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Using continuous plankton recorder data

A.J. Richardson [a,b,c,*], A.W. Walne [a], A.W.G. John [a], T.D. Jonas [a], J.A. Lindley [a], D.W. Sims [d], D. Stevens [a], M. Witt [e]

[a] *Sir Alister Hardy Foundation for Ocean Science (SAHFOS), The Laboratory, Citadel Hill, Plymouth PL1 2PB, UK*
[b] *CSIRO Marine and Atmospheric Research, Cleveland, Qld. 4163, Australia*
[c] *Department of Mathematics, University of Queensland, St. Lucia, Qld. 4072, Australia*
[d] *Marine Biological Association of the UK, The Laboratory, Citadel Hill, Plymouth PL1 2PB, UK*
[e] *Centre for Ecology and Conservation, University of Exeter in Cornwall, Tremough TR10 9EZ, UK*

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Abstract

The continuous plankton recorder (CPR) survey is the largest multi-decadal plankton monitoring programme in the world. It was initiated in 1931 and by the end of 2004 had counted 207,619 samples and identified 437 phyto- and zooplankton taxa throughout the North Atlantic. CPR data are used extensively by the research community and in recent years have been used increasingly to underpin marine management. Here, we take a critical look at how best to use CPR data. We first describe the CPR itself, CPR sampling, and plankton counting procedures. We discuss the spatial and temporal biases in the Survey, summarise environmental data that have not previously been available, and describe the new data access policy. We supply information essential to using CPR data, including descriptions of each CPR taxonomic entity, the idiosyncrasies associated with counting many of the taxa, the logic behind taxonomic changes in the Survey, the semi-quantitative nature of CPR sampling, and recommendations on choosing the spatial and temporal scale of study. This forms the basis for a broader discussion on how to use CPR data for deriving ecologically meaningful indices based on size, functional groups and biomass that can be used to support research and management. This contribution should be useful for plankton ecologists, modellers and policy makers that actively use CPR data.

Keywords: Time series; Monitoring; CPR; Phytoplankton; Zooplankton; Diet; Size

1. Introduction

The continuous plankton recorder (CPR) survey is the largest multi-decadal plankton monitoring programme in the world. The Survey was initiated by Alister Hardy in 1931 (Hardy, 1939) and has since evolved into a unique marine monitoring programme that provides the scientific community with its best long-term measure of the state of oceanic plankton in the North Sea and North Atlantic. Currently data

* Corresponding author. Tel.: +61 7 38267183; fax: +61 7 38267222.
E-mail address: anthony.richardson@csiro.au (A.J. Richardson).

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on the near-surface abundance of phyto- and zooplankton are available monthly from 1946, and these will shortly be supplemented by historical CPR data from 1931 to 1938 currently only in paper format (Stevens, Richardson, & Reid, in press). To the end of 2004, this dataset amounts to 207,619 samples counted for 437 phyto- and zooplankton taxa, many of which are identified to the species level. Since 1991, the CPR survey and the dataset have been managed by the Sir Alister Hardy Foundation for Ocean Science (SAHFOS). This dataset has been the foundation for high-impact research over more than five decades, forming the basis of 23 *Nature* and *Science* articles and almost 1000 publications (see reviews by Reid, Colebrook, Matthews, Aiken, & Continuous Plankton Recorder Team, 2003; Stevens et al., in press). Over recent years, CPR data have become increasingly important as a baseline to assess impacts of global change on pelagic ecosystems (Beaugrand, Brander, Lindley, Souissi, & Reid, 2003; Beaugrand, Reid, Ibanez, Lindley, & Edwards, 2002; Edwards & Richardson, 2004; Greene et al., 2003; Hays, Richardson, & Robinson, 2005; Richardson & Schoeman, 2004). This role helps fulfil regional, national, and international marine obligations concerned with biodiversity loss, climate change, eutrophication, pollution, harmful algal blooms and sustainable fisheries (Brander, Dickson, & Edwards, 2003).

Historically, data from the CPR survey have not been easily available to the research community. At the end of the 20th century, however, there was a significant change in the philosophy of data accessibility at SAHFOS (Stevens et al., in press). CPR data are now freely available through a licence agreement, and some data are currently available via the web and more are likely to be in the future. With this new, more-open data-access policy, the number of data requests for CPR data has been growing steadily over recent years (Stevens et al., in press).

In view of the scientific importance of the CPR dataset, its expanded use by the research community, and its recently enhanced role underpinning marine management, it is timely to provide practical recommendations on how best to use CPR data, and for the first time present a comprehensive description of the taxa counted in the Survey. We begin by providing the necessary background, such as information on the CPR itself, the routes sampled, how samples are analysed, and many of the biases associated with the data. We then supply information essential to using CPR data, including descriptions of each CPR taxonomic entity, the idiosyncrasies associated with counting many of the taxa, the logic behind taxonomic changes in the Survey, the semi-quantitative nature of CPR sampling, and recommendations on accounting for missing data. This information forms the basis for a broader discussion on how to use CPR data for deriving ecologically meaningful indices that underpin marine research and management. Procedures for developing indices based on size, functional groups and biomass are detailed. We conclude by providing information on concomitant environmental data and the data access policy.

We limit our discussions here to the core survey in the North Atlantic, but draw the attention of the interested reader to the North Pacific CPR survey operated by SAHFOS since 1997 (e.g., Batten, Welch, & Jonas, 2003), and CPR surveys operated by other organisations in the Southern Ocean (e.g., Hunt & Hosie, 2003) and the Western Atlantic (e.g., Jossi, John, & Sameoto, 2003). As these surveys have some differences in the CPRs themselves, the instrumentation attached, the counting methodology (Reid et al., 2003), and the different species and stages counted, they will not be discussed here. We hope that this critical look at how best to use CPR data will prove indispensable for plankton ecologists and modellers actively using CPR data or wishing to do so.

2. The continuous plankton recorder

The longevity of the CPR survey is a testament to its ingenious and robust design by Sir Alister Hardy. A prototype device was towed over 1300 miles in Antarctic waters in 1925–1926 (Hardy, 1926). This device was then modified and has remained relatively unchanged since 1931 (Reid et al., 2003). The self-contained automatic plankton recorder collects plankton continuously from a standard depth of ~7 m (Hays & Warner, 1993). A fixed depth close to the surface was chosen to give the most consistent results in the relatively shallow North Sea (Hardy, 1939). Water enters the CPR through a square aperture 1.27 cm on a side (1.61 cm^2), about the size of a thumbnail, and flows down an expanding tunnel, which effectively reduces the water pressure to minimise damage to the captured plankton, and exits through the rear of the device (Fig. 1). The movement of the water past the CPR turns an external propeller at the

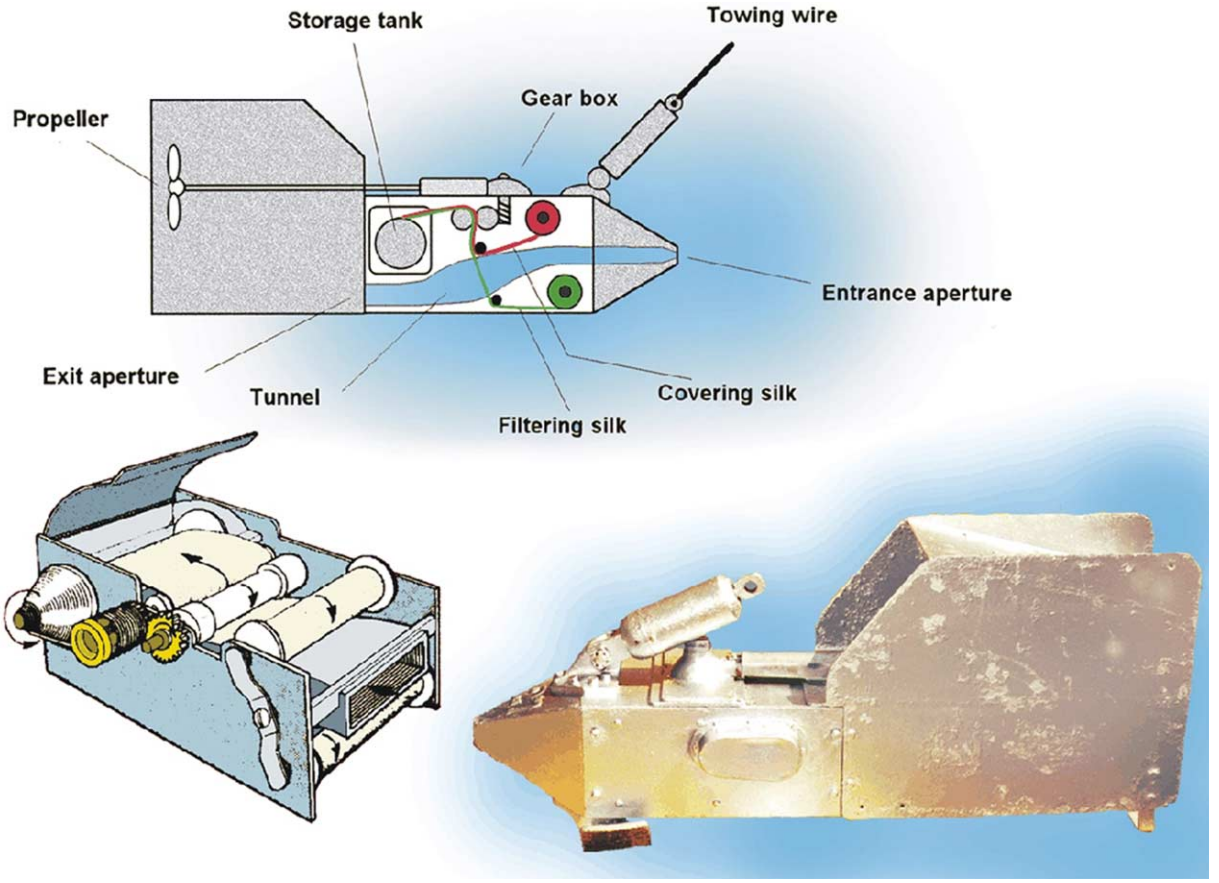


Fig. 1. A cross-section of the CPR, its internal mechanism and CPR body.

rear of the device that operates a drive shaft and gear system, which advances the silk filtering mesh. Plankton in the water are filtered onto this constantly moving band of silk. The filtering silk meets a second band of covering silk, effectively sandwiching the plankton, and is then wound onto a spool in a storage tank containing formalin. The mesh size of the silk is 270 μm. This mesh size was chosen not only to give an adequate representation of copepods, cladocera, pteropods, and chaetognaths, but also to give an indication of blooms of large phytoplankton, while reducing clogging by small phytoplankton cells (Hardy, 1939). Despite the relatively large size of the mesh, small phytoplankton are still retained on the silk (this is explained more fully in Section 7.2). Detailed descriptions of the CPR device, its sampling characteristics, and modifications in its design over the lifespan of the Survey, such as changes to the diving plane and box tail, can be found in Batten, Clark, et al. (2003); John and Reid (2001); Jonas, Walne, Beaugrand, Gregory, and Hays (2004); Reid et al. (2003) and Warner and Hays (1994).

3. Sampling routes

The ability of the CPR survey to collect hundreds of samples throughout an ocean basin is only possible because the CPR is a simple, robust device towed behind ships of opportunity (SOOPs) on their normal trading routes at their conventional operating speeds, usually 15–20 knots, unaccompanied by SAHFOS staff. This is in stark contrast with conventional net and bottle sampling of phyto- and zooplankton, which is generally restricted to expensive research vessels with limited spatial and temporal coverage.

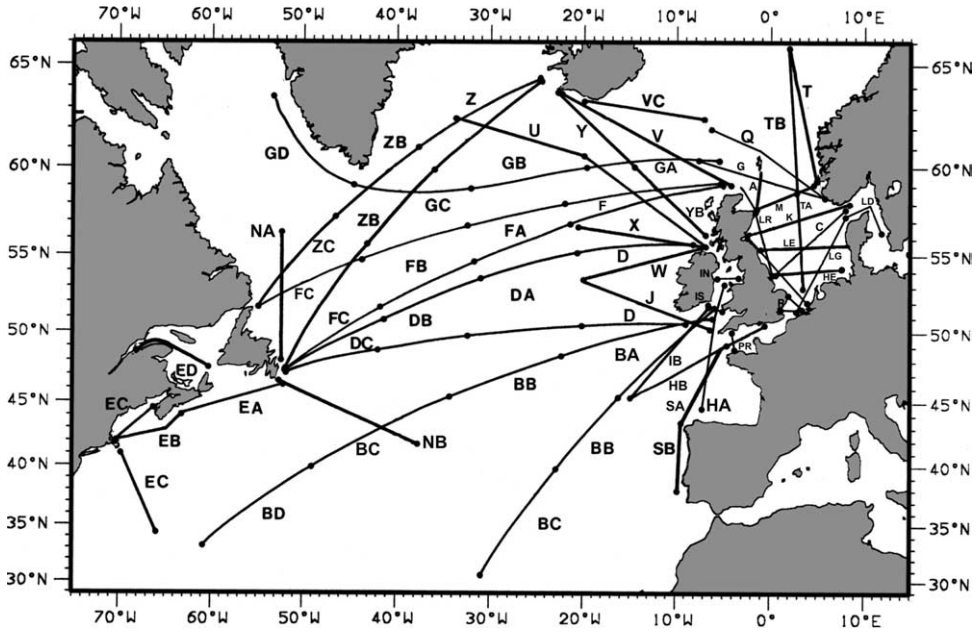


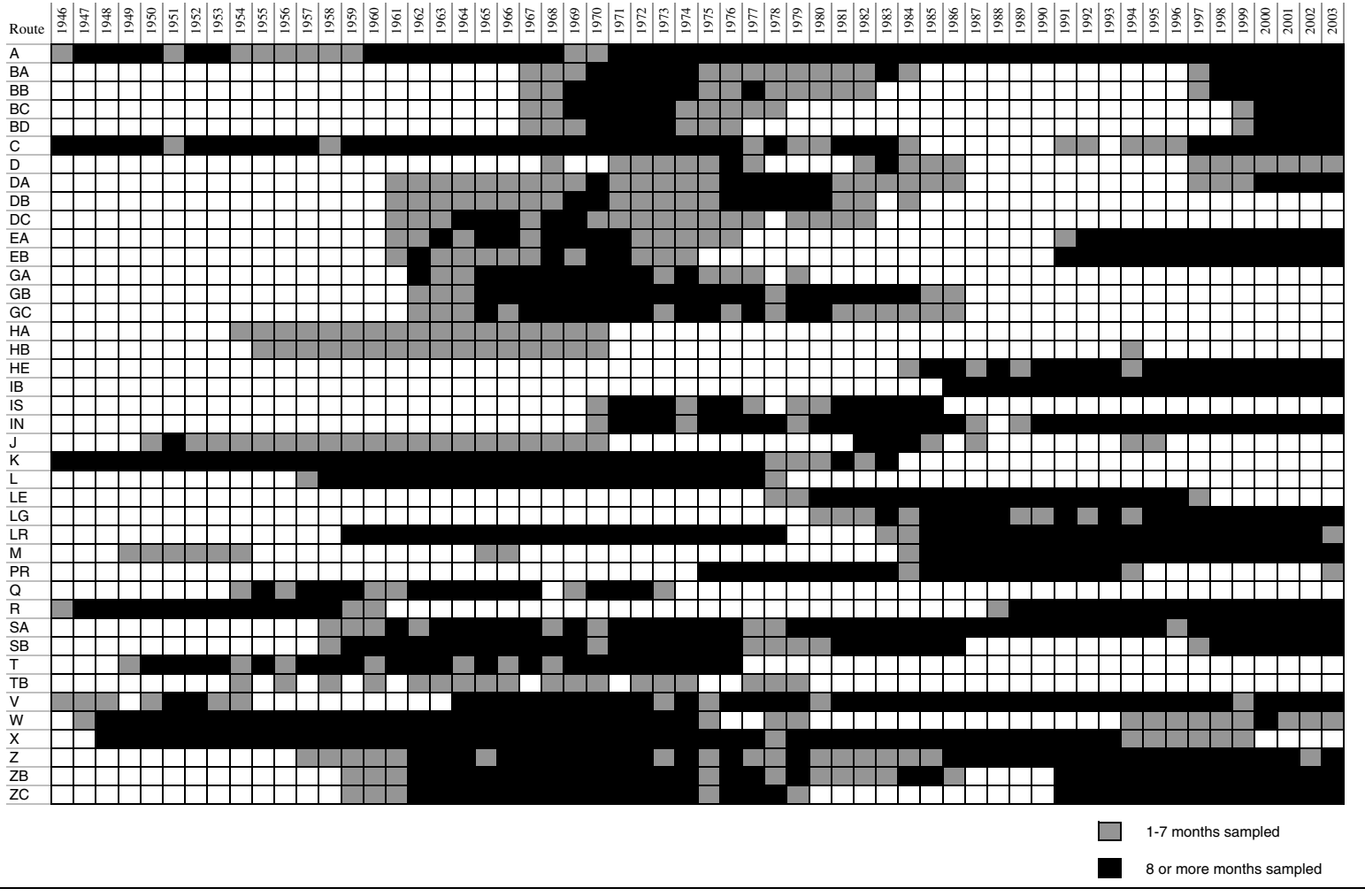
Fig. 2. Map of major routes towed. The number of years each route has been towed is shown in Table 1. Some routes have been shifted in position (e.g., BC, ZB, ...) but their designation has been retained because they were sampling in the same general vicinity and plankton regime.

With the ability to collect samples monthly over large space scales come some associated biases. The restriction to commercial shipping routes means that large areas of the North Atlantic are not sampled (Fig. 2). Another spatial bias is that the same CPRs are usually used for the same route each month because of logistical considerations, rather than being randomly assigned to a route. This maintains consistent sampling for each route but may lead to systematic biases if each CPR has slightly different sampling characteristics. The CPR also misses some localised coastal features, as it does not generally sample closer than 1 nautical mile from the coast, as the crew usually deploy and retrieve the instrument when the vessel is in sufficiently deep water outside the harbour. There are also breaks in the temporal sampling of routes. Occasional short breaks in tows, usually less than several months, occur when vessels towing CPRs break down or have to dry dock for routine maintenance. There are longer breaks when a vessel is redeployed or a shipping company stops towing a certain route, and another vessel plying the same route has to be found and then fitted with a specialised towing point (davit). Breaks of many years and terminations of routes are a result of funding difficulties; routes can be reinstated only when sufficient funding is available. The number of years each route has been towed is shown in Table 1; some such as the A, X and V routes have been towed for most of the last 50 years (although the X route is no longer towed), while others such as the SB, EA and EB routes have had long hiatuses before being reinstated.

These constantly evolving additions and cessations of routes have led to an expansion and contraction of the sampling over the history of the Survey (Fig. 3). Maps of sampling each year from 1946 to 2003 are shown on the SAHFOS website (www.sahfos.org). These changes in the coverage of the survey through time can lead to additional biases. For example, a region sampled by several CPR routes may through time show a shift in the mean sampling position (e.g., in latitude) if some routes have been introduced or discontinued (Southward et al., 2005). Although such biases are often overlooked, they should be considered when interpreting CPR results (see Beaugrand, Ibanez, & Lindley (2003) for more details).

The Survey reached its greatest coverage in the late 1960s and early 1970s, with a peak of 5506 samples in 1970, before it contracted in the 1980s (Fig. 3; Table 1). This decline was a worldwide phenomenon; 40% of the long-term oceanographic monitoring programmes initiated after World War II were terminated during the 1980s because environmental monitoring was considered poor science by administrators

Table 1
Chart of the long-term status of continuous plankton recorder routes



All routes with more than 15 years sampling are included. Location of routes shown in Fig. 2.

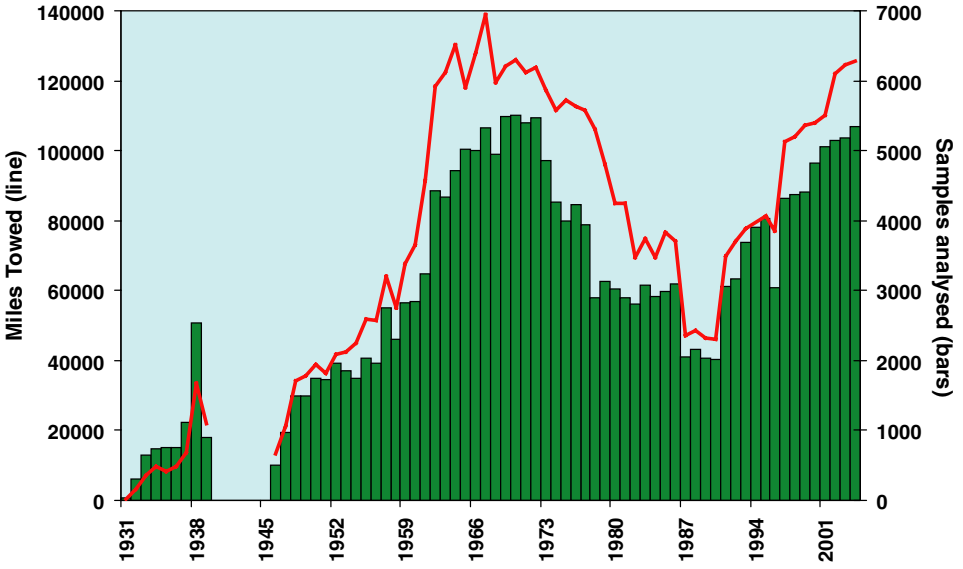


Fig. 3. Miles towed and number of samples analysed by the CPR survey since 1931.

(Duarte, Cebrián, & Marbá, 1992). In the UK this culminated in the Survey ceasing to operate as part of the Natural Environment Research Council in 1989 and all staff being declared redundant (Reid et al., 2003; Southward et al., 2005). A rescue operation led to the creation of the Sir Alister Hardy Foundation for Ocean Science (SAHFOS) in 1990, which has continued with funding primarily from the UK, with additional support by other countries. The negative perception of long-term monitoring only reversed during the mid-1990s, when the consequences of global change were seen as important both politically and scientifically. This change has markedly improved the fortunes of the CPR survey. In 2004, the Survey reached a total of 5,000,000 nautical miles sampled, equivalent to a distance 12 times to the moon and back.

4. Sample pre-processing

When the CPR is returned to the laboratory after towing, the filtering silk, a continuous record of the plankton on that tow, is removed from the internal mechanism and unwound (typically a 500 nautical mile tow will use about 5 m of silk). For ease of plankton counting, the silk is then divided into samples representing 10 nautical miles of tow. The start and end cutting points for each sample are calculated from the exact length of the filtering silk, the speed of the silk advance through the mechanism (assumed constant for each tow), and from information on a log sheet completed by the officers of the towing vessel. The log sheet records the exact time and position of CPR deployment and recovery, in addition to intermediate times and positions of alterations in the course. Calculations assume the vessel does not alter course or speed between successive points on the log sheet.

Position (latitude and longitude) and local time for each sample are also calculated, corresponding to the geographic position of the CPR when the mid-point of the sample is in the middle of the filtering tunnel. Comparison between the calculated position and data from vessels where a GPS record was available suggests the position assigned to CPR samples is accurate to within 10–20 nautical miles. The volume of water filtered for each 10 nautical mile sample is $\sim$3 m^3 (mean = 3.27 m^3, SD = 0.71 m^3, $n = 1723$, Jonas et al., 2004; see also Walne, Hays, & Adams, 1998). Although samples represent 10 nautical miles of tow, the continuously advancing nature of the CPR filtering silk (as opposed to a stepped advance used in modern plankton recorders) results in a sample containing plankton from 15 nautical miles of towing. (Note that this was reported by Batten, Clark, et al. (2003) as 20 nautical miles.) Of the plankton on the cut samples, 50% comes from the central 5-mile section of tow, and 25% from each of the preceding and following 5-mile sections (see Fig. 4 for more details).

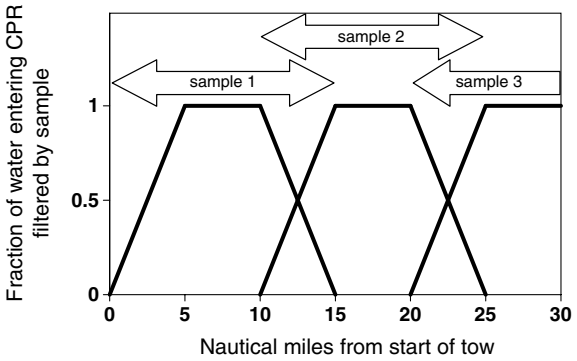


Fig. 4. Collection of plankton on a continuously moving band of silk. The start of Sample 1 enters the CPR filtering tunnel at mile 0. As it advances across the filtering tunnel, the proportion of the water that is filtered by Sample 1 increases until the sample start leaves the tunnel at mile 5 and all the water entering the CPR is filtered by Sample 1. At mile 10, the end of Sample 1 (and start of Sample 2) enters the tunnel. As this boundary advances across the tunnel, a decreasing proportion of the filtered sea water passes through Sample 1 and an increasing proportion is filtered by Sample 2. The boundary leaves the tunnel at mile 15 and then all the sea water entering the CPR is filtered by Sample 2. The time and position assigned to each sample corresponds to when the mid-point of each sample is in the middle of the filtering tunnel. Sample 1 is assigned a position 7.5 nautical miles from the start of the tow and Sample 2 a position 17.5 nautical miles from the start.

5. Sample processing

Alternate 10 nautical mile samples are counted on most routes, except short routes such as the PR and IN (Fig. 2) where every sample is counted. Samples are distributed to CPR staff (known as analysts) in a semi-random manner, so that an individual does not receive successive samples on a route.

There are four separate stages of analysis carried out on each CPR sample, with each focusing on a different aspect of the plankton: viz. (1) overall chlorophyll (the phytoplankton colour index; PCI); (2) larger phytoplankton cells (phytoplankton); (3) smaller zooplankton (zooplankton traverse); and (4) larger zooplankton (zooplankton eyecount). The phytoplankton and zooplankton traverse counting methods are on-silk counting procedures, whereas specimens are removed from the silk for zooplankton eyecount. It is intended here to provide sufficient context to understand later sections on changes in the way taxonomic entities are counted, and on deriving integrated indices from CPR data. A more exhaustive description of analysis procedures used to analyse CPR samples can be found elsewhere (e.g., Colebrook, 1960).

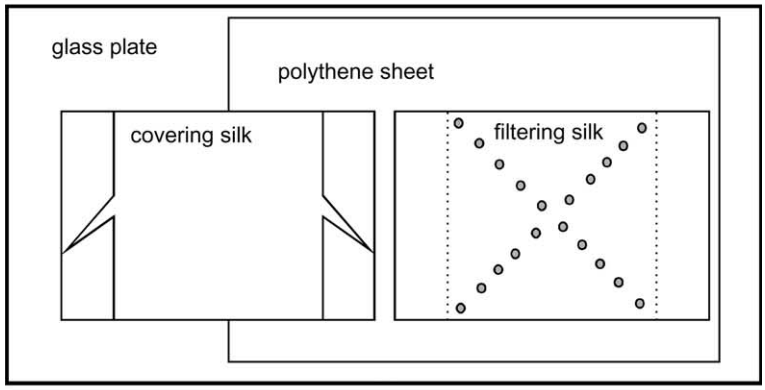
5.1. Phytoplankton colour index

After the silk has been marked into 10 nautical mile samples but prior to cutting, each sample is visually assigned a greenness index by comparison with standard colour charts: viz. no colour, very pale green, pale green, and green (Robinson & Hiby, 1978). These four levels of the phytoplankton colour index (PCI) represent the amount of phytoplankton pigment on the silk and have been assigned numerical values on a ratio scale based on acetone extracts using spectrophotometric methods (Colebrook & Robinson, 1965).

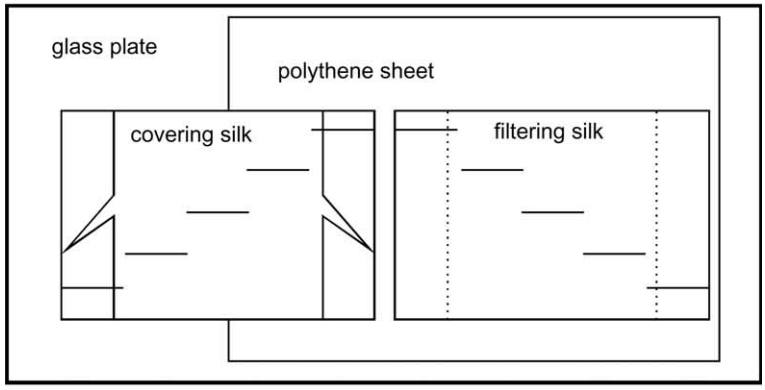
5.2. Phytoplankton analysis

Following the assessment of PCI, the silk is cut into sections (samples), representing 10 nautical miles of tow. Each sample is then laid out on a purpose-built stage (Fig. 5(a)) and 10 fields on each of two diagonals of the filtering silk are counted at 450× magnification (using the Watson Bactil microscopes; Table 2) for phytoplankton (Fig. 5(b)). These 20 fields amount to 1/10,000 of the area of the filtering silk. (Note that Reid et al. (2003) describe the current methodology since 1958 as diagonal transects across both the covering and filtering silks, and Warner & Hays (1994) and Batten, Clark, et al. (2003) give the proportion of the silk counted as 1/8000.) The analyst centres the field of view (295 μm across) on a grid square of the mesh and records the taxa present (and not the more time-consuming total number of individuals of each species per field). This

(a) Mobile glass stage



(b) Phytoplankton Analysis



(c) Zooplankton Traverse

Fig. 5. (a) Mobile glass stage used for sample analysis. Microscope removed so silk and stage are clearly visible. (b) Phytoplankton analysis showing 20 fields (295 μm across) of the filtering silk. (c) Zooplankton traverse showing the stepped traverse (field of view 2.05 mm) across the filtering and covering silk.

is repeated for 20 fields, giving the total number of fields (20 abundance 'categories') in which each taxon has been seen. Each of these 20 categories has an associated accepted value (Table 3), representing the total number of individuals of a species that are likely in the fields examined. This has been derived from the Poisson distribution, which assumes organisms are randomly distributed on the silk (Colebrook, 1960). These accepted values are then multiplied by 10,000 to estimate the phytoplankton abundance on the filtering silk. Unfortunately, because of historical data storage limitations before computers were used, these 20 abundance values

Table 2
A summary of the microscopes used throughout the history of the CPR survey for phytoplankton analysis and zooplankton traverse

Years	Make	Type	Field size (mm)		Magnification	
			Phytoplankton	Zooplankton	Phytoplankton	Zooplankton
1932–1958	Unknown	Monocular, traversing	Unknown	Unknown	2/3″ obj ×10 eye	2/3″ obj 6× eye
1958-present	Watson Bactil	Binocular	0.295 ± 0.01	2.06 ± 0.05	30× obj 10× eye 1.5× head	6× obj 6× eye 1.5× head
1995-present	Micro Instruments	Mark 1, Trinocular	0.295 ± 0.01	2.06 ± 0.05	40× obj 12.5× eye	5× obj 15× eye
2004-present	Micro Instruments	Mark 2, Trinocular, Ergonomic head	0.295 ± 0.01	2.06 ± 0.05	50× obj 12.5× eye	5× obj 12.5× eye

Table 3
Phytoplankton analysis: calculating abundance of a particular taxonomic entity in a CPR sample

Total number of fields	Accepted value	Abundance per sample	Recorded abundance per sample
1	1	10,000	15,000
2	2	20,000	15,000
3	3	30,000	35,000
4	4	40,000	35,000
5	6	60,000	65,000
6	7	70,000	65,000
7	9	90,000	95,000
8	10	100,000	95,000
9	12	120,000	130,000
10	14	140,000	130,000
11	16	160,000	170,000
12	18	180,000	170,000
13	21	210,000	225,000
14	24	240,000	225,000
15	28	280,000	300,000
16	32	320,000	300,000
17	38	380,000	420,000
18	46	460,000	420,000
19	60	600,000	750,000
20	90	900,000	750,000

The total number of fields out of 20 in which the taxon was present is then converted to an accepted value, representing the total number of cells of that taxon present in those 20 fields (based on the Poisson distribution). This is then then multiplied by 10,000 to give the abundance per sample, and then compressed into 10 values (because of historic data limitations) to give the recorded abundance per sample in the database.

are compressed into 10 by averaging (Table 3). Phytoplankton abundance values are thus restricted to 10 discrete values and can be considered semi-quantitative estimates.

5.3. Zooplankton traverse

The second stage of the microscopic analysis is a stepped traverse of the CPR filtering silk and covering silk (Fig. 5(c)) at 54× magnification (using the Watson Bactil microscopes; Table 2). The field of view is 2.06 mm and all zooplankton organisms <2 mm total length are counted. Although we assume retained organisms are uniformly distributed on the silk, the design of the phytoplankton analysis and zooplankton traverse procedures ensures all areas of the silk receive equal weighting. The zooplankton traverse procedure examines 1/50

of the silk. (Note that Reid et al. (2003) and Warner & Hays (1994) report that this procedure examines an area 1/40 of the covering silk and filtering silk, and Batten, Clark, et al. (2003) reports that 1/49 of the sample is viewed. Despite the different values reported, abundance calculations at the Survey have always been based on a subsample of 1/50.)

5.4. Zooplankton eyecount

The final CPR analysis procedure counts all zooplankton greater than *Metridia lucens* stage V in size (>2 mm total length: Rae, 1952). Individuals are removed from the filtering silk and covering silk for identification. Generally all individuals are counted, but for particularly dense samples a sub-sample may be counted.

5.5. Scaling factors

The speed that the silk is wound through the machine is regulated so that 10 nautical miles of tow is captured on ~4 in. (~9.16 cm) of silk (Colebrook, 1960). However, sometimes each 10 nautical mile sample is more or less than 4 in. depending on the tension in the silk, and in such situations a scaling factor is used to estimate abundance in analysis stages where a sub-sample of the silk is counted (phytoplankton analysis and zooplankton traverse).

5.6. The category system for zooplankton

To reduce the time taken to count the large number of CPR samples processed each year, a category counting system is employed. This makes abundance estimates from CPR samples semi-quantitative in nature, although still reflecting real changes in abundance. The individual counts of organisms present in zooplankton traverse and the zooplankton eyecount stages of analysis are recorded in logarithmic categories (Table 4). For example, any number between 12 and 25 individuals of a particular taxon is recorded as category 5. Each category has an accepted value (e.g., accepted value of category 5 is 17), which is based on raw counts of individuals collected in 1938 and 1939 (Rae & Rees, 1947). The accepted value for each category is lower than the average of its upper and lower bounds because lower counts are more common than higher counts (Warner & Hays, 1994). Although there is a loss of information in the category system, it is used to save time processing dense samples. For example, as soon as it becomes evident that there are more than 500 but less than 1000 individuals of a particular species on a sample, the abundance of this species is assigned category 10. The categorical counting system is viewed as a necessary tradeoff: although it reduces the precision of the abundance estimate for each sample, it allows large numbers of samples to be counted every year.

Table 4
Zooplankton traverse and zooplankton eyecount: calculating abundance of a particular taxonomic entity in a CPR sample

Number counted	Category	Accepted value	Abundance per sample for zooplankton traverse
1	1	1	50
2	2	2	100
3	3	3	150
4–11	4	6	300
12–25	5	17	850
26–50	6	35	1750
51–125	7	75	3750
126–250	8	160	8000
251–500	9	310	15,500
501–1000	10	640	32,000
1001–2000	11	1300	65,000
2001–4000	12	2690	134,500

The number counted is converted to a category, which has an accepted value. For zooplankton traverse the accepted value is multiplied by 50 to give the abundance per sample, and for zooplankton eyecount the accepted value is the abundance per sample because the entire sample is counted.

As all zooplankton on the entire silk are counted during zooplankton eyecount, the accepted value for a category is actually the abundance per sample. By contrast, as a sub-sample of the silk is analysed during zooplankton traverse, the accepted value is multiplied by 50 to give the abundance per sample. Because of the category counting system and the use of accepted values, abundances of zooplankton taxa for individual samples have discrete values.

An undesirable consequence of the category counting system and use of accepted values is that taxonomic entities that should sum perfectly within a higher taxonomic group do not always do so. Consider the taxonomic entity "*Calanus* V–VI total", which includes all stage V–VI "*Calanus finmarchicus*", "*Calanus helgolandicus*", and "*Calanus glacialis*" seen during the zooplankton eyecount procedure, and should theoretically equal the sum of the abundances for each species counted individually. (Note that throughout this contribution, taxonomic entities recorded explicitly in the database are enclosed within double quotations.) If 10 individuals of each species were counted these would be recorded in the CPR database as category 4 (4–11 specimens) for each species, and category 6 (26–50 specimens) for "*Calanus* V–VI total". However, the numerical values extracted from the database would show the accepted value of 6 for each of the three individual species and 35 for the combined taxon. This would mean the abundance of each of the individual *Calanus* species does not sum to that for "*Calanus* V–VI total". In such situations, if the abundance of all three *Calanus* taxa is needed, then it is better to use the combined taxonomic entity "*Calanus* V–VI total", rather than summing the abundances of the individual taxa.

5.7. Changes in the counting system

In the early years of the Survey, counting procedures evolved in response to insight garnered through analysing CPR samples. Prior to 1958, phytoplankton were counted in 5 fields on each of the filtering silk and covering silk. Since then, the phytoplankton analysis procedure has involved counting 20 fields on the filtering silk only. (Note that Reid et al. (2003) report that this procedure examines the covering silk and filtering silk.) This means that direct quantitative comparisons of phytoplankton before 1958 cannot be made with subsequent data, although relative changes prior to 1958 can be assessed. Most zooplankton taxa have been counted consistently since March 1948 (Reid et al., 2003). However, for some organisms in zooplankton traverse, such as "Cladocera total" and the small gastropod "*Limacina retroversa*", a restricted category system was used until 1957 (Colebrook, 1960). This was abandoned from 1958 onwards.

5.8. Changes in microscopes

Since the start of the Survey, four different types of microscopes have been used for routine analysis (Table 2). The first, a traversing microscope, was used from 1932 until the 1950s. The second type was the Watson Bactil microscope. This microscope was fixed to the bench and a new travelling stage was designed to accommodate the silk. This microscope is still in use today at the Survey. In 1995 one new Micro Instruments CPR microscope (Mark 1) was commissioned, and in 2004 a further four Micro Instruments microscopes (Mark 2) were brought into service with their own design of mobile stage. The more recent microscopes have the same field sizes for analysis as the old Watson Bactils, though their magnifications are slightly different (Table 2). Since 2004, with the introduction of the latest microscopes, a record is kept of which microscope is used for anlaysis.

6. Taxa in database

6.1. Taxa recorded

To use CPR data effectively it is necessary to have detailed information on each taxonomic entity. Table 5 provides the first comprehensive list of all taxa in the CPR database, together with clarifying descriptions and counting idiosyncrasies where useful. The CPR survey identifies and records a total of 437 taxa in the North Atlantic, with 117 of these taxa occurring in more than 1% by frequency (i.e., >1952 samples) of the 195,176 samples (from 1946 to 2003). These taxa represent an incredible diversity of plankton (Fig. 6), and

Table 5
All taxa counted in the North Atlantic CPR survey, arranged alphabetically within major taxonomic groups

Group	Taxon	Description	ID	Stage	No.	Diet	Size
Bacillariophyceae (diatoms)	*Actinocyclus octonarius ralfsi*		964	P	1		
	Actinoptychus spp.*,+	Mainly *A. undulatus*	151	P	174		
	Amphiprora hyperborea		979	P	4		0.0415[a]
	Asterionella bleakeleyi	Now *Bleakeleya notata* (Hasle & Syvertsen, 1996)	983	P	2		0.00083[a]
	*Asterionella glacialis**,+	Now *Asterionellopsis glacialis* (Hasle & Syvertsen, 1996)	115	P	2999		
	Asterionella kariana	Now *Asterionellopsis kariana* (Hasle & Syvertsen, 1996)	202	P	2		0.000623[a]
	Asteromphalus spp.		152	P	28		
	Aulacodiscus argus		982	P	17		
	*Bacillaria paxillifer**,+	Now *B. paxillifera* (Hasle & Syvertsen, 1996)	153	P	1150		
	Bacteriastrum spp.*,+		154	P	2712		
	Bacteriosira fragilis		959	P	2		0.00614[a]
	*Bellerochea malleus**,+		155	P	1190		
	*Biddulphia alternans**,+		156	P	291		
	*Biddulphia aurita**,+	Now *Odontella aurita* (Hasle & Syvertsen, 1996)	157	P	2123		0.0169[a]
	Biddulphia biddulphiana		948	P	1		
	*Biddulphia granulata**,+	Now *Odontella granulata* (Hasle & Syvertsen, 1996)	158	P	278		0.033[a]
	*Biddulphia regia**,+	Now *Odontella regia* (Hasle & Syvertsen, 1996)	160	P	1921		
	*Biddulphia rhombus**,+	Now *Odontella rhombus* (Hasle & Syvertsen, 1996)	161	P	322		0.03[a]
	*Biddulphia sinensis**,+	Now *Odontella sinensis* (Hasle & Syvertsen, 1996)	114	P	8746		
	Campylosira cymbelliformis		954	P	2		
	*Cerataulina pelagica**,+		162	P	78		0.00325[a]
	Chaetoceros (Hyalochaete) spp.*,+		112	P	34,285		
	Chaetoceros (Phaeoceros) spp.*,+		113	P	39,323		
	Climacodium frauenfeldianum		163	P	30		
	*Corethron criophilum**,+	Now *C. hystrix* (Crawford et al., 1998)	164	P	1339		0.0367[a]
	*Coscinodiscus concinnus**,+		165	P	2318		1.9[a]
	Coscinodiscus spp.	Includes damaged "*Coscinodiscus concinnus*" and "*Coscinodiscus wailesii*" not identifiable to species, as well as other *Coscinodiscus* species	166	P	7926		
	*Coscinodiscus wailesii**,+	Invasive; first recorded in European waters in the English Channel in 1977 (as *C. nobilis*). Details in Edwards, John, et al. (2001)	976	P	1480		
	*Dactyliosolen antarcticus**,+	Does not have symbiotic flagellate (see "*Dactyliosolen mediterraneus*")	104	P	1784		

Table 5 (*continued*)

Group	Taxon	Description	ID	Stage	No.	Diet	Size
	*Dactyliosolen mediterraneus**,+	Now *Leptocylindrus mediterraneus* (Hasle & Syvertsen, 1996). Symbiotic flagellate *Rhizomonas setigera* attached (see "*Dactyliosolen antarcticus*")	105	P	7916		
	*Detonula confervacea**		167	P	234		0.00171[a]
	Diploneis spp.		947	P	22		
	*Ditylum brightwellii**,+		168	P	1745		0.19[a]
	Eucampia groenlandica		962	P	7		
	*Eucampia zodiacus**,+		169	P	984		0.00481[a]
	Fragilaria spp.*,+	May include some chain-forming "*Navicula* spp."	170	P	2871		
	*Guinardia flaccida**,+		171	P	318		
	Gyrosigma spp.*,+	"*Gyrosigma* spp." and *Pleurosigma* spp. not separated, although most are probably *Pleurosigma* spp. (Derek Harbour, pers. comm.)	172	P	1463		
	Hemiaulus spp.*		173	P	287		
	Hemidiscus cuneiformis		206	P	7		
	*Lauderia borealis**,+	Now *Lauderia annulata* (Hasle & Syvertsen, 1996)	174	P	1311		0.00988[a]
	*Leptocylindrus danicus**,+		175	P	641		0.00228[a]
	Lithodesmium undulatum		1590	P	2		
	Melosira arctica		958	P	2		0.0331[a]
	Melosira lineate		957	P	1		
	*Navicula planamembranacea**	Now *Ephemera planamembranacea* (Hasle & Syvertsen, 1996). Species first described in May 1962 from CPR samples in the Northwest Atlantic. Details in Hendey (1964)	120	P	1058		
	Navicula spp.*,+	May include other Naviculoid genera. Does not include "*Navicula planamembranacea*"	176	P	3843		
	Neodenticula seminae	Invasive; first observed in CPR samples from western North Atlantic in 1999. Originally from North Pacific	1568	P	65		
	*Nitzschia closterium**,+	Now *Cylindrotheca closterium* (Hasle & Syvertsen, 1996). Responsible for foam and mucilage	177	P	2802		0.000148[a]
	*Nitzschia delicatissima**,+	Now *Pseudo-nitzschia delicatissima* (Hasle & Syvertsen, 1996). Small and sometimes missed. Accurate specific identification of this species complex is not possible in routine CPR analysis and requires clean valves in a high refractive index medium (Hasle & Syvertsen, 1996). A strain from Canada and one from New Zealand found to produce domoic acid. Other strains examined so far non-toxic (Moestrup, 2004)	119	P	14,601		0.000105[a]

(*continued on next page*)

Table 5 (*continued*)

Group	Taxon	Description	ID	Stage	No.	Diet	Size
	Nitzschia longissima		981	P	30		
	Nitzschia seriata[*,+]	Now *Pseudo-nitzschia seriata* (Hasle & Syvertsen, 1996). Accurate specific identification of this species complex is not possible in routine CPR analysis and requires clean valves in a high refractive index medium (Hasle & Syvertsen, 1996). Several clones of this species have been found to produce domoic acid (Moestrup, 2004)	118	P	13,871		0.000422[a]
	Nitzschia sigma rigida[*]		975	P	59		
	Nitzschia spp.	Does not include "*Nitzschia closterium*", "*Nitzschia delicatissima*", "*Nitzschia longissima*", "*Nitzschiaseriata*" or "*Nitzschia sigma rigida*"	199	P	437		
	Odontella mobiliensis[*]		200	P	73		
	Odontella obtusa		159	P	5		
	Paralia sulcata[*,+]		101	P	11,340		0.0083[a]
	Planktoniella sol[*]		179	P	77		0.1[a]
	Podosira stelliger[*]		272	P	244		
	Rhaphoneis amphiceros[*]		178	P	496		
	Rhizosolenia acuminate[*]		180	P	433		
	Rhizosolenia alata alata[*,+]	Now *Proboscia alata* (Hasle & Syvertsen, 1996)	110	P	17,845		0.0346[a]
	Rhizosolenia alata curvirostris[*]	Now *Proboscia curvirostris* (Hasle & Syvertsen, 1996)	181	P	145		
	Rhizosolenia alata indica[*,+]	Now *Proboscia indica* (Hasle & Syvertsen, 1996)	109	P	4865		
	Rhizosolenia alata inermis[*,+]	Now *Proboscia inermis* (Hasle & Syvertsen, 1996)	111	P	4074		
	Rhizosolenia bergonii[*]		182	P	507		
	Rhizosolenia calcar avis[*]	Now *Pseudosolenia calcar avis* (Hasle & Syvertsen, 1996)	183	P	111		
	Rhizosolenia cylindrus		184	P	12		
	Rhizosolenia delicatula[*]	Now *Guinardia delicatula* (Hasle & Syvertsen, 1996)	185	P	931		0.039[a]
	Rhizosolenia fragilissima[*,+]	Now *Dactyliosolen fragilissimus* (Hasle & Syvertsen, 1996)	186	P	592		0.013[a]
	Rhizosolenia hebetata semispina[*,+]		108	P	13,444		0.0269[a]
	Rhizosolenia imbricata shrubsolei[*,+]	Now *R. imbricata* (Hasle & Syvertsen, 1996)	106	P	10,113		
	Rhizosolenia pungens	Only separated from "*Rhizosolenia setigera*" in 2003	1596	P	12		
	Rhizosolenia robusta		970	P	29		
	Rhizosolenia setigera[*,+]	See "*Rhizosolenia pungens*"	187	P	532		0.0371[a]
	Rhizosolenia stolterfothii[*,+]	Now *Guinardia striata* (Hasle & Syvertsen, 1996)	188	P	2707		
	Rhizosolenia styliformis[*,+]	See Robinson and Colbourn (1970) for more details	107	P	18,661		0.775[a]
	Schroederella delicatula[*,+]	Now *Detonula pumila* (Hasle & Syvertsen, 1996)	189	P	128		
	Skeletonema costatum[*,+]		102	P	3219		0.000339[a]

Table 5 (*continued*)

Group	Taxon	Description	ID	Stage	No.	Diet	Size
	Stauroneis membranacea	Now *Meuniera membranacea* (Hasle & Syvertsen, 1996)	205	P	15		
	Stephanopyxis spp.*,+		190	P	503		
	Streptotheca tamesis	Now *Helicotheca tamesis* (Hasle & Syvertsen, 1996)	191	P	41		
	Surirella spp.		192	P	10		
	Thalassionema nitzschioides[*,+]		117	P	27,152		0.00092[a]
	Thalassiosira spp.*,+		103	P	38,669		
	Thalassiothrix longissima[*,+]	Only counted if the end of a cell is observed within the field of view	116	P	18,920		0.0251[a]
	Triceratium favus		971	P	9		
Dinophyceae (Dinoflagellates)	*Actiniscus pentasterias**	Species is unarmoured; only the siliceous internal skeleton of 2 star-shaped pentasters observed	980	P	105		
	Amphidoma caudata		960	P	1		
	Amphisolenia spp.*		220	P	89		
	Blepharocysta paulsenii		956	P	5		
	Centrodinium spp.		265	P	4		
	*Ceratium arcticum**		128	P	6542		0.0741[a]
	*Ceratium arietinum**		221	P	398		0.159[a]
	*Ceratium azoricum**		222	P	828		
	*Ceratium belone**		223	P	68		
	Ceratium breve		219	P	3		
	Ceratium bucephalum[*,+]		224	P	872		0.159[a]
	*Ceratium buceros**		225	P	104		0.144[a]
	*Ceratium candelabrum**		226	P	713		
	*Ceratium carriense**		227	P	993		
	*Ceratium compressum**		228	P	214		
	Ceratium concilians		260	P	4		
	Ceratium contortum		261	P	20		
	*Ceratium declinatum**		229	P	213		
	*Ceratium extensum**		230	P	955		
	Ceratium falcatiforme		262	P	34		
	Ceratium falcatum		217	P	13		
	Ceratium furca[*,+]		122	P	39,776		0.0658[a]
	Ceratium fusus[*,+]		121	P	60,435		0.0625[a]
	Ceratium geniculatum		218	P	1		
	*Ceratium gibberum**		231	P	451		
	*Ceratium hexacanthum**		232	P	3424		
	Ceratium horridum[*,+]		126	P	20,902		0.144[a]
	Ceratium inflatum		233	P	18		
	Ceratium karstenii		234	P	33		
	Ceratium kofoidii		131	P	9		
	*Ceratium lamellicorne**		235	P	82		
	Ceratium limulus		1591	P	3		
	Ceratium lineatum[*,+]		123	P	14,233		0.0412[a]
	Ceratium longipes[*,+]		127	P	15,644		0.106[a]
	Ceratium longirostrum		263	P	32		
	Ceratium lunula		236	P	30		
	Ceratium macroceros[*,+]		125	P	24,965		0.12[a]
	*Ceratium massiliense**		237	P	2199		
	Ceratium minutum[*,+]		238	P	1490		0.00971[a]
	Ceratium pavillardii		239	P	7		

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Table 5 (*continued*)

Group	Taxon	Description	ID	Stage	No.	Diet	Size
	Ceratium pentagonum[*]		240	P	302		
	Ceratium petersii		241	P	4		
	Ceratium platycorne		242	P	52		
	Ceratium praelongum		243	P	4		
	Ceratium pulchellum		244	P	56		
	Ceratium ranipes		269	P	38		
	Ceratium setaceum		245	P	19		
	Ceratium symmetricum		1579	P	2		
	Ceratium teres[*]		246	P	255		
	Ceratium trichoceros[*]		247	P	1398		
	Ceratium tripos[*,+]		124	P	34,236		0.114[a]
	Ceratium vultur[*]		248	P	130		
	Ceratocorys spp.[*]		249	P	90		
	Cladopyxis spp.[*]		250	P	788		
	Corythodinium spp.	Includes "*Murrayella* spp." (Dodge, 1982)	953	P	18		
	'*Cystodinium*'[*]	A cyst stage of *Dissodinium pseudolunula*, a dinoflagellate parasitic on copepod eggs. Another cyst of *D. pseudolunula* recorded as "Pyrocystis". Details in John and Reid (1983)	266	P	341		
	Dinoflagellate cysts[*]	Presence recorded since 1974, counted since 1993. For species, see Reid (1978). "*Polykrikos schwartzii* cysts" counted separately. Cysts of *Gonyaulax* spp. (*Spiniferites*), *Scrippsiella* spp., *Protoperidinium* spp., and *Warnowia* cf. *rosea*? are often recorded in comments	130	P	6019		
	Dinophysis acuminata	Counted from 2004. Included in "*Dinophysis* spp." before and since. Producer of okadaic acid, a toxin implicated in diarrhetic shellfish poisoning (Moestrup, 2004)	1601	P	0		0.017[a]
	Dinophysis acuta	Counted from 2004. Included in "*Dinophysis* spp." before and since. Producer of okadaic acid and dinophysistoxin-1 or dinophysistoxin-2, toxins implicated in diarrhetic shellfish poisoning (Moestrup, 2004)	1602	P	0		0.0405[a]
	Dinophysis caudata	Counted from 2004. Included in "*Dinophysis* spp." before and since. Producer of okadaic acid, a toxin implicated in diarrhetic shellfish poisoning (Moestrup, 2004)	1603	P	0		
	Dinophysis norvegica	Counted from 2004. Included in "*Dinophysis* spp." before and since. Producer of okadaic acid and dinophysistoxin-1, toxins implicated in diarrhetic shellfish poisoning (Moestrup, 2004)	1604	P	0		0.0212[a]

Table 5 (*continued*)

Group	Taxon	Description	ID	Stage	No.	Diet	Size
	Dinophysis rotundata	Counted from 2004. Included in "*Dinophysis* spp." before and since. Production of dinophysistoxin-1, a toxin implicated in diarrhetic shellfish poisoning, demonstrated in Japan, but North American strains apparently non-toxic (Moestrup, 2004)	1605	P	0		0.0307[a]
	Dinophysis sacculus	Counted from 2004. Included in "*Dinophysis* spp." before and since. producer of okadaic acid, a toxin implicated in diarrhetic shellfish poisoning (Moestrup, 2004)	1606	P	0		
	Dinophysis spp.*,+	Species also counted separately from 2004. Generally associated with diarrhetic shellfish poisoning (Moestrup, 2004)	251	P	9764		
	Dinophysis tripos	Counted from 2004. Included in "*Dinophysis* spp." before and since. Producer of dinophysistoxin-1, a toxin implicated in diarrhetic shellfish poisoning (Moestrup, 2004)	1607		0		
	Exuviaella spp.	Mainly *E. marina* probably. Not included in "*Prorocentrum* spp.", although genus *Exuviaella* is now *Prorocentrum*. Generally produce toxins implicated in diarrhetic shellfish poisoning (Moestrup, 2004)	252	P	2710		
	Glenodinium spp.*	Now *Dissodium asymmetricum* (Dodge, 1982)	271	P	253		
	Gonyaulax spp.*	Includes other genera in Gonyaulaceae (e.g., *Alexandrium*). Counted since 1965. Genus *Alexandrium* produces paralytic shellfish poisoning toxins and fish mass mortality causative substance (Moestrup, 2004)	253	P	3871		
	Gossleriella tropica		201	P	1		
	Gymnodinium spp.	Genus is unarmoured and therefore very undercounted. Members of this genus produce toxins causing paralytic shellfish poisoning and can cause fish and invertebrate mortailities (Moestrup, 2004)	275	P	17		
	Gyrodinium spp.*	Genus is unarmoured and therefore very undercounted. Most are *G. aureolum* (now *Karenia mikimotoi*), which is responsible for fish and invertebrate mortality (Moestrup, 2004)	984	P	82		
	Histioneis spp.		256	P	6		
	Katodinium spp.		276	P	2		

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Table 5 (*continued*)

Group	Taxon	Description	ID	Stage	No.	Diet	Size
	Murrayella spp.	Now counted in "*Corythodinium* spp."	274	P	2		
	Noctiluca scintillans[*]	Counted since 1981. Usually identified by its striated flagellum	750	P	1777		
	Ornithocercus spp.		267	P	29		
	Oxytoxum spp.[*]	Mainly *O. scolopax*	254	P	2279		0.00647[a]
	Parahistioneis spp.		1575	P	1		
	Phalacroma spp.	Many authors consider *Phalacroma* to be synonymous with *Dinophysis* (Steidinger & Tangen, 1996)	818	P	67		
	Podolampas spp.[*]	*P. palmipes*, *P. spinifer* and *P. bipes*	257	P	463		
	Polykrikos schwartzii cysts[*]	Also called 'Umrindetencysts' (Lohmann, 1910). Presence recorded since 1975, counted since 1993. Unarmoured motile cells not found in CPR samples. Details in Reid (1978)	133	P	2499		
	Pronoctiluca pelagica		258	P	23		0.00431[a]
	Prorocentrum spp.[*,+]	Mainly *P. micans*. Although genus now includes "*Exuviaella* spp." these are still counted separately. Genus *Prorocentrum* generally produce toxins for diarrhetic shellfish poisoning (Moestrup, 2004)	259	P	2752		
	Protoceratium reticulatum	Now *Gonyaulax grindleyi* (Steidinger & Tangen, 1996). Producer of yessotoxin, which may accumulate in bivalves; effect on humans unknown (Moestrup, 2004)	129	P	17		
	Protoperidinium spp.[*]	Includes some records of "*Glenodinium* spp." and "*Gonyaulax* spp."; also included "*Scrippsiella* spp." prior to 1982	255	P	22,659		
	Ptychodiscus noctiluca[*]		264	P	136		
	Pyrophacus spp.[*]		132	P	187		
	'*Pyrocystis*'[*]	Probably is '*Pyrocystis*' around the Azores. In Northwest European waters probably not *Pyrocystis lunula* but lunate 2nd cyst stage of *Dissodinium pseudolunula*. See '*Cystodinium*'	268	P	73		
	Scrippsiella spp.[*]	Counted in CPR samples from 1982, before this included in "*Protoperidinium* spp.". Most records are *S. trochoidea*	950	P	2116		
	Triadinium polyedricum[*]	Now *Goniodoma polyedricum* (Steidinger & Tangen, 1996)	952	P	177		
Other phytoplankton	Coccolithaceae[*]	Presence recorded since 1965, counted since 1993. Records weighted toward larger species such as *Coccolithus pelagicus*, but 7 other species, including *Emiliania huxleyi*, and holococcolithophorids have been recorded (Hays et al., 1995)	195	P	6683		

Table 5 (*continued*)

Group	Taxon	Description	ID	Stage	No.	Diet	Size
	Halosphaera spp.*	Presence recorded in phytoplankton analysis 1948–1957 and 1965–1992. Counted in phytoplankton analysis 1993–1995. Counted in zooplankton traverse since 1996	197	T/P	2477		
	Oscillatoria spp.*	Now *Trichodesmium* spp. (cyanobacteria)	193	P	1609		
	Pachysphaera spp.		203	P	100		
	*Phaeocystis pouchetii**	Abundance recorded in 3 categories from 1948 to 1957, and presence recorded since 1958. Details in Owens et al. (1989). Found to be toxic to cod larvae in Norway (Moestrup, 2004)	194	P	1305		
	Pterosperma spp.*	Usually identified to species using Parke et al. (1978), but species is only recorded in comments	196	P	412		
	Silicoflagellatae*	Presence recorded in 1948–1957 and from 1965 to 1992. Counted since 1993	198	P	22,962		
Protozoa	Acantharia	Counted since 2004. Included in ''Radiolaria'' before and since	1608	T	0		
	Foraminifera*	Presence recorded since 1948, counted since 1993. Details in John (1987)	354	T	27,307		
	Radiolaria*	Presence recorded 1948–1957, counted since 1993. Includes ''Acantharia''. From 2004, ''Acantharia'' also recorded separately	355	T	12,453		
Ciliophora	*Dictyocysta* spp.*	Counted since 1996, and within ''Tintinnidae'' both before and since. For species see Lindley (1975)	134	T	1983		
	*Favella serrata**	Counted since 1996, and within ''Tintinnidae'' both before and since. See Lindley (1975) for more details	270	T	255		
	'Fusopsis'*	Probably cyst of an oligotrich ciliate	974	T	218		
	*Parafavella gigantea**	Counted since 1996, and within ''Tintinnidae'' both before and since. See Lindley (1975) for more details	135	T	1105		
	Ptychocylis spp.*	Counted since 1996, and within ''Tintinnidae'' both before and since. See Lindley (1975) for more details	634	T	289		
	Tintinnidae*	Presence recorded 1948–1957, counted since 1993. Includes all tintinnids: ''*Dictyocysta* spp.'', ''*Favella serrata*'', ''*Parafavella gigantea*'', ''*Ptychocylis* spp.'' and ''*Tintinnopsis* spp.'' are included as well as recorded separately since 1996. Many other species noted as comments. Details in Lindley (1975)	356	T	19,467		

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Table 5 (*continued*)

Group	Taxon	Description	ID	Stage	No.	Diet	Size
	Tintinnopsis spp.*	Counted since 1996, and within ''Tintinnidae'' both before and since. See Lindley (1975) for more details	805	T	712		
	*Zoothamnium pelagicum**	Pelagic colonial ciliate. Presence recorded since 1964, counted (as number of colonies) since 1993	357	T	823		
Platyhelminthes	'Spindelei'*	Eggs of *Kuhnia scombri*, a monogenean gill parasite of mackerel *Scomber scombrus*. Counted since 1983	951	T	133		
Cnidaria	Coelenterata tissue	Presence recorded only. Often identified by nematocysts	451	E	28,531		
	Siphonophora	Calycophorans only. Usually identified by bell, but maybe difficult to separate from ''Coelenterata tissue'' if bell not found. Not included in ''Coelenterata tissue''	452	E	1457		
Rotifera	Rotifer eggs*	Counted since 1984. Adults not identifiable in CPR samples	946	T	253		
Annelida	Polychaeta Larvae*,+	Does not include ''*Tomopteris* spp.'', which is recorded separately	450	E	2470		
	Tomopteris spp.*,+	Not included in ''Polychaete larvae''	80	E	5887		
Copepoda	*Acartia danae**		300	T	150	O	1.08[b,c,d]
	*Acartia longiremis**	Usually not differentiated in counts of ''*Acartia* spp.''	327	T	74	O	1.04[b,d]
	Acartia negligens		328	T	27	O	1.05[c,d]
	Acartia spp.*,+	Not identified to species. Mainly *A. clausi* and some ''*Acartia longiremis*''. Details in Colebrook (1982)	5	T	50,620	O	1.15[d]
	Acrocalanus spp.	Not identified to species	301	T	3		
	*Aetideus armatus**		370	E	553	O	1.73[c,d,e]
	Alteutha spp.	Not identified to species. Mainly *A. interrupta* (M. Gee, pers. comm.). Not included in ''Harpacticoida total''. Counted from 1994	985	E	103		
	Amallothrix spp.	Not identified to species	371	E	1		
	*Anomalocera patersoni**,+		372	E	574	C	3.20[d]
	Augaptilus spp.	Not identified to species	604	E	1		
	*Calanoides carinatus**		48	E	1474	H	2.18[c,d,f]
	*Calanus finmarchicus**,+	CV–CVIs. Recorded as a separate species from 1958. Included in ''*Calanus* V–VI total''. Separated from ''*Calanus helgolandicus*'' by shape of inner margin of coxa of P5, and occasionally on shape of head and genital pore. Where large numbers of *Calanus* present, 20 individuals identified to species, and scaled up to total number of ''*Calanus finmarchicus*'' and ''*Calanus helgolandicus*''	40	E	67,557	H	2.70[d,f]

Table 5 (*continued*)

Group	Taxon	Description	ID	Stage	No.	Diet	Size
	Calanus glacialis[*]	CV–CVIs. Recorded since 1958. Separated from *C. finmarchicus* based on size alone (adult females >4.6 mm total length). Included in "*Calanus* V–VI total"	42	E	1838	H	4.60
	Calanus helgolandicus[*,+]	CV–CVIs. Recorded as a separate species from 1958. Included in "*Calanus* V–VI total". Separated from "*Calanus finmarchicus*" by shape of inner margin of coxa of P5, and occasionally on shape of head and genital pore. Where large numbers of *Calanus* present, 20 individuals identified to species, and scaled up to total number of "*Calanus finmarchicus*" and "*Calanus helgolandicus*". See Bonnet et al. (2005) for more details	41	E	41,097	H	2.68[c,d]
	Calanus hyperboreus[*,+]	Mainly CV–CVIs, but probably also includes CIII–CIVs. Not included in "*Calanus* V–VI total"	44	E	1476	H	6.95[d,f]
	Calanus I–IV[+]	Juveniles of "*Calanus finmarchicus*", "*Calanus helgolandicus*" and "*Calanus glacialis*"	1	T	63,164	H	1.65[g]
	Calanus tenuicornis[*]	Now *Mesocalanus tenuicornis* (Razouls, 1995)	46	E	778	H	1.74[c,d,f]
	Calanus total traverse[#]	Includes "*Calanus* I–IV" and V–VIs of *C. finmarchicus*, *C. helgolandicus* and *C. glacialis* seen in zooplankton traverse	12	T	66,420	H	
	Calanus V–VI total[+,#]	Includes "*Calanus finmarchicus*", "*Calanus helgolandicus*" and "*Calanus glacialis*" seen in zooplankton eyecount	43	E	110,446	H	2.48[h]
	Caligoida[*,+]	Nearly all records are *Caligus elongatus* (J. Roskell, pers. comm.). Usually found in association with fish, but not attached in CPR samples	426	E	361		
	Calocalanus spp.[*]	Not identified to species. Now includes genus *Ischnocalanus* (Bradford-Grieve, 1994)	302	T	782	H	
	Candacia aethiopica[*]		375	E	347	C	
	Candacia armata[*,+]		61	E	5788	C	2.18[d,i]
	Candacia bipinnata		373	E	67	C	1.95[c,d]
	Candacia curta		374	E	31	C	
	Candacia giesbrechti	Only found in Mediterranean	819	E	9	C	
	Candacia I–IV		303	T	1316	C	
	Candacia longimana		376	E	24	C	3.41[c,d,i]
	Candacia norvegica		377	E	2	C	2.75[d,i]
	Candacia pachydactyla[*]		378	E	101	C	2.15[d]
	Candacia spp.	Specimens identifiable to genus but not species	429	E	375	C	2.31
	Candacia tenuimana		379	E	2	C	2.14[c,d,i]

(*continued on next page*)

Table 5 (*continued*)

Group	Taxon	Description	ID	Stage	No.	Diet	Size
	Candacia varicans		430	E	4	C	2.20[c,d,i]
	Centropages bradyi[*]		380	E	682	O	1.87[c,d,h]
	Centropages chierchiae eyecount[*]	Counted since 1958. Species also recorded in traverse as "*Centropages chierchiae* traverse" from 1997 to 2003 (see Lindley and Daykin, 2005)	381	E	598	O	
	Centropages chierchiae traverse[#]	Counted from 1997 to 2003. Discontinued in 2004. See also "*Centropages chierchiae* eyecount" (see Lindley and Daykin, 2005)	972	T	159	O	
	Centropages furcatus		19	T	38	O	
	Centropages hamatus[*,+]	Details in Lindley and Hunt (1989)	7	T	7479	O	1.30[d]
	Centropages spp.	Specimens identifiable to genus but not species	431	T	831	O	1.63
	Centropages typicus[*,+]	Details in Lindley and Reid (2002)	6	T	32,320	O	1.55[d,h]
	Centropages violaceus[*]		382	E	178	O	1.80[c,d,h]
	Clausocalanus spp.[*]	Not identified to species. 7 species found (Williams & Wallace, 1975)	9	T	11,948	H	1.15[j]
	Clytemnestra spp.[*]	Not identified to species. Not included in "Harpacticoida total"	305	T	93		
	Copepod eggs	Presence recorded 1948–1957 and from 1974 to 1992. Counted since 1993. Individual eggs of free and sac spawners are counted. *Centropages* spp. eggs most common. Only "Spiny eggs" (probably *Candacia armata* eggs) recorded separately	347	T	14,249	_	
	Copepod nauplii[+]	Presence recorded since 1946 and counted from 1958. Not included in "Copepoda total"	326	T	24,267	H	
	Copepoda total[+,#]	Includes all copepods seen in zooplankton traverse	13	T	132,702	_	
	Copilia spp.[*]	Not identified to species	383	E	80		
	Corycaeus speciosus	Only counted from 1997	997	E	41	C	
	Corycaeus spp.[*,+]	Not identified to species. Mainly *C. anglicus* around Britain, but other species in warm oceanic waters	11	T	6310	C	1.57[j]
	Ctenocalanus vanus[*]		304	T	232	H	0.94[c,d,k]
	Diaixis hibernica		329	T	4		1.20[d]
	Diaixis pygmoea		330	T	2		0.95[d]
	Euaetideus giesbrechti		384	E	9	O	2.04[d]
	Euaetideus spp.	Not identified to species	1598	E	2	O	
	Eucalanus attenuatus[*]	Now *Pareucalanus attenuatus* (Razouls, 1995)	385	E	102	H	3.94[c,d,l]
	Eucalanus crassus[*]	Now *Subeucalanus crassus* (Razouls, 1995)	49	E	971	H	2.85[c,d,l]
	Eucalanus elongates[*]	Revision of Eucalanidae has shown that our material is not *E. elongatus* but is almost certainly *E. hyalinus* (Razouls, 1995)	386	E	326	H	4.69[c,d,l]
	Eucalanus monachus[*]	Now *Subeucalanus monachus* (Razouls, 1995)	387	E	71	H	2.13[d]

Table 5 (*continued*)

Group	Taxon	Description	ID	Stage	No.	Diet	Size
	Eucalanus mucronatus	Now *Subeucalanus mucronatus* (Razouls, 1995)	388	E	7	H	
	Eucalanus pileatus	Now *Subeucalanus pileatus* (Razouls, 1995)	390	E	2	H	
	Eucalanus spp.	Specimens identifiable to genus but not species	389	E	197	H	3.40
	Euchaeta acuta[*]		53	E	1965	C	3.84[c,d]
	Euchaeta glacialis	Now *Paraeuchaeta glacialis* (Razouls, 1995)	391	E	4	C	
	Euchaeta gracilis[*]	Now *Paraeuchaeta gracilis* (Razouls, 1995)	392	E	102	C	6.60[c,d]
	Euchaeta hebes[*,+]	Now *Paraeuchaeta hebes* (Razouls, 1995)	54	E	3035	C	2.80[c,d]
	Euchaeta marina[*]		393	E	560	C	2.72[c,d]
	Euchaeta media		394	E	54	C	3.65[c,d]
	Euchaeta norvegica[*,+]	Now *Paraeuchaeta norvegica* (Razouls, 1995)	52	E	12,143	C	7.00[d]
	Euchaeta pubera		395	E	14	C	3.94[c,d]
	Euchaeta spinosa		396	E	4	C	6.32[c,d]
	Euchaeta spp.	Specimens identifiable to genus but not species	436	E	2482	C	4.82
	Euchaeta tonsa	Now *Paraeuchaeta pseudotonsa* (Razouls, 1995)	397	E	18	C	6.50[d]
	Euchirella amoena		398	E	2	H	
	Euchirella brevis		399	E	1	H	3.50[m]
	Euchirella curticauda		400	E	8	H	3.90[c,d,m]
	Euchirella messinensis		401	E	25	H	4.84[c,d,m]
	Euchirella pulchra		402	E	3	H	3.00[m]
	Euchirella rostrata[*]		51	E	1545	H	2.95[d,m]
	Euchirella spp.	Specimens identifiable to genus but not species	428	E	87	H	4.24
	Euterpina acutifrons[*]	Not included in ''Harpacticoida total''	307	T	88		0.50[d]
	Farranula gracilis		21	T	33		
	Farranula spp.	Specimens identifiable to genus but not species	22	T	20		
	Gaetanus minor		403	E	2		1.93[d,n]
	Gaidius spp.	Not identified to species	437	E	1		
	Gaidius tenuispinus		556	E	2		3.10[c,d,o]
	Halithalestris croni	Now *Parathalestris croni*. Not included in ''Harpacticoida total''	308	E	43		
	Haloptilus acutifrons		601	E	1		2.86[c,d]
	Haloptilus longicornis		404	E	12		1.96[c,d]
	Haloptilus spiniceps		405	E	2		4.14[c,d]
	Harpacticoida total[*,+]	Mainly *Microsetella* spp. Does not include eyecount harpacticoids such as ''*Alteutha* spp.'', ''*Macrosetella gracilis*'', ''*Miracia efferata*'', ''*Oculosetella gracilis*'', ''*Parathalestris croni*'' or two traverse species ''*Clytemnestra* spp.'' and ''*Euterpina acutifrons*'', which are all recorded separately	306	T	4452		
	Hemicyclops aberdonensis	Commensal or parasitic copepod of family Clausidiidae	1589	T	2		

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Table 5 (*continued*)

Group	Taxon	Description	ID	Stage	No.	Diet	Size
	Heterorhabdus cf *abyssalis*	Although included in the European list of marine species by Boxshall (2001); Park (1999) found them only in the Pacific	406	E	13	C	2.40[d]
	Heterorhabdus cf *clausi*	Although included in the European list of marine species by Boxshall (2001); Park (1999) found them only in the Pacific	597	E	3	C	2.20[d]
	Heterorhabdus norvegicus[*]		407	E	377	C	2.77[c,d]
	Heterorhabdus papilliger[*]		408	E	492	C	1.76[c,d]
	Heterorhabdus spinifer		364	E	2	C	
	Heterorhabdus spp.	Specimens identifiable to genus but not species	369	E	46	C	2.49
	Heterostylites longicornis		432	E	1	C	3.00[d]
	Ischnocalanus spp.	Not identified to species. Now recombined with genus *Calocalanus* (Bradford-Grieve, 1994). Discontinued	1586	T	1	H	
	Isias clavipes[*,+]		8	T	686		1.25[d]
	Labidocera acutifrons		961	E	7	C	3.00[d]
	Labidocera aestiva		440	E	10	C	
	Labidocera spp.	Specimens identifiable to genus but not species	62	E	17	C	2.60
	Labidocera wollastoni[*,+]	Details in Lindley and Hunt (1989)	63	E	1438	C	2.20[d]
	Lophothrix spp.	Not identified to species	433	E	1		
	Lubbockia spp.	Not identified to species	311	T	21		
	Lucicutia spp.[*]	Not identified to species. Mainly *L. flavicornis*	312	T	868		
	Macrosetella gracilis	Not included in "Harpacticoida total"	309	E	33		1.40[d]
	Mecynocera clausi[*]		313	T	827	H	0.84[d,l]
	Metridia I–IV	Included in "*Metridia* total traverse"	314	T	2228	O	0.93[g]
	Metridia longa[*]		56	E	2343	O	4.10[d,p]
	Metridia lucens[*,+]		55	E	33,002	O	2.27[c,d,p]
	Metridia total traverse[#]	Includes *Metridia* CV–CVI and "*Metridia* I–IV" seen in zooplankton traverse	315	T	4922	O	
	Microcalanus spp.	Not identified to species. Rare, but some may be included in "*Para-Pseudocalanus*" (Rae, 1952)	316	T	42		
	Miracia efferata	Not included in "Harpacticoida total"	310	E	44		
	Nannocalanus minor[*]		60	E	4632	H	1.71[d,f]
	Neocalanus gracilis[*]		45	E	2419	H	2.76[c,d,f]
	Neocalanus robustior		423	E	21	H	3.42[c]
	Neocalanus spp.	Specimens unidentifiable to species	1570	E	9	H	
	Oculosetella gracilis	Not included in "Harpacticoida total"	963	E	2		
	Oithona spp.[*,+]	Not identified to species	10	T	52,633	O	0.68[j]
	Oncaea spp.[*,+]	Not identified to species	317	T	2976	O	
	Paracandacia bispinosa[*]		409	E	91		1.67[c]

Table 5 (*continued*)

Group	Taxon	Description	ID	Stage	No.	Diet	Size
	Paracandacia simplex[*]		424	E	125		1.75[c]
	Paracandacia spp.	Specimens identifiable to genus but not species	427	E	22		1.7
	Parapontella brevicornis[*,+]		318	T	119		1.37[d]
	Para-Pseudocalanus spp.[*,+]	Includes *Paracalanus* spp., adults of "*Pseudocalanus* spp.", and any inidentifiable small copepods (<2 mm)	3	T	83,130	H	0.70[j]
	Phaenna spinifera		410	E	9		1.80[d]
	Pleuromamma abdominalis[*]	Distinct from other "large" *Pleuromamma* spp. (*P. robusta* and *P. xiphias*) from CV	58	E	3031	O	2.67[c,d,q]
	Pleuromamma borealis[*]	Distinct from other "small" *Pleuromamma* spp. (*P. gracilis* and *P. piseki*) at CVI. Usually identified based on females; males more difficult to identify (but also rarer) and included in "*Pleuromamma* spp."	59	E	5376	O	1.97[c,d,q]
	Pleuromamma gracilis[*]	Distinct from other "small" *Pleuromamma* spp. (*P. borealis* and *P. piseki*) at CVI. Usually identified based on females; males more difficult to identify (but also rarer) and included in "*Pleuromamma* spp."	47	E	4619	O	1.76[c,d,q]
	Pleuromamma piseki[*]	Distinct from other "small" *Pleuromamma* spp. (*P. borealis* and *P. gracilis*) at CVI. Usually identified based on females; males more difficult to identify (but also rarer) and included in "*Pleuromamma* spp."	411	E	1169	O	1.73[c,d]
	Pleuromamma spp.	Specimens identifiable to genus but not species	434	E	1469	O	2.56
	Pleuromamma robusta[*]	Distinct from other "large" *Pleuromamma* spp. (*P. abdominalis* and *P. xiphias*) from CV	57	E	8197	O	3.13[c,d,q]
	Pleuromamma xiphias[*]	Distinct from other "large" *Pleuromamma* spp. (*P. abdominalis* and *P. robusta*) from CV	412	E	639	O	4.13[c,d,q]
	Pontellidae	Specimens unidentifiable to species	1593	E	5	C	
	Pontellina plumata[*]		319	E	62	C	1.69[c,d]
	Pontellopsis regalis		988	E	1	C	
	Pseudocalanus elongatus[*,+,#]	Includes only adult females and males. In the Northeast Atlantic and North Sea these are mainly *P. elongatus* with some *P. acuspes* and *P. minutus*, but in the Northwest Atlantic several other species may be present (Frost, 1989). Details in Colebrook (1982). Also included in "*Para-Pseudocalanus*"	2	T	23,680	H	1.20[r]
	Pseudochirella spp.	Not identified to species	955	E	1		
	Rhincalanus cornutus		413	E	56	H	3.21[c,d]
	Rhincalanus nasutus[*,+]		50	E	1395	H	3.99[c,d,l]

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Table 5 (*continued*)

Group	Taxon	Description	ID	Stage	No.	Diet	Size
	Saphirella tropica		20	T	1		
	Sapphirina spp.*	Not identified to species	414	E	803		
	Scaphocalanus echinatus		320	E	13		1.92[d]
	Scaphocalanus spp.	Specimens identifiable to genus but not species	425	E	16		
	Scolecithricella spp.*	Not identified to species	321	T	2366	H	1.40[d]
	Scolecithrix bradyi		415	T	10	H	1.16[c,d]
	*Scolecithrix danae**		416	E	355	H	2.05[c,d]
	Scolecithrix spp.	Specimens identifiable to genus but not species	1576	E	3	H	
	Scottocalanus persecans		417	E	3		4.80[d]
	Scottocalanus securifrons		575	E	1		4.30[c,d]
	'Spiny eggs'	Probably *Candacia armata* eggs. Eggs of other copepod species are recorded together in "Copepod eggs". Counted from 1997	813	T	99	_	
	*Temora longicornis**,+		4	T	30,409	H	1.00[d]
	*Temora stylifera**		322	T	773	H	1.45[c,d]
	Temora turbinata		323	T	32	H	
	*Tortanus discaudatus**	Recorded regularly on EA route (between Newfoundland and Nova Scotia) in 1960s and 1970s but rare recently because route towed further offshore	324	T	250		2.00[s]
	*Undeuchaeta major**		418	E	74	C	4.55[c,d,t]
	*Undeuchaeta plumosa**		419	E	2282	C	3.18[c,d,t]
	Undeuchaeta spp.	Specimens identifiable to genus but not species	435	E	40	C	3.86
	*Undinula vulgaris**		421	E	296		
	Urocorycaeus spp.*	Not identified to species	325	E	100	C	1.76[j]
	Xanthocalanus spp.	Not identified to species	422	E	2		5.80[d]
Malacostraca	Caprellidea*,+		453	E	1036		
	Cumacea*,+		454	E	1577		
	Decapoda larvae*,+	For species see Lindley (1987). Includes "Sergestidae", which are also counted separately	83	E	38,710		
	Euphausiacea adults	Counted from 1968 to 1988. Included in "Euphausiacea total". Details in Lindley (1977)	86	E	29,256		
	Euphausiacea calyptopis+	Occasional large calyptopis (e.g., *Thysanopoda acutifrons*) are of eyecount size	351	T	4899		
	Euphausiacea eggs	Counted since 1961	353	T	238		
	Euphausiacea juveniles	Counted from 1968 to 1988. Included in "Euphausiacea total". Details in Lindley (1977)	87	E	17,342		
	Euphausiacea nauplii		352	T	791		
	Euphausiacea total*,+	Counted since 1946. Includes "Euphausiacea adults" and "Euphausiacea juveniles". Details in Glover (1952); Jones (1969) and Lindley (1977)	88	E	87,236		

Table 5 (*continued*)

Group	Taxon	Description	ID	Stage	No.	Diet	Size
	Gammaridea*,+	For species see Vane (1951)	81	E	7745		
	Heterophryxus appendiculatus	Isopod parasitic on euphausiids. See Lindley (1977) for further details. Included in "Parasites of the plankton" until end of 2002 (22 records in comments) and recorded separately since 2004	1599	E	3		
	Hyperiidea*,+	For species see Vane (1951) and McHardy (1970)	82	E	45,100		
	Isopoda*,+		456	E	341		
	Lucifer spp.	Also included in "Sergestidae" and "Decapoda larvae"	999	E	90		
	Mysidacea*,+	Identified by statocysts. Mysids collected are of the sub-order Mysida, which have statocysts. Mysids of the order Lophogatrida live in oceanic waters below the sampling depth of the CPR	458	E	1690		
	Sergestidae*	Counted since March 1962. For species see Lindley (1987). Includes "*Lucifer* spp.", which are also counted separately. Included in "Decapoda larvae"	455	E	2049		
	Stomatopoda*	Larval and juvenile stages only	509	E	90		
Other arthropoda	Cirripede larvae*,+	Presence recorded 1947–1957, counted since 1958. These are Balanidae and Verrucidae larvae. For species see Edinburgh Oceanographic Laboratory (1973). Does not include "*Lepas* nauplii" or "*Lepas* cypris"	350	T	4740		
	Cladocera total	Discontinued in 1957	38	T	4250		
	Evadne spp.*,+	Recorded within "Cladocera total" (now discontinued) from 1948 to 1957, and separately since 1958. Details in Gieskes (1971a)	31	T	15,554		
	Lepas cypris	First found in 2002. Not included in "Cirripede larvae". See *Lepas* nauplii	1592	E	6		
	Lepas nauplii*	*Lepas anatifera*, *L. fascicularis*, *L. pectinata* and 1 unidentified species (Roskell, 1975; Bainbridge & Roskell, 1966). Not included in "Cirripede larvae"	457	E	497		
	Ostracoda*	13 taxa of ostracods found (Williams, 1975)	459	E	3291		
	*Penilia avirostris**	Introduced into the North Sea in early 1990s, probably by ballast water (Johns et al., 2005)	148	T	222		
	Podon spp.*,+	Recorded within "Cladocera total" (now discontinued) from 1948 to 1957, and separately since 1958. Details in Gieskes (1971a, 1971b)	30	T	10,157		
	Pycnogonida		449	E	20		

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Table 5 (*continued*)

Group	Taxon	Description	ID	Stage	No.	Diet	Size
Chaetognatha	Chaetognatha eyecount*,+	All Chaetognaths ⩾ 8 mm total length. *Sagitta serratodentata*, *S. elegans*, *S. setosa*, and *Eukrohnia hamata* have been recorded. Details in Bainbridge (1963). Also see "Chaetognatha traverse"	89	E	50,379		
	Chaetognatha traverse+	All chaetognaths. *Sagitta serratodentata*, *S. elegans*, *S. setosa*, and *Eukrohnia hamata* have been recorded. Details in Bainbridge (1963). Also see "Chaetognatha eyecount"	34	T	20,821		
Bryozoa	Cyphonautes larvae*,+	Presence recorded from 1946 to 1957, counted since 1958. Ectoproct bryozoan larvae	35	T	4448		
Mollusca	*Atlanta* spp.*	May contain some "*Oxygyrus* spp."	470	E	240		
	Carinaria spp.		475	E	5		
	Cavolinia spp.*		461	E	121		
	Cephalobrachia spp.		348	E	2		
	Cephalopoda larvae*	May include post larvae. Some identification may be suspect (C. Yau, pers. comm.)	471	E	525		
	Clio spp.*		464	E	383		
	Clione limacina+	The most reliably identified Gymnosome. Both the large arctic form *C.l.l.* forma *limacina* and the small southern form *C. l. l.* forma *minuta* are included	84	E	3716		
	Clione shells	Juvenile *Clione*	39	T	29		
	Creseis spp.		462	E	39		
	Cuvierina spp.		476	E	8		
	Diacria spp.*		463	E	98		
	'Echinospira' larvae	Veliger larvae of *Lamellaria perspicua* (Gastropoda: Prosobranchia). Counted since 1999	1543	T	11		
	Firoloida spp.		472	E	28		
	Gymnosomata	Gymnosomata unidentifiable to species	480	E	124		
	Lamellibranchia larvae*,+	Recorded as present 1946–1948, and counted since 1949. For species see Rees (1954a)	33	T	9070		
	Limacina retroversa+	This represents all thecosomes. *L. retroversa* is the overwhelmingly dominant species in the North Sea and Northeast Atlantic, but other species may be included elsewhere. Presence recorded 1946–1957, counted from 1958. Recorded when spiral is seen.	32	T	35,774		
	Mollusca	Molluscs unidentifiable to species	1577	E	33		
	Notobranchaea spp.		473	E	1		
	Oxygyrus spp.	May contain some "*Atlanta* spp."	477	E	17		

Table 5 (*continued*)

Group	Taxon	Description	ID	Stage	No.	Diet	Size
	Paedoclione doliiformis	Records of "*Pneumodermopsis paucidens*" from western Atlantic shelf waters are likely to be "*Paedoclione doliiformis*" (G.A. Cooper, pers. comm.)	448	E	26		
	Peraclis spp.		488	E	16		
	Pneumoderma spp.		478	E	11		
	Pneumodermopsis canephora		358	E	1		
	Pneumodermopsis ciliata[*]	Details in Cooper and Forsyth (1963)	465	E	67		
	Pneumodermopsis paucidens[*]	Records of "*Pneumodermopsis paucidens*" from western Atlantic shelf waters are likely to be "*Paedoclione doliiformis*" (G.A. Cooper, pers. comm.). Details in Cooper and Forsyth (1963)	474	E	237		
	Pneumodermopsis spp.[*]	Includes only those *Pneumodermopsis* not specifically identified. Most records since 1977 of *Pneumodermopsis* only identified to genus. Details in Cooper and Forsyth (1963)	85	E	149		
	Pterotrachea spp.		466	E	12		
Echinodermata	Echinoderm larvae[*,+]	16 species and higher taxa found (Rees, 1954b). Counted since 1949	36	T	21,304		
	Echinoderm post-larvae[*,+]	Presence recorded before 1958, and counted since	460	E	2516		
Chordata	*Branchiostoma lanceolatum*[*,+]	Identified by notochord and pigment spots	510	E	227		
	Doliolidae[*]	*Dolioletta gegenbauri*, *Doliolina mülleri*, *Doliolum nationalis*. Details in Hunt (1968). Included in "Thaliacea"	978	E	1137		
	Fish eggs[*,+]		90	E	8160		
	Larvacea[*,+]	Presence recorded 1946–1957, counted since 1958. *Oikopleura dioica*, *O. labradoriensis*, *Fritillaria borealis* and *F. pellucida* found	37	T	24,041		
	Salpidae[*,+]	Species include *Salpa fusiformis*, *Thalia democratica*, *Iasis zonaria* and *Ihlea asymmetrica*. Details in Hunt (1968). Included in "Thaliacea"	977	E	1164		
	Thaliacea[*]	Includes "Salpidae" and "Doliolidae". Presence recorded since 1946	469	E	5203		
	Young fish[*,+]	42 species or coarser taxa found (Coombs, 1980)	91	E	26,767		
Miscellaneous taxa	'Hexasterias problematica'	Cyst or resting stage of unknown origin. Counted from 1996	806	P	54		0.00088[a]
	'*Pacillina arctica*'	Unknown biological affinity, but probably a ciliate cyst. Counted from 1996	807	T	58		

(*continued on next page*)

Table 5 (*continued*)

Group	Taxon	Description	ID	Stage	No.	Diet	Size
	Parasites of the plankton	Includes dinoflagellates, Ellobiopsids, Protozoa and parasitic metazoans. It serves to draw the attention of specialists to parasitised material for further examination	468	E	512		
	Parasitic Nematoda	Seen in chaetognaths, copepods, euphausiids and decapods. See Lindley (1977) for records from euphausiids, and Lindley (1992) for a record from a decopod larva	467	E	402		
	Phytoplankton Colour Index^{+} (PCI)	Measured in four categories: no colour, very pale green, pale green, and green. Recorded consistently since 1946	100		88,517		
	Pinus pollen*	Terrestrial pollen grain of genus *Pinus*. Counted from 1996	812	P	483		
	Plastics	Counted since 2004. See Thompson et al. (2004)	1610	P/T/E	0		
	'Stellate bodies'*	Land plant hair. Counted from 1996	814	P	660		

For each taxon, there is information on its unique CPR identification number (ID), stage of analysis in which it is counted (Stage: P, phytoplankton; T, traverse; E, eyecount), and the number of samples it has been found on up to the end of 2003 (No.). Also given is a brief description of taxa where appropriate. The dietary preference (H, herbivore; O, omnivore; C, carnivore) for copepods is given (see Section 8.2). The last column gives total length (mm) for copepods and mass (μg per cell) for phytoplankton (see Sections 8.2, 8.3). Distribution maps of taxa marked* are included in the CPR Atlas (Continuous Plankton Recorder survey team, 2004; http://www.int-res.com/abstracts/meps/CPRatlas/contents.html). Gridded and time-series products for taxa marked^{+} are included in WinCPR (Vezzulli et al., 2004; http://www.network-research-group.org/wincpr/). To calculate total copepod abundance or biomass, all copepod taxa should be summed except those marked$^{\#}$. Note that taxa in double quotations in the text are taxonomic entities within the CPR database, and those in single quotes are not strict taxonomic entities. Unless otherwise stated, consistent time series are available since 1958 for phytoplankton, and from 1948 for zooplankton. All other years given for when a taxon was counted from are for January, unless otherwise stated.

[a] Biological Atlas of the Arctic Seas 2000: Plankton of the Barents and Kara Seas (available online at: http://www.nodc.noaa.gov/OC5/BARPLANK/WWW/HTML/bioatlas.html).
[b] Farran (1948b).
[c] Roe (1972).
[d] Rose (1933).
[e] Vervoort (1952a).
[f] Vervoort (1951a).
[g] Conway and Minton (1975).
[h] Farran (1948a).
[i] Farran (1948c).
[j] Boltovskoy (1999).
[k] Vervoort (1951d).
[l] Vervoort (1951b).
[m] Vervoort (1952d).
[n] Vervoort (1952c).
[o] Vervoort (1952b).
[p] Farran (1948d).
[q] Farran (1948e).
[r] Vervoort (1951c).
[s] Wilson (1932).
[t] Vervoort (1952e).

include members of Bacillariophyceae (Diatoms), Dinophyceae (Dinoflagellates), Coccolithophoridae, Coelenterata, Platyhelminthes, Rotifera, Protozoa, Ciliophora (Tintinnids), Copepoda (Calanoids, Harpacticoids and Poecilostomatoids), Malacostraca (Decapods, Mysids and Euphausiids), Branchiopoda (Cladocerans), Cirripedia, Ostracoda, Mollusca, Echinodermata, Annelida, Bryozoa, Chaetognatha and Chordata. Some of the truly unusual taxa that are counted are "*Pinus* pollen" (pollen from terrestrial pine

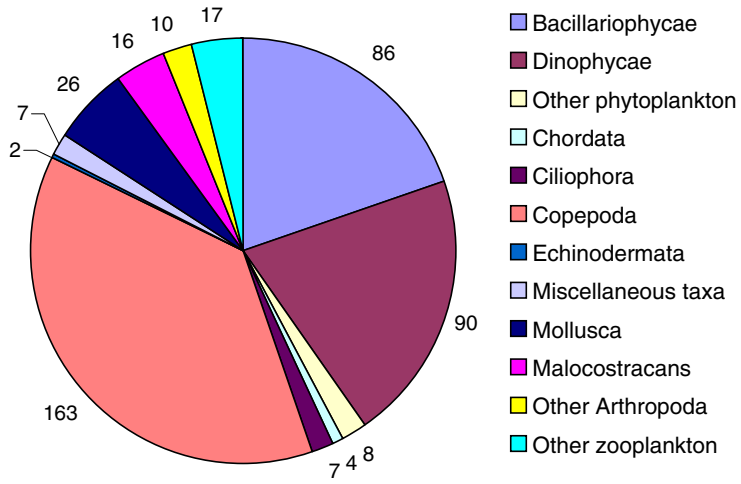

Fig. 6. The number of taxa counted in the CPR survey separated into higher taxonomic groups.

trees), "Stellate bodies" (land plant hairs), "Spindelei" (eggs of the trematode *Kuhnia scombri*), and "Plastics" (microplastics adrift in the ocean). Distribution maps in the North Atlantic of 240 taxa (marked * in Table 5) are provided in the latest CPR Atlas (Continuous Plankton Recorder Survey Team, 2004) available online at http://www.int-res.com/abstracts/meps/CPRatlas/contents.html. Gridded and time-series products for 112 North Sea plankton taxa (marked + in Table 5) are included in WinCPR (Stevens et al., in press; Vezzulli, Dowland, Reid, Clarke, & Papadaki, 2004), a data visualisation and export tool available online at http://www.network-research-group.org/wincpr/. Note that taxonomic names in use at the Survey tend to remain unchanged over the years despite the renaming of species; Table 5 includes new taxonomic names as well as the names used at the Survey.

Plankton identification at the Survey is a trade-off between providing the highest taxonomic identification possible and the time taken to analyse the large number of CPR samples each year (currently totalling >5000). Copepods, diatoms and dinoflagellates are the groups most commonly recorded in the database (Fig. 6) because their members are common in the plankton and are robust, remaining relatively intact during CPR sampling. Within these groups, specimens are usually identified to species or at least to genus. Other common and robust crustaceans such as decapods and euphausiids are not speciated. This is partly because of factors such as the high diversity and lack of a comprehensive range of larval descriptions in Decapoda, but also because of the susceptibility to damage of the prominent spines of many larval decapods and the damage to larger adult euphausiids and post-larval decapods. The size and compact morphology of most copepods usually makes identification reasonably straightforward despite specimens being partially flattened. By contrast, many gelatinous and delicate taxa are damaged irrevocably and are not easily identifiable in CPR samples. These include "Coelenterata tissue", "Doliolidae", "Salpidae", "Siphonophores" and to a lesser extent "Chaetognatha". The nature of CPR sampling therefore unfortunately reinforces the traditional bias towards copepods and away from gelatinous taxa in zooplankton ecological research.

Copepods identified usually represent stage CVs and adults both because the CPR preferentially retains these larger copepods (Robertson, 1968) and because they are easier to speciate than juveniles. In addition, females are generally more easily identified to species than are males. For example, females of three smaller species within the genus *Pleuromamma* are speciated ("*Pleuromamma borealis*", "*Pleuromamma gracilis*", "*Pleuromamma piseki*"), whereas their males are normally recorded as "*Pleuromamma* spp.". Males of other genera such as *Euchaeta* are readily identifiable and are included with the females (see Table 5 for more details).

Juveniles of some relatively common, distinctive, larger copepod genera can be easily identified and are counted separately in the traverse procedure ("*Calanus* I–IV", "*Metridia* I–IV" and "*Candacia* I–IV"). Note that juveniles of the genus *Centropages* may be counted as "*Centropages* spp." when the specimens are at a

stage of development where differentiation between species that may be present is not possible or the damage to adults prevents identification. No other juvenile copepods are counted explicitly as a separate taxonomic entity, although some may be included with their adults if distinctive (e.g., *Euchaeta* juveniles). Other juveniles that are not identifiable may be included in the "*Para-Pseudocalanus* spp." entity. This entity contains any small (<2 mm) unidentifiable copepods (particularly juveniles but also any small damaged specimens that cannot be assigned to another taxonomic entity), as well as the genera *Paracalanus* and "*Pseudocalanus* spp." themselves. Specimens of some relatively common copepod genera that are not identifiable to species because they are juvenile or are damaged can be assigned to higher taxonomic levels, e.g., "*Euchaeta* spp.", "Pontellidae" (see Table 5 for more details).

For many taxonomic groups that have not routinely been speciated at the Survey, focused studies have been carried out periodically by specialists at the Survey, and can provide valuable insights into the species present. These groups include "Chaetognatha", "Cirripede larvae", "*Clausocalanus* spp.", "Coccolithaceae", "Decapoda larvae", "Dinoflagellate cysts", "Doliolidae", "Echinoderm larvae", "Young fish" (larvae and juveniles), "Gammaridea", "Hyperiidea", "Lamellibranchia larvae", "*Lepas* nauplii", "Ostracoda", the pteropod *Pneumodermopsis* spp, "Salpidae", "Sergestidae" and "Tintinnidae" (see Table 5 for more details).

6.2. Taxa recorded as present

All taxa in the CPR database are counted numerically except for two that are only ever recorded as present: viz. "*Phaeocystis pouchetii*" and "Coelenterata tissue". The colonial Prymnesiophyte "*Phaeocystis pouchetii*" appears as a dense mass of nondescript cells under the microscope, making abundance estimates very difficult. Unusually, *Phaeocystis* is most easily identified on CPR samples by its slimy, mucilaginous feel when gently brushing a finger across the silk. Coelenterates are delicate and extremely damaged during CPR sampling and consequently cannot be speciated or given a numerical abundance. They are only recorded as present under "Coelenterata tissue". Coelenterates are identified by a combination of their appearance as acellular tissue strewn over the silk in zooplankton eyecount, and the presence of nematocysts during phytoplankton analysis and zooplankton traverse.

All other taxa that are usually counted numerically can also be recorded as present in some samples when they are seen but cannot be assigned a numerical abundance value. This happens when a taxon is observed outside its typical stage of analysis. For example, a particular phytoplankton taxon may not be seen during phytoplankton analysis but could be observed during zooplankton traverse (especially larger phytoplankton taxa). This taxon would be recorded as present in the sample, but cannot be assigned a numerical abundance value. A similar situation can arise because each type of organism has a reference point, and if the reference point is not observed within the field of view then the taxon cannot be counted but only recorded as present. This is particularly important for organisms larger than a single field of view. For example, the elongate dinoflagellate "*Ceratium extensum*" is only counted (as are all dinoflagellates) if the girdle is present within the field of view. Abundances would be overestimated if they were based on observing any part of the body because a single specimen of *C. extensum* usually covers several fields of view; if any part of the cell other than the girdle is observed during phytoplankton analysis then the taxon is recorded as present. Other reference points for organisms include the base of the antenna of copepods and the eyes of euphausiids. In addition, some taxa are recorded as present but not counted numerically when an organism is extremely damaged. Although this occurs rarely, it is more common with large organisms such as euphausiids or fish larvae. Examples such as these, where taxa are recorded as present, can be extremely valuable. Recent work on calanoid copepod diversity from the CPR survey (based on the number of species per sample) incorporates many zooplankton traverse taxa that were often only seen in zooplankton eyecount and recorded as present on a sample (Beaugrand, 2004; Beaugrand et al., 2002).

Examination of CPR records shows that some organisms are more frequently recorded as present than counted numerically. This may be because the organism is particularly distinctive or is more often identified in a counting procedure not designed for that taxon. For example, "*Polykrikos schwartzii* cysts" have been recorded as present in zooplankton traverse more often than counted in phytoplankton analy-

sis. This is also the case for the chain-forming phytoplankton cells "*Paralia sulcata*" and "*Oscillatoria* spp." (*Trichodesmium* spp.).

6.3. Taxa recently added

The Survey is responsive to changes in research focus and marine management imperatives (Brander et al., 2003) and adds new taxa to those that are counted as appropriate. Effectively this means that a new Taxon ID number is allocated in the CPR database and analysts are trained to identify and record the taxon. For example, the genus *Dinophysis*, which has many species that are defined as harmful algal bloom species and are responsible for diarrhetic shellfish poisoning (Moestrup, 2004), had historically only been identified to the genus level. Since January 2004, "*Dinophysis acuminata*", "*Dinophysis acuta*", "*Dinophysis caudata*", "*Dinophysis norvegica*", "*Dinophysis rotundatum*", "*Dinophysis sacculus*" and "*Dinophysis tripos*" are now recognised and counted (Table 5). The entity "*Dinophysis* spp." has been counted since 1958 and will continue to be counted into the future to preserve the time series, alongside the more detailed species information begun in 2004. Another recent addition to the taxa counted at the Survey from January 2004 is the non-biological entity marine "Plastics". This was initiated in response to recent findings that marine plastics have increased over the last 40 years in CPR samples (Thompson et al., 2004). "Plastics" are not counted numerically but just recorded as present. There are several other recent additions to the taxa counted. Prior to 2003, the isopod "*Heterophryxus appendiculatus*", which is parasitic on euphausiids, was recorded in "Parasites of the plankton", but has been subsequently counted separately. Since January 2004, "Radiolaria" has been separated into "Acantharia" and "Radiolaria" whilst retaining the original taxon. Other taxa added to the database recently include "*Pinus* pollen" in 1996, the veliger larvae of the gastropod *Lamellaria perspicua* ("Echinospira larvae") in 1999, and "*Neodenticula seminae*" in 2003.

6.4. Taxa discontinued/counted differently

As new taxa have been added, the number of species counted in the Survey has generally increased through time, although a few taxonomic entities have been discontinued or counted differently over the years. For example, "Euphausiacea Juveniles" and "Euphausiacea Adults" were only counted from 1968 to 1988; these taxa are included within "Euphausiacea Total". The taxon "Cladocera Total" was discontinued in 1957, although individual taxa ("*Evadne* spp." and "*Podon* spp.") are now counted separately. Those few taxa that have been discontinued are given in Table 5.

As with many long biological time-series, there have been some changes in the counting procedures for a few taxa (see Table 5). For example, "Coccolithaceae" were recorded as present from 1965, and numerically from 1993. "Thaliacea" were counted numerically from 1948 to 1960, and have since been recorded as present, but since 1960 "Salpidae" and "Doliolidae" (which comprise "Thaliacea") have been counted. "*Phaeocystis pouchetii*" was actually counted numerically from 1948 to 1957, and has just been recorded as present since.

6.5. Taxa recorded in comments

Supplementary information, such as the presence of species that are not routinely recorded (i.e., they do not have a taxon ID number in the CPR database), is entered as comments in the CPR database. Such taxonomic entities include filamentous green algae, stalked vorticellids (protozoans), hydroid colonies, 'wagon wheels' (ossicles from holothurian larvae), barnacle exuviae (no other crustacean exoskeletons are noted), tintinnid cysts, and cysts of the dinoflagellates *Gonyaulax* spp. ('*Spiniferites*'), *Scrippsiella*, *Protoperidinium* spp. and *Warnowia* cf. *rosea*. Taxa new to the Survey may first appear as comments by some analysts in the CPR database, prior to being given a taxon ID number in the CPR database and counted numerically by all analysts. Comments may also record aspects of the sample itself, such as the presence of oil or the preservation status of the plankton. Although comments may lack consistency and reflect the personal experience of the analyst, they can be useful for targeting samples for study of specific taxa in the CPR archive.

6.6. Consistency of identification

The identification of taxa has remained as consistent as possible over the 70-year history of the Survey. This achievement has been made possible both by the large number of people who have analysed CPR samples at the Survey, nearly 100 at the last count (Reid et al., 2003), and by the relatively large size of the analysis team at any one time (currently 16 analysts, two of whom each have almost 40 years of experience analysing CPR samples). The Survey thus maintains a critical mass of skilled para-taxonomists. There is also a system of reanalysing a sample for a particular taxonomic entity when it has an anomalous count compared with neighbouring samples, or if the entity is extremely rare in the particular area. These practices have helped to maintain consistency throughout the history of the Survey.

Generally all phytoplankton and most zooplankton including copepods have been consistently identified throughout the history of the Survey. However, some difficult-to-identify zooplankton taxa may have been identified more regularly to species or genus while an expert in the group was within the analysis team, but have not been consistently identified by all analysts over the years. For instance, shells of gastropod molluscs when present are almost always broken and soft tissues are often too distorted for specific identification from superficial morphological features; examination of radula structure and (where present) hook sacs is often necessary for reliable identification. There were analysts with such expertise on molluscs from 1948 to 1977 and the identifications in Vane (1961); Vane and Colebrook (1962); Cooper and Forsyth (1963), and Edinburgh Oceanographic Laboratory (1973) were supported by this specialist knowledge that is not currently available.

7. Interpreting CPR data

Here, we describe the semi-quantitative nature of CPR data, and how these data can be used to derive indices of seasonal and inter-annual abundance and biomass based on functional groups.

7.1. Time series

Although most taxa have been counted since 1946, there have been some changes in counting procedures since then (see Section 5.7). This means that there are consistent time series for most phytoplankton taxa since 1958, and for zooplankton taxa since 1948.

Exceptions to these rules are given in Table 5 and fall into two types. First, many taxa are only recorded when a management decision is taken to do so. For example, the abundant dinoflagellate "*Noctiluca scintillans*" has only been counted from 1981, and the common tintinnids "*Dictyocysta* spp.", "*Favella serrata*", "*Parafavella gigantea*", "*Ptychocylis* spp." and "*Tintinnopsis* spp." have only been counted separately since 1996, when management decisions were taken to record them. More recent examples of such management decisions are given in Section 6.3. Second, advances in taxonomy can result in a new taxon being recorded. This happened when the diatom *Ephemera planamembranacea* was actually discovered and first described as "*Navicula planamembranacea*" (Hendey, 1964) from CPR samples in 1962. This species almost certainly occurred on earlier samples but had not been described. Another example is that of "*C. helgolandicus*", which was only confirmed as a separate species from "*C. finmarchicus*" in the 1950s (see Matthews, 1966) and so was only counted separately in CPR samples from 1958. Before this, *C. helgolandicus* individuals existed, although we did not count them explicitly. Such taxa cannot be regarded as truly absent before they had been first recorded, so that their time series are only valid from the time the taxon was first counted in the Survey (shown in Table 5).

Note that this situation is entirely different from that of taxa truly absent before they were first recorded. Time series for these taxa can be taken from 1948 for zooplankton and from 1958 for phytoplankton. This situation can arise when a taxon may not have historically occurred in the survey area, but has been introduced or has extended its range. For example, the diatom "*Coscinodiscus wailesii*" was introduced through translocation of non-indigenous oysters for mariculture into the Northeast Atlantic in 1977 (Boalch & Harbour, 1977; Edwards, John, Johns, & Reid, 2001) from the Pacific Ocean; the Pacific diatom "*N. seminae*" was introduced, by ballast water or altered currents, into the North Atlantic in 2003; and the cladoceran "*Penilia avirostris*" was found in the North Sea in the 1990s, possibly introduced by ballast water (Johns, Edwards,

Greve, & John, 2005). These taxa were certainly not present before they were first recorded in CPR samples. This situation can also arise when rare taxa may only be found for the first time many years (or decades) after the beginning of the Survey. For example, the copepod "*Gaetanus minor*" was only seen for the first time in the Survey after sampling for 13 years and it was a further 23 years until a second specimen was found. A substantial proportion of taxa in the database are rare (105 taxa have been found fewer than 20 times). The infrequent recording of some rare phyto- and zooplankton taxa may be further compounded if they are not distinctive, making them more likely to be misidentified as similar species. Such 'new' taxa can also be found when the Survey expands into new areas. For example, many cold-water taxa were found when the Survey started sampling the Northwest Atlantic in 1959, and many warm-water taxa were first recorded when the Survey expanded south of 40°N in the late 1960s.

7.2. Semi-quantitative abundances

We recommend that CPR data not be used as an absolute measure of abundance, but as semi-quantitative estimates that reflect real inter-annual and seasonal patterns. Although no device measures the abundance of plankton perfectly (Wiebe & Benfield, 2003), there is increasing evidence that the CPR substantially underestimates absolute numbers (Batten, Clark, et al., 2003; Clark, Frid, & Batten (2001); John, Batten, Harris, & Hays, 2001; Richardson, John, Irigoien, Harris, & Hays, 2004). The relatively large size of the silk mesh (270 μm) of the CPR undoubtedly under-samples phytoplankton, and this is particularly true for the smaller species. Despite this, phytoplankton down to 10 μm in size, such as "Coccolithaceae" and "*Nitzschia delicatissima*" (now *Pseudo-nitzschia delicatissima*), are regularly captured in CPR samples (Table 5). One reason for this may be that phytoplankton are caught on the leno weave (a single strand in one direction and a double twisted strand in the other) of the relatively thick silk strands in the mesh used for filtering in the CPR. Silk mesh has been retained for data consistency. Standard mesh for most modern plankton sampling is a simple weave of fine nylon strands that are heat-fused at the crossings of warp and woof. The silk strands of CPR mesh constitute 30–40% of the mesh area. There may also be an effect of clogging by phytoplankton and zooplankton (John et al., 2002; Jonas et al., 2004), particularly gelatinous forms, which may lead to retention of smaller phytoplankton species. Even for zooplankton, abundances from other samplers are generally 1–40 times more than those from the CPR (Clark et al., 2001; Hunt & Hosie, 2003; John et al., 2001; Richardson et al., 2004). A detailed description of the difficulties in calculating quantitative conversions between abundance estimates from the CPR and conventional net samplers can be found in Richardson et al. (2004). Small zooplankton are likely to be under-sampled because of the relatively large mesh size compared with other standard nets (usually 200 μm) for sampling mesozooplankton (Sameoto et al., 2000). Work on the retention of organisms on the silk during CPR tows found that organisms with widths <300 μm were not fully retained, and that those with widths <287 μm had only 50% retention (Robertson, 1968; c.f. Hays (1994) and Batten, Clark, et al. (2003)). In addition, some small taxa such as "*Oithona* spp." may be underestimated because they are relatively transparent and thus difficult to see in the on-silk analysis during zooplankton traverse. Although on-silk analysis may be sub-optimal for some taxa, it is continued to maintain consistency of the time series; changing this procedure would alter the results.

Large zooplankton are likely to be under-sampled by the CPR because of active avoidance (Clark et al., 2001; Hunt & Hosie, 2003; Richardson et al., 2004). Despite the relatively fast speed of the CPR (7.5 m s^{-1}) compared to many nets (1–2 m s^{-1}), the small inlet aperture of the CPR (1.27 cm × 1.27 cm) compared with a typical net (typically 50 cm diameter) may allow large zooplankton to escape capture if they can sense the approach of the CPR through changes in hydrostatic pressure (Clark et al., 2001; Richardson et al., 2004). Numerical modelling and flow-tank studies are needed to answer questions associated with CPR hydrodynamics and zooplankton avoidance.

Notwithstanding the semi-quantitative nature of CPR sampling, there is considerable evidence that it captures a roughly consistent fraction of the in situ abundance of each taxon and thus reflects the major patterns observed in the plankton (Batten, Clark, et al., 2003). Seasonal cycles estimated from CPR data for relatively abundant taxa are repeatable each year, and are sufficiently resolved to detect the earlier seasonal peaks in response to warmer sea temperatures of recent years (Edwards & Richardson, 2004). There is also generally

good agreement between seasonal cycles measured by the CPR and from other samplers such as WP-2 nets (Clark et al., 2001; John et al., 2001) and the LHPR (Richardson et al., 2004).

Inter-annual changes in plankton abundance are also captured relatively well by the CPR (Clark et al., 2001; John et al., 2001) because the time-series has remained internally consistent, with few changes in the design of the CPR or in counting procedures. This agreement between the CPR and other devices is not as strong as seasonal comparisons (Batten, Clark, et al., 2003), although this may simply reflect the greater auto-correlation in seasonal plankton cycles. A major potential bias in decadal time series of abundance from the CPR is related to the general increase in ship speed from an average of 10.5 knots in 1953 to 14.8 knots in 1999. Faster ship speeds have not influenced the depth of tow (Batten, Clark, et al., 2003; Hays & Warner, 1993), but have slightly decreased the volume of water filtered by the CPR (Jonas et al., 2004). Although this bias could potentially lead to a perceived general long-term decline in abundance, inter-annual changes are large relative to this small bias (Jonas et al., 2004). Moreover, long-term trends in abundance are generally increasing for many taxa counted in CPR samples including the "phytoplankton colour index" (Reid, Edwards, Hunt, & Warner, 1998), "*C. helgolandicus*" (Bonnet et al., 2005), and meroplankton (Lindley & Batten, 2002). Problems associated with changes in the volume of water filtered per sample may be solved by the routine use of flowmeters. Unfortunately, flowmeters are not routinely fitted to the >20 CPRs deployed each month because of a lack of resources.

A consequence of using CPR data to capture relative patterns and not as estimates of absolute abundance is that data are normally expressed in numbers per sample. As each sample represents ~3 m^3 of filtered seawater, abundance estimates should be divided by 3 to obtain estimates per m^3. Because CPR samples provide relative estimates of abundance that are useful for assessing relative patterns, abundance estimates are seldom converted to per m^3 estimates in practice.

8. Using CPR data

8.1. Forms of data output

Plankton abundances from each sample can be used to create gridded maps to explore changes in the distribution of key taxa such as "*C. finmarchicus*" (Planque & Fromentin, 1996) and the diversity of calanoid

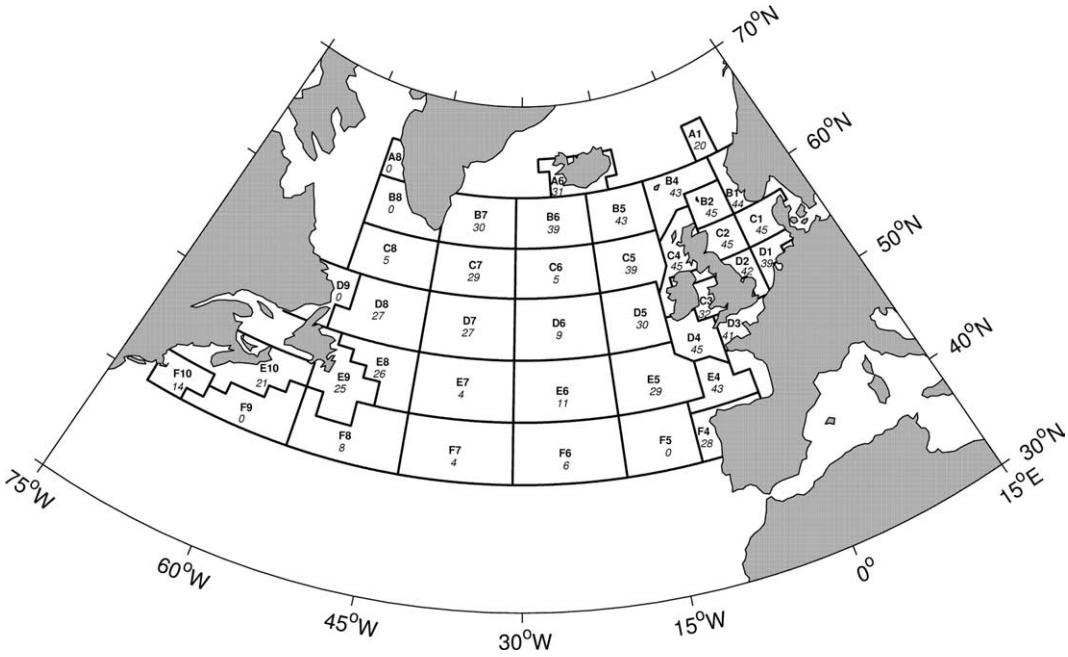

Fig. 7. CPR standard areas, with the number of years where eight or more months have been sampled since 1958.

copepods (Beare, Batten, et al., 2003; Beaugrand et al., 2002). They have also been used to delve into the diel vertical migratory behaviour of zooplankton (Hays, Proctor, John, & Warner, 1994). There are, however, restrictions on access to raw CPR data (see Section 10 for details).

Abundance estimates from individual plankton samples are inherently imprecise because of variable zooplankton behaviour such as diel vertical migration and local weather conditions that can concentrate or disperse fine-scale patches (Robertson, 1968), as well as the 'broad-brush' counting procedures. To subsume much of this fine-scale variability, CPR data are commonly averaged spatially in geographic areas of interest and temporally as monthly or annual means.

The most common relatively large regions used historically have been CPR standard areas (Fig. 7). These have been used to describe seasonal and inter-annual changes in phyto- and zooplankton abundance throughout the North Atlantic (e.g., Colebrook, 1975). They have also been employed recently as comparative replicate study areas to test hypotheses concerning the propagation of environmental forcing up the plankton foodweb (Richardson & Schoeman, 2004). The positioning and size of CPR standard areas is not entirely arbitrary; the edges of many of the standard areas follow the edge of the continental shelf (defined as the 100 fathom (~200 m) contour) and the size of the boxes on the shelf are smaller to reflect the more dynamic physical environment, larger biological variability and greater CPR sampling.

Monthly and annual means for plankton taxa can also be derived for any area of interest, but when considering the size of the area to choose it should be remembered that there is a trade-off between the precision of plankton estimates and their bias. For example, averaging over too small an area leads to fewer estimates of plankton abundance resulting in less confidence in mean monthly or annual values, as well as the increased likelihood of data gaps for particular months or years. By contrast, averaging over too large an area may combine disparate hydrographic regimes. Averaging over large areas also introduces spatial biases due to the changing positions of tow routes, possibly leading to non-representative estimates, but does reduce the error associated with the category counting system. In practice, reasonably large regions (about the size of CPR standard areas) should be considered, but smaller regions are possible in well-sampled areas.

Calculating estimates of seasonal cycles and annual time series from highly seasonal plankton data is problematic when some months have not been sampled. Rather than averaging over the months where data are available, a more robust annual estimate is obtained by first estimating the abundance of plankton for months when there are no data. There are various interpolation options, but the standard way used at the Survey to estimate a missing monthly mean (Colebrook, 1975) is

$$\overline{M} \times \frac{Y}{\overline{Y}},$$

where $\overline{M}$ is the long-term mean of that month, Y is the annual mean of the particular year, and $\overline{Y}$ is the long-term annual mean. At least eight months need to be sampled in a year to have an adequate estimate of the seasonal cycle to estimate the annual abundance, otherwise the year is excluded. Fig. 7 shows the number of years since 1958 when eight or more months were sampled for each CPR standard area.

8.2. Indices based on functional groups

Integrated indices based on functional groups are increasingly being used to summarise changes in communities and ecosystems, forming the basis for ecological indicators that underpin the management of marine systems (Brander et al., 2003). Indices from the CPR survey can provide information pertinent to management issues such as eutrophication (Edwards, Reid, & Planque, 2001), spread of non-indigenous species (Edwards, John, et al., 2001), and particularly climate impacts on biodiversity (Beaugrand et al., 2002), phenology (Edwards & Richardson, 2004) and the abundance of plankton (Richardson & Schoeman, 2004). Examples of such indices can be found in the annual Ecological Status Report produced by SAHFOS (Edwards, Richardson, Batten, & John, 2004; see SAHFOS website). There is a rich variety of potential indices for phyto- and zooplankton, and here we focus on some of these for common functional groups.

There are several simple phytoplankton indices that can be easily derived from CPR data. One such simple index is the ratio of diatoms to dinoflagellates; such a ratio can be easily calculated by direct summation of

individual diatom and dinoflagellate taxa since 1958 (see Table 5). It has been suggested that climate warming will favour dinoflagellates over diatoms, and this has been observed in the Northeast Atlantic from CPR samples (Edwards, Reid, et al., 2001). Another simple index, total phytoplankton, is not so easy to calculate, however, as some phytoplankton taxa have not been counted consistently since 1958: "Coccolithophores" have been counted numerically since 1993; "*N. scintillans*" since 1981; "Silicoflagellates" since 1993. Indices of harmful and nuisance algal blooms can also be derived from CPR samples. For example, the Survey records "*Prorocentrum* spp." (mainly *P. micans*) responsible for diarrhetic shellfish poisoning (DSP), "*Nitzschia seriata*" (now *Pseudo-nitzschia seriata*) and "*N. delicatissima*" (now *P. delicatissima*) responsible for amnesic shellfish poisoning (ASP), and "*Nitzschia closterium*" (now *Cylindrotheca closterium*) responsible for production of foam and mucilage. In addition, the genus "*Dinophysis* spp." is responsible for DSP and is now speciated (see Section 6.3).

To estimate the total abundance of copepods, there are two options. The first and simplest is to use "Copepoda total" (Table 5). This collective entity includes each copepod (whether <2 or >2 mm total length) that is observed during the zooplankton traverse stage of analysis (note that the base of the copepod antennae must be observed). Although this provides a straightforward estimate of copepod abundance, there are two possible weaknesses. The first is that "Copepoda Total" cannot be separated into finer functional groups if desired (e.g., based on diet or size). The second is that the precision of the estimate of total copepod abundance may not be as good as summing individual taxa because large taxa are not well represented in "Copepoda Total". This is a consequence of only 2% of the sample being examined in zooplankton traverse, compared with the entire sample being counted for copepods >2 mm in zooplankton eyecount.

The second and more robust, but labour-intensive, estimate of total copepod abundance is derived by summation of individual abundances of each copepod taxon counted in zooplankton traverse and zooplankton eyecount. This procedure has been used in recent studies (Richardson & Schoeman, 2004). Although this approach would seem straightforward, it is complicated by the fact that some copepods are counted in more than one taxonomic entity simultaneously, so that summing all copepod taxa will over-estimate total copepod abundance. It may seem perplexing that copepods are counted in more than one taxonomic group, but it is a necessary consequence of the increasing taxonomic resolution of the Survey through time and the desire to continue existing time series. For example, before 1958 all *Calanus* (except the much larger congener "*Calanus hyperboreus*") were known as "*C. finmarchicus*". From 1958 onwards, *C. finmarchicus* s.l. was separated into "*C. finmarchicus*", "*C. helgolandicus*" and "*C. glacialis*". Thus to maintain the existing time series for "*C. finmarchicus*" after 1958, an equivalent "*Calanus* V–VI Total" entity comprising the summed abundances was introduced. Thus, individuals counted in "*C. finmarchicus*", "*C. helgolandicus*" and "*C. glacialis*" are also included in "*Calanus* V–VI Total". There are several other examples of the same individual copepod being counted in more than one taxonomic entity: e.g., all adult *Pseudocalanus* spp. are not only counted in their own taxonomic entity but also in "*Para-Pseudocalanus*", and both "*Metridia* total traverse" and "*Calanus* total traverse" contain their juveniles that are also contained in "*Metridia* I–IV" and "*Calanus* I–IV". The zooplankton traverse and zooplankton eyecount taxa that contain no duplicates and so can be summed to obtain total copepod abundance are marked with a # in Table 5. Once estimates of total copepod abundance are calculated, they can then be used to produce useful products such as maps of copepod abundance (Fig. 8(a)) that can be partitioned in meaningful ways seasonally or inter-annually. It should be noted that some other taxa are also recorded in more than one taxonomic group (see "Cladocera Total" (now discontinued), "Dinophysis spp.", "Euphausiacea Total", "Radiolaria", "Sergestidae", "Thaliacea" and "Tintinnidae" in Table 5).

Another useful partitioning of copepods is into broad functional groups that reflect their dominant mode of nutrition. Although almost all zooplankton are omnivorous to some degree (Turner, 1984), here we broadly classify them as herbivores, omnivores or carnivores (Table 5) based on their dominant mode of nutrition gleaned from published sources (Mauchline, 1998; Turner, 1984), from discussion with other plankton ecologists, and from our own knowledge. This information has been used to show that effects of climate warming propagate up the plankton foodweb because of tight trophic coupling (Richardson & Schoeman, 2004), and has been used for initialisation and validation of plankton ecosystem models (e.g., Allen et al., 2001); it may also be useful in other studies.

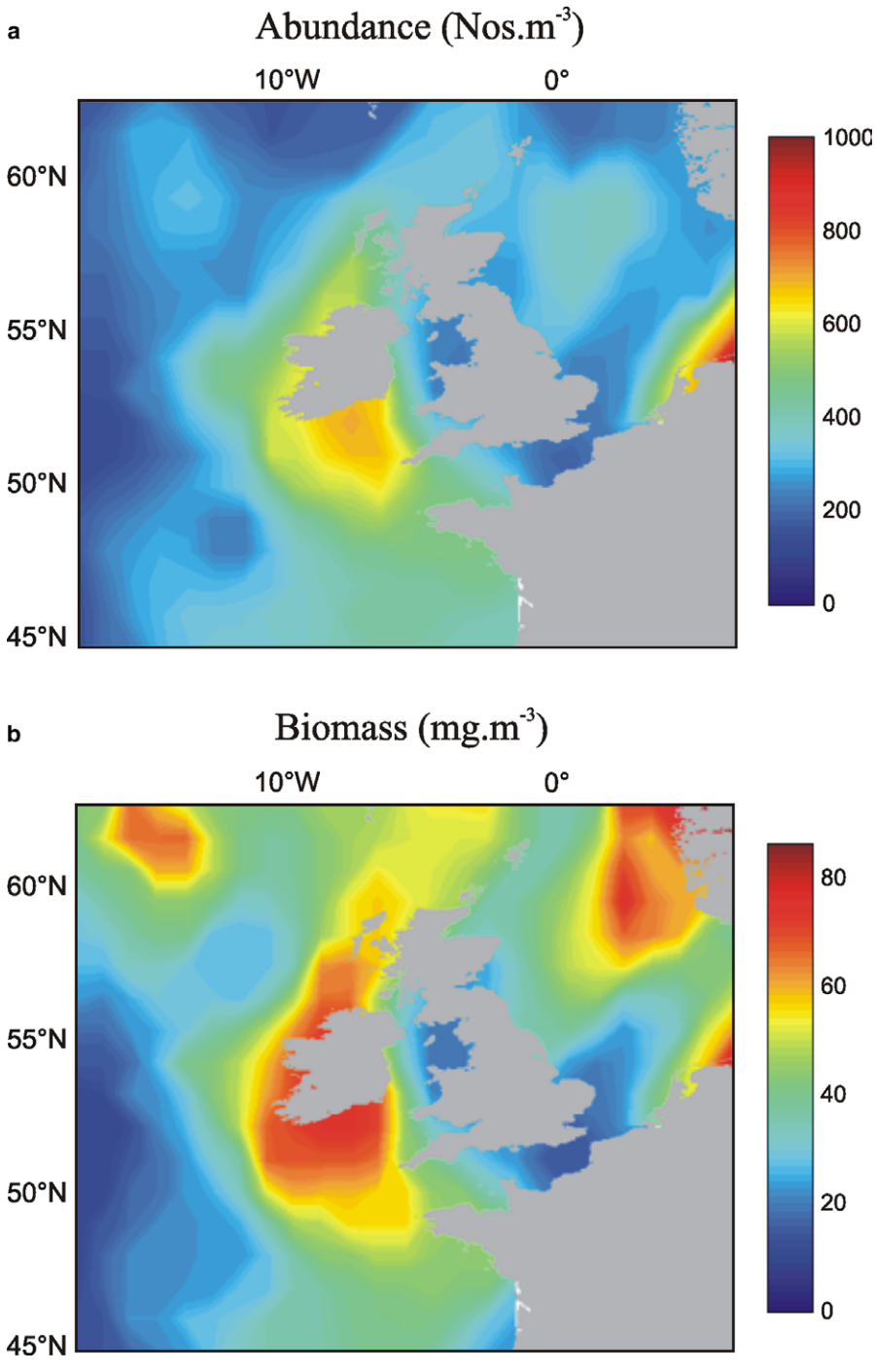

Fig. 8. Map of total copepod (a) abundance, and (b) biomass.

CPR samples can also be used to estimate one of the most important properties of a community, the size of its constituent members (Peters, 1983). Allometric relationships based on organism size allow the derivation of a plethora of rate processes (e.g., respiration and turnover times), and size is probably the major determinant of predatory relationships in the ocean (Verity & Smetacek, 1996). For zooplankton counted from CPR

samples, sizes can only easily be assigned to the copepods because they are generally identified to the species level, whereas many of the larger zooplankton taxa are simply grouped as decapod larvae, euphausiids, or fish larvae and range widely in size. Although no direct estimates of the size of each copepod are available for each sample, as it is clearly not feasible to measure all copepods in all CPR samples, it is still possible to obtain size-based indices.

The simplest way is to calculate the average size of the copepod community ($\overline{L}$) in a sample, by multiplying the total length (L) of each species i obtained from the literature (see Table 5) by its abundance (X_i), summing over all species (N) in the community, and dividing by the total abundance:

$$\overline{S} = \frac{\sum_{i=1}^{N}(L_i \times X_i)}{\sum_{i=1}^{N} X_i}.$$

Such an approach has been used in a number of recent studies (Beaugrand, Brander, et al., 2003) and is useful where the focus is on substantial changes in average community size based on changes in species contribution rather than finer-scale, intra-specific variations related to factors such as temperature. However, in assigning an average size to each copepod species in Table 5, two difficulties had to be overcome. The first was that for each species a range of stages are captured. The CPR does, however, preferentially retain the larger sizes, particularly adults (Robertson, 1968). Of these, relatively few are male; this situation is relatively common in many copepod species (Mauchline, 1998). We have thus used female length to represent the size of a species. The second difficulty was that some copepods are only identified to genus. In these situations we used the size of the dominant species in the core Northeast Atlantic area of the CPR survey to be representative of that genus.

Another useful index that can be calculated from CPR data is the timing of the seasonal cycle (Colebrook, 1975; Colebrook & Robinson, 1965; Edwards & Richardson, 2004). The timing of the seasonal peak throughout the entire growing season (the central tendency, T) can be derived using the month co-ordinate of the centre of gravity of the area below graphs of monthly means:

$$T = \frac{\sum_{i=1}^{12} M \cdot x_{\mathrm{m}}}{\sum_{i=1}^{12} x_{\mathrm{m}}},$$

where x_{m} is the mean abundance in month M (January $= 1, \ldots,$ December $= 12$).

This index is sensitive to changes in the timing of the seasonal cycle. The average seasonal cycle over the entire time series can be used to assess whether seasonal cycles are unimodal or bimodal (spring and autumn peaks). For unimodal taxa the timing of the seasonal peak is calculated throughout the entire year, whereas for bimodal taxa the timing of the seasonal peak is calculated separately for the first six and last six months of the year (Edwards & Richardson, 2004).

8.3. Estimating biomass

Biomass estimates are often needed in ecosystem models, for fisheries research, and in general ecological studies investigating energy transfer between trophic levels. The currency of many ecosystem models is not in numbers of individuals but in biomass such as carbon. Such models require biomass fields of the biological compartments of phytoplankton and zooplankton for initialisation, and biomass time series for validation (Allen et al., 2001; Broekhuizen, Heath, Hay, & Gurney, 1995; Bryant, Heath, Gurney, Beare, & Robertson, 1997; Heath, Scott, & Bryant, 1997; Smith & Tett, 2000). Biomass estimates of copepods probably also represent the best index of food available to fish larvae (Beaugrand, Brander, et al., 2003) and planktivorous fish such as herring and basking sharks, and they are needed for bio-energetic models of fish feeding.

The best estimate of total phytoplankton biomass from CPR data is the "phytoplankton colour index" (PCI). Although the exact nature of the PCI has been questioned because it is assessed visually and on a four-point scale (see Section 5.1), there is strong agreement between the PCI and chlorophyll measured fluo-

rometrically from CPR samples (Batten, Walne, Edwards, & Groom, 2003; Hays & Lindley, 1994), as well as with chlorophyll measured by satellite (Batten, Walne, et al., 2003; Raitsos, Reid, Lavender, Edwards, & Richardson, 2005). The PCI not only reflects the biomass of diatoms and dinoflagellates, but also the pigments from delicate naked micro- and nanoflagellates that tend to disintegrate when preserved in formalin (Gieskes & Kraay, 1977; Reid, Robinson, & Hunt, 1987). These small phytoplankton cells can not be identified in microscopic analysis and therefore are not contained in any phytoplankton counts.

As well as being a better measure of chlorophyll than total phytoplankton, PCI has three advantages over phytoplankton data from microscopic analysis. First, it is assessed on all of the >350,000 samples at the Survey (and not just alternate samples as for other CPR data), although only data on alternate samples is currently entered into the database. In future, PCI for all samples will be entered (Stevens et al., in press). Second, the PCI is measured on return of the CPR to the laboratory and data are potentially available within 4 weeks after sampling, whereas standard data release based on microscopic analysis is ~1 year. Last, there is a longer time series of PCI available than for entities from phytoplankton analysis because the PCI has been evaluated consistently since 1946, whereas phytoplankton analysis has only remained unchanged since 1958.

There are, however, several caveats that should be considered when using PCI data. First, it is a relatively imprecise, seemingly arbitrary visual assessment. On the other hand, it is probably not as arbitrary as it seems, as the few analysts that assess the PCI initially use standard colour charts and train for a year with other more-experienced analysts before undertaking assessments themselves. Moreover, the assessment of PCI is remarkably consistent amongst analysts who perform this job (Hays & Lindley, 1994). Second, having only four categories can present some statistical limitations if the PCI for each sample is used. However, it becomes a continuous (ratio-scale) variable once samples are averaged spatially (e.g., over CPR standard areas) and temporally (e.g., monthly), allowing easier statistical examination. Third, green colouration may be obscured by the presence of other pigments. For example, high abundances of echinoderm larvae, as have been common in recent years (Lindley & Batten, 2002), can have a strong brown colouration, which may overshadow greenness attributable to phytoplankton.

Another estimate of phytoplankton biomass could be derived from mass estimates of individual phytoplankton taxa. Although such estimates are relatively rare in the literature, many are given in Table 5. These can be used to derive time series or maps of biomass for particular taxa.

Estimates of total copepod biomass are relatively straightforward from CPR samples, but require some assumptions because no direct measurements of mass are made. A detailed procedure for estimating copepod biomass based on measuring the size of individual copepods on each CPR sample and combining this information with species-specific mass–length relationships derived for each species was proposed and applied on a small number of CPR samples by Robertson (1968). This method, however, is not practical for the large numbers of samples and copepod taxa routinely counted in the Survey. As estimates of copepod length are far more common than for mass in the literature, a simpler approach is to use the general size information for each copepod taxon (presented in Section 8.2; see Table 5) to estimate the mass of each copepod using an allometric relationship. There are many such length–weight relationships for copepods (e.g., Mauchline, 1998), but the one by Peters (1983) has been used previously at the Survey (Beaugrand, Brander, et al., 2003). This relationship ($W = 0.08\,L^{2.1}$) estimates mass (W, mg wet weight) from total body length (L, mm) for copepods/zooplankton. Such mass estimates for a species i (W_i) can be multiplied by its abundance (X_i) and then summed for all species (N) in a sample to obtain total biomass per sample (B):

$$B = \sum_{i=1}^{N} (W_i \times X_i).$$

An example of using this method to derive a mean map (1958–2002) of total copepod biomass in the Northeast Atlantic is shown in Fig. 8(b). It is clear that this method assumes no change in average body mass for a species over time, but it does allow an interesting comparison with the map of total copepod abundance (Fig. 8(a)). There is a preponderance of biomass in cooler northern areas, contrasting with higher abundance (numbers) of total copepods in the warmer southern areas. This is a consequence of generally larger copepods being found in cooler northern areas. Such maps based on relevant subsets of CPR data enable examination of seasonal and regional variations in biomass of various species and functional groups.

Clearly the same caveats apply to biomass estimates from the CPR as apply to abundance estimates. Total copepod biomass will undoubtedly be under-estimated, although again the relative consistency of the sampling procedures through time should ensure relative changes are meaningful. The method proposed here also does not consider geographical and seasonal variations in mean body weight (e.g., Robertson, 1968). Although the procedure described here enables estimates of total copepod biomass from CPR samples, it is very difficult to estimate total zooplankton biomass because non-copepod zooplankton taxa are only crudely identified to family or class and vary widely in size.

9. Environmental data

There has been no consistent collection of environmental data concomitant with CPR samples over the 70-year history of the Survey because the technology did not exist. However, several parameters are now measured semi-regularly over more recent times. Instruments measuring conductivity, temperature, depth and fluorescence have been fitted in the rear bay of the CPR below the propeller shaft (Fig. 1) along some CPR routes since 1993. The use of instruments measuring temperature alone has been more widespread, particularly since 1996. Despite cost and staff constraints precluding the routine collection of temperature measurements on every tow, data for over 420 CPR tows together with their time and location information are freely available from the SAHFOS website. These data facilitate the study of plankton data in relation to mesoscale features such as fronts along selected CPR routes over the last decade.

Investigation of plankton in relation to environmental variables over longer time scales is best accomplished by global products available freely on the Internet (Hays et al., 2005). SST, wind speed and direction, and cloudiness are available from the International Comprehensive Ocean Atmosphere Datasets (ICOADS; www.cdc.noaa.gov/coads/) at a 1° (1960–2002) and 2° (1860–2002) spatial resolution globally. Updates are released every 5 years. More-regularly updated SST data at a 1° spatial resolution are available from the UK Met Office (HadISST; www.badc.nerc.ac.uk/; Rayner et al., 2003). Salinity data can be obtained from the International Commission for the Exploration of the Sea (ICES; www.ices.dk). The temporal scale (monthly) of these products is comparable to that of the CPR data. Values from these products can be assigned to each CPR sample based on its position and month of sampling.

10. Data availability

In May 1999, SAHFOS amended its data policy to comply with the Global Ocean Observing System (GOOS) programme, making the data freely available for non-profit research (Stevens et al., in press). As part of this commitment to GOOS, the SAHFOS website hosts data on important indicators of primary (''phytoplankton colour index'') and secondary (''*C. finmarchicus*'' since 1958) productivity as monthly means for CPR Standard Areas. Also as part of the GOOS policy, data for all taxa as monthly and annual means are available by completing, signing, and returning a Data Licencing Agreement available on the SAHFOS website. This agreement enables SAHFOS to monitor the number of researchers using CPR data. Data are usually provided within several working days. We ask that any publication resulting from CPR data include an acknowledgement of the data source, and that a copy of the publication be forwarded to SAHFOS. Researchers requiring access to raw sample data are required to visit SAHFOS in Plymouth (UK) to obtain the data themselves. This enables the researcher to better appreciate the strengths and weaknesses of CPR data by witnessing and appreciating first-hand the CPR itself, the process of counting samples, and the idiosyncrasies and complexities of the CPR survey methodology and data.

All samples from 1960 onwards are archived, including those that have been counted as well as those that have not, and they can be used for non-destructive purposes. For example, a number of studies have used samples from the archive to speciate taxa that were only routinely identified to a coarse level, producing maps and seasonal cycles of many taxa including decapods (Lindley, 1987) and fish larvae (Coombs, 1980; see Table 5 for examples). Samples before 1960 were stored in glass tubes, corked and sealed with wax, but had to be discarded recently due to fungal infection and damage during transfer between stores.

11. Summary

The vision of Sir Alister Hardy has provided researchers and managers of the marine environment with their best long-term measure of the state of the oceanic plankton in the North Atlantic. The longevity of the CPR survey is a testament to the ingenious and robust design of his instrument, and the Survey continues to count more than 5000 plankton samples each year. From 1946 to 2004, a total of 207,619 samples have been analysed for 437 taxa in the North Atlantic.

Taxonomic identification in the Survey is a trade-off between providing the highest taxonomic identification possible and the time needed for the large number of samples each year to be analysed, their counts entered and data validated. Copepods, diatoms and dinoflagellates are the most commonly recorded groups because their members are robust and remain relatively intact during CPR sampling, and specimens are usually identified to species. Other common and robust crustaceans such as amphipods, decapods, and euphausiids are not speciated for several reasons including their high diversity and lack of a comprehensive range of larval descriptions. There are also considerable difficulties speciating many gelatinous and delicate taxa, and these are simply recorded in broad taxonomic groups. Table 5 provides the first comprehensive description of the taxa counted in the CPR survey.

The Survey has endeavoured to minimise changes in the counting procedures over the years to maintain a consistent long-term time series. Most phytoplankton taxa have been counted consistently from 1958, and most zooplankton since 1948, although there have been some changes in counting procedures since (detailed in Table 5). These were most dramatic in the early developmental years of the Survey, but they have also occurred in response to improvements in taxonomy, changes in research focus, or evolving marine management imperatives. Examples include the recent speciation of harmful algal bloom taxa of the genus *Dinophysis* responsible for diarrhetic shellfish poisoning and the assessment of marine pollution through counting of marine plastics found on CPR samples.

Although the Survey has maintained consistency of the time series as far as possible, there are two caveats researchers should be particularly conscious of when using CPR data. The first is the sampling bias (both temporal and spatial), a result of the CPR being towed by ships of opportunity and the difficulties this entails. We provide maps of CPR sampling each year on the SAHFOS website and summarise the consistency through time of the major CPR routes (Table 1) so researchers can assess the spatial and temporal sampling of different areas. It is also important to consider the size of the area for any analysis of CPR data, as there is a trade-off between the precision of plankton abundance estimates and their bias. Averaging CPR samples over a small area results in low bias (estimates representative of the area) but relatively imprecise estimates of plankton abundance (because of fewer samples) and the increased likelihood of data gaps for particular months or years. By contrast, averaging over a large area can result in high bias (there can be spatial biases due to the changing positions of tow routes) but relatively precise estimates of plankton abundance (because of the greater number of samples) and fewer data gaps. Thus, the size of the region required for an analysis of CPR data needs to reflect the density of sampling. In practice, the CPR standard areas have been found to be a reasonable trade-off between the precision of plankton abundance estimates and their bias, but smaller regions are possible in well-sampled areas. It should be remembered that individual CPR samples are relatively imprecise because of a host of factors including plankton patchiness, the category counting system and the use of crude indices such as PCI, but averaging over a large number of samples in an area subsumes local variation and smooths the variability introduced by coarse procedures, enabling the emergence of meaningful patterns.

The second qualification that should be considered is that CPR data are semi-quantitative estimates of plankton abundance and not absolute measures. Because of the relatively large mesh size of the CPR, it undoubtedly under-samples phytoplankton, particularly the smaller species. Small zooplankton may also be under-sampled because of the relatively large mesh size compared with other standard nets for sampling mesozooplankton, and large zooplankton may be under-sampled because of active avoidance. Despite the semi-quantitative nature of CPR sampling, there is strong evidence that the CPR captures a roughly consistent fraction of each taxon and thus reflects real inter-annual and seasonal patterns.

Notwithstanding these caveats, indices from the CPR survey can provide information pertinent to environmental management issues such as eutrophication, spread of non-indigenous species, and climate impacts on biodiversity, phenology and the abundance of plankton. There is a rich variety of potential plankton indices

that can be derived from CPR data, and some of the most useful are based on functional groups. We provide information for indices that may be sensitive to climate change (e.g., diatom: dinoflagellate ratios) and indices of harmful and nuisance algal blooms can also be derived. CPR samples can be used to estimate the size of constituent members of the plankton community, and these allow the derivation of a plethora of rate processes. For zooplankton counted from CPR samples, sizes can only easily be assigned to the copepods, because they are generally identified to the species level, whereas many of the larger zooplankton taxa are simply grouped as decapod larvae, euphausiids, or fish larvae and range widely in size. Although no direct estimates of the size of each copepod are available for each CPR sample, we provide estimates of average total length from the literature that can be used to derive changes in average community size.

CPR data can also be used to derive biomass estimates that are needed for ecosystem models, fisheries research, and in general ecological studies investigating energy transfer between trophic levels. The best estimate of total phytoplankton biomass from CPR data is the PCI. Although the exact nature of the PCI has been questioned, there is strong agreement between the PCI and chlorophyll measured fluorometrically from CPR samples, as well as with chlorophyll measured by satellite. The PCI not only reflects the biomass of diatoms and dinoflagellates, but also the pigments from delicate naked micro- and nanoflagellates that tend to disintegrate when preserved in formalin and cannot be identified microscopically. Estimates of total copepod biomass are relatively straightforward from CPR samples, but require some assumptions because no direct measurements of mass are made. A procedure for estimating copepod biomass is given using the general size information for each copepod taxon to estimate the mass of each taxon using an allometric relationship. These mass estimates for each copepod species can then be multiplied by the abundance for each species in each sample and then summed to obtain total biomass per sample.

We hope that this comprehensive description of the taxa counted in the Survey, the strengths and limitations of the sampling and counting methodology, and recommendations on how the data can be used fruitfully will stimulate more robust and imaginative research. Ensuring this invaluable dataset is utilised more widely and effectively in the future will hopefully contribute to the future security of the Survey (as echoed in Hays et al., 2005; Perry et al., 2004; Stevens et al., in press).

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