

Contents lists available at ScienceDirect

# Journal of Sea Research



journal homepage: www.elsevier.com/locate/seares

# Short communication

# Estimating copepods' abundance with paired nets: Implications of mesh size for population studies

# J.C. Antacli <sup>a,b,\*</sup>, D. Hernández <sup>b</sup>, M.E. Sabatini <sup>a,b</sup>

<sup>a</sup> Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina

<sup>b</sup> Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), Paseo Victoria Ocampo N° 1, B7602HSA - Mar del Plata, Argentina

#### ARTICLE INFO

Article history: Received 20 April 2009 Received in revised form 23 September 2009 Accepted 29 September 2009 Available online 9 Ocotber 2009

Keywords: Copepods Population Nets Catchability Southern Patagonian Shelf

#### ABSTRACT

Three representative copepods occurring in the southern Patagonian shelf, *i.e., Calanus australis, Drepanopus forcipatus* and *Oithona helgolandica* were sampled by the first time with paired nets of 66 and 150 µm mesh size. The stage-specific estimates of abundance of their populations were statistically analyzed to assess differences in the catchability by both plankton nets. Differences between nets were significant only for smaller developmental stages and species, with higher catchabilities by the 66 µm net, while no differences were detected for most of the stages of the medium and large size species. A significant effect of the spatial distribution on the estimates of abundance was detected for the majority of the species and stages but the interaction between mesh size and spatial distribution was not significant. This means that differences between both nets were maintained across the latitudinal gradient. Our results strongly suggest the convenience of using the 66 µm plankton net to estimate the abundance of the three copepods' populations. Furthermore, we propose a correction factor to adjust past estimates of abundances from 150 µm mesh collections.

© 2009 Elsevier B.V. All rights reserved.

# 1. Introduction

The catch efficiency of plankton nets for quantitative estimates of (meso)zooplankton has been the issue of numerous studies for many years (*e.g.*, Vanucci, 1968; Regner, 1981; Evans and Sell, 1985; Nichols and Thompson, 1991; Munk et al., 2003; Stehle et al., 2007). The facts show, nevertheless, that there is no single gear and/or mesh size to properly sample all groups, including further all their developmental stages. Therefore, the matter remains still controversial.

Given the overall importance of size structure in marine pelagic food-webs (*e.g.*, Hansen et al., 1994; Calbet and Landry, 1999) and the scaling of vital rates with body mass (*e.g.*, Hansen et al., 1997; Ohman et al., 2002), the assessment of the size-specific abundance of organisms is perhaps one of the most critical aspects of any ecological study. Variations in mesh size have a significant effect on the selection by the sampler (Fraser, 1968) and thus the choice of the mesh size depends on the taxa to be sampled and it varies mainly in relation to the size of the organisms and their ability to avoid the sampler (Vanucci, 1968). It follows that individuals in the lower range of mesozooplankton have been largely ignored in many studies based on standard sampling with 200–330  $\mu$ m plankton nets (Evans and Sell, 1985; Vanucci, 1968; Paffenhöfer, 1998; Hwang et al., 2007; Pitois et al., 2009). Overall, the

200  $\mu$ m mesh nets capture < 10% of the metazooplankton community in terms of numbers, while the biomass is underestimated by one-third and the secondary production by two-thirds. In oligotrophic offshore regions, for example, the 63  $\mu$ m mesh nets have been shown to capture one order of magnitude more individuals than the 200  $\mu$ m nets (Hopcroft et al., 1998; Galliene and Robins, 2001).

Along with the increasing evidence that substantial parts of the mesozooplankton consist of micro-sized stages as well as species, there is been a call for investigations including this smaller fraction to fully understand the structure and dynamics of its populations and their relationships within ecosystems (Paffenhöfer, 1998; Hopcroft et al., 2001). As a result, small-sized species and early stages of copepods are known now as major contributors to the secondary production of marine systems (*e.g.*, Turner, 2004; Gallienne and Robins, 2001; Zervoudaki et al., 2007). In the light of relatively-recent research using fine plankton nets, the small cyclopoids of genus *Oithona*, for instance, have been proven often dominant in many ecosystems worldwide (Gallienne and Robins, 2001).

Taking into account mesozooplankters other than copepods, it has been shown that the abundance of larvaceans is also very much influenced by the use of different mesh sizes. While they are underestimated when 200  $\mu$ m mesh nets are used, they may became the second most-abundant component of the community in oligotrophic areas when smaller mesh nets are utilized (*e.g.*, Jaspers et al., 2009 and references therein).

It is of utmost importance therefore, to acknowledge the implications of different sampling methods to estimate zooplankton abundance

<sup>\*</sup> Corresponding author. Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), Paseo Victoria Ocampo N° 1, B7602HSA - Mar del Plata, Argentina.

E-mail address: antacli@inidep.edu.ar (J.C. Antacli).

<sup>1385-1101/\$ –</sup> see front matter  $\ensuremath{\mathbb{C}}$  2009 Elsevier B.V. All rights reserved. doi:10.1016/j.seares.2009.09.004

(density and biomass) in any ecosystem, as well as to understand their sources of variability.

In the southern Patagonian shelf, zooplankton has been sampled mainly with coarse 390 µm mesh size net, concealing the representation not only of the small species but also that of medium-sized copepods (*e.g.*, Sabatini et al., 2004). More recently, sampling with 150 µm mesh size nets has allowed the recognition of the absolute dominance of the medium-sized clausocalaniid *Drepanopus forcipatus* over both the large calanid *Calanus australis* and the small *Oithona helgolandica* (*sensu* Ramírez, 1966) (Sabatini, 2008a,b).

The copepod community in the region is made up of many other less-abundant species, most of them medium or small-sized (Sabatini, 2008a), which may remain under-represented, even after using a 150 µm mesh size net. These include species such as those of the genus *Oithona* but also the early developmental stages of all other copepods. Hence, a sampling design using paired nets of 66 and 150 µm mesh size was implemented, under the assumption that the estimates of abundance of all developmental stages, and some copepod species, would be differentially determined by mesh size. The aim of this study was then to compare the stage-specific catchability by these two plankton nets for quantitative purposes, focused on population studies of the locally most-abundant copepods. These latter issues will be specifically addressed in a subsequent paper.

Furthermore, the relative catch efficiency between both mesh sizes was estimated for each stage of the dominant species, and hence a correction factor was obtained as progress towards retrospective studies in the region.

#### 2. Methods

#### 2.1. Sampling

Zooplankton sampling was carried out with the RV "Dr. E. L. Holmberg" during late March 2004 at 32 stations located over the continental shelf off southern Patagonia in the SW Atlantic. Stations were arranged in four transects/groups approximately perpendicular to the coast at 47°S, 49°S, 51°S and *ca*. 53°S (Fig. 1). Sampling was performed by vertical tows with a small Bongo sampler, 20 cm mouth opening, fitted with 66 and 150 µm mesh size nets. The advantage of using this kind of sampler is that one single tow allows the simultaneous collection of two plankton samples, *i.e.* paired samples from different mesh-size nets. Tows were smoothly performed from a maximum depth of 130 m to surface. A 5-kg piece was attached to the Bongo frame to depress the sampler. The wire angle was measured relative to the vertical with an inclinometer, and the amount of wire payed out to reach sampling depth was corrected accordingly. Filtered volumes were measured with digital flowmeters (Hydro-Bios, with back-run stop for vertical operation). To account for the likely differential filtration efficiency of each net due to mesh size, two separate flowmeters were used. Each of them was suspended within each ring of the Bongo frame. Mean water volumes filtered by the 66 and 150  $\mu$ m nets were 4.75 m<sup>3</sup> and 5.13 m<sup>3</sup>, respectively. Samples were preserved in 4% buffered formaldehyde for laboratory analysis.



Fig. 1. Southern Patagonian continental shelf. Location of the study area and sampling stations. Transects/groups, (A) 47°S; (B) 49°S; (C) 51°S and (D) ca. 53°S.

# 2.2. Plankton analysis

All individuals in a subsample were identified to the lowest taxonomic level possible. Adults and copepodid stages of the mostabundant species, *i.e., C. australis, D. forcipatus* and *O. helgolandica* were all sexed and staged, while nauplii were not identified to species or stage but pooled. Taxonomic identifications were based on the current literature for the region (*e.g.,* Ramírez, 1970, 1971, 1981; Björnberg, 1981; Bradford-Grieve, 1999; Ramírez and Sabatini, 2000). Stage-specific identifications of the three dominant species were performed after Bradford et al. (1988), Hulsemann (1991) and Grandori (1912), respectively.

In our approach, stages are actually proxies for size, most of our analysis being intended to know how the size spectra of the three dominant species are affected by the different mesh sizes. As a reference, the morphometric features of the target species are then summarized in Table 1.

Counting of the 150 and 66  $\mu$ m mesh samples was carried out with a stereomicroscope *Leica M8* in separate subsamples for each species because of their dissimilar abundances. Increasingly larger subsamples were examined for each species until at least 200 individuals of the most-abundant stage were counted. Thus, paired abundances (individuals m<sup>-3</sup>) were obtained for the 150 and 66  $\mu$ m mesh nets from samples collected simultaneously by a single tow at each station.

### 2.3. Statistical analysis

Statistics were conducted only with *C. australis*, *D. forcipatus* and *O. helgolandica*, which were by far the most-abundant species in both net samples. *C. australis* and *D. forcipatus* were categorized as adult males, adult females and individual copepodid stages (C5, C4, C3, C2 and C1). Female (F) and male (M) C4 and C5 were additionally discriminated in the latter species. In *O. helgolandica*, females, males and C5 were analyzed separately, while C4 to C1 were grouped in one category. Nauplii of all species were introduced in the analysis as a single category, as well as the (unattached) egg sacs of *Oithona* spp. The

#### Table 1

Morphometric features of copepodid developmental stages of *Calanus australis*, *Drepanopus forcipatus* and *Oithona helgolandica*.

| Species/category      | TL (mm)   | PL (mm)     |
|-----------------------|-----------|-------------|
| Calanus australis     |           |             |
| F                     | 3.24      | 2.72        |
| M                     | 3.68      | 2.34        |
| C5                    | 3.52      | 2.16        |
| C4                    | 2.32      | 1.68        |
| C3                    | 1.79      | 1.18        |
| C2                    | 1.44      | 0.83        |
| C1                    | 0.94      | 0.78        |
|                       |           |             |
| Drepanopus forcipatus |           |             |
| F                     | 1.45      | 0.92        |
| M                     | 0.90      | 0.40        |
| C5-F                  | 1.57      | 1.10        |
| C5-M                  | 1.34      | 0.91        |
| C4-F                  | 1.18      | 0.76        |
| C4-M                  | 1.02      | 0.71        |
| C3                    | 0.79      | 0.59        |
| C2                    | 0.58      | 0.39        |
| C1                    | 0.35      | 0.26        |
| Oithong holgolandica  |           |             |
| E                     | 0.00      | 0.50        |
| r<br>M                | 0.00      | 0.55        |
|                       | 0.70      | 0.52        |
|                       | 0.79      | 0.49        |
| C4-1                  | 0.54-0.42 | 0.35 - 0.25 |

Total length (TL) and prosome length (PL) were measured during this study as reference size.

normality and the homogeneity of variances of the abundance data (individuals m<sup>-3</sup>) were examined graphically through categorized normal probability plots (*Statistica v.8.0*). Amongst the commonly-used transformations, the logarithmic was proven the most successful in homogenizing the variances and adjusting values to normality. Hence, abundances values were transformed to  $x'_j = \ln(x_j + 1)$ , being, x: abundance and j: species/categories.

For each species/category *j*, separate bifactorial (*Net* and *Transect*), unbalanced with repeated measures in one factor (*Net*) ANOVA tests were applied to the abundance data in order to evaluate the effect of the 66 and 150 µm mesh sizes on the stage-specific estimates of the three copepods. The catchability by the two nets, the distribution patterns of the dominant species and the possible interaction between both factors were considered. Starting data entry for the ANOVA of each developmental stage *j* were the ln-transformed estimates of abundance from catches by the 150 µm mesh net ( $\ln x_{150} + 1$ ) and the 66 µm mesh net ( $\ln x_{66} + 1$ ), at each sampling station *k*. As mentioned above, these values were estimated from samples collected simultaneously at each station and, as such, they represent repeated measures of the catchability by the two nets over the study area. ANOVAs were performed by routines in *Fortran* language (Hernández, Gabinete de Biomatemática, INIDEP).

Because the distribution pattern of copepods in the southern Patagonian shelf appears to vary with latitude, we considered this effect in the ANOVAs as a *Transect* factor by grouping the data by transects (Fig. 1). When significant differences amongst transects were found at a given category, *Post Hoc* comparisons of the mean abundances estimated for each transect were made with a Scheffé Test (Scheffé, 1959).

#### 3. Results

#### 3.1. Comparison of catches results

The estimates of abundance from the catches of the 66 and 150 µm nets were significantly different only for the smaller stages present in the paired samples, i.e., C1 of D. forcipatus, all copepodid stages and adult females of *O. helgolandica*, as well as their unattached egg sacs and all pooled nauplii. Unexpectedly, differences between nets were not significant for adult males of O. helgolandica, in spite of their relatively small size. Statistical differences were not found for any of the larger stages (*p*-values, Table 2). Hence, while the estimates of abundance derived from the two nets were fairly similar for all stages of *C. australis* and for older than C1 copepodids and adults of D. forcipatus, those of the smaller categories as estimated from the 66 µm samples were on average 5 times higher than those estimated from the 150 µm net (Table 2). These results applied mainly to all stages of O. helgolandica, which were severely under-represented in the 150 µm collection, and also to all species nauplii and unattached egg sacs.

Except for C5 of C. australis and C1 to C3 of D. forcipatus, there was a statistically significant (p < 0.05) effect of the spatial distribution (Transect factor) on the estimates of abundance from catches by the two nets (p-values, Table 2). However, no clear patterns in the distribution of the three species and stages become apparent through comparisons across transects (Scheffé Test, Table 3). The likely reason for this might be that the populations were developing not synchronously but differentially with varying latitude (Figs. 2-4). Yet, it is perhaps more important within the reach of our analysis, that the interaction between the net mesh size factor (Net) and the spatial distribution factor (Transect) on the estimates of abundance was not significant for any stage/species (p-values, Table 2). This result is particularly relevant for the smaller stages analyzed (i.e., C1 D. forcipatus, all stages of O. helgolandica except adult males, nauplii altogether and egg sacs), for which statistically significant differences in the catchability by the two nets were detected through the

# Table 2

Comparison of the catches by 150  $\mu m$  and 66  $\mu m$  mesh nets.

| Species/<br>category           | Mean abundance<br>(ind m <sup>-3</sup> ) |              | p-level              |                         |             |  |
|--------------------------------|--|--------------|----------------------|-------------------------|-------------|--|
|                                | 150 μm<br>net                            | 66 μm<br>net | Nets<br>efficiencies | Spatial<br>distribution | Interaction |  |
| Calanus australis              |  |              |                      |                         |             |  |
| F                              | 10                                       | 13           | 0.5057               | 0.029                   | 0.910       |  |
| М                              | 4  | 5            | 0.4134               | 0.001                   | 0.650       |  |
| C5                             | 47                                       | 77           | 0.2265               | 0.053                   | 0.790       |  |
| C4                             | 22                                       | 32           | 0.5774               | 0.031                   | 0.851       |  |
| C3                             | 21                                       | 34           | 0.3901               | 0.003                   | 0.237       |  |
| C2                             | 6  | 11           | 0.4895               | 0.005                   | 0.190       |  |
| C1                             | 3  | 6            | 0.4277               | 0.001                   | 0.805       |  |
| Drepanopus forcip              | atus                                     |              |                      |                         |             |  |
| F                              | 230                                      | 441          | 0.4250               | 0.005                   | 0.705       |  |
| М                              | 39                                       | 70           | 0.0750               | 0.002                   | 0.427       |  |
| C5-F                           | 693                                      | 965          | 0.3153               | 0.003                   | 0.255       |  |
| C5-M                           | 616                                      | 879          | 0.3173               | 0.007                   | 0.423       |  |
| C4-F                           | 2382                                     | 2945         | 0.4124               | 0.005                   | 0.525       |  |
| C4-M                           | 1547                                     | 1848         | 0.1821               | 0.004                   | 0.288       |  |
| C3                             | 1077                                     | 1677         | 0.1573               | 0.072                   | 0.277       |  |
| C2                             | 353                                      | 656          | 0.1854               | 0.680                   | 0.946       |  |
| C1                             | 118                                      | 311          | 0.0002               | 0.138                   | 0.557       |  |
| Oithona helgoland              | ica                                      |              |                      |                         |             |  |
| F                              | 503                                      | 753          | 0.0160               | 0.004                   | 0.695       |  |
| М                              | 54                                       | 103          | 0.2348               | 0.027                   | 0.904       |  |
| C5                             | 104                                      | 274          | 0.0006               | 0.029                   | 0.106       |  |
| C4-1                           | 99                                       | 736          | 0.0000               | 0.002                   | 0.437       |  |
| Naupliar stages<br>all species | 393                                      | 4873         | 0.0000               | 0.035                   | 0.886       |  |
| Egg sacs<br>Oithona spp.       | 175                                      | 307          | 0.0000               | 0.198                   | 0.145       |  |

Results of the ANOVAs. Statistically significant *p*-level values are in bold. Mean abundance in the first two columns refer to averages across all sampling stations.

ANOVAs, as it means that these differences were maintained across the latitudinal gradient.

The estimates of abundance from either the 66 or 150  $\mu$ m catches resulted in distinct community and population structures. At the community level – though considering only the major components, the relative composition changed because of a higher contribution of nauplii (24% vs. 3%) against *D. forcipatus* (61% vs. 87%) in the 66  $\mu$ m catches. In any case, this medium-sized copepod emerged as the absolute dominant component of the mesozooplankton community, while the relative contributions by *C. australis* and *O. helgolandica* remained similar (Fig. 5). Conversely, the population structures generated by the two nets were almost identical for *C. australis* 

| Table 3            |                   |        |           |               |
|--------------------|-------------------|--------|-----------|---------------|
| Latitudinal effect | (Transect factor) | on the | estimates | of abundance. |

| Transect     | 47°S   | 49°S   | 51°S   |
|--------------|--|--|--|
| 49°S<br>51°S | No differences<br>Ca M ( $F$ =6.44)<br>Ca C3 ( $F$ =3.422)<br>Ca C2 ( $F$ =3.623)<br>Ca C1 ( $F$ =5.489)<br>Df C5-M ( $F$ =3.707)<br>Df C4-F ( $F$ =3.915) | - Ca H $(F=3.013)$<br>Ca M $(F=5.148)$<br>Ca C3 $(F=3.133)$<br>Oh C4-1 $(F=5.287)$<br>Nauplii $(F=3.392)$      | -  |
| ca. 53°S     | Df C4-M (F=4.203)<br>Ca C1 (F=4.491)<br>Oh F (F=3.797)   | Df H ( $F$ =3.554)<br>Df M ( $F$ =4.414)<br>Oh H ( $F$ =3.858)<br>Oh C5 ( $F$ =3.137)<br>Oh C4-1 ( $F$ =3.423) | Ca M ( $F$ =3.482)<br>Ca C5 ( $F$ =3.116)<br>Df H ( $F$ =3.845)<br>Df M ( $F$ =4.722)<br>Df C5-M ( $F$ =4.477)<br>Df C4-H ( $F$ =4.523)<br>Df C4-M ( $F$ =5.080) |

*Post Hoc* comparisons of the mean abundances estimated for each Transect/group (Scheffé Test,  $F_{critical} = 2.947$ ). See Fig. 1 for locations of transects.



Fig. 2. Calanus australis. Abundance (individuals  $m^{-3}$ ) per stage estimated from catches by 150 µm (A) and 66 µm (B) mesh nets.

(Fig. 6A,B) and alike for *D. forcipatus* (Fig. 6C,D) but contrasted strikingly for *O. helgolandica* (Fig. 6E,F).

In summary, it is apparent that the coarser  $150 \,\mu\text{m}$  net undersampled all developmental stages and unattached egg sacs of *O. helgolandica*, the first copepodid stage of *D. forcipatus* and all nauplii present (pooled together). On the other hand, the catchabilities of both nets were not significantly different across all the stages of *C. australis* and from C2 to C6 of *D. forcipatus*. Therefore, only the catch results from the fine 66  $\mu$ m net should be used to estimate the abundance of the former species or categories, while in the latter either mesh size could be used.



**Fig. 3.** Drepanopus forcipatus. Abundance (individuals  $m^{-3}$ ) per stage estimated from catches by 150 µm (A) and 66 µm (B) mesh nets.



**Fig. 4.** *Oithona helgolandica.* Abundance (individuals  $m^{-3}$ ) per stage estimated from catches by 150 µm (A) and 66 µm (B) mesh nets.

# 3.2. Relative catch efficiency between nets

A measure of the relative catch efficiency between both mesh sizes can be defined as the ratio between the efficiency of the coarse net (150  $\mu$ m) relative to the efficiency of the fine mesh net (66  $\mu$ m),

$$e_{150/66} = \frac{e_{150}}{e_{66}}$$

Hence, the estimator of maximum likelihood for such a measure was defined after Irusta et al. (1996) as,

$$\hat{e}_{150/66} = \exp\left(\frac{1}{n}\sum_{k=1}^{n} \ln(x_{150k} / x_{66k})\right),$$

where  $\hat{e}_{150/66}$  is the mean relative efficiency for each stage/species averaged over all *n* sampling stations (excluding those with null values of abundance), and  $x_{150k}$  and  $x_{66k}$  are the abundances (individuals m<sup>-3</sup>) estimated from the catch results of the coarse and fine nets, respectively, at a given *k* station. The mean relative efficiency ( $\hat{e}_{150/66}$ ) was then



Fig. 5. Relative total abundance of species/categories from catches by the 150  $\mu m$  (A) and 66  $\mu m$  (B) mesh nets.



**Fig. 6.** Population structures of *Calanus autralis* (A,B), *Drepanopus forcipatus* (C,D) and *Oithona helgolandica* (E,F) yielded by either 150  $\mu$ m or 66  $\mu$ m mesh nets.

calculated across all sampling stations for all stages/species and the differences examined through the comparison of their confidence intervals (Payton et al., 2003). Values overlapping at least partially would indicate that there are no significant differences amongst their respective mean relative efficiencies.

Therefore, for those species and stages where statistically significant differences in the mean relative efficiency  $\hat{e}_{150/66}$  were found, their confidence intervals were estimated as

$$L_{lower} = \hat{e}_{150/66} \exp(-t_{\alpha/2 (n-1)} \mathbf{s}_{d} / \sqrt{n});$$
  
$$L_{higher} = \hat{e}_{150/66} \exp(t_{\alpha/2 (n-1)} \mathbf{s}_{d} / \sqrt{n}),$$

being  $t_{\alpha/2(n-1)}$  the  $1 - \alpha/2$  percentile of the Student's *t* distribution with n - 1 degrees of freedom and  $s_d$  the standard deviation of the variable *d*, *i.e.*,

$$d_k = \ln(x_{150k}) - \ln(x_{66k}), 1 \le k \le n.$$

As this is a log-normal variable, the standard deviation of  $\hat{e}_{150/66}$  after Kendall and Stuart (1969) is given by,

$$s_{\hat{e}_{150/66}} = \sqrt{\exp(2\overline{d} + s_d^2 / n)(\exp(s_d^2 / n) - 1)},$$

being  $\overline{d}$  y  $s_d^2$  the mean and variance of the variable  $d_k$ ,  $1 \le k \le n$ , respectively.

Overall, the 66  $\mu$ m mesh net captured more individuals of any developmental stage (Table 2) but smaller individuals in particular were significantly missed by the coarse 150  $\mu$ m mesh net, as additionally evidenced by their mean relative efficiencies (MRE) in Table 4. Roughly, the retention of the small-sized categories by the 150  $\mu$ m mesh net was only *ca.* 30% on average of the catch by the fine 66  $\mu$ m mesh net. Total or partial overlapping of the confidence intervals of the mean relative efficiencies of all stages (except adult males) of *O. helgolandica* and C1 of *D. forcipatus* indicated that these are very similar to one another but significantly different from those of nauplii and egg sacs (Fig. 7).

# 3.3. Correction factor for retrospective studies

Because sampling with 150  $\mu$ m mesh size has been conducted rather frequently in the region, we thought it would be worth defining a correction factor to remove the bias introduced by the use of that mesh. This will be necessary if retrospective studies were eventually intended. As inspired by Stehle et al. (2007), on account of the above we propose the following estimator,

$$E_k = \frac{x_{150k}}{\hat{e}_{150/66}},$$

where  $E_k$  is the factor estimator,  $\hat{e}_{150/66}$  is the mean relative efficiency calculated for a given stage/category, averaged over all sampling stations, k is stage/category and  $x_{150k}$  is its (pre-existing) abundance estimated from the 150 µm mesh net for stage/category k. The standard deviation of  $E_k$  can be also estimated (*Delta* method; Seber, 1982) as,

$$S(E_k) = \left(\frac{E_k}{\hat{e}_{150/66}}\right) s_{\hat{e}_{150/66}}$$

The application of such correction should be restricted to estimates of abundance generated by similar sampling design and methods.

# 4. Discussion

This is the first study of the copepod community during summer in the southern Patagonian shelf in which paired nets and smaller mesh sizes ( $66 \mu m$  as opposed to  $150 \mu m$ ) have been used. The benefits of such sampling design were two-fold. On one hand, it allowed the evaluation of both mesh sizes catchabilities in studying the populations of the dominant species, and on the other, our current knowledge of the community structure was expanded.

The estimates of abundance obtained from the catch results of the  $66 \,\mu\text{m}$  and  $150 \,\mu\text{m}$  mesh nets were significantly different in smaller species and early ontogeny stages. In such cases, the fine net  $66 \,\mu\text{m}$  pore

#### Table 4

Mean relative efficiency (MRE) between mesh nets (150 relative to  $66\,\mu\text{m}$ ) and confidence intervals for stages/categories with statistically significant differences in nets efficiencies.

| Species/category            | MRE   | Lower limit (95%) | Higher limit (95%) |
|-----------------------------|-------|-------------------|--------------------|
| Drepanopus forcipatus       |       |                   |                    |
| C1                          | 0.404 | 0.185             | 0.885              |
| Oithona helgolandica        |       |                   |                    |
| F                           | 0.618 | 0.413             | 0.925              |
| C5                          | 0.452 | 0.263             | 0.772              |
| C4-1                        | 0.208 | 0.118             | 0.367              |
| Naupliar stages all species | 0.030 | 0.01              | 0.07               |
| Egg sacs Oithona spp.       | 0.053 | 0.008             | 0.115              |
| Species/category average    | 0.294 |                   |                    |

Averages were estimated over the entire study area (excluding stations with null values of abundance).



**Fig. 7.** Confidence intervals for species/categories whit statistically significant differences in net efficiencies (ANOVAs). Dots refer to mean relative efficiency (probability of 84%) shown in Table 4.

size, was proven more efficient in catching organisms. These findings confirm our initial assumption that minor-size copepod species and smaller developmental stages were underestimated with a 150 µm mesh net. Hence, while both the population structure and total abundance of *O. helgolandica* were severely biased by the coarse net, *D. forcipatus* and *C. australis* populations, species of medium- and large size respectively, appeared to be sampled similarly by the two nets. It was somehow surprising that only the first copepodid stage of *D. forcipatus* were undersampled by the coarse net. Strictly speaking, however, the 150 µm mesh net overall under-represented all species because of the significantly smaller capture of eggs and naupliar stages relative to the fine net.

Böttger-Schnack et al. (2008) compared the copepod abundances sampled with 55  $\mu$ m and 150  $\mu$ m mesh nets in the Red Sea during spring and, in coincidence with our results, found that the abundances of nauplii obtained with the fine mesh net were about two orders of magnitude higher and the numbers of juveniles and adults differed by a factor of 3–7.

An unexpected result in our study concerned the adult males of *O. helgolandica* which, unlike adult females or any other copepodid stage of this species, were similarly captured by either net. Since adult males are smaller than females, this may be a spurious outcome of ANOVA, likely related to their much lower abundance and rather sporadic distribution in nature. In fact, males comprised only 5% of total *O. helgolandica* population (as estimated from the 66 µm catches) and were absent in 10 out of the 64 samples analyzed. However, it should be borne in mind also that the body shape of males, particularly the geniculation of the antenna, might help the retention by a coarser net.

Copepods other than the three dominant species above were not statistically treated either because they were only occasionally present, their abundances were too low or their spatial distributions were very different for comparison. These conditions would produce many null values, thus invalidating the ANOVA. Yet, it is worth mentioning that the total abundance of the small harpacticoid Microsetella norvegica as estimated from the catch results of the 66 µm mesh net was 60 times higher than the estimate from the 150 µm mesh net catches. This is not a trivial piece of information but it highlights the need for a broader view of the copepod community in the southern Patagonian shelf, considering the smaller species and developmental stages. The importance of small-sized copepod species and early developmental stages as key components of the planktonic food web has been demonstrated in a diversity of marine ecosystems worldwide (e.g., Dubischar et al., 2002; Thor et al., 2005; Zervoudaki et al., 2007; Böttger-Schnack et al., 2008). Our results from the 66 µm mesh net catches add support to this view and strongly encourage focusing future studies of the copepod community in the region on the smaller size spectrum. We are currently planning to revisit past scenarios in order to adjust some

former species-specific underestimates by applying the correction factor we are proposing for the dominant species.

# Acknowledgements

Special thanks are given to Fernando Ramírez for his valuable help with taxonomic identifications. We would like to thank people on board the RV "Dr. E. L. Holmberg" during the EH-03/04 cruise, Guillermo Scampini in particular for his help with zooplankton sampling. G. S. passed away suddenly on February 9, 2005. Comments from two anonymous reviewers improved the manuscript. This study was partially funded by CONICET PIP No. 5845 to M. S. This is contribution No. 1560 of the Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), Mar del Plata, Argentina.

# References

- Björnberg, T.K.S., 1981. Copepoda. In: Boltovskoy, D. (Ed.), Atlas del Zooplancton del Atlántico Sudoccidental y Métodos de Trabajo con el Zooplancton Marino. Publicaciones Especiales INIDEP, Mar del Plata, pp. 587–679.
- Böttger-Schnack, R., Schnack, D., Hagen, W., 2008. Microcopepod community structure in the Gulf of Aqaba and northern Red Sea, with special reference to Oncaeidae. J. Plankton Res. 30, 529–550.
- Bradford, J.M., Ohman, M.D., Jillet, J.B., 1988. Larval morphology and development of *Neocalanus tonsus, Calanoides macrocarinatus* and *Calanus australis* (Copepoda: Calanoida) in the laboratory. N. Z. J. Mar. Freshw. Res. 22, 301–320.
- Bradford-Grieve, J.M., 1999. In: Boltovskoy, D. (Ed.), Copepoda. South Atlantic Zooplankton, vol. 2. Backhuys Publishers, Leiden, pp. 869–1098. The Netherlands.
- Calbet, A., Landry, M., 1999. Mesozooplankton influences on the microbial food web: direct and indirect trophic interactions in the oligotrophic open ocean. Limnol. Oceanogr. 44, 1370–1380.
- Dubischar, C.D., Lopes, R.M., Bathmann, U.V., 2002. High summer abundances of small pelagic copepods at the Antarctic Polar Front—implications for ecosystem dynamics. Deep-Sea Res. (2 Top. Stud. Oceanogr.) 49, 3871–3887.
- Evans, M.S., Sell, W.S., 1985. Mesh size and collection characteristics of 50-cm diameter conical plankton nets. Hydrobiologia 122, 97–104.
- Fraser, J.H., 1968. Standardization of zooplankton sampling methods at sea. zooplankton sampling. Monogr. Oceanogr. Methodol., vol. 2. Unesco, Paris, pp. 145–169. Gallienne, C.P., Robins, D.B., 2001. Is *Oithona* the most important copepod in the world's
- oceans? J. Plankton Res. 23, 1421–1432. Grandori, R., 1912. Studi sullo sviluppo larvale dei copepodi pelagici. Redia 8, 440–447.
- Hansen, B., Bjørnsen, P.K., Hansen, P.J., 1994. The size ratio between planktonic predators and their prey. Limnol. Oceanogr. 39, 395–403.
- Hansen, P.J., Bjørnsen, P.K., Hansen, B., 1997. Zooplankton grazing and growth: scaling within the 2–2,000 μm body size range. Limnol. Oceanogr. 42, 687–704.
- Hopcroft, R.R., Roff, J.C., Lombard, D., 1998. Production of tropical copepods in Kingston Harbour, Jamaica: the importance of small species. Mar. Biol. 130, 593–604.
- Hopcroft, R.R., Roff, J.C., Chavez, F.P., 2001. Size paradigms in copepod communities: a re-examination. Hydrobiologia 453 (454), 133–141.
- Hulsemann, K., 1991. The copepodid stages of *Drepanopus forcipatus* Giesbrecht, with notes on the genus and a comparison with other members of the family Clausocalanidae (Copepoda, Calanoida). Helgol. Meeresunters. 45, 199–224.
- Hwang, J., Kumar, R., Dahms, H., Tseng, L., Chen, Q., 2007. Mesh size affects abundance estimates of *Oithona* spp. (Copepoda, Cyclopoida). Crustaceana 80, 827–837.
- Irusta, G., Pérez, M., Bambill, G., Hernández, D.R., 1996. Análisis de la eficiencia y del poder de pesca relativos entre los BIPs. "Dr. E. L. Holmberg" y "Cap. Oca Balda" respecto de la merluza común (*Merluccius hubbsi*). INIDEP Inf. Téc. (Mar del Plata) 7, 1–19.

- Jaspers, C., Nielsen, T.G., Carstensen, J., Hopcroft, R.R., Møller, E.F., 2009. Metazooplankton distribution across the Southern Indian Ocean with emphasis on the role of Larvaceans. J. Plankton Res. 31, 525–540.
- Kendall, M.G., Stuart, A., 1969. The Advanced Theory of Statistics. Charles Griffin and Company Ltd., London.
- Munk, P., Hansen, B.W., Nielsen, T.G., Thomsen, H.A., 2003. Changes in plankton and fish larvae communities across hydrographic fronts off West Greenland. J. Plankton Res. 25, 815–830.
- Nichols, J.H., Thompson, A.B., 1991. Mesh selection of copepodite and nauplius stages of four calanoid copepod species. J. Plankton Res. 13, 661–671.
- Ohman, M.D., Runge, J.A., Durbin, E.G., Field, D.B., Niehöff, B., 2002. On birth and death in the sea. Hydrobiologia 480, 55–68.
- Paffenhöfer, G.A., 1998. Heterotrophic protozoa and small metazoa: feeding rates and prey-consumer interactions. J. Plankton Res. 20, 121–134.
- Payton, M.E., Greenstone, M.H., Schenken, N., 2003. Overlapping confidence interval or standard error internal: what do they mean in terms of statistical significance? [Insect Sci. 3134, 1–6.
- Pitois, S.G., Shaw, M., Fox, C.J., Frid, C.L.J., 2009. A new fine-mesh zooplankton time series from the Dove sampling station (North Sea). J. Plankton Res. 31, 337–343.
- Ramírez, F.C., 1966. Copépodos calanoideos marinos del área de Mar del Plata, con la descripción de Pontella marplatensis, n. sp. Boletín del Instituto de Biología Marina (Mar del Plata) 11, 1–24.
- Ramírez, F.C., 1970. Copépodos planctónicos del sector patagónico. Resultados de la Campaña 'Pesquería XI'. Physis 79, 473–476.
- Ramírez, F.C., 1971. Copépodos planctónicos de los sectores bonaerense y norpatagónico. Resultados de la Campaña 'Pesquería III'. Revista del Museo de La Plata, n.s. Zoología 11. 73–94.
- Ramírez, F.C., 1981. Zooplancton y producción secundaria. Parte I. Distribución y variación estacional de los copépodos. In: Angelescu, V. (Ed.), Campañas de investigación pesquera realizadas en el Mar Argentino por los B/I 'Shinkai Maru' y 'Walther Herwig' y B/P 'Marburg', años 1978 y 1979. Resultados de la Parte Argentina: Contrib., vol. 383. Inst. Nac. Invest. Desarr. Pesq., Mar del Plata, pp. 202–212.
- Ramírez, F.C., Sabatini, M.E., 2000. The occurrence of Calanidae species in waters off Argentina. Hydrobiologia 439, 21–42.
- Regner, S., 1981. The catching efficiency of four different plankton nets relative to ichthyoplankton objects. Institut Za Oceanografiju I Ribarstvo – Split SFR. Jugoslavija 44, 1–6.
- Sabatini, M.E., Reta, R., Matano, R., 2004. Circulation and zooplankton biomass distribution over the southern Patagonian shelf during late summer. Cont. Shelf Res. 24, 1359–1373.
- Sabatini, M.E., 2008a. El ecosistema de la plataforma patagónica austral, Marzo–Abril 2000. Composición, abundancia y distribución del zooplancton. Rev. Invest. Desarr. Pesq. 19, 5–20.
- Sabatini, M.E., 2008b. Life history trends of copepods *Drepanopus forcipatus* (Clausocalanidae) and *Calanus australis* (Calanidae) in the southern Patagonian shelf (SW Atlantic). J. Plankton Res. 30, 981–996.
- Scheffé, H., 1959. The Analysis of Variance. John Wiley and Sons, Inc. Proprietor, Canada. Seber, G.A.F., 1982. The Estimation of Animal Abundance, second ed. Charles Griffin and Company Ltd., London.
- Stehle, M., Dos Santos, A., Queiroga, H., 2007. Comparison of zooplankton sampling performance of Longhurst–Hardy Plankton Recorder and Bongo nets. J. Plankton Res. 29, 169–177.
- Thor, P., Nielsen, T.G., Tiselius, P., Juul-Pedersen, T., Michel, C., Møller, E.F., Dahl, K., Selander, E., Gooding, S., 2005. Post-spring bloom community structure of pelagic copepods in the Disko Bay, Western Greenland. J. Plankton Res. 27, 341–356.
- Turner, J., 2004. The importance of small planktonic copepods and their roles in pelagic marine food webs. Zool. Stud. 43, 255–266.
- Vanucci, M., 1968. Loss of organisms through the meshes. In: Tranter, D.J. (Ed.), Zooplankton sampling. Monogr. Oceanogr. Methodol, vol. 2. Unesco, Paris, pp. 77–86.
- Zervoudaki, S., Christou, E.D., Nielsen, T.G., Siokou-Frangou, I., Assimakopoulou, G., Giannakourou, A., Maar, A., Pagou, K., Krasakopoulou, E., Christaki, U., Moraitou-Apostolopoulou, M., 2007. The importance of small-sized copepods in a frontal area of the Aegean Sea. J. Plankton Res. 29, 317–338.