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Review

An overview of *Calanus helgolandicus* ecology in European waters

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Abstract

We review current knowledge and understanding of the biology and ecology of the calanoid copepod *Calanus helgolandicus* in European waters, as well as provide a collaborative synthesis of data from 18 laboratories and 26 sampling stations in areas distributed from the northern North Sea to the Aegean and Levantine Seas. This network of zooplankton time-series stations has enabled us to collect and synthesise seasonal and multi-annual data on abundance, body size, fecundity, hatching success and vertical distribution of *C. helgolandicus*. An aim was to enable comparison with its congener *Calanus finmarchicus*, which has been studied intensively as a key component of European and north east Atlantic marine ecosystems. *C. finmarchicus* is known to over-winter at depth, whereas the life-cycle of *C. helgolandicus* is less well understood. Overwintering populations of *C. helgolandicus* have been observed off the Atlantic coast between 400 and 800 m, while in the Mediterranean there is evidence of significant deep-water populations at depths as great as 4200 m. The biogeographical distribution of *C. helgolandicus* in European coastal waters covers a wide range of habitats, from open ocean to coastal environments, and its contribution to mesozooplankton biomass ranges from 6% to 93%. Highest abundances were recorded in the Adriatic and off the west coast of Spain. *C. helgolandicus* is generally found in 9–20 °C water, with maximum abundances from 13–17 °C. In contrast, *C. finmarchicus* is found in cooler water between 0 and 15 °C, with peak abundances from 0 to 9 °C. As water has warmed in the North Atlantic over recent decades, the range of *C. helgolandicus* and its abundance on the fringes of its expanding range have increased. This review will facilitate development of population models of *C. helgolandicus*. This will not only help answer remaining questions but will improve our ability to forecast future changes, in response to a warming climate, in the abundance and distribution of this important species.
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Contents

1. Introduction

Mesozooplankton biomass is dominated by copepods (Williams, Conway, & Hunt, 1994). This group is responsible for transferring phytoplankton carbon to higher trophic levels such as fish, birds and marine mammals. Members of the genus *Calanus* are among the largest copepods, and their importance in the diet of the juvenile stages of some economically important fish (such as cod, haddock, herring and mackerel) has been demonstrated by several authors (Gaard & Reinert, 2002; Gislason & Astthorsson, 2002; Ringuette, Castonguay, Runge, & Gregoire, 2002). In addition, *Calanus* sp. can contribute >90% of the dry weight biomass of mesozooplankton in various areas (e.g., North Sea or Celtic Sea) (Joint & Williams, 1985; Williams & Lindley, 1980a, 1980b).

During the last two decades there has been considerable research in the North Atlantic focusing on the dominant *Calanus* species, *Calanus finmarchicus*; for example: US GLOBEC (Wiebe, Beardsley, Bucklin, & Mountain, 2001), the EU projects ICOS (Heath, 1999; Heath & Jónasdóttir, 1999; Heath, Dunn, Fraser, Hay, & Madden, 1999; Heath et al., 1999) and TASC (Tande & Miller, 2000), and more recently the NERC "Marine Productivity" thematic programme, a UK contribution to GLOBEC (Heath et al., 2004; Irigoien, Titelman, Harris, Harbour, & Castellani, 2003). *C. finmarchicus* is a good example of the concept of a "target"/"key" species adopted by the GLOBEC programme. The main reason for this focus is the role such species play in the ecosystem, especially in the intensively fished areas of the North Atlantic rim. This work has led to significant advances in our knowledge of the biology and ecology of *C. finmarchicus* in North Atlantic boreal ecosystems. It is thus probably the best understood copepod species in the world and has been the subject of many modelling studies (Carlotti, 1996; Carlotti & Radach, 1996; Carlotti & Wolf, 1998; Heath, Robertson, Mardaljevic, & Gurney, 1997).

An additional interest in *Calanus* has come from research showing the significant impact of climate (North Atlantic Oscillation index and temperature anomalies) on the abundance and distribution of *C. finmarchicus* in this ocean basin. This aspect has been largely developed by the group working on the Continuous Plankton Recorder (CPR) database. Fromentin and Planque (1996) showed that *C. finmarchicus* abundance has decreased in the North Atlantic over the last 50 years, and Reid, Edwards, Beaugrand, Skogen, and Stevens (2003) described the same trend in the North Sea.
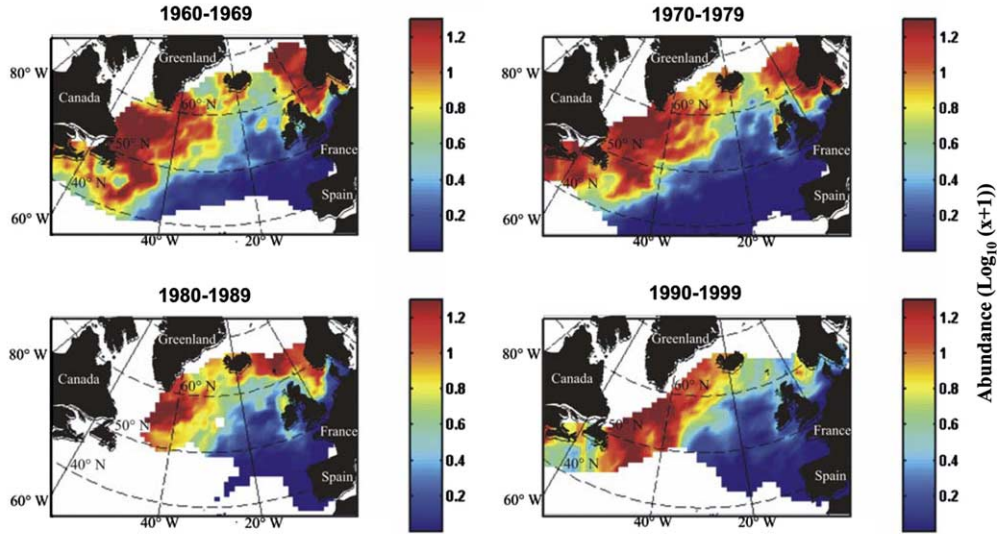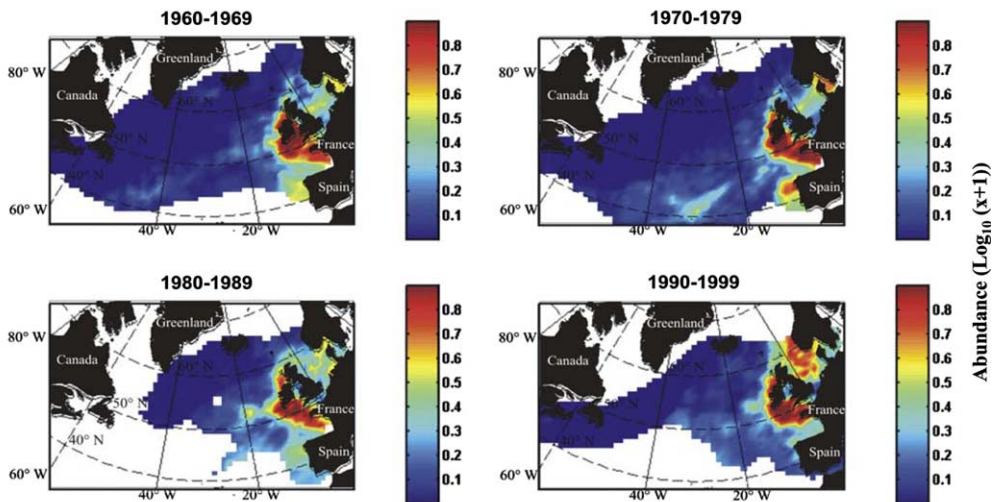
Fig. 1. Long-term changes in the abundance of *C. finmarchicus* (a) and *C. helgolandicus* (b) from the CPR data. The colour scale represents abundance of CV and CVI stages. Maps were generated using the inverse squared distance interpolation method with a search radius of 250 nmiles and a number of neighbours between 5 and 15.

In contrast to *C. finmarchicus*, there has been less focused work on the co-occurring congeneric species *Calanus helgolandicus*, which also has a broad geographical distribution in the northeast Atlantic (Barnard et al., 2004). This species pair is thought to be sensitive to subtle changes in climate, particularly along the European seaboard of the northeast Atlantic. In the last 40 years, there have been dramatic changes in abundance and distribution of *C. finmarchicus* and *C. helgolandicus* in the North Atlantic and the North Sea (Fig. 1). At a European scale and especially in the North Sea, *C. finmarchicus* has shifted progressively northwards, while *C. helgolandicus* appears to have become more abundant and widely distributed in the

1990s. These shifts in distribution demonstrated by the CPR survey provide a strong stimulus for further work on *C. helgolandicus.*

In this paper, we review the ecology of *C. helgolandicus* and make comparisons with *C. finmarchicus*. Comparative aspects are restricted to this species pair, while recognising the presence of both *C. glacialis* and *C. hyperboreus* at high latitudes in the region (Barnard et al., 2004). Only a few studies have examined the ecology of a single copepod species over a range of different environments (Fleminger & Hulsemann, 1977, 1987; Halsband, 2001; Halsband-Lenk, Hirche, & Carlotti, 2002; Halsband-Lenk, Carlotti, & Greve, 2004; Ruyet-Person, Razouls, & Razouls, 1975). Fleminger and Hulsemann (1987) studied the geographical variation in *C. helgolandicus* in the North Atlantic and the Mediterranean basin, but their approach was to determine the number of distinct populations and to explain the gene flow between them. A more recent approach has involved monitoring a species in two different environments in relation to temperature. Halsband-Lenk et al. (2004) found that two congeneric pairs of *Centropages* and *Temora* species at two sites, a cold-temperate shelf sea (Helgoland, North Sea) and a warm-temperate oceanic site (Bay of Villefranche, Mediterranean) showed distinct temperature preferences and specific adaptation of their life cycles to the temperature regime.

Our aim in this study is to identify and compile the long-term datasets available on *C. helgolandicus* in European waters and to answer a number of specific questions. Is the distribution of *C. helgolandicus* influenced by temperature? Has its geographical distribution changed over the last few decades and how may it change in the future? How does its ecology compare with that of the congeneric species, *C. finmarchicus*? We first provide an analysis of the long-term time series of *C. helgolandicus* in European waters in relation to its environment. We then review more broadly the available information on *C. helgolandicus*, placing it in the context of the new findings from our synthesis.

2. Material and methods

Fourteen long-term series (we consider continuous sampling on a regular basis over ∼5 years as long-term) or datasets on *C. helgolandicus* in European waters have been collected. Core data consist of abundances of *C. helgolandicus* copepodites, but data on sex ratio, egg production and hatching success were also available for some sites. Table 1 summarises information on sampling stations, sampling techniques, associated scientific partners, and parameters monitored that have been used in our study.

2.1. Zooplankton collection

Methods for zooplankton collection, egg production and hatching success were broadly consistent in the different time series and are generally based on the ICES Zooplankton Methodology Manual (Harris, Wiebe, Lenz, Skjoldal, & Huntley, 2000). Zooplankton net mesh size ranged from 65 to 500 μm, and abundances were calculated from integration through the water column or represented surface collection (e.g., CPR sampling). Time series and station locations are shown in Fig. 2.

2.2. Chlorophyll and temperature

In the more comprehensive datasets, temperature and Chl*a* were monitored at the same time as the zooplankton collection, although this was not always the case. Where in situ data were not available, we used alternative sources to obtain temperature and Chl*a* values.

Time series of Chl*a* (mg m^{-3}) concentrations were obtained from SeaWiFS ocean colour data using the NASA OC4V4 chlorophyll algorithm (O'Reilly et al., 1998). We used 9 km data for the SeaWiFS retrievals. Sea-surface temperature (SST) values were extracted from AVHRR imagery using the standard NOAA/ NASA algorithms (McClain, Pichel, & Walton, 1985).

Table 1
Sampling stations, parameters monitored and scientific partners

Sampling station	Location	Data available	Years of sampling	Nets used	Contact and e-mail address
Stonehaven (North Sea)	56°57.8′N, 02°06.20′W water depth: 50 m	AB + DS + EP + HS + SR + C/N + L/W,Chla,Ph,Nt,T,S	Weekly since 1997	95/68, 200 and 350 μm vertical net	Steve Hay (marlab) haysj@marlab.ac.uk
Station Z-DOVE (North Sea)	55°07′N, 01°20′W water depth: 54 m	AB	Monthly since 1969	65, 200 and 1000 μm vertical net	Chris Frid (Univ. Newcastle) C.L.J.Frid@newcastle.ac.uk
Norwegian trench (Northern North Sea)	6 stations on 2 transects around 57°5′N, 07°5′W water depth: 30–300 m	AB, VD, EP, T, S	2001	335 μm oblique nets	Rabea Diekmann (IfM-Geomar, Kiel) rdiekmann@ifm-geomar.de Sigrun Jónasdóttir (Denmark) sjo@dfu.min.dk
Helgoland (North Sea)	54°11.18′N, 07°54′W water depth: 10 m	AB, Ph, Nt, T, S	3 times a week since 1975	150 and 500 μm oblique net	Wulf Greve (Hamburg) wgreve@meeresforschung.de
CPR data (North Sea and North Atlantic)	North Atlantic, North Sea, English Channel, Bay of Biscay Sampling at ~10 m depth	AB, DS, Ph, Ph*	1958	270 μm horizontal tow of CPR	Anthony Richardson (SAHFOS) anr@sahfos.ac.uk
L4 (English Channel)	50°15′N, 04°13′W water depth: 55 m	AB + DS + EP + HS + SR + C/N,Chla, Ph, Mz, T, S	Weekly since 1988	200 μm vertical net	Roger Harris (PML) rph@mail.pml.ac.uk www.pml.ac.uk/L4/
Roscoff	48°45′N, 03°58′W water depth 55 m	EP	Weekly in 1993 and 1994	500 μm oblique net	poulet@sb-roscoff.fr
Entrance of Gironde estuary (Bay of Biscay)	Station every 3 nautical miles water depth: 30–1000 m	AB + DS + SR + L/W,Chla, T, S	Once a year in 1995, 1997, 1999, 2001, 2003	150 μm vertical net	Xabier Irigoien/ xirigoien@pas.azti.es Aitor Albaina (AZTI) aalbaina@pas.azti.es
Bay of Biscay	Transects from south Brittany to North of Spain 200 m depth to surface	EP	Once a year in April/May 2000 and 2001	200 μm vertical net	Delphine Bonnet bode@pml.ac.uk
Santander time-series (Bay of Biscay)	43°30′N, 03°47′W; 43°34.4′N, 03°47′W; 43°42.6′N, 03°47′W; water depth: 50 m	AB, Chla, Ph, Nt, T, S	Monthly since 1992	250 μm oblique net	Luis Valdes (Gijon -IEO) luis.valdes@gi.ieo.es
Gijon Station E2 (Cantabrian Sea)	43°36′N,05°41′W; water depth: 40 m 43°42′N, 06°09′W; water depth: 100 m	AB + SD + SR + W, Nt, T, S AB + DS + EP + HS + SR, Chla, Ph, Mz, Nt, T, S	Monthly: 1974–1975 Monthly since 2000	250 and 475 μm oblique net 200 μm vertical net	Sara Ceballos (Oviedo Univ.) ceballos.uo@uniovi.es

Vigo (Atlantic)	42°12.8′N, 08°51.0′W; 42°08.5′N, 08°57.5′W; 42°07.8′N, 09°07.5′W; 42°13.3′N, 08°47.7′W	AB, DS, Chl$a$, T, S	Monthly since 1995	200 and 335 µm oblique net	Ana Miranda (Vigo -IEO) ana.miranda@vi.ieo.es
Portuguese Coast (Atlantic)	Around 40°5′,10°5′W water depth: 50 m	AB, DS, SR,Chl$a$, T, S	Once to 3 times a year from 1998 to 2002	500 µm oblique net	Antonina dos Santos (IPIMAR -Portugal) antonina@ipimar.pt
Baleares (Mediterranean Sea)	39°28.10′N, 02°25.00′W; 39°24.13′N, 02°25.60′W; 39°20.50′N, 02°26.00′W water depth: 75 and 100 m	AB, SR, Chl$a$, Nt, T, S	Monthly from 1994 to 2000 and then seasonally from 2000	250 µm oblique net	Mari Luz Fernandez de Puelles (Mallorca -IEO) mluz.fernandez@ba.ieo.es
DYFAMED site (Mediterranean Sea)	43°25′N, 07°52′E; 43°38′N, 07°23′E surface sampling	AB, Chl$a$, Nt, T, S	Once a year from 1985 to 2001	200 µm horizontal net	Frederic Ibanez (Paris VI Univ.) frederic.ibanez@obs-vlfr.fr
Bay of Bizerte (Mediterranean Sea)	37°16.22′N, 09°52.44′E; 37°12.25′N, 09°53.26′E water depth: 8 and 10 m	AB, Chl$a$, Nt, T, S	Monthly for 2000–2001	160 µm oblique net	Nejib Daly (Tunis Univ.) Nejib.daly@fsb.rnu.tn
Trieste (Adriatic Sea)	45°42.06′N, 13°42.60′E water depth:17 m	AB, Chl$a$, Ph, Mz, Nt, T, S	Twice weekly from 1970 to 1980 and then monthly since 1986	200 µm vertical net	Serena Fonda (Trieste Univ.) labbioma@univ.trieste.it
Adriatic Sea	42°12.8′N, 08°51.0′W; 42°08.5′N, 08°57.5′W; 42°07.8′N, 09°07.5′W; 42°13.3′N, 08°47.7′W	AB, DS, Chl$a$, T, S	1999–2002; 1996–1997; 1997–1999 and 2001; 1989–2000	200 µm vertical net	Davor Lucic (Duvrovnik-Croatia) lucic@labdu.izor.hr
Levantine Sea	34°26.01′N, 26°07.06′E water depth: 4125 m to surface	AB, DS, VD, Chl$a$, T, S	January 1987, June 1993 and January 1998	333 µm oblique net	Horst Weikert (Hamburg Univ.) weikert@uni-hamburg.de

AB, *Calanus helgolandicus* abundance; DS, *C. helgolandicus* developmental stages; EP, egg production; HS, hatching success; SR, sex ratio; C/N, carbon and nitrogen values for *C. helgolandicus*; LW, length and weight values for *C. helgolandicus*; VD, vertical distribution; Chl$a$, Chorophyll a; Ph, phytoplankton identification and abundance, Ph*, CPR phytoplankton index colour (see text for explanation); Mz, microzooplankton identification and abundance; Nt, nutrients; T, temperature; S, salinity.
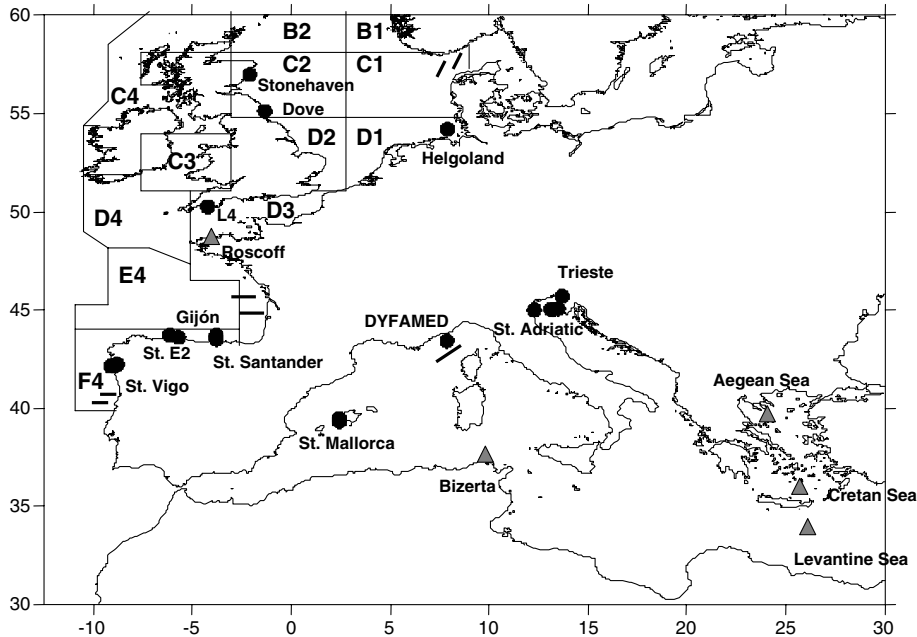
Fig. 2. Map of the stations where *C. helgolandicus* was collected. Full circles: long-term time series, Grey triangles: stations monitored sporadically (e.g., only a few months during the year or only for one year), Lines: cruises, Boxes: CPR survey area.

When stations were too close to the coast to get a good estimate, or the imagery was too cloudy, temperature was downloaded from the UK. Met Office (HadISST Version 1.1 from the Hadley Centre). This SST dataset contains monthly SST data on a $1° \times 1°$ grid and combines in situ sea surface observations and satellite-derived estimates. As many of the stations are coastal, or because the SeaWiFS imagery was contaminated by cloud, accurate Chl*a* retrievals were sometime difficult. In these circumstances, values from the CPR phytoplankton index were converted to Chl*a* concentration (Batten, Walne, Edwards, & Groom, 2003; Batten personal communication; Hays & Lindley, 1994) using the following equations:

For the North Atlantic,

$$Chla \ (mg \ m^{-3}) = (0.2468 \times colour \ category) + 0.1572.$$

For the North Sea,

$$Log \ Chla \ (mg \ m^{-3}) = 0.78 - (0.16 \times colour \ category).$$

2.3. Egg production and hatching success

2.3.1. Stonehaven (North Sea)

Each week, 25 female *C. helgolandicus* were incubated individually for 24 h at ambient field temperatures in 1 L beakers filled with filtered sea water. Each beaker contained a 500 μm mesh to avoid cannibalism. Eggs produced were counted and incubated together in a multiwell plate. Hatching success was measured after 24 h and every day subsequently for a week.

2.3.2. L4 (English Channel)

Female *C. helgolandicus* have been collected weekly since 1992 from station L4 using 500 μm mesh nets towed at the surface. These samples are taken back to the lab and the females isolated for incubation. Five

replicates of five healthy females are incubated for 24 h in 2 L glass beakers. Each beaker contains a Plexiglass egg production tube (mesh 500 μm) and is filled with 0.6 μm filtered seawater at 15 °C.

Twenty four eggs are taken from the egg production experiments and incubated individually in multiwell plates in 0.6 μm filtered seawater at 15 °C. After 24 h, eggs are checked and counted for hatched individuals and checked again every 24 h until either all eggs have hatched or the eggs are certain not to hatch (eggs are considered not viable after 4 days).

2.3.3. Roscoff

In 1997 and 1998, 30 ripe females were sorted weekly using a dissecting microscope and batches of five females were pipetted into six replicate incubators containing 1 L of unfiltered seawater and equipped with a 300 μm partition to prevent egg cannibalism. At the end of the 24 h incubation period, the egg production rate was determined by counting the eggs produced. Hatching success was estimated by incubating 50–100 freshly spawned eggs in 2 or 4 mL bowls containing 0.22 μm filtered seawater for a period up to 72 h (Laabir et al., 1998).

2.3.4. Station E2 (Cantabrian Sea)

From 2000 to 2002, experimental animals were collected monthly with a triple 200 μm mesh WP2 net equipped with filtering cod-ends. Cod-ends were diluted with seawater and transported to the laboratory. Incubation water was collected from the fluorescence maximum or at 5 m when a maximum was not detected.

Between 10 and 15 females were gently sorted under a dissecting microscope, and placed individually in dishes containing 100 mL of 100 μm filtered seawater. Experiments were run for 24 h in an incubator at surface water temperature under conditions of dim light and natural photoperiod. At the end of the incubation, eggs were counted directly in the container. Hatching success was determined 48 h later by adding 25 mL of 95% ethyl alcohol to the crystallizing dishes, and counting the number of hatched nauplii settled to the container bottom. Egg cannibalism (very low) was accounted for by including crumpled egg membranes in the daily egg production counts. Hatching success was calculated as the percentage of nauplii hatched out of all the eggs produced excluding crumpled egg membrane counts. In 2000, eggs were not counted directly in the crystallizing dishes; water from the incubation containers was filtered onto a 33 μm mesh to retain the eggs and then frozen in vials. Counts were performed subsequently in a Petri dish.

2.3.5. Cruise in the Norwegian trench (LIFECO project: 2001)

Calanus females were sampled with a 220 μm mesh net (1 m in diameter) fitted with a 5 L non-filtering cod-end. Contents of the cod-end were gently transferred into a bucket with surface water from the respective station. Immediately 24–30 lively undamaged females were then selected under a stereo-microscope and placed individually in 300 or 600 mL bottles filled with 64 μm screened surface water. Ambient eggs were screened from the incubation water. All females were incubated in darkness for 22–25 h at temperatures appropriate to the station where they were collected. After incubation, eggs were collected by filtering gently onto a 20 μm mesh and immediately counted directly on the mesh. Females were fixed in 4% formalin in seawater for later separation into *C. finmarchicus* and *C. helgolandicus*.

2.3.6. Cruises in the Bay of Biscay: PEL 2000-PEL 2001

At least five female *C. helgolandicus* were sorted individually and placed in 250 mL beakers containing 0.45 μm filtered seawater maintained at 15 °C with a 12 hD:12 hN photoperiod. To avoid cannibalism, a 200 μm mesh was placed at the bottom of each beaker. Beakers were placed in a box containing in situ surface seawater pumped continuously to maintain the incubation temperature at 15 ± 5 °C. After 24 h, contents were filtered onto a 30 μm mesh and preserved in formalin (4% final concentration). Eggs were then counted under a microscope.

Although factors other than temperature and Chl*a* affect egg production and hatching success, more detailed information (e.g., phytoplankton species composition, food quality) was not consistently available for the time series. However, low values of Chl*a* are especially poor at indicating algal biomass available to copepods. This is because at low Chl*a* levels, there can be dominance by either small cells (largely unavailable to copepods) or large cells (see Fig. 9 of Bunker & Hirst, 2004). Additionally, Chl*a* represents biomass rather than primary production and also does not include non-photosynthetic microplankton, which are known to be an important dietary component for copepods (Irigoien et al., 2003).

2.4. Description of the different environments

The European continent is bounded by two seas and one ocean. The circulation of the water masses (Fig. 3) is often strongly affected by local parameters (e.g., freshwater input, winds, depth). A general description of hydrodynamic conditions at each sampling station is provided to aid interpretation of the biological data.

2.4.1. North Sea

Within the northern North Sea, vertical gradients in temperature and salinity are pronounced. High salinity North Atlantic water penetrates through the Norwegian Trench into the Skagerrak, where it is overlain by low salinity Baltic outflow water. The structure of the water column is thus mainly driven by salinity and persists year-round. Warmest water temperatures in late spring to autumn are found at the surface as a seasonal thermocline develops, whereas warmest temperatures during winter are found at intermediate water depths below the permanent halocline. Due to stratification, the spring bloom develops earlier than in other parts of the North Sea. In contrast, the area south of the Norwegian Trench (e.g., stations 3 and 6 sampled during the LIFECO project) is less stratified and is vertically mixed especially in winter. This area is characterized by Central North Sea Water instead of the North Atlantic water mass.

The Stonehaven sampling site has a water column depth of 50 m, which remains well mixed throughout much of the year, except in late summer and autumn when surface heating and stable weather result in a
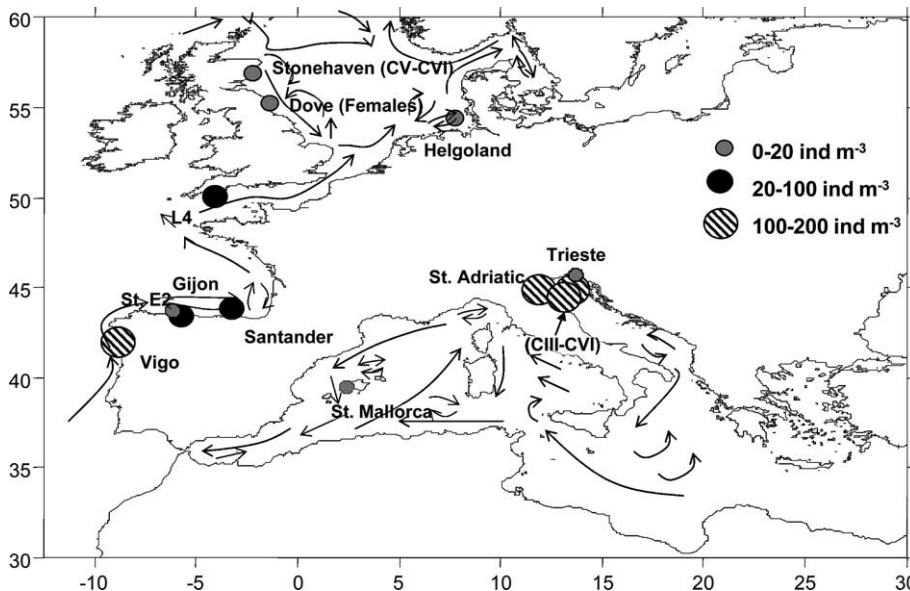

Fig. 3. Average over all months of the time series of *C. helgolandicus* copepodites (CI to CVI) abundance. Size of the circles is proportional to the abundance of the copepodites. Map of the surface currents in the studied area (modified from Ovchinnikov, 1966; Banner et al., 1980; www.mercator-ocean.fr).

temporary thermocline. Coldest temperatures usually occur in the last week of February/first week of March. Water movement is generally southerly, with moderately strong tidal currents. In late summer and autumn, water with a high Atlantic Ocean content usually passes down the Scottish East Coast. These events are particularly clear in the salinity signal (ICES, 2002).

The Dove sampling station, with a depth of ~54 m, is located between the river mouths of the Tyne and Blyth. This area experiences slight stratification in summer, although the timing of the onset, duration and strength varies among years. A thermocline is present with generally lower salinities in the surface water.

Helgoland Island in the North Sea is surrounded by northeasterly coastal currents. The sampling station is located in shallow water (7 m), and no summer stratification of the water column is observed. However, the influence of temperature on mesozooplankton seasonality is well known (Greve, Reiners, Nast, & Hoffmann, 2004).

2.4.2. English channel

Although the two fixed stations in the western English Channel, L4 and Roscoff, have similar water column depth (~55 m), they have different hydrodynamic conditions. Roscoff is characterised by tidally mixed waters (Wafar, Le Corre, & Birrien, 1983) with uniform temperature and Chl*a* concentrations throughout the water column, whereas L4 off Plymouth is weakly stratified throughout spring, summer and autumn (Holligan & Harbour, 1977; Holligan et al., 1984; Pingree, Holligan, & Mardell, 1978). Oceanic waters to the south-west of the British Isles are influenced by North Atlantic drift water and by Mediterranean water flowing north at depth over the slope (Lee & Ramster, 1981).

2.4.3. Bay of Biscay and western Iberian Peninsula

The general oceanic circulation is weak in the Bay of Biscay, and there are frequent cyclonic and anti-cyclonic eddies. In the central Bay of Biscay, the most important hydrographic process seasonally is the existence of strong mixing, from October–November to March–April, followed by the formation of the thermocline and the subsequent thermal stratification during summer. However, several mesoscale features associated with the shelf modulate this general pattern, such as upwelling events during summer, the saline stratification along the coast in winter and spring, and saline intrusions and their associated fronts (see Fernandez et al., 1991, & references therein).

In a cross-shelf section over the continental shelf off Santander and Gijón, the temperature follows the expected seasonal warming and cooling pattern, which drives seasonal stratification and mixing of the water column. The stratified period is between May and October in a layer about 50 m deep at the neritic station (Station Santander 2 and Gijón) beyond the shelf break. Between November and April, the water column remains mixed. During spring and summer, lower surface salinity is found at the surface due to continental runoff and advection from oceanic waters. In late autumn and winter, the salinity pattern is governed by an influx of saline water associated with the poleward current (Lavín, Valdes, Gil, & Moral, 1998).

In waters surrounding Vigo, in spring and summer, northerly winds along the shore are dominant, causing coastal upwelling and producing a southward flow at the surface and a northward undercurrent on the slope. Coastal upwelling breaks down thermal stratification, enriching the surface layers with nutrients and leading to high biological production. In winter the surface circulation is predominantly northward, partially driven by meridional alongshore density gradients (Peliz, Dubert, & Haidvogel, 2003; Peliz, Dubert, Haidvogel, & Cann, 2003), and transporting higher salinity and warmer (subtropical) waters, the Iberian Poleward Current, over the slope and shelf break (Haynes & Barton, 1990; Peliz, Dubert, & Haidvogel, 2003; Peliz, Dubert, Haidvogel, & Cann 2003). Another important feature of the upper layer is the Western Iberian Buoyant Plume (WIBP; Peliz, Rosa, Santos, & Pissarra, 2002), which is a low salinity surface layer fed by winter-intensified runoff from several rivers along the northwest coast of Portugal and from fjord-like lagoons (the Galician rías). Intermediate layers are mainly occupied by a poleward flow of Mediterranean Water (MW), which tends to follow the south-western slope of the Iberian Peninsula (Ambar & Howe, 1979) generating eddies (e.g., Serra & Ambar, 2002).

2.4.4. Mediterranean Basin

The Balearic Sea is a transition region of the western Mediterranean where water masses of southern and northern origin meet in the surface (0–100 m) layer (Fernández de Puelles, Pinot, & Valencia, 2003). Cool and salty northern waters from the windy Gulf of Lions encounter warmer fresher waters of Atlantic origin flowing northward from the southern Algerian basin where weather conditions are milder (Font, Salat, & Tintore, 1988; García, Tintoré, Pinot, Font, & Manriquez, 1994). Three stations (1, 2 and 3) at 75, 100 and 100 m, respectively, are monitored off Mallorca. Sea surface temperature ranges from 13 to 27 °C and the water column is strongly stratified from May to October, whereas it is mixed during winter as expected for these temperate latitudes (Fernández de Puelles, Valencia, & Vicente, 2004).

The Adriatic Sea is unique because it is the site of two different water mass formation processes. The first one is the wintertime Northern Adriatic Dense Water (NADW) mass formation process occurring in the northern half of the basin over the continental shelf along ∼500 km near the shelf break. The NADW is formed in winter in the shallow Gulf of Trieste (maximum depth 26 m) during outbreaks of cold dry winds that induce strong evaporation and cooling. It has a wide range of temperature (6–26 °C) and salinity (38.1–38.4), depending on the region and meteorology (Bergamasco, Oguz, & Malanotte-Rizzoli, 1999; Cardin & Celio, 1997), which affects stations SJ101, SJ105, SJ107 and ZI032 located in the Northern Adriatic. The second process is open ocean deep convection, which occurs in the southernmost part of the basin (∼1200 m depth). This generates the Adriatic Bottom Water (ABW). It is mainly formed by mixing of the surface waters of Ionian origin with the relatively warmer (∼14 °C) and more saline (∼38.5–38.7) Modified Levantine Intermediate Water (MLIW) entering the region at intermediate depths (200–400 m) along the eastern part of the Otranto Strait. Hydrodynamics are controlled by local spring and autumn river inputs from the west and by southern advections of MLIW, which are more frequent in winter.

2.5. Statistical analysis

2.5.1. Relationships between seasonal abundance and environment

Data from the Continuous Plankton Recorder (CPR) were analysed separately from the other datasets with a Principal Component Analysis (PCA) with the aim of identifying long-term changes (examination of principal components) and locating their geographical patterns (mapping of eigenvectors, EV). Numerical procedures and statistical analyses for this dataset are described in Beaugrand and Reid (2003).

To look at similarities among the different time series (CPR and fixed stations), we used non-metric multidimensional scaling (MDS) and cluster analysis. As our time series were of different durations, we worked with a standardised seasonal cycle. Results were plotted on a two-dimensional MDS ordination of the 33 datasets, based on double square-root transformed abundances to investigate similar patterns in the time series rather than similarities in absolute abundances. The Bray Curtis measure of similarity was used. We investigated whether there was any relationship between the grouping of stations and their environmental characteristics by superimposing Chl*a* and temperature, as well as a cluster analysis of stations on the MDS. Three datasets had to be excluded because Chl*a* and/or temperature were not monitored. These stations were either too close to the coast to get a good satellite estimate of Chl*a* or were not located in a CPR box enabling estimation of Chl*a* from the phytoplankton colour index (e.g., in the Mediterranean and in the Adriatic Sea). Analysis was carried out using PRIMER (Clarke & Warwick, 1994).

2.5.2. Relationships between egg production/hatching success and the environment

To elucidate the relative importance of a variety of potential variables in determining egg production and hatching success, we constructed a generalised linear model (GLM). This allows the simultaneous investigation of both categorical and continuous predictors. Predictors tested in the egg production model were those known to be important for egg production (temperature, Chl*a*) or that may be indicative of other broad-scale factors (latitude). Because of the temporal autocorrelation in the time series, a month ef-

fect was also included. A separate GLM was also constructed for hatching success, which included Chl*a* and temperature along with egg production as predictors. However, because fewer data were available for hatching success than for egg production, the analysis was highly sensitive to Chl*a* values > 5 mg m^{-3}; these four points had substantial leverage in the analysis and were removed.

Upon visual inspection of residuals, it was evident that it was necessary to transform egg production ($\log_{10}[X + 1]$) and hatching success (arcsin transform) (Zar, 1984) to improve normality and homoscedasticity. Predictors that had markedly non-linear relationships with the response, from a visual assessment of a preliminary generalised additive model, were parameterised appropriately to reflect the non-linearity in the GLM. GLMs were built using a backward stepwise approach, starting with the full model and then removing non-significant terms sequentially until only significant ($p < 0.05$, F test) terms remained in the final model.

2.5.3. Thermal niche

The thermal niche of *C. helgolandicus* was estimated from all CPR samples collected in the North Atlantic ($n = 190,470$). Sea surface temperature from the HadISST dataset (Hadley Centre, UK Met Office Version 1.1) was assigned to each CPR sample based on its latitude, longitude, month and year. Within each 1 °C temperature bin, the mean abundance of *C. helgolandicus* was calculated. For comparison, the thermal niche for *C. finmarchicus* was also derived.

3. Results

3.1. Abundance and distribution

A simple summary of the datasets is provided by the annual mean abundance based on the monthly averages of copepodite abundances (Fig. 3). CPR data are only semi-quantitative (Richardson, John,
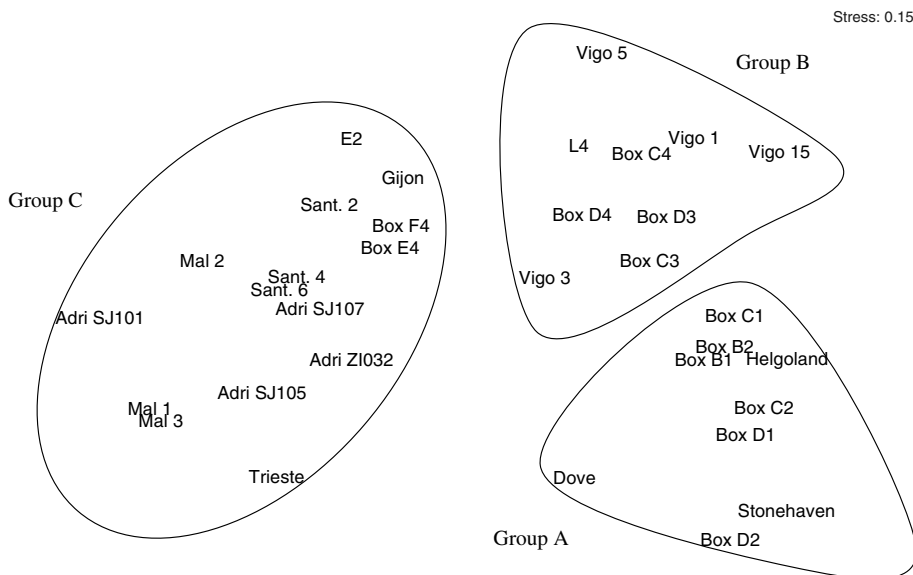

Fig. 4. MDS analysis of the standardised *Calanus helgolandicus* seasonal abundance at the different stations (Mal.: Mallorca, Sant.: Santander, Box: CPR survey area see SAHFOS website for details: www.sahfos.org) Stress: 0.15. Superimposed are the groups formed at similarity of 40.7% by a cluster analysis.

Irigoien, Harris, & Hays, 2004) and are not included here. Interestingly, highest abundances were observed in the Adriatic and off Vigo.

Fig. 4 shows the MDS and cluster analysis of the time series based on their standardised seasonal abundance. The seasonal pattern observed at Vigo is closer to the ones observed at L4 than to some closer stations such as Gijón or Santander. Results of the cluster analysis show that we can divide the datasets into three groups at a similarity of 40.7%. The MDS and cluster analysis of the seasonal abundances between the time-series stations and their corresponding CPR box are in good agreement.

Standardised seasonal cycles for the three groups (A–C) are detailed in Fig. 5. Each group shows different periods of high abundance. The northern group (A) shows high abundances in late summer/autumn,
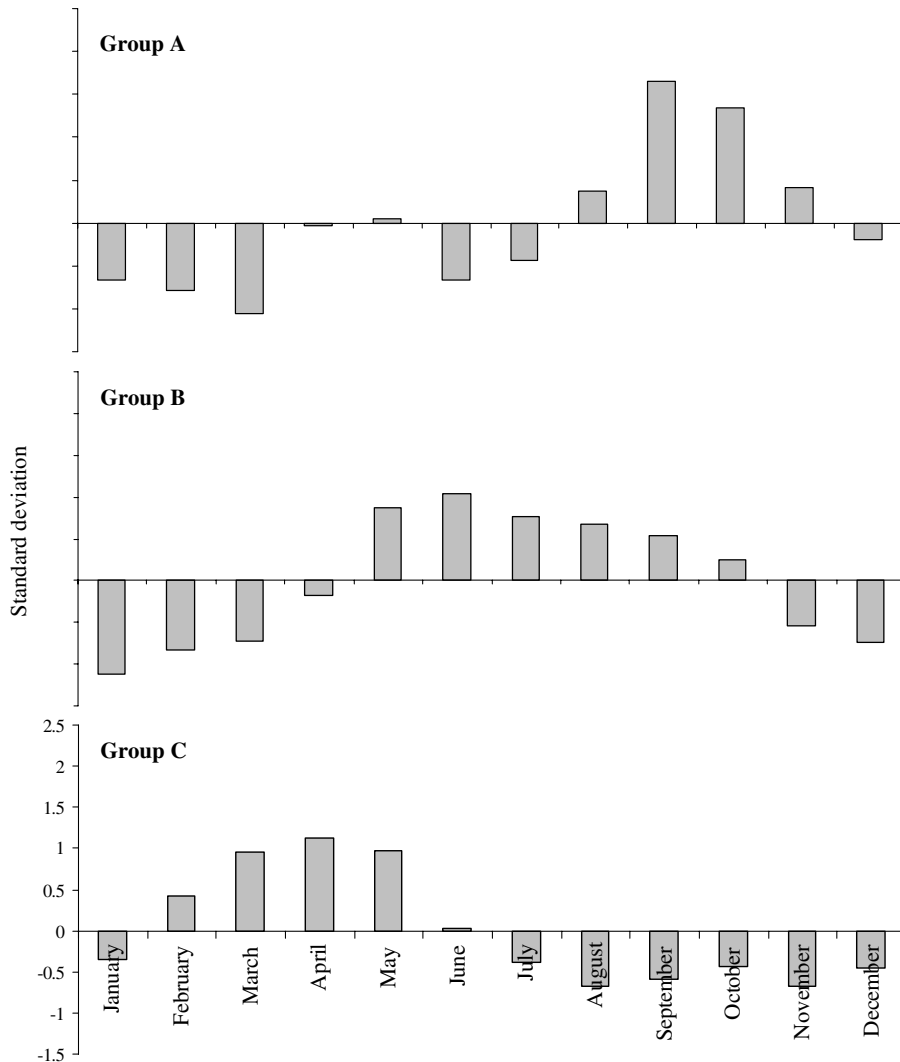

Fig. 5. Average standardised seasonal abundance cycles for the three groups of stations (A to C) identified by the cluster/MDS analyse. Group A: CPR Box B1, B2, C2, C1, D1, D2, Helgoland, Stonehaven and Dove, Group B: CPR Box C4, D3, D4, C3, L4, Vigo 1, 3, 5 and 15 and Group C: CPR Box F4, E4, Gijon, E2, Trieste, ZI032, SJ107, SJ105, SJ101, Santander 2, 4 and 6, Mallorca 1, 2 and 3.
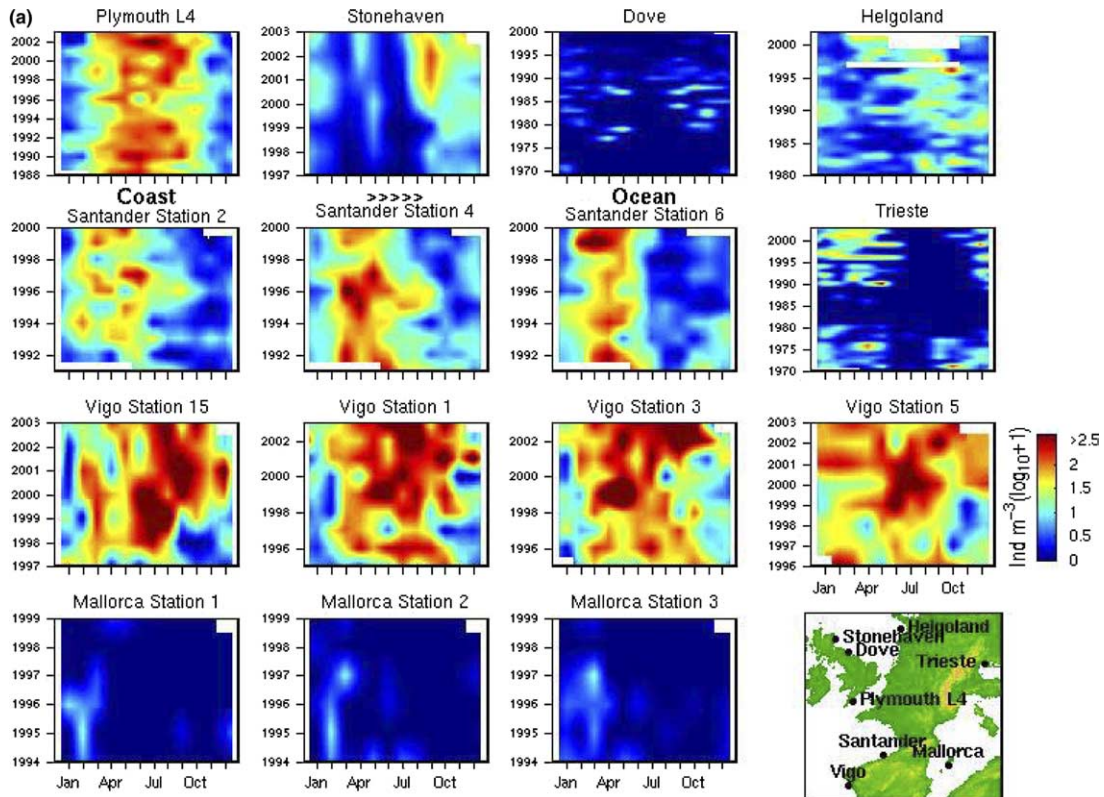
Fig. 6. Changes in *C. helgolandicus* abundance for long-term series >5 years. (a) Fixed sampling stations. (b) CPR boxes.

whereas group (B) has a long period of high abundance from late spring until the beginning of autumn. The group off Spain (C) shows a shorter period of high abundance starting in February and ending in June.

Long-term comparisons between seasonal cycles and time of maximal abundances for time series longer than 5 years are presented in Fig. 6a and b. *C. helgolandicus* has appeared at Stonehaven in early autumn (August–October) since 2000. From this date, more pronounced peaks of abundance also occur earlier in the year (January/February) and in spring (April/May). Peaks of total abundance are also found in early autumn off Helgoland in the early 1980s. However, *C. helgolandicus* first appearance peaks have been noticed earlier in the year since and currently occur in February–March. In the Dove dataset, high abundance also occurs in spring and in early autumn. However, the Dove data do not show any regular seasonal cycle. Station L4, Santander and oceanic stations off Vigo show high total abundances. At L4, *C. helgolandicus* is present all year, with maximum abundances between March and October. Apart from 1996, the same seasonal pattern occurs each year. Off Santander, *C. helgolandicus* is found earlier in the year and for a shorter period (February–July). Abundance seems to increase in more oceanic waters. Inter-annual variability is large at Station 5 off Vigo, with especially low abundances in 1996 and 1997. *C. helgolandicus* is abundant from April to August off Vigo. Low abundances off Mallorca reached their highest values in February from 1994 to 1999.

The latitude range covered by the CPR boxes shows an earlier seasonal cycle of abundance farther south, from August to November in boxes B2 and B1, from April to October in boxes C4, C3 and D4 and from March to June in box E4 (Fig. 6(b)).

Taking the time-series together, as latitude decreases, highest abundances appear earlier in the year (see Figs. 5 and 6). Only a few stations show a trend in the long term series:

Fig. 6 (*continued*)
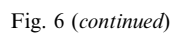
C. helgolandicus abundance peaks seem to have disappeared from the Mallorca station (Mediterranean Sea) since 1998, while higher abundances have been observed at Stonehaven (North Sea) since 1999.
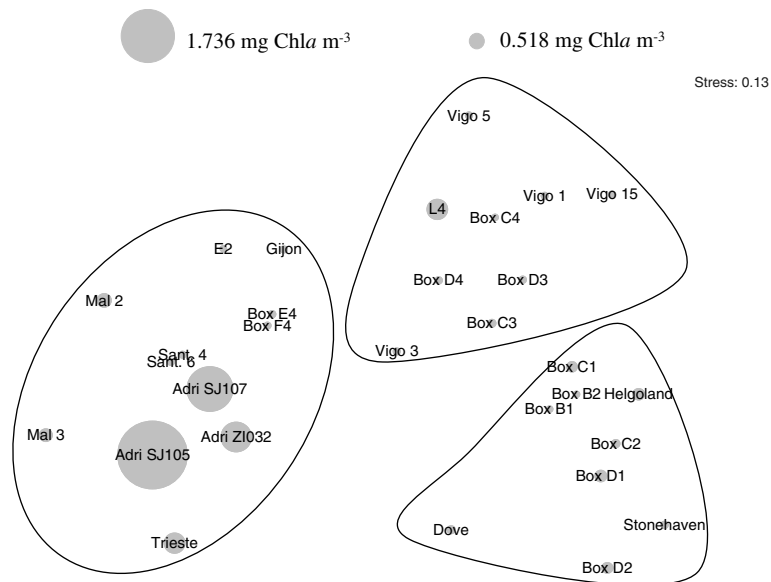
Fig. 7. Average seasonal chlorophyll *a* concentrations (grey circles) superimposed on the MDS analysis of *C. helgolandicus* seasonal abundances (Mal.: Mallorca, Sant.: Santander, Adri: Adriatic, Box: CPR survey area). The size of the shaded circle area is proportional to the Chl*a* concentration.

3.2. Relationships between abundance and environmental data

3.2.1. Chla and Temperature

Annual mean Chl*a* is superimposed on the MDS plot of standardised seasonal cycles in Fig. 7. The size of the circles is proportional to concentration, with increasing diameter representing increasing Chl*a*. No obvious relationship between Chl*a* and the station grouping is evident. Chl*a* patterns are similar for the groups of stations A and B (Fig. 8). Highest peaks are observed in April/May and concentrations remain around 0.6 mg m^{-3} until autumn. In contrast, group C has two phytoplankton bloom periods, in April and November, and shows low Chl*a* values during summer.

A similar analysis, with temperature superimposed, shows that temperature matches the station grouping produced by the MDS analysis reasonably well (Fig. 9). In addition, mean abundances are very well related with temperature (Fig. 10(a)). Seasonal cycles of temperature have similar patterns for the three groups of stations but with different temperature ranges (Fig. 8). Coolest temperatures are observed from January to April. Then temperature warms, reaching a maximum in August followed by a decrease in autumn.

3.2.2. Thermal niche

CPR time series were analysed separately from the fixed coastal stations using Principal Component Analysis (PCA; Fig. 11). In the North Sea and the Shetland Channel, *C. helgolandicus* abundance has increased over the last 50 years, and this increase is correlated positively with Northern Hemisphere Temperature anomalies (Fig. 11(a)). In contrast, no specific trend in *C. helgolandicus* abundance can be observed further south in the Celtic Sea, the English Channel or the Bay of Biscay (Fig. 11(b)). A scatterplot (Fig. 12) of *C. helgolandicus* abundance versus sea surface temperature for the region in red in Fig. 10 (EV > 0.07), with the data adjusted for temporal autocorrelation, shows that *C. helgolandicus* abundance
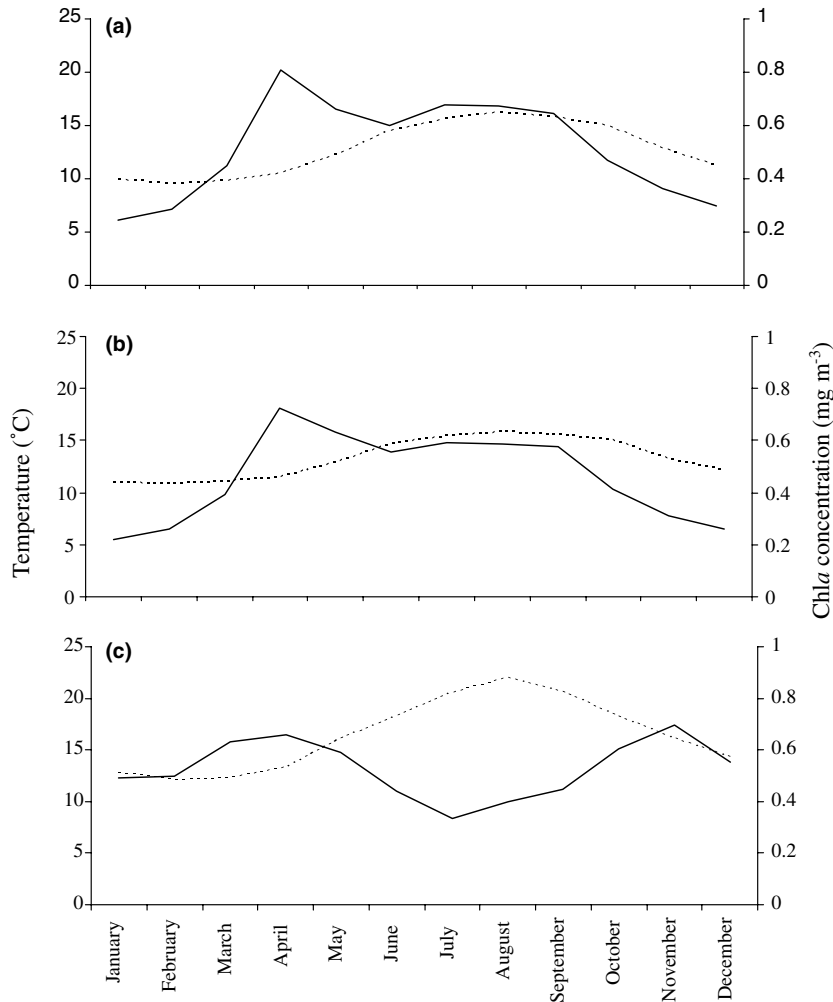
Fig. 8. Temperature (dashed line) and Chl*a* (full line) seasonal cycles in the three groups of stations identified. (a) CPR Box B1, B2, C2, C1, D1, D2, Helgoland, Stonehaven and Dove. (b) CPR Box C4, D3, D4, C3, L4, Vigo 1, 3, 5 and 15. (c) CPR Box F4, E4, Gijon, E2, Trieste, ZI032, SJ107, SJ105, SJ101, Santander 2, 4 and 6, Mallorca 1, 2 and 3.

is well correlated with temperature ($r^2 = 0.46$, $p < 0.05$). However, this subset of CPR data covers a very limited temperature range and at warmer temperatures the abundance declines again (see Fig. 10(a) and (c)).

By considering the abundance of *C. finmarchicus* and *C. helgolandicus* in relation to temperature in all North Atlantic CPR samples, the thermal niche can be defined (Fig. 13). *C. helgolandicus* is generally found in 9–20 °C water, with maximum abundance between 13 and 17 °C. In contrast, *C. finmarchicus* is found in cooler water, generally between 0 and 15 °C, with peak abundances from 0 to 9 °C. This representation of the *C. helgolandicus* thermal niche is supported by our observations at the fixed stations (Fig. 10(a)). Although most of the high abundances are observed between 10 and 17 °C, *C. helgolandicus* is also found over a wide range of temperatures; between 5 °C (in the North Sea, Greve, 2003) and 26 °C (in the Mediterranean off Tunisia).

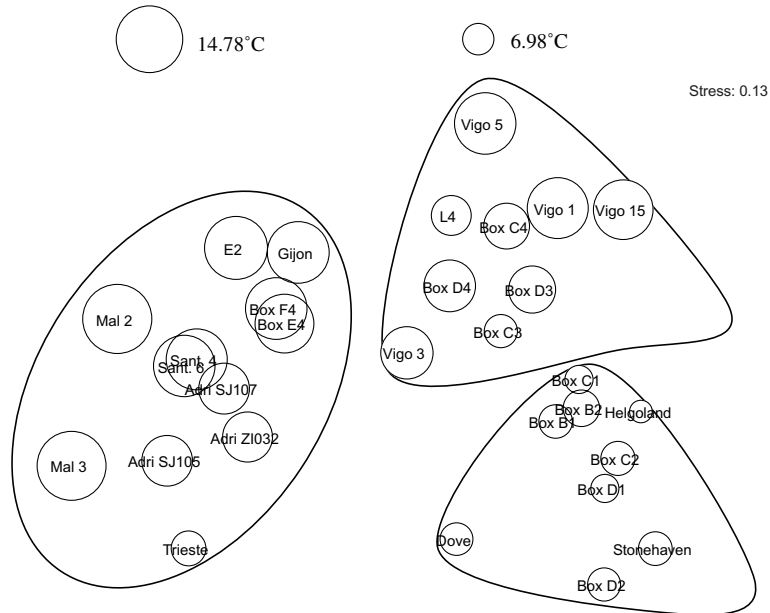Fig. 9. Average seasonal temperatures (circles) superimposed on the MDS analysis of *C. helgolandicus* seasonal abundances (Mal.: Mallorca, Sant.: Santander, Adri: Adriatic, Box: CPR survey area). The size of the circle area is proportional to the temperature.

3.2.3. Phenology

The seasonal cycle of *C. helgolandicus* peaks in spring and autumn in the central North Sea. The timing of these peaks is not significantly related to temperature (see the online Appendix in Edwards & Richardson, 2004). In contrast, the abundance of *C. finmarchicus* peaks only in spring/summer, and is significantly related to temperature ($r = -0.33$), with earlier occurrence in warmer years. The seasonal peak of *C. finmarchicus* has moved earlier in the year by $\sim$10 days from 1958 to 2002.

3.3. Egg production

Despite having only four datasets available, we can still compare the main reproductive periods of *C. helgolandicus* with respect to location (Fig. 14). At Stonehaven (group A), egg production peaks in late summer. The English Channel stations, L4 and Roscoff (group B), show a long reproductive period from early spring to the beginning of winter. At L4, the reproductive period is nearly continuous, as females continue spawning at a low level during winter. The Cantabrian Sea station E2 (group C) is similar to L4, with egg production starting early in the year (mid January) and continuing throughout the year, although the main period of reproduction is from February to the beginning of July. For each geographical area (groups A–C), periods of reproduction match the periods of maximum seasonal abundance (cf. Fig. 5). A maximum egg production of $\sim$28 eggs female^{-1} day^{-1} is observed for all stations monitored, apart from Roscoff where the peak egg production rate was <13 eggs female^{-1} day^{-1}.

The influence of the environment (e.g., temperature and Chl*a*) on egg production was analysed with a generalised linear model (GLM) using all available egg production datasets. The final model ($n = 684$) for *C. helgolandicus* egg production, explaining 43.7% of the total variance, is shown in Fig. 15. The plots illustrate the relationship between egg production and each predictor (adjusted for all other predictors in
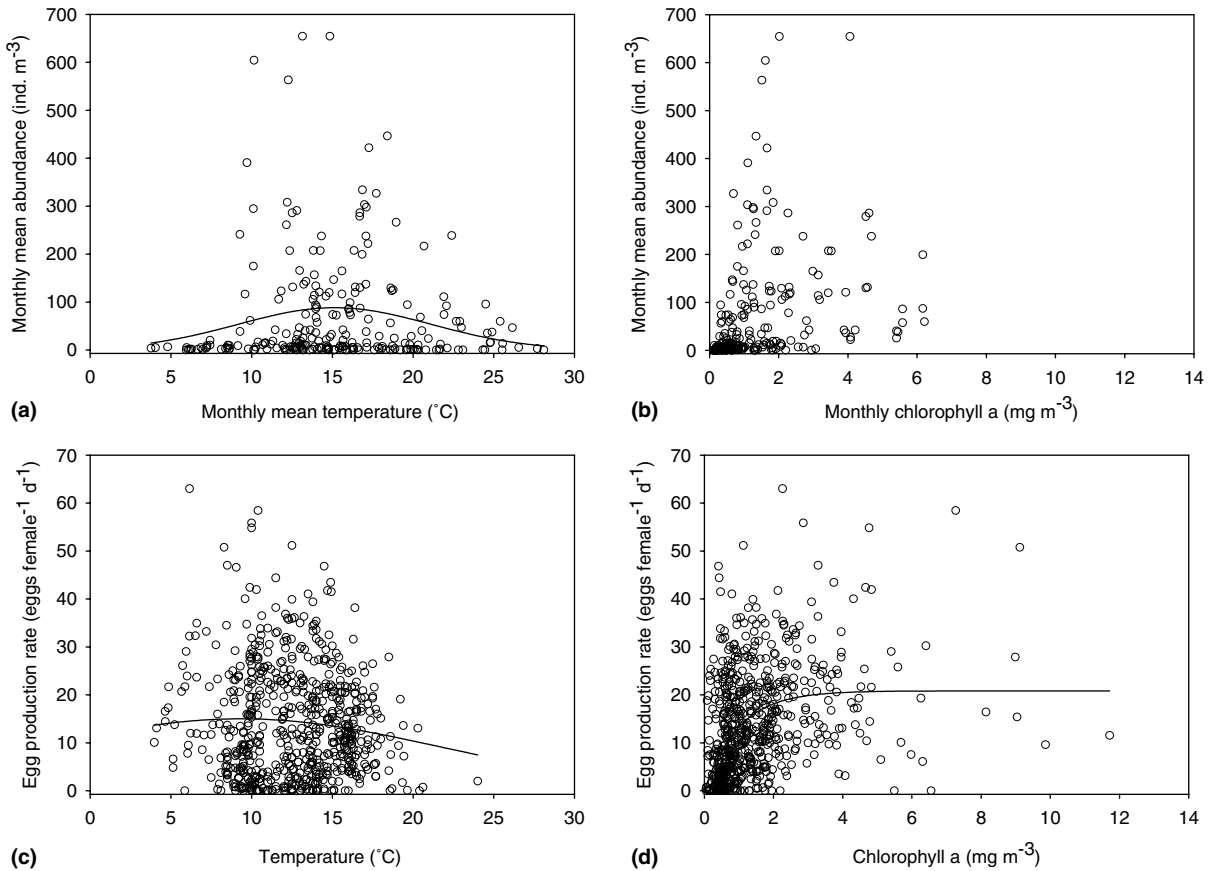
Fig. 10. Mean abundance and egg production rates of *C. helgolandicus* versus temperature and Chl*a* concentration. Data taken from L4, Stonehaven, E2, Roscoff and the Norwegian trench. Bell-shaped curves describing monthly mean abundance (a) and egg production rates (c) versus temperature determined using a Pseudo-voight four parameter fit.

the model). The *y*-axis is a relative scale, so that a *y*-value of zero is the mean effect of the adjusted environmental variable on egg production, a positive *y*-value indicates a positive effect on egg production, and a negative *y*-value indicates a negative effect on egg production. The 95% confidence intervals are shown in each plot.

Month was the most important predictor and reflects the overall seasonal cycle of egg production across all stations, peaking in spring and summer. Chl*a* was the next most important predictor, with the rate of egg production increasing at higher Chl*a* (see also Fig. 10(d)). This was modelled as log(Chl*a*) to capture the non-linear relationship identified by a preliminary generalised additive model. The last significant predictor was latitude; high egg production rates were found at latitudes farther north. Temperature was not a significant predictor of egg production.

Egg production for the total population (eggs $m^{-2} d^{-1}$) was calculated at stations E2 (Cantabrian Sea), L4 (Plymouth) and at Stonehaven by multiplying egg production (eggs female^{-1} d^{-1}) by the female abundance (female m^{-2}). Maximum total egg production reached 256,000, 35,146 and 11,764 eggs m^{-2} d^{-1} for E2, L4 and Stonehaven, respectively.
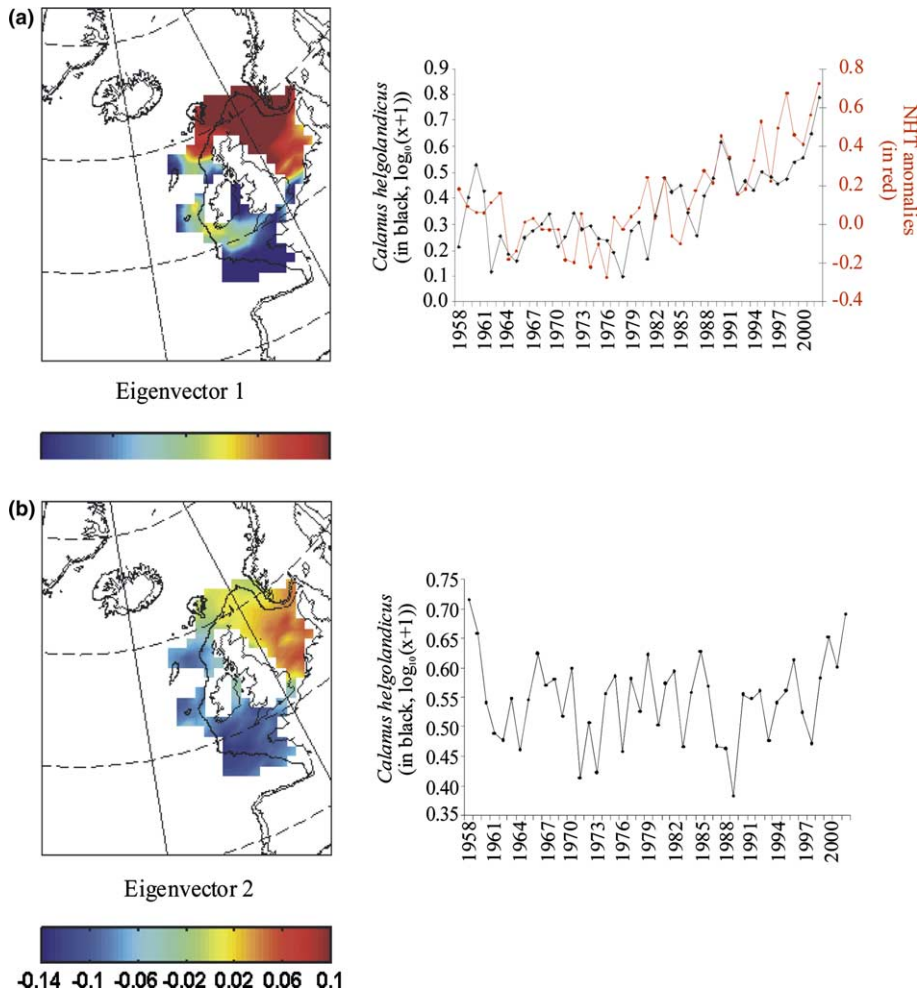
Fig. 11. CPR data analysis. (a) Long-term change in the abundance of *C. helgolandicus* (1958–2002). First eigenvector, EV, (34.23% of the total variance) and re-estimation of abundance value in regions in blue (EV > 0.07). (b) Long-term change in the abundance of *C. helgolandicus* (1958–2002). Second eigenvector, EV, (13.70% of the total variance) and reestimation of abundance value in regions in blue (EV > 0.04).

3.4. Hatching success

The final model ($n = 91$) for predicting *C. helgolandicus* hatching success, explaining 28.4% of the total variance, is shown in Fig. 16. Hatching success was not found to vary with month, Chl*a* or latitude. Temperature was the most significant predictor, with better hatching success at warmer temperatures (range 4–24 °C). Hatching success was also weakly related to egg production rate, with slightly poorer hatching success at higher rates of egg production.

3.5. Vertical distribution and migration

A prominent feature of the ecology of copepods is vertical migration. Vertical migration is usually per-formed daily by copepodites and adults by descending during daylight to escape predators, and ascending
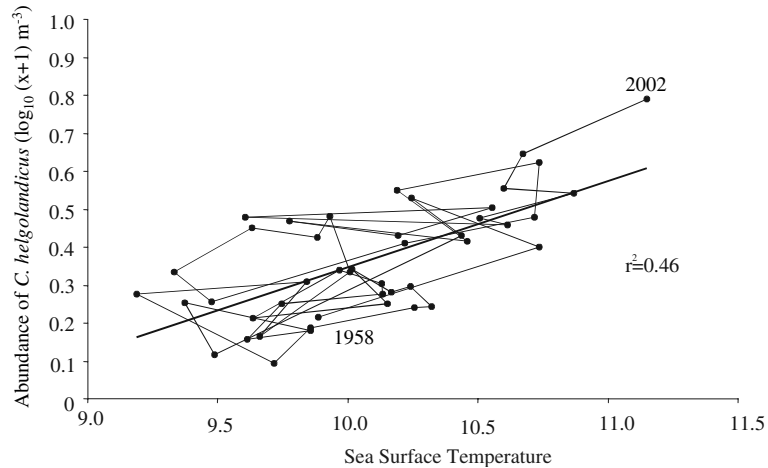
Fig. 12. Scatterplot of *C. helgolandicus* CPR abundance versus temperature. Data are from the CPR region in red in Fig. 10 (EV > 0.07).
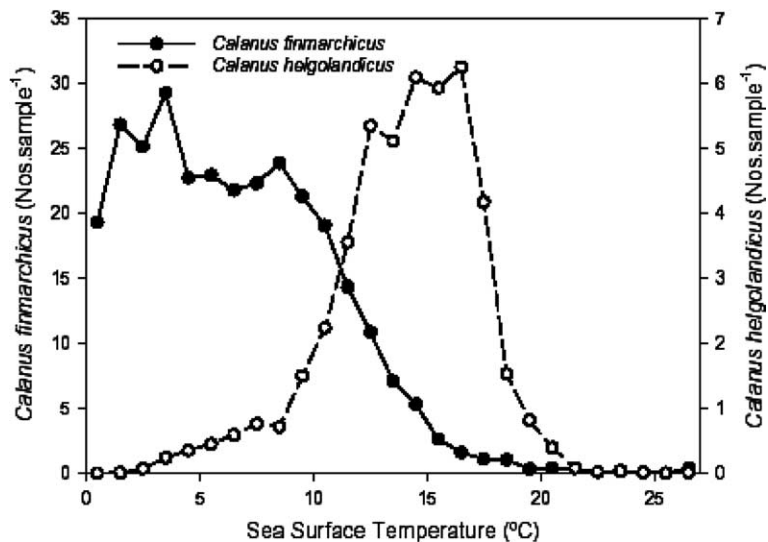
Fig. 13. Mean abundance of *C. finmarchicus* and *C. helgolandicus* species for all the CPR samples in relation to temperature.

to surface waters during the night to feed. However, a much deeper seasonal ontogenetic migration takes place in *Calanus* sp. when diapausing during the winter (stage CV). This behaviour has been shown to be characteristic of *C. finmarchicus* but less is known about diapause in *C. helgolandicus* (e.g., Hirche, 1983, 1996; Williams, 1985; Williams & Conway, 1982, 1984).

3.5.1. The Mediterranean Basin

Fig. 17(a) and (b) presents the vertical distribution of CIV, CV and female *C. helgolandicus* in June 1993 in the Levantine Sea. The water column was stratified, with a temperature gradient of 6 °C in the first 100 m (Fig. 17(c)). Daily vertical migration was not observed for any of the stages studied (Fig. 17). Indeed, in the
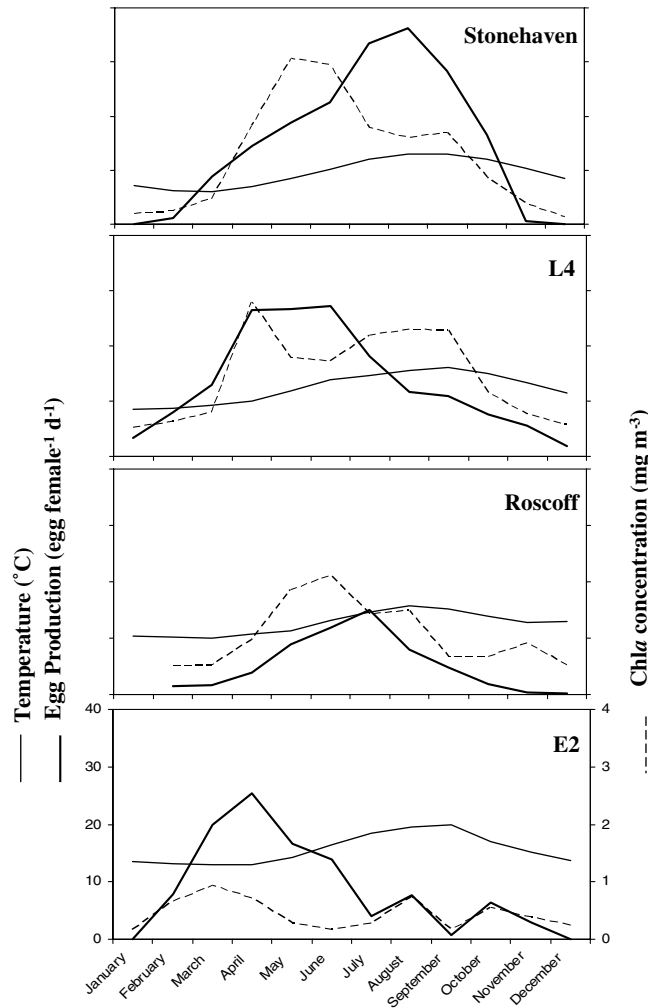
Fig. 14. *C. helgolandicus* egg production cycle (full thick line), temperature (full thin line) and Chl*a* concentration (dashed line) at four different locations. Egg production, temperature and Chl*a* values off Roscoff were taken from Laabir et al. (1998).

first 1025 m, individuals rarely ascended above 575 m by day or night. *C. helgolandicus* abundance in the water column during the night and day combined (Fig. 17(a)) shows peaks around 3000 m depth for CVs and females. Overall, the abundance of *C. helgolandicus* in this area increases with depth relative to that of total zooplankton (Weikert, Koppelmann, & Wiegratz, 2001), contributing > 25% below 1225 m and reaching a maximum in the abyssopelagic zone with 40–60% of the abundance between 2225 and 3725 m.

The sequence of stations in January 1998 (Fig. 18) suggests that the maximum abundance of *C. helgolandicus* at intermediate depths was ~150 m deeper in the Levantine Sea (Ierapetra Deep, Caso Strait South) than at the three sites in the Aegean Sea (450–600 m). Quantitative data on the ontogenetic composition in January 1998 are not available, but both males and females occurred in addition to the numerically dominant CVs. Males were only occasionally found at the two sites in the Levantine Sea. In the Aegean Sea, they seemed to be more abundant in the Cretan Sea and attained highest
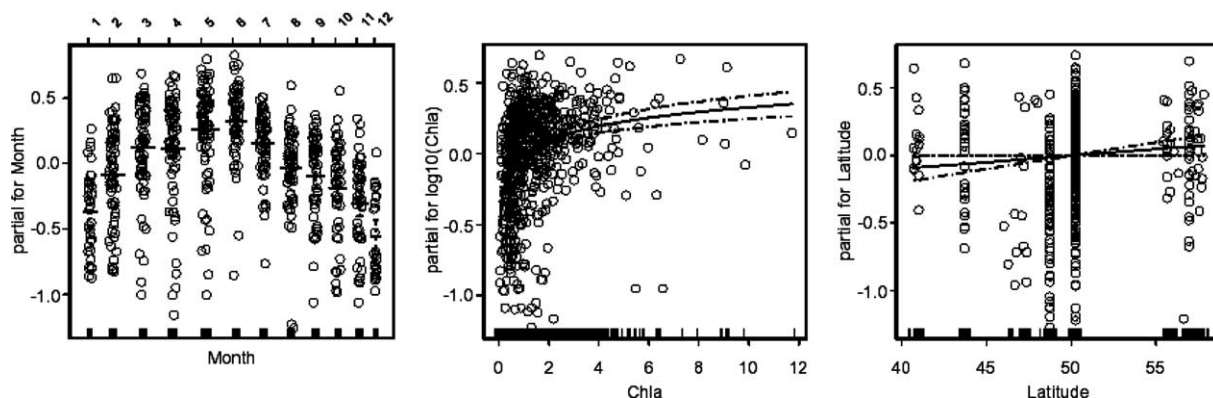
Fig. 15. A graphical representation of the final generalised linear model (GLM) showing the influence of environmental variables on *C. helgolandicus* egg production (*y*-axis). The 95% confidence interval for each variable is shown by the dashed line.
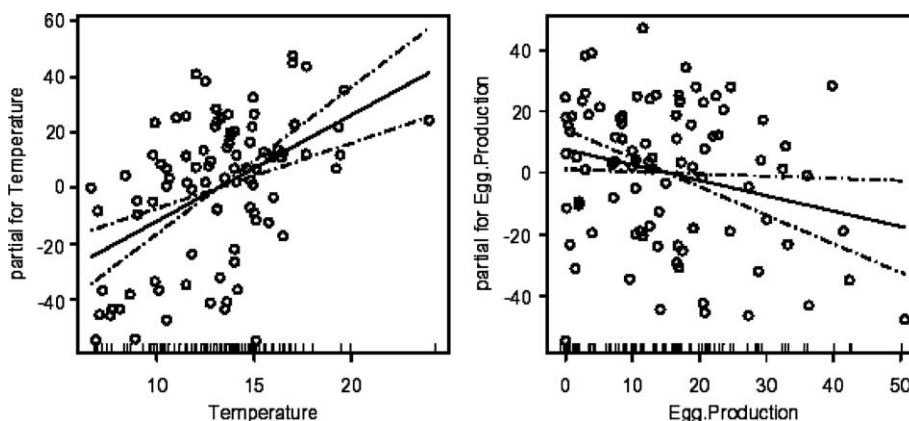
Fig. 16. A graphical representation of the final generalised linear model (GLM) showing the influence of temperature and egg production on *C. helgolandicus* hatching success (*y*-axis). The 95% confidence interval for each variable is shown by the dashed line.

numbers in the Sporades Basin. Here, in the 0–450 m sample, counts of males and CVs were lower than those of females by a factor of four to five (300 ind. $1000 \, m^{-3}$). Of the four deeper intervals, samples from 450–600 m and 900–1050 m have been analysed for stages, yielding relative abundances that varied between 0.4% and 3% (females), 4% and 12% (males) and 85% and 95% (CV).

3.5.2. The North sea

The vertical distribution of *C. finmarchicus* and *C. helgolandicus* was monitored at 6 stations within or near the Norwegian Trench during the LIFECO project (Figs. 19–21). In May, the *Calanus* population was dominated by *C. finmarchicus* at each station, except for station 6 where both species were found in low abundances (Figs. 20 and 21). Vertical distribution patterns were remarkably similar between the two species, although with some interesting differences. In November, abundances were generally much lower than the ones observed in May. *C. helgolandicus* was the dominant species and was found shallower at the northernmost stations (stations 1, 2, 4 and 5) than *C. finmarchicus*, which seems to retreat to deeper water.
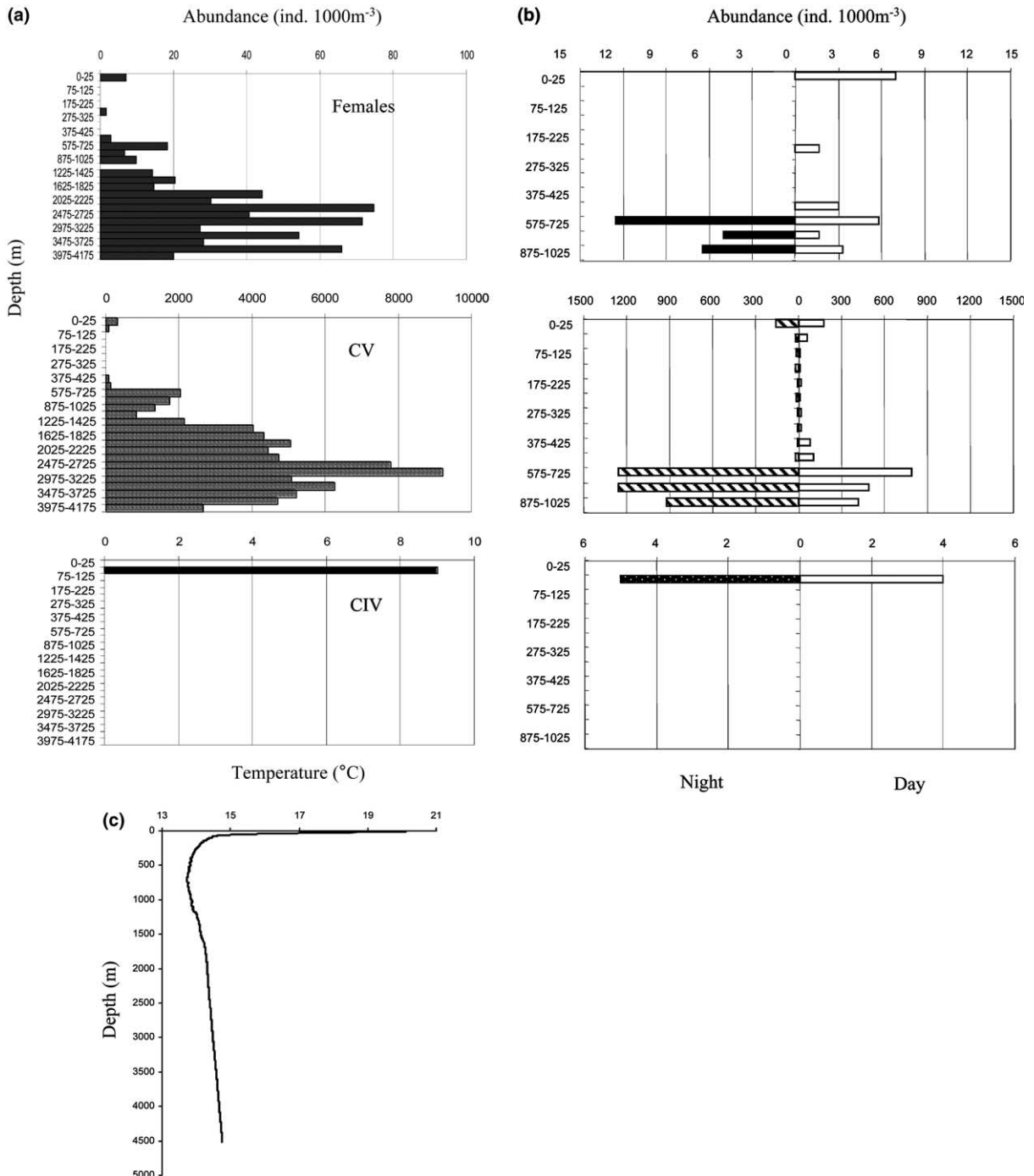
Fig. 17. Vertical distribution of *C. helgolandicus* at 34° 20′N and 25° 50′E (Levantine Sea, sounding depth 4250 m) in 11–19 June 1993. (a) Mean of night and day abundance for the water column. (b) Day and night vertical distribution for the upper 1025 m of the water column. (c) Profile of potential temperature (°C).
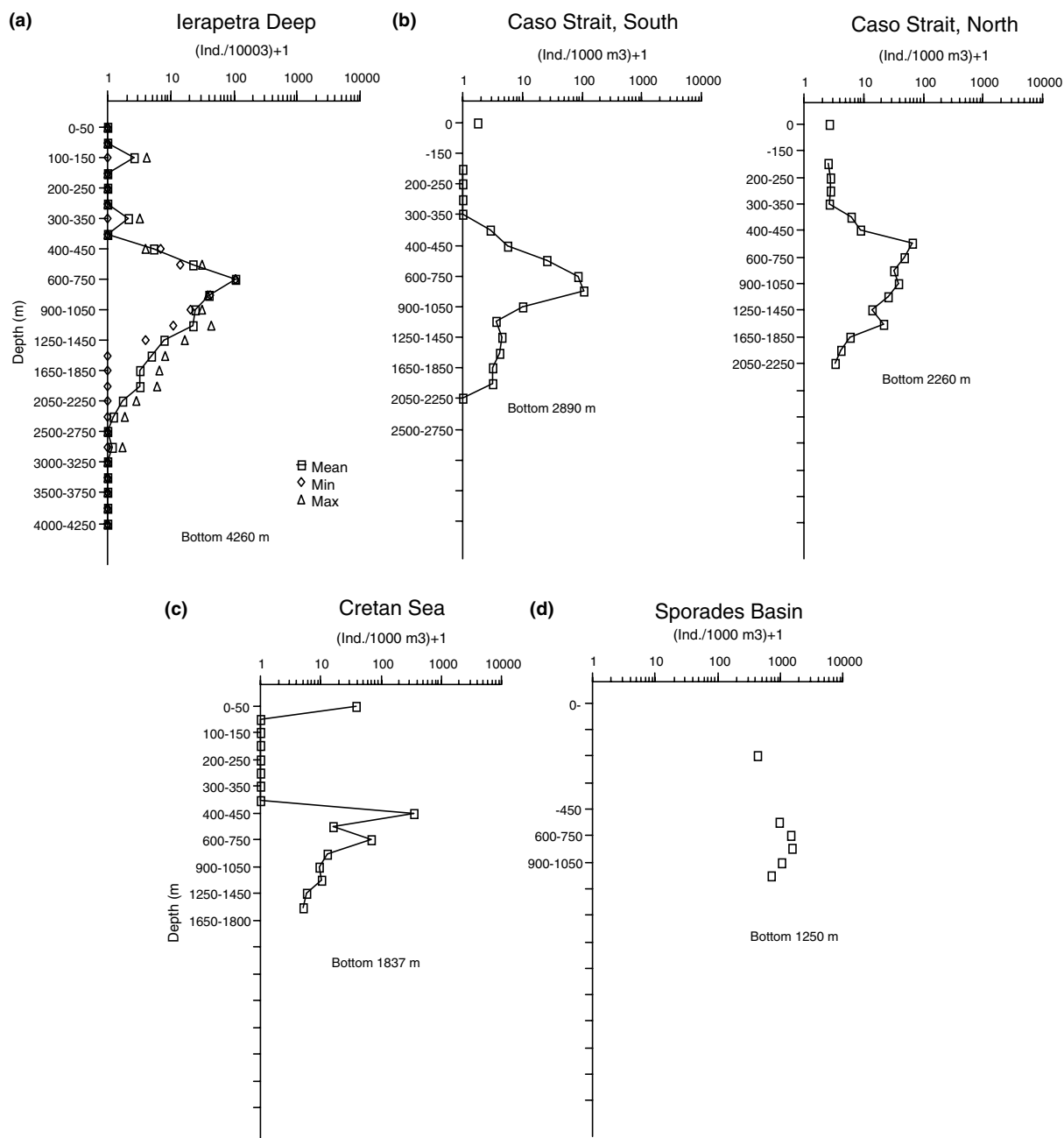
Fig. 18. Vertical distribution of *C. helgolandicus* at stations in the Levantine Sea and the Aegean Sea (Caso Strait, North and following stations) in January 1998 (cruise RV Meteor 40/3). (a) Levantine Sea; (b) Strait connecting the Levantine Sea and the Cretan Sea which is separated by an ∼800 m shallow sill; (c) Cretan Sea; (d) Northern Aegean Sea.

Sampling at certain stations over a full day–night cycle revealed negligible diurnal vertical migration in this area. Temperature was warmest in the upper 50–70 m during November and may additionally regulate the vertical distribution of the two species.
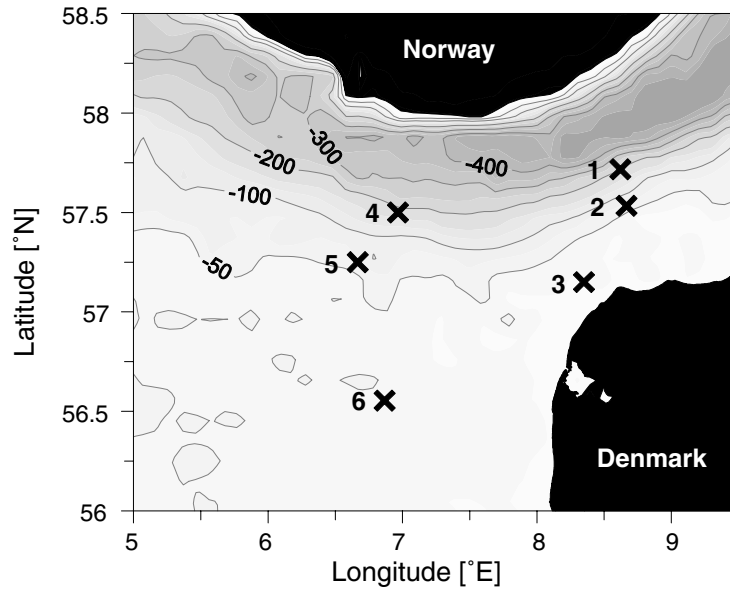
Fig. 19. Map of the stations in the North Sea during the LIFECO project (cruises in April, May/June, September and November 2001).
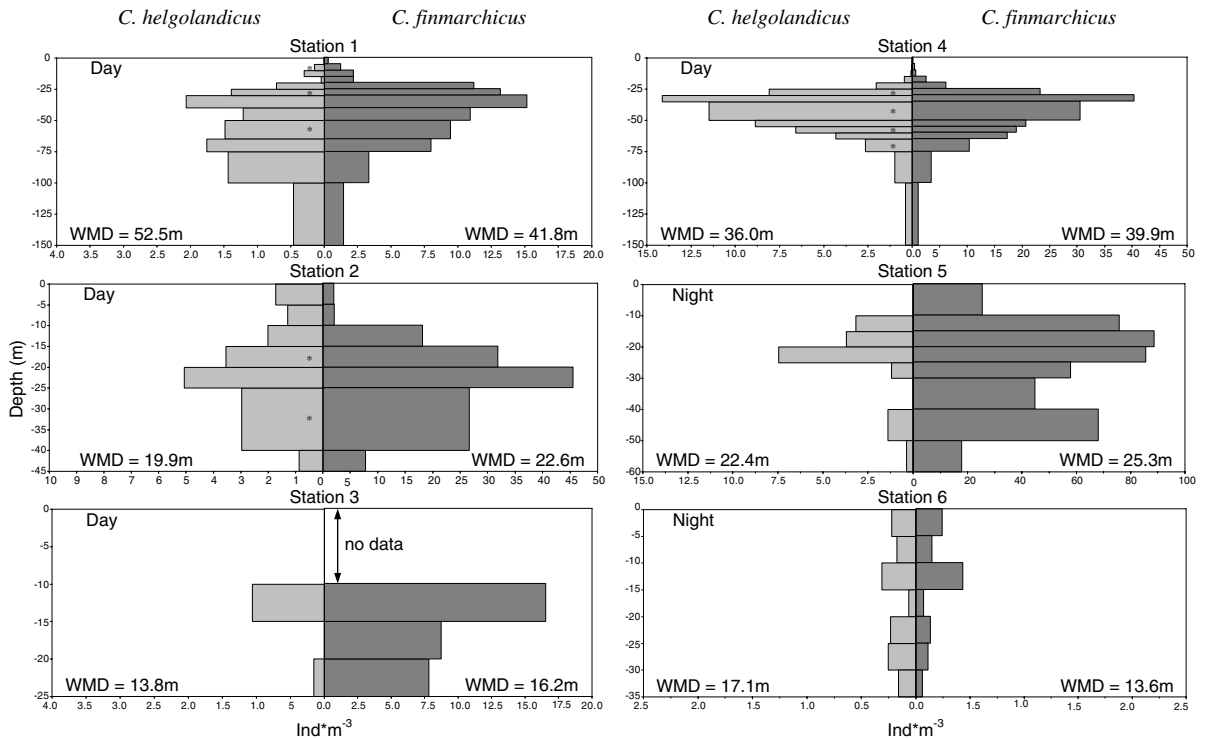
Fig. 20. Vertical distribution of *C. finmarchicus* and *C. helgolandicus* (ind m⁻³) in May 2001 at LIFECO stations 1–6 (see Fig. 19). Asterisks indicate values that were linearly interpolated between adjacent strata.
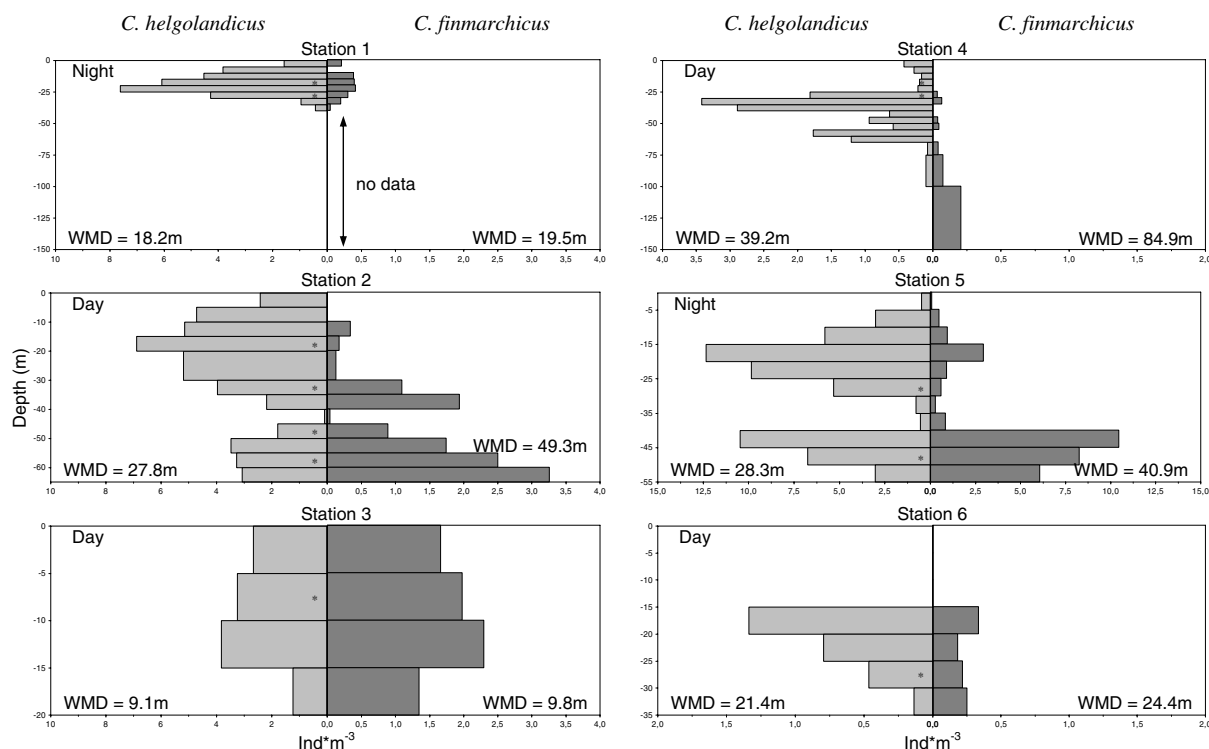
Fig. 21. Vertical distribution of *C. finmarchicus* and *C. helgolandicus* (ind m^{-3}) in November 2001 at stations LIFECO 1–6 (see Fig. 19). Asterisks indicate values that were linearly interpolated between adjacent strata.

4. Discussion

4.1. Distribution and abundance

C. helgolandicus abundance and geographical distribution in the North Atlantic have been previously found to be strongly related to temperature. Indeed, Beaugrand, Reid, Ibanez, Lindley, and Edwards (2002) have shown that in the North Sea during the last 50 years, species associated with warm waters such as *C. helgolandicus* have shifted north by 10° of latitude. These results correlate with the North Atlantic Oscillation index and with the increase in Northern Hemisphere Temperatures. Our Fig. 6 shows a dramatic increase of *C. helgolandicus* in waters off Stonehaven since 2000, and a slight increase in the *C. helgolandicus* abundance peak off Helgoland during the last 20 years. However, results at the Dove station do not show any trend. At the other stations, no clear long-term trends can be observed regarding adult abundance. However, off Mallorca, the low abundance peaks of *C. helgolandicus* seem to have become even smaller since 1997. The increase in abundance off Stonehaven, CPR boxes B1 and B2 and no general increase anywhere else conforms to the expectation that, with warming, abundances increase on the range edge (opening up new environments) but do not markedly change abundances in the centre of a species range. This may be because regulatory mechanisms are already controlling the species in a familiar environment.

In the North Atlantic and the North Sea, the geographical distribution of *C. helgolandicus* has been well described from the Continuous Plankton Recorder survey (Barnard et al., 2004; Colebrook, 1972;

Edinburgh Oceanographic Laboratory, 1973; Lindley & Reid, 2002). Furthermore, the variability in abundance of *C. helgolandicus* in the CPR survey has been analysed and discussed in detail in a number of publications (Colebrook, 1982; Fromentin & Planque, 1996; Matthews, 1969; Rees, 1957; Williams et al., 1994). In the eastern north Atlantic, *C. helgolandicus* is most abundant in European Shelf waters and in oceanic waters to the south-west of the British Isles. Planque and Fromentin (1996) and Fromentin and Planque (1996) have shown that the long-term variations in abundance of *C. helgolandicus* in the area between Iceland and the southern Bay of Biscay, including the North Sea, are positively correlated with temperature in the previous year. The distribution of *C. helgolandicus* extends along the Norwegian coast, a number of fjord populations having been identified using molecular probes (Lindeque, Harris, Jones, & Smerdon, 1999, 2004).

Calanus species are associated with the North Atlantic Oscillation (NAO) index in the North Atlantic and in the Irish Sea (Fromentin & Planque, 1996; Nash & Geffen, 2004). High densities of *C. finmarchicus* coincided with negative NAO index values and high densities of *C. helgolandicus* with positive NAO index values. Fromentin and Planque (1996) suggested a one-year lag before the NAO influences *C. helgolandicus* abundance, although this is not notable in the Irish Sea (Nash & Geffen, 2004). The link between the NAO index and *Calanus* abundance is complex and involves the recent past as well as current environmental conditions and population dynamics (overwintering populations, advection and water inflows). This strong relationship has broken down since 1996 (Planque & Reid, 1998), illustrating the complex nature of interactions between the environment and copepods. This change in the environmental control may be because of the marked change in distribution of *C. finmarchicus* over the last decade in response to climate warming. Williams and Conway (1984) highlighted the variability of the average abundance and the timing of the seasonal maximum of *C. helgolandicus* in the Celtic Sea. The most likely causes of this variability are probably small-scale thermal distribution, stratification of the water column, and food type and quality, and, therefore, are unlikely to be correlated with broad-scale sea surface temperature patterns (Nash & Geffen, 2004). Predation can also be important in regulating *Calanus* population dynamics (Greve, 2003).

Off La Coruña, in the southern Bay of Biscay, *C. helgolandicus* is the sixth most numerically abundant copepod species, representing 4% of the total relative abundance of copepods (Valdés, Álvarez-Osorio, Lavín, Varela, & Carballo, 1991). On the Galician continental shelf, Valdés, Álvarez-Osorio, and Varela (1990) observed that *C. helgolandicus* contributes 6% of the copepod abundance in summer (June), but less than 2% in autumn (September). In October and in November, *C. helgolandicus* is found in the Bay of Biscay at depths ranging from 100 to 1100 m, while during spring and because of ontogenic migration, *C. helgolandicus* appears in the surface layer, which advects animals to the north east.

In the Mediterranean Sea, there is no regular CPR coverage and data are mainly available from cruises or fixed monitoring stations. The zooplankton of the north-western Mediterranean and Adriatic Sea has been studied more intensively than that from the eastern basin and southern coasts (Champalbert, 1996; Gaudy, 1985; Hure & Krsinic, 1998). While *C. helgolandicus* is common in the neritic zone of the Atlantic Ocean and adjacent seas it appears in Mediterranean shelf waters only during winter or occasionally during the rest of the year associated with upwelling. Its abundance in the Western Mediterranean is generally low, except off Marseille where two generations develop (Gaudy, 1972) and in the vicinity of the Ligurian Sea (Boucher, 1984). The rest of the year this species inhabits deep waters between 500 and 1000 m in the Ligurian basin (Gasser, Payet, Sardou, & Nival, 1998), and up to 1000–1500 m in the Naples region (Hure & Scotto di Carlo, 1968). In the western Mediterranean Basin, *C. helgolandicus* tends to dominate along the northern shelf and slope regions (Gaudy, 1985). In the Eastern Mediterranean, *C. helgolandicus* is abundant in the Adriatic Sea (Hure & Scotto di Carlo, 1968; Vućetić, 1965a, 1965b) and present also seasonally in relatively small numbers in the Aegean Sea (Moraitou-Apostolopoulou, 1985). As *C. helgolandicus* is recognised as a temperate, pseudo-oceanic species

(a member of this assemblage indicator group; Beaugrand et al., 2002), we expected lower abundances in the eastern part of the Mediterranean. On the southern coast of the western basin, high concentrations of *C. helgolandicus* have been observed at two stations (the Bizerta Canal and the Bizerta lagoon) off Tunisia at certain times of year. Maximum abundance occurs in December at both stations. In the Bizerta Canal, *C. helgolandicus* abundance peaks at ∼240 ind m^{-3}, whereas in the lagoon the maximum abundance observed is ∼155 ind m^{-3}. Large variations in temperature (range of 15 °C in the canal) and salinity (change of 2.6 psu) occur during the year at both sites, highlighting the tolerance of *C. helgolandicus* to variations in temperature and salinity. It is worth noting that high densities of this species off Tunisia could be associated with Atlantic inputs via the Algerian Current, namely as the flow of Modified Atlantic Water (MAW; Puillat, Taupier-Letage, & Millot, 2002). The Algerian Current generates mesoscale meanders and eddies and may indeed reach the Sicilo-Tunisian Channel. Such transport could explain high abundances of *C. helgolandicus* observed in the non-optimal environments (i.e., high temperatures and salinities) of the Canal and Lagoon.

C. helgolandicus has also been reported from as far east as Lebanese shelf waters (Lakkis, 1976), but appears to be absent throughout most of the central and southern half of the Eastern Mediterranean (Dowidar & El-Maghraby, 1970; Furnestin, 1979; Halim, 1976; Pasteur, Berdugo, & Kimor, 1976). The Eastern Mediterranean Transient (EMT), which is an intensified circulation between the Aegean and Levantine Seas and a reduced flux between the latter and the Ionian Sea (Malanotte-Rizzoli et al., 1999), allows specimens of *C. helgolandicus* to be imported from the Cretan Sea into the Levantine Sea. This was observed in January 1998 as increasing abundances at 400–450 m in the area of the Ierapetra Deep (Fig. 18). According to water mass analyses (Begler, Karsten, Süling, & Lappe, 1999), the increase was below the Levantine Intermediate Water (LIW) and associated with Eastern Mediterranean Deep Water, which is produced by mixing of LIW with cold, saline deep water originating from the Cretan and Adriatic Seas, the core of which was at 1000 m. In the Cretan Sea, the population was mainly below 350–400 m in the Cretan Deep Water, which underlies the LIW that flows in from the Levantine Sea. Apart from lateral transport, results from June 1993 suggest that the population in the Levantine Sea was sustained by local reproduction during the course of upwelling south of Crete and south west of Cyprus (Weikert et al., 2001; Weikert, unpublished results). Regular, seasonal reproduction of *C. helgolandicus* in the Levantine Sea remains uncertain.

Jaschnov (1960,1961,1962,1963; in Vućetić, 1965a) considers *C. helgolandicus* to be characteristic of the Lusitanian fauna and uses it as an indicator of Mediterranean waters. Vućetić (1965a) presents maps of *C. helgolandicus* seasonal distribution in the Adriatic (Fig. 22). The population is located in the central and northern parts of the Adriatic Basin from March to September (with high abundances in spring), while the winter population is found in the south of the basin where the topography is much deeper. This is probably explained by an over-wintering migration into deeper waters. The location of the Trieste station in the north of the Adriatic, where there are shallow waters and strong anthropogenic influences may explain the low abundances of *C. helgolandicus* observed there in our study.

4.2. Seasonal cycle

Peaks of seasonal abundance of *C. helgolandicus* occurred at different times of the year in the (a) North Sea, (b) English Channel/northern Bay of Biscay/Vigo and (c) South Bay of Biscay/Mediterranean and Adriatic Sea (Figs. 5 and 6). Several authors (Halsband, 2001; Halsband-Lenk et al., 2002; Halsband-Lenk et al., 2004; Molinero, 2003), when studying the distribution of *Centropages typicus*, also noticed different annual cycles in several areas (Mediterranean Sea, North Sea, Gulf of Maine). They suggested two possible reasons for this shift in the timing of maximum abundance: (i) a low predation pressure on the dominant species at high latitudes and/or (ii) an optimal temperature favouring fecundity and hatching. Although we
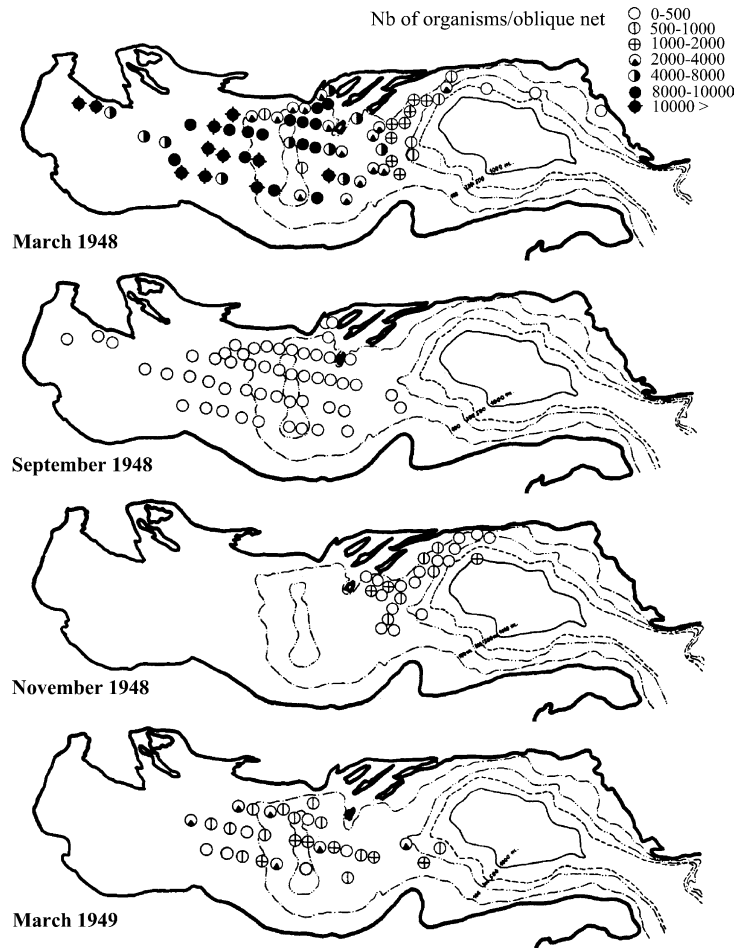
Fig. 22. Seasonal variations of *C. helgolandicus* abundance in the Adriatic (From Fig. 1, Vućetić, 1965a). Data represent the total number of organisms collected in an oblique ring-trawl net (53 m to surface) during a 30 min tow.

do not have data available to test the first hypothesis, the second hypothesis is consistent with our results that show a strong correlation between *C. helgolandicus* seasonal abundance and temperature in three distinct geographic areas (Figs. 9 and 10(a)). This hypothesis is supported by the fact that peak *C. helgolandicus* adult abundance occurs earlier in the year for southern stations than for northern stations (Fig. 5). This timing of abundance peaks is likely to be due to temperature rather than food quality or quantity. Indeed, it is unlikely that a phytoplankton bloom will occur in January in waters off Mallorca.

4.3. Temperature

Several workers have examined how the temperature range of a species relates to it's demographic and physiological characteristics. One approach has been the comparison of the optimal temperature at which species centre and are most abundant with the biological zero of development (i.e., the temperature at which development ceases). Biological zero for a species development is determined using the Bělehrádek equation, $D = a(T - \alpha)^b$, where D is the development time (this time can be egg hatch, egg to maturity or

stage-specific), *T* is temperature (°C) and *a*, *α* and *b* are constants. The value of *α* is the temperature at which development time is infinite (i.e., biological zero for the species). For *C. helgolandicus*, egg development has a biological zero between −4.9 °C (Corkett, 1972) and −10.9 °C (Corkett, McLaren, & Sevigny, 1986). McLaren, Corkett, and Zillioux (1969) found for ten species of copepod that egg development times had biological zeros that were on average 15–20 °C lower than the average environmental temperature where the species were found. Fig. 10(a) shows that abundance of *C. helgolandicus* is greater at around 15 °C, thus ∼20 °C greater than the expected biological zero for this species, and is similar in that regard to abundance in other copepods. Interestingly, *C. helgolandicus* continues to produce large numbers of eggs at temperatures cooler than 15 °C, and indeed the peak egg production rate is also at a cooler temperature than the peak in numbers (see Fig. 10(a) and (c)). Although eggs are readily produced at cooler temperatures, these take longer to develop through every stage, so that if mortality does not decline with cooler temperatures as much as development slows, then the population abundance will be reduced. A copepod that develops at a faster rate than *C. helgolandicus* at cooler temperatures, but has a similar egg production rate, will have the ability to withstand higher natural mortality rates. *C. finmarchicus* has development times suited to a colder environment, and at temperatures below 10 °C has faster development rates than *C. helgolandicus* (Corkett et al., 1986), so its numerical abundance also increases. It is clear that *C. helgolandicus* is broadly confined by temperature in its geographic range. Its abundance falls off rapidly above and below the temperature of maximum abundance, 15 °C. The upper temperature limits controlling a species success may relate to physiological inhibition. There are insufficient data on *C. helgolandicus* development or growth rates to describe this upper range limitation well.

We have suggested that one way temperature controls the distribution of a species results from its impacts upon development rate. Of course there are many other and more complex interactions, but nonetheless there is a strong link between temperature and distribution. If distributional range and peak abundance are strongly linked to temperature, then as regions warm and cool we may expect dramatic changes in abundance and dominance of different copepods (Richardson & Schoeman, 2004) and this would apply to the distribution of *C. helgolandicus* in European waters.

4.4. Influence of the physical environment

Hydrography (e.g., water column stratification, upwelling, fronts) is likely to have a substantial influence on zooplankton distribution, life strategy and thus population dynamics (Boucher, 1984; Longhurst, 1967; Peterson, Miller, & Hutchinson, 1979). Abundances at Vigo are more similar to those observed at L4 than to those at closer stations such as Gijón or Santander. This was previously observed by Stöhr, Schulz, and John (1996) when comparing the population structure and reproduction of *C. helgolandicus* along the Iberian and Moroccan slope with the results of Green, Harris, and Duncan (1993) obtained in the English Channel on the population fluctuations of *C. helgolandicus*. We suggest that the hydrodynamics observed at these stations could explain these differences in seasonal abundance compared with the other Spanish stations. Indeed, off Vigo, from March to September, the eastern North Atlantic Central Water is upwelled from deep water layers. This results in cool sea-surface temperature during the summer and provides productive waters to sustain development and reproduction. Ceballos, Cabal, and Álvarez-Marqués (2004) showed that *C. helgolandicus* can take full advantage of high phytoplankton availability induced by the summer upwelling events off the Galician coast, responding with high reproductive activity. These authors found highest egg production rates at coastal stations due to the ascent of cold nutrient-rich upwelled waters that enhanced phytoplankton productivity (Ceballos et al., 2004). However, Chl*a* concentrations at Vigo, E2 and Santander seem to be of the same order of magnitude (Fig. 8), while egg production rates are lower. This discrepancy probably reflects a limitation of our work, because we had to rely on the CPR phytoplankton colour index to estimate Chl*a* concentration. Estimates were made for the whole F4 CPR box area, masking the coastal productivity due to the upwelling off Vigo.

Valdés and Moral (1998) found that zooplankton abundance off Santander shows a slight, long-term decreasing trend, which contrasts with the upward trend of the water column stratification index (Lavíin et al., 1998; see Fig. 6(a)). They suggested that the duration of water column stratification is very important, as it can limit the input of nutrients from deeper to surface waters and consequently retard phytoplankton and zooplankton growth. A similar hypothesised relationship between an increasing trend in water column stratification and a decline in zooplankton biomass has been suggested by (Roemmich & McGowan, 1995) off the Californian coast (CALCOFI series) and in the north east Atlantic (Richardson & Schoeman, 2004).

Ibañez (unpublished data) and Molinero (2003) both studied the distribution of *C. helgolandicus* in the Ligurian Front during the spring bloom in May 1985 and April 2001, respectively, (Figs. 23 and 24). Late developmental stages (CV–CVI) seem to be located mainly in the central and coastal area (Fig. 23(b)), while in May 1985 there were high densities within the frontal zone (Fig. 24(c)). These results agree with previous observations of Boucher (1984) in the same area in March 1980. He showed that CIV and CV were responsible for the increasing abundance in the frontal zone, and that their numbers decrease in the peripheral zone. In contrast, adults have a lower abundance and do not show such an increase, but have a more or less uniform distribution in the area. He suggested that copepodites appear in the Ligurian Front at a specific period of their life cycle corresponding to a phase in their ontogenic migration. The localisation of juveniles in the upper layer during periods of high primary production (upwelling, spring blooms and coastal fronts) is favourable to the development of the species (e.g., Verheye & Field, 1992).

4.5. Feeding

A large number of studies on the feeding ecology of *Calanus* have been made during the last half century, and the main results are presented in the review by Harris (1996, & references therein). Copepods can discriminate different foods on the basis of particle size and nutritional quality. In laboratory experiments, both *C. finmarchicus* and *C. helgolandicus* showed no selectivity due to the intrinsic nutritional quality of the cells (measured by either lipid composition or C:N ratio) (Meyer, Irigoien, Graeve, Head, & Harris, 2002). Factors other than size that govern selective feeding from natural particulate
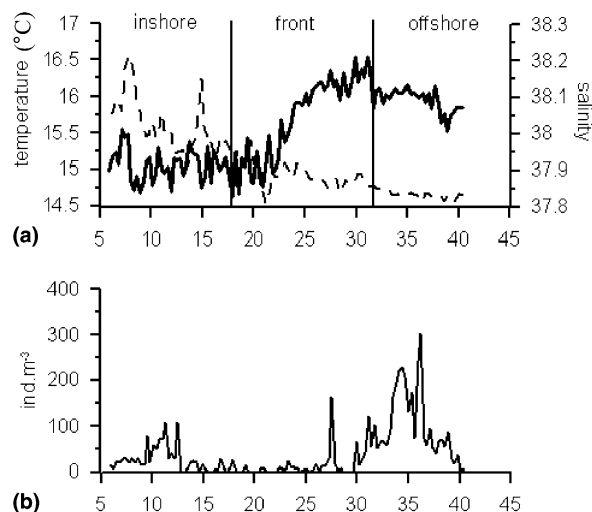
Fig. 23. Surface distribution of *C. helgolandicus* during the spring bloom (12th April 2001) in the Ligurian front. (a) Salinity and temperature within the frontal zone. (b) CV and CVI *C. helgolandicus* distribution (ind m^{-3}).
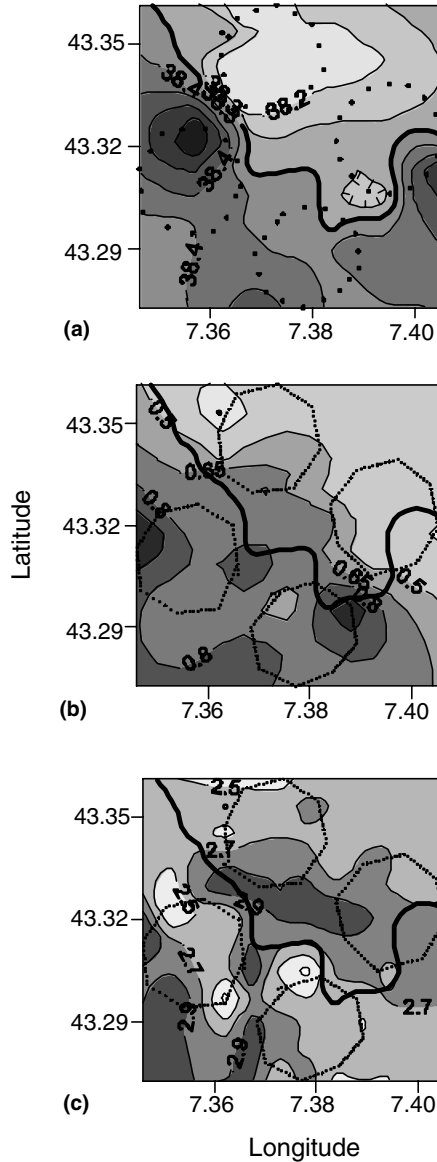
Fig. 24. Spatial distribution of *C. helgolandicus* within the frontal zone in the Ligurian Sea during the spring bloom (May 1985). (a) Salinity. (b) Chlorophyll (mg m^{-3}). (c) *C. helgolandicus* abundance (log(ind m^{-3})).

assemblages are still doubtful. Irigoien et al. (2000) found that *C. helgolandicus* showed little selective feeding behaviour with only a slight preference for diatoms during a one-year study in the English Channel. In contrast, Meyer-Harms, Irigoien, Head, and Harris (1999) found that *C. finmarchicus* in the Norwegian Sea had non-saturated but clearly selective feeding behaviour, with a significant number of cyanobacteria ingested in the field. These cells can be considered too small to be actively eaten, and if excluded from the analysis, the results suggest non-selective feeding (Irigoien et al., 2000; Irigoien personal communication).

As Harris (1996) pointed out, most of the research on *Calanus* feeding has been carried out on later developmental stages (mainly adult females) and the biology of nauplii, in comparison, has been poorly studied. Nauplius stage III is generally considered as the first-feeding stage in *Calanus*. One of the main assumptions in copepod feeding ecology has been that nauplii and adult development stages have different optimal ranges of particle size ingested (Harris, 1996; Richardson & Verheye, 1999). The optimal size of food particles has been estimated to be 2–5% of the prosome length (Berggreen, Hansen, & Kiørboe, 1988). Naupliar stages of *C. helgolandicus* have been reared with low mortality on *Isochrysis galbana* (∼5 μm) (Green, Harris, & Duncan, 1991; Irigoien et al., 2000; Thompson, 1982) and Green, Harris, and Duncan (1992) presented evidence that *C. helgolandicus* nauplii could also derive significant nutrition from small faecal pellets produced by the nauplii of *Pseudocalanus elongatus*. However, Meyer et al. (2002) showed that all *Calanus* developmental stages exhibit a similar selective behaviour, so that behaviour and ingestion rates of nauplii can be extrapolated reasonably well from those of the adults. This is supported by the recent study of Irigoien et al. (2003) on *C. finmarchicus* in the Irminger Sea. They show that *C. finmarchicus* nauplii IV–VI had highest feeding efficiencies on large cells (e.g., diatoms and ciliates), whereas small flagellates were ingested at very low rates. Dietary requirements should be taken into account to explain distribution and abundance of *C. helgolandicus*.

4.6. Reproduction, development and recruitment

The reproductive period of *C. helgolandicus* differs between areas (shown in Fig. 14). Egg production by most calanoid copepods is related at least partially to Chl*a* (Bautista, Harris, Rodriguez, & Guerrero, 1994; Bunker & Hirst, 2004; Williams & Lindley, 1980a, 1980b). Egg production of *C. helgolandicus* is correlated with Chl*a* off Roscoff and Plymouth. The GLM shows that seasonality, Chl*a* and latitude all affect egg production (Fig. 15). Our results are confirmed by Bautista et al. (1994), who found a similar correlation between Chl*a* and egg production for *C. helgolandicus* and three other co-occurring copepod species off Plymouth. In addition, Laabir et al. (1998) showed that *C. helgolandicus* egg production in the English Channel varies seasonally and correlates with Chl *a*, but not with surface temperature. However, in their study for the stations off Plymouth and Roscoff, the increase in *C. helgolandicus* reproduction during spring and summer coincided with a temperature increase from 9 to 15 °C, after which spawning declined during late summer and autumn. These authors found that the seasonal pattern of fecundity differed between the two sites. Off Plymouth, spawning occurred earlier, lasted longer and egg production was significantly higher than in waters off Roscoff. From their results, food quality, as well as quantity, appeared to be important for reproductive success.

Several factors contribute in explaining egg production. For example, Rey-Rassat et al. (2004) observed very low egg production for *C. helgolandicus* at L4 off Plymouth on some dates when both temperature and Chl*a* were high. On these dates, the number of unfertilised females was higher than that of fertilised females, which means that females were newly moulted, not yet fertilised or not yet matured. (Marshall & Orr, 1955) indicated that female fertilisation is a relatively rapid process whose speed varies according to the sex ratio. For a particularly low male to female ratio, fertilisation may take longer. In addition, energy for gonad development in newly moulted females has to come from an increased ingestion rate as the animals mature after reduced rates during moulting, before eggs are produced (Marshall & Orr, 1955; Rey, Carlotti, Tande, & Hygum, 1999; Runge, 1985). The role of lipids in the reproduction of *C. helgolandicus* should also be considered. Rey-Rassat, Irigoien, Harris, Head, and Carlotti (2002a, 2002b) showed that a buffer of lipids is necessary for egg production, and that both current and past feeding history should be taken into account.

Reports of the variation of hatching success in both time and space are scarce in the literature (Ianora, Mazzocchi, & Grottoli, 1992; Ianora & Poulet, 1993; Laabir et al., 1998; Turner, Ianora, Esposito, Carotenuto, & Miralto, 2002). Furthermore, causes of varying egg mortality and viability remain

uncertain. They have been attributed to predation (Liang, Uye, & Onbé, 1994), disease (Peterson & Kimmerer, 1994), food limitation (Guisande & Harris, 1995; Jónasdóttir, 1994), the absence of certain fatty acids essential for egg development (Jónasdóttir & Kiørboe, 1996; Kleppel & Burkhart, 1995; Turner et al., 2002), the low organic content of the eggs (Guisande & Harris, 1995), and the presence of possible inhibitory compounds in the food blocking egg development (Ban et al., 1997; Ianora, Poulet, & Miralto, 1995; Poulet, Ianora, Miralto, & Meijer, 1994; Miralto et al., 1999). Surprisingly our GLM model shows a positive correlation between hatching success and temperature (Fig. 16). Temperature may be a proxy for another factor that may affect hatching success (e.g., phytoplankton community composition or size), but unfortunately none of the factors previously cited and likely to affect hatching success were monitored in parallel with hatching success. A weak negative relationship between hatching success and egg production is also observed (Fig. 16). To our knowledge such a relationship has not been described previously, but it could be because the average egg size may be smaller when more eggs are laid in a clutch, affecting egg viability and reducing hatching success. Another hypothesis is that at low latitudes, small females produce smaller eggs but the similar numbers to the bigger ones at high latitudes. The small eggs will hatch earlier at low latitude and so may not need reserves. In this case, hatching success will be more dependent on qualitative rather than quantitative nutrition of females.

Indeed, copepod body size has been shown to be related to temperature, food quality and quantity (Mauchline, 1998 and references therein). Size is also an important morphological parameter affecting reproduction (Mauchline, 1998). Numbers of eggs in an egg mass or clutch vary seasonally and partially correspond to seasonal changes in body size of adult females (Mauchline, 1998).

Several authors have noticed a difference in size of individuals of the same species living in different areas (Fleminger & Hulsemann, 1977, 1987; Halsband-Lenk et al., 2004; Le Ruyet-Person et al., 1975). The variation in the length of *C. helgolandicus* is generally low in the Mediterranean Sea (Boucher, 1984; Gaudy, 1972). However, length can be quite variable on a larger geographical scale (Fig. 25). Fleminger and Hulsemann (1987) showed that *C. helgolandicus* female prosome length ranges between 2.05 and 2.36 mm in seven different geographic areas. In their study, the largest females were found in the English Channel and in the Bay of Biscay, while smallest individuals were observed in the Aegean Sea. In European waters, the size of the female prosome length varies between 1.94 and 2.6 mm (Fig. 25).

In our study, egg production tends to increase with latitude (Fig. 15), and our GLM model shows that egg production is also partly explained by Chl*a* concentration and seasonality. *C. helgolandicus* size is also affected by latitude and seasonality (see Fig. 25; Fleminger & Hulsemann, 1987; Pond, Harris, Head, & Harbour, 1996), and, therefore, it is likely to have an effect on egg production. Larger females, at high latitudes, would have higher egg production rates.

If prosome length and temperature are correlated, this will be a result of the fact that as temperature increases development time decreases and growth increases. However, development time decreases proportionally faster than growth increases, hence at warmer temperatures animals reach adulthood (or any other fixed stage) at a smaller size.

Several studies have investigated the influence of temperature (Diel & Breteler, 1986; Thompson, 1982) and of food quantity and quality (Rey, Harris, Irigoien, Head, & Carlotti, 2001; Rey-Rassat et al., 2002a, 2002b) on *C. helgolandicus* development rate. In her paper, Thompson (1982) specified that she did not differentiate *C. finmarchicus* from *C. helgolandicus*. Despite her comment "it is probable that the samples of live plankton which were obtained mainly from an area offshore from Flamborough Head contained both species", Corkett et al. (1986) suggested that Thompson used *C. helgolandicus*, and her work has been used since as a reference for *C. helgolandicus* development time (Kiørboe & Sabatini, 1995). To our knowledge, the only other dataset on *C. helgolandicus* development time in relation to temperature (5 and 10 °C only) is the study of Diel and Breteler (1986). A summary of the studies on *C. helgolandicus* development time available in the literature is presented in Fig. 26.
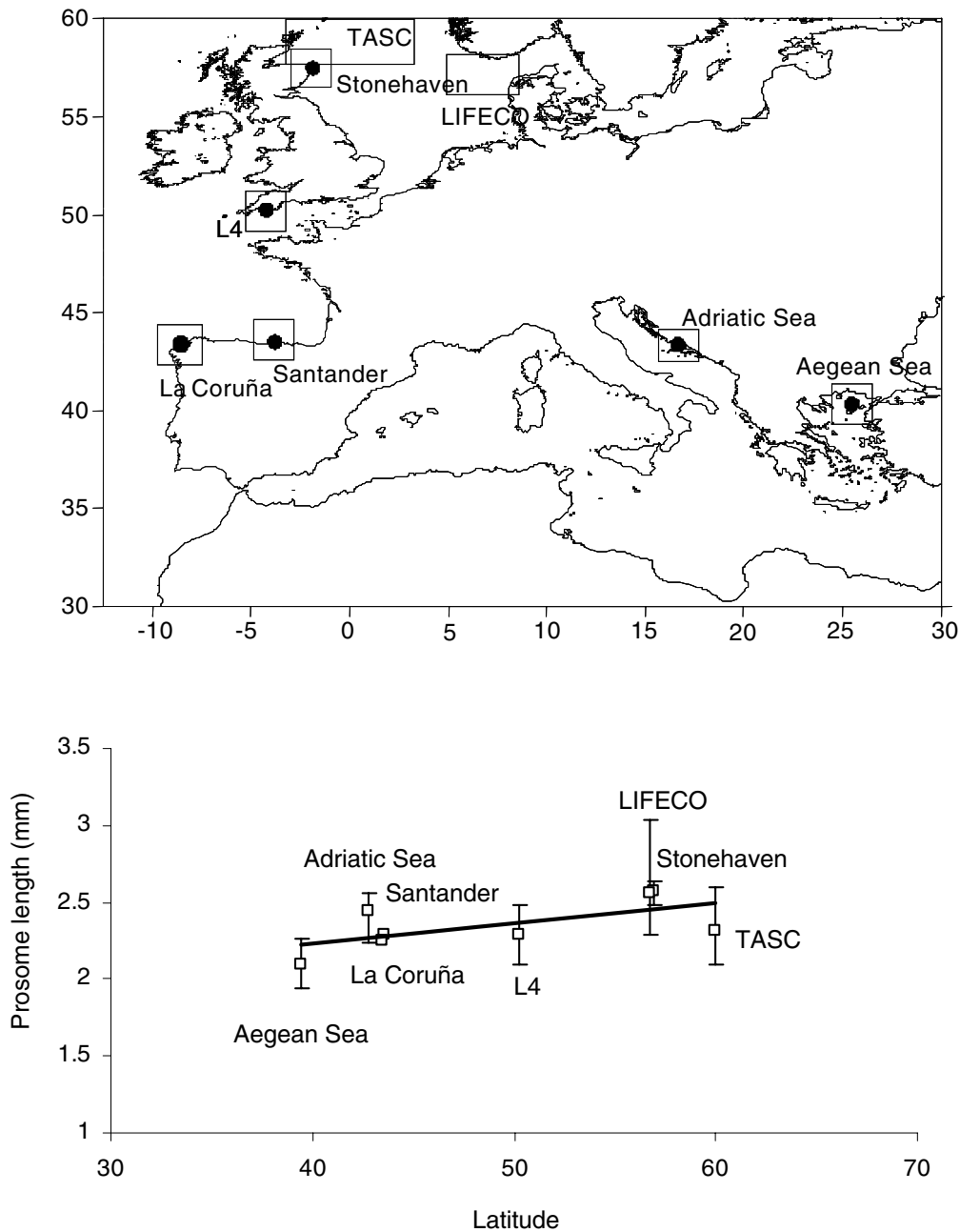
Fig. 25. Diagram of prosome length of *C. helgolandicus* females at various latitudes. The square represents the mean value and the vertical line the range of values.

Shreeve, Ward, and Murray (1998) estimated the mean times for copepodites to moult from stages CII to CV. In their study, development times were all within ±1.5 days of those reported by Thompson (1982).
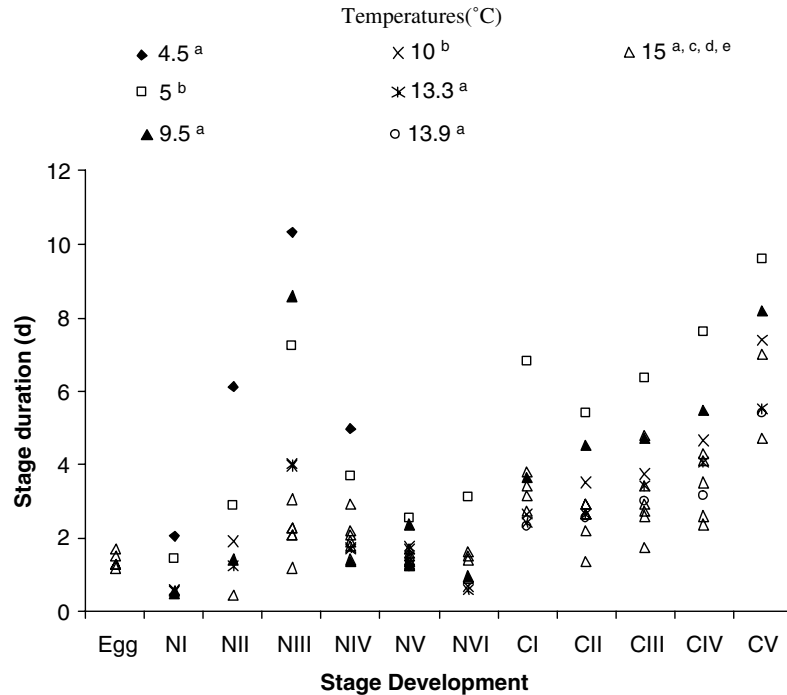
Fig. 26. Literature review of *C. helgolandicus* stage duration in relation to temperature. [a]Thompson (1982); [b]Diel and Breteler (1986); [c]Rey-Rassat et al. (2002a, 2002b); [d]Rey et al. (2001); [e]Shreeve et al. (1998).

The duration of the developmental stages is an important determinant of mortality. The longer their development time, the more likely they are to be preyed upon. Early development stages are unable to migrate vertically and remain at the surface. Eiane and Ohman (2004) suggested that vertical migration of late developmental stages of *C. finmarchicus* may help to reduce mortality risk. Later stages are less heavily preyed upon because they migrate vertically, but also because they are more able to escape. Titelman and Kiørboe (2003) showed differences in behaviour and ability to detect or escape a predator among different development stages of *C. helgolandicus*. Early stage nauplii are better than later stages at detecting fluid signals, while later stages escape at higher speeds (Titelman & Kiørboe, 2003).

At Helgoland Roads, Greve (2003) showed that the annual dynamics of *C. helgolandicus* changed in the 1990s compared to the 1980s due to the change in annual dynamics of *Pleurobrachia pileus*, a voracious predator. *Pleurobrachia pileus* and *C. helgolandicus* prey on each other at appropriate developmental sizes and thereby determine the dominance within the ecosystem (Greve, 1995). They are mutually exclusive, and lower abundances of *P. pileus* enable the earlier growth of *C. helgolandicus*.

During periods of high population densities, cannibalism on eggs and on early nauplii may contribute substantially to mortality rates and thus be important for structuring *Calanus* populations (Bonnet, Titelman, & Harris, 2004). In the field, cannibalism is more likely to act on eggs and early stages (Ohman & Hirche, 2001). In contrast, when adult *Calanus* are present at low abundance, other predators are likely to be responsible for mortality (Ohman & Hirche, 2001; Ohman, Runge, Durbin, Field, & Niehoff, 2002). Irigoien, Conway, and Harris (2004) have recently shown that *Calanus* displays flexible diel vertical migration behaviour depending on its development stage, but also on the position of predators in the water column, rather than predator abundance.

Colebrook (1985) suggested that long-term trends in *Calanus* populations could result from winter mortality. The scarce data available in the literature (Longhurst & Williams, 1992; Østvedt, 1955) generally suggest a winter survival of ~10–30%. Bagøien, Kaartvedt, and Øverås (2000) also suggested that predation is important for *Calanus* winter mortality. However, their study showed that the rate of decrease of the *C. finmarchicus* and *C. helgolandicus* assemblage was only ~0.1–0.3% per day, considerably lower than expected considering the high krill abundance, their predation potential on *Calanus*, and the data on krill stomach contents. In other locales, the *Calanus* overwintering mortality rate is generally > 0.7% per day (Bagøien, 1999; Østvedt, 1955). Bagøien et al. (2000) suggest a potentially continuous advective sy of *Calanus* to the overwintering populations in Oslofjorden. However, the advective supply of *Calanus* to overwintering populations is only of importance to non-closed populations such as in shallower fjords. A subsequent investigation by Bagøien, Kaartvedt, Aksnes, and Eiane (2001) estimated mortality in "closed" populations such as in Sognefjorden. The fjords were characterised by different densities of potential predators, and thus mortality rates were variable between fjords, ranging from 0.008 to 0.027 per day.

Irigoien and Harris (2003), based on a 10-year time-series of *C. helgolandicus* reproduction and abundance at station L4 in the English Channel, investigated the factors responsible for interannual variability in population dynamics. In particular they considered transport, predation, temperature and the possible deleterious effect of diatoms on hatching success. The conclusion was that advection and mortality are the most important factors at L4 and that a single mechanism does not control abundance, but different mechanisms may play major roles during different periods.

4.7. Diapause and vertical distribution

The overwintering phase, which is crucial in the life cycle of *Calanus* due to its consequences for population recruitment, is poorly understood. Information on ecophysiology of *C. helgolandicus* resting copepodites in deep layers during overwintering remains rather limited, but information on the better-studied diapause stage of *C. finmarchicus* could certainly apply to its congener. The ecophysiology of *C. finmarchicus* overwintering has been widely studied (see review by Hirche, 1996). It is well recognized that CV of this species undergoes true diapause at depth, showing arrested development, reduced metabolism, low digestive enzyme activity and torpidity. Nevertheless, there are several questions still open to debate, such as the cues that trigger the onset of diapause and emergence, and the role of lipid storage during overwintering (e.g., Campbell, 2004; Fiksen, Varpe, & Kaartvedt, 2004; Irigoien, 2004). *C. helgolandicus* accumulates lipids, particularly wax esters that enable it to survive periods of poor feeding or starvation (Gatten, Corner, Kilvington, & Sargent, 1979). These are used as an energy source as they diapause in cold deep water, usually as CV stage (Hirche, 1983, 1984; Stöhr et al., 1996; Williams & Conway, 1988), helping the population to withstand periods of low food abundance. In the North Sea, the *C. helgolandicus* population is able to recover from low abundance (due to the combination of cool temperature, late phytoplankton bloom and short reproductive period), and to return to normal population levels by using its lipid reserves, despite low phytoplankton abundance in winter (Lindley & Reid, 2002).

The existence of two populations vertically separated in the water column has been reported for both *C. finmarchicus* and *C. helgolandicus* by Nicholls (1933), and Marshall, Nicholls, and Orr (1934) for the Clyde Sea, by Østvedt (1955) and Krause (1978) for the southern Norwegian Sea, and by Hirche (1983) for Swedish and Norwegian fjords. In the surface layer, copepods are smaller and more active, whereas the deep population is torpid, with large oil sacs and empty guts (Hirche, 1983). Only the deep population is diapausing. At temperate latitudes such as the Celtic Sea, Bay of Biscay or Mediterranean Basin, *C. helgolandicus* also undertakes seasonal descents to deep waters. Williams and Conway (1988) found overwintering CV of *C. helgolandicus* below 400 m to the southwest of the British Isles, whereas in spring all stages occurred mainly in the upper 200 m. Farther south, along the Iberian and Moroccan slope, Stöhr et al. (1996) also remarked that the preferred depth of the *C. helgolandicus* population (CV and adults) in autumn and winter

was 400–600 m south of the Mediterranean outflow water, and 400–800 m north of it. In addition, Andersen, Gubanova, Nival, and Ruellet (2001) observed a deepening of the *C. helgolandicus* population between the beginning of May and the beginning of June 1995 in the open northwest Mediterranean. As the population consists essentially of copepodites CV (about 96%), these authors suggest that this deepening could correspond to the seasonal downward migration of overwintering stages. Generally, the timing of seasonal migrations seems to have been less studied for *C. helgolandicus* than for *C. finmarchicus* (Bagøien et al., 2000).

The preferred over-wintering depth of *C. helgolandicus* populations remains unclear. What evidence there is, generally points to populations at mid-depth, ranging from 400 to 800 m (Stöhr et al., 1996; Williams & Conway, 1988). This depth range is shallower than that for over-wintering *C. finmarchicus*, and there remains the possibility that the over-wintering strategies of the two species differ. However, in contrast to relatively shallow over wintering along the Atlantic margin, the occurrence of high abundances of *C. helgolandicus* at depths > 2000 m in the Mediterranean (Fig. 17) is similar to *C. finmarchicus.* In fact the occurrence of *C. helgolandicus* as deep as 4200 m is significantly deeper than that for the congeneric species in the North Atlantic (Heath et al., 2004).

Understanding the over-wintering strategies of *C. helgolandicus* populations in nearshore waters needs further work. We estimated the distance between the time-series stations and the closest 500 and 1000 m isobaths (Fig. 27). In the southern Bay of Biscay or around the Balearic Islands, the continental shelf is narrow and the 500 and 1000 m isobaths are <100 km from shore. For the stations in the North of the Adriatic, the North Sea and the English Channel, *C. helgolandicus* would have to be transported a distance of at least 300 km before encountering waters deep enough for diapausing at depth.

Williams and Conway (1982, 1984) showed that on the Celtic Sea shelf the overwintering stock in shallow waters consists of adults and CV distributed homogeneously through the water column. These animals did not undergo a true diapause. They showed slow metabolic rates, but were still feeding and probably produced eggs. However, as has been noted previously, *C. helgolandicus* seems to diapause at a reduced depth over deep waters close to the Celtic shelf region. It would be interesting to investigate whether the over-wintering pattern of the Celtic Sea is similar to other off-shelf populations in order to obtain a more comprehensive view of its life cycle and of its population dynamics.
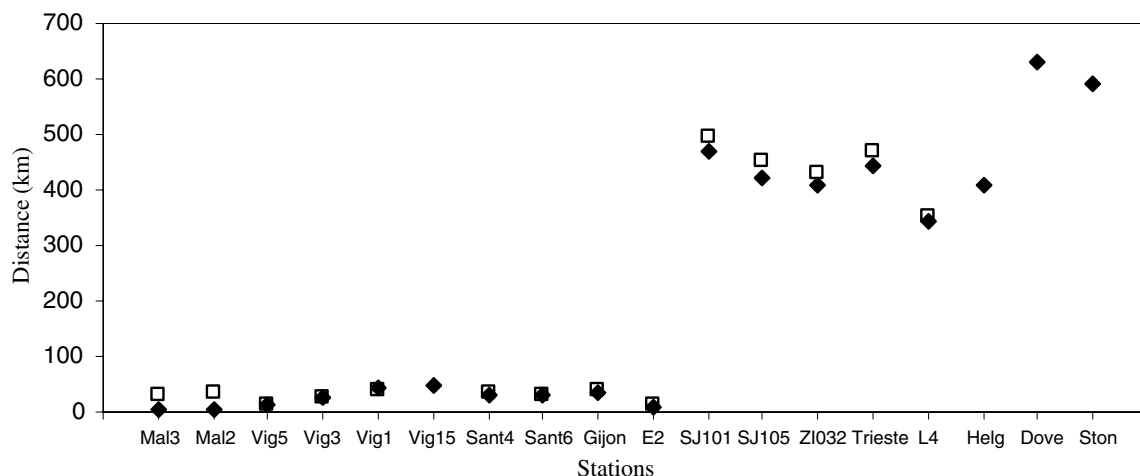

Fig. 27. Distance (km) between the sampling stations and the nearest 500 m (♦) and 1000 m (□) deep water.

4.8. Populations

Fleminger and Hulsemann (1987) carried out a geographic analysis of some morphometric characters across a wide range of *C. helgolandicus* populations (western North Atlantic, mid-North Atlantic, eastern North Atlantic-Europe, eastern North Atlantic Africa, western Mediterranean Sea, Adriatic Sea, Aegean Sea). The distinguishing morphometric character, i.e., the ratio of prosome to urosome length, indicated only one population in the entire Mediterranean Sea and Atlantic Ocean. However, significant differences in the frequency of supernumerary pores provided evidence of two populations of *C. helgolandicus* s.l., one encompassing the Atlantic and western Mediterranean and the second the eastern Mediterranean. The gene flow between the east and west Mediterranean populations maintains homogeneity in morphometry, with the intermediate frequency of supernumerary pores in the west Mediterranean population suggesting interbreeding with both the eastern Mediterranean and the Atlantic populations (Fleminger & Hulsemann, 1987).

The genetic structure of *C. finmarchicus* (i.e., genetic differences between geographic populations) has been analysed in several studies using a variety of molecular tools. At an ocean basin-scale, Bucklin, Sundt, and Dahle (1996) found significant differences between populations inhabiting the North West Atlantic and the Norwegian Sea. In the current system surrounding Iceland, across the boundary region between Atlantic and Arctic waters, Bucklin et al. (2000) reported genetic variation in *C. finmarchicus*, pointing to different areas of origin (NW Atlantic, Norwegian Sea, North Sea and Iceland waters) and likely a mixing among populations. However, no genetic difference between close populations has been detected when comparing *C. finmarchicus* from the Labrador Sea, the Gulf of St. Lawrence, the Gulf of Maine and Georges Bank (Bucklin & Kocher, 1996). To date, the work of Unal, Frost, Armbrust and Kideys (personal communication) has been the only study of the population structure of *C. helgolandicus* using genetic molecular analyses, but these authors compared only two true *C. helgolandicus* populations (Adriatic Sea and English Channel). They showed that English Channel and Adriatic Sea populations showed a distinct clustering in terms of halotype diversities. The knowledge of the genetic structure of *C. helgolandicus* over its entire range may help to understand whether the geographical and ecological divergences found in this study may be genetically supported, or whether they are local, ecophenotypic adaptations to the environment. The genetic structure of *C. helgolandicus* in European waters could be used to assess whether the source area of this species is located in the Mediterranean Sea as suggested by Conover (1988). Stöhr et al. (1996) and John, Mittelstaedt, and Schulz (1998) reported evidence for a transport of diapausing copepodites by undercurrents that could connect the Mediterranean and the Atlantic populations; these would then flow along the Iberian continental slope towards the inner Bay of Biscay and reach the south of the British Isles. A study of the genetic structure of *C. helgolandicus* along its range could be useful to evaluate the role of such transport in the dispersion of *C. helgolandicus* and in ensuring the gene flow between different geographic populations. *C. helgolandicus* has also been found off the eastern North American coast, and this population should be included in the genetic analysis. It would be informative to quantify the differences between western and eastern Atlantic populations, as well as the dispersal mechanism operating at this large scale.

4.9. Comparison with C. finmarchicus

C. helgolandicus and *C. finmarchicus* are closely related species. Table 2 presents a summary comparison of some characteristics of *C. helgolandicus* and *C. finmarchicus*. Their morphological similarity and overlapping geographical ranges have resulted in persistent identification problems. Particularly, immature stages of the North Atlantic species *C. helgolandicus*, *C. finmarchicus* and *C. glacialis* are difficult to distinguish on the basis of morphology. *C. helgolandicus* was formerly considered to be a southern form of *C. finmarchicus* (Rose, 1933). In 1901, Sars redescribed *C. finmarchicus* and distinguished it from *C. helgolandicus*. Among

Table 2
Comparison *of Calanus helgolandicus* and *Calanus finmarchicus*

	Calanus helgolandicus	*Calanus finmarchicus*
Latitudinal range	15–65°N[a,b]	30–80°N[a]
Temperature range (°C)	5–28[c]	0–16[d]
Diapause	Yes? everywhere?[c,e]	yes[e,f]
Female prosome size range (μm)	1.78–2.8[b,g]	1.95-3.28[h]
Development time: NI-adult (days)	26.2–41.7[i]	45.5–128[j,k]
Number of generations per year	3–5[l,m]	1–4[n,o]
Maximum egg production (egg female^{-1} d^{-1})	30-60[p]	40–70[q,r]
Spawning time	Midnight, midday[s]	12.00–16.00, dawn[t,u]
Feeding behavior	Size selective but non-selective for similar size[v,w]	Size selective but non-selective for similar size cells[w,x]

[a] Continuous Plankton Recorder Survey team (2004).
[b] Fleminger and Hulsemann (1987).
[c] This study.
[d] Mauchline (1991).
[e] Hirche (1983).
[f] Hirche (1996).
[g] Rose (1933).
[h] Frost (1974).
[i] Thompson (1982).
[j] Hansen et al. (2003).
[k] McLaren (1978).
[l] Green et al. (1993).
[m] Vućetić (1966).
[n] Tande (1982).
[o] Sameoto and Herman (1990).
[p] Laabir et al. (1998).
[q] Hirche (1989).
[r] Hirche (1990).
[s] Laabir et al. (1995).
[t] Marshall and Orr (1955).
[u] Runge (1987).
[v] Irigoien et al. (2000).
[w] Meyer et al. (2002).
[x] Meyer-Harms et al. (1999).

other characteristics, he found that *C. helgolandicus* differs from *C. finmarchicus* with a more pointed head, a slenderer body, and in the male a considerably longer exopod on the fifth foot. According to (Frost, 1974) and (Fleminger & Hulsemann, 1977), *C. helgolandicus* and *C. finmarchicus* can be separated morphologically only when they are in copepodite stages CV–CVI. The method is based on the shape of the fifth pair of swimming legs (P5) that have to be dissected and on the head-shape criteria also described by Jaschnov, 1957. The CPR programme started to distinguish between the two species in 1958 (Matthews, 1967; Rees, 1949). However, diagnostic morphological characteristics of *Calanus* species are restricted essentially to minor variations in their secondary sex characteristics, presenting a persistent problem in the identification of individuals to species level.

Discussion of the validity of these species has persisted until the 1990s when the application of molecular methods has enabled the systematics to be clarified (e.g., Bucklin, Frost, & Kocher, 1995) showing that *C. helgolandicus* groups with *C. pacificus* and *C. sinicus*, whereas the *C. finmarchicus* group includes *C. glacialis* and *C. marshallae*. Such techniques have also allowed unambiguous identification of both species at earlier developmental stages (Bucklin, Guarnieri, Hill, Bentley, & Kaartvedt, 1999; Hill, Allen, & Bucklin, 2001;

Lindeque et al., 1999). These methods are based on the sequencing of the 16S ribosomal RNA gene or on the DNA sequence of a 633 bp region of the mitochondrial cytochrome oxidase I (mtCOI).

The geographical distributions of *C. helgolandicus* and *C. finmarchicus* are generally distinct, though there is significant overlap in some regions (Table 2). From an analysis of CV and CVI animals collected in the subsurface layer, Planque and Fromentin (1996) estimated that the region of co-occurrence of *C. finmarchicus* and *C. helgolandicus* extended from 52°N to 57°N in the North Sea and Northeast Atlantic. However, Lindeque et al. (1999, 2004) showed in a molecular study that the area of overlap of these two species extends well north of 57°N.

In addition, under different surface temperature patterns 18,s000 years ago, the two species were extensively sympatric in the North Atlantic and at least in the western Mediterranean (Fleminger & Hulsemann, 1987). Moreover, they probably had overlapping breeding periods as well. Because the two species remained separate, mechanisms to prevent cross-breeding are presumed to have been favoured (Fleminger & Hulsemann, 1987).

The 14 °C isotherm in the North Atlantic Ocean marks the position of the southern distribution boundary of the major part of the oceanic *C. helgolandicus* population (Williams, 1985). From the CPR coverage, the *C. finmarchicus* thermal boundary seems to be around 11 °C (Fig. 13). However, 14 °C is also the approximate temperature which vertically separates the *C. finmarchicus* and *C. helgolandicus* populations in the Celtic Sea (Williams, 1985). Williams and Conway (1988) showed that *C. finmarchicus* migrates out of the mixed layer when the water temperature is warmer than 14 °C. In contrast, Irigoien et al. (2004) showed that in the Irish Sea there was no significant difference in diel vertical migration amplitude or vertical position between *C. finmarchicus* and *C. helgolandicus* even during stratification. In addition, in the western Irish Sea, Gowen, Dickey-Collas, and Cullough (1997) found that both species were distributed uniformly in the water column whatever the season (e.g., in stratified and non-stratified waters).

When both species co-occur there is a tendency for high abundance of *C. finmarchicus* earlier in the year than *C. helgolandicus* (Gowen et al., 1997; Herdman, 1918; Matthews, 1969; Nash & Geffen, 2004; Planque & Fromentin, 1996). There is also clear evidence of thermal niche differentiation between these two species and also of successional partitioning in the North Sea. For example, in the North Sea, *C. finmarchicus* occurs most abundantly in spring, whereas *C. helgolandicus* is most abundant in autumn. When these species coexist, it tends to be at low population densities compared to their centres of distribution. The *C. finmarchicus*/*C. helgolandicus* ratio is currently being used by the European Environmental Agency as a climate change impact indicator.

Harris (1996) summarised results of studies that compared the feeding of co-occurring *Calanus* sp. (see Table 2 in that work). Only a few direct comparisons between *C. finmarchicus* and *C. helgolandicus* have been made (Meyer et al., 2002; Williams, 1985; Williams & Conway, 1988). Meyer et al. (2002) show that despite temperature and probable gradients in the size distribution of food between their ranges, *C. finmarchicus* and *C. helgolandicus* exhibit no significant differences in the specific ingestion and filtration rates of their developmental stages. Their results also show that when feeding on algal cells without a clear distinction in external morphology, the main selection factor for both *C. finmarchicus* and *C. helgolandicus* is cell size (Meyer et al., 2002).

4.10. Towards a model of Calanus helgolandicus

The general purpose of population models of plankton species is to describe and eventually predict changes in abundance, distribution, and production of target populations under forcing of the abiotic environment, food conditions and predation. During the last 15 years, and mainly under the auspices of the 'Trans Atlantic study of *Calanus* (TASC)' project, a large number of population models, some coupled with the physical environment, have advanced our understanding of the ecology of *C. finmarchicus* (see Carlotti, Giske, & Werner, 2000; Coombs, Harris, Perry, & Alheit, 1998, for review). These physiologically structured

population models and individual-based models have been built for three main objectives: (i) to estimate the survival of individuals and the persistence of populations in their physical and biological environments, and to look at the factors and processes which regulate their variability, (ii) to estimate the role of *C. finmarchicus* populations in ecosystem flow budgets; and (iii) to study different aspects of behavioural ecology. Several models of physiological processes have also been published.

Production of so many published models for one planktonic organism is unique: this is due to the cumulative research effort started in the first part of the 20th century, synthesised in the book by Marshall and Orr (1955), continued over the second part of the century, and culminating in extensive field and laboratory studies in TASC. Modeling becomes a particularly powerful and valuable tool when a large body of information on physiological and demographic processes is acquired, so that missing information can be estimated, and model results can be validated.

In contrast to *C. finmarchicus*, no model has been built specifically for *C. helgolandicus* populations. However, all types of models built for *C. finmarchicus* could be applied to *C. helgolandicus*, but the individual budget model by Carlotti and Hirche (1997), the structured population model of Carlotti and Radach (1996) and the individual-based population model by Carlotti and Wolf (1996) may provide good starting points. To support such models, current effort should be devoted to collecting an extensive body of information on physiological and demographic rates for all stages of *C. helgolandicus*, and a good field dataset of stage-resolved distributions. The present review describes the current information on *C. helgolandicus*, providing the foundation to start such a model. At the initial TASC meeting in 1996, Carlotti (1996) described the basic knowledge required to build a model of *C. finmarchicus*, and the same is needed for *C. helgolandicus* (see Table 2 in Carlotti & Hirche, 1997).

Parameterisation of such a model can range from the simplistic to extremely complex, depending upon the amount of information known about the population under consideration. Bioenergetic processes (ingestion, egestion, excretion, respiration and egg production) are usually modeled from experimental results, whereas biometrics (e.g., size, weight) and demographic (e.g., development rate, mortality rate) parameters are estimated by combining life table data collected in the field or from laboratory studies.

To summarise, the key rates that need to be defined as a basis to start a population model of *C. helgolandicus* are (see also Carlotti, 1996 his Table 1):

- The ingestion function should be known for different food concentrations (functional response), for all the stages, and for all temperatures. A consistent set of data exists, mainly for adults and there are few data for early developmental stages, but no mathematical functions have been suggested for *C. helgolandicus* itself. How feeding rates change with temperature is a sensitive function in such models.
- The assimilation rate, basic and active metabolic rates, and their changes with temperature, and if possible for stages (nauplii, copepodite, and adult). The information on these processes is rather scarce.
- The reproductive rate for adult females as a function of weight, food and temperature. Reproduction rates from laboratory and in situ observations are well documented. However, as for the ingestion, it is still difficult to define functions relating egg production with food and temperature. The present paper suggests some relationships.
- The mortality rates for all stages due to starvation. This is easy information to get from starving animals.
- The development rates for all stages (including hatching rate for the eggs) at various food levels and temperatures. Valuable information exists and has been synthesised in the present paper.

To calibrate and validate such a model, the time-series synthesised in the present paper are valuable. As for *C. finmarchicus*, coupled hydrodynamical-population models at regional scales could help to answer

many questions and hypotheses raised in this paper, particularly those related to the exchanges between open sea and shelf areas.

5. Conclusions and future perspectives

Our study highlights the value of large-scale, long-term datasets for understanding the population distribution and changes of *C. helgolandicus*, a dominant copepod species in European coastal seas. Without the data from the Continuous Plankton Recorder survey and the fourteen coastal long-term time series stations, this work would not have been possible. However, even in a synthesis based on this considerable body of information there are many aspects of the ecology of *C. helgolandicus* that remain unclear. The continuation of such time series is essential to answer these questions, along with new time-series and surveys to obtain integrated datasets of key variables using standard techniques.

Conclusions of this overview of *C. helgolandicus* ecology in European waters are:

- Highest abundances of *C. helgolandicus* were recorded in the Adriatic and off the west coast of Spain.
- Long-term series in the North Sea have shown an increase in the abundance of *C. helgolandicus* adults during the last 40 years, and the Mallorca time-series shows a decrease in abundance since 1997.
- Data from the Levantine Sea seem to indicate the extension of the species beyond the previously known border of its southern distribution.
- Three station groups were identified based on the seasonal abundance patterns reflecting a continuous gradient in the seasonal cycle with latitude. Thus, the peak of maximum abundance is generally earlier in the year farther south. This latitudinal shift was identified to be associated with temperature variation but not chlorophyll.
- *C. helgolandicus* occupies a thermal niche between 9 and 20 °C, with maximum abundance between 13 and 17 °C.
- Surprisingly, *C. helgolandicus* has been found in deeper waters in the Levantine Sea than in the North Atlantic. Atlantic populations overwintering off-shelf occur between 400 and 800 m; in the Mediterranean there is evidence of significant populations at depths exceeding 4000 m.
- Populations living over deep waters are known to diapause, but more information is needed regarding near-shore populations.
- Egg production is affected by seasonality, chlorophyll and latitude, all partially modulated by body size.
- The optimum temperature for egg production is between 10 and 15 °C.
- Hatching success is greater in warmer water and appears to be lower at high egg production rates.

The recent work of Beaugrand, Brander, Lindley, Souissi, and Reid (2003) on the effect of plankton on cod recruitment in the North Sea has clearly demonstrated how rising temperatures modify the plankton ecosystem and result in reduced survival of young cod. The progressive substitution of *C. finmarchicus* by *C. helgolandicus* since the mid-1980s has delayed the occurrence of *Calanus* prey from spring to late summer, resulting in a mis-match with the food requirements of larval cod and hence reduced survival and recruitment. The phenological mismatch has two components: besides the change from *C. finmarchicus* to *C. helgolandicus*, the precession [I know about precession of orbital features, not of cod. What do you mean here?] of larval cod with warmer temperatures causes a mismatch with *Calanus* juvenile stages and smaller copepods following the phytoplankton bloom period. This and other recent studies clearly indicate the need for detailed understanding of the role of key species such as *C. helgolandicus*, as the marine ecosystems of European waters are increasingly impacted by climate change.

If climate warming continues, we can wonder how far *C. helgolandicus* is likely to expand geographically. Will it become the dominant *Calanus* species in the North Sea? Is *C. helgolandicus* going to supersede

C. finmarchicus in the Atlantic, and will it become one of the most important, ocean-wide copepod species in the future? This will have significant consequences for ecosystem functioning. To answer these questions, future monitoring strategies, using standardised approaches, should be co-ordinated on a broadscale, as has been initiated by the ICES Working Group on Zooplankton Ecology. There remains much to be done, but we trust that this synthesis and review of *C. helgolandicus* will help direct future research on this important species in the 21st century.

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