

Summer distribution of the planktonic copepod, *Calanus finmarchicus*, along the coast of the Gulf of Maine.

Jeffrey A. Runge
Rebecca J. Jones
Nicholas R. Record
Andrew J. Pershing

School of Marine Sciences, University of Maine, and Gulf of Maine Research Institute
350 Commercial Street
Portland, Maine 04101

Abstract

The planktonic copepod, *Calanus finmarchicus*, typically dominates the zooplankton biomass in deep waters of the Gulf of Maine. The sources and processes controlling the population dynamics of *C. finmarchicus* in the Gulf of Maine, particularly on the coastal shelves and ledges along the Maine coast, where lipid-rich copepodid stages of *C. finmarchicus* serve as a primary source of nutrition for planktivorous fish such as herring and mackerel, are not well understood. Knowledge of coastal *C. finmarchicus* abundance and distribution patterns is particularly important for evaluation of risks associated with right whale foraging in the vicinity of high nearshore densities of fixed fishing gear. Here we document the seasonal patterns and summer distribution of *C. finmarchicus* copepodid stage abundance in Maine coastal waters of the Gulf of Maine, based on three plankton surveys conducted in July or August in three successive years and concomitant time series of plankton collections at two mid-coast stations. *C. finmarchicus* copepodid stages CV-CVI, the most energy-rich prey for planktivores, were most abundant in spring (April-May), and again from mid-July through September at the coastal time series station. Abundances of these stages in mid summer (Jul-Aug) were significantly higher, by a factor of 2-47 for stage CV-CVI at offshore coastal stations > 100m depth than shallower nearshore coastal stages. Very few older stage *C. finmarchicus* were observed in the Damariscotta Estuary at any time of year. Our observations are most consistent with the hypothesis that local coastal production originating upstream from Jordan Basin or the Eastern Maine Coastal Current is the first-order source of *C. finmarchicus* in the coastal ocean. Abundance of later copepodid stages that develop from this coastal production is diminished in summer by planktivorous predation and possibly by offshore, cross-shelf drift of stage CV entering dormancy. Estimated concentrations of late, lipid-rich copepodid stages based on profiles with a Laser Optical Plankton counter were not sufficiently high to attract right whale foraging behavior inshore of the 100 m isobath; dense layers generally occurred at stations deeper than 150 m.

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 2006; Kane 2009). Wilkinson Bay in the western Gulf of Maine harbors overwintering stage CV *C. finmarchicus* at abundances ($40\text{-}60 \times 10^4 \text{ m}^{-2}$) that are equal to or higher than levels observed in more northern coastal seas (Maps et al. 2012; Melle et al. in prep.). In spring and summer in coastal regions of the GoM, *C. finmarchicus* can dominate 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 in press).

Research on the ecological role of *C. finmarchicus* in the region indicates that the abundance of its lipid-rich late copepodid stages have key functional significance (Johnson et al. 2011), perhaps more so than the availability of its early life stages as a biological factor influencing recruitment, as has been emphasized other regions of the North Atlantic (e.g. Runge et al. 1999; Beaugrand et al. 2003). The lipid-rich stage CV are a primary prey for planktivorous fish, such as herring, mackerel and sand lance (e.g. Darbyson et al. 2003; Jones et al. in prep.) that are fundamental trophic links in the Gulf of Maine coastal ecosystem. For example, changes in condition of bluefin tuna captured in the Gulf of Maine are correlated with the condition of Atlantic herring and the abundance of stage CV from GoM Continuous Plankton Recorder data (W. Golet, A. Pershing et al., Univ. Maine, in prep.) Since there is no apparent functional redundancy for *C. finmarchicus* in the Gulf of Maine system, significant shifts in abundance of GoM *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).

C. finmarchicus is also the primary prey of the endangered northern right whale (*Eubalaena glacialis*), whose seasonal foraging pattern in the Gulf of Maine appears to exploit the *C. finmarchicus* phenology (Kenney et al. 1995). The Gulf of Maine is the primary foraging ground for right whales. During the winter, when *C. finmarchicus* abundance is low, right whales are generally dispersed, with the only major feeding area being Cape Cod Bay. During this season, whales forage on a mix of prey, including smaller copepods such as *Pseudocalanus* spp. (Mayo & Marx 1990, Pendleton et al. 2009). In the late spring and early summer, right whales migrate offshore to exploit the peak concentrations of *C. finmarchicus* in the Great South Channel (Kenney et al. 1995). As larger portions of the *C. finmarchicus* begin to enter diapause in summer, right whales migrate to deeper habitats in the eastern Gulf of Maine and Bay of Fundy (Murison & Gaskin 1989). Use of these feeding habitats by right whales is significantly correlated with high mean abundance of copepods (Pendleton et al. 2009; Pershing et al. 2009, Patrician and Kenney 2010). Direct observations of feeding are always associated with high density patches or layers of copepods (Wishner et al. 1995, Baumgartner et al. 2003), and Mayo and Marx (1990) suggest that densities must exceed $1,000 \text{ m}^{-3}$ to elicit feeding.

The relative roles of local production and advective transport, both within and from external sources, in determining abundance and distribution of *C. finmarchicus* developmental stages in the Gulf of Maine are not well understood. Local production is clearly substantial in the Gulf of Maine (Durbin et al. 2003; Runge et al. 2006); however a 1-D life history model that simulates well the population dynamics of *C. finmarchicus* in an adjacent coastal sea does not

reproduce the observed demographic structure in Wilkinson Basin (Appendix 1, figure 1), suggesting that advective transport is an important source of overwintering *C. finmarchicus* within the Gulf of Maine's deep basins (Maps et al. 2012). The production of *C. finmarchicus* on the nearshore shelf and shelf edge along the coast of Maine, and the contribution of transport of the coastal production to Wilkinson Basin, are not well known. The coastal shelf and ledges have not been sampled very much, and the coastal abundance and distribution of *C. finmarchicus* is not well described. Knowledge of coastal *C. finmarchicus* abundance and distribution patterns is particularly important for evaluation of risks associated with right whale foraging in the vicinity of high nearshore densities of fixed fishing gear (Singer and Ludwig 2005).

Here, we investigate seasonal patterns and summer distribution of *C. finmarchicus* copepodid stage abundance in coastal waters of the Gulf of Maine. Our study is based on three plankton surveys conducted in July or August in three successive years and concomitant time series of plankton collections at two mid-coast stations. We address basic questions about the seasonal availability of *C. finmarchicus* in coastal waters, including its alongshore and cross shore distribution in summer. We focus on midsummer, when *C. finmarchicus* are known to be increasing in abundance of lipid-rich late copepodid stages and right whales commence migrations to feeding grounds in the eastern Gulf of Maine and Bay of Fundy. We evaluate the suitability of coastal nearshore waters as right whale habitat with respect to food availability and interpret the results in light of present understanding of *C. finmarchicus* population dynamics in coastal Gulf of Maine waters.

Methods

Time series stations

Sampling for seasonal annual cycles of *C. finmarchicus* abundance in Maine coastal waters was conducted at a station in the Damariscotta Estuary (lat. 43°54'.08, lon. 69° 34'.70; 32 m depth) and at a station located on the mid-Maine coastal shelf approx. 5 NM from the mouth of the Damariscotta Estuary (lat. 43°44'.69, lon. 69° 30'.70; 105 m depth) (Fig. 1). Each station was sampled at approximately semi-monthly intervals (more frequently in spring and summer) between April, 2008 and December, 2010, using the 40' University of Maine research vessel, R/V *Ira C*, which is based at the University of Maine's Darling Marine Center.

The sampling methods were based on protocols established for the Canadian Atlantic Zonal Monitoring Program (Mitchell et al. 2002). Zooplankton samples were collected at all stations with a 0.75 m diameter, 200- μ m mesh ring net, in the mouth of which a General Oceanics flowmeter was suspended. The ring net was deployed in duplicate to within 5 meters off the bottom and then towed vertically to the surface at a rate of 40 m/min. All samples were preserved in a 4% seawater-buffered formaldehyde solution. In the laboratory, all zooplankton samples were split in half using a Folsom Plankton Splitter, and half of the sample was archived for identification and enumeration of zooplankton. To estimate *C. finmarchicus*, one split was diluted and 5-10 mL subsamples were taken with a Stempel pipette to obtain a target number of 75-200 *C. finmarchicus* copepodid stages. All *C. finmarchicus* were identified to developmental stage. Other copepod species were enumerated from a single 5-10 mL subsample. The counts were normalized to abundance (number m⁻²), taking into account the subsample dilution and split factors and volume sampled by the net from the flow meter reading.

A SeaBird 19Plus with a WetLabs fluorometer was deployed at each visit to the fixed stations. Typically Niskin water bottle samples were also collected at several depths. Results from these measurements will be reported elsewhere.

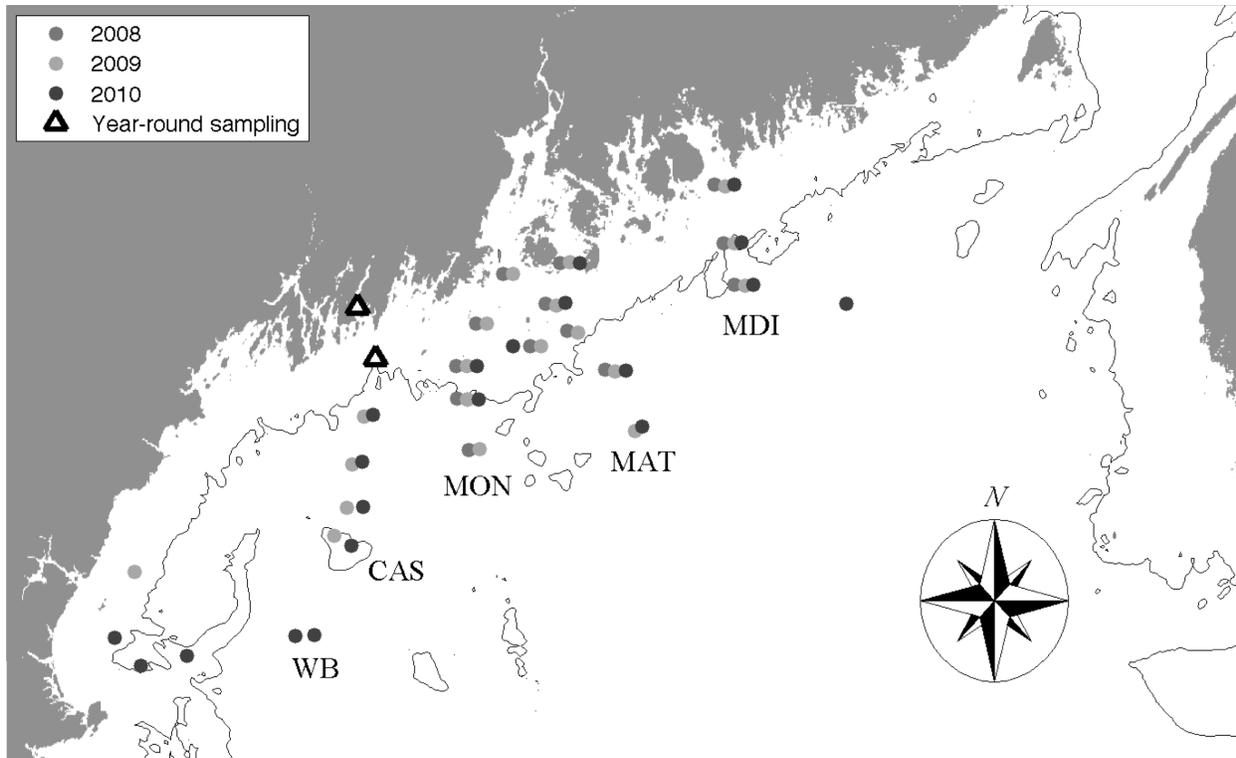


Figure 1. Sampling station locations and transect names. WB: Wilkinson Basin; CAS: Casco line; MON: Monhegan line; MAT: Matinicus line; MDI: Mount Desert Island line. Circles: stations sampled in Jul/Aug 2008-2010. Triangles: time series station in the Damariscotta Estuary and on the mid-coastal shelf.

Coastal surveys

The coastal waters in the northern Gulf of Maine were surveyed in mid-summer (8 July-14 August) in three consecutive years (2008-2010; Fig. 1 and Table 1). The western coast of the Gulf of Maine was divided into 5 transects oriented from nearshore to offshore of the coastal shelf (Fig. 1). In 2010, one transect extending from New Hampshire to Wilkinson Basin was added, and two of the other transects were extended (Table 1).

At each station, a SeaBird-19Plus conductivity, temperature and depth (CTD) profiler outfitted with a Biospherical Photosynthetically Available Radiance (PAR) sensor and Wetlabs Fluorometer was deployed from surface to 5 meters off bottom. A double ring, 0.75 m² diameter, 200 µm mesh plankton net fitted with a General Oceanics flow meter was towed vertically from 5 meters off bottom to the surface at a rate of 40 meters min⁻¹. A Laser Optical Plankton Counter (LOPC) was deployed in profiling mode and towed vertically from 1-2 meters off the bottom to the surface.

If the concentrations of *C. finmarchicus* were above a minimum threshold of approximately 100 liter⁻¹ (estimated by eye), an Open Seas Tucker Trawl configured with three

300 μm plankton nets was deployed to collect depth-stratified samples for use in verifying the LOPC data. The depth strata were 0-15 m, 16-35 m and 40 m to bottom.

Zooplankton abundance was estimated by splitting one ring net sample in half with a Folsom plankton splitter, and then diluting the sample to obtain approximately 200 animals with a 5 mL Stempel pipette aliquot. Additional aliquots were taken as needed to count a minimum of 200 *C. finmarchicus* when they constituted more than 10% of the total zooplankton abundance in the initial aliquot. All copepods were identified to species and sex where possible and all *C. finmarchicus* were identified to stage. All other zooplankton were identified to the lowest possible taxonomic grouping.

Laser optical profiles

A laser optical plankton counter (LOPC) was deployed at each station for a vertical profile. The instrumentation included a CTD sensor, and was lowered and raised at 40 m min^{-1} . Analysis used the upcast data, filtered to include particles with properties associated with large copepods. Particles with a computed equivalent spherical diameter (d) in the range $1000 \mu\text{m} < d < 2500 \mu\text{m}$, and with attenuation proportion (α) in the range $0.25 < \alpha < 0.6$, were included. Attenuation proportion of a particle is similar to the attenuation index (Checkley 2008), but takes into account the relative durations of photodiode occlusion. The range of d was based on the equivalent spherical size of copepodid *C. finmarchicus*, and the ranges of α was based on the *in situ* laser optical properties of a population of diapausing copepods observed in Wilkinson Basin. The total number of particles in each 5 m depth bin from the bottom to the surface of the cast was integrated, giving a profile $P(z)$, the number of particles at each depth z , from which the proportion of particles at each depth was computed,

$$\rho(z) = \frac{P(z)}{\sum P(z)}$$

If \bar{C} is the mean concentration of the full water column copepod count, taken from the ring net data and converted to number m^{-3} , and z_{max} is the depth of the tow, then the concentration of copepods in each depth bin is

$$C(z) = \bar{C} z_{\text{max}} \frac{\rho(z)}{\Delta z}$$

where Δz is the size of the depth bins. This adjusted profile was used to compute the maximum concentration of late-stage *C. finmarchicus* at each station.

This method rests on the assumption that the vertical distribution of *C. finmarchicus* follows the vertical distribution of particles in the 1000-2500 μm range. This assumption is based on the fact that *C. finmarchicus* dominates this size class in the ring net tows, and others have used the LOPC under this assumption (Checkley et al. 2008, Gaardsted et al. 2010). It is possible that there are similarly sized particles not collected by the ring net, such as large detrital particles, but it is unlikely that these particles are abundant enough or deviate enough from the vertical distribution to significantly alter the profile of proportions. To account for this assumption, optical data were not used for a direct abundance estimate; the ring nets provided these numbers. The optical profile is used only to proportion the abundance into depth strata.

Table 1. All transect and station names and locations for surveys completed in 2008-2010.

Transect	Station ID	2008	2009	2010	Depth (m)	LOPC		
						2008	2009	2010
Wilkinson Basin- WB	PI	-	7/8	7/16	79		✓	✓
	PII	-	-	7/16	120	✓		✓
	S	-	-	7/16	51			✓
	WB-7	-	-	7/16	238			✓
	WB-D	-	-	7/22 (N)	233			✓
Casco-CAS	CAS-1	8/14	7/9	7/17	145	✓	✓	✓
	CAS-2	8/14	7/9	7/17	152	✓	✓	✓
	CAS-3	8/14	7/9	7/17	165		✓	✓
	CAS-4	8/14	7/9	7/17	75		✓	✓
Monhegan - MON	MON-1	8/7	7/13	7/18	22	✓	✓	✓
	MON-2	8/7	7/13	7/18	67	✓	✓	✓
	MON-3	8/7	7/13	7/18	96		✓	✓
	MON-4	8/7	7/9 (N)	7/18	182		✓	✓
	MON-5	8/7	7/13	7/18	140	✓	✓	✓
	MON-6	-	-	7/18	115			✓
Matinicus-MAT	MAT-1	8/6	7/10	7/19	48	✓	✓	✓
	MAT-2	8/6	7/10	7/19	96	✓	✓	✓
	MAT-3	8/6	7/10	7/19	70	✓	✓	✓
	MAT-4	8/6 (n)	7/10	7/19	98	✓	✓	✓
	MAT-5	8/6	7/10	7/19	142	✓	✓	✓
	MAT-6	-	7/10	7/19	171		✓	✓
Mount Desert Isl- MDI	MDI-1	8/5	7/11	7/20	47	✓	✓	✓
	MDI-2	8/5	7/11	7/21	106	✓	✓	✓
	MDI-3	8/5	7/11	7/20	202	✓	✓	✓
	JORD	-	-	7/20	202			✓

Results

Observations of *C. finmarchicus* abundance at the time series station DMC-2 (Fig. 2) indicate highest abundances of stage CI-CIII in spring (April – June: mean 21,348 m⁻² over three years). The timing of peak spring abundance of *C. finmarchicus* varied between early April and June from year to year, and the abundance of stage CI-CIII in summer and fall also showed considerable interannual variability. Stage CIV are approximately two times more abundant in spring (mean over three years: 5,037 m⁻²) than in June, then show an extended peak from July - September (mean: 6,752 m⁻²) in some years. Stage CV-CVI are more abundant in summer (mean: 11,146 m⁻²) than in spring (mean: 5,921 m⁻²). Most of the spring stage CV-CVI are females, not the lipid rich stage CV. The highest abundances of stage CV-CVI (mean: 26,488 m⁻²), mostly stage CV, were observed in September.

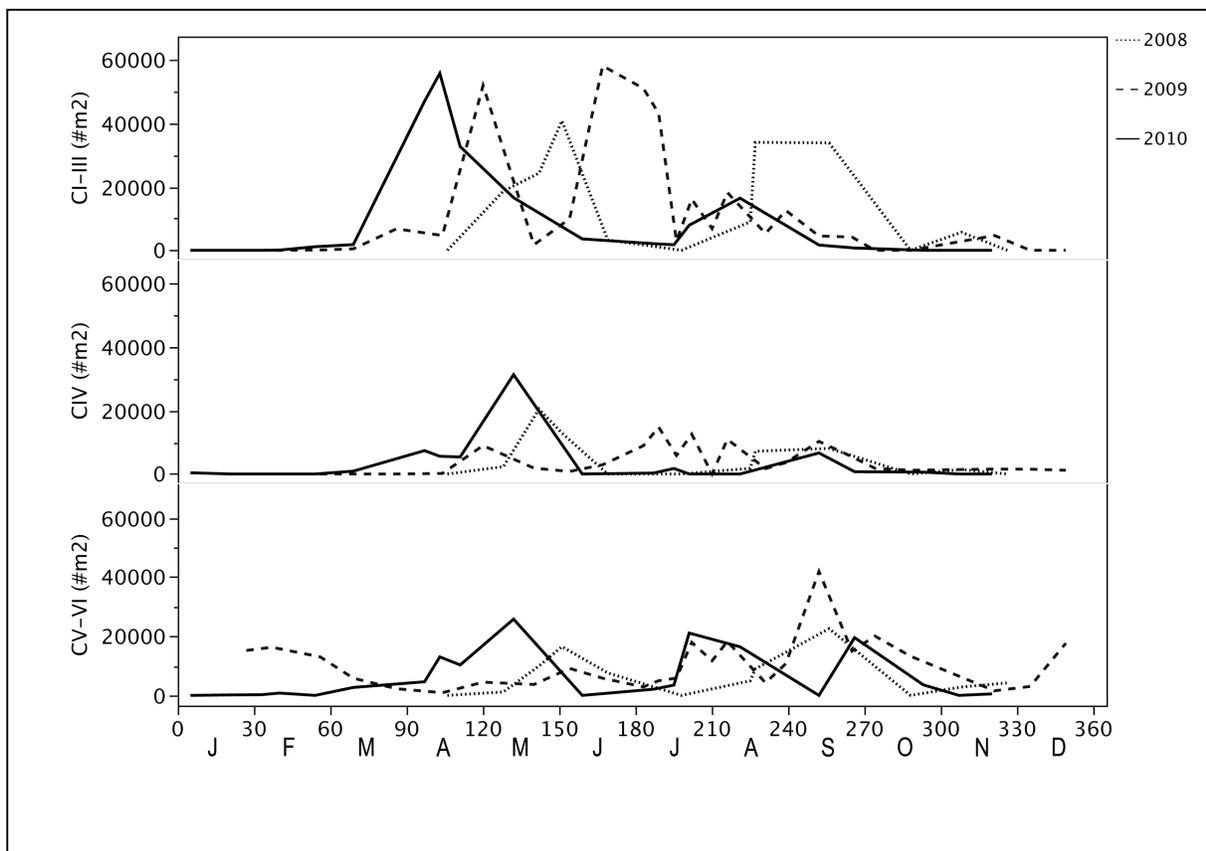


Figure 2. Time series of abundance (number m⁻²) of *C. finmarchicus* copepodid stages at the mid-coastal station (105 m depth), 2008-2010.

C. finmarchicus abundance was very low at all times of year in the Damariscotta Estuary (Table 2). Stage CI-CIII were observed in the estuary in spring, but at approximately <1% of levels measured at the same time at DMC-2 on the coastal shelf. At other times of year, and for stages CIV-CVI at all times of year, abundances in the estuary were negligible.

Our analysis of summer distribution of *C. finmarchicus* is based on 59 samples collected over 3 years between July 8-Aug 14 at stations (including time series station DMC-2) concentrated along the mid-Maine coastal shelf, but also including Wilkinson Basin and the coastal shelf off New Hampshire (Fig. 1). There was no clear alongshore or interannual pattern of abundance (Fig. 3). Observations of stage CI-CIII abundance appear to be higher in 2009 at several stations, but the timing of this survey was in early July, closer to the maximum spring abundances found in the time series at DMC-2. A Kruskal-Wallis One Way ANOVA on Ranks test indicated a marginal ($P=0.04$) significant difference in abundance of stage CIV among years (Table 3), for stations grouped as offshore coastal shelf (>100 m depth).

Analysis of cross shore gradient in *C. finmarchicus* abundance indicates that later stages are much more abundant at the deeper stations (Table 3, Fig. 4). Combining all years, differences in abundance of stages CV-CVI at offshore coastal shelf stations are significantly higher than abundance at nearshore coastal stations (Mann-Whitney Rank Sum test: Table 3), by a factor of 2-47 based on comparison by means or medians, respectively (Table 4). Nearshore-offshore differences in abundance are not significant for stage CIV and for the youngest copepodid stages (Table 3).

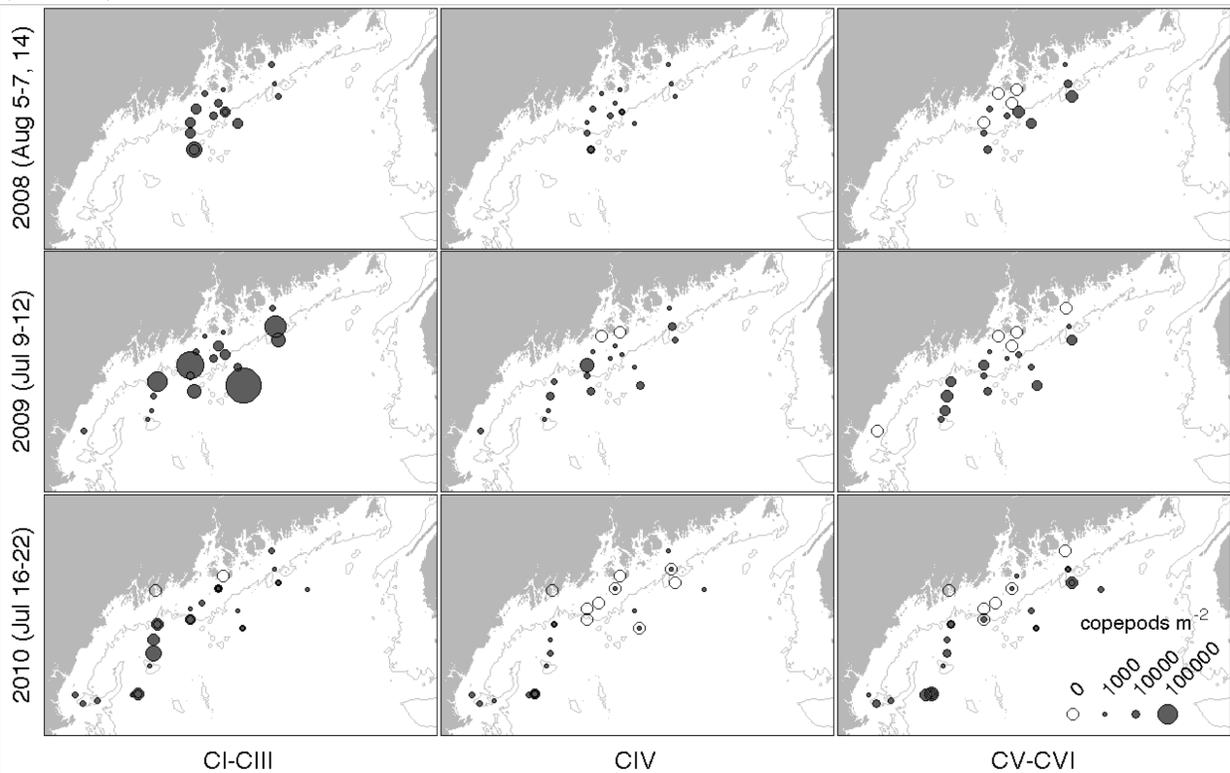


Figure 3. Distribution of abundance (circle area represents number m^{-2} , in logarithmic scale) of *C. finmarchicus* copepodid stages at stations sampled in Jul/Aug 2008-2010. Unfilled circles shows stations at which abundance was zero.

Table 2. Mean abundance (s.e.), median and abundance range of *C. finmarchicus* copepodid stages by season (Winter: Jan., Feb., Mar.; Spring: Apr., May, Jun.; Summer: Jul., Aug., Sep.; Fall: Oct., Nov., Dec.) in the Damariscotta Estuary, 2008-2010. Values represent number m⁻².

	Winter (N= 11)			Spring (N= 15)		
	Mean (SE)	Median	Range	Mean (SE)	Median	Range
CI-III	0 (0)	0	0	1,229 (524)	0	0-7,147
CIV	7 (7)	0	0-77	88 (65)	0	0-920
CV-CVI	170 (87)	0	0-843	0 (0)	0	0

	Summer (N= 23)			Fall (N= 14)		
	Mean (SE)	Median	Range	Mean (SE)	Median	Range
CI-III	1,700 (1386)	0	0-31,883	0 (0)	0	0
CIV	481 (376)	0	0-8,583	0 (0)	0	0
CV-CVI	644 (639)	0	0-14,715	170 (170)	0	0-2,382

Table 3. Non-parametric analysis of differences in abundance among years (2008-2010) in each stage grouping (Krusdal-Wallis One Way ANOVA on Ranks) and between nearshore (<100 m depth) and offshore (>100 m depth) coastal stations (Mann-Whitney Rank Sum test). NS = Not significant.

	Among years: Offshore	Among years: Nearshore	Nearshore- Offshore
CI-III	NS	NS	NS
CIV	P=0.04	NS	NS
CV-VI	NS	NS	P= <0.001

Table 4. Mean abundance (s.e.), median and abundance range of *C. finmarchicus* copepodid stages at nearshore coastal stations (<100 m depth) and offshore coastal stations (>100 m depth) sampled between 8 Jul and 14 Aug, 2008-2011. All values represent number m⁻².

	Nearshore (N= 31)			Offshore (N= 33)		
	Mean	Median	Range	Mean	Median	Range
CI-III	14,228 (6334)	4,835	0-186,973	29,082 (9,302)	12,566	0-296,471
CIV	3,183 (1408)	1,289	0-41,043	5,228 (850)	4,559	0-17,820

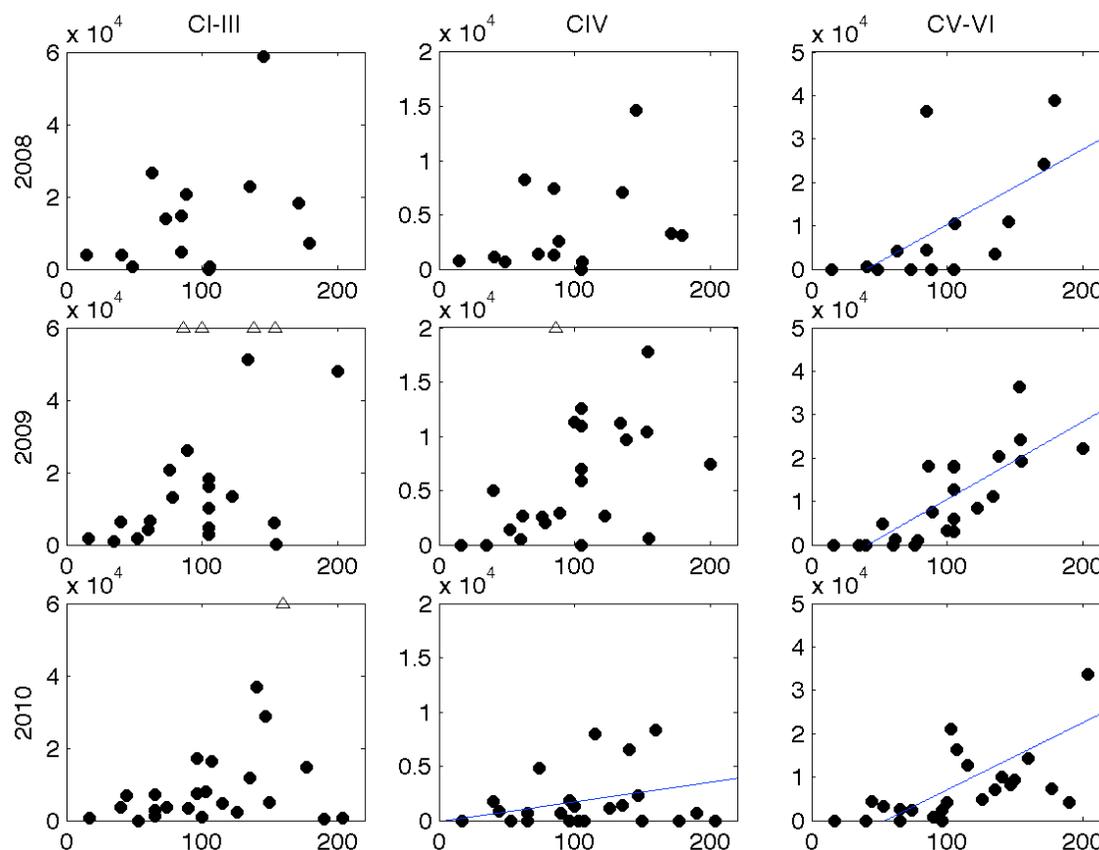


Figure 4. *C. finmarchicus* stage abundance as a function of depth. A linear model was fit relating station depth to abundance for each year-stage combination. If the fit was significant ($p < 0.05$), it is plotted on the corresponding panel. CIV 2010 : $r^2 = 0.15$, CV-VI 2008: $r^2 = 0.37$, 2009: $r^2 = 0.62$, 2010: $r^2 = 0.58$. Triangles indicate points beyond axis limits.

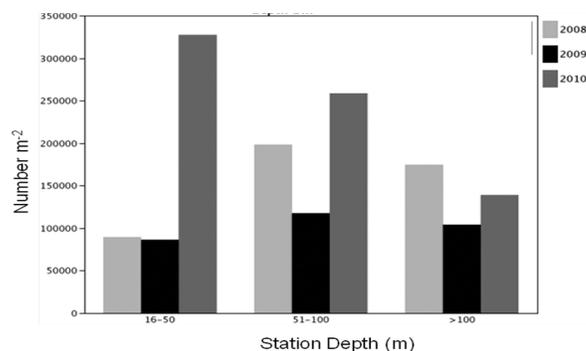


Figure 5. Abundance (number m⁻²) of other dominant copepod taxa in cruise samples, arranged by year (2008-2010) and in bins of station depth where collected. Dominant copepod taxa include species of *Oithona*, *Temora*, *Pseudocalanus*, *Microcalanus* and *Centropages*.

Other copepod species abundant in the 200- μm mesh plankton tows included species of *Oithona*, *Temora*, *Pseudocalanus*, *Microcalanus* and *Centropages*. The combined mean abundance of these species ranged from 80,000 to 320,000 m^{-2} across years and station depth, with no clear pattern of difference in abundance between nearshore and offshore coastal stations (Fig. 5). In 2010, mean abundance of these copepod taxa was two times greater than mean abundance in offshore stations, but this pattern was not observed in Aug 2008 or Jul 2009, when abundances of the other dominant species were similar in the nearshore and offshore coastal stations.

The daytime vertical distribution of late-stage *C. finmarchicus* at stations along the CAS, MAT, and MDI transects (Figs. 6-8) indicate that late stage *C. finmarchicus* are typically distributed throughout the water column, but with peaks in abundance at varying depth layers. The minimum thickness of the depth layers showing maximum concentration is on the order of 30-40m. There appears to be a tendency for *C. finmarchicus* to avoid temperatures $>13\text{-}15^\circ\text{C}$ in the surface 10 m of the water column. In some instances (CAS 3 in 2009; MDI 2 in 2009), *C. finmarchicus* were concentrated near bottom in a layer approx. 40 m. thick. Observations of diel distributions in the deep Wilkinson Basin in 2010 suggest that the majority of late-stage *C. finmarchicus* were residing at depth (mode at 140-180 m) day and night (Fig. 9). Approximately 25% of the late stage *C. finmarchicus* population was present in the surface 30 m (temperature ranging from $8\text{-}14^\circ\text{C}$) day and night. At a few stations, the concentration of late stage *C. finmarchicus* at the depth of maximum concentration (i.e. the densest layer) approached or exceeded the right whale feeding threshold of $1,000\text{ m}^{-3}$ suggested by Mayo & March (1990). All of these stations were at depths greater than 140 m (Fig. 10). There is generally a trend of increasing concentration of the densest layer with increasing station depth ($r^2 = 0.63, p < 0.001$).

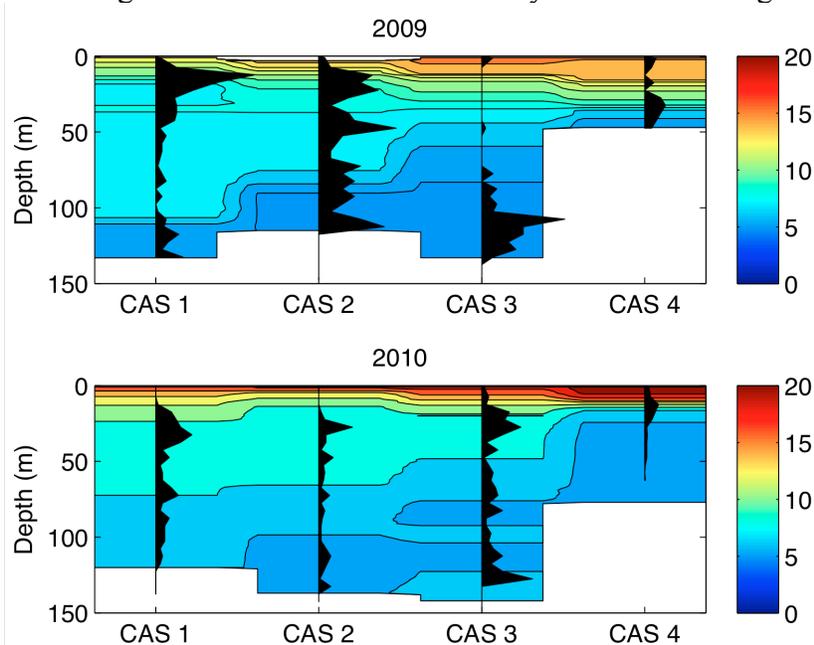


Figure 6. Vertical distribution of estimated late-stage *C. finmarchicus* concentration along the CAS transect, for 2009 (top) and 2010 (bottom). Black shaded area shows the relative abundance (m^{-3}) by depth at each station. Colored contours show temperature ($^\circ\text{C}$).

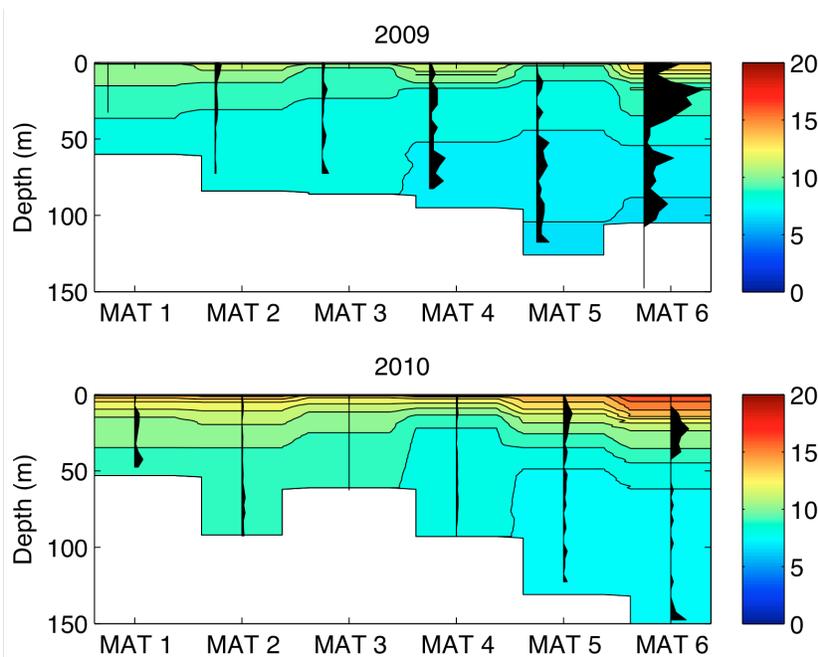


Figure 7 Vertical distribution of estimated late-stage *C. finmarchicus* concentration along the MAT transect, for 2009 (top) and 2010 (bottom). Black shaded area shows the relative abundance (m^{-3}) by depth at each station. Colored contours show temperature ($^{\circ}C$).

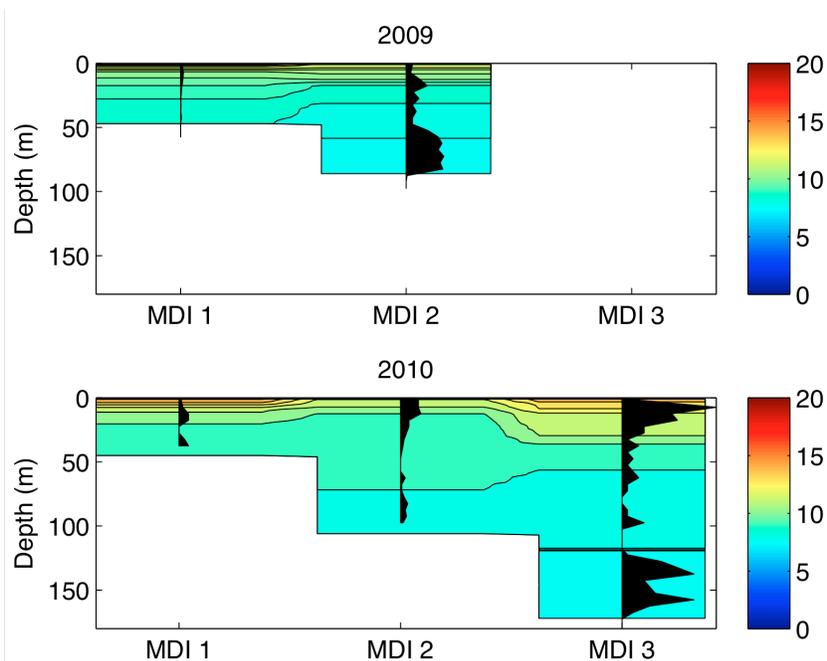


Figure 8 Vertical distribution of estimated late-stage *C. finmarchicus* concentration along the MDI transect, for 2009 (top) and 2010 (bottom). Black shaded area shows the relative abundance (m^{-3}) by depth at each station. Colored contours show temperature ($^{\circ}C$).

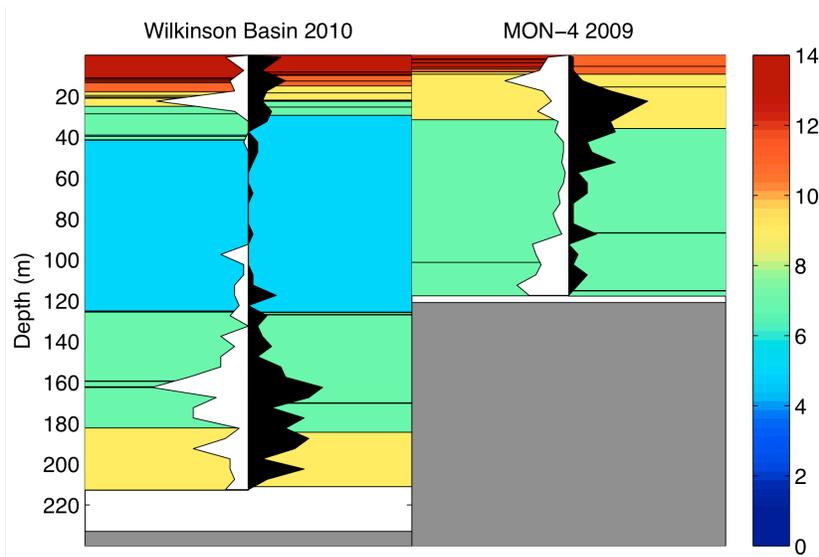


Figure 9 Vertical distribution of estimated late-stage *C. finmarchicus* concentration for daytime tows (white shaded areas) and nighttime tows (black shaded areas). Colored contours show temperature ($^{\circ}\text{C}$).

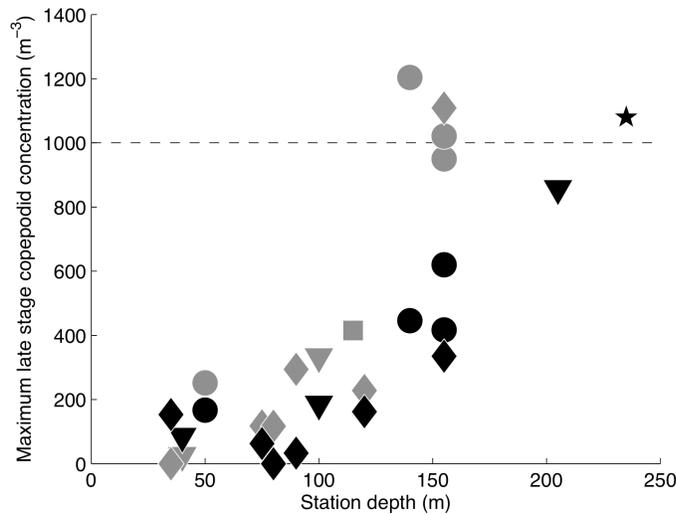


Figure 10 Concentration of late stage *C. finmarchicus* (CIV-adult) at the layer for maximum concentration for each station (triangle = MDI, circle = CAS, diamond = MAT, square = MON, star = WB; grey = 2009, black = 2010). Dashed line indicates the right whale feeding threshold.

Discussion

The results from time series station DMC-2 on Maine's mid-coastal shelf indicate that late stage *C. finmarchicus* abundance is highest in September, with a sharp decrease during October-December. This finding is similar with the abundance pattern observed in the adjacent, deep Wilkinson Basin (Appendix Fig. 1), where *C. finmarchicus* stage CIV-V are abundant after mid-June. The observations of deep, day-night residence of *C. finmarchicus* late stages in Wilkinson Basin (Fig. 9) are consistent with the hypothesis that the Wilkinson Basin population has mostly transitioned to dormancy by early July. The more uniform distribution of late stages in the water column on the coastal shelf (Figs. 6-8), however, suggests a population that is not in diapause. Whether this state is caused by vertical mixing on the more shallow coastal shelf, inhibiting entry into diapause (Durbin et al. 1997), or simply represents actively growing *C. finmarchicus* stage CV drifting downstream in the Maine Coastal Current, is not known.

If the coastal shelf *C. finmarchicus* stage CV are actively growing and are capable at some point of downward descent to deeper water (e.g. CAS-3 in 2009: Fig. 6, or MDI-3 in 2010: Fig. 8) in order to enter dormancy, then a possible mechanism for the observed lower early-fall abundances of stage CV-VI is a gradual offshore drift of deep residing older stages toward deeper water. The physical mechanism supporting this mode of cross-shelf transport of older stages from shallow to deeper water is not clear, however. Alternatively, fewer late stage *C. finmarchicus* in summer may be due to higher mortality due to predation by visual predators, such as herring, mackerel and other planktivorous fish, that are more abundant on the coastal shelf than deeper offshore. Late-stage, lipid-rich *C. finmarchicus* are especially visible on the shallower shelf, where they cannot escape to darker, deep water by diel vertical migration. Results showing strongly significant, lower abundance of stage CV-CVI at nearshore stations (<100 m) than at offshore stations (>100 m), yet marginally significant differences active (not ready for diapauses) stage CIV, and no significant difference for stage CI-CIII distribution are consistent with both hypothetical mechanisms. Likewise, the low abundance of late stage *C. finmarchicus* in the Damariscotta Estuary is likely due to a combination of intense predation on older copepodid stages and flushing before reproduction is possible.

Based on estimates from combined net and LOPC data, the nearshore (<100 m) abundances of *C. finmarchicus* stages CIV and CV-CVI observed in July-August during the three year survey were not sufficiently high enough to attract foraging right whales. There was only one station shallower than 150 m with concentrations of late-stage *C. finmarchicus* > 1,000 m⁻³ in the densest layer (CAS-1, 2009, 145 m). At stations deeper than 150 m, not all profiles contained a dense layer with concentration > 1,000 m⁻³, but concentrations were generally, and statistically significantly higher. It is reasonable to expect, considering the sum prey abundance in the full zooplankton community, that many of these deeper stations are potential foraging sites for right whales.

The dynamics of *C. finmarchicus* in the coastal region of the Gulf of Maine need to be considered in the context of the physical oceanography of the Gulf of Maine. The Gulf of Maine circulation is characterized by cyclonic gyres in the deep interior basins (Jordan Basin and Wilkinson Basin), anti-cyclonic gyres over shallow banks (Georges Bank and Brown Bank), and a southwestward Gulf of Maine Coastal Current [the East Maine Coastal Current (EMCC) and West Maine Coastal Current (WMCC)] (Fig. 1). The EMCC and WMCC normally separate in midcoast, Maine, near Penobscot Bay, with a branch of the EMCC flowing toward the central GoM. In some years, particularly during northeasterly winds, the EMCC continues to flow along the coast to form a straight coastal, flow-through system (e.g. Pettigrew et al. 2005). The

WMCC is not, in a strict sense, a coastal flow. In all observations it is seen some distance from the coast, often centered near the 100-m isobath (Churchill et al. 2005). Wilkinson Basin functions like an “end-point” region where the water derives from buoyancy-dominated river outflow, the WMCC with connection to EMCC and remote upstream flow from the Nova Scotian shelf. A cyclonic eddy circulation has been identified near the surface of Wilkinson Basin, which is weak in winter but intensifies during spring through fall. Due to seasonal variation in wind forcing, local freshwater runoff, and water mass influx into the Gulf, there are substantial seasonal and inter-annual differences in circulation (Pettigrew et al. 2005; Hetland and Signell 2005).

The results of this study are consistent with the hypothesis that local production, rather than cross-shelf advection (see Appendix 2), occurring in early spring and throughout summer in and shoreward of the coastal current serve to supply late stage *C. finmarchicus* to Wilkinson Basin, where they accumulate and overwinter at depth in dormant phase, and to the coastal shelf, ledges and channels in the southern Gulf of Maine (e.g. Jeffreys Ledge, Great South Channel). Abundances of stage CIV and CV-CVI on the coastal shelf are attenuated during summer, due especially to predation by planktivorous fish and perhaps also to cross-shelf export of diapausing stage CV at depth. The source of *C. finmarchicus* to the mid-coastal shelf is likely Jordan Basin and the EMCC, depending on the particular conditions of coastal circulation in a given year. The timing of stage CI-CIII production is also dependent on the annual timing of physical events (light, nutrients, local freshwater discharge and stratification) influencing primary production. Timing of local freshwater discharge may affect coastal *C. finmarchicus* abundance by increasing flow and perhaps also displacing to the east the WMCC. The intensity of alongshore winds may also affect abundance by exporting or importing *C. finmarchicus* across shelf in surface layers, depending on whether the winds are, respectively, upwelling or downwelling in character. Precise mechanisms by which these forces act to control *C. finmarchicus* abundance on the coastal shelf need to be worked out by a combination of physical-biological modeling and further observations. Meanwhile, the present result concerning coastal abundances is that *C. finmarchicus* populations rarely attain concentrations sufficient to attract right whale feeding shoreward of the 100 m isobath.

Acknowledgements

This research was funded by an award from Maine Department of Marine Resources. J.R. and A.P. also acknowledge NSF award OCE-0815336. We thank C. Thompson, P. Stetson, P. Jekielek and the crews of the *R/V Stellwagen* and *R/V Gulf Challenger* for assistance during survey collections. The support of E. Summers, Maine DMR, during all phases of this research is gratefully acknowledged.

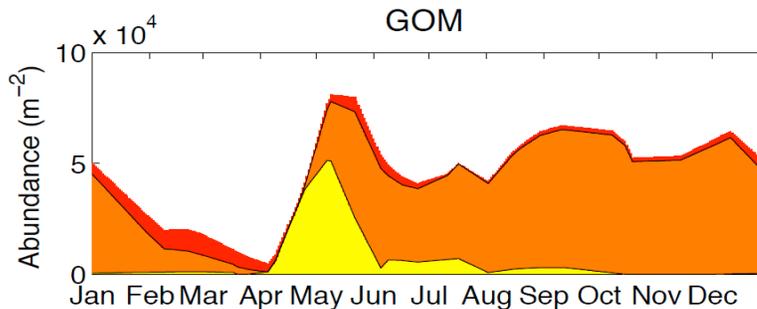
References

- Baumgartner MF, Cole TVN, Clapham PJ, Mate BR. 2003. North Atlantic right whale habitat in the lower Bay of Fundy and on the SW Scotian Shelf during 1999-2001. *Marine Ecology Progress Series* (264): 137-154.
- Beaugrand, G. 2003. Long-Term Changes in Copepod Abundance and Diversity in the North-East Atlantic in Relation to Fluctuations in the Hydroclimatic Environment. *Fisheries Oceanography* 12 (4/5): 270-283.
- Checkley, D. M., R. E. Davis, A. W. Herman, G. A. Jackson, B. Beanlands, L. A. Regier. 2008. Assessing plankton and other particles in situ with the SOLOPC. *Limnology and Oceanography* 53(5): 2123-2136.
- Churchill, J. H., N. R. Pettigrew, and R. P. Signell. 2005. Structure and variability of the Western Maine Coastal Current. *Deep-Sea Research II* (52): 2392-2410.
- Darbyson, E, DP Swain, D Chabot, and M Castonguay. 2003. Diel Variation in Feeding Rate and Prey Composition of Herring and Mackerel in the Southern Gulf of St Lawrence. *Journal of Fish Biology* 63 (5): 1235–1257.
- Durbin, E., J.A. Runge, R. Campbell, P. Garrahan, M. Casas and S. Plourde. 1997. Late fall-early winter recruitment of *Calanus finmarchicus* on Georges Bank. *Marine Ecology Progress Series* (151): 103-114.
- Durbin, E. G., R. G. Campbell, M. C. Casas, M. D. Ohman, B. Niehoff, J. Runge, and M. Wagner. 2003. Interannual variation in phytoplankton blooms and zooplankton productivity and abundance in the Gulf of Maine during winter. *Marine Ecology Progress Series* (254): 81-100.
- Durbin, E., and M. Casas. 2006. Abundance and spatial distribution of copepods on Georges Bank during the winter/spring period. *Deep-Sea Research II* (52): 2537-2569.
- Gaardsted, F., K. S. Tande, and S. L. Basedow. 2010. Measuring copepod abundance in deep-water winter habitats in the NE Norwegian Sea: Intercomparison of results from laser optical plankton counter and multinet. *Fisheries Oceanography* 19(6): 480-492.
- Hetland, R.,D., and R. P. Signell. 2005. Modeling coastal current transport in the Gulf of Maine. *Deep Sea Research (Part II, Topical Studies in Oceanography)*, 52(19-21): 2430-2449.
- Ji, R., C. Davis, C. Chen, and R. Beardsley, 2008. Influence of local and external processes on the annual nitrogen cycle and primary productivity on Georges Bank: A 3-D biological-physical modeling study. *Journal of Marine Systems*, 73:31-47.
- Johnson, C., J. Runge, A. Bucklin, K. A. Curtis, E. Durbin, J. A. Hare, L. S. Incze, J. Link, G. Melvin, T. O'Brien and L. Van Guelpen. 2011. Biodiversity and ecosystem function in the Gulf of Maine: pattern and role of zooplankton and pelagic nekton. *PLoS One* (6): 1-18.
- Jones, R.J, J.A. Runge, J. Stockwell and K. Wurtzell. In preparation. Diet composition of Atlantic herring in the western Gulf of Maine.
- Kane, J., and J. Prezioso. 2009. Distribution and multi-annual abundance trends of the copepod *Temora longicornis* in the US Northeast Shelf Ecosystem. *Journal of Plankton Research* (30): 619-632.
- Kenney RD, Winn HE, Macaulay MC. 1995. Cetaceans in the Great South Channel, 1979–1989: right whale (*Eubalaena glacialis*). *Continental Shelf Research* (15): 385-414.
- Manning, J. P., D. J. McGillicuddy, N. R. Pettigrew, J. H. Churchill, L. S. Incze. 2009. Drifter Observations of the Gulf of Maine Coastal Current. *Continental Shelf*

- Research (29): 835-845.
- Maps, F., J. Runge, A. Leising, A. Pershing, N. Record, S. Plourde, and J. Pierson. 2012. Modeling the timing and duration of dormancy in populations of *Calanus finmarchicus* on the northwest Atlantic shelf. *Journal of Plankton Research* (34): 36-54.
- Mayo, C.A. and M.K. Marx. 1990. Surface foraging behaviour of the North Atlantic right whale, *Eubalaena glacialis*, and associated zooplankton characteristics. *Canadian Journal of Zoology* (68): 2214-2220.
- Mitchell, M. R., G. Harrison, K. Pauley, A. Gagné, G. Maillet, and P. Strain. 2002. Atlantic Zonal Monitoring Program Sampling Protocol. Canadian Technical Report of Hydrography and Ocean Sciences (223).
- Murison LE, Gaskin DE. 1989. The distribution of right whales and zooplankton in the Bay of Fundy, Canada. *Canadian Journal of Zoology* (67): 141-1420.
- Patrician MR, Kenney RD. 2010. Using the continuous plankton recorder to investigate the absence of North Atlantic right whale (*Eubalaena glacialis*) from the Roseway Basin feeding ground. *Journal of Plankton Research* (32): 1685-1695.
- Pendleton DE, Pershing AJ, Brown MW, Mayo CA, Kenney RD, Record NR, Cole TVN. 2009. Regional-scale mean copepod concentration indicates relative abundance of North Atlantic right whales. *Marine Ecology Progress Series* (378): 211-225.
- Pershing, A. J., N. R. Record, B. C. Monger, D. E. Pendleton and L. A. Woodard. 2009. Model-based estimates of *Calanus finmarchicus* abundance in the Gulf of Maine. *Marine Ecology Progress Series* (378): 227-243.
- Pettigrew, N. R., J. H. Churchill, C. D. Janzen, L. J. Mangum, R. P. Signell, A. C. Thomas, D. W. Townsend, J. P. Wallinga, and H. Xue. 2005. The kinematics and hydrographic structure of the Gulf of Maine Coastal Current. *Deep-Sea Research II* (52): 2369-2391.
- Runge, J.A., M. Castonguay, Y. De Lafontaine, M. Ringuette and J.L. Beaulieu. 1999. Covariation of climate, zooplankton biomass and mackerel recruitment in the southern Gulf of St. Lawrence. *Fisheries Oceanography* (8:2): 139-149.
- Runge, J. A., S. Plourde, P. Joly, E. Durbin and B. Niehoff. 2006. Characteristics of egg production of the planktonic copepod, *Calanus finmarchicus*, on Georges Bank: 1994-1999. *Deep-Sea Research II* (53): 3618-2631.
- Singer, L., and L. Ludwig. 2005. Right whale foraging in nearshore waters of the northern Gulf of Maine. Proceedings of a workshop, April 15, 2005. Gulf of Maine Research Institute.
- Sundby, S. (2000). Recruitment of Atlantic cod stocks in relation to temperature and advection of copepod populations. *Sarsia*, 85(4): 277-298.
- Wishner KF, Schoenherr JR, Beardsley R, Chen CS. 1995. Abundance, distribution and population structure of the copepod *Calanus finmarchicus* in a springtime right whale feeding area in the southwestern Gulf of Maine. *Continental Shelf Research* (15): 475-507.

Appendix 1. Wilkinson Basin *Calanus finmarchicus* climatology

Annual climatology of *Calanus finmarchicus* abundance in Wilkinson Basin, based on data collected over three years (2005-2007) at a time series station (250 m depth) located on the northwest edge of the basin (from Maps et al. 2012). Yellow: Stage CI-III; Orange: Stage CIV-CV; Red: adult females.



Appendix 2. Modeling the Transport of *C. finmarchicus* to Maine's Coastal Waters

Introduction

Our summer zooplankton surveys identified a strong boundary in the distribution of late stage *Calanus finmarchicus*, with high abundances occurring only in areas deeper than 100m. One hypothesis that could explain this discontinuity is a lack of cross isobath flow along the coast. To investigate the frequency of incursions of offshore water into the coastal region, we conducted a simple particle simulation using reconstructions of near-surface currents.

Methods

We used high resolution hindcasts of the currents in the Gulf of Maine from 2005-2009 provided by Changsheng Chen at SMAST (University of Massachusetts, Dartmouth). The flow fields were produced using the Finite Volume Coastal Ocean Model (FVCOM), forced by observed winds and surface heat flux and realistic tides. FVCOM has been used extensively to explore physical-biological interactions in the Gulf of Maine (e.g. Ji et al. 2007). For our study, we averaged the modeled currents over the top 25 m.

Our main goal is to quantify where along the coast and in what season are particles most likely to be transported inshore. At noon on every model day, we placed 45 artificial drifters at regular intervals along the 50 fathom (91 m) depth contour (Fig. A1). We assumed that the particles drifted passively in the flow field and tracked their movement over 16 days. We recorded whether or not each drifter crossed into a region corresponding with Maine state waters, excluding Matinicus Island, based on the exemption line.

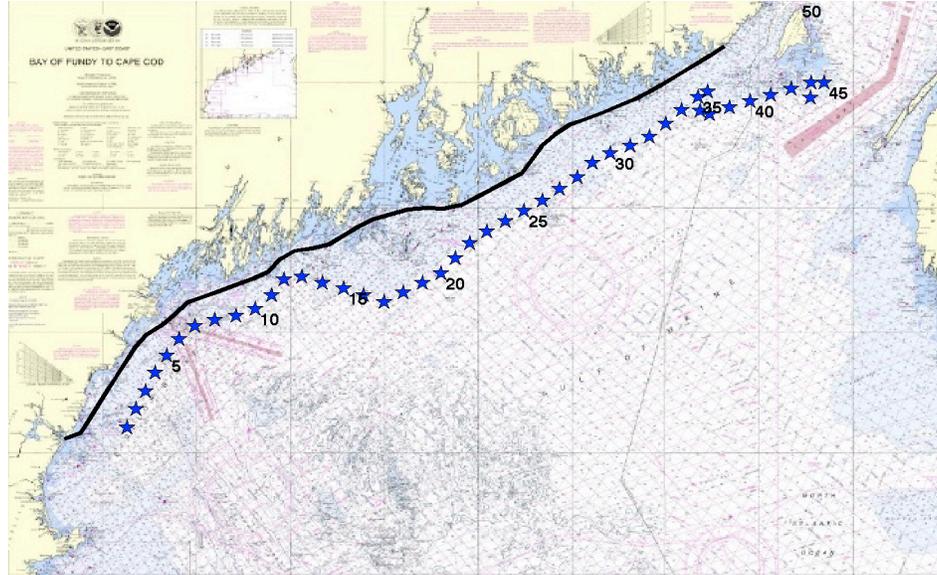


Figure A1. Initial starting positions (blue stars) for the particle experiment. Inshore waters are defined by the black polygon (exemption line), roughly 3 nm from shore.

Results

Whether a particle crossed into state waters depended critically on the time of year and the initial starting position. Particles that started on the section of the coast east of Matinicus to near Mt Desert Rock (stations 20-30), rarely crossed into state waters (Fig. A2). The only crossings from this region occurred during a brief period centered on day 125. The sector to the west had occasional crossings, with a slight increase in the late spring (around day 100) and fall (around day 250). The downeast section, stations 35-45, produced the most frequent crossings. In most years, particles released in this region between day 125 and 160 incurred into state waters. Most of these incursions took place east of Isle au Haut and west of Jonesport. A smaller cluster of crossings also occurred in autumn. Our three cruises all occurred during the period of fewest crossings.

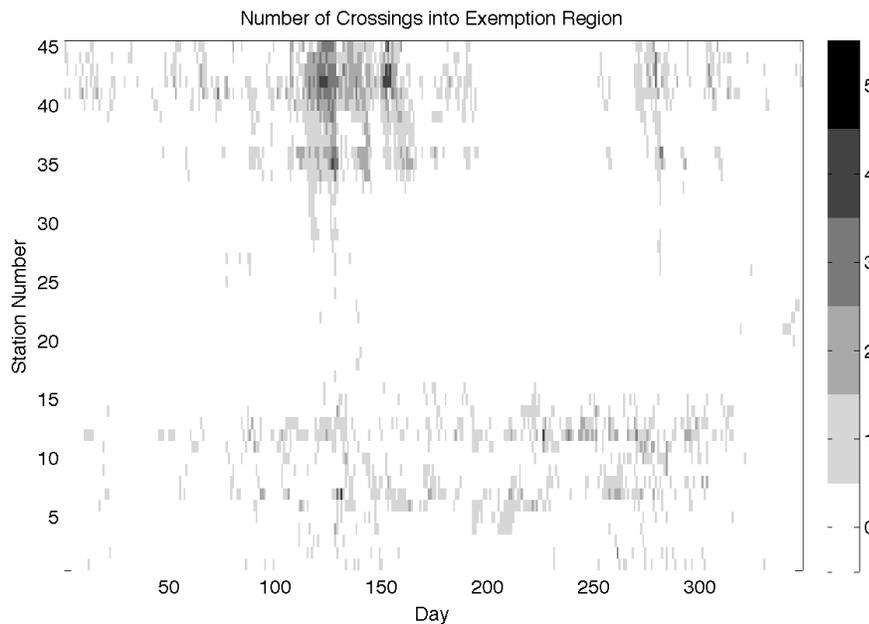


Figure A2. Number of times a particle released on a particular day (x-axis) and station (y-axis) crossed into the black polygon in Figure A1. The number of crossings (out of five years) is indicated by the shades of gray.