Annual variation in the nutritional value of Stage V *Calanus finmarchicus*: implications for right whales and other copepod predators

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ABSTRACT: Stage V (C5) *Calanus finmarchicus* is a central prey item for animals feeding at several trophic levels in the Bay of Fundy, Canada, especially the highly endangered North Atlantic right whale *Eubalaena glacialis*. Here, we show that the energy and lipid content of C5 *C. finmarchicus* collected twice monthly (July to September) from the Grand Manan Basin exhibited significant variation over multiple years (2006 to 2010). Mean ± SD wet mass energy (6.77 ± 0.65 kJ g^{-1}) was highest in 2007 and lowest in 2009 (5.82 ± 0.90 kJ g^{-1}); lipid content followed the same pattern. Significant decreases in individual energy content were observed over the summer during 2006 and 2010. Lipid content was significantly correlated with energy content. Overall, energy content of copepods was 13% lower in 2009 than in 2006–2007, which could alter foraging patterns and activity budgets of predators such as the North Atlantic right whale and have implications for assessment of whale habitat based on models of energy requirements. Variation in C5 quality may be linked to annual changes in the lipid content of Bay of Fundy herring, which consume copepods and are in turn a main prey item of seabirds, fishes, and marine mammals. Our study emphasizes that variation in quality, not just quantity, of prey should be considered when formulating predator consumption models and in tracking trophic transfer.

KEY WORDS: *Eubalaena glacialis* · Zooplankton · Energy content · Lipid · Prey quality · Food web · Bay of Fundy

INTRODUCTION

Understanding the foraging requirements of marine predators is important to our understanding of their ecology and physiology, and for conservation issues. For zooplanktivorous megafauna, the nutritional value of prey is determined by both abundance (quantity) and energy richness (quality). In the case of the Endangered North Atlantic (NA) right whale *Eubalanea glacialis* (Reilly et al. 2012), reduced quantity and quality of their main prey, calanoid copepods, has been implicated in hampering reproductive rates that impede the recovery of this

cetacean (Kenney et al. 1986, Baumgartner & Mate 2003, Greene & Pershing 2004). While technological advances such as modeling software, innovative statistical packages, and optical plankton counters (OPC) have allowed fairly accurate quantification of right whale prey fields, determining the variation in the energetic quality of prey has often been ignored. To date, energetic variation in right whale prey has been recorded over the course of only one summer in the Bay of Fundy (2002; described by Michaud & Taggart 2007, 2011); these authors reported significant changes in energy content on both spatial and temporal scales. These findings and others (see

below) suggest that significant variation in prey quality may also occur on annual scales, which could, in part, account for the documented variability in the number of right whale calves born each year. Such information points to the need to quantify the energy content of copepods over greater time scales.

The NA right whale faces imminent extinction due to low reproductive rates and anthropogenic threats (Clapham et al. 1999, Fujiwara & Caswell 2001, Kraus et al. 2007, Moore et al. 2007). One-third of the population summers in the lower Bay of Fundy, where high densities of *Calanus finmarchicus* are predictably present (Murison & Gaskin 1989, Baumgartner & Mate 2003). NA right whales feed primarily on diapausing Stage V *C. finmarchicus* copepodids (C5), a life stage that has both a high lipid content and energy value (Baumgartner & Mate 2003, Michaud & Taggart 2007, Swaim et al. 2009, Davies et al. 2012). High concentrations of C5s are found at depth (below 100 m), and how right whales forage on these deep layers has been well documented (Murison & Gaskin 1989, Baumgartner & Mate 2003, Baumgartner et al. 2003a,b).

Existing prey consumption models for NA right whales (e.g. Kenney et al. 1986, Baumgartner & Mate 2003) are based on parameters that measure how many copepods per unit time a whale can eat, the assimilation efficiency and metabolic rate of the whale, and a constant (and arbitrary) energy value of those copepods. To date, a single value to represent the energy content of their copepod prey (Comita et al. 1966) has been applied, even though previous studies have demonstrated significant temporal and spatial variation in quality of zooplankton species (Bakke & Valderhaug 1978, DeLorenzo Costa et al. 2006, Michaud & Taggart 2007, 2011). Small changes in energy values can result in large changes in consumption estimates (Kenney et al. 1986), which makes assessment of habitat use all the more difficult.

Assessment of the lipid and energy content of prey has been used to investigate reproductive health in many populations and across a wide range of species. For example, in the Gulf of Alaska, the energy density of forage fishes for seabirds is largely determined by lipid content (Anthony et al. 2000). In this region, a 5-fold range of energy content in 39 species of fishes affected diet selection in breeding seabirds, especially during chick provisioning. Furthermore, the major breeding failure of common guillemots *Uria aalge* in the North Sea in 2004 was attributed to the unusually low energy density (<25% of the typical measured value) of fishes consumed by the parents (Wanless et al. 2005).

The Bay of Fundy (BoF), located between Maine, USA, and Nova Scotia, Canada, is characterized by a large daily tidal flux (>16 m; Dalton 1951) that induces nutrient upwelling to fuel large blooms of spring and autumn primary production. The BoF retains high productivity during the summer months compared to nearby neritic systems because of the tidal regime (Huettmann & Diamond 2000, Thomas et al. 2003, Johnston et al. 2005, Hlista et al. 2009). These processes allow *Calanus finmarchicus* nauplii to mature into the lipid-rich (4.5 to 9.9% wet mass) C5 copepodids during the late spring (Murison & Gaskin 1989, Lee et al. 2006, Michaud & Taggart 2007, Swaim et al. 2009). C5s then aggregate above the sea floor (>150 m) and undergo a fasting period (diapause) supported by their lipid stores until the following winter/spring months (Hirche 1996, Durbin et al. 1997, McLaren et al. 2001, Plourde et al. 2001, Baumgartner et al. 2003a). These swarms comprise the prey base to supply energy to basking sharks *Cetorhinus maximus*, Atlantic herring *Clupea harengus*, seabirds, and the NA right whale. However, little is known about the variation of C5 lipid physiology and energy value in this region.

Our objectives for the present study were to (1) investigate the inter-annual variation in energy and lipid content of C5s collected in the summers of 2006 to 2010, (2) determine whether a pattern of variation exists throughout each summer, and (3) discuss the implications any variation may have on right whale foraging patterns in the context of previously published consumption models. Based on Michaud & Taggart (2007), we hypothesized that C5s would show considerable seasonal and inter-annual variation. Furthermore, we hypothesized that if such variation is not included in predator–prey consumption models, these may misrepresent the amount of prey needed by that predator to meet daily metabolic requirements, a result that can have cascading effects for species management and conservation.

MATERIALS AND METHODS

Copepod collection

The majority of C5s in the Grand Manan Basin (GMB) congregate during the day in discrete layers approximately 100 m below the surface and 50 m above the sea floor (Murison & Gaskin 1989, Baumgartner & Mate 2003, Baumgartner et al. 2003a,b, Michaud & Taggart 2011). We followed the methods reported in Swaim et al. (2009) to collect copepods

biweekly during July to September of 2006 to 2010. Vertical plankton tows were made using a MARMAP 61 cm bongo frame with two 300 µm mesh nets (Sea-Gear) at North (44° 40.00′ N, 66° 25.00′ W) and South (44° 35.00′ N, 66° 25.00′ W) stations within the GMB (Fig. 1). These sites were selected based on areas with the highest sighting probabilities of right whales (sightings data collected 1987 to 2000; NARWC 2008). Water depths for each tow (190 to 210 m) were recorded using a depth sounder (Raytheon 850). Immediately after the nets were hauled onboard, the sampled zooplankton was gently scooped from the cod end and placed into 15 ml cryogenic vials (Nalgene). The vials were then placed in liquid nitrogen on board. These vials remained in liquid nitrogen until transferred to a –80°C freezer at the University of North Carolina at Wilmington.

Energy and total lipid content

After thawing, C5s were sorted and counted on ice under a stereo microscope until approximately 4 g of C5s per tow was reached (mean ± SD: 2670 ± 344 individuals); the number of C5s in each 4 g sample was recorded. Damaged copepods with perforated oil sacs or prosomes were excluded from analyses. Wet mass of C5s was determined by an analytical balance after excess water had been removed by blotting the samples dry with a paper towel. These C5s were then homogenized using a disperser (IKA) and reweighed to account for sample lost to the disperser. Of this 4 g homogenate, 3 g were used to assess energy content. Three pre-weighed calorimeter crucibles were filled with 1 g of C5 homogenate each to yield 3 replicates for each tow. These replicates were then dried to constant mass (5 to 6 d) at 60°C in a drying oven and finally combusted in an IKA 2000 Basic Calorimeter. The accuracy of the calorimeter was verified every 10 samples by combusting 1 g of benzoic acid with a known energy density of 26.460 kJ g^{-1}. Total lipid content of copepods for each tow was quantified using a modified Folch technique (Folch et al. 1957) using 1 g of the homogenate.

Data analysis

The following variables were calculated (Table 1) and used in the analysis: EC_D, the average energy content (kJ g^{-1}) from a single tow (3 replicates) reported as dry mass; EC_W, the average energy content (kJ g^{-1}) of copepods from a single tow (3 replicates) reported as wet mass; $C5_{EC}$, the energy content (J) of an individual; $C5_{WM}$, the average wet mass (µg) of an individual; $C5_{DM}$, the average dry mass of an individual; LC, the total lipid content from each tow (% wet mass); and $C5_{LC}$, the lipid content (µg) of an individual. A paired t-test using the energy and lipid content variables detailed above showed no significant spatial differences (p > 0.05) between North and South stations; therefore, data from both stations were used together in the analysis. To eliminate sampling bias, only the most consistently sampled months (August and September of 2006, 2007, 2009, and 2010) were used to calculate yearly means. Because of this, inter-annual variation (effects between years) and monthly variation (July to September) throughout each summer season were tested for significance using 1-way ANOVA (α = 0.05). The small sample size in 2008 prohibited inclusion of that year in our analysis. Levene's test of equality of error variances determined homogeneity of data groups. Post hoc testing included Bonferroni pairwise
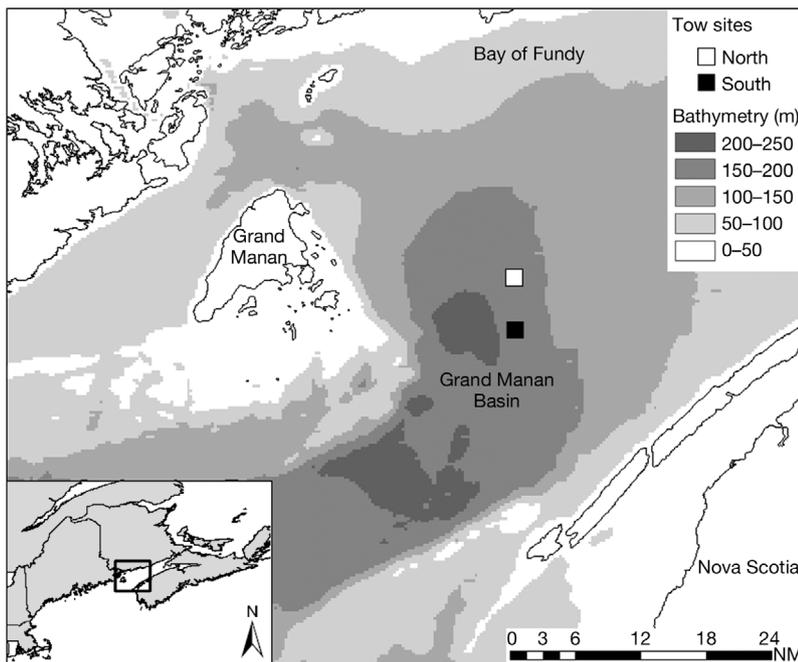

Fig. 1. Zooplankton sampling sites in the Bay of Fundy, Canada. North and South sites (squares) were located in the Grand Manan Basin in regions where right whales are most often seen (see 'Materials and methods'). NM: nautical miles

Table 1. *Calanus finmarchicus.* Variables and equations used to determine energy content, number of individuals analyzed, mass, and lipid content of C5 copepods used in the analyses

Variable	Equation	Definition
Wet mass energy content (kJ g^{-1})	$EC_W = EC_D \times \dfrac{D}{W}$	EC_D = dry mass energy content (kJ g^{-1}) D = final oven-dry mass (g)
Number of wet individuals in a gram	$C5g^{-1} = \dfrac{C5_N}{W}$	W = initial wet mass before drying (g) $C5_N$ = number of individuals in a sample
Mass of a wet individual (µg)	$C5_{WM} = \dfrac{1}{C5g^{-1}} \times 1\,000\,000$	
Mass of a dry individual (µg)	$C5_{DM} = C5_{WM} \times \dfrac{D}{W}$	
Individual energy content (J)	$C5_{EC} = EC_W \times C5_{WM}$	
Lipid content by wet mass (%)	$LC = \dfrac{L_M}{W} \times 100$	L_M = mass of lipid after extraction (g)
Individual lipid content (µg)	$C5_{LC} = C5_{WM} \times \dfrac{LC}{100}$	

comparisons (equal variances) or Tamhane's test (un-equal variances). Linear regression was used to evaluate relationships between variables such as LC and EC_W, and $C5_{WM}$ and $C5_{LC}$. All data were analyzed using SPSS 16.0.

RESULTS

Mass-based energy content

Zooplankton samples from 62 tows were collected and analyzed from the GMB during the summers of 2006 to 2010 (Table 2). In 2009, zooplankton was also sampled in May and June. The highest mean ± SD annual energy content (EC_W; July to September) was observed in 2007 (6.77 ± 0.65 kJ g^{-1}) while the lowest (5.82 ± 0.90 kJ g^{-1}) was recorded in 2009. Significant inter-annual variation in EC_W (p = 0.008) was observed: 2009 was lower than 2006 and 2007 but not different from 2010. Within years, none of the summer months showed significant variation in EC_W (p > 0.05; Table 2). We observed significant inter-annual variation (p < 0.001) in EC_D, where 2009 (28.1 ± 1.5 kJ g^{-1}) was lower than both 2007 (29.8 ± 0.5 kJ g^{-1}) and 2010 (30.3 ± 1.2 kJ g^{-1}). Variation among months in a given summer was not observed during any year (p > 0.05) in EC_D.

Individual energy content and mass

$C5_{EC}$ showed significant inter-annual variation (p < 0.001), where 2006 (10.54 ± 1.11 J) was significantly higher than 2010 (8.02 ± 1.17 J) but lower than 2007 (12.03 ± 0.81 J). In 2007, $C5_{EC}$ was significantly higher than all other years. Significant variation throughout the summer was observed in 2006 and 2010. In July 2006, the energy content of $C5_{EC}$ was higher (12.67 ± 0.45 J) than August (10.25 ± 0.87 J) or September (10.14 ± 0.58 J; p < 0.001). In 2010, the mean for September (7.34 ± 0.67 J) was significantly lower than August (9.37 ± 0.11 J; p = 0.016; Table 2). This indicates that the energy content of individuals decreased over the summer in 2006 and 2010. $C5_{EC}$ and $C5_{WM}$ were significantly correlated (R^2 = 0.44, p < 0.05), confirming that larger copepods have a higher energy content.

The mean $C5_{WM}$ from 2010 (1256.47 ± 115.79 µg) was significantly lower (p < 0.001) than all other years (Table 2). In addition, $C5_{WM}$ in 2007 (1771.33 ± 131.66 µg) was significantly greater than in 2006 (1566.47 ± 158.59 µg) and 2010. $C5_{WM}$ in 2007 and 2009 (1633.36 ± 153.47 µg) did not differ significantly, even though all energy content variables were higher in 2007 than in 2009. Variation in $C5_{WM}$ over the summer was only significant in 2009 (p = 0.01); $C5_{WM}$ between August (1786.71 ± 95.94 µg) and July (1818.08 ± 36.97 µg) were not significantly different from one another but showed a significant decrease in September (1541.35 ± 91.6 µg).

Lipid content

LC showed significant inter-annual variation, similar to EC_W (Table 2; p = 0.016), where 2009 was lower than both 2006 and 2007. No significant variation

Table 2. *Calanus finmarchicus.* Summary of Stage V copepod dry mass (EC_D) and wet mass (EC_W) energy content (kJ g^{-1}), energy density of an individual (J; $C5_{EC}$), average dry mass of an individual (µg; $C5_{DM}$), average wet mass of an individual (µg; $C5_{WM}$), lipid content (% wet mass; LC), and individual lipid content mass ($C5_{LC}$) by month for the 2006 to 2010 summer seasons presented as means ± SD

Date	Tows	EC_D	EC_W	$C5_{EC}$	$C5_{DM}$	$C5_{WM}$	LC	$C5_{LC}$
2006	21	29.52±0.94	6.62±0.69	10.54±1.11	356.95±35.16	1601.51±172.86	9.74±1.18	154.88±16.85
July	3	29.75±0.35	7.01±0.52	12.67±0.45	426.02±16.91	1811.71±87.71	10.08±0.46	182.46±5.23
August	8	29.28±1.50	6.56±1.07	10.25±0.87	349.80±25.25	1591.44±229.10	9.73±1.84	151.75±18.00
September	10	29.64±0.31	6.56±0.21	10.14±0.58	341.95±17.38	1546.50±75.40	9.65±0.62	149.10±8.59
2007	19	29.84±0.54	6.77±0.65	12.03±0.81	403.19±27.94	1787.08±147.79	10.03±1.33	177.96±15.39
July	5	29.79±0.87	6.50±0.50	11.83±0.58	397.82±29.45	1831.19±196.61	10.22±2.04	184.03±15.42
August	10	29.84±0.42	6.94±0.75	12.30±0.96	412.17±29.43	1782.41±136.28	9.94±1.17	176.43±17.37
September	4	29.90±0.42	6.67±0.54	11.58±0.39	387.47±16.83	1743.64±134.01	10.03±0.94	174.21±10.53
2008	4	29.44±0.27	6.67±0.44	12.22±0.85	414.45±26.84	1835.10±102.29	9.96±0.87	182.43±14.90
July	1	29.49	7.13	13.39	451.30	1876.51	10.88	204.22
August	2	29.26±0.23	6.30±0.10	11.89±0.56	406.23±15.87	1886.75±58.29	9.22±0.02	173.95±4.93
September	1	29.74	6.93	11.72	394.00	1690.38	10.51	177.59
2009	12	28.06±1.42	5.72±0.96	9.86±2.03	349.51±60.70	1722.69±188.49	8.36±1.29	144.17±28.58
2009[a]	10	28.10±1.48	5.82±0.90	9.76±1.94	345.57±57.57	1670.30±156.64	8.41±1.27	140.75±24.23
May	1	28.89	6.24	12.71	439.09	2036.26	9.42	191.85
June	1	26.77	4.14	8.01	299.33	1933.01	6.76	130.68
July	2	29.13±0.37	6.45±0.12	11.73±0.45	402.55±10.32	1818.08±36.97	9.40±0.29	171.03±8.82
August	3	27.94±2.12	5.91±1.19	10.49±1.74	374.00±38.65	1786.71±95.94	8.24±1.98	146.12±30.12
September	5	27.78±1.41	5.52±0.90	8.53±1.64	305.71±49.69	1541.35±91.61	8.12±1.01	125.42±18.89
2010	6	30.30±1.23	6.38±0.76	8.02±1.17	264.11±34.46	1256.47±115.79	9.50±1.50	119.07±19.27
August	2	30.93±1.75	6.97±0.83	9.37±0.11	303.53±20.92	1355.63±178.66	10.26±1.74	137.60±5.23
September	4	29.99±1.04	6.09±0.63	7.34±0.67	244.39±16.70	1206.89±43.29	9.11±1.46	109.81±16.33
Overall	62	29.40±1.17	6.47±0.81	10.73±1.75	364.41±55.84	1663.51±221.94	9.55±1.37	158.19±26.55

[a]Annual mean excluding May and June 2009

over the summer was observed during any year ($p > 0.05$). As expected, LC was highly correlated with EC_W ($R^2 = 0.79$, $p = 0.001$). Dry mass LC was also correlated with EC_D ($R^2 = 0.39$; $p < 0.001$). In addition, $C5_{WM}$ was strongly correlated with $C5_{LC}$, such that heavier copepods contained more lipid ($R^2 = 0.70$; $p < 0.001$).

DISCUSSION

Variation in copepod quality

During this study, C5 quality varied significantly among years. Overall, C5s from 2007 were either equivalent to or had significantly more energy content, lipid content, and mass than 2006, 2009, or 2010 (Table 2). For example, EC_W 2009 represented a 14% decrease compared to EC_W 2007. Comparing only September of these years, a larger decrease of 17% was observed. The differences in EC_W were larger than those obtained by comparing EC_D (5% for the years overall and 7% for September only), which might suggest that wet mass values exaggerate variation. However, LC showed variation on a similar scale to EC_W (Table 2). Because these 2 different measures of copepod quality exhibited the same level of variation between 2007 and 2009, it is reasonable to conclude that copepods sampled in 2009 exhibited a decline in quality by 15% (combined EC_W and LC). In addition, the scale of variation in quality at the level of the individual C5 ($C5_{EC}$, which is independent of whether the sample is wet or dry) between 2007 and 2009 (19%) was similar to the value obtained using EC_W.

This points to the potential drawbacks of using dry mass values as the metric of energy density in animals, as differences may be masked or artificially deflated. In practice, the value that is immune to any variation in dry:wet weight ratios is J $C5^{-1}$ ($C5_{EC}$; individual energy density is the same whether in dry or wet terms). Nonetheless, many studies report energy density as J per mass units of dry matter, which we feel can be a little misleading in terms of actual tissue value when masses/volumes of prey are consumed by predators. Intuitively, dry mass calculations decrease variation associated with water content. However, such data do not represent all of the variables that contribute to total energy content invested in an individual

copepod; e.g. a copepod that is only 20% dry matter by mass is of less quality than one that is 30% dry matter by mass, even if the dry matter of both individuals has the same mass-specific energy density. In reality, predators do not consume copepods on a dry mass basis. Wet values and lipid content describe living zooplankton in their environment and represent what is eaten by zooplanktivorous predators. Energy content on a wet mass basis is demonstrably appropriate for assessing and comparing relative prey quality (Anthony et al. 2000). However, because many of the studies reporting energy content in prey do so only as dry mass (e.g. Comita et al. 1966, Tyler 1973, Davis et al. 1998, Michaud & Taggart 2007), dry mass variables are also reported here to permit comparisons to such studies.

Significant trends within a given summer were only observed based on $C5_{EC}$, which showed a 20% decrease in energy content between July and September 2006, and a 22% decrease between August and September 2010 (Table 2). In contrast to our observations, $C5_{EC}$ increased by 63% from May to September in 2002 (Michaud & Taggart 2007). This suggests that there may be large inter-annual variation in the pattern of individual *Calanus finmarchicus* energy content in the BoF. The July to September $C5_{EC}$ for 2006 to 2009 was at least 3 times higher (Table 2) than that reported by Michaud & Taggart (2007) during the same months in 2002 (approximately 3.3 J). This discrepancy could represent real differences across years or could be methodically related to the number of individuals that were processed (present study: ca. 625 per replicate; Michaud & Taggart: 20 per replicate). Smaller numbers can translate to larger relative error as seen in the high SD and SE values reported by Michaud & Taggart (2007). The within-sample variation reported by those authors was also much greater (overall mean ± SD: 32.1 ± 13.5 kJ g^{-1} dry wt.; CV of 0.42) than reported in the present study (overall mean 29.5 ± SD: 1.17 kJ g^{-1}; CV of 0.04). Our samples were dried and combusted in calorimeter crucibles to restrict manipulation of the sample and reduce any potential loss of lipids to a pelletizer such as the one used by Michaud & Taggart (2007) to compress 20 individuals. In comparison, our range of $C5_{EC}$ values (~7 to 12 J) was closer to the range obtained in the nearby Roseway Basin in September 2007 (~3 to 11 J) by Davies et al. (2012), although our mean value for this time period (11.6 J; Table 2) was still higher than that reported by the latter authors (6.9 J).

Possible sources of variation in energy and lipid content

The variation in prey quality seen here is likely based on environmental changes such as water temperature. Larger C5s have more energy overall, and store more lipid, the same patterns observed by Miller et al. (2000) and Davies et al. (2012). Over the course of a summer, however, mean C5 size and energy content decreased (Table 2, Fig. 2). Such trends follow the temperature–size rule that describes how ectotherm growth and development are affected by temperature (Forster & Hirst 2012). According to this rule, the growth rate of *Calanus finmarchicus* exposed to warmer water during the summer yields smaller, faster-growing copepods than those that develop in colder early spring waters (Michaud & Taggart 2007). In laboratory experiments, Campbell et al. (2001b, p. 168) suggested similar trends. C5s reared at 4°C 'did not appear to be feeding and RNA:DNA ratios of these copepods declined over time to levels approaching those of diapausing copepods from the field,' unlike C5s reared at higher temperatures.

Food limitation also impacts growth rates in these copepods (Campbell et al. 2001a,b), but the role that future changes in climate will have on phytoplankton abundance or copepod quality in this region is not well understood. Dramatic changes in water temperature and the subsequent effects on plankton have been documented in other systems. Due to increased
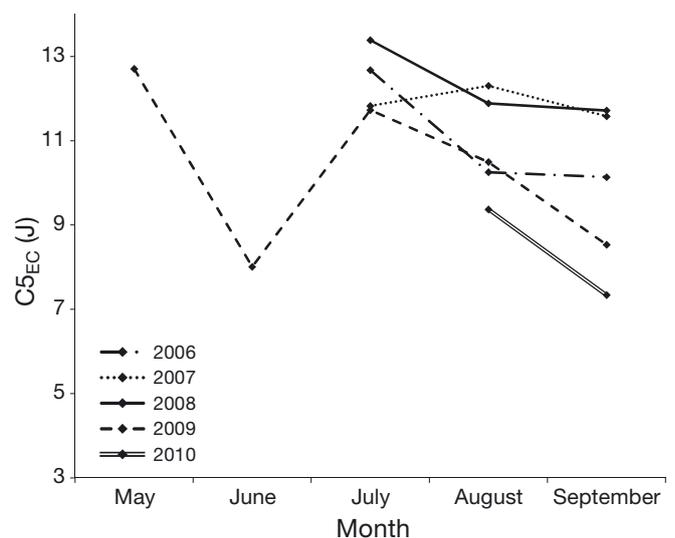
Fig. 2. *Calanus finmarchicus*. Variation in energy content of individual C5 copepods ($C5_{EC}$; J) over the summer based on monthly averages. Standard deviations of each month can be found in Table 2

sea surface temperature (SST) altering upwelling magnitude, reduction of inorganic nutrients available for primary productivity resulted in a smaller zooplankton population (70% from 1951–1957 to 1987–1993) in the California Current System (Roemmich & McGowan 1995a,b). This observed pattern also coincided with a decline (95%) of zooplanktivorious northern anchovy *Engraulis mordax* biomass between 1966 (66.67 g m^{-2}) and 1977 (3.33 g m^{-2}; Smith & Eppley 1982) in the region. In the eastern North Atlantic and North Sea, the past 50 yr have seen an increase in the relative abundance of diatoms while dinoflagellate relative abundance has decreased. This was directly related to increased SST and wind activity during the summer (Hinder et al. 2012). Some evidence does suggest that the BoF may be highly variable in terms of phytoplankton bloom intensity both seasonally and annually (Thomas et al. 2003, Hlista et al. 2009). Because the amount of lipid C5s can store is dependent on bottom-up trophic dynamics (Campbell et al. 2001a), yearly variation of phytoplankton abundance and composition may influence *Calanus finmarchicus* in BoF by altering lipids accumulated for diapause during Stages C4 and C5 (Campbell et al. 2001b, McLaren et al. 2001, Baumgartner et al. 2003a). The inter-annual variation in C5 lipid content we observed and, more specifically, potential variation in fatty acid/alcohol composition (data not shown; see McKinstry 2011) may indicate shifts in food available to copepods. Further monitoring of this system focusing on phytoplankton and copepods is imperative to fully understand the consequences climatic shifts will have on higher trophic level organisms.

Potential implications for predator consumption models

As shown here, prey quality available to predators in BoF is not predictably consistent. A low energy density of copepods, and zooplankton overall, can have detrimental impacts on higher-level predators (Foy & Norcross 1999, Abraham & Sydeman 2004, Ainley et al. 2006, Lane et al. 2011). The significant changes in the lipid and energy content of *Calanus finmarchicus* observed here could potentially impact the foraging ecology of predators such as right whales (DeLorenzo Costa et al. 2006). Environmental changes influencing the abundance and variation of energy density in copepods may help predict when right whales enter or leave the GMB to feed. The late summer arrival and numbers of right whales observed

in the GMB documented since 1980 have been linked with copepod abundance and concentration (Murison & Gaskin 1989, Michaud & Taggart 2007, Pendleton et al. 2009), but could also reflect the overall quality of energy content of copepods available to whales.

The results of this study demonstrate the importance and utility of measuring prey quality at the appropriate temporal and spatial scales. Several authors (e.g. Kenney et al. 1986, Baumgartner & Mate 2003) have attempted to model the prey field density required to meet the energetic demands of feeding NA right whales. Such models are important for considering metabolism in these animals and for identifying areas of suitable right whale habitat on the summer feeding grounds off Cape Cod and in the BoF. Both studies relied on the same single point value for the energy content of an individual C5, viz. the mean value of 6.78 J obtained more than 40 yr ago from waters off Western Scotland by Comita et al. (1966), a data point that is neither temporally nor spatially relevant to contemporary models of feeding right whales in the western North Atlantic. Based on this value, Kenney et al. (1986) estimated that threshold copepod densities required to maintain the metabolism of a right whale ranged from 4.7×10^3 to 1.48×10^6 ind. m^{-3} (with variation depending on a series of caveats). Baumgartner & Mate (2003) refined these models and estimated that a minimum C5 concentration of 3.6×10^3 m^{-3} was needed to meet the energy demands of a right whale, with the caveat that this would require feeding 24 h d^{-1}. Mean peak C5 densities in known right whale feeding areas in the BoF measured via OPC (Baumgartner & Mate 2003) were 6.6×10^3 m^{-3}, supporting the idea that whales in this area are likely feeding on C5 densities on the 10^3 m^{-3} order of magnitude rather than the upper estimate of 10^6 m^{-3} calculated by Kenney et al. (1986). For the purpose of this example, let us then assume that right whales require C5 densities somewhere in the neighborhood of $(3 \text{ to } 6) \times 10^3$ m^{-3} to meet their metabolic demands, where an individual C5 is worth 6.78 J. If, instead, our overall mean energy content (C5$_{EC}$ = 10.73 J C5^{-1}) is used in the model, the corresponding range of required copepod densities drops to $(1.9 \text{ to } 3.8) \times 10^3$ m^{-3}, i.e. a decrease of 37%. Such a change would mean that copepod patches with lower C5 densities would become 'suitable' for whales, expanding potential feeding habitat in a year in which C5s contained high amounts of energy.

Even within only 5 yr of sampling, we observed the annual mean energy content of a C5 (C5$_{EC}$) to vary

from 12.2 (2008) to 8.02 J (2010), representing a decrease in 2010 of 34%. Still greater differences are found in the monthly means, ranging from an extreme low of 7.34 J in September 2010 to a high of 13.39 J in July 2008 (Table 2), which translates into a 45% drop in 2010. Substituting these values, and our mean of 10.73 J, into Baumgartner & Mate's (2003) model of minimum C5 density yields a wide range of required copepod densities (Fig. 3) — emphasizing the influence that variation in prey quality can have on predator models.

Changes in copepod energy content may mean that zooplankton patches of different densities can be sufficient to meet the metabolic demands of predators, but this variation can also affect activity budgets. Consider Baumgartner & Mate's (2003) calculated minimum C5 density of 3.6×10^3 m^{-3} with foraging required 24 h d^{-1}. If this density is available to whales on a steady basis, but the energy content of C5s varies, then whales will need to spend more or less time foraging for the same net energy intake. Whales needing to feed for 24 h d^{-1} on copepods worth 6.78 J would only need to forage for 15 h d^{-1} if C5 energy content increased to our mean of 10.7 J, leaving time for the social, travel, and resting activities that occur on the summer feeding grounds. Although they measured energy content of copepods indirectly (using C:N ratios as a proxy for energy content), DeLorenzo Costa et al. (2006) also found significant ranges in predicted densities of copepods required to meet right whale energy demands in
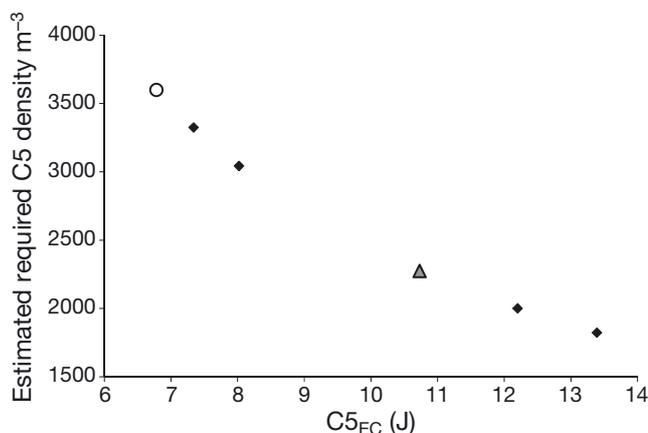
Cape Cod Bay during January to May of 2003, as their C:N ratios varied close to 40% over the period of only a few months. It should also be noted that relative quality of copepods can be followed using less laboratory-intensive methods, such as measuring the size of the oil sac, as has been shown by Hays et al. (2001).

Finally, differences in the quality of one trophic level are useful for interpreting variation in another from the same ecosystem, particularly if they are directly linked. Lane et al. (2011) reported significant variation in the lipid content of Atlantic herring *Clupea harengus* from the BoF during 2005 to 2008 but were unable to determine the specific source of this variation. Herring feed on copepods but are in turn consumed by seabirds, larger fish such as tuna, and porpoises, seals, and fin and humpback whales; thus herring link secondary production to higher trophic levels. In the 3 yr of overlap between the study of Lane et al. (2011) and our study (2006 to 2008), the energy content of individual C5s (C5$_{EC}$) was mirrored by changes in lipid content collected from herring in September (after spending the summer feeding on the copepods whose quality we measured; Fig. 4). We recognize that as this is only a short time frame and that not much weight can be placed on the absolute strength of this relationship, but these data were collected synoptically from 2 different, yet connected,
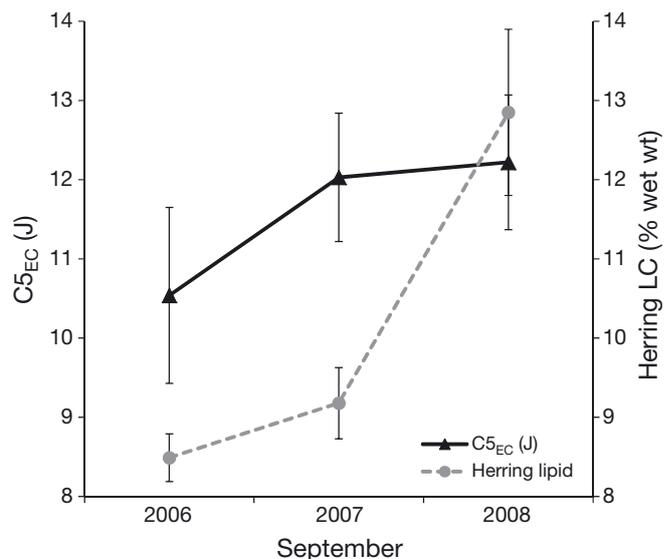

Fig. 3. *Calanus finmarchicus.* Reductions in estimated required densities for feeding right whales *Eubalaena glacialis* (based on Baumgartner & Mate 2003) as a function of changing energy content of individual C5 copepods (C5$_{EC}$). Circle represents value obtained using Comita et al. (1966), triangle represents value obtained using our overall mean, and diamonds represent our lowest and highest annual and monthly means

Fig. 4. *Clupea harengus* and *Calanus finmarchicus.* Mean lipid content of Atlantic herring collected during September from the Bay of Fundy (data from Lane et al. 2011) in relation to changes in the energy content of individual C5 copepods (C5$_{EC}$), their main prey item, during the summers of 2006 to 2008. Sample sizes: herring 2006 (117), 2007 (66), 2008 (10); C5s 2006 (21 tows), 2007 (19 tows), 2008 (4 tows)

trophic levels in the same ecosystem, which is not all that common. Fig. 4 does suggest that herring lipids could be associated with copepod energy content. This provides the first evidence for a source of variation in herring lipid content, which can lead to alterations in herring health and reproduction, and consequently on foraging patterns of herring predators.

The above examples illustrate the pitfalls of using only 1 value for nutritional quality of prey items, and the benefits of measuring quality over several years. In-depth investigations into how the value of copepods for predators varies between years in the BoF are imperative to fully understand predator physiology. Not only will this information help address management issues of fisheries stocks and endangered cetaceans (Smith & Eppley 1982, DeLorenzo Costa et al. 2006), it will also help to monitor the effects on marine food webs of the continuing global warming trend seen in the past 50 yr (Roemmich & McGowan 1995a). Our study provides a foundation for future investigations into the effects of variability of C5 energy/lipid content, C5 mass, and relative C5 abundance in the BoF on predators and other members of the ecosystem. As variation in copepod energy density is likely to be very important in a range of systems, we hope that our efforts will aid in the development of the most precise and accurate models to describe and predict trophic interactions in similar systems that rely heavily on calanoid copepods as a major prey item either directly, in the case right whales, or indirectly via transfer through intermediate trophic levels.

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