

Field calibration of the Optical Plankton Counter with respect to *Calanus finmarchicus*

MICHAEL R. HEATH,^{1*} JOHN DUNN,¹ JOHN G. FRASER,^{1,2} STEPHEN J. HAY¹ AND HEATHER MADDEN^{1,2}

¹FRS Marine Laboratory, PO Box 101, Victoria Road, Aberdeen, UK

²Department of Zoology, University of Aberdeen, Tillydrone Avenue, Aberdeen, UK

ABSTRACT

Zooplankton in the Faroe–Shetland Channel and north-western North Sea were sampled concurrently with a profiling serial net system and an Optical Plankton Counter (OPC) during January and March 1995. *Calanus finmarchicus*, together with a small proportion of *Calanus helgolandicus* (< 3% overall), made up > 75% of the zooplankton in the region, with *C. finmarchicus* being predominant below 500 m depth. Sensitivity analysis of the OPC data was carried out to determine the particle size range providing the highest correlation between the concentrations of stage CIV–CV and stage CVI *C. finmarchicus* estimated from net catches, and particle concentrations from the OPC. Significant correlations were obtained for particle size ranges that corresponded closely with microscopic measurements of the dimensions of copepodites. The highest correlations were obtained for stages CIV–CV in January.

According to the net sampling, the concentration of *C. finmarchicus* in January varied by at least four orders of magnitude over the survey region (< 0.05 to > 500 m⁻³), although only 4% of the samples contained > 100 m⁻³. When *C. finmarchicus* was present at concentrations of around 120 m⁻³, similar estimates of its abundance were obtained from the OPC data as from the net samples. At lower concentrations, the OPC increasingly overestimated the net catches, and the overestimate reached 40:1 at the detection limit of the nets (0.05 m⁻³). The average overestimate, taking into account the distribution of concentrations, was 2.5:1. This over-estimate could not be wholly accounted for by the occurrence of other zooplankton

species or potential errors associated with the OPC or net system, and the conclusion was that it arose mainly from the detection of detrital aggregates by the OPC. Thus, the OPC was effective at resolving the peak concentrations (> 100 m⁻³) of *C. finmarchicus* in the survey region, but was less effective at delineating the marginal areas of the distribution where *C. finmarchicus* was outnumbered by other similarly sized particles. Nevertheless, the results indicated that, with the application of calibration data such as described here, the OPC is a valuable tool for broad scale surveys of the spatial distribution of *C. finmarchicus* during the winter, when the animals are concentrated at depths > 500 m in areas such as the Faroe–Shetland Channel.

Key words: *Calanus finmarchicus*, Faroe–Shetland Channel, instruments, OPC, plankton net, zooplankton

INTRODUCTION

Fine mesh nets have been used for a long time for collecting samples in order to estimate the abundance of plankton organisms (Fraser, 1968). However, the labour costs of generating quantitative data from the samples is high, and increase rapidly as the requirements for taxonomic resolution become more demanding. In addition, the spatial resolution of sampling that can be achieved with net systems is generally low in relation to the variability in abundance and composition of plankton. There are numerous other problems associated with net sampling, such as progressive degradation of filtration efficiency by clogging of meshes. For these reasons there have been several attempts at developing sensor systems for enumerating and identifying organisms *in situ*. These have ranged from simple particle counting devices based on acoustic, conductivity or optical principles, to sophisticated acoustic or optical imaging systems with the potential for near real-time identification of organisms using modern digital processing technology (Herman and Mitchell, 1981; Davis *et al.*, 1992, 1996; Herman, 1992; Sprules *et al.*, 1992; Lenz *et al.*, 1995; Wiebe *et al.*, 1997). The Optical Plankton Counter (OPC, Focal Technologies Inc., Canada; Herman, 1992) is a relatively cheap intermediate technology that is now in relatively widespread usage (e.g. Sameoto and Herman, 1990; Heath, 1995; Huntley *et al.*, 1995; Stockwell and Sprules, 1995;

*Correspondence. E-mail: heathmr@marlab.ac.uk

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Checkley *et al.*, 1997; Osgood and Checkley, 1997; Wieland *et al.*, 1997; Gallienne and Robins, 1998). The OPC system counts and estimates the size of individual particles passing through a light beam. However, the limitations of the system are that (a) the sensor cannot discriminate between living organisms and detritus in the same size range, and (b) the size of each particle as measured by the sensor is difficult to relate to the dimensions of plankton organisms that can be measured under a microscope.

The OPC is produced in two versions, one to operate in the laboratory on net-caught samples or as an in-line flow through device, and another to operate *in situ* as a towed device. Details of the design have been thoroughly described by Herman (1992). Briefly, the *in situ* version may be towed at up to 6 m s^{-1} , the water passing through a $2 \text{ cm} \times 22 \text{ cm}$ cross-section tunnel. A collimated $2 \text{ cm} \times 0.4 \text{ cm}$ light beam is orientated across the tunnel and the projected cross-section area of individual particles interrupting the beam is measured by a photodiode array, digitized, and transmitted to a logging system. A calibration relationship is used to convert the digitized shadow area of each particle to Equivalent Spherical Diameter (ESD), this being the diameter of a sphere with a cross-sectional area equal to that of the measured particle. In the laboratory version, water is pumped through an in-line flow chamber and the path length of the light beam is shorter (2 cm) than in the towed version.

Comparisons between the particle size spectra generated by the OPC and microscopically measured size distributions of the material passing through it, indicate that the system is capable of generating reliable data (Herman, 1992; Wieland *et al.*, 1997; Sprules *et al.*, 1998). However, most such comparisons have been performed in the laboratory rather than *in situ*, due to the difficulty of quantitatively collecting the material passing through the towed instrument. As a consequence, it has been difficult to judge the extent of contamination of *in situ* particle counts by nonliving material, since many of these may be fragile detrital aggregates easily destroyed by nets or other collection systems. Under some circumstances, e.g. following the spring plankton bloom in continental shelf waters, detrital aggregates or 'marine snow' may be the most abundant particles in the water (e.g. Davis *et al.*, 1996; Gorsky *et al.*, 1992).

The present paper reports on the use of a towed *in situ* OPC in a situation where the zooplankton community was dominated by *C. finmarchicus*. The OPC was deployed in conjunction with a concurrently operated net system that resulted in the collection of > 1600 individual plankton samples from two cruises, each with comparative OPC data. These conditions provided a valuable opportunity to evaluate the potential of the

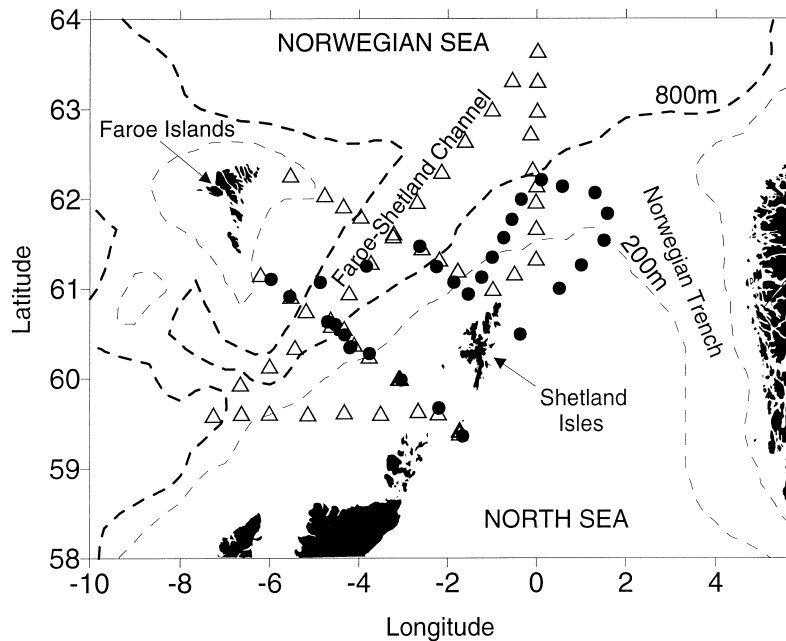
OPC as a rapid survey tool for this particular species, and to derive intercalibration relationships between OPC data and plankton net catches.

MATERIALS AND METHODS

A towed system referred to as ARIES (Dunn *et al.*, 1993) was used to collect data and samples during two cruises in the Faroe-Shetland Channel and NW Scottish shelf by RV DANA (January and March 1995, Fig. 1). ARIES comprised a serial plankton collecting net similar in general concept to the Longhurst-Hardy Plankton Recorder (LHPR; Longhurst *et al.*, 1966), a water sampling rosette, a Mark II *in situ* OPC (Focal Technologies Inc., Canada), and a CTD system. The complete sampling package included a submersible data logging system with an integral pressure sensor and input of data from a flowmeter in the plankton collecting net. Data on the depth of the vehicle, flow in the plankton net and status of the sampling systems were stored every 1 s during each deployment. On recovery of the system, the data were downloaded over a serial line to a computer for merging with navigational data and further analysis. In the surveys described here, the ARIES net system was configured to sequentially collect samples from a 200- μm mesh, 30-cm mouth diameter collecting net at 120-s time intervals during each deployment. The system was towed at $1.5\text{--}2.0 \text{ m s}^{-1}$ (3–4 kn) and the descent and ascent rates were controlled at around 30 cm s^{-1} by adjusting the wire deployment rate. Thus, each net sample represented an integral over $10\text{--}15 \text{ m}^3$ of water from a 40-m depth interval, and around 50 such samples were collected on a typical deployment to the maximum depth of 1000 m.

The *in situ* OPC was mounted on the vehicle in an area of clear water flow alongside the mouth of the net. The instrument had been modified for self-recording, battery powered operation and a submersible logging unit integrated the data on individual particles over user specified size and time intervals. The data were stored in memory and downloaded over a serial link to a computer after recovery of the system. During the cruises described here, particles in the range $100\text{--}5540 \mu\text{m}$ ESD were integrated over 128 size 'bins' and 60-s time intervals. Between 0.25 and 0.5 m^3 of water passed through the OPC during each integration interval, and each net sample collected by ARIES corresponded to two successive OPC integration periods. The size bins were of equal width in terms of digitized shadow area, but the relationship between digitized area and ESD was non-linear, so one of the first tasks in processing the data was to redistribute the logged data across 'classes' of equal

Figure 1. Chart showing locations where comparative OPC and net samples were collected. \triangle , January 1995; \bullet , March 1995.



width in terms of ESD. This resulted in the 128 bins used to record the data being transformed into 136 classes each of 40- μm ESD width. The lower limit of the first class was 100 μm , although the nonlinearity of the calibration and the minimum size detection setting resulted in loss of size resolution for particles smaller than 500 μm ESD.

The submersible data logging unit also incorporated data inputs at 1-s intervals from the pressure sensor and flowmeter. The flowmeter was situated alongside the OPC, and orientated into the water flow. The time and pressure at the start and end of each 60-s integration period were logged together with the particle count data. At the end of each integration period the arithmetic mean pressure and flowmeter revolution rate were also stored. The volume of water passing through the OPC was then the product of the tunnel cross-section area, the flow rate, the duration of the integration period, and a term for flow resistance in the OPC tunnel as specified in the manufacturer's literature.

Individual samples of plankton from the ARIES net were preserved at sea in 4% formaldehyde solution and returned to the laboratory for microscopic analysis. All organisms in the samples were enumerated but detailed taxonomic discrimination was restricted to *Calanus* species. *Calanus finmarchicus* and *C. helgolandicus* occur together in the survey area and are of similar size and morphology in copepodite stages CI–CV. Hence, these two species were identified to stage (CI–CVI), but discriminated from each other only for female stage CVI

specimens, where the distinguishing features are most easily observed. *Calanus hyperboreus* was also identified to development stage for copepodite CI–CVI. *Calanus tenuicornis* was differentiated into only three stage categories (male and female stage CVI and all other stages combined). Other zooplankton were identified to genus only, or other general groupings (Table 1). Numbers in analysis categories were subsequently expressed in terms of concentration (m^{-3}) by reference to the flowmeter data logged by the ARIES system.

The particle concentrations (number m^{-3}) in each pair of OPC integration periods corresponding to the net samples were first averaged and then the concentrations in each of the 40- μm ESD classes integrated over various coarser size ranges defined according to a matrix of the mid-size and span of the range (Table 2). Instances of OPC counts with zero corresponding catch of *C. finmarchicus* and *C. helgolandicus* were then discarded, and the remaining data log-transformed. Finally, the coefficient of correlation between particle concentration and the corresponding *C. finmarchicus* and *C. helgolandicus* concentration was calculated for each combination of mid-size and span, and with various selections of the data according to depth criteria.

RESULTS

A total of 1666 plankton samples from the two cruises were analysed, each having comparative *in situ* OPC

Table 1. Categories applied to the analysis of zooplankton samples collected by the ARIES net system. Samples from the cruise in March 1995 were analysed for all categories, but for the samples collected in January 1995, *Metridia* spp., *Oithona* spp., *Paraeuchaeta* spp. and *Rhincalanus* spp. were not discriminated and were included in the small copepod category

Copepoda	Other crustacea	Noncrustacean invertebrate	Vertebrate
Small copepods	Cirripede nauplii	Chaetognatha	Teleost eggs
<i>C. fin/hel</i> CI	Cirripede cyprids	<i>Clione</i> spp.	Teleost larvae
<i>C. fin/hel</i> CII	Decapoda	Coelenterata	
<i>C. fin/hel</i> CIII	Euphausea	Cumacea	
<i>C. fin/hel</i> CIV	Isopoda	Gastropoda	
<i>C. fin/hel</i> CV	Mysidacea	Lamellibranch	
<i>C. fin/hel</i> CVI male	<i>Parathemisto</i> spp.	Mollusca	
<i>C. finmarchicus</i> CVI female		Ophiuroidea	
<i>C. helgolandicus</i> CVI female		Polychaeta	
<i>C. hyperboreus</i> CI		<i>Tomopteris</i> spp.	
<i>C. hyperboreus</i> CII		Salpa	
<i>C. hyperboreus</i> CIII			
<i>C. hyperboreus</i> CIV			
<i>C. hyperboreus</i> CV			
<i>C. hyperboreus</i> CVI male			
<i>C. hyperboreus</i> CVI female			
<i>C. tenuicornis</i> CI–CV female			
<i>C. tenuicornis</i> CVI male			
<i>C. tenuicornis</i> CVI female			
<i>Metridia</i> spp.			
<i>Oithona</i> spp.			
<i>Paraeuchaeta</i> spp.			
<i>Rhincalanus</i> spp. CI–CV			
<i>Rhincalanus</i> spp. CVI female			

Table 2. Matrix of combinations of the mid-size and span of particle ESD (μm) ranges used to aggregate OPC data for comparison with concentrations of *C. finmarchicus* stages from ARIES net samples. Span refers to the difference between the maximum and minimum particle ESD in a given range, whilst the mid-size was the mid-point between the maximum and minimum. Crosses indicate combinations used for comparison with concentrations of both stage CV and stage CVI copepodites, whilst combinations indicated by circles were used for comparison with data on stage CVI copepodites only

Span (μm)	Mid-size (μm)						
	860	1060	1260	1460	1660	1860	2060
400	×		×		×		○
600		×		×		○	
800	×		×		×		○
1000		×		×		○	
1200	×		×		×		○

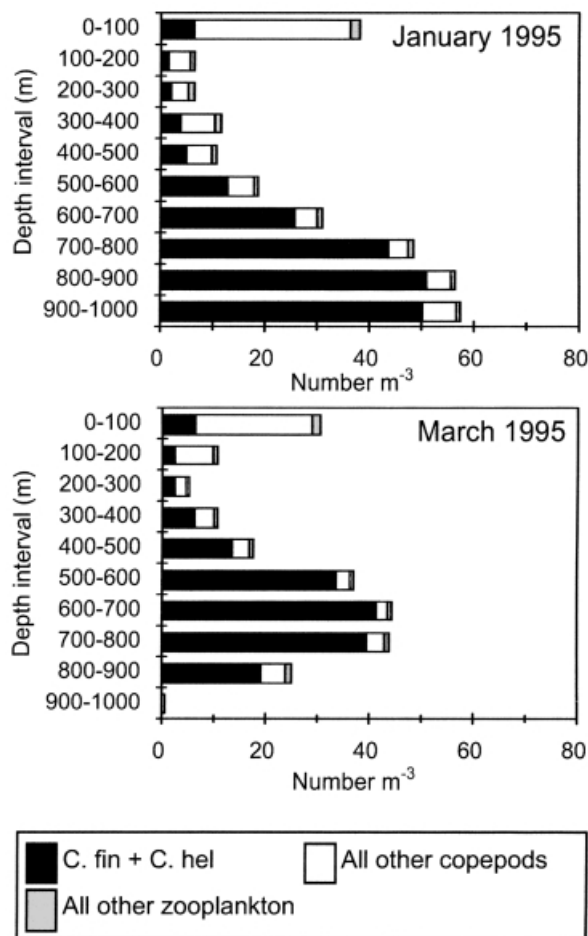
data (Table 3). Copepods dominated the numbers of zooplankton organisms caught by the nets in both January (97.6%) and March (96.7%). Of the copepods, *C. finmarchicus* and *C. helgolandicus* were the dominant species (61.7% of copepods in January, 46.5% in March). However, the contribution of *C. finmarchicus* and *C. helgolandicus* to the total copepod population varied systematically with depth, being greatest below 500 m (85% in January, 91% in March), and decreasing

towards the surface where the small copepod category was the most important group (Fig. 2). The small copepod category was composed largely of *Acartia* spp., *Pseudocalanus* spp., *Temora* spp. and *Oithona* spp.

The distribution of *C. finmarchicus* and *C. helgolandicus* stages with respect to depth and hydrographic features, and the relative abundances of the two species, have been described elsewhere (Heath and Jónasdóttir, 1999; Heath, 1999; Madden *et al.*, 1999). Briefly, stage

Table 3. Numbers of valid ARIES plankton samples and OPC integration periods available from each cruise

Cruise	ARIES deployments	Plankton samples collected	Plankton samples analysed	OPC integrations
January 1995	52	1184	1020	2593
March 1995	30	665	646	1231

Figure 2. Mean concentration (m^{-3}) of *C. finmarchicus* plus *C. helgolandicus* (*C. fin* + *C. hel*), other copepod species, and other zooplankton (not copepods) in 100 m depth intervals from net samples. (a) January 1995; (b) March 1995.

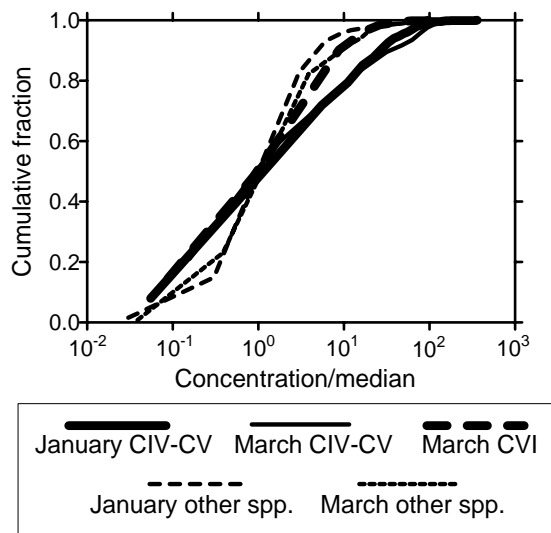
CIV to CVI copepodites accounted for > 99% of the population in both January and March. In both months, stage V made the up the largest component (88% in January, 66% in March). Stage CVI animals contributed < 2% in January, which increased to 13% by March as the population emerged from overwintering. *Calanus finmarchicus* and *C. helgolandicus* were not discriminated for CI–CV copepodite stages. However, of the CVI females sampled in January, *C. finmarchicus* constituted > 99% of the combined *C. finmarchicus*

plus *C. helgolandicus* population at depths below 500 m, 87% in the 200–500 m layer and 54% in the upper 200 m. In March, *C. finmarchicus* constituted > 96% of the female CVI population throughout the water column. Taking into account the vertical distribution of stage CIV–CVI *C. finmarchicus* plus *C. helgolandicus* (Fig. 2; January, 93% in the 500–100 m layer, 3% in the 200–500 m layer, 4% in the upper 200 m; March, 87% in the 500–100 m layer, 9% in the 200–500 m layer, 4% in the upper 200 m), and applying the species proportions found for female CVI specimens, the estimated contribution of *C. finmarchicus* to the combined abundance of both species in the survey region was 97% in January, and 99% in March. Thus, most of animals identified as *C. finmarchicus*/*C. helgolandicus* were in fact *C. finmarchicus*, and for the remainder of this paper the combined group is referred to as *C. finmarchicus* alone.

The distributions of individual sample estimates of *C. finmarchicus* concentration from each survey were highly positively skewed. The data were adequately described by either an exponential or a log-normal distribution (Fig. 3). The detection limit of the net sampling ($0.05 \text{ individuals m}^{-3}$) in relation to the median value was such that it was not possible to discriminate between the two types. The proportions of samples below the detection limit (recorded as zero concentration) were 5.2% for CIV–CV in January, 13.9% for CIV–CV in March, and 12.7% for CVI in March. The relative variance in CIV–CV concentrations remained constant between January and March, but concentrations of CVI in March were slightly less variable (Fig. 3). The other copepod species (as a combined group) were clearly log-normally distributed, with higher median concentrations and less variability than *C. finmarchicus*. The lower variability was primarily reflected in a more uniform distribution of the other copepod category with respect to depth.

Considering only net samples from deeper than 500 m where *C. finmarchicus* was numerically dominant in the plankton, the correlation between log-transformed particle concentrations as measured by the OPC and the log-transformed concentrations of stage CIV–CV *C. finmarchicus* copepodites, was strongly dependent on the mid-size of the range used to integrate particle counts, and to a lesser extent on the span of the range

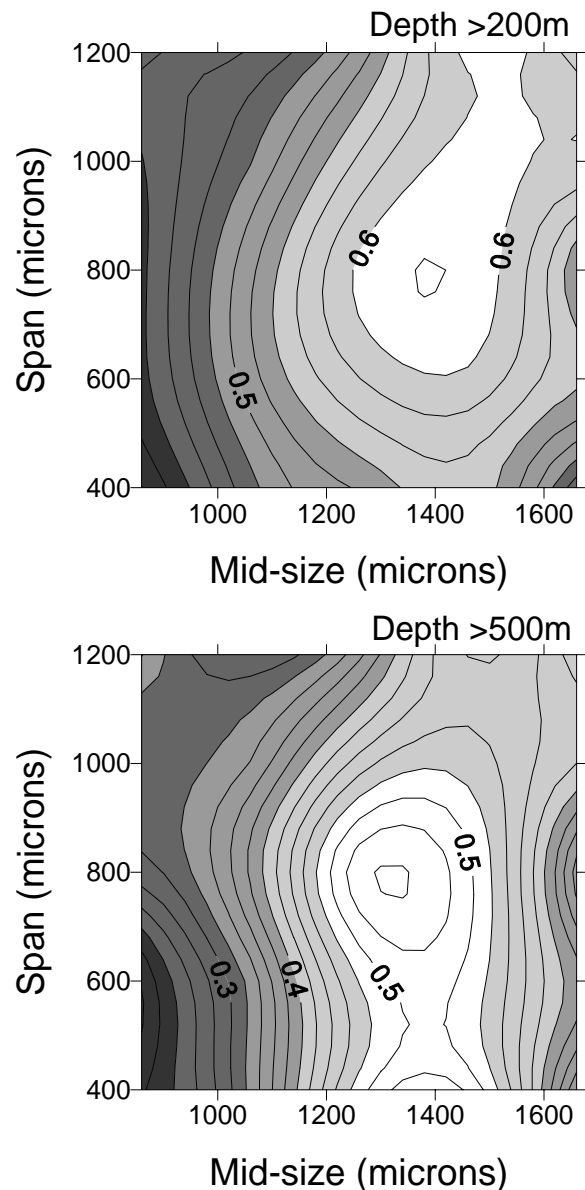
Figure 3. Cumulative frequency distributions of *C. finmarchicus* copepodite stages, and other copepod species, with respect to individual net sample estimates of concentration (m^{-3}). Concentration estimates have been normalized to the median for each category. Median values were: January, CIV–CV, 1.82 m^{-3} ; March, CIV–CV, 0.636 m^{-3} ; March, CVI, 0.569 m^{-3} ; January, other species, 3.30 m^{-3} ; March, other species, 2.58 m^{-3} .



(Figs 4 and 5). The peak correlation corresponded to combinations of mid-size and span of $1300 \mu\text{m}$ and $800 \mu\text{m}$, respectively, in January 1995 (i.e. a range of $900 \mu\text{m}$ to $1700 \mu\text{m}$). In March 1995 the peak correlation with CIV–CV occurred at a mid-size and span of $1380 \mu\text{m}$ and $720 \mu\text{m}$ (range $1020 \mu\text{m}$ to $1740 \mu\text{m}$). In comparison, the highest correlation with the concentration of stage CVI animals in the net samples from the March survey was obtained with mid-size and span of $1520 \mu\text{m}$ and $600 \mu\text{m}$ (i.e. range $1220 \mu\text{m}$ to $1820 \mu\text{m}$; Fig. 6). In all cases, the correlations were significant ($P < 0.01$; Table 4), although the relationship with CVI animals was weaker than for CIV–CV. The mid-sizes associated with maximum correlations agreed well with measurements of *C. finmarchicus* cephalothorax volume on preserved specimens collected during the cruises (S.H. Jónasdóttir, Danish Institute for Fisheries Research, unpublished data) and with reported results of bench tests on OPC systems using preserved specimens (Herman, 1992; Wieland *et al.*, 1997).

Using the optimum ESD ranges for integrating OPC data obtained from analysis of samples collected below 500 m depth (Table 4), the relationships between copepodite and particle concentrations were deter-

Figure 4. Sensitivity of the correlation (r^2) between *C. finmarchicus* stages CIV–CV concentration (m^{-3}) estimated from net samples and corresponding particle concentrations (m^{-3}) from the OPC in January 1995, to the mid-size (μm) and span (μm) of the size range used to integrate the OPC data. (a) All samples from depths $> 200 \text{ m}$; (b) all samples from depths $> 500 \text{ m}$.



mined for the $200\text{--}500 \text{ m}$ and $0\text{--}200 \text{ m}$ depth intervals in each survey. The results (Fig. 7; Table 5) showed that in each case the relationships became weaker with decreasing depth, and explained $< 10\%$ of the variance in the $0\text{--}200 \text{ m}$ depth layer. Combining the data from $200\text{--}500 \text{ m}$ and $500\text{--}1000 \text{ m}$ depth intervals into a

Figure 5. Sensitivity of the correlation (r^2) between *C. finmarchicus* stages CIV–CV concentration (m^{-3}) estimated from net samples and corresponding particle concentrations (m^{-3}) from the OPC in March 1995, to the mid-size (μm) and span (μm) of the size range used to integrate the OPC data. (a) All samples from depths > 200 m; (b) all samples from depths > 500 m.

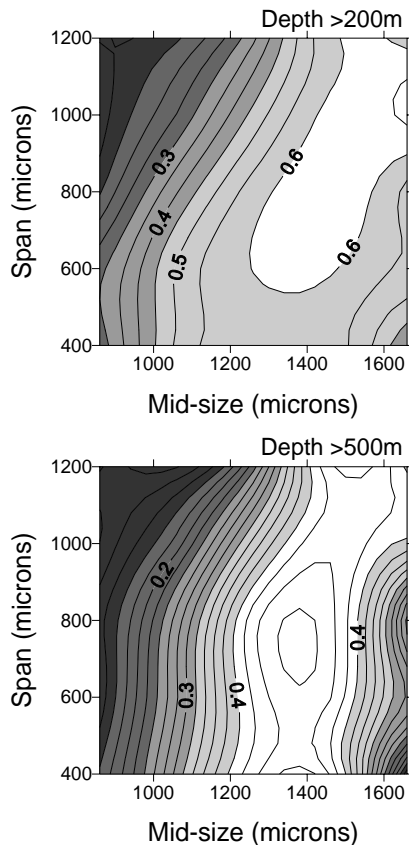
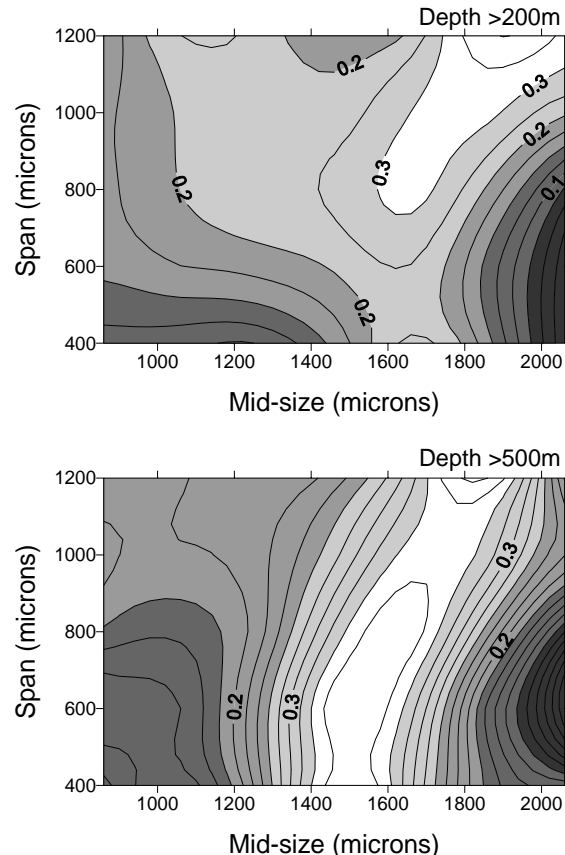


Figure 6. Sensitivity of the correlation (r^2) between *C. finmarchicus* stage CVI concentration (m^{-3}) estimated from net samples and corresponding particle concentrations (m^{-3}) from the OPC in March 1995, to the mid-size (μm) and span (μm) of the size range used to integrate the OPC data. (a) All samples from depths > 200 m; (b) all samples from depths > 500 m.



single analysis, resulted in increases in the correlation with CIV–CV concentrations from the January and March surveys, but a decrease in correlation with CVI concentrations in March (Table 6). The maximum correlations between OPC data and net samples from 200 to 1000 m were obtained with ESD ranges that were close or identical to those based on samples collected from > 500 m.

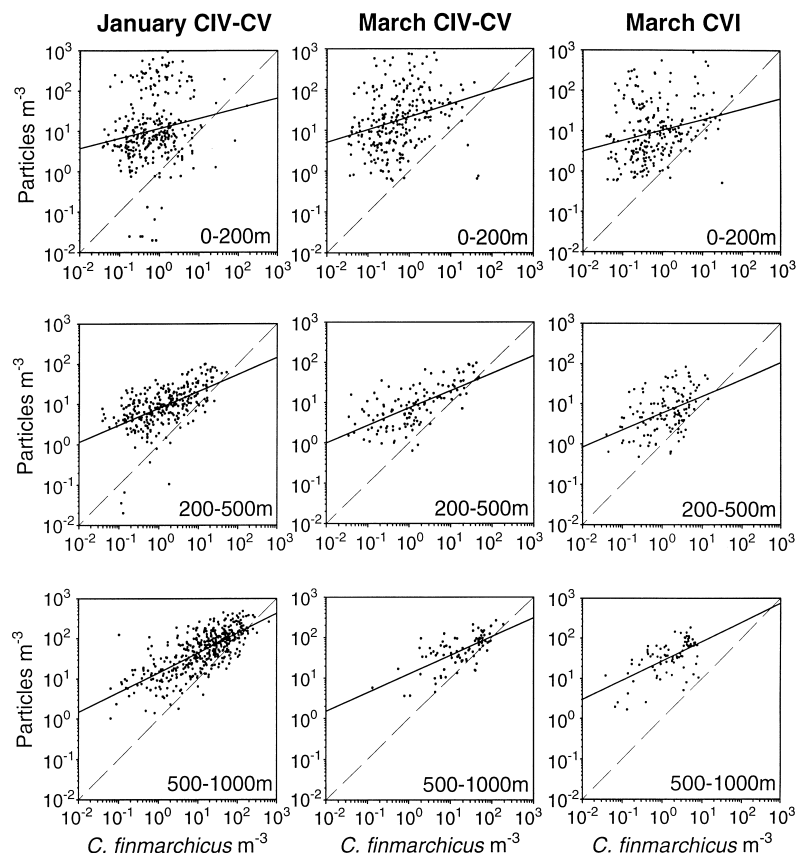
Considering the results from the net samples, the concentrations of particles in the ESD ranges corresponding to *C. finmarchicus* in each month were approximately log-normally distributed (Fig. 8). However, the median concentration estimated by the OPC was higher than that from the nets (by a factor of 10), and the variance was lower. The over-estimate of concentration by the OPC relative to nets was not uniform across the concentration range. The regression relationships ob-

tained for all samples > 200 m indicated that at the detection limit of the nets (0.05 m^{-3}) the OPC over-estimated *C. finmarchicus* concentration by a factor of 40.1, i.e. $\text{OPC}/\text{net} = 40.1$. This factor decreased with increasing concentration such that at a net concentration of 1 m^{-3} the OPC over-estimated by an average factor of 9.6, at a net concentration of 10 m^{-3} by a factor of 3.3, and at a net concentration of 100 m^{-3} by a factor of 1.1. Concentration estimates from the nets equalled those from the OPC at around 120 m^{-3} , and the OPC provided underestimates compared with the nets at higher concentrations. Net samples containing $> 100 \text{ m}^{-3}$ *C. finmarchicus* constituted only a small proportion of the total (January CIV–CV, 4% $> 100 \text{ m}^{-3}$, 5% $> 90 \text{ m}^{-3}$; March CIV–CV, 1% $> 100 \text{ m}^{-3}$, 5% $> 50 \text{ m}^{-3}$; March CVI, 0% $> 100 \text{ m}^{-3}$, 5% $> 10 \text{ m}^{-3}$). Taking into account the skewed distribution of individual sample

Table 4. ESD intervals for integration of OPC data resulting in maximum correlations with ARIES net catches of *C. finmarchicus* from depths in the range 500–1000 m in January and March 1995. The regression equation linking the concentration of particles (m^{-3}) in the given ESD range from the OPC with the concentration (m^{-3}) of *C. finmarchicus* stages from the net samples was of the form $\text{OPC} = A(\text{NET})^B$

Month	<i>C. finmarchicus</i> stage	ESD range (μm)	A	B	Number of samples	Max. r^2
January	CIV–CV	900–1700	14.203	0.492	437	0.534
March	CIV–CV	1020–1740	12.592	0.461	87	0.453
March	CVI	1220–1820	27.126	0.480	83	0.368

Figure 7. Relationships between the concentration of *C. finmarchicus* stages (m^{-3}) estimated from net samples, and corresponding particle concentration (m^{-3}) from the OPC, in different depth layers and surveys. OPC data were integrated over the particle size intervals given in Table 4. Top row, 0–200 m depth interval; middle row, 200–500 m depth interval; bottom row, 500–1000 m depth interval. Left column, stages CIV–CV in January 1995; middle column, stages CIV–CV in March 1995; right column, stage CVI in March 1995. Each dot represents one net sample and the corresponding OPC data. The dashed lines represent a 1:1 relationship between the net and OPC samples. The solid lines represent the regression relationships between the net and OPC data, parameters of which are given in Tables 4 and 5.



estimates over the surveys as a whole (Fig. 3), the regression relationships indicated that the OPC would overestimate the spatially integrated abundance of CIV–CV stages by factors of 2.3 and 2.5 in January and March, respectively. However, the results indicated that the integrated abundance of CVI in March from OPC data

would be overestimated by a factor of 11.1 compared with the value from net sampling.

In summary, the analysis identified the size intervals of particles detected by the OPC that corresponded most closely to development stages of *C. finmarchicus*. In general, the OPC overestimated the concentration

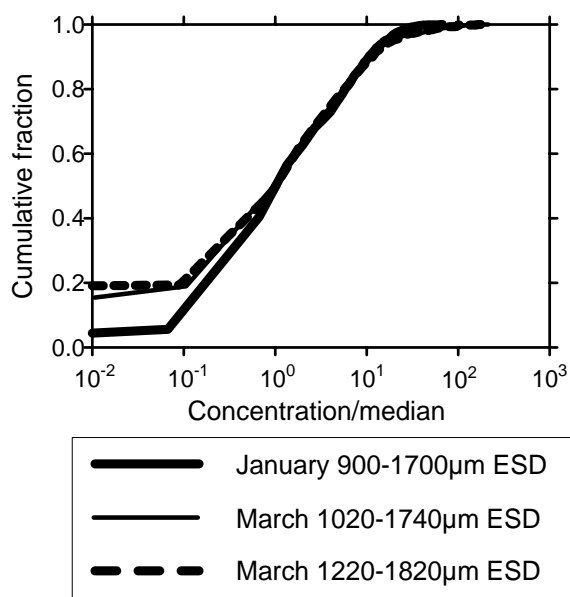
Table 5. Regression relationships between particle concentrations from the OPC and corresponding ARIES net catches of *C. finmarchicus* in the depth range 0–200 m and 200–500 m. The ESD integration interval for the OPC data was that determined from analysis of samples from > 500 m depth (Table 4). The parameters A and B refer to the regression equation given with Table 4

Month	<i>C. finmarchicus</i> stage	Depth interval	A	B	Number of samples	r^2
January	CIV–CV	0–200 m	11.734	0.249	311	0.031
January	CIV–CV	200–500 m	7.988	0.421	283	0.312
March	CIV–CV	0–200 m	22.040	0.317	259	0.079
March	CIV–CV	200–500 m	7.392	0.434	124	0.440
March	CVI	0–200 m	10.437	0.261	250	0.066
March	CVI	200–500 m	5.849	0.419	129	0.192

Table 6. Correlation and regression results obtained from a comparison of particle concentrations from the OPC with corresponding ARIES net catches of *C. finmarchicus* from depths in the range 200–1000 m in January and March 1995. The ESD integration interval for the OPC data was that determined from analysis of samples from > 500 m depth. The parameters A and B refer to the regression equation given in Table 4. For comparison, the last two columns show the maximum attainable correlation with net samples from > 200 m and the corresponding ESD range for integration of OPC data

Month	<i>C. finmarchicus</i> stage	A	B	Number of samples	r^2	Max. r^2	ESD range at max. r^2
January	CIV–CV	10.101	0.556	720	0.604	0.621	980–1780
March	CIV–CV	8.381	0.529	211	0.633	0.633	1020–1740
March	CVI	10.544	0.495	212	0.203	0.261	1240–2080

Figure 8. Cumulative frequency distributions of OPC size categories, with respect to individual sample estimates of concentration (m^{-3}). Concentration estimates have been normalized to the median for each category. Median values were: January 900–1700 μm (corresponding to CIV–CV), 14.94 m^{-3} ; March 1020–1740 μm (corresponding to CIV–CV), 9.46 m^{-3} ; March 1220–1820 μm (corresponding to CVI), 5.54 m^{-3} .



of animals compared with net catches. The overestimate was proportionately greatest at low concentrations and approached 1:1 at around 120 m^{-3} . Thus, the OPC was effective at resolving the peak concentrations ($> 100 \text{ m}^{-3}$) of *C. finmarchicus* in the survey region, but was less effective at delineating the marginal areas of the distribution where *C. finmarchicus* was outnumbered by other particles.

DISCUSSION

In this paper the effectiveness of the OPC as a means of estimating the concentration of *Calanus* species was compared with that of a plankton net. However, there are numerous problems associated with quantitative sampling of plankton with towed nets (Longhurst and Williams, 1976), and they should not be automatically regarded as the standard against which to judge other systems. Avoidance of the mouth opening of the net is a well known phenomenon (Clutter and Anraku, 1968; Barkley, 1972), but this may well be at least as great a problem for the OPC. In this case, the evidence from other sampling during the cruises was that a high proportion of the *C. finmarchicus* were in a diapause state and incapable of avoidance reactions (Ingvarsdóttir *et al.*, 1999). Extrusion of specimens through the meshes of the net is a recognized problem, but should not occur with *C. finmarchicus* or *C. helgolandicus*.

copepodites and 200- μm aperture mesh (Nichols and Thompson, 1991). Retention of organisms in the concentrating net of generic LHPR type systems leads to underestimation of abundance from analysis of cod-end material (Haury *et al.*, 1976). This was undoubtedly a feature of the ARIES system but, in a separate study, comparisons between the integral over all samples collected during individual ARIES deployments, and the total catch by a separate integrating net attached to the same towing frame, indicated a maximum discrepancy of around 10% (unpublished data), which is insufficient to account for the difference between the OPC and net catches described here. Estimation of the volume of water is one of the other main areas of uncertainty in net sampling (Harding and Arnold, 1971; Brander *et al.*, 1993). Errors arise from cross-correlation between filtering rate and the concentration of plankton during a tow, progressive clogging of meshes, and misalignment of the filtering net in relation to the towing axis. Cross-correlation effects were catered for in the ARIES system by the short integration period of the serial discrete samples within each tow. Mis-alignment of the net was checked by installing pitch and roll sensors on the system, which showed that the orientation varied by no more than $\pm 10^\circ$ within a tow, which represents $\pm 3\%$ uncertainty in the effective mouth area of the net. In addition, this error should apply equally to the OPC as both were mounted on the same vehicle. Clogging of the nets was catered for, as far as possible, by situating the flowmeter inside the mouth of the net so that reductions in filtering rate should be reflected in the data from the flowmeter. Finally, the pattern of the discrepancy between the net and OPC estimates of concentration was not consistent with a volume estimation error, which would be expected to result in a constant proportionality between the two. The results showed that the proportionality was inversely related to the concentrations estimated from net sampling, consistent with a constant background concentration effect in the OPC data.

Errors in concentration estimates from the OPC include coincidence quenching, and inaccuracies in measurement of the flow rate through the sampling tunnel. Coincidence errors occur when two or more particles pass through the detection beam of the OPC so close together that they cannot be resolved as separate objects. This phenomenon is primarily a function of particle concentration, towing speed, and instrument sensitivity. The maximum count rate by the OPC during the surveys was 40 particles s^{-1} (4500 m^{-3}), which is below the minimum level at which coincidence is considered to become significant (5000 m^{-3} ; Herman, 1992; Sprules *et al.*, 1992, 1998). Measuring

the volume of water passing through the OPC is also problematic due to the rectangular cross-section of the sampling tunnel. A Mark II OPC with a straight tunnel was used in this study, and flow resistance was assumed to be zero in accordance with the manufacturer's guidance. Sample volume was calculated from speed through the water measured outside the instrument. This approach provides a maximum estimate of the volume sampled and hence a minimum estimate of particle concentration. Thus, errors in estimation of the volume sampled cannot account for the discrepancy between the OPC and net data.

Even though *C. finmarchicus* was by far the most abundant component of the zooplankton over much of the survey region, especially below 500 m depth, other species clearly must have contributed to the particle counts from the OPC. Based on the composition of the net catches, the majority of such organisms would have been other copepods. As a group, the other copepod species were more uniformly distributed with respect to depth than *C. finmarchicus*, and could therefore be considered to represent a relatively constant background source of particles. However, their concentration seems too low to fully account for the difference between the OPC data and the net samples (January, median concentration of all other copepods 3.3 m^{-3} , mean 10.0 m^{-3} ; March, median 2.58 m^{-3} , mean 10.91 m^{-3}). In addition, the majority of these animals were much smaller than *C. finmarchicus*, and certainly would not be expected to appear in the size intervals that produced the highest correlation in the OPC data. The main species in the other copepod category that might be expected to overlap in size with *C. finmarchicus* were *Metridia* spp., but these constituted on average only 11% of the category. Hence, although other plankton besides *C. finmarchicus* would have contributed to the OPC results, they seem unlikely to be the sole source of discrepancy between the OPC data and the net sampling results.

The principal problem with the OPC is that it discriminates particles solely on the basis of size and does not distinguish between living organisms and detritus. Detrital aggregates in the water column should be registered by the OPC, but are typically very fragile and would be destroyed or degraded by any net system, and in any case are not easily analysed in net catches. Concentrations of such material can be significant in relation to zooplankton organisms. For example, Davis *et al.* (1996) recorded an average of > 1200 aggregate particles m^{-3} from analysis of *in situ* video recordings in the Georges Bank area, compared with concurrent measurements of around 200 *C. finmarchicus* m^{-3} . Only a proportion of these aggregates would have been in the

same size range as *C. finmarchicus*, but even so, it is clear that *in situ* particle counts would be expected to overestimate the concentration of zooplankton. Maximum concentrations of particles $> 500 \mu\text{m}$ ESD detected by the OPC during the surveys exceeded 4500 m^{-3} (median concentrations, 40 m^{-3} in January and 210 m^{-3} in March), whilst net catches suggested maxima of $650\text{--}700 \text{ m}^{-3}$ and medians of $7\text{--}8 \text{ m}^{-3}$ in both January and March. Superficially, these results seem in marked contrast to those, e.g. Gallienne and Robins (1998), who found a close to 1:1 relationship between total counts from an OPC and microscopic counts of zooplankton. However, their results were obtained using a laboratory flow through version of the OPC and any detrital aggregates would have already been destroyed by the centrifugal pump used to collect the seawater. Thus, there is circumstantial evidence that the discrepancies between *in situ* OPC counts and net catches described here are due to detection of detritus by the OPC. None of the other inherent uncertainties associated with plankton nets and the OPC seems able convincingly to account for the magnitude of these discrepancies.

The question remains as to whether the OPC is a useful tool for surveying the distribution and abundance of overwintering *C. finmarchicus*, compared with net systems. Nets clearly have deficiencies for quantitative sampling of plankton, but are the long-standing and routinely available standard. In this study, the OPC clearly performed well at resolving the general distribution of stage CIV–CV animals, especially in January. The high correlation between the data from net catches and those from the OPC, and the large variability in concentration over the survey area (four orders of magnitude) suggest that, in future surveys, the abundance of overwintering animals could reasonably be estimated using calibration relationships applied to OPC data, thereby reducing the requirement for analysis of plankton samples. However, the calibrations would clearly be survey specific and restricted to depths $> 200 \text{ m}$ in the Faroe–Shetland Channel, or in other areas where *C. finmarchicus* is abundant and dominates the zooplankton. The high incidence of detrital aggregates would seem to preclude the use of the OPC in this way in continental shelf waters. For stage CVI animals in March, the OPC seemed less useful since this development stage was present only at relatively low concentrations, and the size range overlapped to a large extent with the more abundant stages CIV–CV. With these restrictions, the OPC is a valuable addition to, but not a replacement for, net sampling, allowing estimation of the deep overwintering distribution and abundance of *C. finmarchicus*

within time scales that are impractical by analysis of net catches alone.

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