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Biochemical composition of the mesopelagic coronate jellyfish *Periphylla periphylla* from the Gulf of Mexico

CATHY H. LUCAS

School of Ocean & Earth Science, University of Southampton, National Oceanography Centre, European Way, Southampton, SO14 3ZH

The size–weight relationships, percentage water, ash-free dry weight and biochemical (protein, lipid and carbohydrate) contents of the coronate jellyfish species Periphylla periphylla *have been analysed. A total of 48 medusae ranging in size from 13 to 80 mm bell diameter were collected from mesopelagic depths in the eastern Gulf of Mexico. The dry mass of whole medusae ranged from 1.12 to 10.53% of wet weight (mean 5.49%), while ash-free dry weight, a proxy for organic content, varied between 25.19 and 34.89% of dry weight (mean 30.14%). Preservation in 2% glutaraldehyde resulted in shrinkage in >75% of the medusae, with preserved bell diameters 2.9% to 28.6% smaller than the original fresh bell diameters. Preservation also produced a significant adjustment to the bell diameter to wet weight relationship. With regard to biochemical content, the typical gelatinous zooplankton trend of low carbohydrate (mean 8.99 mg gDW^{-1}), intermediate lipid (mean 20.57 mg gDW^{-1}) and high protein (mean 63.71 mg gDW^{-1}) was observed. Although there was a high degree of variability in biochemistry, there was no apparent trend with size.*

Keywords: *Periphylla periphylla*, jellyfish, biochemistry, water content, preservation

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INTRODUCTION

Jellyfish are no longer considered to be trophic dead ends but instead are important members of pelagic communities, both as predators, and as food for fish (Purcell & Arai, 2001), turtles (Witt *et al.*, 2007) and even other jellyfish (Arai, 2005). One of the ultimate aims in current jellyfish research is to incorporate them into ecosystems models used to predict population dynamics and ecosystem effects. However, such efforts usually suffer from insufficient information on jellyfish biomass and biology (see Purcell, in press). Knowledge of the biochemical and elemental composition of organisms is essential in order to calculate biomass, quantify the transfer of energy through the pelagic food web, and estimate the supply of organic matter to the deep seabed through dead and decaying medusae. For example, a mass deposition of the jellyfish *Crambionella orsini* to the seafloor between 300 and 3300 m depth in the Arabian Sea was estimated to have a standing stock of between 1.5 to 78 g C m^{-2} (Billett *et al.*, 2006); a significant input of carbon.

Over the years there have been comparatively few morphometric and biochemical studies on jellyfish (e.g. Schneider, 1988; Arai *et al.*, 1989; Clarke *et al.*, 1992; Lucas, 1994), and by far the vast majority of these have been for coastal and shallow water species. Data for mesopelagic species are extremely rare. Typically, jellyfish have high water (~95%) and mineral ash (~70%) contents; and in relative terms, high protein (~5–30% of dry weight (DW)), intermediate lipid (~2–10% of DW) and very low carbohydrate (~0.5–1.7% of DW) contents. Proteins are thought to be the main storage product in gelatinous zooplankton, as lipids, comprising mainly phospholipids, have a more structural role.

The coronate jellyfish *Periphylla periphylla* (Péron & Lesueur, 1810) is widely distributed at mesopelagic depths in several oceans (e.g. Mauchline & Harvey, 1983; Roe *et al.*, 1984; Larson *et al.*, 1991; Pagès *et al.*, 1996; Mianzan & Cornelius, 1999; Osborn *et al.*, 2007; Gershwin & Zeidler, 2008). Permanent and highly abundant populations have also been observed in several Norwegian fjords (Lurefjorden, Sognefjorden and Halsafjorden) in abundances of up to 2.5 ind m^{-3}. Research into these Norwegian populations has greatly increased our understanding of the biology and ecology of *P. periphylla*. Recent publications have focused on distribution, abundance and biomass (Fosså, 1992; Youngbluth & Båmstedt, 2001), life cycle and development (Jarms *et al.*, 1999, 2002), patterns of diel vertical migration (Båmstedt *et al.*, 2003; Kaartvedt *et al.*, 2007), causes of mass occurrence (Sornes *et al.*, 2007), trophic ecology and functional morphology (Soetje *et al.*, 2007), impacts on foodweb structure (Riemann *et al.*, 2006), and the fate of jellyfish biomass following population crashes (Titelman *et al.*, 2006). Little information exists on the mass, chemical and biochemical composition of this, and other mesopelagic coronate species such as *Atolla* spp. and *Nausithoe* spp. (but see Clarke *et al.*, 1992; Nelson *et al.*, 2000; Youngbluth & Båmstedt, 2001).

Abundances of gelatinous zooplankton, including *P. periphylla*, are unlikely to be as consistently high in open oceans

Corresponding author:
C.H. Lucas
Email: chl1@noc.soton.ac.uk

as in semi-enclosed fjords (Sornes *et al.*, 2007). Indeed, abundance estimates of *P. periphylla* from net tows in the open ocean are usually <1 ind 1000 m^{-3} (Pagès *et al.*, 1996; Dalpadado *et al.*, 1998). However, their ubiquitous distribution and periodic numerical dominance of oceanic communities suggest that they could, at times, be significant consumers in pelagic food webs and influence the transfer of organic material between the surface and deep sea. As part of a wider study of the distribution, reproductive biology and development of mesopelagic jellyfish, this paper describes the size–weight relationships, percentage water and mineral ash contents, and biochemical composition (protein, lipid and carbohydrate) of the coronate jellyfish *Periphylla periphylla* medusae collected from mesopelagic depths in the eastern Gulf of Mexico.

MATERIALS AND METHODS

Sampling

Periphylla periphylla medusae were collected from the eastern Gulf of Mexico (running along the 1000 m depth contour between 26°24′N 84°51′W and 27°04′N 85°09′W) in mid-September 1995. Medusae were collected using the 'Johnson-Sea-Link' submersible and by Tucker Trawl. A total of 18 medusae were captured using the 'Johnson-Sea-Link', from depths of between 638 m and 831 m. The temperature recorded at these depths varied between 5.45 and 6.80°C. A total of 30 medusae were collected using the Tucker Trawl, primarily during night trawls, from depths ranging between 130 m and 850 m.

Water and mineral ash content

Within 2 hours of collection, the bell diameters of all medusae were measured (mm) and their sex and state of maturity noted where possible (i.e. immature with no gametes visible, male and female). Undamaged individuals selected for size–weight and/or biochemical analyses were then either individually bagged and frozen at −20°C, or preserved in 2% gluteraldehyde for later analysis.

Wet weight (WW, g) of frozen individuals was obtained after carefully 'blotting' the medusae to remove superficial water and excess salt. After wet-weighing, seven individuals were used for dry weight analysis. With the remaining medusae, each individual was cut in half; one-half for biochemical (protein, lipids and carbohydrate) analyses, the remainder for further analyses (dry, ash and ash-free dry weights). To determine dry weight (DW, g), individuals were placed in weighed pre-ashed crucibles and dried at 70°C for 24 hours, or until a constant weight was obtained. The dried samples were ashed at 550°C for 24 hours to burn off organic material, and then cooled in a desiccator prior to re-weighing to determine ash weight (AW, g) and ash-free dry weight (AFDW, g). Following the cruise, the bell diameters of preserved individuals were re-measured and re-weighed so that the effect of preservation on size could be quantified. In addition, the 8 gonads were dissected out from their location peripheral to the central stomach to measure WW and DW according to the methods described above.

Biochemical composition

For the biochemical assays, between 30 mg and 60 mg of freeze dried tissue was weighed out, homogenized with 5 ml of distilled water, and then divided into 10 equal subsamples of 0.5 ml each. For every individual, each assay (i.e. total proteins, total lipids and total carbohydrates) was carried out in duplicate. Following the addition of 0.1 N NaOH, total proteins were measured using the modified Folin–Ciocalteau method of Lowry *et al.* (1951). Bovine serum albumen (BSA) diluted with 0.9% w/v KCl was used as the standard. Total carbohydrates were measured using the phenol–sulphuric acid method of Dubois *et al.* (1956), with D-glucose used as the standard. Total lipids were extracted from the duplicate subsamples using 2:1 chloroform/methanol (Bligh & Dyer, 1959). Phase separation was allowed to take place overnight. The lower chloroform layer was removed, and the crude extract washed with 0.05 N KCl. The amount of lipid was determined gravimetrically according to Folch *et al.* (1957).

RESULTS AND DISCUSSION

Size–weight relationships are important for quantifying population stocks and allow population biomass to be estimated from size–frequency distributions. Two commonly applied measures of biomass, production and material fluxes in the marine environment are dry weight and ash-free dry weight as both these weight types are relatively easy to determine. While these measurements are basic, they are useful from an ecological point of view and they have very rarely been determined for mesopelagic gelatinous species.

A total of 48 *Periphylla periphylla* medusae were captured on the cruise, ranging in size from 13 mm to 80 mm bell diameter (BD). The catch comprised 21 females, 9 males, 10 immature and 8 unidentified. In the seven medusae (13–41 mm BD) used for size–weight analysis, both wet weight (WW) and dry weight (DW) increased linearly with a high degree of correlation (Table 1). Dry mass for whole medusae (N = 21) ranged from 1.12% to 10.53% of WW (mean 5.49%), and ash-free dry weight (AFDW) varied between 25.19% and 34.89% of DW (mean 30.14%). The dry mass value is slightly lower than a previously published value (mean 3.24 ± 0.2% WW, range 2.0–3.9% WW) for *P. periphylla* from the Norwegian fjords (Youngbluth & Båmstedt, 2001) but similar to that found for the related *Atolla wyvillei* (4.92 ± 0.28% WW) (Clarke *et al.*, 1992). The high ash contents, ~65–75%, are typical of all gelatinous zooplankton (Arai *et al.*, 1989; Clarke *et al.*, 1992; Lucas, 1994) although as has been discussed in previous papers these values are biased by 'water of hydration', which is water retained during drying at 60°C and lost during ignition at 550°C (Larson, 1986b; Clarke *et al.*, 1992; Lucas, 1994). Water of hydration is also used to explain the difference between ash-free dry weight and total organic weight determined biochemically (see below).

The effect of preservation in 2% gluteraldehyde on bell diameter and wet weight was determined. Individuals that had been measured fresh were re-measured following preservation for 40 days. Shrinkage of the bell, which is a well known phenomenon in gelatinous zooplankton (e.g. Möller, 1980) occurred in >75% of the medusae. A significant ($r = 0.970$, $P < 0.001$, $N = 40$) relationship was observed between the

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Table 1. Summary of the morphometric measurements of *Periphylla periphylla* from the Gulf of Mexico (BD, bell diameter (mm); WW, wet weight (g); DW, dry weight (g); AFDW, ash-free dry weight (g); ranges and means of WW[1] and DW[2] in medusae 13–41 mm BD,[3] medusae 13–60 mm BD; regressions based on log–log transformed data).

Parameter	N	Range	Mean (±SD)	Regression coefficients			
				a	b	r	p
BD v WW	7	0.71–8.29[1]	3.65 (2.64)	−2.248	1.941	0.926	0.001
BD v DW	7	0.07–0.40[2]	0.20 (0.28)	−2.867	1.496	0.851	0.01
DW % WW[3]	21	1.12–10.53	5.49 (2.04)	–	–	–	–
AFDW % DW[3]	21	25.19–34.89	30.14 (3.39)	–	–	–	–

fresh and preserved bell diameters, such that larger medusae experienced a relatively greater degree of shrinkage (Figure 1). On average, medusae shrank by 9.1%, although the greatest reduction in bell diameter was 28.6%, observed in an individual 42 mm BD (fresh). This is very similar to the findings of Möller (1980) for the coastal jellyfish *Aurelia aurita*. In that study, ephyrae and medusae bell diameter shrank by between 15% and 28.6% following 6 weeks' preservation in 4% formalin, with the greatest shrinkage also found in the largest individuals. The wet weights of whole preserved *P. periphylla* medusae were also measured, with the relationships between fresh bell diameter and fresh WW (N = 7) and fresh bell diameter and preserved WW (N = 26) illustrated on log–log transformed data in Figure 2. A *t*-test showed that the slopes of the least-squares linear regressions were significantly different from each other.

Of the 26 preserved medusae, the gonads in 16 individuals were dissected out and weighed. Preserved gonad WW represented between 0.52% and 4.69% of the total medusa preserved wet mass (mean 2.02 ± 1.27%). Preserved dry mass of the gonads ranged between 3.72% and 9.90% of the wet weight (mean 6.76 ± 2.00% WW). This compares with a mean dry mass in whole medusae, albeit fresh, of 5.49% of WW. Isolated organs, in particular gonads, can be more informative than whole medusae in providing information about nutritional state (Arai *et al.*, 1989) and maturity/gonad size (Lucas, 1994). *Periphylla periphylla* produce few large eggs continuously throughout the year (Jarms *et al.*, 1999); the large size indicative of a direct development (Larson 1986a; Jarms *et al.*, 1999). In other jellyfish species, gonadal tissue has previously been found to represent a substantial fraction of the total carbon or organic (i.e. sum of biochemical fractions) content of medusae (Larson, 1986b; Schneider, 1988; Lucas, 1994), which is primarily attributed to proteins and carbohydrates (Lucas, 1994). It is likely, although untested, that the gonads of *P. periphylla* are organic-rich, reflecting a high degree of investment that would be required to prepare the large oocytes for their time in deep water as non-motile organisms going through several non-feeding stages (Jarms *et al.*, 1999).

The biochemical content (i.e. total proteins, total lipids and total carbohydrates) of whole fresh medusae (22–80 mm BD) is summarized in Table 2. The typical gelatinous zooplankton trend of low carbohydrate (mean 0.49 mg gWW^{-1}), intermediate lipid (mean 1.14 mg gWW^{-1}) and high protein (mean 3.45 mg gWW^{-1}) content was observed, although there was a high degree of variability. In this study, total organics (i.e. sum of proteins, lipids and carbohydrates) were in the region of 5 mg g WW^{-1} (~92 mg gDW^{-1}). In *Atolla wyvillei* from the Southern Ocean, mean contents as

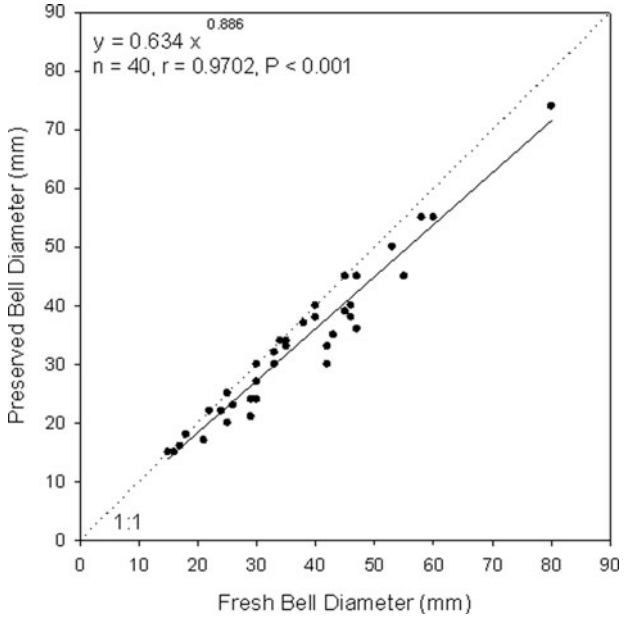

Fig. 1. Effect of preservation on bell diameter (mm) on *Periphylla periphylla*.

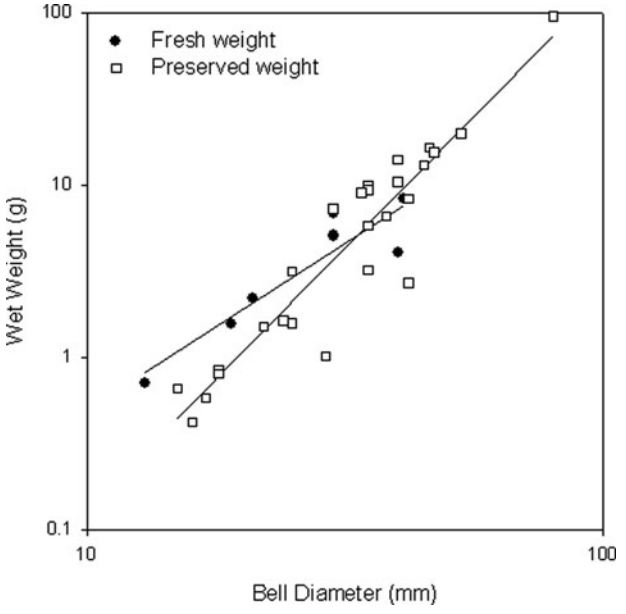

Fig. 2. Effect of preservation on the bell diameter versus wet weight relationship in *Periphylla periphylla* (• b = 1.941, r = 0.926, N = 7, $P < 0.01$; □ b = 3.057, r = 0.935, N = 26, $P < 0.001$).

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Table 2. Summary of the biochemical composition of whole *Periphylla periphylla* medusae (BD (mm) of medusae analysed: mean 34.10 ± 13.59 mm).

Parameter	N	Range	Mean (±SD)
Total proteins			
mg gWW	21	0.85–6.74	3.45 (1.52)
mg gDW	21	34.14–108.21	63.71 (17.18)
Total lipids			
mg gWW	21	0.23–2.74	1.14 (0.65)
mg gDW	21	11.53–48.12	20.57 (8.42)
Total carbohydrates			
mg gWW	21	0.14–1.03	0.49 (0.23)
mg gDW	21	5.06–14.45	8.99 (2.34)

a percentage of wet mass were 0.83% protein, 0.21% lipid and 0.08% carbohydrate (Clarke *et al.*, 1992). Overall, these findings are similar to those reported for a variety of coastal and shallow water species (see review tables in Arai *et al.*, 1989; Lucas, 1994) and the very few published values for mesopelagic and deep sea species.

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Correspondence should be addressed to:
C.H. Lucas
School of Ocean & Earth Science
University of Southampton
National Oceanography Centre, European Way
Southampton, SO14 3ZH
email: chl1@noc.soton.ac.uk

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