Comparison of zooplankton sampling performance of Longhurst–Hardy Plankton Recorder and Bongo nets

MARIA STEHLE[1], ANTONINA DOS SANTOS[1]* AND HENRIQUE QUEIROGA[2]

[1]INSTITUTO NACIONAL DE INVESTIGAÇÃO AGRÁRIA E DAS PESCAS-IPIMAR, AV. BRASÍLIA S/N, 1449-006 LISBOA, PORTUGAL AND [2]CESAM AND DEPARTAMENTO DE BIOLOGIA, UNIVERSIDADE DE AVEIRO, CAMPUS UNIVERSITÁRIO DE SANTIAGO, 3810-193 AVEIRO, PORTUGAL

*CORRESPONDING AUTHOR: antonina@ipimar.pt

Data on the abundance and biomass of zooplankton off the northwestern Portuguese coast, separately estimated with a Longhurst–Hardy Plankton Recorder (LHPR) and a Bongo net, were analysed to assess the comparative performance of the samplers. Zooplankton was collected along four transects perpendicular to the coast, deployments alternating between samplers. Total zooplankton biomass measured using the LHPR was significantly higher than that using the Bongo net. Apart from Appendicularia and Cladocera, abundances of other taxa (Copepoda, Mysidacea, Euphausiacea, Decapoda larvae, Amphipoda, Siphonophora, Hydromedusae, Chaetognatha and Fish eggs) were also consistently higher in the LHPR. Some of these differences were probably due to avoidance by the zooplankton of the Bongo net. This was supported by a comparative analysis of prosome length of the copepod Calanus helgolandicus sampled by the two nets that showed that Calanus in the LHPR samples were on average significantly larger, particularly in day samples. A ratio estimator was used to produce a factor to convert Bongo net biomass and abundance estimates to equate them with those taken with the LHPR. This method demonstrates how results from complementary zooplankton sampling strategies can be made more equivalent.

INTRODUCTION

Variation between zooplankton samples is typically high, usually attributed to the patchy distribution of plankton. However, this variance also contains an unknown amount of sampling error, of which the sampling performance of the equipment can be an important component (Webster and Anderson, 1987). This can be further complicated by the necessity to use different types of samplers, often with different mesh sizes, during the same survey, or to compare results from surveys using different samplers. For example, the zooplankton of an area is often characterised by rapid survey coverage using simple equipment, followed by intensive work at selected sites using more sophisticated sampling equipment (Conway *et al.*, 1998; dos Santos *et al.*, 2007). Examples of commonly used simple survey nets are a Bongo net (McGowan and Brown, 1966) or a WP-2 net (UNESCO, 1968) and of more sophisticated ones, a Longhurst–Hardy Plankton Recorder (LHPR; Longhurst *et al.*, 1966; Williams *et al.*, 1983) or a MOCNESS (Wiebe *et al.*, 1976).

The Bongo net and LHPR were originally designed during the 1960s. The Bongo net has become a standard in plankton research and was originally developed to collect icthyoplankton in horizontal, vertical or oblique tows at low speeds, typically 1–2 knots (Kloppmann, 1990). The LHPR was designed to take a series of consecutive samples on a single haul for studies of vertical distribution at high speed (~4 knots). However, the comparative efficiency of these two nets has never been assessed.

The LHPR and Bongo nets have been individually compared with other sampling systems. Halliday *et al.* (Halliday *et al.*, 2001) compared zooplankton abundance

estimates made with the LHPR and the Optical Plankton Counter (Herman, 1992) from vertical sampling in a Norwegian fjord. Other studies, Richardson et al. (Richardson et al., 2004) and Batten et al. (Batten et al., 1999), compared zooplankton abundance estimated from the Continuous Plankton Recorder (CPR; Hardy, 1935) with samples collected by the LHPR, and John et al. (John et al., 2001) compared CPR with WP-2 nets' samples taken on shelf waters. Other authors (Ohman and Smith, 1995) compared the efficiency of different sampling techniques for zooplankton biomass, using a bridle-less Bongo net and a bridled ring CalCOFI net (Ahlstrom, 1948).

The objective of this study was to compare the LHPR and Bongo net sampling results of a survey in which both were deployed and use a ratio estimator to make the results equivalent.

METHODS

Zooplankton sampling was carried out from the research vessel RV 'Noruega' from 15 to 17 May 2002, over a grid of stations located on the continental shelf off the northwest coast of Portugal (Fig. 1). Samples were collected along four transects perpendicular to the coast, alternating between LHPR and Bongo nets along
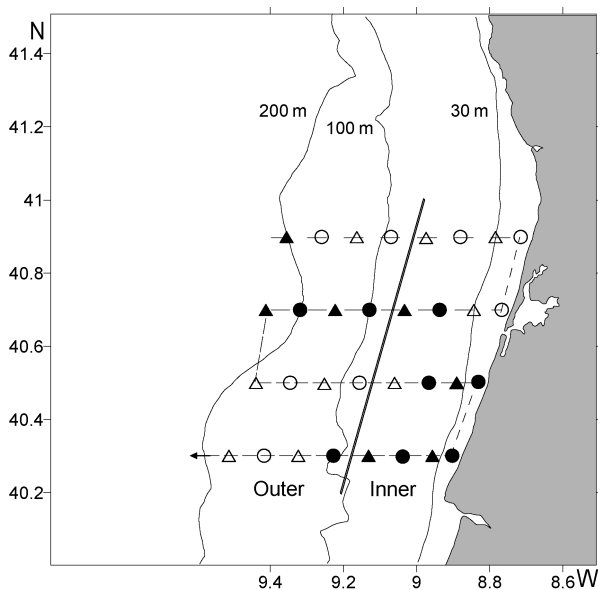

Fig. 1. Study area off the northwest Portuguese coast, showing the location of sampling stations. Broken arrows indicate the direction of sampling. The broken line separates the stations on the inner and outer shelves. Triangles, stations sampled with the LHPR system; circles, stations sampled with the Bongo net; open symbols, day stations; filled symbols, night stations.

the sequence of stations. The LHPR with an inlet aperture of 42 cm and the Bongo net with a 60 cm diameter aperture were fitted with nets of mesh size 280 and 335 μm, respectively. The LHPR net terminates in a cod-end unit, inside which the filtered zooplankton is collected between two rolls of gauze, which are advanced at set time intervals. On each haul, a continuous series of depth stratified samples were collected at 3–4 knots on oblique tows from the surface to 10 m above the bottom. The Bongo net was towed on depth-integrated double oblique hauls at 1–2 knots from surface to 10 m above the bottom. Flow rate was monitored using a calibrated digital flow meter mounted on the mouth aperture of both samplers, and the mean volume of water filtered by the LHPR and Bongo nets was ~230 m³ and ~1180 m³, respectively. Both samplers were towed with the same winch and cable. All samples were preserved in 4% borax-buffered formaldehyde prepared using seawater.

Samples were subsequently sorted and counted for the most abundant taxa. Samples containing >400 individuals per taxon were sub-sampled using a Folsom splitter, usually only for copepods. Abundances were expressed in ind m^{-3}. In order to compare estimates made with the two nets, all samples from each haul of the LHPR were combined into a single sample. Both nets of the Bongo net were of the same mesh size, and abundance values are the mean of the two nets.

Within the most abundant group, the Copepoda *Calanus helgolandicus*, a common large species in the area, was selected for length analysis to see if both samplers captured the same size spectrum within a species. The prosome lengths of *C. helgolandicus* adults from four day and four night stations located in the inner shelf, where the copepods were abundant, were measured; two LHPR and two Bongo net samples in each period. Using a Wild M5 stereomicroscope, 100 individuals were randomly measured from each sample.

The biomass of zooplankton from the grid samples was estimated using displacement volume. Measurement of displacement volume has the advantage of being non-destructive, permitting the use of the entire sample for other quantitative studies (Wiebe et al., 1975). Conversion from displacement volume to biomass was made using an equation given by Wiebe (Wiebe, 1988):

$$DW = 10^{(\log DV + 1.842)/0.865}$$

where DV is displacement volume (mL) and DW is dry weight (mg C). Dry weight is a proxy of biomass and is expressed in mg C m^{-3}.

Differences in biomass, abundance of each taxon and *C. helgolandicus* body size according to type of sampler (LHPR and Bongo nets), time of day (day and night) and location on the shelf (inner and outer shelves; Fig. 1) were analysed with a three-way orthogonal analysis of variance (ANOVA). Several of the most commonly used transformations were applied to the values of biomass and taxa abundance, but none was successful in homogenising the variances. Following the suggestions of Zar (Zar, 1984), we substituted the values of biomass and abundance by their ranks, which homogenised the variances, and performed the ANOVA after this transformation. In the case of *C. helgolandicus* data, since variances were homogeneous, the data were not transformed.

To calculate a factor to convert the abundance and biomass estimates of the Bongo net to make them equivalent to LHPR values and for assessing horizontal distribution, the following ratio estimator was used:

$$\hat{R} = \frac{\sum_{i=1}^{n} y_i}{\sum_{i=1}^{n} x_i}$$

where $\hat{R}$ is the ratio estimator, y_i and x_i are the abundance or biomass values obtained by the Bongo net and LHPR at each sampling station, respectively, n is the number of stations, and the subscript i refers to the sampling station. This estimator is asymptotically centred and has a lower mean square error than the average of the ratio of the bivariated sample when there is no strong correlation between the two variables (Barnett, 1991). Assuming that the sampling fraction is negligible, the standard error of the ratio estimator can be obtained by,

$$S(\hat{R}) = \frac{1}{\bar{x}\sqrt{n}}$$

$$\frac{\sqrt{\sum_{i=1}^{n}(y_i^2) - 2\hat{R}\sum_{i=1}^{n}(y_i x_i) + \hat{R}^2 \sum_{i=1}^{n}(x_i^2)}}{\sqrt{n-1}}$$

where S is the standard deviation of ratio estimator, $\bar{x}$ is the average of the values of abundance or biomass given by the LHPR and y_i and x_i have the same meaning as described earlier. Considering that the distribution of the ratio estimator approximates normality, the 95% confidence interval for the ratio estimator was calculated as (Barnett, 1991):

$$\mathrm{IC}_{0.95}(R) =]\hat{R} \pm 1.96 \times S(\hat{R})[$$

where $\mathrm{IC}_{0.95}$ is the 95% confidence interval.

RESULTS

Zooplankton total biomass

Estimates of zooplankton total biomass from the LHPR were approximately five times higher than those from the Bongo net (Fig. 2, Table I). According to the ANOVA based on the ranks of the observations, this difference was highly significant. None of the other factors or of the interactions was significant (Table I).

Abundances by taxa

A comparison was made between the abundances of selected taxa collected by the two samplers (Table II). Their order of abundance in both samplers was the same, but numbers caught by the LHPR were approximately six times higher than with the Bongo net and were higher for all taxa except Cladocera and Appendicularia.

An ANOVA based on the ranks of the observations of an extended group of taxa (Tables III and IV), showed that the estimates of abundance were significantly different between samplers for most of the taxa: Euphausiacea larvae, Chaetognatha, Decapoda zoea, total Decapoda megalopae, Brachyura megalopae and total Copepoda, *C. helgolandicus* and *Calanoides carinatus*, but not for Cladocera and Appendicularia. None of the interactions between the sampler and the other factors was significant, except for Euphausiacea larvae and total Decapoda megalopae, where the interaction of all three factors was statistically significant (Fig. 3). The main effects of location and time of day were significant in some groups (Table IV). *Calanoides carinatus*, Euphausiacea larvae and Euphausiacea adults were more abundant on the outer shelf, whereas Chaetognatha and Anomura megalopae were more abundant on the inner shelf. Highest numbers of Mysidacea, Amphipoda, Euphausiacea adults, total Decapoda megalopae and Anomura megalopae were collected during the night. The effects of location and time of day were statistically significant in a few cases.

Size of *C. helgolandicus*

A highly significant effect of the interaction between the sampler and time of day on size of *C. helgolandicus* was detected (Table IV). A *post hoc* test indicated that average size of *C. helgolandicus* collected by the Bongo net during the day was significantly smaller than the average size obtained in the other combinations, and that differences among the other combinations were not significant.
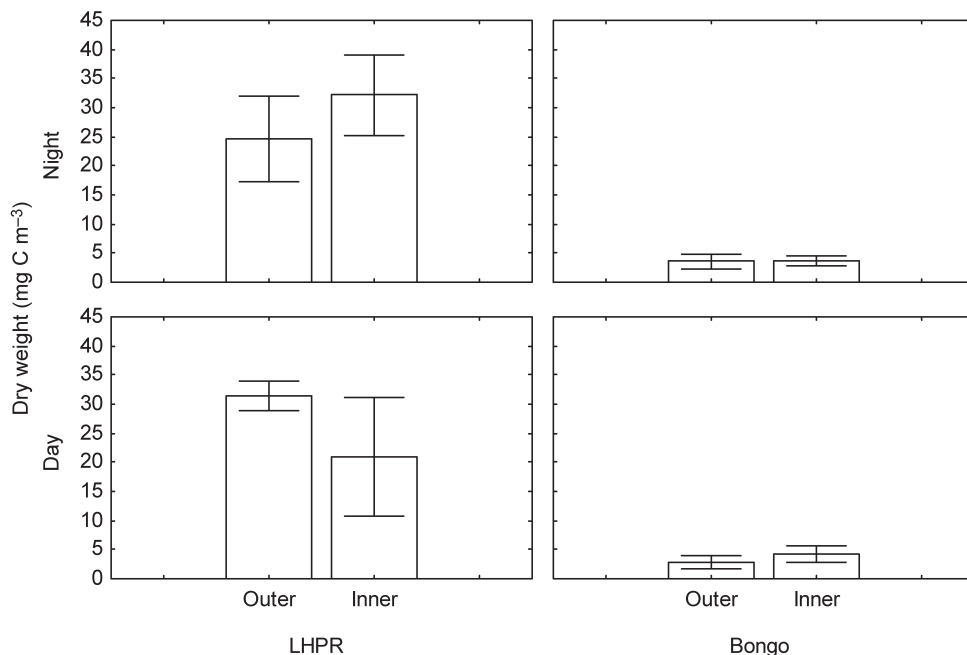
Fig. 2. Mean values of zooplankton biomass in relation to sampler type, location on the shelf and time of day. Error bars represent ±1 standard error.

Ratio estimator

The values of the ratio estimator and the 95% confidence interval are shown in Table V. The ratio estimator for the total biomass has an absolute error of 4%. Depending on the taxon, the maximum error associated with 95% confidence interval ranged between 4% and 83%, with the exception of one value of 345% for Appendicularia. As an example of the application of the ratio estimator, Fig. 4 shows estimates of the horizontal distribution of total biomass collected by the two samplers, before and after the conversion of the Bongo values.

Table I: Analysis of variance (ANOVA) of the ranks of zooplankton biomass

Source of variation	df	MS	F	P-level
Sampler	1	1692.627	65.5898	≪ 0.001
Location	1	0.816	0.0316	>0.50
Time of day	1	0.015	0.0006	>0.50
Location versus sampler	1	18.436	0.7144	>0.40
Location versus time of day	1	1.943	0.0753	>0.50
Sampler versus time of day	1	0.700	0.0271	>0.50
Location versus sampler versus time of day	1	41.697	1.6158	>0.20
Error	24	25.806		

df, degrees of freedom; MS, mean squares; F, F-test values. P-level, probability level.

DISCUSSION

Estimates of total zooplankton biomass and numbers collected by the LHPR were significantly higher than with the Bongo net, apart from numbers of Appendicularia and Cladocera. Differences in catch between the two samplers could be attributed to

Table II: Comparison of the abundances (ind m^{-3}), ANOVA at 95% confidence interval, taxa collected by the two nets

Taxa	Samplers	
	LHPR	Bongo net
Total Copepoda	989.82 ± 281.88	160.29 ± 286.39
Calanus helgolandicus	64.44 ± 19.50	14.69 ± 19.81
Calanoides carinatus	34.51 ± 9.54	8.62 ± 9.69
Mysidacea	14.05 ± 6.36	0.37 ± 6.46
Cladocera	2.94 ± 1.80	4.00 ± 1.82
Appendicularia	2.15 ± 2.74	9.82 ± 2.79
Siphonophora	2.40 ± 0.66	0.44 ± 0.67
Euphausiacea larvae	2.22 ± 0.46	0.43 ± 0.47
Decapoda zoeae	1.90 ± 0.34	0.84 ± 0.35
Fish eggs	1.76 ± 0.37	0.52 ± 0.38
Chaetognatha	0.91 ± 0.22	0.50 ± 0.22
Amphipoda	0.51 ± 0.24	0.04 ± 0.24
Euphausiacea adults	0.50 ± 0.22	0.01 ± 0.22
Hydromedusae	0.21 ± 0.06	0.19 ± 0.06
Total Decapoda megalopae	0.25 ± 0.04	0.05 ± 0.04
Brachyura megalopae	0.21 ± 0.04	0.04 ± 0.04
Anomura megalopae	0.02 ± 0.01	0.01 ± 0.01

Values are mean and standard deviation.

Table III: Significance (P-levels) of the main effects and interactions of the ANOVAs of the ranks of abundance for each zooplankton taxon

Taxa	Source of variation						
	Location	Time of day	Sampler	Location versus time of day	Location versus sampler	Time of day versus sampler	Location versus time of day versus sampler
Total Copepoda	>0.50	>0.50	<0.001	>0.10	>0.50	>0.50	>0.10
Calanus helgolandicus	>0.05	>0.10	<0.01	>0.50	>0.50	>0.50	>0.10
Calanoides carinatus	<0.05	>0.10	<0.01	>0.50	>0.50	>0.50	>0.50
Mysidacea	>0.50	<0.001	>0.10	<0.01	>0.10	>0.50	>0.10
Cladocera	>0.05	>0.10	>0.10	>0.10	>0.10	>0.50	>0.50
Appendicularia	>0.10	>0.05	>0.10	>0.50	>0.50	>0.10	>0.50
Siphonophora	>0.10	>0.50	>0.10	>0.05	>0.50	>0.50	>0.50
Fish eggs	>0.10	>0.10	>0.05	>0.50	>0.50	>0.50	>0.50
Euphausiacea larvae	<0.001	>0.50	<0.01	>0.50	>0.50	>0.10	<0.05
Decapoda zoea	>0.50	>0.10	<0.05	>0.10	>0.50	>0.10	>0.50
Chaetognatha	<0.001	>0.10	<0.01	<0.05	>0.10	>0.10	>0.10
Amphipoda	>0.10	<0.01	>0.10	>0.05	>0.10	>0.50	>0.10
Euphausiacea adult	<0.05	<0.05	>0.10	>0.10	>0.50	>0.10	>0.10
Hydromedusae	>0.10	>0.50	>0.50	>0.10	>0.50	>0.10	>0.50
Total Decapoda megalopae	>0.10	<0.05	<0.001	<0.05	>0.10	>0.50	<0.05
Brachyura megalopae	>0.10	>0.10	<0.001	>0.10	>0.50	>0.50	>0.05
Anomura megalopae	<0.001	<0.001	>0.10	<0.001	>0.50	>0.10	>0.50

differences in mesh sizes, since the LHPR was fitted with a 280-μm mesh net and the Bongo with 335-μm mesh. However, all the organisms analysed in this study had minimum dimensions >335 μm and biomass and number values from the LHPR of five to six times higher than with the Bongo net are higher than could be explained by net selection. Extrusion of organisms through the meshes is dependent on towing speed (Nichols and Thompson, 1991), and since the LHPR is towed at 3–4 knots, approximately twice the speed of the Bongo net, it should be more vulnerable to extrusion although the results did not indicate this. Shape of organisms and their plasticity can also facilitate extrusion. Although not statistically significant, the Bongo net captured more Cladocera and Appendicularia than the LHPR. Morphologically, Cladocera have rounded shape and a body without long and strong spines or protuberances that may facilitate extrusion through the mesh of a high-speed sampler (Vannucci, 1968) as is the case of the LHPR.

Table IV: ANOVA of the size of Calanus helgolandicus

Source of variation	df	MS	*F*	*P*-level
Sampler	1	16.877	240.76	<0.001
Time of day	1	21.118	301.27	<0.001
Sampler versus time of day	1	14.719	209.98	<0.001
Error	796	0.070		

Clogging of the Bongo net could not have explained the differences found between nets, since the volume filtered by the Bongo net was on average ~1180 m^3 for each haul, and there was no indication of a clogging problem.

Differences between samplers could not be attributed to zooplankton patchiness. Although the vertical and horizontal heterogeneity of zooplankton could have an impact on the difference between samplers (Harris *et al.*, 2000), by sampling from the surface to the bottom with the Bongo net and combining each LHPR haul into a single sample and by alternating deployments of the two samplers along the transect lines, we integrated vertical variation in the first case and averaged out horizontal differences in the second.

The active avoidance of the Bongo net may be an explanation for the observed differences between nets. Avoidance depends on factors such as towing speed, net mouth diameter and net design (Fleminger and Clutter, 1965; McGowan and Fraundorf, 1966). There is evidence that higher towing speeds result in higher catches, attributable to the reduction of the evasion time available for the individual organisms. However, high-speed samplers usually have smaller mouth apertures, which reduces the distance that the animals need to displace themselves to avoid capture. The differences obtained in the present study are consistent with the possible avoidance by zooplankton of the slower Bongo net.

A comparison between catches made off South Georgia, in the Southern Atlantic, with a LHPR
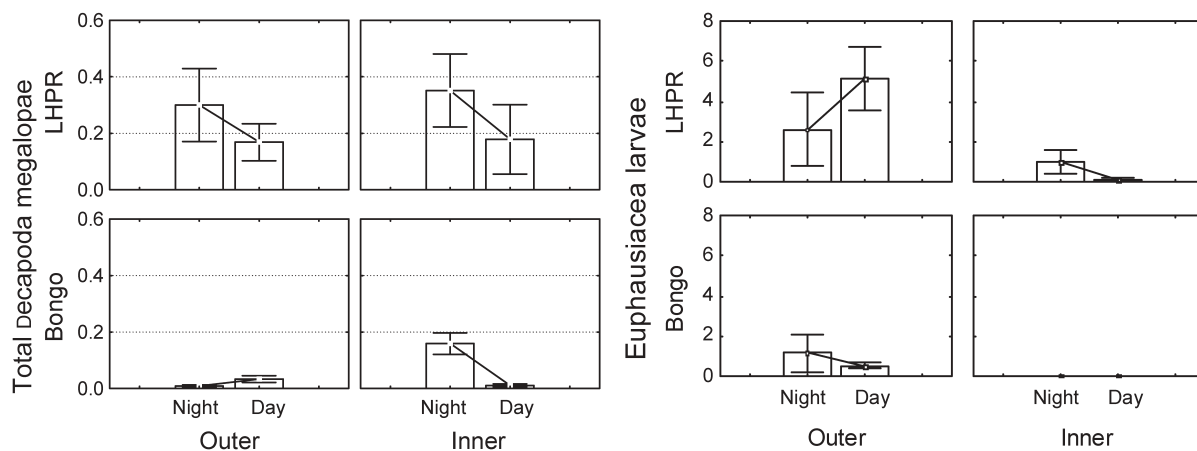
Fig. 3. Mean values of abundance of total Decapoda megalopae and Euphausiacea larvae according to sampler, location and phase of day. Error bars represent ± 1 standard error.

sampler (mesh size 200 and 500 µm towing speed 4 knots) and a Rectangular Midwater Trawl (RMT1; Clarke, 1969) which take depth stratified samples with lower resolution (mesh size 330 µm towing speed 2.5 knots), was made by Ward et al. (Ward et al., 1995). The RMT1 collecting fewer organisms than the LHPR, attributed to avoidance by highly motile species such as Euphausiids.

The LHPR used in the present study had a smaller inlet diameter (42 cm) than the Bongo net (60 cm), however this difference could hardly be considered likely to affect the catches. The detection by an organism of the approach of a net with a large mouth area at a greater distance offsets the smaller distance that organisms need to swim to escape a smaller net (Wiebe et al., 1982). However, there is some controversy concerning the influence of net mouth diameter in catching efficiency. Fleminger and Clutter (Fleminger and Clutter, 1965) concluded that nets with smaller diameter mouths were more effectively avoided and the degree of avoidance varied among species. Consistent with this finding, McGowan and Fraundorf (McGowan and Fraundorf, 1966) demonstrated that estimates of both number of species and species abundance were

Table V: Values of the ratio estimator related to total biomass (mg C m⁻³), taxa abundance (ind m⁻³) and total abundance (ind m⁻³), the 95% confidence interval and the maximum error associated with it

Taxa	Ratio estimator	Confidence interval	Absolute error (%)
Total biomass	0.1228	[0.0855; 0.1601]	4
Mysidacea	0.0315	[0.0000; 0.0687]	4
Euphausiacea adult	0.0279	[0.0000; 0.0687]	4
Siphonophora	0.1824	[0.0878; 0.2771]	9
Amphipoda	0.0812	[0.0000; 0.1766]	10
Total Copepoda	0.1605	[0.0509; 0.2700]	11
Total abundance	0.1716	[0.0563; 0.2868]	12
Euphausiacea larvae	0.1623	[0.0315; 0.2930]	13
Total Decapoda megalopae	0.2641	[0.0806; 0.4477]	18
Calanus helgolandicus	0.2091	[0.0140; 0.4041]	20
Brachyura megalopae	0.2152	[0.0091; 0.4213]	21
Calanoides carinatus	0.2481	[0.0224; 0.4738]	23
Fish eggs	0.3101	[0.0667; 0.5535]	24
Decapoda zoea	0.4491	[0.0762; 0.8220]	37
Anomura megalopae	0.8932	[0.5045; 1.2818]	39
Hydromedusae	0.9194	[0.4027; 1.4362]	52
Chaetognatha	0.6469	[0.0000; 1.3145]	67
Cladocera	1.3820	[0.5513; 2.2127]	83
Appendicularia	3.8526	[0.4068; 7.2984]	345

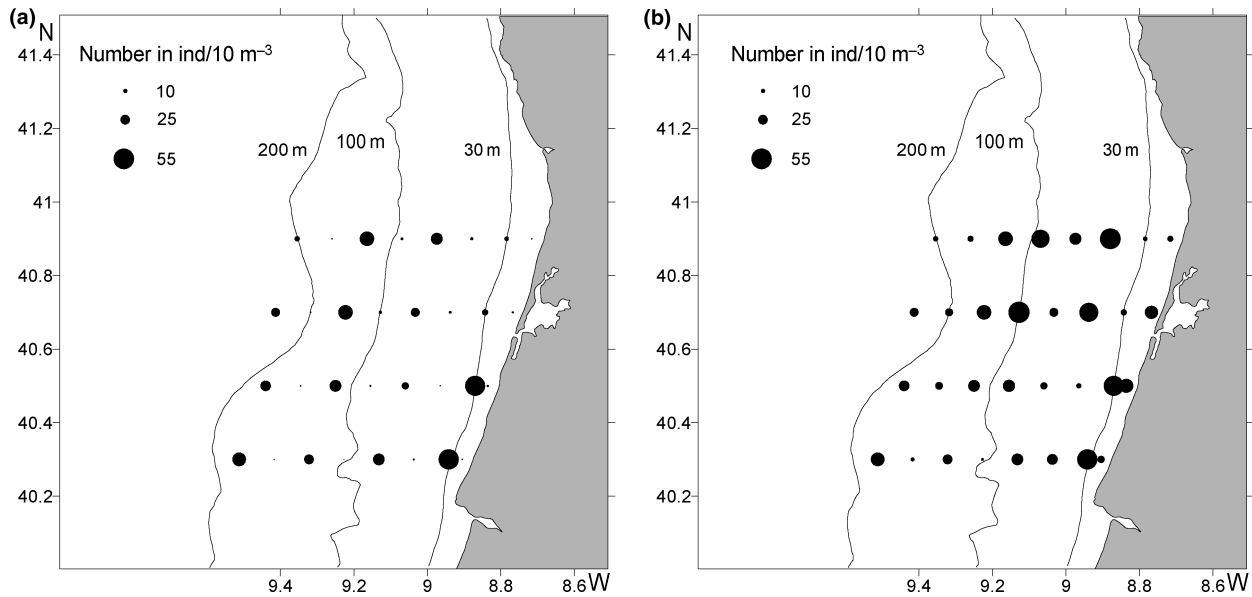Negative values of the lower limit of the confidence interval were set to zero.

Fig. 4. Horizontal distribution of total biomass: (**a**) before conversion; (**b**) after conversion using the ratio estimator.

lower with the smaller nets. In contrast, comparisons between nets with different size mouth opening showed that increasing the area of the net aperture will not reduce net avoidance by the euphausiid *Nematoscelis megalops*, because the potential advantage of greater mouth area of the larger net is effectively cancelled out by individuals reacting to the approach of the net at a greater distance (Wiebe *et al.*, 1982). Thus, there is no evidence that increasing the size of the mouth area of zooplankton nets increases the efficiency of the sampler (Pearcy *et al.*, 1983). Thus, the net aperture in our study should not be relevant, the difference of 18 cm in the mouth net diameter, between the LHPR and the Bongo net, does not seem important in relation to the difference in speed.

There is insufficient information concerning the flow patterns associated with the form of plankton sampler design on which avoidance is dependent. The design of the nets influences their performance dynamics in the water. Turbulence in front of the net, created by the movement of the net through water can be sensed. The use of a mouth-reduction inlet cone as used in the LHPR could reduce this compared to the Bongo net (Tranter and Smith, 1968). This hydrodynamic design feature of the LHPR could also explain the differences in catches between the two devices.

Calanus helgolandicus collected by the LHPR were on average significantly larger than those collected with the Bongo net, a difference that was much greater in samples collected during the day, indicating avoidance. Although they are not visual animals they possess accessory photoreceptors (Frost, 1974) that will probably be important to signalise approaching objects during daylight. Smaller organisms show less avoidance than closely related larger forms (Fleminger and Clutter, 1965; McGowan and Fraundorf, 1966) and this effect can be enhanced during the day by visual detection of the net. This finding appears to contradict results obtained by Fleminger and Clutter (Fleminger and Clutter, 1965) who demonstrated that the use of an artificial light did not lead to a decrease in the catch of calanoid copepods.

Significant sampler versus location versus time of day interactions were detected in total Decapoda megalopae and in Euphausiacea larvae. These were the only significant interactions of sampler with the other factors. Total Decapoda megalopae were more abundant during the night and in the LHPR samples. On the basis of strong swimming capabilities of these organisms (Mileikovsky, 1973; Young, 1995), we would expect a significant difference related to the time of day and sampler associated with avoidance of the Bongo net during the day. The increased abundances recorded during the night dependent on location may be related with upward migration from the lower levels in the water column during the night at different locations, associated with a differential distribution of species along the transects (Conway and Williams, 1986; Conway *et al.*, 1997; Cohen and Forward, 2005). A similar explanation could apply to the significant 3-way interaction in the case of Euphausiacea larvae.

During an oceanographic survey it is common to use different types of zooplankton samplers (Conway *et al.*, 1998; dos Santos *et al.*, 2007) as a compromise between quick spatial or temporal coverage and the need to sample interesting phenomena in greater detail. Surprisingly, we do not know of any previous study that has developed any statistical tool allowing comparison of data from different nets in the same study. A similar situation arises when one is faced with the need to compare data from different studies using different samplers. Recognising this, we suggest that the ratio estimator allows conversion of Bongo net data into LHPR equivalents. In our case, according to the ratio estimator, zooplankton biomass recorded by the LHPR ranged between 10 and 53 times higher than that recorded by the Bongo net. However, a recent paper by Ward *et al.* (2006) shows a summary of LHPR and Bongo net catches of mesozooplankton abundances and biomass collected in Antarctica, where it is apparent that there can be differences in abundance estimates favouring either net depending on taxa. Therefore, the clear trend towards lower estimates obtained with the Bongo in the present study may in part be related to geographical area or species assemblage, and we suggest that this question be further investigated.

The differences in performance between the LHPR and Bongo nets detected in the present study are relevant for future studies on zooplankton ecology, improving the efficiency of the sampling programmes.

ACKNOWLEDGEMENTS

REFERENCES

Ahlstrom, E. H. (1948) A record of pilchard eggs and larvae collected during surveys made in 1939 and 1941. *Special Scientific Report*, United States Fish and Wildlife Service Fisheries, pp. 54–76.

Barnett, V. (1991) *Sample Survey Principles and Methods*. Edward Arnold, London.

Batten, S. D., Hirst, A. G., Hunter, J., *et al.* (1999) Mesozooplankton biomass in the Celtic Sea: a first approach to comparing and combining CPR and LHPR data. *J. Mar. Biol. Assoc. UK*, **79**, 179–181.

Clarke, M. R. (1969) A new midwater trawl for sampling discrete depth horizons. *J. Mar. Biol. Assoc. UK*, **49**, 945–960.

Cohen, J. H. and Forward, R. B. (2005) Diel vertical migration of the marine copepod *Calanopia americana*. II. Proximate role of exogenous light cues and endogenous rhythms. *Mar. Biol.*, **147**, 399–410.

Conway, D. V. P. and Williams, R. (1986) Seasonal population structure, vertical distribution and migration of the chaetognath *Sagitta elegans* in the Celtic Sea. *Mar. Biol.*, **93**, 377–387.

Conway, D. V. P., Coombs, S. H. and Smith, C. (1997) Vertical distribution of fish eggs and larvae in the Irish Sea and southern North Sea. *ICES J. Mar. Sci.*, **54**, 136–147.

Conway, D. V. P., Coombs, S. H. and Smith, C. (1998) Feeding of anchovy *Engraulis encrasicolus* larvae in the northwestern Adriatic Sea in response to changing hydrobiological conditions. *Mar. Ecol. Prog Ser.*, **175**, 35–49.

Dos Santos, A., Santos, A. M. P. and Conway, D. V. P. (2007) Horizontal and vertical distribution of cirripede cyprid larvae in an upwelling system off the Portuguese coast. *Mar. Ecol. Prog Ser.*, **329**, 145–155.

Fleminger, A. and Clutter, R. I. (1965) Avoidance of towed nets by zooplankton. *Limnol. Oceanogr.*, **10**, 96–104.

Frost, B. W. (1974) *Calanus marshallae*, a new species of Calanoid Copepod closely allied to the sibling species *C. finmarchicus* and *C. glacialis*. *Mar. Biol.*, **26**, 77–99.

Halliday, N. C., Coombs, S. H. and Smith, C. (2001) A comparison of LHPR and OPC data from vertical distribution sampling of zooplankton in a Norwegian fjord. *Sarsia*, **86**, 87–99.

Hardy, A. C. (1935) The Continuous Plankton Recorder. A new method of survey. Rapports et Proces-Verbaux des Reunions. *Journal du Conseil Permanent International pour l' Exploration de la Mer*, **95**, 35–47.

Harris, R. P., Wiebe, P. H., Lenz, J., *et al.* (eds) (2000) *ICES Zooplankton Methodology Manual*. Academic Press, USA.

Herman, A. W. (1992) Design and calibration of a new optical plankton counter capable of sizing small zooplankton. *Deep-Sea Res.*, **39**, 395–415.

John, E. H., Batten, S. D., Harris, R. P. and Hays, G. C. (2001) Comparison between zooplankton data collected by the Continuous Plankton Recorder survey in the English Channel and by WP-2 nets at station L4, Plymouth (UK). *J. Sea Res.*, **46**, 223–232.

Kloppmann, M. (1990) The sampling efficiency of a horizontally towed Bé Multiple-Opening–Closing net. ICES C.M. 1990/ L:97.

Longhurst, A. R., Reith, A. D., Bower, R. E., *et al.* (1966) A new system for the collection of multiple serial plankton samples. *Deep-Sea Res.*, **13**, 213–222.

McGowan, J. A. and Brown, D. M. (1966) A new opening-closed paired zooplankton net. *Scripps Institute of Oceanography*, University of Calfornia, Ref 66-23, pp.1–56.

McGowan, J. A. and Fraundorf, V. J. (1966) The relationship between size of net used and estimates of zooplankton diversity. *Limnol. Oceanogr.*, **11**, 456–469.

Mileikovsky, S. A. (1973) Speed of active movement of pelagic larvae of marine bottom invertebrates and their ability to regulate their vertical position. *Mar. Biol.*, **23**, 11–17.

Nichols, J. H. and 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. and Smith, P. E. (1995) A comparison of zooplankton sampling methods in the CalCOFI time series. *California Cooperative Oceanic Fisheries Investigations Reports*, **36**, 153–158.

Pearcy, W. G, Greenlaw, C. F. and Pommeranz, T. (1983) Assessment of euphausiids with five nets and a 120-kHz echosounder in fjords of northern Norway. *Biol. Oceanogr.*, **2**, 151–177.

Richardson, A. J., John, E. H., Irigoien, X., *et al.* (2004) How well does the Continuous Plankton Recorder (CPR) sample zooplankton? A comparison with the Longhurst Hardy Plankton Recorder (LHPR) in the northeast Atlantic. *Deep-Sea Res. Pt I*, **51**, 1238–1294.

Tranter, D. J. and Smith, P. E. (1968) Filtration performance. In Tranter, D. J. (ed.), *Zooplankton Sampling*. UNESCO Monographs on Oceanographic Methodology, pp. 27—56.

UNESCO. (1968) *Zooplankton Sampling*, Tranter, D. J. (ed.), UNESCO Monographs on Oceanographic Methodology, Paris.

Vannucci, M. (1968) Loss of organisms through the meshes. In Tranter, D. J. (ed.), *Zooplankton Sampling*. UNESCO Monographs on Oceanographic Methodology, pp. 77–86.

Ward, P., Atkinson, A., Murray, A. W. A., *et al.* (1995) The summer zooplankton community at South Georgia: biomass, vertical migration and grazing. *Polar Biol.*, **15**, 195–208.

Ward, P., Shreeve, R. and Tarling, G. A. (2006) The autumn mesozooplankton community at South Georgia: biomass, population structure and vertical distribution. *Polar Biol.* DOI 10.1007/s00300-006-0136-3.

Webster, I. and Anderson, J. T. (1987) A model for simulating the towing performance of the Bongo sampler. *Deep-Sea Res.*, **34**, 1277–1291.

Wiebe, P. H. (1988) Functional regression equations for zooplankton displacement volume, wet weight, dry weight, and carbon: a correction. *Fish. Bull.*, **86**, 833–835.

Wiebe, P. H., Steven, B. and James, L. C. (1975) Relationships between zooplankton displacement volume, wet weight, dry weight, and carbon. *Fish. Bull.*, **73**, 777–786.

Wiebe, P. H., Burt, K. H., Boyd, S. H., *et al.* (1976) A multiple opening/closing net and environmental sensing system for sampling zooplankton. *J. Mar. Res.*, **34**, 313–326.

Wiebe, P. H., Boyd, S. H., Davis, B. M., *et al.* (1982) Avoidance of towed nets by the euphausiid *Nematoscelis megalops*. *Fish. Bull.*, **80**, 75–91.

Williams, R. N., Collins, R. and Conway, D. V. P. (1983) The double LHPR system, a high speed micro- and macroplankton sampler. *Deep-Sea Res. Pt I*, **30**, 331–342.

Young, C. N. (1995) Behaviour and locomotion during the dispersal phase of larval life. In McEdward (ed.), *Ecology of Marine Invertebrate Larvae*. Boca Raton, CRC Press, pp. 249–277.

Zar, J. H. (1984) *Biostatistical Analysis*. Prentice-Hall Inc., Englewood Cliffs, New Jersey.