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Behavioral responses of juvenile golden gray mullet *Liza aurata* to changes in coastal temperatures and consequences for benthic food resources☆

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ABSTRACT

Temperature is an important factor for fish. Yet, little is known about temperature effects on the feeding behavior of fish and the subsequent consequences of these behavioral changes on the spatial distribution of resources. We analyzed the differences in the feeding behavior of two size classes of juvenile *Liza aurata* at two water temperatures (i.e. 10 °C and 20 °C), using laboratory mesocosms. We also examined whether potential temperature-induced changes in feeding behavior of the smaller size of *L. aurata* would affect the spatial distribution of the microphytobenthos (MPB) biomass, an important resource in coastal systems.

Both the number of feeding events and the swimming velocity during feeding were higher at 20 °C than at 10 °C, independent of the fish size. The time spent feeding did not vary between 10 °C and 20 °C, while the distance covered during feeding was significantly smaller at 20 °C than at 10 °C. Grazing did not affect the mean MPB biomass, but did increase its spatial variance at the smaller scale (i.e. a few centimeters) at 20 °C.

A high number of feeding events, a high swimming velocity during feeding and a small distance covered during feeding in 20 °C-acclimated *L. aurata* most likely represented an adaptation to an increase in metabolism, as well as to the need to reduce the energy costs of feeding at 20 °C. Results also indicated that changes in feeding behavior of the 20 °C-acclimated *L. aurata* were responsible for the increase in small-scale spatial variability in the MPB biomass but not an overall significant effect on the MPB mean. We suggested that the enhanced spatial patchiness due to grazing by fish at 20 °C might yield a local increase in the mean MPB biomass, probably increasing photosynthetic efficiency of cells and algal growth that counterbalance the negative effect of algal removal by fish.

1. Introduction

Temperature is one of the most important environmental factors for the physiology and metabolism of fish (McKenzie and Claireaux, 2010). Consequently, it can affect all the behavioral traits of fish, including feeding behavior, as well as influence the outcomes of the consumer–resource interactions. If few studies have explicitly investigated the effect of temperature on the feeding behavior of fish (e.g., Nowicki et al., 2012; Theodorou et al., 2012), even less has been done to understand how these behavioral changes influence the spatial or temporal distribution of resources in coastal areas (Polunin and Klumpp, 1992; Smith, 2008). Furthermore, most of these studies have been focused on tropical herbivorous fish in coral reef systems. Very little is known about the effects of temperature on the feeding behavior of other fish inhabiting coastal systems. An example is the gray mullet (Mugilidae), one of the most abundant fish in coastal areas worldwide (Cardona, 2006; Laffaille et al., 2002; Lebreton et al., 2011; Whitfield et al., 2012).

Rises in temperature (within naturally occurring ranges) are usually accompanied by an increase in metabolism and energy demands (Biro et al., 2007, 2010; Ferreira et al., 1998) and, consequently, in food consumption and feeding activity (Polunin and Klumpp, 1992; Smith, 2008). In particular, an increase in the number of feeding events (Ferreira et al., 1998; Floeter et al., 2005; Nowicki et al., 2012; Polunin and Klumpp, 1989; Smith, 2008), the amount of time spent feeding (Biro et al., 2007) and the distances covered during feeding (Biro et al., 2010; Theodorou et al., 2012) have been observed with temperature increases.

In general, empirical evidence illustrates that the addition of grazers or predators results in the reduction of the mean biomass (or density) of

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their resources (Armitage et al., 2009; Berlow, 1999). If a consumer reduces the mean biomass of a resource, this should also cause a reduction in spatial variance of the biomass itself, due to the relationship between the mean and the variance (Taylor, 1961). In coral reef systems, Polunin and Klumpp (1992) showed that the increase in the number of feeding events at increasing temperatures can lead to increases in algal consumption. It is therefore possible that the amount of algae removed and the amount of variance lost in an area both increase as water temperatures increase, even if the density of grazers and the availability of their resources do not vary in that area (Beukers-Stewart et al., 2011; Polunin and Klumpp, 1989).

However, whether or not grazing has negative effects on the mean and the spatial variance of the algal biomass depends on the timescale of measurement and the interplay between the rates of algal removal and algal growth. Grazing is effective in reducing the mean and the spatial variance of algal biomass only if the rates of algal removal exceed the rates of algal growth. Furthermore, whether or not grazing decreases the overall spatial variance of a resource biomass depends not only on the mean effect of the trophic interaction, the overall biomass of the resource and the mathematical relationship between the mean and the variance, but also on the variance of the trophic interaction as well as the residual variability of the resource (i.e. the component of variation that is not due to grazing) (Benedetti-Cecchi, 2000, 2003; Benedetti-Cecchi et al., 2005). The overall spatial variance of the resource is expected to decrease if the loss of variance caused by the reduction in the mean abundance of the resource is larger than the residual variability in the resource abundance, and if the negative effect caused by the reduction in the mean abundance of the resource is larger than the positive effect due to increased spatial variance of grazing.

In this study, we tested the effects of changes in water temperature on the feeding behavior of juvenile golden gray mullet *Liza aurata*, one of the most abundant European gray mullets inhabiting the Northwestern Atlantic coasts and the Mediterranean Sea (Cardona, 2006; Lebreton et al., 2011). The feeding behavior was analyzed at 10 °C and 20 °C, two temperatures representing low and high seasonal values (which occur naturally during winter and summer, respectively) in the geographic distribution of *L. aurata* (Cardona, 2006; Lebreton et al., 2011). We were also interested in understanding whether potential temperature-induced changes in the feeding behavior of *L. aurata* would affect the mean and spatial variance of the microphytobenthos (MPB) biomass, an important benthic food resource for *L. aurata* (Laffaille et al., 2002; Lebreton et al., 2011; Pasquaud et al., 2010). We used a series of laboratory experiments in mesocosm with natural sediment, where we measured the feeding behavior of juvenile *L. aurata* and the mean and the spatial variance of MPB biomass at each temperature (i.e. 10 °C and 20 °C). As mullets must meet higher metabolic rates and energy demands at increasing temperatures (Cucco et al., 2012), we expected (i) the number of feeding events, (ii) the total time spent feeding and/or (iii) the distance covered during feeding to be higher at increasing temperatures; as temperature can affect swimming performance in fish (Claireaux et al., 2006; Deslauriers and Kieffer, 2012), we also expected (iv) the velocity of swimming during feeding to be higher at higher temperatures. Whether or not the spatial or temporal variance of grazing by gray mullets would be able to enhance the spatial patchiness of MPB is not known. Gray mullets, however, feed in schools (Whitfield et al., 2012) and their gregarious behavior should increase the likelihood of homogeneous grazing in an area (Adler et al., 2001). At each experimental temperature, it is possible that the amount of spatial variance in the MPB biomass caused by a heterogeneous grazing would be lower than the amount of MPB variance lost due to the reduction in the mean MPB biomass. Therefore, we expected grazing to have a negative effect (v) on the mean of the MPB biomass and (vi) on the amount of spatial variability of MPB but we also expected that (vii) the amount of microalgae removed and the amount of variance lost due to grazing would be higher at 20 °C than at 10 °C. Because feeding activity in juveniles often varies with fish size (Buckle and Booth, 2009; Choat and Clements, 1993), tests on the feeding behavior were repeated with two sizes of juveniles (i.e. J0 and J1). However, only J0 was taken into account to test for the grazing effects on MPB, as this size dominates the natural populations in shallow coastal areas (Hotos and Katselis, 2011; Lebreton et al., 2011).

2. Material and methods

2.1. Experimental fish

Thirty-six J0 juveniles and 36 J1 juveniles (mean total length (TL) ± SE: 9.71 ± 0.23 cm and 16.10 ± 0.12 cm, respectively) were used in this experiment. The fish were collected along the Sardinian coast of Italy and then transported to the Marine Station of the University of La Rochelle (France), where the experiment was carried out. Fish were maintained for one month in 1000 liter holding tanks (1 × 1 × 1 m) filled with re-circulated filtered sea water. Temperatures and salinity ranged between 14 and 19 °C (mean ± S.E.: 17 °C ± 0.2, n = 30) and 29 and 35 psu (mean ± S.E.: 32 psu ± 0.3, n = 30), respectively. After the mullets were transferred into experimental tanks, water temperatures were adjusted by 0.5 °C per day, until experimental temperatures were reached (10 °C and 20 °C). The fish were then allowed to acclimate to the experimental temperature for at least three months. During this period fish were under natural photoperiod of the location (46°10 N) and fed with natural periphyton daily and with dry pellets (BioMar®) twice a week as an integration of proteins and vitamins. The use of natural periphyton allowed us to maintain the fish in laboratory conditions without compromising their natural foraging behavior (Richard et al., 2010). Natural periphyton was developed on artificial substrates in an adjacent pond, following the methods described in Richard et al. (2010).

2.2. Protocol

Gray mullets are a gregarious fish and exhibit schooling behavior (Whitfield et al., 2012). Therefore, we used 3 fish for each run of the experiment. Each fish was used only once. Before being transferred into the mesocosm (4 × 1 × 1 m; Fig. 1), fish were marked on the opercula with plastic tags of different colors using Krazy glue®, following the procedure described in Lefrancois et al. (2005). For marking, fish were lightly sedated with MS222 ($0.08\,\mathrm{g\,l^{-1}}$). Each tagging procedure took <2 min and fish ventilated continuously with no noticeable decrease in ventilation rate. Fish never lost balance and resumed swimming as soon as they were transferred to the acclimatization chamber (Como pers. obs.). Each fish group was placed in the acclimatization chamber of the mesocosm under natural photoperiod and was left undisturbed for 12 h before the experiment in order to allow them to recover from any stress caused by this handling. Fish were not fed during this period.

An hour and a half before the beginning of the experiment, the water level of the working chamber of the mesocosm was raised by about 50 cm and the fish were encouraged to move from the acclimatization to the working chamber (where the sediment was positioned; see below). This was done by opening the sliding door and lifting up the floor of acclimatization chamber (Fig. 1). In general, the fish entered rapidly (less than 3 min for transfer). The experiment began when the fish started feeding on the sediment placed on the floor and lasted for 3 h. The cameras were turned on as the fish entered the working chamber and recorded their foraging for the entire duration of the experiment. At the end, the fish were encouraged to move back to the acclimatization chamber as the water level was progressively reduced in the working chamber. All the experimental runs were performed in the same period of the day (in the morning) in order to avoid a bias in the results done by daily variations in the fish feeding activity (Almeida, 2003). All precautions were taken to limit fish stress during