

Energy Density of Patagonian Aquatic Organisms and Empirical Predictions Based on Water Content

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Abstract.—We measured the energy density for key species in the freshwater and marine ecosystems of Patagonia, providing the first database of such information for poorly known fauna, including fish, cephalopods, crustaceans, gastropods, annelids, and insects. We then considered an empirical model linking energy density (which is costly to estimate) to water content (which is easy to estimate) and compared the fit of the model with data from different taxonomic groups. Finally, we evaluated the predictive power of models with different levels of taxonomic aggregation to estimate energy density from water content. Fish (7,148–3,443 J/g of wet weight) had the highest energy density, followed by crustaceans (5,906–2,507 J/g), insects (5,794–1,334 J/g), mollusks (5,014–1,661 J/g), and annelids (4,542–1,954 J/g). The use of water content as a predictor of energy density provided greatly improved predictions as compared with use of the mean energy density value. As expected, the predictive power improved when more specific levels of taxonomic aggregation were employed. Nevertheless, we were able to identify levels of aggregation that provided high levels of predictive power. We regard the data generated as primary products for future research on energy fluxes in Patagonian aquatic ecosystems.

Energy density (ED) has been used to evaluate diet quality (Wanless et al. 2005), compare the relative importance of prey items (Harris and Hislop 1978), correct gastric evacuation rates used as input in models (Pedersen and Hislop 2001), explain the foraging behavior of predators (Benoit-Bird 2004), and determine the physiological status of organisms (Schultz

and Conover 1997). During the past 20 years, bioenergetics models, when supplied with data on diet composition, growth, size structure, thermal experience, and estimates of consumer abundance, have provided an effective method for quantifying trophic interactions between predators and their prey (Ney 1993). Bioenergetics models have also been used to investigate environmental problems, such as the potential effects of fish introductions (Ruzycki et al. 2003), global warming (Hill and Magnuson 1990), predation as a factor in recruitment failure (Hartman and Margraf 1993), and other issues in fish ecology (Brandt and Hartman 1993; Trudel and Rasmussen 2001; Harvey et al. 2002), and are especially sensitive to changes in energy density of the consumer and its prey (Kitchell et al. 1977; Beauchamp et al. 1989).

Hence, accurate estimates of energy density constitute a central piece of information for generating accurate estimates of consumption, growth, the relative importance of prey items, gastric evacuation rates, and foraging behavior. Adiabatic bomb calorimetry and proximate analysis are time-consuming processes commonly employed to measure energy density in organisms (Craig et al. 1978). Although energy densities for aquatic invertebrates and vertebrates are slowly being published, representative values for many functional groups and for whole geographic regions are still unavailable. Moreover, energy densities for the same species can vary considerably with size or among seasons. Effective and affordable approaches for acquiring representative values for new regions, new taxa, or new times of the year are required. Empirical relationships between energy density and less costly variables are an appealing option. Hartman and Brandt (1995) presented one such empirical model to estimate the energy density in fish from its negative relationship with water content in tissues (measured as percent dry

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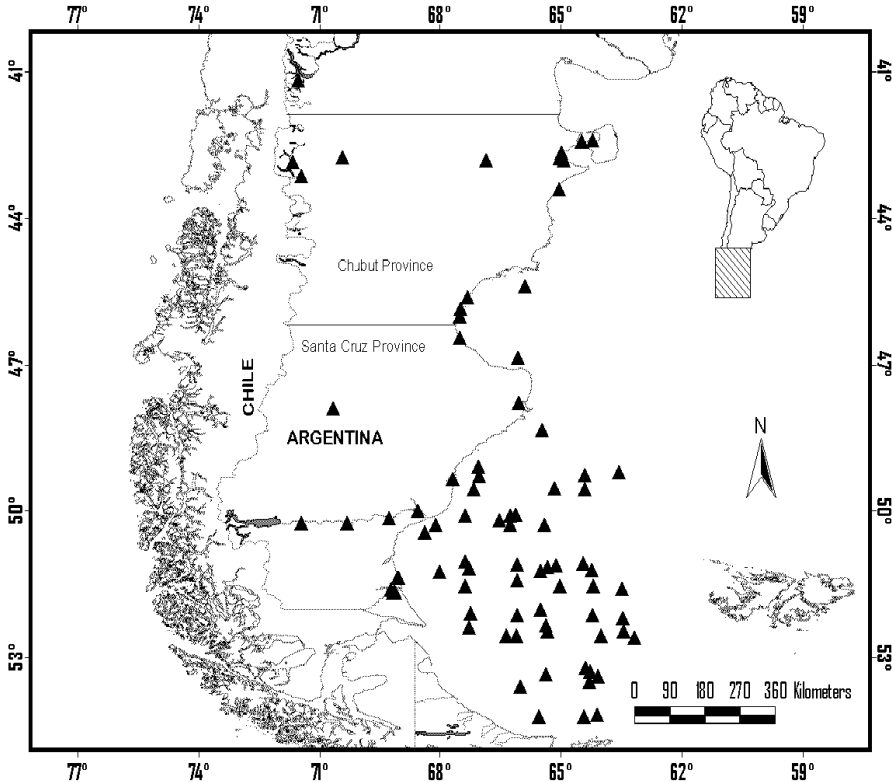


FIGURE 1.—Map showing the area sampled from 2000 to 2005 to determine the energy density of Patagonian aquatic organisms. Triangles show the locations where freshwater and marine organisms were collected.

weight [DW]). Yet, no formal assessment has been made of such methods in terms of their predictive power. For instance, it is not clear how much we have to gain in predictions by considering water content as compared with just using the average energy density for the species.

In Patagonia, few attempts have been made to estimate the energy density of aquatic ecosystem components (Lomovasky et al. 2001; Eder and Lewis 2005; Romero et al. 2006; Ciancio and Pascual 2006) despite an increasing demand for information by models that explore different fisheries and conservation-managing actions (Koen-Alonso and Yodzis 2005). In view of this evident information void, the main objectives of this work are to (1) determine the energy density for a large collection of samples of key marine and freshwater species in Patagonia, including fish, cephalopods, crustaceans, gastropods, annelids, and insects; (2) generate empirical models correlating energy density with water content, comparing the performance of different taxonomic aggregation schemes; and (3) evaluate the predictive power of these models.

Methods

Samples were collected from the locations shown in Figure 1. Freshwater samples were collected from different rivers and lakes of Patagonia in 2000–2001. Invertebrates were captured with a Surber sampler, and fish and crayfish were captured with a fishing basket. Marine samples were collected from the harvests of artisanal fisheries, commercial bottom trawlers, and research cruises (sampling depth, 0–341 m) in 2001–2005 (Table 1; Figure 1). Samples were placed in bags to prevent dehydration and then frozen.

Samples were chopped, homogenized, dried in an oven at 60–80°C for 24–72 h, and then ground to powder. Shells were removed from mollusks (*Aulacomya ater*, *Perumytilus purpuratus*, *Mytilus edulis*, and *Patinigera magellanica*) eaten primarily by birds, which typically ingest prey without the shell (Millones et al. 2005), and *Chilina* spp. were homogenized with shells. The wet and dry weights were determined to the nearest 0.001 g by weighing the homogenate before and after drying.

One-gram pellets were pressed and burned at 30 atmospheres of oxygen in a bomb calorimeter (Parr

TABLE 1.—General information on the 37 taxa analyzed in this study of the energy density of Patagonian aquatic organisms. The letter *N* stands for the number of pellets burned in the calorimeter; no./pellet is the number of individuals included on each pellet. Energy density (ED) is expressed as joules per gram and is on a wet-weight basis except where noted. Size refers to total length. Ranges are provided when more than one individual was analyzed.

Group and species	<i>N</i>	Size (mm)	No./pellet	Dry weight %	ED
Fish					
Freshwater					
Otuno <i>Diplomyste viedmensis</i> ^a	1	250	1	24.0	5,658
<i>Hatcheria macraei</i>	1	80	1	16.4	3,596
Creole perch <i>Percichthys trucha</i>	1	120	1	25.3	5,917
Inanga <i>Galaxias maculatus</i>	1	50–60	2	15.4	3,443
<i>Odontheistes hatchery</i>	1	210	1	27.9	5,783
Steelhead <i>Oncorhynchus mykiss</i>	1	80	1	26.3	6,318
Marine					
<i>Eleginops maclovinus</i>	3	150–200	1	21.6	3,659
Argentine anchovy <i>Engraulis anchoita</i>	6	110–155	1	27.6	5,553
Steelhead	47	300–800	1	29.6	6,850
Patagonian sprat <i>Sprattus fuegensis</i>	15	35–140	1	29.7	7,148
<i>Odontheistes smitti</i>	3	150–152	1	21.4	4,571
<i>Patagonotothen tesellata</i>	2	118–120	1	22.8	4,034
<i>Patagonotothen ramsayi</i>	8	60–140	1	23.6	4,798
Southern blue whiting <i>Micromesistius australis</i>	3	140–150	1	21.5	4,544
Argentine hake <i>Merluccius hubbsi</i>	3	140–146	1	22.7	4,076
<i>Genypterus blacodes</i>	3	200–230	1	22.8	3,692
Invertebrates					
Freshwater					
Crustaceans					
<i>Aegla</i> spp.	2	20–30	2	23.0	3,680
<i>Hyaella fossamacinii</i>	2	3–10	60	15.3	2,547
<i>Samastacus spinifrons</i>	2	40–60	1	28.2	3,892
Annelids					
<i>Oligochaeta</i>	2	30–60	1	13.5	1,954
Insects					
Ephemeroptera					
<i>Ephemeroptera</i>	2	10–20	20	12.7	2,725
Odonata					
<i>Odonata</i>	2	15–20	1	6.3	1,334
Plecoptera					
<i>Plecoptera</i>	2	5–15	30	25.3	5,366
Coleoptera					
<i>Coleoptera</i>	1	15	1	24.9	5,794
Mollusks					
<i>Chilina</i> ssp.	2	5–10	5	35.6	1,661
Marine					
Crustaceans					
<i>Pleoticus muelleri</i>	3	39–45	1	30.7	5,906
<i>Peisos petrunkevitchi</i>	3	16–17	10–20	17.5	3,338
<i>Cyrtograpsus angulatus</i>	3	20–30	1	33.7	3,150
<i>Euphausia lucens</i>	1	2–13	50	13.8	2,507
<i>Themisto gaudichaudii</i>	3	3–12	50	14.0	3,107
<i>Munida gregaria</i>	3	70–50	1		11,008 ^b
Mollusks					
<i>Aulacomya ater</i>	3	47–63	1	21.6	4,139
<i>Perumytilus purpuratus</i>	3	34–36	1	18.0	3,604
<i>Mytilus edulis</i>	3	49–63	1	16.6	2,979
<i>Patinigera magellanica</i>	3	44–46	1	25.0	4,999
<i>Loligo gahi</i>	8	60–90	1	23.4	4,952
<i>Illex argentinus</i>	4	210–415	1	23.7	5,014
Annelids					
<i>Halosidna patagonica</i>	2	40	1	23.3	4,542
All groups	140				

^a Also known as *Olivaichthys viedmensis*.

^b Dry-weight basis.

Model 1241) to determine the gross energetic content. Fuse wire corrections were determined after each combustion event. One to three pellets of each sample were burned, and the mean was used to estimate the energy density of the item. For small individuals (e.g., insects and gastropods), a sampling unit consisted of

whole-body samples of numerous individuals. For large specimens (e.g., fish), a sampling unit consisted of a whole-body homogenate of a single individual. Energy density is expressed in Joules per gram of wet weight.

Empirical relationship between water content and energy density.—We used an empirical linear model.

TABLE 2.—Linear regressions relating energy density to percent dry weight for the species and larger groupings in this study. The letter *a* represents an intercept, the letter *b* a slope. The predictive power of each regression is expressed as the median and 90th percentile of error. The regressions for the European anchovy (Tirelli et al. 2006) and sprat (Pedersen and Hislop 2001) pertain to Northern Hemisphere fish; all other regressions are from the present study and are based on data for Southern Hemisphere fish.

Taxa	<i>r</i> ²	<i>P</i>	<i>a</i>	<i>b</i>	% Error		<i>N</i>
					Median	90th percentile	
Species							
Steelhead	0.98	<0.0001	-2,609	319	1.7	4.3	47
Argentinean anchovy	0.94	0.001	-1,189	243	6.7	8.9	6
European anchovy <i>Engraulis encrasicolus</i>	0.82		-3,316	321			161
Patagonian sprat <i>Patagonotothen ramsayi</i>	0.93	0.02	-2,208	280	4.5	5.7	8
<i>Sprattus fuegensis</i>	0.96	<0.0001	-2,020	310	5.4	9.6	15
Sprat <i>Sprattus sprattus</i>	0.97		-2,996	354			3
<i>Loligo gahi</i>	0.93	<0.0001	-319	219	2.3	4.8	8
<i>Illex argentinus</i>	0.99	0.02	-1,308	266	1	5.5	4
Larger groupings							
Marine fish	0.94	<0.0001	-2,868	326	3.6	15.9	91
Marine invertebrates							
Cephalopods ^a	0.96	<0.0001	-1,070	254	5.7	13	12
Mollusks ^b	0.94	<0.0001	-1,088	250	5.6	10.7	23
Crustaceans ^c	0.98	<0.0001	313	181	7.1	15.8	10
Freshwater taxa							
Fish ^d	0.99	0.0002	-432	254	1.7	2.8	6
Crustaceans ^e	0.91	0.009	748	120	3.1	14.4	5
Insects ^f	0.99	0.03	-115	226	7.4	9.2	4
Marine and freshwater fish	0.93	<0.0001	-2,412	311	3.5	18.3	98
Marine and freshwater crustaceans	0.85	<0.0001	337	166	11.3	18.1	15
All taxa	0.93	<0.0001	-2,056	296	5.2	17.1	140

^a *Loligo gahi* and *Illex argentinus*.

^b *Aulacomya ater*, *Perumytilus purpuratus*, *Mytilus edulis*, *Patinigera magellanica*, *Loligo gahi*, and *Illex argentinus*.

^c *Pleoticus muelleri*, *Peisos petrunkevitchi*, *Euphausia lucens*, and *Themisto gaudichaudii*.

^d Otuno, *Hatcheria macraci*, creole perch, inanga, and steelhead.

^e *Aegla* spp., *Hyaella fossamachinii*, and *Samastacus spinifrons*.

^f Ephemeroptera, Odonata, Plecoptera, and Coleoptera.

The ED was the dependent variable, and the percent DW was the independent variable (Hartman and Brandt 1995):

$$ED = a + b \cdot DW.$$

To compare the fit of the model for different taxonomic groups, we used a likelihood ratio test (Hilborn and Mangel 1997). The null hypothesis was that there were no differences in slope and intercept in pairwise group comparisons. Two types of regressions were tried, with different levels of aggregation (species and grouped regressions). We first made groups as disaggregated as possible, keeping species as groups only for cases where the sample size was larger than four individuals (species regressions). All other species were aggregated (grouped regression) by taxonomic group (e.g., marine fish). Hence, we considered the following species regressions: Patagonian sprat, steelhead, *Patagonotothen ramsayi*, Argentine anchovy, *Loligo gahi*, and *Illex argentinus*, along with the following grouped regressions: marine fish, freshwater fish, cephalopods, mollusks, marine and freshwater

crustaceans, immature and adult freshwater insects, and all species combined (Table 2).

The predictive power of the regressions was evaluated using a goodness-of-fit criterion that depends on prediction errors. For each of the *n* individual samples available, a prediction for energy density was obtained from its observed dry weight and the linear model fitted to the remaining points; the proportional distance between the prediction obtained in this manner and the observed energy density was used as a prediction error for that observation (one-item-out cross validation; Linhart and Zucchini 1986). We used the median and 90th percentile of observed errors as measures of the predictive power of different regression models.

To evaluate the benefits of using water content as a predictor of energy density, for each of the fish species (steelhead, Argentine anchovy, *Patagonotothen ramsayi*, and Patagonian sprat) and each of the cephalopod species (*Loligo gahi* and *Illex argentinus*) we compared the prediction errors from the specific regression with those resulting from simply assigning the average

energy density for the species. To evaluate the costs of aggregating species in the estimation of specific caloric contents, we compared prediction errors from each of the species-specific regressions with those derived from regressions for aggregated taxonomic groups, excluding the species under scrutiny. In this fashion, we compared the errors in the estimated caloric contents in individual fish and cephalopod species from the specific regressions and those provided by grouped regressions (marine fish for fish and mollusks for cephalopods). To evaluate the costs of deriving predictions from models built for "similar species," we compared the errors associated to the specific regressions for Argentine anchovy and Patagonian sprat with those provided by using models proposed for European anchovy and sprat from the Northern Hemisphere (fourth column in Table 3).

Results

Individuals sampled ranged from 35 to 800 mm for teleost fishes and from 3 to 415 mm for invertebrates, and percent dry weight ranged from 15.4% to 29.7% for teleost fishes and from 6.3% to 35.6% for invertebrates (Table 1). The energy density ranged from 3,443 to 7,148 J/g of wet weight for teleosts (3,443–6,318 J/g for freshwater species and 3,659–7,148 J/g for marine and anadromous species) and from 1,334 to 5,906 J/g for invertebrates (1,334–5,794 J/g for freshwater species and 2,507–5,906 J/g for marine species).

Energy density was strongly and positively correlated with percent dry weight (Table 2) for individual species ($r^2 = 0.93\text{--}0.99$), for broader taxonomic-habitat groups ($r^2 = 0.85\text{--}0.99$), and for all taxa combined ($r^2 = 0.93$; Figure 2). Slopes and intercepts were more similar to those of related taxa than to those

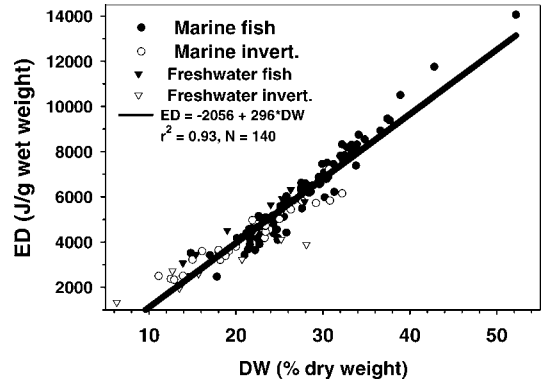


FIGURE 2.—General relationship between energy density (ED) and dry weight (DW) as a percentage of total wet mass for all Patagonian freshwater and marine fish and invertebrate samples combined.

of less-related taxa. For fish, intercepts were the most negative (−432 to −2,609), but slopes were generally higher (243–319). Marine invertebrates had less negative or positive intercepts (−1,088 to +313) and lower slopes (181–266). Freshwater and marine crustaceans were the only groups with positive intercepts (313 and 748) and had the lowest slopes of all the groups analyzed (120 and 181). But even when related taxa had more similar ED–DW relationships, all pairwise species comparisons of slopes and intercepts were significantly different between all pairs of species (likelihood ratio test: P -value = 0.00001–0.04), except for Argentine anchovy and *Patagonotothen ramsayi* (P -value = 0.43).

The median prediction errors were always under 7%, and the 90th percentiles of error were under 10% for individual species regressions (Table 2). Prediction errors were larger for species grouped regressions, but

TABLE 3.—Median and 90th percentile (in parentheses) prediction errors (%) for energy density for selected species when the predictions are based on (1) the average energy density (ED) for that species and (2) regressions relating ED to percent dry weight for various taxonomic groupings. The group regressions (marine fish or mollusks) are based on data for all species in the group except the species being evaluated; the combined-groups regressions are based on data for all of the species in both groups except the species being evaluated.

Species	Average ED, same species	ED from regression with % dry weight			
		Same species	Related species	Group Combined groups	
Marine fish					
Steelhead	14.0 (24.8)	1.7 (4.3)		2.4 (5.3)	5.6 (8.2)
Argentine anchovy	16.0 (29.5)	6.7 (8.9)	7.5 (12.1) ^a	13.3 (18.6)	27.9 (35.2)
<i>Patagonotothen ramsayi</i>	9.0 (17.9)	4.5 (5.7)		7.2 (12.7)	11.1 (16.1)
Patagonian sprat	32.0 (91.0)	5.4 (9.6)	4.5 (16.7) ^b	17.7 (22.6)	9.6 (21.6)
Mollusks					
<i>Loligo gahi</i>	10.0 (21.0)	2.3 (4.8)		4.4 (7.2)	3.2 (9.6)
<i>Illex argentinus</i>	3.0 (22.3)	1 (5.5)		6.5 (7.8)	1.9 (8.5)

the median was always under 20% and the 90th percentile under 25% (except for the predictions for Argentine anchovy with the model combining all species).

To evaluate the overall value of empirical ED–DW models, we compared the prediction errors of species-specific models with those emerging from just using the mean energy density for the species (Table 3, first two columns). Species-specific regression models provided much smaller prediction errors (median error = 1–6.7%) than just using mean values (median error = 3–32%).

To evaluate how much prediction deteriorates as a function of taxonomic aggregation, we compared species-specific prediction errors with those emerging from using data for more aggregated taxonomic groups (Table 3, last three columns). As expected, species-specific models provided the most accurate predictions of energy density. Using regressions from the same genus (regressions of European anchovy and sprat from the Northern Hemisphere to predict energy density of the Argentine anchovy and Patagonian sprat) also provided small prediction errors. The effect of aggregation depends on the specific taxonomic group considered. For instance, while aggregated regressions performed relatively well for most groups, aggregated fish models provided poor predictions for energy density in anchovies and sprats.

Discussion

The data set presented in this paper provides the first estimates of energy density for marine, anadromous, and freshwater fishes and for some of the major prey of species targeted by commercial and sport fisheries in aquatic ecosystems of Patagonia. Based on their proximal composition, Eder and Lewis (2005) estimated the ED of various species of teleosts, elasmobranchs, and cephalopods of the central continental shelf of Patagonia. In this study, we included direct estimation of the ED of key species of southern areas of the Patagonian Continental Shelf and the main components of zooplankton in the region. For example, the amphipod *Themisto gaudichaudii* is the main prey of major commercial species such as the squid *Illex argentinus* (Ivanovic and Brunetti 1994), Argentine hake, and hoki *Macroronus magellanicus*, the principal targets of trawl fisheries in the area (Wholer et al. 1997) as well as of several seabirds in the sub-Antarctic waters (Bocher et al. 2001). The Patagonian sprat is the main prey of magellanic penguins *Spheniscus magellanicus* (Frere et al. 1996) in southern continental colonies of Patagonia, and squids *Loligo gahi* and lobster crabs constitute important prey items for gentoo penguins *Pygoscelis papua* (Clausen and Putz 2003), magellanic

penguins, and rockhopper penguins *Eudyptes chrysocome chrysocome* breeding in the Falkland Islands (Croxall et al. 1985; Clausen and Putz 2002).

Empirical relationships between ED and DW have been extensively used (Unwin et al. 1999; Pedersen and Hislop 2001; Tirelli et al. 2006), but their value as ED predictors have not formally been evaluated. Hartman and Brandt (1995) used independent data sets to compare the fit of a model to different levels of aggregations (combined model, order, and family). They also ran bioenergetics simulations and compared the estimated final weight and consumption using different levels of aggregation against using the mean ED value. They recommended using the lowest practical taxon whenever possible, especially in species with significant seasonal changes in ED (e.g., anchovies). In that way, we explored the prediction error of different levels of aggregation and found results similar to the comparisons described by Hartman and Brandt (1995). We also found that using same-genus models could produce results similar to those of the species-specific regression models. Obviously, the level of accuracy expected will depend on the application. In general, however, accuracy deteriorated as more aggregated regressions were used. Some groups, such as anchovies and sprats, appeared to be less well represented by aggregated models, indicating that accurate ED predictions for those species require specific models.

The significant differences in intercepts and slopes among models may be explained by the variation in the amount of the components of organisms. For the case of fish, Hartman and Brandt (1995) postulated that these variations among models could be explained by the amounts of bones or basic lipid levels. Crustaceans exhibited the lowest slopes of all taxa analyzed on this study. This could be explained by the high proportion of calcareous structures on these invertebrates.

Our data will be useful for bioenergetic modeling of the key trophic linkages in aquatic ecosystems of Patagonia. For instance, governments and private companies have promoted salmonid introductions and restocking of existing populations as part of large-scale aquaculture and to support an increasing sport fishing tourism industry (Pascual and Ciancio 2007). Bioenergetics modeling has been an effective approach for evaluating the impact of predation or competition imposed by nonnative salmonids in North America (Stewart and Ibarra 1991; Rand et al. 1993; Ruzzycki et al. 2003).

Although the direct measures of ED reported here can be used when specific information for a species in a system is lacking, the empirical relationship between ED and DW will enable future modeling to account for

temporal and ontogenetic variation in ED. Seasonal changes in ED have been reported for a diverse array of aquatic species (Brawn et al. 1968; Pedersen and Hislop 2001). Hartman and Brandt (1995) demonstrated that combined species models of ED versus percent DW were adequate for describing seasonal or ontogenetic changes in the ED of fish. Pedersen and Hislop (2001) found no seasonal differences in the relationship between ED and DW for seven marine fish species of the North Sea. The direct estimations of ED presented in this paper may be used carefully for modeling without taking into account seasonal changes, ontogeny, and sexual status of organisms, but the relationships between ED and DW appear not to be affected by these variables.

In this paper, we present the first step in the bioenergetic modeling of aquatic ecosystems in Patagonia, whether by the direct estimation of the ED of key species or by the empirical relationship between ED and DW. Our data set is intended as baseline information for modeling the energy fluxes in Patagonian ecosystems.

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