Resource partitioning in a tropical goby assemblage

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DANKWOORD

Furahini ... Kuja kucheza ... Baada ya kazi, Tusker baridi ... voilà ce ce Mama

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Heidi

Voor Thalia

Contents

Outline of the thesis

In this thesis, we focussed on the coexistence of gobies (Teleostei, Gobiidae) in a tropical mangrove ecosystem. We aimed at describing species richness and analysing patterns of resource utilisation and niche characteristics, in an effort to obtain insight in the processes that might be important in regulating this assemblage.

Chapter 1 gives a general introduction to the theoretical background, the study object and the study area. As the identification of tropical gobies still creates considerable confusion in the literature, we started with a clear description of the goby species encountered during the survey (Chapter 2). Specific morphological characters are described and current knowledge on habitat use and geographical distribution patterns of the species are given. Chapter 3 describes the fish community of the western mangrove creek in Gazi Bay. Although several studies have attempted to describe the fish community of Gazi Bay, our approach differed in some important aspects. Contrary to previous studies, we focussed on local variation in microhabitat within a limited part of the Bay (β-diversity), since habitat heterogeneity, even at a local scale, can be a major cause in the possible coexistence of species. Furthermore, as gobies were the main target, different fishing techniques with smaller mesh sizes were employed. Within this chapter, the importance of the gobies in terms of density and diversity is analysed, and the major factors affecting habitat choice of the Gobiidae are discussed. Chapter 4 is a technical paper assessing the evacuation rate and daily ration of *Gnatholepis anjerensis* through *in situ* methods. For the evacuation rate, estimates derived from a field cage experiment were compared with data from a 24 h field study. Knowledge on evacuation rate is important in the interpretation of temporal variation in feeding intensity. Our sampling design, which involved nine 24 h cycles obtained at consecutive spring and neap tides, allowed us to analyse the importance of short-term variation in food consumption rates. Chapter 5 explores the coexistence of two sympatric goby species *Gnatholepis anjerensis* and *Asterropteryx semipunctatus,* within the seagrass beds. In this analysis, we focussed on temporal resource partitioning. We analysed tidal, day/night and semilunar patterns in occurrence and feeding. The findings are discussed in terms of temporal segregation and alternative mechanisms of niche diversification. Chapter 6 deals in detail with three niche dimensions (food, space and time) of potential significance to the coexistence of the five most abundant gobiid species within the study area (*Favonigobius reichei*, *Gnatholepis anjerensis*, *Glossogobius biocellatus*, *Amoya signatus* and *Acentrogobius audax*). The importance of resource partitioning as a structuring mechanism in the assemblage is assessed, and the potential importance of other factors in structuring the local goby assemblage are discussed. Chapter 7 brings the results of the previous chapters together in a general discussion.

CHAPTER 1

GENERAL INTRODUCTION

Theoretical background

Studies on species coexistence not only describe the richness of species co-occurring in an area at a particular point in time, but should also try to elucidate underlying processes which produce and maintain such coexistence (Tokeshi 1999). One of the approaches that has been useful in the analysis of coexistence in multispecies assemblages is to consider ecological niches and resource utilisation patterns (Schoener 1974, Roughgarden 1974).

Many aspects of the ecological niche of a fish can be inferred from examination of morphological features: shape and position of the mouth, dentition characters and relative gut length often relate to food type and foraging strategy (Keast and Webb 1966, Motta 1988, Motta *et al.* 1995), whereas fin dimensions and body shape are often adapted to habitat characteristics and locomotion (Webb 1984). However, several factors can confound ecomorphological relationships (Motta *et al.* 1995). Indeed, while the potential niche of a species is largely determined by physiological and morphological constraints, the realised niche depends on the interaction with other species. The two most prevalent biotic interactions are predation and competition (Pianka 1994).

According to the optimal foraging theory, an organism will occupy the habitat where a maximal foraging efficiency can be realised. It is thereby able to assess relative profitabilities of different habitats and can monitor the dynamics of the resources (Mittelbach 1981, Werner *et al.* 1983a, Pyke 1984). However, increased risk of predation can alter the choice of the habitat in which to forage (Werner *et al.* 1983b), or change the foraging strategy in an attempt to reduce detectability (Dill 1983). Organisms maximise fitness by balancing the trade-off between foraging profitability and predator avoidance. Several ethological studies provided evidence for fish changing their behaviour adaptively when costs and benefits of feeding and predator avoidance varied (Milinski 1993).

If competition is important in the organisation of a species assemblage, then species must ultimately segregate along one or more niche dimensions to maintain a minimum level of niche separation. This is the principle of limiting similarity, as formulated by Abrams (1983). An alternative possibility for species to coexist in a resource-limited environment is to evolve to equal competitive strength (Aarssen 1983). Differential resource use has often been viewed as evidence for the existence of competition in the evolutionary past (invoked as "ghost of the competition past"), and as a mechanism by which ongoing competitive interactions are minimised (Schoener 1974, Connell 1980). Within an evolutionary context, avoidance of competition can be facilitated by divergent changes in morphological characteristics (so-called character displacement). It is, however, important to note that resource partitioning may arise from a variety of mechanisms. A number of evolutionary scenarios may be thought to lead to large overlap in resource utilisation. Firstly, species diversifying from a common ancestor can have undergone niche differentiation with respects to characters other than resource utilisation. Secondly, species can come to use resources in a similar way through evolutionary and/or ecological optimisation processes. Thirdly, the general morphological and developmental characteristics of a group of species can have predisposed them to use resources in a similar way (Tokeshi 1999). Surely, the interaction between a certain pattern of resource use overlap and competition is complex. Species may also coexist simply because they never competed, and the observed niche partitioning then reflects an independent evolutionary diversification in niche characteristics (Tokeshi 1999). Ultimate demonstration of competition as structuring mechanism needs experimental field manipulations, in which one species is removed or added to the community, and the responses of the other species are monitored (MacNally 1983, Begon *et al.* 1996). Although considerable debate exists on the evaluation of non-experimental evidence (Abrams 1980, Connor and Simberloff 1986), the observational approach still forms the basic starting-point in the analysis of species coexistence, especially in diverse and complex communities (Norton 1991, Tokeshi 1999).

The classical competition theory has been one of the major ideas of community ecology in history (Roughgarden 1986, Morin 1999). However, during the last decades, a more pluralistic view on community organisation has been developed. Wiens (1984) has summarised this pluralistic theory and discussed communities in terms of equilibrium / non-equilibrium dynamics. The equilibrium theory assumes that ecosystems are in a steady state, with overall species composition and relative abundances being stable throughout time, as a result of firm biotic interactions among members. Such systems return to their original structure after perturbation. The non-equilibrium theory predicts that ecosystems are primarily structured by stochastic events, and species composition fluctuates strongly through differential responses to unpredictable environmental changes rather than through biological interactions (DeAngelis and Waterhouse 1987, Reice 1994). These changes either reduce populations to levels at which competitive exclusion can not occur, or cause a limiting resource to become available in an unpredictable way (Grossman *et al.* 1982).

Menge and Sutherland (1987) designed a theoretical framework whereby the relative importance of disturbance, competition or predation were related to the variation in environmental conditions (Figure 1). At high levels of environmental stress, abiotic disturbance might be the overriding force in structuring the community. At low levels of environmental stress, predation can reduce both prey populations and competition. According to this theory, coexistence is promoted through reduction of density dependent interactions, which would otherwise lead to competitive exclusion (Chesson and Case 1986). In marine benthic communities, recruitment is often decoupled from possible species interactions in the benthic habitat because of a planktonic larval phase (Connolly and Roughgarden 1999). As a result, models of benthic communities have been modified to account for the effect of recruitment variation on the intensity and importance of species interactions (Sale 1991, Levin *et al.* 1997). For coral reef fish communities, two models have been proposed to describe the importance of presettlement processes. The lottery model assumes that coral reef fishes compete for space and that the relative abundances of individual species are the result of stochastic recruitment events (Sale 1977). Contrary, the recruitment limitation model predicts that larval supply is normally insufficient for total population size to reach a carrying capacity determined by resource levels. Population changes then reflect variation in input rather than post-recruitment events (Doherty 1983, Jones 1991). Field evidence has been provided for both models, depending mainly on the timing, the microhabitat and the geographical location of the study (Connolly and Roughgarden 1999, Swearer *et al.* 1999).

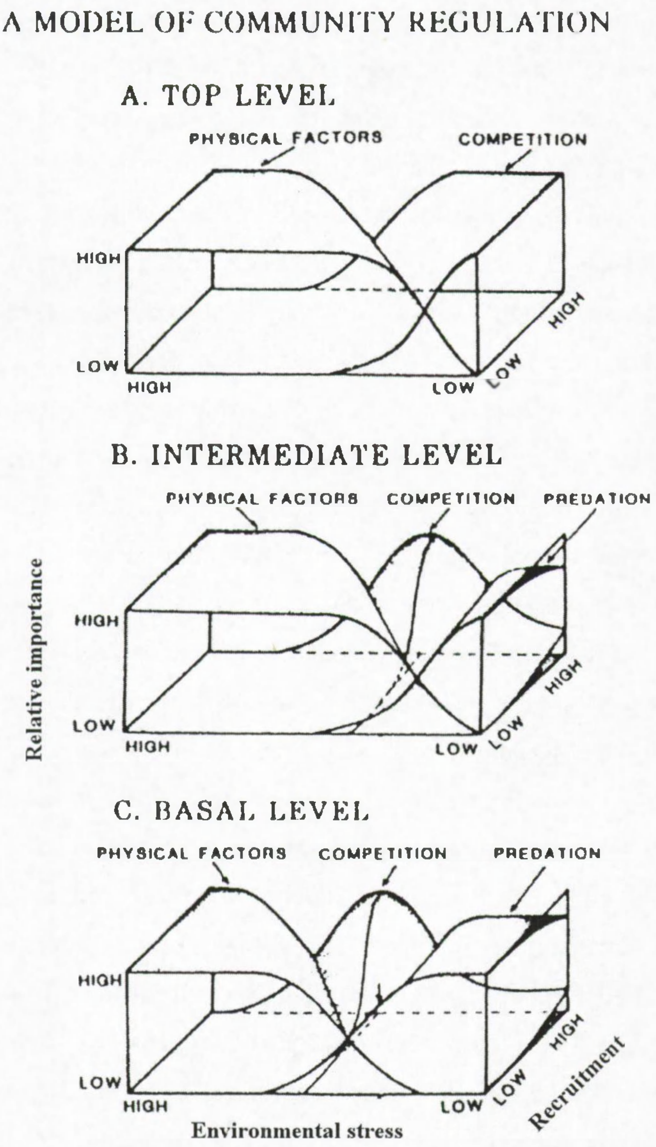

Figure 1: Model of community regulation, showing the relative importance of disturbance, competition and predation in relation to environmental stress and recruitment density at three trophic levels (Menge and Sutherland 1986).

Tropical ecosystems are differing from temperate ecosystems by the number of coexisting species. Although some exceptions have been reported, there seems to be a typical latitudinal gradient in species richness (Rozenzweig 1997). Within a deterministic context, greater numbers of coexisting species are assumed to be associated with greater number of species interactions, higher levels of niche diversification and ecological specialisation, and thus an enhanced resource partitioning (Tokeshi 1999). In theory, this can be achieved through two mechanisms: by expanding the resource spectrum (through exploitation of new resources) or by species packing (by increased subdivision of previously utilised core resources). Winnemiller (1991) investigated the relationship between species diversity and community structure by analysing morphological evidence of niche differentiation in freshwater fish assemblages along a biotic diversity gradient. More speciose tropical fish assemblages showed higher ecomorphological diversification than their temperate counterparts. Several guilds were found to be unique to tropical assemblages. There was an increased subdivision of the aquatic environment, represented by specialised body forms (ecomorphotypes) related to fine-scaled space utilisation. Furthermore, some feeding specialisations were only found in the tropics. While some of these specialisations could be interpreted as expansion of the resource base (e.g. fruit crushing), other specialisations supported the resource subdivision interpretation (e.g. scale feeding, mucus feeding). Winnemiller (1991) concluded that, on a global scale, interspecific competition for food and foraging space strongly influenced the evolution of ecomorphological diversity in tropical freshwater fishes. Not all tropical fish communities are, however, characterised by adaptive radiations leading to extreme specialisation. Several studies on tropical rivers and floodplains found high ecological overlap among species, even those with dissimilar body shapes (Lowe-McConnell 1991). Moreover, recent research on tropical coral reef fishes has suggested that also non-equilibrium systems may harbour highly diverse assemblages (Sale 1991).

The study object

Gobiidae of the temperate region have been the focus of several studies on niche dynamics, resource partitioning and structuring mechanisms promoting the coexistence of species (Edlung and Magnhagen 1981, Thorman 1982, Magnhagen and Wiederholm 1982, Evans 1983, Thorman and Wiederholm 1983, 1986, Evans and Tallmark 1985, Wiederholm 1987, Wilkins and Myers 1992, 1995, Hamerlynck and Cattrysse 1994). These studies have provided evidence for a spectrum of mechanisms regulating community structure, whereby the relative importance of different structuring mechanisms mainly depended on the environmental conditions. Parallel studies on tropical Gobiidae are scarce, although Gobiidae are essentially warm-water fishes and their diversity is most marked in tropical ecosystems such as coral reefs and mangrove swamps (Miller 1993). The importance of Gobiidae as a dominant component of the residential fish fauna in mangrove estuaries has been reported all-over (Krishnamurthy *et al.* 1984, Blaber *et al.* 1985, 1989, 1992, Winterbottom and Emery 1986, Robertson and Duke 1987, 1990, Blaber and Milton 1990, Blaber 1997).

Gobies are typically small-sized fish, mostly smaller than 15 cm. The typical benthic goby has a cylindrical body form, dorsolateral eyes, large pectoral fins and a rounded caudal fin. The pelvic fins are fused to form a suction disk, which allows them to attach to the substrate and withstand relative strong currents. The independent evolution of goby-like morphologies in African ciclids illustrates that the morphological concept of the Gobiidae is successful (Hamerlynck 1993). The basic plan – the generalised benthic goby – has radiated into a wide diversity of forms (Figure 2) that match highly specialised environments and lifestyles (Miller 1993). The Gobiidae indeed include very diverse forms, ranging from amphibious mudskippers to neotenous pelagic gobies, all adapted to various specialised ecological niches (Miller 1973a, b). There is strong evidence that the gobies form a monophyletic group, within which there have been many lines of specialised divergence (Pezold 1993). The estuarine and nearshore character of the group makes them ideal candidates for allopatric speciation through the effect of sea level changes and other paleoclimatological dynamics of coastal areas (Miller 1990, McKay and Miller 1991, Hamerlynck 1993).

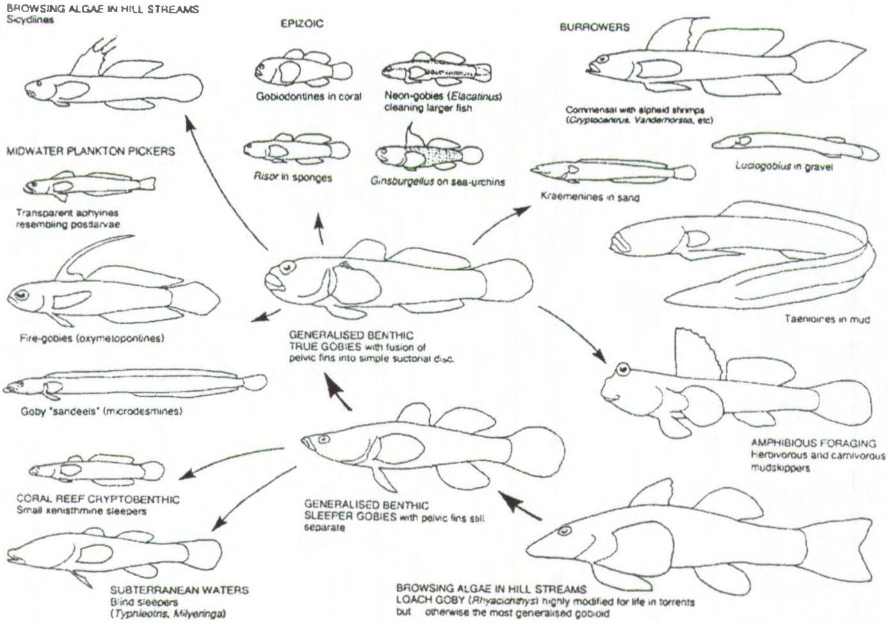

Figure 2: Ecological radiation of the gobioid fishes (Miller 1993).

Small size has important implications for the ecology of gobiids. Adaptiviness of small size in fish relates to efficiency of feeding on small prey and possibilities for exploitation of spatially restricted habitats (Horn and Gibson 1988, Werner and Hall 1988, Miller 1993). However, small size also implicates greater susceptibility to predation. Furthermore, the intensity of predation has been assumed to be higher in the tropics, as there is some evidence that tropical organisms are better equipped with anti-predator adaptations (Thiery 1982). The highest number of specialised morphological traits in fish, including diverse coloration patterns and fin morphologies, has indeed been observed in mature tropical ecosystems such as the African Great Lakes and reef fish communities (Lowe-McConnell 1991). The higher predation risk associated with small size can promote co-existence of more species in the same ecotope. Size can thus be a potentially important factor in the evolution and diversity of fish in tropical ecosystems (Miller 1979).

Gobiidae are essentially demersal repeat-spawners. They produce benthic eggs, which may stick to the substrate by adhesive filaments or special attachment areas. Batch fecundity is relatively low: typically a few hundred to a few thousand eggs are produced within each clutch. This is related to the small size of the adults and is characteristic for fishes exhibiting brood care. Larvae hatching from demersally-spawned eggs tend to be larger and more developed than larvae of pelagic spawners, and may actively maintain their position nearshore (Leis 1991, Potter and Hyndes 1999). Parental care is excerted by the male, guarding the nest and fanning the eggs. Within the classification of Balon (1984), gobies belong to the more precocial reproductive guild of the guarders. However, gobies can exhibit a wide range of life history styles, ranging from early sexual maturation with high reproductive effort and short lifespan to delay of sexual maturation and lowered reproductive effort, several breeding seasons and a long lifespan (Miller 1984, Bruton 1989, Southwood 1996). In addition, several goby species exhibit considerable phenotypical plasticity and can alter their reproductive tactics in response to environmental changes (Wootton 1990, Bouchereau 1997, Pampoulie *et al.* 1999).

The study area

Gazi Bay (Figure 3) is a shallow, well-flushed tropical coastal water system with a mean depth of less than 5 m. The total area, excluding the mangrove swamp, is 10 km². The mangrove forest covers an additional 5 km² and is dominated by *Rhizophora mucronata*, *Sonneratia alba*, *Ceriops tagal*, *Bruguieria gymnorrhiza* and *Xylocarpus granatum* (Kitheka 1997). The bay opens into the Indian Ocean through a relatively wide and shallow entrance in the south. The central part of the Bay is dominated by seagrasses. There are two tidal creeks (Kidogoweni and Kinondo) draining the upper region, which is dominated by mangrove vegetation. The Mkurumuji river discharges into the southwestern part of the Bay. The discharge of rivers is highly seasonal (Kitheka 1997). The semi-diurnal tidal regime is the main forcing function for water circulation in Gazi Bay. The tides generate strong and reversing currents in the deep and narrow tide channels in the mangrove zone, but have a much weaker influence in the seagrass zone and coral reef. The Bay has high rates of water exchange (60% to 90% per tide) and short residence times (3 to 4 h). Tidal asymmetry, with relatively stronger ebb than flood currents in the mangrove creek, promotes the net export of nutrients from the river mouth and of organic detritus from the mangroves to the seagrass beds. The seagrass zone functions as an important buffer between the mangroves and the coral reef, by trapping mangrove particulate organic matter and protecting the coral reef from sedimentation (Hemminga *et al.* 1994). Phytoplankton and zooplankton production increases during the rainy season, but rates of primary and secondary production are relatively low compared with other tropical creeks, probably as a consequence of the high rates of tidal flushing (Kitheka *et al.* 1996, Ohowa *et al.* 1997, Osore *et al.* 1997).

Three important coastal ecosystems can be found along the Kenyan coast: fringing coral reefs along the entire coastline, extensive areas of seagrass beds in backreef lagoons and mangroves on the shores of the brackish parts of the rivers and along coastal creeks. These ecosystems are connected by the tidal water, which carries abiotic and biotic elements to and from the systems. Along the Kenyan Coast, two large river systems enter the Indian Ocean: the rivers Tana and Sabaki. Besides these, there are many smaller rivers coming from the highlands and running through the fossil coral beds, forming creeks with extensive mangrove growth. This is also the case for Gazi Bay (Heip *et al.* 1995). Tropical estuaries or embayments differ in several important features from those of the higher latitudes. While changes in daylength and temperature are the overriding forces creating seasonality in the temperate regions, tropical coastal ecosystems are influenced mainly by changing winds, coastal and oceanic currents, rainfall and river affluence (Lowe-McConnell 1991).

The East African coast has two distinctive and alternating seasons associated with the prevailing trade winds: the Southeast monsoon (SEM) season from March to October and the Northeast monsoon (NEM) season from October to March. The SEM tradewinds blow over the Indian Ocean, and cause the greatest amount of rainfall. The NEM trade winds are coming from the Sahara and Arabian landmasses and provoke a

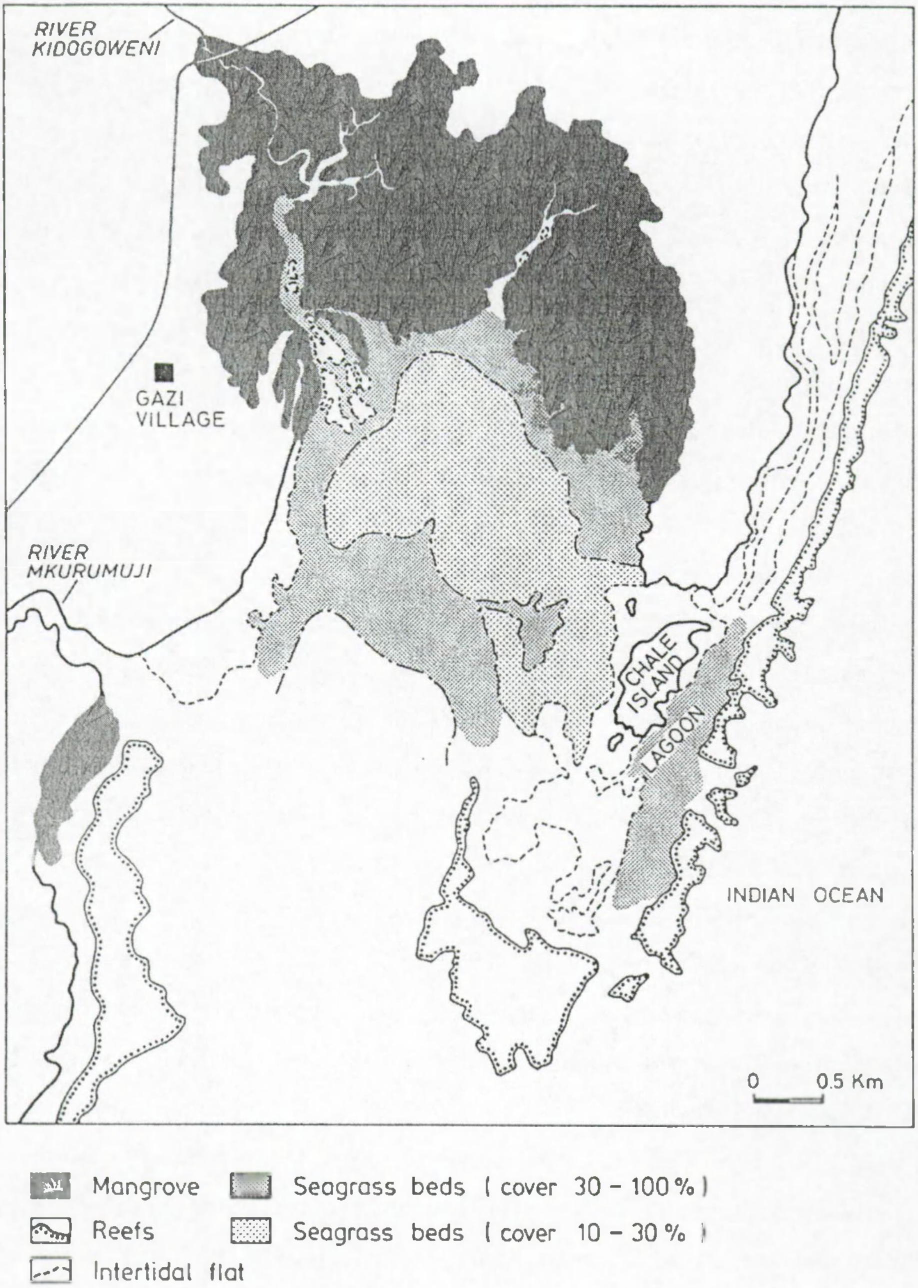

Figure 3: Map of the study area Gazi Bay (adapted from Kitheka 1997).

dry period. The SE monsoons are characterised by rain, high wind energy and decreased temperature and light. This is in contrast to NE monsoons when variables are reversed (McClanahan 1988). Currents along the coast are affected by wind patterns, the continent and the Coriolis force (Figure 4). The permanently west-flowing South Equatorial Current (SEC) dominates the circulation in the Western Indian Ocean. When passing the northern tip of Madagascar, the SEC splits into the Mozambique Current southwards and the East African Coastal Current (EACC) northwards. During the SEM season, the EACC flows into the northwards flowing Somali Current (SC) and continues all the way to the Horn of Africa and into the Arabian Sea. However, during the NEM, the SC reverses direction southwards and meets the EACC along the Kenyan-Somalian coasts, causing a local upwelling at the confluence and an eastward flow, the Equatorial Counter Current (ECC), north of the SEC (Richmond 1997). These reversals have a profound influence on the productivity and cause a north-south dichotomy between ecosystems along the coast of the western Indian Ocean. The northern section (Somalia) is a productive upwelling region with cooler nutrient-rich water, higher plankton productivity and lower benthic productivity. The southern section (Tanzania- Kenya) is associated with low-nutrient water, low phytoplankton biomass but higher benthic productivity (McClanahan 1988, Mantoura *et al.* 1993, Duineveld *et al.* 97, Mengesha *et al.* 1999).

Foodwebs of mangrove ecosystems

Our present understanding of the structure and function of mangrove-based food chains (Figure 5) is based primarily on work done in Florida (Odum and Heald 1972, 1975, Lugo and Snedaker 1974, Snedaker 1989). This research ascertained that vascular plant detritus is the major component of the diet of primary consumers and supports the heterotrophic community. Leafs are rapidly fragmented through grazing of crabs and amphipods. Decomposition then continues through fungal and bacterial decay of detritus and utilisation and re-utilisation (through coprophagy) of detritial particles by a variety of detritivores (Robertson 1986). Later work on the more species-rich mangrove ecosystems of the Indo-Pacific region showed that detritus,

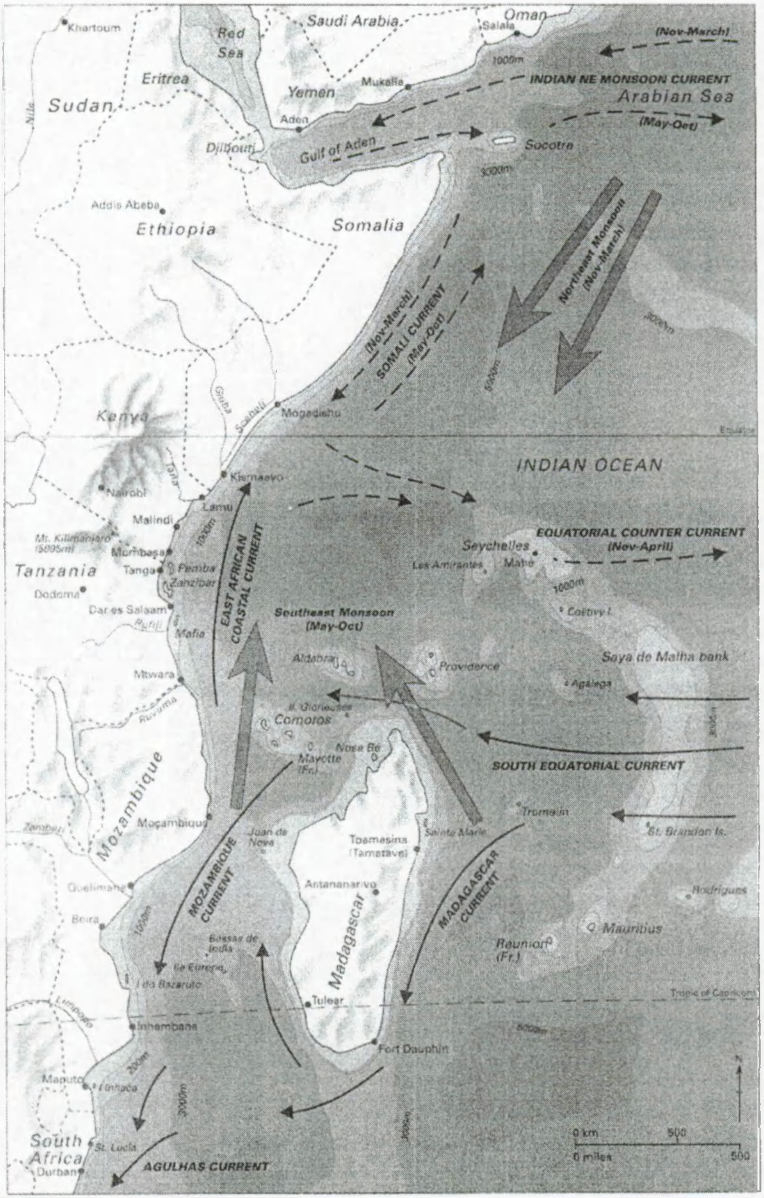

Figure 4: Ocean currents, monsoon winds and water depths at the East African coast (Richmond 1997).

phytoplankton and benthic algae could all be a major source of organic carbon to the heterotrophic food chain, depending on the geomorphological characteristics of the mangrove forest. Input of nutrients and turbidity can greatly affect the trophodynamic functioning of the system (Blaber *et al.* 1985, Thollot *et al.* 1999).

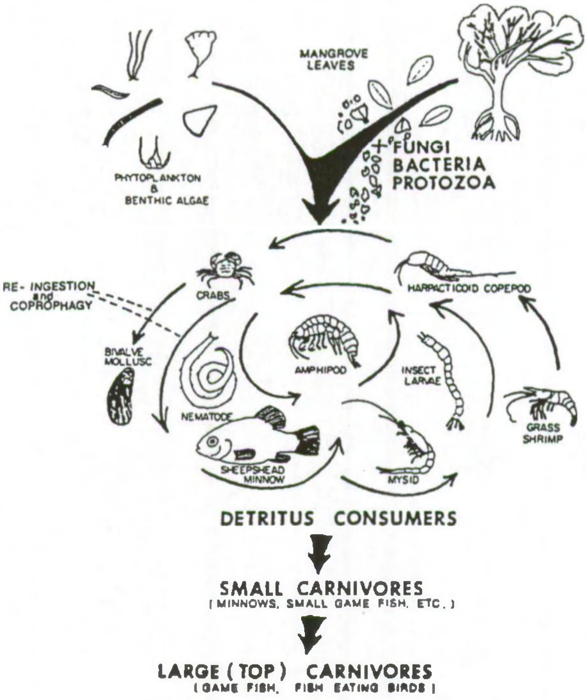

Figure 5: A simplified foodweb of mangrove ecosystems (Odum and Heald 1972).

Furthermore, in contrast to American mangrove ecosystems, the mangrove crab fauna (mainly *Uca* and *Sesarma*) is an important functional component of Indo-Pacific mangrove ecosystems, as they represent an essential pathway in litter processing (Robertson 1986, Smith *et al.* 1991).

Several parts and links of the food web in Gazi Bay have been studied so far: mangrove vegetation (Gallin *et al.* 1989), seagrass and macroalgal cover (Coppejans *et al.* 1992), litterfall (Slim *et al.* 1996), litter decomposition (Woitchik *et al.* 1997, Rao *et al.* 1994, Slim *et al.* 1997, Dahdouh-Guebas *et al.* 1999), zooplankton community structure (Osore *et al.* 1997), macro- and meiofauna (Vanhove *et al.* 1992, Schrijvers *et al.* 1995, 1996, 1998), fish (Van der Velde *et al.* 1995, De Troch *et al.* 1996, Kimani 1996, Marguillier *et al.* 1997, Wakwabi 1999) and parasites (Geets and Ollevier 1996, Geets *et al.* 1997).

Fish communities of mangrove ecosystems have received considerable attention recently. Major topics included: (1) the role of mangroves as nursery and/or feeding ground for commercially important species (Robertson and Duke 1987, Little *et al.* 1988, Chong *et al.* 1990), (2) spatial distribution of fish species in function of habitat heterogeneity (Thayer *et al.* 1987, Blaber *et al.* 1989, Blaber and Milton 1990, Sedberry and Carter 1993, Pinto and Punchihewa 1996, Vance *et al.* 1996, Rönnbäck *et al.* 1999), (3) temporal patterns in species composition and abundance (Robertson and Duke 1990, Rooker and Dennis 1991, Laroche *et al.* 1997), and (4) the trophic ecology of specific groups (Blaber 1986, Brewer and Warburton 1992, Yanez-Arancibia *et al.* 1993, Brewer *et al.* 1995). Under a variety of conditions, mangrove ecosystems function as valuable habitats for fish. However, the ichthyofauna of mangrove habitats greatly varies in species composition and relative densities, partly due to differences in physico-chemical features of the habitat (Blaber *et al.* 1985, Ley *et al.* 1999) and differences in regional species pools (Robertson and Blaber 1992, Laegdsgaards and Johnson 1995).

Wakwabi (1999) synthesised community structure and trophic organisation of the ichthyofauna in Gazi Bay. Characteristic assemblages were linked to the major habitat types: seagrass beds, mangrove creeks, river mouths and coral reef. Seasonal patterns were not very pronounced, although the dry season was characterised by higher densities and a higher diversity than the wet season. More than 63% of the species were carnivorous. Despite the relatively low number of species, the guild of the herbivores was represented by the highest densities, especially in the seagrass beds in the central part of the bay.

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CHAPTER 2

GENERAL DESCRIPTION OF THE GOBIIDAE IN GAZI BAY

Introduction

This chapter gives an overview of all goby species encountered in Gazi Bay during this research. A short note on the three sampling surveys (inclusive sampling gear, methods and locations) is given. Furthermore, we provided a practical key to the genera and a species diagnosis with some distinctive morphological characteristics. Notes on the geographical distribution and habitat choice are given for each species.

Sampling program

Three major sampling campaigns were organised within the scope of this study. In a pilot survey (July to August 1993), three locations within Gazi Bay were explored: the western creek, the eastern creek and Chale Island (situated near the coral reef). Biotopes included sandy beaches, mudflats, seagrass patches, tidal channels and pools. Different types of sampling gear were tested: handnet, fyke nets, trawling net and beach seine. During the second sampling survey (July to August 1994), we focussed on the fish community within the downstream part of the western creek (see Chapters 3 & 6). Three major habitat types were distinguished: sandy beaches, mudflats and seagrass beds. Sampling was done by hand with a trawling net (1.5 m beam length, 6 m long bag with 3-mm stretch size of the inner net) and beach seine (15 by 1.5 m with 3-mm stretch size). Samples were taken at low tides both by day and at night. During the third sampling campaign (July to November 1995), we took samples during ten 24 h surveys in the seagrass beds of the western creek (see chapter 4 & 5). Samples were collected from a dinghy by towing a small beam trawl (1.5 m beam length, 6 m long bag with 3-mm stretch size of the inner net). An overview of the species caught during these campaigns is given in Table 1.

Species identification

We primarily used the key of Hoese (1986) for the Gobiidae in the Southern African region. We further examined the pioneer work of Koumans (1953) for the Indo-Australian Archipelago and the keys of Smith (1958, 1959, 1960) for South Africa. For some genera, we further employed more recent publications (cited below). Most of the identifications were checked by Dr. Helen Larson from the Northern Territory Museum (Ichthyology Section) in Darwin (Australia). For the identification of the *Oxyurichthys* species, specimens were sent to Dr. Frank Pezold from the Museum of Zoology at the Northeast Louisiana University in Monroe (USA).

Table 1: Overview of goby species encountered in the different localities of Gazi Bay during the three sampling surveys, with indication of subfamilies (following the classification of Hoese 1984). A1 = western creek; A2 = eastern creek; A3 = Chale Island; B1 = non-vegetated sites; B2 = seagrass sites; C = seagrass beds.

	Survey 1			Survey 2		Survey 3
	A1	A2	A3	B1	B2	C
Gobiinae						
Acentrogobius audax	x			x	x	x
Amblygobius albimaculatus				x	x	x
Amoya signatus	x			x	x	x
Asterropteryx semipunctatus					x	x
Bathygobius fuscus			x			
Bathygobius sp. 9				x	x	
Cristatogobius lophius				x		
Drombus key				x		x
Favonigobius melanobranchus				x	x	x
Favonigobius reichei	x	x	x	x	x	x
Glossogobius biocellatus	x			x	x	x
Gnatholepis anjerensis	x		x	x	x	x
Istigobius ornatus			x			
Monishia sordida				x	x	
Mugilogobius durbanensis	x	x				
Oplopomus oplopomus				x		x
Oxyurichthys lonchotus				x		
Oxyurichthys ophthalmonema	x			x		x
Oxyurichthys papuensis	x			x	x	x
Oxyurichthys takagi				x		
Psammogobius knysnaensis	x					
Yongeichthys nebulosus	x			x	x	x
Oxudercinae						
Periophthalmus argentilineatus				x	x	
Periophthalmus kalolo	x	x		x	x	x

Identification of gobies to genus-level is often difficult, requiring microscopic examination. Head pores and sensory papillae are of particular interest in characterising genera. Their importance in the classification of gobies has long been recognised, and structural comparisons have been useful in determining phylogenies (Hoese 1983, Miller 1993). Head pores are microscopic openings in the lateral-line head canals (including nasal, interorbital and postorbital canals). Two basic pore patterns can be distinguished: a primitive pattern (= Type B) with an anterior nasal pore and paired anterior interorbital pores, and a more advanced pattern (= Type A) without an anterior nasal pore and with a single anterior interorbital pore (Hoese 1986).

Two basic patterns are recognised in the sensory papillae on the head: a transverse pattern with several vertical papilla lines and two horizontal lines, and a longitudinal pattern with only horizontal lines. Several variations can occur: a reduced transverse pattern, with few papillae scattered on the head, or a multiple longitudinal pattern, with 3 or more horizontal rows between other longitudinal rows, superficially resembling a transverse pattern (Hoese 1986).

We continue with an overview of the genera and species encountered during this research. For the identification of the genera, we designed a key based on Koumans (1953), Hoese (1984) and Murdy (1988). For each species, the location in the work of Koumans (1953) and Smith (1958, 1959, 1960) is noted. If appropriate, other reference work is mentioned. The notes on the geographical distribution and habitat characteristics are summarised from Koumans (1953), Hoese (1986), Maugé (1986), Winterbottom and Emery (1986) and Goren and Dor (1994). Figures are taken from Koumans (1953), Smith (1959, 1960), Hoese (1986) or from specialised literature for the genus. When available, pictures of locally collected specimens were included.

Table 2: Identification key of the gobiid genera encountered during our survey. Genera with asterisk did not occur in our samples but were identified from collections at Tudor Creek in cooperation with Dr. E. Wakwabi (KMFRI, Mombasa).

N°	Key	Genera
1a	Eyes elevated, with lower eyelid and deep sockets; first D spines 7-17, P base elongate	*Periophthalmus*
1b	Eyes not elevated, without eyelid, 1st D spines 6, P base short	2
2a	Head compressed, scaled from above opercle, neck with longitudinal dermal crest	*Cristatogobius*
2b	No longitudinal dermal crest	3
3a	First spine in 1st and 2nd D stiff and thickened, preopercle with 1-3 flat spines	*Oplopomus*
3b	D spines all thin and flexible	3
4a	Preopercle with 1-9 spines (cheek scaled)	*Asterropteryx*
4b	No preopercle spines	5
5a	Cheek with large scales, teeth at sides of upper jaw directed medially, anterior interorbital pore paired, mouth horizontal, inferior	*Gnatholepis*
5b	Cheek naked, teeth at sides of jaws vertical or directed posteriorly	6
6a	Head pores absent	*Mugilogobius*
6b	Head pores present	7
7a	Lower jaw curved upward at tip, C longer than head in adult, head pores type B	8
7b	Lower jaw normal, C longer or shorter than head, head pores type A	9
8a	Head compressed, D VI+I, 6-8	**Redigobius*
8b	Head rounded, D VI+I, 12-13	*Oxyurichthys*
9a	Gill opening extending to below rear margin of preopercle	10
9b	Gill opening restricted to P base or slightly below	12
10a	Tongue tip bilobed or branchiostegal membranes forming free fold across isthmus, predorsal scaled at least to above opercle	11
10b	Tongue tip truncate, branchiostegal membranes attached to sides of isthmus, predorsal naked	**Mahidolia*
11a	Snout much greater than eye, tongue bilobed	*Glossogobius*
11b	Snout subequal to or less than eye, tongue weakly notched	*Psammogobius*
12a	D VI+I, 13-15, upper gill arch with finger-like projections, 10-15 short vertical papillae rows under eye, operculum with several scales dorsally	*Amblygobius*
12b	D VI+I, 7-15, upper gill arch without finger-like projections, 4-6 long vertical papillae rows or longitudinal rows only under eye, operculum naked or with 1 scale	13

13a	Mouth small, almost horizontal, snout broadly rounded, ending above front of upper lip, PD 6-9, reaching eye	*Istigobius*
13b	Mouth small to large, oblique, snout gently or steeply sloping, not broadly curved in lateral view, ending behind upper lip, PD 0-20	14
14a	D VI+I, 7-9, several longitudinal rows of head papillae	*Favonigobius*
14b	D VI+I, 9-15, head papillae pattern transverse or longitudinal	15
15a	Head papillae pattern longitudinal	16
15b	Head papillae pattern transverse	19
16a	Upper P rays free, silk-like, small bump under anterior nostril, cheek with a fold behind upper lip, a prominent truncate or curved mental frenum	*Bathygobius*
16b	Upper P rays normal, no bump under anterior nostril, cheek without fold, mental frenum indistinct	17
17a	Predorsal naked	18
17b	Predorsal scaled	*Acentrogobius*
18a	C peduncle and midside with dark spots larger than eye	*Yongeichthys*
18b	C peduncle without enlarged spots	*Amoya*
19a	LS 33-63, D VI+I, 9-15	**Caffrogobius*
19b	LS 25-34, D VI+I, 9-11	20
20a	Mouth reaching below rear half of eye, upper P rays often free, anterior nostril often with a small flap, no white spot on upper P base	*Monishia*
20b	Mouth reaching below front half of eye, no free P rays, no flap on anterior nostril, white spot at upper P base	*Drombus*

Acentrogobius audax Smith, 1959
(in Smith 1959: p. 201)
Common name: mangrove goby
Diagnosis: longitudinal head papillae pattern, Type A head pores. Predorsal scales to near eye, operculum scaled, second to fourth dorsal spines elongated, third spine longest, dark marks on midline of body, prominent oblique bar on opercle and below eye.
Distribution: Indo-Pacific tropical species
Habitat: on mud and sand bottoms in mangroves and coastal bays

Amblygobius albimaculatus (Rüppell, 1830)
(in Koumans 1953: p. 141 and Smith 1959: p. 204)
Common name: butterfly goby
Diagnosis: transversal head papillae pattern, Type A head pores. Filamentous projections on upper part of first gill arch, body relative high and compressed, first dorsal fin with middle spines distinctly prolonged, 5 dark transversal crossbars on body, black blotch above pectoral base and another on base of caudal fin, 2-5 black spots on caudal fin and 3 on second dorsal fin, colours when alive are reddish green with lower parts yellow.
Distribution: Red Sea, western Indian Ocean, Indonesia, Australia and south Pacific Islands
Habitat: on coral reefs and in weedy areas

Amoya signatus (Peters, 1855)
(*Ctenogobius criniger*: in Koumans 1953: p. 178; *Acentrogobius signatus*: in Smith 1959: p. 202; *Ctenogobius pavidus*: in Smith 1959: p. 196)
Common name: tusk goby
Diagnosis: longitudinal head papillae pattern, Type A head pores. Midline of predorsal naked. Side of body with dark spots about equal to eye along midline, blue spots on head when alive, blue ocellus behind fifth and sixth dorsal spine, tip of ventral fin in males dark. Easily distinguished from *Acentrogobius audax* by the absence of predorsal scales and the striped first spine of first and second dorsal fin.
Distribution: Indo-Pacific tropical species
Habitat: in estuaries and bays over fine sand and mud, often in burrows

Asterropteryx semipunctatus Rüppell, 1830
(in Koumans 1953: p. 290 and Smith 1958: p. 143)
(Unpublished key of D. Hoese)
Common name: starryfin goby
Diagnosis: head papillae pattern not clear, Type A head pores. Preoperculum with 3-9 short spines. Cheek and operculum with large scales. Third dorsal spine filamentous. First dorsal fin with a basal stripe, body brown-black with numerous light spots.
Distribution: Red Sea, Indian Ocean and tropical western and central Pacific Ocean
Habitat: on coral reefs and in turbid waters; in mangrove areas or muddy waters

Bathygobius fuscus (Rüppell, 1830) & ***Bathygobius sp. 9*** Hoese, 1986
(in Koumans 1953: p. 187 and Smith 1959: p. 212)
Description of *B. fuscus* in Akihito & Meguro (1980) for the Japanese waters
Common names: Dusky frill goby & brownlined goby
Diagnosis: longitudinal head papillae pattern, head pores Type A.
B. fuscus: Upper 3 pectoral rays free from membrane, uppermost ray with 2-3 branches, mental frenum with straight margin; transverse dark bands over back.
B. sp. 9: Upper 4-5 pectoral rays free from membrane, mental frenum broad with short lateral lobes; body with numerous brown longitudinal lines.
Distribution: Red Sea and Indian Ocean, western Pacific Ocean
Habitat: around corals, rocks, or mangroves, intertidal, can enter estuaries and rivers

Cristatogobius lophius Herre, 1927
(In Koumans 1953: p. 95 – not recorded in Smith 1959, 1960 & Hoese 1986)
Diagnosis: longitudinal head papillae pattern, head pores type A. Neck with a longitudinal dermal crest, mouth nearly vertical, caudal fin pointed, colour dark brown with 5 or 6 pale transverse bands, two large black spots on base of pectoral fin, black dots on head and anterior half of body.
Distribution: Indo-Pacific region
Habitat: unknown

Drombus key (Smith, 1947)
(*Acentrogobius triangularis* & *Ctenogobius key* in Smith 1959: p. 199 & 195)
Common name: key goby
Diagnosis: transversal head papillae pattern, head pores Type A. Third and fourth spine of first dorsal fin longest, prolonged in adults, dark blotch on upper pectoral base with white area in front. Body elongate and compressed, colour dark brown. Can be distinguished from *Monishia* by the absence of free pectoral rays and the absence of a flap on anterior nostrils.
Distribution: East African coast to western Pacific Ocean
Habitat: inhabiting mangroves and coastal bays

Favonigobius reichei (Bleeker, 1953) **& *Favonigobius melanobranchus*** (Fowler, 1934)
(*Acentrogobius reichei*: Koumans 1953: p. 77 and Smith 1959: p. 201)
(*Rhinogobius melanobranchus*: Koumans 1953: p. 77-79)
Common names: tropical sand goby & blackthroat goby
Diagnosis: Multiple longitudinal head papillae pattern, head pores type A. Body yellowish with numerous small spots, midside with 4 or 5 slightly enlarged groups of black spots. The two species are very similar in appearance. *F. melanobranchus* has black spots on the upper edge of the caudal fin; *F. melanobranchus* has 7 transverse scales and *F. reichei* has 8-9 transverse scales. Membranes at sides of isthmus are black in *F. melanobranchus* (Hoese and Winterbottom 1979).
Distribution: East African coast, Indian Ocean to Indonesia
Habitat: on sandy and muddy bottom, weedy areas, intertidal, can enter estuaries, lagoons and rivers

Glossogobius biocellatus (Valenciennes, 1837)
(In Koumans 1953: p. 163)
Common name: sleepy goby
Diagnosis: Longitudinal head papillae pattern, head pores Type A. Head depressed, snout elongate, colour dark brown to black, with small black spots in longitudinal rows, easily distinguished by the lappet over the iris and deeply bilobed tongue.
Distribution: East African coast to western Pacific Ocean
Habitat: in mangroves, entering estuaries, lagoons and coastal rivers

Gnatholepis anjerensis (Bleeker, 1850)
(*Acentrogobius cauerensis*: Koumans 1953: p. 68 and Smith 1959: p. 202)
Common name: weeper
Diagnosis: transversal head papillae pattern, head pores Type B. Large cheek and opercular scales, colour yellow to brown, with many lines of dark spots and irregular blotches along midside, dark spots on caudal and dorsal fins, pronounced vertical black streak from eye to lower opercular edge.
Distribution: Red Sea, east African coast, most Indian Ocean Islands, Indonesia, Philippines and south China
Habitat: on sandy bottoms and coral reefs, intertidal, can enter estuaries

Istigobius ornatus (Rüppell, 1830)
(*Acentrogobius ornatus*: Koumans 1953: p. 71 and Smith 1959: p. 202)
Common name: ornate goby
Diagnosis: longitudinal head papillae pattern, head pores Type A. Snout very obtuse, lips thick, upper pectoral rays free, 6 to 9 predorsal scales reaching eye, colour pale yellowish with several rows of small dark spots along body.
Distribution: Red Sea, East African coast and western Pacific
Habitat: in sandy areas and on coral reefs, can enter estuaries

Monishia sordida Smith, 1959
(in Smith 1959: p. 206) - Description in Goren (1985)
Common name: epaulette goby
Diagnosis: transversal head papillae pattern, head pores type A. Head depressed, upper P rays free near tips, P base scaled, upper P base with a large dark spot, body brownish with irregular dark blotches.
Distribution: Red Sea and western Indian Ocean
Habitat: turbid inshore waters, mainly sheltered areas

Mugilogobius durbanensis (Barnard, 1927)
(*Stigmatogobius durbanensis* Smith 1960: p. 306)
Common name: Durban goby

Diagnosis: longitudinal head papillae pattern, head pores absent. Head depressed, interorbital broad, operculum with 6 rows of scales, preoperculum naked, body with faint irregular cross-bars, double curved bar across caudal base
Distribution: southeast African coast
Habitat: usually found in burrows among mangroves, also in brackish and fresh waters

Oplopomus oplopomus (Valenciennes, 1837)
(In Koumans 1953: p. 29 and Smith 1959: p. 188)
Common name: spinecheek goby
Diagnosis: multiple longitudinal head papillae pattern, head pores Type A. Preoperculum with 1 to 3 spines, first spine in each dorsal fin thickened and stiff, body yellow with dark spots on side, a larger spot above operculum and on caudal base.
Distribution: Red Sea and Indian Ocean
Habitat: on sand often near coral reefs

Oxyurichthys lonchotus (Jenskins, 1903), ***O. ophthalmonema*** (Bleeker, 1857), ***O. papuensis*** (Valenciennes, 1837) ***& O. takagi*** Pezold 1998
Common names: unknown & eyebrow goby & frogface goby & sea newt
Diagnosis: transversal head papillae pattern, head pores type B, pointed caudal fin longer than head, crest on the nape.
O. lonchotus: well-defined dark spots on the upper portion of the cornea, lateral series of large elongate blotches on trunk, large prominent spot on the upper pectoral fin base, gular marks and spots at the base of the anal fin rays.
O. ophthalmonema: adults with clear tentacles on the eye, juveniles with a range of cornifications on the eye (from nubs to tentacles), well developed crest on nape, anterior scales cycloid, ctenoid behind first dorsal fin.
O. papuensis: no distinct tentacle on the eye, adults with callus on eye, callus in juveniles weakly developped, sometimes small bump dorsally, scales cycloid anteriorly and ctenoid from second dorsal fin origin posteriorly, 7 to 8 vertical dark brown bars on body.
O. takagi: no spot, cirrus or callus on eye, low crest on nape from first dorsal fin origin to above preopercle, all scales are cycloid, 4 to 5 dark bands on body, large dark spot on upper pectoral base.
Distribution: Red Sea, Indian Ocean and Indonesia
Habitat: in mangrove areas and shallow coastal waters with bottom substrates of silt or other fine sediments

Periophthalmus argentilineatus Valenciennes, 1837 ***& P. kalolo*** Lesson, 1830
P. argentilineatus in Koumans 1953: p. 214; *P. sobrinus* in Smith 1959: p. 220
P. koelreuteri in Koumans 1953: p. 207 and Smith 1959: p. 219
For this genus the species names as in the specialised key of Murdy (1988) were used
Common names: Bigfin mudhopper & African mudhopper
Diagnosis: head papillae pattern reduced, head pores absent. Eyes elevated, with lower eyelid, pectoral base elongated and muscular.
P. argentilineatus: ventral fins partly connected, first dorsal fin with 11 to 16 spines, fin base longer than height, with margin usually convex, with black stripe and numerous small white spots posteriorly on fin.
P. kalolo: ventral fins separated, first dorsal fin with 11 to 15 spines, fin height greater than length of base, with margin slightly rounded, with black stripe and numerous white spots proximally on fin.
Distribution: *P. argentilineatus*: from the Southern Red Sea and East coast of Africa eastwards to Japan and Oceania; *P. kalolo*: from East Africa to Samoa
Habitat: Found in tropical muddy habitats, especially among mangroves, spending considerable time out of water

Psammogobius knysnaensis Smith, 1936
In Smith 1960: p. 306
Common name: Knysna sand goby
Diagnosis: longitudinal head papillae pattern, head pores Type A. Gill opening extends to below eye, predorsal scaled to above rear end of operculum, colour brown, scattered with dark spots on back, midside with 3-6 elongate dark brown spots.
Distribution: known only from the east African coast
Habitat: sandy beaches and mangrove areas

Yongeichthys nebulosus (Forsskal, 1775)
(*Ctenogobius criniger* in Koumans 1953: p. 178 and *Ctenogobius nebulosus* in Smith 1959: p. 197)
Common name: shadow goby
Diagnosis: longitudinal head papillae pattern, head pores Type A. No predorsal scales, head and dorsal part of body with irregular blackish spots, three larger blackish spots: the first below the first dorsal fin, the second below the second dorsal fin and the third at middle of base of caudal fin, margins of median fins often black.
Distribution: Red Sea, western Indian Ocean, Indonesia, north Australia, China and Micronesia
Habitat: shallow sheltered waters; on muddy bottoms in mangroves or continental shelf mud, can enter estuaries and rivers

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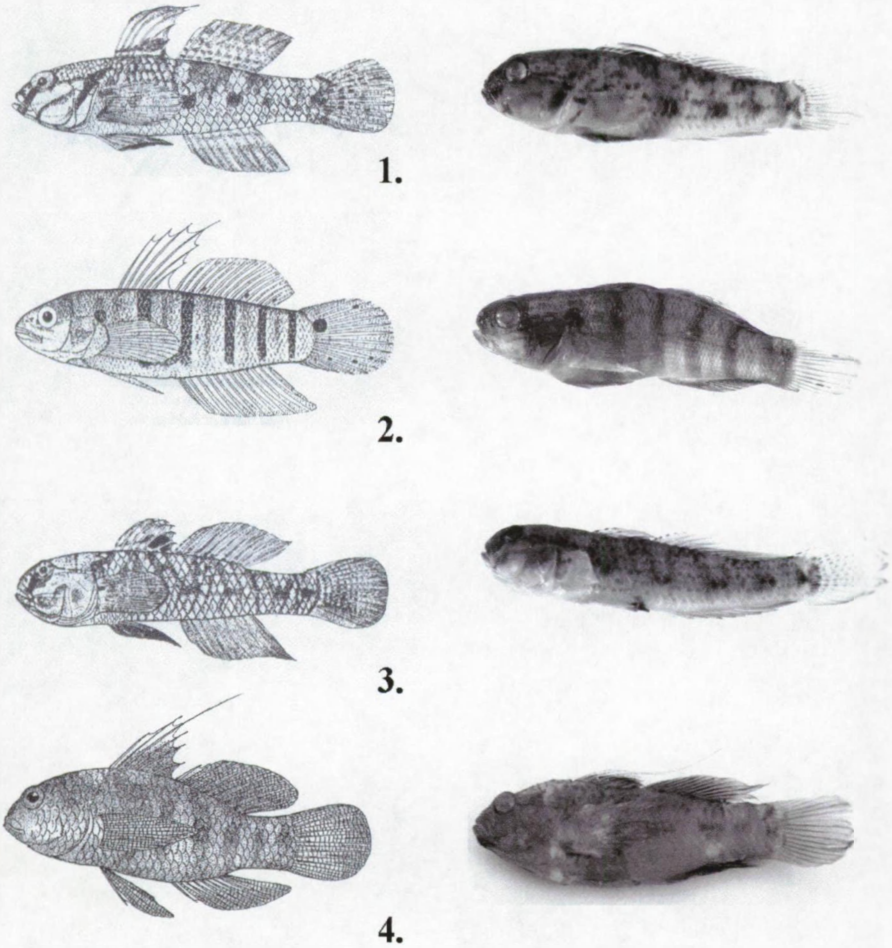
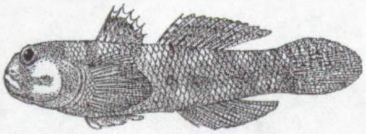


Figure1a: The Gobiidae of Gazi Bay
1. *Acentrogobius audax* (from Hoese 1986), Dr. 55 mm, Pi. 55 mm
2. *Amblygobius albimaculatus* (from Hoese 1986), Dr. 135 mm, Pi. 45 mm
3. *Amoya signatus* (from Hoese 1986), Dr. 65 mm, Pi. 42 mm
4. *Asterropteryx semipunctatus* (from Hoese 1986), Dr. 55 mm, Pi. 39 mm
(abbreviations: Dr.=drawing, Pi.=Picture)



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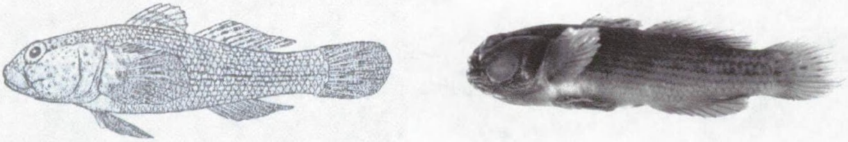

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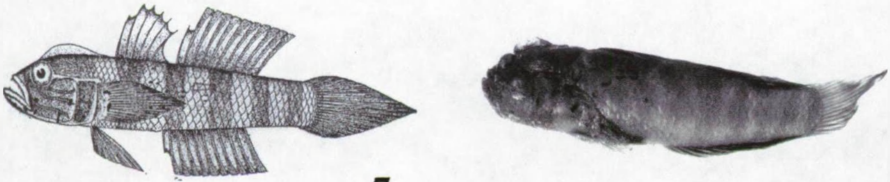

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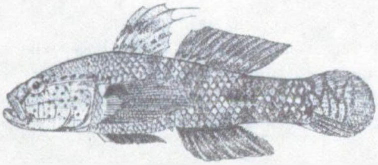

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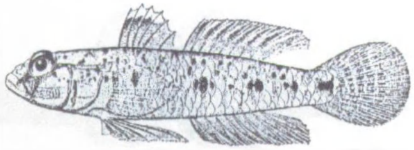
Figure 1b: The Gobiidae of Gazi Bay
5. *Bathygobius fuscus* (from Koumans 1953), Dr. n.s.
6. *Bathygobius sp. 9* (from Hoese 1986), Dr. 40 mm, Pi. 40 mm
7. *Cristagobius lophius* (from Koumans 1953), Dr. n.s., Pi. 53 mm
8. *Drombus key* (from Hoese 1986), Dr. 60 mm
(abbreviations: Dr.=drawing, Pi.=Picture, n.s.=not scaled)



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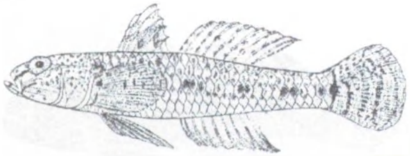

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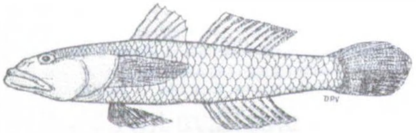

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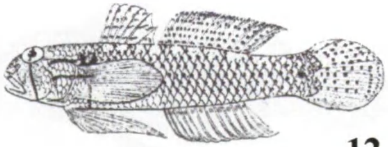
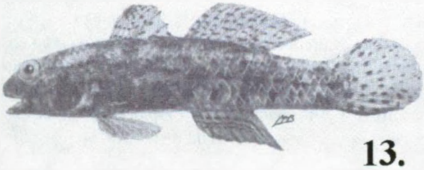


12.

Figure 1c: The Gobiidae of Gazi Bay
9. *Favonigobius melanobranchus* (from Hoese 1986), Dr. 30 mm
10. *Favonigobius reichei* (from Hoese 1986), Dr. 50 mm, Pi. 50 mm
11. *Glossogobius biocellatus* (from Hoese 1986), Dr. 75 mm, Pi. 55 mm
12. *Gnatholepis anjerensis* (from Smith 1959), Dr. 50 mm, Pi. 40 mm
(abbreviations: Dr.=drawing, Pi.=Picture)



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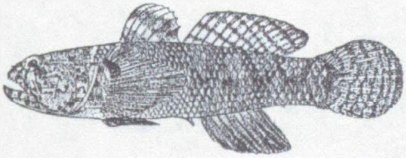

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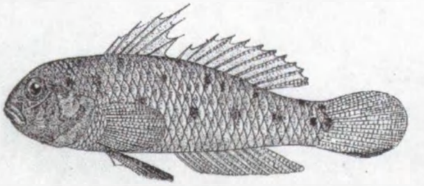

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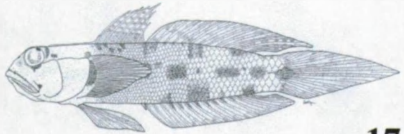
Figure 1d: The Gobiidae of Gazi Bay
13. *Istigobius ornatus* (from Hoese 1986), Dr. 75 mm, Pi. 42 mm
14. *Monishia sordida* (from Hoese 1986), Dr. 45 mm
15. *Mugilogobius durbanensis*, Pi. 35 mm
16. *Oplopomus oplopomus* (from Koumans 1953), Dr. n.s., Pi. 46 mm
(abbreviations: Dr.=drawing, Pi.=Picture, n.s.=not scaled)



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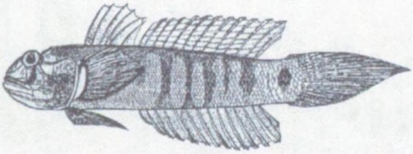

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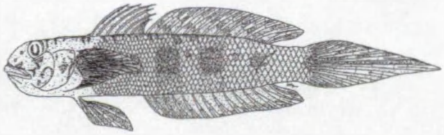

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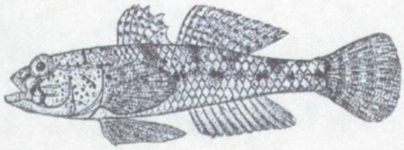

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Figure 1e: The Gobiidae of Gazi Bay
17. *Oxyurichthys lonchotus* (from Pezold 1998), Dr. 43 mm
18. *Oxyurichthys ophthalmonema*, Pi. 85 mm
19. *Oxyurichthys papuensis* (from Hoese 1986), Dr. 180 mm
20. *Oxuyrichthys takagi* (from P. Regan, unpublished), Dr. n.s.
21. *Periophthalmus argentilineatus*, Pi. 140 mm
22. *Periophthalmus kalolo*, Pi. 95 mm
23. *Psammogobius knysnaensis* (from Hoese 1986), Dr. 55 mm
24. *Yongeichthys nebulosus*, Pi. 70 mm
(abbreviations: Dr.=drawing, Pi.=Picture, n.s.= not scaled)

CHAPTER 3

DISTRIBUTION PATTERNS IN THE FISH COMMUNITY OF A TROPICAL BAY, WITH EMPHASIS ON THE HABITAT CHOICE OF THE GOBIIDAE

Coene Heidi, Beuls Ingrid, Silence Jurgen and Ollevier Frans

ABSTRACT

This paper reports on the fish species composition at nine adjacent shallow water sites in a mangrove creek, differing mostly in terms of substrate type and seagrass cover. A total of 9,805 individuals covering 95 species and belonging to 42 families were collected during the survey. The Gobiidae was by far the most species-rich family (19 species) and contributed 40% of all individuals caught. Two major assemblages could be distinguished: an assemblage in the seagrass sites and one in the unvegetated areas. The seagrass sites harboured typical vegetation-associated species such as syngnathids, scorpaenids, labrids, siganids and scarids. They showed the highest species richness and diversity. The unvegetated sites were clearly dominated by Gobiidae, both in terms of density and diversity. Atherinids, sillaginids, bothids, synodonts and the goby species of the genera *Favonigobius* and *Oxyurichthys* were characteristic on sandy bottoms. Besides the overall dominance of gobies, pursemouths (Gerreidae) and thornfishes (Teraponidae) were typical for muddy sites.

These results are comparable to those obtained in previous surveys on the fish community of Gazi Bay. There was a comparable species richness and diversity, even at a microhabitat scale. This is, however, the first report identifying the Gobiidae as a major component of the fish community. We propose that our fishing methods and mesh sizes were adapted to capture small benthic species.

The commonly accepted hypothesis that densities of small fish species are positively correlated with vegetation cover does not hold for the gobies in our study area. Based on the presumed high predation pressure on gobies in Gazi Bay and their observed dominance and distribution patterns, we might expect that they possess adaptive predator avoidance strategies, as described for their counterparts in temperate regions.

INTRODUCTION

Tropical shallow marine ecosystems are often characterised by a high species diversity. In many tropical regions, habitat heterogeneity, even at a local scale, can be a major factor promoting coexistence of a high number of species (Lowe-McConnell 1991). It is a general feature of mangrove embayments to contain diverse habitat types, including seagrass beds, mudflats, sand banks, main channels and small creeks, covering a range of different abiotic and biotic conditions (Blaber 1997).

The presence or absence of a species and its numerical abundance in any habitat are regulated by physiological tolerances, morphological constraints, habitat preferences related to reproductive strategies, biological interactions such as competition and predation, and chance events (Begon *et al.* 1996). Specific species assemblages may be formed as a result of either differential survival, species-specific recruitment or post-settlement preferences for different habitat units (Greenfield and Johnson 1990). Based on the equilibrium/non-equilibrium concept, the relative importance of biotic or abiotic mechanisms in structuring these assemblages will depend on the predictability (or harshness) of the environment (Grossman *et al.* 1982). When biotic mechanisms are considered, habitat selection is supposed to be affected mainly by foraging profitability (Werner *et al.* 1983a) traded-off against risk of predation (Werner *et al.* 1983b). Especially for small-sized species like Gobiidae, predation pressure is often high (Miller 1979).

There have been several field surveys on the fish species composition in Gazi bay, including identification of major communities in the different parts of the bay on a macrohabitat scale (Van der Velde *et al.* 1995, De Troch *et al.* 1996, Wakwabi 1999) and an assessment of seasonal patterns in the community structure (Kimani *et al.* 1996, Wakwabi 1999). Van Der Velde *et al.* (1995) found distinct differences in fish assemblages between samples from sites in seagrass meadows near the mangrove area and those from sites in seagrass beds in the bay, both at family and species level. They concluded that fish assemblages in seagrass beds were dense and rich compared with those in unvegetated areas. Although there was a high similarity between clusters, the distinction was maintained because of the occurrence of specific families. The Gobiidae (together with Muraenidae, Teraponidae, Haemulidae & Blennidae) were found to be specific for the catches near the mangrove area. De Troch *et al.* (1996) identified two major fish communities in the western creek of Gazi bay: a first community occurred in the downstream part (sandy bottom station with sparse vegetation) and was characterised by a low density and diversity; a second community occurred in the upstream part of the same creek (station with dense seagrass vegetation), with high density and diversity. The study of Kimani *et al.* (1996) comprised monthly samples during one year at three sites. They stated that Gobiidae were not abundant in Gazi bay, contrary to other mangrove estuaries with soft substratum. Dominant species reported by Kimani *et al.* (1996) were *Gerres oyena*, *Atherinomorus lacunosus* and *Herklotsichthys quadrimaculatus*. These are pelagic species typically caught in large schools with a beach seine. Other common species belonged to the Teraponidae, Monodactylidae, Lethrinidae and Lutjanidae. The study of Wakwabi (1999) comprised a detailed spatial survey, using a trawling net towed from a zodiac at high water during neap tides. He suggested that the following spatial structures are important in determining the community patterns: the fringing reef, the distribution and intensity of seagrass beds, the mangrove swamps and the river mouths. Scorpaenidae, Siganidae, Blenniidae and Scaridae were found to be indicator species for the seagrass beds, both in the seagrass beds in the main bay lagoon as well as in the mixed seagrass beds of the downstream part of the western creek. Little *et al.* (1988) presented the results of a beach seine survey (mesh size of 6-mm) in Tudor Creek, situated some 50 km north of Gazi bay. Their sampling sites included a variety of substrate types. They found Gobiidae, Clupeidae, Gerreidae, Ambassidae and Engraulidae dominating the catches. They reported 14 goby species, although only 4 were identified. The dominance of Gobiidae in Tudor Creek (Mombasa), both in terms of density and diversity, was also reported by Wakwabi (1999), who took beam trawl samples (2-mm mesh size) in two shallow mangrove creeks with silty substrates.

We focussed on the local variation in microhabitats (ß-diversity), with the sampling area covered in the present study being limited to the downstream part of the western creek of Gazi Bay. The sampling sites differed in terms of substratum type, entrained largely by the prevalent water currents in the creek. Special attention was devoted to the occurrence and habitat choice of the Gobiidae, a family that has been recognised as a typical component of the residential fish fauna of shallow areas in mangrove ecosystems world-wide (Krishnamurthy *et al.* 1984, Little *et al.* 1988, Blaber *et al.* 1989, Blaber and Milton 1990, Blaber 1997). Data on the prevalence and habitat choice of gobies within the fish community of Gazi Bay are presented and their occurrence in the Indo-Pacific region reviewed.

MATERIAL AND METHODS

Description of study area and sampling sites

Gazi bay is a shallow, tropical coastal water lagoon with the mean depth in most areas less than 5 m. The Bay (39°30'E and 4°25'S) is situated in southern Kenya, approximately 47 km south of Mombasa. The reef zone in front of the bay is part of the fringing reef that forms a nearly uninterrupted belt along the Kenyan coast (Kitheka *et al.* 1996). There are two major tidal creeks penetrating the mangrove forest. The western creek is the mouth of the seasonal river Kidogoweni, while the eastern creek is a tidal creek. This investigation focuses on the downstream part of the western creek. This creek is characterised by a very diversified substrate: the lowest parts are extremely silty because of the low tidal current and subsequent sedimentation of the finest particles. The higher parts have a more sandy substrate. Two major sandbanks occur which are only exposed at low tide. Seagrasses occur in the lower subtidal areas of the creek. The mangrove vegetation along the western creek is a species-rich mixed mangal, with *Sonneratia alba*, *Rhizophora mucronata* and *Avicennia marina* occurring closest to the tidal channel (Gallin *et al.* 1989). The tidal regime is semi-diurnal and causes strong and reversing currents in the mangrove creek. Tidal amplitude varies between 70 cm (neap tides) and 290 cm (spring tides).

Sampling took place between 21st of July and the 25th of August 1994, which corresponds with the dry season (McClanahan 1988). During this season, freshwater influx is minimal, resulting in moderate hypersaline and relatively clear water (Kitheka 1997). Surface water temperature and salinity were measured with a mercury thermometer and a refractometer, respectively. Temperature ranged between 24 and 29°C and salinity varied between 30 and 36 ppt.

Nine shallow water sites (Figure 1) within the western creek were selected according to substrate type (grain sizes) and including three main habitat types (mud, seagrass and sand). Site 1 (MUD 1) is a muddy sand flat situated in front of a sand beach. It is used as a landing base for the local fishermen. Site 2 (MUD 2) is sandy mudflat situated between two mangrove stands. Site 3 (MUD 3) is a small muddy creek between a dense mangrove stand and a sand bank. Site 4 (MUD 4) is a sandy mudflat situated at the mouth of the western creek in the bay and adjacent to an extensive sand beach. Site 5 (MUD 5) is situated most upstream of the western creek and consists of a silty substrate surrounded by mangrove stands. All these non-vegetated sites are situated at the western side of the creek. The eastern site of the creek is covered with seagrass beds. Site 6 (SG 1) is situated at the mouth of the western creek and consists of the major entrance channel with an extensive seagrass bed at the eastern site of a sand bank. Site 7 (SG 2) is situated in the upstream region of the western creek on the left side of a large sand bank (which is exposed at low tide) and bordered to the right by mangrove stands. The most abundant seagrass species are *Cymodocea rotundata* and *C. serrulata*, *Halophila stipulacea* and *H. ovalis*, and *Thalassia hemprichii* (Coppejans *et al.* 1992). Site 8 (SAND 1) is a subtidal sand bank between MUD 2 and SG 1; site 9 (SAND 2) is a more upstream sand flat adjacent to SG 2. Sediment characteristics of the non-vegetated sites were taken from Schrijvers *et al.* (1995). They determined the granulometric variables and the amount of organic material in approximately the same sites (Table 1). The lowest mud content and % of organic material was found in SAND 1 and SAND 2. Median particle size in these sites was higher than 500 µm. The sites MUD 1, MUD 3 and MUD 5 showed the highest mud content and organic material.

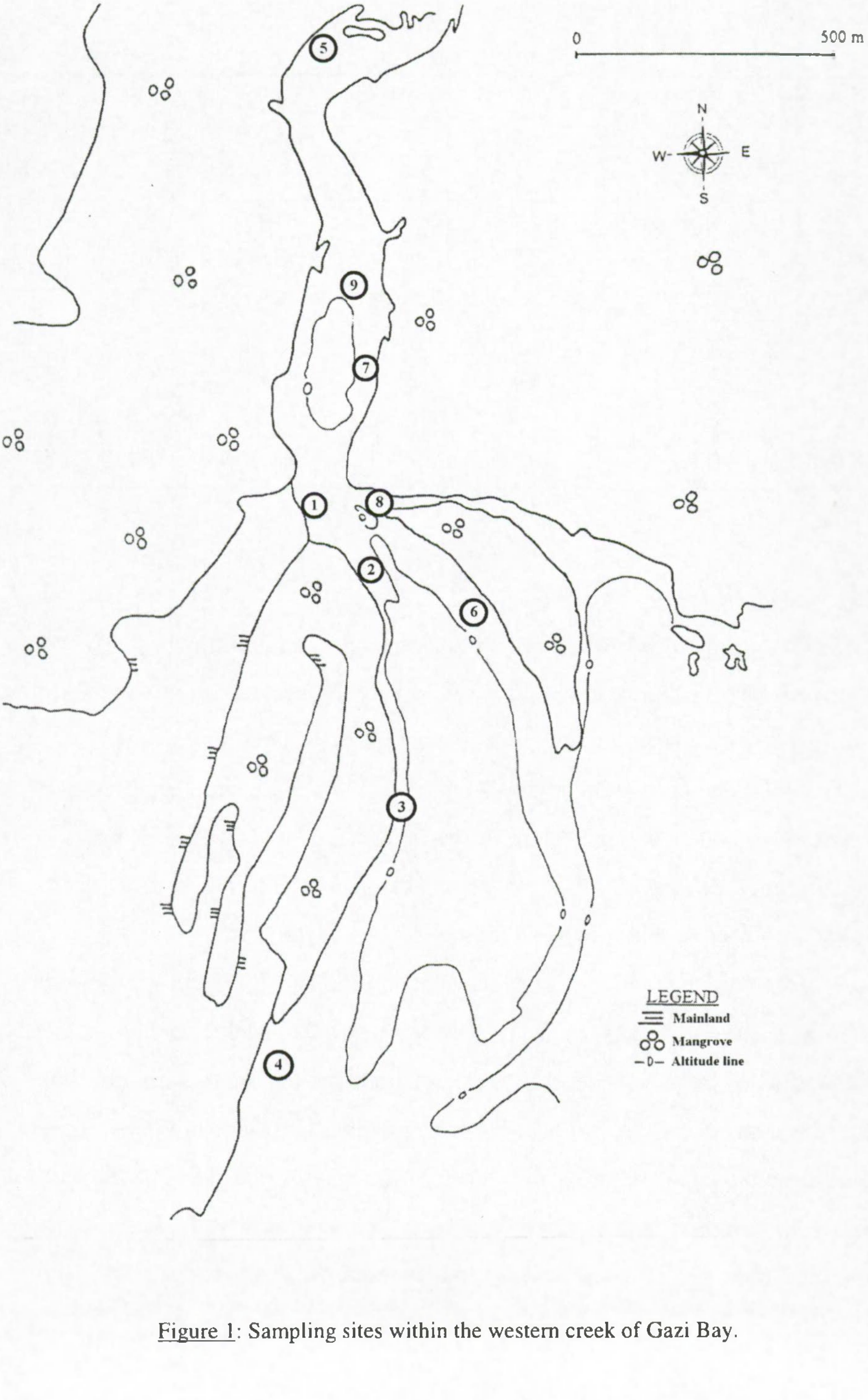

Figure 1: Sampling sites within the western creek of Gazi Bay.

Table 1: Sediment characteristics for the non-vegetated sites, taken from Schrijvers *et al.* (1995): codes of sampling sites; percentage of mud, sand and coarse sand; median grain size (in μm); and percentage of organic matter.

Sampling site (this study)	Sampling site (Schrijvers *et al.*)	Mud %	Sand %	Coarse sand %	Median grain size	% Organic matter
MUD 1	G 10	3.30	79.83	16.87	334.9	6.44
MUD 2	G 6	2.52	92.30	5.18	357.7	3.09
MUD 3	G 7	3.78	90.93	5.29	281.2	7.38
MUD 4	G 8	2.37	84.42	13.21	366.5	1.30
MUD 5	G 1	3.35	93.20	3.45	369.8	19.41
SAND 1	G 11	0.78	87.42	11.80	544.5	0
SAND 2	G 9	0.32	93.87	5.81	518.7	0

Sampling procedure

Two sampling methods were used: beach seining and hand trawling. The beach seine measured 15 by 1.5 m with 3-mm stretched mesh and was fitted with a ground rope and floats. A standardised haul was considered to sweep an area of 18 m². The small beam trawl of 1.5-m width had a bag-net of 6-m long with stretched meshes of 25- and 20-mm of the outer net and 3-mm of the inner net. The trawling net was fitted with a ground rope and tickler chain and was dragged at constant speed over a minimal distance of 20-m parallel to the shoreline.

Sampling was always conducted at low tide (± 2 hours) and four tows were taken at each sampling site. Beach seining was only conducted during the daytime, while trawling was done during day and night at the same sampling site. Not all sampling sites could be sampled by both methods: in the sandy sites, only trawling could be conducted, whereas only beach seining was possible in the most silty site (MUD 5). A total of 223 nettings were taken. An overview of the sampling schedule is given in Table 2. The fishes were sorted, anaesthetised in benzocaine and preserved in

4% formaldehyde-seawater solution. Species were identified using the keys provided by Smith and Heemstra (1986).

Table 2: Overview of the sampling schedule with number of tows at each sampling site for both beach seining (BS) and trawling (TR).

	MUD 1	MUD 2	MUD 3	MUD 4	MUD 5	SG 1	SG 2	SAND 1	SAND 2
BS	15	10	16	15	13	13	12	4	11
TR	21	9	22	0	0	41	3	18	0
total	36	19	38	15	13	54	15	22	11

Data analysis

Diversity of the fish assemblages in the different sampling sites was measured with Simpson's diversity (D) and equitability (E) index:

$$D = 1 / \sum_{i=1}^{s} p_i^2 \text{ and } E = D / D_{\max} \text{ with } D_{\max} = 1 / S$$

with S the number of observed species and p_i the (numerical) proportion of species i to the total number of fish individuals (Krebs 1989a). The Simpson's index was preferred above other commonly used diversity measures as it is less sensitive to sample size effects and emphasize dominant rather than rare species (Hill 1973). The rarefaction method was used to compare species richness between sampling sites obtained from different sample sizes. The rarefaction plot estimates the number of species expected in a random sample of individuals taken from a collection (Krebs 1989a). Calculations were made with the Biodiversity Professional Program.

Similarity between the fish assemblages in the different sampling sites was assessed with the Jaccard's coefficient of similarity (J):

$$J = \frac{x}{(s + x)}$$

with x the number of co-occurrences and s the sum of the non-co-occurrences of the recorded fish species (Krebs 1989b). The coefficient of similarity only takes presence-absence data into account.

A forward stepwise discriminant analysis was used to identify the set of species which contributed most to the discrimination between habitat types. In addition, a Bray-Curtis cluster analysis and principal component analysis were employed to explore species distribution patterns, to detect structure in the relationship between species and to summarize most of the variation with only few components (James and McCulloch 1990). These analyses were carried out with STATISTICA 4.1 for Windows and the Biodiversity Professional Program.

Assumptions for ANOVA were not met for all species, so we preferred to perform non-parametric statistics where necessary. To compare densities, Kruskal-Wallis ANOVA was used and multiple comparisons were carried out following Siegel and Castellan (1988).

RESULTS

Overall community structure

The species composition of the observed fish community at the nine sampling sites is given in Table 3. A total of 9,805 individuals and 95 species belonging to 42 families were collected during this survey. Although relative importance differed, most families occurred in all habitat types. The fish community of the mud sites was strongly dominated by the Gobiidae, with more than 40% of the individuals belonging to this family. Other abundant families were Gerreidae (8%), Sillaginidae (6%), Synodontidae (6%) and Ambassidae (6%). In the seagrass beds, the Siganidae (17%) and Gobiidae (15%) were dominant, followed by Apogonidae (11%), Scaridae (10%) and Scorpaenidae (8%). The sand flats harboured both families that are typical for the mud biotope (Gerreidae (8%)) and for the seagrasses (Apogonidae (14%) and Siganidae (4%)), but the most abundant families were the Atherinidae (24%) and the Gobiidae (20%).

Table 3: Fish families and species encountered during the sampling campaign in the western creek of Gazi Bay: comparison of mean densities (per 30 m²) between the nine sampling sites.

(abbr = abbreviations of species names used in graphs; m = MUD sites; sg = SG sites; s = SAND sites)

	abbr	**m1**	**m2**	**m3**	**m4**	**m5**	**sg1**	**sg2**	**s1**	**s2**
Muraenidae										
Siderea picta	*Sidpic*	0.16	0.34	0.09		0.33	0.48	0.24	0.28	
Clupeidae										
Herklotsichthys quadrimaculatus	*Herqua*					2.08		1.11		
Engraulidae										
Stolephorus indicus	*Stoind*		5.55	0.08		8.00	1.34		0.24	0.19
Synodontidae										
Saurida gracilis	*Saugra*	4.08	3.24	3.11	6.15	7.67	1.61	1.91	0.71	14.8
Synodus indicus	*Synind*	1.27	0.22	0.32		0.25	0.38	0.89		0.19
Antenariidae										
Histrio histrio	*Hishis*						0.02			
Atherinidae										
Atherinomorus duodecimalis	*Athduo*	1.02	0.77	2.35			0.06	0.13	17.9	
Belonidae										
Tylosaurus crocodilus	*Tylcro*			0.02			0.03			
Hemiramphidae										
Hyporhamphus affinis	*Hypaff*	0.08				0.58	0.56	0.11	1.05	
Fistulariidae										
Fistularia commersonii	*Fiscom*	0.58					0.79	1.11		
Syngnathidae										
Hippichthys cyanospilos	*Hipcya*	0.32		0.11		0.17	0.35	0.11	0.08	
Hippichthys spicifer	*Hipspi*	2.11	0.83	1.56		2.17	0.40	0.67	0.58	
Hippocampus histrix	*Hiphis*	0.02	0.06	0.05				0.22		
Syngnathoides biaculeatus	*Synbia*	0.17	0.06	0.14	0.10		1.57	1.69	0.75	
Solenostomidae										
Solenostomus cyanopterus	*Solcya*							0.22		
Scorpaenidae										
Dendrochirus brachypterus	*Denbra*	0.07		0.09			0.04	0.24	0.12	
Pterois miles	*Ptemil*						0.38	0.11	0.03	
Scorpaenopsis gibbosa	*Scogib*						0.01			
Sebastapistes strongia	*Sebstr*	0.95	0.41	1.30		0.75	2.66	5.31	1.67	
Synanceia verrucosa	*Synver*		0.05			0.02				
Plathycephalidae										
Cociella crocodila	*Coccro*	0.05	0.12	0.03					0.12	0.19
Ambassidae										
Ambassis gymnocephalus	*Ambgym*	0.95	2.65	0.08			0.06			
Ambassis natalensis	*Ambnat*	0.97	7.06	0.90					0.48	
Serranidae										
Epinephelus sp.	*Episp*	0.02				0.33				
Epinephelus malabaricus	*Epimal*	0.07		0.04						
Grammistidae										
Grammistes sexlineatus	*Grasex*			0.05						
Teraponidae										
Pelates quadrilineatus	*Pelqua*	0.64	0.29				0.11	4.98	0.10	
Terapon jarbua	*Terjar*	3.18		1.12	0.10	0.83	0.15			0.56
Apogonidae										
Apogon lateralis	*Apolat*		0.06	0.40					2.48	
Foa brachygramma	*Foabra*	4.57	3.52	1.05		1.50	3.75	8.40	1.46	
Fowleria aurita	*Fowau*	0.14	0.06				0.05		1.30	
Sphaeramia orbicularis	*Sphorb*		0.35	0.19					1.40	

		m1	m2	m3	m4	m5	sg1	sg2	s1	s2
Haemulidae										
Plectorhinchus gibbosus	*Plegib*	0.05	0.10	0.04	0.10		0.01	0.56		0.93
Pomadasys furcatum	*Pomfu*			0.04						
Lutjanidae										
Lutjanus ehrenbergii	*Lutehr*	2.06	0.91	1.33	0.21	6.25	2.01	3.62	0.94	
Lethrinidae										
Lethrinus harak	*Lethar*	3.06	1.59	0.10		10.1	1.33	7.11	0.81	
Scorpididae										
Neoscorpis lithophilus	*Neolit*				0.42					0.74
Ephippidae										
Platax teira	*Platei*	0.05				0.08	0.03	0.11		
Tripterodon orbis	*Triorb*						0.03			
Monodactylidae										
Monodactylus argenteus	*Monagr*	0.43	0.18	0.12		0.08			0.24	
Gerreidae										
Gerres acinaces	*Geraci*	7.73	2.35	7.00	1.46	9.42	2.10	1.67	3.75	8.33
Gerres filamentosus	*Gerfil*	0.16	0.18	0.11		0.67				1.48
Sillaginidae										
Sillago sihama	*Silsih*	5.30	6.40	4.60	2.19	2.42	0.01		0.18	12.4
Leiognathidae										
Gazza minuta	*Gazmin*		0.10		0.52	0.42				
Chaetodontidae										
Chaetodon lunula	*Chalun*			0.03						
Carangidae										
Caranx sexfasciatus	*Carsex*	0.14		0.09		0.25				
Pomacentridae										
Chrysiptera annulata	*Chrann*						0.02		0.05	
Noepomacentrus fallax	*Noefal*					0.17			0.03	
Labridae										
Cheilio inermis	*Cheine*						0.03	0.07		
Labrid sp.	*Labsp*	0.05	0.12				0.23	0.89	0.05	
Scaridae										
Leptoscarus vaigiensis	*Lepvai*	1.56	0.82			3.00	3.07	9.69	0.25	
Scarus sp.	*Scasp*	0.09		0.03				0.33	0.06	
Mugilidae										
Liza sp.	*Lizsp*	0.20		1.71		0.17			0.05	
Sphyraenidae										
Sphyraena barracuda	*Sphbar*	0.42	0.20	0.28	0.21	3.83	0.05	0.78	0.50	
Blennidae										
Petroscirtes breviceps	*Petbre*	0.68		0.19	0.21	1.50	0.69	1.44		0.19
Petroscirtes mitratus	*Petmit*	0.18	0.59	0.45			0.56	0.24	0.30	
Gobiidae										
Acentrogobius audax	*Aceaud*	1.15	0.29	3.10		2.22		0.37		
Acentrogobius sp.	*Acesp*					0.53				
Amblygobius albimaculatus	*Ambalb*					0.97	0.32			
Amoya signatus	*Amosig*	3.76	0.20	3.21	2.43	3.31	1.39	0.56	0.67	1.54
Asterropteryx semipunctatus	*Astsem*							0.07		
Bathygobius sp.9	*Batsp9*	0.04	0.62	0.37			0.69		0.06	
Cristatogobius lophius	*Crilop*					0.28				
Drombus key	*Drokey*	0.17	0.39	0.52	0.17					
Favonigobius melanobranchus	*Favmel*	2.19	6.29	0.15	0.35	1.58	0.46	1.11	0.40	0.62
Favonigobius reichei	*Favrei*	12.3	10.7	3.99	10.0	2.92	2.82	0.93	6.21	13.5
Glossogobius biocellatus	*Globio*	2.00	3.60	5.96	0.52	4.78	1.15	1.30	1.44	0.31
Gnatholepis anjerensis	*Gnaanj*	19.9	2.24			0.75	1.35	4.79	0.61	
Monishia sordida	*Monsor*	0.22					0.04	0.19	0.13	

		m1	m2	m3	m4	m5	sg1	sg2	s1	s2
Oplopomus oplopomus	*Oplopl*			0.03						
Oxyurichthys ophthalmonema	*Oxyoph*	0.08		0.79	0.35	3.31				5.56
Oxyurichthys papuensis	*Oxypap*	0.62		1.74	4.34	3.28		0.19	0.14	19.7
Periophthalmus argentilineatus	*Perarg*	0.29		0.36			0.19			
Periophthalmus kalolo	*Perkal*	0.08					0.01			
Yongeichthys nebulosus	*Yonneb*	0.03		1.00		0.47		0.56		
Siganidae										
Siganus sutor	*Sigsut*	3.71	0.59	0.43	0.83	13.9	3.93	15.8	1.60	
Siganus stellatus	*Sigste*			2.78					0.57	
Bothidae										
Bothus pantherinus	*Botpan*	0.29	1.31	0.16			0.28	0.11	1.36	0.74
Pseudorhombus arsius	*Psears*	0.05	0.06	0.06		0.17			0.09	
Syacium micrurum	*Syamic*	0.02								
Cynoglossidae										
Cynoglossus durbaniensis	*Cyndur*	0.03	0.10	0.06	0.10		0.06			
Monacanthidae										
Paramonacanthus barnardi	*Parbar*		0.22			0.08		0.13		
Ostraciidae										
Lactoria sp.	*Lacsp*	0.05					0.37			
Ostracion cubicus	*Ostcub*	0.10	0.12			0.17	0.10			
Tetraodontidae										
Amblyrhynchotes honckenii	*Ambhon*	0.48			2.40		0.12	0.22	0.23	
Arothron hispidus	*Arohis*						0.02		0.24	
Arothron immaculatus	*Aroimm*	0.13	0.12			0.25	0.04	0.04	0.03	
Canthigaster bennetti	*Canben*	0.05					0.01			
Chelonodon sp.	*Chesp*	0.26	0.24				0.12	0.07	0.03	
Tylerius spinosissimus	*Tylspi*	0.74	0.35	0.05	0.21		0.04	0.67	0.04	

Diversity patterns

Most families were represented by only one or two species. The Gobiidae family was by far the most species-rich, being represented by 19 species. The Tetraodontidae were represented by 6 species and the Scorpaenidae by 5 species (Table 3). Figure 2 shows the rarefaction plot of the sampling sites, showing the pattern of increase in species richness in relation to sampling effort. This plot indicates that the saturation value has not been reached yet for most of the sampling sites, which might affect our estimates of total diversity at these sites. We suggest to interpret results obtained for sites MUD 4, MUD 5 and SAND 2 with caution. Figure 3 shows that the mean number of species caught per netting (only BS samples) was significantly lower for the MUD 4 and SAND 2 sites than for the other sites, and highest for the MUD 1, MUD 5 and SG sites (Kruskal-Wallis, df = 8, $p < 0.05$, multiple comparisons). The pattern observed for the Simpson's diversity measure is very similar to that of the species richness (Kruskal-Wallis, df = 8, $p < 0.05$, multiple comparisons; Figure 3). The comparison of evenness measures per netting for the nine sampling sites (Figure 3) revealed no significant differences (Kruskal-Wallis, df = 8, $p > 0.05$).

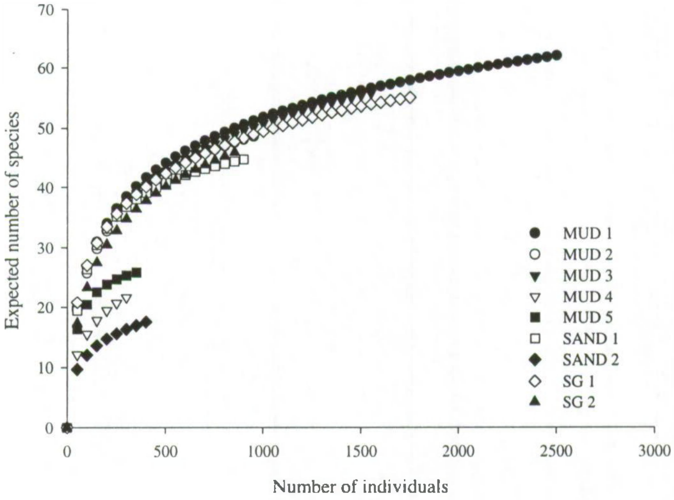

Figure 2: Rarefaction plot of the nine sampling sites, indicating the expected number of species for a given sample size (in number of individuals).

Species composition

Despite the high species richness, only a limited number of species dominated the community in terms of abundances. *Favonigobius reichei*, *Gnatholepis anjerensis*, *Saurida gracilis*, *Foa brachygramma*, *Gerres acinaces*, *Siganus sutor*, *Sillago sihama*, *Glossogobius biocellatus* and *Atherinomorus duodecimalis* accounted for 50% of the total number of individuals in the catches. Sixteen species had a relative abundance higher than 1%. There was generally high overlap in species presence between sites, as indicated by Jaccard's similarity coefficients (Table 4). Besides the lower similarities for the sites MUD 4 and SAND 2 (which may be due to the limited sample size), most similarity measures exceeded 40%. Of the 30 most abundant species, only

3 species occurred in less than 5 sampling sites. Six species were found in all sampling sites: 4 goby species (*Favonigobius reichei*, *Glossogobius biocellatus*, *Amoya signatus* and *Favonigobius melanobranchus*), *Gerres acinaces* (pursemouth) and *Saurida gracilis* (lizardfish).

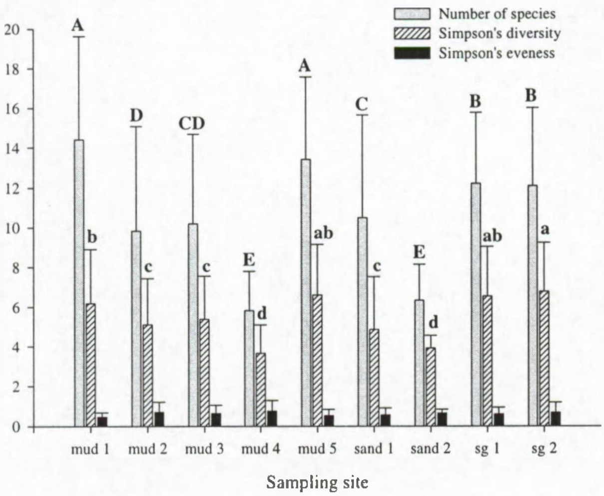

Figure 3: Comparison of the mean species number, diversity and eveness measures among the nine sampling sites. Error bars represent 1 SD. Characters represent the results of Kruskal-Wallis ANOVA multiple comparisons for the data on species number (capitals) and diversity (lower cases). Means with different characters are significantly different ($p < 0.05$).

Differences in density estimates between the two sampling techniques were tested for the 30 most dominant species. *Ambassis gymnocephalus* and *Apogon lateralis* were only caught with the trawling net, whereas the clupeid *Herklotsichthys quadrimaculatus* only appeared in the beach seine catches. Density estimates for *Gerres acinaces*, *Saurida gracilis*, *Sphyraena barracuda* and the schooling pelagic species *Sillago sihama* and *Atherinomorus duodecimalis* were significantly higher for the beach seine than for the trawling catches (Mann-Whitney U-test, $p < 0.05$, Bonferroni corrected). For the other species, no significant differences were found.

Table 4: Jaccard's similarity matrix for the nine sampling sites based on the presence-absence data of all fish species.

	MUD 1	MUD 2	MUD 3	MUD 4	MUD 5	SG 1	SG 2	SAND 1	SAND 2
MUD 1	-								
MUD 2	0.59	-							
MUD 3	0.62	0.55	-						
MUD 4	0.31	0.30	0.33	-					
MUD 5	0.49	0.43	0.42	0.30	-				
SG 1	0.61	0.47	0.41	0.27	0.36	-			
SG 2	0.58	0.47	0.40	0.28	0.44	0.54	-		
SAND1	0.55	0.59	0.48	0.24	0.41	0.51	0.55	-	
SAND2	0.25	0.25	0.30	0.48	0.30	0.20	0.21	0.19	-

A forward stepwise discriminant analysis (with the 50 most dominant species) was performed to investigate in which way the species composition in the three main habitat types was different. Twenty-eight species were retained in the model. A graphic representation of the analysis is shown in Figure 4. Irrespective of the high overlap in species presence, the three habitat types (seagrass, mud and sand) are quite clearly separated. This indicates that both typical and ubiquitous species are composing the fish fauna in each habitat type. *Syngnathoides biaculeatus* (pipefish), *Leptoscarus vaigiensis* (parrotfish), *Sebastopistes strongia* (scorpionfish) and Labrid sp. (wrasse) had highest catch rates in the seagrass sites. The sand community consisted typically of *Apogon lateralis* (cardinal fish), *Bothus pantherinus* (flounder), *Atherinomorus duodecimalis* (silverside) and *Oxyurichthys papuensis* (goby). Typical mud site species were the gobies *Glossogobius biocellatus* and *Acentrogobius audax*. Some species occurred prominently in both sand and muddy habitat sites: *Saurida gracilis* (lizardfish), *Sillago sihama* (sillago), *Gerres acinaces* (pursemouth) and the gobies *Favonigobius reichei* and *Oxyurichthys ophthalmonema*.

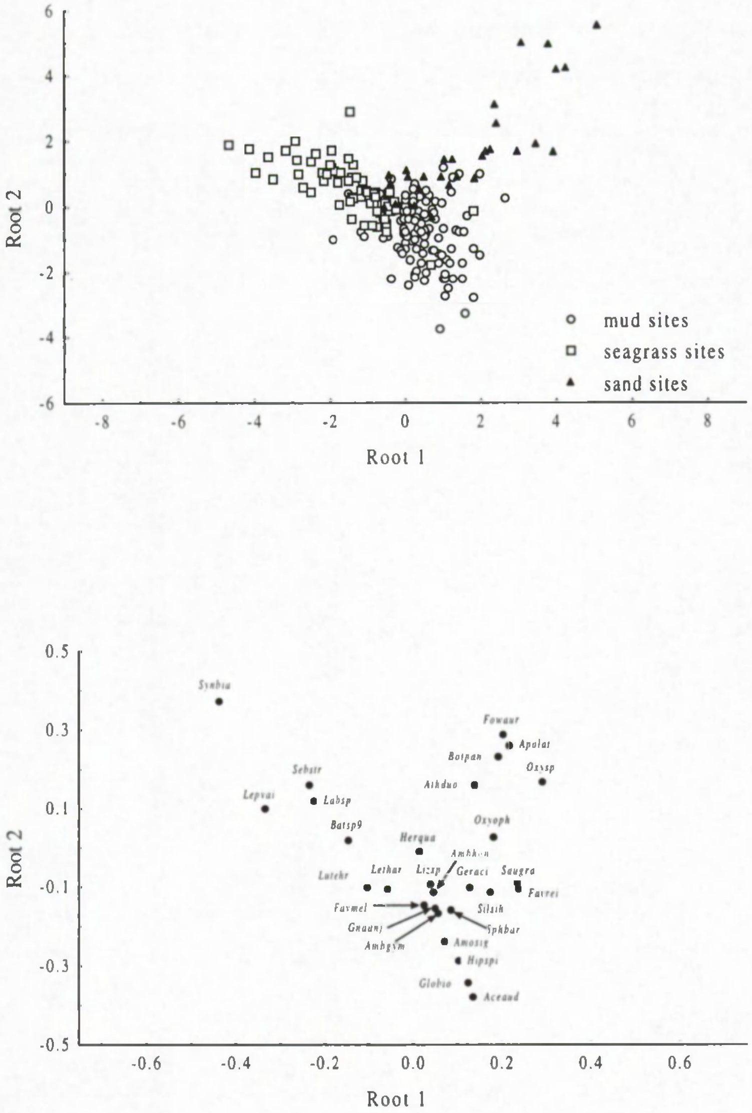

Figure 4: Plot of stepwise forward discriminant analysis (root 1 vs. root 2) of the catch rates of the 50 most abundant fish species in the three main habitat types of the study area. Upper panel: sample plot; lower panel: species plot. For abbreviations of species see Table 3.

A Bray-Curtis cluster analysis based on the procentual contribution of the 30 most dominant species in the nine sampling sites is shown in Figure 5. In a first step, two sites were separated: the SAND 2 and MUD 4 (group A), which were the two sites with the smallest sample size. In a second step, two main groups could be distinguished. Group B consisted of the two SG sites with high similarity, whereby at a lower level the MUD 5 site was added. Within group C, MUD 1 and MUD 2 were most similar, joined by MUD 3 at the 50% similarity level. SAND 1 was characterised by the lowest similarity within this group.

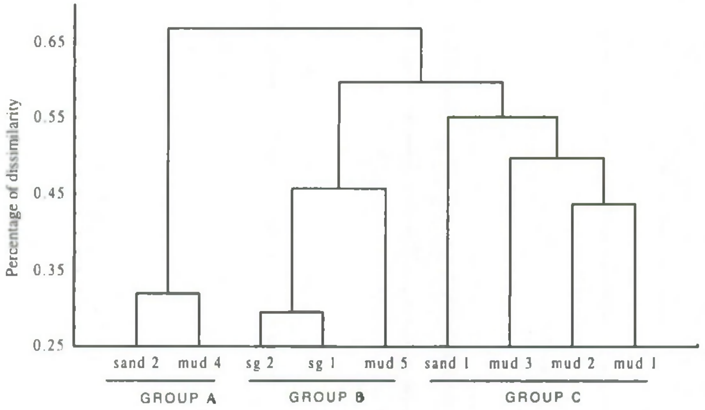

Figure 5: Result of Bray-Curtis Cluster analysis (group average link method) on the nine sampling sites, based on the catch rates of the 30 most abundant fish species.

Figure 6 shows the results of a principal component analysis on the mean catch rates of the 30 most dominant species in the nine sampling sites. The first two factors accounted for 51% of the total variance. The first principal component axis separated the seagrass sites from the non-vegetated sites. In the plot of loadings, a large number of species was significantly correlated to the negative X-axis. *Leptoscarus vaigiensis* (parrotfish), *Foa brachygramma* (cardinal fish), *Siganus sutor* (rabbitfish), *Sebastopistes strongia* (scorpionfish), *Petroscirtes breviceps* (blenny), *Fistularia commersonii* (flutemouth), *Lutjanus ehrenberghii* (snapper), *Lethrinus harak*

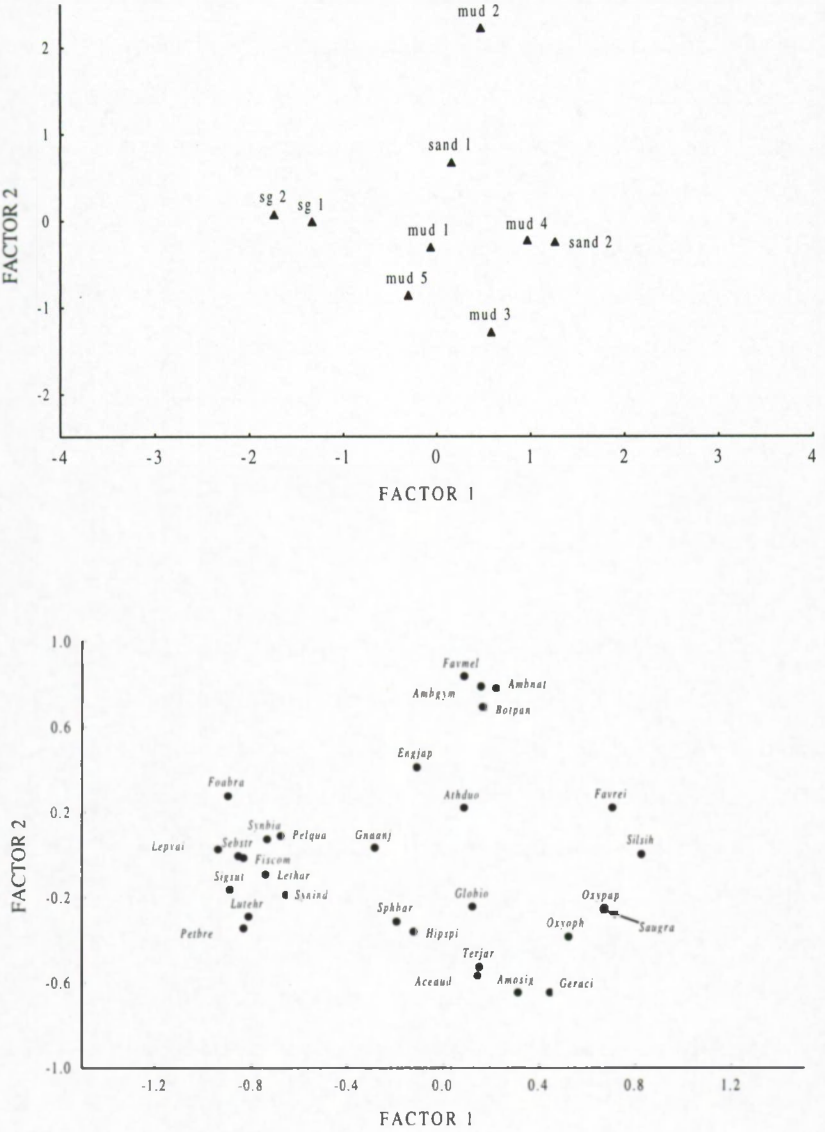

Figure 6: Results of principal component analysis (factor 1 vs. factor 2) on the catch rates of the 30 most dominant species in the nine sampling sites. Upper panel: plot of scores; lower panel: plot of loadings. For abbreviations of species, see Table 3.

(emperor) and *Syngnathoides biaculeatus* (pipefish) were all identified as typical seagrass species. The second principal component mainly resolved the variation within the non-vegetated sites. The MUD 2 and SAND 1 sites were separated mainly on the occurrences of the goby *Favonigobius melanobranchus*, the ambassids *Ambassis gymnocephalus* and *A. natalensis* and the flounder *Bothus pantherinus*. The MUD 4 and SAND 2 sites were both characterised by the occurrence of *Sillago sihama*, the gobies *Favonigobius reichei* and *Oxyurichthys papuensis* and the lizardfish *Saurida gracilis*. MUD 3 and MUD 5 had the highest scores for the pursemouth *Gerres acinaces*, the gobies *Acentrogobius audax* and *Amoya signatus*, and the thornfish *Terapon jarbua*.

Gobiidae contribution

The Gobiidae represented more than 40% of all individuals caught, although this varies among sites (Figure 7). Comparison of the mean density of gobies revealed highest mean densities for the SAND 2 and MUD 1 sites (> 40 ind / 30 m^2); whereas the SAND 1 and SG sites harboured the lowest densities of gobies (< 10 ind / 30 m^2). The mean density of non-gobies was highest (> 70 ind / 30 m^2) in the MUD 5 and SG 2 site and lowest (< 20 ind / 30 m^2) in the MUD 4 site (Kruskal-Wallis ANOVA, df = 8, $p < 0.05$, multiple comparisons).

A total of 19 species of Gobiidae were encountered during this survey (Table 2). Only one species was never caught in the unvegetated sites, namely *Asterropteryx semipunctatus*. Other species with restricted distribution were *Acentrogobius sp. 2* and *Callogobius maculipinnis*, both ocurring only at site MUD 5, and *Oplopomus oplopomus* at the MUD 3 site. Within the seagrasses, 14 species of gobies were caught, while the sand habitat harboured 9 species. The mean number of gobiid species caught per netting was significantly higher in three of the non-vegetated sites (MUD 1, MUD 3 and MUD 5) than in the other sites (Kruskal-Wallis ANOVA, df = 8, $p < 0.05$, multiple comparisons).

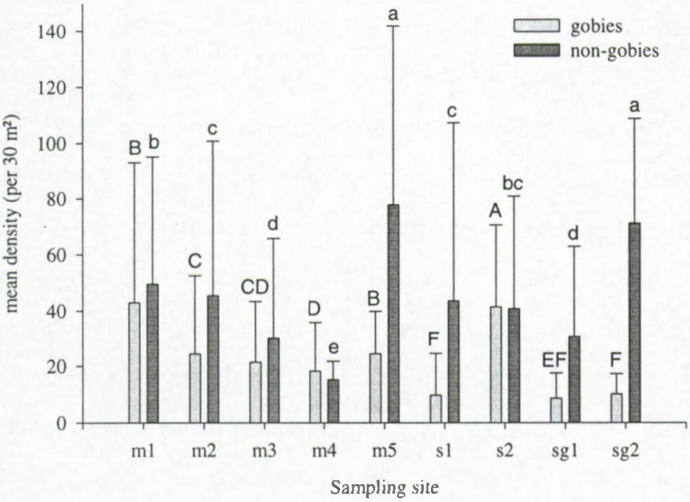

Figure 7: Comparison of goby and non-goby densities among the sampling sites: mean, standard deviation. Characters represent the results of Kruskal-Wallis ANOVA multiple comparisons for the data on gobies (capitals) and non-gobies (lower cases). Means with different characters are significantly different ($p < 0.05$).

DISCUSSION

The fish community of Gazi Bay

The benthic fish community of this mangrove creek is clearly characterised by a high species richness, but at the same time strongly dominated by a limited number of species. This seems to be a general feature of tropical shallow water habitats (Blaber 1997). We observed a high overlap in overall species composition among sampling sites. The dominant species occurred in several sites, indicating a low degree of habitat specialisation for these species. Nevertheless, there was a consistent pattern in the relative abundances of species among habitat types, as discriminant analysis enabled us to identify typical species groups for each habitat type. The seagrass sites harboured syngnathids, scorpaenids, labrids, siganids and scarids, which are known to be typically vegetation-associated species (Smith and Heemstra 1986). These sites showed the highest diversity, which could be directly related to the observed high species richness. The unvegetated sites were dominated by Gobiidae. Both species richness and densities of gobies were highest in the mud and sand sites. The principal component and cluster analyses further showed that the mud and sand sites were not clearly separated on the basis of species distributions. Characteristics for the sandy sites (SAND 1, SAND 2, MUD 2 and MUD 4) were atherinids, sillaginids, bothids, synodonts and goby species of the genera *Favonigobius* and *Oxyurichthys*. All these species have a typically light pigmentation. Their association with sandy bottoms has often been related to camouflage advantage (Blaber 1997). Besides the overall dominance of gobies, some other fish species were found to be typical for the muddy sites, including the pursemouths (Gerreidae) and thornfishes (Teraponidae).

When comparing our results with previous studies on the fish community in Gazi bay, it turned out that most of the common families reported by earlier surveys appeared in our catches. Our survey was limited to the downstream part of the western creek, which is only a small part of Gazi Bay. Nevertheless, we found a species richness and diversity comparable to previous surveys. In addition, on the local scale we focussed upon, we found the same distinct assemblages between seagrass beds and non-vegetated areas as in other studies that covered a larger area. The study of De Troch *et al.* (1996) clearly underestimated the importance of microhabitat diversity in the downstream part of the western creek. They only reported on 14 species, whereas we observed 96 species in the same area. This shows that extensive sampling in a balanced design is important in community analysis, especially in tropical regions.

Contrary to the previous surveys, we did not observe the Mullidae, although they seem to prefer muddy unvegetated beaches in mangrove creeks (Blaber 1997). The family of the Ambassidae, small-sized resident fishes that were caught frequently in the unvegetated sites in our study, was only reported by Wakwabi (1999), who caught 4 individuals. This might be related to the specific sampling technique we used, as we showed that *Ambassis gymnocephalus* was only caught with the beam trawl net.

Previous studies mainly used beach seines, with the exception of Wakwabi (1999). This highlights the importance of the choice of the sampling methodology in organising a field survey. The effectiveness of each capture method is species-specific and might therefore underestimate some important species. As we combined both beach seining and trawling, we probably produced a less biased estimate of the fish abundance for each habitat. However, we still need to assume that the differences we found between habitats were not attributable to differences in the effectiveness of the capture method (Connolly 1994).

None of the field surveys cited above had identified the Gobiidae as a major component of the fish community in Gazi Bay. Probably, the mesh sizes used by previous authors were not appropriate to capture the smaller species. The small-sized species group might be of considerable importance in tropical shallow water habitats (Krishnamurthy and Jeyaseelan 1981, Lowe-McConnell 1991). Most goby species tend to be caught with active gear (trawling or beach seining) with small mesh sizes, or with local poisoning methods. This is mainly due to their morphology, small body size and their often territorial, burying or cryptic behaviour. De Troch *et al.* (1996), using a beach seine net with 25 mm stretched mesh size, reported only three goby species in the western creek (*Gnatholepis anjerensis*, *Favonigobius reichei* and *Amblygobius albimaculatus*). Just one species, identified as *Oligolepis keiensis* (probably mistaken for *Oxyurichthys sp.*), was collected by Kimani *et al.* (1996), with a beach seine net of 20 mm stretched mesh size. Van der Velde *et al.* (1995) used a variety of fishing techniques (fyke nets, visual census count technique, beam trawl, beach seine and rotenone) to describe the fish community of Gazi Bay (all nets with mesh size 20 mm) and reported three goby species: *Amblygobius albimaculatus*, *A. sphynx* and *Priolepis inhaca*. Only the survey of Wakwabi (1999) reported a considerable diversity of Gobiidae. He could distinguish between 10 species during his seasonal survey (trawling net with 2 mm mesh size) and 10 species during his short-term spatial survey (beam trawling with 5 mm mesh size), totalling 14 Gobiidae species.

The importance of Gobiidae as a dominant component of the residential fish fauna in mangrove estuaries has been frequently reported. Krishnamurthy *et al.* (1984) described the global distribution pattern of the mangrove ichthyofauna. Among the ichthyofauna reported, the Gobiidae showed the highest number of species (approximately 110). Within the Indo-West Pacific zoogeographical province, several studies confirmed the high diversity and/or density of the family Gobiidae in estuaries, coastal waters and lakes and mangrove embayments (Blaber 1997). Day (1974) reported on the fish fauna of the Morrumbene estuary (Mozambique) and illustrated the dominance of several goby species in the upper reaches of the mangrove forest, small creeks and muddy channels. A checklist of the Red Sea (Goren and Dor 1994) mentioned 96 Gobiidae species. Several of these species occurred also in our catches (*Amblygobius albimaculatus, Amoya signatus, Asterropteryx semipunctatus, Callogobius maculipinnis, Gnatholepis anjerensis, Oplopomus oplopomus, Oxyurichthys papuensis, Periophthalmus kalolo, P. argentilineatus and Yongeichthys nebulosus*). Most of these species have also been reported from the Arabian Gulf (Kuronuma and Abe 1986). Pinto and Punchihewa (1996) reported four goby species in the mangrove prop root habitat and seagrasses in Sri Lanka. *Glossogobius biocellatus,* a species that was also observed by us, was caught in both habitats, with the highest densities in the seagrasses. Rönnback *et al.* (1999) observed 9 species of gobies inhabiting the *Avicennia* and *Rhizophora* microhabitats in the Philippines. Gobiidae have also been found important in several (sub)tropical estuaries of North Australia, especially in small mangrove creeks and adjacent mud/sandflats (Robertson and Duke 1987, 1990, Blaber *et al.* 1985, Blaber *et al.* 1989). Several of the recorded species were identical or related to those observed at Gazi Bay (*Acentrogobius sp.*, *Amoya sp.*, *Drombus sp.*, *Favonigobius melanobranchus*, *Glossogobius biocellatus*, *Gnatholepis sp.* and *Yongeichthys nebulosus*). Blaber and Milton (1990) reported on the species composition, community structure and zoogeography of fishes of 13 mangrove estuaries in the Solomon Islands. Their analysis revealed that Gobiidae were the most numerous taxon in soft, muddy-bottom estuaries. By comparing their results with other mangrove estuaries of the Indo-Pacific region, Blaber and Milton (1990) concluded that there is a characteristic fish fauna typical for mangrove systems throughout the region. A complete checklist of fishes from the Solomon Islands (Blaber *et al.* 1991) included 774 species. The Gobiidae proved to be the largest family with 75 species, followed by the Apogonidae with 46 species.

Habitat preference of the Gobiidae

It is commonly hypothesized that the abundance of small fish species is positively correlated with vegetation cover. In addition to the extensive documentation of the association of small fishes with submerged aquatic vegetation in the field (Humpries and Potter 1993, Connolly 1994), several experimental investigations (mainly field manipulations and tethering experiments) have focused on the relative role of food abundance and refuge in explaining this association (Werner *et al.* 1983a,b, McIvor and Odum 1988, Rozas and Odum 1988, Werner and Hall 1988, Levin *et al.* 1997). The hypothesis of a preference for vegetation cover, however, does not hold in the case of the gobies in our study area, as they were far more diverse and abundant in the adjacent unvegetated habitat. This is surprising, since their small body size makes them highly susceptible to predation throughout their whole lifespan (Miller 1979).

An accurate assessment of the predation pressure on the gobies in our study area is difficult to make at this stage. The only information available on the trophic organisation of the fish community of Gazi bay is provided by Wakwabi (1999). He recorded more than 60% of the species as carnivores, which were especially important in the mangrove-seagrass associated community of the creeks. Most of these species were generalist feeders, some with clear opportunistic tendencies, having wide prey spectra with overlapping diets. The most important resident piscivores were members of the families Synodontidae, Muraenidae, Sphyraenidae and Plathycephalidae. *Saurida gracilis*, *Synodus indicus*, *Sidera picta*, *Sphyraena barracuda* and *Cociella crocodila* all occurred regularly in our samples, both in the seagrasses and unvegetated sampling sites. No assessment has been made so far on migrating piscivores relying on the tidal current to enter the creek, or the importance of birds as predators of small fishes in the creek.

The importance of the piscivorous guild in mangrove embayments or (sub)tropical estuaries is assumed to be in part dependent on basic hydrological features of the site. Turbid areas associated with mangrove creeks can reduce effectiveness of visual piscivorous predators and thus be especially attractive to small-sized fish (Cyrus and Blaber 1987). In a tropical mangrove creek in SW Madagascar, piscivores only represented 18% of the species composition. This was attributed to the high turbidity and low tidal current (Laroche *et al.* 1997). Blaber *et al.* (1985), however, reported on an important piscivorous guild penetrating the mangrove creeks in the Dampier region (NW Australia) at high tides. The combination of clear water conditions, constant seawater salinity and a large tidal range of about 5 m was assumed to favour predation on juveniles and small resident species by piscivorous fishes. This last group was composed of non-selective feeders and their diet consisted mainly of small resident species like Gobiidae and Atherinidae (Blaber 1986). Based on the hydrological features of Gazi bay (low turbidity due to reduced freshwater influence), visual predation is assumed to be favoured.

So far, ethological studies on tropical gobies are very scarce. Only scattered information is therefore available on habitat associations of the goby species encountered during our survey. Given the supposedly high predation pressure on gobiids in Gazi Bay, we expect the trade-off between food gathering and predator avoidance to be important in the species composition and distribution of gobiids.

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CHAPTER 4

IN SITU ESTIMATION OF FOOD EVACUATION RATE AND DAILY RATION IN A TROPICAL GOBY *GNATHOLEPIS ANJERENSIS*

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ABSTRACT

This paper presents data on an *in situ* estimation of food evacuation rate and daily ration of the tropical goby *Gnatholepis anjerensis*. Estimates of stomach and complete digestive tract evacuation rate, obtained from a field cage experiment and from 24 h field data, were compared. Daily ration estimates of Eggers and Elliott & Persson models gave similar results, supporting recent studies. Caution should be made, however, in the selection of the digestive tract section to be analysed: we found considerable differences in daily ration estimates when stomach or complete digestive tract content data were used, contrary to other studies. This might be due to the relative high evacuation rate of the complete digestive tract content of *Gnatholepis anjerensis*. Day-to-day variation in food daily ration, estimated from weekly field sampling, was high. Generalisations based on limited daily ration estimates can thus lead to considerable errors. No pattern in daily ration according to spring-neap tidal cycle was found.

INTRODUCTION

The feeding ecology characterises the role of a species within the ecosystem. Estimates of food consumption have often been used in trophodynamic models and descriptions of multispecies energy budgets (Sainsbury 1982, Evans 1984, Jarre *et al.* 1991). Although temperate goby species have received considerable attention in feeding studies (Doornbos and Twisk 1987, Hamerlynck *et al.* 1993, del Norte-Campos and Temming 1994), their tropical counterparts have been largely neglected. Yet, gobies (Gobiidae, Teleostei) are essentially a tropical taxon that occurs in high densities in a wide range of biotopes (Blaber *et al.* 1989, Blaber and Milton 1990).

Gnatholepis anjerensis has a widespread distribution in tropical and subtropical marine habitats (Hoese and Winterbottom 1979) and is one of the most dominant goby species in the seagrass beds of the mangrove creeks along the Kenyan coast (see

Chapter 3). It is a small sized benthic teleost fish feeding mainly on benthic or epiphytic invertebrates. It is part of the diet of several important piscivores and may therefore play an important role as intermediate fish species in the food web of mangrove ecosystems.

Evacuation rates are best measured *in situ*, as the fish is then subjected to the natural variation in environmental conditions and diet (Bromley 1994). Rates of gastric emptying are generally described by fitting the data to a gastric emptying curve, although the choice of the most appropriate mathematical expression is still controversial (Pennington 1985, Olson and Mullen 1986, Persson 1986). Recent studies have shown that the empirical exponential model approximates well models based on physiological digestion (Jobling 1986, Salvanes *et al.* 1995). In this study we compared estimates of a field cage experiment with estimates from 24 h field data. Boisclair and Marchand (1993) pointed out the importance of selecting the appropriate section of the digestive tract when estimating fish daily ration. Although they did not find significant differences in estimates based on stomach or complete digestive tract content data, they considered the use of the complete digestive tract content more reliable as variances of estimates were considerable lower. We found it appropriate to perform such a comparison between both appraoches with our dataset, given the lack of reference studies.

Several authors have stressed that there is an important diel variation in feeding intensity in natural fish populations (Swenson and Smith 1973, Smagula and Adelman 1982, Hamerlynck *et al.* 1993, Trudel and Boisclair 1993, Grant and Kott 1999). This variation might be the result of short-term abiotic or biotic changes in the environment, such as temperature, salinity, food availability or predation risk. In some cases, feeding intensity has been shown to be related to the spring-neap cycle (Gibson 1978, Hamerlynck *et al.* 1993). As our study area is strongly influenced by a semilunar tidal rhythm, we analysed feeding intensity during nine consecutive neap and spring 24 h cycles.

The aim of this study was to obtain estimates of evacuation rate and daily food intake through *in situ* methods for *Gnatholepis anjerensis.* In addition, we wanted to investigate day-to-day variation in food intake in relation to neap and spring tides. Finally, we compared daily ration estimates derived from stomach or complete digestive tract content data.

MATERIAL AND METHODS

Study area

Gazi Bay (39°30'E and 4°25'S) is a tropical embayment, situated approximately 50 km south of Mombasa (Kenya). The bay is sheltered from the Indian Ocean by a fringing coral reef and Chale Island. Sampling took place between July and October 1995, corresponding with the end of the SE monsoon. The tidal regime of the study area is semidiurnal, causing strong and reversing currents in the mangrove creek. For the hydrodynamics of the bay, we refer to Kitheka *et al.* (1996). The fish community of the bay has been described by De Troch *et al.* (1996) and Wakwabi (1999).

Evacuation rate

The evacuation rate R for *G. anjerensis* was estimated by two methods, both involving field conditions. In a field cage experiment, the decline of stomach/gut fullness of non-feeding fish was followed over time through serial slaughtering (R_{exp}) (Thorpe 1977). As a second approach, the temporal variation in stomach fullness data over a 24 h cycle was used to estimate the evacuation rate (R_{max}) during periods of maximum food decline in the gut, assuming no food intake during these periods (Elliott and Persson 1978). According to Jobling (1986), an exponential function will best describe the emptying of small, easily digestable low energy food from the stomach. *G. anjerensis* corresponds to this assumption, being a typical epibenthic feeder with a diet consisting mainly of amphipods, copepods, isopods and ostracods (see Chapter 5).

The field cage experiment was conducted on 13 and 15 September 1995 in the subtidal seagrasses of the Western Creek in Gazi Bay. Samples were taken during daytime at low water, between 12.00 h and 16.00 h. This coincides with the time of maximal feeding for *G. anjerensis* (Chapter 5). Specimens, ranging between 20 and 53 mm SL, were caught with a beach seine (15 m long and 1.5 m width, with 1.5 x 1.5 mm mesh size) or hand trawling net (beam 1.5 m, mesh size of inner net 1.5 x 1.5 mm) within a time interval of 30 min. A subsample of 6 to 24 specimens was anaesthetised immediately with benzocaine and fixed in 7% formol. The other specimens were divided randomly between two food-free cages which were placed on the sampling location. The cages were made of PVC frames (1 m by 0.5 m and 0.5 m deep) and were covered with a gauze of 250 μm, allowing circulation of water but excluding food organisms. Subsamples of both cages were taken and processed in the same way. On day 1, subsamples of 10 fish were fixed every 30 minutes; on day 2, the time interval between two subsamples was 60 minutes. To attain sufficient sample sizes, fishes from both cages were pooled. In the laboratory, each goby was dissected and the digestive tract was subdivided in 4 sections: stomach, intestine 1, intestine 2 and intestine 3. All intestine sections had the same length. Food content of each section was placed in a preweighted vial and dried overnight at 60°C. Dry weights were measured at 1 μg precision. Fullness indices were standardised using dry weight (DW) of the fish, derived from a standard length - dry weight regression, estimated from a subsample of 50 specimens *G. anjerensis*:

$$\ln \mathrm{DW}\ (\mathrm{mg}) = -6.45 + 3.36 \ln \mathrm{SL}\ (\mathrm{mm})\ (r^2=0.97,\ p<0.001)$$

The fullness index of a section of the alimentary tract (FI_{sec}) is given by:

$$FI_{sec} = (\mathrm{DW\ section/DW\ fish}) \times 100$$

where the section refers to either the stomach (sto), or sections of the intestine (int1, int2 and int3).

The fullness index of the complete digestive tract (CDT) is calculated as:

$$FI_{CDT} = \sum FI_{sec}$$

It is important to check the underlying assumptions before using fullness indices, as the standardisation of a variable by dividing individual values by the corresponding body weight is based on the implicit assumption that the variable varies isometrically with body size (Héroux and Magnan 1996). A regression analysis on our data showed that the fullness index removes the effect of fish size (linear regression analysis: ß = -0.13; $p > 0.05$; N = 671).

The decrease of mean gut fullness of unfed fish can be described by an exponential function:

$$\overline{FI_{t+1}} = \overline{FI_t}\ e^{-RT}$$

which becomes in its semilogarithmic form

$$\ln \overline{FI_{t+1}} = \ln \overline{FI_t}\ - RT$$

where $\overline{FI_{t+1}}$ and $\overline{FI_t}$ are the mean fullness indices at the end and the beginning of time interval T, respectively. The evacuation rate R_{exp} represents the slope of the relationship between $\ln \overline{FI_t}$ and time. Since we use ln-transformed values, empty stomachs are automatically removed from the analysis. This is justified because the time at which the stomach became empty is not known, and therefore empty stomachs could bias results. However, it has been shown that removal of empty stomachs from the analysis may influence evacuation rate estimates, especially if the proportion of empty stomachs increases significantly during the last time intervals (Bromley 1988). In our experiment, the percentage empty stomachs fluctuated randomly, and no significant increase with time was found (linear regression analysis, $p>0.05$).

The 24 h field data were taken from an intensive field campaign between 21 July and 3 October 1995 in the subtidal seagrasses of the Western creek in Gazi Bay. A total of nine 24 h cycles, each with sampling intervals of two hours, were obtained at consecutive spring and neap tides (Table 1). As catch rates were variable over time, the number of analysed specimens varied between time intervals and sampling dates. A total of 671 *G. anjerensis* individuals were dissected and analysed for dry weight of their stomach and intestine content. The method was identical to the field cage experiment. Mean FI_{sto} and FI_{cdt} for each 2 h interval were calculated. As sample sizes were rather low at night, we could not calculate specific evacuation rates for each sampling date separately. Assuming that evacuation rate did not change during the sampling period, the pooled dataset was used to estimate maximal evacuation rate for stomach and complete digestive tract.

The instantaneous evacuation rate $R_{(T)}$ is given by

$$R_{(T)} = \frac{(\ln \overline{FI_{t+1}} - \ln \overline{FI_t})}{T} \qquad \text{Equation (1)}$$

where $\overline{FI_t}$ and $\overline{FI_{t+1}}$ are the mean fullness indices at the beginning and the end of the interval, T is the duration of each sampling interval.

$R_{(T)}$ was calculated for all two consecutive time intervals and the maximum value of $R_{(T)}$ was defined as the maximal evacuation rate (R_{max}) estimate (assuming a period of food evacuation only).

Table 1: Dates, tidal status and number of analysed specimens (N) for the different 24 h sampling dates.

Experimental code	Date (1995)	Tidal status	N
24 h nr. 1	21-22 July	neap	43
24 h nr. 2	27-28 July	spring	83
24 h nr. 3	5-6 August	neap	31
24 h nr. 4	11-12 August	spring	116
24 h nr. 5	19-20 August	neap	47
24 h nr. 6	27-28 August	spring	115
24 h nr. 7	3-4 September	neap	79
24 h nr. 8	24-25 September	spring	68
24 h nr. 9	2-3 October	neap	68

Daily ration

In the exponential Elliott and Persson (1978) model the amount of food consumed is determined for each two successive time intervals by the formula:

$$C_t = \frac{(\overline{FI}_{t+1} - \overline{FI}_t e^{-RT})RT}{1 - e^{-RT}} \qquad \text{Equation (2)}$$

where R represents the gastric evacuation rate.

Daily ration is then calculated as the sum of C_t over 24 h.

$$C_{24(E\&P)} = \sum C_{ti} \qquad \text{Equation (3)}$$

This model assumes that food evacuation is exponential and that the rate of food consumption within the sampling interval is constant.

To estimate daily ration following the linear model of Eggers (1977), one calculates

$$C_{24(E)} = 24R\overline{FI_{24}} \qquad \text{Equation (4)}$$

where $\overline{FI_{24}}$ is the mean fullness index over 24 hours.

As the number of observations was not equally distributed, the overall mean was calculated from the mean values of all two hour sampling intervals.

Day-to-day variation

To quantify the amount of variation between the daily ration estimates, the day-to-day variation (DTDV) was calculated as in Trudel and Boisclair (1993):

$$\text{DTDV} = 100\left|\frac{C_d - C_m}{C_m}\right|$$

where C_d is the daily ration on day d and C_m is the average daily ration of all sampling days.

Statistical analysis

As fullness data are expressed in percentages; we based calculations on the arcsinus squareroot-transformation and used the backtransformed data to present the results (Sokal and Rohlf 1995). With respect to the 24 h field data, an ANOVA on transformed data was used to test differences in the mean FI among the different time intervals within each sampling day. A Wilcoxon matched pairs test was used to compare evacuation rate and daily ration estimates based on stomach versus complete digestive tract contents, and daily ration estimates based on Eggers versus Elliott and Persson methods. The Mann-Withney U-test was used to compare evacuation rate and daily ration estimates between neap and spring tide samples.

Bootstrap simulations (1000 replica's) were used to estimate 95% confidence intervals for evacuation rate and daily ration estimates (Crowley 1992). For R_{max} the values obtained at each of the two consecutive time intervals, yielding the maximum evacuation rate were randomly resampled; a new mean FI was calculated and a simulated value of R_{max} was computed using equation (1). For the daily ration estimates, each 2 h interval was resampled and a new set of mean FI calculated. The simulated values for daily ration following the Eggers model were calculated using equation (4). The evacuation rate estimated from both pooled data and specific sampling dates were used in the computation of simulated daily rations. The sets of new mean FI for each time interval were used to calculate the overall mean FI_{24}. For the Elliott and Persson daily ration, the same sets of mean FI for each time interval were used to calculate the consumption rate between two consecutive time intervals using equation (2). Summation revealed simulated values (equation 3). Values were declared significantly different when the 95% confidence intervals did not overlap (Boisclair and Marchand 1993).

RESULTS

Field cage experiment and estimation of R_{exp}

An overview of the changes in FI over time after caging for the different tract sections is given in Figure 1. All sections showed the same temporal pattern: the mean FI remains high during the first 120 min after catching. The highest decline of mean FI appears between 120 and 150 min. Between 150 and 210 min, mean FI remained low and variability decreased. Post-hoc multiple comparisons (Tukey 's Honest Significant Difference Test for unequal sample sizes) revealed two major groups of time-intervals during which the mean FI did not differ: a first group between 0 and 120 min after caging and a second group between 150 and 210 min. The stomach had always the lowest fullness, even after correction for section length. Although the three intestine sections had the same length, the mean fullness of Intestine 2 was highest for each time interval. Mean FI for Intestine 3 was lower than Intestine 1 during the first 60 min, but raised gradually and became higher than Intestine 1 fullness after 60 min.

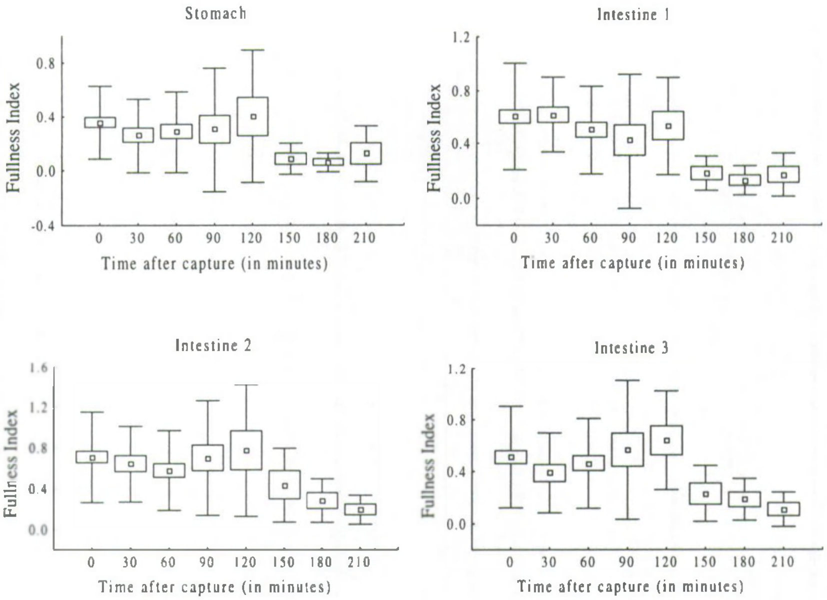

Figure 1: Changes in fullness index of caged *G. anjerensis* with time (in minutes after capture) for the different digestive sections, with indication of mean (square), standard error (box) and standard deviation (whisker).

The experimental estimates of evacuation rate for the different sections are given in Table 2. The stomach and first intestine section had higher evacuation rates compared to second and third intestine sections. To evacuate 50% of the food out of the stomach or the complete digestive tract, it takes 1.6 h and 1.8 h, respectively. 90% evacuation is completed after 5.2 h and 5.9 h for stomach and CDT, respectively.

24 h field data and estimation of R_{max}

An overview of the changes in stomach and CDT fullness over a 24 hour cycle for the different sampling dates and for the pooled data is presented in Figure 2. Overall mean stomach and CDT fullness ranged from 0.16 (24 h nr. 9) to 0.50 mg DW (24 h nr. 2) and from 1.20 (24 h nr. 1) to 2.71 mg DW (24 h nr. 8), respectively. Differences in stomach fullness between time intervals within a 24 h period were highly significant for all sampling dates (ANOVA, $p<0.01$). Although some variability exists, a predominant feeding at daytime was consistently observed throughout the whole study period. Mean stomach fullness starts to decline around sunset and remains very low until sunrise. In most cases, all gobies have emptied their stomachs completely by midnight. Only for two of the 24 h cycles (nr. 4 and nr. 8), CDT fullness did not change significantly during a 24 h period (ANOVA, $p>0.05$). The CDT fullness pattern shows more variation between sampling dates than the stomach fullness pattern. On most occasions, however, the same day-night pattern was observed for stomach fullness, with the major CDT fullness decline occurring a few hours later than the decline in stomach fullness. In contrast to the pattern for stomach fullness, the mean CDT fullness almost never reaches zero. Estimates of maximal stomach and complete digestive tract evacuation rates (R_{max}) were respectively 0.92 h^{-1} for the stomach and 0.56 h^{-1} for the CDT.

Table 2: Data summary of linear regression analysis to obtain experimental evacuation rate R_{exp} estimation for the different gastric sections, including variance (R^2) and significance level (p-level).

Gastric section	R_{exp} (h^{-1})	R^2	p-level
Stomach	0.56	0.74	0.006
Intestine 1	0.49	0.79	0.002
Intestine 2	0.35	0.81	0.002
Intestine 3	0.47	0.63	0.019
CDT	0.47	0.76	0.008

Daily ration estimates

A comparison of daily ration estimates calculated with both models and based on both stomach versus CDT fullness data is given in Figure 3 and 4. Point estimates always fell within the bootstrap simulated confidence interval when the Eggers model was used. With the Elliott & Persson model, however, point estimates of daily ration (based on CDT data) sometimes deviated markedly from the simulated estimate, making the accuracy of the estimate doubtful. The size of the C.I. fell in the same range when models or evacuation rate estimates were compared, though C.I. tended to be somewhat larger when CDT data were employed.

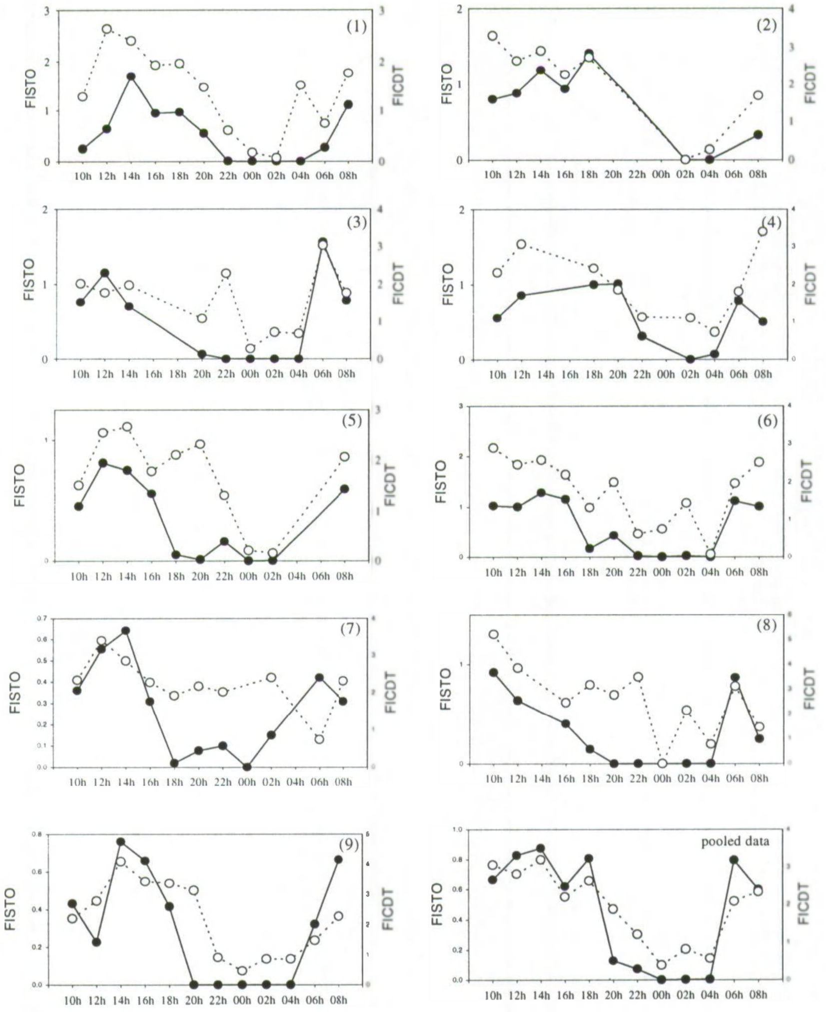

Figure 2: Overview of the changes in stomach (●) and complete digestive tract (○) fullness over a 24 h cycle for the different sampling dates and for the pooled data (arcsinsqrt-backtranformed means).

FISTO = stomach fullness index; FICDT = complete digestive tract fullness index

The two models gave always similar daily ration estimates (Wilcoxon matched pairs test, $p>0.05$, $n = 13$). Daily ration estimates based on CDT were significantly higher compared to stomach-based daily rations (Wilcoxon matched pairs test, $p<0.05$, $n = 12$).

Day-to-day variation

Day-to-day variations in daily ration are presented in Table 3. Mean DTDV did not differ between estimates from both methods, but mean DTDV was higher for stomach content based than for complete digestive tract based estimates.

Comparison of daily rations from neap and spring tides did not reveal any significant difference (Mann-Whitney U-test, $p > 0.05$, $n = 9$).

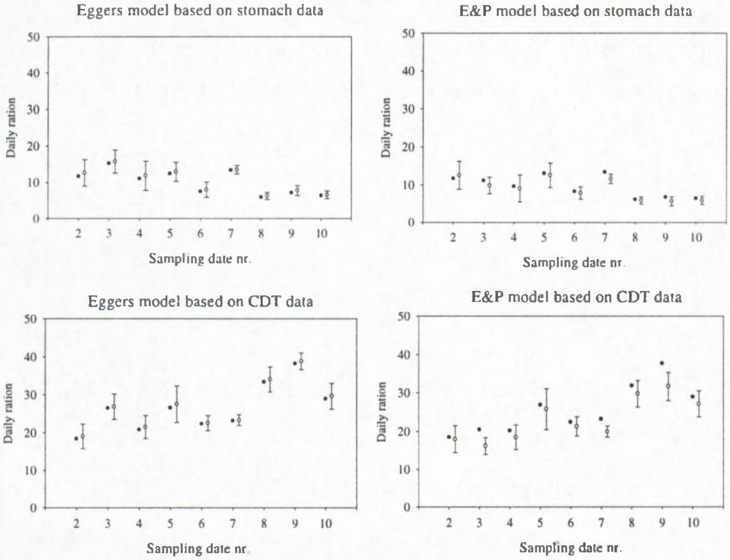

Figure 3: Point (●) and bootstrap simulated (O) estimates (+95 % C.I.) of daily rations for both models and digestive tract sections. Specific evacuation rates were used.

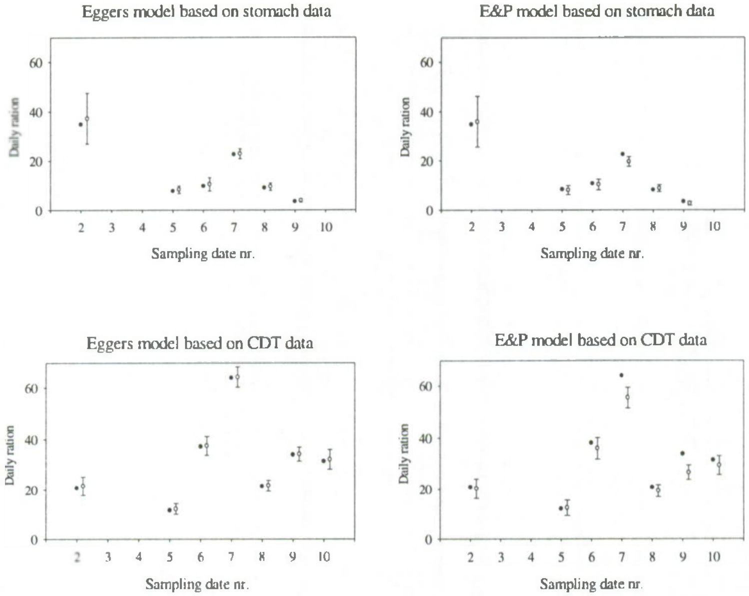

Figure 4: Point (●) and bootstrap simulated (○) estimates (+95 % C.I.) of daily rations for both models and digestive tract sections. Pooled evacuation rate was used.

DISCUSSION

Evacuation rate

In general, the digestion process is characterised by three stages: (1) a brief initial emptying delay, (2) a period of maximal digestion rate, and (3) a time-lag in the later stages of digestion with removal of undigestable food. These stages do not always occur and may differ in length and form depending on, among others, food composition, caloric content of the food, meal size, temperature, starvation and hormonal status (Windell *et al.* 1969, Jobling 1981, MacDonald and Waiwood 1982, Persson 1986). Depending on these factors, food evacuation may best be described by a certain model (Jobling 1986). The results of our field experiment clearly show three phases in the digestion process: an initial lag-phase, a very short period of higher

Table 3: Estimations of daily ration and day-to-day variation (DTDV) for the different sampling dates determined with the Eggers ($C_{24}(E)$) and Elliott and Persson ($C_{24}(E\&P)$) model, based on stomach and complete digestive content data (in % body dry weight day^{-1}).

	Stomach				Complete digestive tract			
Code	$C_{24}(E)$	DTDV	$C_{24}(E\&P)$	DTDV	$C_{24}(E)$	DTDV	$C_{24}(E\&P)$	DTDV
24 h nr. 1	11.7	16.3	11.7	22.1	18.5	30.4	18.5	27.9
24 h nr. 2	15.2	51.1	11.1	16.0	26.5	0.1	20.5	19.9
24 h nr. 3	11.1	9.7	9.7	0.5	20.9	21.3	20.2	21.2
24 h nr. 4	12.4	23.2	13.0	35.7	26.6	0.3	26.9	5.1
24 h nr. 5	7.5	25.6	8.3	13.9	22.4	15.6	22.5	12.2
24 h nr. 6	13.4	32.8	13.4	39.4	23.3	12.3	23.3	9.2
24 h nr. 7	5.9	41.6	6.1	36.3	33.4	25.9	31.9	24.6
24 h nr. 8	7.1	29.4	6.7	30.0	38.3	44.3	37.8	47.7
24 h nr. 9	6.4	36.6	6.4	33.4	28.9	9.1	28.9	13.0
mean	10.1	29.6%	9.6	25.3%	26.5	17.7%	25.6	20.1%

digestion rate and a period of low fullness without further significant decline. An initial emptying delay has been described mainly from experiments in which large prey items or nutrient-rich food were used. The lag-phase could then be explained by the time needed to break down the food and to allow enzyme penetration, or as a strategy to gain higher absorption efficiencies (Jobling 1986). However, this explanation does not seem applicable to our data, as the food of *G. anjerensis* consists of small prey items with relatively low caloric content. An alternative explanation for our observations may be an effect of stress due to capture and handling. Stress (due to force feeding in laboratory conditions) can indeed lead to an underestimation of evacuation rates (Swenson and Smith 1973). Thorpe (1977) found lower evacuation rates of caged compared to free fish. Boisclair and Leggett (1988) conducted laboratory experiments where time for acclimatisation was incorporated. They compared field and laboratory-derived estimates of evacuation rates at the same temperature, and suggested that stress was the major factor for the significantly greater values of laboratory-derived estimates. They recommend the use of field-corrected rather than laboratory estimates of evacuation rates in the calculation of daily ration. Many other authors prefer field rather than laboratory estimates due to the better integration of all possible environmental and physiological variability (Héroux and Magnan 1996).

An indication that stress occurred and slowed down the digestion in our cage experiment is the observation that stomach and intestine sections started emptying simultaneously and at the same speed after a delay. As a result, there was almost no difference between the evacuation rates of stomach or complete digestive tract. The number of empty stomachs did not increase significantly with time, probably because the duration of the experiment was not sufficiently long lasting .

As we observed a very distinct and synchronical non-feeding phase throughout the field study, the R_{max} estimate obtained in the field might be more reliable. Yet, we should not exclude the existence of natural variation in digestion rate, as this physiological process may be influenced by numerous internal and external factors (Jobling 1981, Andersen 1999). Estimates of R_{max} evacuation rates for stomach data were on average 1.69 times higher than those for CDT data. The same result was found for the R_{exp} estimates. This difference between stomach and CDT data appeared to be considerably smaller than the differences recorded in other studies. Boisclair and Marchand (1993) reported a 2.8 times difference comparing stomach and CDT evacuation rates for *Lepomis gibbosus*. Grove and Crawford (1980) examined the digestion rate in the stomachless *Blennius pholis* and found considerable differences between foregut and complete digestive emptying. The biological explanation for our observation remains unresolved, but this lack in difference may explain in part the relatively high daily ration estimates we found for the CDT data.

Daily ration

Our study confirms the findings of previous studies that both the lineair model of Eggers (1977) and the exponential model of Elliott and Persson (1978) result in similar estimates of daily ration (Boisclair and Leggett 1988, Boisclair and Marchand 1993, Héroux and Magnan 1996). These authors recommended the use of the Eggers model because of lower variance as well as its logistical simplicity and robustness in case of variable sampling intervals.

Boisclair and Marchand (1993) did not find a significant difference in daily ration values estimated using data on stomach or CDT content. As stomach content data gave higher variances in daily ration and were more sensitive to increasing sampling time intervals, they suggested the use of CDT data. We obtained clearly different results when using stomach or CDT data. Daily rations estimated from stomach data were much lower than those from CDT data, the difference being significant. Our results thus suggest that caution should be made in the choice of the digestive tract section used to estimate daily ration.

Substantial day-to-day variations (DTDV) in food consumption have been observed in several studies. Trudel and Boisclair (1993) estimated daily ration of minnows in field conditions over different series of consecutive days, and found average DTDV in food consumption rates ranging between 7 to 16%. We used an analogous field procedure, only differing in shorter time intervals and a varying number of fishes per sample. Our results, however, did not confirm their observation. Although the daily feeding rhythm did not change, the overall daily food intake showed significant variation between weekly sampling dates. Although this variation may be due to sometimes small sample sizes, Boisclair and Leggett (1988) did not find a significant effect of the number of sampled fish on the daily ration estimate. Therefore, it seems more likely that the observed variation is due to other factors such as differences in food availability or feeding motivation of individual fish. Some authors found a relation between feeding intensity and the spring-neap tidal cycle (Gibson 1978, Hamerlynck *et al.* 1993). The results we obtained for *G. anjerensis* did not indicate a pattern in daily ration coinciding with the semilunar cycle. It should, however, be pointed out that there is a semilunar pattern for catch rates (Chapter 5).

Smagula and Adelman (1982) studied variation in food consumption of largemouth bass under laboratory conditions and found substantial variation even with constant prey densities. As they could not detect any periodic behavior, they assumed a random endogenous variation in diel food consumption. Variation in field studies may, however, also be increased due to diel variation induced by exogenous factors and due to error as a consequence of the indirect estimation of food consumption through mathematical models. Therefore, the natural variation should not be underestimated and generalisations based on daily ration estimates obtained from limited field data, may result in considerable errors.

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CHAPTER 5

SHORT-TERM TEMPORAL CHANGES IN CATCH RATES AND FEEDING ACTIVITY OF TWO GOBY SPECIES IN A TROPICAL TIDAL MANGROVE CREEK: RESOURCE PARTITIONING OF *GNATHOLEPIS ANJERENSIS* AND *ASTERROPTERYX SEMIPUNCTATUS*

Coene Heidi, Owino Robert, Wenseleers Tom and Ollevier Frans

ABSTRACT

Resource partitioning between the tropical gobies *Gnatholepis anjerensis* (Bleeker, 1850) and *Asterropteryx semipunctatus* Rüppell, 1830 was studied, with emphasis on the temporal aspect. Analysis of spatial, tidal, day/night and semilunar patterns in occurrence and feeding clearly indicated that the niche of both goby species was different. There was only a weak distinction in habitat choice: both species occurred in the same seagrass sites at the same time, though, *A. semipunctatus* attained the highest densities in the sites with dense seagrass cover. Feeding intensity of *G. anjerensis* was highest in the scarcely vegetated site. No correlation between tidal status and densities or feeding intensity of the gobies was found. The day/night cycle affected the species in a different way. For *G. anjerensis,* we observed higher catch rates during the daytime, and this coincided with a diurnal feeding pattern. In the case of *A. semipunctatus,* catch rates were irregular during a 24-hour cycle and feeding occurred throughout the diel cycle, without any restriction in time. A semilunar periodicity was observed in the catch rates of both species: *G. anjerensis* and *A. semipunctatus* were most abundant during the neap tides. A semilunar rhythm was also apparent in the feeding intensity of *A. semipunctatus*, as significant higher stomach fullness was found for this species during neap tides. No such pattern was observed for *G. anjerensis*. The diet composition of the species was very similar with respect to the animal fraction: amphipods, copepods and isopods were dominating food categories. The stomachs of *A. semipunctatus*, however, contained a considerable amount of plant material and debris. Moreover, the low rating of animal prey in *A. semipunctatus* might indicate the importance of plants in supplementing the diet. It is suggested that the species employ a different feeding strategy: while *G. anjerensis* is an active predator, that hunts on benthic crustaceans, *A. semipunctatus* has an omnivorous feeding behaviour. This might, at least in part, explain the observed temporal segregation.

INTRODUCTION

Resource partitioning may arise from either competitive or non-competitive factors. Irrespective of its origin, however, it helps to alleviate potential competitive interactions and maintain the coexistence of species (Tokeshi 1999). The principle of limiting similarity predicts that related species exploiting the same resources must ultimately segregate along one or more niche dimensions to maintain a minimum level of niche separation (Schoener 1974).

There is still considerable debate on the relative importances of niche dimensions along which species tend to segregate. Studying marine fish assemblages, Ross (1986) suggested that, unlike in terrestrial systems, trophic segregation plays a more important role than spatial segregation in aquatic ecosystems. He argued that increased mobility allows aquatic predators to efficiently partition food resources while remaining in the same general habitat. In addition, habitats may be of limited duration, especially in many riverine or coastal marine systems, limiting the potential for high levels of habitat specialisation. The importance of temporal segregation appears to vary between ecosystem types. However, in tidally fluctuating habitats, temporal habitat segregation might be an important mechanism in structuring the assemblage (Butler 1982, Cattrijsse *et al.* 1994, Lafaille *et al.* 1999).

Within the framework of a general study of resource utilisation and coexistence of tropical gobies, the present paper compares the temporal occurrence and feeding patterns of two abundant goby species (*G. anjerensis* and *A. semipunctatus*) in the subtidal seagrasses of a mangrove creek (Gazi Bay, Kenya). Gobioids are a very diverse and abundant group of fishes, which are distributed worldwide in almost all types of water. Their diversity is most marked in tropical ecosystems such as coral reefs and mangrove swamps (Miller 1993). So far, however, almost nothing is known about their ecology and the mechanisms that mediate coexistence within these systems.

Gobiidae of the temperate region have been the focus of several studies on niche dynamics, resource partitioning and mechanisms regulating assemblages of species (Evans and Tallmark 1985, Wilkins and Meyers 1992, 1995, Hamerlynck and Cattrijsse 1994). We expect, however, some major differences in tropical environments. As there are more species sharing the same assemblage in tropical systems, they may be exposed to a higher number of pathways for direct and indirect biotic interactions. Higher prevalence of competition or predation might significantly affect mechanisms regulating assemblage structure (Winnemiller 1991).

Within the mangrove creek of Gazi Bay, gobies form a dominant component of the resident ichthyofauna (see Chapter 2). The habitat of these species is strongly subjected to short-term temporal changes, including tidal rhythms, as well as diel and semilunar cycles. These factors may influence the physiology of the fauna directly or may entrain physical as well as biotic changes in the characteristics of the environment, such as temperature, salinity, food availability and predation risk (e.g. McIvor and Odum 1988, Boujard and Leatherland 1992, Gibson 1992). In this paper, we focus on the impact of short-term temporal fluctuations on densities and feeding behaviour of two co-existing and dominant gobiid species. We further evaluate the relative role of the food, spatial and temporal dimensions in the niche segregation of these species.

MATERIAL AND METHODS

Study area

Gazi bay is a tropical mangrove embayment in Kenya covering a total area of 15 km², situated approximately 50 km south of Mombasa (4°25’ S and 39°30’ E). The bay is sheltered from the Indian Ocean by a fringing coral reef and Chale Island. There are two major tidal creeks, which are entering the mangrove stands: the western creek, which receives the seasonal river Kidogeweni, and the Eastern creek, which has no freshwater input. Seagrasses occur in the central part of the bay and in the tidal creeks. Dominant seagrass species in the sampling sites are *Cymodocea rotundata*, *C. serrulata*, *Thalassia hemprichii*, *Halophila ovalis* and *H. stipulacea* (Coppejans *et al.*

1992). The mangrove vegetation along the western creek is a species-rich mixed mangal, with *Sonneratia alba*, *Rhizophora mucronata* and *Avicennia marina* occurring closest to the tide channel (Gallin *et al.* 1989). The tidal regime of the study area is semi-diurnal and causes strong and reversing currents in the mangrove creek. The hydrodynamics of the bay have been described by Kitheka *et al.* (1996). Variations in salinity follow the tidal cycle. The temperature fluctuates between 25°C and 32°C, and is influenced by both tidal and day/night changes. The tidal amplitude during the sampling period ranged from 0.7 m to 3.5 m.

Sampling site

Samples were taken at four seagrass sites (A, B, C, D) in the western creek (Figure 1). This creek is characterised by a very diversified substrate: the lowest parts are silty because of the slow tidal current and associated sedimentation of the finest particles. The highest parts have a more sandy substrate. There are two major sandbanks, which are only exposed at low tide (Slim *et al.* 1996). Seagrasses occur in the lower subtidal areas of the creek. Site A is situated at the mouth of the creek, at the eastern side of the most downstream sandbank; site B lays in front of a landing base for the local fishermen; site C is situated near a local oyster bed and next to the upstream sandbank, and site D lays most upstream. Site C and D are covered with dense seagrass beds, while the seagrass coverage is sparse in site A and B.

Sampling procedure

Sampling took place between July and October 1995, which corresponds with the end of the SE monsoon, a period characterised by dense cloud cover, abundant rains, high wind energy, decreased temperatures and light intensity (McClanahan 1988). To investigate a semilunar pattern, ten 24 h cycles were sampled at consecutive spring and neap tides (Table 1). Samples of the epibenthic fauna were collected from a small dinghy by towing a 1.5 m beam trawl with a 3 mm stretched mesh size of the inner net during 10 min over an average distance of 300 m. Every two hours, each of the four localities were sampled, which made a total of 48 samples per 24 h. At low water spring tide, the water level was too low to sample all localities. At this time, samples were only taken at site B, using handtrawling over the same distance. The fishes were sorted on board, anaesthetised in benzocaine and preserved in 4 % formaldehyde solution.

Figure 1: Indication of the sampling sites within the western creek.

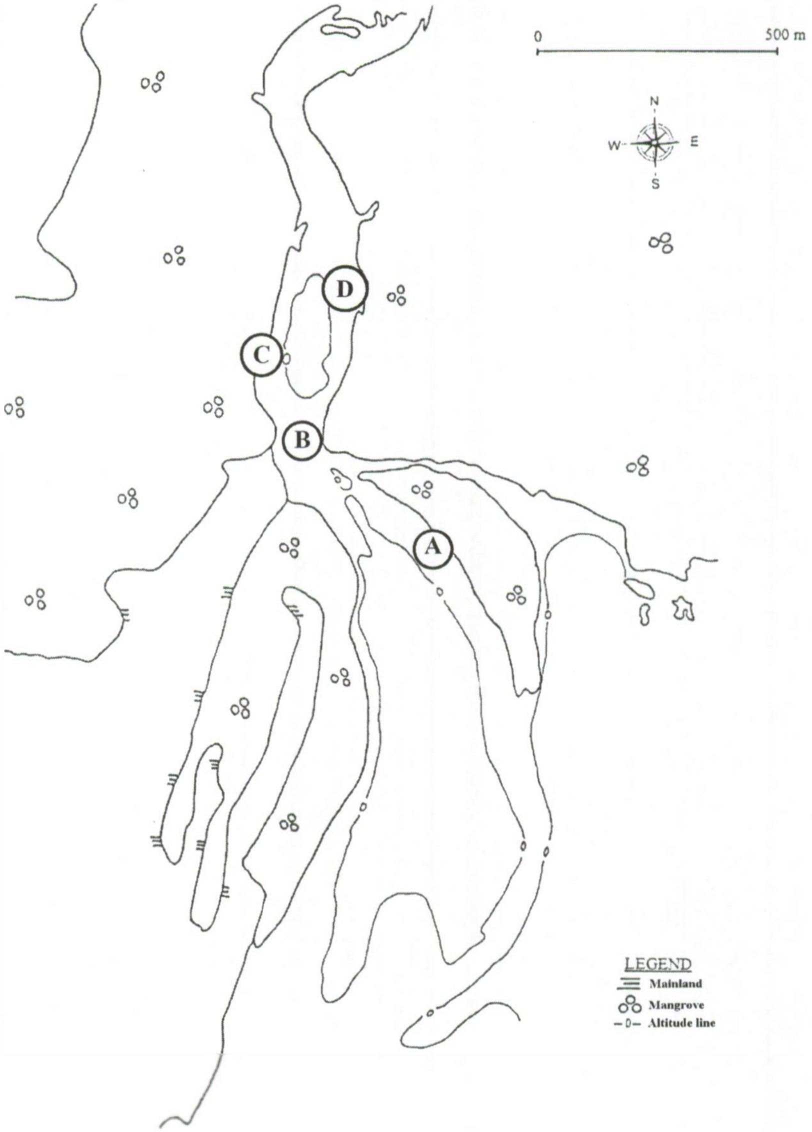

Table 1: Overview of the sampling schedule, including date, time and height of low (LW) and high water (HW) and semilunar phases (adapted from Kilindini tide table, Kenya Ports Authority 1995).

Experimental code	Date (1995)	Time and height of LW	Time and height of HW	spring / neap
24 h nr. 1	21 - 22 July	17.54 h (1.3 m)	23.37 h (2.2 m)	neap
		05.46 h (1.2 m)	12.36 h (2.6 m)	
24 h nr. 2	27 - 28 July	10.04 h (0.6 m)	16.24 h (3.3 m)	spring
		22.39 h (0.4 m)	04.48 h (3.0 m)	
24 h nr. 3	5 - 6 August	17.02 h (1.2 m)	23.03 h (2.2 m)	neap
		05.01 h (1.1 m)	11.58 h (2.8 m)	
24 h nr. 4	11 - 12 August	10.25 h (0.2 m)	16.47 h (3.7 m)	spring
		22.55 h (0.0 m)	05.10 h (3.5 m)	
24 h nr. 5	19 - 20 August	16.46 h (1.4 m)	22.31 h (2.1 m)	neap
		04.39 h (1.4 m)	11.39 h (2.4 m)	
24 h nr. 6	27 - 28 August	10.49 h (0.3 m)	17.06 h (3.5 m)	spring
		23.09 h (0.2 m)	05.21 h (3.4 m)	
24 h nr. 7	3 - 4 September	16.36 h (1.2 m)	22.47 h (2.2 m)	neap
		04.43 h (1.2 m)	11.41 h (2.7 m)	
24 h nr. 8	24 - 25 September	09.54 h (0.3 m)	16.11 h (3.4 m)	spring
		22.08 h (0.3 m)	04.24 h (3.5 m)	
24 h nr. 9	2 - 3 October	16.15 h (1.2 m)	22.42 h (2.3 m)	neap
		04.43 h (1.3 m)	11.25 h (2.6 m)	
24 h nr. 10	8 - 9 October	09.56 h (0.2 m)	16.11 h (3.4 m)	spring
		22.03 h (0.3 m)	04.24 h (3.7 m)	

Some general assumptions were made about the fishing technique. Catchability was treated as a constant, mainly because no adequate information was available on possible temporal changes in catch efficiency. We assumed that boat disturbance, net escape and mesh selection were similar for both goby species, such that our sampling method was appropriate to study the relative occurrence of the two species.

The gobies were sorted and identified according to Hoese (1986), but final identifications were done using unpublished identification keys of Randall and Hoese communicated by F. Pezold and H. Larson. Standard lengths (SL) of each individual were recorded to the nearest mm. Standard length – dry weight regressions were estimated using 50 specimens of varying SL dried for 5 days at 65°C. This resulted in the following regressions:

G. anjerensis $\ln(DW) = 3.4 \ln(SL) - 6.4$ $r = 0.98$ $p = 0.001$

A. semipunctatus $\ln(DW) = 3.3 \ln(SL) - 5.6$ $r = 0.97$ $p = 0.001$

Stomach content analysis

To elucidate the temporal feeding pattern of *G. anjerensis* and *A. semipunctatus,* a qualitative and quantitative stomach content analysis was performed. As catches were rather low, we examined all specimens with standard lengths above 25 mm for *G. anjerensis* (665 individuals) and above 20 mm for *A. semipunctatus* (364 individuals). To analyse the stomach contents, food items were counted and measured under a dissecting microscope with a drawing mirror. Plant material and debris that could not be counted were not included in this analysis. Ash-free dry weight prior to digestion was estimated for each food item using length-weight regressions or assigned values (De Troch *et al.* 1998). Percentage occurrence (%O), numerical (%N) and gravimetrical (%G) percentages were calculated based on the definition of Berg (1979) to describe the general diet composition. Fullness indices (FI) were calculated using dry weight values of stomach content (dried for 24 h at 65°C). No significant correlation was found between the fullness index and the standard length of the fish, so no adjustment for size differences was made (Spearman rank correlation; *G. anjerensis*: $R = -0.15$, $p > 0.05$; *A. semipunctatus*: $R = -0.05$; $p > 0.05$).

Statistical analysis

(1) Categorical approach

To analyse the catch rate data, we used mainly Friedman ANOVA (neither raw nor transformed data were normally distributed). Data were pooled and means of a given time-interval were compared. To compare catch rates among sampling sites, data were aligned according to time (2 h intervals). For the tidal and day/night analysis, we compared means that were calculated from data every full cycle separately (over 12.4 and 24 hour intervals, respectively). To test for the effect of tidal status, data for each 12 hour sampling (day or night) were grouped in four categories: low (LW) and high water (HW), which correspond to two-hour intervals while incoming (IT) and outgoing tide (OT) represent four-hour intervals. In this way, a clear difference was made between slack and running water. To analyse the day/night cycle, we averaged and compared data collected during the day (6.30 h to 18.30 h) and during the night.

We could not use the same statistical approach for the feeding intensity analysis, since the number of analysed specimens was not equally distributed over a 24 hour cycle. For this analysis, data were pooled according to spring or neap sampling dates. This is relevant because tidal conditions (and co-occurring variables) always occur on the same time of the day within spring or neap 24 hours (see also Table 1).

(2) Temporal multiple regression approach

Categorising essentially uninterrupted time series as under (1) results in a loss of information and a reduction in statistical power when testing for periodic temporal effects. To circumvent this limitation, an alternative method was devised based on least-squares regression. A computer programme was designed in Visual Basic, which allowed us to fit a periodic model analytically, with the function written as a linear combination of sinusoidal waves with known periods:

$$y = a_0 + b_1 * \sin(\frac{2\pi}{T_1} * t - \varphi_1) + b_2 * \sin(\frac{2\pi}{T_2} * t - \varphi_2) + b_3 * \sin(\frac{2\pi}{T_3} * t - \varphi_3)$$

The known periods T_1, T_2 and T_3 were equal to 750, 1,440 and 20,808 minutes (12.5 h, 24 h and 28.7 days, respectively), corresponding to the tidal, day-night and neap-spring cycles, respectively. For each cycle, the amplitude and the phase parameter were then estimated by the least-squares method. The amplitudes give information on the relative importance of the three cycles, while the phase parameters can be used to estimate the maxima of each cycle (first observation was done at 10.00 h during 24 h nr. 1). Standard errors on all parameters and significance of each cycle were estimated using a Monte Carlo procedure.

RESULTS

Catch rates

Overall mean catch rates

During the whole sampling campaign, a total of 3,457 gobies were caught, belonging to 13 species (Table 2). For further analyses on temporal changes in catch and feeding rates, the two most abundant species with mean SL higher than 20 mm were selected, namely the wheeper *G. anjerensis* and the starryfin goby *A. semipunctatus*. Mean and peak catches rates were respectively 0.9 and 12.2 individuals per 100 m² for *G. anjerensis* and 0.2 and 4.4 individuals per 100 m² for *A. semipunctatus*.

Table 2: List of Gobiidae species caught in Gazi Bay during ten 24 h cycles, including number of collected specimens (N), standard length (SL) range, mean (in mm) and standard deviation.

Species	N	SL range	SL mean ± SD
Gnatholepis anjerensis	1897	11-53	23.4 ± 8.2
Favonigobius melanobranchus	688	11-31	18.3 ± 2.1
Asterropteryx semipunctatus	383	12-40	29.7 ± 4.5
Favonigobius reichei	181	10-38	18.0 ± 4.5
Amoya signatus	117	12-47	25.6 ± 7.9
Glossogobius biocellatus	98	13-52	32.9 ± 10.6
Amblygobius albimaculatus	69	13-85	35.2 ± 16.7
Oxyurichthys sp.	13	12-38	21.6 ± 7.9
Periophthalmus kalolo	4	24-35	64.3 ± 30.8
Acentrogobius audax	3	14-46	30.7 ± 16.0
Drombus key	2	21-22	21.5 ± 0.7
Oplopomus oplopomus	1		40
Yongeichthys nebulosus	1		75

Spatial pattern

For *G. anjerensis,* no significant difference in catch rates among localities was apparent (Table 3). Samples taken with handtrawling at site B at low water spring tide were not taken into account. These handtrawling samples corresponded with the highest catch rates observed, but we could not distinguish whether this was due to the sampling method or to the extreme low water level. For *A. semipunctatus,* catch rates tended to be high at sites C and D than at sites A and B, but this observation was only marginally significant (Table 3). Therefore, we did not distinguish between sites in further analyses.

Table 3: Results of Friedman ANOVA on the catch rates of *Gnatholepis anjerensis* and *Asterropteryx semipunctatus* for the variables locality (2 h), tidal phase (12.4 h) and day/night (24 h), including degrees of freedom (df), number of comparisons (N) and significance level (p). Significant values are in bold.

Species	Source of variation	df	N	p
Gnatholepis anjerensis	Locality	3	120	0.36
	Tidal phase	3	20	0.12
	Day/Night	1	10	**0.04**
Asterropteryx semipunctatus	Locality	3	120	0.06
	Tidal phase	3	20	0.47
	Day/Night	1	10	0.32

Tidal pattern

The tidal status (LW, IT, HW, OT) did not affect the densities of the gobies (Table 3). No significant cycle with a tidal periodicity was found by periodic regression analysis (Table 4).

Day/night pattern

Mean day and night densities were compared for the ten 24 h sampling dates. *G. anjerensis* showed highest densities during the daytime (Friedman ANOVA, Table 3). Only on two sampling dates (24 h nr. 3 and nr. 9), the mean density at night was slightly higher. For *A. semipunctatus,* a clear day-night pattern could not be observed: day versus night densities changed randomly. The periodic regression analysis revealed the same result: only for *G. anjerensis,* a significant cyclic pattern with a 24 h periodicity was found (Table 4).

Semilunar pattern

For both species, catch rates were significantly higher during neap tides than during spring tides (Periodic regression analysis, Table 4).

Feeding intensity

Spatial pattern

G. anjerensis had the highest median stomach fullness at site B (Kruskal-Wallis ANOVA, $p = 0.01$). For *A. semipunctatus,* overall median stomach fullness did not differ significantly between sampling sites (Kruskal-Wallis ANOVA, $p = 0.08$).

Tidal pattern

Periodic regression did not reveal a significant tidal cycle in feeding intensity for either species (Table 4).

Day-night pattern

For *G. anjerensis,* mean stomach fullness was highest during the daytime (Friedman ANOVA, $p = 0.01$). The periodic regression analysis revealed a highly significant day-night cycle, with peak stomach fullness around midday (Table 4). The changes in stomach fullness over 2 h time intervals within a 24 h period are shown in Figure 2. Although some variability existed, the relative pattern of peaks in stomach fullness during the daytime was congruent over all sampling dates. Mean stomach fullness starts to decline around sunset and remains very low until sunrise. In most cases, all gobies had emptied their stomachs completely after midnight.

For *A. semipunctatus,* no differences in stomach content fullness were found between day and night (Table 4). Data were grouped in 4 h intervals and compared for spring and neap tides (Figure 3). For neap tides, a decline of mean fullness during the first part of the night was observed, although the mean stomach fullness never reached zero. The spring tide results showed a less clear-cut pattern. The peculiar position of the 14 h sample (spring tide) may be caused by a sampling error, as about 90% of the individuals came from one trawling and the percentage empty stomachs within this sample was exceptionally high, suggesting regurgitation.

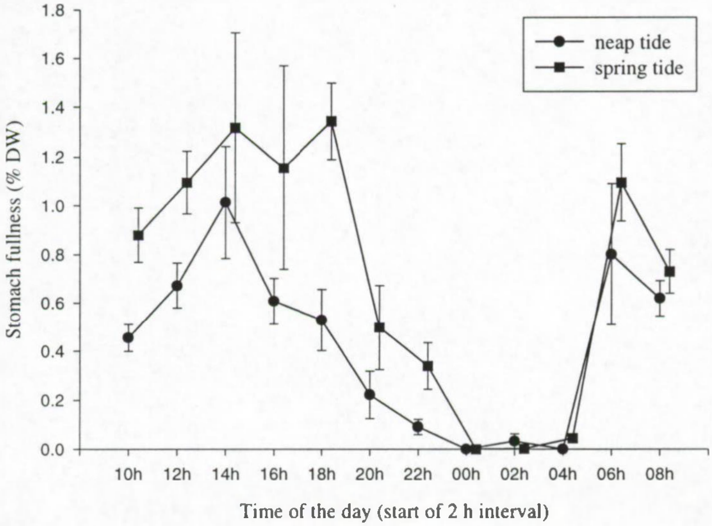

Figure 2: Changes in mean stomach fullness (± S.E.) over a 24 hour neap and spring tide cycle for *Gnatholepis anjerensis.*

The pattern of empty stomachs over a 24 h cycle may provide additional information on the feeding behaviour of the species (Figure 4). For *G. anjerensis,* a very high percentage of the analysed fishes had empty stomachs during the night.

During spring tides, the emptying of stomachs started a few hours later than during neap tides. In contrast, empty stomachs were found throughout the 24 h cycle in *A. semipunctatus*. During neap tides, the percentage of empty stomachs remained very low. When comparing the percentage of empty stomachs between tidal phases, high tide samples scored highest for both species, respectively 48% for *G. anjerensis* and 32% for *A. semipunctatus*.

Semilunar pattern

In *G. anjerensis*, we found a tendency for higher values for overall mean stomach fullness during spring tides than during neap tides, but this pattern was not significant (Table 4). In *A. semipunctatus,* stomach fullness indices were significantly higher during neap tides than during spring tides (Table 4).

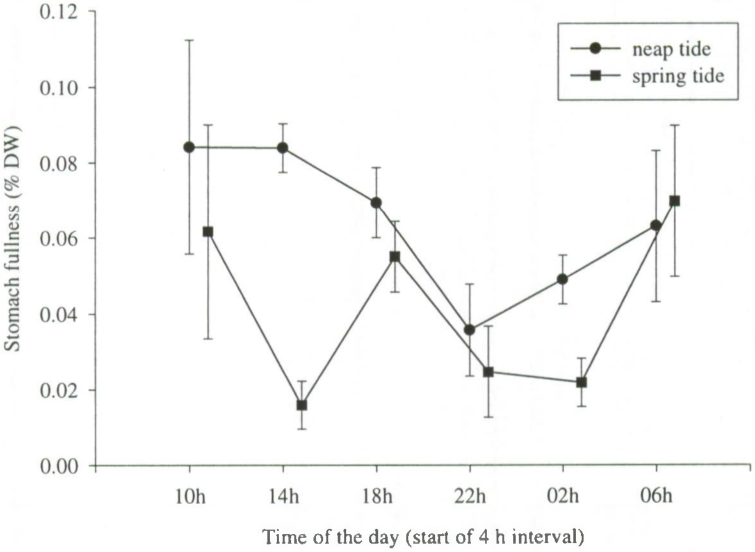

Figure 3: Changes in mean stomach fullness (± S.E.) over a 24 hour neap and spring tide cycle for *Asterropteryx semipunctatus.*

Table 4: Results of periodic regression on the temporal changes in catch rates and stomach fullness indices of *Gnatholepis anjerensis* and *Asterropteryx semipunctatus*. Estimated parameters were b (amplitude) and φ (phase) of the respectively fitted sinus-functions. Catch rates were ln-transformed; stomach fullness indices were arcsinussquareroot-transformed. Significant values are in bold.

		Catch rates		Fullness Index	
Cycle	Parameter	*G. anjerensis*	*A. semipunctatus*	*G. anjerensis*	*A. semipunctatus*
	a_0	1.10 ± 0.051	0.290 ± 0.029	0.058 ± 0.002	0.017 ± 0.001
Tidal cycle	b_1 (± SE)	0.148 ± 0.061	0.062 ± 0.004	0.004 ± 0.002	0.002 ± 0.001
	φ_1 (± SE)	82.2 ± 79.5	77.98 ± 62.46	57.9 ± 53.3	53.2 ± 44.9
	p-level	0.085	0.34	0.392	0.21
24h cycle	b_2 (± SE)	0.303 ± 0.060	0.005 ± 0.029	0.041 ± 0.002	0.002 ± 0.001
	φ_2 (± SE)	75.2 ± 49.7	72.21 ± 47.56	58.2 ± 3.6	56.6 ± 40.8
	p-level	**0.001**	0.99	**0.001**	0.12
Spring/Neap cycle	b_3 (± SE)	0.441 ± 0.162	0.275 ± 0.008	0.010 ± 0.003	0.009 ± 0.003
	φ_3 (± SE)	10.5 ± 14.1	7.50 ± 17.50	82.2 ± 70.0	5.9 ± 16.1
	p-level	**0.018**	**0.014**	0.130	**0.014**
	explained variance	10.8%	7.5%	34.8%	12.3%

Diet composition

Fifteen food categories were observed in the stomachs of the two species (Table 5). Diets of *G. anjerensis* and *A. semipunctatus* were very similar with respect to the animal fraction. Copepods (harpacticoids), amphipods and isopods were the most common prey items. Gastropods, mysids and decapods (shrimps) occurred only in the stomachs of *G. anjerensis,* whereas bivalves were only found in *A. semipunctatus*. The gravimetrical contribution of copepods, ostracods and kinorhynchs were more important in the diet of *G. anjerensis*. Isopods were significantly more important in the diet of *A. semipunctatus* (Kruskal-Wallis ANOVA, $p<0.05$, Bonferroni corrected). The same size ranges of copepods, amphipods and isopods were ingested by both species (Figure 5). The median size of ingested copepods was significantly higher for *G. anjerensis*, while the median size of isopods was significantly higher for *A. semipunctatus* (Mann-Whitney U-test, $p<0.05$). For none of the species, a significant correlation between mean length of ingested copepod, amphipod or isopod and standard length of the fish was found (Spearman rank order correlation, $p>0.05$). The relative importance of the prey categories did not change over the observed period for neither species. The number of food items per stomach was very low for *A. semipunctatus:* the overall mean was 3 items per stomach with half of the examined stomachs containing only two food items. For *G. anjerensis,* the number of food items per stomach ranged from 0 to 133, with a mean of 27 per stomach.

The stomachs of *A. semipunctatus* contained high amounts of benthic algae and weeds, plant materials and debris. *G. anjerensis* had a considerable amount of sand particles in their stomachs.

DISCUSSION

Because the study area is subjected to a semi-diurnal tidal regime, this might have important implications for the habitat use and feeding behaviour of the gobiid fish. A

Table 5: Frequency of occurrence (%O), numerical (%N) and gravimetrical (%G) percentages for the prey categories of *Gnatholepis anjerensis* and *Asterropteryx semipunctatus*.

	G. anjerensis			*A. semipunctatus*		
Food items	%O	%N	%G	%O	%N	%G
Copepoda	80.0	47.0	21.0	48.1	36.8	9.6
Amphipoda	62.1	15.0	54.6	49.7	36.6	69.1
Isopoda	62.4	21.7	2.9	22.1	12.2	3.4
Ostracoda	53.2	7.7	15.9	9.0	3.2	4.0
Gastropoda	12.5	0.7	0.1	0.0	0.0	0.0
Kinorhyncha	37.6	3.8	1.1	0.8	0.2	0.1
Cumacea	15.6	0.7	0.9	9.0	3.2	3.5
Bivalva	0.0	0.0	0.0	6.3	2.2	8.1
Polychaeta	22.7	1.2	0.4	2.2	0.8	0.1
Acarina	18.3	0.9	0.2	4.1	2.2	0.4
Nematoda	9.4	1.1	0.5	0.8	0.3	0.1
Tanaidacea	1.8	0.1	0.4	4.4	1.5	0.3
Mysidacea	0.2	0.0	0.8	0.0	0.0	0.0
Pycnogonida	0.4	0.0	0.3	1.9	0.6	1.5
Decapoda	0.2	0.0	0.8	0.0	0.0	0.0

large number of studies have shown tidally-related activity and feeding patterns for fishes living in estuaries, salt marches and swamps (Gibson 1992, Horn *et al.* 1999). Both feeding requirements and predator avoidance may be at the cause of this behaviour. Several species use tides for intertidal movements to exploit food resources, with the fish entering the intertidal area with empty stomachs during flooding tide and turning back after feeding when water is ebbing (Weisberg *et al.* 1981, Cattrijsse *et al.* 1994, Laffaille *et al.* 1999). Other studies demonstrated how small fishes were feeding at low tide in the depositional subtidal area of a creek and entering the marsh/mangrove surface at rising tides to avoid predation (Kneib 1987, McIvor and Odum 1988, Vance *et al.* 1996). However, no tidally related patterns have been observed during our survey. Neither for *G. anjerensis* nor *A. semipunctatus*, a significant correlation between catch rates and tidal phases was observed. Neither did the time of feeding, which was indirectly assessed by the mean stomach fullness, reflect a tidal pattern. These observations suggest that the gobies do not use the tidal current to enter the mangrove forest; feeding takes place within the subtidal creek. Probably, the energy demanding intertidal movements are irrelevant, as there is a high and appropriate food availability within the mangrove creek (Alongi 1989, Schrijvers *et al.* 1995).

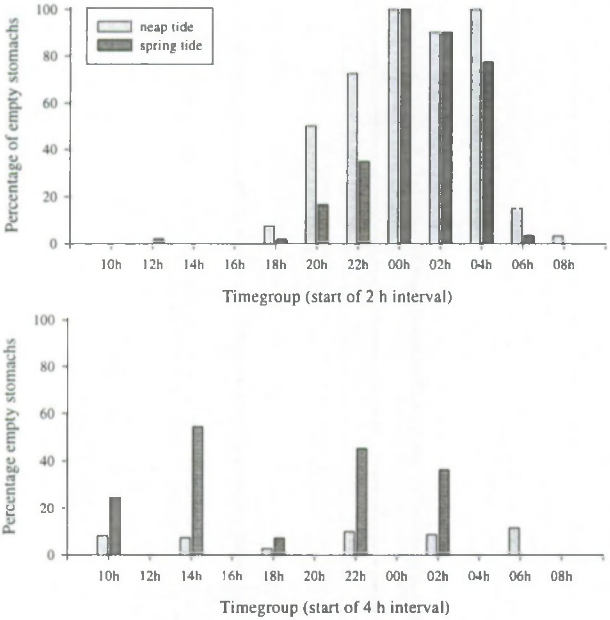

Figure 4: Diel fluctuations of empty stomach rates in *Gnatholepis anjerensis* (above) and *Asterropteryx semipunctatus* (below) for spring and neap tide cycles.

It is a generally accepted idea that morphological characteristics of a fish species determine to some extent its habitat use, prey type and feeding behaviour (Norton 1995, Wainwright and Richard 1995). Body shape and fin structures are often

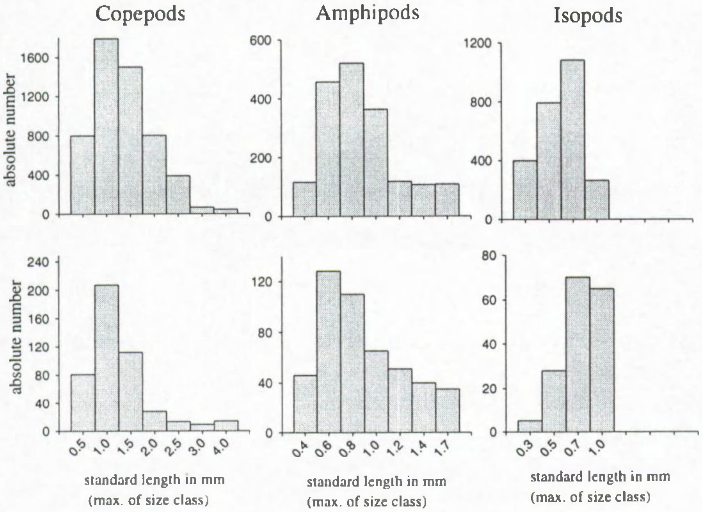

Figure 5: Standard length frequency distributions of the ingested copepods, amphipods and isopods for *Gnatholepis anjerensis* (above) and *Asterropteryx semipunctatus* (below).

adapted to locomotion and fouraging area (Webb 1984). Shape and position of mouth, dentition and relative gut length often relate to food type and fouraging strategy (Keast and Webb 1966, Motta *et al.* 1995). Both goby species studied by us are typically benthic fish. They differ, however, in general body shape and coloration pattern. *G. anjerensis* has an elongated cylindrical body shape and life colours are yellow to brown. *A. semipunctatus* has a laterally compressed, high body shape and life colours are dark brown to black. The ventral fins of *G. anjerensis* are typically united into an adhesive disc; the ventral fins of *A. semipunctatus* are only partly connected. This differential functional morphology may be the cause of interspecific differences in habitat use and fouraging strategy. *A. semipunctatus* might be better shaped to fourage within dense seagrass patches, whereby its dark colour matches to the dense vegetation. On the contrary, *G. anjerensis* is better shaped to fourage in less dense seagrass patches, or in more open sandy patches, which might relate to the lighter coloration pattern. Our observations are in agreement with this hypothesis: *A.*

semipunctatus attained highest densities in the sites with dense seagrass cover and feeding intensity of *G. anjerensis* was highest in the scarcely vegetated site.

The hypothesis that *A. semipunctatus* is better adapted to densely vegetated sites whereas *G. anjerensis* is better adapted to less vegetated sites can also explain our observation that the diet of the two species differed. The dominant food components for both species were small crustaceans. However, the stomachs of *A. semipunctatus* contained a low number of prey items and a supplementary amount of plant material, which suggest a more omnivorous diet. No plant material was found in the stomach of *G. anjerensis*, but sand particles were prevalent. Therefore, *G. anjerensis* is expected to be an active predator, hunting specifically on epibenthic invertebrates, while *A. semipunctatus* is ingesting a large amount of plant material, and the invertebrate prey found in the stomach might be to a large extent epiphytic or plant-associated organisms. This different fouraging strategy may explain the feeding restriction of *G. anjerensis* to daytime, as active hunting requires light, whereas the omnivorous feeding behaviour of *A. semipunctatus* may be more flexible in this context.

Temporal changes in feeding activities are common among fishes, and have been attributed to predator and competitor avoidance, as well as differential availability of prey (Gliwicz 1986, Grossman *et al.* 1980). Diurnal or nocturnal activity and feeding have been observed in many goby species (Butler 1982, Hamerlynck *et al.* 1993, del Norte-Campos and Temming 1994). Especially for gobies, the trade-off between feeding and predator avoidance might be of significant importance. The small size of gobies is an appropriate adaptation for the exploitation of small-sized food resources in shallow water habitats. But small size also implicates high susceptibility to predation (Miller 1979). Many goby species are essentially intermediate components in food webs (Blaber 1986, Doornbos and Twisk 1987, Hamerlynck and Cattrijsse 1994). So far, few studies have been carried out on the piscivorous fishes and their fouraging habits in Gazi Bay (De Troch *et al.* 1996, Wakwabi 1999). Among the possible resident predators for Gobiidae, we mention Muraenidae, Plathycephalidae, Synodontidae, Sphyraenidae, Fistularidae and

Belonidae. Screening of the stomach contents of these predators showed that gobies are an important component in their diet (unpublished data). Further detailed analysis is needed to quantify relative predation pressure on the different goby species. Besides fish, also birds might be important goby predators, especially at low tides (Crawford *et al.* 1985). So far, however, no information about predation by birds from the study area is available.

So far, one ethological study on predator-recognition behaviour has been reported on *A. semipunctatus* and *G. anjerensis* (Smith 1989, Smith and Smith 1989). Both species responded heavily to a visual contact with the predator, and these responses were transmitted within and between species. Only for *A. semipunctatus* was a chemical alarm response observed. This species showed reduced movement and increased bobbing behaviour in response to chemical stimuli from injured conspecifics or predators. In this way, *A. semipunctatus* could be more efficient in avoiding predators, and the time of feeding might therefore be less constrained. This hypothesis remains, however, speculative and needs further examination.

In most studies on short-term temporal patterns in density and feeding of fish species, the effect of semilunar phases on feeding intensity has been largely neglected. One exception is the study of Gliwicz (1986) in a tropical lake, which related a lunar cycle in zooplankton density to changes in predation efficiency of zooplanktivorous fish according to moon light intensities. Most documented examples of semilunar rhythms in fish are, however, associated with spawning and/or migratory activities (Gibson 1978, Horn *et al.* 1999). Moon phase effects on fish assemblages in mangroves have been little studied; some exceptions are the studies by Davis (1988) and Rooker and Dennis (1991). We observed a semilunar periodicity in the catch rates of both species: both *G. anjerensis* and *A. semipunctatus* were most abundant during the neap tides. A semilunar rhythm was also apparent in the feeding intensity of *A. semipunctatus*, with significantly higher stomach fullness being observed during neap tides. A semilunar rhythm in occurrence and feeding can be expected in benthic-feeding fishes that exploit intertidal flats during high tides (Northcott 1991). However, our data did not suggest any tidal migration for feeding. More information on temporal changes in prey availability and/or predation pressure is needed to interpret these observations.

Conclusion

In our general search for processes determining the coexistence of goby species in a tropical lagoon, we analysed the observed patterns of occurrence and feeding behaviour in terms of niche segregation. The present study shows that *G. anjerensis* and *A. semipunctatus* occur in the same seagrass biotope, but their actual fouraging sites probably differed. General diet composition was similar, but feeding strategies differed. In addition, a temporal segregation was observed, both in terms of day/night and semilunar behaviour. The day/night differences could be related to the differences in feeding strategy. This differential resource use might be interpreted as avoidance of current competition or through competitive interactions in the past (Schoener 1974, Connell 1980). However, it may also reflect historical constraints imposed by species divergences over evolutionary time (Tokeshi 1999). In this context, differences in resource use reflect unique adaptations and not co-evolutionary interactions between species (Norton 1991). Whatever the ultimate cause, *G. anjerensis* and *A. semipunctatus* are actually not competing.

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CHAPTER 6

RESOURCE UTILISATION OF FIVE SYMPATRIC GOBY SPECIES IN A TROPICAL MANGROVE CREEK

Coene Heidi and Ollevier Frans

ABSTRACT

The niche characteristics of five sympatric gobies, *Favonigobius reichei*, *Gnatholepis anjerensis*, *Glossogobius biocellatus*, *Amoya signatus* and *Acentrogobius audax* were studied in a tropical mangrove embayment (Gazi Bay, Kenya). The spatial distribution patterns of the goby species over nine sampling sites were overlapping. Some differential habitat use was apparent, which may be related to species-specific camouflage properties. *F. reichei* was dominant at the sandy sites, whereas *G. biocellatus*, *A. signatus* and *A. audax* attained the highest densities at the silty sites. *G. anjerensis* was mostly found at the seagrass sites. With the exception of *G. biocellatus*, which appeared to be a non-selective piscivore, all species had a very similar diet composition, feeding on a wide range of benthic invertebrates. Both diet composition and size distributions of copepods and amphipods, the dominant prey taxa, were very similar among species. *G. anjerensis* differed from the other species in having a more generalist feeding strategy, whereby individual feeding diversity attributed mostly to the total feeding niche breadth. Ontogenetic differences were only observed in the spatial niche, and may relate to size differentiated social hierarchy and/or intraguild predation of *G. biocellatus* or predation by other fishes. Complementarity along the spatial and trophic dimension was observed both in diet breadth and niche overlap. Trophic overlap was generally higher than spatial overlap. In the absence of data on prey availability, predation intensity, abiotic disturbance levels or recruitment variation, the discussion on possible mechanisms regulating the assemblage structure remains speculative. Our observations are, however, in agreement with the view of an r-selected assemblage, of which the members are largely opportunistic and independent, as has been repeatedly observed for tropical fish living in a seasonal environment. There is some evidence that predation might be important, especially when considering the distribution patterns of the different goby species and ontogenetic stages. Exploitative competition is, however, unlikely to be the main driving force currently structuring the assemblage.

INTRODUCTION

In order to understand the community organisation and patterns of species coexistence, it is important to measure niche parameters and overlap in resource utilisation among the different species composing local guilds. In some cases, interspecific competition has been proven to be important in shaping communities, by determining which and how many species can coexist (Connell 1983, Schoener 1983). This equilibrium approach is based on the theory of limiting similarity, which states that niche differentiation is essential for the coexistence of species (Schoener 1974). In other cases, it has been shown that non-equilibrium factors, like stochasticity and the level of disturbance, may be important (Wiens 1984, Sale 1991, Reice 1994).

Menge and Sutherland (1987) provided a general, conceptual framework in which the relative importance of disturbance, competition or predation as structuring agents are related to variation in environmental conditions (including environmental stress and recruitment density). At high levels of environmental stress, abiotic disturbance might be the overriding force in structuring the community. At low levels of environmental stress, predation can reduce densities of prey populations and the importance of competition. In marine benthic communities, recruitment is often decoupled from species interactions in the benthic habitat because of a planktonic larval phase (Connolly and Roughgarden 1999). Presettlement processes and all mechanisms producing variation in recruitment may be important in determining community structure (Sale 1991, Levin *et al.* 1997). For coral reef communities, two models have been proposed to describe the importance of presettlement processes. The lottery model assumes that coral reef fishes compete for space and that the relative abundances of individual species are the result of stochastic recruitment events (Sale 1977). Contrary, the recruitment limitation model predicts that larval supply is normally insufficient for total population size to reach a carrying capacity determined by resource levels (Doherty 1983).

Temperate Gobiidae have been the focus of several studies on niche dynamics, resource partitioning and structuring mechanisms in the coexistence of species (Edlung and Magnhagen 1981, Thorman 1982, Magnhagen and Wiederholm 1982, Evans 1983, Thorman and Wiederholm 1983, 1986, Evans and Tallmark 1985, Hamerlynck *et al.* 1986, Wiederholm 1987, Costello 1992, Wilkins and Myers 1992, 1995). Parallel studies on tropical Gobiidae are scarce, although gobiids are essentially warm-water fishes and their diversity is most marked in tropical ecosystems such as coral reefs and mangrove swamps (Miller 1993). One of the most obvious differences between temperate and tropical ecosystems is the number of coexisting species. Within a deterministic context, greater numbers of coexisting species can be associated with greater numbers of species interactions, which may enhance niche specialisation and resource partitioning (Tokeshi 1999). Examples of fine and extensive resource segregation among tropical fishes may be found in the African Great Lakes (Lowe-McConnell 1996, Bouton *et al.* 1997) and in reef ecosystems (Gladfelter and Johnson 1983, Ebeling and Hixon 1991). However, marked seasonality in tropical ecosystems can prevent niche specialisation, as species have to cope with the changing environment (Lowe-McConnell 1991).

Within the mangrove creek of Gazi Bay, the Gobiidae family is by far the most diverse with 19 species, and attains the highest densities in the subtidal unvegetated areas (see Chapter 2). The tropical sand goby *Favonigobius reichei* (Bleeker), the weeper *Gnatholepis anjerensis* (Bleeker), the sleepy goby *Glossogobius biocellatus* (Valenciennes), the tusk goby *Amoya signatus* (Peters) and the mangrove goby *Acentrogobius audax* Smith are the most common goby species in the study area and are the focus of this study.

Although considerable debate exists on the evaluation of non-experimental evidence with respect to the importance of competition in structuring communities (Abrams 1980, Connor and Simberloff 1986, Ross 1986), the observational approach still forms a basic starting-point for research in this field, especially in diverse and complex communities (Norton 1991, Tokeshi 1999).

In the present study, we analysed the three major niche dimensions (habitat, food and time) of the five dominant goby species in Gazi Bay, and examine the importance of resource partitioning as a structuring agent in this assemblage. Niche characteristics of juveniles and adults were compared in an effort to detect whether there are ontogenetic shifts, and we report on some life history traits of the gobies.

Our field observations were tested against current theories on causal processes underlying community organisation.

MATERIAL AND METHODS

Sampling area and strategy

The study area was Gazi Bay, a shallow tropical mangrove embayment with two major tidal creeks penetrating in the mangrove forest. The Bay (39°30'E and 4°25'S) is situated along the western Indian Ocean, at approximately 50 km south of Mombasa. The mangrove vegetation has been described by Gallin *et al.* (1989), seagrass composition was addressed in Coppejans *et al.* (1992), and more information on tidal regime and seasonal patterns of abiotic conditions can be found in Kitheka *et al.* (1996). Sampling took place between 21st of July and 25th of August 1994. This corresponds with the dry season (McClanahan 1988).

Samples were taken in the downstream part of the Western creek, because of the local availability of different substrate types. Nine shallow water sites were selected according to substrate (grain size) from three main habitat types (mud, sand and seagrass). For a detailed description of these locations and characteristics, we refer to Chapter 3.

Two sampling procedures were used: beach seine (15 by 1.5 m with 3-mm stretch size) and beam trawl (1.5 m width, 6 m long bag, and 3-mm stretch size of inner net). A standardised beach seine haul was estimated to sweep an area of 18 m^2. The trawling net was dragged at constant speed over a minimal distance of 20 m parallel to the shoreline. Sampling was only conducted at low tide (± 2 hours). Four tows were taken on each sampling occasion. Beach seining was only conducted during the daytime, while trawling was done during day and night at the same sampling site. Not all sampling sites could be sampled by both methods: in the sandy sites only trawling could be conducted, whereas in the siltiest site (MUD 5), only beach seining was possible. In total 223 nettings were taken.

Stomach content analysis

Species were sorted out and identified according to Koumans (1953), Smith (1959, 1960) and Hoese (1986). Identifications were checked by H. Larson and F. Pezold (personal communication). Standard lengths of the specimens were measured to the nearest 1 mm. The Bhattacharya method, followed by a NORMSEP method (Gayanilo *et al.* 1996), were applied for the detection of cohorts from the length-frequency data. Observed versus expected frequencies were compared with a χ^2-test.

Table 1: Overview of samples used for stomach content analysis: number of analysed and empty stomachs of the five goby species for the different sampling sites and sampling times in the diel cycle (A = number of analysed stomachs; E = number of empty stomachs).

	F. reichei		*G. anjerensis*		*G. biocellatus*		*A. signatus*		*A. audax*	
SITE	A	E	A	E	A	E	A	E	A	E
MUD 1	33	15	23	2	16	3	29	2	30	5
MUD 3	29	10			56	21	42	7	50	3
MUD 4	17	2								
MUD 5					20	6	15	1	20	1
SAND 2	23	3								
SG 1	19	4	85	11	28	9	42	0		
TIME										
Day	76	18	76	2	81	25	92	8	74	8
Night	45	16	32	11	39	14	36	2	26	1

The stomach content of 577 gobies belonging to 5 species was analysed. The number of specimens analysed per sampling site was determined according to the relative importance in the distribution patterns of the different species and comprised both day and night samples (Table 1). The range in standard lengths of analysed specimens was 21-49 mm for *F. reichei*, 22-50 mm for *G. anjerensis*, 22-64 mm for *G. biocellatus*, 20-56 mm for *A. signatus* and 21-72 mm for *A. audax*. Stomach contents were removed under a dissecting binocular and transferred onto a slide for further examination under a microscope (100x). Prey items were identified to the taxonomic level indicated in Table 3, counted and measured (SL) with a calibrated ocular or drawn using a drawing mirror and subsequently measured using a digitalizing tablet. The numerical percentage (N%) of each prey category to the total stomach content was calculated for each fish. Gravimetrical percentage (G%) was defined as the relative contribution of the prey category to the total ash-free dry weight (AFDW) of the stomach content. We used SL-AFDW regressions or assigned AFDW values for the relevant prey categories as described in previous studies from the study area (De Troch *et al.* 1998, Wakwabi 1999). Frequency of occurrence (O%) was calculated for each prey category as the percentage of examined stomachs containing the prey category. Empty stomachs were not included in the calculations. For the analysis of prey size selectivity, mean prey length for each individual fish was used in the analysis.

To explore the general diet composition and the feeding strategies of the five goby species, the Tokeshi (1991) method and the modified graphical Costello (1990) method as described in Amundsen *et al.* (1996) were used. Both methods distinguish between the niches of individuals and those of the whole population. Two components can be identified to contribute to the population's total feeding niche width: the within-phenotype component, showing the variation of each individual in its resource use, and the between-phenotype component comprising the variation between individuals. In the Tokeshi graph, the mean individual feeding diversity (D_I) is plotted against the population feeding diversity (D_P) whereby:

$$D_I = \frac{(-\sum P_{ij} \ln P_{ij})}{N}$$

$$D_P = -\sum P_i \ln P_i$$

with P_{ij} = proportion of prey type i in the j^{th} fish, N= total number of fish and P_i = proportion of prey type i in the entire fish population.

In the modified Costello's method, the relative occurrence of each prey category (O%) is plotted against the prey-specific gravimetrical contribution, which is calculated as the percentage that a prey category comprises of all prey items in those predators in which the prey type occurs.

To measure stomach fullness, the contents were dried for 24 hours in a furnace at 60°C, and weighted on an electronic microbalance with a precision of 1 µg. Feeding intensity was estimated with the fullness index (FI):

$$\mathrm{FI} = (\mathrm{DWstomach})/(\mathrm{DWfish})*100$$

A SL-DW regression was established for the 5 goby species, whereby 50 individuals per species of various lengths were dried for 5 days at 65°C, giving the following results:

Favonigobius reichei	$\ln(DW) = 3.4 * \ln(SL) - 7.1$	$r=0.96$
Gnatholepis anjerensis	$\ln(DW) = 3.4 * \ln(SL) - 6.4$	$r=0.98$
Glossogobius biocellatus	$\ln(DW) = 3.2 * \ln(SL) - 6.5$	$r=0.99$
Amoya signatus	$\ln(DW) = 3.2 * \ln(SL) - 6.1$	$r=0.96$
Acentrogobius audax	$\ln(DW) = 3.1 * \ln(SL) - 5.6$	$r=0.99$

Differences in feeding intensity among habitats were assessed by comparing the mean stomach fullness indices. In doing this, we assume that feeding took place within the sampling site prior to capture. This seems reasonable, since the stomach content evacuation rate of the gobiids was estimated to be high (Chapter 4).

Niche breadth

Niche breadth was estimated for the spatial and trophic dimension with Levin's standardized measure B_A:

$$B_A = \frac{(B-1)}{(n-1)} \text{ with } B = \frac{1}{\sum p_i^2}$$

with p_i = proportion of resource category i to the total resources and n = the total number of resource categories (Krebs 1989a).

For classifying a species as generalist or specialist, niche breadth measures were represented relative to the upper and lower bounds of extreme values found for all species combined (Colwell and Futuyma 1971).

Niche overlap

To measure ecological similarities between species-pairs, niche overlap was estimated with the simplified Morisita overlap index O_{jk}:

$$O_{jk} = \frac{2\sum_{i=1}^{n} p_{ij} p_{ik}}{\sum_{i=1}^{n} p_{ij}^2 + p_{ik}^2}$$

with p_{ij}, p_{ik} = the proportion of resource category i to the total resources used by the two species j and k and n = total number of resource categories (Krebs 1989a). The Morisita niche overlap is nearly identical to the traditionally used Pianka measure, but recommended on the basis of its robustness (Smith and Zaret 1982). To compare niche overlap indices among species-pairs, adjustments relative to the extreme values were used (Colwell and Futuyma 1971).

Additionally to the spatial niche overlap index, the Jaccard similarity coefficient J was calculated for the distribution data:

$$J = \frac{x}{(s+x)}$$

with x = the number of co-occurrences and s = the sum of the non-co-occurrences. The Jaccard coefficient is based on presence-absence data and the number of co-occurrences, irrespective of densities (Krebs 1989b). Using this index, we make an assessment of co-occurrence of species on a microhabitat scale.

As species respond to local resource availability, trophic niche overlap between species should be considered primarily within each habitat. To estimate total trophic niche overlap (O_{jk}) between a species pair, we adjusted the site-specific overlap measures for differences in relative densities between sites:

$$O_{jk} = \sum_{x=1}^{n} O_{jk,x} \left[\frac{R_{j,x} + R_{k,x}}{2} \right]$$

with $O_{jk,x}$ = the overlap index of species j and k at site x; $R_{j,x}$ the proportional abundance of species j at site x to the total abundance of species j in n sites, with n = number of sites at which species j and k are co-occurring.

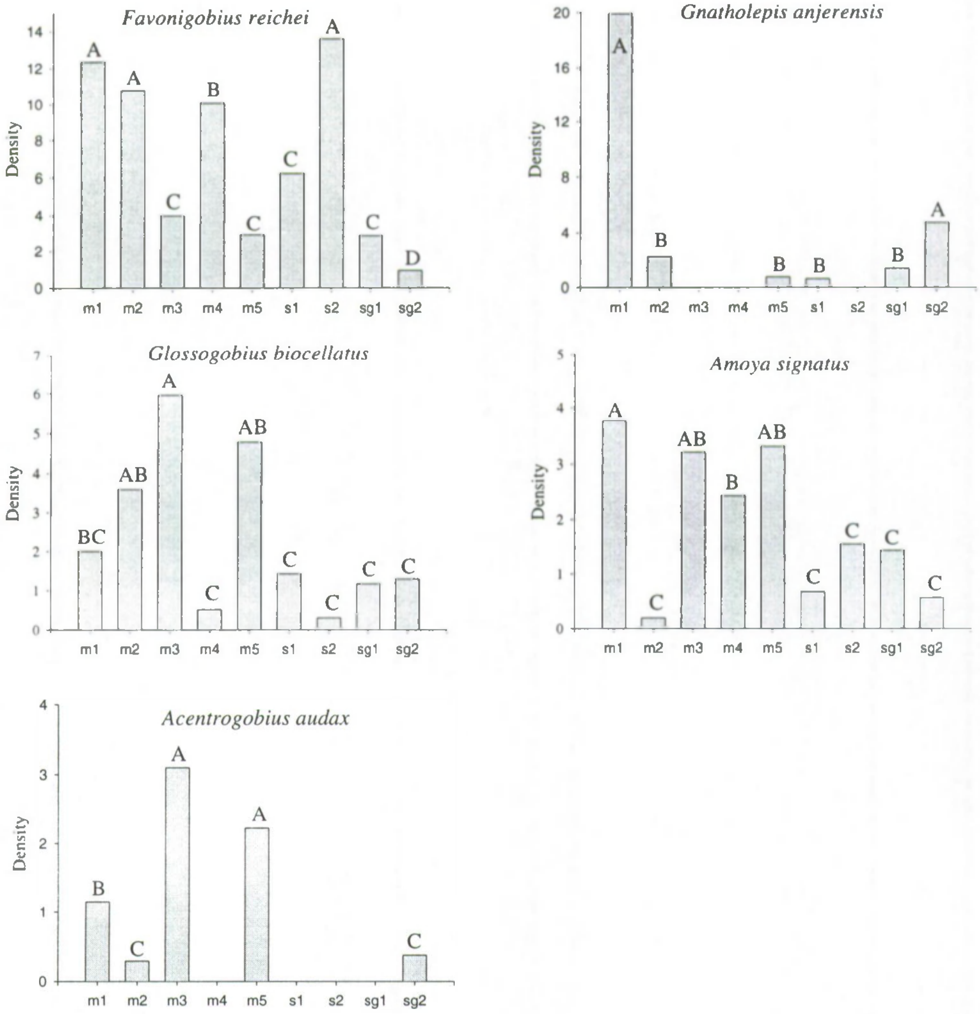

Figure 1: Distribution patterns over the nine sampling sites: mean densities (per 30 m²) and Kruskal-Wallis ANOVA post-hoc comparisons. Means sharing the same character are not significantly different. m = MUD, s = SAND, sg = SG.

To visualise the habitat and food interaction within and between species, we performed a Principal Component Analysis on the site-specific diet composition for the five species. We analysed the interaction of day/night (temporal dimension) with the spatial and trophic dimension. Caution should be made in interpreting these interactions. While the temporal and spatial interaction reflects a direct interaction of species capturing space, the temporal and trophic dimension do not interact directly as the time of the day at which resources are depleted will not make any difference when considering exploitative competition (Piet *et al.* 1999).

Statistical analysis

Whenever possible, ANOVA and post-hoc comparisons were employed. If ANOVA assumptions were not met and no appropriate transformation could be found, non-parametric analogues (Mann-Withney U-test, Kruskal-Wallis ANOVA and Friedman ANOVA) were used, with post-hoc multiple comparisons being calculated as in Siegel and Castellan (1988).

RESULTS

The spatial niche

General distribution pattern

Initially, differences in density estimates obtained by the two sampling methods were tested. The catch rates obtained with beach seining and trawling at daytime for each species within each sampling site revealed no significant differences (Mann-Withney U-test, all $p>0.05$ and Bonferroni corrected). Therefore, further analysis was based on pooled data.

For each of the five goby species, densities between sites differed significantly (Kruskal-Wallis ANOVA, d.f.=8, $p<0.05$. Results of multiple comparisons are shown in Figure 1. *F. reichei* was most abundant at sites MUD 1, MUD 2 and SAND 2, followed by site MUD 4 (mean densities 0.3 - 0.5 ind./m^2). At the MUD 3 and SAND 1 site, mean densities were lower, although occasionally high densities (1 - 1.8

ind./m²) were observed. *G. anjerensis* occurred with highest mean density at the MUD 1 site and at the SG sites. At the MUD 1 site, variation in catch rates was very high, with extreme densities of 1.3 - 6.3 ind./m². *G. biocellatus* was most abundant at sites MUD 2, MUD 3 and MUD 5, with mean densities 0.1-0.2 ind./m². *A. signatus* was found mostly at sites MUD 1, MUD 3 and MUD 5 (mean densities 0.1 ind./m²), attaining maximal densities at MUD 3, with 0.9 ind./m². *A. audax* was most abundant at the MUD 3 and MUD 5 sites, with a mean density of 0.1 ind./m². The highest recorded density for this species was 0.4 ind./m² at site MUD 3.

To compare equitability in distribution among sites between the goby species, spatial niche breadths were calculated. *F. reichei*, *G. biocellatus* and *A. signatus* had the broadest niches, ranging from 0.71 to 0.76. These species occurred at all sampling sites. *G. anjerensis* and *A. audax* had the narrowest spatial niches, 0.34 and 0.32, respectively. These species did not occur at all sites and attained a high density at one or two sites.

Similarities in distribution and co-occurrence patterns of species pairs, assessed by the Morisita niche overlap index and the Jaccard similarity coefficient, are given in Table 2. The Morisita niche overlap revealed a high number of similarities exceeding 50%. The Jaccard similarity coefficient highlighted a high percentage of co-occurrences for three species pairs: *F. reichei - G. biocellatus*, *F. reichei - A. signatus* and *G. biocellatus - A. signatus*.

Temporal variation in distribution

Day and night catch rates of trawl sampling were compared at each site for the five goby species. No significant differences between day and night were found (Mann-Withney U-test, all $p > 0.05$).

Population structure and ontogenetic variation in distribution

The population of the different species differed in length frequency distribution and population structure (Figure 2). *F. reichei* and *G. anjerensis* consisted of 2 cohorts, of which the smaller cohort was far most abundant. Maximal recorded length did not exceed 50 mm for both species. Gravid females were observed from 20 mm SL onwards. When SL was higher than 35 mm, all females of both species were gravid. In *G. biocellatus* and *A. signatus,* two cohorts of approximately equal size were distinguished. SL ranged between 8 and 64 mm. The minimal SL for mature females was 47 mm for *G. biocellatus* and 26 mm for *A. signatus.* For *A. audax*, separation of cohorts was less clear. Two possibilities are proposed, whereby respectively 2 or 3 cohorts were observed. Probably, the number of observed specimens was too low to make the distinction among both possibilities. The minimal SL for mature females was 55 mm.

Table 2: Pair-wise similarities in distribution patterns between the five goby species studied: the Morisita niche overlap (relative abundances) and Jaccard similarity coefficient (presence-absence) for species pairs.

Morisita niche overlap

	1.	*2.*	*3.*	*4.*	*5.*
1. F. reichei	100				
2. G. anjerensis	47	100			
3. G. biocellatus	55	29	100		
4. A. signatus	73	51	79	100	
5. A. audax	34	32	88	76	100

Jaccard similarity coefficient

	1.	*2.*	*3.*	*4.*	*5.*
1. F. reichei	1.00				
2. G. anjerensis	0.27	1.00			
3. G. biocellatus	0.53	0.28	1.00		
4. A. signatus	0.49	0.26	0.51	1.00	
5. A. audax	0.20	0.09	0.29	0.30	1.00

Relative abundances and equitability of distribution over sites differed between juveniles and adults within species (Figure 3). Spatial niche breadth measures for juveniles and adults of *F. reichei* were similar. At the two most occupied sites, however, the relative abundances between juveniles and adults differed most: at MUD 1 juveniles were strongly dominating (86% of the sample), while at SAND 2 juveniles contributed only 64%. Although juveniles and adults of *G. anjerensis* occurred at the same sites, niche breadth of juveniles was markedly lower, due to their high relative

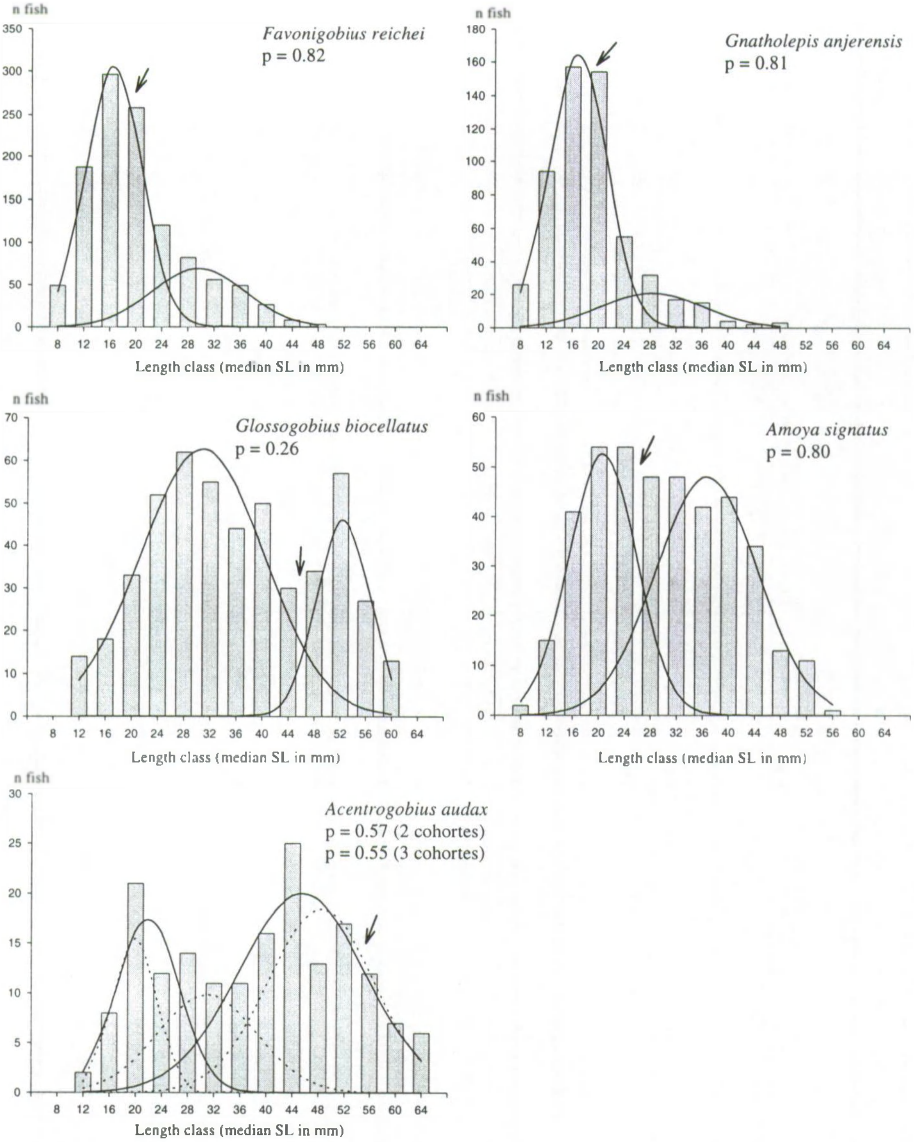

Figure 2: Standard length frequency distributions for the five goby species, separation of cohorts (Gauss curves), minimal SL for mature females (arrows) and results of χ^2-test analysing for differences among the expected and observed length frequency distributions (p-level).

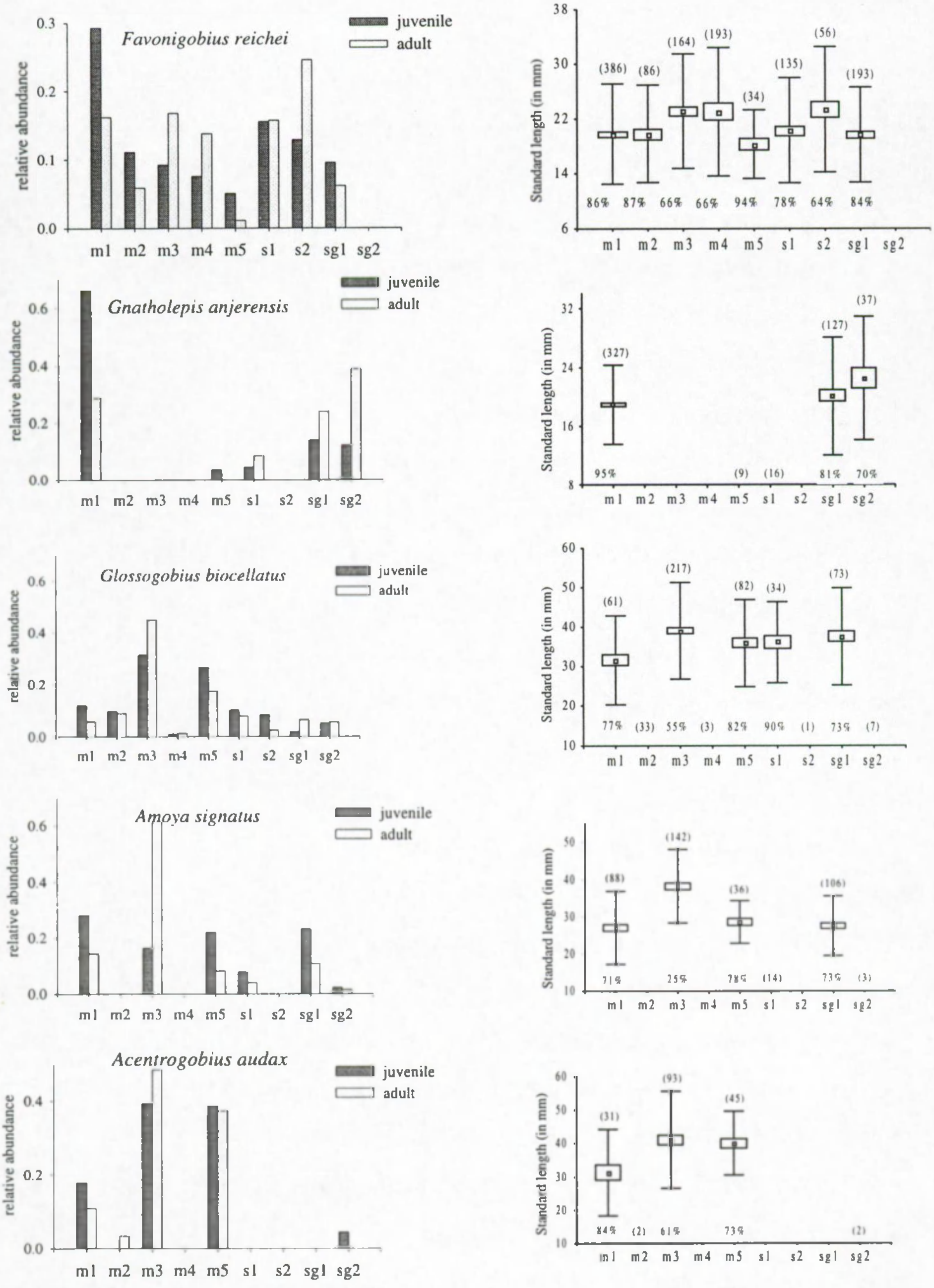

Figure 3: Comparison of distribution patterns between juveniles and adults: (LEFT) proportional abundance within each sampling site, calculated independently for juveniles and adults; (RIGHT) box-whisker plot for observed standard length in the relevant sampling sites. Mean (square), st.err. (box) and st.dev. (whisker); (n) above box-whiskers indicates number of observed specimens; n% under box-whiskers gives the proportion of juveniles within the sample.

abundance at the MUD 1 site. Adults were more equally distributed. *G. biocellatus* occurred at all nine sampling sites, both as juveniles and adults. The niche breadth of juveniles was slightly higher than that of the adults. The adults were most abundant at the MUD 3 site, where only 55% of the individuals were juveniles. For *A. signatus*, a quite equal distribution over habitats was found for juveniles. The adults, however, were most abundant at site MUD 3. Only 25% of the specimens at this site were juveniles, compared to 71-78% at the other sites. For *A. audax*, juveniles and adults showed a very similar distribution pattern.

In summary, there seemed to exist a tendency for the juveniles of the two smallest species (*F. reichei* and *G. anjerensis*) to concentrate at the MUD 1 site, whereas most of the adults of the three bigger species (*G. biocellatus*, *A. signatus* and *A. audax*) were found at the MUD 3 site.

Spatial niche overlap was highest for all combinations of *G. biocellatus*, *A. signatus* and *A. audax*, and also for *F. reichei* and *A. signatus* (Figure 3).

The feeding niche

General feeding strategy and diet composition

Tokeshi's method clearly separated *G. biocellatus* from the other species (Figure 4). In this species, both individual and population feeding diversity were very low, indicating a specialised feeding strategy. All other species were characterised by a high population feeding diversity. Of these, *G. anjerensis* was characterised by the highest individual feeding diversity, reflecting a generalist and opportunistic feeding strategy.

The results of Costello's modified method are represented in Figure 5. *G. biocellatus* showed a population specialisation towards one specific prey item, namely fishes. These fishes were mostly juveniles of various species, including other gobies and conspecifics. Small proportions of amphipods and mysids were included in the diet of a small subset of individuals. For *G. anjerensis,* several food categories are positioned towards the lower right part of the graph, indicating that many individuals share the same prey types and that the diet of each individual is also very diverse. Most of the important prey taxa (copepods, ostracods, amphipods, kinorhynchs and isopods) were taken by more than half of the individuals, but their average contribution to the stomach content was low. This species clearly has a generalist feeding strategy. The feeding strategy of *F. reichei*, *A. signatus* and *A. audax* is characterised by a high interindividual variation, as most of the prey types are positioned towards the upper left corner of the graph. Fishes, mysids and decapods (crabs) were taken by only a limited fraction of the predator population, but if taken they contributed substantially to the stomach content weight. For all three species, amphipods and harpacticoid copepods were dominant and general prey taxa. For *A. signatus* and *A. audax*, also polychaetes and nematodes represented prey taxa often taken.

Feeding niche breadth of *G. biocellatus* and *F. reichei* was significantly lower than niche breadth of *G. anjerensis*, *A. signatus* and *A. audax* (ANOVA & Tukey's HSD post-hoc comparisons for unequal sample size).

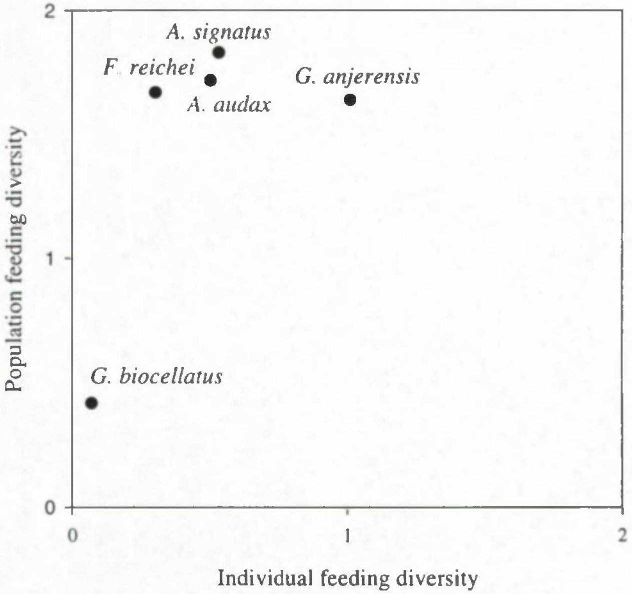

Figure 4: Tokeshi (1991) graphical method, comparing individual and population feeding diversity of the five goby species.

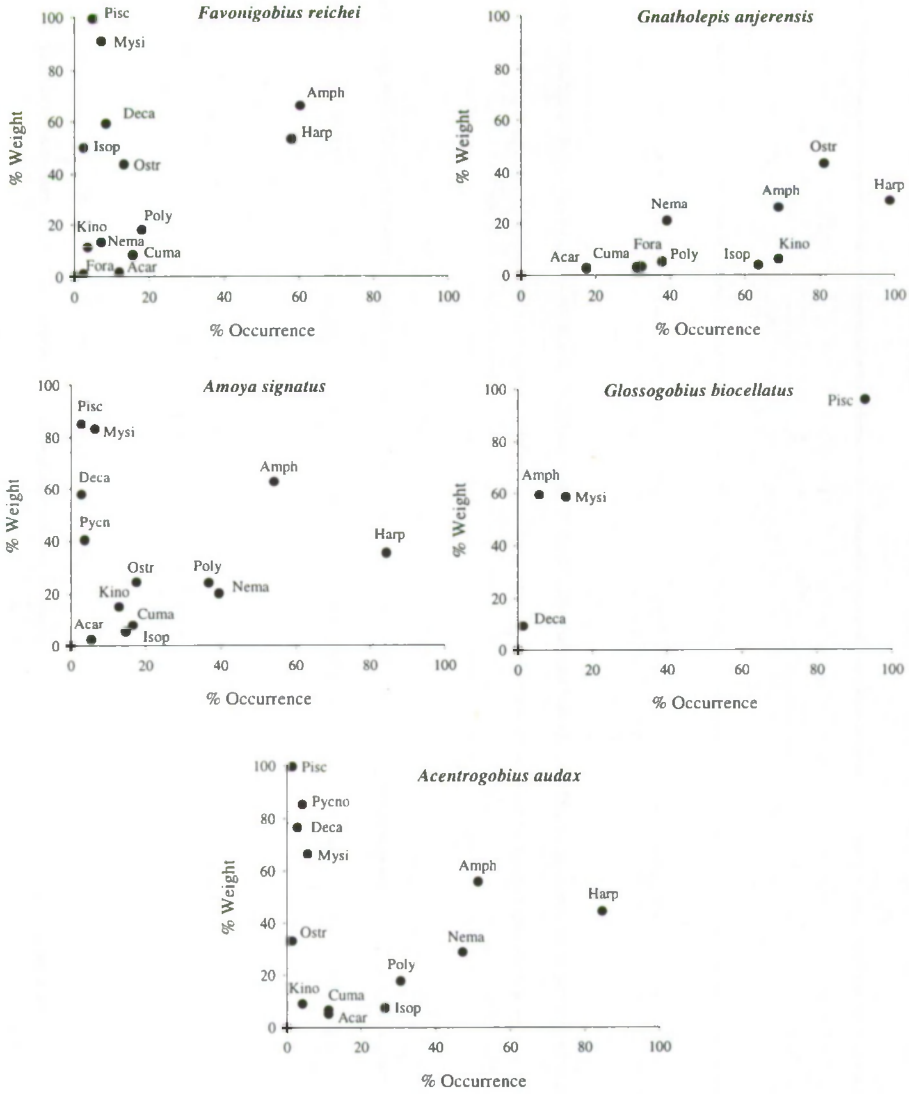

Figure 5: Modified Costello (1990) graphical representation of the stomach content for the five goby species studied: percent frequency of occurrence (% Occurrence) against prey-specific gravimetrical contribution (% Weight). For prey abbreviations see Table 3.

Table 3: Spatial patterns in diet composition: gravimetrical proportions of prey types for five goby species at different sampling sites (not all species were caught at all sampling sites in sufficient numbers for analysis).

Prey type abbreviations: Harp = Harpacticoida; Amp = Amphipoda; Isop = Isopoda; Ostr = Ostracoda; Poly = Polychaeta; Kino = Kinorhyncha; Cuma = Cumacea; Acar = Acarina; Nema = Nematoda; Mysi = Mysidacea; Pycn = Pycnogonida; Pisc = Pisces; Deca = Decapoda; Fora = Foraminifera. "<" indicates proportion < 0.01

	Harp	Amp	Isop	Ostr	Poly	Kino	Cuma	Acar	Nema	Mysi	Pycn	Pisc	Deca	Fora
F. reichei														
MUD 1	0.02	0.48		0.06	0.03	<	<		0.02	0.27		0.06	0.06	
MUD 3	0.28	0.36		0.07	0.03	<	0.10	0.02	<	0.03		0.05	0.05	<
MUD 4	0.20	0.55			0.10			<	0.01			0.13		
SAND 2	0.66	0.26		0.04	0.01		<	<	0.01					
SG 1	0.24	0.42	0.07	0.12	0.08	<	<	<				0.07		<
G. anjerensis														
MUD 1	0.17	0.17	<	0.40	<	0.05	<	<	0.20					<
SG 1	0.33	0.20	0.06	0.28	0.04	0.04	<	<	0.03					<
G. biocellatus														
MUD 1										<		0.99		
MUD 3		0.18								0.15		0.64	0.02	
MUD 5										0.07		0.93		
SG 1		0.02								0.12		0.85	<	
A. signatus														
MUD 1	0.28	0.36	<	<	0.07	0.04	<		0.09	0.04	0.09	0.04		
MUD 3	0.22	0.49	<	<	0.09	0.03	0.04	<	0.07	0.01	<	0.04		
MUD 5	0.50	0.19	0.02		0.13		0.01		0.04	0.06			0.05	
SG 1	0.32	0.33	0.01	0.08	0.06	<	<		0.08	0.09			0.02	
A. audax														
MUD 1	0.48	0.10	0.05	<	0.03	<	<	<	0.14	0.10	0.04	0.04		
MUD 3	0.28	0.37	<	0.05	0.07	0.01	<	0.02	0.13	<	0.02	0.01	0.03	
MUD 5	0.58	0.11	<		0.12	0.01	<		0.13		0.04			

Spatial variation in feeding

General diet composition (Table 3) and niche breadth (Table 4) were calculated for each species in different habitat types. For *F. reichei*, the stomach contents of individuals from the sand habitat differed significantly from those of fishes collected at other sampling sites. Copepods were far most abundant in the sandy sites (Kruskal-Wallis ANOVA, df=3, p=0.005). The feeding niche breadth at this habitat tended to be narrower than in the other habitat types, although this was not significant. For *G. anjerensis*, nematods were significantly more eaten at the MUD 1 site compared to the SG site (Kruskal-Wallis ANOVA, df=1, p=0.001), with the niche breadth measure in this mud site being significantly lower than in other sites. In the diet of *A. audax*, copepods were dominant at the MUD 1 and MUD 5 sites, whereas amphipods were more important at MUD 3 (Kruskal-Wallis ANOVA, df=3, p=0.006 and p=0.02, respectively). Other prey taxa did not differ among habitats. Dietary breadth did not differ among sites. There were no dietary differences between sites for *G. biocellatus* and *A. signatus*. Only the niche of *G. biocellatus* was significantly broader at the SG site than at the other sites.

Table 4: Comparison of mean diet breadth B_A ± S.D. among sampling sites. (p-level = probability associated with one-way ANOVA). Significant values are in bold.

	Mud 1	Mud 3	Mud 4	Mud 5	Seagrass	Sand	p-level
F. reichei	0.17 ± 0.24	0.31 ± 0.29	0.12 ± 0.23		0.30 ± 0.34	0.09 ± 0.09	0.06
G. anjerensis	0.26 ± 0.16				0.40 ± 0.24		**0.01**
G. biocellatus	0.02 ± 0.08	0.10 ± 0.23		0.00 ± 0.00	0.20 ± 0.32		**0.04**
A. signatus	0.26 ± 0.36	0.28 ± 0.28		0.33 ± 0.29	0.33 ± 0.30		0.75
A. audax	0.40 ± 0.33	0.28 ± 0.28		0.32 ± 0.31			0.32

Table 5: Morisita feeding niche overlap: adjusted overall pattern and habitat-specific niche overlap.

Overall Pattern

	1.	*2.*	*3.*	*4.*	*5.*
1. F. reichei	1.00				
2. G. anjerensis	0.45	1.00			
3. G. biocellatus	0.07	0.01	1.00		
4. A. signatus	0.86	0.59	0.09	1.00	
5. A. audax	0.64	0.48	0.05	0.76	1.00

Mud 1 site

	1.	*2.*	*3.*	*4.*	*5.*
1. F. reichei	1.00				
2. G. anjerensis	0.39	1.00			
3. G. biocellatus	0.10	0.00	1.00		
4. A. signatus	0.81	0.52	0.11	1.00	
5. A. audax	0.36	0.48	0.07	0.71	1.00

Mud 3 site

	1.	*2.*	*3.*	*4.*	*5.*
1. F. reichei	1.00				
2. G. anjerensis	-	-			
3. G. biocellatus	0.05	-	1.00		
4. A. signatus	0.93	-	0.14	1.00	
5. A. audax	0.94	-	0.06	0.94	1.00

Mud 5 site

	1.	*2.*	*3.*	*4.*	*5.*
1. F. reichei	-				
2. G. anjerensis	-	-			
3. G. biocellatus	-	-	1.00		
4. A. signatus	-	-	0.04	1.00	
5. A. audax	-	-	0.03	0.59	1.00

SG 1 site

	1.	*2.*	*3.*	*4.*	*5.*
1. F. reichei	1.00				
2. G. anjerensis	0.87	1.00			
3. G. biocellatus	0.08	0.01	1.00		
4. A. signatus	0.90	0.93	0.04	1.00	
5. A. audax	-	-	-	-	-

As species respond to local food availability, feeding niche overlap between species pairs was calculated within each site (Table 5). There was considerable variation in feeding niche overlap according to sites. Highest values were recorded for combinations of *F. reichei*, *A. signatus* and *A. audax*. For all these species-combinations, lowest values were recorded at the MUD 1 site, except for *A. signatus* and *A. audax*, which had lowest diet overlap at the MUD 5 site.

The relative importance of intra- and interspecific differences in diet composition is shown in Figure 6. The PCA plot clearly shows the separation of *G. biocellatus* on the basis of fish and mysids and of *G. anjerensis* on the basis of ostracods, foraminifers and kinorhynchs. For *F. reichei*, *A. signatus* and *A. audax*, however, no separation between species was apparent. Intraspecific differences between sites were as important as interspecific differences.

Differences in feeding intensity among habitats were assessed by comparing the mean stomach fullness indices (Table 6). For *G. anjerensis*, *A. signatus* and *A. audax*, a significant negative correlation between relative fullness and body size was found (Spearman rank order correlation, Table 7). Therefore, standard length was considered as covariate in the comparative analysis among species (ANCOVA). The stomach fullness of *G. biocellatus* was significantly higher at the MUD 1 site than at the other sites. In contrast, stomach fullness was significantly higher at the SG site than at the other sites for *A. signatus*. *A. audax* had higher stomach fullness at the MUD 3 than at the MUD 1 site. No differences were found for the other species.

Table 6: Comparison of feeding intensity among sampling sites: mean stomach fullness ± S.D. and significance level of appropriate test. Significant values are in bold. (*)=ANOVA and (**)=ANCOVA (see also text)

	Mud 1	Mud 3	Mud 4	Mud 5	Seagrass	Sand	p-level
F. reichei	0.35 ± 0.47	0.58 ± 0.75	0.53 ± 0.58		1.03 ± 1.08	0.48 ± 0.17	0.19 (*)
G. anjerensis	0.42 ± 0.33				0.87 ± 0.61		0.17 (**)
G. biocellatus	6.50 ± 5.70	1.70 ± 2.70		1.80 ± 2.10	2.50 ± 4.50		**0.001** (*)
A. signatus	0.36 ± 0.32	0.41 ± 0.42		0.40 ± 0.40	1.12 ± 1.06		**0.001** (**)
A. audax	0.26 ± 0.34	0.62 ± 0.51		0.43 ± 0.29			**0.001** (**)

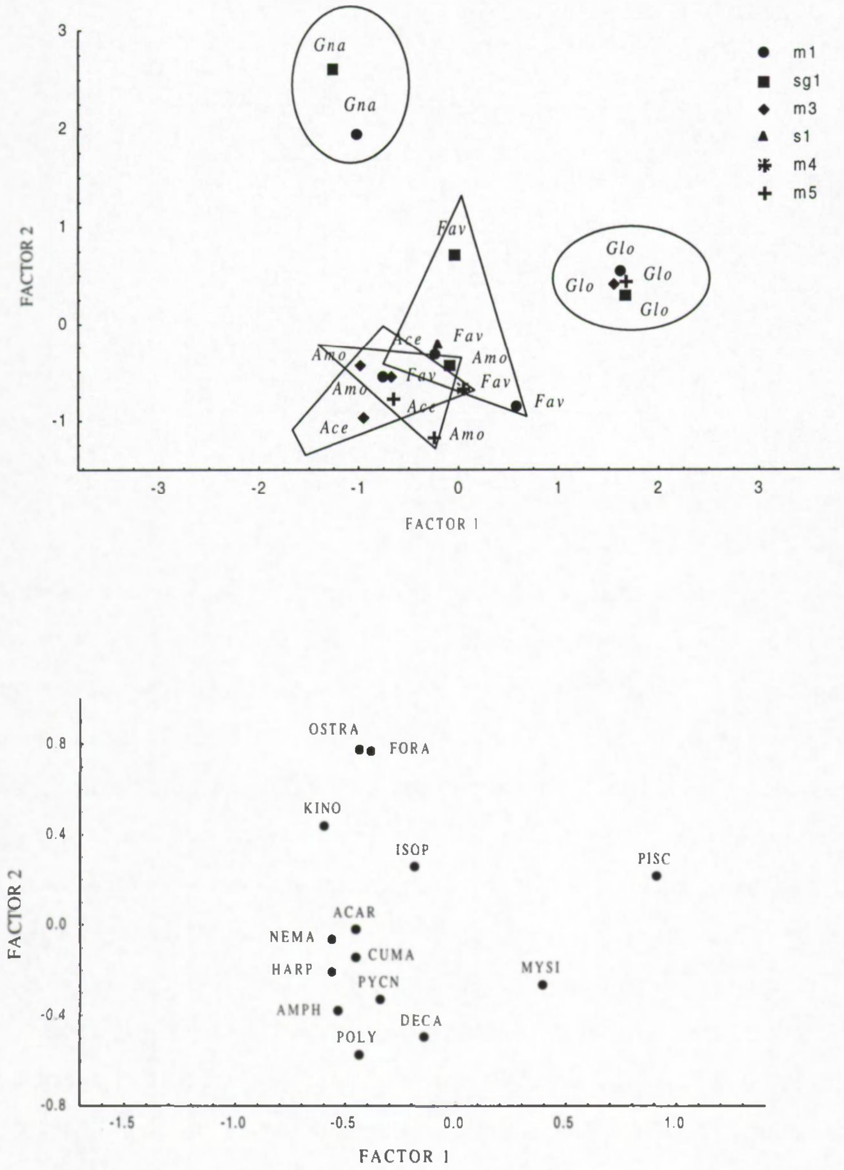

Figure 6: Results of Principal Component Analysis (factor 1 vs. factor 2) on the site-specific diet compositions of the five goby species. Upper panel: plot of scores; lower panel: plot of loadings. Abbreviations: *Fav* = *F. reichei*; *Gna* = *G. anjerensis*; *Glo* = *G. biocellatus*; *Amo* = *A. signatus*; *Ace* = *A. audax*.

Table 7: Correlation between stomach fullness index and standard length for five goby species at Gazi Bay: Spearman Rank Order Correlation. Significant values are in bold. N = number of analysed specimens; R = correlation coefficient; p = significance level.

	N	R	p-level
F. reichei	112	-0.13	0.17
G. anjerensis	76	-0.56	**0.001**
G. biocellatus	100	-0.14	0.15
A. signatus	117	-0.40	**0.001**
A. audax	81	-0.25	**0.02**

Temporal variation in feeding

Day-night differences in diet composition were minor (Table 8). For *G. anjerensis,* isopods were more eaten at night than during the day, whereas consumption of ostracods was significantly higher during the day. Day-night differences were most marked for *G. biocellatus.* While fishes were the most important prey during the day, amphipods and mysids were added to the diet during the night. In the diet of *A. audax,* differences were observed in the secondary prey. Ostracods, kinorhynchs and acarids were all predominantly taken at night. No differences were detected for the other goby species (Kruskal-Wallis ANOVA for each species and post-hoc comparisons between prey items). For all species, there was a tendency for a higher feeding niche breadth at night, but none of the differences were significant (Table 9; Kruskal-Wallis ANOVA, $p > 0.05$). A comparison of fullness indices of day and night samples revealed a significant difference only for *G. anjerensis* (Table 9). For this species, stomach fullness during daytime was significantly higher than stomach fullness during the night (Kruskal-Wallis ANOVA, $p < 0.05$).

Ontogenetic variation in feeding

Ontogenetic patterns (juveniles versus adults) in diet composition and feeding niche

Table 8: Temporal patterns in diet composition: gravimetrical proportions of the prey types for the five goby species in day and night samples (For prey type abbreviations see Table 3; "<" indicates proportion < 0.01).

	Harp	Amp	Isop	Ostr	Poly	Kino	Cuma	Acar	Nema	Mysi	Pycn	Pisc	Deca	Fora
F. reichei														
Day	0.29	0.40	0.02	0.04	0.03	<	0.02	<	<	0.07		0.06	0.06	<
Night	0.32	0.37		0.08	0.08	<	0.04	0.01	0.01	0.05		0.03		<
G. anjerensis														
Day	0.28	0.18	0.02	0.35	0.02	0.04	<	<	0.08					0.01
Night	0.33	0.25	0.14	0.14	0.07	0.03	0.02	<						0.02
G. biocellatus														
Day		<								0.07		0.93		
Night		0.22								0.25		0.49		
A. signatus														
Day	0.28	0.33	<	0.04	0.08	0.02	0.01	<	0.08	0.07	0.02	0.03	0.01	
Night	0.33	0.43	<	0.03	0.08	<	<		0.06	<	0.03		0.03	
A. audax														
Day	0.38	0.29	0.02	<	0.05	<	<	<	0.14	0.04	0.04	0.01	0.02	
Night	0.49	0.10	<	0.09	0.11	0.03	<	0.03	0.11	<		0.01		

Table 9: Temporal patterns in diet breadth (B_A) and feeding intensity (FI): mean ± S.D. for day and night samples, and Kruskal-Wallis ANOVA (p-level). Significant values are in bold.

Species		B_A	p-level	FI	p-level
F. reichei	Day	0.35 ± 0.22	0.16	0.96 ± 2.09	0.08
	Night	0.43 ± 0.28		0.38 ± 0.78	
G. anjerensis	Day	0.17 ± 0.25	0.25	0.67 ± 0.64	**0.01**
	Night	0.24 ± 0.28		0.20 ± 0.31	
G. biocellatus	Day	0.09 ± 0.24	0.33	7.91 ± 19.29	0.49
	Night	0.16 ± 0.28		5.54 ± 13.29	
A. signatus	Day	0.30 ± 0.32	0.96	1.12 ± 2.43	0.08
	Night	0.30 ± 0.26		0.40 ± 0.49	
A. audax	Day	0.32 ± 0.32	0.57	0.41 ± 0.77	0.22
	Night	0.35 ± 0.22		0.22 ± 0.29	

breadth were analysed for *G. biocellatus*, *A. signatus* and *A. audax.* No significant differences in diet composition between juveniles and adults were observed (Table 10; Kruskal-Wallis ANOVA, all p>0.05). Feeding niche breadths did not differ significantly between juveniles and adults in any of the studied species (Table 11; Kruskal-Wallis ANOVA, all p>0.05).

Prey size selectivity

As copepods and amphipods were the primary prey items for *F. reichei*, *G. anjerensis*, *A. signatus* and *A. audax,* we investigated in detail whether there was size selectivity for these prey items within and among species. For none of the species, a significant correlation between the mean length of ingested copepods and the standard length of the predator was found (Spearman rank order correlation, all p>0.05). There was, however, a significantly positive correlation between mean length of ingested

Table 10: Ontogenetic changes in diet composition: gravimetrical proportions of the different prey types for juvenile and adult *Glossogobius biocellatus*, *Amoya signatus* and *Acentrogobius audax* (For prey type abbreviations see Table 3; "<" indicates proportion < 0.01).

	Harp	Amp	Isop	Ostr	Poly	Kino	Cuma	Acar	Nema	Mysi	Pycn	Pisc	Deca	Fora
G. biocellatus														
Juvenile		0.09								0.09		0.81	<	
Adult		0.08								0.13		0.77	0.02	
A. signatus														
Juvenile	0.34	0.28	0.01	0.07	0.06	<	<	<	0.09	0.08	<	0.04	0.02	
Adult	0.26	0.44	<	0.01	0.11	0.03	0.02	<	0.06	0.02	0.04		0.01	
A. audax														
Juvenile	0.47	0.17	0.03	0.02	0.04	0.02	<	<	0.16	0.03	0.02	0.02	0.01	
Adult	0.35	0.30	<	0.03	0.09	<	<	0.02	0.10	0.03	0.03	<	0.02	

Table 11: Ontogenetic changes in diet breadth (B_A): mean ± S.D. for juveniles and adults, and ANOVA (p-level).

Species		B_a	p-level
G. biocellatus	Juvenile	0.12 ± 0.26	0.33
	Adult	0.05 ± 0.16	
A. signatus	Juvenile	0.32 ± 0.32	0.96
	Adult	0.28 ± 0.30	
A. audax	Juvenile	0.32 ± 0.30	0.57
	Adult	0.33 ± 0.30	

amphipods and the standard length of the fish for *G. anjerensis* (N=29, r=0.20, p=0.005). This correlation was not found for the other species (Spearman rank order correlation, p>0.05).

The mean ingested prey size between species was compared over four sampling sites separately (Table 12). At the MUD 1 site, *A. signatus* selected significantly larger copepods than the other species. At the SG habitat, *G. anjerensis* took smaller copepods than the other species. At the MUD 3 and MUD 5 site, no significant differences were observed among species. The stomachs of *F. reichei* and *A. signatus* contained larger amphipods than the stomachs of the other species at all sites (Kruskal-Wallis ANOVA, Table 12).

Comparisons of prey sizes among relevant sampling sites within species are also shown in Table 12. Larger copepods dominated in the stomachs of *A. signatus* from the MUD 1 and MUD 5 sites compared to animals from other sites. Copepods in the stomachs of *A. audax* were significantly larger at the MUD 5 site than at the other sites. No differences in mean size of copepods were observed for the other species. The mean sizes of ingested amphipods did not differ among sites for any of the studied species (Table 12).

Table 12: Mean length (mm) of copepods and amphipods in the stomachs of the predators according to species and sampling site: mean ± S.D., (range) and p-level of Kruskal-Wallis ANOVA. Significant values are in bold.

	COPEPODA					AMPHIPODA				
species	MUD 1	MUD 3	MUD 5	SG 1	p-level	MUD 1	MUD 3	MUD 5	SG 1	p-level
F. reichei	0.4 ± 0.1 (0.2 – 0.6)	0.5 ± 0.2 (0.1 - 1.5)		0.5 ± 0.2 (0.2 - 1.0)	0.16	3.1 ± 1.1 (0.8 - 5.0)	2.6 ± 1.0 (0.7 – 5.0)		2.6 ± 0.8 (1.0 - 4.0)	0.71
G. anjerensis	0.3 ± 0.1 (0.1 – 1.0)			0.4 ± 0.1 (0.1 - 1.2)	0.27	1.4 ± 0.5 (0.6 - 5.0)			1.2 ± 0.5 (0.7 - 3.0)	0.13
A. signatus	0.8 ± 0.4 (0.2 – 2.0)	0.5 ± 0.2 (0.2 - 1.2)	0.8 ± 0.2 (0.2 - 2.0)	0.5 ± 0.2 (0.2 - 2.0)	**0.001**	2.6 ± 2.4 (1.0 - 9.0)	2.6 ±1.1 (1.0 - 8.0)	2.4 ± 1.1 (1.0 - 5.0)	2.7 ± 1.3 (1.0 - 5.0)	0.60
A. audax	0.4 ± 0.1 (0.1 - 1.0)	0.5 ± 0.2 (0.2 - 1.3)	0.7 ± 0.2 (0.2 - 1.2)		**0.001**	2.2 ± 0.8 (0.8 - 5.0)	1.9 ± 0.7 (0.7 - 7.0)	1.5 ± 0.7 (0.8 - 4.0)		0.08
p-level	**0.001**	0.96	0.17	**0.05**		**0.002**	**0.04**	0.11	**0.001**	

Comparison of niche characteristics

In Figure 8, the spatial niche breadth is plotted against the trophic niche breadth for all species. Three main patterns can be distinguished. For *F. reichei* and *G. biocellatus*, spatial niche was far broader than food niche. For *G. anjerensis* and *A. audax*, the inverse pattern was observed. For *A. signatus*, both spatial and food niches were broad. A comparison of spatial and feeding niche overlap values for all species pairs is given in Figure 9. Most species pairs were clearly separated through either the food or the spatial dimension. Two species pairs had both high food and spatial overlap: *A. signatus* - *A. audax* and *F. reichei* - *A. signatus*.

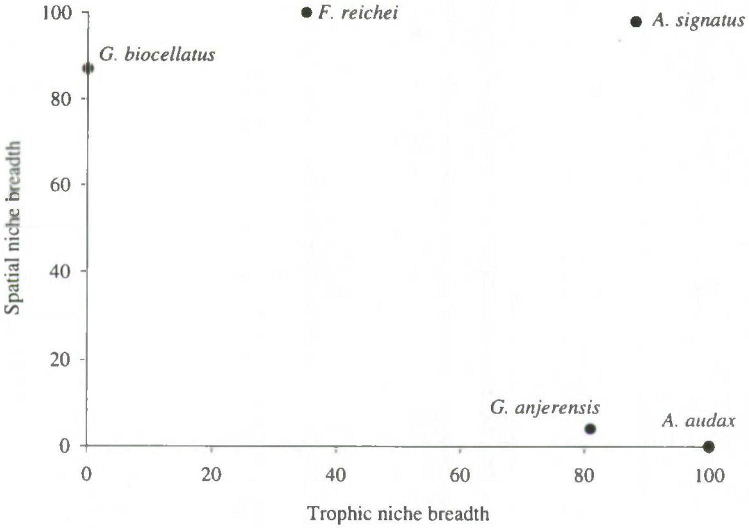

Figure 7: Comparison of adjusted trophic and spatial niche breadth for five goby species in Gazi Bay.

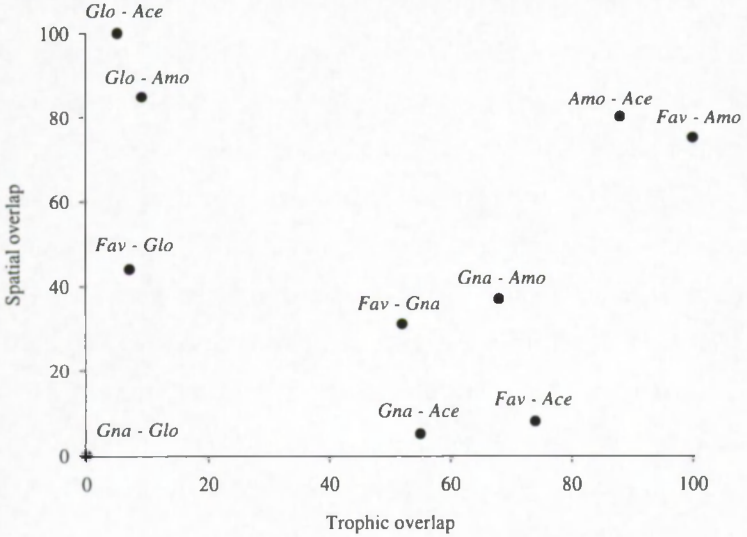

Figure 8: Comparison of trophic and spatial niche overlap between species-pairs. Abbreviations: *Fav = F. reichei, Gna = G. anjerensis, Glo = G. biocellatus, Amo = A. signatus, Ace = A. audax.*

DISCUSSION

The spatial niche

For each species, substrate preferences were observed. It has been suggested that differences in habitat preference of goby species are primarily a consequence of various predator-avoidance strategies (Tallmark and Evans 1986, Wilkins and Myers 1992). Behaviour patterns like burrowing in the sand, schooling, reduced activity or changing colour to achieve maximal camouflage have been observed in gobiids and are considered to be adaptations to reduce vulnerability to predation in open habitats (Tallmark and Evans 1986, Magnhagen 1988, Magnhagen and Forsgren 1991, Gill and Potter 1993). Tallmark and Evans (1986) have shown that gobies residing on less preferred substrate are subject to higher predation pressure than gobies that were free to choose their substrate. Gill and Potter (1993) observed that the typical burrowing behaviour in sand-dwelling gobies could cause gill clogging and even death when transferred to aquaria containing muddy substrate. Thus, morphological and physiological adaptations to substrate can be important in habitat choice. The observed habitat distribution of the species in our study can be partly related to species-specific camouflage properties. *F. reichei* has a light skin pigmentation and attained the highest densities at the sandy sites, while *G. biocellatus*, *A. signatus* and *A. audax* have a dark skin pigmentation and were most abundant at the muddy sites. These differential distribution patterns can be the result of either differential survival, species-specific recruitment or post-settlement preferences between sites (Greenfield and Johnson 1990). However, habitat choice can also be influenced by intra- and/or interspecific interactions. No disjunct ontogenetic patterns in distribution were apparent for the goby species in our study area. However, one sampling site harboured mostly juveniles of especially the small-sized species, while the adults of the larger species dominated another sampling site. This partial size segregation may be explained as a result of social interactions (Kneib 1987, Wiederholm 1987, Wissinger 1992, Wilkins and Myers 1995), including cannibalism and within-guild predation of *G. biocellatus*.

The feeding niche

With the exception of *G. biocellatus,* which appeared to be a non-selective piscivore, the observed goby species had a very similar diet composition, feeding on a wide range of benthic invertebrates. Whereas the heterogeneity of food items in the diet of *G. anjerensis* was largely due to intra-individual variability, most of the variation in *F. reichei*, *A. signatus*, and *A. audax* was attributed to differences among individuals. Copepod and amphipod prey size distributions were highly overlapping between species. There were minor differences in diet composition among sampling sites, but no consistent differences among species were found. Habitat variability can affect predator behaviour as well as prey availability, resulting in habitat-specific fouraging strategies (Ehlinger 1989). Many benthic gobiids have been described to have a flexible feeding strategy (Hamerlynck *et al.* 1993, Swenson and McCray 1996), and this feature has been proposed to contribute to the success of this family (Miller 1979, Antholz *et al.* 1991).

The examined species fed both during the day and at night. One exception was *G. anjerensis*, which is a diurnal feeder (see also Chapter 4). Qualitative differences were most obvious in *G. biocellatus.* This species fed only on fish during the day, whereas it consumed a higher fraction of more slow-moving prey items such as amphipods and mysids at night. This observation can be explained as the result of an altered feeding strategy in the absence of light.

Ontogenetic changes in diet are common in many fishes, including gobies (Grossman 1980, Aarnio and Bonsdorff 1993). They function as adaptations for maximising energy intake, which, through a concomitant increase in growth rate, typically decrease vulnerability to predation and increase reproductive output (Werner and Gilliam 1984). Fish assemblages are often strongly size-structured, so that a variety of interactions may potentially occur between different life stages of species (Ross 1986). Our results, however, did not show ontogenetic differences in feeding, even though we did sample the whole size range of the examined goby species (except the larval pelagic stage), as the observed maximal length corresponds with the maximal length of the respective species given in literature (Hoese 1986). Probably, the small size difference between juveniles and adults of the examined goby species does not necessitate ontogenetic feeding changes.

The high interindividual variation in the diet of some species, the site-related diet differences and the altered feeding during the night were all indicative of an opportunistic feeding strategy.

Comparison of niche characteristics

When comparing niche breadth of the goby species along the spatial dimension, we could distinguish *F. reichei*, *G. biocellatus* and *A. signatus* as generalists, and *G. anjerensis* and *A. audax* as specialists. Along the trophic dimension, *G. anjerensis*, *A. signatus* and *A. audax* was found to be generalists and *G. biocellatus* a specialist. So only *A. signatus* showed no complementarity in relative niche specialisation along the two dimensions. Niche complementarity has often been interpreted as a strategy to achieve niche segregation between species. It is hereby predicted that species, which are not segregated along one niche dimension, tend to be segregated along another dimension. For most species pairs, we observed a complementarity between spatial and trophic overlap indices. Only two species pairs (*A. signatus* - *A. audax* and *F. reichei* - *A. signatus*) overlapped equally high along both dimensions.

For all combinations of *F. reichei*, *G. anjerensis*, *A. signatus* and *A. audax*, trophic overlap was higher than spatial overlap. This is in contrast with the findings of Ross (1986), who reviewed resource partitioning in fish assemblages and found that the trophic dimension is the most important dimension for segregating species. It should, however, be noted that prey items could only be identified to higher taxonomic levels, due to the digestion process and the lack of taxonomic knowledge on available prey species. This might have caused an underestimation of the importance of trophic niche segregation in our study, as the diet composition of the goby species might have differed on a lower, not detected taxonomic prey level.

Competition

The mere observation of the degree of niche overlap does not allow one to conclude on the importance or intensity of competition (Abrams 1980, Connell 1980, Holbrook and Schmitt 1989). A high niche overlap might be an indication of strong ongoing competition, with species not being able to develop resource partitioning due to evolutionary, developmental constraints or ecological needs (Tokeshi 1999), but it can also be interpreted as a sign of the insignificance of competition. Indeed, niche overlap does not need to result in competition unless resources are in short supply. Therefore, the ratio of demand to supply is of vital concern in the relationship between ecological overlap and competition (Pianka 1994). Several authors have provided evidence that gobies have no significant impact on the benthic macro- and meiofauna they feed on (Berge and Hesthagen 1981, Evans 1983, Thorman and Wiederholm 1986, Gee 1987, Aarnio *et al.* 1991). Others report on a considerable predation impact of gobies on their food resources (Pihl 1985). These opposing results might be related to methodological aspects such as the use of different conversion coefficients by various authors (Hamerlynck and Cattrysse 1994). In general, small Gobiidae are considered to be controlled by predation rather than being food-limited (Miller 1979).

The resource availability of the study area was not quantified, but one expects high productivity levels of benthic invertebrates, given that tropical mangrove creeks are considered among the most productive detritus-based ecosystems in the world (Odum and Heald 1975, Por and Dor 1984, Parrish 1989).

Although there was considerable overlap in overall habitat use between the species examined, it should be mentioned that we did not include microhabitat utilisation in our analysis. As MacNally (1983) pointed out, territoriality can lead to spatial segregation without resource partitioning, resulting in a mosaic or patchy distribution. This might in part explain the differences we observed between the Morisita niche overlap index and the Jaccard similarity coefficient: while several species pairs showed a strong overlap in general habitat use, the actual co-occurrence in the same nettings was only high for three species. Gobies are often territorial (Miller 1979, Wilkins and Myers 1993, 1995). Within the context of competition, it might be meaningful to distinguish between exploitative competition which deals with the depletion of resources and interference competition which is determined by direct behavioural interaction between organisms capturing space (Mac Nally 1983). At least in some cases, segregation maintained by interspecific territoriality has been shown to be an important mechanism regulating guild structure of epibenthic predators (Evans and Tallmark 1985, Faria *et al.* 1998). Although exploitative competition is less likely to occur among the goby guild in Gazi Bay, interference competition may be important in governing the use of the habitat at a local scale.

Predation

In several studies on temperate gobies, predation has been shown to reduce competition among goby species (Evans and Tallmark 1985, Magnhagen 1988). Although the predation pressure excerted on the Gobiidae in the study area has not been quantified so far, there is some indirect evidence that predation might be important. The studies of De Troch *et al.* (1998) and Wakwabi (1999) indicated a high proportion of piscivores in the fish community of Gazi Bay. In addition, the clear water conditions of the bay may favour visual predation. In general, the intensity of predation has been assumed to be high in the tropics, and this has been proposed to contribute to the higher species diversity (Thiery 1982). If predation pressure on the gobiid species in our study area is important, this might strongly reduce competitive interactions, and may then relax selection for niche differences.

Abiotic conditions

Adverse abiotic conditions may keep populations below the abundance level at which competition is likely to occur (Thorman and Wiederholm 1983, 1986). The overriding local climatic features in the study area are the reversing monsoons (Richmond 1997). These winds, together with the changes in the major coastal and oceanic currents in the region, create a marked seasonality in rainfall, temperature and productivity (Nzioka 1979, McClanahan 1988, Kitheka *et al.* 1996, Ohowa *et al.* 1997, Osore *et al.* 1997). Tropical coastal fishes living under seasonal conditions are acknowledged to be generalists, as they have to cope with a changing environment. In contrast, aseasonal tropical environments are characterised by specialists (Lowe-McConnell 1991). The predominant type of selection in seasonal environments seems to be for rapid population increase, similar as in pioneer communities (Southwood 1996). Gazi Bay has been described as an important nursery and feeding ground for juveniles of commercially important coastal species. Most of these species were reported as generalist and opportunistic feeders (Wakwabi 1999). This is in agreement with our results, as four out of five examined goby species had a generalised feeding strategy with clear opportunistic tendencies.

Some aspects of life history

The Hutchinsonian niche concept involves more than the three most commonly studied dimensions (food, habitat and time). Species may also segregate along other dimensions. One of these is related to life-history patterns (Tokeshi 1999). No specific information on the life histories of the examined goby species is available. Nevertheless, we can invoke some differences from the observed length distribution patterns and maturity stages. Regarding the length frequency distributions of the species, two patterns are apparent. *F. reichei* and *G. anjerensis* consisted of two cohorts, whereby the smallest cohort was far the most abundant, and both species were characterised by a limited maximal length. For *G. biocellatus* and *A. signatus*, two cohorts of approximately equal size were distinguished, and these two species generally grew bigger. For *A. audax*, the pattern was less clear, probably due to the lower number of observed specimens. The maximal observed SL corresponds well with the maximal recorded length in literature (Hoese 1986), which indicates that the species spend their entire lifespan within the mangrove creek, and can thus be considered as permanent residents.

Conclusion

Although at first sight, the niches of the goby species were highly overlapping, some resource partitioning patterns were apparent. While *G. biocellatus* was clearly different along the trophic dimension, segregation of the other species was more important along the spatial dimension. The observed patterns of habitat segregation might be related to species-specific camouflage properties and/or social interactions. Exploitative competition was not likely to be important among the goby guild, at least not during the observation period. Our observations are largely in agreement with both the predation and abiotic disturbance hypothesis. Both hypotheses remain potentially important in structuring the goby assemblage of Gazi Bay.

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CHAPTER 7

GENERAL DISCUSSION

The present study has aimed to investigate the patterns in the coexistence of tropical gobies in a mangrove creek. In this chapter, we will review the major conclusions of our work and discuss our observations in the framework of plausible mechanisms structuring the assemblage.

The diversity of the Gobiidae in the study area was high. We identified 24 species belonging to 18 genera. This diversity might even be underestimated, as our sampling effort mainly focussed on the subtidal habitats in the downstream part of the western creek of the bay, and other sites in the bay (eastern creek, central part of the bay, river mouths, coral reef) were only sampled occasionally. Also, no samples were taken within the mangrove forest, however, several studies in mangrove ecosystems have reported on goby species either residing in the forest or entering the forest with tidal currents (Thayer *et al.* 1987, Vance *et al.* 1996, Horn *et al.* 1999). The diversity of a local community is in part determined by the regional species pool (Cornell and Lawton 1992, Southwood 1996, Caley and Schluter 1997). Gazi Bay is an open coastal ecosystem that is closely linked with the western Indian Ocean. This region is acknowledged as one of the most species-rich biogeographical zones and harbours a diverse fish fauna (Smith and Heemstra 1986, Blaber 1997). The gobioid fauna of this region is very rich and is composed primarily of widespread tropical Indo-west Pacific genera, with at least 88 genera having been recognized so far (Hoese and Winterbottom 1979).

Although our survey was limited to the downstream part of one mangrove creek, we found a comparable species richness and diversity in the fish community as was obtained for the whole bay in previous surveys (Van der Velde *et al.* 1995, De Troch *et al.* 1996, Kimani *et al.* 1996, Wakwabi 1999). Mangrove ecosystems are often characterised by diverse habitats, including open water channels, seagrass beds, small creeks and inlets, intertidal mudflats, sandy mud beaches and mangrove prop root habitats. Several studies have shown that this habitat heterogeneity contributes significantly to the fish community diversity (Blaber *et al.* 1989, Pinto and Punchihewa 1996, Vance *et al.* 1996, Rönnbäck *et al.* 1999). This is also shown in our study. All previous surveys underestimated the local diversity in the western creek, as they neglected the high beta diversity in microhabitats. Habitat heterogeneity indeed appeared important for the goby diversity, as each habitat type had typical goby species.

The Gobiidae dominated the fish assemblage of the unvegetated areas in Gazi Bay, both in terms of density and diversity. Therefore, the commonly accepted hypothesis that densities of small fish are positively correlated with vegetation cover does not hold for the gobies in our study area. Given the supposedly high predation pressure on the gobies, we expected the trade-off between food gathering and predator avoidance to be important in the species composition and distribution of gobies. Some indirect observations were in agreement with this hypothesis. When analysing the distribution patterns of the five dominant goby species over nine sampling sites differing in substrate type, we observed that body colouration matched with preferred substrate type. This might indicate a predator avoidance strategy, as has been described for several temperate goby species (Tallmark and Evans 1986, Magnhagen and Forsgren 1991, Gill and Potter 1993). Furthermore, we observed a partial size-related habitat segregation of *Glossogobius biocellatus* and other gobiid species. *G. biocellatus* is a piscivore, feeding on a variety of juvenile fish, including conspecifics and other goby species, and we hypothesise that the habitat segregation can be attributed to this intra-"guild" predation and other social hierarchy interactions. Further experimental demonstration is needed to validate this hypothesis.

In a comparative study of temporal and trophic niches of two gobiid species, *G. anjerensis* and *A. semipunctatus* in the seagrass beds of the mangrove creek, we observed a differential resource use. Ou data suggest that the species employ a different feeding strategy, which might, at least in part, explain the observed day/night segregation. We suggest that autecological differences are important in explaining the resource partitioning of *G. anjerensis* and *A. semipunctatus*. Several morphological differences, such as different body shapes and coloration patterns related to different habitat use, suggest that the two species occupy a different fundamental niche. The hypothesis of differing food requirements can in part explain differing temporal resource use.

No tidally related pattern in occurrence and feeding was observed for *G. anjerensis* and *A. semipunctatus*, suggesting that these species do not enter the mangrove forest and feeding takes place within the subtidal creek. It was suggested that the high and appropriate food availability in the creek makes energy demanding intertidal movements irrelevant. However, so far, we should not extrapolate this observation too far. Samples should also be taken inside the mangrove forest, which requires a completely different sampling strategy.

In a comparative study of the temporal, food and spatial niche axes of the five dominant gobiid species in Gazi Bay, no support for a clearcut niche partitioning was found. Spatial distribution patterns were overlapping, although some differential habitat preferences were apparent. With the exception of *Glossogobius biocellatus,* a piscivore, all species had a similar diet composition, feeding on benthic crustaceans. The diet of *Gnatholepis anjerensis* differed from the other species in its high intra-individual diet diversity. The diets of *Favonigobius reichei*, *Amoya signatus* and *Acentrogobius audax* where not distinguishable, and differences between sites were as important as interspecies differences. The high inter-individual variation in diet, the site-related diet differences and the altered feeding during the night in these species were all indicative of a largely opportunistic and flexible feeding strategy.

Our observations can be interpreted in two alternative ways with respect to the importance of competition in structuring the assemblage. High niche overlap can indicate high levels of competition, whereby species are not able to partition resources. However, the observation of high niche overlap may also indicate low competition, if resources are not limited or carrying capacities are not reached (Tokeshi 1999). We have some indirect evidence of low competition in the study area. Firstly, the observed gobies are probably not food limited, given that (1) goby species in temperate regions are not able to impact their prey populations (Evans 1983, Thorman and Wiederholm 1986, Gee 1987, Aarnio *et al.* 1991) and (2) the benthic productivity of tropical mangrove creeks is high (Por and Dor 1984, Alongi 1989, Schrijvers *et al.* 1995). Gazi bay has been described as an important feeding ground for a high number of residents and visiting fish species. More than half of these species are generalist benthic carnivores, with wide prey spectra and overlapping diets

(Wakwabi 1999). This has also been observed in other tropical coastal areas (Brewer *et al.* 1995).

Still, it has been suggested that competition is often strongly episodic rather than constant. Competition is then only important during occasional bottlenecks in resource abundance and virtually undetectable when resources are abundant. In this view, competition is an occasional structuring force in communities rather than a pervasive influence on community patterns (Morin 1999). Therefore, seasonal fluctuations in niche overlap measures are essential to detect the importance of competition. Wakwabi (1999) reported on seasonal patterns in prey selection for fishes in Gazi Bay. He found that peaks in primary and secondary production at the end of the rainy season (August) coincided for some fish species with higher stomach fullness and selection of larger prey items. General diet composition did, however, not differ significantly between seasons. If our sampling period (July-September) coincides with high food availability, the observed high food niche overlap among gobies might indeed be interpreted as relaxed exploitative competition. Further research on seasonal patterns in food choice and food availability of the gobies is essential to weigh the importance of exploitative competition. Ultimate demonstration of exploitative competition strength will need carefully designed experimental field manipulations.

So far, we can not exclude that other mechanisms reduce the effect of competition by keeping population densities below carrying capacities. Both the predation and abiotic disturbance hypothesis remain potentially important in structuring the observed goby assemblage, and in explaining the high diversity of gobies inhabiting the mangrove creek.

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SUMMARY

In this thesis, we focussed on the coexistence of gobies (Teleostei, Gobiidae) in a tropical mangrove ecosystem (Gazi Bay, Kenya). We aimed at describing the species richness and analysing the patterns of resource utilisation and niche characteristics, in an effort to get insight in the processes that might be important in regulating this assemblage.

Our survey on the fish species composition in the mangrove creek revealed 95 species belonging to 42 families. The Gobiidae was by far the most species-rich family (24 goby species) and contributed 40% of all individuals caught. This high diversity could be linked to the high diversity of the regional species pool (Indian Ocean). However, also the habitat heterogeneity in the mangrove creek was shown to be important. Comparison with previous surveys on the fish community of Gazi Bay revealed comparable species richness and diversity at a microhabitat level.

We further explored the importance of niche differentiation in the coexistence of *Gnatholepis anjerensis* and *Asterropteryx semipunctatus* in the subtidal seagrasses, with emphasis on the temporal aspect. No tidally related pattern in occurrence and feeding was observed. However, we did observe differences in spatial and day/night resource use. Different feeding strategy and autecological aspects were suggested to explain these observations.

A field study at nine sampling sites was conducted to describe spatial, trophic and time niche for the five most abundant goby species. The niche of two species was different along the trophic dimension. However, no support for clear-cut niche partitioning among the other three species was found. If we presume a high food availability, we might conclude that niche differentiation was not essential for the coexistence of these species within the covered period. Further research on seasonal patterns in food choice and food availability is essential to weight the importance of exploitative competition. Both the predation and abiotic disturbance hypothesis remain potentially important in structuring the assemblage and in explaining the high diversity and success of the gobies inhabiting the mangrove creek.

SAMENVATTING

In deze thesis werd de coëxistentie van grondels (Teleostei, Gobiidae) in een tropisch mangrove ecosysteem (Gazi Bay, Kenya) onderzocht. Een analyse van de soortenrijkdom en de ecologische niche van de grondelsoorten had tot doel een inzicht te verwerven in de regulerende factoren van deze gemeenschap.

Onderzoek naar de soortensamenstelling van de benthische visgemeenschap in de mangrovekreek leverde 95 soorten uit 42 families op. De familie van de Gobiidae was veruit het meest soortenrijk (24 soorten) en vertegenwoordigde 40 % van de totale abundantie. Deze hoge diversiteit kon deels gelinkt worden aan de hoge soortenrijkdom van de regionale soortenverzameling (Indische Oceaan). Ook de habitat heterogeniteit in de mangrovekreek bleek belangrijk. Vergelijking met vorige studies op de visgemeenschap in Gazi Bay toonde aan dat dezelfde soortenrijkdom en diversiteit teruggevonden werd op microhabitat niveau.

De niche differentiatie tussen *Gnatholepis anjerensis* en *Asterropteryx semipunctatus* werd onderzocht in de subtidale zeegrassen, met speciale aandacht voor de tijdsdimensie. Er werd geen effect van getijden op abundantie en voeding vastgesteld. Er waren wel verschillen in dag/nacht ritme en habitatgebruik. We suggereren dat een verschillende voedingsstrategie en autecologische verschillen een mogelijke verklaring bieden voor deze differentiatie.

De ecologische niche van de vijf meest abundante grondelsoorten werd verder in detail onderzocht. Hoewel er voor twee soorten verschillen werden gevonden volgens de trofische dimensie, werd er voor de drie andere soorten geen duidelijke niche differentiatie vastgesteld. De hoge interindividuele variatie in dieet, de lokaliteit-gerelateerde dieetverschillen en een gewijzigde voeding 's nachts waren een indicatie voor een grotendeels opportunistische en flexibele voedingsstrategie van de grondels. Dit wijst erop dat mogelijks ook andere mechanismen dan de besproken aspecten van niche differentiatie belangrijk zijn in de regulatie van deze gemeenschap. Verder onderzoek naar seizoenale patronen in voedselkeuze en voedselaanbod is essentieel om exploitatieve competitie als regulerende factor te evalueren. Zowel de predatie als abiotische verstoringshypothese blijven potentieel belangrijk in het verklaren van de diversiteit en het succes van de grondels in dit mangrove ecosysteem.