
Long-term changes of euphausiids in shelf and oceanic habitats southwest, south and southeast of Iceland

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Abstract:

Generalized additive models (GAMs) were used to test the hypothesis that changes in physical and biological environmental conditions affected by current climatic warming would negatively impact the euphausiid populations in the North Atlantic. Two zooplankton time series were used, one collected by the Marine Research Institute (MRI) on a transect south of Iceland during spring (1990–2011) and the other by the Continuous Plankton Recorder (CPR) survey (1958–2007) in the oceanic waters south of Iceland covering all months. Due to limitations of the sampling gears used, the results mainly reflect the variations of the early stages of euphausiids. On a spatial scale, results reveal a general decline of euphausiid abundance from the east coast of Greenland to the Faroe Islands. On a temporal scale, euphausiid numbers decreased in most CPR areas from 1958 to 2007. Conversely, an increase was observed in numbers of larvae during spring 1990–2011 for the shelf south of Iceland. Single variable-based GAMs indicated that phytoplankton biomass was generally the main environmental factor regulating euphausiid abundance. Multiple variable-based GAMs showed that phytoplankton biomass was the strongest predictor of euphausiid abundance in the west, whereas in the east temperature appears to be most important. In addition, the onset of the spring bloom also affected the long-term changes in euphausiid abundance. For the oceanic areas, it is concluded that a weakened temporal synchrony between the development of young euphausiids and the phytoplankton bloom influenced by recent climate warming may have led to the observed decrease in euphausiid populations.

Keywords: euphausiids ; long-term changes ; Icelandic waters ; Northeastern Atlantic Ocean ; Continuous Plankton Recorder ;

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40 **INTRODUCTION**

41 Euphausiids are an important zooplankton group in the Icelandic marine ecosystem as they
42 constitute the second largest component of the zooplankton biomass after copepods (Astthorsson
43 and Gislason, 1995; Astthorsson *et al.*, 2007), and at least in some regions (e.g. north of Iceland)
44 dominate the zooplankton community in winter months (Astthorsson and Gislason, 1992).

45 Euphausiids prey on both phytoplankton and small zooplankton, while being an important food for
46 top predators such as cod, saithe, capelin, herring, blue whiting, whales and sea birds (Pálsson,
47 1983; Astthorsson and Pálsson, 1987; Vilhjálmsón, 1994; Astthorsson and Gislason, 1997b;
48 Sigurjónsson and Víkingsson, 1997; Jaworski and Ragnarsson, 2006; Pálsson and Björnsson, 2011).

49 Einarsson (Einarsson, 1945) reviewed the distribution pattern and the general biology of
50 euphausiids in the Northeastern Atlantic and around Iceland. The later studies used material from
51 the Continuous Plankton Recorder (CPR) survey of the Sir Alistair Hardy Foundation for Ocean
52 Science (SAHFOS) further to describe the distribution and population dynamics of euphausiids in
53 the North Atlantic Ocean (Lindley, 1977, 1978, 1980, 1982a, 1982b; Lindley and Williams, 1980;
54 Williams and Lindley, 1982). More recent studies in Icelandic waters have focused on the
55 distribution and life cycles of euphausiids in a fjord on the north-western peninsula (Astthorsson,
56 1990; Astthorsson and Gislason, 1992), over the shelf north of Iceland (Astthorsson and Gislason,
57 1997a), and in the subarctic waters of the Iceland Sea, to the north of Iceland (Gislason and Silva,
58 2012). The most recent studies investigated the distribution and population patterns of euphausiids
59 in the Irmirger Sea and over the northern Mid-Atlantic ridge (Saunders *et al.*, 2007; Letessier *et al.*,
60 2009; Letessier *et al.*, 2011). These studies showed that *Thysanoessa raschii*, *T. inermis*, *T.*
61 *longicaudata* and *Meganycitiphanes norvegica* were the most common euphausiid species in these
62 regions.

63 Research has shown that bottom-up rather than top-down effects regulate the marine
64 ecosystem north and east of Iceland (Astthorsson and Vilhjálmsón, 2002; Astthorsson *et al.*, 2007).
65 Changes in hydrographic conditions, mainly due to variable inflow of Atlantic water, influence the
66 stratification of the water column and consequently the magnitude and timing of the phytoplankton
67 spring bloom, which in turn affects zooplankton abundance and composition (Astthorsson and
68 Gislason, 1995; Astthorsson and Gislason, 1998; Gislason *et al.*, 2009). These variations have
69 further been shown to affect growth of fish in the area (Astthorsson and Vilhjálmsón, 2002;

70 Astthorsson *et al.*, 2007). In the more biologically complex southern and western areas causal
71 events are harder to identify (Astthorsson *et al.*, 2007).

72 The rise in seawater temperature driven by climate change appears to have altered the
73 phenology, abundance and diversity of plankton in the Northeastern Atlantic Ocean (Reid, 2001;
74 Beaugrand and Reid, 2003; Beaugrand *et al.*, 2003; Edwards and Richardson, 2004; Reid and
75 Valdés, 2011). Thus, climate-induced changes in the plankton community have affected higher
76 trophic levels by asynchrony between production at the base of the food web and at higher levels
77 (Beaugrand and Reid, 2003; Edwards and Richardson, 2004). Several studies have related a decline
78 in the stocks of key Antarctic euphausiid species (*Euphausia superba*) in the Southern Ocean to
79 climate warming and its implications on the abiotic and biotic environment (e.g. Atkinson *et al.*,
80 2004; Flores *et al.*, 2012).

81 We hypothesize that changes in physical and biological environmental conditions affected
82 by the rise in sea water temperatures would negatively impact the euphausiid populations. Thus, it
83 is the main purpose of this study is to describe the long-term and seasonal changes of euphausiids in
84 Icelandic waters and adjacent sea areas. In particular, we aim to evaluate how environmental
85 variables and the onset of the phytoplankton spring bloom and biomass affect the multidecadal
86 variability of the euphausiids.

87

88 **METHODS**

89 For this study, two time series of euphausiid abundance were used, one collected by the Marine
90 Research Institute (MRI) at a transect south of Iceland in May-June 1990 to 2011, (the Icelandic
91 spring survey) and the other by the CPR survey covering a wider area of the Northeastern Atlantic
92 Ocean and the whole year (1958–2007) (Fig.1).

93

94 *The Icelandic spring survey*

95 From 1990 to 1991 zooplankton samples were collected with Hensen nets (0.42 m² mouth area, 200
96 µm mesh size) whereas from 1992 to 2011 with WP2 nets (0.25 m² mouth area, 200 µm mesh size).
97 The plankton nets were towed from 50 m depth (or from ~2 m above the bottom where depth was
98 <50 m) to the surface at a velocity of ~0.75 m s⁻¹. HydroBios flowmeters were fitted in the net
99 mouth to measure the volume of water filtered.

100 The samples were preserved in 4% buffered formaldehyde until analysed in the laboratory
101 ashore. The procedure consisted in counting and identifying under a stereomicroscope the larger
102 zooplankters such as adult euphausiids in the whole sample, and smaller ones in sub-samples
103 obtained by a Motoda splitter containing at least 400 zooplankters (Motoda, 1959). Adult
104 euphausiids were identified to the species level and the earlier developmental stages were separated

105 into the following categories: eggs, and nauplius, metanauplius, calytopsis and furcilia stages. For
106 the present analysis the larval stages were treated as one group (nauplii, metanauplii, calyptope and
107 furciliae).

108

109 *The Continuous Plankton Recorder survey*

110 The CPR (0.013 m² mouth area, 270 µm mesh size) collects plankton at approximately monthly
111 intervals sampling in continuous along standard routes crossing the North Atlantic Ocean (Fig. 1).
112 The instrument is towed by ships of opportunity at an estimated mean depth of ~7 m and at an
113 average velocity of ~6.6 m s⁻¹ (Batten *et al.*, 2003). The distance corresponding to one CPR sample
114 is equivalent to filtering ~3 m³ of seawater (i.e. 10 nautical miles). At SAHFOS, the samples were
115 processed and the plankton taxa identified and counted using standard procedures (Batten *et al.*,
116 2003; Richardson *et al.*, 2004, 2006). Monthly data from 1958 to 2007, collected in the CPR
117 standard areas southwest, south and southeast of Iceland were used (58–66°N, 43°W–3°E, Fig. 1).
118 In the analysis, euphausiid furcilia, juveniles and adult counts (Lindley, 1977; Richardson *et al.*,
119 2006) were combined and converted to total numbers per m³.

120

121 *Explanatory variables*

122 Concurrent with the zooplankton sampling in the Icelandic spring survey, temperature and salinity
123 were measured on each station with a CTD (Sea Bird Electronics SBE-9) and water samples
124 collected from five depths (0, 10, 20, 30 and 50 m) for chlorophyll *a* (Chl *a*) analysis. The water
125 was filtered through GF/C glass fibre filters, that were homogenized in 90% aqueous acetone and
126 the Chl *a* extracted and measured by a spectrophotometer. Temperature, salinity and Chl *a* values
127 were averaged from the surface down to 50 m depth.

128 Data on monthly Sea Surface Temperature (SST) from 1958 to 2011 were obtained from the
129 UK Met Office Hadley Centre (HadISST v 1.1 available at <http://badc.nerc.ac.uk>) and averaged for
130 each CPR area (Fig. 1). Monthly sea surface salinity data at ~5 m depth were obtained from the
131 Global Ocean Data Assimilation System (GODAS available at <http://www.esrl.noaa.gov/psd/>), and
132 averaged for each CPR area from 1980 to 2011. Monthly means of the North Atlantic Oscillation
133 (NAO) index from 1958 to 2011 were obtained from the National Weather Service – Climate
134 Prediction Center (available at <http://www.nws.noaa.gov/>). The index is a measure of the pressure
135 difference between the Icelandic low and the Azores high. Daily NAO index is constructed by
136 projecting the daily (00Z) 500mb height anomalies over the Northern Hemisphere onto the loading
137 pattern of the NAO. For the present analysis, the NAO winter index was used (average from
138 December to April) as suggested by Fromentin and Planque (Fromentin and Planque, 1996).

139 Data on surface Chl *a* concentrations were obtained from the European Space Agency's
140 GlobColour project (<http://www.globcolour.info>). Weekly Chl *a* concentrations from 1998 to 2011,
141 on a 25 km grid, were averaged for the same geographic locations as the Selvogsbanki stations (an
142 area 25x25 km with the station in center) and for the CPR areas (Fig. 1).

143 For all regions (Selvogsbanki transect and CPR areas), the onset of the phytoplankton spring
144 bloom was estimated from the surface Chl *a* concentrations data of the GlobColour project. To
145 avoid errors in the estimation due to missing data around the date of interest, a Generalized
146 Additive Model (GAM) fit was first applied to the surface Chl *a* concentrations to estimate its
147 seasonality. The start of the spring bloom was defined as the first week of the year in which the Chl
148 *a* concentration increased by 5% above the annual median value (Siegel *et al.*, 2002; Henson *et al.*,
149 2009).

150

151 *Data analysis*

152 All the sampling gears used in the present study will inevitably under sample the euphausiids
153 (Brinton and Townsend, 1981; Sameoto *et al.*, 1993, 2000; Nicol, 2003; Wiebe *et al.*, 2004). In
154 order to assess the efficiency of the different gears of catching euphausiids, we calculated the
155 catching efficiency (CE) of the different plankton samplers. The calculations were done based on
156 the methodology of Clutter and Anraku (Clutter and Anraku, 1968), $CE = ((R - K/S_i)/R)^2$, in which
157 CE is the catching efficiency (the percentage of euphausiids that are in the path of the sampler that
158 are captured), R is the net radius (in m), K is the avoidance parameter (detection distance (m) *
159 mean swimming speed (m s⁻¹)) and S_i is the towing speed (m s⁻¹). The calculations were based on
160 the different towing speeds and entrance radii of the samplers. We are not aware of any previous
161 estimates of detection distance of euphausiids, but assume here that the euphausiids would be able
162 to detect the sampling gear within a distance of 0.25 m. Studies on swimming speeds of euphausiids
163 indicate that they range from 1 to 3 body lengths per second (BL s⁻¹) with a mean of ~1.7 BL s⁻¹
164 (Price, 1989; Klevjer and Kaartvedt, 2003, 2006, 2011; Gaten *et al.*, 2010). We used the mean value
165 in relative swimming speed (BL s⁻¹) to calculate swimming speeds in units of m s⁻¹ of euphausiids
166 ranging in size from 1 to 5 cm. The outcome was in turn used to calculate catching efficiency for
167 different size classes of euphausiids (1-5 cm). Using this approach, we found that the efficiency of
168 the WP2 net of catching euphausiids ranged from 0.96 for 1 cm long euphausiids to 0.82 for 5 cm
169 long euphausiids. Calculations for the Hensen net gave very similar values (0.97-0.85). The CPR
170 showed much lower catching efficiencies ranging from 0.87 (1 cm long euphausiids) to 0.43 (5 cm).
171 These simple calculations demonstrate that all the sampling gears of the present study (Hensen,
172 WP2, CPR) catch reasonably well (CE > 0.70) euphausiids up to 2 cm in size, thus including the
173 larval and juvenile stages of the three most common euphausiid species in the North Atlantic (*T.*

174 *longicaudata*, *T. inermis*, *M. norvegica*) as well as the adult stages of the smallest species (*T.*
175 *longicaudata*), which also is the one most common in terms of numbers in the North Atlantic
176 (Lindley, 1982). While we recognize that the calculations presented above can only be considered
177 crude estimates as both detection distance and swimming speed are estimated with great
178 uncertainty, we can still conclude that the catching efficiency of all gears decreases with the size of
179 the euphausiids. Probably, more than 70% of the larvae and juveniles are captured by all samplers.
180 It should, however, be noted that the calculations do not take into account the effects of bow wave
181 pressure on the avoidance behavior of the euphausiids which is likely to be more pronounced for the
182 CPR, being towed behind large container ships at relatively shallow depth, than for the vertically
183 towed Hensen and WP2 nets. Due to the low efficiency of samplers of catching adult euphausiids,
184 for the Icelandic spring survey we only used the data on eggs and larvae for the analysis of temporal
185 and spatial variability. As to the CPR data, the euphausiids are only recorded as total euphausiids
186 when processing the samples at SAHFOS (Batten *et al.*, 2003) and therefore the adults could not be
187 separated from the CPR data. Lindley and co-workers have used the CPR data in a number of
188 studies on abundance and distribution of euphausiids in the North Atlantic (e.g. Lindley, 1977,
189 1978, 1980, 1982a, 1982b; Lindley and Williams, 1980; Williams and Lindley, 1982), while
190 realizing that the CPR samplers do not catch equally all developmental stages (A. Lindley, UK,
191 personal communication). In spite of the limitations posed by the relatively low catching efficiency
192 of the devices used for sampling the euphausiids in the present study, we nevertheless feel confident
193 in using the data as indices of temporal and spatial variability (thus assuming that the catching
194 efficiency does not change with time or region). We realize, however, that they cannot be used in
195 order to compare absolute abundances.

196 Although the basic design of the CPR has remained relatively unchanged since the late
197 1940's, there has been a steady increase in the speed at which it is towed (Batten *et al.*, 2003). This
198 has led to significant decreases in sampled volume due to higher incidence of net clogging, which
199 is not accounted for by the standardized plankton analysis at SAHFOS. It is conceivable that the
200 significant decrease in sampling volume would result in decreases in calculated densities of
201 plankton. The issue is clearly relevant for the consistency and interpretation of the CPR data and it
202 has therefore received considerable attention in research. John *et al.*, (John *et al.*, 2002) quantified
203 the relationship between the volume of water filtered per sample and the extent of clogging using
204 flow metered tows and concluded that the effect of clogging on filtering rates was not great.
205 Similarly, Batten *et al.*, (Batten *et al.*, 2003) reported that although there was some evidence that
206 flow would be reduced with time, estimates of plankton abundance for large areas remained
207 unaffected. The most recent study on the long-term changes of volume filtered by the CPR and their
208 relevance to CPR data interpretation (Jonas *et al.*, 2004), similarly found no significant correlation

209 between the long-term changes in ship speed and two commonly used indicators of plankton
210 variability, phytoplankton colour and the total copepods indices. Based on these studies, we feel
211 confident that the effect of long-term changes in filtered volume on euphausiid abundance is small
212 compared to influences of other factors.

213 For both data sets (Icelandic spring survey and CPR), the distribution of the euphausiid
214 abundance data was strongly skewed to the right and with several zero observations, therefore a
215 logarithmic transformation ($\ln(x+1)$) was applied. To avoid estimation errors because of missing
216 values in the CPR data, an interpolation of the data was made using data interpolating empirical
217 orthogonal functions (Beckers and Rixen, 2003).

218 For both data sets (Icelandic spring survey and CPR), two-way analysis of variance
219 (ANOVA) was used to test statistically if the long-term variability was similar during day and
220 night. Day samples were defined as samples taken between sunrise and sunset and night samples
221 between sunset and sunrise. In a test like this, a significant interaction term (year vs. daytime (day
222 or night)) means that the long-term variability is different during day and night. The interaction
223 term (year vs. day and night) was, however, only significant for one area (B7, ANOVA, $p < 0.05$).
224 As it may be assumed that euphausiids stay shallower in the water column during night than during
225 day (e.g. Eriksen and Dalpadado, 2011), and also as euphausiids probably better avoid the sampling
226 gear during day time (Wiebe *et al.*, 2004), night samples were considered to better represent their
227 abundance. Therefore for area B7, the night data were used to infer the long-term changes. For the
228 remaining regions day and night samples were combined.

229 To visually compare euphausiid abundance values collected by the CPR survey and the
230 Icelandic spring survey, the data were standardized to a mean of zero and standard deviation of one.

231 Generalized Additive Models (GAMs) were used to analyse long-term changes of
232 euphausiid abundance as function of hydrographic and biological variables (Wood, 2006). The data
233 were characterized by a large number of zero observations that would make the use of standard
234 error distribution for GAM analysis (Gaussian) inappropriate. Therefore, an approach combining two
235 models – presence/absence and abundance larger than zero – was used (Stefánsson and Pálsson,
236 1997; Barry and Welsh, 2002). The first model uses the presence/absence of the euphausiids as the
237 response variable assuming a binomial distribution (logit link function). In the second model,
238 euphausiid numbers larger than zero are used as the response variable which is assumed to be
239 Gaussian distributed. In all models, thin plate regression splines were used with a maximum of
240 three effective degrees of freedom as smoothing function for each predictor. In the GAMs,
241 temperature, salinity, Chl *a* (surface values or average from 0–50 m), onset of the phytoplankton
242 spring bloom and NAO winter index were used as predictors.

243 Both single and multiple variable based GAMs were used to study the influence of the
244 predictors on euphausiid abundance. However, as the different explanatory variables did not have
245 the same temporal coverage, the GAMs were limited to the period 1998 to 2007 for the CPR data
246 and 1998 to 2011 for the Icelandic spring survey data, when records for all the environmental
247 predictors were available.

248 The first step in the GAM analysis was to use single variable based GAMs to identify the
249 relationships between individual predictors and the euphausiid abundance in the different regions.
250 The fitted models were evaluated based on 1) the percentage of deviance explained, 2) the Un-
251 Biased Risk Estimator (UBRE) or Generalized Cross Validation (GCV) scores, and 3) the smooth
252 confidence region (Planque *et al.*, 2007).

253 The second step was to use multiple variable based GAMs to estimate the combined effect
254 of more than one predictor on euphausiid abundance. High collinearity between predictors was
255 assessed by pairwise scatterplots, Pearson's correlation coefficients and variance inflation factors
256 with the cut-off value of 5 were used to remove collinear variables as recommended by Zuur *et al.*
257 (Zuur *et al.*, 2009). In the multiple variable based GAMs, the predictors were chosen by a
258 backward-elimination process for the least significant predictor based on χ^2 -statistic for the
259 presence/absence models and the F-statistic for the abundance larger than zero models (Stefánsson
260 and Pálsson, 1997). The multiple variable GAMs with the lowest UBRE or GCV scores were
261 selected as the best fitted models (Wood, 2006). The data analysis was conducted with the mgcv
262 package version 1.7–22 in the statistical software R (Wood, 2011).

263

264 **RESULTS**

265 *1. Sea surface temperature*

266 Interannual variations in sea surface temperatures for all regions from 1958 to 2011 are shown in
267 Fig. 2. All regions showed a general cooling trend during the 1960s. From the early 1970s until mid
268 1990s temperatures fluctuated while being generally low. Thereafter a general warming trend was
269 apparent in all regions with maxima in 2003 and 2008. After 2008 surface temperatures dropped
270 dramatically in all areas (Fig. 2).

271 From 1958 to 2011, the overall mean sea surface temperatures varied from ~ 7.0 to 8.5°C .
272 Area B7 was on average the coldest region (long-term average $\sim 5.7^\circ\text{C}$) and B5 the warmest (long-
273 term average $\sim 9.5^\circ\text{C}$).

274

275 *2. Chlorophyll a*

276 In the areas south of Iceland, the phytoplankton spring bloom began between late April and mid
277 May (i.e. in weeks ~16–20) from 1998 to 2009, whereas after 2009 it started between mid May and
278 early June (i.e. in weeks ~19–22) (Fig. 3A).

279 In most areas there was a more or less gradual increase in the yearly average Chl *a*
280 concentrations from the beginning of the time series (Fig. 3B). In areas B7 and B6, the Chl *a*
281 concentrations peaked around 2003 and 2004, respectively, while for the other areas concentrations
282 were more stable (Fig. 3B). After ~2007 a general increase in Chl *a* concentrations was apparent in
283 all areas.

284 In the CPR areas, the long-term average of Chl *a* concentrations for the whole series
285 (1998–2011) fluctuated between 1.62 mg Chl *a* m⁻³ in area B5 to 2.01 mg Chl *a* m⁻³ in area A6. On
286 average, in spring 2.12 mg Chl *a* m⁻³ were measured along the Selvogsbanki transect.

287 Due to cloud cover, no data on the surface Chl *a* concentrations could be obtained for area
288 B4 and, therefore, neither the onset of the phytoplankton spring bloom nor the long-term variability
289 of Chl *a* can be illustrated.

290

291 *3. Euphausiids*

292 *3.1. Seasonal changes*

293 The seasonal variations in abundance of euphausiids were generally characterized by low
294 abundance during winter and a high abundance during summer months (Fig. 4, right panels). In area
295 A6, numbers started to increase in May–June with the highest values being observed in June and
296 August. Numbers remained high until September when they started to decrease and had reached
297 low winter values by October. In areas B7 and B6 a significant increase had taken place already in
298 March. In these regions, the highest values were observed in June and July. The main decrease in
299 numbers occurred after August and by November abundance had returned to low winter values. In
300 area B5 the main increase took place from April–June. Numbers peaked in June and remained high
301 until August–September, when they started to decrease and had reached low winter values again in
302 November–December. In area B4, the main increase in numbers occurred in May and June.
303 Maximum was reached in June. Numbers remained relatively high until September, but by
304 November they had returned to low winter values (Fig. 4, right panel).

305 The description above is based on the long-term averages (Fig. 4, right panels). However,
306 there is considerable variability in the seasonal pattern among years (Fig 4, left panels). Thus, in
307 several years, there is clearly only one maximum in numbers during the summer (e.g. in the mid
308 1990s in area B7), whereas in other years two maxima are evident (e.g. in the early 1980s in area
309 B7).

310 The mean annual number of euphausiids was highest in CPR areas B7, B6, and B5 (~4–6
311 euphausiids m⁻³) and lowest in area B4 (~3 euphausiids m⁻³). A gradual decrease in mean annual
312 numbers is evident from west to east, i.e. from east of Greenland (B7) to the west of the Faroe
313 Islands (B4) (Figs. 1 and 4).

314

315 3.2. Long-term changes

316 The abundance of euphausiids during 50 years of sampling with the CPR is shown in Fig. 5.
317 The values shown are standardized annual averages. In all areas the numbers fluctuated
318 considerably, while generally showing a decreasing trend in all the CPR areas but B6 (simple linear
319 regressions: B7 $r^2=0.11$, $p<0.05$; A6 $r^2=0.25$, $p<0.001$; B5 $r^2=0.22$, $p<0.001$ and B4 $r^2=0.22$,
320 $p<0.001$). It is noteworthy that in all areas numbers were relatively low at the end of the series and
321 in three areas (B6, B5 and B4) the lowest values were in fact observed during the last year of the
322 series (2007).

323 On the Selvogsbanki transect, the long-term changes of larvae in late May were rather
324 similar to those of the eggs (see smoothed curved in Fig. 6A). Numbers of both eggs and larvae was
325 high at the start of the series (1990) and maxima of both eggs and larvae were observed around
326 1993 to 1994, 2000 and 2005. Around 2008 to 2009 the numbers of larvae peaked again, while the
327 number of eggs was at a low.

328 Linear regression analysis showed no long-term trend for the number of eggs between 1990
329 and 2011 ($p>0.05$) (Fig. 6A) while the number of larvae increased significantly during the same
330 period ($p<0.05$). Thus, at least for the euphausiid larvae, the Icelandic time series (Fig. 5) does not
331 reflect the same overall decreasing trend as the CPR series (Fig. 6), probably mainly because of its
332 much shorter time span.

333 On average, the number of eggs along the Selvogsbanki transect tended to increase from
334 inshore to offshore from 1990 to 2011 (ANOVA, $p<0.001$), with highest numbers observed on
335 station 4 and 5 (Tukey's HSD, $p<0.001$; Fig. 6B). In contrast, the abundance of larvae was similar
336 along the transect (ANOVA, $p>0.05$).

337

338 3.3 Single variable based GAMs

339 For all the CPR areas combined, both the presence/absence and abundance larger than zero models
340 showed similar results (Fig. 7, Table I).

341 For the presence/absence models, Chl *a* was the strongest associated predictor, explaining
342 overall 5.4% of the presence/absence recorded in recent years, followed by salinity (3.2%) and
343 temperature (1.5%) (Table I). The probability of euphausiids being present generally increased with
344 increasing Chl *a* concentrations, while the opposite was true for salinity (Figs. 7A, B). The

345 relationship between euphausiid occurrence and temperature was more complex, the probability of
346 presence showing a decreasing trend from ~ 4 to $\sim 8^{\circ}\text{C}$, and an increasing trend after that (Fig. 7C).
347 It should be noted that the confidence limits were wide at the highest Chl *a* concentrations and
348 lowest salinities due to limited data.

349 For the abundance larger than zero models Chl *a* was the strongest associated explanatory
350 variable (14.4%, Table I) with salinity (8.7%) and temperature (2.1%) being less important. As for
351 the presence-absence models, the abundance of euphausiids where it exceeded zero was generally
352 positively related to Chl *a* up to $\sim 1.5 \text{ mg Chl } a \text{ m}^{-3}$, and negatively related to salinity (Figs. 7D, E).
353 For temperature, the model indicated a decreasing trend from ~ 4 to $\sim 8^{\circ}\text{C}$, and an increasing trend
354 after that (Fig. 7F).

355 On the Selvogsbanki transect, the probability of finding euphausiid eggs in the samples was
356 mainly explained by salinity (12.6%, Table II), with lowest occurrence of eggs being recorded at
357 salinities ~ 34.6 (Fig. 8A). Confidence limits are, however, high at the lower salinity values due to
358 limited data. The abundance of eggs when it was non-zero along the Selvogsbanki transect showed
359 no significant relationship with any of the predictors (Table II).

360 The probability of euphausiid larvae being present along the Selvogsbanki transect exhibited
361 no significant relationship with any of the predictors (Table II). The abundance of larvae was best
362 explained by temperature (14.8%, Table II) following a dome-shaped functional form, peaking at
363 temperatures between ~ 8.5 and 9°C (Fig. 8B).

364

365 *3.4 Multiple variable based GAMs*

366 GAMs based on multiple explanatory variables from the CPR areas were established. For the
367 combined data set, the multiple variable based GAMs significantly improved the predictions of
368 euphausiids abundance (Table III), as compared to the single variable based GAMs (Table I). All
369 the environmental predictors considered, except the onset of the phytoplankton spring bloom,
370 significantly contributed to the overall models (Table III). The multiple variable based GAMs
371 explained respectively $\sim 17.5\%$ and 27.6% of the interannual variability in euphausiid
372 presence/absence and abundance where it was non-zero (Table III).

373 Multiple variable based GAMs were also set up for the CPR areas separately. For the
374 presence/absence models, temperature came out as a significant explanatory variable in majority of
375 the models (B7, A6, B5 and B4) (Table III). Depending on regions, presence of euphausiids was
376 also related to Chl *a* (B7) onset of phytoplankton spring bloom (B5) or NAO (B4).

377 For the abundance larger than zero models, the relative role of the different explanatory
378 variables also varied by CPR areas. East of Greenland (B7), the abundance of euphausiids was
379 related to Chl *a* concentration and the onset of the phytoplankton spring bloom, while south and

380 southwest of Iceland (B6, A6) also salinity and the NAO were relevant. Farther east, abundance was
381 either related to temperature and Chl *a* (B5) or temperature alone (B4).

382 For the more coastal areas south of Iceland (Selvogsbanki transect), the multiple variable
383 based GAMs established a relationship between the presence/absence of eggs and salinity and Chl *a*
384 (together explaining ~25% of interannual variability), while no relationship could predict
385 presence/absence of larvae (Table IV).

386 The multiple variable based GAMs explained ~36% of the abundance of larvae where they
387 exceeded zero, while no relationship could predict the abundance of eggs. The number of larvae
388 were mainly related to temperature, the onset of the phytoplankton spring bloom and NAO (Table
389 IV).

390

391 **DISCUSSION**

392 *Seasonal cycle*

393 In the open waters of the Northeastern Atlantic euphausiids reached maximum abundance from
394 May to August (Fig. 4). This confirms previous findings of Lindley (Lindley, 1978) for a wider area
395 of the North Atlantic and for the shelf areas south (Gislason and Astthorsson, 1995) and north of
396 Iceland (Astthorsson and Gislason, 1997a; Gislason and Astthorsson, 1998). Year-to-year changes
397 in seasonal abundance of euphausiids may be due to different life history traits of different
398 dominant species. Lindley (Lindley, 1978, 1982a) found that in the warm Atlantic waters, *T.*
399 *longicaudata* has two annual generations, while only one generation in the colder waters. In the
400 present material, species were not distinguished so it is impossible to evaluate if a particular species
401 has more than one annual generation, e.g. in warm years. Nonetheless, our results show two annual
402 peaks during the summer in some years (Fig. 4, left panels, B7 and A6).

403 In agreement with Letessier *et al.* (Letessier *et al.*, 2009), we found that euphausiids in
404 surface layers gradually decreased from the east of Greenland to the west of the Faroe Islands (Fig.
405 4). Presumably this pattern reflects the higher production of euphausiids in the western parts of the
406 North Atlantic as opposed to the eastern parts. As suggested by Saunders *et al.* (Saunders *et al.*,
407 2007), the complex water mass dynamics in the Irminger Sea and over the Reykjanes ridge
408 (Holliday *et al.*, 2006), characterised by relatively warm temperatures and high food availability,
409 may allow euphausiids to grow larger and to have a longer life span in these regions compared to
410 other regions. As larger females produce more eggs this would then contribute to a greater
411 productivity of euphausiids in these regions (Cuzin-Roudy, 2000).

412 Physical parameters, such as local topography and water mass dynamics, which in the area
413 of study are complex and in some regions influenced by freshwater runoff from rivers/glaciers, may
414 influence the euphausiid abundance and seasonal occurrence in different ways (Dalpadado *et al.*,

415 2008a, Buchholz *et al.*, 2010, McGinty *et al.*, 2011). In agreement with the study of Lindley
416 (Lindley, 1980), we found low number of euphausiids in the surface layer in the winter months
417 (Fig. 4). The relatively low abundance in the winter months may be related to high mortality during
418 a season when food is scarce and also the fact that euphausiids tend to stay relatively deep in the
419 water column during the winter season (Lindley, 1980; Mackas *et al.*, 2012).

420

421 *Long-term changes*

422 Our findings show that in most of the open seas of the Northeastern Atlantic, euphausiid abundance
423 decreased from 1958 to 2007 (Fig. 5). Similarly, Beaugrand and Reid (Beaugrand and Reid, 2003)
424 and Beaugrand *et al.* (Beaugrand *et al.*, 2003) reported euphausiids to have declined during recent
425 decades in the North Sea and adjacent seas. Our study demonstrates that this declining trend is
426 widespread in the whole Northeastern Atlantic and still ongoing. Although the decrease in area B6
427 was not significant (Fig. 5), the lowest numbers were nevertheless observed during the last years of
428 the time series, thus indicating a decline there also.

429 While the CPR data showed that total numbers of euphausiids generally declined from 1958
430 to 2007 (Fig. 5), the number of larvae along the Selvogsbanki transect showed an increasing trend
431 from 1990 to 2011 (Fig. 6A). The apparent discrepancy between the two time series is most likely
432 related to the much shorter time span of the Selvogsbanki series. However, such an opposite trend
433 may also be related to differences in sampling techniques (WP2 nets vs. CPR) which makes a
434 comparison difficult (Beare *et al.*, 2000), as well as to differences in the frequency and spatial
435 extension of the sampling. Thus, the Icelandic time series refers to the spring period (May–June)
436 only, whereas the CPR data cover the whole year. Additionally, the Selvogsbanki data were mostly
437 collected on the south Icelandic shelf, while the CPR data were mainly collected off shelf (Fig. 1).
438 The different long-term trends exhibited by the CPR data and the Icelandic spring survey data could
439 thus reflect onshore-offshore differences in interannual variability and/or in species composition.
440 Indeed *T. inermis* tends to be most abundant on the Icelandic shelves, *M. norvegica* mainly over the
441 shelve edges, while *T. longicaudata* is mainly found in the oceanic areas (Einarsson, 1945;
442 Mauchline and Fisher, 1969). Finally, euphausiid patchiness and the fact that they spawn in
443 multiple batches (Cuzin-Roudy, 2000) may influence more the data from the relatively small and
444 infrequently sampled Selvogsbanki area compared to the larger and more frequently sampled CPR
445 areas.

446 The spatial distribution of euphausiid eggs along the Selvogsbanki transect showed a
447 distinctive pattern of increasing abundance from onshore to offshore, while the larvae were more or
448 less evenly distributed along the transect (Fig. 6B). This is probably reflecting that the distribution
449 of the larvae was being affected by horizontal advection and mixing processes for a longer period of

450 time than the eggs that stay much shorter time as plankton. Topographical dissimilarities and
451 different water masses characterised the stations along the transect, stations 1 to 3 being influenced
452 by freshwater run-off from land, as opposed to stations 4 and 5, that are more oceanic and mainly
453 under the influence of Atlantic waters (Stefánsson and Ólafsson, 1991; Gislason and Astthorsson,
454 2004). Such cross-shelf environmental differences could partly explain the variability illustrated in
455 Fig. 6. The increasing number of eggs from onshore to offshore probably reflects the distribution of
456 spawning adults with spawning mainly taking place near the shelf edge

457

458 *Drivers of euphausiid abundance*

459 The single variable based GAMs were designed to study the effects of individual explanatory
460 variables on euphausiid abundance. For the combined CPR data set, these analyses showed that
461 phytoplankton biomass was the single most important factor affecting the long-term changes of the
462 euphausiids (Table I). The importance of phytoplankton for the growth and development of
463 euphausiids has been demonstrated in several other studies (see Atkinson *et al.*, 2008 for a review).
464 In our study, the highest abundance of euphausiids was associated with Chl *a* concentrations >1.5
465 mg m⁻³ (Fig. 7D). Letessier *et al.* (Letessier *et al.*, 2009) on the other hand, found temperature to be
466 the single most important factor influencing euphausiid numerical abundance, with Chl *a* playing
467 only a minor role. The reason for this is probably related to the fact that the study of Letessier *et al.*
468 (Letessier *et al.*, 2009) spans the whole Atlantic Ocean from polar to tropical latitudes, so the
469 temperature range is much larger than in the present study. As noted by Zarauz *et al.* (Zarauz *et al.*,
470 2007), GAMs are only statistical models and unable to identify causal relationships. The effects of
471 temperature in our study may thus be masked by the effects of temperature on phytoplankton spring
472 bloom development.

473 The multiple variable based GAMs showed that euphausiid abundance is affected by
474 different factors in different areas, as also observed by McGinty *et al.* (McGinty *et al.*, 2011) for
475 calanoid copepods. In the west Chl *a* is the major predictor of euphausiid abundance, whereas in the
476 east temperature appears most important (Table III). The difference could possibly be related to
477 differences in species composition between west and east, with different species having different
478 requirements/responses to changes in climate and food environment. The limited information that is
479 available on the distribution of euphausiids in the North Atlantic indicates *T. longicaudata* as the
480 numerically dominant species in all regions, while *M. norvegica* appears more abundant in the
481 eastern areas (Einarsson, 1945; Lindley, 1982). Thus, it is possible that the different responses of
482 the euphausiids to the environmental factors partly reflect a longitudinal gradient in euphausiid
483 species composition.

484 Earlier studies have shown that zooplankton composition on the Selvogsbanki transect is
485 mainly governed by salinity and phytoplankton biomass (Gislason *et al.*, 2009). In this study, the
486 probability of occurrence of euphausiid eggs at Selvogsbanki was positively related to salinity >35
487 (Table II, Fig. 8A), indicating that euphausiids prefer spawning in areas of relatively high salinities.
488 In fact, Einarsson (Einarsson, 1945) reported the main spawning of *M. norvegica* and *T.*
489 *longicaudata* to occur in areas with pure Atlantic water.

490 The present study also demonstrates that for the recent warm period (1998–2011), changes
491 in temperature, NAO and in the timing of the phytoplankton bloom influenced the numbers of
492 larvae on Selvogsbanki (Table IV). Lower wind stress during negative NAO may result in a
493 stronger stratification, triggering the phytoplankton bloom (Henson *et al.*, 2009) and in turn an
494 increase in euphausiid numbers. According to Henson *et al.* (Henson *et al.*, 2009), the timing of the
495 phytoplankton spring bloom is linked to the NAO, with a relatively early bloom when the NAO is
496 negative.

497 According to Hátún *et al.* (Hátún *et al.*, 2009), a weak North Atlantic subpolar gyre may
498 lead to an increase of saline and warm water south of Iceland, which in turn may positively affect
499 the annual mean phytoplankton biomass and negatively the abundance of *Calanus finmarchicus* in
500 the Irminger Sea. We observed high Chl *a* concentrations (Fig. 3B), a delay in the phytoplankton
501 spring bloom (Fig. 3A), and low euphausiid numbers (Fig. 5) in years when the subpolar gyre was
502 weak (2000–2010) (Hátún *et al.* 2009; Larsen *et al.*, 2012). As copepods are part of the diet of
503 euphausiids (Falk-Petersen *et al.*, 2000; Dalpadado *et al.*, 2008b), the decline in the stocks of *C.*
504 *finmarchicus* may have also contributed to the decline in euphausiid populations.

505 As stated above, *T. longicaudata* is the most abundant euphausiid species in the North
506 Atlantic. Einarsson (Einarsson, 1945) proposed that the upper temperature limit at which the density
507 of *T. longicaudata* is limited is 15°C, and reproduction would be optimal at temperature <12°C.
508 Given the significant positive effect of temperature on euphausiid densities (Fig. 7F), the observed
509 decrease in densities in the CPR areas in the 2000's (Fig. 5) while surface temperatures increased
510 (Fig. 2) is somewhat surprising. As Chl *a* appears to affect more the long-term variability of the
511 euphausiids than temperature (Table I), it may be argued that the effects of temperature were
512 overridden by the effect of Chl *a*. However, the fact that Chl *a* was generally increasing in the CPR
513 areas in the 2000's (Fig. 3B) while the abundance of euphausiids was decreasing (Fig. 5) seems to
514 contradict this. In addition to temperature and Chl *a*, the onset of the spring bloom was also
515 affecting the long term changes of the euphausiids (Tables I, III). In all the CPR areas there was a
516 gradual delay in the onset of the spring bloom from around 2006 (Fig. 3A). In the beginning of the
517 time series, blooming began between late April and mid May, whereas in the end between mid May
518 and early June. The delay may have translated into a weaker synchrony between the timing of first

519 feeding euphausiid larvae in surface layers and the timing of the spring bloom. We believe that the
520 warming of the surface waters during recent years may thus have been a factor resulting in a weaker
521 temporal synchrony of the developing young euphausiids with the phytoplankton bloom that in turn
522 may have lead to the reduced population sizes of the euphausiids, thus suggesting that large scale
523 climatic factors may have altered conditions during the most important period in the life cycle of the
524 euphausiids.

525 We acknowledge that top-down effects also play a role in regulating euphausiid abundance.
526 For example, the annual consumption of euphausiids by fin whales, estimated to be around 2.5
527 million tonnes (Sigurjónsson and Víkingsson, 1997) may be sufficient to affect the stock sizes of
528 euphausiids in the region. Predation pressure from fin whales may have increased due to the 10%
529 increase in fin whale numbers from 1987 to 2001 in the area between Iceland and Greenland
530 (Vikingsson *et al.*, 2009). A recent study conducted in Icelandic waters on the diet composition of
531 minke whales has shown lower incidence of euphausiids in their diet in the mid 2000s than in the
532 early 1980s (Vikingsson *et al.*, 2014). This may in turn reflect the declining number of euphausiids
533 in the area.

534 Changes in the abundance and distribution pattern of several marine species around Iceland
535 have been related to climatic changes (Astthorsson *et al.*, 2007), for instance the northward
536 migration of many southern rare and vagrant species (Valdimarsson *et al.*, 2012) and the
537 unprecedented feeding migrations of mackerel to the sea areas around Iceland during summer in
538 recent years (Astthorsson *et al.*, 2012). Our findings, of a more or less general decline of
539 euphausiids in the open sea areas southwest, south and east of Iceland are in general agreement with
540 other studies on the long-term changes of zooplankton, such as *Calanus finmarchicus*, in the open
541 waters of the North Atlantic (e.g. Planque and Taylor, 1998; Hátún *et al.*, 2009), and support the
542 hypothesis that bottom-up regulation, driven by climate change forcing, is a major factor affecting
543 interannual changes in abundance of euphausiids. Further studies, emphasizing the trophic
544 interactions of these important groups in Icelandic and adjacent seas, and the underlying
545 mechanisms for the observed relationships, are needed in order to understand how climate change
546 will likely impact the marine ecosystem.

547

548

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837 **LEGENDS TO TABLES**

838 Table I. Results of single variable based presence/absence and abundance larger than zero General
839 Additive Models (GAMs) for euphausiids in CPR areas B7, B6, A6, B5 and B4 in the Northeastern
840 Atlantic based on data from 1998 to 2007 (Fig. 1). Predictors used in the study were sea surface
841 temperature, salinity, surface Chl *a* concentration, onset of the phytoplankton spring bloom (OPB)
842 and North Atlantic Oscillation winter index (NAO). For each predictor, percentage of deviance
843 explained (% Deviance), Un-Biased Risk Estimator (UBRE) or Generalised Cross Validation
844 (GCV) scores, Chi-square (χ^2) or F-test significance (F) are given. Unless otherwise stated 3
845 effective degrees of freedom (edf) were used.

846
847 Table II. Results of single variable based presence/absence and abundance larger than zero General
848 Additive Models (GAMs) for euphausiid eggs and larvae at Selvogsbanki transect based on data
849 from 1998 to 2011 (Fig. 1). Predictors used in the study were temperature, salinity, Chl *a*
850 concentration averaged from 0–50 m, onset of the phytoplankton spring bloom (OPB) and North
851 Atlantic Oscillation winter index (NAO). For each predictor, percentage of deviance explained (%
852 Deviance), Un-Biased Risk Estimator (UBRE) or Generalised Cross Validation (GCV) scores, Chi-
853 square (χ^2) or F-test significance (F) is given. Unless otherwise stated 3 effective degrees of
854 freedom (edf) were used.

855
856 Table III. Results of multiple variable based presence/absence and abundance larger than zero
857 General Additive Models (GAMs) for euphausiids in CPR areas B7, B6, A6, B5 and B4 in the
858 Northeastern Atlantic based on data from 1998 to 2007 (Fig. 1). Predictors used in the study were
859 surface temperature, salinity, surface Chl *a* concentration, onset of the phytoplankton spring bloom
860 (OPB) and North Atlantic Oscillation winter index (NAO). Percentage of deviance explained (%
861 Deviance), Un-Biased Risk Estimator (UBRE) or Generalised Cross Validation (GCV) scores are
862 shown for the best fitted GAMs. Significance is given for each predictor used in the models. Unless
863 otherwise stated 3 effective degrees of freedom (edf) were used. Presence/absence GAMs could not
864 be constructed for area B6.

865
866 Table IV. Results of multiple variable based presence/absence and abundance larger than zero
867 General Additive Models (GAMs) for euphausiid eggs and larvae at Selvogsbanki transect based on
868 data from 1998 to 2011 (Fig. 1). Predictors used in this study were temperature, salinity, Chl *a*
869 concentration averaged from 0-50 m, onset of the phytoplankton spring bloom (OPB) and North
870 Atlantic Oscillation winter index (NAO). Percentage of deviance explained (% Deviance), Un-
871 Biased Risk Estimator (UBRE) or Generalised Cross Validation (GCV) scores are shown for the
872 best fitted GAMs. Significance is given for each predictor used in the models. Unless otherwise

873 stated 3 effective degrees of freedom (edf) were used. Presence/absence GAMs could not be
874 constructed for larvae and abundance larger than zero models could not be constructed for eggs.

875

876 **LEGENDS TO FIGURES**

877 Fig. 1. Map showing the sampling areas in the study with CPR areas indicated. Stations at
878 Selvogsbanki transect are shown by black dots (inside area A6). Gray contours show 200 and
879 1000m bottom depth. The inset map is an enlargement of the Selvogsbanki region with the stations
880 indicated by numbered black dots.

881

882 Fig. 2. Interannual variations in the Sea Surface Temperature (SST, °C) from 1958 to 2011 at the
883 Selvogsbanki transect and in the CPR areas southwest, south and southeast of Iceland. SST values
884 are standardized to zero mean and standard deviation one. Lines show plain loess smoothing with a
885 span of five years. For location of regions see Fig. 1.

886

887 Fig. 3. Interannual variations in the onset of the phytoplankton spring bloom (weeks) (A) and
888 surface Chl *a* concentrations (mg m^{-3}) (B) from 1998 to 2011 at Selvogsbanki transect and in the
889 CPR areas southwest, south and southeast of Iceland. Chl *a* concentrations were standardized to
890 zero mean and standard deviation one. Lines show plain loess smoothing with a span of five years.
891 For location of areas/transect refer to Fig. 1.

892

893 Fig. 4. Seasonal abundance of total euphausiid from 1958 to 2007 in the CPR areas (Fig. 1). Right
894 panel summarizes the information presented in the left panel by boxplots, showing the median,
895 upper and lower quartiles and outliers (open circles). Average values are shown for both day and
896 night time samplings, except for area B7, where night values were used.

897

898 Fig. 5. Interannual variation in abundance of total euphausiid in CPR areas B7, B6, A6, B5 and B4
899 from 1958 to 2007. Abundances are annual averages standardized to zero mean and unit variance.
900 Curved line is a loess smoothed curve with a span of five years. Regression lines significant at
901 $p < 0.05$ level are shown by straight red lines.

902

903 Fig. 6. (A) Interannual variation in the number of euphausiid eggs (light gray) and larvae (black) at
904 Selvogsbanki transect (Fig. 1). Abundances are based on one annual sampling at five stations in late
905 May standardized to zero mean and unit variance. Curved line is a loess smoothed curve with a span
906 of five years. Regression line significant at $p < 0.05$ level is shown by straight red line for larvae
907 estimates. (B) Variation in abundance of eggs and larvae, $\ln(x+1)$, along the Selvogsbanki transect,
908 illustrated by boxplots, showing the median, upper and lower quartiles and outliers (open circles).

909

910 Fig. 7. Results of single variable based presence/absence and abundance larger than zero General
911 Additive Models (GAMs) for euphausiids in all the CPR areas combined based on data from 1998
912 to 2007 (Fig. 1). The figure illustrates the predictors that best explained presence/absence of the
913 euphausiids (A–C) or euphausiid abundance where it exceeded zero. (D–F) (Table I). The solid
914 lines show the smoothing function according to the GAMs. The shaded gray areas represent the
915 regions within two standard errors of the mean (i.e. accounting for 95% of the observations), and
916 open circles show residuals of the curve fit. Short vertical lines on the X-axis indicate the values at
917 which observations were made.

918

919 Fig. 8. Results of single variable based presence/absence and abundance larger than zero General
920 Additive Models (GAMs) for euphausiid eggs (upper) and larvae (lower) at the Selvogsbanki
921 transect south of Iceland based on data from 1998 to 2011 (Fig. 1). The figure illustrates the
922 predictors that best explained presence/absence of euphausiid eggs (A) or abundance of larvae
923 where it was larger than zero (B) (Table II). The solid lines show the smoothing function according
924 to the GAMs. Shaded gray areas represent the regions within two standard errors of the mean (i.e.
925 accounting for 95% of the observations), and open circles show residuals of the curve fit. Short
926 vertical lines on the X-axis show the values at which observations were made. Note that the panels
927 do not illustrate the same predictor.

Table V. Results of single variable based presence/absence and abundance larger than zero General Additive Models (GAMs) for euphausiids in CPR areas B7, B6, A6, B5 and B4 in the Northeastern Atlantic based on data from 1998 to 2007 (Fig. 1). Predictors used in the study were sea surface temperature, salinity, surface Chl *a* concentration, onset of the phytoplankton spring bloom (OPB) and North Atlantic Oscillation winter index (NAO). For each predictor, percentage of deviance explained (% Deviance), Un-Biased Risk Estimator (UBRE) or Generalised Cross Validation (GCV) scores, Chi-square (χ^2) or F-test significance (F) are given. Unless otherwise stated 3 effective degrees of freedom (edf) were used.

All CPR Areas		Temperature	Salinity	Chl <i>a</i>	OPB	NAO
Presence/ Absence	% Deviance	1.5	3.2	5.4	0.2	0.3
	UBRE	-0.02	-0.04	-0.26	-0.14	-0.01
	p (χ^2)	0.05	<0.001	<0.01	0.82	0.61
Abundance >0	% Deviance	2.1	8.7	14.4	3.4	3.3
	GCV	2.92	2.74	2.54	3.12	2.90
	p (F)	**<0.01	<0.001	<0.001	<0.01	<0.01

*1edf, **2edf

Table VI. Results of single variable based presence/absence and abundance larger than zero General Additive Models (GAMs) for euphausiid eggs and larvae at Selvogsbanki transect based on data from 1998 to 2011 (Fig. 1). Predictors used in the study were temperature, salinity, Chl *a* concentration averaged from 0–50 m, onset of the phytoplankton spring bloom (OPB) and North Atlantic Oscillation winter index (NAO). For each predictor, percentage of deviance explained (% Deviance), Un-Biased Risk Estimator (UBRE) or Generalised Cross Validation (GCV) scores, Chi-square (χ^2) or F-test significance (F) is given. Unless otherwise stated 3 effective degrees of freedom (edf) were used.

		Selvogsbanki	Temperature	Salinity	Chl <i>a</i>	OPB	NAO
Presence/ Absence	Eggs	% Deviance	2.3	12.6	7.0	6.5	0.5
		UBRE	0.51	0.37	0.45	0.45	0.54
		$p(\chi^2)$	0.62	0.05	0.14	0.35	0.92
	Larvae	% Deviance	1.7	33.8	6.4	35.7	58.2
		UBRE	-0.48	-0.54	-0.50	-0.60	-0.71
		$p(\chi^2)$	0.49	0.50	*0.30	*0.33	0.42
Abundance >0	Eggs	% Deviance	2.3	11.0	8.6	9.3	11.6
		GCV	2.70	2.46	2.53	2.51	2.44
		$p(F)$	0.88	0.34	0.47	0.43	0.32
	Larvae	% Deviance	14.8	8.2	1.0	5.3	10.1
		GCV	1.54	1.66	1.79	1.71	1.62
		$p(F)$	0.02	0.16	0.89	0.34	0.09

*1edf, **2edf

Table VII. Results of multiple variable based presence/absence and abundance larger than zero General Additive Models (GAMs) for euphausiids in CPR areas B7, B6, A6, B5 and B4 in the Northeastern Atlantic based on data from 1998 to 2007 (Fig. 1). Predictors used in the study were surface temperature, salinity, surface Chl *a* concentration, onset of the phytoplankton spring bloom (OPB) and North Atlantic Oscillation winter index (NAO). Percentage of deviance explained (% Deviance), Un-Biased Risk Estimator (UBRE) or Generalised Cross Validation (GCV) scores are shown for the best fitted GAMs. Significance is given for each predictor used in the models. Unless otherwise stated 3 effective degrees of freedom (edf) were used. Presence/absence GAMs could not be constructed for area B6.

	CPR Areas	Temperature	Salinity	Chl <i>a</i>	OPB	NAO	% Deviance	UBRE/ GCV
Presence/ absence	All areas	0.02	0.008	0.14	-	0.008	17.5	-0.45
	B7	*0.05	-	*0.65	-	-	17.0	-0.56
	B6	-	-	-	-	-	-	-
	A6	<0.001	-	-	-	-	4.0	-0.17
	B5	0.004	-	-	0.037	-	15.4	-0.20
	B4	<0.001	-	-	-	<0.001	8.0	-0.05
Abundance >0	All areas	0.0025	<0.001	<0.001	-	<0.001	27.6	2.33
	B7	-	-	<0.001	0.209	-	41.4	1.27
	B6	-	<0.001	0.002	0.021	0.007	57.0	2.58
	A6	-	0.011	0.033	<0.001	0.002	65.8	1.51
	B5	0.015	-	<0.001	-	-	48.2	1.49
	B4	<0.001	-	-	-	-	27.2	1.36

*1edf; **2edf

Table VIII. Results of multiple variable based presence/absence and abundance larger than zero General Additive Models (GAMs) for euphausiid eggs and larvae at Selvogsbanki transect based on data from 1998 to 2011 (Fig. 1). Predictors used in this study were temperature, salinity, Chl *a* concentration averaged from 0-50 m, onset of the phytoplankton spring bloom (OPB) and North Atlantic Oscillation winter index (NAO). Percentage of deviance explained (% Deviance), Un-Biased Risk Estimator (UBRE) or Generalised Cross Validation (GCV) scores are shown for the best fitted GAMs. Significance is given for each predictor used in the models. Unless otherwise stated 3 effective degrees of freedom (edf) were used. Presence/absence GAMs could not be constructed for larvae and abundance larger than zero models could not be constructed for eggs.

Selvogsbanki		Temperature	Salinity	Chl <i>a</i>	OPB	NAO	% Deviance	UBRE/ GCV
Presence/ absence	Eggs	-	0.02	0.04	-	-	24.9	0.3
	Larvae	-	-	-	-	-	-	-
Abundance >0	Eggs	-	-	-	-	-	-	-
	Larvae	**0.006	-	-	0.03	0.006	35.6	1.5

*1edf; **2edf

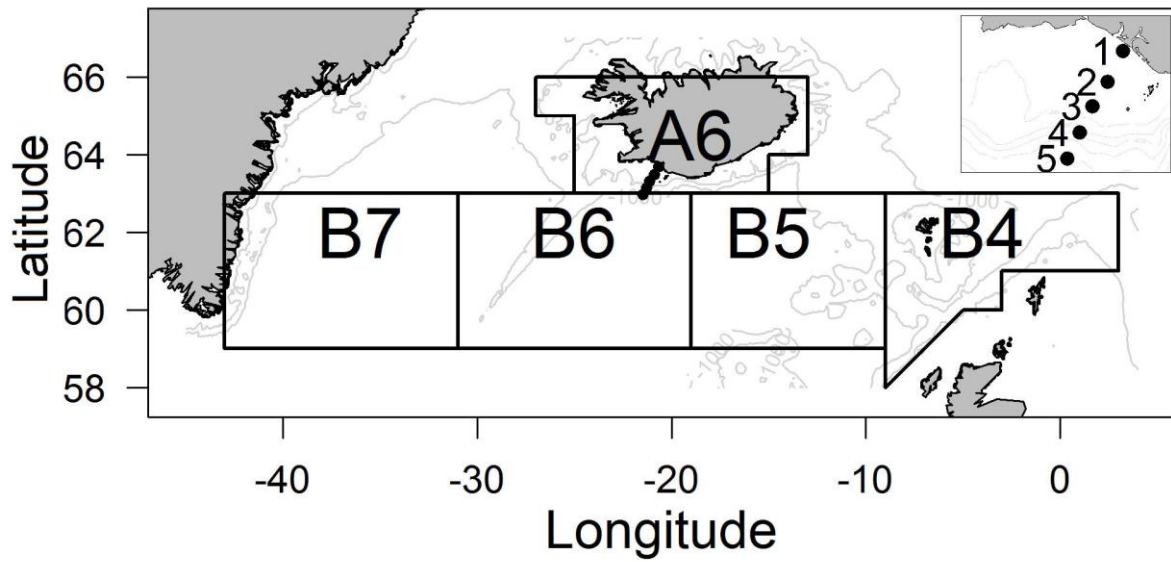


Fig. 8. Map showing the sampling areas in the study with CPR areas indicated. Stations at Selvogsbanki transect are shown by black dots (inside area A6). Gray contours show 200 and 1000m bottom depth. The inset map is an enlargement of the Selvogsbanki region with the stations indicated by numbered black dots.

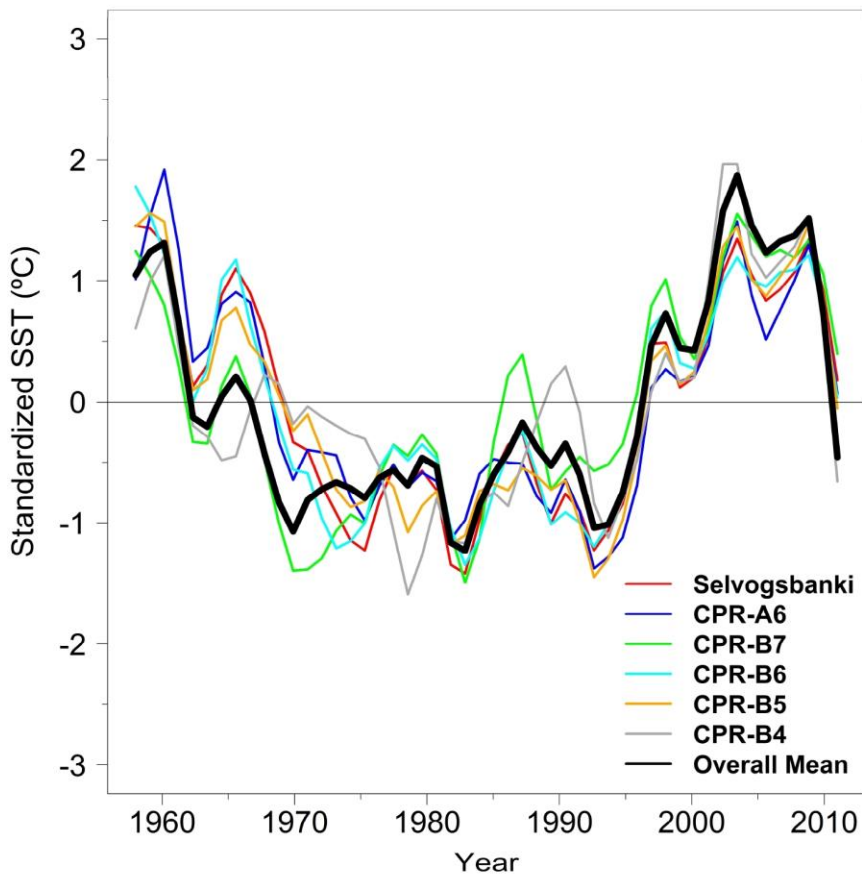


Fig. 9. Interannual variations in the Sea Surface Temperature (SST, °C) from 1958 to 2011 at the Selvogsbanki transect and in the CPR areas southwest, south and southeast of Iceland. SST values are standardized to zero mean and standard deviation one. Lines show plain loess smoothing with a span of five years. For location of regions see Fig. 1.

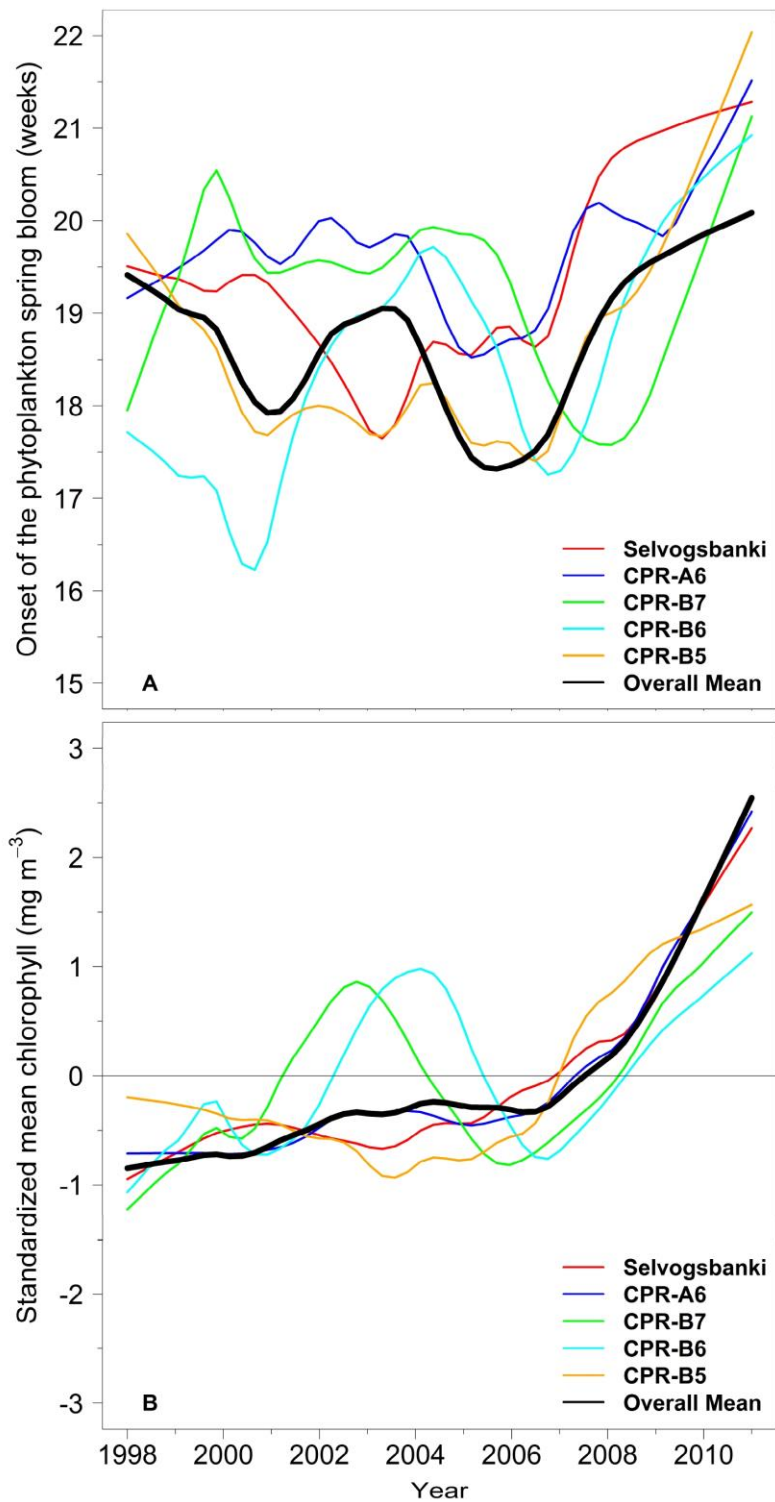


Fig. 10. Interannual variations in the onset of the phytoplankton spring bloom (weeks) (A) and surface Chl *a* concentrations (mg m⁻³) (B) from 1998 to 2011 at Selvogsbanki transect and in the CPR areas southwest, south and southeast of Iceland. Chl *a* concentrations were standardized to zero mean and standard deviation one. Lines show plain loess smoothing with a span of five years. For location of areas/transect refer to Fig. 1.

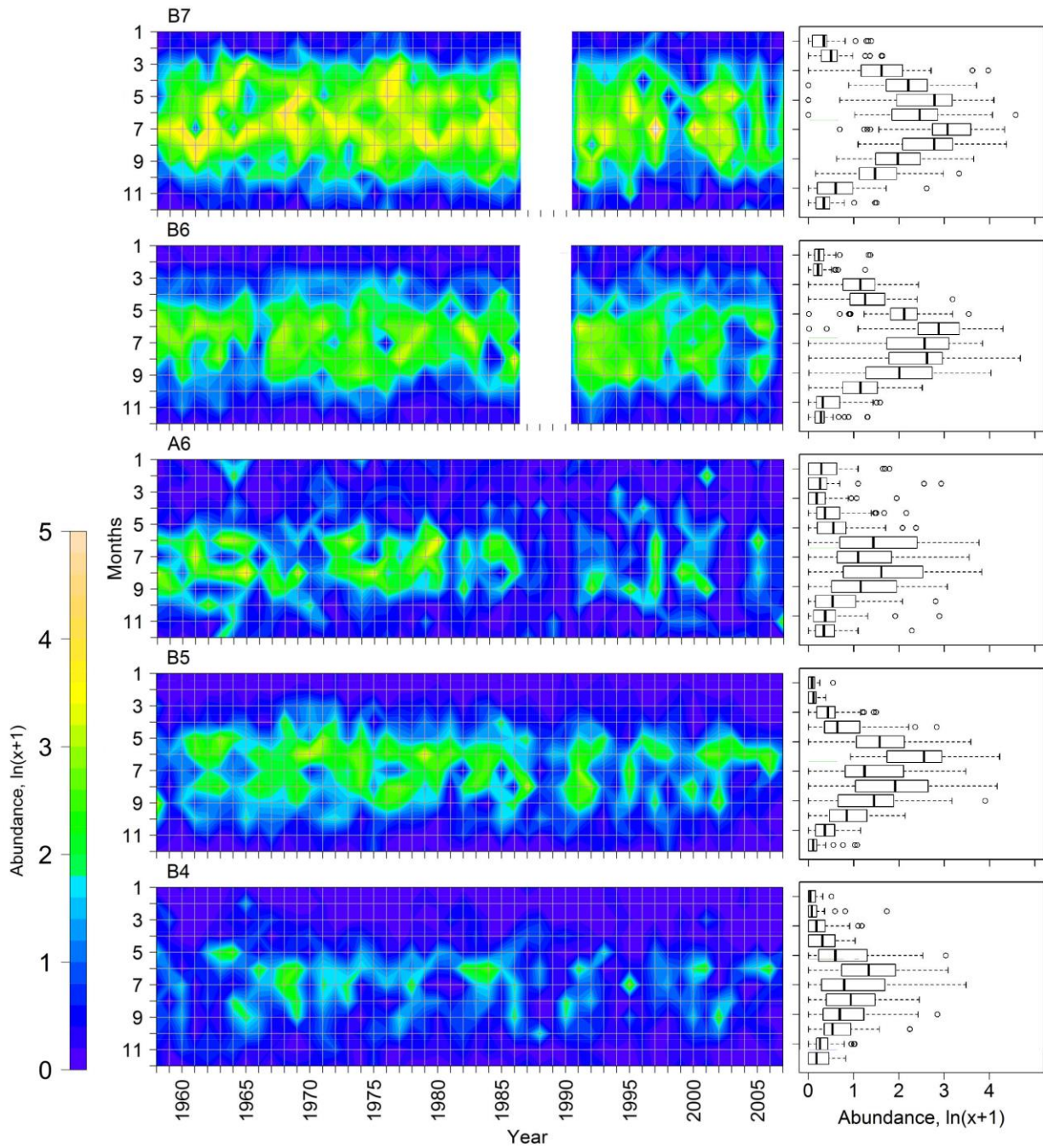


Fig. 11. Seasonal abundance of total euphausiid from 1958 to 2007 in the CPR areas (Fig. 1). Right panel summarizes the information presented in the left panel by boxplots, showing the median, upper and lower quartiles and outliers (open circles). Average values are shown for both day and night time samplings, except for area B7, where night values were used.

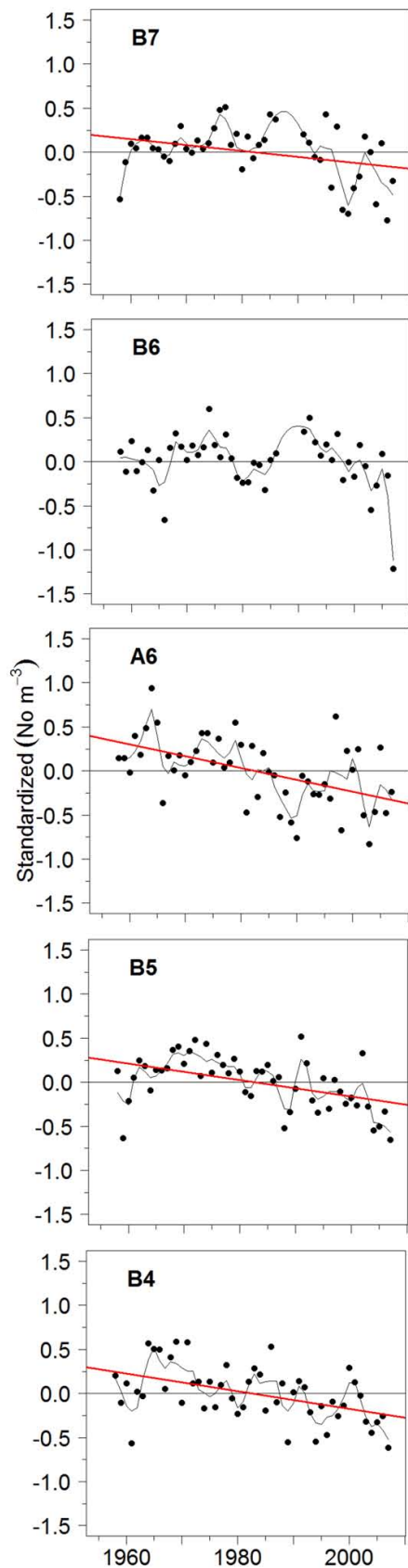


Fig. 12. Interannual variation in abundance of total euphausiid in CPR areas B7, B6, A6, B5 and B4 from 1958 to 2007. Abundances are annual averages standardized to zero mean and unit variance. Curved line is a loess smoothed curve with a span of five years. Regression lines significant at $p < 0.05$ level are shown by straight red lines.

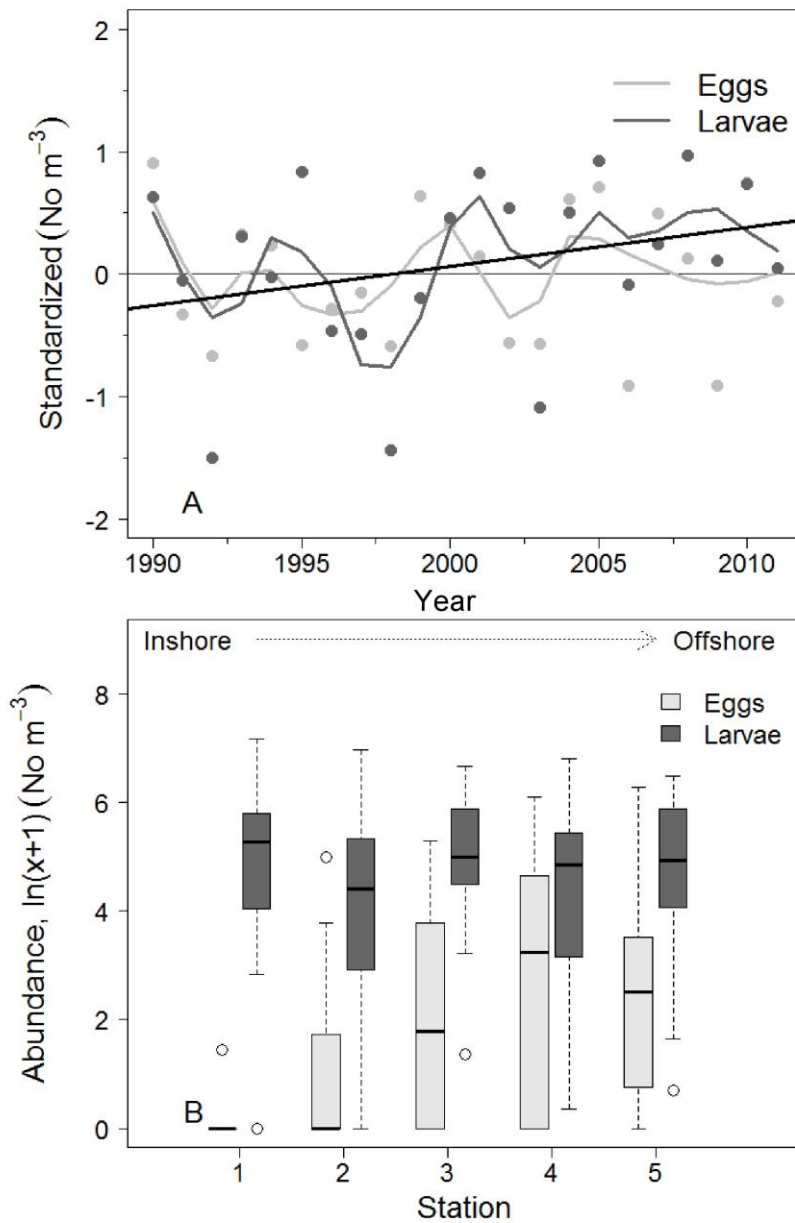


Fig. 13. (A) Interannual variation in the number of euphausiid eggs (light gray) and larvae (black) at Selvogsbanki transect (Fig. 1). Abundances are based on one annual sampling at five stations in late May standardized to zero mean and unit variance. Curved line is a loess smoothed curve with a span of five years. Regression line significant at $p < 0.05$ level is shown by straight red line for larvae estimates. (B) Variation in abundance of eggs and larvae, $\ln(x+1)$, along the Selvogsbanki transect, illustrated by boxplots, showing the median, upper and lower quartiles and outliers (open circles).

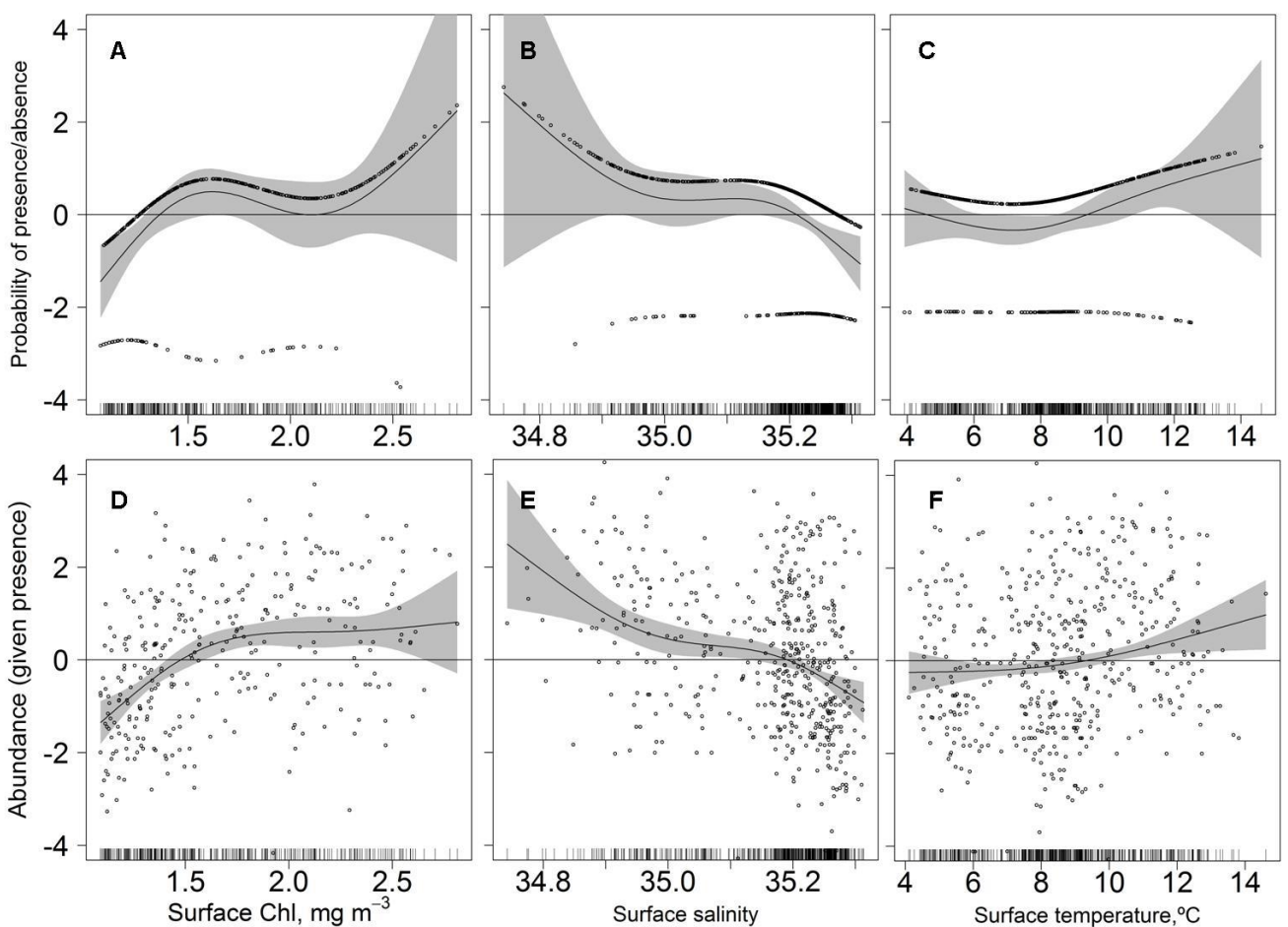


Fig. 14. Results of single variable based presence/absence and abundance larger than zero General Additive Models (GAMs) for euphausiids in all the CPR areas combined based on data from 1998 to 2007 (Fig. 1). The figure illustrates the predictors that best explained presence/absence of the euphausiids (A–C) or euphausiid abundance where it exceeded zero. (D–F) (Table I). The solid lines show the smoothing function according to the GAMs. The shaded gray areas represent the regions within two standard errors of the mean (i.e. accounting for 95% of the observations), and open circles show residuals of the curve fit. Short vertical lines on the X-axis indicate the values at which observations were made.

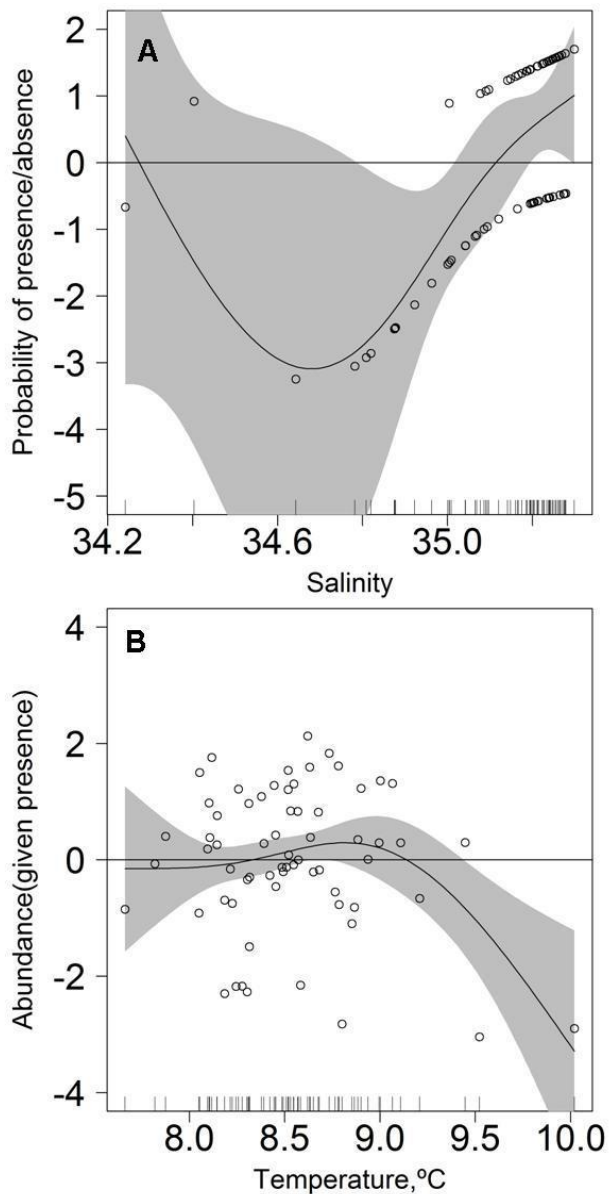


Fig. 8. Results of single variable based presence/absence and abundance larger than zero General Additive Models (GAMs) for euphausiid eggs (upper) and larvae (lower) at the Selvogsbanki transect south of Iceland based on data from 1998 to 2011 (Fig. 1). The figure illustrates the predictors that best explained presence/absence of euphausiid eggs (A) or abundance of larvae where it was larger than zero (B) (Table II). The solid lines show the smoothing function according to the GAMs. Shaded gray areas represent the regions within two standard errors of the mean (i.e. accounting for 95% of the observations), and open circles show residuals of the curve fit. Short vertical lines on the X-axis show the values at which observations were made. Note that the panels do not illustrate the same predictor.