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ABSTRACT

Seagrasses are marine angiosperms widely distributed in both tropical and temperate coastal waters creating one of the most productive aquatic ecosystems on earth. Due to the high primary production and a complex habitat structure, meadows formed by seagrasses support a variety of benthic, demersal and pelagic organisms. Many fish and shellfish species, including those of commercial interest, are attracted to seagrass habitats for foraging and shelter, especially during their juvenile life stages. Thus, seagrass meadows are valuable resources for fisheries at both local and regional scales. The study presented here examined the community structure, size distribution, species composition and spatial variation of fish in two different seagrass habitats dominated by either *Thalassia hemprichii* or *Thalassodendron ciliatum* at Inhaca Island, southern Mozambique. The sampling of fish was conducted in daylight during four consecutive spring tide periods using a small beam trawl. Multivariate analysis revealed significant differences in total fish density and biomass when comparing different seagrass sites. The abundance and species number of fish were greater in *T. ciliatum* meadows than in *T. hemprichii* meadows. The sampling results showed a mean fish density (± SE) of 0.12 ± 0.02 and 0.08 ± 0.03 fishes m^{-2}, respectively, in the two sites of *T. ciliatum*, and 0.02 ± 0.005 and 0.01 ± 0.005 fishes m^{-2}, respectively, in the two sites of *T. hemprichii*. The mean fish biomass (± SE) of the two *T. ciliatum* sites was 1.09 ± 0.26 and 0.67 ± 0.25 g m^{-2}, respectively, and 0.31 ± 0.10 and 0.045 ± 0.02 g m^{-2}, respectively, in the two sites dominated by *T. hemprichii*. Out of 55 different fish taxa from 26 families recorded during the study, four species accounted for more than 60 % of the total abundance: *Siganus sutor*, *Paramonacanthus barnardi*, *Stetojulius interrupta* and *Pelates quadrilineatus.* In addition, only the two species *Siganus sutor* and *Pelates quadrilineatus* represented more than 40 % of the overall weight. The study showed that the abundance, diversity and species composition of fish were generally significantly higher in *T. ciliatum* meadows compared to *T. hemprichii* meadows. Obvious discrepancies between the two seagrass habitats may be explained by various biotic and abiotic mechanisms of which the study suggests ecological differences in architectural structure of dominating seagrass species, habitat complexity and provision of epiphytic food to be of major importance. The study presented here is one of the few quantitative fish studies of seagrass meadows in the whole Western Indian Ocean region. Thus, it is of importance to increase the amount of such studies since they provide valuable baseline data on local fish community structures, information which is essential for the perspectives of fisheries management and protection of seagrass habitats. The need to amplify our presently scarce scientific knowledge is further highlighted by the raised pressure on seagrass meadows in the region, a result of growing coastal populations and human disturbance from e.g. pollution, eutrophication, sedimentation, fishing activities and collection of invertebrates.

Keywords: Seagrass, fish, community structure, spatial variation, structural complexity, Western Indian Ocean region, Mozambique, Inhaca Island

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INTRODUCTION

Seagrass ecosystems constitute an essential part of marine habitats in continental shelf waters throughout the world. The distribution of seagrasses ranges from high intertidal to shallow subtidal soft bottoms, i.e. sandy bays, mud flats, lagoons and estuaries, where they often form extensive mono- and multispecific meadows. In the tropics it is common to find seagrass meadows adjacent to other key ecosystems such as coral reefs and mangroves. Seagrass meadows are among the most productive aquatic ecosystems in the biosphere (Duarte and Chiscano, 1999) and may increase biodiversity of associated organisms (e.g. Edgar *et al.*, 1994; Oshima *et al.*, 1999; Boström and Bonsdorff, 2000). They are important as nursery grounds, foraging areas and predation refuges for numerous fish and invertebrate populations (Adams, 1976; Heck and Thoman, 1984; Orth *et al.*, 1984) and provide crucial benefits for commercial, subsistence and recreational fisheries (Bell and Pollard, 1989; Rooker *et al.*, 1998). Due to the complex architecture of the leaf canopy in combination with the dense network of roots and rhizomes seagrass meadows may stabilize bottom sediments (Fonseca, 1989) and serve as effective hydrodynamic barriers reducing wave energy and current velocity (Koch, 1996), and thereby reduce turbidity (Bulthuis *et al.*, 1984) and decrease coastal erosion (Almasi *et al.*, 1987). Further, seagrass meadows trap large amounts of nutrients and organic matter in the bottom sediment (Smith, 1981; Gacia *et al.*, 1999). Through microbial decomposition, seagrass biomass may enter the marine food-web as detritus and thus support productivity through recycling of nutrients and carbon (Livingston, 1984; Hemminga, *et al.*, 1991).

During the last decades the problems of seagrass degradation have received increased attention worldwide (Short and Wyllie-Echeverria, 1996). Widespread losses of seagrass habitats are reported from many coastal areas including North America (Orth and Moore, 1983), Australia (Walker and McComb, 1992 and references therein), Europe (Pasqualini *et al.*, 1999; Baden *et al.*, 2003) and Africa (Gullström, unpublished data). Seagrass demise might be induced by natural events such as storms (Gallegos *et al.*, 1992) or diseases (den Hartog, 1987). Seagrass loss, however, mainly occurs due to human impacts and the most general explanation to reduction of seagrass is excessive nutrient enrichment, i.e. eutrophication, of coastal waters (e.g. Kemp *et al.*, 1983; Orth and Moore, 1983; Fortes 1988, Tomasko *et al.*, 1996; McGlathery, 2001). Effluent disposal (Larkum and West, 1990) and changes in land use pattern (Shepherd *et al.*, 1989) are other important anthropogenic disturbances that threaten seagrass populations. The decline of seagrass habitats may affect the density and composition of associated fish species (e. g. Kikuchi, 1974; Stoner, 1983; Bell and Pollard, 1989). Connolly (1994) found that the total number of fish in patches of removed seagrass was lower than in undisturbed seagrass meadows, but higher than in unvegetated areas. In general, it has been widely regarded that seagrass meadows support a higher diversity and abundance of associated fish than adjacent unvegetated habitats (e. g. Bell and Pollard, 1989; Sogard and Able, 1991; Connolly, 1994; Jenkins *et al.*, 1997; Mattila *et al.*, 1999), although there are some contradictions (e. g. Heck and Thoman, 1984; Hanekom and Baird, 1984).

As mentioned earlier, seagrass meadows play an important role as nursery areas for fish with a number of species that directly depend on the seagrass habitat for their survival (e.g. Pollard, 1984; Parrish, 1989; Tolan et al., 1997; Guidetti and Bussotti, 2000), while other species have more general preferences (e.g. Blaber *et al.*, 1992; Jenkins and Wheatley, 1998). According to Hemminga and Duarte (2000) fish species living within seagrass meadows can be distinguished by their residence status: (1) *permanent residents* are species that spend their entire life in seagrass meadows, (2) *temporary residents* are species present seasonally or during parts of their life in these habitats, (3) *regular visitors* are fish species that frequently visit seagrass meadows, e.g. through diurnal migrations from an adjacent coral reef, (4) *occasional visitors* are species that migrate to the meadows sporadically.

The dynamics of fish communities in seagrass meadows have been studied in most tropical coastal waters (e.g. Pollard, 1984, Blaber *et al.*, 1989; Sedberry and Carter, 1993; Nagelkerken *et al.*, 2001). In Mozambique, as in the whole Western Indian Ocean (WIO) region, however, such studies are few and deal mainly with species composition and relative abundance (e.g. Mauge, 1967; Vivien, 1974; Harmelin-Vivien, 1983; Almeida *et al.*, 1995; Muhando, 1995; van der Velde *et al.*, 1995; Gell and Whittington, 2002). The study presented here examined the community structure, size distribution, species composition and spatial variation of fish in two different seagrass habitats, dominated by either *Thalassia hemprichii* or *Thalassodendron ciliatum*, around Inhaca Island, Mozambique, and is one of the few investigations that reveal quantitative fish community data from seagrass meadows in the WIO. A hypothesis to be tested is if the two seagrass habitats (*T. hemprichii* and *T. ciliatum*) significantly differ in density, biomass, species composition and spatial distribution of fish species. The results may have importance as baseline data for fisheries management and future conservation of seagrass habitats in Mozambique. The ecological significance of seagrass ecosystems for fish and fisheries in the WIO region has been discussed in a review by Gullström *et al*. (2002).

The coast of Mozambique

Mozambique is situated on the south eastern coast of Africa between latitudes 10 and 26 degrees south and longitudes 30 and 41 degrees east. The most spectacular geographical feature of the country is its long and pristine coastline of 2 515 km influenced by the warm waters of the Indian Ocean (Michler, 1999). The coastal zone is characterised by an assortment of productive ecosystems (e.g. mud flats, sand beaches, algal beds, mangroves, seagrass meadows and coral reefs) important for the increase of biodiversity. The climate in Mozambique is strongly influenced by the warm southward Mozambique Current and varies from tropical in the north to subtropical in the south with one wet (Oct-Mar) and one dry (Apr-Sep) season. Tides range from 0.2 to 6.3 metres.

Mozambique has an estimated population of about 18.5 million people (1997) (Else, *et al*. 1997). During the long civil war (1976-1992) the movement of people to the coast increased drastically and now over 60 % of the inhabitants live along the coastal zone and the annual growth rate, including migration, is 4-7 % (Michler, 1999; UNEP, 2001). In the beginning of the 1990s Mozambique was regarded one of the world's poorest countries with an estimated gross national product (GNP) per capita of only $US 80 (Coughanowr *et al.*, 1995). The human pressure is important and one of the driving forces shaping the coast of Mozambique is the rapid demographic growth. Two-thirds of the human population depend socially and economically of coastal and marine resources such as fisheries, mari-culture, mangrove forestry, and tourism (Massinga and Hatton, 1996). The national fish and shrimp industry is the largest generator of foreign income and shrimp fishing alone contributes to about 50 % of the current export (Macia, 1997). This exerts an enormous pressure on the coastal and marine environment and its resource base. A reduction of the marine resources would not only have socio-economic impacts but also reduce the amount of available protein. The strong pressure from the growing population and expanding development along the coast is reflected in extensive destruction and overuse of natural resources, enhanced pollution problems and severe habitat degradation (Lindén, 1993, Moffat *et al.*, 1998). In the southern part of Mozambique, including Inhaca Island, uncontrolled tourist activities are placing further strain on the environment. However, on Inhaca an integrated coastal zone management plan has focused on sustainable development. The plan has promoted the creation of numerous patch reserves around the island (Gove, 1996).

MATERIALS AND METHODS

Study area

The present study was carried out in the waters surrounding Inhaca Island situated about 35 km eastward of Maputo, southern Mozambique (Lat. 25°58’-26°05’S; Long. 32°55’-33°00’E) (Figure 1). The island is small (~ 42 km^2) and located in an area permanently affected by two different kinds of hydrographical regimes. The eastern coastline of Inhaca is exposed straight towards the Indian Ocean and is characterised by wave actions, a strong ocean current and a steep slope in bottom topography. In contrast, the western coastline, facing Maputo Bay, is relatively protected and shows a fairly even topographic bottom slope with a maximum depth of 20 m (Kalk, 1995). The climate is subtropical with a rainy season lasting from October to March. Rainfall is highly unpredictable and the interannual fluctuations are large. The tide is semi-diurnal and vary with an amplitude of 0.1 to 3.9 m, creating widespread intertidal areas exposed twice daily during low tides (Kalk, 1995). A comprehensive description of the island´s animal and plant species as well as their ecological interrelationships is given by Kalk (1995).

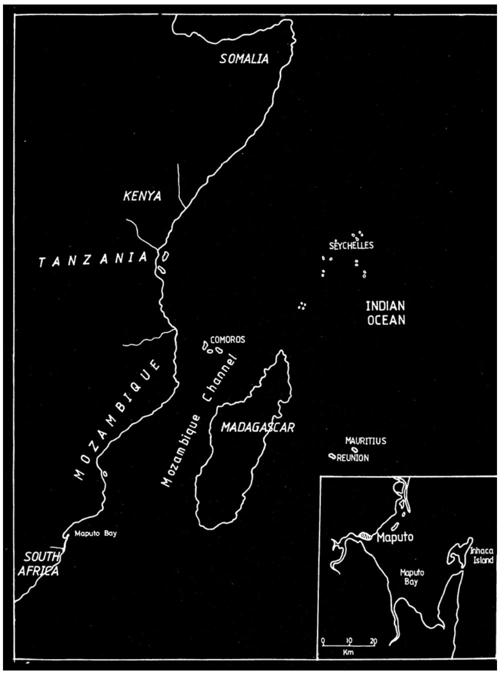

FIGURE 1. Map showing the Western Indian Ocean region and the location of Inhaca Island, southern Mozambique.

Extensive areas of the intertidal zone as well as the subtidal fringe of Inhaca Island are covered by different seagrass communities (Bandeira, 2002). Over 50 seagrass species have been described in the world (den Hartog, 1970; Hemminga and Duarte, 2000), and the coastal zones of the WIO region encompass 13 known species (Bandeira and Björk, 2001). However, the seagrass assemblages at Inhaca are extremely diverse for such a small area and as many as 9 seagrass species distributed in three families have been identified (Bandeira, 2002). The species around the island are *Cymodocea rotundata* Ehrenb. et Hempr. ex Aschers., *C. serrulata* (R. Br.) Aschers. et Magnus, *Halodule uninervis* (Forsk.) Aschers. in Bossier, *H. wrightii* Ascherson, *Halophila ovalis* (R. Br.) Hook. *f.*, S*yringodium isoetifolium* (Ascherson) Dandy, *Thalassodendron ciliatum* (formerly *Cymodocea ciliata*) (Forsk.) den Hartog (Cymodoceaceae), *Thalassia hemprichii* (Ehrenberg) Asherson (Hydrocharitaceae) and *Zostera capensis* Setchell (Zosteraceae). Furtermore, Bandeira (2002) recognised 7 different seagrass community types around Inhaca, each composed of 1 to 9 seagrass species (sometimes interspersed with a considerable amount of algae). Mixed seagrass meadows with a high diversity are common in the whole WIO region. Up to 8 or 10 species at the same locality has been reported for Mozambique (Bandeira, 2000).

The field sampling of this study was conducted in two of the island's most important seagrass communities, *Thalassia hemprichii* / *Halodule wrightii* (TH) and *Thalassodendron ciliatum* / *Cymodocea serrulata* (TC) (mapped and identified by Bandeira, 2002) (see map and illustrations in Figure 2 and 3, respectively). The former community occurs intertidally and is the most diverse seagrass community (including all nine species represented at the island). It covers 44 % of seagrass habitats around Inhaca, while the latter community represents 21 % of which extensive areas are subtidal. Together with *Zostera capensis*, these three seagrass communities represent 88 % of the total seagrass coverage around the island (Bandeira, 2002). The sampling sites of this study were chosen in areas characterised by dense and homogeneous seagrass meadows.

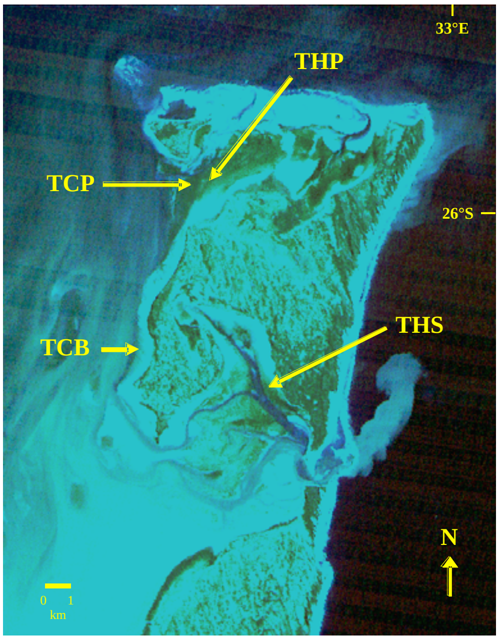

FIGURE 2. Satellite image over the sampling sites of seagrass meadows at Inhaca Island, Mozambique.
TCB = *Thalassodendron ciliatum* / *Cymodocea serrulata* at the Biological station area
TCP = *Thalassodendron ciliatum* / *Cymodocea serrulata* at the Portinho area
THP = *Thalassia hemprichii* / *Halodule wrightii* at the Porthino area
THS = *Thalassia hemprichii* / *Halodule wrightii* at the Saco da Inhaca area

Physical settings

On each sampling occasion, temperature, salinity and conductivity were measured with a Yellow Spring Instrument (YSI) and water depth was recorded using a LCD Digital Sounder (Hondex PS-7). All physical measurements were collected in the middle of the sampling lines before each sampling procedure.

FIGURE 3. Illustrations of dominant seagrass species in meadows at the study sites of Inhaca Island, Mozambique. The images are adopted from Richmond (1997).

(a) *Thalassia hemprichii* and *Halodule wrightii* (TH)

(b) *Thalassodendron ciliatum* and *Cymodocea serrulata* (TC)

Fish sampling

Fish were sampled during four consecutive spring tide periods in October and November 1999 and at four sites in the two seagrass communities TH (*Thalassia hemprichii* meadows at the Porthino area, THP, and the Saco da Inhaca area, THS) and TC (*Thalassodendron ciliatum* meadows at the Biological station area, TCB, and the Porthino area, TCP) (Figure 1). The sampling was conducted in daylight, 0-3 hours before high tide and at depth of 1.4-2.9 m, using a beam trawl with an opening of 1.44 x 0.43 m. 108 individual replicates were randomly taken at the four seagrass sites. The sampling was done over a distance of 100 m for each replicate during the first period (13-15 October) and 200 m for each replicate during the three following periods (25-27 October, 9-12 and 21-24 November) (Table 1). The net had an unstretched mesh dimension of 6 mm and a cod-end of 3 mm in mesh size. The sampling was performed towards the wind with a constant boat speed of approximately 1.9 knots in a straight line between two wooden poles.

In the laboratory, all fish specimens were identified to the lowest taxonomic level possible and counted. The individuals were measured for standard length (SL) to the nearest mm and wet weight to the nearest 0.01 g.

Data analysis

The spatial variation of fish community structures in different seagrass sites was assessed using non-metric multidimensional scaling (nMDS) technique. The similarities of the nMDS ordination were based on a Bray Curtis similarity matrix (Clark, 1993). To reduce the weighting of abundant taxa the data was square-root transformed. Significance tests for differences among sites were done using one-way analysis of similarity (ANOSIM). The similarity of percentages (SIMPER) procedure was used to determine the fish species that contribute to dissimilarity among seagrass sites. All statistics were carried out using Primer for Windows (version 5.2) (Clark and Warwick, 1994).

TABLE 1. Sampling data. Seagrass communities: TC = *Thalassia hemprichii* / *Halodule wrightii*; TH = *Thalassodendron ciliatum* / *Cymodocea serrulata*. Sampling sites: B = the Biological station area; P = the Portinho area; S = the Saco da Inhaca area.

Period	Date	Seagrass community	Sampling site	No. samples (n)	Trawl-length (m)
1	13 - 15 Oct 1999	TC	B	12	100
2	25 - 27 Oct 1999	TC	B	6	200
		TC	P	6	200
		TH	P	6	200
		TH	S	6	200
3	9 - 12 Nov 1999	TC	B	18	200
		TC	P	6	200
		TH	P	6	200
		TH	S	6	200
4	21 - 24 Nov 1999	TC	B	18	200
		TC	P	6	200
		TH	P	6	200
		TH	S	6	200

RESULTS

Physical measurements

The hydrographical data showed no distinct differences between sampling sites (Table 2). The sampling water depth of meadows dominated by *Thalassodendron ciliatum* varied between 1.5 m and 2.9 m in high spring tide, whereas the depth of water in the two *Thalassia hemprichii* meadows was slightly lower and ranged from 1.4 m to 2.3 m during the same tidal period. Those small differences were an outcome of the general distribution of the two seagrass species around the island. *T. hemprichii* meadows are found in the intertidal areas, while *T. ciliatum* spreads along the subtidal zone (Bandeira, 2002).

The mean water temperature was between 20.3 and 25.9 °C and the mean salinity ranged from 32.3 to 41.3 ‰. The conductivity measurements fluctuated between 47.4 and 61.3 S/m (Siemens per meter).

TABLE 2. Hydrographical data. Seagrass sites: TCB = *Thalassodendron ciliatum* / *Cymodocea serrulata* meadows at the Biological station area; TCP = *Thalassodendron ciliatum* / *Cymodocea serrulata* meadows at the Porthino area, THP = *Thalassia hemprichii* / *Halodule wrightii* meadows at the Porthino area; THS = *Thalassia hemprichii* / *Halodule wrightii* at the Saco da Inhaca area.

Seagrass site	Water depth (m)	Temperature (°C)	Salinity (‰)	Conductivity (S/m)
TCB	1.5 – 2.9	20.9 – 25.9	32.3 – 41.3	47.4 – 61.3
TCP	2.1 – 2.6	20.4 – 25.0	34.0 – 40.8	51.6 – 61.0
THP	1.4 – 2.0	20.6 – 25.6	33.7 – 40.6	51.3 – 60.4
THS	1.5 – 2.3	20.3 – 25.7	34.6 – 39.0	50.2 – 58.4

Total abundance, total biomass and dominant fish taxa

A total of 2102 individual fish, representing 55 taxa from 26 families, was recorded at the sampling sites during the study (Table 3). Four species, *Siganus sutor* (23.2 %), *Paramonacanthus barnardi* (15.7 %), *Stethojulis interrupta* (15.0 %) and *Pelates quadrilineatus* (7.9 %) dominated the catch and were estimated for more than 60 % of the total abundance. Including these four species, there were 13 species being the main number of individuals in the catch (86.5 %). *Siganus sutor* (30,8 %) and *Pelates quadrilineatus* (10.4 %) represented more than 40 % of the overall weight. 15 species contributed to the major part of the total biomass (88,8 %). The family Siganidae (represented by only one species, i.e. *Siganus sutor*) dominated the catch and was ranked first by overall abundance (23.2 %) and biomass (30.8 %) (Table 4). Labridae (21.2 %), Monacanthidae (15.7 %) and Teraponidae (7.9 %) were also abundant, while high biomass was found of Teraponidae (10.4 %), Labridae (9.7 %), Lethrinidae (7.5 %), Platycephalidae (7.0 %) and Scaridae (6.6 %). The species diversity of the fish families captured varied between 1 and 7 identified species (Table 3). Labridae was the most diverse family and represented by 7 species. Apogonidae, Syngnathidae and Tetraodontidae were represented by 4 species and Gobiidae as well as Scorpaenidae by 3 species. The remaining fish families had only 1 or 2 species represented.

TABLE 3. Fish data from 4 seagrass sites around Inhaca Island, Mozambique. Commercial importance: A = aquarium, AC = aquaculture, F = fisheries, FH = fisheries - highly commercial, FM = fisheries - minor importance, G = gamefish, SA = show aquarium.

Family	Species	Abundance		Biomass (g)			Length (mm)		Importance
		n	%	mean	range	Total %	mean	range	
Aploactinidae	*Ptarmus jubatus*	17	0.81	3.1	0.6-5.8	0.30	47	24-59	
Apogonidae	*Apogon nigripinnis*	1	0.05	9.3	9.3	0.05	59	59	
Apogonidae	*Apogon taeniatus*	36	1.71	11.0	0.7-20.0	2.27	61	25-79	
Apogonidae	*Apogon timorensis*	5	0.24	2.2	1.6-2.6	0.06	38	35-40	
Apogonidae	*Foa brachygramma*	2	0.10	1.1	0.5-1.8	0.01	29	23-34	A
Blenniidae	*Petroscirtes breviceps*	75	3.57	6.7	0.3-16.1	2.90	48	21-107	A
Blenniidae	*Petroscirtes mitratus*	8	0.38	0.8	0.1-2.0	0.04	28	12-45	A
Bothidae	*Bothus pantherinus*	1	0.05	2.7	2.7	0.02	51	51	F
Centriscidae	*Aeoliscus punctulatus*	52	2.47	3.4	0.5-8.2	1.03	120	65-145	SA
Cynoglossidae	*Cynoglossus durbanensis*	3	0.14	17.3	3.7-27.7	0.30	115	75-137	
Cynoglossidae	*Cynoglossus zanzibarensis*	1	0.05	10.8	10.8	0.06	103	103	F
Diodontidae	*Lophodiodon calori*	1	0.05	110.8	110.8	0.64	124	124	
Gobiidae	*Amblygobius sphynx*	2	0.10	21.5	20.5-22.4	0.25	93	90-96	A
Gobiidae	*Favonigobius melanobranchus*	16	0.76	0.3	0.1-1.1	0.03	28	19-33	
Gobiidae	*Vanderhorstia delagoae*	1	0.05	1.0	1	0.01	47	47	
Gobiidae		3	0.14	0.8	0.6-1.1	0.01	37	33-40	
Haemulidae	*Plectorhinchus flavomaculatus*	1	0.05	4.4	4.4	0.03	59	59	F
Labridae	*Cheilinus digrammus*	1	0.05	5.4	5.4	0.03	55	55	FM, A
Labridae	*Cheilio inermis*	90	4.28	9.6	0.2-70.0	4.96	100	28-223	FM, A
Labridae	*Cymolutes praetextatus*	1	0.05	11.6	11.6	0.07	86	86	
Labridae	*Halichoeres scapularis*	5	0.24	16.4	7.7-22.5	0.47	90	72-102	A
Labridae	*Novaculichthys macrolepidotus*	31	1.47	5.5	0.3-28.0	0.98	56	25-121	A
Labridae	*Stethojulis interrupta*	315	14.99	1.7	0.2-10.8	3.00	41	21-79	A
Labridae	*Pteragogus flagellifer*	2	0.10	17.8	15.1-20.4	0.20	80	73-86	A
Lethrinidae	*Lethrinus lentjan*	50	2.38	19.9	0.3-115.0	5.73	82	20-176	FH
Lethrinidae	*Lethrinus variegatus*	50	2.38	6.0	0.1-26.5	1.73	58	17-91	FM, A
Lethrinidae		18	0.86	0.4	0.1-2.0	0.04	21	12-40	
Lutjanidae	*Lutjanus fulviflamma*	42	2.00	21.7	4.2-48.5	5.24	74	53-122	F, G, A, SA
Monacanthidae	*Paramonacanthus barnardi*	330	15.70	1.6	0.1-20.2	3.00	45	9-84	
Mullidae	*Parupeneus indicus*	8	0.38	16.3	1.6-43.3	0.75	77	42-124	F, G
Mullidae	*Parupeneus rubescens*	3	0.14	3.0	2.4-3.7	0.05	50	46-54	F
Ostraciidae	*Lactoria cornuta*	11	0.52	36.9	8.0-98.3	2.34	74	40-127	A
Ostraciidae	*Ostracion cubicus*	1	0.05	1.9	1.9	0.01	22	22	A
Platycephalidae	*Platycephalus indicus*	3	0.14	203.3	140.0-250.0	3.51	304	278-318	F, AC, G
Platycephalidae	*Sorsogona prionota*	42	2.00	14.4	2.3-66.4	3.48	86	53-183	
Pomacentridae	*Chrysiptera annulata*	11	0.52	3.5	0.4-7.9	0.22	47	22-53	
Pseudochromidae	*Pseudochromis natalensis*	2	0.10	7.4	6.8-8.0	0.08	74	70-77	
Scaridae	*Leptoscarus vaigiensis*	66	3.14	16.6	0.1-105.0	6.30	72	16-163	F, A
Scaridae	*Scarus ghobban*	2	0.10	27.5	16.1-38.9	0.32	92	81-103	F, A
Scaridae		1	0.05	1.0	1	0.01	33	33	
Scorpaenidae	*Dendrochirus brachypterus*	9	0.43	5.4	3.2-6.9	0.28	52	43-58	A
Scorpaenidae	*Parascorpaena mossambica*	29	1.38	13.7	0.7-51.5	2.28	57	26-111	
Scorpaenidae	*Synanceia verrucosa*	1	0.05	13.9	19.9	0.08	66	66	FM, A
Serranidae		1	0.05	1.4	1.4	0.01	38	38	
Siganidae	*Siganus sutor*	488	23.22	10.9	3.5-51.3	30.75	72	50-125	F
Syngnathidae	*Hippichtys cyanospilos*	1	0.05	0.7	0.7	0.00	95	95	
Syngnathidae	*Hippocampus camelopardalis*	16	0.76	2.4	0.9-7.9	0.22	52	33-81	
Syngnathidae	*Syngnathoides biaculeatus*	51	2.43	9.1	5.2-15.7	2.67	127	153-222	SA
Syngnathidae	*Trachyrhampus bicoarctatus*	1	0.05	6.7	6.7	0.04	312	312	
Synodontidae	*Saurida gracilis*	7	0.33	18.8	7.6-26.9	0.76	115	91-127	F
Teraponidae	*Pelates quadrilineatus*	166	7.90	10.8	0.1-20.6	10.35	79	14-99	FM
Tetraodontidae	*Arothron hispidus*	8	0.38	18.9	3.3-38.4	0.87	59	32-90	A
Tetraodontidae	*Arothron immaculatus*	12	0.57	13.7	7.4-22.5	0.95	62	50-80	SA
Tetraodontidae	*Canthigaster solandri*	1	0.05	3.4	3.4	0.02	40	40	A
Tetraodontidae	*Chelonodon laticeps*	1	0.05	31.2	31.2	0.18	84	84	
Total		2102							

TABLE 4. Ranking order of total density and biomass (in percent) of all fish families caught at Inhaca Island, Mozambique.

	Family	Density (%)		Family	Biomass (%)
1	Siganidae	23.22	1	Siganidae	30.75
2	Labridae	21.17	2	Teraponidae	10.35
3	Monacanthidae	15.70	3	Labridae	9.72
4	Teraponidae	7.90	4	Lethrinidae	7.50
5	Lethrinidae	5.61	5	Platycephalidae	6.99
6	Blenniidae	3.95	6	Scaridae	6.63
7	Scaridae	3.28	7	Lutjanidae	5.24
8	Syngnathidae	3.28	8	Monacanthidae	3.00
9	Centriscidae	2.47	9	Syngnathidae	2.94
10	Platycephalidae	2.14	10	Blenniidae	2.94
11	Apogonidae	2.09	11	Scorpaenidae	2.64
12	Lutjanidae	2.00	12	Apogonidae	2.40
13	Scorpaenidae	1.86	13	Ostraciidae	2.35
14	Gobiidae	1.05	14	Tetraodontidae	2.02
15	Tetraodontidae	1.05	15	Centriscidae	1.03
16	Aploactinidae	0.81	16	Mullidae	0.80
17	Ostraciidae	0.57	17	Synodontidae	0.76
18	Mullidae	0.52	18	Diodontidae	0.64
19	Pomacentridae	0.52	19	Cynoglossidae	0.36
20	Synodontidae	0.33	20	Aploactinidae	0.30
21	Cynoglossidae	0.19	21	Gobiidae	0.20
22	Pseudochromidae	0.10	22	Pomacentridae	0.22
23	Bothidae	0.05	23	Pseudochromidae	0.09
24	Diodontidae	0.05	24	Haemulidae	0.03
25	Haemulidae	0.05	25	Bothidae	0.02
26	Serranidae	0.05	26	Serranidae	0.01

Seagrass community comparisons

Multivariate analyses revealed cut separation in fish community structures among seagrass sites. The nMDS plots showed that the distribution pattern of sites was exceedingly similar for total density and total biomass of fish (Figure 4). Seagrass sites were shown to have significant effects on fish assemblages for both density (one-way ANOSIM, Global R = 0.802, P = 0.001) and biomass (Global R = 0.777, P = 0.001) of fish. However, pairwise tests of both fish density and biomass on effects between two specific sites provided significant dissimilarities only between TCB and the three other seagrass sites (TCP, THP and THS), respectively, whereas no significance was observed between TCP and THP, between TCP and THS, and between THP and THS (Table 5).

FIGURE 4. Two-dimensional non-metric multidimensional scaling (nMDS) ordinations on fish density (a) and biomass (b) from 4 seagrass sites around Inhaca Island, Mozambique. Stress = 0.08 (a) and 0.07 (b).

_ = *Thalassodendron ciliatum* / *Cymodocea serrulata* at the Biological station area

_ = *Thalassodendron ciliatum* / *Cymodocea serrulata* at the Portinho area

_ = *Thalassia hemprichii* / *Halodule wrightii* at the Porthino area

Δ = *Thalassia hemprichii* / *Halodule wrightii* at the Saco da Inhaca area

TABLE 5. One-way ANOSIM testing for differences in fish community structures among 4 seagrass sites around Inhaca Island, Mozambique. ns = not significant, * p < 0.05, ** p < 0.01, *** p < 0.001

	Fish density		**Fish biomass**	
	R-value	p	R-value	p
Among sites	0.802	***	0.777	***
Pairwise tests				
TCB vs TCP	0.482	*	0.506	*
TCB vs THP	0.924	**	0.886	**
TCB vs THS	1.000	**	0.964	**
TCP vs THP	0.667	ns	0.704	ns
TCP vs THS	1.000	ns	0.556	ns
THP vs THS	0.926	ns	0.704	ns

A SIMPER analysis showed that the major contributors to dissimilarities within and among seagrass sites were *Siganus sutor*, *Paramonacanthus barnardi* and *Stethojulis interrupta* for fish density, and *Siganus sutor*, *Paramonacanthus barnardi*, *Pelates quadrilineatus* and *Leptoscarus vaigiensis* for fish biomass (Table 6).

TABLE 6. SIMPER analysis of fish species contributing (%) most to dissimilarity within and among all seagrass sites.

FISH DENSITY				FISH BIOMASS			
Site	Fish species	%	cum %	Site	Fish species	%	cum %
TCB	*Siganus sutor*	18.54	18.54	**TCB**	*Siganus sutor*	23.18	23.18
	Paramonacanthus barnardi	14.99	33.53		*Paramonacanthus barnardi*	13.13	36.31
	Stethojulis interrupta	9.68	43.21		*Pelates quadrilineatus*	11.85	48.16
TCP	*Siganus sutor*	17.14	17.14	**TCP**	*Siganus sutor*	21.70	21.70
	Paramonacanthus barnardi	16.65	33.79		*Paramonacanthus barnardi*	15.57	37.27
	Stethojulis interrupta	12.96	46.75		*Leptoscarus vaigiensis*	11.93	49.19
THP	*Siganus sutor*	40.97	40.97	**THP**	*Siganus sutor*	49.51	49.51
	Stethojulis interrupta	14.32	55.29		*Lutjanus fulviflamma*	15.16	64.67
	Pelates quadrilineatus	12.80	68.09		*Pelates quadrilineatus*	12.21	76.88
THS	*Favonigobius melanobranchus*	32.11	32.11	**THS**	*Favonigobius melanobranchus*	18.89	18.89
	Petroscirtes mitratus	18.30	50.14		*Arothron immaculatus*	18.63	37.52
	Stethojulis interrupta	16.68	67.09		*Arothron hispidus*	12,41	49.93
TCB vs TCP	*Siganus sutor*	7.77	7.77	**TCB vs TCP**	*Pelates quadrilineatus*	7.49	7.49
	Stethojulis interrupta	7.40	15.18		*Siganus sutor*	7.30	14.79
	Pelates quadrilineatus	6.85	22.03		*Leptoscarus vaigiensis*	6.77	21.56
TCB vs THP	*Paramonacanthus barnardi*	10.63	10.63	**TCB vs THP**	*Paramonacanthus barnardi*	9.02	9.02
	Siganus sutor	7.94	18.57		*Pelates quadrilineatus*	7.11	16.13
	Stethojulis interrupta	6.98	25.56		*Siganus sutor*	7.10	23.23
TCB vs THS	*Siganus sutor*	13.55	13.55	**TCB vs THS**	*Siganus sutor*	16.40	16.40
	Paramonacanthus barnardi	8.80	22.35		*Pelates quadrilineatus*	8.82	25.22
	Pelates quadrilineatus	7.17	29.52		*Paramonacanthus barnardi*	7.47	32.69
TCP vs THP	*Paramonacanthus barnardi*	12.15	12.15	**TCP vs THP**	*Leptoscarus vaigiensis*	12.10	12.10
	Stethojulis interrupta	10.70	22.85		*Paramonacanthus barnardi*	10.76	22.86
	Leptoscarus vaigiensis	10.01	32.87		*Syngnathoides biaculeatus*	8.27	31.14
TCP vs THS	*Paramonacanthus barnardi*	10.38	10.38	**TCP vs THS**	*Siganus sutor*	14.19	14.19
	Siganus sutor	10.37	20.76		*Leptoscarus vaigiensis*	11.28	25.46
	Stethojulis interrupta	8.59	29.34		*Paramonacanthus barnardi*	9.75	35.21
THP vs THS	*Siganus sutor*	18.46	18.46	**THP vs THS**	*Siganus sutor*	26.10	26.10
	Favonigobius melanobranchus	10.24	28.70		*Platycephalus indicus*	10.40	36.50
	Pelates quadrilineatus	6.73	35.43		*Lutjanus fulviflamma*	7.85	44.35

The mean fish density (± SE) in the sites dominated by *T. ciliatum* was 0.12 ± 0.02 ind. m^{-2} in TCB and 0.08 ± 0.03 ind. m^{-2} in TCP, respectively, and thus higher than in the sites dominated by *T. hemprichii* with a mean fish density (± SE) of 0.02 ± 0.005 ind. m^{-2} in THP and 0.01 ± 0.005 ind. m^{-2} in THS, respectively. Fish biomass showed similar differences among seagrass communities as fish density (Figure 5). The mean biomass of fish (± SE) in the *T. ciliatum* sites was 1.09 ± 0.26 g m^{-2} in TCB and 0.67 ± 0.25 g m^{-2} in TCP, respectively, while the *T. hemprichii* sites revealed mean fish biomasses (± SE) of 0.31 ± 0.10 g m^{-2} in THP and 0.045 ± 0.02 g m^{-2} in THS, respectively.

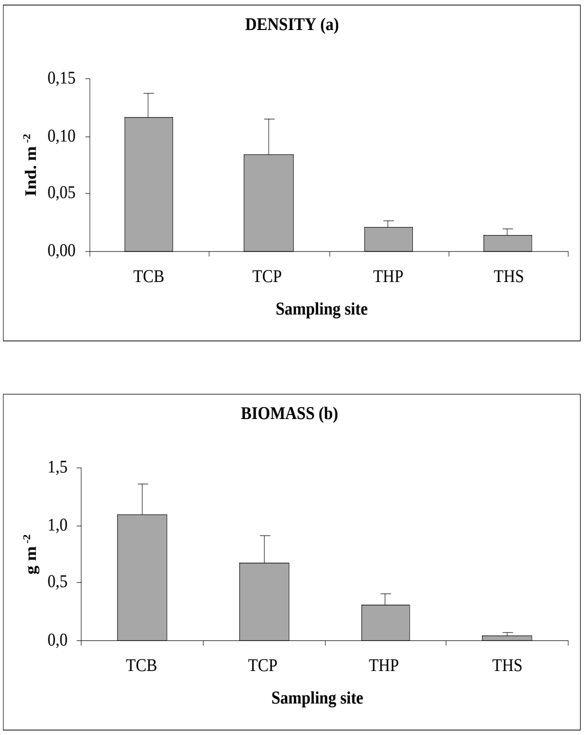

FIGURE 5. Mean density (a) and biomass (b) ± SE of total fish catch from four sites in two different seagrass community types around Inhaca Island, Mozambique.

TCB = *Thalassodendron ciliatum* / *Cymodocea serrulata* at the Biological station area (n = 10)

TCP = *Thalassodendron ciliatum* / *Cymodocea serrulata* at the Portinho area (n = 3)

THP = *Thalassia hemprichii* / *Halodule wrightii* at the Porthino area (n = 3)

THS = *Thalassia hemprichii* / *Halodule wrightii* at the Saco da Inhaca area (n = 3)

Generally, the mean length sizes of fish caught in this study were small and far below adult level of sizes for many fish species (Table 3). The mean size distribution of fish measured for SL ranged from 2.1 cm for Lethrinidae to 31.2 cm for *Trachyrhampus bicoarctatus*. However, the mean fish size of all specimens was 7.4 cm in SL and only 9 taxa had a mean length of more than 10.0 cm in SL.

DISCUSSION

The present study has shown that spatial variation are important for fish community structures in two seagrass habitats, dominated by either *Thalassia hemprichii* (THP and THS) or *Thalassodendron ciliatum* (TCB and TCP), of Inhaca Island, southern Mozambique. The mean density and biomass of fish were higher in the two sites dominated by *T. ciliatum* than in the sites composed of mainly *T. hemprichii*. Observed differences between the two seagrass communities can be explained by various biotic and abiotic mechanisms. As suggested in the literature (e.g. Blaber *et al*., 1992; Heck and Orth, 1980; Heck and Thoman, 1981), the main reasons for spatial heterogeneity of fish in seagrass meadows may be due to differences in plant morphology and structural complexity, significant factors for the efficiency of shelter against predation and foraging success. Contradicting the refuge theory (e.g. Heck and Orth, 1980), Bell and Westoby (1986) found evidence from field experiments that higher densities of fish in structurally more complex seagrass habitats could be explained by preferential recruitment. Hyndes *et al*. 2003 showed that fish assemblages differed noticeably among three distinct seagrass habitats, structurally divergent from each other, due to differences in e.g. leaf canopy, leaf area index and landscape configuration. They suggest that fish species show a preference for seagrasses characterised by different plant and meadow architectures. In conformity with their results, our study assumes that the fish community composition in TC and TH may be separated due to differences in structural architecture of the dominating seagrass species. Like most seagrass species, *T. hemprichii* has strap-like leaves emerged directly from the sediment surface, whereas the leaves of *T. ciliatum* are positioned higher in the water column as vertical rhizomes can extend beyond the sediment surface. Further, the zonation of seagrasses due to the tidal gradient around Inhaca Island may influence the distribution of fish. TC occurs within or in close connection to subtidal areas, whereas TH has its main extension in the intertidal zone and, thus, longer air exposure during low tide. Epiphytic algae on the stems and leaves of seagrasses might also be important for the distribution of fish as they provide food for many marine organisms (Borowitzka and Lethbridge, 1989). Additionally, existing hydrodynamic conditions can also be relevant for the fish-habitat interactions in seagrass meadows as it affects larval supply (Jenkins *et al*., 1998). However, this study shows that the spatial distribution of fish in seagrass meadows is highly variable, but indicates an interaction between fish assemblage structure and seagrass communities.

In Table 7 fish standing stock data from this study has been compared to other studies with quantitative data in different seagrass habitats. Both fish density and biomass seem to be quite low, but are still within the similar range as the comparative studies, where the mean density ranged from 0.02 to 6.08 fishes m^{-2} and the mean biomass from 0.16 to 3.84 g m^{-2}. Fish represented in this study were mainly of juvenile life-stages, possibly a result of the sampling technique used (Petrik and Levin 2000), and in turn this could underestimate the amount of fish. One conceivable limiting factor in the sampling with beam-trawl is avoidance of some large and fast-swimming fish species. Gell and Whittington (2002) showed that the choice of sampling with either seine-nets or bamboo fish traps was very important for the number of fish species caught. Thus, the diversity of fish in the seagrass meadows of Inhaca may potentially be higher using complementary sampling methodology as e.g. seine nets, gill nets, fish traps and visual census technique. Fish assemblages in seagrass meadows are also influenced by diel variation (e.g. Hindell *et al*., 2000), and hence the catch rates of fish in this study might have been higher if the sampling was done during both day and night, and not only during daytime.

TABLE 7. Fish standing stock in seagrass meadows.

Location	**Seagrass community**	**Density (fishes m^{-2})**	**Biomass (g m^{-2})**	**Source**
Puerto Rico	*Thalassia testudinum* and *Syringodium filiforme*		0.65 - 3.15	Martin and Cooper (1981)
North-east Australia	Seagrass areas (mainly *Enhalus acoroides*)		0.5 - 1.8	Blaber *et al.* (1989)
Groote Eylandt, northern Australia	Short seagrass sites		1.31 - 2.21	Blaber *et al.* (1992)
Groote Eylandt, northern Australia	Tall seagrass sites		0.16 - 3.84	Blaber *et al.* (1992)
Cairns, Australia	8 seagrass species (mainly *Zostera capricorni*)	0.88		Coles *et al.* (1993)
Southern Australia	Different seagrasses	3.03 - 6.08	1.67 - 2.58	Edgar *et al.* (1994)
Maine, USA	*Zostera marina*	1.12		Mattila *et al.* (1999)
Fremantle, Australia	*Posidonia sinuosa*	0.08 – 0.29	3.30 - 6.21	Hyndes *et al.* (2003)
Fremantle, Australia	*Amphibolis griffithii*	0.03 – 0.06	4.20 – 5.26	Hyndes *et al.* (2003)
Fremantle, Australia	*Posidonia coriacea*	0.02 – 0.05	0.73 – 1.90	Hyndes *et al.* (2003)
Inhaca Island, Mozambique	*Thalassodendron ciliatum* and *Cymodocea serrulata*	0.11 ± 0.02	0.99 ± 0.21	This study
Inhaca Island, Mozambique	*Thalassia hemprichii* and *Halodule wrightii*	0.02 ± 0.004	0.18 ± 0.08	This study

In the WIO, few studies in fish ecology deal with fish biodiversity associated to seagrass meadows. In reports from Kenya (van der Velde et al., 1995), Tanzania (Muhando, 1995), Mozambique (Almeida *et al*., 1995; Gell and Whittington, 2002; this study) and Madagascar (Mauge, 1967; Vivien, 1974; Harmelin-Vivien, 1983) typical seagrass-associated fish communities have been characterised. The most common species found belong to the families Apogonidae, Blenniidae, Centriscidae, Gerreidae, Gobiidae, Labridae, Lethrinidae, Lutjanidae, Monacanthidae, Scaridae, Scorpaenidae, Siganidae, Syngnathidae and Teraponidae. Some taxa were more restricted in their distribution, including species belonging to Plotosidae in Kenya, Atherinidae and Portunidae in Tanzania, and Pomacentridae and Tetraodontidae in Mozambique. The abundance and diversity of fish of the seagrass habitats in the present study are dominated by juvenile migrant species belonging to the families Siganidae, Labridae, Lethrinidae, Scaridae and Lutjanidae, as well as some stationary species represented in all life-stages belonging to the families Monacanthidae, Teraponidae, Syngnathidae and Blennidae. Pollard (1984) showed in a review on the ecology of seagrass fish communities that the WIO region was similar to other areas in terms of fish family composition. In particular Blenniidae, Gerreidae, Gobiidae, Labridae, Monacanthidae, Sciaenidae, Scorpaenidae, Sparidae, Syngnathidae, and Tetraodontidae were dominant throughout most seagrass habitats and geographical areas.

According to FishBase (2003), about one third of identified fish species in this study are considered important for commercial fisheries (Table 3). However, more species consecutively caught in the subsistence fishery may have significance for local people around Inhaca Island. (de Boer *et al*., 2001). Unfortunately there is little documentation available that permits to evaluate the size and importance of seagrass fisheries in ecological, social and economic terms. Information on the seagrass fisheries from the WIO is either scarce or difficult to access as it may be in report form at local institutions or authorities. However, Gell (2000) and Gell and Whittington (2002) have documented the seagrass fishery and the diversity of fishes in seagrass beds of Montepuez Bay in the north of Mozambique. The results showed that the seagrass fishery was very important at local levels. Seagrass fishery sustains over 400 fishermen in the bay. The total fish catch from an area of 35 km^2 covered by seagrass was estimated at about 500 t yr^{-1} (or 14.3 t km^{-2} yr^{-1}), with a market value of approximately USD 120 000. Part of the catch went to direct consumption and part was traded. A positive correlation was found using catch per unit effort and total seagrass cover as variables. This result indicates that seagrass coverage may influence fish biomass and fishery productivity.

CONCLUDING REMARKS

The present study provides evidence that abundance, diversity and community structure of fish varies between different seagrass sites and habitat compositions around Inhaca Island, Mozambique. Densities and biomasses of fish were generally significantly higher in *T. ciliatum* meadows relative to *T. hemprichii* meadows, and a spatial variation of fish community structures was found. The results suggest a strong interaction between fish and seagrass habitats, at least during parts of their life stages.

Seagrass meadows represent an important component of the tropical coastal zone and show similar magnitudes of productivity and fish biomass as coral reefs and mangroves. Still they have received much less attention than the other systems in terms of research and management. In Mozambique, as in many other countries of the WIO region, the pressure on the seagrass ecosystems is increasing due to a growing coastal population and overexploitation of resources. Inhaca Island is an example of an area strongly influenced by overfishing, verified by local fishermen complaining on diminishing catch rates (de Boer *et al*., 2001), and as seagrass vegetation is an important component of the intertidal flats around the island (de Boer, 2000; Bandeira, 2002) it might also be influenced by the pressure from artisanal fishery. Thus, it is important to increase the presently scarce scientific knowledge on ecological interactions, such as between fish assemblages and seagrass environments, in the region. The study presented here gives valuable information for ecological valuation of seagrass ecosystems, and especially for habitat protection and fisheries management.

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