Journal of Experimental Marine Biology and Ecology 506 (2018) 49–60

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Dynamic habitat use of an estuarine nursery seascape: Ontogenetic shifts in habitat suitability of the European flounder (*Platichthys flesus*)

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ARTICLE INFO

Keywords:
Habitat suitability
European flounder
Ontogenetic shifts
Fish nursery
Estuarine seascape

ABSTRACT

Estuaries have long been recognized as nursery habitats for various marine fish species. As seascapes consisting of a mosaic of habitat patches, estuarine nurseries incorporate ecological processes such as ontogenetic shifts. To improve our understanding of the habitat requirement changes of nursery species within the estuarine seascape, habitat suitability models were built using boosted regression trees for three size classes of European flounder (*Platichthys flesus*) juveniles. The models combined several dynamic and static predictors, from physical and chemical water parameters to biological and physical habitat variables. The relationships between juveniles and predictor variables varied with size, potentially indicating the dynamics of habitat use for the juvenile flounder inside the estuarine nursery. Younger post-settled juveniles tended to be spatially constrained to a shallow upstream area and, with size, there were ontogenetic shifts to the middle estuary. This demonstrates the importance of considering different life stages when developing essential fish habitat maps, which reflect fine scale temporal and spatial distributions. Given the high level of anthropogenic pressures to which estuaries are subjected, the consideration of fish ontogenetic habitat requirements within the estuarine nursery is needed to identify high-value areas, and is valuable for developing effective spatial and temporal management plans. These are essential to fully protect the most sensitive life stages, such as early post-settlement stages occupying transient habitats. Additionally, and as the juvenile-habitat associations can rapidly change, fine-scale connectivity in the estuarine nursery becomes even more relevant in determining recruitment. Connectivity should therefore be central in conservation planning, in order to sustain estuarine and marine adult populations, and ultimately maintaining the fisheries.

1. Introduction

During their life history, the habitat preferences of many coastal marine and estuarine fish change with ontogeny, and early life stages can inhabit very different environments compared with their adult stages (Dando, 2011; Gillanders et al., 2003; Kimirei et al., 2013). The pelagic dispersal stage of eggs and larvae is typically followed by settlement if suitable habitat is found (Cowen and Sponaugle, 2009). In the nursery area, fish juveniles benefit from refuge from predators and high food availability promoting survival and growth until they are ready to move and recruit to the adult population (Beck et al., 2001; Fodrie and Mendoza, 2006; Vasconcelos et al., 2009). Movement patterns, however, can be interpreted at a range of spatial scales (Dance and Rooker, 2015) and, although major ontogenetic habitat shifts can occur at large scales (i.e. hundreds to thousands of km), it is also possible to detect changes in species habitat preferences at small scales, for example, inside nursery areas (Nagelkerken et al., 2015). Ontogenetic movements at smaller scales, such as inside nursery areas, may be more difficult to be detected. They may occur as habitat suitability varies with size, age or development, and due to modifications in food resource requirements (Mendes et al., 2014), predation risk (Kimirei et al., 2013), and habitat availability, which allows an enhancement of the fitness of the fish by seeking optimal habitats (Kahler et al., 2001).

Among nursery habitats, estuaries have been recognized as essential for many marine fish species (Able, 2005; Potter et al., 2015), contributing to the sustainability and conservation of adult populations. Therefore, estuarine nursery grounds have been widely studied (Amara et al., 2009; Pattrick and Strydom, 2014; Rochette et al., 2010; Vasconcelos et al., 2010), and much emphasis has been given to the need to determine their importance for management and conservation. Recent studies, however, have called for a more dynamic approach when assessing nursery areas, emphasizing that these are heterogenous,

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https://doi.org/10.1016/j.jembe.2018.05.011
Received 22 November 2017; Received in revised form 21 May 2018; Accepted 31 May 2018

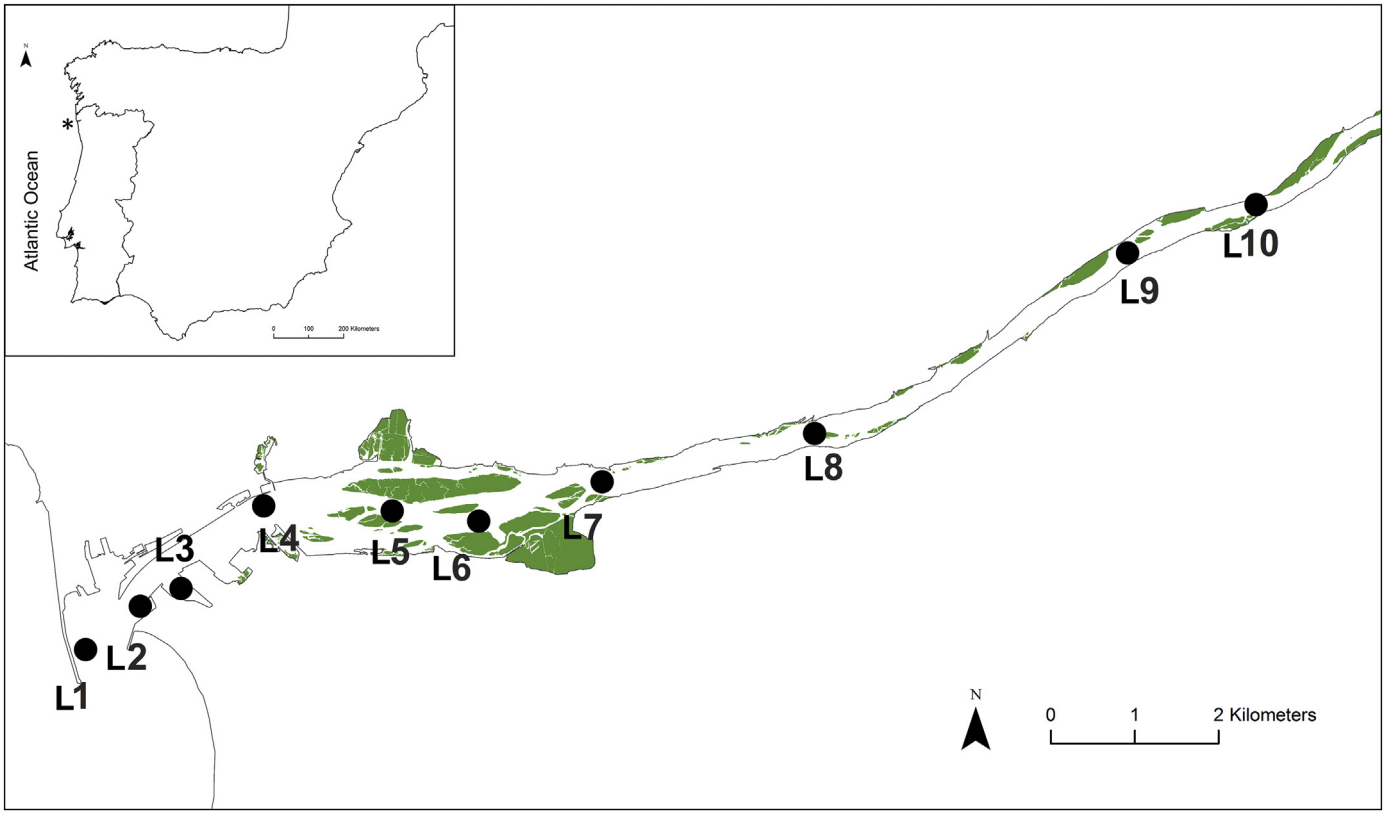

Fig. 1. Lima estuary location in the Northwest Iberian Peninsula (Portugal) and sampling sites.

spatially explicit seascapes where dynamic processes and ontogenetic movements occur (Nagelkerken et al., 2015; Sheaves et al., 2015). Habitat suitability models and predictive mapping have been key to understanding fish distributions based on habitat variables (Le Pape et al., 2014; Vasconcelos et al., 2013) and have been broadly applied to juvenile fish using estuarine and coastal nurseries (Compton et al., 2012; Froeschke and Froeschke, 2011; Le Pape et al., 2007; Nicolas et al., 2007; Trimoreau et al., 2013; Vasconcelos et al., 2010; Zucchetta et al., 2010). However, most habitat suitability studies have focused on the young-of-the-year or overall juvenile distribution and have overlooked ontogenic movements inside the nursery (but see Costa et al., 2015; Furey and Rooker, 2013), despite available evidence that a finer scale change in habitat requirements inside the nurseries is shared by several species (e.g. Manderson et al., 2002; Mendes et al., 2014; Ribeiro et al., 2012; van der Veer et al., 2001).

While being important nursery areas, estuaries are also among the most threatened coastal ecosystems, generally located in areas of high population and large-scale development (McLusky and Elliott, 2004). The high level of anthropogenic pressures to which they are subjected cause degradation, fragmentation and ultimately loss of habitats (Amorim et al., 2017; Lotze et al., 2006). As habitat requirements can change during ontogeny (Werner and Gilliam, 1984), even at fine temporal and spatial scales, it is likely that responses to habitat change (due to fragmentation, loss, increased urbanisation) will also differ among life stages. The knowledge of the different ontogenetic habitat requirements is, therefore, particularly important for management and conservation. Hence, approaches that consider ontogenetic movements within the estuarine nursery habitats, and that identify high-value areas, are necessary to develop effective management plans of marine fishes using anthropogenically-stressed areas, such as estuaries. Furthermore, detailed knowledge of fine-scale habitat preferences, and of which habitat features are potentially limiting, is fundamental to enhance the probability of successful habitat restoration (Bond and Lake, 2003).

In order to improve our understanding of environmental processes governing spatial distributions of nursery species within the estuarine seascape, habitat suitability models were built for the juvenile European flounder (*Platichthys flesus*). The European flounder was chosen as model species due to its estuarine dependence during the early life stages (Elliott et al., 2007; Potter et al., 2015). *P. flesus* is regarded as a semi-catadromous species (Elliott et al., 2007; Potter et al., 2015), known to enter the estuaries in their larval stage, and appear to prefer low salinity upstream habitats to settle (Amorim et al., 2016; Bos and Thiel, 2006; Freitas et al., 2009; Jager, 1998). Later, older juveniles slowly move downstream, until they leave the estuary to breed at sea (Ramos et al., 2010). Although juveniles are generalist feeders, Mendes et al. (2014) showed ontogenetic shifts in prey selection, with post-settled individuals presenting a low diet diversity, and older juveniles presenting a distinct diet from the young-of-the-year. Therefore, and following the hypothesis that the European flounder performs ontogenetic movements within the nursery area, this study aimed to determine i) the ontogenetic shifts in habitats, and ii) the environmental factors that determine the suitability of the habitat at each ontogenetic stage in order to build predictive distribution maps.

2. Material and methods

2.1. Study area

The Lima estuary is a small Atlantic temperate estuary located in the NW coast of the Iberian Peninsula (Portugal), discharging an annual average river flow of 70 $m^3 s^{-1}$ from a catchment of 2446 km^2. The tidal regime is mesotidal semidiurnal (3.7 m range during spring tides) and its influence reaches 20 km upstream. Geomorphologically, the estuary can be divided into 3 distinct sections: the lower estuary (0–3 km from the mouth), near an urbanized area, is a navigational channel, narrow and deep, with artificial channels; the middle estuary (3–7 km from the mouth) is a broad shallow zone with salt marshes and