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Spatial analysis of the trophic interactions between two juvenile fish species and their preys along a coastal–estuarine gradient

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ABSTRACT

Coastal and estuarine systems provide nursery grounds for many marine fish species. Their productivity has been correlated with terrigeneous inputs entering the coastal–estuarine benthic food web, thereby favouring the establishment of fish juveniles. Studies in these ecosystems often describe the nursery as a single large habitat without verifying nor considering the presence of contiguous habitats. Our study aimed at identifying different habitats based on macrozoobenthic communities and morpho-sedimentary characteristics and assessing the trophic interactions between fish juveniles and their benthic preys within these habitats. It included 43 sampling sites covering 5 habitats in which we described taxonomically and quantitatively the invertebrates and fish communities with stable isotopes and gut contents. It suggested that the benthic common sole *Solea solea* displayed feeding plasticity at the population level, separating the juveniles (G0) from the older fish (G1) into different "feeding subpopulations". Size-based feeding plasticity was also observable in the spatial occupancy of that species in the studied bay. The demersal pouting, *Trisopterus luscus*, equally used the different habitats but displayed low feeding plasticity across and inside each habitat. Stable isotopes proved to be powerful tools to study the spatial distribution of trophic interactions in complex ecosystems like the bay of Vilaine and to define optimal habitats for fish that use the coastal–estuarine ecosystem as nursery grounds.

1. Introduction

Located at the sea–continent interface, coastal ecosystems are known as productive areas (Costanza et al., 1997). They foster high primary and secondary productions (Largier, 1993) and sometimes tertiary production as they are inhabited by marine species at various stages of their life cycle (Beck et al., 2001). Coastal zones are characterized by local production and inputs of organic matter originating from different sources (e.g. detritic, algal, planktonic) which vary greatly in time and space. These inputs may considerably boost up the coastal and marine production (Maslowski, 2003) and may significantly modify ecosystem functioning (Baird et al., 2004). For instance, seasonal river floods result in an increase in input of macronutrients leading to an increase in plankton production (Nielsen and Richardson, 1996). Benthic production also varies at various temporal scales via the cycling of nutrients between the sediments at the bottom and the overlying water column (Josefson and Conley, 1997). Nutrient enrichment and eventually eutrophication resulting from the pelagic–benthic coupling has a noticeable impact on food availability to the benthic fauna (Darnaude et al., 2004a). The impact of nutrient enrichment on the fluctuation of species abundance in coastal marine communities can be of prime importance in the functioning of these ecosystems (Salen-Picard et al., 2002). Thus terrestrial organic matter has been shown to play a significant role in the dynamics of coastal macrobenthic communities and on the productivity of commercial fish species and fisheries (Darnaude et al., 2004b).

Research on essential coastal habitats, such as nurseries, often describes them as a single large habitat without considering that it is composed of a mosaic of habitats (i.e. seascape) that provides resources for a diversity of species (Ray, 2005). Generally, when more than one habitat is studied, these are examined separately so that little is known about how they interact and function together. The complexity of the spatial organisation of these habitats and the multiplicity of potential organic matter sources that support secondary and tertiary consumers, make the study of the nursery functioning fairly challenging (Deegan and Garritt, 1997).

Stable isotope tracking is a powerful tool to apprehend the functional aspects of a nursery's spatial organisation, yet allowing the definition of optimal habitats for fish species that use the coastal–estuarine ecosystem as nursery grounds. The basic rationale of the stable isotope approach is that the isotopic composition of consumer tissues reflects this of their diet, which in turn depends on the relative proportions of prey species

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assimilated over a specific time period (De Niro and Epstein, 1978; Minagawa and Wada, 1984; Peterson and Fry, 1987). Stable isotopes of carbon and nitrogen are commonly used to examine consumers' trophic ecology providing a time-integrated measure of trophic position and energy sources. Nitrogen stable isotope ratios in consumers are typically enriched in the heavier (^{15}N) isotope from 2 to 4‰ per trophic level (Minagawa and Wada, 1984; Peterson and Fry, 1987), making δ^{15}N values useful in defining trophic positions of consumers (Post, 2002). The carbon isotope ratios fractionate to a lesser extent (0 to 1‰) and are typically used to define diet compositions or sources of energy (De Niro and Epstein, 1978).

In estuarine-coastal gradients, the natural variations of stable isotopes allow to distinguish coastal from marine areas either on δ^{15}N or δ^{13}C. Terrestrial and estuarine waters traditionally present ^{13}C-depleted values compared to marine waters because carbon in materials originated by photosynthesis (e.g. fixed carbon in terrestrial plants or phytoplankton) is depleted in ^{13}C compared to atmospheric CO_2. Seawater δ^{13}C is supposedly at equilibrium with atmospheric CO_2 (Oana and Deevey, 1960). In the same way, terrestrial waters have traditionally lower δ^{15}N than marine waters (France, 1995), but nowadays, higher values in δ^{15}N are often observed in coastal waters in comparison to marine waters, as coastal ecosystems receive ^{15}N-enriched sewage discharges (anthropisation, agriculture and industries) with river run-offs (Gartner et al., 2002; Schlacher et al., 2005). According to McClelland et al. (1997), wastewater with high NO_3^- derived from human and animal wastes is ^{15}N enriched (+10 to +20‰) and elevates the overall δ^{15}N signatures of water entering the trophic chain in coastal areas. These variations of stable isotope signatures along seaward gradient, make stable isotopes useful in the identification of the primary sources of organic carbon in the diet of organisms. In such conditions, the isotopic approach has been successfully used to trace the transfer of organic matter through estuarine and coastal food webs (Islam and Tanaka, 2006; Vinagre et al., 2008) and identify aspects of life history or movement patterns of species in nursery habitats (Fry, 2008). Stable isotope ratios (δ^{15}N or δ^{13}C) were recently used in coastal areas to infer on the relative contribution of different resources used among juveniles of flatfish species (Kostecki et al., 2010; Le Pape et al., 2013; Vinagre et al., 2008) and to quantify the relative contribution of estuarine and coastal production in supporting juveniles fish (Leakey et al., 2008b). They have also proved to be powerful tools to assess ontogenetic size-based shift in fish diet and associated feeding plasticity (e.g. Leakey et al., 2008a for ages 1+, 2+ and 3+ common sole; Ho et al., 2009).

The present study aimed to answer the following questions: Do juveniles of benthic and demersal fish species use the bay of Vilaine as one large habitat or as multiple habitats? If so, do these habitats display the same trophic interactions? In order to answer these questions, we defined and assessed the spatial organization of habitats along the estuarine-coastal gradient of the bay of Vilaine nursery ground. More precisely, we (i) identified different habitats based on macrozoobenthic communities and morpho-sedimentary characteristics, (ii) described and tested the biological and ecological differences of these biosedimentary habitats using stable isotope analyses and fish stomach contents, and (iii) assessed the trophic interactions within these habitats. We hypothesized that benthic species would be more constrained in their use of habitats due to their close relationships with the substrate and associated fauna compared to demersal fish. In the same way we expected that age-0 fish (G0), due to a high site fidelity, would present lower feeding plasticity than older individuals (G1).

2. Material and methods

2.1. Study area and sampling protocol

The study was conducted in the bay of Vilaine located on the French Atlantic coast, south Brittany (Fig. 1). The bay covers a surface area of 230 km^2 and is characterized by an open shallow muddy estuarine area, under the influence of freshwater inflows. Surveys were carried out at the end of August 2008 using a stratified sampling design relying on a 5-stratum scheme (Fig. 1), in which each stratum was identified by depth range and sediment type. Depths ranged from 5 to 35 m and the sediment types varied from coarse-grained sand and gravel to fine sand and/or coarse silt. Sampling was conducted using a 2.9 m wide and 0.5 m high beam trawl, with a 20-mm-stretched mesh net in the cod-end. Each haul lasted 15 min and covered a mean surface of 4500–5000 m^2. A total of 43 hauls were performed (Fig. 1, see Table 1 for the number of hauls by habitat).

All fish were identified at the species level and weighted. This study focused however on two of the most abundant species in the bay of Vilaine: the benthic common sole and the demersal pouting. Individuals from these two species were aged according to their length-frequency distributions. The two size-classes corresponded respectively to the young-of-the-year group (G0) and age one group (G1): common sole (G0: 9.09 ± 0.76 cm, G1: 16.45 ± 1.25 cm) and pouting (G0: 7.88 ± 0.96 cm, G1: 11.49 ± 0.93 cm). These size classes were consistent with our own database of otolith measures (unpublished data) and other studies (Merayo and Villegas, 1994; Mérigot et al., 2007). Several studies have highlighted the nursery function of the bay of Vilaine for these two species (Le Pape et al., 2003b), yet only the two size classes associated with the juvenile phase were studied. Individuals of the two species were frozen (−24 °C) prior to isotopic and gut content analyses.

Concurrently, the benthic fauna was sampled at the same sites (43 sampling sites with 4 replicates per site) using a Van Veen grab (0.1 m^2). Sediments from the grab were sieved in a cubic screen (1 mm mesh size). Retained fraction (sediments and macro-invertebrates) of 3 of the 4 replicates was fixed and preserved in 10% seawater buffered formaldehyde. The remaining grab replicate was frozen (−24 °C) for isotopic analyses. In the laboratory, invertebrates were sorted from the sediments and identified to the lowest taxonomic level, before counting and weighing. Analyses of the benthic fauna were conducted on the summed biomass of the 3 replicates by site. Benthic invertebrate macrofauna was categorized into trophic guilds for the comparison between the habitats: carnivores, detritivores, and deposit- and suspension-feeders (Appeltans et al., 2011; Fauchald and Jumars, 1979; Hily and Bouteille, 1999; Rosenberg, 1993). Bottom water was sampled using a Niskin bottle and filtered until clogged through precombusted Whatman GF/F filters (0.5 μm) immediately after sampling. Filters were kept frozen until their extraction to obtain particulate organic matter (POM).

2.2. Stable isotope analyses (SIA)

A sample of white dorsal muscle of the fish was dissected and used for SIA (Pinnegar and Polunin, 1999). All samples were frozen individually at −80 °C before freeze-drying. Each dried sample was then ground into a homogeneous powder using a mixer mill. Approximately 0.2 mg of sample was accurately weighed into small tin cups, and stable isotope ratios of carbon and nitrogen were analysed in a Carlo Erba NC2500 elemental analyser coupled to a Thermo Finnigan Mat Delta XP isotope ratio mass spectrometer. Isotope ratios were reported in delta notation as per international standards: Pee Dee belemnite carbonate for δ^{13}C and atmospheric nitrogen for δ^{15}N. Data were corrected using working standards (bass muscle, bovine liver, nicotinamide; SD < 0.2‰ for both δ^{13}C and δ^{15}N) that were previously calibrated against the International Atomic Energy Agency (IAEA) standards.

Benthic invertebrates selected for SIA were those considered as potential preys for the bentho-demersal fish species and dominant in terms of abundance and biomass in the Vilaine coastal–estuarine ecosystem. Isotope analyses were conducted on the muscle of large benthic organisms (i.e. >1 cm), whereas analyses were done on the remaining tissues once the digestive tracts, jaws and cerci were removed for small organisms. The remaining tissues were then washed with distilled