

## **Copepod community from Arctic to Antarctic: large-scale patterns of naupliar and postnaupliar distribution and abundance in the epipelagic layer revealed by citizen science**

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*The use of citizen science and opportunity sampling during commercial or tourist voyages can provide valuable insights into the structuring of the marine plankton community in broad biogeographic areas. With the goal of studying the distribution and abundance of smaller zooplankton using citizen science approach, plankton samples were collected at 33 stations spanning from the Arctic to Antarctic during the cruise of the S/V "Croatian Tern" (1994-1997), using vertical tows with a 53µm mesh size Nansen net in the upper epipelagic layer. In this study, we summarize the observed distribution patterns of planktonic copepods by ontogenetic stages (nauplii, copepodites, adults) and by postnaupliar assemblages (calanoids, oithonids, oncaeiids, harpacticoids, corycaeiids), reporting also on the numerical ratio of nauplii to postnaupliar copepods, as an important indicator of the stability of copepod reproduction. The highest abundances of total copepods were found in the northeastern and southeastern Pacific, while the lowest values were found in the Mediterranean Sea and Southern Ocean. Overall, the copepod community was dominated by naupliar stages, while most postnaupliar assemblages (calanoids, oithonids, and oncaeiids) were dominated by copepodites. Spatially, nauplii and postnaupliar oithonids showed similar latitudinal patterns, with both assemblages dominating in high latitudes of temperate zones on both sides of the equator, while contributions of calanoids, oncaeiids, and corycaeiids increased at lower latitudes. The ratio of nauplii to postnauplii varied from 1.1 to 6.4, and only at five stations was it slightly < 1. Latitudinally, the median values of this ratio varied from 1.1 in the marginal Arctic to 3.1 in the South Pacific, with no statistically significant differences among areas. The sudden change in nauplii/postnauplii ratio could signal disturbances in the copepod community, provided that the average values are determined for all marine areas under different productivity conditions.*

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**Key words:** copepods; nauplii; biogeography; latitudinal change; citizen science

## INTRODUCTION

Marine planktonic copepods represent an important link between primary production and top predators and contribute to the biogeochemical cycling of carbon and other nutrients (BEAUGRAND *et al.*, 2003; TURNER, 2004; VALDÉS *et al.*, 2018). These ecological functions are largely related to their diversity, abundance, and distribution patterns (DUARTE, 2000), which vary greatly across large biogeographic areas. The considerable variation in size both within and among copepod species and their generally patchy distribution pose challenges for copepod studies, particularly with respect to uniformity of sampling methods across the world's oceans (TSENG *et al.*, 2011). Plankton nets made with fine mesh often show poor filtering efficiency in euphotic layer due to phytoplankton density, while on the other hand, small copepods and developmental stages are lost through larger mesh sizes. Still, for a thorough understanding of plankton ecology, it is necessary to take into consideration the entire copepod assemblage, including larvae and juveniles. Ecological functions of pre-adult copepods are often more versatile compared to adults; they represent more abundant prey, highly diversified grazers and, in the case of the nauplii, link the microbial and classical food webs (JUNGBLUTH *et al.*, 2013). Copepod juveniles also represent their secondary production (GARCIA-COMAS *et al.*, 2016) and provide an estimate of the potential productivity of marine ecosystems. Recording only sexually mature individuals of larger copepod species and missing small species and majority of juvenile stages represents a major gap in marine zooplankton research (KRŠINIĆ *et al.*, 2020). The numerical relationship between adult and juvenile copepods is rarely investigated. Yet nauplii are the most numerous copepods and the most numerous metazoans in the ocean, essential to ecosystem functioning as both grazers and prey. Nauplii represent the most vulnerable stage in the copepod life cycle and have higher mortality rates due to predation and environmental stress than post naupliar stages (DEVREKER *et al.*, 2005; CRIPPS *et al.*, 2014).

Nowadays, oceanographic expeditions covering the world's oceans from pole to pole have become extremely rare and, due to the enormous financial requirements, are only possible for relatively few research institutions. Therefore, the use of citizen science and opportunity sampling during commercial or tourist voyages can provide valuable plankton material from less visited or little explored sites over wide geographic areas (PAKHOMOV *et al.*, 2020). One such opportunity occurred during the Arctic-Antarctic cruise aboard the S/V "Croatian Tern," a 19.8 m steel ketch built in a Croatian shipyard. This voyage covered a total of 35,926 nautical miles and lasted almost three years, with the goal of navigating as close as possible to the North and South Poles (described in KRŠINIĆ, 2018). During the cruise, zooplankton samples were collected in different biogeographic zones in both hemispheres, using a uniform sampling method. Due to the small mesh size of the plankton net used (i.e., 53 micrometers), the material collected provided information on the distribution and abundance of different life stages of copepods, from nauplii larvae to copepodites and adults across the world's oceans. Thus, the objective of this study is to describe the observed patterns of abundance and distribution of ontogenetic stages of copepod assemblages in the upper epipelagic layer, focusing on the numerical ratio of nauplii to postnaupliar copepods.

## MATERIAL AND METHODS

During the course of "Croatian tern" journey, zooplankton samples were collected by the crew in the surface layer, 0-50 m or 0-15 m (St6, St7) of 33 stations (Table 1, Fig. 1) with a Nansen net, 45 cm in diameter, 250 cm in length and 53- $\mu$ m mesh size, equipped with a R2 flowmeter (Model 2030, General Oceanics). Temperature was measured with digital thermometer (Greisinger electronic GHT 175/MO) at a depth of 20 - 40 cm. Samples were collected in warmer seasons and ice-free periods in both hemispheres, however, the surface temperatures varied over a large range, between -1.4°C and 21°C in the Northern Hemisphere and between 1.4°C and

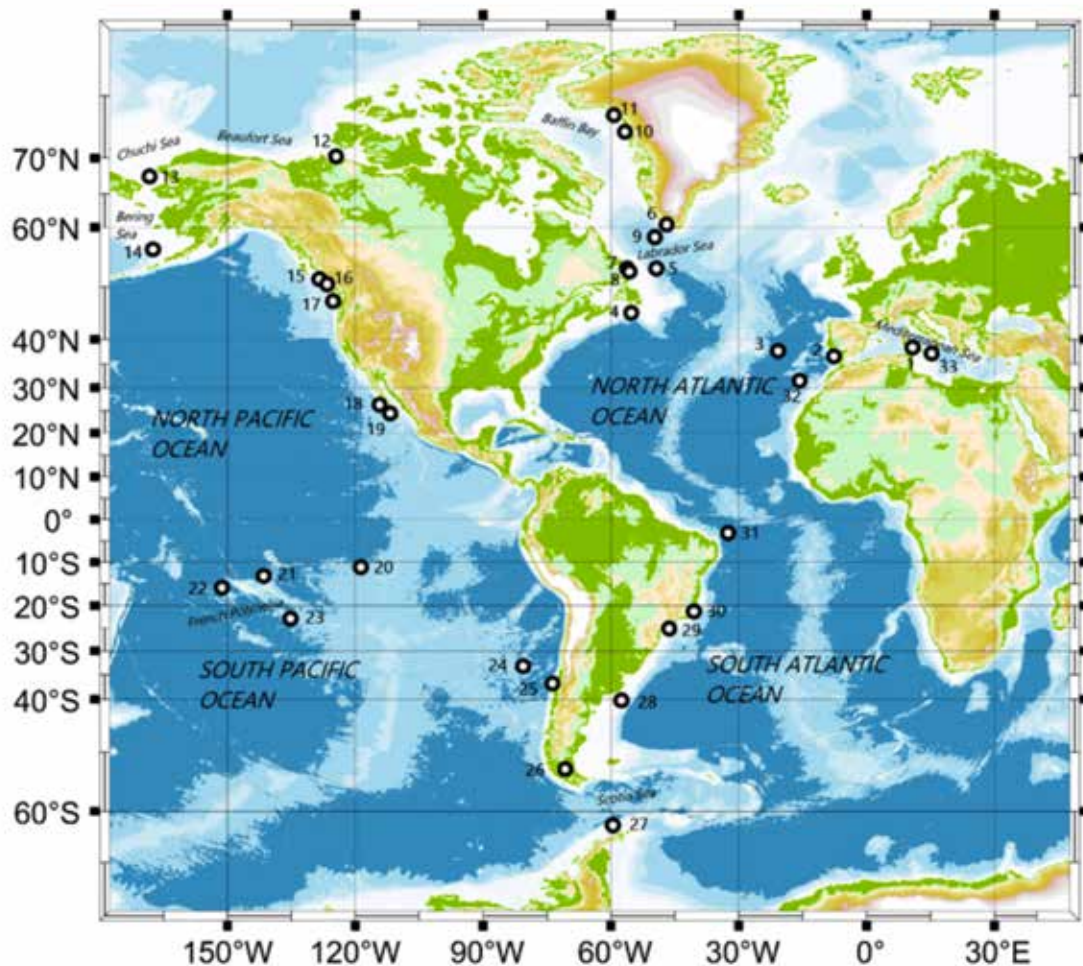


Fig. 1. Distribution of sampling stations during Arctic-Antarctic cruise

27°C in the Southern Hemisphere. During sampling, the wind was weak and the sea was calm (Table 1). The plankton net was deployed with a hand winch using a hauling speed of 0.5 m s<sup>-1</sup>. The volumes filtered by the net were approximately equal at all stations and averaged about 8 m<sup>3</sup> with the exception of stations St6 and St7 where the filtered volume was approximately 2.4 m<sup>3</sup>. Samples were preserved in a 2.5 % formaldehyde-seawater solution neutralized by CaCO<sub>3</sub>.

In the laboratory, subsamples were placed in a glass cell (dimensions 7 x 4.5 x 0.5 cm) and examined with an inverted microscope (Olympus IMT-2) at 100x and 400x magnifications. One-sixteenth of each net sample was counted.

The data were analyzed statistically using the nonparametric Spearman correlation coef-

ficient (Rs) to reveal relationships with surface temperature and among copepod assemblages. Differences in abundance medians among geographical areas were tested with non-parametric Kruskal-Wallis test. Mann-Whitney test was used to reveal differences in medians between stations from the Northern and Southern Hemisphere. The relationship between naupliar and post-naupliar copepods' abundances was expressed as nauplii/postnauplii ratio. In this paper, detailed taxonomic composition of post-naupliar copepods was not analyzed. However, results were obtained for assemblages, at either the order or family level: Calanoida, Harpacticoida, Oithonidae, Oncaeiidae and Corycaeiidae. Adults and copepodites were counted separately, except for harpacticoids and corycaeiids where all postnaupliar stages were pooled.

Table 1: General data for sampling stations during cruise of „Croatian Tern“ from 1995 to 1997 (☼ all samplings are performed during the day).

| Stations | Areas                  | Location                                | Longitude | Latitude | Date       | GTM Time | Houl (m) | Wind | Sea | °C   |
|----------|------------------------|---|-----------|----------|------------|----------|----------|------|-----|------|
| 1        | Mediterranean Sea      | Thyrrhenian Sea                         | 38.2 N    | 11.01 E  | 28.5.1994  | 12:00☼   | 50       | 6    | 1   | 21   |
| 2        | North Atlantic         | Off the Iberian coast                   | 36.4N     | 07.43W   | 11.6.1994  | 14:00☼   | 50       | 4    | 2   | 19   |
| 3        | North Atlantic         | -----                                   | 37.5N     | 20.55W   | 26.6.1994  | 12:30☼   | 50       | 4    | 1-2 | 19   |
| 4        | North Atlantic         | Grand Banks                             | 45.0N     | 55W      | 16.7.1994  | 11:40☼   | 50       | 2    | 0-1 | 13   |
| 5        | Labrador Sea           | West                                    | 53.05N    | 49.10W   | 29.7.1994  | 19:30☼   | 50       | 5    | 1-2 | 13   |
| 6        | Labrador Sea           | East                                    | 60.31N    | 46.70W   | 11.8.1994  | 16:45☼   | 15       | 25   | 1-2 | 2    |
| 7        | Labrador Sea           | Newfoundland-Labrador shelf             | 53.05N    | 56.00W   | 19.8.1994  | 23:00☼   | 15       | 0    | 0   | 5    |
| 8        | Labrador Sea           | Newfoundland-Labrador shelf             | 52.52N    | 55.42W   | 20.8.1994  | 12:40☼   | 50       | 2    | 0-1 | 7    |
| 9        | Labrador Sea           | Central                                 | 58.3N     | 49.5W    | 22.6.1995  | 08:30☼   | 50       | 0    | 0   | 5    |
| 10       | Baffin Bay             | -----                                   | 73.2N     | 56.5W    | 15.7.1995  | 12:15☼   | 50       | 0    | 0   | -1   |
| 11       | Baffin Bay             | -----                                   | 75.2N     | 59.1W    | 19.7.1995  | 11:00☼   | 50       | 0    | 0   | -1.4 |
| 12       | Beaufort Sea           | Amundsen Gulf                           | 70.1N     | 124.3W   | 29.8.1995  | 13:30☼   | 50       | 2    | 1   | 1    |
| 13       | Chukchi Sea            | -----                                   | 67.4N     | 168.1W   | 7.9.1995   | 19:00☼   | 50       | 2    | 1   | 4    |
| 14       | Bering Sea             | Southeast                               | 56.3N     | 167.3W   | 16.9.1995  | 21:00☼   | 50       | 2    | 1   | 8    |
| 15       | Eastern North Pacific  | Queen Charlotte Sound, British Columbia | 51.2N     | 128.2W   | 9.10.1995  | 17:30☼   | 50       | 2    | 1   | 17   |
| 16       | Eastern North Pacific  | Johnston Strait, British Columbia       | 50.5N     | 126.4W   | 11.10.1995 | 19:00☼   | 50       | 0    | 0   | 17   |
| 17       | Eastern North Pacific  | off western Washington coast            | 47.2N     | 125.0W   | 4.5.1996   | 23:50☼   | 50       | 5    | 0-1 | 13   |
| 18       | Eastern North Pacific  | Baja California                         | 26.1N     | 114.1W   | 4.6.1996   | 15:20☼   | 50       | 7    | 1-2 | 19   |
| 19       | Eastern North Pacific  | Baja California                         | 24.2N     | 111.6W   | 8.6.1996   | 17:00☼   | 50       | 0    | 0   | 19   |
| 20       | South Pacific          | Central                                 | 11.4S     | 118.5W   | 28.6.1996  | 14:30☼   | 50       | 8    | 1   | 27   |
| 21       | South Pacific          | Central                                 | 13.4S     | 141.3W   | 24.7.1996  | 03:07☼   | 50       | 4    | 0   | 26   |
| 22       | South Pacific          | Central                                 | 16.1S     | 151.1W   | 7.8.1996   | 21:36☼   | 50       | 7    | 2   | 26   |
| 23       | South Pacific          | Central                                 | 23.1S     | 135.0W   | 19.9.1996  | 20:15☼   | 50       | 5    | 2   | 24   |
| 24       | Eastern South Pacific  | Chilean Sea                             | 33.4S     | 80.4W    | 17.10.1996 | 15:05☼   | 50       | 5    | 1   | 21   |
| 25       | Eastern South Pacific  | Chilean Sea                             | 37.0S     | 73.5W    | 11.11.1996 | 19:15☼   | 50       | 0    | 0   | 22   |
| 26       | Eastern South Pacific  | South of Punta Arenas                   | 53.2S     | 70.5W    | 5.12.1996  | 20:00☼   | 50       | 1    | 0   | 14   |
| 27       | Scotia Sea             | -----                                   | 62.3S     | 59.3W    | 29.12.1996 | 16:14☼   | 50       | 0    | 0   | 1.4  |
| 28       | Western South Atlantic | Argentine Sea                           | 40.4S     | 57.3W    | 13.1.1997  | 11:30☼   | 50       | 4    | 2   | 19   |
| 29       | Western South Atlantic | Off the coast of Brazil                 | 25.3S     | 46.1W    | 16.2.1997  | 14:02☼   | 50       | 0    | 0   | 18   |
| 30       | Western South Atlantic | Off the coast of Brazil                 | 21.5S     | 40.3W    | 27.2.1997  | 16:30☼   | 50       | 10   | 0   | 22   |
| 31       | Western South Atlantic | Off the coast of Brazil                 | 3.4S      | 32.3W    | 26.3.1997  | 19:42☼   | 50       | 0    | 0   | 25   |
| 32       | North Atlantic         | Off the coast of Morocco                | 31.3N     | 15.5W    | 2.5.1997   | 15:07☼   | 50       | 5    | 1   | 19   |
| 33       | Mediterranean Sea      | Ionian Sea                              | 37N       | 15.5E    | 26.5.1997  | 15:30☼   | 50       | 0    | 0   | 19   |

To describe the (dis)similarity patterns of the spatial distribution of copepod assemblages (square root transformed abundances of copepod nauplii, total calanoids, total oithonids, total oncaeids, total harpacticoids and total corycaeids), hierarchical clustering (CA) and multidimensional scaling (nMDS) were applied to the same data matrix, which was transformed into a lower triangular similarity matrix using Bray-Curtis coefficients. The grouping variable “area-climate” (i.e., the geographic area of the global ocean coupled with climatic zone) was used to extract spatial distribution patterns in the data matrix. Clustering was performed using the group average method, applying the permutation test “similarity profile” (SIMPROOF) available in PRIMER 6 (CLARKE & GORLEY, 2006) to test the significance of the internal structure within the constructed clusters. To visualize the 2-D data proximity, MDS diagrams were created with overlaid clusters derived from the cluster dendrogram at different similarity levels and with overlaid bubbles corresponding to abundance ranges of copepod assemblages.

## RESULTS

### Spatial distribution of copepod stages and assemblages

The distribution of total abundances of copepods (nauplii and postnaupliar stages) in areas of the world’s ocean is shown in Fig. 2. The highest ranges were determined in northeastern (1493–63,044 ind. m<sup>-3</sup>) and southeastern Pacific (6524–34,876 ind. m<sup>-3</sup>). Overall, the lowest abundances were found in the Mediterranean Sea (1469–4284 ind. m<sup>-3</sup>) and in the Southern Ocean (184 ind. m<sup>-3</sup>). Median values were not significantly different among the areas (Kruskal-Wallis H = 14.772; p = 0.0637).

Nauplii were the most numerous fraction of copepods that largely determined the fluctuation in total copepod abundances. Naupliar abundances varied from a minimum of 184 ind.m<sup>-3</sup> (St27) to a maximum of 36,864 ind.m<sup>-3</sup> (St17) (Fig.3). In general, the lowest abundances (<10<sup>3</sup> ind. m<sup>-3</sup>) were found in marginal boreal areas

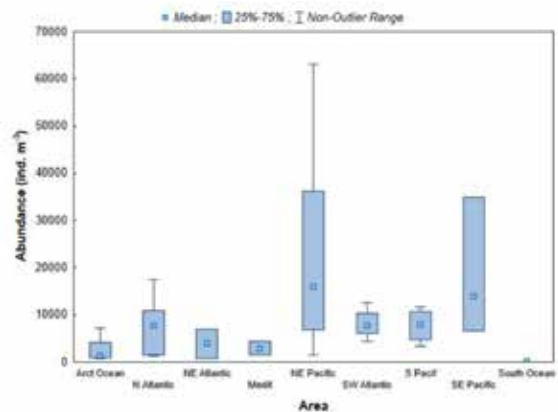


Fig. 2. Boxplot of total copepod abundance ranges in the investigated areas

such as the Scotia Sea (St27), Baffin Bay (St10, St11), and Beaufort Sea (St12), as well as off the Atlantic Iberian coast (St2) and in the Ionian Sea (St 33). Conversely, the abundances increased by an order of magnitude (>10<sup>4</sup> ind. m<sup>-3</sup>) in the Bering Sea (St14), northeastern Pacific (St17, St19), southeastern Pacific (St26) and off the coast of Newfoundland in the northern Atlantic (St4). Median values were not significantly different among the areas (Kruskal-Wallis H = 14.4225; p = 0.071) (Fig. 3).

Abundances of total postnaupliar copepods ranged from 15 ind.m<sup>-3</sup> (St12) to 26,180 ind.m<sup>-3</sup> (St17). The abundance distribution pattern was somewhat consistent with that of nauplii, with the highest values (<10<sup>4</sup> ind.m<sup>-3</sup>) recorded in the northeastern Pacific (St14 -Bering Sea; St17-off the coast of Washington, USA) and lowest values (<500 ind. m<sup>-3</sup>) in marginal Arctic (St12-Beaufort Sea; St11- Baffin Bay), off the Iberian Atlantic coast (St2) and in the northeastern Pacific (St16 - British Columbia). Postnaupliar copepods were not found in one of the samples from the Labrador Sea (St7) and in the Scotia Sea (St27) (Fig. 3). Median values were not significantly different among the areas (Kruskal-Wallis H = 15.27; p = 0.0541) (Fig. 3).

The proportion of copepod assemblages (at order or family level) to the total number of postnaupliar copepods is shown in Fig. 4. Overall, calanoids were dominant in the samples from the stations in Mediterranean Sea, Northeast Atlantic, Southwest Atlantic, Southwest and South Pacific, but their contribution decreased

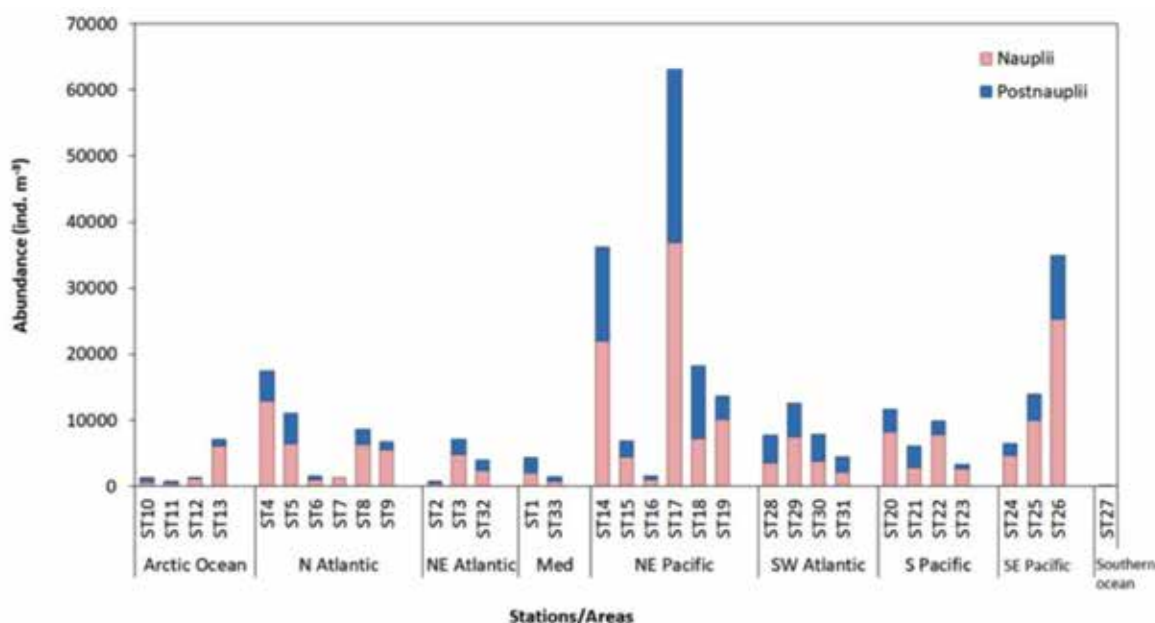


Fig. 3. Distribution of naupliar and total postnaupliar abundances at sampling stations

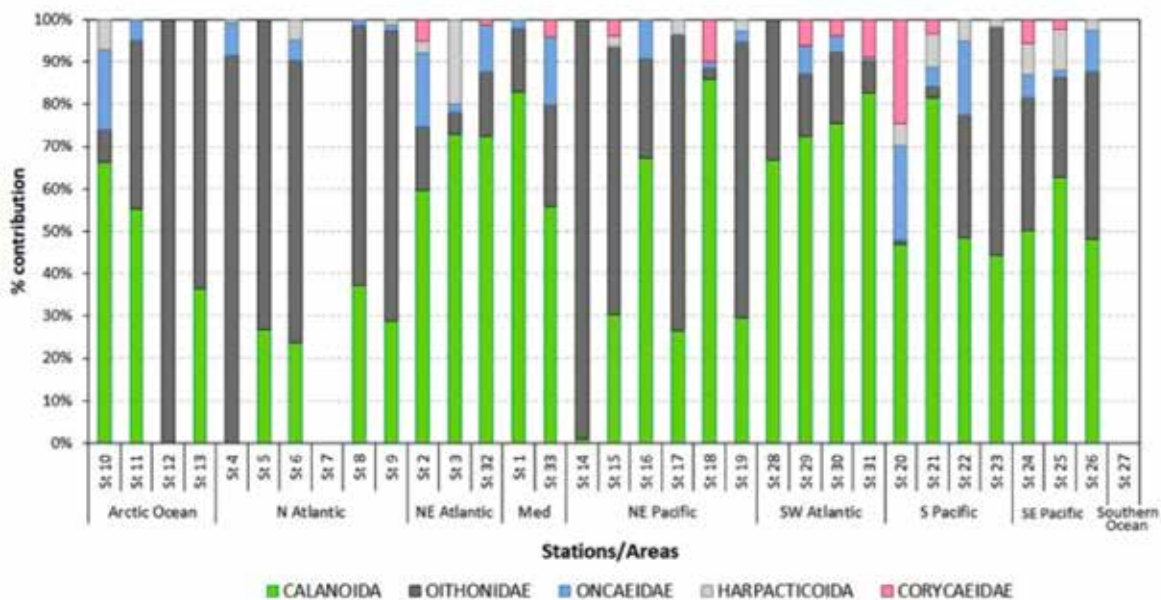


Fig. 4. Percentage contribution of copepod assemblages in total postnaupliar copepods

in the western Arctic, Northern Atlantic and eastern North Pacific stations. At positive stations, abundances of total calanoids (copepodites and adults) ranged from 151 ind.m<sup>-3</sup> at St14 in the Bering Sea to 9,491 ind.m<sup>-3</sup> at St18 in northeastern Pacific (Baja California, Mexico), with a median of 989 ind.m<sup>-3</sup> (Fig. 5). Median values were not significantly different among areas (Kruskal-Wallis H=9.63; p=0.21). Cope-

podite stages dominated over adults, with an average contribution of 85.9%.

Abundances of total oithonids ranged from 15 ind. m<sup>-3</sup> (St12) to 18,247 ind. m<sup>-3</sup> (St17) (Fig. 5). In addition to northeastern Pacific (St17, off the coast of Washington, USA), very high abundances of oithonids were found in the southeastern Bering Sea (St 14; 13,970 ind. m<sup>-3</sup>) and in the southeastern Pacific (St26, 4155

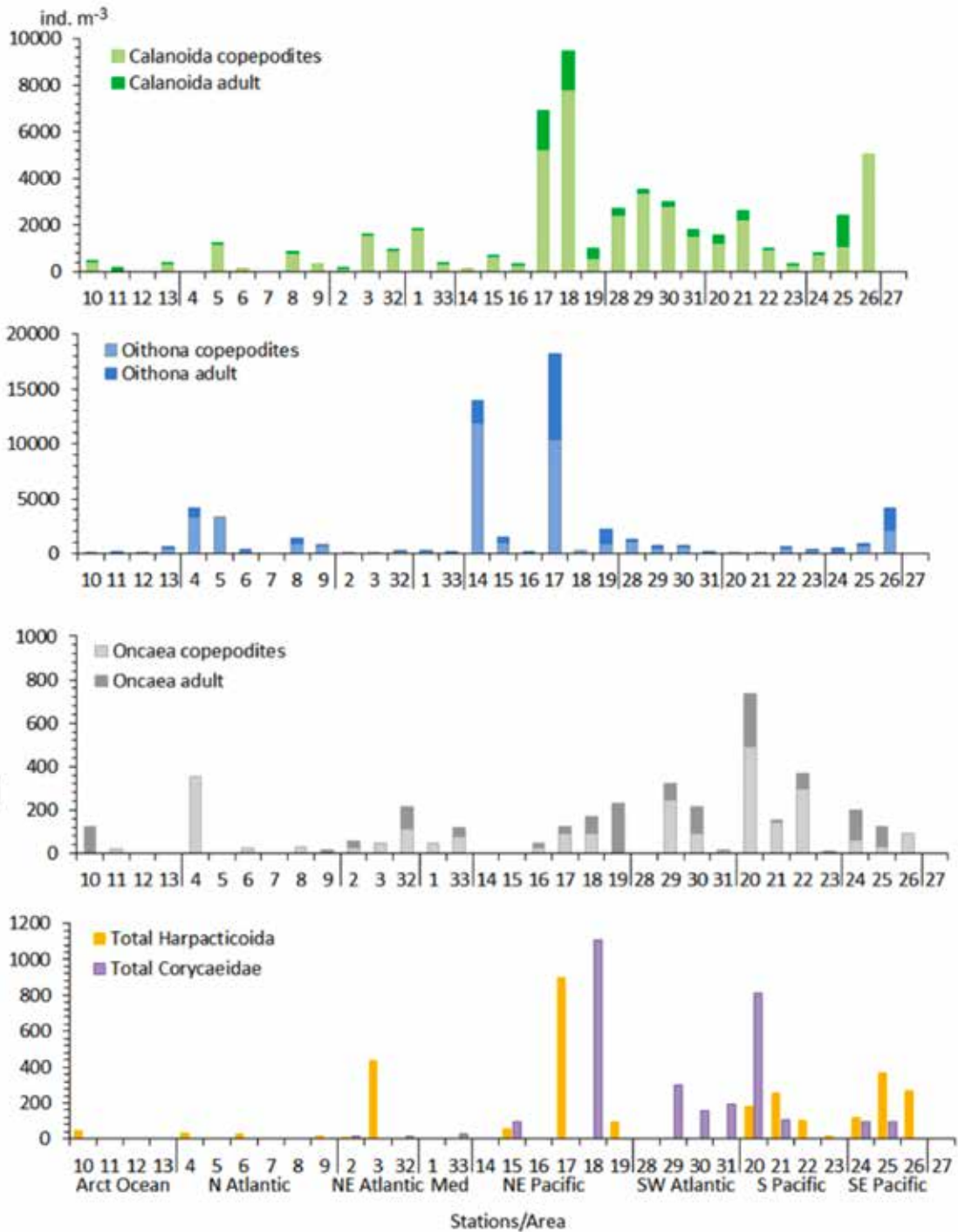


Fig. 5. Spatial distribution of abundances of postnaupliar assemblages at sampling stations

ind. m<sup>-3</sup>), with *Oithona similis* as the dominant species at all three locations. Median values differed significantly among areas (Kruskal-Wallis H=15.45, p<0.05). Of the total postnaupliar oithonids, their copepodites accounted for an average of 70.9 %.

Abundances of total oncaeids ranged from 15 ind.m<sup>-3</sup> in the Labrador Sea (St9), to 736 ind.m<sup>-3</sup> in central South Pacific (St20). At eight stations oncaeids were not found (Fig. 5). Median values were not significantly different among areas (Kruskal-Wallis H=12.77; p=0.12). Domi-

nant species was *Oncaea zernovi* at station 19 in the Northeast Pacific with an abundance of 138 ind.m<sup>-3</sup>. In total number of postnaupliar oncaeids, their copepodites participated with an average of 62 %.

Postnaupliar harpacticoids were registered at 16 stations (Fig. 5), with abundances ranging from 15 ind.m<sup>-3</sup> at St9 in the Labrador Sea, to 900 ind.m<sup>-3</sup> at St17 (off the coast of Washington, USA) in the northeast Pacific. Median values were significantly different among areas (Kruskal-Wallis H=0.000; p<0.001). Dominant species was *Microsetella norvegica*.

Postnaupliar corycaeids were absent above 55°N and below 60°S latitudes, which include a large area of the Arctic, the Subarctic, the Subantarctic and Antarctic (Fig. 5). At 12 positive stations, their abundances ranged from 15 ind.m<sup>-3</sup> in northeastern Atlantic (St 32, off the Moroccan coast) to 1,105 ind.m<sup>-3</sup> in the northeastern Pacific (St18, Baja California). Median values were significantly different among areas (Kruskal-Wallis H=0.000; p<0.001)

### Statistical analysis

The difference in abundances between naupliar and total postnaupliar copepods was statistically significant (t-test, p <0.05). The ratio of naupliar to postnaupliar abundances ranged between 1.1 and 2.8 at 18 stations, with nauplii dominating (Fig. 6). The highest ratios of 4.5

and 6.4 were found in the Labrador Sea (St9) and Chuchi Sea (St13), respectively. The nauplii/postnauplii ratio ranging from 0.7 to 0.9 was determined at five stations (Fig. 6), while postnaupliar copepods were not registered at three stations (St7 in Labrador Sea, St12 in Beaufort Sea and St27 in Scotia Sea). The boxplot distribution of nauplii/postnauplii ratio by sampling area is shown in Fig. 7. Median values were not significantly different among areas (Kruskal Wallis H=10.683; p=0.153)

Spearman rank-order correlation between naupliar and postnaupliar copepods was significant at p<0.05 ( $R_s=0.815$ , n=31). Copepod nauplii were significantly positively correlated with all postnaupliar assemblages, except corycaeids (Table 2). Among postnaupliar assemblages, significant correlations were observed for total calanoids with oncaeids, harpacticoids and with corycaeids (Table 2). With the exception of oithonids, postnaupliar assemblages showed positive relationship with temperature, however, the statistically significant values were obtained only for calanoids and oncaeids (Table 3)

Copepod abundances were tested for differences in medians between Northern and Southern Hemisphere stations. Significant differences were found only for calanoids, with higher median south of the Equator (Table 4).

The levels of similarity in copepod community structure and abundance between the sampling stations within geographical areas-climate

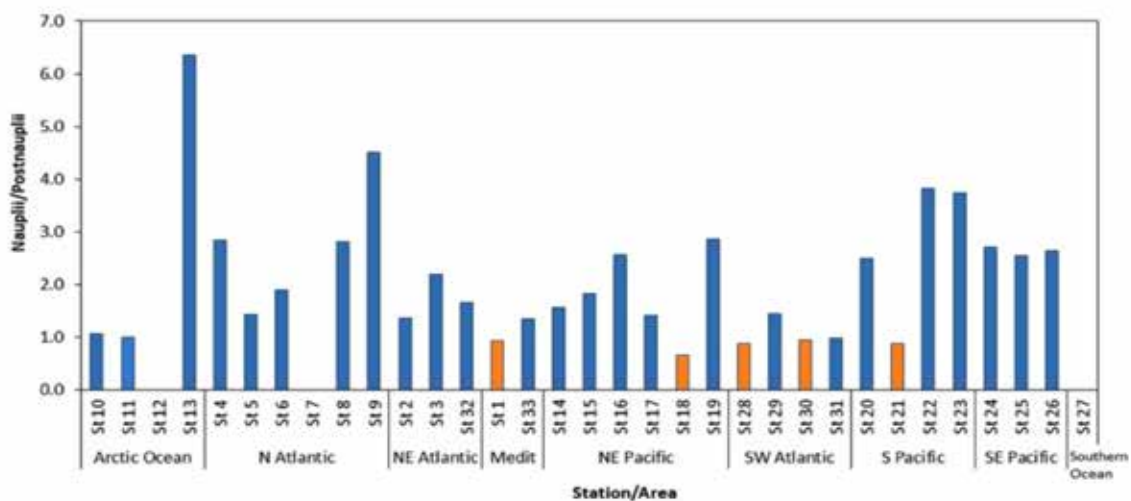


Fig. 6. Distribution of nauplii/postnauplii ratio at sampling stations (orange bars denote ratio <1)



Table 2. Spearman correlations between copepod assemblages; NAUP, nauplii; CAL, calanoids, HARP, harpacticoids, OITH, oithonids, ONC, oncaeids, CORY, corycaeids; (\*, significant at  $p < 0.05$ )

|      | NAUP   | CAL    | HARP  | OITH  | ONC   |
|------|--------|--------|-------|-------|-------|
| CAL  | 0.495* |        |       |       |       |
| HARP | 0.588* | 0.932* |       |       |       |
| OITH | 0.720* | 0.247  | 0.241 |       |       |
| ONC  | 0.450* | 0.461* | 0.364 | 0.004 |       |
| CORY | 0.556  | 0.754* | 0.577 | 0.021 | 0.395 |

Table 3. Spearman rank order correlations between abundances of main copepod groups and temperature (\*, significant at  $p < 0.05$ )

| Copepod assemblage | Temperature |
|--------------------|-------------|
| Nauplii            | 0.231       |
| Calanoida          | 0.397*      |
| Oithonidae         | -0.194      |
| Oncaeidae          | 0.633*      |
| Harpacticoida      | 0.263       |
| Corycaeidae        | 0.312       |

Table 4. Mann-Whitney U test for differences in medians between the northern and southern hemisphere stations (\*, significant at  $p < 0.05$ )

| Copepod assemblages | Mann-Whitney U test (* sign. at $< 0.05$ ) |           |
|---------------------|--|-----------|
| Nauplii             | U=104.000                                  | p=0.421   |
| Calanoida           | U=46.00                                    | p= 0.018* |
| Oithonidae          | U=109.00                                   | p=0.983   |
| Oncaeidae           | U=79.00                                    | p=0.082   |
| Harpacticoida       | U=20.00                                    | p=0.244   |
| Corycaeidae         | U=8.00                                     | p=0.144   |

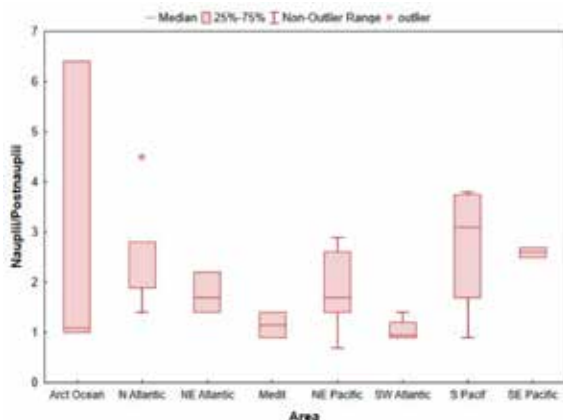


Fig. 7. Boxplot of nauplii/postanauplii ratio in the investigated areas

zones are illustrated by the CA dendrogram (Fig. 8), with the identified clusters superimposed on the MDS plot (up to 69% similarity) (Fig. 9). Cluster analysis revealed one outlier (station 27 in the Southern Ocean, separated at 21.54% similarity level) and two major groupings of stations (1 and 2). The outlier was characterized by the lowest naupliar abundance in the dataset coupled with absence of postnaupliar copepods. According to the SIMPROOF test, apart from the outlier, the following clustering was statistically significant (black lines): Group 1 of stations in high latitudes of northern tem-

perate (stations 7, 16) and polar zone (stations 6, 10, 11, 12) and in/near the subtropical zones (stations 2, 23 and 33), separated at 47.68% similarity level from Group 2. Group 2 branches into two clusters at 55.19% similarity level - a smaller cluster of stations (2a) in the high latitudes of the temperate zones on both sides of the Equator (stations 4, 17, 14 and 26) and a larger mixed cluster (2b) of stations extending from polar (St13) to near-equatorial latitudes (St31), without meaningful climatic grouping. However, temperate-cold stations (stations 5, 8, 9, 13) were projected somewhat closer together than to subtropical/tropical stations.

When abundances of copepod assemblages were overlaid as bubbles on the same MDS plot, the clustering corresponded to abundance gradients represented by increasing bubble size, most visibly for nauplii and oithonids (Fig. 10 A, B). Maximal abundances of both groups were associated with higher latitudes of temperate zones (cluster 2a). This affinity was less expressed in calanoids, oncaeids and harpacticoids (Fig. 10 C, D, E), while corycaeid abundances were exclusive to subtropical/tropical zones (Fig. 10 F).

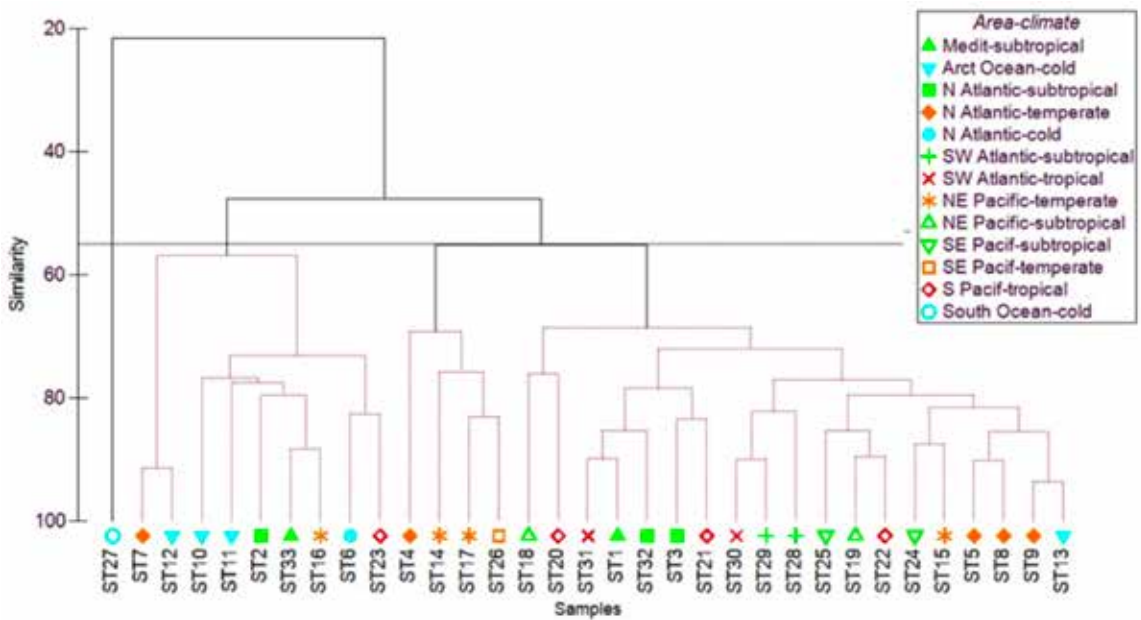


Fig. 8. Dendrogram of the hierarchical clustering of sampling stations using Bray Curtis similarities calculated on square root transformed abundances of copepod assemblages (copepod nauplii, total calanoids, total oithonids, total oncaeids, total harpacticoids and total corycaeids). Statistically significant separations are displayed by the black lines, while the red lines indicate the lack of statistically significant internal structure of the cluster (significance value is set at 5%). Slice (dashed black line) is set at 55% similarity level.

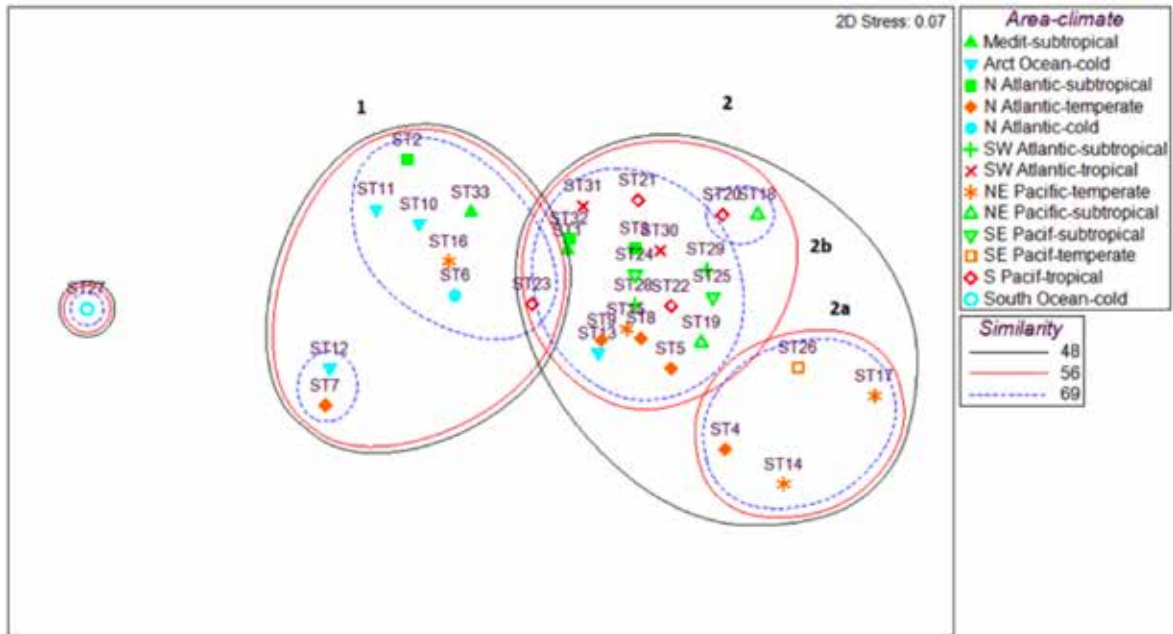


Fig. 9. nMDS 2-D ordination of investigated stations within global ocean's areas and climate zones, coupled to a cluster analysis (stress = 0.07), with superimposed clusters at similarity levels from Fig. 8 dendrogram. Statistically significant clustering is denoted with full lines.

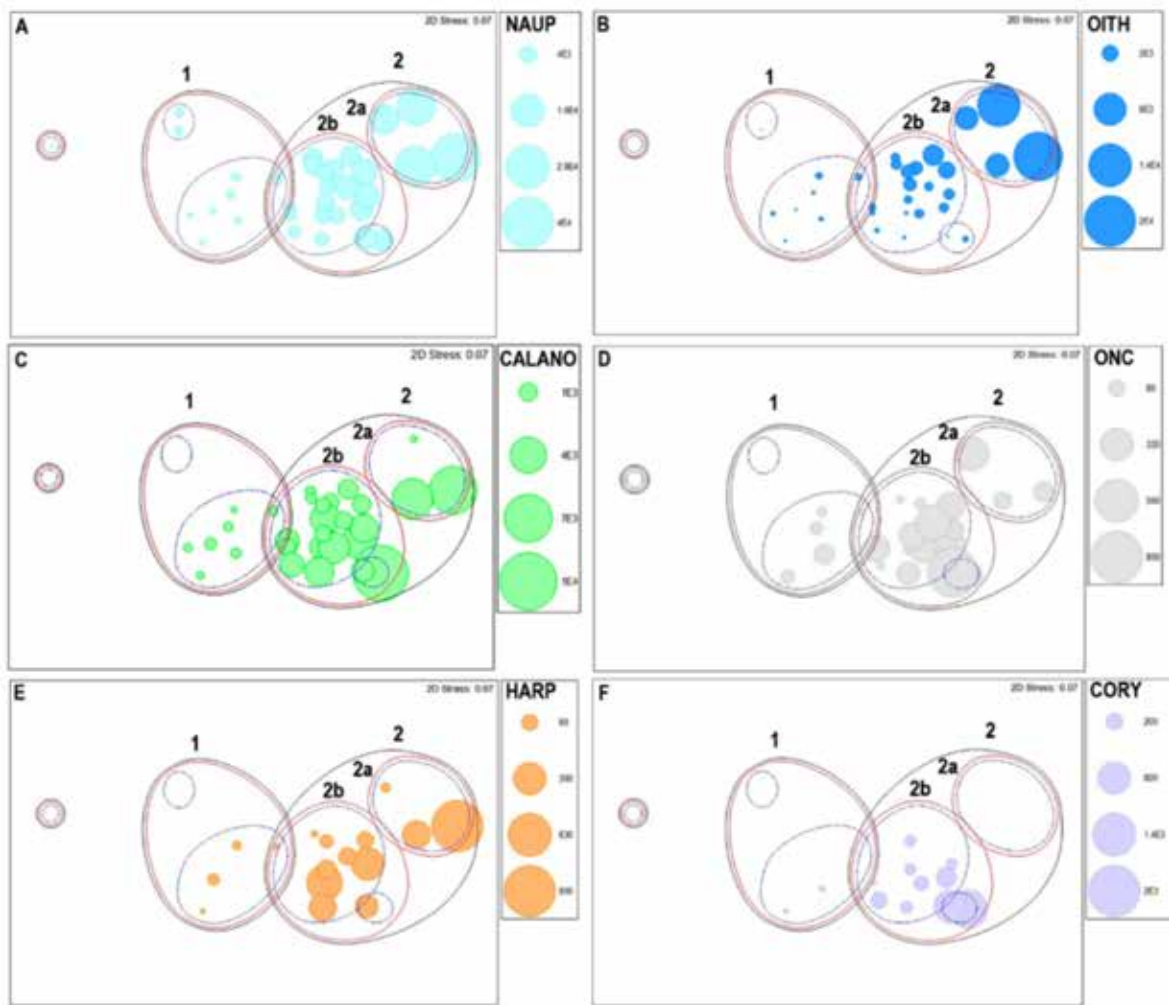


Fig. 10. A-F. Bubble plots of abundances of copepod assemblages at each station depicted as bubbles overlaid on Figure 9 nMDS, with bubble size corresponding to increase in abundance (NAUP=nauplii; OITH=oithonids; CALANO=calanoids; ONC=oncaeids; HARP=harpacticoids, CORY=corycaeids).

## DISCUSSION

There are relatively few recent papers that analyze the global distribution of copepods (e.g., FERNÁNDEZ DE PUELLES *et al.*, 2019; BRANDÃO *et al.*, 2021), and majority are primarily concerned with copepod diversity (WOOD-WALKER *et al.*, 2002; IRIGOIEN *et al.*, 2004; ROMBOUTS *et al.*, 2010). Estimates of diversity, while important, are mostly based on the taxonomy of adult individuals which do not provide information on ontogenetic structure, secondary production, or trophic potential and energy export to higher trophic levels (GARCÍA COMAS *et al.*, 2016). This information is particularly important in the oligotrophic

open ocean, where copepod production contributes a large portion of the energy budget (BODE *et al.*, 2018).

In this study, we summarize the abundance and distribution patterns of planktonic copepod assemblages by ontogenetic stage observed in nine circumglobal zones of the world's oceans (*sensu* BOLTOVSKOY, 1998), extending from the Arctic to Antarctic. Because the ecological role of copepods has been shown to be stage-dependent due to variation in body size during ontogeny (SERRA-POMPEI *et al.*, 2020), differences in ontogenetic structuring of copepod populations can be indicative of disparities in energy flow in different marine ecosystems (IM *et al.*, 2015).

### Abundance and spatial distribution of copepod assemblages

During the Arctic-Antarctic cruise of “Croatian tern”, nauplii were the most abundant copepod stage in the upper epipelagic layer of almost all visited areas. In the temperate and tropical regions of the Pacific and Atlantic, the abundances of nauplii even significantly exceeded those of tintinnids, a dominant protozoan group (KRŠINIĆ, 2018). Moreover, the proportion of copepodite stages in postnaupliar copepods was > 60% and peaked in calanoids (> 85 %). The overwhelming abundance of larval and juvenile copepods is easily overlooked when plankton nets with large mesh sizes are used to collect zooplankton (HOPCROFT *et al.*, 1998, 2001). However, when the community bulk is shifted to the lower size ranges of juveniles, this implies niche shift and a different utilization of resources in the trophic web (OLIVARES *et al.*, 2019).

Copepod abundance and community structure are closely related to temporal patterns of primary production (WOOD-WALKER *et al.*, 2002; CAPUZZO *et al.*, 2018). In examining the role of copepod size in community structuring, GARCIA COMAS *et al.* (2016) found that structuring based on individual size is primarily determined by food availability. The spatial distribution of copepod abundances during the Arctic-Antarctic cruise was largely influenced by the naupliar densities; it is evident that these were increased by an order of magnitude in the highly productive zones of the world ocean, e.g., the Bering Sea (BAIER&TERAZAKI, 2005; EISNER *et al.*, 2013), the British Columbia continental margin (ROBINSON & WARE, 1994), the California Current System (MCGOWAN *et al.*, 1996; WEBER *et al.*, 2021), and the Newfoundland shelf (LEAR, 1998; RICE, 2002). Climatically, these areas correspond to the temperate zone, where the influx of cold water from the subpolar/polar zones promotes upwelling and shapes productivity conditions, and high primary production supports abundant herbivorous zooplankton (MUETER *et al.* 2007; HICKEY & BANAS, 2008; HARRISON *et al.*, 2013). Among postnaupliar groups, the best matched to productivity conditions in the upper epipelagic

layer were oithonids, whose abundance generally coincided with the spatial distribution pattern of nauplii. WOOD-WALKER *et al.* (2002) noted the dominance of *Oithona* spp. in the northern polar biome. Additionally, numerous studies have shown that *Oithona* spp. (and particularly *O. similis s.l.*) are among the most abundant copepods from polar (e.g., WARD & HIRST, 2007; DVORETSKY & DVORETSKY, 2009) to tropical latitudes (WANG *et al.*, 2017), efficiently linking primary production to fish (GALIENNE & ROBINS, 2001; SPINELLI *et al.*, 2012). The global distribution of *Oithona* spp. has been attributed to a generalist diet, opportunistic feeding, and the use of omnivory/detritivory as feeding strategies (KATTNER *et al.*, 2003).

We have noted the typical dominance of calanoids in tropical and subtropical epipelagic waters of the Atlantic and Pacific (MADHUPRATAP and HARIDAS, 1986; MIYASHITA *et al.*, 2009; SCHNACK-SCHIEL *et al.*, 2010; KOZAK *et al.*, 2014), but in the northern subpolar and polar regions, adult calanoids were apparently much less abundant, although samples were collected in the polar summer when feeding conditions for herbivores are expected to be optimal (EL-SAYED and WEBER, 1982; KORB *et al.*, 2010). This alleged poleward decline is most likely related to the structure of the calanoid assemblage at high latitudes and the associated bias in our sampling method, as cold-water communities tend to be dominated by more dispersed, large-bodied copepods (> 2mm) (EISNER *et al.*, 2013; WANG *et al.*, 2019; BRANDÃO *et al.*, 2021), which are undersampled by small-diameter plankton nets. Therefore, in our study, only the abundances of juvenile calanoids are representative of the stations located in Labrador Sea, Beaufort Sea, Chuchi Sea, Bering Sea, and Baffin Bay upper epipelagic layer. The abundances of adults increased southward in both the Atlantic and Pacific, reflecting a shift toward smaller epipelagic calanoids at lower latitudes (WEBBER & ROFF, 1995; MCKINNON *et al.*, 2008). The relationship with temperature was apparently reversed for calanoids and oithonids. However, the lack of data for large calanoids may have biased the relationship between calanoids and

temperature, as well as the higher medians of calanoid abundances found in our study in the Southern Hemisphere.

Oncaeid copepods were less abundant than calanoids and oithonids, because the dominance of this omnivorous assemblage is often shifted to deeper layers, unlike calanoids, whose abundance generally decreases with depth (ROMAN *et al.*, 1995; YAMAGUCHI *et al.*, 2015). KRŠINIĆ *et al.* (2020) found that the core of adult oncaeid populations resided below 100 m depth in the deep southern Adriatic Sea. Similarly, peaks of oncaeid abundances were found below 200 m in the northernmost part of the Red Sea (Gulf of Aqaba; BÖTTGER-SCHNACK *et al.*, 2008). Overall, we found the highest abundances of oncaeids ( $> 700$  ind.  $m^{-3}$ ) in the subequatorial central South Pacific (St20), accompanied by high abundances of corycaeids, indicating the important role of carnivorous copepods in the local food web. The increased proportion of carnivorous copepods in high nutrient and low chlorophyll systems near the equator is attributed to their ability to bypass rapid phytoplankton depletion, which limits herbivorous grazers (WILLETT *et al.*, 2006).

The spatial distribution of abundances of harpacticoids and corycaeids was similar to that of postnaupliar calanoids, with the former two groups increasing at lower latitudes. Nevertheless, their patterns showed low overlap, as the corycaeids were absent above  $55^{\circ}$  N latitude, whereas the harpacticoids occurred over a wider latitudinal range extending as far north as the marginal Arctic (Station 10, Baffin Bay). We found that *Microsetella norvegica* dominated the harpacticoid assemblage at high latitudes, similar to DUGAS & KOSLOW (1984) for the Scotian shelf and ARENDT *et al.* (2013) for the subarctic fjord environment. Corycaeid copepods, on the other hand, are typical of warm water plankton and are associated with warm currents (MOTODA, 1963). Interestingly, in our study, high abundances of corycaeid copepods were found in areas of warm southern equatorial currents in both the Pacific and Atlantic (French Polynesia; MARTINEZ *et al.*, 2009; Brazil Current; LOPES *et al.*, 2006), but an absolute

maximum ( $< 1000$  ind.  $m^{-3}$ ) was recorded in the southern reaches of the California Current. The relative proportions of copepods associated with either warm or cold waters are very important in this large-scale upwelling system, as variations indicate changes in fish feeding conditions and overall productivity (BOGRAD *et al.*, 2000; WEBER *et al.*, 2021).

We must point out that with only two sites sampled during the Arctic-Antarctic cruise the Mediterranean Sea was poorly covered relative to other temperate areas. Due to the large dissimilarities between the western and eastern basins and the strong latitudinal gradients in productivity, the copepod community in the Mediterranean Sea exhibits large spatial and temporal variations (SIOKOU FRANGOU *et al.*, 1997, 2010). Therefore, the corresponding variability in the abundance and distribution of copepods in the Mediterranean is insufficiently illustrated during the Arctic-Antarctic cruise, although the relatively low densities of all copepod assemblages reflect the oligotrophic nature of the basin (POWLEY *et al.*, 2017). Similarly, we had only one station (St27) on the Antarctic shelf, which limits the conclusions for this area. Here, nauplii were represented with a minimal value found, while conversely KRŠINIĆ (2018) found relatively large abundances of tintinnids during the same cruise. The most probable reason for the absence of postnaupliar copepods in the Scotia Sea sample is the patchiness of zooplankton and small diameter of the plankton net, since there is an extensive literature documenting the diversity and abundance of calanoids and cyclopoids in this region (WARD & HIRST, 2007; CORNILS *et al.*, 2018; PAKHOMOV *et al.*, 2020).

The results of the Arctic-Antarctic cruise are consistent with several paradigms of global copepod distribution, *e.g.* the significant contribution of naupliar stages to copepod abundance and production in the open ocean (HIRST & LAMPITT, 1998; HOPCROFT *et al.*, 2001), the seasonally increased copepod productivity at high northern latitudes (DAGG *et al.*, 1984; ARASHKEVICH *et al.*, 2002) and latitudinal variations in abundances of copepod orders (TURNER, 1981; WOOD-WALKER *et al.*, 2002). A recent study

based on global “Tara Expedition” (2009-2013) plankton material revealed very similar patterns in copepod community structure, with contributions from the larger calanoids and oithonids increasing poleward and the smaller calanoids, oncaeids, and corycaeids peaking at lower latitudes. This pattern was apparently driven not only by temperature, but also depended on phytoplankton biomass, size structure, and the predominant feeding strategy within a copepod order (BRANDÃO *et al.*, 2021). Our results also suggest that despite the wide range (-1°C to 27°C), temperature was not the only determinant of copepod assemblage abundance distribution during the Arctic-Antarctic cruise, as feeding conditions, especially for grazers, also played a role. The relationship with temperature/climate zone may have been more pronounced at lower taxonomic levels, as shown by KRŠINIĆ (2018) for tintinnids, which exhibited more distinct preferences across global climate zones at the species level.

We recognize that our results represent a snapshot in time and provide a retrospective view of conditions prior to the 2000s. Due to ongoing climate change, several marine ecosystems have undergone or continue to undergo profound modifications of their biological communities, including changes in copepod abundance, size structure, and diversity (e. g., Bering Sea, MUETER *et al.*, 2007; Northwest Atlantic Shelf, PERSHING *et al.*, 2015; California Current System, MACKAS *et al.*, 2007, WEBER *et al.*, 2021; Arctic Ocean, ARRIGO & van DIJKEN, 2015). Thus, our results contribute a piece of the climate change mosaic against which ongoing changes in copepod biogeography can be compared.

#### **Numerical relationship between nauplii larvae and postnaupliar copepods**

The long-term stability of copepod populations in an area is an indicator of the ecosystem’s resilience to various stressors. This stability can be assessed by the ecology of key species (REBSTOCK, 2001; PROVAN *et al.*, 2009; MAZZOCCHI *et al.*, 2012), trends in abundance (REBSTOCK,

2002), or ontogeny (CONOVER *et al.*, 1995). It is not easy to determine a copepod-based indicator that represents a clear signal of disturbance in the pelagic zone, but instability in copepod reproduction could be considered an important warning sign. Naupliar stages ensure the continuation of copepod populations into the next year, but because survival rates of nauplii are lower than those of adult individuals (HAIRSTON & BOHONAK, 1998), they must be produced abundantly to compensate for increased mortality (OHMAN *et al.*, 2001; PLOURDE *et al.*, 2009). This means that the ratio of abundance of nauplii to all postnaupliar copepods should be at least  $> 1$ , assuming the copepod community is not under increased stress from adverse environmental conditions, predation, or starvation. The ratio of nauplii to postnauplii is expected to vary seasonally, consistent with maximum reproduction of currently dominant copepod species in different marine systems (VARGAS *et al.*, 2007). During the Arctic-Antarctic cruise, the ratio of nauplii to postnauplii varied from 1.1 to 6.4, and only at five stations was it slightly  $< 1$  (Fig. 6). Interestingly, these five stations were stations in the subtropical and tropical zones dominated by calanoids. Latitudinally, the median values of this ratio varied from 1.1 in the marginal Arctic to 3.1 in the South Pacific, with no statistically significant differences between areas.

To date, the relative abundances of naupliar and postnaupliar copepods have been studied in only a few marine ecosystems. KRŠINIĆ and GRBEC (2012) found that the ratio of nauplii to postnauplii varied between 2.2 and 3.3 and between 2.5 and 3.5 in the open and nearshore waters of the Adriatic Sea, respectively. Moreover, during 10 years of research in the deep southern Adriatic, a maximum of postnaupliar copepods was almost always found together with a maximum value of nauplii, with an average ratio of 3.5, and a regular decrease with depth was observed (KRŠINIĆ *et al.*, 2020). In the pigment layer in plankton off La Jolla, California, the ratio of nauplii to postnauplii in the period from April to September was 9.0 at the coastal station and 5.2 at the open-ocean station (BEERS & STEWART, 1970). In the surface waters

of the eastern tropical Pacific this ratio ranged from 2.4 to 7.3 (BEERS & STEWART, 1971).

Therefore, the ratio of nauplii to postnaupliar copepods is an important indicator for characterizing the area, but also for evaluating changes in the pelagic zone. As a relatively simple indicator that is stable within a range, the variability of abundances of nauplii could be useful in monitoring disturbance signals in the copepod community, provided that the average factors are determined for all marine zones under different productivity conditions, as previously noted by KRŠINIĆ *et al.* (2020). Currently, there are several plankton-based indicators investigating the relationship between species functional traits and hydroclimatic variability, trophic pathways, and anthropogenic impacts (BEAUGRAND, 2005; PITOIS *et al.*, 2021), each providing new piece of information on ecosystem functioning and resilience, and we therefore propose to also consider the relationship between copepod nauplii and postnauplii.

## CONCLUSIONS

With the exception of macroscopic zooplankton such as ctenophores or jellyfish, citizen science approach is not often used in plankton studies. Since reliable collection of plankton material demands training and equipment and can be both labor-intensive and time consuming, finding motivated partners among the public for

this kind of collaboration is very important for scientists.

The longest such partnership is the on-going global CPR plankton survey which monitors near-surface plankton communities since 1931 (BATTEN *et al.*, 2019). Valuable plankton material collected during “Croatian tern” cruises show that copepod abundances worldwide are dominated by developmental stages, both naupliar larvae and copepodites. Because their ecological role differs from that of adult individuals, more attention should be paid to the dynamics of the ontogenetic structure of the copepod community. In addition, we propose to use the ratio of nauplii to postnauplii as an indicator of the stability of copepod reproduction in different biogeographical areas, as fluctuations may be indicative of the onset of disturbances in the pelagic zone.

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## Zajednica veslonožaca od Arktika do Antarktike: upotreba „citizen science“ u poznavanju globalne raspodjele brojnosti nauplija i postnauplija u epipelagijskom sloju

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### SAŽETAK

Korištenje „citizen science“ prilikom sakupljanja uzoraka tijekom komercijalnih ili turističkih brodskih putovanja može pružiti vrijedan uvid u strukturu zajednica morskog planktona u širokim biogeografskim područjima. S ciljem proučavanja raspodjele i brojnosti manjeg zooplanktona korištenjem navedenog pristupa, uzorci planktona prikupljeni su u gornjem dijelu epipelagijskog sloja na 33 postaje od Arktika do Antarktike tijekom krstarenja jedrilice “Hrvatska čigra” (1994.-1997.). Uzorci su sakupljeni vertikalnim potezima Nansen planktonske mreže veličine okca od 53 mikrometra. U ovoj studiji saželi smo uočene obrasce raspodjele planktonskih račića veslonožaca po ontogenetskim stadijima (naupliusi, kopepoditi, adulti) i po postnauplijarnim skupinama (kalanoidi, oitonidi, onceidi, harpaktoidi, koriceidi). Izneseni su podaci o brojčanom odnosu naupliusa i postnauplijskih kopepoda, kao pokazatelju stabilnosti razmnožavanja kopepoda. Najveće abundancije ukupnih kopepoda utvrđene su u sjeveroistočnom i jugoistočnom Pacifiku, dok su najmanje vrijednosti utvrđene u Sredozemnom moru i Južnom oceanu. Sveukupno, zajednicom kopepoda prevladavali su nauplijski stadiji, dok su u većini postnauplijskih skupina (kalanoidi, oitonidi i onceide) dominirali kopepoditi. Brojnosti nauplija i postnaupliarni oitonidi pokazali su slične geografske obrasce, pri čemu su obje skupine dominirale na visokim geografskim širinama umjerenih zona s obje strane ekvatora, dok su se udjeli kalanoida, onceida i koriceida povećali na nižim geografskim širinama. Omjer nauplija i postnauplija kolebao je od 1,1 do 6,4, a samo na pet postaja bio je neznatno  $< 1$ . Latitudinalno, srednje vrijednosti ovog omjera varirale su od 1,1 u rubnom Arktiku do 3,1 u južnom Pacifiku, bez statistički značajnih razlika među područjima. Nagla promjena u omjeru brojnosti nauplija i postnauplijarnih stadija mogla bi signalizirati poremećaje u zajednici kopepoda, pod uvjetom da su prosječne vrijednosti određene za sva morska područja pod različitim uvjetima produktivnosti.

**Ključne riječi:** veslonošci; naupliji; biogeografija; geografska širina; citizen science

