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Resource use by three juvenile scarids (*Cryptotomus roseus, Scarus iseri*, *Sparisoma radians*) in Caribbean seagrass beds

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ABSTRACT

The bucktooth parrotfish *Sparisoma radians*, the striped parrotfish *Scarus iseri* and the bluelip parrotfish *Cryptotomus roseus* are three herbivorous fishes commonly found at juvenile stages in Caribbean seagrass beds. While the diet of the three species as adults is relatively well known, few studies have been conducted on the feeding patterns of juveniles. In this study, the resource use of the juveniles of three scarid species were studied using two complementary methods: gut content and stable isotope analyses (^{13}C:^{12}C and ^{15}N:^{14}N ratios). Bayesian mixing model approaches were used to calculate the contribution of each food item to fish diets (SIAR, mixing models). The three parrotfish species appeared to rely essentially on the consumption of fleshy macrophytes. *Cryptotomus roseus* consumed more benthic invertebrates and presented a higher trophic level than the two other scarid species. *Scarus iseri* presented a higher assimilation of benthic biofilm, in accordance with the high percentage of sediment in its gut content, and *Sparisoma radians* assimilated more *Thalassia testudinum* leaves. This research highlighted a food resources partitioning among the juveniles of the three herbivorous fishes, probably to avoid inter-specific competitive interactions for the most palatable food at a critical stage of their life.

1. Introduction

Herbivorous fishes have been widely studied on coral reefs due to their major role in the control of algae and are known to mitigate their competitive interactions with corals (Burkepile and Hay, 2010 and references therein). On tropical seagrass beds, herbivorous fishes, such as parrotfishes (Scarinae), have received less attention (Del Moral et al., 2016). In the Caribbean, three species of herbivorous fishes are commonly found on seagrass beds: the bucktooth parrotfish *Sparisoma radians* (Valenciennes, 1840), the bluelip parrotfish *Cryptotomus roseus* (Cope, 1870) and the striped parrotfish *Scarus iseri* (Bloch, 1789). The first two species are exclusively found on seagrass beds, whereas *Scarus iseri* can also be found on coral reefs at all life stages. During their juvenile stages, these three species cohabit in shallow seagrass meadows which represent their primary nursery habitat (Bouchon-Navaro et al., 2004; Kopp et al., 2010; Layman and Silliman, 2002; Weinstein and Heck, 1979). Indeed, studying seagrass meadows is particularly relevant due to their role as nursery areas for nearshore fishes (Tuya et al., 2014).

Possibly due to anthropic pressures on seagrass meadows, the stocks of these three juveniles have dramatically decreased over the last ten years in Guadeloupe, although they were formerly common in this habitat (Y. Bouchon-Navaro, Pers. com. 2016).

Information on the diet of these herbivorous fishes in the literature is principally available for adults. *Sparisoma radians* mainly ingests turtlegrass *Thalassia testudinum* Banks & Sol. ex König, 1805, fleshy macroalgae like *Dictyota* sp. or *Acanthophora spicifera* (M. Vahl) Børgesen, 1910 and calcified macroalgae such as *Halimeda* sp. (Lobel and Ogden, 1981; Randall, 1967; Targett and Targett, 1990). Depending on the region, *Scarus iseri* is described as a feeder on microalgae from dead coral pavements, fleshy macroalgae or epiphytic filamentous microalgae (McAfee and Morgan, 1996; Nagelkerken et al., 2006; Randall, 1967). *Cryptotomus roseus* is described as strictly herbivorous, feeding on seagrass (Carpenter, 2002), but its diet has not been studied in detail. However, little information is available for the juveniles of these three parrotfish species, although ontogenetic shifts in diet are common for tropical fishes (Cocheret de la Moriniere et al., 2003) or temperate herbivorous fishes (Havelanche et al., 1997). Dietary changes are useful

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to understand their ecological role in seagrass beds, such as the regulation of the algal biomass.

Trophic niches of fishes can be described on the basis of gut content analyses (Ogden, 1976; Randall, 1967) or direct observation of their feeding behaviour in the field by the counting of "bites" (Cardoso et al., 2009; Lobel and Ogden, 1981; McAfee and Morgan, 1996; Overholtzer and Motta, 1999). However, these methods provide a description of a species' diet at a specific time and present several practical problems (Bearhop et al., 2004). With gut content analyses, the principal difficulty results from the ability of herbivorous fishes, such as Scarinae, to grind the ingested matter into small fragments with their fused beak and their pharyngeal mills (Bellwood and Choat, 1990; Randall, 1967). The relative proportions of food items in gut contents are estimated with varying degrees of accuracy by different authors and on the basis of different parameters (occurrence, weight or volume percentages). With field observations, it is difficult to discriminate between potential dietary targets (e.g. between seagrass leaves and epiphytes) and the ingestion of some food items, such as detritus, is difficult to quantify. For these reasons, determining the trophic niches of herbivorous fishes remains challenging.

More recently, stable isotope ratios of fish muscles (^{13}C:^{12}C and ^{15}N:^{14}N) have been used to determine their trophic niche. Isotopic ratios measured in consumer tissues are closely linked to those of their diet and increase in a stepwise fashion with each trophic level.

The mean trophic isotopic enrichment, or fractionation factor ($\Delta^{15}N$ and $\Delta^{13}C$), was estimated at +3.4 ± 1.1‰ for nitrogen (Minagawa and Wada, 1984) and +0.4 ± 1.3‰ for carbon (Post, 2002). However, Mill et al. (2007) demonstrated a higher $\Delta^{15}N$ for herbivorous fishes (4.7‰ for *Acanthurus sohal* and 4.1‰ for *Sparisoma* spp.) and Sweeting et al. (2007) recommended a $\Delta^{13}C$ ranging between 1.5‰ and 2‰ for marine fishes.

Stable isotope analysis is considered to be a powerful tool to reflect the feeding behaviour of individuals over long periods (approximately three months in the muscles of adult fishes), corresponding to the turnover of the tissues of consumers (Bearhop et al., 2004).

Several methods using C and N stable isotopes ratios, expressed as $\delta^{13}C$ and $\delta^{15}N$, have been developed to understand and interpret fish ecology. Isotopic signatures of the consumer and those of its potential food sources can be used in mixing models to calculate and estimate the contribution of several food sources to the diet of a consumer (see Phillips, 2012 and Phillips et al., 2015 for reviews). Results of mixing models can be used to describe and compare trophic niches between fish species (Dromard et al., 2015; Plass-Johnson et al., 2013). Despite the fact that numerous potential organic matter sources occur in seagrass beds, mixing models have been used before for fish species living in this habitat (Benstead et al., 2006; Hyndes and Lavery, 2005; Loneragan et al., 1997). However, few studies have been done in the Caribbean seagrass beds (Nagelkerken and van der Velde, 2004).

In the present study, we analysed the diet of juveniles of three parrotfish species in a Caribbean seagrass bed to describe and compare their trophic niche, combining stable isotope and gut content analyses.

2. Materials and methods

The study was carried out in the Bay of the Grand Cul-de-Sac Marin, located in the northern part of Guadeloupe Island (Lesser Antilles) (Fig. 1). In the south, the bay is bordered by mangroves and the northern part is partially enclosed by a coral barrier reef. Shoals of the bay are colonized by seagrass meadows dominated by the turtlegrass, *Thalassia testudinum*. Sampling was performed in a shallow seagrass bed (<2 m depth), at mid-distance between the coast and the barrier reef, far from the influence of mangroves, at the end of the wet season (October to December 2010). The sampling area covers 1 km^2 approximately.

Table 1
Mean ± SD values of $\delta^{13}C$ and $\delta^{15}N$ signatures and C/N ratio of juvenile scarids and organic matter sources collected in Guadeloupe seagrass beds. N: number of samples. * Sources not taken into account in mixing models.

Sample types	N	$\delta^{13}C$ ‰ ± SD	$\delta^{15}N$ ‰ ± SD	C/N
Fish species				
Cryptotomus roseus	13	−11.5 ± 1.6	7.0 ± 0.7	3.3 ± 0.1
Scarus iseri	11	−11.9 ± 0.9	5.7 ± 0.8	3.3 ± 0.03
Sparisoma radians	13	−9.6 ± 0.8	5.7 ± 0.6	3.1 ± 0.02
Invertebrates	5	−11.8 ± 0.5	5.1 ± 0.2	5.6 ± 0.5
MOP*	9	−18.2 ± 1.5	3.9 ± 0.4	7.1 ± 1.2
Biofilm	6	−19.5 ± 1.7	2.1 ± 0.2	9.4 ± 0.2
Detritus	5	−13.0 ± 0.04	3.3 ± 0.03	8.6 ± 0.1
Fleshy macroalgae				
Anadyomene stellata	3	−13.5 ± 0.3	1.5 ± 0.3	20.0 ± 0.4
Caulerpa cupressoides	3	−8.3 ± 0.1	2.2 ± 0.03	13.5 ± 0.2
Chaetomorpha sp.	3	−17.2 ± 0.7	2.5 ± 0.03	19.5 ± 0.7
Dictyota cf *pulchella*	3	−13.5 ± 0.3	2.8 ± 0.1	23.8 ± 0.5
*Halimeda incrassata**	3	−12.0 ± 0.04	1.6 ± 0.04	9.9 ± 0.1
Padina sp.	3	−5.2 ± 0.1	2.5 ± 0.2	38.0 ± 0.9
*Udotea flabellum**	3	−8.6 ± 0.03	1.2 ± 0.1	10.8 ± 0.1
Epiphytes (*Thalassia*)	6	−13.5 ± 1.2	2.5 ± 0.4	11.8 ± 2.9
Seagrass				
Thalassia testudinum (old)	10	−7.4 ± 0.1	1.8 ± 0.2	23.8 ± 2.1
Thalassia testudinum (young)	5	−7.2 ± 0.1	2.2 ± 0.1	19.7 ± 0.2
*Syringodium filiforme**	5	−4.7 ± 0.1	1.6 ± 0.07	23.0 ± 0.3

Table 2
Mean and range of fish total length (TL) and wet weight (W) of the three fish species. Lengths at maturity (Lm) are taken from Bouchon-Navaro et al. (2006).

Fish species	TL (cm)	W (g)	Lm (cm)
Cryptotomus roseus	5.7 (4.6–6.8)	2.5 (1.3–4.2)	8.6
Scarus iseri	5.0 (4.5–5.5)	2.0 (1.5–2.6)	15.9
Sparisoma radians	6.4 (6.0–6.7)	5.1 (4.5–5.7)	12.0

2.1. Sampling protocol

Three herbivorous fish species (*C. roseus, S. iseri* and *S. radians*) were sampled during 6 purse seine samples (Table 1). The total length of fish was measured to the nearest millimetre and individuals were weighed to the nearest milligram (Table 2). All specimens sampled were below their minimum size at first maturity (Bouchon-Navaro et al., 2006). The main potential organic matter (OM) sources in the seagrass beds were sampled and treated for stable isotope analysis (Table 1). The dominant species or genera of fleshy macroalgae occurring in seagrass beds were collected and cleaned with distilled water: *Anadyomene stellate* (Wulfen) C. Agardh, 1823, *Caulerpa cupressoides* (Vahl) C. Agardh, 1817, *Chaetomorpha* sp., *Dictyota* cf *pulchella* Hörnig & Schnetter, 1988 and *Padina* sp., along with the calcified macroalgae *Halimeda incrassata* (J. Ellis) J.V. Lamouroux, 1816 and *Udotea flabellum* (J. Ellis & Solander) M.A. Howe, 1904. Two seagrasses were collected, *Thalassia testudinum* and *Syringodium filiforme* Kützing, 1860. Samples of *T. testudinum* were sorted into two categories: old leaves (O) and young leaves (Y), both selected without epiphytes. Around 100 g (wet weight) of each species of macroalgae and seagrass were collected on field. Epiphytes colonising old leaves of *Thalassia* were gently scrapped with a scalpel blade and stored apart. Benthic invertebrates (amphipods, copepods, decapods, gastropods) collected with seagrass and macroalgae samples were sorted. When collected, macroalgae and *Thalassia* leaves were preserved in plastic bags in order to retain the detritus, composed of organic matter and bacteria (Crossman et al., 2001), deposited on algal thalli and