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Spatial variations in dietary organic matter sources modulate the size and condition of fish juveniles in temperate lagoon nursery sites

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Effective conservation of marine fish stocks involves understanding the impact, on population dynamics, of intra-specific variation in nursery habitats use at the juvenile stage. In some regions, an important part of the catching effort is concentrated on a small number of marine species that colonize coastal lagoons during their first year of life. To determine the intra-specific variation in lagoon use by these fish and their potential demographic consequences, we studied diet spatiotemporal variations in the group 0 juveniles of a highly exploited sparid, the gilthead seabream (*Sparus aurata* L.), during their ~6 months stay in a NW Mediterranean lagoon ($N = 331$, SL = 25–198 mm) and traced the origin of the organic matter in their food webs, at two lagoon sites with contrasted continental inputs. This showed that the origin (marine, lagoonal or continental) of the organic matter (OM) available in the water column and the sediment can vary substantially within the same lagoon, in line with local variations in the intensity of marine and continental inputs. The high trophic plasticity of *S. aurata* allows its juveniles to adapt to resulting differences in prey abundances at each site during their lagoon residency, thereby sustaining high growth irrespective of the area inhabited within the lagoon. However, continental POM incorporation by the juveniles through their diet (of 21–37% on average depending on the site) is proportional to its availability in the environment and could be responsible for the greater fish sizes (of 28 mm SL on average) and body weights (of 40.8 g on average) observed at the site under continental influence in the autumn, when the juveniles are ready to leave the lagoon. This suggests that continental inputs in particulate OM, when present, could significantly enhance fish growth within coastal lagoons, with important consequences on the local population dynamics of the fish species that use them as nurseries. As our results indicate that continental OM can represent up to 62% of the flesh of the juveniles originating from these ecosystems, particular care should be taken to preserve or improve the chemical quality of riverine inputs to coastal lagoons.

1. Introduction

Mortality rates in fish are maximal during early life stages (Cushing and Horwood, 1982). Therefore, understanding the role, in population dynamics, of nursery habitats use by fish juveniles is particularly important for the effective conservation of marine fish stocks (Jennings and Blanchard, 2004). Environmental variation has been shown to influence ecosystems functioning, with implications for fish ecology and stock recruitment success (Bennett et al., 1995; Islam and Tanaka, 2006; Adams et al., 2009). In particular, the level and nature of continental inputs in coastal ecosystems were shown to modify the composition, abundance and biomass of benthic prey

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(Drake et al., 2002; Salen-Picard et al., 2002; Nicolas et al., 2007; Kostecki et al., 2010), which subsequently influence growth and mortality of fish juveniles (Houde, 2006). As these last two parameters determine the success of recruitment to the adult exploited stock (Barry et al., 1996; Islam and Tanaka, 2006), exploitation of continental inputs within foodwebs sustaining juvenile growth in coastal nursery areas might be central in the conservation of many exploited stocks. However, there is still a lack of knowledge on the degree of spatiotemporal variations in the origin of the organic matter sustaining fish foodwebs, as well as their consequences for population dynamics.

Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotopes analysis constitutes a powerful tool for the description of the structure of coastal foodwebs and organic matter transfer through them (Carlier et al., 2008; McClellan and Braun-McNeill, 2010; Layman et al., 2012). Provided that distinct isotopic signatures can be identified for the primary producers, the method allows assessment of the main organic matter source(s) that sustain animal feeding (Moreno et al., 2010; Kostecki et al., 2012), especially when combined with detailed analysis of predator diets (*e.g.* Darnaude et al., 2004; Darnaude, 2005). The recent development of mixing models based on $\delta^{13}C$ and $\delta^{15}N$ signatures (Phillips and Gregg, 2003; Phillips et al., 2005; Wissel and Fry, 2005; Parnell et al., 2010) has further allowed robust quantification of the contributions of different possible sources of organic matter (OM), both to foodwebs (Abrantes and Sheaves, 2010; Chételat et al., 2010) or to individual consumer diets (Inger et al., 2006; Moreno et al., 2010; Kostecki et al., 2012). However, although patterns in the origin of the OM used by juvenile fish were analyzed in several coastal nursery grounds (*e.g.* Darnaude, 2005; Kostecki et al., 2010; Pasquaud et al., 2010; Vinagre et al., 2010), there is still a lack of quantitative studies in this field (Kostecki et al., 2012; Le Pape et al., 2013). Studies investigating the link between the source(s) of OM to the trophic chains sustaining juvenile fish growth and condition are even fewer (Koussoroplis et al., 2010; Isnard et al., in press).

Among the coastal ecosystems used as nursery areas by fish species, temperate lagoons have so far received little attention in terms of their quality as nursery habitats (Kjerfve, 1994; Isnard et al., in press) and their foodweb structure and functioning (Palomares et al., 1993; Libralato et al., 2002; Carlier et al., 2008). Despite this, numerous fish species targeted by coastal fisheries use them as nursery grounds (Quignard et al., 1983; Parrish, 1989; Beck et al., 2001; Fernandez Delgado et al., 2007). As with estuaries, these transitional ecosystems are thought to offer favorable development conditions for juvenile fish. Indeed, compared to the sea, lagoons provide protection from predation but also present conditions that maximize metabolic rates and lower osmoregulation costs (higher temperatures and productivity, lower salinities), thus increasing the growth potential of juveniles (Gillanders et al., 2003; Dahlgren et al., 2006; Vasconcelos et al., 2010, 2011). As in many transition areas between land and sea, lagoon productivity is modulated by continental inputs in nutrients and particulate OM (Nixon, 1982), which can sustain high primary and secondary productions and benefit to the whole foodweb (Salen-Picard et al., 2002; Darnaude et al., 2004; Whitfield, 2005; Vizzini and Mazzola, 2008). However, temperate lagoons differ widely in their physico-chemical characteristics, depending on the size of their watershed, their depth and the number of their connection to the sea (Mercier et al., 2012). They also are highly variable both spatially and temporally and particularly sensitive to anthropogenic and climatic pressures (Jackson et al., 2001; Anthony et al., 2009).

In this context, we aimed at determining the demographic consequences of (1) lagoon environmental variability and (2) intra-specific diversity in lagoon use by euryhaline juvenile fish. To do so, we studied the spatio-temporal variations in diet, ultimate OM source(s) and body growth of group 0 juveniles of the gilthead seabream (*Sparus aurata*, L.) during their annual stay in two areas of the same lagoon under contrasted freshwater and marine inputs. The gilthead seabream is an euryhaline and eurythermal sparid fish which is abundantly fished in the Mediterranean and in the eastern Atlantic and has consequently a high economic value (Froese and Pauly, 2000). Yet, its biology and ecology in the Gulf of Lions (North Western Mediterranean Sea) are still poorly understood (Libralato and Solidoro, 2008; Bodinier et al., 2010; Mercier et al., 2011, 2012). After hatching at sea in December–February, a large proportion of the juveniles colonize coastal lagoons, where they sustain high growth rates from April–June to October–November (Mercier et al., 2011; Isnard et al., in press), before returning to the open sea to join the adult stock (Audoin, 1962; Lasserre, 1974; Mercier et al., 2012). In the Gulf of Lions (NW Mediterranean), a large part of the juveniles originate from lagoons with shallow and desalted water (Mercier et al., 2012), where incorporation of continental OM is thought to maximize juvenile growth and condition (Isnard et al., in press). Among them, the Mauguio lagoon (Hérault, France) is currently considered as one of the main nursery site for *S. aurata* juveniles in the area (Quinard et al., 1983; Mercier et al., 2012; Isnard et al. in press). However, abiotic and biotic environmental conditions are particularly variable within this lagoon, whose environmental status is listed as "poor" by the local water Agency (Ifremer, 2009, 2012). Therefore, we investigated the consequences of the colonization of two parts of this lagoon differing in their abiotic (temperature, salinity) and biotic (diet and OM sources) environmental conditions, on the size and condition of *S. aurata* juveniles at the end of their first year of life. In particular, we tested the hypothesis that continental inputs in particulate OM (POM) to the lagoon are beneficial for the growth of *S. aurata* juveniles through their positive influence on fish local foodwebs. For this purpose, we compared (1) the temporal variability in the diet of *S. aurata* juveniles, (2) the main origin of the OM they assimilated (lagoonal, continental or marine) and (3) their body size and condition, between two parts of the lagoon under contrasted freshwater influence. By providing knowledge on the variability in continental OM exploitation by juvenile marine fish within coastal lagoons, its causes and its potential consequences for juvenile fish condition, this approach should help decision making for the sustainable management of coastal lagoon ecosystems and the exploited stocks of euryhaline fish that use them as nursery areas.

2. Material and methods

2.1. Study area

With an area of 31.7 km^2 and a drainage area of 410 km^2 (Ifremer, 2008), the Mauguio lagoon is the fourth largest lagoon in the Gulf of Lions (north western Mediterranean sea; 43°57′14″N; 4°03′50″ E, Fig. 1). It is very shallow (maximum depth < 1.3 m) and communicates with the sea through a single channel. Therefore, water characteristics in the lagoon are highly dependent on local weather conditions. Climate in the area is of Mediterranean type, with mild winters and hot summers. Rains occur mainly during spring and winter, with a mean annual amount of 699 mm (Ifremer, 2006, 2008, 2009, 2012). As a result, water temperatures in the lagoon vary from 4 °C in winter to 26 °C in summer (Ifremer, 2006, 2008, 2009, 2012). Salinity ranges from 2 to 32, but with marked spatial differences within the lagoon. Hence, the lagoon sole connection to the sea (M) is located at its southwest end while most sources of continental inputs (*e.g.* C1–C3) are located along its northeastern shore (Fig. 1). This configuration leads to a quasi-permanent gradient of decreasing salinity and increasing