Environmental Biology of Fishes **61:** 213–229, 2001.

The impact of artisanal fishery on a tropical intertidal benthic fish community

Willem F. de Boer[a,b], Annemieke M.P. van Schie[b], Domingos F. Jocene[b], Alzira B.P. Mabote[b] & Almeida Guissamulo[b,c]
[a]*Office for International Cooperation, University of Groningen, P.O. Box 72, 9700 AB Groningen, The Netherlands (e-mail: fred_pat@hotmail.com)*
[b]*Departamento de Ciências Biológicas, Universidade Eduardo Mondlane, C.P. 257, Maputo, Mozambique*
[c]*Museu de História Natural, C.P. 257, Maputo, Mozambique*

Received 28 April 2000 Accepted 4 December 2000

Key words: overfishing, consumption, Q/B ratio, habitat preferences, biomass, abundance

Synopsis

We examined the benthic fishes and artisanal fishery in the intertidal flats of Inhaca Island, Mozambique. Results of a questionnaire indicated that catches had decreased, and that piscivorous fish have disappeared. Results of a catch sampling study indicated that current catch rates are low, <2 kg person^{-1} fishing trip^{-1}. Use of fishing gear was significantly related to season, diel and lunar tidal phase, and habitat. Forty-eight fish species were observed in the catches with eight species comprising 80% of the catch of 1814 specimens. The annual catch was estimated at 26.2 t for the whole bay. Highest fishing pressure was observed in the central section of the bay. A demersal fish survey was carried out with a 2-m beam trawl to sample the fish community. Two different areas were sampled, one area with a low, and one with a high fishing pressure. A total of 19 889 fishes were caught comprising 93 species. Gobies dominated the catches and accounted for 56% of all specimens. Fishes were small with a mean standard length of 29 mm. The Saco area exhibited the highest catch rates and biomass (maximum of 1040 fish 1000 m^{-2} and 1490 g 1000 m^{-2}), and the highest species richness and evenness values. Catch composition was different between the two sampling areas, and was strongly affected by season, but less by habitat. Total fish biomass was estimated at 5.6 t for the whole area. Stomach content varied with habitat, and season, and was dominated by benthic invertebrates. The largest estimates of consumption were obtained in the tidal channel and the *Zostera* beds. Mean consumption of benthic organisms was 1.3 g AFDW m^{-2} yr^{-1}. The area seemed to be overfished. The heavily fished areas exhibited lower catch rates, lower proportion of piscivorous fish, increased proportion of small fish, and a decrease in species diversity.

Introduction

Fishing can contribute considerably to peoples' diet (Andersson & Ngazi 1995, Dayaratne et al. 1995b, McClanahan et al. 1997), and an increase in fishing is generally seen as a way to improve rural conditions (Kent & Josupeit 1989, Kent 1998). Inhaca Island, Mozambique, is no exception to this, in that an increase in fishing pressure is regarded as essential for the Island's development.[1] Fishes are an important component of intertidal ecosystems, through their interactions with other organisms (Kerekes 1994, Christensen 1996, Dahl & Greenberg 1996, Johnson & Kitchell 1996, Proulx et al. 1996, Schlacher & Wooldridge 1996, Beets 1997, Flecker 1997, Irlandi & Crawford 1997, Pierce & Hinrichs 1997).

Fishing can affect the community structure of fishes, and alter abundance and species composition (Polunin & Roberts 1993, Roberts 1995, Christensen 1996, Jennings et al. 1996a,b) and, as such, contribute to an altering predation pressure by the fishes on the benthic community, which could lead to a different community state.

However, the fishing pressure on Inhaca's tidal flats may already be too high, as fishermen have complained

[1] Anon. 1990. Plano de desenvolvimento integrado da Ilha da Inhaca. Commissão Nacional do Plano Moçambique, Maputo. 154 pp.

about diminishing catches. Have the local fishing techniques, such as line and seine net fishing, attained those levels at which the composition and the abundance of the fish fauna has been affected? The aim of this paper is to describe the fish community of Inhaca's intertidal flats, and study the impact of local fisheries on this community. In this study several predictions indicating overfishing were tested: (1) The catches are relatively large compared to the available biomass (King 1995). (2) Overfishing reduces species richness, and can increases dominance (Roberts 1995), hence lower values for species richness and higher values for dominance are expected in the areas with the highest fishing pressure. (3) Piscivorous fish will be less abundant in areas of higher exploitation (Jennings & Polunin 1995, Letourneur 1996). (4) The relative absence of piscivorous fishes will reduce the predation rate, associated with a greater abundance of small fish species (Christensen 1996, Polunin & Jennings 1998). To gain a complete picture of the human impact on the ichthyofauna, the study comprised several components: a questionnaire in which older fishermen were asked to describe historic trends in catches, a catch sampling study of the local catches per activity, a beam-trawl survey, and a fish stomach content analysis.

Materials and methods

Study area

The general ecology of Inhaca Island (latitude 26°07′ S, longitude 32°56′ E) is well described by Kalk (1995). Total rainfall is 880 mm and mean air temperature is 23°C. There is a hot rainy summer (November–April), and a colder and drier winter (March–October). Water temperatures on the tidal flats range from 18°C to 32°C.

The study was conducted in two areas, both lying in the southern bay of Inhaca. The bay, with a total area of 15.4 km^2, is fringed by mangroves (Figure 1). Both areas were subdivided into five different habitat types (de Boer 2000, de Boer et al. 2000). The mudflats are the lower lying areas that are totally inundated during low water neap tide (LWNT). The sandbanks are higher lying areas and contain coarser sand. Some parts of these sandbanks are even exposed during high water neap tide (HWNT). The sandflats are intermediate in depth, consist of finer sands than the sandbanks and cover extensive areas. Both study areas are bordered by tidal channels, the beds of these channels are only exposed during LWNT. The bed of the channel in the Saco is covered by old coral debris and rocks, with patches of *Halodule wrightii* seagrasses. In the Banco area, the channel is mainly composed of coarse sand and small *Cymodocea serrulata* seagrass beds. Other habitat types are mangrove fringes in the Saco, and an extensive *Zostera capensis* seagrass bed in the Banco. The latter two habitats are relatively higher in altitude.

Questionnaire

Older fishermen (N = 39, mean age = 49 years) were asked to estimate their average total daily catch over the last 12 months, and about 30 years ago. They were also asked to name the most important species caught today and in the past, and to provide an explanation for the change in catch size or species composition.

Catch sampling

In total, 80 surveys were carried out by boat to count the number of people engaged in different fishing activities in the southern bay. These surveys were carried out in summer and winter (N = 80), evenly divided between neap and spring tides, and over the four different diel phases of the tide: low, flood, high and ebb. Fishing activities were recorded with reference to fishing gear, number of people involved, location, and main habitat type (tidal channels, bar mud- or sandflats, and seagrass beds). Several gear types were distinguished; these included line fishing, fishing from the shore with beach-seine nets, fishing with seine-nets from boats, floating gill nets, cone-shaped baited fish traps (±1.5 m) made of wooden sticks, and spearfishing with traditional spears. At the end of each survey, catches of fishermen were weighted and counted distinguishing between fish species.

The observed frequencies of the different fishing techniques were compared with expected values based on an equal distribution of the expected values over season (summer or winter), tide (neap or spring), tidal phase (high, low, outgoing, or incoming tide), or based on the area occupied by the habitat types (17% for the tidal channels, 50% for mud- and sandflats, 33% for seagrass beds). Differences between observed and expected values were tested with a χ^2-test. A Kruskal–Wallis test was used to compare total catches.

Trawl survey

A demersal survey was carried out in two study areas, the Saco and the Banco (Figure 1). Fishing was

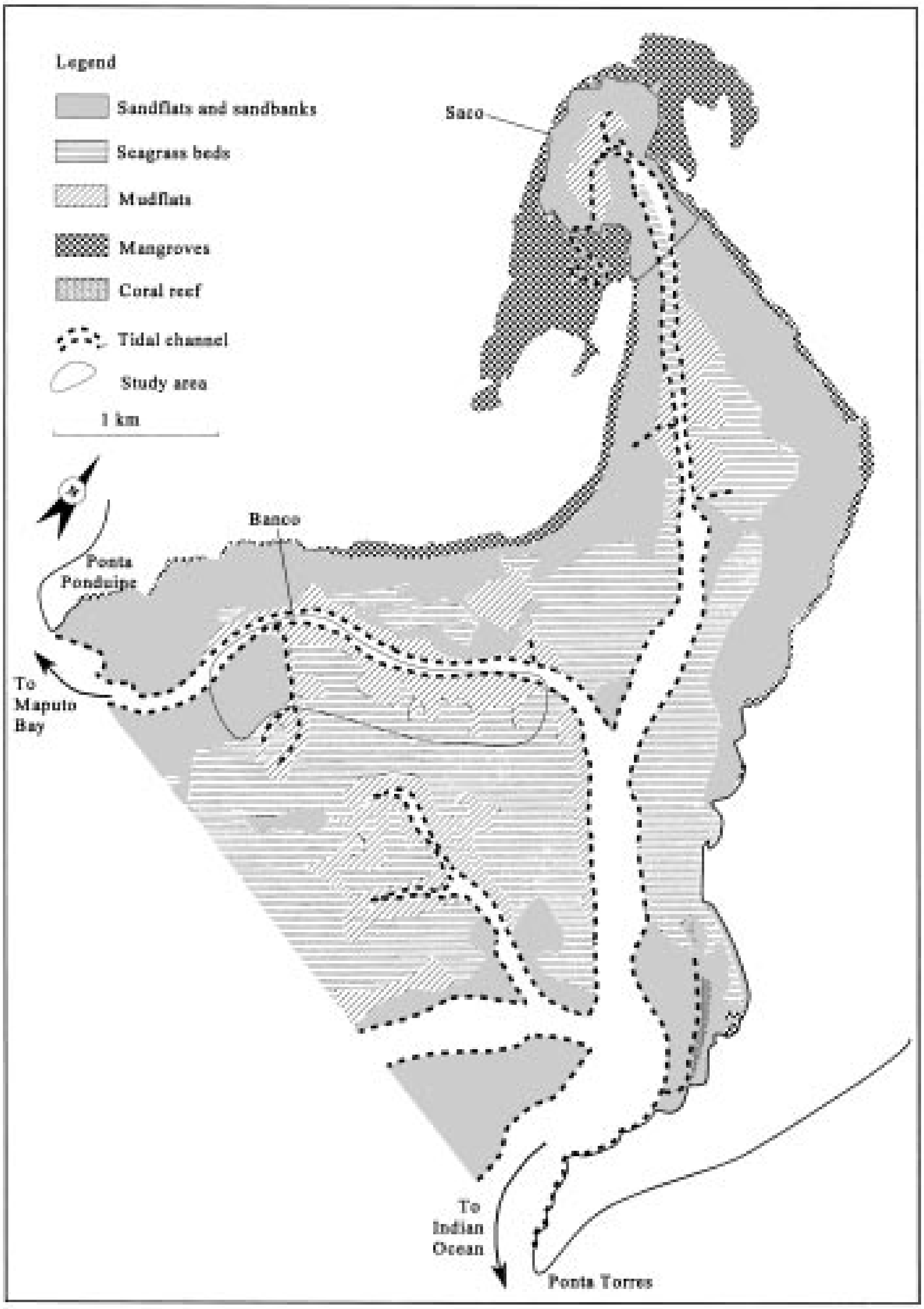

Figure 1. The location of the two study areas, the Saco and the Banco, in the bay of Inhaca Island, with the main habitats.

conducted with a 2-m beam trawl with a mesh size of 5 × 5 mm and a tickler chain in front of the net (Kuipers 1975, Kuipers et al. 1992). The net was towed by a 6 m vessel with a 25 hp outboard motor. Haul duration was standardised to five minutes in which an average distance of 150 m was covered (corresponding to an average velocity of 0.5 m s^{-1}). Haul length was measured by an electronic counter fitted to a wheel next to the frame. Trawling was made from December 1996 to March 1997 (summer) and from June to August 1997 (winter). We conducted 180 day and 100 night trawls, equally divided over tide (neap or spring), over season (summer or winter) and over habitat (5 habitat types per area). All habitats within one area were sampled within a period of one hour before and one hour after high tide. Day catches were sorted the same day, night catches were stored in a 10% formalin and seawater solution and sorted the next day. Fish were identified according to Smith and Heemstra (1991), measured (standard length in mm), and weighed (fresh weight in 0.1 g). A reference collection was checked by taxonomists. Results are presented following the taxonomic order of Smith and Heemstra (1991).

Day and night catches were converted into catches per 1000 m^2, by multiplying haul length with net width, without correcting for net efficiency. Total fish biomass in the bay was estimated by multiplying the mean biomass values per habitat with habitat area. Species richness was compared between areas by using richness, dominance and evenness indices (Magurran 1988), available in the Primer software package (Clarke & Warwick 1994). Differences in catch rates or richness indices were tested with non-parametric Mann-Whitney U, or Kruskal–Wallis tests (Zar 1984). Sample ordination was carried out by a non-metric Multi-Dimensional Scaling (MDS) on Bray-Curtis similarity coefficients calculated from 4th root transformed abundance data (Clarke & Warwick 1994).

Stomach content analysis

The stomach content of 932 fishes was determined. Sample number was evenly distributed over season, habitat, and fish species. After capture, fishes were directly separated from the main catch and preserved in 10% formalin. Fishes were weighed, and the stomach contents identified with a dissection microscope. The percentage of volumetric abundance of different food categories found in a stomach, was obtained by flattening food items in a petri-dish and counting the area in mm^2 covered by each different food item (Cyrus et al. 1993, Weerts et al. 1997).

Consumption was calculated by using consumption/biomass (Q/B) ratios derived from the empirical model of Pauly et al.,[2] based on the mean habitat temperature ($Tk = 1000\ (T^{\circ}C + 273.1)^{-1}$) and the maximum weight (W_{∞}) of the species:

$$Q/B = 10^{6.37}(0.0313^{Tk})(W_{\infty}^{-0.168}).$$

Q/B ratios were calculated for each species by using maximum weights taken from the catch data and mean water temperature for each fishing season. The resulting Q/B_i for fish species i was then multiplied by the fish biomass (M_{ij}) of species i in each habitat j, after which total consumption in fresh weight (C_{jk}, g FW 1000 m^{-2}) was obtained by adding the consumption of all species in a particular habitat and season (*k*)

$$C_{jk} = \sum_{i=1}^{i=N}(Q_i/B_i) \cdot M_{ij}.$$

By multiplying total consumption with habitat- and season-specific fractions of different diet categories, the total consumption per diet category could be calculated. Total annual consumption was obtained by adding the two seasons' totals.

Results

Questionnaire

The average daily catch was 11 kg (±8 sd) presently, versus 29 kg (±23) in the past. Hence, most fishermen (82%) believed that the catch has reduced (Sign test, $p < 0.0001$). The reason for this decrease was attributed to too many fishermen in the bay (64%), climate (38%), lack of adequate fishing gear (18%), or other factors (10%). More species (36) were mentioned as present in historic catches, compared to the number in present catches (27). The species which were named as more abundant in the past were piscivorous or omnivorous fishes such as kingfishes (*Carangoides* spp.), rays (Dasyatidae, Myliobatidae), grunters (*Pomadasys* spp.), snapper (*Lujanus* spp.), queenfish (*Scomberoides* spp.), sea breams (*Rhabdosargus* spp.), and piscivorous squid and cuttlefish.

Catch and sampling effort

Line fishing was the most commonly used fishing technique (Table 1), followed by gill-nets and fish traps. Line-fishing and seine-net fishing were more common in summer, while fish traps were observed more in winter. Gill-nets were used irrespective of season. Line

[2] Pauly, D., V. Christensen & V. Sambilay. 1990. Some features of fish food consumption estimates used by ecosystem modellers. ICES Counc. Meet. 1990/G17: 8.

Table 1. The frequency of the different fishing activities and the number of trips over the seasons, the tides,the tidal phases, and the habitat types, toghether with the number of participants per fishing trip. Frequencies were tested against expected values based on equal distribution over the independent variables. Stastical paramaters (Chi-square, degrees of freedom, and p) are indicated. The last columnns give the estimated total annual catch (t) for the whole bay.

Gear type	Number of fishing trips												Mean number participants trip^{-1}	Total number of participants	Total catch t yr^{1}
	Total fishing trips	Season		Tide		Tidal phase				Habitat					
		Summer	Winter	Spring tide	Neap tide	High water	Low water	Outgoing water	Incoming water	Tidal channel	Mud- and sandflats	Seagrass beds			
Line fishing	289	246	43	187	102	11	205	39	34	40	158	91	1.0	289	5.1
Boat seine net	17	15	2	9	8	1	7	3	6	3	2	12	4.4	75	1.8
Floating gill nets	119	57	62	51	68	32	27	28	32	13	36	70	1.9	226	11.5
Beach seine net	56	43	13	25	31	1	20	8	27	6	16	34	3.0	168	3.9
Spear fishing	14	1	4	3	2	0	4	1	0	1	2	2	1.0	14	0.1
Fish traps	107	14	93	67	40	2	98	5	2	4	38	65	1.0	107	3.7
Total	602	376	217	342	251	47	361	84	101	67	252	274	12	879	26.2
Chi-square		200.741		21.69		202.009				115.229				350.594	
df		5		5		15				10				5	
p		0.0001		0.001		0.0001				0.0001				0.0001	

fishing was conducted during low water spring tides when the water level was lowest. Gill-nets were used regardless of tidal phase. Beach seine nets were applied during low or incoming waters, when the nets can be deployed easily on foot. Choice of fishing method was also significantly related to habitat. Seagrass beds were preferred by all fishing techniques, except for line fishing which was more common on mud- and sandflats. Spearfishing was observed more frequently at the margins of the tidal channels. Season, tidal phase, and habitat were significantly related to the choice of fishing gear (Table 1; all $\chi^2 > 21.000$, $p < 0.001$).

A total of 48 species was caught, representing 1814 specimens. Species composition of the catches differed among gear type (Table 2). Fishing with seine-nets yielded the most species, whilst spear fishing was only directed at one species, mud-burying eels (Ophichthidae). The most abundant species by number were *Liza macrolepis* (22%), Gerreidae (16%), *Crenidens crenidens* (12%), and *Sillago sihama* (11%). By catch weight the dominant species were *Liza macrolepis* (17.3), and Gerreidae (12%).

Mean catches per fishing trip varied from 0.9–5.9 kg, which, corrected for the number of fishermen, yielded 0.8–4.8 kg person^{-1} (Table 2). Summer catches were slightly larger than winter catches, except for beach seines. Catches were significantly different among gear type (Kruskal–Wallis $H = 14.902$, df = 3 and 57, $p < 0.002$). Total catch weight was largest for gill nets and smallest for line and spear fishing. No significant differences were detected between the catch person^{-1} among different gear types ($H = 7.39$, df = 3 and 57, $p = 0.06$).

The annual total catch was estimated at 26.2 t for the bay, of which 44% was taken by gill nets, 22% by boat or beach seine nets and 20% by line fishing (Table 2). Catch area^{-1} (in kg FW 1000 m^{-2} yr^{-1}) was lowest in the Saco and at the borders of the bay (Figure 2). Highest catches area^{-1} (maximum of 6000 kg FW 1000 m^{-2} yr^{-1}) were recorded from the central section of the bay, especially around the channels.

Trawl survey

The total trawled area was 65 612 m^2. Equal areas were sampled in summer (33 418 m^2) and winter (32 194 m^2); and during day spring tides (22 344 m^2), day neap tides (21 628 m^2), and at night (21 640 m^2). The mean water depth for all tows was 1.4 m (±0.4); mean salinity 33‰; and mean water temperature 25°C. A total of 19 889 fishes was identified, comprising 93 species (Table 3, 4). The majority of the species contributed <1% to the total. Only six species contributed more than 5% to the total: *Gerres acinaces* (9.1%), *Sillago sihama* (13.1%), *Favonigobius melanobranchus* (12.8%), *Favonigobius reichei* (20.0%), *Amoya signatus* (12.8%), and *Oxyurichthys ophthalmonema* (8.4%). The Gobiidae (from Gobiidae to *Youngeichthys nebulosus* in Table 3) clearly dominated the catches; 56% of all fishes captured belonged to this family. The mean length was therefore small, 29 mm, and 98% of the fishes were <100 mm. The ratio between the numbers caught during the day to the numbers caught at night, and the difference in seasonal occurrence and habitat differences for each species, are provided in Table 3.

Catches did not decrease over time as a result of the trawl survey (Spearman rank test, $p > 0.05$). Catch rate was not different between spring and neap tides, but night trawls yielded significantly larger catches than day trawls ($N = 3$ and 280, $H = 9.231$, $p < 0.01$). The mean catch was significantly larger in summer, and significantly larger in the Saco area ($U = 7492$, $p < 0.001$, and $U = 5751$, $p < 0.0001$, for season and area respectively), but differences in species richness, evenness and dominance were relatively small. When the 10 different habitats were compared, large differences were detected in catch rate and richness parameters (Kruskal-Wallis tests; $53 < H < 112$, $N = 10$ habitats and 280 trawls, $p < 0.0001$). The general pattern was that catch rates were highest in the mudflats (1040 fish 1000 m^{-2}) and the channel (620 fish 1000 m^{-2}) in the Saco, and the *Zostera* seagrass bed in the Banco (630 fish 1000 m^{-2}, Table 3). These habitats, and especially the tidal channel in the Saco, were also the ones with the highest species diversity (Table 4). Fishes were smaller in the mudflats. The tidal channel in the Saco had the highest fish biomass at 1490 g 1000 m^{-2}. The sandflats and sandbanks exhibited lower catch rates and lower species diversity. The species evenness was generally negative, and dominance was positively related to abundance. The channel in the Saco and the *Zostera* seagrass beds were exceptions, in that both had higher catches, high species diversity, but also high evenness and low dominance values. Total fish biomass in the bay was estimated to be 5.6 t, of which 55% was found associated with seagrass beds, 14% in the channel and 31% on the mud- and sandflats.

A non-parametric sample ordination plotted the trawls in one large cluster, in which area and season were the two major factors explaining the position of

Table 2. The species composition (in %) of the catches as obtained with different fishing techniques in summer and winter. The weighted mean catch rate (Mean-N) and biomass (Mean-G, in g) was corrected for the differences in observed frequencies of the fishing activities. Mean catch weight (+sd) fishing trip^{-1}, and mean catch person^{-1} fishing trip^{-1} is given in g fresh weight. Fishes indicated with * were also caught in the trawl samples.

	Summer (%)					Winter (%)				Mean N	Mean G
	Line	Seine boat	Gill net	Seine beach	Spear	Line	Gill net	Seine beach	Spear		
Ophichthidea unidentified	—	—	—	—	100	—	—	—	100	0.2	0.6
Sardinella albella	—	1.7	—	—	—	—	—	—	—	0.2	0.1
Chirocentrus dorab	—	0.7	—	—	—	—	—	—	—	0.1	0.1
Strongylura leiura	1.3	—	—	—	—	—	—	—	—	0.3	1.0
Hemiramphus far	—	—	—	—	—	—	1	—	—	0.2	0.4
Hyporhamphus affinis	7.0	0.7	—	0.1	—	—	—	—	—	1.8	1.6
Pterois antennata	—	1.2	—	0.1	—	—	—	—	—	0.2	0.0
*Platycephalus indicus**	3.0	—	19	0.8	—	—	7	1	—	4.0	7.7
Sorsogana prionata	—	0.5	—	—	—	—	—	—	—	0.1	0.1
Ambassidae unidentified*	—	0.2	—	—	—	—	—	—	—	0.0	0.0
*Epinephelus malabaricus**	—	1.4	—	0.8	—	—	—	—	—	0.4	0.6
*Pelateus quadrilineatus**	0.9	7.7	—	—	—	—	—	—	—	1.1	0.1
*Terapon jarbua**	2.6	2.9	7	9.5	—	—	7	—	—	5.4	3.8
Pomatomus saltatrix	—	—	—	—	—	—	1	—	—	0.2	2.3
*Diagramma pictum**	0.4	—	—	0.1	—	—	—	—	—	0.1	0.6
Pomadasys maculatum	—	—	—	—	—	—	9	—	—	1.8	2.2
Plectorhinvhus schotaf	—	—	—	0.4	—	—	—	—	—	0.1	0.1
*Lutjanus fulviflamma**	1.7	1.7	11	0.6	—	—	—	—	—	1.7	1.0
*Acanthopagrus berda**	2.2	—	—	0.1	—	—	1	1	—	0.8	0.9
*Crenidens crenidens**	10.0	2.6	—	28.0	—	—	14	2	—	12.4	7.8
*Rhabdosargus thorpei**	4.3	10.8	11	7.7	—	—	1	1	—	5.3	9.0
Lethrinus sp.*	—	1.4	—	0.7	—	—	—	—	—	0.3	0.1
*Lethrinus lentjan**	0.4	5.3	—	—	—	—	—	—	—	0.7	0.5
*Lethrinus mahsena**	—	3.3	—	—	—	—	—	—	—	0.4	0.1
Gerreidae unidentified*	36.5	17.5	37	10.0	—	—	—	—	—	16.4	11.7
*Gerres acinaces**	—	—	—	—	—	—	9	7	—	2.4	1.4
Gerres oyena	—	7.7	—	0.2	—	—	—	—	—	0.9	0.1
*Gerres rappi**	3.0	—	—	—	—	—	—	—	—	0.8	5.7
Parupeneus indicus	—	0.5	—	—	—	—	—	—	—	0.1	0.0
*Sillago sihama**	20.4	1.9	4	1.6	—	75	14	1	—	10.9	6.5
Sciaenidae unidentified	—	0.2	—	—	—	—	—	—	—	0.0	0.0
*Leiognathus equula**	—	2.4	—	0.2	—	—	—	—	—	0.3	0.1
*Heniochus diphreutes**	—	—	—	0.1	—	—	—	—	—	0.0	0.0
Caranx papuensis	—	—	—	—	—	—	—	1	—	0.0	0.1
Caranx sexfasciatus	—	—	—	—	—	8	10	—	—	2.2	6.1
Scomberiodes lysan	—	0.5	—	—	—	—	—	—	—	0.1	0.0
*Cheilio inermis**	—	3.8	—	—	—	—	—	—	—	0.4	0.6
*Halichoeres dussumieri**	0.4	—	—	—	—	—	—	—	—	0.1	0.0
Scarus globiceps	—	0.2	—	—	—	—	—	—	—	0.0	0.0
Scarus sordidus	—	0.7	—	—	—	—	—	—	—	0.1	0.0
Scarus sp.*	—	—	—	0.2	—	—	—	—	—	0.1	0.1
*Mugil cephalus**	—	6.2	—	10.1	—	17	1	—	—	3.8	7.4
*Liza macrolepis**	5.7	2.4	11	26.3	—	—	26	88	—	21.7	17.3
Siganus sp.*	—	4.8	—	1.2	—	—	—	—	—	0.8	1.5
*Siganus sutor**	—	8.6	—	—	—	—	—	1	—	1.0	0.2
Pseudorhombus arsius	—	0.2	—	0.7	—	—	—	—	—	0.2	0.1
Pseudorhombus elevatus	—	0.2	—	—	—	—	—	—	—	0.0	0.0

Table 2. Continued

	Summer (%)					Winter (%)				Mean N	Mean G
	Line	Seine boat	Gill net	Seine beach	Spear	Line	Gill net	Seine beach	Spear		
Lactoria cornuta	—	—	—	0.2	—	—	—	—	—	0.1	0.0
Total number of identified fish	230	418	27	832	9	12	94	189	3		
Total number of species	16	31	7	23	1	3	13	9	1	48	48
Mean catch weight fishing trip^{-1} (g)	930	5740	5900	3720	1242	1210	4750	4280	1150		
sd	40	590	2050	210	390	700	1290	1680	—		
Mean catch person^{-1} (g)	800	1110	2360	1380	1242	1210	4750	1610	1150		

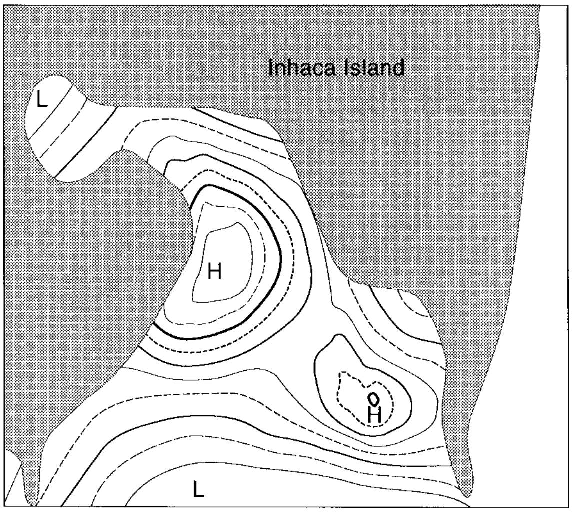

Figure 2. Local differences in catch per unit area by fishermen in the bay (in kg FW 1000 m^{-2} yr^{-1}). The contour lines connect areas with equal catches per unit area, from areas with high (H) to low (L) catches. Mean maximum catch was 6000 kg FW 1000 m^2, subsequent contour lines indicate a decrease in catch size (from high to low) of about 700 kg FW.

the samples in the graph (Figure 3). So trawls taken from different habitats, but from the same area and the same season, had a similar species composition.

Stomach content analysis

The mean contribution of shrimps (21%), crabs (17%), vegetation (15%), fishes (12%), and bivalves (10%), showed that the stomach content was dominated by benthic organisms and that a piscivorous diet was only shown by a minority of the fishes. Prey composition differed between winter and summer, mainly because of the high proportion of bivalves in the stomachs in winter (Figure 4), and the differences in fish communities. Shrimp and crabs were the other two important categories. In winter, fishes consumed no zooplankton and fewer fish than in summer.

Only six small species exhibited sometimes a piscivorous diet. In these species the ratio between the number of stomachs with fish remains to the total number of stomachs examined was > 0.10; for *Platycephalus indicus* (0.30), *Pelateus quadrilineatus* (0.12), *Diagramma picta* (0.13), *Lutjanus fulviflamma* (0.18), *Glossogobius biocellatus* (0.35), and *Pseudorhombus arsius* (0.15). Large predatory piscivorous fish were absent in the trawl samples. The catch rate of these six piscivorous fish species combined was significantly different between the ten habitats, with by far the highest catch rates (172 fish 1000 m^{-2}) in the channel in the Saco compared to the other habitats (1–49 fish 1000 m^{-2}) ($H = 118{,}757$, $df = 9, 280$, $p < 0.0001$). In addition to a larger catch rate in the Saco, these species represented a significantly larger fraction (24%) of the fish community ($H = 78.171$, $df = 9, 280$, $p < 0.0001$). Combining the different habitats, the mean catch rate of these piscivorous fishes was almost three times higher in the Saco compared to the Banco (45 fish 1000 m^{-2} against 16 fish 1000 m^{-2}).

Stomach content also appeared to vary with habitats (Figures 4, 5). Herbivorous diets and zooplankton feeding were found more at the Banco, whilst feeding on polychaetes was typically found in the Saco area. Crab and shrimps were eaten in large quantities, mainly in the sandbanks, sandflats and channel areas. Bivalves were only eaten in large quantities in the *Zostera* seagrass beds. A piscivorous diet was rare, but

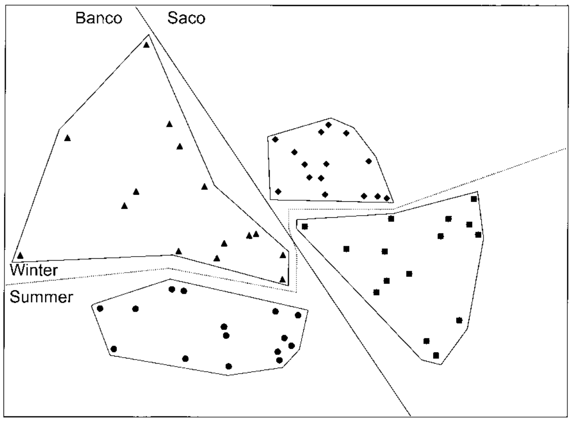

Figure 3. The ordination of the trawls using the non-metric multiple dimension scaling technique on Bray-Curtis similarity coefficients from 4th root transformed abundance data. Every point represents the mean catch from trawls from the same habitat and the same tide. Trawls from particular areas and seasons are enclosed by polygons. The differences between trawls from summer and winter, and from the two study areas, are indicated by the two lines.

slightly more common in the Saco (13%), than in the Banco (10%).

Total consumption by fish depended on fish biomass, fish density and water temperature (respectively 29.9°C and 26.5°C in summer for Saco and Banco, and 20.8°C and 20.1°C in winter). Q/B ratios varied from 5.9–33.1, with an average of 16.5. The mean contribution of the different fish species to the total consumption (Table 3) shows that the role of the smaller but abundant Gobiidae is relatively small compared to the larger, but less abundant species such as *Platycephalus indicus*, *Pelateus quadrilineatus*, *Pseudorhombus arsius* and *Sillago sihama*. Due to the higher catch rates in summer and the warmer water, consumption by fish in summer contributed 65% to the total annual consumption (Table 5). The channel in the Saco was the habitat with the largest consumption rate at 16 kg FW 1000 m^{-2} yr^{-1}. Due to the large differences in the composition of the stomach contents and the difference in the consumption rates per habitat type, large difference were observed in the consumption rate over the different diet categories (Table 5). In the summer, the crab consumption in the channel in the Saco (2299 g AFDW 1000 m^{-2}) is, for instance, larger than the total consumption of all diet categories combined in the sandflats or in the mangrove fringe (636 and 1078 g respectively).

Discussion

According to the results of the questionnaires, catches have decreased considerably over time. This was mainly attributed to overfishing. Although the results of these questionnaires are difficult to confirm, the other parameters studied here seem to support this view. The species mentioned as having disappeared were piscivorous fishes. This is a first indication of an excessive fishing pressure (Jennings & Polunin 1995, 1996).

Line fishing was the most common fishing technique used, because of the low initial investment and equal catches $person^{-1}$ between the different techniques. Fishing gear choice varied by season, (daily and lunar) tide, and habitat. This pattern of changing fishing techniques and fishing intensity over different habitats following the tidal and seasonal patterns corresponds with other studies of traditional fishing methods (Cordell 1974, Johannes 1981), and is assumed to be an answer to the changing availability of fishes. Line fishing was mainly done during low water spring tide, when the fish concentrate in the tidal channels. Seagrass beds were preferred, probably because of the assumed higher fish densities there. Fish traps were only observed at the lowest water, as they were hidden from observation at higher water levels. The use of fish fences, made out of long poles with attached nets, was not observed during the study, although they were frequently seen on other occasions. Fishing was generally directed at the larger fishes, as can be seen by comparing the size-frequency distribution of the fishes caught by fishermen with the distribution from the trawl samples for *Crenidens crenidens* (Figure 6). Some of the species observed were not recorded in the survey, such as *Pomatomus saltatrix*, *Pomadasys maculatum*, and *Caranx sexfasciatus*. This is especially true for the surface feeding fish such as *Hyporhamphus affinis*, or *Strongylura leiura*. However, there was a large overlap in species composition between the fishermen's catches and the trawl sampling program. Of the 48 fish species caught, 27 species (56%) were also present in the trawl-samples. These 27 fish species comprised 85% of the total weight of the catch of the fishermen and 71% of the total survey catch. Large, totally piscivorous predators were absent from the fishermen's catches. This could be an indication that a shift in the catch composition has taken place from species higher in the trophic system to species at lower levels, which is typical of overfishing (Jennings & Polunin 1996).

The mean catch per fishing trip at Inhaca was usually <2 kg $person^{-1}$. McClanahan et al. (1997), and

Table 3. The species composition of the trawls including only those species of which N > 4, with total number of fish caught (N), percentage of total catch (%), mean fresh weight (g), contribution to total biomass (%), mean, minimum and maximum fish standard lengths (mm), the ratios of fish numbers caught per day/night and summer/winter (night = only caught at night), contribution (%) to total consumption by fish (cons.), and the mean catch rate (N 1000 m^{-2}) over the different habitats.

Fish species	Frequency		Biomass		Length		Ratio		Cons.	Catch rates (N 1000 m^{-2})									
										Saco					Banco				
	N	%	Mean (g fish^{-1})	Total (%)	Mean	Min–max	Day : night	Sum : win	%	Mudflat	Sandflat	Mangrove	Sandbank	Channel	Mudflat	Sandflat	Zostera	Sandbank	Channel
Saurida gracilis	13	0.07	2.5	0.13	53	30–72	1.1 : 1	1.5 : 1	0.2	—	—	—	—	0.7	0.7	—	0.1	0.2	0.4
Choeroichthys sculptus	5	0.03	0.7	0.01	98	67–111	day	summer	0.0	—	—	—	—	—	0.3	—	0.3	—	—
Hippichthys cyanospilos	81	0.41	0.8	0.26	93	7–130	1 : 4.5	7.7 : 1	0.5	0.4	0.2	0.2	0.2	13.4	0.6	—	0.2	0.2	—
Scorpaenidae unidentified	9	0.05	0.2	0.01	18	14–28	4 : 1	winter	0.0	0.4	0.2	—	—	0.9	—	—	—	—	—
Parascorpaena mossambica	10	0.05	6.0	0.24	47	30–60	1 : 4.8	3.9 : 1	0.3	—	—	0.2	—	1.4	0.1	—	0.1	—	—
Platycephalus indicus	126	0.63	54.5	27.36	140	19–617	1.7 : 1	1.3 : 1	14.4	3.4	0.1	0.2	2.0	2.8	1.0	2.3	2.8	1.5	2.4
Ambassis commersoni	9	0.05	2.7	0.10	33	6–62	1 : 2.6	winter	0.2	0.4	—	—	—	1.5	—	—	—	—	—
Ambassis natalensis	231	1.16	0.8	0.76	30	10–55	1 : 18.1	1.7 : 1	1.5	1.9	14.7	17.0	9.7	4.7	—	—	—	—	—
Ambassis productus	110	0.55	0.8	0.34	31	16–48	1.7 : 1	1 : 113.1	0.4	1.2	—	9.6	3.1	—	0.1	—	—	—	—
Epinephelus andersoni	19	0.10	2.1	0.16	29	17–50	1 : 2.8	8.2 : 1	0.2	2.1	—	—	—	1.6	0.2	—	—	—	—
Pelateus quadrilineatus	737	3.71	1.9	5.55	36	12–104	1 : 2.2	21.9 : 1	7.7	1.1	—	0.2	—	113.5	5.5	0.1	20.7	0.4	—
Apogon nigripinnis	12	0.06	2.8	0.14	39	23–58	5.5 : 1	2.9 : 1	0.2	—	—	—	—	—	1.1	—	—	—	0.7
Foa brachygramma	26	0.13	1.5	0.16	33	18–46	day	1 : 4.4	0.2	—	—	—	—	—	3.0	—	—	—	—
Apogon new species	9	0.05	0.7	0.02	27	18–39	day	winter	0.1	—	—	—	—	2.1	—	—	—	—	—
Lutjanus fulviflamma	232	1.17	2.8	2.60	31	10–125	1 : 1.6	8.8 : 1	2.4	0.7	—	0.2	0.5	21.8	1.3	0.1	22.3	—	—
Sparidae unidentified	27	0.14	0.1	0.02	17	10–24	1 : 3.5	summer	0.0	—	0.1	0.7	—	—	0.1	0.2	2.2	—	—
Crenidens crenidens	50	0.25	14.9	2.98	67	26–162	1 : 7.3	1.7 : 1	2.0	—	0.2	1.4	—	6.3	0.2	—	1.4	0.1	—
Rgabdosargus sarba	22	0.11	3.5	0.31	48	23–90	1 : 1.2	20.2 : 1	0.3	—	—	0.2	0.2	1.5	—	—	1.1	—	—
Rhabdosargus thorpei	6	0.03	0.1	0.00	14	10–18	night	summer	0.0	—	—	—	—	—	—	—	0.8	—	—
Lethrinus sp.	12	0.06	5.7	0.27	53	15–116	day	winter	0.3	—	—	—	—	2.5	—	—	—	—	—
Lethrinus mahsena	7	0.04	4.1	0.11	53	36–75	day	summer	0.1	—	—	—	—	—	0.7	—	—	—	—
Gerreidae unidentified	331	1.66	1.1	1.45	32	15–58	1 : 49.4	winter	2.6	8.7	2.0	5.4	26.3	26.3	—	—	—	—	—
Gerres acinaces	1810	9.10	1.0	7.09	33	12–85	1 : 1.3	6.3 : 1	6.7	—	0.1	0.1	—	2.7	43.6	58.9	57.4	36.7	52.7
Sillago sihama	2614	13.14	0.8	8.62	33	5–205	1 : 1.1	14.1 : 1	6.7	25.1	44.6	36.8	21.7	15.6	23.2	40.3	22.4	120.4	36.5

Gazza minuta	357	1.79	0.4	0.56	23	10–85	1 : 2.1	winter	1.1	2.1	3.0	11.3	3.3	10.9	16.3	17.0	6.3	0.8	2.4
Chaetodon auriga	13	0.07	1.1	0.06	27	17–55	1 : 1.3	winter	0.1	0.2	—	—	—	2.3	—	—	—	—	—
Cheilio inermis	7	0.04	0.7	0.02	56	25–105	1 : 1.5	winter	0.0	—	—	—	—	1.1	—	—	—	—	—
Stethojulis interrupta	9	0.05	0.6	0.02	27	15–40	day	winter	0.1	0.2	—	—	—	1.7	—	—	—	—	—
Leptoscarus vaigiensis	69	0.35	0.5	0.13	24	15–45	1 : 2.2	winter	0.3	0.2	—	—	0.5	12.7	—	—	—	—	—
Petroscirtes breviceps	27	0.14	2.6	0.28	49	25–70	1 : 4.1	winter	0.6	—	—	—	—	6.3	—	—	—	—	—
Callionymus marleyi	145	0.73	3.7	2.13	54	17–145	1 : 1.7	1.7 : 1	2.7	1.4	—	—	0.3	19.0	1.2	0.9	0.9	1.0	2.2
Gobiidae unidentified	20	0.10	0.4	0.03	26	16–40	1.2 : 1	summer	0.1	2.7	—	0.3	—	0.6	—	—	—	—	—
Amoya signatus	2546	12.80	0.3	3.34	24	9–55	1 : 1.2	3.8 : 1	6.7	278.1	47.8	30.9	29.6	39.2	1.6	0.5	88.6	1.0	—
Drombus key	2	0.11	0.4	0.03	27	18–37	1 : 1.5	1 : 1.7	0.1	3.3	—	—	0.1	0.2	—	—	1.7	—	—
Favonigobius melanobranchus	2545	12.80	0.3	3.23	22	2–53	1 : 1	26 : 1	6.5	165.0	10.1	14.9	13.0	19.0	22.7	25.2	250.3	3.9	5.4
Favonigobius reichei	3975	19.99	0.2	2.86	9	8–58	1 : 2.5	1 : 56.3	4.4	110.8	123.5	115.4	118.1	93.8	9.2	16.0	111.0	0.9	1.1
Glossogobius biocellatus	190	0.96	0.9	0.65	32	10–92	1 : 1.4	1 : 1.4	1.1	21.5	3.0	—	0.9	9.3	1.5	0.1	2.5	—	0.2
Oligolepis keiensis	91	0.46	0.4	0.13	24	16–35	1 : 16.7	42.9 : 1	0.4	0.4	—	0.1	—	—	0.1	—	22.4	—	—
Oxyurichthys ophthalmonema	1671	8.40	0.2	1.46	24	9–36	1 : 1.5	summer	4.7	327.9	91.6	7.4	0.6	17.0	0.4	0.1	0.3	—	—
Vanderhorstia delagoae	27	0.14	1.0	0.10	38	25–75	3.9 : 1	2.3 : 1	0.2	4.7	—	—	0.1	0.6	—	—	—	—	0.3
Youngeichthys nebulosus	9	0.05	0.5	0.02	34	26–50	4 : 1	3.4 : 1	0.0	0.1	—	—	—	0.3	—	—	1.4	—	—
Eleotridae unidentified	5	0.03	1.1	0.02	49	41–52	1 : 3	summer	0.0	—	—	—	—	0.7	—	—	—	—	—
Eleotris melanosoma	5	0.03	0.3	0.01	22	14–29	1 : 3.1	summer	0.0	0.2	—	0.5	—	0.3	—	—	—	—	—
Acanthurus sp.	6	0.03	1.3	0.03	30	25–35	1 : 4.1	winter	0.1	—	—	—	—	1.2	—	—	—	—	—
Siganus sp.	71	0.36	5.2	1.46	41	11–135	1 : 5.2	winter	1.5	0.2	0.7	—	—	10.4	0.3	—	1.1	0.9	—
Siganus sutor	7	0.04	2.8	0.08	43	34–51	day	summer	0.1	—	—	—	—	—	0.7	—	—	—	—
Pseudorhombus arsius	320	1.61	9.1	11.61	63	10–997	1.4 : 1	1.4 : 1	9.0	12.0	1.0	0.3	3.6	25.3	5.3	4.2	1.6	1.6	2.2
Cynoglossus durbanesis	16	0.08	13.8	0.88	86	10–138	1 : 6.1	1.2 : 1	0.8	—	—	—	—	0.1	0.4	—	0.3	—	1.7
Solea bleekeri	821	4.13	2.0	6.61	37	8–303	1 : 1.4	1 : 1.8	6.8	56.0	10.7	2.0	4.4	73.6	9.3	3.8	1.9	1.4	0.9
Paramonacanthus barnardi	11	0.06	0.6	0.03	24	18–30	day	winter	0.0	—	—	—	—	—	1.7	—	—	—	—
Arothron sp.	6	0.03	0.9	0.02	21	11–37	2.5 : 1	1 : 5.2	0.0	—	—	—	—	0.5	—	0.1	0.3	—	—
Arothron hispidus	29	0.15	1.1	0.13	19	6–50	1 : 1.1	8.3 : 1	0.2	1.4	0.7	—	0.2	3.4	—	—	—	—	—
Arothron immaculatus	25	0.13	1.8	0.18	24	8-59	2.6 : 1	1 : 3.3	0.2	0.3	—	1.3	0.3	1.4	—	—	0.9	—	—
Other species*	333	1.67	3.9	5.21	42	8–750	—	—	5.1	2.0	3.0	1.7	0.8	45.6	1.1	0.5	4.8	0.4	1.7
Total	19889	100		100						1040	360	260	240	610	150	170	630	170	110

*comprises unidentified fishes (N = 265) and species of which < 5 fishes were caught:
Strophidon sathete, *Cirrhimuraena playfairii*, *Herklotsichthys* sp., *Gonorynchus gonorhynchus*, *Antennariidae*, *Pegasus volitans*, *Acentronura tentaculata*, *Hippocampus camelopardalis*, *Pterois miles*, *Sebastapistes strongia*, *Sebastes capensis*, *Ptarmus jubatus*, *Cociella punctata*, *Cociella heemstrai*, *Onigocia oligolepsis*, *Epinephelus malabaricus*, *Terapon jarbua*, *Pseudamia gelatinosa*, *Diagramma pictum*, *Acanthopagrus berda*, *Rhabsosargus holubi*, *Lethrinus lentjan*, *Lethrinus variegatus*, *Gerres rappi*, *Leiognathus equula*, *Secutor insidiator*, *Heniochus diphreutes*, *Carangidae*, *Carangoides armatus*, *Labridae*, *Scarus* sp., *Mugil cephalus*, *Liza macrolepis*, *Acentrogobius audax*, *Mugilogobius durbanensis*, *Acanthurus triostegus*, *Bothus pantherinus*, *Tylerius spinosissimus*, *Lophodion*sp.

Table 4. The mean area fished per trawl per habitat together with the total mean fish catch per trawl, fish density (N 1000 m^{-2}), fish biomass (g 1000 m^{-2}), the mean number of fish species per trawl (N-spp), and the mean Margalef and Shannon-Wiener indices of species richness, Pielou's eveness and Hill's dominance ratios.

	Saco					Banco				
	Mudflat	Sandflat	Mangrove	Sandbank	Channel	Mudflat	Sandflat	Zostera	Sandbank	Channel
m^2	183	239	216	203	223	273	254	258	232	262
fish $trawl^{-1}$	162	65	53	42	121	38	37	130	46	30
N 1000 m^{-2}	1040	360	260	240	620	150	170	630	170	110
g 1000 m^{-2}	370	140	150	210	1490	320	290	670	250	240
N-spp $trawl^{-1}$	6.7	4.0	3.9	4.0	11.9	5.9	3.9	8.2	3.0	3.7
Margalef	1.14	0.74	0.84	0.88	2.35	1.43	0.99	1.65	1.09	1.27
Shannon	0.84	0.66	0.82	0.77	1.69	1.26	0.92	1.31	0.74	0.90
Eveness	0.45	0.55	0.72	0.66	0.71	0.76	0.74	0.64	0.68	0.79
Dominance	0.60	0.65	0.55	0.60	0.30	0.38	0.51	0.39	0.60	0.50

Dayaratne et al. (1995b) recorded far higher individual catches for systems in Kenya and Sri Lanka respectively, with mean catches of 4–60 kg $person^{-1}$ $operation^{-1}$. However, the annual catch per area was lower in Kenya, at 1.1–1.8 kg 1000 m^{-2} yr^{-1}. So, fishermen at Inhaca had lower catch rates, but the productivity of the fishing area was ten times higher than areas examined in Kenya. Current catches (17 kg 1000 m^{-2} yr^{-1}) at Inhaca fall within the interval of 1–100 kg FW 1000 m^{-2} yr^{-1} reported for other estuarine catches (Lowe-McConnell 1987). The catches did not vary substantially between the main habitat types, and the ratio between catch (kg m^{-2}) and the total biomass obtained in the trawl samples (kg m^{-2}) was 3.7 for the channel, 4.7 for the seagrass beds, and 5.2 for the combined mud and sandflats. The bay sides had a low catch $area^{-1}$, and no fishing was recorded from the mangrove fringes. The highest catch per area were measured in the central section of the bay, mainly around the tidal channels. The two study areas were, respectively, situated in an area recorded as having the lowest catch $area^{-1}$ (the Saco), and an area with intermediate to high catch $area^{-1}$ (the Banco).

The trawl sampling program yielded 93 different fish species, which is not a high figure for tropical estuaries (Kimani et al.1996, Wantiez et al. 1996, Blaber 1997). Significantly larger catches were recorded from the Saco, especially in gobies-dominated mudflats. The highest biomass was also obtained in the Saco; with the channel having a 2–10 times greater biomass than the other habitats. This channel also exhibited the highest values for species richness, the lowest dominance, and one of the highest evenness values. The trawls were dominated by Gobiidae, a situation typical of intertidal mud- and sandflats (Whitfield et al. 1989, Prochazka & Griffiths 1992, Harrison & Whitfield 1995). The overall mean size of the fishes was extremely small (29 mm). Large fishes (>100 mm) were almost absent from the samples (<2% of total abundance). Species richness was highest in the three habitat types with seagrass vegetation, the two channels and the *Zostera capensis* seagrass beds. This pattern has been reported in other studies (Whitfield et al. 1989, De Troch et al. 1996, Randall et al. 1996, West & King 1996, Jenkins et al. 1997), and attributed to differences in food availability, shelter and other factors. The trawls of the Saco and the Banco exhibited a different species composition, which varied strongly with season, and modestly among habitats (Figure 3).

The stomach content of the fishes was dominated by benthic invertebrates such as crabs, shrimps and bivalves. Herbivorous fish (mainly found in the channels and on the seagrass beds) and piscivorous fish were rare. Stomach content was different between summer and winter, and among habitats. Hence, the fish followed an opportunistic feeding style, which is typical for benthic feeding fishes (Gerking 1994). Q/B ratios, varying from 5.9–33.1, were relatively high, which can be explained by the small maximum size of the fishes and the warm water. The consumption of fish was highest in the channel: 16.1 kg 1000 m^{-2} yr^{-1}. The benthic organisms contributed 64% to this amount and, using an ash-free dry-weight/fresh weight conversion factor of 0.13 (unpublished data), this corresponds with a predation pressure on the benthic stratum of 1.3 g AFDW m^{-2} yr^{-1}. Moreover, the total consumption was probably underestimated because maximum weight values from the trawl samples were used in the calculation of consumption, instead of asymptotic

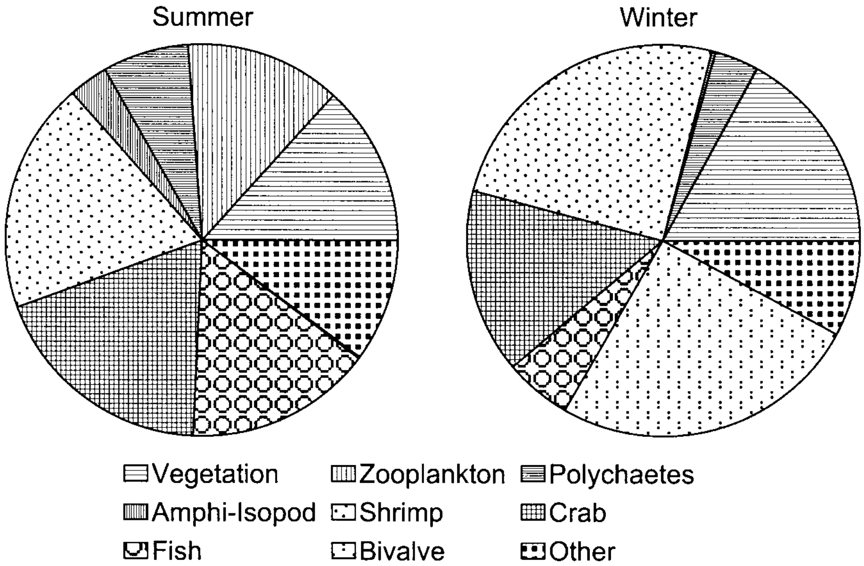

Figure 4. Stomach contents of the fishes in summer and winter by % of volumetric abundance.

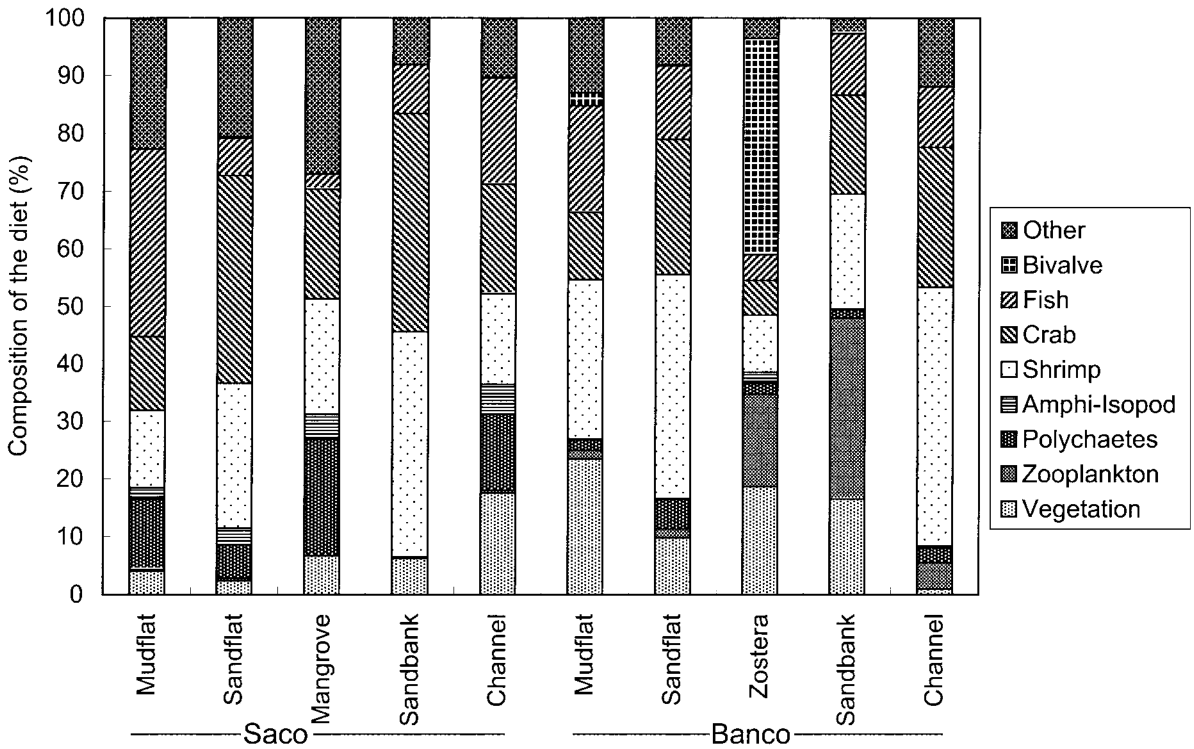

Figure 5. The cumulative percentage of feeding categories in the stomachs of fishes caught at ten different habitats in the Saco and Banco areas.

Table 5. The total consumption of fish in g FW 1000 m^{-2}, over the different habitat types, and broken down over the the different feeding categories and over summer and winter, together with the annual estimated consumption.

Category	Saco					Banco				
	Mudflat	Sandflat	Mangrove	Sandbank	Channel	Mudflat	Sandflat	Zostera	Sandbank	Channel
Summer										
Vegetation	117	15	72	102	2119	402	164	902	292	10
Zooplankton	8	3	0	0	56	25	25	777	557	52
Polychaetes	354	37	217	3	1607	31	86	88	28	29
Amphi-Isopod	59	18	47	1	625	3	2	95	0	3
Shrimp	390	160	217	640	1902	474	648	479	353	510
Crab	374	229	205	620	2299	199	390	291	303	275
Fishes	945	41	29	139	2220	315	212	216	187	118
Bivalve	0	2	0	0	6	39	3	1807	1	0
Other	661	131	291	131	1245	221	135	172	47	135
Total summer	2908	636	1078	1637	12078	1710	1664	4827	1768	1132
Winter										
Vegetation	112	32	61	61	712	353	101	451	88	9
Zooplankton	8	5	0	0	19	22	15	389	168	45
Polychaetes	338	77	184	2	540	27	53	44	8	25
Amphi-Isopod	56	39	40	1	210	3	1	48	0	2
Shrimp	372	336	184	380	640	417	401	240	106	436
Crab	356	481	173	368	773	175	241	146	91	235
Fishes	902	86	24	83	746	277	131	108	56	101
Bivalve	0	4	0	0	2	35	2	904	0	0
Other	630	274	246	78	418	194	83	86	14	115
Total winter	2774	1335	911	972	4061	1502	1028	2416	533	969
Total yr^{-1}	5682	1970	1989	2608	16140	3211	2692	7243	2301	2100

weights. Feeding efficiency was also not included in the model.

The total standing biomass of the benthic fishes was estimated at 5.6 t, whilst fishing harvest was estimated at 26.2 t per year. These values however, should only be compared with caution. No correction has been made for the annual fish production, for the part of the catch that is not made up by benthic fishes, or for the net efficiency of the trawl. Data about the productivity of the fish community, expressed as the production/biomass ratio, are unavailable for this area, but values from St Francis Bay, South Africa, indicated a P/B value of 3 for benthic feeding fish (calculated from Heymans & Baird 1995). The proportion of the fishermen's catch belonging to the benthic community was estimated at 85% of the total biomass of that catch. Net efficiency was estimated by Kuipers (1975) at >50% for flatfish <100 mm. Moreover, the fishing targets the largest fishes, and the example (Figure 6) showed that 90% of the catch of the fishermen comprised only the upper 10% fraction of the available fishes. King (1995) showed that the maximum sustainable yield could be estimated as a fraction of the unexploited population, normally <0.2. Synthesising these data, the picture emerges that the bay is being overfished. Catches may not be sustainable. It should be stressed that the current study is based on correlative data, and nothing is known about the fishing pressure in the past. The impact of the fisheries could only be fully understood, when comparison can be made with an unfished control situation.

Overfishing appeared to have resulted in some alteration of the fish community: (1) The low presence of piscivorous fishes in the trawls samples. No totally piscivorous fishes were found, only benthic feeding fishes that only occasionally included fishes in their diet. Even those fishes comprised 10% of the total abundance, whilst Blaber (1997) mentioned an abundance of 17% for totally piscivorous fishes in the nearby Lake St Lucia, and even higher figures for other similar systems (Blaber 1980). Overfishing is

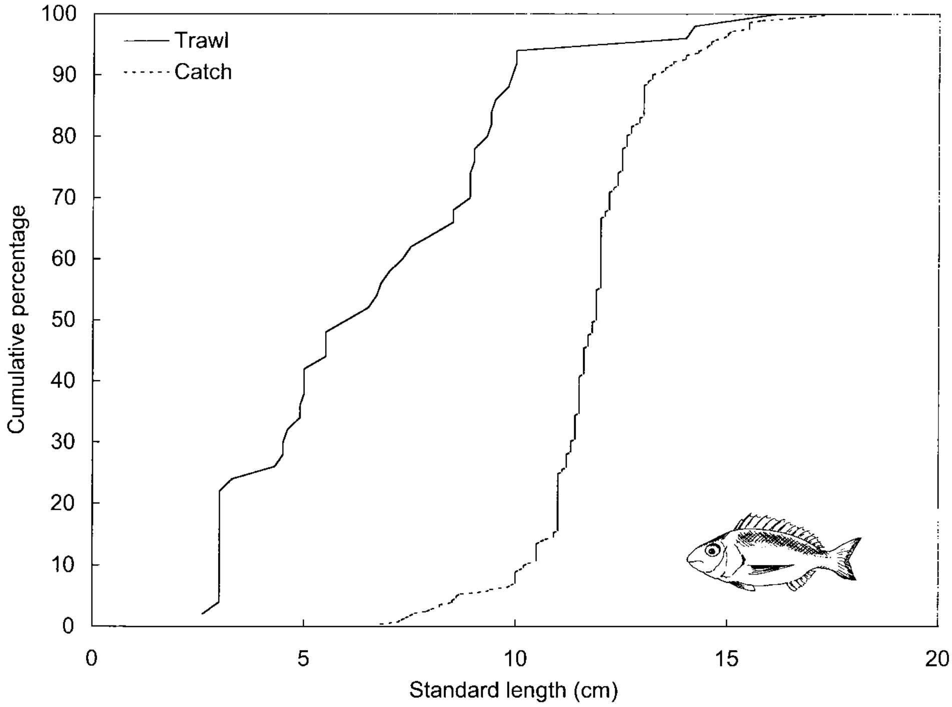

Figure 6. The size-frequency distribution of *Crenidens crenidens* as calculated from the trawl samples (solid line) and the fishermen's catches (broken line).

assumed to generate such a shift in the community structure (Jennings & Polunin 1996). (2) Fishermen mentioned the disappearance of large predators such as rays, grunters and sea breams, and reduced catches for squid and cuttlefish. (3) The low frequency of a piscivorous diet. (4) A high density of small fish. This might be expected for sheltered bays and mangrove areas which have an important nursery function for fish (Blaber 1980, Cyrus & Blaber 1987, Whitfield et al. 1989, Harris et al. 1995, Laroche et al. 1997), but it is also in agreement with the prediction that a release of the predation pressure from larger piscivorous fishes would benefit the smaller fish species. (5) The Saco, which is subject to a relatively lower fishing pressure, had the largest fish catch rates, the largest fish biomass, the highest species richness, and the lowest dominance. Moreover, the greatest abundance of piscivorous fish was found there, and the fraction of piscivorous fish in the trawls was the highest recorded for the whole area.

These patterns are in agreement with the predictions formulated in the introduction. Overfishing appears to have influenced the fish community structure at Inhaca.

Acknowledgements

We would like to thank the staff of the Marine Biology Research Station at Inhaca for their hospitality, and especially Morgado Manganhela, João Canhe, and Castigo Hobjane for their logistical support. The study greatly benefited from the assistance of several students from the Department of Biological Sciences of the Eduardo Mondlane University in Maputo, and we are especially grateful to Phil Heemstra and Ofer Gon of the J.L.B. Smith Institute of Ichthyology for checking our fish reference collection. The manuscript greatly improved through the constructive comments of Wim Wolff, Herbert Prins, Angus Paterson, Phil Heemstra, and two anonymous referees. The research was carried out in the framework of the Deibi Project.

References cited

Andersson, J.E.C. & Z. Ngazi. 1995. Marine resource use and the establishment of a Marine Park: Mafia Island, Tanzania. Ambio 24: 475-481.

Beets, J. 1997. Effects of a predatory fish on the recruitment and abundance of Caribbean coral reef fishes. Mar. Ecol. Prog. Ser. 148: 11–21.

Blaber, S.J.M. 1980. Fish of the Trinity inlet system of North Queensland with notes on the ecology of fish faunas of tropical indo-pacific estuaries. Aust. J. Mar. Freshwater Res. 31: 137–146.

Blaber, S.J.M. 1997. Fish and fisheries of tropical estuaries. Chapman & Hall, London. 367 pp.

Christensen, V. 1996. Managing fisheries involving predator and prey species. Rev. Fish Biol. Fisheries 6: 417–442.

Clarke, K.R. & R.M. Warwick. 1994. Change in marine communities; an approach to statistical analysis and interpretation. Plymouth Marine Laboratory, Plymouth. 144 pp.

Cordell, J. 1974. The lunar-tide fishing cycle in Norteastern Brazil. Ethnology 13: 25–38.

Cyrus, D.P., E.C. Wellmann & T.J. Martin. 1993. Diet and reproductive activity of the estuarine roundherring *Gilchristella aestuaria* in Cubhu, a freshwater coastal lake in Northern Natal, South Africa. S. Afr. J. Aquat. Sci. 19: 3–13.

Cyrus, D.P. & S.J.M. Blaber. 1987. The influence of turbidity on juvenile marine fish in the estuaries of Natal, South Africa. Cont. Shelf Res. 7: 1411–1416.

Dahl, J. & L. Greenberg. 1996. Impact on stream benthic prey by benthic vs drift feeding predators: a meta-analysis. Oikos 77: 177–181.

Dayaratne, P., O. Lindén & M.W.R.N. de Silva. 1995. Puttalam Lagoon and Mundel Lake, Sri Lanka: a study of coastal resources, their utilization, environmental issues and management options. Ambio 24: 391–401.

de Boer, W.F. 2000. Biomass dynamics of seagrasses and the role of mangrove and seagrass vegetation as different nutrient sources for an intertidal ecosystem in Mozambique. Aq. Bot. 66: 225–240.

de Boer, W.F., L. Rydberg & V. Saide 2000. The influence of tidal currents on an intertidal ecosystem at Inhaca Island, Mozambique. Hydrobiol. 428: 187–196.

de Troch, M., J. Mees, I. Papadopoulos & E.O. Wakwabi. 1996. Fish commutities in a tropical bay (Gazi Bay, Kenia): seagrass beds vs. unvegetated areas. Neth. J. Zool. 46: 236–252.

Flecker, A.S. 1997. Habitat modification by tropical fishes: environmental heterogeneity and the variability of interaction strength. J. N. Amer. Benthol. Soc. 16: 286–295.

Gerking, S.D. 1994. Feeding ecology of fish. Academic Press, San Diego. 416 pp.

Harris, S.A., D.P. Cyrus & A.T. Forbes. 1995. The larval fish assemblage at the mouth of the Kosi estuary, Kwazulu-Natal, South Africa. S. Afr. J. Mar. Sci. 16: 351–364.

Harrison, T.D. & A.K. Whitfield. 1995. Fish community structure in three temporarily open/closed estuaries on the Natal Coast. Ichthyol. Bull. 64: 1–80.

Heymans, J.J. & D. Baird. 1995. Energy flow in the Kromme estuarine ecosystem, St Francis Bay, South Africa. Est. Coast Shelf Sci. 41: 39–59.

Irlandi, E.A. & M.K. Crawford. 1997. Habitat linkages: the effect of intertidal saltmarshes and adjacent subtidal habitats on abundance, movement, and growth of an estuarine fish. Oecologia 110: 222–230.

Jenkins, G.P., H.M.A. May, M.J. Wheatley & M.G. Holloway. 1997. Comparison of fish assemblages associated with seagrass and adjacent unvegetated habitat of Port Phillip Bay and Corner Inlet, Victoria, Australia, with emphasis on commercial species. Est. Coast. Shelf Sci. 44: 569–588.

Jennings, S., D.P. Boullé & N.V.C. Polunin. 1996a. Habitat correlates of the distribution biomass of Seychelles' reef fishes. Env. Biol. Fish. 46: 15–25.

Jennings, S., S.S. Marshall & N.V.C. Polunin. 1996b. Seychelles' marine protected areas: comparative structure and status of reef fish communities. Biol. Cons. 75: 201–209.

Jennings, S. & N.V.C. Polunin. 1995. Relationships between catch and effort in Fijian multispecies reef fisheries subject to different levels of exploitation. Fish. Manag. Ecol. 2: 89–101.

Jennings, S. & N.V.C. Polunin. 1996. Impacts of fishing on tropical reef ecosystems. Ambio 25: 44–49.

Johannes, R.E. 1981. Words of the lagoon; fishing and marine lore in the Paulau District of Micronesia. University of California Press, Berkely. 245 pp.

Johnson, T.B. & J.F. Kitchell. 1996. Long-term changes in zooplanktivorous fish community composition: implications for food webs. Can. J. Fish. Aquat. Sci. 53: 2792–2803.

Kalk, M. 1995. A natural history of Inhaca island. Witwatersrand University Press, Johannesburg. 394 pp.

Kent, G. 1998. Fisheries, food security, and the poor. Food Policy 22: 393–404.

Kent, G. & H. Josupeit. 1989. The contribution of fisheries to alleviating malnutrition in Southern Africa. FAO Fisheries Circular 818: 1–49.

Kerekes, J.J. 1994. Aquatic birds in the trophic web of lakes. Kluwer Academic Publishers, Dordrecht. 544 pp.

Kimani, E.N., G.K. Mwatha, E.O. Wakwabi, J.M. Ntiba & B.K. Okoth. 1996. Fishes of a shallow tropical mangrove estuary, Gazi, Kenya. Mar. Freshwater Res. 47: 857–868.

King, M. 1995. Fisheries biology, assessment and management. Fishing News Books, Oxford. 341 pp.

Kuipers, B. 1975. On the efficiency of a two-metre beam trawl for juvenile plaice *(Pleuronectes platessa*). Neth. J. Sea Res. 9: 69–85.

Kuipers, B.R., B. Maccurrin, J.M. Miller, H.W. van der Veer & J.I.J. Witte. 1992. Small trawls in juvenile flatfish research: their development and efficiency. Neth. J. Sea Res. 29: 109–117.

Laroche, J., E. Baran & N.B. Rasoanandrasana. 1997. Temporal patterns in a fish assemblages of a semiarid mangrove zone in Madagascar. J. Fish Biol. 51: 3–20.

Letourneur, Y. 1996. Dynamics of fish communities on Reunion fringing reef, Indian Ocean. I. Patterns of spatial distribution. J. Exp. Mar. Biol. Ecol. 195: 1–30.

Lowe-McConnell, R.H. 1987. Ecological studies in tropical fish communities. Cambridge University Press, Cambridge. 382 pp.

Magurran, A.E. 1988. Ecological diversity and its measurement. Chapman & Hall, London. 179 pp.

McClanahan, T.R., H. Glaesel, J. Rubens & R. Kiambo. 1997. The effects of traditional fisheries management on fisheries yields and the coral-reef ecosystems of southern Kenya. Env. Cons. 24: 105–120.

Pierce, C.L. & B.D. Hinrichs. 1997. Response of littoral invertebrates to reduction of fish density: simultaneous experiments in ponds with different fish assemblages. Freshwater Biol. 37: 397–408.

Polunin, N.V.C. & S. Jennings. 1998. Differential effects of small-scale fishing on predatory and prey fishes on Fijian reefs. pp. 95–124. *In*: D.M. Newberry, H.H.T. Prins & N.D. Brown (ed.) Dynamics of Tropical Communities, Blackwell Science, Oxford.

Polunin, N.V.C. & C.M. Roberts. 1993. Greater biomass and value of target coral-reef fishes in two small Caribbean marine reserves. Mar. Ecol. Prog. Ser. 100: 167–176.

Prochazka, K. & C.L. Griffiths. 1992. The intertidal fish fauna of the west coast of South Africa–species, community and biogeographic patterns. S. Afr. J. Zool. 27: 115–120.

Proulx, M., F.R. Pick, A. Mazumder, P.B. Hamilton & D.R.S. Lean. 1996. Effects of nutrients and planktivorous fish on the phytoplankton of shallow and deep aquatic systems. Ecology 77: 1556–1572.

Randall, R.G., C.K. Minns, V.W. Cairns & J.E. Moore. 1996. The relationship between an index of fish production and submerged macrophytes and other habitat features at three littoral areas in the Great Lakes. Can. J. Fish Aquat. Sci. 53: 35–44.

Roberts, C.M. 1995. Effects of fishing on the ecosystem structure of coral reefs. Cons. Biol. 9: 988–995.

Schlacher, T.A. & T.H. Wooldridge. 1996. Patterns of selective predation by juvenile, benthivorous fish on estuarine macrofauna. Mar. Biol. 125: 241–247.

Smith M.M. & P.C. Heemstra (ed.). 1991. Smiths' sea fishes. Southern Book Publishers, Johannesburg. 1048 pp.

Wantiez, L., M. Harmelin-Vivien & M. Kulbicki. 1996. Spatial and temporal variation in a soft-bottom fish assemblage in St Vincent Bay, New Caledonia. Mar. Biol. 125: 801–812.

Weerts, S.P., D.P. Cyrus & A.T. Forbes. 1997. The diet of juvenile *Sillago sihama* (Forsskål, 1775) from three estuarine systems in KwaZulu-Natal. Water SA 23: 95–100.

West, R.J. & R.J. King. 1996. Marine, brackish, and freshwater fish communities in the vegetated and bare shallows of an Australian coastal river. Estuaries 19: 31–41.

Whitfield, A.K., L.E. Beckley, B.A. Bennett, G.M. Branch, H.M. Kok, I.C. Potter & R.P. Elst. 1989. Composition, species richness and similarity of ichthyofaunas in eelgrass *Zostera capensis* beds of Southern Africa. S. Afr. J. Mar. Sci. 8: 251–259.

Zar, J.H. 1984. Biostatistical analysis. Prentice Hall, Englewood Cliffs. 718 pp.