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Offshore–onshore linkages in the larval life history of sole in the Gulf of Lions (NW-Mediterranean)

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A B S T R A C T

Understanding individual dispersion from offshore natal areas to coastal nurseries during pelagic larval life is especially important for the sustainable management of exploited marine fish species. For several years, the hatching period, the larval life duration, the average growth rate and the otolith chemical composition ($\delta^{13}C$, $\delta^{18}O$, Sr:Ca and Ba:Ca) during the larval life were studied for young of the year (YOY) of sole collected in three main nurseries of the Gulf of Lions (GoL) (Thau, Mauguio and Berre). We investigated the spatial variation in the origin of the sole larvae which colonised the nurseries around the GoL, and whether temporal differences in environmental conditions during this life stage affected growth and larval life duration. The hatching period ranges from October to March, depending on year and site. Average ages at metamorphosis varied between 43 and 50 days, with the lowest and highest values consistently found for Mauguio and Berre, respectively. Otolith growth rates ranged between 2.7 and 3.2 $\mu m\ d^{-1}$, with the lowest values in Thau and Mauguio and the highest in Berre. Otolith chemical composition during the larval life also varied, suggesting contrasted larval environmental histories in YOY among nurseries. In fishes from Berre and Mauguio, larval life was more influenced by the Rhône River, showing consistently higher larval Ba:Ca ratios (10/23 $\mu mol\ mol^{-1}$) and lower $\delta^{13}C$ (−6.5/−6.1‰) and $\delta^{18}O$ values (−1.6/0.1‰) than for Thau (with Ba:Ca ratios < 8 $\mu mol\ mol^{-1}$, $\delta^{13}C$ ~−2.3‰ and $\delta^{18}O$ ~1.5‰). Differences in larval otolith composition were observed for 2004, with higher Ba:Ca and lower $\delta^{13}C$ and $\delta^{18}O$ values than in the two other years. These differences were explained by changes in composition and chemical signatures of water masses after an exceptional flooding event of the Rhône River in late 2003.

1. Introduction

Understanding the links between life history traits at the larval stage and the patterns of dispersion from natal areas to nurseries is especially important for the conservation of many marine fish species. In marine ecosystems, the persistence and resilience of populations in the face of natural and anthropogenic disturbances are largely linked to their degree of connectivity (Botsford et al., 2009). As many fish species are relatively sedentary at the adult stage, dispersion of eggs and/or larvae is one of the most important sources of connectivity of fish populations (Jones et al., 1999; Cowen et al., 2006; Sale et al., 2010). Dispersion success at this stage strongly depends on environmental conditions encountered by eggs and larvae. During the few days or weeks of the larval stage, individual migration can be passive at first, eggs and young larvae being only transported by marine currents, and it is mostly at the very end of this life stage that larvae become active and swim toward nursery grounds. Other larvae can quickly adopt behavioural activities such as oriented swimming activities, and response to sensory cues (Lagardère et al., 1999; Leis, 2007). Eggs and larvae are

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vulnerable and many individuals (90/93% of common sole larvae) are lost for recruitment due to predation, starvation or other processes (Koutsikopoulos, 1991). However, factors such as river floods are known to influence recruitment success by increasing the planktonic production near the river mouth and enhancing the growth and survival of larvae of coastal fish species (Salen-Picard et al., 2002; Le Pape et al., 2003). The description of larval life history is therefore a first essential step in the understanding of the success of larval dispersion and the maintenance of connectivity among populations (Sale et al., 2010).

In this work, the concomitant structural and chemical information stored in otoliths (ear stone) of young-of-the-year (hereafter YOY) of common sole, *Solea solea* (Linnaeus, 1758), a coastal fish species from the Gulf of Lions (hereafter GoL) (NW Mediterranean), was used to investigate the links between larval life history and larval dissemination in this commercially important flatfish species. Its life cycle has been thoroughly studied, but mainly in the northern part of its distribution area (North Sea, Atlantic Ocean, English Channel and Irish Sea). The common sole produces a high number of pelagic eggs (130,000 at 34 cm to 1,300,000 at 54 cm) (Quéro and Vayne, 1997) hatching after 7–8 days (Fonds, 1979). Metamorphosis and benthic recruitment of larvae on nursery grounds occur after 3–7 weeks at a size of ~8.5 mm (Amara et al., 2000; Vinagre et al., 2008). Juvenile sole inhabit coastal or estuarine nurseries for two to three years, before recruiting to adult offshore populations, each constituted of fish originating in various nurseries (Koutsikopoulos et al., 1995; Vasconcelos et al., 2008; Tanner et al., 2011, 2012). There is less knowledge on the life cycle of *S. solea* in the Mediterranean Sea (Mérigot et al., 2007; Morat et al., 2012, 2014), especially in the GoL. Previous studies confirm the general ontogenetic shift of habitat observed elsewhere in its distribution area, with pelagic larvae also found offshore, benthic juveniles in lagoons or shallow marine areas and benthic adults on the continental shelf down to ~200 m depth (Salen-Picard et al., 2002). However, data on the spawning area (suspected near the Rhône River mouth) and on the inter-habitat connectivity in this area, especially at the larval stage, are necessary for the preservation of local populations and sustainable fisheries (Quignard et al., 1984; Mérigot et al., 2007; Morat et al., 2014). Indeed, the common sole is highly exploited in the GoL, where annual catches decreased from 520 to 177 tonnes between 1990 and 2010 (http://www.fao.org). In this context, we aimed to assess (i) whether there is a spatial variation in the origin of the sole larvae among nurseries of the GoL, (ii) if the Rhône River inputs influence this repartition, and (iii) whether inter-annual differences in environmental conditions during this life stage affect growth and larval life duration, especially during years characterized by an exceptionally high discharge from the Rhône River.

The larval life of fish could be directly studied using the egg and larvae dispersions. However, this is time consuming and requires a good knowledge of the main spawning periods and areas. Otoliths can provide useful information on the past conditions of fish life and migrations (Thorrold et al., 1997b). The continuous growth of otoliths by accretion of daily layers of calcium carbonate from the birth to the death of fish (Pannella, 1971) provides access to valuable information regarding fish history, such as daily growth rates (Morales-Ñin, 2000) and larval life duration (Amara et al., 1998). Otoliths are metabolically inert, i.e. otolith material remains unaltered after deposition (Campana and Neilson, 1985; Campana and Casselman, 1993), and their elemental and stable isotope compositions largely reflect the physicochemical characteristics of the environment inhabited by fish during their growth (Fowler et al., 1995; Gallahar and Kingsford, 1996). Therefore, otolith can provide valuable records of the environmental conditions encountered by fish during their larval life, in terms of temperature, salinity and chemical composition of the water masses encountered (Thorrold et al., 1997a; Blamart et al., 2002). In this context, otoliths of YOY sole from distant coastal lagoon nurseries distributed along the coast of the GoL were used to assess inter-annual and inter-site variations of age, average otolith growth, stable isotope and elemental compositions of the material deposited during larval life.

2. Material and methods

2.1. Study area

As with the rest of the NW Mediterranean, the Gulf of Lions (Fig. 1) is mainly oligotrophic (Lochet and Leveau, 1990), except in the area influenced by the inputs of the Rhône River, which is the most important runoff into the Mediterranean since the damming of the Nile in 1970. Its discharge can vary between less than 500 $m^3\ s^{-1}$ in summer and ~10–11,000 $m^3\ s^{-1}$ during flooding periods (Fig. 2), with a centennial mean of 1700 $m^3\ s^{-1}$ (Estournel et al., 2009). Annual Rhône River inputs to the GoL average 6.2×10^6 tonnes of terrestrial particulate material (Pont, 1997) and account for ~50% of the phytoplankton production of the gulf (Lochet and Leveau, 1990). However, the maximum discharge observed for the Rhône River on the 3rd December 2003 (Fig. 2) corresponds to a 100-year return flood event due to huge rainfalls in the south eastern region of France (Miralles et al., 2006). During this extreme

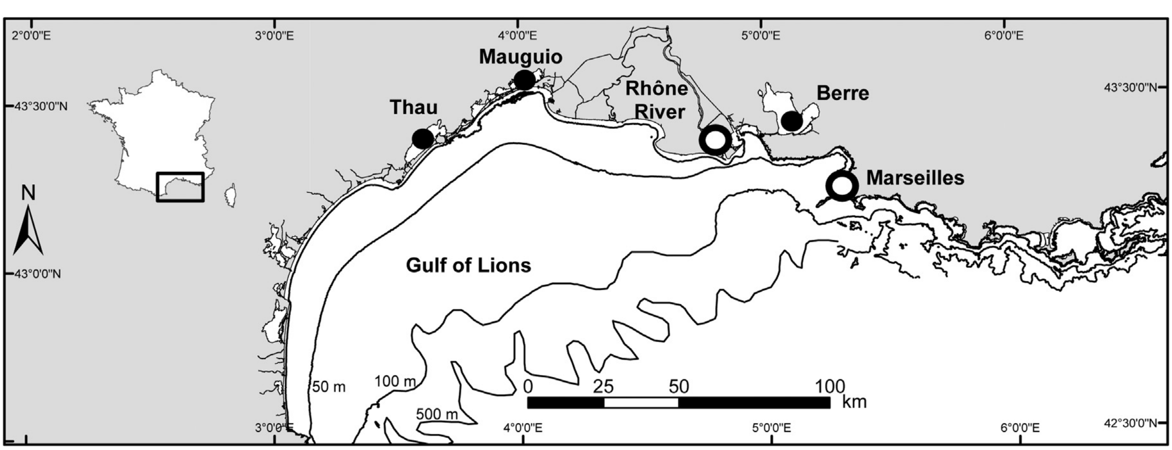

Fig. 1. Location of YOY sole sampled in the Gulf of Lions (black points) and water samples (white points).