

Relative importance of interlinked mangroves and seagrass beds as feeding habitats for juvenile reef fish on a Caribbean island

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ABSTRACT: Mangroves and seagrass beds are important daytime shelter habitats for juvenile Caribbean reef fish species, but little is known about their relative importance as feeding grounds. In the present study, we tested the degree to which these 2 habitats are used as a feeding ground for 4 nocturnally active fish species on Curaçao, Netherlands Antilles. Stable isotope analysis was used as a technique to distinguish between feeding in mangroves and seagrass beds. Individuals of the 4 species which were sheltering during the daytime in permanently inundated fringing mangroves subject to low tidal exchange showed a stable carbon isotope signature indicative of a mixed diet composed of crustaceans from mangroves as well as seagrass beds, with the contribution from mangrove food items lying between 57 and 92%. However, individuals of the same species sheltering on adjacent (<50 m distance) seagrass beds during the daytime showed a carbon signature indicative of almost exclusive feeding on seagrass beds. This indicates that 2 different subpopulations probably exist for the 4 species studied: a population of fishes sheltering in mangroves during the daytime and feeding primarily in the mangroves and secondarily in the seagrass beds at night, and a population of fishes of the same species sheltering in adjacent seagrass beds during the daytime and feeding primarily in seagrass beds at night.

KEY WORDS: Coral reef fish · Mangroves · Seagrass beds · Stable isotopes · Feeding habitats · Interlinkages

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INTRODUCTION

Coastal habitats such as mangroves, seagrass beds, mud flats and patch reefs are often interlinked through diurnal fish feeding migrations (Ogden & Buckman 1973, Ogden & Ehrlich 1977, Rooker & Dennis 1991, Nagelkerken et al. 2000a). Even though these studies have focussed on different aspects of these feeding migrations (e.g. timing, duration, home range, migration routes, associated skin coloration, anatomy of eyes and species-specific behaviour), little evidence is present on the degree to which these interlinked habitats are used as a feeding habitat. Commonly used research techniques such as visual observations on fish

feeding behaviour and fish feeding migrations are only snap-shots, whereas stomach analyses often do not reveal the source of the food and do not provide evidence that ingested food is also assimilated (Gearing 1991).

Stable carbon isotope analysis is a technique for tracing carbon sources in an animal's diet. Various types of marine food sources (e.g. detritus, phytoplankton, zooplankton, seagrass, epiphytes, macroalgae, crustaceans) often have different isotopic signatures, which also differ between habitats (e.g. mangrove vs seagrass bed: Harrigan et al. 1989, Loneragan et al. 1997, Cocheret de la Morinière et al. 2003a). Stable carbon isotope analysis often makes it possible to determine

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the general food composition (i.e. average diet) and its source, assimilated in terms of weeks to months (Gearing 1991).

Mangroves have received particular attention with respect to their role as a source of carbon for fishes. It has been observed that during high tide, fishes from adjacent habitats such as subtidal mud flats and seagrass beds migrate into the mangroves to feed (Vance et al. 1996, Sheaves & Molony 2000). Recent stable isotope studies have confirmed that these fishes assimilate the food sources obtained from the mangroves (Rodelli et al. 1984, Marguillier et al. 1997, Sheaves & Molony 2000). However, the above studies were all done in the Indo-Pacific where tidal differences are in the order of several metres, resulting in movement of large quantities of seawater and fishes between neighbouring habitats. On Caribbean islands, where low tidal differences and slow tidal currents occur, Nagelkerken & van der Velde (2004, this issue) showed that fringing mangroves are not an important feeding habitat for most fish occurring in adjacent seagrass beds. Many other studies have shown, however, that Caribbean mangroves are important feeding sites for fishes, but these studies were often done on resident fish in large mangrove swamps (Odum & Heald 1975, Thayer et al. 1987, Ley et al. 1994), and not on fishes sheltering in fringing mangroves during the daytime and migrating to adjacent seagrass beds at night.

Due to the tidal regime on Caribbean islands, export of particulate organic carbon from mangroves to adjacent systems may be very low. Furthermore, the mangrove prop-roots generally remain inundated during low tide and are therefore permanently accessible to fishes. As a result, they function differently than most Indo-Pacific intertidal mangroves. During the daytime, seagrass beds as well as fringing mangroves on Caribbean islands harbour high densities of mainly nocturnally active zoobenthivorous fish species (Haemulidae, Lutjanidae). In the mangroves, the fishes shelter between the prop-roots, and at night most of these fishes migrate to adjacent seagrass beds to feed, as observed by visual census studies (Rooker & Dennis 1991, Nagelkerken et al. 2000a, 2001, Ley & McIvor 2002). However, the mangroves are not completely empty at night (Nagelkerken et al. 2000a), and fishes may show opportunistic feeding during the daytime while sheltering in the mangroves (Rooker 1995). Therefore, even though it is widely accepted that Caribbean fish species belonging to the families Haemulidae and Lutjanidae migrate from daytime shelter habitats such as mangroves, patch reef and channels to seagrass beds at night to forage (Ogden & Ehrlich 1977, Rooker & Dennis 1991, Nagelkerken et al. 2000a), the role of fringing mangroves as a feeding habitat for

these species remains unclear. In the present study, we used multiple stable isotope analysis to test the hypothesis that seagrass beds are the main feeding grounds for nocturnally active fish species sheltering in fringing mangroves during the daytime.

MATERIALS AND METHODS

Study area. The study was carried out in Spanish Water Bay on the Caribbean island of Curaçao, Netherlands Antilles. The bay has a maple-leaf shape, a total surface area of approx. 3 km², and is mainly <6 m deep (Fig. 1). The shoreline of the bay is fringed by *Rhizophora mangle* mangrove trees of which the prop-roots are always inundated. The inundated part was on average (\pm SD) 1.4 \pm 0.5 m wide (i.e. from the outer mangrove fringe to the shoreline), the water 0.8 \pm 0.2 m deep, and the density of the submerged prop-roots 7.4 \pm 5.9 m⁻² (Nagelkerken et al. 2000b). Monospecific *Thalassia testudinum* seagrass beds are located in front of the mangroves at depths of 0.4 to 3 m. Mean seagrass cover (\pm SD) in the bay was 81 \pm 12%, height of the seagrass canopy above the substratum 22 \pm 8 cm and seagrass shoot density 143 \pm 66 m⁻² (Nagelkerken et al. 2000b). Between about 3 and 6 m depth, the bay consists of subtidal muddy/sandy seabeds with some degree of algal cover (<20%) of *Halimeda opuntia*, *H. incrassata*, *Cladophora* sp. and *Caulerpa verticillata* (Kuenen & Debrot 1995), followed at 6 m by a deep channel (max. 11 to 18 m deep) in the central parts of the bay.

The mangrove and seagrass habitats were clearly separated. The mangrove habitat extended to the outer fringe of the mangrove canopy, and was a dark environment with no vegetation growing on the muddy substrate, which was covered by dark-coloured mangrove detritus. From the fringe of the mangroves outward, seagrass and benthic algae covered the lightly coloured sandy substratum. Seagrass leaves were not encountered in the mangrove habitat, and vice-versa, indicating little exchange of large particulate organic material between habitats. The average daily tidal range is about 30 cm (de Haan & Zaneveld 1959).

Mean (\pm SD) water temperature and salinity on the seagrass beds during November 1997 and August 1998 were 28.3 \pm 0.2°C and 35.4 \pm 0.2 psu, respectively (Nagelkerken et al. 2000b). The bay has relatively clear water with an average horizontal Secchi disk visibility of 6.2 \pm 2.1 m.

Study design. Four of the most abundant juvenile reef fish species found in mangroves and seagrass beds (see Nagelkerken et al. 2000b) were selected for the study: french grunt *Haemulon flavolineatum*,

bluestriped grunt *H. sciurus*, schoolmaster *Lutjanus apodus* and yellowtail snapper *Ocyurus chrysurus*. Between May and September 1998 a number of individuals of each species was caught during the daytime in the mangroves (N = 32) and in adjacent (<50 m distance) seagrass beds (N = 156) in Spanish Water Bay (Fig. 1, Table 1). Fishes were caught on the seagrass beds using a beach seine net, whereas in the mangroves they were caught using hook and line and an Antillean fish trap with bait. In the mangroves, individuals of each species were always caught from the same mangrove stand. On the seagrass beds, individuals of each species were caught at 2 to 3 different sites, except for *L. apodus* which was caught at a single seagrass site.

Because the number of specimens from the mangroves and seagrass beds was highly unbalanced (32 vs 156), a selection of 29 individuals was made from the seagrass bed specimens. For each species, the same number of fishes with similar sizes as in the mangroves were selected from the seagrass beds. In all figures a comparison is made between the mangrove specimens and all seagrass specimens as well as the selection of the seagrass specimens.

Decapoda and Tanaidacea are the most important food items of the 4 fish species (Nagelkerken et al. 2000a, Cocheret de la Morinière et al. 2003a,b) and were collected in both habitats during July 2003. Decapoda were collected from under rocks and stones in both habitats and from the prop-roots in the

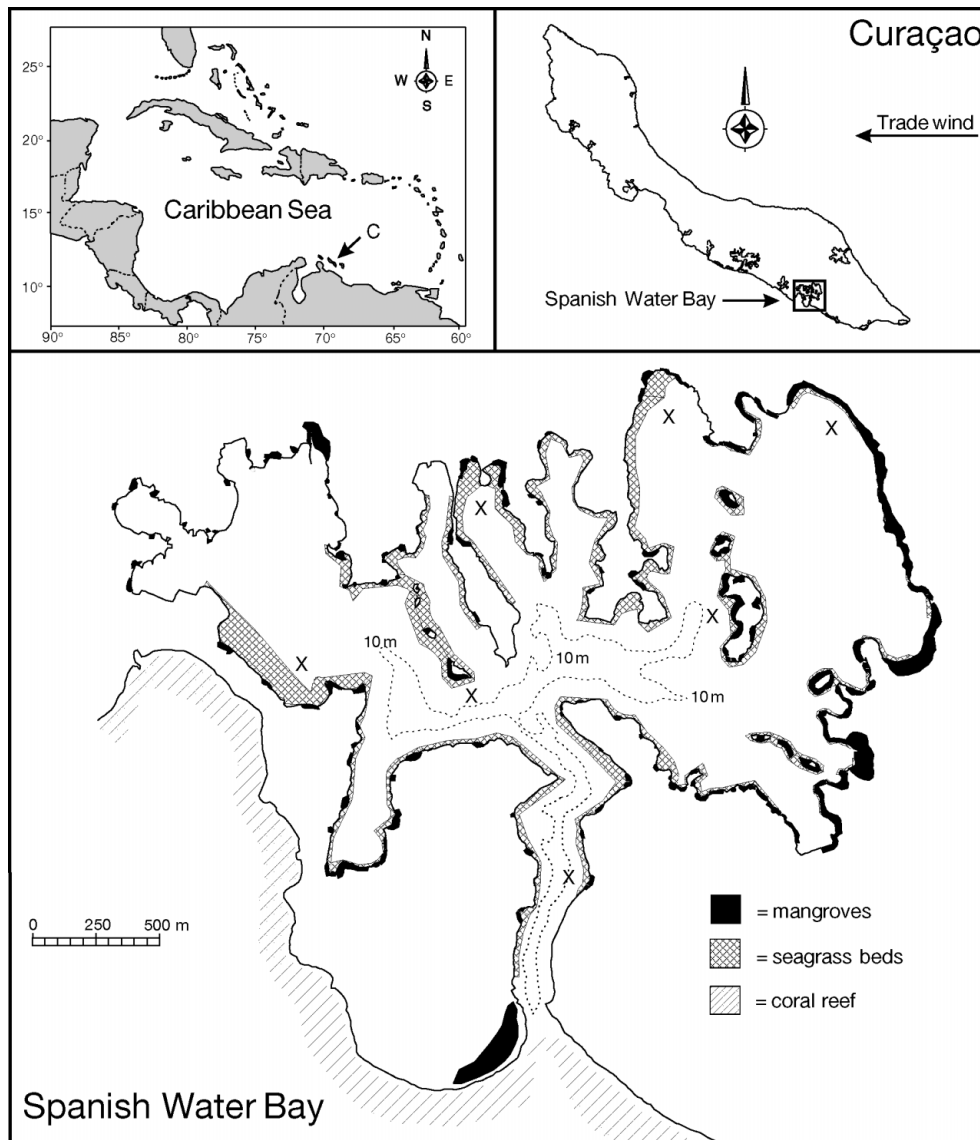


Fig. 1. Location of Curaçao (C) in the Caribbean, location of Spanish Water Bay on the island, and location of the collection sites in Spanish Water Bay (marked 'X')

Table 1. Numbers of individuals (# iso) analysed for stable isotopes for 4 fish species from mangroves and seagrass beds. SL = mean standard length (cm); SE = standard error; Size range = range in SL (cm); Density = mean fish density per 100 m² during the daytime (data from Nagelkerken et al. 2000b). Seagrass beds (N = 29) reflect the sampling regime in the mangroves (# iso, SL, Size range)

Species	Mangroves (N = 32)				Seagrass beds (N = 156)				Seagrass beds (N = 29)		
	# iso	SL (SE)	Size range (cm)	Density (SE)	# iso	SL (SE)	Size range (cm)	Density (SE)	# iso	SL (SE)	Size range (cm)
<i>Haemulon flavolineatum</i>	11	8.3 (0.2)	7.4–9.5	89.4 (18.0)	30	8.1 (0.3)	5.8–11.0	15.1 (2.9)	11	8.4 (0.3)	7.4–9.6
<i>Haemulon sciurus</i>	8	14.8 (2.0)	8.0–25.9	22.9 (3.7)	61	12.1 (0.6)	4.6–21.8	2.0 (0.4)	8	14.4 (1.6)	8.0–21.8
<i>Lutjanus apodus</i>	9	16.0 (1.1)	12.3–21.1	24.5 (2.3)	22	10.1 (0.6)	5.6–15.6	0.1 (0.0)	6	13.6 (0.5)	12.6–15.6
<i>Ocyurus chrysurus</i>	4	9.3 (0.7)	7.5–11.0	3.8 (1.7)	43	12.0 (0.5)	2.7–17.1	1.5 (0.3)	4	9.4 (0.7)	8.3–11.0

mangroves, whereas Tanaidacea were sampled in the laboratory from collected seagrass plants and prop-root epibionts (sponges, algae, etc.). Decapoda were subdivided into crabs and shrimps: 6 and 0 specimens, respectively, were from the mangroves and 11 and 8 specimens from the seagrass beds. Shrimps were not encountered in the mangroves and did not occur in the bay at the high densities typical for many tropical estuaries. Furthermore, the shrimps collected from the seagrass beds were benthic shrimps (50% *Alpheus* sp.) and not free-swimming Penaeidae. Because Tanaidacea are small (<3 mm) about 10 to 20 specimens were pooled to form a single sample. A total of 4 samples of Tanaidacea in the mangroves and 3 samples in the seagrass beds were analysed.

Muscle tissue of fish and complete Decapoda and Tanaidacea were dried for 48 h at 70°C, after which the samples were ground to a fine powder using a mortar, pestle and liquid nitrogen. Fish muscle tissue was used because of its slow turnover rate, resulting in a history of food assimilation over periods of months and excluding short-term variability (Gearing 1991). Carbon and nitrogen stable isotope composition were measured for each sample with a Carlo Erba NA 1500 elemental analyser coupled online via a Finnigan Conflo III interface with a Thermo-Finnigan DeltaPlus mass-spectrometer. Carbon and nitrogen isotope ratios are expressed in the delta notation ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) relative to Vienna PDB and atmospheric nitrogen. Average reproducibilities based on replicate measurements for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were about 0.15‰.

Statistical analysis. A Student's *t*-test was used to compare the $\delta^{13}\text{C}$ values of individual fish species and of pooled fish species between mangroves and seagrass beds. A 1-way ANOVA, followed by a Games-Howell post-hoc test, was used to test the difference in $\delta^{13}\text{C}$ values between specimens from the same species collected from different seagrass beds. Simple 2-end mixing models (e.g. Phillips & Gregg 2001) were used

to calculate the contribution of mangrove food items to the diet of the various fish species using the following formula:

$$f_A = \frac{\delta_M - \delta_B}{\delta_A - \delta_B}$$

where f_A is the mean proportion of Source A in Mixture *M*, and δ_M , δ_A and δ_B represent the mean isotopic carbon signatures for Mixture *M* and Sources A and B, respectively.

RESULTS AND DISCUSSION

The 4 selected fish species occurred in mangroves as well as in the seagrass beds during the daytime, but the mangroves were favoured as a shelter habitat (see Table 1), probably because of their high structural complexity and dark environment which lower the risk of predation (Nagelkerken et al. 2000b, Cocheret de la Morinière et al. 2004). Pooled individuals of the 4 fish species caught in the mangroves showed a frequency distribution of stable carbon isotope values different from that of fishes caught on adjacent seagrass beds (Fig. 2), with the overall mean $\delta^{13}\text{C}$ value (\pm SE) of mangrove fishes ($-15.0 \pm 0.4\text{‰}$) being significantly depleted compared to that of seagrass fishes ($-12.7 \pm 0.1\text{‰}$; $p < 0.000$, *t*-test) and the selection of seagrass fishes ($-12.3 \pm 0.2\text{‰}$; $p < 0.000$, *t*-test).

The sampled fishes had about the same size range in the mangroves as in the seagrass beds, although very small juveniles of 2 to 7 cm were not found in the mangroves (Fig. 3). Individual fishes >10 cm showed increasingly depleted $\delta^{13}\text{C}$ values with an increase in fish size in the mangroves compared to the seagrass beds (Fig. 3). However, several small juveniles in the size range of 7 to 10 cm had comparable $\delta^{13}\text{C}$ values in the mangroves and in the seagrass beds, which is indicative of at least 2 scenarios: (1) very small juveniles sheltering and feeding previously (i.e. at a size of 2 to 7 cm) on the seagrass beds moved permanently to

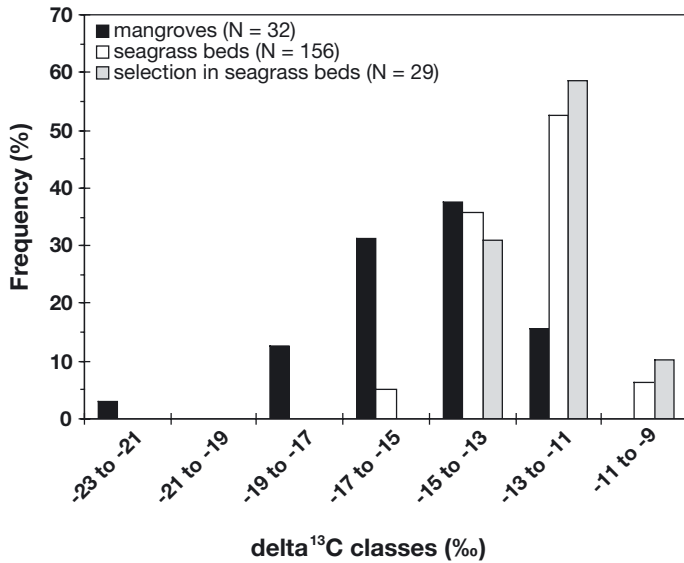


Fig. 2. Frequency distribution of pooled $\delta^{13}\text{C}$ values of the 4 fish species caught in mangroves and seagrass beds during the daytime. Grey bars indicate the selection of the seagrass fishes (based on similar sizes as in the mangroves)

the mangroves when they reached a size of about 7 cm; since it takes several weeks to months before the $\delta^{13}\text{C}$ signature of food is incorporated into the muscle tissue (Gearing 1991, Hesslein et al. 1993), they still show a seagrass $\delta^{13}\text{C}$ signature. (2) Small juveniles (i.e. 7 to 10 cm length) sheltering in the mangroves during the daytime consume a larger proportion of food from the seagrass beds when migrating to the seagrass bed at night than larger juveniles.

At the species level, no significant differences were found within species between $\delta^{13}\text{C}$ values of specimens collected from different seagrass bed sites ($p > 0.124$, Games-Howell post-hoc test). For each of the 4 fish species separately, the $\delta^{13}\text{C}$ values of individuals from the mangroves were significantly lower than those from the seagrass beds ($p < 0.039$, t -tests) and the selection of the seagrass beds ($p < 0.048$, t -tests; Fig. 4). The diet of these species is largely composed of Decapoda (crabs and shrimps) and Tanaidacea (Nagelkerken et al. 2000a). Comparable to the fishes, crabs and Tanaidacea showed a significantly depleted $\delta^{13}\text{C}$ value in the mangroves compared to the seagrass beds ($p < 0.017$, t -tests; Fig. 4). Shrimps were not encountered in the mangroves, but the seagrass bed shrimps had a mean $\delta^{13}\text{C}$ value comparable to that of crabs and Tanaidacea from the seagrass beds.

Stable isotope ratios of animals reflect those of their diet with, on average, 1‰ enrichment in carbon and 3‰ enrichment in nitrogen, although the nitrogen enrichment can vary between approximately 2 and 5‰ (DeNiro & Epstein 1978, Rau et al. 1983, Fry 1988,

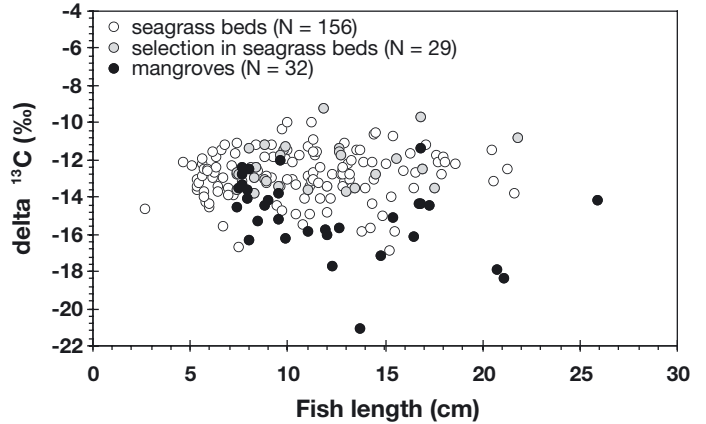


Fig. 3. Relation between $\delta^{13}\text{C}$ values and standard length of all individuals of the 4 studied fish species caught in mangroves and seagrass beds during the daytime. Grey symbols indicate the selection of the seagrass fishes (based on similar sizes as in the mangroves)

Cabana & Rasmussen 1994). Small juveniles of Haemulidae and Lutjanidae in Spanish Water Bay forage almost exclusively on Tanaidacea, whereas larger juveniles show a diet shift towards Decapoda as the main food source (Cocheret de la Morinière et al. 2003a,b). The fishes caught in the Spanish Water Bay seagrass beds can be considered small juveniles, and the stable isotope data indicated that these fishes mainly fed on Tanaidacea from the seagrass beds (Fig. 4).

Studies have shown that these fish species also mainly consume Tanaidacea in the mangroves (Nagelkerken et al. 2000a). However, the stable isotope data indicated that the fishes were too enriched in $\delta^{13}\text{C}$ to

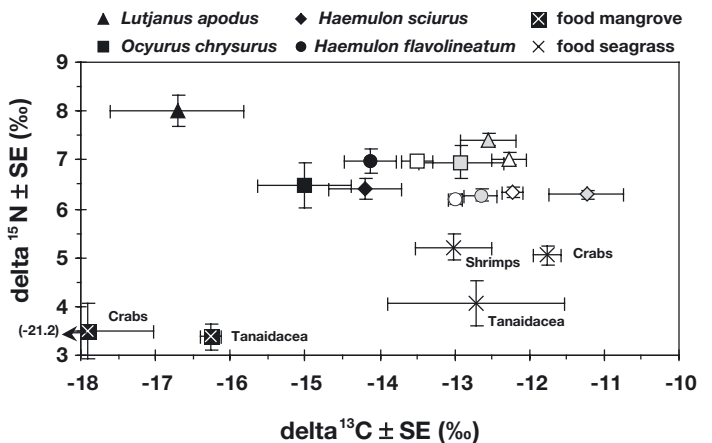


Fig. 4. Mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of the 4 fish species and their most important food items caught during the daytime in mangroves (filled symbols) and seagrass beds (open symbols). Grey symbols indicate the selection of the seagrass fishes (based on similar sizes as in the mangroves)

be feeding exclusively on Tanaidacea from the mangroves (Fig. 4). The data thus suggest that they had a mixed diet composed of Tanaidacea from the mangroves as well as from the seagrass beds. Using a simple 2-end mixing model (e.g. Phillips & Gregg 2001), the contribution of mangrove Tanaidacea to the diet of *Haemulon flavolineatum*, *H. sciurus* and *Ocyurus chrysurus* from the mangroves would range between 67 and 92% if it was assumed that the fishes fed exclusively on Tanaidacea.

Individuals of *Lutjanus apodus* caught in the mangroves showed a much lower $\delta^{13}\text{C}$ value than that of the other fish species from the mangroves (Fig. 4). However, *L. apodus* was much larger in size in the mangroves than on the seagrass bed (Table 1), and had a size in the mangroves at which it mainly feeds on Decapoda instead of Tanaidacea (Cocheret de la Morinière et al. 2003b). Such ontogenetic shifts are commonly found in Lutjanidae (Thayer et al. 1987, Cocheret de la Morinière et al. 2003a). The highly depleted $\delta^{13}\text{C}$ values of mangrove crabs compared to mangrove Tanaidacea (Fig. 4) may thus explain the depleted $\delta^{13}\text{C}$ value of *L. apodus* compared to that of the other fish species in the mangroves. However, the mangrove crabs (–21.2‰) were depleted much more than 1‰ in $\delta^{13}\text{C}$ compared to *L. apodus* (–16.7‰), suggesting that this species probably consumes Decapoda from the mangroves as well as from the seagrass beds. Assuming that *L. apodus* consumes only Decapoda, the contribution of the mangrove Decapoda to its diet would be 57 to 63% (depending on the ratio of crab vs shrimp in the diet).

The present study indicates that nocturnally active fish species sheltering on the seagrass beds during the daytime forage in the same habitat at night, whereas individuals of the same species belonging to the same size class and sheltering in the mangroves during the daytime forage in the mangroves as well as in the seagrass beds at night. Taking the results of the stable carbon isotope analysis into account, at least 3 feeding strategies can be proposed for the nocturnally active fishes sheltering in the mangroves during the daytime: (1) the fishes feed opportunistically during the daytime in the mangroves and migrate to the seagrass beds at night for additional feeding; (2) the fishes start feeding in the mangroves at dusk whilst slowly migrating to the seagrass beds to continue feeding; and (3) after having migrated at dusk to the seagrass beds to feed, the fishes at some point during the night return to the mangroves to feed. Preliminary results of fish behaviour studies in the same mangroves as studied here indicated that at least some of the fish feed in the mangroves during the daytime (M. C. Verweij pers. comm.). Irrespective of the feeding strategy used, the shelter habitat and the stable carbon isotope values of

fishes that occur in the mangrove during the daytime differ from those on the seagrass beds. This suggests the presence of 2 subpopulations utilising different shelter habitats during the daytime and showing only a partial overlap in feeding habitat at night. Although fishes sheltering in the mangroves during the daytime feed primarily in the mangroves, they may still show diurnal migrations to the seagrass beds at night. Whether these mangroves, due to their relatively small size, do not provide sufficient food (Nagelkerken et al. 2000a) for the high density of fish sheltering there, or whether the diurnal migrations are stereotypical behavioural patterns (Helfman 1986) is not known.

In conclusion, the data indicate that individuals of 4 common reef fish species which shelter in the mangroves during the daytime and migrate to the seagrass beds at night consume food primarily from the mangroves and secondarily from the seagrass beds. In contrast, individuals of the same species sheltering during the daytime in seagrass beds adjacent to the mangroves almost exclusively consume food from the seagrass beds. The complete separation in daytime shelter habitat and the partial separation in feeding habitat suggest the presence of 2 different subpopulations.

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