



# Trophic ecology of mullets during their spring migration in a European saltmarsh: A stable isotope study

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## ABSTRACT

Mullet populations are abundant in littoral waters throughout the world and play a significant role in organic matter fluxes. Mulletts are opportunistic feeders: adults have frequently been shown to feed on primary producers (e.g. fresh or detrital plant material, microphytobenthos) but they may also feed on meiofauna. The population structure and stomach contents of mullets that colonize saltmarsh creeks in Aiguillon Bay (French Atlantic coast) were studied to determine if they use saltmarshes as a feeding ground in spring. Stable isotope analyses were carried out on mullets sampled to assess their diet during their spring migration. The mullet population was primarily composed of young-of-the-year (G0), 1 year-old (G1) of both *Liza ramada* and *Liza aurata* species and 3 year-old or older (G3+) *L. ramada* individuals. G0 and G3+ population densities increased during the spring period: catch per unit effort (CPUE) increased from 0.22 to 1.49 ind min<sup>-1</sup> for the G0 age group; but stomach content analyses revealed that only G1 and G3+ feed in the saltmarsh. Isotopic signatures of G1 (spring:  $\delta^{13}\text{C}$ :  $-14.8\text{‰}$ ,  $\delta^{15}\text{N}$ :  $14.1\text{‰}$ ) and G3+ mullets (spring:  $\delta^{13}\text{C}$ :  $-16.9\text{‰}$ ,  $\delta^{15}\text{N}$ :  $13.8\text{‰}$ ) indicate that mullet growth is supported largely by primary consumers, such as benthic meiofauna or small macrofauna. Mulletts are thus positioned at a much higher trophic level than true primary consumers.

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## 1. Introduction

Mulletts are important members of fish communities in estuarine and littoral waters throughout the world. The study of their feeding activity is of particular interest for a better understanding of ecosystem functioning because they are among the few large fish able to feed directly on the lowest trophic levels (Hickling, 1970; Odum, 1970; Laffaille et al., 2002; Gautier and Hussenot, 2005). They inhabit numerous habitats in the littoral zone: mudflats

**Abbreviations:** CPUE, Catch per unit effort; CPUE<sub>n</sub>, Number CPUE; CPUE<sub>m</sub>, Biomass CPUE; DTW, Digestive tract weight; G0, Young-of-the-year; G1, 1 year-olds; G2, 2 year-olds; G3+, 3 year-old and older; IR, Instantaneous ration; SPOM, Suspended particulate organic matter; SSOM, Surface sediment organic matter; TW, Total fish weight; VI, Vacuity index.

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(Almeida et al., 1993), saltmarshes (Lefeuvre et al., 1999; Laffaille et al., 2002) as well as estuaries and even rivers (Lam Hoï, 1969; Keith and Allardi, 2001; Cardona, 2006). Depending on their habitat, mullets can have many feeding strategies (e.g. water filtering, sediment scraping) (Bruslé, 1981; Almeida et al., 1993; Cardona, 1995) to exploit the most accessible food resources, in terms both of quantity and quality (Odum, 1968; Almeida et al., 1993). Due to their high biomass in European saltmarshes (Laffaille et al., 2000; Parlier et al., 2006), mullets play a major role in coastal food webs as biotic vectors of organic matter between littoral habitats and the open sea (Lefeuvre et al., 1999; Laffaille et al., 2002) and also as competitors with other consumers for food resources (Lasserre et al., 1976).

On European Atlantic coasts, mullets spend their reproduction period off-shore, on the continental shelf. Spawning occurs at different periods depending on location and species: from August to February for *Liza aurata* and from autumn to winter for *Liza ramada* (Keith and Allardi, 2001). Recruitment also varies in coastal areas depending on species and generally lasts from the end of winter through to the summer (Hickling, 1970; Gautier and Hussenot, 2005). During that period, young-of-the-year changes from a planktonic to a benthic diet (Albertini-Berhaut, 1973, 1974; Ceccherelli et al., 1981; Ferrari and Chierigato, 1981).

Adult mullets also migrate in early spring to the very littoral areas where they perform daily trophic migrations. They can exploit the full extent of the mudflats, including the lower part of saltmarsh, they can reach via the numerous creeks and channels that fill up at every high tide (Laffaille et al., 2000; Parlier et al., 2006). Stomach content analyses tend to show that mullets have a limno-benthophagous feeding mode in these areas: when foraging, they scrape the superficial sediment layers and ingest a mix of sediment and organic matter. Food selection is achieved by the mechanical (gill-rakers) and gustatory elements (Bruslé, 1981).

Trophic ecology of mullets has mostly been studied through stomach content analysis which provides considerable information on fish food resources but only reveals what has been recently ingested. Stable isotope analyses of tissues are complementary to stomach content studies since they allow the determination of what is actually assimilated (Pinnegar and Polunin, 1999). Stable isotope analyses can also be used to assess changes of diet during migrations (Fry, 2006). The distinction between ingested and assimilated resources is important for mullets because their limno-benthophagous feeding strategy leads them to ingest a large variety of available food items of different degrees of digestibility, including plants or detrital matter (Odum, 1970; Bruslé, 1981), microalgae (Almeida et al., 1993; Laffaille et al., 2002), but also meiofauna (Ezzat, 1963; Lasserre et al., 1976; Laffaille et al., 1998) and small macrofauna (Riera et al., 1999; Bouchard and Lefeuvre, 2000; Quan et al., 2007). Assimilation processes are related to the quality, and thus the digestibility of ingested food items, with better assimilation rates for fresh tissues or tissues with higher nitrogen or nutrient content (Tenore, 1983; Mann, 1988; Cebrián, 1999).

This study aimed to determine the origin of food sources and the trophic level of mullets. It has been carried out in the saltmarshes of the Aiguillon Bay, an intertidal bay on the French Atlantic coast, in which saltmarshes are in the same type of these which have previously been examined using stomach content analyses (Laffaille et al., 1998, 2002). Mullet abundance is high in this bay during the spring (Parlier et al., 2006), when mullets colonize saltmarsh creeks after a winter stay in off-shore waters (Laffaille et al., 1998). In this study, the population structure of mullets was determined to define which age groups colonize the saltmarsh creeks. The feeding activity of each age group entering and leaving the creeks was analyzed by comparing stomach content weight between flood and ebb tides. The instantaneous and long-term diets were determined using stable isotope analyses of stomach content and muscle tissues, respectively.

## 2. Materials and methods

### 2.1. Study site

Aiguillon Bay, located on the French Atlantic coast, covers 56 km<sup>2</sup> in area and includes 38 km<sup>2</sup> of bare mudflats and 18 km<sup>2</sup> of saltmarshes (Fig. 1) (Verger, 2005). It is a semi-diurnal macrotidal system, which causes relatively strong tidal currents (average 0.2–0.6 m s<sup>-1</sup>) (SHOM, 2001). The bay receives most of effluents of the Marais Poitevin, the second largest wetland in France. Freshwater inputs come from the Sèvre Niortaise River, the Lay River and many channels, including the largest, the Curé Channel. Watershed inputs occur mainly from autumn to spring (Meunier and Joyeux, unpublished results) and salinity ranged from 4.5 to 35 during our spring sampling period.

Mullets were collected in a tributary creek of the Curé Channel (Fig. 1) which drains a 10 ha watershed on the southern part of Aiguillon Bay (Parlier et al., 2006). The whole creek is integrated in the saltmarsh part of the bay, dominated by halophytic plants, such as *Halimione portulacoides* (Meunier and Joyeux, unpublished

results). No vegetation was present on creek banks, which were covered with extensive patches of microphytobenthos. The sampling site (46°15'49 N, 01°07'09 W) was located 50 m upstream from the creek mouth and had a cross-section of 15 m wide and 5 m deep.

### 2.2. Fish sampling

Mullets were regularly sampled on 22 occasions during three non-consecutive weeks from the beginning of March to mid-April 2005 (Spring 1: March 8–14; Spring 2: March 24–30; Spring 3: April 6–12). Sampling was performed during spring tides, with tidal ranges from 5.70 to 6.25 m as in the study of Parlier et al. (2006) and assessed the population structure with precision and to obtain sufficient samples for stomach content and stable isotope analyses (muscle tissues and stomach contents). In order to compare stomach contents of mullets before and after their visit to the saltmarsh creek, 16 fish samplings were performed on an ebb tide and 6 on the flood tide (Laffaille et al., 2002).

The whole mullet population was sampled using a series of four successive nets in the creek (Laffaille et al., 1998; Parlier et al., 2006): three trammel nets (70–30 mm mesh size, 2 m high and 30 m long) to capture large individuals and a fyke net (4 mm mesh size, 5 m deep, 1.80 m high, 20 m long) to catch the smallest individuals. To ensure maximum adult capture rates, trammel nets were set out diagonally across the creek and spaced 10 m apart as adult mullets can avoid nets and thereby escape (Laffaille et al., 2002). For ebb tide sampling, nets were set out across the creek at high tide until the creek was totally drained. Nets were set up on the creek for periods of 20 min separated by intervals of 5 min thus covering 80% of the tide. Using this protocol, the number and biomass of fish which migrate into the creek during one tidal cycle can be estimated (Laffaille et al., 1998). Moreover, with this regular sampling, mullets can be frozen quickly, thereby arresting digestion and avoiding regurgitation. For flood tide sampling, nets were set across the empty creek and were left until high tide. The sampling protocol was the same as for the ebb tide. All samples were stored in iceboxes in the field and deep frozen (–20 °C) at the laboratory until analysis.

### 2.3. Population structure

All sampled mullets were measured (fork length) to the nearest mm. Mullets of 50 mm length or more were identified to the species level using the identification keys of Farrugio (1977), Cambrony (1984), synthesized in Keith and Allardi (2001), and Gautier and Hussenot (2005). Mullets were individually weighed to the nearest 0.01 g. Mullets less than 50 mm long, for which identification is very difficult (Cambrony, 1984; Keith and Allardi, 2001), were not identified. These mullets were pooled into size classes to the nearest mm and mean individual weights were calculated for each size class ( $\pm 0.01$  g). Within species, age was defined based on growth curves from Le Dantec (1955) and Lam Hoï (1969), tables in Gautier and Hussenot (2005) and young-of-the-year growth curves for *Liza aurata* and *Liza ramada* from Aiguillon Bay (Parlier, unpublished results).

For all ebb samples (one sample corresponds to a period of 20 min), the number ( $N_i$ ) and biomass ( $M_i$ ) of mullets per sample were defined for each species and each age group (Laffaille et al., 1998). Numbers of non-caught mullets ( $N_j$ ) during the 5 min intervals between samples  $i$  and  $i + 1$  were estimated by extrapolation using the moving average of samples ( $N_i$  and  $N_{i+1}$ ) with the formula:  $N_j = [(N_i/t_i) + (N_{i+1}/t_{i+1})]/2 * t_j$  where  $t_i$  is the sampling time for sample  $i$  (min),  $t_{i+1}$ : sampling time for sample  $i + 1$  (min) and  $t_j$  is the time between sample  $i$  and  $i + 1$  (min). Biomass of non-caught mullets per sample ( $M_j$ ) was determined using  $M_i$  and the same

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