

# 1 **Recruitment of shrimp (*Pandalus borealis*) in the Barents Sea related to spawning stock** 2 **and environment**

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4

## 5 **Abstract**

6

7 The shrimp spawn in autumn, and the females carry their eggs as out roe until spring when the  
8 larvae hatch. Within a period of 2 months the shrimp larvae settle to the bottom. It has been  
9 claimed that the year class strength probably is determined during the larval phase. Today's  
10 assessment and forecast of the shrimp stock productivity and potential fishing yields is weak.  
11 This is partly due to poor knowledge on population dynamics from hatching until the shrimp  
12 are caught in the fishery at the age of 3 or 4 years. We therefore here identify the most  
13 important abiotic and biotic factors that effect recruitment in addition to spawning stock  
14 biomass. Since 1995 a net attached to the underbelly of the survey trawl used at the annual  
15 cruise in the Barents Sea has caught juvenile shrimp. The abundance of settled shrimp larvae  
16 varies in time and space. The recruitment to the fishery has been quite stable with the  
17 exception of the 1996 year-class which was observed as 1 year old but has not been registered  
18 since. The temporal pattern of the three youngest year-classes are studied in relation to abiotic  
19 factors such as sea temperature, ice index and North Atlantic Oscillation, as well as biotic  
20 factors such as spawning stock biomass and presence of copepods, euphausiids and predating  
21 cod. Recruitment indices and factors identified by Spearman correlation to be significantly  
22 correlated with recruitment were used as input in a principal component analysis (PCA) and a  
23 generalized additive model (GAM) was applied. Abundance of 1 year old shrimp is positively  
24 correlated to spawning stock biomass the previous year and temperature the last winter and  
25 negatively correlated with the number of 1 year old cod. Two year old shrimp show  
26 significant correlation with temperature while there is a strong negative correlation with  
27 euphausiids. Three year old shrimp are significantly correlated with the number of 2 year old

28 shrimp the previous year but negatively correlated to temperature at sampling time. This is  
29 probably due to less overlap with the main predator cod when cold. Ricker functions indicate  
30 an increased density dependent mortality with age. When predicting the recruitment of shrimp  
31 to the fishery the spawning stock biomass, the abundance of cod and euphausiids, as well as  
32 the temperature should be included.

33

34 Key words: *Pandalus borealis*, recruitment, Northeast Atlantic, Barents Sea, Spawning stock,  
35 environmental factors

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## 43 **1. Introduction**

44

45 The shrimp (*Pandalus borealis*) is a protandric hermaphrodite changing sex from male to  
46 female at an age of 4 to 7 years in the Northeast Atlantic (Nilssen and Hopkins, 1992). The  
47 shrimp spawn in autumn and the eggs are carried as out roe by the females (ovigerous  
48 females) until spring when the larvae hatch. Within a period of 2–3 months the shrimp larvae  
49 pass through six developmental stages after which they settle to the bottom as post larvae  
50 (Shumway et al., 1985; Ouellet et al. 1990; Bergström, 2000).

51 It is of major importance for the shrimp stock assessment to get information on the strengths  
52 of the recruiting year classes as early as possible. Today's assessment forecast of the shrimp  
53 stock productivity and potential fishing yields is weak, partly due to the lack of knowledge on  
54 the population dynamics from hatching until the shrimp are caught in the fishery. According  
55 to Shumway et al. (1985) the year class strength of shrimp is probably largely established  
56 during the pelagic larval stage. In the Barents Sea shrimp larvae are transported 0–300 km  
57 during the larval phase (Pedersen et al., 2003). It is assumed that the transport processes  
58 influence the recruitment both directly as advective losses of larvae and indirectly through  
59 temperature, food availability and predator-prey interactions (Apollino et al., 1986; Lysy and  
60 Dvinia, 1991; Clarke et al., 1991; Ouellet et al., 1995). Ouellet et al. (2007) found that  
61 survival of the pelagic shrimp larvae was dependent on warming rate and the depth of the  
62 mixed water layer. The object of this study is to define relevant recruitment indices and  
63 identify the environmental factors determining recruitment success. Annual variation in  
64 recruitment and larval survival are related to abiotic factors; temperature, ice coverage, the  
65 North Atlantic Oscillation (NAO), and to biotic factors; spawning stock biomass (SSB)  
66 defined as biomass of ovigerous females the previous year, abundance of zooplankton,  
67 euphausiids and capelin (*Mallotus villosus*). We will also study the effect of the main predator

68 cod (*Gadus morhua*) as predation has been shown to overrule the positive effect of favourable  
69 temperature conditions on shrimp survival (Wieland et al., 2007).

70

## 71 **2. Material and Methods**

72

### 73 *2.1. Study area*

74

75 The Barents Sea is a shelf sea with an average depth of 230 m. The circulation is dominated  
76 by the Norwegian Atlantic Current that enters the Barents Sea through the Bear Island  
77 Trench. Some of the Atlantic Water flow eastward parallel to the coast towards Novaya  
78 Zemlya while another part flows northeast wards and into the Hopen Deep (Fig.1). The  
79 relative strength of these two branches varies with the atmospheric fields (Ingvaldsen et al.,  
80 2003). South of the Atlantic inflow, the Norwegian Coastal Current continues along the  
81 Finnmark and Kola coast. In the northern and eastern parts of the Barents Sea, Arctic water  
82 flow southwest wards near the surface. The Atlantic inflow continues towards northeast  
83 below this layer. The Barents Sea has several bank areas with associated anticyclonic  
84 circulation. The Atlantic inflow to the Barents Sea shows considerable inter-annual variability  
85 (Ådlandsvik and Loeng, 1991). Fig. 1

86

87 The major water masses in the investigated area are Atlantic Water with salinity over 35‰,  
88 and the colder and fresher Arctic Water. These water masses are separated by the Polar Front.  
89 In the western Barents Sea the position of the front is relatively stable, although it seems to be  
90 pushed northwards during warm climatic periods (Loeng, 1991; Ingvaldsen, 2005). In the  
91 eastern part the position of the front has large seasonal, as well as year to year variations. Ice  
92 conditions also show large seasonal and year to year variations. In the winter the ice can cover  
93 most of the northern Barents Sea, while in the summer the whole sea may be ice-free.

94

95 2.2. *Abiotic factors*

96

97 The climate of the Barents Sea shows substantial variations, and the temperature fluctuations  
98 at the Vardø-N section along 31°13'E (Fig. 1) gives a good representation of the climate  
99 variability in the central Barents Sea (Ingvaldsen et al., 2003) and the position of the Polar  
100 Front in the Hopen Deep (Skjoldal et al., 1987). The mean temperature in the section,  
101 between 50–200 m depth, was calculated from 72°15'N to 74°15'N. The section is sampled 4  
102 times a year (January, March, June–July and August–September). In addition to January and  
103 March temperatures (best available measure of winter temperature) the annual mean  
104 temperature was used in the correlation analysis.

105

106 From a temperature atlas where all observations from August–October each year have been  
107 interpolated to a regular grid, a section along the Hopen Deep between 74°N and 76°30'N at  
108 50 to 200 m was defined to provide a time series of temperature in the northernmost parts of  
109 the Barents Sea where shrimp is most abundant (Fig. 1). Temperatures from  
110 August–September each year were used instead of annual means, because by including winter  
111 temperatures the section could not extend as far north. As the temperature level for the rest of  
112 the year is determined by the winter temperature, the annual variation is clear also in the  
113 summer temperature (Ottersen et al., 2000). Bottom temperatures in the Hopen Deep (Fig. 1  
114 Area E) were extracted from a similar temperature atlas and mean temperatures were  
115 calculated. The Russian section defined along the Kola meridian at 33°30' E (Bochkov 1982  
116 and Tereshchenko, 1996) gives a good indication of the temperature variation in the southern  
117 Barents Sea (Ingvaldsen et al., 2003). The annual mean temperature for the upper 200 m from  
118 70°30'N to 72°30' N, were calculated and used in the correlation analysis.

119

120 The North Atlantic Oscillation (NAO) is one of the most prominent and recurrent patterns of  
121 seasonal and long-term atmospheric variability in the North Atlantic Ocean and is there fore

122 used in this study. The NAO index from NCAR (Hurrell, 1995) is a much used, but crude  
123 indicator of the south-westerly winds in the Norwegian and Barents Sea, and has significant  
124 effect on the Barents Sea temperatures (Ottersen et al., 2003).

125

126 The ice index is an integrated value for the ice coverage between 25°E and 45°E in the  
127 Barents Sea and is a good indicator of the climate conditions. A definition of the index is  
128 given by Ådlandsvik and Loeng (1991), and values are updated annually by the Institute of  
129 Marine Research (Skogen et al., 2007). Note that a low index corresponds to heavy ice  
130 conditions.

131

### 132 2.3. *Biotic factors*

133

134 Since 1987, the zooplankton abundance has been monitored on annual surveys during the  
135 Norwegian-Russian 0-group and capelin surveys that are carried out in autumn. The  
136 zooplankton biomass in the Barents Sea is dominated by *Calanus finmarchicus*, and the  
137 biomass estimate is based on net-hauls from bottom to surface (Dalpadado et al., 2003;  
138 Skogen et al., 2007). Euphausiids (*Thysanoessa inermis*, *T. raschii*, *T. longicaudata* and  
139 *Meganyctiphanes norvegica*) have been monitored in the Barents Sea since 1952 at demersal  
140 fish surveys conducted by Russian scientists at PINRO. A net is attached to the survey trawl  
141 and sampled in the autumn and winter period when euphausiids are concentrated close to the  
142 bottom and show no vertical migration (Drobysheva et al., 2003).

143

144 The number of 1 year old capelin sampled in August was included in the correlation analysis  
145 since there may be a relationship between the shrimp and the capelin directly by capelin  
146 feeding on shrimp juveniles or indirectly by both being prey for the cod (Skogen et al., 2007).  
147 The Arctic Fisheries Working Group report (Anonymous, 2006) lists the number of cod in

148 age group 3, whereas Bjarte Bogstad (IMR) provided data on age groups 1 and 2. The number  
149 of cod in each year class is the output of the VPA.

150

#### 151 2.4. *Shrimp spawning stock and recruitment*

152

153 Annual shrimp surveys have been conducted by Norway in the Barents Sea every spring in  
154 the period 1982–2004. Between 100 and 200 stations have been towed with 3 knots<sup>1</sup> for one  
155 hour, 30 minutes or, since 1992 for 20 minutes. Shrimp are sexed and length measured on  
156 board the vessel. The spawning stock biomass is presented as the weight (ton) of reproducing  
157 females (egg carrying females and females with hatched eggs) per square nautical mile<sup>2</sup> (nm<sup>2</sup>).  
158 <sup>2</sup>). Aschan and Sunnanå (1997) described in detail the procedures for sampling, stratification,  
159 length measurements and sex determination.

160

161 As the survey trawl (Campelen 1800) only catches large shrimp (carapace length (CL) >15  
162 mm equals total length > 6 cm) efficiently, sampling techniques for sampling the smallest  
163 shrimp have been tested and evaluated (Larsen et al., 1993; Aschan et al., 2000). In 1995 a  
164 fine meshed (8 mm) juvenile bag with a 1 m<sup>2</sup> opening was attached to the lower trawl belly  
165 one meter in front of the junction to the cod end (Nilssen et al., 1986; Aschan and Sunnanå,  
166 1997). Because the juvenile bag samples both 1 and 2 year old shrimp escaping the trawl  
167 through the belly and thereby does not require additional sampling time, it was chosen as the  
168 main sampling tool for small shrimp. Indices for 3 years old and also for 2 year old shrimp  
169 were produced from the cod end sample.

170

171 The samples were weighted to the shrimp catch at each station and the strata size in a swept  
172 area calculation before calculating the average density by sub-area (A–F, Fig. 1). Number of  
173 shrimp in each 1 mm interval was calculated for the years 1989–2004 and for the belly bag

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<sup>1</sup> 1 knot = 1 nautical mile/h = 1.852 km/h = 0.514 ms<sup>-1</sup>

<sup>2</sup> 1 square nautical mile = (1.852 km)<sup>2</sup> = 3.4299 km<sup>2</sup>

174 for the years 1995–2004. The young shrimp (< 15 mm) are divided into age groups; age 1: CL  
175 <9 mm, age 2: 9 mm ≤ CL < 12 mm and age 3: 12 mm ≤ CL < 15 mm, according to the length  
176 at age key generated from the Hopen Deep (Aschan, 2001). This length at age key is based on  
177 data collected since 1990 and is not necessarily applicable on shrimp collected in the 1980's.  
178 However, when describing the long time spatial recruitment pattern the index of 2 year old  
179 shrimp, defined as above, is presented by area for year class 1980 to 2002.

180

### 181 2.5. Numerical analysis

182

183 Regression analysis between 2 year old shrimp caught in the juvenile bag and same age  
184 shrimp caught in the cod end was run to identify if the latter could be used as a recruitment  
185 index and thereby provide a longer time series.

186

187 The spawning stock recruitment relationship was studied by fitting linear regression and the  
188 Ricker (1954) spawning stock recruitment model to recruitment indices of age 1 (1994–2003  
189 year class), age 2 (1989–2002 year class) and age 3 shrimp (1986–2001 year class) and  
190 spawning stock biomass. The formula for the Ricker model is:

191

$$192 R = a \cdot SSB \cdot e^{(-b \cdot SSB)}$$

193

194 where  $R$  is the recruitment,  $SSB$  is our measure of the spawning stock biomass in the year of  
195 recruitment, and  $a$  and  $b$  are constants.

196

197 We used two criteria for determining the fit of the models, the adjusted  $R^2$  where a larger  
198 value indicates a better fit, and the akaike information criterion (AIC) where smaller value  
199 indicate a better more parsimonious model (Quinn and Keough 2002).

200



201 As the shrimp recruitment is likely to depend on the spawning stock biomass a survival index  
202 was established for age 1 and age 2 as recruitment per unit of SSB which produced these  
203 recruits. For age 3 the survival index is the number of age 3 recruits per age 2 recruits the  
204 previous year.

205  
206 A correlation analysis between recruitment measures, recruitment indices and survival indices  
207 (age 1, age 2 and age 3), and abiotic and biotic parameters was run using Spearman's rho  
208 statistic to estimate a rank-based measure of association. The rank Spearman correlation  
209 coefficient (rho) is calculated after the variables have separately been transformed to ranks  
210 and is a conservative measure on monotonic relationships between the variables. The  
211 Spearman correlation is robust and has been recommended when data do not necessarily  
212 come from a bivariate normal distribution (Quinn and Keough 2002). The populations in  
213 nature, in this study temperature, species abundance etc., seldom have a normal distribution,  
214 and one can not assume that the data are normally distributed. When using our few data  
215 Shapiro–Wilkins normality test indicated normality for some variables (annual mean  
216 temperature Vardø P = 0.02, Capelin P = 0.008, Cod 1 P = 0.05, Cod 2 P = 0.02, Age 2 P =  
217 0.03 and Survivals = Age 3/Age 2 P = 0.01), but normality plots showed that the outermost  
218 points did not follow the normal distribution.

219  
220 All variables were tested for autocorrelation for a lag of one, two and three years. Where  
221 autocorrelation was significant ( $P \leq 0.05$ ), we corrected for it by adjusting the degrees of  
222 freedom used in the Spearman's rho statistics. This adjustment was done in accordance with  
223 Pyper and Peterman (1998):

224

$$225 \frac{1}{N^*} = \frac{1}{N} + \frac{2}{N} \sum_{j=1}^{N/5} r_{xx}(j)r_{yy}(j)$$

226

227 where  $N^*$  is the effective number of degrees of freedom on the time series  $X$  and  $Y$ ,  $N$  is the  
228 sample size and  $r_{xx}(j)$  and  $r_{yy}(j)$  are the autocorrelations of  $X$  and  $Y$  at lag  $j$ . Following the  
229 recommendation by Pyper and Peterman (1998) a maximum of  $N/5$  lags were included in the  
230 calculation of effective number of degrees of freedom. Therefore two lags were included for  
231 1 year old shrimp and three lags for 2 and 3 year old shrimp. All statistical analyses in this  
232 study were run in R 2.5.0 (R Development Core Team, 2007).

233

234 Relevant abiotic and biotic factors identified by the Spearman correlation analysis as  
235 significant, were used as input when running a principal component analysis (PCA). A  
236 generalized additive model (GAM) in the function “ordisurf” in R fits surfaces of density of  
237 recruits (age 1, age 2 and age 3) to the respective principal component ordinations (PC1 and  
238 PC2). The generalized additive model (GAM) is a generalized linear model (GLM), in which  
239 the linear predictor is replaced by a user specified sum of smooth functions of the covariates  
240 plus a conventional parametric component of the linear predictor. The function “gam” uses  
241 thinplate splines in two dimensions, and automatically selects the degree of smoothing by  
242 generalized cross validation (Oksanen, 2007).

243

### 244 **3. Results**

245

#### 246 *3.1. Abiotic factors*

247

248 From 1985 to 1989 there were in general low temperatures in the Barents Sea, while the  
249 period 1990–1995 was characterized by warm conditions (Fig. 2). In 1996 a sudden  
250 temperature drop occurred and it stayed cold until 1998. Since then temperatures have been  
251 high, with the exception of 2003 which was close to the long-term mean. Prior to 2000–2001  
252 the mean temperature, the January and the March temperatures in the Vardø-N section, the  
253 NAO index and the ice index varied much in the same manner indicating warm conditions

254 with small amounts of ice during high NAO, but after 2000–2001 there is not a good  
255 correlation between the NAO and other parameters. The ice index follows in general the  
256 variations in mean temperature, but with a lag of 1–3 years. An exception was in 2003, when  
257 there were large amounts of ice despite the temperatures not being correspondingly low. The  
258 reason was a late onset of melting in spring 2003. In the Hopen Deep the ice edge was close  
259 to 75°N through the entire winter, which is close to normal, but the ice edge reached 76°N  
260 about a month later than in 2002. Fig. 2

261  
262 It was cold in the Hopen section in 1987, 1996 and 2003, while the warmest years were 1989,  
263 1999 and 2004 (Fig. 2). The bottom temperature in the Hopen Deep (area E) shows much of  
264 the same variability as the mean temperature in the Hopen section (50–200 m). However,  
265 some differences are evident, and the most pronounced difference is the strong increase in  
266 bottom temperature in 1987–1992, followed by a rapid decrease in 1993. In 1996 and 2003  
267 the bottom temperatures were low, but the decrease was not as extreme as observed at 50–200  
268 m depth.

269  
270 The temperature along the Hopen section is significantly correlated with the bottom  
271 temperature in the Hopen Deep, with the Vardø annual mean temperature and with the NAO  
272 (Spearman correlation  $\rho = 0.68, 0.70$  and  $0.85$  respectively). The temperature in Hopen  
273 and Kola sections has the same variability, but there are large deviations between the time  
274 series after the year of 1999 and therefore there is no correlation ( $\rho -0.40$ ). The very low  
275 temperatures measured in Hopen in the years 1996 and 2003 were not observed in Kola.

276

277

278 3.2. *Biotic factors*

279

280 The zooplankton and euphausiid biomass increases in the 90's and stay above the long-term  
281 mean until 2004. However, both variables show great variation between years (Fig. 3). Cod  
282 has very good recruitment in the period 1991–1998. Capelin has a negative correlation to cod  
283 of age 1–4 (rho: -0.44 to -0.63) while zooplankton has a positive correlation with cod age 1, 2  
284 and 3 (rho: 0.66-0.69). This is the consequence of low densities of cod giving rise to high  
285 numbers of capelin predating on copepods. Fig. 3

286

287 3.3. *Shrimp spawning stock and recruitment*

288

289 The recruitment indices given for age 2 shrimp caught in the cod end of the survey trawl and  
290 in the juvenile bag attached to the belly of the trawl are well correlated ( $R^2 = 0.80$ ) (Fig. 4).  
291 We therefore used the longer time series for number of age 2 shrimp caught in the cod end in  
292 the correlation analysis. Fig. 4

293

294 The biomass of spawning females, recruitment index for age 2 and age 3 shrimp may vary by  
295 a factor of 4–5, while the recruitment index for 1 year old shrimp vary by a factor of 10. This  
296 indirectly indicate that the greatest mortality occur between age 1 and 2. Recruitment indices  
297 for 2 and 3 year old shrimp and spawning stock biomass sampled in the cod end each year  
298 since 1989 reveals high spawning stock and good recruitment of age 2 shrimp in the early and  
299 the late 90's (Fig. 5). The recruitment indices for 1 year old shrimp sampled in the belly bag  
300 since 1995 show strong year-classes in 1999 and 2000. Both spawning stock biomass and  
301 recruitment of all age classes are on a historically low level in 2004. Fig. 5

302

303 The recruitment of shrimp varies between areas and years (Fig 6). The Hopen Deep (E) is the  
304 most important area for recruitment with the highest density of recruits. The mean density of  
305 age 2 shrimp in the Tiddly Bank (B) and Thor Iversen Bank (C) is less than 30% of the  
306 density in the Hopen Deep (E). Off Finnmark (A), in the Bear Island Trench (D) and off Bear  
307 Island (F) the density of age 2 shrimp is even lower with a mean density less than 15 % of the  
308 mean density in the Hopen Deep. Except for the period 1994–1997, the number of recruits in  
309 the Hopen Deep (E) has a strong covariation with the bottom temperature in the Hopen Deep  
310 (Fig. 2 and Fig. 5). The poor covariation in 1994–1997 is probably due to the high number of  
311 1 and two year cod in that period (Fig. 3), and possibly due to unusual inter-annual variability  
312 in the temperature. Fig. 6

313

314 The spawning stock recruitment relationship fits both to the linear model and the Ricker  
315 model, but F–statistics give the linear model the best fit for all age groups ( $P < 0.001$ ) (Fig. 7  
316 and Table 1). The AIC indicates that the stock recruitment model fit gets weaker for each age  
317 group. That is due to the biotic and abiotic factors affecting the survival rate of young shrimp  
318 over time. Fig. 7

319

320 Some of the variables (SSB, Age 2, Cod 1) turned out to have a significant ( $P \leq 0.05$ )  
321 autocorrelation, but only at lag 1. The correlation between Age 1 and Cod 1 (-0.6) and Age 2  
322 and SSB (-0.46) turned out to be insignificant when degrees of freedom were adjusted for  
323 (Table 2). However, survival (Age 1/SSB) and Cod 1 still have a significant negative  
324 correlation. All abiotic and biotic factors presented were included in the correlation analysis,  
325 but only variables giving significant correlation ( $P \leq 0.05$ ) were included in Table 2. Thereby  
326 the Kola temperature, ice index, zooplankton and cod age 3 are excluded. The correlation  
327 analysis reveals that for age 1 shrimp the most important positive factor, after spawning stock  
328 biomass the previous year, is the temperature in January and March the same year. The  
329 presence of cod age 1 and 2 the previous year is important negative factors (Table 2.). Age 1

330 shrimp is positively correlated with capelin but negatively, although not significantly  
331 correlated ( $\rho = -0.45$ ) with zooplankton. Age 2 shrimp is not significantly correlated with  
332 spawning stock biomass ( $\rho = 0.46$ ), is significantly correlated with temperatures (Vardø and  
333 Hopen sections and Hopen bottom) and NAO the previous year, but has a significant strong  
334 negative correlation with euphausiids ( $\rho = -0.8$ ). Age 3 shrimp is significantly correlated  
335 with age 2 shrimp the previous year and negatively correlated to the temperature at the  
336 sampling time (Vardø in March). Simultaneously, the survival of 3 year old shrimp, as  
337 previously seen for age 1 shrimp, seem to be good when the young capelin thrives.

338  
339 The principal components 1 and 2 contribute 92%, 79% and 70% to the correlation between  
340 factors selected for the PCA ordination to be fitted to the distribution of age 1, 2 and 3 shrimp  
341 (Table 3). The generalized additive model has the best fit to the age 1 and age 2 shrimp while  
342 the deviance explained by the model for age 3 is only 16% (Table 3). The density of shrimp  
343 of age 1 and 2 is projected on the respective PCA ordination plots (Fig. 8). In the PCA plot  
344 the isolines show how the recruitment, of age 1 and age 2 change along the 3 most important  
345 factors. The PCA for age 1 and age 2 visualizes how the recruitment is very dependent on  
346 SSB and temperature. While the presence of young cod and euphausiids reduces shrimp  
347 recruitment. Fig. 8

348

#### 349 **4. Discussion**

350 When evaluating the effect of environmental factors on shrimp recruitment, the ambient  
351 temperature is the most obvious factor to study. The NAO and the ice index were included as  
352 they may represent the large scale climate variability of the Barents Sea. The NAO influences  
353 on the Barents Sea in several ways. It may have an effect through changing the wind field,  
354 thereby changing the position of the Polar Front and the ice edge, and by increasing the  
355 northward flow of Atlantic Water in the Barents Sea. This response is direct with no lag as it  
356 is related to the wind conditions at the time. The NAO has also an indirect effect as it often

357 cause changes to the temperature of the Atlantic Water in the Norwegian Sea which is  
358 subsequently advected into the Barents Sea. Due to this a lag between the NAO and the  
359 Barents Sea temperatures has been identified by several authors (e.g. Furevik, 2001). When  
360 using the ocean temperatures this advected, lagged signal is already in the time series, and  
361 there will therefore be no additional information available by lagging NAO and shrimp.  
362 The influence of the NAO is strongest when it is in a well defined positive or negative phase  
363 with several high- or low-index years following. Prior to 2001 the NAO index had well  
364 defined positive or negative phases, while since 2001 it has been low and irregular (Fig. 2).  
365 This is probably the cause for the poor correlation between the NAO and the other parameters  
366 after 2001. The age 1 and 3 shrimp show no correlation with NAO while the age 2 shrimp is  
367 significantly correlated with this index (Table 2). Age 2 shrimp also show a significant  
368 correlation to the Vardø and Hopen temperatures and as the NAO and these temperatures are  
369 significantly correlated (0.88 for NAO and Hopen), we consider this a temperature effect.

370

371 The best recruitment index for age 1 shrimp is received by using the juvenile bag. However,  
372 the time series is short and because age 2 shrimp caught in the cod end is correlated to the  
373 shrimp caught in the juvenile bag and provides a longer time series they are considered the  
374 best recruitment measure (Fig. 4). Due to high and variable natural mortality from age 1 to  
375 age 3, age 1 shrimp is not the best recruitment indicator to be used for fishery prognosis. The  
376 index of age 2 shrimp is significantly correlated to available abiotic and biotic factors whereas  
377 this correlation is weaker for the index of age 3 shrimp (Table 2 and Table 3). We consider  
378 age 2 shrimp to be the best indicator of recruitment as has also been concluded for shrimp  
379 stocks off West Greenland, Iceland and elsewhere (Wieland, 2004; Skuladottir, 1990).

380

381 The index of 3 year old shrimp from the cod end is hard to predict as the effect of several  
382 abiotic and biotic factors co-occur over time and the correlation to these factors get weak. A  
383 better correlation might have been received if the environmental factors (e.g. temperature and

384 cod) would have been integrated over the last three years before running the correlation  
385 analysis. However, the index of age 3 shrimp gives an indication on the recruitment to the  
386 shrimp fishery the next year, and may be used as a recruitment index in future assessment  
387 work. A problem using this index is however, that a fraction of this age group is caught in the  
388 commercial trawl and may have been exposed to fishing mortality.

389  
390 One year old shrimp are significantly correlated to spawning stock biomass, and the relation  
391 is almost linear (Table 1, Fig. 7). Even if the Cushings match/mismatch hypothesis, effective  
392 for the larval phase, may explain some of the inter annual variability in shrimp recruitment  
393 (Ouellet et al., 2007), the winter temperature and cod predation seem to be of essential  
394 importance as they together with the SBB stand for more than 97 % of the deviance explained  
395 by the GAM function (Fig. 8, Table 3). Crustaceans (krill, amphipods and shrimp) seem to be  
396 the dominant prey of 1 year old cod, composing up to 40–80% of their diet. In some years  
397 *Pandalus borealis* made up for 30–37% of the Total Fullness Index (Dalpadado and Bogstad,  
398 2004). According to Dalpadado and Bogstad (2004) the cod reduces its crustaceans consume  
399 at age 2 and moves to fish prey at age 3, consequently the negative correlation with shrimp  
400 recruits gets weaker with shrimp and cod age (Table 2).

401  
402 The positive correlation between shrimp and the winter temperature may be a direct effect of  
403 decreasing natural mortality, as temperatures below -1 °C are known to result in reduced  
404 abundance and temperatures below -1.6 °C result in extinction of shrimp (Smidt, 1981;  
405 Wieland 2005). However, the positive correlation between one year old shrimp and  
406 temperature and capelin may be related to food competition and overlap between shrimp and  
407 capelin as also shrimp feed on *Calanus finmarchicus* (CI–CVI) (Harvey and Morrier 2003).  
408 During winter the capelin is distributed according to the position of the Polar Front, so during  
409 cold winters the capelin is concentrated in the Hopen Deep while during warm winters it is  
410 spread over a larger area (Gjørseter, 2008). In warm years, the distribution of capelin in



411 summer has a more northerly distribution, north and east of the Hopen Deep, than in cold  
412 years. Consequently there is less overlap between shrimp and capelin in warm years than in  
413 cold years both during summer and winter. Although capelin by far is controlling the  
414 abundance of copepods (Dalpadado and Skjoldahl 1996; Gjørseter et al. 2000), less overlap in  
415 warm years leaves more *C. finmarchicus* available for the shrimp in the Hopen Deep. This  
416 may explain the negative, although not significant, correlation (-0.45) between one year old  
417 shrimp and zooplankton. Dalpadado et al. (2003) found correlation coefficients 0.57–0.72  
418 between temperature and capelin biomass. The positive response of one year old shrimp and  
419 capelin to high temperatures may thereby be the result of less overlap and consequently less  
420 food competition.

421  
422 The 2 year old shrimp show a positive response to temperature (Table 2). This relationship is  
423 common when studying fish recruitment in the Barents Sea. Abundance estimates of 0-group  
424 cod exhibit a close relationship with sea temperature variability at the Kola section (Nilssen et  
425 al., 1994). Covariability in early growth and year class strength of cod, haddock and herring is  
426 explained by their common positive response to temperature (Ottersen and Loeng, 2000). The  
427 striking negative correlation with euphausiid biomass may have several explanations. The  
428 dominating euphausiids in the Barents Sea are *Meganyctiphanes norwegica*, a boreal species  
429 found in Atlantic water, and *Thysanoessa inermis*, *T. raschii* and *T. longicaudata* having an  
430 arctic boreal distribution (Drobysheva et al., 2003). *M. norwegica* reaches the length of 45  
431 mm and is primarily a carnivore aiming for copepod prey, including overwintering *Calanus*  
432 *spp.* (Dalpadado et al., 2003; Kaartvedt et al., 2002). *Thysanoessa spp.* is smaller (25–35 mm)  
433 and has been classified as herbivores although *T. raschii* seems to switch to detritus feeding in  
434 winter (Hopkins et al., 1989, Drobysheva et al., 2003; Pedersen et al., 2008). The age 2  
435 shrimp and *M. norwegica* have the same size and are likely to compete for the same food  
436 source, as juvenile shrimp are known to be active feeders and obtain most of their food,  
437 euphausiids and copepods, from the macro plankton (Berenboim, 1981; Wienberg, 1980;

438 Wienberg 1982). In winter shrimp and *M. norvegica* may crop on overwintering copepods  
439 that may be a scarce food source in deep water also in the Barents Sea (Kaartvedt et al. 2002).  
440 As indicated before the mortality in the second year seems to be high, especially in years after  
441 good recruitment. The reduced food supply may be a limiting factor not only when  
442 euphausiids are abundant, but also when density of 2 year old shrimp is high. This increase in  
443 density-dependent mortality with age is illustrated by the change in the shape of the Ricker  
444 curve with age (Fig. 7). This is probably caused by intra-specific competition due to  
445 limitations in available prey in combination with predation.

446

447 The recruitment indices are influenced by variable natural mortality rates and catchability  
448 (Hannah, 1993). Although the spawning stock number was high in 1996 to 1999 the  
449 recruitment of age 2 shrimp did not show an increase in the same manner as seen previously,  
450 probably as a result of increased natural mortality due to cod predation (Fig. 3). Cold  
451 temperature conditions in the Hopen Deep as observed in 1987, 1996 and 2003 (Fig. 2)  
452 increases the natural mortality of 1 and 2 year old shrimp either directly, or indirectly as the  
453 habitat overlap with cod probably increases as female shrimp and larvae move along  
454 temperature gradients (Rasmussen et al., 2000), and get a more southern distribution as they  
455 escape the cold water. Pedersen et al. (2003) showed by a transport model that high numbers  
456 of larvae settled in the area around Bear Island, that also serves as nursery area for cod  
457 (Skogen et al., 2007). The young cod feed on the young shrimp causing high natural mortality  
458 and low abundance of age 2 shrimp off Bear Island (Fig 6).

459

460 The absence of the 1996 year class in the survey as 3 year olds in year 1999 is thereby caused  
461 by several co-occurring factors, the low spawning stock number and the distribution of the  
462 spawning females in 1996, temperature conditions and cod consumption. Similar  
463 environmental conditions may explain the low abundance of the 1987 and the 2001 year class  
464 at age 3 (Fig. 5). Wieland (2005) concluded that a moderate increase in temperature from 1°C

465 to 3°C above a lower threshold of optimal range in the northern regions off West Greenland  
466 extended the favourable distribution area for shrimp and recruitment of age 2 shrimp. A  
467 similar temperature reduction was observed in the in the Hopen Deep in the northern Barents  
468 Sea in 1987, 1996 and 2003 (Fig. 2). As seen here for shrimp, studies on cod recruitment in  
469 the Barents Sea indicate that the North East Arctic cod is also affected by temperature through  
470 a variety of pathways (Hjermann et al., 2007)

471

472 The spawning stock biomass seem to have a significant effect on the number of age 1 and age  
473 2 shrimp but this correlation is not detectable for age 3 shrimp, probably because the effect of  
474 temperature, predation by 1 and 2 year cod and euphausiids governs the development of the  
475 year classes (Table 1, Fig. 7). So, even if the female biomass may vary with a factor of 5  
476 between years, a low number of female shrimp does not alone cause low recruitment.

477

478 Even if the larval phase is important (Quellet et al., 2007), the year class strength does not  
479 seem to be established during the larval stage as has been claimed by Shumway et al. (1985).

480 The density of 1 year old shrimp is directly dependent on SSB the previous year and is further  
481 influenced by cod predation after the larvae settled.

482

483 Environmental fluctuations rather than changes in spawning female biomass are the primary  
484 causes of shrimp stock fluctuations (Hancock, 1973; Garcia 1983). Therefore approaches  
485 including an environmental factor e.g. natural variability, temperature have been suggested  
486 and three dimensional interpretations have been proposed (Garcia, 1983; Hannah, 1999). This  
487 is supported by our study where the ambient factor temperature, and the biotic factors  
488 spawning stock biomass, cod age 1 and 2 as predators and euphausiids as competitors all  
489 affect the recruitment significantly. When modelling the recruitment of shrimp in the Barents  
490 Sea the spawning stock number, the annual mean Vardø temperature, the number of 1 and 2  
491 year cod, and the euphausiid abundance the previous year should be included.

492

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494

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501

502

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663

664 Figure text:

665

666 Fig.1. A schematic description of the circulation of the Barents Sea. Arrows show the current  
667 of Atlantic water (dark grey) and Arctic water (light gray) (after Aure et al., 2000). Main  
668 survey areas are East Finnmark (A), Tiddly Bank (B), Thor Iversen Bank (C), Bear Island  
669 Trench (D), Hopen Deep (E) and Bear Island (F). The Hopen, the Vardø-North and the Kola  
670 section (stippled lines) are shown.

671

672 Fig. 2. Annual mean, January and March temperature in the Vardø section (50–200 m),  
673 summer temperature (August–September) in the Hopen section (50–200 m) and Kola section  
674 annual mean (0–200 m), bottom temperature in the Hopen Deep (area E in Fig. 1), NAO  
675 winter index and ice index. A low ice index corresponds to heavy ice conditions and vice  
676 versa.

677

678 Fig. 3. Zooplankton biomass, index of euphausiid abundance (updated from Drobysheva et  
679 al., 2003) and number of capelin, cod age 1, age 2 and age 3.

680

681 Fig. 4. Two year old shrimp caught in the juvenile bag attached to the underbelly of the  
682 survey trawl plotted against 2 year old shrimp caught in the cod end, 1995–2004.

683

684 Fig. 5. Recruitment indices for 2 and 3 year old shrimp (standardized to the mean) and  
685 biomass of spawning females (SSB) sampled in the cod end each year. Recruitment indices  
686 for 1 year old shrimp (standardized to the mean) sampled in the belly bag since 1995. The  
687 indices represent the whole Barents Sea.

688

689 Fig. 6. Number of recruits as 2 year old shrimp by each sub area (A–E) in Fig. 1.

690

691 Fig. 7. Number of recruits at age 1 (1994–2003 year class), at age 2 (1989–2002 year class)  
692 and at age 3 (1986–2001 year class) plotted against spawning stock biomass for

693 corresponding year classes. Linear regression and the Ricker stock-recruitment model  $y = a * x$

694  $* \exp(-b*x)$  are fitted, and the parameter values received are given in Table 1.

695

696 Fig. 8. Spline surfaces of shrimp at age 1 (No.  $\times 100 \text{ nm}^{-2}$ ) upper panel and at age 2 (No.  $\times 1000$

697  $\text{nm}^{-2}$ ) bottom panel, fitted to principal component ordinations of selected environmental

698 factors. The years plotted refer to the year-class in both panels.

699

700 Table 1. Parameter values (*a* and *b*) with respective standard error for linear regression  
 701 through origin and the Ricker curve. Adjusted R-squared, the degrees of freedom and,  
 702 P-value for F-test and AIC values are given.

703

	Age 1		Age 2		Age 3	
	Linear	Ricker	Linear	Ricker	Linear	Ricker
<i>a</i>	4.29	1.65	5.71	4.22	22.43	74.61
st. error	0.67	1.36	0.77	2.57	2.99	23.69
<i>b</i>		-0.35		-0.09		0.39
st. error		0.22		0.17		0.12
R <sup>2</sup> (adj.)	0.80	0.78	0.79	0.74	0.77	0.76
d.f.	9	12	13	12	15	14
P	<0.001	ns	<0.001	ns	<0.001	<0.01
AIC	64	105	101	103	136	153

704

705

706 Table 2. Spearman rank correlation between shrimp at age 1, 2 and 3, and survival (Age  
707 1/SSB, Age 2/SSB and Age 3/Age 2) and explanatory abiotic (January and March  
708 temperature Vardø section the same year, mean annual temperature Vardø section, the Hopen  
709 section and bottom temperature from the Hopen Deep, and the the NAO the previous year)  
710 and biotic factors (capelin, euphausiids and cod age 1 and 2). SSB is lagged to the year of  
711 recruitment of each age group. Correlation factor ( $\rho$ ) is given only for significantly  
712 correlating factors ( $P < 0.05$ ). Values given in parenthesis turned out not to be significant  
713 when correction for autocorrelation was conducted.  
714

	Age 1	Age1/SSB	Age 2	Age 2/SSB	Age 3	Age 3/Age 2
Sampling years	1995–2004		1991–2004		1989–2004	
Age 2 shrimp					0.43	
SSB	0.90		(-0.46)			
Temp. Vardø			0.75	0.55		
Temp. Vardø J.	0.77	0.90				
Temp. Vardø M.		0.70			-0.51	
Temp. Hopen			0.62	0.51		
Temp. Hopen b.			0.55			
NAO			0.58	0.48		
Capelin	0.63					0.49
Euphausiids			-0.81	-0.52		
Cod 1 year	(-0.60)	-0.63				
Cod 2 years		-0.62				

715

716 Table 3. Contribution of eigenvalues for PC1, PC2 and PC3 received from the Principal  
 717 Component Analysis and adjusted R<sup>2</sup> values and deviance explained from the Generalized  
 718 Additive model.  
 719

	Age 1 shrimp	Age 2 shrimp	Age 3 shrimp
Principal Component Analysis:			
Contribution to correlation			
PC1	70.8 %	63.6 %	47.0 %
PC2	21.1 %	16.2 %	24.1 %
PC3	5.7 %	14.3 %	22.3 %
Generalized Additive Model :			
R <sup>2</sup> (adj.)	0.92	0.56	0.04
Deviance explained	97.6%	62.6%	16.6%

720