Comparing estimates of zooplankton abundance from CUFES samples with those from a vertical bongo net

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Abstract

The accuracy of using CUFES (continuous underway fish egg sampler) as an alternative method to vertical bongo nets for sampling zooplankton abundance and distribution is assessed. Analysis is based on 14 taxonomic groups representing a wide variety of organism sizes. Samples were collected in March 2004 in the southern Benguela, South Africa. In total, 64 CUFES samples were collected while the ship was underway and 32 CUFES and vertical bongo net on-station samples were collected along four inshore-offshore transects. The frequencies of obtaining the taxa using the CUFES and vertical bongo net samples were the same for small copepods, amphipod adults and juveniles, and *Nannocalanus*. Volumetric abundance estimates of nine taxonomic groups from on-station CUFES (ln no.m^{-3}) were significantly correlated with areal abundance estimates from vertical bongo net samples (ln no.m^{-2}). These groups were mostly small zooplankton and crustacean eggs, showing the usefulness of the CUFES for sampling small zooplankton. There were considerable differences between night and day catches, with higher correlations between catches obtained using the CUFES and vertical bongo nets at night than during the day for *Metridia* adults and juveniles, small copepods, *Cladocera*, *Oithona* and *Centropages* adults, suggesting that these taxa undergo diel vertical migration. Relative abundance plots indicate that small copepods were relatively the most abundant taxonomic group sampled by vertical bongo nets whereas crustacean eggs were relatively the most abundant taxonomic group sampled with the CUFES. There was no good evidence of improved precision by using underway CUFES sampling compared with on-station samples. Generally, there was a greater proportion of large zooplankton in vertical bongo net samples than in CUFES samples and the CUFES was found to be a good sampler of small zooplankton.

Introduction

The Benguela Current ecosystem lies off the west coast of southern Africa in the south-east Atlantic Ocean (14° to 37°S). It is one of the four major eastern boundary current regions of the world's ocean, along with the Canary Current system off the Iberian Peninsula and north-west Africa, the Humboldt Current system off western South America, and the California Current system off the western United States (Andrews and Hutchings 1980, Shannon 1985, Verheye *et al.* 1998). It is divided into northern and southern subsystems in the region of Lüderitz (26°S) where there is a permanent upwelling cell (Shannon 1985). The southern Benguela extends from Lüderitz to the Agulhas Bank (Gibbons 1999), and is affected by physical factors such as changes in bottom topography and longshore wind stress, which result in locally enhanced upwelling, producing longshore variations in water temperature, nutrient concentrations and planktonic biomass (Pitcher *et al.* 1992). Like other upwelling regions, the southern Benguela is dynamic, and a series of wind-driven upwelling events brings cool nutrient-rich subsurface water into the euphotic layer (Shannon and Pillar 1986, Probyn 1992). Newly upwelled waters are characterized by high nutrient concentrations and low chlorophyll concentrations (Brown 1984, Pitcher *et al.* 1992). Phytoplankton blooms subsequently develop, mainly dominated by diatoms and to a lesser extent by dinoflagellates, making the Benguela a highly productive system (Shannon and Pillar 1986, Pitcher *et al.* 1992). A large proportion of this production is consumed by zooplankton or reaches the sediments on the sea bed (Brown and Hutchings 1987).

The strength and intensity of coastal upwelling varies seasonally and annually, responding to changes in wind speed and direction (Hutchings *et al.* 1991). However in the southern Benguela wind-induced upwelling reaches a maximum during spring and summer (Shannon 1985). This results in tongues of productive water which are extremely variable in their extent and distribution. Although zooplankton organisms in the southern Benguela are often exposed to a rich food supply, there is often a wide variation in the quality and quantity of potential food organisms and these are unpredictable (Brown and Hutchings 1987, Stuart and Pillar 1990). This consequently leads to marked variability in zooplankton both in space and in time and may limit the occurrence and productivity of organisms at higher trophic levels in the food web

(Andrews and Hutchings 1980, Borchers and Hutchings 1986, Brown and Hutchings 1987).

It has been estimated that microzooplankton can contribute 14% to mesozooplankton production (Walker and Peterson 1991). According to Porter *et al.* (1985) microzooplankton grazing can play an important role in regulating bacterial populations and regenerating nutrients essential for phytoplankton and microbial growth. Most mesozooplankton are herbivorous and most macrozooplankton are omnivorous (Verheye *et al.* 1992). Both meso- and macrozooplankton are important zooplankton groups in the Benguela ecosystem; within these groups are the copepods and euphausiids which together make up 90% of the standing stock in terms of dry mass of zooplankton (Pillar 1986). Copepods dominate both in terms of abundance and biomass making up 50-60% of the total crustacean zooplankton biomass along the continental shelf. They are a key factor in understanding nutrient and carbon fluxes in the marine environment (Richardson *et al.* 2001).

Zooplankton provide food for some of the most important commercial pelagic fish in the southern Benguela, such as anchovy (*Engraulis encrasicolus*), sardine (*Sardinops sagax*) and round herring (*Etrumeus whiteheadi*) (James 1987, 1988, van der Lingen 1994). It is estimated that zooplankton contribute about 60 to 80% of the diet of sardine (James 1988) and 90% of the annual consumption by pelagic fish in the Benguela system is likely to be derived from meso- and macrozooplankton (Armstrong *et al.* 1991). Zooplankton are therefore a major link between the primary producers and higher trophic levels and, when scarce, may limit fish production in the Benguela ecosystem (Shannon and Field 1985, Verheye *et al.* 1992).

Sardine and anchovy form the mainstay of the South African purse seine fishery, particularly on the west coast. Studies have indicated that these fish are size-selective planktivores consuming different size-fractions of the zooplankton (van der Lingen 1994). Sardine prefer small particles (< 1.2 mm), while anchovy feed more effectively on large particles (>1.0 mm) (James 1987, van der Lingen 1994, van der Lingen *et al.* 2006). Both anchovy and sardine show two modes of feeding: particulate and filter feeding (van der Lingen 1994).

Light intensity and relative energetic costs determine each feeding mode. Filter feeding occurs when light intensity is low and prey are small but present in high densities whereas particulate feeding commences in sufficient light for visual feeding on low concentrations of large prey (Batty *et al.* 1990). The population sizes of anchovy and sardine alternate in the southern Benguela and other upwelling ecosystems with periods of sardine dominance followed by periods of anchovy dominance (Schwartzlose *et al.* 1999). Alternations between sardine and anchovy can be linked to trophodynamic differences (van der Linden *et al.* 2006). Verheye *et al.* (1998) indicated that long-term changes in zooplankton communities coincide with sardine and anchovy alternations in the southern Benguela. Given this information it is possible that any shift in zooplankton community and size structure can drive alternation between these two species. It is therefore important to study abundance and size distribution of zooplankton because they can give indications of the potential feeding conditions for pelagic fish (Verheye and Hutchings 1988).

Distribution and abundance of zooplankton changes over time and space and this can be brought about by changes both in biotic and abiotic factors (Verheye 1991). In the southern Benguela upwelling system, it has been suggested that zooplankton distribution is affected by the seasonal cycle of primary production, which in turn corresponds with seasonal fluctuations in upwelling intensity (Verheye *et al.* 1992). Young copepods occupy shallow depths while older stages live at deeper average depths (Verheye *et al.* 1991, Verheye and Field 1992,). During active upwelling strong winds transport the young zooplankton offshore (Pillar *et al.* 1992). Offshore-inshore and alongshore advection may lead to significant temporal and vertical changes in plankton communities (Verheye *et al.* 1992). Predation, vertical migration and passive horizontal transport of individuals are the biological and physical processes that result in marked fluctuations within zooplankton populations. Many zooplankton undergo diel vertical migration in which animals occupy greater depths (below the thermocline) during the daytime and ascend into near-surface waters during darkness (Stuart and Pillar 1990). This kind of behaviour changes with the developmental stage of zooplankton. Early copepodite stages occur in the wind-mixed surface layers and as they grow older they progressively occupy greater depths (Smith 1984, Pillar *et al.* 1992, Verheye *et al.* 1991, 1992, Verheye and Field 1992,). Such

adaptation thus allows zooplankton to regulate spatial and temporal distributions to a certain extent (Verheye and Field 1992).

Good understanding of the processes that cause changes in population dynamics needs sampling programs and devices that give both accurate measurements of abundance and levels of precision that allow detection of variation in key parameters (Pepin and Shears 1997). Accuracy and precision are determined by the number of collection sites that can be sampled in a reasonable time period and by the efficiency of the gear used (Pepin and Shears 1997). There have been many developments in zooplankton sampling methods since the development of the pelagic fishery on the west coast. Currently, zooplankton are sampled using vertical bongo nets which are deployed when ships are on-station.

The continuous underway fish egg sampler (CUFES) was established in the mid-1990s as a novel survey technique for sampling the highly variable distribution of pelagic fish eggs (Checkley *et al.* 1997). The CUFES consists of a high volume, submersible pump fixed rigidly to the ship's hull, and a device to concentrate egg-sized particles and to collect sequential samples of other large particles in a mesh. The system can operate continuously in nearly all sea conditions, which helps minimize the loss of samples in adverse conditions between stations and leads to increased volumes of water being sampled while at sea (Checkley *et al.* 1997). Sampling occurs simultaneously with other ship activities, underway or on-station, providing estimates of the volumetric abundance of pelagic fish eggs. Sampling usually occurs at a pump depth of 3m but in some systems (including the one used in this study) it is set at 6m depth. CUFES samples yield data series amenable to temporal and spatial analysis. The CUFES is particularly useful for two primary purposes. First, together with environmental data collected simultaneously, CUFES data are able to give insight into the spawning habitat of the target species both between and within regions (Checkley *et al.* 2000). Second, the CUFES can improve the estimation of spawning biomass of the targeted species by use of the daily egg production method (Lo *et al.* 2001).

The CUFES has been used in several regions of the world's oceans, including the western Agulhas Bank in South Africa (van der Lingen *et al.* 1998, Dopolo *et al.* 2005), Onslow Bay in North Carolina (Checkley *et al.* 1997, 1999), southern and

central California (Checkley *et al.* 2000), and Canada (Pepin *et al.* 2005). CUFES sampling is progressively being effectively applied in other countries such as Spain, France, Mexico, Peru, Chile, UK and Norway. The CUFES provides a horizontally integrated estimate of egg density from a single depth along a survey grid and has potential to reduce sampling time (van der Lingen *et al.*1998). However, it has a major limitation in providing the vertical distribution of fish eggs as it only collects samples from a fixed depth (of 3m or 6m). The vertical distribution of fish eggs may vary in space according to changes in environmental conditions (van der Lingen *et al.* 1998).

For zooplankton, high resolution samples are necessary to properly characterize distribution patterns and variability in plankton populations and to detect significant population changes (Sutor *et al.* 2005). Detailed mapping of horizontal zooplankton distributions on a fine scale is difficult and almost impossible with traditional sampling equipment such as bongo nets; time limitations make it difficult to resolve fine scale features. Although vertical bongo net samples are reliable in terms of collecting zooplankton that are distributed vertically or are undergoing vertical migration, sampling is time consuming as it requires the vessel to stop. The CUFES might improve cost and accuracy in estimating abundance and distribution of zooplankton, potentially giving accurate fine scale horizontal distributions.

To determine the potential of the CUFES as an additional sampling method for zooplankton, the consistency of CUFES samples needs to be determined relative to those from vertical bongo nets. This study aimed to examine meso- and macrozooplankton collected in CUFES samples during a pre-recruit survey that was conducted in March 2004 in the region of Cape Columbine off the west coast of South Africa. The main objective of the study was to assess the utility of using the CUFES for determining meso- and macrozooplankton concentrations by comparing both on-station and underway CUFES samples with vertical bongo net hauls.

Material and methods

Zooplankton samples used in the present study were collected during a pre-recruit survey of pelagic fish that was conducted from 5 to 15 March 2004 between Cape Point and Hondeklip Bay, from inshore and offshore waters in the region of Cape Columbine (33°S) off the west coast of South Africa (Fig.1). This area is the centre of the recruitment area for pelagic fish and historically the main commercial pelagic fishing ground on the west coast. Historically, extensive sampling for zooplankton has been carried out in this area since the development of pelagic fisheries.

For this study samples from a survey grid consisting of four inshore/offshore lines were used. Stations were positioned ten nautical miles apart along each line except for a few cases where they were separated by five nautical miles. A total of 94 vertical bongo net samples and 253 CUFES samples were collected. CUFES samples were collected while the ship was on-station and samples were also collected between stations while the vessel was underway. Water was continuously pumped from 6m depth to the concentrator where particles were retained by a 500μm mesh and concentrated in a reduced flow. The flow was then directed to a mechanical sample collector allowing the sequential collection of samples. The sample interval during this survey was 10 minutes for on-station samples and 12-30 minutes for underway samples.

The CUFES operated continuously throughout the survey at a pump flow rate (expressed in terms of volume pumped per m^2 of sea surface covered) of 410 $L.m^{-2}$. The start and end time of each sampling interval and the ship's position at these times was recorded from the ship's GPS (global positioning system). The vertical bongo net samples were collected at each station with a paired bongo net system of 0.57m diameter ($0.25m^2$) fitted with 300 μm mesh dyed black. The mesh size used for vertical bongo net sampling is thus smaller than the one used for the CUFES. The net system was hauled vertically from a maximum depth of 200m or 5m from the bottom. Simultaneously, depth and temperature profiles were recorded with an underwater unit. The volume sampled was recorded with an electronic flowmeter mounted

centrally in the mouth of one net. Immediately after collection, CUFES samples were examined, zooplankton were fixed and all samples were preserved in 5% buffered formalin prior to laboratory analysis. All the samples were labelled with place, date, method and time of collection.

In total, 96 CUFES (64 underway and 32 on-station) samples and 32 on-station vertical bongo samples were selected from the above survey for analysis. Stations were selected where underway samples occurred before and after an on-station sample, and these were designated as downstream and upstream samples. At the laboratory, macrozooplankton (adult and juvenile euphausiids, amphipods and chaetognaths) were removed from samples in which they occurred. They were further sub-sampled using a Folsom Plankton Splitter. Samples were poured into a levelled Folsom Plankton Splitter and split into two equal parts by rotating the splitter. Sea water was added to each sub-sample and split. This was repeated until there were enough sub-samples of the original plankton for effective counting. The aliquots from the macrozooplankton ranged from 1/2 of the sample material to 1/64 of the sample material for samples with more abundant animals. All individuals were identified mostly to genus level and counted under the microscope. The remaining zooplankton were poured into graduated measuring cylinders and were allowed to settle for 24 hours. The settled volume was read and the volume of preservative was adjusted so that the total volume was ten times the settled volume of zooplankton. Following re-suspension of the plankton, 2mL aliquots were removed from each sample with a modified piston pipette for counting. Zooplankton from each 2mL sub-sample were counted and identified under a dissecting microscope.

Vertical bongo net counts were standardized to individuals per m^2. The CUFES counts were standardized to individuals per m^3. To compare the sampling methods, 14 taxonomic groups were chosen from those counted. In selecting these groups, taxa were chosen that represented wide variations in abundance, high numbers, broad distributions over all the sampling area (present in almost all stations), and different sizes.

Among the large copepod species, *Calanus* adult males, females and sub adults (C5) were counted separately and classified as "large *Calanus*". Young stages (C1-C4)

were pooled and classified as "small *Calanus*". *Metridia* males and females were combined into "*Metridia* adults", *Centropages* males and females were pooled into "*Centropages* adults", and *Podon* spp., *Evadne* spp. and *Penilia* spp. were pooled and classified as *Cladocera*. Other taxonomic groups were "small copepods", "*Oithona*", "crustacean eggs", "copepod nauplii", "*Nannocalanus*", "amphipod juveniles" and "amphipod adults".

The presence or absence of zooplankton in samples obtained using each of the two sampling methods (the CUFES and vertical bongo nets) were analyzed using log-likelihood ratios (G statistics) to test whether the two methods have the same probabilities of catching the different taxonomic groups, assuming that the two methods are independent and that each taxonomic group has its own probability of being caught in a sample. Pearson product moment correlation coefficients were used to establish the strengths of the relationships between the abundance of animals collected using onstation CUFES and vertical bongo nets for the different taxonomic groups. To examine differences in vertical migratory behavior of the different taxa, which would affect their susceptibility of being caught by the CUFES, correlations were calculated between abundance estimates from CUFES and vertical bongo net samples after splitting the samples into day and night categories. All counts were log transformed (Log_e (x+1)) to reduce heteroscedasticity and improve normality.

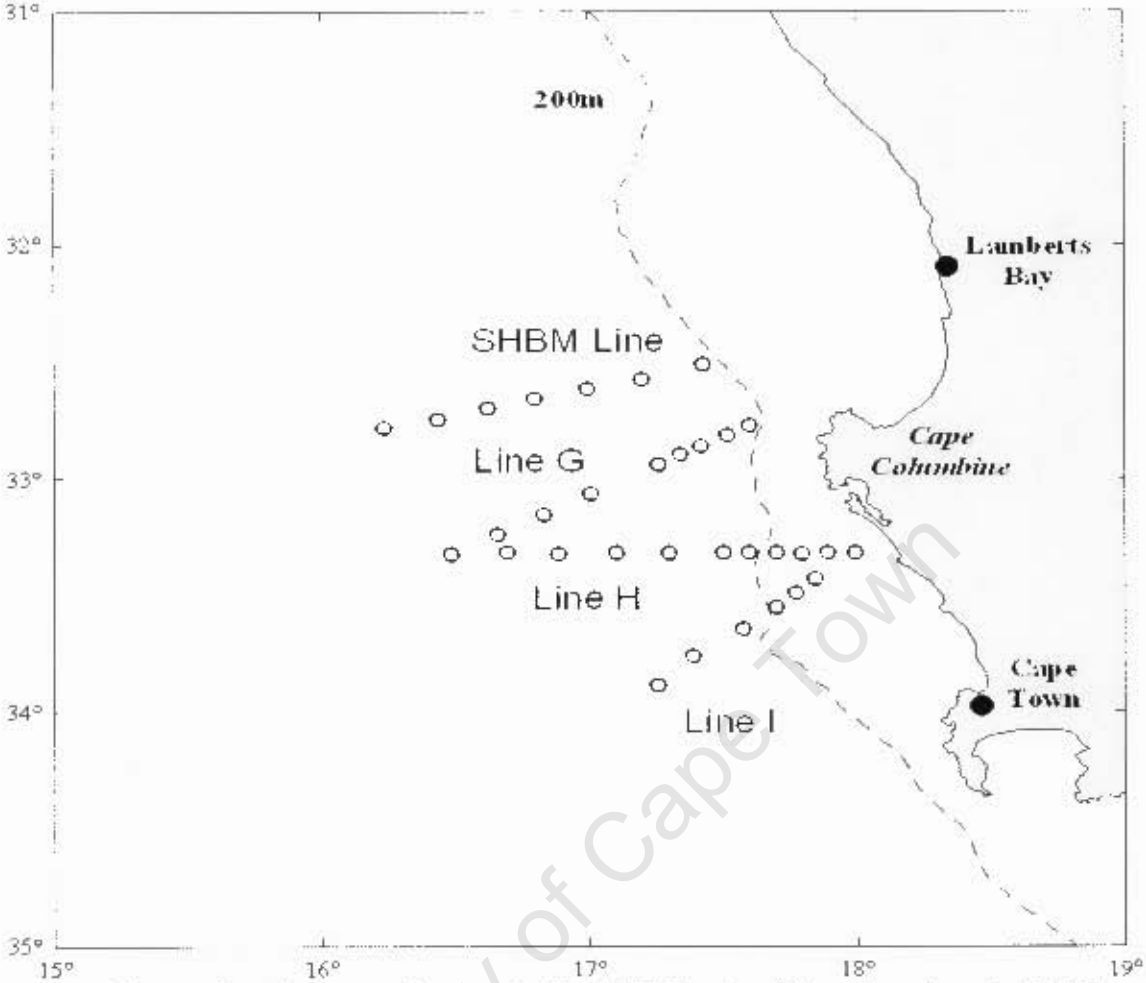

Figure 1. Site map from the pre-recruit survey in March 2004 showing 32 locations where the CUFES and vertical bongo nets were deployed along the St Helena Bay Monitoring (SHBM) line and three additional lines labeled G, H and I.

Results

The analysis of presence and absence of zooplankton taxonomic groups in catches from each sampling gear (Table 1) revealed some significant differences between the two sampling methods. For eight of the 14 zooplankton taxa (Copepod nauplii, *Oithona*, *Centropages* juveniles, *Metridia* juveniles, *Calanus* juveniles, *Centropages* adults, *Metridia* adults and *Calanus* adults) the frequency of obtaining positive results was significantly smaller for the CUFES samples relative to the vertical bongo net samples (i.e. observed frequency was smaller than the expected frequency) (Table 2). This suggests that the CUFES had a lower rate of catching these taxa compared to the vertical bongo nets. Only in the case of small copepods, amphipod larvae,

Nannocalanus and amphipod adults was the frequency of obtaining the taxa using the CUFES consistently similar to the vertical bongo nets. This indicates that the CUFES is able to sample these taxonomic groups with similar efficiency as the vertical bongo nets.

Generally, results showed that the vertical bongo net had a greater probability of catching large zooplankton taxa than the CUFES, whereas both sampling methods had the same probability of catching small zooplankton. For two taxonomic groups, crustacean eggs and *Cladocera*, results were inconsistent, with observed frequencies of occurrence in both samples obtained using the two different methods not reflecting those expected (results not shown in Table 2).

Table 1: The number and percentages of all stations (n=32) that contained individuals of each taxonomic group in both CUFES and vertical bongo net samples, in CUFES samples only, in vertical bongo net samples only, and in samples from neither of the two sampling methods. Taxa are listed from smallest to largest group.

	Number (%) of stations containing individuals in samples				
Taxonomic group	Both Methods	only CUFES	only Bongo	Neither method	Total
Crustacean eggs	21 (66)	3 (9)	1 (3)	7 (22)	32 (100)
Copepod nauplii	7 (22)	0 (0)	21 (66)	4 (12)	32 (100)
Cladocera	9 (28)	13 (41)	3 (9)	7 (22)	32 (100)
Oithona	27 (84)	0 (0)	5 (16)	0 (0)	32 (100)
Small copepods	32 (100)	0 (0)	0 (0)	0 (0)	32 (100)
Centropages juveniles	13 (41)	2 (6)	6 (19)	10 (34)	32 (100)
Metridia juveniles	12 (38)	1 (3)	9 (28)	10 (31)	32 (100)
Calanus juveniles	20 (63)	1 (3)	9 (28)	2 (6)	32 (100)
Amphipod juveniles	17 (53)	6 (19)	5 (16)	4 (12)	32 (100)
Nannocalanus	14 (44)	4 (12)	5 (16)	9 (28)	32 (100)
Centropages adults	17 (53)	1 (3)	11 (34)	3 (10)	32 (100)
Metridia adults	19 (59)	0 (0)	12 (38)	1 (3)	32 (100)
Calanus adults	12 (38)	2 (6)	13 (41)	5 (16)	32 (100)
Amphipod adults	7 (22)	9 (28)	10 (31)	6 (19)	32 (100)

Table 2. Results of goodness of fit tests showing observed and expected probabilities of sampling each taxonomic group using each sampling method, the calculated G statistics and the probability of obtaining the results by chance. Critical values were χ^2=5.991 (df = 2, α = 0.05).

Taxanomic group	p(CUFES) observed	p(CUFES) expected	p(bongo) observed	p(bongo) expected	G statistics	p
Crustacean eggs	0.75	0.72	0.69	0.72	15.95	< 0.01
Copepod nauplii	0.22	0.54	0.88	0.54	246.93	<0.01
Cladocera	0.69	0.53	0.38	0.53	6.74	<0.05
Oithona	0.84	0.92	1.00	0.92	12.65	<0.01
Small copepods	1.00	1.00	1.00	1.00	0.00	ns
Centropages juveniles	0.48	0.54	0.61	0.54	9.48	<0.01
Metridia juveniles	0.41	0.53	0.66	0.53	11.90	<0.01
Calanus juveniles	0.66	0.78	0.91	0.78	7.59	<0.01
Amphipod juveniles	0.72	0.70	0.69	0.70	1.06	ns
Nannocalanus	0.56	0.58	0.59	0.58	5.98	ns
Centropages adults	0.56	0.72	0.88	0.72	9.92	<0.01
Metridia adults	0.59	0.78	0.97	0.78	73.13	<0.01
Calanus adults	0.44	0.61	0.78	0.61	9.02	<0.01
Amphipod adults	0.50	0.52	0.53	0.52	1.20	ns

The relationships between ln-transformed zooplankton densities estimated from the 32 simultaneously sampled stations using on-station CUFES and vertical bongo nets were tested for correlation using the Pearson product moment correlation coefficient. There were positive correlations in most cases (Fig. 2). Significant correlations were apparent for crustacean eggs, *Cladocera*, *Oithona*, small copepods, *Centropages* juveniles, *Metridia* juveniles, *Nannocalanus*, *Centopages* adults and *Metridia* adults. Correlation coefficients (r) ranged from 0.185 to 0.648 for significant comparisons, but there was much scatter in the data. The strongest correlation was found for crustacean eggs (Fig. 2a) and the weakest significant correlation for *Cladocera* (Fig. 2m).

For underway samples a total of 64 CUFES abundance estimates (downstream and upstream) were tested for correlation with ln-transformed zooplankton abundance from vertical bongo nets (Fig. 3). Significant correlations were only apparent for crustacean eggs, copepod nauplii, *Metridia* juveniles, *Calanus* juveniles, *Nannocalanus*, amphipod juveniles and *Calanus* adults with r values ranging from

0.352 to 0.463. Again crustacean eggs showed the highest r values (Fig. 3a) and copepod nauplii the lowest r values (Fig. 3j).

When the zooplankton abundance data from all the CUFES stations, both underway (upstream and downstream) and on-station, were pooled and compared with those from the 32 on-station vertical bongo net samples, there were significant correlations for all taxonomic groups except for amphipod adults and *Oithona.* Strongest correlations were found for crustacean eggs (Fig. 4a).

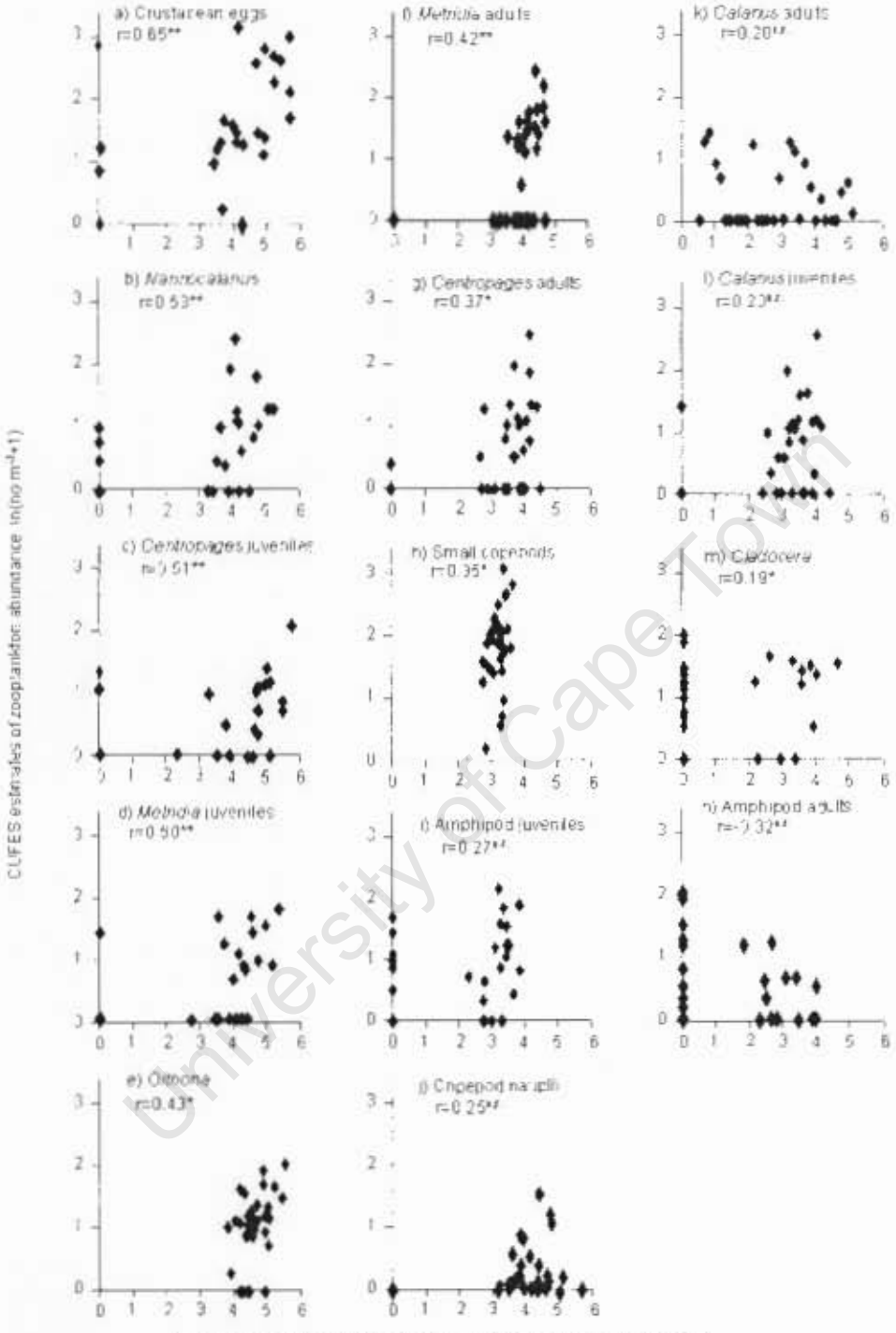

Figure 2. Comparison between zooplankton abundance measured with on-station CUFES and vertical bongo nets (n = 32) showing correlation coefficients r and significance levels (* – $p < 0.05$, ** – $p < 0.01$ and n.s. = not significant).

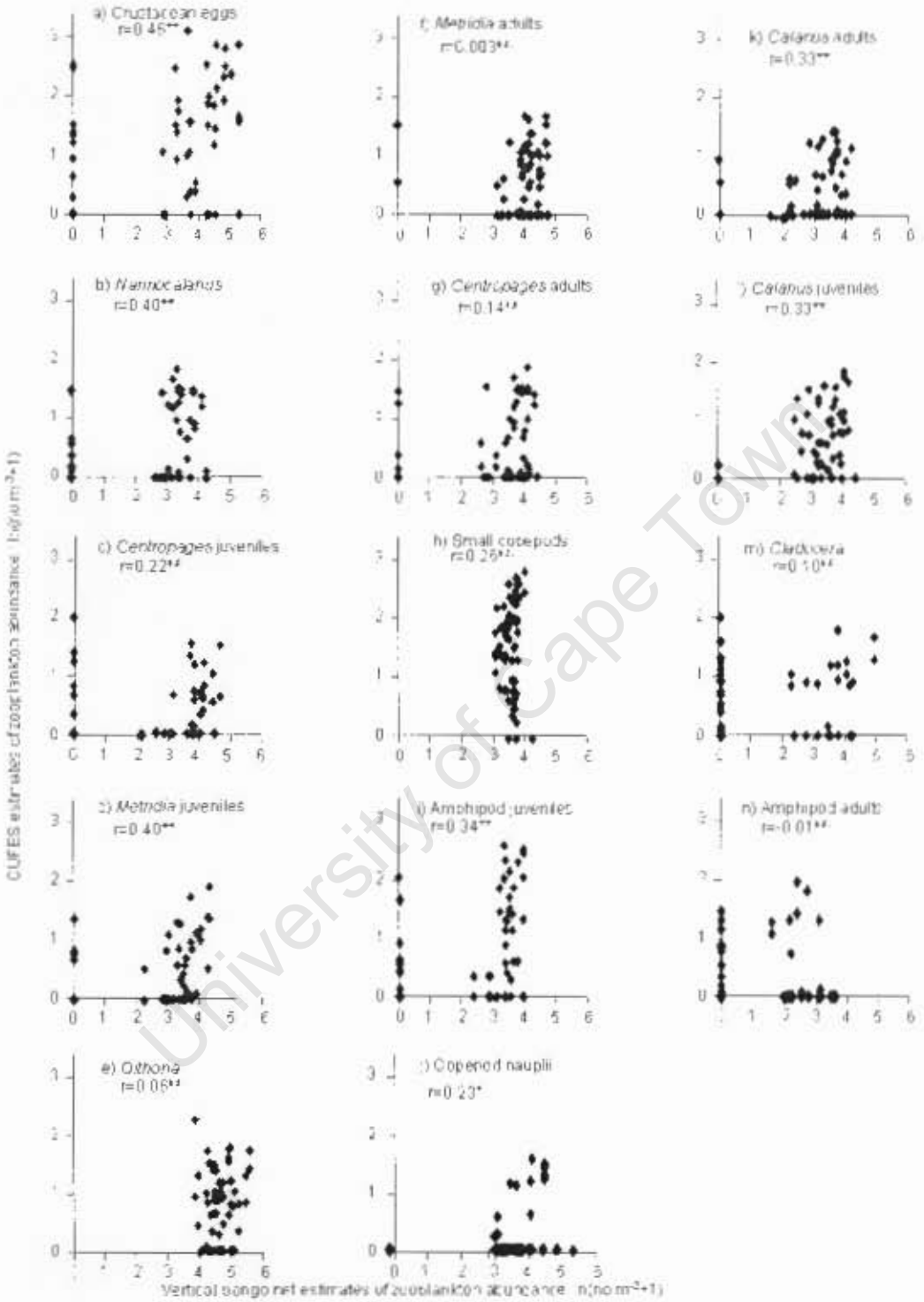

Figure 3. Comparison between zooplankton abundance measured with underway CUFES and vertical bongo nets (n = 64) showing correlation coefficients *r* and significance levels (* $p < 0.05$, ** = $p < 0.01$ and n.s. = not significant).

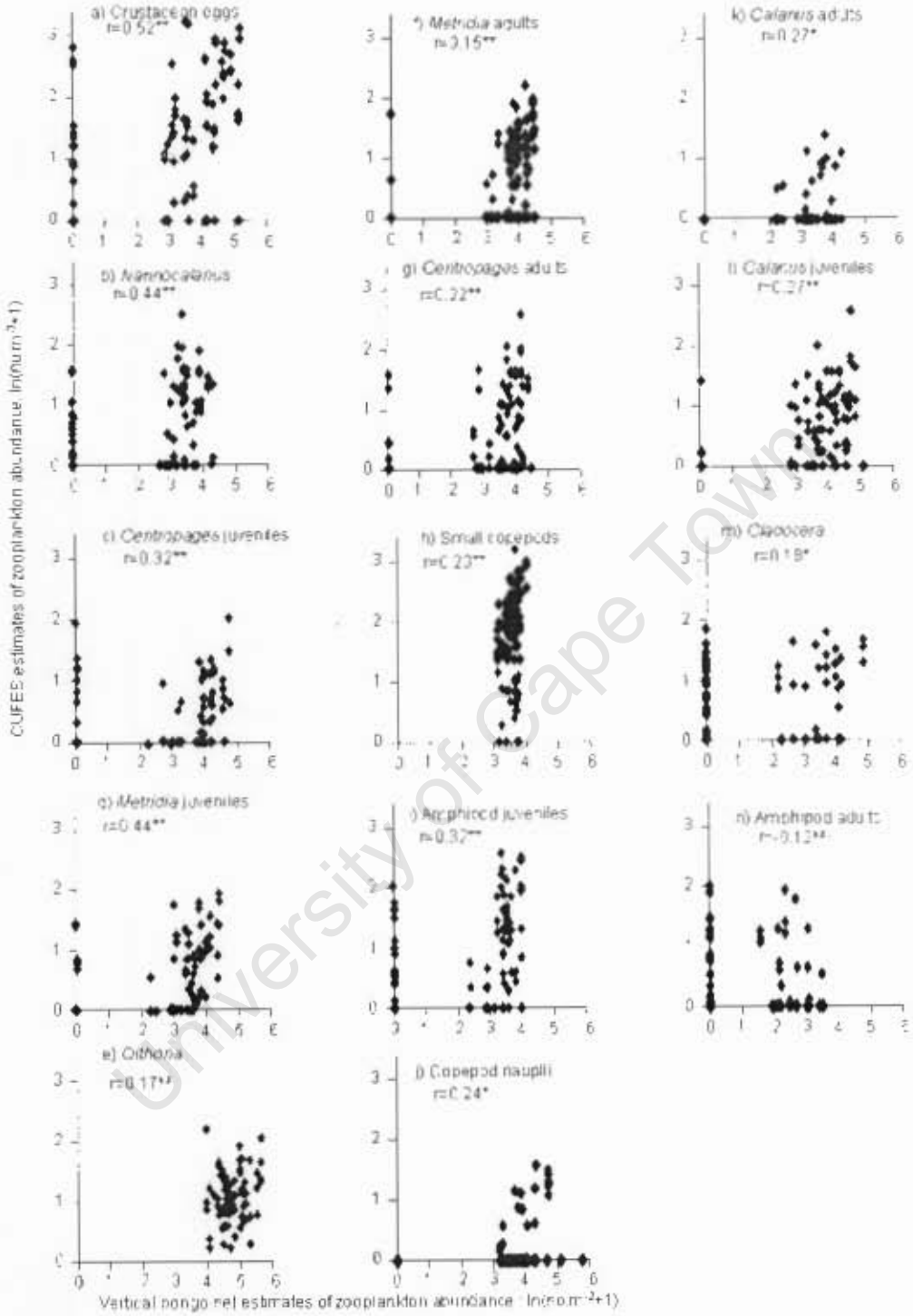

Figure 4. Comparison between zooplankton abundance measured with underway and on-station CUFES and vertical bongo nets (n = 96) showing correlation coefficients r and significance levels (* = $p < 0.05$, ** = $p < 0.01$ and n.s. = not significant).

Marked differences between day and night samples were observed (Table 3), with catches of *Oithona*, *Cladocera*, small copepods, *Metridia* juveniles and *Centropages* adults showing significant correlations during the night compared to the day stations (Fig. 5). Generally correlations were higher for night than day samples, indicating that CUFES and vertical bongo net catches were more similar during the night, as might be expected if many of the taxonomic groups are vertical migrators. For day stations, only catches for crustacean eggs, *Nannocalanus* and *Centropages* juveniles showed significant correlations. This suggests that these taxonomic groups undergo limited vertical migration and were consistently present in surface waters, where they are accessible to the CUFES.

Table 3. The correlation coefficient (r) between ln-transformed volumetric abundance from CUFES ($no.m^{-3}+1$) and vertical bongo nets ($no.m^{-3}+1$) for day and night sampling.

	Day		Night	
Taxonomic group	r	p	r	p
Crustacean eggs	0.540	<0.05	0.756	<0.01
Oithona	0.245	n.s.	0.560	<0.05
Cladocera	-0.040	n.s.	0.300	<0.05
Small copepods	0.109	n.s.	0.569	<0.05
Centropages juveniles	0.695	<0.01	0.500	<0.05
Metridia juveniles	0.096	n.s.	0.684	<0.01
Nannocalanus	0.717	<0.01	0.402	n.s.
Centropages adults	0.193	n.s.	0.502	<0.05
Metridia adults	0.294	n.s.	0.414	n.s.

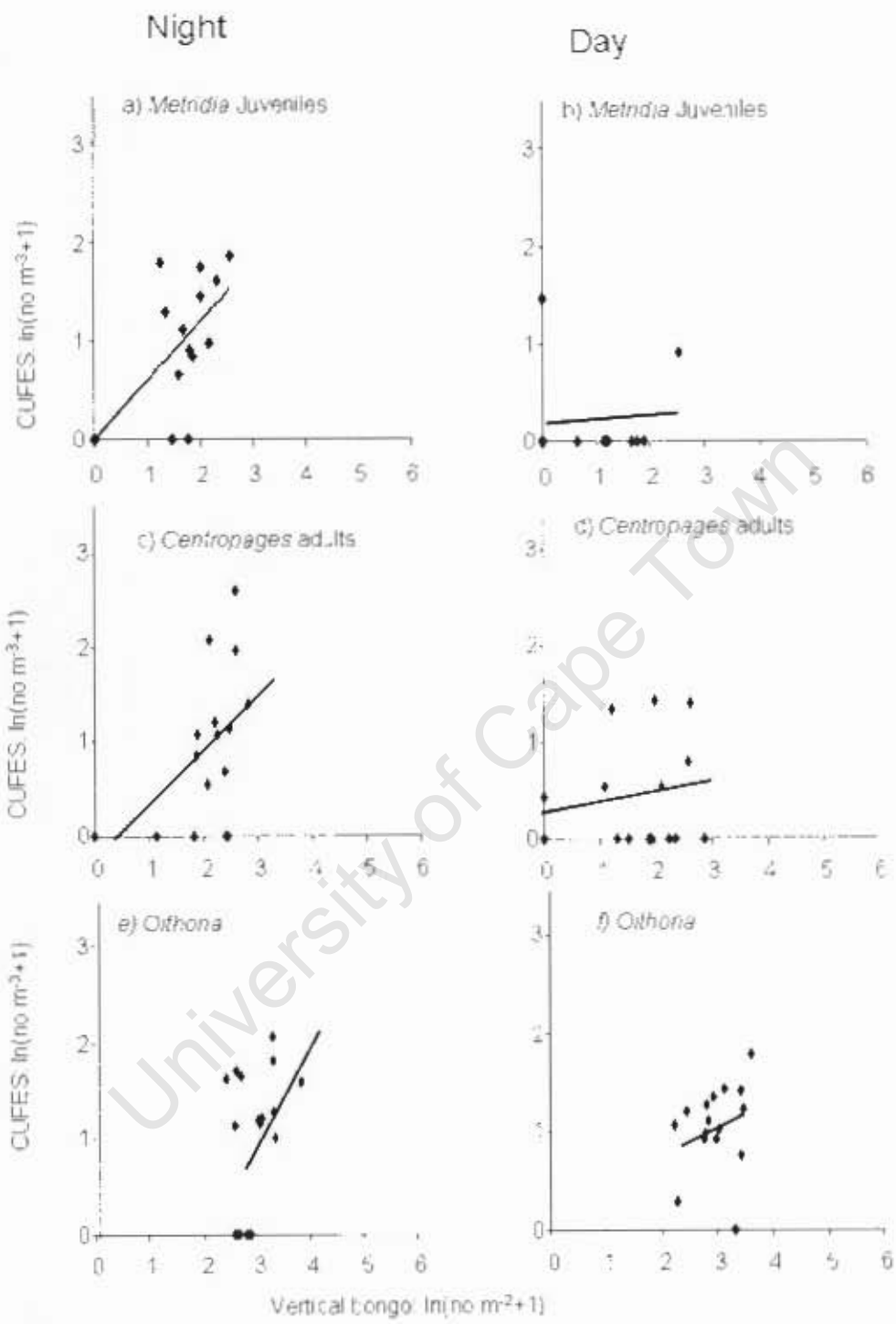

Figure 5. Plots showing the relationships between ln-transformed volumetric abundance for selected species from on-station CUFES and vertical bongo nets split, into day and night. Correlation coefficients r and significance levels are shown in Table 3.

Correlation coefficients (r) from onstation CUFES and vertical bongo net samples were plotted in increasing order of body size for the taxonomic groups that showed significant correlations (Fig. 6). There is no clear pattern in these results.

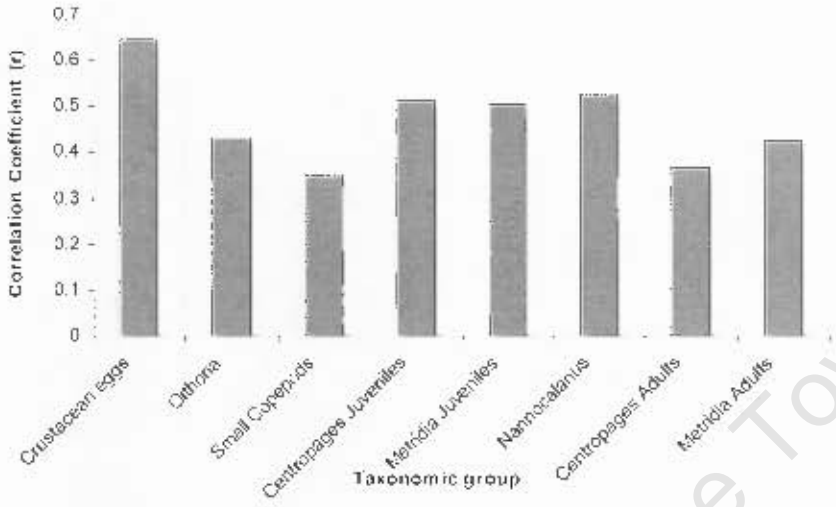

Figure 6. Correlation coefficients calculated between ln-transformed abundance from CUFES ($no.m^{-3}$) and ln-transformed volumetric estimates from vertical bongo net samples ($no.m^{-2}$) for different taxa in increasing order of body size.

The relative mean abundance of each taxonomic group estimated from the two sampling methods (CUFES and vertical bongo net) from four lines is given in Figure 7. These plots show the eight groups that had the highest significant correlations in abundance estimated by the two sampling methods. All eight groups were found in samples from both sampling devices but their relative abundance varied greatly from one sampling method to the other. In vertical bongo net samples, small copepods were the most abundant taxonomic group in all the four lines with highest proportions at line H (Fig. 7c). Other groups present in large relative abundance were *Oithona* and crustacean eggs. In the CUFES samples, small copepods were the most abundant group only along the SHBML (Fig. 7a), followed by *Metridia* adults. For lines G to I crustacean eggs showed the highest relative abundance in the CUFES samples followed by small copepods. Generally, the relative abundance of different taxa were very different between the CUFES and vertical bongo net samples indicating that the two methods are sampling the taxa differently.

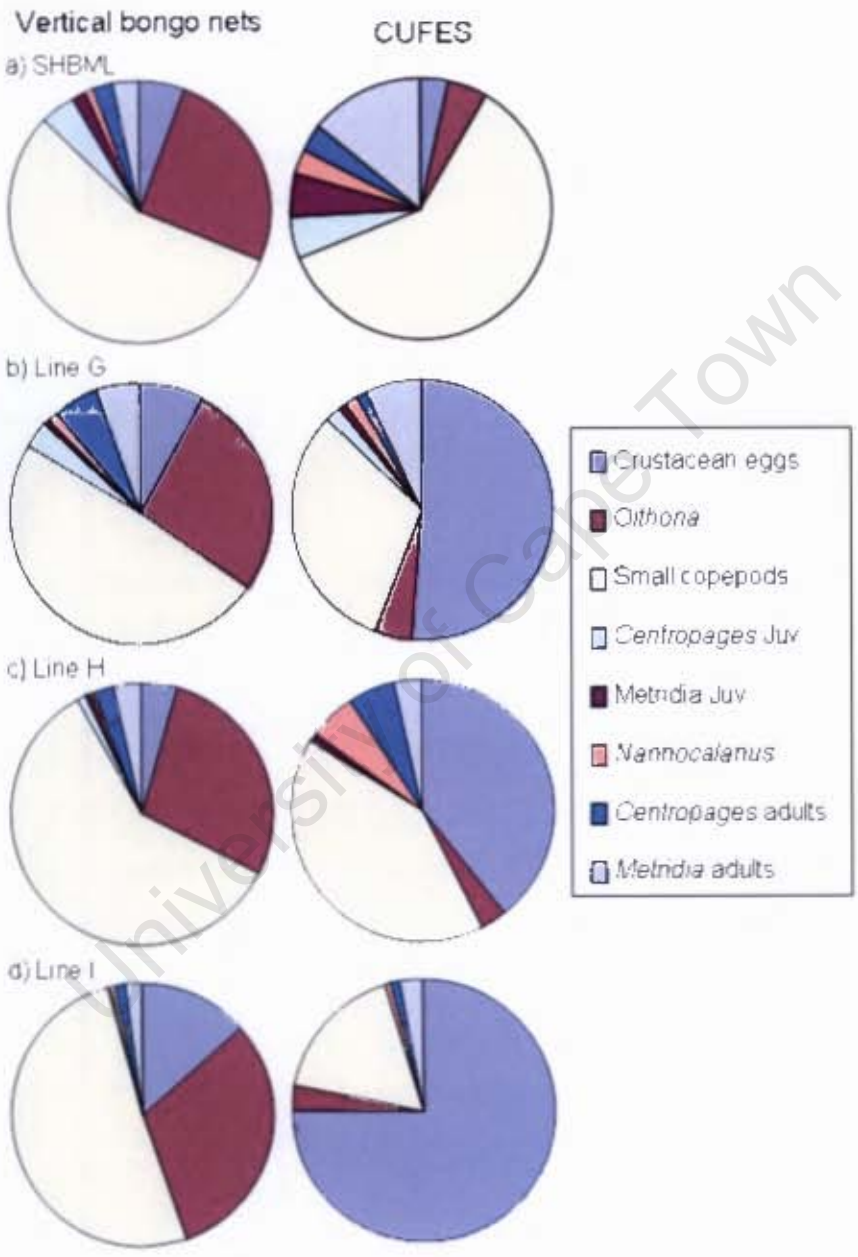

Figure 7. Relative mean abundance of each taxonomic group from vertical bongo net (no.m^{-2}) and CUFES (no.m^{-3}) from four sampled lines (SHBML, Line G, H and I).

Discussion

In this study it has been shown that the CUFES is only partially effective as a method of obtaining a representative sample of zooplankton populations. It has been assumed that samples from vertical bongo nets represent the "true" situation in the sea, so the obvious differences between the CUFES and vertical bongo nets (mesh size, depth of sampling, method of capture) were deliberately ignored in order to address the question of whether the CUFES is an appropriate tool for obtaining routine samples of zooplankton.

CUFES has proved to be a reliable system to sample pelagic fish eggs under virtually all sea conditions (Checkley *et al.* 1997, 1999, 2000, van der Lingen *et al.* 1998). The CUFES is a pump-based sampler that continuously samples from a fixed depth of 6m whereas vertical bongo nets sample (in the present study) over a 200m water column. Vertical distribution and abundance of zooplankton vary in the southern Benguela (Verheye and Field 1992) through processes such as vertical migration of individuals to deep water during the day and surface waters at night (Verheye 1991). This behaviour differs with life cycle stages and species, with larger individuals tending to occur deep at night whereas small individuals show minimal or no changes (Verheye and Field 1992). These difference in behaviour would be expected to affect the sampling efficiency of the CUFES compared with the vertical bongo nets, which has been shown in these results. In all cases there were differences between samples in terms of presence/absence of difference taxonomic groups, their absolute abundance, and relative composition within the samples.

For large zooplankton (*Centropages* juveniles and adults, *Metridia* juveniles and adults, *Calanus* adults and juveniles) the catch ratios using vertical bongo nets were greater than for CUFES. These results demonstrate that the CUFES is not a good sampler for these large-sized taxa, because their populations are mostly absent from the surface waters during the day. In contrast to pronounced vertical migration in large zooplankton, there are minimal changes in smaller zooplankton (Hutchings 1979, 1985 and Pillar 1984). Vertical bongo nets provide more representative samples of the entire population of zooplankton by integrating over the water column (Pepin and Shears 1997). Pepin *et al.* (2005) assessed CUFES accuracy and precision for

three species of temperate fish and attributed the CUFES bias as compared to vertical bongo nets to the incomplete mixing of the population of eggs, suggesting vertical distribution of eggs played a key factor.

The CUFES uses a larger mesh size (500µm) to retain particles than vertical bongo nets (300µm), and this difference might be expected to result in less efficient sampling of small taxa by the CUFES than by vertical bongo nets. This was apparent in the results for *Oithona* and copepod nauplii, which were caught more frequently in vertical bongo nets than in CUFES samples. *Oithona* is a non-migratory species (Hutchings 1979, Pillar 1984), but it is mainly concentrated from 40-60m depth (Pillar 1984), so both vertical location and mesh size could explain the higher catch rate of this group using vertical bongo nets compared to the CUFES. The correlation between CUFES and vertical bongo net samples for *Oithona* were higher at night than during the day, suggesting that this species might undergo vertical migration (Table 3, Fig. 7).

The overall catch ratio for CUFES compared to vertical bongo nets was the same for small copepods, amphipods (adults and juveniles) and *Nannocalanus*. The similarities between CUFES and vertical bongo net catches for these taxa suggest that these taxonomic groups were fairly homogeneously distributed in the water column. Hence both methods were efficiently catching the zooplankton taxa at the same comparable rate. Catches of *Cladocera* juveniles and crustacean eggs from the CUFES and vertical bongo nets were inconsistent. Results showed that CUFES catches of *Nannocalanus* are better correlated with those of vertical bongo nets during the day. These results suggest that these groups undergo limited vertical migration during the day. Pillar (1984) found no convincing evidence of vertical migration for small copepods and concluded that these species are mostly abundant in the upper layers of the water. In addition Hutchings (1979, 1985) and Pillar (1986) found that *Nannocalanus* show little evidence of vertical migration, and this study suggests that *Nannocalanus* might also be concentrated in surface waters.

Significant correlations were observed between zooplankton abundance estimates in samples from on-station CUFES and vertical bongo nets for nine taxonomic groups: crustacean eggs, small copepods, *Cladocera*, *Oithona*, *Nannocalanus, Centopages*

juveniles and adults and *Metridia* juveniles and adults. However, there was great variability in the paired estimates, resulting in low overall r values (Table 4). Crustacean eggs showed relatively high correlations, further mirrored by the high abundance of these eggs in CUFES samples compared to those from vertical bongo nets despite the use of a finer mesh by vertical bongo nets This suggests the suitability of CUFES for sampling crustacean eggs, indicating that they were distributed in the mixed surface water.

The non-significant results observed in this study were mostly related to sampling of large zooplankton by the CUFES. This is expected as it has been shown that large zooplankton undergo vertical migration with maximum day time densities below the thermocline (De Decker 1964, Hutchings 1979, Verheye and Field 1992, Pillar 1984 and Verheye and Hutchings 1988). In addition, copepod nauplii showed no correlations between abundance estimates from the two sampling methods, possibly due to the different mesh sizes used for these two sampling gears. Robertson and Howard (1978) suggested that vertical migration differs with species, time of sampling and habitat. Huggett (2003) argued that vertical migration of zooplankton will be a trade-between getting more food and increased predation pressures .

Evidence from this study suggests that most large zooplankton taxa (*Metridia* juveniles and adults and *Centropages* adults) were more abundant in the surface waters at night than during the day. This is based on the significant correlations observed between samples from the CUFES and vertical bongo nets for the night stations (Table 3). From this we can suggest that groups consisting of large organisms were mostly concentrated deep during the day, where the CUFES could not effectively sample. However this needs to be investigated further. Non significant correlations and reduced catches for large zooplankton using CUFES also could be due to avoidance of the pump intake by large zooplankton, particularly during the day. The CUFES actively pumps water whereas the vertical bongo nets are towed through the water column. Towed nets reduce zooplankton avoidance and are able to capture mobile zooplankton effectively; some of these zooplankton are able to avoid the CUFES (Pepin and Shears 1997). Checkley *et al.* (2000) suggested that large zooplankton have a tendency to not follow the flow of water into the sea chest, resulting in few large zooplankton being sampled by the CUFES.

Checkley *et al* (2000) postulated that underway sampling results in increased sample volumes so we would expect to find more representative samples of zooplankton. We did not find any evidence of this. Correlations were not significant between underway CUFES samples and vertical bongo net samples for most taxonomic groups and r values were very low compared to comparisons between vertical bongo nets and on-station CUFES samples. However it is also possible that the vertical bongo nets did not catch representative samples, as has been assumed.

The relative abundance plots of taxonomic groups from samples obtained using the CUFES and vertical bongo nets showed different compositions, suggesting that the two gears sample different taxonomic groups differently. Small copepods were concentrated in the surface waters along the SHBML, which is indicated by high relative abundance of this group in CUFES and vertical bongo net samples. However CUFES samples from lines G, H and I were dominated by crustacean eggs whereas bongo net samples were dominated by small copepods. It has previously been suggested that distribution can be affected by environmental factors like wind (Pitcher *et al.* 1992). Verheye and Hutchings (1988) have suggested that zooplankton abundance varies between size classes and inshore and offshore, with small copepods being evenly distributed in the water column. Pillar (1986) found that small copepods are limited to the surface which would also explain their high abundance in both the CUFES and vertical bongo net sampling methods. Relative abundances of other taxa (*Metridia* juveniles and adults, *Centropages* juveniles and adults, *Nannocalanus*) were very low using both sampling methods.

Evidence from this study suggests that the CUFES is able to sample effectively for small zooplankton, in particular crustacean eggs. It has previously been found that the CUFES is very efficient for sampling small pelagic eggs (Checkley *et al.* 1997). Evidence for this comes from a study by van der Lingen *et al.* (1998) who studied abundance of sardine and round herring eggs on the western Agulhas Bank and found CUFES to be useful for studying these eggs. Checkley *et al.* (2000) also studied abundance of sardine and anchovy eggs off southern California and found that CUFES is suitable for studying these pelagic eggs. It was suggested from these studies that pelagic eggs are often distributed in the surface layers and the CUFES

efficiently captures these eggs. This study suggests that distributions of both crustacean eggs and small copepods in the surface layers played a role in the efficiency of CUFES in sampling these groups. Van der Lingen *et al.* (1998) and van der Lingen and van der Westhuizen (2000) have also argued that differences in egg buoyancy play a significant role in bias in data from the CUFES as compared with CalVET net samples. They suggested the higher r values for sardine eggs compared with anchovy eggs were due to relative vertical distributions of these eggs because sardine eggs are more concentrated in the surface than anchovy eggs and are therefore more accessible to the CUFES.

In conclusion the CUFES has proved to be a good sampling device for crustacean eggs. Because CUFES is able to obtain samples both underway and on-station, it results in increased numbers of samples. However it was apparent that most of the CUFES samples contain fewer individuals of zooplankton for most large species than vertical bongo net samples, and they provided an inadequate representation of the distribution and abundance of these species compared to vertical bongo nets. Despite the advantages that the CUFES may have over vertical bongo nets, the large variability in the CUFES samples prevents their effective use to sample zooplankton taxa, particularly large zooplankton. In addition, the larger mesh size used by the CUFES compared with the vertical bongo nets will probably result in different efficiencies of the two methods for sampling small zooplankton. Notwithstanding these differences, abundances of crustacean eggs, small copepods, *Cladocera*, *Oithona*, *Nannocalanus, Centopages* juveniles and adults and *Metridia* juveniles and adults that were caught by CUFES were correlated with abundance in vertical bongo net samples. This suggests that, although the CUFES samples do not provide comparable absolute estimates to vertical bongo net samples, the CUFES can be used to understand the dynamics of target group, such as small copepods. The low accuracy of the CUFES for large zooplankton puts a major limitation on its usefulness as a tool for sampling large zooplankton, particularly those that occur at greater depths or undergo vertical migration. For near-surface species that are abundant in the water column with minimal or no vertical migration, the CUFES can provide a reliable measure of their relative abundance. It is important to note that these results are derived from a study that was confined to a small fixed area, sampled during one month. This would place some limitations on the conclusions about the usefulness of

CUFES for sampling zooplankton. Further studies are needed which look at a wide range of areas in different seasons and possibly the use of similar mesh sizes in the two samplers.

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