

COPEPOD DISTRIBUTION IN SURFACE WATERS OF THE DRAKE PASSAGE USING CONTINUOUS PLANKTON RECORDER AND A PUMP-NET ONBOARD SYSTEM

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ABSTRACT

There is no single instrument that can sample quantitatively the complete spectrum of pelagic organisms, or even all the components of zooplankton. Mesh size is the main factor affecting species selectivity in the Continuous Plankton Recorder (CPR), implying a need to use multiple net systems to fully characterize a community. The spatial distribution of copepod communities in the water masses of the western and eastern sectors of Drake Passage were studied using, respectively, a CPR and a Pump Net onboard system. For this purpose, and assuming that copepod community size structures of each of the three water masses were similar in both the sectors studied, the possibility of complementing CPR results using a Pump-Net onboard system was evaluated. The latter system allows the estimation of absolute abundances and has the advantage of solving two problems associated with CPR, namely mesh clogging and low catching efficiency. The contribution of the nauplius forms and species accurately identified with both samplers was analyzed. Although *Oithona similis* dominated both communities, in the western sector small species made a greater contribution than *Calanus simillimus*, the opposite being true for the eastern sector. Nauplii and early copepodite stages of *O. similis* were missing from the CPR samples and represented between 69 and 79% of total copepod communities, whereas small calanoid copepods, *C. simillimus* copepodites and later stages of *O. similis* were inaccurately sampled by the CPR and represented between 14 and 18% of the copepod community. Hence, the Pump Net sampler is useful for complementing the semi-quantitative information of the CPR and for its calibration.

RESUMO

Não há um único instrumento que possa efetuar uma amostragem quantitativa completa para o espectro de organismos pelágicos, ou mesmo, para todos os componentes do zooplâncton. O tamanho da malha é o principal fator que afeta a seletividade de espécies no Registro Contínuo de Plâncton (CPR). Neste trabalho, estudamos a distribuição espacial das comunidades da copépode nas massas de água registradas nos setores ocidentais e orientais da Passagem de Drake, usando um CPR e um equipamento de amostragem que consiste em uma bomba de sucção instalada a uma rede de malha de 20 µm, respectivamente. Para este fim, e supondo que o tamanho das estruturas da comunidade de Copépodes de cada uma das três massas de água são similares em ambos setores estudados, foi avaliada a possibilidade de complementar resultados obtidos com o uso de CPR usando à bordo o sistema de bomba de sucção-rede. Este sistema permite a avaliação da abundância absoluta e possui a vantagem de resolver dois problemas associados à CPR, que são o assoreamento da rede e a baixa eficiência de captura. A contribuição das formas nauplius e das espécies identificadas com os dois amostradores, foram analisadas. Embora *Oithona similis* dominasse ambas as comunidades no setor ocidental, pequenas espécies de calanóides apresentaram contribuição mais elevada do que *Calanus simillimus*, enquanto o inverso foi verdadeiro para o setor oriental. Nauplii e estágios iniciais de copepoditos de *O. similis* faltaram nas amostras de CPR e representaram entre 69-79% das comunidade total de copépode, enquanto as densidades de pequenos calanóides e copepoditos de *C. simillimus* e estágios posteriores de *O. similis* foram imprecisamente estimadas por meio de CPR e representaram entre 14 e 18% da comunidade copépodes. Portanto, o sistema de bomba de sucção-rede é útil para complementar informações semi-quantitativas de CPR e sua calibração.

Descriptors: Copepod, Continuous Plankton Recorder, Pump Net sampler, Drake Passage, Southern Ocean.

Descritores: Copépodos, densidade, Registro Contínuo de Plâncton, sistema bomba de sucção, Passagem de Drake, Oceano Antártico.

INTRODUCTION

There is no single instrument that can sample quantitatively the complete spectrum of pelagic organisms, or even all the components of the zooplankton (ANON., 1964), which is reflected in the diversity of zooplankton samplers currently in use (WIEBE; BENFIELD, 2003). Mesh size is the main factor affecting plankton selectivity (UNESCO, 1968). The Continuous Plankton Recorder (CPR) has been used as the most effective and rapid method to monitor zooplankton patterns to assess the effects of environmental change (HOSIE et al., 2003). CPR has been used to sample zooplankton since the 1920s (HARDY, 1936), with more than four million miles of CPR tows carried out and with the highest concentration of samplings in the North Sea and Northeast Atlantic (REID et al., 2003). About 190,000 samples have been analyzed under microscopes, the phytoplankton and zooplankton of which have been counted and identified into approximately 500 different taxa (REID et al., 2003). The present understanding of the dynamics of plankton at ocean basin scale, over monthly seasonal cycles and in the time-frame of decennial change, would not have been achieved without the CPR (BRANDER et al., 2003). The Indian and Pacific sectors of the Southern Ocean constitute the second best ocean basin sampled by CPR. In contrast, for the Southern Atlantic Ocean, CPR has provided more limited datasets. Annual CPR tows have been conducted in the Scotia Arc by the British Antarctic Survey and Sir Alister Hardy Foundation for Ocean Science since 2006, but the results have not yet been published. Across the Drake Passage, only four transects have been made (MCLEOD et al., 2010) and detailed analysis of data was only completed for one of these CPR surveys (TAKAHASHI et al., 2010), the results of which were used in this study.

The CPR is an ideal sampler over large scales, with resolution on the 5-10 nautical mile scale, and has been used to demonstrate distinct changes in zooplankton patterns in relation to the various fronts across the Southern Ocean (HOSIE et al., 2003; HUNT; HOSIE, 2005; TAKAHASHI et al., 2010). A mesh size of 270 μm has been chosen as appropriate to retain a reasonable proportion of zooplankton (copepods and cladocerans), remaining unchanged over the history of the survey (BATTEN et al., 2003). However, in the last decade, several studies using plankton nets of 100- μm mesh size have indicated that small copepods exceed the abundance and sometimes the biomass of larger ones (METZ, 1996; ATKINSON; SINCLAIR, 2000; GALLIENNE; ROBINS, 2001; DUBISCHAR et al., 2002; TURNER, 2004). The use of very fine mesh sizes (<35 μm) in a high-speed sampler like the CPR has proved

impracticable for regular routine use and does not meet the agreed mesh size of 270 μm standardized for all CPRs as originally used in 1931. Accurate calibration is difficult to achieve, and there is a large reduction in efficiency (NICHOLS; THOMPSON, 1991), together with an increase in clogging of the mesh net. Mesh size is the main factor affecting species selectivity in CPRs (HUNT; HOSIE, 2006), implying a need to use multiple net systems to fully characterize a community. In spite of this, previous research has compared the sampling efficiency of the CPR and other more widely used devices using similar mesh nets (>200 μm). Most frequent comparisons were with vertical or oblique net hauls (e.g.: CLARK et al., 2001; JOHN et al., 2001; HUNT; HOSIE, 2003; KANE, 2009) and with the Longhurst-Hardy Plankton Recorder (LHPR) (RICHARDSON et al., 2004). In these cases, the possibility of differences in abundance due to changes in the sampling depth cannot be ruled out because of the vertical distribution of zooplankton. Richardson et al. (2004) suggested that a comparison between CPR data and surface data from another sampler over a broader spatial scale would be a more valid approach. Hunt and Hosie (2003) have been the only ones to date who have compared multiple net hauls and CPR samples over the same track with the same mesh over a wide area. Nevertheless, in these studies, the biases due to silk mesh clogging and escape through the mesh of the smaller zooplankton remain unsolved. The rapid increase in the use of CPR data which has occurred over recent years makes it necessary to evaluate the quantitative accuracy of the instrument (JOHN et al., 2001).

Nichols and Thompson (1991) suggested that water samples taken by pump or bottles offer a potential solution to the problem of sampling smaller copepod stages. In order to quantify zooplankton, pump samplers have been used together with zooplankton nets since the 1950s (TONOLLI, 1951) and pump-based samplers have gained popularity in recent years, especially to collect the smaller zooplankton (NAYAR et al., 2002; WIEBE; BENFIELD, 2003). An onboard pump-net sampler allows the collection of micro- and small meso-zooplankton data from a series of horizontal samples over a wide area, making it possible to study mesoscale distribution patterns of zooplankton.

The purpose of the present study was to study the spatial distribution of copepod communities in the water masses of the western and eastern sectors of Drake Passage using a CPR and a Pump-Net onboard system, respectively. For this purpose, the possibility of complementing CPR results in the estimation of the abundance of copepod communities, using a Pump-Net onboard system that addresses the issue of filtering performance, i.e. mesh clogging and escapement through the mesh, was evaluated.

Biases within the data set

The Drake Passage region under study covers an area of about 600 x 400 nautical miles. The possibility of longitudinal differences in copepod abundance or population structures between the western sector (CPR transect) and the eastern sector (pump-net transects) could not be excluded because they were separated by distances ranging from 130 to 470 nautical miles.

The patchy distribution of copepods may give rise to misleading comparison results if the two systems are used simultaneously. A high variability has been found when analyzing simultaneous “replicate” samples from a pump-net sampler and a net sampler separated by only 7 m (ARON, 1958). All other factors being equal, each sampler would have an equal chance of passing through a patch; then, it would be expected that the counts would vary considerably between the two devices for each paired haul, but that for many paired hauls there would be no trend of one net outfishing the other (ARON, 1958). There is a high degree of variance between replicates even when identical nets are hauled simultaneously on either side of a ship (UNESCO, 1968). The CPR is no exception, as dissimilar results have been obtained when it was compared with other devices with the same mesh size; Hunt and Hosie (2003) found higher densities in CPR samples than in NORPAC net samples.

Sheldon et al. (1972) discovered that the size distribution of marine particles varies predictably with latitude and thus established four zones, each with similar spectra in the Atlantic and Pacific Oceans: Polar, Temperate, Subtropical and Equatorial. They found similar size distribution patterns in samples located south of 50°S and between 30°W (Atlantic Ocean) and 130°W (Pacific Ocean). Other authors later established that the relative abundance of organisms of different sizes (plankton size spectra) can be remarkably consistent within these large regions when ecological conditions are similar (SHELDON *et al.*, 1972; QUINONES *et al.*, 2003). QUINONES *et al.* (2003) suggested that the planktonic sized-structure of offshore oligotrophic systems (like the region under study) is a conservative property. These authors found similarities between plankton size spectra in places as far apart as the Northwestern Atlantic and the North Pacific Central Gyre. In the Drake Passage, the distributions of sea surface temperature values, primary production values (MOORE; ABBOTT, 2000), SeaWiFS chlorophyll *a* values (ATKINSON *et al.*, 2008; PARK *et al.*, 2010), transport vectors of drifting particles (THORPE *et al.*, 2007) and zooplankton biomass values (O'BRIEN, 2007) become roughly parallel to the Polar and Subantarctic Fronts, rather than changing with longitude, in waters

moving through Drake Passage from the Southeast Pacific Ocean to the Southwestern Atlantic Ocean. In addition, Sprintall (2008), who studied long-term trends and interannual variability of temperature in Drake Passage (from 57 to 67°W) stated that the Polar Front (PF) divides the area into two sub-regions with different dynamics and climatic signals. Sheldon *et al.* (1972) defined the Antarctic Convergence (Polar Front) as the limit between two zones each with its characteristic particle size structure (Polar and Temperate zones). Based on these previous reports, it seems reasonable to regard both fronts as the strongest spatial structuring forces in the region. So dividing each dataset into three parts according to the positions of the fronts contributes to creating regions of similar environmental conditions in both sectors of Drake Passage: 1) South of the Polar Front (Antarctic Zone; AZ); 2) between the Polar and Subantarctic Fronts (Polar Frontal Zone; PFZ), and 3) north of the Subantarctic Front (Subantarctic Zone; SAZ),

In addition, among marine planktonic invertebrates, copepods may account for 90-97% of the biomass (BRADFORD-GRIEVE *et al.*, 1999). In the present study, copepods account for about 94%, in term of numbers, of total zooplankton in CPR samples (TAKAHASHI *et al.*, 2010). According to this, it can be inferred that copepod community size structures were rather similar between both sectors of Drake Passage for each water mass analyzed, and that the contribution of small and large size copepods to total community did not differ significantly between sectors. This assumption will be used to evaluate the possibility of complementing CPR results in the estimation of abundance of copepod communities, using a Pump-Net onboard system.

MATERIAL AND METHODS

Information about the research cruises that study the eastern and western sectors of Drake Passage and a general comparison of the characteristics and methodology of the Pump-Net onboard system and CPR are given in Table 1. For the description, sampling protocol and processing technique of the CPR, see Takahashi *et al.* (2010), Batten *et al.* (2003) and Hosie *et al.* (2003). The western sector of Drake Passage was sampled during the Southern Ocean CPR Survey conducted between 62.31°S 61.77°W and 55.76°S 80.01°W, covering a total of 689.9 nautical miles (nm) between February 7 and 9, 2000. The CPR data of copepods used in this study were collected from tows 68 and 70 (TAKAHASHI *et al.*, 2010). On the other hand, the eastern sector of Drake Passage was covered with two oceanographic transects between 55 and 63°S (40-70°W) during the summer Antarctic Cruise 2000. The first transect was covered between January 3 and 4, 2000 between 55.23°S

62.57°W and 61.65°S 57.38°W, along a total of 424.39 nm of which 351.56 nm (83%) were sampled in eight sections of 23-50 nm (mean 44 nm). The second transect was made between February 10 and 12, 2000 between 55.24°S 65.99°W and 60.16°S 49.65°W, covering a total of 601.67 nm of which 160 nm (26%) were sampled in eight sections of 5-32 nm (mean 25 nm). Samples for copepod studies were taken from a continuous pumping system powered by a centrifugal pump placed at 9 m depth aboard the icebreaker “Almirante Irizar”. Seawater was pumped through a natural rubber hose to the wet laboratory. The seawater flow rate was checked before sampling. Up to 3000 L of seawater were filtered through a modified Nansen 20 µm-mesh net suspended on the roof and the samples collected were preserved in 3% formaldehyde. Prior to the laboratory analyses, each microplankton sample was separated into two fractions by using a 300-µm mesh net. Absolute abundances of nauplii and some small species of copepods in the fraction <300 µm were estimated from three subsamples of each sample, if enough material was available. Otherwise, the entire sample was examined. Counts were made under an inverted microscope at 200x magnification. Larger copepods (fraction >300 µm) were identified under a stereoscopic microscope at 40x magnification and the entire sample was examined.

Table 1. Information on research cruises and characteristics of the Pump-Net system and Continuous Plankton Recorder (CPR).

Place	Western Drake Passage	Eastern Drake Passage
Cruise name	8 th Antarctic expedition	CAV 2000
Ship	R/V Kaiyo Maru	RH “Alte Irizar”
Speed (kn)	15.22 ± 1.22	13.6 ± 1.0
Date	February 2000	January-February 2000
Distance Sampled (without frontal zones)	493 nm	511 nm
SAMPLER	CPR Type II	Pump-Net
Mesh size	270 µm	20 µm
Depth	6-10 m	9 m
Section range	3.8 – 3.9 nm	5-50 nm
Seawater filtered per sample	1.13-1.16 m ³	1.20-3.31 m ³
Clogging	Possible	No
Reduction in flow rate	Possible	No

The distribution of transects for each cruise in Drake Passage is shown in Figure 1. The positions of the Polar and Subantarctic Front in Drake Passage are defined in accordance with Orsi et al. (1995), using AVHRR Oceans Pathfinder Sea Surface Temperature (SST) data obtained for summer 2000 through the online Physical Oceanography Distributed Active Archive Center (PO.DAAC) Ocean ESIP Tool (POET) at the NASA Jet Propulsion Laboratory, Pasadena, CA, USA (<http://podaac.jpl.nasa.gov/poetthe>). In the eastern sector of Drake Passage (Pump-Net), samples were not taken in the sections corresponding to the Polar Front and the Subantarctic Front, and hence the corresponding CPR sections in the western sector of Drake Passage (n: 25 and 26, respectively; TAKAHASHI et al., 2010) were not considered in the analyses.

A three-way ANOVA design with fixed factors was used to detect significant fluctuations in density values (ZAR, 1999). Density values were expressed as individuals (ind.) m⁻³ instead of ind. for each travel section, because the amount of water filtered by the sampler systems per section is different (i.e.: approx. 0.6 m³ for the Pump-Net and 3.11 m³ for the CPR per 10-nautical mile section; JOHN et al., 2002). This has the limitation that the filtration efficiency of the CPR is assumed to remain constant. The analyses of data from both sectors of Drake Passage were run for all copepods and separately only for each copepod species and group identified in both sectors and which contributed, at least 2% of total abundance. Drake Passage sector (Western and Eastern), Location (Subantarctic Zone and Polar Front Zone) and Time of day (daytime and nighttime) were entered as fixed factors. Samples from the Antarctic Zone were not included in the analysis because no samples were taken during the 8-h nocturnal period in the eastern and western sectors of Drake Passage. The ln (X+1) transformation effectively homogenized the variance of the data, except for nauplius stages. On this account, nauplii density values were transformed into ranks and then the ranks were analyzed by a Kruskal–Wallis nonparametric ANOVA (ZAR, 1999). Significant differences in density values were tested using the Tukey’s HSD *a posteriori* multiple-comparison test for unequal sample sizes (ZAR, 1999).

The total length of 1648 copepod specimens recorded in the Pump-Net samples (up to 30 specimens of each species per sample) was measured under a stereoscopic microscope (precision: 0.05 mm) and an inverted microscope (precision: 0.015 mm). Then, they were separated into 12 size-classes to evaluate total length-frequency (TL-F) distribution of copepods.

RESULTS

The SST data determined the presence of three water masses: Antarctic waters south to the Polar Front, the Polar Front Zone between the Subantarctic Front and the PF, and the Subantarctic waters, north to the SAF (Fig. 1). Despite the differences in the total number of sections covered (16 vs. 180), the number of nautical miles in the western sector of Drake Passage was similar to that in the eastern sector (Table 1). For the Antarctic (AZ), Polar Front (PFZ) and Subantarctic (SAZ) Zones, 184, 241 and 87 nm were studied within the eastern sector, respectively, and 131, 116 and 246 nm within the western sector, respectively.

The density values of copepods in the western sector of Drake Passage (CPR samples) ranged between 1 and 1710 ind. m⁻³. A total of 15,575 specimens of copepods were collected (129 sections, without considering the Polar and Subantarctic Front sections), of which 70 (0.5%), 1275 (8.1%), 3928 (25.2%) and 9993 (64.2%) belonged to nauplius forms, *Calanus simillimus*, *Oithona similis* and small calanoid copepods (likely to be adults and copepodites of the more abundant *Ctenocalanus citer*,

Clausocalanus spp., and the rare *Microcalanus pygmaeus*, and copepodites of *C. simillimus*; TAKAHASHI et al., 2010), respectively (Fig. 2). Adults of *Rhincalanus gigas* and *Pleuromamma robusta* (<0.1% of the total) were also present in the samples. The density values of copepods from the eastern sector of Drake Passage (Pump-Net samples) ranged between 0 and 3040 ind. m⁻³; data were pooled for further analysis because no significant differences (T-test 0.69, $P = 0.499$) were found between the two oceanographic transects. A total of 4204 copepods, of which 2984 (71%), 370 (9%) and 390 (10%) specimens corresponded to nauplius forms, *C. simillimus* and *O. similis*, respectively, were assigned to 10 species (Fig. 2). Small calanoid copepods (such as *C. citer* and *Clausocalanus* spp.), *Microsetella norvegica* and *Oncaea curvata* contributed with 5% and large calanoids such as *Calanoides acutus* (Calanidae), *Metridia gerlachei* (Metridiidae) and *Subeucalanus longiceps* (Eucalanidae) contributed 5% to the total (Fig. 2). There was variability in the contribution of each copepod category among the three water masses analyzed both in the western and eastern sectors of Drake Passage (Fig. 2).

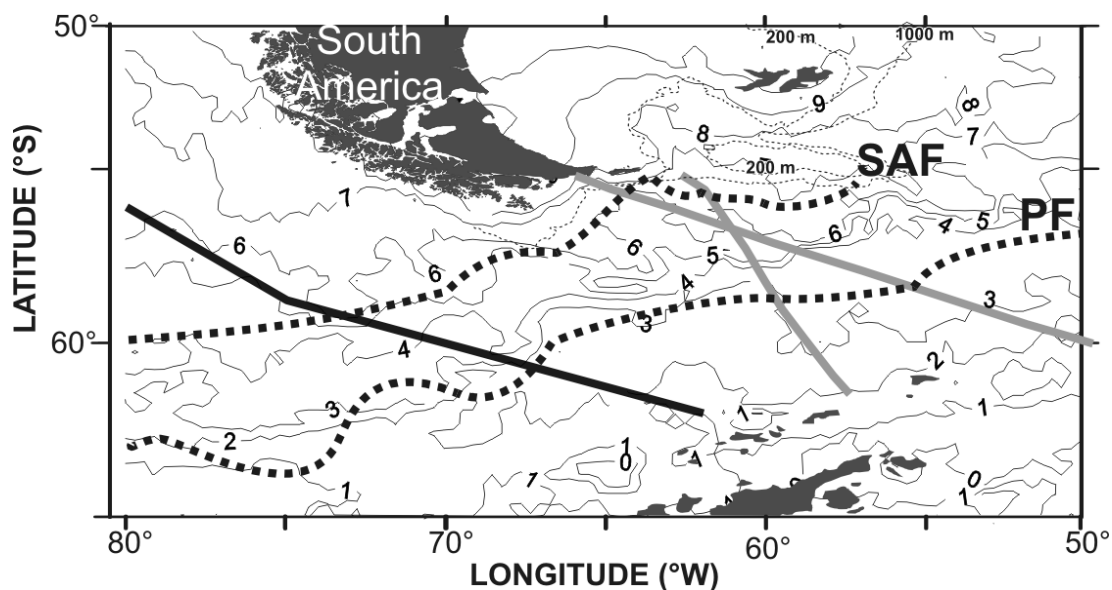


Fig. 1. Transect locations of the Pump-Net system (gray) and Continuous Plankton Recorder (CPR, black) surveys in the eastern and western sectors of Drake Passage during summer 2000. Sea-surface temperature(°C) distributions are also shown. SAF: Subantarctic Front; PF: Polar Front.

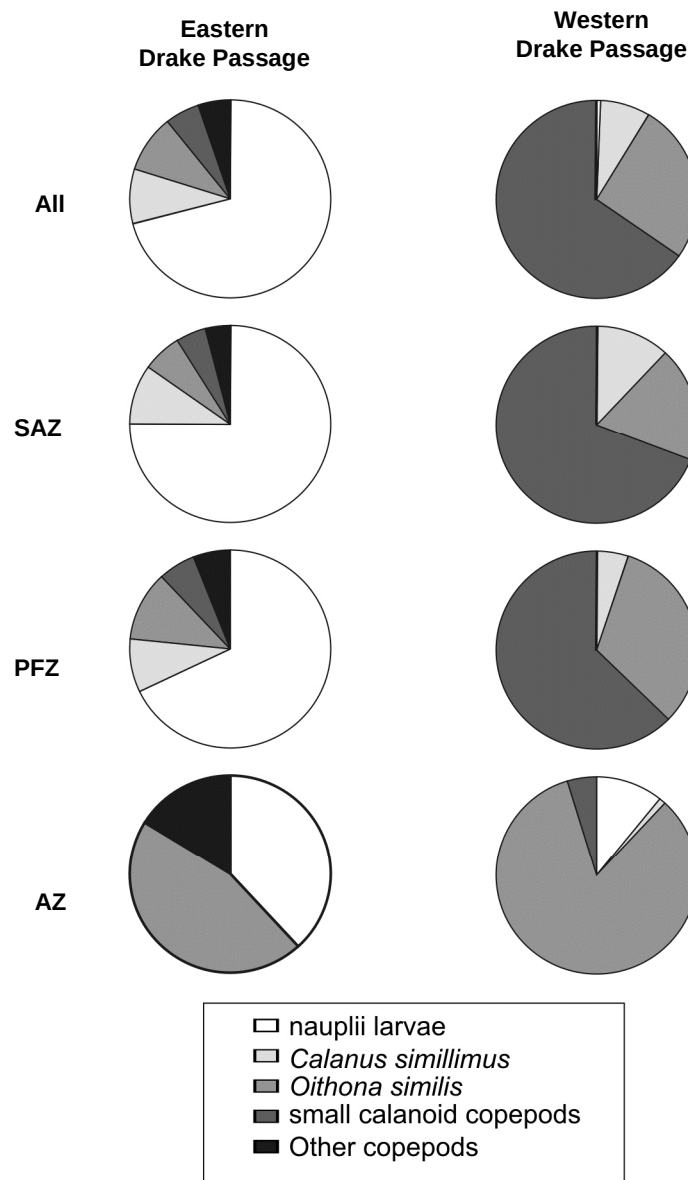


Fig. 2. Comparison of copepod community structures from the eastern and western sectors of Drake Passage compiled from mean density values of each water mass. Small calanoid copepods: copepodites and adults of *Ctenocalanus citer* and *Clausocalanus* spp. for both sectors and copepodites of *C. simillimus* (western). AZ: Antarctic Zone; PFZ: Polar Front Zone; SAZ: Subantarctic Zone.

The density distribution for total copepods, nauplii forms, *O. similis*, *C. simillimus*, *R. gigas* and small calanoid copepodites and copepodis shown in Figure 3. The density values of total copepods, nauplius larvae and *C. simillimus* were significantly higher for the eastern sector of Drake Passage (Table 2, Fig. 3). The mean density values of *R. gigas* nauplii and *O. similis* were slightly higher

for the eastern sector than for the western sector of Drake Passage (1.1 and 49 ind. m⁻³, respectively, vs. 1.0 and 33 ind. m⁻³, respectively), while the opposite was true for small calanoid copepods (53 and 85 ind. m⁻³ for the eastern and western sector, respectively), but none of these differences were statistically significant (Table 2, Fig. 3). The distribution of density values of *O. similis* in the western sector of

Drake Passage showed the presence of extreme values, which could affect ANOVA results. An outlier value from the western sector dataset was detected using Grubbs' test (GRUBBS, 1969), so a further comparison between Drake Passage sectors was made without the outlier, and *O. similis* densities obtained in the eastern sector were significantly higher than those obtained in the western sector ($F_{1,139} = 5.67$, $P = 0.018$). It is worth noting that most differences in copepod density values between eastern and western sectors of Drake Passage were an artifact related to the different sampling systems used, as discussed below.

The main effects of Location and Time of day were significant in some groups (Table 2); the abundances of total copepods, *C. simillimus*, *O. similis* and small calanoid copepods were significantly higher at nighttime than in the daytime. Nauplii of *R. gigas* were more abundant in PFZ than in SAZ. *O. similis* was the only one showing a significant simultaneous effect of Drake Passage sector and Location; density values were significantly higher in PFZ than in SAZ in the western sector samples, but similar in the eastern sector samples. The Tukey's HSD *a posteriori* test indicated that the abundances of *C. simillimus* and *O. similis* from the western sector (CPR samples) were significantly higher at nighttime than in the daytime for both PFZ and SAZ ($P < 0.04$). Although in the eastern sector densities were higher at nighttime than in the daytime, differences were significant for *C.*

simillimus (Tukey's HSD, $P < 0.02$), but not for *O. similis* (Tukey's HSD, $P > 0.20$).

DISCUSSION

The mesh selectivity model of Nichols and Thompson (1991) shows that a mesh size of 75% of the copepod width catches 95% of all the individuals of that size. Taking into account that the filtering silk of the CPR has a mesh of 270 μm and considering the length-to-width formula of Gallienne and Robins (2001), the CPR quantitatively retains copepods of at least 360 in body width and 1250 μm in total body length. Experimentally, the rest of the copepods might be caught in different proportions (or undersampled), with values near zero for body lengths below 600-700 μm (NICHOLS; THOMPSON, 1991). Unfortunately, the degree of CPR undersampling is hard to quantify because it would be closely related to the presence of large phytoplankton during the time of sampling. Phytoplankton could decrease the aperture size or porosity of the silk, thus increasing the catching efficiency of small copepods by reducing the possibility of escape through the mesh. At the same time, however, phytoplankton would increase clogging of the filtering silk, reducing the filtration efficiency of the CPR by up to 60% (HUNT; HOSIE, 2006). Phytoplankton has been observed in the silk only around SAZ (K.T. pers. obs.).

Table 2. Significance (P-levels) of the main effects and interactions of the three-way ANOVAs for the density of each copepod taxon and total copepods. Significant values in bold. Sector: Western and Eastern Drake Passage. Location: Subantarctic and Polar Front Zones. Time of day: daytime and nighttime.

Taxa	Source of variation						
	Sector	Location	Time of day	Sector x Location	Sector x Time of day	Location x Time of day	Sector x Location x Time of day
<i>Calanus simillimus</i>	<0.0001	0.55	<0.0001	0.11	0.28	0.13	0.44
<i>Oithona similis</i>	0.47	0.009	0.031	0.048	0.44	0.52	0.81
Nauplii indet (small)	<0.0001	0.66	0.96	0.72	0.99	0.75	0.86
<i>Rhincalanus gigas</i> nauplii	0.24	<0.0001	0.91	0.39	0.87	0.99	0.78
Small calanoid copepods	0.55	0.26	0.003	0.14	0.26	0.13	0.50
TOTAL	0.0006	0.054	0.032	0.19	0.08	0.31	0.67

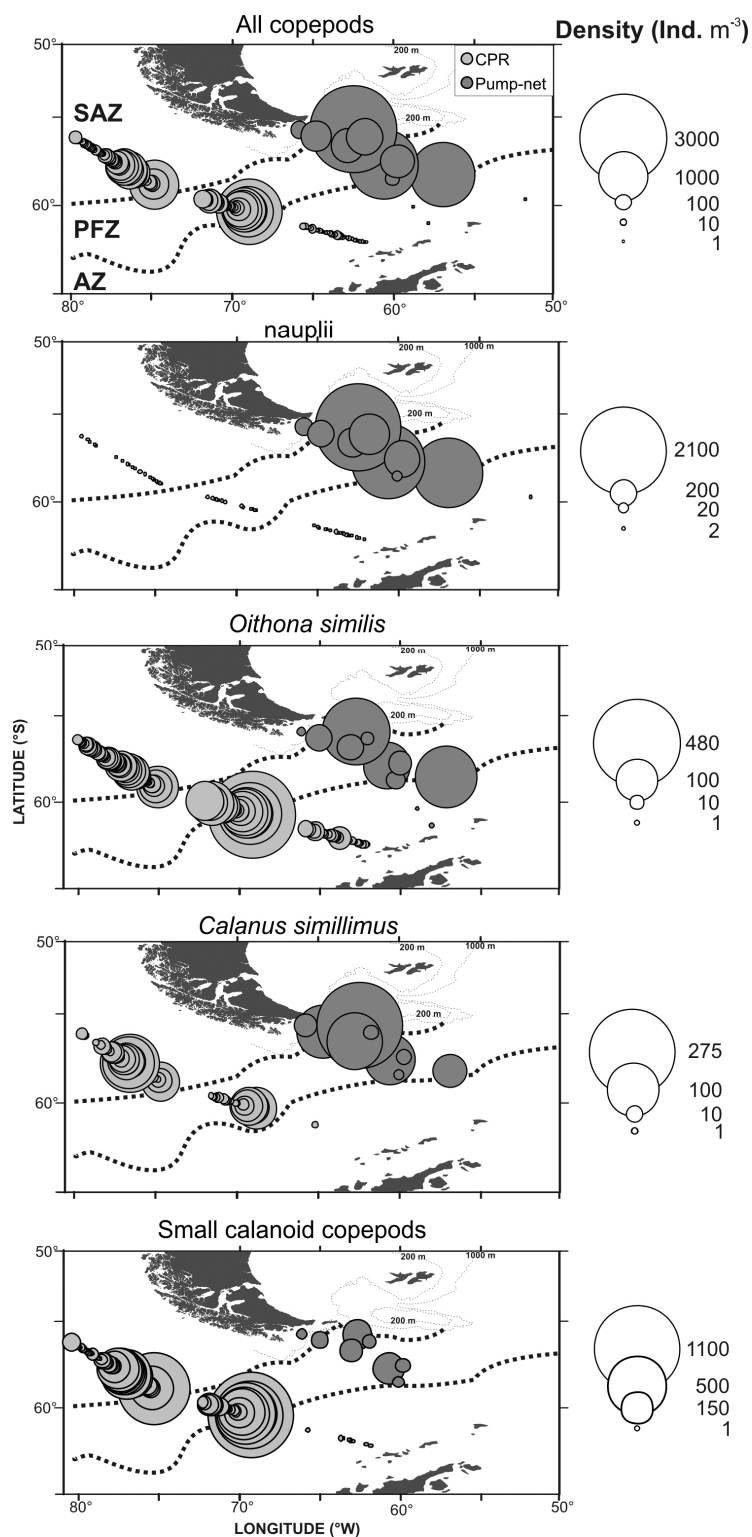


Fig. 3. Density of total copepods, *Calanus simillimus*, *Oithona similis*, small calanoid copepods and nauplius forms from Pump-Net and Continuous Plankton Recorder (CPR) samples. The circle size is proportional to absolute density values. AZ: Antarctic Zone; PFZ: Polar Front Zone; SAZ: Subantarctic Zone.

According to the analysis of total length-frequency (TL-F) distribution of copepods of the on-board pump-net system and assuming similar TL-F distribution structures for the copepod communities in both sectors of Drake Passage (see “Biases within the data set”), approximately 10% of total copepods were quantitatively caught by the CPR, because they are larger than 1250 μm in total length (Fig. 4). In addition, it is likely that about 75% of the copepod community (<650 μm in total length, Fig. 4) was completely missing from the CPR samples, while 15% of the copepods probably suffered from some degree of undersampling related to the clogging of the

filtering silk, mainly around the SAZ. The high dispersion of density values for each group and water mass (Fig. 3) in both sectors of Drake Passage might be explained by the fact that the sampler systems used have been designed for large-scale sampling with a resolution of 5-10 nautical miles. Although this may mask evidence of a patchy distribution, it is possible that the extreme and short-term physico-chemical variability in the Southern Ocean would have led to fluctuations in copepod abundance of up to three orders of magnitude in these waters (i.e.: *O. similis*; PINKERTON et al., 2010; MCLEOD et al., 2010).

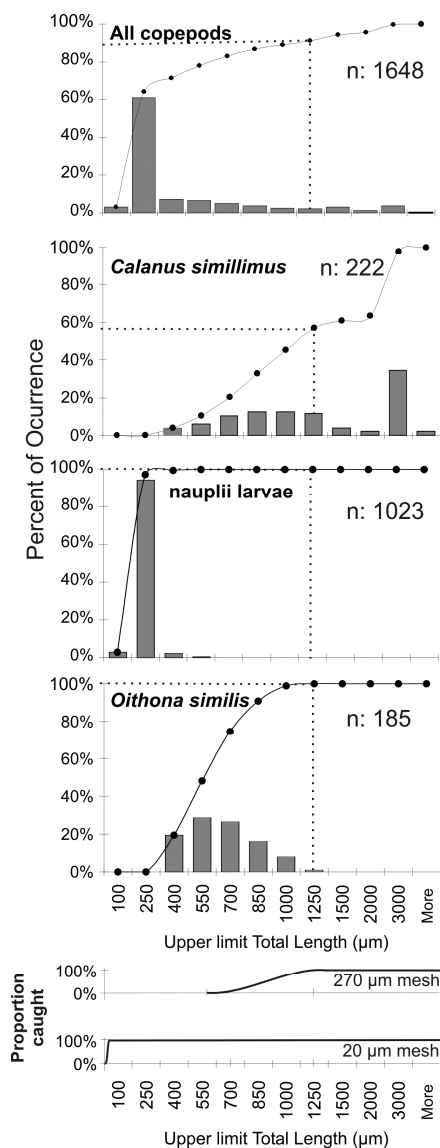


Fig. 4. Size frequency distribution and cumulative frequency distribution of each copepod taxon and total copepods. The proportions of specimens caught with 270- μm mesh size (CPR) and 20- μm mesh size (P-N), estimated according to the mesh selectivity model of Nichols and Thompson (1991), and the length-to-width formula of Gallienne and Robins (2001) are also shown.

Small nauplii provide a clear example of the fact that the pump-net can complement the information obtained from the CPR. They may pass through the 270- μm mesh of the CPR due to their small size, and if caught, their identification is often very difficult because of their small size. The copepod dimensions recorded in the present study (40-220 μm in width and 70-650 μm in length) indicate that almost all the small nauplius forms were quantitatively sampled with the 20- μm mesh of the on-board pump-net system. There was neither clogging effect nor changes in filtration efficiency. Nauplii showed the highest abundances of all copepod groups considered, with values decreasing southward with increasing body length and width (Figs 4, 5). There has been no previous attempt to quantify nauplius abundances from CPR samples, except for *Rhincalanus gigas* nauplii, which were quantitatively caught by both devices (Fig. 4). Pitois and Fox (2008) developed a production model for estimating nauplius abundance from that of adult copepods sampled by the CPR. In this model, nauplius abundance is a function of temperature, adult copepod biomass and egg production estimated from fecundity values. Unfortunately, the model lacks the backing of reliable data and contains a number of assumptions and deterministic relationships. In this study, the density values of nauplii may be considered among the highest of an annual cycle, because nauplii reach their maximum abundance in surface waters during summer (VERVOORT, 1965; ATKINSON; SINCLAIR, 2000). Considering that copepod nauplii are, by and large, the main component of small mesozooplankton (WARD et al. 2011), it can be inferred that copepod nauplii in the western sector of Drake Passage (CPR samples) might represent 38%, 68% and 71% of total copepods for AZ, PFZ and SAZ, respectively, as in the eastern sector (Pump-Net sample).

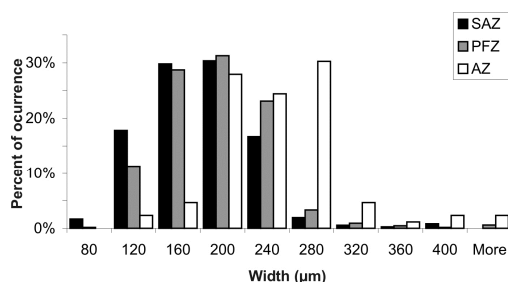


Fig. 5: Width frequency distribution of nauplii from the eastern sector of Drake Passage (Pump-Net samples) for each water mass. AZ: Antarctic Zone; PFZ: Polar Front Zone; SAZ: Subantarctic Zone.

Calanus simillimus is an important species of the Southern Ocean because of its high abundance and biomass (ATKINSON; SINCLAIR, 2000; PAKHOMOV et al., 2000; TAKAHASHI et al.,

2010). The analysis of total length-frequency distribution of *C. simillimus* based on the mesh selectivity model (NICHOLS and THOMPSON, 1991) suggests that copepodites I-IV were undersampled by the CPR and quantitatively sampled by the pump-net sampler (Fig. 4). If some of these early stages were occasionally retained in the CPR mesh, they were difficult to identify and classified as small copepodites. The CPR dataset showed that *C. simillimus* copepodites represent only 0.7 % of *C. simillimus* numbers (G.H. pers. obs.). In pump-net samples, copepodites I-IV represented on average 53% and 68% of the *C. simillimus* population for SAZ and PFZ respectively, which is in agreement with previous summer reports that showed older populations north of the Polar Front (WARD et al., 1996). Considering that only *C. simillimus* (CV-CVI) is quantitatively retained by both samplers, this species was somewhat more abundant in the eastern sector (Pump-Net samples; average 52 ind. m^{-3} and 23 ind. m^{-3} for SAZ and PFZ respectively) than in the western sector (CPR samples: average 12 ind. m^{-3} and 16 ind. m^{-3} for SAZ and PFZ respectively).

For *Oithona similis*, only stages IV-VI were found in studies using high-speed samplers such as the LHPR or CPR (ATKINSON et al., 1996a,b; PINKERTON et al., 2010). Copepodites I-III might have been missed in CPR samples or, as is the case for nauplii, if any of the copepodites I-III of *O. similis* are trapped on the mesh due to net clogging, then they are difficult to identify accurately due to their small size and the conditions of sampling process. This fraction represents on average 61% of the *O. similis* population for the three water masses studied (this study, DUBISCHAR et al., 2002). In addition, the on-board pump-net system was expected to quantitatively catch all copepodite stages. Considering only stages IV-VI, *O. similis* was more abundant in the AZ and PFZ of the western sector of Drake Passage (average 5 and 72 ind. m^{-3} respectively against 0.1 and 44 ind. m^{-3} respectively for the eastern sector). Although similar densities values were recorded for SAZ in both sectors (eastern: 29 ind. m^{-3} and western: 23 ind. m^{-3} Pump-Net samples), probably this species was somewhat more abundant in the western part of SAZ, because it was underestimated. These results are in agreement with the prediction of the boosted regression tree (BRT) model of Pinkerton et al. (2010), which indicated that the median nighttime relative abundance of *O. similis* adults for the longitudinal ranges of the western sector of Drake Passage (65-80°W) was higher than that for the eastern sector (50-65°W) during January-February. Moreover, Pinkerton et al. (2010) predicted that an area somewhat to the south of the location of the CPR transect (about 65°S, 80°W), was one of the five hotspots of *O. similis* abundance which deserve further attention.

Large copepods such as *Calanoides acutus* and *Metridia gerlachei* with densities of up to 40-70 ind. m⁻³ were only caught in the eastern sector of Drake Passage. They are epi- to mesopelagic species (RAZOULS et al., 2005-2011), and their presence has been documented in the study area (Ocean Biogeographic Information System, 2011) and in the Atlantic and Pacific sectors of the Southern Ocean (RAZOULS et al., 2000), where they are among the most numerous calanoid species (SCHNACK-SCHIEL; HAGEN, 1994). On the other hand, the large copepods *Rhincalanus gigas* and *Pleuromamma robusta* were found in very low abundances (six and one specimens, respectively) in the western sector (CPR sampler) in samples taken mainly at nighttime; they inhabit deeper waters (mesopelagic-bathypelagic species) and undertake nocturnal migrations (ATKINSON et al., 1996a). These species had lengths over 2 mm, which represents a narrow overlapping with the species recorded in both sectors of Drake Passage. In addition, their lower contribution to the copepod community did not influence the total length-frequency (TL-F) distribution of copepods.

The size range fractions of copepods evaluated and the contribution of each size fraction to the copepod community in each water mass studied are summarized in Table 3. There was a narrow overlapping of the copepod groups found in the lower size range: nauplii were mostly below 400 µm length

(Fig. 5, Table 3) and *O. similis* CI-CIII mostly between 400 and 700 µm. According to pump-net samples, these two groups together represent 66%, 75% and 79% of the copepod communities for AZ, PFZ and SAZ, respectively. These two groups were the only copepod specimens in this size range (the harpacticoid *Microsetella norvegica* was in this size range but its contribution was below 3%) which were almost completely missing in the CPR samples. Taking into account that copepod community size structures were rather similar in both sectors of Drake Passage, we may suggest that CPR average values of total copepod density for AZ, PFZ and SAZ should be at least multiplied by 3, 4 and 5 respectively to obtain a more accurate picture of total copepod abundances. The middle size range was characterized by copepod groups with a wide overlap in their size ranges and represented between 14 and 18% of the copepod communities analyzed. This fraction was partially underestimated in CPR samples but the degree of undersampling was hard to quantify directly. In spite of this, it may be suggested that the total underestimation of this copepod size fraction in the communities was not significant when compared with the lower size fraction. The higher size fraction was characterized by *C. similis* and some other large calanoid species with low densities. Although their contribution to the copepod community was the lowest, they were quantitatively retained by both samplers.

Table 3. Relative contribution of copepod communities, divided into three size ranges, to each water mass analyzed and how well they were characterized with the CPR sampler. AZ: Antarctic Zone; PFZ: Polar Front Zone; SAZ: Subantarctic Zone.

Length size range	Copepods species / groups	Characterization with CPR sampler	Percent of occurrence in copepod community (Pump – Net samples)		
			AZ	PFZ	SAZ
< 700 µm	Nauplii larvae <i>Oithona similis</i> (CI-CIII) <i>Microsetella norvegica</i>	Fraction missing	66%	75%	79%
700 – 1250 µm	<i>Oithona similis</i> (CIV-CVI) <i>Calanus similis</i> copepodites Small calanoid copepods	Fraction underestimate	18%	15%	14%
> 1250 µm	<i>Calanus similis</i> (adults) Some adults of small calanoid copepods Other large calanoids	Fraction quantitatively retained	16%	10%	7%

We may conclude that abundance of copepod communities was dissimilar as between the western and eastern sectors of Drake Passage, and that the same was true for population structure. *O. similis* dominated both communities with dissimilar distribution among the three water masses of both sectors and its density was higher in the western sector than in the eastern sector of Drake Passage. Small calanoid copepods (*Clausocalanus* spp., *Ctenocalanus citer*) had a higher contribution than *C. similis* in the western sector, while the opposite was true for the eastern side. Although the Pump-Net is not an autonomous system, it allows the estimation of absolute abundances and has the advantage of solving two problems associated with the use of CPR, namely mesh clogging when phytoplankton are recorded and low catching efficiency of small zooplankton through the 270- μ m mesh. Nauplii and early copepodite stages of calanoid and cyclopoid species which were inaccurately sampled by the CPR were possible to quantify with the on-board pump-net sampler. Hence, the pump-net sampler is useful for complementing the semi-quantitative information from the CPR and for its calibration when used in the Southern Ocean. The comparative study of these two kinds of gear should be performed on a 1-year cycle because the retention efficiency of zooplankton is seasonally dependent (RICCARDI, 2010).

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