

## ENERGY DENSITY EMPIRICAL PREDICTOR MODELS FOR THREE COASTAL CRAB SPECIES IN THE SOUTHWESTERN ATLANTIC OCEAN

Javier Ciancio<sup>1,\*</sup>, Nicolás Suárez<sup>1</sup>, and Pablo Yorio<sup>1,2</sup>

<sup>1</sup> Centro Nacional Patagónico-CONICET, Blvd. Brown 2915, 9120 Puerto Madryn, Chubut, Argentina

<sup>2</sup> Wildlife Conservation Society, Amenábar 1595, P 2, Of. 19, C1426AKC, Ciudad de Buenos Aires, Argentina

### ABSTRACT

Energy density was measured for key intertidal and subtidal crab species in the Southwestern Atlantic Ocean. Empirical models were developed to link energy density to water content (expressed as dry weight) and the fit to data was compared between different taxonomic and gender aggregations. Predictive power of models with different levels of aggregation and the effect of using a model of a surrogate species or group were also evaluated. *Neohelice granulata* (Dana, 1851) (3728 J/g wet weight) contained the highest energy density followed by *Cyrtograpsus angulatus* Rathbun, 1914 (3365 J/g wet weight), and *C. altimanus* Dana, 1851 (3042 J/g wet weight). Females (3645 J/g wet weight) showed higher energy density compared to males (3074 J/g wet weight). Dry weight of whole individuals provided good energy density predictions, with low predictive error when using species or same genus models (6.4-9.6% for the median error). Predictive power improved when more specific levels of taxonomic aggregation were employed. Interestingly, the two congeneric *Cyrtograpsus* did not differ in their energy density predictor model, suggesting a unique model could be used for this genus. This paper provides valuable inputs for bioenergetic modeling in coastal ecosystems in the Southwestern Atlantic.

**KEY WORDS:** crabs, energy density, salt marsh, water content

**DOI:** 10.1163/1937240X-00002178

### INTRODUCTION

Energy is a common exchange currency for any living organism, and the way it is used is crucial for individual survival and is strongly shaped by natural selection. Individual behavior and life history, population dynamics, and ecosystem metabolism could be studied in a bioenergetic perspective (McNab, 2002; Brown et al., 2004). The first step in any bioenergetic study is the estimation of energy density, either by direct or indirect methods. As Ciancio et al. (2007) pointed out, energy density by itself could be used to evaluate a diverse array of ecological hypothesis, e.g., relate diet quality to offspring growth or breeding performance (Wanless et al., 2005), explain the foraging behavior of predators (Benoit-Bird, 2004), and determine the physiological status of organisms (Schultz and Conover, 1997). In addition, bioenergetic models, which are very sensitive to energy density of organisms, are widely used to investigate a diverse array of environmental problems such as the potential effects of fish introductions (Ruzycki et al., 2003; Ciancio et al., 2010), global warming (Hill and Magnuson, 1990), as well as other related problems in aquatic ecology (Brant and Hartman, 1993; Trudel and Rasmussen, 2001; Harvey et al., 2002).

Despite the relevance of energy density for ecological studies, information is still unavailable for many key species in several regions. Moreover, the energy density for the same species can vary considerably with individual size or among seasons (e.g. Hislop et al., 1991; Zwarts and

Wanink, 1993; Pedersen and Hislop, 2001; Brey et al., 2010). The traditional methods to estimate energy density, adiabatic bomb calorimetry and proximate analysis, are resource and time consuming processes (Craig et al., 1978). Hartman and Brant (1995) presented empirical relationships between energy density and less costly variables to estimate fish energy density, based on its negative relationship with water content in tissues (measured as percent dry weight). Ciancio et al. (2007) validated these empirical models for a large and diverse data set of Patagonian aquatic invertebrate and vertebrate organisms, and demonstrated that their use resulted in a low predictive error. More recently, James et al. (2012) found similar results in a meta-analysis for aquatic and terrestrial invertebrates, showing that these models are not affected by taxonomic, seasonal, or spatial variability.

Given the growing interest and potential applicability of bioenergetic modelling in aquatic systems, energy density values or predictor models for additional taxa are needed. This is more evident for crabs, for which there are a few available estimations. *Neohelice granulata* (Dana, 1851), *Cyrtograpsus altimanus* Rathbun, 1914, and *C. angulatus* Dana, 1851 are widely distributed crab species inhabiting brackish coastal lagoons, salt marshes, mudflats, and rocky shores of the Southwestern Atlantic Ocean in Brasil, Uruguay, and Argentina (Spivak, 1997; Boschi, 2000). These species, particularly the burrowing crab, *N. granulata*, constitute key species for coastal ecosystems (Bortolus and Iribarne, 1999; Botto et al., 2005; Gutiérrez et al., 2006), and are prey of several waterbird, fish and other crab

\* Corresponding author; e-mail: ciancio@cenpat.edu.ar

ies (Spivak, 1997; García et al., 2008; Josens et al., 2010; Berón et al., 2011; Suárez et al., 2011). The aim of this study was to: (1) determine the energy density by direct bomb calorimetry of these three Southwestern Atlantic Ocean crab species, and (2) generate empirical models correlating energy density with water content and evaluate their predictive power and error.

## MATERIALS AND METHODS

Fifty five individuals were sampled with size ranging from 8.3 to 34.3 mm carapace length. Samples of *N. granulata* and *C. angulatus* were collected from the Bahía San Blas protected area, Buenos Aires Province, Argentina (40°33'S, 62°16'W) during November 2011 and of *C. altimanus* from Bahía Nueva, Chubut Province, Argentina (42°45'S, 65°02'W) during December 2011. Crabs were randomly collected from intertidal areas, and body size of each individual was measured as maximum carapace width (CW) with digital callipers to the nearest 0.1 mm. Crabs were then categorized as "small" (CW ≤ 15 mm), "medium" (15 < CW ≤ 25 mm) and "large" (CW > 35 mm). Sex was identified by the shape of the pleon, and the reproductive status of females (presence of eggs) was noted. Individuals were chopped, homogenized, dried in an oven at 60-80°C for 24-72 hours, and then ground to powder. Wet and dry weights were recorded with a precision of 0.001 g by weighing the homogenate before and after drying. One-gram pellets, consisting of whole-body samples of 1-6 individuals (Table 1), were pressed and burned at 30 atmospheres of oxygen in a bomb calorimeter (Parr model 1241) to determine gross energetic content. Fuse wire corrections were determined after each combustion event. Energy density is expressed in Joules/gram (J/g) wet weight (WW) and Joules/gram wet weight ash free, estimated in the same way as WW but extracting the mass of ashes from the mass of the pellet (AFWW = J/(mass pellet - mass of ashes after combustion)). Energy density is expressed in AFWW to explore the effect of the large exoskeleton of crabs, which could constitute

a large fraction of the dry mass but produce a small amount of heat during the combustion and remain mostly as ashes.

An empirical linear model with energy density (ED) as the dependent variable and percent dry weight (DW) as independent variable was used:

$$ED = a + bDW$$

A likelihood ratio test was used in order to compare the fit of the model to different species, with the null hypothesis being that there were no differences in slope and intercept in pair wise group comparisons (Hilborn and Mangel, 1997). Four types of regressions were calculated, with different levels of aggregation of the data (species, genus, sex, and all data). Hence, the following regressions were considered: *C. altimanus*, *C. angulatus*, *N. granulata*, *Cyrtograpsus* spp., males, females, and all individuals (Table 2).

The predictive power of regressions was evaluated using a goodness-of-fit criterion that depends on prediction errors. For each of the  $n$  individual samples available, we obtained a prediction for energy density from its observed dry weight and the linear model fitted to the remaining points. The proportional distance between the prediction obtained in such manner and the observed energy density was used as a prediction error for that observation ("one item-out cross validation," Linhart and Zucchini, 1986). Median and 90th percentile of observed errors were used as measures of the predictive power of different regression models. To evaluate the costs of aggregating species or using "surrogate" species models in the estimation of specific caloric contents, prediction errors from each of the species-specific regressions were compared with those derived from regressions for aggregated taxonomic group (All species or models of *Cyrtograpsus*, Table 3), with the species under scrutiny excluded. The effect of species and sex on energy density was explored using a two-way ANOVA. Normality of data was visually inspected using qqplot and homogeneity of variances by the Bartlett's test. All statistical analyses were performed in R software version 2.15.1 (R Development Core Team, 2011).

Table 1. Summary of the energy density estimated for male and female *Neohelice granulata*, *Cyrtograpsus altimanus* and *C. angulatus* of different size and reproductive status. N/pellet is the number of individuals included in each pellet burned in the calorimeter. Energy density is expressed in Joules per gram wet weight (WW) and as Joules per gram ash free wet weight (AFWW). The size range is expressed in millimetres. Means are presented ± 1 SD.

Species	Sex	Size category	Size range	N/pellet	% dry weight	ED (J/gWW)	ED (J/gAFWW)
<i>C. altimanus</i>	Male	small	8.3-13.6	6	32.8	2717	3113
	Male	medium	15.1-23.2	3	34.2	3101	4141
	Male	medium	15.8-24.4	2	30.7	2905	3820
	Female	small	8.8-13.8	6	37.3	3380	4768
	Female	medium	19.3-24.4	2	34.5	3221	4272
	Female	medium	16.4-23.0	4	25.4	2929	2841
<i>C. angulatus</i>	Male	small	9.8-14.7	4	28.7	2487	3879
	Male	medium	12.3-13.8	2	25.9	2287	2916
	Male	large	34.3	1	35.8	3354	4646
	Female	small	11.3-14.9	3	43.6	4116	4694
	Female	medium	18.4-23.8	2	41.3	3946	5509
	Female	large	32.6	1	31.8	3363	4194
	Female	large	29.4	1	28.9	3785	3869
<i>N. granulata</i>	Male	small	8.9-13.2	5	41.3	3887	4475
	Male	medium	15.4-18.5	2	34.2	3581	4600
	Male	large	33.6	1	28.2	3352	4711
	Female	small	9.5-13.9	4	40.2	4289	5138
	Female	medium	16.2-23.4	2	32.5	3637	4320
	Female	large	32.9	1	29.8	3442	4497
	Female	medium	18.1-23.7	2	26.8	3889	5041
	Female	large	29.4	1	25.3	3750	4797
Mean <i>C. altimanus</i>						3042 ± 239	3826 ± 729
Mean <i>C. angulatus</i>						3334 ± 707	4244 ± 817
Mean <i>N. granulata</i>						3728 ± 297	4697 ± 283
Mean males						3074 ± 523	4033 ± 664
Mean females						3646 ± 393	4495 ± 690

Table 2. Linear regression models between energy density and percent dry weight for all species and groups of species analyzed with intercept  $a$ , slope  $b$ , and their predictive power, expressed as the median and 90th percentile of error. The first value corresponds to the model fitted to energy density expressed in Joules per gram wet weight and the second value to energy density expressed in Joules per gram ash free wet weight.

	Regression			Error		N
	$r^2$	$a$	$b$	Median	90th percentile	
All sp.	0.28/0.26	1721/2167	51/64	8.0/8.4	26.3/36.5	21
Males	0.62/0.24	193/1744	88/70	11.2/9.7	17.8/35.4	9
Females	0.26/0.29	2589/2533	31/59	10.1/9.5	15.7/21.9	12
<i>Cyrtograpsus</i> spp.	0.55/0.72	740/70	74/120	6.2/9.6	20.4/19.3	13
<i>C. altimanus</i>	0.38/0.72	1868/-1105	36/151	6.4/8.3	18/21.9	6
<i>C. angulatus</i>	0.62/0.77	536/656	82/106	6.6/5.7	28/26	7
<i>N. granulata</i>	0.3/00	2844/4813	27/3.5	7.8/6.6	11.2/11.4	8

## RESULTS

The percent dry weight ranged from 24.30 to 43.50% (Table 1). Energy density ranged from 2287 to 4289 J/g WW and 2841 to 4289 J/g AFWW (Table 1). Two-way ANOVA indicated that energy density mean values differed among species and between sexes expressed both in WW ( $P = 0.006$  and  $0.008$ , respectively) and AFWW ( $P = 0.033$  and  $0.036$ , respectively). The interaction between sex and species was not significant for both models ( $P = 0.07$  and  $0.49$ ). *Neohelice granulata* showed the highest ED values, and females showed higher values than males (Table 1).

Energy density, expressed either in J/g wet weight, or expressed in J/g ash free wet weight was positively correlated with percent dry weight for species specific models ( $r^2 = 0.30-0.77$ ), males ( $r^2 = 0.24-0.62$ ), females ( $r^2 = 0.26-0.29$ ), *Cyrtograpsus* spp. ( $r^2 = 0.55-0.72$ ), all the data grouped together ( $r^2 = 0.28-0.26$ ) except for the model that included the energy density expressed in an ash free base for *N. granulata* ( $P = 0.85$ ) (Fig. 1; Table 2). Most of the models had positive intercepts (70-2844) and low slope values (27-151). Species pairwise comparisons of slopes and intercepts showed that *C. angulatus* and *C. altimanus* regressions were not significantly different for values expressed as WW and AFWW (likelihood ratio test  $P = 0.21$  and  $0.26$ , respectively) and differed from *N. granulata* (both  $P_{\text{values}} < 0.001$ ) for energy density expressed in a WW base. Sex regressions differed for values expressed as WW (likelihood ratio test  $P = 0.015$ ) but no difference was found when comparing energy density expressed in an AFWW base (likelihood ratio test  $P = 0.24$ ).

Table 3. Predictive error of using surrogate species regressions, derived from regressions for aggregated taxonomic group, with the species under scrutiny excluded. The first value corresponds with the model fitted to energy density expressed in Joules per gram wet weight and the second value fitted to energy density expressed in Joules per gram ash free wet weight.

	All sp. model		<i>Cyrtograpsus</i> model	
	Median	90th percentile	Median	90th percentile
<i>C. altimanus</i>	13.7/12.2	23.3/44.3	6/3.4	7/25
<i>C. angulatus</i>	6.4/10.3	28.3/23.5	7/11.9	16.5/16.7
<i>N. granulata</i>	14/7.5	30.1/15.1		

The median prediction errors were under 9% in all regressions, and the 90th percentiles of error were under 26% for individual species regressions (Table 2). Prediction errors were larger for species grouped regressions (median = 6.20-11.20%, 90th percentile = 19.30-36.50). While the prediction error did not vary significantly for energy density expressed in WW or AFWW, the variance explained by the models (expressed here by  $r^2$ ) was larger for the species of *Cyrtograpsus* when the energy density was expressed in AFWW. Using surrogate regressions also provided low prediction errors. The errors for the median ranged from 6 to 12% in the case of the genus model (*Cyrtograpsus* model), and from 6 to 14% for the all sp. model (Table 3).

## DISCUSSION

The present work provides the first estimate of the energy density of *C. altimanus* and energy density predictor models for the three main crab species inhabiting the southwestern Atlantic coast of South America. Previous studies of the energy content of *N. granulata* and *C. angulatus* report estimates that were based only on their soft tissues (García et al., 2008; Josens et al., 2010; Berón et al., 2011), yet whole body energy density values provided in this study are more appropriate for bioenergetic modeling of predator-prey interactions (Hanson et al., 1997). Interestingly the two congeneric *Cyrtograpsus* species showed similar values and did not differ in their energy density predictor model.

Because pellets consisted of whole individual crabs, including exoskeleton, our energy density predictor models did not fit as well ( $r^2 = 0.24-0.77$ ) compared to other taxa in which hard structures represent a smaller fraction of dry weight, such as many species of fish or molluscs ( $r^2$  range 0.93-0.99, Ciancio et al., 2007). Therefore, energy density expressed in AFWW was included in the analysis in an attempt to compensate the effect of exoskeleton on predictor models. As expected, models using values expressed in AFWW offered a better fit for both *Cyrtograpsus* species models ( $r^2$  WW = 0.38 and 0.62;  $r^2$  AFWW = 0.72 and 0.77 for *C. altimanus* and *C. angulatus* respectively). Using same-genus regression models, with similar prediction errors (Table 3). *N. granulata* showed a different and weak relationship between energy density and DW, which could be driven by a different body composition than *Cyrtograpsus* crabs. The clear differences among models

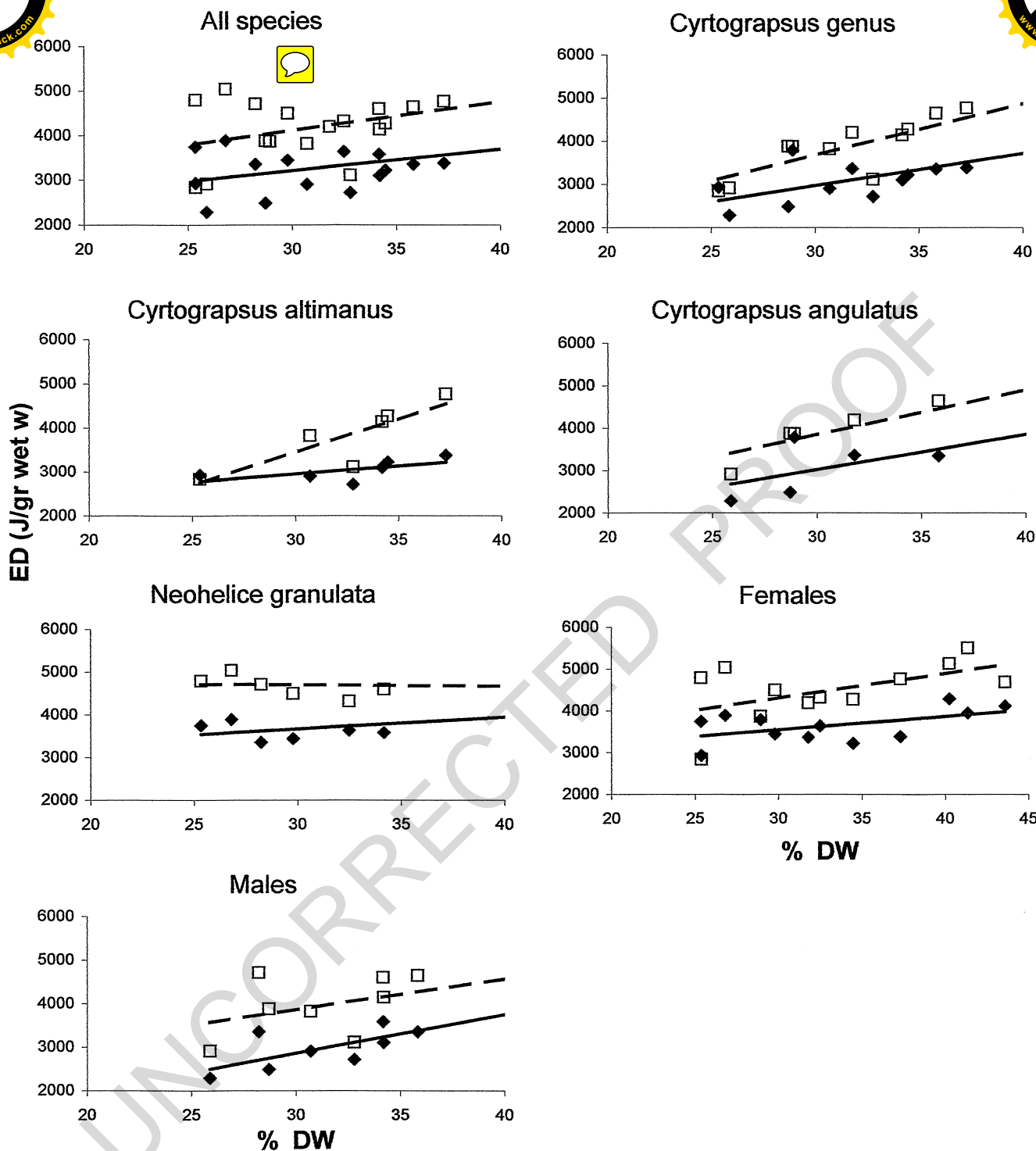


Fig. 1. Empirical relationship between energy density and % of dry weight for the three species and groups analyzed in this study. Energy density is expressed in Joules per gram wet weight (WW, filled symbols) and as Joules per gram ash free wet weight (AFWW, open squares).

in intercepts and slopes may be explained by the variation in the amount of different body components (Zwarts and Wanink, 1993), very likely the different proportion of calcareous structures among these crab species. Females showed higher mean energy density than males, likely as a result of the accumulation of lipids in gonads which are larger in females than in males.

Seasonal and ontogenetic changes in energy density have been reported for a diverse array of aquatic species (Brawn et al., 1968; Pedersen and Hislop, 2001; Breck, 2008). Therefore, the energy density estimates obtained in this study (Table 1) should be carefully used when bioenergetic modelling without considering seasonal or ontogenetic changes and the sexual or physiological status of



ps. However, the empirical relationships between energy density and dry weight (Table 2) are not affected by these variables (Ciancio et al., 2007; James et al., 2012), providing energy density predictors that could be used under any condition.

#### ACKNOWLEDGEMENTS

We thank the Wildlife Conservation Society and Agencia Nacional de Promoción Científica y Tecnológica (PICT 2010-203) for financial support, Centro Nacional Patagónico (CONICET) for institutional support, and Dirección de Administración de Áreas Protegidas (Ministerio de Asuntos Agrarios Provincia de Buenos Aires) for the permits to work at Bahía San Blas Reserve.

#### REFERENCES

- Benoit-Bird, K. J. 2004. Prey caloric value and predator energy needs: foraging predictions for wild spinner dolphins. *Marine Biology* 145: 435-444.
- Berón, M. P., G. O. García, T. Luppi, and M. Favero. 2011. Age-related prey selectivity and foraging efficiency of Olrog's Gulls (*Larus atlanticus*) feeding on crabs in their non-breeding grounds. *Emu* 111: 172-178.
- Bortolus, A., and O. Iribarne. 1999. Effects of the SW Atlantic burrowing crab *Chasmagnathus granulata* on a *Spartina* salt marsh. *Marine Ecology Progress Series* 178: 79-88.
- Boschi, E. E. 2000. Species of decapod crustaceans and their distribution in the American marine zoogeographic provinces. *Revista de Investigación y Desarrollo Pesquero* 13: 7-136.
- Botto, F., I. Valiela, O. Iribarne, and J. Alberti. 2005. Impact of burrowing crabs on C and N sources, control, and transformations in sediments and food webs of SW Atlantic estuaries. *Marine Ecology Progress Series* 293: 155-164.
- Brant, S. B., and K. J. Hartman. 1993. Innovative approaches with bioenergetics models: future applications to fish ecology and management. *Transactions of the American Fisheries Society* 122: 731-735.
- Brawn, V. M., D. L. Peer, and R. J. Bentley. 1968. Caloric content of the standing crop of benthic and epibenthic invertebrates of St. Margaret's Bay, Nova Scotia. *Journal of the Fisheries Research Board* 25: 1803-1811.
- Breck, J. E. 2008. Enhancing bioenergetics models to account for dynamic changes in fish body composition and energy density. *Transactions of the American Fisheries Society* 137: 340-356.
- Brey, T., C. Müller-Wiegmann, Z. M. C. Zittier, and W. Hagen. 2010. Body composition in aquatic organisms – a global data bank of relationships between mass, elemental composition and energy content. *Journal of Sea Research* 64: 334-340.
- Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a metabolic theory of ecology. *Ecology* 85: 1771-1789.
- Ciancio, J. E., D. A. Beauchamp, and M. A. Pascual. 2010. Marine effect of introduced salmonids: prey consumption by exotic steelhead and anadromous brown trout in the Patagonian Continental Shelf. *Limnology and Oceanography* 55: 2181-2192.
- , M. A. Pascual, and D. A. Beauchamp. 2007. Energy density of Patagonian aquatic organisms and empirical predictions based on water content. *Transactions of the American Fisheries Society* 136: 1415-1422.
- Craig, J. F., M. J. Kenley, and J. F. Talling. 1978. Comparative estimations of the energy content of fish tissue from bomb calorimetry, wet oxidation and proximate analysis. *Freshwater Biology* 8: 585-590.
- Dana, J. D. 1851. *Crustacea Grapsoidea, (Cyclometopa, Edwardsii)*: *Conspectus Crustacearum quae in Orbis Terrarum circumnavigatione, Carolo Wilkes e classe Reipublicae Foederatae Duce, lexit et descriptis J.D. Dana*. Proceedings of the Academy of Natural Sciences of Philadelphia 5: 247-254 (printed in 1852).
- García, G. O., M. Favero, and R. Mariano-Jelicich. 2008. Red-gartered Coot *Fulica armillata* feeding on the grapsid crab *Cyrtograpsus angulatus*:

- advantages and disadvantages of an unusual food resource. *Ibis* 150: 114.
- Gutiérrez, J. L., C. G. Jones, P. M. Groffman, S. E. G. Findlay, O. Iribarne, P. D. Ribeiro, and C. M. Bruschetti. 2006. The contribution of crab burrow excavation to carbon availability in surficial salt-marsh sediments. *Ecosystems* 9: 647-658.
- Hanson, P. C., T. B. Johnson, D. E. Schindler, and J. F. Kitchell. 1997. *Fish Bioenergetics 3.0*. University of Wisconsin Sea Grant Institute, WISCU-T-97-001, Madison, WI.
- Hartman, K. J., and S. B. Brant. 1995. Estimating energy density of fish. *Transactions of the American Fisheries Society* 124: 347-355.
- Harvey, C. J., P. C. Hanson, T. E. Essington, P. B. Brown, and J. F. Kitchell. 2002. Using bioenergetics models to predict stable isotope ratios in fishes. *Canadian Journal of Fisheries and Aquatic Sciences* 59: 115-124.
- Hilborn, R., and M. Mangel. 1997. *The Ecological Detective: Confronting Models with Data*. Princeton University Press, Princeton, NJ.
- Hill, D. K., and J. J. Magnuson. 1990. Potential effects of global climate warming on the growth and prey consumption of Great Lakes fish. *Transactions of the American Fisheries Society* 119: 265-275.
- Hislop, J. R. G., M. P. Harris, and J. G. M. Smith. 1991. Variation in the caloric value and total energy content of the lesser sandeel (*Ammodytes marinus*) and other fish preyed on by seabirds. *Journal of Zoology* 224: 501-517.
- James, D. A., I. J. Csargo, A. Von Eschen, M. D. Thul, J. M. Baker, C. A. Hayer, J. Howell, J. Krause, A. Letvin, and S. R. Chipps. 2012. A generalized model for estimating the energy density of invertebrates. *Freshwater Science* 31: 69-77.
- Josens, M. L., M. S. Bó, and M. Favero. 2010. Foraging ecology of the Great Grebe *Podiceps major* in Mar Chiquita Lagoon (Buenos Aires, Argentina). *Ardeola* 57: 133-141.
- Linhart, H., and W. Zucchini. 1986. *Model Selection*. Wiley, New York, NY.
- McNab, B. K. 2002. *The Physiological Ecology of Vertebrates: a View from Energetics*. Cornell University Press, London, 576 pp.
- Pedersen, J., and J. R. G. Hislop. 2001. Seasonal variations in the energy density of fishes in the North Sea. *Journal of Fish Biology* 59: 380-389.
- R Development Core Team. 2011. *R: a Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna.
- Rathbun, M. J. 1914. New genera and species of American *brachyrrhynchous* crabs. *Proceedings of the United States National Museum* 47: 117-129.
- Ruzycki, J. R., D. A. Beauchamp, and D. L. Yule. 2003. Effects of introduced lake trout on native cutthroat trout in Yellowstone Lake. *Ecological Applications* 13: 23-37.
- Schultz, E. T., and D. O. Conover. 1997. Latitudinal differences in somatic energy storage: adaptive responses to seasonality in an estuarine fish (*Atherinidae: Menidia menidia*). *Oecologia* 109: 516-529.
- Spivak, E. D. 1997. Los crustáceos decápodos del Atlántico sudoccidental (25°-55°S): distribución y ciclos de vida. *Investigaciones Marinas Valparaíso* 25: 69-91.
- Suárez, N., V. Retana, and P. Yorio. 2011. Temporal changes in diet and prey selection in the threatened Olrog's gull *Larus atlanticus* breeding in Southern Buenos Aires, Argentina. *Ardeola* 58: 35-47.
- Trudel, M., and J. B. Rasmussen. 2001. Predicting mercury concentration in fish using a mass balance model. *Ecological Applications* 11: 517-529.
- Wanless, S., M. P. Harris, P. Redman, and J. R. Speakman. 2005. Low energy values of fish as a probable cause of a major seabird breeding failure in the North Sea. *Marine Ecology Progress Series* 294: 1-8.
- Zwarts, L., and J. H. Wanink. 1993. How the food supply harvestable by waders in the Wadden Sea depends on the variation of energy density, body weight, biomass, burying depth, and behaviour of tidal-flat invertebrates. *Netherlands Journal of Sea Research* 31: 441-476.

RECEIVED: 10 April 2013.

ACCEPTED: 10 June 2013.

AVAILABLE ONLINE: ???.