

Trophic relationships in an interlinked mangrove-seagrass ecosystem as traced by $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$

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ABSTRACT: The food web structure of a mangrove forest and adjacent seagrass beds in Gazi Bay, Kenya, was examined with stable carbon and nitrogen isotope ratio techniques. A carbon isotopic ratio gradient was found from mangroves with mean (\pm SD) $\delta^{13}\text{C}$ value of $-26.75 \pm 1.64\text{‰}$ to seagrass beds with $-16.23 \pm 4.35\text{‰}$. Seagrasses close to the mangroves were more depleted in ^{13}C than seagrasses close to the major coral reef. Macroinvertebrates collected along this mangrove seagrass bed transect showed a similar $\delta^{13}\text{C}$ gradient. Fishes collected near the mangroves were depleted in ^{13}C compared to fishes collected in the seagrass meadows. The fish community was differentiated on the basis of its carbon isotopic ratios and the site where individuals were collected. Three groups were identified: (1) species occurring in seagrass meadows in the close vicinity of the mangrove swamps; (2) species migrating between mangroves and the seagrass meadows, together with species occurring throughout the entire seagrass area, from close to the mangroves to the outer bay; and (3) species that use the seagrass meadows proper as a lifetime habitat. The results show that seagrass stands are the main feeding grounds providing food for all fish species studied. $\delta^{15}\text{N}$ signatures allowed to the identification of the following trophic levels: (1) fish species feeding on seagrasses and macroalgae (herbivores); (2) fish feeding on zoo/benthos-plankton (zoobenthoplanktivores); and (3) other fish and/or macro-crustacea (piscivores/benthivores). A ^{15}N isotope enrichment of $<2\text{‰}$ was found between successive trophic levels suggesting significant omnivory.

KEY WORDS: $\delta^{13}\text{C}$ · $\delta^{15}\text{N}$ · Mangroves · Seagrasses · Fishes · Trophic relationships

INTRODUCTION

Measurements of natural $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$ isotopic ratios provide a powerful tool in determining respectively sources of nutrition for consumers and trophic relationships among organisms and have often been used in the study of marine food webs (e.g. Hobson & Welch 1992, Rau et al. 1992, Newell et al. 1995). Stable carbon and nitrogen isotopic ratios in animals are largely determined by those of their diet (Fry & Sherr 1984). As a consequence of isotopically selective excretion or respiration of the lighter isotopes, heavy isotope enrichment can occur over a trophic gradient.

However, for ^{13}C , this enrichment is small and the $^{13}\text{C}/^{12}\text{C}$ ratio of an animal reflects the $^{13}\text{C}/^{12}\text{C}$ of its diet (0 to 1‰ increase of $\delta^{13}\text{C}$ per trophic level; Fry & Sherr 1984). Thus, $\delta^{13}\text{C}$ measurements primarily indicate the main sources of carbon to consumers. On the other hand, enrichment of ^{15}N in consumers relative to food is larger than for ^{13}C , thus $\delta^{15}\text{N}$ values rather inform on trophic distance of consumers from the foodbase (Minagawa & Wada 1984). The simultaneous use of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values therefore allows the elucidation of trophic relationships in food webs.

Hemminga et al. (1994) and Rao et al. (1994) reported a non-overlapping $\delta^{13}\text{C}$ signal range for mangrove leaves and seagrasses in Gazi Bay, Kenya. Furthermore, Hemminga et al. (1994) reported a $\delta^{13}\text{C}$ gradient in the seagrass *Thalassodendron ciliatum*

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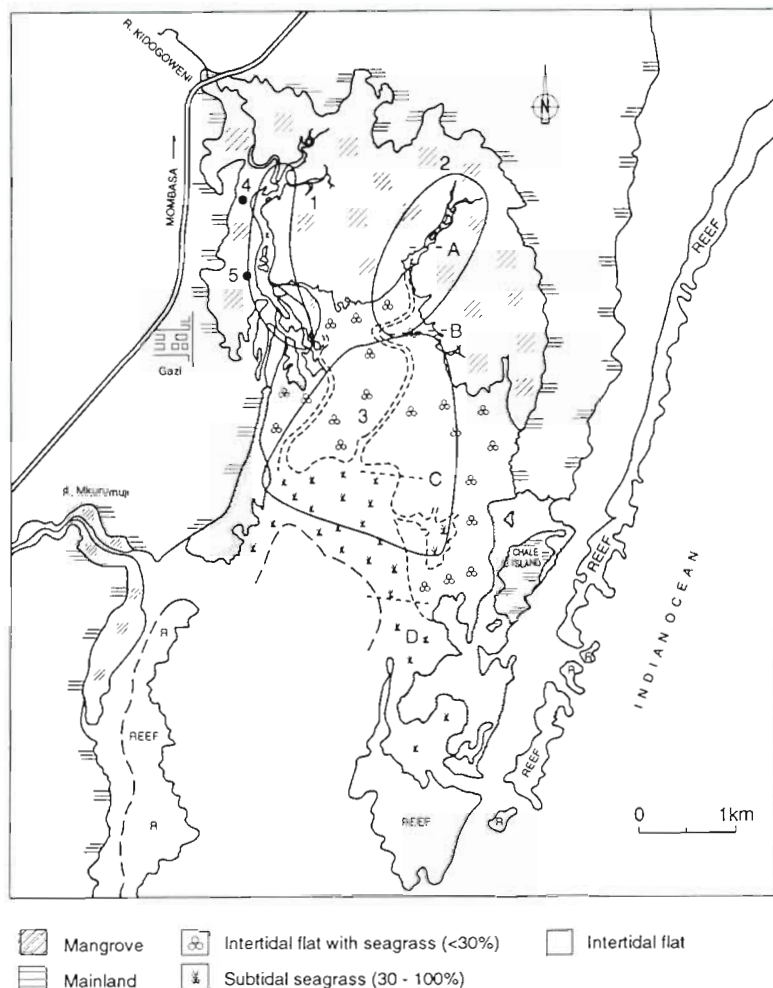


Fig. 1. Map of Gazi Bay, Kenya. 1: western creek; 2: eastern creek; 3: seagrass meadows; 4: sampling site in the *Ceriops tagal* mangrove stand; 5: oyster nursery; A, B, C and D: sampling sites in the seagrass meadows of zones 2 and 3

from the mangroves towards the coral reef. The first objective of the work reported here was to determine if a similar $\delta^{13}\text{C}$ gradient is present in the higher trophic levels, allowing the determination of the feeding sites of the fishes. The second objective was to reveal the trophic relations between the fish of Gazi Bay.

STUDY AREA AND METHODS

Study area. The study was carried out in Gazi Bay, south of Mombasa, Kenya ($4^{\circ}25'S$, $39^{\circ}30'E$) (Fig. 1). Gazi Bay is characterised by a zonation of mangrove forest, seagrass meadows and coral reef. There are 2 major tidal creeks with seagrasses penetrating the mangrove forest. The western creek is the mouth of the

river Kidogoweni, a seasonal river, while the eastern creek (Kinondo creek) is a small tidal creek (Slim & Gwada 1993). The vegetation in these creeks is described by van Avesaath et al. (1993), van der Velde et al. (1995) and Slim et al. (1997).

Sampling. Samples for isotopic analysis were collected during the Coastal Research Programme of the Netherlands Indian Ocean Programme (1990 to 1995) and the European Community (EC) STD-3 project on 'Interlinkages between Eastern-African coastal ecosystems' (1992 to 1995). Mangrove leaves of 8 species occurring in Gazi Bay were collected from zones 1, 2 and 4 (Fig. 1) and the samples were pooled for each species. These species were: *Rhizophora mucronata*, *Ceriops tagal*, *Sonneratia alba*, *Avicennia marina*, *Bruguiera gymnorhiza*, *Xylocarpus granatum*, *Lumnitzera racemosa* and *Heritiera littoralis*. Fresh leaves of the same physiological age were collected by choosing the second one from the terminal bud. The leaves were dried at 80°C for 5 h. Further details on sampling were provided by Rao et al. (1994). *Thalassodendron ciliatum* is the dominant seagrass of the subtidal area (Coppejans et al. 1992) and leaves were taken at 4 different distances from the mangroves towards the coral reef (Fig. 1). The pooled seagrass samples were dried at 60°C . Four species of molluscs, 2 species of macrocrustaceans and 12 of the most abundant fish species were caught in the eastern and

western creeks and in the seagrass meadows. For the invertebrates (molluscs and crustaceans), at least 5 whole individuals were pooled. In the case of fishes, muscle tissues were carefully excised from each specimen with a clean scalpel. Only muscle tissue was used because its slow turnover rate results in integrating diet effects over months, and thus allows the exclusion of short-term variability effects (Gearing 1991). In each analysis, dried samples were pretreated with 20% HCl for removing carbonates since carbonates are known to interfere with C signatures. Dry animal tissue and leaf tissue were ground to a fine powder using a mortar, pestle and liquid nitrogen.

Isotopic analysis. Mass spectrometric measurements were performed using a Delta E, Finnigan Mat isotope ratio mass spectrometer. For carbon isotopic ratios, the organic material was combusted in an Elemental

Analyser (Carlo Erba NA1500). The CO₂ generated during the combustion was automatically trapped in an on-line Finnigan Mat trapping box for cryopurification before injection into the mass spectrometer. For the nitrogen isotopic ratios, the N₂ gas produced during combustion was cryogenically trapped in stainless steel tubes filled with a molecular sieve, and samples were manually introduced into the mass spectrometer. A graphite reference material (USG-24) was used as a standard for carbon isotopic ratio measurements. Values are expressed relative to the VPDB (Vienna Pee Dee Belemnite) standard (Coplen 1996). High purity tank nitrogen gas was used as a working standard for the nitrogen isotope ratio measurements. This working standard was calibrated against N1 and N2 ammonium sulphate (IAEA, Vienna). δ¹⁵N values are reported relative to nitrogen in air. Stable carbon and nitrogen isotopic ratios are presented as δ values:

$$\delta R = [(X_{\text{sample}} - X_{\text{standard}}) / X_{\text{standard}}] \times 10^3$$

(‰)

where R = ¹³C or ¹⁵N and X = ¹³C/¹²C or ¹⁵N/¹⁴N.

Reproducibility for the analysis of different aliquots of the same tissue sample was generally better than 0.2‰ for both isotopes. δ¹⁵N analysis was duplicated for pooled samples of molluscs, crustaceans and fishes (*Parascorpaena mossambica*, *Paramonacanthus barnardi* and juvenile *Siganus sutor*). The standard deviations varied from 0.08 (*Terebralia palustris*) to 0.22 (Cypraeidae) for molluscs, 0.46 (*Metopograpsus thukuhar*) to 0.62 (*Uca lactea*) for crustaceans, and 0.06 (*P. barnardi*) to 0.11 (*P. mossambica*) for fishes.

RESULTS

Flora

The most important primary producers were the mangrove trees and the seagrasses. The mangrove leaves had a signal range between -24.28 and -29.71‰, typical for C₃ plants (Table 1). The carbon isotopic ratios for the seagrasses were observed to

Table 1. Stable carbon and nitrogen isotopic ratios for samples collected in the mangrove ecosystem of Gazi Bay, Kenya. Number of individuals in parentheses. The values for the mangrove and seagrass leaves were obtained from pooled samples of more than 10 leaves

Species	Sampling site ^a	δ ¹³ C (‰)	SD	δ ¹⁵ N (‰)	SD
Mangrove leaves					
<i>Avicennia marina</i> (fringing)		-29.71 ^b		+1.63	
<i>Heritiera littoralis</i>		-28.78 ^b		+0.76	
<i>Lumnitzera racemosa</i>		-27.17 ^b		+0.57	
<i>Avicennia marina</i>		-26.62 ^b		+2.18	
<i>Sonneratia alba</i>		-26.50 ^b		+1.66	
<i>Rhizophora mucronata</i>		-26.09 ^b		+1.25	
<i>Xylocarpus granatum</i>		-25.87 ^b		+0.15	
<i>Bruguiera gymnorrhiza</i>		-25.77 ^b		+0.86	
<i>Ceriops tagal</i>		-24.28 ^b		+0.89	
Seagrass leaves					
<i>Thalassodendron ciliatum</i>					
from Site A		-19.82		+1.60	
B		-18.67		+0.82	
C		-16.34		+0.81	
D		-10.07		+2.81	
Fishes					
<i>Siganus sutor</i> (juvenile) (5) ^c	1 & 2	-21.20		+3.52	
<i>Valamugil seheli</i> (6)	1 & 3	-19.31	0.56	+5.88	0.15
<i>Sphaeramia orbicularis</i> (9)	3	-18.85	2.58	+8.55	0.54
<i>Siganus sutor</i> (24)	1, 2 & 3	-17.28	2.26	+7.90	0.91
<i>Tylosurus crocodilus</i> (2)	1, 2 & 3	-16.50	0.06	+11.36	0.03
<i>Conger cinereus</i> (13)	3	-16.11	3.63	+9.77	0.51
<i>Sphyraena barracuda</i> (10)	1, 2 & 3	-15.95	2.35	+11.05	0.84
<i>Paramonacanthus barnardi</i> (5) ^f	1	-14.46		+6.60	
<i>Plotosus lineatus</i> (11)	1 & 3	-14.22	0.50	+10.30	0.49
<i>Lutjanus fulviflamma</i> (24)	1, 2 & 3	-14.17	1.79	+10.04	0.62
<i>Cheilo inermis</i> (21)	3	-14.05	0.77	+9.10	0.64
<i>Parascorpaena mossambica</i> (5) ^c	3	-13.91		+6.29	
<i>Leptoscarus vaigiensis</i> (46)	1 & 2	-12.80	3.02	+6.62	0.74

^aSee Fig. 1 for abbreviations. Most dominant foraging groups in bold
^bData from Rao et al. (1994)
^cPooled sample

range from -10.02 to -19.82‰. The more negative values were observed for seagrass leaves from sites close to the mangrove forest, while seagrass leaves in the vicinity of the coral reef had the least negative values. The mean δ¹⁵N values for the mangrove leaves and seagrasses were +1.11 and +1.51‰, respectively (Table 1).

Molluscs and crustaceans

The gastropods *Terebralia palustris* and *Cerithidea decollata* and the crabs *Uca lactea* and *Metopograpsus thukuhar* were collected in the *Ceriops tagal* stands (Fig. 1). *T. palustris* exhibited a more negative δ¹³C value (-24.23‰) than the other 3 species (-20.64, -18.96 and -19.83‰, respectively; Fig. 2).

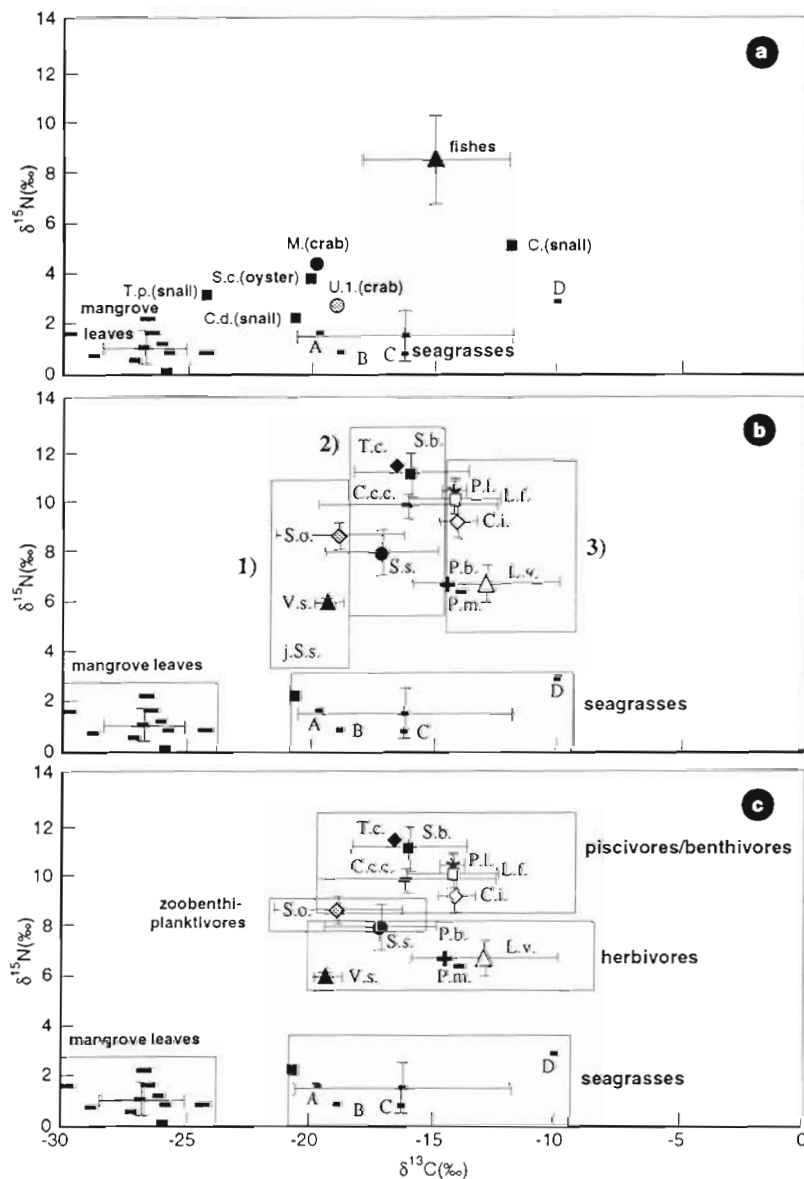


Fig. 2. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of different mangroves, seagrasses, molluscs, crustaceans and fish species. Mangrove leaves (leaves of 8 different species); seagrasses (*Thalassodendron ciliatum* from sites A, B, C and D); molluscs (T.p. = *Terebralia palustris*, C.s. = *Cerithidea decollata*, S.c. = *Saccostrea cucullata*, C. = *Cypraeidae*); crabs (U.l. = *Uca lactea*, M. = *Metopograpsus thukuhar*); 12 fish species [total length in cm] (T.c. = *Tylosurus crocodilus* [30.2], S.b. = *Sphyræna barracuda* [12 to 32], P.l. = *Plotosus lineatus* [8 to 20.5], C.c.c. = *Conger cinereus* [51 to 76.5], L.f. = *Lutjanus fulviflamma* [7.9 to 24.5], C.i. = *Chelodactylus inermis* [10.6 to 21.6], S.o. = *Sphaeramia orbicularis* [5 to 11], S.s. = *Siganus sutor* [8.4 to 25.7], j.S.s. = juvenile *S. sutor* [6], L.v. = *Leptoscarus vaigiensis* [5 to 24.7], V.s. = *Valamugil seheli* [14.7 to 16], P. = *Paramonacanthus barnardi* [8 to 10], P.m. = *Parascorpaena mossambica* [7 to 11]). (a) Differentiation of isotopic signatures of plants and between producers and consumers. (b) Differentiation of fish species on the basis of foraging site and $\delta^{13}\text{C}$: (1) Fish species occurring in seagrass meadows in the close vicinity of the mangrove swamps; (2) fish species migrating between mangroves and seagrass meadows, together with species occurring throughout the entire seagrass covered area from close to the mangroves to the coral reef; and (3) fish species that use the seagrass meadows proper as a lifetime habitat. (c) Differentiation of fish species on the basis of feeding habitats and $\delta^{15}\text{N}$. Error bars on the figures represent ± 2 SD

The oyster *Saccostrea cucullata* was collected from an oyster nursery located in the western creek and had a $\delta^{13}\text{C}$ value of -20.08‰ . The gastropods (*Cypraeidae*) collected in the seagrasses near sites C and D (see Fig. 1) had a $\delta^{13}\text{C}$ value of -11.88‰ (Fig. 2).

The $\delta^{15}\text{N}$ values of the molluscs and crabs ranged from $+2.20\text{‰}$ (*Cerithidea decollata*) to $+5.08\text{‰}$ (*Cypraeidae*) (Fig. 2).

Fishes

The $\delta^{13}\text{C}$ values for the fishes collected in Gazi Bay ranged from -22.20‰ (*Conger cinereus*) to -9.35‰ (*Leptoscarus vaigiensis*), and $\delta^{15}\text{N}$ values ranged from $+5.32\text{‰}$ (*L. vaigiensis*) to $+12.16\text{‰}$ (*Sphyræna barracuda*) (Table 1).

DISCUSSION

Flora

Hemminga et al. (1994) and Rao et al. (1994) reported that mangrove leaves and seagrasses in Gazi Bay do not overlap in their $\delta^{13}\text{C}$ signal, and have average (\pm SD) values of -26.75 ± 1.64 and $-16.23 \pm 4.35\text{‰}$, respectively. The seagrasses exhibit a very large range in their $\delta^{13}\text{C}$ values (Fig. 2), an observation also reported by others (McMillan et al. 1980, Fry & Sherr 1984, Lin et al. 1991, Hemminga & Mateo 1996). The $\delta^{13}\text{C}$ values for most seagrasses are within the range usually associated with C_4 metabolism (Hatch-Slack cycle) (Fry & Sherr 1984). However, it has been observed that carboxylation in seagrasses occurs through the C_3 rather than the C_4 pathway (Benedict et al. 1980). Aquatic plants use the dissolved inorganic carbon (DIC) pool during photosynthesis and therefore the $\delta^{13}\text{C}$ value of these aquatic plants is affected by the isotopic composition of the DIC pool. The $\delta^{13}\text{C}$ signal of DIC set by the CO_2 air-sea exchange processes also

depends on the production of respiratory CO₂ during decomposition of plant material such as mangrove detritus. During decomposition, mangrove leaves or mangrove-derived material show little change in the δ¹³C signal (Zieman et al. 1984). Since the δ¹³C signal of the mangroves is very negative (close to -27‰), mineralisation of mangrove detritus induces a shift in δ¹³C of DIC to more negative values (Mook & Tan 1991). This process may explain the more negative δ¹³C values (-19.82‰) for seagrasses near the mangroves and the less negative δ¹³C values (-10.09‰) for seagrasses near the coral reef, as discussed by Hemminga et al. (1994). The observed δ¹⁵N values for the mangrove leaves and seagrasses are 2‰ lower than those reported by Zieman et al. (1984) and Newell et al. (1995).

Molluscs and crustaceans

The herbivorous gastropod *Terebralia palustris*, collected in the *Cerriops tagal* stands (sampling station 4, Fig. 1), had a δ¹³C signal of -24.23‰, which is close to that of the *C. tagal* leaves (-24.28‰), indicating that leaves of this species are the main carbon source for the gastropod (Fig. 2a). This agrees well with field observations of *T. palustris* feeding behaviour (Slim et al. 1997). In contrast, the gastropod *Cerithidea decollata* and the crabs *Uca lactea* and *Metopograpsus thukuhar*, which occur also in the *C. tagal* stands, have tissue δ¹³C values showing enrichment in ¹³C (Fig. 2a). Inundation of the stands during spring tides imports carbon from the seagrass meadows (Hemminga et al. 1994, Slim et al. 1996). A possible explanation for the observed less negative δ¹³C signal for *C. decollata*, *U. lactea* and *M. thukuhar* is that they feed on a mixture of inwelled seagrass and local mangrove detritus. The oyster *Saccostrea cucullata* was collected from sampling station 5 and has a δ¹³C signature of -20.08‰ (Fig. 2a). Kazungu (1996) reported a δ¹³C value of particulate organic matter (POM) at station 5 of -21.39‰ at high tide when the oyster nursery is inundated. This δ¹³C value, and the fact that the C/N atom ratio of POM was very low (8.14) relative to the mangroves and seagrasses, suggests that phytoplankton contributed significantly to POM composition and the oyster diet. The cypraeid snails were collected between sampling sites C and D and had a δ¹³C signature (-11.88‰) close to the one of the local seagrass leaves (Fig. 2a). Kazungu (1966) reported a mean δ¹³C value of POM at site D of -18.39‰, which indicates that the main carbon source for the cypraeid snails is not derived from POM, and must originate from local seagrasses and seagrass derived material.

Fishes δ¹³C

Valamugil seheli and *Sphaeramia orbicularis*, with average δ¹³C values of -19.31 and -18.85‰, respectively (Fig. 2b), were most abundant in the mangrove creeks. Mwamsojo (1994) reported that *S. orbicularis* is restricted to the mangrove area and that it is a true resident of mangrove creeks. Individuals of this species were collected at the edge of the mangrove creeks, close to the seagrasses. δ¹³C values of muscle tissue of *S. orbicularis* suggest this species also consumes carbon from outside the mangroves, i.e. from the nearby seagrasses. We believe that *S. orbicularis* looks for shelter between the roots of the mangrove trees but feeds outside or near the edge of the mangroves. Individuals of *Leptoscarus vaigiensis* and *Siganus sutor* were found over the entire seagrass area and this was confirmed by their wide δ¹³C range: -21.26 to -9.35‰ for *L. vaigiensis* and -21.58 to -14.36‰ for *S. sutor* (Fig. 2b). Juvenile *S. sutor* had a δ¹³C value of -21.2‰, suggesting mangrove derived material was the basis of its diet. *Cheilo inermis*, *Plotosus lineatus* and *Lutjanus fulviflamma* were most abundant in the outer bay seagrass zone (seagrass δ¹³C between -16.34 and -10.07‰) and had a mean carbon isotopic signature of -14.05, -14.22, and -14.17‰, respectively, similar to that of the local seagrasses. This indicates a strong dependency on seagrass material via seagrass-supported trophic intermediates. The carnivorous species *Sphyraena barracuda* and *Conger cinereus* were collected in the mangrove creeks, but had average δ¹³C signals of -15.95 and -16.11‰, respectively. These values fall within the range observed for seagrasses. Observations indicate that these fishes migrate between the seagrasses and the mangroves but feed on fish and/or macrocrustacea located in the seagrasses.

The fish community was differentiated into subgroups on the basis of carbon isotopic composition and collection site of individuals. Three different groups were distinguished: (1) species occurring in seagrass meadows in the close vicinity of mangrove swamps and showing the largest depletions (lowest δ¹³C values) (*Valamugil seheli* and *Sphaeramia orbicularis*); (2) species migrating between mangroves and the seagrass meadows, together with species occurring throughout the entire seagrass-covered area from close to the mangroves to the coral reef, showing intermediate δ¹³C values (*Sphyraena barracuda*, *Tylosurus crocodilus*, *Conger cinereus* and *Siganus sutor*); and (3) species that use the seagrass meadows as a lifetime habitat and show the least negative δ¹³C values (*Plotosus lineatus*, *Lutjanus fulviflamma*, *Cheilo inermis*, *Leptoscarus vaigiensis*, *Paramonacanthus barnardi* and *Parascorpaena mossambica*) (Fig. 2b).

Fishes $\delta^{15}\text{N}$

A rough distinction in the feeding patterns of the fish species was made based on literature data (Smith & Heemstra 1986). Three feeding guilds were distinguished: (1) species feeding on mainly or partly on seagrasses and macroalgae (herbivores) (*Valamugil seheli*, *Leptoscarus vaigiensis*, *Paramonacanthus barnardi* and *Siganus sutor*); (2) species feeding on zoo/benthos-plankton: (zoobenthoplanktivores) (*Sphaeramia orbicularis*); and (3) species feeding on other fish and/or macro-crustacea (piscivores/benthivores) (*Sphyraena barracuda*, *Tylosurus crocodilus*, *Conger cinereus*, *Plotosus lineatus*, *Lutjanus fulviflamma* and *Cheilo inermis*). *Parascorpaena mossambica* showed a remarkably low $\delta^{15}\text{N}$ value, indicating that this predator may feed on e.g. macroinvertebrates that feed on seagrass detritus.

These groups were also differentiated on the basis of their $\delta^{15}\text{N}$ signature. The first group had a range of mean $\delta^{15}\text{N}$ values from +5.88‰ (*Valamugil seheli*) to +6.62‰ (*Leptoscarus vaigiensis*) (Fig. 2c). However, *Siganus sutor*, also a herbivorous fish, showed more enriched values (+7.90‰) than the former species. Together with its negative $\delta^{13}\text{C}$ values, this observation suggests that not all *S. sutor* are herbivorous, but that some individuals are also omnivorous.

Sphaeramia orbicularis had a mean $\delta^{15}\text{N}$ of +8.55‰. Mwamsojo (1994) reported that the gut content of this species consisted of epibenthic and hyperbenthic crustaceans and a few molluscs. Taking into account literature data (Smith & Heemstra 1986), this species can therefore be classified as zoobenthoplanktivorous.

Plotosus lineatus, *Conger cinereus*, *Lutjanus fulviflamma* and *Cheilo inermis*, which are classified as zoobenthivores and piscivores (Smith & Heemstra 1986), had a range of mean $\delta^{15}\text{N}$ values from +9.10‰ (*Cheilo inermis*) to +10.30‰ (*Plotosus lineatus*).

Sphyraena barracuda and *Tylosurus crocodilus* were the top predators observed in this study, and their $\delta^{15}\text{N}$ values were the highest, reaching +11.05 and +11.36‰, respectively.

For all fishes taken together, the $\delta^{15}\text{N}$ signature ranged from +5.32‰ (for a *Leptoscarus vaigiensis*) to +12.16‰ (for a *Sphyraena barracuda*), showing about a 2‰ increase per trophic level (Fig. 2c). Cabana & Rasmussen (1994) reported that $\delta^{15}\text{N}$, as a tracer of trophic position, reflects variations in the underlying food web structure, rather than variable fractionation along the food chain. According to them, an average increase between trophic pairs in a food chain smaller than +3.4‰, which is the $\delta^{15}\text{N}$ change per trophic level as reported by Minagawa & Wada (1984), may indicate significant levels of omnivory in these food webs. In the present study, the overlaps in the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$

ratios of the various groups and an enrichment in $\delta^{15}\text{N}$ smaller than 2‰ suggests a high contribution by omnivory.

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LITERATURE CITED

- Benedict CR, Wong WWL, Wong JHH (1980) Fractionation of the stable isotopes of inorganic carbon by seagrasses. *Plant Physiol* 65:512–517
- Cabana G, Rasmussen JB (1994) Modelling food chain structure and contaminant bioaccumulation using stable nitrogen isotopes. *Nature* 372:255–257
- Coplen TB (1996) New guidelines for reporting stable hydrogen, carbon and oxygen isotope-ratio data. *Geochim Cosmochim Acta* 60:3359–3360
- Coppejans E, Beeckman H, De Wit M (1992) The seagrass and associated macroalgal vegetation of Gazi Bay (Kenya). *Hydrobiologia* 247:59–75
- Fry BM, Sherr EB (1984) $\delta^{13}\text{C}$ measurements as indicators of carbon flow in marine and freshwater ecosystems. *Cont Mar Sci* 27:13–47
- Gearing JN (1991) The study of diet and trophic relationships through natural abundance ^{13}C . In: Coleman DC, Fry B (eds) Carbon isotope techniques. Academic Press, London, p 201–218
- Hemminga MA, Mateo MA (1996) Stable carbon isotopes in seagrasses: variability in ratios and use in ecological studies. *Mar Ecol Prog Ser* 140:285–298
- Hemminga MA, Slim FJ, Kazungu J, Ganssen GM, Nieuwenhuize J, Kruyt NM (1994) Carbon outwelling from a mangrove forest with adjacent seagrass beds and coral reefs (Gazi Bay, Kenya). *Mar Ecol Prog Ser* 106:291–301
- Hobson KA, Welch HE (1992) Determination of trophic relationships within a high Arctic marine food web using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis. *Mar Ecol Prog Ser* 84:9–18
- Kazungu JM (1996) Nitrogen transformational processes in a tropical mangrove ecosystem (Gazi Bay, Kenya). PhD thesis, Free University of Brussels
- Lin G, Banks T, Da Silva Lobo O'Reilly Sternberg L (1991) Variation in $\delta^{13}\text{C}$ values for the seagrass *Thalassia testudinum* and its relations to mangrove carbon. *Aquat Bot* 40:333–341
- McMillan C, Parker PL, Fry B (1980) $^{13}\text{C}/^{12}\text{C}$ ratios in seagrasses. *Aquat Bot* 9:237–249
- Minagawa M, Wada E (1984) Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between $\delta^{15}\text{N}$ and animal age. *Geochim Cosmochim Acta* 48:1135–1140
- Mook WG, Tan FC (1991) Stable carbon isotopes in rivers and estuaries. In: Degens ET, Kempe S, Richey JE (eds) Biochemistry of major world rivers. John Wiley & Sons, Chichester, p 245–264
- Mwamsojo GUJ (1994) The feeding ecology of the chubby cardinalfish *Sphaeramia orbicularis* (Pisces: Apogonidae)

- in a tropical mangrove creek. MSc thesis, Free University of Brussels
- Newell RI, Marshall N, Sasekumar A, Chong V (1995) Relative importance of benthic microalgae, phytoplankton, and mangroves as sources of nutrition for penaeid prawns and other coastal invertebrates from Malaysia. *Mar Biol* 123:595–606
- Rao RG, Woitchik AF, Goeyens L, Van Riet A, Kazungu J, Dehairs F (1994) Carbon, nitrogen contents and stable carbon isotope abundance in mangrove leaves from an East African coastal lagoon (Kenya). *Aquat Bot* 47:175–183
- Rau GH, Ainley DG, Bengtson JL, Torres JJ, Hopkins TL (1992) $^{15}\text{N}/^{14}\text{N}$ and $^{13}\text{C}/^{12}\text{C}$ in Weddell Sea birds, seals, and fish: implications for diet and trophic structure. *Mar Ecol Prog Ser* 84:1–8
- Slim FJ, Gwada P (1993) The mangrove vegetation. In: Woitchik AF (ed) Dynamics and assessment of Kenyan mangrove ecosystems. EC STD-3 Programme final report no. TS 2-0240-C, Free University of Brussels, p 6–35
- Slim FJ, Hemminga MA, Cocheret de la Morinière E, van der Velde G (1996) Tidal exchange of macrolitter between a mangrove forest and adjacent beds (Gazi Bay, Kenya). *Neth J Aquat Ecol* 30:119–128
- Slim FJ, Hemminga MA, Ochieng C, Jannink N, Cocheret de la Morinière E, van der Velde G (1997) Leaf litter removal by the snail *Terebralia palustris* (Linnaeus) and sesarmid crabs in an East African mangrove forest (Gazi Bay, Kenya). *J Exp Mar Biol Ecol* (in press)
- Smith MM, Heemstra PC (1986) *Smiths' sea fishes*. Springer-Verlag, Berlin
- van Avesaath PH, van der Velde G, Coppejans E (1993) The submerged vegetation of the tidal creeks. 1. Seagrasses and macro-algae of eastern and western creeks. In: Woitchik AF (ed) Dynamics and assessment of Kenyan mangrove ecosystems. EC STD-3 Programme final report no. TS 2-0240-C, Free University of Brussels, p 35–62
- van der Velde G, Dehairs F, Marguillier S, Mwatha GK, Op't Veld RLJM, Rajagopal S, van Avesaath PH (1995) Fish fauna of mangrove creeks, seagrass meadows and sand flats in Gazi Bay: a study with nets and stable isotopes. In: Hemminga MA (ed) Interlinkages between Eastern-African coastal ecosystems. Report no. TS-CT92-0114, Netherlands Institute of Ecology, Yerseke, p 132–157
- Zieman JC, Macko SA, Mills AL (1984) Role of seagrasses and mangroves in estuarine food webs: temporal and spatial changes in stable isotope composition and amino acid content during decomposition. *Bull Mar Sci* 35:380–392

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