



## Research papers

# Habitat usage by the cryptic copepods *Pseudocalanus moultoni* and *P. newmani* on Georges Bank (Northwest Atlantic)



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## ABSTRACT

The cryptic copepod species, *Pseudocalanus moultoni* and *P. newmani*, co-occur on Georges Bank and in the Gulf of Maine (Northwest Atlantic); even recent studies have reported results and conclusions based on examination of the combined species. Species-specific PCR (SS-PCR) based on mitochondrial cytochrome oxidase I (COI) sequence divergence was used in this study to discriminate the species. Species-specific descriptions of habitat usage and predicted patterns of transport and retention on Georges Bank were made by mapping distributions and calculating abundances of each species from January to June, 1999 for four vertical strata (0–15 m, 15–40 m, 40–100 m, and 0–100 m) and five regions (Northern Flank, Bank Crest, Northeast Peak, Southern Flank, and Slope Water) identified on the basis of bathymetry and circulation. Patterns of distribution and abundance for the two species during January to June, 1999 were largely consistent with those described based on vertically integrating mapping and analysis for the same period in 1997 by McGillicuddy and Bucklin (2002). The region-specific and depth-stratified analyses allowed further discrimination in habitat usage by the species and confirmed the distinctive patterns for the two species. The observed differences between the species in abundances among the five regions and three depth strata over Georges Bank impact their transport trajectories. The concentration of *P. moultoni* in deep layers likely explains the higher rates of retention and lower rates of advective loss of this species from the Bank, compared to *P. newmani*, which may be more subject to wind-driven transport in the surface layer. Accurate identification and discrimination of even closely-related and cryptic species is needed to ensure full understanding and realistic predictions of changes in diversity of zooplankton and the functioning of pelagic ecosystems.

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## 1. Introduction

The planktonic copepod sibling species *Pseudocalanus moultoni* and *P. newmani* occur sympatrically during the spring and summer on Georges Bank in the NW Atlantic Ocean (Bucklin et al., 2001; McGillicuddy and Bucklin, 2002). The species cannot be reliably distinguished using morphological characters and even recent studies have reported the combined abundances of the sibling species (e.g., O'Brien et al., 2013; Kane, 2007, 2014). However, genetic divergence between the species for the mitochondrial cytochrome oxidase I (COI) barcode region of 18% is consistent with that of other copepod species (Bucklin et al., 2003, 2011; Blanco-Bercial et al., 2014), allowing design of a rapid and inexpensive molecular protocol, species-specific PCR (SS-PCR), that can be used for routine species identification for samples

preserved in alcohol or frozen in liquid nitrogen (Bucklin et al., 1998, 1999, 2001).

Despite their marked morphological similarity, species of *Pseudocalanus* differ in many aspects of their life history, ecology, biogeography, and seasonal timing of reproduction (Frost, 1989; and e.g., Napp et al., 2008; Hopcroft and Kosobokova, 2010). *P. moultoni* and *P. newmani* have similar development and reproductive rates; without discriminating the species, models developed by Ji et al. (2009) used rates of development and reproduction that fall between those of the two species (Davis, 1987; Jonasdottir, 1989; McLaren et al., 1989). However, potentially important behavioral differences between the species, such as vertical positioning in the water column, were not considered. The biogeographical distributions for *P. moultoni* and *P. newmani* were discriminated by Frost (1989), who considered that *P. moultoni* is a coastal species, while *P. newmani* has more open-ocean affinities. Subsequent discoveries of *P. moultoni* in coastal waters surrounding Svalbard in the Northeast Atlantic Ocean by Aarbakke et al. (2011, 2014) appear consistent with this designation.

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The biological and physical dynamics underlying the pelagic community dynamics over Georges Bank were the focus of a U.S. GLOBEC field program during 1994–1999 (Wiebe et al., 2006) and continuing efforts have sought to understand impacts of climate variability and change on the critically-important Northwest Atlantic continental shelf ecosystem (Friedland et al., 2013). During the Georges Bank Study, broad-scale surveys were used to examine the population dynamics of key species on the Bank by monthly sampling at a set of standard stations from January to June each year. Analysis of the resultant patterns of species distribution and abundance was facilitated by mapping to a standard grid, with regions delimited by bathymetry and hydrography (Chu, 2004), including a persistent and predictable tidal-mixing front between the shallow, well-mixed waters of the Bank Crest and the deeper seasonally-stratified waters of the Southern Flank (Bigelow, 1927; Garrett et al., 1978; Butman and Beardsley, 1987). A number of studies reported characteristic differences in the species composition of the zooplankton assemblage over the Bank (e.g., Durbin and Casas, 2006; Wishner et al., 2006). Shifts in zooplankton composition, associated with climate variability and change, impact the entire Northwest Atlantic shelf ecosystem (Mountain and Kane, 2010). In particular, it is important to understand the response of *Pseudocalanus* spp. in the Georges Bank region to climate change, since the species are primary prey for cod and haddock larvae; in warmer waters, there is a shift toward the copepod, *Centropages typicus*, which is difficult for the fish larvae to capture and can lead to fisheries collapse (Stegert et al., 2010, 2012; Petrik et al., 2009, 2014).

The U.S. GLOBEC Georges Bank Study offered an opportunity to examine patterns of distribution and abundance – and hypothesize about the underlying physical and biological processes that determined them – of the co-occurring cryptic sibling species of *Pseudocalanus* (Bucklin et al., 1998, 2001). Based on monthly sampling during broad-scale surveys during January to June, 1997 and adjoint physical–biological modeling, McGillicuddy and Bucklin (2002) described the species-specific patterns. The spring–summer 1997 increase of *P. moultoni* on the crest of the Bank was shown to result both from increased transport of copepods onto the Bank from surrounding regions and by local reproduction and recruitment, with populations maintained within the clockwise gyre on Georges Bank. In contrast, the spring increase for *P. newmani* was caused by transport from these upstream source regions on the Scotian Shelf, with copepods carried along the Southern Flank of Georges Bank; both species became very abundant on the Bank Crest when the around-bank circulation intensified (McGillicuddy and Bucklin, 2002).

The results reported here build upon earlier biological (Bucklin et al., 2001) and physical–biological modeling studies (McGillicuddy et al., 1998; McGillicuddy and Bucklin, 2002) of *Pseudocalanus* species on Georges Bank. In order to better understand the physical–biological mechanisms by which *P. moultoni* and *P. newmani* may persist and proliferate in the complex and variable flow field over Georges Bank, distributions and abundances of the cryptic species were examined for 1999 and compared to previous results for 1997, with separate analyses for five regions and three depth strata. The ultimate goal is to predict changes in the distribution and abundance of each of the cryptic sibling species of *Pseudocalanus* as a result of changes in their physical and biotic environment and to anticipate how their populations might respond to climate change.

## 2. Methods

### 2.1. Sample collection and analysis

Vertically-stratified zooplankton samples were collected during U.S. GLOBEC Georges Bank Study broad-scale surveys carried out monthly from January to June, 1999 (Fig. 1). Collections were made using a 1-m<sup>2</sup> Multiple Opening and Closing Net and Environmental Sensing System (MOCNESS; Wiebe et al., 1985) with 150  $\mu$ m mesh nets, which effectively capture the adults of both *Pseudocalanus* species. Samples were split at sea, with a one-half preserved for molecular analysis in 95% ethyl alcohol and one-half preserved in buffered formalin for taxonomic analysis. Alcohol-preserved samples from 15 to 20 net tows (stations), with 3–4 net samples per tow, were analyzed from each of the six broad-scale survey cruises in 1999.

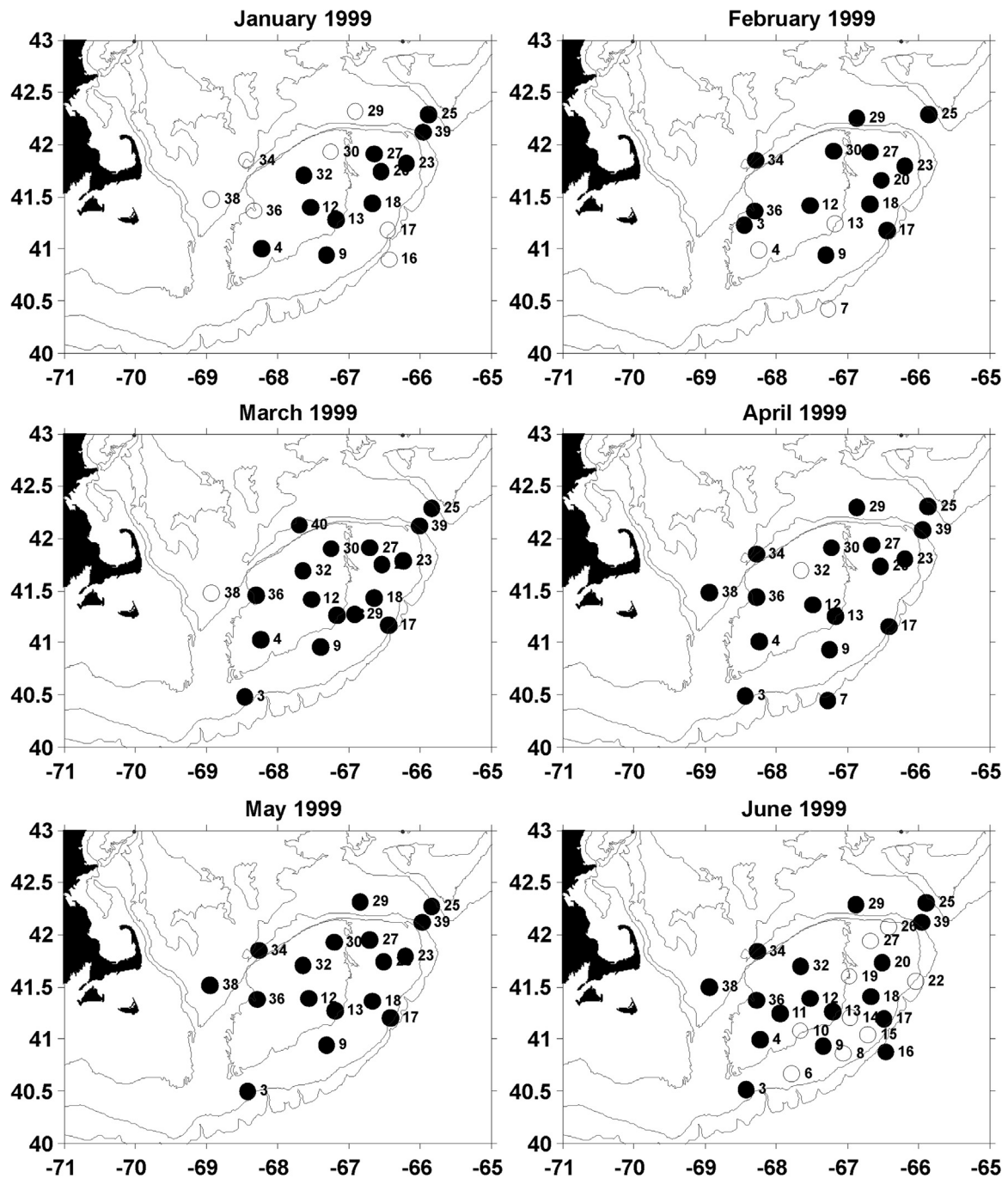
### 2.2. Determination of species abundances

Aliquots of MOCNESS samples collected at each depth and station were removed to a petri dish in a wide-mouth plastic pipette. Each Petri dish was scanned under a dissecting microscope for adult female *Pseudocalanus* species. At least 20 copepods were removed from each sample and placed in a separate vial for each net sample. Adult females were used in all cases when sufficient numbers were available; fifth-stage juveniles (CV copepodites) were used as necessary to meet the minimum aliquot of 20 *Pseudocalanus* spp. Regression analysis showed that, for each of the six months regardless of depth, adult females and CVs were significantly correlated ( $p < .0005$ ), indicating that there was no discernable bias due to the inclusion of CVs in subsamples for SS-PCR analysis. Counts of *Pseudocalanus* spp. females from net tows for 0–15, 15–40, and 40–100 m depths during the monthly 1999 broad-scale cruises were used to determine species-specific patterns of distribution, which were reported as per m<sup>2</sup>.

Discrimination of the cryptic species and identification of individual copepods was done by species-specific PCR (SS-PCR) following previously-published protocols (Bucklin et al., 2001). All three PCR primers (LCO-1490, PM-COI, and PN-COI) were added to a competitive, multiplexed PCR reaction cocktail, which allowed discrimination of the species with a one-step protocol. Reactions were done in 96-well plates; each plate included one negative (no-DNA) control. The relative abundances of the two species for each aliquot were determined based on SS-PCR (for detailed description of methods, see Bucklin et al., 1998). Absolute abundances of each species were determined by multiplying the relative proportions of the species in subsamples determined using SS-PCR by the total *Pseudocalanus* spp. counts in the formalin-preserved split of the same sample as determined by the URI Zooplankton Sorting Group (<http://www.bco-dmo.org/resources>). On average, 50 samples were examined for each broad-scale survey (3–4 net samples at 15–20 stations) for a total of 350 samples over the six broad-scale cruises. In all, 4201 individual copepods were analyzed using SS-PCR in order to document the distribution and abundance of the two species on Georges Bank and in adjacent regions at sufficiently high spatial resolution.

### 2.3. Patterns of species' distribution and abundance

Comparisons of habitat usage, including predicted patterns of transport and retention by the two species on Georges Bank, were made by analyzing Bank-wide and regional patterns of distribution and abundance. *P. moultoni* and *P. newmani* abundance distributions determined using the SS-PCR determined ratios for four strata (0–15 m, 15–40 m, 40–100 m, and 0–100 m) were mapped individually in monthly snapshots from January to June, 1999,



**Fig. 1.** Station locations and numbers where samples were collected for analysis of *Pseudocalanus* spp. abundances during monthly broad-scale surveys of the U.S. GLOBEC Georges Bank Study. On the crest of the Bank, water depths are often less than 40 m deep, allowing only two depth strata to be sampled. Open circles represent stations that lack data for one or more depth intervals; filled circles indicate that data were available and species abundances were estimated for all depth intervals, including integrated abundances.

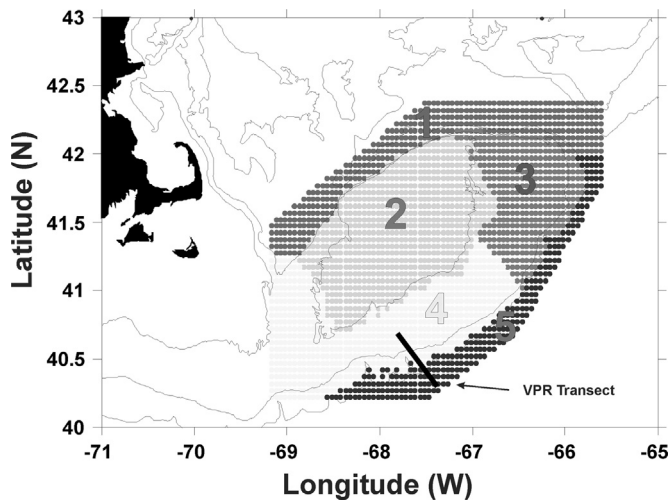
using the same objective analysis procedure described in [McGillucuddy and Bucklin \(2002\)](#), which is based on [He et al. \(1997\)](#).

In addition, high-resolution vertical and horizontal distributional data for *Pseudocalanus* spp. across the Southern Flank and adjacent Slope Water were obtained from the Video Plankton Recorder (VPR; [Davis et al., 2004](#)). The VPR towyo sampling was done on June 16, 1995, starting at 0440 UTC (0040 local EDT) on Georges Bank at the 75 m isobath (40.69°N; 67.81°W) and ending off-Bank at 1300 UTC (1100 EDT) (40.31°N; 67.38°W). The hydrographic data are given in [Gallager et al. \(2004\)](#). The plankton image data were obtained from the VPR's low magnification camera, which had an imaged volume of 36 × 27 × 44 mm (=43 mL)

sampled at 60 frames per second (=155 L/min or 77 m<sup>3</sup> sampled during the 8.33 h towyo). For complete and detailed description of VPR sampling methodology see [Davis et al. \(2004\)](#).

Species abundances for each stratum were computed for each of five regions using Easykrig software ([Chu, 2004](#)), which is specifically tailored for analysis of U.S. GLOBEC broad-scale survey data ([http://globec.who.edu/jg/serv/globec/gb/broadscale\\_grid.html](http://globec.who.edu/jg/serv/globec/gb/broadscale_grid.html)). The five regions are based on bathymetry and circulation patterns and include Northern Flank, Bank Crest, Northeast Peak, Southern Flank, and Slope Water ([Fig. 2](#)).

Analysis of Variance (ANOVA) was implemented in MATLAB<sup>®</sup> (The Mathworks, Inc.) to statistically evaluate the effects of four



**Fig. 2.** Standard grid for Georges Bank, showing five regions defined by bathymetry and circulation patterns. Regions are: (1) Northern Flank, (2) Bank Crest, (3) Northeast Peak, (4) Southern Flank, and (5) Slope Water. Also shown is a Video Plankton Recorder (VPR) transect made on June 16, 1995 between 0040 local EDT (40.69°N; 67.81°W) and 1100 EDT (40.30°N; 67.37°W). Additional results from the VPR transect are provided in [Gallager et al. \(2004\)](#); methods are described in [Ji et al. \(2013\)](#).

different sources of variation: differences between the two species, five regions, six months (January to June, 1999), and three depth strata (0–15 m, 15–40 m, and 40–100 m). Abundances (numbers/m<sup>2</sup>) of the species were log<sub>10</sub> transformed for analysis. The null hypothesis tested was that the effects of the four sources of variance did not differ. Effects of the variables and their pairwise interactions were evaluated for statistical significance.

#### 2.4. Temperature and salinity distributions

The relationship between the two *Pseudocalanus* species and temperature and salinity data collected on the 1999 broad-scale cruises were analyzed. Average temperature and salinity values were computed for each of the three depth strata sampled on the broad-scale cruises in 1999 where *Pseudocalanus* spp were counted. The mean values were then kriged to the standard grid for Georges Bank, which was subdivided into five regions based on bathymetry and circulation patterns ([Fig. 2](#)). Averages of the kriged values for each bank region, depth interval, and month were computed to match the *Pseudocalanus* species data. Portions of the bank that were shallower than the deepest depth interval (40–100 m) were excluded from this calculation.

### 3. Results

#### 3.1. Bank-wide patterns of abundance

Month-to-month patterns of distribution and abundance for the two species in 1999 were largely consistent with those described for spring 1997 by [McGillicuddy and Bucklin \(2002\)](#). In vertically-integrated (0–100 m) distribution maps, early spring distributions (source regions) were apparently distinct, with marked concentrations of *P. newmani* on the Southern Flank of the Bank during March and April, while summer distributions (destination regions) were overlapping on top of Georges Bank ([Fig. 3a](#)). In January, *P. moultoni* was concentrated in surface waters along the southern flank, while populations of *P. newmani* spanned an area from the adjacent Brown's Bank, over the Northeast Peak, and along the Southern Flank, where the two species' distributions

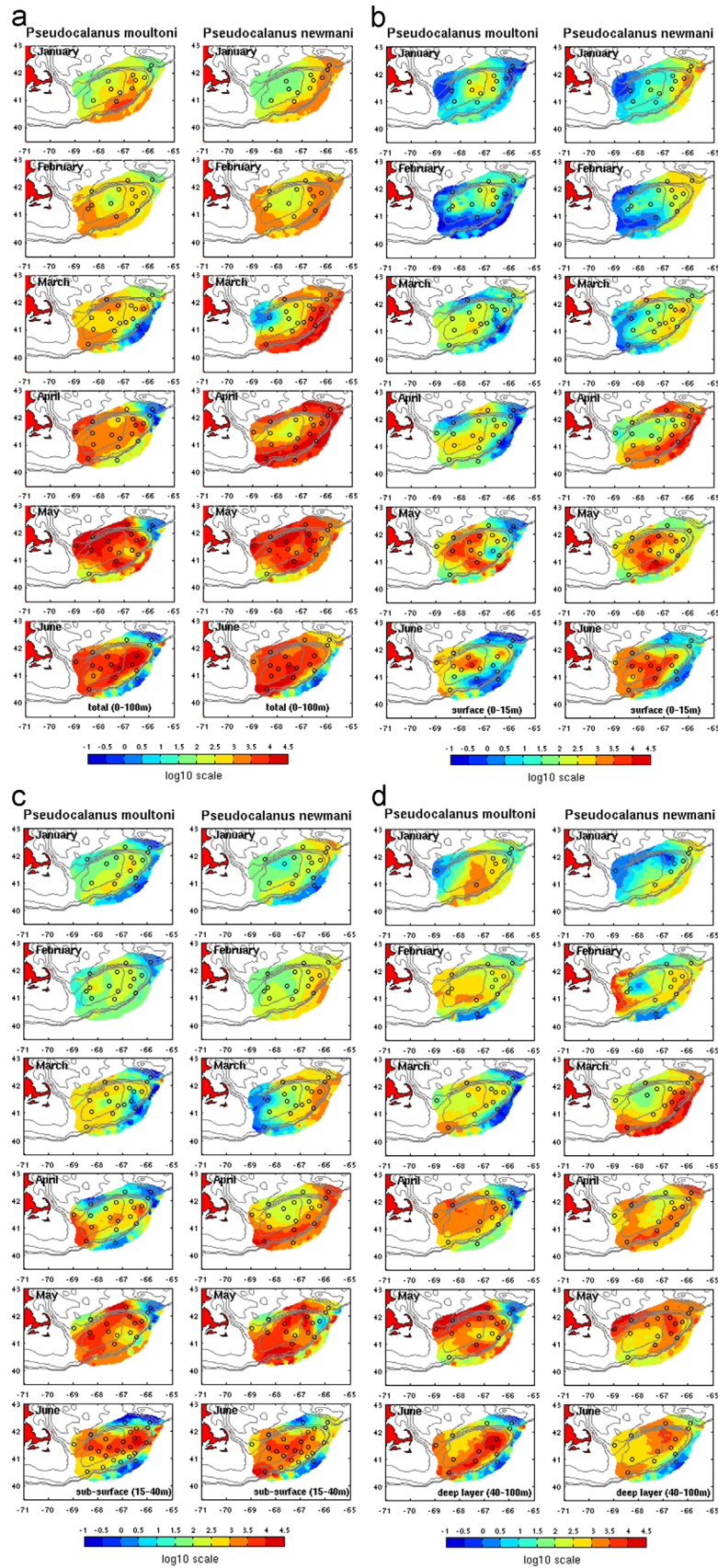
overlapped. These patterns persisted into February, although concentrations diminished for *P. moultoni*. In March, population growth was marked for *P. newmani*, especially along the Southern Flank of the Bank. In April, *P. moultoni* concentrations increased over the Bank Crest, while *P. newmani* predominated along the entire Southern Flank and Northeast Peak. During May and June, patterns of distribution and abundance were similar for the two species, with highest concentrations of both species usually found over the Bank crest.

Bank-wide distributions also showed distinctive patterns for the two species by depth stratum: 0–15 m ([Fig. 3b](#)), 15–40 m ([Fig. 3c](#)), and 40–100 m ([Fig. 3d](#)). At the surface (0–15 m), *P. moultoni* were consistently concentrated over the Bank Crest, showing a slight increase from February to March, and building steadily to a maximum in May ([Fig. 3b](#)). In distribution maps of the top-most layer, *P. newmani* showed the marked concentrations on the Northeast Peak and Southern Flank in April, followed by May–June concentrations on the Bank Crest ([Fig. 3b](#)). At mid depths (15–40 m), most notable is the later population increase of *P. moultoni*, with dense concentrations spreading across the Bank by April and persisting through June ([Fig. 3c](#)). This layer also shows the characteristic earlier peak of *P. newmani* on the Northeast Peak, with subsequent increases on the Southern Flank in April that expanded across the Bank by May and June ([Fig. 3c](#)). Maps of the deepest layer (40–100 m) showed a high concentration of *P. moultoni* on the Northeast Peak in February, which was not seen in other layers ([Fig. 3d](#)). With the exception of this novel feature, the month-to-month distributional patterns of the two species were similar to the shallower layers described above.

Summed over all depth strata, Bank-wide abundance of *P. moultoni* was lowest in February, while *P. newmani* was least abundant in January ([Fig. 4](#)). The month of the greatest difference in total abundance was April, when *P. newmani* showed a markedly larger seasonal increase than *P. moultoni*. In May, total abundances were at their maximum levels for both species; in June, *P. newmani* abundances decreased, while *P. moultoni* remained high ([Fig. 4](#)). Considering bank-wide abundances for the species in each depth stratum separately, notable features are the low relative abundances of *P. moultoni* in the top-most (0–15 m) layer throughout all six months ([Fig. 4](#)). Summed over the sampled broad-scale collections, *P. moultoni* had nearly equal abundances in the two subsurface layers (15–40 m and 40–100 m; [Fig. 4](#)). The species differed in month-to-month abundances in the deepest waters analyzed (> 40 m). The largest relative concentration of *P. newmani* in the deepest layers (40–100 m) was in March; most of the population was found in the middle layer (15–40 m) in May. In contrast, *P. moultoni* concentrations in deep waters were greatest in May and June ([Fig. 4](#)).

#### 3.2. Comparisons among Georges Bank regions

Calculation of depth-stratified and total abundances of the two species in five Georges Bank regions defined by bathymetry and circulation allowed more detailed examination of habitat usage ([Fig. 5](#)). *P. moultoni* increased gradually from March to April, with a marked increase from April to May, and seasonal maxima in May on the Northern Flank, Bank Crest, and Southern Flank; starting in May, *P. moultoni* is more abundant in deeper strata ([Fig. 5](#)). *P. newmani* showed a similar pattern of total and depth-stratified abundance on the Bank Crest, except for a more marked decrease in abundance in June. The Northeast Peak, Southern Flank, and Slope Water abundances of *P. newmani* all showed a March increase in the deepest layer (40–100 m) that was not seen for *P. moultoni*. On the Southern Flank, this was followed by a sharp April increase in the middle layer (15–40 m), a marked May increase in the surface layer (0–15 m) resulting in peak total



**Fig. 3.** Abundances of *Pseudocalanus moultoni* and *P. newmani* based on broad-scale surveys over Georges Bank for January to June, 1999 for 0–100 m (a), 0–15 m (b), 15–40 m (c), and 40–100 m (d). Data were objectively analyzed onto a finite element mesh (see [McGillicuddy and Bucklin, 2002](#)). Scale bar: number of individuals per square meter; open circles: sample collection locations; geographic coverage of each map is confined to that area where the expected error computed in the objective analysis, averaged over all time periods and both species, is less than ~70 percent. This error threshold was subjectively chosen to define a consistent mapping area that encompasses all of the broad-scale survey stations. (a) Abundances of *P. moultoni* and *P. newmani* for 0–100 m. (b) Abundances of *P. moultoni* and *P. newmani* for 0–15 m. (c) Abundances of *P. moultoni* and *P. newmani* for 15–40 m. (d) Abundances of *P. moultoni* and *P. newmani* for 40–100 m.

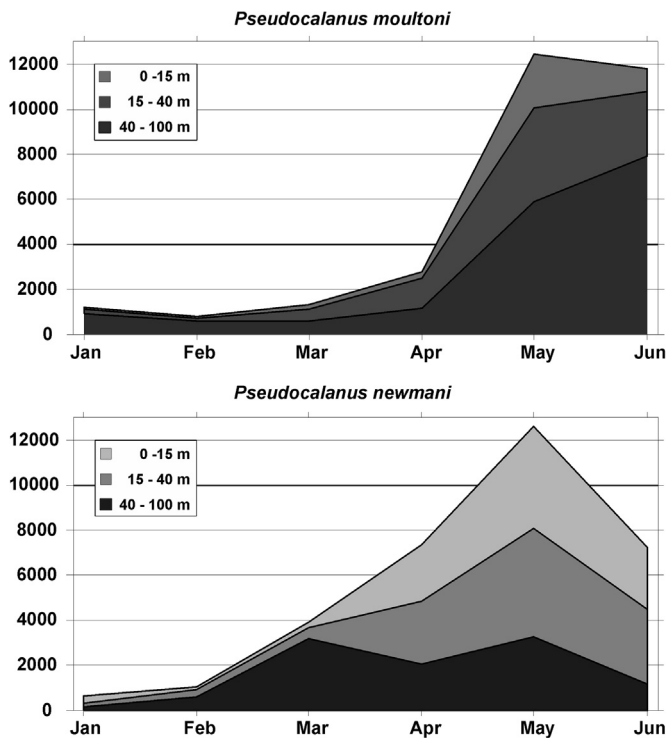


Fig. 4. Total Bank-wide abundances of female *Pseudocalanus moultoni* and *P. newmani* for three depth strata (0–15 m, 15–40 m, and 40–100 m) in samples collected during U.S. GLOBEC broad-scale surveys from January to June, 1999.

abundance, and then a June decrease (Fig. 5). On the Northern Flank, *P. moultoni* had a marked spike in abundance in the deepest layer in May, much higher than the deep-water May increase of *P. newmani*. The Northeast Peak had distinctive seasonal patterns for both species: *P. moultoni* abundances were highest in June, not May, and the surface layer abundances of *P. newmani* did not show the May increase.

### 3.3. Sources of variation

The effects of the four different sources of variation (species, regions, months, and depth strata) were significantly different based on mean square values in an Analysis of Variance (ANOVA; Table 1). The largest effect was months ( $p < 0.001$ ), reflecting the marked changes in abundances of each species in each region from January to June 1999. The second largest effect was depth stratum ( $p < 0.001$ ), clearly demonstrating that the species were not homogeneously distributed throughout the water column. The difference between species ( $p = 0.015$ ) and regions ( $p = 0.026$ ) explained less of the overall variation and had lower significance values (Table 1). Notably, all pairwise interactions that included species were highly significant, clearly indicating that the two species displayed distinctive habitat preferences with regard to these three variables; other interaction terms were not statistically significant ( $p > 0.010$ ; Table 1).

### 3.4. Relationship with temperature and salinity

Average temperatures on Georges Bank ranged from about 5 °C to about 13 °C, and varied monthly with March the coldest and June the warmest (Fig. 6). From January through April, the deepest depth was the warmest and the surface interval was the coldest. In May and June the pattern was reversed and deepest depth interval was coldest and the surface depth interval was the warmest. Except for the Bank Crest region, the other four regions reflected the

general pattern of seasonal and vertical temperatures. On the Crest there was very little difference in the vertical due to the shallow depths and strong tidal mixing (Fig. 7). Across the Bank, the average salinity values ranged from ~32.2 to 33 PSU and were lowest in January. The deepest depth interval always had the highest salinities and the surface the lowest (Fig. 6). Regionally the salinities varied with lower values on the Northern Flank, Bank Crest, and Northeast Peak; higher values were observed on the Southern Flank and Slope Water regions (Fig. 7).

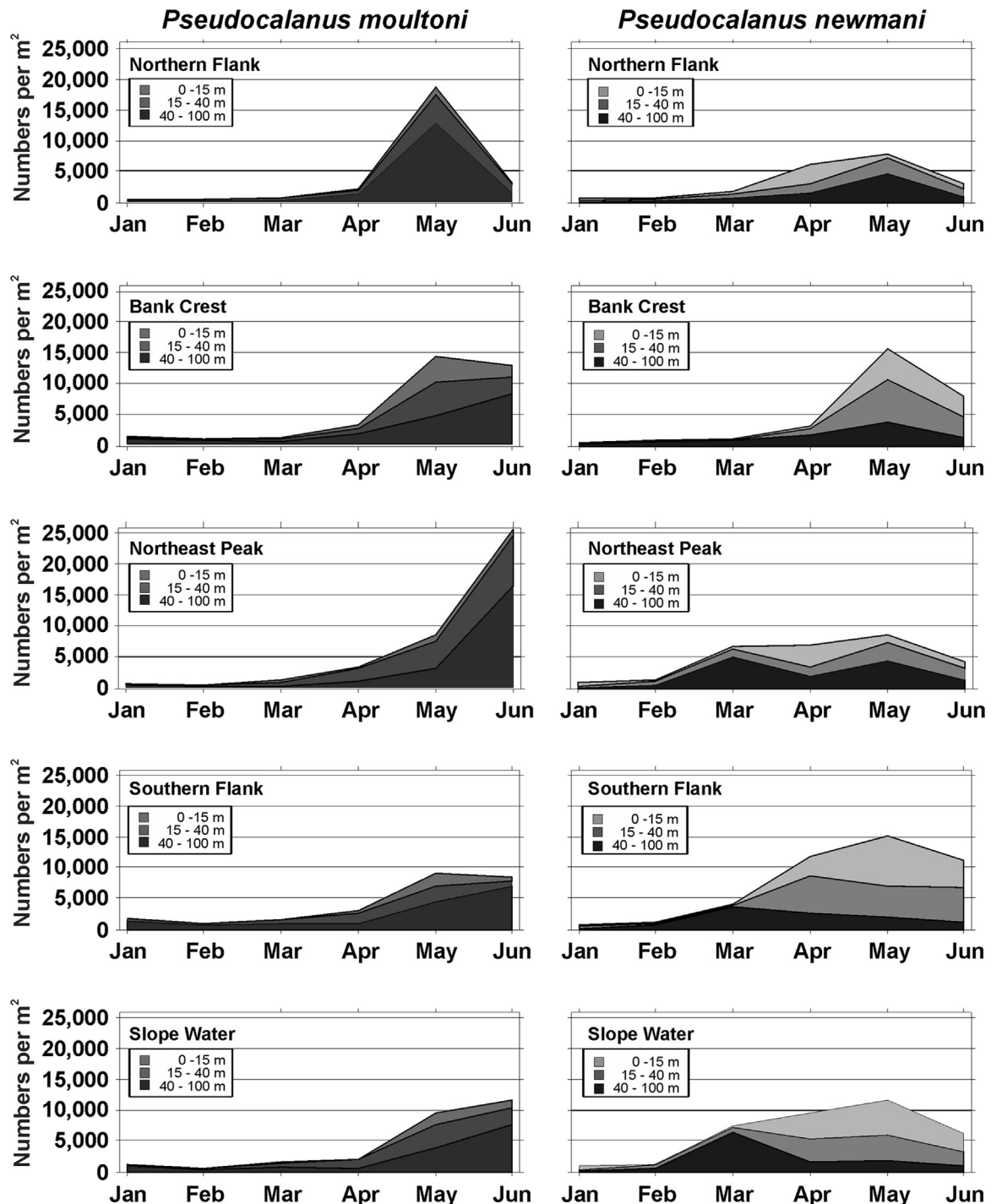
A 3-way ANOVA was performed on the temperature and salinity to determine the effects of regions, months, and depth. For temperature, the regions, months, and depths were significantly different ( $p < .05$ ), as were the interaction terms for regions  $\times$  months and months  $\times$  depths (Table 2). For salinity, the regions, months, and depths were also significantly different ( $p < .05$ ), as were the interaction terms for regions  $\times$  months and regions  $\times$  depths, but not months  $\times$  depths (Table 3).

A multiple linear regression analysis was performed to examine the relationship between the two *Pseudocalanus* species and temperature and salinity. The species were the dependent variable and temperature, salinity, and a temperature/salinity interaction term were the independent variables. Both regressions were significant ( $p < .05$ ). For *P. moultoni*, the regression explained about 26% of the variance; for *P. newmani*, it explained about 21%. The abundance data were plotted as a function of temperature and salinity and the regression equations were used to plot a predicted model surface (Fig. 8). The model surfaces for the two species show subtle differences that reflect the spatial differences in the species distributions on Georges Bank. However, the differences are not statistically significant, likely due to the variability of the data and overlap in the confidence limits of the regression coefficients.

## 4. Discussion

Although *P. moultoni* and *P. newmani* can be discriminated using morphological characters (Frost, 1989), the differences are subtle and requires time consuming high resolution microscope examination key morphological characters not practical for large numbers of samples. By using total counts of *Pseudocalanus* spp. and determining proportions of the two species by species-specific PCR (SS-PCR) reactions based on DNA sequence differences of the COI barcode region, the cryptic species were shown to have distinct patterns of distribution and abundance on Georges Bank during January to June, 1999. These findings are consistent with an earlier study using adjoint physical–biological modeling of the two species' abundances based on vertically-integrated broad-scale surveys on Georges Bank from January to June 1997 (McGillicuddy and Bucklin, 2002). Fully comparable analyses from multiple years is especially important, and the similarity of the overall findings is particularly noteworthy, given the importance of large-scale forcing and associated interannual variability of ocean dynamics in this region (Petrie and Drinkwater, 1993; Loder et al., 1998; Smith et al., 2001, 2012; Mountain and Kane, 2010; and see Wiebe et al., 2002). Also, in contrast to the 1997 results, we report here analysis of depth-stratified samples from the 1999 collections, which allows comparative analysis of three-dimensional habitat usage by the cryptic species. Although these analyses do not allow conclusions of the underlying dynamic causes of the observed and analyzed distributions, the mapping and analysis of species abundances in three depth strata and the separate calculation of abundances in five regions defined by bathymetry and circulation allow inferences of species-specific patterns of transport, retention, and maintenance.

McGillicuddy and Bucklin (2002) speculated that concentrations of *P. newmani* on the northeastern edge of the sampled



**Fig. 5.** Abundances of *Pseudocalanus moultoni* and *P. newmani* for three depth strata (0–15 m, 15–40 m, and 40–100 m) in the five regions of Georges Bank, based on collections from U.S. GLOBEC broad-scale surveys during January–June 1999. Regions are: Northern Flank, Bank Crest, Northeast Peak, Southern Flank, and Slope Water (see Fig. 2).

domain represented either the southern edge of a Scotian Shelf population or the nearshore extension of an offshore population. The persistence of *P. newmani* in waters to the north and east of the Bank was consistent with an earlier study by McLaren et al. (1989), who found the species on Browns Bank almost throughout the year. We concluded that these populations may be the source of *P. newmani* populations on Georges Bank; the species may be transient along the Southern Flank of Georges Bank where the populations are unlikely to be retained or self-maintained. The spring–summer 1997 increase of *P. moultoni* on the Bank Crest, while later than that of *P. newmani*, was shown to result both from

increased transport of copepods onto the Bank from surrounding regions and from local reproduction and recruitment, with populations maintained within the clockwise gyre on Georges Bank. Copepods from the two distinct source regions were intermixed by circulation on the Bank, and the species' distributions overlapped by early summer (Bucklin et al., 2001; McGillicuddy and Bucklin, 2002). The objectively-analyzed maps for vertically-integrated (0–100 m) distribution and abundance during January to June 1999 showed strong parallels with the 1997 maps, models, and cartoons for the same months (McGillicuddy and Bucklin, 2002). Notable differences include: the relatively high abundance of *P. moultoni*

**Table 1**

Results of Analysis of Variance (ANOVA) of log<sub>10</sub> transformed abundances for the two species in the five Georges Bank regions, over six months (January to June, 1999), and three depth strata (0–15 m, 15–40 m, and > 40 m). Columns indicate: (1) source of the variability; (2) sum of squares (SS) due to each source; (3) degrees of freedom (d.f.) associated with each source; (4) mean squares, calculated as the ratios of SS/d.f.; (5) *F* statistics, calculated as the ratios of the mean squares; and (6) significance levels (*p*-values).

Source	Sum Sq.	d.f.	Mean Sq.	<i>F</i>	<i>p</i> -Values
Species	0.767	1	0.76669	8.62	0.004
Regions	0.749	4	0.18721	2.10	0.085
Months	40.54	5	8.10816	91.17	< 0.0001
Depths	5.921	2	2.96033	33.28	< 0.0001
Interactions					
1) Species × Regions	1.3703	4	0.34257	3.85	0.0056
2) Species × Months	2.0231	5	0.40462	4.55	0.0008
3) Species × Depths	2.2420	2	1.12100	12.60	< 0.0001
4) Regions × Months	2.0606	20	0.10303	1.16	0.3028
5) Regions × Depths	0.2762	8	0.03453	0.39	0.9251
6) Months × Depths	1.6605	10	0.16605	1.87	0.0565
Error	10.4948	118	0.08894		
Total	68.1046	179			

on the Southern Flank (rather than the northwest region of the Bank) in January and the widespread abundance and overlap of both species in May and June. Interannual differences in transport events, including noteworthy – and anomalous – cross-over of Scotian Shelf water onto Georges Bank in 1997 (Bisagni et al., 1996; Ji et al., 2006) likely contributed to the differences between the two years.

The deeper abundance of *Pseudocalanus* spp. on the Southern Flank in June was also observed in VPR data from June, 1995 (Fig. 9). Although VPR images cannot discriminate the two species, the data show clearly that *Pseudocalanus* spp. were abundant deeper in the water column, below the seasonal thermocline. While this pattern in vertical distribution is consistent with the net-based sampling from 1999, the abundances were much lower. The VPR-based abundances of egg-carrying *Pseudocalanus* spp. averaged over the Southern Flank were 20 m<sup>-2</sup> (0–15 m), 277 m<sup>-2</sup> (15–40 m), 1686 m<sup>-2</sup> (40–100 m), and 1983 m<sup>-2</sup> (0–100 m). However, these differences may reflect interannual variability, as the abundance of *Pseudocalanus* spp. (as well as other small copepods) increased by a factor of two-to-three on Georges Bank between 1995–1999 (Kane, 2007; Ji et al., 2013). Based on our 1997 (Bucklin et al., 2001) and 1999 (Figs. 3d and 5) observations, it seems likely that the deep *Pseudocalanus* observed with the VPR on the southern flank in 1995 were predominantly *P. moultoni*.

#### 4.1. Bank-wide patterns of distribution and abundance

Mapping of distributions (Fig. 3a–d) and calculations of Bank-wide abundances (Fig. 4) in three distinct depth strata provided

further evidence of differences between the species in habitat usage. The complex temporal and spatial patterns of temperature and salinity variation across the Georges Bank region – with marked variability among grid zones, depth strata, and months – provided an exceptional opportunity to explore the habitat preferences of the two *Pseudocalanus* species. Based on our statistical analysis (see Section 3), patterns of distribution and abundance of the two species were associated with temperature and salinity (26% of the variance for *P. moultoni*; 21% for *P. newmani*, based on multiple linear regression). Also, there were subtle (not statistically-significant) species-specific differences in these associations (Fig. 8). This result is noteworthy, since the Georges Bank region is a small fraction of the rather extensive geographic ranges of both species (Frost, 1989).

Time-series analysis for 1995–2012 by Erikson (2015) also showed differences in the responses of the two species to temperature and salinity on Georges Bank, based on intensive sampling and environmental observations by NOAA-NEFSC Ecosystem Monitoring (EcoMon) Surveys and U.S. GLOBEC broad-scale surveys during May–June each year. *P. moultoni* abundances were significantly positively correlated with depth-averaged temperature during this period, while *P. newmani* abundances were not. There were significant differences between the abundance anomalies of each species during a number of years, with no consistent pattern in relative abundances (Erikson, 2015). These analyses provided further indications that the two species may respond differently to environmental conditions, and suggested that there may be other species-specific differences in responses to conditions of their pelagic environment.

Both species had peak abundances in May, with somewhat greater concentrations of *P. moultoni* in middle and deep layers, compared to concentrations of *P. newmani* in the surface and middle layers (Fig. 4). The June increase in *P. moultoni* was largely explained by increased concentrations in deeper waters (40–100 m). Concentrations of *P. newmani* along the Southern Flank were most evident in the middle and deep layers in March (Fig. 3c and d) and in the surface layer in April (Fig. 3b). In contrast, *P. moultoni* on the Northern Flank was most evident in deep layer in May (Fig. 3d).

#### 4.2. Region-specific patterns of distribution and abundance

Analysis of depth-stratified abundances for the two species in each of the five regions allowed further discrimination of habitat usage by the cryptic species on the Bank. In three regions (Northeast Peak, Southern Flank, and Slope Water), *P. newmani* abundance increased in the deep layer in March (not seen for *P. moultoni*), followed by a sharp April increase and slight May decrease in the middle layer. In contrast, the seasonal increase for *P. moultoni* started in April in all five regions; with notable concentrations in the deep layer during May on the Northern Flank and during June on the Northeast Peak.

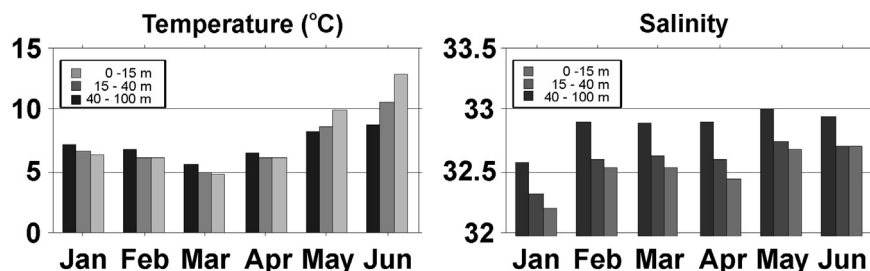


Fig. 6. Bank-wide average temperatures and salinities as a function of depth interval and month.



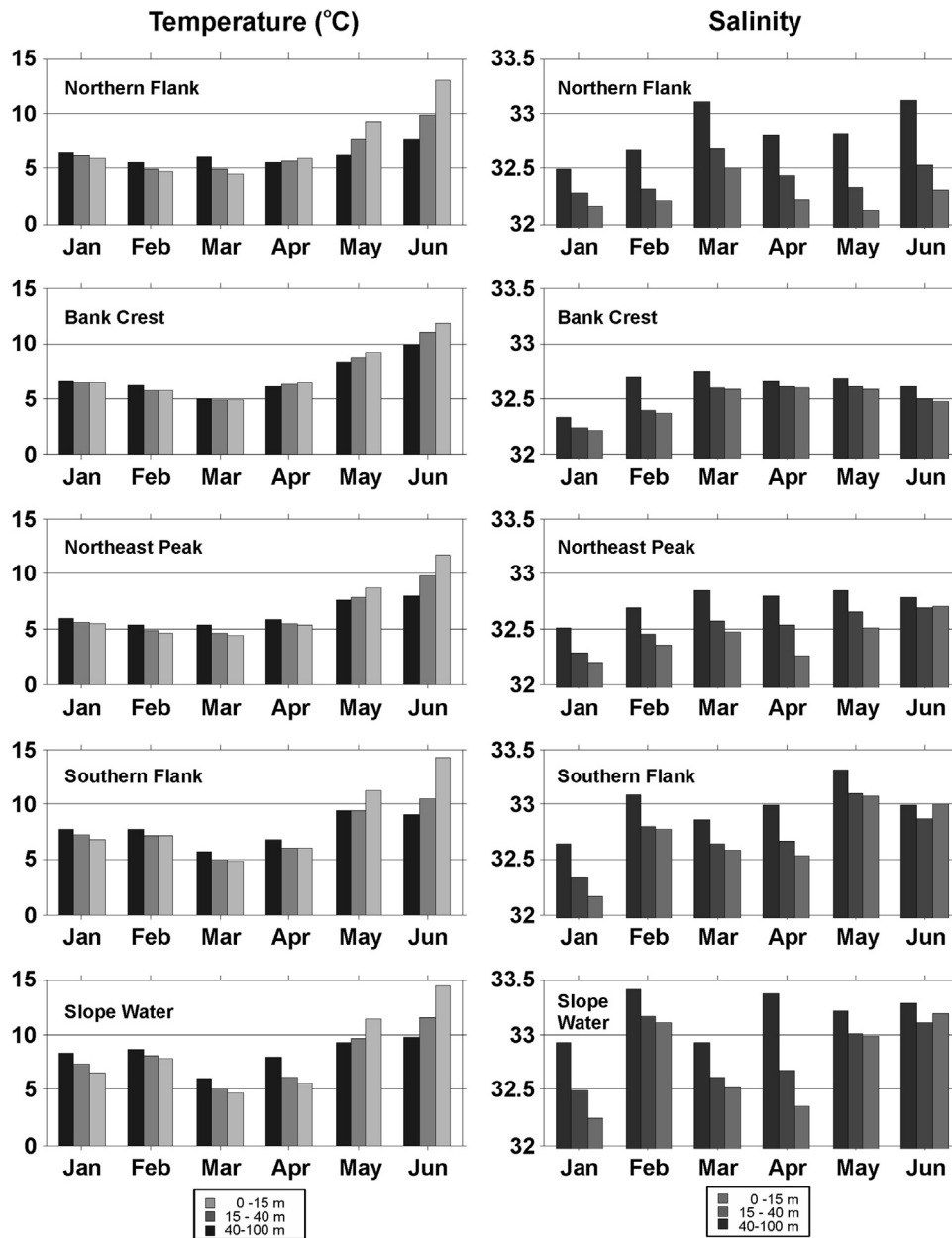


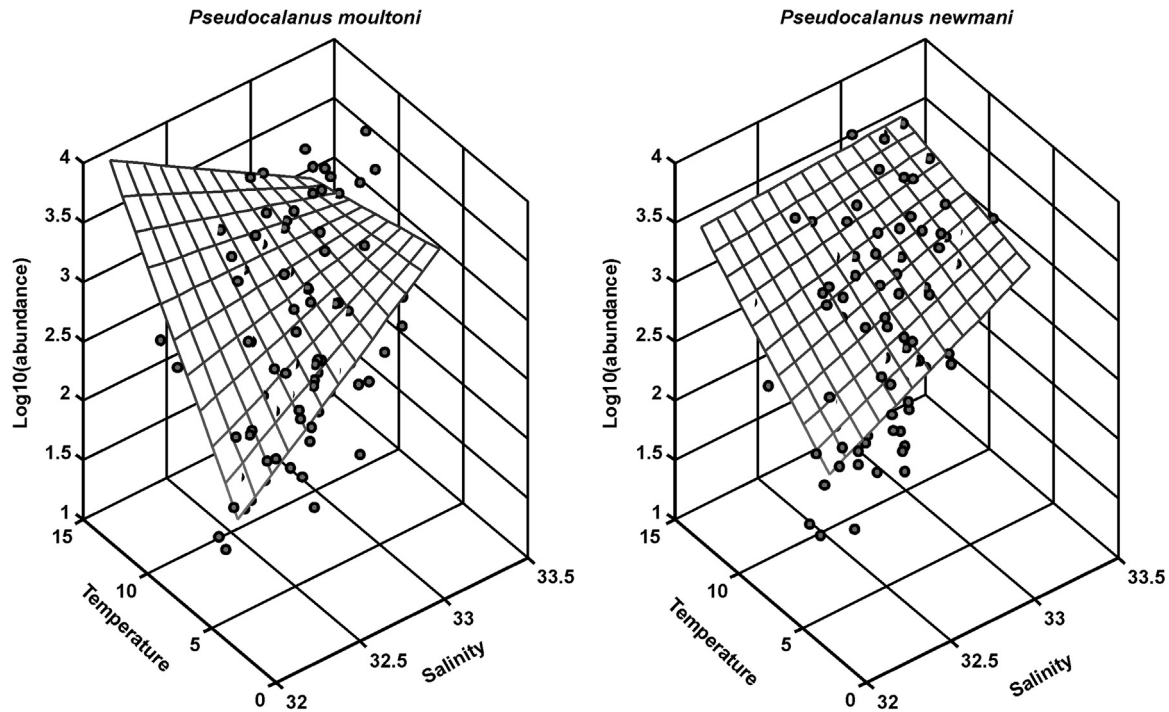
Fig. 7. Regional average temperatures and salinities as a function of depth interval and month.

**Table 2**  
Results of Analysis of Variance (ANOVA) of temperature data for the five Georges Bank regions, over six months (January to June, 1999), and three depth strata (0–15 m, 15–40 m, and 40–100 m).

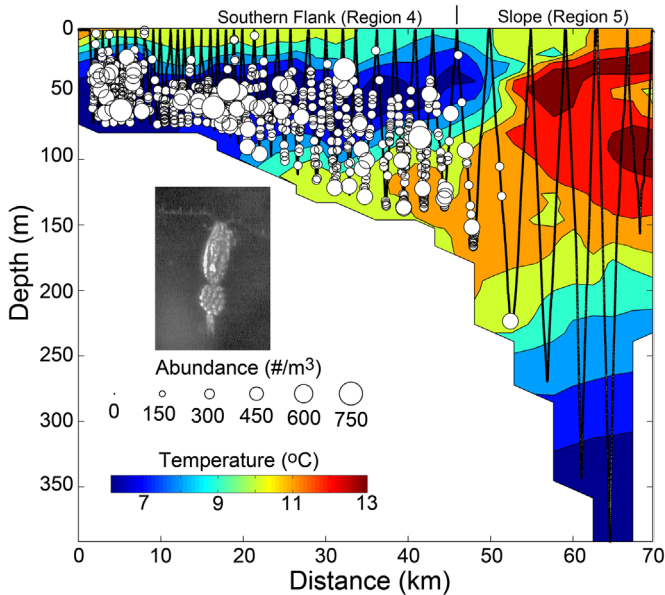
Source	Sum Sq.	d.f.	Mean Sq.	F	p-values
Regions	40.55	4	10.1375	44.13	< 0.0001
Months	343.787	5	68.7573	299.29	< 0.0001
Depths	4.884	2	2.4421	10.63	0.0002
Interactions					
1) Regions × Months	15.075	20	0.7538	3.28	0.0007
2) Regions × Depths	1.607	8	0.2008	0.87	0.5461
3) Months × Depths	54.148	10	5.4148	23.57	< 0.0001
Error	9.189	40	0.2297		
Total	469.24	89			

**Table 3**  
Results of Analysis of Variance (ANOVA) of salinity data for the five Georges Bank regions, over six months (January to June, 1999), and three depth strata (0–15 m, 15–40 m, and 40–100 m).

Source	Sum Sq.	d.f.	Mean Sq.	F	p-Values
Regions	2.49727	4	0.62432	61	< 0.0001
Months	1.89448	5	0.3789	37.02	< 0.0001
Depths	2.10203	2	1.05101	102.7	< 0.0001
Interactions					
1) Regions × Months	1.39655	20	0.06983	6.82	< 0.0001
2) Regions × Depths	0.346	8	0.04325	4.23	0.001
3) Months × Depths	0.13487	10	0.01349	1.32	0.2544
Error	0.40937	40	0.01023		
Total	8.78056	89			



**Fig. 8.** Abundance of *Pseudocalanus moultoni* and *P. newmani* versus temperature and salinity (solid dots) and the predicted model surface based on a multilinear regression of abundance versus temperature and salinity.



**Fig. 9.** Distribution of *Pseudocalanus* spp. females with eggs on Georges Bank on June 16, 1995 based on VPR data. The contours indicate seawater temperature (°C); scale is shown in color bar. Circles represent abundance in number of individual copepods per  $m^3$ . Georges Bank regions sampled were Southern Flank (Region 4) and Slope Water (Region 5), as defined in Fig. 2. Inset: VPR image of *Pseudocalanus* with attached egg sac.

#### 4.3. Vertical distributions of the cryptic species

Differences in vertical distributions were most apparent in the proportional abundances of the two species in each depth stratum during January to June, 1999. The proportional concentration of *P. moultoni* in the deepest layer (40–100 m) was apparent in May and June in the Bank-wide analysis (Fig. 4); the species showed proportional concentrations on the Northeast Peak and Southern Flank in June in the regional analyses (Fig. 5), consistent with the

1997 genetic data (Bucklin et al., 2001) and the 1995 VPR data (Fig. 9). In contrast, *P. newmani* was concentrated in the deep waters on the Bank Crest in May and the Southern Flank in April and May (Fig. 5); the Bank-wide analysis showed larger proportional concentration in deep waters in March (Fig. 4). Similar differences in the vertical distributions of the two species were observed by Manning and Bucklin (2005) in a time-series study of zooplankton in coastal waters of the western Gulf of Maine. There, *P. moultoni* was less abundant above the pycnocline in spring and summer, and *P. newmani* was generally more abundant in surface samples throughout the year.

#### 4.4. Species-specific patterns of habitat usage

We may hypothesize that differing behaviors and vertical distributions of *P. moultoni* and *P. newmani* – especially in the complex hydrographic regime of the Bank – may result in the species' differential transport and retention over Bank regions. The mechanism(s) of differential flux and retention are unclear, but may include vertical distribution in the stratified flows of frontal regions, differential responses to turbulence, and differential micro-habitat preferences.

The tidal mixing front, which typically sets up during spring around the periphery of the Bank Crest (Loder et al., 1993; Ullman et al., 2003), may help retain deeper-dwelling copepods on the Bank. Copepods in near-surface waters are subject to advection by Ekman transport, while copepods below the Ekman layer are less subject to transport. Hannah et al. (1997) identified a mechanism for convergence of drifting particles on the Bank crest, owing to the decrease in surface layer transport due to the increase in thickness of the Ekman layer associated with tidal mixing. Chen et al. (2003) modeled particle transport on Georges Bank, showing distributions of particles with tidal forcing plus realistic wind stress, and demonstrating that remaining deeper in the water column may represent a strategy to aid retention. Downward vertical migration by the chaetognath *Sagitta elegans* has been postulated as a key mechanism for on-Bank retention (Lough and Trites, 1989).

Vertical positioning in the water column, resulting in characteristic distributional depth ranges, is typical of many zooplankton species of diverse taxonomic and functional groups, including copepods (e.g., Gallager et al., 2004). On Georges Bank, concentration of abundances in deep layers may represent a strategy to avoid advective transport and loss for small copepods like *Pseudocalanus* spp. We hypothesize that the deeper distribution of *P. moultoni* will prove advantageous if significant warming of the northwest Atlantic Ocean takes place as a result of climate change. The observed differences in species-specific patterns of vertical distribution between *P. moultoni* and *P. newmani* require additional analysis to understand their relationships to environmental variation (biological and physical parameters), the behavioral mechanisms that generate and maintain them, and the consequences for advective transport, retention, and loss from the Bank.

#### 4.5. Ecological significance of cryptic species in pelagic biodiversity assessments

It is critically important that cryptic species be routinely and accurately discriminated in analyses of pelagic biodiversity. Although the importance of these species in determining ecosystem dynamics and responses to climate change is currently unclear, species identification is the foundation of understanding niche parameters, physiological tolerance limits, characterization of trophic relationships, and sensitivities of species, food webs, and communities to environmental variability. The goal of complete and accurate characterization of species diversity is clearly in reach with use of DNA-based detection and identification approaches.

*Pseudocalanus* spp. offer a useful case history of the complexities of zooplankton diversity and biogeographical distributions. Recent investigations by Aarbakke et al. (2011, 2014) have continued to document new findings in this regard. It is unclear whether the emerging and more complicated patterns, which appear to confirm broader habitat preferences and biogeographic distributions, result from recent responses and rearrangements due to changing conditions, species introductions (e.g., ballast water transport), insufficient sampling, and/or prior inability in species identification. In any case, the emerging and more accurate global view of zooplankton species diversity will provide a sound and valuable basis for examining and predicting species- and community-level responses of zooplankton to bio-physical changes driven by climate change.

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