Comparison of the epipelagic zooplankton samples from a U-Tow and the traditional WP2 net

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The performance of a new mesozooplankton sampler, the U-Tow, was compared to that of the traditional WP2 net. The U-Tow significantly underestimated species abundance, but gave a very good representation of species composition and community size structure. WP2 net samples could be used to calibrate the U-Tow, allowing absolute abundance to be determined. It is recommended that the U-Tow, in its current configuration, be used in conjunction with WP2 net samples to give measures of abundance, so as to identify areas of change in plankton communities.

INTRODUCTION
The assessment of the abundance, species composition and size distribution of mesozooplankton is a fundamental goal of biological oceanography (UNESCO, 1968; Mitson et al., 1996; Greene et al., 1998). Traditionally, however, mesozooplankton have been sampled with simple ring nets that sample over very restricted spatial scales, with individual deployments being made over a few tens of metres. The resulting lack of spatial detail in mesozooplankton surveys limits our ability to understand, for example, the trophic interactions and biogeochemical impact of mesozooplankton, their life-history strategies, and the impact of physical and biological processes on secondary production (Piontkovski et al., 1995; Stockwell and Sprules, 1995; Greenstreet et al., 1997; Benfield et al., 1998; Liao et al., 1999; Zhang et al., 2000).

Consequently, there is an urgent need for techniques that allow mesozooplankton to be sampled over extended spatial scales (tens or even hundreds of kilometres) (Marine Zooplankton Colloquium, 1989). To this end, acoustic and optical techniques have been extensively explored in recent years, although both techniques have limited ability to resolve species composition and may also suffer from the presence of too many, or non-living, particles in the water (Mitson et al., 1996; Stanton et al., 1996; Ongood, 1997; Benfield et al., 1998a; Brierley et al., 1998b; Liao et al., 1999; Zhang et al., 2000). Systems that actually collect zooplankton samples at high speed and over extended transects would, therefore, be most valuable.

To date, the only system capable of such sampling is the Continuous Plankton Recorder (CPR). This instrument has been routinely, and consistently, surveying the North Sea and North Atlantic plankton since 1948 (Oceano-graphic Laboratory Edinburgh, 1973; Warner and Hays, 1994). The main reason that the CPR is not used more widely is its inability to sample physical parameters and confinement to sampling at one depth (Hays et al., 1998).

Due to these limitations in the performance of the CPR, a new vehicle, the U-Tow, has been designed in recent years for sampling mesozooplankton and physical parameters at high speeds (maximum tested speed of 22 km h⁻¹) and over extended spatial scales (Hays et al., 1998). The original version of the U-Tow was designed and built by Valeport Limited (Dartmouth, Devon) in collaboration with the Sir Alister Hardy Foundation for Ocean Science (SAHFOS) in 1994. It is fitted with a Plankton Sampling Mechanism (PSM, Valeport Model 140) (Figure 1), which is based on the mechanisms used in the CPR and Longhurst Hardy Plankton Recorder (LHPR) (Hays et al., 1998), and a Conductivity Temperature Depth sensor (CTD). It can also be configured to carry additional sensors, and can be fitted with a servo control module to actively control depth; in this way an undulating depth profile can be achieved. This design has since been modified by W. S. Ocean Systems Limited (Alton, Hants) to have improved undulating capabilities and an increased potential payload (Mills et al., 1998). However, both models use the same PSM (Figure 1). Water enters the PSM via an aperture at the front of the U-Tow, and passes through a filtering mesh supported by a series of fine stainless steel...
At pre-determined intervals, the filtering mesh and a covering mesh advance on to a take-up spool, situated in a storage chamber that contains a formaldehyde reservoir, giving a series of discrete samples. The U-Tow has a comparatively small inlet aperture (18 mm diameter) which prevents problems with clogging of the mesh when too large a volume of water is filtered.

Ideally, the performance of any new piece of equipment should be investigated before use so that results can be reliably compared with other studies, and so that temporal and spatial variation in the plankton can be distinguished from variation in sampler performances (Aron et al., 1965). Gear inter-comparisons, although not ‘exciting’ science, are a vital component of sampling. For example, Hernroth (Hernroth, 1987) found that the sampling and filtration efficiency of the Nansen net was 50–70% compared to the WP2 net under ideal conditions and 25–30% during periods of high particle abundance or long hauls; while DeVries and Stein (DeVries and Stein, 1991) discovered a discrepancy in densities of the rotifer *Daphnia* found by a tube sampler, a vertical tow net and the Schindler–Patalas trap, although they performed equally for most species, emphasizing the need for a taxon-specific approach when evaluating samplers. More recently, whilst calibrating an optical plankton counter (OPC), Sprules et al. (Sprules et al., 1998) found it to be accurate up to concentrations of 100 organisms l⁻¹. Above this concentration, there was an increasing level of coincident counts, where multiple animals were counted as one, resulting in underestimation of zooplankton abundance and inaccurate size distributions. Similarly, Zhang et al. (Zhang et al., 2000) suggest that the OPC is able to produce reasonable estimates of zooplankton abundance in waters with less than 100 detritus particles l⁻¹ but only after correcting for the influence of background detritus. The most extensive gear inter-comparisons have concentrated on acoustic techniques. For example, Greene et al. (Greene et al., 1998) used a Dual-Beam Acoustics Deployed on a Multiple Opening/Closing Net and Environmental Sensing System (D-BAD MOCNESS) to collect acoustic data and net samples simultaneously. The results from the two samplers were consistent, except for samples with high quantities of siphonophores where predicted backscattering coefficients exceeded observed backscattering coefficients.

The most widely used mesozooplankton sampler is the simple ring net, or WP2 net (UNESCO, 1968), which has been shown to be suitable for quantitative sampling (Hernroth, 1987). The WP2 net is generally used to give an integrated sample of mesozooplankton from either a vertical or a horizontal haul at slow speeds, usually net more than 3.7 km h⁻¹, and therefore it samples over a relatively small distance (metres). The aim of this study is to compare the performance of the U-Tow with that of the traditional WP2 net. Estimates of abundance, species composition and community size structure are evaluated from samples collected in Swansea Bay, the North Sea and the Irish Sea.

**METHOD**

Three different U-Tow systems were used in this study. A fixed depth Valeport Ltd. U-Tow (Hays et al., 1998) was...
deployed in Swansea Bay (December 1997, April, May, September and November 1998), an undulating Valeport Ltd. U-Tow (Hays et al., 1998) was deployed in the North Sea (February 1998); and an undulating W. S. Ocean Systems Ltd. U-Tow (Mills et al., 1998) was deployed in the Irish Sea (June and July 1998). This gave a total of 28 deployments over about 1668 km. Tow speeds ranged between 13 and 18.5 km h⁻¹. All U-Tows were fitted with the same PSM and 200 µm filtering mesh. The only difference in the three systems with respect to sampling zooplankton was the electromagnetic flow meter fitted to the PSM used in the Valeport systems (Valeport Model 802) (Hays et al., 1998). The W. S. Ocean Systems Ltd. model did not have a flow meter fitted to the PSM. In these cases, the volume of water filtered per sample was calculated from the distance towed multiplied by the area of the inlet to the PSM, with the standard EM flowmeter measuring the volume of water entering the PSM, and an impellor flow meter (Kent Water Meter) measured the volume of water exiting. An impellor flow meter was used in the Valeport trials because the PSM was not equipped with a flow meter reading. However, the flow rate was monitored by using a real-time depth sensor and Aladin Pro dive computer, for an accurate reading of depth, was deployed. After each deployment the undulation profile to the surface. In all cases, a 56 cm vertical net hauls were taken from the maximum depth of 9 m, made possible by using a real-time depth sensor, followed by a triangular course, with each leg approximately 4.5 km, for approximately 3 h. The PSM was set at sample intervals of 15 min. Five-minute WP2 net tows at 9 m, made possible by using a real-time depth sensor, were taken at each corner of the triangular course. Deployments in the North Sea and Irish Sea involved towing the undulating U-Tow along a straight-line course, with a vertical WP2 net haul taken at the beginning and end of each tow. As the purpose of these cruises was to test the capabilities of the U-Tow, the length of tow and depth range varied between tows. Tow duration ranged between 1.5 h and 16 h (average 4.5 h); and depth ranged between 5 m and 40 m. The PSM was set at sample intervals between 15 and 30 min (average 22.5 min). For each tow, vertical net hauls were taken from the maximum depth of the undulation profile to the surface. In all cases, a 36 cm diameter WP2 net fitted with a General Oceanics flow meter and Aladin Pro dive computer, for an accurate reading of depth, was deployed. After each deployment samples were immediately washed off the mesh and preserved in 4% borax-buffered seawater formaldehyde.

Animals from both sets of samples were identified as far as possible, to at least genus for copepods and at least order for other animals, using a binocular microscope. Where possible the whole sample was analysed but in some cases, where total zooplankton abundance was very high, a sub-sample was analysed. Where possible, at least a hundred animals of a size that is caught 95% quantitatively by a 200 µm mesh [calculated using mesh-selection curves calculated by (Nichols and Thompson, 1991)] were counted from each sample. Measurements of length and width were also made of at least 100 animals, or all the animals present if the total was less than 100, from each sample using a calibrated eyepiece graticule. Animal lengths were sorted into length groups of 50 µm intervals between 100 µm and 1000 µm, and 1000 µm intervals between 1000 µm and 10 000 µm.

In the analysis to compare the two gear types, only the U-Tow samples at either end of the tow, and therefore directly comparable to the net samples, were used. However, samples left on the filtering section of the PSM during retrieval of the U-Tow were discarded. This was due to the possibility of plankton being washed off by turbulent water from the ship’s wash, and as water is drained out of the PSM. Bray–Curtis similarity coefficients between individual sample measures of species abundance (numbers m⁻³), species composition (proportion contributed by each species to total abundance) and length frequency distributions were calculated using the CLUSTER routine from Plymouth Routines In Multivariate Ecological Research (PRIMER) (Clarke and Warwick, 1994). These were mapped as non-metric multi-dimensional scaling (MDS) plots. Analyses of similarities (ANOSIM) were performed to test for differences between all WP2 net samples and all U-Tow samples with respect to species abundance, species composition and length frequency distribution. These multivariate techniques were used as they compare samples on the extent to which particular species are found at similar levels of abundance (Clarke and Warwick, 1994). This was shown previously to be important (DeVries and Stein, 1991).

To further examine the proportion of animals retained by the PSM, in the laboratory a known number of adult Calanus (a large copepod) and Sagitta (a large chaetognath) (both animals that are quantitatively retained by a 200 µm mesh), were pumped through the PSM at flow rates comparable to those on operational tows (average 1958 l h⁻¹). The number of animals retained on the mesh and the number of animals found floating in the tank having passed through the PSM were then counted. In these trials an impellor flow meter (Kent Water Meter) measured the volume of water entering the PSM, with the standard EM flowmeter measuring the volume exiting.

**RESULTS**

**Absolute abundance**

Fifty-one WP2 net samples and 66 U-Tow samples were analysed. In total, about 25 000 animals were identified...
and about 13,000 were measured. In almost all cases, the average total zooplankton abundance estimated using U-Tow samples was markedly lower than that estimated using WP2 net samples (Figure 2a). This observation was confirmed by a one-way ANOSIM analysis which showed that sample similarities between species abundance measures from the U-Tow and WP2 net groups were significantly different to sample similarities within groups (Global $R = 0.219$, $P = 0.027$). To test whether this difference was due to skewing by unusually high measures of abundance in some samples, the analysis was repeated with a ln(abundance + 1) transformation. The abundance estimated from U-Tow samples was still lower than that estimated from WP2 samples (Figure 2b). An ANOSIM showed this difference to be significant (Global $R = 0.203$, $P < 0.001$).

The average abundance from U-Tow samples, expressed as a percentage of abundance from WP2 net samples, of all taxa was 24.41% ($n = 66$, SD = 44.02), although this was very variable even within tows (Figure 3) and a paired $t$-test showed the values from the beginning and end of a tow to be significantly different ($t_{28} = 2.3$, $P < 0.05$). To test whether WP2 net measures of abundance could be used to calibrate the U-Tow measures of abundance, a correlation analysis was performed between the average abundance from U-Tow samples, expressed as a percentage of abundance from WP2 net samples, at the beginning and end of tows where the values were less than 100%, and would therefore need calibrating. A significant positive correlation was found at the 1% level ($t_{17} = 5.73$, $r^2 = 0.68$, $P < 0.001$) (Figure 4) showing that a reasonable measure of abundance could be estimated using the WP2 net samples to calibrate abundance measures. From Figure 4 it appears that the average abundance from U-Tow samples, expressed as a percentage of abundance from WP2 net samples, decreases from the beginning to the end of the tow. However, regression analysis showed no significant relationship between the change in performance during the tow and the length of tow ($t_{17} = 2.61$, $r^2 = 0.09$, $P > 0.05$). Figure 5 shows the result of assuming a linear relationship between the average abundance from U-Tow samples, expressed as a percentage of abundance from WP2 net samples, at the beginning and end of the June tows in the Irish Sea and, using this relationship, calibrating the intermediate U-Tow samples.

The laboratory trials showed that on average 27.45% ($n = 3$, SD = 6.74) Calanus and 37.83% ($n = 3$, SD = 4.36) Sagitta were retained on the mesh. Overall an average of 29.04% ($n = 3$, SD = 5.86) of all the animals were retained on the mesh inside the PSM. These trials showed that all the water entering the PSM also exited via the outlet (Figure 1), i.e. some animals were able to pass through the PSM and out via the outlet without being retained.

Species composition and size structure

When species composition was considered (i.e. for each sample, the abundances of individual species were expressed as a percentage of the total zooplankton abundance) the samples from the U-Tow and WP2 net gave very similar values (Figure 6a) and an MDS plot showed no obvious separation of similarity coefficients (Figure 6b). A one-way ANOSIM analysis (Global $R = 0.000$, $P = 0.451$) showed that, on average, similarities between groups and within groups were the same.

Similarly, when comparing the size structure (i.e. proportion contributed by each length interval, as described in the method section, to the total number of animals measured) from samples taken by the U-Tow and WP2 net, the average length frequency distributions were comparable (Figure 7a) and an MDS plot showed no separation of sample similarity coefficients (Figure 7b). This was confirmed by a one-way ANOSIM analysis with $P$ value of 0.39 (Global $R = 0.002$).

DISCUSSION

Data from any sampler may, broadly speaking, be internally consistent (e.g. the CPR) but combining or comparing...
Fig. 3. Ratios of U-Tow abundance : WP2 net abundance, expressed as a percentage, for the beginning (filled) and end (open) of each tow.
data from other samplers is not possible unless the performance of that sampler has been thoroughly investigated. However, all too frequently, this important component of sampling is ignored and rigorous intercomparisons are hard to find in the literature.

One of the most common parameters investigated in zooplankton studies is the abundance of different species (numbers m$^{-3}$). In this investigation it is obvious that the U-Tow seriously underestimates levels of abundance (Figure 2a) even after a ln(abundance + 1) transformation to reduce the effect of any skewing by unusually high measures of abundance (Figure 2b). There are several potential reasons that could lead to differing estimates of absolute abundance. The first consideration is the patchiness of plankton. The long tows of the U-Tow mean that patches of plankton will be integrated to give an estimate of average abundance. On the other hand, when sampling with the net, the samples may come entirely from a very dense or a very sparse patch of plankton. If this were the case, one would expect occasions where the U-Tow greatly overestimated abundance compared to the WP2 net but overall levels of abundance in the two nets would be the same. However, this was not the case since the U-Tow is always underestimating abundance (Figure 2).

Further variation could be introduced by the extrusion of smaller plankton through the mesh and avoidance of the sampler by the larger and more mobile animals. It is generally expected that extrusion will be higher in high-speed samplers due to the higher water pressures pushing animals through the mesh. In contrast, avoidance will be lower in high-speed samplers due to the animal's speed not being sufficient to escape. However, small inlet

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**Fig. 4.** Comparison between average abundance from U-Tow samples, expressed as a percentage of abundance from WP2 net samples, at the beginning and end of tows, showing the line of best fit.

**Fig. 5.** Absolute abundance measured in U-Tow samples (□) and WP2 net samples (•) during June tows in the Irish Sea, and calibrated abundance from the U-Tow samples using the WP2 net samples (•).
Apertures are also associated with increased avoidance as the distance that has to be crossed to escape the sampler is so much smaller (Clutter and Anraku, 1968). In this case, extrusion and avoidance cannot explain the discrepancy between the U-Tow and WP2 nets. Firstly, there is no difference in percentage species composition relative to total abundance (Figures 5a and b), whereas you would expect to find fewer of the smaller species in the U-Tow compared to the WP2 net due to increased extrusion, and also fewer of the larger species in the net suffering most from avoidance. Secondly, and most obviously, there is no difference in the size structure of the samples (Figures 6a and b). Thus, despite the much increased speed and reduced inlet aperture, there appears to be no increase in extrusion or avoidance in the U-Tow relative to the WP2 net.

Additional considerations for deriving absolute abundance are the filtration efficiency of the samplers, which decreases as the mesh clogs, and the measurement of the flow rates. Filtration efficiency is defined as the percentage of the water presented to a sampler that is filtered (UNESCO, 1968). A drop in efficiency causes a larger acceleration front that is more easily detected by animals. Consequently, this could cause an increase in avoidance. If flow is underestimated, the volume of water filtered will be underestimated and, therefore, the measure of abundance will be overestimated. It is possible that, due to the lack of a flow meter on the PSM, the volumes of water filtered in samples from the Irish Sea tows were overestimated, resulting in an underestimation of abundance. However, a one-way ANOVA, performed on the average ratios of U-Tow abundance to...
WP2 net abundance, showed no significant differences between tows from Swansea Bay, the North Sea or the Irish Sea ($F = 1.575, P > 0.05$), i.e. our assumption of flow rates through the PSM when no flow meter was fitted are probably valid.

Pumping experiments in the laboratory resulted in an average 29.04% of animals being retained on the PSM mesh, the rest being found in the outlet water or in other parts of the PSM. The animals were not extruded through the mesh since they were much wider than the mesh size (Nichols and Thompson, 1991), implying that they travelled an alternative route through the PSM that avoided the mesh, most probably travelling underneath the mesh.

This would explain why, although there are large discrepancies in abundance estimates, species composition and size structure do not differ between the two samplers. Variations in the tautness of the mesh, which could differ with each tow and between PSMs, could also allow different numbers of animals to pass under the mesh. This could explain the variation in the levels of discrepancy between the WP2 net and the U-Tow. In a recent comparison between CPR data and those derived from WP2 nets, it has been shown that levels of abundance were much lower in the CPR (Clark et al., 2001). It may therefore be a general feature that high speed samplers may underestimate zooplankton abundance. It is widely
known that for many samplers performance may vary from deployment to deployment due to changes in conditions, e.g. particle abundance in the Nansen net (Hernroth, 1987) and the OPC (Sprules et al., 1998). It is also possible that some of the variation is caused by differences in the performance of the WP2 net, although this has been shown to be relatively stable (UNESCO, 1968).

Evidence suggests that if the average abundance from U-Tow samples, expressed as a percentage of abundance from WP2 net samples, is low at the beginning of a tow it will also be low at the end of a tow, and vice versa. Therefore, it is probably justifiable to assume a linear relationship of sampling performance within a tow.

The main conclusion from this study is that the U-Tow cannot be the only sampler used for investigations that require accurate measures of abundance or, therefore, biomass. It is necessary to take samples with another sampler, such as the WP2 net, at the beginning and end of a tow to calibrate the results from the U-Tow. However, it would be perfectly acceptable to use the U-Tow in studies based on the species composition and size structure of plankton communities. The U-Tow would be an ideal tool to use between sampling stations to identify where changes in plankton communities occur.

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