Dynamic Energy Budget model parameter estimation for the bivalve *Mytilus californianus*: Application of the covariation method

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ABSTRACT

Dynamic Energy Budget (DEB) models serve as a powerful tool for describing the flow of energy through organisms from assimilation of food to utilization for maintenance, growth and reproduction. The DEB theory has been successfully applied to several bivalve species to compare bioenergetic and physiological strategies for the utilization of energy. In particular, mussels within the *Mytilus edulis* complex (*M. edulis*, *M. galloprovincialis*, and *M. trossulus*) have been the focus of many studies due to their economic and ecological importance, and their worldwide distribution. However, DEB parameter values have never been estimated for *Mytilus californianus*, a species that is an ecological dominant on rocky intertidal shores on the west coast of North America and which likely varies considerably from mussels in the *M. edulis* complex in its physiology. We estimated a set of DEB parameters for *M. californianus* using the covariation method estimation procedure and compared these to parameter values from other bivalve species. Model parameters were used to compare sensitivity to environmental variability among species, as a first examination of how strategies for physiologically contending with environmental change by *M. californianus* may differ from those of other bivalves. Results suggest that based on the parameter set obtained, *M. californianus* has favorable energetic strategies enabling it to contend with a range of environmental conditions. For instance, the allocation fraction of reserve to soma (κ) is among the highest of any bivalves, which is consistent with the observation that this species can survive over a wide range of environmental conditions, including prolonged periods of starvation.

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1. Introduction

Mussels in the genus *Mytilus* form beds on temperate shores worldwide, and have served as the cornerstone of much modern intertidal ecological theory (Paine, 1974). On the Pacific coast of North America, many ecological studies have focused on *Mytilus californianus*, which spans a broad geographic range, from southern Mexico to the Aleutian Islands (Morris et al., 1980). Over much of its range *M. californianus* forms beds in the mid intertidal zone, that in turn drive levels of biodiversity in this ecosystem (Gutiérrez et al., 2003). As ecosystem engineers, mussel beds enhance the diversity and abundance of organisms within the bed through the provision of three-dimensional habitat (Seed and Suchanek, 1992; Smith et al., 2006). Conversely, as competitive dominants, their presence can pre-emptively exclude other large organisms such as macroalgae (Paine, 1994; Robles and Desharnais, 2002). For example, Paine (1974) showed that the experimental removal of the predatory seastar *Pisaster* resulted in a downward movement in the lower zonation of *M. californianus*, which then effectively replaced macroalgae in the lower intertidal zone. Understanding the dynamics of growth, survival, and reproductive potential in this species thus has significant implications for predicting how changes in the physical environment due to climate change and other stressors will likely affect intertidal ecosystem dynamics.

While the physiology of *M. californianus* has been reasonably well studied (Bayne et al., 1976a,b; Logan et al., 2012; Place et al., 2008), several holes still exist in our knowledge which prevent a quantitative, predictive framework for anticipating how this key species will likely respond to future and ongoing environmental change. In particular, and as is true for many other species, such forecasts are complicated by a lack of information about how multiple stressors affect physiological performance (Howard et al., 2013); how environmental change affects sublethal responses such as changes in growth and reproduction (Petes et al., 2007); and how food and allocation of energy interact with environmental stress (Schneider et al., 2010). Dynamic Energy Budget (DEB) models offer a means of addressing such questions, but require thorough parameterization (Freitas et al., 2007). Recently, Kearney et al. (2010) linked biophysical models of intertidal body temperature to DEB models to examine how changing climates may affect *M. californianus* mussels in central California. Because parameters were unavailable for this species, Kearney et al. (2010) based the DEB

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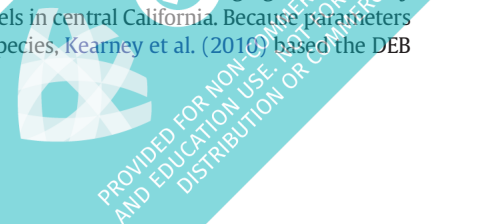
model on parameters calculated for *Mytilus edulis* (Rosland et al., 2009; van der Veer et al., 2006).

Importantly, there are several reasons to expect that the physiological responses of *M. californianus* may differ substantially from those of its congeners. This species is particularly long-lived and characteristically can live upwards of 50–100 years, unlike species in the *M. edulis* complex, which typically live for approximately 18–24 years (Seed and Suchanek, 1992; Shaw et al., 1988; Suchanek, 1981). Like its congeners (Lesser et al., 2010), *M. californianus* growth and reproductive rates are strongly affected by food availability and temperature (Bayne et al., 1976a,b; Blanchette et al., 2007). However, while species replacement among mussels in the *M. edulis* complex occurs as environmental conditions change across local (Schneider and Helmuth, 2007) and geographic (Hilbish et al., 2010) scales, *M. californianus* inhabits exposed rocky shores over a much wider latitudinal range. Thus, *M. californianus* is potentially exposed to a much broader range of environmental conditions than any one species in the *M. edulis* complex (Fly and Hilbish, 2013). These observations suggest that this species may lend itself well to the application of the DEB theory.

Here we use the covariation method described in Lika et al. (2011a,b) to estimate DEB parameters for *Mytilus californianus*. While we recognize that many of these parameters may change with patterns of local acclimatization (and particularly along an intertidal zonation gradient) these estimates are meant to serve as an initial exploration of how this ecologically important species may differ in its response to changing environmental conditions from its more well-studied congeners.

2. Materials and methods

2.1. Covariation method

We applied the covariation method for DEB parameter estimation as described in Lika et al. (2011a,b), which has been augmented by the "Add_my_pet" collection (http://www.bio.vu.nl/thb/deb/deblab/add_my_pet/index.php). Within the estimation procedure, there are constraints on parameter values to ensure that predictions are within a biologically possible range (Lika et al., 2011a,b). These constraints are defined by the use of 2 types of (single-point) *zero-variate* data: (i) *real data* (actual observations of the species of interest at specified temperatures) and (ii) '*pseudo-data*' (a set of parameters for the generalized animal at a reference temperature of 20 °C). *Real data* consist of observations such as maximum weight, age and reproduction rate as well as weight and age at birth, metamorphosis, and puberty. '*Pseudo-data*' consist of a set of parameters representative of a generalized animal, and are determined from parameter estimates of a wide range of species (Kooijman, 2010). The culmination of both types of zero-variate data constrain the range of values for each parameter estimate and allow the estimation of (abstract) parameters to fit real world observations (Lika et al., 2011a). Uni-variate data in the covariation method typically consist of sets of time-series observations of an organism in the form of independent (i.e. time) and dependent (i.e. length) variables. Weight coefficients are assigned to both the real observations and pseudo-data, reflecting the certainty in each data set, where a high weight coefficient suggests high confidence in the data used (Lika et al., 2011a). Thus, more weight is assigned to the real data than the pseudo-data, and on measurements of weight than measurements of length. Very little weight is given to length at birth, given the difficulty and uncertainty associated with the metric. Regressions within the estimation routine produce the best set of parameters that fit such observations.

The "Add_my_pet" collection provides a set of routines to estimate all parameters from all available datasets simultaneously. In this way, all information interacts to provide the most biologically realistic result. The routine effectively searches for parameters within the possible parameter space to find a set of parameter values with the least deviation between predictions and observations, done so by minimizing the weighted sum of squared difference between the two (Lika et al., 2011a,b). The routines in the Add_my_pet collection (written for MatLab® and Octave) were used to estimate DEB parameters for *M. californianus*, as well as obtain a goodness of fit value (defined as $10 (1 - \text{mean relative error})$) and completeness mark (described in Lika et al., 2011a,b). Our goal for this study was to assess the energy allocation potential of *M. californianus* rather than energy allocation strategies as a result of stress. Accordingly, we modeled subtidal individuals only, and the functional response f was set to an idealized value of 1 (*ad libitum* food supply).

Standard DEB theory assumes isomorphy, meaning the organism does not change in shape during growth (Kooijman, 2010). For this study, we extended the standard DEB to include metabolic acceleration between birth and metamorphosis, which occurs in all bivalve larval development (Kooijman, In review; Kooijman et al., 2011). In the DEB context, this means the early juvenile stages (larvae) grow as a V1-morph: surface area increases proportionally with volume, and therefore the surface-area specific assimilation rate $\dot{p}_{Am}$ and energy conductance $\dot{v}$ increase proportionally with length (Kooijman et al., 2011). At late juvenile and adult stages, isomorphic growth occurs, where the surface area is proportional to volume$^{2/3}$ (Kooijman, 2010).

2.2. Zero-variate data

Life stage and physical characteristics used for the estimation procedure were obtained from the literature, with exception of ultimate wet weight, for which realistic published data were unavailable (see Table 1 for zero-variate data from the literature and field observations used in estimation procedure). Maximum wet weights reported in literature corresponded to maximum shell lengths ~14 cm, but this is an underestimate given the reported maximum length of *M. californianus* at approximately 20 cm (Paine, 1976). To account for this discrepancy, we used an average somatic wet tissue weight of the largest mussels (approximately 19 cm) that we recorded from collections in central Oregon, US (described below). Age and physical characteristics were obtained from literature for (i) "birth", the time when feeding begins (for *M. californianus*, at the veliger larval stage, first 24–48 h following fertilization) (Bayne, 1976); (ii) metamorphosis, occurring from the pediveliger larval stage in *Mytilus californianus*; and (iii) puberty, when animals are first able to reproduce. We recognize that the use of intertidal individuals may represent a potential source of error due to potential influences of aerial exposure on age–length relationships, but because of predation no subtidal populations were available for analysis.

2.3. Uni-variate data

Uni-variate datasets used to estimate parameters via the covariation method (Lika et al., 2011a,b) include observations of: (i) length vs. dry weight (Fox and Coe, 1943) and field observations of (ii) length vs. total tissue weight and (iii) age vs. length of low intertidal individuals.

Animals were collected in June 2012 from the low intertidal zone at Strawberry Hill, OR (44.250° N, −124.115° W) over the full range of size classes available to represent biometrics of subtidal individuals. Approximately 5 animals were sacrificed per size class (size class = every 2 cm, ranging from 1 cm to 19 cm) over 3 transects spanning the low rocky intertidal zone. Biometric data include shell length and somatic tissue weight. To obtain a time vs. length curve, shells were cross-sectioned and aged by counting annual lines near the umbo region (Sarà et al., 2013). While this is an accepted method of age determination for other bivalve species (Lutz, 1976; Seed and Suchanek, 1992), it has not been commonly used for *M. californianus*. We therefore made the simplifying assumption that rings were produced annually, as in other species in the genus.

Table 1
Observed vs. predicted zero-variate data with associated temperatures used in estimation procedure. Weight refers to the weight coefficient applied to each data point in the estimation procedure.

Parameter description	Symbol	Unit	Observed value	Predicted value	Weight	Reference
Age at birth	a_b	d	1	1.143	1000	Seed (1976)
Temperature for a_b	T_{ab}	°C	18	–	–	Fox and Coe (1943)
Age at metamorphosis	a_j	d	3	3.151	10	Bayne (1976)
Temperature for a_j	T_{aj}	°C	18	–	–	Fox and Coe (1943)
Age at puberty	a_p	d	365	390.5	10	Seed (1976)
Temperature for a_p	T_{ap}	°C	18	–	–	Fox and Coe (1943)
Life span	a_m	d	7300	8065	10	Suchanek (1981)
Temperature for a_m	T_{am}	°C	18	–	–	Fox and Coe (1943)
Physical length at birth	L_{wb}	cm	0.0180	0.01603	0	Bayne (1976)
Physical length at metamorphosis	L_{wj}	cm	0.0260	0.03641	10	Bayne (1976)
Physical length at puberty	L_{wp}	cm	4	4.886	10	Suchanek (1981)
Ultimate physical length	L_{wm}	cm	20	16.21	100	Paine (1976)
Dry weight at puberty	W_{dp}	g	0.325	0.337	1000	Fox and Coe (1943)
Ultimate wet weight	W_{wm}	g	100	102.5	10,000	Field measurements described in this study
Maximum reproduction rate	$\dot{R}_m$	# eggs d^{-1}	12e6/365	2.965E+04	10	Seed, (1976) and Widdows (1991)
Temperature for R_m	$T_{\dot{R}m}$	°C	18	–	–	Fox and Coe (1943)

Notation after Kooijman (2010).

2.4. Inter-specific comparisons

Primary parameter values for Bivalvia inter-specific comparisons were obtained from the website http://www.bio.vu.nl/thb/deb/deblab/addmypet/html/primaryparameters.html, with the exception of *Mytilus californianus* (this study) and *Brachidontes pharaonis* (Montalto et al., in this 2014). Published parameter sets are standardized for body temperature, food availability, and body size to permit comparisons between species in the following way: rates are fixed to a common temperature T_{ref} of 20 °C, scaled functional response f is set to 1, and maximum structural length L_M is set to 1 cm.

3. Results and discussion

Table 1 shows observed and predicted real zero-variate data for *M. californianus*, as well as weight coefficients used. Table 2 presents primary DEB parameters obtained for *M. californianus* which were compared against those for other bivalve species at a reference temperature of 20 °C (Table 3). Comparison of model predictions against observed (uni-variate) datasets for *M. californianus* are shown in Fig. 1. It is important to note that while the parameters presented in Table 3 represent the most up to date values from "add_my_pet collection" database, which includes corresponding references, they may not necessarily represent the most recent (or all of the) published parameter values in the literature.

3.1. Size and shape

Comparisons of primary parameters among bivalve species in the context of DEB assume that the physical design (and physical design parameters) of an organism depend on its maximum size, while parameters influencing the biochemical environment of an organism are size-independent, both inter- and intra- specifically (Kooijman, 2010). Three physical design parameters depend on maximum size in the standard DEB model: surface-area-specific assimilation rate $\{\dot{p}_{Am}\}$ maturity threshold at birth E_H^b, and maturity threshold at puberty E_H^p. Since maximum size differs among species, a dimensionless zoom factor z is applied, and is used for comparison of physical parameters of an organism to a "reference organism" of maximum length $(L_{Mref}) = 1$ cm (Kooijman, 2010). Most compound parameters are derived in some way using the zoom factor. Zoom factors between bivalve species differ substantially, ranging from 0.02 (*Mytilaster mimimus*) to 4.69 (*Mytilus edulis*). *M. californianus* fell within the middle of this range at 1.72.

The shape coefficient converts physical lengths (in this study shell length) to structural length, following from the equations $L = \delta_M L_w$ and $V = (\delta_M L)^3$. The relationship between volume and length, which varies significantly between species of different morphologies, is captured using the shape coefficient. The shape coefficient of *M. californianus* (0.24) fell within the range of the rest of the bivalve species, with a mean of 0.28 and coefficient of variation between all bivalve species of 0.34 (Table 3). However, this value only applies to the growth of late juveniles and adults, as animals exhibiting metabolic acceleration likely have a

Table 2
Parameter values and standard deviations (reference temperature $T_{ref} =$ 20 °C) obtained using the covariation method estimation procedure (Lika et al., 2011a,b). Parameters without standard deviations shown were not estimated, but fixed *a priori*.

Parameter description	Symbol	Unit	Value	Standard deviation
Maximum specific searching rate	$\{\dot{F}_m\}$	L cm^{-2} d^{-1}	128	–
Digestion efficiency of food to reserve	κ_X	–	0.7193	–
Energy conductance	$\dot{v}$	cm^{-1}	0.01431	5.674E−02
Allocation fraction to soma	κ	–	0.9885	–
Reproduction efficiency	κ_R	–	0.9165	–
Volume-specific somatic maintenance rate	$[\dot{p}_M]$	J cm^{-3} d^{-1}	15.15	33.63
Maturity maintenance rate coefficient	$\dot{k}_J$	d^{-1}	0.002	–
Specific cost for structure	$[E_G]$	J cm^{-3}	3140	4140
Maturity at birth	E_H^b	J	2.125E−06	3.79E−05
Maturity at metamorphosis	E_H^j	J	2.495E−05	5.185E−04
Maturity at puberty	E_H^p	J	74.55	976.5
Zoom factor	z	–	1.724	2.023
Shape coefficient	δ_M	–	0.2417	0.185

Notation after Kooijman (2010).

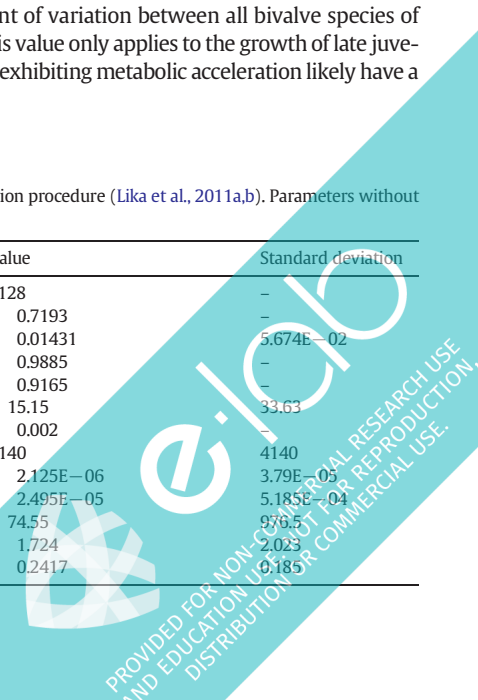**Table 3**

Some DEB primary parameters of bivalve species at reference temperature $T_{ref} = $ 20 °C; all data obtained from the add_my_pet collection (http://www.bio.vu.nl/thb/deb/deblab/add_my_pet/Species.html).

Bold text indicates values published in this issue; symbol notation from Kooijman (2010) see text.

Species	z	δ_m	κ_X	p_{Am}	v	κ	κ_R	$[p_M]$	$[E_G]$	E_H^b	E_H^j	E_H^p
M. arenaria	3.06	0.27	0.80	52.50	0.01	0.896	0.95	15.37	3069	2.46E−04	5.53E−04	2.45E+01
B. pharaonis	**0.04**	**0.31**	**0.75**	**16.4**	**0.02**	**0.998**	**0.95**	**14.24**	**2478**	**1.33E−07**	**3.71E−03**	**4.80E−01**
M. minimus	0.02	0.43	0.80	0.61	0.02	0.999	0.95	39.61	2420	2.89E−08	4.54E−03	6.39E−02
M. californianus	**1.72**	**0.24**	**0.72**	**26.42**	**0.01**	**0.989**	**0.92**	**15.15**	**3140**	**2.13E−06**	**2.50E−05**	**7.46E+01**
M. edulis	4.69	0.29	0.53	79.70	0.07	0.809	0.95	13.74	4783	2.00E−05	2.00E−05	4.48E+01
P. viridis	0.88	0.16	0.70	26.79	0.01	0.990	0.95	30.19	3123	2.51E−06	1.34E−04	5.35E−01
C. gigas	1.40	0.12	0.33	61.04	0.01	0.290	0.95	12.69	2674	4.54E−04	4.00E−01	8.56E−01
P. maximus	2.01	0.38	0.80	72.08	0.02	0.812	0.95	29.05	2976	6.24E−04	1.28E−01	3.45E+03
C. edule	0.67	0.35	0.80	11.02	0.02	0.980	0.95	16.13	2527	5.19E−06	1.16E−04	4.49E+00
E. directus	0.55	0.16	0.80	39.27	0.01	0.991	0.95	70.51	2491	5.10E−07	5.68E−05	1.33E+01
M. balthica	0.30	0.29	0.80	21.36	0.01	0.990	0.95	69.48	2279	7.95E−06	2.01E−04	9.01E+00
R. philippinarum	0.09	0.35	0.70	2.57	0.01	0.987	0.95	28.24	3050	2.52E−06	1.28E−01	1.52E−01

different shape coefficient during larval growth due to their morphology at the early juvenile (V1-morphic) stage (Kooijman et al., 2011).

In DEB theory, accelerating species undergo a metabolic switch at metamorphosis. In the early juvenile phase, larvae follow the DEB rules of a V1-morph and grow exponentially (surface area increases proportionately with volume). Post-metamorphosis stages assume isomorphy and follow von Bertallanffy growth (Kooijman, 2010; Kooijman et al., 2011). The DEBtool routine 'get_tj' was used to determine the scaled time since birth at metamorphosis τ_j, scaled maturity at birth and metamorphosis ($v_H^j = 11.74 v_H^b$ in this case), and from there, scaled length at birth l_b and metamorphosis l_j (0.0022 and 0.0051, respectively). Since $l_j/l_b = 2.27$, we can infer that maximum specific assimilation as well as energy conductance (the primary parameters relating surface area and volume) increase by a factor of 2.27 from birth until metamorphosis.

3.2. Feeding and assimilation

The specific maximum assimilation rate follows from the relationship $z L_{mref} = \frac{\kappa \{\dot{p}_{Am}\}}{[\dot{p}_M]}$, and was estimated at 26.42 for *M. californianus*. There is a broad range of $\{\dot{p}_{am}\}$ values reported for bivalve species (0.61 for *M. minimus* to 79.70 for *M. edulis*). Additionally, under optimal food conditions, *M. californianus* exhibits a higher digestion efficiency κ_X than *M. edulis*, increasing the fraction of energy in food that is fixed in reserve by 26% (0.72 vs. 0.53 in *M. californianus* and *M. edulis*, respectively). A higher efficiency of energy acquisition from food is likely an energetic advantage under low food conditions, or in the presence of other stressors such as elevated temperature (Schneider et al., 2010) or ocean acidification (Thomsen et al., 2013) which may in part explain why *M. californianus* is a dominant competitor in rocky intertidal communities (Paine, 1974; Robles and Robb, 1993; Robles et al., 1995).

3.3. Maintenance

The somatic maintenance cost $[\dot{p}_M]$ for *M. californianus* was estimated to be 15.15 J cm^{-3}, a value only slightly higher than that of *M. edulis* (13.74 J cm^{-3}). This value falls in the lower range reported across all bivalve species (12.69–70.51 J cm^{-3}; Table 1). $[E_G]$ is the amount of reserve energy required to synthesize a unit volume of structure, including the energy stored in tissue and overhead costs for anabolism. This value was lower in *M. californianus* (3140 J cm^3) than in *M. edulis* (4783 J cm^3), however these species had the highest value for $[E_G]$ in comparison with the other bivalves listed. The energetic investment in life cycle transitions (maturity) E_H^b, E_H^j and E_H^p for *M. californianus* were 2.13E^{-06}, 2.50E^{-05} and 7.46E^{+01} J cm^3, respectively. Interestingly, the difference between maturity at birth E_H^b and maturity at metamorphosis E_H^j was the smallest in comparison with other bivalves implying *M. californianus* may reduce the time spent between these two phases and therefore complete metamorphosis sooner. After metamorphosis, the larvae reach the pediveliger stage, byssus threads begin to form and the pediveliger is able to settle. At least theoretically, the short time spent completing metamorphosis could be an adaptive strategy of *M. californianus* to pre-emptively settle before other larvae in the water column, potentially explaining the competitive-dominant nature of this species. These results demonstrate the importance of using mechanistic approaches to understand relative ability of California mussels to survive in extreme and highly variable intertidal zones.

3.4. Allocation fraction to soma

DEB theory assumes that energy assimilated from food directly enters the reserve, which is then spent on growth and somatic maintenance at a fixed fraction (κ). The remaining amount (1-κ) is spent on
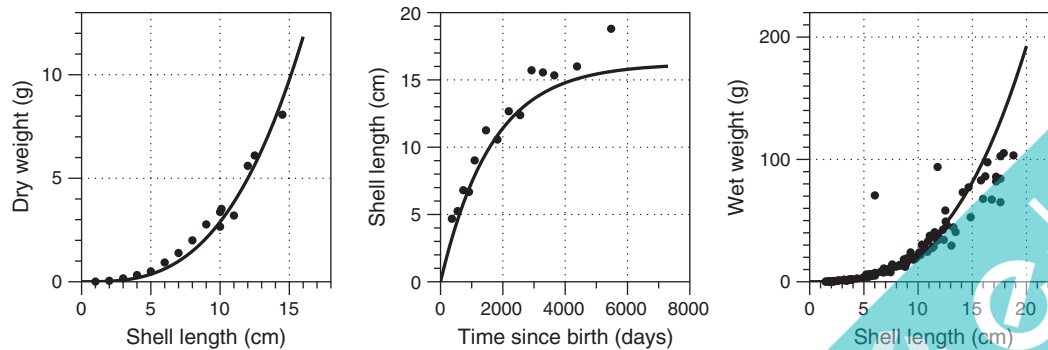

Fig. 1. Observed uni-variate data sets (points) and predictions (lines) resulting from the covariation method. Completeness mark and goodness of fit value (Lika et al., 2011a,b) of 2.5 and 8.1, respectively. It is important to note that the age vs length and length vs wet weight data here are taken from field measurements, and lifetime body temperatures and functional responses are variable and unknown.

maturation/reproduction and maturity maintenance. The κ value for *M. californianus* fell within the high range of the rest of the bivalve species at 0.99, 18% higher than *M. edulis*. These results are consistent with the comparatively long life span of *M. californianus* when compared to mussels in the *M. edulis* complex in that more energy appears to be devoted to somatic maintenance than reproduction.

3.5. Completeness and goodness of fit

The covariation method uses many types of real data sets in the parameter estimation procedure, and generally, the more data used in the estimation imply more trustworthy parameters. However, there is an inherent risk of error with variable sources of data. For example, data taken from the field will likely vary between geographic locations or from lab experiments and may be affected by the history of temperature and feeding. For example, while we aimed to model subtidal individuals only, two of our uni-variate datasets were from low intertidal populations. Previous studies with *M. edulis* have shown that aerial exposure has a clear effect on shell length (Saraiva et al., 2011), thus comparisons with true subtidal populations will be an important step in the future, as will be the incorporation of the effects of aerial exposure for intertidal populations.

In addition to evaluating the quality of the data used to estimate a parameter set, a completeness mark (ranked 1–10) and a goodness of fit value (10(1 − mean relative error)) are assigned to each parameter set as estimates of reliability. Using the completeness scale provided in Lika et al. (2011a), we assigned a completeness mark of 2.5 to our data and calculated a goodness of fit mark of 8.1. See Fig. 1 for observed uni-variate data and predictions.

4. Conclusion

At the most basic level, Dynamic Energy Budget models provide a framework from which we can describe the utilization of energy at the individual level in response to changes in its environment. Having a basic understanding of energy allocation allows us to understand important bioenergetic strategies, which are captured in the parameter values. For example, coupled DEB and biophysical models have been proven as an effective means for predicting spatial and temporal patterns in reproduction and growth under changing environmental conditions (Kearney et al., 2010, 2013; Sarà et al., 2011). Importantly, these models have shown that without a detailed understanding of physiological performance, incorrect predictions of how species and populations will likely respond to environmental change can occur. For example, Kearney et al. (2012) showed that the return time of sublethal exposures can significantly affect reproductive output in lizards, and that these patterns cannot be assessed using traditional climate envelope approaches.

While understanding the response of a species at the individual level is a key first step, successful predictions of ecosystem-level responses to environmental change will require an understanding of how populations of organisms, and species interactions between populations, are affected by environmental change. The DEB theory can provide a valuable tool in our arsenal for making predictions that extend far beyond simple predictions of mortality, and may potentially emerge as a means of examining processes occurring at multiple levels of complexity.

Acknowledgments

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