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Continuous Plankton Records: Plankton Atlas of the North Atlantic Ocean (1958–1999). I. Introduction and methodology

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ABSTRACT: The Continuous Plankton Recorder (CPR) survey is one of the largest plankton monitoring programmes in the world. Data from this programme have been used to investigate many ecological issues such as biogeography, biodiversity and relationships between plankton and global change. A CPR Atlas on the geographical distribution of plankton in the North Atlantic Ocean was first published by the Edinburgh Oceanographic Laboratory (1973). This atlas, based on about 40 000 CPR samples collected from 1958 to 1968, contributed greatly to our knowledge of the biogeography of ~260 species or taxa in the North Atlantic Ocean. The data of the CPR Atlas were updated in the last 30 years. In this introduction to the revised CPR Atlas, which is based on data for 1958–1999, new numerical procedures and features used in preparing the updated maps are described.

KEY WORDS: Continuous Plankton Recorder survey · Atlas · Plankton · North Atlantic Ocean

INTRODUCTION

The Continuous Plankton Recorder (CPR) survey is one of the largest plankton monitoring programmes in the world. Results from the survey have been used to investigate many ecological issues (Reid et al. 2003). Biogeographical studies have been conducted showing spatial distribution of more than 250 species throughout the North Atlantic Ocean and its shelf seas (Colebrook et al. 1961a,b, Edinburgh Oceanographic Laboratory 1973). Recently, the mapping protocol has been improved using the Lambert projection (Planque & Fromentin 1996) and mapping techniques such as kriging (Planque & Fromentin 1996, Planque et al. 1997). A number of papers have allowed a better characterisation of seasonal cycles and spatial changes for many taxa (Glover 1957, Colebrook 1979, 1984, 1991). Other studies have examined long-term changes in phytoplankton and zooplankton (Colebrook 1981, Reid et al. 1998, Beaugrand & Reid 2003). Results show that long-term variability in standing stock, production and community structure of the plankton might be related to the North Atlantic Oscillation (NAO) (Fromentin & Planque 1996, Reid & Planque 2000). Other studies have recently shown a major reorganisation in the biodiversity of calanoid copepods related to regional warming (Beaugrand et al. 2002, Beaugrand 2003). Some studies have focussed on diel vertical migration of calanoid copepods (Hays et al. 1994, Hays 1995, 1996, Hirst & Batten 1998), spatial and temporal changes in the diversity of decapod crustacean larvae or calanoid copepods (Lindley 1998, Beaugrand et al. 2000, Beaugrand 2001). Monitoring of non-indigenous species (Edwards et al. 2001) and unusual events (Lindley et al. 1990, 1993, Edwards et al. 1999) have been undertaken as well. The CPR data have led to a better understanding of the ecology and functioning of North Atlantic ecosystems.

A CPR Atlas on the geographical distribution of plankton in about 40 000 CPR samples collected from 1958 to 1968 from the North Atlantic Ocean was published by the Edinburgh Oceanographic Laboratory (1973). This Atlas contributed substantially to our knowledge of the biogeography of 255 species or taxa in the North Atlantic Ocean. However, no update of this monograph has been published in the last 30 years.

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Most of the maps presented in 1973 have been recreated in the new CPR Atlas, which summarises the work of the Continuous Plankton Recorder team (CPR Survey Team 2004; this issue), based on 155 669 samples collected from 1958 to 1999. Here in Part I, I briefly describe the methodology of collection and analysis of CPR samples and outline the new numerical procedure employed. New symbols and features have been added to the maps to increase the information and improve the interpretation.

CONTINUOUS PLANKTON RECORDER SURVEY

The CPR survey is an upper layer plankton monitoring programme that has regularly collected samples in the North Atlantic and North Sea at monthly intervals since 1946 (Warner & Hays 1994). The CPR was first used during the RV 'Discovery' expedition to the Antarctic Ocean in 1925 to 1927. From 1931 it was regularly deployed along certain routes in the North Sea. The original idea was to use a similar methodology to that used in meteorological research to investigate causes and effects of changes in the abundance of marine plankton and to relate them to varying hydroclimatic conditions and catches of pelagic fishes such as herring (Hardy 1939). As the number of sampling years increased, it became possible to study changes in the abundance and composition of species through time. Since the start of the programme, data on the abundance of more than 400 species or taxa have been gathered by about 178 000 CPR samples collected up to the year 2000, which represents ~2 million entries and ~80 million data-points (Beaugrand et al. 2003). The spatial distribution of CPR samples collected from 1958 to 1999 is presented in Fig. 1.

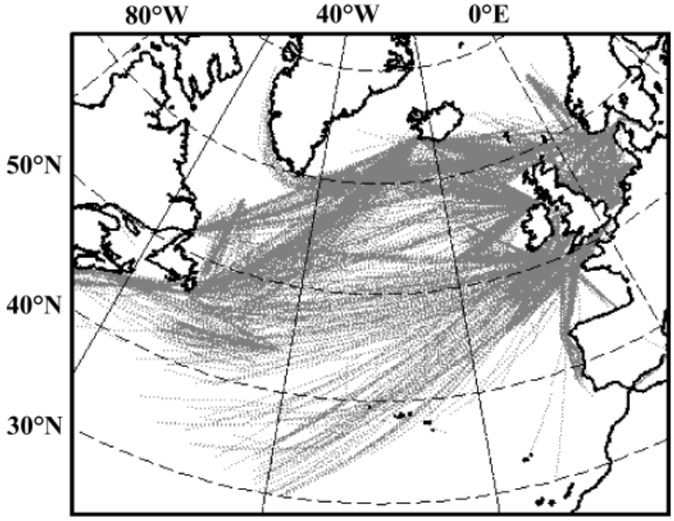

Fig. 1. Geographical location of samples collected by the CPR survey from 1958 to 1999

The CPR programme is operated by a high-speed plankton recorder that is towed behind merchant ships at an average speed of 20 km h^{-1} and a depth of approximately 6.5 m (Hays & Warner 1993). Despite the limitation to near-surface sampling, studies have shown that this device gives a satisfactory assessment of the epipelagic zone (Lindley & Williams 1980, Batten et al. 1999). Water enters the recorder through a square aperture of 1.62 cm^2 and flows to an area with a cross-section of 5 × 10 cm, where plankton is filtered by a slowly moving band of silk with an average mesh size of 270 µm. A second band of silk covers the organisms to form a sandwich that is reeled into a tank containing 4% formaldehyde. The speed of silk movement is adjusted to the speed of the ship by means of an impeller and a gearbox located above the internal mechanism; 1 cm on the silk corresponds to 1 nautical (n mile) mile of tow.

At the laboratory, the silk roll is unwound and cut into sections corresponding to 10 n miles (18.5 km) or approximately 3 m^3 of seawater filtered (Warner & Hays 1994). Positions and times of samples are calculated from data on the start and end of deployment as well as changes in the course and speed of the ship.

Plankton identification and counting is realised in 4 steps:

Step 1. Estimation of the colour of the silk into 4 categories: nil, very pale green, pale green, and green. This gives an index of chlorophyll concentration, also called the 'greenness index'. This protocol has not changed since 1958.

Step 2. Identification and quantification of phytoplankton taxa, to species level where possible. More than 200 phytoplankton species or taxa are identified. Subsampling of the filtering silk is conducted by examining 20 fields at 450 magnification (295 µm diameter view) in 2 diagonals of 10 fields across the silk. This corresponds to a subsample of about 1/8000 of the silk. Abundance of each phytoplankton taxonomic category is determined by counting the number of fields in which each taxon is detected. The methodology of this analysis has remained unchanged since 1958.

Step 3. Examination of zooplankton, generally <2 mm. Over 70 species or taxa are identified at this stage. Subsamples of 1/40 of both silks are examined in a traverse at 54 magnification (2.05 mm diameter view).

Step 4. Identification of zooplankton >2 mm on both filtering and covering silks. More than 150 species or taxa may be identified at this step. For counting zooplankton, a category system similar to a logarithmic progression of abundance is used to reduce the time of analysis. Methods of counting and data processing are described in more detail in Colebrook (1960, 1975), Warner & Hays (1994), Batten et al. (2003) and Reid et al. (2003).

NUMERICAL PROCEDURE FOR MAPPING SPATIAL DISTRIBUTIONS

The new CPR Atlas is based on 155 669 CPR samples collected from 1958 to 1999 (see Fig. 1). Results for 240 species or taxonomic groups are presented in CPR Survey Team (2004, this volume). Other species are not included, as the data were often limited to a few records or in some cases to a single occurrence. The 1973 CPR Atlas presented the geographical distribution of 255 species or taxa. The numerical procedure used for the present CPR Atlas was divided into 2 main stages (Fig. 2).

Stage 1: Spatial regularisation of species for each 2-month and day/night period. This stage consists of 3 steps: (1) transformation of latitudes and longitudes into Lambert coordinates, (2) spatial regularisation and (3) mapping (Fig. 2).

Step 1. Transformation of latitudes and longitudes into Lambert coordinates: In the 1973 CPR Atlas, the Mercator projection was used to map the geographical distribution of species. This projection, however, is not suitable for the mapping of large regions far away from the equator. For this updated version of the CPR Atlas, the Lambert Conic Conformal Projection was used (Planque & Fromentin 1996, Beaugrand et al. 2000,

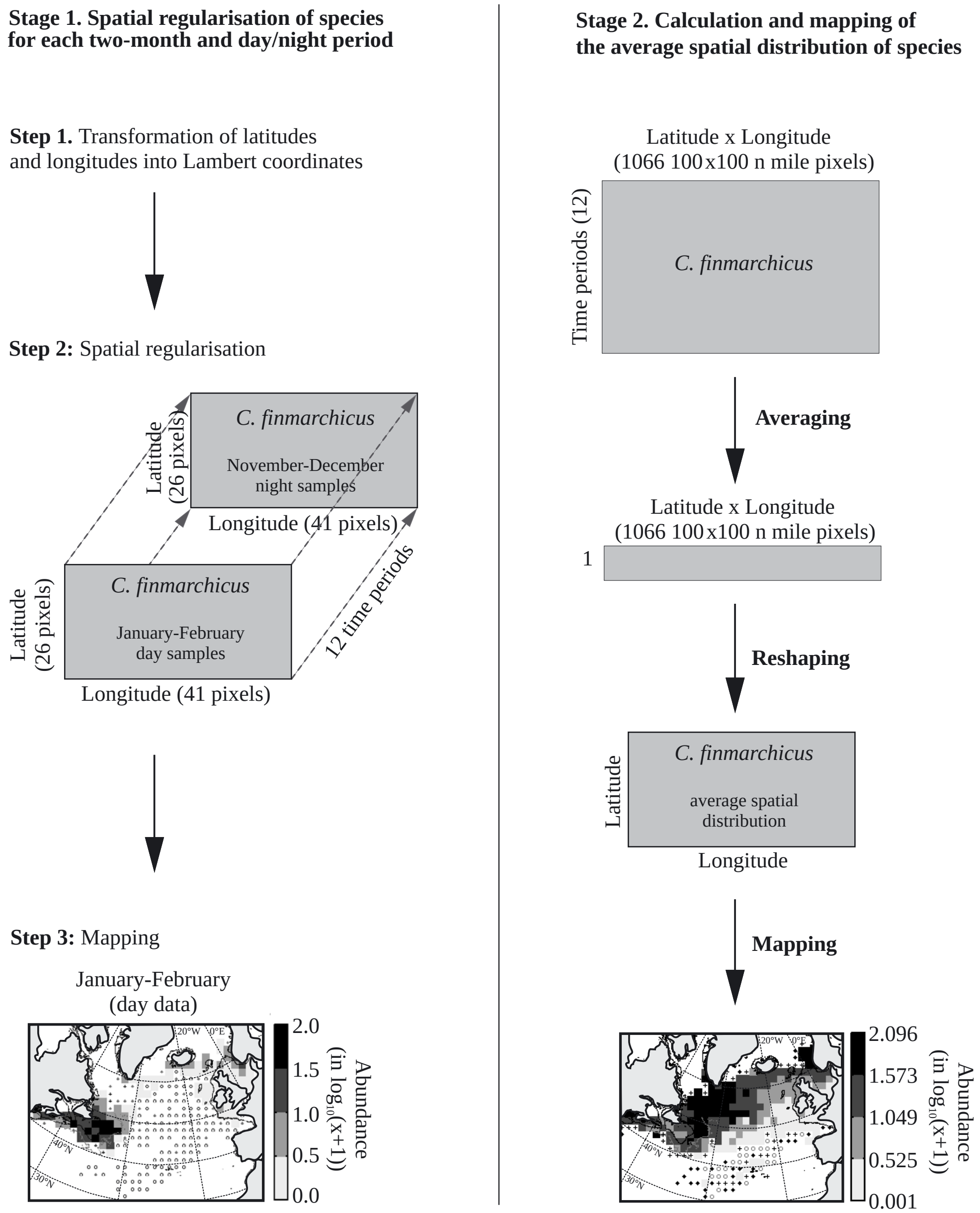

Fig. 2. Analysis stages and steps towards the production of the species distribution maps

2001), to avoid a strong deformation of distance on the maps.

Step 2. Spatial regularisation: Sampling by the CPR is irregular in space, as the samples follow the tracks of 'ships of opportunity'. Fig. 1 shows the spatial heterogeneity of CPR sampling. A regular grid (70° W to 20° E; 30 to 70° N) was defined on the basis of Lambert coordinates. The size of the geographical square for the spatial regularisation was fixed by trial and error to 100 × 100 n miles. This represents the best compromise between the number of missing geographical squares and the size of the spatial resolution. No spatial interpolation was used in the biogeographical charts. The spatial resolution was slightly improved in comparison to the 1973 CPR Atlas (geographical rectangle 1° latitude × 2° longitude).

Spatial regularisation needs to be realised for homogeneous time periods. In the pelagic realm, diel and seasonal scales represent a source of variability often greater than at the interannual scale (van der Spoel 1994, Piontkovski et al. 1999, Beaugrand et al. 2003). Therefore, a numerical procedure was included to account for temporal scales of variability; 12 spatial regularisations were produced for each 2-month period (January-February; March-April; May-June; July-August; September-October; November-December) for both day and night periods using the function in Beaugrand et al. (2001) (see their Fig. 1).

The procedure had to address the problem of including both abundance and presence data, and it distinguished 3 cases: (1) species with only presence/absence data; (2) species with only abundance data; (3) species with both presence and abundance data. Fig. 3 summarises the procedure implemented for each geographical square and time period. An average value of abundance was only calculated when the number of abundance data was >2. A distinction was made between 1 and only 1 record (abundance or presence; symbolised by a '◆') and >1 record (abundance or presence; symbolised by a '**+**'). This was to differentiate the exceptional occurrence of a species in a region, possibly due to misidentification, contamination of a sample, miscalculation of the location of a sample, or a real occurrence related to atypical hydroclimatic forcing. When no abundance was calculated and the occurrence of a species was not detected for a pixel, a zero for no occurrence (symbolised by a '○') was added on the map if the number of samples in the pixel was >2 (fixed by trial and error). This was to avoid indications of no occurrence related to regions

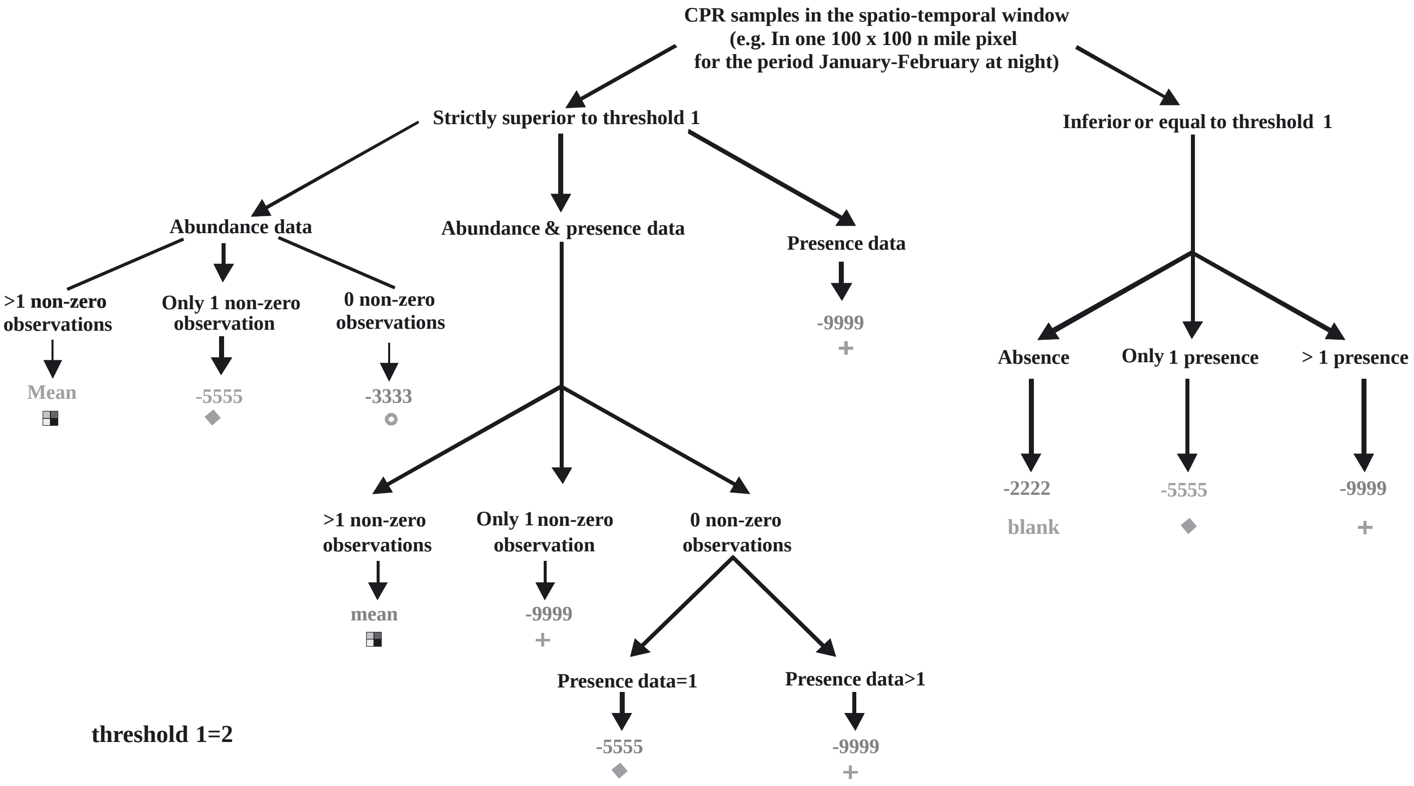

Fig. 3. Procedure of spatial regularisation of species distributions. A '**+**' (–9999): more than one occurrence in a geographical square for a given time period. ◆ (–5555): one and only one occurrence in a geographical square. ○ (–3333): no occurrence in a geographical square. Blank (–2222): no occurrence in an undersampled region (≤2 samples for a given time period); these data are not distinguished from unsampled regions

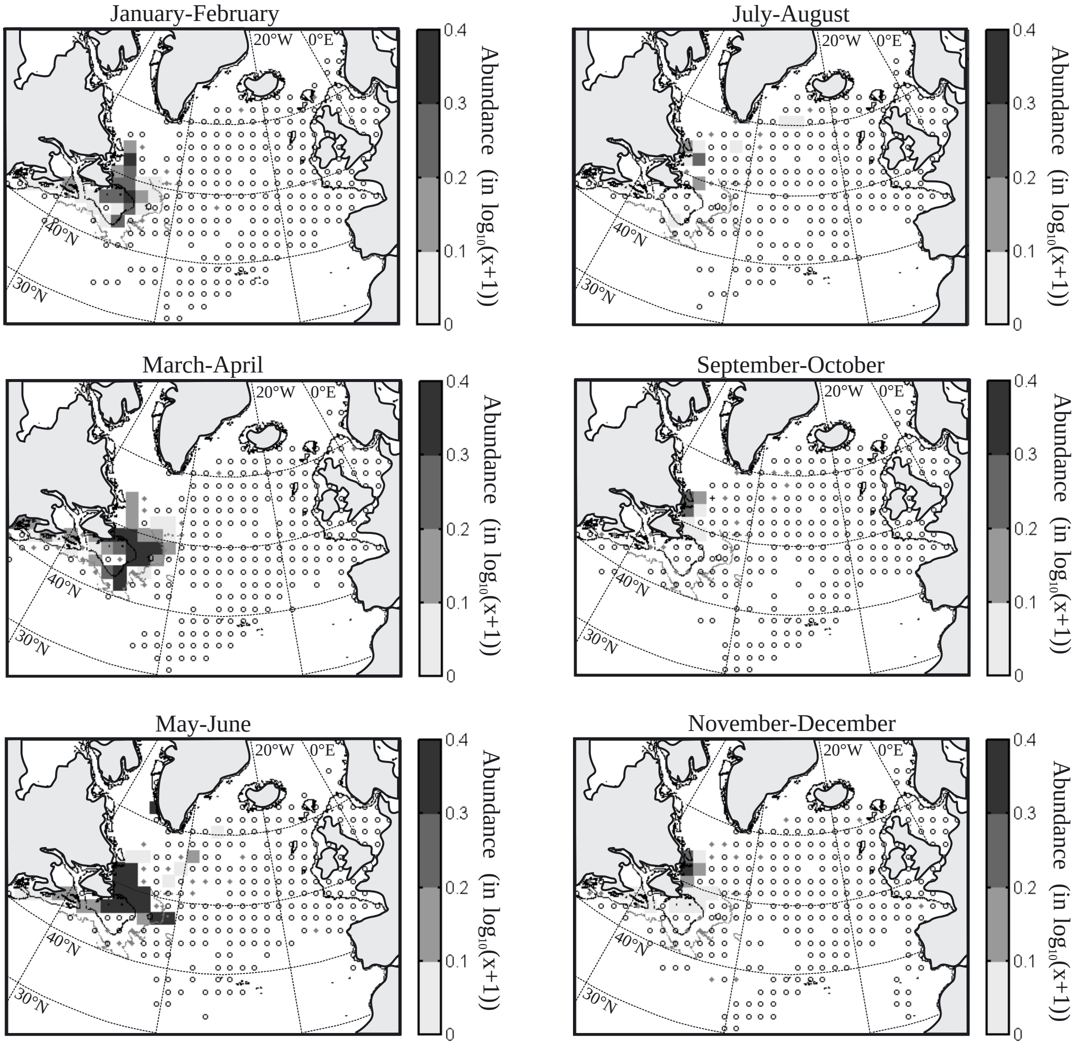

Fig. 4. *Calanus glacialis*. Seasonal changes in geographical distribution (nighttime data)

that were poorly sampled. No distinction was made between the latter regions and regions never sampled by the CPR, to avoid too much complexity in the maps.

Step 3. Mapping: Although not shown in the CPR Atlas, mapping of the geographical distribution of each species for each of the 12 time periods is possible. Fig. 4 displays seasonal changes in the abundance of *Calanus glacialis*. This species was only common in the near surface water of the Labrador Current from January to June, emphasising the importance of seasonal variability in the spatial regulation. Diel vertical migration should also be taken into consideration (Fig. 5). For example, *Pleuromamma abdominalis* is mainly detected in near-surface waters during dark periods. Abundance categories were transformed using Colebrook's (1975) function.

Stage 2: Calculation and mapping of the average spatial distribution of species. Fig. 6 summarises the procedure used to average the information (abundance and presence/absence) from the 12 maps. Thresholds used in that procedure were fixed to 6 time periods by trial and error. An average estimation of the abundance of a species for a geographical square was calculated when the number of 2-month time periods for which data on abundance were available was >6 (out of a possible 12; 6 day and 6 night). An indication of presence (**+**) was added when a taxon was detected in >2 samples (all time periods considered). An indication of an absence (○) was added in a geographical square when the absence of a taxon was confirmed in >6 time periods (thresholds 2 and 3) and presence was never recorded. This ensured that absence of a species was reported in a relatively well-sampled region. Fig. 7 shows an example of maps produced by the procedure for the calanoid copepod *Calanus finmarchicus*.

Table 1 summarises the main differences between the 1973 CPR Atlas and the present one.

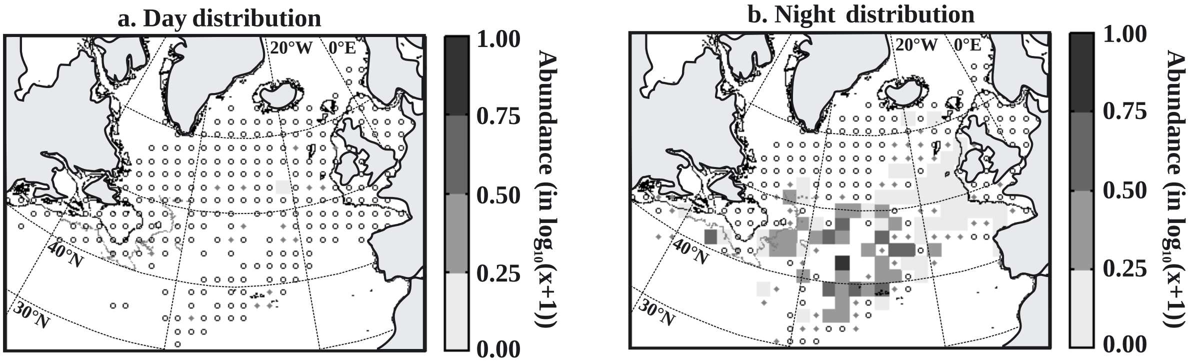

Fig. 5. *Pleurommama abdominalis.* Geographical distribution (a) during the daytime and (b) at night for September-October

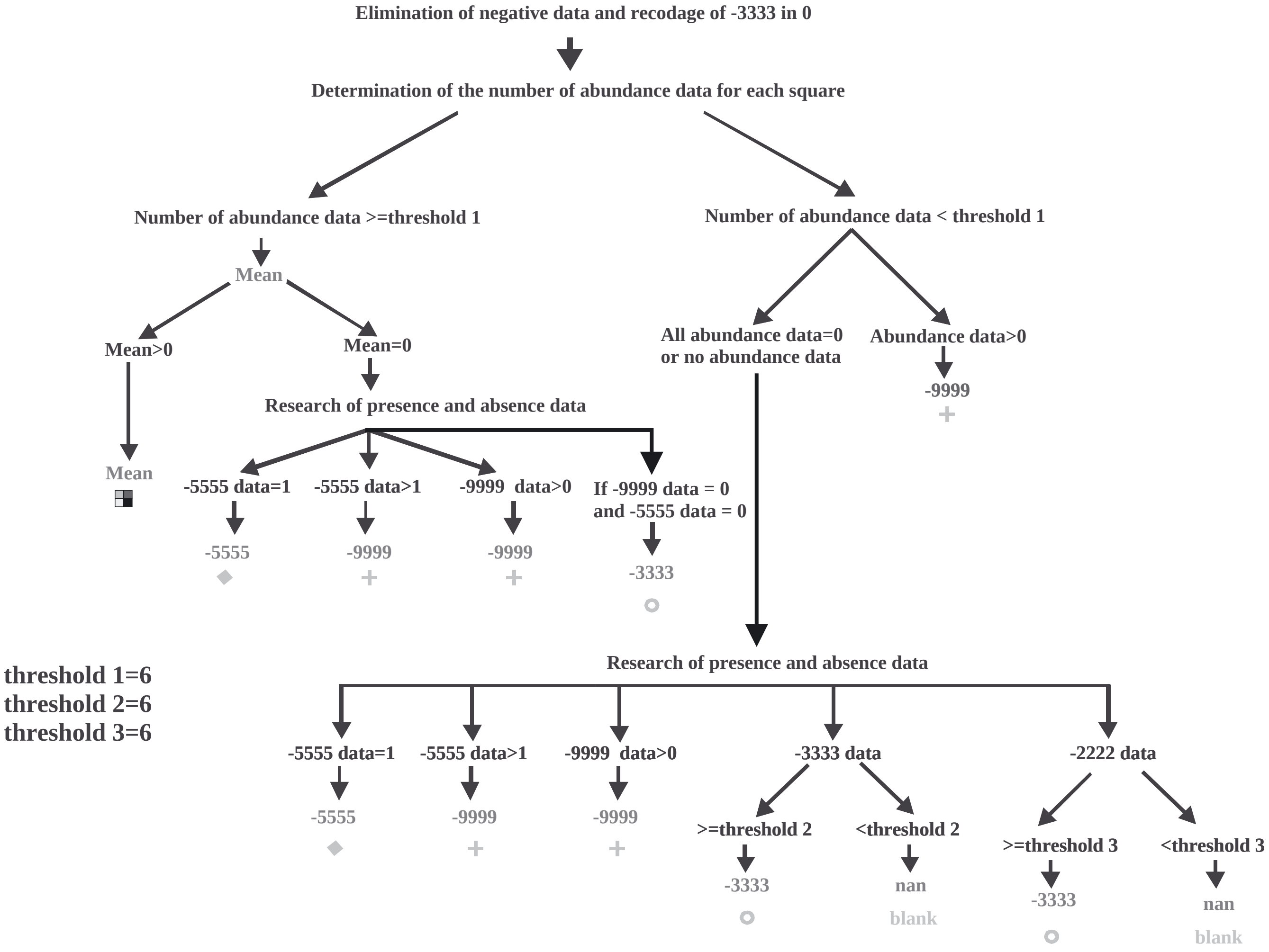

Fig. 6. Procedure for averaging the monthly information (abundance and presence/absence). Same symbols as in Fig. 3. Threshold 1 = threshold 2 = threshold 3 = 6 (see main text)

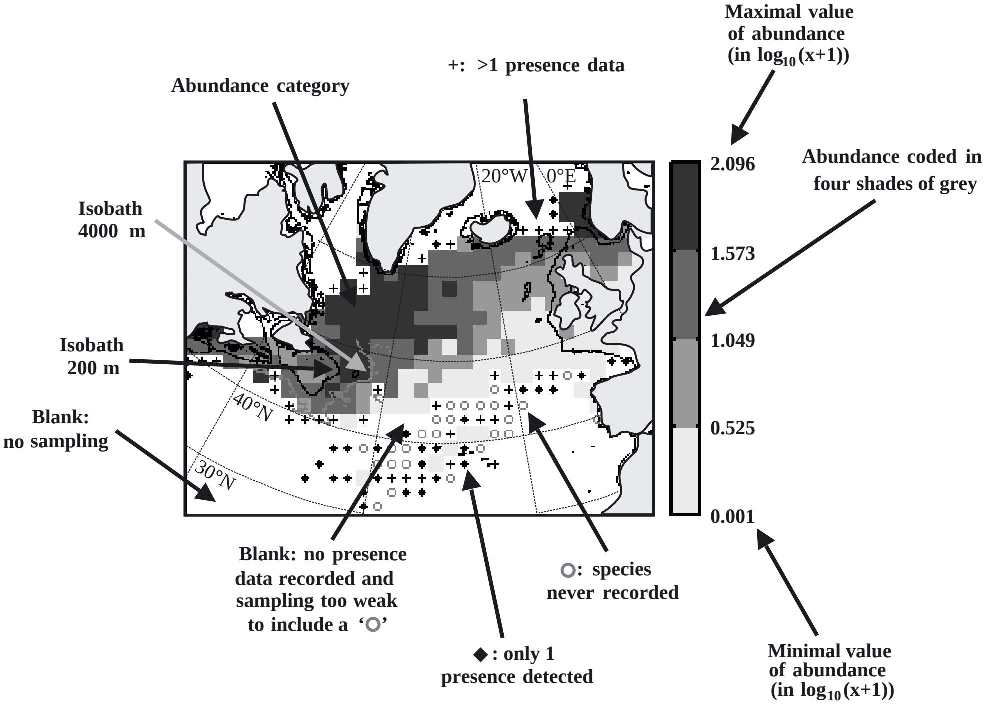

Fig. 7. *Calanus finmarchicus*. Spatial distribution. Arrows indicate the main features on the map

Table 1. Comparison between the 1973 CPR Atlas and the present Atlas

	1973 CPR Atlas	Present Atlas
Number of taxa	255	240
Time period	1958–1968	1958–1999
Number of data	40 000	155 669
Projection	Mercator	Lambert Conic Conformal
Resolution	1° lat. × 2° long.	100 × 100 n miles
Abundance category	Up to 3	Up to 4
No. of symbols per map	Up to 4	Up to 7
Variability	No	Seasonal and diel variability[a]
Other features	Land mask	Land mask and bathymetry

[a]Available at: www.sahfos.org/CPR_atlas.htm

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