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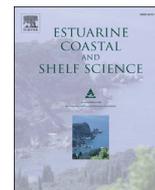
Predictive mechanistic bioenergetics to model habitat suitability of shellfish culture in coastal lakes

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ABSTRACT

Quantitative tools based on mechanistic modelling of functional traits able to enhance the sustainability of aquaculture and most other human activities (i.e. reducing the likelihood of detrimental impacts optimising productions), are especially important factors in the decision to site aquaculture facilities in coastal lakes, ponds and lagoons and, in the case of detrimental impact, to adopt mitigation measures. We tested the ability of mechanistic functional trait based models to predict life history traits of cultivable shellfish in shallow coastal lakes. Dynamic Energy Budget (DEB) models were run to generate spatially explicit predictions of Mytilus galloprovincialis life history (LH) traits (e.g. body size and fecundity). Using fortnightly data of food supply and hourly data of body temperatures, and exploiting the power of mechanistic rules, we estimated the amount of faeces ejected by a fixed quantity of organisms cultivated in two shallow Southern Mediterranean (Sicily) lakes. These differed in terms of temperature and food density, implying large differences in life history traits of mussels in the two study areas. This information could help facilitate the selection of sites where environmental conditions are more suitable for aquaculture and contextually compatible with sustainability. The validation exercise obtained by comparing the predicted and observed data was nearly consistent. Therefore, a mechanistic functional traits-based model seems able to capture the link between habitat characteristics and functional traits of organisms, delineating the fundamental portion of an ecological niche, the possibility of predicting LH traits and potential ecological applications in the management of natural coastal resources.

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1. Introduction

The considerable expansion of shellfish culture (e.g. bivalves) in shallow habitats such as lagoons, ponds and coastal lakes may pose serious threats to local natural biodiversity assets due to the focal impacts exerted by large amounts of cultivated biomasses (Sarà, 2007a). Currently, such detrimental impacts are reduced by using sites for a certain period of time, and then moving shellfish facilities to another location, far removed from the original site (IUCN, 2009). Each time, however, stakeholders must decide again to where facilities should be moved, in order to optimise production and minimise the impacts of cultivation. This decision process is primarily based on ecological information and socio-economic consequences. Some decision-based methods also rely on statistic-correlative approaches (e.g. Geographic Informative Systems and integrated stat-mathematical models; Vincenzi et al., 2011; Melaku Canuet al., 2012). In correlative approaches, habitat characteristics are linked through geographical information systems (GIS) to a statistical description that implicitly captures biological processes (e.g. growth or species presence) to the extent that they are statistically associated with the predictors (Kearney and Porter, 2009). Within an aquaculture context, useful predictors can be ambient factors such as water columns and sedimentary chemical (e.g. salinity), trophic (e.g. quality and quantity of food) and physical (e.g. sedimentary texture, hydrodynamics) variables (IUCN, 2009). On this basis alone, however, stakeholders have few decision tools with which to identify the best places to start new culture initiatives, i.e. where (i) shellfish growth will be maximised and (ii) there will be a smaller likelihood of impact through biodeposits released by the cultivated shellfish.

While the application of correlative modelling tools helps increase knowledge of habitat characteristics (IUCN, 2009), potentially assignable to accommodate new farming, they do not provide

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information on functional (individual) traits of the potential cultivated organisms (Sarà et al., 2011, 2012). Detailed knowledge of species-specific characteristics for every cultivated species is crucial in enhancing our discriminative ability to make correct environmental choices (*sensu* Diaz and Cabido, 2001) whilst also increasing economic income.

In the present context, functional means all those specific traits defining species in terms of their ecological roles (Diaz and Cabido, 2001), and thereby the species identity. In ectotherms such as cultivated bivalves and fish, these traits usually include tolerance and sensitivity to environmental conditions such as physiological thermal tolerance limits (Kearney and Porter, 2009) delimiting the ability of each species to maintain its metabolic machinery (Sokolova et al., 2012), to obtain energy from food, or those behavioural (e.g. swimming behaviour, habitat use, mating system) and morphological (e.g. shape) traits (Schoener, 1986) which allow optimisation of energetic income (Krebs and Davies, 1992) and ultimate fitness (Roff, 1992). Since flows of energy and matter (and time) through habitats and organisms are subjected to Conservation Laws (Kooijman, 2010) and are traceable processes, we may use these principles to quantitatively and mechanistically predict the functioning of each species and thereby the magnitude of and variability in these traits (the so-called mechanistic trait-based approach; Kearney et al., 2010, 2012) based on eco-mechanics principles (Sarà et al., in 2014).

Thus, such an approach offers new opportunities to predict reliable estimates of life history (LH) traits of every species, including in an aquaculture context (Sarà et al., 2012). This includes the eventual commercial size and time needed to reach it, the fecundity (the number of eggs produced per gram of biomass as an estimate of hatchery potential), and the number of reproductive events per life span. The ability to predict the magnitude of these traits, the ultimate fitness of a cultivated species (Stearns, 1992) and its potential role in contributing to the bulk organic matter through faecal deposits (continually released in the surroundings) and their link in a spatially-explicit environmental context (i.e. running models using local environmental to get LH results of the target species which are contextualized in a specific geographical location; Sarà et al., 2012) is recognised as especially important for the decision-making process. This could also help increase the cost-benefit thresholds between the maximization of production and the mitigation of aquaculture impacts in coastal ecosystems (IUCN, 2009).

Fortunately, coastal and estuarine management and the application of conservation science can be assisted by functional ecology and bioenergetics, thanks to recent individual-trait-based mechanistic models based on the Dynamic Energy Budget theory (DEB; Kooijman, 2010). DEB helps to gain more complete information on possible environmental conservation strategies to be adopted in exploiting aquatic resources, as in the case of aquaculture. Recent applications have shown the high reliability of DEB approaches in many ecological contexts, mostly with ectotherms such as bivalves and fish (e.g. Pouvreau et al., 2006; Sarà et al., 2011, 2012, 2013a,b; Saraiva et al., 2011a). Bivalves acquire energy from available food and transform it into biological structures (e.g. flesh and shells) at a rate directly influenced by external temperature (Kooijman, 2010). Temperature is, as in most ectotherms, the major driver controlling and regulating metabolism and biochemical kinetics (Kooijman, 2010). The mechanistic approach based on DEB depicts temperature-dependent metabolic processes with precision, and enables us to more accurately predict the growth performance of an animal, as has been successfully demonstrated recently on land with lizards (Kearney, 2012; Kearney et al., 2012) and in marine habitats with bivalves (e.g. Pouvreau et al., 2006; Kearney et al., 2010; Sarà et al., 2011, 2012, 2013a; Saraiva et al., 2012), crustaceans and fish (e.g. Jusup et al., 2011; Pecquerie et al., 2011). Moreover, DEB seems

to have a potential to predict distributions of invasive organisms (Sarà et al., 2013b) or threatened species (*sensu* Kearney, 2012), as well as a simple tool which, starting from organismal functional traits and a few mechanistic rules (Kooijman, 2010), is able to provide basal information (viz. based on species identity) about the suitability of areas potentially designated to aquaculture.

Here, we present a field and laboratory-validated, theoretical exercise conducted in eastern Sicily (Southern Mediterranean), where two brackish marine coastal lakes (Faro and Ganzirri; Fig. 1) offer a great opportunity to verify whether mechanistic models are sufficiently reliable in testing the suitability of lagoon waters for shellfish culture. We chose these habitats as a study system because large amounts of environmental data (e.g. Manganaro et al., 2009) are available for DEB modelling (i.e. water temperature and food density), and also because there has been local debate about the suitability of these lakes for shellfish culture; even though, as reported in Manganaro et al. (2009), the shellfish industry has only been banned in the Ganzirri lake since 1995, while the Faro lake is still used as enclosure of mussels from Northern Italy.

We thus tested if a functional trait-based approach referring to DEB theory is useful in mechanistically predicting life history traits of the bivalve *Mytilus galloprovincialis* in the spatially explicit context of Ganzirri and Faro lakes. In doing so, the predictions were improved by accounting for the effects of water temperature on body temperature (and metabolic rates) and local food densities. We obtained life history traits of mussels such as: (i) the habitat-specific maximum length of mussels using real data (local hourly series of water temperatures and fortnightly series of food density expressed as chlorophyll-a levels); (ii) the maturation time under two conditions; (iii) the total number of eggs produced during a life span of about 4 years, and (iv) the number of reproductive events. Lastly, exploiting the mechanistic power of DEB, we estimated (v) the quantity of faeces released by a theoretical quantity of bivalves (50 tonnes) cultivated in each lake.

2. Materials and methods

2.1. The study area

The study was carried out in two brackish coastal lakes located close to Capo Peloro (Eastern Sicily; 38° 15′ 57″ N; 15° 37′ 50″ E): Ganzirri and Faro (Fig. 1). The Ganzirri lake is larger (surface 34 ha; entire volume 9.8×10^5 m^3), and shallower (6 m maximum depth) than Faro (surface 26 ha, entire volume 2.5×10^6 m^3; about 9.0×10^5 m^3 0–5 m in depth, with a maximum depth of 30 m). The Ganzirri pond has muddy sediments, and primary production is sustained essentially by phytoplankton (Manganaro et al., 2009). Faro is a small meromictic marine lake (~26 ha), characterised by sandy-muddy bottoms seasonally covered by green algal mats, although primary production there is mainly sustained by phytoplankton. Both lakes exhibit similar fetches (Manganaro et al., 2009), are characterised by wind-driven circulation, are connected to each other by a channel and have salinity levels close to that of the sea (~33–37). Seawater entering the lakes through narrow channels plays an almost negligible role in their internal circulation and hydrodynamics (Giacobbe et al., 1996; Manganaro et al., 2009).

2.2. Water temperature and food density

An important step in this study was to place the modelling exercise in a spatially explicit environmental context. To do this, we ran DEB models with mussel body temperature (BT) and food as driving forces in the life history of mussels throughout the study area (Fig. 1). We performed DEB simulations of water temperature
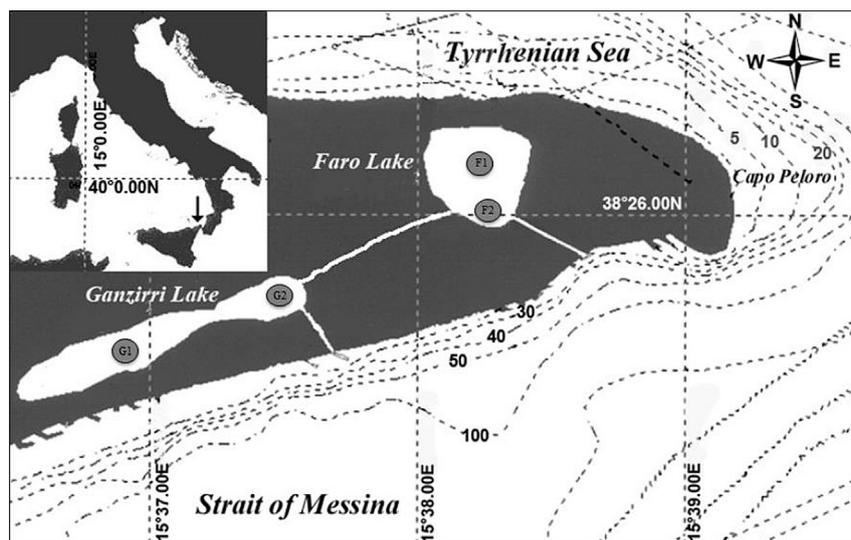
Fig. 1. Map of the study area (G1and G2 are, respectively, Sites 1 and 2 of the Ganzirri lake; F1 and F2 are Sites 1 and 2 of the Faro lake).

obtained by two clusters of three thermo-loggers each, positioned in each lake. The thermo-logger (Type 22 iButton; http://www.alphamach.com/Eng/ibutton.htm; Lima and Wethey, 2009) hardware was programmed to record up to 4096 readings at 0.5 °C for one year (1 January 2010–31 January 2011) and they were positioned in the two lakes in two different sites (hereafter referred as Ganzirri Site 1 and Site 2, and Faro Site 1 and Site 2) at a depth of about 1 m, previously chosen as study sites in Manganaro et al. (2009). For our study, these were chosen to better represent the environmental condition of two lakes. While there are many potential ways to express food available to bivalves (Mann, 1988; Langdon and Newell, 1990; Sarà et al., 2003; Sarà, 2007b), we used suspended chlorophyll-a (CHL-a; $\mu g\ l^{-1}$) as a proxy for phytoplankton biomass. Bi-weekly CHL-a data in two sites at Ganzirri (Fig. 2a) and two at Faro (Fig. 2b) were obtained from Manganaro et al. (2009), where water samplings were collected from May 1998 to April 1999.

2.3. The Dynamic Energy Budget (DEB) model and a species' functional traits

DEB captures whole-organism bioenergetics, connecting individual behaviours to population growth via estimates of reproductive output (Kooijman, 2010). As mentioned above, the most important factor driving the metabolic machinery in organisms is body temperature, which, in ectotherms, e.g. bivalves, is a direct function of the external environment (Lima et al., 2011). For submerged organisms, BT generally closely approximates the temperature of the surrounding water. BT drives metabolic rates according to specific rules (viz. First Principles) allowing predictions about changes in metabolic functioning and estimates of biological responses to changes in environmental variables (i.e. water temperature, available energy from food, etc.). The mechanistic nature of a DEB model (Kooijman, 2010) can be briefly explained as follows: (1) energy and matter assimilated from food are assumed to be proportional to the organism surface area following a type II functional response (i.e. *f*; Holling, 1959); (2) these are directed to the reserves (e.g. fat, protein); (3) the reserve flux is mobilised according to the κ-rule (i.e. a fixed fraction κ is allocated to growth and somatic maintenance, while the remaining 1-κ is allocated to maturity maintenance, maturation or reproduction), and (4) maintenance has priority over growth, and growth ceases when all reserves are required for somatic maintenance. By thus applying the DEB model,
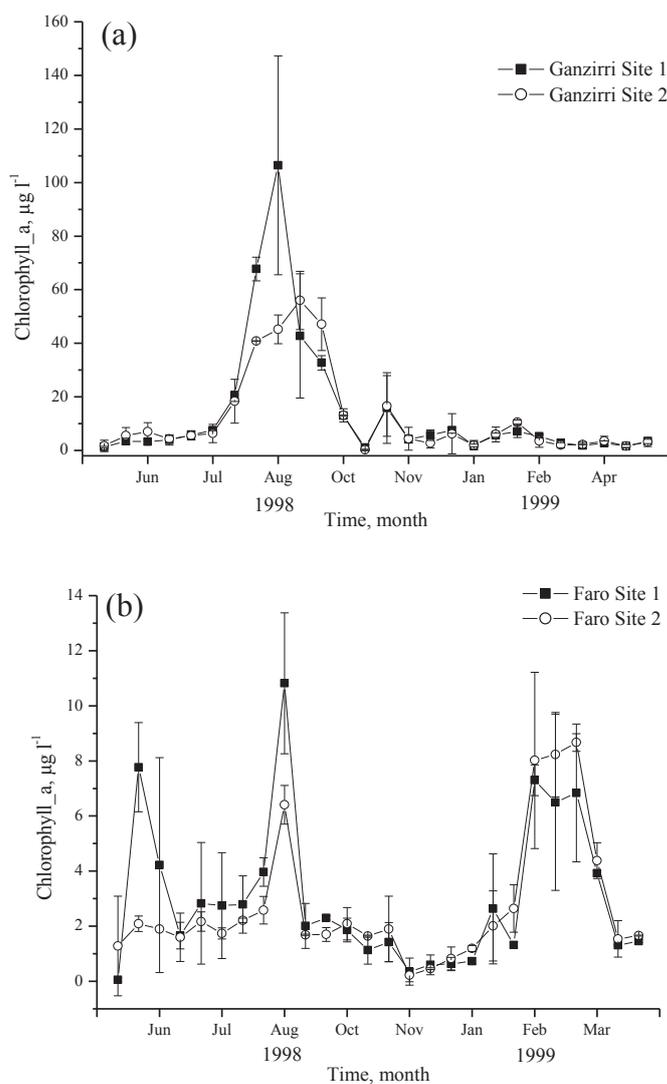

Fig. 2. Bi-weekly chlorophyll-a data in the two lakes (from Manganaro et al., 2009): Ganzirri (a) and Faro (b).

we obtained the following outputs: (1) Maximal individual habitat size (MIHS) which in a DEB context is equal to the amount of energy mobilized from reserves by the ratio between the assimilated energy minus that spent on maintenance; (2) Maturation Time (MT), i.e. the time (in days) required to reach the minimal size that allows for gamete development and maturation; (3) Reproductive Events (RE), the number of times that the amount of energy has reached a certain density in the reproduction buffer and overflow as gametes, and (4) Total Reproductive Output (TRO) which depends on the amount of energy available for reproduction coming from reserves and stored into a reproduction buffer (whose extent is species-specific). Further details of how DEB works and how the main LH outputs have been estimated are reported in Kearney (2012), Kearney et al. (2012), Sarà et al. (2011, 2012, 2013a,b, in press), Saraiva et al. (2011b; 2012).

DEB models must be tailored to the organism in question. It is therefore necessary to obtain functioning parameters of target species by integrating experimental and mathematical procedures. In this case, parameters used in building the *Mytilus* 'DEB model were obtained from the literature (Sarà et al., 2011, 2012; Saraiva et al., 2012).

2.4. Estimates of faeces quantities

We aimed to estimate the potential amounts of faeces released by mussels into water masses and lake sediments. The DEB model enables this, estimating the hourly production of faeces released into the surroundings using the following relationships (Kooijman, 2010; but see; Saraiva et al., 2012;; Sarà et al., 2013a):

$$\text{Faeces}\left(\text{mgh}^{-1}\right) = \left(J_x - p_A\right)\big/20.3\,\text{J} \quad \times \quad \text{mg POM}$$

where J_x is the flux of energy ingested, p_A is the flux of energy absorbed (here assuming an assimilation efficiency of 0.88 estimated through the Conover ratio; Conover, 1966) and 20.3 J is the conversion factor used to estimate the energetic value of 1 mg of ingested food (mg POM). Using the hourly amount in mg, we summed the total amount per approx. 35,000 h (i.e. 4 years) and obtained the total quantity of faeces deposited throughout the life span. We then standardised this amount to 1 kg of adult mussels (composed of about 50 individuals in Ganzirri and more than 100 in Faro – the latter were smaller, according to our simulations). To obtain the approximate quantity of faeces released in the lakes by a theoretical farm of 50 tons, we multiplied the amount of faeces produced per kg by 50,000 (i.e. 50 tons).

2.5. DEB model validation

The reliability of DEB has been tested on many occasions, including very recently (i.e. successfully estimating ultimate size and other LH traits in bivalves – Saraiva et al., 2012; Sarà et al., 2013a,b). Nevertheless, once simulations had been obtained using each lake fortnightly food supply and hourly temperatures and integrating *Mytilus galloprovincialis* DEB parameters into the model (Table 1), we validated the model outcomes as in Sarà et al. (2013a). Bivalve culture has not been allowed in Ganzirri since 1995, but in Faro farming practices are currently active (Manganaro et al., 2009). Thus we collected there, in summer 2011, 100 mussels on ropes positioned at a depth of about 1.0 m. These animals were used for validation and measured using a digital calliper (total umbonal length; ±0.1 mm) and weighed using an analytical scale (±0.001 g). Estimates of age were obtained according to the method reported in Sarà et al. (2013a) and for bivalve size validation in the Ganzirri lake, we referred to data from Genovese (1970). Whilst the model outcome would ideally be validated with data on fecundity, we were prevented from doing so by laboratory logistic restrictions. Despite this, we were highly confident about our validation; it is well known that there is a very strong (positive) relationship between body size and gonadic mass (and then fecundity) in ectothermic invertebrates such as bivalves, as has been shown several times in the literature (Strathman and Strathman, 1982; Gosling, 1992; Kooijman, 2010).

Comparisons between the model and observations were made graphically and also by computing the overall error as $E = e^{\sigma^2} - 1$, where σ^2 is the variance of ε and $\varepsilon = \sqrt{\log^2(\widehat{Y}_{\text{pred}}/Y_{\text{obs}})}$ for each data point. A null value of E is assumed to be a perfect match between modelled and observed data (Saraiva et al., 2011a).

3. Results

3.1. Water temperature and food density

Hourly temperatures were higher in Ganzirri lake, which is generally shallower than Faro. In particular, Ganzirri Site 1 temperatures ranged between 10.5 and 33.0 °C, Ganzirri Site2 between

Table 1
DEB parameters for *Mytilus galloprovincialis* (1 = Sarà et al., 2012; 2 = Saraiva et al., 2012); L_b, L_p = length at birth and puberty; d_{Vw} = specific density to convert weight into volume; f = functional response type II $f = X/(X_K + X)$; μx = chemical potential to convert moles into food energy; SMI is the somatic mass index of both starved and well-fed animals, expressed as somatic ash free dry mass (AFDM, mg); X_K = saturation coefficient expressed as a concentration of chlorophyll a (µg CHL-a l^{-1}), where the ingestion rate is half of the maximum.

Symbol	Description	Formulation	Units	*Mytilus galloprovincialis*	
				Value	Ref.
V_b	Structural volume at birth	$V_b = (L_b \times \delta_m)^3$	cm^3	0.0000013	1
V_p	Structural volume at puberty	$V_p = (L_p \times \delta_m)^3$	cm^3	0.06	1
δ_m	Shape coefficient	$\delta_m = (Ww \times d_{Vw}^{-1}) \times L^{-1}$	–	0.2254	1
$\{J_{Xm}\}$	Maximum surface area-specific ingestion rate	$\{J_{Xm}\} = J_X/\left(f \times V^{\frac{2}{3}}\right)$	J cm^{-2} h^{-1}	8.2	1
ae	Assimilation efficiency	$ae = (\mu x \times J_X)/p_A$	–	0.88	1
X_K	Saturation coefficient	–	µg l^{-1}	2.1	1
$[E_G]$	Volume-specific cost of growth	$[E_G] = \text{SMI}_{\text{starved}} \times 23 \times (\delta_m^3)^{-1}$	J cm^3	5993	2
$[E_m]$	Maximum storage density	$[E_m] = (\text{SMI}_{\text{fed}} - \text{SMI}_{\text{starved}}) \times 23 \times (\delta_m^3)^{-1}$	J cm^3	2190	1
$[p_M]$	Volume-specific maintenance cost	$[p_M] = p_M/V$	J cm^{-3} h^{-1}	1	1
κ	Fraction of utilized energy spent on maintenance and growth	–	–	0.7	1
K_R	Fraction of reproductive energy	–	–	0.8	1
T_A	Arrhenius temperature	$T_A = \ln\left|k_{(T_0)}/k_{(T_1)}\right| \times \frac{(T_1 \times T_0)}{(T_0 - T_1)}$	°K	7022	2
T_L	Lower boundary of tolerance range		°K	275	1
T_H	Upper boundary of tolerance range		°K	296	1
T_{AL}	Rate of decrease at lower boundary		°K	45,430	1
T_{AH}	Rate of decrease at upper Boundary		°K	31,376	1

9.5 and 32.5 °C, while Faro Sites 1 and 2 were very similar, ranging between 12.5 and 28 °C. The hourly patterns of combined thermo logger series for both lakes are reported in Fig. 3 (a–b). Food density, expressed in values of suspended CHL-a, was significantly higher (more than fourfold) in the shallower Ganzirri (13.3 ± 21.0 μg l^{-1} on average) than in Faro (average 2.9 ± 2.7 μg l^{-1}). This reflects the findings by Manganaro et al. (2009).

3.2. DEB model and a species' functional traits

The combination of food and temperature at all sites led to substantial differences in the expression of ultimate size and the other LH traits over four years between the two lakes (Table 2; Fig. 4a–b). In Ganzirri, *Mytilus galloprovincialis* exceeded 8 cm in total length and 8 g in total weight; in contrast, in Faro, mussels barely reached 7 cm and 4 g. Similarly, all other examined LH traits reached larger values in Ganzirri than in Faro, as with the reserve capacity (Fig. 4b) and the egg production which exceeded 3 million per year commenced 8 months after birth. The only exception was that the number of spawning events was lower (Table 2; Fig. 4a–b).
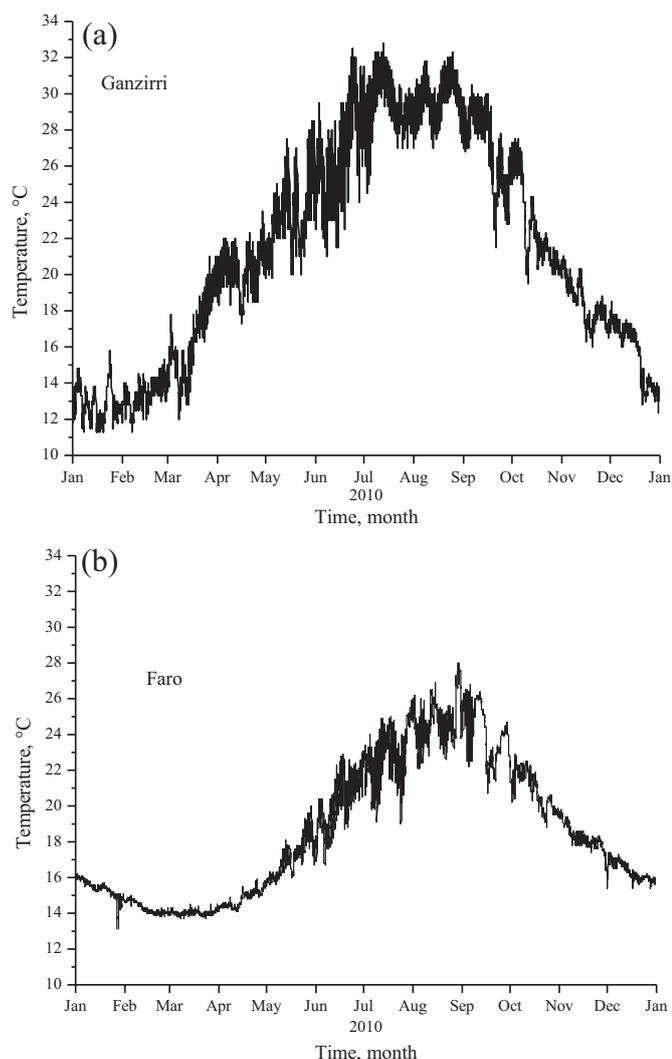

Fig. 3. Hourly thermo logger data of the column water deployed in the study area: (a) mean water temperature of the Ganzirri lake; (b) mean water temperature of the Faro lake.

Table 2
Life history traits of *Mytilus galloprovincialis* under environmental conditions in the study area (TL, cm = total length; TWw, g = tissue wet weight; MT = maturation time, days; TRO = total reproductive output as expressed by total amount of eggs emitted in 4 years; RE = number of reproductive events in 4 years; Faeces production rate, mg h^{-1} = mean of faeces production rate in 4 years).

Site	LT (cm)	TWw (g)	Time to maturity (days)	Reproduction (# eggs)	RE	Faeces production (mg h^{-1})
Faro Site 1	7.28	4.84	201	6,522,266	19	0.02 (±0.02)
Faro Site 2	7.22	4.74	196	6,585,351	19	0.02 (±0.01)
Ganzirri Site 1	8.67	9.53	225	11,325,161	17	0.03 (±0.03)
Ganzirri Site 2	8.32	8.31	239	13,661,937	10	0.17 (±0.03)

The validation procedure carried out with Faro animals demonstrated a good agreement between the predicted *vs.* observed data and, overall, DEB estimates of total length and tissue wet weight differed by less than 1 cm and 0.10 g over three years (three years is, in fact, the greatest age reached by mussels found in the Faro lake). Indeed, according to shell ring analysis, size of animals collected in Faro (*n* = 100) resulted in: (i) 1.75 ± 0.05 cm in mussels of about six months; (ii) 2.72 ± 0.05 cm for those one year old; (iii) 3.70 ± 0.06 cm in animals reaching two years; and (iv) 5.28 ± 0.27 cm for three year old mussels. These results were consistent with modelled data outputs for which predicted sizes were of 1.60 cm, 2.66 cm, 4.60 cm, 6.13 cm, and 1.65 cm, 2.65 cm, 4.58 cm, 6.13 cm for mussels of the same age classes in Site 1 and Site 2, respectively (Fig. 5a).

For Ganzirri lake, shell lengths predicted by the model were compared with the only record reported in literature (Genovese, 1970). Mussel total length has been reported to reach 3.04 cm (*n* = 49) and 5.17 cm (*n* = 74) after 12 and 24 months of cultivation, respectively. The model integrating the environmental conditions data recorded in both Ganzirri sites returned 2.96 cm in Site 1 and 2.81 cm in Site 2 after 12 months of cultivation, and 5.29 cm and 5.05 cm after 24 months under (Fig. 5a). The overall error between predicted and observed data in both lakes was 0.040 (Fig. 5a). Dealing with tissue wet weight, model validation has been performed only for the Faro lake population. Observed mussels weighted 0.26 ± 0.02 g, 0.63 ± 0.03 g, 1.43 ± 0.12 g, and 2.78 ± 0.44 g for 0.5, 1, 2, and 3 year old individuals, respectively. The model for the same age classes predicted 0.05 g, 0.24 g, 1.23 g, 2.90 g, and 0.06 g, 0.24 g, 1.22 g, 2.86 g for Sites 1 and 2, respectively (Fig. 5b). For this comparison the value of overall error was 0.335 (Fig. 5b).

3.3. Estimation of faeces

Quantities of faeces produced hourly per individual over four years are reported in Table 2. However, by assuming a theoretical farm of 50 tons (see above), the models returned faeces production rate of 86,984 (±75,565) mg h^{-1} and 86,153 (±68,608) mg h^{-1} in Faro (Site 1 and Site 2, respectively), while in Ganzirri faeces production amounted to 66,466 (±64,178) mg h^{-1} in Site 1 and 417,459 (±414,289) mg h^{-1} in Site 2.

4. Discussion

Shellfish culture is an important aquaculture reserve (Gibbs, 2004) since it does not require supplementary food input, as with fish aquaculture (Naylor et al., 2000; Garen et al., 2004). It represents the core of integrated multi-trophic aquaculture worldwide (Troell et al., 2009). In addition, although shellfish culture produces sizable environmental impacts (Chamberlain et al., 2001), cultured bivalves provide a top-down control strategy of eutrophication
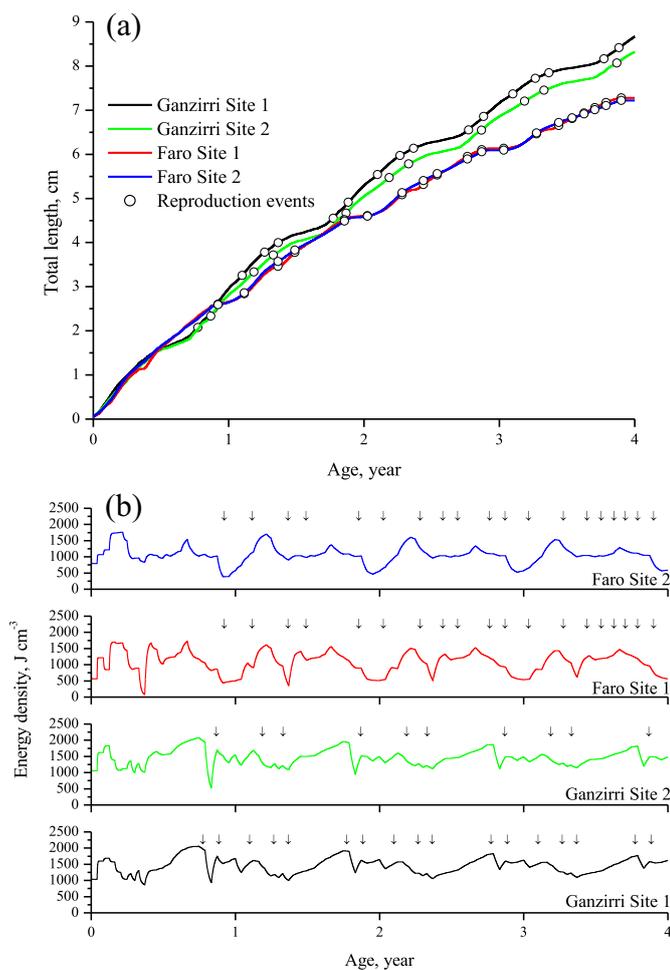
Fig. 4. Model outputs: (a) Von Bertalanffy growth functions of *Mytilus galloprovincialis* and numbers of reproductive events (circle) as estimated by DEB model (Total length, cm = ultimate valve length reached at the end of 4 years) under environmental conditions in the: Ganzirri lake, Site 1 (black line), Site 2 (green line), and Faro lake, Site 1 (red line), Site 2 (blue line); (b) Energy density as estimated by DEB model under environmental condition in: Ganzirri lake, Site 1 (black line), (green line) Site 2, and Faro lake, Site 1 (red line), Site 2 (blue line); the arrows indicate the drop of energy density into reserve due to the occurrence of spawning events. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

symptoms associated with excessive loading of nutrients to the coastal zone (Ferreira et al., 2007; Xiao et al., 2007). Indeed, on a global scale, aquaculture of suspension-feeding bivalves such as clams, cockles, oysters and mussels is becoming one of the most valuable productive activities from the sea (FAO, 2010). In the Mediterranean and Black Sea areas, the production of cultured bivalves in marine and brackish water from 2000 to 2010 amounted to 2,038,592 tons: a value of 3.6 billion USD (FAO, 2010). Shellfish culture is among the best candidates of the so-called Blue Growth, a global strategy model designed to use exploited resources available all across European oceans and coasts, where the waste of one product becomes the source of new initiatives for jobs and growth (EC, 2012). As such, it could be a reliable tool to: (1) reduce the ecological impact of artisanal fishery; (2) promote the reversion of eutrophication effects, and (3) restore water quality in degraded estuaries, coastal lakes and lagoons (Jackson et al., 2001). Results of the present DEB model simulations fitwell into this framework, providing indications about the habitat suitability to shellfish aquaculture. Such indications are important at local levels, where

harvesting represents a threat to natural shellfish populations such as mussels, clams and cockles. DEB showed that both the thermal and trophic conditions occurring within the two lakes were favourable to *Mytilus galloprovincialis* growth and reproduction. Indeed, while models returned larger and more reproductive individuals in one of the two lakes (Ganzirri), under all conditions DEB predicted mussels to reach the most frequent commercial size (5 cm; Peteiro et al., 2006) after only 24 months. Such an outcome was highly consistent with the field observations made by Genovese (1970), which reported 5.2 cm as the mean size for two-year-old *M. galloprovincialis* in Ganzirri lake. However, from a management perspective, the large imbalance between faeces production modelled in the Ganzirri sites would suggest a diversification of farming activity. The Ganzirri lake sites could serve as hatcheries for mussels to be subsequently transplanted and cultivated until commercial size is attained in the Faro Lake. Ganzirri has great potential to sustain the reproductive requirements of a 'source population' since the habitat conditions of this site in terms of temperature and food density would guarantee the required healthy status of the adults. In turn, the adult healthy status is a crucial aspect, as it drives through the maternal effect (Kooijman, 2010), the ability to sustain an adequate production of juveniles. This maternal effect comprises the amount of energy reserve that mothers allocate to eggs, allowing embryos to develop and hatch completely with a reserve density equalling that of the mother at egg formation (Jager, 2012); 'healthy parents give rise to healthy offspring'. This parental investment is a temperature-dependent process and is, therefore, closely linked to the body's temperature profile that adults display during life span. The appreciation of temperature and CHL-a annual time series in this study showed that Ganzirri and Faro lakes are characterized by seasonal inter-lagoon variation, characteristic of worldwide distributed coastal lagoon habitats (Pérez-Ruzafa et al., 2007, 2011). Indeed, it is the strong and diversified fluctuations of biotic and abiotic parameters in Ganzirri and Faro that contribute to making these sites such interesting models of lagoons, ponds and coastal lakes. For example, both lakes differ remarkably in their trophic levels, which range from oligotrophic in Faro to mesotrophic in Ganzirri (Caruso et al., 2006). Similarly, Ganzirri shows a range of salinity typical of polyhaline waters (18 to <30 PSU), while Faro displays euhaline conditions (30 to <40 PSU) (Pérez-Ruzafa et al., 2011). The fact that this robust mechanistic method could be developed and validated in such highly variable environments seems to support the general applicability of this approach to those habitats where natural variability is less marked (e.g. sub-tropical lagoons). The application of a DEB-based mechanistic approach made it possible to capture local differences in life history traits, which were likely due to higher food concentrations allowing mussels to invest more energy in egg production. Such information is also highly valuable at local levels, as it can be used to advise stakeholders on the more suitable areas to promote shellfish culture activities. In contrast, under the Faro lake conditions, DEB predicted a smaller amount of faeces produced per individual; this would allow individuating where the impact on shellfish farming could be minimised. This would aid the ability to decide whether to cultivate shellfish culture in closed environments such as ponds, lakes and lagoons. DEB was able to capture the two key aspects — less time required to reach commercial size, thereby minimising the risk of environmental impact by biodeposits on the surroundings — to be considered when choosing where to site a farm (Sarà et al., 1998).

5. Potential bias of mechanistic model

A possible criticism of the functional trait-based mechanistic modelling approach is that it is based on characteristics of the
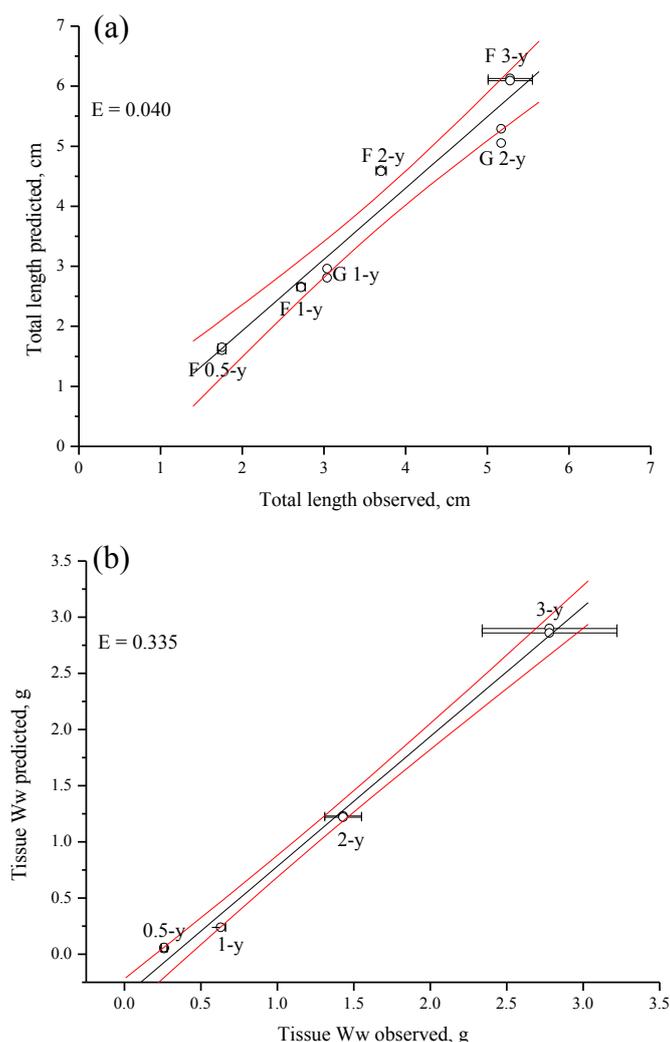
Fig. 5. Regression (black line) and 95% confidence limits (red lines) between observed and predicted data of: (a) Total Length (TL, cm; circle) of *M. galloprovincialis* in Faro (F; 0.5, 1, 2, 3 years) and Ganzirri (G; 1 and 2 years) lakes, for Site 1 and Site 2; $TL_{predicted} = -0.45 \ (\pm 0.36) + 1.19 \ (\pm 0.09) * TL_{observed}$ ($r^2 = 0.94$; $p < 0.0001$; $F = 156.62$); (b) Tissue wet weight (TWw, g; circle) of mussels 0.5, 1, 2, 3 years old in Faro lake for Site 1 and Site 2; $TWw_{predicted} = -0.37 \ (\pm 0.06) + 1.15 \ (\pm 0.04) * TWw_{observed}$ ($r^2 = 0.99$; $p < 0.0001$; $F = 865.05$). E-value reflects the variance of error obtained for each data point; assuming a null value for a perfect match and increasing value for increasing errors (Saraiva et al., 2011a). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

species fundamental niche. While the species presence in a certain area is determined by its functional tolerance limits (Kearney and Porter, 2009), its presence in ecological communities is shaped by biotic interactions such as competition (Chase and Leibold, 2003; Laughlin et al., 2012). Application in aquaculture contexts is probably the best way of testing and validating mechanistic functional models. Assuring positive economic incomes in aquaculture is achieved by reducing competition for food and mortality due to predators. In this context, predictions via these models are particularly reliable, as shown by validation exercises carried out across the recent literature (Saraiva et al., 2012; Sarà et al., 2013a) and in the present paper. Here, the deviations between predicted and observed data in Faro and Ganzirri lakes were small (see Results section). According to Sarà et al. (2013a) this slight difference could be due to the coarse resolution of environmental food concentration used in the present work that, although sufficient to depict the feeding (and growth) performance of organisms inhabiting both lakes, was probably not sufficiently fine–grained to catch such differences in size. While this is useful (CHL-a being the most common measure of particulate organic matter used across the current literature; Sarà, 2007a), it may still be an oversimplification

when describing the feeding habits of shellfish (Dame, 1996; Mazzola and Sarà, 2001; Saraiva et al., 2011a, 2012). Indeed, detritus from various sources other than fresh organic matter (Sarà et al., 2003), which is often less labile than the latter (as expressed by CHL-a) may contribute to the bivalve diet (Mazzola and Sarà, 2001; Sarà et al., 2003; Bourlès et al., 2009; Saraiva et al., 2011a,b, 2012). For example, Saraiva et al. (2011a) showed that the total particulate matter (TPM) has a sizable effect on feeding processes, inducing a reduction in ingestion rate and high production of pseudo faeces with ensuing effects on growth performance. Differences in food quality (apart from food quantity) may affect feeding traits (functional response, assimilation, etc.) and in turn individual energetic dynamics, influencing the magnitude of LH traits (viz. body size). As is widely reported in the literature (van der Meer, 2006; van der Veer et al., 2006; Rosland et al., 2009; Filgueira et al., 2011; Thomas et al., 2011), we recognize that the choice of CHL-a as a unique food descriptor for bivalves may imply a potential bias in LH trait predictions within this habitat. However, we believe that it could have resulted as minimized, particularly in the case of Faro lake, which is characterized by high depth, low residence time of superficial water and trophic conditions typical of

oligotrophic systems (Ferrarin et al., 2013). Also, an enclosed basin is characterized by very low systemic energy (minimal wave and current action) in terms of coastal environments, which probably further limits provisions of detrital food available to mussels within the lake. Finally it is of note that temperature and food data were collected for one single year. Therefore, the model prediction regarding the LH traits of *Mytilus galloprovincialis* may underestimate the inter-annual variability.

6. Functional trait-based models capture ecological and biological differences at local level

The functional mechanistic trait-based approach adopted in this study, implemented with high-resolution data such as hourly temperature, was able to capture how local environmental differences rebound on mussel growth and biodeposits production. Such a result is in line with a recent companion study showing that adopting high temporal data resolution in predictive modelling is necessary to increasing the accuracy of DEB predictions (Montalto et al., 2014). The functional mechanistic trait-based model is a reliable tool for identifying suitable habitats to house shellfish cultures and this has both ecological and economic-productive implications. A mechanistic based model is invoked from several sides as a core approach, able to increase the accuracy of our predictions in a changing world (e.g. Loreau and de Mazancourt, 2013). In a context of aquaculture and environmental impact assessment, adopting such an approach means changing the viewpoint from one based on statistical inference to one based on mechanistic quantification. The core of the GIS approach (Buckley et al., 2010) is represented, for example, by habitat characteristics, which are statistically used to infer on biological traits and ecological processes (e.g. species growth or presence/absence). In contrast, the starting point in a mechanistic trait-based approach comprises functional traits of the target organisms, which are used to mechanistically quantify ecologically relevant variables such life history traits (Kooijman, 2010; Matzelle et al., 2014) as body size, fecundity and number of spawning events. The power of this approach lies within the further integration of biological and ecological traits into the local environmental conditions (the so-called spatially-explicit environmental process; Kearney et al., 2010) which provides quantitative predictions of the ecological process; the higher the environmental temporal data resolution, the higher the accuracy of functional trait-based predictions will be (*sensu* Montalto et al., 2014).

7. Potential environmental implications related to aquaculture deriving from the functional trait-based approach

As mentioned earlier, the quantitative estimate of LH traits is a key feature of mechanistic trait-based models, representing the most important difference with respect to correlative GIS habitat-based models (Buckley et al., 2010). Most approaches to coastal resources management are based on LH traits of organisms, although this aspect is often neglected in current resource conservation programmes in aquaculture. Trait-based models can help in this regard, as quantification of these traits may be necessary to estimating local aquaculture carrying capacity (e.g. Sarà and Mazzola, 2004) and in other coastal management contexts, e.g. Allocated Zone for Aquaculture (AZA) studies. In AZA, the choice of an area in which to start new production is based first on the optimization of the cultivable species growth, irrespective of its potential environmental impact on the surroundings. The amount of faeces produced by single specimens is also important information for predicting the potential impact of production (Brigolin

et al., 2009); this is crucial in Allowable Zone of Effect (AZE) studies. In such cases, information provided by functional trait-based models integrated with that of transport hydrodynamics models (e.g. DEPOMOD; IUCN, 2009) is useful in establishing the zone extension of possible environmental effects, i.e. the AZE.

In conclusion, the present modelling exercise also shows how to apply functional trait-based models to the human exploitation of coastal waters, in our case with lagoon aquaculture. Such an approach provides opportunities to link habitat characteristics (food and water temperature) with functional traits of organisms (through depicting the fundamental portion of an ecological niche) in order to yield reliable predictions of organismal LH traits (body size and fecundity). The fine-tuned quantification of LH traits will be important when assessing the potential exploitation of coastal natural habitats for human needs and assessing potential impacts of human action in the context of global changes (see Hughes et al., 2005; Schwartz, 2012). Overall, it would seem that a scientific path towards obtaining sufficient, high-resolution information on habitat features and organismal functional traits should be at the core of future collaborative projects. It would help build the basal informative platform of the Integrated Coastal Zone Management (ICZM; Marinov et al., 2007; Nobre and Ferreira, 2009) and it should be part of the decision making process required to achieve the best threshold of environmental sustainability (CMP, 2007). Finally, the approach described in the present paper combined with population (Bacher and Gangnery, 2006), hydrodynamics (Ferrarin et al., 2013), bio-deposition (DEPOMOD; IUCN, 2009), and economic models, provides a very important tool for management strategy to optimize aquaculture production from a sustainable ecosystem standpoint, according to FAO recommendations (Soto et al., 2008).

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