The impact of increasing temperatures on dormancy duration in *Calanus finmarchicus*

JAMES J. PIERSON[1]*, HAROLD BATCHELDER[2], WHITLEY SAUMWEBER[3], ANDREW LEISING[4] AND JEFFREY RUNGE[5]

[1]HORN POINT LABORATORY, UNIVERSITY OF MARYLAND CENTER FOR ENVIRONMENTAL SCIENCE, 2020 HORNS POINT ROAD, CAMBRIDGE, MD 21613, USA, [2]OCEAN, AND ATMOSPHERIC SCIENCES, OREGON STATE UNIVERSITY, COLLEGE OF EARTH, 104 CEOAS ADMINISTRATION BUILDING, CORVALLIS, OR 97331-5503, USA, [3]NOAA OCEAN SERVICE, 1305 EAST WEST HIGHWAY, SILVER SPRING, MD 20910, USA, [4]NOAA-SWFSC-ERD, 1352 LIGHTHOUSE DR, PACIFIC GROVE, CA 93950, USA AND [5]SCHOOL OF MARINE SCIENCES, GULF OF MAINE RESEARCH INSTITUTE, UNIVERSITY OF MAINE, 350 COMMERCIAL STREET, PORTLAND, ME 04101, USA

*CORRESPONDING AUTHOR: jpierson@umces.edu

Dormancy is a key life history trait of planktonic calanoid copepods in the genus *Calanus*. Empirical evidence suggests that duration of dormancy is controlled by ambient temperature driving lipid metabolism in individuals. Here, we use the temperature-dependent metabolic rates of overwintering individuals to show that increasing temperatures, associated with global climate change over the next several decades, may reduce dormancy duration for the north Atlantic species *C. finmarchicus* by up to 40 days. Our calculations are based on comparing predicted dormancy duration for individuals of a given size at specific temperatures to dormancy duration at warmer temperatures and smaller size. We also provide corrections to the relationship of dormancy duration described by Saumweber and Durbin [Estimating potential diapause duration in Calanus finmarchicus. Deep Sea Res. Pt. II., 53, 2597–2617.]. Our calculations indicate that changing temperatures in the sea may lead to phenological shifts in life histories of *C. finmarchicus* and congeners, which may have implications for planktonic food web and trophic dynamics.

INTRODUCTION

The known impacts of climate-driven temperature increases on marine zooplankton populations, often dominated by copepods, have been reviewed by Hays *et al.* (Hays *et al.*, 2005) and Richardson (Richardson, 2006). They include biogeographic shifts (Beaugrand and Ibañez, 2002; Beaugrand *et al.*, 2002, 2009) and changes in biomass (Roemmich and McGowan, 1995a,b), and size of dominant taxa (Beaugrand *et al.*, 2002). Discerning climate-related shifts require inferences based on changes in zooplankton populations observed over long periods of time, usually decades or more. Less information is available about the response of individual zooplankton to climate change, although individuals are the agents on which the consequences of climate change, for example increasing temperatures, will act. Despite recent technological advances, such as optical imaging, that have enhanced the ability to sample individual zooplankton *in situ*, analysis of trends is constrained by population-based measurements from existing time series. This constraint in observation requirements precludes direct information of individual zooplankter response to climate change.

Nevertheless, the biological and physiological effects of increasing temperature on individual marine calanoid copepods are studied well. Relationships between temperature and metabolism (Ikeda *et al.*, 2001), respiration (Ikeda *et al.*, 2007), fecundity (Bunker and Hirst, 2004), growth (Huntley and Lopez, 1992; Hirst and Bunker, 2003), development (Forster *et al.*, 2011) and dormancy duration (Saumweber and Durbin, 2006) have been investigated and have been reported in the literature. These studies provide insight into the possible impacts of climate forcing on processes determining population dynamics and food web structure, and provide the empirical basis on which numerical models of planktonic food webs and life histories have been developed.

One of the key life history traits for some pelagic copepod species is dormancy. Dormancy may occur in various life stages and for various durations depending on the species (reviewed by Dahms, 1995). Dormancy in copepods is believed to be a strategy enabling individuals (populations) to persist through seasonally adverse conditions, e.g. generally, periods of presumed high mortality, which may be due to low food availability or unsuitably high or low temperatures (Dahms, 1995). In calanoids of the genus *Calanus*, dormancy generally occurs in the fifth copepodid (CV) stage during winter, at depths of $100-1000$ m depending on the local conditions (Heath, 2000; Heath *et al.*, 2004). Many of the studies on dormancy in *Calanus* have been conducted on *C. finmarchicus*, which is found throughout the North

Atlantic from approximately 40 to 65°N. The mechanisms controlling the onset and termination of dormancy have not been unambiguously elucidated, and a number of hypotheses have been put forth implicating food, photoperiod and temperature (reviewed by Johnson *et al.*, 2008 and references therein), as well as predation (Ji, 2011). Recent modeling studies suggest that dormancy timing may be controlled by accumulation and metabolism of lipids in the later copepodid stages, driven by temperature and food availability, as described in the Lipid Accumulation Window (LAW) hypothesis (Johnson *et al.*, 2008; Maps *et al.*, 2012). Lipid-rich stages of *C. finmarchicus* are abundant in coastal and oceanic food webs across its subarctic range, where they are prominent mesozooplankton grazers and primary prey for planktivorous fish, such as herring, mackerel, northern sand lance, capelin and young blue whiting (e.g. Gilman, 1994; Dalpadado *et al.*, 2000; Darbyson *et al.*, 2003; Dommasnes *et al.*, 2004; Skjoldal, 2004; Langøy *et al.*, 2012). Northern right whales feed on lipid-rich *C. finmarchicus* in coastal northwest Atlantic waters (Baumgartner *et al.*, 2003) and mesopelagic fish feed on dormant *C. finmarchicus* in deep basins of the North Atlantic (Kaartvedt, 2000). The larvae of a number of fish species also feed, sometimes almost exclusively, on the eggs and nauplii of *C. finmarchicus* (e.g. Runge and de Lafontaine, 1996; Ringuette *et al.*, 2002; Heath and Lough, 2007).

Parameterization of dormancy duration and timing of entry into and exit from dormancy in these models is largely based on the empirical relationships derived by Saumweber and Durbin (Saumweber and Durbin, 2006). The metabolic rate of dormant animals was determined empirically in shipboard and laboratory experiments, and relationships based on these measurements were subsequently used to prescribe dormancy duration in life history models of *C. finmarchicus*. Results from the modeling efforts reproduced the broad patterns from observational data in some cases but not in others (Maps *et al.*, 2012). In places where the model did not agree with observations, the discrepancy was concluded to be more likely the result of advection of animals with different life histories into the study area than a weakness of the hypothesis.

Here, we examine how increasing temperature may impact dormancy duration of overwintering *C. finmarchicus*. We use results from Saumweber and Durbin (Saumweber and Durbin, 2006), including the empirical relationships between the volume of storage lipids and metabolic rate of dormant animals, and make simple calculations to determine how changes in temperature and animal size might affect potential dormancy time. Four scenarios are tested to examine the effects on lipid

metabolism that may be experienced by overwintering stage CV over the next century. In each case, we considered not only temperature change, but also changes in individual size that may accompany the environmental changes, using the growth and development relationships from Campbell *et al.* (Campbell *et al.*, 2001). These relationships were used in the modeling efforts to explore the LAW hypothesis, and provide the basis for growth and development rate in these models (Johnson *et al.*, 2008; Maps *et al.*, 2012). In addition, we present corrections to the originally published models by Saumweber and Durbin (Saumweber and Durbin, 2006), correcting typographic errors in coefficients and equations, and most importantly introducing a new linear equation to relate the length and oil sac volume (OSV) of individual CV copepodites to carbon content (replacing equation 8 in Saumweber and Durbin, 2006). This new linear equation replaces an exponential equation that can generate incorrect conditions for larger animals.

METHOD

The model of dormancy duration (t, in days) developed by Saumweber and Durbin (Saumweber and Durbin, 2006, equation 30) was determined from empirical measurements of lipid content and nitrogen-specific respiration rate of dormant CV *C. finmarchicus* in the deep basins of the Gulf of Maine. Here, we have simplified the equation:

$$t = \frac{\mathrm{Log}_e[(Q(625 \times \mathrm{OSV}_{min} + 7.5) + 40.1657 \times L^3 - 28.8737)/}{(Q(625 \times \mathrm{OSV}_{max} + 7.5) + 40.1657 \times L^3 - 28.8737 + 12)]}{-0.04065 \times R}$$

(1)

where Q is the proportion of wax ester that is composed of carbon (0.74), OSV_{max} and OSV_{min} (equations 6 and 7 in Saumweber and Durbin 2006, respectively) are maximum and minimum OSVs (μL) predicted for a given prosome length (L, mm), the value 12 in the denominator is the initial carbon weight (μg) of triacylglyceride (TAG) storage lipids in dormant animals and R is defined as the daily nitrogen-specific respiration rate in units of carbon (μgC μg N^{-1} day^{-1}). The equation for R is a function of temperature:

$$R = \frac{24 \times Q \times 12.011 \times 10^{(0.0442 \times T + 2.1154)}}{10^6}$$
$$= 2.1331 \times 10^{-4} \times 10^{(0.0442 \times T + 2.1154)}, \quad (2)$$

where Q is 0.74 as defined above, T is temperature in degrees Celsius, and the 24, 12.011 and 10^6 terms are

Table I: List of equations used in calculation of dormancy duration, from Saumweber and Durbin (Saumweber and Durbin, 2006)

Source equation	Units/description
$\mathrm{OSV}_{max} = 0.274052$ $L^2 - 0.5987 L + 0.254568$	OSV_{max} (μL) as a function of prosome length (L, mm)
$\mathrm{OSV}_{min} = 0.279779$ $L^2 - 1.06674 L + 1.060073$	OSV_{min} (μL) as a function of prosome length (mm)
$N = 1.63287$ $L^3 + 18.80358$ $\mathrm{OSV} - 0.94817$	The relationship between nitrogen weight (N; μg), oil sac volume (OSV; μL) and prosome length (L; mm)

unit conversions from hours to days, μmol CO_2 to μg C, and from gN to μgN, respectively. Details are given by Saumweber and Durbin (Saumweber and Durbin, 2006) for derivation of the model, and additional details are shown in Table I for the calculation of OSV_{min} and OSV_{max}.

It is important to note here that there are two typographical errors in the original Saumweber and Durbin (Saumweber and Durbin, 2006) paper and one equation that is not valid for larger sized dormant individuals. In Table 5 the parameter m, which is used to calculate the relationship between OSV and N weight in equation 9 should have a value of 1.63287 μg mm^{-3} (Saumweber, unpublished results). The correct coefficient was used in the calculations that led to the results published in the work of Saumweber and Durbin (Saumweber and Durbin, 2006), but the printed values of m in equation 9 and Table 5 are incorrect. An additional typographic error is in equation 19 of Saumweber and Durbin (Saumweber and Durbin, 2006), in which the denominator should be 10^6 (μgN gN^{-1}).

For completeness, we include one additional correction in the equation of Saumweber and Durbin (Saumweber and Durbin, 2006), which relates to the estimation of the total carbon (TOTC, μg C) using OSV and the length of individuals (L, in mm), as shown in equation 8 of Saumweber and Durbin (Saumweber and Durbin, 2006). Using the original equation, the potential amount of wax ester carbon (WEC) was actually greater than TOTC for individuals with prosome lengths (L) greater than 2.79 mm. This condition (WEC:TOTC > 1) is not possible, and is resulted from an exponential term (with an exponent < 1) for OSV in the equation describing TOTC. Saumweber (unpublished results) subsequently calculated a linear equation for the relationship between TOTC, OSV and the length of individuals (L, in mm),

$$\mathrm{TOTC} = 7.67365(L^3) + 308.17835(\mathrm{OSV}) - 7.41910,$$

(3)

that has a slightly lower R^2 value ($R^2 = 0.908$) than the original exponential equation (Saumweber and Durbin, 2006, equation 8), but satisfies the necessary constraint that WEC < TOTC. The new equation for TOTC was not used in this study on dormancy duration, but may have implications for modeling *C. finmarchicus* growth and respiration (Fig. 1).

To calculate the changes in dormancy duration for a given change in temperature, size or both, we first calculated dormancy duration from the corrected dormancy duration equation from Saumweber and Durbin (Saumweber and Durbin, 2006), for a range of temperatures ($0-12°C$) and prosome lengths ($1.8 - 3$ mm), to generate a matrix of dormancy duration times (days). We then examined how the duration of dormancy would change for four different temperature–size scenarios that might be expected to occur with global warming. The scenarios we tested were: temperature increase of $1°C$ with prosome length decreases of 0.03 and 0.13 mm, and a temperature increase of $2°C$ with prosome length decreases of 0.07 and 0.17 mm. Temperature increases of up to $2°C$ are predicted in the North Atlantic, although there is considerable uncertainty about predictions in the upper 500 m of the ocean (Meehl *et al.*, 2007). The smaller size changes at each of the two temperatures were based on linear relationships between prosome length and temperature described by Campbell *et al.* (Campbell *et al.*, 2001). The larger size changes were included to account for the effects of possible food limitation, as described in

the Campbell *et al.* paper for their $8°C$ treatment, in which CV individuals in the low food treatment size were 1.4 mm smaller than the high food treatment. The change in dormancy duration was calculated as the difference between the dormancy duration calculated for a given temperature and prosome length and the dormancy duration at the increased temperature and decreased prosome length described for each of the four scenarios.

In addition to testing how dormancy duration changed in response to increased temperature and decreased size, we also examined potential dormancy duration changes in response to decreased lipid sac volume. This could occur if the individual copepods are unable to fulfill their quota of lipid storage (OSV_{max}) before entering dormancy. We calculated the duration of diapause for OSV reserves corresponding to 95, 75 and 50% of OSV_{max} for the same range of temperatures ($0-12°C$) and prosome lengths ($1.8-3$ mm) as described above.

RESULTS

The original Saumweber and Durbin (Saumweber and Durbin, 2006) result and corrected total carbon content described in the methods section are shown in Fig. 1. Using a linear term for the relationship with OSV (μL) increases the predicted total carbon content for prosome lengths > 2.45 mm compared with using the original exponential term, and the ratio of WEC to TOTC never exceeds 0.9 (Fig. 1).

Calculated changes in dormancy duration caused by increased temperature and decreased PL are shown in Fig. 2. In general, the greatest decreases in dormancy duration occur for the largest animals at the coldest temperatures in each scenario. For the smallest temperature and size change that we considered (Fig. 2a), estimates of dormancy duration were shortened by more than 20 days for 2.57 mm PL animals living initially at $0°C$ (Fig. 2b). In contrast, at the largest temperature increase and size decrease, the dormancy duration decreased by 42 days for 2.66 mm animals living initially at $0°C$ (Fig. 2d). For the smallest animals, there was an increase in dormancy duration of up to 30 days. Prolonged dormancy of small individuals occurred for both warming scenarios and the greatest decreases in prosome length (Fig. 2d).

For each of the four scenarios, we also calculated the change in dormancy duration for animals reared under the environmental conditions described by Campbell *et al.* (Campbell *et al.*, 2001), assuming they attained OSV_{max} (Fig. 2; Table II). Consistent with the overall findings, the greatest change in dormancy duration
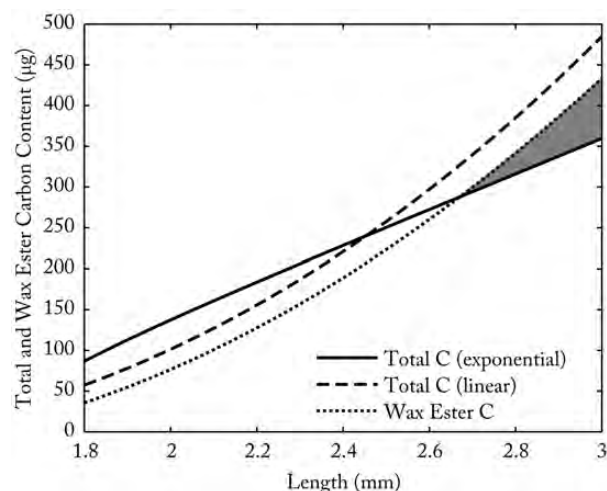
Fig. 1. Relationship between prosome length (mm) and carbon content (μg) in wax esters (WEC) and total (TOTC) for individual dormant *C. finmarchicus* CV. TOTC is shown using models with exponential OSV and linear OSV terms. The shaded region illustrates conditions for which the exponential model predicts WEC is greater than TOTC.
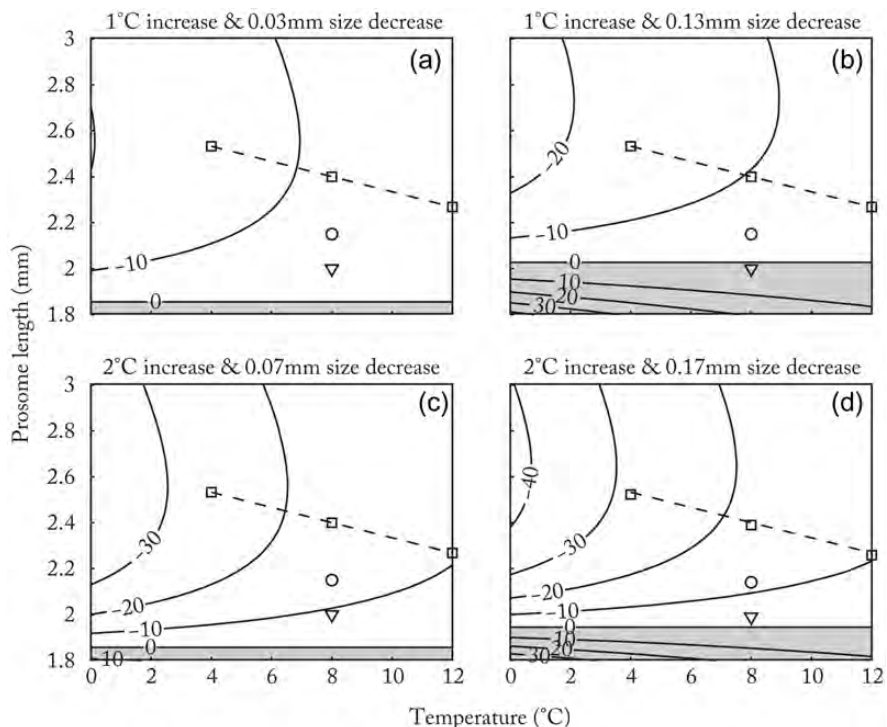
Fig. 2. Contours of dormancy duration changes (days) for four different scenarios with temperature increases ($1-2°C$) and stage CV prosome length decreases ($0.03-0.17$ mm) using corrected dormancy duration calculations when compared with original equations provided by Saumweber and Durbin (Saumweber and Durbin, 2006). Shaded area shows region where dormancy duration increases with temperature. Symbols show the prosome length (mm) of animals reared at given temperatures from Campbell *et al.* (Campbell *et al.*, 2001) under food replete conditions at 4, 8 and 12°C (squares), and medium (circle) and low food (inverted triangle) at 8°C.

Table II: Change in the duration of dormancy (days) for copepodite V of a given size (PL; mm) and at a given temperature (Temp; °C), calculated from Campbell (Campbell, 2001), for each of the four scenarios

|	Temp [PL]	+1°C— 0.03 mm	+1°C— 0.13 mm	+2°C— 0.07 mm	+2°C— 0.17 mm
High food	4 [2.53]	−13	−14	−26	−25
High food	12 [2.27]	−6	−7	−11	−12
High food	8 [2.4]	−9	−8	−17	−15
Medium food	8 [2.15]	−7	−3	−15	−8
Low food	8 [2.0]	−4	2	−10	−1

occurred for animals at the lowest temperature (0°C). For animals reared at low food levels at 8°C, the model predicts dormancy will be lengthened by 2 days for a 1°C increase in experienced temperature (Fig. 2b).

Reduced OSV at diapause initiation that would likely accompany less than maximal food conditions always shortened estimated dormancy duration, and this had a larger effect at the lowest temperatures and for animals with intermediate PL's centered on ~2.4 mm (Fig. 3). A 5% decrease in OSV (i.e. 95% of OSV$_{max}$) reduced

dormancy by 10 days or less, but a 25% decrease (75% of OSV$_{max}$) reduced dormancy by up to 40 days. At 50% of OSV$_{max}$, the duration of dormancy duration was greatly shortened, by up to 85 days for 2.4 mm PL animals at 0°C.

DISCUSSION

Dormancy is a key life history trait for *C. finmarchicus*, and the duration depends on both the temperature at which the copepod resides and the amount of storage lipid it has accumulated. Saumweber and Durbin (Saumweber and Durbin, 2006) found that dormancy duration could last up to 9 months (~280 days) for 2.34 mm PL animals at 0°C. Our findings suggest that this duration could change by more than a month (~39 days) with a 2°C temperature increase and concomitant size decrease. The dependence of development (progression through life history stages) and growth (increasing individual mass) on temperature has been shown to differ in copepods, resulting in smaller stage-specific lengths and weights at higher temperatures (Miller *et al.*, 1977; Forster *et al.*, 2011). To account for this, we used
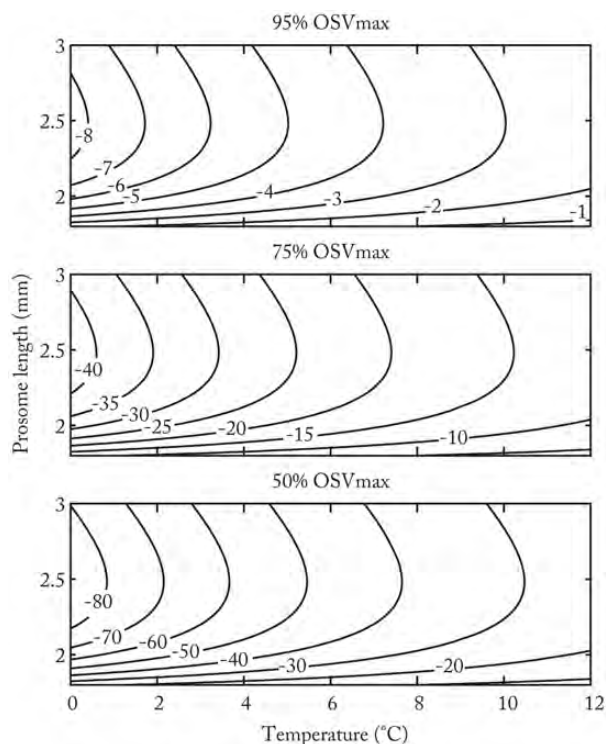
Fig. 3. Contours of change in dormancy duration (days) with varying initial oil sac volumes (OSVs) as a percentage of the maximum possible volume (OSV$_{max}$). Upper panel shows data for 95% of maximum volume, middle panel for 75% and lower panel for 50%.

the development and growth relationships from Campbell *et al.* (Campbell *et al.*, 2001) to calculate a mean decrease in prosome length that would occur with increasing temperatures of 1 and 2°C, and included those size decreases in our scenarios to calculate changes in dormancy duration. Because the relationship we used was determined from experiments at food saturation, we also included scenarios with animals that decreased in PL. It should be noted that the decreased PL used here was smaller (0.1 mm PL) than the change observed by Campbell *et al.* (Campbell *et al.*, 2001) when food was reduced from saturating to their "medium" levels (~0.2 mm PL), suggesting that the shortened durations of dormancy may be conservative. It should be noted that the smallest animals actually had increased dormancy duration for all four of the scenarios we tested; however, animals smaller than 2 mm were rarely observed in studies on *C. finmarchicus* CVs (Miller *et al.*, 1998, 2000; Saumweber, 2005). Further, the respiration equations from the work of Saumweber and Durbin (Saumweber and Durbin, 2006) that are used here are weight specific, but respiration is parameterized only as a function of temperature over the duration of dormancy, so size-specific changes in respiration for individuals are not directly accounted

for in this study. Our intent was to develop and test a simple model of the potential decrease in dormancy duration associated with animals overwintering in warmer water, but a more complex life history model that accounts for changing respiration throughout dormancy is beyond the scope of this study. It is unlikely that diapause duration of any sized individuals would actually lengthen as temperature increases, so the equation describing diapause duration in Saumweber and Durbin (Saumweber and Durbin, 2006) as modified here that yields lengthened diapauses of the smallest individuals as temperatures warm should be used with caution, or not at all, for small-sized CVs.

We also examined how dormancy duration could change for individuals at a given temperature and PL if OSV was not at its maximum at the beginning of dormancy. At 75% of OSV$_{max}$, dormancy duration could be shortened by as much as 40 days. At 50% of OSV$_{max}$, dormancy duration could be shortened by 80 days; however, the minimum OSV that would allow an individual to enter dormancy is unclear. The LAW hypothesis, as it is parameterized in Maps *et al.* (Maps *et al.*, 2012) model, uses a threshold for lipid accumulation in the fourth copepodid (CIV) stage derived from a genetic algorithm procedure (Record *et al.*, 2010). The internal molecular and hormonal cues that control the initiation of dormancy in *C. finmarchicus* (Hill, 2009) are not well known, and experiments to empirically determine minimum thresholds are hampered by the lack of success in experimentally inducing dormancy of *C. finmarchicus* in laboratory settings.

Using the incorrect parameter values published in Saumweber and Durbin (Saumweber and Durbin, 2006) led to up to 2 weeks greater change in the duration of dormancy for each of the four scenarios compared with using the corrected relations used here (data not shown). In the published models (Johnson *et al.*, 2008; Maps *et al.*, 2012), the errors in the published Saumweber and Durbin (Saumweber and Durbin, 2006) parameters were corrected, but had they not been, the error would not have been trivial. The other correction to Saumweber and Durbin (Saumweber and Durbin, 2006) presented here, the change from an exponential to a linear fit for the relationship of carbon content to length and OSV (Fig. 1), is essential to ensure that the model does not predict individuals with more carbon content in the lipid fraction than the total. Even though the R^2 value of the exponential model is slightly higher than the linear model (Saumweber, unpublished results), the impossibility of having higher lipid carbon content per individual than total carbon content precludes the use of an exponential equation here.

Our calculations indicate that changing temperatures in the sea may lead to changes in phenology for *C. finmarchicus* and likely other species with similar life histories. Kjellerup *et al*. (Kjellerup *et al*., 2012) showed that egg production of *C. finmarchicus* increased with increasing temperature as long as food was available, and that the rate of increase in temperature was higher than for the congener *C. glacialis*. This combined with faster development times for *C. finmarchicus* under increasing temperatures (e.g. Campbell *et al*., 2001) may confer a competitive advantage over *C. glacialis* in some cases. However, it should be noted that timing changes have been inferred for both *C. finmarchicus* and *C. helgolandicus* in the temperate northeast Atlantic, with *C. helgolandicus* abundance increasing in regions historically dominated by *C. finmarchicus* (Beaugrand *et al*., 2002). This suggests that climate change may have different effects on a species throughout it's range. The present study relies on the data collected in the Gulf of Maine and if populations of *C. finmarchicus* in other parts of its range are differently adapted to local conditions, the relationships described here may not be appropriate to predict dormancy for those animals. Recent genetic evidence based on a suite of markers suggests two to four distinct populations throughout the North Atlantic basin (Unal and Bucklin, 2010), but we do not currently have the empirical data to evaluate the potential impact that phenotypic variability has on dormancy duration. Further, other marine calanoids employ a similar life history strategy (Falk-Petersen *et al*., 2009), and in particular the evaluation of dormancy timing for congeners of *C. finmarchicus* is less well constrained simply because of fewer studies on the dormancy metabolism and respiration of those congeners.

This study represents one means of exploring the impact of changes in dormancy timing based on a model fit to available empirical data, but it does not preclude other mechanisms affecting timing of dormancy or the response of individuals to local conditions. It is intended to explore the potential effects of dormancy duration using a fairly simple approach to determine the range of magnitudes that can be expected under reasonable climate change scenarios. However, as Pepin and Head (Pepin and Head, 2009) note, CV individuals not only need to survive dormancy, but to complete the life cycle by developing gonads and molting, which has an associated metabolic cost. Thus, different local conditions could lead to varying strategies for resource allocation that in turn may lead to a variety of dormancy strategies throughout the species' range. For example, dormancy depth has been shown to vary across the range of *C. finmarchicus* (Heath, 2000; Heath *et al*., 2004), and some of these differences have been concomitant with changes in lipid content (Pepin and Head, 2009). The exact mechanisms leading to this variability have not been elucidated, but warrant further empirical study to better understand the nature of dormancy.

The timing of dormancy entry and exit for *C. finmarchicus* will likely impact coastal and oceanic North Atlantic food webs through its influence on the spatial and temporal overlap between *Calanus* and its predators and prey. As such, phenological shifts have been identified as a key component to structuring marine food webs and productivity, most famously through the "Match–Mismatch Hypothesis" (Cushing, 1990; Ji *et al*., 2010; Thackeray, 2012). Analysis of zooplankton time series data has supported these findings and suggested potential future impacts, should observed trends continue (Mackas and Beaugrand, 2010). In our study, we provide a mechanism to estimate how one major life history trait, dormancy, of this dominant copepod species could be impacted by climate change.

There are presently few data sets with enough resolution to accurately determine dormancy duration and temperature at the depth of dormancy using the methods presented here, precluding a direct test of the current hypothesis with existing data. Observing the timing of spring blooms from satellites has shown climate-related changes (e.g. Kahru *et al*., 2011), but sampling zooplankton in deep water provides challenges that cannot presently be met with remote sensing technology. However, advances in optical (e.g. Baumgartner, 2003; Baumgartner *et al*., 2003) and acoustic (e.g. Gaardsted *et al*., 2010) methods may provide the enhanced resolution needed to estimate the timing and depth of dormancy more accurately. When paired with moored or autonomous underwater vehicle data, more rigorous testing of the hypotheses proposed here would be possible. Such observations are likely to prove important as the indirect effects of climate change become more pronounced with increasing temperatures.

FUNDING

REFERENCES

Baumgartner, M. F. (2003) Comparisons of *Calanus finmarchicus* fifth copepodite abundance estimates from nets and an optical plankton counter. *J. Plankton Res.*, **25**, 855–868.

Baumgartner, M. F., Cole, T. V. N., Campbell, R. G. *et al.* (2003) Associations between North Atlantic right whales and their prey, *Calanus finmarchicus*, over diel and tidal time scales. *Mar. Ecol. Prog. Ser.*, **264**, 155–166.

Beaugrand, G. and Ibañez, F. (2002) Spatial dependence of calanoid copepod diversity in the North Atlantic Ocean. *Mar. Ecol. Prog. Ser.*, **232**, 197–211.

Beaugrand, G., Luczak, C. and Edwards, M. (2009) Rapid biogeographical plankton shifts in the North Atlantic Ocean. *Global Change Biol.*, **15**, 1790–1803.

Beaugrand, G., Reid, P. C., Ibañez, F. *et al.* (2002) Reorganization of North Atlantic marine copepod biodiversity and climate. *Science*, **296**, 1692–1694.

Bunker, A. J. and Hirst, A. G. (2004) Fecundity of marine planktonic copepods: global rates and patterns in relation to chlorophyll a, temperature and body weight. *Mar. Ecol. Prog. Ser.*, **279**, 161–181.

Campbell, R. G., Wagner, M. M., Teegarden, G. J. *et al.* (2001) Growth and development rates of the copepod *Calanus finmarchicus* reared in the laboratory. *Mar. Ecol. Prog. Ser.*, **221**, 161–183.

Cushing, D. H. (1990) Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. *Adv. Mar. Biol.*, **26**, 249–293.

Dahms, H. U. (1995) Dormancy in the Copepoda—an overview. *Hydrobiologia*, **306**, 199–211.

Dalpadado, P., Ellertsen, B., Melle, W. *et al.* (2000) Food and feeding conditions of Norwegian spring-spawning herring (*Clupea harengus*) through its feeding migrations. *ICES J. Mar. Sci.*, **57**, 843–857.

Darbyson, E., Swain, D. P., Chabot, D. *et al.* (2003) Diel variation in feeding rate and prey composition of herring and mackerel in the southern Gulf of St Lawrence. *J. Fish Biol.*, **63**, 1235–1257.

Dommasnes, A., Melle, W., Dalpadado, P. *et al.* (2004) Herring as a major consumer in the Norwegian Sea. *ICES J. Mar. Sci.*, **61**, 739–751.

Falk-Petersen, S., Mayzaud, P., Kattner, G. *et al.* (2009) Lipids and life strategy of Arctic *Calanus*. *Mar. Biol. Res.*, **5**, 18–39.

Forster, J., Hirst, A. G. and Woodward, G. (2011) Growth and development rates have different thermal responses. *Am. Nat.*, **178**, 668–678.

Gaardsted, F., Zhou, M., Pavlov, V. *et al.* (2010) Mesoscale distribution and advection of overwintering *Calanus finmarchicus* off the shelf of northern Norway. *Deep Sea Res. Pt. I*, **57**, 1465–1473.

Gilman, S. L. (1994) An energy budget for northern sand lance, *Ammodytes dubius*, on Georges Bank, 1977–1986. *Fish. Bull.*, **92**, 647–654.

Hays, G. C., Richardson, A. J. and Robinson, C. (2005) Climate change and marine plankton. *TRENDS Ecol. Evol.*, **20**, 337–344.

Heath, M. R. (2000) Winter distribution of *Calanus finmarchicus* in the Northeast Atlantic. *ICES J. Mar. Sci.*, **57**, 1628–1635.

Heath, M. R. and Lough, R. G. (2007) A synthesis of large-scale patterns in the planktonic prey of larval and juvenile cod (*Gadus morhua*). *Fish. Oceanogr.*, **16**, 169–185.

Heath, M. R., Boyle, P. R., Gislason, A. *et al.* (2004) Comparative ecology of over-wintering *Calanus finmarchicus* in the northern North Atlantic, and implications for life-cycle patterns. *ICES J. Mar. Sci.*, **61**, 698–708.

Hill, K. A. J. (2009) Changes in gene expression, lipid class and fatty acid composition associated with diapause in the marine copepod *Calanus finmarchicus* from Loch Etive, Scotland. PhD Thesis. University of St Andrews, St Andrews, UK, pp. 133.

Hirst, A. G. and Bunker, A. J. (2003) Growth of marine planktonic copepods: global rates and patterns in relation to chlorophyll a, temperature, and body weight. *Limnol. Oceanogr.*, **48**, 1988–2010.

Huntley, M. E. and Lopez, M. D. G. (1992) Temperature-dependent production of marine copepods: a global synthesis. *Am. Nat.*, **140**, 201–242.

Ikeda, T., Kanno, Y., Ozaki, K. *et al.* (2001) Metabolic rates of epipelagic marine copepods as a function of body mass and temperature. *Mar. Biol.*, **139**, 587–596.

Ikeda, T., Sano, F. and Yamaguchi, A. (2007) Respiration in marine pelagic copepods: a global-bathymetric model. *Mar. Ecol. Prog. Ser.*, **339**, 215–219.

Ji, R. (2011) *Calanus finmarchicus* diapause initiation: new view from traditional life history-based model. *Mar. Ecol. Prog. Ser.*, **440**, 105–114.

Ji, R., Edwards, M., Mackas, D. L. *et al.* (2010) Marine plankton phenology and life history in a changing climate: current research and future directions. *J. Plankton Res.*, **32**, 1355–1368.

Johnson, C. L., Leising, A., Runge, J. *et al.* (2008) Characteristics of *Calanus finmarchicus* dormancy patterns in the Northwest Atlantic. *ICES J. Mar. Sci.*, **65**, 339–350.

Kaartvedt, S. (2000) Life history of *Calanus finmarchicus* in the Norwegian Sea in relation to planktivorous fish. *ICES J. Mar. Sci.*, **57**, 1819–1824.

Kahru, M., Brotas, V., Manzano-Sarabia, M. *et al.* (2011) Are phytoplankton blooms occurring earlier in the Arctic? *Glob. Change Biol.*, **17**, 1733–1739.

Kjellerup, S., Dünweber, M., Swalethorp, R. *et al.* (2012) Effects of a future warmer ocean on the coexisting copepods *Calanus finmarchicus* and *C. glacialis* in Disko Bay, western Greenland. *Mar. Ecol. Prog. Ser.*, **447**, 87–108.

Langøy, H., Nøttestad, L., Skaret, G. *et al.* (2012) Overlap in distribution and diets of Atlantic mackerel (*Scomber scombrus*), Norwegian spring-spawning herring (*Clupea harengus*) and blue whiting (*Micromesistius poutassou*) in the Norwegian Sea during late summer. *Mar. Biol. Res.*, **8**, 442–460.

Mackas, D. L. and Beaugrand, G. (2010) Comparisons of zooplankton time series. *J. Mar. Syst.*, **79**, 286–304.

Maps, F., Runge, A., Leising, A. *et al.* (2012) Modelling the timing and duration of dormancy in populations of *Calanus finmarchicus* from the Northwest Atlantic shelf. *J. Plankton Res.*, **34**, 36–54.

Meehl, G. A., Stocker, T. F., Collins, W. D. *et al.* (2007) Global Climate Projections. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K. B., Tignor, M. and Miller, H. L. (eds), *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK and New York, NY, USA.

Miller, C. B., Crain, J. A. and Morgan, C. A. (2000) Oil storage variability in *Calanus finmarchicus*. *ICES J. Mar. Sci.*, **57**, 1786–1799.

Miller, C. B., Johnson, J. K. and Heinle, D. R. (1977) Growth rules in the marine copepod genus *Acartia*. *Limnol. Oceanogr.*, **22**, 326–335.

Miller, C. B., Morgan, C. A., Prahl, F. G. *et al.* (1998) Storage lipids of the copepod *Calanus finmarchicus* from Georges Bank and the Gulf of Maine. *Limnol. Oceanogr.*, **43**, 488–497.

Pepin, P. and Head, E. J. H. (2009) Seasonal and depth-dependent variations in the size and lipid contents of stage 5 copepodites of *Calanus finmarchicus* in the waters of the Newfoundland Shelf and the Labrador Sea. *Deep-Sea Res. I*, **56**, 989–1002.

Record, N. R., Pershing, A. J., Runge, J. A. *et al.* (2010) Improving ecological forecasts of copepod community dynamics using genetic algorithms. *J. Mar. Syst.*, **82**, 96–110.

Richardson, A. J. (2006) In hot water: zooplankton and climate change. *ICES J. Mar. Sci.*, **33**, 279–295.

Ringuette, M., Castonguay, M., Runge, J. A. *et al.* (2002) Atlantic mackerel (*Scomber scombrus*) recruitment fluctuations in relation to copepod production and juvenile growth. *Can. J. Fish. Aquat. Sci.*, **59**, 646–656.

Roemmich, D. and McGowan, J. (1995a) Climatic warming and the decline of zooplankton in the California current. *Science.*, **267**, 1324–1326.

Roemmich, D. and McGowan, J. (1995b) Sampling zooplankton: correction. *Science*, **268**, 352–353.

Runge, J. A. and de Lafontaine, Y. (1996) Characterization of the pelagic ecosystem in surface waters of the northern Gulf of St. Lawrence in early summer: the larval redfish-*Calanus*-microplankton interaction. *Fish. Oceanogr.*, **5**, 21–37.

Saumweber, W. (2005) Energetic constraints on diapause in Calanus finmarchicus: implications for population dynamics in the Gulf of Maine. PhD Thesis. University of Rhode Island, Kingston, RI, USA, pp. 262.

Saumweber, W. and Durbin, E. (2006) Estimating potential diapause duration in *Calanus finmarchicus*. *Deep Sea Res. Pt. II*, **53**, 2597–2617.

Skjoldal, H. R. (ed.) (2004) *The Norwegian Sea Ecosystem*. Tapir Academic Press, Trondheim, Norway.

Thackeray, S. J. (2012) Mismatch revisited: what is trophic mismatching from the perspective of the plankton? *J. Plankton Res.*, **34**, 1001–1010.

Unal, E. and Bucklin, A. (2010) Basin-scale population genetic structure of the planktonic copepod *Calanus finmarchicus* in the North Atlantic Ocean. *Prog. Oceanogr.*, **87**, 175–185.