Ocean & Coastal Management 107 (2015) 16–27

Contents lists available at ScienceDirect

Ocean & Coastal Management

journal homepage: www.elsevier.com/locate/ocecoaman

Cascade effects and sea-urchin overgrazing: An analysis of drivers behind the exploitation of sea urchin predators for management improvement

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ARTICLE INFO

Article history:
Received 5 June 2014
Received in revised form
16 December 2014
Accepted 11 January 2015
Available online

Keywords:
Food web changes
Fisheries management
Overgrazing
Small-scale fisheries
Social-ecological drivers
LEK
Trophic cascades
Kenya
Zanzibar

ABSTRACT

Marine ecosystems generate a wide variety of goods and services, but are globally deteriorating due to multiple drivers associated with anthropogenic activities. Intense fishing pressure can lead to changes in structure and function of marine food webs. Particularly overfishing of predatory species at high trophic levels can cause cascading effects leading to ecosystem degradation, affecting both marine organisms and people dependent on them. In the Western Indian Ocean region, intensive fishing takes place and degradation of coral reefs and seagrass beds has been documented. One reason behind this degradation is overgrazing by increasing numbers of sea urchins. An essential step towards better management is to thoroughly understand the drivers leading to such changes in ecosystems. Against this background, the general aim of this study was to gain understanding about whether sea urchin predators in the WIO region are fished, and to identify the drivers behind the fishing of these species. The study had four objectives: (i) to document if and how predatory fish eating sea urchins are caught in smallscale fisheries, (ii) to assess if, and if so why, sea urchin predators are targeted species, (iii) to assess if and to what degree local ecological knowledge (LEK) on ecological complexity involving sea urchins and their predators (e.g. trophic cascades) is present among local fishers, and (iv) to identify fishers' suggestions for management that can reduce problems linked to sea urchin overgrazing. The results show that all investigated species of sea urchin predators are fished by local small-scale fishers. Most sea urchin predators are not actively targeted, are not popular local food fish, and have minor use and economic importance for fishers. This stands in sharp contrast to their ecological keystone role by controlling sea urchin populations. The fishers' awareness and LEK were weak and partly lacking. Management suggestions targeted mostly the symptoms of food web changes rather than the drivers behind them.

Based on the results we suggest that management of degraded ecosystems, as a result of food web changes, should encompass a wide variety of strategies and scales. Specific suggestions for sea urchin predator management are education of local stakeholders on destructive gear effects and food web complexity, further investigations of catch- and release fishing as well as the use of selective gears.

1. Introduction

Anthropogenic disturbances cause increasingly negative changes to marine ecosystems around the globe, threatening the livelihoods of people depending on their goods and services (Halpern et al., 2008; Jackson et al., 2001; Lotze et al., 2006; MEA, 2003). One such disturbance is intense fishing pressure, which may lead to considerable changes in structure and functioning of marine ecosystems, like alterations of marine food webs (Jackson et al., 2001; Pauly et al., 1998). The drivers behind human

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http://dx.doi.org/10.1016/j.ocecoaman.2015.01.010
0964-5691/

activities leading to ecosystem changes are highly diverse. An essential first step to counteract or prevent negative changes is to understand the underlying drivers (MEA, 2003), such as those behind overfishing. A high fishing pressure on predatory species at the top of food webs can cause community-wide changes and cascading effects, which may potentially affect other levels of the food web (Menge, 1995; Pace et al., 1999; Pinnegar et al., 2000). Such trophic cascades are likely to develop in simple food webs (Pauly and Watson, 2005) involving keystone predators, which often are few in numbers and are specialized to prey on morphologically well-defended organisms such as sea urchins (Terborgh and Estes, 2010; Pinnegar et al., 2000).

Over the past four decades, increasing densities of sea urchins leading to overgrazing of seagrasses and bioerosion of corals have been documented more frequently (Alcoverro and Mariani, 2002; Eklöf et al., 2008; Heck and Valentine, 1995; McClanahan and Muthiga, 1988). One factor leading to such high sea urchin abundances and destructive grazing in seagrass beds and on coral reefs is the loss of top-down control due to intense fishing of sea urchin predators (Eklöf et al., 2009; McClanahan, 1992; McClanahan and Muthiga, 1989; McClanahan and Shafir, 1990). Alarmingly, coral reefs and seagrass beds are globally declining due to human disturbances (Bellwood et al., 2004; Duarte et al., 2008; Pandolfi et al., 2003; Waycott et al., 2009), and additional food web alterations could have further devastating effects (Baden et al., 2010; Duarte, 2002; Jackson et al., 2001; Moksnes et al., 2008). These shallow-water habitats provide a broad range of ecosystem services, which makes them indispensable for the everyday lives of people in many coastal areas, primarily as valuable fishing grounds in small-scale fisheries (de la Torre-Castro et al., 2014; Moberg and Folke, 1999; Unsworth and Cullen, 2010). In the Western Indian Ocean region (WIO), seagrass- and coral-associated fish contribute to a large part of the economy as well as the protein intake of coastal communities (de la Torre-Castro et al., 2014; de la Torre-Castro and Rönnbäck, 2004; Gullström et al., 2002; McClanahan, 2010; Thyresson et al., 2011). However, the use of destructive fishing methods like beach seines (used as drag-nets) leads to physical damage to seagrasses and corals, while gears with very small mesh sizes catch high proportions of juvenile fish and by-catch (Jiddawi and Öhman, 2002; Mangi and Roberts, 2006; Ochiewo, 2004). The use of such destructive gears, the open access character of the fishery, insufficient management, increasing tourism and a lack of livelihood alternatives has led to overexploitation and depletion of fish stocks throughout the WIO region, including both the Kenyan coast and Zanzibar (Jiddawi, 2012; Jiddawi and Öhman, 2002; McClanahan and Mangi, 2001; Ochiewo, 2004).

In the WIO in general, and along the Kenyan coast in particular, several events of seagrass overgrazing by dense sea urchin populations have been documented (Alcoverro and Mariani, 2002; Crona, 2006; Eklöf et al., 2009). Previous studies have shown that fishing of sea urchin predators (particularly finfish like the redlined triggerfish *Balistapus undulatus*) has led to increased urchin densities on coral reefs and seagrass beds (McClanahan, 1992, 2000; McClanahan and Muthiga, 1989; McClanahan and Shafir, 1990). McClanahan (2000) found densities of sea urchin predators to be higher and sea urchin densities to be lower in protected areas, compared to fished ones, and McClanahan and Shafir (1990) suggested that the fishing of sea urchin predators is thought to have "disproportionate consequences" in the food web.

Examples from other parts of the world show comparable trophic cascades from overfishing, but that the drivers behind sea urchin predator overharvest can vary between ecosystems. For example, the overfishing of lobster on rocky reefs in Northeastern New Zealand was driven by its high commercial value and led to an ecological release of sea-urchins and overgrazing of kelp (Shears and Babcock, 2002). Along the Pacific coast of North America, overhunting of fur seals offshore forced their main predator – the killer whale *Orca orca* – to move inshore and switch to feeding on sea otters. This led to a trophic cascade where sea urchins – the main prey of sea otters – increased greatly in abundance, and subsequently overgrazed giant kelp, the habitat-forming species in the system (Estes et al., 1998). Understanding the drivers behind the exploitation of species with crucial ecological functions, such as sea urchin predators, is especially important for adequate management design. Although the drivers of overfishing in general in the WIO are well documented (McClanahan et al., 2008, 2005; McClanahan and Mangi, 2004), the specific drivers behind the exploitation of sea urchin predators are poorly understood. Therefore it is important to gain a better understanding of the factors contributing to the fishing of these species, to be able to design management that leads to well-functioning marine ecosystems.

Before designing management measures, it is further important to assess the local ecological knowledge (LEK) and awareness of local fishers about ecological complexity such as interactions between sea urchins and their predators. This is important as such assessments can provide a basis to address resource users' and stakeholders' knowledge gaps (Crona, 2006). It has further been shown that including LEK besides scientific knowledge can add valuable information when designing management schemes (Moller et al., 2004; Olsson and Folke, 2001), and that the inclusion of LEK can benefit managers when designing awareness programs aimed at enhancing compliance with management measures.

Against this background, the overall aim of this study was to gain understanding about whether sea urchin predators in the WIO region are fished, and to identify the drivers behind the fishing of these species. The study had four specific objectives: (i) to document if and how sea urchin fish predator species are caught in smallscale fisheries; (ii) to assess if, and if so why, sea urchin predators are target species; (iii) to assess if and to what degree local ecological knowledge (LEK) is present among local fishers (on ecological complexity involving sea urchins and their predators, e.g. trophic cascades); and (iv) to identify the fishers' suggestions for management strategies that can reduce problems with sea urchin overgrazing.

2. Material and methods

2.1. Theoretical framework

In this study, we used the term "drivers" as defined by the Millennium Ecosystem Assessment (MEA): "natural or anthropogenic factors causing changes in ecosystems" (MEA, 2003). Drivers can have direct impacts on ecosystem processes (e.g. physical, biological or chemical factors), as well as influence their wider scope (e.g. demographic, economic, sociopolitical, scientific, technological, cultural and religious factors). Many major ecosystem alterations are known to originate from multiple drivers on local, regional and/or global scales (MEA, 2003).

2.2. Study sites

The study was carried out in two areas of the WIO region: (1) the larger Mombasa area in the Coast province of Kenya, and (2) the coast of Unguja Island in the Zanzibar archipelago, Tanzania (from here on referred to as "Zanzibar") (Fig. 1). Typical features for these areas are intertidal lagoons characterized by seagrass beds, patch- and fringing coral reefs, and also mangroves. The fisheries are small-scale, artisanal and generate lowincome. Fishers targeting finfish are predominantly male, and use a variety of traditional and

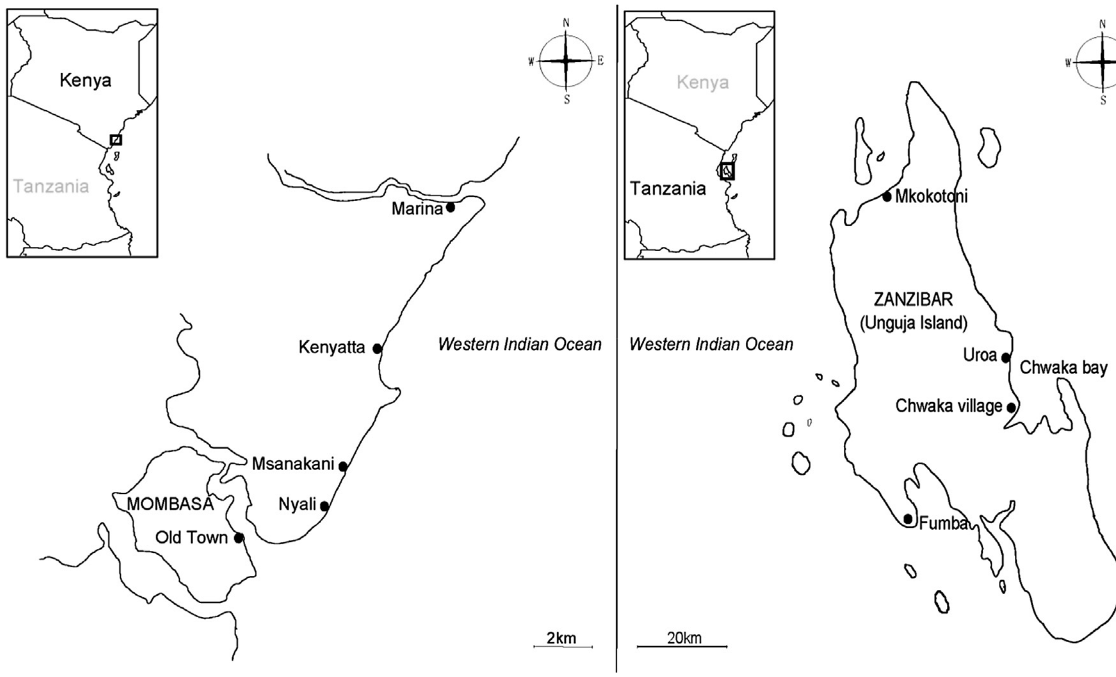

Fig. 1. The study sites in the WIO region: the larger Mombasa area, Kenya, and Unguja Island, Zanzibar, Tanzania.

non-traditional gears that target a high diversity of species. Catches are sold to fish traders, local households, restaurants, and the tourist industry (Jiddawi and Öhman, 2002; McClanahan and Mangi, 2004). Traditional gears include basket traps ('malema' in Kenya and 'madema' in Zanzibar), nets and hand lines, whereas more modern gears include beach seines, gill nets and spear guns (Jiddawi and Öhman, 2002; Mangi and Roberts, 2006). Due to the predominant use of small, non-motorized fishing vessels (e.g. dugout canoes), as well as the low-technology gear, fishing is mostly conducted in shallow inshore waters (Jiddawi, 2012; Jiddawi and Öhman, 2002; McClanahan and Mangi, 2000). Consequently, seagrass- and coral ecosystems close to the shore are under heavy fishing pressure (de la Torre-Castro et al., 2014; McClanahan and Mangi, 2004).

2.3. Data collection

A combination of interviews, literature research, and observations was used to collect the data for this study. Both quantitative and qualitative data was gathered to assess the current situation concerning the exploitation of sea urchin predators in the WIO area. We focused on two of the most common and most well studied sea urchin species in the area: 1) *Tripneustes gratilla*, a generalist herbivore feeding on seagrasses and macroalgae (Alcoverro and Mariani, 2002; Crona, 2006; de la Torre-Castro and Jiddawi, 2005) and 2) *Echinometra mathaei*, a generalist omnivore often feeding on hard substrate in areas where macroalgae are lacking (Herring, 1972; Hutchings, 1986; McClanahan and Muthiga, 1989; McClanahan and Shafir, 1990; Russo, 1980). A list of fish species feeding on sea urchins in the study areas was collated from the literature and used in the interviews. Eight fish species were identified to feed on sea urchins (Table 1). The red-lined triggerfish *B. undulatus* has been shown to be the most important predator or "keystone species" (due to the fact that it stands for a majority of sea urchin predation observed in the field), followed by the male terminal wrasses *Coris formosa* and *Cheilinus trilobatus* (McClanahan, 1995, 2000).

Table 1
Sea urchin predator fish species in the WIO, divided by fish family.

Balistidae	Labridae	Lethrinidae
Balistapus undulatus[a,b,c,d,e,f]	*Coris formosa*[a,b,c,d]	*Lethrinus mahsena*[a,b,c,d,f]
Balistoides viridescens[a,b,d,f]	*Cheilinus trilobatus*[a,b,c,d]	
Pseudobalistesfuscus[a,b,c,d,f]	*Coris aygula*[a,b,c,d]	
	Coris gaimard [b,c,d]	

Seaurchin predator fish species reported in the study areas.
[a] Froese and Pauly, 2013.
[b] Lieske and Myers, 2001.
[c] McClanahan, 1995.
[d] McClanahan, 2000.
[e] McClanahan and Shafir, 1990.
[f] Watson and Ormond, 1994.

2.4. Interviews

Primary data was collected through semi-structured interviews conducted in Kenya from October to December 2008, and in Zanzibar during July and August 2009. A total of 167 fishers were

Table 2
Numbers of interviewed fishers from the investigated landing sites.

Fishery landing site	Number of respondents
Mombasa area, Kenya	
Bamburi (Kenyatta beach)	20
Marina Port	20
Nyali	20
Nyali Msanakani	20
Old Town	20
	total = 100
Zanzibar (Unguja Island), Tanzania	
Chwaka Bay	20
Fumba	21
Mkokotoni	26
	total = 67

interviewed (Table 2); 100 at five different fishery landing sites in the larger Mombasa area in Kenya (Old Town, Nyali, Nyali Msanakani, Kenyatta and Marina), and 67 at three different sites around Zanzibar's coast (Chwaka Bay, Fumba and Mkokotoni). Prior to the interviews, meetings were held with fishers representing the respective landing sites (chairpersons of “beach management units” in Kenya and beach recorders or “Bwana Dikos” in Swahili in Zanzibar) to introduce the study and ask for the cooperation of fishers.

In both study areas, finfish (as the investigated sea urchin predator species) are traditionally almost exclusively fished by men (Fröcklin et al., 2013; Ochiewo, 2004). Hence, all respondents in this study were male fishers.

The interviews were conducted at the fishery landing sites. However, depending on the preferences of the respondents, some interviews took place at the respondents' homes or at public meeting points. To ensure a realistic representation of the investigated groups of fishers, the interviewees were randomly selected among those willing to participate in this study, disregarding age, experience or fishing practices. A semi-structured interview schedule (Denscombe, 1998; Kvale and Brinkmann, 1997) was used for all interviews to allow a flexible succession of questions, as well as follow-up questions and deeper discussions. Question themes to identify the drivers behind the fishing of sea urchin predators encompassed demographic information, fishing practices, the exploitation of sea urchin predators, local ecological knowledge, awareness of ecosystem alterations and exploitation effects, as well as management ideas (for the interview form, see Appendix I). All investigated fish- and sea urchin species were presented to the interviewees using color photographs to avoid confusion or misinterpretation. Most interviews were conducted in Swahili with the help of interpreters affiliated to local research institutions (Kenya Marine and Fisheries Research Institute in Mombasa and Institute of Marine Sciences in Zanzibar). The interviews took between 30 and 90 min, and the answers were noted, as well as voice recorded when approved by the respondents. To ensure data triangulation, additional information was collected through informal discussions with local researchers (from the Kenyan Marine and Fisheries Research Institute and the Wildlife Conservation Society in Kenya and the Institute of Marine Sciences in Zanzibar), fish traders and beach-management unit chairmen in Mombasa and beach recorders (“Bwana dikos”) in Zanzibar. Further, fishers and fisheries-related activities (preparations of fishing gears, fishers leaving and returning from fishing, landing the catch, selling of the catch) were observed at the landing sites, and local fish markets were visited.

2.5. Data analysis

For the quantitative data analysis, the provided answers were transcribed and coded into answer groups. To statistically test for differences between groups (Kenyan vs. Zanzibari fishers, age groups, bait-users vs. non-bait users, users of different gears), bivariate statistics and the Chi-square test and Fisher's exact test were used. Where data is presented for both Kenya and Zanzibar combined, separate tests were conducted for the two areas, to be able to exclude possible significant differences in associations. To test for differences in gear use depending on age or experience, the Kruskal Wallis test was used, and the Spearmen test was used to test for correlations between factors. All statistical analyses were performed using the program “Stata”, version 13. Only p-values <0.05 were considered as statistically significant. For the presentation of qualitative data, answers were pooled and arranged in different topics discussed. For these results, a descriptive representation was used presented as percentages of respondents.

3. Results and discussion

3.1. General overview of fishers and their practices

The interviewed fishers were between 16 and 77 years old, with younger fishers in Kenya (46% under 31 years, $n = 100$) compared to Zanzibar (24% under 31 years, $n = 67$). Years of fishing experience varied between six months and 50 years, with the larger proportion of younger fishers in Kenya also having less fishing experience (45% less than 11 years of fishing experience) compared to Zanzibar (19% less than 11 years).

In total 84% of the fishers ($n = 116$) conducted fishing as a fulltime occupation, and 70% ($n = 100$) fished 6–7 days per week throughout the year. These results are consistent with earlier studies in the region (McClanahan and Mangi, 2004; Thyresson et al., 2013) and imply a steady, daily fishing pressure.

A total of 61% of the fishers stated that they usually fish in seagrass beds, and 58% in coral reef areas ($n = 161$, multiple answers were allowed). Considering the two study areas separately, 58% of the Kenyan respondents fished in seagrass beds, and 53% in coral habitats ($n = 95$), and in Zanzibar, 71% fished in coral- and as many in seagrass habitats ($n = 66$). This demonstrates that both coral reefs and seagrass ecosystems are of high importance for local small-scale fisheries as fishing grounds.

As is typical for small-scale fisheries around the world, a variety of fishing gears were used in the study areas. When comparing the Kenyan and Zanzibar study areas, the use of certain gears varied (Fig. 2). The results of this study show that differences in gear use emerge for fishers of different age, and for fishers of different fishing experience ($p = 0.00016$ for age and $p = 0.000026$ for years of fishing experience). The youngest and least experienced fishers used beach seines, followed by gill nets, hook and line, and finally traps were used by the oldest and most experienced respondents. Age and fishing experience were strongly correlated (Spearman's rho = 0.83).

Beach seines – which are among the most destructive gears in the region (McClanahan and Mangi, 2001; Jiddawi and Öhman, 2002) – were the most frequently used gear at the Kenyan sites, whereas few fishers mentioned using beach seines in the Zanzibar sites. This could be related to the greater proportion of younger fishers in the Kenyan study sites, where, compared to the Zanzibar sites, nearly twice as many fishers were under 30 years old. Other studies have also shown that young people often use gears like beach seines or spear guns instead of traditional gears, despite their destructiveness (Mangi and Roberts, 2006) or disapproval by elders (de la Torre-Castro and Lindström, 2010; Mangi et al., 2007; McClanahan et al., 1997). However, during the data collection for a later study in 2013, a use of beach seines was observed in Zanzibar as well (Wallner-Hahn, unpublished data). During the data

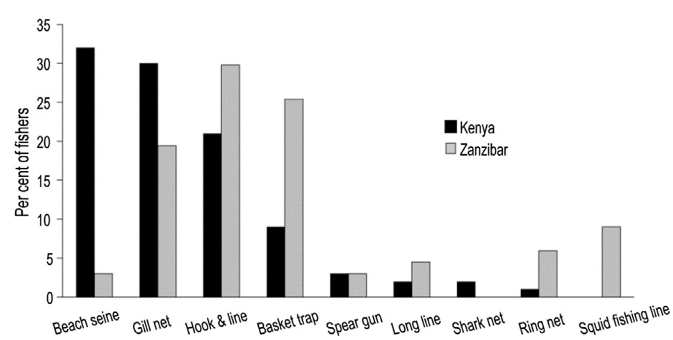

Fig. 2. Main fishing gears used (in % of fishers per study area; Kenya: $n = 100$; Zanzibar: $n = 67$).

collection to this study, beach seines were especially prevalent in two of the Kenyan landing sites (Marina and Nyali Msanakani), where 56% of the respondents reported their use. Meanwhile at the Zanzibar study sites, the most frequently used gear was hook and line, followed by traditional basket-traps. Such basket-traps require a large amount of knowledge to construct and use, and are usually used by older fishers (see also de la Torre-Castro and Rönnbäck, 2004; Mangi et al., 2007). This could indicate the existence of a more traditional fishing background among the respondents in the relatively more rural study sites in Zanzibar compared to the more urban Mombasa area in Kenya. This also coincides with the higher proportion of elder fishers with more fishing experience found in Zanzibar (see also de la Torre-Castro and Rönnbäck, 2004).

Concerning the use of bait, 64% of all respondents (n = 167) – mostly hook and line- and trap fishers – used different kinds of bait (e.g. pieces of squid, fish, octopus, worms, sea urchins, starfish, algae and seagrass).

Seventy-four percent of the fishers from Kenyan study sites (n = 100) perceived declining catches of sea urchin predators. This could indicate that sea urchin predator numbers have been decreasing, and presuming no changes in daily fishing pressure, could continue to do so, leading to impaired predation control of sea urchin populations.

An issue that may be contributing to the increasing fishing pressure in the WIO region is the continuous increase in tourism, which results in a growing demand for high-value food fish (de la Torre-Castro, 2012; Gössling, 2003; Thyresson et al., 2013). Moreover, increasing migration from rural areas leads to growing coastal populations (Glaesel, 2000; Hinrichsen, 1999) that increase the market for finfish.

3.2. Are sea urchin predator fish species caught in small-scale fisheries of Kenya and Zanzibar?

All of the interviewed fishers caught at least one of the eight identified sea urchin predator fish species, and 50% of all respondents reported to catch all eight species (Table 3). More importantly, the three ecologically most important predators – the triggerfish *B. undulatus* and the wrasses *C. formosa* and *C. trilobatus* (McClanahan, 1995, 2000) – were caught by a majority (67%–81%) of the fishers (Table 3). The species most commonly caught was the emperor *Lethrinus mahsena*, which is thought to be the least important from a predation control perspective (McClanahan, 1995). Comparing Kenya and Zanzibar, the same patterns of predator fishing can be seen in both countries. However, several of the species were caught by more fishers at the Zanzibar sites.

However, only *L. mahsena* was caught daily, followed by the wrasses, while triggerfish were not part of everyday catches, and by some fishers only caught rarely (on average, a fisher caught 1.2 individuals of *B. undulatus* per week). These results correspond to those found by McClanahan (2000), and are not surprising since triggerfish have naturally low population densities, and their populations have slow growth and long recovery periods following the cessation of fishing (McClanahan, 2000). During the field work for this study, catches of undersized sea urchin predator species were observed (personal observation by Wallner-Hahn in Mombasa, Kenya), which concurs with another study in the area (Mangi and Roberts, 2006), where catches of the key predator *B. undulatus* were found to contain up to 25% juvenile fish, and catches of *Pseudobalistes fuscus* of even 100%. The high incidence of juveniles indicates probable overexploitation and unsustainable fisheries. This could have cascading effects on seagrass- and coral reef habitats, as triggerfish are among the few species specifically adapted to feed on armored prey like spiny sea urchins, which makes them especially important and not easily replaceable in the food web (McClanahan, 1995; Pinnegar et al., 2000; Sala, 1997). Furthermore, since triggerfish usually occur in low densities, they are particularly vulnerable to overfishing (McClanahan and Shafir, 1990; Young and Bellwood, 2012).

Table 3
Sea urchin fish predator species reported to be caught by local fishers.

Preadator fish species	Both sites (n = 167)	Kenya (n = 100)	Zanzibar (n = 67)
Balistapus undulatus	67%	59%	79%*
Balistoides viridescens	66%	56%	82%*
Pseudobalistes fuscus	64%	56%	76%*
Coris formosa	60%	47%	80%*
Cheilinus trilobatus	81%	81%	81%
Coris aygula	54%	46%	67%*
Coris gaimard	58%	48%	73%*
Lethrinus mahsena	90%	93%	85%

The results are shown in % of fishers. Values with significant differences ($p < 0.05$) between Kenya and Zanzibar are shown as *.

3.3. Are sea urchin predators actively targeted, and if so, why?

Only one of the eight species – *L. mahsena* – was actively targeted by the majority of the respondents (Fig. 3). Slightly higher percentages of fishers targeted this species actively in Zanzibar, compared to Kenya, but no significant statistical difference emerged (p = 0.067). This shows that *L. mahsena* is an important target species in both study areas. Very few fishers (1–6%) targeted the other seven sea urchin predators, including the keystone predator *B. undulatus*. This indicates that the catches of these seven species can largely be categorized as by-catch.

The three main sea urchin predator species *B. undulatus*, *C. formosa* and *C. trilobatus* were caught as by-catch by all gears (Fig. 4).

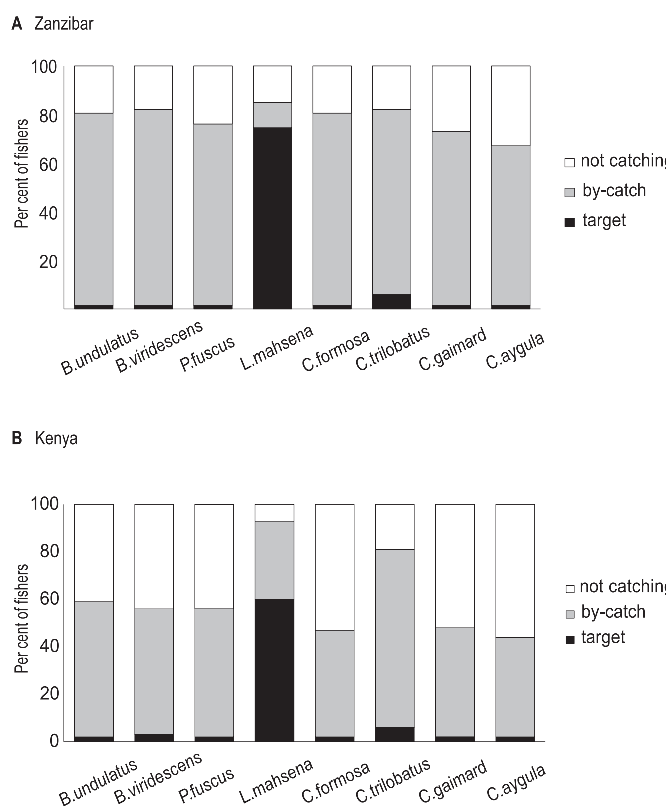

Fig. 3. Percentages of fishers targeting/by-catching/not catching the sea urchin predator fish species in the study sites in Zanzibar (n = 67) and Kenya (n = 100) (based on the fishers' responses, in % of the total number of fishers).

Basket trap fishers reported catching these three species most frequently, followed by hook and line fishers. As these gears often use bait, they may attract the predators since they are invertivorous and/or piscivorous (Froese and Pauly, 2013). When comparing the catches of the three main predator species between bait users and non-bait users, significant differences emerged: *B. undulatus* and *C. formosa* were reported to be caught at higher rates by bait-users in both Kenya and Zanzibar (*B. undulatus* by 82% of the total number of bait users (n = 106) compared to 42% of the non-bait users (n = 57) (p = 4.008e-07) and *C. formosa* by 72% (n = 107) compared to 42% (n = 57) (p = 0.00035). For *C. trilobatus*, this difference was only found in Zanzibar (94% of bait-users (n = 50) compared to 50% of non-bait users (n = 14) (p = 0.00019)). As traps were used to a higher extent in the Zanzibar study sites compared to the Kenyan ones, this could also explain the generally higher proportions of fishers reporting catching the sea urchin predators in the Zanzibar sites. In many cases, fish caught by traps and hook and line were landed live and hence, a straightforward management strategy may be to encourage fishers to carefully return sea urchin predators to the ocean (so called 'catch-and-release' management). This type of management strategy should only be taken into consideration after thorough explanations of the ecological background, consultations and discussions with the fishers, and biological assessments ensuring sufficient survival of released fish. Furthermore, an increased use of traps might also benefit sustainable fisheries in general (Mangi et al., 2007) as they, with the right mesh size and volume, are considered to be among the least damaging gears (de la Torre-Castro, 2006; de la Torre-Castro, 2012; Mangi and Roberts, 2006).

L. mahsena was the species being marketed at the highest rates by the vast majority of fishers (Fig. 5). The wrasse *C. trilobatus* was sold by 81% of the fishers catching it, which indicates that even though very few fishers target it, it still provides an income.

In addition, *L. mahsena* was the only predator species which fishers categorized as of economically high value (Fig. 6). *C. trilobatus* was classified as medium value, while the six remaining species were mostly categorized as low value fish. This further indicates why the two main sea urchin predators, *B. undulatus* and *C. formosa*, as well as *Balistoides viridescens*, *P. fuscus*, *Coris aygula* and *Coris gaimard* are not actively targeted by fishers.

Triggerfish like *B. undulatus*, *B. viridescens* or *P. fuscus* were found to be among the least preferred species by the fishers, which is supported by earlier work (Mangi et al., 2007; McClanahan and Muthiga, 1989). This may be explained by their very tough and poisonous skin (McClanahan and Muthiga, 1989), which has to be

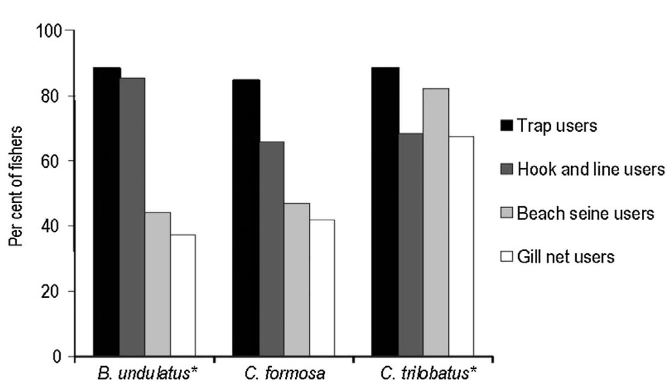

Fig. 4. Percentages of the different gear users catching the three main predator species as by-catch (based on the fishers' responses from both Kenyan and Zanzibar sites; gill net users: n = 43, hook and line users: n = 41, beach seine users: n = 34, trap users: n = 26). Significant differences ($p < 0.05$) in the catches by the different gears shown as *.

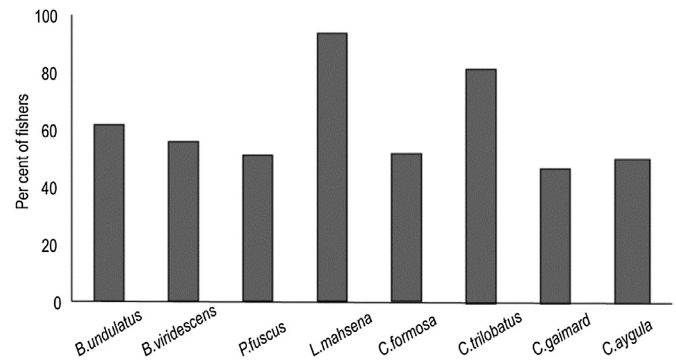

Fig. 5. Fishers selling sea urchin predator fish species (based on the fishers' responses, in % of the total number of fishers from Kenyan and Zanzibar sites (n = 167)).

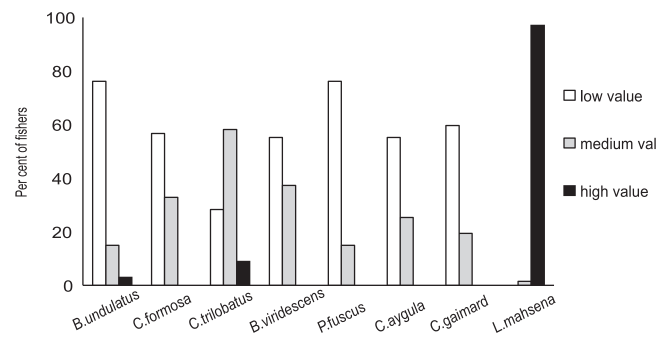

Fig. 6. Sea urchin predators' economic value according to the fishers (in % of fishers, n = 67).

removed before they are eaten or sold (personal observation, S. Wallner-Hahn) (Fig. 7).

Fishers who did not sell the predator species stated that they either used them for their own consumption, gave them away to those in need, or used them as bait. Consequently, despite numerous species being caught without being targeted, there is minimal discard as most species are either sold or needed for the fishers' subsistence (see also Mangi et al., 2007; Obura, 2001). Fish species of high commercial value are often sold to hotels or bigger markets, rather than to local people, while lower-value species (like triggerfish) are sold in small local markets or are kept for home consumption (de la Torre-Castro and Rönnbäck, 2004; Thyresson et al., 2013). Against this background, the mentioned straightforward management measure of returning live-caught sea urchin predators to the sea becomes a lot more complex, as it might deprive fishers of much-needed, low priced protein.

In the Kenyan sites, the fishers stated that sea urchin predator species were also caught for the live aquaria trade (mainly wrasses and triggerfish). In the Zanzibar sites, the triggerfish species were used for traditional medicine, as sandpaper (triggerfish skin) or ornaments, indicating a more traditional use. As the majority of the fishers from the Zanzibar study sites caught triggerfish as by-catch, it can be assumed that fish already caught are skinned for these uses, rather than being specifically targeted for them.

3.4. Awareness and Local Ecological Knowledge (LEK)

3.4.1. Perceived changes in sea urchin populations

Sixty-eight percent of all respondents (n = 167) stated that sea urchin numbers were increasing (for the two study areas separately: 54% of the Kenyan fishers and 88% of the fishers from

Fig. 7. A fisherman showing a freshly caught individual of *B. undulatus* (above), and a skinned individual on a local fish market in Mombasa (below).

Zanzibar, which shows a significant difference between the two sites ($p = 3.450e-06$)). The higher percentages of Zanzibari fishers perceiving an increase in sea urchin numbers could be due to a higher awareness of changes in the marine ecosystem and/or a bigger increase in sea urchin numbers compared to the Kenyan study sites. However, data allowing a comparison to support either hypothesis is lacking. The fishers' presumed causes for this increase are shown in Table 4. Interestingly, only 6% mentioned a lack of sea urchin predators as a possible cause for increases in sea urchin densities; a belief which strongly contrasts with most research studies (see Eklöf et al., 2009; McClanahan, 1992; McClanahan and Muthiga, 1989; McClanahan and Shafir, 1990).

Furthermore, less than 50% of the respondents were aware of the fact that the eight investigated fish species (Table 2) feed on sea urchins. This illustrates relatively low degrees of knowledge concerning food web interactions, trophic cascades and the impacts of fishing on marine ecosystems.

Only 21% ($n = 167$) of the respondents thought that fishing of the predator species could affect sea urchin numbers, indicating low levels of awareness about the fishers' own impact as an additional part of the food web. Some fishers stated, however, that the predators would be so disproportionally few, that they could not possibly have any effect on the high numbers of sea urchins and consequently, their fishing could not impact sea urchin numbers. However, as triggerfish naturally occur in low densities (McClanahan and Shafir, 1990; Young and Bellwood, 2012), and fishing reduces their numbers further, it is possible that their ecological importance as predators is misjudged by the fishers because of their low abundances.

3.4.2. Local ecological knowledge about seagrasses

In the Zanzibar sites, 70% of the fishers perceived seagrasses as declining ($n = 67$). The most frequently mentioned reason was sea urchin overgrazing (Table 5), while only 6% of the fishers mentioned a lack of sea urchin predators as a possible indirect cause. Further, more than half of the fishers from the sites in Zanzibar (54%, $n = 67$) perceived the increasing sea urchin numbers as a problem for seagrasses. When they were asked if they thought seagrass ecosystems were affected by the increasing sea urchin populations, 49% ($n = 67$) agreed, all of which referring to overgrazing as the main cause to seagrass decline. Together with the low LEK about trophic interactions between predators and sea urchins (see above), this shows higher degrees of LEK and awareness concerning simpler concepts like herbivory, but less understanding about complex concepts like indirect food web interactions.

3.5. Fishers' suggestions for how to manage sea urchin overgrazing

During the interviews, the fishers from both Kenyan and Zanzibar sites were asked to give their ideas and proposals about how management can reduce the problem of seagrass overgrazing and coral reef bioerosion caused by sea urchins (Table 6). The main suggestion was the physical removal of sea urchins – a reactive management response that has been shown to reduce sea urchin densities in the short term, but also has limited or potentially adverse effects in the long term (Eklöf et al., 2008). The fishers who suggested an increased use of sea urchins as bait, argued partly for a broader reintroduction of a smaller type of wooden "Madema/Malema" basket traps, which can use sea urchins as bait, and have declined in use. Most importantly, very few fishers (3%) considered reducing catches of sea urchin predators as a potential solution. A few fishers argued for turning sea urchins into a business of any kind, which could contribute to a reduction in numbers. In the study areas, sea urchins are currently not exploited or used for any purpose other than as bait (Alcoverro and Mariani, 2002), while the collection of *T. gratilla* for consumption or local marketing is common in some WIO countries such as Madagascar or Mozambique. An increased use of sea urchins might contribute to a reduction in numbers as well as potential benefits as a livelihood.

The results show that a vast majority of the fishers suggested solutions targeting the "symptoms" of overgrazing (high densities of sea urchins, overgrazing of seagrasses and overconsumption of

Table 4
The fishers' assumed causes for increasing sea urchin numbers.

Presumed causes for sea urchin increase	Percent of fishers
High reproduction rates of sea urchins	27%
Lack of exploitation	23%
Seasonal changes	21%
Decreased use of sea urchins as bait	12%
Lack of sea urchin predators	6%

The results are shown in % of fishers perceiving an increase ($n = 113$).

Table 5
The fishers' assumed causes for declining seagrasses.

Presumed causes for seagrass decrease	Percent of fishers
Sea urchin overgrazing	47%
Coastal erosion/increased water motion	21%
Seaweed farming	17%
Use of destructive gears	8.5%
Lack of sea urchin predators	6%

The results are shown in % of the fishers earlier mentioning a seagrass decrease ($n = 47$).

Table 6
The fishers' management proposals concerning sea urchin overgrazing.

Management proposals – sea urchin overgrazing	Percent of fishers
Removal of sea urchins	51%
Nothing can be done	8%
Increase use of sea urchins as bait	7%
Reduction of catches of sea urchin predator species	3%
Turning sea urchins in business	1.5%
Education and cooperation with scientists	1.5%
Replanting of seagrasses	1%

The results are shown in % of fishers (n = 136).

corals), rather than the drivers behind overgrazing (e.g. overfishing of urchin predators and the underlying reasons for it). Only a few respondents mentioned solutions aimed at the drivers (like the reduction of predator catches, education for a better understanding of ecosystem functioning and cooperation with scientists and/or the government), which is indicative of higher degrees of awareness, a broader perspective, and better understanding of social-ecological linkages.

The fishers from study sites in Kenya were further asked to give general management proposals concerning overexploited predator fish species and declining catches. The suggested management proposals (Table 7) are examples of higher degrees of LEK and show awareness concerning the problems and shortcomings, which artisanal fisheries in the WIO are facing. All suggestions could in theory contribute to higher catches, but also a more sustainable use of marine resources and a development towards more balanced seagrass – sea urchin – predator interactions.

LEK seems to be higher concerning fishing benefits and ecosystem structure, rather than ecosystem linkages and processes like trophic cascades, which was also shown in another study in southern Kenya (Crona, 2006). LEK among fishers can nevertheless be substantial, although highly variable among resource user groups and individuals (Crona, 2006; de la Torre-Castro and Rönnbäck, 2004). As LEK is argued to be an important factor contributing to more sustainable resource use (Olsson and Folke, 2001), additional education about trophic cascades and ecosystem functioning should be desirable components in future management.

3.6. Synthesis: drivers behind the overharvest of sea urchin predators

Multiple factors operating at different scales seem to have contributed to the overexploitation of sea urchin predator fish species in the WIO (Table 8). Despite local differences concerning management regimes, fishing techniques, traditional-, cultural- and geographical settings, the same patterns were observed in the studied areas in Kenya and Zanzibar.

Our study identified a number of direct drivers which might influence the exploitation of sea urchin predators in the WIO, such as fishing techniques using bait, destructive gears like beach seines leading to catches of juveniles and discard (see also Mangi and Roberts, 2006), and overlapping selectivity of fishing gears (see also McClanahan and Mangi, 2004). The drivers in a regional socio-economic context are likely to be overexploitation of coastal ecosystems (illustrated by poor catches), as well as poverty forcing fishers to use bycatch species like sea urchin predators for subsistence. These drivers are in turn influenced by governance regimes and management plans, as well as the condition of the available resources. Overexploitation of marine resources is a global problem, as fish populations are driven to local- or global extinction, which can result in unexpected and far-reaching impacts in marine ecosystems (Jackson et al., 2001; Pauly, 2008). Overgrazing of seagrass beds and coral reefs due to overexploited sea urchin predator populations is a clear example of the above. Nonetheless, there is a growing demand for high value food fish as tourism increases (Gössling, 2003). Simultaneously, there is an increasing demand for fish as a protein source to feed growing populations, which is reflected in an increased consumption of low-value food fish particularly in developing countries. However, the per-capita fish consumption in Sub-Saharan Africa steadily decreases (Delgado et al., 2003), indicating a high, non-saturated demand for food fish, rising prices and overexploited resources (Thyresson et al., 2013). It can therefore be assumed that countries like Kenya and Tanzania are facing a high fishing pressure on marine resources throughout the food web, leading to decreasing catches and ecosystem changes indirectly driven by the effects of globalization. Consequently, serious management problems arise, and the welfare of small-scale fishers and coastal populations, depending on these marine resources for their daily livelihoods, is threatened.

Table 7
Suggested management proposals concerning overexploited sea urchin predator fish species and declining catches.

Management proposals – declining catches	Percent of fishers
Banning of destructive fishing gears	31%
Recovery periods for inshore ecosystems	18%
Supply of gear for offshore fishing	18%
Supply of less destructive gear	18%
Controls	14%
Stronger regulations for commercial ships and trawlers	8%
Avoiding catches of juveniles	6%
Fishers' cooperatives	5%
Rotational fishing/recovery periods	5%
Reduction of the numbers of fishers	4%
Education	1%
Reduction of sea urchins	1%

The results are shown in % of fishers (n = 100).

4. Conclusions

The results of this study contribute to a further understanding of the problem of ecosystem degradation due to cascading effects of overfishing. Its main contribution is the identification and investigation of underlying drivers from a social-ecological perspective. While knowledge about the ecological dynamics of such changes already existed (Alcoverro and Mariani, 2002; Eklöf et al., 2008; Heck and Valentine, 1995; McClanahan and Muthiga, 1988) the fishers' motivations to fish and use key predators as well as the associated values and driving forces were to a great extent unknown. Specifically, this study indicates that:

(i) all investigated sea urchin predator fish species are exploited by small-scale fisheries in Kenya and Zanzibar in the WIO;
(ii) the predator species are (with the exception of the emperor *L. mahsena*) not actively targeted and have low economic value on the fish market;
(iii) the majority of the fishers were aware of an increase in sea urchin numbers and the negative effects sea urchins may have on seagrass beds and coral reefs. On the other hand, LEK on trophic cascades deriving from fishing of sea urchin predators was found to be generally low;
(iv) awareness concerning fisheries-related problems like high fishing pressure, declining catches, use of destructive gears and management approaches relevant for the WIO was present among fishers;

Table 8
Identified drivers behind the exploitation of sea urchin predators, causes and management suggestions.

Identified drivers	Causes	Consequences	Management suggestions
Bait use	Fishing methods like hook and line or basket traps using different kinds of bait attract sea urchin predators because of their invertivorous/piscivorous diet.	Catches of sea urchin predators.	Education on food web interactions and cascading effects; cooperation with fishers to explore the possibility of returning sea urchin predators to the sea (as most fish caught with these gears are caught alive); introduction of modified traps that allow triggerfish to escape (Gomes et al., 2013; Mbaru and McClanahan, 2013).
Multi-gear fisheries and non-sustainable fishing methods	High numbers of fishers in multi-gear fisheries using more and more effective gears as catches are declining. High and increasing numbers of fishers fishing in shallow coastal waters deplete local fish stocks. Use of destructive gears like beach seines or nets with too small mesh sizes catching juvenile fish or even eggs. Fishing methods like spear guns that target the biggest individuals and make it easy to catch triggerfish (susceptible because of their territorial nature).	Intense fishing pressure causing potential imbalances in the food web structure. Depleted fish stocks and destruction of important habitats like seagrass beds and coral reefs.	Education on destructive gears and their effects on marine ecosystems, better management of gears, banning of destructive gears/gear exchange programs and control routines; enforcement of existing laws and better regulations on fishing gears.
"Everything caught is taken", even less valuable fish species	Need of protein and cash. Lack of alternative livelihoods. Most fishers live under poverty lines and are, due to declining catches and increasing fish prices, forced to take up low value species for their own protein intake.	High fishing pressure on fish species throughout the food web as higher value species are sold and lower value species kept for fishers' own protein intake.	Education on food web interactions and cascading effects and cooperation with fishers to explore the possibility of returning important species like sea urchin predators. Introduction of modified traps that allow triggerfish to escape (Gomes et al., 2013; Mbaru and McClanahan 2013. Coordination with other government ministries to promote realistic alternative livelihoods.
Lack of knowledge on ecosystem processes and cascading effects	New actors engaged in fisheries lacking traditional and local ecological knowledge due to lack of job opportunities.	Erosion of traditional- and local ecological knowledge Erosion of institutions such as respect of elders' knowledge.	Coordination with other government ministries to promote realistic alternative livelihoods. On-going educational seminars and information to fishers. Special education for "new fishers", and their inclusion into existing institutions and organizations such as fishers committees.
Growing global demand for both high value and low value food fish	Growing populations and increasing tourism in developing countries lead to an increasing demand for low- and high value fish.	Overexploitation of marine resources throughout the food web leads to depleted fish stocks and small-scale fishers struggling for their livelihoods. Overfishing of species of high trophic levels leads to food web changes and cascading effects (Pauly et al., 1998).	Consider planetary boundaries and global governance procedures as well as awareness raising about connections between local, regional and global factors.

(v) there is no strong trade-off between the fishing of keystone predators and societal gains. Fishing of species like *B. undulatus* can have devastating effects on seagrasses and corals, but provides minor benefits to the population (due to the low market value and limited uses of these species).

Several factors driving the fishing of sea urchin predators were identified in this study, suggesting that management of degraded ecosystems, as a result of food web changes, should encompass a wide variety of strategies and scales. In the WIO context, one key issue is the human dependence on coastal/marine resources, which should be considered in management and governance strategies (Cinner et al., 2009; de la Torre-Castro, 2012; McClanahan et al., 2009). The technical aspects of management (e.g. design of selective gears) as e.g. described in Mbaru and McClanahan (2013) of key predator species like sea urchin predators is essential, but can only be one component striving towards productive ecosystems.

Management suggestions derived from this study require actions on multiple scales, including education, gear management, strengthening of local institutions, the enforcement of existing rules and regulations and the introduction of adequate alternative livelihood options. It is furthermore important that the connections between regional and global processes (like market dynamics) are taken into consideration. Finally, management and governance actions have to be coordinated and undertaken in cooperation with local actors, and the integration of fishers as well as the exchange of scientific-, local- and traditional ecological knowledge between the different groups of stakeholders and scientists should be emphasized.

Acknowledgments

We are deeply grateful for the valuable cooperation and kindness of all fishers in Mombasa and Zanzibar. In Mombasa, we would like to thank the Kenya Marine and Fisheries Research Institute (KMFRI), especially Jacob Ochiewo and Fridah Munyi-Leshan, for valuable support and input, as well as Edward Waiyaki for precious help in the field. In Zanzibar, we thank our colleagues at the Institute of Marine Sciences (IMS) for great assistance, especially Narriman Jiddawi, Muumin Abdulaziz, Fatma Iddi and Said Juma Shabaan. At Stockholm University, we thank Caroline Raymond, who provided key assistance in the field, and Charlotte Berkström, Sara Fröcklin and Lars Lindström for valuable inputs on this manuscript. We are grateful for dissemination grants from the Western Indian Ocean Marine Science Association (WIOMSA), which made this study possible as part of the Marine Science for Management (MASMA) program (to the project "Seagrass and Sea Urchin Interactions Overgrazing and Resource Use in the WIO Region"). MTC was supported by Sida and The Swedish research Council (VR, Proj. nr. 344-2011-5448). JSE was funded by the Swedish International Development Cooperation Agency Sida (grant SWE-2009-018) and the Swedish Research Council (Vetenskapsrådet/Uforsk grant SWE-2012-086). MG was supported by Sida, Vetenskapsrådet, Formas and the Sida/SAREC Marine Science bilateral program between Tanzania and Sweden.

Appendix I

Semi-structured interview guideline for fishers used in this study

An analysis of drivers behind the exploitation of sea urchin predators in the WIO

Demographic information

- Respondent's name:
- Sex: male female
- Age in years:
- Marital status: single/married (number of wifes)/divorced/widowed
- Number of children (under 18 year/over 18 years):
- Number of other relatives supported by the respondent:
- Education: no education/primary school/secondary school/university

Fishing practices

- For how long have you been working as a fisher:
- Is fishing your main occupation: yes/no
- *(If no)* Which other occupations do you have:
- Was your father a fisher as well:
- In which types of habitats do you most oftenly fish: make a ranking:
  - seagrass beds
  - coral reef
  - sand flat
  - mangroves
  - rocky ground
- Do you usually fish:
  - in the intertidal zone
  - subtidal close to shore
  - subtidal deep sea
- Do you use a boat: yes/no
- (I*f yes*) which kind of boat do you use:
- What kind of fishing gears do you use:
- Which of these gears do you use: most often/second most often/etc.:
- Why are you using that kind of gear:
- *(For trap and hook & line fishermen)* Are you using any bait: yes/no
- *(If yes)* Which kind of bait are you using:
- *(If not mentioned)* Do you use sea urchins as bait: yes/no
- *(If yes)* Do you use these species as a bait: *Tripneustes gratilla/Echinometra mathaei*
- Do you know if these sea urchin species are collected for some other purpose:
- Which fish species do you usually catch:
- Which fish species have you caught today, and how much of each in (in kg or pieces):
- Do you usually fish any of these particular species on the pictures:
  - *Balistapus undulatus*
  - *Balistoides viridescens*
  - *Peudobalistes fuscus*
  - *Coris formosa*
  - *Coris aygula*
  - *Coris gaimard*
  - *Cheilinus trilobatus*
  - *Lethrinus mahsena*
  - *Rhinecantus aculeatus*
  - *Rhinecantus rectangulus*
- Do you specifically target these species *(asked for the same species individually)*: yes/no
- How much of these species (in kg per species) do you usually catch per day *(asked for the same species individually)*:

Ecology and LEK

- Have there been changes in the catch trend of these species since you started fishing, and which (no change/increase/decrease):
- *(If change)* Why do you think the catches of these species have changed:
- Have there been any changes in the size of these fish over time (since you started fishing):
  - increase
  - decrease
  - no change
- *(If change)* Why do you think the size of these species has changed:
- What do these fish species eat:
- Do any of these species eat sea urchins *(asked for each species individually)*:
- *(If yes)* Do they eat these particular sea urchin species:
  - *T. gratilla*
  - *E. mathaei*
- Are there any other animals eating sea urchins, and which:
- Have you seen any changes in the number of urchins since you started fishing:
  - increase
  - decrease
  - no change
- In which habitats have you observed these changes:
  - coral reef
  - seagrass bed
  - sandflats
  - rocky ground
- What do you think is causing these changes in urchin numbers: *(If fishing is not mentioned as a cause)* Do you think fishing of these particular fish species could affect the number of urchins: yes/no
- Have you observed any changes in the seagrass meadows in your fishing grounds:
  - increase
  - decrease
  - no change
- Do you think that seagrasses are affected by increasing numbers of sea-urchins: yes/no
- Do you think fishing in general affects the seagrass and coral reef ecosystem: yes/no
- *(If yes)* explain how (positively/negatively):

- Does the Mombasa marine park affect your fishing: yes/no
- *(If yes)* explain how (positively/negatively):

Market information

- What is your daily income from fishing (in KES/TZS):
- How much did you earn today (in KES/TZS):
- Do you sell these species *(show pictures of sea urchin predator species individually)*: yes/no
- How much do you usually get for these species (per kg in KES/TZS):
- How would you rank their economic importance *(show pictures of sea urchin predator species individually)*:
  low
  medium
  high
- Who buys these fish species from you:
- *(If selling to a middleman)* Who are the final users of these species:
- Are some of these fish exported: yes/no
- (*If yes*) to which countries?
- Do you usually keep any of these fish species for your own use: yes/no
- Are these fish species eaten: yes/no
- Do you eat them yourself: yes/no
- *(If yes)* Why do you eat them (taste good/cheap/protein source/etc.):
- Are these species used for anything else:
- (*If not mentioned*) are these species used for:
  the production of medicine
  ornamental trade
  aquaria trade
- Do you eat sea urchins: yes/no
- If yes, which species:
- (If *not mentioned*) Do you eat the following species: *E. mathaei/T. gratilla*

Management

- *(If increasing numbers of sea urchins mentioned)* Would you consider increasing numbers of sea urchins as a problem: yes/no
- *(If yes)* explain how:
- *(If yes)* How could the problem of increasing sea urchin numbers be solved:
- Which management strategies could benefit to higher numbers of sea urchin predators?
- How could seagrasses be protected from sea urchin overgrazing?

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