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The influence of habitat structure on energy allocation tactics in an estuarine batch spawner

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ABSTRACT

Trade-off between fecundity and survival was tested in a batch spawner, the Mediterranean killifish *Aphanius fasciatus*, using an integrated modelling-data approach based on previously collected empirical data. Two sites of the lagoon of Venice (Northern Adriatic sea, Italy) were selected in order to compare the energy allocation between growth and reproduction in two contrasting habitats. These were characterised by high and comparable level of richness in basal resources, but showed two different mortality schedules: an open natural salt marsh, exposed to high level of predation, and a confined artificial site protected from piscivorous predation. By means of a bioenergetic Scope for Growth model, developed and calibrated for the specific goals of this work, we compared the average individual life history between the two habitats. The average individual life history is characterised by a higher number of spawning events and lower per-spawning investment in the confined site exposed to lower predation risk, compared to the site connected with the open lagoon. Thus, model predictions suggest that habitat structure with different extrinsic mortality schedules may shape the life history strategy in modulating the pattern of energy allocation. Model application highlights the central role of energy partitioning through batch spawning, in determining the life history strategy. The particular ovary structure of a batch spawner seems therefore to allow the fish to modulate timing and investment of spawning events, shaping the optimal life history in relation to the environmental conditions.

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1. Introduction

Transitional water systems, such as estuaries and coastal lagoons, typically show high degree of heterogeneity, due to the presence of multiple habitat types and the high spatio-temporal variability of environmental conditions (Irlandi and Crawford, 1997). This remarkable level of heterogeneity does not only support a large fish production (Elliott and Hemingway, 2002), but it is also expected to shape the life history strategies of fish populations by influencing many biological interactions, such as foraging behaviours, competition and predation (Irlandi and Crawford, 1997). According to Reznick et al. (2002), the optimal life history strategy is largely shaped by environmental factors that are represented by both extrinsic mortality schedules, related for example to predation, and by intrinsic and energetic habitat constraints. A number of empirical studies suggest especially the primacy of predation pressure in shaping life history strategies in small-sized freshwater fish species, occurring in fragmented populations subjected to different habitat characteristics (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). Similarly, estuarine resident fish, whose isolated populations occur into different habitat types, represent an optimal model to test for the effects of contrasting habitat characteristics on the optimal life history strategy. Within the Mediterranean and Northern American salt-marsh habitats, killifish constitute an excellent candidate for these kind of studies, as they are small-sized, resident fish, occurring in fragmented, shallow water habitats characterised by variable degree of structural complexity, confinement and food richness. Recently, the relationships between habitat structure and life history tactics have been investigated in the Mediterranean killifish *Aphanius fasciatus* (Valenciennes, 1821) (Cavraro et al., 2014a), suggesting that the optimal life history strategy is mainly shaped by food richness and morphological structure of the habitat. In particular, this study

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indicated that a different degree of confinement, by influencing the presence of predator and thus adult mortality, would influence the patterns of energy allocation. The two sites selected to compare the energy allocation tactics were characterised by high and comparable level of richness in basal resources (similar level of organic matter in the sediment), but showed two different mortality schedules: an open natural salt marsh (Campalto, CA) exposed to high level of predation, due to the connection with the open lagoon, and a confined, artificial site (Vignole, VI), composed of a system of small ditches, protected from piscivorous predation (Cavraro et al., 2014a). Despite having similar fish densities, these sites differed strongly in mortality, showing an overall mortality of 57% in CA and 28% in VI (Cavraro et al., 2014a), confirming that the degree of confinement is able to influence the susceptibility of this species to predation. Results showed that fish experiencing higher predation pressure, and thus suffering from higher adult mortality, presented a higher reproductive allotment and a shorter life span (Cavraro et al., 2014a). On the contrary, predation intensity seemed not to influence the age/size at maturity, although this species shows a precocious maturity and differences in the magnitude of days or months were not easy to be detected with scale reading. Furthermore, a major peak in the gonado-somatic index was observed during the spawning season in the site subjected to tidal influence (open, natural salt marsh) while the artificial creek showed a lower reproductive allotment, that was apparently allocated into more different GSI peaks within the breeding season (Cavraro et al., 2014a). According to traditional life history theories (Stearns, 1992; Roff, 1992), higher investment in reproduction should have a negative influence on survival. The energy allocation tactic in the open natural saltmarsh should therefore favour a higher reproductive investment at the expense of survival, decreasing the fitness of older fish, accelerating growth, and reducing the number of spawning events over the life span. By contrast, in the confined habitat, where reproductive allotment is higher, slower growth rate, higher number of spawning events and higher fitness of older individuals should be favoured.

To test for these habitat-dependent differences in energy allocation, a bioenergetic model is here applied, using the previously collected empirical data (Cavraro et al., 2014a). The model, developed and calibrated for the specific goals of this paper, could be a proper tool to assess and compare the energy allocation tactics characterising the average individual life history in the two contrasting habitats. While the previous empirical work showed evidence of differences in reproductive allotment within a single breeding season, the present bioenergetic model should allow calculation of the number of reproductive events, the per-event reproductive investment and the somatic growth rate over the entire life span of the species in the two contrasting habitats.

2. Materials and methods

A standard bioenergetic model formulation (Ursin, 1967) was modified to capture *A. fasciatus* batch spawning dynamics. In accordance with the modelling strategy adopted by Wang and van Cappellen (1996), model parameters were divided in two categories:

i) reaction specific parameters, such as metabolic rates and temperatures, considered independent from the site, and set on the basis of previous studies on the eco-physiology of this species;
ii) parameters governing reproduction, which were considered as 'site-specific', and estimated independently at the two sites where the model was applied. These parameters vary in response to the relative exposure to predation (process occurring externally from the individual). The influence on the metabolism of food availability and water temperature, considered to be other important environmental drivers, was standardized by forcing the model with site-specific values for these parameters.

The present methodological section will first focus on the aspects related to model identification, and therefore provide a detailed description of data and methods used for model application.

2.1. Model theory

The bioenergetic model used in this work is based on a Scope for Growth (SfG) formulation (Winberg, 1956; Paloheimo and Dickie, 1965; Ursin, 1967). The growth of *A. fasciatus* is described in terms of somatic (W), and gonadic (G) tissue wet weight. The rate of change of fish body weight is the difference between the net energy available through feeding, the net anabolism term A, and the energy used for basic metabolic activities, the fasting catabolism term C, converted in mass by ε_W and ε_G (the energy density of, respectively, somatic and gonadic tissues):

$$\begin{cases} \dfrac{dW}{dt} = (1 - k \cdot H_1) \cdot \dfrac{A - C}{\varepsilon_W} \\ \dfrac{dG}{dt} = H_1 \cdot \left[k \cdot \dfrac{A - C}{\varepsilon_G} - H_2 \cdot (1 - k_R) \cdot G \right] \end{cases} \quad (1)$$

The bioenergetic model of *A. fasciatus* considers only the female adult stage, partitioning the typical year in two periods, a reproductive and a non-reproductive one, on the basis of the H_1 function (see Eq. (1.11), Table 1). As suggested by the values of Gonado Somatic Index (*GSI*) reported in Cavraro et al. (2013), the reproductive period lasts for approximately 7 months, from the beginning of February until late August. During this period only part of the energy assimilated, *(1-k)* in Eq. (1), is invested in somatic tissues, and the remaining fraction k is used for gonads development. Spawning happens when the gonads reach a certain degree of maturation, which is measured by a threshold *GSI* value, T_{GSI}. At each spawning event, a batch of mature eggs is released, corresponding to the fraction k_R of the ovary in volume. This is described in the model by means of Eq. (1.11) (see Table 1). Subsequent spawning events are separated by a minimal time of two weeks (Cavraro et al., 2014b).

Both anabolic and catabolic processes are strongly affected by two major environmental forcings: water temperature and food availability. This is accounted in the model by means of $f_a(T)$ and $f_c(T)$ (respectively Eqs. 1.4–1.5, 1.6–1.7 in Table 1). This function varies between 0 and 1, considering the optimal temperature and maximum lethal temperature for *A. fasciatus*, based on a Lassiter and Kearns (1974) formulation. The second forcing function is the availability of food in the environment. This is quantified in the model by *f(F)*, the fraction of available food over a site-specific maximum. In the adopted formulation (see Brigolin et al., 2014a) the anabolism is linearly proportional to the ingested food, through an assimilation efficiency coefficient (see Eq. (1.1)), and I_{max} represents a theoretical maximum ingestion rate when food availability is not a limiting factor. The effective ingestion, I, is estimated by considering that below a minimum temperature, T_{feed}, the fish has no appetite, and ingestion becomes null (see Eq. (1.2)–(1.3)).

If in the reproductive period the net anabolism is lower than the

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