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ECOSYSTEMS

Mangrove Fish Production is Largely Fuelled by External Food Sources: A Stable Isotope Analysis of Fishes at the Individual, Species, and Community Levels from Across the Globe

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ABSTRACT

Coastal ecosystems are energetically connected through passive transport of nutrients but also by migrations of motile organisms. Mangroves are highly productive tropical ecosystems that replenish offshore populations of many species, but we know little about the degree to which this production is fuelled by prey from mangroves, especially in the cases in which mangroves are only accessible at high tide. Different results have been obtained on the importance of mangroves as feeding habitats, confounded by differences in species composition, seascape configuration, and methodology. In the present study, we took a more holistic approach by exploring reliance by fishes on mangroves as a feeding habitat at multiple ecological levels: from individuals to species to communities in mangrove ecosystems from across the globe, using a stable isotope approach. A two end-member mixing model showed a wide range (12–72%) in degree of reliance on mangrove food sources by fishes from different studies across the globe. However, analyzed at the levels of individual fish and species, reliance was low (for example, <25% for 55% of the species worldwide, or <50% for 85% of species, respectively) even though they were collected from sites that differed in geographical location, tidal regime, seascape structure, and species composition. The high fisheries productivity of mangroves appears to be energetically supported largely by food sources from adjacent habitats. In light of the ongoing rapid demise and fragmentation of mangrove and adjacent ecosystems, loss of ecosystem connectivity is likely to affect the productivity and functioning of tropical coastal ecosystems and the services they provide.

Key words: stable isotopes; mangrove; carbon flux; connectivity; seagrass.

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INTRODUCTION

Ecosystem connectivity is a pervasive feature of ecosystems worldwide that supports their biodiversity, productivity and functioning (Polis and others 1997). Water bodies of many freshwater (for example, van de Wolfshaar and others 2011; Rypel and others 2012) and marine (for example, Heck and others 2008; Granek and others 2009) ecosystems are intricately linked through active migration of animals as well as passive transport of nutrients and particulate organic matter facilitated by river flows or tidal exchanges (Cowen and others 2000; Gibson 2003). Tropical coastal seascapes in particular have received increasing attention from studies with a focus on elucidating the underlying mechanisms of ecosystem connectivity (Duarte and Cebrian 1996; Mumby and others 2004; France and Duffy 2006; Verweij and others 2008), as they form an ideal model system due to the juxtaposition of highly productive ecosystems such as mangrove forests, seagrass beds, and coral reefs. Although these systems can thrive in isolation, it has commonly been observed that where they occur close to one another they subsidize productivity in adjacent systems (Bouillon and others 2000; Bouillon and others 2008), show higher species richness at their interfaces (Nagelkerken and others 2001; Dorenbosch and others 2005), and show strong ecological linkages through tidal and diurnal migration by decapods and fish (Meyer and Schultz 1985; Sheaves and Molony 2000; Dorenbosch and others 2004). The interplay of tidal flow speed, hydrology of the system, the spatial and temporal distribution of predators and prey, the presence of aquatic vegetation, and difference in fish body size and fish species, among other things, result in a highly complex degree of connectedness among coastal habitats (Nagelkerken 2009).

Mangrove forests are one of the world's most productive ecosystems (Costanza and others 1997), and are typified by high densities of motile fauna (Robertson and Duke 1987; Nagelkerken 2007). Offshore fisheries and fish stocks have been correlated to the presence and extent of shoreline mangrove forests (Manson and others 2005; Meynecke and others 2008). Before the availability of advanced techniques to trace pathways of carbon flow through marine food webs, it was proposed that mangrove leaf detritus and particulate organic matter were responsible for subsidizing coastal food webs, a concept that has been referred to as ''mangrove outwelling'' (Lee 1995). The current consensus, however, is that the contribution of mangrove leaves as a source of nutrition for marine organisms from adjacent subtidal habitats is relatively low (Sheaves and Molony 2000; Kieckbusch and others 2004; Lin and others 2007). Recent stable isotope studies have shown that the dependence on carbon from primary producers such as phytoplankton, microphytobenthos, macroalgae, and epiphytes is much larger than previously thought (Bouillon and others 2008; Nagelkerken and others 2008). Although the relatively small role of mangrove detritus as a carbon source for most fauna is generally accepted, we know little about the degree to which mangroves energetically support resident and adjacent food webs at higher trophic levels through secondary production of prey items. Studies have shown that mangrove carbon can indirectly enter food webs through predators visiting mangroves at high tide to feed on crabs that primarily depend on mangrove leaves for their nutrition, a process that has been referred to as a ''short-circuit in the mangrove food chain'' (Sheaves and Molony 2000).

Tidal and diurnal migrations by motile fauna are ubiquitous in coastal ecosystems, and include entering as well as exiting inshore habitats during different times of the day or at different tidal amplitudes (Boström and others 2011). Tidal and diurnal inter-habitat migrations in mangroves occur daily and are highly structured in time and space (Krumme 2004; Verweij and Nagelkerken 2007). They are thought to be driven by changes in feeding opportunities or temporal changes in predation risk related to time of day or tidal stage (Laegdsgaard and Johnson 2001; Verweij and others 2006a; Hammerschlag and others 2010). In general, fringe mangroves can be separated into those that are permanently inundated with continuous access to motile animals and those that are only available at high tide. Whereas in microtidal areas permanently inundated mangroves seem to function mainly as shelter habitat (Verweij and others 2006b), studies suggest that in macro-tidal areas where mangroves are drained during low tides they serve as feeding habitats during high tides (Krumme and others 2008). There has been an ongoing debate as to whether motile fauna use high-intertidal habitats such as mangroves for feeding as opposed to refuge habitat (Laegdsgaard and Johnson 2001; Lugendo and others 2007). Different studies have found very different degrees of dependencies of motile fauna on mangrove-associated prey items (Nagelkerken and van der Velde 2004a). Confounding factors that have contributed to disparate results include: (1) terminology: different mangrove microhabitats have all been referred to as ''mangroves,'' (2) tidal regime: studies have been done in areas with widely differing tidal amplitudes, (3) species selection: different outcomes are observed for species with a different ecology, (4) spatio-temporal variability: fish occurrences and abundance may greatly vary in space and time, and (5) methodology: techniques were used that do not unambiguously show that mangrove food sources are ingested and/or assimilated. For example, the migration by fishes into the mangrove root habitat at high tide does not necessarily mean that they also feed there (Krumme and others 2008), whereas studies which show that fish leave the mangroves at ebbing tides with full stomachs (for example, Sheaves and Molony 2000; Krumme and others 2008) cannot quantify to what degree these mangrove food items are (1) assimilated (Michener and Shell 1994), or (2) contribute to the overall diet, as some soft-body prey items are quickly assimilated and therefore rarely found in the stomach (Gee 1989) or feeding takes place in additional adjacent habitats (Lugendo and others 2007; Kruitwagen and others 2010). Stable isotope analysis provides a more reliable technique in these cases to establish the main sources of food (Dittmar and others 2009).

Understanding the complex ecological interactions among ecosystems that support their productivity is of critical importance for their management and conservation. Intertidal tropical ecosystems that harbor high species diversity and show great variability in seascape structure and geomorphology are particularly difficult to study. Yet, there is an urgent need to better understand the processes that sustain the important role that they play in replenishing offshore populations and regulating population dynamics of a variety of species, especially in the light of their rapid and continuing demise (Duke and others 2007; Waycott and others 2009). In the present study, we took a more holistic approach than previously done by focusing on multiple fish species, at multiple ecological levels (individuals, species, communities) from multiple regions across the globe to come to a broader view of how ecological connectivity affects energy flow in complex seascapes. We use mangroves as a model ecosystem as they are known for their high densities of motile fauna (shrimp, crabs, fish; see Figure 1C) and for their high subsidy of new recruits to animal populations in adjacent marine ecosystems. We analyzed stable isotope ratios of fish tissue and stomach contents, and of potential food sources collected from mangroves and adjacent seagrass beds to examine the reliance on mangroves as a feeding habitat by intertidal fishes. Furthermore, we searched the literature for comparable studies in permanently inundated as well as intertidal mangroves that used a stable isotope approach. The end product is a global overview of the potential role that mangrove habitats play as a feeding habitat for fish. This not only provides us with a better understanding of the complexity and functioning of coastal food webs by fish that connect multiple habitats by their daily movements, but also sheds a light on the potential underlying mechanisms that lead to differences in trophic connectivity across habitats, with consequences for fishes, fisheries, and ecosystem functioning.

MATERIALS AND METHODS

Study Area

The collection of fishes was carried out between February 2007 and March 2010 at Kunduchi (mainland Tanzania, 6°40′29.39″S 39°13′6.60″E) and at the islands of Semama and Panjang (East Kalimantan—Indonesia, 2°08′38.26″N 118°20′02.18″E and 2°22′42.55″N 118°12′09.07″E, respectively).

The Kunduchi creek harbors mangrove forests with an estimated total surface area of 68.7 ha (Wang and others 2003). The creek has a narrow entrance to the ocean of ~300 m wide, and is 2.2 km long from entrance to the origin (Figure 1). The area has an average tidal difference of 3.5 m, and during low tide (spring and neap), the mangrove area is completely drained (see Figure 4A). Besides rainwater, the Kunduchi creek has no freshwater input. The creek is fringed by the mangrove *Sonneratia alba* which has upright roots. Off the Kunduchi coast (about 600 m) lays an extensive seagrass bed extending from the spring low water mark to a depth of about 5 m further offshore. *Thalassia hemprichii* and *Thalassodendron ciliatum* are the dominant seagrass species.

Semama and Panjang are two small coral reef islets off the coast of East Kalimantan, Borneo (Indonesia). The western shoreline of Panjang is lined with a narrow (~4 m wide) fringe of mangroves. Adjacent to the mangroves there is a slowly sloping intertidal sand flat of ~1 km wide that harbors patches of seagrass vegetation. The sand flat ends at a deep (>9 m depth) tidal channel which hydrologically connects the sand flat to the adjacent open ocean. The narrow fringe of intertidal mangroves along the western coastline of Semama is followed by a shallow intertidal sand flat of ~300–600 m wide and with patches of low seagrass cover (<25%), ending in a drop off zone

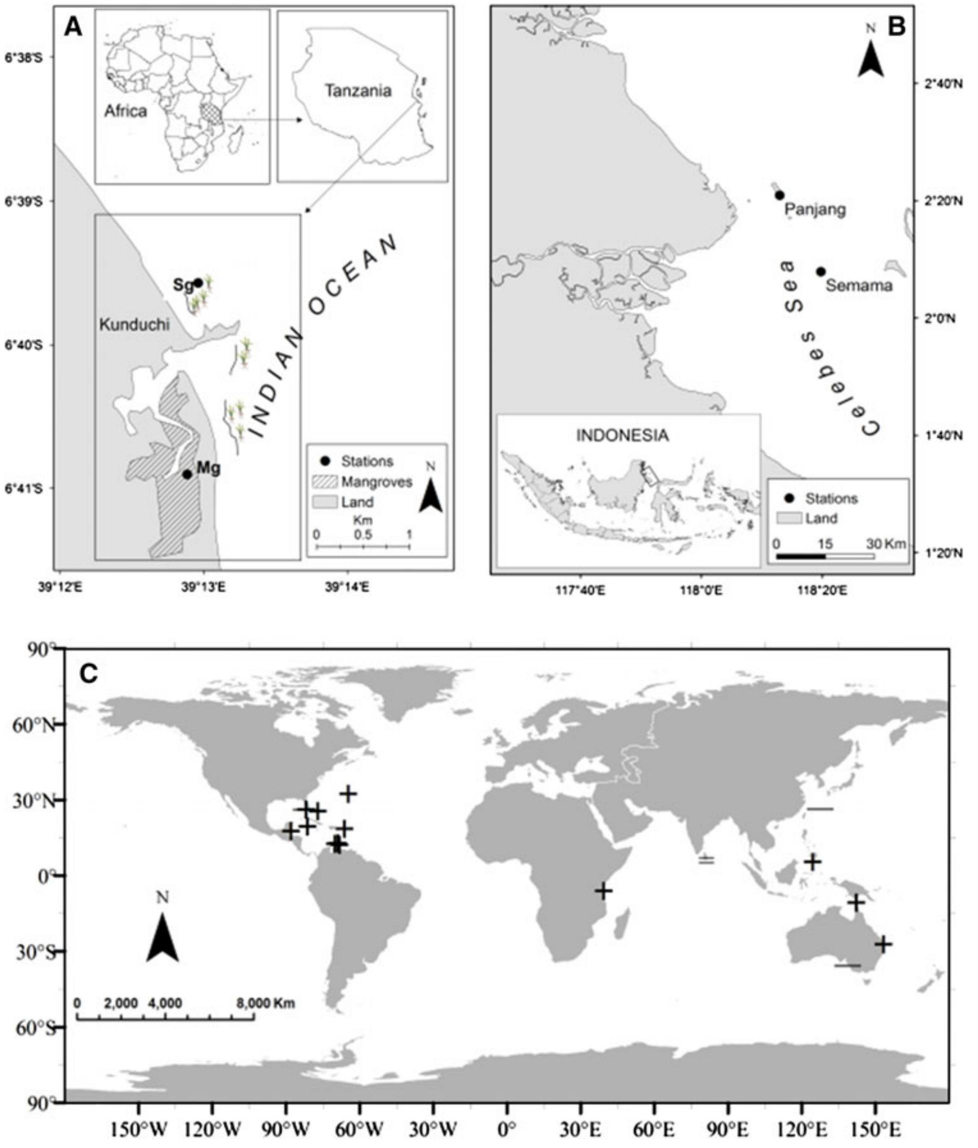

Figure 1. Location of collection sites of fishes and their prey items in Tanzania and Indonesia (**A**, **B**) and study locations for data obtained from the literature (**C**). *Mg* mangroves, *Sg* seagrass beds. We searched Thomson Reuters' Web of Science (Topic = mangrove and seagrass and fish; Topic = density or abundance or community) for studies that quantified complete fish communities in mangroves and their adjacent seagrass beds, complemented by references from Nagelkerken and van der Velde (2002) and our own unpublished data. Total fish density in mangroves versus seagrass is indicated by ''+'' (if higher in mangrove), ''−''(if lower in mangrove), or ''='' (if similar in both habitats). References used: Robertson and Duke (1987), Thayer and others (1987), Blaber and others (1989), Sheridan (1992), Sedberry and Carter (1993), Laegdsgaard and Johnson (1995), Pinto and Punchihewa (1996) Nagelkerken and van der Velde (2002), Eggleston and others (2004), Bloomfield and Gillanders (2005), Lugendo and others (2005), Dorenbosch and others (2007), Aguilar-Perera and Appeldoorn (2008), Shibuno and others (2008), Unsworth and others (2009), Hylkema and others (unpublished data), and Nagelkerken (unpublished data).

where a fringing reef is located. As the intertidal flats at both islands harbor only low coverage of seagrass they are hereafter referred to as sand flats. The mangroves at both islands fall completely dry at low tide. The average tidal amplitude is ~1.5 m (spring tide 2.7 m).

Sample Collection

Fishes and potential food items were collected at high tide in the mangroves and at low tide on the seagrass beds (Tanzania) or sand flats (Indonesia), using a beach seine net with a stretched mesh size of 10 mm. We intensively sampled four species (*Lutjanus fulviflamma*, *Lethrinus harak*, *Lethrinus lentjan*, and *Siganus sutor*) which occur in both mangrove and seagrass beds habitat at the study site in Tanzania. In addition we collected other fish species at the three locations (*Apogon lateralis*, *Apogon* sp., *Carangoides* sp., *Gerres abbreviates*, *Gerres oyena*, *Leiognathus equulus*, *Sphyraena barracuda*, and *Terapon jarbua*) that utilize mangrove during high tide. Captured fish were frozen prior to the processing. During processing, total length of each fish was measured to the nearest millimeter and white muscle tissue and stomach content were collected.

Samples of macroinvertebrates and macroalgae that formed the predominant food items for the selected fish species (see Suppl. Table 1) were collected from the mangrove roots, sand flats and seagrass beds by scoop nets or were handpicked. Sampling in the mangrove was done at low tide to assure that all collected food items were permanently associated with the mangrove root habitat independent of the tides. Sample sizes of fishes are presented in Table 1.

Sample Preparation and Analysis

All samples were analyzed for stable carbon and nitrogen isotope ratios. Stable carbon and nitrogen isotopes values of an organism's tissue reflect assimilation and turnover from its diet (Peterson and Fry 1987; Grey 2001). Stable isotope signatures of stomach contents provide an estimation of the diet of the preceding few hours, whereas stable isotope signatures of muscle tissue provide integrated information of the diet over the course of several weeks to months (Hesslein and others 1993; Guelinckx and others 2007). Because different food items get digested at different rates, stomach con-

Table 1. Stable Carbon and Nitrogen Isotope Signatures (Mean and Standard Deviation) of Fish Species from the Three Sampling Locations in Tanzania and Indonesia

Location	Species	Habitat	*N*	Size (cm)	%Mg	Mean δ^{13}C	SD	*p* value	Mean δ^{15}N	SD	*p* value
Kunduchi	*Apogon* sp.	Mg	9	4–7	52	−18.7	2.7	**0.020**	10.3	0.3	0.071
		Sg	4	3–8	33	−14.8	1.1		9.7	0.9	
	Carangoides sp.	Mg	8	3–8	65	−17.6	0.9	0.475	10.4	0.3	<**0.001**
		Sg	13	4–10	56	−17.4	0.6		9.1	0.7	
	Gerres oyena	Mg	17	4–7	62	−18.3	1.3	<**0.001**	10.1	1.0	<**0.001**
		Sg	8	3–8	–	−11.2	0.8		7.6	0.9	
	Lutjanus fulviflamma	Mg	119	3–16	12	−14.0	1.5	0.997	10.2	1.2	0.967
		Sg	86	2–25	21	−14.0	2.2		10.2	1.3	
	Lethrinus harak	Mg	12	3–11	22	−13.9	2.0	**0.024**	9.1	1.4	0.052
		Sg	64	5–30	18	−12.7	1.6		8.4	1.1	
	Lethrinus lentjan	Mg	7	3–9	10	−13.8	1.0	0.797	9.1	0.5	0.205
		Sg	87	4–30	21	−13.9	1.7		9.4	1.3	
	Siganus sutor	Mg	16	3–10	38	−17.3	1.1	0.600	9.8	0.8	0.654
		Sg	52	2–24	47	−17.5	2.3		9.7	1.2	
	Sphyraena barracuda	Mg	13	8–15	45	−16.7	0.3	0.584	11.6	0.6	0.698
		Sg	12	10–20	40	−16.6	0.5		11.5	0.4	
Semama	*A. lateralis*	Mg	5	3–6	77	−15.2	0.9		8.5	0.2	
	G. abbreviatus	Mg	11	10–13	14	−11.2	0.6	<**0.001**	7.7	0.4	**0.001**
		Sf	6	11–13	25	−9.8	0.6		8.3	0.2	
	G. oyena	Mg	3	3–10	18	−10.3	1.1	0.949	7.6	0.2	0.629
		Sf	14	3–14	18	−10.3	1.1		7.3	0.9	
	Terapon jarbua	Mg	4	3–6	67	−14.1	3.3		7.1	1.7	
Panjang	*Apogon* sp.	Mg	4	3–6	48	−14.7	1.8		8.2	0.8	
	G. abbreviatus	Mg	12	8–13	35	−13.0	1.2		7.4	0.7	
	G. oyena	Mg	10	4–14	30	−12.9	1.2	<**0.001**	7.4	0.4	<**0.001**
		Sf	12	5–10	8	−9.5	0.9		6.8	0.3	
	Leiognathus equulus	Mg	6	3–4	40	−13.7	0.3	<**0.001**	6.7	0.2	0.625
		Sf	8	3–4	16	−10.7	0.1		6.9	0.8	
	Sphyraena barracuda	Mg	3	5–34	49	−13.3	2.0		9.3	0.4	

p values in bold indicate significance differences in tissue stable isotope signatures between fishes collected from mangroves (Mg) and sand flats (Sf)/seagrass beds (Sg), based on independent sample t-tests ($p \leq 0.05$). % Mg indicates the percent contribution of mangrove food items to the fish diet based on the IsoSource stable isotope mixing analysis. Habitat capture habitat for fish, N sample size of collected fishes, size total fish length.

tents can provide a biased view of the true diet and are therefore less reliable. In the natural environment, carbon stable isotope signatures of primary producers show variation due to differential discrimination of ^{13}C. These differences are also reflected in their consumers and higher trophic levels. Habitats that harbor different types of primary producers often show distinct stable carbon isotope signatures (Lugendo and others 2007; Kristensen and others 2008; Nyunja and others 2009), which is also the case for seagrass and mangrove habitats (Marguillier and others 1997; Nagelkerken and van der Velde 2004b; Lugendo and others 2007). Marine organisms that use these habitats as feeding grounds can therefore acquire a stable carbon isotope signature in their tissue that reflects the various food sources consumed from these habitats (Deniro and Epstein 1981). On average, muscle tissues of consumers are enriched by about 0.5‰ for δ^{13}C and 3.4‰ for δ^{15}N, respectively, compared to their food sources (Vander Zanden and Rasmussen 2001; McCutchan and others 2003).

Fish muscle tissue was taken from the musculature below the dorsal fin and above the lateral line. All samples were oven-dried at 70°C for 48 h. Dried samples were ground to a fine powder using a ball mill (Retsch MM2). Samples were weighed accurately in pre-combusted tin containers. Carbon and nitrogen stable isotopes composition were measured with a Carlo Erba NA 1500 elemental analyzer coupled on-line with a ThermoFinnigan DeltaPlus mass spectrometer. Carbon and nitrogen isotope ratios are expressed in the standard delta notation (δ^{13}C, δ^{15}N) relative to Vienna Pee Dee Belemnite and atmospheric nitrogen. Every 12 runs, sucrose (IAEA-CH-6), ammonium sulfate (IAEA-N-2), and caffeine were added as a reference standard. Average reproducibility based on replicate measurements of standard δ^{13}C and δ^{15}N ranged (1 SD) between 0.15 and 0.17‰ for δ^{13}C and between 0.13 and 0.21‰ for δ^{15}N.

Literature Search

We searched for studies that analyzed stable isotope ratios of fish tissue and prey items from mangroves and adjacent sand/seagrass beds. Studies were grouped into two categories: intertidal mangrove forests that are completely drained during low tide and secondly, mangrove forests that remain inundated during low tide. We used the IsoSource mixing model (Phillips and others 2005) to calculate the degree of dietary dependence on mangrove food items for each species considered in each study (see below under statistical and data analysis). As stable isotope studies on tropical coastal fishes often do not report stable isotope signatures of food items from mangroves as well as from adjacent habitats many studies had to be excluded because dietary dependence cannot be calculated based on a single source habitat. In total, we were able to use 14 different studies from across the globe (Figure 1C; Table 2). We excluded all planktivorous, piscivorous and detritivorous fish in this analysis [except juvenile *Sphyraena barracuda* and *Carangoides* sp. which are known to feed on crustaceans (Lugendo and others 2006)] and only focused on zoobenthivores and herbivores, as these two feeding guilds consume food sources that are permanently associated with the mangrove or sand/seagrass habitats. This contrasts fish from other feeding guilds that also consume prey items that are transported across habitat borders by tidal movements (for example, plankton and particulate organic matter), making it impossible to determine if these fish feed on these food items in the mangroves at high tide or in adjacent habitats at low tide. This exclusion of species did not down-scale the importance of our conclusions, as almost half of the fish species in mangrove estuaries are represented by zoobenthivores alone (Sheaves 2012), and this number is higher for their biomass and density. For intertidal mangroves we excluded shrimps and other highly motile potential food sources in the mixing model as described below, but they were included for inundated mangroves. We only considered stable isotope signatures of fish species with $N > 2$ collected individuals.

Statistical and Data Analysis

Statistical tests were performed using SPSS 17.0 for Windows (SPSS Inc. 2007). Normality of the data was checked with a Shapiro–Wilkinson test and homogeneity of variances was tested with a Levene's test. Independent samples *t*-tests were used to statistically test the difference in δ^{13}C and δ^{15}N between fishes belonging to the same species collected from mangroves and sand/seagrass beds in Tanzania and Indonesia. Differences in stable carbon and nitrogen isotope signatures of potential food sources between habitats (for Kunduchi, Semama, and Panjang) and between habitats as well as between inundated and drained mangroves (for study sites from around the globe) were tested with MANOVA (General Linear Model) followed by a Tukey post-hoc test. For testing the differences between habitats for potential food sources,

Table 2. Mean Contribution of Carbon from Mangrove Food Items to the Diet of Fishes Collected from Mangroves (Mg) and/or Adjacent Sand/Seagrass Beds, Based on the IsoSource Mixing Model

Reference	Study (#)	Location	Inundation	Type	% Mg contribution (mean ± SD) all species	Total # of species	Species with ≥75% Mg contribution	% Mg contribution (per selected species)
Lugendo and others (2007)	1	Tanzania (Kaole)	Drained	F, P	60 ± 7	3		
	1	Tanzania (Nunge)	Drained	F, P	29 ± 22	7		
Kruitwagen and others (2010)	2	Tanzania (Mtoni)	Drained	F, P	26 ± 15	28		
Nyunja and others (2009)	3	Kenya	Drained	F, P	29 ± 30	5	*Siganus sutor*	79
Igulu and others (this study)	4	Tanzania (Kunduchi)	Drained	F, P	22 ± 26	10	*Apogon* sp.	75
	4	Indonesia (Semama)	Drained	F, P	37 ± 27	6	*A. lateralis*	84
	4	Indonesia (Pajang)	Drained	F, P	32 ± 14	7		
Marguillier and others (1997)	5	Kenya	Drained	P	–			
Heithaus and others (2011)	6	Australia	Drained	P	–			
Sheaves and Molony (2000)	7	Australia	Drained	P	–			
Melville and Connolly (2003)	8	Australia	Drained	P	–			
					Mean: 33 ± 13			
Kieckbusch and others (2004)	9	USA (Florida)	Inundated	P	–			
	9	Bahamas	Inundated	F, P	12 ± 4	2		
Lugendo and others (2007)	10	Tanzania (Mapopwe)	Inundated	F, P	65 ± 34	9	*Gerres filamentosus*	89
			Inundated				*Leiognathus equluus*	89
			Inundated				*Lethrinus lentjan*	91
			Inundated				*Lutjanus fulviflamma*	92
			Inundated				*Monodactylus argenteus*	97
			Inundated				*Zenarchopterus dispar*	100
Lugendo and others (2007)	10	Tanzania (Mbegani)	Inundated	F, P	72 ± 12	17	*Monodactylus argenteus*	76
			Inundated				*L. argentimaculatus*	86
			Inundated				*Hemirhamphus* sp.	89
Harrigan and others (1989)	11	USA (Florida)	Inundated	P				
Nagelkerken and van der Velde (2004b)	12	Curaçao	Inundated	F, P	33 ± 23	4		
Nagelkerken and van der Velde (2004a)	13	Curaçao	Inundated	F	21 ± 19	15		
Lee (2000)	14	China	Inundated	F, P	23 ± 12	5		
					Mean: 38 ± 35			

Per study, the % mangrove contribution was averaged across all collected species (see total # of species per study). Study # indicates the study numbers used in Suppl. Figure 2. Type depicts whether the study was used to calculate mean isotope signatures of potential prey items (P) in mangroves/seagrass beds (results shown in Suppl. Figure 2) or used in a IsoSource mixing model to calculate % contribution of mangrove food items to the diet of fish (F), the results of which are shown in Figure 4B. Inundation refers to whether mangroves are intertidal (drained at low tide) or permanently inundated. The last two columns indicate for each study which species showed high dependence (≥75%) on mangrove food items, and the degree of this dependence (% contribution), respectively.

sampling habitat and potential food items were treated as fixed factors. For testing differences between potential food sources from inundated and drained mangroves, inundation type and sampling habitat were treated as fixed factors. Comparable to the food item analysis, MANOVA was used to test differences in δ^{13}C and δ^{15}N signatures between fishes from different habitats and inundation type for the global comparison, using individual fish species and inundation type as dependent variables. Differences in signatures among size classes of fish were tested using a 1-way ANOVA, followed by a Tukey post-hoc test. For all tests, significance was accepted at a level of $p \leq 0.05$.

The IsoSource mixing model for stable isotopes was used to examine all possible source contributions by potential food items from mangroves or sand/seagrass beds to the fish diets. Due to large variability in prey selection, as shown by stomach contents of fishes from various locations and studies (de Troch and others 1998; Hajisamae and others 2003; Nakamura and others 2003; Lugendo and others 2006), we analyzed overall habitat contribution in terms of food provisioning and not contribution per individual food item from a habitat. Mean values of potential food items were used as source contributor and a 2% source increment and 0.1‰ mass balance tolerance were used as suggested by Phillips and Gregg (2003). Only δ^{13}C signatures were entered into the calculation because we were interested in the carbon contribution per habitat. All signatures of potential food items were corrected for trophic fractionation, calculated per species from individuals for which we had stable isotope values of stomach contents as well as muscle tissue. In the cases where we did not have both stomach content and muscle tissue signatures to calculate the enrichment factor, a common enrichment factor (0.5‰, Deniro and Epstein 1978) for carbon was used. For our own data from Tanzania and Indonesia, source contribution was first calculated per individual fish and then averaged for each species. This approach was chosen to more objectively determine the source contribution, because using the mean value for calculating the source contribution for a species (as done in the majority of the published studies) would imply that all individual fish consume the same food items, whereas in nature individuals target a variety of food items. For the source contributions (IsoSource) we used crabs, hermit crabs, polychaetes, isopods, amphipods and mantis shrimps for carnivorous/zoobenthivorous fish, and macroalgae for herbivorous fish (Supplementary Figures 1 and 2).

RESULTS

Mangrove Feeding at Individual and Species Level

Stomach Content Isotope Signatures (Indicative of Short-term Feeding Patterns)

Stable isotope signatures of stomach contents from *L. fulviflamma* showed no significant differences between fish collected from the mangroves and those from the seagrass beds (independent *t*-tests, δ^{13}C: $p = 0.144$, but with a difference in δ^{15}N: $p = 0.016$). Of 23 and 29 fish collected from mangroves and seagrass beds, only five and six individuals, respectively, showed a δ^{13}C stomach content signature that overlapped with those of mangrove food sources (Figure 2A). The IsoSource stable isotope mixing model estimated that of the *L. fulviflamma* individuals caught from both habitats, on average 37% of their diet was obtained from mangrove food sources. For individuals of the other three species collected from seagrass beds (Figures 2B–D), mixing models calculated the contribution of mangrove food items to the diet to be 19% for both *Lethrinus harak* and *Lethrinus lentjan* and 39% for *Siganus sutor*, respectively.

Muscle Tissue Isotope Signatures (Indicative of Long-term Feeding Patterns)

δ^{13}C and δ^{15}N signatures of fish muscle tissue did not differ significantly (Table 1) between fish caught in mangroves as opposed to seagrass beds (except δ^{13}C of *Lethrinus harak*), and largely overlapped with the range of food item signatures for the seagrass beds (Figures 2E–H). Only a small percentage of all individuals showed a tissue δ^{13}C that overlapped with that of mangrove food items (*L. fulviflamma*: 2%; *Lethrinus harak*: 4%; *Lethrinus lentjan*: 2%; *S. sutor*: 16%). The IsoSource stable isotope mixing model estimated that of all fishes caught in the mangroves and seagrass beds, the mean percentage diet contribution from mangrove food items was 15, 12, 21, and 45% for *L. fulviflamma*, *Lethrinus harak*, *Lethrinus lentjan*, and *S. sutor*, respectively. Calculations on mangrove contribution to fish diets were not confounded by fish body size, as no significant increase or decrease was found for tissue δ^{13}C as a function of fish length (Suppl. Table 1).

Mangrove Feeding at Community Level

In Tanzania (Kunduchi) only three out of eight species (*Apogon* sp., *G. oyena* and *Lethrinus harak*) showed significantly depleted δ^{13}C tissue values for

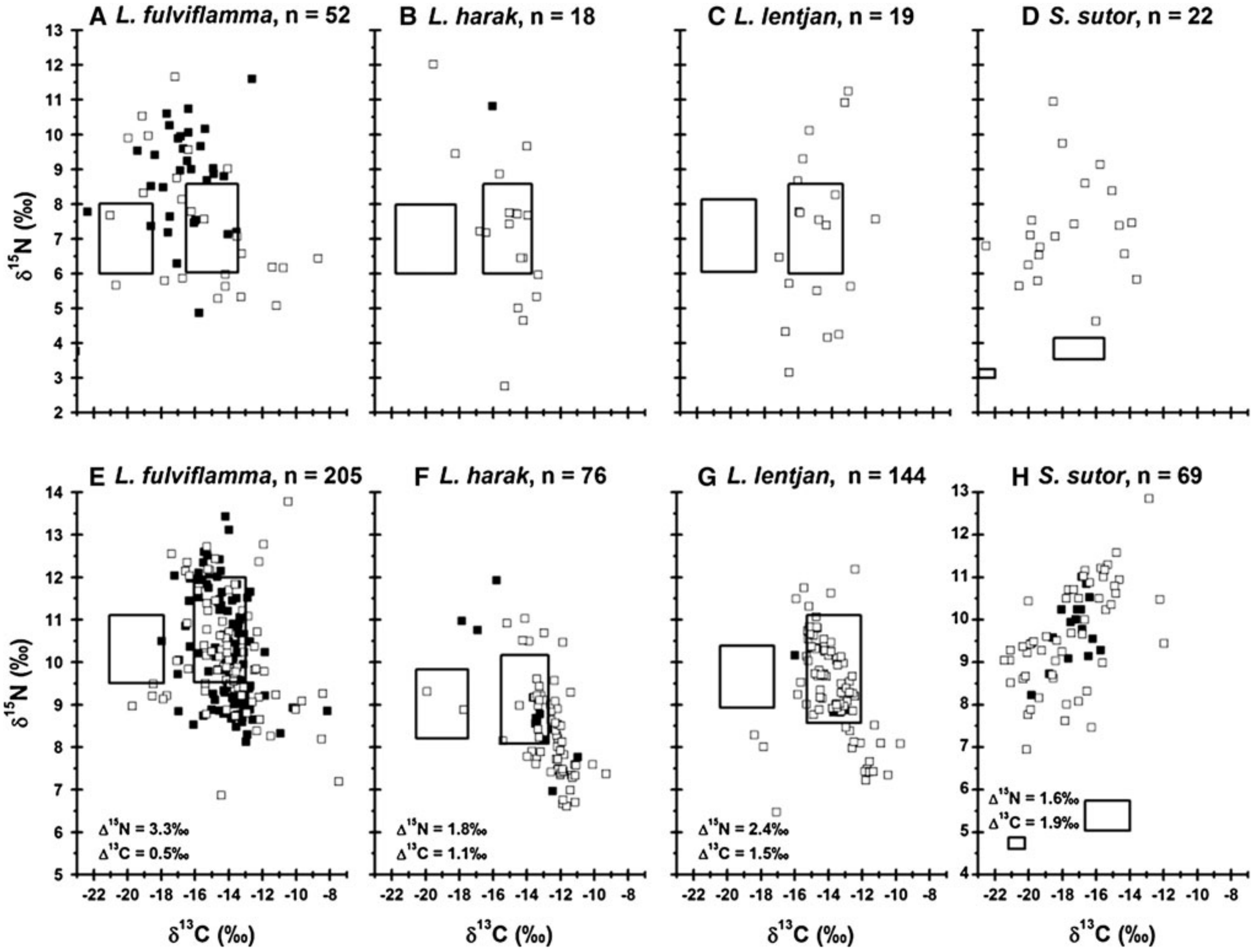

Figure 2. δ^{15}N and δ^{13}C values of stomach contents (**A**–**D**) and muscle tissue (**E**–**H**) for individual fish belonging to the species *L. fulviflamma*, *Lethrinus harak*, *Lethrinus lentjan*, and *Siganus sutor* collected from the mangrove root habitat (*filled symbols*) and the adjacent seagrass beds (*open symbols*) at Kunduchi. The *boxes* in **A**–**D** indicate the range of the mean values (see Suppl. Figures 1A, B) for potential food samples from mangroves (*left hand boxes*) and seagrass (*right hand boxes*) habitats, whereas *boxes* in **E**–**H** indicate the same range in mean values for food items, but adjusted for fractionation between prey and consumer. Fractionation was calculated by comparing signatures (δ^{15}N as well as δ^{13}C) between muscle tissue and stomach for the same fish, and calculating mean enrichment per species (means shown *bottom-left* of each panel). *N* = sample size of fish analyzed.

individuals caught in mangroves as opposed to seagrass beds (Table 1; Figure 3A). Of these, *G. oyena* was the only species who had multiple individuals collected from the mangroves overlapping in their tissue δ^{13}C with that of mangrove food items (11 out of 17 individuals). For three species (*Lethrinus harak*, *Lethrinus lentjan*, *L. fulviflamma*) δ^{13}C tissue signature overlapped with those of seagrass bed food items, whereas *G. oyena* collected from the seagrass beds showed highly enriched tissue signatures. For the remainder of the species, fishes showed a δ^{13}C tissue signature that fell in-between that of mangrove and seagrass bed food items. The IsoSource mixing model showed the average contribution of mangrove food sources to the diet of fish species to range between 10 and 65% (Table 1), with highest contributions for *Sphyraena barracuda* and *Carangoides* sp. from both habitats and for *G. oyena* and *Apogon* sp. that were caught in the mangroves.

In Indonesia (Semama), only two species (*Terapon jarbua* and *A. lateralis*) collected from mangroves showed highly depleted δ^{13}C tissue signatures that partly overlapped with those of mangrove prey items, and the IsoSource mixing model estimated the contribution of mangrove food

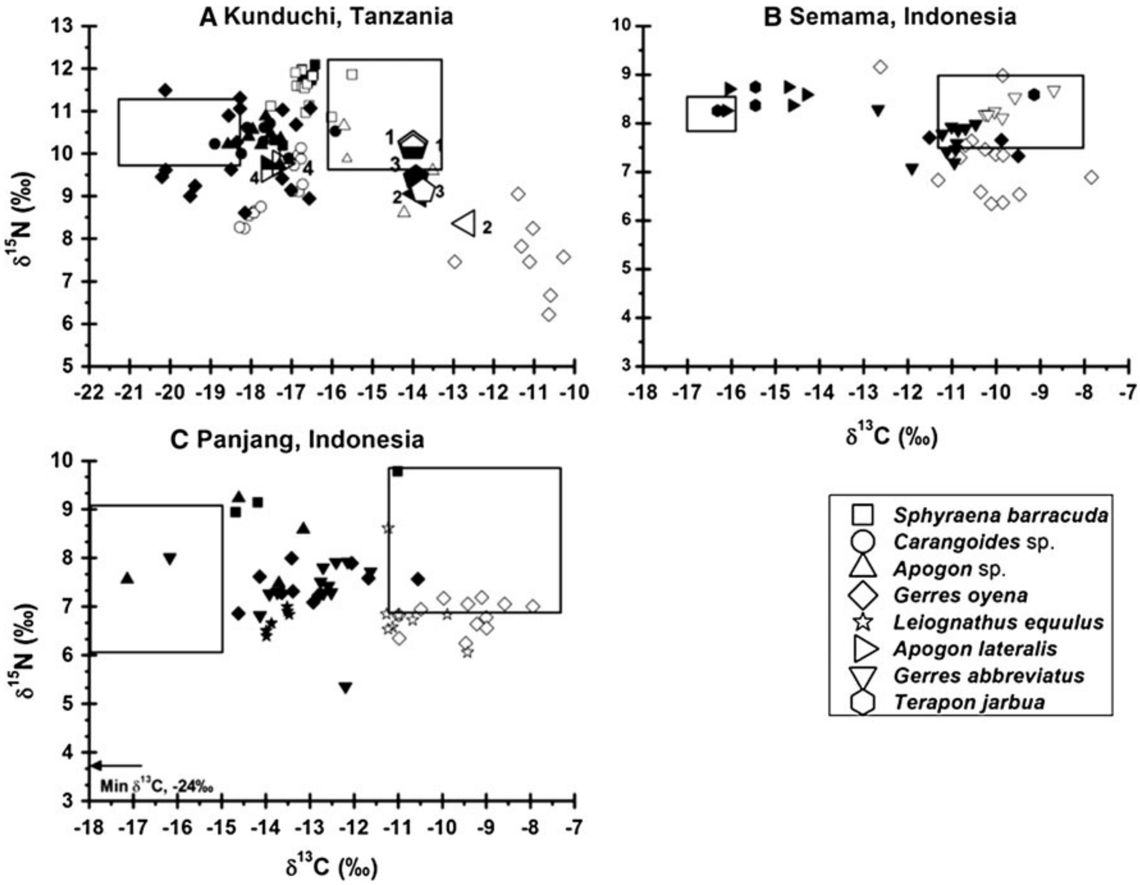

Figure 3. δ^{15}N and δ^{13}C tissue values for species of the fish communities in mangroves (*filled symbols*) and sand/seagrass beds (*open symbols*) at Kunduchi (**A**), Semama (**B**), and Panjang (**C**). *Each symbol* represents one individual fish. *Boxes* indicate the range (based on mean values) of potential food items (see Suppl. Figure 1) from mangroves (*left hand boxes*) and sand/seagrass (*right hand boxes*) habitats, for each location separately and adjusted for fractionation. As degree of fractionation per species was not available, we used the commonly used average enrichment of 0.5‰ for δ^{13}C and 3.4‰ for δ^{15}N, respectively (Vander Zanden and Rasmussen 2001; McCutchan and others 2003). *Large symbols* and associated numbers in **A** indicate the average signature at Kunduchi (see Table 1) for: 1 *L. fulviflamma*, 2 *Lethrinus harak*, 3 *L. lentjan*, and 4 *Siganus sutor* in the mangroves and seagrass beds.

items to their diet to be 67 and 77%, respectively (Figure 3B). Two other species collected from mangroves as well as seagrass beds (*G. oyena* and *G. abbreviatus*) all showed δ^{13}C signatures that mainly overlapped with those of seagrass bed prey items, with a dependency on mangrove food sources of 25% or less (Table 1). Nevertheless, *G. abbreviatus* collected from the mangroves showed significantly depleted δ^{13}C tissue values compared to those collected from the seagrass beds.

In Pajang (Indonesia), all fishes collected from the seagrass beds overlapped in their δ^{13}C tissue signatures with that of seagrass food items, whereas those collected from the mangroves showed significantly depleted values that fell in-between that of prey items from mangroves and seagrass beds (Table 1; Figure 3C). Only two individual fish showed a δ^{13}C signature similar to that of mangrove prey items. The Isosource mixing model estimated the average contribution of mangrove food items to the diet to range between 8 and 49%, with highest contributions for two species that were caught in the mangroves only (*Sphyraena barracuda*: 49%, and *Apogon* sp.: 48%).

Global Trends of Mangrove Feeding

Fish communities from neither intertidal nor permanently inundated mangroves showed a disparate pattern in their degree of dependence on mangrove food items (overall mean: 33 vs. 38%, respectively) when analyzed at the level of individual studies, and both mangrove types showed a wide range of dependency values (12–72%;

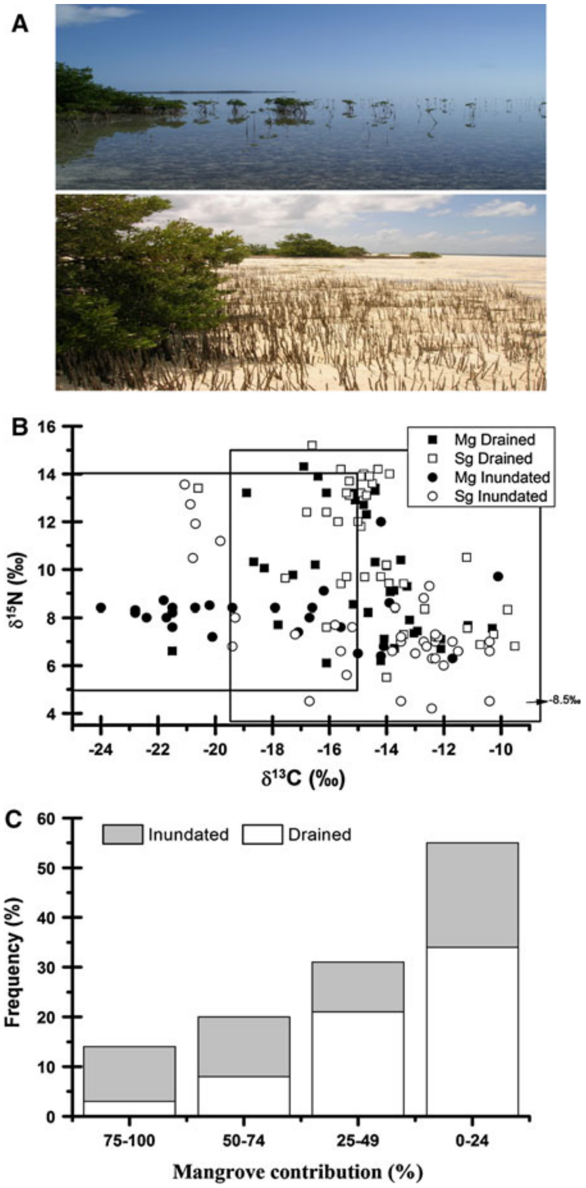

Figure 4. **A** Example of an inundated mangrove forest at high tide (*upper panel*) and at low tide (*lower panel*). **B** Mean δ^{15}N and δ^{13}C tissue values for individual species (indicated as separate data points) of studies from across the globe (listed in Table 2), indicating capture habitat (*Mg* mangrove, *Sg* seagrass/sand bed) and inundation type. *Boxes* indicate the range (based on mean values) of potential food items (see Suppl. Figure 2) from mangroves (*left hand boxes*) and sand/seagrass (*right hand boxes*) habitats, adjusted for fractionation. As degree of fractionation per species was not available, we used the commonly used average enrichment of 0.5‰ for δ^{13}C and 3.4‰ for δ^{15}N, respectively (Vander Zanden and Rasmussen 2001; McCutchan and others 2003). **C** Frequency distribution at fish species level for the degree of dietary dependence on mangrove food items. For each species in each study (see **B**), the percent contribution of carbon from mangrove food items was calculated using the IsoSource mixing model.

Table 2). Analyzed at the species level (Figure 4B), however, it was evident that more species from permanently inundated mangroves had depleted mean δ^{13}C tissue values than those collected from mangroves that are drained at low tide (MANOVA, $F_{(2,104)} = 27.23$, $p \leq 0.001$), and this was also true for fishes collected from their respective adjacent seagrass/sand habitats (MANOVA, $F_{(2,104)} = 3.19$, $p = 0.045$). The absolute number of species that overlapped only with δ^{13}C signatures of mangrove food items was relatively low, however, and was predominated by species collected from permanently inundated mangroves and their adjoining habitat (Figure 4B). Consequently, about 85% of the species considered on a global scale showed a dietary dependence of $<50\%$ on mangrove prey items, with species from drained mangroves contributing more to this pattern than those from permanently inundated mangroves (Figure 4C). Only few species showed a mangrove food dependence of at least 75%, including several species of cardinalfish (Apogonidae) and snappers (Lutjanidae) (Table 2).

DISCUSSION

Whereas many studies have focused on the role of carbon from mangrove vegetation (leaf litter and detritus) as a source of nutrition for intertidal and subtidal animal communities, we still know very little about the role that mangroves play as a feeding habitat where motile fauna can forage on the high abundance of macroinvertebrates, such as crabs and gastropods that are permanently associated with the mangrove root habitat. In the present study, we show that few fish species show high dietary reliance on food items associated with mangroves, as indicated by isotope mixing models using our own data from Tanzania and Indonesia as well as those extracted from the literature from around the globe. This finding applied to resident fishes in permanently inundated mangrove forests as well as to fishes entering intertidal mangroves at high tide. Mangroves have been widely acknowledged as important nurseries due to the high numbers of juvenile fish that they harbor (Mumby and others 2004; Nagelkerken and others 2008), and the paradigm is that increased survival from predation and enhanced growth resulting from abundant food supplies underlie their nursery role (Parrish 1989; Faunce and Layman 2009; Nagelkerken 2009). However, contrary to this assertion, very little evidence was found in the present study in support of the mangrove food-supply hypothesis. Our study is novel in that we evaluated fish dependency patterns both on the short-term (using stomach content) and long-term (using muscle tissue) at individual, species, and community levels of fishes collected from mangroves with different inundation types as well as their adjacent ecosystems, from around the globe. This holistic approach showed that although there was a clear distinction in stable carbon isotope signatures of all collected food sources between mangroves and adjacent ecosystems (seagrass beds/sand flats), the stomach content and muscle tissue signatures of fishes collected from these systems were decoupled from this pattern at all levels studied. The overall reliance on food sources in the mangroves was low for the majority of fish species collected from mangroves as well as from adjacent ecosystems, indicating that fringing mangrove systems in general do not appear to function as primary feeding areas for most species, irrespective of whether they are residents or temporary immigrants.

Previous studies that have shown a low reliance of fishes on mangrove food items have mostly based their conclusions on average signatures of fish tissues, but average values only tell part of the story. Our understanding of this phenomenon may be skewed due to the fact that individuals within a fish species, but also within prey species, may show specialization in terms of diet or use different niches (Layman and others 2007). This means that analysis at the level of individual consumers may show patterns that are masked by averages. Nevertheless, our analysis at this level also showed a pattern of low dependence of fish on mangrove food sources. Less than 16% of the individuals for any of our four selected fish species from the Tanzania study site had a δ^{13}C muscle tissue signature that overlapped with those of mangrove food items, and calculations from the mixing model showed that the dietary reliance of fish on these food items ranged merely between 12 and 21% for the three zoobenthivorous species and 45% for the herbivore *Siganus sutor*. This indicates that a low importance of mangrove root systems as feeding habitats for fish is quite ubiquitous across individuals within our study species, and if individual specialization occurred at all (for example, Layman and others 2007) this was not expressed as a differential selection of feeding habitats. For prey items, our meta-analysis showed quite some variability. As their stable isotope values are used as sources to calculate mangrove food contribution to the fishes' diets, spatio-temporal and individual variability in prey signatures could thus affect the patterns observed for their fish consumers. Even though variability in the prey signature was observed, the signatures of prey items collected from mangrove and adjacent habitats showed a very good separation even when studies from across the globe (done in different seasons, at different locations, on different prey species, and so on) were combined. Furthermore, the degree of fractionation may differ between species, but differences in stable carbon signatures of prey items from mangrove and adjacent habitats were much larger (2–4.5‰ on average) than the typical degree of fractionation for carbon (0–1‰). Therefore, the overall conclusion related to degree of fish reliance on mangrove food items is unlikely to change due to variability in prey signatures. Hence, most individual fish caught in the mangroves seemed to be nutritionally dependent predominantly on food items from the sand/seagrass beds indicating strong energetic linkages between neighboring coastal marine ecosystems, resulting from regular tidal and feeding migrations.

The literature shows different outcomes with respect to the importance of mangroves as fish feeding habitats, which may have partly resulted from differences in the species studied, tidal regime, geographic location, methodology, and spatio-temporal variability in fish community structure as well as stable isotope tissue signatures. This may significantly alter our ability to detect important spatial subsidies; for example, discrete, seasonally-driven recruitment events that link ecosystems could be missed by the typical small-scale fish sampling regimes. The present study collected data at multiple levels, from different species and locations around the world, from different types of mangrove habitat with different tidal regimes, and based on sampling done in different years. There was clearly some variability visible in our meta-analysis, which was probably attributed to the above factors. Nevertheless, the overall patterns at multiple levels of study were consistent and led to the same conclusions. However, the results also warrant that individual studies may provide very different conclusions, due to variability caused by the above-mentioned factors. Our mixing models using data from our study sites in Tanzania and Indonesia and from the literature showed average values for mangrove food dependence that ranged between 12 and 72% across studies (species pooled) and between 0 and 100% across individual fish species, underpinning how multiple abiotic and biological factors can affect, and have previously affected, conclusions related to this concept. From our overarching analyses, it can be deduced that biogeography had a relatively small effect, whereas tidal regime and species identity had a larger effect. The higher reliance on mangrove food items observed for some fish species seems to be partly related to their feeding ecology. For example, a reasonably high reliance was found for the top predator *Sphyraena barracuda* which is known to shelter in mangrove roots to ambush prey fish (Verweij and others 2006a). Fish species that forage on the sea bottom or by scooping up sediment and sieve out the associated macroinvertebrates (for example, *Gerres*; Blaber 2000) likely have more surface area available for foraging on the typically vegetation-poor substratum under the dark mangrove canopy as opposed to seagrass beds in which dense vegetation may obstruct bottom feeding. Finally, herbivores (for example, *Siganus sutor*) and epiphyte consumers (*Monodactylus argenteus*) can forage on the filamentous algae and macroalgae growing on mangrove prop-roots (Blaber 2000; Verweij and others 2006a) and may therefore show a higher reliance on mangrove food items than species belonging to other feeding guilds. Although most of the fish species caught in mangroves showed δ^{13}C tissue signatures that were similar to those caught from the adjacent sand/seagrass beds, some mangrove-caught species did show partly depleted δ^{13}C tissue values, suggesting that their main source of food originates from the seagrass beds but that they feed opportunistically on mangrove prey items when they occupy this habitat at high tide. Importantly, even in the cases (Semama, Pajang) in which no dense seagrass vegetation was present that could provide shelter while foraging there, fishes did not seem to feed significantly in the adjacent mangroves that provided protection from predation. The fact that for very few fish species a difference in tissue or stomach content δ^{13}C was found between individuals caught from seagrass beds and mangroves suggests that there are single assemblages of fishes within species that perform regular migrations and support flow of energy between mangrove and seagrass ecosystems.

The degree of mangrove inundation had a significant effect on the reliance of fish on mangrove food items. Averaged across studies, the degree of mangrove food reliance was quite similar for fish species caught from permanently inundated versus drained mangrove forests, but when separated at the species level the difference became evident, showing more fish species with depleted δ^{13}C signatures or with high mangrove food reliance in the former than in the latter. Inundation type and tidal amplitude have previously been suggested to regulate the extent to which fishes utilize mangrove habitats (Fry and Ewel 2003), whereas the duration of access to the mangrove habitat has been shown to play a role in mangrove resource utilization by fishes and decapods (Fry and Ewel 2003; Lugendo and others 2007). Our results further indicated that out of 12 fish species that showed high (≥75%) mangrove reliance nine were associated with permanently inundated mangroves (Table 2). However, this does not explain why many other fish species also move into mangroves at high tide, and this may be driven by processes other than food acquisition.

Different hypotheses have been put forward to explain why aquatic animals migrate into mangroves at high tide, including seeking shelter from predators (Haywood and Kenyon 2009). The refuge hypothesis is based on the presence of structural complexity created by the mangrove prop-roots (Nagelkerken and Faunce 2007, 2008) and a turbid environment (Blaber 2000; Chong, 2007; Nagelkerken and others 2010) that reduce predation risk. Although most studies have shown higher fish densities in mangroves than adjacent seagrass beds (Figure 1C), mangrove occupancy does not appear to considerably enhance growth rates of fishes and they seem to harbor equal or lower densities of food items like macroinvertebrates or zooplankton compared to seagrass beds (Kitheka and others 1996; Grol and others 2008; Kimirei and others 2013). It is therefore more likely that the perceived or realized safety of the dark, structure-rich mangrove root habitat is the immediate driver for fish to show an attraction towards mangrove root-habitats (Huijbers and others 2011), in particular when the refuge value of adjacent seagrass beds is reduced during high tide when higher water levels allow predator intrusion (Sheaves 2005) or is reduced during daytime when fish are easier to detect by visual predators (Nagelkerken and van der Velde 2004b).

The overall results of the current study have important implications for management and conservation of coastal marine and estuarine habitats and their fish communities. More than 50% of the world's mangroves have already been lost and they continue to disappear at a rate of 1–2% per year (Duke and others 2007). Fragmentation of mangrove and seagrass habitats due to coastal development (for example, mangrove clearing, construction of dams and causeways, dredging of navigation channels) may disrupt the strong ecological linkages between mangrove and seagrass ecosystems (Layman and others 2007). Loss of (vegetated) migration corridors due to human impacts could lead to higher mortality rates in seagrass beds due to fishes being obstructed to safely retreat into nearby mangrove areas at high tide. Moreover, studies have shown that cross-ecosystem transfer of nutrients by fishes that feed in one habitat and then release nutrients through defecation in their shelter habitats enhances benthic productivity or even the presence of vegetation in the recipient habitat (Meyer and Schultz 1985; Granek and others 2009; Layman and others 2012). Mangroves have typically been highlighted and protected based on their perceived nursery role for (commercial) shrimp and fish. While strong correlations have been found globally between offshore stock sizes of fish and crustaceans and the mangrove habitat presence (Aburto-Oropeza and others 2008), the present study suggests that it is the habitats that are located adjacent to mangrove fringes which energetically sustain this productivity in many cases. It is clear from the current study that management and conservation of coastal ecosystems should not be based solely on identifying the ecosystems or habitats which harbor highest animal densities or show highest secondary productivity, but should identify the suite of ecological factors that support such production, in particular the energetic linkages among ecosystems that arise from, and form a critical part of, the complex life histories of many coastal fish populations.

CONCLUSIONS

Our study suggests that mangrove food items may only contribute little to the overall diet of fishes from interlinked mangroves-seagrass ecosystems. At all levels studied—individual fish, species and community levels across the globe—similar patterns of low dietary reliance on mangrove-associated prey were generally observed. Inundation type had a noticeable effect on the degree of mangrove reliance. The results strongly suggest that mangrove root systems act mainly as refuge areas instead of critical feeding grounds for the majority of fish species studied so far. The ongoing, rapid loss and fragmentation of mangrove and seagrass habitats and loss of cross-ecosystem connectivity are likely to have strong effects on the productivity and ecosystem services provided by such coastal marine habitats. With many fish species moving across ecosystem borders, conservation efforts should be geared towards protecting habitat mosaics rather than individual habitats or ecosystems.

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