

The energy density of jellyfish: Estimates from bomb-calorimetry and proximate-composition

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Received 20 October 2006; received in revised form 11 November 2006; accepted 11 December 2006

Abstract

Two techniques are described to calculate energy densities for the bell, gonad and oral arm tissues of three scyphozoan jellyfish (*Cyanea capillata*, *Rhizostoma octopus* and *Chrysaora hysoscella*). First, bomb-calorimetry was used, a technique that is readily available and inexpensive. However, the reliability of this technique for gelatinous material is contentious. Second, further analysis involving the more labour intensive proximate-composition analysis (protein, fat and carbohydrate) was carried out on two species (*C. capillata* and *R. octopus*). These proximate data were subsequently converted to energy densities. The two techniques (bomb-calorimetry and proximate-composition) gave very similar estimates of energy density. Differences in energy density were found both amongst different species and between different tissues of the same species. Mean (\pm S.D.) energy density estimates for whole animals from bomb-calorimetry were 0.18 ± 0.05 , 0.11 ± 0.04 , and 0.10 ± 0.03 kJ g wet mass⁻¹ for *C. capillata*, *R. octopus*, and *C. hysoscella* respectively. The implications of these low energy densities for species feeding on jellyfish are discussed.
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Keywords: Bioenergetic models; *Chrysaora*; *Cyanea*; Foraging ecology; Leatherback turtle; Marine food webs; *Rhizostoma*

1. Introduction

Food quality has fundamental implications for the ecology of all species. For example, vertebrates that feed on nutritionally high quality food (e.g. carnivores) typically spend a large proportion of their time resting or socialising in-between foraging bouts. Conversely, animals that feed on nutritionally lower quality foods

(e.g. herbivores) often need to allocate more time to foraging (Fortin et al., 2002; Shrader et al., 2006). However, for some predators, information on the nutritional quality of their prey is lacking or poorly documented. This is clearly illustrated by ‘scyphozoan medusae’ of the Phylum Cnidaria (from hereon referred to as ‘jellyfish’) which were once considered unimportant and energetic dead ends in pelagic food webs but are now considered intrinsic dietary components for an increasing range of vertebrate and invertebrate species (Arai, 2005; Houghton et al., 2006a,b). For example, leatherback sea turtles (*Dermodochelys coriacea* Vandelli)

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are regularly seen in areas where jellyfish are abundant at the surface, and have been observed to consume up to 200 kg of jellyfish a day (Duron, 1978; James and Herman, 2001; Houghton et al., 2006b). Other examples of predators now known to prey on jellyfish include many arthropods, fish and birds (Arai, 2005); however, their importance as prey items does not end in the pelagic realm. Recent research has shown that large aggregations of moribund jellyfish may be important vectors for carbon transport to the deep sea in many areas of the world ocean with jellyfish detritus possibly acting as a good food source for benthic fauna (Billett et al., 2006). Furthermore, considering that jellyfish may become more important in some marine systems as a result of climate change and/or overfishing (Mills, 2001; Lynam et al., 2006), their overall ecosystem impact as prey (and predators) may similarly increase. Unfortunately, as the energy density of jellyfish is relatively poorly documented when compared to other pelagic taxa (Arai, 1997), constructing bioenergetic models for species that prey on jellyfish (Davenport, 1998; Lynam et al., 2006; Wallace et al., 2006), and trophic dynamic models that incorporate jellyfish, may be problematic.

The lack of information on the energy density of jellyfish is partly caused by methodological problems associated with the high salt content, high water content (95–98% wet mass) and extremely low energy density of this group (Larson, 1986; Lutcavage and Lutz, 1986; Clarke et al., 1992; Lucas, 1994; Arai, 1997). More specifically, in proximate composition analysis, the sum of protein, lipid and carbohydrate fractions (g) are termed ‘total organics’ and taken to be synonymous with ash free dry mass (AFDM) or the mass combusted when samples are ashed in a furnace (Lucas, 1994). However, for gelatinous zooplankton there is a discrepancy or an unaccounted difference between ‘total organics’ and ‘AFDM’. This difference is thought to be residual/bound water that remains in the dried jellyfish, even after drying to constant mass. The amount of ‘water of hydration’ remaining after drying, was estimated to be ~11.7% by Madin et al. (1981) for salps and Larson (1986) for *Aurelia aurita* L. and *Cyanea capillata* L. This bound water, combined with a low energy density may render traditional methods for estimating energy density, such as bomb-calorimetry, unreliable (Lutcavage and Lutz, 1986).

To tackle these uncertainties and provide baseline data for future bioenergetic studies, we compared two techniques for measuring the energy density of jellyfish: bomb-calorimetry and proximate-composition. Bomb-calorimetry is relatively quick, inexpensive and thus appropriate for large sample sizes if the analytical

uncertainties of this approach when applied to jellyfish can be resolved. Bomb-calorimetry measures the heat liberated when ‘food/or a sample’ is combusted in a sealed chamber (the bomb) surrounded by water. The heat liberated (heat of combustion) represents the food’s total energy or gross energy value (GE). The second approach, proximate-composition analysis, provides more reliable estimates of energy density but is time consuming (Arai, 1997), expensive and requires much more sample material. Proximate composition measures the protein, carbohydrate and lipid content of a sample. The measured fractions are then multiplied by the combustion equivalents of these compounds. Importantly, it provides a good benchmark for assessing the reliability of bomb-calorimetry. Our aim, therefore, was to compare results derived from the same material, using both methods. We applied the techniques to three species of jellyfish, *C. capillata*, *Rhizostoma octopus* L., and *Chrysaora hysoscella* L., all of which are often abundant at high latitudes (Doyle et al., in press) and hence may play important ecosystem roles.

2. Materials and methods

2.1. Collection and drying process

Fresh specimens of *C. hysoscella* ($n=10$) were collected from the side of a jetty in Dingle Harbour, County Kerry, Ireland (52.13°N, 10.36°W), using a dip net. Freshly stranded specimens of *C. capillata* ($n=27$) were collected from Laytown Beach, County Meath, Ireland (53.67°N, 6.23°W). These specimens were either freshly stranded on the beach or were in the process of stranding (i.e. still in the water) when collected. Samples that were directly removed from the beach were gently dipped in a bucket of seawater to remove any sand. Fresh specimens of *R. octopus* ($n=10$) were collected from Rosslare Harbour, County Wexford, Ireland (52.37°N, 6.36°W), using a dip net. In all the above sampling events, the wet mass of individual specimens was measured to the nearest gram, and the bell (umbrella) diameter measured to the nearest centimetre. Each jellyfish was then dissected into three distinct body components (or tissues): bell, oral arms and gonads. These tissues were individually stored in plastic bags, weighed, and within 1–2 h were frozen at -20°C . All jellyfish were collected during July–October 2004.

During November 2004, samples were removed from the freezer and allowed to thaw. Samples were homogenized into a ‘jelly soup’ using a blender, and poured into pre-weighed aluminium cartons. Individual

samples (component plus aluminium carton) were weighed and then placed in an oven at a constant temperature of 65 °C and dried to constant mass. During the drying process, samples were removed and weighed once or twice a day. Prior to weighing, samples were first allowed to cool to room temperature in a desiccator, and immediately after weighing returned to the oven if a constant mass had not been achieved. On occasions it was necessary to 'scrape and stir' the sample to remove or prevent a surface layer (skin) forming that slowed the drying process. As large granules sometimes formed during this process, it was necessary to use a mortar and pestle to grind these samples into a fine powder. These ground samples were then returned to the oven for additional drying.

2.2. Determination of gross energy (GE) using bomb-calorimetry

The gross energy (GE) was determined for individual tissue samples of *C. capillata* ($n=25$), *R. octopus* ($n=17$), and *C. hysoscella* ($n=29$) using a Gallenkamp Autobomb™ adiabatic calorimeter. The calorimeter had two stainless steel bombs and two calorimeter chambers, A and B. Each bomb was always used with the same calorimeter chamber during GE determinations. The heat capacity (hc) of each separate pair of bomb and calorimeter chamber, plus the mass of water within the calorimeter chamber, was determined as follows: $hc = [(GE \times wt) + 0.167] / \Delta T$. Where, hc=heat capacity of bomb ($\text{kJ } ^\circ\text{C}^{-1}$), GE=gross energy of benzoic acid (26.46 kJ g^{-1}), wt=weight of pellet in grams and ΔT =final temperature–initial temperature (in °C). The heat capacity for each bomb chamber was $10.822 \text{ kJ } ^\circ\text{C}^{-1}$. As is standard practice in adiabatic bomb calorimetry methodology, the same mass of water ($\pm 0.5 \text{ g}$) was always used for each bomb and calorimeter chamber pairing between GE determinations in order to maintain a constant heat capacity.

Each chamber was also calibrated for the heat of combustion of 1 g of benzoic acid (26.46 kJ g^{-1}) on a daily basis. Typically, 0.70 g of sample material (e.g. food or animal tissue) would be combusted for determination of GE in this system. However, to ensure combustion of the ground jellyfish samples, 0.50 g of sample was mixed with 0.50 g of benzoic acid in a weighing boat to give a composite sample, and manually pelleted using a hydraulic pelleting press (Enerpac™). Once pelleted, samples were kept in a silica gel dessicator. The change in temperature to a constant temperature due to combustion of the sample (approximately 10 min post-ignition) was detected using

a Beckmann thermometer, accurate to $0.001 \text{ } ^\circ\text{C}$. The GE of each composite sample was determined using standard procedures (McLean and Tobin, 1987) and calculated as; $GE = [(TrK \times 10.822 / \text{sample weight}) K \text{ kJ g}^{-1}]$. Where Tr is the change in temperature of the calorimeter between initial and post-combustion of the sample, and $10.822 \text{ (kJ } ^\circ\text{C}^{-1})$ is the heat capacity constant for the chambers. The GE value was corrected for the contribution that 0.50 g of benzoic acid made to the combustion of the composite sample, to give the equivalent of a 1 g jellyfish sample. As is standard practice, the GE values were not corrected for the potential small effect of nitric or sulphuric acid formed during the combustion process (McLean and Tobin, 1987).

2.3. Proximate-composition analysis

2.3.1. Ash determination

The inorganic matter or ash content of samples was determined for individual tissues samples of *C. capillata* ($n=39$) and *R. octopus* ($n=8$) using the AOAC 16.267 method (AOAC, 1990). Insufficient sample material of *C. hysoscella* prevented similar ash/proximate composition analysis for this species. A known mass of sample ($\sim 1 \text{ g} \pm 0.1 \text{ mg}$) that had been dried to constant mass, was ashed in a furnace at $600 \text{ } ^\circ\text{C}$ for 6 h. The ash content was calculated by the difference between initial and final mass of the sample. Analysis was carried out in triplicate per sample.

2.3.2. Protein, lipid and carbohydrate determination for individual tissue samples

The protein content was determined for individual tissue samples of *C. capillata* ($n=47$) and *R. octopus* ($n=8$) using the macro-Kjeldahl method (Association of Official Analytical Chemists (AOAC, 1990) method, International Dairy Federation (IDF) Standard 20B: 1993). For calculation of the % protein in a sample, the % N was multiplied by a conversion factor of 5.8 (Gnaiger and Bitterlich, 1984; Clarke et al., 1992). All protein analysis was carried out in triplicate.

The fat content of individual tissues was determined for *C. capillata* ($n=9$) and *R. octopus* ($n=7$) using a Soxtec 2055 Avanti instrument (Foss, Ireland). All fat analyses were carried out in duplicate.

The carbohydrate content of the samples was determined colorimetrically by measuring glycogen content (Cary Varian UV–Visible spectrophotometer) after acid digestion of individual tissue samples of *C. capillata* ($n=9$) and *R. octopus* ($n=7$). All carbohydrate analysis was carried out in duplicate.

2.3.3. Data analysis

To calculate the energy content of *C. capillata* and *R. octopus* from proximate-composition, the measured

quantities (in grams) of the various fractions (protein, lipid and carbohydrate), were multiplied by the known mean combustion equivalents of these compounds (i.e.

Table 1

Wet and dry mass (g) for individual tissues of *C. hysoscella*, *C. capillata* and *R. octopus* with associated bell diameters

Species	ID #	Bell diameter (cm)	Wet mass (g)				Dry mass (g)			
			G	OA	B	W	G	OA	B	W
<i>C. hysoscella</i>	1	17	78	47	277	402	4.1	1.8	10.2	16.0
<i>C. hysoscella</i>	2	24	184	187	500	871	8.9	7.0	18.4	34.4
<i>C. hysoscella</i>	3	18	48	36	188	272	2.4	1.6	7.0	10.9
<i>C. hysoscella</i>	4	21	109	123	383	615	5.0	4.7	14.0	23.7
<i>C. hysoscella</i>	5	22	133	212	417	762	6.2	8.1	16.0	30.2
<i>C. hysoscella</i>	6	24	266	135	480	881	11.7	5.2	17.7	34.5
<i>C. hysoscella</i>	7	24	130	143	487	761	6.1	5.3	18.4	29.9
<i>C. hysoscella</i>	8	17	96	19	152	266	4.2	0.8	5.7	6.6
<i>C. hysoscella</i>	9	17	89	36	299	423	4.2	1.6	10.9	16.6
<i>C. hysoscella</i>	10	19	61	49	231	341	3.3	2.1	8.5	13.9
Mean (±S.D.)		20.1 (3.0)	119 (65)	99 (70)	341 (129)	559 (246)	5.6 (2.8)	3.8 (2.6)	12.7 (4.8)	21.7 (10.2)
<i>C. capillata</i>	1	47	135	546	1008	1689	7.8	26.3	42.6	76.8
<i>C. capillata</i>	2	40	176	832	1562	2570	11.0	41.9	66.4	119.3
<i>C. capillata</i>	3	33	61	553	1154	1768	3.1	27.0	46.8	76.9
<i>C. capillata</i>	4	28	32	365	693	1089	1.4	17.4	28.0	46.8
<i>C. capillata</i>	5	35	101	574	1337	2011	5.1	28.1	52.4	85.6
<i>C. capillata</i>	6	37	67	623	1418	2108	3.5	31.5	58.6	93.6
<i>C. capillata</i>	7	28	13	21	211	244	0.6	1.4	9.0	11.0
<i>C. capillata</i>	8	31	42	295	902	1239	2.5	14.2	29.7	46.4
<i>C. capillata</i>	9	33	70	129	1157	1356	4.2	7.2	47.0	58.4
<i>C. capillata</i>	10	29	112	262	803	1177	7.0	12.8	32.8	52.5
<i>C. capillata</i>	11	33	118	301	1272	1692	9.4	17.8	47.4	74.5
<i>C. capillata</i>	12	26	20	55	475	551	1.2	4.3	19.1	24.5
<i>C. capillata</i>	13	36	108	107	1329	1544	5.3	6.3	49.5	61.1
<i>C. capillata</i>	14	36	420	868	1234	2521	24.2	36.1	46.9	107.2
<i>C. capillata</i>	15	27	42	74	620	736	1.9	3.7	22.4	28.0
<i>C. capillata</i>	16	27	20	154	524	698	1.0	7.1	19.8	27.8
<i>C. capillata</i>	17	36	198	621	1018	1838	9.9	25.8	37.3	73.0
<i>C. capillata</i>	18	29	76	369	552	997	3.7	16.2	20.4	40.2
<i>C. capillata</i>	19	24	34	73	349	456	1.6	3.9	12.7	18.2
<i>C. capillata</i>	20	37	69	461	1453	1984	3.2	20.5	55.6	79.3
<i>C. capillata</i>	21	30	125	724	617	1466	6.3	30.4	23.3	60.0
<i>C. capillata</i>	22	28	147	75	970	1192	6.8	4.7	36.5	48.0
<i>C. capillata</i>	23	20	50	141	293	484	2.9	6.8	11.3	21.0
<i>C. capillata</i>	24	23	48	388	448	885	2.4	17.4	16.7	36.5
<i>C. capillata</i>	25	27	20	132	754	906	1.1	6.6	29.5	37.2
<i>C. capillata</i>	26	15	12	5	171	188	0.7	0.3	6.8	7.8
<i>C. capillata</i>	27	24	51	228	437	716	2.6	10.3	17.5	30.4
Mean (±S.D.)		30.3 (6.6)	88 (83)	332 (258)	843 (415)	1263 (662)	4.8 (4.9)	15.8 (11.6)	32.8 (16.7)	53.4 (29.3)
<i>R. octopus</i>	1	36	213	1372	822	2407	9.0	57.0	29.9	95.9
<i>R. octopus</i>	2	57	1522	3920	3412	8854	64.9	176.0	80.8	321.6
<i>R. octopus</i>	3	48	72	2871	4319	7262	5.6	115.5	156.5	277.6
<i>R. octopus</i>	4	51	581	3093	4068	7742	26.1	122.0	172.7	320.8
<i>R. octopus</i>	5	23	12	413	177	602	0.5	16.8	6.4	23.8
<i>R. octopus</i>	6	23	21	328	570	919	0.5	15.4	11.4	27.3
<i>R. octopus</i>	7	18	15	70	241	326	0.7	2.9	10.0	13.6
<i>R. octopus</i>	8	15	9	67	183	259	0.5	2.4	6.3	9.3
<i>R. octopus</i>	9	13	14	24	31	69	0.2	1.3	1.2	2.7
<i>R. octopus</i>	10	11	–	20	52	72	–	1.2	2.3	3.4
Mean (±S.D.)		29.5 (17.1)	246 (483)	1218 (1510)	1388 (1787)	2851 (3605)	10.8 (20.6)	51.0 (64.1)	47.8 (66.0)	109.6 (139.1)

G=gonads, OA=oral arms, and B=bell. Values for whole jellyfish (W) are derived from the sum of the three tissues (gonads, oral arms and bell).

23.9 kJ g⁻¹ for protein, 39.5 kJ g⁻¹ for lipid and 17.5 kJ g⁻¹ for carbohydrate; see Clarke et al., 1992). All the proximate-composition data (including ash content) and subsequent energy density estimates were corrected for the effect of bound water by assuming a ‘water of hydration’ of 11.7% DM (Larson, 1986; Lucas, 1994). The following equations can be used to determine revised energy densities kJ g DM⁻¹, assuming 11.7% water of hydration. Revised GE kJ g⁻¹ = [(proportion of protein × a) + (proportion of lipid × b) + (proportion of carbohydrate × c)] × d. Where: a = 23.9 (gross energy value for protein in kJ g⁻¹); b = 39.5 (gross energy value for lipid in kJ g⁻¹); c = 17.5 (gross energy value for carbohydrate in kJ g⁻¹); d = water of hydration correction factor of 1.13 (i.e. water of hydration = 11.7% or 0.117; therefore 1 – 0.117 = 0.883; 1/0.883 = 1.13). For example: if a dried jellyfish gonad sample was 27.3% DM protein, 0.58% DM lipid, and 0.94% DM carbohydrate, then the energy density would be 1/0.883 [(0.273 × 23.9) + (0.0058 × 39.5) + (0.0094 × 17.5)] = 7.83 kJ g DM⁻¹. Similarly, to correct for the dilution effect of the bound water of hydration, the energy density values from bomb-calorimetry were multiplied by 1.13.

All percentage data were arcsine square root transformed prior to statistical analysis, and untransformed back to get means and S.D. in percentages.

To test the difference between two slopes we used the test statistic $t = (b_1 - b_2) / (SE_1^2 + SE_2^2)^{1/2}$, described by Fowler et al. (1998), where b₁ = slope 1; b₂ = slope 2, SE₁ = Standard error coefficient of slope 1; SE₂ = Standard error coefficient of slope 2.

3. Results

3.1. Raw results before correcting for bound water of hydration

3.1.1. Wet mass, DM and water content

A summary of wet and dry mass (g) for each species and their tissues is found in Table 1. It took 82–410 h to dry the jellyfish samples to a constant mass, with the length of time required being largely determined by the initial wet mass of specimen and the amount of wet sample exposed to drying air (Fig. 1).

Mean water contents for whole jellyfish were 95.8, 96.1 and 96.2% of wet mass (*C. capillata*, *R. octopus*, and *C. hysoscella* respectively) (Table 2). *Cyanea capillata* had a significantly lower water content than the other two species (one-way ANOVA: $F_{2, 37} = 4.75$, $p < 0.05$). There was a significant difference between the component tissues of *C. capillata*, with bell tissue having higher water content than both the gonad and

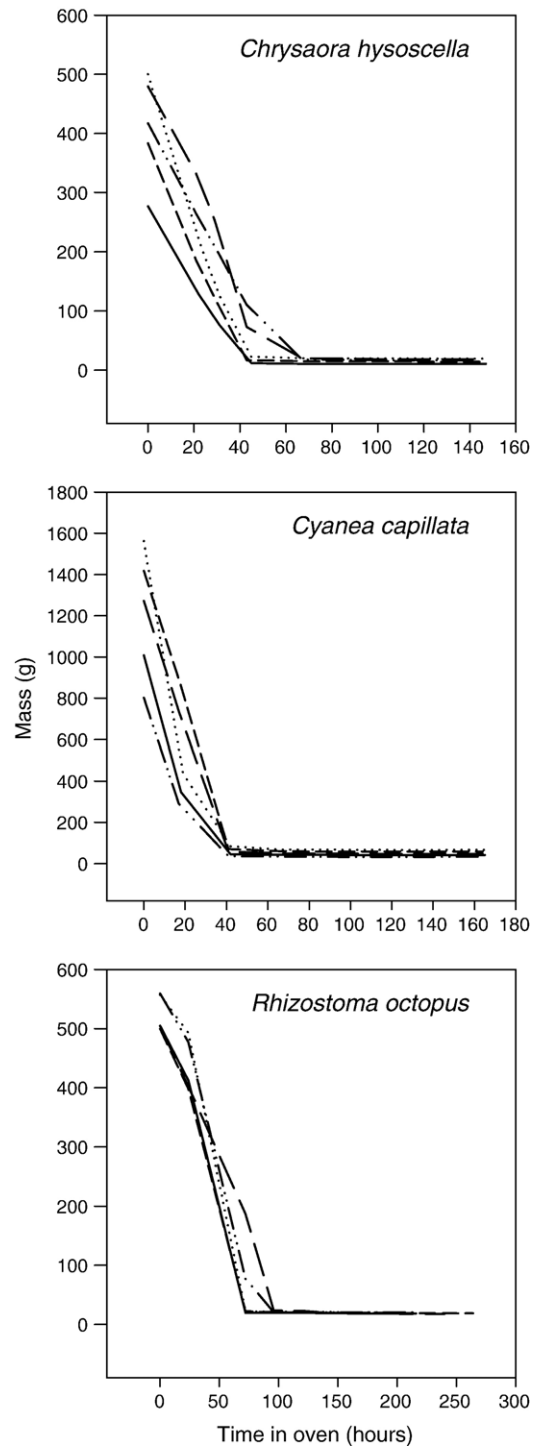


Fig. 1. Drying curves for *C. hysoscella*, *C. capillata* and *R. octopus* bell tissues. For each species separate drying curves are shown for five individuals. Mass at time zero is initial wet mass of individual analysed.

Table 2

Dry mass and water content as % of wet mass for individual tissues of *C. hysoscella*, *C. capillata* and *R. octopus*

Species	ID #	Dry mass (% WM)				Water content (%WM)			
		G	OA	B	W	G	OA	B	W
<i>C. hysoscella</i>	1	5.2	3.9	3.7	4.0	94.8	96.1	96.3	96.0
<i>C. hysoscella</i>	2	4.8	3.8	3.7	3.9	95.2	96.2	96.3	96.1
<i>C. hysoscella</i>	3	4.9	4.3	3.7	4.0	95.1	95.7	96.3	96.0
<i>C. hysoscella</i>	4	4.6	3.8	3.6	3.9	95.4	96.2	96.4	96.1
<i>C. hysoscella</i>	5	4.6	3.8	3.8	4.0	95.4	96.2	96.2	96.0
<i>C. hysoscella</i>	6	4.4	3.8	3.7	3.9	95.6	96.2	96.3	96.1
<i>C. hysoscella</i>	7	4.7	3.7	3.8	3.9	95.3	96.3	96.2	96.1
<i>C. hysoscella</i>	8	4.4	4.4	3.8	2.5	95.6	95.6	96.2	97.5
<i>C. hysoscella</i>	9	4.7	4.4	3.6	3.9	95.3	95.6	96.4	96.1
<i>C. hysoscella</i>	10	5.3	4.4	3.7	4.1	94.7	95.6	96.3	95.9
Mean (±S.D.)		4.8 (0.3)	4.0 (0.3)	3.7 (0.1)	3.8 (0.5)	95.2 (0.3)	96.0 (0.3)	96.3 (0.1)	96.2 (0.5)
<i>C. capillata</i>	1	5.8	4.8	4.2	4.5	94.2	95.2	95.8	95.5
<i>C. capillata</i>	2	6.3	5.0	4.2	4.6	93.7	95.0	95.8	95.4
<i>C. capillata</i>	3	5.1	4.9	4.1	4.3	94.9	95.1	95.9	95.7
<i>C. capillata</i>	4	4.4	4.8	4.0	4.3	95.6	95.2	96.0	95.7
<i>C. capillata</i>	5	5.1	4.9	3.9	4.3	94.9	95.1	96.1	95.7
<i>C. capillata</i>	6	5.2	5.1	4.1	4.4	94.8	94.9	95.9	95.6
<i>C. capillata</i>	7	4.8	6.7	4.3	4.5	95.2	93.3	95.7	95.5
<i>C. capillata</i>	8	6.0	4.8	3.3	3.7	94.0	95.2	96.7	96.3
<i>C. capillata</i>	9	6.0	5.6	4.1	4.3	94.0	94.4	95.9	95.7
<i>C. capillata</i>	10	6.2	4.9	4.1	4.5	93.8	95.1	95.9	95.5
<i>C. capillata</i>	11	7.9	5.9	3.7	4.4	92.1	94.1	96.3	95.6
<i>C. capillata</i>	12	5.7	7.7	4.0	4.5	94.3	92.3	96.0	95.5
<i>C. capillata</i>	13	4.9	5.9	3.7	4.0	95.1	94.1	96.3	96.0
<i>C. capillata</i>	14	5.8	4.2	3.8	4.3	94.2	95.8	96.2	95.7
<i>C. capillata</i>	15	4.6	4.9	3.6	3.8	95.4	95.1	96.4	96.2
<i>C. capillata</i>	16	4.8	4.6	3.8	4.0	95.2	95.4	96.2	96.0
<i>C. capillata</i>	17	5.0	4.1	3.7	4.0	95.0	95.9	96.3	96.0
<i>C. capillata</i>	18	4.8	4.4	3.7	4.0	95.2	95.6	96.3	96.0
<i>C. capillata</i>	19	4.6	5.4	3.6	4.0	95.4	94.6	96.4	96.0
<i>C. capillata</i>	20	4.6	4.4	3.8	4.0	95.4	95.6	96.2	96.0
<i>C. capillata</i>	21	5.0	4.2	3.8	4.1	95.0	95.8	96.2	95.9
<i>C. capillata</i>	22	4.6	6.3	3.8	4.0	95.4	93.7	96.2	96.0
<i>C. capillata</i>	23	5.8	4.8	3.9	4.3	94.2	95.2	96.1	95.7
<i>C. capillata</i>	24	5.0	4.5	3.7	4.1	95.0	95.5	96.3	95.9
<i>C. capillata</i>	25	5.5	5.0	3.9	4.1	94.5	95.0	96.1	95.9
<i>C. capillata</i>	26	5.7	4.8	4.0	4.1	94.3	95.2	96.0	95.9
<i>C. capillata</i>	27	5.0	4.5	4.0	4.2	95.0	95.5	96.0	95.8
Mean (±S.D.)		5.3 (0.8)	5.1 (0.8)	3.9 (0.2)	4.2 (0.2)	94.7 (0.8)	94.9 (0.8)	96.1 (0.2)	95.8 (0.2)
<i>R. octopus</i>	1	4.2	4.2	3.6	4.0	95.8	95.8	96.4	96.0
<i>R. octopus</i>	2	4.3	4.5	2.4	3.6	95.7	95.5	97.6	96.4
<i>R. octopus</i>	3	7.8	4.0	3.6	3.8	92.2	96.0	96.4	96.2
<i>R. octopus</i>	4	4.5	3.9	4.2	4.1	95.5	96.1	95.8	95.9
<i>R. octopus</i>	5	4.5	4.1	3.6	4.0	95.5	95.9	96.4	96.0
<i>R. octopus</i>	6	2.6	4.7	2.0	3.0	97.4	95.3	98.0	97.0
<i>R. octopus</i>	7	4.6	4.1	4.2	4.2	95.4	95.9	95.8	95.8
<i>R. octopus</i>	8	6.0	3.6	3.5	3.6	94.0	96.4	96.5	96.4
<i>R. octopus</i>	9	1.8	5.2	3.9	3.9	98.2	94.8	96.1	96.1
<i>R. octopus</i>	10	–	5.8	4.4	4.8	–	94.2	95.6	95.2
Mean (±S.D.)		4.0 (2.2)	4.4 (0.7)	3.5 (0.8)	3.9 (0.5)	95.5 (1.7)	95.6 (0.7)	96.5 (0.8)	96.1 (0.5)

G=gonads, OA=oral arms, B=bell, and W=whole jellyfish.

oral arm tissues (ANOVA: $F_{2, 57}=36.83$, $p<0.001$). There was also a significant difference between tissue types in *C. hysoscella*, but in this case, the gonads had lower water content than both bell and oral arm tissues

(ANOVA: $F_{2, 27}=48.45$, $p<0.001$). There was no significant difference in the water content of the different tissue types in *R. octopus* tissues (ANOVA: $F_{2, 27}=1.92$, $p>0.05$).

Table 3

Gross energy (GE) density values for *C. capillata* and *R. octopus* measured from proximate-composition analysis (PC), proximate-composition analysis assuming 11.7% water of hydration (revised PC), bomb-calorimetry (BC), and bomb-calorimetry revised assuming 11.7% water of hydration

Species	ID #	Raw GE kJ g DM ⁻¹ (BC)				Revised GE kJ g DM ⁻¹ (BC)				ID #	Raw GE kJ g DM ⁻¹ (PC)				Revised GE kJ g DM ⁻¹ (PC)			
		G	OA	B	W	G	OA	B	W		G	OA	B	W	G	OA	B	W
<i>C. capillata</i>	1	8.81	7.23	2.28	4.64	9.98	8.19	2.58	5.26	3	5.79	7.54	2.15	4.18	6.56	8.54	2.43	4.74
<i>C. capillata</i>	2	9.57	7.73	2.01	4.72	10.84	8.75	2.28	5.34	4	7.13	7.74	1.84	4.19	8.08	8.77	2.08	4.75
<i>C. capillata</i>	5	4.68	6.28	0.89	2.88	5.30	7.11	1.01	3.27	6	6.36	8.83	2.14	4.55	7.21	10.00	2.43	5.15
<i>C. capillata</i>	10	6.86	6.04	1.07	3.05	7.77	6.84	1.21	3.45	8	8.70	7.26	1.93	3.92	9.85	8.23	2.18	4.44
<i>C. capillata</i>	11	6.59	–	–	–	7.46	–	–	–	9	8.00	8.36	1.63	2.92	9.06	9.47	1.85	3.31
<i>C. capillata</i>	13	6.09	–	0.91	–	6.90	–	1.03	–	14	6.43	6.92	2.15	4.72	7.28	7.84	2.43	5.35
<i>C. capillata</i>	14	5.92	–	–	–	6.70	–	–	–	18	7.12	7.51	2.23	4.81	8.07	8.51	2.53	5.44
<i>C. capillata</i>	17	7.55	6.48	1.75	4.21	8.55	7.34	1.98	4.77	19	6.49	8.20	2.23	3.89	7.35	9.29	2.52	4.40
<i>C. capillata</i>	21	4.72	5.63	1.57	3.96	5.35	6.38	1.78	4.48	20	7.22	7.08	1.88	3.44	8.18	8.02	2.13	3.89
<i>C. capillata</i>	22	5.92	9.92	1.08	2.62	6.70	11.23	1.22	2.97	24	8.55	7.65	2.67	5.43	9.69	8.66	3.02	6.15
<i>C. capillata</i>	–	–	–	–	–	–	–	–	–	27	7.30	8.80	2.87	5.26	8.27	9.97	3.26	5.95
Mean (±S.D.)		6.67 (1.45)	7.04 (1.60)	1.45 (0.53)	3.73 (0.87)	7.55 (1.81)	7.98 (1.65)	1.64 (0.60)	4.22 (0.98)		7.19 (0.92)	7.81 (0.66)	2.16 (0.36)	4.30 (0.75)	8.14 (1.05)	8.84 (0.74)	2.44 (0.41)	4.87 (0.85)
<i>R. octopus</i>	1	–	2.98	3.73	–	–	3.37	4.22	–	1	1.63	3.46	1.51	2.68	1.85	3.92	1.71	3.04
<i>R. octopus</i>	2	4.74	3.42	2.20	3.38	5.37	3.87	2.49	3.83	2	4.82	3.46	2.41	3.47	5.46	3.92	2.73	3.93
<i>R. octopus</i>	3	7.99	2.44	0.62	1.53	9.05	2.76	0.70	1.73	3	3.29	3.39	1.54	2.35	3.72	3.84	1.74	2.66
<i>R. octopus</i>	4	4.03	4.18	1.10	2.51	4.56	4.73	1.25	2.84	–	–	–	–	–	–	–	–	–
<i>R. octopus</i>	5	–	2.37	2.30	–	–	2.68	2.60	–	–	–	–	–	–	–	–	–	–
<i>R. octopus</i>	8	–	3.79	0.58	–	–	4.29	0.66	–	–	–	–	–	–	–	–	–	–
<i>R. octopus</i>	9	–	6.17	2.57	–	–	6.99	2.91	–	–	–	–	–	–	–	–	–	–
Mean (±S.D.)		5.59 (2.11)	3.62 (1.31)	1.87 (1.16)	2.47 (0.93)	6.33 (2.39)	4.10 (1.48)	2.12 (1.31)	2.80 (1.05)		3.25 (1.59)	3.44 (0.04)	1.82 (0.51)	2.83 (0.58)	3.68 (1.81)	3.89 (0.04)	2.06 (0.57)	3.21 (0.65)
<i>C. hysoscella</i>	1	7.17	1.82	0.04	2.05	8.12	2.06	0.05	2.32	–	–	–	–	–	–	–	–	–
<i>C. hysoscella</i>	2	6.16	0.85	0.15	1.85	6.98	0.96	0.17	2.10	–	–	–	–	–	–	–	–	–
<i>C. hysoscella</i>	3	5.42	2.64	0.16	1.64	6.14	2.99	0.18	1.86	–	–	–	–	–	–	–	–	–
<i>C. hysoscella</i>	4	4.98	2.13	0.55	1.80	5.64	2.41	0.62	2.03	–	–	–	–	–	–	–	–	–
<i>C. hysoscella</i>	5	4.76	1.77	0.49	1.70	5.39	2.00	0.55	1.93	–	–	–	–	–	–	–	–	–
<i>C. hysoscella</i>	6	3.88	1.86	1.01	2.11	4.39	2.11	1.14	2.39	–	–	–	–	–	–	–	–	–
<i>C. hysoscella</i>	7	5.22	1.97	1.23	2.18	5.91	2.23	1.39	2.47	–	–	–	–	–	–	–	–	–
<i>C. hysoscella</i>	8	3.83	3.69	1.54	2.60	4.34	4.18	1.74	2.94	–	–	–	–	–	–	–	–	–
<i>C. hysoscella</i>	9	2.96	3.22	3.98	3.65	3.35	3.65	4.51	4.14	–	–	–	–	–	–	–	–	–
<i>C. hysoscella</i>	10	5.15	–	0.98	1.81	5.83	–	1.11	2.05	–	–	–	–	–	–	–	–	–
Mean (±S.D.)		4.95 (1.21)	2.22 (0.85)	1.01 (1.16)	2.14 (0.60)	5.61 (1.37)	2.26 (1.21)	1.15 (1.31)	2.42 (0.68)	–	–	–	–	–	–	–	–	–

Raw BC and revised BC values are also shown for *C. hysoscella*. Energy is expressed as kJ g dry mass⁻¹.

3.1.2. Energy density from bomb-calorimetry

Mean gross energy density estimates obtained using bomb-calorimetry ranged from 2.14 to 3.73 kJ g DM⁻¹, for whole jellyfish (Table 3). There was a significant difference in GE between species, with *C. capillata* having a higher mean GE content (3.73 kJ g DM⁻¹) than the two other species (ANOVA: $F_{2, 17}=9.53, p<0.01$). Within species, there were significant differences between the GE of the different tissues. In the case of *C. capillata* the bell tissue had significantly lower energy density (mean: 1.45 kJ g DM⁻¹) than both the gonad (mean: 6.67 kJ g DM⁻¹) and oral arm (mean: 7.04 kJ g DM⁻¹) tissues (ANOVA: $F_{2, 22}=46.09, p<0.01$) (Table 3). With *C. hysoscella*, the gonads had significantly higher energy content (mean: 4.95 kJ g DM⁻¹) than both oral arm (mean: 2.22 kJ g DM⁻¹) and bell (mean: 1.01 kJ g DM⁻¹) tissues (ANOVA: $F_{2, 26}=34.15, p<0.01$). In a similar fashion, the gonad tissue of *R. octopus* had significantly higher energy content (mean: 5.59 kJ g DM⁻¹) than both oral arm (mean: 3.62 kJ g DM⁻¹) and bell (mean: 1.87 kJ g DM⁻¹) tissues (ANOVA: $F_{2, 14}=7.88, p<0.01$) (Table 3).

3.1.3. Proximate-composition results

3.1.3.1. Inorganic composition (ash content). The mean ash content for whole *C. capillata* was 67.8% DM. There was a significant difference between the ash content of the different tissues, where the gonads and oral arms had a significantly lower ash content than the bell tissue (ANOVA: $F_{2, 36}=141.37, p<0.001$) (Table 4). Although the sample size was limited for *R. octopus*, the ash content was higher than that of *C. capillata* (Table 4).

3.1.3.2. Organic composition (protein, lipid and carbohydrate content). Protein was by far the largest fraction of the organic matter present in *C. capillata* dried samples, which contained only minor amounts of either lipids or carbohydrates. The protein content ranged from 10.1% to 22.6% DM for whole specimens (Table 5), and varied significantly between the component tissues (ANOVA: $F_{2, 30}=249.24, p<0.001$). Both the gonads and oral arms had a far greater protein content than did the bell component (mean±S.D. expressed as % DM: gonads=28.4±3.9, oral arms=29.8±3.1, bell=7.9±

Table 4

Ash content values (both measured and revised) for individual tissues of *C. capillata* and *R. octopus*

Species	ID #	Ash (% DM)				Ash (% DM) revised			
		G	OA	B	W	G	OA	B	W
<i>C. capillata</i>	1	–	52.0 (1.22)	67.8 (0.31)	–	–	58.9	76.7	–
<i>C. capillata</i>	2	–	51.2 (0.43)	68.1 (1.06)	–	–	58.0	77.1	–
<i>C. capillata</i>	3	57.7 (1.10)**	58.2 (0.20)**	74.9*	68.3	65.3	65.9	84.8	77.4
<i>C. capillata</i>	4	–	59.2 (0.10)	74.8 (0.20)**	–	–	67.0	84.7	–
<i>C. capillata</i>	6	56.1*	52.3 (0.10)**	75.0 (0.26)	66.6	63.5	59.3	84.9	75.5
<i>C. capillata</i>	8	–	58.8 (0.14)	78.1 (0.13)	–	–	66.6	88.5	–
<i>C. capillata</i>	9	52.6 (1.40)**	51.4 (0.24)	74.6 (0.30)**	70.2	59.6	58.3	84.5	79.5
<i>C. capillata</i>	10	–	–	71.3 (0.32)	–	–	–	80.7	–
<i>C. capillata</i>	11	–	51.5 (0.03)	78.0 (0.06)	–	–	58.3	88.3	–
<i>C. capillata</i>	13	–	–	72.2 (0.45)	–	–	–	81.6	–
<i>C. capillata</i>	14	62.9 (0.26)	59.6 (0.05)	74.3 (0.92)	66.8	71.3	67.5	84.1	75.6
<i>C. capillata</i>	17	–	–	70.6 (0.32)	–	–	–	79.9	–
<i>C. capillata</i>	18	50.9 (0.10)**	56.2 (0.47)	75.7 (0.16)	65.6	57.6	63.7	85.7	74.3
<i>C. capillata</i>	19	–	48.5 (0.40)**	72.7 (0.30)**	–	–	54.9	82.3	–
<i>C. capillata</i>	20	51.5 (0.20)**	58.5 (0.12)	74.2 (0.19)	69.2	58.3	66.2	84.1	78.4
<i>C. capillata</i>	21	–	53.0 (0.31)	–	–	–	60.0	–	–
<i>C. capillata</i>	22	–	–	70.3 (0.65)	–	–	–	79.6	–
<i>C. capillata</i>	24	–	54.0 (0.38)	73.1 (0.15)	–	–	61.1	82.8	–
<i>C. capillata</i>	27	–	51.9 (0.30)	73.7 (0.30)**	–	–	58.8	83.4	–
Mean (±S.D.)		55.3 (4.61)	54.4 (3.63)	73.3 (2.90)	67.8 (1.75)	62.6 (5.2)	61.6 (4.1)	83.0 (3.3)	76.8 (2.0)
<i>N</i>		6	15	18	6	6	15	18	6
<i>R. octopus</i>	1	79.7*	72.3 (0.03)**	80.2 (0.20)	75.4	90.3	81.9	90.8	85.4
<i>R. octopus</i>	2	66.1 (0.37)	72.0 (0.85)	75.7 (0.43)	71.8	74.9	81.5	85.7	81.3
<i>R. octopus</i>	3	–	72.4 (0.40)	80.0 (0.07)	–	–	82.0	90.6	–
Mean (±S.D.)		72.9 (9.57)	72.2 (0.17)	78.7 (2.52)	73.6 (2.59)	82.6 (10.9)	81.8 (0.2)	89.1 (2.9)	83.4 (2.9)
<i>N</i>		2	3	3	2	2	3	3	2

G=gonads, OA=oral arms, B=bell, and W=whole jellyfish. All samples were analysed in triplicate unless otherwise indicated (*single, **duplicate).

Table 5
Protein, lipid and carbohydrate content values for individual tissues of *C. capillata* and *R. octopus*

Species	ID #	Protein (% DM)				Lipid (% DM)				Carbohydrate (% DM)			
		G	OA	B	W	G	OA	B	W	G	OA	B	W
<i>C. capillata</i>	1	–	32.5 (0.50)	8.9 (0.39)	–	–	–	–	–	–	–	–	–
<i>C. capillata</i>	2	–	31.5 (0.66)	8.7 (0.29)	–	–	–	–	–	–	–	–	–
<i>C. capillata</i>	3	22.6 (0.20)	29.1 (0.06)	8.2 (0.17)	16.1	–	0.98 (0.02)	0.16 (0.00)	0.46	–	1.17 (0.02)	0.70 (0.01)	0.87
<i>C. capillata</i>	4	28.2 (0.90)	29.7 (0.51)	6.8 (0.01)	16.0	–	–	–	–	–	–	–	–
<i>C. capillata</i>	5	–	26.1 (1.25)	7.1 (0.15)	–	–	–	–	–	–	–	–	–
<i>C. capillata</i>	6	25.0 (0.18)	34.4 (0.32)	8.2 (0.09)	17.7	–	1.08 (0.71)	0.10 (0.00)	0.45	–	1.01 (0.01)	0.77 (0.00)	0.86
<i>C. capillata</i>	8	34.7 (0.30)	27.7 (0.20)	7.2 (0.14)	15.0	–	–	–	–	–	–	–	–
<i>C. capillata</i>	9	31.8 (1.00)	32.3 (0.50)	6.0 (0.06)	11.1	–	–	–	–	–	–	–	–
<i>C. capillata</i>	10	–	–	6.3 (0.28)	–	–	–	–	–	–	–	–	–
<i>C. capillata</i>	11	–	32.8 (0.22)	6.5 (0.15)	–	–	–	–	–	–	–	–	–
<i>C. capillata</i>	13	–	–	5.9 (0.11)	–	–	–	–	–	–	–	–	–
<i>C. capillata</i>	14	25.2 (0.16)	27.3 (0.26)	7.9 (0.07)	18.4	0.58 (0.02)	0.60 (0.03)	0.26 (0.13)	0.45	0.94 (0.01)	0.90 (0.00)	0.89 (0.03)	0.90
<i>C. capillata</i>	17	–	–	8.6 (0.10)	–	–	–	–	–	–	–	–	–
<i>C. capillata</i>	18	28.1 (0.07)	28.7 (0.47)	8.5 (0.05)	18.4	–	–	–	–	–	–	–	–
<i>C. capillata</i>	19	25.5*	31.6 (0.22)	8.5 (0.13)	14.9	–	–	–	–	–	–	–	–
<i>C. capillata</i>	20	28.6 (0.37)	25.5 (0.50)	7.0 (0.25)	12.7	–	2.01 (0.19)	0.16 (0.02)	0.66	–	1.10 (0.00)	0.78 (0.01)	0.87
<i>C. capillata</i>	21	–	24.4 (0.23)	9.8 (0.44)	–	–	–	–	–	–	–	–	–
<i>C. capillata</i>	22	–	–	6.5 (0.16)	–	–	–	–	–	–	–	–	–
<i>C. capillata</i>	24	34.1 (0.24)	29.3 (2.88)	10.3 (0.08)	20.9	–	–	–	–	–	–	–	–
<i>C. capillata</i>	27	28.9 (0.33)	34.1 (0.01)	11.2 (0.00)	20.5	–	–	–	–	–	–	–	–
Mean±S.D.		28.4 (3.86)	29.8 (3.09)	7.9 (1.46)	16.5 (3.05)	0.58	1.17 (0.60)	0.17 (0.07)	0.50 (0.10)	0.94	1.05 (0.12)	0.79 (0.08)	0.88 (0.02)
N		11	16	20	11	1	4	4	4	1	4	4	4
<i>R. octopus</i>	1	5.2 (0.26)	13.8 (0.15)	5.2 (0.27)	11.8	–	0.18 (0.04)	0.38 (0.10)	–	–	0.41 (0.01)	0.72 (0.00)	–
<i>R. octopus</i>	2	19.1 (0.54)	13.2 (0.18)	9.3 (0.08)	14.5	0.30 (0.08)	0.42 (0.08)	0.13 (0.01)	0.32	0.84 (0.02)	0.88 (0.02)	0.70 (0.02)	0.83
<i>R. octopus</i>	3	–	13.1 (0.07)	5.4 (0.18)	–	–	0.26 (0.15)	0.28 (0.02)	–	–	0.85 (0.00)	0.72 (0.01)	–
<i>R. octopus</i>	4	–	–	–	–	0.94 (0.26)	–	–	–	0.88 (0.00)	–	–	–
Mean±S.D.		12.1 (9.81)	13.4 (0.40)	6.6 (2.32)	12.8 (2.33)	0.62 (0.45)	0.29 (0.12)	0.26 (0.13)	0.32	0.86 (0.03)	0.71 (0.26)	0.71 (0.01)	0.83
N		2	3	3	2	2	3	3	1	2	3	3	1

G=gonads, OA=oral arms, and B=bell. Values for whole jellyfish (W) are derived from the sum of the three tissues (gonads, oral arms and bell). All protein samples were analysed in triplicate, unless otherwise indicated (*single, **duplicate). Lipids and carbohydrates were analysed in duplicate, unless otherwise indicated (*single).

1.5) (Table 5). Both the lipid and carbohydrate fractions were normally less than 1.2% of DM for all tissue types; however small sample size limited further analysis (Table 5). A similar picture emerged for the organic content of *R. octopus*, which comprised relatively large amounts of protein, and relatively minor amounts of lipids and carbohydrates (Table 5). However, these differences between individual tissue types were not as large as the protein differences observed between both gonads and oral arms and the bell components of *C. capillata*.

3.1.3.3. Energy density from proximate composition.

Mean gross energy density estimates obtained using proximate composition ranged from 2.83 to 4.30 kJ g DM⁻¹, for whole jellyfish (Table 3). *C. capillata* had a higher mean GE content (4.30 kJ g DM⁻¹) than *R. octopus*. For *C. capillata*, there were significant differences between the GE of the different tissues i.e. bell tissue had significantly lower energy density (mean: 2.16 kJ g DM⁻¹) than both the gonad (mean: 7.19 kJ g DM⁻¹) and oral arm (mean: 7.81 kJ g DM⁻¹) tissues (ANOVA: $F_{2, 30}=224.78$, $p<0.001$). Sample size limited further analysis of *R. octopus* (Table 3), although similar to *C. capillata*, the bell tissue had the lowest GE (mean: 1.87 kJ g DM⁻¹) (Table 3).

3.1.3.4. Total biochemical composition and unmeasured fraction.

The chemical analysis of whole *C. capillata* highlights the fact that that the dried samples mostly comprised inorganic matter, i.e. the mean ash content was 76.8% DM (Table 4). Within the organic proportion of the jellyfish samples, protein was by far the most abundant fraction (10.1–22.6% DM), with the sum of lipids and carbohydrates contributing to less than 1.4% of DM (see *C. capillata* id number 14, Table 5). This is equivalent to approximately 7–16 times more protein in whole specimens of *C. capillata* than the sum of lipids and carbohydrates. Note that the sum of all fractions did not add up to 100% DM (e.g. see *C. capillata* #14 Tables 4 and 5: 66.8 ash+(18.4+0.45+0.90) total organic matter=86.55% DM). This implies that there was a large fraction of matter in the samples that was not measurable by the methods employed in the study. A similar unmeasured fraction was found for *R. octopus* (i.e. see *R. octopus* #2 Tables 4 and 5: 71.8 ash+(14.5+0.32+0.83) total organics=87.45% DM).

3.2. Revised results after correcting for bound water of hydration

Both bomb-calorimetry and proximate-composition raw GE values were revised assuming 11.7% DM ‘water

of hydration’ calculated by Madin et al. (1981), Larson (1986), Clarke et al. (1992), and Lucas (1994). Importantly, after revision, the sum of all fractions measured by proximate-composition was ~100% DM (e.g. see *C. capillata* id number 14 Tables 4 and 5).

Revised mean energy densities from bomb-calorimetry were 4.22, 2.80 and 2.42 kJ g DM⁻¹ for *C. capillata*, *R. octopus* and *C. hysoscella* respectively. Individual tissues of *C. capillata* differed significantly (ANOVA: $F_{2, 22}=46.09$, $p<0.001$) with bell tissue (1.64 kJ g DM⁻¹) having much lower energy content than both oral arm (7.98 kJ g DM⁻¹) and gonad (7.55 kJ g DM⁻¹) tissues (Table 3).

Revised mean energy densities from proximate-composition were 3.21 and 4.73 kJ g DM⁻¹ for *R. octopus* and *C. capillata* respectively. Individual tissues of *C. capillata* differed significantly (ANOVA: $F_{2, 30}=79.22$, $p<0.001$) with bell tissue (2.44 kJ g DM⁻¹) having much lower energy content than both oral arm (8.39 kJ g DM⁻¹) and gonad (8.14 kJ g DM⁻¹) tissues (Table 3).

There was no significant difference between the revised GE values derived from both methods for *C. capillata* whole jellyfish, and its gonad and oral arm tissues (ANOVA: $p<0.05$). However, GE values obtained from bomb-calorimetry for *C. capillata* bell tissue were significantly different from the corresponding proximate-composition values (ANOVA: $F_{1, 17}=12.10$, $p<0.01$). Small sample sizes for *R. octopus* limited similar analysis.

There was a significant relationship between revised ash content and energy density of individual tissues derived from proximate composition ($p<0.001$). Similarly, there was a significant relationship between revised ash content and energy density of individual

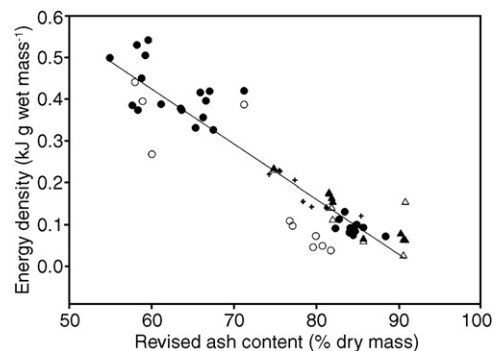


Fig. 2. Relationship between revised ash content and energy density (kJ g wet mass⁻¹) for individual tissues of jellyfish. Circles=*Cyanea capillata*, triangles=*Rhizostoma octopus*, open symbols=proximate-composition, filled symbols=bomb-calorimetry, crosshairs=whole jellyfish (spp. or method not specified). Energy density (kJ g wet mass⁻¹) = 1.21–0.0132 (% revised ash), $r^2=0.847$, $p<0.001$.

tissues derived from bomb-calorimetry ($p < 0.001$). There was no difference between these two regression lines ($t = 0.9351$, $df = 59$). The relationship between revised ash content and energy density of individual tissues from both methods combined, gave the following equation: Energy density ($\text{kJ g wet mass}^{-1}$) = $1.21 - 0.0132$ (% revised ash), $r^2 = 0.847$, $p < 0.001$ (Fig. 2). There was no difference between the regression lines of ‘whole’ jellyfish samples and ‘tissue’ samples, such that the equation above can be used to determine the energy density for whole jellyfish samples.

The revised mean bomb-calorimetry values for whole jellyfish equate to 0.18, 0.11, 0.10 $\text{kJ g wet mass}^{-1}$, for *C. capillata*, *R. octopus*, and *C. hysoscella* respectively. The revised mean proximate-composition values for

whole jellyfish equate to 0.20, and 0.12 $\text{kJ g wet mass}^{-1}$, for *C. capillata* and *R. octopus* respectively.

4. Discussion

Estimating the energy density of jellyfish is not straightforward, but our results help resolve some of the problems associated with different approaches (Lutcuage and Lutz, 1986; Arai, 1997). We can consider our revised proximate-composition estimates to be close to the true energy density of jellyfish because, (1) this method accounted for the bound water of hydration, and (2) subsequently, when the sum of all measured fractions were added they equalled $\sim 100\%$ of DM. Hence the revised values from proximate-composition

Table 6
Gross energy (GE) density values of different foodstuffs (expressed as $\text{kJ g dry weight}^{-1}$ and as $\text{kJ g dry mass}^{-1}$ when available)

Feedstuff/tissue	Species	GE $\text{kJ g dry mass}^{-1}$	GE $\text{kJ g wet mass}^{-1}$	Comment	Source
Red algae	<i>Gelidium</i> and <i>Centroseras</i>	13.8±2.1		Based on stomach contents of marine iguanas	Wikelski et al. (1997)
Green algae	<i>Ulva</i> species	10.0±2.7		Based on stomach contents of marine iguanas	Wikelski et al. (1997)
Sea grass	<i>Thalassia</i> species	14			Bjorndal (1997)
Sponge		16			Bjorndal (1997)
Hydrozoan	<i>Calycopsis borchgrevinki</i>	4.79		Calculated from carbon content	Clarke et al. (1992)
Hydrozoan	<i>Botrynema brucei</i>	1.96		Calculated from carbon content	Clarke et al. (1992)
Siphonophores	<i>Diphyes antarctica</i>	2.98		Calculated from carbon content	Clarke et al. (1992)
Pyrosomas	<i>Pyrosoma atlantica</i>	4.96±1.56	0.31±0.07	Proximate-composition	Davenport and Balazs (1991)
Jellyfish	<i>Atolla wyvillei</i>	5.95		Calculated from carbon content	Clarke et al. (1992)
Jellyfish	<i>Aurelia aurita</i>	2.3–3.6			Arai (1997)
Jellyfish	<i>Pelagia noctiluca</i>	3.1–4.1			Arai (1997)
Jellyfish	<i>Cyanea capillata</i>	4.22±0.98	0.18±0.05	Based on corrected bomb-calorimetry estimates	This study
Jellyfish	<i>Chrysaora hysoscella</i>	2.42±0.68	0.10±0.03	Based on corrected bomb-calorimetry estimates	This study
Jellyfish	<i>Rhizostoma octopus</i>	2.80±1.05	0.11±0.04	Based on corrected bomb-calorimetry estimates	This study
Ctenophore	<i>Beroe ovata</i>	2.7±0.4	0.07		Finenko et al. (2001)
Ctenophore	<i>Pleurobrachia</i>	0.47		Calculated from carbon content	Clarke et al. (1992)
Ctenophore	<i>Beroe</i> sp.	4.33		Calculated from carbon content	Clarke et al. (1992)
Polychaete	<i>Tomopteris carpenteri</i>	16.33		Calculated from carbon content	Clarke et al. (1992)
Squid		20.71±0.95	3.81±0.24		Van Pelt et al. (1997)
Salp	<i>Salpa fusiformis</i>	5.45		Calculated from carbon content	Clarke et al. (1992)
Adult sand lance	<i>Ammodytes hexapterus</i>	14.23–22.79			Robards et al. (1999)
Sandeels	<i>Ammodytes marinus</i>	5.8±0.5		Samples taken from guillemot regurgitates	Wanless et al. (2005)
Sprat	<i>Sprattus sprattus</i>	7.6±0.7		Samples taken from guillemot regurgitates	Wanless et al. (2005)
Flatfish		16.5±0.23	3.61±0.01		Anthony et al. (2000)
Pacific cod	<i>Gadus marcocephalus</i>	17.1±0.22	3.65±0.08		Anthony et al. (2000)
Pacific herring	<i>Clupea harengus pallasi</i>	21.3±0.19	5.84±0.11		Anthony et al. (2000)
Myctophid fish	E.g. <i>Krefflichys</i> spp.	24.1	6.9	Obtained from stomach samples of birds	Kooyman et al. (1992)
Various fish	From north Pacific	15.57–27.92	2.37–8.05		Van Pelt et al. (1997)
Typical carbohydrate		17.5			Clarke et al. (1992)
Typical lipid		39.5			Clarke et al. (1992)
Typical protein		23.9			Clarke et al. (1992)
Foliage	<i>Eucalyptus</i> mix	21.05	7.9		Ullrey et al. (1981)

provide a good benchmark for comparison with bomb-calorimetry values.

Although bomb-calorimetry is frequently used to quantify the energy density of a wide range of taxa, estimates for jellyfish (and other gelatinous zooplankton) have previously been problematic due to the low energy density of samples, uneven distribution of the inorganic and organic matter in the dried samples and the fact that some residual/bound ‘water of hydration’ always remains after the drying process (Clarke et al., 1992; Lucas, 1994; Arai, 1997). Our corrected estimates of energy density derived from bomb-calorimetry ranged from 2.91 to 5.07 kJ g DM⁻¹. These values are comparable to our proximate composition values and the few published estimates obtained from proximate-composition and carbon content analysis: 2.3–6.0 kJ g DM⁻¹ (Clarke et al., 1992; Arai, 1997) and suggest that with suitable modification (outlined in methods), bomb-calorimetry can provide reliable estimates of energy density for jellyfish.

Importantly, these results highlight differences in energy density both between species and between body components. For example, whole *C. capillata* jellyfish were almost twice as nutritious as *C. hysoscella* (energy densities 0.22 and 0.12 kJ g wet mass⁻¹ respectively), and *C. capillata* bell tissue had ~5 times less energy than either gonad or oral arm tissue. In short, our jellyfish energy densities illustrate the variation between seemingly similar species and reiterate the importance for collecting energy density data for a wide range of species and their associated tissues (Tierney et al., 2002).

Both our bomb-calorimetry and proximate-composition energy estimates confirm that jellyfish have a very low energy density when compared with other taxa and foodstuffs (Table 6). This low energy density is a combination of (a) the high ash content, so that energy densities per g dry mass are low, and also the high water content which means that low energy densities per g dry mass translate to even lower relative energy densities on a wet mass basis (Table 7). For example, jellyfish may have up to 58 times less energy per gram of wet mass than herring flesh.

The clear relationship we found between jellyfish energy density and ash content, suggests that ash content, which is cheap and easy to measure, may provide a good proxy for jellyfish energy density where other data are lacking. The search for similar proxies for energy density in others groups is well developed. For example, for fish in the north Pacific there are strong negative relationships between energy density and both ash free dry weight and ash contents (Van Pelt et al., 1997). In the absence of other data, therefore, the

empirical relationship we established: Energy (kJ g wet mass⁻¹) = 1.21 – 0.0132 (% revised ash) can be used to estimate jellyfish energy density.

Although jellyfish as a food resource may seem very improbable with such low energy densities, some animals have adopted anatomical, physiological and/or behavioural adaptations to survive on food items that are equally as energetically challenging. For example, the koala (*Phascolarctos cinereus*) survives exclusively on a nutritionally taxing diet of eucalyptus leaves (low in protein and high in deterrent compounds such as terpenes) by being inactive for up to 20 h a day, moving slowly, and possessing a large cecum (the most capacious of any mammal) with a microbial fauna that aids digestion efficiency (Ullrey et al., 1981; Lawler et al., 1998; Feldhamer et al., 1999). The white rhino (*Ceratotherium simum*), a non-ruminant and the largest extant ‘pure grass feeder’ can attain a size of 2300 kg on this low quality food source by foraging 50% of the diel cycle (Shrader et al., 2006). So for some, particularly large animals, survival may be simply a matter of quantity, rather than quality of prey (Shrader et al., 2006). Indeed, larger animals can survive better on lower quality foods than smaller animals as body size helps determine metabolic requirements (Nagy et al., 1999). It is therefore perhaps unsurprising that the

Table 7

Tissue	<i>C. capillata</i>	<i>R. octopus</i>	<i>C. hysoscella</i>
<i>(a) Mean GE kJ g DM⁻¹ (n, ±S.D.)</i>			
Gonad (PC)	8.14 (11, 1.81)	3.68 (3, 1.81)	–
Oral arms (PC)	8.84 (11, 0.74)	3.89 (3, 0.04)	–
Bell (PC)	2.44 (11, 0.41)	2.06 (3, 0.57)	–
Whole (PC)	4.87 (11, 0.85)	3.21 (3, 0.65)	–
Gonad (BC)	7.55 (10, 1.81)	6.33 (3, 2.39)	5.61 (10, 1.37)
Oral arms (BC)	7.98 (7, 1.65)	4.10 (7, 1.48)	2.26 (9, 1.21)
Bell (BC)	1.64 (8, 0.60)	2.12 (7, 1.31)	1.15 (10, 1.31)
Whole (BC)	4.22 (7, 0.98)	2.80 (3, 1.05)	2.42 (10, 0.68)
<i>(b) Mean GE kJ g WM⁻¹ (n, ±S.D.)</i>			
Gonad (PC)	0.42 (11, 0.08)	0.20 (3, 0.11)	–
Oral arms (PC)	0.42 (11, 0.08)	0.16 (3, 0.01)	–
Bell (PC)	0.09 (11, 0.02)	0.06 (3, 0.00)	–
Whole (PC)	0.20 (11, 0.04)	0.12 (3, 0.02)	–
Gonad (BC)	0.43 (10, 0.15)	0.38 (3, 0.28)	0.27 (10, 0.08)
Oral arms (BC)	0.40 (7, 0.15)	0.17 (7, 0.06)	0.10 (9, 0.05)
Bell (BC)	0.06 (8, 0.03)	0.07 (7, 0.05)	0.04 (10, 0.05)
Whole (BC)	0.18 (7, 0.05)	0.11 (3, 0.04)	0.10 (10, 0.03)

PC=proximate-composition, and BC=bomb-calorimetry assuming. (a): Mean gross energy (GE) density values for individual tissues and whole samples of *C. capillata*, *R. octopus* and *C. hysoscella* (expressed as kJ g dry mass⁻¹, n, ±S.D.). (b): Mean gross energy (GE) density values for individual tissues and whole samples of *C. capillata*, *R. octopus* and *C. hysoscella* (expressed as kJ g wet mass⁻¹).

largest sea turtle, the leatherback (*D. coriacea*), and the largest teleost fish, the oceanic sunfish (*Mola mola*), are both able to survive largely on a nutritionally challenging diet of jellyfish (Davenport, 1998; Wallace et al., 2005, 2006; Houghton et al., 2006b).

A salient finding of this study is the disparity of energy densities between the different jellyfish tissues that may have some bearing on the foraging decisions of jellyfish predators. Indeed, there are precedents elsewhere e.g. green turtles (*Chelonia mydas*) selectively graze on young leaves of seagrass (*Thalassia testudinum*) that are lower in lignin and hence higher in nutritional quality (Bjorndal, 1980). Similarly, in Alaska, bears (*Ursus arctos* and *U. americanus*) selectively target the energy rich salmon *Oncorhynchus* spp. (i.e. those that have not spawned) or the energy rich body parts (i.e. eggs in females and brain in males) when availability of salmon is high (Gende et al., 2001). Unfortunately, observations of predators foraging on jellyfish are comparatively rare (James and Herman, 2001), however, one example are the hyperiid amphipods that are facultative parasites of jellyfish. Buecher et al. (2001) have shown that the preferred food of the adult *Hyperia medusarum* are the gonads, and as such supports the assertion that variation in the quality of prey tissues may alter feeding behaviour. Considering a five-fold difference in the energy density of *C. capillata* tissues, it would be interesting to observe if leatherback turtles selectively target the more nutritious gonads and oral arms. As Wallace et al. (2006) suggested, variations in the quality and amount of prey consumed might lengthen or shorten the remigration interval of leatherback turtles. Clearly, observations of predators feeding on jellyfish are warranted.

In summary, we have critically examined the energy density of jellyfish using two different approaches. We have shown that with suitable modifications, bomb-calorimetry can be used (and therefore may be more widely employed) to measure the energy density of gelatinous zooplankton. Our findings illustrate the variation in energy densities between species and within species, and importantly highlight that jellyfish have a very low energy density per wet mass when compared with other marine taxa. These values of energy density can be confidently applied to construct bioenergetic models for jellyfish predators such as leatherback turtles and oceanic sunfish.

Acknowledgements

Funding was provided by INTERREG IIIA (European Regional Development Fund), the Countryside Council

for Wales Species Challenge Fund and the Marine Conservation Society. The Marine Institute (Ireland), under the National Development Plan, provided additional funds for T.K. Doyle. Special thanks to Therese Uniacke, Ciara Brickley, Nidhi Bansal, and Tom O'Connor of the Department of Food and Nutritional Science, University College Cork, who carried out the proximate-composition analysis. Thanks are also due to Aine Healy, David Jones, Vincent, Sean and Christina Rooney, Jim and Rose Hurley, Kevin McCormack, Eithne Lee, Maria Doyle, Kate Williamson, Irena Kruszona and colleagues, Vernon Jones and Tom Stringell. [SS]

References

- Anthony, J.A., Roby, D.D., Turco, K.R., 2000. Lipid content and energy density of forage fishes from the northern Gulf of Alaska. *J. Exp. Mar. Biol. Ecol.* 248, 53–78.
- Arai, M.N., 1997. *A Functional Biology of Scyphozoa*. Chapman & Hall, London.
- Arai, M.N., 2005. Predation on pelagic coelenterates: a review. *J. Mar. Biol. Assoc. UK* 85, 523–528.
- Billett, D.S.M., Bett, B.J., Jacobs, C.L., Rouse, I.P., Wigham, B.D., 2006. Mass deposition of jellyfish in the deep Arabian Sea. *Limnol. Oceanogr.* 51 (5), 2077–2083.
- Bjorndal, K.A., 1980. Nutrition and grazing behavior *Chelonia mydas*. *Mar. Biol.* 56, 147–154.
- Bjorndal, K.A., 1997. Foraging ecology and nutrition of sea turtles. In: Lutz, P.L., Musick, J.A. (Eds.), *The Biology of Sea Turtles*. CRC Press, pp. 199–231.
- Buecher, E., Sparks, C., Brierley, A., Boyer, H., Gibbons, M., 2001. Biometry and size distribution of *Chrysaora hysoscella* (Cnidaria, Scyphozoa) and *Aequorea aequorea* (Cnidaria, Hydrozoa) off Namibia with some notes on their parasite *Hyperia medusarum*. *J. Plankton Res.* 23, 1073–1080.
- Clarke, A., Holmes, L.J., Gore, D.J., 1992. Proximate and elemental composition of gelatinous zooplankton from the Southern-Ocean. *J. Exp. Mar. Biol. Ecol.* 155, 55–68.
- Davenport, J., 1998. Sustaining endothermy on a diet of cold jelly: energetics of the leatherback turtles *Dermochelys coriacea*. *Brit. Herp. Soc. Bull.* 62, 4–8.
- Davenport, J., Balazs, G.H., 1991. “Fiery pyrosomas” — are pyrosomas an important items in the diet of leatherback turtles? *Brit. Herp. Soc. Bull.* 37, 33–38.
- Doyle, T.K., Houghton, J.D.R., Buckley, S.M., Hays, G.C., Davenport, J., in press. The broad-scale distribution of five jellyfish species across a temperate coastal environment. *Hydrobiologia*. doi: 10.1007/s10750-006-0362-2.
- Duron, M., 1978. Contribution à l'étude de la biologie de *Dermochelys coriacea* (Linné) dans les Pertuis Charentais. PhD Thesis, University of Bordeaux, Talence, France.
- Feldhamer, G.A., Drickamer, L.C., Vessey, S.H., Merritt, J.F., 1999. *Mammalogy: Adaptation, Diversity, and Ecology*. McGraw-Hill.
- Finenko, G.A., Anninsky, B.E., Romanova, Z.A., Abolmasova, G.I., Kideys, A.E., 2001. Chemical composition, respiration and feeding rates of the new alien ctenophore, *Beroe ovata*, in the Black Sea. *Hydrobiologia* 451, 177–186.
- Fortin, D., Fryxell, J.M., Pilote, R., 2002. The temporal scale of foraging decisions in bison. *Ecology* 83, 970–982.

- Fowler, J., Cohen, L., Jarvis, P., 1998. Practical Statistics for Field Biology. John Wiley & Sons.
- Gende, S.M., Quinn, T.P., Willson, M.F., 2001. Consumption choice by bears feeding on salmon. *Oecologia* 127, 372–382.
- Gnaiger, E., Bitterlich, G., 1984. Proximate biochemical composition and caloric content calculated from elemental CHN analysis — a stoichiometric concept. *Oecologia* 62, 289–298.
- Houghton, J.D.R., Doyle, T.K., Davenport, J., Hays, G.C., 2006a. The ocean sunfish *Mola mola*: insights into distribution, abundance and behaviour in the Irish Sea and Celtic Seas. *J. Mar. Biol. Assoc. UK* 86, 1237–1243.
- Houghton, J.D.R., Doyle, T.K., Wilson, M.W., Davenport, J., Hays, G.C., 2006b. Jellyfish aggregations and leatherback turtle foraging patterns in a temperate coastal environment. *Ecology* 87, 1967–1972.
- James, M.C., Herman, T.B., 2001. Feeding of *Dermochelys coriacea* on medusae in the northwest Atlantic. *Conserv. Biol.* 4, 202–205.
- Kooyman, G.L., Cherel, Y., Lemaho, Y., Croxall, J.P., Thorson, P.H., Ridoux, V., 1992. Diving behavior and energetics during foraging cycles in king penguins. *Ecol. Monogr.* 62, 143–163.
- Larson, R.J., 1986. Water-content, organic content, and carbon and nitrogen composition of medusae from the Northeast Pacific. *J. Exp. Mar. Biol. Ecol.* 99, 107–120.
- Lawler, I.R., Foley, W.J., Eschler, B.M., Pass, D.M., Handasyde, K., 1998. Intraspecific variation in *Eucalyptus* secondary metabolites determines food intake by folivorous marsupials. *Oecologia* 116, 160–169.
- Lucas, C.H., 1994. Biochemical composition of *Aurelia aurita* in relation to age and sexual maturity. *J. Exp. Mar. Biol. Ecol.* 183, 179–192.
- Lutcavage, M., Lutz, P.L., 1986. Metabolic-rate and food-energy requirements of the leatherback sea-turtle, *Dermochelys coriacea*. *Copeia* 796–798.
- Lynam, C.P., Gibbons, M.J., Axelsen, B.E., Sparks, C.A.J., Coetzee, J., Heywood, B.G., Brierley, A.S., 2006. Jellyfish overtake fish in a heavily fished ecosystem. *Curr. Biol.* 16, R492–R493.
- Madin, L.P., Cetta, C.M., McAlister, V.L., 1981. Elemental and biochemical composition of salps (Tunicata, Thaliacea). *Mar. Biol.* 63, 217–226.
- McLean, J.A., Tobin, G., 1987. Animal and Human Calorimetry. Cambridge University Press, pp. 24–30.
- Mills, C.E., 2001. Jellyfish blooms: are populations increasing globally in response to changing ocean conditions? *Hydrobiologia* 451, 55–68.
- Nagy, K.A., Girard, I.A., Brown, T.K., 1999. Energetics of free-ranging mammals, reptiles, and birds. *Annu. Rev. Nutr.* 19, 247–277.
- Robards, M.D., Anthony, J.A., Rose, G.A., Piatt, J.F., 1999. Changes in proximate composition and somatic energy content for Pacific sand lance (*Ammodytes hexapterus*) from Kachemak Bay, Alaska relative to maturity and season. *J. Exp. Mar. Biol. Ecol.* 242, 245–258.
- Shrader, A.M., Owen-Smith, N., Ogutu, J.O., 2006. How a mega-grazer copes with the dry season: food and nutrient intake rates by white rhinoceros in the wild. *Funct. Ecol.* 20, 376–384.
- Tierney, M., Hindell, M.A., Goldsworthy, S., 2002. Energy content of mesopelagic fish from Macquarie Island. *Antarct. Sci.* 14, 225–230.
- Ullrey, D.E., Robinson, P.T., Whette, P.A., 1981. *Eucalyptus* digestibility and digestible energy requirements of adult male koalas, *Phascolarctos cinereus* (Marsupialia). *Aust. J. Zool.* 29, 847–852.
- Van Pelt, T.I., Piatt, J.F., Lance, B.K., Roby, D.D., 1997. Proximate composition and energy density of some North Pacific forage fishes. *Comp. Biochem. Physiol.* 118, 1393–1398.
- Wallace, B.P., Williams, C.L., Paladino, F.V., Morreale, S.J., Lindstrom, R.T., Spotila, J.R., 2005. Bioenergetics and diving activity of interesting leatherback turtles *Dermochelys coriacea* at Parque Nacional Marino las Baulas, Costa Rica. *J. Exp. Biol.* 208, 3873–3884.
- Wallace, B.P., Kilham, S.S., Paladino, F.V., Spotila, J.R., 2006. Energy budget calculations indicate resource limitation in Eastern Pacific leatherback turtles. *Mar. Ecol. Prog. Ser.* 318, 263–270.
- Wanless, S., Harris, M.P., Redman, P., Speakman, J.R., 2005. Low energy values of fish as a probable cause of a major seabird breeding failure in the North Sea. *Mar. Ecol. Prog. Ser.* 294, 1–8.
- Wikelski, M., Carrillo, V., Trillmich, F., 1997. Energy limits to body size in a grazing reptile, the Galapagos marine iguana. *Ecology* 7, 2204–2217.