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Title: THE INFLUENCE OF HABITAT STRUCTURE ON ENERGY ALLOCATION TACTICS IN AN ESTUARINE BATCH SPAWNER

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Keywords: iteroparity; semelparity; batch spawning; habitat structure; bioenergetic model; individual based model

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Abstract: We tested the iteroparity-semelparity continuum in a batch spawner, the Mediterranean killifish *Aphanius fasciatus* by means of an integrated modelling-data approach. Two sites of the lagoon of Venice (Northern Adriatic sea, Italy) were selected as a test-case. These were characterised by high and comparable level of richness in basal resources, but showing 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 SFG (Scope for Growth) model, here developed and calibrated for the specific goals of this work, we compared the average individual life history between the two habitats. Results showed that 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 with 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. The application of the SFG model strongly suggests 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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Venezia, 26/05/2015

To the attention of the editorial board,

Dear editor,

please find attached a copy of the ms entitled: "THE INFLUENCE OF HABITAT STRUCTURE ON ENERGY ALLOCATION TACTICS IN AN ESTUARINE BATCH SPAWNER" by Daniele Brigolin, Francesco Cavraro, Veronica Zanatta, Roberto Pastres and Stefano Malavasi.

The enclosed ms is submitted to *Estuarine, Coastal and Shelf Science* for consideration.

The ms is new and has not been previously submitted to other journals. The study adopts an integrated modelling-data approach to test the iteroparity-semelparity continuum in a batch spawner. The work focuses on habitat influence and the role of energy partitioning through batch spawning in determining life history strategies. The Mediterranean killifish *Aphanius fasciatus* was selected as a model species for this study.

We are confident that you can take care of the reviewing process in the best possible way.

Looking forward to hearing from you, I remain.

Sincerely yours,

Daniele Brigolin

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

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5 **Abstract**  
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8 We tested the iteroparity-semelparity continuum in a batch spawner, the Mediterranean  
9 killifish *Aphanius fasciatus* by means of an integrated modelling-data approach. Two  
10 sites of the lagoon of Venice (Northern Adriatic sea, Italy) were selected as a test-case.  
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12 These were characterised by high and comparable level of richness in basal resources,  
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14 but showing two different mortality schedules: an open natural salt marsh, exposed to  
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16 high level of predation, and a confined artificial site protected from piscivorous  
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18 predation. By means of a bioenergetic SFG (Scope for Growth) model, here developed  
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20 and calibrated for the specific goals of this work, we compared the average individual  
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22 life history between the two habitats. Results showed that the average individual life  
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24 history is characterised by a higher number of spawning events and lower per-spawning  
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26 investment in the confined site exposed to lower predation risk, compared with the site  
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28 connected with the open lagoon. Thus, model predictions suggest that habitat structure  
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30 with different extrinsic mortality schedules may shape the life history strategy in  
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32 modulating the pattern of energy allocation. The application of the SFG model strongly  
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34 suggests the central role of energy partitioning through batch spawning, in determining  
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36 the life history strategy. The particular ovary structure of a batch spawner seems  
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38 therefore to allow the fish to modulate timing and investment of spawning events,  
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40 shaping the optimal life history in relation to the environmental conditions.  
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56 **Keywords** iteroparity; semelparity; batch spawning; habitat structure; bioenergetic  
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58 model; individual based model  
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5 **1 Introduction**  
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8 Transitional water systems, such as estuaries and coastal lagoons, typically show high  
9 degree of heterogeneity, due to the presence of multiple habitat types and the high  
10 spatio-temporal variability of environmental conditions (Irlandi and Crawford, 1997).  
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12 This remarkable level of heterogeneity does not only support a great fish production  
13 (Elliott and Hemingway, 2002), but it is also expected to shape the life history strategies  
14 of fish populations by influencing many biological interactions, such as foraging  
15 behaviours, competition, and predation (Irlandi and Crawford, 1997). According to  
16 Reznick et al. (2002), the optimal life history strategy is largely shaped by  
17 environmental factors that are represented by both extrinsic mortality schedules, related  
18 for example to predation, and by intrinsic and energetic habitat constraints. A number of  
19 empirical studies suggest especially the primacy of predation pressure in shaping life  
20 history strategies in small-sized freshwater fish species, occurring in fragmented  
21 populations subjected to different habitat characteristics (Jennions and Telford, 2002;  
22 Johnson and Belk, 2001; Reznick and Endler, 1982; Reznick et al., 2001, 2002; Rodd  
23 and Reznick, 1991; Walsh and Reznick, 2008, 2009, 2010a,b). Similarly, estuarine  
24 resident fish, whose isolated populations occur into different habitat types, represent  
25 therefore an optimal model to test for the effects of contrasting habitat characteristics on  
26 the optimal life history strategy. Within the Mediterranean and Northern American salt-  
27 marsh habitats, killifish constitute an excellent candidate for these kind of studies, as  
28 they are small-sized, resident fish, occurring in fragmented, shallow water habitats  
29 characterised by variable degree of structural complexity, confinement and food  
30 richness. Recently, the relationships between habitat structure and life history tactics  
31 have been investigated in the Mediterranean killifish *Aphanius fasciatus* (Valenciennes,  
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5 1821) (Cavraro et al., 2014a), suggesting that the optimal life history strategy is mainly  
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7 shaped by food richness and morphological structure of the habitat. In particular, this  
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9 study indicated that a different degree of confinement, by influencing the presence of  
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11 predator and thus adult mortality, would influence the patterns of energy allocation.  
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13 Results showed that under comparable levels of food richness, fish experiencing higher  
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15 predation pressure, and thus suffering from higher adult mortality, presented a higher  
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17 reproductive allotment and tended to concentrate the reproductive effort in few  
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19 spawning events along a short spawning season (Cavraro et al., 2014a). On the other  
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21 side, predation intensity seemed not to influence the age/size at maturity. This was  
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23 indicated by a major peak in the gonado-somatic index during the spawning season  
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25 observed in one site subjected to tidal influence (open, natural salt marsh) compared  
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27 with an artificial creeks showing a lower reproductive allotment along a longer period  
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29 (Cavraro et al., 2014a).  
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36 Organisms, both plant and animals, can adopt two main strategies to cope with that, that  
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38 is semelparity (a single reproductive event followed by spawner death) or iteroparity  
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40 (organisms reproduce more than once before dying). Within these two general  
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42 categories, an iteroparity-semelparity continuum may be described, identifying many  
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44 different intermediate situations. According to traditional life history theories, high  
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46 adult mortality, with respect to that experienced during the juvenile phase, would select  
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48 for semelparity, while low adult mortality would select for iteroparity.  
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53 The south european Toothcarp is a quite long-living small teleost (up to 7 years  
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55 recorded life span), characterized by early maturity and batch-spawning, as clearly  
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57 appears from the structure of the ovary (Leonardos and Sinis, 1998; Cavraro et al.,  
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59 2014a). Females usually lay many batches of eggs during the reproductive season,  
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5 probably with a semi-lunar periodicity (Cavraro et al., 2014b). The results found by  
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7 Cavraro et al. (2014a) opened the question whether populations exposed to higher  
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9 predation pressure, leading to a high adult mortality and a shorter life span, respond  
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11 changing their energy allocation schedules towards a higher degree of semelparity, by  
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13 partitioning the reproductive energy into fewer reproductive events with a higher per-  
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15 event investment. Most of the models dealing with this iteroparity-semelparity  
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17 continuum predict that all the demographic changes decreasing adult value, respect to  
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19 juvenile, should favour semelparity (Stearns, 1992, Roff, 1992). This also implies a  
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21 trade-off between fecundity and survival, since the part of energy devoted to  
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23 reproduction is no longer available for survival.  
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29 In this paper, we tested the iteroparity-semelparity continuum in a batch spawner, the  
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31 Mediterranean killifish, applying a bioenergetic model to the *Aphanius fasciatus* life  
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33 history data obtained from Cavraro et al. (2014a). We selected the two sites  
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35 characterised by high and comparable level of richness in basal resources (similar level  
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37 of organic matter in the sediments) but showing two different mortality schedules: an  
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39 open natural salt marsh (Campalto, CA) exposed to high level of predation, due to the  
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41 connection with the open lagoon, and a confined, artificial site (Vignole, VI),  
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43 constituted by a system of small ditches, protected from piscivorous predation (Cavraro  
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45 et al. 2014a). By means of a bioenergetic SFG (Scope for Growth) model, here  
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47 developed and calibrated for the specific goals of this paper, we compared the average  
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49 individual life history between the two habitats, modelled on the basis of the empirical  
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51 data obtained from Cavraro et al. (2014a).  
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57 Our main test hypothesis was that higher predation exposure should lead to an energy  
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59 allocation tactic closer to the semelparous extreme of a semelparity-iteroparity  
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5 continuum, that is characterised by lower number of reproductive events with higher  
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7 per-event investment over the life span.  
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## 10 11 12 **2 Material & Methods**

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15 A standard bioenergetic model formulation (Ursin, 1967) was modified to capture *A.*  
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17 *fasciatus* batch spawning dynamics. In accordance with the modelling strategy adopted  
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19 by Wang and Van Cappellen (1996), model parameters are divided in two categories:  
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24 i) reaction specific parameters, such as metabolic rates and temperatures, considered  
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26 independent from the site, and set on the basis of previous studies on the eco-  
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28 physiology of this species;  
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32 ii) parameters governing reproduction, which were considered as "site-specific", and  
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34 estimated independently at the two sites in which the model was applied. These  
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36 parameters vary in response to the relative exposure to predation (process occurring  
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38 externally from the metabolism of the individual). The influence on the metabolism of  
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40 food availability and water temperature, considered to be other important environmental  
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42 drivers, was standardized, by forcing the model with site-specific values for these  
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44 parameters.  
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49 The present methodological section will first focus on the aspects related to model  
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51 identification and therefore provide a detailed description of data and methods used for  
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53 model application.  
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## 2.1 Model theory

The bioenergetic model used in this work is based on a Scope for Growth formulation (Winberg, 1960; Paloheimo & Dickie, 1965; Ursin, 1967). The growth of *A. fasciatus* is described in terms of somatic (W), and gonadic (G) tissues wet weight. The rate of change of fish body weight is the difference among 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  $\varepsilon_W$  and  $\varepsilon_G$  (the energy density of, respectively, somatic and gonadic tissues):

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

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 less than the fasting catabolism, meaning that we are in a critical situation, the energy is only used for growth. In the winter period energy is used only for maintenance and growth. Total length ( $L$ ) is estimated as a diagnostic state variable, based on a species-specific allometry (Eq. 1.10).

**Table 1: Functional expressions used in the *Aphanius fasciatus* bioenergetic model.**

| Functional expression:   |         |
|--|---------|
| $A = (1 - \alpha) AE I$  | ( 1.1 ) |
| $\begin{cases} I = f_{food} I_{max} W^m f_a(T) & , T > T_{feed} \\ I = 0 & , T \leq T_{feed} \end{cases}$  | ( 1.2 ) |
| $\begin{cases} f_a(T) = \left( \frac{T_{max_A} - T}{T_{max_A} - T_{opt_A}} \right)^{b_{A(T-T_{opt_A})}} e^{b_{A(T-T_{opt_A})}} & , T > T_{feed} \\ f_a(T) = 0 & , T \leq T_{feed} \end{cases}$ | ( 1.3 ) |
| $\begin{cases} f_a(T) = \left( \frac{T_{max_A} - T}{T_{max_A} - T_{opt_A}} \right)^{b_{A(T-T_{opt_A})}} e^{b_{A(T-T_{opt_A})}} & , T > T_{feed} \\ f_a(T) = 0 & , T \leq T_{feed} \end{cases}$ | ( 1.4 ) |
| $\begin{cases} f_a(T) = \left( \frac{T_{max_A} - T}{T_{max_A} - T_{opt_A}} \right)^{b_{A(T-T_{opt_A})}} e^{b_{A(T-T_{opt_A})}} & , T > T_{feed} \\ f_a(T) = 0 & , T \leq T_{feed} \end{cases}$ | ( 1.5 ) |

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|---|
| $C = \varepsilon_{O_2} k_{max} f_c(T) W^n \quad (1.6)$  |
| $\begin{cases} f_c(T) = \left( \frac{T_{max_C} - T}{T_{max_C} - T_{opt_C}} \right)^{b_C(T - T_{opt_C})} e^{b_C(T - T_{opt_C})}, T > T_{feed} \\ f_c(T) = 0, \quad , T \leq T_{feed} \end{cases} \quad \begin{matrix} (1.7) \\ (1.8) \end{matrix}$   |
| <p>Output Variables:</p>  |
| $W = G + w \quad (1.9)$   |
| $L = a l (w + G)^{bl} \quad (1.10)$   |
| $H_1(t) = \begin{cases} 0 & , t < t_{ri} \vee t > t_{Rf} \\ 1 & , t_{ri} \leq t \leq t_{Rf} \end{cases} \quad (1.11)$   |
| $H_2(t) = \begin{cases} 0 & , (t - t') < t_L \vee GSI < T_{GSI} \\ 1 & , (t - t') \geq t_L \wedge GSI \geq T_{GSI} \end{cases} \quad (1.12)$  |
| <p>t: time [days]<br/>t': time at which the last spawning event occurred [days]</p> <p><i>Prognostic state variables:</i></p> <p>W: wet somatic weight of A. fasciatus [g]<br/>G: wet gonadic weight of A. fasciatus [g]</p> <p><i>Diagnostic state variables:</i></p> <p>W: Total weight of A. fasciatus (gonads + Somatic weight) [g]<br/>L: length of A. fasciatus[mm]</p> <p><i>Forcing:</i></p> <p>T: Water temperature [ °C]<br/>f<sub>food</sub>: organic fraction in the sediment [-]</p> |

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5 *Rate and processes:*

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7 A: net Anabolism [ $\text{J d}^{-1}$ ]

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9 C: Fasting Catabolism [ $\text{J d}^{-1}$ ]

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12 *Parameters:*

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14 AE: Assimilation Efficiency [-]

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16  $T_{\text{feed}}$ : Lowest feeding temperature [ $^{\circ}\text{C}$ ]

17  
18  $T_{\text{max}_A}$ : maximum lethal temperature for the anabolic process [ $^{\circ}\text{C}$ ]

19  
20  $T_{\text{opt}_A}$ : optimal temperature for the anabolic process [ $^{\circ}\text{C}$ ]

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22  $b_A$ : shape coefficient for temperature function for the anabolic process ( $f_a(T)$ ) [-]

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24  $I_{\text{max}}$ : maximum ingestion rate [ $\text{J g}^{-\text{m}} \text{d}^{-1}$ ]

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26 m: weight exponent for net anabolism [-]

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28  $\alpha$ : feeding catabolism coefficient [-]

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30  $T_{\text{max}_C}$ : maximum lethal temperature for the catabolic process [ $^{\circ}\text{C}$ ]

31  
32  $T_{\text{opt}_C}$ : optimal temperature for the catabolic process [ $^{\circ}\text{C}$ ]

33  
34  $b_C$ : shape coefficient for temperature function for the catabolic process ( $f_c(T)$ ) [-]

35  
36  $k_{\text{max}}$ : fasting catabolism at  $0^{\circ}\text{C}$  [ $\text{d}^{-1} \text{g}^{-\text{n}}$ ]

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38  $\epsilon_{O_2}$ : energy consumed by the respiration of 1 g of oxygen [ $\text{kJ g}^{-1}$ ]

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40 n: weight exponent for the catabolism [-]

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42 K: reproduction investment energy fraction [%]

43  
44  $\epsilon_W$ : energy content of somatic tissue [ $\text{kJ g}^{-1}$ ]

45  
46  $\epsilon_G$ : energy content of gonadic tissue [ $\text{kJ g}^{-1}$ ]

47  
48 a: Coefficient for weight – length conversion [-]

49  
50 b: Exponent for weight – length conversion [-]

51  
52  $t_{Ri}$ : Start of reproductive period (1<sup>ST</sup> February) [day]

53  
54  $t_{Rf}$ : End of reproductive period (31<sup>TH</sup> August) [day]

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56  $t'$ : day of last spawning [day]

57  
58  $t_L$ : minimum spawning time-step (15 days) [day]

T<sub>GSI</sub>: Upper threshold for GSI [day]

Model parameters, along with their units, references and values are reported in Table 2: values for 20 over 23 parameters were set based on eco-physiological studies carried out on killifishes. These first 20 are referred in Table 2 as "general parameters", opposed to the 3 "site-specific parameters", for which different values are selected at each site of model application. Since the studies on *A. fasciatus* did not allow to cover all the aspects required by model parameterization, we consulted the literature for other killifish species having comparable biological, physiological and life history traits, which were namely: *Aphanius dispar*, *Fundulus heteroclitus*, *Fundulus notatus* and *Fundulus parvipinnis*. Minimum, optimal and maximum feeding and respiration temperatures were set by comparing the indications by different studies: were sources did not agree different values were averaged.  $k_{\max}$  and  $\beta$  were estimated based on a non-linear regression on experimental oxygen consumption data (Skadhauge & Lotan, 1974). AE and  $\alpha$  were estimated from experimental tests carried out on *F. heteroclitus* (Weisberg & Victor A, 1982; Stewart, 1972). The energy density of somatic and gonadic tissues of a female specimen was estimated by averaging the results of 3 different studies (Stewart, 1972; Nixon et al., 1976; Madon et al., 2001). Based on the different studies consulted, the maximum ingestion rate,  $I_{\max}$ , resulted to be highly variable, ranging between 334 and 2627.5 J days<sup>-1</sup> g<sup>-m</sup>, most probably as a result of variable experimental conditions, and particularly of diet composition: a value of 1084.5 J days<sup>-1</sup> g<sup>-m</sup> (Weisberg and Victor, 1982) was considered to be the most representative of the diet composition typical of the lagoon of Venice. Parameters  $a_L$  and  $b_L$ , defining the weight-length allometry were estimated by performing a linear regression on log-

transformed data (Cavraró, 2012).  $\epsilon_{O_2}$  is the energy consumed by the respiration of 1 g of oxygen ( $\text{kJ g}^{-1}$ ),  $k_{\text{max}}$  is the respiration rate at  $0^\circ\text{C}$  ( $\text{mg O}_2 \text{ g WW}^{-1} \text{ day}^{-1}$ ).  $k_{\text{max}}$  was obtained by linearly interpolating log transformed data of basal respiration rates at different temperatures (Skadhauge and Lotan, 1974).

**Table 2. Parameters used in the *Aphanius fasciatus* bioenergetic model and their sources.**

| General parameters                              | Description        | Value  | Unit                                      | Source   |
|---|--------------------|--------|---|--|
| Assimilation efficiency                         | AE                 | 0.81   | -   | (Stewart, 1972; Weisberg & Victor A, 1982)                                 |
| Lowest feeding temperature                      | $T_{\text{feed}}$  | 5      | $^\circ\text{C}$                          | (Leonardos, 2008),(Rinaldi A., 2014),(Cavraró F., 2014; Cavraró F. , 2013) |
| Optimal temperature for the anabolic process    | $T_{\text{opt}_a}$ | 25.1   | $^\circ\text{C}$                          | (Leonardos, 2008),(Rinaldi A., 2014),(Cavraró F., 2014; Cavraró F. , 2013) |
| Maximum lethal temperature for anabolic process | $T_{\text{max}_A}$ | 39     | $^\circ\text{C}$                          | (Leonardos, 2008),(Rinaldi A., 2014),(Cavraró F., 2014; Cavraró F. , 2013) |
| Shape coefficient for $f_a$ and $f_c$           | b                  | 0.238  | -   | (Kidder et al., 2006), (Skadhauge & Lotan, 1974)                           |
| Weight exponent for anabolism                   | m                  | 2/3    | -   | (Ursin, 1967)  |
| Maximum ingestion rate                          | $I_{\text{max}}$   | 1084.5 | $\text{J g}^{-\text{m}} \text{ day}^{-1}$ | (Weisberg & Victor A, 1982)  |
| Feeding catabolism coefficient                  | $\alpha$           | 0.86   | -   | (Stewart, 1972)  |
| Optimal temperature for the catabolic process   | $T_{\text{opt}_c}$ | 25.1   | $^\circ\text{C}$                          | (Leonardos, 2008),(Rinaldi A., 2014),(Cavraró F., 2014; Cavraró F. , 2013) |

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|---|-----------------|---|-------------------|---|
| Maximum lethal temperature for catabolic process    | $T_{max\_C}$    | 39  | °C                | (Leonardos, 2008),(Rinaldi A., 2014),(Cavraro F., 2014; Cavraro F. , 2013)                      |
| Fasting catabolism at 0°C                           | $k_{max}$       | 1.79  | $g^{-n} day^{-1}$ | (Skadhauge & Lotan, 1974)   |
| Energy consumed by the respiration of 1 g of oxygen | $\epsilon_{O2}$ | 13.6  | $kJ g^{-1}$       | (Brafield AE, 1972)   |
| Weight exponent for catabolism                      | $n$             | 0.7   | -                 | (Fonds, 1973)   |
| Energy content of somatic tissue                    | $\epsilon_W$    | 4680  | $J g^{-1}$        | (Nixon & Oviatt, 1973; Stewart, 1972)   |
| Energy content of gonadic tissue                    | $\epsilon_G$    | 6284  | $J g^{-1}$        | (Nixon & Oviatt, 1973; Stewart, 1972)   |
| Coefficient for weight – length conversion          | $a_L$           | 39.6  | -                 | Linear regression on the whole set of data collected by Cavraro et al. (2014a) (see Appendix A) |
| Exponent for weight – length conversion             | $b_L$           | 0.29  | -                 | Linear regression on the whole set of data collected by Cavraro et al. (2014a) (see Appendix A) |
| Start of reproductive period                        | $t_{Ri}$        | February 1  | [day]             |   |
| End of reproductive period                          | $t_{Rf}$        | August 31   | [day]             |   |
| Minimum time between subsequent spawning events     | $t_L$           | 15  | [day]             |   |
| <b>Site-specific parameters</b>                     |                 |   |                   |   |
| Reproduction energy investment fraction             | $k$             | CA<br>( $\mu=0.42$ ;<br>$\sigma=0.1009$ )<br><br>VI ( $\mu=0.44$ ;<br>$\sigma=0.0715$ ) | -                 | Values were calibrated within the 0.2-0.6 range   |
| Batch spawning factor                               | $k_R$           | CA=0.21<br><br>VI=0.31  | -                 | Site-specific field data  |
| Upper threshold for GSI                             | $T_{GSI}$       | CA=16.18  | -                 | Site-specific field data  |

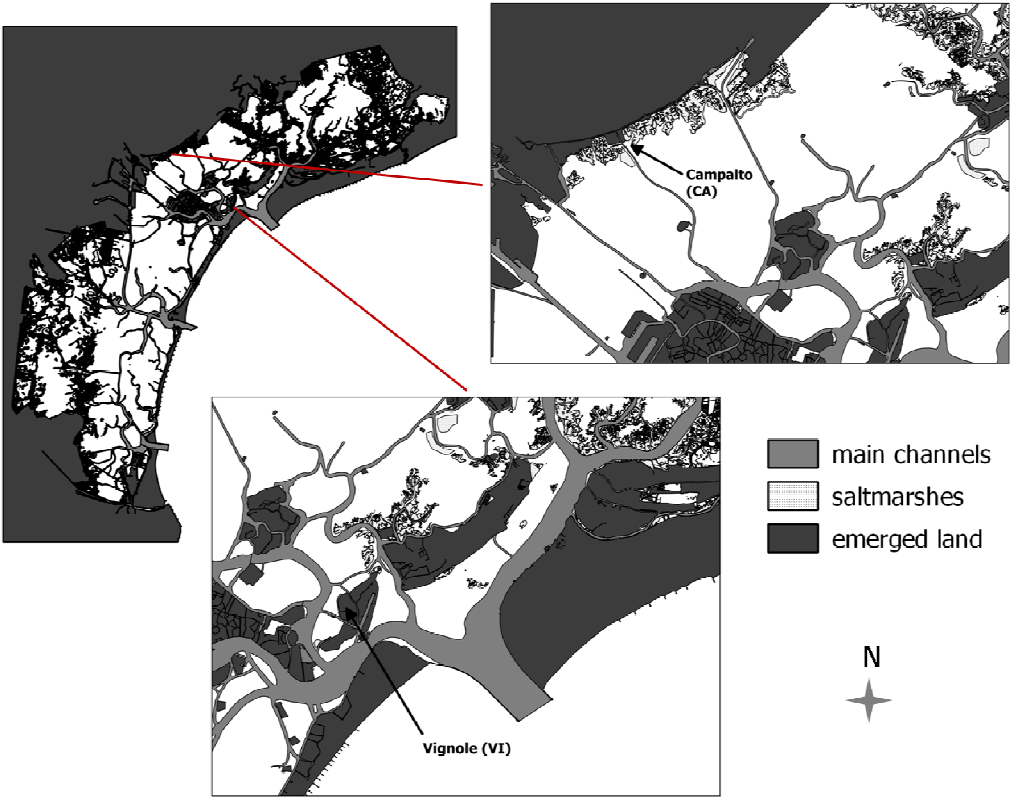


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| VI=10.60 | 90%le |
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2.2 Model application: study site and field data description

As outlined in the Introduction section, two sites characterized by a comparable level of richness in basal resources (organic matter in the sediments), similar fish density, but different level of adult mortality (due to the different degree of tidal influence and connectivity with the open lagoon) were selected: Campalto (CA) and Vignole (VI) (see Fig. 1). A summary of the main characteristics of the two sites in terms of location, habitat morphology and life history traits of the two inhabiting fish populations are given in Appendix A1.



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5 **Figure 1. Location of the two sites studied in this work, Campalto (CA) and**  
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7 **Vignole (VI), within the lagoon of Venice.**  
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11 Observed data used in model calibration are the total wet weight (W), gonads weight  
12 (G) and body length (L) collected in CA and VI in 2010 (Cavraro et al., 2014). Only  
13 data regarding mature female specimens were considered, selecting specimens  $\geq 1$  years  
14 old (Leonardos and Sinis, 1998; Cavraro et al., 2014a). For *A. fasciatus* the best  
15 reproductive period is between April and July (Leonardos & Sinis, 1998), although  
16 values of GSI observed in the Venice lagoon increase since February, and until the end  
17 of August (Cavraro, 2010): the reproductive period was therefore set between February  
18 1<sup>st</sup> and August 31<sup>st</sup>. The absolute age in days was determined as follows: i) the age in  
19 years was first estimated by reading annulus in scales (Leonardos and Sinis, 1999); ii)  
20 birthday was arbitrarily set on May 15<sup>th</sup>, central date of the reproductive period; ii) the  
21 period between the end of the last year and the sampling date was added to the total age  
22 of the individual. Data concerning specimens having the same age were thus  
23 aggregated, and mean and standard deviation of the distributions calculated. For single  
24 values, a synthetic value of the standard deviation was calculated from the coefficient of  
25 variation (standard deviation/mean) of the entire time series. In this way four time series  
26 were obtained at each station (CA-VI), for W, G, L and GSI (G/W).  
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48 Water temperature was recorded monthly during sampling in 2010: daily water  
49 temperature used to force the model was estimated by linearly interpolating the time  
50 series of data at each site. According to Leonardos (2008) *A. fasciatus* feeds mostly on  
51 the benthic compartment (microbenthivorous/ detritus feeder). Based on this, the  
52 percentage of organic matter in the upper 15-20 cm of sediment was used to quantify  
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5 the relative level of food availability at each site ( $f_{\text{food}}$ ). Details on the construction of  
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7 model forcing functions are reported in Appendix A2.  
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10 Three of the parameters involved in the reproduction were considered to be site-  
11 specific, these were  $T_{\text{GSI}}$ ,  $k_{\text{R}}$ , and  $k$ .  $T_{\text{GSI}}$  was quantified on the basis of the maximum  
12 GSI value observed at each site. The  $k_{\text{R}}$  parameter, defining the fraction of an ovary  
13 invested in a single batch, was quantified independently at each site, by analyzing in  
14 laboratory a sample of 120 and 141 individuals, respectively for CA and VI. On a  
15 fraction corresponding approximately to 1/3 of ovary, the cumulative volume of mature  
16 eggs was assessed by assuming that mature eggs to have a diameter  $\geq 0.25$  mm (Kneib  
17 & Stiven, 1978). This cumulative volume was therefore divided by the total volume of  
18 gonads. The  $k$  parameter was calibrated, by fitting the model to the observed data of  $W$   
19 and  $G$ .  
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### 37 *2.3 Simulation set-up and calibration procedure*

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40 At each site, two types of simulations were carried out:

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42 a) repeated runs, based on a Monte-Carlo approach, for model calibration;  
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44 b) single runs, using nominal and test values of the parameters. These latter runs were  
45 aimed at exploring the behavior of batch-spawning dynamics in different conditions,  
46 and carried out by systematically checking  $W$  and  $G$  trajectories under all possible  
47 combinations of minimum and maximum values for  $k$ ,  $k_{\text{R}}$  and  $T_{\text{IGS}}$ .  
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54 Within step a), a single model parameter was calibrated at each site:  $k$ . Uncertainty on  
55 this parameter reflects the variability in phenotypes of individuals within a population,  
56 and were estimated by considering the dispersion of  $W$  and  $G$  data around their average  
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values. A bootstrapping technique (Shao and Tu, 1995) was used, by carrying out a set of 5000 independent runs. The number was set based on an exploratory analysis of model results, carried out on the basis of the same methodology adopted in Brigolin et al. (2014). Each run was carried out as follows: i) a synthetic time-series of observations was generated by randomly extracting the value of each state variable, W and G, from the pdf available at each time ( $t_i$ ) in which observations were carried out; ii) values of k minimizing the distance between model predictions and field data were searched between the 0.2-0.6 interval set on the basis of the literature analysis (see Table 2). A weighted cost function was applied:

$$\Gamma = \sum \frac{(\widehat{W}_i - W_i)^2}{\sigma_{W_i}^2} + \sum \frac{(\widehat{G}_i - G_i)^2}{\sigma_{G_i}^2} \quad (2)$$

where  $\widehat{W}_i$  and  $\widehat{G}_i$  represent predicted values at the time  $t_i$ , at which synthetic observations  $W_i$  and  $G_i$  were available;  $\sigma_{W_i}^2$  and  $\sigma_{G_i}^2$  are the respective variances of W and G at time  $t_i$ ; iii) the pdf of k was reconstructed from the set of 5000 calibrations and statistics regarding the distribution were calculated. The model was coded in MATLAB<sup>TL</sup>. A 4<sup>th</sup> order Runge-Kutta scheme was used to integrate the system of ordinary differential equations and the MATLAB<sup>TL</sup> function "fminbnd" was used to search the minimum of the goal function. The model simulation starts from the maturity age, set up at 365 days for both sites.

### 3 Result

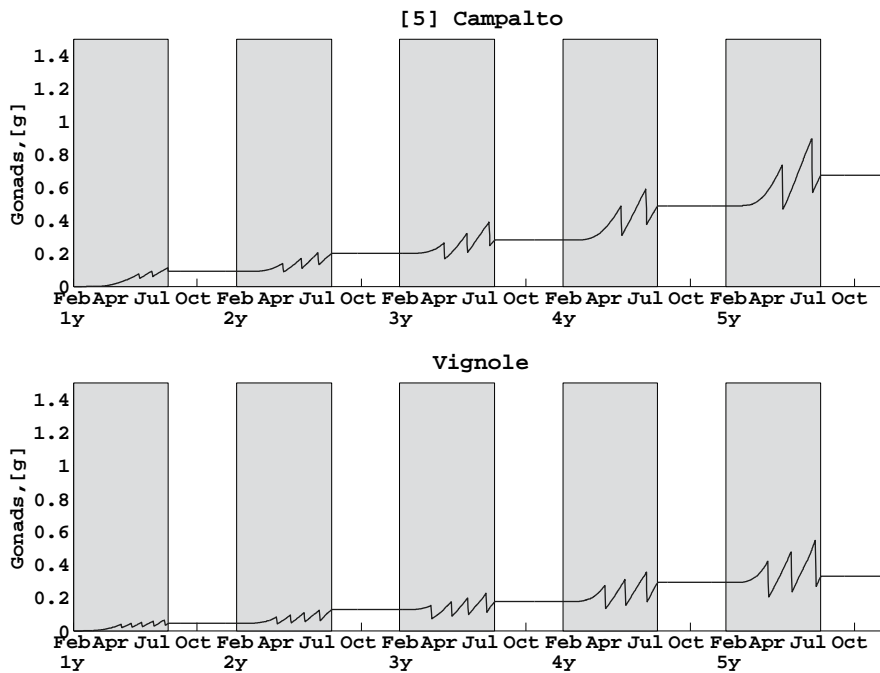
#### 3.1 Comparing the average individual life histories between the two sites

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5 The results of the calibration of the k parameter are presented in detail in Appendix B.  
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7 Figure 2 and Table 3 show a comparison among two single model runs, which were  
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9 performed with average values of calibrated k (i.e. 0.42 in CA and 0.44 in VI). Two  
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11 different dynamics of G can be observed:  
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15 i) in CA characterized by at maximum 3 important events per year (years IV and V have  
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17 only 2 events), and spawning concentrated in the last part of the reproductive time  
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19 window (marked in gray in the figures);  
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23 ii) in VI an higher number of spawning events occurs (up to 5), and are more  
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25 systematically distributed all along the reproductive time window.  
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28 Rate of energy allocation in gonads is slightly higher in VI (see Table 3), were more  
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30 events occur during the life span. At this site, both average and maximum GSI are lower  
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32 compared to CA. The relative size (fraction of eggs released over the entire ovary) of  
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34 the batch is higher at VI, but the average energy loss per spawning (absolute value) is  
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36 lower at this site compared to CA. This is related to the lower size of the gonads at VI  
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38 (again, see the mean GSI), which is ultimately governed by an higher number of  
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40 spawning events per season. The cumulative energy loss in spawning during life is  
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42 higher at VI, and this reflects on a lower performance in terms of weight reached at this  
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44 site, compared to CA.  
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**Figure 2. Model results: G trajectories showing the spawning dynamics at the two sites. Results were produced by performing a single model run, with k corresponding to the mean value estimated from calibration at each site.**

**Table 3. Model results, synthesis of life history characteristics in the two sites.**

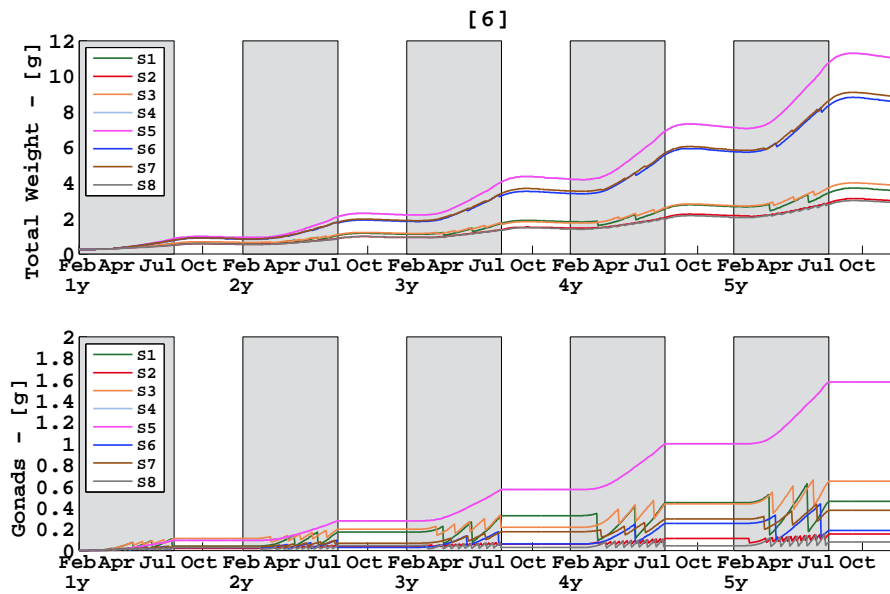
|   | Source       | VI   | CA    |
|---|--------------|------|-------|
| Rate of energy allocation in gonads (fraction of the total energy available instantaneously) ( $k$ parameter [-]) | Model output | 0.44 | 0.42  |
| Tot. n° of spawning events [-]  | Model output | 20   | 12    |
| Upper threshold for GSI ( $T_{GSI}$ parameter [-])  | Field data   | 10.6 | 16.18 |
| Mean GSI during reproductive periods [-]  | Model output | 7.6  | 12.3  |
| Batch size (as a fraction of the ovary) ( $k_R$ parameter [-])  | Field data   | 0.31 | 0.21  |

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|---|--------------|-------|-------|
| Avg. energy loss per spawning event [joule]     | Model output | 648.6 | 793.8 |
| Cumulative energy loss in spawning [joule]      | Model output | 12972 | 9525  |
| Weight achieved at the 6 <sup>th</sup> year [g] | Model output | 5.22  | 5.63  |

### 3.2 Scenario analysis

Spawning dynamics was further studied at VI: figure 3 shows the results of the scenario analysis (parameter values used in the different scenarios are reported in table B1, Appendix B). Results indicate that the batch-spawning dynamics predicted by the model responds to variations in the values of  $k$ ,  $k_R$  and  $T_{IGS}$ , (these 3 parameters, governing reproduction dynamics in the model, and which were considered to be site-specific). Remarkable changes are visible in the overall growth performance (e.g.  $S_5$  vs  $S_2$ - $S_8$ ), as well as in the dynamics of batch-spawning. Interestingly, a simple combination of minimal and maximal values of the three parameters produced a variety of dynamics ranging from the non-reproduction ( $S_5$ ) to the single-batch spawn ( $S_6$  at year IV) and different degrees of multiple-batch release (e.g.  $S_3$  to  $S_8$ ).



**Figure 3. Scenarios: W and G trajectories at VI (Vignole) under different values of the parameters  $k$ ,  $k_R$  and  $T_{IGS}$  (parameter values are provided in Table B1, appendix B).**

#### 4 Discussion

The average individual life history strategy of *Aphanius fasciatus*, as resulting from the application of a SFG model to the empirical data obtained by Cavraro et al. (2014a) in the two contrasting habitats of CA and VI, revealed that fish in VI invest slightly more energy in reproduction than in somatic growth over the entire life span. In this site, fish allocate the reproductive energy into more spawning events (20 vs 12), being the investment for single spawning event smaller in comparison with that observed in CA. On the other side, in CA fish showed a higher reproductive investment and a smaller number of spawning events during the spawning season, with a slightly lower total



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5 reproductive investment counterbalanced by a higher somatic growth rate. From a  
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7 demographic point of view, the main difference between the populations from the two  
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9 sites is the higher adult mortality in CA, likely due to the exposure to piscivorous  
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11 predation, in turn related to a strong connection of this habitat with lagoon deeper  
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13 waters. This difference in adult mortality can explain the differences between the two  
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15 life history strategies, in the light of a trade-off between reproductive effort and  
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17 survival, in line with some theoretical models and empirical evidence (Stearns, 1992).  
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19 In a habitat type such that of CA, the higher mortality rate reduces the fitness value of  
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21 older fish, respect to that of younger specimens. According to these theories, in such  
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23 conditions a tendency toward semelparity would evolve. In fact, the model developed in  
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25 the present study indicates a higher somatic growth rate and a higher investment in each  
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27 spawning event in this site. According with Cole (1954), semelparity is the life history  
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29 strategy involving only a single reproductive event, followed by death, whereas  
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31 iteroparity implies a higher number of reproductive events during life-span. In fish, a  
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33 continuum between semelparity and iteroparity could be observed in some families,  
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35 such as gobies (Wootton 1990). Despite the empirical data did not show any significant  
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37 difference in the age/size at maturity between the two sites, both these observations  
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39 suggest a tendency, for fish inhabiting CA site, to attain more rapidly the maturity size.  
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41 On the contrary, the population in VI, characterized by a lower growth rate and a higher  
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43 life expectancy, would delay maturity, shifting in the direction of iteroparity, with an  
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45 extended reproductive period and a lower amount of energy allotted to each spawning  
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47 event. Iteroparity can be termed abbreviate and protracted, with abbreviate iteropares  
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49 displaying a long breeding season with several spawning events and a relatively short  
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51 life cycle. This is made possible by the ovary structure of repeated spawners, where  
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5 different groups of oocytes can reach maturity at different time intervals (Wootton  
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7 1990). *Aphanius fasciatus* is a typical batch spawner, with ovaries containing immature  
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9 and hydrated oocytes together (Leonardos and Sinis, 1998). Despite a not extremely  
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11 short life cycle, since a maximum age of seven years has been recorded (Cavraro et al.,  
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13 2014a), within this framework this species seems to adopt the abbreviate iteroparous  
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15 strategy, considering both the extended reproductive period, up to six months, and the  
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17 early sexual maturity, with well developed gonads in specimens less than one year old  
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19 (Leonardos and Sinis, 1998; Cavraro et al., 2014a).  
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24 The test-case presented in the scenario analysis allowed to virtually explore the  
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26 iteroparity-semelparity continuum (Figure 3). Although this was done by considering  
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28 only 8 possible combinations for the site-specific parameters  $k$ ,  $T_{GSI}$  and  $k_R$ , meaningful  
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30 differences were predicted in terms of somatic growth performance (higher S1-S4, and  
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32 S8 weights at the end of the 5<sup>th</sup> year), and number of spawning events (lower for S6 and  
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34 S7; no-spawning for S5). S1 and S3 represent a sort of intermediate situation, closer to  
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36 the real examples of CA and VI, in which a high fraction of the energy available is  
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38 invested in reproduction, but this occurs when ovaries have an higher degree of  
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40 maturation. This test case was provided as a "proof of concept" on the possible use of  
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42 the model to explore systematically the influence of environmental factors on the  
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44 dynamics of batch spawning.  
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50 Our results show that habitat structure with different extrinsic mortality schedules may  
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52 shape the life history strategy in modulating the pattern of energy allocation through a  
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54 different way of energy partitioning within the ovary, determining a different number of  
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56 spawning events and a different intensity of per-event investment, at the expense of  
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58 somatic investment. Interestingly, the total fecundity in VI is larger than in CA, but this  
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5 appears to be the combined effect of a different energy partitioning over the life span,  
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7 that is higher degree of iteroparity, and a lower somatic growth rate. Other factors,  
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9 besides the differential extrinsic adult mortality schedules, cannot be ruled out in  
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11 explaining the different life history trajectories observed in the two sites. For example,  
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13 differential pattern and intensity of predation on the juvenile phase between the two  
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15 sites: the artificial creeks of VI lack of shallow water pools that represent an elective  
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17 habitat for juvenile *A. fasciatus* during the first months of life (Cavraro et al., 2014b).  
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19 Thus young fish would experience higher mortality rates than in natural salt marshes.  
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21 Also the resource available to each individual may vary between the two sites, due to  
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23 slight differences in fish density and food richness (Cavraro et al. 2014a). Together with  
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25 mortality rates, these factors could play a role in shaping the different life history tactics  
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27 observed. However, the application of the SFG model strongly suggests the central role  
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29 of energy partitioning through batch spawning, in determining the life history strategy.  
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31 The particular ovary structure of a batch spawner seems therefore to allow the fish to  
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33 modulate timing and investment of spawning events, shaping the optimal life history in  
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35 relation to the environmental conditions.  
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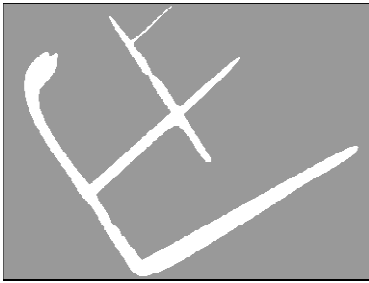
## Appendix A

### A1 - Study sites description: Campalto (CA) and Vignole (VI)



#### Campalto - CA

The salt marsh comprise a network of small intertidal creeks connected with a mudflat. It is an open system, where predator fish can access to the creeks during high tide. Furthermore, the drying of the creeks at each tide cycle forces toothcarps to move into deeper water.

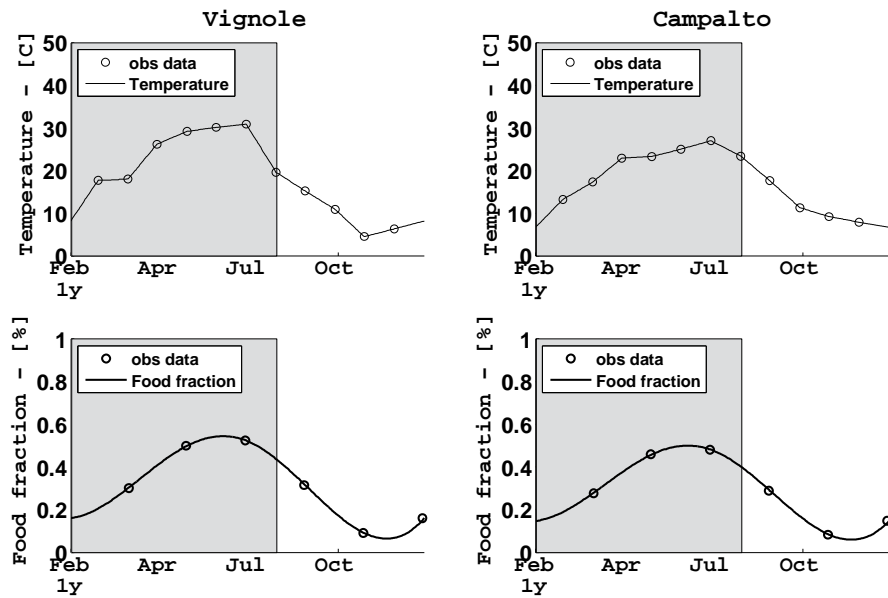


#### Vignole - VI

It is a close system of artificial creeks within a lagoon island once used for fish farming. No predator fish are present, and the fish community is composed by only three species, with *A. fasciatus* being the most abundant.

| Site     | Mortality (%) | Density (ind 100 m <sup>-2</sup> ) | Mean size (mm) | Mean age (year) | Fecundity (n. eggs g <sup>-1</sup> eviscerated weight) |
|----------|---------------|------------------------------------|----------------|-----------------|--|
| Campalto | 57 ± 0.02     | 81.3 ± 64.6                        | 31.26 ± 0.87   | 1.7±0.15        | 820.95±38.52   |
| Vignole  | 28 ± 0.01     | 103.0 ± 29.3                       | 38.86 ± 1.22   | 2.6±0.18        | 417.10±22.59   |

### A2 - construction of model forcing functions



**Figure A2. Water temperature and food fraction dynamic used in the model for Vignole and Campalto sites.**

Food availability is expressed in the model as a fraction of food over a theoretical maximum. Model forcing was constructed by calculating the ratio between the value of organic matter measured at each site (CA and VI) and the highest value of organic matter found in site-specific studies for the Venice Lagoon (i.e. 20%; Consorzio Venezia Nuova, 2003). Seasonal variability was reconstructed starting from a time-series analysis of mesozobenthos abundances, recorded at 6 different stations of the Venice lagoon (Consorzio Venezia Nuova, 2005). This diet was reconstructed on the basis of *A. fasciatus* stomacal contents analyses (Leonardos, 2008) and of a food web model of the three main habitats of the lagoon of Venice (Brigolin et al., 2014b).

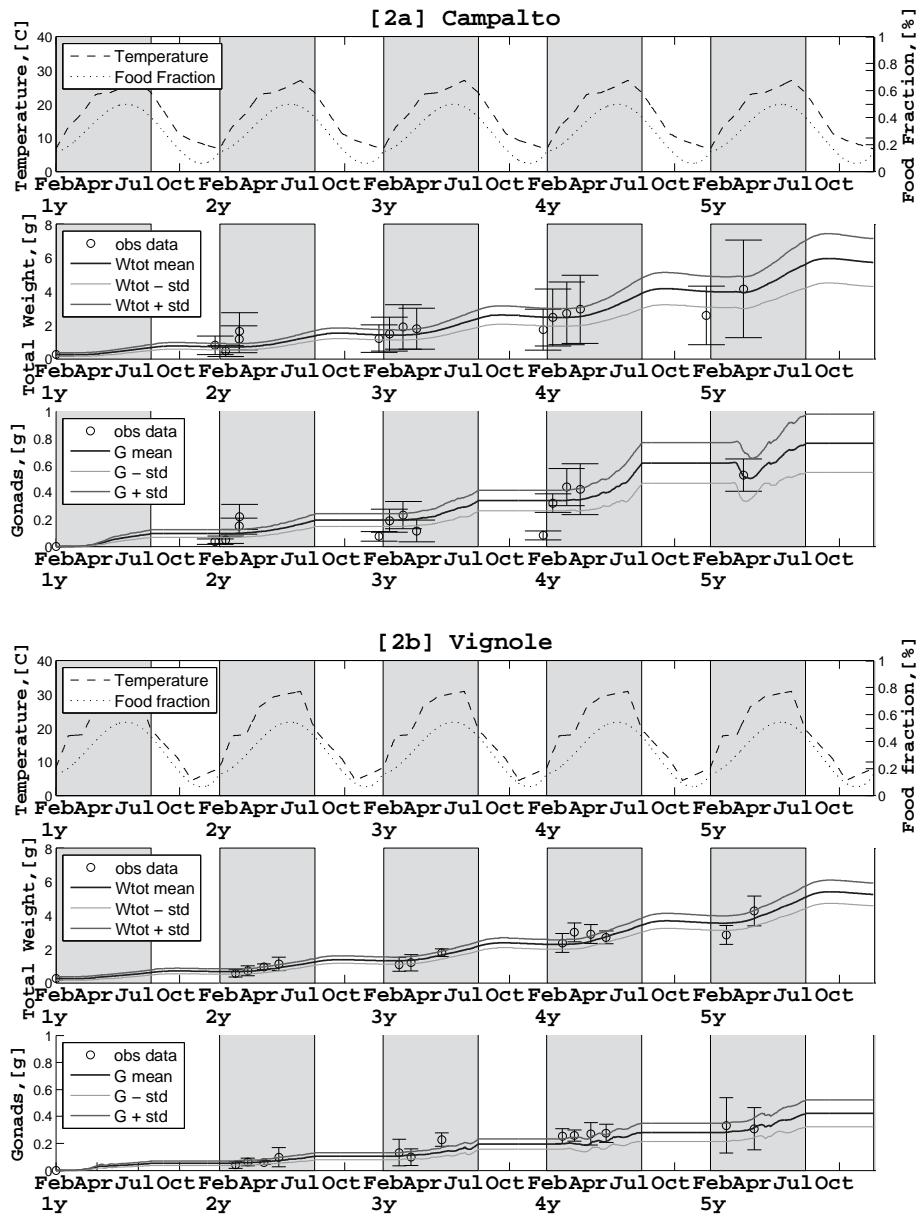
## Appendix B

### *B1. Model calibration results*

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5 The results of the calibration of the  $k$  parameter are presented in Figs. B1 and B2.  
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7 Model trajectories of the mean total and gonads weights,  $W$  and  $G$ , along with their  
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9 standard deviations, are compared with the samples means and standard deviations in  
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11 Campalto (Figs. B1a) and Vignole (Figs. B1b). As one can see, the model fits both the  
12  
13 average observed growth and its variance. A notable exception is the gonads weight in  
14  
15 Campalto at the beginning of the III and IV years: in these cases the calibrated model  
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17 overestimates the observed data. A higher variability is predicted around the average  
18  
19 values in Campalto with respect to Vignole, indicating that the algorithm used in  
20  
21 calibration for quantifying parameters uncertainty is correctly responding to the  
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23 differences in the variability of the observed data. Fish growth decreases during winter,  
24  
25 as a result of the lower water temperatures (see dashed lines in Fig. B1a,b), and stops in  
26  
27 VI between November 28 and December 8, when water temperature goes below 5 °C,  
28  
29 value set for the feeding threshold  $T_{\min}$ .  $G$  trajectories are discontinuous, as a result of  
30  
31 the succession of reproductive (marked in gray in the figures) and non-reproductive  
32  
33 periods. Fluctuations of  $G$ , decrease associated to spawning and subsequent increase,  
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35 are spread all along the reproductive window in Vignole, and more confined around a  
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37 limited period of time in Campalto. The smooth trajectory reported in the graph  
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39 represents the average reproductive behavior of the population at each site, and result  
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41 from the average of the 5000 individual simulations. As one can see from the box-plot  
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43 reporting statistics on the values which minimized the goal function  $\Gamma$  (Figure B2),  
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45 central values of  $k$  (means) for CA and VI are, respectively, 0.42 and 0.44. Although  
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47 very limited, this difference was statistically significant (two-sided t-test;  $p < 0.001$ ),  
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49 indicating that a fraction of energy invested in gonads growth during the reproductive  
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51 period, is approximately 5 % lower in CA than in VI. As shown in Figure B3, it was  
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also possible to compare model predictions with field data regarding two additional morfometric parameters, L and IGS, which were treated as diagnostic state variables in the model. Also in this case, results indicate a satisfactory agreement between model and field data, with the notable exception of the IGS in CA at the beginning of the III and IV years, directly related to the extremely low values recorded for G, and probably related to a systematic bias in the February sampling.



**Figure B1a-b. Calibration results: model predicted versus observed values for W and G at a) Campalto; b) Vignole. Water temperature and food fraction imposed as model forcing are represented in the figure.**



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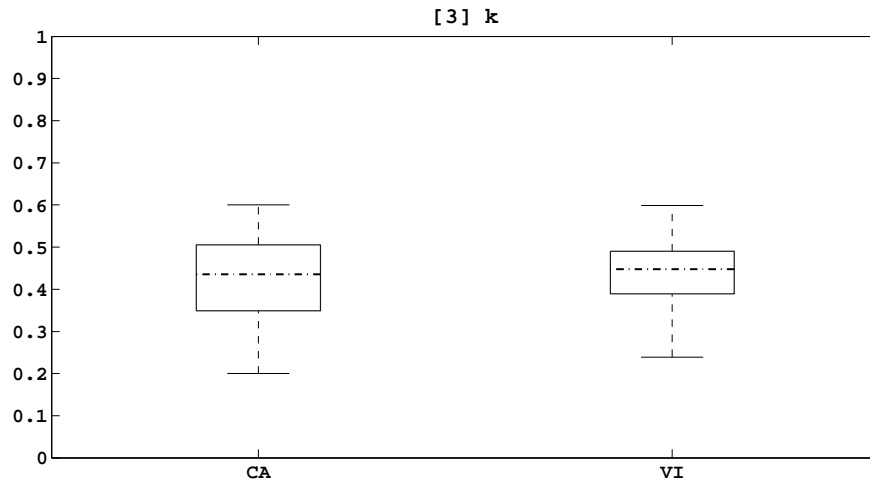
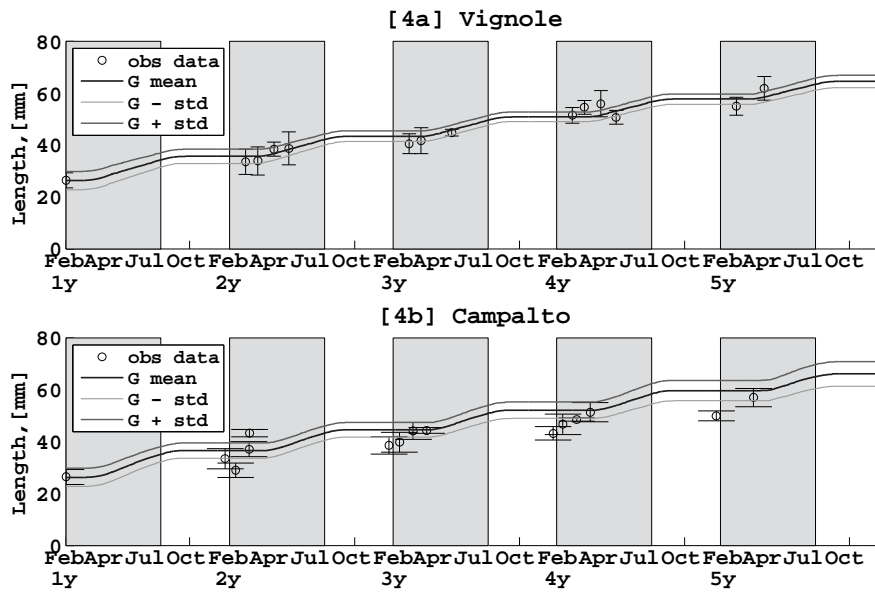
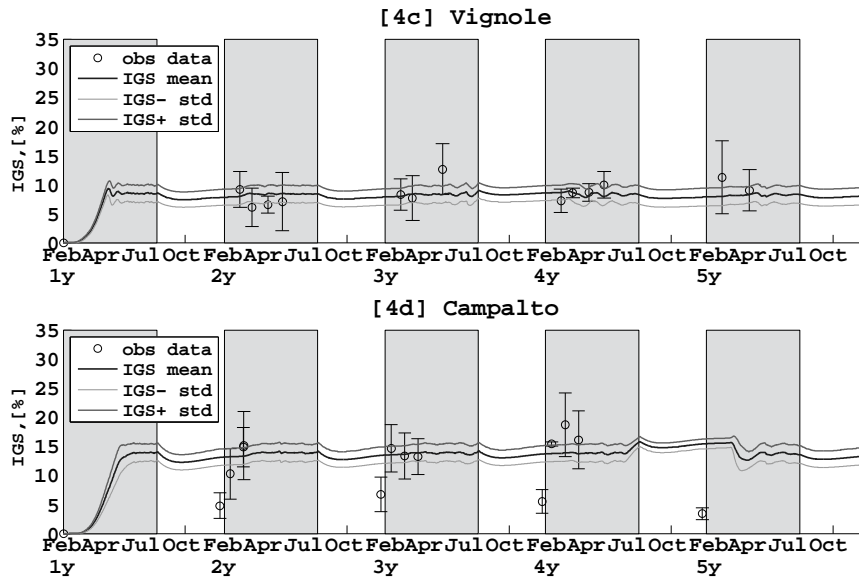


Figure B2. Calibration results: k parameter values.





**Figure B3. Model results: predicted versus observed values for total body length (L), and the gonado-somatic index (IGS), at Campalto (B1b,d), and Vignole (B1a,c).**

**Table B1. Site-specific parameters value used in different scenario to simulate the spawning dynamics,  $k_{min}, k_{max}$ : [0.2 0.6],  $K_{R_{min}}, K_{R_{max}}$ : [0.21 0.48],  $IGS_{min}, IGS_{max}$ : [5.3 18.73].**

|    |           |               |             |
|----|-----------|---------------|-------------|
| S1 | $K_{max}$ | $K_{R_{max}}$ | $IGS_{max}$ |
| S2 | $K_{max}$ | $K_{R_{min}}$ | $IGS_{min}$ |
| S3 | $K_{max}$ | $K_{R_{min}}$ | $IGS_{max}$ |
| S4 | $K_{min}$ | $K_{R_{min}}$ | $IGS_{max}$ |
| S5 | $K_{min}$ | $K_{R_{max}}$ | $IGS_{max}$ |
| S6 | $K_{min}$ | $K_{R_{max}}$ | $IGS_{min}$ |
| S7 | $K_{min}$ | $K_{R_{min}}$ | $IGS_{min}$ |
| S8 | $K_{max}$ | $K_{R_{max}}$ | $IGS_{min}$ |

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5 **References**  
6  
7

8 Brafield AE, S. D. (1972). Oxy-calorific coefficients for animals respiring nitrogenous  
9 substrates. *Comparative Biochemistry and Physiology Part A: Physiology*,  
10 43(4), 837-841.  
11  
12  
13

14 Brigolin, D., Meccia, V.L., Venier, C., Tomassetti, P., Porrello, S., Pastres, R., 2014a.  
15 Modelling the interactions between offshore fish cages and elemental  
16 biogeochemical cycles in the Mediterranean sea. *Aquaculture Environment*  
17 *Interactions* 5, 71-88.  
18  
19  
20  
21  
22

23 Brigolin, D., Facca, C., Franco, A., Franzoi, P., Pastres, R., Sfriso, A., Sigovini, M.,  
24 Soldatini, C., Tagliapietra, D., Torricelli, P., Zucchetta, M., Pranovi, F. , 2014b.  
25 Linking food web functioning and habitat diversity for an ecosystem based  
26 management: a Mediterranean lagoon case-study. *Marine Environmental*  
27 *Research* 97, 58-66.  
28  
29  
30  
31  
32  
33

34 Cole, L. C., 1954. The population consequences of life history phenomena. *Quarterly*  
35 *Review of Biology* 29, 103–137.  
36  
37

38 Consorzio Venezia Nuova, 2005. Ciclo annuale e composizione tassonomica dei  
39 popolamenti planctonici nella laguna di Venezia (aprile 2003–marzo 2004)  
40 ICSREL-T039.0. Technical report, 96 pp. (in Italian).  
41  
42  
43  
44

45 Consorzio Venezia Nuova, 2003. Valutazione integrata dello stato qualitativo attuale  
46 dei sedimenti lagunari superficiali. Progetto ICSEL. Campionamento 1995-  
47 2001. In: *Indagini sperimentali sui rilasci dei sedimenti e biodisponibilità dei*  
48 *microinquinanti*. Technical report, 209 pp. (in Italian).  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
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- 1  
2  
3  
4  
5 Cavraro, F., Fiorin, R., Riccato, F., Zucchetta, M., Franzoi, P., Torricelli, P., Malavasi,  
6  
7 S., 2010. Distribuzione e habitat di *Aphanius fasciatus* (Valenciennes, 1821) in  
8  
9 laguna di Venezia. Boll. Mus. St. Nat. Venezia 62: 125-134  
10  
11 Cavraro, F., 2012. Genetica, Ecologia e Comportamento di un Biomonitore della  
12  
13 Variabilità di Sistemi Acquatici di Transizione . Ca' Foscari University Venice,  
14  
15 101 pp  
16  
17  
18 Cavraro, F., Torricelli, P., Franzoi, P., Malavasi., S., 2013. Productivity in natural and  
19  
20 artificial habitats in brackish water systems: an example from *Aphanius fasciatus*  
21  
22 populations. Transitional Waters Bulletin, 7, 23-31.  
23  
24  
25 Cavraro, F., Daouti I., Leonardos I., Torricelli P and Malavasi S., 2014a. Linking  
26  
27 habitat structure to life history strategy: Insights from a Mediterranean killifish.  
28  
29 Journal of Sea Research 85,205–213.  
30  
31  
32 Cavraro, F., Varin, C. & Malavasi, S., 2014b. Lunar-induced reproductive patterns in  
33  
34 transitional habitats: Insights from a Mediterranean killifish inhabiting northern  
35  
36 Adriatic saltmarshes. Estuarine, Coastal and Shelf Science 139, 60–66.  
37  
38  
39 Elliott, M. & Hemingway, K. L., 2002. Fishes in Estuaries. (Elliott, M. & Hemingway,  
40  
41 K. L. Eds.) Blackwell, Oxford, 636 pp.  
42  
43  
44 Fonds, M. V., C. . (1973). The oxygen consumption of four *Pomatoschistus* species  
45  
46 (Pisces, Gobiidae) in relation to water temperature. Netherlands Journal of Sea  
47  
48 Research, 7, 376-286.  
49  
50  
51 Frisk, C., Andersen, K.H., Temming, A., Herrmann, J.P., Madsen, K.S., Kraus, G.,  
52  
53 2015. Environmental effects on sprat (*Sprattus sprattus*) physiology and growth  
54  
55 at the distribution frontier: A bioenergetic modelling approach. Ecological  
56  
57 Modelling 299, 130-139.  
58  
59  
60  
61  
62  
63  
64  
65

- 1  
2  
3  
4  
5 Jennions, M. & Telford, S., 2002. Life-history phenotypes in populations of  
6  
7 *Brachyrhaphis episcopi* (Poeciliidae) with different predator communities.  
8  
9 Oecologia 132(1), 44–50  
10  
11 Johnson, J.B. & Belk, M.C., 2001. Predation environment predicts divergent life-history  
12  
13 phenotypes among populations of the livebearing fish *Brachyrhaphis*  
14  
15 *rhabdophora*. Oecologia 126(1),142–149.  
16  
17  
18 Kidder, G. W., 3rd, Petersen, C. W., & Preston, R. L. (2006). Energetics of  
19  
20 osmoregulation: I. Oxygen consumption by *Fundulus heteroclitus*. J Exp Zool A  
21  
22 Comp Exp Biol, 305(4), 309-317.  
23  
24  
25 Kneib, R. T., & Stiven, A. E. (1978). Growth, reproduction, and feeding of *Fundulus*  
26  
27 *heteroclitus* (L.) on a North Carolina salt marsh. Journal of Experimental Marine  
28  
29 Biology and Ecology, 31(2), 121-140.  
30  
31  
32 Kooijman, S.A.L.M., 1986. Energy budgets can explain body size relations. J. Theor.  
33  
34 Biol. 121, 269–282.  
35  
36  
37 Irlandi, E.A. & Crawford, M.K., 1997. Habitat linkages: the effect of intertidal  
38  
39 saltmarshes and adjacent subtidal habitats on abundance, movement, and growth  
40  
41 of an estuarine fish. Oecologia 110, 222–230.  
42  
43  
44 Lassiter RR, Kearns DK (1974) Phytoplankton population changes and nutrient  
45  
46 fluctuations in a simple aquatic ecosystem model. In: Middlebrookers EJ,  
47  
48 Falkenberger DH, Maloney TE (eds) Modelling the eutrophication process. Ann  
49  
50 Arbour Science, Ann Arbor, MI, p 131-188  
51  
52  
53 Leonardos I. and Sinis, A., 1998. Reproductive strategy of *Aphanius fasciatus* Nardo,  
54  
55 1827 (Pisces: Cyprinodontidae) in the Mesolongi and Etolikon lagoons (W.  
56  
57 Greece). Fisheries Research 35,171–181.  
58  
59  
60  
61  
62  
63  
64  
65

- 1  
2  
3  
4  
5 Leonardos, I. & Sinis, A., 1999. Population age and sex structure of *Aphanius fasciatus*  
6  
7 Nardo, 1827 (Pisces: Cyprinodontidae) in the Mesolongi and Etolikon lagoons  
8  
9 (W. Greece). Fisheries Research 40, 227–235.  
10  
11 Leonardos, I., 2008. The feeding ecology of *Aphanius fasciatus* (Valenciennes, 1821) in  
12  
13 the lagoonal system of Messolongi (western Greece). Scientia Marina 72(2),  
14  
15 393–401.  
16  
17  
18 Madon, S. P., Williams, G. D., West, J. M., & Zedler, J. B. (2001). The importance of  
19  
20 marsh access to growth of the California killifish, *Fundulus parvipinnis*,  
21  
22 evaluated through bioenergetics modeling. Ecological Modelling, 136(2–3),  
23  
24 149-165.  
25  
26  
27 Maltagliati, F. (1999). Genetic divergence in natural populations of the Mediterranean  
28  
29 brackish-water killifish *Aphanius fasciatus*. Marine Ecology Progress Series,  
30  
31 179, 155-162.  
32  
33  
34 Nixon, S. W., & Oviatt, C. A. (1973). Ecology of a New England Salt Marsh.  
35  
36 Ecological Monographs, 43(4), 463-498.  
37  
38  
39 Nixon, S. W., Oviatt, C. A., Garber, J., & Lee, V. (1976). Diel Metabolism and Nutrient  
40  
41 Dynamics in a Salt Marsh Embayment. Ecology, 57(4), 740-750.  
42  
43  
44 Paloheimo, J. E. & Dickie, L.M. (1965). Food and growth of fishes. I. A growth curve  
45  
46 derived from experimental data. J. Fish. Res. Bd Can. 22, 521-42.  
47  
48  
49 Reznick, D.N., Endler, J.A., 1982. The Impact of Predation on Life History Evolution in  
50  
51 Trinidadian Guppies (*Poecilia reticulata*). Evolution 36(1), pp.160–177.  
52  
53  
54 Reznick, D.N., Butler Iv, M.J. & Rodd, H., 2001. Life-history evolution in guppies. VII.  
55  
56 The comparative ecology of high- and low-predation environments. The  
57  
58 American naturalist 157(2), 126–40.  
59  
60  
61  
62  
63  
64  
65

- 1  
2  
3  
4  
5 Reznick, D.N., Bryant, M.J. & Bashey, F., 2002. r- and K-Selection Revisited: The  
6  
7 Role of Population Regulation in Life-History Evolution. *American Naturalist* 83(6), 1509–  
8  
9 1520.  
10  
11 Rodd, F.H. & Reznick, D.N., 1991. Life History Evolution in Guppies: III. The Impact  
12  
13 of Prawn Predation on Guppy Life Histories. *Oikos* 62(1), 13.  
14  
15 Roff, D. A., 1992. The Evolution of Life Histories: Theory and Analysis. *Reviews in*  
16  
17 *Fish Biology and Fisheries* 3(4), 384-385  
18  
19 Sarà, G., Rinaldi, A., & Montalto, V. (2014). Thinking beyond organism energy use: a  
20  
21 trait-based bioenergetic mechanistic approach for predictions of life history traits  
22  
23 in marine organisms. *Marine Ecology*, n/a-n/a.  
24  
25  
26  
27 Shao, J., Tu, D., 1995. The Jackknife and Bootstrap. Springer Series in Statistics, 516  
28  
29 pp.  
30  
31 Skadhauge, E., & Lotan, R. (1974). Drinking Rate and Oxygen Consumption in the  
32  
33 Euryhaline Teleost *Aphanius Dispar* in Waters of High Salinity. *Journal of*  
34  
35 *Experimental Biology*, 60(2), 547-556.  
36  
37  
38 Stearns, S. C., 1992. The evolution of Life Histories. Oxford University Press, New  
39  
40 York, 249 pp.  
41  
42  
43 Stewart, G. L. A. a. K. W. (1972). Food, Feeding Selectivity and Ecological  
44  
45 Efficiencies of *Fundulus notatus* (Cyprinodontidae). *American Midland*  
46  
47 *Naturalist*, 88(1), 76-89.  
48  
49  
50 Ursin E. (1967). A mathematical model of some aspects of fish growth, respiration and  
51  
52 mortality. *J Fish Res Board Can*, 24, 2355–2453.  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

- 1  
2  
3  
4  
5 Walsh, M.R. & Reznick, D.N., 2008. Interactions between the direct and indirect effects  
6  
7 of predators determine life history evolution in a killifish. PNAS 105(2), 594–  
8  
9 599.  
10  
11 Walsh, M.R. & Reznick, D.N., 2009. Phenotypic Diversification Across an  
12  
13 Environmental Gradient: a Role for Predators and Resource Availability on the  
14  
15 Evolution of Life Histories. Evolution 63(12), 3201–3213.  
16  
17  
18 Walsh, M.R. & Reznick, D.N., 2010a. Influence of the indirect effects of guppies on  
19  
20 life-history evolution in *Rivulus hartii*. Evolution; international journal of  
21  
22 organic evolution 64(6), 1583–93.  
23  
24  
25 Walsh, M.R. & Reznick, D.N., 2010b. Experimentally induced life-history evolution in  
26  
27 a killifish in response to the introduction of guppies. Evolution; international  
28  
29 journal of organic evolution 65(4), 1021–36.  
30  
31  
32 Winberg, G.G. (1956). Rate of Metabolism and Food Requirements of Fishes.  
33  
34 Belorussian State University, Minsk. (Translated from Russian by J. Fish. Res.  
35  
36 Board Can. 194, 1–202.  
37  
38  
39 Weisberg, S. B., & Victor A, L. (1982). Ingestion, egestion, excretion, growth, and  
40  
41 conversion efficiency for the mummichog, *Fundulus heteroclitus* (L.). Journal of  
42  
43 Experimental Marine Biology and Ecology, 62(3), 237-249.  
44  
45  
46 Wootton, R.J. 1990. Ecology of Teleost Fishes. Chapman & Hall, London, 404 pp.  
47  
48  
49  
50  
51  
52  
53  
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55  
56  
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