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Trophic shift in young-of-the-year mullets during salt marsh colonization

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RUNNING HEAD

Trophic shift in YoY mullets in salt marshes

ABSTRACT

This study investigated the trophic shift of young-of-the-year (YoY) thinlip grey mullets
Liza ramada and golden grey mullets *Liza aurata* during their recruitment in a salt marsh
located on the European Atlantic coast. Stable isotope signatures ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of the fishes
followed a pattern, with enrichments in ^{13}C and ^{15}N to increasing length: $\delta^{13}\text{C}$ in fishes < 30

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mm ranged from -19.5 to -15.0‰, whereas in fishes > 30 mm $\delta^{13}\text{C}$ ranged from -15.8 to -12.7‰, closer to the level in salt marsh food resources. Large differences between the $\delta^{15}\text{N}$ values of mullets and those of food sources (6.0‰ on average) showed that YoY are secondary consumers, like older individuals, when feeding in the salt marsh. YoY mullets shift from browsing on pelagic prey to grazing on benthic resources from the salt marsh before reaching 30 mm in length. The results highlight the role of European salt marshes as nurseries for juvenile mullets.

KEY WORDS

Diet; *Liza ramada*; *Liza aurata*; juveniles; stable isotopes; schorre.

INTRODUCTION

Salt marshes are among the most productive ecosystems on Earth (McLusky, 1989). Their high level of primary production (*e.g.*, halophytic plants, benthic microalgae) provides food resources for benthic macrofauna and supports a complex food web (Currin *et al.*, 1995; Deegan & Garritt, 1997; Riera *et al.*, 2000). Salt marsh habitats are important feeding grounds for transient species (*e.g.*, fishes, crustaceans), which perform tidal migrations to feed on salt marsh primary producers and locally produced fauna (Kneib, 1997; Zimmerman *et al.*, 2000; Laffaille *et al.*, 2001; Gibson, 2003; Lebreton *et al.*, 2011). These habitats also provide other ecosystem services, including serving as refuges, particularly for juveniles, against fish predation (Craig & Crowder, 2000; Zimmerman *et al.*, 2000). As a result, salt marshes are considered major nurseries for fishes and crustaceans (Beck *et al.*, 2001). Along the European Atlantic coast, numerous fish juveniles, including valuable commercial species, colonize creeks to forage on salt marsh resources (Laffaille *et al.*, 1998; Laffaille *et al.*, 2001; Lebreton *et al.*, 2011).

Mullets are widespread in tropical and temperate marine waters (Nelson, 1994) and, due to their high abundance and daily feeding migrations (Laffaille *et al.*, 1998; Lebreton *et al.*, 2011), they fulfil an important ecological role as exporters of organic matter from salt marshes to adjacent areas and fuel offshore food webs. Mullets turn the organic matter they forage on into high quality matter (*i.e.*, fish tissues) as well as low quality matter (*i.e.*, feces) (Laffaille *et al.*, 1998; Lefeuvre *et al.*, 1999; Deegan *et al.*, 2000).

Along the European Atlantic coasts, two species of mullets migrate in intertidal salt marsh creeks: the thinlip grey mullet *Liza ramada* (Risso 1827) and the golden grey mullet *Liza aurata* (Risso 1810) (Laffaille *et al.*, 1998; Parlier *et al.*, 2006; Lebreton *et al.*, 2011). In these

habitats, mullets exploit benthic food resources by scraping mud surfaces and sorting food items using their gill rakers (Hickling, 1970). Most studies about *L. ramada* and *L. aurata* food sources focus on adults (Lam Hoï, 1969; Bruslé, 1981; Almeida *et al.*, 1993; Cardona, 1996; Laffaille *et al.*, 2002; Almeida, 2003) whereas there has been less focus on young-of-the-year (YoY) (Albertini-Berhaut, 1973; Albertini-Berhaut, 1974; Ferrari & Chieregato, 1981; Lebreton *et al.*, 2011). These two species reproduce on the continental shelf: from August to February for *L. aurata* and from autumn to winter for *L. ramada*, but the spawning period can vary depending on location and species (Keith *et al.*, 2011). Recruitment also varies in coastal areas and generally lasts from the end of winter through to the summer (Hickling, 1970; Gautier & Hussenot, 2005).

In Aiguillon Bay (French Atlantic coast), YoY mullet recruitment begins in March, and then the fishes start performing daily migrations into salt marsh creeks. However, YoY are still foraging on neritic zooplankton even when visiting salt marsh creeks (Lebreton *et al.*, 2011) just after their recruitment, whereas one- and three-year-old and older mullets use salt marsh resources from the very moment when they colonize the salt marshes in spring (Laffaille *et al.*, 2002; Lebreton *et al.*, 2011). YoY undergo a diet shift as they grow, switching from pelagic resources (*i.e.* zooplankton) to benthic resources (Albertini-Berhaut, 1973; Albertini-Berhaut, 1974). The aim of this study was to determine at what size and when this diet shift occurs, to determine when YoY become dependent on salt marsh food resources. To that aim, food sources used by YoY mullets were determined in summer by using stable isotope ratio analyses. This approach allows the determination of food sources actually assimilated by fishes (Pinnegar & Polunin, 1999) and is thus regularly used to assess changes in diet during migrations (Fry, 2006). The summer results were compared with those from spring (Lebreton *et al.*, 2011). The relationship between stable isotope signatures and

fish length allows a determination of the size at which YoY shift from neritic to salt marsh food resources.

MATERIALS AND METHODS

Study site

Aiguillon Bay, located on the French Atlantic coast, is an embayment of 56 km², including 38 km² of bare mudflats and 18 km² of salt marshes (Fig. 1) (Verger, 2005). Aiguillon Bay is very shallow, with a depth not exceeding 1m below the hydrographic zero (Verger, 1968). It is a semi-diurnal macrotidal system, with a tidal range higher than 5 m at mean high water springs, which generates relatively strong tidal currents (0.2 – 0.6 m.s⁻¹) (SHOM, 2001). Fresh water inputs come from the Sèvre Niortaise River, the Lay River and many channels, of which the largest one is the Curé Channel. Inputs of fresh water in the bay are man-managed thanks to gates: fresh water inputs occur mainly from autumn to spring and are very scarce after March or April, following closure of the gates (Meunier and Joyeux, unpublished results). The gates were closed in mid-March during the sampling year. As a result, salinities were low at the beginning of March (3.5 to 4.5) and were close to those of oceanic waters (29 to 35) afterward. The sampling site (46°15'49 N, 01°07'09 W), located in the salt marsh and exposed to the air at every low tide, is the same as in Lebreton *et al.* (2011). It is a tributary creek of the Curé channel, which drains a 10 ha watershed on the southern part of Aiguillon Bay (Parlier *et al.* 2006). This site is located 50 m upstream from the creek mouth and has a cross-section 15 m wide and 5 m deep. In this area, the salt marsh

vegetation is dominated by halophytic plants, such as *Halimione portulacoides* (Meunier and Joyeux, unpublished results). No vegetation is present on the creek banks, which are covered with extensive patches of microphytobenthos.

Fish sampling

Young-of-the-year mullets were sampled in summer (22 July 2005) during spring tides. Fish collection was carried out following the same procedure as in Lebreton *et al.* (2011), using a fyke net (4 mm mesh size, 5 m deep, 1.80 m high, 20 m long) set up across the creek. The net was set up on the creek for periods of 20 minutes, then removed for 5 minutes to empty it. Sampling was therefore efficient for 80% of the whole tide (20 minutes of sampling every 25 minutes) allowing collection of representative samples of the YoY fish community (Laffaille *et al.*, 1998; Parlier *et al.*, 2006). All samples were stored in iceboxes in the field and frozen (-20°C) at the laboratory until analysis.

Stable isotope ratio analysis

Sample processing was the same as in Lebreton *et al.* (2011). All individuals were measured (fork length) to the nearest mm. Age of fishes was defined based on: 1. population structure defined during the same year (Lebreton *et al.* 2011); 2. growth curves from Le Dantec (1955), Lam Hoï (1969) and Parlier (unpublished results), and tables in Gautier &

Hussenot (2005). All these data show a very good relationship between length and age of YoY. Individuals used for stable isotope analyses were sub-sampled so as to be representative of the size structure of the YoY population. Mulletts 50 mm in length or more were identified to the species level using the identification keys of Farrugio (1977), Cambrony (1984), also reviewed in Gautier & Hussenot (2005), and Keith *et al.* (2011). Mulletts less than 50 mm long, for which identification is very difficult (Cambrony, 1984; Keith *et al.*, 2011), were not identified.

Stable isotope analyses were performed on whole eviscerated fishes with the head removed for mulletts less than 50 mm long and on white dorsal muscle for fishes > 50 mm long. Muscles were dissected with the greatest care to avoid the presence of bone fragments. All samples were freeze-dried and ground using a ball mill. Fish samples from mulletts < 50 mm were acidified with 1 mol L⁻¹ HCl to remove carbonates, then dried in a dry bath at 60°C and ground again. Since acidification may have an effect on $\delta^{15}\text{N}$ values, these samples were analysed separately for determination of $\delta^{15}\text{N}$ (raw samples) and $\delta^{13}\text{C}$ (acidified samples) values. Preliminary tests were performed on samples to check for a possible effect of lipids on $\delta^{13}\text{C}$ values. Since no significant effect of lipids was observed, no delipidation process was carried out.

Samples were analysed using an EA-IRMS (Isoprime, Micromass, UK). Isotope ratio values were expressed in δ unit notation as deviations from standards (Vienna Pee Dee Belemnite for $\delta^{13}\text{C}$ and atmospheric N₂ for $\delta^{15}\text{N}$) following the formula: $\delta^{13}\text{C}$ or $\delta^{15}\text{N} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3$, where R is $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$. Calibration was done using reference materials (USGS-24, IAEA-CH6, IAEA-600 for carbon; IAEA-N1, -N2, -N3, -600 for nitrogen). Analytical precision based on analyses of acetanilide (Thermo Scientific) used as an internal laboratory standard was 0.15‰ and 0.2‰ for carbon and nitrogen, respectively.

Data and statistical analyses

Length, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of YoY mullets sampled in summer 2005 were compared to those observed in spring 2005 (Lebreton *et al.*, 2011). Stable isotope compositions of YoY were compared with those of potential food sources and prey from the same bay (Riera *et al.*, 1999; Lebreton *et al.*, 2011; Richard, unpublished results). The $\delta^{15}\text{N}$ primary producer baseline was computed by averaging $\delta^{15}\text{N}$ values for phytoplankton and microphytobenthos, since they were not statistically different. Primary and secondary consumer theoretical baselines were determined by adding the average and standard deviation values of trophic fractionation from Vander Zanden & Rasmussen (2001) to the $\delta^{15}\text{N}$ baseline: $2.5 \pm 2.5\text{‰}$ from primary producers to primary consumers and $3.2 \pm 0.4\text{‰}$ from primary consumers to secondary consumers.

RESULTS

Population characteristics

Two hundred and twenty three mullets were collected in the field. Among them, 74 were *L. ramada* and 29 were *L. aurata* ≥ 50 mm in length. Mullet length was 45 ± 20 mm on average. The smallest individuals were 21 mm long and the longest ones were 90 and 94 mm long for *L. aurata* and *L. ramada*, respectively. In spring, the average length of YoY (\pm

standard deviation) was 20 ± 2 mm and ranged from 16 to 42 mm (Lebreton *et al.*, 2011). Taking both species together, the length of YoY was higher in summer than in spring (Student test; d.f. = 1663; $p < 0.001$).

Stable isotope ratios

Muscle stable isotope composition was determined in 26 individuals. Signature ranges were wide in summer, with values ranging from -19.5 to -12.7‰ for $\delta^{13}\text{C}$ and from 9.7 to 13.3‰ for $\delta^{15}\text{N}$ (Fig. 2). A distribution pattern was observed for $\delta^{13}\text{C}$ values, with a ^{13}C -enrichment related to increasing length. The smallest mullets (< 30 mm) showed a wide range of $\delta^{13}\text{C}$ values, from -19.5 to -15.0‰, whereas the largest mullets (> 30 mm) presented a narrower range of $\delta^{13}\text{C}$, with values from -15.8 to -12.7‰. Mulletts larger than 30 mm were thus more ^{13}C -enriched than mullets < 30 mm (Student test; d.f. = 82; $p < 0.001$). The same pattern of distribution was observed for $\delta^{15}\text{N}$ (Fig. 2): smallest individuals (< 30 mm) presented lower $\delta^{15}\text{N}$ values (from 9.7 to 12.0‰) than largest ones (from 10.7 to 13.3‰) (Student test; d.f. = 82; $p < 0.001$).

Due to the wide range of values, $\delta^{13}\text{C}$ for mullets sampled in summer were close to the $\delta^{13}\text{C}$ values of many potential food sources, from phytoplankton, SPOM and SSOM to vegetal or animal salt marsh resources (microphytobenthos, fresh or detrital *Spartina maritima*, plant detritus, nematodes or annelids) (Fig. 3). A group of 6 individuals with $\delta^{13}\text{C}$ values lower than -18‰ could be identified; these mullets all measured less than 30 mm in length (Fig. 2 and 3).

In spring, $\delta^{13}\text{C}$ values ranged from -22.3 to -18.4‰ and $\delta^{15}\text{N}$ values ranged from 8.0 to 12.4‰ (Lebreton *et al.*, 2011). $\delta^{13}\text{C}$ values of mullets < 30 mm sampled in summer were

higher than those of mullets sampled in spring (Fig. 2) (Student test; d.f. = 57; $p < 0.001$). $\delta^{15}\text{N}$ value of mullets < 30 mm sampled in summer ($11.7 \pm 0.9\text{‰}$ on average) were more ^{15}N -enriched than in spring (average = $9.9 \pm 1.3\text{‰}$; Student test; d.f. = 35; $p = 0.032$; figure 2 and 3) and very close to the theoretical secondary consumer $\delta^{15}\text{N}$ value ($11.2 \pm 0.4\text{‰}$).

DISCUSSION

Young-of-the-year population characteristics in summer and comparison with spring

Two species of YoY mullets colonized the salt marsh during summer: *L. ramada* and *L. aurata*, as already described by Parlier et al. (2006). Both species are known to colonize salt marsh creeks for the purpose of feeding, either when they are one year old (*L. ramada* and *L. aurata*) or adults (*L. ramada*) (Laffaille et al., 2002; Almeida, 2003; Lebreton et al., 2011). *Liza ramada* and juveniles of *L. aurata* are very euryhaline (Lasserre & Gallis, 1975; Shusmin, 1990), and can thus access this part of the salt marsh, where large and sudden salinity variations can occur. YoY mullets have already been observed in salt marsh creeks during spring and summer (Laffaille et al., 1998; Parlier et al., 2006). Nevertheless, Lebreton et al. (2011) observed that YoY were not exploiting salt marsh food resources but neritic food resources (*i. e.* zooplankton) in spring just after coastal recruitment.

Mullets presented a wider range of lengths in summer (21 to 94 mm) than in spring (16 to 42 mm). The relatively close values observed for the smallest fishes between spring and summer suggest that coastal recruitment of mullets was ongoing at the end of July in Aiguillon Bay, as at some other locations on the French Atlantic coast (Lam Hoï, 1969;

Labourg, 1985; Keith *et al.*, 2011). On the contrary, the maximum lengths observed in summer mullets were strikingly larger than those of spring mullets. These maximum lengths observed in summer correspond well with a 4 month period of growth since the mullets were recruited in coastal areas, following the growth curves of YoY *L. aurata* and *L. ramada* from Aiguillon Bay (Parlier, unpublished results). This shows that YoY recruited during spring have grown and that they still colonize salt marsh creeks. This sampling and data from Lebreton *et al.* (2011) thus represent a large range of mullet lengths in two seasons. It is therefore possible to determine the shift in mullet diet in relation with their growth.

Dietary shift in YoY mullets between spring and summer

In summer, the large range of YoY $\delta^{13}\text{C}$ values demonstrates that YoY could access a large range of food sources. Very ^{13}C -depleted YoY mullets had a diet based on neritic food resources (SPOM, phytoplankton), like in the spring (Lebreton *et al.*, 2011). This group of ^{13}C -depleted individuals was only composed of very small – and thus very young - mullets with $\text{FL} < 30$ mm. The young ages of the fishes and the neritic origin of their food resources demonstrate that they had just arrived in coastal areas, confirming that YoY recruitment was ongoing and continuous during the summer (Koussoroplis *et al.*, 2010). Their high $\delta^{15}\text{N}$ values in comparison with those of neritic food sources (SPOM, phytoplankton) demonstrate that these mullets were secondary consumers when feeding in neritic ecosystems, with a diet probably based on zooplankton, as already observed in the spring (Lebreton *et al.*, 2011). Some other fishes with $\text{FL} < 30$ mm were a few more enriched, suggesting that the diet of these individuals was shifting.

Older mullets (FL > 30mm) were ^{13}C -enriched, showing that they were using food resources from the salt marsh. It therefore appears that YoY can exploit food resources from the salt marsh as soon as they reach a fork length of 30 mm. Some stomach content observations revealed some sediment (Lebreton, unpublished results), providing support for a shift from a pelagic to a limno-benthophagous diet. This confirms the assumption made by Lebreton *et al.* (2011) that YoY mullets undergo a trophic shift in relation to their size when they colonize salt marshes. Many authors have demonstrated that an ontogenic dietary shift occurs for numerous species of mullets, with fishes passing from browsing on pelagic prey to grazing on benthic resources (Odum, 1970; Bruslé, 1981; Eggold & Motta, 1992; Koussoroplis *et al.*, 2010).

Differences between the $\delta^{15}\text{N}$ values of individuals > 30 mm and those of salt marsh primary sources (*Spartina maritima*, microphytobenthos), reaching on average 6.0‰, showed that these mullets were not primary consumers, and were at least secondary consumers. When mullets have a limno-benthophagous diet in the salt marsh, the bulk of ingested sediment and organic matter contains large quantities of meiofauna and small macrofauna (Lebreton, personal observation). These items are easily digestible and the assimilation rates of these food sources are higher than those of fresh and detrital plant organic matter, explaining why mullets are secondary consumers (Lebreton *et al.*, 2011).

This shift from a pelagic to a limno-benthophagous diet between spring and summer is clearly related to the length – and thus to the age – of individuals, as shown by the sharp increases in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of mullets from 20 to 30 mm long. This range of fork lengths fits well with observations made by Albertini-Berhaut (1973; 1974) and Ceccherelli *et al.* (1981), who determined that this dietary shift occurred at the post-larval stage (15–25mm) for *L. ramada* and *L. aurata*. This change in feeding habit has also been observed in other species of mullets of similar lengths (Odum, 1970; Bruslé, 1981; Eggold & Motta, 1992;

Koussoroplis *et al.*, 2010). Eggold & Motta (1992) determined with *Mugil cephalus* that the observed trophic shift was not related to morphological changes in the mouth and gill rakers of YoY. This change in diet appears mostly related to a change in trophic behaviour before YoY reach a size of 30 mm.

After this trophic shift, the diet of YoY is similar to these of G1 and G3+ mullets when they colonize salt marshes for the purpose of feeding (Lebreton *et al.*, 2011). As assumed for G1 and G3+ individuals (Lebreton *et al.*, 2011), the migration of YoY into salt marshes is probably related to the large quantities of high quality food resources in this habitat (Kneib, 1997; Cattrijsse & Hampel, 2006). This is particularly the case for nematodes, whose abundance can be several times higher in salt marshes (Heip *et al.*, 1985; Giere, 1993) than in the bare mudflats adjacent to the marshes (Rzeznik-Orignac *et al.*, 2003). Colonization of salt marshes at feeding purpose may be necessary for YoY mullets because high quantities of energetic food resources would allow them to maximize food intake and growth (Gibson, 2003).

Salt marshes are known to be essential habitats for aquatic organisms, particularly juvenile fishes, because they provide food resources and refuge. They are thus considered to be very good nurseries because fishes can optimize their foraging, growth and survival (Beck *et al.*, 2001; Cattrijsse & Hampel, 2006). This study thus highlights the role of European salt marshes as feeding areas for YoY mullets along the French Atlantic coast.

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FIGURE CAPTIONS

Figure 1. Location of Aiguillon Bay and the sampling site.

Figure 2. Relationships between stable isotope ratios in muscle ($\delta^{13}\text{C}$ & $\delta^{15}\text{N}$) and fork length of YoY in spring and summer 2005.

Figure 3. Stable isotope signatures ($\delta^{13}\text{C}$ & $\delta^{15}\text{N}$) of YoY and of potential food sources and prey. For YoY, each point represents one individual. Dotted lines represent theoretical $\delta^{15}\text{N}$ baselines for primary producers, and primary and secondary consumers (see Materials and Methods for calculations). Potential food sources and preys: Ann: annelids, Mpb: microphytobenthos, Nem: nematodes, Phy: phytoplankton, Pma: *Plantago maritima*, Sma: alive *Spartina maritima*. Sma det: detritic *Spartina maritima*, SPOM: suspended particulate

481 organic matter, SSOM: sediment surface organic matter, Pla det: plant detritus. Food source
482 data taken from Lebreton *et al.* (2011) are in bold face type, those from Richard (1998,
483 unpublished results) are italicized, those from Richard (2004, unpublished results) are
484 underlined and those from Riera *et al.* (1999) are in normal face type.





