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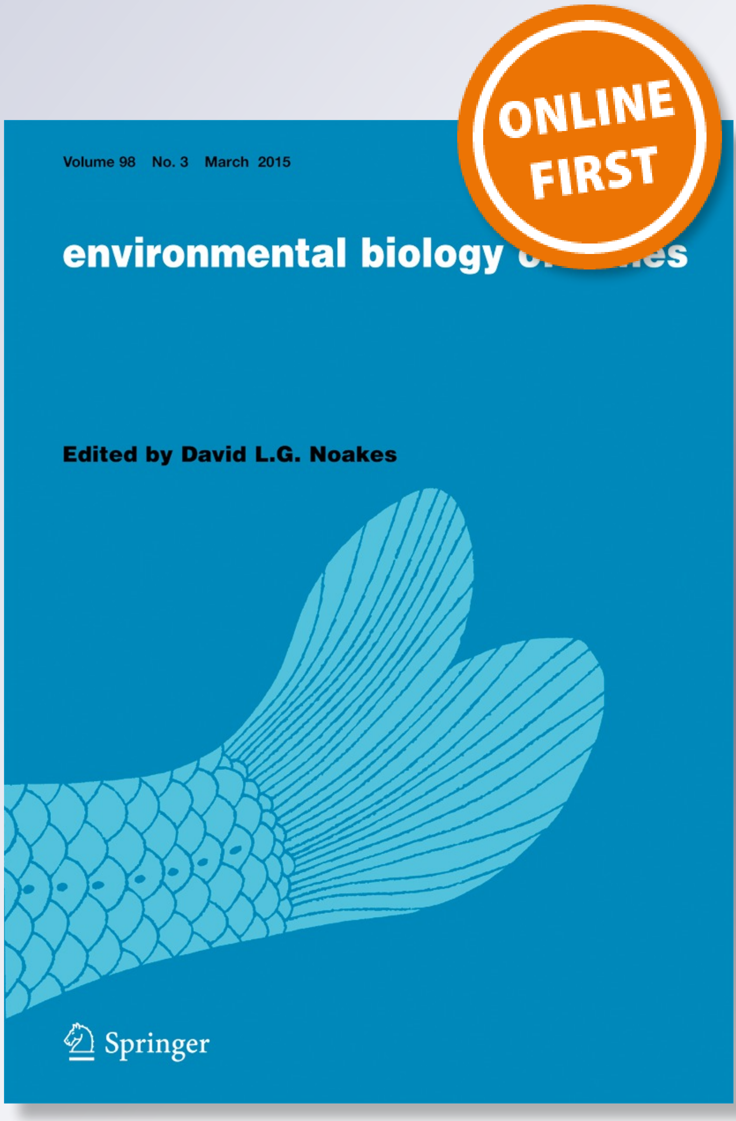

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Abstract The tropical rocky intertidal is a poorly studied ecosystem of great ecological and commercial importance, warranting consideration when implementing coastal management strategies. Icthyofaunal diversity was studied at low tide in intertidal pools in the Watamu Marine National Park, Kenya (Western Indian Ocean). A total of 235 individuals in 15 families (34 species) were observed in 78 sampled quadrats. Gobiidae was the most prevalent family, comprising 25.5 % of individuals (five species), followed by Blenniidae with 18.3 % of individuals (five species), Pomacentridae with 15.7 % of individuals (ten species), and Labridae with 14 % of individuals (seven species). A Chao2 asymptotic richness estimate gave an expected asymptotic richness value of 96.36 (s.d.=6.26), but is likely an underestimate of actual species richness due to limitations of visual census techniques. Half of species observed (52.7 %) were only observed as juveniles, indicating that these habitats may function as nurseries for reef-associated and deeper water fish. Other species were resident in this zone, with ten species being found in no other habitat in the surrounding area. This study suggests that the rocky intertidal contributes greatly to adjacent subtidal reef fish populations, which may support continuing local fisheries commerce through spillover of valuable species into the fishable waters. Conservation of this habitat may be of more importance than was previously considered due to its recent discovery as a possible nursery ground for offshore coral reef fish and the presence of species not found in other habitats in the area.

Keywords Species richness · Biodiversity · Tidepool · Kenya · Connectivity · Conservation

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Introduction

Coral reef fish use their habitats non-randomly and are often closely associated with a particular substrate type, such as live coral (Faria and Almada 2001; Garpe and Öhman 2003). Juveniles have been shown to be more specialized in microhabitat selection than conspecific adults, often associating with a specific coral species or growth form (Garpe and Öhman 2007). Microhabitat selection has also been documented between and within intertidal pools. For example, Faria and Almada (2001) showed that habitat use varies greatly between different species and different life history

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stages of the same species, with species showing highly specific microhabitat use.

The extreme environmental conditions observed in intertidal habitats compared to those encountered in habitats that stay submerged throughout the tidal cycle (Metaxas and Scheibling 1993) result in a variety of physiological adaptations in resident tidepool fish species (Gibson and Yoshiyama 1999). However, these are not the only fish to make use of the challenging intertidal environment. While some large reef fish and pelagic species use the intertidal for foraging and may end up accidentally trapped in pools as the tide goes out, other species exist in tidepools as temporary residents (Griffiths 2003), using the habitat during specific seasons or life history stages (Gibson and Yoshiyama 1999). Often these temporary residents are larval or juvenile fish recruits which leave the intertidal once they reach a certain body size or maturity, making tidepools an important nursery area for ecologically and commercially important deep water species in some locations (Gibson and Yoshiyama 1999; Almada and Faria 2004; Cunha et al. 2008). In Barbados, for example, tidepools house many juvenile reef species and are thought to form a reservoir of biodiversity, capable of replenishing surrounding reef populations (Mahon and Mahon 1994).

The rocky intertidal is a relatively well-studied habitat in the field of ecology, however the vast majority of these studies have been conducted on temperate coastlines. Very few intertidal studies have focused on tropical shores (Gibson and Yoshiyama 1999) and fewer on those in the Western Indian Ocean region (Table 1). This study will describe for the first time the low-tide fish assemblage of the rocky intertidal platforms in the Watamu Marine National Park (WMNP), North coast of Kenya, and examine the importance of these habitats to offshore coral reefs and fisheries biodiversity and conservation.

Methods

Study area

The Malindi/Watamu Marine National Reserve (Fig. 1) covers a total area of 20,000 hectares of near-shore

Table 1 Comparison of fish biodiversity found in previous tropical rocky intertidal surveys, and corresponding subtidal fish surveys for some of the same regions. H' = Shannon-Wiener diversity index, not available for all studies

Location	Method	Individ.	Families	Species	H'	Reference
Intertidal						
WMNP, Kenya (WIO)	Stationary visual census	235	22	55	3.15	This study
Goa, W. India	Clove oil anaesthetic	386	5	9		Lobsang et al. 2012
Oahu, Hawaii	Water removal, collection	342	10	19	2.4	Cox et al. 2011
Espírito Santo, SE Brazil	Rotenone icthyocide	3448	27	88		Macieria and Joyeux 2011
Glorieuses Island (WIO)	Clove oil anaesthetic	155	14	32		Durville and Chabanet 2009
Cerará, NE Brazil	Underwater visual census	8914	25	43		Cunha et al. 2008
Martins Bay, Barbados	Rotenone icthyocide	2078	63			Mahon and Mahon 1994
Subtidal						
WMNP, Kenya (WIO)	Underwater visual census			375		Cowburn, unpublished data
Glorieuses Island (WIO)	Underwater visual census		57	332		Durville et al. 2003
Goa, W. India	Underwater visual census			49		Sluka 2013

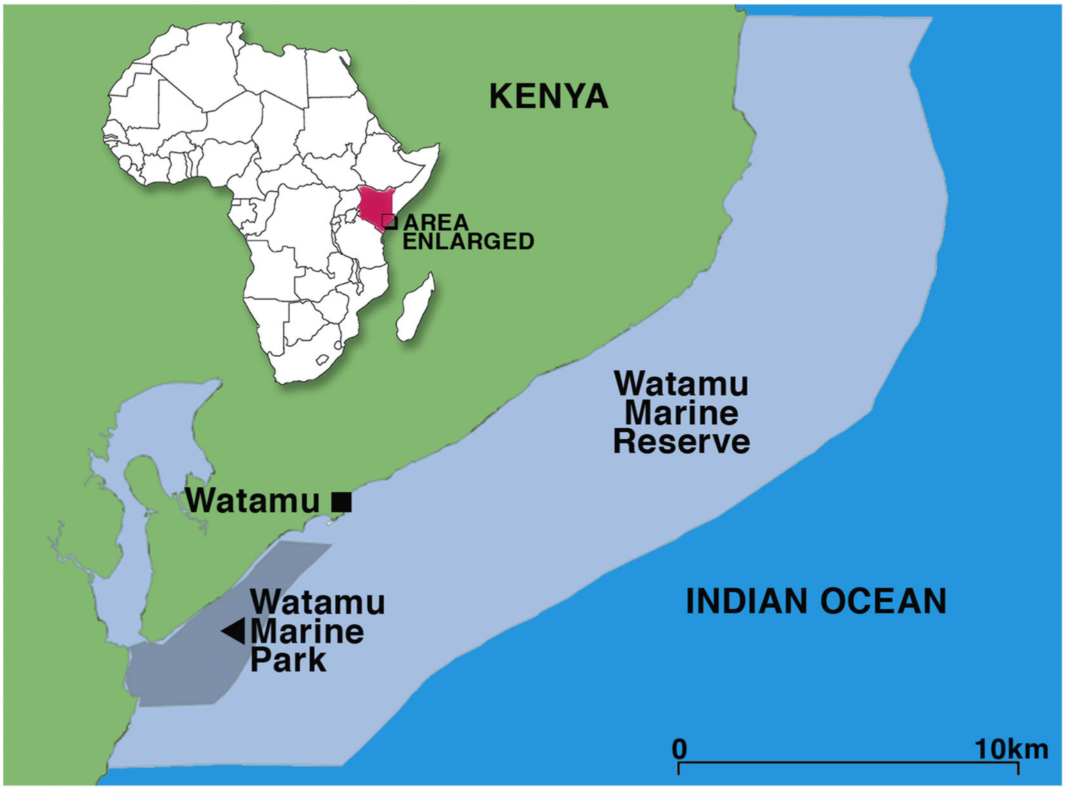

Fig. 1 Location of study area on the North Coast of Kenya. The smaller dark area just south of Watamu Town is the Watamu Marine National Park (WMNP), which is completely protected from fishing or collection. The larger lighter area is the Watamu/Malindi Marine National Reserve, which extends north to join the Malindi Marine National Park. This area is open to artisanal fisheries using traditional methods. Rocky platforms surveyed in this study were entirely within the WMNP

lagoon, bordered by a fringing reef that runs nearly continuously along the Kenyan coast, about 200 km (Aloo 2000). Embedded within this reserve, the WMNP encompasses a total area of 10 km^2, bounded by a linear fringing reef located 1–2 km from shore. This smaller park is completely protected from any sort of fishing or collection, however tourism operations are prevalent and occasional poaching has been reported (Kenya Wildlife Service (KWS), personal communication). The Park is bordered to the north and south by the Reserve, which limits fishing activities to traditional, artisanal methods, though in recent years there has been an increase in illegal ringnet fishing reported (KWS, personal communication).

Kenya experiences two monsoonal seasons: the Northeast (October-March) and Southeast (March-October) monsoons. The Northeast Monson is characterized by low cloud cover, lack of rain, reduced wind energy, and higher temperatures with the opposite being true for the Southeast Monsoon (McClanahan 1988). The tidal range in Kenya is 4 m (Brakel 1982 in McClanahan 1988), with mixed semidiurnal highs and lows.

Tidepool characterization

The shallow (maximum depth=10 m) lagoon of the WMNP is punctuated by nearshore platforms of hard substrate that form pools, shelves, and interconnected matrices, resulting in a range of tidepool habitats. These platforms tend to be flat across the top, not existing on any sort of shore slope, with little to no intertidal zonation (authors' observation) so that there is seemingly little within-platform difference in tidal exposure. Thirteen of these platforms were selected for sampling out of 22 mapped rocky platforms within the park. Platforms were selected based on accessibility (two were far offshore, one of which surrounded a protected island) and presence of life. Pools within many of the smaller, very nearshore platforms were observed to be filled in with sand and seagrass blades and no fish were observed at these locations throughout the months of April-July 2013. Pools in the 13 studied platforms had an average depth of 14.50 cm (±8.05 sd) and an average opening width of 39.24 cm (±33.51 sd).

Icthyofaunal richness sampling

Random sampling of ichthyofaunal richness and abundance was accomplished by using a computer generated random numbers list to place 1×1 m quadrats along a coordinate system spanning the length and width of each platform (Littler and Littler 1985). Approximately 12 quadrats were surveyed on each platform (78 total quadrats sampled), each of which typically encompassed 1–3 pools or partial pools, for a total of approximately 24 pools surveyed per rocky platform. All fish surveys were conducted at low spring tides within 3 days of the full/new moon, when the tidal height was 0.46–0.93 m.

Due to national park regulations, it was not possible to collect and count fish using anesthetics or by draining pools. For that reason, underwater stationary visual census techniques (Barrett and Buxton 2002) were combined with those developed by Faria and Almada (1999) for non-invasive tidepool fish censusing. Two-minute fish counts were performed for each quadrat, during which time two observers actively searched pool areas for cryptic fish by prodding crevices with blunt probes and recording all fish that swam through the quadrat within the 2 min. Photos were taken of any fish for which definite field identification was not possible for later analysis. The interconnected nature of many of the sampled pools made censusing challenging, but we feel confident with the results obtained through these methods. All fish identifications were made using Lieske and Myers (1997) and Froese and Pauly (2013).

Statistical analyses

Variation in depth and richness between platforms were analyzed with one-way, fixed factor ANOVAs. Normality was confirmed for all datasets using a one-sample K-S test, and homogeneity of variance was confirmed using Levene's test. Shannon-Wiener diversity indices (H') and Sørensen dissimilarity coefficients were calculated for each platform as well as all platforms overall. The species accumulation curve and chao2 asymptotic estimator were also calculated. All statistical tests were performed in R (R Core Team 2013).

Results

A total of 235 individuals in 15 families (34 species) were observed in the 78 sampled quadrats. Gobiidae was the most prevalent family, comprising 25.5 % of individuals (five species) of the total, followed by Blenniidae with 18.3 % of individuals (five species), Pomacentridae with 15.7 % of individuals (four species), and Labridae with 14.5 % of individuals (six species).

One-way, fixed factor ANOVA tests showed that the 13 studied rocky platforms did not differ significantly from each other in terms of either depth ($F_{9,115}=1.87$, $p=0.06$) or species richness ($F_{9,115}=1.40$, $p=0.19$). Because of this, all sites were grouped together for calculations of overall biodiversity.

Overall, the studied rocky platform area had a Shannon-Weiner diversity index of 3.15, with a Pielou's evenness score of 0.85. The average Sørensen index of dissimilarity of all pair-wise comparisons between sites was 0.79. A sample-based species accumulation curve was constructed using Kindt's exact method (Oksanen 2013; Fig. 2). The extrapolated richness value for the area overall using the non-parametric Chao2 asymptotic estimator is 96.36 (6.26 SE).

In addition to these calculations based on species recorded in the 78 sampled quadrats, we also made an incidental sightings list wherein we recorded any new species we happened to see during surveys and in photographs, but that did not occur in sampled quadrats.

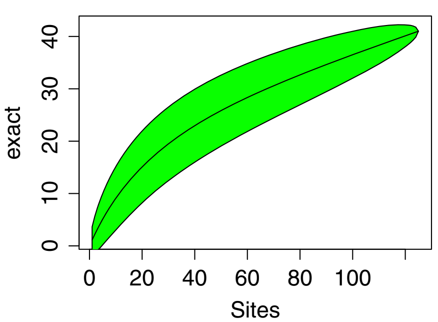

Fig. 2 Species accumulation curve for 34 fish species observed in 78 quadrats (sites), using the Kindt's exact method to determine "exact" species richness by sampling effort. Envelope gives 95 % confidence interval

These data were not incorporated into statistical analyses, but are included in Tables 1 and 2. The total number of species observed (including those on the incidental sightings list) was 55 (Table 1). Of these, 38.2 % were observed as both juveniles and adults, 52.7 % were observed only in a juvenile or sub-adult stage/size, and 9.1 % were only observed as adults. It was determined that 35.7 % of all observed species were of value to commercial fisheries (Anam and Mostarda 2012; Table 2).

Discussion

The rocky intertidal areas surveyed in this study had a total of 55 species in 22 families (235 individuals), with an overall Shannon-Weiner biodiversity index of H'= 3.15. There are very few reports of tropical intertidal fish to compare this study to, and fewer from the Western Indian Ocean area (Table 1). Making comparisons is difficult due to different sampling methods and efforts, however it appears that the intertidal platforms of Watamu are of medium richness when compared to other sites at a species level, but of high richness when compared at the family level. The patterns of diversity observed will be linked to the biogeographic region of the site (Randall 1998) and habitat characteristics such as the size, structural complexity, and relief of the intertidal area (Jennings et al. 1996; Arakaki et al. 2014). Other studies showed a low species richness of 9 in Goa, India, which is an offshore site heavily influenced by fluvial effects, and 32 in a study of a small island near Madagascar. The lower intertidal biodiversity at Goa is reflected in a similar lower biodiversity subtidally of 49 species (Sluka 2013). At Glorieusus Island, there was a similar subtidal diversity as at Watamu (332 vs 375), but a relatively smaller number of intertidal species (32 vs 55). With so few data points from around the world to compare to it is difficult to interpret the biodiversity of Watamu in the context of other sites, and points to the need for more work on tropical intertidal shores.

The sample-based species accumulation curve for this habitat (Fig. 2) does not reach a clear asymptote, which is expected in very diverse areas such as tropical marine communities (Ugland et al. 2003). The Chao2 non-parametric estimator predicts a total species richness of 96.36 (6.26 SE) for the rocky intertidal as a whole. This should be considered a lower-bound estimate (Gotelli and Colwell 2001; Walther et al. 2005),

Table 2 Taxonomic list of fish species observed in intertidal rockpools in Watamu Marine National Park, Kenya, combined total from quadrat surveys (*N* number observed) and incidental sightings (I). Residency status (R) as defined by Griffiths (2003): permenant resident (Pr), temporary (Tp), transient (Tr). Commercial importance (CI) as described in Anam and Mostarda (2012): aquarium trade (Aq), fisheries (F)

Family and Taxa	*R*	N	CI
Acanthuridae			
Acanthurus triostegus	Tp	2	F
Apogonidae			
Apogonichthyoides taeniatus	Tp	I	Aq
Cheilodipterus quinquelineatus	Tp	1	Aq
Ostorhinchus cookii	Pr	17	Aq
Ostorhinchus taeniophorus	Pr	5	Aq
Pristiapogon kallopterus	Tr	I	Aq
Balistidae			
Pseudobalistes flavimarginatus	Tp	I	F
Rhinecanthus aculeatus	Tp	I	F
Blenniidae			
Antennablennius variopunctatus	Pr	21	Aq
Blenniella cyanostigma	Pr	19	Aq
Hirculops cornifer	Pr	1	Aq
Istiblennius unicolor	Pr	1	Aq
Salarius fasciatus	Pr	1	Aq
Chaetodontidae			
Chaetodon auriga	Tp	I	Aq
Chaetodon lunula	Tp	I	Aq
Gobiidae			
Gnatholepis anjerensis	Pr	I	Aq
Gnatholepis caurensis	Pr	12	Aq
Gnatholepis scapulostigma	Pr	4	Aq
Istigobius ornatus	Pr	16	Aq
Stenogobius kenyae	Pr	13	
unidentified larvae	Pr	12	
Kuhliidae			
Kuhlia mugil	Tp	I	Aq
Labridae			
Coris caudimacula	Tr	1	F
Halichoeres hortulanus	Tr	2	F
Halichoeres scapularis	Tp	I	F
Labroides dimidiatus	Tp	4	F
Stethojulis albovittata	Tr	1	F
Thalassoma amblycephalum	Tp	1	F
Thalassoma hebraicum	Tp	8	F
unidentified larvae	Tp	17	
Lutjanidae			
Lutanus fulviflamma	Tp	1	F

Table 2 (continued)

Family and Taxa	*R*	N	CI
Lutjanus kasmira	Tp	I	F
Mullidae			
Parupeneus barberinus	Tp	I	F
Muraenidae			
Echidna leucotaenia	Pr	1	F/Aq
Echidna nebulosa	Pr	1	F/Aq
Siderea picta	Pr	I	F/Aq
Nemipteridae			
Scolopsis ghanam	Tp	I	F
Pempheridae			
unidentified larvae	Tp	20	
Pleuronectidae			
unidentified larvae	Tp	1	
Plotosidae			
Plotosus lineatus	Tp	I	Aq
Pomacentridae			
Abudefduf sexfasciatus	Pr	I	Aq
Abudefduf sparoides	Pr	I	Aq
Abudefduf vaigiensis	Pr	21	Aq
Chrysiptera annulata	Tp	I	Aq
Chrysiptera biocellata	Tp	I	Aq
Chrysiptera brownriggii	Pr	7	Aq
Chrysiptera glauca	Tp	I	Aq
Pomacentrus aquilus	Pr	5	Aq
Pomacentrus caeruleus	Tp	I	Aq
Pomacanthus chrysurus	Tp	1	Aq
unidentified larvae	Tp	3	
Scorpaenidae			
Scorpaenopsis oxycephala	Tp	8	
Serranidae			
Grammistes sexlineatus	Tp	1	F
Signidae			
Siganus sutor	Tp	1	F
Syngnathidae			
Micrognathus andersonii	Tr	1	
Synodontidae			
Saurida gracilis	Tp	4	F
Tetraodontidae			
Canthigaster solandri	Tp	1	

especially taking into account the likelihood of underestimation with visual census methods (Gibson 1999; Willis 2001). Unfortunately, richness estimates and species accumulation models were not available for studies in Table 1, which would have yielded more accurate comparisons of area richness (Gotelli and Colwell 2001).

Over 375 fish species have been identified in the Watamu Marine National Park over the past 3 years (Cowburn, unpublished data). The low tide intertidal fish surveys conducted through this study have added ten new species to the list, all in families Gobiidae and Blenniidae. The most common of these were *Antennablennius variopunctatus* (n=21), *Blenniella cyanostigma* (n=19), and *Istigobius ornatus* (n=16). These species represent a component of biodiversity in the national park that are unique to the intertidal area and would be overlooked in conventional reef surveys. Other species use the intertidal zone to varying degrees, at different times of tide and/or life cycle (Griffiths 2003). Usage of the intertidal zone can be divided into three main categories: permanent residents - those that spend their entire life history (from juvenile through adult) in the intertidal; temporary (opportunistic/secondary) residents - those that spend only part of their lives in the intertidal (often as juveniles); transients - those that are only occasionally present in low-tide pools (likely trapped by an outgoing tide while foraging) (Griffiths 2003). Based on these definitions we can tentatively assign those fish found in WMNP tidepools as both adults and juveniles as permanent residents, those that are found only as juveniles temporary as residents, and those found only as adults as transients (Table 2).

Several prominent reef-associated species were observed in tidepools during this study. These include species such as: *Acanthurus triostegus* (convict tang), *Pseudobalistes flavimarginatus* (yellowmargin triggerfish), *Rhinecanthus aculeatus* (white-banded triggerfish), *Chaetodon spp*. (butterflyfish), *Lutjanus spp.* (snapper), and *Parupeneus barberinus* (Dash-and-dot goatfish). Family-wise, several groups identified are characteristic of coral reef fish families: Acanthuridae, Chaetodontidae, Labridae, and Pomacentridae (Choat and Bellwood 1991). The high percentage of reef-associated species found only as juveniles during this survey (Temporary residents; 52.7 %, Table 2) suggests that these areas may provide nursery habitat for subtidal reef fish. This nursery habitat concept has been suggested for other intertidal habitats as well, including mangroves (Robertson and Duke 1987), intertidal beaches (Van der Veer et al. 2001), mud flats (Chong et al. 1990), and estuaries (Boehlert and Mundy 1988). Durville and Chabanet (2009) found 13 species present in rockpools only as juveniles, including species from families Lutjanidae, Chaetodontidae, Pomacentridae, Labridae, Mugilidae, Acanthuridae, and Bothidae - all reef associated species. Similarly, Macieria and Joyeux (2011) found that 7.3 % of fish collected from tidepools in SE Brazil were non-resident, reef-associated species, many of which were only observed in a small body size. Mahon and Mahon (1994) found that 44 % of the 2078 fish (63 species) collected in E. Barbados were temporary residents and suggested that these habitats might represent an overflow from the deeper reef areas and could function as a reservoir to replenish subtidal reef populations. However, the significance of intertidal habitats as nurseries seems to vary greatly by location and season (Gibson and Yoshiyama 1999). Further investigation is necessary to definitively label this area a nursery habitat. Beck et al. (2001) point out that in order for a habitat to classify as a nursery, it must make a substantial contribution to juvenile density, growth, survival, and movement to adult habitat. Surveys over different seasons, at different times of day and including more rocky platforms may be necessary to account for temporal and spatial variation (Almada and Faria 2004; Arakaki and Tokeshi 2006; Faria and Almada 2006). Investigations into size class distributions of fish, mark and recapture studies to establish movement between habitats, and comparisons with other juvenile reef fish habitats will be necessary to fully establish the rocky intertidal habitat as a nursery for subtidal reef fish.

It is likely that nearly all reef fish species use intertidal habitats at some point in their life cycle for reproduction, shelter, foraging, etc. Transient residents – those fish that use the intertidal area primarily during high tide for foraging, but may become trapped in pools as the tide goes out, or seek refuge from larger predators in these areas for short times – were represented by only 2.1 % of individuals (five species) in this study. However, as surveys were only performed at low tide, this number does not account for all fish species that make use of this habitat. High tide underwater visual census could provide a better understanding of the importance of this habitat to subtidal reef fish for foraging (Faria and Almada 2006).

If the rocky intertidal habitats in the Watamu MNP do indeed provide important foraging and nursery grounds for subtidal reef fish, this habitat has the potential to make a substantial contribution to local commerce by supporting marine fisheries. We recorded several commercially important species in the rocky intertidal, including *Siganus sutor* (Whitespotted rabbitfish), *Scolopsis ghanam* (Arabian monacle bream), *L. fulvivlamma* (Black-spot snapper), *L. kasmira* (Bluestripe snapper), and *P. barberinus* (Dash-and-dot goatfish), which are commonly reported in fisheries catches at Malindi and Watamu landing sites (Kuaunda-Arara and Rose 2004a, b). A total of 35.7 % of observed species are noted as having importance to Kenyan fisheries by the FAO guide to Kenyan fisheries resources (Anam and Mostarda 2012). Though the subtidal area immediately adjacent to these rocky intertidal platforms are completely protected from fishing and collection, the Watamu MNP is bounded to the north and south by the Malindi/Watamu Marine National Reserve which allows artisanal fishing using traditional methods (Fig. 1). Spillover from protected MNP waters into the MNR seems to be low, but higher out of Watamu MNP than the Malindi MNP (25 km north), likely due to the presence of a fringing reef at Watamu compared to a series of patch reefs at Malindi (Kaunda-Arara and Rose 2004b). However, fish movements within the Watamu MNP do seem to be directional to the south (Kaunda-Arara and Rose 2004a), so it is possible that spillover is just a slower process here than elsewhere. McClanahan and Mangi (2000) reported findings of a 10 year long study of spillover from the Mombasa Marine National Park (70 km south of WMNP) to fishable areas which revealed that the park closure increased both catch per fisher and catch per area by more than 50 %. The dominant fisheries species they found spilling into exploitable waters were in the families Siganidae (rabbitfish), Lethrinidae (emperors), and Acanthuridae (surgeonfish). These findings suggest that the rocky intertidal habitat of WMNP is of value to local marine commercial interests by sheltering juvenile fisheries species and supporting the high-tide foraging of adults and that similar processes may be at work along other areas of the coastline where spillover from protected parks to fishable reserves is of greater importance.

The tropical rocky intertidal is an understudied habitat and often overlooked by coastal managers and conservation organizations. This study in the Watamu Marine National Park of Kenya demonstrates their ecological and commercial importance, which should make a strong case for their inclusion in research and conservation efforts. More research should be done to help managers better understand the role of these unique habitats in the biodiversity, health, and ecosystem functioning of tropical coastal areas and their contribution to coastal livelihoods.

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