

# Expansion and homogeneity of the vertical distribution of zooplankton in a very deep mixed layer

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**ABSTRACT:** During stratification over 70% of the zooplankton >100 µm in the Gulf of Aqaba (Eilat), Red Sea, resided in the upper 100 m. In the course of winter mixing, the vertical pattern became more homogeneous, reaching an almost complete uniformity when the vertical mixing exceeded 500 m depth. The zooplankton expanded its vertical distribution throughout the mixed layer. However, full homogeneity, such as would be expected for a passive tracer and observed for phytoplankton, occurred for zooplankton only in the upper section of the mixed layer. Homogeneity occurred for zooplankton passing through 750 µm mesh but not for larger crustaceans. The copepod *Pleuromamma indica* retained its diel vertical migration regardless of mixing but expanded its nocturnal range under mixing conditions. The observed homogeneity of zooplankton could have been reached either by passive entrainment with the mixing water or by isotropic swimming of the animals, or both. The ecological implications of the expansion of zooplankton distribution for predator-prey relationships and particle fluxes are discussed.

**KEY WORDS:** Plankton · Vertical mixing · Red Sea

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## INTRODUCTION

Previous studies addressing the relationship between the vertical distribution of zooplankton and water column stratification focused on small-scale patterns within the photic layer (≤100 m depth) (Buckley & Lough 1987, Checkley et al. 1992, Incze et al. 1996), indicating a more even zooplankton distribution in well-mixed than in stratified columns. For example, Checkley et al. (1992) compared the vertical distribution of zooplankton >100 µm in 2 different neritic sites, a tidally mixed column near Japan and a stratified column in the Gulf of Mexico. While a roughly uniform vertical distribution was found in the well-mixed site, discrete vertical patterns occurred in the stratified site. A similar homogeneity extending to 100 m in a well

mixed water column and a segregated vertical distribution in stratified water columns were reported for *Calanus finmarchicus* and *C. helgolandicus* in the Celtic Sea (Williams 1985).

Deep winter mixing reaching aphotic layers occurs in the Sargasso Sea (Menzel & Ryther 1960, Longhurst 1998), in high latitudes (Longhurst 1998) and in warm-core eddies (Tranter et al. 1980, Bradford et al. 1982, Zohary et al. 1998). The consequent changes in the vertical distribution of phytoplankton, but not zooplankton, under such mixing conditions are well documented (Sverdrup 1953, Bradford et al. 1982, Lindell & Post 1995, Zohary et al. 1998).

Unusually deep mixing occurs every winter in the northern part of the Gulf of Aqaba (Eilat) in the Red Sea (Genin et al. 1995). Seasonal conditions change; from stratification with a very shallow (0 to 30 m) wind-mixed layer during the warm months (May to September) to deep convective mixing, extending several

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hundred meters below the surface during the winter (Reiss & Hottinger 1984, Wolf-Vecht et al. 1992, Genin et al. 1995). Reports from that region attributed the observed seasonality in the community structure of ultraphytoplankton (Lindell & Post 1995), coccolithophores (Winter et al. 1979) and microplankton (Kimor & Golandsky 1977) to water-column stability and the degree of mixing. For example, ultraphytoplankton, including *Synechococcus* and small eukaryotic cells, were uniformly distributed throughout a 600 m deep mixed layer during the cold winter of 1992/1993 (Lindell & Post 1995), indicative of their passive entrainment by mixing. A similar homogeneous distribution in the mixed layer was reported for large (>65 µm) diatoms and dinoflagellates during winter 1975 (Kimor & Golandsky 1977) and for coccolithophores in February 1976 (Winter et al. 1979). Likewise, the extended distribution of typical Red Sea epipelagic oncaeid species down to 300 m depth in the Gulf during winter 1999 was also ascribed to the nearly homogeneous and well oxygenated water column (Böttger-Schnack et al. 2001). This study further explores the effect of the deep convective mixing in the Gulf of Aqaba (Eilat) on the vertical distribution of zooplankton and on the vertical migration of the calanoid copepod *Pleuromamma indica* Wolfenden, 1905.

## MATERIALS AND METHODS

The study was carried out at Stn A (29° 28' N, 34° 56' E), a 600 to 700 m deep site, 3 km off the H. Steinitz Marine Biology Laboratory in the northern part of the Gulf of Aqaba (Eilat), Red Sea. Reiss & Hottinger (1984), Wolf-Vecht et al. (1992) and Genin et al. (1995) described the climatic and oceanographic conditions at this site. The photic layer (1% light level) is around 100 m.

This report is part of a 2 yr study (January 1991 through June 1993) of zooplankton dynamics at Stn A. Here we present the results of all our winter cruises, carried out when the vertical mixing surpassed 100 m (December 1991, January, February and December 1992, January and February 1993) and representative cruises from summer when the water column was stratified (August to September 1992, June 1993). Zooplankton samples were taken aboard the RV 'Jadran' using a WP2 net (HydroBios) of 57 cm mouth diameter, and 100 µm mesh, with a pre-calibrated flow meter (TSK). The net was hauled vertically at approx. 0.8 m s<sup>-1</sup> and choke-closed at the top of the sampled layer using a messenger. Samples were preserved upon retrieval in a 4% buffered formalin-sea water solution. Two sets of net hauls were performed on each cruise in 1991 and 1992, one around midday, the other around

midnight. Each set consisted of 6 vertical hauls, each sampling a 100 m layer from 600 m to the surface. The average volume filtered per sample was 26 ± 11 m<sup>3</sup> (n = 102). A full profile took 3 to 4 h to complete. For logistical reasons, only the midday tow was made in each of the 1993 cruises. The data presented here are based on a total of 15 vertical profiles (9 midday, 6 nighttime; Table 1).

Zooplankton samples were counted in the laboratory using a dissecting microscope. Sub-samples were taken using a Stempel pipette so that at least 400 specimens were counted per sample. In order to examine the effect of body size on the level of vertical homogeneity in 2 profiles (noon in February and September 1992), the samples were size-fractionated using a column of 100, 400, and 750 µm mesh filters. The counted specimens were sorted into the following groups: large phytoplankton (dinoflagellates and diatoms), tintinnids, sarcodines, nauplii of copepods, copepods (copepodites and adults), molluscs, chaetognaths, and a combined category of all other specimens. Profiles having less than 1500 specimens per 1 m<sup>2</sup> for a particular group were omitted from the analysis. In order to compare the distribution of the strong diel migrating copepod *Pleuromamma indica* between extreme conditions of stratification and deep mixing, all the copepodites and adults of this species sampled in the day and night profiles from 3 summer and 3 winter cruises from 1992 were counted.

Temperature and salinity profiles were measured on accompanying cruises using a STD (Applied Microsystems, STD-12) within 13 d prior to or after each zooplankton sampling. The stratification at the study site is determined mostly by temperature, with a negligible effect of salinity (Reiss & Hottinger 1984, Genin et al. 1995). Hence, the bottom of the mixed layer was defined as the shallowest depth at which the tempera-

Table 1. Dates and times of zooplankton sampling and the corresponding mixed layer depth (MLD) at 'Stn A' in the Gulf of Aqaba (see 'Materials and methods' for the calculation of the MLD in the winter months)

Zooplankton	Day	Night	MLD (m)
11–12 Dec 1991	+	+	146
16–17 Jan 1992	+	+	316
13–14 Feb 1992	+	+	510
14–15 Jul 1992	+	+	12
11–12 Aug 1992	+	+	24
17–18 Sep 1992	+	+	20 <sup>a</sup>
9–10 Dec 1992	+	+	214
6 Jan 1993	+		309
9 Feb 1993	+		549
23 Jun 1993	+		17

<sup>a</sup>Calculated according the summer average

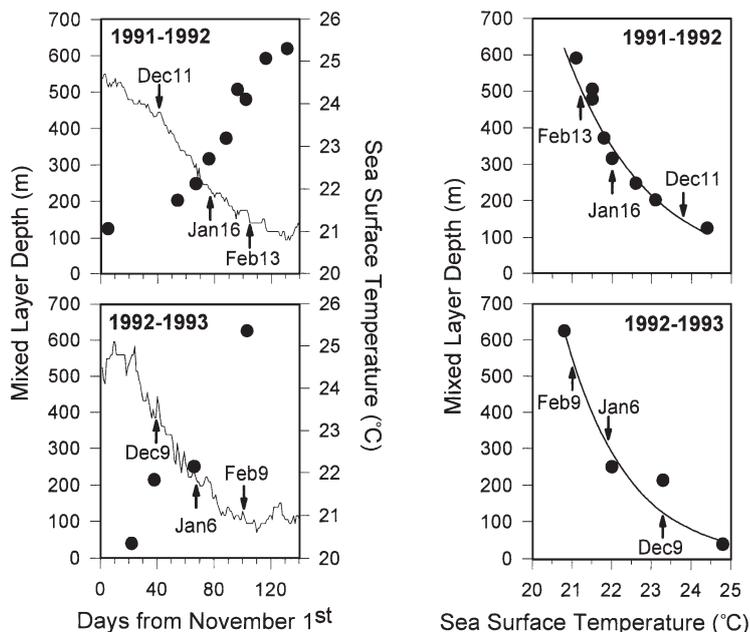


Fig. 1. Left panels: Variations in the SST (line), measured daily from the pier of the marine underwater observatory, and MLD (closed circles), measured in Stn A, during the winter months of 1992 and 1993 (November to March). Right panels: MLD plotted against the corresponding SST. The exponential regression equations are  $MLD = 13 \times 10^6 e^{-0.48SST}$  ( $R^2 = 0.97$ ,  $n = 8$ ) for winter 1991/1992 and  $MLD = 38 \times 10^7 e^{-0.64SST}$  ( $R^2 = 0.92$ ,  $n = 4$ ) for winter 1992/1993. Arrows in both panels indicate the date of our plankton cruises

ture declined by at least  $0.1^\circ\text{C}$  (Simó & Pedrós-Alió 1999). The mixed layer depth (MLD) was fairly constant during summer, never exceeding 30 m; therefore, a separation of 13 d between the zooplankton and STD measurements in this season was not critical for the subject addressed in this work. However, an accurate determination of mixing depths at the time of zooplankton sampling was important in the winter. Sea surface temperature (SST) was measured daily from the pier of the Marine Underwater Observatory north to the Marine Biology Laboratory (Genin et al. 1995). The MLD and the daily change in the SST, measured between November and March in 1992 and 1993, are presented in Fig. 1. During these periods the MLD at Stn A increased continuously corresponding to the progressive decline in the SST measured from the pier (see Fig. 1, left panels). Note that the maximal MLD was at least 600 m in both March 1992 and February 1993. The MLD increased exponentially with the decrease in the SST: in winter 1991/1992,  $MLD = 13 \times 10^6 e^{-0.48 \times SST}$ ,  $R^2 = 0.97$ ,  $n = 8$ ; and in winter 1992/1993,  $MLD = 38 \times 10^7 e^{-0.64 \times SST}$ ,  $R^2 = 0.92$ ,  $n = 4$  (Fig. 1, right panels). For zooplankton samples taken within 1 d of direct STD measurement, the measured MLD value was used. Otherwise, the MLD was extrapolated based on the above exponential regression lines.

As mixing depths did not exceed 30 m during the summer (Genin et al. 1995, B. Lazar unpubl. data), all samples from June through September were pooled for the quantitative analyses into a single category, termed 'Summer'. All other samples were separated based on cruise dates into 3 monthly periods: December, January, and February, corresponding to intermediate (146 to 214 m), deep (309 to 316 m), and very-deep (510 to 549 m) mixing, respectively (Table 1).

Vertical profiles of chlorophyll *a* (chl *a*) were measured between the surface and 500 to 550 m on 10 February 1992, when the MLD was 478 m, and on 11 August 1992, when the water column was stratified. Chlorophyll measurements were made using the standard technique of 24 h dark extraction in 90% acetone using water samples of 250 ml collected with Niskin bottles and filtered on GF/F filters. The chlorophyll concentration in the extracted solution was read with a pre-calibrated Turner Design Model 10 Fluorometer.

The abundance of zooplankton was calculated in terms of both the density ( $\text{no. m}^{-3}$ ) and the proportion (%) found in each 100 m layer. Two ratios were used to characterize

the vertical homogeneity:  $R_1$ —the abundance in the top 100 m divided by that in the 100 to 200 m layer; and  $R_2$ —the abundance in the 0 to 200 m divided by that in the 200 to 400 m layer.  $R_1$  and  $R_2$  were expected to be highest during the summer and lowest, near unity, after the vertical mixing had reached 200 and 400 m, respectively. The effect of the period (4 'levels') on each of the ratios ( $R_1$  and  $R_2$ ) was tested using 1-way ANOVA followed by Tukey's HSD post-hoc test (non-equal N) after log transforming the ratios to comply with the requirement for homogeneity of variance ( $p > 0.05$ , Cochran Test). Statistical tests were performed using Statistica (1999 Edition, StatSoft).

## RESULTS

The depth of the mixed layer was shallower than 24 m in all summer cruises (June to September), around 150 to 200 m in December, ca. 300 m in January, and exceeded 500 m in February (Table 1).

Changes in the vertical distribution of zooplankton co-varied with changes in the mixed-layer depth (Fig. 2). Under stratified conditions in the summer, 60 to 90% of the zooplankton in the water column was found in the photic layer (upper 100 m) with less than

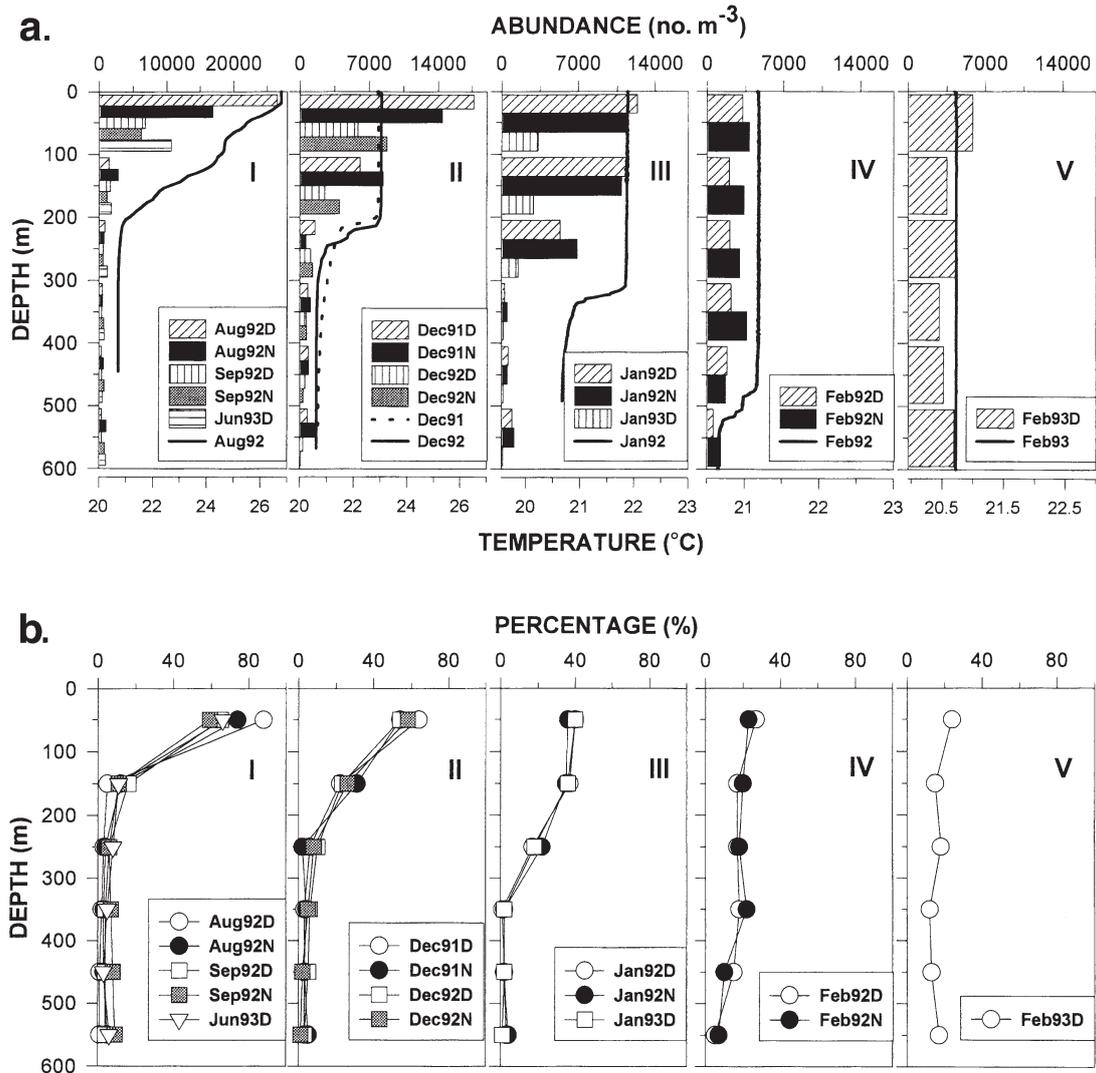


Fig. 2. Vertical profiles of total zooplankton and temperature in Summer (I), December (II), January (III) and February 1991 to 1993 (IV, V). (a) Zooplankton abundance (bars) and temperature (lines); (b) percentages of zooplankton in each layer of the total integrated over the 600 m water column during the same periods as in a. The letters D and N to the right of the date in the legends indicate day or night profile, respectively. Note the different ranges and scales used for temperature in the different plots

16% in the layer just below it (100 to 200 m). In December, when vertical mixing reached ca. 150 to 200 m, only 54 to 64% of the zooplankton resided in the upper 100 m, with 22 to 31% in the 100 to 200 m layer. When mixing exceeded 300 m, over 90% of the zooplankton in the water column was evenly distributed within the mixed layer. A nearly uniform distribution of zooplankton was observed throughout the upper 400 to 500 m in February. This pattern was evident in both day and night and in different years (Fig. 2b) despite substantial inter-annual differences in the overall abundance of the zooplankton (Fig. 2a).

Values for  $R_1$  and  $R_2$  spanned an order of magnitude throughout the year, ranging from 18 to 19 in summer to nearly 1.0 in winter (Fig. 3).  $R_1$  sharply declined in

December, when the vertical mixing of the water reached 146 to 214 m, reaching unity in January after mixing had exceeded 200 m.  $R_2$  declined more gradually, approaching unity only in February, after the water-column mixing had surpassed 400 m depth (Fig. 3). The effect of period on each of the ratios  $R_1$  and  $R_2$  was highly significant (ANOVA,  $p < 0.001$ ; Table 2). Post-hoc tests (Tukey HSD) indicated significant differences ( $p < 0.01$ ) between  $R_1$  during the summer and  $R_1$  during each of the 3 winter months, with non-significant differences ( $p > 0.1$ ) between winter months. Significant differences in  $R_2$  were found only between February and each of the 3 other periods (Table 2).

Nauplii, copepods, chaetognaths, molluscs, tintinnids, sarcodines, and phytoplankton, passing through



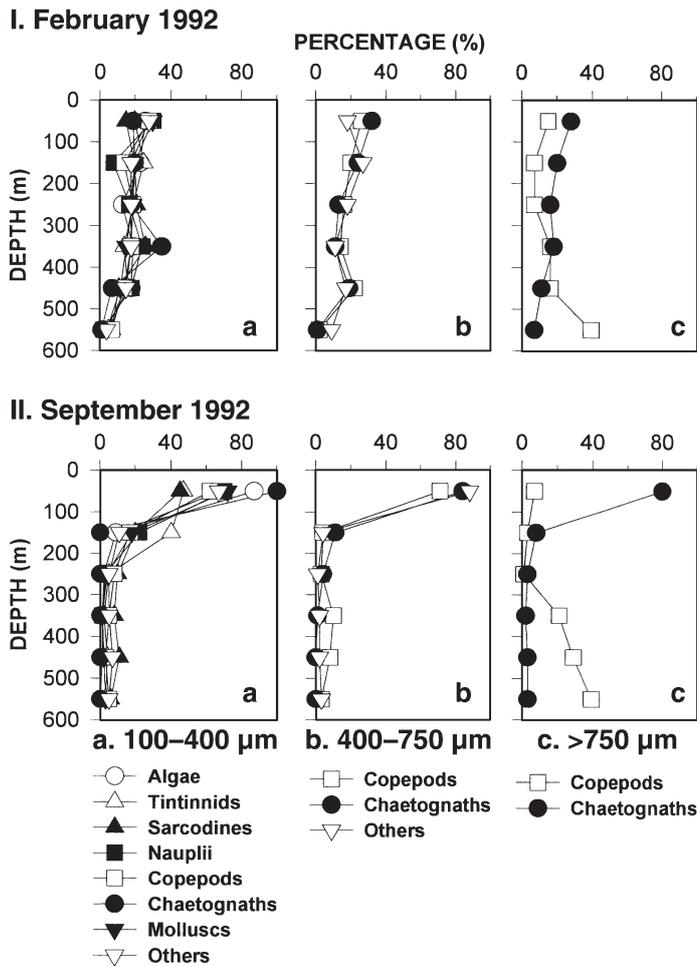


Fig. 4. Vertical profiles of size-fractionated zooplankton groups during the day in February 1992 when the mixed layer depth was 510 m (I, upper panels) and in September 1992, when the mixed layer was approx. 20 m deep (II, lower panels). (a) The group of smallest animals, passing through 400 µm and retained on 100 µm mesh; (b) the group of intermediate animals, passing through 750 µm and retained on 400 µm mesh; (c) the group of largest animals, retained on 750 µm mesh. Zooplankton abundance is presented as percentages in each 100 m thick layer of the total integrated over the 600 m water column. See Table 3 for the total number of animals in each group. Profiles with less than a total of 1500 ind. m<sup>-2</sup> (integrated over the entire water column) were omitted from the analysis

Table 3. Abundance (ind. m<sup>-2</sup>) of the size-fractionated groups integrated over the 600 m deep column in diurnal hauls in February 1992, when the mixed layer depth was 510 m, and September 1992, when the mixed layer depth was around 20 m

Mesh size (µm)	Month	Algae	Tintinnina	Sarcodina	Nauplii	Copepoda	Chaetognatha	Mollusca	Others
100–400	Feb	$2.2 \times 10^5$	$7.0 \times 10^4$	$1.5 \times 10^4$	$1.0 \times 10^5$	$5.7 \times 10^5$	$2.9 \times 10^3$	$3.8 \times 10^4$	$1.1 \times 10^5$
	Sep	$3.6 \times 10^4$	$3.4 \times 10^4$	$2.3 \times 10^4$	$1.1 \times 10^5$	$5.7 \times 10^5$	$2.5 \times 10^3$	$7.9 \times 10^4$	$1.1 \times 10^5$
400–750	Feb					$4.6 \times 10^4$	$5.7 \times 10^3$		$3.5 \times 10^3$
	Sep					$6.7 \times 10^4$	$2.5 \times 10^3$		$8.2 \times 10^3$
>750	Feb					$1.5 \times 10^3$	$5.2 \times 10^3$		
	Sep					$4.8 \times 10^3$	$3.5 \times 10^3$		

bly stratified,  $R_1$  ranges from 3.6 and higher year-round (Hopkins 1982, Böttger 1987, Schneider et al. 1994, Mazzocchi et al. 1997), with extreme values of 13 to 16 in the Red Sea (Weikert 1982, Beckmann 1984).

For logistical reasons, temperature profiles could not be obtained simultaneously with zooplankton profiles during this study. Nevertheless, simultaneous measurements of sea-surface temperature and mixed layer depth (Fig. 1, right panel) indicated that within a season the former variable was a reliable predictor of the latter. Thus, our error in inferring mixed layer depth based on a SST during the days of our zooplankton sampling unlikely exceeded 50 m.

Our coarse sampling protocol (once a month) and lack of replication (single day and night profiles per cruise) weakened our conclusion regarding the correspondence between mixing and animal distribution. Nevertheless, the repetition of the same pattern during the 2 winters of our study strengthened that conclusion, as did the reports by Almeida Prado-Por (1983) and Böttger-Schnack et al. (2001) from our study site during 2 additional winters (1975, 1999). Almeida Prado-Por (1983) observed a fairly uniform vertical distribution of calanoid copepods between the surface and 500 m during winter 1975, while Böttger-Schnack et al. (2001) reported homogeneity of epipelagic cycloids throughout the upper 350 m in late winter 1999.

The effect of vertical mixing on the spreading and homogeneity of zooplankton distribution was reported from other oceans but on much smaller spatial and temporal scales (20 to 80 m; a few days). Incze et al. (1990) reported such homogeneity for microzooplankton throughout the upper 70 m of the water column in the north-western Gulf of Alaska, Haury et al. (1990) observed it for larvaceans in the upper 80 m in Monterey Bay, California, while Lagadeuc et al. (1997) reported such homogeneity throughout the

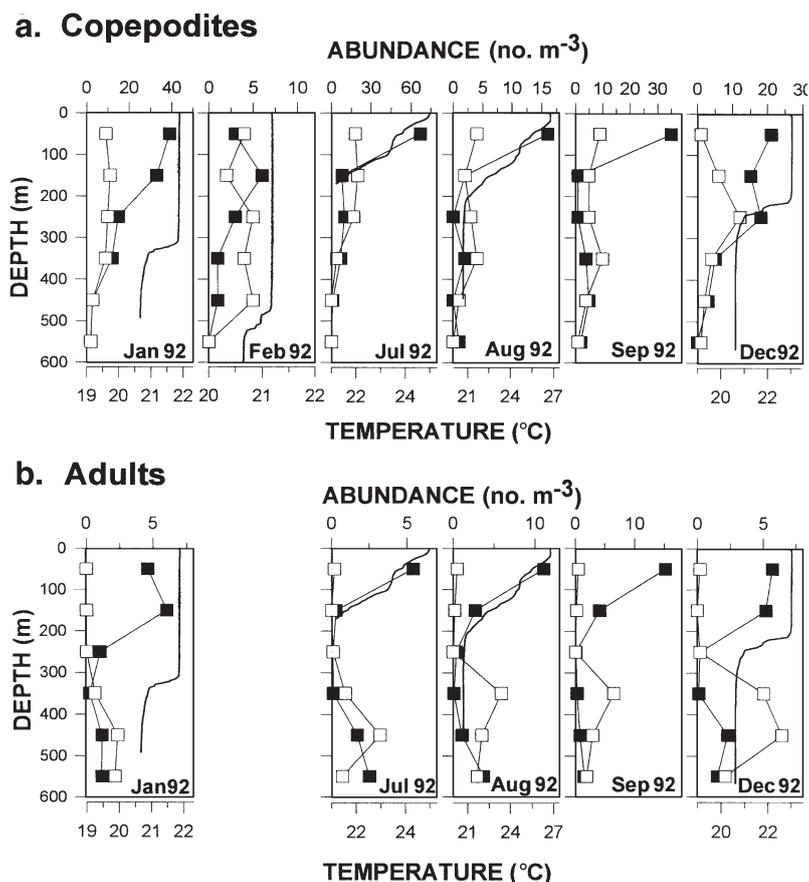


Fig. 5. *Pleuromamma indica*. Diurnal (□) and nocturnal (■) profiles of copepodites (a, upper panels) and adults (b, lower panels) and the corresponding temperature profiles (heavy lines) in 3 winter and 3 summer months in 1992. The plot of adults in February 1992 was omitted due to the scarcity of these animals ( $\approx 300 \text{ ind. m}^{-2}$ )

upper 20 m for copepod nauplii in the Baie des Chaleurs, Canada.

Spreading and homogeneity in the vertical distribution of phytoplankton in deeply mixed water columns were observed at our study site (Kimor & Golandsky 1977, Winter et al. 1979, Lindell & Post 1995) as well as at many

other regions worldwide (Sverdrup 1953, Pingree et al. 1975, Bradford et al. 1982, Zohary et al. 1998). Deep mixing is obviously deleterious for phytoplankton, as the cells which are mixed down to aphotic layers (as much as 85% in the Gulf of Aqaba in February) cannot photosynthesize. For herbivorous zooplankton, however, the spreading to aphotic layers may not be similarly deleterious as their food (phytoplankton) is also spread throughout the mixed layer.

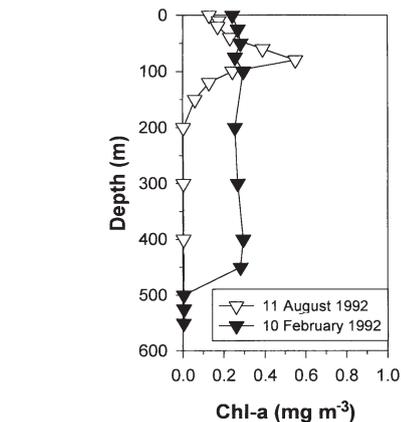


Fig. 6. Vertical profiles of chl a collected with niskin bottles at Stn A in winter (February) and in summer (August) 1992

The changes from stratified distribution in the summer to vertical homogeneity in the winter were most distinctive for small zooplankters. Large chaetognaths (retained on 750  $\mu\text{m}$  mesh), which are found in the upper 100 m in the Gulf of Aqaba, displaying little, if any, diel vertical migration (Schmidt 1973), exhibited a change from stratified to homogeneous distribution identical to that of the smaller zooplankton (Fig. 4c). Conversely, large copepods (Fig. 4c) such as *Pleuromamma indica* (Fig. 5), a group likely consisting of many diel migrators (Brooks & Mullin 1983, Bennett &

Table 4. Ratios  $R_1$  and  $R_2$  for the size-fractionated groups in the diurnal hauls in February 1992, when the mixed layer depth was 510 m, and September 1992, when the mixed layer depth was around 20 m. –: 100% of the specimens were found in the upper 100 m of the water column

Mesh size ( $\mu\text{m}$ )	Month	Algae		Tintinnina		Sarcodina		Nauplii		Copepoda		Chaetognatha		Mollusca		Others	
		$R_1$	$R_2$	$R_1$	$R_2$	$R_1$	$R_2$	$R_1$	$R_2$	$R_1$	$R_2$	$R_1$	$R_2$	$R_1$	$R_2$	$R_1$	$R_2$
100–400	Feb	1.1	1.6	0.8	1.3	0.8	0.8	3.5	0.9	2.0	1.2	0.9	0.8	1.5	1.5	1.5	1.3
	Sep	9.7	44	1.2	13	2.3	3.6	3.2	27	3.7	6.1	–	–	4.0	18	5.9	7.9
400–750	Feb									1.3	1.5	1.4	2.3			0.7	1.6
	Sep									18	5.9	7.5	19			24	33
>750	Feb									2.1	1.0	1.4	1.4				
	Sep									2.6	0.5	10	15				

Hopkins 1989), retained their diel migration pattern even when the water column was deeply mixed. The only apparent change in the vertical migration of *P. indica* was a sharp decrease in their nocturnal  $R_1$ . That is, while under stratified conditions these copepods ascended at night to the upper 100 m (= the photic zone), under deep mixing conditions their distribution was homogeneous throughout the upper 200 m of the mixed layer ( $R_1 = 0.8 \pm 0.3$  for copepodites). This nocturnal pattern was likely a result of the homogeneity of their food. In adjacent waters in the Red Sea south of the Gulf, where the water column is stratified year round, most ( $95 \pm 10\%$ ) of *P. indica* ascend daily to the upper 100 m (equivalent to  $R_1 \approx 19$ ) even in the winter (March 1979, Beckmann 1984).

What is the mechanism that produces vertical extension and homogeneity in the distribution of zooplankton? Two, not mutually exclusive mechanisms, are likely: One is 'active', in which homogeneous distribution is reached by isotropic swimming of the zooplankton; the other is 'passive', in which similarly to phytoplankton, the animals are passively entrained by the mixing water. The active mechanism could be an optimal response as predicted by the model of Ideal Free Distribution (Fretwell & Lucas 1970, Begon et al. 1990), as a homogeneous distribution of grazers throughout the volume in which their food is uniformly distributed would minimize competition for food. It might also be a reaction to vertical changes in the intensity of the ambient turbulence, as suggested by Mackas et al. (1993) for the copepods *Neocalanus plumchrus* and *N. flemingeri* in the subarctic Pacific. On the other hand, the passive mechanism should depend on the turbulence intensity, the vertical current shear, and the zooplankton ability to overcome vertical displacement. It is likely that under conditions of high turbulence and strong vertical current shear strong migrators (but not weak ones) will either be able to retain their vertical position or evade the mixed layer. These expectations are supported by the observations of Lagadeuc et al. (1997), showing that the distribution of nauplii but not adult copepods became homogeneous throughout a 20 m wind-mixed layer. Haury et al. (1990) demonstrated that weak swimmers such as shallow-living larvae and deep-living *Oithona* that were vertically separated under calm sea conditions became vertically mixed during a storm. Conversely, they found that the strong swimmer and migrator *Metridia pacifica* Copepodite stage V retained its position at the same depth. Also in our study, the large copepod *Pleuromamma indica* retained its diel migration behavior regardless of water mixing. Its migration consisted of a bi-daily swim of 300 to 500 m, clearly indicating its good swimming ability. Euphausiids, which are good swimmers, by and large avoided the vertical net used in this study.

For qualitative examination of their vertical migration, in February 2000 (mixing depth 430 m) a large Bongo net (70 cm mouth diameter, 300  $\mu\text{m}$  mesh) was obliquely towed by 2 of us (V. Farstey & A. Genin) at  $150 \text{ cm s}^{-1}$  from 100 m to the surface (bottom depth 600 to 700 m). The Bongo net minimizes the avoidance problem, and is reliably used to sample euphausiids and similarly sized zooplankton (Brinton 1967). The nocturnal Bongo hauls caught large quantities ( $>10 \text{ ind. m}^{-3}$ ) of the krill *Euphausia diomedea* Ortmann, 1894 (10 to 12 mm in length) and several other large decapods, none of which were present in that layer during the day. Evidently, large strong swimmers retained their diel vertical migration behavior in spite of mixing. The diel vertical migration is possibly a 'fixed' behavior, determined by proximal factors such as light, yet with a limited flexibility to 'fine tune' the nocturnal depth based on food availability (Huntley & Brooks 1982, Daro 1988). Such a modulation of nocturnal range apparently caused the observed decrease (10 to 20 fold) of *P. indica*'s  $R_1$  with the onset of deep mixing (Fig. 5).

In order to evaluate the extent of zooplankton homogeneity in the mixed layer, the observations were compared with the distribution expected for a passive tracer. A simple model used a 'sampling procedure' based on 100 m intervals identical to those used in the field. Thus the proportion of the 'population' of the passive tracer found in the upper 100 m (of the total found in the mixed layer only) was expected to follow a  $X^{-1}$  curve, where  $X$  is the number of full 100 m intervals in the mixed layer. Note that the depth of the mixed layer in this comparison was considered to be the number of 100 m intervals that were fully included in the actual mixed layer. For example, in a case of actual 316 m mixing (January 1992), 3 such intervals were included in the mixed layer, so that the expected proportion in the upper 100 m is 1/3. The comparison of the expected and observed data (Fig. 7) indicated that the zooplankton followed the trend expected for a passive tracer, although the observed proportion near the surface was, on average,  $11 \pm 6\%$  higher. Accordingly, the exponent value of the power regression line was  $-0.8$ , compared with the expected value of  $-1.0$  ( $R^2 = 0.98$ ; Fig. 7). The fraction of strong swimming zooplankton was too small (typically  $<0.1\%$  of the total; Table 3) to explain this difference from the model. A possible explanation is that the mixed layer consisted of 2 parts. An upper part, comprising most of the mixed layer, in which mixing was more intense and the distribution of organisms was homogeneous, and a lower part, adjacent to the deepening thermocline, in which the mixing was weaker allowing gradients. The first evidence for this pattern is based on the results: the density of zooplankton in the bottom 100 m of the

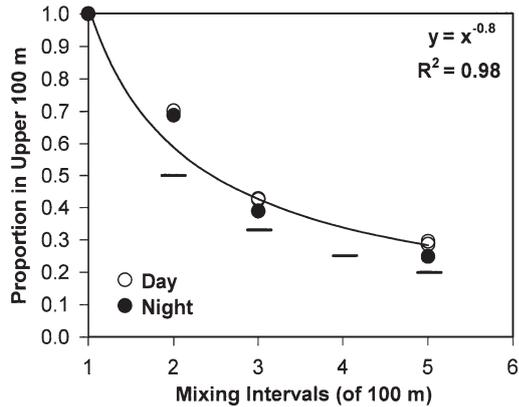


Fig. 7. Comparison between the observed and expected proportion of zooplankton in the upper 100 m under different depths of vertical mixing. See text for a description of the model. Circles: observed data; horizontal bars: predicted values. The observed data power regression line and its parameters are indicated on the top right

mixed layer (i.e. the 100 to 200 m layer in December 1992, the 200 to 300 m layer in January, and the 400 to 500 m layer in February 1992) was consistently lower than the density in shallower parts of the corresponding mixed layer (see Fig. 2). On average, in this lower section of the mixed layer the zooplankton density was  $47 \pm 13\%$  lower than in the almost perfectly homogeneous layer above (Fig. 2a,b). The second evidence is based on a similar trend observed for phytoplankton: vertical profiles of *in vivo* fluorescence measured by B. Lazar (unpublished data from November 1999 through December 2001; maximum mixing depth of 640 m in February) showed uniform fluorescence in the top part but a decline in the lower part (10s of meters). These 2 biological trends possibly indicated the occurrence of weaker mixing near the thermocline, allowing zooplankton to resist downward entrainment in that layer (and causing phytoplankton to remain in darkness long enough to change their *in vivo* fluorescence). Thus, it is likely that strong convective mixing in the winter causes zooplankton to spread throughout the mixed layer. However, zooplankton attains a full homogeneity comparable to that of a passive tracer only in the upper section of the mixed layer.

How should vertical expansion and homogeneity of zooplankton affect the community? First, as mentioned above, it should minimize competition for food among herbivorous zooplankters. Second, a dramatic decline in the absolute zooplankton density was observed in the upper 100 m as mixing deepened, reaching a  $\times 5$  dilution by February (Fig. 2a). This dilution could significantly lower zooplankton predation by visual predators in the upper, illuminated portion of the water column due to the linear functional response of

zooplanktivorous fish (Gerking 1994). However, this reduced predation could have been offset by a parallel increase in the zooplankton density in the deeper layers, although predation is much reduced at aphotic layers. No clear trend was apparent in the integrated zooplankton abundance throughout the water column between mixed and stratified conditions. Zooplankton predators residing in the upper layer, which rely on high prey density for their growth and survival, may severely suffer from the reduced prey density during mixing (Lasker 1975, Buckley & Lough 1987). On the other hand, deep-water predators, as well as the deep-sea bottom community, should benefit from the higher densities of prey during the mixing period and the shorter time it takes sinking particles to reach great depths. To the best of our knowledge, this is the first description of such a remarkable extension and homogeneity of zooplankton distribution driven by deep convective mixing. These findings may have relevance for other areas where such deep winter mixings occur.

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