Chemical composition and oxygen consumption rates of the ctenophore *Bolinopsis infundibulum* from the Gulf of Maine

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Abstract. Quantitative determinations of chemical composition and oxygen consumption rates were made for a deep-living population of the lobate ctenophore *Bolinopsis infundibulum*. Animals were collected in the Gulf of Maine with the submersible 'Johnson-Sea-Link' during September 1989 at depths ranging from 120 to 240 m. Carbon and nitrogen contents were similar to values reported for epipelagic ctenophores. Lipid and protein levels were lower than values typical of epipelagic ctenophores, but higher than those of mesopelagic species. Carbohydrate was nearly an order of magnitude higher than previously recorded for *B.infundibulum*. Oxygen consumption rates ranged from 0.004 to 0.235 $\mu l\ O_2\ mg^{-1}$ dry weight h^{-1} at temperatures ranging from 5 to 7°C. Carbon-specific metabolic rates ranged from 0.21 to 12.73 $\mu l\ O_2\ mg^{-1}\ C\ h^{-1}$. Energy expenditures estimated from respiration data (~3% body C day^{-1}) indicated that up to 350 small copepods (e.g. *Pseudocalanus* sp.) or 23 larger copepods (e.g. *Calanus finmarchicus*) would be necessary to provide the daily maintenance ration required by a 92 mm *B.infundibulum*. These metabolic characteristics suggest that *B.infundibulum* could have a significant impact on prey populations in the Gulf of Maine.

Introduction

Midwater environments of the ocean have become a focus for research over the past decade, principally because water column processes at midwater depths may significantly influence the cycling of biogenic materials between the surface ocean and the deep sea. A particularly important biological finding has been the discovery that many gelatinous zooplankton are widespread and often abundant at mesopelagic depths (Wiebe *et al.*, 1979; Alldredge, 1984; Youngbluth *et al.*, 1990). The broad spectrum of living and detrital particles consumed by these animals qualify salps, appendicularians, ctenophores, siphonophores and medusae as undoubtedly important regulators of biogeochemical flux (Alldredge, 1984). The ubiquitous distribution of gelatinous zooplankton and their periodic numerical dominance in oceanic communities suggest that their metabolic activities, at times, represent a significant fraction of the total macrozooplankton energy budget. Furthermore, many gelatinous species (e.g. ctenophores, siphonophores and medusae) are predators of smaller zooplankton and larval fishes and, when abundant, can have major impacts on prey populations (Fraser, 1962; Larson, 1987; Mackie *et al.*, 1987). Indeed, in the Gulf of Maine, ctenophores, along with other gelatinous species (e.g. medusae and siphonophores), are among the major predators of small planktonic crustaceans, fish eggs and larval fishes (Rogers *et al.*, 1978; Davis, 1984).

Bolinopsis infundibulum is a boreal–Arctic lobate ctenophore which inhabits coastal waters from New England to Labrador in the northwestern Atlantic, across the Arctic Seas, and along Scotland and Norway in the eastern Atlantic and into the Baltic (Bigelow, 1926; Zelickman, 1972; Lenz, 1973). Although

often reported as a surface dweller, *B.infundibulum* is generally found in deeper water (Morris *et al.*, 1983). In the Gulf of Maine, this species is most numerous in the uppermost 100 m from July until September (Bigelow, 1926). Seasonality in the abundance of deeper-living populations is unknown (Gamble, 1977; Morris *et al.*, 1983). Investigations of *B.infundibulum* collected from surface waters indicate that this species is a voracious, opportunistic predator of small copepods (e.g. *Acartia*, *Temora*, *Pseudocalanus*, *Centropages* and *Calanus* copepodite stages IV and V) and cladocerans (*Podon* and *Evadne*) (Nagabhushanam, 1959; Kamshilov, 1960; Anderson, 1974; Gamble, 1974, 1977).

Because *B.infundibulum* is an extremely delicate planktonic animal (Bigelow, 1926; Greve, 1970; Lenz, 1973; Gamble, 1974, 1977; Reeve and Walter, 1978; Morris *et al.*, 1983), information regarding its biology is scarce. What little biological data that are available for *B.infundibulum* have been derived from studies of epipelagic specimens. Most of these investigations have focused on feeding, techniques for laboratory maintenance, chemical composition and fecundity (Nagabhushanam, 1959; Kamshilov, 1960; Greve, 1970; Gamble, 1974, 1977; Reeve and Walter, 1978; Hoeger, 1983; Morris *et al.*, 1983; Schulze-Röbbecke, 1984; Andrew *et al.*, 1987). No quantitative data have been published on the ecology or physiology of deeper-living populations. The only data on metabolic rates for *B.infundibulum* were taken from eight small specimens collected with a net at the surface off Helgoland, FRG (Gyllenburg and Greve, 1979).

This paper presents the first quantitative assessments of the chemical composition and rates of oxygen consumption for *B.infundibulum* from deep-living populations. Minimum daily rations derived from these data provided estimates of the predatory role of this species.

Method

Individual *B.infundibulum* were collected in the Gulf of Maine (Wilkinson Basin; 42°20'N, 69°47'W) from the 'Johnson-Sea-Link' submersible during September 1989, at depths ranging from 120 to 240 m (Table I). Temperature, salinity and oxygen recorded at the sampling depths varied from 5.0 to 6.3°C, 32.6 to 33.0‰ and 10.7 to 11.9 mg O_2 l^{-1}, respectively (Table I; Figure 1). Metabolic rates were measured in a shipboard environmental room at *in situ* temperatures (6.0 ± 1.0°C).

An array of four specially designed 6.5-l respirometers attached to the submersible were used to gently trap the ctenophores (Youngbluth, 1984). The 1.25-cm-thick acrylic samplers provided sufficient insulation to maintain *in situ* temperatures within the samplers during ascent to the surface and during the 10–15 min period required after recovery to transfer them to the environmental room aboard ship.

On each of four dives, two or three ctenophores were collected. The remaining respirometers were used as controls; water was collected from the same depth as that of the experimental animals. Once the animals and controls had been collected, the submersible made a slow ascent to the surface. Aboard

Table 1. Collection and environmental data. Temperature and salinity are the values recorded at the collection depths. *n* is the number of *B.infundibulum* collected in respirometers

Date	Dive time	Bottom depth (m)	Collection depth (m)	Temperature (°C)	Salinity (‰)	*n*
September 13	06:44–08:18	282	235–238	6.3	33.0	2
September 14	06:17–07:41	232	187–189	6.1	32.8	2
September 17	10:09–12:08	255	133–145	5.1	32.7	3
September 18	06:58–08:15	258	124–130	5.0	32.6	3

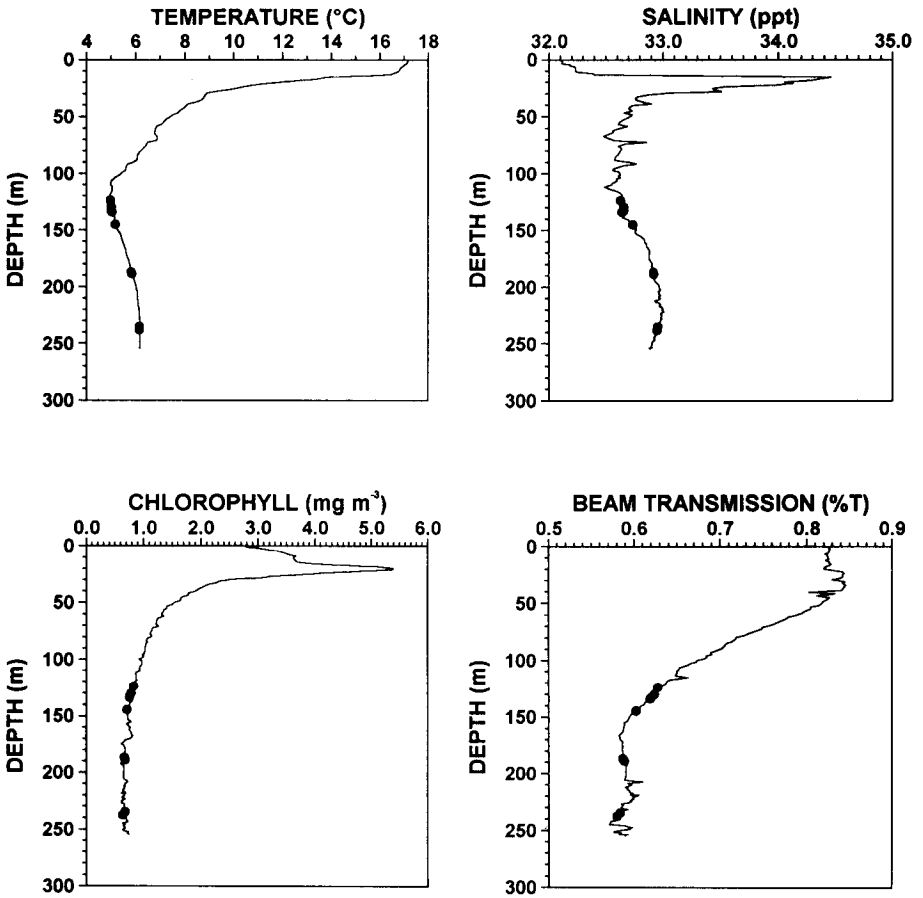

Fig. 1. Temperature, salinity, chlorophyll fluorescence and transmissometer data as a function of depth on September 9, 1989. Closed circles represent depths at which the *B.infundibulum* used in respiration trials were collected during the cruise.

ship, the respirometers were quickly detached from the submersible and transferred to the incubation chamber. Sampling was conducted at night in order to minimize any possible effects of light shock. Incubations were likewise conducted in the dark.

Endeco pulsed oxygen probes were used to monitor pO_2 within each respirometer. The pulse interval for the probes was 15 min. These sensors were profoundly affected by rapid changes in temperature and pressure during a dive. Once constant temperature and pressure were re-established in the shipboard environmental room, the probes stabilized after 3–5 h. Data used to determine rates of oxygen consumption were taken after an 8–11 h acclimatization period in order to allow recovery of both probes (3–5 h) and animals (5–6 h) after ascent to the surface (see Results). Data from the sensors were recorded with an Onset Tattletale datalogger. The datalogger and batteries to power the probes

were contained in a pressure can mounted on the submersible during the dive. The probes and datalogger were activated prior to launching the submersible, and ran continuously until the experiment was terminated ~20 h later.

The respirometers were cleaned with 1 N HCl and then filled with seawater before each dive. As soon as the submersible was launched and the respirometers were submerged, the lids were opened in order to flush the samplers. As the submersible began its descent, the lids were closed to prevent intrusion of material during transit to the operating depth. Prior to collecting ctenophores and controls, the samplers were flushed with seawater from the operating depth.

After each experiment, ctenophores were measured (total length) before removing them from the respirometers. The specimens were then placed in tared jars and frozen at −10°C for subsequent weight and proximate chemistry determinations. In the shore-based laboratory, jars containing the ctenophores were weighed to the nearest 0.01 g and then dried at 60°C to constant weight. Subsequently, dried individuals were homogenized for analyses of elemental and proximate chemistry using established methods (Youngbluth *et al.*, 1988; Reisenbichler and Bailey, 1992).

Additional specimens of *B.infundibulum* were collected with unmodified samplers (i.e. samplers without oxygen electrodes). These animals were used for determinations of morphometric correlations and proximate chemical composition.

Results

The water column at the study site was characterized by a shallow (~10 m) layer of Maine Surface Water (MSW) at the surface. Below the MSW was a broad (~40 m) layer of relatively high-salinity water, presumably Slope Water (SLW). Beneath the SLW was a region of relatively low temperature and salinity, characteristic of Maine Intermediate Water (MIW; Hopkins and Garfield, 1979). This MIW extended from ~50 m to the bottom (~270 m). A region of relatively warmer and more saline and turbid water, present in the deepest part of MIW (~210 m to the bottom), is herein defined as the benthic boundary layer (BBL). A pronounced thermocline and chlorophyll maximum layer were present in the upper 40 m (Figure 1).

Distribution

In the upper 100 m, the numerically dominant ctenophore was *Pleurobrachia pileus*. *Bolinopsis infundibulum* were rare in this portion of the water column. Although encountered throughout the MIW, most individuals of *B.infundibulum* appeared in a relatively narrow layer, ~30 m in vertical extent (120–150 m), which coincided with the region of lowest temperatures and salinities of the MIW (Figure 1). Within the depth interval of maximum abundance, *B.infundibulum* were widely scattered. Occasions when more than one individual were present in the field of view from the submersible were uncommon; therefore, estimates of abundance based on nearest-neighbor distances were not possible. Within the relatively warmer and more saline BBL,

Table II. Means, ranges and regression coefficients for morphometric measurements of *B.infundibulum*. A linear regression of log–log transformed data ($Y = aX^b$) was used to derive the slope (b) and intercept (a) for the relationship between dry weight (DW) and total length (TL = apical to oral length). Relationships between DW and wet weight (WW), ash-free dry weight ($AFDW$) and carbon content (CC) were derived from linear regressions of untransformed data ($Y = a + bX$, where b = slope and a = intercept). The coefficient of determination (r^2) is given for each regression. n is the number of individuals analyzed. Numbers in parentheses are standard error (±SE). $Y = DW$ for all regressions

Morphometric parameter	n	Mean (±SE)	Range	Regression coefficients		
				a (intercept)	b (slope)	r^2
DW	44	1921 (±291)	120–8790	–	–	–
TL	44	81 (±6)	25–216	0.161	2.096	0.943
WW	44	50 740 (±7490)	3040–227 820	−61.151	0.039	0.988
$AFDW$	13	370 (±93)	36–1155	67.554	4.963	0.992
CC	21	62 (±15)	2–259	422.677	31.977	0.926

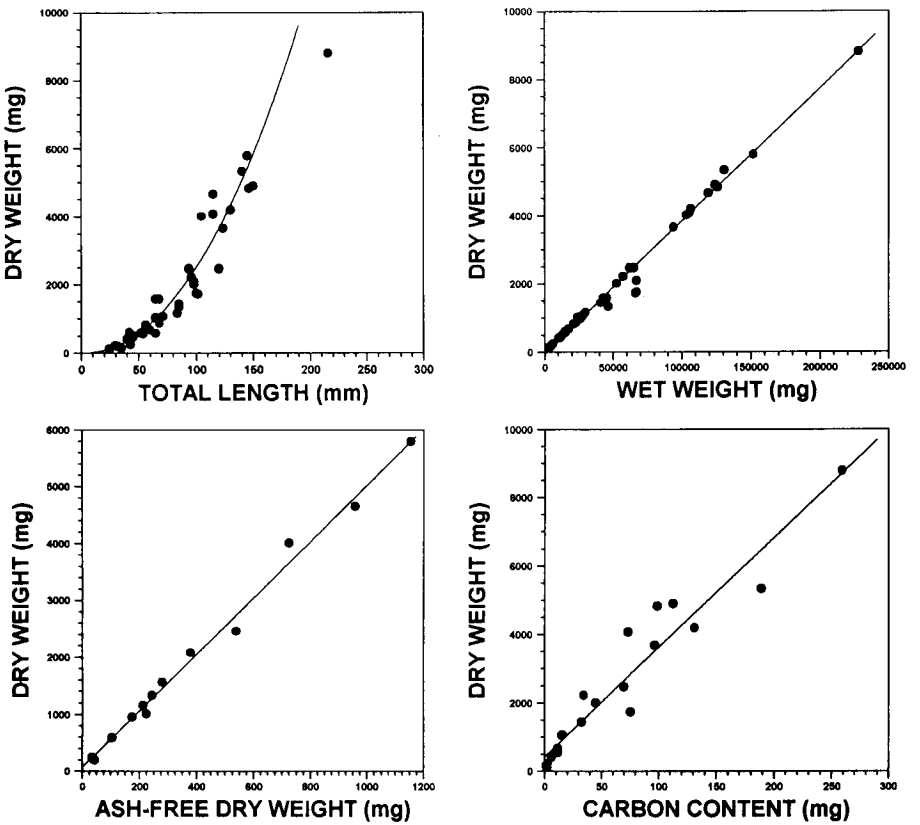

Fig. 2. Morphometric regressions. A linear regression of log–log transformed data ($Y = aX^b$) was used for the relationship between dry weight and total length. Linear regressions of untransformed data ($Y = aX + b$) were used to determine the relationships between dry weight and wet weight, ash-free dry weight and carbon content (see Table II for values of slopes, intercepts and correlation coefficients).

populations of *B.infundibulum* were, for the most part, replaced by a midwater cydippid ctenophore, *Euplokamis* sp. (Widder *et al.*, 1992). Visibility ranged from 3–5 m above the BBL to 1–2 m within the BBL.

Morphometrics

In this paper, all expressions of physiological parameters are based on weight. Lengths of individuals were measured for comparison with literature values. However, because the bodies of lobate ctenophores are elastic, length is not always a reliable standardization parameter (Youngbluth *et al.*, 1988). However, elasticity did not appear to be a problem with *B.infundibulum*, as indicated by the relatively high degree of correlation between total length and dry weight (Table II; Figure 2). There were strong positive relationships between the wet weight, dry weight and carbon content of *B.infundibulum*.

Elemental and proximate composition

The mean carbon and nitrogen contents of *B.infundibulum*, expressed as percent dry weight (%DW), were within the range of values reported for epipelagic ctenophores and substantially higher than values reported for the midwater ctenophore *Bathocyroe fosteri* (Table III). The carbon and nitrogen contents of ctenophores in this study were similar to those of *Bolinopsis infundibulum* collected from epipelagic depths (Hoeger, 1983; Table III). Levels of protein in *B.infundibulum* were lower than those of epipelagic species, but nearly twice those reported for *Bathocyroe fosteri* (Youngbluth *et al.*, 1988). Lipid values were about half those observed for *B.fosteri*, and substantially lower than those of the epipelagic ctenophores *P.pileus* and *Beroe gracilis* (Hoeger, 1983). Carbohydrate was nearly an order of magnitude higher than previously recorded for epipelagic specimens of *Bolinopsis infundibulum*.

There was a significant positive correlation between DW and weight-specific carbon content ($P < 0.05$; Table IV), but not with nitrogen content ($P > 0.05$). Likewise, there were significant positive correlations between body size (DW) and weight-specific levels of lipid and carbohydrate ($r \geq 0.7$ in both cases), but not with protein ($r < 0.2$). When standardized to carbon content (g protein g^{-1} C), protein was significantly correlated with DW, whereas lipid and carbohydrate were not (Table IV).

Oxygen consumption rates

Weight-specific oxygen consumption by ctenophores was positively correlated ($P < 0.05$; Pearson product–moment correlation) with the incubation time. These results support our visual observations that experimental animals remained healthy (i.e. ctenes beating normally, animals suspended in the water column of the chamber) throughout the respiration trials. However, the rate of oxygen consumption was not constant over the duration of incubation. After probe stabilization (~3–5 h), oxygen consumption rates declined rapidly during the next 5–6 h and continued to decline thereafter at a relatively low, but

Table III. Chemical composition (%DW) of the ctenophore *B.infundibulum* and 12 other mesopelagic and epipelagic ctenophore species. Chemical parameters include carbon (C), nitrogen (N), protein, lipid and carbohydrate. *n* is the number of individuals measured. n.d. indicates no data available

Species	C	N	C:N	Protein	Lipid	Carbohydrate	*n*	Source
Bolinopsis infundibulum	2.18	0.45	4.8	1.1	0.2	1.0	21	Present study
Bolinopsis infundibulum	1.9	0.52	3.7	n.d.	n.d.	n.d.	48	Hoeger (1983)
Bolinopsis infundibulum	nd	n.d	n.d.	1.57	0.58	0.11	2	Kremer[a]
Mesopelagic								
Bathocyroe fosteri	0.82	0.20	4.1	0.57	0.38	0.24	35	Youngbluth *et al.* (1988)
Epipelagic								
Bolinopsis vitrea	0.60	0.13	4.6	n.d.	n.d.	n.d.	73	Kremer *et al.* (1986)
Ocyropsis spp.	1.18	0.30	3.9	n.d.	n.d.	n.d.	20	Kremer *et al.* (1986)
Eurhamphaea vexilligera	0.88	0.24	3.7	n.d.	n.d.	n.d.	44	Kremer *et al.* (1986)
Mnemiopsis mccradyi	1.90	0.51	3.8	n.d.	n.d.	n.d.	18	Reeve and Baker (1975)
Mnemiopsis leidyi	1.70	0.50	3.4	n.d.	n.d.	n.d.	40	Kremer (1975)
Pleurobrachia brachei	3.28	0.87	3.8	n.d.	n.d.	n.d.	10	Reeve *et al.* (1978)
Pleurobrachia brachei	4.99	1.21	4.1	n.d.	n.d.	n.d.	62	Kremer[a]
Pleurobrachia pileus	3.68	0.74	4.9	n.d.	n.d.	n.d.	26	Schneider (1982)
Pleurobrachia pileus	n.d.	n.d.	n.d.	3.06	1.70	0.44	35	Hoeger (1983)
Beroe ovata	3.72	0.99	3.9	n.d.	n.d.	n.d.	19	Kremer *et al.* (1986)
Beroe cucumis	10.16	2.61	3.9	n.d.	n.d.	n.d.	9	Kremer[a]
Beroe gracilis	n.d.	n.d.	n.d.	4.86	4.24	0.88	14	Hoeger (1983)

[a] P.Kremer (unpublished data from Friday Harbor, Washington).

Table IV. Correlations between size (dry weight; DW) and weight- and carbon-specific levels of body carbon (C), nitrogen (N), protein, lipid and carbohydrate (CHO) for *B.infundibulum*. Significance was determined at the 95% confidence level ($P = 0.05$)

C % DW	N % DW	Protein ($g\ g^{-1}$ DW)	Lipid ($g\ g^{-1}$ DW)	CHO ($g\ g^{-1}$ DW)	Protein ($g\ g^{-1}$ C)	Lipid ($g\ g^{-1}$ C)	CHO ($g\ g^{-1}$ C)
0.66[a]	0.29	−0.20	0.66[a]	0.69[a]	−0.80[a]	0.01	0.46

[a] Significant ($P < 0.05$).

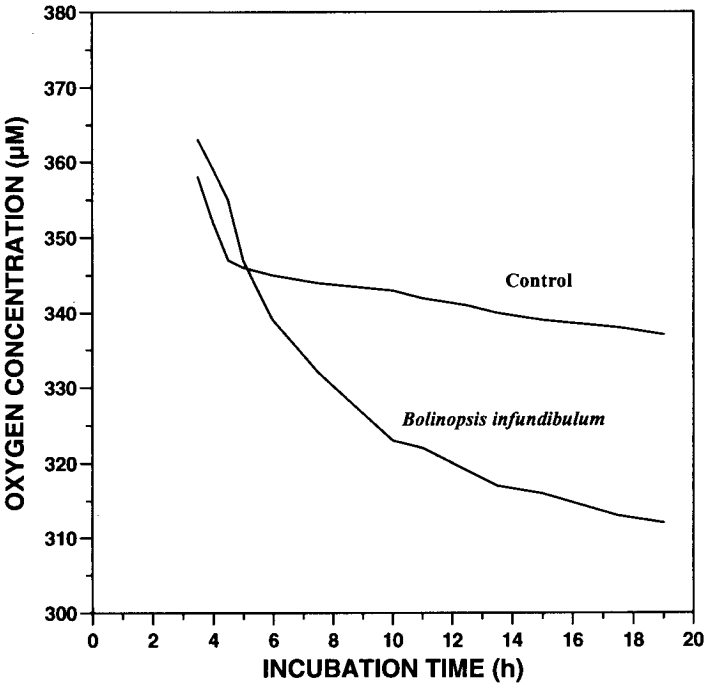

Fig. 3. Typical respiration runs for *B.infundibulum* and a control respirometer. The oxygen concentration within each of the two respirometers is plotted as a function of time, beginning at the point when the respirometers were transferred to the incubation chamber aboard ship.

constant rate until the experiment was terminated (Figure 3). The initial period of rapidly declining consumption rate was assumed to represent a 'disturbed' response to conditions after capture, e.g. ascent from capture depth, recovery of the submersible and/or feeding effects, whereas the subsequent period may represent a response to decompression and/or container effects (see Discussion). Oxygen consumption data reported in this paper were taken after the initial 5–6 h period of rapid decline in consumption rate. Decreases in the oxygen content of water in control chambers during incubation were significant ($P < 0.05$; paired t-test). Because no effort was made to filter the water used in the respirometers, consumption of oxygen in controls was presumed to be due to microzooplankton (e.g. ciliates) and microorganisms (e.g. bacteria). It was further assumed that similar levels of consumption by these organisms were included in experimental respirometers. Differences in the rates of decrease of oxygen content between controls and experimental respirometers were significant in every case ($P < 0.01$; t-test).

There was a high degree of variability among individuals in the rate of oxygen consumption as a function of size (Figure 4). Because of this variability, statistical tests for outliers failed to eliminate any of the data points. Consequently, results of regressions of oxygen consumption as a function of body weight were ambiguous. The linear regression of log–log transformed data

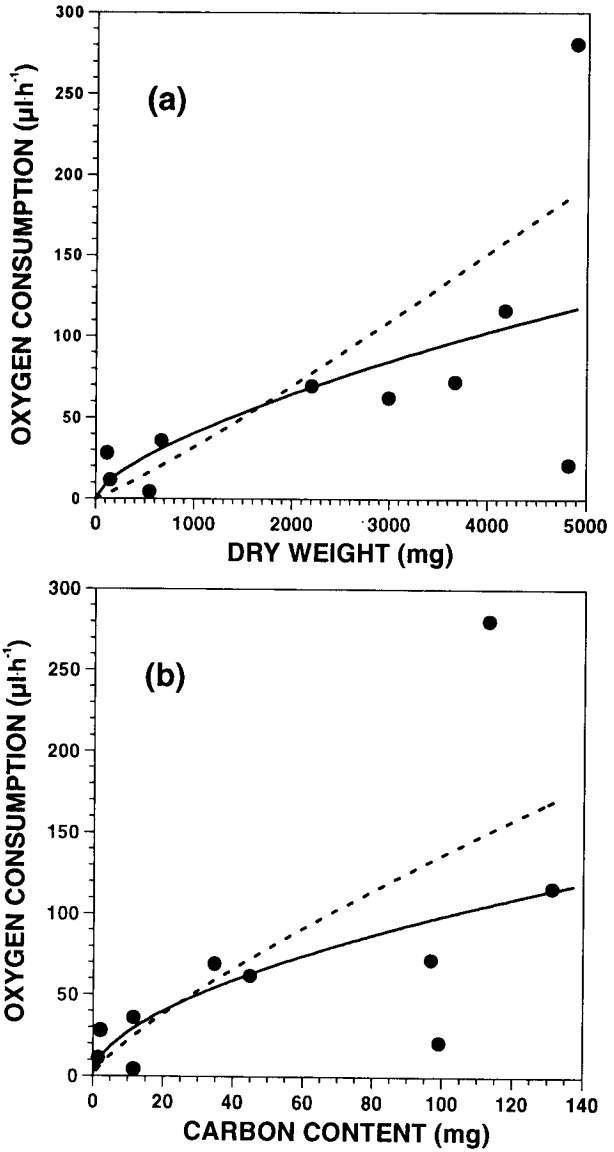

Fig. 4. Oxygen consumption plotted against dry weight (**a**) and carbon content (**b**). Data points are represented by closed circles. Two types of regression, geometric and non-linear, are represented by solid and dashed lines, respectively.

(geometric regression) for oxygen consumption as a function of DW resulted in an exponent of 0.67 for the allometric equation $Y = aX^b$, where Y = oxygen consumption rate, X = weight, a = intercept and b = slope. The non-linear regression (Bevington, 1969) of oxygen consumption versus DW gave a substantially higher value for the exponent of the allometric equation (b = 1.12) than that of the simple geometric regression.

The results of the geometric regression suggested that specific metabolic rates of *B.infundibulum* were weight dependent. In contrast, the results of the non-linear regression indicated that metabolism was weight independent. Leverage coefficients for these data were generally low. The two relatively high coefficients did not exceed the criteria for exclusion from the data set (Sokal and Rohlf, 1981). Furthermore, the two 'high' values had correspondingly low standardized residuals (Sokal and Rohlf, 1981). These results indicated that our metabolic measurements were consistent with the least-square regression model.

Both geometric and non-linear regressions of oxygen consumption, as a function of carbon content, indicated a weight-dependent relationship between respiration and total body carbon content (b = 0.61 and 0.79, respectively; Figure 4). Mean weight-specific respiration rates were 0.054 μl O_2 mg^{-1} DW h^{-1} (range = 0.004–0.235 μl O_2 mg^{-1} DW h^{-1}) and 3.05 μl O_2 mg^{-1} C h^{-1} (range = 0.21–12.73 μl O_2 mg^{-1} C h^{-1}).

Metabolic demand

Metabolic demand for *B.infundibulum*, expressed as carbon-specific respiration (% body C day^{-1}, assuming an RQ of 0.8) averaged 3.1 ± 1.3 SE. This value was lower than the range of values (5–11%) reported for epipelagic and mesopelagic ctenophores (Kremer *et al.*, 1986; Youngbluth *et al.*, 1988) and ~25% of the value reported for an epipelagic population of *B.infundibulum* (Hoeger, 1983). Data on the size or weight of animals were not given by Hoeger (1983). Our value was, however, similar to that reported for one of two treatments of the mesopelagic ctenophore *Bathocyroe fosteri* (2.8 %C day^{-1}; Youngbluth *et al.*, 1988).

Discussion

Distribution and abundance

Values for chemical composition and oxygen consumption rate may reflect seasonal variability in these parameters. After a peak in abundance during July–September, *Bolinopsis infundibulum* virtually disappears from the surface waters of the Gulf of Maine and adjacent waters of Georges Bank (Bigelow, 1926). Similarly, populations of *B.infundibulum* off Scotland also decline precipitously throughout the water column in the fall, leaving a relatively small number of individuals to overwinter and subsequently repopulate the area in the following spring and summer (Gamble, 1977). The cause of this annual population crash has been speculatively attributed to 'population senescence' (defined as a reduction in fecundity and feeding efficiency, an increase in parasitism and a large proportion of deformed, eroding individuals; Gamble, 1977). The absence of *B.infundibulum* in surface waters and the relatively low abundance at midwater depths in the Gulf of Maine may also be due to 'senescence'. However, a more likely explanation is that late-season conditions of lower surface temperatures, along with low levels of productivity and reduced prey abundance, result in a decline in abundance of *B.infundibulum*. Levels of

primary productivity and potential prey abundance for *B.infundibulum* were not measured in our study. However, copepod populations in the Gulf of Maine and Georges Bank typically decline to relatively low levels during the fall and winter (Davis, 1984). In a situation of low levels of available food, metabolic rates of *B.infundibulum* may be correspondingly low. Metabolic rates of epipelagic ctenophores have been shown to be directly related to food availability (Kremer, 1982). Likewise, chemical composition, as measured by the C:N ratio, is directly related to food availability in epipelagic ctenophores (Kremer, 1982).

Chemical composition

Data reported for epipelagic lobate ctenophores generally indicate weight-independent metabolism with a corresponding lack of correlations between body size and weight-specific chemical content (Kremer *et al.*, 1986). The correlations between body size and weight-specific chemical content of *B.infundibulum* support our assessment of the dependence of metabolic rates on body size. Weight-dependent metabolic rates have been reported for other ctenophore species: *Bolinopsis vitrea* and *Beroe ovata* (Kremer *et al.*, 1986), and *Eurhamphaea vexilligera* (Biggs, 1977).

Metabolic rates

In most investigations of ctenophore metabolism, the method of linear least squares has been used to regress log–log transformed data. Values of $b = 0.6$ for the allometric exponent support strong weight dependence and values of 1.0 have been interpreted to indicate weight independence (Schmidt-Nielsen, 1979; Larson, 1987). There is evidence that the use of a non-linear regression for oxygen consumption data may avoid errors associated with mathematical transformations (Zar, 1968; Glass, 1969; Silvert, 1979; Zimmerman *et al.*, 1987). An exponent of 1.1 derived from our non-linear regression, in contrast to a b value of 0.7 with linear regression of transformed data, reflects uncertainty in the results. However, analyses based on body carbon support weight-dependent rates, regardless of the method used.

The absence of a consistent physiological pattern in weight-independent or weight-dependent respiration among most ctenophore species is probably related as much to methodological treatments as to the relatively small number of individuals examined in most studies (Table III). Physiological stress incurred by transferring ctenophores from sampling devices to respirometers can be sufficient to compromise physiological measurements (Youngbluth *et al.*, 1988; Bailey *et al.*, in press). *Bolinopsis infundibulum* is a fragile animal and consequently easily damaged during capture and subsequent manipulations aboard ship (Greve, 1970; Gamble, 1974, 1977; Reeve and Walter, 1978). Our procedures precluded handling and transfer of captured individuals. The ctenophores we obtained remained active during the course of our experiments. Consequently, we believe that the variability we observed can be related to factors other than mechanical stress.

Subsequent to re-establishing electrode stability after each dive, rates of

oxygen consumption in experimental respirometers decreased rapidly over a period of 5–6 h before establishing a relatively low, but constant decline. Oxygen consumption rates during this initial 5–6 h period averaged 12 times higher than those recorded afterward. In contrast, rates of decrease of oxygen in control respirometers were constant after probe stabilization. An initial period of elevated oxygen consumption is common with this type of respirometry, particularly with more active animals which require a period of acclimatization to conditions after containment and ascent to the surface (Childress, 1977). Although *B.infundibulum* is not a fast-swimming animal, such as a fish or crustacean, our data suggest that this species requires a period of time to acclimatize to experimental conditions. Serial-incubation experiments with salps have shown that oxygen consumption rates decreased by 50%, 4–5 h after initial capture (Cetta *et al.*, 1986). With *B.infundibulum*, containment for periods exceeding ~24–30 h usually resulted in a substantial reduction in activity level and consequent settling to the bottom of the chamber. We have observed similar reductions in the activity levels of many species of deep-living gelatinous zooplankton (Bailey *et al.*, 1994). Whether these reductions in activity are the result of physiological responses to decompression (Bailey *et al.*, 1994) or simply to container effects are currently unresolved.

Feeding within the respirometers must also be considered as a factor affecting our observed metabolic rates. For example, respiration of fresh (3 h after collection) and unfed (11 h after collection) lobate ctenophores (*Mnemiopsis mccradyi*) differed by 20% (Kremer, 1982). It is possible that during the first part of each run, animals were not only acclimatizing, but were also feeding on zooplankton within the respirometers, although small zooplankton (e.g. copepods) were rarely collected in the respirometers. *Bolinopsis infundibulum* has a relatively rapid (~1–2 h) digestion rate for copepods (Nagabhushanam, 1959; Kamshilov, 1960; E. Widder, personal communication); therefore, we believe our rates were characteristic of unfed ctenophores.

The mean value for weight-specific respiration of *B.infundibulum* was generally lower than those of epipelagic ctenophores, but similar to that of the midwater species *Bathocyroe fosteri* (Youngbluth *et al.*, 1988; Table V). These data support our observations that *Bolinopsis infundibulum* is behaviorally similar to *Bathocyroe fosteri* in being a relatively passive predator that relies primarily on random encounters with prey. This passive behavior contrasts with the more active feeding strategies used by epipelagic species such as *Pleurobrachia* spp. or *Mnemiopsis* spp. (Kamshilov, 1960; Gamble, 1977; Harbison *et al.*, 1978).

Prey requirements

Calculations based on an average metabolic demand (3% body C day^{-1}) indicated that a medium-sized (92 mm) *Bolinopsis infundibulum* (2.3 g DW) would require an input of ~2 mg C day^{-1} as a maintenance ration. Daily carbon rations for several species of epipelagic and mesopelagic ctenophores ranged from 0.15 to 1.50 mg C day^{-1} (values are standardized to a length of 40 mm;

Table V. Oxygen consumption rates of *B.infundibulum* and 10 other mesopelagic and epipelagic ctenophore species. Data are means of measured values. Numbers in parentheses are standard errors and numbers of individuals analyzed (±SE, *n*). n.d. indicates no data available

Species	ml O_2 mg^{-1} DW h^{-1}	ml O_2 mg^{-1} protein h^{-1}	Temperature (°C)	Source
Bolinopsis infundibulum	0.054 (±0.021, 10)	0.002 (±0.01, 10)	5–6	Present study
Bolinopsis infundibulum	0.033[a] (8)	n.d.	8	Gyllenberg and Greve (1979)
Mesopelagic				
Bathocyroe fosteri	0.042 (±0.021, 49)	0.049 (±0.01, 35)	9–12	Youngbluth *et al.* (1988)
Ocyropsis sp.	0.126 (±0.028, 6)	n.d.	9–12	Youngbluth *et al.* (1988)
Epipelagic				
Bolinopsis vitrea	0.070 (± 0.01, 55)	n.d.	25	Kremer *et al.* (1986)
Ocyropsis spp.	0.126 (16)	n.d.	25	Kremer *et al.* (1986)
Ocyropsis maculata	0.12 (3)	n.d.	25	Kremer *et al.* (1986)
Eurhamphaea vexilligera	0.063 (±0.01, 47)	n.d.	25–29	Biggs (unpublished data)
Mnemiopsis mccradyi	0.098 (±0.01, 22)	n.d.	21	Kremer (1982)
Mnemiopsis leidyi	0.070 (±0.01, 19)	n.d.	10	Kremer (1977)
Mnemiopsis leidyi	0.231 (±0.01, 21)	n.d.	25	Kremer (1977)
Cestum sp.	n.d.	0.21 (3)	29	Biggs (unpublished data)
Beroe ovata	0.273 (±0.02, 22)	n.d.	25	Kremer *et al.* (1986)

[a] Extrapolated value; conversion of WW to DW using our regression equation (Table II).

Kremer *et al.*, 1986; Youngbluth *et al.*, 1988). When standardized to a length of 40 mm, *B.infundibulum* (430 mg DW; 7 mg C) would require 0.2 mg C day^{-1}. Thus, although the absolute carbon requirement for the individuals reported in this study is substantially higher, the standardized value falls within the range of values reported for other ctenophores, albeit at the low end of the range. Assuming a conservative assimilation efficiency of 70% (Reeve *et al.*, 1978) at steady state (i.e. no growth or reproduction), the daily maintenance ration for a 92 mm *B.infundibulum* could be supplied by 350 small copepods (e.g. ~0.008 mg C $individual^{-1}$ for *Pseudocalanus* sp.), or 23 larger copepods (e.g. ~0.124 mg C $individual^{-1}$ for *Calanus finmarchicus*; Davis, 1984) or 140 fish larvae (e.g. 0.02 mg C $individual^{-1}$ for the cod, *Gadus morhua*; Jorgensen, 1985). *Bolinopsis infundibulum* collected in 1989 and 1992 from the Gulf of Maine were observed to have calanoid copepods in their guts (1989 = present study; 1992 = E.Widder, personal communication). *Bolinopsis infundibulum* has been described as an important predator of zooplankton, including copepods, copepod nauplii, cirripede nauplii and fish larvae (Nagabhushanam, 1959; Kamshilov, 1960; Fraser, 1970; Gamble, 1974; Morris *et al.*, 1983). Given the low abundance of *B.infundibulum* found at the time of our study, they probably had little effect on their prey populations. However, midsummer densities of *B.infundibulum* from areas other than the Gulf of Maine have been reported as high as 400 m^{-3} (Kamshilov, 1960). Clearly, such densities of ctenophores could have a very significant impact on prey populations.

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