Biological Connectivity and Nursery Function of Shallow-Water Habitats in Chwaka Bay

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INTRODUCTION

Chwaka Bay encompasses a range of shallow-water habitats such as coral reefs, seagrass and algal beds, mangrove forests, and sand/mudflats that harbour diverse assemblages of fauna and offer a wide variety of ecosystem services. These habitats are not isolated but connected with each other through a number of biological, geochemical and physical mechanisms that operate at multiple spatial and temporal scales. An insight into the degree of connectivity among shallow-water habitats is essential, especially in attempting sustainable use and proper resource management. To understand linkages between shallow-water systems and hence to be able to prioritize areas for conservation (e.g. selection of marine protected areas), one of the most important processes to identify and evaluate is the nursery function value of an area (Nagelkerken 2009a). Beck et al. (2001) defined the nursery concept as: “a habitat is a nursery for juveniles of a particular species if its contribution per unit area to the production of individuals that recruit to adult populations is greater, on average, than production from other habitats in which juveniles occur”, and in addition they argued that “the ecological processes operating in nursery habitats, when compared to other habitats, must support greater contributions to adult recruitment from any combination of four factors: (1) density, (2) growth, (3) survival of juveniles and (4) movement to adult habitats”. An additional definition to the nursery concept was provided by Dahlgren et al. (2006), who argued that it is highly important to assess the overall contribution of a nursery habitat to the adult population, and not only use the contribution per-unit-area that may
exclude habitats with a small per-unit-area contribution to adult populations. This makes sense for marine resource managers, since there is a need to identify the most important habitats for supporting adult populations (Dahlgren et al. 2006).

During the last two decades, various studies have been conducted at Unguja Island and within Chwaka Bay. These studies provide data that can be aggregated to determine the function of shallow-water habitat types with respect to habitat connectivity and nursery function. Almost all studies on this topic that have been conducted in Chwaka Bay have focused on migration of organisms, although Mohammed (1998) partly investigated nutrient transport from mangroves to adjacent seagrass and unvegetated habitats (see also chap. 9). In this chapter, we therefore focus on biological connectivity and nursery function, and with respect to Chwaka Bay our specific objectives are to (1) describe various types of migration and the seascape mosaic of the Bay, (2) identify cross-habitat linkages at multiple scales and the nursery role of different Bay habitats, and (3) highlight scientific gaps and future research. For a comprehensive review on the subject of connectivity among tropical coastal ecosystems see Nagelkerken (2009b).

MIGRATION AND MOVEMENT OF ORGANISMS IN TROPICAL SHALLOW-WATER SEASCAPES

Daily Migrations

The tidal and/or diel cycle can affect the availability of shallow-water habitats for feeding or sheltering species. Large areas of Chwaka Bay are intertidal and devoid of water during low tide. Consequently, these habitats are used by fish species only during high tide. However, in some areas, inundated creek systems may provide habitat for fish during low tide (Lugendo et al. 2007a; Mwandya et al. 2009). Regular tidal migrations by fish connect the intertidal habitats with adjacent deeper habitats where species retreat during low tide (Dorenbosch et al. 2004). Furthermore, a number of species have a nocturnal feeding strategy, characterized by species that are inactive and seek cover in sheltered habitats during day-time hours, while during the night they distribute over their feeding grounds. Conversely, diurnal species show the opposite behaviour. Such diel habitat shifts by nocturnal and diurnal species are often characterized by specific twilight-triggered migrations between feeding and sheltering habitats. Both tidal and diel migrations occur on a regular daily basis.

Seasonal Migrations

Various species are known to undertake seasonal migrations associated with spawning events (Robertson 1992; Sadovy 1996). Individuals from a large area aggregate together at a single location for simultaneous spawning, which often result
in specific locations or habitats being used during successive years (Claydon 2004). Spawning migrations are often directed towards the open ocean and subsequently multiple habitats such as mangroves, seagrass and algal beds, mud/sand flats and coral reefs are connected through fish spawning migrations (Johannes 1978). A number of fish species that exist in seagrass and mangrove habitats of Chwaka Bay, e.g. *Lutjanus argentimaculatus* and *Siganus canaliculatus*, are known to cross habitats when migrating to outer reef slopes in Palau, Micronesia (Johannes 1978; Pittman and McAlpine 2003). It seems likely that such spawning migrations might occur in Chwaka Bay, although no such observations have been made.

Seasonal events, such as heavy rainfall during wet seasons, may result in reduced salinity in coastal areas affecting patterns of fish abundance and distribution in nearshore habitats like mangrove creeks (Lugendo et al. 2007b). Likewise, seasonal events may also result in periodic abundance of food sources (for example, increased productivity due to mixing and turbulence generated by trade winds and water currents or temperature increases), resulting in aggregations of feeding species. Such seasonal effects are often accompanied by specific migrations of species, in which they temporarily use a specific habitat type during a short period of the year. Chwaka Bay is typically affected by heavy rainfall during the rainy season in April–May and various studies have found changes in mangrove and seagrass fish assemblages during this season (Lugendo et al. 2007b; Mwandya et al. 2010a; b).

**Ontogenetic Migrations**

Many species use different habitats during juvenile and adult life stages. The juvenile and adult habitats are connected by means of ontogenetic migrations where larvae first settle in their juvenile habitat and subadults join the adult population in an adjacent habitat when nearing maturity. This phenomenon is encompassed in the nursery hypothesis (Fig. 1). In marine tropical shallow-water seascapes (like Chwaka Bay), the nursery hypothesis requires that species strongly associated with the coral reef during their adult life phase predominantly use shallow-water habitats located away from the coral reef such as seagrass beds and mangroves during their juvenile life phase. After a pelagic larval phase, these species settle in seagrass beds and mangroves where they spend their entire juvenile life phase (Fig. 1). Unlike coral reefs, seagrass beds and mangroves are attractive juvenile habitats because of high food availability, high structural complexity and reduced underwater visibility (Blaber and Blaber 1980; Shulman 1985; Laegdsgaard and Johnson 2001; Cocheret de la Morinière et al. 2004; Verweij et al. 2006; Gullström et al. 2008; Kimirei et al. 2011). These habitat characteristics result in high growth rates and reduced predation and hence low mortality rates, making the non-reef habitats suitable nurseries for juvenile coral reef fishes (Dahlgren and Eggleston 2000). When approaching maturity, individuals become too large to benefit from the advantages (e.g. structural protection) of the nursery habitats (i.e. habitats characterized by high densities of juveniles), and they migrate to their adult habitat (the coral reef) – referred to as an ontogenetic migration (Fig. 1).
Although the nursery hypothesis has not been directly proven by following tagged individuals during ontogenetic migration, various studies in the Caribbean and the Indo-Pacific region have shown that for various coral reef fish species, seagrass beds and mangroves harboured the highest densities of small-sized fishes (i.e. juveniles), while in contrast the coral reefs harboured the large-sized fishes, i.e. adults (see reviews by for example Parrish 1989; Robertson and Blaber 1992; Beck et al. 2001). Likewise, a large number of juvenile coral reef fish have been recorded in mangroves and seagrass beds of Chwaka Bay (Dorenbosch 2005a; b; 2006a; Lugendo et al. 2006; 2007a; b; c; Gullström et al. 2008), and it is obvious that the embayment harbours extensive areas of potential nursery grounds (mangroves and seagrass beds) for many of the coral reef fish species found around the entrance of the Bay. Based on studies from the Caribbean and the Indo-Pacific region (and some evidence from East Africa), it is now generally assumed that seagrass beds and mangroves are important juvenile habitats for coral reef fishes. The nursery hypothesis and the underlying ontogenetic migrations are therefore important phenomena when considering conservation of these shallow-water ecosystems. The use of one habitat type (e.g. juvenile or adult habitat) may have wide-reaching effects that extend outside that particular single habitat; therefore, for conservation planning well-connected habitats should be treated as a single entity.
SEASCAPE MOSAIC OF CHWAKA BAY

Chwaka Bay comprises a complex mosaic of patches of different shallow-water habitats. Similar to many other sheltered tropical coastal environments worldwide, Chwaka Bay is arranged as an interconnected mangrove-seagrass-coral reef continuum, commonly referred to as the tropical seascape (Ogden 1988) and constituting one of the richest repositories of marine biodiversity. This highly diverse coastal seascape provides numerous natural resources and ecosystem services, including functioning as an ecological basis for fisheries production, which has significant implications for sustainable livelihood and food security (Ngoile and Shunula 1992; Moberg and Rönnbäck 2003; de la Torre-Castro 2006).

In general, biogenic deposits and erosion products derived from fossil limestone terraces characterize the sea bottom of Chwaka Bay (Tobisson et al. 1998; Muzuka et al. 2005; see also chap. 2 and 8). An extensive network of channels with north-south directed tidal water currents strongly influences movement patterns of organisms, and consequently the strength of energy flow and habitat connectivity across the embayment. The seascape surrounding this complex channel system is primarily characterized by a mixture of shallow intertidal and subtidal seagrass meadows and unvegetated sand and mud flats. Deeper seagrass beds are found off the coast of Marumbi as well as in the vicinity of the coral reef area at the Bay entrance. The large and widespread dominance of seagrass habitat, and in particular the remarkable diversity of seagrass species in such a small area as Chwaka Bay, is rare (see chap. 5). This is an important reason why this embayment shows such high density and diversity of mobile and migrating seagrass-associated species, including fish (e.g. Dorenbosch, 2005a; b; Gullström et al. 2008) and sea urchins (Asplund et al. unpublished data). Seagrass meadows not only comprise seagrass plants but also intermingling seaweed vegetation, most commonly the calcareous algae Halimeda spp. (Muzuka et al. 2005; Gullström et al. 2006; see chap. 8). In addition, the intertidal areas in the south (bordering the mangroves) are widespread and include mixed habitats of seagrass and macroalgae (e.g. of the genera Sargassum and Turbinaria) (Gullström et al. 2006).

Extensive mangroves and associated shallow creek systems fringe the southern shoreline of the embayment (see chap. 4). While the prominent mangrove forest itself creates a low-energy intertidal area functioning as important juvenile habitat for fish and various crustaceans, the associated creeks provide the main water exchange route between the forest and other Bay habitats, hence facilitating migration of fishes (Mwandya et al. 2009; 2010b). Within mangrove forests, the high structural complexity provided by the forest's prop roots and pneumatophores offers rich food supply and high sheltering capacity for juvenile fish species (Laegdsgaard and Johnson 2001). Some fish species exclusively use mangrove creeks during low-water (Lugendo et al. 2007a; Mwandya et al. 2009).

The mouth of the Bay comprises heterogeneous coral reefs. Patch and fringing reefs, fragmented reef boulders and limestone notches are scattered at the entrance,
protecting the Bay from the open ocean. The reef system also acts as a temporary migration destination for various fish and invertebrate species seeking refuge during low tides when other embayment habitats like seagrass beds and mangroves are exposed (see chap. 6).

CONNECTIVITY AT DIFFERENT SCALES IN CHWAKA BAY

The degree of connectivity is fundamentally linked to spatial and temporal scales. With respect to scale, migration patterns of fish and decapods can be distinguished by the range of consequences for the functioning of the shallow-water seascape. A number of community- and population-based studies have focused on migrating animals in Chwaka Bay, predominantly examining the fish fauna. Most of these studies have typically described and compared fish assemblage patterns in the different Bay habitats, with several attempting to address the strength of habitat connectivity and/or the nursery function value at different scales.

Diel and tidal fish migrations between interlinked shallow-water habitats usually extend short distances, varying between meters and kilometres (Dorenbosch et al. 2004). Such short-distance migrations between adjacent habitats are usually performed for the purpose of feeding, shelter or reducing risk of predation, and avoidance of competition (Krumme 2009). This may explain regular changes in a number of community features, including biomass, diversity, as well as flux of energy between adjacent habitats (Sheaves 2009). At a larger scale, fish can undertake migration from a few to hundreds of kilometres. This can also be achieved through larval transport whereby pelagic larvae are transported far away from their natal habitats by ocean currents, over large geographical distances (Roberts 1997). During later life stages, after the larval phase, inter-habitat migrations regularly occur as seasonal and/or ontogenetic migrations (Kimirei et al. 2011). In Chwaka Bay, various types of cross-habitat migrations operating at different scales have been studied and are described below.

REGULAR CROSS-HABITAT MIGRATIONS

Tidal Migrations

Tagging as well as acoustic tracking studies have been used to follow the movements of juvenile fishes in real time. Data from the only tagging study in Chwaka Bay conducted by Dorenbosch et al. (2004) indicate that a large part of juvenile populations of *Lutjanus fulviflamma* and *L. ehrenbergii* may move from a subtidal channel to shallow tidal notches on the fossil reef terrace in the western side of the Bay as a response to tidal changes, most likely for sheltering purposes. Although this type of environment stretches from the intertidal to the subtidal areas of the Bay, the tagging study showed that juvenile fishes move over relatively small areas.
Furthermore, individual fishes showed a high degree of site fidelity, demonstrating homing in both the channels and the small tidal creeks (Dorenbosch et al. 2004).

**Foraging Migrations**

On a daily basis, some fish species regularly migrate from their main shelter habitat to forage in an adjacent habitat (Harborne et al. 2006; Verweij et al. 2006). In Chwaka Bay, two studies have focused on foraging migration (Lugendo et al. 2006; 2007c), examining utilization of shallow-water habitats as important feeding grounds for various fish species of commercial importance. Stable isotope results revealed that all Bay habitats were important feeding grounds for several fish species, e.g. *Gerres filamentosus*, *Lethrinus lentjan*, *Lutjanus fulviflamma* and *Siganus sutor*. These species had δ^{13}C values which were in-between those of food items from two neighbouring habitats, suggesting that foraging migrations take place between different Bay habitats. In Chwaka Bay, foraging migrations may often coincide with tidal migrations, i.e. intertidal flats can only be used for foraging during high tides.

**LIFE-CYCLE AND SEASONAL TRIGGERED MIGRATIONS**

**Seasonal Migrations**

During the period of heavy rains in this part of the western Indian Ocean, in April and May, significant variations in fish community variables including density, biomass and species richness have been observed in mangrove and mud/sand flat habitats of Chwaka Bay (Lugendo et al. 2007b; Mwandya 2010b). Many species disappeared from these habitats during this season. Furthermore, those species that persisted showed a remarkable decrease in density (Lugendo et al. 2007b). The changes in fish community composition were explained by alterations in water temperature and salinity due to freshwater supply from the heavy rains. In contrast to the mangrove and mud/sand flat habitats, fish assemblages in seagrass beds were hardly affected and therefore remained more or less steady (Lugendo et al. 2007b).

**Ontogenetic Migrations from Nursery Habitats**

The most studied subject with respect to fish migration in Chwaka Bay is on their distribution within different habitats, in turn related to the concept of ontogeny and nursery function. A general finding from these studies is that shallow-water habitats like mangrove creeks, seagrass beds and mudflats of Chwaka Bay are dominated by juvenile fishes of both ecological and commercial importance (e.g. Dorenbosch et al. 2005a; b; Lugendo et al. 2005; 2007a; Gullström et al. 2008), with several species living on coral reefs as adults (Dorenbosch et al. 2005a; b).
This is not a very surprising phenomenon since mangroves and seagrass beds have been reported to commonly support high densities of juvenile fish worldwide (Parrish 1989; Robertson and Blaber 1992; Nagelkerken 2009a), and are well known to function as nursery grounds for reef-fish populations (Adams et al. 2006). However, factors such as seascape configuration (Pittman et al. 2007), habitat patch composition (Grober-Dunsmore et al. 2007) and species- and life stage-specific preferences for food and shelter (Shulman 1985), may likely influence fish-habitat interactions in an exclusive way across the embayment.

A seine net study by Lugendo et al. (2005; 2007a) examining the fish community composition in different shallow-water habitats of Chwaka Bay showed clear links to the nursery function and subsequently to ontogenetic migration. Within the seagrass habitat, the most diverse fish assemblages ($H' = 3.4$) were found in beds near the mangrove forest, while seagrass beds further out in the Bay harboured the least diverse assemblages (Lugendo et al. 2007a). The mudflat area showed the lowest species diversity, which was attributed to the numerical dominance of one species, viz. *Gerres oyena*. In terms of density, mangrove creeks had a significantly higher mean density compared to other habitats. Overall, Lugendo et al. (2005) found that 76% of all fishes caught in their study were small juveniles and another 16% large juveniles or subadults. Many species were of commercial interest (e.g. *Lutjanus fulviflamma*, *Hipposcarus harid*, *Monodactylus argenteus*, *Scolopsis ghanam*, *Siganus sutor* and *Sphyraena barracuda*) and believed to utilize these nearshore habitats as nurseries (Dorenbosch et al. 2005b), sometimes in relatively high densities (Lugendo et al. 2007a), confirming Chwaka Bay as providing an important nursery environment.

As described by Lugendo et al. (2005; 2007a) fishes in the shallow waters of Chwaka Bay exhibited spatial variability across habitats in terms of size distribution. Generally, mangrove habitats harboured smaller-sized juveniles as compared to individuals of the same species that were found in the seagrass beds. For example, small-sized juveniles of *Lethrinus lentjan*, *L. variegatus*, *Pelates quadrilineatus*, *Siganus sutor* and *Sphyraena barracuda* were found in shallow and turbid mangrove creek areas, whereas large-sized juveniles were observed in slightly deeper and less turbid seagrass beds. Furthermore, juveniles of *Gerres filamentosus* and *Monodactylus argenteus* occurred in high densities only within the mangroves, while no adults were observed in any of the studied shallow-water habitats.

Ontogenetic migration patterns of fish species in Chwaka Bay seem to some degree be linked to aspects of habitat preference; some fish species were found in multiple habitats, while others were restricted to a single habitat type (Lugendo et al. 2007a). Juveniles of *Gerres oyena*, *Lethrinus lentjan*, *Lutjanus fulviflamma* and *Sphyraena barracuda* were generalists (found in all studied embayment habitats). In contrast, juveniles of *Cheilio inermis*, *Hipposcarus harid*, *Leptoscarus vaigiensis*, and *Scolopsis ghanam* were found in seagrass beds only, while those of *Gerres filamentosus* and *Monodactylus argenteus* were mainly found in the mangrove habitats (Lugendo et al. 2007a).
As mentioned above, most studies performed in Chwaka Bay describing connectivity and the nursery function have focused on fish assemblages or populations of certain fish species. However, some studies have focused on other animal groups. Subramaniam (1980) conducted an investigation of the nursery phase of penaeid prawns between 1977 and 1979. The peak post-larval immigrations were recorded during the warmer months (February-March) and poor recruitment during cooler months (June-August). The post-larval recruitment represented all the species of commercially important shallow-water prawns in Tanzania including Penaeus latisulcatus, Fenneropenaeus indicus, Metapenaeus monoceros, P. monodon, P. semisulcatus and Parapenaeopsis spp. In terms of occurrence, P. latisulcatus (75%) and F. indicus (15%) were the dominant species for most parts of the year. Oceanographic factors including the East African Coastal Current and the tides are considered important in the transport and dispersal of the larval and post-larval penaeids from the breeding grounds to the nursery area. Subramaniam (1990) revealed that the greatest post-larval incursions occur at night during flood spring tides when the tidal flow is strongest.

The juvenile population as described by Subramaniam (1980; 1990) consists of P. latisulcatus distributed in the intertidal sand flats with rich growth of seagrass and F. indicus inhabiting the muddy areas of the mangrove forests. The clear distribution range exhibited by the two species has considerable ecological implications. Subramaniam (1990) pointed out that despite an overlap of peak post-larval incursions, the spatial partitioning of the two species enables them to efficiently utilize food available in the different biotopes without any significant inter-specific competition. This has also been demonstrated in a study at Inhaca Island, southern Mozambique, by Macia (2004), which showed that different penaeid shrimp species have obvious habitat preferences, in turn emphasising their spatial partitioning to reduce competition for food and space.

Subramaniam (1980; 1990) found that while in the nursery area, P. latisulcatus grows to maturity (60-70 mm) in 5-6 months, whereas F. indicus attains maturity (110-120 mm) in 6-8 months; subsequently, specimens of both species migrate back to the sea. It is suggested that low salinity as a result of freshwater runoff during the rainy season is responsible for triggering emigration of prawns from the nursery areas. Subramaniam (1980) argued that the estuarine environment is not absolutely necessary for the completion of life history of all penaeid species. He considered the provision of food and shelter as equally important factors for nursery dependence by these crustaceans.

**Larval Transport**

Ocean current patterns and the spatial setting of shallow-water habitats in Chwaka Bay can influence recruitment patterns that result in distinct fish assemblages in seagrass habitats. Dorenbosch et al. (2006a) showed differences in fish species
assemblages in seagrass beds of Chwaka Bay compared to seagrass habitats in other locations around Unguja Island. These species assemblage differences suggested variations in recruitment patterns that may directly reflect differences in ocean current patterns, which are not likely to be similar at all seagrass locations around the island. Consequently, this may result in different recruitment peaks of species around Unguja Island and likewise, also different seagrass fish assemblages. However, it may also be the case that Chwaka Bay has a unique chemical or acoustic signature and is recognized by certain larvae of species that subsequently directly recruit into seagrass beds of Chwaka Bay, and not to other coastal seagrass beds, e.g. in adjacent intertidal areas. Rather than passively floating with the main ocean current, these larvae may actively search for specific habitat types for settlement. The embayment of Chwaka Bay is relatively large compared to other shallow-water areas around the coastline of Unguja Island. Furthermore, the system of subtidal areas and intertidal flats intermingled with deep channels is unique to the island and results in diverse and abundant seagrass assemblages. This may in turn result in an environmental setting that influences spatial recruitment patterns of larval fishes that settle in shallow waters around Unguja Island. However, although such direct recruitment, independent from the main ocean current has been shown for the Caribbean (Nagelkerken 2007; Pollux et al. 2007), it remains unclear whether recruitment patterns of seagrass-associated fishes around Unguja island are random or directed at certain locations or habitat configurations (such as Chwaka Bay).

**Genetic Connectivity**

Species with pelagic larval life phases are most likely genetically connected over large distances, i.e. multiple kilometres. On the scale of a 1,000 km gradient in the western Indian Ocean (Mombasa in Kenya to the Comoros), based on DNA fingerprinting, Dorenbosch et al. (2006a) showed that populations of *Lutjanus fulviflamma* were not genetically distinct, suggesting a regular exchange of genetic material. Although Chwaka Bay was not part of the sampling design, a similar population structure has been shown along the East African coast for the fiddler crab *Uca annulipes* (Silva et al. 2010). Most likely, populations of marine species with a pelagic larval phase exchange larvae over long distances and can influence or replenish each other over longer distances than previously expected. For these pelagic larval species (such as the commercially important *Lutjanus* family), Chwaka Bay seems to be part of a large meta-population and the present fish assemblage is heavily dependent on recruitment peaks, most likely also from abroad (Dorenbosch et al. 2006b).
INFLUENCE OF SPATIAL SCALE ON PATTERNS OF FISH CONNECTIVITY

Visual census and beach seine surveys that have been conducted in Chwaka Bay during the last years suggest connectivity of fish assemblages between the Bay habitats – seagrass beds and mangroves – and the adjacent coral reef. This could either play a role on the scale level of 10s to 100s of meters (in this case a 60 m gradient), or on the scale level of the entire Bay (i.e. 10-15 km), as illustrated in figures 2 and 3.

In a small-scale study by Dorenbosch et al. (2005a), the influence of the coral reef on adjacent seagrass beds was demonstrated over a 60 m gradient at the entrance zone of Chwaka Bay (Fig. 2). This 60 m long coral reef–seagrass gradient is characterized by decreasing species richness with increasing distance from the coral reef–seagrass interface. This pattern is predominantly characterized by decreasing species richness and density of reef-associated species. The farther away from the reef edge, the more dominant seagrass-associated and nursery species become. The latter are those species that show high juvenile densities in the seagrass habitat and low densities on the coral reef, and of which the adults show the opposite pattern and are mainly concentrated on the reef. Reef-associated species use the adjacent seagrass edge for foraging, but only within a narrow distance. Additionally, nursery species occur along the entire gradient, but already at a 60 m distance there is a clear habitat shift of juveniles that predominantly use the seagrass beds, whereas the adults are located around the adjacent coral reef.

With respect to the entire area of Chwaka Bay, it could be suggested that predominantly the shallow seagrass beds off Chwaka and Marumbi villages are utilized by coral reef species (the nursery species), in comparison with the deeper seagrass beds or mangroves. Although the mangroves and adjacent mudflats are also used by some reef-associated species, the fish assemblages in these habitats are dominated by species that do not occur on the reef. In general, the seagrass beds in Chwaka Bay are likely to be more strongly connected with the coral reef than the mangroves (see also chap. 9).

The influence of shallow seagrass beds in Chwaka Bay on the coral reef is also likely to extend farther out beyond the reefs. Based on visual census surveys in 2005, high densities of small, juvenile Cheilinus undulatus were found in seagrass beds of Chwaka Bay (Dorenbosch et al. 2006c). Similar surveys in different shallow-water habitats (mangroves, seagrass beds and coral reefs) around Unguja Island in the same year showed that juveniles of this reef-fish were mostly absent or occurred only in very low densities (Dorenbosch et al. 2006c). It is therefore likely that the seagrass beds in Chwaka Bay are an important source of juvenile Cheilinus undulatus on a geographic scale that may influence large parts of the eastern coast of Unguja Island.
Figure 2. Connectivity of fish assemblages over a 60 m coral reef–seagrass gradient at the entrance zone of Chwaka Bay, based on visual census surveys (Dorenbosch et al. 2005a). Connectivity is illustrated by (a) total species richness, (b) species similarity (expressed as % of co-occurring species), and (c) mean fish density of species groups (Dorenbosch et al. 2005a) of the four habitat zones.
Figure 3. Connectivity of fish assemblages in the coral reef – seagrass – mangrove gradient in Chwaka Bay based on visual census surveys (Dorenbosch et al. 2005a) and beach seine hauls (Lugendo et al. 2005). Connectivity is illustrated by (a) total species richness of the coral reef (entrance of Chwaka Bay) and seagrass beds in Chwaka Bay (entrance and Chwaka village), (b) species similarity (expressed as % of co-occurring species) between three zones (coral reef, seagrass beds at the Bay entrance and seagrass beds near Chwaka village), and (c) similarity of fish assemblages in the mangrove (creeks, channels and mudflats) and seagrass zone (Marumbi and Chwaka) of Chwaka Bay with respect to the reef (% of co-occurring species). Data in (c) is based on beach seine hauls, whereas the species assemblage on the coral reef is determined by visual census surveys. Numbers above the bars in (c) indicate species richness of the habitat zones.
INFLUENCE OF MULTIPLE SPATIAL SCALES AND LANDSCAPE CONFIGURATION ON FISH CONNECTIVITY

The structuring of species assemblages is determined by interacting processes operating across different scales (Levin 1992). To date, with respect to connectivity of fish, relatively few studies have considered multiple scales (Pittman and McAlpine 2003; Grober-Dunsmore et al. 2009). Nevertheless, in contrast to other fish studies in Chwaka Bay, Gullström et al. (2008; 2011) focused explicitly on fish-habitat interactions in seagrass habitats at various scales, partly using a landscape ecology approach (Grober-Dunsmore et al. 2009). Focusing on seagrass meadows dominated by *Thalassia hemprichii* or *Enhalus acoroides* (three sites each) and one mixed meadow (*T. hemprichii*, *E. acoroides* and *Thalassodendron ciliatum*), both studies examined how the spatial variability of fish is determined by factors at scales ranging from local within-meadow attributes to landscape configuration. Gullström et al. (2008) showed that the pooled number of fish species found in different seagrass habitats was clearly dominated by species associated with coral reefs (40), while few species (5) were associated with mangroves. Thirteen species were associated with both mangrove and coral-reef habitats, while three species were associated with unvegetated mud/sand flats, and nine species used seagrass habitats exclusively. In contrast to species diversity, the highest densities and biomass of fish were recorded for seagrass residents and coral-seagrass associated fish. Combined with the fact that specimens were mostly juveniles and (to a lesser extent) subadults, the findings highlight the potential importance of the seagrass meadows of Chwaka Bay as transient and nursery areas. This is further strengthened by the fish assemblage structure being clearly defined by distance to mangrove and coral-reef habitats (Gullström et al. 2008). Furthermore, in a study focusing on the seagrass-grazing parrotfish *Leptoscarus vaigiensis*, Gullström et al. (2011) found 22 potential predator species of this parrotfish, most of which were coral-reef associated and hence providing more evidence for cross-habitat connectivity in the Bay. The findings from these two studies demonstrate the complexity of scale and the importance of considering different scales (temporal as well as spatial) in attempting to understand connectivity across a shallow-water seascape like that of Chwaka Bay.

SCIENTIFIC GAPS AND FUTURE RESEARCH

Despite the vast amount of research carried out in Chwaka Bay, little information is available on connectivity in terms of cross-habitat linkages and the importance of nursery functions. The energy-exchange between habitats is difficult to understand since few studies have focused on quantification of the flow of energy, nutrients and organisms within the Bay. Also from a global point of view, few studies have acknowledged the exchange of energy and ecological processes across tropical shallow-water seascapes (see reviews by Nagelkerken 2009b; Berkström et al. 2012). To improve the understanding of connectivity between coastal habitats
it is of importance to consider a number of complex themes in ecology including trophic dynamics related to migration patterns (Sheaves 2009), habitat connectivity over relevant scales (Mumby 2006), and ecological processes and mechanisms across different scales (Nagelkerken 2009b).

With respect to cross-habitat interactions in shallow coastal waters, one of the most highlighted subjects is the nursery role hypothesis, yet few studies have been able to evaluate the nursery function according to the theoretical nursery concept (see Beck et al. 2001; Heck et al. 2003; Nagelkerken 2009a). Hence, an observation of high abundance of juvenile fish in the mangrove and seagrass habitats, with proportionally more adults on the coral reefs, is not sufficient to qualify Chwaka Bay as a nursery habitat. For a habitat to be qualified as a nursery habitat it should disproportionately (compared to other habitats) contribute to the production of specimens recruiting to the adult population. To elucidate the importance of different shallow-water habitats as nursery area for fish and decapods, tag-/mark-recapture surveys is one established method to obtain reliable estimates of juvenile fish abundance, and duration of residency within the nursery areas. Nagelkerken (2007) alludes to availability of new (and advanced) techniques such as DNA analysis, stable isotope analysis, otolith microchemistry, and the use of internal micro-tags or transponders which offer new opportunities for investigating seascape connectivity by fish. It is also of importance to take area coverage of each habitat type into account to fully understand the efficiency of nursery habitats (Dahlgren et al. 2006).

In summary, to successfully manage and conserve the resources of Chwaka Bay, it is of great importance to improve the understanding of energy-exchange dynamics across the seascape mosaic. This includes quantification of migration patterns, trophic dynamics and functional processes at a range of spatial and temporal scales.

ACKNOWLEDGEMENTS

We wish to thank various anonymous reviewers for useful comments. We are also grateful to all people in Chwaka who have assisted during the field surveys.

REFERENCES


