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Instruments and Methods

How well does the Continuous Plankton Recorder (CPR) sample zooplankton? A comparison with the Longhurst Hardy Plankton Recorder (LHPR) in the northeast Atlantic

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Abstract

The Continuous Plankton Recorder (CPR) survey has collected data on basin-scale zooplankton abundance in the North Atlantic since the 1930s. These data have been used in many studies to elucidate seasonal patterns and long-term change in plankton populations, as well as more recently to validate ecosystem models. There has, however, been relatively little comparison of the data from the CPR with that from other samplers. In this study we compare zooplankton abundance estimated from the CPR in the northeast Atlantic with near-surface samples collected by a Longhurst-Hardy Plankton Recorder (LHPR) at Ocean Weather Station India (59°N, 19°W) between 1971 and 1975. Comparisons were made for six common copepods in the region: *Acartia clausi*, *Calanus finmarchicus*, *Euchaeta norvegica*, *Metridia lucens*, *Oithona* sp., and *Pleuromamma robusta*. Seasonal cycles based on CPR data were similar to those recorded by the LHPR. Differences in absolute abundances were apparent, however, with the CPR underestimating abundances by a factor of between 5 and 40, with the exception of *A. clausi*. Active avoidance by zooplankton is thought to be responsible. This avoidance is species specific, so that care must be taken describing communities, as the CPR emphasises those species that are preferentially caught, a problem common to many plankton samplers.

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1. Introduction

Since the 1930s, zooplankton distribution and abundance in the northeast Atlantic has been

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estimated by the Continuous Plankton Recorder (CPR) survey. This survey was instigated by Alistair Hardy following his development of the CPR: an instrument that can be towed at high speed from ships-of-opportunity during their normal operations. The fundamental design of the CPR and methods of analysis for zooplankton sampling have remained relatively unchanged since 1948 (Colebrook and Robinson, 1986). This consistency has provided an extensive data set widely used by the scientific community (Colebrook, 1978; Fromentin and Planque, 1996; Greenstreet et al., 1997; Reid et al., 2003), enabling long-term changes in plankton populations to be studied (Aebischer et al., 1990; Planque and Taylor, 1998; Reid et al., 1998; Beaugrand et al., 2002).

As CPRs routes are sampled monthly, the resulting data have often been used to examine seasonal patterns in zooplankton abundance (Colebrook, 1984; Planque and Fromentin, 1996; Beare and Mackenzie, 1999). More recently, CPR data have also been used to provide estimates of zooplankton biomass for use in statistical and numerical models (Broekhuizen and McKenzie, 1995; Bryant et al., 1997; Heath et al., 1997; Smith and Tett, 2000; Allen et al., 2001). As modellers increasingly use CPR data, and given that the time series has now been in operation for many decades, information on its ability to collect samples representative of the entire plankton community and performance with respect to other samplers is desirable.

One criticism of the CPR is that despite being internally consistent, abundance estimates from this device have only rarely been compared with other more widely used gears (but see Clark et al., 2001; John et al., 2001; Batten et al., 2003). These few studies have generally shown strong agreement between seasonal cycles and community changes measured with the CPR and WP2 nets, although there is generally a weaker relationship for inter-annual abundance. The major difference in abundance estimates between the devices was that abundance estimates using the WP2 net were between 1 and 40 times more than that of the CPR (Clark et al., 2001; John et al., 2001). Owing to differences in mesh size (CPR: 270 μm ; WP2:

200 μm) and the sampling depth (CPR: near-surface; WP2: vertically-integrated) in these studies, it was not possible to resolve whether differences in abundance were related to mesh size (for the smaller species), the vertical distribution of zooplankton, or zooplankton avoidance.

One other more recent study has compared CPR sampling with a vertical net haul over the top 20 m (Hunt and Hosie, 2003). This work was conducted in the Southern Ocean and used different counting procedures than that employed at the CPR survey in the North Atlantic. They found that the CPR had higher abundances than the net sampler for many of the smaller copepod taxa but lower abundances for larger copepods, and suggested this difference may be due to active avoidance.

In this study we compare the abundance of zooplankton collected with the CPR with near-surface samples of the Longhurst Hardy Plankton Recorder (LHPR) collected with almost identical mesh sizes. We used the LHPR because it takes a quantitative near-surface sample, whereas most other zooplankton sampling techniques obtain samples integrated over the upper water column. If differences in abundance are still noted, then they are more likely to be due to differing selectivity of the devices. We have chosen for comparison with the CPR a sampling site in the deep ocean, Ocean Weather Station India (OWSI) in the northeast Atlantic (Williams, 1988), rather than a site over the shelf as in previous studies (Clark et al., 2001; John et al., 2001) in an attempt to minimise local hydrographic effects on abundance that are more likely in shallow coastal regions. An area without strong local effects is best for comparison, as the semi-quantitative nature of CPR sampling requires large spatial areas to be investigated.

2. Materials and methods

2.1. LHPR samples from Ocean Weather Station India (OWSI)

Data for zooplankton abundance were collected from OWSI situated in the northeast Atlantic about 420 km south of Iceland (59°N, 19°W).

Sampling was carried out with a Longhurst-Hardy Plankton Recorder (LHPR) fitted with a 280 μm mesh and towed obliquely at 1.5–2.5 knots (0.77–1.03 m s^{-1}). The original design of the LHPR was based on the CPR (Wiebe and Benfield, 2003), and as such it may be expected to provide a better comparison with the CPR than other nets. Samples were collected approximately weekly between March and October 1971–1975 (for a more detailed description of sampling see Williams (1988)). Although the LHPR collects high-resolution data on vertical distributions of plankton, here we use only near-surface abundance (per m^3) estimates. As the near-surface sample from an LHPR is not taken over standard depth ranges on different tows, we used data interpolated over the top 10 m for comparison. All samples included in this analysis were taken during daylight.

2.2. CPR samples

CPRs are towed at a depth of ~ 7 m (Hays and Warner, 1993). Water enters through an inlet aperture of 1.61 cm^2 then passes through a 270 μm silk filtering mesh (see Warner and Hays (1994) for a full description). Samples corresponding to 10 nautical miles (18.5 km) of tow are then counted in a standard way (Colebrook and Robinson, 1986; Warner and Hays, 1994) and converted to abundances per m^3 from the amount of water filtered per sample. Although the volume of water filtered has not been measured historically for CPR samples, it was estimated using a predictive relationship between filtered volume and plankton abundance, which accounts for the effect of clogging on filtered volume (John et al., 2002).

CPRs have been towed at monthly intervals in the northeast Atlantic on several routes resulting in the collection of 5086 samples in the area 49–69°N and 9–29°W during 1971–1975. Such a large area was chosen so that there were sufficient samples to generate robust seasonal cycles. For the dominant copepod species, a preliminary analysis of the seasonal cycles and abundances in different sub-areas within the region revealed generally similar patterns throughout.

3. Results

The most abundant copepods in both data sets were *Acartia clausi*, *Calanus finmarchicus*, *Euchaeta norvegica*, *Metridia lucens*, *Oithona* sp., and *Pleuromamma robusta*, so comparisons were restricted to these common taxa. Although the CPR survey does not routinely speciate the genus *Acartia*, *A. clausi* probably constitute 95% of this genus in the region.

3.1. Seasonal patterns of abundance

To compare changes in the abundance of these taxa, time series of monthly means from the CPR and LHPR are shown in Fig. 1. There is generally good agreement in the shape of the seasonal cycles from the two devices through the years, except for short periods: e.g. *C. finmarchicus* midway through 1972 (Fig. 1a).

A visual assessment of the seasonal cycles each year showed they were generally consistent, suggesting they can be usefully averaged over the 5-year study period. Fig. 2 shows the average seasonal cycle over the 5 years for the two time series. Similar seasonal cycles were estimated from the LHPR and CPR for all species. There was a broad peak in *C. finmarchicus* abundance during most of spring and summer collected with both the LHPR and CPR (Fig. 2a). There was also strong agreement in the seasonal cycles for *A. clausi*, with a single peak in Aug–Sep (Fig. 2b). There was generally a late spring and autumn peak of abundance for *M. lucens*, although the exact timing was not synchronous in both time series (Fig. 2d). *E. norvegica* (Fig. 2e) had similar seasonal cycles measured by the CPR and LHPR, although the peak identified by the CPR was slightly later than that observed by the LHPR. The abundance estimated by the LHPR in Jan was relatively higher than that from the CPR. *P. robusta* (Fig. 2f) was generally low over the first half of the year, with higher levels in Aug–Dec peaking in Sep. The CPR found this species in relatively high numbers in Dec but there was no sampling at OWSI in this month for comparison.

Correlation coefficients show significant relationships between monthly mean abundances for

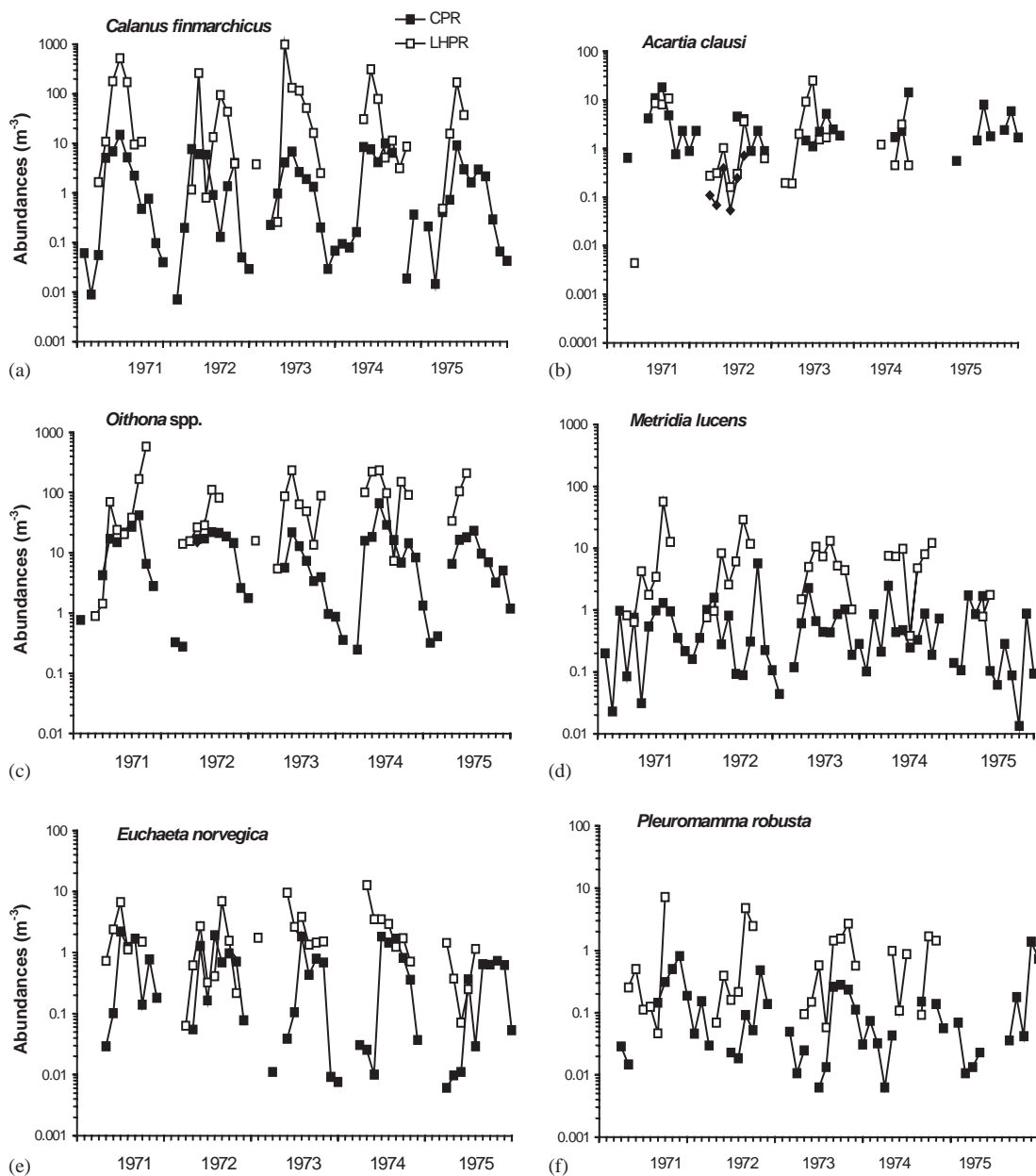


Fig. 1. Copepod abundance: monthly time series recorded by the CPR and LHPR over a 5-year period for (a) *A. clausi*, (b) *C. finmarchicus*, (c) *Oithona* sp., (d) *M. lucens*, (e) *E. norvegica* and (f) *P. robusta*.

C. finmarchicus, *A. clausi*, *M. lucens* and *P. robusta* (Table 1). Correlations for *E. norvegica* and *Oithona* sp. were positive but not statistically significant. Although no adjustment was made

for temporal autocorrelation, the seasonal cycles for each species were quite distinct and did not follow a standard single peak seasonal cycle, making it less likely to identify spurious correla-

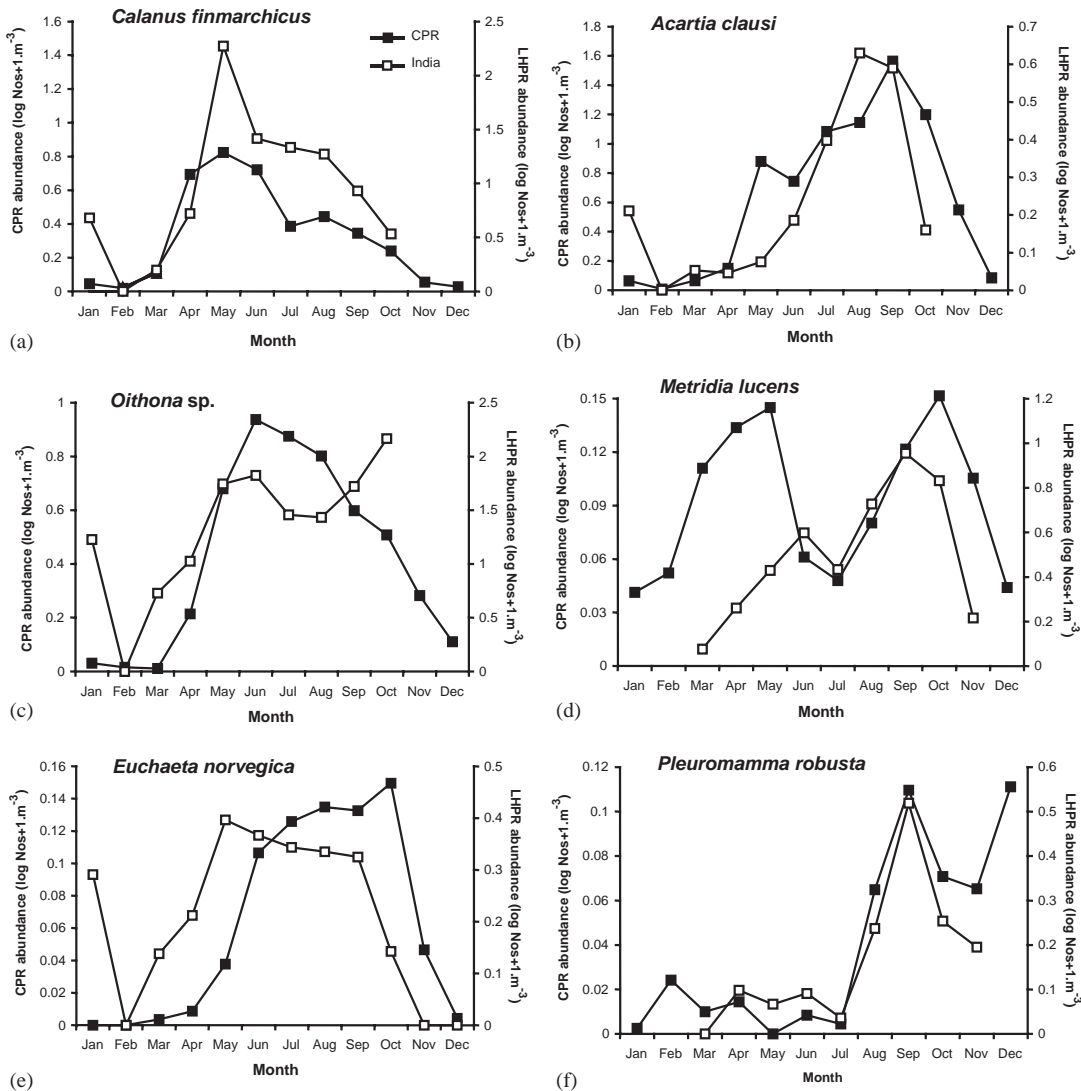


Fig. 2. Copepod abundance (log): mean seasonal cycle for (a) *A. clausi*, (b) *C. finmarchicus*, (c) *Oithona* sp., (d) *M. lucens*, (e) *E. norvegica* and (f) *P. robusta*.

tions. Inter-annual abundances would have less autocorrelation but were not investigated because of the short (5 year) time series available.

3.2. LHPR:CPR ratios

On close inspection of Fig. 2, it is clear that abundances recorded in the LHPR surface samples were considerably higher than those from the CPR (note the log-transformed y-axis scale). The ratio

between monthly abundances recorded by the LHPR at OWSI and those recorded by the CPR was always greater than one, indicating that the CPR generally underestimates abundances (Table 1). The ratio for *A. clausi* was closest to unity with a value of 1.7. Ratios between the WP2 net and the CPR from other studies are also shown in Table 1, but are not directly comparable as they were collected with a different mesh size and from a vertically-integrated sample. The ratio shows

Table 1

Correlation coefficients between mean monthly abundances for various zooplankton taxa, ratios of abundance recorded by the CPR and LHPR, and copepod sizes (from Rose, 1933, except maximum size of *C. finmarchicus* from Matthews, 1967)

Copepod taxa	Correlation	LHPR:CPR	WP2:CPR English Channel	WP2:CPR North Sea	Total length (mm)
<i>Oithona</i> sp.	0.25 (0.49)	10	43.3	47.5	0.8
<i>Acartia clausi</i>	0.92 (0.000)	1.7	2.3	13.2	1.15–1.22
<i>Metridia lucens</i>	0.74 (0.023)	11	20	-	2.5–2.9
<i>Calanus finmarchicus</i>	0.83 (0.003)	40	2.1	2.8	2.7–4.6
<i>Pleuromamma robusta</i>	0.73 (0.026)	8	—	—	3–4.3
<i>Euchaeta norvegica</i>	0.42 (0.175)	5	—	—	7–11

Significance levels for correlation coefficients are given in brackets and those that are significant ($p < 0.05$) are shown in italics. Ratios between WP2 net sampling and the CPR in two shelf areas for the English Channel (Clark et al., 2001) and North Sea (John et al., 2001) are presented for comparison.

strong seasonal and interannual variations (Fig. 3) at OWSI. This is a consequence of the very variable abundance time series from both samplers: Fig. 1 shows that the difference between the two time series is not constant. The overall ratio between surface LHPR:CPR samples for the other copepods varied between 5 (*E. norvegica*) and 40 (*C. finmarchicus*) with the other species differing by a factor of about 10 (Table 1).

3.3. Relative proportion of copepod species and total abundance

Differences in the LHPR:CPR abundance ratios for the different species leads to discrepancies in the estimated relative composition of the copepod assemblage. The variability in the proportion of each copepod species as a percentage of the total abundance is illustrated in Fig. 4. It is evident that *A. clausi* is relatively more abundant in CPR than in LHPR samples. Differences in the LHPR:CPR ratio among species leads to differences in the timing of peaks in total copepod abundance measured with the two devices. Peak total abundance measured by the CPR was mainly a result of high abundance of *A. clausi*, whereas the peak in the LHPR corresponds to maximum abundance of *C. finmarchicus* (Fig. 4).

4. Discussion

This is the first study to compare abundance estimates from the CPR survey in the North Atlantic

with a near-surface net sampler having a similar mesh size. It must be remembered when interpreting the findings from this study that all zooplankton samplers give biased estimates of species abundance because of loss of zooplankton (UNESCO, 1968). The LHPR can have problems with stalling of animals in the net causing loss of animals and smearing of their distributions (Haurly et al., 1976), although if the net has a moderate taper, as was the case for the net used with the LHPR at OWSI, these problems are minimised. There is also a degree of variability introduced into abundance estimates from the LHPR by differences in operating procedures and the experience of the personnel, which invariably changed during the OWSI programme. The CPR has a number of sampling biases, including a decrease in filtration efficiency when the CPR body is not properly sealed (Hays, 1994) and a decrease in filtered volume as ship speed increases (Jonas et al., submitted).

Despite these device-specific limitations, there was good agreement in the seasonal cycles described by the CPR and LHPR. The seasonal succession of copepod abundance was apparent from both data sets with maxima for *C. finmarchicus*, *Oithona* sp., *A. clausi*, and *P. robusta* observed in May, June, August and September, respectively (see also Planque et al., 1997). Strong correlation between seasonal cycles was also observed between the CPR and integrated WP2 net hauls in the shallow (55 m) western English Channel (John et al., 2001) and at a coastal station (54 m) in the central western North Sea (Batten et al., 2003).

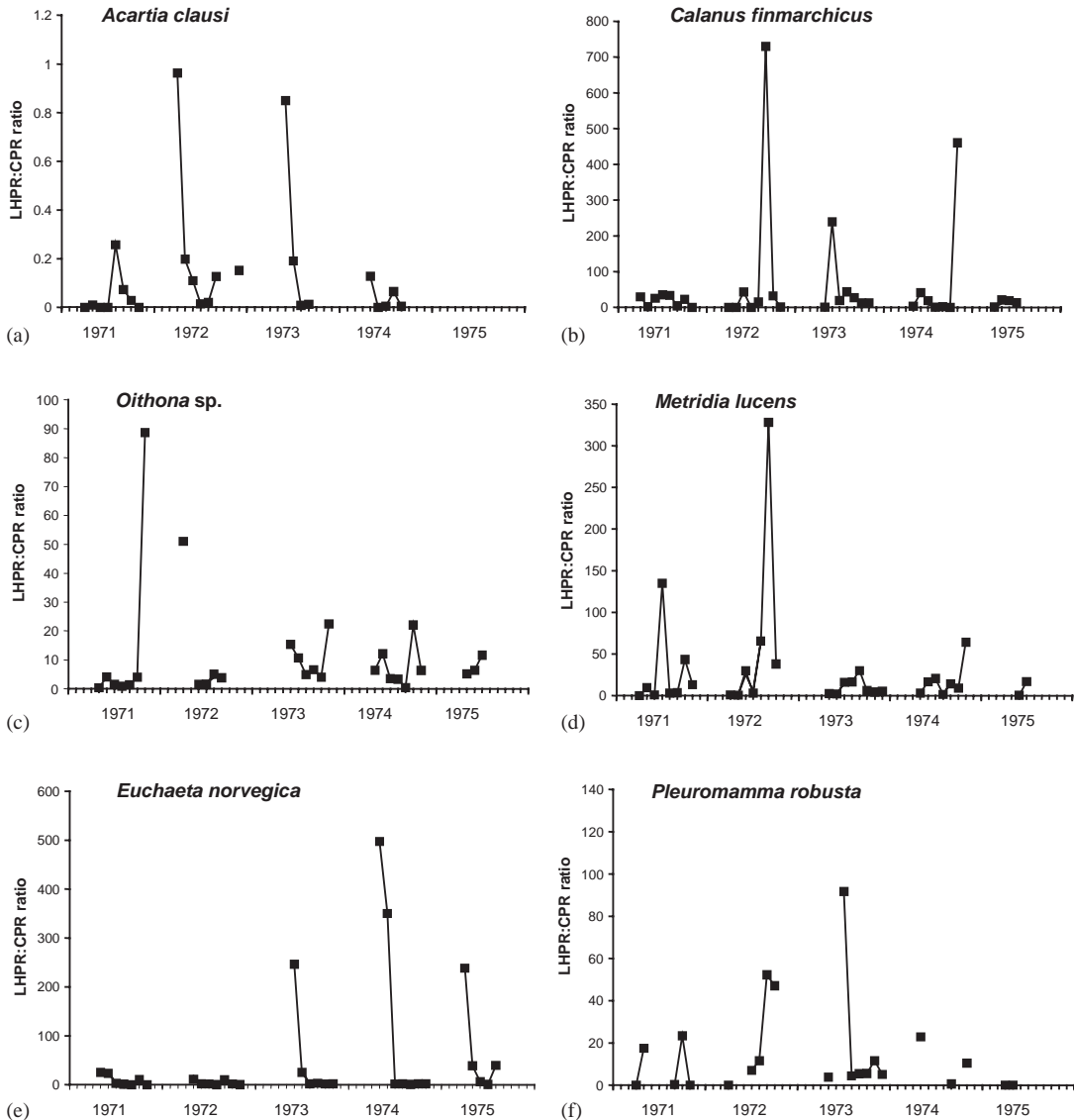


Fig. 3. Ratio of LHPR:CPR abundance for (a) *A. clausi*, (b) *C. finmarchicus*, (c) *Oithona sp.*, (d) *M. lucens*, (e) *E. norvegica* and (f) *P. robusta*.

Even though the seasonal cycles from the two devices compared well, estimated abundances were substantially lower for the CPR than the LHPR, except for *A. clausi*. Williams and Lindley (1980) also found significant differences in the maximum abundance of *C. finmarchicus* recorded by CPR and near-surface LHPR samples. Comparisons of integrated net hauls from WP2 nets with CPR samples have also been shown to under-estimate

abundance of many taxa (Clark et al., 2001; John et al., 2001). The present study, in conjunction with recent results in the Southern Ocean (Hunt and Hosie, 2003), now confirms that the under-estimation is not due to the fact that the CPR only samples at the surface.

The difference in abundance estimates between samplers is not likely to be due to the difference in mesh. The mesh size of the CPR is actually 10 μm

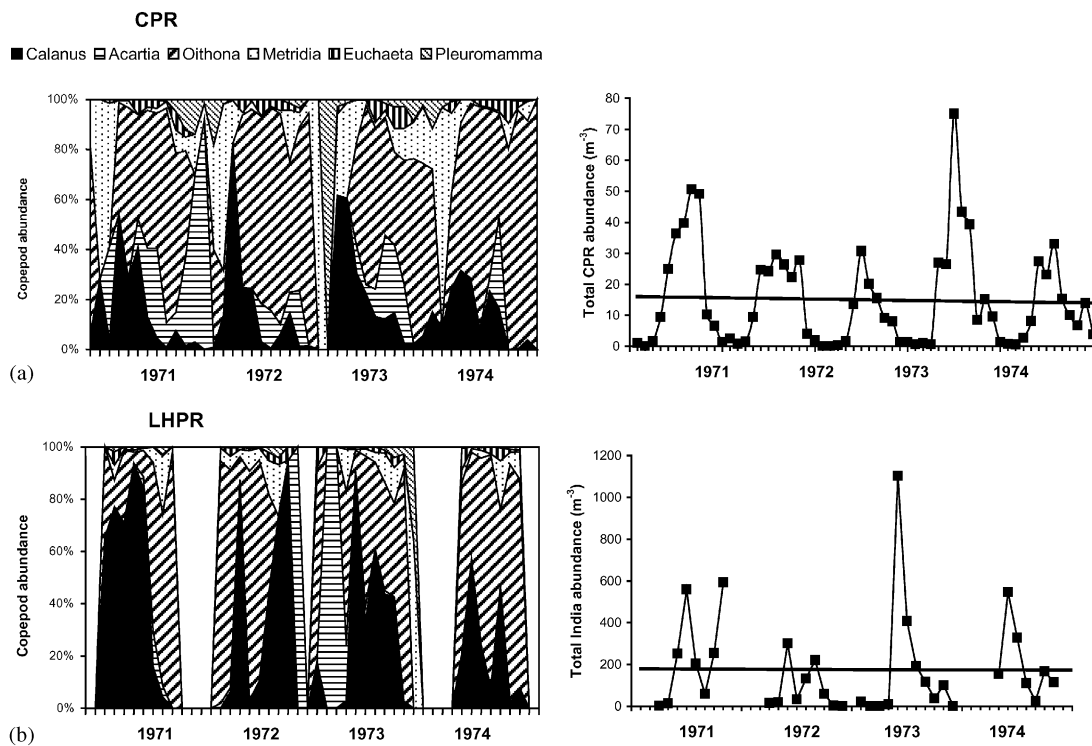


Fig. 4. Proportion of zooplankton abundance (% of total, left panel) for each species and total abundance (right panel) as recorded by (a) CPR samples and (b) LHPR samples.

smaller than the LHPR mesh size used in this study. The difference in composition of the mesh (CPR: silk; LHPR: nylon) is also unlikely to lead to the marked underestimate of zooplankton that was observed: the leno weave of the silk maintains the shape of the mesh and tends to retain organisms that get caught in it.

The difference in abundance estimates between samplers is also unlikely to be because of the vertical distribution of zooplankton in the surface water column. The mean CPR depth is 6.7 m, with almost all tow depths between 2 and 10 m (Hays and Warner, 1993); this is very similar to the depth of the interpolated surface LHPR sample (0–10 m). In addition, the water behind a fast moving vessel that tows the CPR is likely to be mixed to the towing depth (Batten et al., 2003).

The difference in abundance is also unlikely to be due to the counting system employed at the CPR survey. Each species is assigned an abun-

dance category during counting, which is later converted to a numerical abundance value based on an accepted mean for that category. This categorical system is a tradeoff between numerical accuracy and speed of processing. This system results in only a small (~4%) underestimate of abundance (Clark et al., 2001).

Another possible explanation for the lower abundances measured by the CPR may be extrusion through the CPR mesh because of fast tow speeds, although this is also unlikely. Extrusion through the CPR mesh is minimised by the water passing through a widening tunnel after the inlet aperture, resulting in the water speed across the filtering mesh being only 3.2% of that of the tow speed (Hays, 1994). This results in all copepods wider than 375 μm , such as adult *C. finmarchicus*, *M. lucens*, *P. robusta* and *E. norvegica* (widths > 900 μm) being retained by the CPR at normal tow speeds (Hays, 1994). The retention of smaller

species such as *Oithona* sp. and *A. clausi* adults (widths <375 µm) by the CPR silk at normal tow speeds is similar to that of a nylon net with the same mesh size. Moreover, if extrusion was a serious problem, fragments of organisms may be expected. Fragments are commonly found for delicate organisms such as coelenterates, but most hard-shelled copepods found on the CPR filtering silk are intact, albeit squashed.

A possible explanation for the undersampling of some species may be that they are difficult to identify during counting. For example, the CPR underestimated *Oithona* sp. compared with the LHPR. Undersampling of this species has been reported in other studies (Fransz et al., 1991; Clark et al., 2001; John et al., 2001). In comparative studies using WP2 nets (integrated abundance) and the CPR, the WP2 net captured 45 times more *Oithona* sp. than the CPR, which was attributed to the difference in mesh size (WP2: 200 µm, CPR: 270 µm; Clark et al., 2001; John et al., 2001). In the current study using similar mesh sizes the ratio of LHPR:CPR abundance for *Oithona* sp. was still high (10:1) but substantially lower than these previous studies. The study by Hunt and Hosie (2003) in the Southern Ocean comparing CPR samples from those vertical nets collected in the top 20 m found that *Oithona similis* was sampled well by the CPR; this may be because their CPR samples were washed off the mesh and counted in a dish. *Oithona* sp. are small and transparent, making them difficult to identify in the on-silk analysis that is used at the CPR in the North Atlantic survey. Unfortunately the samples cannot be washed off the silk into a Bogorov tray, which would probably provide a more accurate estimate of abundance for this species, as this would jeopardise the continued consistency of the time series. It is doubtful that other species examined in this study were underestimated for the same reason as *Oithona* sp., as they are larger (*C. finmarchicus*, *E. norvegica*, *M. lucens* and *P. robusta*) or are relatively opaque (*A. clausi*) and are therefore more easily seen during counting.

The most likely reason for the discrepancy in estimated abundances of the larger species between the two devices is their catch efficiency. This is related to the speed of the device, the mouth area

of the device, and the avoidance capability of the zooplankton. Avoidance by zooplankton is reduced when nets are towed more quickly (UNESCO, 1968) or have larger mouth areas (McGowan and Fraundorf, 1966; Ware and Lambert, 1985).

Avoidance capability is related to three factors: viz. the flow dynamics of the sampler and in particular the ‘bow-wave’ in front of the device, the ability of a particular species to detect that ‘bow-wave’, and the escape speed of the species. Flow dynamics around the CPR are not known because there have not been studies using flow tanks or numerical models. Moreover, the reaction distance to an approaching device and the escape velocities of individual copepods are also poorly known.

In view of the lack of information on flow dynamics, reaction distances and escape velocities, probably the simplest method to compare catch efficiencies of the CPR and the LHPR is to use the approach adopted by Clark et al. (2001). Catch efficiency (CE), defined as the proportion of individuals in the sampling path that are caught (UNESCO, 1968), can be calculated as

$$CE = \left(\frac{R - K/S_i}{R} \right),$$

where R is the entrance radius, K is the avoidance parameter, and S_i is the speed of tow. We use this equation with the knowledge that it was developed for a conical net and may not apply directly to a CPR that may have different flow characteristics (Clark et al., 2001). As with many other high-speed samplers, no detailed comparative experiments between the CPR and conical nets have been conducted.

The mean towing speed for the CPR in 1971–1975 was ~12.8 knots (6.6 m s^{-1}), much faster than the usual speed of the LHPR of ~1.75 knots (0.9 m s^{-1}). The radius for the CPR, however, is only ~0.00898 m (half the diagonal of the 1.27×1.27 cm inlet aperture Clark et al. 2001), much smaller than the diameter of the LHPR of 0.5 m (Wiebe and Benfield, 2003). Estimates of the catch efficiency for both devices (Fig. 5) show that it decreases as the avoidance parameter increases. What is most noticeable, however, is the much

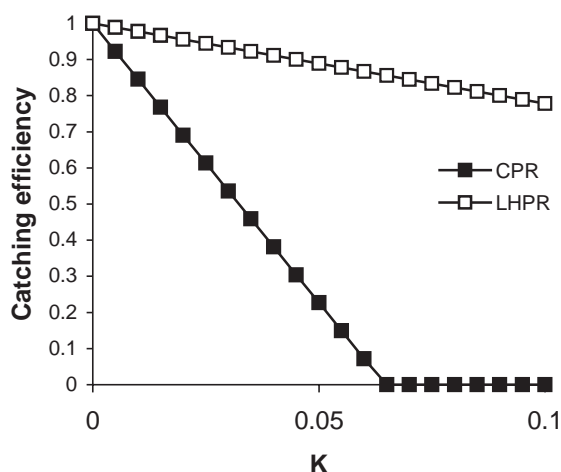


Fig. 5. Catch efficiencies of the LHPR and CPR for values of K (detection distance \times mean escape speed). Note that when catch efficiencies were calculated to be less than 0 for the CPR they were set to 0.

steeper decline in estimated catchability of zooplankton for the CPR than for the LHPR. This suggests that the underestimation by the CPR may be mainly attributable to active avoidance by zooplankton, similar to the conclusion reached by Clark et al. (2001). Compared with the LHPR, the easier avoidance by zooplankton of the small aperture of the CPR may not be compensated for by the fast tow speed of the device. Although it has been suggested that the amount of turbulence behind a ship towing a CPR may act to disorientate zooplankton making it difficult for them to avoid the aperture, this does not seem to be supported by the present analysis.

If avoidance was responsible, one may expect that larger copepods would have a greater escape response, so underestimates of their abundance would be greater than for smaller species. This is not clear from Table 1. The ability of an animal to escape not only depends on its swimming speed, but also on its ability to perceive the sampling device through a variety of visual, acoustical and hydrostatic stimuli (Fleminger and Clutter, 1965; UNESCO, 1968), which may not be directly related to species size.

Finally a caveat is necessary: there is a mismatch of scales when comparing CPR data with

time series collected at a point as in the present and most previous comparative studies. Because of the patchiness of plankton, the semi-quantitative nature of CPR sampling, and the large area each sample represents (a single CPR sample represents over 20 nautical miles), analysis of CPR data usually involves selecting a large area of interest. By contrast, previous comparisons by Clark et al. (2001), John et al. (2001) and the present study compare CPR data over a large scale with data from a single location, which is likely to be influenced by local forcing. This problem is analogous to comparing output from general circulation models on a coarse grid scale with measurements of temperature or rainfall at a single site, a situation that is not strictly valid because of local effects (Busioc et al., 2001). A common way around this problem of downscaling in climate research is to compare synoptic output from general circulation models with data averaged from a number of point stations. Therefore, a more valid approach would be to compare CPR data with surface data from another sampler over a broader spatial scale than in the present study. We suggest that future comparisons with the CPR should be made on a complimentary scale, such as with a network of sampling stations (e.g. the ICES Working Group on Zooplankton Ecology, <http://www.ices.dk/reports/occ/>). In the present study, we did minimise the likely impact of local forcing on plankton abundance by choosing an oceanic rather than shelf site to compare with CPR data.

In conclusion, this and other comparative studies show that seasonal cycles and to a lesser degree the inter-annual variation measured by the CPR is similar to other samplers. However, the CPR does underestimate the abundance of many species, probably because of active avoidance of the device by zooplankton. This avoidance is species specific, so that care must be taken describing communities, as the CPR emphasises those species that are preferentially caught, a problem common to many plankton samplers. Although it is known that the CPR focuses on species with a surface distribution (Hunt and Hosie, 2003), a general question in zooplankton ecology that remains to be adequately answered is how representative a surface sample is of the entire

zooplankton community throughout the water column. This question has been addressed for phytoplankton using chlorophyll profiles and the concept of biogeochemical provinces (Longhurst et al., 1995). Such an approach for zooplankton would probably best be addressed by using the extensive vertically resolved zooplankton data available from MOCNESS, BIONESS, RMT and LHPR without recourse to the CPR (for example, Halliday et al., 2001; Wiebe et al., 2002).

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