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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 xxx

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 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. 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 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 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

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