Regional Studies in Marine Science 3 (2016) 49–57

Contents lists available at ScienceDirect

Regional Studies in Marine Science

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

Lunar, diel, and tidal changes in fish assemblages in an East African marine reserve

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HIGHLIGHTS

- Short-term changes in fish assemblages were visually observed in a coral reef and in a seagrass bed.
- Fish assemblages changed during lunar, diel, and tidal cycles in the coral reef and during diel and tidal cycles in the seagrass bed.
- Fish movement governed by natural cycles can cause predictable short-term variations in fish communities.
- The consideration of natural cycles in the survey design of fish community studies is essential.

ARTICLE INFO

Article history:
Received 13 January 2015
Received in revised form
3 May 2015
Accepted 5 May 2015
Available online 18 May 2015

Keywords:
Coral reef
Seagrass bed
Community structure
Underwater visual census (UVC)
Species diversity
Trophic groups

ABSTRACT

Fish assemblages in tropical habitats like coral reefs or seagrass beds vary with natural cycles (e.g., lunar, diel or tidal) on several spatio-temporal scales. However, the dimensions of these variations are rarely being quantified despite their strong implications for ecosystem functioning and conservation of exploited stocks. Ignoring these predictable changes hinders the identification of structuring forces of fish assemblages and may lead to incorrect interpretations of the results and evaluation of habitats. To assess natural variation on short timescales, fish assemblages at a small tropical island (Chumbe Island, Tanzania) in the western Indo-Pacific were investigated and compared among two coastal habitats (coral reef and seagrass bed) at different lunar, diel, and tidal phases using underwater visual census methods. Results of multivariate analyses suggested two distinct fish communities in the two habitat types with the coral reef comprising a higher species richness and heterogeneity than the seagrass bed. In the coral reef, community composition and trophic diversity was influenced by all three natural cycles, while in the seagrass bed they were mainly driven by tidal phases. Mean fish densities were slightly different in the two habitat types during daytime but increased significantly in the seagrass bed during twilight hours. For the investigated habitats on Chumbe Island our results indicate that (i) through their routine migrations mobile fishes can provide important functional links between habitats, (ii) seagrass beds have lower species richness and diversity, and emphasize that (iii) fish movement governed by natural cycles can cause predictable short-term variations in fish communities.

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1. Introduction

Coastal shallow water regions in the tropics are mainly characterized by diverse and highly productive habitats like seagrass beds and coral reefs, which fulfil important ecological functions and ecosystem services, like nursery and foraging grounds for fishes or food and income for the coastal population (Costanza et al., 1997; De la Torre-Castro and Rönnbäck, 2004; Jackson et al., 2015; Mumby, 2006). Dependency on coastal marine resources for daily protein needs is particularly high throughout the Indo-Pacific region (Unsworth and Cullen, 2010), where artisanal fisheries in inshore waters is one of the main sources of livelihood for many coastal communities. Despite this importance, coastal ecosystems are at risk worldwide, due to anthropogenic activities such as coastal development or overexploitation of marine resources. On Zanzibar, Tanzania, as one example of a tropical rural

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http://dx.doi.org/10.1016/j.rsma.2015.05.001
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economy in the Indo-Pacific region, coastal ecosystems provide 30% of the gross domestic product mainly through coastal fisheries and reef-based tourism (Lange and Jiddawi, 2009; Muhando, 2008). However, overfishing and the uncontrolled expansion of tourism is causing a drastic degradation of ecosystems (Spalding et al., 2001) and fishery yields per unit effort have been decreasing in the last 20 years (Mkenda and Folmer, 2001; Berachi, 2003). To ensure sustainable use of exploited fish stocks and correctly identify environmental factors affecting fish communities, reliable information on local community structure is necessary.

An important monitoring tool to detect long-term changes in fish assemblages is underwater visual census (UVC) (Bijoux et al., 2013). UVC is non-destructive, quick, inexpensive, adaptable to various habitats and species, and permits the collection of a wide range of biological data *in situ* (Gilbert et al., 2005). It is therefore one of the main methods used in coral reef systems and particularly suited for assessing density and biomass of coral reef fishes. However, to be an effective tool for conservation planning and provide valuable information for managing fisheries, it is necessary to distinguish variations in fish assemblages due to changes in recruitment or mortality from those due to fish movement in response to natural cycles like the lunar, diel or tidal phases (Bijoux et al., 2013). These cycles are long known to cause predictable fluctuations in fish communities by inducing different behavioural patterns in diel activity (Helfman, 1986; Hobson, 1973; Ogden and Quinn, 1994), foraging (Ogden and Zieman, 1977; Robblee and Zieman, 1984), and spawning (Colin and Bell, 1991; Taylor, 1984). Yet, the scales over which these variations occur are rarely being quantified or considered in the experimental design of fish community studies (see Bijoux et al., 2013 for review). This may lead to misinterpretations of empirical data and ultimately, to less efficient conservation and management practices. Moreover, regular short-term movements of adult and juvenile fishes can temporally alter the diversity or even the functional diversity, which can be of great importance for ecosystem dynamics, stability and productivity (Mumby, 2006; Berkström et al., 2013). Movement also affects the functional role a species has within a system: individuals of certain species might, for instance, be functionally important while foraging in one habitat type, but exert no significant functional impact, when resting in another (Nash et al., 2013). Through their routine migrations mobile fishes further link adjacent habitat types (Appeldoorn et al., 2009; Dorenbosch et al., 2006; Nagelkerken and van der Velde, 2002; Unsworth et al., 2008) influencing cross-habitat food-web dynamics and energy transfer. These so-called mobile links (Welsh and Bellwood, 2014) are thus key to ecosystem functioning and have shown to improve the resilience against disturbances (Olds et al., 2012; Welsh and Bellwood, 2014). Hence, if sampling does not consider temporal scales (e.g. diel) and does not cover relevant cyclic environmental changes (e.g. tides), important temporary residents may be missed and results will provide an incomplete picture of the actual fish community and the overall role of certain species or habitats may be assessed inaccurately (Jackson et al., 2002, 2001).

The main goal of our study was to determine short-term temporal patterns in the habitat use of tropical marine fishes in two coastal habitats (coral reef and seagrass bed) and assess the influence of these patterns on the structure of fish communities. We conducted observational studies in the no-take reserve of Chumbe Island, Zanzibar (Tanzania) during different time periods (high/low tide during day/twilight at spring/neap tide) to analyse (i) how fish community composition, species diversity, and fish densities are influenced by the lunar, diel, and tidal cycle, (ii) how the structure and diversity of trophic groups vary with these natural cycles, and (iii) if significant differences occur, which species are mainly responsible for the observed variation.

2. Material and methods

2.1. Study site

Chumbe Island (6°17′S, 39°10′E), a small coral island of approximately 0.22 km^2 in the western Indo-Pacific, is located 12 km south-west of Unguja Island, one of the two main islands of the Zanzibar Archipelago (Fig. 1(A)). In 1992, Chumbe and its surrounding waters on the western side were declared a no-take area and registered as a UN recognized Protected Area in 1994, whilst the eastern side of the island is still exploited by artisanal fisheries.

The study was carried out on the sheltered south-western coast of Chumbe, a relatively shallow area (<7 m) with a tidal range of 2.0 m during neap tides and 3.5 m during spring tides. Within this area three main habitats could be identified: sandy bottom, seagrass beds and coral reef (mangroves are absent on Chumbe Island). Seagrass beds were dominated by *Thalassodendron ciliatum* with a mean density of 576 ± 123.48 shoots m^{-2} and a mean length of 37.9 ± 10.0 cm while the coral reef habitat was characterized by a mixture of hard coral (26%), rubble and sand (56%), and rocky surface (18%). Salinity (measured using the Practical Salinity Scale) varied between 37 and 40 in the coral reef and between 36 and 39 in the seagrass bed, and temperature ranged in both habitats from 28 to 30 °C. Fish assemblage data were collected in the seagrass bed and coral reef area from December 2011 to February 2012 during the north-east monsoon and southern hemisphere summer.

2.2. Sampling procedure

To assess short-term temporal changes in fish community structure and fish density in different habitats a hierarchical sampling design was used (Fig. S1). Within each of the two investigated habitat types (coral reef and seagrass bed) fish were sampled at three different temporal scales (lunar, diel, and tidal cycle). At each factor combination at least four square quadrats of 25 m^2 with a minimum distance of 10 m to each other were surveyed using stationary point counts (Dorenbosch et al., 2006; Polunin and Roberts, 1993). Point counts can provide accurate data on mobile and conspicuous fish species, but may be biased by the experience of the observer and also require high water clarity (Murphy and Jenkins, 2010). Thus quadrats were surveyed on condition of underwater visibility >5 m by two observers independently after thorough training of species identification (English et al., 1997) until results were comparable. This same sampling technique was used across the entire experimental design balancing other known biases inherent to visual sampling methods (e.g. under- or over-estimation of fish densities) and thus allowing comparisons to be made across habitats and temporal cycles. Point counts were performed by placing a 5 m tape measure as a visual reference for quadrat size perpendicular to two permanent 50 m transects (at 5 m, 30 m and 45 m) in each habitat type (Fig. 1(B)). After placing the tape measure, the observer waited for at least 4 min to minimize fish disturbance before counting all fish species within or swimming through the quadrat over a period of 10 min. The first 8 min the observer stayed on the edge of the quadrat, while during the last 2 min the observer moved through the quadrat to search for sedentary species and fish hiding under seagrass leaves or coral boulders. All fishes observed were counted and identified to lowest possible taxa. Depending on water depth surveys were conducted using either snorkelling or SCUBA. Sampling was carried out at spring high/low tides and neap high/low tides during both daylight hours (9:00–16:30) and twilight (5:30–7:30 and 17:30–19:30). With $n \geq 4$ square quadrats surveyed per factor combination there were a total of 117 observational units in the data set (Table S1). Due to time restrictions not all factor combinations could be

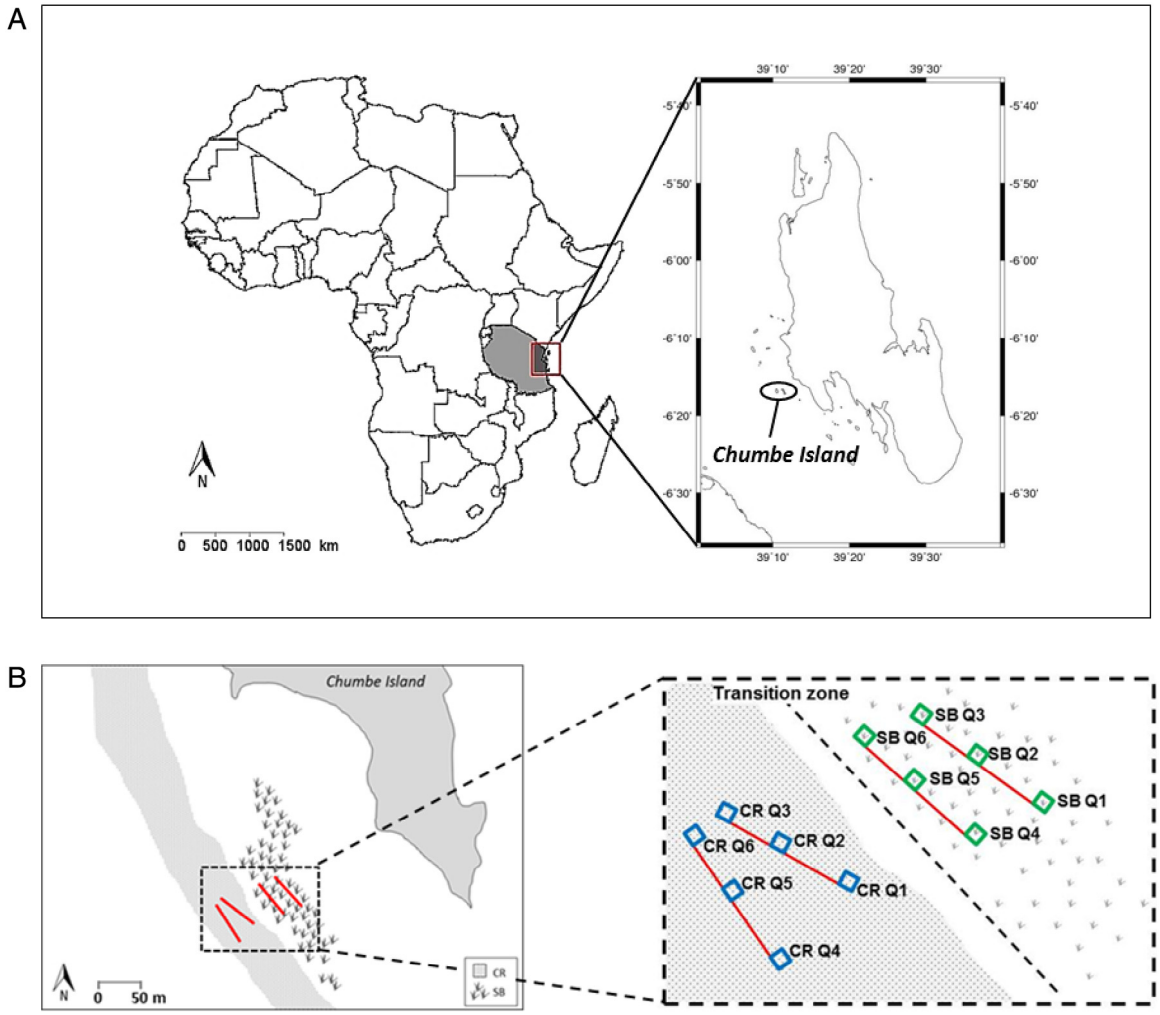


Fig. 1. (A) Study site *Chumbe Island* (black circle), south-west of the main island of the Zanzibar Archipelago in the western Indo-Pacific with (B) an overview of the sampling area (south-western side of Chumbe Island) and positions of sampling quadrats (25 m^2) in the coral reef (CR, blue) and seagrass bed (SB, green). Squares were laid along two 50 m transects (red line) at 0–5 m, 25–30 m and 45–50 m. Distance between transects is approximately 15–30 m. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

sampled to an equal extent and impracticalities of night sampling prevented the implementation of full day–night cycles.

2.3. Data analysis

2.3.1. Fish community composition and diversity

The experimental design consisted of the factors habitat (H, two levels, fixed), sampling quadrat (Q, six levels, random, nested in habitat), moon (M, two levels, fixed), daytime (D, two levels, fixed), and tide (T, two levels, fixed). The sampling quadrats were treated as random to account for inter-quadrat variation and thus, a 5-factorial mixed-effects model was applied to the study design (Millar and Anderson, 2004). Prior to multivariate analysis, fish assemblage data were transformed by 4th-root to reduce the influence of abundant species relative to rare ones (Clarke and Warwick, 2001). With these data, Bray–Curtis similarity matrices were calculated and used as input for (i) a non-metric multidimensional scaling analysis (nMDS) and (ii) non-parametric permutational multivariate analysis of variances (PERMANOVA) to test for habitat—(coral reef and seagrass bed) and time-related (lunar, diel, and tidal cycle) differences in fish community structure and composition. PERMANOVA are less stringent in their assumptions than the traditional multivariate analogues and thus preferable for ecological multivariate data sets like fish counts which usually contain many zeros (Anderson and Millar, 2004; Anderson, 2001). The test statistic (pseudo-F values) was calculated directly from the similarity matrix and the P-values were then obtained using 4999 permutations of residuals under the reduced model (Anderson and ter Braak, 2003). We first investigated the statistical significance and relative importance of the main factors (H, Q, M, D, T) and the spatio-temporal interactions (H × M, H × D, H × T) and then conducted posteriori pairwise comparisons with the PERMANOVA t-statistics for the factors of interest (interaction terms) to elucidate temporal differences within one habitat type. If significant differences occurred (P-values < 0.05), similarity matrices were further analysed using similarity percentage analysis (SIMPER) to identify the species that contributed most to the between-group differences (Clarke and Warwick, 2001). For comparison of species evenness, richness and heterogeneity among habitats two commonly used measures for species diversity, Pielou's evenness (J') and the Shannon index (H'), were calculated (Magurran, 1988) and statistically compared using a non-parametric Kruskal–Wallis test (assumptions for parametric testing could not be met). Pielou's evenness, a measure of the distribution of individuals over species, is constrained between 0.0 and 1.0 with 1.0 representing a situation in which all species are equally abundant. The Shannon index, on the other hand, accounts for both species richness and evenness of the species present: the more species present and the more evenly abundances are distributed among these species, the higher

the value of H' (typical values vary between 1.5 and 3.5, only rarely exceeding 4.5). Furthermore, each species was assigned a feeding category (herbivorous, omnivorous, piscivorous, planktivorous, corallivorous, detrivorous fishes, and invertebrate feeders) based on data in FishBase (Froese and Pauly, 2012) to compare trophic groups (Tilman, 2001) between assemblages. Based on these categories the 4th-root transformed fish assemblage data were aggregated and analysed analogous to fish community data. All multivariate analyses were performed using the PRIMER v6 software with the PERMANOVA + add-on package (Plymouth Marine Laboratory).

2.3.2. Fish density

For hypotheses testing of the univariate mean fish density data we used a generalized linear mixed-effects model (GLMM) (Bolker et al., 2009) with fish density as the response variable and the factors habitat (H), sampling quadrat (Q), moon (M), daytime (D), and/or tide (T) as the explanatory variables. Similar to the multivariate analysis, the factor sampling quadrat (Q) was introduced and treated as random to account for the spatial dependencies of sampling quadrats within habitats (Zuur et al., 2009). Because fish density data followed a gamma distribution, a gamma GLMM with an inverse link was used and fitted by maximum likelihood (Laplace Approximation). To identify the important variables in determining fish densities a suitable set of alternative mixed-effects models with different combinations of explanatory variables was specified and then compared using second-order Akaike's information criterion (AICc) and the according Akaike weights (w_m). The AICc is a well-established model-selection criterion, which is based on the maximum log-likelihood function and also accounts for sampling size (Burnham and Anderson, 2002). The AICc increases the relative penalty for model complexity with small data sets and is therefore more suitable for our data set than the AIC. However, the AICc measures only the relative quality of a statistical model, and thus Akaike weights – the relative likelihood of each of the candidate models given the data (Johnson and Omland, 2004) – were also taken into account. The predictive model with the minimum AICc and highest w_m was regarded the preferred representation for the data set tested (Anderson et al., 2000) and selected for further analyses. Following AICc determination of the best fitting model, term significance was determined using a Wald t-test. All univariate analyses were carried out using R Statistics (the R Foundation for Statistical Computing, http://www.r-project.org/) and the *lme4* package (Bates et al., 2012).

3. Results

In total, 138 species from 32 families (Table S2) were recorded during point count samplings. We found 125 species in the coral reef (CR) and 66 species *n* the seagrass bed (SB) with 53 species occurring in both habitat types. The species accumulation curves for both habitat types approached an asymptote and it can therefore be assumed that our sampling effort has been sufficient to collect most of the species present (Fig. S2). The most dominant families in terms of species numbers per family were Pomacentridae (CR = 23 spp., SB = 12 spp.), Labridae (CR = 21 spp., SB = 15 spp.), Scaridae (CR = 12 spp., SB = 6 spp.), and Acanthuridae (CR = 10 spp., SB = 6 spp.), while by abundance, Pomacentridae (CR = 34.2%, SB = 31.6%), Sphyraenidae (CR = 16.4%, SB = 15.0%), Labridae (CR = 13.1%, SB = 11.1%), and Scaridae (CR = 8.6%, SB = 5.5%) were most dominant in both habitat types. In the coral reef Acanthuridae (8.0%) was also relatively abundant, whereas in the seagrass bed Siganidae (21.2%) was the second most dominant fish family.

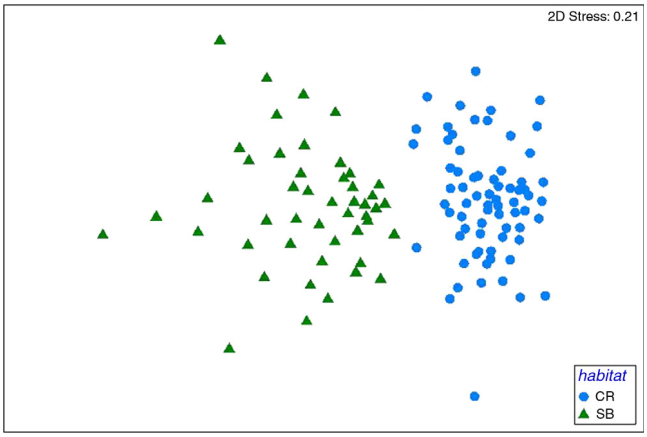


Fig. 2. Two-dimensional MDS plot for 4th-root transformed count data in the coral reef (CR, blue dots) and seagrass bed (SB, green triangles). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.1. Community structure and composition

The nMDS (Fig. 2) and PERMANOVA analyses (Table 1(A)) of the 4th-root transformed count data revealed significant differences between coral reef and seagrass bed indicating two distinct fish communities in the two habitat types. Also, the locations of the sampling quadrats within one habitat type had an impact on community composition highlighting the spatial heterogeneity of fish assemblages at small scales. Posteriori pairwise comparisons of the interaction terms habitat (H) with lunar (M), diel (D), and tidal (T) phases (H × M, H × D, H × T) (Table 1(B)) showed a consistent response to all three natural cycles in the coral reef and to the tidal phases in the seagrass bed with distinct high (H) and low tide (L) assemblages. The differences between groups were generally caused by several species, each contributing 7% or less to the overall dissimilarity (Table 2) indicating species rich and diverse fish assemblages. SIMPER analysis showed an average dissimilarity of 59.6% between the two habitat types (Table 2(A)), which was mainly caused by the shoemaker spinefoot *Siganus sutor* (4.7%) and the two damselfishes *Chromis viridis* (3.5%) and *Plectroglyphidodon lacrymatus* (3.3%). *S. sutor* and *C. viridis* were very abundant in the seagrass bed and rare in the coral reef, while the opposite was true for *P. lacrymatus*. In the coral reef (Table 2(B)–(D)) the lunar (M), diel (D), and tidal (T) phases primarily influenced the abundances of *C. viridis* (M = 3.3%, D = 3.3%, T = 3.5%), the Daisy parrotfish *Chlorurus sordidus* (M/D = 2.4%, T = 2.3%), and the surgeonfish *Ctenochaetus striatus* (M = 2.4%, D = 2.4%, T = 2.4%). All three species were more abundant during neap tide leading to an average dissimilarity of 63.4% between neap and spring tide samples. During daytime and low tides *C. viridis* and *C. striatus* were more common than during twilight and high tides while the *C. sordidus* showed a reverse pattern with an average dissimilarity of 63.2% of daytime vs.twilight and 64.1% of high vs. low tide samples.

Conversely, in the seagrass bed solely the tidal phases significantly structured community composition. The relatively high overall dissimilarity (69.9%) between low and high tide assemblages was mainly due to higher abundances of *S. sutor* (7.0%), the yellowtail barracuda *Sphyraena flavicauda* (6.3%), *C. viridis* (5.5%) and *C. sordidus* (5.3%) during high compared to low tides (Table 2(E)).

3.2. Diversity

Average values for the Shannon index varied significantly between the two habitat types (Kruskal–Wallis test, $\chi^2 = 46.842$,

Table 1
(A) Non-parametric multivariate analysis and (B) subsequent pairwise comparisons of 4th-root transformed fish assemblage data based on a Bray–Curtis similarity matrix testing for differences between habitats (H) and lunar (M), diel (D), and tidal (T) cycles.

(A) PERMANOVA					(B) Pairwise comparisons		
Source	df	MS	Pseudo-*F*	*P*-value	Groups	*t*	*P*-value
H	1	68 224	11.437	**0.0002**			
Q(H)	10	7057.4	4.2892	**0.0002**			
M	1	1518.6	0.9230	0.5534			
D	1	4183.6	2.5426	**0.0006**			
T	1	2847.1	1.7304	**0.0288**			
H × M	1	2297.4	1.3963	0.1262	CRN vs. CRS	1.6717	**0.0002**
					SBN vs. SBS	0.5838	0.9516
H × D	1	2092.0	1.2714	0.2136	CRD vs. CRT	1.4091	**0.009**
					SBD vs. SBT	1.3322	0.0644
H × T	1	4545.4	2.7625	**0.0002**	CRH vs. CRL	1.557	**0.0006**
					SBH vs. SBL	1.4243	**0.0334**
Residuals	99	1645.4					
Total	116						

P-values were obtained using 4999 permutations for each of the given permutable units. Fish were sampled using underwater visual census in square quadrats (Q, nested in habitat (H)) of two benthic habitat types (CR = coral reef, SB = seagrass bed) at the different time periods (N = neap tide, S = spring tide, D = day, T = twilight, H = high tide, and L = low tide). Bold values: $p < 0.05$.

Table 2
Results of the SIMPER analysis to assess which species are primarily responsible for the observed differences between (A) the two habitat types (CR = coral reef, SB = seagrass bed), (B) neap (N) vs. spring tide (S) samples within the coral reef, (C) day (D) vs. twilight (T) samples within the coral reef, and high (H) vs. low tide (L) samples within (D) the coral reef and (E) the seagrass bed.

(A) CR and SB		(B) CRN and CRS		(C) CRD and CRT		(D) CRH and CRL		(E) SBH and SBL	
Fish species	%	Fish species	%	Fish species	%	Fish species	%	Fish species	%
Siganus sutor	4.7	*Chromis viridis*	3.3	*Chromis viridis*	3.3	*Chromis viridis*	3.5	*Siganus sutor*	7.0
Chromis viridis	3.5	*Chlorurus sordidus*	2.4	*Chlorurus sordidus*	2.5	*Chlorurus sordidus*	2.3	*Sphyraena flavicauda*	6.3
Plectroglyphidodon lacrymatus	3.3	*Ctenochaetus striatus*	2.4	*Ctenochaetus striatus*	2.4	*Ctenochaetus striatus*	2.4	*Chromis viridis*	5.5
Sphyraena flavicauda	2.9	*Chaetodon trifascialis*	2.3	*Chromis atripectoralis*	2.3	*Plectroglyphidodon lacrymatus*	2.3	*Chlorurus sordidus*	5.3
Chaetodon trifasciatus	2.8	*Meiacanthus mossambicus*	2.2	*Meiacanthus mossambicus*	2.2	*Chromis atripectoralis*	2.4	*Stethojulis bandanensis*	4.6
Chlorurus sordidus	2.7	*Centropyge multispinis*	2.2	*Chromis weberi*	2.2	*Meiacanthus mossambicus*	2.2	*Cheilio inermis*	4.3
Gomphosus caeruleus	2.6	*Chromis atripectoralis*	2.2	*Parupeneus macronemus*	2.1	*Chaetodon trifascialis*	2.1	*Thalassoma hebraicum*	4.1
Canthigaster valentini	2.5	*Plectroglyphidodon lacrymatus*	2.2	*Chaetodon trifascialis*	2.1	*Parupeneus macronemus*	2.1	*Leptoscarus vaigiensis*	4.0
Ctenochaetus striatus	2.4	*Ctenochaetus binotatus*	2.1	*Plectroglyphidodon dickii*	2.1	*Plectroglyphidodon dickii*	2.1	*Pomacentrus trilineatus*	3.6
Thalassoma hebraicum	2.3	*Plectroglyphidodon dickii*	2.1	*Acanthurus leucosternon*	2.1	*Centropyge multispinis*	2.1	*Canthigaster valentini*	3.6

SIMPER results were obtained based on a Bray–Curtis similarity matrix, which was calculated from 4th-root transformed fish assemblage data sampled with underwater visual census. Only the first 10 species contributing most to the dissimilarity (% = percent dissimilarity contribution) are listed.

P-value < 0.0001) showing a higher species richness and heterogeneity in the coral reef (125 spp., $H' = 3.623$) compared to the seagrass bed (66 spp., $H' = 2.558$). Average values for Pielou's evenness (J′), however, were similar (Kruskal–Wallis, $\chi^2 = 0.022$, *P*-value = 0.8821) between the coral reef (J′ = 0.7515) and the seagrass bed (J′ = 0.6106). The values for both habitat types suggest that species proportions in the two communities were relatively equal with no dominance of any single species. Variations in trophic groups of fish assemblages followed a similar pattern as those of fish community composition (Table 3), i.e. assemblages of trophic groups changed significantly with lunar phases (N = neap tide, S = spring tide) and the tidal cycle (H = high tide, L = low tide) in the coral reef (CR) and with the diel (D = daytime, T = twilight) and tidal cycle (H = high tide, L = low tide) in the seagrass bed (SB).

Planktivorous (CRN = 27.6%, CRS = 21.1%, CRH = 21.2%, CRL = 32.2%) and omnivorous fishes (CRN = 23.1%, CRS = 25.2.%, CRH = 22.7%, CRL = 25.82%) were the most abundant, with the omnivores also being the most diverse (regarding number of species present) trophic groups in the coral reef at all sampling times (Fig. 3). Not surprisingly, in the seagrass bed herbivores were generally one of the most dominant trophic groups (SBD = 30.2%, SBT = 34.5%, SBH = 30.3%, SBL = 39.0%) together with either planktivorous fishes (SBH = 30.6%) or invertebrate feeders and piscivorous fishes, respectively (SBD = 22.7%, SBT/SBL = 28.1%, Fig. 3).

3.3. Fish density

Despite the differences in community composition, four of the five most abundant species were the same in both habitat types (CR = coral reef, SB = seagrass bed): the damselfishes *C. viridis* (CR = 13.2%, SB = 19.6%) and *C. atripectoralis* (CR = 5.1%, SB = 5.3%), the barracuda *S. flavicauda* (CR = 10.5%, SB = 12.4%), and the parrotfish *C. sordidus* (CR = 6.9%, SB = 4.1%). The most abundant species in the seagrass bed, however, was the rabbitfish *S. sutor* (26.32%) which was rarely observed in the coral reef (0.3%). To statistically compare mean fish densities between all samples, 17 candidate GLMMs (gamma distribution, inverse link) were tested (Table S3). Our results for the second-order Akaike information criterion (AICc = 416.04) and the Akaike weights ($w_m = 0.80$) show that the preferred probabilistic model is the one that considers a multiplicative effect for the habitat and daytime (with the factors H = habitat, D = daytime, and IA = interaction

Table 3
(A) Non-parametric multivariate analysis and (B) subsequent pairwise comparisons of aggregated 4th-root transformed fish assemblage data based on feeding categories (COR = corallivore, DET = detrivore, HER = herbivore, INV = invertebrate feeders, OMNI = omnivore, PIS/INV = fish and invertebrate feeders, PLA = planktivore, nd = no data) testing for differences between habitats (H) and lunar (M), diel (D), and tidal (T) cycles.

(A) PERMANOVA					(B) Pairwise comparisons		
Source	df	MS	Pseudo-*F*	*P*-value	Groups	*t*	*P*-value
H	1	42 306	22.118	**0.0002**			
Q(H)	10	2279.5	4.9277	**0.0002**			
M	1	0468.0	1.0117	0.4262			
D	1	2226.0	4.8121	**0.0004**			
T	1	1455.1	3.1456	**0.0178**			
H × M	1	1329.5	2.8740	**0.0194**	CRN vs. CRS	2.5352	**0.0002**
					SBN vs. SBS	0.4374	0.9040
H × D	1	1313.6	2.8396	**0.0224**	CRD vs. CRT	1.1065	0.3106
					SBD vs. SBT	2.0743	**0.0054**
H × T	1	1534.9	3.318	**0.0098**	CRH vs. CRL	1.9340	**0.0018**
					SBH vs. SBL	1.5940	**0.0434**
Residuals	99	462.6					
Total	116						

Results are based on a Bray–Curtis similarity matrix and *P*-values were obtained using 4999 permutations for each of the given permutable units. Fish were sampled using underwater visual census in square quadrats (Q, nested in habitat (H)) of two benthic habitat types (CR = coral reef, SB = seagrass bed) at the different time periods (N = neap tide, S = spring tide, D = day, T = twilight, H = high tide, and L = low tide). Bold values: $p < 0.05$.

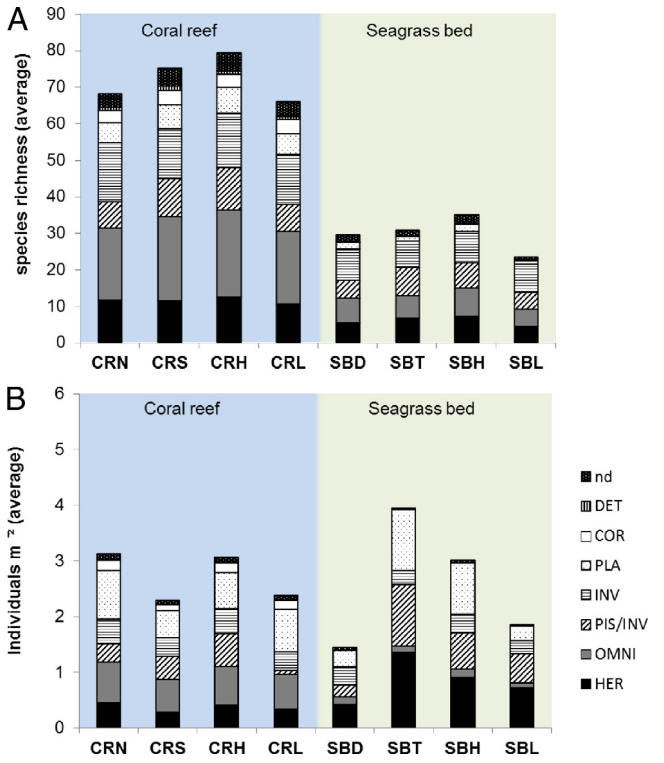


Fig. 3. (A) Average species richness and (B) mean densities (individuals m^{-2}) for the different trophic groups (HER = herbivorous, OMNI = omnivorous, PIS/INV = fish and invertebrate feeders, INV = invertebrate feeders, PLA = planktivorous, COR = corallivorous, DET = detrivorous fishes, nd = no data) in the fish assemblages at the different sampling periods (CR = coral reef, SB = seagrass bed, N = neap tide, S = spring tide, D = day, T = twilight, H = high tide, L = low tide).

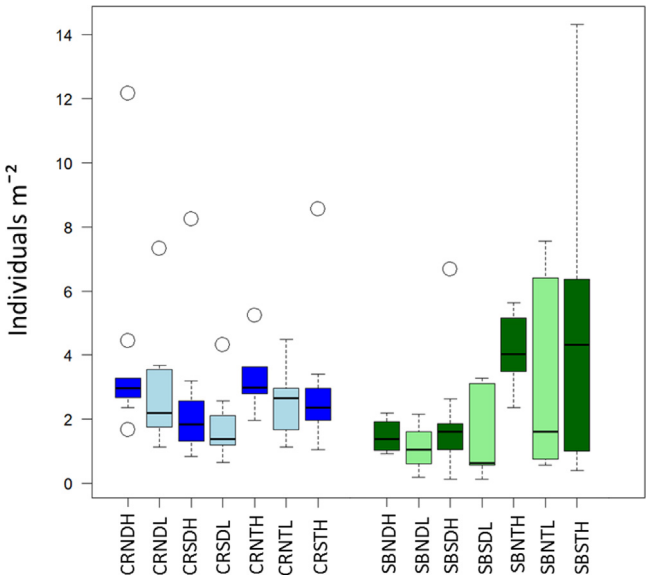


Fig. 4. Comparison of mean fish densities (individuals m^{-2}) between coral reef (CR, blue) and seagrass bed (SB, green) at the different sampling periods (N = neap tide, S = spring tide, D = day, T = twilight, H = high tide, and L = low tide). Note: due to time restrictions no samples could be taken at spring low tide during twilight hours in either habitat type (CRSTL/SBSTL). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

term H × D). This model (HDIA) was therefore selected for further data analysis.

The results of the Wald *t*-test for model term significance (Table 4) show significant differences in fish densities between habitats ($p = 0.04$), with slightly higher predicted values for the coral reef (predicted values without random effects are 2.32 and 1.30 for CR and SB, respectively). The effect of daytime (day vs. twilight) was not significant in coral reef samples ($p = 0.64$) but was highly significant in the seagrass bed ($p < 0.001$), with significantly higher values during twilight (see Fig. 4) (4.10 ± 3.36 ind. m^{-2}). This increase and the high variance of individual numbers were mainly caused by shoaling fishes like the rabbitfish *S. sutor*, the damselfish *C. viridis*, and the barracuda *S. flavicauda*.

4. Discussion

We found high variability in fish abundance and species composition between the two studied habitat types (coral reef and seagrass bed). In the coral reef changes in assemblages were associated with lunar, diel, and tidal phases, while in the seagrass bed only the tidal phases influenced species composition. However, fish densities and the trophic structure of seagrass bed assemblages were also distinctly influenced by the diel cycle. Mainly vagile fishes from the families Scaridae, Pomacentridae, Sphyraenidae, and Siganidae dominated the two shallow water fish assemblages indicating that these assemblages are in a dynamic state, therefore, suggesting migration between habitats. These fishes (with the exception of Pomacentridae) also constitute the

Table 4
Summary statistics of best-fit HDIA model (H = habitat, D = daytime, IA = interaction term H × D) with Wald *t*-tests of term significance.

Model terms*	Estimate	Standard error	*t*-value	*P*-value
Intercept (CR, day)	0.43158	0.10426	4.14	3.48E−05***
Habitat (SB)	0.33673	0.16409	2.052	0.04016*
Daytime (twilight)	−0.02289	0.0493	−0.464	0.64245
Habitat (SB) × daytime (twilight)	−0.27638	0.09136	−3.025	2.48E−03**

CR = coral reef, SB = seagrass bed.
* *P*-value significance level < 0.05.
** *P*-value significance level < 0.01.
*** *P*-value significance level < 0.001.

main target species for fisheries on Zanzibar with Siganidae having the highest number in catches of artisanal fisheries (J. Rehren, unpublished data from Chwaka Bay). Even though it is not possible to quantify individual movements based on observational UVC data, we interpret our UVC data as an indication of fish activity and related lunar, diel, and tidal patterns as fishes moving between habitats. For movement data of individual fishes further research based on hydro-acoustic telemetry or mark–recapture studies is required.

4.1. Lunar cycle

Regarding fish community composition the lunar cycle had no significant influence in the seagrass bed, but seems to be an important structuring force in the coral reef. Our results are in agreement with previous studies e.g. Letourneur (1996) or Galzin (1987) which suggests that about 30% of variance in coral reef fish abundances could be related to the lunar cycle. Moon phases are known to trigger reef fish behaviour like the spawning periodicity of Scaridae (e.g. *Chlorurus sordidus*) or Acanthuridae (e.g. *Ctenochaetus striatus*) (Claydon et al., 2014) which were among the species contributing most to the observed differences between neap and spring tide samples. Spawning of these species commonly takes place at well-defined sites (Claydon et al., 2014), and migration from/to spawning sites could be a possible reason for the differing abundances of these species during neap tides. Due to their predictability in time and space spawning migrations also have direct consequences for fish catchability (Bos and Gumanao, 2012) and hence for conservation and management strategies of exploited stocks (Robinson et al., 2011).

4.2. Diel cycle

The diel cycle (encompassing the time interval between sunrise and sunset due to nocturnal limitations) had no deterministic impact on species diversity or community composition of fish assemblages in the seagrass bed, but significantly affected fish assemblages in the coral reef and overall fish densities and the structure of trophic groups in the seagrass bed mainly due to a higher activity of shoaling fishes like *C. viridis*, *S. sutor*, and *S. flavicauda* during twilight periods. This increase in activity was also reported for seagrass beds in other regions (Sogard et al., 1989) and contrasts the observed 'quiet period' during dusk and dawn within coral reefs (McFarland et al., 1979). Strong diel patterns are well documented within habitats such as seagrass beds (Jackson et al., 2002, 2001) or for fish families like Haemulidae (Hitt et al., 2011; McFarland et al., 1979). This phenomenon can often be attributed to behavioural patterns in foraging like avoiding predators and/or following prey activity. During darkness, invertebrate abundance in seagrass beds is known to be higher than during the day (Guest et al., 2003) and higher than in coral reefs (Nagelkerken et al., 2000) due to in the water column emerging zooplankton, benthic crustaceans, and polychaetes (Hobson and Chess, 1978; Yahel et al., 2005). Thus, the increased activity of the planktivorous damselfish *C. viridis* during twilight periods can possibly be linked to vertical migrations of its main prey items (zooplankton) rising in the water column at dusk. We also found the herbivore rabbitfish *S. sutor* to be more abundant in the seagrass bed during twilight periods, which is in accordance with findings from Thompson and Mapstone (2002) showing that daily variation in abundance was highest for Lutjanidae, Serranidae and Siganidae. Furthermore, studies of the plasticity of diel activity patterns of a closely related species (*Siganus lineatus*) revealed that rabbitfishes are also feeding during crepuscular periods, possibly to reduce the pressure of predation or competition (Fox and Bellwood, 2011; Fox et al., 2009). The fish and invertebrate feeding barracuda *S. flavicauda* was observed in both habitats during the day, but during twilight periods abundances decreased in the coral reef while increasing in the seagrass bed possibly due to changing prey availability or movement between the two adjacent habitat types. Transient piscivorous fishes are known to be important contributors to the variability in small-fish abundances within seagrass beds by directly increasing mortality and/or modifying fish behaviour (Hindell et al., 2000). Thus, the observed habitat use patterns of *S. flavicauda* provides an example that Indo-Pacific coral reefs and seagrass beds are connected through fish migrations, but further research is required to determine the functional impact of the above mentioned species in structuring fish assemblages.

4.3. Tidal cycle

The tidal state is an important factor controlling fish assemblages in shallow water systems by making shallow areas accessible for larger species during high tide and thus altering fish assemblage structure and/or behavioural interactions (Gibson, 2003; Unsworth et al., 2007). During extreme low tides, water levels in the seagrass bed at Chumbe Island can reach values below 1.0 m, while in the coral reef the water depth always stays above 2 m. Hence, in the seagrass bed the ebbing tide resulted in a reduction in fish abundance and diversity compared to high tide samples (Fig. 3), most likely due to fishes migrating to deeper water areas to avoid stranding or the increasing risk of avian predation. Again, mobile species like *S. sutor, S. flavicauda, C. viridis*, and *C. sordidus* contributed most to the observed differences (Table 2(E)) and were more abundant during high compared to low tides. Our results are consistent with previous studies (Pogoreutz et al., 2012; Sogard et al., 1989; Unsworth et al., 2007) and support the hypothesis that fish utilization of seagrass habitats are related to both availability of prey (diel patterns) and water levels (tidal patterns). In particular, patterns for planktivorous fish species like *C. viridis*, whose feeding strategy is strongly related to water currents and which were at the same time less abundant in the coral reef, indicate foraging movements from adjacent habitat types to the seagrass bed. Furthermore, species from the family Siganidae and Scaridae are known to migrate between coral reef and seagrass bed (Unsworth et al., 2008). Thus, our study indicates that seagrass beds may temporarily appear less important to certain species, when sampled, e.g. only during low tides and the importance of these habitats may be assessed inaccurately (Jackson et al., 2001).

4.4. Diversity and habitat effects

Our results reveal two distinct fish communities in the two adjacent habitat types with higher species diversity in the coral reef. Similar habitat effects were also found in studies at comparable locations in the Indo-Pacific (Unsworth et al., 2007). Species richness and diversity (H') in the seagrass beds were similar to those reported for other seagrass meadows in Zanzibar (Lugendo et al., 2007) with a dominance of similar species and fish families like the ones found in seagrass beds in Mozambique (Gell and Whittington, 2002) or Indonesia (Pogoreutz et al., 2012). Further, the seagrass beds at Chumbe Island showed a common feature for inshore fish assemblages, where less than six species comprised about 70% of the total abundance, even though many more species were present (Quinn, 1980). The differences in diversity can have important functional consequences and several studies suggest that systems with high species richness and functional diversity should be relatively stable and insensitive to perturbations (McCann, 2000). Based on our findings the seagrass system may therefore be more susceptible to species loss and less resilient to disturbances than the coral reef. Also, the relatively high value for the Shannon index ($H' = 3.623$) in the coral reef indicates a system less susceptible to disturbance because abundance is not concentrated on one species and potential losses of single species may be better compensated (Naeem and Li, 1997).

4.5. Benthic seascape

Habitat characteristics like the complexity of the benthic substratum or the percentage of live coral cover are known to influence movement and community structure of coral reef fishes (Gullström et al., 2008; McClanahan and Arthur, 2001; Mwandya et al., 2010) and can be important in regulating the extent of movement associated with natural cycles (Bijoux et al., 2013). Some species, for instance, are reluctant to leave their preferred substratum and cross large gaps of habitats of low structural complexity such as sand (Chapman and Kramer, 2000). Consequently, the habitat composition and configuration can regulate fish movement and thus spatio-temporal dynamics in fish assemblages. Our findings indicate that the location of the sampling quadrats along the cross-shelf gradient had a distinct influence on fish assemblage structure in both habitat types. Unfortunately, replicates were not sufficient for statistical analysis as these sub-locations were not considered in the sampling design. Hence, we recommend considering the underlying benthic habitat structure in future studies to determine the importance of habitat complexity as a structuring force in tropical shallow water fish assemblages.

5. Conclusions

The present study on Chumbe Island illustrates that community composition, densities and trophic diversity of fish assemblages in tropical shallow water habitats may fluctuate over short timescales depending on different natural cycles. These changes were predictable in space and time and can have important implications for ecosystem functioning. To correctly evaluate how environmental change is affecting fish assemblages it therefore seems necessary to distinguish the different causes of variation in fish assemblages. Hence, for UVC to be an effective monitoring tool and to facilitate the design of much needed conservation measures for exploited fish stocks, the inclusion of natural cycles in the survey design is essential. If samples are not taken at relevant temporal scales, the role of certain species or habitats may be assessed inaccurately. In coral reefs and seagrass habitats at Chumbe Island tidal, diel, and lunar phases exert strong influences on the movement behaviour of mobile fishes, which can thus be important for the functional linkages between adjacent habitats.

Acknowledgements

We thank the staff of *Chumbe Island Coral Park* (CHICOP) for their logistic support and we are grateful to M. Klaus for field assistance. Many thanks also to C. Roder and E. Acevedo-Trejos for their statistical advice and valuable comments.

Appendix A. Supplementary data

Supplementary material related to this article can be found online at http://dx.doi.org/10.1016/j.rsma.2015.05.001.

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