

Title: On the surprising lack of differences between two congeneric calanoid copepod species, *Calanus finmarchicus* and *C. helgolandicus*

Authors: Robert J. Wilson¹, Douglas C. Speirs¹, Michael R. Heath¹

¹University of Strathclyde

Corresponding author: Robert J. Wilson, robert.wilson@strath.ac.uk, +44 0141 548 3809

Address: Department of Mathematics, University of Strathclyde, 26 Richmond Street, Glasgow, G1 1XH, Scotland, United Kingdom

Abstract:

The important calanoid copepod species *Calanus finmarchicus* and *C. helgolandicus* have distinct geographic ranges which are changing under the influence of climate change. Understanding the mechanisms underlying their distributions is becoming increasingly important as a result of the possible ecological impacts of these range shifts. Here we review inter-species differences in key life cycle traits that influence each species' geographic distribution, in particular development and growth, fecundity, feeding behaviour, vertical migration and overwintering behaviour. The distinct temperature niche of each species leads to an a priori assumption that the response of life cycle traits to temperature is a key determinant of their contrasting geographic distributions. A new development model was created to reconcile published experimental development times for each species. Model

output indicates that at temperatures below approximately 12-13 °C, *C. finmarchicus* is the faster developing species, but above these temperatures *C. helgolandicus* develops more quickly. Conventionally *Calanus* development time is assumed to decrease monotonically with temperature; however our model indicates that the response of development time to temperature is instead U-shaped. Differences in life cycle aspects such as seasonality and vertical structuring are interpreted in light of this development model. Body size and lipid accumulation abilities could be significant influences on each species' geographic distribution; however evidence is consistent with inter-species differences not existing for these traits. Published evidence shows that inter-species differences in egg production may exist, but do not follow a clear pattern. Diapause is an important and well studied life cycle adaptation of *C. finmarchicus*, but has received little attention in *C. helgolandicus*. We synthesised knowledge of diapause and suggest the hypothesis that *C. helgolandicus* is restricted to continental shelf regions as a result of an inability to diapause for significant periods. This synthesised view of each species' respective life cycle traits is that response of growth and development to temperature is the only known difference between each species, which indicates a promising direction for the extension of population models of *C. finmarchicus* to *C. helgolandicus*.

Keywords: *Calanus finmarchicus*; *Calanus helgolandicus*; copepod, diapause; distribution; niche

Acknowledgements: This work was undertaken as part of PhD research, gratefully funded by Marine Alliance for Science and Technology Scotland.

45

46

47

48 **Abstract:** The important calanoid copepod species *Calanus finmarchicus* and *C.*
49 *helgolandicus* have distinct geographic ranges which are changing under the influence of
50 climate change. Understanding the mechanisms underlying their distributions is becoming
51 increasingly important as a result of the possible ecological impacts of these range shifts.
52 Here we review inter-species differences in key life cycle traits that influence each species'
53 geographic distribution, in particular development and growth, fecundity, feeding behaviour,
54 vertical migration and overwintering behaviour. The distinct temperature niche of each
55 species leads to an a priori assumption that the response of life cycle traits to temperature is a
56 key determinant of their contrasting geographic distributions. A new development model was
57 created to reconcile published experimental development times for each species. Model
58 output indicates that at temperatures below approximately 12-13 °C, *C. finmarchicus* is the
59 faster developing species, but above these temperatures *C. helgolandicus* develops more
60 quickly. Conventionally *Calanus* development time is assumed to decrease monotonically
61 with temperature; however our model indicates that the response of development time to
62 temperature is instead U-shaped. Differences in life cycle aspects such as seasonality and
63 vertical structuring are interpreted in light of this development model. Body size and lipid
64 accumulation abilities could be significant influences on each species' geographic
65 distribution; however evidence is consistent with inter-species differences not existing for
66 these traits. Published evidence shows that inter-species differences in egg production may
67 exist, but do not follow a clear pattern. Diapause is an important and well studied life cycle
68 adaptation of *C. finmarchicus*, but has received little attention in *C. helgolandicus*. We

69 synthesised knowledge of diapause and suggest the hypothesis that *C. helgolandicus* is
70 restricted to continental shelf regions as a result of an inability to diapause for significant
71 periods. This synthesised view of each species' respective life cycle traits is that response of
72 growth and development to temperature is the only known difference between each species,
73 which indicates a promising direction for the extension of population models of *C.*
74 *finmarchicus* to *C. helgolandicus*.

75 **1. Introduction**

76 Calanoid copepod species play critical roles in marine food webs throughout the North
77 Atlantic, and often dominate the mesozooplankton biomass (Head et al., 2003). Congeneric
78 species typically have largely non-overlapping environmental niches (Helaouët and
79 Beaugrand, 2007) and geographic ranges. Existing literature has therefore largely focused on
80 congeneric species in isolation. However, many ecosystems are now seeing ongoing, and
81 often poorly understood, changes in calanoid copepod regimes (Beaugrand, 2012), with
82 congeneric species replacing each other. Inter-species differences may profoundly influence
83 both the extent and the consequences of these changes. Therefore a fuller understanding of
84 inter-species differences appears necessary. Here we consider the species *Calanus*
85 *finmarchicus* and *C. helgolandicus*, which have partially overlapping geographic
86 distributions.

87 *C. finmarchicus* dominates the mesozooplankton biomass in much of the North Atlantic. Its
88 range covers a large part of the sub-polar North Atlantic, from eastern Canada to the North
89 Sea (Melle et al., 2014). The North Sea marks the northern extent of the range of *C.*
90 *helgolandicus*, which extends as far south as the Mediterranean Sea (Bonnet et al., 2005).
91 Historically, research has focused on *C. finmarchicus*, with less attention on *C.*
92 *helgolandicus*. This is largely a result of the vital role *C. finmarchicus* plays in the sub-polar

North Atlantic ecosystem (Heath et al., 2000; Aksnes and Blindheim, 1996), with it being a key prey species for many commercially important fish (Lynch et al., 2001). This focus is reflected by the number of papers published with titles including the words “*C. finmarchicus*” (582) and “*C. helgolandicus*” (192) that were published until 2013 (Web of Science). However, significant changes in both species’ geographic distribution in recent decades, and the potential impacts of these changes, have resulted in an increased interest in both species’ comparative ecology and biology.

During recent decades the geographic range of *C. finmarchicus* has shifted northwards (Barnard et al., 2004), while a recent analysis of Continuous Plankton Recorder data concluded that *C. helgolandicus* is possibly expanding in every direction (Chust et al., 2014). These range shifts are understood to have largely been driven by increased oceanic temperatures (Reygondeau and Beaugrand, 2011), and are likely to continue as a result of future climate change (IPCC, 2007). Evidence also indicates that neither species has undergone significant thermal adaptation to changing temperature regimes (Hinder et al., 2014).

Recent decades have seen a significant regime shift in the North Sea. *C. helgolandicus* abundance now exceeds that of *C. finmarchicus*, a reversal of the situation in the 1960s (Reid et al., 2003). Debate remains over the causes of this regime shift (Reid et al., 2003; Beaugrand, 2004), however the change in temperature regime appears to be the most influential factor (Beaugrand, 2012).

These regime shifts may have significant ecosystem impacts. The suitability of *C. finmarchicus* to act as prey for fish species is strongly influenced by its size, lipid stores and seasonality (Frederiksen et al., 2013; van Deurs et al., 2009; van Deurs et al., 2014). Inter-

116 species differences in these traits may determine the suitability of *C. helgolandicus* to replace
117 *C. finmarchicus* in terms of ecosystem function.

118 Due to their morphological similarities, *C. finmarchicus* and *C. helgolandicus* were originally
119 thought to be the same species, until Sars distinguished them in 1901 (Sars, 1903). This was
120 disputed for many decades (Frost, 1974), but was resolved in the 1990s when molecular
121 studies confirmed them as distinct species (e.g. Bucklin et al., 1995). They are generally
122 thought to be morphologically indistinguishable, except for the fifth copepodite and adult
123 stages (Fleminger and Hulsemann, 1977). Long term time series, such as the Continuous
124 Plankton Recorder, reflect this, with only species specific abundance for CV and adult stages
125 being reported.

126 The biology and ecology of *C. finmarchicus* (Melle et al., 2014) and *C. helgolandicus*
127 (Bonnet et al., 2005) have been separately reviewed in recent studies. The review of Bonnet
128 et al. (2005) carried out a short comparison of the differences between each species.
129 However, the statistics reported were arguably not very comparable and, in particular, may
130 provide an incomplete reflection of the relative growth rates and development times for both
131 species when they co-occur. Our review is the first extensive comparative analysis of the key
132 differences between *C. finmarchicus* and *C. helgolandicus*.

133 Geographic distributions of populations are largely driven by the response of species to
134 temperature, food and ocean circulation (Speirs et al., 2006). Our a priori assumption is that
135 biogeographic differences between each species are a result of different quantitative
136 responses of life cycle traits to environmental conditions. Some researchers (e.g. Møller et al.,
137 2012) suggest that inter-species differences in the response of growth to temperature explain
138 these large scale differences. Here we provide a critical quantitative comparative review of

139 the relationship between temperature and the following key life cycle traits: growth,
140 development and egg production rates.

141 A key aspect of the life cycle of *C. finmarchicus* is that it undergoes a period of
142 overwintering at depth, commonly referred to as diapause (Hirche, 1996). However, the
143 overwintering behaviour of *C. helgolandicus* has been poorly studied; and the extent of the
144 ability of *C. helgolandicus* to diapause is not clear. We suggest that differences in
145 overwintering behaviour are an important determinant of the two species' geographic
146 distributions. In particular, the potential inability to diapause for significant periods of time
147 may limit *C. helgolandicus* largely to continental shelf regions.

148 The motivation of this study is to inform possible future modelling studies of both species.
149 Process-based models have shed important light on a range of aspects of *C. finmarchicus*' life
150 cycle. A stage-structured population model has aided understanding of its large-scale
151 biogeography (Speirs et al., 2006). An understanding of the importance of advection for some
152 populations has also been strengthened by process-based models (Heath et al., 1999). At the
153 smaller scale, this class of model has enhanced our understanding of the relationship between
154 *C. finmarchicus* and phytoplankton (Carlotti and Radach, 1996), the role of diel vertical
155 migration (Fiksen and Carlotti, 1998) and diapause behaviour (Maps et al., 2012). In contrast,
156 with the exception of a recently published stage structured model of populations of both
157 species in the North Sea (Maar et al., 2013), to date process-based modelling studies have not
158 been carried out on *C. helgolandicus*.

159 The probable biogeographic shifts of both species due to climate change raises a need for
160 predictive process-based modelling of these species. A key question is the rate at which each
161 species will shift northwards, and the extent to which community composition will change. A
162 more complete understanding of the differences and similarities between each species will

163 indicate which elements of existing *C. finmarchicus* models can be transferred over to new
164 models of *C. helgolandicus* and potentially to multi-species models (Ji et al., 2012) including
165 *C. finmarchicus* and *C. helgolandicus*.

166 **The Life Cycle of *Calanus finmarchicus* and *C. helgolandicus***

167 Both species develop through thirteen development stages: egg, six naupliar (NI-NVI), five
168 copepodite (CI-CV), and a male or female adult stage (CVIm/CVIf). CV of *C. finmarchicus*
169 are known to diapause during winter, and sometimes this is viewed as a separate sub-stage
170 (CVd). Laboratory experiments demonstrate that feeding does not occur until stage NIII in
171 both species (e.g. Cook et al., 2007). Lipids play an important role in the life cycle of *C.*
172 *finmarchicus* (Hirche, 1996), with lipid accumulation mostly beginning in stage CIII (Hygum
173 et al., 2000b). *C. helgolandicus* accumulates lipids, however their importance in its life cycle
174 are less clear.

175 Throughout most of its geographic range, *C. finmarchicus* has an annual life cycle (e.g. Heath
176 et al., 2000). However, in colder extremes generation time can exceed one year (Heath et al.,
177 2008), whereas in warmer environments there can be multiple generations each year (Hirche
178 et al., 2001). Reflecting its warmer temperature regime *C. helgolandicus* typically has
179 multiple generations each year (Bonnet et al., 2005).

180

181 **2 Development in surface waters**

182 **2.1 Body Size**

183 Quantitative aspects of key traits such as ingestion (Wirtz, 2013), metabolism (Saiz and
184 Calbet, 2007) and egg production rate (Campbell and Head, 2000) are strongly influenced by
185 body size. Inter-species differences in body size are therefore expected to influence the

respective population dynamics of both species. Size differences may also result in different ecosystem function, with a recent paper (Frederiksen et al., 2013) invoking lower body size of *C. helgolandicus* as a reason it cannot be a full replacement for *C. finmarchicus* as prey for some fish.

Growth experiments show a negative relationship between body size and temperature (e.g. Campbell et al., 2001a). This should be reflected by geographic patterns of body size. This was analysed by considering the geographic pattern in female body size. Published female prosome lengths for each species were compared with mean annual sea surface temperature (SST) in the region studied (figure 1). We excluded laboratory studies, because our proxy for the temperature at which individuals developed, mean annual SST, is not fully comparable with those of laboratory experiments. Our comparison shows that the relationship between annual sea surface temperature and female prosome length across both species is approximately linear, indicating that temperature is the most significant influence on geographic patterns of body size.

Prosome lengths of females in co-occurring populations have been reported in the North Sea by two studies (Jónasdóttir et al., 2005; Jónasdóttir and Koski, 2011). Combining their data indicates that no biologically significant differences in female body occur in the North Sea (figure 2), with *C. helgolandicus* having a marginally larger mean female prosome length (2.58 mm) than *C. finmarchicus* (2.56 mm). We therefore conclude that existing evidence is consistent with both species developing to the same body size under identical environmental conditions.

2.2 Influence of temperature on development and growth

209 Inter-species differences in growth rate and development time are likely to be strong
210 determinants of differences in the viability of each species in a particular environment. Here
211 we critically review published development times for each species to see if there are inter-
212 species differences.

213 **2.2.1 Comparison of published experimental development times**

214 The most extensive study of growth and development in *C. finmarchicus* is the classic work
215 of Campbell et al. (2001a), which has been used in a number of population models (Melle et
216 al., 2014). A key finding was that *C. finmarchicus* follows the equiproportional rule of
217 development (Corkett et al., 1986). This important rule states that the relative duration of
218 each stage is independent of temperature. A notable departure from equiportionality was
219 observed for the CV stage, which was prolonged at a temperature of 4 °C, however the
220 reasons for this were unclear. Additional evidence that *C. finmarchicus* undergoes
221 equiproportional development is given by the laboratory study of Hygum et al. (2000a).
222 Tande (1988) concluded that *C. finmarchicus* does not undergo equiproportional
223 development. However, they compared individuals from different geographic regions, and
224 did not control for food conditions. Campbell et al. (2001a) found that between 4 and 12 °C,
225 the relationship between development time and temperature followed a Belehrádek function
226 (Belehrádek, 1935). Development time from egg to adult was approximately 91, 45 and 32
227 days at 4, 8 and 12 °C respectively. Comparison with other published estimates of *C.*
228 *finmarchicus* development time from egg to adult (Corkett et al., 1986; Tande, 1988) show
229 very close agreement in development times across studies. The work of Campbell et al.
230 (2001a) therefore appears to be a solid basis for the many modelling studies that have used it.

231 Development and growth of *C. helgolandicus* has been studied less extensively. The first
232 published study of its growth from egg to adult was that of Thompson (1982), which

233 concluded that *C. helgolandicus* does not develop equiproportionally. However, they did not
234 perform species identification checks (Thompson 1982), which possibly resulted in a large
235 number of *C. finmarchicus* individuals being used. Apart from this, the recent work of
236 Bonnet et al. (2009) is the only laboratory study of *C. helgolandicus* growth from egg to adult
237 to consider the influence of temperature on stage duration. Analysis of stage durations at
238 temperatures of 9, 12 and 15 °C indicated that naupliar stages develop equiproportionally,
239 however they concluded that copepodite stages did not. A comparison of stage durations of
240 this study with two others (Rey et al., 2001; Cook et al., 2007) showed very consistent
241 relative stage durations for naupliar stages across each study, providing further confirmation
242 that naupliar stages develop equiproportionally.

243 We plotted published relationships between egg to adult development time and temperature
244 for both species (figure 3). This illustrates apparently clear differences between each species
245 at temperatures at and below 12 °C. All development times from egg to adult for *C.*
246 *helgolandicus* (Bonnet et al., 2009; Thompson, 1982; Diel and Klein Breteler, 1986) are
247 longer at the relevant temperature than would be expected for *C. finmarchicus* based on the
248 classic work of Campbell et al. (2001). Development times for naupliar stages of *C.*
249 *helgolandicus* were also found to be longer at 8 and 12 °C by Cook et al. (2007) in
250 comparison with published naupliar development times for *C. finmarchicus* (Campbell et al.,
251 2001; Cook et al., 2007).

252 However, published development times for *C. helgolandicus* are not consistent with each
253 other. This makes inferring the quantitative differences between each species problematic.
254 The experimental results of Bonnet et al. (2009) indicate that at 12 °C, *C. helgolandicus* takes
255 approximately 10 days longer to develop from egg to adult than *C. finmarchicus* (Campbell et
256 al., 2001), and that development time from egg to adult for *C. helgolandicus* at 15 °C is
257 approximately 5 days longer than for *C. finmarchicus* at 12 °C. These differences are not

258 consistent with other published results. Cook et al. (2007) found that *C. helgolandicus* had a
259 shorter development time from egg to final naupliar stage at 15 °C than *C. finmarchicus* did
260 at 12 °C. *C. helgolandicus* development time from egg to C1 was also 4 and 6 days shorter at
261 12 and 15 °C respectively in Cook et al. (2007) than in Bonnet et al. (2009). Similarly, Rey et
262 al. (2001) reported *C. helgolandicus* development times from egg to C1 under multiple food
263 regimes at 15 °C, finding development time under 10 days for all regimes. This is in contrast
264 to the 14 days reported in Bonnet et al. (2009).

265 After comparing their results with those of Thompson (1982), Bonnet et al. (2009) concluded
266 that the experiment of Thompson (1982) probably contained significant numbers of *C.*
267 *finmarchicus* individuals. However, the development time to final naupliar stage at 12 °C
268 recorded by Thompson is very similar to those reported for *C. helgolandicus* by Cook et al.
269 (2007) and Rey et al. (2001). Similarly, the development time from egg to adult reported by
270 Thompson (1982) (26.21 days) is similar to the time (24.4 days) reported by Rey-Rassat et al.
271 (2002c). The difference between the development times to adult reported by Rey-Rassat et al.
272 (2002c) and Bonnet et al. (2009) is 12 days, and this is particularly anomalous given that the
273 same food regime was used in both studies (*Prorocentrum micans*). The development time
274 reported by Diel and Klein Breteler (1986) at 10 °C (39 days) is also reasonably consistent
275 with that reported by Thompson (1982) at 9.57 °C (41.72 days).

276 This suggests that the development times published by Thompson (1982), Rey et al. (2001),
277 Cook et al. (2007) and Diel and Klein Breteler (1986) are broadly consistent. In contrast,
278 Bonnet et al. (2009) appears to be an outlier, reporting significantly longer development
279 times than the other studies.

280 After reviewing the methodology in these studies it appears that differences in dietary
281 regimes is likely the reason for these disparities in published *C. helgolandicus* development

282 times. As shown by Diel and Klein Breteler (1986), diet can have a significant influence on
283 the development time of *Calanus* species. Bonnet et al. (2009), Cook et al. (2007), Rey et al.
284 (2001) and Rey-Rassat et al. (2002c) all reported development times under the same dietary
285 regime (*Prorocentrum micans*). However, Bonnet et al. (2009) appears to have grown
286 individuals at below food saturated conditions. Total volume of water was 0.5 mL/individual
287 in Bonnet et al. (2009) in contrast to 6.25 (Cook et al., 2007), 4 (Rey et al., 2001) and 6
288 mL/individual (Rey-Rassat et al., 2002c) in the other studies. Bonnet et al. (2009) replenished
289 food supply every 12 hours, however clearance rates for stages NIII-NVI are approximately 3
290 mL/individual/day (Rey et al., 2001) when fed on a *P. micans* diet. In addition, the mean
291 prosome length of females reported by Bonnet et al. (2009) at 15 °C was 1.95 mm,
292 significantly lower than the mean of 2.59 mm reported by Rey-Rassat et al. (2002a). It
293 therefore appears probable that the lower development times reported by Bonnet et al. (2009)
294 are a direct result of the dietary regime used.

295 If we accept that the *C. helgolandicus* development times reported by Bonnet et al. (2009)
296 cannot be compared directly with the published times for *C. finmarchicus* then we can draw
297 the following conclusions. *C. finmarchicus* has shorter development times than *C.*
298 *helgolandicus* at and below temperatures of 12 °C. However, a lack of published data means
299 we do not know if there are inter-species differences above 12 °C.

300 We are therefore faced with two questions. First, what explains the inter-species differences
301 in development times? And second, are there inter-species differences at temperatures above
302 12 °C? We consider these questions by developing a model of the growth and development of
303 each species. In turn, we are asking a third question. Can known differences in development
304 time between the two species be explained by known differences in the key drivers of growth
305 rate?

306 Growth in *Calanus* species in essence is the net change in body weight that results from the
307 following key processes: ingestion and assimilation of food, egestion, excretion and
308 metabolism. Differences in development time for each species must result from quantitative
309 differences in how one or more of these processes are influenced by temperature and/or diet,
310 or in absolute differences at each temperature.

311 Before detailing our growth and development model we will review existing knowledge of
312 inter-species differences in these life cycle traits.

313

314 **2.2.2 Metabolism and excretion**

315 Metabolism plays a key role in determining the thermal niche and the potential to diapause of
316 each species (Ingvarsdóttir et al., 1999). Recently, Maps et al. (2014) summarised published
317 metabolic rates for *Calanus* species. In total, five papers have reported respiration rates for *C.*
318 *finmarchicus* (Hirche, 1983; Marshall and Orr, 1958; Saumweber and Durbin, 2006;
319 Ingvarsdóttir et al., 1999; Ikeda et al., 2001). These studies provide valuable quantitative
320 insight into the metabolism of *C. finmarchicus* in both a diapausing and non-diapausing state.
321 Only one of these papers (Hirche, 1983) is sometimes referenced as reporting *C.*
322 *helgolandicus* respiration rates. Hirche (1983) reported *C. finmarchicus* respiration rates
323 which were based exclusively on *C. finmarchicus* individuals. However, *C. helgolandicus*
324 individuals were not distinguished from *C. finmarchicus* in the experiments sometimes
325 referred to as showing *C. helgolandicus* respiration rates. A knowledge gap therefore exists in
326 our understanding of metabolism in *C. helgolandicus*. However, the strong relationship
327 between body size and metabolism (Ikeda et al., 2001) suggests that metabolic rates for *C.*
328 *finmarchicus* and *C. helgolandicus* should be very similar. In addition, Maps et al. (2014)
329 concluded that there was an almost identical inter-species pattern in allometric scaling of

330 metabolism with body size across *Calanus* species. However, apparent inter-species
331 differences in response of ingestion to temperature (Møller et al., 2012) suggests that the
332 energetics of each species differ, which may result in different metabolic rates.

333 Assimilation and excretion play critical roles in determining growth rate in zooplankton. A
334 number of studies have reported assimilation efficiencies for *Calanus* species under different
335 dietary regimes (summarised in Mayor et al., 2011). However, the lack of directly
336 comparable data means that inter-species comparisons are currently not possible and remain
337 an open question.

338 **2.2.3 Influence of food on growth**

339 A small number of studies have considered the influence of food concentration on growth in
340 each species, however discerning the existence of inter-species differences from these studies
341 is difficult. The laboratory study of Campbell et al. (2001a) considered the relationship
342 between relative stage duration and carbon and nitrogen growth rates and food concentration.
343 Stage durations were only recorded for low, medium and high food concentration; however
344 there was a clear trend, with both nauplii and copepodite stages exhibiting longer stage
345 durations at lower food concentrations. Carbon and nitrogen specific growth rates were found
346 to saturate at high food concentrations.

347 The influence of food concentration on *C. helgolandicus* development from egg to naupliar
348 stages (Cook et al., 2007) and from egg to adult stages (Rey-Rassat et al., 2002c) have been
349 studied experimentally. Both studies only considered diets that could be described as having
350 low and high food concentration, and they indicated that development is significantly slower
351 at lower food concentrations.

352 Influences of both diet (Rey et al., 2001) and food concentration (Rey-Rassat et al., 2002c) on
353 *C. helgolandicus* growth have been studied experimentally. Low food concentration has a
354 significant negative influence on *C. helgolandicus* carbon and nitrogen growth rate (Rey-
355 Rassat et al., 2002c). Growth rates also appear to be influenced by dietary composition, with
356 Rey et al. (2001) reporting different carbon and nitrogen growth rates under varying dietary
357 regimes. These studies only considered growth at the temperature of 15 °C, therefore due to
358 the influence of temperature and body size on ingestion growth rates in each species cannot
359 be reliably compared.

360 We are therefore only able to make general descriptions of the relationship between growth
361 and food concentration for each species. The nature of the functional response (Gentleman et
362 al., 2003) of growth rate to food concentration in each species is uncertain. However, global
363 patterns (Hirst and Bunker, 2003) and that for *C. finmarchicus* (Campbell et al., 2001a)
364 indicates that this functional response may follow a Michaelis-Menten relationship. Further
365 study is necessary to provide evidence of inter-species differences.

366 Similarities in feeding behaviour were indicated by the study of Meyer et al. (2002), which
367 found that neither *C. finmarchicus* or *C. helgolandicus* fed selectively on different algal
368 groups of the same size, concluding that only size selective algal feeding occurred in each
369 species. Harris et al. (2000) also studied *C. finmarchicus* and *C. helgolandicus* in the field
370 and concluded that size-selective feeding predominated. However, in general, non-size
371 selective-feeding has been observed in both species (e.g. Meyer-Harms et al., 1999; Irigoien
372 et al., 2000).

373 Temperature and body size both have significant influences on ingestion rates in *Calanus*
374 species (Harris, 1996). A consequence is that quantitative comparisons of individuals of each
375 species from different geographic regions need to be interpreted carefully. This difficulty is

376 raised by the two existing comparative studies of feeding in each species (Meyer et al., 2002;
 377 Møller et al., 2012), with both studies raising each species at significantly different
 378 temperatures. The smaller size of *C. helgolandicus* than *C. finmarchicus* in existing feeding
 379 studies is likely to partially explain any inter-species differences in absolute ingestion rate,
 380 due to allometric scaling of ingestion rate (Wirtz, 2013). The results of Meyer et al. (2002)
 381 showed higher ingestion rates for nauplii, copepodite and adult female *C. finmarchicus* than
 382 for *C. helgolandicus*. However, the temperature at which individuals were raised and feeding
 383 experiments conducted, 10 °C for *C. finmarchicus* and 15 °C for *C. helgolandicus*, means
 384 that differences between the two species' ingestion rates cannot be confidently related to
 385 inter-species differences rather than the influence of temperature on body size and ingestion.

386 The recent study of Møller et al. (2012), which measured clearance rate over a wide
 387 temperature range for both species, provides a more accurate quantification of the differences
 388 between each species' ingestion rates. Clearance rate for females, normalized to the fraction
 389 of its maximum clearance rate, was higher for *C. finmarchicus* below 11 °C, but higher for *C.*
 390 *helgolandicus* above 11 °C (figure 4). A dome shaped response of ingestion rate to
 391 temperature was found for both species, with optimum temperature for *C. finmarchicus* being
 392 approximately 11 °C and *C. helgolandicus* being 13 °C. The significant differences of the
 393 temperature at which individuals were raised; 5 °C for *C. finmarchicus* and 15 °C for *C.*
 394 *helgolandicus* would have resulted in *C. finmarchicus* females being significantly larger than
 395 *C. helgolandicus*. This, coupled with potential acclimatization effects, means that future
 396 study of clearance rates of individuals raised under identical conditions is needed to clarify
 397 our understanding of inter-species differences.

398 It was generally assumed that *Calanus* species do not consume small cells, i.e. those that are
 399 “filtered” (Meyer et al., 2002). However, evidence indicates that *C. helgolandicus* consumes
 400 small cells (Meyer et al., 2002), and has been raised to adult stages on a diet of *Isochrysis*

galbana (Irigoien et al., 2000). Naupliar stages of *C. helgolandicus* appear to require higher food concentrations and develop more slowly when feeding on smaller cells (Cook et al., 2007). *C. finmarchicus* is also known to consume small cells (Harris et al., 2000; Båmstedt et al., 1999). Feeding studies of both species grown under the same environmental conditions will be needed to confirm if there is an inter-species difference in feeding on small cells.

2.2.4 Growth and Development Model

Reviewing published studies of ingestion, ability to assimilate food and metabolism indicates that we can only make direct quantitative comparisons of the relationship between ingestion rate and temperature. We therefore hypothesised that inter-species differences in the response of ingestion rate to temperature alone can explain a large part of the difference in published development times, and we tested this by developing a new development model. Published development times for *C. finmarchicus* (Campbell et al., 2001a, Corkett et al., 1986) and *C. helgolandicus* (Bonnet et al., 2009; Rey-Rassat et al, 2002c; Thompson, 1982; Diel and Klein Breteler, 1986) were used for parameterisation and model testing purposes.

Allometric scaling of key functions with body size suggests that stage based development can be dispensed with and replaced with a more simplified view of development that will maintain the key quantitative aspects of development. Ingestion and metabolic rates are therefore assumed to be stage independent in our model, i.e. they only depend on body size and temperature. Molting between stages is influenced strongly by body weight, and we assume that molting body weight is pre-determined, referring to this as the critical molting weight (Carlotti et al., 1993). Consideration of published body sizes (figure 2) indicates that terminal body size is the same for both species under identical environmental conditions, and that body size under food saturated conditions is determined by temperature (Campbell et al., 2001a). We therefore assume that terminal adult body weight is determined by temperature.

Carbon weight was used as our measure of body weight. Development in stage CV of *C. finmarchicus* is a combination of structural growth and lipid accumulation. Lipid accumulation occurs on a large scale in CV of *C. finmarchicus* as a precursor to overwintering, however *C. helgolandicus* may not accumulate lipids on the same scale. Consequently, we have parameterised our development model only up to the start of CV. As a result of a lack of comparable experimental data on the relationship between development time and food concentration for each species we assume food-saturated conditions throughout.

Ingestion of carbon is governed by two processes: the relationship between maximum carbon ingestion rate (units: $\mu \text{ g h}^{-1}$) and body size (units: $\mu \text{ g}$), f_1 , and the relationship between carbon ingestion rate and temperature, f_2 . Ingestion rate in zooplankton is understood to be strongly influenced by body size (Wirtz, 2013). Saiz and Calbet (2007) showed that maximum ingestion rate has approximately three quarter power scaling with body size, therefore we set f_1 to be $\mu w^{0.75}$, where w is carbon weight ($\mu \text{ g}$) and μ is a parameter to be fitted within boundaries estimated from Saiz and Calbet (2007). The form of f_2 is a dome shaped response (figure 4) taken from Møller et al. (2012). Some of the food ingested is egested or excreted and therefore not assimilated into body carbon. We define the assimilation efficiency, A as the percentage of food ingested that is assimilated, and this is parameterised within boundaries derived from Mayor et al. (2011). This is then applied to the ingestion rate to give us the rate at which food is assimilated into body carbon.

Metabolic costs are understood to have approximately three quarter power scaling with body weight in general (Gillooly et al., 2001) and the review by Maps et al. (2014) indicates that this holds for *Calanus*. Metabolism also increases with temperature, and that this relationship follows a Q10 relationship, i.e. each increase in temperature of 10 °C will result in respiration

449 rates increasing by a factor of Q10. Therefore we use the equation $Q10^{T/10} \lambda w^{0.75}$ to
 450 represent metabolic costs (units: $\mu \text{ g h}^{-1}$), where T is temperature ($^{\circ}\text{C}$) and with $Q10$ and λ
 451 being parameterised within reasonable bounds derived from the literature review contained in
 452 Maps et al. (2014). Minimum and maximum published $Q10$ are 2.3 (Marshall and Orr, 1958)
 453 and 3.4 (Hirche, 1983) respectively.

454 Thus our growth model is a differential equation of the form:

$$\frac{dw}{dt} = f_2 A w^{0.75} - Q10^{T/10} \lambda w^{0.75}$$

455 where

$$f_2 = \frac{P_5}{\left[1 + \exp\left(\frac{P_3}{T + 273} - \frac{P_3}{P_1}\right) + \exp\left(\frac{P_4}{P_2} - \frac{P_4}{T + 273}\right)\right]}$$

456 For *C. finmarchicus* $P_1 = 293, P_2 = 284, P_3 = 13,282, P_4 = 29,725$, and $P_5 = 6.05$, and for
 457 *C. helgolandicus* $P_1 = 289, P_2 = 275, P_3 = 39,429, P_4 = 14,123$ and $P_5 = 12.12$ (Møller et
 458 al., 2012). P_5 is a typo corrected from Møller et al. (2012) (Møller, personal communication).

459 Individuals are assumed to molt to the next stage when their carbon weight reaches the
 460 respective critical molting weight. We estimated the relationship between molting weight for
 461 CV individuals and temperature using published data on length-weight (Hygum et al., 2000b)
 462 and temperature-length relationships (Campbell et al., 2001a). CV molting weight was
 463 therefore assumed to relate to temperature using the equation $C_m = 2.037 * 10^{-10} * (-27.4 * T + 2084)^{3.52}$, where C_m is the CV molting carbon weight in $\mu \text{ g}$ and T is
 464 temperature in $^{\circ}\text{C}$.

466 First we parameterise our model completely for *C. finmarchicus*, using the development
 467 times at 4, 8 and 12 $^{\circ}\text{C}$ under food-saturated conditions reported by Campbell et al. (2001a).

468 The parameterisation of development to CV was performed by minimising the least squares
 469 of our model fit. This provides a general parameterisation of growth to CV for *C.*
 470 *finmarchicus*, and our parameter values are $A = 0.488, Q_{10} = 3.19, \mu = 0.0415, \lambda =$
 471 0.000101 . The relationship between development time and temperature given by the model
 472 (figure 3) departs from the conventional Belehrádek function, which sees development time
 473 decrease monotonically with temperature. In contrast, our model indicates that there is a U-
 474 shaped relationship between development time and temperature. This U-shape is a result of
 475 the differing relationships between ingestion rate and metabolism and temperature. Ingestion
 476 rate appears to decrease with increasing temperatures above a temperature of approximately
 477 12 °C for *C. finmarchicus* (Møller et al., 2012). However, metabolic costs will continue to
 478 increase with temperature. As a result, carbon-specific growth rate will have a dome-shaped
 479 response to temperature, and development time will have a U-shaped response in turn.

480 We then changed the ingestion rate parameters to model *C. helgolandicus* and compared the
 481 results with published development times for *C. helgolandicus*. Our model results for *C.*
 482 *helgolandicus* (figure 3) show development times that are reasonably consistent with those of
 483 Thompson (1982) and Rey-Rassat et al. (2002c). However, as expected, they are considerably
 484 shorter than those reported by Bonnet et al. (2009); approximately 8 days at 12 and 15 °C.
 485 This implies that the development times published by Thompson (1982), Cook et al. (2007),
 486 Rey et al. (2001) and Rey-Rassat et al. (2002c) are more directly comparable with those of *C.*
 487 *finmarchicus* published by Campbell et al. (2001).

488 Published differences in ingestion rate therefore appear to be able to explain most of the known
 489 inter-species differences in development time. However, future study is needed to clarify
 490 these issues. Quantitative understanding of inter-species differences in absolute ingestion and
 491 respiration rates is currently lacking, along with knowledge of the influence of temperature
 492 on respiration rate. Dietary regime can have a significant influence on growth (Rey et al.,

2001), and therefore future studies of potential inter-species differences in the influence of food quality on development appears to be useful.

In addition, the *C. helgolandicus* individuals captured by Møller et al.(2012), were from a geographically identical region, L4 English Channel, to those used by Bonnet et al. (2009). However Møller et al. (2012) (Gullmar fjord, Norway) captured individuals from a geographically distinct region from those in Campbell et al. (2001a) (Gulf of Maine). Genetic differentiation exists between eastern and western North Atlantic populations (Unal and Bucklin, 2010). Whether this differentiation results in significant quantitative differences in life cycle parameters remains an open question (Melle et al., 2014), however our parameterised model may be sensitive to such differences.

The relationship between development time and temperature produced here is unconventional; however it is consistent with that produced by Møller et al. (2012), who used the same ingestion rate-temperature relationship to model development in *C. finmarchicus* and *C. helgolandicus*. Currently, there is no data to test whether, as predicted, this relationship departs from the conventional Belehrádek function. This is because development time has yet to be measured at temperatures above the turning points implied by our model. However, there is considerable evidence that this may be the case. The relationship between egg production rate and temperature appears to be dome-shaped for most zooplankton species where egg production rate is reported at a broad enough temperature range (e.g. Halsband-Lenk et al., 2002; Holste and Peck, 2006; Pasternak et al., 2013). In addition to Møller et al. (2012), a dome-shaped response has been found between ingestion rate and temperature in other zooplankton species (e.g. Garrido et al. 2013; Alcaez et al., 2014). This indicates that a dome-shaped response of growth to temperature may be a regular occurrence in zooplankton species.

Our model also indicates that there is an upper temperature limit, above which *Calanus* species cannot exist. At around 18 °C, the development time for *C. finmarchicus* is extremely protracted. High metabolic costs and lowered ingestion rates in this temperature region are likely to result in high mortality rates and an inability of *C. finmarchicus* populations to persist. This temperature range coincides with that seen in regions just south of the southerly latitudinal extent of *C. finmarchicus*. Similarly, development time for *C. helgolandicus* is extremely protracted at temperatures below 9 °C. We therefore hypothesise that the inability of Bonnet et al. (2009) to raise *C. helgolandicus* to adult at 9 °C results from ingestion being too low at that temperature to offset metabolism. This suggests that both species may only be able to exist within particular thermal windows. These windows are of particular interest in the context of climate change. Alcaez et al. (2014) recently synthesised research on thermal thresholds and concluded that differences in the temperature response of positive and negative elements of metabolic balance can result in an upper temperature threshold for zooplankton. Further quantification of these relationships will provide useful insights into the likely impacts of climate change on *Calanus* species.

2.3 Egg Production

Environmental influences on egg production play a significant role in influencing the population dynamics of zooplankton. Inter-species differences in egg production rate are therefore a candidate mechanistic explanation of the large geographic differences in populations of *C. finmarchicus* and *C. helgolandicus*. Spawning time of each species has been reported by a small number of papers. *C. helgolandicus* and *C. finmarchicus* have been reported to spawn at midnight and mid-day (Laabir et al., 1998), and mid-day and dawn

(Marshall and Orr, 1955; Runge, 1987) respectively. Whether these studies indicate interspecies differences in spawning behaviour remains inconclusive.

2.3.1 Environmental influences on egg production

Temperature (Hirche et al., 1997), body size (Campbell and Head, 2000), and food quantity and quality (Diel and Tande, 1992; Jónasdóttir et al., 2002; Bunker and Hirst, 2004; Campbell et al., 2001b) all influence egg production rate (EPR). In broad terms, temperature has two key influences. Higher temperatures result in lower female body sizes, which has a negative influence on EPR (Campbell and Head, 2000). In contrast for a given female, EPR will increase with temperature (Hirche et al., 1997). Comparisons of EPR in different geographic regions are therefore challenging.

The laboratory study of Hirche et al. (1997) considered the influence of temperature and food on *C. finmarchicus* EPR and has been used in population models (e.g. Speirs et al., 2006). However, no comparable studies of EPR in *C. helgolandicus* have been carried out to date. Consequently, field-based studies have to be relied on when considering interspecies differences.

2.3.2 Comparison of egg production rate in both species

We reviewed published studies of maximum EPR for each species (figure 5). In the majority of studies the maximum EPR is higher for *C. finmarchicus* than for *C. helgolandicus*. This indicates that EPR for *C. finmarchicus* is in general higher than for *C. helgolandicus* at each species' "optimal" temperature, however this is not overwhelming confirmation of biological differences in egg production rate. Body size is significantly lower in *C. helgolandicus* than *C. finmarchicus* at "optimal" temperatures, therefore the strong positive relationship between

body size and EPR (Campbell and Head, 2000; Jónasdóttir et al., 2005) possibly explains a large part of the difference between each species in these studies.

The apparent reduction in maximum EPR with increased annual temperature indicates that body size variation explains a significant part of the large scale geographic variation in EPR across both species. However, the broad scale relationship between temperature and egg production rate is still a matter of debate. A recent study (Bonnet et al., 2005) compared EPR for *C. helgolandicus* at four separate stations, finding that temperature did not have a discernibly large influence. This inability to predict the influence of temperature on egg production over large geographic scales has also been demonstrated by a multi-station analysis of *C. finmarchicus* EPR (Melle et al., 2014). In contrast, laboratory studies have found that temperature does have a significant influence on egg production rate (Runge and Plourde, 1996; Hirche et al., 1997; Jónasdóttir et al., 2005; Jónasdóttir and Koski, 2011). This lack of quantitative understanding of the influences on geographic variations in egg production rate within species means that comparison of individuals living in very similar, or identical, environments is needed if we are to draw inferences about inter-species differences in egg production rate.

Rigorous comparison of egg production rates of co-occurring *C. finmarchicus* and *C. helgolandicus* faces a number of difficulties. Ages of co-occurring females may be significantly different as a result of inter-species differences in development time. This can have an impact on relative EPR of each species for several reasons: young females can take a significant time to reach full reproductive maturity (Plourde and Runge, 1993; Niehoff et al., 1999), older females can have lower EPR (Diel and Tande, 1992; Hirche et al., 1997), and feeding history can have a significant impact on EPR (Rey-Rassat et al., 2002a; Hirche et al., 1997; Niehoff, 2000; Ceballos and Alvarez-Marquez, 2006).

586 To date two studies, both carried out in the Dogger Bank, North Sea, have recorded EPR for
 587 co-occurring populations (Jónasdóttir et al., 2005; Jónasdóttir and Koski, 2011). These
 588 studies show that inter-species differences, if they exist, do not follow a clear pattern.
 589 Jónasdóttir and Koski (2011) reported egg production rates for the years 2001, 2002 and
 590 2005, finding no statistically significant differences between the two species' EPR.
 591 Jónasdóttir et al. (2005) reported that *C. finmarchicus* had higher per capita EPR in March,
 592 April and June 2001, whereas it was higher in *C. helgolandicus* in May and September of that
 593 year. It is possible that these differences result from differing levels of maturity of females.
 594 Maturity of females from March to September 2001 in the North Sea was reported by
 595 Jónasdóttir et al. (2005), and these show monthly differences between each species. These
 596 differences may result from the contrasting seasonal cycles of each species in the North Sea,
 597 however more research is needed if we are to properly quantify seasonal differences in
 598 maturity.

599 Dome-shaped responses between egg production rate and temperature have been observed for
 600 a large number of zooplankton species (Halband-Lenk et al., 2002; Holste and Peck, 2006;
 601 Holste et al., 2009; Rhyne et al., 2009; Koski and Kuosa, 1999; Pasternak et al., 2013.) Egg
 602 production and ingestion rates are strongly correlated in calanoid copepods (Peterson and
 603 Dam, 1996), therefore the dome-shaped response between ingestion rate observed in both
 604 species (Møller et al., 2012) implies that there will also be a dome-shaped response between
 605 egg production rate and temperature in both species. The form of the ingestion rate-
 606 temperature relationship for each species (figure 4) implies that *C. finmarchicus* will have a
 607 peak egg production rate at lower temperatures. Evidence to support this is given by studies
 608 of hatching success rate at high temperatures. *C. finmarchicus* egg hatching success has been
 609 observed to be significantly reduced at temperatures of 22 °C (Preziosi and Runge, 2014),
 610 whereas *C. helgolandicus* egg hatching success appears to be unaffected at these

temperatures (Laabir et al., 1995). However, studies of EPR at a wider range of temperatures is needed to confirm the exact quantitative nature of any inter-specific differences. This potential temperature response may also be a further influence on the thermal niche of each species.

We conclude that at its optimal temperatures of 15 °C, *C. helgolandicus* will have significantly lower egg production rate than for *C. finmarchicus* at its optimal temperature of 10 °C. Studies of co-occurring individuals show no clear evidence of clear inter-species differences. However, we hypothesis that the differing responses of ingestion rate to temperature will result in inter-species differences in egg production rate.

620

2.4 Vertical population structuring and diel vertical migration

Both *C. finmarchicus* (Heath et al., 2004) and *C. helgolandicus* (Andersen et al., 2001) display vertical population structuring where a seasonal thermocline has developed. Studies in the Irish Sea (Williams, 1985) and the Dogger Bank, North Sea (Jónasdóttir and Koski, 2011) indicate a distinct pattern of vertical structuring in each species. Prior to the development of the seasonal thermocline there is no evidence of differences in vertical structuring. In contrast, the development of the thermocline and warmer temperatures results in *C. finmarchicus* largely living in cooler deep waters, with *C. helgolandicus* remaining at the surface in warmer waters. Irigoien et al. (2004) also found no significant difference between the vertical positioning of each species in the water column in the Irish Sea. However, the temperatures in this study region were significantly lower than for Williams (1985) and Jónasdóttir and Koski (2011), where living in deeper waters may be necessary for *C. finmarchicus* to survive. The extent of vertical separation between the two species may therefore be strongly influenced by the temperature profile of the water column.

635 Differences in vertical distribution of both species are likely a reflection of each species
636 positioning itself at an optimal point in the water column to maximize growth. Our
637 development time model indicates that this position is probably different for both species,
638 with *C. helgolandicus* expected to prefer warmer surface waters.

639 Diel vertical migration plays an important role in *Calanus* species, allowing individuals to
640 avoid predation, and to feed at optimal times (Lampert, 1993). Comparisons of vertical
641 structuring during the day and night show that both species undertake diel vertical migration
642 (Jónasdóttir and Koski, 2011; Andersen et al., 2004). The only study of diel vertical
643 migration of co-existing *C. finmarchicus* and *C. helgolandicus* (Irigoien et al., 2004) found
644 no significant difference between each species' diel vertical migration behaviour in the Irish
645 Sea. Both species migrated to the surface at night in the central part of the Irish Sea, but at
646 coastal regions this pattern was reversed. No significant differences were found between the
647 diel vertical migration amplitude of each species.

648

649 **2.5 Overwintering Behaviour**

650 *C. finmarchicus* experiences long periods during winter where there is minimal food in
651 surface waters. To survive this period *C. finmarchicus* undergoes a long period of
652 overwintering, commonly referred to as diapause, spent in deep waters with reduced
653 respiration rates (reviewed in Hirche, 1996). The reasons for this period of overwintering are
654 thought to be multiple, including the need to survive long periods of low food supply and
655 avoiding high predation rates (Ji, 2011). Individuals normally enter diapause during the fifth
656 copepodite stage (Heath and Jónasdóttir, 1999), however significant numbers of CIV
657 copepodites have been observed in some overwintering populations (Head and Pepin, 2007).

659 Diapause usually begins in summer or autumn when individuals swim to depths (Hirche,
660 1996) and remain there for a period of up to six months. Median dormancy duration has been
661 estimated as 200 days in the western North Atlantic and 250 days in the eastern North
662 Atlantic (Melle et al., 2014). Exit from diapause normally occurs in the second half of winter,
663 but there is significant geographic variation in timing (Jónasdóttir et al., 2008). This
664 overwintering period is known to occur at a temperature range of -1 to 11 °C (Dupont and
665 Aksnes, 2012) and a depth range of 500 to 1,500 metres (Heath and Jónasdóttir, 1999).

666

667 Some uncertainty persists in our understanding of the causes and mechanisms behind
668 diapause in *C. finmarchicus*, however a large body of evidence (synthesised in Irigoien,
669 2004) indicates that lipids play a fundamental role. Before diapause commences individuals
670 build up significant lipid reserves. These lipid reserves are primarily composed of wax esters
671 (WE), the proportion of which is normally in excess of 80% (Kjellerup et al., 2012). Lipids
672 then act as the primary energy reserve for respiration during diapause (Ingvarsdóttir et al.,
673 1999), with lipid sacs often taking up in excess of 60% of body volume (Perrin et al., 2012),
674 but being continuously depleted as diapause proceeds.

675

676 Diapause requires individuals to maintain neutral buoyancy at depths for a significant period
677 of time. Visser and Jónasdóttir (1999) proposed that the thermo-physical properties of lipids
678 enable *C. finmarchicus* to attain neutral buoyancy in deep waters. This ability however has
679 been challenged due to its sensitivity to the relative biochemical composition of individuals
680 (Campbell and Dower, 2003). Visser and Jónasdóttir's (1999) model results were also based
681 on the properties of the lipids in the Pacific species *Neocalanus plumchrus*, and it is unclear if
682 the properties of lipids in *C. finmarchicus* are the same (Wilson et al., 2013; Pond and

683 Tarling, 2013).

684

685 Recently, the level of unsaturation in lipids has been proposed as a partial determinant of the
686 neutral buoyancy depth of zooplankton (Pond, 2012). The temperature at which lipids can
687 undergo liquid-solid phase transitions is dependent on the level of unsaturation (Pond and
688 Tarling, 2011), and selective catabolism of saturated and unsaturated wax esters may play a
689 key role in aiding neutral buoyancy during overwintering (Clark et al., 2012). The physical
690 properties of *C. finmarchicus* lipids in general needs further study, and so the relative
691 importance of lipids to buoyancy regulation remains unclear.

692

693 After exiting diapause, individuals molt to the next development stage, primarily from CV to
694 adult. CV individuals that are to become female predominantly exit diapause after males
695 (Heath, 1999) and then lay eggs in proportion to food supply, however there is some evidence
696 that remaining lipid reserves may fuel pre-spring bloom egg production (Richardson et al.,
697 1999; Mayor et al., 2009).

698

699 It remains unclear what triggers diapause entrance and exit. Photoperiod was proposed as a
700 potential trigger for diapause initiation and exit (Miller et al., 1991), however this failed to
701 reproduce the observed geographic variations in diapause onset and duration (Hind et al.,
702 2000). More recently, Johnson et al. (2008) analysed patterns of dormancy duration for *C.*
703 *finmarchicus*, concluding that no individual environmental cue triggered diapause initiation
704 or termination. However, they could not rule out the Lipid Accumulation Window hypothesis
705 to explain the onset of diapause, or a lipid-modulated endogenous timer as the control of
706 diapause duration. Pond (2012) recently synthesised research to suggest that wax ester un-
707 saturation level may influence the timing of both diapause entrance and exit.

708

709 In contrast to *C. finmarchicus*, the overwintering behaviour of *C. helgolandicus* remains less
710 clear. The study of Hirche (1983) is sometimes cited as showing that *C. helgolandicus*
711 undergoes diapause. This showed reduced respiration rates during winter, a key indication of
712 genuine diapause, however this study did not distinguish *Calanus* species. Therefore its
713 conclusions about the behaviour of *C. helgolandicus* remain uncertain. The only other study
714 reporting respiration rates for *C. helgolandicus* during winter (Williams and Conway, 1984)
715 concluded that it did not undergo true diapause in the Irish Sea. Further indications of
716 differences in overwintering behaviour is provided in the North Sea, where *C. finmarchicus*
717 largely retreats to deeper water by November, in contrast to *C. helgolandicus* which mostly
718 remains in shallower waters (Bonnet et al., 2005).

719

720 Differences in overwintering behaviour between the two species could also be inferred from
721 first principles, assuming that lipids are the principle driver of diapause, by comparative
722 analysis of lipid content of both species. These differences may also have broader ecological
723 impacts. A recent study argued that *C. helgolandicus* would not be a full replacement for *C.*
724 *finmarchicus* as part of the diet for some fish species (Frederiksen et al., 2013) partly as a
725 result of its lower lipid content.

726

727 Reported values of wax ester content of stage C5 *C. helgolandicus* are significantly lower
728 than those for *C. finmarchicus* (tables 1 and 2). For example, a laboratory study found that
729 CV of *C. finmarchicus* had three times more wax ester than those of *C. helgolandicus* (Rey-
730 Rassat et al., 2002b). However, individuals were raised at different temperatures in this study:
731 *C. finmarchicus* at 8 °C and *C. helgolandicus* at 15 °C. A consequence is that the *C.*
732 *finmarchicus* individuals would have been significantly larger, and it is further known that

733 smaller *C. finmarchicus* individuals have lower lipid levels (Miller et al., 2000). The same
734 difficulty exists for comparison of other studies of lipid levels in both species.

735

736 We therefore have two possibilities: there is an inter-species difference in lipid accumulation
737 in the two species, or that observed differences between the two species are largely because
738 smaller individuals have lower lipid levels. The relationship between body length and wax
739 ester content in *C. finmarchicus* is very significant, with CV individuals of prosome length 2
740 mm having total absolute wax ester content over 5 times lower than those of individuals with
741 prosome lengths of 2.7 mm (Pierson et al., 2013; Pepin et al., 2011; Saumweber and Durbin
742 2006). The majority of reported wax ester levels for *C. helgolandicus* CV have been in the
743 English Channel, and the highest reported value value is 55 $\mu\text{g C}$ (Rey-Rassat et al., 2002b).
744 *C. finmarchicus* CV have on average 50 $\mu\text{g C}$ of wax ester (Pierson et al., 2013) when their
745 prosome lengths are 2 mm. This is approximately the size of *C. helgolandicus* CV in the
746 English Channel. Therefore the recorded wax ester levels for *C. helgolandicus* are not
747 significantly different to those in *C. finmarchicus* of the same size. This indicates that there
748 are no significant inter-species differences in lipid accumulation ability.

749

750 Comparison of the lipid composition of co-occurring *C. finmarchicus* and *C. helgolandicus*
751 populations is currently lacking, however a study of lipid composition of both species in
752 relatively similar regions of the North Sea found no inter-species differences (Kattner and
753 Krause, 1989), and that observed differences can probably be explained by environmental
754 differences. Existing observations are therefore consistent with a lack of inter-species
755 differences in lipid accumulation rate.

756

757 An open question is the actual behaviour of *C. helgolandicus* during winter. Populations exist

758 in regions with sea bed depths ranging from 1,000 to 4,000 metres (Bonnet et al., 2005; Stohr
759 et al., 1996; John et al., 1998; Andersen et al., 2001). It has been observed living
760 predominantly at depths of 2,000 metres in June in the Levantine Sea (Bonnet et al., 2005)
761 which indicates a seasonal vertical migration may occur. This over-summering behaviour is
762 probably a necessary life cycle adaptation given *C. helgolandicus*'s possible metabolism-
763 ingestion trade off. Temperatures at the surface during summer in the Levantine Sea are
764 potentially too high for *C. helgolandicus* to offset metabolic losses by ingesting food,
765 therefore a seasonal migration to deeper, cooler waters may be necessary.

766

767 There are currently no studies of the duration and timing of any possible diapause period for
768 *C. helgolandicus*. However, consideration of our knowledge of the duration of diapause for
769 *C. finmarchicus* can be used to make some credible predictions about the maximum duration
770 of diapause for *C. helgolandicus*. Diapause can be seen as an extended period of low
771 respiration rates without feeding (Ingvarsdóttir, 1999), therefore diapause must end before an
772 individual starves. The two main influences on time to starvation are total lipid content at the
773 start of diapause and in situ temperature (Saumweber and Durbin, 2006). Throughout most of
774 its geographic range, *C. helgolandicus* would overwinter at temperatures greater than 10 °C,
775 and CV individuals would have body size below 2 mm. Extension of the diapause duration
776 model of Saumweber and Durbin (2006) (updated by Pierson et al., 2013) to *C. helgolandicus*
777 would indicate a maximum diapause duration of less than 60 days, more than three times
778 shorter than for *C. finmarchicus*. Respiration rates for overwintering *C. helgolandicus* are not
779 available in the literature; therefore this is a preliminary prediction.

780

781 Importantly, an inability to survive without food for much longer than two months may be an
782 explanation for *C. helgolandicus* largely being restricted to continental shelf regions. Oceanic

regions experience more prolonged periods of low food supply, typically in excess of 90 days, than shelf regions. Therefore the inability of *C. helgolandicus* to diapause for long periods may result in low viability of populations in off-shelf regions.

2.6 Mortality

Estimates of mortality in stage-structured *Calanus* populations face many problems and uncertainties. Advection, patchiness of populations, and uncertainties in estimates of stage duration, among other factors, has led to the general view that the problem is intractable (Ohman, 2012). As a result there has been relatively little attempt to quantify the impact of mortality on populations. However, some recent research has attempted to provide a clearer direction for the rigorous quantification of mortality in *Calanus* (Ohman, 2012; Gentleman et al., 2012).

A limited number of studies have made field-based estimates of mortality in *C. finmarchicus* (e.g. Eiane et al., 2002; Eiane and Ohman, 2004, Ohman and Hirsch, 2001; Ohman et al., 2002; Ohman et al., 2004) and *C. helgolandicus* (Hirst et al., 2007). These estimates of *Calanus* mortality have been used in population models of *C. finmarchicus* (Speirs et al., 2006) and *C. helgolandicus* (Maar et al., 2013). Both species see significantly higher mortality in egg and early naupliar stages than in later stages. However, inferring inter-species differences from these studies is very difficult. The only existing studies of each species have been in distinct geographic regions, with distinct predation and temperature regimes. Mortality can vary significantly with predation regime (Eiane et al., 2002) and temperature (Hirst et al., 2007). Therefore published mortality estimates are not directly comparable and we cannot make particularly credible conclusions about inter-specific differences.

808 We can however infer some general differences between each species given the apparent
809 response of their development times to temperature. Below 12 °C *C. finmarchicus* develops
810 faster than *C. helgolandicus*. As a result, we would expect mortality pressures to be stronger
811 on *C. helgolandicus* at these temperatures. Similarly, our development time model indicates
812 that the converse is true for temperatures above 13 °C, where *C. finmarchicus* is likely to see
813 more significant mortality pressures. *C. finmarchicus* also appears to have significantly lower
814 egg survival rates at higher temperatures (Preziosi and Runge, 2014). The dome-shaped
815 response of each species' ingestion rate to temperature (Møller et al., 2012) implies that
816 starvation mortality will be different in each species. The low ingestion rates of *C.*
817 *helgolandicus* at temperatures of around 7 °C and below imply that it will have very high
818 levels of mortality at these temperatures, and that this will be particularly pronounced during
819 periods of low food. Similarly, *C. finmarchicus* is likely to see pronounced levels of mortality
820 at temperatures close to 20 °C because the lowered ingestion rates are likely to fail to offset
821 increased respiratory costs at these temperatures. Mortality may therefore play a key role in
822 limiting the geographic extent of each species.

823

824 **3 Biogeography and environmental niches of *C. finmarchicus* and *C. helgolandicus***

825 Inter-species differences can be discerned by evaluating the ecological niches of species in
826 relation to the environment. A recent study (Helaouët and Beaugrand, 2007) considered the
827 environmental niches of each species in relation to a range of environmental variables. They
828 found that the most influential factors on the abundance of each species, as recorded by the
829 Continuous Plankton Recorder, are temperature and its correlates, and bathymetry.

830 An additional question is the ability of environmental variables to explain the large scale
831 geographic distribution of each species. Here we consider this question, restricting our

analysis to those variables considered by Helaouët and Beaugrand (2007) which have high quality spatial coverage in the North Atlantic, that is temperature, bathymetry and salinity. We used the statistical modelling method of general additive modelling (GAMs) to relate average monthly abundance of both species to average annual sea surface temperature, monthly salinity and bathymetry during the period from 1958 to 2002, with seasonality, when considered, accounted for by including a monthly component in GAM models. Monthly sea surface temperature is from the HadISST dataset (Rayner et al., 2003). Bathymetry was taken from the General Bathymetric Chart of the Oceans. Monthly salinity data is taken from the World Ocean Atlas (2009) (Antonov et al., 2010).

Biological and environmental data was resolved to a 1 degree resolution, with *Calanus* abundance averaged in each cell by month. We used monthly CPR data from 1958 to 2002. Initially there were 170,149 observations, which were reduced to 85,007 after resolving to a 1 by 1 degree resolution. Abundance data was then log transformed, i.e. we used $\log_{10}(\text{abundance} + 1)$. We then considered the success of these models in predicting the geographic distribution of each species, and inferred each species' environmental niche to the key environmental variables temperature and bathymetry. Model results are summarized in table 3.

3.1 Geographic Range

The geographic distributions of each species over the period 1960-2000 are shown in figure 6. *C. finmarchicus* has a range covering a large part of the North Atlantic, with known population centres in the Irminger Sea, Labrador Sea, Iceland Basin, Norwegian Trench and the Faroe Shetland Channel (Heath et al., 2004). *C. helgolandicus* has a range stretching from the Leventine Sea in the eastern Mediterranean Sea (Weikert et al., 2001) to the North Sea (Bonnet et al., 2005). *C. finmarchicus* is largely located within the Atlantic Polar Biome north

of the Oceanic Polar Front, whereas *C. helgolandicus* occurs in waters south of the Oceanic Polar Front (Helaouët and Beaugrand, 2007). *C. helgolandicus* predominantly lives in waters with significantly lower oxygen, silicates and nutrients (Longhurst, 1998; CPR).

The large scale geographic distribution of both species were reasonably successfully reproduced (figure 7 illustrates this for the period 1960-1969) using the predictions from the GAM model relating abundance with temperature, bathymetry and salinity (te(MON,SAL,TEMP,BATH)) in table 3). The R^2 value for the *C. finmarchicus* model, 0.5, is higher than for *C. helgolandicus*, 0.4, indicating greater predictive ability. However, spatial bias in the CPR data means that this should not necessarily be interpreted as meaning that these variables are stronger predictors of *C. finmarchicus* abundance than *C. helgolandicus*. Our temperature and month only model was much stronger for *C. finmarchicus* than for *C. helgolandicus*. However, the inclusion of bathymetry results in a marked improvement in the ability of the model to predict the geographic distribution of *C. helgolandicus*. *C. helgolandicus* is largely a continental shelf species, so the greater importance of bathymetry for *C. helgolandicus* than *C. finmarchicus* implied by our models is in line with expectations.

3.2 Environmental niches in relation to temperature and bathymetry

The southern extent of *C. finmarchicus* is thought to be the 11 °C isotherm (Planque and Fromentin, 1996), which also coincides closely with the northern extent of *C. helgolandicus*. *C. finmarchicus* has a known temperature range of 0-16 °C (Mauchline, 1991), whereas *C. helgolandicus* ranges from 5-28 °C (Bonnet et al., 2005).

We derived the relationship between the abundance of each species and temperature and bathymetry using our GAM models, as shown in figure 8. The annual temperature optimum is approximately 4 °C for *C. finmarchicus* and 14 °C for *C. helgolandicus* (in agreement with Helaouët and Beaugrand, 2007). The derived thermal niche also indicates that the

880 temperature tolerance range for *C. finmarchicus* is greater than for *C. helgolandicus*, which
881 accords with Helaouët and Beaugrand (2007).

882 *C. finmarchicus* is predominantly an oceanic species and this is reflected by the wide range of
883 its bathymetry niche. In contrast, *C. helgolandicus* has a geographic range that is largely
884 restricted to the Continental Shelf, and its bathymetry niche indicates that it is largely
885 restricted to waters shallower than 1,000 metres. The population map for *C. helgolandicus*
886 also indicates a very abrupt decline in population numbers at the continental shelf to the south
887 west of the British Isles. The reasons for this restriction are not fully known. Studies in the
888 Mediterranean Sea (e.g. Anderson et al., 2001) indicate that *C. helgolandicus* is capable of
889 living at depths of up to 4000 m. However, we hypothesised in our section on overwintering
890 that this restriction may be explained by an inability of *C. helgolandicus* to undergo a
891 significant period of diapause during winter.

892 **4 Seasonality and inter-species interactions**

893 **4.1 Seasonal cycles**

894 Geographic differences exist in the patterns of seasonality for each species. *C. finmarchicus*
895 shows a clear seasonal cycle, with a single peak in spring occurring throughout its geographic
896 range (Planque and Fromentin, 1996). In contrast, *C. helgolandicus* mostly has a seasonal
897 peak that varies significantly with latitude, with peak seasonal abundance occurring in spring
898 in the Mediterranean, whereas peak abundance occurs in autumn in the North Sea and North
899 East Atlantic (Bonnet et al., 2005; Planque and Fromentin, 1996).

900 The main region where both species overlap, the North Sea, sees very clear differences in
901 seasonality, which is shown in the Stonehaven time series (Bonnet et al., 2005). This time
902 series, starting in 1997, shows that *C. helgolandicus* has a seasonal peak in autumn, with an

903 earlier smaller peak in spring also evident. In contrast, *C. finmarchicus* has a seasonal peak
904 significantly earlier in the year during spring.

905 Here we consider the trend in the region around Stonehaven since 1960 by analysing CPR
906 records. Figure 9 shows the seasonal pattern in abundance in the region around Stonehaven
907 over four decades from 1960 to 2000, derived from CPR data using a GAM model that
908 relates monthly abundance of each species purely with month. Our derived time series
909 reflects the decline in the abundance of *C. finmarchicus*, and increase in *C. helgolandicus*
910 over the period 1960-2000 (Reid et al., 2003), and as in the Stonehaven time series it
911 indicates that abundance peaks significantly later in the year for *C. helgolandicus* than for *C.*
912 *finmarchicus* throughout the time period. Interestingly, there appears to be indications that the
913 spring *C. helgolandicus* peak did not develop until the 1980s.

914 This mismatch in seasonality between the two species has led some researchers to conclude
915 that *C. finmarchicus* is more important as prey in the diets of many fish species in the North
916 Sea (e.g. van Deurs et al., 2009). The causes of this mismatch between the seasonal cycle of
917 the two species are unclear. Different development responses to temperature probably play a
918 role, with our review of development time showing *C. helgolandicus* developing more slowly
919 at the temperatures experienced in this region. The stark difference between seasonality also
920 suggests that different advective routes into the North Sea may play a role. *C. finmarchicus* is
921 known to require annual advection into the North Sea to maintain a summer population
922 (Heath et al., 1999), however to date the role of advection in North Sea populations of *C.*
923 *helgolandicus* has not been studied. A greater understanding of the influences of seasonality
924 on each species is therefore necessary to aid predictions of ecosystem impacts of *C.*
925 *finmarchicus* being replaced by *C. helgolandicus*.

926 **4.2 Inter-species competition**

927 It remains unclear if there is significant inter-species competition where the two species co-
928 exist. Meyer et al. (2002) is the only existing study comparing the feeding behaviour of each
929 species in co-existing field populations. No significant differences between the two species in
930 terms of feeding behaviour were found. This implies that some level of competition for
931 resources should occur between the two species where they physically co-exist. However,
932 studies of the vertical structuring of co-occurring *C. finmarchicus* and *C. helgolandicus*
933 populations indicate that there is often a lack of vertical overlap for the two species, thus
934 possibly limiting the potential for inter-species competition. Jónasdóttir and Koski (2011)
935 found that in the Dogger Bank, North Sea, *C. helgolandicus* stayed predominantly in the
936 warm surface waters, with *C. finmarchicus* staying in the cooler, deep waters. This difference
937 however appears to be dependent on the existence of a thermocline.

938 Williams and Conway (1985) studied differences in vertical distribution in the Irish Sea.
939 They found that after the development of the thermocline, there were distinct differences in
940 the vertical distribution of the two species, but prior to this there was no significant difference
941 in their vertical distributions. There is also a temporal mismatch in the seasonal population
942 peaks (Bonnet et al., 2005) and egg production rates (Jónasdóttir et al., 2005) of co-occurring
943 *C. finmarchicus* and *C. helgolandicus*. This may further limit the importance of inter-species
944 competition.

945 **5 Conclusions**

946 We have reviewed the ecological and biological differences between *C. finmarchicus* and *C.*
947 *helgolandicus* and our key conclusions are as follows:

- 948 • *C. finmarchicus* has an annual temperature optimum of approximately 5 °C, while *C.*
949 *helgolandicus* has an optimum of 14 °C.

- Experimental studies indicate that *C. finmarchicus* develops faster than *C. helgolandicus* at temperatures below 12 °C. We have produced a new development model which indicates that *C. helgolandicus* develops faster than *C. finmarchicus* above 13 °C.
- Reviewed published data indicates that both species grow to the same body size under identical environmental conditions, with large geographic differences in body size apparently being determined by in situ temperature.
- Comparative evidence shows that, if they exist, inter-species differences in egg production do not follow a clear pattern.
- There is no direct evidence that *C. helgolandicus* undergoes a period of diapause, and we hypothesise that due to high overwintering temperatures any period of diapause will be short in duration.
- Broad scale differences in lipid levels in each species can be explained without invoking inter-species differences, and are consistent with the lower lipid levels of *C. helgolandicus* resulting from temperature driven differences in body size.
- Both species undertake diel vertical migration, and existing evidence implies no inter-species differences in behaviour.
- Significant differences in seasonal cycle exist, with *C. helgolandicus* abundance peaking significantly later in the year in the North Sea, where the species co-occur.

Ongoing climate change is likely to result in the continued replacement of *C. finmarchicus* by *C. helgolandicus* in many ecosystems, in particular the North Sea. Our review sheds some light on the prospects of these changes, and uncertainties in our knowledge of their impacts. The ecosystem impacts of these changes rest in part on the ability of *C. helgolandicus* to “replace” *C. finmarchicus*. Importantly, many inter-species differences, in particular in body size and lipid content, appear to be lower than has been assumed in some literature

975 (Frederiksen et al., 2013). However, current mismatch between seasonality in each species
976 results in *C. finmarchicus* playing a much more important role in the diets of some fish
977 species (van Deurs et al., 2009). A fuller understanding of the potential future evolution of *C.*
978 *helgolandicus* seasonality is necessary to get a more complete picture of the extent to which
979 *C. helgolandicus* can replace *C. finmarchicus* in ecosystems.

980 The strong similarities between each species lead to the possibility of hybridisation between
981 *C. finmarchicus* and *C. helgolandicus* where they co-exist. Recent research has shown that *C.*
982 *finmarchicus* and *C. glacialis* can inter-breed (Parent et al., 2012), the first known instance in
983 any zooplankton species. Hybrids often outnumbered the population of *C. finmarchicus* or *C.*
984 *glacialis* in the Labrador Sea and Scotian Shelf (Parent et al., 2012). Whether hybridisation
985 occurs, and has the effect of masking inter-species differences, between *C. finmarchicus* and
986 *C. helgolandicus* remains an open question. Other recent work has shown that there is more
987 overlap in body size of *C. finmarchicus*, *C. glacialis* and *C. hyperboreus* than previously
988 thought (Parent et al., 2011). This confirms the need to look at traits where species co-exist if
989 we want to identify differences between the species. Identification of the extent of overlap of
990 key traits where *Calanus* species co-exist will be a good indicator of the potential ecosystem
991 changes that may result from future regime shifts.

992 A key research question is whether geographic genetic differences have significant
993 quantitative influences on populations. We parameterised our growth model using
994 development times of western North Atlantic *C. finmarchicus* and ingestion rates from
995 eastern North Atlantic *C. finmarchicus*. Similarly, quantitative inferences based on traits
996 measured for *C. helgolandicus* in the North Sea may not accurately reflect those found in the
997 Mediterranean. Our model therefore may be sensitive to geographic variations in genetics.

998 An important area for future research is the potential expansion of *C. helgolandicus* into
999 oceanic environments. Its population is currently largely restricted to continental shelf
1000 regions, a phenomenon we hypothesise is determined by higher temperatures causing shorter
1001 potential diapause periods. A more complete understanding of the mechanisms explaining *C.*
1002 *helgolandicus*' current restriction to continental shelf is necessary to predict whether it will
1003 continue to be restricted to continental shelf regions, which may have significant impacts on
1004 ecosystems.

1005

1006

1007 **Acknowledgements**

1008 We thank Marine Alliance for Science and Technology Scotland and the University for
1009 Strathclyde, whose funding made this work possible.

1010 **References**

1011

1012 Aksnes, D.L., Blindheim, J., 1996. Circulation patterns in the North Atlantic and possible
1013 impact on population dynamics of *Calanus finmarchicus*. *Ophelia* 44, 7-28.

1014

1015 Alcaraz, M., Felipe, J., Grote, U., Arashkevich, E., Nikishina, A., 2014. Life in a warming
1016 ocean: thermal thresholds and metabolic balance of arctic zooplankton. *Journal of Plankton*
1017 *Research* 36, 3-10.

1018

1019 Andersen, V., Gubanova, A., Ruellet, N.P., 2001. Zooplankton community during the
1020 transition from spring bloom to oligotrophy in the open NW Mediterranean and effects of
1021 wind events. 2. Vertical distributions and migrations. *Journal of Plankton Research* 23, 243-
1022 261.

1023

1024 Andersen, V., Devey, C., Gubonova, A., Picheral, M., Melnikov, V., Tsarin, S., et al., 2004.
1025 Vertical distributions of zooplankton across the Almeria-Oran frontal zone (Mediterranean
1026 Sea). *Journal of Plankton Research* 26 (3), 275-293.

1027

1028 Antonov, J. I., D. Seidov, T. P. Boyer, R. A. Locarnini, A. V. Mishonov, H. E. Garcia, O.K., et al.,
1029 2010. *World Ocean Atlas 2009, Volume 2: Salinity*. S. Levitus, Ed. NOAA Atlas NESDIS 69, U.S.
1030 Government Printing Office, Washington, D.C., 184 pp.

1031

1032 Båmstedt, U., Nejstgaard, J.C., Solberg, P.T., 1999. Utilisation of small-sized food algae by
1033 *Calanus finmarchicus* (Copepoda, Calanoida) and the significance of feeding history. *Sarsia*
1034 84, 19–38.

1035

1036 Barnard, R., Batten, S.D., Beaugrand, G., Buckland, C., Conway, D.V.P., Edwards, M., et
1037 al., 2004. Continuous Plankton Records: Plankton Atlas of the North Atlantic Ocean (1958-
1038 1999). II - Biogeographical charts. Marine Ecology Progress Series (Supplement) 11-75.

1039

1040 Beaugrand, G., 2004. The North Sea regime shift: evidence, causes, mechanisms and
1041 consequences. Progress in Oceanography 60, 245-262.

1042

1043 Beaugrand, G., 2012. Unanticipated biological changes and global warming. Marine
1044 Ecology Progress Series 445, 293-301.

1045

1046 Belehrádek, J., 1935. Temperature and living matter. Protoplasma Monograph 8, 1-277.

1047

1048 Bonnet, D., Richardson, A.J., Harris, R., Hirst, A., Beaugrand, G., Edwards, M. et al., 2005.
1049 An overview of *Calanus helgolandicus* ecology in European waters. Progress in
1050 Oceanography 65, 1-53.

1051

1052 Bonnet D., Harris R.P., Yebra, L. Guilhaumon, F., Conway, D.V.P., Hirst, A.G.,
1053 2009. Temperature effects on *Calanus helgolandicus* (Copepoda: Calanoida) development
1054 time and egg production. Journal of Plankton Research 31, 31-34.

1055

1056 Bucklin, A., Frost, B.W., Kocher, T.D., 1995. Molecular systematics of six *Calanus* and
1057 three *Metridia* species (Calanoida: Copepoda). Marine Biology 121, 655-664.

1058

1059 Bunker, A.J., Hirst, A.G., 2004. Fecundity of marine planktonic copepods: global rates and
1060 patterns in relation to chlorophyll *a*, temperature and body weight. Marine Ecology Progress
1061 Series 279, 161–181.

1062

1063 Campbell, R.W., Head, E.J.H., 2000. Egg production rates of *Calanus finmarchicus* in the
1064 western North Atlantic: effect of gonad maturity, female size, chlorophyll concentration,
1065 and temperature. Canadian Journal of Fisheries and Aquatic Sciences 57, 518-529.

1066

1067 Campbell, R.G., Wagner, M.W., Teegarden, G.J., Boudreau, C.A., Durbin, E.G., 2001a.
1068 Growth and development rates of the copepod *Calanus finmarchicus* in the laboratory.
1069 Marine Ecology Progress Series 221, 161-183.

1070

1071 Campbell, R.G., Runge, J.A., Durbin, E.G., 2001b. Evidence for food limitation of *Calanus*
1072 *finmarchicus* production rates on the southern flank of Georges Bank during April 1997.
1073 Deep Sea Research II 48, 531-549.

1074

1075 Campbell, R.W., Dower, J.F., 2003. Role of lipids in the maintenance of neutral buoyancy
1076 by zooplankton. Marine Ecology Progress Series 263, 93–99.

1077

1078 Carlotti, F., Krause, M., Radach, G., 1993. Growth and development of *Calanus*
1079 *finmarchicus* taking into account the effect of temperature. Limnology and Oceanography
1080 38, 1125–1134.

1081

1082 Carlotti, F., Radach, G., 1996. Seasonal dynamics of phytoplankton and *Calanus*
1083 *finmarchicus* in the North Sea as revealed by a coupled one-dimensional model.

1084 Limnology and Oceanography 41, 522-539.

1085

1086 Ceballos, S., Cabal, J.A., Alvarez-Marque S.F., 2004. Reproductive strategy of *Calanoides*

1087 *carinatus* and *Calanus helgolandicus* during a summer upwelling event off NW Spain.

1088 Marine Biology 145, 739–750.

1089 Ceballos, S., Alvarez-Marques, F., 2006. Reproductive activity and physiological status of

1090 the calanoid copepods *Calanus helgolandicus* and *Calanoides carinatus* under food-limiting

1091 conditions. Journal of Experimental Marine Biology and Ecology 339, 189–203.

1092

1093 Ceballos, S., Viesca, L., Alvarez-Marques F., 2006. Copepod egg production during highly

1094 productive late spring conditions: importance of freshly ingested food and lipid storage.

1095 Marine Ecology Progress Series 317, 171-186.

1096

1097 Chust, G., Castellani, C., Licandro, P., Ibaibarriaga, L., Sagarminaga, Y., Irigoien, X., 2014.

1098 Are *Calanus* spp. shifting poleward in the North Atlantic? A habitat modelling approach.

1099 ICES Journal of Marine Science 71, 241-253.

1100

1101 Clark, K.A., Brierley, A.S., Pond, D.W., 2012. Composition of wax esters is linked to

1102 diapause behaviour of *Calanus finmarchicus* in a sea loch environment. Limnology and

1103 Oceanography 57, 65-75.

1104

1105 Cook, K.B., Bunker, A., Hirst, A.G., Speirs, D.C., 2007. Naupliar development times and

1106 survival of the copepods *Calanus helgolandicus* and *Calanus finmarchicus* in relation to

1107 food and temperature. Journal of Plankton Research 29, 757-767.

1108

1109 Corkett, C.J., McLaren, I.A., Sevigny, J.M., 1986. The rearing of the marine calanoid
 1110 copepods *Calanus finmarchicus* (Gunnerus), *C. glacialis* Jaschnov and *C. hyperboreus*
 1111 Kroyer with comment on the equiproportional rule. Syllogeus 58, 539-546.
 1112
 1113 Diel, S., Klein Breteler, C.M., 1986. Growth and development of *Calanus* spp. (Copepoda)
 1114 during spring phytoplankton succession in the North Sea. Marine Biology 91, 85-92.
 1115
 1116 Diel, S., Tande, K., 1992. Does the spawning of *Calanus finmarchicus* in high latitudes
 1117 follow a reproducible pattern? Marine Biology 113, 21-31.
 1118
 1119 Dupont, N., Aksnes, D.L., 2012. Effects of bottom depth and water clarity on the vertical
 1120 distribution of *Calanus* spp. Journal of Plankton Research 34, 263-266.
 1121
 1122 Durbin, E.G., Campbell, R.G., Casas, M.C., Ohman, M.D., Niehoff, B., Runge, J., et al.,
 1123 2003. Interannual variation in phytoplankton blooms and zooplankton productivity and
 1124 abundance in the Gulf of Maine during winter. Marine Ecology Progress Series 254, 81-100.
 1125
 1126 Eiane, K., Aksnes, D.L., Ohman, M.D., Sood, S., Martinussen, M.B., 2002. Stage-specific
 1127 mortality of *Calanus* spp. under different predation regimes. Limnology and Oceanography
 1128 47, 636–645.
 1129
 1130 Eiane, K., Ohman, M.D., 2004. Stage specific mortality of *Calanus finmarchicus*,
 1131 *Pseudocalanus elongates* and *Oithona similis* on Fladen Ground, North Sea, during a spring
 1132 bloom. Marine Ecology Progress Series 268, 183–193.
 1133

1134

1135 Fiksen, O., Carlotti, F., 1998. A model of optimal life history and diel vertical migration in
1136 *Calanus finmarchicus*. Sarsia 83, 129-147.

1137

1138 Fileman, E., Petropavlovsky, A., Harris, R., 2010. Grazing by the copepods *Calanus*
1139 *helgolandicus* and *Acartia clausi* on the protozooplankton community at station L4 in the
1140 Western English Channel. Journal of Plankton Research 32, 709-724.

1141

1142 Fleminger, A., Hulsemann, K., 1977. Geographical range and taxonomic divergence in
1143 North Atlantic *Calanus* (*C. helgolandicus*, *C. finmarchicus* and *C. glacialis*). Marine
1144 Biology 40, 233-248.

1145

1146 Frederiksen, M., Anker-Nilssen, T., Beaugrand, G., Wanless, S., 2013. Climate, copepods
1147 and seabirds in the boreal Northeast Atlantic – current state and future outlook. Global
1148 Change Biology 19, 364–372.

1149

1150 Frost, B.W., 1974. *Calanus marshallae*, a new species of calanoid copepod closely allied
1151 to the sibling species of *C. finmarchicus* and *C. glacialis*. Marine Biology 26, 77-79.

1152

1153 Garrido, S., Cruz, J., Santos, A.M.P., et al., 2013. Effects of temperature, food type and
1154 concentration on the grazing of the calanoid copepod, *Centropages chierchiae*. Journal of
1155 Plankton Research 35, 843 – 854.

1156

1157 Gatten, R.R., Corner, E.D.S., Kilvington, C.C., Sargent, J.R., 1979. A seasonal survey of
1158 the lipids of *Calanus helgolandicus* Claus from the English Channel. In E. Naylor and R.G.

1159 Hartnol (eds). Cyclic Phenomena in Marine Plants and Animals. Pergamon Press, Oxford,
1160 pp. 275-284.
1161

1162 Gentleman, W., Leising, A., Frost, B., Storm, S., Murray, J., 2003. Functional responses
1163 for zooplankton feeding on multiple resources: a review of assumptions and biological
1164 dynamics. Deep Sea Research Part II - Topical Studies in Oceanography 50, 2847-2875.
1165

1166 Gentleman, W.C., Pepin, P., Doucette, S., 2012. Estimating mortality: clarifying
1167 assumptions and sources of uncertainty in vertical methods. Journal of Marine Systems 105-
1168 108, 1–19.
1169

1170

1171 Gillooly, J.F., Brown, J.H., West, G.B., Savage, V.M., Charnov, E.L., 2001. Effects of size
1172 and temperature on metabolic rate. Science 293, 2248–2251.
1173

1174 Gislason, A., Astthorsson, O.S., 2000. Winter distribution, ontogenetic migration and rates
1175 of egg production of *Calanus finmarchicus* southwest of Iceland. ICES Journal of Marine
1176 Science 57, 1727-1739.
1177

1178 Halsband-Lenk, C., Hans-Jurgen, H., Carlotti, F., 2002. Temperature impact on reproduction
1179 and development of congener copepod populations. Journal of Experimental Marine Biology
1180 and Ecology 271, 121–153.
1181

1182 Harris, R.P. 1988. Interactions between diel vertical migratory behaviour of marine
1183 zooplankton and the subsurface chlorophyll maximum. Bulletin of Marine Science 43,

1184 663–674.

1185

1186 Harris, R.P., Irigoien, X., Head, R.N., Rey, C., Hygum, B.H., Hansen, B.W., et al., 2000.

1187 Feeding, growth and reproduction in the genus *Calanus*. ICES Journal of Marine Science

1188 57, 1708-1726.

1189

1190 Harris, R.P., 1996. Feeding ecology of *Calanus*. Ophelia 44, 85-109.

1191

1192 Hay, S., 1995. Egg production and secondary production of common North Sea copepods:

1193 field estimates with regional and seasonal comparisons. ICES Journal of Marine Science 52,

1194 315-327.

1195

1196 Head, E.J.H., Harris, L.R., Campbell, R.W., 2000. Investigations on the ecology of *Calanus*

1197 spp. in the Labrador Sea. I. Relationship between the phytoplankton bloom and reproduction

1198 and development of *Calanus finmarchicus* in spring. Marine Ecology Progress Series 193,

1199 53-73.

1200

1201 Head, E.J.H., Harris, L.R., Yashayaev, I., 2003. Distributions of *Calanus* spp. and other

1202 mesozooplankton in the Labrador Sea in relation to hydrography in spring and

1203 summer (1995–2000). Progress in Oceanography 59, 1–30.

1204

1205 Head, E., Pepin, P., 2007. Variations in overwintering depth distributions of *Calanus*

1206 *finmarchicus* in the slope waters of the NW Atlantic continental shelf and the Labrador

1207 Sea. Journal of Northwest Atlantic Fishery Science 39, 49-69.

1208

1209 Heath, M.R., Astthorsson, O.S., Dunn, J., Ellertsen, B., Gaard, E., Gislason, A., et al., 2000.
 1210 Comparative analysis of *Calanus finmarchicus* demography at locations around the
 1211 northeast Atlantic. ICES Journal of Marine Science 57, 1562-1580.
 1212
 1213 Heath, M.R., Boyle, P.R., Gislason, A., Gurney, W.S.C., Hay, S.J., Head, E.J.H., et al.,
 1214 2004. Comparative ecology of overwintering *Calanus finmarchicus* in the northern North
 1215 Atlantic, and implications for life cycle patterns. ICES Journal of Marine Science 61(4),
 1216 698-708.
 1217
 1218 Heath, M.R., Jónasdóttir, S., 1999. Distribution and abundance of overwintering *Calanus*
 1219 *finmarchicus* in the Faroe-Shetland Channel. Fisheries Oceanography 8 (Suppl 1), 40-60.
 1220
 1221 Heath, M.R., 1999. The ascent migration of *Calanus finmarchicus* from overwintering
 1222 depths in the Faroe-Shetland Channel. Fisheries Oceanography 8 (Suppl 1), 84-99.
 1223
 1224 Heath, M.R., Backhaus, J.O., Richardson, K., McKenzie, E., Slagstad, D., Beare, D., et al.,
 1225 1999. Climate fluctuations and the spring invasion of the North Sea by *Calanus*
 1226 *finmarchicus*. Fisheries Oceanography 8 (Suppl 1), 163-176.
 1227
 1228 Heath, M. R., Rasmussen, J., Ahmed, Y., Allen, J., Anderson, C.I.H., Brierley, A.S., et al.,
 1229 (2008) Spatial demography of *Calanus finmarchicus* in the Irminger Sea. Progress in
 1230 Oceanography 76, 39-88.
 1231
 1232 Helaouët, P., Beaugrand, G., 2007. Macroecology of *Calanus finmarchicus* and *C.*
 1233 *helgolandicus* in the North Atlantic Ocean and adjacent seas. Marine Ecology Progress

1234 Series 345, 147-165.

1235

1236 Hind, A.T., Gurney, W.S.C., Heath, M.R., Bryant, A., 2000. Overwintering strategies in
 1237 *Calanus finmarchicus*. Marine Ecology Progress Series 193, 95-107.

1238

1239 Hinder, S.L., Gravenor, M.B., Edwards, M., Ostle, C., Bodger, O.G., Lee, P.L.M., et al.,
 1240 2014. Multi-decadal range changes vs. thermal adaptation for north east Atlantic oceanic
 1241 copepods in the face of climate change. Global Change Biology 20, 140–146.

1242

1243 Hirche, H.J., 1983. Overwintering of *C. finmarchicus* and *C. helgolandicus*. Marine
 1244 Ecology Progress Series 11, 281-290.

1245

1246 Hirche, H.J., 1996. Diapause in the marine copepod *Calanus finmarchicus* - a review.
 1247 Ophelia 44, 129-143.

1248

1249 Hirche, H.J., Meyer, U., Niehoff, B., 1997. Egg production of *Calanus finmarchicus*: effect
 1250 of temperature, food and season. Marine Biology 127, 609-620.

1251

1252 Hirche, H. J., Brey, T. and Niehoff, B., 2001. A high frequency time series at Ocean Weather
 1253 Ship Station M (Norwegian Sea): population dynamics of *Calanus finmarchicus*. Marine
 1254 Ecology Progress Series 219, 205–219.

1255

1256 Hirst, A.G., Bunker, A.J., 2003. Growth of marine planktonic copepods: global rates and
 1257 patterns in relation to chlorophyll *a*, temperature, and body weight. Limnology and
 1258 Oceanography 48, 1988–2010.

1259

1260 Hirst, A.G., Bonnet, D., Harris, R.P., 2007. Seasonal dynamics *Calanus helgolandicus* and
1261 mortality rates of over two years at a station in the English Channel. Marine Ecology
1262 Progress Series 340, 189–205.

1263

1264 Holste, L., Peck, M.A., 2006. The effects of temperature and salinity on egg production and
1265 hatching success of Baltic *Acartia tonsa* (Copepoda: Calanoida): a laboratory investigation.
1266 Marine Biology 148, 1061–1070.

1267

1268 Holste, L., St. John, M.A., Peck, M.A., 2009. The effects of temperature and salinity on
1269 reproductive success of *Temora longicornis* in the Baltic Sea: a copepod coping with a tough
1270 situation. Marine Biology 156, 527–540

1271

1272 Hygum, B.H., Rey, C., Hansen, B.W., 2000a. Growth and development rates of *Calanus*
1273 *finmarchicus* nauplii during a diatom spring bloom. Marine Biology 136, 1075–1085.

1274

1275 Hygum, B.H., Rey, C., Hansen, B.W., Tande, K.S., 2000b. Importance of food quantity to
1276 structural growth rates and neutral lipid reserves accumulated in *Calanus finmarchicus*.
1277 Marine Biology 136, 1057–1073.

1278

1279 Ikeda, T., Kanno, Y., Ozaki, K., Shinada, A., 2001. Metabolic rates of epipelagic marine
1280 copepods as a function of body mass and temperature. Marine Biology 139, 587–596.

1281

1282 Intergovernmental Panel on Climate Change WGI, 2007. Climate Change 2007: The

1283 physical science basis. Cambridge University Press Cambridge.

1284

1285 Ingvarsdóttir, A., Houlihan, D.F., Heath, M.R., Hay, S.J., 1999. Seasonal changes in
 1286 respiration rates of copepodite stage V *Calanus finmarchicus* (Gunnerus). Fisheries
 1287 Oceanography 8 (Suppl 1), 73-83.

1288

1289 Irigoien, X., Head, R.N., Harris, R.P., Cummings, D., Harbour, D., Meyer-Harms, B.,
 1290 2000. Feeding selectivity and egg production of *Calanus helgolandicus* in the English
 1291 Channel. Limnology and Oceanography 45, 44-54.

1292

1293 Irigoien X., 2004. Some ideas about the role of lipids in the life cycle of *Calanus*
 1294 *finmarchicus*. Journal of Plankton Research 26, 259-263.

1295

1296 Irigoien, X., Conway, D.V.P., Harris, R.P., 2004. Flexible diel vertical migration behaviour
 1297 of zooplankton in the Irish Sea. Marine Ecology Progress Series 267, 85-97.

1298

1299 Ji, R., 2011. *Calanus finmarchicus* diapause initiation: new view from traditional life history-
 1300 based model. Marine Ecology Progress Series 440, 105-114.

1301

1302 Ji, R., Ashjian, C. J., Campbell, R. G., Chen, C., Gao, G., Davis, C.S., et al., 2012. Life
 1303 history and biogeography of *Calanus* copepods in the Arctic Ocean: an individual-based
 1304 modelling study. Progress in Oceanography 96, 40-56.

1305 John, H.C., Mittelstaedt, E., Schulz, K., 1998. The boundary circulation along the European
 1306 continental slope as transport vehicle for two calanoid copepods in the Bay of Biscay.
 1307 Oceanologica Acta 21, 307-318.

1308

1309 Johnson, C. L., Leising, A. W., Runge, J. A., Head, E.J, Pepin, P., Plourde, S., et al., 2008.

1310 Characteristics of *Calanus finmarchicus* dormancy patterns in the Northwest Atlantic. ICES

1311 Journal of Marine Science, 65, 339–350.

1312

1313 Jónasdóttir, S.H., Gudfinnsson, H.G., Gislason, A. Assthorsson, O.S., 2002. Diet

1314 composition and quality for *Calanus finmarchicus* egg production and hatching success of

1315 south-west Iceland. Marine Biology 140, 1195-1206.

1316

1317 Jónasdóttir, S.H., Trung, N., Hansen, F., Gärtner, S., 2005. Egg production and hatching

1318 success in the calanoid copepods *Calanus helgolandicus* and *Calanus finmarchicus* in the

1319 North Sea from March to September 2001. Journal of Plankton Research 27, 1239-1259.

1320

1321 Jónasdóttir, S.H., Richardson, K., Heath, M.R., Ingvarsdóttir, A., Christofferson, A., 2008.

1322 Spring production of *Calanus finmarchicus* at the Iceland-Scotland Ridge. Deep Sea

1323 Research 55, 471-489.

1324

1325 Jónasdóttir, S., Koski, M., 2011. Biological processes in the North Sea: comparison of *C.*

1326 *helgolandicus* and *C. finmarchicus* vertical distribution and production. Journal of

1327 Plankton Research 33, 85-103.

1328

1329 Jónasdóttir, S. H., 1999. Lipid content of *Calanus finmarchicus* during overwintering in the

1330 Faroe Shetland Channel. Fisheries Oceanography 8 (Suppl 1), 61-72.

1331

1332 Kattner, G., Krause, M., 1987. Changes in lipids during the development of *Calanus finmarchicus* s.l.

1333 from copepodid I to adult. Marine Biology, 96, 511–518.

1334

1335 Kattner, G., Krause, M., 1989. Seasonal variations of lipids (wax esters, fatty acids and

1336 alcohols) in calanoid copepods from the North Sea. Marine Chemistry 26, 261-275.

1337

1338 Kjellerup, S., Dunweber, M., Swalethorp, R., Nielsen, T.G., Møller, E.F., Markager, S., et

1339 al., 2012. The effects of a future warmer ocean on the coexisting copepods *Calanus*

1340 *finmarchicus* and *C. glacialis* in the Disko Bay Western Greenland. Marine Ecology

1341 Progress Series 447, 87-108.

1342

1343 Koski, M., Kuosa, H., 1999. The effect of temperature, food concentration and female size on

1344 the egg production of the planktonic copepod *Acartia biflosa*. Journal of Plankton Research

1345 21, 1779-1789.

1346

1347 Laabir, M., Poulet, S.A., Ianora, A., 1995. Measuring production and viability of eggs in

1348 *Calanus helgolandicus*. Journal of Plankton Research 17, 1125–1142.

1349

1350 Laabir, M., Poulet, S.A., Harris, R.P., Cuef, A., Head, R.N., Ianora, A., 1998. Comparative

1351 study of the reproduction of *Calanus helgolandicus* in well-mixed and seasonally stratified

1352 coastal waters of the western English Channel. Journal of Plankton Research 20, 407-421.

1353

1354 Lampert, W., 1993. Ultimate causes of diel vertical migration of zooplankton: new evidence

1355 for the predator-avoidance hypothesis. Ergebnisse der Limnologie 39, 79-88.

1356

1357 Longhurst, A., 1998. Ecological geography of the sea. Academic Press, London.

1358

1359 Lynch, D.R., Lewis, C.V.W., Werner, F.E., 2001. Can Georges Bank larval cod survive on
1360 a calanoid diet? Deep Sea Research II 48, 609-630.

1361

1362 Maar, M., Møller, E.F, Gurkan, Z., Jónasdóttir, S., Nielsen, T.G., 2013. Sensitivity of
1363 *Calanus* spp. copepods to environmental changes in the North Sea using life-stage
1364 structured models. Progress in Oceanography 111, 24-37.

1365

1366 Madsen, S.J., Nielsen, T.G., Tervo, O.M., Soderkvist, J., 2008. Importance of feeding for
1367 egg production in *Calanus finmarchicus* and *C. glacialis* during the Arctic spring.
1368 Marine Ecology Progress Series 353, 177–190.

1369

1370 Maps, F., Runge, J.A., Leising, A., Pershing, A.J., Record, N.R., Plourde, S., et al., 2012.
1371 Modelling the timing and duration of dormancy in populations of *Calanus finmarchicus*
1372 from the Northwest Atlantic shelf. Journal of Plankton Research 34, 36-54.

1373

1374 Maps, F., Record, N.R., Pershing, A.J., 2014. A metabolic approach to dormancy in pelagic
1375 copepods helps explaining inter- and intra-specific variability in life-history strategies.
1376 Journal of Plankton Research. In press. doi:10.1093/plankt/fbt100

1377

1378

1379 Marker, T., Andreassen, P., Arashkevich, E., Hansen., B.W., 2003. Lipid deposition and
1380 sexual maturation in cohorts of *Calanus finmarchicus* (Gunnerus) originating from Bergen
1381 (60 °N) and Tromsø (69 °N) reared in Tromsø, Norway. Marine Biology 143, 283–296.

1382

1383 Marshall, S.M., Orr, A.P., 1955. The biology of a marine copepod *Calanus finmarchicus*
 1384 (Gunnerus). London Oliver and Boyd.
 1385
 1386 Marshall, S.M., Orr, A.P., 1958. On the biology of *Calanus finmarchicus*. X. Seasonal
 1387 changes in oxygen consumption. Journal of the Marine Biological Association of the UK 37,
 1388 459-472.
 1389
 1390 Mauchline, J., 1991. Some modern concepts in deep-sea pelagic studies patterns of growth
 1391 in the different horizons. In J. Mauchline and T. Nemoto (Eds.) Marine Biology its
 1392 accomplishment and future prospect (pp. 107-130). Tokyo, Hokusen-sha.
 1393
 1394 Mayor, D.J., Anderson, T.R., Pond, D.W., Irigoien, X., 2009. Egg production and associated
 1395 losses of carbon, nitrogen and fatty acids from maternal biomass in *Calanus finmarchicus*
 1396 before the spring bloom. Journal of Marine Systems 78, 505 – 510.
 1397
 1398 Mayor, D.J., Cook, K., Thornton, B., Walsham, P., Witte, U.F.M., Zuur, A.F., et al., 2011.
 1399 Absorption efficiencies and basal turnover of C, N and fatty acids in a marine Calanoid
 1400 copepod. Functional Ecology 25, 509–518.
 1401
 1402
 1403 McLaren, I.A., Head, E.J.H., Sameoto, D.D., 2001. Life cycles and seasonal distributions of
 1404 *Calanus finmarchicus* on the central Scotian Shelf. Canadian Journal of Fisheries and
 1405 Aquatic Sciences 58, 659–670.
 1406
 1407 Melle, W., Runge, J.A., Head, E., Plourde, S., Castellan, C., Lecandro, P., et al., 2014. The

1408 North Atlantic Ocean as habitat for *Calanus finmarchicus*: environmental factors and life
 1409 history traits. Progress in Oceanography. In press.
 1410
 1411 Meyer, B., Irigoien, X., Graeve, M. Head., R.N., Harris., R.P., 2002. Feeding rates and
 1412 selectivity among nauplii, copepodites and adult females of *Calanus finmarchicus* and
 1413 *Calanus helgolandicus*. Helgoland Marine Research. 56, 169-176.
 1414
 1415 Meyer-Harms, B., Irigoien, X., Head, R., Harris, R., 1999. Selective feeding on natural
 1416 phytoplankton by *Calanus finmarchicus* before, during and after the 1997 spring bloom in
 1417 the Norwegian Sea. Limnology and Oceanography 44 (1), 154–165.
 1418
 1419 Miller, C.B., Crain, J.A., Morgan, C.A., 2000. Oil storage variability in *Calanus*
 1420 *finmarchicus*. ICES Journal of Marine Science 57, 1786-1800.
 1421
 1422 Miller, C.B., Cowles, T.J., Wiebe, P.H., Copley, N.J., Grigg, H., 1991. Phenology in
 1423 *Calanus finmarchicus*, hypotheses about control mechanisms. Marine Ecology Progress
 1424 Series 72, 79-91.
 1425
 1426 Møller, E.F., Maar, M., Jónasdóttir, S.H., Nielsen, T.G., and Tonnesson, K., 2012. The effect
 1427 of changes in temperature and food on the development of *Calanus finmarchicus* and
 1428 *Calanus helgolandicus* populations. Limnology and Oceanography 57, 211 – 220.
 1429
 1430 Munk, P., Hansen, B.W., Nielsen, T.G., Thomsen, H.A., 2003. Changes in plankton and fish
 1431 larvae communities across hydrographic fronts off West Greenland. Journal of Plankton
 1432 Research 25, 815-830.

1433

1434 Niehoff, B., Klenke, U., Hirche, H.J., Irigoien, X., Head, R., Harris, R., 1999. A high
1435 frequency time series at Weathership M, Norwegian Sea, during the 1997 spring bloom: the
1436 reproductive biology of *Calanus finmarchicus*. Marine Ecology Progress Series 176, 81-91.

1437

1438 Niehoff, B., 2000. Effect of starvation on the reproductive potential of *Calanus*
1439 *finmarchicus*. ICES Journal of Marine Science 57, 1764–1772.

1440

1441 Niehoff, B., 2004. The effect of food limitation on gonad development and egg production of
1442 the planktonic copepod *Calanus finmarchicus*. Journal of Experimental Marine Biology and
1443 Ecology 307, 237-259.

1444

1445 Ohman, M.D., Runge, J.A., 1994. Sustained fecundity when phytoplankton resources are in
1446 short supply: omnivory by *Calanus finmarchicus* in the Gulf of St. Lawrence. Limnology
1447 and Oceanography 39, 21–36.

1448

1449 Ohman, M.D., Hirche, H.J., 2001. Density dependent mortality in an oceanic copepod
1450 population. Nature 412, 638–641.

1451

1452 Ohman, M.D., Runge, J.A., Durbin, E.G., Field, D.B., Niehoff, B., 2002. On birth and death
1453 in the sea. Hydrobiologia 480, 55–68.

1454

1455 Ohman, M.D., Eiane, K., Durbin, E.G., Runge, J.A., Hirche, H.-J., 2004. A comparative
1456 study of *Calanus finmarchicus* mortality patterns at five locations in the North Atlantic.
1457 ICES Journal of Marine Science 61, 687–697.

1458

1459 Ohman, M.D., 2012. Estimation of mortality for stage-structured zooplankton
1460 populations: what is to be done? *Journal of Marine Systems* 93, 4-10.

1461

1462 Parent, G.J., Plourde, S., Turgeon, J., 2011. Overlapping size ranges of *Calanus* spp. off the
1463 Canadian Arctic and Atlantic Coasts: impact on species' abundances. *Journal of Plankton*
1464 *Research* 33, 1654-1665.

1465

1466 Parent, G.J., Plourde, S., Turgeon, J., 2012. Natural hybridization between *Calanus*
1467 *finmarchicus* and *C. glacialis* (Copepoda) in the Arctic and Northwest Atlantic. *Limnology*
1468 *and Oceanography* 57, 1057–1066.

1469

1470 Pasternak, A. F., Arashkevich, E. G., Grothe, U., Nikishina, A. B., Solovyev, K. A., 2013.
1471 Different effects of increased water temperature on egg production of *Calanus finmarchicus*
1472 and *C. glacialis*. *Oceanology* 53, 547-553.

1473 Pepin, P., Parrish, C.C., Head, E.J.H., 2011. Late autumn condition of *Calanus finmarchicus*
1474 in the northwestern Atlantic: evidence of size-dependent differential feeding. *Marine Ecology*
1475 *Progress Series* 423, 155-166.

1476

1477 Perrin, G., Dibacco, C., Plourde, S., and Winkler, G., 2012. Assessing stable isotope
1478 dynamics of diapausing *Calanus finmarchicus* and *C. hyperboreus* during the overwintering
1479 period: a laboratory experiment, *Journal of Plankton Research* 34, 685-699.

1480

1481 Peterson, W.T., Dam, H.G., 1996. Pigment ingestion and egg production rates of the
1482 calanoid copepod *Temora longicornis*: implications for gut pigment loss and omnivorous

1483 feeding. Journal of Plankton Research 18, 855–861.

1484

1485 Pierson, J.J., Batchelder, H., Saumweber, W., Leising, A., Runge, J., 2013. The impact of
 1486 increasing temperatures on dormancy duration in *Calanus finmarchicus*. Journal of Plankton
 1487 Research 35, 504-512.

1488

1489 Planque, B., Fromentin, J.M., 1996. *Calanus* and environment in the eastern North
 1490 Atlantic. I. Spatial and temporal patterns of *C. finmarchicus* and *C. helgolandicus*. Marine
 1491 Ecology Progress Series 134, 101-109.

1492

1493 Plourde, S., Runge, J.A., 1993. Reproduction of the planktonic copepod *Calanus*
 1494 *finmarchicus* in the Lower St. Lawrence Estuary: relation to the cycle of phytoplankton
 1495 production and evidence for a *Calanus* pump. Marine Ecology Progress Series 102, 217-
 1496 227.

1497

1498 Pond, D.W., Tarling, G.A., 2011. Phase transitions of wax esters adjust buoyancy in
 1499 diapausing *Calanoides acutus*. Limnology and Oceanography 56, 1310-1318.

1500

1501 Pond, D.W., 2012. The physical properties of lipids and their role in controlling the
 1502 distribution of zooplankton in the oceans. Journal of Plankton Research 34, 443-453.

1503

1504 Pond, D.W., Tarling, G.A., 2013. Solid evidence or fluid ideas on the importance lipid phase
 1505 transitions to diapausing copepods: reply. Journal of Plankton Research 35, 441-443.

1506

1507 Preziosi, B.M., Runge, J.A., 2014. The effect of warm temperatures on hatching success of

1508 the marine planktonic copepod, *Calanus finmarchicus*. Journal of Plankton Research. In
 1509 press doi:10.1093/plankt/fbu056.

1510

1511 Rayner, N.A., Parker, D.E., Horton, E.B., Folland, C.K., Alexander, L.V., Rowell, D.P., et
 1512 al., 2003. Global analyses of SST, sea ice and night marine air temperature since the late
 1513 nineteenth century. Journal of Geophysical Research 108, 4407.

1514

1515 Reid, P.C., Edwards, M., Beaugrand, G., Skogen, M., Stevens, D., 2003. Periodic changes in
 1516 the zooplankton of the North Sea during the twentieth century linked to oceanic inflow.
 1517 Fisheries Oceanography 12, 260-269.

1518

1519 Rey, C., Harris, R. P., Irigoien, X., Head, R., Carlotti, F., 2001. Influence of algal diet on
 1520 growth and ingestion of *Calanus helgolandicus* nauplii. Marine Ecology Progress Series
 1521 216, 151–165.

1522

1523 Rey-Rassat, C., Irigoien, X., Harris, R., Head, R., Carlotti, F., 2002a. Egg production rates
 1524 of *Calanus helgolandicus* females reared in the laboratory: variability due to present and
 1525 past feeding conditions. Marine Ecology Progress Series 238, 139-151.

1526

1527 Rey-Rassat C., Irigoien X., Harris R., Carlotti, F., 2002b. Energetic cost of gonad
 1528 development in *Calanus finmarchicus* and *C. helgolandicus*. Marine Ecology Progress
 1529 Series 238, 301-306.

1530

1531 Rey-Rassat, C., Irigoien, X., Harris, R., Head, R., Carlotti, F., 2002c. Growth and development
 1532 of *Calanus helgolandicus* reared in the laboratory. Marine Ecology Progress Series 238,

1533 125–138.

1534

1535 Reygondeau, G., Beaugrand, G., 2011. Future Climate-driven shifts in distribution of

1536 *Calanus finmarchicus*. *Global Change Biology* 17, 756-766.

1537

1538 Rhyne, A.L., Ohs, C.L., Stenn, E., 2009. Effects of temperature on reproduction and survival

1539 of the calanoid copepod *Pseudodiaptomus pelagicus*. *Aquaculture* 292, 53-59.

1540

1541 Richardson, K., Jónasdóttir, S.H., Hay, S.J., Christofersen, A., 1999. *Calanus finmarchicus*

1542 egg production and food availability in the Faroe-Shetland Channel and northern North

1543 Sea: October-March. *Fisheries Oceanography* 8, 153-162.

1544

1545 Runge, J.A., Plourde, S., Joly, P., Niehoff, B., Durbin, E., 2006. Characteristics of egg

1546 production of the planktonic copepod, *Calanus finmarchicus*, on Georges Bank: 1994-

1547 1999. *Deep-Sea Research II* 53, 2618-2631.

1548

1549 Runge, J.A., 1987. Measurement of egg production rate of *Calanus finmarchicus* from

1550 preserved samples. *Canadian Journal of Fisheries and Aquatic Science* 44, 2009-2012.

1551

1552 Runge, J.A., Plourde, S., 1996. Fecundity characteristics of *Calanus finmarchicus* in coastal

1553 waters of eastern Canada. *Ophelia* 44, 171-187.

1554

1555 Saiz, E., Calbet, A., 2007. Scaling of feeding in marine calanoid copepods. *Limnology and*

1556 *Oceanography* 52, 668–675.

1557

1558 Sargent, J.R., Gatten, R.R., Corner, F.D.S., Kilvington, C.C., 1977. On the nutrition and
 1559 metabolism of zooplankton. XI. Lipid in *Calanus helgolandicus* grazing *Biddulphia*
 1560 *sinensis*. Journal of the Marine Biological Association of the United Kingdom 57, 525-533.
 1561
 1562 Sars, G.O., 1902. An Account of the Crustacea of Norway. Copepoda Calanoida. Vol. IV.
 1563 Published by the Bergen Museum, Norway.
 1564
 1565 Saumweber, W., Durbin, E. G., 2006. Estimating potential diapause duration in *Calanus*
 1566 *finmarchicus*. Deep-Sea Research II 53, 2597-2617.
 1567
 1568 Speirs, D.C., Gurney, W.S.C., Heath, M.R., Horbelt, W., Wood, S., de Cuevas, A., 2006.
 1569 Ocean-scale modelling of the distribution, abundance, and seasonal dynamics of the
 1570 copepod *Calanus finmarchicus*. Marine Ecology Progress Series 131, 183-192.
 1571
 1572 Stenevik, E.K., Melle, W., Gaard, E., Gislason, A., Broms, C.T.A., Prokopchuk, I., Ellertsen,
 1573 B., 2007. Egg production of *Calanus finmarchicus* - a basin-scale study. Deep-Sea Research II
 1574 54, 2672-2685.
 1575
 1576 Svensen, C., Tande, K., 1999. Sex change and female dimorphism in *Calanus finmarchicus*.
 1577 Marine Ecology Progress Series 176, 93–102.
 1578
 1579 Stohr, S., Schulz, K., John, H. C., 1996. Population structure and reproduction of *Calanus*
 1580 *helgolandicus* (Copepoda Calanoida) along the Iberian and Moroccan slope. Helgolander
 1581 Meeresuntersuchungen 50, 457-475.
 1582

1583 Tande, K.S., 1982. Ecological investigations on the zooplankton community of Balsfjorden,
 1584 Northern Norway - generation cycles, and variations in body- weight and body content of
 1585 carbon and nitrogen related to overwintering and reproduction in the copepod *Calanus*
 1586 *finmarchicus* (Gunnerus). Journal of Experimental Marine Biology and Ecology 62, 129-
 1587 142.

1588

1589 Tande, K.S., 1988. Aspects of developmental and mortality rates in *Calanus finmarchicus*
 1590 related to equiproportional development. Marine Ecology Progress Series 44, 51-58.

1591

1592 Thompson, B. M., 1982. Growth and development of *Pseudocalanus elongatus* and
 1593 *Calanus* sp. in the laboratory. Journal of the Marine Biological Association UK 62, 359-
 1594 372.

1595

1596 Tiselius, P., Hansen, B., Calliari, D., 2012. Fatty acid transformation in zooplankton: from
 1597 seston to benthos. Marine Ecology Progress Series, 446, 131 – 144.

1598

1599 Unal, E., Bucklin, A., 2010. Basin-scale population genetic structure of the planktonic
 1600 copepod *Calanus finmarchicus* in the North Atlantic Ocean. Progress in Oceanography 87,
 1601 175–185.

1602

1603 van Deurs M., van Hal R., Tomczak M., Jonasdottir, S.J., Dolmer, P., 2009. Recruitment of
 1604 lesser sandeel *Ammodytes marinus* in relation to density dependence and zooplankton
 1605 composition. Marine Ecology Progress Series 381, 249-258.

1606

1607 van Deurs, M., Koski, M., Rindorf, A., 2014. Does copepod size determine food
 1608 consumption of particulate feeding fish? ICES Journal of Marine Science 71, 35-43.
 1609
 1610 Visser, A.W., Jónasdóttir S.H., 1999. Lipids, buoyancy and the seasonal vertical migration
 1611 of *Calanus finmarchicus*. Fisheries Oceanography 8, 100-106.
 1612
 1613 Weikert, H., Koppelman, R., Wiegratz, S., 2001. Evidence of episodic changes in deep-
 1614 sea zooplankton abundance and composition in the Levantine Sea (Eastern Mediterranean).
 1615 Journal of Marine Systems 30, 221-239.
 1616
 1617 Williams, R., Conway, D.V.P., 1984. Vertical distribution and seasonal and diurnal
 1618 migration of *Calanus helgolandicus* in the Celtic Sea. Marine Biology 79, 63-73.
 1619
 1620 Williams, R., 1985. Vertical distribution of *Calanus finmarchicus* and *C. helgolandicus* in
 1621 relation to the development of the seasonal thermocline in the Celtic Sea. Marine Biology
 1622 86, 145-149.
 1623
 1624 Wilson, R.J., Speirs, D.C., Heath, M.R., 2013. Solid evidence or fluid ideas on the
 1625 importance lipid phase transitions to diapausing copepods. Journal of Plankton Research 35,
 1626 438-440.
 1627
 1628 Wirtz, K., 2013. How fast can plankton feed? Maximum ingestion rate scales with digestive
 1629 surface area Journal of Plankton Research 35, 33-48.
 1630

1631 Yebra, L., Bonnet, D., Harris, R.P., Lindeque, P.K., Peijnenburg, K., 2011. Barriers in the
1632 pelagic: population structuring of *Calanus helgolandicus* and *C. euxinus* in European waters.
1633 Marine Ecology Progress Series 428, 135–149.

1634 **Figure and Table Captions**

1635 Figure 1: Comparison of published female prosome lengths of *C. finmarchicus* and *C.*
1636 *helgolandicus* with annual average sea surface temperature in the year prosome length
1637 was recorded. *C. finmarchicus* references: Tande, 1982; Richardson et al., 1999; Runge
1638 and Plourde, 1996; Ohman and Runge, 1994; Kjellrup et al., 2012; Svensen and Tande,
1639 1999; Niehoff et al., 1999; McLaren et al., 2001; Niehoff, 2004; Runge et al., 2006; Munk
1640 et al., 2003; Madsen et al., 2008; Jónasdóttir et al., 2008; Stenevik et al., 2007.
1641 *C. helgolandicus*: Jónasdóttir et al., 2005; Ceballos et al., 2004; Ceballos et al., 2006; Rey-
1642 Rassat et al., 2002b; Jónasdóttir and Koski, 2011; Yebra et al., 2011; Bonnet et al. 2009.
1643 Annual average sea surface temperature was estimated using the HadSST3 data set
1644 (Rayner et al., 2003), and in the HadSST3 grid cell the prosome length was measured
1645 within. Line shows linear model: Prosome length = $2.869 - 0.0358 \text{ Temperature}$ ($r^2 =$
1646 0.63 .)

1647

1648 Figure 2: Comparison of female prosome lengths for co-occurring *C. finmarchicus* and *C.*
1649 *helgolandicus* published in Jónasdóttir et al., 2005 and Jónasdóttir and Koski 2011. Line
1650 shows linear model: *C. finmarchicus* PL = $0.579 + 0.767 \text{ } C. \text{ helgolandicus PL}$ ($r^2 = 0.70$.)

1651

1652 Figure 3: Development time for *C. finmarchicus* and *C. helgolandicus* from egg to start of
1653 CV stage. Model was parameterised for *C. finmarchicus* using Campbell et al. (2001a).
1654 Solid lines are modelled development times assuming that the only inter-species
1655 difference is the relationship between ingestion rate and temperature, whereas symbols are
1656 published experimental development times for each species.

1657

1658 Figure 4: The relationship between clearance rate and temperature for *C. finmarchicus*
1659 and *C. helgolandicus*. Reproduced from Møller et al. (2012).

1660

1661 Figure 5: Comparison of published maximum egg production rates and annual average sea
1662 surface temperatures for *C. finmarchicus* and *C. helgolandicus*. *C. finmarchicus*: Head et
1663 al., 2000; Diel and Tande, 1992; Jónasdóttir et al., 2008; Niehoff et al., 1999; Niehoff et al.,
1664 2004; Durbin et al., 2003; Jónasdóttir et al., 2005; Jónasdóttir and Koski, 2011; Gislason and
1665 Astthorsson, 2000; Hay, 1995; Runge et al., 2006; Campbell and Head, 2000. *C.*
1666 *helgolandicus*: Fileman et al., 2010; Harris, 1988; Tiselius et al., 2012; Ceballos et al., 2004;
1667 Ceballos and Alvarez-Marques, 2006; Ceballos et al., 2006; Jónasdóttir et al., 2005;
1668 Jónasdóttir and Koski, 2011. Line shows linear model: Max. EPR = $115.35 - 4.438$
1669 Temperature ($r^2 = 0.175$.)

1670

1671 Figure 6: Decadal changes in *C. finmarchicus* and *C. helgolandicus* total stages CV and
1672 CVI abundances, from CPR data. Data was interpolated using Loess smooths, with a span
1673 of 0.05. We exclude any one by one degree grid cells where there are less than 5 total
1674 monthly observations in the cell and its direct neighbours during the respective decade.
1675 Colour scale represents annual abundance of CV and CVI stages.

1676

1677 Figure 7: Average annual abundances of *C. finmarchicus* and *C. helgolandicus* stages CV
1678 and CVI during the period 1960-69 as predicted by a GAM model, which related abun-

1679 dance to annual temperature, monthly salinity, bathymetry and month. Colour scale
1680 represents predicted average annual abundance of CV and CVI stages.

1681

1682 Figure 8: Relationship of annual average abundance to temperature and bathymetry for *C.*
1683 *finmarchicus* and *C. helgolandicus*. Relationship is derived using a GAM model relating
1684 abundance with temperature, bathymetry, and month. Colour scale represents predicted
1685 annual abundance of CV and CVI stages.

1686

1687 Figure 9: Seasonal cycles in the North Sea for *C. finmarchicus* (dashed line) and *C.*
1688 *helgolandicus* (solid line). Derived from CPR abundance data using a GAM model relating
1689 monthly abundance with month

1690

1691 Table 1: Published papers reporting *C. finmarchicus* lipid levels for stage C5

1692

1693 Table 2: Published papers reporting *C. helgolandicus* lipid levels for stage C5

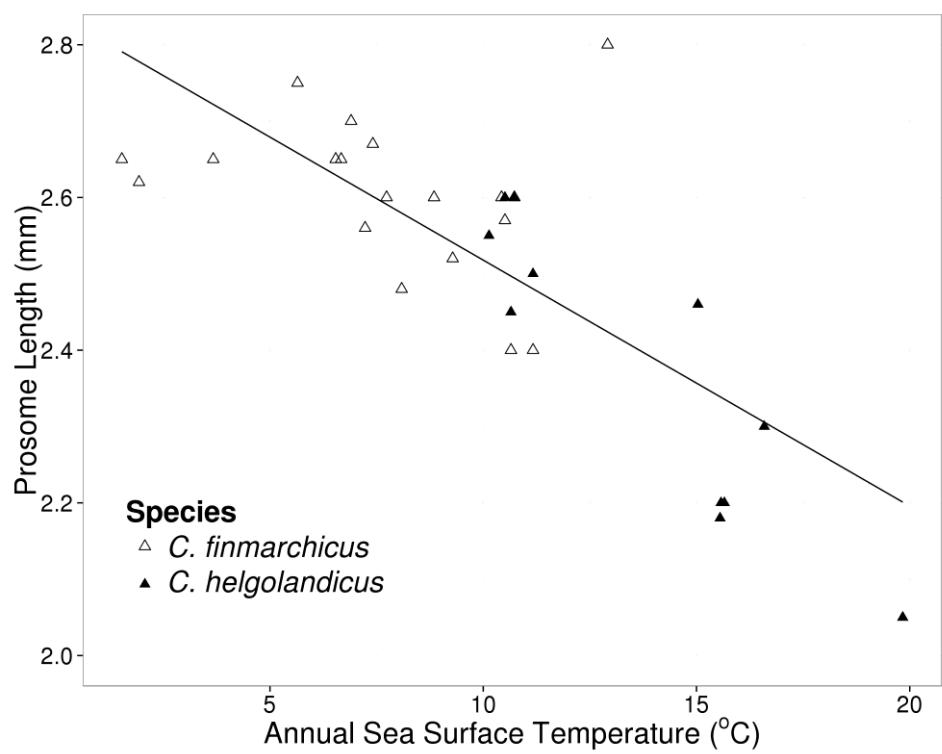
1694

1695 Table 3: R^2 values for single and multi-variable GAMs for *Calanus finmarchicus* and
1696 *Calanus helgolandicus*. Models related abundance of *C. finmarchicus* and *C.*
1697 *helgolandicus*, from Continuous Plankton Recorder data over the period 1958-2002,
1698 with annual temperature (**TEMP**), salinity (**SAL**) and bathymetry (**BATH**), with
1699 seasonality accounted for using month (**MON**). We used tensor product smooths (te).
1700 All p-values were less than 0.01.

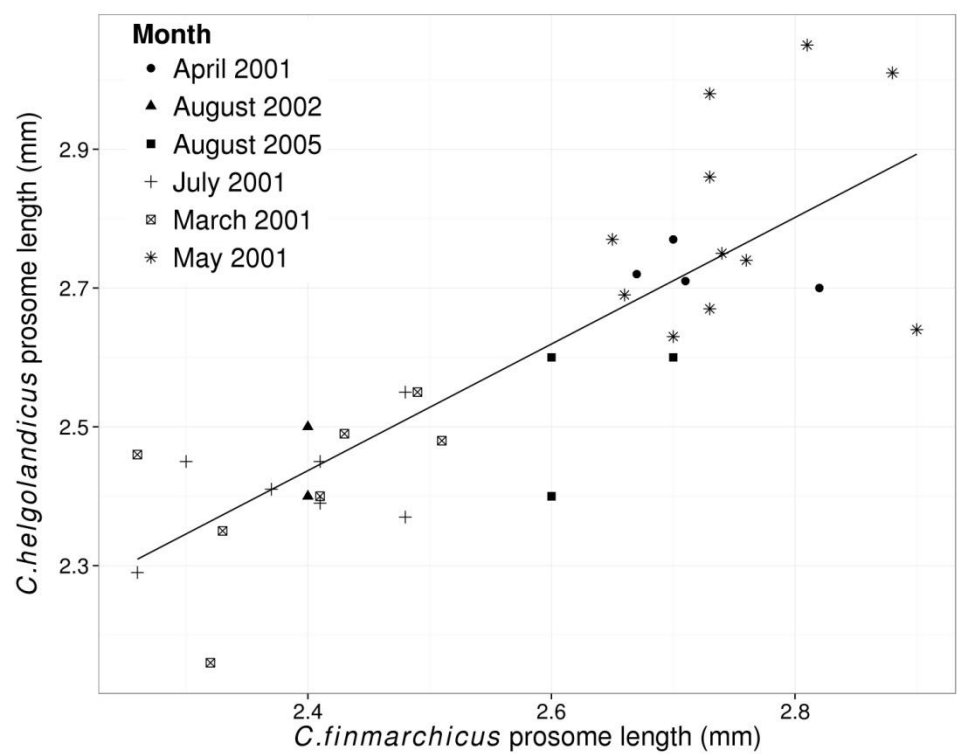
1701

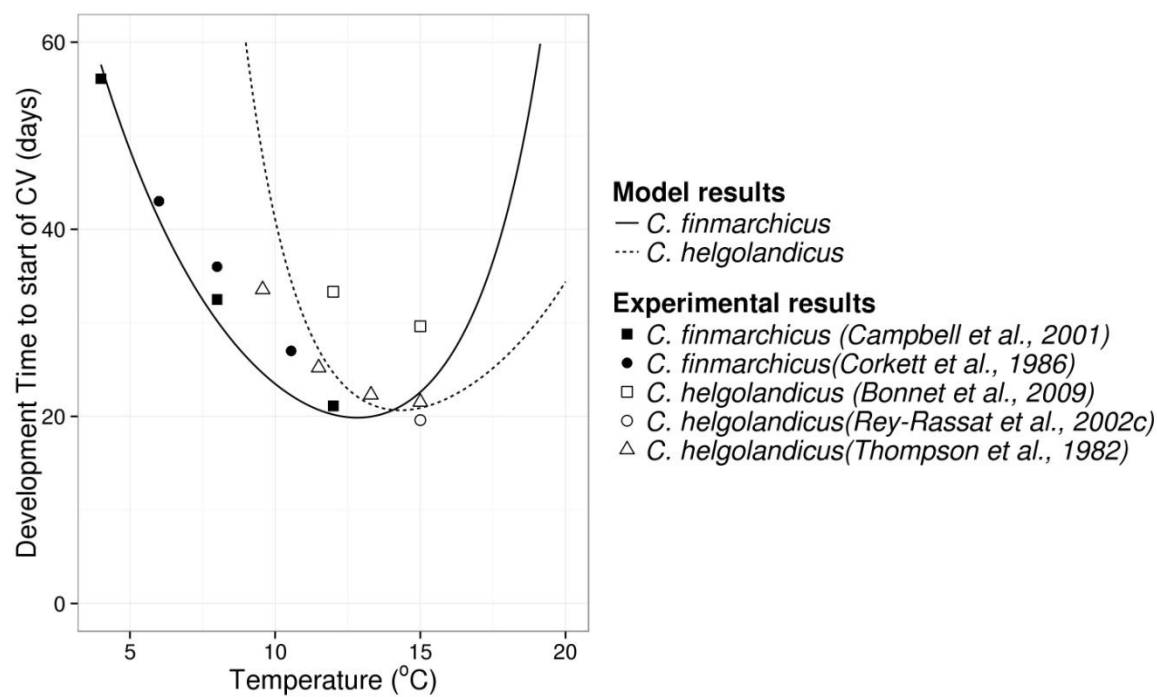
1702

1703 Figure 1

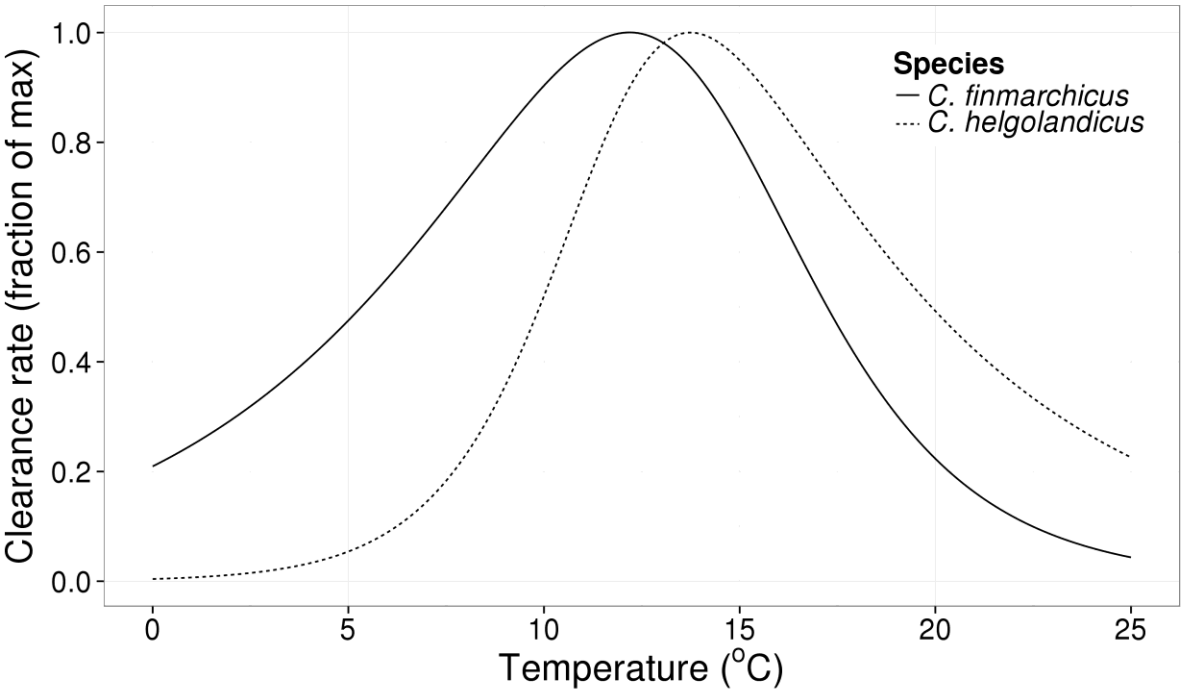


1704





1709 Figure 4

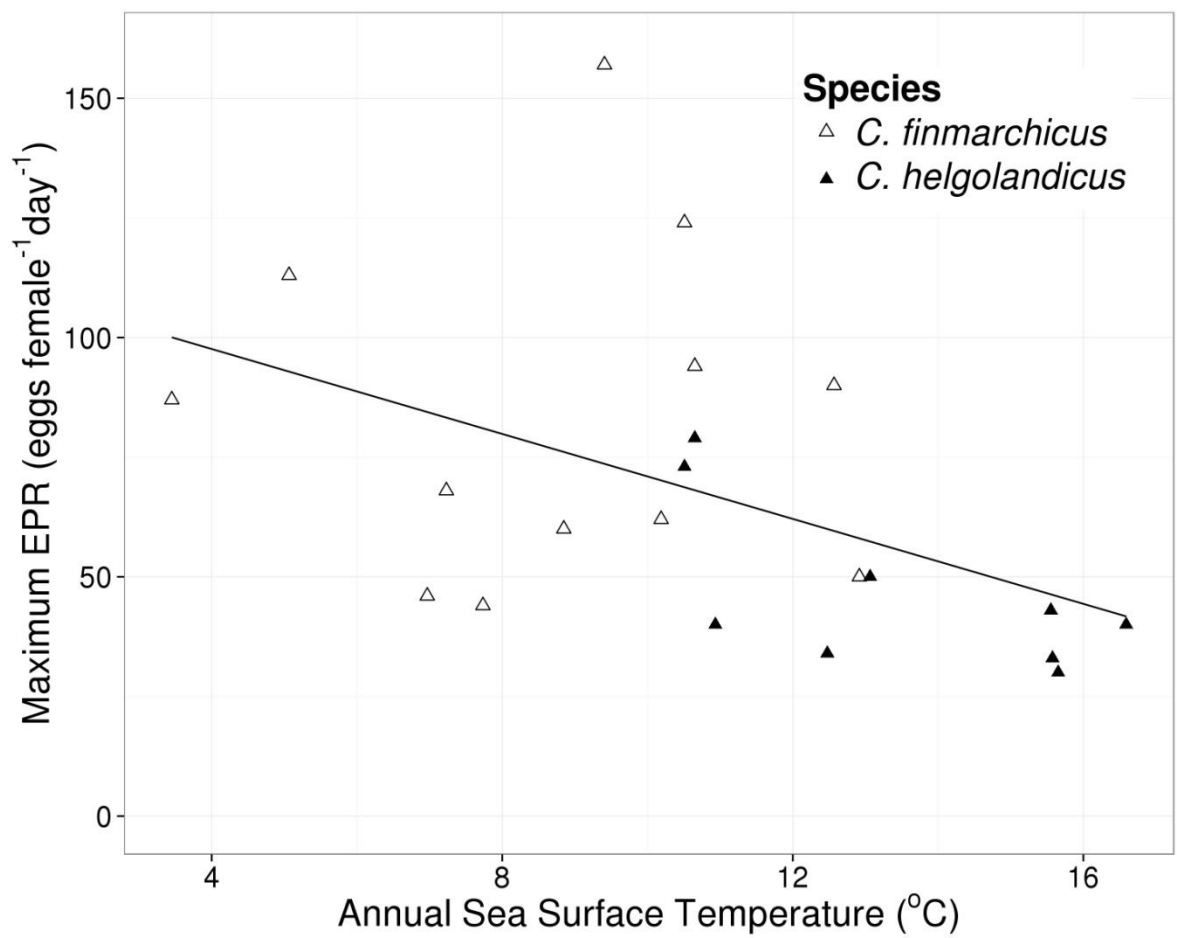


1710

1711

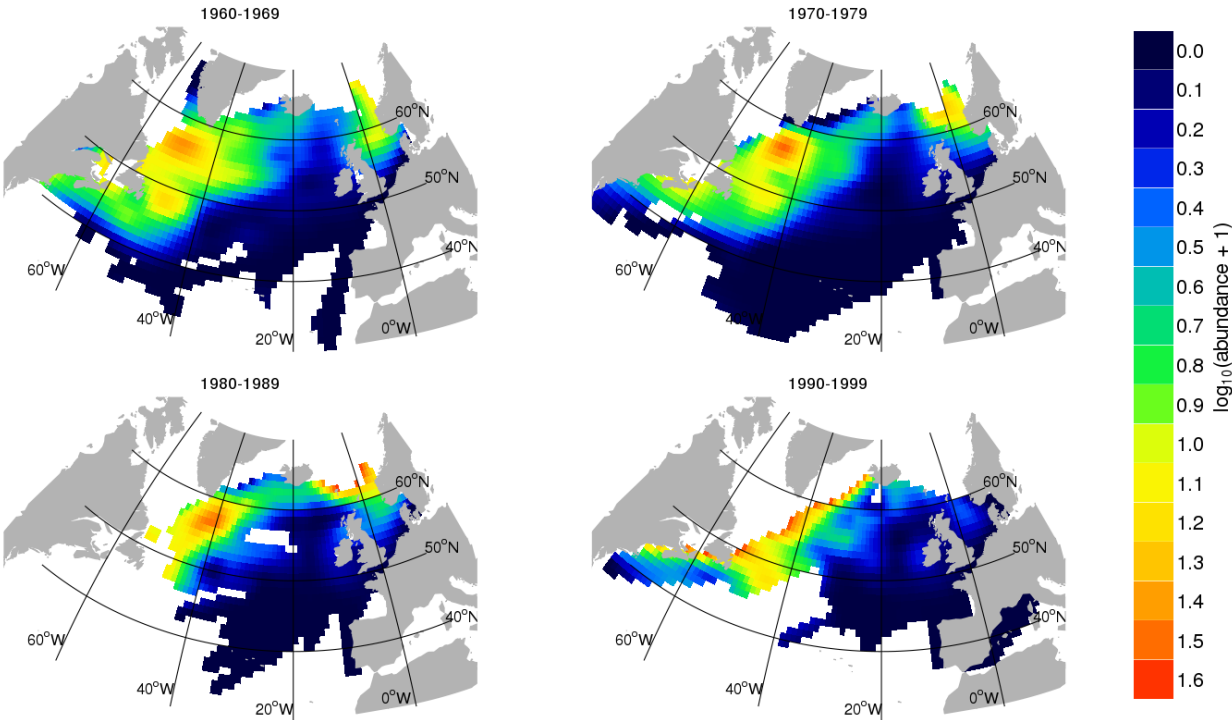
1712

1713 Figure 5



1714
1715

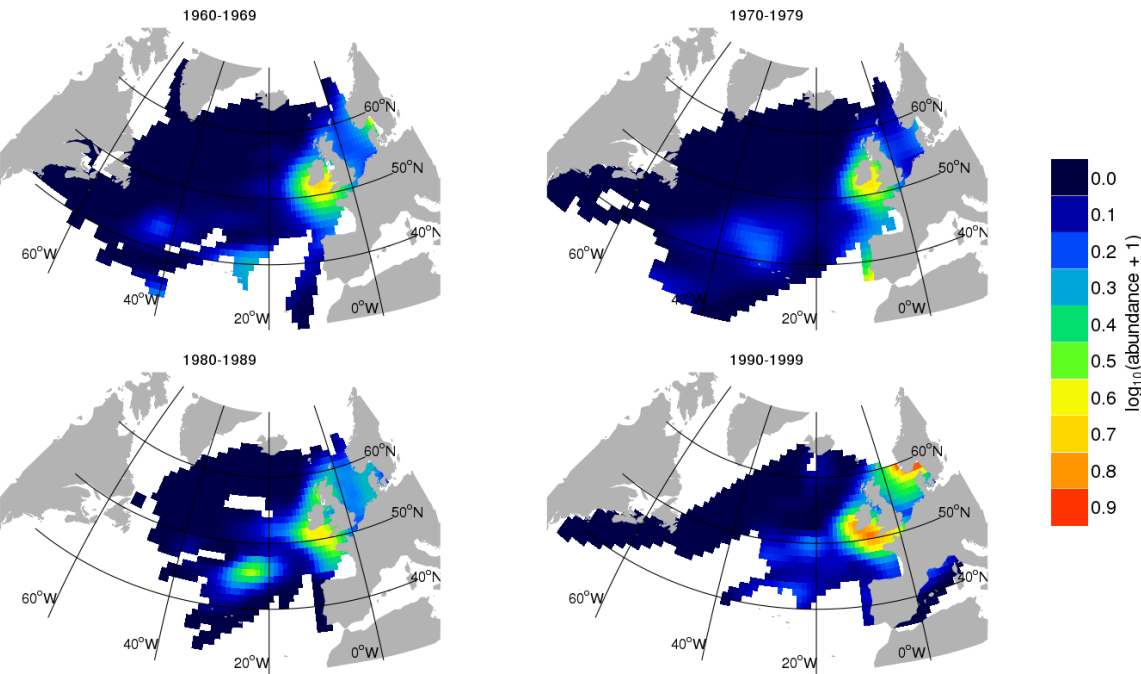
1716 Figure 6



1717

C. finmarchicus

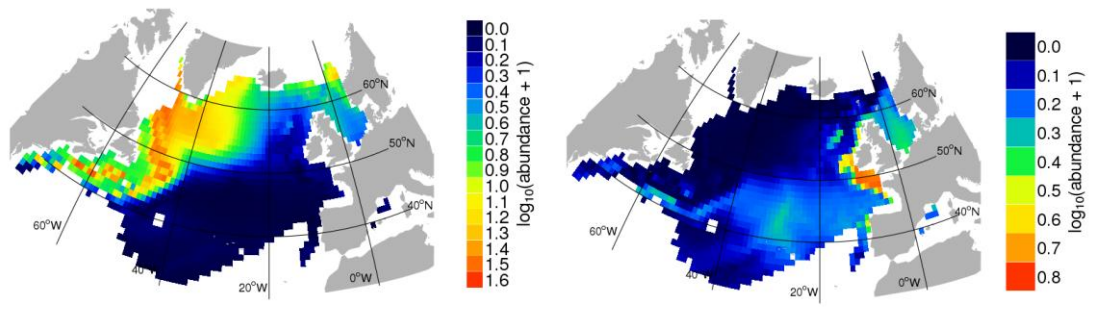
1718



1719

C. helgolandicus

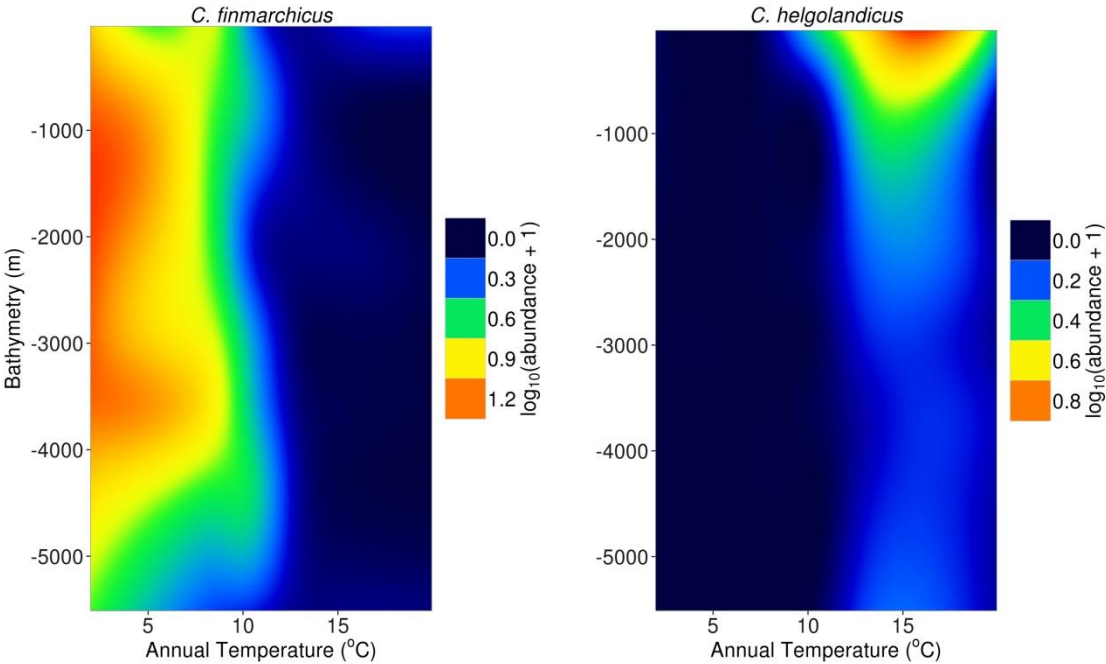
1720 Figure 7



1721

1722

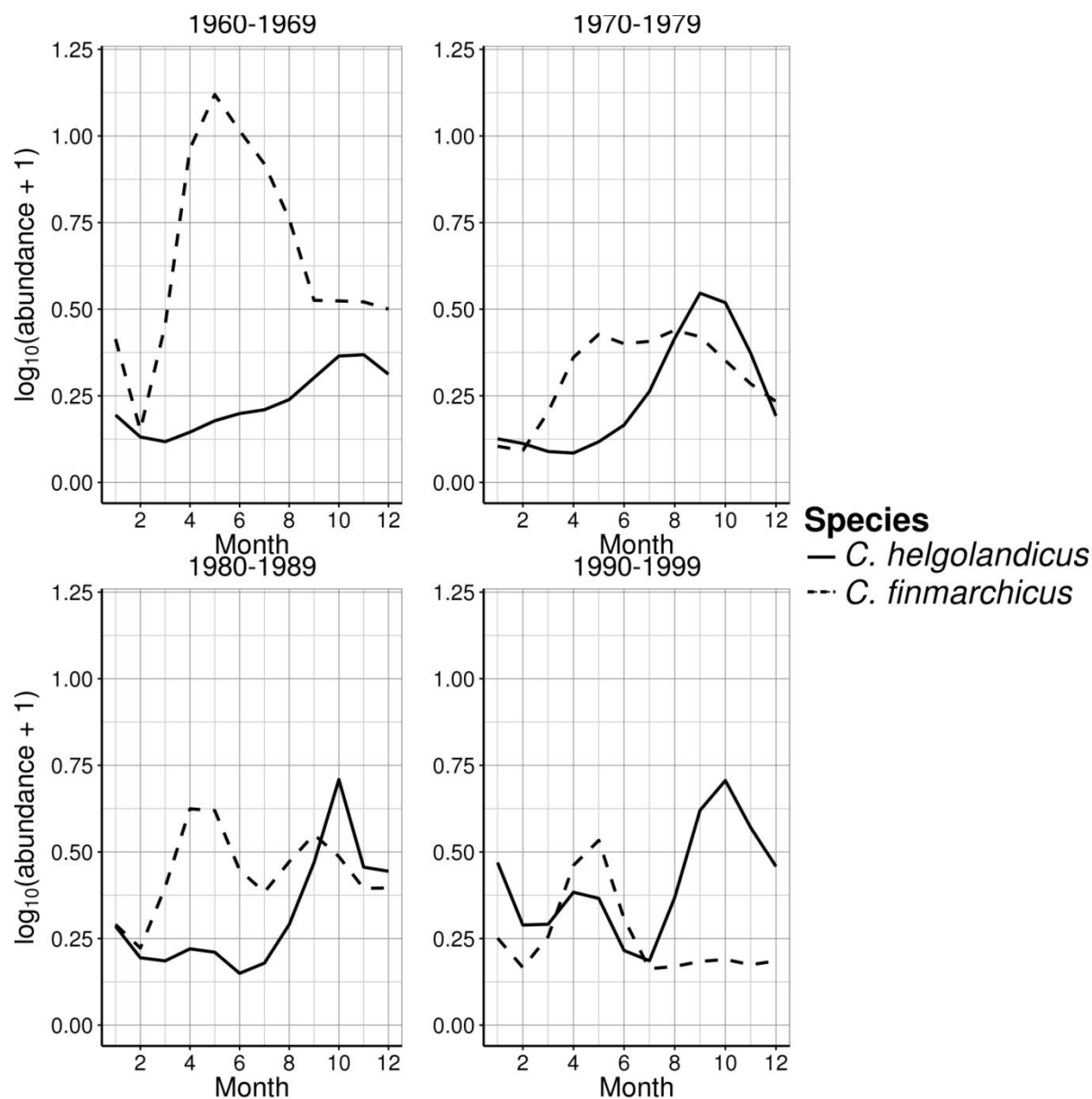
1723 Figure 8



1724

1725

1726 Figure 9



1727

1728

1729

1730

1731

1732

1733 Table 1

1734	Reference	Location	Maximum WE ($\mu\text{g C}$)
1735	Kattner and Krause, 1987	North Sea	30
1736	Kattner and Krause, 1989	North Sea	49.808
1737	Ohman and Runge, 1994	St. Lawrence	11.356
1738	Heath and Jónasdóttir, 1999	Faroe-Shetland Channel	100
1739	Clark et al., 2012	Loch Ewe	100
1740	Marker et al., 2003	Bergen	77
1741	Marker et al., 2003	Tromsø	82
1742	Hygum et al., 2000a	Mesocosms	60
1743	Hygum et al., 2000b	Mesocosms	72
1744	Rey-Rassat et al., 2002b	Mesocosms	142
1745	Jónasdóttir, 1999	Faroe-Shetland Channel	200
1746			

1747 Table 2

1748

1749	Reference	Location	Maximum WE ($\mu\text{g C}$)
1750	Gatten et al., 1979	English Channel	50.31
1751	Kattner and Krause, 1989	North Sea	36
1752	Ceballos et al., 2006	Cantabrian Sea	21.3
1753	Sargent et al., 1977	English Channel	19.9
1754	Rey-Rassat et al., 2002b	Mesocosms	55

1755

1756

1757	Table 3		
1758			
1759	Model	<i>Calanus finmarchicus</i>	<i>Calanus helgolandicus</i>
1760	te(MON)	0.094	0.014
1761	te(SAL)	0.118	0.008
1762	te(TEMP)	0.243	0.113
1763	te(BATH)	0.033	0.115
1764	te(MON,TEMP)	0.371	0.253
1765	te(SAL,TEMP)	0.26	0.206
1766	te(TEMP,BATH)	0.25	0.183
1767	te(MON,SAL)	0.237	0.173
1768	te(SAL,BATH)	0.21	0.158
1769	te(MON,BATH)	0.153	0.051
1770	te(MON,TEMP,BATH)	0.448	0.349
1771	te(MON,SAL,TEMP)	0.427	0.296
1772	te(MON,SAL,BATH)	0.385	0.293
1773	te(SAL,TEMP,BATH)	0.301	0.264
1774	te(MON,SAL,TEMP,BATH)	0.498	0.399
1775			