Journal of Sea Research 85 (2014) 205–213

Contents lists available at ScienceDirect

Journal of Sea Research

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

Linking habitat structure to life history strategy: Insights from a Mediterranean killifish

Francesco Cavraro [a,*], Irini Daouti [b], Ioannis Leonardos [b], Patrizia Torricelli [a], Stefano Malavasi [a]

[a] CEMAS — Centre for Estuarine and Coastal Marine Science c/o Department of Environmental Sciences, Informatics and Statistics, Università Ca' Foscari Venezia, Campo della Celestia, Castello 2737/b, 30122 Venice, Italy
[b] Laboratory of Zoology, Department of Biological Applications and Technology, University of Ioannina, 45110 Ioannina, Greece

ARTICLE INFO

Article history:
Received 6 March 2012
Received in revised form 9 May 2013
Accepted 20 May 2013
Available online 2 June 2013

Keywords:
Salt Marsh
Predation
Energy
Demography
Reproduction

ABSTRACT

Modern theories of life history evolution deal with finding links between environmental factors, demographic structure of animal populations and the optimal life history strategy. Small-sized teleost fish, occurring in fragmented populations under contrasting environments, have been widely used as study models to investigate these issues. In the present study, the Mediterranean killifish *Aphanius fasciatus* was used to investigate the relationships between some habitat features and life history strategy. We selected four sites in the Venice lagoon inhabited by this species, exhibiting different combinations of two factors: overall adult mortality, related to intertidal water coverage and a consequent higher level of predator exposure, and the level of sediment organic matter, as indicator of habitat trophic richness. Results showed that these were the two most important factors influencing demography and life history traits in the four sites. Fish from salt marshes with high predator pressure were smaller and produced a higher number of eggs, whereas bigger fish and a lower reproductive investment were found in the two closed, not tidally influenced habitats. Habitat richness was positively related with population density, but negatively related with growth rate. In particular the synergy between high resources and low predation level was found to be important in shaping peculiar life history traits. Results were discussed in the light of the interactions between selective demographic forces acting differentially on age/size classes, such as predation, and habitat trophic richness that may represent an important energetic constraint on life history traits. The importance to link habitat productivity and morphology to demographic factors for a better understanding of the evolution of life history strategy under contrasting environments was finally suggested.

1. Introduction

Theories on life history evolution shifted during the last decades from *r*- and *K*-selection paradigms to a more analytical view, creating a direct mechanistic link between environmental factors, demographic structure of populations and optimal life history strategies (Reznick et al., 2002). This view is mostly based on demographic selective forces, and especially on extrinsic mortality schedules, that act differentially on age/size classes, shaping life history traits of locally adapted populations.

Small-sized teleost species, such as those belonging to the families Poeciliidae and Cyprinodontidae, live often in fragmented ecosystems or microhabitats. Some species of these families have been used as study models to investigate the relationships between environmental factors, selective demographic forces and life history traits. A number of studies showed the primacy of predation as the selective agent that shapes life history traits (Jennions and Telford, 2002; Johnson and Belk, 2001; Reznick and Endler, 1982; Reznick et al., 2001, 2002; Rodd and Reznick, 1991; Walsh and Reznick, 2008, 2009, 2010a,b). Results of these studies are consistent in showing that the intensity of predation on the adults can determine smaller size at maturation and higher reproductive effort (with more and smaller eggs). However, when other factors (such as predation on juveniles or competition, food abundance, growth rates and density regulation) are controlled for, more complicated patterns may arise (Walsh and Reznick, 2008, 2009, 2010a,b). As concluded by Reznick et al. (2002), the optimal life history strategy is not only under the influence of demographic selective forces, such as predation, but also of further "additive" environmental factors, which interact with demographic forces, even in complicated, indirect and unexpected ways. In the present study, a Mediterranean killifish inhabiting brackish confined habitats, the South European Toothcarp *Aphanius fasciatus* (Valenciennes, 1821), was used as a study model to test for the effects on life history traits of the interaction between predation intensity and habitat richness in environmental basal resources. Considering the spectrum of habitat types inhabited by this species in the Venice lagoon (Cavraro et al., 2011), predation intensity was assumed to be related to the tidal influence on the salt marsh creeks. In creeks of natural origin, lying within the intertidal zone and connected with near subtidal mudflats, adult *A. fasciatus* are forced to leave refuge habitat within the creeks for deeper waters, undergoing predation by large

* Corresponding author. Tel.: +39 041 234 7732; fax: +39 041 52 81 494.
E-mail address: cavraro@unive.it (F. Cavraro).

1385-1101/$ – see front matter © 2013 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.seares.2013.05.004

piscivorous fish. Other creeks are of artificial origin (man-made creeks created within lagoon islands for traditional fish farming or as line of defense) and are regulated through barriers, so that connection with external mudflats and/or the complete drainage of the creek is prevented. In this case, tidal influence is unimportant and the creek constitutes a refuge area even during low tides, avoiding predation by large piscivorous fish from external lagoon. We predict that populations inhabiting creeks of natural origin are subjected to overall higher predation intensity compared to those from artificial creeks, so they are expected to show higher reproductive allotment and smaller size at reproduction, according to the current available literature (Reznick et al., 2002). While predictions on the effects of predation on life history phenotype are easy to formulate due to the abundance of previous studies on this subject (Jennions and Telford, 2002; Johnson and Belk, 2001; Reznick and Endler, 1982; Reznick et al., 2001; Rodd and Reznick, 1991; Walsh and Reznick, 2008, 2009, 2010a,b), studies on the effects of habitat richness on life history traits are quite scarce in the current literature (Furness et al., 2012; Walsh and Reznick, 2008, 2010a,b). Some aquatic habitats, such as transitional waters, are known to be detritus-based systems, with trophic richness directly related to the level of organic matter entrapped into sediments (Howes et al., 1984; Mitsch and Gosselink, 2000; Odum, 1988). Furthermore, studies on aquatic benthic invertebrates indicate that biomass, density and some life history traits, such as growth and reproduction, are positively related to the level of organic matter in the sediments (Figueiredo-Barros and Leal, 2006; Kevrekidis, 2005). Since these invertebrates are the main component of the diet of small resident fish, including killifishes *A. fasciatus* (Leonardos, 2008), we predict that sediment organic matter may directly influence demographic and life history traits at the higher trophic levels represented by fish populations. Evidence that benthic organic matter can affect elemental stoichiometry of the neotropical killifish *Rivulus hartii* is provided by a recent work (El-Sabaawi et al., 2012), suggesting that reproduction, somatic growth and lipid content of fish may be directly influenced by the quality of the basal resources of their habitats. El-Sabaawi et al. (2012) hypothesized that the main mechanism explaining these relationships is that the quality of basal resources constraints the elemental composition at higher trophic levels. We therefore predict that habitat richness may interact with predation intensity, acting on life history traits, either directly, by influencing some somatic and reproductive traits, or indirectly, through the mediated effects of density and biomass. High food levels may enhance not only fish density, but also the individual size, increasing the amount of energy devoted to growth and to reproduction *i.e.* more trophic resources would determine higher fecundity and bigger eggs. On the contrary, low resource availability would decrease fish density, and would force fish to a trade-off of the amount of energy devoted to growth or to reproduction.

To test for these effects, we selected four sites that could represent four combinations of predation intensity and habitat richness, according to a 2×2 design: 1) High trophic richness and low predation intensity, 2) high trophic richness and high predation intensity, 3) low trophic richness and high predation intensity, and 4) low trophic richness and low predation intensity. This design allowed us to assess to what extent environmental basal resources are able to modulate the effects of extrinsic mortality schedules on life history traits.

To achieve this goal, we proceeded with two subsequent steps. (1) First we assessed the influence of the measured environmental factors on the demographic structure of local female populations sampled from the four sites during the breeding season, in terms of density, growth rates, and age/size structure. (2) Then we assessed the influence of the same factors on life history traits in a sub-sample of female populations, measured as size and age-specific reproductive investment, egg size and size at maturity. We focused our study on this sex because females express a larger reproductive effort than males (Johnston and Leggett, 2002). By comparing the paralleled effects of the same environmental factors on both demographic structures and life history traits of local populations, we addressed the influence of the interplay between demographic selective forces and habitat richness on optimal life history strategy.

2. Materials and methods

2.1. Study species

The South European Toothcarp *A. fasciatus* is a small euryhaline killifish, inhabiting shallow brackish waters in the central and eastern coastal zones of the Mediterranean Sea. It is an estuarine resident, commonly found in lagoons and other brackish water ecosystems. In the Venice lagoon it is mainly found in salt marsh systems (Franco et al., 2006), where it feeds mainly on small sized benthic invertebrates, algae and diatoms (Leonardos, 2008). Reproductive strategies of *A. fasciatus* show the typical adaptations to the unstable and unpredictable environment of transitional waters, such as batch spawning and early sexual maturation (Leonardos and Sinis, 1998).

2.2. Collection sites

Four sampling stations were chosen within the Venice lagoon (Online Resource 1), differing for both chemico-physical and morpho-structural characteristics.

Alberoni — AL (low predation, low resources): this site, situated in the proximity of Malamocco sea inlet, in the central basin of the lagoon, is a ring-shaped artificial ditch, with an average depth of 1 m. The direct connection with the shipway gives typical marine chemico-physical features to the water. The bottom is permanently covered with a dense mat of green algae (*Ulva* sp. pl.) and a rich and diversified nektonic community is present in this site, with species belonging to different families (Online Resource 2).

Campalto — CA (high predation, high resources): Campalto station is placed in a natural salt marsh systems in the Northern basin of the Venice lagoon. It is a shallow brackish water area, organized in a complex network of small intertidal creeks connected with a wide mudflat. Tide influence is quite strong, determining the drying of the creeks at each tide cycle and forcing the fishes to abandon the most confined area for deeper water in the open lagoon.

Conche — CO (high predation, low resources): as Campalto, this site is located in a wide salt marsh area in the Southern basin of the Venice lagoon, in front of Chioggia sea inlet. As in Campalto, a strong influence of tide cycles characterizes the area.

Vignole — VI (low predation, high resources): samplings were conducted within inland artificial ditches in Vignole island, in the Northern basin of the Venice lagoon. The original connection with the lagoon is almost closed, so a limited water exchange is still present with a negligible tidal influence, while the poor nektonic community (three fish and one decapod species) is in fact isolated from the rest of the lagoon and protected from large piscivorous fish, as in AL.

2.3. Rationale and study design

These four sites were chosen first to reflect variations in the level of the two factors mentioned in the introduction, whose influence on population structure and life history traits was investigated as main goal of the present study. Adult mortality was linked to the percentage of intertidal waters within 1 km range (Table 1) and thus to the tidal regime of the site, which exposes adult toothcarps to piscivorous predators. Habitat trophic richness was expressed as level of organic matter in the sediments, measured performing the loss on ignition method, according to Heiri et al. (2001).