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Persistence of *Calanus finmarchicus* in the western Gulf of Maine during recent extreme warming

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The planktonic copepod, *Calanus finmarchicus*, resides at the southern edge of its subarctic range in the Gulf of Maine (GoM). Here we investigate the population response of *C. finmarchicus* to record warming in the GoM in 2012. Demographic data from two time series stations and a plankton survey conducted in early autumn 2012 show that *C. finmarchicus* did not produce an autumn generation as predicted, despite warm summer and overwintering temperatures. On the contrary, we observed high abundances of the overwintering stage CV in the western GoM and a new cohort in early spring 2013 likely originating from egg production during a winter phytoplankton bloom. This spring cohort was the most abundant ever recorded in the 8-year time series. To account for these observations, we hypothesize that production of females originating from the eastern GoM and Scotian Shelf, combined with growth of copepodid stages in the Maine Coastal Current and local egg production, are the primary sources of supply maintaining high abundances in Wilkinson Basin, the primary repository of *C. finmarchicus* in the western GoM. Predicting fluctuations in abundance or circumstances for disappearance of *C. finmarchicus* in the northwest Atlantic will need models that address the roles of local production and advection.

KEYWORDS: *Calanus finmarchicus*; Gulf of Maine; warming; climate change; resilience; population dynamics

INTRODUCTION

The predominance of the planktonic copepod, *Calanus finmarchicus*, in the mesozooplankton assemblage throughout the North Atlantic is well known. In the Gulf of Maine (GoM), *C. finmarchicus* resides at the southern edge of its subarctic range (Sundby, 2000). The species is nevertheless a prominent component of the zooplankton in the GoM system (e.g. Durbin *et al.*, 2003; Durbin and Casas, 2006; Kane, 2009). Wilkinson Basin, in the western GoM, harbors overwintering stage CV *C. finmarchicus* at abundances ($>3.0 \times 10^4$ inds. m^{-2}) that are equal to or higher than levels observed in the species' more northern habitat (Maps *et al.*, 2012; Melle *et al.*, 2014). In coastal regions of the GoM in spring and summer, *C. finmarchicus* dominates not only biomass (Manning and Bucklin, 2005) but also abundance of zooplankton in the catch of plankton nets with $>200 \mu\text{m}$ mesh size (Runge and Jones, 2012).

Calanus finmarchicus has key functional significance in the GoM ecosystem (Bigelow, 1924; Johnson *et al.*, 2011). The lipid-rich stage CV are a primary prey for planktivorous fish, such as herring and sand lance (e.g. Payne *et al.*, 1990; Collette and Klein-MacPhee, 2002) that are fundamental trophic links in regional fisheries. Since there is no apparent functional redundancy for *C. finmarchicus* in the GoM ecosystem, significant shifts in abundance of *C. finmarchicus* may have substantial impacts on the region's metazoan energy budget and consequently affect local distribution and abundance of planktivores and higher trophic-level predators (Johnson *et al.*, 2011). Wilkinson Basin plays a particularly important role in the western GoM because it serves as a primary source of supply of *C. finmarchicus* to fishing and northern right whale feeding grounds in waters off southern New England, including the Great South Channel and Georges Bank (Wishner *et al.*, 1995; Miller *et al.*, 1998; Pendleton *et al.*, 2009).

Statistical-based modeling of *C. finmarchicus* habitat characteristics, notably sea surface temperature, across the North Atlantic predicts that climate-driven ocean warming will force distribution of the species northward over the next several decades (Reygondeau and Beaugrand, 2011). This prediction has particular relevance for the western GoM, where water column temperatures are historically several degrees higher than more northern *C. finmarchicus* habitats (Maps *et al.*, 2012; Melle *et al.*, 2014). Over the past decade, water column temperatures in surface and deep waters of the GoM have been rising at a rate ($0.2^\circ\text{C year}^{-1}$) that is more than ten times the observed average temperature rise ($0.01^\circ\text{C year}^{-1}$) over the past century (Shearman and Lentz, 2011; Mills *et al.*, 2013). In 2012, identified as an especially anomalous year for the GoM, sea surface temperatures in summer were as much as 5°C higher than the long-term average and the mean annual

SST was fully 2°C higher than normal (Mills *et al.*, 2013). In addition to possible adverse effects of higher surface temperatures on physiological rate processes, for example egg hatching success (Preziosi and Runge, 2014), warmer temperatures at depth during summer and autumn may force early exit from dormancy of the overwintering, pre-adult stage CV, with consequences for the timing of winter-spring reproduction. In a one-dimensional life history model, Maps *et al.* (Maps *et al.*, 2012) predicted that the already warm overwintering temperatures in Wilkinson Basin in the western GoM force exit from dormancy in late summer/early autumn. In the model, the emergence of new females aligns with the autumn phytoplankton bloom, resulting in a new, autumn cohort that sustains the western GoM population through to reproduction in spring.

Here we investigate the response of *C. finmarchicus* in the GoM to the 2012 warming event. Using data from two time series stations and from a research cruise conducted in early autumn 2012, we compare the seasonal abundance and demographic patterns of the 2012 *Calanus* population in the western GoM with recent historical data. We use the observations to (i) evaluate the extent to which abundance of *C. finmarchicus* was sustained in the western GoM and (ii) test the hypothesis (Maps *et al.*, 2012) that the warm, overwintering waters in the GoM bring about early exit from diapause and subsequent production of an autumn cohort during the autumn phytoplankton bloom. The results of our study lead us to consider a new hypothesis, involving local production and transport of copepodid stages in the Maine Coastal Current, that may make the *C. finmarchicus* population in the western GoM more resilient to climate forcing than previously predicted.

METHOD

Samples were collected at survey stations (Fig. 1) during research cruise CH 0712 on the R/V *Cape Hatteras* between 24 September and 3 October 2012 and at two time series stations (Fig. 1), the Coastal Maine Time Series station (CMTS) located at the landward margin of the Maine Coastal Current (Lat. $43^\circ44.8'\text{N}$, Lon. $69^\circ30.1'\text{W}$; depth: 105 m), and the Wilkinson Basin Time Series station (WBTS) located in the northwestern corner of Wilkinson Basin (Lat. $42^\circ51.7'\text{N}$, Lon. $69^\circ51.8'\text{W}$; depth: 225 m). The CMTS was sampled at semi-monthly to monthly intervals (with some longer gaps) between August 2008 to December 2013, using the University of Maine research vessel, R/V *Ira C*, based at the Darling Marine Center. The WBTS was sampled at monthly or longer intervals between January 2005 to July

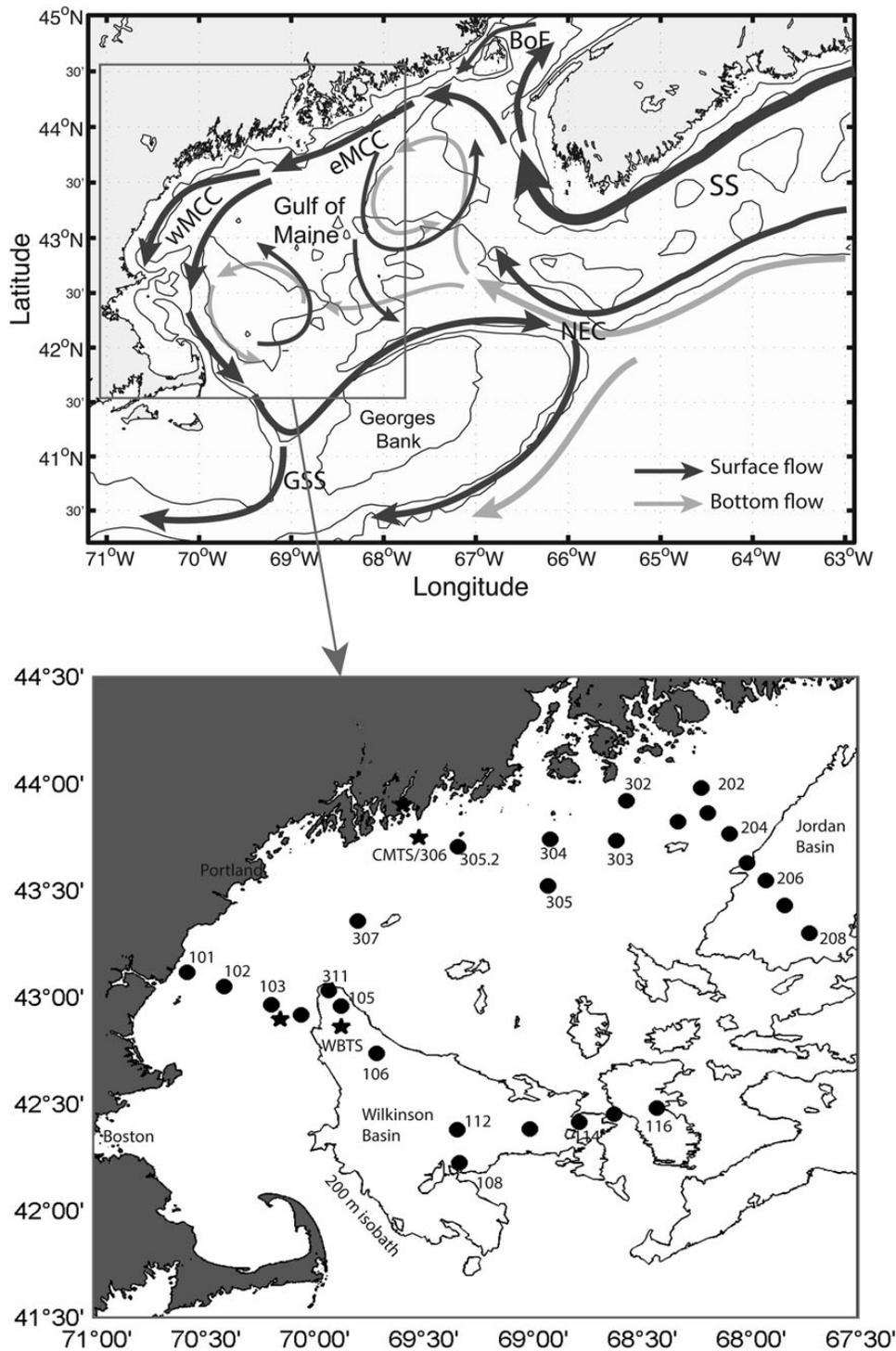


Fig. 1. Gulf of Maine showing general circulation of surface and deep flows, plankton survey station locations (inset: circles) and time series stations (inset: stars) in Wilkinson Basin (WBTS) and midcoast Maine (CMTS). SS, Scotian Shelf; BoF, Bay of Fundy; NeC, Northeast Channel; eMCC, eastern Maine Coastal Current; wMCC, western Maine Coastal Current; GSS, Great South Channel.

2010 and at monthly intervals between April 2012 and May 2013, using the University of New Hampshire research vessel, R/V *Gulf Challenger*.

The methods for sampling environmental variables and *C. finmarchicus* abundance at the sampling stations followed, with variations indicated below, the protocols

established by the Canadian Atlantic Zone Monitoring Program (Mitchell *et al.*, 2002). Salinity and temperature were measured with a Seabird 19 plus at the CMTS, a Seabird 19 or 49 at WBTS and a Seabird 911 equipped with a Wetlabs fluorometer during research cruise CH 0712. Concentrations of chlorophyll *a* were routinely measured at WBTS and during CH 0712, but not at the CMTS. At WBTS, duplicate, 100 mL or 500–550 mL water samples were collected with Niskin bottles at the surface, 10, 20 and 40 m. During CH0712, duplicate 100 mL samples were collected with a rosette at the surface, 10, 20, 30 and 50 m as well as at the depth of maximum chlorophyll as determined with the *in situ* fluorometer. The samples were filtered under low vacuum onto Whatman GFF glass fiber filters (0.8 μm) and also frequently onto 5- μm and 20- μm Nucleopore filters at selected depths. The filters were placed in 5 mL of 90% acetone and cold extracted for 24 h, after which fluorescence was measured with a Turner AU-10 fluorometer. Chlorophyll *a* concentrations were calculated using equations in Strickland and Parsons (Strickland and Parsons,

1972). For the time series plot of chlorophyll *a* concentrations (Fig. 2), bottle sample data were interpolated linearly in time and with depth from the surface to the bottom of the mixed layer, below which chlorophyll *a* concentration was assumed to be zero. The mixed layer depth was determined as the depth showing a difference of 0.2°C with the temperature at 10 m (Maps *et al.*, 2012).

Calanus finmarchicus abundance was estimated from zooplankton samples collected with 0.75 m diameter, 200- μm mesh ring nets, in the mouth of which a General Oceanics flowmeter was suspended. The nets were deployed, in single-ring or dual-ring (two ring nets connected side-by-side) configurations, to within 5 m off the bottom and then towed vertically to the surface at a rate of 40 m min^{-1} . Two replicate samples from separate casts were preserved in a 4% seawater-buffered formaldehyde solution. In the laboratory, all formalin preserved zooplankton samples were split into half using a Folsom Plankton Splitter. Half of the sample was archived for identification and enumeration of zooplankton, and the other half was processed for biomass determination. To

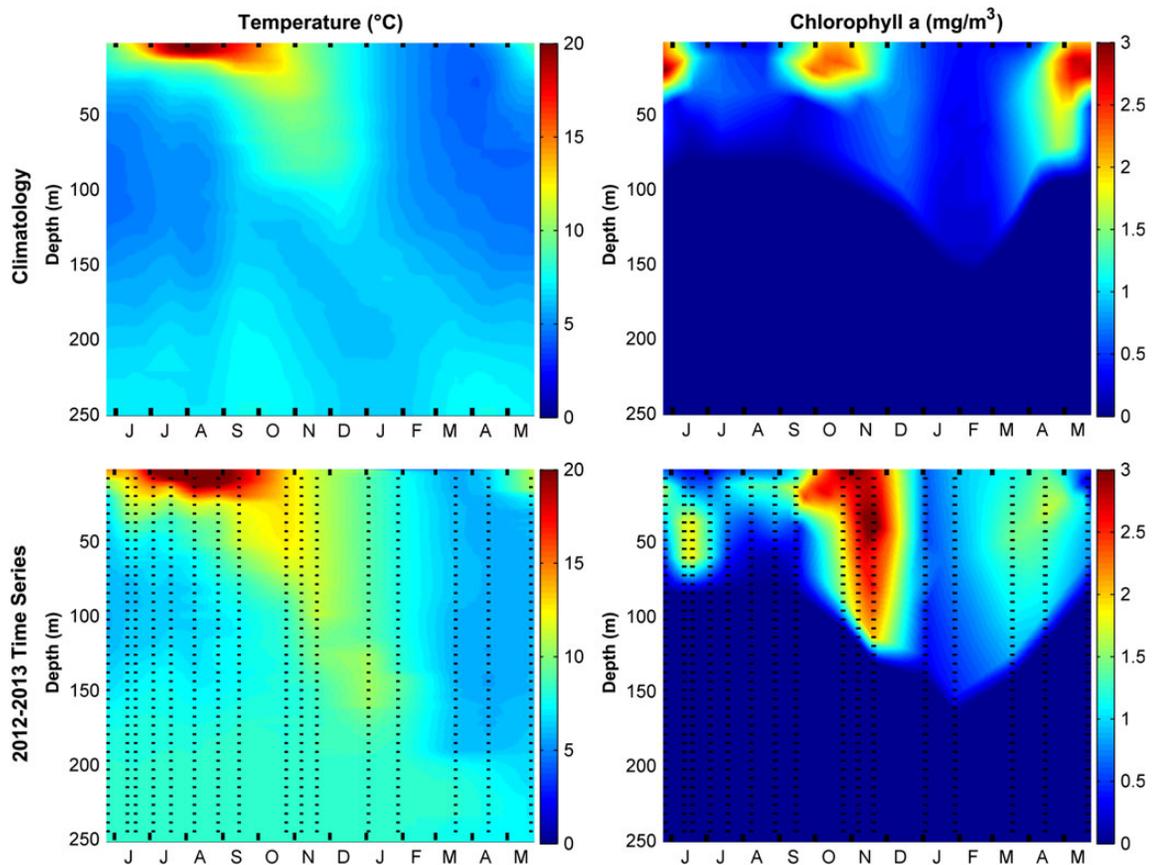


Fig. 2. Observed temperature (°C: left panels) and chlorophyll *a* concentrations ($\text{mg chl } a \text{ m}^{-3}$: right panels) at time series station WBTS in Wilkinson Basin. Top panels: Climatology based on data collected between 2005 and 2012 by the Coastal Observing Center, University of New Hampshire. Bottom panels: data collected between 1 June 2012 and 31 May 2013 at WBTS. Dotted vertical lines indicate sampling dates. Note that in all panels the time series starts in June.

estimate abundances, the archival split was diluted and sub-sampled with a 5 mL Stempel pipette. Depending on abundance in the sample, multiple subsamples were taken until a target number of 75–150 *C. finmarchicus* copepodids were enumerated and staged and in addition at least 200 specimens in total were counted and identified to the lowest possible taxonomic level. The counts were normalized to abundance (number m^{-2}), taking into account the subsample dilution, the split, and volume sampled by the net at the station. Because of faulty flowmeter readings during cruise CH 0712, we calculated volume filtered by the net from net area and net depth. The filtered volume calculated geometrically, as we have done here, is closely related to the flowmeter volume when flowmeters were working properly.

On cruise CH 0712, live *C. finmarchicus* for shipboard observations of molting and egg production rates were captured with a 1-m diameter, 333 μm mesh ring net fitted with a non-filtering cod end. The net was towed obliquely from near bottom to the surface while the vessel maintained a speed of 1–2 kt. The contents of the cod end were transferred with minimum handling into 3.8 L clear plastic containers filled with sub-surface seawater. The containers were placed in coolers in which the temperature was maintained between 4 and 8°C. Females and copepodid stage CIV–CV were sorted within 2 h of capture for use in the molting and egg production observations. Females were pipetted separately into individual petri dishes and incubated for 24 h in a refrigerator (5–8°C) to measure egg production rate (Runge *et al.*, 2006). Copepodid stages, also sorted individually into separate petri dishes, were incubated for 24–48 h for observations of molting rate (Runge *et al.*, 1985).

RESULTS

The water temperature climatology (Fig. 2) for Wilkinson Basin shows the start in May of a seasonal thermocline that warms and intensifies over the course of the summer. Maximum mean temperatures of 17–18°C are attained in late August in a surface layer ~25 m deep. Mixing of the warm surface layer to a depth of ~110 m occurs between mid-September and mid-October. Warmer water in the surface 100 m persists until late December, after which the well-mixed upper 100–150 m cools to a surface layer minimum average temperature of 4°C in late winter. The underlying deep water at 150 m is coolest (5°C) in early spring, warming to 7–8°C by late November.

In 2012, Wilkinson Basin surface water temperatures in spring and summer were 4–5°C warmer than the seasonal average (Fig. 2). The maximum surface temperature in

late August reached 22°C. Warming of the underlying deep water, which was already warmer than average in late spring, occurred sooner and persisted later, until late January. Deep water at 150 m was 7–8°C by June and 11–12°C by late November.

T – S diagrams (Fig. 3) illustrate the seasonal evolution of water column properties from May 2012 to May 2013. This general seasonality agrees with the climatological pattern, featuring the formation of a mid-depth water mass, located at the elbow in the T – S curves, from convective mixing driven by winter cooling. During 2012 this intermediate water was noticeably warmer and saltier and thus less pronounced when compared with climatology. This was probably due to weaker convective mixing leading to shallower mixed layers during the preceding winter (Fratantoni *et al.*, 2013). The T – S diagrams show no sign of abnormal flushing of water mass throughout the water column.

Differences in the seasonal cycle of phytoplankton, as represented by the concentration of chlorophyll *a*, between 2012 and 2013 and the climatological average, are also evident. For most of the year, except during January 2013, chlorophyll concentrations in 2012–2013 (Fig. 2) were at least half of the estimated critical concentration, 1.8 mg chl *a* m^{-3} (Runge *et al.*, 2006), required for maximum *C. finmarchicus* egg production. The autumn bloom in 2012, which was greater than average in magnitude, vertical extent and duration, persisted through November to mid-December, attaining highest concentrations in a deep (40 m) chlorophyll maximum in mid-November. Notable as well is the late-winter phytoplankton bloom in 2013, which reached concentrations, 1–1.5 mg chl *a* m^{-3} , capable of sustaining egg production as early as mid-February and persisted through May. This bloom started earlier than the climatological bloom, although it was smaller in magnitude.

The *C. finmarchicus* climatology at the WBTS (Fig. 4) shows highest abundances of all copepodid stages in May and June, during the spring bloom and post-bloom period. During the summer months, the population accumulates as the dormant stage CV, which persists through the autumn until awakening in winter. The rate of accumulation of stage CV between May and July appears variable among years (Fig. 5) and high CV abundance was not consistently observed each year until mid-July. The average abundance of stage CV in 2012 between 15 July and 1 December (3.7×10^4 ind. m^{-2} ; $n = 7$ station visits) is not significantly different, either by Student's *t* test ($P = 0.08$) or non-parametric rank-sum test ($P = 0.08$) from the historical average CV abundance in 2005–2011 (5.2×10^4 ind. m^{-2} ; $n = 12$ station visits).

Notable is the increase in abundance of stage CI–IV in April 2013, to 9.6×10^4 ind. m^{-2} , fully 6 weeks earlier

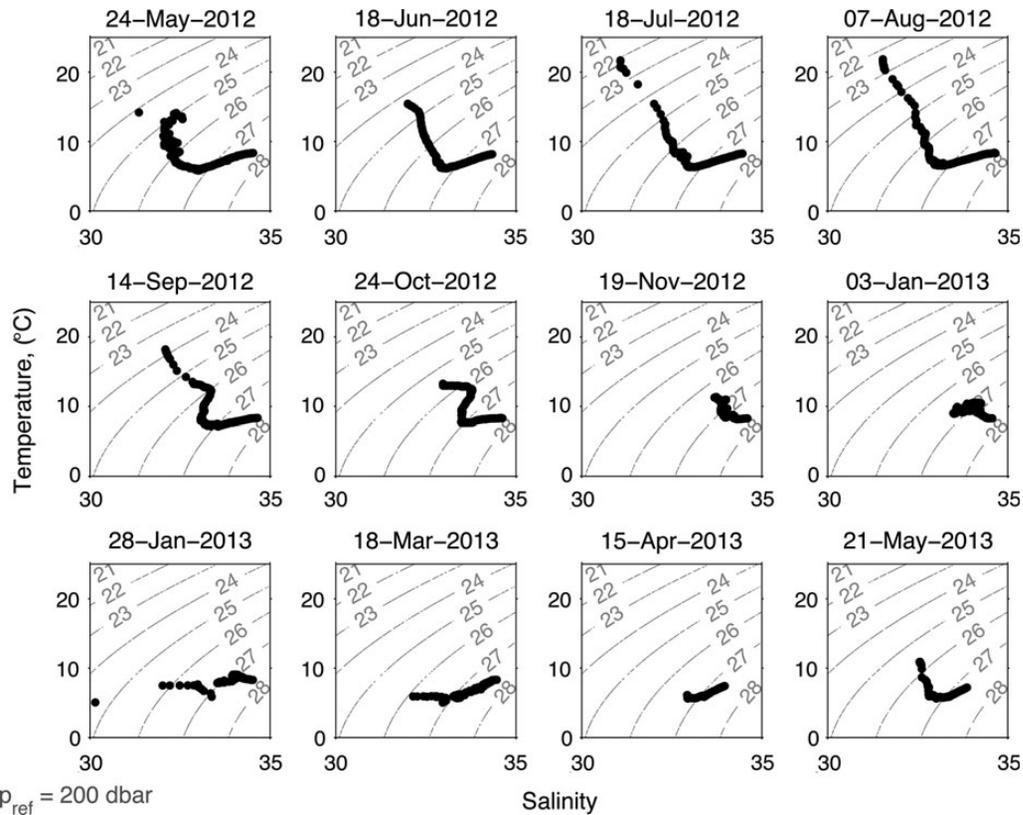


Fig. 3. Representative monthly T-S plots at WBTS sampled between May 2012 and May 2013.

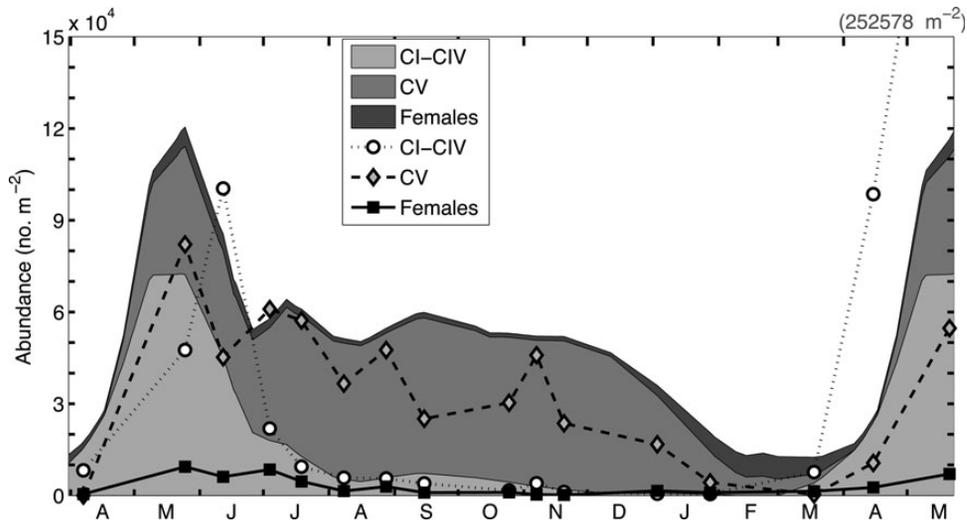


Fig. 4. Abundance (number $\times 10^4 \text{ m}^{-2}$) of *C. finmarchicus* copepodid stages at WBTS. Shaded pattern shows a 2005–2013 climatology. Symbols and associated lines show 2012–2013 data (open circles: CI-CIV abundance; filled diamonds: CV abundance; filled squares: adult female abundance). Note that the database for the climatology is limited, particularly in the autumn.

than the climatological average (Fig. 4). In May 2013, stage CI-IV abundance was at the highest level ($25.3 \times 10^4 \text{ ind. m}^{-2}$) ever observed in the time series. This precocious spring development is consistent with the timing of the late winter bloom in 2013.

The abundance of *C. finmarchicus* sampled in the vicinity of the WBTS at Sta. 105 was $3.5 \times 10^4 \text{ m}^{-2}$ during the *Cape Hatteras* cruise in late September/early October 2012 (Fig. 6). The mean stage CV abundance across Wilkinson Basin (Fig. 6: Stations 105–116 and 311) was

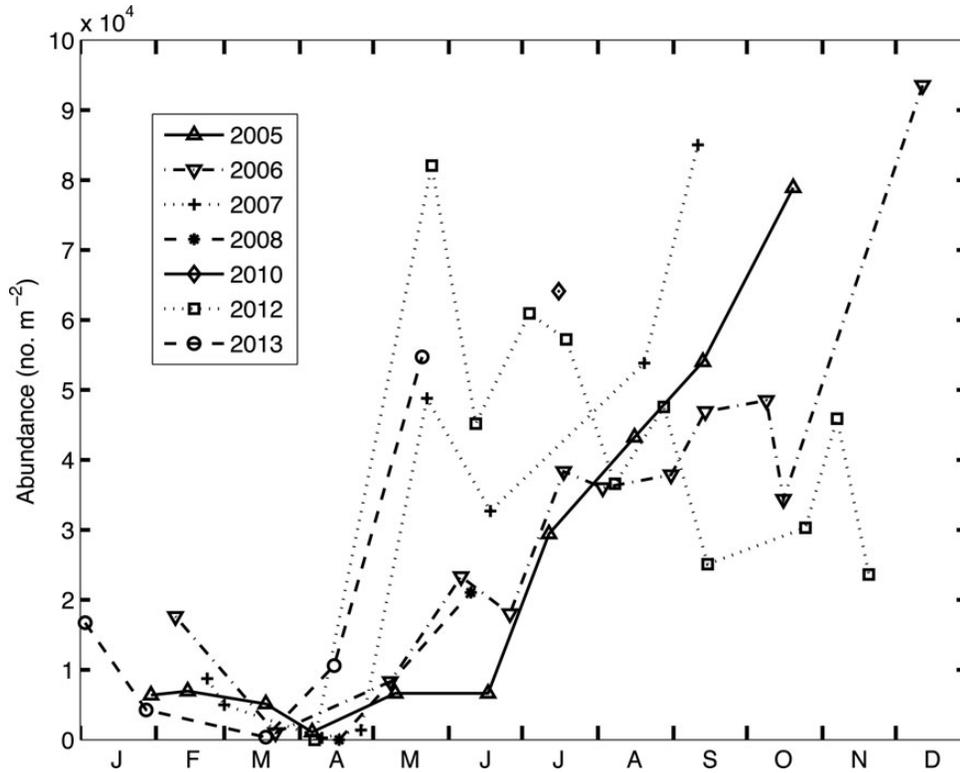


Fig. 5. *Calanus finmarchicus* CV abundance (number $\times 10^4 \text{ m}^{-2}$) measured at WBTS between 2005 and 2013, showing all sampling dates in each year of collection.

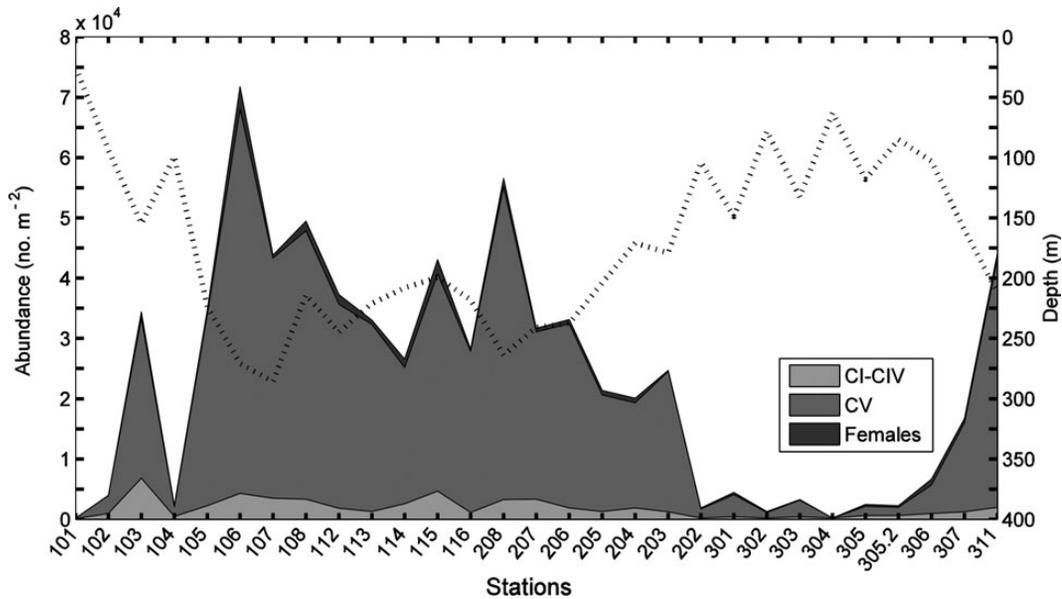


Fig. 6. *Calanus finmarchicus* copepodid stage abundance (number $\times 10^4 \text{ m}^{-2}$) in Wilkinson Basin (Sta. 105–116) and at all stations sampled during the September–October, 2012 survey. Station locations shown in Figure 1. Broken line shows bottom depth (m) at each station.

$3.6 \times 10^4 \text{ ind. m}^{-2}$ (95% CI: 0.63; $n = 11$). These observations indicate that *C. finmarchicus* abundances from samples at the WBTS are representative of the species

abundance across Wilkinson Basin. Stage CV abundance levels in Jordan Basin (Fig. 6: Stations 206–208) were similar to Wilkinson Basin. Abundances in the eastern

Maine Coastal Current (Fig. 6: Stations 202–305) were relatively low, which is consistent with the climatological time series observations at the CMTS station.

The average (2008–2012) seasonal abundance of *C. finmarchicus* copepodid stages at the CMTS is shown in Figure 7. The peak abundance of all copepodid stages ($7.8 \times 10^4 \text{ m}^{-2}$) occurs later (mid-June) than in Wilkinson Basin. There is a smaller, secondary abundance peak ($3.7 \times 10^4 \text{ m}^{-2}$), more than half of which are stage CI-CIV, in September. Overwintering stage CV do not accumulate in late summer and autumn because the station is shallower than the usual overwintering depth; either the CV's have moved off to deeper water or they suffered high mortality from predation.

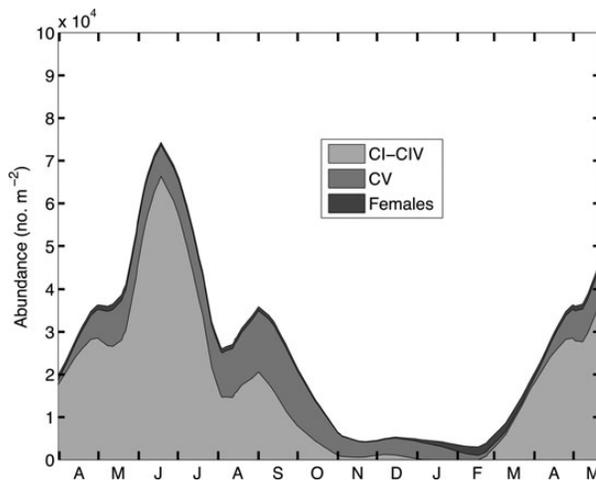


Fig. 7. Averaged (2008–2012) monthly (starting in April) abundance (number $\times 10^4 \text{ m}^{-2}$) of *C. finmarchicus* copepodid stages at CMTS.

Observations of *C. finmarchicus* molting (Table I) and egg production rates (Table II) in Wilkinson Basin were conducted in late September/early October 2012. The majority of the population comprised lipid-filled Stage CV, and no Stage CV were observed to molt into females, consistent with dormancy. Estimates of Stage CIV molting rates ($11\% \text{ day}^{-1}$) indicated that they were actively molting into Stage CV, presumably to enter dormancy. There were few females relative to stage CV, and egg production rates were low ($3 \text{ eggs female}^{-1} \text{ day}^{-1}$). There were also very few early copepodid stages, indicating the absence of reproduction in late summer/early autumn. The low egg production rates reflected low chlorophyll *a* concentrations in Wilkinson Basin in late September 2012. Estimates of integrated (0–50 m) chlorophyll *a* concentrations were $30\text{--}70 \text{ mg m}^{-2}$ (based on bottle samples) and $30\text{--}50 \text{ mg m}^{-2}$ (based on the *in situ* fluorometer), about half of which passed through a $5\text{-}\mu\text{m}$ Nucleopore filter.

DISCUSSION

Our observations in autumn 2012 through spring 2013 show that the abundance of *C. finmarchicus* in the western GoM was sustained in 2012 despite record high temperatures in surface and deep waters. The mean abundance levels of stage CV in Wilkinson Basin between mid-July and December 2012 were high and not significantly different from the historical average. The historical average abundance in autumn and winter is based on a small number of samples over a period of only 7 years (Fig. 5), highlighting a regional need for sustaining WBTS as a

Table I: Observation of molting rates of *C. finmarchicus* stage CIV and CV

Station	Date	Start time	Duration (h)	Stage	Number of individuals	Number molting	Molting rate (% d ⁻¹)
102	9/27.2012	18:00	72	CIV	2	1	
103	9/27.2012	21:00	72	CIV	7	2	
Combined				CIV	9	3	11
102	9/27.2012	18:00	72	CV	40	0	
103	9/27.2012	21:00	72	CV	35	0	
Combined				CV	75	0	0

Animals incubated individually in petri dishes in a refrigerator (6–8°C).

Table II: Observations of egg production rates of *C. finmarchicus*

Station	Date	Start time	Duration (h)	Number of females	Number spawning	Mean clutch number	EPR Eggs fem ⁻¹ d ⁻¹
103	9/27.2012	21:30	24	4	1	29	7
105	9/26.2012	18:00	24	32	3	21	2
112	9/28.2012	17:30	24	19	3	13	2
116	9/29.2012	10:00	24	28	4	31	4
Combined				83	11	24	3

Adult females incubated individually in petri dishes in a refrigerator (6–8°C).

long time series fixed station in the western GoM. Nevertheless, the historical average is very similar to abundances observed earlier by Greene *et al.* (Greene *et al.*, 2003) in Wilkinson Basin in years before and after an unusual minimum observed in 1998 (see Discussion). In late winter in 2012, Stage CV abundances dropped to relatively low levels, perhaps due to a combination of predation and advective losses (Johnson *et al.*, 2006), without a corresponding increase in female abundance. Nevertheless, there were sufficient females to take advantage of the unusual, prolonged late-winter primary production to produce a massively abundant cohort 6 weeks earlier than normal. *Calanus finmarchicus* females have prolific reproductive potential, up to 60–80 eggs female⁻¹ day⁻¹, and the integrated chl *a* standing stocks in late February and March were close to the critical concentration needed to sustain near maximum egg production rates (Runge *et al.*, 2006). The reason for the absence of an increase in female abundance corresponding to the decline of stage CV, which were presumably molting into adult stages is not known. One possibility is that newly molted females resided in the surface layer to feed (Marshall and Orr, 1972) and were subject to increased mortality by planktivorous fish.

We did not find evidence for early exit from dormancy as predicted by a 1-D life history model (Maps *et al.*, 2012) developed for *C. finmarchicus* populations in the Gulf of St. Lawrence and the GoM. The model explicitly includes a mechanism to account for dormancy, based on accumulation of storage lipids in late copepodite stages to a threshold value signaling dormancy entry and a temperature-dependent metabolic depletion rate controlling dormancy duration and timing of exit. Because of the relatively warm overwintering temperatures in the GoM, the model predicted rapid lipid depletion and consequently a dormancy timing on the order of 3 months, which would force stage CV that developed during the spring phytoplankton bloom and entered dormancy in late spring/early summer to exit dormancy in late summer/early autumn. While the life history model successfully simulated observations of the life cycle, abundance and body weight of *C. finmarchicus* at the Anticosti Gyre station in the northwestern Gulf of St. Lawrence, where overwintering temperatures allow lipid stores to last 7 months or more, our results are not consistent with the model prediction of emergence from diapause and production of an autumn cohort at the WBTS station in Wilkinson Basin. During the research cruise conducted in early autumn 2012 we observed a stage CV population in Wilkinson Basin that was lipid-rich, not lipid-depleted, deep dwelling, behaviorally sluggish, and not molting, all signs of a population in deep diapause. These observations suggest that the CV population in Wilkinson Basin comprised individuals entering diapause later in summer,

rather than individuals entering diapause earlier in the season. Egg production rates were low among the rare females, reflecting the very low chlorophyll *a* concentrations that clearly were not sufficient to sustain high egg production, either directly as food or indirectly by supporting microzooplankton prey, during the sampling period. We would expect egg production to have increased later during the intense, November bloom (Fig. 2), however, and this production may have contributed individuals to the early cohort in 2013.

The success of the 1-D life history model in the north-west Gulf of St. Lawrence, where advective influences are constrained, but its failure to predict *C. finmarchicus* demography in Wilkinson Basin in autumn and winter, leads us to consider scenarios for advective sources to maintain overwintering abundance of *C. finmarchicus* in the western GoM. Using Lagrangian tracking of individuals in the Finite Volume Coastal Ocean Model, Johnson *et al.* (Johnson *et al.*, 2006) investigated transport and retention of dormant stage CV from sources within and external to the GoM. Wilkinson Basin, where self-retention was high, received 45–50% of passively drifting individuals residing at 150 m or 100 m depth originating from Jordan Basin, 5–25% of individuals originating from the Scotian Shelf and <5% of individuals originating from the external, upstream slope waters entering the GoM from the Northeast Channel. Since abundances of stage CV were low in 2012 in the Scotian Shelf waters supplying not only Wilkinson Basin but also Jordan Basin (Johnson *et al.*, 2013), these deep upstream sources of overwintering stage CV do not seem to be sufficient to account for the sustained overwintering abundance in Wilkinson Basin.

We put forward here an alternative source of stage CV to Wilkinson Basin that involves the Maine Coastal Current as the primary vector supplying copepodid stages to the western GoM. This concept has roots in earlier work by Bigelow (Bigelow, 1924), Fish (Fish, 1936) and Durbin *et al.* (Durbin *et al.*, 1995). Early life stages of *Calanus* produced in early summer in the Bay of Fundy and perhaps Jordan Basin are entrained in the Maine Coastal Current and develop to late copepodid stages as they drift southwestward (Fig. 1) along a broad path centered on the 100 m isobath (Churchill *et al.*, 2005). Supplied by nutrient-rich waters from the eastern GoM, the Maine Coastal Current supports high primary production (Tian *et al.*, 2014) sustaining *C. finmarchicus* growth throughout the summer months. The mean 20-m temperature during summer (July–Aug) at NERACOOS Buoy E, located at the landward edge of the Maine Coastal Current near the Maine Coastal Time Series Station, is 9.7°C (<http://www.neracoos.org/datatools/climatologies>). Development times from egg to mid-stage

CV at MCC summer temperatures are therefore on the order of 3–6 weeks (Campbell *et al.*, 2001). Given current velocities of $0.15\text{--}0.3\text{ m s}^{-1}$ in the eastern MCC and $0.05\text{--}0.15\text{ m s}^{-1}$ in the western Maine Coastal Current (Pettigrew *et al.*, 2005), eggs produced by females in the Bay of Fundy or the eastern GoM in early summer would arrive at the landward edge of Wilkinson Basin in late summer. We hypothesize that individuals arriving as stage CV in the western GoM in late summer are prepared to enter diapause and therefore tend to reside deeper in the water column (e.g. Plourde *et al.*, 2001). On the shallow (<120 m) nearshore shelf, these diapausing stage CV are advected by cross-shelf bottom currents into Wilkinson Basin, where they accumulate in deep water layers centered between 150 and 200 m. If this is the case, variability in along and cross-shelf transport of late stage *C. finmarchicus* in the Maine Coastal Current may be source of variability in supply to Wilkinson Basin.

The proposed mechanism of internal GoM supply to Wilkinson Basin therefore involves a combination of transport (of early life stages from the nutrient-rich eastern GoM) and local production (growth of copepodite stages in the Maine Coastal Current). The supply vector requires the presence of females and egg production in late spring and early summer in the eastern GoM. As demonstrated by observations of high cohort production in spring from a low initial abundance of females in late winter (Durbin *et al.*, 2003; data from this study: Fig. 4), not many females are needed to input large numbers of eggs into the water column. Even in 2012, a year of relatively low abundance of *C. finmarchicus* in the Bay of Fundy (Johnson *et al.*, 2013), we estimate that sufficient females were available to supply abundant early life stages to the Maine Coastal Current. The source of adults in the eastern GoM is the Nova Scotia Current and, ultimately, the Gulf of St. Lawrence. Sustained abundance in the western GoM will also depend on the timing of primary production supplying sufficient food ($>1\text{ mg chl } a\text{ m}^{-3}$ as a useful proxy) for egg production in Wilkinson Basin in late winter/early spring and for growth of copepodites in the Maine Coastal Current during summer. Food availability for females in Wilkinson Basin and copepodids in the Maine Coastal Current may be a source of variability in the resiliency response of *C. finmarchicus* in the western GoM, since the timing, duration and magnitude of primary production is also under climate forcing.

The emphasis on control from supply routes and production within the GoM contrasts with a mechanism of external supply in which slope-water intrusions and/or upstream transport processes are the primary drivers of *C. finmarchicus* abundance. Greene *et al.* (Greene *et al.*, 2003, 2004) hypothesized that the minimum and

maximum modes of a coupled upper-layer slope water system in the northwest Atlantic south of Newfoundland are related to the negative and positive states of the North Atlantic Oscillation (NAO); during negative NAO states the deep GoM basins are invaded by fresher and cooler Labrador Subarctic Slope Water (LSSW) associated with much lower abundances of *C. finmarchicus*. Under this scenario, the extremely low presence of *C. finmarchicus* in the deep basins in 1998, when abundances of overwintering stages were an order of magnitude lower than adjacent years, is related to the very negative NAO in 1996, which forced the coupled slope water system into a minimum state and consequently LSSW into the deep GoM basins, with a 2 year lag to take into account transport from eastern Canada. Interestingly, the station-based winter NAO index in 2010 was -4.64 , even more intense than the previous very negative (-3.78) 1996 NAO winter index (<http://www.cgd.ucar.edu/cas/jhurrell/indices.html>). If a 2-year lagged relationship between very negative NAO winter indices and *Calanus* abundance in the GoM was valid, dramatically lower *Calanus* abundances in the GoM basins would have been expected in 2012. On the other hand, hydrographic evidence from the Scotian Shelf indicates that the LSSW did not extend down the Scotian Shelf into the GoM in 2012, the way it did in 1998 (Greene *et al.*, 2013; Hebert *et al.*, 2013). Thus, whether LSSW in the GoM is associated with low *C. finmarchicus* abundance cannot be evaluated. The difference in circumstances between 1996–1998 and 2010–2012 may reflect increased anthropogenic climate forcing in the Arctic and associated teleconnections linking atmosphere–ocean interactions in the Arctic Ocean with the northwest Atlantic shelf (Greene *et al.*, 2013).

Under our alternative hypothesis, the very low abundance of overwintering *C. finmarchicus* observed in 1998 in Wilkinson Basin may well have been the result of an exceptional disconnect in that year between the eastern and western branches of the Maine Coastal Current. The degree of connectivity between the eastern and western branches is variable, depending on the extent to which the eastern branch deflects offshore along the mid-Maine coast (Pettigrew *et al.*, 2005; Fig. 1). Observations of current flow conditions in the summer of 1998 indicate that the “gate” between the two branches was closed (Pettigrew *et al.*, 2005) suggesting that the primary supply of *Calanus* to the western GoM was shut off. In other years, the “gate” is more or less open; an analysis of satellite SST for the coastal GoM did not show any evidence of a disconnect in 2012 (D. Vandemark, unpublished data). Similarly, abundance of lipid-rich *C. finmarchicus* may be low in the Bay of Fundy and Jordan Basin and yet normal in Wilkinson Basin, due to the capacity for production and growth via the nutrient-rich Maine Coastal Current.

If the alternative mechanism of coastal supply and transport proposed here is borne out, there are implications for predicting the fate of *C. finmarchicus* at the southern edge of its range in the northwest Atlantic. The conventional method for forecasting species distributions under changing climate scenarios is the bioclimate envelope approach, essentially quantifying a species' realized niche in present day, and mapping it onto future conditions (e.g. Reygondeau and Beaugrand, 2011). In addition to being difficult to validate, application of this method in the ocean does not account for the role of advective transport. The rapid warming in the GoM over the past decade has provided a window into how ecological changes might play out in a warmer climate. The absence of a decline in *C. finmarchicus* abundance, despite habitat conditions outside its normal bioclimate envelope, suggests that our climate forecasting strategy for planktonic species should account for advection and transport as well as local production and life history. Predicting the decline or disappearance of *C. finmarchicus* from the GoM based on surface temperature or external, basin scale drivers like the NAO will need to involve models that address the roles of local production and advection within the GoM.

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