Biological-physical processes determining *Pseudocalanus* spp. (Crustacea; Copepoda) distribution and abundance on Georges Bank in the Northwest Atlantic

Ann Bucklin, Dennis J. McGillicuddy, and Christopher A. Manning

Abstract

The planktonic copepod sibling species, *Pseudocalanus moultoni* and *P. newman*i, co-occur on Georges Bank (Northwest Atlantic), but differ in Spring-time evolution of distribution and abundance. Previous studies have described Bank-wide species' distribution and abundance in monthly snap-shots from January to June of 1997 and 1999, using species-specific PCR (SS-PCR) to discriminate the sibling species. Numerical models were used to infer the biological sources and sinks implied by the observed changes in abundance between monthly surveys and the flow during the intervening periods. Based on such observation, visualization, and modeling, the two species appeared to have distinct sources in the early spring, but overlapping distributions by early summer, with the springtime increase for both species driven by a complex mixture of hydrodynamic transport and species-specific population dynamics. New observations have examined distribution and abundance of the two species at smaller scales. We describe here studies of *Pseudocalanus* spp. vertical distributions with respect to stratification and mixing, and the distributions of other biological, chemical, and physical moieties in the water column. Field collections were done along transects in two areas: across a tidal-mixing front on Georges Bank, and along in near-shore water of western Gulf of Maine. Both field studies demonstrated that water column stratification and stratified flow may differentially affect the two *Pseudocalanus* spp. The previously observed differences in Bank-wide patterns of *P. moultoni* and *P. newmani* may result from processes at small-scales, including different vertical distributions under stratified conditions, different responses to turbulence, and different micro-habitat preferences

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Introduction

The planktonic copepod sibling species, *Pseudocalanus moultoni* and *P. newman*i, occur sympatrically during the spring and summer on Georges Bank. Despite their marked morphological similarity, the species differ in many aspects of their ecology, including patterns of distribution and abundance; preferred habitat; and seasonal timing of reproduction. The two species cannot be reliably distinguished using morphological characters, but DNA sequence variation of mitochondrial DNA (mtDNA) indicates that they are old and genetically diverged species (Bucklin et al., 1998). A simple molecular protocol, species-specific PCR (SS-PCR), was developed to reliably identify and discriminate individuals of *P. moultoni* and *P. newmani* (see Bucklin et al., 1999, 2001).

McGillicuddy and Bucklin (2002) reported the results of numerical modeling experiments using observed distributions in a known physical field. Physical and biological controls on the springtime distributions of *P. moultoni* and *P. newmani* were examined by assimilating the 1997 broadscale observations into a coupled physical-biological model. The forward problem was posed as an advection - diffusion - reaction equation for the copepod concentration. The adjoint method of data assimilation was used to invert for the biological sources and sinks implied by the observed changes in abundance between surveys and the flow during the intervening period (for details, see McGillicuddy and Bucklin, 2002).

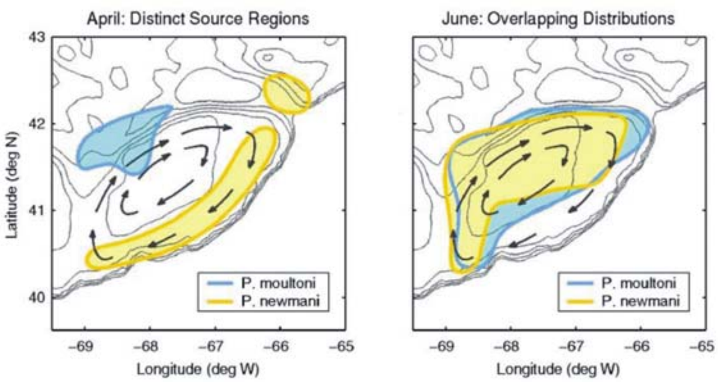

Fig. 1. Intermingling of *P. moultoni* and *P. newmani* during Spring 1997 on Georges Bank. Contours outline population centers of the two species and are adapted from the results of a data assimilative coupled physical-biological model. The clockwise circulation on Georges Bank is depicted by arrows. (Figure from McGillicuddy and Bucklin, 2002)

Both species' overall abundances increased during Spring 1997 and 1999, with maximum abundances peaking in May or June of each year. However, the seasonal evolution of abundance patterns differed between the two species and, to a lesser degree, between the two years. McGillicuddy and Bucklin (2002) speculated that the spring-summer increase of *P. moultoni* on the crest of the Bank in 1997 resulted both from increased transport of copepods onto the Bank from surrounding regions and from reproduction of individuals that persisted within the anticyclonic gyre over the Bank, although they could not discriminate between these processes based on the observed distributions. They further speculated that concentrations of *P. newmani* on the northeastern edge of the sampled domain represented either the southern edge of a Scotian Shelf population or the nearshore extension of an offshore population. If so, 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 persistence of *P. newmani* in waters to the north and east of the Bank is consistent with an earlier study by McLaren et al. (1989), who found the species on Browns Bank almost throughout the year. These speculations are also consistent with the biogeographic distributions described for the two species by Frost (1989), who considered *P. moultoni* to be a coastal species and *P. newmani* to be a cosmopolitan, oceanic species.

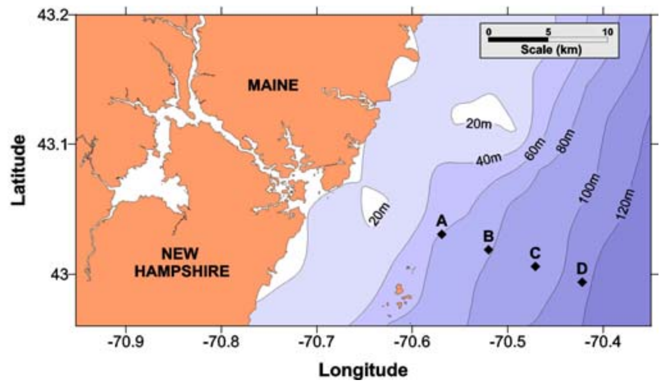

Fig. 2. Project REACH sampling transect in near-shore waters of the western Gulf of Maine. Collections were made a stations locations indicated by A, B, C, and D. (Figure from Manning, 2003)

In order to understanding the mechanisms and processes underlying the differences in the species' Bank-wide patterns of distribution and abundance, we examined small-scale patterns of abundance in vertically-stratified collections along a transect across a tidal mixing front on Georges Bank. The tidal-mixing front on the southern flank of Georges Bank is a persistent and predictable feature which defines a boundary between physical (the shallow, well-mixed waters of the Bank crest vs. the deeper seasonally-stratified waters of the flank; Garrett et al., 1978) and biological regimes (see e.g., Mountain and Taylor, 1996). Within the well mixed area, chlorophyll levels and rates of primary production are higher than in surrounding stratified waters (O'Reilly et al., 1987); the phytoplankton assemblage is dominated by diatoms in well-mixed regions vs. dinoflagellates in stratified waters (Cura, 1987). There are characteristic differences in the species composition of the zooplankton assemblage (Casas et al., 1995).

Another study to resolve the vertical distributions of the two *Pseudocalanus* spp. is being carried out in near-shore waters of the western Gulf of Maine, as part of the Regional Ecology and Coastal Hydrography (REACH) project (see http://www.REACH.unh.edu; Manning, 2003; Fig. 2). The Western Maine Coastal Current which flows generally south through this region, is stratified in summer months, and mixed to a depth of approximately 100m in winter (Bisagni et al. 1996). This flow may feed Massachusetts Bay and Georges Bank, acting as a supply for copepod species to these areas (Durbin 1997), although the degree to which this occurs is still debated (McGillicuddy et al. 1998). These coastal waters are nutrient-rich, with high phytoplankton productivity (Durbin 1997) that in turn supports an abundant copepod community (Bigelow 1924, Turner 1994). This is a useful study area, since as in most coastal oceans in temperate zones, the temporal/spatial patterns of stratification and vertical mixing exert considerable control on the biological system.

Intercomparison between these studies in different ocean areas – Georges Bank vs. near-shore waters – is intended to work toward mechanistic understanding of the small-scale processes that determine differences observed in Bank-wide patterns of distribution and abundance of the two sibling species of *Pseudocalanus*. Field studies in different ocean regions are needed, since patterns of distribution and abundance at any scale for a given copepod species may be strongly influenced by habitat and environmental differences.

Methods and Approach

A simple molecular protocol, species-specific PCR (SS-PCR), was used to identify and discriminate female *P. moultoni* and *P. newmani* in sample aliquots (see Bucklin et al., 1999, 2001). Proportions of the two species determined by SS-PCR were applied to counts of *Pseudocalanus* spp., provided by K. Wishner (University of Rhode Island) for the cross-frontal study and done by C.A. Manning (UNH) for the near-shore study (Manning, 2003).

Vertically-stratified zooplankton samples were collected during a June 1999 cruise to examine cross-frontal exchange at the tidal-mixing front on the southern flank of Georges Bank. Samples were collected at closely-spaced stations, with the timing of collections designed to reflect different points in the tidal cycle. Concentrations of the two species were estimated for samples taken from 10m strata throughout the 40m to 50m deep water column.

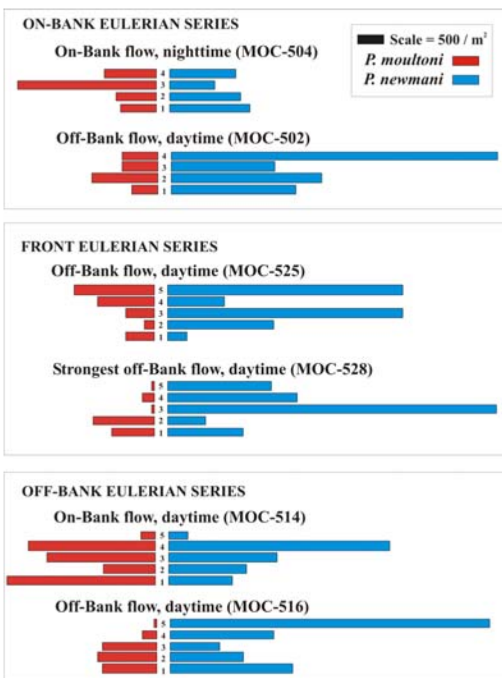

Fig. 3. Abundances of *Pseudocalanus* spp. in vertically-stratified samples collected in samples across the tidal-mixing front on Georges Bank in June 1999

Zooplankton samples were also collected along a cross-shelf transect in near-shore waters of the western Gulf of Maine from April 2002 to March 2003 (Fig. 2). Estimates of female *Pseudocalanus* spp. abundance in vertically-stratified samples were made by counting the mixed species and determining their relative abundance in a sample aliquot using SS-PCR (Manning, 2003). Data were analyzed and visualized to compare seasonal patterns of abundance and vertical distributions of the two species with respect to stratification and mixing of the water column.

Results and Discussion

Small-scale processes across a tidal-mixing front: Analysis of concentrations of *Pseudocalanus* spp. along a transect across the tidal mixing front revealed significant differences between the two species (Fig. 3). In all samples, *P. moultoni* was less abundant. Notably, *P. moultoni* showed relatively lower abundance in surface strata. In contrast, *P. newmani* was more frequently most abundant in the surface layers. Analysis of fluxes (or transport of copepods in currents as measured by the ADCP) supported our hypothesis that *P. moultoni* are retained and concentrated within the 60 m isobath (Fig. 4). The mechanism 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. Future studies of these patterns and their causes are planned to examine distributional patterns, if possible with measurements of transport and flux. These results will be integrated and assimilated into biological / physical models, in order to provide mechanistic understanding of the processes determining the patterns observed at both small- and Bank-wide scales.

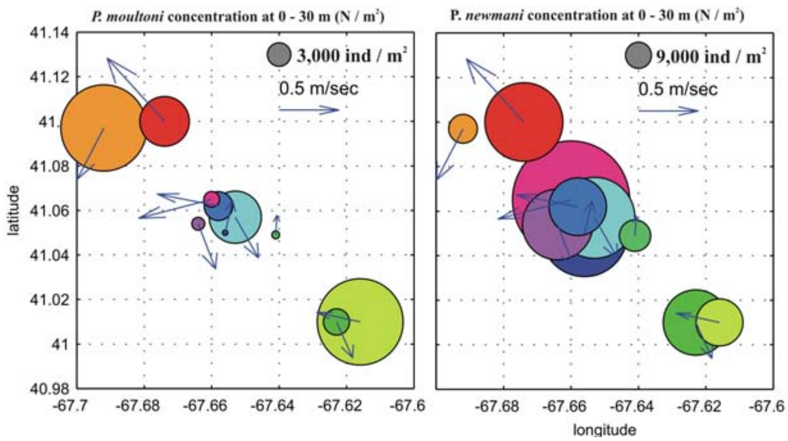

Fig. 4. Concentrations of *P. moultoni* and *P. newmani* (numbers m-2) vs. ADCP velocity measurements (m sec-1, averaged over 0 - 30 m) during the southern flank cross-frontal exchange experiment in June 1999.

Near-shore waters of the western Gulf of Maine: Both *P. moultoni* and *P. newmani* were present throughout the year in the western Gulf of Maine. Stratification of the water column had a marked effect on the vertical distributions of both species, which showed strong vertical gradients in samples taken during Summer. Under stratified conditions, *P. moultoni* was almost absent from surface waters, while *P. newmani* was present in the surface at much higher levels than in deep samples (Fig. 5). This pattern of vertical segregation was no longer evident after the water column became fully mixed. These differences suggest that individuals of the two species respond differently to the vertical distribution of some biological, chemical, or physical property of the water column. Such differences in vertical distribution under stratified conditions will have significant consequences for rates and directions of advective transport, and thus for patterns of distribution and abundance at meso- to large spatial scales.

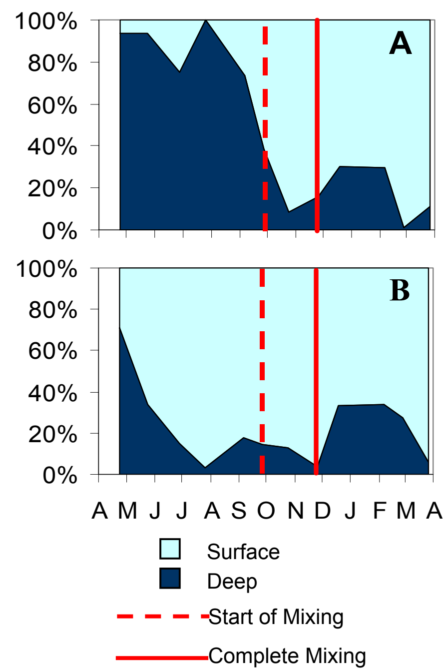

Fig. 5. Relative abundances of *Pseudocalanus moultoni* (A) and *P. newmani* (B) in pooled surface and deep samples from REACH stations. Figure from Manning (2003)

Conclusions

Despite their morphological similarity, two sibling species of *Pseudocalanus, P. moultoni* and *P. newmani*, differ markedly in patterns of distribution and abundance on Georges Bank. Observations and numerical modeling of these patterns through the period of Spring population increase during 1997 (with comparative observations during 1999) suggested that the two species may have different mechanisms of population retention on Georges Bank. Small-scale examination of vertical distributions of the two species across a tidal-mixing front on Georges Bank, during June 1999, revealed significant differences between *P. moultoni* and *P. newmani*. Comparative studies of *Pseudocalanus* spp. in near-shore waters of the Gulf of Maine during 2002-2003 similarly revealed distinctive differences in their vertical distributions under stratified conditions. We hypothesize that the different Bank-wide patterns may result from differential vertical distributions in stratified flows of frontal regions, differential responses to turbulence, and differential micro-habitat preferences. Future studies are planned of the two species' seasonal patterns of abundance, including description of their vertical distributions, in diverse regions and spanning a range of spatial scales from micro- to meso-scales.

Acknowledgments

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