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Influence of food availability on the spatial distribution of juvenile fish within soft sediment nursery habitats

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ABSTRACT

Soft sediments in coastal shallow waters constitute nursery habitats for juveniles of several flatfishes. The quality of a nursery is defined by its capacity to optimize the growth and the survival of juvenile fish. The influence of biotic factors, such as food availability, is poorly studied at the scale of a nursery ground. Whether food availability limits juvenile survival is still uncertain. A spatial approach is used to understand the influence of food availability on the distribution of juvenile fish of various benthic and demersal species in the Bay of Vilaine (France), a productive nursery ground. We quantified the spatial overlap between benthic macro-invertebrates and their predators (juvenile fish) to assess if the latter were spatially covering the most productive areas of the Bay. Three scenarios describing the shapes of the predator–prey spatial relationship were tested to quantify the strength of the relationship and consequently the importance of food availability in determining fish distribution. Our results underline that both food availability and fish densities vary greatly over the nursery ground. When considering small organisational levels (e.g., a single fish species), the predator–prey spatial relationship was not clear, likely because of additional environmental effects not identified here; but at larger organisational level (the whole juvenile fish community), a strong overlap between the fish predators and their prey was identified. The evidence that fish concentrate in sectors with high food availability suggests that either food is the limiting factor in that nursery or/and fish display behavioural responses by optimising their energetic expenditures associated with foraging. Further investigations are needed to test the two hypotheses and to assess the impact of benthic and demersal juvenile fish in the food web of coastal nurseries.

1. Introduction

Soft substrates in coastal shallow waters constitute nursery habitats for juveniles of several flatfishes of commercial interest (e.g., *Solea solea*, *Pleuronectes platessa*) and also of other demersal species (e.g., *Trisopterus luscus*, *Merlangius merlangus*) (Gibson, 1994; Elliott and Hemingway, 2002; Able, 2005; Franco et al., 2006). For most of those fishes, the juvenile phase is characterised by high growth and mortality rates, followed by a migration towards deeper zones at sexual maturity (Dorel et al., 1991; Le Pape et al., 2003). Thus, the juvenile phase represents a bottleneck with regard to recruitment, making a large proportion of commercial species highly dependent on coastal habitats to complete their life cycle (Seitz et al., 2014).

The total number of juvenile fish produced yearly by all nursery habitats related to a fish stock shows large temporal variability (e.g., Rijnsdorp et al., 1992). These variations are notably influenced not only by the surface area but also the quality of the nursery grounds (Rijnsdorp et al., 1992; Rochette et al., 2010) and by environmental fluctuations such as those in temperature (Van der Veer et al., 2000), salinity (Pasquaud et al., 2012), and river discharge (Le Pape et al., 2003; Kostecki et al., 2010). Within a nursery area, high spatial and interannual variations of juvenile density are also observed (e.g., Dorel et al., 1991; Rogers, 1992; Kopp et al., 2013). The variations are directly related to the complexity and spatial heterogeneity in the physico-chemical properties of these coastal habitats; a main reason is that physico-chemical properties can exceed the physiological tolerance of certain juvenile fishes (e.g., hypoxic stress, salinity or temperature tolerance). Predation and food availability, although less often studied (Johnson et al., 2013), are two main biotic factors impacting the growth, survival, and spatial distribution of juveniles within nursery grounds (Gibson, 1994).

Competition for food is expected to regulate growth and survival rates of juveniles but the impact level of food availability is still widely controversial (Le Pape and Bonhommeau, 2015). Some authors argue

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that food limits the carrying capacity of nurseries (e.g., Gibson, 1994; Nash and Geffen, 2000; Van der Veer et al., 2010), whereas others strongly argue that there is enough food for all the species in nurseries (e.g., Van der Veer and Witte, 1993; Hampel et al., 2005; Vinagre and Cabral, 2008). These competing viewpoints lead to two different expectations regarding the distribution of juvenile fish. (1) In the case of food limitation, juvenile fish are expected to be more concentrated in sectors where prey are abundant; indeed, the mobility of benthic invertebrates being negligible in comparison to benthic and demersal juvenile fish, starved juvenile fish should migrate towards nursery sectors with higher food availability (the order of magnitude of potential daily distances travelled by juvenile flatfish is about 1 km: Berghahn, 1987; Burrows et al., 1994, 2004; Gibson et al., 1998; Morrison et al., 2002, Vinagre et al., 2006; Le Pape and Cognez, 2016). Therefore, juvenile fish distribution should follow the feeding potentials of a nursery habitat. (2) Where food is not limiting, we expect a weak (or no) spatial relationship between fish and their prey. Indeed, because food is in excess, the influence of food quantity on fish distribution should be minimal. Juvenile fish should be more responsive to food quality and select a nursery sector more for the composition of its prey community than for the total food availability. In this case, food factor may be less determining than local variations of abiotic factors such as temperature or granulometry.

Liebig's law of the minimum states that ecological processes, such as the growth of juveniles, may be influenced by a multitude of factors, but are only controlled by the scarcest resource (Cade et al., 1999; Hiddink and Kaiser, 2005); e.g., oxygen concentration or food availability (Gibson, 1994). The factors are thus not additive but multiplicative; indeed, only one unfavourable factor among all is enough to penalise the response. This concept can be broadened to give a general framework within which to discuss the food limitation hypothesis (Johnson et al., 2012) in nurseries, by characterizing the spatial relationships between the fish and their prey. Three scenarios are thus expected (Fig. 1). (1) In the first scenario, the relationship between predators and prey is highly predictive; high food densities involve necessarily high juvenile fish densities. If the other influencing factors are independent from predator and prey distributions, food availability will likely drive the behaviour of juveniles, either because of a food limitation effect, or because these predators optimise their energetic expenditures associated with foraging (Rose and Leggett, 1990). It is also possible that unmeasured abiotic factors define both predators and prey distributions; therefore, this first scenario must be considered along with available information on abiotic factors influencing benthic communities within the nursery. (2) In the second scenario, there is no predictive relationship between the fish and its prey. The juveniles are found in high densities even in sectors where prey abundance is relatively low. This suggests that food seems to be in excess and consequently is not a limiting factor. (3) In the third scenario, high densities of juveniles are restricted to areas of high prey densities, suggesting either food limitation or a behavioural response of the predator optimising its probability of catching a prey. But, unlike the first scenario, low densities of juveniles in sectors with high prey abundance indicate that other unmeasured factors are potentially limiting (Johnson et al., 2012). This scenario also suggests that the factor(s) determining fish density vary from one sector to another.

The present study aims to assess the influence of benthic prey availability on the spatial distribution of benthic and demersal juvenile fish in a nursery ground, the Bay of Vilaine (France). It was conducted in two steps. We first explored the influence of the organisational level of predators (species level, morphological group level, and community level) on the predator–prey relationship. Considering several benthic and demersal juvenile fishes together to study the predator–prey relationship is relevant because they display similar prey spectra (Piet et al., 1998). We secondly tested the three aforementioned scenarios by quantifying the spatial correspondence between the abundances of juveniles and their prey, in order to infer the regulation potential of food availability on juvenile fish distribution in the studied nursery.

2. Materials and methods

2.1. Study site

The Bay of Vilaine (Fig. 2) is a soft-bottom ground used as a nursery by several benthic and demersal fishes of commercial interest (Desaunay et al., 1981; Dorel et al., 1991). It has been studied for more than 30 years, producing valuable knowledge on its fish (Marchand, 1991; Le Pape et al., 2003; Nicolas et al., 2007; Kopp et al., 2013) and benthic invertebrate communities (Le Bris and Glemarec, 1995; Brind'Amour et al., 2009, 2014). Given such data and knowledge-rich

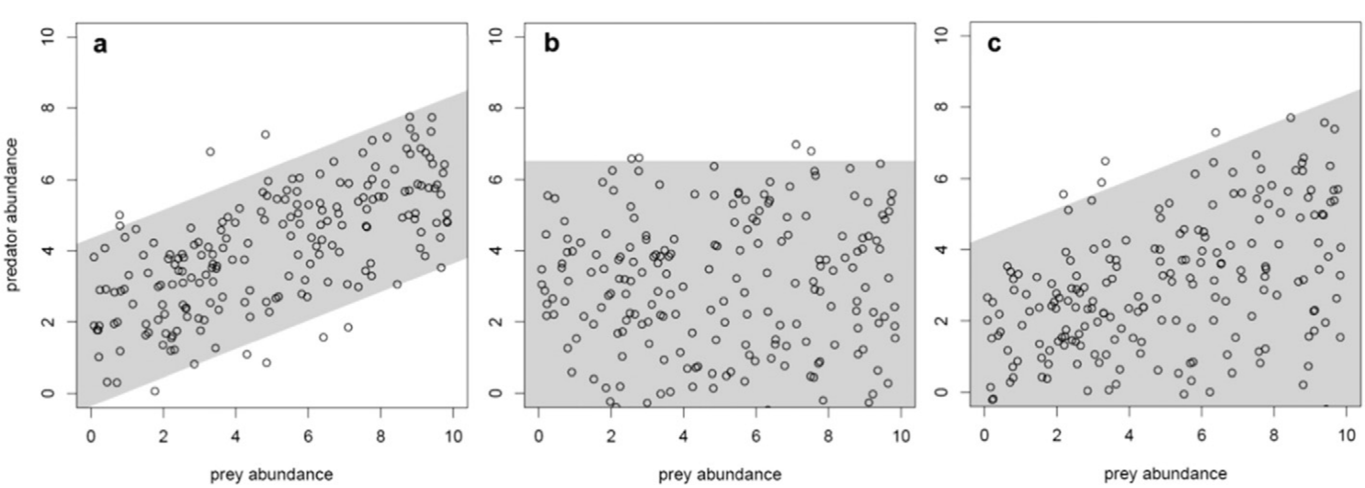

Fig. 1. Graphical description of the three scenarios used to infer the strength of the food limitation hypothesis in explaining juvenile fish distribution within nursery habitat (simulated data). (a) Prey density is the main factor influencing the spatial distribution of the predators. Natural variability constitutes the noise (variability) in the signal. (b) Prey density is independent of the predator density; in this scenario, food is not limiting. (c) Prey density partially regulates the predator spatial distribution, but other unmeasured factors seem also to be locally-limiting.