Aquat. Living Resour. 23, 399–416 (2010)

DOI: 10.1051/alr/2011006
www.alr-journal.org

Aquatic
Living
Resources

Changes in an East African social-ecological seagrass system: invertebrate harvesting affecting species composition and local livelihood

Lina Nordlund[1,2,a], Johan Erlandsson[2], Maricela de la Torre-Castro[3] and Narriman Jiddawi[4]

[1] Department of Systems Ecology, Stockholm University, S-106 91 Stockholm, Sweden
[2] ARONIA Coastal Zone Research Team, Åbo Akademi University / Novia University of Applied Sciences, 10600 Ekenäs, Finland
[3] Department of Systems Ecology and Stockholm Resilience Center, Stockholm University, S-106 91 Stockholm, Sweden
[4] Institute of Marine sciences, University of Dar Es Salaam, P.O. Box 668, Zanzibar, Tanzania

Received 22 July 2010, Accepted 19 November 2010

Abstract – Seagrass meadows support high biodiversity and are important for invertebrate harvesting activities in developing countries. The aim of this study was to estimate the social and ecological effects of invertebrate harvesting, i.e. how this exploitation may affect/has affected seagrass variables (biomass, shoot density and canopy height), macrofaunal community structure, the use and importance of these resources for the livelihood of local people over time. A multi-disciplinary approach was used, including interviews with harvesters, observations of the number/activities of invertebrate harvesters, and a biological field study in Zanzibar, Tanzania. The study showed that women/children harvest invertebrates, and they prefer large seagrass patches, high to medium shoot density, and high seagrass cover. All interviewees said they had noticed a decline in seagrass distribution over the last decade, >20% considered it a large decline. Interviewees also reported decreased numbers of animals, but no change in the number of animal species over the last decade. The main reasons for the decline of seagrass and animals according to interviewees, are an increase in the number of harvesters, and a change in attitude, i.e. people being less careful about the intertidal zone and seagrasses. Invertebrate harvesting was found important for food security and provision of cash income. The current average catch weight was ca. 2 kg/collection day/person, and 3 kg and 5 kg, 5–10 and 30 years ago respectively according to interviewees. At present, the harvesting women earn ca 60–70% and ca 40% of what they would have if catches were the same sizes as they were 5–10 and 30 years ago respectively, according to our calculations. The field sampling within seagrass beds showed that an inaccessible/remote site had significantly higher invertebrate abundance and species richness/diversity than an exploited site (ANOVA). Multivariate statistics further revealed weak but significant differences for animal abundance and biomass between these sites. By combining findings from both interviews and field sampling this study shows that invertebrate harvesters can influence macrofaunal community structure in seagrass meadows, which in turn results in negative impacts on local harvesters' economy and livelihood.

Key words: Biodiversity / Disturbance / Human exploitation / Shellfish / Local livelihood / Seagrass beds / Social-ecological systems / Marine protected area / Zanzibar / East Africa

1 Introduction

Ecosystem goods and services, e.g. resources that can be used or provided from an ecosystem, are vital to humans. In tropical developing countries, rural communities are often directly dependent upon these natural resources for their livelihood and therefore more immediately vulnerable to changes in nature. There is an extensive utilization of the coastal resources which has led to a significant decline in the productivity and biodiversity of marine fisheries (Jiddawi and Öhman 2002). For example, the inshore fishing areas and shallow reefs surrounding the coasts of e.g. Tanzania and Zanzibar are considered overexploited and degraded (Jiddawi and Öhman 2002; Silva 2006). Further the coastal human population is growing rapidly along the East African coast (Silva 2006; Human development report 2006), and the coastal ecosystems are under increasing exploitation pressure from a number of human activities, of which fishing is only one.

Food security and livelihood opportunities are crucial for the survival of local poor people living close to coastal ecosystems. Tropical and subtropical intertidal areas, e.g. mangroves, rocky shores and seagrass meadows, provide local people with e.g. marine invertebrates, shoreline protection, fishing and

[a] linanordlund@gmail.com

harvesting grounds (Moberg and Folke 1999; de Boer et al. 2002; de la Torre–Castro and Rönnbäck 2004; Rius et al. 2006; Lange and Jiddawi 2009; Crawford et al. 2010; Unsworth and Cullen 2010). Thus, a common activity in the intertidal area, in Zanzibar and many other tropical and subtropical coastal countries, is invertebrate subsistence harvesting in the intertidal area. Invertebrate harvesting is also known as invertebrate collection or gleaning and any intertidal area that is dry enough to walk on is potentially good for invertebrate harvesting but there is a preference for mussel and seagrass beds (Keough et al. 1993; de la Torre–Castro and Rönnbäck 2004; Rius et al. 2006; Nordlund 2007; Crawford et al. 2010). In Zanzibar, many women and children living in coastal villages collect invertebrates such as gastropods, octopus and bivalves for both food security as well as some cash income (Håkansson 2006; Crawford et al. 2010). A study of the effects of shell collection on the abundance of gastropods on Tanzanian shores determined that commercially valuable species were less abundant on shores in Dar es Salaam and Zanzibar than on the sparsley populated Mafia Island (south of Zanzibar and Dar es Salaam), which is relatively unexploited with very little shell collecting. This suggests that shell collecting can potentially influence intertidal mollusc populations (Gaudian 1990; Newton et al. 1993). Furthermore an earlier study by Nordlund (2007) at Inhaca Island, Mozambique, showed that invertebrate harvesting and harbour activity can negatively affect animal abundance, biomass and species composition in seagrass meadows.

Seagrass meadows are vital invertebrate harvesting grounds and are commonly distributed in tropical and subtropical coastal intertidal areas. Seagrasses are marine angiosperms that assist in stabilizing the seafloor with their root systems and filtering or trapping harmful pollutants or particles derived from land. They are also *ecosystem engineers* (Jones et al. 1994; Coleman and Williams 2002) since they develop the habitat structure and function of the system and therefore profoundly affect community structure, resulting in an ecosystem with high diversity and many processes, such as plant and animal production (Howard et al. 1989; Duarte and Chiscano 1999). Fish and invertebrates use these habitats for foraging, protection against predators and as nursery grounds (Orth et al. 1984; Bell and Pollard 1989; Nagelkerken et al. 2000). A healthy seagrass meadow is important for the functionality of the whole seascape e.g. for coral reef ecosystems which are closely interlinked with seagrass systems (Dorenbosch 2006). Associated coral reefs may also be affected by invertebrate migration (e.g. through larval dispersal) from seagrass beds close-by, as well as by available food for reef-associated animals foraging within the seagrass ecosystem.

Seagrass habitats are rapidly decreasing worldwide due to natural causes such as storms, but primarily due to anthropogenic activities such as habitat destruction from nutrient enrichment, sediment overloading and coastal development (Green and Short 2003; Waycott et al. 2009). Globally seagrass habitats have been reduced at a rate of 110 km^2 per year during the last 30 years and ca 30% of the known seagrass area has been lost during the last century (Waycott et al. 2009). This makes seagrass meadows one of the most threatened ecosystems in the world, comparable to coral reefs, mangroves and tropical rainforests (World Seagrass Conference 2010). In the tropical regions from East Africa to Hawaii, where seagrasses are widespread, abundant, very diverse, and of vital importance for local livelihood, data gaps of seagrass distribution due to lack of research are serious (de la Torre Castro and Rönnbäck 2004; Waycott et al. 2009; Unsworth and Cullen 2010). Both the decline of seagrass habitat and the higher stress levels on the substrate from e.g. pollution could reduce species diversity and abundance of associated organisms. With fishing as a major source of protein and income, the need for healthy seagrass meadows and surrounding habitats should be over-emphasized.

This multi-disciplinary study examined the social and ecological effects (i.e. using a socio-ecological approach) of invertebrate harvesting in Zanzibar seagrass meadows. Our aims were to estimate how exploitation in the form of invertebrate harvesting has affected/may affect seagrass characteristics, macrofaunal community structure, and the use and importance of these resources for the livelihoods of local people over time. Our main hypotheses were that (1) seagrass cover and the abundance and species number of invertebrates have decreased over time because of harvesting of invertebrates (from interviews), which in turn affect catch weights and cash income negatively, (2) invertebrate harvesters are aware of many different anthropogenic factors disturbing the seagrass habitat and associated animals, and (3) a remote (i.e. virtually unexploited) site has higher invertebrate abundance, biomass and diversity than an exploited site.

2 Materials and methods

2.1 Study sites

The present study was conducted in the north-east part of Unguja Island (Zanzibar Island) in Tanzania (Fig. 1). The island is 100 km from north to south and around 30 km from east to west. The main economic activities among the local people are fishing and agriculture. Tourism on this tropical island is increasing and employs directly and indirectly almost 10% of the population (pers. comm. Jula Bishop, chairman Zanzibar Association of Tourism Investors). The tides are semi-diurnal and the tidal range is large, varying from 3–4 m during spring tide and about 1 meter for neap tide.

The north eastern part of Unguja Island has an intertidal area characterized with a hard bottom (pavement) covered with a layer of sand and patchy seagrass meadows. Thirteen different seagrass species can be found in the Western Indian Ocean (Gullström et al. 2002), and eight species in northern Zanzibar, of which the most common are *Thalassia hemprichii* and *Thalassodendron ciliatum* (formerly *Cymodocea ciliate*). Close to the beach there is a mixture of seagrass species: *Halodule* sp.(Forsk.) Aschers, in Bossier, *Cymodocea rotundata* Ehrenb. and Hempr. ex Aschers, *T. hemprichii* (Ehrenberg) Asherson. Further out in the intertidal area, where the seagrass is coverd by seawater to a greater extent i.e. less exposed, there is a domination of *T. ciliatum* (formerly *C. ciliata*) (Forskål) den Hartog. Also *Halophila ovalis* (R. Br.) Hook. *f*., *Syringodium isoetifolium* (Ascherson) Dandy and *Cymodocea serrulata* (R. Br.) Aschers. and Magnus, *Halophila stipulacea* (Forssk.) Ascher. can be found in the area. The intertidal area is lined by a coral reef (pers. observation).

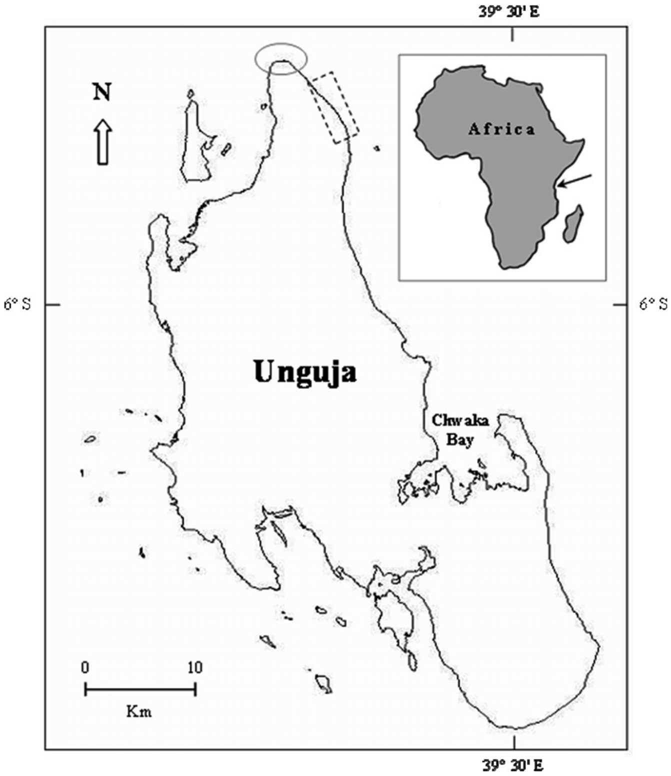

Fig. 1. Map showing the location of Unguja Island (i.e. Zanzibar), Nungwi intertidal area (the exploited site) within the grey circle and the remote site in the dashed box.

Two sites were chosen at the northern part of Unguja Island for this study, one exploited site (Nungwi village) and one inaccessible/remote site (Fig. 1). The exploited site is positioned at the very northern tip of the island, around 05°43′S and 039°17′E (Fig. 1). There are approximately 560 people in Nungwi village and 7900 people living in the surrounding area, Nungwi – Rural Sheiha (National Bureau of Statistics, Tanzania). Along the beach in Nungwi there are mostly budget hotels, and larger hotel complexes can be found further away from the village. On the beach shells are sold to tourists. Outside Nungwi village the intertidal area where invertebrate harvesting occurs are around 2 km^2. We found that the village of Nungwi was suitable for the interview study and for representing the exploited site for the biological field sampling due to its many invertebrate harvesters. The inaccessible/remote site is located further down south on the east coast (about 10 km by boat from Nungwi; Fig. 1). The intertidal area resembles the site outside Nungwi, but there were no invertebrate harvesters due to lack of habitation for its remoteness and lack of access without boat and traditionally women do not use fishing boats. The site chosen for the biological field sampling was around 2 km^2, i.e. of similar size to the exploited site.

2.2 Interviews

Structured interviews with mainly open-ended questions were performed with local coastal people in Nungwi village between November 2007 and January 2008 (Appendix 1). All eighteen interviewees were randomly selected and the sample size about 10% of the potential invertebrate harvesters in Nungwi village (National Bureau of Statistics, Tanzania). Eighteen females between the age of 9 and 92 years (of whom 5 were children) were interviewed, both current harvesters as well as harvesters in the past. Only a small fraction of all invertebrate harvesters are males in Nungwi, i.e. young boys and some men spearfishing octopus (pers. observation). The interview questions were planned to reflect social-ecological data about invertebrate harvesting activities and the seagrass habitat. We carried out interviews to: (1) examine when, how often and where invertebrate harvesting occurred/occurs and which animals were/are collected, (2) estimate whether seagrass cover has changed over the last 10–30 years, (3) estimate if animal abundance and species richness have decreased over the last 10–30 years, (4) determine if the invertebrate harvesting activity and local livelihood have changed, (5) evaluate subsistence and economic importance of invertebrate harvesting, (6) evaluate if there are signs of overexploitation from the invertebrate harvesting activity (Appendix 1; Table 1). The interviews were conducted in Kiswahili with the assistance of an interpreter. The answers were written down during the interview process. Pictures of different species etc. were shown for some of the interview questions for the interviewees to refer to when selecting their preferred choice. Pictures of different seagrass characteristics i.e. density (shoots), cover and patch size (drawn by Nordlund; Appendix 1) and seagrass species as well as 337 pictures of invertebrate species were shown derived from Richmond (2002). The duration of each interview was between 40 min to 1 h. A matrix containing all gathered answers was created to obtain a systematic overview prior to analyzing the interview. The interviews were analyzed qualitatively by grouping the answers in themes or categories and quantified by simply counting the number of respondents giving a certain answer (e.g. Kvale 1996). Furthermore, the number of replies obtained directly from the interviews, or the categorization, was expressed as percentage. Observations of the number of invertebrate harvesters were carried out at both the exploited and inaccessible/remote site. The number of harvesters was counted during spring tide for 3 months (a total of 15 days during low spring tide at each site). No harvester was ever observed in the inaccessible/remote site. Observations were also performed to get a rough overview of the spatial distribution of harvesters in the exploited site.

2.3 Biological field sampling

We carried out a biological inventory to estimate if there was a difference in biomass, shoot density and canopy height of seagrasses between an inaccessible/remote and an exploited site, and if there was a higher invertebrate abundance, biomass and species richness in the inaccessible/remote site than the exploited site. The biological field sampling was performed between October 2007 and December 2007. Within the exploited and the unexploited sites 20 and 22 seagrass patches were chosen respectively, both sites dominated by *Thalassodendron ciliatum*. The seagrass patches were chosen by firstly identifying the sites on a satellite image, followed up by travelling to the site by boat. The specific seagrass patches were selected around the anchored boat. A quadrate (size: 0.25 m^2)

Table 1. Answers by interviewees/harvesters to some important questions discussed in the text (n = 18 interviewed people).

Question	Answer	Percentage (%) of replies	Absolute numbers of replies	Total number of answers
14. Have you noticed any changes in the seagrass distribution during your lifetime? (what are the changes? How has the distribution changed, and why in your opinion?)	No change	0	0	18
	Small decrease	78	14	
	Great decrease	22	4	
15. Have changes in the seagrass meadows affected your collection activities? If yes, How?	Yes	83	15	18
	No	17	3	
16. Has the number of animals changed the last years? How and why?	Yes	94	17	18
	No	6	1	
17. Have the animal species changed the last years? How and why?	Yes	6	1	18
	No	94	17	
19. Why do/did you collect animals?	Food	28	5	18
	Food and sell	72	13	
21. If you sell/sold animals, what is the income? (average per day; TZS)	0-1000	8	1	13
	1001-2000	38	5	
	2001-3000	23	3	
	3001-4000	0	0	
	4001-5000	15	2	
	5001-6000	15	2	
	6001-	0	0	
23. Have tourist activities affected your collection activities? If yes, How?	Yes	0	0	17
	No	100	17	
25. Can you describe a normal catch when you collect one day (pics, kilo)	1 kg	21	3	14
	2 kg	50	7	
	3 kg	21	3	
	> 4 kg	7	1	

was thrown haphazardly in the middle of the seagrass patch. All above-ground seagrasses and animals (>0.5 cm) in the quadrate were collected and stored in a frozen condition until the laboratory was reached. The sampling of organisms was performed simultaneously as invertebrate harvesting was carried out by villagers, i.e. during low spring tide, so that comparable data were sampled.

In the laboratory, the animals sampled during the biological inventory were identified to species level (otherwise to the lowest taxonomic level possible). The animals were counted, dried and then weighed (Short and Coles 2001). The shoots from *T. ciliatum* and its associated seagrass species were cleaned in fresh water, dried and weighed, and then the shoots were counted separately to obtain shoot density. The plants were measured for mean length (i.e. canopy height) per quadrate (Short and Coles 2001). Drying of both animals and plants was executed until no weight loss was recorded, but always for a minimum of 48 h at 90 °C (method adopted from

Table 2. List of animals found during the biological inventory for the exploited site (20 quadrates with a total of 5 m^2) and the inaccessible/remote site (22 quadrates with a total of 5.5 m^2) with animal abundance and biomass (absolute numbers) shown. H-herbivores, C-carnivores, O-omnivores, F-filter feeder, S-suspension feeder, M-macrophages.

EXPLOITED (5 m^2)		
Species/taxa	Abundance/ species (*n*)	Dry weight/ species (g)
Anadara antiquata (F)	1	6.1
Arca avellana (F)	1	0.3
Astropectinidae (C,H or S)	1	9.5
Bivalvia (F)	2	0.8
Bryozoa (F)	1	0.3
Conus betulinus (C)	4	19.3
Demospongiae (F)	5	8.9
Diogenidae (H, C? and S)	1	0.3
Fulvia sp. (F)	1	2.5
Holothuria edulis (S)	2	7.0
Isogonium sp. (F)	2	2.3
Limidae (F)	1	13.1
Ophiurida (C or M)	1	0.9
Paguroidea (F)	2	1.2
Pinctada margaritifera (F)	7	108.0
Stombus gibberulus (H)	1	10.3
Stomopneustes variolaris (H?)	1	9.2
Tectus sp. (H)	3	0.7
Tridacna maxima (F)	1	329.0
Tripneustes gratilla (H)	1	33.0
Unknown	2	1.8
21 different taxa Total:	41	564.0

INACCESSIBLE/REMOTE (5.5 m^2)		
Species/taxa	Abundance/ species (*n*)	Dry weight/ species (g)
Acrosterigma elongatum (F)	1	24.0
Amphipholis squamata (C or M)	1	0.1
Anadara antiquata (F)	6	51.0
Arca avellana (F)	1	5.3
Bivalvia (F)	1	3.3
Cardiidae (F)	2	30.0
Ciliopagarus strigatus (C and S)	1	3.8
Conus lividus (C)	1	1.4
Conus sp. (C)	3	6.0
Cypraea annulus (H)	4	11.0
Cypraea citrina (H)	1	1.2
Demospongiae (F)	14	70.0
Diodon liturosus (C)	1	45.0
Echinometra mathaei (H)	9	109.0
Gafrarium sp.(F)	2	10.0
Gastropoda (H,C and/or S)	3	5.3
Harpa costata (C)	1	7.5
Holothuria edulis (S)	1	28.0
Majidae (O)	1	0.2
Ophionereis porrecta (D)	1	1.7
Paguroidea (F)	5	20.0
Phasianella nivosa (H)	1	1.4
Phasianella sp. (H)	3	3.0
Pinna muricata (F)	12	80.0
Pitar hebraea (F)	1	2.2
Portuniinae (C and H)	1	0.1
Stombus gibberulus (H)	1	1.6
Tectus sp. (H)	14	3.4
Terebra sp.*(C)*	1	0.3
Unknown	1	12.0
Veneridae (F)	1	5.9
31 different taxa Total:	96	542.0

Short and Coles 2001). Molluscs and hermit crabs were dried and weighed including shells.

2.4 Statistical analyses

Unpaired two-tailed or one-tailed 2-sample *t*-tests (depending on the hypothesis tested), were used to determine significant differences between sites for animal and seagrass data (Quinn and Keough 2002). One-tailed 2-sample unequal variance *t*-tests (according to Keselman et al. 2004 and Ruxton 2006 this is a very robust, reliable and underused test) were used to test hypotheses of the variables of macrofaunal estimates (abundance, richness, biomass) being greater in the inaccessible/remote site than in the exploited site. Data were log or square root-transformed when needed to meet basic statistical assumptions, i.e. homoscedasticity and normal distribution. Mann-Whitney U-test was used when data were non-normally distributed. Correlation analyses (Pearson correlation coefficient) were performed for animal and seagrass variables to investigate their different relationships. Spatial patterns of invertebrate communities were examined for animal abundance and biomass with a non-parametric multivariate technique, which is considered sensitive for detecting community composition patterns in seagrass assemblages (Bowden et al. 2001). One-way analysis of similarities (ANOSIM) tested for differences in invertebrate community structure among localities (Clarke and Warwick 1994). The similarity of percentages (SIMPER) procedure was carried out to determine which animal species contributed most to similarities and dissimilarities within and between sites (Clarke 1993). The multivariate analyses were carried out using Primer version 5.2.4 (Clarke and Gorley 2001).

3 Results

3.1 Interviews

3.1.1 The Interviewees

Most women were housewives (n = 8) or students (n = 3) but also farmer (n = 1) and small business women (n = 1) were represented.

Almost half of the 18 interviewees had been harvesting invertebrates for more than 20 years outside Nungwi. The age span among the interviewees was 9–92 years with a mean age of 33.3 and median age of 30.0. Twelve of the interviewees were at present harvesters and six had been invertebrate harvesters in the past. The reasons given as to why these six harvesters were not collecting anymore were that they were either too old (n = 2), not physically fit (n = 4), have other jobs (n = 2) and/or due to unprofitability (n = 2), with some of them fitting into more than one category. A compilation of the most important interview results that are discussed can be seen in Table 1.

3.1.2 Invertebrate harvesting activity

All women were collecting invertebrates during spring low tide and 11% (n = 2) were also collecting during neap low tide. During spring tide the women collected between 2 and 7 days per spring tide, with an average of 3.8 days, and students were collecting on weekends or their days off. The two women who collected during neap tides did so for one day and 2 to 5 days per neap tide respectively. The amount of time harvesters spend collecting regardless of spring or neap tide is 1–5 h, with an average of 2.6 h per day. There was also a tendency that the women stay out longer towards the end of the spring tide period. Up to 150 people were observed in the intertidal site outside Nungwi when observations of the invertebrate harvesting activities were made during low spring tide for a total of 15 days. Some of the respondents also mentioned that there were usually over one hundred harvesters in the area outside Nungwi during spring tide. We estimated that ca 130 people collect during one day of low spring tide based on personal observations and the answers from the interviewees. We estimated that on average a person collects invertebrates for 40.5 days per year, based on answers from the interviewees.

The invertebrate harvesting activity starts early in life, at the age of 5–7 years. The young harvesters often follow their mothers or other relatives to learn how to harvest invertebrates.

3.1.3 Collection grounds

The interviewed harvesters were evenly distributed over the intertidal area close to the shore when collecting invertebrates outside the village, but less harvesteres were present as distance from the shore increased. Ninety four percent (94%, n = 17) of the women preferred seagrass as collecting grounds. One interviewee also mentioned coral rubble and one mentioned sand as good grounds.

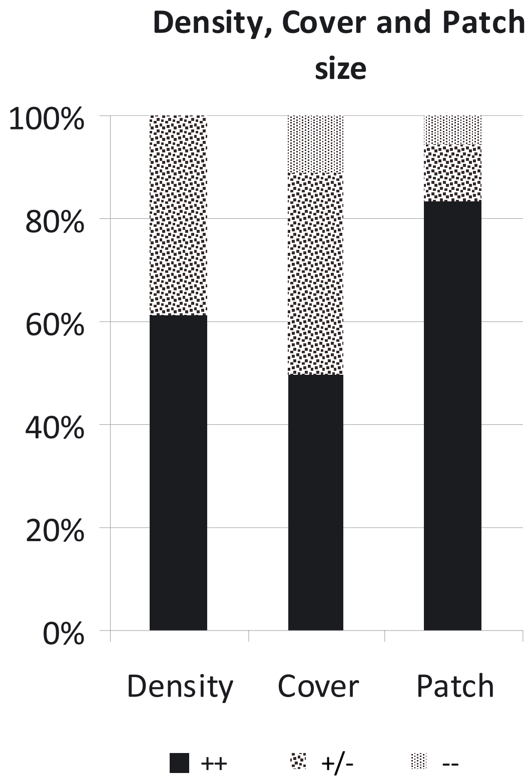

Fig. 2. The preferred choice of the invertebrate harvesters for three seagrass characteristics (n = 18 harvesters): seagrass shoot density, seagrass cover and seagrass patch size (in black = high or large ++; dotted = medium +/-; in grey = low or small –).

All seagrass species in the area were shown on pictures where harvesters could point to their preferred choice of seagrass habitat. *Thalassodendron ciliatum* was the first choice of seagrass for 44% (n = 8) of the women, followed by *Thalassia hempricii, Halodule* sp. and *Cymodocea* sp.

Pictures of characteristics of seagrass meadows were shown to the respondents (Appendix 1) resulting in preferred seagrass characteristics of high (n = 11) to medium (n = 7) shoot density, high (n = 8) to medium (n = 6) seagrass cover and large patch size (n = 15) (Fig. 2).

3.1.4 Ecological changes and their effects

All interviewees reported a change in the seagrass cover outside Nungwi over the time that they have been invertebrate harvesters (which in general meant up to the last 2–3 decades as most women have been active during this time). They all reported that there has been a decline in cover, but the experience of the level of decline differed between the respondents. 78% mentioned a small decrease and 22% mentioned a decrease of ≥50% within the last 15 years. The greater reduction was mentioned mostly by women in their 30's and 40's (Table 1).

Almost all of the women (94%, n = 17) said that the number of animals has decreased in the last 5–10 years (Table 1). Only the youngest interviewee (age 9) responded that she was not sure if she witnessed a change in animal abundance. Eighty three percent (83%, n = 15) of the interviewees said that the

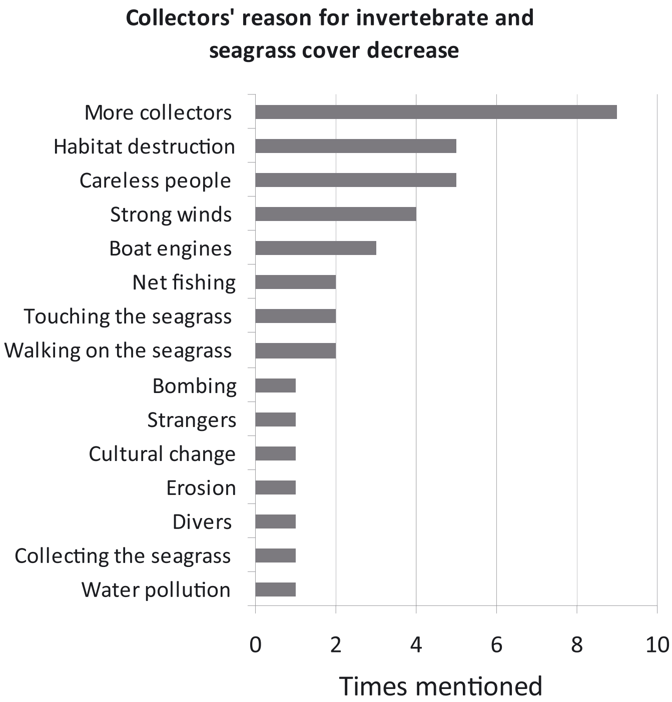

Fig. 3. Frequency of the different reasons for the decline of invertebrates and seagrass cover reported by invertebrate harvesters.

changes regarding seagrass meadows have had an impact on their harvesting activity (Table 1). Many mentioned that they need to collect during a longer period of time in order to get the same amount of animals as before, thus clearly showing that the effort has increased. Furthermore, they noted that they received less income because of fewer animals; two women declared that it is hardly worth the effort of collecting today due to the small catch size. Only one of the eighteen women mentioned a change in invertebrate species compared to before; however, she started collecting invertebrates in the 1920's. Nonetheless, some of the other women voiced that it is harder to find some species nowadays, thus inferring that the abundance and species diversity (but not species richness) have decreased.

The reasons mentioned for the decrease of invertebrates and seagrass cover were diverse, but the most common ones mentioned by harvesters included "more invertebrate harvesters", "careless people" (people not caring about the intertidal area and the seagrass environment), "habitat destruction", "strong winds", and "boat engines" (Fig. 3). When asked whether tourist activities have affected the harvesting activities all of the respondents said no ($n = 18$), but one also added that she sometimes can sell shells to tourists.

3.1.5 Invertebrate harvesting as a subsistence activity

Invertebrate harvesting is above all a subsistence activity in Nungwi. All interviewees collect to increase food security in the household, but 72% ($n = 13$) also said they sell or sold parts of their catch as a complement to food collection (Table 1). The catch range among the present harvesters is 1–3 kg, with an average catch weight of 2 kg, during 2–4 hours of invertebrate harvesting in one day of spring tide (Table 1). The very young harvesters are in the lower catch range. Some of the respondents mentioned that the catch weight range 5–10 years ago were 3–5 kg (estimations from 82% of the interviewees) and that 30 years ago the catch weight was around 5 kg (estimations from 67% of the interviewees). These estimations are based on memories and the interviewees showing how the bucket was filled 5–10 and 30 years ago. The strategy today among many of the harvesters is to collect everything they can find that they know can be eaten or sold. Only 24% of the interviewees felt that collection is also a social activity while the majority 76% said it is simply work.

Animals collected were identified by the respondents ($n = 14$) from 337 pictures of different common invertebrate species in the intertidal area. A list of invertebrates generally exploited by the respondents is shown in Appendix 2. The species used for home consumption and commercial purposes were noted, with molluscs being the main harvested group. An estimated weight of the invertebrates collected is around 10 metric ton per year based on answers by present harvesters in the exploited site. This calculation is based on an average of 130 people/collection day collecting for 40.5 days per year and with an average catch weight of ca 2 kg per person and day of collection. If the catch weight per person and day is increased to 3 kg (5–10 years ago) the yearly catch would be ca 16 metric ton, and if the catch is increased to 5 kg (30 years ago), the estimated catch of invertebrates would be ca 26 metric ton per year.

3.1.6 Socio-economic aspects

The average income range for the invertebrate harvesters that sell parts of or the whole catch is 0.85-2.55 USD /catch (1000-3000 TZS) for 2–4 hours of invertebrate harvesting during one day of spring tide (exchange rate: 1 USD – 1176 TZS). The absolute maximum income on an extremely profitable day is 8.51-17.01 USD/catch, in which case it was reported to be attributed to the presence of a couple of octopuses in the catch. One of the respondents also sold shells directly to tourists. Species collected to be sold are shown in Appendix 2. An estimation of the total cash income for all invertebrate harvesters together in the exploited area is ca. 10 264 USD per year which yields approximately 79 USD per person and year. This calculation is based on an average of 130 people/collection day collecting for 40.5 days per year and with an average income of ca 2 USD per person and day of collection. The individual harvester nowadays collects on average ca 2 kg per day and collected ca. 3 kg 5–10 years ago and 5 kg thirty years ago. Thus, at present the harvesting women earn ca 60–70% and 40% of what they would have done if catches were of the same sizes as 5–10 and 30 years ago respectively.

3.2 Biological inventory of seagrasses and animals

3.2.1 Seagrass inventory

No significant differences in seagrass biomass ($df = 38$, $t = 0.05$, $p = 0.96$) and total seagrass shoot abundance

(df = 39, t = −0.11, p = 0.91) were found between the exploited and inaccessible/remote sites. Overall there was a dominance of *T. ciliatum* and very few *T. hemprichii* shoots at both sites. Canopy height was not significantly different between the sites, although slightly taller shoots were present at the inaccessible/remote site than at the exploited site (Mann-Whitney Test; W = 354, p = 0.057).

3.2.2 Animal inventory

During the biological sampling, a total of 21 different animal species/taxa in all 20 sampled quadrates were found in the exploited site outside Nungwi. In the inaccessible/remote site 31 different animal species/taxa in 22 sampled quadrates were identified (Table 2). The total determined animal abundance was 41 in the exploited site and 96 in the inaccessible/remote site (Table 2), and the Shannon Wiener Diversity Index for the exploited site and inaccessible/remote site was estimated to 1.65 and 3.05 respectively. Regarding animal abundance, the variance was 4.05 for the exploited site and more than 6 times higher (25.85) for the inaccessible/remote site. Furthermore, the inaccessible site had ca two times higher species richness of collected/commercial invertebrates than at the exploited site (Table 2, Appendix 2).

Animal abundance was significantly higher at the inaccessible/remote site than at the exploited site (Fig. 4; df = 34, t = 1.84, p = 0.037). A significant difference in species richness was found between the sites, with greater richness at the inaccessible/remote site than at the exploited site (df = 27, t = 1.97, p = 0.03; Fig. 4). No significant difference in animal biomass was found between the sites (df = 24, t = −0.02, p = 0.58), but one sample from the exploited site outside Nungwi contained a Giant clam (*Tridacna maxima*) with a shell weight of more than half of the total animal weight of that site (Fig. 4). If the Giant clam shell is excluded from the test there was a significantly higher animal biomass at the inaccessible/remote site than at the exploited site (df = 36, t = 1.75, p = 0.044; Fig. 4).

3.2.3 Relationships among animal and seagrass variables

There was no significant relationship between animal abundance and the number of seagrass shoots in the exploited site (r = 0.31, p = 0.18) or for the remote site (r = 0.17, p = 0.44). No significant relationships between animal abundance and seagrass biomass were detected at either site, or when sites were pooled (r = −0.07 to 0.25, p = 0.29–0.93).

No significant relationships between animal biomass and seagrass biomass or between animal biomass and the number of seagrass shoots were found at each site and no significant relationship was found when sites were pooled (r = −0.04 to 0.11, p = 0.57–0.87). The correlation analyses between seagrass variables revealed that only the correlation between seagrass biomass and shoot density was significant at both sites (exploited site: r = 0.55, p = 0.01; inaccessible/remote site: r = 0.80, p = 0.0001), and seagrass biomass vs canopy height was significant at the inaccessible/remote site (r = 0.56, p = 0.006).

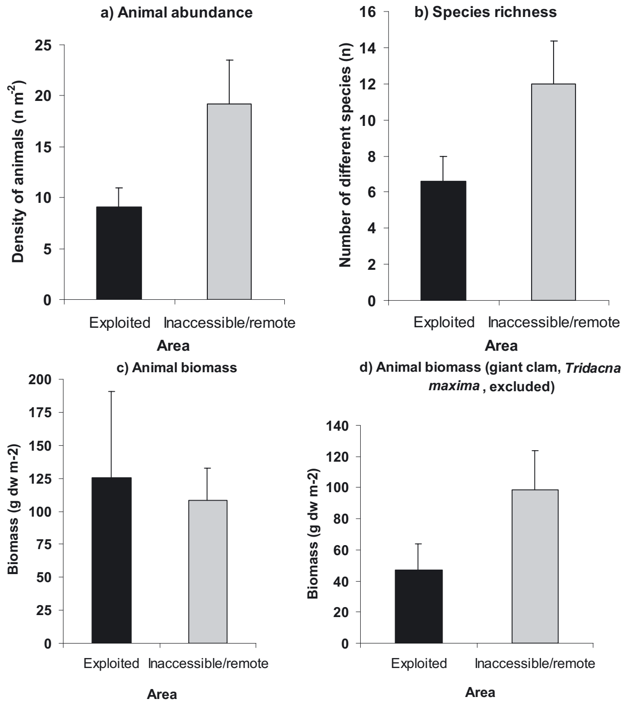

Fig. 4. Means of animal abundance was significantly higher at the inaccessible/remote site than at the exploited site (a), species richness was significantly higher at the inaccessible/remote site (b), animal biomass showed no difference between sites (c) and animal biomass with the giant clam excluded was significantly higher at the inaccessible/remote site (d). Bars denote mean ± SE.

3.2.4 Animal community structure

Multivariate analyses of animal abundance and animal biomass showed weak but significant separations in invertebrate community structure between the exploited and inaccessible/remote sites (ANOSIM; abundance: global R = 0.13, p = 0.005 biomass: global R = 0.16, p = 0.002. The average similarity (calculated with the SIMPER analysis) at the exploited site was mainly attributed to Demospongiae and *Pinctada* sp. for the abundance and *Pinctada* sp. and *Holothuria edulis* for the biomass (Tables 3 and 4). At the inaccessible/remote site it was mainly attributed to Demospongiae and *Echinometra mathaei* for the abundance and to Demospongiae and *Pinna muricata* for the biomass (Tables 3 and 4). The average dissimilarity (calculated with the SIMPER analysis) between sites was mostly explained by Demospongiae and *Tectus* sp. (abundance) and by Demospongiae and *Echinometra mathaei* (biomass; Tables 3 and 4).

4 Discussion

In this study the main findings were that invertebrate harvesters have observed or experienced a decline in animal abundance and seagrass cover over the last two decades. This situation seems to have affected catch weights and subsistence for harvesters in negative ways during this time period. Our calculations (based on the answers by interviewees) show that

Table 3. Average similarity (%) and species contributing to similarities within the exploited and inaccessible/remote site, and average dissimilarity (%) and species contributing (<2%) to dissimilarities between the sites based on animal abundance.

Exploited (E)	Inaccessible/remote (C)	Exploited vs. inaccessible/remote (E vs. C) (E vs. C)
Average similarity: 5.7%	Average similarity: 14.0%	Average dissimilarity: 93.4%
Demospongiae (30.1%)	Demospongiae (51.3%)	Demospongiae (14.0%)
Pinctada sp. (22.6%)	*Echinometra mathaei* (13.4%)	*Tectus* sp.(7.7%)
Tectus sp. (14.1%)	*Pinna muricata* (9.9%)	*Echinometra mathaei* (7.6%)
Holothuria edulis (8.4%)	Paguroidea (6.2%)	*Pinctada* sp. (6.1%)
Conus betulinus (7.5%)	*Anadara antiquata* (4.6%)	*Pinna muricata* (5.9%)
Unknown (6.7%)	*Tectus* sp. (4.2%)	Paguroidea (4.3%)
Paguroidea (4.8%)	Gastropoda (3.1%)	*Anadara antiquata* (4.3)
		Conus betulinus (3.3%)
		Cypraea annulus (3.3%)
		Holothuria edulis (3.2%)
		Unknown (3.2%)
		Gastropoda (2.8%)
		Cardiidae (2.4%)
		Conus sp. (2.4%)

Table 4. Average similarity (%) and species contributing to similarities within the exploited and inaccessible/remote site, and average dissimilarity (%) and species contributing (<2%) to dissimilarities between the sites based on animal biomass.

Exploited (E)	Inaccessible/remote (C)	Exploited vs. inaccessible/remote (E vs. C)
Average similarity: 2.8%	Average similarity: 8.4%	Average dissimilarity: 97.8%
Pinctada sp. (28.6%)	Demospongiae (42.5%)	Demospongiae (11.7%)
Holothuria edulis (24.3%)	*Pinna muricata* (18.2%)	*Echinometra mathaei* (10.8%)
Conus betulinus (19.4%)	*Echinometra mathaei* (16.4%)	*Pinctada* sp. (8.9%)
Demospongiae (16.7%)	*Anadara antiquata* (7.6%)	*Pinna muricata* (7.6%)
Unknown (7.3%)	*Cypraea annulus* (6.4%)	*Anadara antiquata* (6.8%)
		Tridacna maxima (6.3%)
		Holothuria edulis (4.3%)
		Tripneustes gratilla (4.0%)
		Conus betulinus (3.8%)
		Cardiidae (3.6%)
		Unknown (3.4%)
		Cypraea annulus (3.0%)
		Harpa costata (2.6%)
		Stomopneustes vairolaris (2.3%)
		Acrosterigma elongatum (2.3%)
		Paguroidea (2.2%)
		Diodon liturosus (2.1%)
		Astropectinidae (2.0%)

the value of catches at present would have been ca 1.5–2.5 times higher if catches were of the same sizes as 10–30 years ago. Furthermore, the inaccessible/remote site had higher animal abundance and species richness than the exploited site confirming the observations by invertebrate harvesters that an intense and frequent harvesting can affect animal communities in seagrass meadows.

4.1 Importance of invertebrate harvesting for harvesters' livelihood

Invertebrate harvesting has a strong gender aspect and a long tradition with almost exclusively women collecting (this study; Håkansson 2006). Some men occasionally come onto intertidal areas to collect invertebrates, as reported from Chwaka Bay 70 km southeast of Nungwi (de la Torre-Castro and Rönnbäck 2004). Women in Tanzania have a significant role in fishing outside the formal fishing sector (Jiddawi and Öhman 2002). Most women harvest invertebrates during spring low tide, and seagrass is the preferred ground for invertebrate harvesting. This points out how important the seagrass meadows are for the harvesters. The preferred seagrass characteristics are high to medium shoot density, high to medium seagrass cover and large patch size. This implies that fragmentation and attenuation of the seagrass meadows could be negative for the harvesters.

The main driving force for invertebrate harvesting is subsistence, mainly for food consumption in Nungwi, even though many of the harvesters occasionally sell parts of their catch for some cash income. However, Håkansson (2006) found the contrary for Chwaka Bay in Zanzibar, where invertebrate harvesting is primarily for economic reasons and harvesting for food consumption is secondary, although still important as a safety net function and to add variety in protein consumption. Even though the harvesting is mainly for food securing in Nungwi the present yearly catch in the area generates roughly 10 300 USD per year, which averages to around 79 USD per harvester and year. This is an important cash income for the household, so a decrease in catch weight could result in lost or reduced cash income. The comprehensive understanding among the women is that the amount of invertebrates has declined over the last decade or more on the collection grounds outside Nungwi, and the effort has clearly increased. The amount of available food and cash income have decreased for the villagers. At present the invertebrate harvesting women seem to earn only 40% and 60–70% of what they would have done if catches today were of the same sizes as 30 and 5–10 years ago respectively.

4.2 Perceptions of changes and damages in the seagrass meadows

The interviewees report that the seagrass cover outside Nungwi has declined during the last 1–2 decades. However, seagrass patches are very dynamic; they move, become denser or less dense, arise or disappear and these natural changes were also mentioned by some of the interviewees, but the women seem to agree on a general decline in seagrass cover outside Nungwi. Remote sensing can be used to investigate changes in seagrass distribution and biomass (Knudby and Nordlund, in press). Gullström and Lundén (2007) detected small overall changes in submerged aquatic vegetation (SAV), i.e. seagrass and macroalgal cover, from 1986 to 2001 on the north eastern coast of Unguja Island (remote sensing of both sites in the present study), but important losses and gains at the local scale had occurred. The overall change was a total loss of about 8% in SAV distribution. According to the interviewees the decrease they mentioned has occurred during the last 10–15 years but unfortunately there is no remote sensing data over distribution changes between 2001 and 2009. Remote sensing data from Chwaka Bay south-east of Nungwi showed a general pattern that the deeper, outer parts of the bay revealed fewer changes in seagrass dominated SAV compared to the near-shore environment (Gullström et al. 2006). This kind of information would also be very interesting to gather from the site outside Nungwi. Healthy seagrass meadows hold a high invertebrate diversity and studies have shown that seagrass meadows have significantly greater species richness than unvegetated habitats (Edgar 1990; Boström and Bonsdorff 1997; Nakamura and Sano 2005). The decline in seagrass cover, reported by interviewees, may have negatively affected the abundance of invertebrates due to habitat loss and fragmentation.

The general opinion among the invertebrate harvesters is that the abundance of invertebrate species has decreased in the site outside Nungwi village, especially so during the last decade, although it may also have been a gradual decline during 30 years (e.g. ca. 5 kg/catch 30 years ago, 3 kg/catch 10 years ago, 2 kg/catch at present). This observation by the interviewees is alarming, since the livelihood component is so important and since the sustainability thresholds are unknown. There was only one respondent who answered that the animal species composition has changed, a woman who started to collect invertebrates in the 1920's, while many mentioned that some species are more difficult to find today. This implies that the species richness is almost the same but that abundance and species diversity (e.g. Shannon index) are lower now. The actual situation with great difficulties and efforts in finding many species may be an early warning sign showing that relevant changes are taking place in the area.

Some possible reasons for the decline in animal abundance could include the increasing human population, resulting in higher numbers of harvesters. The number of invertebrate harvesters in Zanzibar seagrass meadows has been limited in the past due to small village populations, but significant demographic changes have occurred over the last 10–15 years. The population and migration have increased and tourism has grown, resulting in higher resource pressure. A change in attitude, i.e. people caring less about the environmnet in general and about seagrass ecosystems in particular, was recognized among the harvesters. One of the reasons of increased carelessness might be the higher pressure on local people's livelihoods, which can create a higher pressure on the seagrass ecosystem. Around twice the numbers of generally collected/commercial invertebrate species were found in the inaccessible site compared to the exploited site, suggesting that the exploited site is negatively affected.

One of many reasons for the decrease in seagrass cover might be due to boat anchoring causing broken and uprooted seagrass shoots (Francour et al. 1999). The general opinion among the harvesters is that tourism activities do not affect the harvesting activity *per se*. However, some of the reasons mentioned for the decrease in animals and seagrass cover were habitat destruction through e.g. construction and boat engines, which is directly related to increased tourism and boating activities. But the women interviewed did not link this destruction with the tourism increase in the area (from 56 415 to 134 954 tourists/year in Zanzibar 1995-2009, ZATI Tourism Statistics).

4.3 Comparison between exploited and inaccessible sites

The biological inventory revealed that the two sites were very similar regarding seagrass characteristics, e.g. seagrass biomass and shoot abundance. However, the inaccessible site showed greater animal abundance, species richness, and a five-fold larger variance of the total animal abundance. This larger variance of animal abundance at the inaccessible site supports the hypothesis that there are fewer animals and therefore less spatial variability in the exploited site. The Shannon-Wiener index was also higher at the inaccessible site. One potential reason for the difference between the two sites in invertebrate community structure is the invertebrate harvesting activity, and as a consequence some species are more difficult to find. Since there were hardly any differences in seagrass characteristics between the two sites, the meadows characteristics are unlikely to cause the observed differences in macrofaunal community structure. No relationships were found between seagrass characteristics and animal abundance/biomass in the present study.

An earlier study with an extensive biological inventory showed a positive relationship between seagrass biomass and animal abundance/biomass in another East African area (Nordlund 2007).

Invertebrate harvesting and harbour action have been shown to negatively affect animal abundance, biomass and species composition in seagrass meadows (Nordlund 2007). The present study similarly points out negative effects on animal abundance and animal diversity due to extensive harvesting pressure in the exploited site. Replication of exploited and unexploited sites was not possible, as unexploited seagrass localities are very rare in Zanzibar. The present study has strong multi-disciplinary components. The recognition of marine systems as social and ecological integrated units has lately been highlighted in coral fisheries of the Western Indian Ocean (Cinner et al. 2009). In a similar way, we argue that an integrated approach is needed to understand invertebrate harvesting activities. In our study we used a biological study comparing the invertebrate community between sites with different degrees of exploitation, a social study investigating local people's perceptions of changes, due to exploitation, and effects on their local livelihood. The combination of these two data sets provide a better understanding of the problem and indicates that long-term invertebrate harvesting may locally reduce macrofaunal diversity, while diversity in inaccessible seagrass meadows can be sustained. A reduced diversity or abundance of key species due to invertebrate harvesting may also affect ecosystem function negatively (Cardinale et al. 2006). The present study showed that functional groups like filter-feeders and carnivores (e.g. bivalves and gastropods respectively) are harvested to a larger degree than other groups (Appendix 2). Also on the east coast of South Africa local people have mainly been harvesting bivalves and gastropods, reducing the intertidal mussel beds there to almost non-existence, with a change in community structure and dramatic declines in biodiversity and ecosystem function (Lasiak 1991; Dye 1992; Lasiak and Field 1995). These mussel beds also have extreme difficulties to recover through natural recruitment, since there are strong adult-recruit relationships and high post-settlement mortality (Erlandsson et al. 2006; Erlandsson et al. 2008). This is also an example of the classic theory "the tragedy of the commons", which will deplete biological resources and impoverish local people (Hardin 1998). Zanzibar seagrass beds seem to be not as heavily affected by invertebrate harvesters, although ecosystem function can be impaired when drastically changing animal associated communities. The use of the optimal foraging theory showed that differences in prey choice and spatial variation in exploitation by invertebrate harvesting women and children can be understood as a strategy aimed at maximizing intake and the relative value of a prey species (de Boer et al. 2002), and this could seriously affect the abundance of e.g. molluscs and the function of the system. Signs of overexploitation can be difficult to identify due to lack of information about the life history of species. Tropical seagrass beds are very complex (Waycott et al. 2009) and understudied socio-ecological systems (de la Torre-Castro 2006), and in order to being able to maintain the flow of goods and services from this ecosystem the life history of seagrass associated organisms needs to be investigated further. To conclude we show in this socio-ecological study that invertebrate harvesting can influence macrofaunal community structure in seagrass meadows, which in turn affects the livelihood of local harvesters negatively.

Acknowledgements. This study would not have been possible without the help from Kombo Mohamed Haji, Seif Hamza Makame, all the interviewees, Mohammed Sheha Mohammed, the staff at Institute of Marine Science, Zanzibar, team Sweden, Frida Lanshammar, Abdallah Ame Mtwana, Gary and Caroline Naude, Pete and Sensation Divers, Bengt Lundén, and especially Martin Gullström. This research was supported by Department of Systems Ecology, Stockholm University, Formas (The Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning) and Anita Marklund.

Appendices are only available after the references.

References

Bell J.D., Pollard D.A., 1989, Ecology of fish assemblages and fisheries associated with seagrasses. In: Larkum A.W.D., McComb A.J., Shepherd S.A. (eds.) Biology of seagrasses - a treatise on the biology of seagrasses with special reference to the Australian region. Elsevier, Amsterdam, pp. 565–609.

Boström C., Bonsdorff E., 1997, Community structure and spatial variation of benthic invertebrates associated with *Zostera marina* (L.) beds in SW Finland. J. Sea Res. 37, 153–166.

Bowden D.A, Rowden A.A., Attrill M.J., 2001, Effect of patch size and in-patch location on the infaunal macro-invertebrate community of *Zostera marina* seagrass beds. J. Exp. Mar. Biol. Ecol. 259, 133–154.

Cardinale B.J., Srivastava D.S., Duffy J.E., Wright J.P., Downing A.L., Sankaran M., Jouseau C., 2006, Effects of biodiversity on the functioning of trophic groups and ecosystems. Nature 443, 989–992.

Cinner, E.J., McClanahan T.R., Daw, T.M., Graham, N.A.J, Maina J., Wilson, S.K., Hughes, T.P., 2009, Linking social and ecological systems to sustain coral reef fisheries. Curr. Biol. 19, 206–212.

Clarke K.R., Warwick R.M., 1994, Change in marine communities: an approach to statistical analysis and interpretations. Plymouth Marine Laboratory, Plymouth.

Clarke K.R., 1993, Non-parametric multivariate analysis of change in community structure. Aust. Ecol. 18, 117–143.

Clarke K.R., Gorley R.N., 2001, PRIMER v5: User Manual/Tutorial. Primer-E Ltd.

Coleman F.C., Williams S.L., 2002, Overexploiting marine ecosystem engineers: potential consequences for biodiversity. Trends Ecol. Evol. 17, 40–44.

Crawford B., Herrera M.D., Hernandez N., Leclair C.R., Jiddawi N., Masumbuko S., Haws M., 2010, Small scale fisheries management: lessons from cockle harvesters in Nicaragua and Tanzania. Coast. Manage. J. 38, 1–21.

de Boer W.F., Blijdenstein A.F., Longamane F., 2002, Prey choice and habitat use of people exploiting intertidal recourses. Environ. Conserv. 29, 238–252.

de la Torre-Castro M., Rönnbäck P., 2004, Links between humans and seagrasses – an example from tropical East Africa. Ocean Coast. Manage. 47, 361–387.

de la Torre-Castro M., 2006, Humans and seagrasses in East Africa – A social-ecological systems approach. PhD. Dissertation Stockholm University, Stockholm.

Dorenbosch M., 2006, Connectivity between fish assemblages of seagrass beds, mangroves and coral reefs: evidence from the Caribbean and the western Indian Ocean. PhD Dissertation Radboud University Nijmegen.

Duarte C.M., Chiscano C.L., 1999, Seagrass biomass and production: a reassessment. Aquat. Bot. 65, 159–174.
Dye A.H., 1992, Experimental studies of succession and stability in rocky intertidal communities subject to artisanal shellfish gathering. Netherlands J. Sea Res. 30, 209–217.
Edgar G.J., 1990, The influence of plant structure on the species richness, biomass and secondary production of macrofaunal assemblages associated with Western Australian seagrass beds. J. Exp. Mar. Biol. Ecol. 137, 215–240.
Erlandsson J., Pal P., McQuaid C.D., 2006, Re-colonisation rate differs between co-existing indigenous and invasive intertidal mussels following major disturbance. Mar. Ecol. Prog. Ser. 320, 169–176.
Erlandsson J., Porri F., McQuaid C.D., 2008, Ontogenetic changes in small-scale movement by recruits of an exploited mussel: implications for the fate of larvae settling on algae. Mar. Biol. 153, 365–373.
Francour P., Ganteaume A., Poulain M., 1999, Effects of boat anchoring in *Posidonia oceanica* seagrass beds in the Port-Cros National Park (north-western Mediterranean Sea). Aquat. Cons. Mar. Freshw. Ecol. 9, 391–400.
Gaudian G., 1990, Reef survey of Mafia Island, Tanzania. Reef Encounter, 7 July 1990, 14-15. In: Newton L.C., Parkes E.V.H., Thompson R.C., 1993, The effects of shell collecting on the abundance of gastropods on Tanzanian shores. Biol. Conserv. 63, 241–245.
Green E.P., Short F.T., 2003, World atlas of seagrasses. University of California Press, Berkeley.
Gullström M., de la Torre Castro M., Bandeira S.O., Björk M., Dahlberg M., Kautsky N., Rönnback P. Öhman M.C., 2002, Seagrass ecosystems in the western Indian Ocean. Ambio 31, 588–596.
Gullström M., Lundén B., 2007, Changes in submerged aquatic vegetation on Zanzibar as mapped by satellite remote sensing. Poster presentation at The 7th International Seagrass Biology Workshop (ISBW7) - Zanzibar, Tanzania
Gullström M., Lundén B., Bodin M., Kangwe J.W., Öhman M.C., Mtolera M.S.P. Björk M., 2006, Assessment of changes in the seagrass-dominated submerged vegetation of tropical Chwaka Bay (Zanzibar) using satellite remote sensing. Estuar. Coast. Shelf Sci. 67, 399–408.
Håkansson E., 2006, Invertebrate harvesting in Chwaka village, Zanzibar with special focus on women and the importance of seagrasses. Dissertation, Stockholm University.
Hardin G., 1998, Extensions of "The Tragedy of the Commons". Science 280, 682–683.
Howard R.K., Edgar G.J. Hutchings P.A., 1989, Faunal assemblages of seagrass beds. In: Larkum A.W.D., McComb A.J., Sheperd S.A. (Eds.), Biology of seagrasses – a treatise on the biology of seagrasses with special reference to the Australian region. Elsevier, Amsterdam, pp. 536–564.
Human development report, 2006, http://hdr.undp.org/hdr2006/.
Jiddawi N.S., Öhman M.C., 2002, Marine Fisheries in Tanzania. Ambio 31, 518–527.
Jones C.G., Lawton J.H. Shachak M., 1994, Organisms as ecosystem engineers. Oikos 69, 373–386.
Keough M.J., Quinn G.P. King A., 1993, Correlations between human collecting and intertidal mollusc populations on rocky shores. Conserv. Biol. 7, 378–391.
Keselman H.J., Othman A.R. Wilcox R.R. Fradette K., 2004, The new and improved two-sample *t*− test. Psychol. Sci. 15, 47–51.
Knudby A., Nordlund L., in press, Remote sensing of seagrasses in a patchy multi-species environment. Int. J. Remote Sens DOI: 10.1080/01431161003692057.
Kvale S., 1996, InterViews: An introduction to qualitative research interviewing. Thousand Oaks, CA: Sage Publications, Inc.
Lange G-M., Jiddawi N., 2009, Economic value of marine ecosystem services in Zanzibar: Implications for marine conservation and sustainable development. Ocean Coast. Manage. 52, 521–532.
Lasiak T., 1991, The susceptibility and/or resilience of rocky littoral molluscs to stock depletion by the indigenous coastal people of Transkei, southern Africa. Biol. Conserv. 56, 245–264.
Lasiak T.A., Field J.G., 1995, Community-level attributes of exploited and non-exploited rocky infratidal macrofaunal assemblages in Transkei. J. Exp. Mar. Biol. Ecol. 185, 33–53.
Moberg, F., Folke, C., 1999, Ecological goods and services of coral reef ecosystems. Ecol. Econ. 29, 215–233.
Nagelkerken I., Dorenbosch M., Verberk W.C.E.P., Chocheret de la Morinière E., van der Velde G., 2000, Importance of shallow-water biotopes of a Caribbean bay for juvenile coral reef fishes: patterns in biotope association, community structure and spatial distribution. Mar. Ecol. Prog. Ser. 202, 175–192.
Nakamura Y., Sano M., 2005, Comparison of invertebrate abundance in seagrass bed and adjacent coral and sand areas at Amitori Bay, Iriomote Island, Japan. Fish. Sci. 71, 543–550.
National Bureau of Statistics, Tanzania, 2008, www.nbs.go.tz/. Government site.
Newton L.C., Parkes E.V.H., Thompson R.C., 1993, The effects of shell collecting on the abundance of gastropods on Tanzanian shores. Biol. Conserv. 63, 241–245.
Nordlund L., 2007, Human impact on invertebrate abundance, biomass and community structure in seagrass meadows - a case study at Inhaca Island, Mozambique. MSc, dissertation Uppsala University.
Orth R.J., Heck K.L. Jr., van Montfrans J., 1984, Faunal communities in seagrass beds: A review of the influence of plant structure and prey characteristics on predator-prey relationships. Estuaries 7, 339–350.
Quinn G.P., Keough M.J., 2002, Experimental design and data analysis for biologists. Cambridge, Cambridge University Press.
Richmond M.D., 2002, A Field Guide to the Shores of Eastern Africa and the WIO Islands. 2nd edn. Sida/Department for Research Cooperation, SAREC, and University of Dar es Salaam.
Rius M., Kaehler S., McQuaid C.D., 2006, The relationship between human exploitation pressure and condition of mussel populations along the south coast of South Africa. S. Afr. J. Sci. 102, 130–136.
Ruxton G.D., 2006, The unequal variance t-test is an underused alternative to Student's *t*-test and the Mann-Whitney U test. Behav. Ecol. 17, 688–690.
Short F.T., Coles R.G. (eds.), 2001, Global seagrass research methods. Elsevier, Amsterdam, pp. 143–153.
Silva P., 2006, Exploring the linkages between poverty, marine protected area management, and the use of destructive fishing gear in Tanzania. World Bank Policy Research Working Paper No. 3831.
Unsworth R.K.F., Cullen L.C., 2010, Recognising the necessity for Indo-Pacific seagrass conservation. Conserv. Lett. 3, 63–73.
Waycott M., Duarte C.M., Carruthers T.J.B., Orth R.J., Dennison W.C., Olyarnik S., Calladine A., Fourgurean J.W., Heck Jr. K.L., Hughes A.R., Kendrick G.A., Kenworthy W.J., Short F.T., Williams S.L., 2009, Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proc. Natl. Acad. Sci. USA 106, 12377–12381.
ZATI Tourism Statistics, 2010, www.zati.org.

Appendix 1. Interview Sheet

Interviews were chosen randomly, by visiting 18 different households in a haphazard way. The people (only women/females) that opened the doors were chosen to be interviewed (all agreed to this). Questions were asked in the same way, but further explanations and follow-up questions might have varied between the 18 interviewees. All women were interviewed by the same person. When asked regarding changes over time all interviewees have given answers referring to the time period during which they have been actively collecting invertebrates (mainly within a time period of 10–30 years ago since a majority of harvesters have been active during this time period).

Interview sheet for potential invertebrate harvesters
Date:
Interview nr:

Name? (optional)
1. Profession?
2. Age?
3. Family? Single, Married, Divorced or Widowed
4. Children, how many and age?
5. Do you collect invertebrates nowadays? Yes or no. If no, change tempus for following questions.
6. How often do you collect invertebrates during spring tide?
7. How often do you collect invertebrates during neap tide?
8. For how many hours do you collect animals per day?
9. When you are colleting animals, how many other women are collecting in the same area (as far as you can see), outside Nungwi?
10. For how many years have you been collecting animals in the sea?
11. Where are you colleting animals, which location?
12. What collecting grounds do you prefer and why is that?
13. What type of seagrass species do you prefer?
(Pictures of seagrass from a field guide to the seashores of East Africa and the Western Indian Ocean Islands by Richmond 2002 was shown)
13.1 Density? (Fig. 1S)
13.2 Cover? (Fig. 1S)
13.3 Patch size? (Fig. 1S)
14. Have you noticed any changes in the seagrass distribution during your lifetime? (what are the changes? How has the distribution changed, and why in your opinion?)
15. Have changes in the seagrass meadows affected your collection activities? If yes, How?
16. Has the number of animals changed the last years? How and why?

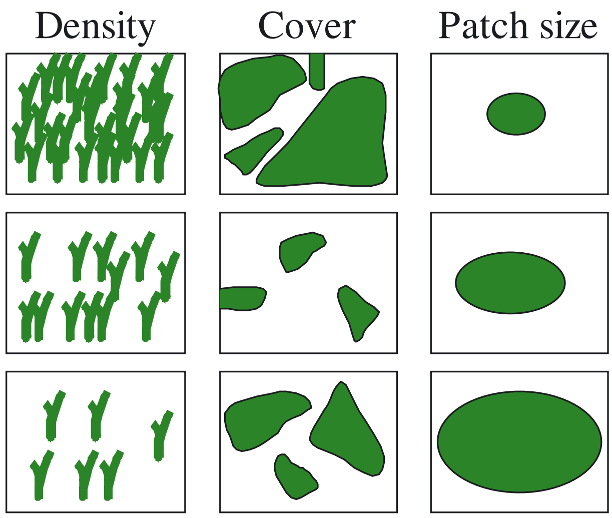

Fig. 1S.

17. Have the animal species changed the last years? How and why?
18. Would you collect more often if you had access to a boat, which could take you further away? And why?
19. Why do you collect animals?
20. Is collecting also a social activity? e.g. meeting and talking with other harvesters?
21. If you sell animals, what is the income? (per catch or per animal)
22. Have activities or changes in the village affected your collection activities? If yes, How?
23. Have tourist activities affected your collection activities? If yes, How?
24. Which animals do you collect? Which are for food and which are sold?
(Pictures from A field guide to the seashores of East Africa and the Western Indian Ocean Islands by Richmond 2002 was shown together with shells of different animals and not only species collected)
25. Can you describe a normal catch when you collect one day (pics, kg)?
26. What are the general negative/positive changes in your collection activities the last couple of years?
PART II; if not collecting nowadays
27. If you are not collecting anymore, when did you stop?
28. What is the reason that you changed your invertebrate harvesting?

Appendix 2. Invertebrate species collected

Table 1S. Pictures of 337 invertebrate species were shown to all the interviewees in Nungwi, where they were asked to point out if and why they generally collect the animal. Definition of numbers in Table: 1- first and foremost collected for food, 2 - first and foremost collected to sell and 3 - is collected to eat or to sell, or primarily to eat and secondarily to sell (e.g. gastropods), 4 - as fish food. * indicates that this collection happens rarely. 14 of the 18 interviewees answered the question of animal species collected, and each column represents one interviewee. Pictures of the animal species were from: A field guide to the seashores of East Africa and the Western Indian Ocean Islands by Richmond, 2002. This table was created to get an overview of animals collected and their use.

Interviewee no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14
ARTHROPODA														
Crustacea														
Palinurellus wieneckii	1			1				1	1		1			
Panulirus delagoae	1			1				1	1		1			
Panulirus homarus	1			1				1	1		1			
Panulirus longipes longipes	1			1				1	1		1			
Panulirus ornatus	1			1				1	1		1			
Panulirus versicolor	1			1				1	1		1			
Thenus orientalis	1			1										
Uca tetragonon		1		1	1		1	1	1					
Crabs, not shown	1			1	1	1	1	1	1			1	1	1
MOLLUSCA														
Polyplacophora														
Acanthopleura brevispinosa					1						1			
Acanthopleura gemmata					1						1			
Gastropoda														
Amaea acuminata								1	1		1	1		
Ancilla castanea								1	2		3		2	
Architectonica perspectiva				1		2		1	2			2	2	
Bursa lampas		1	1	1	1	2	1	1	2	2	2	1	3	
Bursa rosa		1			1	2	1	1	2	2	2	1	3	
Cantharus fumosus			1	1	1			1	1	1		1	3	
Cantharus undosus			1	1	1			1	1	1		1	3	
Cassis cornuta	1	1		2	1	2	1	3	1		2	3	3	3
Cerihidea decollata				1				1						
Cerithium caeruleum								1			1	1	1	
Cerithium nodulosum								1			1	1	1	
Charonia tritonis			1	1	1	2		3	2		2	3	3	
Cheilea papyracea								1						
Chicoreus ramosus	1	1		1	1	2	1	1	2	3	3	1	1	
Clanculus puniceus	1			2				1				2		
Clypeomorus bifasciatus								1	1			1	1	
Clypeomorus bifasciatus								1	1			1	1	
Conus arenatus				2		2		2	2	2		2	2	2
Conus catus				2		2		2	2	2		2	2	2
Conus coronatus				2		2		2	2	2		2	2	2
Conus ebraeus				2		2		2	2	2		2	2	2
Conus generalis				2		2		2	2	2		2	2	2
Conus geographus				2		2		2	2	2		2	2	2
Conus imperialis				2		2		2	2	2		2	2	2
Conus litoglyphus				2		2		2	2	2		2	2	2
Conus litteratus				2	1	2		2	2	2		2	2	2
Conus lividus				2		2		2	2	2		2	2	2
Conus marmoreus				2	1	2		2	2	2		2	2	2
Conus miles				2		2		2	2	2		2	2	2
Conus rattus				2		2		2	2	2		2	2	2
Conus striatellus				2		2		2	2	2		2	2	2
Conus striatus				2		2		2	2	2		2	2	2
Conus textile				2		2		2	2	2		2	2	2
Coralliophilia violacea								1			1	1	2	

Table 1S. continued.

Interviewee no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Cronia konkanensis								1		2	3	1	2	
Cymatium lotorium					1	2		1	2	2	2	1	3	
Cymatium muricinum					1	2		1	2	2	2	1	3	
Cypraea annulus				2		2		2	2	2	3	2	2	2
Cypraea arabica				2		2		2	2	2	3	2	2	2
Cypraea caputserpentis				2		2		2	2	2	3	2	2	2
Cypraea carneola				2		2		2	2	2	3	2	2	2
Cypraea helvola				2		2		2	2	2	3	2	2	2
Cypraea isabella				2		2		2	2	2	3	2	2	2
Cypraea mappa				2		2		2	2	2	3	2	2	2
Cypraea mauritiana				2		2		2	2	2	3	2	2	2
Cypraea moneta				2		2		2	2	2	3	2	2	2
Cypraea tastudinaria				2		2		2	2	2	3	2	2	2
Cypraea tigris	1	1		2		2		2	2	2	3	2	2	2
Cypraea vitellus				2		2		2	2	2	2	2	2	2
Cypraecassis rufa				2	1	2	1	2	2			3	3	3
Diala lauta								1	1		1	1	1	
Drupa fusconigra								1			3	1	2	
Drupa morum								1			3	1	2	
Drupa ricina								1			3	1	2	
Drupella corunus								1		2	3	1	2	
Drupella rugosa										2		1		
Engina mendicaria				2					2				2	
Ficus subintermedia						2		1	2		2	1	3	
Fusinis colus		1	1	1	1			1	1			1	3	
Gena varia								1	2			2	2	
Gibbula townsendi								1				2		
Gyroscala lamellosa								1	1		1	1	1	
Hapra amouretta	2			2	1	3	1	3	2	2	3		2	
Harpa harpa	2			2	1	3	1	3	2	2	3		2	
Hastula lanceata									2		3		2	
Hipponix conicus								1						
Janthina janthina								1	1		1	1	1	
Janthina prolongata								1	1		1	1	1	
Lambis chiragra arthritica	1	1		2	1	2	1	3	3		3	1	3	3
Lambis lambis	1	1		2	1	2	1	3	3	3	3	1	3	3
Lambis truncata	1	1		2	1	2	1	3	3	3	3	1	3	3
Latirus polygonus			1	1	1			1				1	3	
Littoraria glabrata								1	2	1			2	
Littoraria pallescens								1		1			2	
Littoraria scabra								1	2	1			2	
Littoraria undulata								1	2	1			2	
Lophiotoma cingulifera								1	2			3	2	
Lunella coronata			1					1		1		11		
Melampus sp.								1			1	1	2	
Merica melanostoma								1			3	3	2	
Mitra chrysalis				2				1	2	2	3		2	
Mitra cucumerina				2				1	2	2	3		2	
Mitra paupercula				2				1	2	2	3		2	
Mitra pellisserpentis								1	2	2	3		2	
Monodonta labio								1				1		
Morula granulata								1			3	1	2	
Morula margiticola								1					2	
Murex brevispina	2					2		1	2	2	3	2	2	
Murex pecten	2							1	2	2	3	2	2	
Nassarius albescens gemmuliferus	1	1	1	1	1			1	1				3	
Nassarius arcularia plicatus	1	1	1	1	1			1	1			1	3	
Nassarius coronatus	1	1	1	1	1			1	1			1	3	

Table 1S. continued.

Interviewee no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Nassarius echinatus	1	1	1	1	1			1	1			1	3	
Nautica gualteriana		1			1			1	1		1		3	
Nerita albicilla		1						1	2	1			2	
Nerita plicata		1						1	2	1			2	
Nerita polita		1						1	2	1			2	
Nerita textilis		1						1	2	1			2	
Nerita undata		1						1	2	1			2	
Nodilittorina natalensis								1	2	1			2	
Nodolittorina africana africana								1	2	1			2	
Oliva bulbosa				2				1	2	2	3	2	2	
Oliva episcopalis				2				1	2	2	3	2	2	
Oxystele tabularis												2		
Phalium glaucum						2			2		2	1	3	
Phasianella nivosa								1	2	1				
Phasianella variegata								1	2	1				
Planaxis sulcatus								1					2	
Pleuroploca filamentosa	1	1	1	1	1		1	1	1	1		1	3	1
Pleuroploca trapezium	1	1	1	1	1		1	1	1	1		1	3	1
Polinices mammilla					1			1	1		1		3	
Pterygia nucea	2			2				1	2		3		2	
Purpura (Thais) persica								1			3	1	2	
Rhinoclavis sinensis								1	1		1	1	1	
Septa gemmata					1	2			2			1	3	
Stomatella orbiculata														
Strombus decorus decorus	1	1			1		1	1	1	1	1	1	2	
Strombus gibburulus	1	1			1		1	1	1	1	1	1	2	
Strombus lentiginosus	1	1			1		1	1	1	1	1	1	2	
Tectus mauritianus					1			1				2		
Terebra crenulata	2			2				2	2	2	3	3	2	
Terebra dimidiata	2			2				2	2	2	3	3	2	
Terebra nebulosa	2			2				2	2	2	3	3	2	
Terebralia palustris	1				1			2	1		1	1	1	
Tonna canaliculata					1	2	1	3	2		2	3	3	
Tonna perdix					1	2	1	3	2		2	3	3	
Trochus maculatus		1	1	1	1		1	1		1		2	2	
Trochus virgatus		1	1	1	1		1	1		1		2	2	
Turbo argyrostomus	1	1	1	1	1		1	1	3	1	2	1	1	
Turbo marmoratus	1	1	1	1	1		1	1	3	1	2	1	1	
Vasum ceramicum	1	1		1	1		1	1	1		3	3	1	1
Vasum rhinocerus	1	1		1	1		1	1	1		3	3	1	1
Vasum turbinellus	1	1		1	1		1	1	1		3	3	1	1
Vasum turbinellus var. Cornigerum	1	1		1	1		1	1	1		3	3	1	1
Vexillium rugosum				2				1	2		3		2	
Volema paradisiaca	1	1		1	1		1	1	1	1	3	1	1	1
Volema pyrum	1	1		1	1			1	1	1	3	1	1	1
Xenophora corrugata								1					3	
Zeuxius olivaceus					1				1			1	3	
Ophisthobranchia														
Bulla ampulla											2			
Bivalvia														
Acrosterigma rubicundum	1		1	1	1			1	1	1	1	1	1	1
Anadara antiquata	1	1	1	1	1		1	1	1	1	1	1	1	1
Anadara erythraeonensis	1	1	1	1	1		1	1	1	1	1	1	1	1
Anodontia edentula	1	1			1	1		1	1	1	1	1	1	1
Asaphis violascens									1				1	
Atactodea glabrata			1		1			1	1				1	
Atrina vexillum			1	1	1		1	1	1	1	1	1	1	1
Bankia sp.														

Table 1S. continued.

Interviewee no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Barbatiia decussata				1	1			1	1			1	1	
Barnea manilensis			1									1	1	
Bassina calophylla									1			1	1	
Beguina gubernaculum	1		1		1			1	1			1	1	
Branchidontes variabilis	1		1	1	1			1	1			1	1	
Brechites attahens								1						
Cardita variegata								1	1			1	1	
Chama brassica					1			1	1			1	1	
Chione toreuma			1		1				1	1	1	1	1	
Chlamys senatorius			1		1			1	1	1		1	1	
Circe scripta			1		1			1	1	1		1	1	1
Clementina papyracea			1		1			1	1				1	
Codakia punctata	1			1	1	1		1	1	1		1	1	1
Corbula tatensis			1						1	1		1		
Dicyathifer mannii								1						
Donax faba			1		1	1		1	1			1	1	1
Donax incarnatus			1		1	1		1	1			1	1	1
Donax madagascariensis			1		1	1		1	1			1	1	1
Dosinia hepatica					1			1	1			1	1	1
Eumarcia paupercula			1		1			1	1			1	1	
Gafrarium divaricatum			1		1	1		1	1	1	1	1	1	1
Gafrarium pectinatum			1		1	1		1	1	1	1	1	1	1
Gastrochaena gigantea												1		
Glycymeris pectunculus			1	1	1			1	1	1	1	1	1	1
Glycymeris quecketti			1	1	1			1	1	1	1	1	1	1
Hyotissa hyotis		1	1		1	1		1				1	1	
Irus macrophylla								1	1			1	1	
Isogonium ephippium	1	1	1	1	1	1		1	1	1		1	1	1
Isognomon isognomon	1	1	1	1	1	1		1	1	1		1	1	1
Isognomon nucleus	1	1	1	1	1	1		1	1	1		1	1	1
Lima lima					1			1	1			1	1	
Lioconcha castrensis		1			1			1	1	1			1	
Lithophaga teres					1			1	1			1	1	
Lopha cristagalli					1			1	1				1	
Loripes clausus					1			1	1			1	1	
Lunulicardia auricula			1		1			1	1			1	1	
Macoma litoralis			1		1			1	1		1	1	1	1
Mactra cuneata			1		1			1	1		1	1	1	1
Mactra lilacea			1		1			1	1		1	1	1	1
Mactra lurida			1		1			1	1		1	1	1	1
Mactra ovalina			1		1			1	1		1	1	1	1
Malvufundus normalis								1						
Martesia striata			1											
Meretrix meretrix					1			1	1			1	1	
Meropesta nicobarica			1		1			1	1	1	1		1	1
Modiolus auriculatus	1		1	1	1	1		1	1	1	1	1	1	1
Modiolus philippinarium	1		1	1	1	1		1	1	1	1	1	1	1
Perna picta	1		1	1	1	1		1	1			1	1	1
Petricola lapicida						1			1			1	1	
Pinctada margaritifera	1	1		1	1	1		1	1	1	1	1	1	1
Pinna muricata		1	1	1	1	1	1	1	1	1	1	1	1	1
Pitar hebracea			1		1	1		1			1	1	1	1
Plagiocardium pseudolima	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Plicatula australis								1		1		1		
Protapes sinuosa								1	1	1		1	1	
Pteria chinesis			1		1			1	1			1	1	
Saccostrea cucllata		1	1		1			1	1			1	1	1
Scinitella oblonga					1			1	1				1	

Table 1S. continued.

Interviewee no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Semele radiata					1				1				1	
Semipallium tigris	1		1						1			1	1	
Septifer bilocularis			1	1				1	1				1	1
Siliqua radiata			1	1	1			1	1				1	
Solen ceylonesis														1
Spondylus hysterix									1			1	1	
Squilia polita				1	1			1	1		1	1		
Striostera margaritacea		1	1		1			1	1			1	1	1
Sunetta contempta					1			1				1	1	
Tapes literatus	1		1					1	1		1	1	1	1
Tapes sulcarius	1		1					1	1		1	1	1	1
Tellina capsoides			1	1	1	1		1	1		1	1	1	1
Tellina madagascarensis			1	1	1	1		1	1		1	1	1	1
Tellina perna			1	1	1	1		1	1		1	1	1	1
Tellina platum			1	1	1	1		1	1		1	1	1	1
Tellina staurella			1	1	1	1		1	1		1	1	1	1
Tellina virgata			1	1	1	1		1	1		1	1	1	1
Thracia sp.												1		1
Timoclea subnodulosa								1	1			1		
Trachycardium pectiniforme	1		1	1	1	1		1	1	1	1	1	1	1
Trapezium bicarinatum								1	1			1	1	
Tridacna maxima	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Tridacna squamosa	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Tugonia divaricata					1				1			1		
Cephalopoda														
Loligo duvaucelli	3	1	3	3				3	3		3		3	3
Octopus macropus	3	1	3	3	1	1	1	3	3	3	3	3	3	3
Sepia pharaonis	3	1	3					3	3		3	3	3	3
Sepioteuthis lessoniana	3	1	3	3				3	3		3	3	3	3
ECHINODERMATA														
Asteroidae														
Archaster lorioli											4			
Asaterodiscides belli											2			
Asterina burtoni											4			
Astropecten monacanthus											2			
Astropecten polyacanthus											2			
Astropsis carinifera											4			
Culcita schmideliana											4			
Dactyloaster cylindricus											4			
Leiaster coriaceus											4			
Linckia laevigata											4			
Luidia maculata											4			
Pentaceraster mammilatus											4			
Pentaceraster tuberculatus											4			
Protoreaster lincki											4			
Holothurioidea														
Actinopyga mauritiana											2*			
Actionopyga echinites											2*			
Bohadschia atra										2				
Holothuria atra								2*	2*		2*			
Holothuria edulis								2*	2*		2*			
Holothuria nobilis								2*	2*		2*			
Holothuria scabra								2*	2*		2*			
Stichopus hermanni											2*			
Stichopus horrens											2*			