RESEARCH ARTICLE

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Caribbean mangroves and seagrass beds as daytime feeding habitats for juvenile French grunts, *Haemulon flavolineatum*

Abstract Caribbean seagrass beds are important feeding habitats for so-called nocturnally active zoobenthivorous fish, but the extent to which these fishes use mangroves and seagrass beds as feeding habitats during daytime remains unclear. We hypothesised three feeding strategies: (1) fishes feed opportunistically in mangroves or seagrass beds throughout the day and feed predominantly in seagrass beds during night-time; (2) fishes start feeding in mangroves or seagrass beds during daytime just prior to nocturnal feeding in seagrass beds; (3) after nocturnal feeding in seagrass beds, fishes complete feeding in mangroves or seagrass beds during the morning. We studied the effect of habitat type, fish size, social mode and time of day on resting and feeding behaviour of large juvenile (5–10 cm) and sub-adult (10–15 cm) *Haemulon flavolineatum* in mangroves and seagrass beds during daytime. Sub-adults occurred in mangroves only, spent most time on resting, and showed rare opportunistic feeding events (concordant with strategy 1), regardless of their social mode (solitary or schooling). In contrast, large juveniles were present in both habitat types and solitary fishes mainly foraged, while schooling fishes mainly rested. Exceptions were small juveniles (±5 cm) in seagrass beds which foraged intensively while schooling. Large juveniles showed more feeding activity in seagrass beds than in mangroves. In both habitat types, they showed benthic feeding, whereas pelagic feeding was observed almost exclusively in the seagrass beds. In both habitat types, their feeding activity was highest during 8:00–10:30 hours (concordant with strategy 3), and for seagrass fishes, it was also high during 17:30–18:30 hours (concordant with strategy 2). The study shows that both mangroves and seagrass beds provide daytime feeding habitats for some life-stages of *H. flavolineatum*, which is generally considered a nocturnal feeder.

Introduction

Mangroves and seagrass beds are used as shelter habitats during daytime by juveniles and sub-adults of nocturnally active species of grunts (Haemulidae) and snappers (Lutjanidae) (e.g. Cocheret de la Morinière et al. 2004; Verweij et al. 2006). On Caribbean islands tidal fluctuations are small (see http://www.tidesandcurrents.noaa.gov/) and mangroves are often permanently inundated and accessible for fish. At dusk, Haemulidae and Lutjanidae leave their daytime shelter and migrate to adjacent seagrass beds and sandy seabeds to feed on macro-invertebrates during the night (e.g. Rooker and Dennis 1991; Burke 1995; Nagelkerken et al. 2000b; Ley and McIvor 2002). Based on these nocturnal feeding migrations and on the high abundance of invertebrate prey species in seagrass beds, it has always been hypothesised that seagrass beds are important feeding grounds for nocturnally active fish species (Ogden and Zieman 1977; Orth et al. 1984; Pollard 1984; Nagelkerken et al. 2000b). In the Indo-Pacific, where most mangroves are only inundated and accessible during high tide due to large tidal fluctuations, for some fish species mangroves function as a feeding habitat too. These fishes perform tidal feeding movements from creeks, mud flats and seagrass beds to adjacent mangroves at high tide (Sasekumar et al. 1984; Robertson and Duke 1990; Vance et al. 1996; Sheaves

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and Molony 2000). In contrast to the Indo-Pacific, Caribbean mangroves do not appear to function as important feeding habitats for fishes from adjacent seagrass beds (Nagelkerken and van der Velde 2004a, b).

To what extent Caribbean fringing mangroves function as feeding habitats for fishes that reside in the mangroves during daytime, as opposed to those residing in seagrass beds, remains unclear. Stable carbon isotope analysis of juvenile Haemulidae and Lutjanidae has indicated that fishes sheltering in seagrass beds during daytime primarily feed in the seagrass beds, whereas those sheltering in mangroves during daytime primarily feed in the mangroves (Nagelkerken and van der Velde 2004b). Also, gut content analysis of juvenile Lutjanidae collected from the mangroves has shown that these fishes feed there (Thayer et al. 1987; Rooker 1995). This raises questions on the exact frequency and timing of diurnal feeding by so-called nocturnally active zoobenthivores. Although for nocturnally active zoobenthivores, the function of the mangroves and seagrass beds during daytime is probably more closely related to providing shelter than to supplying food (Cocheret de la Morinière et al. 2004; Verweij et al. 2006) opportunistic feeding may take place during the day (Nagelkerken and van der Velde 2004b). Qualitative studies and gut content analyses indeed suggest opportunistic daytime feeding for Lutjanidae (Starck 1971; Rooker 1995; Kamukuru and Mgaya 2004) and Haemulidae (Hobson 1965).

Based on Nagelkerken and van der Velde (2004b) the following hypotheses were formulated for nocturnally active zoobenthivores that spend their daytime in the mangroves or in seagrass beds: (1) fishes feed opportunistically in the mangroves or seagrass beds throughout the day and feed predominantly in seagrass beds during the night; (2) fishes start feeding in mangroves or seagrass beds during daytime just prior to nocturnal feeding in the seagrass beds; (3) after nocturnal feeding in the seagrass beds, the fishes complete feeding in the mangroves or seagrass beds during a certain part of the morning. Which feeding strategies are used by supposedly nocturnally active zoobenthivores that dwell in mangroves and seagrass beds remains largely unanswered due to a lack of in-depth quantitative behavioural studies.

The present study therefore investigated the diurnal behaviour of juvenile and sub-adult *Haemulon flavolineatum* in mangroves and seagrass beds of a bay on the Caribbean island of Curaçao. In this bay, the smallest juveniles of this species shelter in seagrass beds and mangroves during daytime and show increasing preference for the mangrove habitat with increasing body size (Cocheret de la Morinière et al. 2002; Nagelkerken et al. 2000a). It was expected that these size-related sub-populations show different feeding strategies, because recently settled grunts are zooplanktivores that feed during daytime, whereas larger individuals are nocturnally active zoobenthivores that apparently do not feed during the day (Ogden and Ehrlich 1977; McFarland 1980; Helfman et al. 1982). We therefore hypothesised that diurnal feeding is more important for the smaller than for the larger

fishes. The primary goal of this study was to investigate how the two suggested sub-populations of different size classes of *H. flavolineatum* spend their diurnal time-budget in mangroves and seagrass beds, with emphasis on the feeding strategies as hypothesised above.

Materials and methods

Study area

The study was carried out during January–March 2004, and during June–August 2005 in the Spanish Water Bay (surface area $\pm$ 3 km^2) at the south-western coast of Curaçao, Netherlands Antilles (Fig. 1). The bay has a narrow (70 m wide) and shallow (5–6 m deep) mouth, and a relatively long (1.1 km) and deep (11–18 m) channel that connects the inland bay to the sea and a fringing reef. Other parts of the bay are relatively shallow (<6 m). The mean daily tidal range is about 30 cm (de Haan and Zaneveld 1959). Besides rainwater, the bay has no freshwater input. The shoreline of the bay consists partly of fossil coral reef and is fringed by mangroves, predominantly *Rhizophora mangle*, which roots are permanently inundated. Seagrass beds, predominantly *Thalassia testudinum*, and macro-algal flats cover the bottom of the bay (Kuenen and Debrot 1995).

Behaviour observations were carried out in six fringing *R. mangle* stands and in two monospecific *T. testudinum* beds (Fig. 1). At all sites, mangroves were separated from the adjacent seagrass bed by a strip of mud and sand of approximately 3 m wide. Shoot density and leaf height were measured at one of the two seagrass beds and were on average ($\pm$ SD) 338$\pm$67 m^{-2} and 14.1$\pm$4.7 cm, respectively. The mean water depth at the border of the mangrove stands and at the seagrass bed was 1–2 m. The mean underwater visibility as measured by horizontal Secchi distance at the border of the mangrove stands and at the seagrass bed was 5–6 m.

Observations

Behavioural observations were carried out at three time intervals during daytime in mangroves and seagrass beds: 8:00–10:30 hours (T1), 11:45–14:15 hours (T2) and 15:30–17:30 hours (T3). Fishes in the seagrass bed were observed at an additional fourth time interval just before sunset: 17:30–18:30 hours (T4). At T4, light intensities diminished quickly and hence detailed behaviour observations inside the shaded mangroves were not possible. Nevertheless, a few superficial observations were conducted at this time, during which small groups of individuals were observed for 15 min, and the number of foraging and non-foraging fish was recorded after each minute. Night-time behaviour observations could not be performed because fishes were startled and either froze or swam away when lit by a flashlight. Several aspects of the night-time feeding in the Spanish

Fig. 1 Map of the Spanish Water Bay in Curaçao (*C*) with the study sites (*encircled*). Fish behaviour in the mangroves was studied at sites 2–7, whereas that in the seagrass beds was studied at sites 1 and 4
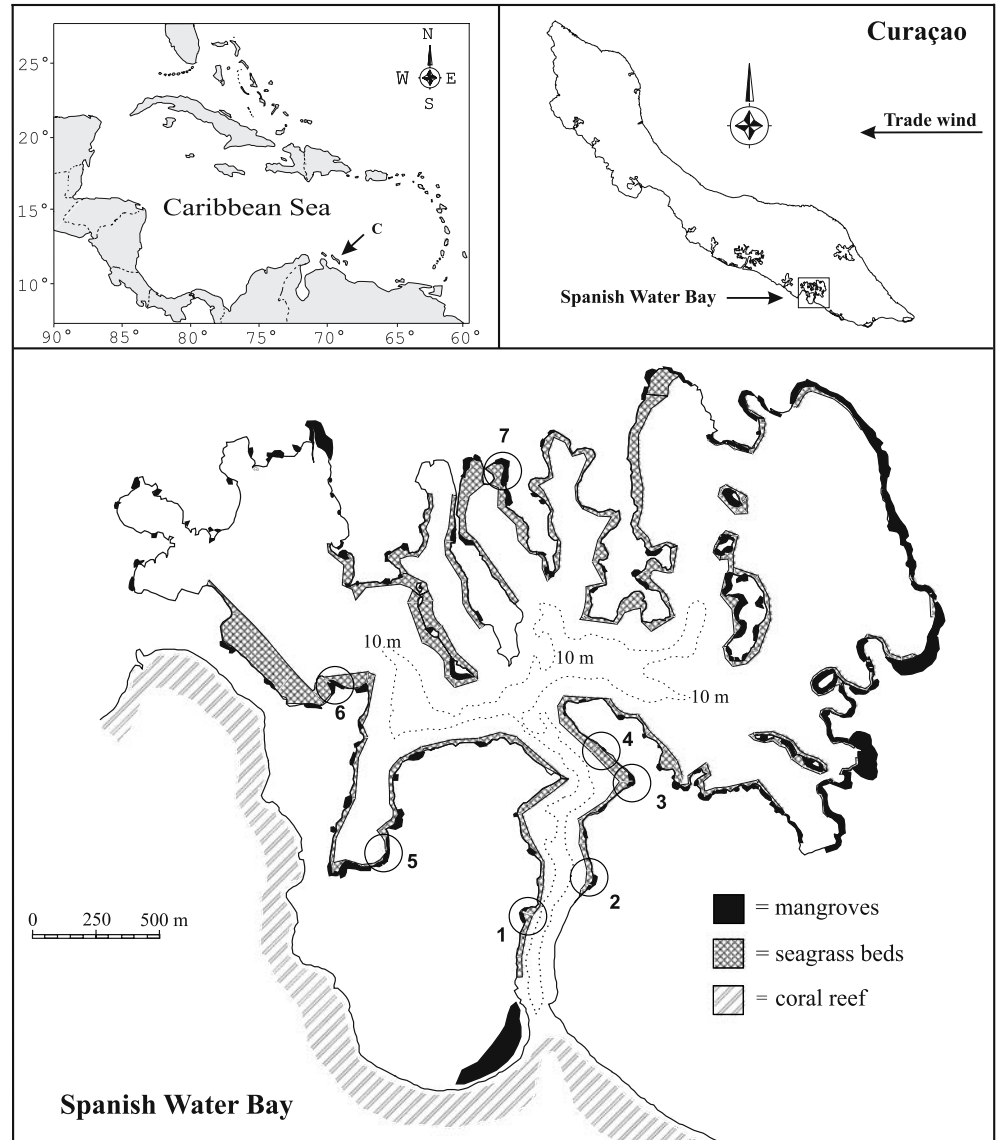

Water Bay have been reported in Nagelkerken et al. (2000b).

Fishes could be ascribed to two social modes: schooling or solitary. A fish was regarded to be in a school when it was closer than 20 cm to at least two conspecifics. The size of observed fishes was between 5 and 15 cm, and because the maturation size of this species is about 15.5 cm (Starck 1971; Claro 1983; Munro 1983) all individuals observed in this study were juveniles or sub-adults. Fishes were furthermore ascribed to two size classes: large juveniles (5–10 cm) that occurred both in the mangroves and in the seagrass bed and sub-adults (10–15 cm) that occurred exclusively in the mangroves. The size of observed fish was estimated visually in 2.5 cm length classes or to the nearest centimetre.

The number of fishes observed was 8 or 9 per habitat type, per social mode, per size class and per time interval (see Fig. 2), with a total of 156 observed fishes. The following combinations of factors could not be studied: observations in the mangroves were not possible during T4, schooling fishes were not present in seagrass beds during T2, and sub-adults were not present in seagrass beds at any time interval.

All observations were carried out by two snorkelling observers. Individual fishes were observed for 15 min by one observer during which the time budget (measured in seconds) of resting, swimming, and feeding behaviour (see Table 1) was recorded. Agonistic interactions were recorded as well, but results were omitted due to lack of trends. Observations were aborted before 15 min had passed if an individual was lost from sight or changed from social mode or habitat type. When referring to "feeding behaviour" or "feeding activity" both "searching for food" and "taking a bite" is meant.

a) Large juveniles in mangroves

b) Sub-adults in mangroves

c) Large juveniles in seagrass beds
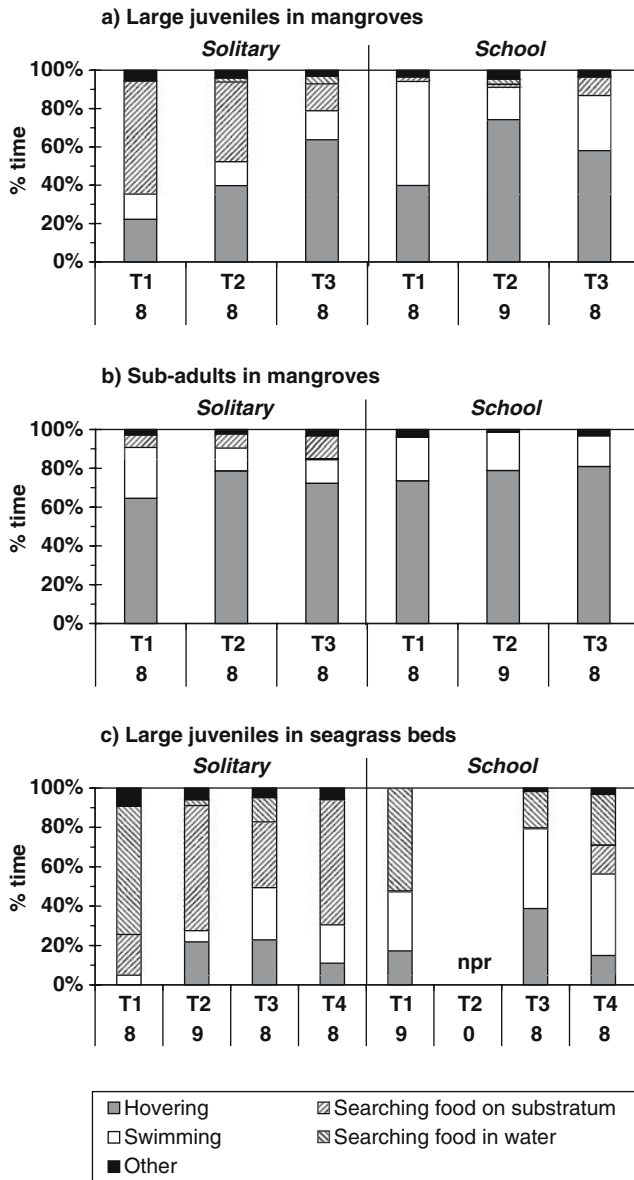
Fig. 2 Time budget (mean % of time) of all types of behaviour of *Haemulon flavolineatum*: **a** large juveniles (5–10 cm) in the mangroves, **b** sub-adults (10–15 cm) in the mangroves and **c** large juveniles (5–10 cm) in the seagrass beds during different time (*T*) intervals. *Left parts* of the graphs show averages for solitary juveniles while *right parts* show averages for schooling juveniles. Numbers below time intervals (*x*-axis) represent number of fishes observed. Observations during T4 were not possible in the mangroves and during T2 no schooling were fishes present ("npr") in the seagrass beds. "Other" refers to short behavioural events: taking bites (see Fig. 3) and agonistic interactions

Data analysis

Because we were primarily interested in resting and feeding behaviour, the behavioural types that we analysed statistically were the percentage time spent on "hovering" and on "searching for food" (for which searching for food in the water column and on a substratum were pooled), and the number of bites taken per minute.

To determine whether there was size-based variation in behaviour within the two 5 cm size classes we assigned, simple linear regressions were performed (SPSS version 11.5) between fish size and all behavioural types analysed statistically (see above) for both habitat types (mangroves and seagrass beds) and both size classes (5–10 and 10–15 cm) separately. For fishes of which the size was estimated in 2.5 cm size classes we used the middle value of this size class as an approximate of individual fish size (e.g. size class 5.0–$7.5 = 6.25$ cm). There was no strong linear relationship between fish size and behaviour (% time hovering: $R^2 \leq 0.088$, $P \geq 0.024$, % time searching for food: $R^2 \leq 0.069$, $P \geq 0.068$, number of bites: $R^2 \leq 0.097$, $P \geq 0.030$) per habitat type, within each size class. Therefore, fish size was not included as a covariable in other statistical tests, and we assume that the size-variation within the two size classes did not affect the results.

All further analyses were performed with Statistica 7.0. Arcsine-square root transformations did not improve normality of the percentage data, mainly because the data tended to have a bimodal distribution. Therefore, percentage data were divided in four categories: 0–$25\% =$ category 1; 25–$50\% =$ category 2; 50–$75\% =$ category 3; 75–$100\% =$ category 4. These ordinal categorical data were analysed with a multinomial ordinal regression (MO) using a logit link function (e.g. Ananth and Kleinbaum 1997). The number of bites were analysed using a Poisson regression (PO). Since these observed counts tended to be overdispersed compared to Poisson variance, a correction was applied using the scaled deviance as an estimate for the dispersion parameter (McCullagh and Nelder 1989).

Because there were no observations during T4 in the mangroves, T4 observations in the seagrass bed were omitted from MO and PO regressions. Fully factorial models could not be fitted for all fish in the mangroves and the seagrass beds because sub-adults were not present in the seagrass beds. Therefore, we fitted two separate models that partly overlapped. The first model included only fishes in the mangroves, with independent factors being: size class (large juveniles and sub-adults), time interval (T1, T2, T3) and social mode (solitary or schooling). The second model included only large juveniles (present in both mangroves and seagrass beds), with independent factors being: habitat type (mangroves or seagrass beds), time interval (T1, T2, T3) and social mode (solitary or schooling). Full models included all factors and all two-way interactions. Three-way interactions could not be fitted due to lack of data. Final models were analysed by using standard log-likelihood ratio Type III tests (McCullagh and Nelder 1989).

When analysing time spent on searching for food by fishes in mangroves, the MO test could not incorporate schooling individuals, because they all belonged to category "1" (0–25% of time spent on searching for food, see Fig. 2a, b) and variation within this group was too low to enable statistical analysis. Therefore, schooling individuals were omitted from the MO regression when testing

Table 1 Description of all analysed types of behaviour of *Haemulon flavolineatum*

Resting (hovering)	Staying in one spot in the water column, manoeuvering only in order to maintain the same position (resting behaviour).
Swimming	Moving to another location by moving body and fins.
Feeding: searching for food (foraging)	
On a substratum	Systematically searching a substratum (e.g. sand, seagrass leaves, macro-algae) for food. The head is pointed downwards and the fish scans the substrate with its eyes.
In water column	Jerkily swimming short distances, while clearly spotting and focussing their eyes on food particles floating in the water column.
Eating	Putting mouth to the substratum or particle in the water column and taking a bite. When taking a mouthful of sand, the grunt was often seen "chewing" (the opercula moved and the mouth opened and closed) and ejecting the sand particles through mouth and gills after a few seconds.[a]

[a] Pushing sediment through the gill-rakers is a way to filter out small zoobenthos, e.g. also shown by cichlids (Baerends and Baerends-van Roon 1950)

time spent on searching for food by fishes in mangroves, and the test was performed for solitary fishes only (see Table 2). A non-parametric Mann–Whitney *U* test examined the single effects of social mode on % time spent on searching for food by mangrove fishes.

Results

Resting behaviour

In the mangroves, *H. flavolineatum* on average spent most of their time on hovering (Fig. 2a, b). This behaviour was significantly affected by fish size and time of day (Table 2). In the mangroves, sub-adult fishes spent more time on hovering than large juveniles (Fig. 2a, b). The effect of time was only clearly visible for large solitary juveniles that spent an increasing amount of time on hovering as time of day proceeded (Fig. 2a).

For large juveniles in seagrass beds and mangroves, the percentage time spent hovering was significantly affected by habitat type, social mode and time (Table 2). Large juveniles in the seagrass beds spent less time on hovering than large juveniles in the mangroves (Fig. 2a, c). Schooling fishes in both habitat types on average spent more time on hovering than solitary fishes (Fig. 2a, c). Large juveniles spent less time on hovering during T1 than during T2 and T3 (Fig. 2a, c), and for fishes in the seagrass beds, time spent on hovering was low during T4 as well (Fig. 2c).

Feeding behaviour

In the mangroves, solitary *H. flavolineatum* spent significantly more time on searching for food than schooling fishes (Fig. 2a, b; Mann–Whitney *U* test, $Z = -3.029$, $P = 0.002$) and solitary fishes took significantly more bites per minute than schooling fishes that practically did not feed (Fig. 3, Table 2). Large juveniles spent significantly more time on searching for food than sub-adults

Table 2 Results of the multinomial ordinal regressions ('MO') and Poisson regressions ('PO'), testing the effects of habitat type ('Hab'), social mode ('SoMo'), size class ('Size') and time of day ('Time') on fish behaviour

	Mangroves only (large juveniles and sub-adults)			Large juveniles only (habitat: mg and sg)		
Type test	MO	MO	PO	MO	MO	PO
Type behaviour	Hov.	SF all	# Bites	Hov.	SF all	# Bites
Single factors						
Hab	–	–	–	**	***	***
SoMo	NS	MWU	***	**	***	***
Size	***	**	***	–	–	–
Time	**	NS	NS	**	*	**
Interactions						
Hab × SoMo	–	–	–	NS	NS	NS
Hab × Size	–	–	–	–	–	–
Hab × Time	–	–	–	NS	NS	NS
SoMo × Size	NS	NS	NS	–	–	–
SoMo × Time	NS	NS	NS	NS	NS	NS
Time × Size	NS	NS	**	–	–	–

MWU Mann–Whitney *U* test, which analysed the effect of social mode on time spent on 'SF all' for fishes in mangroves; the results are given in the text of the Results section

Hov. time spent on hovering, *SF all* time spent on searching for food in the water column and on a substratum pooled together, *# Bites* number of bites, *mg* mangroves, *sg* seagrass beds, – factors not possible to test, *NS* not significant

*$0.01 < P < 0.05$, **$0.001 < P < 0.01$, ***$P < 0.001$
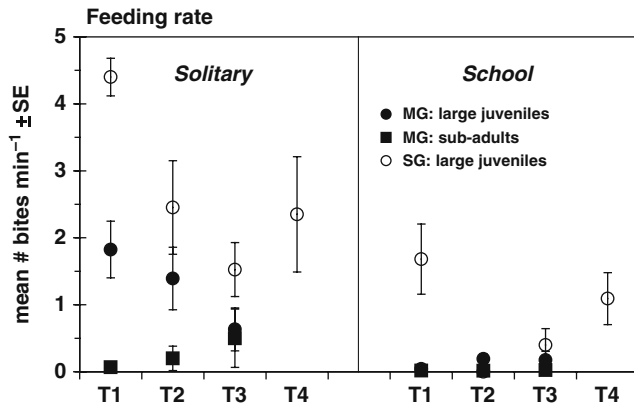
Feeding rate

Fig. 3 Feeding rate expressed as mean number of bites per minute of total observation time for large juvenile and sub-adult *Haemulon flavolineatum* in the mangroves ('MG'), and for large juveniles in the seagrass beds ('SG'). The *left part* of the graph shows averages for solitary fishes per time interval; the *right part* for schooling fishes. Observations during T4 were not possible in the mangroves and during T2 no schooling fishes were present in the seagrass beds

(Fig. 2a, b, Table 2). The effect of size was also reflected by the feeding rate of fishes in the mangroves: there was a significant size × time effect on the feeding rate (Table 2). For solitary large juveniles the feeding rate decreased during the day, whereas solitary sub-adults had a much lower feeding rate that increased slightly during the day (Fig. 3).

The superficial observations on fish behaviour in the mangroves during T4 indicated that almost no feeding behaviour took place in this habitat type at dusk. However, large juveniles were seen moving out of the mangroves to the adjacent strip of muddy substratum at T3 and T4, where they foraged actively and were feeding alone or in small schools.

In mangroves and seagrass beds, large juveniles spent significantly less time on searching for food and showed a lower feeding rate when schooling than when solitary (Figs. 2a, c, 3, Table 2). Solitary juveniles spent more time on searching for food and showed a higher feeding rate in the seagrass bed than in the mangroves (Figs. 2a, c, 3, Table 2). A different type of food searching behaviour was observed between fishes in the mangroves and seagrass bed. Large juveniles in seagrass beds were searching for food both in the water column (mostly during T1) and on a substratum (i.e. sand, deposited sediment on macro-algae and seagrass leaves), whereas those in the mangroves almost exclusively searched for food on a substratum (i.e. sand, mud, deposited sediment on macro-algae and mangrove prop-roots) (Fig. 2b, c). The fishes that were searching for food in the water column were all approximately 5 cm in size. The feeding rate was higher when searching for food in the water column than when searching for food on a substratum: large juveniles in the seagrass bed searching for food in the water column took 1.4 times more bites per minute of foraging compared to fishes in the mangroves and seagrass bed that were searching for food on a substratum (Table 3).

Table 3 Feeding rate of foraging *Haemulon flavolineatum* in the mangroves ('MG') and seagrass beds ('SG'), expressed as mean (± SE) # bites taken per minute of searching for food on a substratum ('SF sub') and in the water column ('SF wat')

	SF sub	SF wat	N (SF sub, SF wat)
Large juveniles MG	3.0 (±0.3)	2.9 (±0.4)	19, 4
Sub-adults MG	2.1 (±0.5)	no	10, 0
Large juveniles SG	3.0 (±0.4)	4.1 (±0.3)	30, 27

For sub-adults in the mangroves, searching for food in the water column was not observed ('no'). *N* is the total number of individuals observed searching for food on a substratum and in the water column, respectively

Another difference between habitat types was that schooling juveniles (size approx. 5 cm) in seagrass beds spent substantial time on searching for food in the water column and were seen to take bites, whereas schooling juveniles in the mangroves only very rarely showed any feeding behaviour (Figs. 2a, c, 3). In both habitat types feeding behaviour decreased over the period T1–T2–T3, except for schooling large juveniles in the mangroves (Figs. 2a, c, 3). Additionally, for fishes in the seagrass beds, time spent on searching for food and the feeding rate increased during T4, compared to T3 (Figs. 2c, 3).

Discussion

The present study shows that during daytime *H. flavolineatum* use fringing mangroves both as a shelter and feeding habitat and seagrass beds mainly as a feeding habitat. *H. flavolineatum* used mangroves more intensively as a shelter habitat than seagrass beds, since: (1) fishes in mangroves showed lower feeding activity and higher resting activity compared to those in the seagrass beds, (2) inactive resting schools were present all day in mangroves, whereas they were absent during mid-day in seagrass beds and (3) resting sub-adults were only present in the mangroves. The inactivity of diurnal resting schools of juvenile grunts on patch reefs is generally known (e.g. Ogden and Ehrlich 1977; McFarland and Hillis 1982) and the daytime shelter function of mangroves and seagrass beds to these fish has been established before (Cocheret de la Morinière et al. 2004; Verweij et al. 2006). In contrast, the importance of mangroves and seagrass beds as daytime feeding habitats has not been quantitatively studied before.

The higher benthic feeding activity observed for solitary large juvenile *H. flavolineatum* in seagrass beds compared to those in the mangroves can possibly be explained by a higher availability of prey species in the seagrass habitat. *H. flavolineatum* primarily feeds on macro-invertebrates, and specifically on Tanaidacea (Nagelkerken et al. 2000b; Cocheret de la Morinière et al. 2003), which are more abundant in the seagrass beds than in the mangroves of the Spanish Water Bay (Nagelkerken et al. 2000b; Cocheret de la Morinière 2002). This is prob-

ably also true for the schooling juveniles of 5 cm in the seagrass beds that are known to feed mainly on Copepoda (Cocheret de la Morinière et al. 2003). Copepoda showed high abundances on the seagrass beds of Spanish Water Bay (Nagelkerken et al. 2000b). The high feeding rate observed for seagrass fishes was due to the high occurrence of pelagic feeding in the seagrass bed, for which the feeding rate was 1.4 times higher compared to that of benthic feeding. The feeding rate may be higher for pelagic foraging compared to benthic foraging because prey items swimming freely in the water column are probably easier to catch compared to those hidden in the sediment. Nagelkerken et al. (2001) showed that the seagrass beds harboured the lowest density of piscivores (together with shallow algal flats) of 11 different habitat types in or adjacent to Spanish Water Bay. This suggests that for the small and vulnerable fishes of 5 cm, feeding on the seagrass beds where there is more food and a lower density of predators is favourable.

When fishes were feeding, this occurred mostly solitary (except foraging schools of 5 cm small grunts). Correspondingly, Hobson (1965) noted that schooling *Haemulon sexfasciatum* in sand and rock bay habitat types showed no feeding activity, whereas solitary individuals did feed. Schooling is probably used as an anti-predator mechanism (Ehrlich and Ehrlich 1973). Ogden and Quinn (1984) suggested that it may be more favourable to break up from the school when foraging to avoid competition for feeding space, as each grunt may need an exclusive feeding area because invertebrate prey are dispersed across the seafloor (Ogden and Quinn 1984).

As expected, diurnal feeding was a more common practice for large juvenile *H. flavolineatum* than for sub-adults. Similarly, for a number of snapper species, smaller fishes showed a higher degree of diurnal feeding than larger fishes (Starck 1971; Mueller et al. 1994; Rooker 1995). Our results may be explained by the fact that as juvenile *H. flavolineatum* grow larger they shift from being predominantly diurnal zooplanktivores to being predominantly nocturnal zoobenthivores (Ogden and Ehrlich 1977; McFarland 1980; Helfman et al. 1982). In the seagrass bed large juveniles showed benthic feeding and only the smallest fishes (approx. 5 cm) also showed pelagic feeding, whereas all large juveniles in the mangroves almost exclusively showed benthic feeding. Sub-adults almost exclusively sheltered during daytime. The above suggests that juvenile *H. flavolineatum* may show the following ontogenetic transition in feeding behaviour: they settle in seagrass beds as exclusive diurnal zooplanktivores, when attaining a larger size they shift to diurnal benthic and/or pelagic feeding in mangroves but primarily in seagrass beds, and then gradually adopt a nocturnal benthic feeding mode in seagrass beds which is supplemented by opportunistic feeding while sheltering in the mangroves during daytime.

Sub-adults appear to supplement their nocturnal feeding by feeding opportunistically during daytime, as was visible for the mangrove sub-population. This is in support of strategy 1 suggested in the introduction, which

stated that fishes feed opportunistically in the mangroves or seagrass beds throughout the day and feed predominantly in seagrass beds during the night. Such supplementary opportunistic diurnal feeding has also been suggested to occur for other species of Lutjanidae and Haemulidae in various bay and reef habitats (Hobson 1965; Starck and Davis 1966; Starck 1971; Rooker 1995; Kamukuru and Mgaya 2004) but the present study is the first that provides evidence for this based on quantitative behavioural analyses. Even though large juveniles may feed nocturnally as well, diurnal feeding for this size class did not seem to be opportunistic at all because on average 45 and 65% of the diurnal time-budget was spent on feeding behaviour by solitary large juveniles of the mangrove and the seagrass-subpopulation, respectively.

Large juveniles in both habitat types showed higher feeding activity during 8:00–10:30, compared to midday and late afternoon, which is possibly related to a completion of feeding after night-time feeding. This is in agreement with strategy 3 as suggested in the introduction, which stated that after nocturnal feeding in the seagrass beds, the fishes complete feeding in the mangroves or seagrass beds during a certain part of the morning. There was no evidence in the present study that Haemulidae in the mangrove habitat used strategy 2 as formulated in the introduction, which stated that fishes start feeding in mangroves or seagrass beds during daytime prior to nocturnal feeding in the seagrass beds. Feeding in the mangroves did not intensify in the late afternoon and superficial behaviour observations indicated no increased feeding in the mangroves at dusk. However, during T3 and T4 (between 15:30 and 18:30), some large juvenile grunts did forage intensively on the muddy substratum adjacent to the mangroves. So, feeding may indeed start before moving to the seagrass beds at dusk, but it apparently does not start inside the mangrove habitat, but on the muddy substratum between the mangroves and seagrass beds, which may function as a transitional foraging habitat in this specific study area. Unlike the mangrove sub-population, for the seagrass sub-population feeding behaviour did increase again during 17:30–18:30 hours (in agreement with strategy 2). Comparably, intense feeding before 10:00 and after 15:00, compared to low feeding activity during mid-day has also been observed for *Lutjanus analis* on artificial reefs, and has been linked to twilight activity of their prey items (Mueller et al. 1994). Contrastingly, *Lutjanus apodus* ($<$7 cm) in mangroves showed higher stomach fullness during midday (11:00–13:00), compared to morning and late afternoon (Rooker 1995), indicating species- and habitat-specific differences.

Conclusions

During daytime resting schools of large juvenile (5–10 cm) and sub-adult (10–15 cm) *H. flavolineatum* use mangroves as shelter habitats, whereas mainly solitary

large juvenile *H. flavolineatum* use mangroves and especially seagrass beds as feeding habitats. Sub-adults feed opportunistically in mangroves throughout the day (concordant with hypothesis 1), while large juveniles in mangroves and seagrass beds showed much more feeding behaviour. In both habitat types, large juveniles showed peak feeding activity during 8:00 and 10:30, which is possibly a completion of nocturnal feeding during the morning (concordant with hypothesis 3), and seagrass fishes also showed high feeding activity during 17:30–18:30, which is just prior to possible nocturnal feeding in the seagrass beds (concordant with hypothesis 2).

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