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Ecophys.Fish perspectives on growth of juvenile soles, *Solea solea* and *Solea senegalensis*, in the Tagus estuary, Portugal

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ABSTRACT

Ecophys.Fish, an ecophysiological framework to simulate fish growth in time-varying environments, was parameterized for two sole species, *Solea solea* (Linnaeus, 1758) and *Solea senegalensis* Kaup, 1858. The model gave reliable predictions of soles' growth and metabolic rates from published data under controlled environments. Differences in model parameters reflected specie's different environmental optima and were in accordance with their distributional range — northern range of *S. solea* and a southern range of *S. senegalensis*.
Field application of this model to resolve the effects of varying habitat conditions on juvenile soles' growth in the Tagus estuary (Portugal), during the spring–summer period from 2003 to 2006, highlighted spatial and temporal differences in soles' metabolic scope for growth and estimated growth rates. Higher growth estimates were obtained for *S. solea* and *S. senegalensis* in Vila Franca de Xira during 2006, and for *S. senegalensis* in Alcochete during 2003, 2004 and 2006, and were fairly well explained by natural variation in abiotic conditions.
Overall, the Ecophys.Fish model gave accurate field predictions of each sole species' growth rate and proved to be a useful tool for monitoring and assessment of habitat quality for juvenile sole.

1. Introduction

Metabolism can power the activities of organisms and it is only through metabolism that the environment has its effects on those activities — e.g. feeding, digestion, excretion, swimming, and growth (Fry, 1947, 1971). According to Fry's "physiological classification of the environment" there are five categories of environmental factors: lethal (e.g. predators); loading or masking factors that increase maintenance costs (e.g. salinity); controlling factors that determine the inherent metabolic pace at both maximum and minimum activity levels (e.g. temperature); limiting factors that restrict maximum metabolism (e.g. oxygen); and directive factors that guide individual regulatory behaviour and physiological acclimatory processes on both maximum and minimum metabolism (e.g. photoperiod).These factors affect the available metabolic power to sustain activities above the obligatory minimum for life (standard metabolic rate, SMR) and below the physiological maximum (active or maximum metabolic rate, MMR). The difference between MMR and SMR is termed metabolic scope (Fry, 1947, 1971). In this context, the metabolic scope for growth (MSg) can be considered as the available power for growth after all routine activities have been performed corresponding to the difference between MMR and routine metabolic rate (RMR).

Growth in fish is assumed to be a comprehensive measure of habitat quality and fish health, as it integrates the effects of environmental factors (e.g. food resources, salinity, temperature) and individual fitness (e.g. Able et al., 1999; Meng et al., 2000; Fonseca et al., 2006). Metabolic scope for growth is strongly correlated with growth rates, and can be used to predict fish growth given respirometric determination of the metabolic scope (Neill and Bryan, 1991). Building on this concept, Neill et al. (2004) developed an ecophysiological framework for simulating fish growth under varying conditions of multiple environmental variables, the Ecophys.Fish model. The model mechanistically describes the interaction of Fry's classes of environmental factors and their joint effects on growth, coupling metabolism and bioenergetics. It depicts the way the available energy is partitioned within the fish so it can perform all activities (including food processing and excretion) according to abiotic constraints on the metabolic capacity. Model components have been tested in specific scenarios, which measured fish growth and metabolic performance with varying temperature and oxygen (Del Toro-Silva et al., 2008) and with simultaneous variation in temperature and feed energy (Fontaine et al., 2007), and proved effective in both cases.

Yamashita et al. (2001) described the ecophysiology of flatfish in nursery grounds based on Fry's environmental classification and discussed the possibility of an ecophysiological model to predict growth and subpopulation production. Using growth as an evaluative endpoint, the Ecophys.Fish model can also be used for habitat quality assessment under realistic time-varying environments. Del Toro-Silva (2008) adapted the Ecophys.Fish model for southern flounder

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(*Paralichthys lethostigma* Jordan and Gilbert, 1884) and applied it to evaluate habitat quality of nursery areas in North Carolina estuaries.

In the present study, Ecophys.Fish was parameterized for two sole species, the common sole *Solea solea* (Linnaeus, 1758) and the Senegalese sole *Solea senegalensis* Kaup, 1858. These sole species are very similar in terms of morphology and ecology, but have different distributional ranges: the common sole has a more northern distribution ranging from the North Sea to North Africa, including the Mediterranean, while the Senegalese sole occurs from the Bay of Biscay to Senegal (Quéro et al., 1986). Both species use the Tagus estuary (Portugal) as an important nursery ground (Costa and Bruxelas, 1989; Cabral and Costa, 1999), occurring in sympatry in this area providing the opportunity to assess how the model performs under field conditions, i.e. to determine the metabolic scope for growth and estimate juvenile sole growth in the Tagus estuary. Although estuarine conditions are highly dynamic, in nursery areas juvenile fishes usually benefit from abundant food resources, favourable temperature ranges and low predatory pressure (Miller et al., 1985). Ecophys.Fish model was thus used as a tool to resolve the effects of varying habitat conditions on juvenile soles' growth in the Tagus, during the spring–summer period from 2003 to 2006.

Information for constructing the models was retrieved from several studies focusing on these species metabolic rates and growth patterns under controlled conditions (e.g. Fonds, 1975; Howell and Canário, 1987; van den Thillart et al., 1994; Lefrançois and Claireaux, 2003; Salas-Leiton et al., 2008).

2. Materials and methods

2.1. Model description and parameterization

The Ecophys.Fish model has two functional modules dealing with fish metabolism and bioenergetics. The metabolism subroutine describes how time-varying environmental factors, namely temperature, salinity, pH, food and dissolved oxygen influence metabolic rates and thus the metabolic scope for growth. Standard metabolic rate (SMR) is a function of the loading effects of salinity, temperature (as a controlling factor) and fish weight, where modelled fish partially compensate for temperature change. SMR is defined as: $\mathrm{SMR} = S * \exp(q1\ T\mathrm{accl}) * \exp(q2\ T\mathrm{stress})$; where S is the intercept value, which is a function of salinity, fish weight and temperature, elevated as an exponential function both of acclimation temperature (Taccl and $q1$, the steady state component and rate constant) and of the difference between ambient and acclimation temperatures (Tstress and $q2$, the transient state component and rate constant) in order to account for both the Ahrennius effect and thermal acclimation. Maximum metabolic rate (MMR) is determined by the limiting effects of dissolved oxygen (DO) with regard to the controlling effects of temperature and pH and the effects of fish weight. Thus, $\mathrm{MMR} = MMSO * DO\mathrm{a} * pH\mathrm{factor} * DO\mathrm{lim} * DO\mathrm{accl} * W\mathrm{effect}$, where *MMSO* is the intercept of marginal metabolic scope (a determinant of intrinsic metabolic efficiency); *DO*a is ambient dissolved oxygen concentration; *pH*factor is a dimensionless pH transformation to account for a crude Bohr effect; *DO*lim is a power-hyperbolic function of the temperature-dependent DO that limits MMR; *DO*accl is the DO acclimation component that accounts for DO changes at a given rate proportional to SMR; and *W*effect is the effect of fish weight on metabolic rates. In addition, routine metabolic rate (RMR) is defined as 2.0*SMR based on Winberg's empiricism, which results in a metabolic scope for growth (MSg) equal to the difference between MMR and 2.0*SMR.

In the bioenergetics subroutine, the fish partitions the consumed food energy between obligatory expenditures, namely standard and routine activities, feed-processing costs, wastes and the residual energy is then converted to new biomass — fish growth. Under the model a fish eats all appropriate food encountered or until available digestive or metabolic capacity becomes insufficient to support further food processing, thus representing a metabolic limitation of food intake. Neill et al. (2004) describe in full detail the above-intertwined relationships between environmental factors and fish physiological processes.

Ecophys.Fish model parameterization for *S. solea* and *S. senegalensis* (with STELLA® software) was based on published data describing the two species' respective environmental preferences and limits (*e.g.* salinity, temperature, dissolved oxygen), as well as biological constrains (*e.g.* feeding rate) (Table 1). The model's inputs are time series of temperature, pH, dissolved oxygen, salinity, food availability and energy content, and initial size and energy density of juvenile fish (Neill et al., 2004). Metabolic rate data were also compiled from previous studies on sole species, providing estimates of oxygen uptake rates during standard, routine or maximum activity (Table 1). In the complete absence of requisite data, some model parameters were retained as in the original version of the model, such as the functions describing the variable acclimation rate coefficients for DO and temperature changes. Model parameters were progressively adjusted and tested by simulating growth and respirometry trials documented in these published studies. The models' adequacy or goodness of fit was checked by linear regression analysis of observed (references in Table 1) and simulated growth rates (as weight percent change per day relative to fish initial weight).

2.2. Field application

The Tagus estuary (38°40′N 9°15′W) is a large system (325 km^2), partially mixed and with a tidal range of about 4 m. Intertidal and saltmarsh areas account for *ca.* 40% of the total estuarine area. Mean river flow discharge is 400 $\mathrm{m}^3\mathrm{s}^{-1}$ although it varies considerably with season and year (Bettencourt and Ramos, 2003). The upper part of the estuary is shallow and fringed by salt marshes. The two main nursery areas for sole (Vila Franca de Xira — VFX and Alcochete — ALC) identified by Costa and Bruxelas (1989) and Cabral and Costa (1999) are located in the upper estuary (Fig. 1). In VFX nursery area both sole species occur, but in ALC nursery only *S. senegalensis* is present (Cabral and Costa,

Table 1
Main sources of reference data for Ecophys.Fish model parameterization for *Solea solea* and *Solea senegalensis*.

Model parameterization	*S. solea*	*S. senegalensis*	References
Temperature			
Topt (°C)	20	25	Fonds (1975), Fonds et al. (1989); Howell (1997); Cabral and Costa, 1999; Amara (2004); Imsland et al. (2003); Lefrançois and Claireaux (2003);
Tinfl (°C)	12	16	
q1 (1/°C)	0.052	0.054	
Dissolved oxygen and metabolic rates			
DOlim, intercept ($\mathrm{mg\ O_2\ L^{-1}}$)	0.175	0.35	Howell and Canário (1987); van den Thillart et al. (1994); Aragão et al. (2003); Lefrançois and Claireaux (2003); Davoodi and Claireaux (2007); Salas-Leiton et al. (2008)
DOlim, Max ($\mathrm{mg\ O_2\ L^{-1}}$)	1.75	2.00	
Smino ($\mathrm{mg\ O_2\ g^{-1}\ h^{-1}}$)	0.037	0.042	
Hill parameter	1.9	2.25	
Salinity			
SalOpt	10	20	Imsland et al. (2003); Arjona et al. (2005); Vinagre et al. (2006); Vinagre et al. (2007);
Feeding rate			
FeedRateMax ($\mathrm{g_{feed}/g_{fish}{}^{*}day}$)	0.20	0.25	Cabral (2000); Vinagre et al. (2007); Vinagre and Cabral (2008)
Growth rate			Fonds (1975); Day et al. (1997); Dias et al. (2004); Rodiles et al. (2005); Rodríguez et al. (2005); Palazzi et al. (2006); Pinto et al. (2007); Costas et al. (2008); Salas-Leiton et al. (2008)

For detailed description of model parameters see Neill et al. (2004).