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Highlights (for review)**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.

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1

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

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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.

Keywords: coral reef; seagrass bed; community structure; underwater visual census (UVC); species diversity; trophic groups;

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 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 km² 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. 1A). 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 characterised by a mixture of hard coral (26 %), rubble and sand (56 %), and rocky surface (18 %). Salinity (measured using the Practical Salinity Scale) varied between 37-40 in the coral reef and between 36-39 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 m² 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 overestimation 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. 1B). 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 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 (HxM, HxD, HxT) 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, detritivorous 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 were

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 in 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 %) were also relatively

abundant, whereas in the seagrass bed Siganidae (21.2 %) were the second most dominant fish family.

3.1 Community structure and composition

The nMDS (Fig. 2) and PERMANOVA analyses (Table 1A) 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 (HxM, HxD, HxT) (Table 1B) 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 2A), 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 2B-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 2E).

3.2 Diversity

Average values for the Shannon index varied significantly between the two habitat types (Kruskal-Wallis test, $\chi^2 = 46.842$, 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 group (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 term HxD). 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 ($4.10 \pm 3.36 \text{ ind. m}^{-2}$). 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 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 2E) 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 utilisation 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.

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References

- Anderson, D.R., Burham, K.P., Thompson, W.L., 2000. Null hypothesis testing: problems, prevalence, and an alternative. *J. Wildl. Manage.* 64, 912–923.
- Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecol.* 26, 32–46.
- Anderson, M.J., Millar, R.B., 2004. Spatial variation and effects of habitat on temperate reef fish assemblages in northeastern New Zealand. *J. Exp. Mar. Bio. Ecol.* 305, 191–221.
doi:10.1016/j.jembe.2003.12.011

- Anderson, M.J., ter Braak, C.J.F., 2003. PERMUTATION TESTS FOR MULTI-FACTORIAL ANALYSIS OF VARIANCE. *J. Stat. Comput. Simul.* 73, 85–113.
- Appeldoorn, R.S., Aguilar-Perera, A., Bouwmeester, B.L.K., Dennis, G.D., Hill, R.L., Merten, W., Recksiek, C.W., Williams, S.J., 2009. Movement of fishes (Grunts: Haemulidae) across the coral reef seascape: A review of scales, patterns and processes. *Caribb. J. Sci.* 45, 304–316.
- Bates, D.M., Maechler, M., Bolker, B., 2012. Linear mixed-effects models using S4 classes. R package version 0.999999-0.
- Berachi, I.G., 2003. Bioeconomic analysis of artisanal marine fisheries of Tanzania (Mainland). University of Tromsø, Norway.
- Berkström, C., Lindborg, R., Thyresson, M., Gullström, M., 2013. Assessing connectivity in a tropical embayment: Fish migrations and seascape ecology. *Biol. Conserv.* 166, 43–53. doi:10.1016/j.biocon.2013.06.013
- Bijoux, J.P., Dagorn, L., Gaertner, J.-C., Cowley, P.D., Robinson, J., 2013. The influence of natural cycles on coral reef fish movement: implications for underwater visual census (UVC) surveys. *Coral Reefs* 32, 1135–1140.
- Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H., White, J.S.S., 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol. Evol.* 24, 127–135. doi:10.1016/j.tree.2008.10.008
- Bos, A.R., Gumanao, G.S., 2012. The lunar cycle determines availability of coral-reef fishes at fish markets. *J. Fish Biol.* 81, 2074–2079. doi:10.1111/j.1095-8649.2012.03454.x
- Burnham, K.P., Anderson, D.R., 2002. Model selection and multimodel inference : a practical information-theoretic approach. Springer Science & Business Media, New York.
- Chapman, M., Kramer, D., 2000. Movements of fishes within and among fringing coral reefs in Barbados. *Environ. Biol. Fishes* 57, 11–24.
- Clarke, K., Warwick, R., 2001. Change in marine communities: an approach to statistical analysis and interpretation. PRIMER-E, Plymouth.
- Claydon, J.A.B., McCormick, M.I., Jones, G.P., 2014. Multispecies spawning sites for fishes on a low-latitude coral reef: spatial and temporal patterns. *J. Fish Biol.* 84, 1136–1163. doi:10.1111/jfb.12355
- Colin, P.L., Bell, L.J., 1991. Aspects of the spawning of labrid and scarid fishes (Pisces : Labroidei) at Enewetak Atoll, Marshall Islands with notes on other families. *Environ. Biol. Fishes* 31, 229–260.
- Costanza, R., D'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R. V., Paruelo, J., Raskin, R.G., Sutton, P., van den Belt, M., 1997. The value of the world's ecosystem services and natural capital. *Nature* 387, 253–260.

- De la Torre-Castro, M., Rönnbäck, P., 2004. Links between humans and seagrasses — an example from tropical East Africa. *Ocean Coast. Manag.* 47, 361–387. doi:10.1016/j.ocecoaman.2004.07.005
- Dorenbosch, M., Grol, M.G.G., Nagelkerken, I., van der Velde, G., 2006. Different surrounding landscapes may result in different fish assemblages in East African seagrass beds. *Hydrobiologia* 563, 45–60. doi:10.1007/s10750-005-1428-2
- English, S., Wilkinson, C., Baker, V., 1997. *Survey Manual for Tropical Marine Resources*, 2nd ed. Australian Institute of Marine Science, Townsville.
- Fox, R.J., Bellwood, D.R., 2011. Unconstrained by the clock? Plasticity of diel activity rhythm in a tropical reef fish, *Siganus lineatus*. *Funct. Ecol.* 25, 1096–1105. doi:10.1111/j.1365-2435.2011.01874.x
- Fox, R.J., Sunderland, T.L., Hoey, A.S., Bellwood, D.R., 2009. Estimating ecosystem function: contrasting roles of closely related herbivorous rabbitfishes (Siganidae) on coral reefs. *Mar. Ecol. Prog. Ser.* 385, 261–269. doi:10.3354/meps08059
- Froese, R., Pauly, D.E., 2012. FishBase [WWW Document]. World Wide Web Electron. Publ. version. URL www.fishbase.org (accessed 8.1.12).
- Galzin, R., 1987. Structure of fish communities of French Polynesian coral reefs. II . Temporal scales. *Mar. Ecol. Prog. Ser.* 41, 137–145.
- Gell, F., Whittington, M.W., 2002. Diversity of fishes in the Quirimba Archipelago, northern Mozambique. *Mar. Freshw. Res.* 53, 115–121.
- Gibson, R.N., 2003. Go with the flow: tidal migration in marine animals. *Hydrobiologia* 503, 153–161. doi:10.1023/B:HYDR.0000008488.33614.62
- Gilbert, M., Rasmussen, J.B., Kramer, D.L., 2005. Estimating the density and biomass of moray eels (Muraenidae) using a modified visual census method for hole-dwelling reef fauna. *Environ. Biol. Fishes* 73, 415–426. doi:10.1007/s10641-005-2228-2
- Guest, M.A., Connolly, R.M., Loneragan, N.R., 2003. Seine nets and beam trawls compared by day and night for sampling fish and crustaceans in shallow seagrass habitat. *Fish. Res.* 64, 185–196. doi:10.1016/S0165-7836(03)00109-7
- Gullström, M., Bodin, M., Nilsson, P.G., Öhman, M.C., 2008. Seagrass structural complexity and landscape configuration as determinants of tropical fish assemblage composition. *Mar. Ecol. Prog. Ser.* 363, 241–255. doi:10.3354/meps07427
- Helfman, G., 1986. Fish Behaviour by Day, Night and Twilight, in: Pitcher, T. (Ed.), *Behaviour of Teleost Fishes*. Croom-Helm, London, pp. 366–387.
- Hindell, J.S., Jenkins, G.P., Keough, M.J., 2000. Variability in abundances of fishes associated with seagrass habitats in relation to diets of predatory fishes. *Mar. Biol.* 136, 725–737.

- Hitt, S., Pittman, S., Nemeth, R., 2011. Diel movements of fishes linked to benthic seascape structure in a Caribbean coral reef ecosystem. *Mar. Ecol. Prog. Ser.* 427, 275–291. doi:10.3354/meps09093
- Hobson, E.S., 1973. Diel feeding migrations in tropical reef fishes. *Helgoländer Wissenschaftliche Meeresuntersuchungen* 24, 361–370. doi:10.1007/BF01609526
- Hobson, E.S., Chess, J.R., 1978. Trophic relationships among fishes and plankton in the lagoon at Enewetak Atoll, Marshall Islands. *Fish. Bull.* 76, 133–153.
- Jackson, E.L., Rees, S.E., Wilding, C., Attrill, M.J., 2015. Use of a seagrass residency index to apportion commercial fishery landing values and recreation fisheries expenditure to seagrass habitat service. *Conserv. Biol.* 00, 1–11. doi:10.1111/cobi.12436
- Jackson, E.L., Rowden, A.A., Attrill, M.J., Bossey, S.J., Jones, M.B., 2001. The Importance of Seagrass Beds as a Habitat for Fishery Species. *Oceanogr. Mar. Biol. an Annu. Rev.* 39, 269–303.
- Jackson, E.L., Rowden, A.A., Attrill, M.J., Bossy, S.F., Jones, M.B., 2002. Comparison of fish and mobile macroinvertebrates associated with seagrass and adjacent sand at St. Catherine Bay, Jersey (English Channel): Emphasis on commercial species. *Bull. Mar. Sci.* 71, 1333–1341.
- Johnson, J.B., Omland, K.S., 2004. Model selection in ecology and evolution. *TRENDS Ecol. Evol.* 19, 101–108. doi:10.1016/j.tree.2003.10.013
- Lange, G.-M., Jiddawi, N., 2009. Economic value of marine ecosystem services in Zanzibar: Implications for marine conservation and sustainable development. *Ocean Coast. Manag.* 52, 521–532. doi:10.1016/j.ocecoaman.2009.08.005
- Letourneur, Y., 1996. Dynamics of fish communities on Reunion fringing reefs, Indian Ocean. I. Patterns of spatial distribution. *J. Exp. Mar. Bio. Ecol.* 195, 1–30.
- Lugendo, B.R., Nagelkerken, I., Jiddawi, N., Mgaya, Y.D., van der Velde, G., 2007. Fish community composition of a tropical nonestuarine embayment in Zanzibar, Tanzania. *Fish. Sci.* 73, 1213–1223. doi:10.1111/j.1444-2906.2007.01458.x
- Magurran, A., 1988. *Ecological Diversity and its Measurements*. Princeton University Press, New Jersey.
- McCann, K.S., 2000. The diversity-stability debate. *Nature* 405, 228–233. doi:10.1038/35012234
- McClanahan, T.R., Arthur, R., 2001. The effect of marine reserves and habitat on populations of East African coral reef fishes. *Ecol. Appl.* 11, 559–569.
- McFarland, W.N., Ogden, J.C., Lythgoe, J.N., 1979. The influence on light on the twilight migrations of grunts. *Environ. Biol. Fishes* 4, 9–22.
- Millar, R.B., Anderson, M.J., 2004. Remedies for pseudoreplication. *Fish. Res.* 70, 397–407. doi:10.1016/j.fishres.2004.08.016

- Mkenda, A.F., Folmer, H., 2001. The Maximum Sustainable Yield of Artisanal Fishery in Zanzibar: A Cointegration Approach. *Environ. Resour. Econ.* 19, 311–328.
- Muhando, C.A., 2008. Approaches to Coral Reef Monitoring in Tanzania, in: *CORDIO Status Report*. pp. 129–138.
- Mumby, P.J., 2006. Connectivity of reef fish between mangroves and coral reefs: Algorithms for the design of marine reserves at seascape scales. *Biol. Conserv.* 128, 215–222.
doi:10.1016/j.biocon.2005.09.042
- Murphy, H.M., Jenkins, G.P., 2010. Observational methods used in marine spatial monitoring of fishes and associated habitats: a review. *Mar. Freshw. Res.* 61, 236–252.
- Mwandya, A.W., Mgaya, Y.D., Öhman, M.C., Bryceson, I., Gullström, M., 2010. Distribution patterns of striped mullet *Mugil cephalus* in mangrove creeks, Zanzibar, Tanzania. *African J. Mar. Sci.* 32, 85–93. doi:10.2989/18142321003714575
- Naeem, S., Li, S., 1997. Biodiversity enhances ecosystem reliability. *Nature* 390, 507–509.
- Nagelkerken, I., Dorenbosch, M., Verberk, W.C.E.P.C.E.P., Cocheret de la Morinière, E., van der Velde, G., Eocheret de la Morinière, E., 2000. Day-night shifts of fishes between shallow-water biotopes of a Caribbean bay, with emphasis on the nocturnal feeding of Haemulidae and Lutjanidae. *Mar. Ecol. Prog. Ser.* 194, 55–64.
- Nagelkerken, I., van der Velde, G., 2002. Do non-estuarine mangroves harbour higher densities of juvenile fish than adjacent shallow-water and coral reef habitats in Curaçao (Netherlands Antilles)? *Mar. Ecol. Prog. Ser.* 245, 191–204.
- Nash, K.L., Graham, N.A.J., Bellwood, D.R., 2013. Fish foraging patterns, vulnerability to fishing, and implications for the management of ecosystem function across scales. *Ecol. Appl.* 23, 1632–1644.
- Ogden, J.C., Quinn, T.P., 1994. *Migration In Coral Reef Fishes: Ecological Significance and Orientation Mechanisms, Mechanisms of Migration in Fishes*. Plenum Press, New York.
- Ogden, J.C., Zieman, J.C., 1977. Ecological aspects of coral reef-seagrass bed contacts in the Caribbean, in: Taylor, D.L. (Ed.), *Proceedings of Third International Coral Reef Symposium Vol. 1: Biology*. Rosenstiel School of Marine and Atmospheric Science, Miami, pp. 377–382.
- Olds, A.D., Connolly, R.M., Pitt, K.A., Maxwell, P.S., 2012. Habitat connectivity improves reserve performance. *Conserv. Lett.* 5, 56–63. doi:10.1111/j.1755-263X.2011.00204.x
- Pogoreutz, C., Kneer, D., Litaay, M., Asmus, H., Ahnelt, H., 2012. The influence of canopy structure and tidal level on fish assemblages in tropical Southeast Asian seagrass meadows. *Estuar. Coast. Shelf Sci.* 107, 58–68. doi:10.1016/j.ecss.2012.04.022
- Polunin, N.V.C., Roberts, C.M., 1993. Greater biomass and value of target coral-reef fishes in two small Caribbean marine reserves*. *Mar. Ecol. Prog. Ser.* 100, 167–176.
- Quinn, N.J., 1980. Analysis of temporal changes in fish assemblages in Serpentine Creek, Queensland. *Environ. Biol. Fishes* 5, 117–133.

- Robblee, M.B., Zieman, J.C., 1984. Diel Variation in the Fish Fauna of a Tropical Seagrass Feeding Ground. *Bull. Mar. Sci.* 34, 335–345.
- Robinson, J., Samoilys, M.A., Grandcourt, E., Julie, D., Cedras, M., Gerry, C., 2011. The importance of targeted spawning aggregation fishing to the management of Seychelles' trap fishery. *Fish. Res.* 112, 96–103. doi:10.1016/j.fishres.2011.08.015
- Sogard, S.M., Powell, G.V.N., Holmquist, J.G., 1989. Utilization by fishes of shallow, seagrass-covered banks in Florida Bay: 2 . Diel and tidal patterns. *Environ. Biol. Fishes* 24, 81–92.
- Spalding, M.D., Ravilious, C., Green, E.P., 2001. *World Atlas of Coral Reefs*. University of California Press, Berkeley.
- Taylor, M., 1984. Lunar synchronization of fish reproduction. *Trans. Am. Fish. Soc.* 113, 484–493.
- Thompson, A.A., Mapstone, B.D., 2002. Intra- versus inter-annual variation in counts of reef fishes and interpretations of long-term monitoring studies. *Mar. Ecol. Prog. Ser.* 232, 247–257.
- Tilman, D., 2001. Functional diversity, in: Levin, S.A. (Ed.), *Encyclopedia of Biodiversity*. Academic Press, San Diego, pp. 109–120.
- Unsworth, R.K.F., Bell, J.J., Smith, D.J., 2007. Tidal fish connectivity of reef and sea grass habitats in the Indo-Pacific. *J. Mar. Biol. Assoc. UK* 87, 1287–1296. doi:10.1017/S002531540705638X
- Unsworth, R.K.F., Cullen, L.C., 2010. Recognising the necessity for Indo-Pacific seagrass conservation. *Conserv. Lett.* 00, 1–11. doi:10.1111/j.1755-263X.2010.00101.x
- Unsworth, R.K.F., De León, P.S., Garrard, S.L., Jompa, J., Smith, D.J., Bell, J.J., 2008. High connectivity of Indo-Pacific seagrass fish assemblages with mangrove and coral reef habitats. *Mar. Ecol. Prog. Ser.* 353, 213–224. doi:10.3354/meps07199
- Welsh, J.Q., Bellwood, D.R., 2014. Herbivorous fishes, ecosystem function and mobile links on coral reefs. *Coral Reefs* 33, 303–311. doi:10.1007/s00338-014-1124-7
- Yahel, R., Yahel, G., Berman, T., Jaffe, J.S., Genin, A., 2005. Diel pattern with abrupt crepuscular changes of zooplankton over a coral reef. *Limnol. Oceanogr.* 50, 930–944.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. *Mixed Effects Models and Extensions in Ecology with R*. Springer Science & Business Media, New York.

Figure legends

Figure 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 m²) 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.

Figure 2 Two-dimensional MDS plot for 4th-root transformed count data in the coral reef (CR, blue dots) and seagrass bed (SB, green triangles).

Figure 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 = detritivorous 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).

Figure 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).

Tables

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- <i>F</i>	<i>P</i> -value	Groups	<i>t</i>	<i>P</i> -value
H	1	68224	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			
HxM	1	2297.4	1.3963	0.1262	CRN vs. CRS	1.6717	0.0002
					SBN vs. SBS	0.5838	0.9516
HxD	1	2092.0	1.2714	0.2136	CRD vs. CRT	1.4091	0.009
					SBD vs. SBT	1.3322	0.0644
HxT	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 & SB		B) CRN & CRS		C) CRD & CRT		D) CRH & CRL		E) SBH & SBL	
Fish species	%	Fish species	%	Fish species	%	Fish species	%	Fish species	%
<i>Siganus sutor</i>	4.7	<i>Chromis viridis</i>	3.3	<i>Chromis viridis</i>	3.3	<i>Chromis viridis</i>	3.5	<i>Siganus sutor</i>	7.0
<i>Chromis viridis</i>	3.5	<i>Chlorurus sordidus</i>	2.4	<i>Chlorurus sordidus</i>	2.5	<i>Chlorurus sordidus</i>	2.3	<i>Sphyræna flavicauda</i>	6.3
<i>Plectroglyphidodon lacrymatus</i>	3.3	<i>Ctenochaetus striatus</i>	2.4	<i>Ctenochaetus striatus</i>	2.4	<i>Ctenochaetus striatus</i>	2.4	<i>Chromis viridis</i>	5.5
<i>Sphyræna flavicauda</i>	2.9	<i>Chaetodon trifascialis</i>	2.3	<i>Chromis atripectoralis</i>	2.3	<i>Plectroglyphidodon lacrymatus</i>	2.3	<i>Chlorurus sordidus</i>	5.3
<i>Chaetodon trifascialis</i>	2.8	<i>Meiacanthus mossambicus</i>	2.2	<i>Meiacanthus mossambicus</i>	2.2	<i>Chromis atripectoralis</i>	2.4	<i>Stethojulis bandanensis</i>	4.6
<i>Chlorurus sordidus</i>	2.7	<i>Centropyge multispinis</i>	2.2	<i>Chromis weberi</i>	2.2	<i>Meiacanthus mossambicus</i>	2.2	<i>Cheilio inermis</i>	4.3
<i>Gomphosus caeruleus</i>	2.6	<i>Chromis atripectoralis</i>	2.2	<i>Parupeneus macronemus</i>	2.1	<i>Chaetodon trifascialis</i>	2.1	<i>Thalassoma hebraicum</i>	4.1
<i>Canthigaster valentini</i>	2.5	<i>Plectroglyphidodon lacrymatus</i>	2.2	<i>Chaetodon trifascialis</i>	2.1	<i>Parupeneus macronemus</i>	2.1	<i>Leptoscarus vaigiensis</i>	4.0
<i>Ctenochaetus striatus</i>	2.4	<i>Ctenochaetus binotatus</i>	2.1	<i>Plectroglyphidodon dickii</i>	2.1	<i>Plectroglyphidodon dickii</i>	2.1	<i>Pomacentrus trilineatus</i>	3.6
<i>Thalassoma hebraicum</i>	2.3	<i>Plectroglyphidodon dickii</i>	2.1	<i>Acanthurus leucosternon</i>	2.1	<i>Centropyge multispinis</i>	2.1	<i>Canthigaster valentini</i>	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.

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 = detritivore, 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- <i>F</i>	<i>P</i> -value	Groups	<i>t</i>	<i>P</i> -value
H	1	42306	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			
HxM	1	1329.5	2.8740	0.0194	CRN vs. CRS	2.5352	0.0002
					SBN vs. SBS	0.4374	0.9040
HxD	1	1313.6	2.8396	0.0224	CRD vs. CRT	1.1065	0.3106
					SBD vs. SBT	2.0743	0.0054
HxT	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: $p < 0.05$.

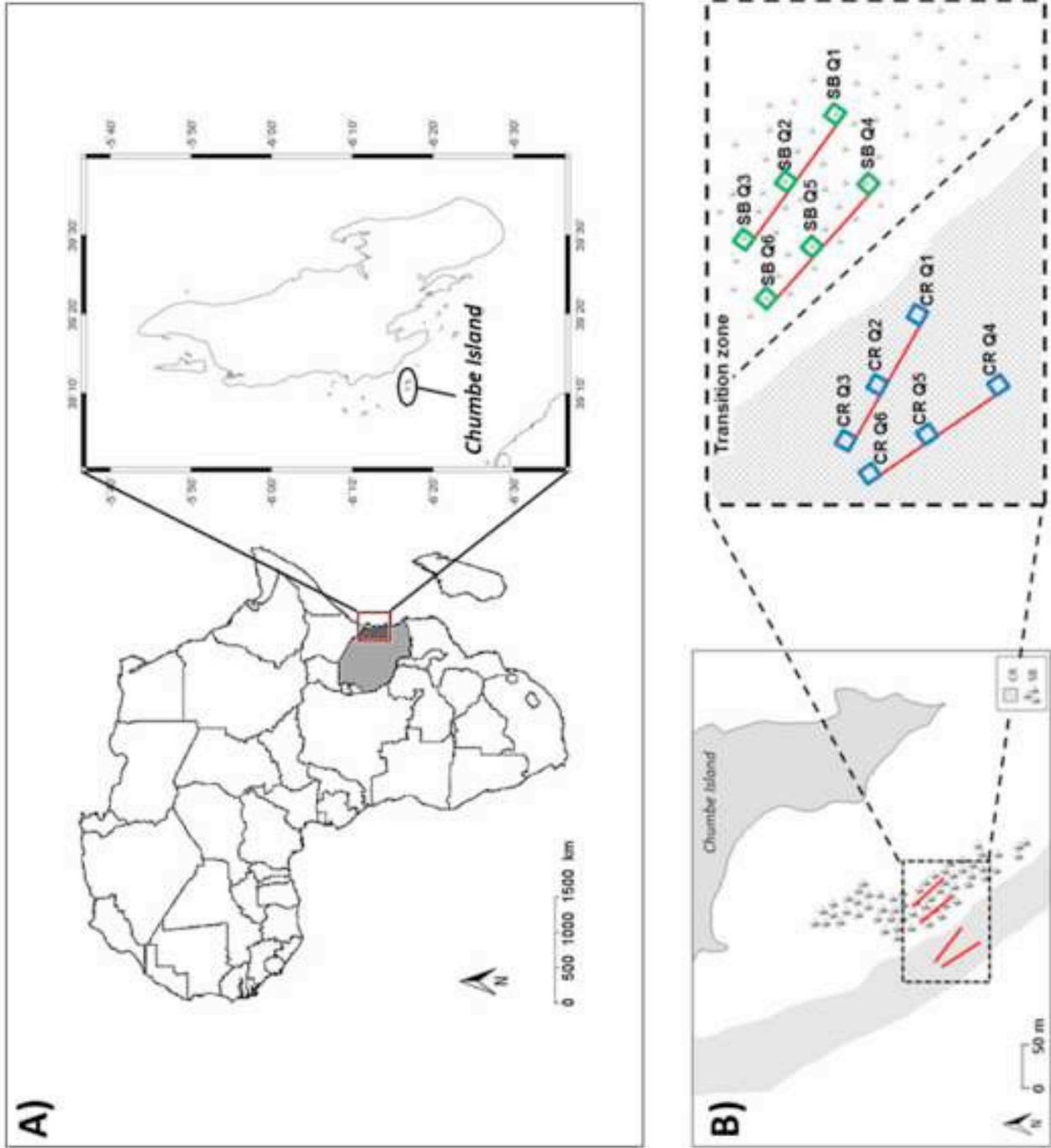
Table 4 Table 4. Summary statistics of best-fit HDIA model (H = habitat, D = daytime, IA =interaction term HxD) with Wald t-tests of term significance.

Model terms*	Estimate	Standard Error	t-value	<i>P</i> -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) x daytime (twilight)	-0.27638	0.09136	-3.025	2.48E-03**

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

Figure 1 Overview study site
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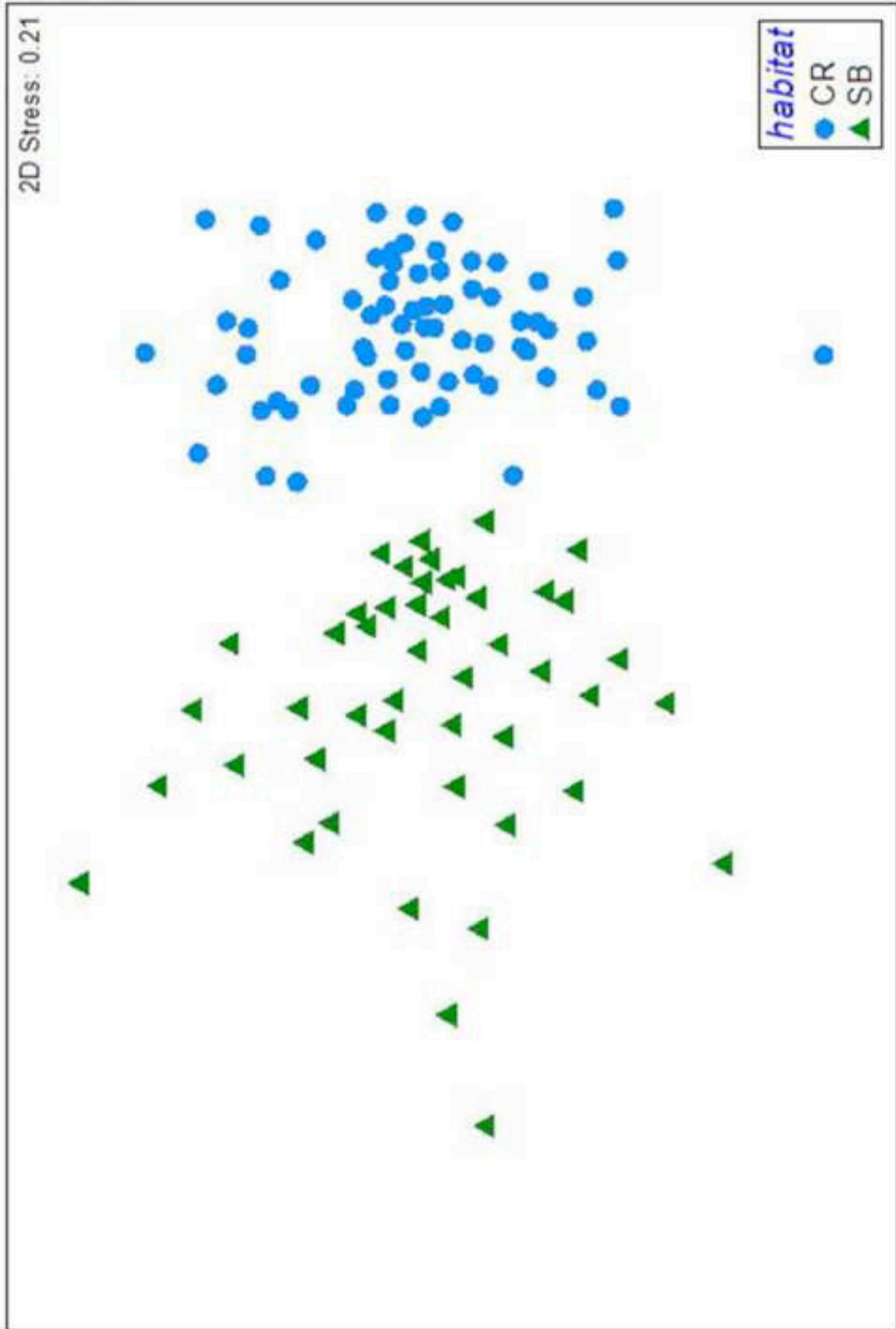
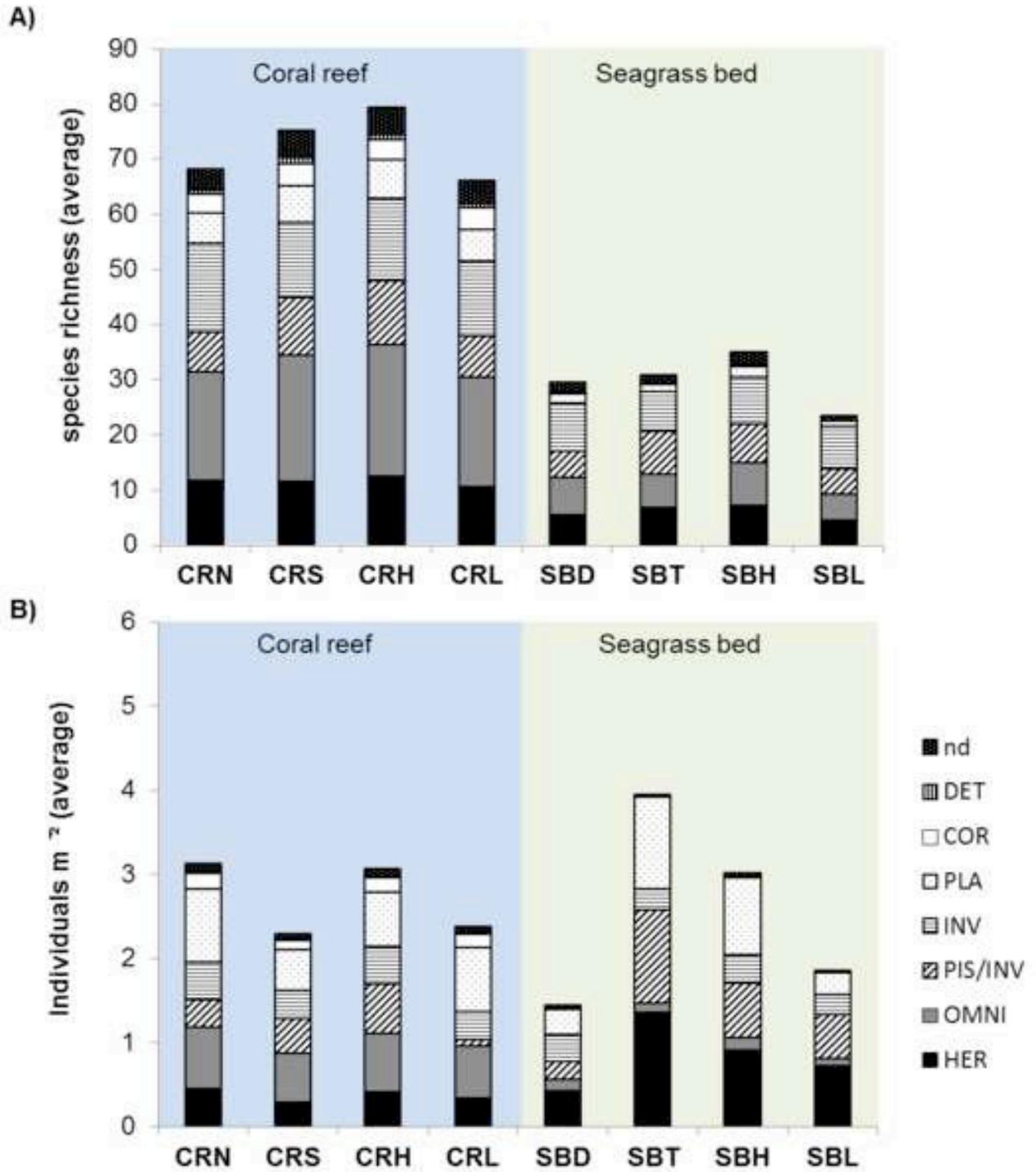


Figure 2 MDS plot
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Figure 3 Bar charts species richness
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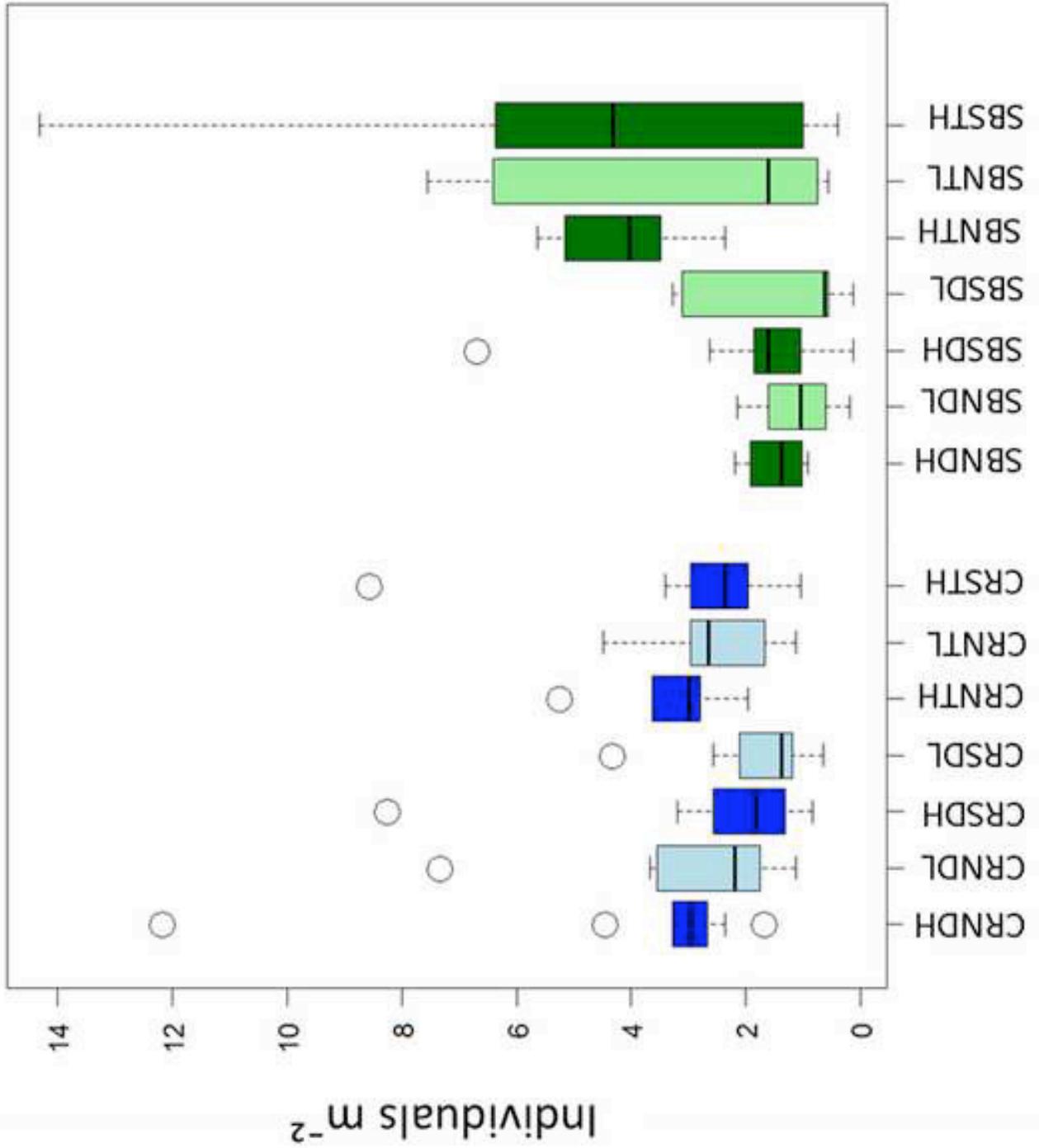


Figure 4 Fish densities box plot
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