Continuous plankton records stand the test of time: evaluation of flow rates, clogging and the continuity of the CPR time-series

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The Continuous Plankton Recorder (CPR) survey is one of the most extensive biological time-series in existence and has been in operation over major regions of the North Atlantic since 1932. However, there is little information about the volume of water filtered through each sample, but rather a general assumption has persisted that each sample represents 3 m$^3$. Data from electromagnetic flowmeters, deployed on CPRs between 1995 and 1998, was examined. The mean volume filtered through samples was 3.11 m$^3$ and the effect of clogging on filtration efficiencies was not great. Consequently, even when the likely variations in flow due to clogging are taken into account, previously identified links between zooplankton abundance and climatic signals remain strong.

INTRODUCTION

Long term ecological time-series are becoming increasingly important research datasets with the expansion of studies documenting how biological systems have responded to climate change (Colebrook, 1986; Forchhammer et al., 1998; Reid et al., 1998a; Post and Stenseth, 1999; Beaugrand et al., 2000; Forchhammer and Post, 2000). However, funding constraints mean there are relatively few such time-series that span many decades, particularly in marine systems. Without question, one of the most extensive marine biological time-series is provided by the Continuous Plankton Recorder (CPR) survey. This survey, which is currently managed by the Sir Alister Hardy Foundation for Ocean Science, was initiated by Alister Hardy in the 1930s following his development of the CPR (Hardy, 1939). The CPR is an instrument that can be towed at high speed from ships-of-opportunity (i.e. non-research ships) over extended tracts. The fundamental design of the CPR, and methods of analysis for zooplankton and phytoplankton, have remained unchanged since 1948 and 1958, respectively (Colebrook and Robinson, 1986), with over 400 taxa being identified and counted (Warner and Hays, 1994), enabling long term changes in plankton populations to be studied.

As the CPR time-series has lengthened, so the value of the data has increased. Beginning in the 1980s, CPR data began to reveal systematic changes in the zooplankton communities of the NE Atlantic, with these changes being linked to annual weather indices and with parallel trends also occurring at other trophic levels (Colebrook, 1978; Aebischer et al., 1990; Dickson et al., 1988; Reid et al., 1998b). More recently, long term trends in the abundance of certain key zooplankton taxa have been shown to be strongly correlated with the North Atlantic Oscillation, a widely used index for annual weather patterns in Northern Europe (Fromentin and Planque, 1996; Planque and Taylor, 1998).

Despite this wide use of the CPR data, doubt has remained surrounding the continuity of the time-series. While the abundance of plankton in the samples is determined using standard microscopic analysis, the volume of water filtered in the collection of these organisms has not been routinely measured (Valne et al., 1998). Therefore, it has been assumed that a constant volume of water is filtered through each sample. However, it is well known that when plankton is abundant, the filtering meshes of nets...
can become clogged with material, which then reduces the subsequent flow rate (Brander et al., 1993; Walne et al., 1998). Hence if the extent of clogging has varied systematically throughout the CPR time-series, artefacts may have been introduced into the time-series.

Recently, electromagnetic flowmeters have been developed which can measure the flow rate through CPRs (Walne et al., 1998). Here we examine data from the first 4 years of these flowmeter deployments and quantify the relationship between the volume of water filtered per sample and the extent of clogging. We then use this relationship on historically collected samples to predict the respective volumes of water filtered in the collection of each sample, and in this way we objectively reconstruct the CPR time-series. Hence we establish the true continuity of the CPR time-series, and validate the trends in zooplankton abundance that have previously been identified.

**METHOD**

**Background to CPR survey**

To date, over 200 000 samples have been analysed by the CPR survey, representing extensive spatial and temporal coverage. CPRs are towed at a depth of 6–7 m (Hays and Warner, 1993). Water enters through an inlet aperture of 1.61 cm² and passes through a 270 µm silk filtering mesh [for a full description on how CPRs sample see (Warner and Hays, 1994)]. Samples corresponding to 10 nautical miles (18.5 km) of tow (equivalent to 3 m³ of water filtered assuming 100% filtration efficiency) then undergo standard analysis: phytoplankton abundance is first estimated from a visual assessment of the coloration and accorded a greenness index (from 0 to 6.5) by reference to standard colour charts, then the organisms collected on the silk are identified and counted (Colebrook and Robinson, 1986; Warner and Hays, 1994). The level of identification varies: some organisms are identified to species, others to genus or class only.

**Electromagnetic flowmeters**

The electronic flowmeter designed for the CPR is described by Walne et al. (Walne et al., 1998). Flow rate (recorded in l min⁻¹) is stored on electronic loggers and then downloaded onto a computer on return of the CPR to the laboratory. Time and position of deployment and retrieval are recorded so that the volume of water filtered can be determined for each sample (Walne et al., 1998). Preliminary screening of the raw data was carried out and tows with large variances in their flow rate (due to poor flowmeter performance) were discarded from analysis. The volume (m³) filtered per sample was then calculated from the corresponding average flow rate.

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Fig. 1. Map of tow routes with operational flowmeters, 1995–1999, illustrating the three spatial scales used to subdivide the data. The four regions (divided by dotted lines) were separated according to oceanographic area: R1, North Sea; R2, Northern Atlantic; R3, Central Atlantic; R4, Irish Sea.
RESULTS

Assessment of flow data collected on operational CPR tows

Flowmeters were deployed on CPRs between 1995 and 1999 on 15 routes covering several areas of the North Sea and North Atlantic (Figure 1). In total, they were deployed on 286 tows, generating flow data for nearly 2000 samples. The expected flow rate to produce a total filtered volume of 3 m$^3$ per sample is generally ~70–80 l min$^{-1}$ and many examples of flow rates that lay close to this range of values were recorded (Figure 2).

Quantification of the relationship between the volume filtered and extent of clogging

The mean volume filtered per sample was 3.11 m$^3$ (SD = ± 0.8 m$^3$, Figure 3). As an initial examination of the importance of clogging, we examined the mean volume filtered at different levels of mesh coloration, total phytoplankton numbers and total small (<2 mm) zooplankton numbers (Figure 4). The mean volume filtered decreased with increased coloration of the mesh and increased plankton numbers. However, even with the highest plankton numbers recorded, maximal clogging only decreased the volume filtered per sample by ~20%. It was readily apparent that the observed variation in volumes filtered per sample was relatively trivial when compared with seasonal differences in plankton numbers.

We derived empirical relationships between the volume filtered and plankton numbers per sample over three spatial scales (shown in Figure 1): first, for the individual tow routes, then for data grouped into four geographical

\begin{figure}[h]
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\includegraphics[width=\textwidth]{fig2.png}
\caption{Two examples of raw flow rate data recorded on CPRs. These tows were on route R in the southern North Sea during December 1997 (solid line) and September 1998 (heavy solid line).}
\end{figure}

\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{fig3.png}
\caption{Frequency histogram of the recorded volumes filtered (m$^3$) per sample.}
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\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{fig4.png}
\caption{The relationship between the mean volume filtered per sample (SEM bars) and sample colour (greenness index, a), total phytoplankton abundance (b), and for total traverse (i.e. small) zooplankton (c).}
\end{figure}
areas which corresponded roughly to oceanographic areas, and finally for the entire dataset. When stepwise multiple regression analyses were performed, the amount of variation in the volume filtered per sample that could be explained by plankton numbers decreased from a maximum of 95% to a minimum of 20% as the spatial scale increased.

To produce a single generic equation relating the volume filtered per sample to plankton numbers on the filtering meshes, we ran a stepwise multiple regression using the 19 phytoplankton and nine zooplankton taxa that had the greatest overall abundance, and therefore might be expected to have the most significant effect on flow. In addition, the remaining plankton taxa were grouped into general taxonomic categories (e.g. total centric diatoms, total dinoflagellates, total copepods) and also included in analyses. This analysis showed that in the entire dataset, 15% of the variation in the volume filtered per sample could be explained by the following six variables: numbers of total phytoplankton, *Thalassiosira* sp., *Noctiluca scintillans*, total centric diatoms, *Nitzschia seriata* and total *Rhizosolenia* sp. In order to verify that a linear relationship was the most appropriate type to use for this particular dataset, the analyses were repeated using a number of data transformations. However, these did not improve the goodness of fit.

**Use of empirically derived relationship to predict the volumes filtered for historically collected samples**

Using the various equations (one generic and four regional) relating the volume filtered to the extent of clogging, we recalculated plankton abundances for samples collected between 1995 and 1998, and then compared them with the absolute abundances derived from the measured flow as well as abundances calculated by assuming 3 m$^3$ were filtered per sample. The coefficients of determination ($r^2$) between these different abundance measurements indicated that while the assumption of 3 m$^3$ per sample is reasonably sound, using the volumes filtered predicted from the extent of clogging gave improved estimates of absolute abundance (Table I). This is exemplified by an $r^2$ of 0.99 between actual and recalculated abundance of *Calanus finmarchicus* (Figure 5).

The generic equation to predict the volume filtered per sample was applied to the historical dataset (1948–present, representing nearly 173 000 samples), and the resulting ‘predicted’ plankton abundance values compared with those calculated when assuming that the volume filtered remained constant at 3 m$^3$. Annual means of *C. finmarchicus*, for 1958–1998, did not differ significantly ($P > 0.05$ in a paired sample $t$-test) when using a constant value or the predicted values for the volume filtered. The relationship between the predicted abundance of *C. finmarchicus* and the NAO index (Fromentin and Planque, 1996) was strong for 1958–1995 (Figure 6).

**DISCUSSION**

The importance of long term monitoring of biological systems to study and detect responses to environmental change has long been established. A prerequisite of long term studies is that data collection is carried out in a consistent manner to establish the continuity of such time-series. However, in reality, the logistical difficulties involved often mean that consistency is not always achieved. For example, data from the California Cooperative Oceanic Fisheries Investigations (CalCOFI) have provided hydrographic measurements in the southern California bight since 1949. However, methods for zooplankton sampling have been changed twice (Ohman and Smith, 1995), potentially disrupting the continuity of the time-series. Under international programmes such as the Joint Global Ocean Flux Study (JGOFS), which involves

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Abundance$^a$</th>
<th>Abundance$^b$</th>
<th>Abundance$^c$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total copepods</td>
<td>0.97</td>
<td>0.90</td>
<td>0.92</td>
</tr>
<tr>
<td>Calanus finmarchicus</td>
<td>0.94</td>
<td>0.98</td>
<td>0.99</td>
</tr>
<tr>
<td>Total zooplankton</td>
<td>0.96</td>
<td>0.94</td>
<td>0.98</td>
</tr>
</tbody>
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$^a$Calculated using a constant volume filtered of 3 m$^3$ per sample.
$^b$Sample volumes predicted using generic equations.
$^c$Sample volumes predicted using regional regression equations.
over 20 countries with six time-series stations spanning three oceans, standardized protocols are followed (Knap et al., 1996) to enable spatial and temporal inter-comparisons of biological and hydrographic measurements. To maintain the true continuity of the CPR survey, methods for the collection and analysis of samples have remained unchanged since 1948, with the exception of a modification to the tail fin (between 1975 and 1986) for improving the stability of the instrument at high speeds (Hays and Warner, 1993). One anomaly in the sampling protocol has been the absence of information on the volume of water passing through each sample, due to lack of flow measurements on CPRs. The importance of determining filtration efficiencies of plankton nets to enable the calculation of absolute plankton abundances has been recognized for decades (McQueen and Yan, 1993). However, flowmeters have not been used on CPRs historically because meters that are small enough to fit into the narrow water tunnel of the instruments, and that are able to record and store data over long periods, were not available. It is only relatively recently that electromagnetic (EM) flowmeters have been developed for the CPR that do not impede the flow of water through the instrument, and are able to log results over extensive towing (Walne et al., 1998).

There were several clear findings from our results. First, the flow recorded by EM flowmeters during the period 1995–1998, over an extensive spatial scale, had a mean of 3.11 m$^3$, close to the previously assumed value of 3 m$^3$. Second, the effect of clogging is present (Figure 4) but the absolute effects on water flow are relatively small. There is very little information available regarding the clogging and filtration coefficients of high-speed plankton samplers (Hays, 1994); however, samplers often filter more than the theoretical quantity of water that would be expected from the inlet area, leading to filtration efficiencies in excess of 100% (LeFèvre, 1973). Two factors that may mitigate the extent of clogging in CPRs are the relatively small size of the inlet aperture and the movement of the mesh. Reduction in the size of the inlet aperture decreases the amount of water entering, which prevents clogging under normal working conditions, hence improving the reliability of quantitative data from samplers (LeFèvre, 1973). Furthermore, as the CPR silk is continuously moving during towing, the effect of clogging is less than expected when compared with other samplers (e.g. U-Tow) (Hays et al., 1998).

Third, analysis of the dataset on three spatial scales indicated that it was possible to establish much stronger relationships between clogging and flow for individual tow routes compared with the entire dataset. This is presumably due to spatial variations in the plankton taxa sampled in different areas. For instance, centric diatoms and dinoflagellates were most abundant in the North Sea and Atlantic regions, whilst the diatom Thalassiosira sp. was more abundant in the North and South Atlantic, with the dinoflagellate N. scintillans accounting for nearly 20% of the total plankton in the Irish Sea samples.

Finally, the variation between the volumes filtered per sample (coefficient of variation = 0.26) was relatively trivial compared with the variation in taxon abundance (e.g. C. finmarchicus coefficient of variation = 9.8) and hence the implications of variable flow rates for recalculating absolute plankton abundances were relatively minor, especially since CPR data are usually presented as monthly or annual means. As a consequence of these
REFERENCES


