Interlinkage between Caribbean coral reefs and seagrass beds through feeding migrations by grunts (Haemulidae) depends on habitat accessibility

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ABSTRACT: Tropical marine habitats are often energetically linked through feeding migrations by fish. A widely accepted assumption is that species of Haemulidae (grunts) undertake nocturnal feeding migrations from coral reefs to seagrass beds. This has been based on studies investigating migrations between small patch reefs and surrounding seagrass beds located in lagoons. Due to the size and location of these patch reefs, we argue that this does not represent migration from coral reef to seagrass ecosystems, and a literature search shows limited proof for such migration. We hypothesised that the spatial arrangement of these habitats in the seascape may have profound effects on the degree to which such migrations occur. *Haemulon flavolineatum* caught from seagrass beds located in semi-enclosed embayments, and thus isolated to a high degree from adjacent reefs, showed a diet and stable isotope signature of muscle tissue that differed from those collected from the coral reef. In contrast, fishes from open seagrass systems without restricted access from the reef showed the same stable isotope signature as those collected from the coral reef, suggesting feeding from the same habitat, viz. the seagrass beds. Additional visual census data showed that semi-enclosed seagrass beds did not have elevated densities of large-sized fish at night, which would be expected if large individuals from the reef migrated to the seagrass beds to feed. The data thus show that interlinkages between coastal ecosystems, such as coral reefs and seagrass beds, by fishes may strongly depend on the spatial arrangement of habitats within the seascape.

KEY WORDS: *Haemulon flavolineatum* · Coral reef · Seagrass · Feeding migrations · Habitat linkages · Stable isotopes · Diet analysis

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INTRODUCTION

Mangroves, seagrass beds and coral reefs occur along many shallow-water tropical shorelines. These ecosystems are connected through physical, biological and chemical processes, including exchange of nutrients, organic matter, sediment, water bodies and animals (Parrish 1989, Lee 1995, Wolanski 2007). In particular, fish and decapods link these systems through spawning, feeding, tidal and ontogenetic migrations. Various shrimp and reef fish use mangroves and seagrass beds as juvenile habitats before migrating to offshore adult habitats (Manson et al. 2005, Nagelkerken 2007, Verweij et al. 2008). Many species also show consistent tidal or diurnal migrations between habitats, alternatively using them as shelter and feeding areas (Helfman et al. 1982, Vance et al. 1996, Nagelkerken & van der Velde 2004, Verweij et al. 2006b). The scale,

timing and duration of these migrations are highly variable, however, and depend on a variety of biotic and environmental factors. The arrangement of mangrove, seagrass and reef habitats within the seascape has profound effects on the degree and type of ecological linkages between these habitats, and affects the spatial distribution of fishes (Pittman et al. 2004, 2007, Dorenbosch et al. 2007, Grober-Dunsmore et al. 2007).

Seagrass beds are attractive juvenile habitats for various fish species because of the high abundance of food, lowered predation risk resulting from the high structural complexity of the habitat at the small scale, a lower number of predators and reduced water clarity compared to the reef (Parrish 1989, Verweij et al. 2006a). For similar reasons, many crustaceans and other macroinvertebrate fauna utilise seagrass beds as shelter habitats (Orth et al. 1984), providing potentially high food abundance to fishes. Seagrass beds have therefore been recognised as important feeding habitats for fishes in the Indo-Pacific (e.g. Kochzius 1999, Unsworth et al. 2007) as well as the Caribbean (e.g. Ogden & Ehrlich 1977, Nagelkerken et al. 2000a), although most evidence comes from the latter region. Several studies have shown that fishes undertake nocturnal feeding migrations from structurally complex shelter habitats, such as mangroves, patch reefs, coral reefs, undercut notches and boulders, to more open habitats such as seagrass and algal beds (Ogden & Ehrlich 1977, Helfman et al. 1982, McFarland & Hillis 1982, Burke 1995, Nagelkerken et al. 2000a).

We tested whether the spatial arrangement of coral reefs relative to seagrass beds in the coastal seascape affects habitat linkages through feeding migrations by fishes. The reason for this is that there appears to be a discrepancy in the literature between the evidence and assumptions on feeding by reef fishes in seagrass beds. It is widely accepted that grunt species (Haemulidae), in particular *Haemulon flavolineatum*, *H. plumieri* and *H. sciurus*, undertake nocturnal feeding migrations from the reef to seagrass beds (e.g. Ogden & Ehrlich 1977, Helfman et al. 1982, McFarland & Hillis 1982). Reef habitats discussed in these studies are coral boulders or small patch reefs completely surrounded by seagrass beds and are all located within lagoons. Hence, they do not represent 'coral-reef-to-seagrass' migrations, but more so feeding migrations 'among back-reef habitats' located in the same lagoon. In the present study we argue that (1) there is little proof so far for true coral-reef-to-seagrass feeding migrations, (2) the studies that focused on feeding migrations to seagrass beds by grunts have been misinterpreted in many other studies and (3) nocturnal feeding in seagrass beds by Haemulidae from coral reefs depends on the degree of accessibility of the seagrass beds. Clearly, seagrass beds are attractive feeding sites for

grunts if they surround small patch reefs that provide daytime shelter sites. Whether this is also true for spatially separated seagrass beds and patch or fringing reefs, or for seagrass beds that are less accessible to fishes, remains unclear.

We first review the literature for studies of nocturnal fish feeding migrations to seagrass beds in the Caribbean, and provide examples of studies that have misinterpreted these results. We only refer to studies that have directly investigated migration of fishes (i.e. based on observations of fish migration by e.g. visual observations or fish tagging), and not studies inferring between-habitat migrations based on differences in size frequencies of fishes or based on qualitative observations. Furthermore, we provide gut content, stable isotope and visual census survey data to support our hypothesis that nocturnal feeding in seagrass beds by *Haemulon flavolineatum* from adjacent coral reefs depends on the accessibility of the seagrass beds. We expect that for spatially isolated seagrass beds, feeding migrations by reef-associated grunts towards the seagrass beds are less pronounced than has thus far been observed.

MATERIALS AND METHODS

Study area. To test the effect of accessibility of seagrass beds on nocturnal feeding by *Haemulon flavolineatum* from coral reefs, 3 'open' and 3 'semi-enclosed' seagrass systems were selected at various islands in the Western Atlantic (Fig. 1). Open seagrass beds were defined as systems located adjacent to coral reefs without any barriers in between the 2 habitats (Bermuda; Grand Cayman, Cayman Islands; St. Thomas, US Virgin Islands), whereas semi-enclosed seagrass beds were defined as systems located in semi-enclosed lagoons or bays devoid of any patch reef development with only a narrow entrance connecting them to the adjacent coral reef (Aruba; Spanish Water Bay and Piscadera Bay in Curaçao, Netherlands Antilles). Semi-enclosed seagrass systems occur circumtropically, typically in areas where environmental conditions (e.g. water turbidity, salinity, temperature) in embayments or lagoons are suitable for seagrass growth but not for patch reef growth, such as Caribbean embayments in Belize, Bermuda, Bimini, Bonaire and Grand Cayman. Open systems, which are very prominent in the Indo-Pacific region, are found circumtropically in areas where the shallow-shelf area is large with clear and calm water, allowing for seagrass as well as coral reef growth.

In Bermuda, the study area was located within Castle Harbour, a semi-enclosed basin at the eastern end of the island (Fig. 1). Well-developed seagrass beds consisting of *Thalassia testudinum* and *Syringodium*
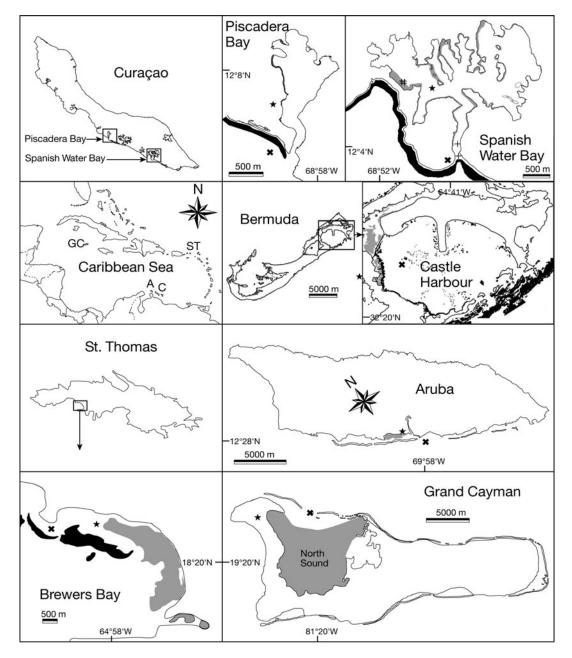
Fig. 1. Map of the study areas, showing the location of the seagrass beds (light grey), coral reefs (black), and fish collection sites (✖ = coral reef sites, ★ = seagrass sites). The continuous fringing coral reefs along the shorelines of Aruba and Grand Cayman are not shown. + = sites for visual census surveys on Curaçao. Fishes for which stable isotope analysis was done on the gut contents were collected at Spanish Water Bay from the sites marked with ✖, ★, and #. Inset Caribbean Sea: GC = Grand Cayman, A = Aruba, C = Curaçao, ST = St. Thomas. Bermuda is not shown on the inset but is located approx. 1540 km directly north of St. Thomas

filiforme occurred along the shallow western edge of the basin, which is bordered on the outside by a poorly developed fringing reef. There were numerous patch reefs scattered across the basin, and the large patch reef from which the samples were taken was located approximately 750 m from the nearest seagrass beds. The seagrass beds were separated from the patch reefs by bare sand at a depth of 6 to 9 m.

In the Cayman Islands, the seagrass beds were located in the North Sound of Grand Cayman (Fig. 1). This is a large marine lagoon connected on its outer edge to an emergent fringing reef. The substratum of the southern three-quarters of the North Sound was covered by *Thalassia testudinum* with associated macroalgal species. The substratum of the northern quarter was covered by a mixture of sand, rock bottom

and coral communities. The 'Wreck of the Pilot' seagrass collection site is a small wreck within a large area of *T. testudinum*, around which Haemulidae, Lutjanidae and other fish species congregated. The 'Barra Alley' reef site is a small channel through the emergent fringing reef with a small ledge along which *Haemulon flavolineatum* aggregated.

In St. Thomas, the seagrass beds located in Brewers Bay consisted of *Syringodium filiforme* mixed with sparse *Thalassia testudinum*. The seagrass and coral reef habitats were separated by a stretch of 100 to 400 m of bare sand (Fig. 1). At the east end of Brewers Bay, the coral reef consisted of large patch reefs at 4 to 6 m depth that merged to form a continuous fringing reef to the west.

In Aruba, the seagrass beds consisted of monospecific stands of *Thalassia testudinum* located in a shallow lagoon which was separated from the adjacent fringing reef by coral cays and a reef crest (Fig. 1). The open connection between the reef and the lagoon was about 0.5 to 4 m deep and about 450 m wide. The reef terrace was about 150 m wide and turned into a reef slope at 7 to 9 m depth up to a depth of about 25 m, where a sandy plain started.

In Curaçao, the seagrass beds consisted of monospecific stands of *Thalassia testudinum* in Spanish Water Bay and of *Syringodium filiforme* in Piscadera Bay. The seagrass beds in each bay were connected to the reef by only a narrow channel. The mouth of Spanish Water Bay was about 85 m wide and 6 m deep, while the mouth of Piscadera Bay was about 70 m wide and 6 m deep (Fig. 1). The adjacent fringing coral reef started from the shore as a gradually sloping submarine terrace of about 150 m wide, until it reached the 'drop-off' at a depth of approximately 7 to 9 m. At the drop-off, the reef sloped off steeply to about 50 to 60 m depth.

Sampling design. Although previous studies on grunt feeding migrations were carried out by following individual fishes (tagged or not tagged), we used stable isotope analysis of muscle tissue as an indicator of feeding migrations. The reason for this is that nocturnal fish feeding migrations or behaviour can be disturbed by using strobes during underwater surveys, and fish feeding may be difficult to observe in detail during night observations. By measuring stable isotopes in fish tissue, no effect of the methodology on fish migration or behaviour was present. At each reef site per island, 5 to 15 adult *Haemulon flavolineatum* ranging on average between 14.3 and 16.5 cm in fork length (FL) were collected at depths of 1.5 to 6 m, while at each seagrass site per island 9 to 30 juveniles ranging on average between 8.1 and 8.9 cm FL were collected at depths of 0.5 to 2 m (Table 1). *H. flavolineatum* reaches adulthood from approximately 14 cm FL (Gaut & Munro 1983). *H. flavolineatum* shows a strong ontogenetic shift in habitat use: juveniles are predominantly found in lagoonal habitats such as mangroves and seagrass beds, whereas adults mainly live and shelter on reefs at least during the daytime (Nagelkerken 2007). Hence, a comparison between adults from the 2 habitats was not possible. Sampling was carried out during daytime, in 1998 at Spanish Water Bay and 2001 to 2003 at the other localities. At each island the reef and seagrass fishes were collected simultaneously during the same time period.

For the stable isotope analysis, a small piece of muscle tissue was removed from each fish, dried for 48 h at 70°C, and ground to a fine powder using a mortar, pestle and liquid nitrogen. 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). Stable isotopes are well-suited to trace migrations of many animal species (see review by Hobson 1999). Carbon and nitrogen stable isotope compositions were measured with a Carlo Erba NA 1500 elemental analyser

Table 1. *Haemulon flavolineatum*. Sampling for stable isotope analysis. Length = mean fork length

Island	Location	Sampling habitat	Sampling depth (m)	No. of fish sampled	Length ± SD (cm)
Aruba	Mangel Alto	Coral reef	4–6	5	14.3 ± 1.3
		Seagrass bed	0.5	10	8.2 ± 0.7
Bermuda	Castle Harbour	Coral reef	2–4	9	15.9 ± 2.4
		Seagrass bed	1	9	8.9 ± 2.3
Curaçao	Piscadera	Coral reef	1.5–6	15	15.3 ± 1.0
		Seagrass bed	0.5–2	15	8.6 ± 1.2
	Spanish Water Bay	Coral reef	4–6	12	15.5 ± 0.8
		Seagrass bed	1–2	30	8.1 ± 1.5
Grand Cayman	Barra Alley	Coral reef	4.5	10	16.5 ± 0.6
	Wreck of the Pilot	Seagrass bed	1.5	10	8.7 ± 0.6
St. Thomas	Brewer's Bay	Coral reef	4–6	10	15.4 ± 1.2
		Seagrass bed	1–2	10	8.3 ± 0.8

coupled on-line via a Finnigan Conflo III interface with a ThermoFinnigan DeltaPlus mass spectrometer. Carbon and nitrogen isotope ratios are expressed in the delta notation ($\delta^{13}C$, $\delta^{15}N$) relative to the Vienna PeeDee Belemnite standard and atmospheric nitrogen. Average reproducibilities based on replicate measurements of standards (acetanilide, ammonium sulphate, and sucrose) for $\delta^{13}C$ and $\delta^{15}N$ were within 0.15‰.

For Curaçao, fish densities and diet data collected during earlier studies (Nagelkerken et al. 2000a) were also included to support the interpretation of the stable isotope data. Use of >1 method allows for stronger conclusions, and we therefore included these data from Curaçao even though they were not part of the original study design. Fish densities of *Haemulon flavolineatum* were estimated using visual census surveys during the daytime and at night in size classes of 2.5 cm at a reef site and seagrass site located 200 m from one another (Fig. 1). On the reef, 32 belt transects (3×50 m) distributed over the 2, 5, 10 and 15 m reef depth zones were sampled during the daytime, while at night 16 transects were surveyed. In the seagrass bed, a total of 4 transects were sampled at night and 8 transects during the daytime. For further details see Nagelkerken et al. (2000a).

Gut contents of fish caught in Curaçao were studied for the same fish used in the stable isotope analysis. Fish analysed for the reef were larger in size than those from the seagrass beds due to the strong differences in ontogenetic habitat use by this species. To test for the effects of ontogeny in the comparison between the reef and seagrass beds we therefore additionally analysed gut contents for the largest size class of *Haemulon flavolineatum* that we could find in the seagrass bed (mean ± SD: 12.7 ± 0.3 cm FL; see Table 3). 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 Amphipoda, Annelida, Bivalvia, Copepoda, Decapoda, Echinoidea, fish, Gastropoda, Isopoda, Mysidacea, sediment, Tanaidacea or unidentified. Diet composition was determined by estimating the relative volumetric quantity of food items, using a stereomicroscope.

During a consecutive field study in Curaçao in October 2007, we additionally collected gut contents of *Haemulon flavolineatum* for stable isotope analysis (Fig. 1) to confirm the different signatures of prey from the coral reef and seagrass food webs. We collected gut contents instead of living prey items, because it was difficult to (1) identify the specific prey species consumed from the gut contents, (2) identify the microhabitats where these prey species occurred and (3) sample these specific prey items due to their small size. Gut contents, on the other hand, reflect the true diet of the

fishes and could thus indicate differences in stable isotope values of consumed prey items between habitats. Gut contents could only be collected in Curaçao at Spanish Water Bay. Fish measured 13.2 ± 2.3 cm FL (mean ± SD) on the coral reef (n = 18) and 9.6 ± 1.1 cm on the seagrass beds (n = 14). Gut contents were treated and analysed for stable isotope analysis in the same way as the tissue samples.

RESULTS AND DISCUSSION

Current knowledge on nocturnal feeding migrations by Haemulidae

Only a few studies have investigated nocturnal feeding migrations of Haemulidae to seagrass beds (Table 2). The majority of these were done in the US Virgin Islands and assessed various aspects of the nocturnal migration behaviour of Haemulidae sheltering during daytime on coral boulders or (small) patch reefs that were completely surrounded by seagrass beds within a lagoon. These studies showed that the feeding migrations are linked to changing light levels, are often precisely timed, and take place along fixed migration pathways, as much as 1 km long, which gradually bifurcate into a dendritic pattern with an individual fish at the tip of each branch. These studies from the 1970s and early 1980s (Table 2) have been widely cited in the literature as proof of the existence of nocturnal feeding migrations from coral reefs to seagrass beds (e.g. by Tulevech & Recksiek 1994, Burke 1995, Kochzius 1999, Beets et al. 2003, Grober-Dunsmore et al. 2007, Unsworth et al. 2007), but in fact they report migrations from coral heads or small patch reefs located in lagoons to the directly surrounding seagrass beds within the same lagoon. The problem lies in the definition of a coral reef. Patch reefs located in seagrass beds within Caribbean lagoons are typically small areas of a few m^2 to a few 100s of m^2 in size. They are not comparable to a coral reef ecosystem, which is an entity covering large surface areas in excess of 10s to 100s of km^2 and functioning as a fairly independent ecosystem, such as atolls, and fringing and barrier reefs. Simply referring to 'reef to seagrass bed migration' based on results from patch reefs in lagoons leads to confusion.

True coral reef to seagrass migrations, i.e. between 2 ecologically and spatially separated coastal ecosystems, have not really been shown (Table 2). Burke (1995) and Beets et al. (2003) presented some preliminary data on the existence of nocturnal feeding migrations between spatially separated coral reefs and seagrass beds. Hence, the widely accepted idea that coral reef and seagrass ecosystems are energetically con-

Table 2. *Haemulon* spp. Studies assessing nocturnal feeding migrations from reef-like structures to adjacent seagrass beds. *M. annularis* = *Montastrea annularis, T. testudinum* = *Thalassia testudinum, S. filiforme* = *Syringodium filiforme*, np = data not provided, bordering = reef borders seagrass bed, FL = fork length, SL = standard length, TL = total length, USVI = US Virgin Islands. Formulas for conversion (from www.fishbase.org): SL = 0.5 + 0.83 × FL, TL = 1.1 + 1.09 × FL. Only fish tracking studies (visual, transponders, external tags) were included; anecdotal size-frequency-based studies that provide indirect data of movement were excluded

Location	Type of coral structure (max. diameter)	Location of coral structure (water depth)	Seagrass species	Distance coral to seagrass bed	Fish species	Fish size (cm)	Migration distance (m)	Source
Migration between patch reefs in lagoons and surrounding seagrass beds								
St. Croix, USVI	Patch reefs (<100 m)	In lagoon (2–3 m)	*T. testudinum* & *S. filiforme*	1–10 m	*H. flavolineatum* & *H. plumieri*	<15 and >15 SL	100–300	Ogden & Ehrlich (1977)
St. Croix, USVI	Patch reefs (<100 m)	In lagoon (2–3 m)	*T. testudinum* & *S. filiforme*	1–10 m	*H. flavolineatum* & *H. plumieri*	np; juveniles (< ~15)	100–150	Ogden & Zieman (1977)
St. Croix, USVI	Patch reefs (<100 m)	In lagoon (2–3 m)	*T. testudinum* & *S. filiforme*	1–10 m	*H. flavolineatum* & *H. plumieri*	~5–10 TL	~90	McFarland et al. (1979)
St. Croix, USVI	Patch reefs (~30 m)	In lagoon (4–6 m)	*T. testudinum* & *S. filiforme*	1–10 m	*H. flavolineatum* & *H. plumieri*	3–12 TL	8–30	Helfman et al. (1982)
St. Croix, USVI	*M. annularis* domes (<5 m)	In lagoon (2–3 m)	*T. testudinum* & *S. filiforme*	np	*H. flavolineatum* & *H. plumieri*	<12 SL	np	McFarland & Hillis (1982)
Key Largo, Florida	Patch reefs (<150 m)	On shallow shelf (<5 m)	np	0 to a few m	*H. plumieri*	21.0–25.5 TL	130–560	Tulevech & Recksiek (1994)
Migration between coral reefs and nearby seagrass beds								
Tobacco Caye, Belize	Gorgonian patch reef & coral rubble	On barrier reef (2–4 m)	*T. testudinum* & *S. filiforme*	~20–150 m	*H. flavolineatum* & *H. sciurus*	12.4–16.0 14.7–20.5 FL	0–199	Burke (1995)
St. John, USVI	*M. annularis* reef	On fringing reef (3–20 m)	*T. testudinum* & *S. filiforme*	np; bordering	*H. sciurus*	17.4–28.0 FL	87–767	Beets et al. (2003)

nected via fish feeding migrations should be re-evaluated by defining the type of reef that is referred to and by specifically designed experimental studies in order to gain a better understanding of migration between coral reef ecosystems and seagrass beds. Studies on this topic have largely been executed in the Caribbean. The few studies done so far in the Indo-Pacific were based on beach seine netting where the density data suggested nocturnal feeding migrations between coral reefs and seagrass beds by various fish species (Kochzius 1999, Unsworth et al. 2007).

Effect of accessibility of seagrass beds on cross-habitat feeding migrations

At island level, no significant difference in $\delta^{13}C$ (p > 0.228, *t*-test) was found for the 3 open seagrass systems between *Haemulon flavolineatum* from the seagrass beds and those from the adjacent coral reef (Fig. 2A). This indicates that the adult fish from the coral reef have a diet consisting of food items with a similar $\delta^{13}C$ as those from the seagrass beds. As stable carbon isotope signatures of food items typically differ between coral reefs and seagrass beds (Fry et al. 1983, Hemminga et al. 1994), this suggests that *H. flavolineatum* from the reef and the seagrass beds feed in the same habitat, which in this case would be the seagrass beds because juvenile *H. flavolineatum* are not known to migrate from the seagrass beds to the reef for feeding.

For the semi-enclosed seagrass systems juvenile *Haemulon flavolineatum* from the seagrass bed were significantly depleted in $\delta^{13}C$ (p < 0.013, *t*-test) compared to the adults from the adjacent coral reef (Fig. 2B). The gut contents of fish collected at Spanish Water Bay showed the same pattern (p = 0.046, *t*-test); $\delta^{13}C$ of gut contents were depleted by roughly 1‰ compared to that of the fish muscle tissues, which is a typical isotope fractionation between predator and prey (e.g. Fry 1988). The above clearly indicates that
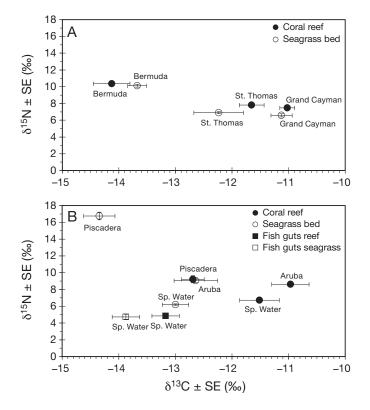
Fig. 2. *Haemulon flavolineatum*. Mean $\delta^{15}N$ and $\delta^{13}C$ values for muscle tissue of fish collected on the coral reef, and on (A) 'open' seagrass beds versus (B) 'semi-enclosed' seagrass beds. For Spanish Water Bay (Sp. Water), mean stable isotope values are additionally shown for gut contents

whereas individuals from the seagrass bed mainly consumed Tanaidacea (Table 3). Although gut contents differed between large fish on the reef and medium-sized fish in the seagrass beds, ontogenetic shifts in $\delta^{13}C$ and $\delta^{15}N$ can be ruled out as a factor causing the observed differences between stable isotope signatures on the reef versus the semi-enclosed seagrass beds. First, if stable isotope values were influenced by ontogeny then this effect would also be visible for the open seagrass systems, but here stable isotope values did not differ significantly between reef and seagrass beds, although different size classes were compared. Second, for none of the islands did $\delta^{15}N$ differ between different-sized fish from the 2 habitat types (for both open and closed systems), indicating that they act at the same trophic level. An exception was a much higher $\delta^{15}N$ value for medium-sized seagrass fishes in the eutrophicated Piscadera Bay than for large fish from the coral reef, which is opposite to the usual increase in trophic level for adult fish (e.g. Jennings et al. 2002).

The absence of feeding in semi-enclosed seagrass beds by adults from the coral reef in this setting is further supported by size frequency data of *Haemulon flavolineatum* from both habitats during day and night in Curaçao (Fig. 3). First, no increase in fish density was observed in the seagrass beds at night compared to daytime, which could have been caused by individuals migrating from the coral reef to the seagrass beds. Second, the larger size classes (10 to 20 cm), which likely possess a larger home range than the small individuals, were completely absent from the seagrass beds but remained present on the coral reef by day and night. The distance between the reef and the seagrass beds could not have played a major role because the sampled seagrass beds in the mouth of the Spanish Water Bay were located about 200 m away from the coral reef, and Haemulidae are known to undertake nocturnal feeding migrations up to 1 km (Ogden & Zie-

individuals from the 2 habitats consume food sources with a different $\delta^{13}C$, suggesting that they feed in different habitats. A difference in stable isotope signatures of prey items between the 2 habitats is supported in Curaçao by the different gut content signatures. The difference in diet is additionally supported by gut content data from Curaçao, where individuals from the reef fed primarily on Annelida, fish and Decapoda,

Table 3. *Haemulon flavolineatum*. Gut content (% volume) analysis from the Spanish Water Bay area, for adults from the coral reef and for juveniles from the seagrass bed (see Table 1), and additionally for large individuals (mean fork length ± SD: 12.7 ± 0.3 cm) from the seagrass beds. Values in bold indicate a relative identifiable food abundance of >10% in the gut. Amphi = Amphipoda, Anne = Annelida, Bival = Bivalvia, Cope = Copepoda, Deca = Decapoda, Echino = Echinoidea, Gastro = Gastropoda, Iso = Isopoda, Mysi = Mysidacea, Sed = sediment, Tana = Tanaidacea, Unid = unidentifiable

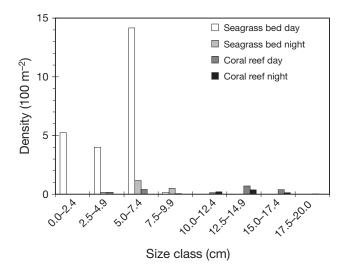| Location, type of fish	n	Amphi	Anne	Bival	Cope	Deca	Echino	Fish	Gastro	Iso	Mysi	Sed	Tana	Unid
Coral reef, large fish	12	4	**27**	3	2	**12**	2	**18**	6	2	1	20	0	1
Seagrass bed, juveniles	30	1	0	0	0	**11**	0	3	6	0	0	13	**39**	26
Seagrass bed, large fish	6	0	3	0	0	0	0	0	0	0	0	0	**55**	41

Fig. 3. *Haemulon flavolineatum*. Density distribution for different size classes (fork length [FL]) on the seagrass beds and coral reef in the Spanish Water Bay area, at night and during the daytime

man 1977; Table 2). The restricted width and depth of the channels connecting the coral reefs to the lagoon in Aruba and the 2 bays in Curaçao (Fig. 1), respectively, may reduce the likelihood of reef individuals finding and entering the seagrass beds compared to open seagrass systems. Hence, the larger the interface is between the reef and the adjacent seagrass beds, the higher the number of fish which may find and migrate to the seagrass beds.

One might argue that adult *Haemulon flavolineatum* from the reef do feed in semi-enclosed seagrass systems, but consume food items with a different $\delta^{13}C$ than the juveniles in the seagrass beds, resulting in the observed difference in $\delta^{13}C$ between individuals from the reef and those from the seagrass beds. This argument can be discarded on the basis of 3 different observations. First, large juvenile *H. flavolineatum* (mean length: 12.7 cm, range: 12.3 to 13.0 cm) resident in the seagrass beds of Spanish Water Bay primarily consumed Tanaidacea, just as the medium-sized juveniles (mean: 8.1 cm, range: 5.8 to 11.0 cm) in the seagrass beds did, whereas adult individuals (mean: 15.5 cm, range: 14.4 to 16.7 cm) on the coral reef never consumed Tanaidacea (Table 3). The similarity in diet between medium- and large-sized individuals from the seagrass beds suggests that primary feeding on Tanaidacea does not change through ontogeny as long as the fish are residing in the seagrass beds. On the coral reef they must depend on other food items as Tanaidacea occur in low abundances there: 5 vs. 229 Tanaidacea dm^{-3} in the substratum, and 2 vs. 1172 Tanaidacea m^{-3} in the water layer above the substratum, on the reef and seagrass

beds, respectively (I. Nagelkerken unpubl. data). Hence, large individuals collected on the reef would be expected to show a diet largely based on Tanaidacea (just as the large individuals collected on the seagrass beds), should they indeed feed on the seagrass beds at night. However, their diet did not include a single specimen of Tanaidacea. Second, Piscadera Bay is highly eutrophicated with sewage effluent overflow from the nearby municipal sewage treatment plant at Klein Hofje (Buth & Ras 1992), which caused the highly enriched $\delta^{15}N$ values of juveniles in the seagrass beds of the bay compared to the fish from the reef (Fig. 2B). When marine habitats are eutrophicated by sewage effluents, nearly the entire food web is enriched in $\delta^{15}N$ (e.g. Schlacher et al. 2005). Hence, independent of what specific food items the individuals from the reef consume, their significant depletion of 7.6‰ in $\delta^{15}N$ (p < 0.001, *t*-test) compared to the individuals from the seagrass beds of Piscadera Bay shows that they do not consume any food from the seagrass beds or other bay habitats, as this would have resulted in an enrichment in $\delta^{15}N$ for the reef individuals. Third, it has been shown worldwide that stable carbon signatures of food webs typically differ between coral reefs and seagrass beds (Fry et al. 1983, Hemminga et al. 1994), which would explain the observed difference in $\delta^{13}C$ between fish from, and foraging within, different habitat types. The effect of seasonality on feeding and stable isotope values was not investigated here, but samples for seagrass–reef comparisons were taken at the same time for the various study locations.

The present study demonstrates that the spatial arrangement of habitats is an important factor influencing their ecological linkages. Distance to other habitats and patch size affect the composition of tropical coastal fish communities (Dorenbosch et al. 2007, Grober-Dunsmore et al. 2007). Likewise, distance to coral reefs seems to affect the fish assemblage of seagrass beds significantly (Weinstein & Heck 1979, Nagelkerken et al. 2000b). This means that resource management should be based on managing habitat mosaics and their configuration rather than single habitats. This is important for management-related issues such as location and size selection of marine protected areas (MPAs).

In conclusion, the present study suggests that the degree of accessibility of the seagrass beds determines the degree to which adult *Haemulon flavolineatum*, and possibly other fish species, migrate from coral reefs to adjacent seagrass beds to feed. The configuration of habitat patches within a seascape influences their degree of interlinkage by fish migration, affects fish migration patterns, and has a strong impact on the feeding ecology of reef fishes.

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