Biological activities in the North Sea I. Comparison of Calanus helgolandicus and Calanus finmarchicus vertical distribution and production.

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Editor of Journal of Plankton Research

Please find attached a revised manuscript and figures entitled "Biological activities in the North Sea I. Comparison of *Calanus helgolandicus* and *Calanus finmarchicus* vertical distribution and production".

I have now carefully gone through each of the reviewer's comments and found most of the suggestions and comments very helpful and took most of them into account, in the revised manuscript. We believe that it has improved our manuscript greatly and helped eliminate possible misunderstandings and shortfalls.

Please note that we refer (in our new Table I) to the accompanying MS by Koski, Jónasdóttir and Bagøien that is due for revision next week.

I hope we have made clear improvements and answered the questions and comments to the satisfaction of both editor and reviewers.

Yours sincerely,

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First I would like to thank the reviewers for constructive criticism of the MS which has helped to improve the MS. In the response below, "I" refers to the first author. In addition to my response to the authors listed below I have now

- slightly changed the title of the manuscript exchanging "on the Dogger Bank" with "in the North Sea" to match the accompanying manuscript by Koski et al. (in response to the reviewer's comments on the title of that MS)
- removed superfluous headings in the result section under "In situ egg production and hatching" in addition to minor corrections and clarifications.
- made small improvements, mainly related to better clarification, in results and discussion.

Reviewer: 1

General evaluation

The paper compares vertical distribution and production of Calanus helglolandicus and Calanus finmarchicus in the North Sea, as estimated from data collected during four years. To my mind this is an interesting study that casts novel light on the productivity and life strategies of the sibling Calanus species in an area where they co-exist.

On the whole, I enjoyed reading the paper. Its content clearly falls within the scope of Journal of Plankton Research. I have but a few relatively minor comments to make, and advice publication assuming the authors will consider them.

A few minor comments

Page 4, l.1-2: The information presented here ('Peak production for C. helgolandicus occurred in July compared to April for C. finmarchicus') is inconsistent with what is stated on the same subject on P.14, l.4-5, where it is stated that the production of C.fin peaked in March and that of C.helg in May. This apparent inconsistency must be resolved.

These two turned out to be quite mixed up in our text and has both been corrected and clarified. We are glad it was caught – while quite embarrassed over the mistake.

In the Methods section I miss a description on how the samples for abundance estimation were treated, i.e. if the samples were split before counting and if so by which method. The description indicates that only female Calanus were counted, while results on all stages are presented in the Results section. The relevant paragraph in the Methods section should be improved so as to reflect this.

This has been added to the method section. Revised MS Page 5

Page 7, First line in Results: Minor typos: replace 14.6 with 14.7, and 18.3 with 18.4.

Corrected

Page 7, last line: As to if the separation is distinct or not this may be disputed, particularly in light of that at one stn in 2003 C.fin did in fact stay in warm water above the thermocline as did C.helg (Fig. 3). The same error is repeated in the Abstract by stating that a 'clear separation was evident', and in the Discussion on Page 12. In my view, and from inspecting Fig. 2, the spatial separation of the species is not at all clear in August 2003, and therefore I feel the words 'distinct' or 'clear' are unfortunate here. This may have some consequences to the discussion. So please be more careful in the wording, and tell the reader that you are aware of this exception and included it in the discussion.

Yes, this is true, and the wording has been changed at these places, and awareness on the distinction written on page 12 line 3 in *vertical distribution*. In response to Rev 2 we have now added a statistical test on the abundance of the species in the 2 water masses that show a highly significant difference in the abundance above and below thermocline (see page 8).

Page 8, lines 2-3: I do not understand how yearly densities were standardized to maximum density. Can you please explain the calculations?
This is now changed after discussion with 2 statisticians and other colleagues about best presentation and statistical test of the data (see comment to the figure 4 here below). The statisticians suggested against standardizing the data, and suggested plotting the sum in the water masses. If standardizing the data, then it should be weighted with the number behind the data, so it would be the same as presenting the original abundance. Therefore we added up the abundance data per temperature bins, to better show the separation of the females and stages and for more straight forward statistical comparison of the data. Additionally, I replaced the word density with the words abundance and concentration.

Page 9, l.12: From Table IV I read that EPR differed between years (2001 different from 2002) so the statement that the EPR of C. helgolandicus did not differ between years is incorrect. In addition the EPR ranged from 8-29 eggs fem-1 d-1 (instead of 9-29).
This has been corrected

Page 12, 1st line: a word is missing after 'understanding', add 'of'.
P.13, l.9: replace 'be' with 'been'.
P.14, l.22: Delete 'this'?
All corrected

P.14, l.4-5: Inconsistent with what is stated on P.4, as mentioned before. This one is correct – the other is now corrected.

P.14, l.5-7: I think you are confusing names here (C.fin and C.helg). According to Jónasdóttir et al. (2005, their Fig.5) C. helg is showing generally low rates (<50 eggs m-3 d-1), while C.fin has max EPR in May (~150 eggs m-3 d-1). Please check if this has consequences for the discussion on this matter. Yes this is mixed up (see above). It does not change the discussion as it was correct in the mind, but not on paper!

P.14, l.26: The temperature difference is rather ~7°C. The abstract gives temperatures as 9°and 16°. This accords also better with the temperature intervals reported in Results. Changed to 7 °C

Table I: What do the blank spaces for CHc5 and CFc5 in 2001 mean? Are they zeros or not measured. Explain in Table legend what 'nm' means. Clarified – changed to na (not analysed).

Table IV: Why do you not indicate significance for hatching as for the other variables? The comparison was mistakenly left out, and it now in and in accordance to the text.

Fig. 2: In my version of the MS, the figure that is meant to show vertical distribution of C.fin in July (the uppermost panel) is rotated 90°. Must be improved. – The reason is (as stated in the methods) that in 2001 the zooplankton abundance was unfortunately only from a total vertical tow, not depth separated. This has now been pointed out in figure legend, and the graph made clearer including station numbers on x-axes to avoid misunderstanding of the orientation of the plot. (New Table I – as suggested by Rev 2, should also clarify this).

Fig. 4: Impossible to see which curve is for Cfin and which is for C.helg. Must be improved. What is meant by relative abundance here? Please explain. I am also a bit confused if the Fig shows females only as the legend suggests, or if younger stages are included also, as the discussion on this Fig in main text (P. 8), implies that the younger stages are also included. This could be made clearer. This figure has been changed – after discussion with statisticians on best way of presenting this data (see answer to comment above). In the new figure the separation of species is clear. Figure legend has been corrected to include the stage 5 copepodides.

I have not checked if all the cited references are listed in the reference list or vice versa.
After revision, some new references have been added and other removed. I have now gone over the references 2 times before this re-submission and would surprised if it is not correct.

Reviewer: 2
Comments to the Author
The data on depth distribution and reproduction at the Dogger Bank, North Sea, are interesting, and as it is stated in the manuscript, there are only few studies, comparing directly depth distribution and reproduction of the two sibling species. Unfortunately, the paper seems a bit superficial and parts of Method and Results sections are slovenly written. I therefore recommend the publication of this manuscript in JPR only after major revisions.

Introduction and Discussion are mostly concise and well written. There are a few mistakes (left-out words mainly, please check). Both parts nevertheless lack deeper insight and the manuscript would benefit from a more thorough discussion, including data from other areas and information on the physiology, which are available for both species (e.g. Williams 1980, Hirche 1983, Pond et al. 1996, both MEPS). For example, the discussion on food and feeding (page 12/13) includes only 4 references and all of these present data on C. finmarchicus, literature on C. helgolandicus is not included. (Given, that there are so many tables on this topic, the discussion is surprisingly short anyway.)
I admit our bias towards *Calanus finmarchicus* studies and have now made an effort to corrected that bias. In the **Introduction** I have added a sentence on a study I had missed before on a lab study on CF and CH food selection. In the **Discussion** I have now improved and deepened out discussion on selection and feeding and effects of diets on EPR for both species (current page 14). We did not go in our discussion (or introduction) much beyond the scope of our study – comparison of the 2 species and their importance on the Dogger Bank. The results did not give a major reason to go into food quality studies (then I would cite more of my own papers too) or egg composition. Williams 1980 was (and is) in the paper (discussion). The suggested study of Hirche 1983 does not fit into this paper. In that paper he does not compare the species and over-wintering is not an issue here.

Moreover, the authors often rely on reviews (e.g. Bonnet et al. 2005, Harris et al. 2000) instead of citing original publications, which I find irritating.
We totally agree about using original references before reviews. However, in our case there are 3 citations to Bonnet et al.; one to their comparison of the 2 species (their table 2), as a reference to the surprisingly few comparisons of the 2 species (even though they compiled the data from different sources, the mini-comparison is theirs). The other 2 citations refer to a study conducted by Rabea Diekman and only published in this review on the vertical co occurrence of the 2 species in the North Sea during spring. The reference to Harris et al 2000 is now removed and we refer to Niehoff et al. 1999 that has the original population egg production estimates.

Methods and Results sections need thorough work as the paper presents many data and lacks some focus. As I have quite a few comments, I'll go through them consecutively:

page 4 line 29: 3 North Sea cruises – abstract says 4 page 4 line 41: "…described in (Jonasdottir et al., 2005)" – to my knowledge this does not match the JPR layout, consult Instructions for authors
We added into the abstract that comparison was done on data collected on 4 cruises. The correct citation format is now used and we checked the whole MS (and references) to correct the citation formats.

page 4 line 59: 2-4 intensive stations…
- There is some confusion in the text about which station was sampled when. Is it two or four stations? Please, add a table on sampling dates and stations and indicate which measurements (abundance, EPR, temperature of incubation) have been done. The sampling procedure seems rather inconsistent (2001, depth integrated, 2002, 10 m intervals at buoy station: why are two sampling sites indicated in Fig 1, 2003 and 2005 5m interval sampling of transect stations). Wouldn't it make sense to only use the latter two years, sine these are the ones, which can be compared in terms of sampling procedure?
I have added a table (current Table I) with our sampling procedure to clarify our admittedly somewhat inconsistent sampling between years. From start we did seriously evaluate if to include abundance data from 2003 as we did not focus on *Calanus* production on that cruise in favour of other copepod species. However, as the distribution of the cousin species is also a focus of our paper, we decided to include the 2003 data, also to show the yearly variation in abundance. Station locations *per se* do not matter in this case, as all environmental measures are taken at the same stations as the production measurements are conducted. The problem arises when the abundance and production are not measured at the same location as was the case in 2002. This is however, pointed out and is only used for approximate estimate of population egg production rates in the discussion.

Obviously based on the following comment the method description was not clear enough and we use the reviewer's comments to clarify the method section.
page 5 egg production measurements - sampling for egg production was done at which stations?
Line 24: sampling depth was 50 or 70m. Did you sample at that depth only?
Meaning: did you take horizontal catch net tows – if yes at which speed was the net towed, what was the sampling depth for surface sampling, what was the depth for Chlorophyll max? The water depth in our sampling area is maximum 70 m. We now clarify that we took a vertical tow from about 5 m above the bottom and up. We have now added in the towing speed.

Did you incubate 40 females at a time in a 600ml bottle? Absolutely not, this we NEVER would do!
Were the numbers of females per bottle (volume) the same in the two species? If not, is it possible that the lacking difference in EPR between the two species can be attributed to the incubation method (which does not match the standard according to Runge and Roff 2000 ICES manual)? With increasing female abundance, cannibalism increases (see Ohman and Hirche 2001, Nature).
The method says that females were "individually introduced into 300 or 600 mL bottles" Therefore the rest of the reviewers comment does not apply. Because we cannot recognize the 2 species from life samples with 100% certainty, the species were randomly introduced into these bottles, but NB individually.

What do you mean: Separate incubations were carried out on each station two times (line 47)?
Clarified – we sailed the transect back and forth 4 - 7 times during the cruises. In 2002 we conducted egg production experiments on two of these transect routes. This is also included in the new Table I.

Why is there only one bar for each station (Figure 5)?
I am not sure I understand the question, but the bars represent the average egg production (combined surface and chl max as there was no significant difference between those (as explained in the text current p. 9), and pellet production at chl max and surface for each station. In 2002 the replicate incubations for each station are combined to increase number of replicate incubations as the second incubation had new animals. In 2005 the bars represent only the first day of incubation to be comparable to the other years. This is explained in the result section page 9 but to clarify I have added clarification in the figure text.

What do you mean: In 2005 females were only sampled once on route to transect? Figure 5 shows EPR data from 4 stations (1, 3, 5, 8). What is the purpose of incubating the female for 4 days? The results are not very enlightening either, thus, you may want remove these parts from the manuscripts.
After visiting the site for several years, we wanted to improve our understanding of the importance of the bloom for secondary production. In the back of our mind was the idea to test if the quality of the bloom decreased away from the bank – where the nutrient input is highest and we could use that to generate a natural experiment with changing food quality. The best way to compare the species in changing food environment is to use a bioassay – that is, to incubate the same population of copepods in waters at stations with increased distance from the bank. In 2003 we used cultured *Acartia tonsa* (accompanying MS by Koski et al) and in 2005 we sampled *Calanus* from one station (on our way to the transect). We can use the first day to compare with the incubations in 2001 and 2002, while the cumulative egg production or final 4 day egg production can show us how the 2 species react to the immediate food environment. We find this study important for the manuscript and do not want to remove it from the paper but have tried to make the purpose of the study more enlightening for the potential reader. To avoid misunderstanding I have clarified this in the methods, results and in the discussion.

page 7, line 23: chlorophyll was DIFFUSED between the years - What do you mean?
This has been reworded.

page 7, line 43: total fatty acid composition…was correlated with the chl a content – how can COMOSITION correlate to chl a CONTENT? Statistics correct? (Spearman rank test not mentioned in Method section)
The reviewer is absolutely correct here, that the fatty acid composition is not correlated… this has been corrected to that seston fatty acid concentration (total) was correlated to cha. The Spearmen rank test is now mentioned in the Method section.

Page 8: Plotting Gaussian 3 parameter curves without any statistical significance does not make much sense, does it? It seems rather arbitrary.
As pointed out in our response to Reviewer 1 we have now re-plotted the figure after a discussion with couple of statisticians and colleagues. I copy here the answer to reviewer 1.: *The statisticians suggested against standardizing the data, and suggested plotting the sum in the water masses in temperature ranges (we used 2 degree bins). If standardizing the data, then it should be weighted with the number behind the ratio, so in the end it would be the same as presenting the original abundance.* Therefore we added up the abundance data per temperature bins, to better show the separation of the cousin females and C5 stages, and to be able to do a clear statistical test on the data. Therefore we do not use Gaussian curves anymore – it also turns out it requires rather complicated statistical test to compare such curves. As we are interested to test if there is a different temperature preference by these

species the statisticians suggested that we use a simple chi square test making the temperature cut where there were equal abundance on each side. This was done and the text changed accordingly.

page 8 line 52: First you refer to egg production and hatching, then it is "however pellet production in only compared for the chlorophyll max incubations" Compared to what anyway? Among each other? Relation to egg production? Why is this remark not included in the fecal pellet production chapter, page 9?
This has been corrected and moved to a one combined faecal pellet section; *Faecal pellet production* as I agree the faecal pellet paragraphs were too scattered in the MS.

page 9, lines 6 to 16: How did you calculate clutch sizes if you have not incubated single females and if you have not checked for eggs more often? At these temperatures, there were likely some females, which had spawned more than once within 23-24hrs, while others may not had spawned at all.
The reviewer is correct and this should not be called clutch size but more correctly maximum egg production at each station. I have come across many researchers that insist on excluding zero producing females in their average EPR and while I see problems with that approach (depends on the purpose of the production measure) I feel this should be separately reported. The reviewer is absolutely correct that I should not use clutch size as it is has another meaning. This has been corrected and clarified in the manuscript and now called either maximum egg production or EPR_{max}

page 9 – bioassay – and then again fecal pellet production? Why? Which stations are compared, here you seem to refer to the surface layer – line 27, FP was significantly higher in chl.max layer for both species (higher than what?), See comment above on faecal pellets. We have now added an explanation to the bioassay in our introduction and again in the method section page. We also have combined the faecal pellet discussion in one paragraph as it was obviously not very clear.

line 33, C. finmarchicus had significantly higher FP in BOTH layers compared to C. helgolandicus – how does that relate to page 8, line 52? See comment above.
These are 2 different approaches and now they are combined – and hopefully better explained in the result section. In 2002 there is not surprisingly a big difference in FP production between the surface and chl max and between species in the chl max. There is no explanation for why there are more pellets in the surface 2005 compared to 2002 and a sentence on this matter is now added to the discussion.

page 10, line 41, females at station 3 and 5 were significantly larger at station 1 and 5???? That does not make sense. No I agree, and it is a typo. This has been corrected and simplified, as basically station 1 had the smallest *C. helgolandicus* size and that is how it is now written.

page 10, Interaction between environmental factors and production; pearsons product moment correlation between female properties does not appear in the Statistics chapter. More important, I wonder what the purpose of some of these tests is: What do you expect from a correlation between female size and FP, the latter in terms of number of FP per female? Does this imply any biological consequences?
This comment made me realize that it is not necessary to show the correlation matrix in the paper, as it is only a tool to help us to see if the data is reasonable and if correlations make sense – and as in this case to make a size normalization of egg production data. I have removed the table and only included the relevant information in the text. I agree with the reviewer that there is nothing biological interesting in the correlation of size and FPproduction (or some other correlations shown).

page 11: Why did you transform length to volume? What is EPvol? Please, explain!

It is just one way of normalizing to length. Most often size is normalized to a carbon content based on standardized length, but as we do not trust carbon conversions of *Calanus* based on size (due to variable lipid contents and a lack of a good standardized value) we mean that volume might be a better indicator of size that prosome length. EPvol is now explained in the text (now EPRvol).

page 11 line 20 versus page 10 line 60: page 11 says "EPR of C. helgolandicus could not be explained by any of the environmental parameters, neither microplankton nor fatty acid concentrations" page 10 states "The in-situ egg production of C. helgolandicus was best explained by the concentration of ciliates, heterotrophic dinoflagellates and flagellates…."This is contradictory, isn't it?
This is due to the two different methods used, immediate measure v.s. a bioassay approach. We mean that the results from those are now better explained and discussed (due to this and the previous comments - thanks).

page 11, line 46: "assuming 250 µg C per egg" – must be 0.25 µg C per egg, same mistake has been made in the discussion. Oops, this has been corrected.

page 11, line 46-47, the references for egg carbon content seem not to be all correct: I did not find any reference to egg carbon measurements in Hygum et al. 2000 (only CI to females) and Koski (2007) did not measure egg carbon but cites unpublished data by E. Arahkevich; I suggest to refer to these unpublished data in the present manuscript, too, rather than giving the somewhat misleading impression that there are actually egg carbon data published. There are 3 Hygum et al. 2000 papers and the reviewer may have looked at a wrong paper. The egg C value is given in their table 1 in the cited paper and mentioned in the text under the section "Carbon content of *Calanus finmarchicus* eggs". One of the other papers (Importance of food..) also gives egg carbon value, but cites the "Growth and development" paper which we use. The citation to Koski is now removed, but an additional paper by Cabal et al. 1997 is now added. The values are corrected accordingly (did not change much – a decimal point in GGR).

Reference list: the list is not yet well formated - number of pages are missing (Mauchline 1998); Madsen et al. (2008): Ref Type Journal (see line 17/18), same in Rees (line 54); some journal are abbreviated with points (Mar. Biol.) other are not (Mar Biol), some references end with a point, some do not (Nejstgaard et al, Daan et al.) We have carefully gone over the reference list, and corrected according to JPR standards.

Eiane and Ohman are not cited in the text Yes they are - see previous MS page 14 line 39 (current page 15).

Biological processes in the North Sea: Comparison of *Calanus helgolandicus* and *Calanus finmarchicus* vertical distribution and production

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Keywords: *Calanus helgolandicus*, *Calanus finmarchicus*, egg production, Dogger Bank

Abstract

Comparison of abundance, vertical distribution and reproduction of the cousin species, the boreal *Calanus finmarchicus* and temperate *Calanus helgolandicus* was carried out on 4 cruises in July and August north of the Dogger Bank, North Sea. During this period the water column was highly stratified with a tidally generated deep chlorophyll maximum at 30 m depth. When co-occurring, a separation of the species was evident, where *C. finmarchicus* preferred colder (9°C) deeper waters while *C. helgolandicus* stayed in the warmer (16°C) surface waters. Egg production rates were not statistically different between the species, and the population egg production depended primarily on female abundance and was generally higher for *C. finmarchicus*. Egg production rates of the *Calanus* spp. were best explained by the abundance of autotrophic and heterotrophic dinoflagellates, flagellates and ciliates. Hatching success remained over 90% at all times but the estimated naupliar survival (N1-6) was only 9%. The chlorophyll maximum supported highest faecal pellet production and egg production at the stations close to the bank. This study shows that *C. finmarchicus* can remain reproductively active in the North Sea ecosystem longer than previously thought, and with warmer surface temperatures retreat to cooler, deeper waters utilizing the deep chlorophyll maximum. This implies that *C. finmarchicus* cannot be reliably sampled with the Continuous Plankton Recorder during summer.

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Introduction

The Dogger Bank is situated in the central North Sea and is a well known feeding ground for planktivorous fish (Daan et al., 1990). While thermally stratified during summer, the area north of Dogger Bank is characterized by subsurface chlorophyll blooms the primary production of which has been estimated to be greater than the spring production in the same area (Richardson et al., 2000). The area around Dogger Bank is also the area where the two *Calanus* species, the boreal *Calanus finmarchicus* and the more temperate *Calanus helgolandicus* overlap. *C. finmarchicus* is usually located north of the bank in deeper waters while *C. helgolandicus* is more evenly distributed in the North Sea basin (Planque and Fromentin, 1996; Jónasdóttir et al., 2005).

Calanus helgolandicus and *C. finmarchicus* are of major importance as food for planktivorous fish in the North Sea ecosystem (Munk and Nielsen, 1994) and numerous studies have been able to correlate fish recruitment to the presence of one or other of these species (Beaugrand et al., 2003; Heath and Lough, 2006). There is an indication that *Calanus finmarchicus* is more important for recruitment of many fish stocks in the North Sea than is *C. helgolandicus*, and this may be related to the timing of their abundance and seasonal production (van Deurs et al., 2009; Beaugrand et al., 2003). *Calanus finmarchicus* enters the North Sea in early spring from its over-wintering in the Faroe Shetland Channel and Norwegian Sea (Heath et al., 1999) while *C. helgolandicus* is generally a Mediterranean species and disperses in the North Sea from south. Long term data from the Continuous Plankton Recorder (CPR) suggest that *C. finmarchicus* is retreating north from the North Sea and *C. helgolandicus* is gaining ground due to warmer temperatures (Planque and Fromentin 1996). This has been shown to have affected the survival of fish larvae (Beaugrand et al., 2003; van Deurs et al., 2009) probably due to the mismatch with the production of *C. helgolandicus*, which occurs later in the season (Jónasdóttir et al., 2005; van Deurs et al., 2009). However, whether the reduction of the population *C. finmarchicus* is due to increased temperatures in the North Sea or a failure in restocking in the spring from the over-wintering habitat off the shelf is debated (Beare and McKenzie, 1999).

There is actually remarkably little known on the biology of these two closely related species co-occurring in the North Sea. Therefore a comparison of the two *Calanus* species is of considerable interest in evaluating their importance in the North Sea ecosystem and understanding how/if they interact while overlapping. Only one direct comparative study on *C. finmarchicus* and *C. helgolandicus* egg production has been conducted (Jónasdóttir et al., 2005) on a one year seasonal production of these species. Here it was demonstrated that *C. finmarchicus* and *C. helgolandicus* distribution differed both spatially and seasonally where *C. helgolandicus* had lower egg production

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rates most of the season compared to *C. finmarchicus*. Peak egg production for *C. helgolandicus* occurred in May compared to March for *C. finmarchicus.* Bonnet and co-workers (Bonnet et al., 2005) list in their review on *C. helgolandicus* some comparative aspects between *C. finmarchicus* and *C. helgolandicus* (their Table 2) where they demonstrate differences in distribution and temperature ranges, as well as their differences in maximum egg production rates and development times. A concurrent comparison on feeding selection by most of the development stages of both species has been conducted in the laboratory by Meyer and co workers (Meyer et al., 2002). They showed that there were no differences between the species in selection of the food mixtures offered.

The purpose of this paper is to compare the production and abundance of these two congeneric species at the northern/southern edge of their distribution during summer. Sampling was conducted off the northern flank of the Dogger Bank and was a part of a long term study on the biology and production of the subsurface chlorophyll maximum off the Dogger Bank. The questions asked are if there is a spatial overlap between *C. helgolandicus* and *C. finmarchicus* and if their production is controlled by the same factors, lending insight into the relative importance of these two species in this highly productive area.

Method

Physical, chemical and biological measurements were carried out during 4 North Sea cruises on R/V Dana (DTU-Aqua) 7-11 August 2002, 2003 and 27 July – 7 August 2005, along a transect across the northern flank of Dogger Bank and at 4 stations 19 July 2001(Fig. 1). The transect had 15-17 CTD stations of which 4 were sampled intensively for other biological measurements. On these intensively sampled stations, shipboard egg production and hatching success experiments on *C. finmarchicus* and *C. helgolandicus* were carried out, fatty acid analysis of seston and samples for zooplankton vertical distribution and abundance were taken (see though exceptions in Table I). In 2001 samples were taken as described by Jónasdóttir and co-workers (Jónasdóttir et al., 2005).

Measurements of the physical environment, chlorophyll and zooplankton abundance were taken on each station shown in Fig. 1. Temperature, salinity, and fluorescence profiles were taken with a Seabird® CTD (model 911+) equipped with a Wetstar fluorometer. Stratification was calculated as the energy needed to mix the water column (Simpson, 1981). Simultaneously, samples of chlorophyll *a* were taken with Niskin bottles from various depths to calibrate the fluorometer measurements. An overview of the experiments and sampling is given in Table I.

Abundance

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On the 2 - 4 intensive stations (Table I) zooplankton was sampled with a submersible pump. Additionally, in 2002 sample profiles were taken 12 times with ca 6 hour intervals at a drifting buoy station north of the transect (Fig. 1) and in 2005 additional night profiles were taken at 2 stations. The water was pumped directly into an attached 30 µm plankton net protected by an outer 200 µm mesh net bag. The submersible pump (Homa, H-500, with the plankton net fitted to the outlet) was lowered to a pre-determined depth where it sampled for 3 minutes (1.2 m^3 min^{-1}). In 2002 samples were taken at 10 m depth intervals, while at 5 m intervals in 2003 and 2005. In 2001 a depth integrated sample was taken where the pump was lowered to 50 m depth or to 5 m above the bottom depth, if shallower, and sampled (1.2 m^3 min^{-1}) while towed vertically to the surface at an average rate of 15 cm sec^{-1}. The samples were fixed in 4% borax buffered formalin. Zooplankton were counted from a 1/4 to 1/64 fraction of the total sample, so the counts exceeded 200 individuals from the main copepod species. From these samples *C. finmarchicus* and *C. helgolandicus* females and copepodite stages 5 (not in 2001) were identified. Copepodite stages 1-4 (stage 5 included in 2001) were counted but these stages cannot be differentiated morphologically between the species. In 2001 and 2005 *Calanus* nauplii were specifically identified. Species separation was done on the basis of the different morphology of the 5th swimming legs (Rees, 1949)

Measurement of egg production and hatching success

In 2001 and 2002 *Calanus* females were sampled at the intensive stations (Fig 1; Table I) with a 220 µm mesh size plankton-net (1 m in diameter) fitted with a 5 L non-filtering cod-end. No females were found at station A in 2001. The sampling depth was usually about 5 m off the bottom depth, usually 50 or 70m and the net was towed vertically with a towing speed of ca 4 m min^{-1}. The contents of the cod-end were gently transferred into a bucket with surface (4 m) water from the respective station. Immediately after sampling 14 to 40 active undamaged females were selected under a stereomicroscope and individually introduced into 300 or 600 mL bottles filled with 64 µm screened ambient water. Screening was done in order to remove all ambient eggs from the incubation water. Females were incubated in darkness for 22-25 hours at temperatures appropriate for the ambient temperatures (Table I) at the station where they were collected. There was no physical barrier between the females and their eggs. However, in order to minimize cannibalism on eggs the incubation bottles chosen were tissue culture flasks. The bottles were kept upright (not rotating) during incubation and the eggs sank to the bottom of the bottle. The temperature controlled room was mid ship on lower level so physical stirring due to the ships movement was minimal. While these actions do not eliminate the possibility of cannibalism it was minimized. In 2002 females were incubated in either surface or chlorophyll max waters for 24 hours. This procedure was repeated when visiting the stations 3 days later with new net tows and incubations. In 2005 we

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ran a bioassay approach (Müller-Navarra and Lampert, 1996) to further test how the two species responded to potentially different food quality at the different stations. Over 200 females were sampled on route to the transect, in Skagerrak at 57.66 N and 7.33 W and incubated as above, individually in 24 replicates in both chlorophyll max and surface waters from each of the 4 intensive stations. The water changed every day for 4 days when the station was re-visited at approximately 24 hours intervals. Egg production was not measured on *Calanus* spp. in 2003 but incubations for 2001 are described in (Jónasdóttir et al., 2005).

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After the 24 hr incubations, eggs and faecal pellets were collected by filtering the bottle content gently through a 20 µm mesh and immediately counted directly on the mesh through a stereo microscope. The prosome lengths of the females were measured after which they were fixed in 4% formalin in seawater for later identification as *C. finmarchicus* or *C. helgolandicus*. Eggs from all females from a specific station were incubated in one or two 600 mL glass bottles containing 20 µm previously screened incubation water. Because of the pooling of the eggs separate hatching data for *C. finmarchicus* and *C. helgolandicus* eggs are not available. The eggs were further incubated for 48 h after which time nauplii and un-hatched eggs were preserved in 4% Lugol's solution for later estimation of hatching success. Unfortunately hatching samples taken in 2005 were destroyed.

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Phytoplankton and lipid sampling

Water samples for protist counts were taken from the surface and chlorophyll maximum at the intensive stations with Niskin bottles attached to the CTD rosette from several depths. Water samples were fixed in 4% acidic Lugol's solution for phytoplankton and ciliates, and gluteraldehyde for separation of autotrophic versus heterotrophic organisms. Lugol's samples were allowed to settle in a settling chamber (Uttermöhl, 1958; Hasle, 1979) and gluteraldehyde samples handled according to Haas (Haas, 1982). Phytoplankton and ciliates were enumerated and geometrical axes measured under inverted microscope (Lugol's samples) or epifluorescence microscope (gluteraldehyde samples). Volumes were calculated using the software program Planktonsys 3.11 from BioConsult A/S, and carbon content calculated according to Edler (Edler, 1979) and Mullin and co-workers (Mullin et al., 1966). Additional data on ciliate counts from the cruises were obtained from Arendt and co-workers (Arendt et al., 2005).

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One to 5 L of water from surface and chlorophyll maximum were filtered onto combusted GF/C (Whatman) filters and immediately frozen in cryo-vials -80°C. Fatty acids were extracted from filters containing the field collected seston using chloroform:methanol (2:1 by volume). A known amount of the fatty acid C23:0 was added to the sample and used as an internal standard for

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quantification of specific fatty acids. After at least 24 hours extraction at –20°C, the chloroform:methanol phase was collected and the filters were washed three times with chloroform:methanol. The extracts were washed according to the modified Folch method (Hamilton et al., 1993). After saponifcation, the samples were transmethylated to fatty acid methyl esters (FAME) using boron trifluoride (BF_3) and then stored in air-tight vials in an argon atmosphere at -80°C until GC analysis. The FAME sample was injected into a gas chromatograph (Hewlett Packard 5809A, with a 30 m omegawax 320 µm column, and equipped with a split/splitless injection system) using helium as a carrier gas at 1.8 mL min^{-1}. Fatty acid methyl esters were identified based on comparison with retention times of several standards; Larodan PUFA standard, fatty acid from the dinoflagellate *Prorocentrum minimum* to locate 18:5(n-3), Matreya PUFA-3 and Supelco 18919, resulting in identification of 42 fatty acids.

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Statistics

Test of associations between the female properties were made by Pearson product moment correlation. Egg production, spawning percentage, brood size and prosome length were tested for differences between stations within years using one-way ANOVA or Kruskal Wallis ANOVA on ranks if the requirement of equal variances were not met. Tukey HSD or Dunn's *post hoc* pair-wise comparisons were carried out when ANOVAs gave significant differences. Principle component analysis (PCA) was used to reduce the number of environmental variables to be used in the multiple regressions and correlations. Chi-square analysis of contingency tables was used to compare the temperature preference of *C. helgolandicus* and *C. finmarchicus* based on preference for above and below thermocline. Spearman rank test was used for nonlinear correlations and a Pearsons product moment correlation matrix was generated between female properties The statistical programs SPSS and Sigma Stat were used for the analyses.

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Results

Physical and biological environment

The average temperature in the upper 20 m differed between the years, being 14.7, 17.5, 18.4 and 14.8 °C in 2001, 2002, 2003 and 2005 respectively (Table II). The thickness and concentration of the chlorophyll maximum layer also differed between the years (Fig. 2), with a strong chlorophyll maximum in 2001 and 2002 and more vertically diffused in 2003 and 2005. The stratification in 2003 was 131 Joules m^{-3} and markedly higher than in the other years where it was 98, 105 and 95 Joules m^{-3} for 2001, 2002 and 2005, respectively. Average chlorophyll concentrations in the chlorophyll maximum layer varied from 1.4 to 4.1 µg L^{-1} (Table III). The dominant microplankton class was autotrophic dinoflagellates of which *Ceratium* species were the major group in both years.

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The surface chlorophyll concentrations were highest in 2001 (ca 1 µg L^{-1}) but between 0.4 and 0.6 µg chl *a* L^{-1} in 2002 and 2005. There were no dominant groups of microplankton in the surface waters but the assemblage was equally composed of flagellates, autotrophic and hetetrotrophic dinoflagellates, and ciliates but with slightly lower contribution of flagellates in 2005. Diatoms were only found in comparable amounts to other groups in the chlorophyll maximum at station 8 in 2005. Carbon:chlorophyll ratios of the counted microplankton ranged from 21 to 102 (Table III). Total seston fatty acids were positively correlated with the chl *a* content (Spearman Rank Order Correlation: ρ = 0.52, p = 0.03, n = 17). Polyunsaturated fatty acids were most abundant in the chlorophyll maximum in 2001 and 2005 or 7 to 27 µg L^{-1}, but were more uniformly low (about 1 µg L^{-1}) in 2002 (Table IV).

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Abundance

Both *Calanus finmarchicus* and *C. helgolandicus* were found at the transect stations in all years, but abundances varied both annually and spatially. In 2001 and 2003 *C. finmarchicus* was found in higher abundance than *C. helgolandicus* but the reverse was true in 2002. The species occurred in similar numbers in 2005. In 2002 *C. finmarchicus* was found in very low concentrations (1 indiv. m^{-3}) at the transect stations (Fig. 2; Table II), but at the buoy station (Fig. 3) the abundance of both species was similar. A vertical separation of the species was observed in 2003 and 2005 and at the buoy station in 2002 where *C. finmarchicus* females were below the thermocline while *C. helgolandicus* females were in the upper warmer surface waters. To better compare the optimal temperature ranges that the two congeneric species occupied, female and C5 concentrations were plotted against their respective sampling temperatures. Peak abundance was at 9 and 16 °C for *C. finmarchicus* and *C. helgolandicus* respectively (Fig. 4a). There was a highly significant difference in the abundance of the 2 species above and below the thermocline (Chi-square = 666, df = 1, P<0.001). The copepodite stage 5 (C5) stages had a similarly significant vertical distribution (Chi-square = 815, df =1, P<0.001); *C. finmarchicus* having higher abundances in deeper cooler layers (max at 7.5 °C) while the C5 stage of *C. helgolandicus* were in the upper layers in 2002 and 2005 but more evenly distributed through the water column in 2003 (Table II; Fig. 4b) resulting in broader temperature preference with a maximum abundance at 13.5°C. Stages C1-4 were most abundant in the upper 40 m all years, and nauplii only separated for *Calanus* in 2005 were in the upper 20 m (Table II).

There was no indication of diel vertical migration of either species at the buoy station in 2002, while there was some indication of upward migration to 15 m during night by *C. finmarchicus* at station 3 in 2005 Fig. 3b).

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Size

In 2001 and 2005 no difference was observed in the size between *C. finmarchicus* and *C. helgolandicus* (Table V). However, in 2002 *C. helgolandicus* was significantly larger than *C. finmarchicus* (2.46 ± 0.01 v.s. 2.40 ± 0.01 mm, Kruskal-Wallis One Way Analysis of Variance on Ranks, $H_1 = 19.4$, $P = <0.001$) and both species were significantly larger in 2005 compared to 2001 and 2002 (Kruskal-Wallis One Way Analysis of Variance on Ranks, *C. helgolandicus* $H_2 = 36.3$; $P = <0.001$ and *C. finmarchicus* $H_2 = 93.1$; $P = <0.001$.

In situ egg production and hatching.

For comparisons between years, we only used data from day 1 in 2005. There were no significant differences in egg production rates (EPR) between surface water and chlorophyll maximum incubations in any of the years after 1 day incubation. Therefore, to increase the number of replicates, surface and chlorophyll maximum data are pooled.

The proportion of spawning females was 75-83 % for *C. helgolandicus* and 58-79 % *C. finmarchicus* during the 3 years (Table V). However, this difference was not significant between the species ($F_1 = 2.3$; $P = 0.15$) and not different between years for either species ($F_{2, 1} = 1.15$; $P = 0.3$). The highest egg production rate for an individual *C. helgolandicus* was 79 eggs d^{-1} (Table V) and the EPR_{max} (EPR from spawning females only) were significantly higher in 2002 than the other years (Kruskal-Wallis ANOVA, $H_2 = 23.1$; $P < 0.001$, Dunn's *post-hoc* pairwise comparison). The highest EPR of a single *C. finmarchicus* was 94 eggs d^{-1}. No differences were observed in EPR_{max} between years for *C. finmarchicus*. The difference between the species was significant in 2001 (33 ± 4 and 21 ± 3 eggs female^{-1}day^{-1}; $F_1 = 5.7$; $P = 0.02$) and 2005 (38 ± 2 and 20 ± 5 eggs female^{-1}day^{-1}; $F_1 = 11.7$; $P < 0.001$) for *C. finmarchicus* and *C. helgolandicus* respectively.

The average egg production rate (EPR, zero production included) for *C. helgolandicus* ranged from 8-29 eggs female^{-1} d^{-1} and was significantly lower in 2001 compared to 2002 (Kruskal-Wallis ANOVA, $H_2 = 10.5$; $P = 0.005$, Dunn's *post-hoc* pairwise comparison). EPR ranged from 8-43 eggs female^{-1} d^{-1} for *C. finmarchicus* and was significantly higher in 2005 compared to the 2001 and 2002 (Kruskal Wallis ANOVA, $H_2 = 7.9$, $P = 0.02$; Fig. 5, Table V). No statistically significant difference was observed in EPR between species in any of the years.

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Hatching success was always over 90% with the exception of station 3 in 2002 (Table V). There was a significant difference ($F_3 = 6.1$; $P = 0.009$) between stations in 2002 and hatching was significantly lower in 2002 than 2001, 91% compared to 98% respectively ($F_1 = 12.2$; $P = 0.013$).

Bioassay 2005

In 2005 the females were collected at a single station at the start of the cruise and the same females incubated for 4 days in either surface or chlorophyll maximum waters at the 4 intensive stations to assess potential difference in the food environment in the incubations. This should also show if the two species respond differently with time to the same food environment.

Significant differences were found in total number of *C. helgolandicus* eggs produced over the 4 days (cumulative egg production) between stations in the surface layer ($F_2 = 4.3$; $p = 0.04$) but not in the chlorophyll maximum layer (Fig. 6 a). The opposite was true for *C. finmarchicus* where the difference between stations in chlorophyll maximum was significant ($F_3 = 3.3$; $p = 0.03$) but not in the surface layer. The difference between surface and chlorophyll maximum total egg production was significant for *C. finmarchicus* ($F_1 = 89.8$; $p = 0.003$) but not for *C. helgolandicus*. *C. finmarchicus* produced significantly more eggs in the chlorophyll maximum than did *C. helgolandicus* (H1=7.9; p=0.005), but the difference was not significant between the species feeding in the surface water. EPR decreased from day 1 to 4 at different rates for both species at all stations.

When we separate the analyses between the surface and chlorophyll maximum layer, *C. helgolandicus* differed in size between stations in the surface incubations (significant interaction between water layer and station, 2-way ANOVA $F_{3, 35} = 75$; $p = 0.008$) where the female at station 1 was significantly smaller than at the other stations (Holm Sidack $p < 0.05$). No difference was observed in *C. finmarchicus* size between stations or in *C. helgolandicus* in the chlorophyll maximum layer where more females were behind the mean measurements.

Interaction between environmental factors and production

A Pearsons product moment correlation between female properties showed a significant positive correlation between size of *C. finmarchicus* females and egg production ($r = 0.49$, $n = 39$, $p < 0.001$). A negative correlation was found between faecal pellet production and hatching success for both species ($r = -0.70$, $n = 12$, $p < 0.05$).

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The *in-situ* egg production of *C. helgolandicus* (after 1 day of incubation all years) was best explained by the concentration of ciliates, heterotrophic dinoflagellates and flagellates resulting in a predictive model with r^2=0.87 p = 0.01 (Stepwise Regression, Table VI). None of the fatty acid concentrations of the seston could contribute to explain the observed *C. helgolandicus* EPR. As egg production of *C. finmarchicus* was highly correlated with female prosome length it was standardized to female volume calculated according to (Mauchline, 1998):

logV (mm^3) = 3.614 log PL (µm) – 10.69

where V is female volume, and PL is prosome length. EPR normalized to size, EPR_{vol} was best explained with the fatty acid 22:6n3 that is typical for dinoflagellates (Stepwise Regression, Table VI).

The egg production rates of *C. finmarchicus* after the 4 days of acclimation to the chlorophyll maximum and surface food sources were best explained with the concentration of autotrophic dinoflagellates and flagellates as well as diatoms (stepwise regressions r^2 = 0.87; F_3= 17, p = 0.01; Table VI) . However the EPR of *C. helgolandicus* could not be explained with any of the environmental parameters measured, neither microplankton nor fatty acid concentrations.

Secondary production

The population egg production rate (EPR_{pop}) for *C. finmarchicus* was on average 3 times higher than of *C. helgolandicus* in both 2001 and 2005 but the reverse in 2002 when the EPR_{pop} measured was about 10 times higher for *C. helgolandicus* (Table VII). The secondary production of *C. helgolandicus* and *C. finmarchicus* was highest in 2005 for both species with highest production of about 21 mg C m^{-2} d^{-1} at station 5 respectively, for *C. helgolandicus* and *C. finmarchicus* assuming 0.254 µg C per egg for both species (average value from Ohman and Runge, 1994; Cabal et al., 1997; Hygum et al., 2000; Mayor et al., 2006). At other stations and years the secondary production ranged from 0-5 mg C $m^{-2}d^{-1}$ (Table VII). Naupliar survival was estimated from egg production, hatching and female abundance, and compared to observed naupliar densities. The highest naupliar survival was estimated to be only 8 % from egg to N6.

Faecal pellet production

The comparison of faecal pellet production (FP) between years was only conducted on copepods that could actively feed, that is in the chlorophyll maximum layer even though some pellet production was measured in surface waters in 2005 (Fig. 5). There was a significant difference in *C. helgolandicus* faecal pellet production between stations in 2002 (H_3 = 30.5 P <0.001) but not for *C. finmarchicus*. In 2005 the FP differed between station for both species (F_3 = 11.1, P<0.01 for *C.*

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finmarchicus and H_3 = 9.9; P = 0.02 *C. helgolandicus*). There was a significant difference in FP between years for both species (H_1 = 15.1 and 21.3; P<0.001 for both) with higher production in 2005. When pooled, no significant difference was found between FP of the two species.

The sum of 4 days of feeding (the bioassay in 2005) resulted in a significant difference between stations in faecal pellet production (FP) in the surface waters for both *C. helgolandicus* and *C. finmarchicus* (F_3 = 5.8; p = 0.02 and H_3 = 18.5; p < 0.001, respectively; Fig. 6 b). The difference between stations in chlorophyll maximum was only significant for *C. finmarchicus* (F_3 = 16.6; p < 0.001) where highest production was at stations 5 and 8. FP was significantly higher in the chlorophyll maximum layer for both species (F_1 = 12.5; p < 0.001 for *C. helgolandicus* and H_1 = 45.1; p < 0.001 for *C. finmarchicus*). *C. finmarchicus* had significantly higher faecal pellet production in both layers compared to *C. helgolandicus* (H_1 = 6.6; p = 0.01, F_1 = 11.8; p < 0.001 in surface and chlorophyll maximum, respectively).

Faecal pellet production of *C. finmarchicus* was best explained with the *in situ* concentration of autotrophic flagellates (stepwise regressions r^2 = 0.81; F_1 = 31, p = 0.001) while the faecal pellet production of *C. helgolandicus* was best explained with both *in situ* concentrations of autotrophic flagellates and ciliates (stepwise regressions r^2 = 0.96; F_2 = 77, p < 0.001).

Discussion

The congeneric species, the temperate *C. helgolandicus* and the boreal *C. finmarchicus* overlap both in time and space in the northern North Sea. As species identification is difficult with live specimens, comparative studies of their reproduction and physiology under natural conditions have been limited to date. Therefore this study is an important piece in a larger puzzle, improving our understanding of the co-occurrence and dynamics of these species especially under changing climatic conditions in the North Sea.

Vertical distribution

The present study shows that when *C. helgolandicus* and *C. finmarchicus* co-occur *C. finmarchicus* prefers to stay in deeper, cooler waters (7.5-9 °C) and *C. helgolandicus* above the thermocline in 15-16°C waters. While *C. finmarchicus* was also found above the thermocline and *C. helgolandicus* below the thermocline (e.g. in 2003 station closest to the bank, Fig .2) the majority of the population in all 3 years was separated by the thermocline and the separation is highly significant. Separation of *C. finmarchicus* and *C. helgolandicus* in different water masses has been observed

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before in the North Atlantic (Williams, 1985) where the vertical distribution also was associated with thermal stratification. Such separation of *C. finmarchicus* and *C. helgolandicus* was however, not reported in the North Sea in May 2001 in the review by Bonnet et al (Bonnet et al., 2005) where both species stayed below 10m depth with maximum abundance at 20-40 m. However, during this period the water column was well mixed with Simpson's stability index <10 Joules m^{-3} (Jónasdóttir et al., 2005) with little vertical temperature contrast. Instead of retreating from the North Sea as surface temperatures increase, as may be inferred from CPR data (Beaugrand et al., 2003), it appears that *C. finmarchicus* could just as likely migrate down into cooler waters in summer. This deep maximum in *C. finmarchicus* abundance would not be observed in the CPR data, as the CPR samples to a maximum of 10 m depth. Diel vertical migration appears to be minimal and when taking place, *C. finmarchicus* ascends to about 15 m depth, still below the range of the CPR sampling depth. The high abundance in 2005 shows that *C. finmarchicus* may stay active longer in the North Sea than previously believed (Bonnet et al., 2005; Jónasdóttir et al., 2005). There is however, a large yearly variation in abundance of both species between the years reported here. This yearly variation is most likely due to variation in the strength of the spring invasion into the North Sea from the Faroe Shetland Channel (Beare and McKenzie, 1999; Heath et al., 1999), which is the prerequisite for the success of *C. finmarchicus* in the North Sea.

We cannot explain the vertical separation of the species most prominent in 2005 and at the Buoy station in 2002. There are several possible reasons; interspecies competition for food, avoiding predation of each other's eggs and nauplii and differences in optimal temperature tolerance. Most *Calanus* nauplii were found in the upper 20 m (Table II) where temperature would augment their development time. At this depth they are also out of reach of the females of both *Calanus* species and can therefore avoid cannibalism that can be high at high naupliar concentrations (Bonnet et al 2004). However, different temperature preference is the most likely explanation for the vertical separation at this southern/northern boundary of the species (Fig 4).

Food and feeding

New production is continuously taking place at the deep chlorophyll maximum along the flanks of the Dogger Bank due to tidal pumping of nutrient rich water from the deeper layer (Richardson et al., 2000). It is an area of plentiful and high quality food, promoting copepod growth and survival, at a time when the surface waters are mostly depleted in food (Table III, Fig. 2). The quality of the food ingested is also reflected in the high hatching success of the eggs produced. The faecal pellet production indicated that feeding in the chlorophyll maximum was highest at the stations closest to the bank, decreasing away from the bank (Figs. 5 and 6b). Typically, for summer and subsurface

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blooms, the microplankton community in the chlorophyll maximum was mainly composed of autotrophic and heterotrophic dinoflagellates, and flagellates. While we cannot use our faecal pellet data to calculate ingestion rates as we did not measure the faecal pellet sizes, it is probable that ingestion rates must have been higher for *C. finmarchicus,* having higher faecal pellet production compared to *C. helgolandicus.* Either the ingestion rates were lower or the assimilation efficiency higher in *C. helgolandicus* as the egg production rates of the species were similar and we can assume similar respiration rates during incubation as the temperatures were the same. There is however, no clear explanation for higher pellet production for both species in the surface layer in 2005 compared to 2002. The food abundance and composition was similar these years (Table III).

C. helgolandicus has been shown to be able to feed efficiently on *Ceratium furca* in the North Sea (Jansen et al. 2006); *Ceratium* sp. was the dominant dinoflagellate in the subsurface maximum during the present study. No comparison on feeding, between the congeneric species has been conducted in the field, and was not done in the present study. Studies conducted separately on these species show that both species can be non selective (e.g. *C. helgolandicus*: Irigoien et al. 2000 ; *C. finmarchicus*: Meyer et al., 2002), and selective for ciliates (e.g. *C. helgolandicus*: Nejstgaard et al., 2001; *C. finmarchicus:* Mayor et al., 2006, Ohman and Runge, 1994) or for diatoms (e.g. *C. helgolandicus*: Kleppel et al., 1991; *C. finmarchicus:* Koski, 2007). However, food particle size does seem to affect selectivity for both *Calanus* species (e.g. *C. helgolandicus*: Fileman et al 2007 and *C. finmarchicus*: Meyer et al. 2002) while no selectivity is observed when cell sizes are similar (Meyer et al. 2002).

Reproduction and food environment

The environmental parameters found to affect the immediate egg production rates (1 day *in-situ* incubation) were similar for both species, indicating they are likely to be feeding on similar diets. Both were significantly correlated to the autotrophic dinoflagellates, flagellates and ciliates while the specific nutritionally important fatty acids could not explain any of the variation in the observed egg production rates which may indicate that essential fatty acids were not limiting in the copepod diet. Hirche (Hirche, 1996) reports that egg production of *C. finmarchicus* reduced sharply after 2 days of starvation at 0 ºC. Therefore, in the one day incubations the egg production was based on food they encountered approximately 1-2 days before the incubation. Only few studies have made a simultaneous measure of egg production and selection for these two species and their results show both positive (Meyer-Harms et al. 1999; Niehoff et al. 1999; Koski 2007) and negative (Nejstgaard et al., 2001) relation between EPR and diatom diets and both positive (Irigoien et al 2000) and negative (Nejstgaard, et al., 2001) relation between EPR and the haptophyte *Phaeocystis* spp. Most

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studies, like the present one, make a correlation with microplankton biomass, bypassing ingestion. One of these shows that ciliates can be important for egg production of both *Calanus finmarchicus* and *C. helgolandicus* (Jónasdóttir et al., 2005).

The bioassay study that ran over 4 days gives a better indication of the food environment in the deep chlorophyll maximum layer and how the congeneric species can utilize the subsurface bloom. The differences in feeding and reproduction between the two species became more pronounced showing higher egg- and faecal pellet production for *C. finmarchicus* compared to *C. helgolandicus*. *C. finmarchicus* production was again highly significantly correlated to autotrophic flagellates and dinoflagellates, and to lesser extent diatoms, even though they were present in low concentrations. No measured variables could explain the EPR of *C. helgolandicus* while faecal pellets of both species were highly correlated to the abundance of autotrophic flagellates. Both species had reduced EPR with time, which indicates that they may have had a better food source for production at their original sampling location, in the Skagerrak. This lack of correlation for *C. helgolandicus* underlines the importance of making an estimate of food ingestion and selection to better understand how the food environment affects egg production rates.

Population egg production

The timing of production and distribution of *C. helgolandicus* varies with location in the North Sea (Bonnet et al., 2005) but a seasonal study in a similar area as in the present study (Jónasdóttir et al., 2005) strongly indicated that the peak production season for both species was drawing towards the end in July and August. These authors showed the 2001 peak egg production of *C. finmarchicus* in March and *C. helgolandicus* in May; with relatively constant low population egg production rates (EPR_{pop}) of *C. helgolandicus* (< 50 eggs m^{-3} d^{-1}) and the highest average rates in May for *C. finmarchicus* (150 eggs m^{-3} d^{-1}). Our measurement shows remarkably higher EPR_{pop} in July and August of 21 - 1600 eggs m^{-3} d^{-1} (160 - 82000 eggs m^{-2} d^{-1}) for *C. finmarchicus* and 15 – 890 eggs m^{-3} d^{-1} (450 - 44000 eggs m^{-2} d^{-1}) for *C. helgolandicus* (Table VII). The contribution of *C. finmarchicus* was therefore on the average 15 times larger in August 2005 compared to its highest in 2001 but similar for *C. helgolandicus* and 2 times higher in August 2005 compared to May 2001 (Jónasdóttir et al., 2005). Our measurements are in the same order of magnitude as the spring EPR_{pop} of *Calanus finmarchicus* at the peak of their spring production in Northern Norwegian Fjords; 60000-120000 eggs m^{-2} d^{-1} (Koski, 2007) and the maximum reported for Station M in the Norwegian Sea in June of about 35000 eggs m^{-2} d^{-1} (Niehoff et al., 1999). It was somewhat surprising that *C. finmarchicus* had a larger contribution to total production during late summer for 2 years, based on the fact that this species was not expected to be dominant in the North Sea in late

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summer. During 2002 *C. finmarchicus* was in much lower abundance on the Dogger Bank transect resulting in 10 times higher EPR_{pop} for *C. helgolandicus*. However, at the buoy station the abundances were similar and if assuming the same egg production rates there for both species as measured at the transect stations, the EPR_{pop} of the species was the same. However, only 2-20% of this production may make past the N6 stage, but according to Eiane and Ohman (Eiane and Ohman, 2004) mortality is highest in naupliar stages 1-3 for *C. finmarchicus.*

The individual egg production rate of the two species did not appear to differ at any time. The incubations of both species were carried out at the same temperatures, while the copepods inhabit *in-situ* water masses of about 7 °C difference. We do not know if the production rates of the species at the same incubation temperature would be affected by their previous *in-situ* temperature preference, but as there was no significant difference in the instant (day 1) egg production rates in the surface (ca 15°C) and chlorophyll maximum (ca 7°C) incubations in 2002 and 2005 (Table V) we can conclude that the previous temperatures do not affect the immediate production rates. The EPR of *C. finmarchicus* was always higher than of *C. helgolandicus* but due to high variation in some of the measurements the difference was never significant. However, *C. finmarchicus* had a significantly higher maximum rate compared to *C. helgolandicus*. The highest EPR of 79 and 94 eggs for *C. helgolandicus* and *C. finmarchicus* respectively represents about 80 and 85 % of their reproductive potential based on their size and are therefore high for the end of the reproductive season (see Fig. 6a in Jónasdóttir et al., 2005) in the North Sea. It is difficult to calculate the specific egg production rates for *Calanus* due to the variable content of their lipid reserve that can give them a relatively high carbon weight. However, if we use a carbon weight of 77 µg C $female^{-1}$ (estimated from dry weight of similar sized lipid free females from the North Sea, Jónasdóttir unpublished, assuming carbon to be ca 47% of dry weight; Båmstedt 1986) and an egg weight of 0.254 µg C (see above) the specific egg production was 4 -9% and 3-15% for *C. helgolandicus* and *C. finmarchicus* respectively. This is similar to the values for *C. finmarchicus* production in Greenland waters (Madsen et al., 2008), but lower than that reported by Koski for Norwegian fjords (Koski, 2007). Those studies use higher carbon content for females which means that our values are in the lower range. No published specific egg production values of were found for *C. helgolandicus.*

The general conclusion of this study is that when *C. helgolandicus* and *C. finmarchicus* co-occur during July and August off Dogger Bank, they are vertically separated and this is best explained by the different temperature preference of the species. Due to the difference in abundance *C. finmarchicus* is a more important species during late summer than *C. helgolandicus* off Dogger Bank.

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The deep chlorophyll maxima in the North Sea appears to give both species a refuge, offering both a high quality food away from the surface waters where highest predation pressure may occur, as well as offering optimal temperatures for both species. This suggests that the summer productivity of both species is as high as during the spring bloom, further underscoring the central importance of subsurface primary production in fuelling the North Sea ecosystem.

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Table I. Measurements conducted on the Dana cruises in the years 2001- 2003 and 2005. Egg production and hatching incubations of *Calanus finmarchicus* and *C. helgolandicus* and environmental measurements, Station numbers are as in Fig. 1. For fatty acids and microplankton data in 2003 see Koski et al. (submitted).

Table II. Dogger Bank 2001 - 2003 and 2005. Average temperature (T °C) chlorophyll concentration (µg L^{-1}) and abundance of *C. finmarchicus* (CF) and *C. helgolandicus* (CH) females (no m^{-2}), stages, C5, C1-4 and nauplii integrated over depth layers 0-20m, 20-40m and 40-60 m and averaged over the whole transect. Abundance numbers in 2001 are averaged over the whole water column and C1-4 includes stage C5. na: not analysed.

Table III. Chl-*a* and the carbon concentration of the main microplankton groups (µg L^{-1}), as well as the POC (microplankton C): Chl-*a* ratio at the four Dogger Bank transect stations in 2001, 2002 and 2005 (mean ± SD of the 2-3 times when the station was visited). The depth of the chlorophyll maximum layer is given in parenthesis; the surface water was always sampled at ca 5 m.

Table IV. Fatty acid composition (µg L^{-1}) of seston on the Dogger Bank transects. Stations as in Fig. 1, Chl max: sub surface chlorophyll maximum. SAFA, MUFA and PUFA: saturated, monounsaturated and polyunsaturated fatty acids and include minor fatty acids not shown in the table.

Table V. *Calanus helgolandicus* and *C. finmarchicus*. Average female length (mm ± SE), spawning females, EPR_{max} (eggs $female^{-1}$ day^{-1}) of producing females only with highest individual EPR shown in parenthesis, EPR (eggs $female^{-1}$ day^{-1}) and hatching success of eggs (n = total number of eggs incubated, na: not available) at different stations on the Dogger Bank in 2001, 2002 and 2005. 2005 data shows results from after 1 day of incubation. * From Jónasdóttir et al. 2005, + measurement from incubation day 2. Significant differences between stations within each year are indicated by different lower case letters (Holm Siddak *a posteriori* all pair wise comparison $p<0.05$). The capital letters describe significant differences ($p<0.05$) between years, pooling all stations (one way ANOVA).

Table VI. *C. helgolandicus* and *C. finmarchicus*. Results from multiple stepwise regression on *in situ* (2001-2005) and bioassay egg production rates in 2005 (eggs $female^{-1}$ d^{-1} or eggs mm^{-3} d^{-1}) the

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food environment , chlorophyll a (µg L^{-1}), auto- and heterotrophic flagellates, diatoms, auto- and heterotrophic dinoflagellates and ciliates (µgC L^{-1}). The stepwise process selects only those variables (labelled "in") that contribute to the best regression. Variables not in the regression are labelled "out". Model statistics show R^2: coefficient of determination of the multiple regression, F_{df} : the F ratio with *df*: degrees of freedom, and significance value *p* of the multiple regression. For each variable in the model, "F-to-remove" is the F statistic for its coefficient within the regression; for each variable not in the model, "F-to-enter" is the F statistic that its coefficient would have if it were the next variable added in the regression. p_{var}: significance of the variable within the regression where * : $p<0.05$, ** $p<0.01$.

Table VII. *C. helgolandicus* and *C. finmarchicus.* Population dynamics on the Dogger Bank. Population egg production rates (eggs m^{-2} d^{-1}) and secondary production (C m^{-2} d^{-1}) for CH: *C. helgolandicus* and CF: *C. finmarchicus* and N1-6 produced: Nauplii stages 1-6 produced per m^{-2} based on observed hatching success assuming 1 stage per day for 6 stages. Nauplii observed are the depth integrated naupliar stages 1 – 6 at each station (no m^{-2}) and % survival is the estimated survival of the nauplii produced.

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Figure 1. Stations sampled in 2002, 2003 and 2005(stars) where intensive stations are filled stars and CTD stations are all stars. Stations used from the cruise in 2001 are marked with A, B, C and D (Jónasdóttir et al., 2005). The drifting buoy station B in 2002 is labelled with open triangles.

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Figure 2. A) Vertical distribution of chlorophyll *a* (filled contours in µg L^{-1}) and temperature (line contours °C) on the transects north of Dogger Bank in the years 2001, 2002, 2003 and 2005. B) Vertical distribution of female *Calanus helgolandicus* (hatched bars) and *Calanus finmarchicus* (white bars) abundance (numbers m^{-3}). In 2001 bars represent abundance at stations B, C and D based on a vertically integrated tow (no *Calanus* found at station A).

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Figure 3. a) Diurnal variation in the vertical distribution of chlorophyll *a* (filled contours in µg L^{-1}), temperature (line contours °C) and the female abundance (numbers m^{-3}) of *Calanus helgolandicus* (hatched bars) and *Calanus finmarchicus* (white bars) at the buoy station B in 2002. Whiskers are +1 SE of average 2-5 pump profiles). b) Abundance (numbers m^{-3}) of female *Calanus helgolandicus* (hatched bars) and *Calanus finmarchicus* (white bars) at day and night at stations 3 and 5 in 2005.

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Figure 4. *C. helgolandicus* (hatched bars) and *C. finmarchicus* (open bars). a) Female and b) C5 abundance (no m^{-3}) in temperature bins of 3 degrees.

Figure 5. *C. helgolandicus* and *C. finmarchicus.* Station averages of egg production rates (EPR: eggs $female^{-1}$ d^{-1}) surface and chlorophyll max waters combined, and of faecal pellet production (pellets $female^{-1}$ d^{-1}) in surface waters and chlorophyll max in 2001, 2002 and 2005. Whiskers are +1 SE.

Figure 6. *C. helgolandicus* and *C. finmarchicus*. Cumulative a) egg production and b) faecal pellet production in chlorophyll max and surface waters at the 4 stations in 2005. Whiskers are ± 1 SE.

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Table I

	2001 19 July	2002 7-13 August	2003 14-19 August	2005 27 July – 2 August
Egg production	*In situ* surface 16°C stations A*, B, C, D	*In situ* surface 15°C & Chl_{max} 9°C Two times stations 1, 3, 5, 7		Bioassay, 4 day incubations surface 15°C & Chl_{max} 9°C stations 1, 3, 5, 8
Hatching	surface stations A*, B, C, D	surface Two times stations 1, 3, 5, 7		Lost
Chl *a* and T	profile 6 stations (1 time)	profile 15 stations (4 times)	profile 17 stations (6 times)	profile 15 stations (7 times)
Fatty acids seston	Chl_{max} stations A, B, C, D (1 time)	Chl_{max} and surface stations 1, 3, 5, 7 (2 times)	Chl_{max} and surface stations 1, 3, 5, 8 (2 times)	Chl_{max} stations 1, 3, 5, 8 Surface station. 1 (2 times)
Microplankton	Ciliates station D	Chl_{max} and surface stations 1, 3, 5, 7 (2 times)	Chl_{max} and surface stations 1, 3, 5, 8 (4 times)	Chl max and surface stations 1, 3, 5, 8
Zooplankton abundance	Integrated vertical stations A, B, C, D	10 m depth intervals Day: stations 2, 4 Buoy: Time series, 12 times	5 m depth intervals Day: stations 3, 5, 8	5 m depth intervals Day stations 1, 3, 5, 8 Night stations 3, 5

*No females found at station A in 2001

Table II:

	Depth layer	T °C	Chl a µg L^{-1}	CH females m^{-2}	CF females m^{-2}	CH_{C5} m^{-2}	CF_{C5} m^{-2}	C1-4 m^{-2}	nauplii m^{-2}
2001	0-20	14.7 ± 0.5	1.2 ± 0.2	131 ± 87	310 ± 87	na	na	4720 ± 2333 (incl. C5)	2257 ± 1495
	20-40	9.6 ± 2.8	2.3 ± 0.9						
	40-60	6.4 ± 0.4	1.4 ± 0.2						
2002	0-20	17.5 ± 1.2	0.6 ± 0.1	358 ± 197	6 ± 6	253 ± 181	6 ± 6	486 ± 103	na
	20-40	12.8 ± 3.1	1.1 ± 0.8	246 ± 79	63 ± 4	385 ± 226	53 ± 33	125 ± 19	na
	40-60	7.3 ± 0.8	0.6 ± 0.2	6 ± 4	0	0	22 ± 0	14 ± 10	na
2002 Buoy	0-20	17.6 ± 0.1	0.5 ± 0.01	361 ± 158	55 ± 14	na	na	157 ± 62	na
	20-40	10.8 ± 0.5	1.3 ± 0.2	92 ± 54	251 ± 78	na	na	102± 17	na
	40-60	7.8 ± 0.00	0.9 ± 0.0	17 ± 5	48 ± 5	na	na	34± 4	na
2003	0-20	18.4 ± 0.5	0.4 ± 0.1	59 ± 59	140 ± 81	188 ± 97	30 ± 17	619 ± 185	na
	20-40	13.0 ± 3.5	0.7 ± 0.5	62 ± 38	348 ± 240	104 ± 51	797 ± 570	648 ± 286	na
	40-60	7.5 ± 0.7	0.8 ± 0.6	31 ± 31	78 ± 78	410 ± 56	219 ± 52	302 ± 264	na
2005	0-20	14.8 ± 0.4	0.5 ± 0.1	605 ± 350	121 ± 53	39 ± 24	237 ± 98	444 ± 295	12480 ±7435
	20-40	11.6 ± 2.6	0.8 ± 0.4	106 ± 71	658 ± 353	0	2960 ± 1326	222 ± 107	342 ± 195
	40-60	7 .0 ± 0.7	0.6 ± 0.3	0	258 ± 206	0	1826 ± 1110	163 ± 128	389 ± 304

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Table III

Group	**Chl-max**				**Surface**			
2001	**St A (35)**	**St B (33)**	**St C (26)**	**St D (29.5)**	**St A (5)**	**St B (5)**	**St C (5)**	**St D (5)**
Chl-*a*	2.9	4.0	3.6	2.7	1.2	1.1	1.1	1.0
Ciliates				4.6				
2002	**St 1 (36.5)**	**St 3 (35)**	**St 5 (33.5)**	**St 7 (30.5)**	**St 1 (5)**	**St 3 (5)**	**St 5 (5)**	**St 7 (5)**
Flagellates	39 ± 5.4	8 ± 7	12	9 ± 2	5 ± 1	7 ± 2	5	14 ± 0
Diatoms	0.002 ± 0.002	0.005 ± 0.001	0.02	0.0003 ± 0.0004	0 ± 0	0 ± 0	0.1	0.0 ± 0.0
Autotrophic dinoflagellates	334 ± 65	192 ± 37	21	120 ± 149	5 ± 4	3 ± 1	5	5 ± 1
Heterotrophic dinoflagellates	32 ± 13	20 ± 1	6	19 ± 17	4.5 ± 5	3 ± 1	3	6 ± 2
Ciliates	12 ± 11	12 ± 3	6	6 ± 3	1 ± 0.3	2 ± 0.4	5	4 ± 2
Total	416 ± 46	232 ± 34	45	153 ± 167	16 ± 11	15 ± 4	18	29 ± 2
Chl-*a*	4.1 ± 0.7	3.8 ± 0.3	1.4 ± 0.4	2.2 ± 0.8	0.4 ± 0.02	0.5 ± 0.05	0.6 ± 0.59	0.6 ± 0.59
POC: Chl-*a*	102	62	41	60	31	40	31	50
2005	**St 1 (40.5)**	**St 3 (37)**	**St 5 (37.5)**	**St 8 (33)**	**St 1 (5)**	**St 3 (5)**	**St 5 (5)**	**St 8 (5)**
Flagellates	6 ± 3	6.7 ± 2.3	7.3 ± 3.3	5.5 ± 3.5	1.6 ± 0.7	1.8 ± 0.5	1.3 ± 0.3	1.9 ± 0.4
Diatoms	0.4 ± 0.6	0.07 ± 0.1	0.006 ± 0.01	7.0 ± 5.1	0.2 ± 0.2	0.5 ± 0.4	0.7 ± 0.6	0.2 ± 0.3
Autotrophic dinoflagellates	147 ± 147	119 ± 55	26 ± 3.9	12 ± 11	3.1 ± 1.2	4.1 ± 1.8	3.5 ± 1.4	6.1 ± 4.0
Heterotrophic dinoflagellates	10 ± 8	4.7 ± 2.0	5.8 ± 3.6	4.4 ± 3.9	1.3 ± 0.4	1.6 ± 0.9	3.2 ± 1.9	2.4 ± 2.0
Ciliates	5 ± 1	3.0 ± 3.5	2.1 ± 1.1	1.9 ± 1.0	3.2 ± 1.8	1.2 ± 0.1	4.1 ± 1.2	3.0 ± 1.7
Total	168 ± 154	133 ± 53	41 ± 4.1	31 ± 15	11 ± 5.1	12 ± 5.2	14 ± 6.3	16 ± 9.2
Chl-*a*	2.3 ± 0.8	1.6 ± 0.5	1.9 ± 0.8	1.4 ± 0.5	0.4 ± 0.1	0.4 ± 0.1	0.4 ± 0.1	0.5 ± 0.1
POC: Chl-*a*	74	82	21	23	28	29	35	35

Table IV.

Year:	2001				2002				2005								
Station:	A	B	C	D	1	3	5	7	1	3	5	7	1	3	5	8	1
	Chl max				Chl max				Surface				Chl max				Surface
Depth (m)	30	27	34	35	38	37	35	31	5	8	12	11	37	34	35	27	5
14:0	2.58	5.78	12.31	7.92	19.70	9.89	5.05	5.35	2.60	2.69	4.93	3.85	23.93	17.28	11.01	19.08	8.93
16:0	7.85	13.18	21.32	14.65	28.27	19.38	16.19	14.80	9.52	6.52	12.53	9.74	25.49	15.98	8.57	16.92	11.32
18:0	3.18	3.79	5.00	3.44	8.32	6.08	6.31	5.97	10.52	4.28	6.67	6.28	10.30	3.21	2.46	6.24	4.13
SAFA	14.22	22.86	38.70	26.06	56.62	35.60	27.80	26.33	23.00	13.58	24.40	20.11	62.19	37.08	22.45	43.11	25.07
16:1n7	1.33	2.37	4.28	5.82	0.10	0.04	0.07	0.07	0.03	0.01	0.08	0.07	6.99	8.17	3.47	8.38	4.59
18.1n9	2.05	2.13	4.29	2.81						0.01	0.01	0.01	2.29	1.05	0.51	1.11	1.09
20:1n9	0.04	0.03	0.03	0.04	0.00			0.01					2.12	0.34	0.30		0.89
MUFA	4.50	5.72	11.49	10.49	0.14	0.04	0.07	0.09	0.04	0.04	0.08	0.08	18.36	11.61	5.41	13.16	9.82
16:2n4	0.05	0.79	1.07	0.67	0.12	0.07	0.07	0.07	0.08	0.02	0.08	0.05					
16:4nx	0.35	0.82	0.56	1.50				0.01				0.01	1.94	0.21	0.20	0.36	0.26
18:2n6	0.79	1.15	2.95	1.10									1.97	0.68	0.35	0.63	0.34
18:2n4	0.33	0.01			0.09	0.01	0.06	0.03	0.07	0.01	0.10						
18:3n6	0.01				0.51		0.15	0.13	0.22	0.13	0.10	0.07					
18:3n3	0.73	1.03	2.79	1.01	0.11	0.02	0.03	0.05	0.03	0.03	0.02	0.05	1.13	1.03	0.62	0.85	0.35
18:4n3	0.85	2.05	3.52	1.64				0.01					2.15	2.98	1.46	2.50	0.95
18.5n3	0.28	4.06	7.78	2.75						0.04			3.87	6.18	2.26	2.94	1.36
20:2n6	0.08	0.02	0.01	0.17						0.01			0.01	0.17		0.10	0.11
20:3n6	0.40			0.02	0.24	0.01	0.14	0.09	0.08	0.04	0.05	0.06	0.01		0.23		0.05
20:3n3	0.05	0.03			0.22	0.10	0.43	0.29	0.21	0.06	0.18	0.13					
20:5n3	0.97	1.95	2.71	4.64	0.00	0.00	0.01	0.01	0.04	0.01			0.48	0.74	0.23	0.32	0.19
22:6n3	1.90	3.15	5.79	1.91	0.03	0.03	0.01	0.03					4.20	8.70	2.17	2.77	1.71
PUFA	7.40	15.11	27.25	16.72	1.55	0.39	1.01	0.84	0.77	0.39	0.63	0.41	15.96	20.68	7.52	10.63	5.39
Total	**26.12**	**43.69**	**77.44**	**53.27**	**58.30**	**36.04**	**28.88**	**27.27**	**23.81**	**14.01**	**25.11**	**20.60**	**96.51**	**69.37**	**35.37**	**66.89**	**40.27**
n3/n6	2.49	5.39	3.87	7.19	0.70	20.92	1.95	2.00	1.08	0.81	1.42	1.38	3.56	15.65	5.50	5.43	5.53
22/20	1.96	1.62	2.13	0.41	-	-	0.67	2.15	0	0.00	-	-	8.72	11.75	9.63	8.54	9.03

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Table V

	Length *mm ± 1SE*		*spawning females / total females*		*EPR_{max}; eggs female^{-1} d^{-1}* *(highest individual EPR)*		*EPR* *eggs female^{-1} d^{-1}*		*Hatching* *% (n)*
	C. helgolandicus	*C. finmarchicus*	*C. helgolandicus*	*C. finmarchicus*	*C. helgolandicus*	*C. finmarchicus*	*C. helgolandicus*	*C. finmarchicus*	
2001:	A	A	A	A	A	A	A	A	A
Station A	[a] 2.5 ± 0.03	[a,b] 2.4 ± 0.09	6/10	2/4	[a] 18 ± 4 (31)	[a] 25 ± 9 (33)	[a] 13 ± 4	[a] 12 ± 8	[a] 98 (217)*
Station B	[a] 2.4 ± 0.02	[a,b] 2.4 ± 0.06	11/15	3/9	[a] 24 ± 2 (36)	[a] 24 ± 8 (39)	[a] 17 ± 3	[a] 8 ± 4	[a] 96 (222)*
Station C	[a] 2.5 ± 0.02	[a] 2.5 ± 0.04	2/2	15/22	[a] 24 ± 0 (24)	[a] 45 ± 4 (80)	[a] 23 ± 0	[a] 29 ± 5	[a] 98 (196)*
Station D	[a] 2.4 ± 0.08	[b] 2.3 ± 0.03	8/9	8/13	[a] 20 ± 4 (35)	[a] 37 ± 8 (69)	[a] 18 ± 4	[a] 23 ± 7	[a] 99 (155)*
2002	A	A	A	A	B	A	B	A	B
Station 1	[a,b] 2.5 ± 0.01	[a] 2.4 ± 0.12	37/51	3/3	[a] 27 ± 2 (61)	[a] 23 ± 10 (35)	[a] 20 ± 2	[a] 23 ± 10	[a] 93 ± 4 (1295)
Station 3	[a] 2.5 ± 0.01	[a] 2.4 ± 0.03	35/43	25/31	[a] 32 ± 2 (62)	[a] 40 ± 4 (88)	[a,b] 26 ± 3	[a] 32 ± 4	[b] 85 ± 9 (1537)
Station 5	[b] 2.4 ± 0.02	[a] 2.4 ± 0.02	39/44	21/25	[a] 31 ± 3 (79)	[a] 27 ± 3 (55)	[a,b] 28 ± 3	[a] 16 ± 3	[a,b] 92 ± 3 (1406)
Station 7	[a,b] 2.5 ± 0.01	[a] 2.4 ± 0.02	59/65	4/8	[a] 32 ± 2 (75)	[a] 25 ± 12 (54)	[b] 29 ± 2	[a] 13 ± 7	[a] 93 ± 6 (1565)
2005 day 1:	B	B	A	A	A	A	AB	B	
Station 1	[a] 2.4± 0.10	[a] 2.6 ± 0.03	1/3	15/29	[a] 17 (31)	[a,c] 46 ± 5 (73)	[a] 8 ± 8	[a] 33 ± 7	na
Station 3	[a] 2.6 ± 0.02	[a] 2.7 ± 0.03	8/9	21/29	[a] 22 ± 3 (36)	[c] 47 ± 5 (94)	[a] 24 ± 5	[a] 43 ± 7	na
Station 5	[a] 2.6 ± 0.05	[a] 2.6 ± 0.03	12/13	19/25	[a] 20 ± 3 (37)	[a,b] 32 ± 5 (67)	[a] 23 ± 4	[a] 32 ± 6	na
Station 8	[a] 2.6 ± 0.04	[a] 2.6 ± 0.03	9/11	19/22	[a] 21 ± 4 (40)	[b] 30 ± 3 (56)	[a] 19 ± 5	[a] 27 ± 4	na

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Table VI.

	variable		*F*-to-remove	*F*-to-enter	p_{var}
C. helgolandicus					
eggs female^{-1} d^{-1}	chl *a*	out	-	0.3	0.605
R^2 = 0.87	heterotrophic dinoflagellates	in	14.4	-	0.004*
F_3 = 17.0	autotrophic dinoflagellates	out	-	0.01	0.919
p= 0.01	ciliates	in	6.4	-	0.065*
	flagellates	in	37.6	-	0.019*
	diatoms	out	-	2.1	0.217
C. finmarchicus					
eggs mm^{-3} d^{-1}	chl *a*	out	-	0.5	0.52
	heterotrophic dinoflagellates	out	-	1.8	0.23
R^2 = 0.65	autotrophic dinoflagellates	in	7.7	-	0.04*
F_2 = 4.7	ciliates	in	5.9	-	0.06
p= 0.07	flagellates	out	-	0.7	0.45
	diatoms	out	-	1.0	0.37
2005 (day 4)					
C. finmarchicus					
eggs female^{-1} d^{-1}					
	heterotrophic nanoflagellates	out	-	1.0	0.382
R^2 = 0.87	autotrophic nanoflagellates	in	50.1	-	0.002**
F_3 = 17.0	heterotrophic dinoflagellates	out	-	3.7	0.128
p= 0.01	autotrophic dinoflagellates	in	25.3	-	0.007*
	ciliates	out	-	0.5	0.527
	diatoms	in	9.8	-	0.035*

Table VII.

YR	Station	CH Population EPR egg m^{-2} d^{-1}	CF Population EPR egg m^{-2} d^{-1}	CH Secondary production mg C m^{-2} d^{-1}	CF Secondary production mg C m^{-2} d^{-1}	N1-6 produced m^{-2}	Nauplii observed m^{-2}	% survival
2001	A	111*	42*	0.0	0.0	-	-	-
	B	5146	1453	1.3	0.4	38010	1211	3.2
	C	1490	20668	0.4	5.2	130292	777	0.6
	D	443	819	0.1	0.2	7496	331	4.4
2002	1							
	3	23183	2222	5.8	0.6	129568	-	-
	5	9178	1067	2.3	0.3	56549	-	-
	7							
2005	1	4850	14331	1.2	3.6	109334+	10021	9.2
	3	4217	49954	1.1	12.5	308771+	6534	2.1
	5	44355	81667	11.1	20.4	718327+	36048	5.0
	8	2568	162	0.6	0.0	15561+	193	1.2

* No females found in quantitative plankton tow, but enough found in qualitative tows for egg production incubations. Abundance artificially set for 0.2 female m^{-3}. + Hatching success in 2005 was assumed to be 95% (average from all hatching measurements).

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There was as significant difference between stations in faecal pellet production (FP) in the surface waters for both *C. helgolandicus* and *C. finmarchicus* ($F_3 = 5.8$; $p = 0.02$ and $H_3 = 18.5$; $p < 0.001$, respectively; Fig. 6 b). The difference between stations in chlorophyll max was only significant for *C. finmarchicus* ($F_3 = 16.6$; $p < 0.001$) where highest production was on stations 5 and 8. FP was significantly higher in chlorophyll max layer for both species ($F_1 = 12.5$; $p < 0.001$ for *C. helgolandicus* and $H_1 = 45.1$; $p < 0.001$ for *C. finmarchicus*). *C. finmarchicus* had significantly higher faecal pellet production in both layers compared to *C. helgolandicus* ($H_1 = 6.6$; $p = 0.01$, $F_1 = 11.8$; $p < 0.001$ in surface and chlorophyll max, respectively).

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The same correlations were found for *C. finmarchicus* but in addition female length and egg production (and clutch size) were positively correlated.

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C. helgolandicus	Clutch n = 19	Egg production n = 19	Spawning frequency n = 19	Faecal pellet production n = 19	Hatching n = 12
Length	-0.25	0.14	0.22	**0.54***	-0.41
Clutch		**0.80*****	0.22	-0.342	-0.49
Egg production			**0.66***	-0.12	-0.30
Spawning frequency				0.178	0.07
Faecal pellet production					**-0.70***
C. finmarchicus	n = 39	n = 39	n = 39	n = 39	n = 12
Length	0.229	**0.493****	0.234	**0.602*****	-0.411
Clutch		**0.779*****	-0.012	0.108	-0.485
Egg production			**0.446***	0.284	-0.300
Spawning frequency				0.048	0.072
Faecal pellet production					**-0.703***

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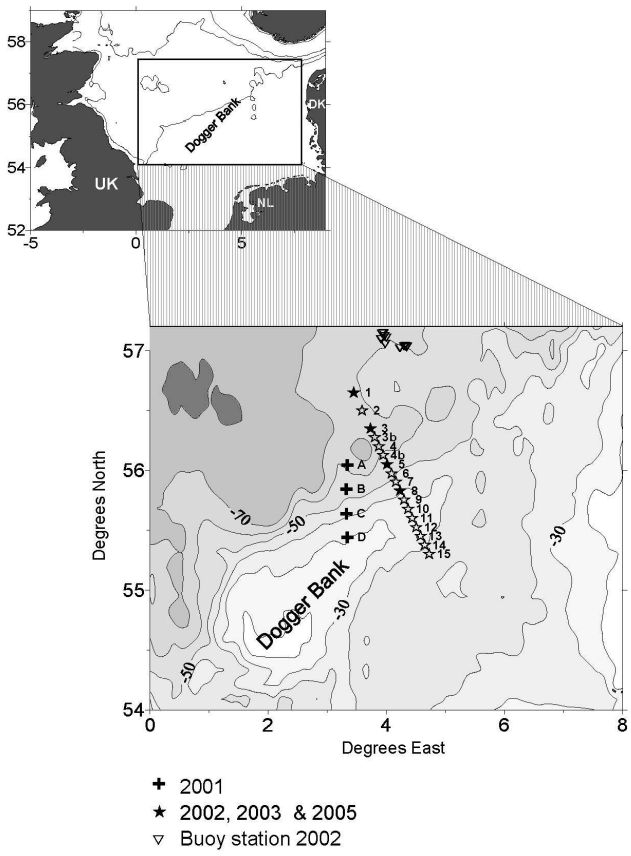

Jonasdottir & Koski Figure 1

Figure 1. Stations sampled in 2002, 2003 and 2005(stars) where intensive stations are filled stars and CTD stations are all stars. Stations used from the cruise in 2001 are marked with A, B, C and D (Jónasdóttir et al., 2005). The drifting buoy station B in 2002 is labelled with open triangles.
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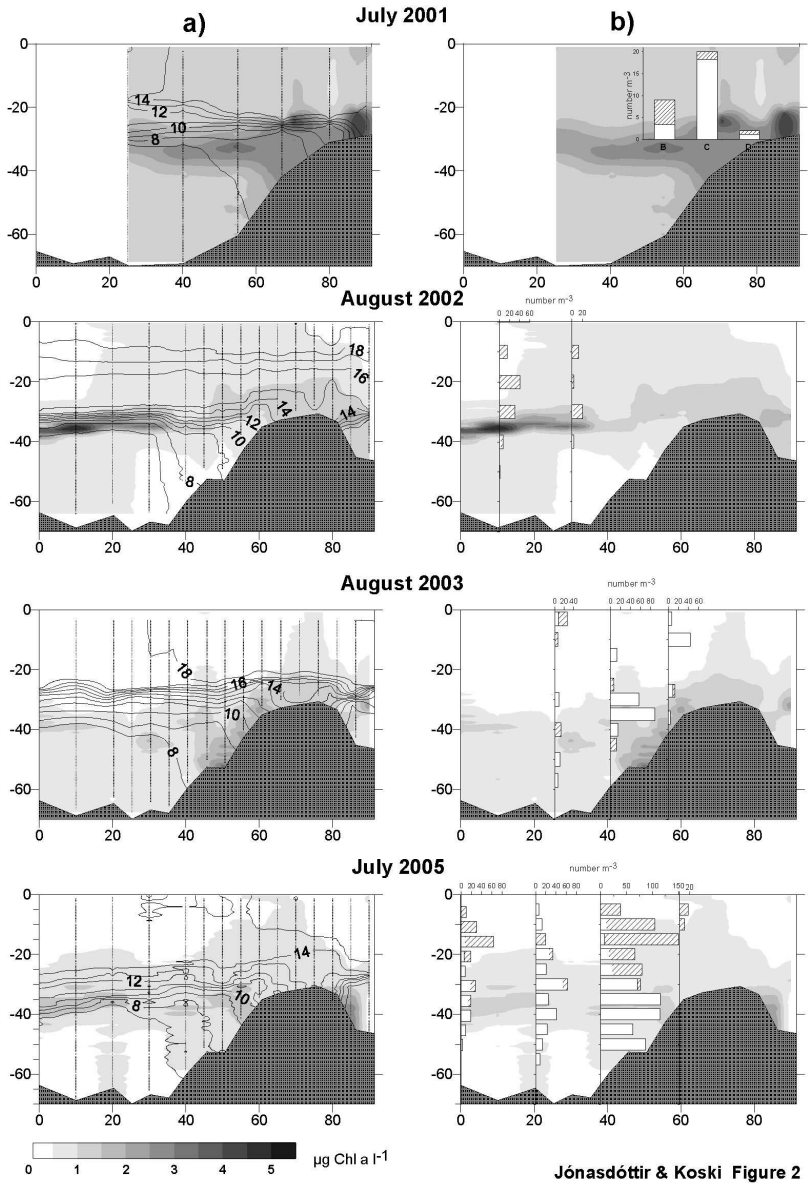


Figure 2. A) Vertical distribution of chlorophyll a (filled contours in μg L-1) and temperature (line contours °C) at the transects north of Dogger Bank in the years 2001, 2002, 2003 and 2005. B) Vertical distribution of female Calanus helgolandicus (hatched bars) and Calanus finmarchicus (white bars) abundance (numbers m-3). In 2001 bars represent abundance at stations B, C and D based on a vertically integrated tow (no Calanus found at station A).
210x297mm (200 x 200 DPI)

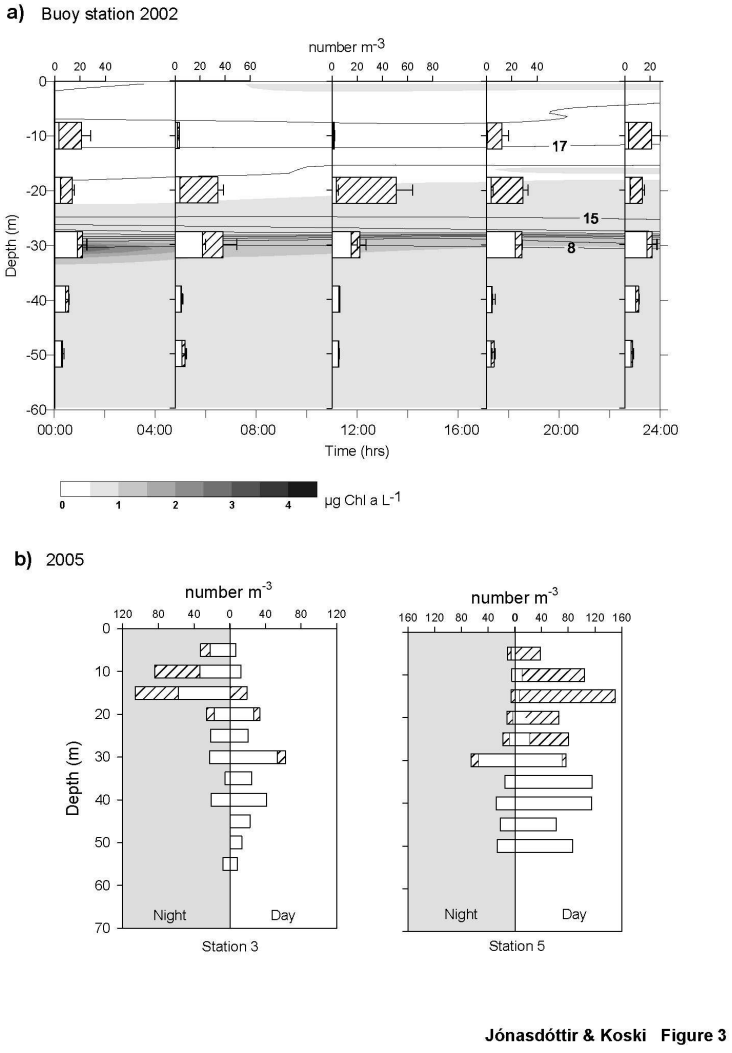
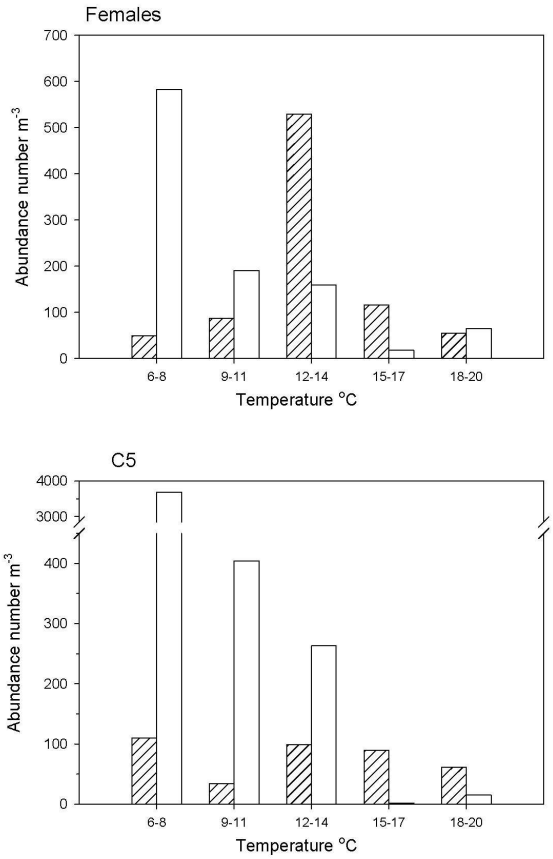


Figure 3. a) Diurnal variation in the vertical distribution of chlorophyll a (filled contours in µg L-1), temperature (line contours °C) and the female abundance (numbers m-3) of Calanus helgolandicus (hatched bars) and Calanus finmarchicus (white bars) at the buoy station B in 2002. Whiskers are +1 SE of average 2-5 pump profiles). b) Abundance (numbers m-3) of female Calanus helgolandicus (hatched bars) and Calanus finmarchicus (white bars) at day and night at stations 3 and 5 in 2005.
210x297mm (200 x 200 DPI)



Jónasdóttir & Koski Figure 4

Figure 4. C. helgolandicus (hatched bars) and C. finmarchicus (open bars). a) Female and b) C5 abundance (no m-3) in temperature bins of 3 degrees.
210x297mm (200 x 200 DPI)

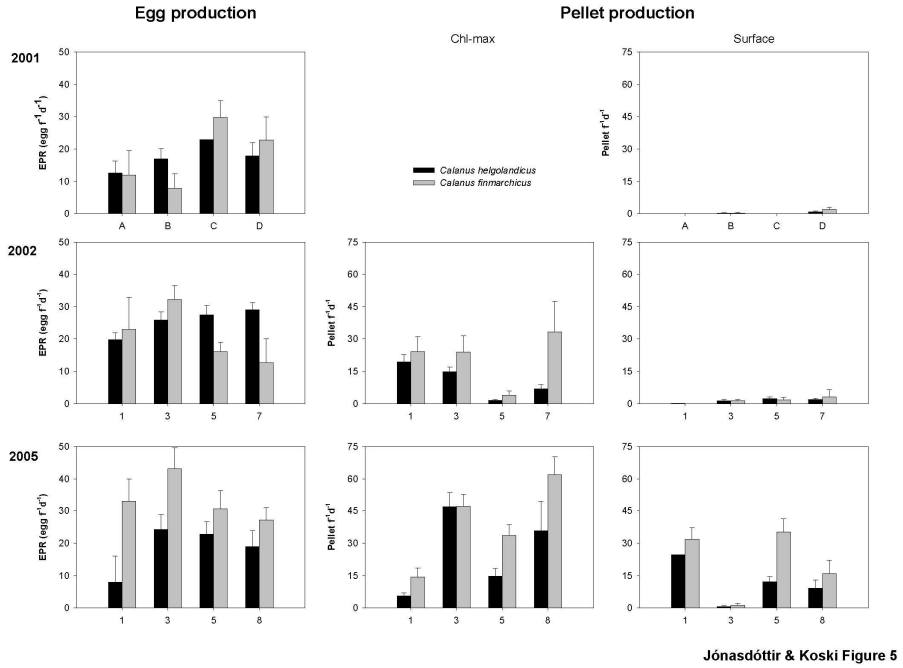


Figure 5. C. helgolandicus and C. finmarchicus. Station averages of egg production rates (EPR: eggs female-1 d-1) surface and chlorophyll max waters combined, and of faecal pellet production (pellets female-1 d-1) in surface waters and chlorophyll max in 2001, 2002 and 2005. Whiskers are +1 SE. 297x210mm (200 x 200 DPI)

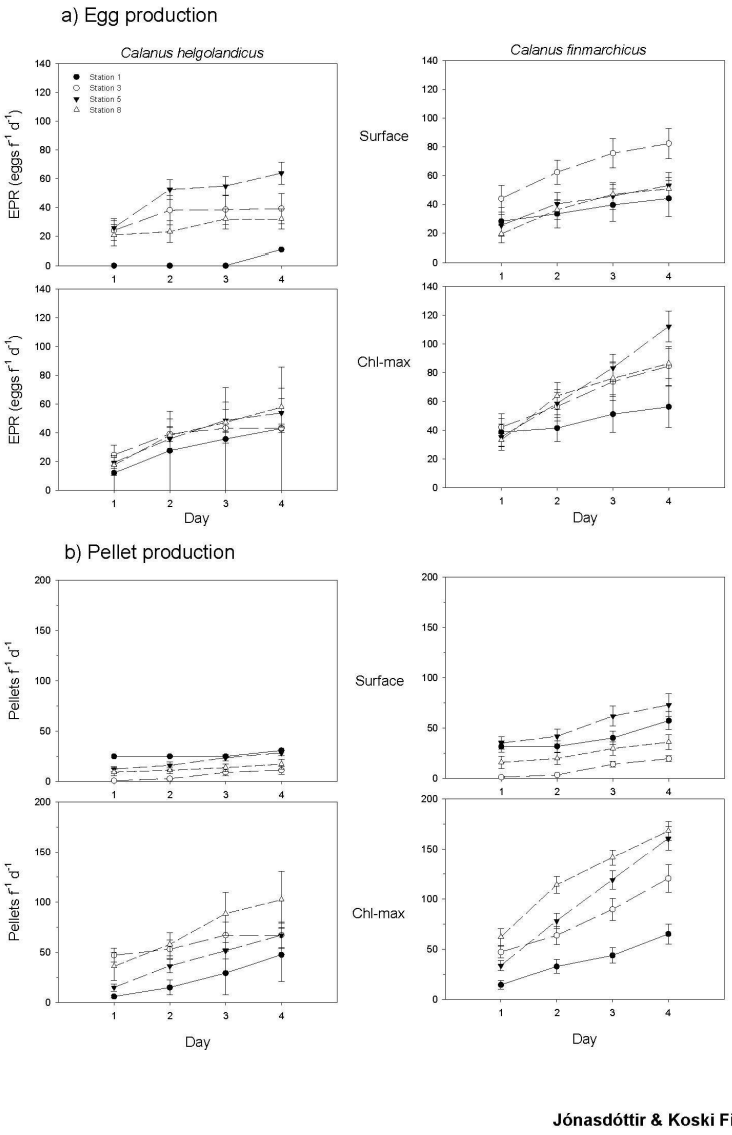


Figure 6. C. helgolandicus and C. finmarchicus. Cumulative a) egg production and b) faecal pellet production in chlorophyll max and surface waters at the 4 stations in 2005. Whiskers are ± 1 SE. 210x297mm (200 x 200 DPI)