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Research paper

Potential fishing-related effects on fish life history revealed by otolith microchemistry

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ABSTRACT

Although inferring habitat selection and movement in wild fishes using otolith microchemistry has been the subject of much debate, experimental results suggest that complex environmental vs. life history interactions affect the incorporation of certain chemical elements into otoliths. We hypothesized that under relatively homogeneous hydrographic conditions, individual life history trait strategies should dominate signals of geochemical signatures. We tested our hypothesis by analyzing individual chronologies of otolith signals of strontium to calcium (Sr:Ca) and barium to calcium (Ba:Ca) ratios in a sedentary coastal fish (*Diplodus annularis*). Two areas from the same northwest Mediterranean region with different levels of fishing pressure were sampled: (1) a no-take marine protected area where the "bigger-is-better" strategy should prevail (energy allocation is biased toward growth to compensate for high natural mortality at small sizes) and (2) a highly exploited population where the "smaller-is-better" strategy should dominate (energy allocation is biased toward reproduction to compensate for high fishing mortality at large sizes). Significant differences in reproduction vs. growth trade-offs were observed between the sub-populations. Sr:Ca and Ba:Ca chronologies were compared between back-calculated ontogenetic stages (larvae, juveniles and adults) and sub-populations/life histories using a general linear mixed model. The Sr:Ca chronology successfully reproduced the allocation of energy for growth or reproduction according to the life history strategy of the individual, whereas correlation between ontogeny and otolith microchemistry was less obvious for Ba:Ca. We contend that the direct and/or indirect (e.g., the removal of large predators) effects of fishing pressure on microchemical signals should receive more attention in field studies, as trade-offs between mortality and growth/reproduction might alter microchemical patterns under a given a set of conditions.

1. Introduction

Coupled analysis of otolith microchemistry and age from individual fishes has become a widely used approach to exploring relevant aspects of fish ecology, such as associating individuals with a particular habitat through their life cycle and elucidating migrations and population structures (Campana, 1999; Elsdon et al., 2008; Phillis et al., 2011; Sturrock et al., 2012, and references therein). Strontium (Sr) and barium (Ba) are the most studied elements used to infer the past locations of fishes due to the positive relationship between the ambient relative concentrations of these elements and their relative concentrations in otoliths (Elsdon and Gillanders, 2005; Elsdon et al., 2008; Tabouret et al., 2010). Marine fishes typically derive between 83% and 98% of their otolith Sr and Ba contents from the surrounding water, and the changes produced by marked variations in water properties (i.e., salinity, chemical composition) or productivity are indicative of a specific habitat (Chen and Jones, 2006; Walther and Thorrold, 2006).

Although it is clear that minor or trace elements that accumulate in otoliths might be associated with ambient concentrations (Limburg, 1995; Campana, 1999; Milton and Chenery, 2001; Zimmerman, 2005; Ranaldi and Gagnon, 2010), the relative bioavailability of different elements taken up by fishes has received less research attention (reviewed in Elsdon et al., 2008). It is likely that these elements will be fractioned during transport across the gut and gills from water and food to the blood, eventually being transported to the endolymph and, finally, to the otolith (Borelli et al., 2001; Payan et al., 2010). Furthermore, the proportions of these elements with respect to calcium also depend on the calcium deposition rate and organic matrix content (McFadden et al., 2016). Kalish (1991) was among the first authors to argue that in addition to environmental factors, physiological factors

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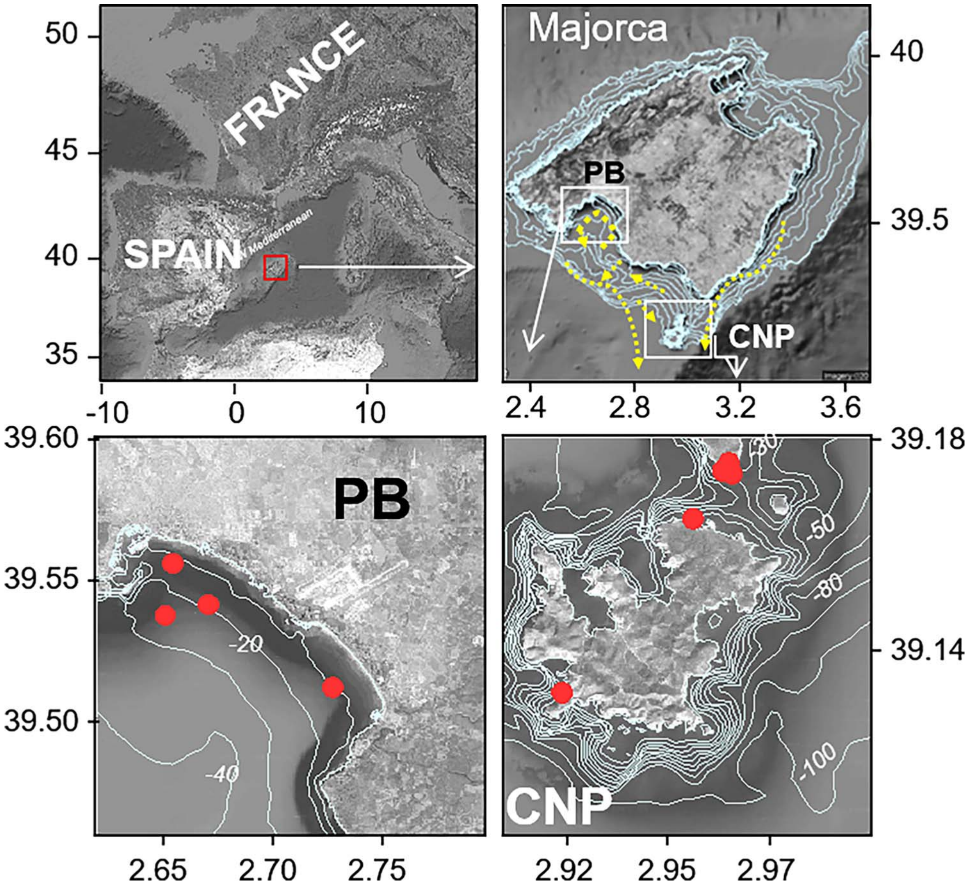

Fig. 1. Location of the two sampling areas: Palma Bay (PB, Majorca Island) and the national maritime-terrestrial Park of Cabrera (CNP). The specific collection sites for geochemical analyses of the otoliths are shown in red. In the top-right map, the main summer coastal surface currents in the area of study are superimposed in yellow (after Basterretxea et al., 2012; Álvarez et al., 2015). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

influence the chemical composition of otoliths. He suggested that changes in blood plasma composition during gonad development, specifically the composition and concentration of ion-binding proteins, is important and that the apparent relationship between temperature and otolith elemental composition is due to the effect of temperature on gonad development. Since then, it has been believed that changes in otolith microchemistry do not solely reflect ambient water concentrations; indeed, mounting evidence has revealed the important roles of ontogeny and physiology, which might lead to the misinterpretation of the field patterns inferred from microchemical analyses (Hoff and Fuiman, 1995; Brown and Severin, 1999; Clarke and Friedland, 2004; Miller and Kent, 2009; Morales-Nin et al., 2014; Miller, 2011; Gronkjaer, 2016; Alós et al., 2017). For example, several studies have demonstrated that otolith Sr:Ca and Ba:Ca ratios correspond to seasonal variations in water temperature, and negative relationships between the somatic growth rate and both Sr:Ca (Sadovy and Severin, 1994) and Ba:Ca ratios (Miller, 2011) have been reported. Brown and Severin (2009) concluded that the water Sr:Ca ratio is the primary factor affecting otolith Sr:Ca ratios in freshwater and estuarine fishes but not in marine species. Although the lifetime Sr:Ca profiles of the analyzed marine fishes varied as much as those of the estuarine fishes, there was no apparent relationship with water chemistry, suggesting that other factors are able to introduce significant variability in the Sr:Ca ratio. Recently, Sturrock et al. (2015) showed experimentally that physiological biokinetic factors (e.g., those associated with the reproductive stage) likely have a strong impact on otolith microchemistry.

Fishes of the same species can vary widely in their life history strategies. Indeed, the course imposed by local sources of mortality should inevitably generate populations that respond to local selective pressures by allocating energy for growth or reproduction according to an optimal life history strategy (Reznick et al., 1990; Hutchings, 1993; Puebla et al., 2007). For instance, the natural mortality imposed by predators on small-sized individuals should shift the trade-off between growth and reproduction in life history, whereby individuals allocate more energy toward somatic growth according to the “bigger-is-better” strategy (Reznick, 1982; Hutchings, 1993; Edeline et al., 2007; Olsen and Moland, 2011). In contrast, the selective properties of fishing shift mortality toward large-sized individuals and should therefore indirectly induce a higher investment in reproduction and a lower allocation of energy toward somatic growth; the outcome at the population level is to maximize life-span fitness in exploited environments according to the “smaller-is-better” strategy (Olsen and Moland, 2011; Alós et al., 2014). Thus, we hypothesized that in cases in which the hydrographic conditions and seawater composition are rather similar (i.e., within the same water mass), the effects of life history optimization in response to contrasting mortality pressures might strongly imprint a geochemical tag throughout the life of a fish. This idea is supported by the findings of Sturrock et al. (2014, 2015), who suggested that physiological influences were especially strong for Sr and Ba contents, even stronger than variations in water chemistry. In fishes kept in captivity, significant relationships have been observed between element/calcium ratios and physiological-related factors in terms of body length and condition, sex, growth rate, and spawning. In this respect, our hypothesis is also based on the theory that individual growth curves can actually be modeled as functions of energy investment driven by combinations of temperature, life stage, sex and reproductive stage (Lester et al., 2004; Pecquerie et al., 2011).

Existing data suggest that in areas located away from major river plumes, Sr and Ca in seawater of the northwestern (NW) Mediterranean are relatively stable, even at great depths (Bernat et al., 1972). In the Balearic Archipelago (NW Mediterranean), the absence of permanent rivers and scarce industrial pollution (Moukhchan et al., 2013) creates a good environment for examining the effects of differential pressures on life history traits in wild fishes in their natural environment. Moreover,