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## Using continuous plankton recorder data

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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.

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### 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 on the near-

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33 surface abundance of phyto- and zooplankton are available monthly from 1946, and these will shortly be sup-  
34 plemented by historical CPR data from 1931 to 1938 currently only in paper format (Stevens, Richardson, &  
35 Reid, in press). To the end of 2004, this dataset amounts to 207,619 samples counted for 437 phyto- and zoo-  
36 plankton taxa, many of which are identified to the species level. Since 1991, the CPR survey and the dataset  
37 have been managed by the Sir Alister Hardy Foundation for Ocean Science (SAHFOS). This dataset has been  
38 the foundation for high-impact research over more than five decades, forming the basis of 23 *Nature* and *Sci-*  
39 *ence* articles and almost 1000 publications (see reviews by Reid, Colebrook, Matthews, Aiken, & Continuous  
40 Plankton Recorder Team, 2003; Stevens et al., in press). Over recent years, CPR data have become increas-  
41 ingly important as a baseline to assess impacts of global change on pelagic ecosystems (Beaugrand, Brander,  
42 Lindley, Souissi, & Reid, 2003; Beaugrand, Reid, Ibanez, Lindley, & Edwards, 2002; Edwards & Richardson,  
43 2004; Greene et al., 2003; Hays, Richardson, & Robinson, 2005; Richardson & Schoeman, 2004). This role  
44 helps fulfil regional, national, and international marine obligations concerned with biodiversity loss, climate  
45 change, eutrophication, pollution, harmful algal blooms and sustainable fisheries (Brander, Dickson, &  
46 Edwards, 2003).

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

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

65 We limit our discussions here to the core survey in the North Atlantic, but draw the attention of the inter-  
66 ested reader to the North Pacific CPR survey operated by SAHFOS since 1997 (e.g., Batten, Welch, & Jonas,  
67 2003), and CPR surveys operated by other organizations, in the Southern Ocean (e.g., Hunt & Hosie, 2003)  
68 and the Western Atlantic (e.g., Jossi, John, & Sameoto, 2003). As these surveys have some differences in the  
69 CPRs themselves, the instrumentation attached, the counting methodology (Reid et al., 2003), and the differ-  
70 ent species and stages counted, they will not be discussed here. We hope that this critical look at how best to  
71 use CPR data will prove indispensable for plankton ecologists and modellers actively using CPR data or wish-  
72 ing to do so.

## 73 2. The continuous plankton recorder

74 The longevity of the CPR survey is a testament to its ingenious and robust design by Sir Alister Hardy.  
75 A prototype device was towed over 1300 miles in Antarctic waters in 1925–1926 (Hardy, 1926). This  
76 device was then modified and has remained relatively unchanged since 1931 (Reid et al., 2003). The  
77 self-contained automatic plankton recorder collects plankton continuously from a standard depth of  
78 ~7 m (Hays & Warner, 1993). A fixed depth close to the surface was chosen to give the most consistent  
79 results in the relatively shallow North Sea (Hardy, 1939). Water enters the CPR through a square aperture  
80 1.27 cm on a side (1.61 cm<sup>2</sup>), about the size of a thumbnail, and flows down an expanding tunnel, which  
81 effectively reduces the water pressure to minimise damage to the captured plankton, and exits through the  
82 rear of the device (Fig. 1). The movement of the water past the CPR turns an external impeller at the rear

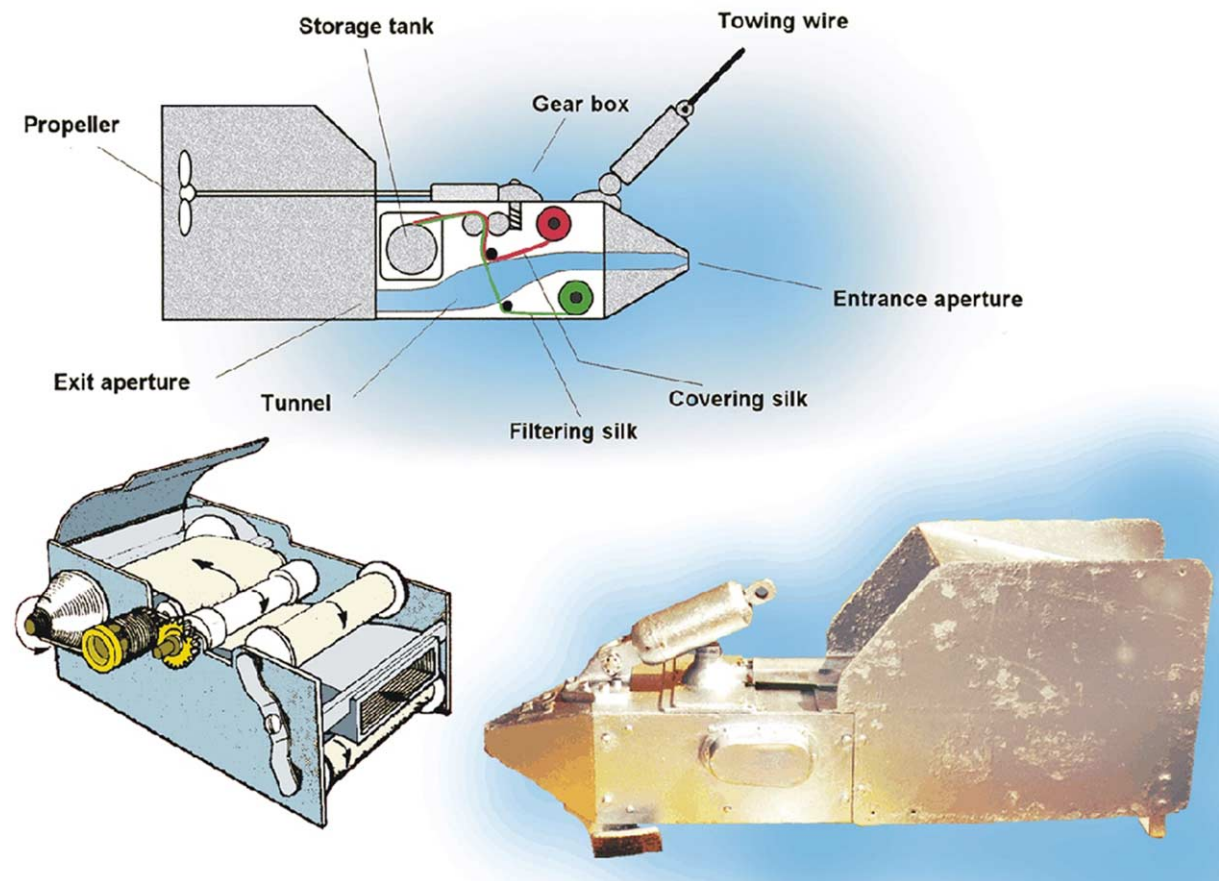


Fig. 1. A cross-section of the CPR, its internal mechanism and CPR body.

83 of the device that operates a drive shaft and gear system, which advances the silk filtering mesh. Plankton  
 84 in the water are filtered onto this constantly moving band of silk. The filtering silk meets a second band of  
 85 covering silk, effectively sandwiching the plankton, which is then wound onto a storage spool in a tank  
 86 containing formalin. The mesh size of the silk is 270  $\mu\text{m}$ . This mesh size was chosen not only to give  
 87 an adequate representation of copepods, cladocera, pteropods, and chaetognaths, but also to give an indi-  
 88 cation of blooms of large phytoplankton, while reducing clogging by small phytoplankton cells (Hardy,  
 89 1939). Despite the relatively large size of the mesh, small phytoplankton are still retained on the silk (this  
 90 is explained more fully in Section 7.2). Detailed descriptions of the CPR device, its sampling characteris-  
 91 tics, and modifications in its design over the lifespan of the Survey, such as changes to the diving plane  
 92 and box tail, can be found in Batten, Clark, et al. (2003); John and Reid (2001); Jonas, Walne, Beau-  
 93 grand, Gregory, and Hays (2004); Reid et al. (2003) and Warner and Hays (1994).

### 94 3. Sampling routes

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

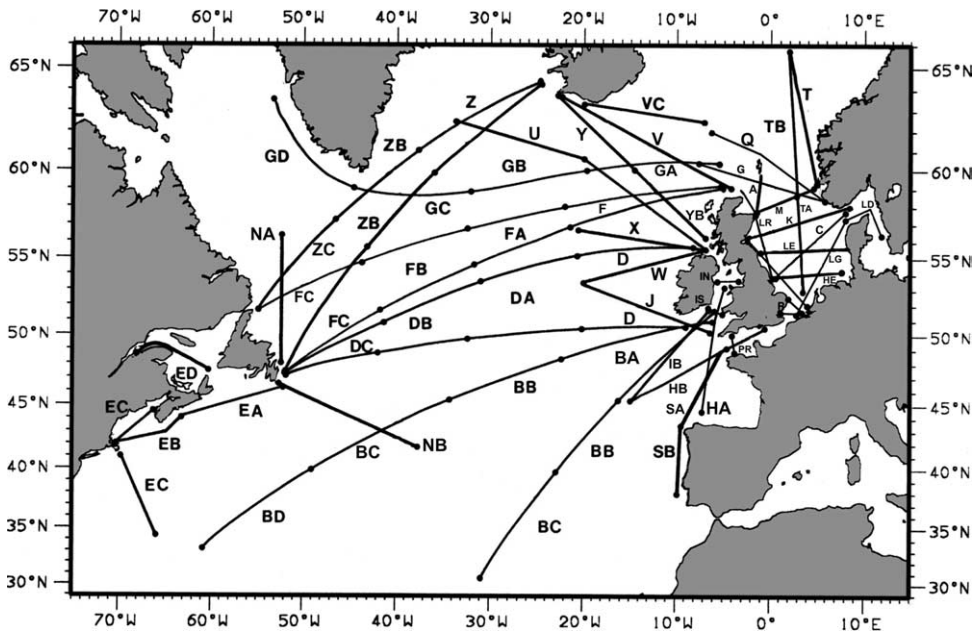


Fig. 2. Map of major routes towed. The number of years each route has been towed is shown in Table 1. Some routes have been shifted in position (e.g., BC, ZB, ...) but their designation has been retained because they were sampling in the same general vicinity and plankton regime.

100 With the ability to collect samples monthly over large space scales come some associated biases. The restric-  
 101 tion to commercial shipping routes means that large areas of the North Atlantic are not sampled (Fig. 2).  
 102 Another spatial bias is that the same CPRs are usually used for the same route each month because of logis-  
 103 tical considerations, rather than being randomly assigned to a route. This maintains consistent sampling for  
 104 each route but may lead to systematic biases if each CPR has slightly different sampling characteristics. The  
 105 CPR also misses some localised coastal features, as it does not generally sample closer than 1 nautical mile  
 106 from the coast, as the crew usually deploy and retrieve the instrument when the vessel is in sufficiently deep  
 107 water outside the harbour. There are also breaks in the temporal sampling of routes. Occasional short breaks  
 108 in tows, usually less than several months, occur when vessels towing CPRs break down or have to dry dock for  
 109 routine maintenance. There are longer breaks when a vessel is redeployed or a shipping company stops towing  
 110 a certain route, and another vessel plying the same route has to be found and then fitted with a specialised  
 111 towing point (davit). Breaks of many years and terminations of routes are a result of funding difficulties;  
 112 routes can be reinstated only when sufficient funding is available. The number of years each route has been  
 113 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  
 114 (although the X route is no longer towed), while others such as the SB, EA and EB routes have had long hia-  
 115 tuses before being reinstated.

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

123 The Survey reached its greatest coverage in the late 1960s and early 1970s, with a peak of 5506 samples  
 124 in 1970, before it contracted in the 1980s (Fig. 3; Table 1). This decline was a worldwide phenomenon;  
 125 40% of the long-term oceanographic monitoring programmes initiated after World War II were terminated  
 126 during the 1980s because environmental monitoring was considered poor science by administrators



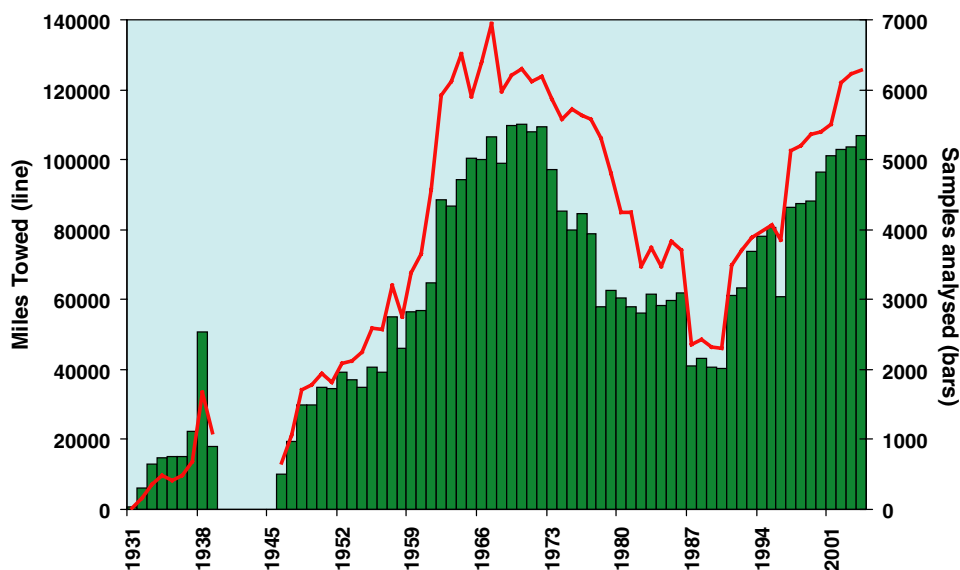


Fig. 3. Miles towed and samples analysed by the CPR survey since 1931.

(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  $\sim 3 \text{ m}^3$  (mean =  $3.27 \text{ m}^3$ , SD =  $0.71 \text{ m}^3$ ,  $n = 1723$ , 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).

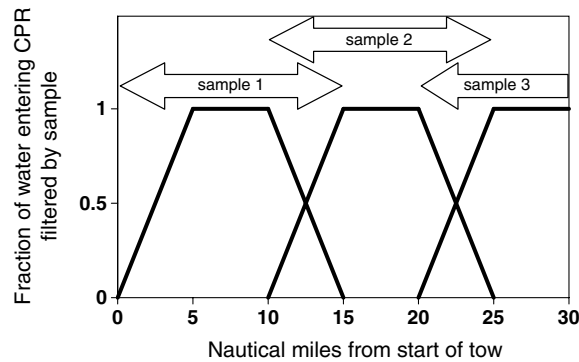


Fig. 4. Collection of plankton on a continuously moving band of silk. The start of Sample 1 enters the CPR filtering tunnel at mile 0. As it advances across the filtering tunnel, the proportion of the water that is filtered by Sample 1 increases until the sample start leaves the tunnel at mile 5 and 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.

## 156 5. Sample processing

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

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

### 167 5.1. Phytoplankton colour index

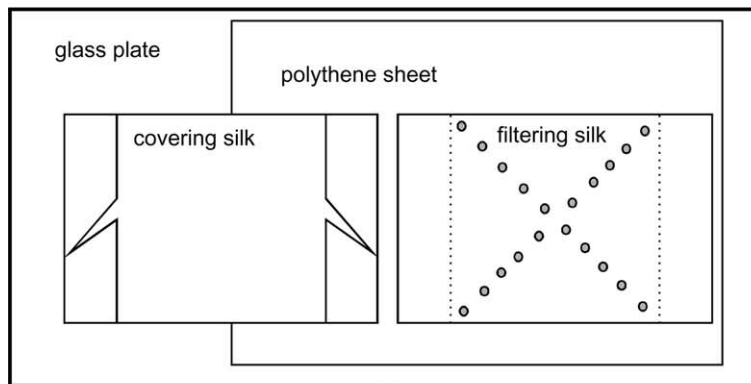
168 After the silk has been marked into 10 nautical mile samples but prior to cutting, each sample is visually  
 169 assigned a greenness index by comparison with standard colour charts: viz. no colour, very pale green, pale  
 170 green, and green (Robinson & Hiby, 1978). These four levels of the phytoplankton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

### 173 5.2. Phytoplankton analysis

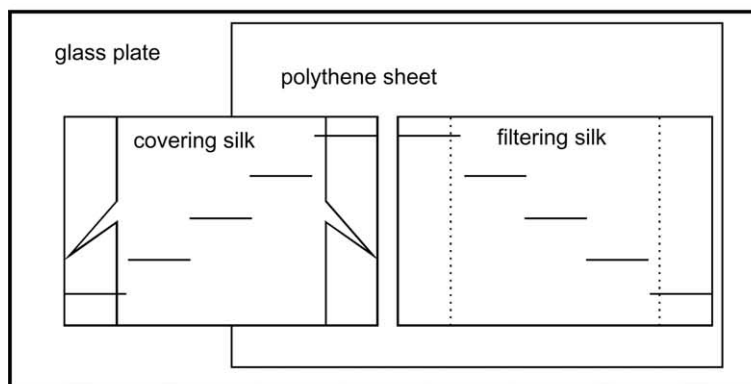
174 Following the assessment of PCI, the filtering silk is cut into sections (samples), representing 10 nautical  
 175 miles of tow. Each sample is then laid out on a purpose-built stage (Fig. 5(a)) and 10 fields on each of two  
 176 diagonals of the filtering silk are counted at 450 $\times$  magnification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



(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  $\mu\text{m}$  across) of the filtering silk. (c) Zooplankton traverse showing the stepped traverse (field of view 2.05 mm) across the filtering and covering silk.

183 taxon has been seen. Each of these 20 categories has an associated accepted value (Table 3), representing the  
 184 total number of individuals of a species that are likely in the fields examined. This has been derived from the  
 185 Poisson distribution, which assumes organisms are randomly distributed on the silk (Colebrook, 1960). These  
 186 accepted values are then multiplied by 10,000 to estimate the phytoplankton abundance on the filtering silk.  
 187 Unfortunately, because of historical data storage limitations before computers were used, these 20 abundance  
 188 values are compressed into 10 by averaging (Table 3). Phytoplankton abundance values are thus restricted to  
 189 10 discrete values and can be considered semi-quantitative estimates.

Table 2

A summary of the microscopes used throughout the history of the CPR survey

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.

### 190 5.3. Zooplankton traverse

191 The second stage of the microscopic analysis is a stepped traverse of the CPR filtering and covering silk  
 192 (Fig. 5(c)) at 54× magnification (using the Bactil microscopes; Table 2). The field of view is 2.05 mm and  
 193 all zooplankton organisms <2 mm total length are counted. Although we assume retained organisms are  
 194 uniformly distributed on the filtering silk, the design of the phytoplankton analysis and zooplankton traverse

195 procedures ensures all areas of the silk receive equal weighting. The zooplankton traverse procedure examines  
 196 1/50 of the silk. (Note that Reid et al. (2003) and Warner & Hays (1994) report that this procedure examines  
 197 an area 1/40 of the covering and filtering silk, and Batten, Clark, et al. (2003) reports that 1/49 of the sample is  
 198 viewed. Despite the different values reported, abundance calculations at the Survey have always been based on  
 199 a subsample of 1/50.)

#### 200 5.4. Zooplankton eyecount

201 The final CPR analysis procedure counts all zooplankton greater than *Metridia lucens* stage V in size  
 202 (>2 mm total length; Rae, 1952). Individuals are removed from the filtering and covering silks for identifica-  
 203 tion. Generally all individuals are counted, but for particularly dense samples a sub-sample may be counted.

#### 204 5.5. Scaling factors

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

#### 210 5.6. The category system for zooplankton

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

## 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. These taxa represent an incredible diversity of plankton (Fig. 6), and include members of

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)	<i>Actinocyclus octonarius ralfsi</i>		964	P	1		
	<i>Actinopterychus</i> spp.*,+	Mainly <i>A. undulatus</i>	151	P	174		
	<i>Amphiprora hyperborea</i>		979	P	4		0.0415 <sup>a</sup>
	<i>Asterionella bleakeleyi</i>	Now <i>Bleakeleya notata</i> (Hasle & Syvertsen, 1996)	983	P	2		0.00083 <sup>a</sup>
	<i>Asterionella glacialis</i> *,+	Now <i>Asterionellopsis glacialis</i> (Hasle & Syvertsen, 1996)	115	P	2999		
	<i>Asterionella kariana</i>	Now <i>Asterionellopsis kariana</i> (Hasle & Syvertsen, 1996)	202	P	2		0.000623 <sup>a</sup>
	<i>Asteromphalus</i> spp.		152	P	28		
	<i>Aulacodiscus argus</i>		982	P	17		
	<i>Bacillaria paxillifer</i> *,+	Now <i>B. paxillifera</i> (Hasle & Syvertsen, 1996)	153	P	1150		
	<i>Bacteriastrum</i> spp.*,+		154	P	2712		
	<i>Bacteriosira fragilis</i>		959	P	2		0.00614 <sup>a</sup>
	<i>Bellerochea malleus</i> *,+		155	P	1190		
	<i>Biddulphia alternans</i> *,+		156	P	291		
	<i>Biddulphia aurita</i> *,+	Now <i>Odontella aurita</i> (Hasle & Syvertsen, 1996)	157	P	2123		0.0169 <sup>a</sup>
	<i>Biddulphia biddulphiana</i>		948	P	1		
	<i>Biddulphia granulata</i> *,+	Now <i>Odontella granulata</i> (Hasle & Syvertsen, 1996)	158	P	278		0.033 <sup>a</sup>
	<i>Biddulphia regia</i> *,+	Now <i>Odontella regia</i> (Hasle & Syvertsen, 1996)	160	P	1921		
	<i>Biddulphia rhombus</i> *,+	Now <i>Odontella rhombus</i> (Hasle & Syvertsen, 1996)	161	P	322		0.03 <sup>a</sup>
	<i>Biddulphia sinensis</i> *,+	Now <i>Odontella sinensis</i> (Hasle & Syvertsen, 1996)	114	P	8746		
	<i>Campylosira cymbelliformis</i>		954	P	2		
	<i>Cerataulina pelagica</i> *,+		162	P	78		0.00325 <sup>a</sup>
	<i>Chaetoceros</i> (Hyalochaete) spp.*,+		112	P	34,285		
	<i>Chaetoceros</i> (Phaeoceros) spp.*,+		113	P	39,323		
	<i>Climacodium frauenfeldianum</i>		163	P	30		
	<i>Corethron criophilum</i> *,+	Now <i>C. hystrix</i> (Crawford et al., 1998)	164	P	1339		0.0367 <sup>a</sup>
	<i>Coscinodiscus concinnus</i> *,+		165	P	2318		1.9 <sup>a</sup>
	<i>Coscinodiscus</i> spp.	Includes damaged “ <i>Coscinodiscus concinnus</i> ” and “ <i>Coscinodiscus walesii</i> ” not identifiable to species, as well as other <i>Coscinodiscus</i> species	166	P	7926		
	<i>Coscinodiscus walesii</i> *,+	Invasive; first recorded in European waters in the English Channel in 1977 (as <i>C. nobilis</i> ). Details in Edwards, John, et al. (2001)	976	P	1480		
	<i>Dactyliosolen antarcticus</i> *,+	Does not have symbiotic flagellate (see “ <i>Dactyliosolen mediterraneus</i> ”)	104	P	1784		

Table 5 (continued)

<i>Dactyliosolen mediterraneus</i> *,+	Now <i>Leptocylindrus mediterraneus</i> (Hasle & Syvertsen, 1996). Symbiotic flagellate <i>Rhizomonas setigera</i> attached (see “ <i>Dactyliosolen antarcticus</i> ”)	105	P	7916	
<i>Detonula confervacea</i> *		167	P	234	0.00171 <sup>a</sup>
<i>Diploneis</i> spp.		947	P	22	
<i>Ditylum brightwellii</i> *,+		168	P	1745	0.19 <sup>a</sup>
<i>Eucampia groenlandica</i>		962	P	7	
<i>Eucampia zodiacus</i> *,+		169	P	984	0.00481 <sup>a</sup>
<i>Fragilaria</i> spp.*,+	May include some chain-forming “ <i>Navicula</i> spp.”	170	P	2871	
<i>Guinardia flaccida</i> *,+		171	P	318	
<i>Gyrosigma</i> spp.*,+	“ <i>Gyrosigma</i> spp.” and <i>Pleurosigma</i> spp. not separated, although most are probably <i>Pleurosigma</i> spp. (Derek Harbour, pers. comm.)	172	P	1463	
<i>Hemiaulus</i> spp.*		173	P	287	
<i>Hemidiscus cuneiformis</i>		206	P	7	
<i>Lauderia borealis</i> *,+	Now <i>Lauderia annulata</i> (Hasle & Syvertsen, 1996)	174	P	1311	0.00988 <sup>a</sup>
<i>Leptocylindrus danicus</i> *,+		175	P	641	0.00228 <sup>a</sup>
<i>Lithodesmium undulatum</i>		1590	P	2	
<i>Melosira arctica</i>		958	P	2	0.0331 <sup>a</sup>
<i>Melosira lineate</i>		957	P	1	
<i>Navicula planamembranacea</i> *	Now <i>Ephemera planamembranacea</i> (Hasle & Syvertsen, 1996). Species first described in May 1962 from CPR samples in the Northwest Atlantic. Details in Hendey (1964)	120	P	1058	
<i>Navicula</i> spp.*,+	May include other Naviculoid genera. Does not include “ <i>Navicula planamembranacea</i> ”	176	P	3843	
<i>Neodenticula seminae</i>	Invasive; first observed in CPR samples from western North Atlantic in 1999. Originally from North Pacific	1568	P	65	
<i>Nitzschia closterium</i> *,+	Now <i>Cylindrotheca closterium</i> (Hasle & Syvertsen, 1996). Responsible for foam and mucilage	177	P	2802	0.000148 <sup>a</sup>
<i>Nitzschia del icatissima</i> *,+	Now <i>Pseudo-nitzschia delicatissima</i> (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 <sup>a</sup>

(continued on next page)

Table 5 (continued)

Group	Taxon	Description	ID	Stage	No.	Diet	Size
	<i>Nitzschia longissima</i>		981	P	30		
	<i>Nitzschia seriata</i> *,+	Now <i>Pseudo-nitzschia seriata</i> (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 <sup>a</sup>
	<i>Nitzschia sigma rigida</i> *		975	P	59		
	<i>Nitzschia</i> spp.	Does not include “ <i>Nitzschia closterium</i> ”, “ <i>Nitzschia delicatissima</i> ”, “ <i>Nitzschia longissima</i> ”, “ <i>Nitzschiaseriata</i> ” or “ <i>Nitzschia sigma rigida</i> ”	199	P	437		
	<i>Odontella mobiliensis</i> *		200	P	73		
	<i>Odontella obtusa</i>		159	P	5		
	<i>Paralia sulcata</i> *,+		101	P	11,340		0.0083 <sup>a</sup>
	<i>Planktoniella sol*</i>		179	P	77		0.1 <sup>a</sup>
	<i>Podosira stelliger*</i>		272	P	244		
	<i>Rhaphoneis amphiceros*</i>		178	P	496		
	<i>Rhizosolenia acuminata*</i>		180	P	433		
	<i>Rhizosolenia alata alata</i> *,+	Now <i>Proboscia alata</i> (Hasle & Syvertsen, 1996)	110	P	17,845		0.0346 <sup>a</sup>
	<i>Rhizosolenia alata curvirostris*</i>	Now <i>Proboscia curvirostris</i> (Hasle & Syvertsen, 1996)	181	P	145		
	<i>Rhizosolenia alata indica</i> *,+	Now <i>Proboscia indica</i> (Hasle & Syvertsen, 1996)	109	P	4865		
	<i>Rhizosolenia alata inermis</i> *,+	Now <i>Proboscia inermis</i> (Hasle & Syvertsen, 1996)	111	P	4074		
	<i>Rhizosolenia bergonii*</i>		182	P	507		
	<i>Rhizosolenia calcar avis*</i>	Now <i>Pseudosolenia calcar avis</i> (Hasle & Syvertsen, 1996)	183	P	111		
	<i>Rhizosolenia cylindrus</i>		184	P	12		
	<i>Rhizosolenia delicatula*</i>	Now <i>Guinardia delicatula</i> (Hasle & Syvertsen, 1996)	185	P	931		0.039 <sup>a</sup>
	<i>Rhizosolenia fragilissima</i> *,+	Now <i>Dactyliosolen fragilissimus</i> (Hasle & Syvertsen, 1996)	186	P	592		0.013 <sup>a</sup>
	<i>Rhizosolenia hebetata semispina</i> *,+		108	P	13,444		0.0269 <sup>a</sup>
	<i>Rhizosolenia imbricata shrubsolei</i> *,+	Now <i>R. imbricata</i> (Hasle & Syvertsen, 1996)	106	P	10,113		
	<i>Rhizosolenia pungens</i>	Only separated from “ <i>Rhizosoleniasetigera</i> ” in 2003	1596	P	12		
	<i>Rhizosolenia robusta</i>		970	P	29		
	<i>Rhizosolenia setigera</i> *,+	See “ <i>Rhizosolenia pungens</i> ”	187	P	532		0.0371 <sup>a</sup>
	<i>Rhizosolenia stalterfothii</i> *,+	Now <i>Guinardia striata</i> (Hasle & Syvertsen, 1996)	188	P	2707		
	<i>Rhizosolenia styliformis</i> *,+	See Robinson and Colbourn (1970) for more details	107	P	18,661		0.775 <sup>a</sup>
	<i>Schroederella delicatula</i> *,+	Now <i>Detonula pumila</i> (Hasle & Syvertsen, 1996)	189	P	128		
	<i>Skeletonema costatum</i> *,+		102	P	3219		0.000339 <sup>a</sup>

Table 5 (continued)

	<i>Stauroneis membranacea</i>	Now <i>Meuniera membranacea</i> (Hasle & Syvertsen, 1996)	205	P	15	
	<i>Stephanopyxis</i> spp.*,+		190	P	503	
	<i>Streptotheca tamesis</i>	Now <i>Helicotheca tamesis</i> (Hasle & Syvertsen, 1996)	191	P	41	
	<i>Surirella</i> spp.		192	P	10	
	<i>Thalassionema nitzschioides</i> *,+		117	P	27,152	0.00092 <sup>a</sup>
	<i>Thalassiosira</i> spp.*,+		103	P	38,669	
	<i>Thalassiothrix longissima</i> *,+	Only counted if the end of a cell is observed within the field of view	116	P	18,920	0.0251 <sup>a</sup>
	<i>Triceratium favus</i>		971	P	9	
Dinophyceae (Dinoflagellates)	<i>Actiniscus pentasterias</i> *	Species is unarmoured; only the siliceous internal skeleton of 2 star-shaped pentasters observed	980	P	105	
	<i>Amphidoma caudata</i>		960	P	1	
	<i>Amphisolenia</i> spp.*		220	P	89	
	<i>Blepharocysta paulsenii</i>		956	P	5	
	<i>Centrodinium</i> spp.		265	P	4	
	<i>Ceratium arcticum</i> *		128	P	6542	0.0741 <sup>a</sup>
	<i>Ceratium arietinum</i> *		221	P	398	0.159 <sup>a</sup>
	<i>Ceratium azoricum</i> *		222	P	828	
	<i>Ceratium belone</i> *		223	P	68	
	<i>Ceratium breve</i>		219	P	3	
	<i>Ceratium bucephalum</i> *,+		224	P	872	0.159 <sup>a</sup>
	<i>Ceratium buceros</i> *		225	P	104	0.144 <sup>a</sup>
	<i>Ceratium candelabrum</i> *		226	P	713	
	<i>Ceratium carriense</i> *		227	P	993	
	<i>Ceratium compressum</i> *		228	P	214	
	<i>Ceratium concilians</i>		260	P	4	
	<i>Ceratium contortum</i>		261	P	20	
	<i>Ceratium declinatum</i> *		229	P	213	
	<i>Ceratium extensum</i> *		230	P	955	
	<i>Ceratium falcatifforme</i>		262	P	34	
	<i>Ceratium falcatum</i>		217	P	13	
	<i>Ceratium furca</i> *,+		122	P	39,776	0.0658 <sup>a</sup>
	<i>Ceratium fusus</i> *,+		121	P	60,435	0.0625 <sup>a</sup>
	<i>Ceratium geniculatum</i>		218	P	1	
	<i>Ceratium gibberum</i> *		231	P	451	
	<i>Ceratium hexacanthum</i> *		232	P	3424	
	<i>Ceratium horridum</i> *,+		126	P	20,902	0.144 <sup>a</sup>
	<i>Ceratium inflatum</i>		233	P	18	
	<i>Ceratium karstenii</i>		234	P	33	
	<i>Ceratium kofoidii</i>		131	P	9	
	<i>Ceratium lamellicorne</i> *		235	P	82	
	<i>Ceratium limulus</i>		1591	P	3	
	<i>Ceratium lineatum</i> *,+		123	P	14,233	0.0412 <sup>a</sup>
	<i>Ceratium longipes</i> *,+		127	P	15,644	0.106 <sup>a</sup>
	<i>Ceratium longirostrum</i>		263	P	32	
	<i>Ceratium lunula</i>		236	P	30	
	<i>Ceratium macroceros</i> *,+		125	P	24,965	0.12 <sup>a</sup>
	<i>Ceratium massiliense</i> *		237	P	2199	
	<i>Ceratium minutum</i> *,+		238	P	1490	0.00971 <sup>a</sup>
	<i>Ceratium pavillardii</i>		239	P	7	
	<i>Ceratium pentagonum</i> *		240	P	302	

(continued on next page)

Table 5 (continued)

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

Table 5 (continued)

<i>Dinophysis rotundata</i>	Counted from 2004. Included in “ <i>Dinophysis</i> spp.” before and since. Production of dinophysistoxin-1 (DTX1), a toxin implicated in diarrhetic shellfish poisoning, demonstrated in Japan, but North American strains apparently non-toxic (Moestrup, 2004)	1605	P	0	0.0307 <sup>a</sup>
<i>Dinophysis sacculus</i>	Counted from 2004. Included in “ <i>Dinophysis</i> spp.” before and since. producer of okadaic acid, a toxin implicated in diarrhetic shellfish poisoning (Moestrup, 2004)	1606	P	0	
<i>Dinophysis</i> spp.*,+	Species also counted separately from 2004. Generally associated with diarrhetic shellfish poisoning (Moestrup, 2004)	251	P	9764	
<i>Dinophysis tripos</i>	Counted from 2004. Included in “ <i>Dinophysis</i> spp.” before and since. Producer of dinophysistoxin-1 (DTX1), a toxin implicated in diarrhetic shellfish poisoning (Moestrup, 2004)	1607		0	
<i>Exuviaella</i> spp.	Mainly <i>E. marina</i> probably. Not included in “ <i>Prorocentrum</i> spp.”, although genus <i>Exuviaella</i> is now <i>Prorocentrum</i> . Generally produce toxins implicated in diarrhetic shellfish poisoning (Moestrup, 2004)	252	P	2710	
<i>Glenodinium</i> spp.*	Now <i>Dissodinium asymmetricum</i> (Dodge, 1982)	271	P	253	
<i>Gonyaulax</i> spp.*	Includes other genera in Gonyaulaceae (e.g., <i>Alexandrium</i> ). Counted since 1965. Genus <i>Alexandrium</i> produces paralytic shellfish poisoning toxins and fish mass mortality causative substance (Moestrup, 2004)	253	P	3871	
<i>Gossleriella tropica</i>		201	P	1	
<i>Gymnodinium</i> spp.	Genus is unarmoured and therefore very undercounted. Members of this genus produce toxins causing paralytic shellfish poisoning and can cause fish and invertebrate mortalities (Moestrup, 2004)	275	P	17	
<i>Gyrodinium</i> spp.*	Genus is unarmoured and therefore very undercounted. Most are <i>G. aureolum</i> (now <i>Karenia mikimotoi</i> ), which is responsible for fish and invertebrate mortality (Moestrup, 2004)	984	P	82	
<i>Histioneis</i> spp.		256	P	6	
<i>Katodinium</i> spp.		276	P	2	

(continued on next page)

Table 5 (continued)

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

Table 5 (continued)

	<i>Halosphaera</i> spp.*	Presence recorded in Phytoplankton 1948–1957 and 1965–1992. Counted in Phytoplankton 1993–1995. Counted in zooplankton traverse since 1996	197	T/P	2477
	<i>Oscillatoria</i> spp.*	Now <i>Trichodesmium</i> spp. (cyanobacteria)	193	P	1609
	<i>Pachysphaera</i> spp.		203	P	100
	<i>Phaeocystis pouchetii</i> *	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
	<i>Pterosperma</i> 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	<i>Dictyocysta</i> spp.*	Counted since 1996, and within “Tintinnidae” both before and since. For species see Lindley (1975)	134	T	1983
	<i>Favella serrata</i> *	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
	<i>Parafavella gigantea</i> *	Counted since 1996, and within “Tintinnidae” both before and since. See Lindley (1975) for more details	135	T	1105
	<i>Ptychocylis</i> 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: “ <i>Dictyocysta</i> spp.”, “ <i>Favella serrata</i> ”, “ <i>Parafavella gigantea</i> ”, “ <i>Ptychocylis</i> spp.” and “ <i>Tintinnopsis</i> spp.” are included as well as recorded separately since 1996. Many other species noted as comments. Details in Lindley (1975)	356	T	19,467

(continued on next page)

Table 5 (continued)

Group	Taxon	Description	ID	Stage	No.	Diet	Size
	<i>Tintinnopsis</i> spp.*	Counted since 1996, and within “Tintinnidae” both before and since. See Lindley (1975) for more details	805	T	712		
	<i>Zoothamnium pelagicum</i> *	Pelagic colonial ciliate. Presence recorded since 1964, counted (as number of colonies) since 1993	357	T	823		
Platyhelminthes	‘Spindelei’*	Eggs of <i>Kuhnia scombri</i> , a monogenean gill parasite of mackerel <i>Scomber scombrus</i> . 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* <sup>+</sup>	Does not include “ <i>Tomopteris</i> spp.”, which is recorded separately	450	E	2470		
	<i>Tomopteris</i> spp.* <sup>+</sup>	Not included in “Polychaete larvae”	80	E	5887		
Copepoda	<i>Acartia danae</i> *		300	T	150	O	1.08 <sup>b,c,d</sup>
	<i>Acartia longiremis</i> *	Usually not differentiated in counts of “ <i>Acartia</i> spp.”	327	T	74	O	1.04 <sup>b,d</sup>
	<i>Acartia negligens</i>		328	T	27	O	1.05 <sup>c,d</sup>
	<i>Acartia</i> spp.* <sup>+</sup>	Not identified to species. Mainly <i>A. clausi</i> and some “ <i>Acartia longiremis</i> ”. Details in Colebrook (1982)	5	T	50,620	O	1.15 <sup>d</sup>
	<i>Acrocalanus</i> spp.	Not identified to species	301	T	3		
	<i>Aetideus armatus</i> *		370	E	553	O	1.73 <sup>c,d,e</sup>
	<i>Alteutha</i> spp.	Not identified to species. Mainly <i>A. interrupta</i> (M. Gee, pers. comm.). Not included in “Harpacticoida Total”. Counted from 1994	985	E	103		
	<i>Amalothrix</i> spp.	Not identified to species	371	E	1		
	<i>Anomalocera patersoni</i> * <sup>+</sup>		372	E	574	C	3.20 <sup>d</sup>
	<i>Augaptilus</i> spp.	Not identified to species	604	E	1		
<i>Calanoides carinatus</i> *		48	E	1474	H	2.18 <sup>c,d,f</sup>	
<i>Calanus finmarchicus</i> * <sup>+</sup>	CV–CVIs. Recorded as a separate species from 1958. Included in “ <i>Calanus</i> V–VI Total”. Separated from “ <i>Calanus helgolandicus</i> ” by shape of inner margin of coxa of P5, and occasionally on shape of head and genital pore. Where large numbers of <i>Calanus</i> present, 20 individuals identified to species, and scaled up to total number of “ <i>Calanus finmarchicus</i> ” and “ <i>Calanus helgolandicus</i> ”	40	E	67,557	H	2.70 <sup>d,f</sup>	

Table 5 (continued)

<i>Calanus glacialis</i> *	CV–CVIs. Recorded since 1958. Separated from <i>C. finmarchicus</i> based on size alone (adult females >4.6 mm total length). Included in “ <i>Calanus</i> V–VI Total”	42	E	1838	H	4.60
<i>Calanus helgolandicus</i> *,+	CV–CVIs. Recorded as a separate species from 1958. Included in “ <i>Calanus</i> V–VI Total”. Separated from “ <i>Calanus finmarchicus</i> ” by shape of inner margin of coxa of P5, and occasionally on shape of head and genital pore. Where large numbers of <i>Calanus</i> present, 20 individuals identified to species, and scaled up to total number of “ <i>Calanus finmarchicus</i> ” and “ <i>Calanus helgolandicus</i> ”. See Bonnet et al. (2005) for more details	41	E	41,097	H	2.68 <sup>c,d</sup>
<i>Calanus hyperboreus</i> *,+	Mainly CV–CVIs, but probably also includes CIII–CIVs. Not included in “ <i>Calanus</i> V–VI Total”	44	E	1476	H	6.95 <sup>d,f</sup>
<i>Calanus</i> I–IV <sup>+</sup>	Juveniles of “ <i>Calanus finmarchicus</i> ”, “ <i>Calanus helgolandicus</i> ” and “ <i>Calanus glacialis</i> ”	1	T	63,164	H	1.65 <sup>g</sup>
<i>Calanus tenuicornis</i> *	Now <i>Mesocalanus tenuicornis</i> (Razouls, 1995)	46	E	778	H	1.74 <sup>c,d,f</sup>
<i>Calanus</i> total traverse <sup>#</sup>	Includes “ <i>Calanus</i> I–IV” and V–VIs of <i>C. finmarchicus</i> , <i>C. helgolandicus</i> and <i>C. glacialis</i> seen in zooplankton traverse	12	T	66,420	H	
<i>Calanus</i> V–VI Total <sup>+,#</sup>	Includes “ <i>Calanus finmarchicus</i> ”, “ <i>Calanus helgolandicus</i> ” and “ <i>Calanus glacialis</i> ” seen in zooplankton eyecount	43	E	110,446	H	2.48 <sup>h</sup>
Caligoida*,+	Nearly all records are <i>Caligus elongatus</i> (J. Roskell, pers. comm.). Usually found in association with fish, but not attached in CPR samples	426	E	361		
<i>Calocalanus</i> spp.*	Not identified to species. Now includes genus <i>Ischnocalanus</i> (Bradford-Grieve, 1994)	302	T	782	H	
<i>Candacia aethiopica</i> *		375	E	347	C	
<i>Candacia armata</i> *,+		61	E	5788	C	2.18 <sup>d,i</sup>
<i>Candacia bipinnata</i>		373	E	67	C	1.95 <sup>c,d</sup>
<i>Candacia curta</i>		374	E	31	C	
<i>Candacia giesbrechti</i>	Only found in Mediterranean	819	E	9	C	
<i>Candacia</i> I–IV		303	T	1316	C	
<i>Candacia longimana</i>		376	E	24	C	3.41 <sup>c,d,i</sup>
<i>Candacia norvegica</i>		377	E	2	C	2.75 <sup>d,i</sup>
<i>Candacia pachydactyla</i> *		378	E	101	C	2.15 <sup>d</sup>
<i>Candacia</i> spp.	Specimens identifiable to genus but not species	429	E	375	C	2.31
<i>Candacia tenuimana</i>		379	E	2	C	2.14 <sup>c,d,i</sup>

(continued on next page)

Table 5 (continued)

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

Table 5 (continued)

<i>Eucalanus mucronatus</i>	Now <i>Subeucalanus mucronatus</i> (Razouls, 1995)	388	E	7	H	
<i>Eucalanus pileatus</i>	Now <i>Subeucalanus pileatus</i> (Razouls, 1995)	390	E	2	H	
<i>Eucalanus</i> spp.	Specimens identifiable to genus but not species	389	E	197	H	3.40
<i>Euchaeta acuta</i> *		53	E	1965	C	3.84 <sup>c,d</sup>
<i>Euchaeta glacialis</i>	Now <i>Paraeuchaeta glacialis</i> (Razouls, 1995)	391	E	4	C	
<i>Euchaeta gracilis</i> *	Now <i>Paraeuchaeta gracilis</i> (Razouls, 1995)	392	E	102	C	6.60 <sup>c,d</sup>
<i>Euchaeta hebes</i> * <sup>+</sup>	Now <i>Paraeuchaeta hebes</i> (Razouls, 1995)	54	E	3035	C	2.80 <sup>c,d</sup>
<i>Euchaeta marina</i> *		393	E	560	C	2.72 <sup>c,d</sup>
<i>Euchaeta media</i>		394	E	54	C	3.65 <sup>c,d</sup>
<i>Euchaeta norvegica</i> * <sup>+</sup>	Now <i>Paraeuchaeta norvegica</i> (Razouls, 1995)	52	E	12,143	C	7.00 <sup>d</sup>
<i>Euchaeta pubera</i>		395	E	14	C	3.94 <sup>c,d</sup>
<i>Euchaeta spinosa</i>		396	E	4	C	6.32 <sup>c,d</sup>
<i>Euchaeta</i> spp.	Specimens identifiable to genus but not species	436	E	2482	C	4.82
<i>Euchaeta tonsa</i>	Now <i>Paraeuchaeta pseudotonsa</i> (Razouls, 1995)	397	E	18	C	6.50 <sup>d</sup>
<i>Euchirella amoena</i>		398	E	2	H	
<i>Euchirella brevis</i>		399	E	1	H	3.50 <sup>m</sup>
<i>Euchirella curticauda</i>		400	E	8	H	3.90 <sup>c,d,m</sup>
<i>Euchirella messinensis</i>		401	E	25	H	4.84 <sup>c,d,m</sup>
<i>Euchirella pulchra</i>		402	E	3	H	3.00 <sup>m</sup>
<i>Euchirella rostrata</i> *		51	E	1545	H	2.95 <sup>d,m</sup>
<i>Euchirella</i> spp.	Specimens identifiable to genus but not species	428	E	87	H	4.24
<i>Euterpina acutifrons</i> *	Not included in "Harpacticoida Total"	307	T	88		0.50 <sup>d</sup>
<i>Farranula gracilis</i>		21	T	33		
<i>Farranula</i> spp.	Specimens identifiable to genus but not species	22	T	20		
<i>Gaetanus minor</i>		403	E	2		1.93 <sup>d,n</sup>
<i>Gaidius</i> spp.	Not identified to species	437	E	1		
<i>Gaidius tenuispinus</i>		556	E	2		3.10 <sup>c,d,o</sup>
<i>Halithalestris croni</i>	Now <i>Parathalestris croni</i> . Not included in "Harpacticoida Total"	308	E	43		
<i>Haloptilus acutifrons</i>		601	E	1		2.86 <sup>c,d</sup>
<i>Haloptilus longicornis</i>		404	E	12		1.96 <sup>c,d</sup>
<i>Haloptilus spiniceps</i>		405	E	2		4.14 <sup>c,d</sup>
Harpacticoida Total* <sup>+</sup>	Mainly <i>Microsetella</i> spp. Does not include eyecount harpacticoids such as " <i>Alteutha</i> spp.", " <i>Macrosetella gracilis</i> ", " <i>Miracia efferata</i> ", " <i>Oculosetella gracilis</i> ", " <i>Parathalestris croni</i> " or two traverse species " <i>Clytemnestra</i> spp." and " <i>Euterpina acutifrons</i> ", which are all recorded separately	306	T	4452		
<i>Hemicyclops aberdonensis</i>	Commensal or parasitic copepod of family Clausidiidae	1589	T	2		
<i>Heterorhabdus cf abyssalis</i>	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 <sup>d</sup>

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Table 5 (continued)

Group	Taxon	Description	ID	Stage	No.	Diet	Size
	<i>Heterorhabdus cf clausi</i>	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 <sup>d</sup>
	<i>Heterorhabdus norvegicus*</i>		407	E	377	C	2.77 <sup>c,d</sup>
	<i>Heterorhabdus papilliger*</i>		408	E	492	C	1.76 <sup>c,d</sup>
	<i>Heterorhabdus spinifer</i>		364	E	2	C	
	<i>Heterorhabdus</i> spp.	Specimens identifiable to genus but not species	369	E	46	C	2.49
	<i>Heterostylites longicornis</i>		432	E	1	C	3.00 <sup>d</sup>
	<i>Ischnocalanus</i> spp.	Not identified to species. Now recombined with genus <i>Calocalanus</i> (Bradford-Grieve, 1994). Discontinued	1586	T	1	H	
	<i>Isias clavipes*+*</i>		8	T	686		1.25 <sup>d</sup>
	<i>Labidocera acutifrons</i>		961	E	7	C	3.00 <sup>d</sup>
	<i>Labidocera aestiva</i>		440	E	10	C	
	<i>Labidocera</i> spp.	Specimens identifiable to genus but not species	62	E	17	C	2.60
	<i>Labidocera wollastoni*+*</i>	Details in Lindley and Hunt (1989)	63	E	1438	C	2.20 <sup>d</sup>
	<i>Lophothrix</i> spp.	Not identified to species	433	E	1		
	<i>Lubbockia</i> spp.	Not identified to species	311	T	21		
	<i>Lucicutia</i> spp.*	Not identified to species. Mainly <i>L. flavicornis</i>	312	T	868		
	<i>Macrosetella gracilis</i>	Not included in “Harpacticoida Total”	309	E	33		1.40 <sup>d</sup>
	<i>Mecynocera clausi*</i>		313	T	827	H	0.84 <sup>d,l</sup>
	<i>Metridia</i> I–IV	Included in “ <i>Metridia</i> Total traverse”	314	T	2228	O	0.93 <sup>g</sup>
	<i>Metridia longa*</i>		56	E	2343	O	4.10 <sup>d,p</sup>
	<i>Metridia lucens*+*</i>		55	E	33,002	O	2.27 <sup>c,d,p</sup>
	<i>Metridia</i> total traverse <sup>#</sup>	Includes <i>Metridia</i> CV–CVI and “ <i>Metridia</i> I–IV” seen in zooplankton traverse	315	T	4922	O	
	<i>Microcalanus</i> spp.	Not identified to species. Rare, but some may be included in “ <i>Para-Pseudocalanus</i> ” (Rae, 1952)	316	T	42		
	<i>Miracia efferata</i>	Not included in “Harpacticoida Total”	310	E	44		
	<i>Nannocalanus minor*</i>		60	E	4632	H	1.71 <sup>d,f</sup>
	<i>Neocalanus gracilis*</i>		45	E	2419	H	2.76 <sup>c,d,f</sup>
	<i>Neocalanus robustior</i>		423	E	21	H	3.42 <sup>c</sup>
	<i>Neocalanus</i> spp.	Specimens unidentifiable to species	1570	E	9	H	
	<i>Oculosetella gracilis</i>	Not included in “Harpacticoida Total”	963	E	2		
	<i>Oithona</i> spp.*+*	Not identified to species	10	T	52,633	O	0.68 <sup>j</sup>
	<i>Oncaea</i> spp.*+*	Not identified to species	317	T	2976	O	
	<i>Paracandacia bispinosa*</i>		409	E	91		1.67 <sup>c</sup>
	<i>Paracandacia simplex*</i>		424	E	125		1.75 <sup>c</sup>
	<i>Paracandacia</i> spp.	Specimens identifiable to genus but not species	427	E	22		1.7
	<i>Parapontella brevicornis*+*</i>		318	T	119		1.37 <sup>d</sup>

Table 5 (continued)

<i>Para-Pseudocalanus</i> spp.*,+	Includes <i>Paracalanus</i> spp., adults of “ <i>Pseudocalanus</i> spp.”, and any unidentifiable small copepods (<2 mm)	3	T	83,130	H	0.70 <sup>j</sup>
<i>Phaenna spinifera</i>		410	E	9		1.80 <sup>d</sup>
<i>Pleuromamma abdominalis</i> *	Distinct from other “large” <i>Pleuromamma</i> spp. ( <i>P. robusta</i> and <i>P. xiphias</i> ) from CV	58	E	3031	O	2.67 <sup>c,d,q</sup>
<i>Pleuromamma borealis</i> *	Distinct from other “small” <i>Pleuromamma</i> spp. ( <i>P. gracilis</i> and <i>P. piseki</i> ) at CVI. Usually identified based on females; males more difficult to identify (but also rarer) and included in “ <i>Pleuromamma</i> spp.”	59	E	5376	O	1.97 <sup>c,d,q</sup>
<i>Pleuromamma gracilis</i> *	Distinct from other “small” <i>Pleuromamma</i> spp. ( <i>P. borealis</i> and <i>P. piseki</i> ) at CVI. Usually identified based on females; males more difficult to identify (but also rarer) and included in “ <i>Pleuromamma</i> spp.”	47	E	4619	O	1.76 <sup>c,d,q</sup>
<i>Pleuromamma piseki</i> *	Distinct from other “small” <i>Pleuromamma</i> spp. ( <i>P. borealis</i> and <i>P. gracilis</i> ) at CVI. Usually identified based on females; males more difficult to identify (but also rarer) and included in “ <i>Pleuromamma</i> spp.”	411	E	1169	O	1.73 <sup>c,d</sup>
<i>Pleuromamma</i> spp.	Specimens identifiable to genus but not species	434	E	1469	O	2.56
<i>Pleuromamma robusta</i> *	Distinct from other “large” <i>Pleuromamma</i> spp. ( <i>P. abdominalis</i> and <i>P. xiphias</i> ) from CV	57	E	8197	O	3.13 <sup>c,d,q</sup>
<i>Pleuromamma xiphias</i> *	Distinct from other “large” <i>Pleuromamma</i> spp. ( <i>P. abdominalis</i> and <i>P. robusta</i> ) from CV	412	E	639	O	4.13 <sup>c,d,q</sup>
Pontellidae	Specimens unidentifiable to species	1593	E	5	C	
<i>Pontellina plumata</i> *		319	E	62	C	1.69 <sup>c,d</sup>
<i>Pontellopsis regalis</i>		988	E	1	C	
<i>Pseudocalanus elongatus</i> *, +, #	Includes only adult females and males. In the Northeast Atlantic and North Sea these are mainly <i>P. elongatus</i> with some <i>P. acupes</i> and <i>P. minutus</i> , but in the Northwest Atlantic several other species may be present (Frost, 1989). Details in Colebrook (1982). Also included in “ <i>Para-Pseudocalanus</i> ”	2	T	23,680	H	1.20 <sup>f</sup>
<i>Pseudochirella</i> spp.	Not identified to species	955	E	1		
<i>Rhincalanus cornutus</i>		413	E	56	H	3.21 <sup>c,d</sup>
<i>Rhincalanus nasutus</i> *, +		50	E	1395	H	3.99 <sup>c,d,l</sup>
<i>Saphirella tropica</i>		20	T	1		
<i>Sapphirina</i> spp.*	Not identified to species	414	E	803		
<i>Scaphocalanus echinatus</i>		320	E	13		1.92 <sup>d</sup>

(continued on next page)

Table 5 (continued)

Group	Taxon	Description	ID	Stage	No.	Diet	Size
	<i>Scaphocalanus</i> spp.	Specimens identifiable to genus but not species	425	E	16		
	<i>Scolecithricella</i> spp.*	Not identified to species	321	T	2366	H	1.40 <sup>d</sup>
	<i>Scolecithrix bradyi</i>		415	T	10	H	1.16 <sup>c,d</sup>
	<i>Scolecithrix danae</i> *		416	E	355	H	2.05 <sup>c,d</sup>
	<i>Scolecithrix</i> spp.	Specimens identifiable to genus but not species	1576	E	3	H	
	<i>Scottocalanus persecanus</i>		417	E	3		4.80 <sup>d</sup>
	<i>Scottocalanus securifrons</i>		575	E	1		4.30 <sup>c,d</sup>
	'Spiny eggs'	Probably <i>Candacia armata</i> eggs. Eggs of other copepod species are recorded together in "Copepod eggs". Counted from 1997	813	T	99	—	
	<i>Temora longicornis</i> * <sup>+</sup>		4	T	30,409	H	1.00 <sup>d</sup>
	<i>Temora stylifera</i> *		322	T	773	H	1.45 <sup>c,d</sup>
	<i>Temora turbinata</i>		323	T	32	H	
	<i>Tortanus discaudatus</i> *	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 <sup>s</sup>
	<i>Undeuchaeta major</i> *		418	E	74	C	4.55 <sup>c,d,t</sup>
	<i>Undeuchaeta plumosa</i> *		419	E	2282	C	3.18 <sup>c,d,t</sup>
	<i>Undeuchaeta</i> spp.	Specimens identifiable to genus but not species	435	E	40	C	3.86
	<i>Undinula vulgaris</i> *		421	E	296		
	<i>Urocorycaeus</i> spp.*	Not identified to species	325	E	100	C	1.76 <sup>j</sup>
	<i>Xanthocalanus</i> spp.	Not identified to species	422	E	2		5.80 <sup>d</sup>
Malacostraca	Caprellidea* <sup>+</sup>		453	E	1036		
	Cumacea* <sup>+</sup>		454	E	1577		
	Decapoda larvae* <sup>+</sup>	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 <sup>+</sup>	Occasional large calyptopis (e.g., <i>Thysanopoda acutifrons</i> ) 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* <sup>+</sup>	Counted since 1946. Includes "Euphausiacea adults" and "Euphausiacea juveniles". Details in Glover (1952); Jones (1969) and Lindley (1977)	88	E	87,236		
	Gammaridea* <sup>+</sup>	For species see Vane (1951)	81	E	7745		
	<i>Heterophryxus appendiculatus</i>	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		

Table 5 (continued)

	Hyperiidæ* <sup>+</sup>	For species see Vane (1951) and McHardy (1970)	82	E	45,100
	Isopoda* <sup>+</sup>		456	E	341
	<i>Lucifer</i> spp.	Also included in “Sergestidae” and “Decapoda larvae”	999	E	90
	Mysidacea* <sup>+</sup>	Identified by statocysts. Mysids collected are of the sub-order Mysida, which have statocysts. Mysids of the order Lophogatrada 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 “ <i>Lucifer</i> spp.”, which are also counted separately. Included in “Decapoda Larvae”	455	E	2049
	Stomatopoda*	Larval and juvenile stages only	509	E	90
Other arthropods	Cirripede larvae* <sup>+</sup>	Presence recorded 1947–1957, counted since 1958. These are Balanidae and Verrucidae larvae. For species see Edinburgh Oceanographic Laboratory (1973). Does not include “ <i>Lepas</i> nauplii” or “ <i>Lepas</i> cypris”	350	T	4740
	Cladocera Total	Discontinued in 1957	38	T	4250
	<i>Evadne</i> spp.* <sup>+</sup>	Recorded within “Cladocera Total” (now discontinued) from 1948 to 1957, and separately since 1958. Details in Gieskes (1971a)	31	T	15,554
	<i>Lepas</i> cypris	First found in 2002. Not included in “Cirripede larvae”. See <i>Lepas</i> nauplii	1592	E	6
	<i>Lepas</i> nauplii*	<i>Lepas</i> anatifera, <i>L. fascicularis</i> , <i>L. pectinata</i> 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
	<i>Penilia avirostris</i> *	Introduced into the North Sea in early 1990s, probably by ballast water (Johns et al., 2005)	148	T	222
	<i>Podon</i> spp.* <sup>+</sup>	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
Chaetognatha	Chaetognatha eyecount* <sup>+</sup>	All Chaetognaths $\geq$ 8 mm total length. <i>Sagitta serratodentata</i> , <i>S. elegans</i> , <i>S. setosa</i> , and <i>Eukrohnia hamata</i> have been recorded. Details in Bainbridge (1963). Also see “Chaetognatha traverse”	89	E	50,379

(continued on next page)

Table 5 (continued)

Group	Taxon	Description	ID	Stage	No.	Diet	Size
	Chaetognatha traverse <sup>+</sup>	All Chaetognaths. <i>Sagitta serratodentata</i> , <i>S. elegans</i> , <i>S. setosa</i> , and <i>Eukrohnia hamata</i> have been recorded. Details in Bainbridge (1963). Also see “Chaetognatha eyecount”	34	T	20,821		
Bryozoa	Cyphonautes Larvae <sup>*+†</sup>	Presence recorded from 1946 to 1957, counted since 1958. Ectoproct bryozoan larvae	35	T	4448		
Mollusca	<i>Atlanta</i> spp.*	May contain some “ <i>Oxygyrus</i> spp.”	470	E	240		
	<i>Carinaria</i> spp.		475	E	5		
	<i>Cavolinia</i> spp.*		461	E	121		
	<i>Cephalobranchia</i> spp.		348	E	2		
	Cephalopoda larvae*	May include post larvae. Some identification may be suspect (C. Yau, pers. comm.)	471	E	525		
	<i>Clio</i> spp.*		464	E	383		
	<i>Clione limacina</i> <sup>*+†</sup>	The most reliably identified Gymnosome. Both the large arctic form <i>C.l.l. forma limacina</i> and the small southern form <i>C. l. l. forma minuta</i> are included	84	E	3716		
	<i>Clione</i> shells	Juvenile <i>Clione</i>	39	T	29		
	<i>Creseis</i> spp.		462	E	39		
	<i>Cuvierina</i> spp.		476	E	8		
	<i>Diacria</i> spp.*		463	E	98		
	‘Echinospira’ larvae	Veliger larvae of <i>Lamellaria perspicua</i> (Gastropoda: Prosobranchia). Counted since 1999	1543	T	11		
	<i>Firoloida</i> spp.		472	E	28		
	Gymnosomata	Gymnosomata unidentifiable to species	480	E	124		
	Lamellibranchia larvae <sup>*+†</sup>	Recorded as present 1946–1948, and counted since 1949. For species see Rees (1954a)	33	T	9070		
	<i>Limacina retroversa</i> <sup>*+†</sup>	This represents all thecosomes. <i>L. retroversa</i> 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		
	<i>Notobranchaea</i> spp.		473	E	1		
	<i>Oxygyrus</i> spp.	May contain some “ <i>Atlanta</i> spp.”	477	E	17		
	<i>Paedoclione doliiformis</i>	Records of “ <i>Pneumodermopsis paucidens</i> ” from western Atlantic shelf waters are likely to be “ <i>Paedoclione doliiformis</i> ” (G.A. Cooper, pers. comm.)	448	E	26		
	<i>Peraclis</i> spp.		488	E	16		
	<i>Pneumoderma</i> spp.		478	E	11		
	<i>Pneumodermopsis canephora</i>		358	E	1		

Table 5 (continued)

	<i>Pneumodermopsis ciliata</i> *	Details in Cooper and Forsyth (1963)	465	E	67	
	<i>Pneumodermopsis paucidens</i> *	Records of “ <i>Pneumodermopsis paucidens</i> ” from western Atlantic shelf waters are likely to be “ <i>Paedoclione doliiformis</i> ” (G.A. Cooper, pers. comm.). Details in Cooper and Forsyth (1963)	474	E	237	
	<i>Pneumodermopsis</i> spp.*	Includes only those <i>Pneumodermopsis</i> not specifically identified. Most records since 1977 of <i>Pneumodermopsis</i> only identified to genus. Details in Cooper and Forsyth (1963)	85	E	149	
	<i>Pterotrachea</i> spp.		466	E	12	
Echinodermata	Echinoderm larvae* <sup>+</sup>	16 species and higher taxa found (Rees, 1954b). Counted since 1949	36	T	21,304	
	Echinoderm post-larvae* <sup>+</sup>	Presence recorded before 1958, and counted since	460	E	2516	
Chordata	<i>Branchiostoma lanceolatum</i> * <sup>+</sup>	Identified by notochord and pigment spots	510	E	227	
	Doliolidae*	<i>Dolioletta gegenbauri</i> , <i>Doliolina mülleri</i> , <i>Doliolum nationalis</i> . For species see Hunt (1968). Included in “Thaliacea”	978	E	1137	
	Fish eggs* <sup>+</sup>		90	E	8160	
	Larvacea* <sup>+</sup>	Presence recorded 1946–1957, counted since 1958. <i>Oikopleura dioica</i> , <i>O. labradoriensis</i> , <i>Fritillaria borealis</i> and <i>F. pellucida</i> found	37	T	24,041	
	Salpidae* <sup>+</sup>	Species include <i>Salpa fusiformis</i> , <i>Thalia democratica</i> , <i>Iasis zonaria</i> and <i>Ihleia asymmetrica</i> . Details in Hunt (1968). Included in “Thaliacea”	977	E	1164	
	Thaliacea*	Includes “Salpidae” and “Doliolidae”. Presence recorded since 1946	469	E	5203	
	Young fish* <sup>+</sup>	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 <sup>a</sup>
	‘ <i>Pacillina arctica</i> ’	Unknown biological affinity, but probably a ciliate cyst. Counted from 1996	807	T	58	
	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 decapod larva	467	E	402	

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Table 5 (continued)

Group	Taxon	Description	ID	Stage	No.	Diet	Size
	Phytoplankton Colour Index <sup>+</sup> (PCI)	Measured in four categories: no colour, very pale green, pale green, and green. Recorded consistently since 1946	100		88,517		
	<i>Pinus</i> pollen*	Terrestrial pollen grain of genus <i>Pinus</i> . 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 ( $\mu\text{g}$  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<sup>+</sup> 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<sup>#</sup>. 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.

<sup>a</sup> 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>).

<sup>b</sup> Farran (1948b).

<sup>c</sup> Roe (1972).

<sup>d</sup> Rose (1933).

<sup>e</sup> Vervoort (1952a).

<sup>f</sup> Vervoort (1951a).

<sup>g</sup> Conway and Minton (1975).

<sup>h</sup> Farran (1948a).

<sup>i</sup> Farran (1948c).

<sup>j</sup> Boltovskoy (1999).

<sup>k</sup> Vervoort (1951d).

<sup>l</sup> Vervoort (1951b).

<sup>m</sup> Vervoort (1952d).

<sup>n</sup> Vervoort (1952c).

<sup>o</sup> Vervoort (1952b).

<sup>p</sup> Farran (1948d).

<sup>q</sup> Farran (1948e).

<sup>r</sup> Vervoort (1951c).

<sup>s</sup> Wilson (1932).

<sup>t</sup> Vervoort (1952e).

269 Bacillariophyceae (Diatoms), Dinophyceae (Dinoflagellates), Coccolithophoridae, Coelenterata, Platyhel-  
 270 minthes, Rotifera, Protozoa, Ciliophora (Tintinnids), Copepoda (Calanoids, Harpacticoids and Poecilos-  
 271 tomatoids), Malacostraca (Decapods, Mysids and Euphausiids), Branchiopoda (Cladocerans), Cirripedia,  
 272 Ostracoda, Mollusca, Echinodermata, Annelida, Bryozoa, Chaetognatha and Chordata. Some of the truly  
 273 unusual taxa that are counted are "*Pinus* pollen" (pollen from terrestrial pine trees), "Stellate bodies" (land  
 274 plant hairs), "Spindelei" (eggs of the trematode *Kuhnia scombri*), and "Plastics" (microplastics adrift in the  
 275 ocean). Distribution maps in the North Atlantic of 240 taxa (marked \* in Table 5) are provided in the latest  
 276 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  
 277 (marked <sup>+</sup> in Table 5) are included in WinCPR (Stevens et al., in press; Vezzulli, Dowland, Reid, Clarke, &  
 278 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  
 279 years despite the renaming of species; Table 5 includes new taxonomic names as well as the names used  
 280 at the Survey.  
 281  
 282

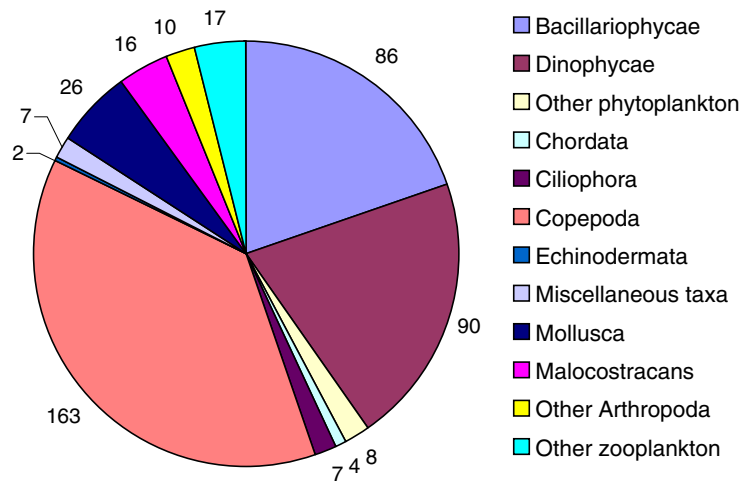


Fig. 6. The number of taxa counted in the CPR survey separated into higher taxonomic groups.

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

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

304 Juveniles of some relatively common, distinctive, larger copepod genera can be easily identified and are  
 305 counted separately in the traverse procedure (“*Calanus* I–IV”, “*Metridia* I–IV” and “*Candacia* I–IV”). Note  
 306 that juveniles of the genus *Centropages* may be counted as “*Centropages* spp.” when the specimens are at a  
 307 stage of development where differentiation between species that may be present is not possible or the damage  
 308 to adults prevents identification. No other juvenile copepods are counted explicitly as a separate taxonomic  
 309 entity, although some may be included with their adults if distinctive (e.g., *Euchaeta* juveniles). Other juveniles  
 310 that are not identifiable may be included in the “*Para-Pseudocalanus* spp.” entity. This category is effectively  
 311 an entity of any small (<2 mm) unidentifiable copepods (particularly juveniles but also any small damaged  
 312 specimens that cannot be assigned to another taxonomic entity), as well as the genera *Paracalanus* and “*Pseudocalanus*  
 313 spp.” themselves. Specimens of some relatively common copepod genera that are not identifiable to  
 314 species because they are juvenile or are damaged can be assigned to higher taxonomic levels, e.g., “*Euchaeta*  
 315 spp.”, “*Pontellidae*” (see Table 5 for more details).

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

## 322 6.2. Taxa recorded as present

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

332 All other taxa that are usually counted numerically can also be recorded as present in some samples when  
333 they are seen but cannot be assigned a numerical abundance value. This happens when a taxon is observed  
334 outside its typical stage of analysis. For example, a particular phytoplankton taxon may not be seen during  
335 phytoplankton analysis but could be observed during zooplankton traverse (especially larger phytoplankton  
336 taxa). This taxon would be recorded as present in the sample, but cannot be assigned a numerical abundance  
337 value. A similar situation can arise because each type of organism has a reference point, and if the reference  
338 point is not observed within the field of view then the taxon cannot be counted but only recorded as present.  
339 This is particularly important for organisms larger than a single field of view. For example, the elongate dino-  
340 flagellate “*Ceratium extensum*” is only counted (as are all dinoflagellates) if the girdle is present within the field  
341 of view. Abundances would be overestimated if they were based on observing any part of the body because a  
342 single specimen of *C. extensum* usually covers several fields of view; if any part of the cell other than the girdle  
343 is observed during phytoplankton analysis then the taxon is recorded as present. Other reference points for  
344 organisms include the base of the antenna of copepods and the eyes of euphausiids. In addition, some taxa  
345 are recorded as present but not counted numerically when an organism is extremely damaged. Although this  
346 occurs rarely, it is more common with large organisms such as euphausiids or fish larvae. Examples such as  
347 these, where taxa are recorded as present, can be extremely valuable. Recent work on calanoid copepod diver-  
348 sity from the CPR survey (based on the number of species per sample) incorporates many zooplankton tra-  
349 verse taxa that were often only seen in zooplankton eyecount and recorded as present on a sample (Beaugrand,  
350 2004; Beaugrand et al., 2002).

351 Examination of CPR records shows that some organisms are more frequently recorded as present than  
352 counted individually. This may be because the organism is particularly distinctive or is more often identified  
353 in a counting procedure not designed for that taxon. For example, “*Polykrikos schwartzii* cysts” have been  
354 recorded as present in zooplankton traverse more often than counted in phytoplankton analysis. This is also  
355 the case for the chain-forming phytoplankton cells “*Paralia sulcata*” and “*Oscillatoria* spp.” (*Trichodesmium*  
356 spp.).

## 357 6.3. Taxa recently added

358 The Survey is responsive to changes in research focus and marine management imperatives (Brander et al.,  
359 2003) and adds new taxa to those that are counted as appropriate. Effectively this means that a new Taxon ID  
360 number is allocated in the CPR database and analysts are trained to identify and record the taxon. For exam-  
361 ple, the genus *Dinophysis*, which has many species that are defined as harmful algal bloom species and are  
362 responsible for diarrhetic shellfish poisoning (Moestrup, 2004), had historically only been identified to the  
363 genus level. Since January 2004, “*Dinophysis acuminata*”, “*Dinophysis acuta*”, “*Dinophysis caudata*”, “*Dinophy-*

364 *ysis norvegica*”, “*Dinophysis rotundatum*”, “*Dinophysis sacculus*” and “*Dinophysis tripos*” are now recognised  
365 and counted (Table 5). The entity “*Dinophysis* spp.” has been counted since 1958 and will continue to be  
366 counted into the future to preserve the time series, alongside the more detailed species information begun  
367 in 2004. Another recent addition to the taxa counted at the Survey from January 2004 is the non-biological  
368 entity marine “Plastics”. This was initiated in response to recent findings that marine plastics have increased  
369 over the last 40 years in CPR samples (Thompson et al., 2004). “Plastics” are not counted numerically but just  
370 recorded as present. There are several other recent additions to the taxa counted. Prior to 2003, the isopod  
371 “*Heterophryxus appendiculatus*”, which is parasitic on euphausiids, was recorded in “Parasites of the plank-  
372 ton”, but has been subsequently counted separately. Since January 2004, “Radiolaria” has been separated into  
373 “Acantharia” and “Radiolaria” whilst retaining the original taxon. Other taxa added to the database recently  
374 include “*Pinus pollen*” in 1996, the veliger larvae of the gastropod *Lamellaria perspicua* (“Echinospira” lar-  
375 vae”) in 1999, and “*Neodenticula seminae*” in 2003.

#### 376 6.4. Taxa discontinued/counted differently

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

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

#### 389 6.5. Taxa recorded in comments

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

#### 400 6.6. Consistency of identification

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

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

## 418 7. Interpreting CPR data

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

### 421 7.1. Time series

422 Although most taxa have been counted since 1946, there have been some changes in counting procedures  
423 since then (see Section 5.7). This means that there are consistent time series for most phytoplankton taxa since  
424 1958, and for zooplankton taxa since 1948.

425 Exceptions to these rules are given in Table 5 and fall into two types. First, many taxa are only recorded  
426 when a management decision is taken to do so. For example, the abundant dinoflagellate “*Noctiluca scintil-*  
427 *lans*” has only been counted from 1981, and the common tintinnids “*Dictyocysta* spp.”, “*Favella serrata*”,  
428 “*Parafavella gigantea*”, “*Ptychocylis* spp.” and “*Tintinnopsis* spp.” have only been counted separately since  
429 1996, when management decisions were taken to record them. More recent examples of such management  
430 decisions are given in Section 6.3. Second, advances in taxonomy can result in a new taxon being recorded.  
431 This happened when the diatom *Ephemera planamembranacea* was actually discovered and first described  
432 as “*Navicula planamembranacea*” (Hendey, 1964) from CPR samples in 1962. This species almost certainly  
433 occurred on earlier samples but had not been described. Another example is that of “*C. helgolandicus*”, which  
434 was only confirmed as a separate species from “*C. finmarchicus*” in the 1950s (see Matthews, 1966) and so was  
435 only counted separately in CPR samples from 1958. Before this, *C. helgolandicus* individuals existed, although  
436 we did not count them explicitly. Such taxa cannot be regarded as truly absent before they had been first  
437 recorded, so that their time series are only valid from the time the taxon was first counted in the Survey (shown  
438 in Table 5).

439 Note that this situation is entirely different from that of taxa truly absent before they were first recorded.  
440 Time series for these taxa can be taken from 1948 for zooplankton and from 1958 for phytoplankton. This  
441 situation can arise when a taxon may not have historically occurred in the survey area, but has been intro-  
442 duced or has extended its range. For example, the diatom “*Coscinodiscus wailiesii*” was introduced through  
443 translocation of non-indigenous oysters for mariculture into the Northeast Atlantic in 1977 (Boalch & Har-  
444 bour, 1977; Edwards, John, Johns, & Reid, 2001) from the Pacific Ocean; the Pacific diatom “*N. seminae*” was  
445 introduced, by ballast water or altered currents, into the North Atlantic in 2003; and the cladoceran “*Penilia*  
446 *avirostris*” was found in the North Sea in the 1990s, possibly introduced by ballast water (Johns, Edwards,  
447 Greve, & John, 2005). These taxa were certainly not present before they were first recorded in CPR samples.  
448 This situation can also arise when rare taxa may only be found for the first time many years (or decades) after  
449 the beginning of the Survey. For example, the copepod “*Gaetanus minor*” was only seen for the first time in the  
450 Survey after sampling for 13 years and it was a further 23 years until a second specimen was found. A sub-  
451 stantial proportion of taxa in the database are rare (105 taxa have been found fewer than 20 times). The infre-  
452 quent recording of some rare phyto- and zooplankton taxa may be further compounded if they are not  
453 distinctive, making them more likely to be misidentified as similar species. Such ‘new’ taxa can also be found  
454 when the Survey expands into new areas. For example, many cold-water taxa were found when the Survey  
455 started sampling the Northwest Atlantic in 1959, and many warm-water taxa were first recorded when the Sur-  
456 vey expanded south of 40°N in the late 1960s.

## 457 7.2. Semi-quantitative abundances

458 We recommend that CPR data not be used as an absolute measure of abundance, but as semi-quantitative  
459 estimates that reflect real inter-annual and seasonal patterns. Although no device measures the abundance of  
460 plankton perfectly (Wiebe & Benfield, 2003), there is increasing evidence that the CPR substantially underes-  
461 timates absolute numbers (Batten, Clark, et al., 2003; Clark, Frid, & Batten (2001); John, Batten, Harris, &  
462 Hays, 2001; Richardson, John, Irigoien, Harris, & Hays, 2004). The relatively large size of the silk mesh  
463 (270  $\mu\text{m}$ ) of the CPR undoubtedly under-samples phytoplankton, and this is particularly true for the smaller  
464 species. Despite this, phytoplankton down to 10  $\mu\text{m}$  in size, such as “Coccolithaceae” and “*Nitzschia delica-*  
465 *tissima*” (*Pseudo-nitzschia delicatissima*), are regularly captured in CPR samples (Table 5). One reason for this  
466 may be that phytoplankton are caught on the leno weave (a single strand in one direction and a double twisted  
467 strand in the other) of the relatively thick silk strands in the mesh used for filtering in the CPR. Silk mesh has  
468 been retained for data consistency. Standard mesh for most modern plankton sampling is a simple weave of  
469 fine nylon strands that are heat-fused at the crossings of warp and woof. The silk strands of CPR mesh con-  
470 stitute 30–40% of the mesh area. There may also be an effect of clogging by phytoplankton and zooplankton  
471 (John et al., 2002; Jonas et al., 2004), particularly gelatinous forms, which may lead to retention of smaller  
472 phytoplankton species. Even for zooplankton, abundances from other samplers are generally 1–40 times more  
473 than those from the CPR (Clark et al., 2001; Hunt & Hosie, 2003; John et al., 2001; Richardson et al., 2004). A  
474 detailed description of the difficulties in calculating quantitative conversions between abundance estimates  
475 from the CPR and conventional net samplers can be found in Richardson et al. (2004). Small zooplankton  
476 are likely to be under-sampled because of the relatively large mesh size compared with other standard nets  
477 (usually 200  $\mu\text{m}$ ) for sampling mesozooplankton (Sameoto et al., 2000). Work on the retention of organisms  
478 on the silk during CPR tows found that organisms with widths <300  $\mu\text{m}$  were not fully retained, and that  
479 those with widths <287  $\mu\text{m}$  had only 50% retention (Robertson, 1968; c.f. Hays (1994) and Batten, Clark,  
480 et al. (2003)). In addition, some small taxa such as “*Oithona* spp.” may be underestimated because they are  
481 relatively transparent and thus difficult to see in the on-silk analysis during zooplankton traverse. Although  
482 on-silk analysis may be sub-optimal for some taxa, it is continued to maintain consistency of the time series;  
483 changing this procedure would alter the results.

484 Large zooplankton are likely to be under-sampled by the CPR because of active avoidance (Clark et al.,  
485 2001; Hunt & Hosie, 2003; Richardson et al., 2004). Despite the relatively fast speed of the CPR  
486 ( $7.5 \text{ m s}^{-1}$ ) compared to many nets ( $1\text{--}2 \text{ m s}^{-1}$ ), the small inlet aperture of the CPR ( $1.27 \text{ cm} \times 1.27 \text{ cm}$ ) com-  
487 pared with a typical net (typically 50 cm diameter) may allow large zooplankton to escape capture if they can  
488 sense the approach of the CPR through changes in hydrostatic pressure (Clark et al., 2001; Richardson et al.,  
489 2004). Numerical modelling and flow-tank studies are needed to answer questions associated with CPR hydro-  
490 dynamics and zooplankton avoidance.

491 Notwithstanding the semi-quantitative nature of CPR sampling, there is considerable evidence that it cap-  
492 tures a roughly consistent fraction of the in situ abundance of each taxon and thus reflects the major patterns  
493 observed in the plankton (Batten, Clark, et al., 2003). Seasonal cycles estimated from CPR data for relatively  
494 abundant taxa are repeatable each year, and are sufficiently resolved to detect the earlier seasonal peaks in  
495 response to warmer sea temperatures of recent years (Edwards & Richardson, 2004). There is also generally  
496 good agreement between seasonal cycles measured by the CPR and from other samplers such as WP-2 nets  
497 (Clark et al., 2001; John et al., 2001) and the LHPR (Richardson et al., 2004).

498 Inter-annual changes in plankton abundance are also captured relatively well by the CPR (Clark et al.,  
499 2001; John et al., 2001) because the time-series has remained internally consistent, with few changes in the  
500 design of the CPR or in counting procedures. This agreement between the CPR and other devices is not as  
501 strong as seasonal comparisons (Batten, Clark, et al., 2003), although this may simply reflect the greater auto-  
502 correlation in seasonal plankton cycles. A major potential bias in decadal time series of abundance from the  
503 CPR is related to the general increase in ship speed from an average of 10.5 knots in 1953 to 14.8 knots in  
504 1999. Faster ship speeds have not influenced the depth of tow (Batten, Clark, et al., 2003; Hays & Warner,  
505 1993), but have slightly decreased the volume of water filtered by the CPR (Jonas et al., 2004). Although this  
506 bias could potentially lead to a perceived general long-term decline in abundance, inter-annual changes are  
507 large relative to this small bias (Jonas et al., 2004). Moreover, long-term trends in abundance are generally

508 increasing for many taxa counted in CPR samples including the “phytoplankton colour index” (Reid,  
 509 Edwards, Hunt, & Warner, 1998), “*C. helgolandicus*” (Bonnet et al., 2005), and meroplankton (Lindley & Bat-  
 510 ten, 2002). Problems associated with changes in the volume of water filtered per sample may be solved by the  
 511 routine use of flowmeters. Unfortunately, flowmeters are not routinely fitted to the >20 CPRs deployed each  
 512 month because of a lack of resources.

513 A consequence of using CPR data to capture relative patterns and not as estimates of absolute abundance is  
 514 that data are normally expressed in numbers per sample. As each sample represents  $\sim 3 \text{ m}^3$  of filtered seawater,  
 515 abundance estimates should be divided by 3 to obtain estimates per  $\text{m}^3$ . Because CPR samples provide relative  
 516 estimates of abundance that are useful for assessing relative patterns, abundance estimates are seldom con-  
 517 verted to per  $\text{m}^3$  estimates in practice.

## 518 8. Using CPR data

### 519 8.1. Forms of data output

520 Plankton abundances from each sample can be used to create gridded maps to explore changes in the dis-  
 521 tribution of key taxa such as “*C. finmarchicus*” (Planque & Fromentin, 1996) and the diversity of calanoid  
 522 copepods (Beare, Batten, et al., 2003; Beaugrand et al., 2002). They have also been used to delve into the diel  
 523 vertical migratory behaviour of zooplankton (Hays, Proctor, John, & Warner, 1994). There are, however,  
 524 restrictions on access to raw CPR data (see Section 10 *Data Availability* for details).

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

530 The most common relatively large regions used historically have been CPR standard areas (Fig. 7). These  
 531 have been used to describe seasonal and inter-annual changes in phyto- and zooplankton abundance through-  
 532 out the North Atlantic (e.g., Colebrook, 1975). They have also been employed recently as comparative repli-  
 533 cate study areas to test hypotheses concerning the propagation of environmental forcing up the plankton

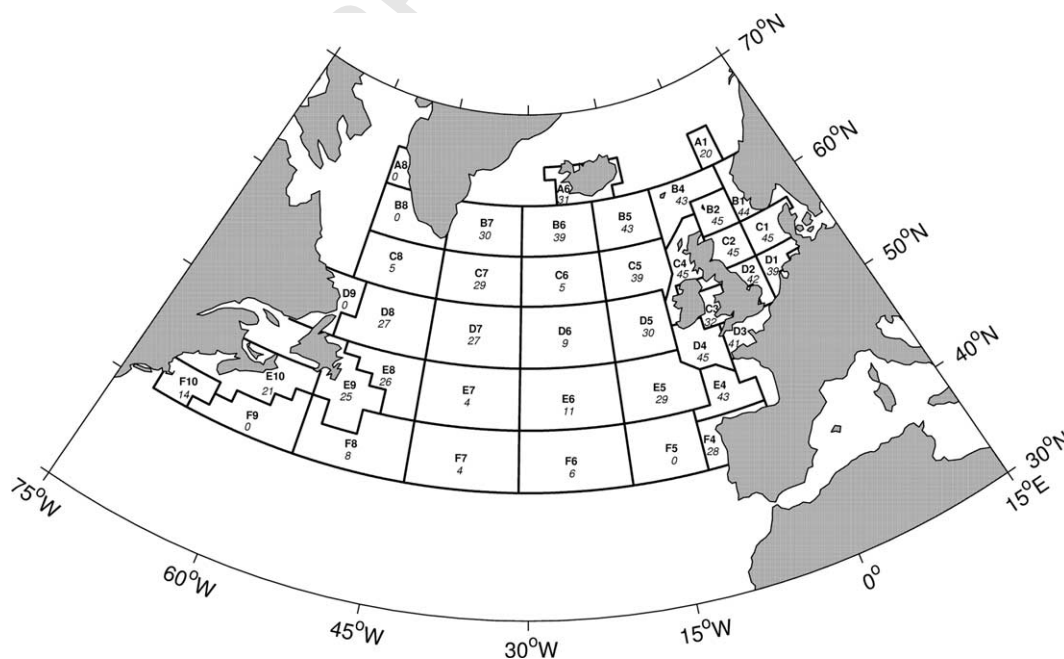


Fig. 7. CPR standard areas, with the number of years where eight or more months have been sampled since 1958.

534 foodweb (Richardson & Schoeman, 2004). The positioning and size of CPR standard areas is not entirely arbi-  
 535 trary; the edges of many of the standard areas follow the edge of the continental shelf (defined as the 100  
 536 fathom (~200 m) contour) and the size of the boxes on the shelf are smaller to reflect the more dynamic phys-  
 537 ical environment, larger biological variability and greater CPR sampling.

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

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

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

553 where  $\bar{M}$  is the long-term mean of that month,  $Y$  is the annual mean of the particular year, and  $\bar{Y}$  is the long-  
 554 term annual mean. At least eight months need to be sampled in a year to have an adequate estimate of the  
 555 seasonal cycle to estimate the annual abundance, otherwise the year is excluded. Fig. 7 shows the number  
 556 of years since 1946 when eight or more months were sampled for each CPR standard area.  
 557

## 558 8.2. Indices based on functional groups

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

568 There are several simple phytoplankton indices that can be easily derived from CPR data. One such simple  
 569 index is the ratio of diatoms to dinoflagellates; such a ratio can be easily calculated by direct summation of  
 570 individual diatom and dinoflagellate taxa since 1958 (see Table 5). It has been suggested that climate warming  
 571 will favour dinoflagellates over diatoms, and this has been observed in the Northeast Atlantic from CPR sam-  
 572 ples (Edwards, Reid, et al., 2001). Another simple index, total phytoplankton, is not so easy to calculate, how-  
 573 ever, as some phytoplankton taxa have not been counted consistently since 1958: “Coccolithophores” have  
 574 been counted numerically since 1993; “*N. scintillans*” since 1981; “Silicoflagellates” since 1993. Indices of  
 575 harmful and nuisance algal blooms can also be derived from CPR samples. For example, the Survey records  
 576 “*Prorocentrum* spp.” (mainly *P. micans*) responsible for diarrhetic shellfish poisoning (DSP), “*Nitzschia seri-*  
 577 *ata*” (now *Pseudo-nitzschia seriata*) and “*N. delicatissima*” (*P. delicatissima*) responsible for amnesic shellfish  
 578 poisoning (ASP), and “*Nitzschia closterium*” (now *Cylindrotheca closterium*) responsible for production of  
 579 foam and mucilage. In addition, the genus “*Dinophysis* spp.” is responsible for diarrhetic shellfish poisoning  
 580 and is now speciated (see Section 6.3).

581 To estimate the total abundance of copepods, there are two options. The first and simplest is to use  
 582 “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.

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 ( $\bar{L}$ ) 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:

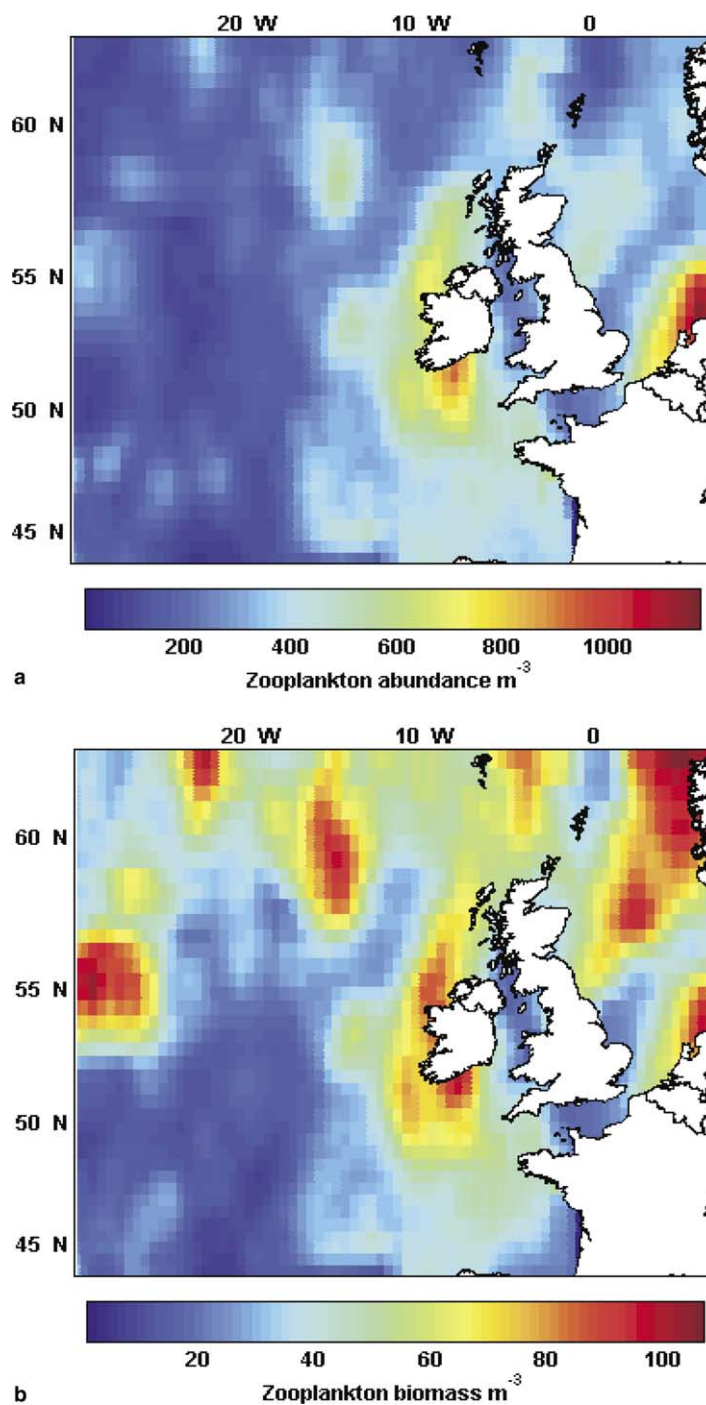


Fig. 8. Map of total copepod (a) abundance, and (b) biomass.

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

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Such an approach has been used in a number of recent studies (Beaugrand, Brander, et al., 2003; Sims, Witt, Richardson, & Metcalfe, in press) 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:

$$T = \frac{\sum_{i=1}^{12} M \cdot x_m}{\sum_{i=1}^{12} x_m},$$

where  $x_m$  is the mean abundance in month  $M$  (January = 1, ..., 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 (Sims et al., in press), 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 fluorometrically 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 (Kirby et al., in press; 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; Sims et al., in press). 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 North-east 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

734 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.

739 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/](http://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/](http://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](http://www.ices.dk)). The temporal scale (monthly) of these products is comparable to that of the CPR data. Values of these products can be assigned to each CPR sample based on its position and month of sampling.

## 748 10. Data availability

749 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.

762 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.

## 768 11. Summary

769 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.

774 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 sim-

781 ply recorded in broad taxonomic groups. Table 5 provides the first comprehensive description of the taxa  
782 counted in the CPR survey.

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

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

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

816 Notwithstanding these caveats, indices from the CPR survey can provide information pertinent to environ-  
817 mental management issues such as eutrophication, spread of non-indigenous species, and climate impacts on  
818 biodiversity, phenology and the abundance of plankton. There is a rich variety of potential plankton indices  
819 that can be derived from CPR data, and some of the most useful are based on functional groups. We provide  
820 information for indices that may be sensitive to climate change (e.g., diatom: dinoflagellate ratios) and indices  
821 of harmful and nuisance algal blooms can also be derived. CPR samples can be used to estimate the size of  
822 constituent members of the plankton community, and these allow the derivation of a plethora of rate pro-  
823 cesses. For zooplankton counted from CPR samples, sizes can only easily be assigned to the copepods,  
824 because they are generally identified to the species level, whereas many of the larger zooplankton taxa are sim-  
825 ply grouped as decapod larvae, euphausiids, or fish larvae and range widely in size. Although no direct esti-  
826 mates of the size of each copepod are available for each CPR sample, we provide estimates of average total  
827 length from the literature that can be used to derive changes in average community size.

828 CPR data can also be used to derive biomass estimates that are needed for ecosystem models, fisheries  
829 research, and in general ecological studies investigating energy transfer between trophic levels. The best esti-  
830 mate of total phytoplankton biomass from CPR data is the PCI. Although the exact nature of the PCI has  
831 been questioned, there is strong agreement between the PCI and chlorophyll measured fluorometrically from  
832 CPR samples, as well as with chlorophyll measured by satellite. The PCI not only reflects the biomass of dia-

toms 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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