Day-night shifts of fishes between shallow-water biotopes of a Caribbean bay, with emphasis on the nocturnal feeding of Haemulidae and Lutjanidae

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ABSTRACT: Day-night changes in fish communities were quantified in 6 associated shallow-water biotopes within a single bay: mangroves, seagrass beds, algal beds, channel, fossil reef boulders, and notches in fossil reef rock. All biotopes, except the algal beds, showed a strong reduction in fish density and species richness at night, caused by absence of diurnally active fishes and migrations of Haemulidae and Lutjanidae to the seagrass beds. The fish fauna of the different biotopes showed a relatively high dissimilarity between day and night. This dissimilarity is largely caused by absence of Acanthuridae, Chaetodontidae, Labridae, Pomacentridae, Scaridae and Sparidae at night. These fishes seek shelter at night in, amongst others, the channel, notches and boulders. The balloonfish *Diodon holocanthus* utilised almost all biotopes as shelter as well as feeding sites. The wide distribution of its preferred food (molluscs) probably explains its distribution in most biotopes at night. The nocturnally active Haemulidae and Lutjanidae, on the other hand, migrated from their daytime shelter sites to the seagrass beds at night to feed. Some of these fishes also migrated to the algal beds to feed. The preference of Haemulidae and Lutjanidae for the seagrass bed as a feeding biotope, instead of other bay biotopes, appears to be related to the relatively high availability of their preferred food (Tanaidacea and Decapoda) as determined by digestive tract analysis. Other bay biotopes showed much lower densities of such food items compared to the seagrass beds.

KEY WORDS: Shallow-water biotopes · Coral reef fishes · Day-night shifts · Community structure · Diet · Food abundance · Feeding sites

INTRODUCTION

Activity patterns of many coral reef fish species show large differences between day and night. Species of Acanthuridae, Chaetodontidae, Labridae, Pomacentridae and Scaridae are diurnally active fishes. These species migrate from their feeding sites at night to rocks, corals, holes, crevices, ledges, seagrass beds, and sediment, where they find shelter (Starck & Davis 1966, Randall 1967, Collette & Talbot 1972, Sbikin 1977). Nocturnally active species of Apogonidae, Diodontidae, Haemulidae, Lutjanidae, Holocentridae and

Sciaenidae shelter during daytime and migrate to their feeding sites at night (Starck & Davis 1966, Randall 1967, Collette & Talbot 1972, Sbikin 1977). Studies which have focussed on the day-night changeover of fish communities have been mostly qualitative (e.g. Starck & Davis 1966, Collette & Talbot 1972, Hobson 1973, Sbikin 1977). Few quantitative studies have been carried out and only on single biotopes such as seagrass beds (Weinstein & Heck 1979, Robblee & Zieman 1984) and mangroves (Rooker & Dennis 1991). Day-night changes of fish assemblages between several shallow-water biotopes within a single bay or lagoon are hardly studied. Studies of the importance of different shallow water biotopes as shelter or feeding sites, and an understanding of the

interactions between associated shallow-water biotopes are necessary.

Feeding migrations of both nocturnal and diurnal fish species are often precisely timed. They occur at dusk and at dawn along specific and constant routes (Ogden & Buckman 1973, Ogden & Ehrlich 1977). They are linked to changing light levels (McFarland et al. 1979, Helfman et al. 1982). Especially Haemulidae (grunts) show a marked migration behaviour. In lagoons, juvenile Haemulidae school together and seek shelter on patch reefs or in the mangroves by day and migrate to the adjacent seagrass beds at night to feed on invertebrates (Ogden & Ehrlich 1977, Rooker & Dennis 1991). The migration routes are more or less fixed over the long term and may cover distances of up to 1 km (Ogden & Ehrlich 1977, Ogden & Zieman 1977). Adult Haemulidae and Lutjanidae shelter on the coral reef by day and migrate to the adjacent seagrass beds to feed at night (Starck & Davis 1966, Weinstein & Heck 1979, Baelde 1990).

Haemulidae and Lutjanidae supposedly feed at night to reduce risk of predation, and because their preferred food (i.e. crustaceans) emerges at night (Hobson 1965, Starck & Davis 1966). Seagrass beds harbour high densities of several crustacean species due to their structural complexity (Orth et al. 1984). It has been suggested that seagrass beds function as important feeding sites for nocturnally active benthic carnivores, including Haemulidae and Lutjanidae (Randall 1967, Ogden & Zieman 1977, Orth et al. 1984, Pollard 1984). Few studies have investigated in detail why Haemulidae and Lutjanidae especially feed on the seagrass beds at night, and not in other associated lagoon biotopes, such as mangroves, patch reefs, algal beds, etc. Other lagoon biotopes may also contain high densities of crustaceans. The question is whether Haemulidae and Lutjanidae migrate to the seagrass beds, instead of other lagoon biotopes, because they contain higher densities of (preferred) food organisms, or merely because the seagrass beds cover a much larger area than other lagoon biotopes, thus reducing competition for food. For a better understanding of the selection of feeding sites by fishes within a lagoon, not only their diets should be studied, but also availability of the selected food organisms in all other associated biotopes.

Species of Haemulidae and Lutjanidae were selected in the present study because they show marked migration behaviour and because they often constitute a large part of the fish population in lagoons and bays. The 2 questions addressed in this study, carried out in different biotopes within 1 bay, are: (1) What is the effect of the day-night changeover in fish community structure (i.e. structure of the fish fauna) on the densities of individual fish species in 6 different but associ-

ated bay biotopes? and (2) Does the absence or presence of the most commonly consumed food organisms in different bay biotopes explain why species of Haemulidae and Lutjanidae normally select seagrass beds as nocturnal feeding biotopes?

MATERIALS AND METHODS

Study area. The study was carried out in the Spanish Water bay in Curaçao, Netherlands Antilles (Fig. 1). The mouth of this bay is situated at the sheltered south-western coast of the island and is 85 m wide and protected by a sill of maximum 6 m deep. The bay is connected to the sea by a relatively long (1.1 km) and deep channel that partly continues into the central part of the bay. Apart from the channel the bay is relatively shallow (depth <5 m). The daily tidal range is on average 30 cm (de Haan & Zaneveld 1959). Mean (±SD) water temperature and salinity during the study period (November 1997 through August 1998) at the 12 study sites in the bay were 28.3 ± 0.2°C and 35.4 ± 0.2‰, respectively, while on the reef in front of the bay 27.5 ± 1.2°C and 35.0 ± 0.2‰, respectively, were measured. The restricted range of salinities demonstrates the oceanic nature of the bay. The bay has relatively clear water with an average of 6.2 ± 2.1 m horizontal Secchi disk visibility. Highest mean visibility was found near the mouth (8.1 ± 3.1 m) and in the western part of the bay (7.4 ± 2.2 m), while the lowest mean visibility was found in the eastern part (4.4 ± 1.2 m). The mean visibility on the reef in front of the bay measured 17.5 ± 4.6 m. The bottom in the eastern part is dominated by fine sediment, while in the western part it is largely composed of coarse sediment (Kuenen & Debrot 1995).

A pre-study survey in the Spanish Water bay revealed 6 main biotopes. These are the mangroves, seagrass beds, algal beds, channel, notches in fossil reef rock, and fossil reef boulders. Data were collected in each of these biotopes, and on the coral reef along the coast of the island.

The red mangrove *Rhizophora mangle* dominates the coastline of the bay and is most abundant in the eastern part of the bay (Fig. 1). In other parts of the bay, the mangroves consist of isolated stands. The mangrove stands selected for this study had submerged root systems measuring, on average, 27 ± 11 m in length and 1.4 ± 0.5 m in width, at water depths of 0.8 ± 0.2 m.

The shallow parts of the bay are dominated by the turtle grass *Thalassia testudinum* (Fig. 1). This seagrass is found along almost the entire coastline of the bay, at depths of approximately 40 cm to a maximum of 3 m. In the turbid parts of the bay the seagrass extends to about 1.5 m depth, while in the clearer part it extends to about 3 m. Mean seagrass cover was 81 ± 12%,
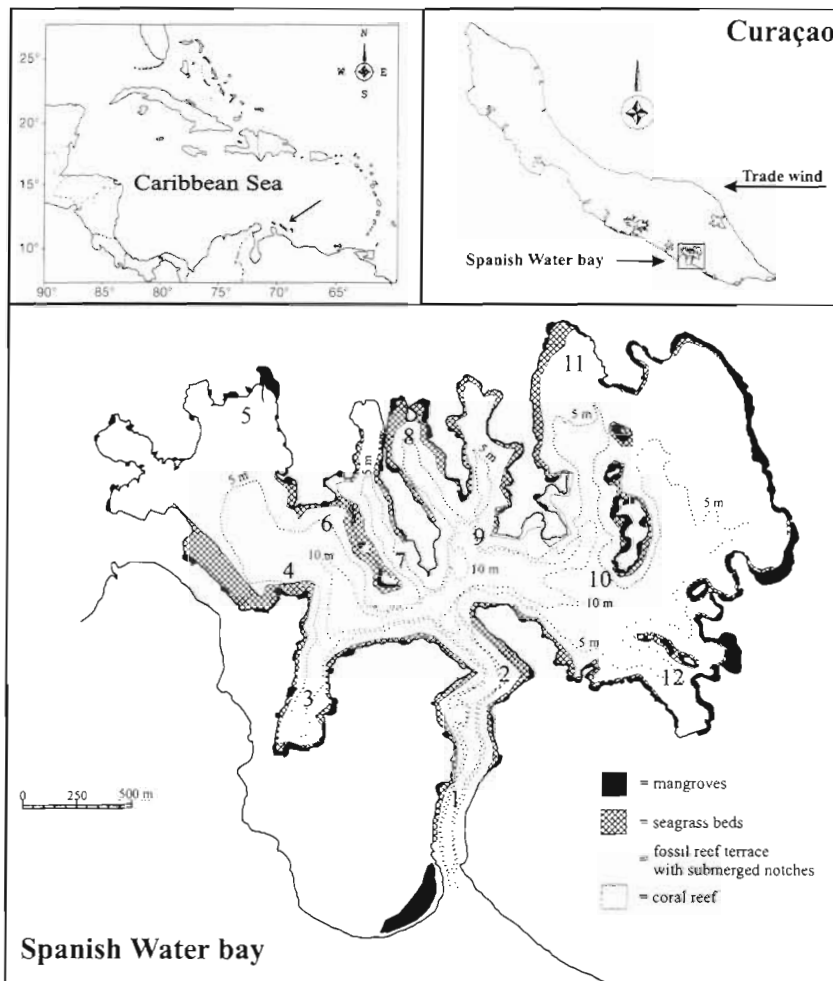
Fig. 1. Map of the Spanish Water bay showing the location of the study sites (1 to 12). The algal beds generally cover the area between the seagrass beds and the channel (rated at the 10 m isobath); the boulders are located directly in front of the fossil reef terrace

covered with filamentous algae. The soft bottom of the channel is almost completely devoid of vegetation. Compared to the other biotopes the deeper part of the channel is very turbid.

The shore on the southern part of the bay largely consists of a fossil reef terrace (up to 3 m high) which partly extends into the water (Fig. 1). At the water/surface interface and under water, biochemical solution and biochemical abrasion have formed notches in the fossil reef terrace (de Buisonjé & Zonneveld 1960). The water height of the notches selected for this study was approximately 0.5 m and the notches extended about 0.8 m under the reef terrace. As they are located under the reef terrace, the notches receive little ambient light and are relatively dark. The rocky substratum of the notches is mainly covered by fleshy and filamentous algae. Small to medium-sized rocks are often located just in front of the notches.

Massive boulders which have broken off from the fossil reef terrace in the past and tumbled into the water are regularly found at a distance of 0.5 to 2 m in front of the reef terrace (Fig. 1). The boulders partly extend above the sea water level. The mean circumference of the selected boulders measured 7.7 ± 3.1 m, while the mean water height measured 0.6 ± 0.2 m. At the bottom/water interface the boulders often contain shallow cracks and holes. On average the height of the holes was 0.13 ± 0.09 m, while they extended on average along $30 \pm 26\%$ of the total circumference of the boulder. The rocky substratum of the boulders is mainly covered by fleshy and filamentous algae.

Sampling design. The total fish abundance in the bay was largely accounted for by juvenile fish using the bay as a nursery. Fish densities and species richness (i.e. number of species) were determined during both day and night at 12 study sites in the 6 associated biotopes. The selected study sites were located throughout the bay. Not all biotopes were present at each site (Fig. 1). The number of sites and transects for the different biotopes were: mangroves (12, 44), seagrass beds (11, 44), algal beds (10, 60), channel (4, 16),

height of the seagrass blades 22 ± 8 cm, and seagrass shoot density 143 ± 66 m^{-2}.

As depth increases and light levels decrease, *Thalassia testudinum* is almost completely replaced by macroalgal species such as *Halimeda opuntia*, *H. incrassata*, *Cladophora* sp. and *Caulerpa verticillata* (Kuenen & Debrot 1995). The algal beds fill up almost the complete area between the seagrass beds and the channel, and are generally found on the soft bottom at 2 to 5 m depth. The density, cover and elevation of the algae is very low. Hence, the algal beds are scarcely vegetated and provide little shelter for fish.

In the central parts and at the entrance of the bay, at about 5 m depth, the bottom abruptly turns into a deep channel with a steep slope (Fig. 1). The channel is 11 to 18 m deep, reaching its greatest depth near the entrance of the bay. On the slope of the channel some small and large boulders of fossil reef rock are found

notches in fossil reef rock (7, 24), and fossil reef boulders (6, 22).

At each site of each biotope, 4 replicate transects were randomly selected. As the algal beds were distributed over a depth range of about 2 to a maximum of 6 m, the replicate transects were taken close to the shore at 2 m depth as well as in the deeper parts of the bay at 5 m depth (total = 8 replicates per site). The data of the 2 depth zones were pooled in all analyses. The size of the transects on the seagrass beds and algal beds measured 3 × 50 m, while in the channel they measured 3 × 25 m. For the mangroves, isolated stands of mangrove were selected and surveyed completely. The mangrove stands were narrow (up to a maximum of 2 m), permitting a complete and accurate census. Isolated fossil reef boulders were also surveyed completely. The notches in the fossil reef rock are continuous and were studied at each site in 4 sections of 25 m long. For all transects in the mangroves, notches, and boulders the total transect area was estimated by measuring the depth at intervals of 5 m (for the boulders at intervals of 1 m) and multiplying the mean depth with the total length of the transect.

The transects were marked by a fine rope, placed at least 30 min before the survey in order to minimise disturbance effects. Snorkeling gear was used during the visual surveys. SCUBA gear was used on the algal beds at 5 m and in the channel. For the night census the light beam of the dive lights was adjusted for a wide angle which covered the entire transect width. Most fish species did not appear to be greatly disturbed by the light beam. Due to the relatively low fish abundance at night, fishes were not easily missed.

Per transect, the surveys were done once by 2 observers during daytime and at night in the period December 1997 to March 1998. Species identification and quantification of fishes was first thoroughly practised in test transects. As most fish remained more or less in the same area, the observers effect on fish abundance estimates seems to be relatively small. The moon phase was not taken into account at night in the various transects in the different biotopes. No significant effect of the moon cycle on the density of any abundant fish species was demonstrated, except *Diodon holocanthus*, in a pilot study done in all bay biotopes during the 4 different moon phases. Additionally, observations on the migration behaviour of fishes sheltering in the mangroves, boulders, notches and seagrass beds were made at dusk. The surveys included almost all encountered species with the exception of small or cryptic fish species (Gobiidae, Blenniidae, Apogonidae, Muraenidae) and species forming large schools (Atherinidae, Clupeidae, Engraulidae).

Diets of abundant species of Haemulidae (grunts) and Lutjanidae (snappers) were quantified by examining the entire digestive tract. The gut contents were categorised as: algae (calcareous, filamentous, macro, and unicellular), Amphipoda, Annelida, Bivalvia, Copepoda, Decapoda (mainly crabs and sometimes shrimps), Echinodermata, fish, Foraminifera, Gastropoda, Isopoda, Mysidacea, Nematoda, Ostracoda, other, seagrass, sediment, and Tanaidacea. The number of crustaceans was too high for quantification as percent composition by total number, and the biomass too low for quantification as percent composition by total weight. The abundance of each group was therefore quantified as the percent composition by volume of the digestive tract (Bowen 1992). For diet analysis fishes were caught with a beach seine on the seagrass beds and notches and boulders, and with an Antillean fish trap in the mangroves. As these fishes feed at night they were caught during the early morning to facilitate diet analysis. Ontogenetic shifts in diets are present in several species of Haemulidae and Lutjanidae. Only the most abundant size class of the fishes was therefore used for diet analysis.

Densities of macro-invertebrates were determined in the top layer of the substratum as well as in the vegetation, at 3 sites in the mangroves, seagrass beds, algal beds and channel. Per biotope 6 bottom cores (diameter = 5.4 cm) were taken. Macro-invertebrates from the vegetation were also sampled by hauling a plankton net (diameter of mouth = 25 cm) through the seagrass and algal blades along a transect of 3 m long. The plankton net samples were taken at the same locations as the bottom cores. Samples were taken at dusk after 17:00 h.

Only the upper 3 cm of the bottom cores were analysed for their contents since this fraction contained the majority of benthic organisms. The cores were sieved over a sieve with a mesh size of 250 μm. The bottom cores and plankton net samples were incubated with Bengal Rose for 12 h to colour small crustaceans and other organisms red and facilite quantification. For each core and plankton net sample the total number and type of macro-invertebrates were determined using a stereomicroscope. The macro-invertebrates were categorised as: Acaridae, Amphipoda, Annelida, Bivalvia, Copepoda, Cumacea, Decapoda, Echinodermata, Gastropoda, Isopoda, Mysidacea, Nematoda, Nemertea, Ostracoda, Platyhelminthes, and Tanaidacea.

Statistical analysis. Mean fish density and species richness during day and night were compared for each biotope using a paired *t*-test on log-transformed data. Homogeneity of variances was tested with a Bartlett test while normality was tested with a Kolmogorov-Smirnov 1-sample test (Sokal & Rohlf 1995). Day-night differences in density were also compared for individual fish species in each biotope using a Wilcoxon test

for matched pairs (Sokal & Rohlf 1995). Differences in densities of macro-invertebrates between biotopes were tested using a Kruskal-Wallis test or a Mann-Whitney U-test. Cluster analysis was carried out on log-transformed data of the fish species densities in the different biotopes during daytime and at night, using the computer programme CLUSTAN1C2 (Wishart 1978). The average-linkage method (Sokal & Michener 1958) was used in combination with the Bray-Curtis coefficient.

RESULTS

Fish densities decreased significantly at night (p < 0.002, t-test) in the boulders, mangroves, channel, notches and seagrass beds (Fig. 2a), showing mean decreases of 86 to 97 % with respect to daytime densities. The fish density at night in the algal beds, however, was as low as during daytime. Also, fish species richness decreased significantly at night (p < 0.036,
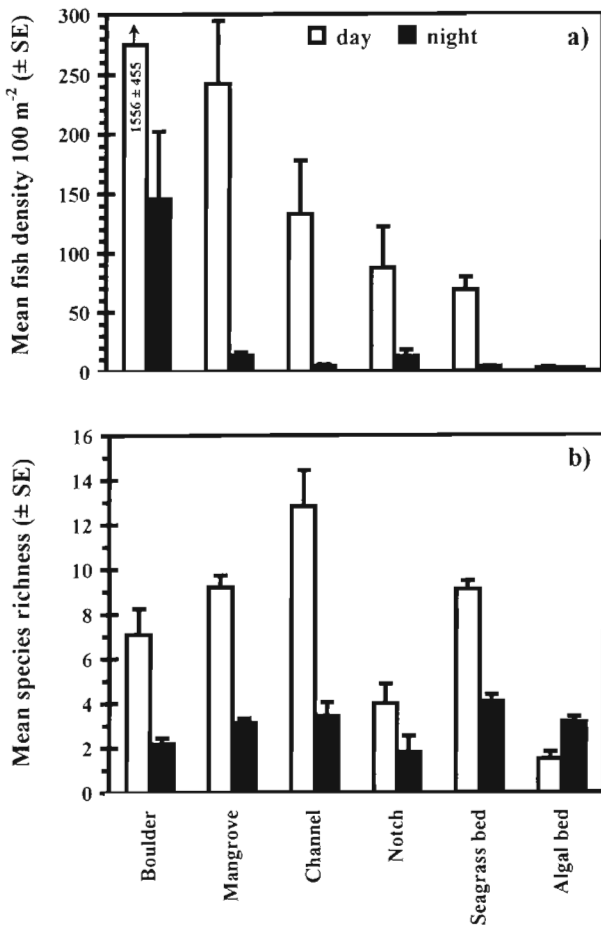

Fig. 3. Cluster analysis for fish species densities in 6 different bay biotopes during daytime and night-time

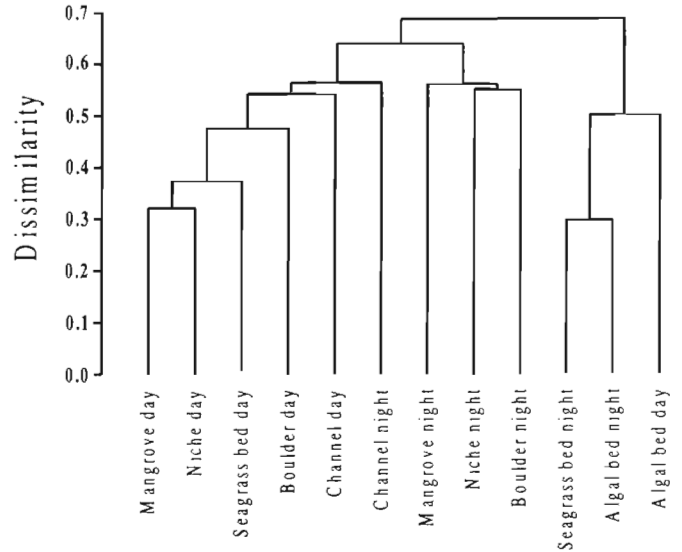Fig. 2. (a) Mean density and (b) species richness of fishes in 6 different bay biotopes during daytime and night-time

t-test) in the boulders, mangroves, channel, notches and seagrass beds (Fig. 2b), showing mean decreases of 55 to 73 % with respect to the daytime values. The algal beds, on the other hand, showed a mean increase in species richness at night of 112 % (p = 0.012, t-test). So, except for the algal beds, the density and species richness in all biotopes decreased substantially at night.

Cluster analysis of fish species densities in each biotope showed a relatively high dissimilarity in the fish community structure between day and night (Fig. 3). Lowest dissimilarity was found between the fish community of seagrass beds and algal beds at night.

Table 1 shows the day-night changes in densities of abundant fish species in the different biotopes. In the seagrass beds, the most noticeable difference between day and night was a high abundance of Scaridae during daytime in contrast to an almost complete absence at night. Diodontidae were hardly observed during daytime, while at night their densities increased significantly and at that time they contributed significantly to the total fish density.

In the mangroves, Gerreidae, Pomacentridae, Scaridae, and Sparidae were relatively abundant by day but formed only a very small part of the total fish abundance at night (Table 1). Densities of Diodontidae increased significantly at night, and they became dominant together with the Haemulidae and Lutjanidae.

On the algal beds, Scaridae and Sparidae formed an important part of the total daytime fish abundance, but at night they were almost completely absent. The densities of Diodontidae and Haemulidae increased significantly at night and they became dominant, which was not the case by day.

Table 1. Mean densities per 100 m^{-2} (SD) of the most abundant fishes in the 6 different bay biotopes by day and at night. Less abundant and rare species are not shown. Numbers in rows of family names are total fish densities for each family, including species not shown. Day-night densities were compared using a Wilcoxon test for matched pairs. >, >>: significantly higher (p < 0.05, respectively, p < 0.01), and <, <<: significantly lower; the others showed no significant difference

	Seagrass bed Day	Seagrass bed Night	Mangrove Day	Mangrove Night	Algal bed Day	Algal bed Night	Channel Day	Channel Night	Notch Day	Notch Night	Boulder Day	Boulder Night
Acanthuridae	1.6	0.05	1.1	0.1	0.1	0.01	5.8	0.3	6.7	–	55.2	1.7
Acanthurus chirurgus, doctorfish	0.8 (1.1) >	0.05 (0.1)	1.0 (1.8)	0.1 (0.3)	0.1 (0.3)	0.01 (0.04)	5.8 (3.3) >	0.3 (0.3)	5.0 (8.8)	–	55.2 (68.6) >	1.7 (3.9)
Chaetodontidae	1.6	0.02	10.9	1.2	0.1	–	6.6	0.3	2.3	–	13.7	–
Chaetodon capistratus, foureye butterflyfish	1.6 (1.1) >>	0.02 (0.1)	10.9 (10.9) >>	1.2 (3.6)	0.1 (0.2)	–	6.6 (4.8)	0.3 (0.2)	2.3 (4.9)	–	13.7 (16.6)	–
Diodontidae	0.1	0.8	0.3	1.8	0.01	0.3	0.3	0.5	0.3	3.0	1.1	–
Diodon holocanthus, balloonfish	0.1 (01) <<	0.8 (0.5)	0.3 (0.5) <	1.7 (1.9)	0.01 (0.04) <<	0.3 (0.3)	0.3 (0.3)	0.5 (0.6)	0.3 (0.5)	2.7 (2.5)	1.1 (2.8)	–
Gerreidae	3.5	0.2	18.0	0.5	0.4	0.3	0.2	–	0.9	–	25.4	–
Gerres cinereus, yellowfin mojarra	0.3 (0.4)	0.1 (0.3)	16.2 (32.4) >>	0.5 (1.4)	0.1 (0.3)	0.2 (0.3)	0.2 (0.3)	–	0.1 (0.4)	–	25.4 (42.8)	–
Eucinostomus spp., mojarra spp.	2.0 (3.8)	–	0.3 (0.5)	–	0.3 (0.8)	0.04 (0.1)	–	–	–	–	–	–
Haemulidae	31.5	1.9	129.3	4.5	0.1	1.3	4.2	1.4	10.2	2.7	748.9	18.3
Haemulon flavolineatum, french grunt	27.8 (22.2) >>	1.4 (0.8)	99.1 (123.6) >>	3.4 (3.9)	0.1 (0.3) <<	0.9 (0.7)	3.9 (3.4)	1.3 (1.7)	8.7 (13.6)	2.7 (3.7)	601.9 (580.9) >	16.5 (26.3)
Haemulon sciurus, bluestriped grunt	3.5 (2.8) >>	0.4 (0.4)	26.4 (24.8) >>	1.1 (1.4)	0.03 (0.1) <	0.3 (0.5)	0.2 (0.2)	0.1 (0.2)	1.4 (1.9)	–	109.5 (182.1)	1.8 (4.0)
Holocentridae	–	0.05	0.1	0.3	–	–	1.4	–	–	1.9	10.8	23.4
Holocentrus adscensionis, squirrelfish	–	0.05 (0.1)	0.1	0.2 (0.4)	–	–	1.4 (2.0)	–	–	1.9 (2.0)	9.2 (10.0)	19.4 (20.3)
Labridae	2.0	–	–	–	–	–	11.0	–	8.4	–	68.2	–
Halichoeres bivittatus, slippery dick	1.3 (3.5)	–	–	–	–	–	6.8 (11.5)	–	0.4 (1.0)	–	8.5 (20.9)	–
Thalassoma bifasciatum, bluehead	0.2 (0.8)	–	–	–	–	–	1.4 (2.8)	–	5.8 (15.4)	–	21.1 (51.7)	–
Lutjanidae	4.1	0.4	48.4	3.2	0.6	0.2	11.7	0.5	13.8	2.2	291.9	15.8
Lutjanus apodus, schoolmaster	0.2 (0.3)	0.1 (0.1)	36.2 (14.8) >>	3.2 (2.3)	0.02 (0.1)	0.03 (0.1)	0.5 (0.6)	0.2 (0.2)	12.6 (7.0) >	1.7 (2.6)	269.3 (242.0) >	13.4 (19.4)
Lutjanus griseus, gray snapper	0.7 (1.0) >	0.02 (0.1)	3.6 (2.9)	–	0.3 (0.7)	0.1 (0.1)	7.8 (6.4)	0.1 (0.2)	0.4 (1.0)	–	5.1 (8.5)	–
Ocyurus chrysurus, yellowtail snapper	3.0 (2.3) >>	0.2 (0.3)	7.8 (16.4)	–	0.2 (0.4)	0.1 (0.2)	3.1 (3.1)	0.1 (0.2)	0.4 (1.1)	–	–	–
Pomacentridae	1.7	–	7.1	0.1	0.04	–	27.6	–	35.1	1.5	204.3	73.5
Abudefduf taurus, night sergeant	–	–	–	–	–	–	–	–	–	1.1 (1.6)	–	36.1 (64.6)
Stegastes dorsopunicans, dusky damselfish	–	–	0.5 (1.1)	–	–	–	0.6 (1.2)	–	24.9 (32.4) >	0.4 (0.8)	162.0 (99.8) >	37.4 (17.4)
Stegastes partitus, bicolor damselfish	–	–	–	–	–	–	13.8 (26.6)	–	–	–	1.4 (3.5)	–
Scaridae	21.3	0.03	14.9	0.1	0.3	0.01	58.1	0.7	4.1	0.5	70.0	1.6
Scarus iserti, striped parrotfish	19.7 (16.3)	–	10.8 (29.6)	–	0.3 (0.8)	–	46.3 (44.2)	–	3.5 (9.2)	–	41.3 (80.7)	–
Sparisoma chrysopterum, redtail parrotfish	0.6 (0.5)	–	2.2 (4.6)	–	–	0.01 (0.04)	4.9 (4.9)	0.4 (0.6)	–	0.5 (1.2)	23.1 (43.9)	1.6 (3.6)
Sparidae	0.7	0.1	6.8	0.04	0.5	0.05	–	–	–	–	–	–
Archosargus rhomboidalis, sea bream	0.7 (0.6) >>	0.1 (0.5)	6.8 (13.3) >	0.04 (0.1)	0.5 (1.3)	0.03 (0.1)	–	–	–	–	–	–
Summed density of abundant species	68.7	3.8	242.0	13.1	2.4	2.3	132.4	4.6	86.8	12.5	1556.4	145.5
% of total fish density	91.0	87.5	91.8	86.4	83.7	86.7	78.1	91.8	75.9	87.9	86.6	87.9

In the channel, Labridae and Pomacentridae were relatively abundant by day but completely absent at night, while *Pseudupeneus maculatus* (spotted goatfish) increased in density from 0.0 per 100 m^2 by day to 0.6 per 100 m^2 at night (not included in Table 1 because of low abundance in other biotopes). In contrast to the other biotopes, Acanthuridae and Scaridae were still relatively abundant in the channel at night. These were sleeping fishes, however, seeking shelter for the night between scattered rocks and boulders on the bottom of the channel.

In the notches, Acanthuridae and Labridae were relatively abundant by day but completely absent at night, while Pomacentridae showed a strong decrease in density at night. Further, Diodontidae and Holocentridae increased in density at night becoming relatively abundant. The Pomacentridae were still relatively abundant at night, but these were inactive fishes sheltering in holes and crevices.

At the boulders, Chaetodontidae, Gerreidae and Labridae were absent at night, while the density of Holocentridae increased at night. As for the notches, Pomacentridae were still abundant at night, but these were inactive fishes sheltering in holes and crevices. The boulders were the only biotope where *Diodon holocanthus* was absent at night.

Observations at dusk in the seagrass beds revealed that Haemulidae and Lutjanidae migrated from the mangroves, boulders, and notches to the adjacent seagrass beds at night. The smaller fishes generally descended between the seagrass shoots to search for food at the bottom, while the larger individuals were more often observed swimming above the seagrass blades. Nocturnal feeding migrations of Haemulidae

and Lutjanidae from the adjacent coral reef to the seagrass beds in the bay were not observed. No larger fishes and adults of the coral reef were observed at night in any of the bay biotopes near the mouth of the bay nor further inwards of the bay.

Haemulidae and Lutjanidae showed a strong diet preference for specific types of macro-invertebrates. The proportions in which they were consumed sometimes differed somewhat between fishes from different biotopes (Table 2). The diets of *Haemulon flavolineatum*, *H. sciurus* and *Ocyurus chrysurus* consisted largely of Tanaidacea, while Decapoda (mainly crabs) constituted the largest part of the diets of *Lutjanus apodus* and *L. griseus*. Other macro-invertebrates which were frequently consumed were Copepoda by *H. flavolineatum* and *H. sciurus*, Mysidacea by *O. chrysurus*, Annelida by *H. flavolineatum*, and small fishes by *O. chrysurus* and *L. apodus*. Amphipoda and Gastropoda formed a small part of the diets of *H. flavolineatum* and *H. sciurus*.

The macro-invertebrates most commonly consumed by Haemulidae and Lutjanidae were found to be most abundant in bottom sediment of the seagrass beds, and for some macro-invertebrates this was also the case for the algal beds (Table 3). Tanaidacea and Annelida were very abundant in the seagrass and algal beds, but were absent in the mangroves, and only occurred at very low densities in the channel. Amphipoda were found in higher densities in the seagrass beds and algal beds than in the other biotopes, while Mysidacea were abundant in the seagrass beds and absent in most other biotopes. Copepoda and Gastropoda were found in all 4 biotopes, but were most abundant in the seagrass beds. Densities of the different macro-inverte-

Table 2. Composition of diets of several species of Haemulidae and Lutjanidae. Only the most important groups of macro-invertebrates are shown, and composition for each group is expressed as percentage of the total food volume in the entire digestive tract of a fish. Size refers to the size range (total length) of the fishes studied, while N refers to the number of stomachs analysed. Tana: Tanaidacea, Cope: Copepoda, Mysi: Mysidacea, Deca: Decapoda, Amphi: Amphipoda, Gastro: Gastropoda, Anne: Annelida

	Size (cm)	N	Tana	Cope	Mysi	Deca	Amphi	Gastro	Anne	Fish	Total
Haemulon flavolineatum											
Seagrass bed	5 – 13	39	58	0	0	3	4	2	1	1	68
Boulder, notch	4 – 13	6	15	33	0	0	10	0	18	0	76
Haemulon sciurus											
Seagrass bed	6 – 14	38	54	10	1	1	1	5	3	0	75
Mangrove	8 – 12	5	43	0	0	0	0	0	0	0	43
Ocyurus chrysurus											
Seagrass bed	6 – 13	34	34	5	19	23	1	1	1	7	91
Mangrove	2 – 10	4	55	3	10	0	0	0	0	33	100
Lutjanus apodus											
Seagrass bed	7 – 18	39	14	0	3	68	1	0	0	7	93
Mangrove	12 – 21	10	0	0	0	72	0	0	0	26	98
Boulder, notch	9 – 22	4	0	0	0	68	0	0	0	33	100
Lutjanus griseus											
Seagrass bed	7 – 16	14	10	0	2	68	0	0	0	7	87

Table 3. Densities (SD) of the most commonly consumed macro-invertebrates by Haemulidae and Lutjanidae in the bottom sediment of different biotopes, and between the seagrass and algal blades. –: no significant difference, na: not applicable. S: seagrass bed, A: algal bed, M: mangrove, C: channel

| | Density in top layer of bottom (dm^{-3}) | | | | | | Density between blades (m^{-3}) | | |
	Seagrass bed	Algal bed	Mangrove	Channel	Difference	p-value	Seagrass bed	Algal bed	p-value
Tanaidacea	284 (549)	391 (687)	0 (0)	17 (17)	S > M; A > M,C	<0.036	2619 (1407)	60 (112)	0.001
Copepoda	240 (367)	46 (51)	10 (18)	10 (12)	–	>0.087	1005 (454)	80 (76)	<0.001
Gastropoda	184 (83)	49 (47)	68 (66)	70 (36)	S > A,M,C	<0.016	324 (361)	79 (66)	0.025
Annelida	143 (108)	133 (101)	0 (0)	2 (6)	S,A > M,C	<0.003	360 (244)	11 (14)	<0.001
Mysidacea	29 (44)	2 (6)	0 (0)	0 (0)	S > M,C	=0.022	699 (912)	10 (6)	<0.001
Amphipoda	19 (25)	15 (24)	2 (6)	5 (8)	–	>0.181	165 (119)	1 (3)	<0.001

brates between the blades of the seagrasses were in all cases significantly higher than between the algal blades (Table 3). In the notches and boulders, these macro-invertebrates are probably lacking because only rocky substratum is present.

DISCUSSION

With the exception of the algal beds, all biotopes of the Spanish Water bay showed a strong reduction in fish density and species richness at night, and a high dissimilarity in the fish fauna between day and night. The dissimilarity in fish fauna was largely caused by daily migrations of Acanthuridae, Chaetodontidae, Labridae, Pomacentridae, Scaridae and Sparidae. These diurnally active fishes (Starck & Davis 1966, Randall 1967, Collette & Talbot 1972) were generally abundant in most bay biotopes by day, but completely absent or found at very low densities at night. Species belonging to these families are known to migrate away from their diurnal feeding sites and seek shelter at night (Starck & Davis 1966, Randall 1967, Collette & Talbot 1972, Sbikin 1977). This probably explains the relatively high densities at night of inactive Acanthuridae and Scaridae in the channel, and of Pomacentridae in the notches and boulders of the Spanish Water bay. These biotopes contain small rocks and boulders with holes and crevices which provide shelter for the night.

The nocturnally active Diodontidae utilised most biotopes as shelter sites during daytime, but at night no predominant migration to the seagrass beds or algal beds was observed. Instead, all biotopes were used as shelter as well as feeding sites at night. The main food of Diodon holocanthus consists largely of molluscs (Randall 1967, Nagelkerken et al. unpubl data), and the presence of Gastropoda in the seagrass beds, algal beds, mangroves as well as the channel may explain the presence of this fish species in all of these biotopes at night.

Studies have shown that during daytime Haemulidae and Lutjanidae seek shelter on patch reefs and in mangroves located in lagoons (Ogden & Ehrlich 1977,

Rooker & Dennis 1991). The present study suggests that any bay biotope with sufficient shelter (i.e. boulders, channel, seagrasses, mangroves, notches) is used as a daytime shelter site by these species. The only biotope not used as such were the algal beds. This is likely the result of the low structural complexity and consequently the low degree of shelter provided by this biotope (Nagelkerken et al. in press a). The seagrass beds in the Spanish Water bay (this study) and Lac bay in Bonaire (Nagelkerken et al. in press b) form an important daytime shelter site for juvenile Haemulidae and Lutjanidae. Lack of these fishes in the seagrass beds of St. Croix (Ogden & Zieman 1977, Robblee & Zieman 1984) may be explained by the relatively narrow and short seagrass blades which provide a relatively low degree of shelter (J. Ogden pers. comm.).

The nocturnally active Haemulidae and Lutjanidae (Starck & Davis 1966, Randall 1967) were very abundant in almost all biotopes during daytime but, in contrast to the diurnally active fish species, generally did not feed. This is supported by analysis of the diets of these fishes in the Spanish Water bay caught at midday and in the afternoon which showed that their digestive tracts were largely empty. When feeding at night, it appeared for these fish species that no large differences were present in their diet between the different biotopes. A similar result was found by Brewer et al. (1995) in Australia, who suggested that feeding behaviour may not entirely be opportunistic but also determined by species-specific preferences.

Studies have shown, so far, that at night juvenile Haemulidae and Lutjanidae migrate out of the mangroves and patch reefs to the adjacent seagrass beds to feed on invertebrates (Ogden & Ehrlich 1977, Robblee & Zieman 1984). The present study shows that not only the mangroves, but all shelter sites show strong reductions in fish densities (including Haemulidae and Lutjanidae) at night. For the notches, boulders and mangroves it was confirmed that the nocturnal fish migration was toward the adjacent seagrass beds. The most commonly consumed macro-invertebrates by Haemulidae and Lutjanidae, viz. Tanaidacea, Cope-

poda, Mysidacea and Annelida, were absent or occurred at low densities in the mangroves and channel, and most likely also in the notches and boulders. In the sediment of the seagrass beds and between the seagrass blades these food organisms were abundant, however. This probably explains why Haemulidae and Lutjanidae, at least in the Spanish Water bay, largely migrate out of their shelter biotopes towards the seagrass beds at night to feed, instead of staying in their diurnal shelter sites to find food. Likewise, Brewer et al. (1995) showed that for most fish species living in a seagrass bed in Australia predation on penaeid shrimps appeared to be density dependent, while Blaber et al. (1992) suggested that larger fish species were more abundant in denser seagrass beds because the smaller fishes on which they feed had the same pattern of abundance.

Another factor to consider with respect to the nocturnal feeding migrations is the accessibility of the prey, viz. how fishes search and capture their prey in relation to the type of biotope. One hypothesis which relates to this, but has never been tested, is that Haemulidae favour the seagrass beds for feeding because of the more extensive surface areas as compared to other biotopes. Haemulidae lack high-precision sight, and effective feeding may depend on fluorescence by micro-organisms to signal moving prey (J. Ogden pers. comm.). This method of food capture necessitates a large surface area to avoid competition for space between fishes.

Decapoda, which formed the main food type for Lutjanidae, were not found in the bottom cores and plankton hauls sampled during the present study. Neither of these 2 sampling methods is very effective in sampling Decapoda, however. These invertebrates are probably able to hold onto the seagrass and algal blades when the plankton net is passing through the vegetation, and are too large to be sampled by the bottom cores. However, as seagrass blades and shoots provide excellent shelter for different species of crustaceans (Stoner 1980, Lewis & Stoner 1983), Decapoda are likely to be more abundant in the seagrass beds than in the other biotopes with little bottom vegetation, such as the boulders, channel, mangroves and notches. Likewise, several studies have found higher densities of crustaceans in seagrass beds than in areas with little vegetation (see review by Orth et al. 1984).

Although Haemulidae and Lutjanidae showed nocturnal migrations from the mangroves, notches and boulders to the seagrass beds, their densities in the seagrass beds were lower at night than during daytime. In the seagrass beds larger size classes of fishes were present at night than during daytime, suggesting that the small-sized individuals were missed during the night census. Field observations showed that the small fishes sink between the seagrass blades at night, and as such

can be easily missed. The larger individuals were always found swimming above the seagrass blades. Because other bay biotopes had very little or no bottom vegetation this problem was not encountered there.

Only in the algal beds was there no strong decrease in fish density and species richness at night, and the latter even showed an increase at night. Densities of Haemulon flavolineatum and H. sciurus increased at night on the algal beds, suggesting that these fish species also use this biotope as a feeding area. The macroinvertebrates which were most commonly consumed by these fish species, viz. Tanaidacea and Copepoda, were relatively abundant in the bottom sediment of the algal beds. This probably explains why H. flavolineatum and H. sciurus not only migrate to the seagrass beds but also to the algal beds at night to feed.

Adult Haemulidae, Lutjanidae and other fish species which shelter on the coral reef by day often migrate to the adjacent seagrass beds at night to feed (Starck & Davis 1966, Weinstein & Heck 1979, Baelde 1990, Blaber et al. 1992). In the present study such a migration was not evident and this may be caused by 2 factors. Firstly, the total area of seagrasses in the Spanish Water bay is relatively small compared to the total area of the coral reef. As juvenile fish which live in the bay also feed on the seagrass beds at night, migration of adult coral reef fish into the relatively small seagrass beds of the bay would increase competition for food and space. Secondly, the mouth of the bay is small, measuring 85 m in width and 6 m at its deepest. The entrance of the Spanish Water bay may hence be more difficult to find compared to wide lagoons protected by a barrier with many connections to the main reef. The small mouth of the bay probably limits large-scale nocturnal migrations from the reef into the bay. Instead, it was observed that the adult Haemulidae of the reef appear to, at least partly, use the shallow reef terrace as a feeding site.

CONCLUSIONS

All bay biotopes of the Spanish Waterbay, except the algal beds, showed a strong reduction in fish density and species richness at night. This was largely caused by (1) diurnally active Acanthuridae, Chaetodontidae, Labridae, Pomacentridae, Scaridae and Sparidae which sought shelter at night in biotopes such as the channel, notches and boulders, and (2) nocturnally active Haemulidae and Lutjanidae which migrated out of their diurnal shelter sites at night towards the seagrass beds, and to a lesser extent also to the algal beds, to forage on benthic crustaceans. Diodontidae, on the other hand, sheltered in almost all biotopes during daytime but did not show obvious migrations to a spe-

cific biotope at night. The selection of the seagrass beds as a nocturnal feeding site by Haemulidae and Lutjanidae appears to be determined by the presence and abundance of their preferred food organisms, viz. Tanaidacea, Copepoda and Mysidacea. Also for Diodontidae the nocturnal feeding in almost all biotopes appears to be related to the presence of their preferred food, molluscs, in most biotopes.

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