Estimation of dynamic energy budget parameters for the Mediterranean toothcarp (*Aphanius fasciatus*)

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ABSTRACT

Organisms adopt different sets of physiological, behavioural and morphological trade-offs in order to cope with natural environmental fluctuations. This has consequential rebounds on ecological processes and population dynamics. Such aspects become crucial for sex-dimorphic species, where sex-specific growth variation could mirror different tactics both in energy acquisition and investment between maximum female and male body size with cascading effects on population demography. To date, different approaches have been used in order to understand the causes of individual growth rate changes in ectotherm indeterminate growers, most of which failed. Here, we propose the use of a mechanistic model based on the Dynamic Energy Budget theory (DEB; Koojiman, 2010) to investigate potential differences in energy allocation strategies adopted by individuals of different genders with the Mediterranean toothcarp *Aphanius fasciatus* (Valenciennes, 1821) as the model species. We collected literature and field data in order to study differences in energy allocation strategies between females and males of the same species by generating projections of possible growth performances: (1) throughout their entire life span and (2) under a context of varying functional responses. Generally, the present exercise of simulations returned different patterns of growth performance among females and males of *A. fasciatus*, with the former being able to better optimize energetic trade-offs under optimal environmental conditions. The present DEB parameterization exercise represents an essential step towards developing a mechanistic approach to depict metabolic strategies, which are at the base of observed sexual differences, and how such differences may impair ultimate fitness at individual and, therefore, population levels.

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1. Introduction

Trade-offs occur amongst a variety of traits in a diversity of organisms, and can have major effects on ecological and evolutionary processes, population dynamics (Beckerman et al., 2002) and the evolution of physiological, behavioural, morphological and life-history traits (Roff, 2002; Stearns, 1992; Zera and Harshman, 2001). Age-specific body size and growth rates represent complex organismal trade-offs reflecting energy allocation partitioned among growth, maintenance, storage and reproduction, so as to maximize fitness (*sensu* Bozinovic et al., 2011). Also, they may vary among sexes and populations due to genetic and environmental processes leading to profound differences in life-history traits with consequential rebounds in terms of demography. A sex-specific growth variation (in sexual size dimorphic species) is a natural phenomenon that probably reflects different tactics both in energy acquisition and investment between maximum female and male body size (Henderson et al., 2003; Holtby and Healey, 1990; Roff,

1983) and in the amount of energy allocated to gonads - more often used as the most common quantitative estimate of individual reproductive potential (*sensu* Rennie et al., 2008). However, such an approach is difficult to execute, as there are other 'costly' behaviours which may be related to reproduction, such as activity related to finding and competing for mates and/or reduced feeding during mating (Henderson et al., 2003; Rennie et al., 2008). Several issues have been addressed in order to understand the causes of individual growth rate changes in ectotherm indeterminate growers, mostly due to failure to accommodate some aspects related to the first life stages (e.g. embryo development; Lika and Kooijman, 2011) or ignoring the individual based autocorrelation in growth rate data as a function of varying latitudes (Buckley et al., 2010). Thus, here, we propose the use of a mechanistic model based on the Dynamic Energy Budget theory (DEB; Kooijman, 2010) to investigate potential differences in energy allocation strategies adopted by individuals of different genders with the Mediterranean toothcarp *Aphanius fasciatus* (Valenciennes, 1821) as the model species. Indeed, unlike the previous bioenergetic models, the most powerful aspect of the DEB theory relies on the possibility of tracking the metabolic process of an organism through the entire life cycle as an explicit function of

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body temperature and food availability (Kearney, 2012; Kooijman, 2010).

A. fasciatus is the most abundant Cyprinodontid fish endemic of Mediterranean shallow waters, and inhabits areas such as lagoons, salt marshes, shallow brackish waters and occasionally freshwaters (Wildekamp, 1993). As it shows sexual dimorphism, it is a perfect species to test the reliability of DEB model in studying the difference in growth performance and Darwinian fitness. This fact applies both to different striped colorations (Cavraro et al., 2013; Gandolfi et al., 1991) and different life history strategies, with females usually being bigger and living longer than males (e.g. Leonardos and Sinis, 1999; Newman, 1907). While males of this species seem to be more vagrant at the spatial scale of a lagoon (as suggested for other congeneric; e.g. Vargas and De Sostoa, 1997), there is evidence that females caring for eggs attached to stones or seagrass leaves (e.g. *Ruppia maritima*; Mannino and Sarà, 2006) are more linked to a specific territory. As a main consequence, this makes females more vulnerable to highly changing environments such as shallow waters of lagoons and ponds. In this study, we report a collection of literature and field data aiming to develop a mechanistic modelling approach for the Mediterranean toothcarp *A. fasciatus* in order to study differences in energy allocation strategies between females and males of the same species by generating projections of possible growth performances: (1) throughout their entire life span and (2) under a context of varying functional responses.

2. Materials and methods

The Dynamic Energy Budget [DEB] theory, along with other bioenergetics models, is explicitly based on certain physical principles such as the conservation of mass, isotopes, energy and time, including the inherent degradation of energy associated with all processes (Kooijman, 2010; Fig. 1). DEB uses surface area and volume relationships to keep track of three state variables of an organism: (i) the structural volume (volume of structural biomass), (ii) the reserve (energy and biomass available for direct use) and (iii) maturity (amount of energy spent in organismal development). Energy and matter (e.g. organic and inorganic) assimilated from food are assumed to be proportional to the organisms' surface area following a Holling's type II functional response curve. They are initially directed to the reserve (e.g. fat, carbohydrate, protein) pool, then distributed throughout the tissue. Structural biomass (e.g. proteins and membranes) requires energy for its maintenance in direct proportion to structural volume. Reserve is mobilized at a rate that corresponds to the weak homeostasis assumption (i.e. at

constant food density, reserve plus structure has a constant chemical composition during growth; Kooijman, 2010). This flux is allocated according to the κ-rule: a fixed fraction (κ) is allocated to growth and somatic maintenance whilst the remainder fraction (1-κ) is allocated to maturity maintenance plus maturation or reproduction. Life stages exploit energy in different ways: (i) juveniles mature and increase their complexity (i.e. develop new organs and regulation systems), and (ii) adults reproduce. Hence, the energy spent on development in juveniles will be exploited on reproduction in adults. If the general condition of the external environment in which organisms live is poor (i.e. deviated values of temperature and food availability with respect to the common natural patterns), reproduction and growth are reduced. In extreme situations, such as starved conditions, shrinking events or rejuvenation might occur; this means that an organism allocates the energy meant for reproduction towards somatic maintenance. The latter has priority over growth and, consequently, growth ceases when all the mobilized reserve is required for it. The standard DEB model also assumes isomorphy (i.e. no change in shape during growth, like shellfish).

One of the caveats of the DEB model application by using the covariation method (Lika et al., 2011a) is that first, it is necessary to estimate the core and auxiliary parameters for the species to be modelled. The core DEB parameters (e.g. digestion efficiency, energy conductance etc.) are related to processes controlling state variable dynamics; auxiliary parameters quantify effects of temperature on rates and time, allowing the conversion of measurements related to abstract quantities (e.g. structural volume) to real world observations (e.g. wet mass; *sensu* Kearney, 2012). The covariation method is based on a collection of observations (zero-variate and uni-variate data) and on a set of 'pseudo-data' that usually represent constant parameter values for a generalised animal (i.e. typical value for a wide variety of animals at a reference temperature of 20 °C; Kooijman, 2010). Zero-variate data represent single values of a quantity of interest at a particular state (such as maximum weight, age at birth, etc.), while the uni-variate data consist of sets of observations in the form of independent (i.e. age) and dependent (i.e. length) variables (Lika et al., 2011a). Parameter estimates are based on the simultaneous minimization of a weighted sum of squared deviations between a number of data sets and model predictions, in a single-step procedure (Lika et al., 2011a, 2011b).

2.1. Collection of zero-variate data

These kinds of data constitute the physical characteristics directly measurable at different stages of species development in the field: age, length and wet weight at birth (when they start to feed), at puberty (when first reproduction takes place) and at adult (the maximum values they reach). The zero-variate data for both males and females of *Aphanius fasciatus* were obtained from literature and field observations and related values are reported in Table 1.

Fig. 1. A simple dynamic energy budget (DEB) model as reported in Kooijman (2010) describing the energy fluxes through a feeding individual (from Sarà et al., 2013).

Table 1
Observed and estimated zero-variate data for males and females of *Aphanius fasciatus* (Ref: 1 = Sezen and Olmez, 2012; 2 = Zerunian, 2004; 3 = Leonardos and Sinis, 1999; 4 = this study; 5 = Kleanthidis et al., 1999; 6 = Leonardos, 2008).

Zero-variate data	Unit	Male		Female		Ref
		Obs.	Est.	Obs.	Est.	
a_b, age at birth	d	11	10.98	11	11.35	1,2
a_p, age at puberty	d	365	593	365	433	3,4
L_b, length at birth	cm	0.51	0.62	0.51	0.57	1
L_p, length at puberty	cm	2.37	2.39	2.02	2.10	4
L_i, ultimate length	cm	6.81	7.36	7.06	8.38	3
Ww_p, wet weight at puberty	g	0.193	0.18	0.116	0.115	5
Ww_i, ultimate wet weight	g	5.38	5.29	7.46	7.33	5
R_i, maximum reprod rate	# d^{-1}	1.25	1.25	1.40	1.40	6
a_m, life span	d	2190	2171	2190	2172	3

2.2. Collection of univariate data

The univariate data are represented by a relationship between one independent (e.g. body size) and one dependent variable (e.g. age). In this study, univariate data result from field observations, while laboratory measurements were carried out in order to obtain the temperature correction factors for this species, as expressed by the Arrhenius (1889) relationship: such a relationship is useful to describe the dependency of all metabolic rates on the body temperature (Kooijman, 2010).

2.3. Field collection

Between March 2010 and May 2011, individuals of *Aphanius fasciatus* were collected monthly from the Stagnone di Marsala (Trapani, Western Sicily; 37° 52′ N, 12° 28′ E) by means of a fishing net (5 x 1.5 m) with a mesh size of 2.5 mm (Mazzola et al., 1999).

Every month 100 individuals were randomly sampled, stored in previously labelled plastic bags and then brought back to the laboratory. Samples were thus immediately sorted by sex, and for each specimen, total length (TL; cm) was measured using a digital calliper (DIGI-Kanon; ±0.001 cm), while the wet weight (WW, g) was measured using an analytical balance (Mettler Toledo PL 602-5). Contextually, sex was confirmed for each individual through the analysis of other sexual characteristics. The age was determined on a total of 1,308 individuals through the analysis of otolith (sagitta) rings (Campana, 2001; Campana and Thorrold, 2001). Using a stereomicroscope (Leica EZ 150), age was estimated by counting the number of annual rings. Biometric, gravimetric and age data were combined with each other and the following relations were determined: (1) Total Length – Wet-weight, (2) Age – Total Length and (3) Age – Wet-weight. These datasets are included in the estimation procedure.

2.4. Laboratory experiments

Laboratory experiments were based on oxygen consumption measurements at different temperatures and performed in order to estimate the Arrhenius temperature and both upper and lower boundaries of the thermal range. Briefly, during the field phase, about 80 *A. fasciatus* were grouped into a 60-l seawater tank (20 °C, 37-38 PSU) where they were left to acclimate for three weeks under *ad libitum* food conditions. After this period, 40 individuals were divided into 8 tanks (n = 5) containing filtered seawater and starting from a seawater temperature of 20 °C; within each tank, temperature changed at a constant rate (1 °C per hour). Temperature was manipulated till 8 experimental temperatures were reached: 5 °C, 10 °C, 15 °C, 20 °C, 25 °C, 30 °C, 35 °C and 40 °C, respectively. After a further 24 h of acclimation at different temperatures during which organisms were not fed, individuals of *A. fasciatus* were placed singularly into respirometric chambers and the amount of oxygen consumed over one hour was measured according to the procedure reported in Ezgeta-Balic et al. (2011) and Sarà et al. (2008, 2013). The oxygen consumption rates were used to estimate the Arrhenius temperature through the calculation of the linear regression slope resulting from a log-log plot of the metabolic rate against the inverse of temperature in Kelvin (Fig. 2; Freitas et al., 2010; Kooijman, 2010; Sarà et al., 2013). The integration of all these data, according to the rules of the covariation method, allowed us to perform the estimation procedure with a dataset comprising 9 zero-variate data, 3 sets of univariate data and all temperature correction factors.

2.5. Model simulations

DEB model simulations were performed in order to investigate potential variation in growth performance resulting from differences in the way males and females of *A. fasciatus* managed the energy from food. Here, the hypothesis was posited in terms of reduced food
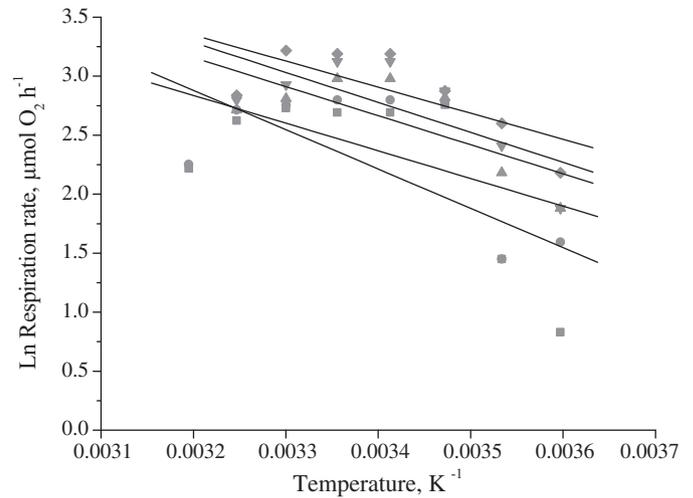
Fig. 2. Plot of the ln of oxygen consuption rates against the inverse of temperatures expressed in Kelvin. The Arrhenius temperature for *A. fasciatus* has been calculated as the mean value of the slopes (n = 5).

availability; the DEB parameters estimated for this species were applied under a range of different functional responses (0.2, 0.4, 0.6, 0.8 and 1.0).

3. Results and discussion

Throughout the sampling period, more than 2,000 individuals of *A. fasciatus* were collected; about 62% were females, 37% males and the remaining 1% were classified as indeterminate (i.e. too small to recognize the sex). Generally, females were bigger than males, with a mean (±SD) total length of 2.30 ± 0.79 cm and a wet weight of 0.24 ± 0.32 g compared to males (2.09 ± 0.68 cm and 0.16 ± 0.17 g) and apparently they were also living longer, as no 5-year old males were caught over the 14 months of field collection (the oldest was 4 years old). Oxygen consumption measurements showed significant differences at varying temperatures, with respiration rates ranging between 5.84 ± 2.43 and 22.51 ± 2.86 μmol O_2 l^{-1} h^{-1} at 5° and 20 °C, respectively. By plotting these data we estimated a thermal window of 35 °C (5 °C - 40 °C), although as shown in Fig. 2, the sample size was reduced to two individuals for the estimate at highest temperature, while the Arrhenius temperature resulted in 2,579°K (Table 2, Fig. 2). Although this value is far from the value of 8,000°K for a generalized animal (Kooijman, 2010), it is consistent with eurythermal characteristics of this species. Furthermore, the thermal tolerance window estimated in this study (Table 2) well reflected the thermal geographic distribution of *A. fasciatus* that is reported at a range between 4 °C and 40 °C (Leonardos, 1996, 2008).

Primary DEB parameters for both sexes of *A. fasciatus* derived from the estimation procedures are listed in Table 3. Of the standard DEB model the remaining parameters that are not listed here (specific searching rate {Fm} (l d^{-1} cm^{-2}), digestion efficiency κ_X (-) and Gompertz stress coefficient s_G (-)) could not be estimated from the

Table 2
Thermal range of *Aphanius fasciatus* as expressed by Arrhenius temperature, and lower and upper tolerance boundaries estimated through measurements of oxygen consumption at different temperatures.

Temperature parameters	Units	Value
T_{ref}, reference temperature	K	293
T_A, Arrhenius temperature	K	2,579
T_L, lower tolerance temperature	K	278
T_H, upper tolerance temperature	K	313
T_{AL}, lower boundary of the Arrhenius temp	K	7,786
T_{AH}, upper boundary of the Arrhenius temp	K	3,696

Table 3
Primary DEB parameters obtained through the estimation procedure – covariation method (Lika et al., 2011a).

Parameter values	Unit	Male	Female
z, zoom factor	–	1.685	1.889
δ_M, shape coefficient	–	0.229	0.225
{Fm}, max spec searching rate	l d^{-1} cm^{-2}	6.5	6.5
κ_X, digestion efficiency of food to reserve	–	0.8	0.8
v, energy conductance	cm d^{-1}	0.0703	0.0594
κ, allocation fraction to soma	–	0.3976	0.6381
κ_R, reproduction efficiency	–	0.95[*]	0.95[*]
[p_M], vol-specific somatic maintenance	J d^{-1} cm^{-3}	8.099	8.014
{p_T}, surface-specific som. maintenance	J d^{-1} cm^{-2}	0	0
k_J, maturity maint. rate coefficient	d^{-1}	0.002[*]	0.002[*]
[E_G], spec cost for structure	J cm^{-3}	5,237	5,237
E_{Hb}, energy maturity at birth	J	22.18	6.28
E_{Hp}, energy maturity at puberty	J	1,212	294.4
h_a, Weibull aging acceleration	d^{-1}	1.35 10^{-8}	1.80 10^{-8}
s_G, Gompertz stress coefficient	–	0.0001	0.0001

[*] Fixed at the values of the generalized animal.

available data. However, as showed in Fig. 3a–f, their results seemed to help us confidently depict growth performances and resource allocation strategies of organisms living under natural conditions. The goodness of fit between predicted and observed data quantified by 10 (1- mean relative error) (Lika et al., 2011b), was higher than 8.5 for both sexes. Such values are good, given that the goodness of fit measure takes on value in

[−∞, 10] (*sensu* Lika et al., 2011a, 2011b). Although we assumed that there are no differences in habitat use (in terms of both temperature and food availability) between females and males, they differ mainly in two aspects: (1) the amount of energy invested in reaching the first stage of their life cycle and (2) the energy invested in building new biomass relative to that of reproduction, i.e. κ. Females are able to reduce the energy investment to produce eggs by only one order of magnitude, (or embryonic development) and become mature compared to males, and they increase the fraction of energy to be allocated to growth by almost 50% (Table 3). These results would suggest that in optimal environmental conditions, females could better optimize energetic trade-offs, at least during the first stages of their life cycles, where the individual ability to reach a certain body size (e.g. size of first reproduction) becomes crucial in indeterminate growers. Indeed, as suggested by Strathmann and Strathmann (1982), with increased body size, the capacity for egg production may increase faster than space for brooding. The results of present simulation exercise showed different patterns of growth performance among females and males of *A. fasciatus*, with the former reaching the largest size in terms of body length and weight for all functional responses tested (Table 4; Fig. 4a-b). Such a model outcome is corroborated in nature as reported many times across the current literature (Cavraro et al., 2013; Gandolfi et al., 1991; Leonardos and Sinis, 1999). In addition, decreasing values of functional response resulted, for both sexes, in a significant reduction in size and reproductive rates. With a functional response ranging from 1 (simulating the food *ad libitum* condition) and 0.4 (a severe reduction of amount of
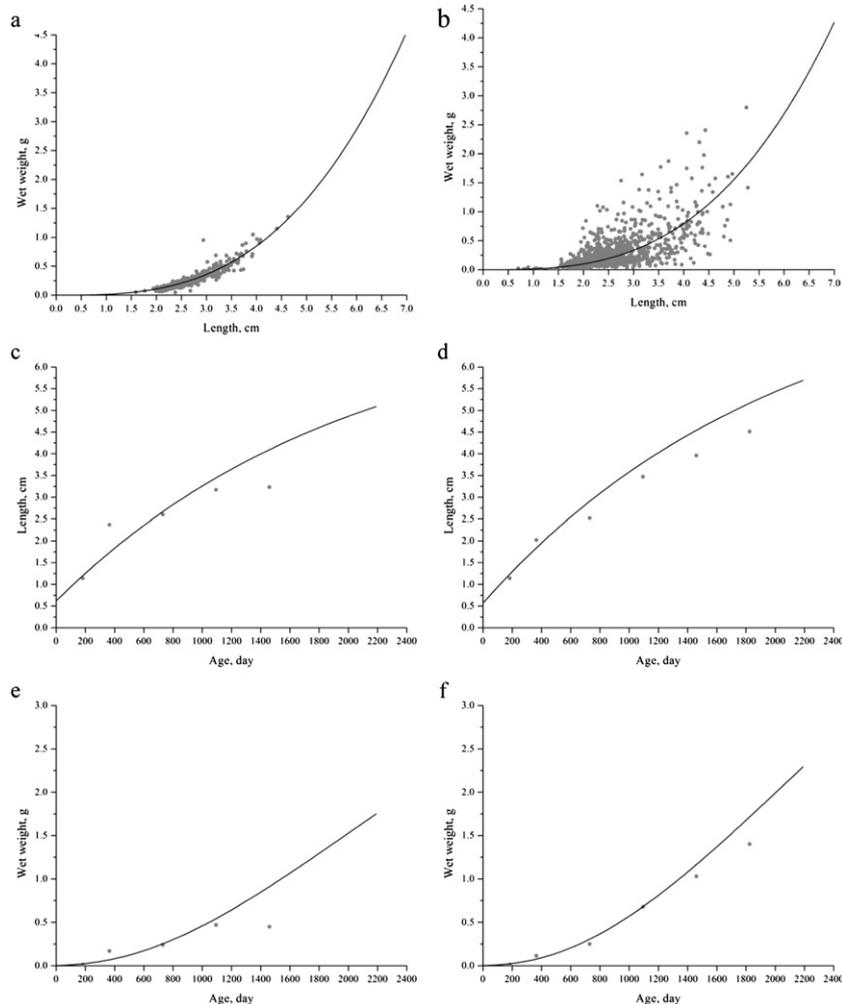
Fig. 3. Comparisons between model predictions (solid lines) and observed data (dots) for male (left) and female (right) A. fasciatus collected in the Stagnone di Marsala. (a) and (b) show length-weight relationships, (c) and (d) length as function of age and (e) and (f) wet weight as function of age.

Table 4
Zero-variate data for *A. fasciatus* using different functional responses.

Zero-variate data	Unit	Male						Female					
		obs	f = 1	f = 0.8	f = 0.6	f = 0.4	f = 0.2	obs	f = 1	f = 0.8	f = 0.6	f = 0.4	f = 0.2
ab, age at birth	d	11	11	11	12	13	14	11	11	12	12	13	14
ap, age at puberty	d	365	593	797	1237	3123	6.10E + 22	365	433	566	830	1626	6.17E + 22
Lb, length at birth	cm	0.51	0.62	0.62	0.62	0.62	0.62	0.51	0.57	0.57	0.57	0.57	0.57
Lp, length at puberty	cm	2.37	2.39	2.41	2.44	2.51	7.36	2.02	2.10	2.11	2.13	2.17	8.38
Li, ultimate length	cm	6.81	7.36	5.89	4.42	2.94	1.47	7.06	8.38	6.71	5.03	3.35	1.68
Ww$_p$, wet weight at puberty	g	0.193	0.180	0.183	0.186	0.197	4.886	0.116	0.115	0.115	0.116	0.121	6.858
Ww$_i$, ultimate wet weight	g	5.38	5.29	2.66	1.10	0.32	0.04	7.46	7.33	3.69	1.53	0.45	0.06
Ri, maximum reprod. rate	# d^{-1}	1.25	1.25	0.62	0.23	0.03	−0.04	1.40	1.40	0.71	0.29	0.07	-0.02
am, life span	d	2190	2171	2172	2172	2173	2173	2190	2172	2172	2173	2173	2173

energy ingested) the amount of gametes produced varied accordingly (from 1.25 to 0.03 and 1.40 to 0.07 in males and females, respectively). Both trait values dropped below zero for f = 0.2 (Table 4). However, our results suggested that females have are better able to manage the energy available from food, and this trait could allow them to cope better with changing environments. Moreover, females should be closer linked to a specific habitat, as it has been observed that they provide care at the nest (Ribeiro et al., 2008). By contrast, males are observed to be more vagrant and thus, in highly changing conditions, they can move and seek contiguous habitats where the environment is more stable. Our simulations support such behaviours, and as a main consequence males resulted less able than females to face poorer trophic conditions (as shown by simulations carried out by setting the value of functional response equal to 0.4; Table 4). At that functional response males

deviated far from reality, showing values that are not biologically significant (*sensu* Kearney, 2013; Lika et al., 2011b).

4. Conclusions

Aphanius fasciatus seems a perfect model species to study the different strategies played by males and females in coping with highly changing habitats such as lagoons, ponds and other shallow waters. As shown here, somatic growth dynamics of individuals can significantly diverge between the two genders within each species and this may have profound repercussions in terms of body size, fecundity, life-history traits and, lastly, in population dynamics. The present DEB parameterization exercise represents an essential step towards developing a mechanistic approach to depict metabolic strategies, which are at the base of observed sexual differences. The ability to mechanistically predict all potential expressions of life history traits in sexual size dimorphic species, such as in *A. fasciatus*, could indeed be crucial in understanding how potential variations in *A. fasciatus* fitness will affect population size, structure and dynamics (*sensu* Chevin et al., 2010). Already, Darwin noted that sexual size dimorphism might impair ultimate fitness at individual levels through indirect ecological (e.g. habitat and/or food choice) and behavioural (e.g. foraging and reproduction) effects (Blanckenhorn, 2005). These effects are expected to be complicated in areas of shallow water, as such habitats are particularly sensitive to environmental changes due to anthropogenic alterations like local (e.g. sediment remotion, harvesting etc.) and global (e.g. sea level rise, increasing temperature) factors (Sarà, 2009). All these aspects need to be taken into account, not only for predictive, but also for conservation purposes. Indeed, although widely distributed in most shallow waters across a very wide geographical area, the presence of *A. fasciatus* is now seriously threatened by multiple human stressors such as habitat degradation, pollution of continental and coastal waters, destruction and reduction of saltworks and introduction of alien species (Galil, 2009). Many studies have provided evidence that this species can become locally extinct (e.g. Ferrito and Tigano, 1995, 1996; Lorenzoni and Esposito, 2012) and for this reason, it was ranked among Least Concern species (LC) by the International Union for Conservation of Nature and Natural Resources (IUCN) (Baillie and Groombridge, 1996). The present study allowed us to get a first set of bioenergetic information about this species, supporting the need to also include sex differences into mechanistic functional trait based modelling, which is a good way to improve our predictive ability. The possibility of building mechanistic models based on reliable parameters could be an useful tool to feed population models, which in turn would inform management plans about where critical thresholds lie, or what might affect the potential resilience of particular species or ecological communities (Chevin et al., 2010).
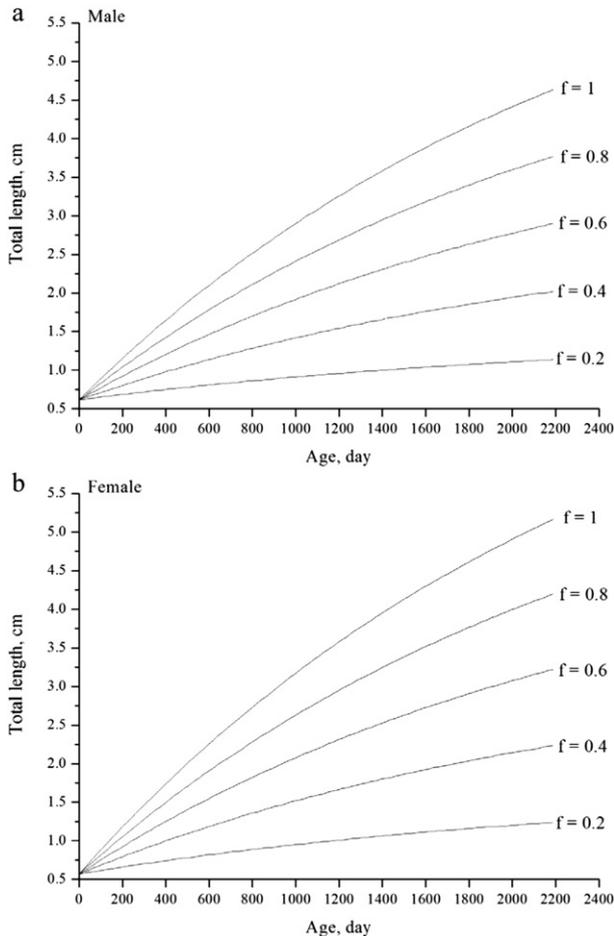
Fig. 4. Simulation of growth trajectory of *A. fasciatus* at varying functional response; (a) male, (b) female.

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