Available online at www.sciencedirect.com

SCIENCE DIRECT

Estuarine, Coastal and Shelf Science 57 (2003) 1079–1089

ESTUARINE
COASTAL
AND
SHELF SCIENCE

Diet shifts of Caribbean grunts (Haemulidae) and snappers (Lutjanidae) and the relation with nursery-to-coral reef migrations

E. Cocheret de la Morinière, B.J.A. Pollux, I. Nagelkerken, G. van der Velde*

Department of Animal Ecology and Ecophysiology, University of Nijmegen, Toernooiveld 7, 6525 ED Nijmegen, The Netherlands

Received 20 December 2001; accepted 6 January 2003

Abstract

The spatial size distribution of grunts and snappers have previously indicated the separation of juveniles in nursery habitats from the adults on the coral reef. This implies life cycle migrations from nursery habitats (such as seagrass beds and mangroves) to the coral reef. If diet shifts are related to such migrations, then the diets of these fish must change before or around the fish size at which such migrations take place. A wide size range of juveniles of two grunt species (*Haemulon sciurus* and *Haemulon flavolineatum*) and of two snapper species (*Lutjanus apodus* and *Ocyurus chrysurus*) were caught in seagrass beds and mangroves, and their gut contents identified and quantified. Regression analysis between fish size and dietary importance of small crustaceans showed a negative relationship in all four species. Positive relations were found for *H. sciurus*, *L. apodus* and *O. chrysurus* between fish length and the dietary importance of decapods, and for *L. apodus* and *O. chrysurus* between fish length and prey fish importance. Critical changes in the fish diets with fish size were examined by application of a Canonical Correspondence Analysis (CCA). The CCA yielded three clusters of size-classes of fishes with similar diets, and application of a Mantel test showed that each of these clusters had significantly different diets, and that each cluster diet was significantly specialised. The size at which a fish species 'switched' from one cluster to another was compared with size-at-maturity data and with the typical size at which these species migrate from the nursery habitats to the coral reef. *H. sciurus* and *H. flavolineatum* may be prompted to migrate from the nursery habitats to coral reef habitats because of dietary changes, or because of the development of the gonads. For *L. apodus* and *O. chrysurus*, a dietary changeover forms a more likely explanation for nursery-to-reef migrations than does sexual maturation because these species reach maturity at sizes much larger than the maximum size of individuals found in nursery habitats. Although other factors may theoretically initiate or promote the migration patterns, the results of this study indicate that ontogenetic dietary changes may crucially influence the nursery-to-coral reef migrations of these reef fish species.

Keywords: nursery habitats; nursery-to-reef migration; diet shifts

1. Introduction

The role of seagrass beds and mangroves as 'nursery' habitats for some fish species has received considerable attention as a link with adjacent coral reef or off-shore habitats (e.g. Beck et al., 2001; Parrish, 1989; Pollard, 1984), even though the relative importance of these habitats for different size-classes of fishes has rarely been adequately quantified (Adams & Ebersole, 2002; Cocheret de la Morinière, Pollux, Nagelkerken, & van der Velde, 2002; Nagelkerken, Dorenbosch, Verberk, Cocheret de la Morinière, & van der Velde, 2000a). The value of such nursery habitats for fish has been explained by several authors in terms of shelter against predators, high interception rate of the vegetation to planktonic larvae, temporary alleviation of competition, or high food availability (Blaber & Blaber, 1980; Carr & Adams, 1973; Cocheret de la Morinière et al., 2002; Heck & Crowder, 1991; Laegdsgaard & Johnson, 2001; Odum & Heald, 1972; Ogden & Zieman, 1977; Parrish,

---

* Corresponding author.
E-mail address: gerardv@sci.kun.nl (G. van der Velde).

0272-7714/03/$ - see front matter © 2003 Elsevier Ltd. All rights reserved.
doi:10.1016/S0272-7714(03)00011-8

1989; Robertson & Blaber, 1992; Shulman, 1985). This size-related preference of juvenile fishes for particular shallow-water habitats can be described as life cycle migration patterns (e.g. Appeldoorn, Recksiek, Hill, Pagan, & Dennis, 1997; Cocheret de la Morinière et al., 2002; Yáñez-Arancibia et al., 1988), since the spatial separation of size-classes of a fish species suggests movement from one habitat to another with ontogeny. Indeed, such migrations have been inferred for many fish species with larger individuals found progressively off-shore (Ross, 1986; Werner & Gilliam, 1984). This inference applies to the nursery concept as well: it intrinsically proposes that sub-adult reef fishes migrate from nursery habitats (in many cases seagrass beds and/or mangroves) to the coral reef.

In Spanish Water Bay (Curaçao, Netherlands Antilles), a number of reef fish species were identified as nursery species (Nagelkerken et al., 2000a). The use of nursery habitats in this bay by the most abundant of those fish species was confirmed by Cocheret de la Morinière et al. (2002). The spatial size-frequency distributions described by Cocheret de la Morinière et al. (2002) not only suggested nursery-to-reef migrations, but also size-related migrations at a smaller scale, from one nursery habitat to another. Possible biological and physical mechanisms instigating these migrations from one habitat to another are: (a) physical environmental factors (turbidity, temperature, salinity, depth, habitat complexity, etc.), or gradients and seasonal changes therein, mark the migratory pathways (derived from e.g. Blaber, 1997); (b) physiological or morphological changes in the juveniles (e.g. photon receptor sensitivity, development of gonads, development of swimming or navigational capabilities) increase their home range or susceptibility to environmental gradients (derived from e.g. Gerking, 1994; Helfman, Meyer, & McFarland, 1982; Hyndes, Platell, & Potter, 1997); (c) the spatial distribution of food abundance or food types determines choice of habitats (derived from e.g. Brook, 1977; Edgar & Shaw, 1995a,b; Parrish & Zimmerman, 1977); (d) ontogenetic changes in feeding strategy (e.g. from zoobenthivory to piscivory) lead to larger home ranges, thereby increasing the chance of accidentally finding the reef habitat (derived from e.g. Edgar & Shaw, 1995a,b; Muñoz & Ojeda, 1998).

Many fish species show ontogenetic changes in diet (e.g. Ross, 1986; Werner & Gilliam, 1984), and the ontogeny of resource partitioning may directly influence life cycle migration patterns of coastal fishes (Hyndes et al., 1997; Livingstone, 1982). Literature on trophic studies in seagrass and mangrove fish communities in general is scant, however, and most authors have not distinguished separate size-classes of fishes in nursery areas (but see Blaber, 1997; Heck & Weinstein, 1989; Livingston, 1982; Muñoz & Ojeda, 1998).

The present study focused on the diet shifts of a selection of four carnivorous grunt (Haemulidae) and snapper (Lutjanidae) species that inhabit seagrass beds and mangroves during their juvenile and sub-adult stages (Cocheret de la Morinière et al., 2002; Nagelkerken et al., 2000a). Gut contents of *Haemulon flavolineatum*, *H. sciurus*, *Lutjanus apodus*, and *Ocyurus chrysurus* were analysed for each size-class that occurred in the nursery habitats (seagrass beds and mangroves) in the bay.

The main questions in this study were:

1. Do ontogenetic diet changes occur in these reef fish species while they are still in the nursery habitats (i.e. before they migrate to the coral reef)?
2. Can these diet shifts be related to nursery-to-reef migrations?

2. Materials and methods

2.1. Study area

The present study was carried out in Spanish Water Bay in Curaçao, Netherlands Antilles (Fig. 1). This 3-km^2 bay is shallow (largely <6 m), harbours extensive seagrass meadows and is fringed by mangroves (*Rhizophora mangle*). Most mangrove stands studied consist of strips of vegetation hanging over from fossil reef ledges, hence providing little structural complexity from prop roots or branches in the water column beneath the mangrove canopy. Water depths under mangrove canopies varied between 0.8 and 1.8 m. These canopies provide dark habitats (average light extinction underwater was 85%, as opposed to 40% over seagrass beds). The seagrass beds consist of monospecific stands of *Thalassia testudinum* (Kuenen & Debrot, 1995). Mean shoot density (±SD) in the seagrass transects was 246 m^{-2} (±110) and seagrass canopy height averaged 28.0 cm (±11.5).

There is no freshwater input into the bay other than rain, and salinity (average 35.4) was slightly higher than on the reef (average 34.6). Bay water surface temperature averaged 30.1 °C (±0.8), while water surface temperature on the reef averaged 28.4 °C (±0.9). Underwater visibility was high at all sites, and varied between an average of 6.5 m (±1.8) in the bay and 21.4 m (±3.1) on the reef as measured by horizontal Secchi disk distance. The average tidal amplitude in the area is 30 cm (De Haan & Zaneveld, 1959).

The bay has a long (1 km) and narrow (70 m) entrance that connects it to the adjacent fringing reef. This reef is part of a marine park that stretches up to the southeast tip of the island. A detailed description of the reefs in the Netherlands Antilles can be found in Bak (1975).

2.2. Sampling design

In various parts of Spanish Water Bay, beach seine nets were used to collect fishes inhabiting seagrass beds

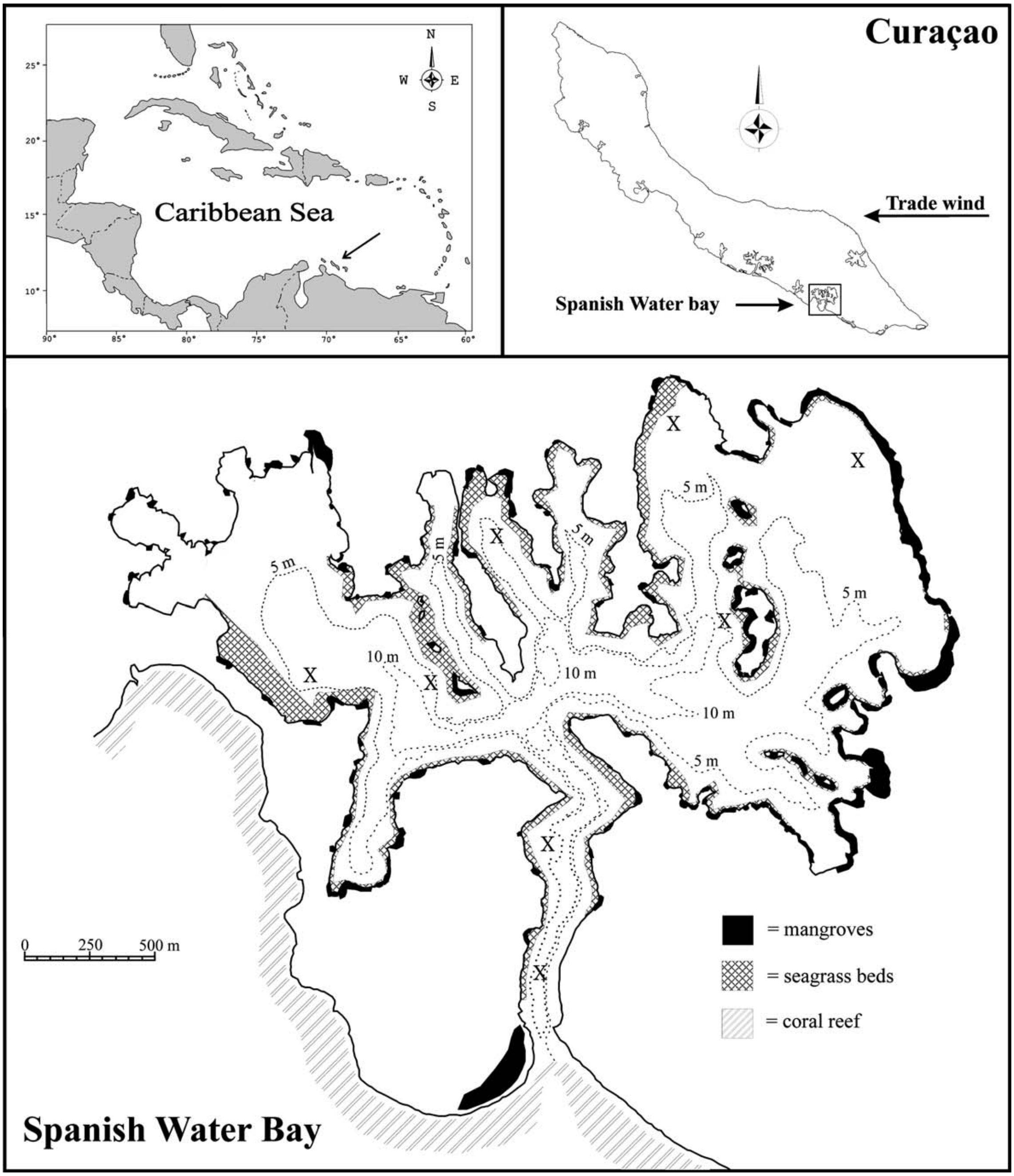

Fig. 1. Map of Spanish Water Bay and various habitats. Bathymetry is indicated with 5 and 10 m isobaths. Sites where fish collection took place are indicated by 'X'.

(fish collection sites were indicated with 'X' in Fig. 1). Fish collection took place in the same period in which the spatial size distribution patterns of the fish species were surveyed (Cocheret de la Morinière et al., 2002), during May through to September 1998. Antillean fish traps were used in mangrove habitats. Since these fish species feed in seagrass beds at night while they inhabit the bay (Nagelkerken, Dorenbosch, Verberk, Cocheret de la Morinière, & van der Velde, 2000b), fish collection took place overnight or early in the morning. The smallest individuals were captured from isolated patches of seagrass, mangroves or boulders by use of the ichtyocide rotenone. Data on gut contents of fishes from mangroves were pooled with data on fish guts from seagrass bed communities, since fishes in Spanish Water Bay mainly feed from the seagrass beds and not from the mangroves (Nagelkerken et al., 2000b). No fishes were caught on the nearby coral reef, since the main aim of the study was to investigate if diet shifts occur in the nursery habitats (i.e. before they migrate to the coral reef).

A total number of 392 fishes were captured in the bay, of which 287 stomachs had sufficient contents for gut analysis. The gut contents of the individuals were preserved in ethanol (70% v/v) and dyed with Rose Bengal before identification and quantification. All fishes were measured (Fork Length) and weighed. Food components in the digestive tracts were classified to Class level (Oligochaeta, Polychaeta, Bivalvia, Gastropoda, Echinoidea) or Order/Subclass level (Tanaidacea, Mysidacea, Ostracoda, Isopoda, Copepoda, Amphipoda, Decapoda), while prey fish, sediment and plant material (seagrass or algae) found in the guts were categorised as fish, seagrass, sediment, foraminifers, filamentous algae, calcareous algae or macro-algae. Using a stereomicroscope, the relative volumetric quantity of the food items was estimated, i.e. the volume of the contents of the digestive tract was set to 100%, and the food items found were estimated by eye, as volumetric percentage of total stomach volume (Nielsen & Johnson, 1992). A volumetric measure was chosen because it is an estimation of biomass, whereas gravimetric methods would produce large errors in these small volumes because of water content (blotting would damage the samples in some cases), and methods that involve frequencies would underestimate large food items and overestimate small food categories (Hyslop, 1980).

2.3. Data processing and statistical analysis

Gradual dietary changes with increasing fish size were examined by least squares linear regression (fish size against the relative volumes of food items in the fish guts).

Ordination of the food categories was performed using the Canoco software package (Ter Braak & Smilauer, 1998). All stomach content data were $\log(1+X)$ transformed prior to analysis. Detrended Correspondence Analysis (DCA) of the pooled gut contents data calculated a gradient length of 4.8, and therefore a unimodal method was used (Ter Braak & Smilauer, 1998). In each Canonical Correspondence Analysis (CCA) that was subsequently applied, scaling was focused on inter-sample distances (Hill's scaling), and rare 'species' were downweighted.

First, a CCA was applied on the composition of the diets of all individual fish stomachs, with 'size' of the fishes and 'species identity' as 'environmental variables', to test which of these factors best explains the variation in the gut contents of these fishes.

A second CCA was then applied, with each size-class of the selected fish species entered separately as 'environmental variables', to find which of the size-classes best explain the variation in the gut contents of these fishes. The size at which the most critical diet change occurs (indicated by the separation of different clusters of size-classes in the CCA) was then compared with size-at-maturity data (Munro, 1983) and with the typical size at which these species move from the nursery habitat to the adjacent coral reef (Cocheret de la Morinière et al., 2002). The clusters of size-classes appearing in this CCA were regarded as separate diet groups (ontogenetic feeding guilds, see Muñoz & Ojeda, 1998), and the difference among the group diets were tested with a Mantel test (see subsequently).

Although the collection of compositional data is a common practice in ecology, few authors have attempted to develop satisfactory statistical testing (Lawlor, 1980; Manly, 1991; Patterson, 1986). Many authors refer to Keast's suggestion that a diet overlap index value (Schoener, 1974) of 0.3 or less indicates little overlap in the diets of the groups, whereas an index value of 0.7 or more indicates a high degree of overlap (Keast, 1978). Others have used jackknife or bootstrap methods or cluster analysis, but the estimation of confidence intervals with those methods is complicated or the analyses do not involve actual testing of differences (Sevenster & Bouton, 1998). Sevenster and Bouton (1998) improved methods developed by Manly (1991) and Patterson (1986), in which dietary differences are tested using the Mantel test (Sokal & Rohlf, 1995). Sevenster and Bouton (1998) show that a significant difference in diet among species does not necessarily imply that interspecific overlap is smaller than intraspecific overlap, and apply significance testing on both the interspecific and intraspecific level. In the present study, diet overlaps among individual fish stomachs within a cluster (identified in a CCA of size-classes, as described earlier) were calculated using Schoener's index (Schoener, 1974), yielding an overlap matrix. Randomisation (1000 permutations) generates the null-distribution for the statistics, which is compared to the observed average overlaps between and within groups. If less than 5% of the simulated interspecific overlaps are smaller than the observed interspecific overlaps, we decide that the diets of the groups differ significantly more than expected if all individuals belonged to the same dietary background. The overlaps within the two groups are judged in a similar way. If less than 5% of the simulations produce an intraspecific overlap larger than the observed value, we conclude that the species under consideration is significantly more specialised than expected if all individuals were from the same background (Sevenster & Bouton, 1998). Mantel test *p*-values were corrected for multiple comparisons by use of a sequential Bonferroni correction (Peres-Neto, 1999). Sample size and inequality of sample sizes have proved to greatly influence the test statistic in the Mantel test (Luo & Fox, 1996). The larger the sample sizes are, the more sensitive the test becomes to detecting differences in diet composition among groups. The effect of inequality of sample sizes on the test statistic is much stronger than the effect of sample size alone: sensitivity of the test increases strongly with increasing equality of the sample sizes. Differences in diets may therefore not be detected when the data consist of small sample sizes or with large differences in sample sizes. With the present data, the Mantel test produced significant *p*-values ($p < 0.05$) with each comparison (within group or among groups), and a correction for inequality of sample sizes (as developed by Luo & Fox, 1996) would only make differences more significant (smaller *p*-values). This correction was therefore not applied.

3. Results

Individuals of the collected species ranged from 1.8 to 27.4 cm (FL). Dietary overlap (Schoener's index) was generally high among the species' overall diet compositions (34% up to 70%). Table 1 shows the mean composition of the diets of the fish species for each size-class. Clearly, these grunts and snappers belong to the feeding guild of carnivores, with a large variety of invertebrates (mainly crustaceans) and prey fish representing more than 80% of the species' diets on average. *Haemulon sciurus* and *H. flavolineatum* are invertebrate consumers, while the two snapper species feed on both invertebrates and fishes. The average proportion of decapods was larger in the diets of the snappers as compared to the diets of the grunts (Table 1). The proportion of tanaids was high in all species (Table 1). Copepods are important dietary components for small fishes (0.0–5.0 cm), especially for the juveniles of *H. flavolineatum* and *Ocyurus chrysurus*.

3.1. Gradual dietary changes

When size of the individuals and their species identity were entered as environmental factors in a CCA, size appeared to have a much stronger effect on diet composition of the individuals than species identity. The correlation between the first ordination axis (explaining 23.5%) and the size of the individuals was 0.66, while for species identity this was 0.29. Correlations with the second axis (explaining 10.3%) were 0.32 for the factor 'size', and 0.05 for 'species identity'. Inflation factors were low (<2), indicating no interaction between the two factors. The influence of fish size on diet composition can be explained by the increasing proportion of prey fishes and decapods and the decreasing importance of other (smaller) crustaceans in the diets of these carnivores with increasing fish size (Table 1). Regression analysis between size-classes and proportions of small crustaceans (not decapods) showed significantly negative relationships for all four fish species (Table 2), indicating a steady decline of the importance of crustaceans for these species with increasing fish size. Except for *H. flavolineatum*, all species showed significantly positive correlations for decapod importance with fish size. Additionally, *L. apodus* and *O. chrysurus* showed significant positive relations between fish size and the importance of prey fish (Table 2).

3.2. Critical diet shifts

CCA of diet composition of individual stomachs and size-classes of the four species showed three clusters (Fig. 2). Cluster A consisted of the smallest juveniles of *Haemulon flavolineatum* and *Ocyurus chrysurus*. The separation of cluster A from the others was mainly due to the relatively large volume of copepods consumed by small juveniles of *H. flavolineatum* and *O. chrysurus* (Fig. 3). Cluster B in Fig. 2 consisted of a group of size-classes of individuals that predominantly fed on a variety of small benthic invertebrates, with an important contribution of Tanaidacea (Fig. 3). Cluster C was formed by the largest fishes that had changed their diet to larger crustaceans (crabs) and prey fish. Dietary overlap (Schoener's index) between cluster A and cluster B was 41%, while overlap between cluster B and C was only 7%. Each cluster was significantly different from the other (among groups $p < 0.05$, Mantel test), and each cluster was significantly more specialised than the other (within groups $p < 0.05$, Mantel test).

3.3. Feeding strategy vs. migration pattern

The average size at which *Haemulon sciurus* becomes sexually mature (Table 3), was also the size at which the major dietary change occurred (from cluster B to C, Fig. 2), and corresponds to the average size of individuals found on the adjacent reef (Table 3). *H. flavolineatum* drastically changed its diet only once, at the 5.0–7.5 size-class (Fig. 2), which did not correspond to any of the relevant sizes in Table 3. The size at sexual maturity of *H. flavolineatum* does correspond to the average size at which they occur on the coral reef.

In the ontogeny of *Lutjanus apodus* and *Ocyurus chrysurus*, a major change in diet (Fig. 2) occurred at a size-class that corresponds to the size at which these individuals were first observed on the coral reef (Table 3). Sexual maturity sets in at sizes much larger than the size of major diet change for these two snappers.

4. Discussion

In a recent study, the spatial size-frequency distributions of nine coral reef fish species, including those of the present study, were surveyed in seagrass beds and mangroves in Spanish Water Bay and the adjacent coral reef, using a single visual census method (Cocheret de la Morinière et al., 2002). All of the fish species (including the grunts and snappers in the present study) appeared to grow up in nursery habitats after which they migrate to the coral reef to take up permanent residence there.

Table 1
Average percent volume of each food category

N caught	Size-class (cm)	Tanaidacea	Copepoda	Isopoda	Amphipoda	Mysidacea	Bivalvia	Gastropoda	Decapoda	Fish	Sediment	Rest	Unidentified
Haemulon flavolineatum													
11	0.0–2.5	12.7	66.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	20.9
15	2.5–5.0	12.0	83.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.2
13	5.0–7.5	66.9	0.4	0.0	8.5	0.0	0.0	0.0	8.5	0.0	0.0	7.7	8.1
12	7.5–10.0	75.0	0.0	0.0	4.6	0.0	0.0	3.3	0.0	0.0	0.0	0.0	17.1
12	10.0–12.5	22.5	0.2	0.0	3.8	1.2	2.1	2.9	0.0	1.7	7.5	0.4	57.8
6	12.5–15.0	50.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.5	5.0	42.2
Haemulon sciurus													
16	2.5–5.0	63.5	30.4	2.5	0.1	0.0	0.1	0.0	0.6	0.0	0.0	0.8	2.0
16	5.0–7.5	79.1	7.9	1.9	0.6	0.0	0.0	0.1	0.0	0.0	0.1	0.1	10.3
9	7.5–10.0	53.8	13.3	0.0	0.0	2.9	2.8	6.1	0.0	0.0	0.0	7.2	13.9
7	10.0–12.5	41.4	17.1	0.7	0.0	0.0	3.9	4.7	0.0	0.0	17.0	5.1	10.0
14	12.5–15.0	25.9	2.2	8.7	2.6	0.0	5.3	6.3	1.4	0.0	7.5	16.6	23.4
5	15.0–17.5	22.0	1.2	6.0	5.0	0.0	8.2	0.0	0.0	0.0	17.0	26.0	14.6
4	17.5–20.0	12.0	0.5	0.0	1.3	0.0	16.3	7.5	15.0	0.0	22.5	17.5	7.5
4	20.0–22.5	0.5	0.0	0.0	0.0	0.0	0.0	0.0	50.0	0.0	0.0	30.8	18.8
1	25.0–27.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	90.0	0.0	0.0	0.0	10.0
Lutjanus apodus													
5	0.0–2.5	91.0	9.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
9	2.5–5.0	48.7	9.7	3.9	20.7	7.7	0.1	0.0	7.8	0.0	0.0	0.0	1.6
8	5.0–7.5	37.5	5.0	0.1	15.6	10.0	0.0	0.0	23.0	0.0	0.0	0.6	8.1
11	7.5–10.0	24.0	0.0	0.0	1.0	7.3	0.0	0.0	47.3	18.2	0.0	0.5	1.8
13	10.0–12.5	5.8	0.2	4.6	1.4	0.0	0.0	0.0	77.7	4.2	0.0	0.0	6.2
14	12.5–15.0	3.6	0.0	0.0	0.0	0.0	0.0	0.0	86.4	4.3	0.0	0.0	5.7
6	15.0–17.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	83.3	16.7	0.0	0.0	0.0
2	17.5–20.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	50.0	50.0	0.0	0.0	0.0
3	20.0–22.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	46.7	53.3	0.0	0.0	0.0
Ocyurus chrysurus													
9	0.0–2.5	49.9	49.0	0.0	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
16	2.5–5.0	21.9	66.6	0.0	0.0	0.0	0.3	0.0	0.3	0.0	0.0	0.0	10.9
8	5.0–7.5	78.6	5.9	0.3	0.9	14.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0
15	7.5–10.0	23.0	8.7	0.7	0.7	28.1	1.5	3.0	12.7	13.6	0.3	1.1	6.5
10	10.0–12.5	37.2	1.2	0.5	0.0	14.6	0.0	0.2	31.0	3.0	6.0	0.2	6.1
8	12.5–15.0	2.5	0.0	0.0	0.0	11.9	2.5	0.0	59.4	15.6	0.6	3.8	3.8
5	15.0–17.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	63.0	20.0	4.0	13.0	0.0

Food items that never exceeded 2% estimated volume of gut contents, were grouped in a ‘Rest’ group (i.e. Oligochaeta, Polychaeta, Echinoidea, Ostracoda, seagrass, foraminifers, filamentous algae, calcareous algae, macro-algae).

Table 2
Slopes and regression coefficients (R^2, in brackets) of linear regressions between fish size and food item

	Small crustaceans	Decapods	Prey fish
Haemulon flavolineatum	−0.57 (0.32)	ns	ns
Haemulon sciurus	−0.83 (0.67)	0.55 (0.30)	no
Lutjanus apodus	−0.78 (0.61)	0.58 (0.33)	0.34 (0.11)
Ocyurus chrysurus	−0.68 (0.46)	0.58 (0.33)	0.27 (0.11)

Only statistically significant slopes ($p < 0.05$) and regression coefficients are shown. 'ns' indicates not significant, and 'no' indicates that the food item was not observed in the species.

The role of dietary changes and other factors as possible drives for these post-settlement migrations is discussed subsequently.

4.1. General diet

Small crustaceans were very important in the diets of *Haemulon flavolineatum*, *H. sciurus*, *Lutjanus apodus* and *Ocyurus chrysurus*, as is generally the case for seagrass and mangrove inhabiting fishes (Pollard, 1984). Although penaeid and caridean shrimps were also found to be highly important food items in grunts and snappers in many studies (Austin & Austin, 1971; Carr & Adams, 1973; Claro, 1983; Croker, 1962; Edgar & Shaw, 1995a,b; Harrigan, Zieman, & Macko, 1989; Heck & Weinstein, 1989; Randall, 1967; Rooker, 1995; Sanchez, 1994; Starck & Schroeder, 1971; Thayer, Colby, & Hettler, 1987), they were not observed in any of the examined guts in this study. Here, the volumes of tanaids and crabs were especially high in the guts of the juvenile grunts and snappers. Few authors have reported the importance of tanaids in nursery fish diets as a separate food category (Austin & Austin, 1971; Hyndes et al., 1997; Nagelkerken et al., 2000b; Randall, 1967) of which only Nagelkerken et al. (2000b) observed similarly high relative dietary contributions in Spanish Water Bay. On fish species level, the present data on the qualitative and quantitative diet description of these species are coherent with data of the authors cited above, with the exception of shrimp and tanaid importance. Overall diet overlap (Schoener's index) was generally high among the selected species (33–70%), reflecting interspecies similarity in resource utilisation.

4.2. Gradual dietary changes

Ontogenetic diet changes of coral reef fishes in seagrass beds and mangroves are rarely studied (but see Edgar & Shaw, 1995a; Hettler, 1989; Rooker, 1995; Starck & Schroeder, 1971). Even though the method used to estimate relative volumetric quantities is rough and subject to a fair amount of bias (Hyslop, 1980), ontogenetic diet changes of the selected fish species are very clear. Regression analysis of diet composition vs. fish size showed gradual diet changes in all selected species. A negative relationship was found for the volume of the smaller crustaceans (mostly tanaids and copepods) in the stomachs of *Haemulon sciurus*, *H. flavolineatum*, *Lutjanus apodus* and *Ocyurus chrysurus* with increasing fish body size. A positive relationship with fish size was found for decapods in *H. sciurus*, *L. apodus* and *O. chrysurus*, and for prey fish in the stomachs of *L. apodus* and *O. chrysurus*. Differences in digestion capability or efficiency at different ontogenetic stages could theoretically bias the observed decrease in relative importance of small crustaceans with fish size, but that argument provides no plausible explanation for

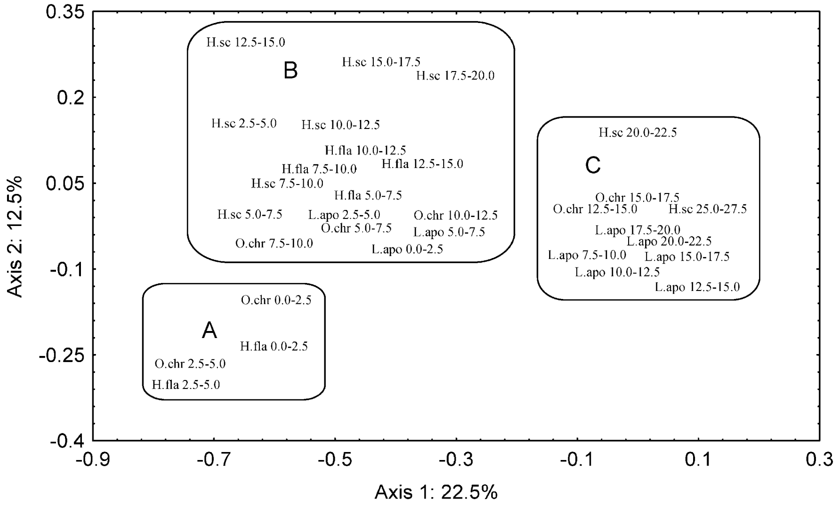

Fig. 2. Correlations with first two axes (CCA) for all size-classes: H.sc = *Haemulon sciurus*; H.fla = *Haemulon flavolineatum*; L.apo = *Lutjanus apodus*; O.chr = *Ocyurus chrysurus*. Size-classes (in cm) are indicated by the numbers behind the species codes. Percentages of variance explained by the ordination axis are shown near the axis.

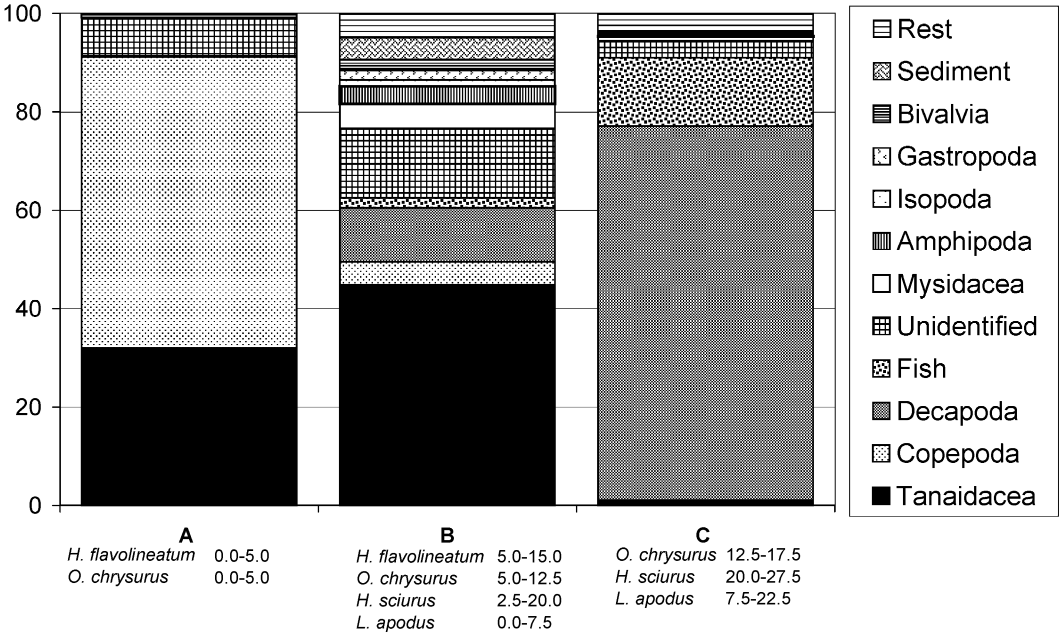

Fig. 3. Average diet composition of the fishes from the three clusters derived from CCA in Fig. 2. Food items that never exceeded 2% estimated volume of the gut contents, were grouped in a 'Rest' group (i.e. Oligochaeta, Polychaeta, Echinoidea, Ostracoda, seagrass, foraminifers, filamentous algae, calcareous algae, macro-algae). Species and size-classes (cm) below the graph indicate the size-classes of species belonging to the clusters.

the observed increase in the preference for larger crustaceans and prey fish with increased fish size. Other authors (e.g. Edgar & Shaw, 1995a; Hyndes et al., 1997) have also reported patterns of increasing prey size with increasing fish size for other species.

The highly mobile grunt and snapper species that feed on ever larger food items as they grow, may theoretically need to expand their foraging radius, since the biomass of prey fish and decapod crabs per unit area is much less than that of smaller crustacean prey such as tanaids (Nagelkerken et al., 2000b). Observations of tagged individuals confirm that larger fishes show diurnal migrations over greater distances than smaller fishes in Spanish Water Bay (Cocheret de la Morinière, unpublished data): the percentage of tag return at the initial site was much less for larger individuals, which were recovered farther away from the location where they were tagged. When these fishes start foraging in a larger radius, the chance of accidentally finding the narrow entrance of the bay (to them now an exit to the reef) increases. Especially in the case of piscivorous species it is favourable to take up residence on the coral reef, because of the clear water conditions on the reef habitats as opposed to the more turbid water in the bay. Also, all of the selected species are known to spawn on the coral reef (Munro, 1983), which presents another reason for these fish species to move to the coral reef. Once arrived on the coral reef, which stretches over an area much larger than the surface area of the bay and its narrow entrance, these fishes stay in the reef habitat, over which they can migrate over large distances. The migration from the nursery habitats to the coral reef can thus theoretically be promoted by gradual dietary changes during the fish' life cycle.

4.3. Critical diet shifts

The statistical separation of groups of size-classes with different diets indicates the largest diets shifts. The CCA of the diet composition of individual size-classes of the selected fish species yielded three clusters. The first cluster consisted of the 0.0–2.5 and 2.5–5.0 cm size-classes of *Haemulon flavolineatum* and *Ocyurus chrysurus*. These juveniles predominantly fed on copepods, possibly reflecting the shift from zooplanktivory to a zoobenthic

Table 3
Average size (cm) of fishes observed on the coral reef adjacent to Spanish Water Bay, and the size-class at which the individuals were first encountered on nearby reef habitats (Cocheret de la Morinière et al., 2002)

	Average size on reef	First size on reef	Cluster B–C changeover	Size at sexual maturity
Haemulon flavolineatum	15.1	7.5–10.0	–	15.5
Haemulon sciurus	21.5	12.5–15.0	20.0	20.0
Lutjanus apodus	18.5	10.0–12.5	7.5	25.0
Ocyurus chrysurus	17.1	10.0–12.5	12.5	26.0

Approximate sizes at which the fish species reach sexual maturity were adopted from Claro (1983), Munro (1983) and Starck and Schroeder (1971). Size at changeover from cluster B to cluster C (Fig. 3) was not available for *Haemulon flavolineatum*, since it did not occur in cluster C.

feeding strategy after settlement. The second cluster consisted of individuals that fed on a wide range of invertebrates, mostly small crustaceans. The third cluster was formed by the largest individuals of fish species that predominantly fed on larger crustaceans (decapod crabs) and prey fish. Each of the three clusters had a diet composition that was significantly different from the other and was significantly specialised (Mantel test, $p \leq 0.05$).

The size at which a species 'moves' from one cluster to another cluster of size-classes with a different diet, was compared with size-at-maturity data (Munro, 1983) and with the size at which the species is known to migrate to the adjacent coral reef (Cocheret de la Morinière et al., 2002). In *Haemulon sciurus*, the size at the critical diet shift (20 cm) corresponds to the size at which the first individuals become sexually mature, viz. approximately 20 cm (Munro, 1983), which is also the average size at which they occur on adjacent reef sites (Cocheret de la Morinière et al., 2002). It does not correspond to the smallest size-class that was observed on nearby reefs (12.5–15.0 cm). At 12.5–15.0 cm, however, diet change from small crustaceans to decapod crabs has already set in. Thus, the largest change in diet of *H. sciurus* occurs at size-classes at which conspecifics have already begun to migrate to coral reef habitats, but diet change starts much earlier, at sizes that are similar to the smallest observed individuals on nearby reefs. It is not clear whether sexual maturity or change in dietary needs instigates migration from nursery habitat to coral reef for this species.

Haemulon flavolineatum consumes large portions of small crustaceans throughout the size range that occurs in the bay. Since it did not occur in cluster 3, the minimum size of individuals observed on the coral reef could not be related to any discrete dietary change. The maximum size of this species in bay habitats corresponds to average size at sexual maturity (Munro, 1983). Given the gradual diet changes before the size at which this species moves to the coral reef and the concurrence with the size-at-maturity, the development of gonads (and subsequent search for sex partners) as well as dietary shifts may explain its migratory patterns.

In the case of *Lutjanus apodus* and *Ocyurus chrysurus*, the size at the critical diet shift corresponded to the smallest size at which these species were observed on the adjacent reef. Sexual maturity is reached at sizes much larger than fish size at the major diet shift, and diet change may thus play a more important role in determining their migration patterns.

A large number of other factors may theoretically initiate or promote nursery-to-reef migrations of reef fish species. For instance, Helfman et al. (1982) and McFarland, Ogden, and Lythgoe (1979) found that *Haemulon flavolineatum* becomes increasingly more sensitive to light with fish size, and that it possesses compass navigational abilities. Also, the fishes may migrate along physicochemical gradients, or their habitat requirements may change with age (see Section 1). This study, however, merely indicates that the importance of dietary changes in determining fish migration patterns cannot be dismissed.

4.4. Conclusions

The juveniles of reef fish species show ontogenetic dietary changes while they are still in the nursery habitats (i.e. before migration to the coral reef). Positive relationships were found between fish size and prey size in all species. The grunts may be prompted to migrate from the nursery habitats to coral reef habitats because of dietary changes, or because of the development of the gonads. For the snappers, a dietary shift forms a more likely explanation for nursery-to-reef migrations than does sexual maturation because these species reach maturity at sizes much larger than the maximum size of individuals found in nursery habitats. Although other factors may theoretically initiate or promote the migration patterns, the results of this study indicate that ontogenetic dietary changes may crucially influence the nursery-to-coral reef migrations of these reef fish species.

Acknowledgements

We would like to thank all personnel of the Carmabi Foundation, where the research was carried out, and M. Dorenbosch and W. Verberk for their support during fieldwork. We thank E. Kardinaal for supplying us with a map of the Spanish Water Bay and the Winkel family for the use of their pier. Jan Sevenster has helped a great deal with properly applying the Mantel statistics. Finally, we thank Ruth Fisher for supplying rotenone and Prof. P.H. Nienhuis for his comments and suggestions on the manuscript. The research was funded by the Netherlands Foundation for the Advancement of Tropical Research (WOTRO). The Stichting Nijmeegs Universiteitsfonds (SNUF) funded B.J.A.P.

References

Adams, A. J., Ebersole, J. P. (2002). Use of back-reef lagoon habitats by coral reef fishes. *Marine Ecology Progress Series 228*, 213–226.

Appeldoorn, R. S., Recksiek, C. W., Hill, R. L., Pagan, F. E., Dennis, G. D. (1997). Marine protected areas and reef fish movements: the role of habitat in controlling ontogenetic migration. *Proceedings of the 8th International Coral Reef Symposium 2*, 1917–1922.

Austin, H., Austin, S. (1971). The feeding habits of some juvenile marine fishes from the mangroves in Western Puerto Rico. *Caribbean Journal of Science 11*, 171–178.

Bak, R. P. M. (1975). Ecological aspects of the distribution of reef corals in the Netherlands Antilles. *Bijdragen tot de Dierkunde 45*, 181–190.

Beck, M. W., Heck, K. L., Jr., Able, K. W., Childers, D. L., Eggleston, D. B., Gillanders, B. M., Halpern, B., Hays, C. G., Hoshino, K., Minello, T. J., Orth, R. J., Sheridan, P. F., Weinstein, M. P. (2001). The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *Bioscience 51*, 633–642.

Blaber, S. J. M. (1997). *Fish and fisheries of tropical estuaries* (Vol. 22, 353 pp.). London: Chapman and Hall.

Blaber, S. J. M., Blaber, T. G. (1980). Factors affecting the distribution of juvenile estuarine and inshore fish. *Journal of Fish Biology 17*, 143–162.

Brook, I. M. (1977). Trophic relationships in a seagrass community (*Thalassia testudinum*), in Card Sound, Florida. Fish diets in relation to macrobenthic and cryptic faunal abundance. *Transactions of the American Fisheries Society 106*, 219–229.

Carr, W. E. S., Adams, C. A. (1973). Food habits of juvenile marine fishes occupying seagrass beds in the estuarine zone near Crystal River, Florida. *Transactions of the American Fisheries Society 102*, 511–540.

Claro, R. (1983). Ecologia y cicle de vida del caballerote, *Lutjanus griseus* (Linnaeus), en la platforma cubana. I. Identidad, distribucion y habitat, nutricion y reproduccion. *Reportajes y Investigaciones del Instituto por Oceanologia de la Academia de Sciencia de Cuba 7*, 1–30.

Cocheret de la Morinière, E., Pollux, B. Y. A., Nagelkerken, I., van der Velde, G. (2002). Post-settlement life cycle migration patterns in relation to biotope preference of coral reef fish that use seagrass and mangrove habitats as nurseries. *Estuarine, Coastal and Shelf Science 55*, 309–321.

Croker, R. A. (1962). Growth and food of the Gray snapper, *Lutjanus griseus* in Everglades National Park. *Contributions from the Institute of Marine Science Miami 403*, 379–383.

De Haan, D., Zaneveld, J. S. (1959). Some notes on tides in Annabaai harbour, Curaçao, Netherlands Antilles. *Bulletin of Marine Science of the Gulf and Caribbean 9*, 224–236.

Edgar, G. J., Shaw, C. (1995a). The production and trophic ecology of shallow-water fish assemblages in southern Australia. II. Diets of fishes and trophic relationships between fishes and benthos at Western Port, Victoria. *Journal of Experimental Marine Biology and Ecology 194*, 83–106.

Edgar, G. J., Shaw, C. (1995b). The production and trophic ecology of shallow-water fish assemblages in southern Australia. III. General relationships between sediments, seagrasses, invertebrates and fishes. *Journal of Experimental Marine Biology and Ecology 194*, 107–131.

Gerking, S.D. (Ed.). (1994). *Feeding ecology of fish* (416 pp.). California, USA: Academic Press Inc.

Harrigan, P., Zieman, J. C., Macko, S. A. (1989). The base of nutritional support for the gray snapper (*Lutjanus griseus*): an evaluation based on a combined stomach content and stable isotope analysis. *Bulletin of Marine Science of the Gulf and Caribbean 44*, 65–77.

Heck, K. L., Crowder, L. B. (1991). Habitat structure and predator-prey interactions in vegetated aquatic ecosystems. In S. S. Bell, E. D. McCoy, & E. R. Mushinsky (Eds.), *Habitat structure: The physical arrangements of objects in space* (pp. 281–299). London: Chapman and Hall.

Heck, K. L., Jr. Weinstein, M. P. (1989). Feeding habits of juvenile reef fishes associated with Panamanian seagrass meadows. *Bulletin of Marine Science of the Gulf and Caribbean 45*, 629–636.

Helfman, G. S., Meyer, J. L., McFarland, W. N. (1982). The ontogeny of twilight migration patterns in grunts (Pisces: Haemulidae). *Animal Behaviour 30*, 317–326.

Hettler, W. F. (1989). Food habits of juveniles of Spotted seatrout and Gray snapper in Western Florida Bay. *Bulletin of Marine Science of the Gulf and Caribbean 44*, 155–162.

Hyndes, G. A., Platell, M. E., Potter, I. C. (1997). Relationships between diet and body size, mouth morphology, habitat and movements of six sillaginid species in coastal waters: implications for resource partitioning. *Marine Biology 128*, 585–598.

Hyslop, E. J. (1980). Stomach contents analysis—a review of methods and their application. *Journal of Fish Biology 17*, 411–429.

Keast, A. (1978). Trophic and spatial interrelationships in the fish species of an Ontario temperate lake. *Environmental Biology of Fishes 3*, 7–31.

Kuenen, M. M. C. E., Debrot, A. O. (1995). A quantitative study of the seagrass and algal meadows of the Spaanse Water, Curaçao, The Netherlands Antilles. *Aquatic Botany 51*, 291–310.

Laegdsgaard, P., Johnson, C. (2001). Why do juvenile fish utilise mangrove habitats? *Journal of Experimental Marine Biology and Ecology 257*, 229–253.

Lawlor, L. R. (1980). Overlap, similarity and competition coefficients. *Ecology 6*, 245–251.

Livingston, R. J. (1982). Trophic organization of fishes in a coastal seagrass system. *Marine Ecology Progress Series 7*, 1–12.

Luo, J., Fox, B. J. (1996). A review of the Mantel test in dietary studies: effects of sample size and inequality of sample sizes. *Wildlife Research 23*, 267–288.

Manly, B. F. J. (1991). *Randomization and Monte Carlo methods in biology*. London, UK: Chapman and Hall.

McFarland, W. N., Ogden, J. C., Lythgoe, J. N. (1979). The influence of light on the twilight migrations of grunts. *Environmental Biology of Fishes 4*, 9–22.

Muñoz, A. A., Ojeda, F. P. (1998). Guild structure of carnivorous intertidal fishes of the Chilean coast: implications of ontogenetic dietary shifts. *Oecologia 114*, 563–573.

Munro, J.L. (Ed.), (1983). *Caribbean coral reef fishery resources* (2nd ed., 276 pp). Philippines: ICLARM.

Nagelkerken, I., Dorenbosch, M., Verberk, W. C. E. P., Cocheret de la Morinière, E., & van der Velde, G. (2000a). Importance of shallow-water biotopes of a Caribbean bay for juvenile coral reef fishes: patterns in biotope association, community structure and spatial distribution. *Marine Ecology Progress Series 202*, 175–192.

Nagelkerken, I., Dorenbosch, M., Verberk, W. C. E. P., Cocheret de la Morinière, E., & van der Velde, G. (2000b). Day–night shifts of fishes between shallow-water biotopes of a Caribbean bay, with emphasis on the nocturnal feeding of Haemulidae and Lutjanidae. *Marine Ecology Progress Series 194*, 55–64.

Nielsen, L.A. & Johnson, D.L. (Eds.), (1992). *Fisheries techniques* (468 pp.). Bethesda, USA: American Fisheries Society.

Odum, W. E., & Heald, E. J. (1972). Trophic analyses of an estuarine mangrove community. *Bulletin of Marine Science 22*, 671–738.

Ogden, J. C., & Zieman, J. C. (1977). Ecological aspects of coral reef–seagrass bed contacts in the Caribbean. *Proceedings of the 3rd International Coral Reef Symposium 1*, 377–382.

Parrish, J. D. (1989). Fish communities of interacting shallow-water habitats in tropical oceanic regions. *Marine Ecology Progress Series 58*, 143–160.

Parrish, J. D., & Zimmerman, R. J. (1977). Utilization by fishes of space and food resources on an offshore Puerto Rican coral reef and its surroundings. *Proceedings of the 3rd International Coral Reef Symposium 1*, 297–303.

Patterson, G. B. (1986). A statistical method for testing dietary differences. *New Zealand Journal of Zoology 13*, 113–115.

Peres-Neto, P. R. (1999). How many statistical tests are too many? The problem of conducting multiple ecological inferences revisited. *Marine Ecology Progress Series 176*, 303–306.

Pollard, D. A. (1984). A review of ecological studies on seagrass–fish communities, with particular reference to recent studies in Australia. *Aquatic Botany 18*, 3–42.

Randall, J. (1967). Feeding habits of West Indies reef fishes. *Studies in Tropical Oceanography 5*, 847 pp.

Robertson, A. I., & Blaber, S. J. M. (1992). Plankton, epibenthos and fish communities. In A. I. Robertson, & D. M. Alongi (Eds.), *Tropical mangrove ecosystems*, *Coastal and estuarine studies*

No. 41 (pp. 173–224). Washington D.C.: American Geophysical Union.

Rooker, J. R. (1995). Feeding ecology of the Schoolmaster snapper *Lutjanus apodus* (Walbaum), from Southwestern Puerto Rico. *Bulletin of Marine Science 56*, 881–894.

Ross, S. T. (1986). Resource partitioning in fish assemblages: a review of field studies. *Copeia 2*, 332–388.

Sanchez, A. J. (1994). Feeding habits of *Lutjanus apodus* (Osteichthyes: Lutjanidae) in Laguna de Terminos, Southwest Gulf of Mexico. *Revista de Investigaciones Marinas 15*, 125–134.

Schoener, T. W. (1974). Resource partitioning in ecological communities. *Science 185*, 27–39.

Sevenster, J. G., & Bouton, N. (1998). The statistical significance of diets and other resource utilization patterns. *Netherlands Journal of Zoology 48*, 267–272.

Shulman, M. J. (1985). Recruitment of coral reef fishes: effects of distribution of predators and shelter. *Ecology 66*, 1056–1066.

Sokal, R. R., & Rohlf, F. J. (1995). *Biometry* (3rd ed., 887 pp. New York: WH Freeman and Company.

Starck, W. A., & Schroeder, R. E. (1971). Investigations on the gray snapper *Lutjanus griseus. Studies in Tropical Oceanography 10*, 224 pp.

Ter Braak, C. J. F., & Smilauer, P. (1998). Reference manual and user's guide to Canoco for Windows: Software for canonical community ordination (version 4). Ithaca, NY, USA: Microcomputer Power.

Thayer, G. W., Colby, D. R., & Hettler, W. F. Jr. (1987). Utilization of the red mangrove prop root habitat by fishes in south Florida. *Marine Ecology Progress Series 35*, 25–38.

Werner, E. E., & Gilliam, J. F. (1984). The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics 15*, 393–425.

Yáñez-Arancibia, A., Lara-Dominguez, A. L., Rojas-Galaviz, J. L., Sánchez-Gil, P., Day, J. W., & Madden, C. J. (1988). Seasonal biomass and diversity of estuarine fishes coupled with tropical habitat heterogeneity (southern Gulf of Mexico). *Journal of Fish Biology 33*(Suppl. A), 191–200.