

Are Caribbean mangroves important feeding grounds for juvenile reef fish from adjacent seagrass beds?

I. Nagelkerken^{1,2,*}, G. van der Velde¹

¹Department of Animal Ecology and Ecophysiology, University of Nijmegen, Toernooiveld 1, 6525 ED Nijmegen, The Netherlands

²Carmabi Foundation, PO Box 2090, Piscaderabaai z/n, Curaçao, Netherlands Antilles

ABSTRACT: Little evidence is available on how juvenile fishes utilise seagrass beds and adjacent mangroves as feeding habitats. In this study we tested the degree to which Caribbean mangroves are utilised as feeding grounds by the fish community from adjacent seagrass beds. Stable carbon and nitrogen isotope analyses were performed on several potential food items from seagrass beds and adjacent mangroves, on muscle tissue of 23 fish species from seagrass beds on a Caribbean island (Curaçao, Netherlands Antilles), and on juveniles of 2 common reef fish species, *Haemulon flavolineatum* and *Ocyurus chrysurus*, from seagrass beds in 7 bays on 5 Caribbean islands. Only the herbivore *Acanthurus chirurgus* and the carnivore *Haemulon chrysargyreum* appeared to feed predominantly in the mangrove habitat, whereas the carnivores *Mulloidichthys martinicus* and *O. chrysurus* (only on 2 islands) showed a stable carbon signature suggestive of food intake from the mangrove as well as the seagrass habitat. The piscivore *Sphyraena barracuda* foraged on fish schooling at the mangrove/seagrass interface. For the other 18 seagrass fish species, which contributed 86% of the total seagrass fish density, the contribution of food sources from the mangroves was minor to negligible. The same was true for *H. flavolineatum* and *O. chrysurus* on most of the other Caribbean islands. The results contrast with the situation in the Indo-Pacific, where intertidal mangroves serve as important feeding habitats for fishes from adjacent systems during high tide. This difference is most probably explained by both the absence of large tidal differences on Caribbean islands and the greater food abundance in seagrass beds than in mangroves.

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

Resale or republication not permitted without written consent of the publisher

INTRODUCTION

Stable isotope analyses have been used to test whether mangrove faunal communities are detritus-based. Several studies have shown that outwelling of mangrove carbon (as POC, DOC, DIC, detritus or leaves) can occur to adjacent systems up to a few kilometres away (Rodelli et al. 1984, Hemminga et al. 1994, Newel et al. 1995). Furthermore, seagrasses, invertebrates and fishes often show an enrichment in stable carbon isotope ratio with increasing distance to the mangroves (Lin et al. 1991, Marguillier et al. 1997, Lee 2000, Chong et al. 2001, Bouillon et al. 2002). It

was therefore well accepted that mangrove carbon significantly fuelled food webs of adjacent coastal habitats (Mann 1972, Odum & Heald 1975). Recent stable isotope studies have shown, however, that these food webs are mostly based on phytoplankton or benthic algae (Stoner & Zimmerman 1988, Primavera 1996, Bouillon et al. 2002). In the case of *Rhizophora* mangroves bordering seagrass beds, the mangroves can also be the recipients of carbon and nutrients from the seagrass litter (Hemminga et al. 1994, Slim et al. 1996).

Irrespective of the degree to which different primary sources contribute to the mangrove food web, mangrove invertebrates such as crabs and shrimps show

*Email: i.nagelkerken@sci.kun.nl

stable carbon values which are significantly depleted compared to those from seagrass beds (Fry et al. 1982, 1983, Kitting et al. 1984, Rodelli et al. 1984, Stoner & Zimmerman 1988, Harrigan et al. 1989, Fleming et al. 1990, Primavera 1996, Marguillier et al. 1997, Lee 2000, Schwamborn et al. 2002). The few stable isotope studies done on fishes in mangrove-lined estuaries or bays also show depleted carbon signatures in mangroves (Rodelli et al. 1984, Marguillier et al. 1997, Lee 2000, Sheaves & Molony 2000). The latter studies were all done in the Indo-Pacific, where carnivorous fishes from adjacent ecosystems, such as seagrass beds and sand flats, are known to migrate into inundated mangroves at high tide to feed on macro-invertebrates (Sasekumar et al. 1984, Robertson & Duke 1990, Vance et al. 1996). Sheaves & Molony (2000) showed that this resulted in a short-cut of carbon pathways (i.e. shortening of the food chain) in the mangrove food web, as a result of which these carnivorous fish showed stable carbon signatures close to those of the mangrove macrofauna.

In contrast to many mangrove forests in the Indo-Pacific, the prop-root system of Caribbean mangroves along the water's edge are often continuously inundated and are subject to small tidal differences of only about 30 to 60 cm (de Haan & Zaneveld 1959, see also <http://co-ops.nos.noaa.gov/tides03/tpred2.html>). As a result, high densities of nocturnally active carnivorous fish seek shelter in the mangrove prop-roots during the daytime and migrate to adjacent seagrass beds and algal muddy/sandy seabeds at night to feed (Rooker & Dennis 1991, Nagelkerken et al. 2000a). Fishes of the same nocturnally active species, although smaller in size, seek shelter in adjacent seagrass beds during the daytime (Cocheret de la Morinière et al. 2002). These seagrass beds also contain many diurnally active fish species. Little is known, however, about the importance of mangroves in the Caribbean as a feeding habitat for diurnally and nocturnally active fish species found in seagrass beds during the daytime. Many Caribbean studies have focussed on the feeding of fishes which are resident in mangroves, but do not study the interaction with adjacent habitats such as seagrass beds (e.g. Odum & Heald 1975, Ley et al. 1994, Rooker 1995).

Since the mangroves on Caribbean islands are continuously inundated and accessible to fishes from adjacent seagrass beds, and probably offer better protection against predation by piscivores (Cocheret de la Morinière et al. 2004), we hypothesised that, even though large tidal differences such as in the Pacific are lacking, mangroves would form an additional feeding ground for fishes resident on adjacent seagrass beds. In the present study, we tested this hypothesis for 23 species of Caribbean reef fish, using stable carbon and nitrogen isotope analyses.

MATERIALS AND METHODS

Study areas. The study was mainly carried out in Spanish Water Bay on the Caribbean island of Curaçao, Netherlands Antilles. This bay has a maple-leaf shape, a total surface area of approx. 3 km², and is mostly <6 m deep (Fig. 1). The shoreline of the bay is fringed by *Rhizophora mangle* mangrove trees, whose prop-roots are always inundated. 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 %, while the height of the seagrass canopy above the substratum was 22 \pm 8 cm and the seagrass shoot density was 143 \pm 66 m⁻² (Nagelkerken et al. 2000b). At depths between about 3 and 6 m, 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 other study sites (see Fig. 1) were located in Fuik Bay and St. Joris Bay on Curaçao, at Mangel Alto within the lagoon along the SW coast of Aruba, in Lac Bay on Bonaire, in Scotland Bay on Trinidad and in Well Bay on Tortola. All these bays, except Scotland Bay, were dominated by *T. testudinum* seagrass beds adjacent to *R. mangle* mangroves. In Scotland Bay, seagrass beds consisted of *Halophila decipiens* adjacent to *R. mangle*.

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.

All bays were marine with no river influence, and with small tidal differences (<50 cm, de Haan & Zaneveld 1959). In Spanish Water Bay, mean (\pm SD) water temperature and salinity on the seagrass beds were 28.3 \pm 0.2°C and 35.4 \pm 0.2 psu, respectively. This bay has relatively clear water with an average horizontal Secchi disk visibility of 6.2 \pm 2.1 m. Details of Fuik Bay and St. Joris Bay can be found in Nagelkerken et al. (2001a), those of Lac Bay in Nagelkerken et al. (2000c).

Study design. Fishes (predominantly juvenile coral reef fish, see Table 1) were collected during the daytime between May and September 1998 from various seagrass localities in Spanish Water Bay, close (0 to 50 m) to the mangrove fringe (Fig. 1), using a beach

seine net. At the same localities, potential food items from the seagrass beds and mangroves were collected between May and September 1998 and in July 2003. Macroalgae were represented by fleshy green and brown algae, and Echinoidea by sea urchins. 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. The study was extended to other bays for 2 very common juvenile fish species, *Haemulon flavolineatum* and *Ocyurus chrysurus*, which were collected with a beach seine net or with hook and line during the daytime from seagrass beds adjacent to mangroves. During June and July 1998, 6 to 7 individuals of each species were caught in Fuik Bay as well as in St. Joris Bay on Curaçao (Fig. 1), and in July 2001 and July 2002,

7 to 10 individuals of each species were caught at each of the 4 other islands.

Fish tissues and the potential food items were dried for 48 h at 70°C, and ground to a fine powder using a mortar, pestle and liquid nitrogen. For fishes, only 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). For mangroves, the first leaves following the terminal bud were used, whereas for seagrasses all green leaves of the entire plant were used, since no variation has been found between young and old leaves or between the tip and base of the leaf (Lin et al. 1991). Food items containing calcium carbonate were decalcified to allow us to focus solely on organic carbon (Nieuwenhuize et al. 1994); this was not done for the nitrogen isotope analysis, since nitrogen content is affected by acid washing (Bunn et al. 1995). Car-

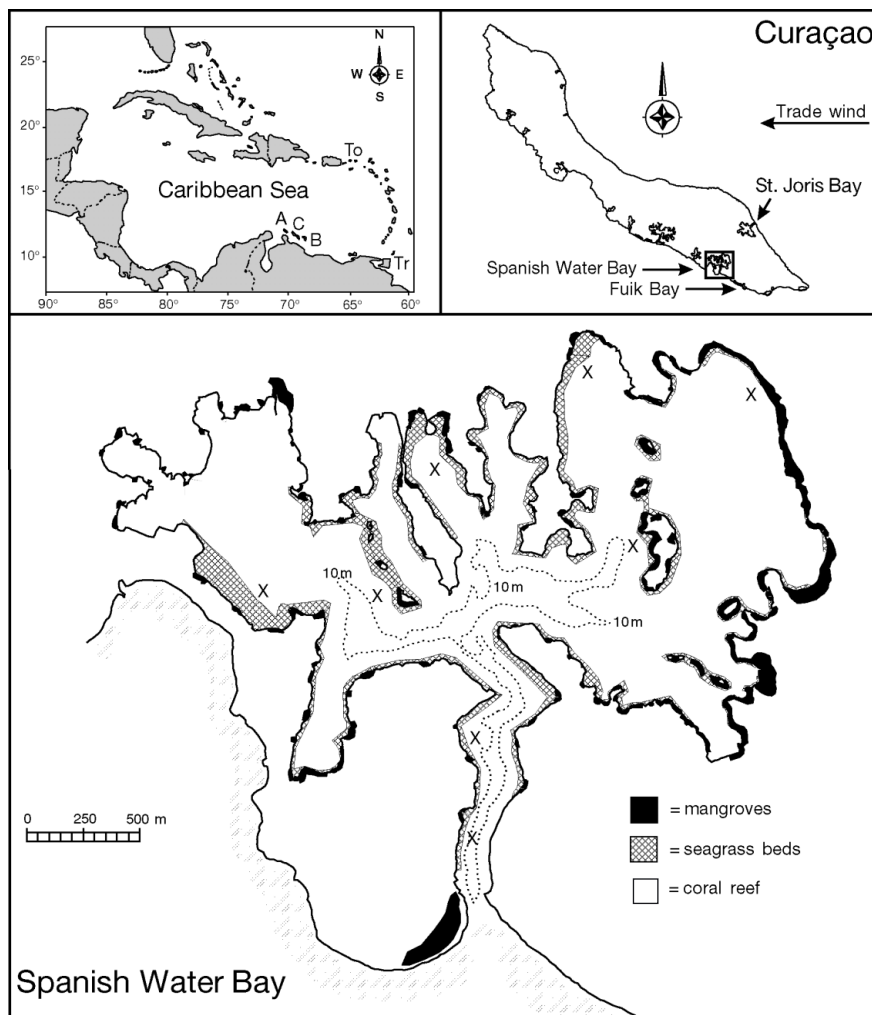


Fig. 1. Map showing the Caribbean islands sampled (A = Aruba, C = Curaçao, B = Bonaire, Tr = Trinidad, To = Tortola), the 3 bays sampled in Curaçao, and the location of the seagrass beds and sites of fish collection (marked 'X') in Spanish Water Bay

bon and nitrogen stable isotope compositions were measured with a Carlo Erba NA 1500 elemental analyser coupled online via a Finnigan Conflo III interface with a ThermoFinnigan 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 of standards for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were about 0.15%.

Diet composition was determined for the fishes caught in Spanish Water Bay. All fishes caught were immediately put on ice to avoid further food digestion. The entire digestive tract of each fish was removed and food items were quantified for the groups Nematoda, Bivalvia, Copepoda, Echinoidea, Gastropoda, Polychaeta, Oligochaeta, Osteichthyes, Ostracoda, Amphipoda, Decapoda, Foraminiferida, Isopoda, Mysidacea, Tanaidacea, seagrass, algae (unicellular, filamentous, calcareous, macro), sediment, or other. Diet composition was determined by estimating the relative volumetric quantity of food items, using a stereomicroscope (Nielsen & Johnson 1992).

RESULTS AND DISCUSSION

The $\delta^{13}\text{C}$ values of potential fish food items from the mangroves and seagrass beds in Spanish Water Bay ranged between -27.0 and -10.5‰ (Fig. 2). The various primary producers and macroinvertebrates all showed different stable carbon signatures, but could be divided into a group associated with the mangroves (range: -27.0 to -14.1‰) and a group associated with the seagrass beds (-15.4 to -10.5‰). Other studies have shown a similar range of $\delta^{13}\text{C}$ values for various types of algae and macroinvertebrates from mangroves (± -29 to -15‰ ; Rodelli et al. 1984, Stoner & Zimmerman 1988, Primavera 1996, Marguillier et al. 1997, Lee 2000, Schwamborn et al. 2002) and from seagrass beds (± -16 to -6‰ ; Fry et al. 1982, 1983, Kitting et al. 1984, Harrigan et al. 1989, Fleming et al. 1990).

Stable isotope ratios in animals reflect those of their diet, with an average of 1‰ carbon enrichment and 3‰ nitrogen enrichment, although nitrogen enrichment can vary between approximately 2 and 5‰ (DeNiro & Epstein 1978, Fry & Arnold 1982, Rau et al. 1983, Minagawa & Wada 1984, Fry 1988, Cabana & Rasmussen 1994). The 3 herbivorous fish species

Acanthurus bahianus, *Scarus iserti* and *Sparisoma chrysopterum* collected from the seagrass beds showed stable carbon and nitrogen ratios indicative of feeding on the seagrass bed (Fig. 2a), with a diet consisting primarily of seagrass epiphytes (filamentous algae) or leaves (Table 1). For *Acanthurus chirurgus*, which feeds mainly on macroalgae (Table 1), the data suggest a diet consisting of a mixture of mangrove and seagrass macroalgae. Using a simple 2-end mixing model for mixed diets (e.g. Phillips & Gregg 2001), the data suggest that the average contribution of mangrove macroalgae to its diet was 55%.

Of the 15 carnivorous fish species collected from the seagrass bed, the only piscivorous species, *Sphyraena barracuda*, feeds mainly on silversides, herrings and anchovies in Spanish Water Bay (Nagelkerken et al. 2001b). This is borne out by the $\delta^{13}\text{C}$ value of -14.2‰ for the common silverside *Atherinomorus stipes* (Nagelkerken et al. unpubl.), compared to -13.6‰ for *S. barracuda* (Fig. 2b). These fish species mostly seek shelter in schools at or near the mangrove/seagrass interface, where *S. barracuda* is often observed feeding on them. This suggests that although *S. barracuda* does not feed in the actual mangroves, its feeding behaviour is often associated with the presence of mangroves.

All of the remaining 14 carnivorous species, except *Haemulon chrysargyreum* and *Mulloidichthys martinicus*, showed $\delta^{13}\text{C}$ values indicating a diet consisting of seagrass macroinvertebrates (Fig. 2b). In their juvenile stage, species of the genera *Eucinostomus*, *Gerres*, *Haemulon* and *Lutjanus* feed largely on Tanaidacea, and secondarily on Decapoda in Spanish Water Bay (Nagelkerken et al. 2000a, unpubl.), which is in contrast to fishes from other Caribbean mangroves where shrimps and Amphipoda are an important food source (e.g. Thayer et al. 1987, Rooker 1995). The mean $\delta^{13}\text{C}$ values and standard error for Tanaidacea and Decapoda (shrimps and crabs) in the mangrove and the seagrass beds clearly show that the fish species of these 4 genera (excluding *H. chrysargyreum*) obtain these food items primarily from the seagrass bed (Fig. 2b). If we assume that these fish species only consume Tanaidacea and if we ignore the range in $\delta^{13}\text{C}$ values for seagrass Tanaidacea, a simple 2-end mixing model (e.g. Phillips & Gregg 2001) suggests that the contribution of mangrove Tanaidacea to their diet would be at most 29% (in the case of *H. flavolineatum*),

Fig. 2. (Facing page.) Mean (\pm SE) $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of potential fish food collected from mangroves (filled circles) and seagrass beds (open circles) and of 23 fish species collected from seagrass beds (filled squares) for (a) primary producers and herbivorous fish, (b) macrofauna and carnivorous fish, (c) macrofauna and omnivorous fish from Spanish Water Bay, and (d) 2 fish species collected from seagrass beds in 2 other Curaçao bays (St. Joris Bay and Fuik Bay) and from seagrass beds at 4 other Caribbean islands (Aruba, Bonaire, Trinidad, Tortola). See Table 1 for full genus names

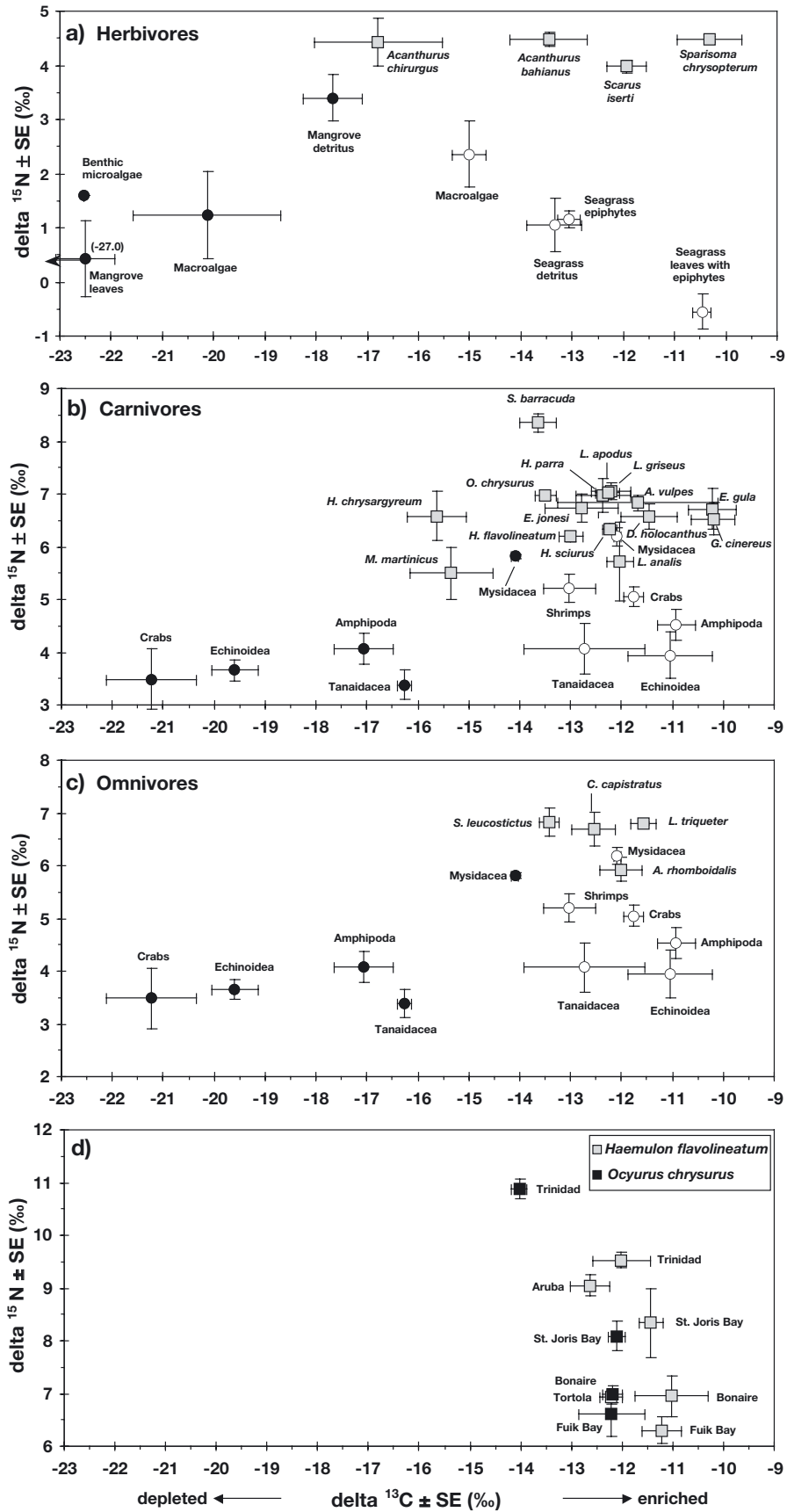


Table 1. Feeding guild, relative abundance on seagrass bed (calculated from Nagelkerken et al. 2000b), mean standard length (SL) and its range, number of stable isotope samples (# iso) and guts analysed (# guts), and diet composition for each fish species; H = herbivore, ZB = zoobenthivore, O = omnivore, ZP = zooplanktivore, P = piscivore; * = pooled abundance of *Eucinostomus gula* and *E. jonesi*. Diet composition shows only values >15%. Tana = Tanaidacea, Deca = Decapoda, Cope = Copepoda, Mysi = Mysidacea, Ostra = Ostracoda, Bival = Bivalvia, Gastro = Gastropoda, Fila = filamentous algae, Macro = macroalgae, Calc = calcareous algae, Gras = *Thalassia testudinum*

Species	Common name	Feeding guild	Relative abundance (%)	SL (range) (cm)	# iso guts	# guts	Diet composition													
							Tana	Deca	Cope	Mysi	Ostra	Bival	Gastro	Fish	Fila	Macro	Gras			
<i>Acanthurus bahianus</i>	Ocean surgeon	H	0.0	11.4 (4.9–17.2)	8	10											45			20
<i>Acanthurus chirurgus</i>	Doctofish	H	1.8	13.2 (8.0–18.6)	4	11											35			55
<i>Albula vulpes</i>	Bonfish	ZB	0.0	15.9 (13.0–18.0)	2	0														
<i>Archosargus rhomboidalis</i>	Sea bream	O	1.5	9.8 (6.1–13.5)	7	10														
<i>Chaetodon capistratus</i>	Fourey butterflyfish	O	2.0	5.8 (5.0–6.5)	8	11														
<i>Diodon holocanthus</i>	Balloonfish	ZB	0.1	15.3 (13.8–16.4)	7	19														49
<i>Eucinostomus gula</i>	Silver jenny	ZB	6.2*	6.0 (6.0)	4	10														93
<i>Eucinostomus jonesi</i>	Slender mojarra	ZB	6.2*	6.8 (5.0–8.0)	7	21														70
<i>Gerrus cinereus</i>	Yellowfin mojarra	ZB	0.6	5.9 (4.8–7.1)	7	7														50
<i>Haemulon chrysargyreum</i>	Smallmouth grunt	ZB	0.6	7.8 (5.9–9.0)	4	3														63
<i>Haemulon flavolineatum</i>	French grunt	ZB	35.3	8.1 (5.8–11.0)	30	28														60
<i>Haemulon parra</i>	Sailors choice	ZB	0.1	6.8 (6.5–7.3)	4	4														73
<i>Haemulon sciurus</i>	Bluestriped grunt	ZB	4.8	12.1 (4.6–21.8)	61	63														47
<i>Lactophrys triquetra</i>	Smooth trunkfish	O	0.0	13.2 (12.3–14.0)	3	0														
<i>Lutjanus analis</i>	Mutton snapper	ZB	0.1	16.9 (12.3–21.4)	2	2														100
<i>Lutjanus apodus</i>	Schoolmaster	ZB	0.3	10.1 (5.6–15.6)	22	40														17
<i>Lutjanus griseus</i>	Gray snapper	ZB	0.8	11.1 (6.5–18.8)	17	17														74
<i>Mulloidichthys martinicus</i>	Yellow goatfish	ZB	0.1	10.4 (9.7–11.0)	4	10														16
<i>Ocyurus chrysurus</i>	Yellowtail snapper	ZP/ZB	3.6	12.0 (5.7–17.1)	43	64														20
<i>Scarus iserti</i>	Striped parrotfish	H	32.6	6.9 (4.1–11.0)	25	26														17
<i>Sparisoma chrysopterum</i>	Redtail parrotfish	H	0.6	23.1 (15.2–26.5)	4	7														
<i>Sphyræna barracuda</i>	Great barracuda	P	0.2	18.5 (16.1–36.2)	11	12														100
<i>Stegastes leucostictus</i>	Beaugregory	O	0.7	6.4 (4.3–7.4)	7	8														81

but much lower for fish species showing more depleted $\delta^{13}\text{C}$ values (-13.0 to -10.2‰ ; see Fig. 2b). At $\delta^{13}\text{C}$ values of -11.7‰ and higher, the contribution of mangrove Tanaidacea to the fish diets would be 0%. The contribution of the mangroves will be lower in reality, however, because these fish species feed secondarily on Decapoda. The mangrove Decapoda (crabs) are much more depleted than the mangrove Tanaidacea, and if they were included in the calculations, the contribution of mangrove macrofauna to the diets of these seagrass fishes would be much lower. The data for *H. flavolineatum* from seagrass beds in 2 other Curaçao bays and on 4 other Caribbean islands also suggest that the seagrass beds are the main feeding habitats (Fig. 2d).

The zooplanktivore/zoobenthivore *Ocyurus chrysurus* has a mixed diet composed of Decapoda, Mysidacea and Tanaidacea (Table 1). Its depleted $\delta^{13}\text{C}$ value compared to these food items from the seagrass bed suggests that this species obtains some of its food from the mangroves (i.e. Mysidacea and Tanaidacea, Fig. 2b). The $\delta^{13}\text{C}$ values of *O. chrysurus* from seagrass beds in 2 other Curaçao bays and on 2 other Caribbean islands suggest that its food is primarily obtained from the seagrass beds, except in Trinidad, where there may be some contribution from the mangroves (Fig. 2d).

Of all carnivorous fish species from the seagrass bed, *Haemulon chrysargyreum* and *Mulloidichthys martinicus* showed the most depleted $\delta^{13}\text{C}$ values, which fell within the range of mangrove food items (Fig. 2b). The diet of *M. martinicus* is mainly composed of Copepoda, Decapoda and Tanaidacea (Table 1), and the data suggest that its diet is composed either entirely of mangrove food items or of a mixture of mangrove and seagrass food items. The diet of *H. chrysargyreum* consists primarily of Tanaidacea, and the data indicate that this food source is obtained from the mangrove habitat and not from the seagrass beds.

The omnivores showed $\delta^{13}\text{C}$ values indicating a diet consisting of seagrass

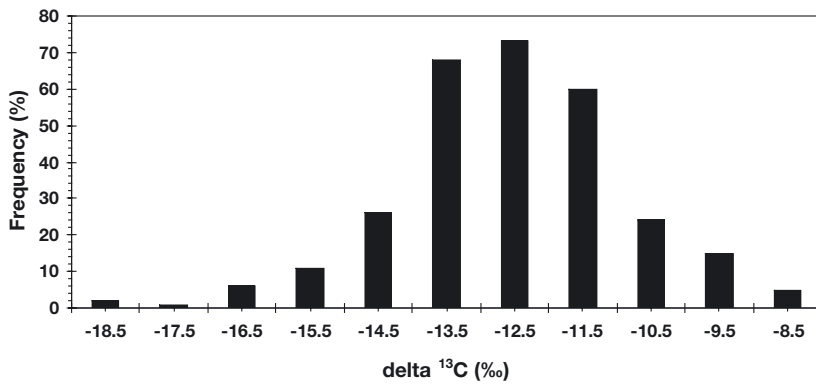


Fig. 3. Frequency distribution of $\delta^{13}\text{C}$ values of all fishes ($N = 291$) from the seagrass beds of Spanish Water Bay

macroinvertebrates (Fig. 2c). *Archosargus rhomboidalis* forages on macroinvertebrates as well as seagrass (Table 1). A contribution of seagrass to its diet may thus explain the lower $\delta^{15}\text{N}$ value compared to that of the other 3 omnivorous species.

In summary, the data show that of the 23 species collected from the seagrass bed, 18 (relative abundance = 85.7% of the total seagrass fish community, see Table 1) obtained their food primarily from the seagrass beds, even though they were caught at distances of less than 50 m from the mangrove fringe. For the species *Acanthurus bahianus*, *Ocyurus chrysurus*, *Haemulon chrysargyreum* and *Mulloidichthys martinicus*, the data suggest a diet composed either partly or completely of food items from the mangrove. *Sphyraena barracuda* does not obtain its food from the mangroves, but feeds at the mangrove/seagrass interface. Hence, the mangroves do not appear to be a major source of food for the majority of the fish species and individuals on seagrass beds adjacent to mangroves. This conclusion is also supported by the frequency distribution of $\delta^{13}\text{C}$ values of individual fishes, which shows that most fishes had a signature which fell within the range of seagrass food items (Fig. 3).

The relatively minor importance of the studied Caribbean mangroves as feeding grounds for most fishes from adjacent systems seems to contrast with the situation in the Indo-Pacific, where many estuarine and juvenile marine fishes have been observed to migrate into inundated mangroves at high tide to feed (Sasekumar et al. 1984, Chong et al. 1990, Robertson & Duke 1990, Vance et al. 1996). Stable isotope studies have confirmed that these fishes do indeed feed in the mangroves. Rodelli et al. (1984) concluded that approximately 14 fish species ($\delta^{13}\text{C} = -27$ to -16%) caught in a Malaysian mangrove ecosystem derived about 60% of their carbon from mangrove swamps, while Sheaves & Molony (2000) showed that 5 fish species ($\delta^{13}\text{C} = -23$ to -21%) caught in Australian estu-

aries fed on sesamid crabs in adjacent mangroves during high tide. In a marine bay in Kenya, Marguillier et al. (1997) found that 3 fish species ($\delta^{13}\text{C} = -21$ to -19%) from adjacent seagrass beds depended on mangrove carbon. Fishes caught from a mangrove estuary in China showed similar $\delta^{13}\text{C}$ values (around -20% , Lee 2000). In Florida, fishes collected from intertidal mangroves showed depleted $\delta^{13}\text{C}$ values (-24 to -22%) compared to those caught from distant seagrass beds (-15 to -13%) (Harrigan et al. 1989, Fleming et al. 1990). Also in the Caribbean a wide variety of studies have shown that mangroves are an important feeding habi-

tat for fishes (Odum & Heald 1975, Thayer et al. 1987, Ley et al. 1994, Rooker 1995). However, these studies were done on fishes resident in large mangrove swamps, and hence no insight has been obtained into the degree to which these mangroves are used as feeding sites by fishes from adjacent habitats.

The absence of large tidal differences on Caribbean islands may be the primary cause of the minor importance of the mangroves as a feeding habitat for seagrass fishes. Quinn & Kojis (1987) postulated that in estuaries with a tidal range less than 1 m, tidal currents have little effect on fish distribution. Secondly, the fringing mangroves in the marine bays and lagoons of many Caribbean islands are much smaller in surface area than the mangroves forests in estuaries, while seagrass beds contain higher densities of food than the mangroves (Nagelkerken et al. 2000a). Finally, the difference between the Caribbean and Indo-Pacific may be explained by differences in the diversity and structure of mangroves and seagrass beds. Mangrove and seagrass species richness is greater in the Indo-Pacific, which may cause differences in structural complexity, food abundance and hydrological factors in these habitats, affecting their utilisation as feeding habitats by fishes.

It can be concluded that the degree to which mangroves are utilised as a feeding ground by fishes from adjacent habitats may be primarily related to the tidal regime. On Caribbean islands with small tidal differences, the continuously inundated mangrove prop-roots do not play a primary role as a feeding habitat for most fishes from adjacent seagrass beds, except for *Acanthurus chirurgus*, *Haemulon chrysargyreum*, *Mulloidichthys martinicus* and *Ocyurus chrysurus*. The question remains whether fish species sheltering in the mangroves during the daytime (see Nagelkerken et al. 2000a) do not use the mangroves as an important feeding habitat either. This question is addressed in Nagelkerken & van der Velde (2004, this issue).

Acknowledgements. This study was funded by the Schure-Beijerinck-Popping Fonds, with logistic support provided by the MSV 'Freewinds'. We are indebted to the captain Mr. M. Napier, the officers and crew of the MSV 'Freewinds' for all their support and help. We wish to thank the following persons for their help with catching the fish in the various bays and islands: E. Cocheret de la Morinière, M. Dorenbosch, B. Pollux, W. Verberk, M. Versteeg, M. Wiltjer, R. Kishore, J. Munro, R. Power and F. Franken. We also thank J. Eygensteyn for analysing the stable isotopes. This is Centre for Wetland Ecology publication no. 325.

LITERATURE CITED

- Bouillon S, Raman AV, Dauby P, Dehairs F (2002) Carbon and nitrogen stable isotope ratios of subtidal benthic invertebrates in an estuarine mangrove ecosystem (Andhra Pradesh, India). *Estuar Coast Shelf Sci* 54:901–913
- Bunn SE, Loneragan NR, Kempster MA (1995) Effects of acid washing on stable isotope ratios of C and N in penaeid shrimps and seagrass: implications for food-web studies using multiple stable isotopes. *Limnol Oceanogr* 40:622–625
- Cabana G, Rasmussen JB (1994) Modelling food chain structure and contaminant bioaccumulation using stable nitrogen isotopes. *Nature* 372:255–257
- Chong VC, Sasekumar A, Leh MUC, D'Cruz R (1990) The fish and prawn communities of a Malaysian coastal mangrove system, with comparisons to adjacent mud flats and inshore waters. *Estuar Coast Shelf Sci* 31:703–722
- Chong VC, Low CB, Ichikawa T (2001) Contribution of mangrove detritus to juvenile prawn nutrition: a dual stable isotope study in a Malaysian mangrove forest. *Mar Biol* 138:77–86
- Cocheret de la Morinière E, Pollux BJA, Nagelkerken I, van der Velde G (2002) Post-settlement life cycle migration patterns and habitat preference of coral reef fish that use seagrass and mangrove habitats as nurseries. *Estuar Coast Shelf Sci* 55:309–321
- Cocheret de la Morinière E, Nagelkerken I, van der Meij H, van der Velde G (2004) What attracts juvenile coral reef fish to mangroves: habitat complexity or shade? *Mar Biol* 144:139–145
- de Haan D, Zaneveld JS (1959) Some notes on tides in Annabaai harbour, Curaçao, Netherlands Antilles. *Bull Mar Sci Gulf Caribb* 9:224–236
- DeNiro MJ, Epstein S (1978) Influence of diet on the distribution of carbon isotopes in animals. *Geochim Cosmochim Acta* 42:495–506
- Fleming M, Lin G, da Silveira Lobo Sternberg L (1990) Influence of mangrove detritus in an estuarine ecosystem. *Bull Mar Sci* 47:663–669
- Fry B (1988) Food web structure on Georges Bank from stable C, N, and S isotopic compositions. *Limnol Oceanogr* 33:1182–1190
- Fry B, Arnold C (1982) Rapid $^{13}\text{C}/^{12}\text{C}$ turnover during growth of brown shrimp (*Penaeus aztecus*). *Oecologia* 54:200–204
- Fry B, Lutes R, Northam M, Parker PL (1982) A $^{13}\text{C}/^{12}\text{C}$ comparison of food webs in Caribbean seagrass meadows and coral reefs. *Aquat Bot* 14:389–398
- Fry B, Scalan RS, Parker PL (1983) $^{13}\text{C}/^{12}\text{C}$ ratios in marine food webs of the Torres strait, Queensland. *Aust J Mar Freshw Res* 34:707–715
- 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, San Diego, p 201–218
- Harrigan P, Zieman JC, Macko SA (1989) The base of nutritional support for the gray snapper (*Lutjanus griseus*): an evaluation based on a combined stomach content and stable isotope analysis. *Bull Mar Sci* 44:65–77
- Hemminga MA, Slim FJ, Kazungu J, Ganssen GM, Nieuwenhuize J, Kruijff 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
- Kitting CL, Fry B, Morgan MD (1984) Detection of inconspicuous epiphytic algae supporting food webs in seagrass meadows. *Oecologia* 62:145–149
- Kuenen MMCE, Debrot AO (1995) A quantitative study of the seagrass and algal meadows of the Spaanse Water, Curaçao, The Netherlands Antilles. *Aquat Bot* 51:291–310
- Lee SY (2000) Carbon dynamics of Deep Bay, eastern Pearl River estuary, China. II. Trophic relationship based on carbon- and nitrogen-stable isotopes. *Mar Ecol Prog Ser* 205:1–10
- Ley JA, Montague L, McIvor CC (1994) Food habits of mangrove fishes: a comparison along estuarine gradients in northeastern Florida Bay. *Bull Mar Sci* 54:881–899
- Lin G, Banks T, da Silveira 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
- Mann K (1972) Macrophyte production and detritus food chains in coastal waters. In: Melchiorri-Santolini U, Hopton JW (eds) Proc IBP-UNESCO Symp Detritus and Its Ecological Role in Aquatic Ecosystems, Rome. *Mem Ist Ital Idrobiol* 29:353–383
- Marguillier S, van der Velde G, Dehairs F, Hemminga MA, Rajagopal S (1997) Trophic relationships in an interlinked mangrove-seagrass ecosystem as traced by $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. *Mar Ecol Prog Ser* 151:115–121
- Minagawa M, Wada E (1984) Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between d^{15}N and animal age. *Geochim Cosmochim Acta* 48:1135–1140
- Nagelkerken I, van der Velde G (2004) Relative importance of interlinked mangroves and seagrass beds as feeding habitats for juvenile reef fish on a Caribbean island. *Mar Ecol Prog Ser* 274:153–159
- Nagelkerken I, Dorenbosch M, Verberk WCEP, Cocheret de la Morinière E, van der Velde G (2000a) Day-night shifts of fishes between shallow-water biotopes of a Caribbean bay, with emphasis on the nocturnal feeding of Haemulidae and Lutjanidae. *Mar Ecol Prog Ser* 194:55–64
- Nagelkerken I, Dorenbosch M, Verberk WCEP, Cocheret de la Morinière E, van der Velde G (2000b) Importance of shallow-water biotopes of a Caribbean bay for juvenile coral reef fishes: patterns in biotope association, community structure and spatial distribution. *Mar Ecol Prog Ser* 202:175–192
- Nagelkerken I, van der Velde G, Gorissen MW, Meijer GJ, van't Hof T, den Hartog C (2000c) Importance of mangroves, seagrass beds and the shallow coral reef as a nursery for important coral reef fishes, using a visual census technique. *Estuar Coast Shelf Sci* 51:31–44
- Nagelkerken I, Kleijnen S, Klop T, van den Brand RACJ, Cocheret de la Morinière E, van der Velde G (2001a) Dependence of Caribbean reef fishes on mangroves and seagrass beds as nursery habitats: a comparison of fish faunas between bays with and without mangroves/seagrass beds. *Mar Ecol Prog Ser* 214:225–235
- Nagelkerken I, van der Velde G, Cocheret de la Morinière E (2001b) Fish feeding guilds along a gradient of bay biotopes and coral reef depth zones. *Aquat Ecol* 35:73–86

- Newell RIE, Marshall N, Sasekumar A, Chong VC (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
- Nielsen LA, Johnson DL (1992) Fisheries techniques. American Fisheries Society, Bethesda
- Nieuwenhuize J, Maas YEM, Middelburg JJ (1994) Rapid analysis of organic carbon and nitrogen in particulate materials. *Mar Chem* 45:217–224
- Odum WE, Heald EJ (1975) The detritus-based food web of an estuarine mangrove community. In: Cronin LE (ed) *Estuarine research*. Academic Press, New York, p 265–286
- Phillips DL, Gregg JW (2001) Uncertainty in source partitioning using stable isotopes. *Oecologia* 127:171–179
- Primavera JH (1996) Stable carbon and nitrogen isotope ratios of penaeid juveniles and primary producers in a riverine mangrove in Guimaras, Philippines. *Bull Mar Sci* 58: 675–683
- Quinn NJ, Kojis BL (1987) The influence of diel cycle, tidal direction and trawl alignment on beam trawl catches in an equatorial estuary. *Environ Biol Fish* 19:297–308
- Rau GH, Mearns AJ, Young DR, Olson RJ, Schafer HA, Kaplan IR (1983) Animal $^{13}\text{C}/^{12}\text{C}$ correlates with trophic level in pelagic food webs. *Ecology* 64:1314–1318
- Robertson AI, Duke NC (1990) Mangrove fish-communities in tropical Queensland, Australia: spatial and temporal patterns in densities, biomass and community structure. *Mar Biol* 104:369–379
- Rodelli MR, Gearing JN, Gearing PJ, Marshall N, Sasekumar A (1984) Stable isotope ratio as a tracer of mangrove carbon in Malaysian ecosystems. *Oecologia* 61: 326–333
- Rooker JR (1995) Feeding ecology of the schoolmaster snapper, *Lutjanus apodus* (Walbaum), from southwestern Puerto Rico. *Bull Mar Sci* 56:881–894
- Rooker JR, Dennis GD (1991) Diel, lunar and seasonal changes in a mangrove fish assemblage off southwestern Puerto Rico. *Bull Mar Sci* 49:684–698
- Sasekumar A, Ong TL, Thong KL (1984) Predation on mangrove fauna by marine fishes. In: Soepadmo E, Rao AN, Macintosh DJ (eds) *Proc Asian Symp Mangrove Environment: Research and Management*. UNESCO, Kuala Lumpur, p 378–384
- Schwamborn R, Ekau W, Voss M, Saint-Paul U (2002) How important are mangroves as a carbon source for decapod crustacean larvae in a tropical estuary? *Mar Ecol Prog Ser* 229:195–205
- Sheaves M, Molony B (2000) Short-circuit in the mangrove food chain. *Mar Ecol Prog Ser* 199:97–109
- Slim FJ, Hemminga MA, Cocheret de la Morinière E, van der Velde G (1996) Tidal exchange of macrolitter between a mangrove forest and adjacent seagrass beds (Gazi Bay, Kenya). *Neth J Aquat Ecol* 30:119–128
- Stoner AW, Zimmerman RJ (1988) Food pathways associated with penaeid shrimps in a mangrove-fringed estuary. *Fish Bull* 86:543–551
- Thayer GW, Colby DR, Hettler WF (1987) Utilization of the red mangrove prop root habitat by fishes in south Florida. *Mar Ecol Prog Ser* 35:25–38
- Vance DJ, Haywood MDE, Heales DS, Kenyon RA, Lonergan NR, Pendrey RC (1996) How far do prawns and fish move into mangroves? Distribution of juvenile banana prawns *Penaeus merguensis* and fish in a tropical mangrove forest in northern Australia. *Mar Ecol Prog Ser* 131: 115–124

Editorial responsibility: Otto Kinne (Editor), Oldendorf/Luhe, Germany

Submitted: March 3, 2003; Accepted: March 18, 2004
Proofs received from author(s): June 11, 2004