Upscaling from individual-level bioenergetic balance to population-level dynamics for improving fisheries management

Connectant el balanç energètic a nivell individual amb la dinàmica poblacional per a millorar la gestió pesquera

Irene MORO-MARTÍNEZ[1], Joaquim TOMÀS-FERRER[2], Gaetano CATANESE[3] and Miquel PALMER[4]

1,2,3 Laboratori d'Investigacions Marines i Aqüicultura (LIMIA-IRFAP), Govern de les Illes Balears, Av. Gabriel Roca 69, Port d'Andratx 07157, Illes Balears.
4 Institut Mediterrani d'Estudis Avançats (IMEDEA), UIB-CSIC. C. Miquel Marquès, 21. Esporles, Illes Balears. imoro@sgaip.caib.es

Abstract: Marine resources represent 17% of the proteins consumed by humans. Thus, in a scenario where the outcomes of climate change on fisheries remain poorly known, resources management should be carefully designed for maximizing profitability and sustainability. Nowadays, conventional management strategies are based on reference points at the population level (e.g., maximum sustainable yield). However, the emerging properties at the population level related with between-fish variability are rarely considered, despite that evidence on their strength and extend is accumulating. Agent-based modelling (ABM) is an emerging strategy for exploring the outcomes of individual variability. However, ABM requires precise description of individual variability. Here, we report an example of the large between-fish variability in the growth rate of seabass (*Dicentrarchus labrax*), even when the individuals monitored are genetically close, and they have experienced the same environmental conditions. Moreover, we demonstrate how bioenergetic models (specifically, the dynamic energy budget model, DEB) allow to disentangle the biological processes involved (e.g., energy assimilation versus energy mobilization rates). This experiment is part of a broader plan aimed to better understand the potential resilience against climate change conferred by individual variability, and to provide updated tools for improving fisheries management at the local level (Balearic Islands).
Keywords: Fisheries, management, population dynamics, individual variability, DEB

Resum: *Els recursos marins representen el 17% de les proteïnes consumides pels humans. Per tant, en un escenari on els resultats del canvi climàtic sobre la pesca segueixen sent poc coneguts, la gestió dels recursos s'hauria de dissenyar acuradament per tal de maximitzar la seva rendibilitat i sostenibilitat. Actualment, les estratègies de gestió convencionals es basen en punts de referència a nivell de població (per exemple, el màxim rendiment sostenible). No obstant això, les propietats emergents a nivell de població relacionades amb la variabilitat entre peixos rarament es tenen en compte, malgrat que s'acumulen les evidències sobre la seva rellevància i extensió. El modelatge basat en agents (ABM) és una estratègia emergent per explorar els resultats de la variabilitat individual. Tanmateix, els ABMs requereixen una descripció precisa de la variabilitat individual. Aquí, reportam un exemple de la gran variabilitat entre peixos en la taxa de creixement en el llobarro (*Dicentrarchus labrax*), fins i tot quan els individus monitoritzats són genèticament propers i han experimentat les mateixes condicions ambientals. A més, demostram com els models bioenergètics (concretament, el model DEB) permeten dilucidar els processos biològics implicats (per exemple, assimilació d'energia versus taxes de mobilització d'energia). Aquest experiment forma part d'un pla més ampli que té com a objectiu comprendre millor la resiliència potencial davant el canvi climàtic que atorga la variabilitat individual i proporcionar eines actualitzades per millorar la gestió de la pesca a nivell local (Illes Balears).*
Paraules clau: *Pesca, gestió, dinàmica poblacional, variabilitat individual, DEB*

INTRODUCTION

Marine resources represented 17% of the proteins of animal origin consumed in 2019 by humans (*FAO*, 2021). Given their importance, and in a scenario where the effects of climate change on fisheries remain poorly understood, marine resources management must therefore be carefully designed to maximize profitability and sustainability. Nowadays, the assessment and management of fish stocks are usually based in monitoring some population level indicators. The stock status is typically inferred from statistical models fed by the total biomass landed and the fishing effort. These models are designed for estimating some reference points (e.g., Maximum Sustainable Yield (*MSY*)), which in turn are used to support specific management decisions (Restrepo, 1999; Punt *&* Smith, 2001). However, these models assume that fish are all equal and ignore between-individual variability, in spite that it has long been known that the effects of individual variation may be substantial and can affect population growth, equilibrium density and stability (Bjørnstad & Hansen,1994). The topic of how individual variation affects population-level features is still poorly explored but is attracting a growing interest. In a recent review of experimental and comparative evidences on this topic, it has been suggested that more variable populations are less vulnerable (Forsman & Wennerste, 2016).

Therefore, provided that individual fish are the foundation from which population- and ecosystem-level traits emerge, fish variation should be of central importance for any approach to fisheries management (Ward *et al.*, 2016).

Agent-based (ABMs) also known as individual-based models (IBMs) are modelling approaches that consider individuals as discrete, single entities. Individuals carry on several properties (e.g., weight) that changes over the life cycle (Grimm, 1999). Thus, ABMs, among others, emerge as suitable tools for designing management strategies that explicitly consider individual variation and account for its outcomes. ABMs has been already successfully coupled with bioenergetic models for understanding and predicting fish population dynamics (Beaudouin *et al.*,2015). However, practical application to fisheries management is particularly challenging because these coupled models require an in-depth knowledge of individual variability in bioenergetic rates. In spite that advances in fish biotelemetry are impressive, monitoring metabolism of wild fish is still troublesome, and applications addressing these issues in fisheries management are still scarce (Crossin *et al.*, 2017).

Therefore, as a preliminary prove-of-concept, here we focus in describing fish variation in bioenergetic rates of lab-reared fish because repeated measures of the same fish can be easily obtained. Moreover, we monitored fish from a single aquaculture line that have experienced the same environmental conditions, in order to assess the amount of fish variability not explainable by neither genetic nor environmental differences. The bioenergetic model chosen for assessing metabolic rates was the Dynamic Energy Budget (DEB). The DEB theory is an especially attractive bioenergetic framework because it provides a mechanistic understanding of growth (among other biological processes) under a specific history of external forcing variables (e.g., the specific history of food and temperature experienced by a given fish throughout all its lifespan) (Kooijman, 2010). However, estimating DEB parameters at the fish level is challenging too (Lika *et al.*, 2020).

Therefore, the goals of this communication are two-fold: (1) from the biological side, we report the extend and strength of fish variation in growth and disentangle the relative importance of energy assimilation and mobilization in shaping those growth patterns; and (2) from the methodological side, we demonstrate that fish-level DEB parameters can be estimated using a Bayesian framework. This communication is part of a broader study aimed to better understanding the resilience potential against climate change, conferred by the existence of individual variability. This knowledge, in turn, may be later used for developing updated tools to improve fisheries management at the local level (Balearic Islands).

MATHERIALS AND METHODS

Twenty-two individuals of *Dicentrarchus labrax* that were born at the same day, were tagged, and individually monitored for a period of 60 days (between 140 and 200 days old). Fish come to the same selection line; thus, genetic diversity is expected to be small when compared with wild fish. Fish were randomly distributed into three tanks at LIMIA (Marine Research and Aquaculture Lab, Port d'Andratx). Total length was measured using a conventional ictiometer to the nearest mm. Wet weight was measured with a digital balance to the nearest 0.001g. Five repeated measures of wet weight and total length were obtained. Water temperature was daily recorded. Fishes were fed *ad libitum* with commercial pellets.

For DEB theory we refer the reader to Kooijman (2010). Briefly, DEB theory is a formal metabolic theory which provides a single quantitative framework to dynamically describe the main aspects of metabolism (energy and mass budgets) of all living organisms at the individual level, based on assumptions about energy uptake, storage, and utilization. From the statistical side, the DEB model is a system of coupled differential equations, which implies specific challenges for estimating DEB parameters (Lika *et al.*, 2020). Here, for shake of simplicity, (1) the initial time for numerical integration (t_0) was set at 139 days, one day before the first of our observations for length and weight; (2) we just consider one time-varying forcing variable (temperature) and two observable variables (length- and weight-at-age); and (3) we focus on estimating inter-individual variability for only two parameters: maximum assimilation rate ($\dot{p}Am$), and energy conductance ($\dot{v}$). These two parameters are related with two key metabolic processes: energy assimilation and energy mobilization. The remaining DEB parameters were obtained from Add-my-Pet (https://www.bio.vu.nl/thb/deb/deblab/add_my_pet/). Both, population-level means and fish-level values were estimated using a Bayesian approach. Samples from the joint posterior distribution of the parameters, given the data (fish length- and wet weight-at-age) and the priors, were obtained using *STAN* (Stan Development Team, 2020) and the *cmdstanr* library from the R package (R Core Team, 2021).

RESULTS AND DISCUSSION

Form the methodological side, the experimental and analytical strategy followed in this work has allowed to successfully estimate two key parameters of the DEB model at the fish level: maximum assimilation rate ($\dot{p}Am$), and energy conductance ($\dot{v}$), at individual level. Model predictions using those fish-level parameters are very close to the observed values for length- and weight-at-age (Fig.1B). Thus, the Bayesian framework developed here seems to be a promising analytical tool for estimating DEB parameters at the individual level.

Form the biological side, the between-fish differences in growth pattern are impressive (Fig. 1A). At the end of the experiment (when fish were 200 days old), fish weight ranged between 22.4 and 49.2 gr, which implied that the largest fish was more than twice as heavier than the smallest fish. The between-fish variability in length at the same age was also noticeable (between 133 and 167 mm). It should be emphasized that all those fish (1) come from the same aquaculture breeding family, thus between-fish genetic variability should be small; (2) they have been born the same day and have experienced the same environment during all lifespan.

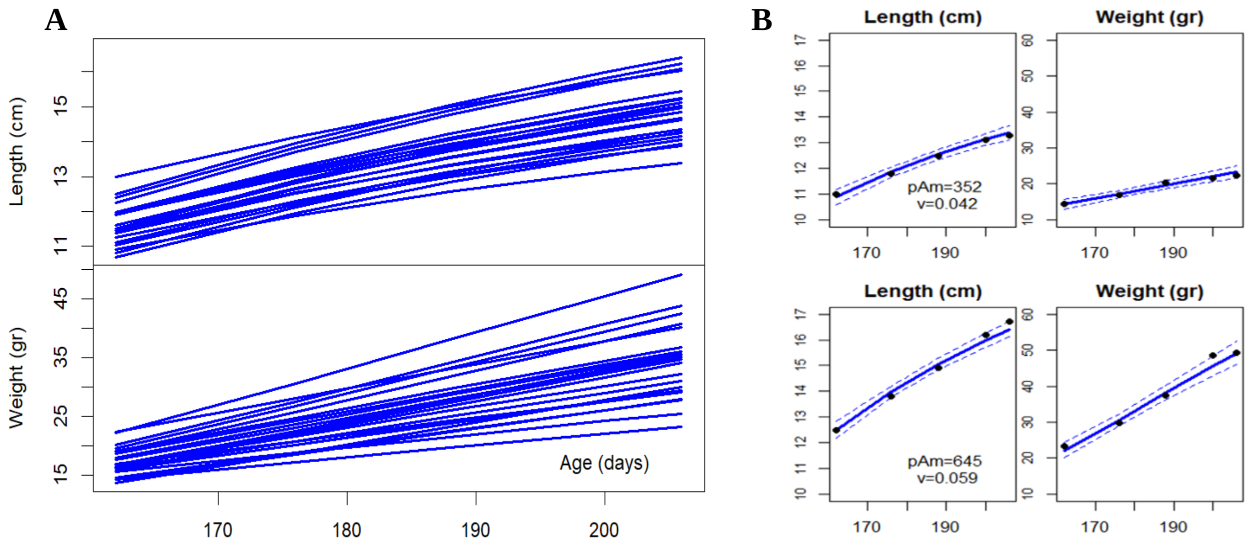

FIGURE 1. A*: Expected growth pattern for the 22 fishes monitored in this work. Each line corresponds to an individual fish. B: Observed (points) and expected (predicted by DEB) values for length- and weight-at-age (blue lines) for 2 selected individual fish. The solid line is the median expectation. The dashed lines denote 95% Bayesian credibility interval*.

The extend of between-fish variability can be better visualized after comparing the estimated values of *pAm* and *v* for the 22 fish analyzed (Fig. 2), where these two parameters seem to be correlated (correlation coefficient = 0.81). Thus, fish with large assimilation rate tend to display large mobilization rate too.

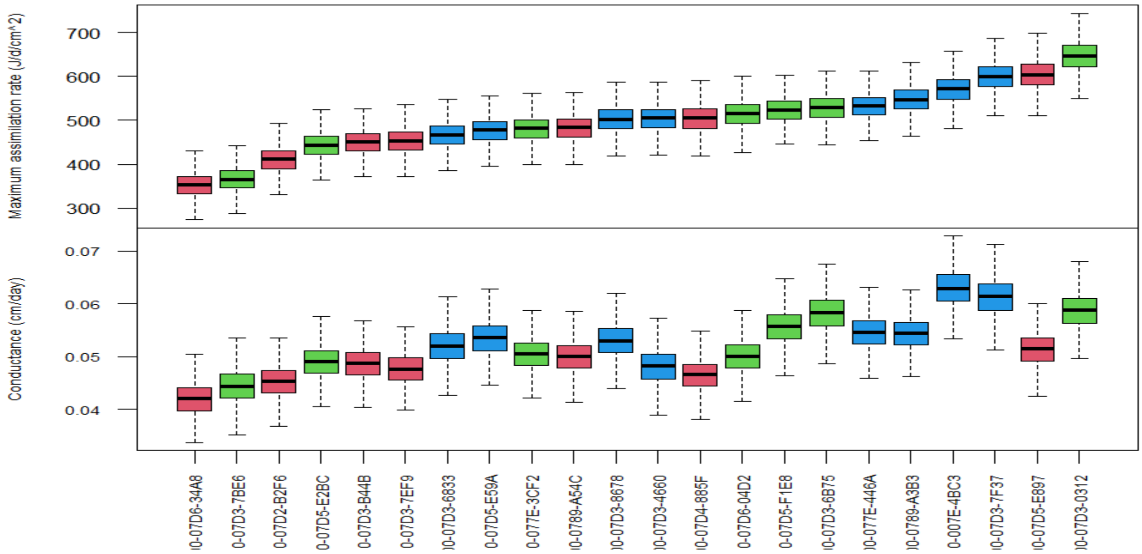

FIGURE 2. *Estimated values for pAm and v at the individual level. Each box-plot represents one fish (median and 95% Bayesian credibility interval). Fish are sorted in increasing order for pAm, in both panels, thus pAm and v are correlated (r = 0.81). Colors denote tanks, thus between-tank differences were negligible.*

The experiment reported here is part of a broader study. After (1) solving several technical problems related with estimating DEB parameters at the fish level; and (2) demonstrating that between fish variability is noticeable even when fish are genetically close and they have experienced the same environmental conditions, the next challenge will be to explore and compare the between-fish variation in growth pattern and DEB parameters when fish are submitted to an increasing range of temperatures. The underlaying hypothesis to be tested is that fish variability is conferring more resilience against climate change. Moreover, we are planning to enlarge the scope of observed variables, including measures of (1) oxygen basal consumption rate; (2) otolith optical density; and (3) quantification of several growth-related gene expression. It is expected that this additional data will improve the precision of DEB parameter estimates and contribute to better understand the underlying biological processes. The final objective is to develop a coupled AMB-DEB for better understanding and predicting the dynamic of resource abundance, which could be used for improving the fisheries management at the Balearic Islands.

ACKNOWLDGMENTS

IMM and JTF were supported by a PhD fellowship (FPI-INIA) from the National Institute for Agricultural and Food Research and Technology (INIA) and is a contribution of the Joint Research Unit IMEDEA-LIMIA. This study has been supported by CLOCK'S project from the Spanish Government (PID2019-104940GA-I00). The seabass individuals were provided by Acuicultura Balear S.A.U.

REFERENCES

Beaudouin, R., Goussen, B., Piccini, B., Augustine, S., Devillers, J., Brion, F., & Péry, A. R. 2015. An individual-based model of zebrafish population dynamics accounting for energy dynamics. PloS one, 10(5): e0125841.

Bjørnstad, O. N., & Hansen, T. F. 1994. Individual variation and population dynamics. *Oikos*, 69(1): 167-17.

Crossin, G. T., Heupel, M. R., Holbrook, C. M., Hussey, N. E., Lowerre-Barbieri, S. K., Nguyen, V. M., ... & Cooke, S. J. 2017. Acoustic telemetry and fisheries management. *Ecological Applications*, 27(4): 1031-1049.

FAO. 2021. World Food and Agriculture - Statistical Yearbook 2021. Rome. https://www.fao.org/documents/card/en/c/cb4477en

Forsman, A. & Wennersten, L. 2016. Inter-individual variation promotes ecological success of populations and species: evidence from experimental and comparative studies. *Ecography* 39: 630–648

Grimm, V. 1999. Ten years of individual-based modelling in ecology: what have we learned and what could we learn in the future? *Ecological Modelling* 115(2-3): 129–148.

Kooijman, B. 2009. Dynamic Energy Budget Theory for Metabolic Organisation (3rd ed.). *Cambridge: Cambridge University Press*.

Lika, K., Augustine, S., & Kooijman, S. A. 2020. The use of augmented loss functions for estimating dynamic energy budget parameters. *Ecological Modelling*, 428: 109110.

Punt, A.E. & Smith, A.D.M. 2001. The gospel of maximum sustainable yield in fisheries management: birth, crucifixion and reincarnation. In: Reynolds, J.D., Mace, G.M., Redford,K.H. & Robinson,J.G.(Eds.), Conservation of Exploited Species. *Cambridge University Press*, Cambridge, UK, pp. 41–66.

Restrepo, V.R. (Ed.). 1999. Proceedings of the fifth national NMFS stock assessment workshop: providing scientific advice to implement the precautionary approach under the Magnuson-Stevens Fishery Conservation and Management *Act. NOAA Tech. Memo*. NMFS-F/SPO-40, 161 p.

Ward, T. D., Algera, D. A., Gallagher, A. J., Hawkins, E., Horodysky, A., Jørgensen, C., ... & Cooke, S. J. 2016. Understanding the individual to implement the ecosystem approach to fisheries management. *Conservation Physiology*, 4(1).