DTU Library

Periodic fluctuations in recruitment success of Atlantic cod

Rindorf, Anna; Cadigan, Noel G.; Howell, Daniel; Eero, Margit; Gislason, Henrik

1   **Periodic fluctuations in recruitment success of Atlantic cod**

2   Anna Rindorf[1*], Noel Cadigan[2], Daniel Howell[3], Margit Eero[1], Henrik Gislason[1],

3   [1]Technical University of Denmark, National Institute of Aquatic Resources, Kemitorvet 1,

4   DK2800 Lyngby, Denmark.

5   [2] Marine Institute of Memorial University of Newfoundland, Centre for Fisheries Ecosystems

6   Research. St. John's, NL, Canada A1C 5R3.

7   [3] Institute of Marine Research, Postboks 1870 Nordnes, 5817 Bergen, Norway

8   [*]Corresponding author. Tel. +45 33 96 33 78. Email: ar@aqua.dtu.dk

9   **Abstract**

10   Autocorrelation in recruitment success of fish is frequently reported, but the underlying

11   mechanisms are generally only vaguely alluded to. We analysed recruitment success of cod

12   21 stocks in the North Atlantic to investigate possible common causes of autocorrelation in

13   recruitment. We found autocorrelation and periodic fluctuations in recruitment success and

14   adult growth in just above half of the stocks considered and investigated six possible

15   underlying mechanisms. With three exceptions, the variations in recruitment success were not

16   significantly related to temperature or growth anomalies, indicating that the variation was not

17   caused by temperature dependent survival or growth dependent spawning products. Further, a

18   link between recruitment and subsequent spawning biomass could not explain the observed

19   recruitment patterns. Slow-growing cod stocks tended to exhibit longer cycles and positive

20   autocorrelations consistent with dilution of predation mortality by adjacent large year classes

21   or age reading errors whereas fast growing cod stocks showed shorter cycles and no

22   significant autocorrelation at lag 1. Both types exhibited significant negative autocorrelations

23   consistent with cannibalism at one or more lags greater than lag 1.

1

24 Key words: Atlantic cod, recruitment, periodic fluctuations, autocorrelation, cannibalism,

25 growth

26

Introduction

28 Periodic fluctuations in the number of recruits per weight of spawning fish occur in numerous

29 exploited fish stocks (Fogarty et al. 2001; Thorson et al. 2014; Ricard et al. 2016). These

30 changes in recruitment success may be generated by a number of processes, including links to

31 climatic conditions, quality of spawning products, predation, cannibalism, or competition.

32 Climatic conditions can potentially influence recruitment success directly or act as a proxy

33 for relevant factors such as food abundance and temperature that impact the growth and

34 survival of juveniles (Beaugrand et al. 2003; Mantzouni and MacKenzie 2010; Drinkwater et

35 al. 2014). Changes in growth conditions can influence the quality and quantity of spawning

36 products (Morgan and Lilly 2006) and through this influence, cyclic growth patterns,

37 generated e.g. by inter cohort competition for food, can potentially introduce cycles in

38 recruitment success (Skjæraasen et al. 2012). Recurrent changes in predation mortality can

39 occur for a variety of reasons; periodic fluctuations in the abundance of alternative prey, limit

40 cycles generated by cannibalism (Bjørnstad et al. 1999; Ricard et al. 2016), or because other

41 individuals of comparable size shelter juveniles from predation (apparent mutualism, Holt

42 1977). Another possibility is that the link between recruitment and size of subsequent

43 spawning stock biomass (SSB) leads to positive correlations between the recruitment success

44 in a given year and stock size several years later (Gilbert 1997). This may occur when the

45 relationship between SSB and recruitment is weak and recruitment includes occasional spikes

46 as is the case in several stocks of haddock (ICES 2017c). A high recruitment leads to a

47 subsequent high SSB with no change in the following level of recruitment and therefore a

2

48 low number of recruits per spawner when the strong cohort matures. This may lead to cycle

49 lengths that are correlated to the age of 50% maturity. Spurious positive correlations between

50 adjacent age classes can be introduced by ageing errors (Bradford 1991), as a large age class

51 is misidentified into the two adjacent yearclasses. In addition, there is a general tendency for

52 late maturing stocks to exhibit greater positive autocorrelation in recruitment (Thorson et al.

53 2014), though the cause of this has not been determined. Identifying the actual causes of

54 significant autocorrelations is necessary for a greater understanding of population regulation

55 in fish stocks and for practical stock management.

56 The high potential abundance of Atlantic cod (*Gadus morhua*) throughout the North Atlantic

57 combined with piscivory, cannibalistic behaviour and large adult size makes it a key regulator

58 in the ecosystems it inhabits, and makes it likely that density dependence is an important

59 feature of its ecology. Furthermore, its well-documented population ecology and cannibalism

60 makes cod an ideal case for investigating the possible causes of periodic recruitment patterns.

61 The numerous processes that can generate fluctuations in the recruitment success of cod

62 could affect the occurrence of cycles in a number of stocks systematically. Changes in the

63 occurrence of food and predators are likely to differ from stock to stock, resulting in

64 differences in oscillations between stocks. Similarly, local climatic changes may introduce

65 periodicities (Casini et al. 2009), where the duration of the periods are likely to vary between

66 regions according to e.g. local temperature. In contrast, large-scale changes such as the NAO

67 may lead to cycles with the same approximately 10 year (decadal) wavelength in all regions

68 and significant correlation across stocks (Hurrell 1995; Beaugrand, et al. 2003). Local

69 changes with wavelengths above 5 years are also expected where slow cycles in the

70 abundance of predators such as marine mammals occur. With the exception of NAO related

71 climatic variables, local changes in food (i.e. changes not related to NAO or similar large-

72 scale impacts), climatic conditions and predation are expected to produce periodicities of

3

73 variable length with no apparent pattern across stocks. Hence, if fluctuations between stocks

74 are random, it can be a sign of varying local conditions, with short wavelength fluctuations

75 being more likely to result from local variations in feeding conditions and predation by short-

76 lived predators, while longer wavelengths may indicate changes in climate or long lived

77 predator stocks.

78   Here, we analyse cod recruitment success in order to investigate the occurrence of periodic

79 fluctuations and identify the underlying causes. We investigate seven different hypotheses:

80   1. There are no significant periodic patterns in cod recruitment success;

81   2. Recruitment success of cod is linked to climate;

82   3. Patterns in the somatic growth of adults generate patterns in recruitment success;

83   4. The link between recruitment and the subsequent SSB causes negative

84   autocorrelations in recruitment success at the age of maturity;

85   5. A large year class dilutes the predation mortality of adjacent year classes (apparent

86   mutualism);

87   6. A large year class decreases the growth and thereby increases the mortality of the

88   subsequent year class (inter-cohort competition);

89   7. Autocorrelations are introduced by cannibalism.

90 To test these hypotheses, we perform time series analyses of recruitment success, age at 50%

91 maturity, annual sea surface temperature and weight at age for 21 cod stocks in the North

92 Atlantic.

93

4

94 **Methods**

95 **Definitions and hypotheses**

96   A time series may show both long term and short term periodic changes (Fig. 1).

97 Recruitment success can respond to large-scale ecosystem changes and often declines when

98 the biomass of spawning fish increases. This may introduce long-term recruitment (20 years)

99 trends (termed 'regime shifts' in Szuwalski et al. 2015). Here, we focus on periodic

100 fluctuations with a wavelength of less than 20 years and detrend the observed time series

101 (Fig. 1a) to derive time series of deviations from the long-term patterns (Fig. 1b). When these

102 detrended time series show cycles (periodicity), the wavelength is given by the number of

103 years between successive peaks (Fig. 1c) and the lag at which the highest negative correlation

104 is observed is the time between a peak and the successive trough, which by definition equals

105 half of the wavelength of symmetric fluctuations.

106 Local fluctuations in sea surface temperature may impact recruitment success (hypothesis 2,

107 Beaugrand et al 2003; Mantzouni and MacKenzie 2010). In contrast, decadal wavelengths are

108 consistent with recruitment cycles driven by approximately decadal cycles such as NAO

109 (Hurrel 1995). If all stocks show similar periodicities with a wavelength around 10 years, this

110 would indicate a panregional climatic influence on recruitment across stocks, in accordance

111 with the many studies, which have demonstrated climate impacts on fish stocks (Sundby

112 2000; Beaugrand et al. 2003; Mantzouni and MacKenzie 2010).

113 In contrast to hypotheses 1 and 2, hypotheses 3 to 7 may result in systematic differences

114 between stocks. Under hypothesis 3, periodicity in weight of spawners affect recruitment

115 success, and accounting for this relationship will eliminate periodicity in recruitment success.

116 Hypothesis 4 expects a match between the age at 50% maturity of a stock and the lag at

117 which the highest negative correlation in recruitment success occurs (Fig. 2). Hence, we

118 would expect the wavelength to vary between stocks in accordance with the differences in

5

119   age at 50% maturity between stocks. Hypotheses 5 to 7 are expected to generate short-term

120   autocorrelation. If a large year class dilutes the predation mortality of adjacent year classes

121   (hypothesis 5), recruitment success will show positive autocorrelation in stocks with slow

122   individual growth where there is a considerable overlap in length distribution between ages

123   for younger fish (Fig. 2). For stocks with rapid individual growth, the length overlap between

124   successive cohorts is less or non-existing, and the possibility to 'hide' among members of a

125   different cohort decreases. Therefore, we expect less or no autocorrelation in fast growing

126   stocks. Inter cohort competition (hypothesis 6) will promote negative short-term

127   autocorrelation in weight at age and cohort strength (Fig. 2). Cannibalism (hypothesis 7) also

128   leads to negative autocorrelation in cohort strength (Fig. 2). In both cases, the negative

129   autocorrelation will peak at the lag corresponding to the size difference where the interaction

130   is most important. For cannibalism, the lag at which a negative autocorrelation occurs

131   depends on the time required to reach the size where cannibalism is possible. As the size at

132   which cannibalism occurs varies considerably less across stocks than weight at age (Kikkert

133   1993; Bogstad et al. 1994; Brander 1995), the negative effect of a large cohort on subsequent

134   cohorts should occur more rapidly in fast growing populations. In stocks with slow somatic

135   growth, the effects of apparent mutualism (hypothesis 5), inter cohort competition

136   (hypothesis 6) and cannibalism (hypothesis 7) may occur simultaneously. If this is the case,

137   large cohorts may be followed by one or a few additional large cohorts as the large cohort

138   acts to shelter the subsequent cohorts from predation by saturating predators (Holt 1977), or

139   by smaller cohorts as inter cohort competition reduces their growth and cannibalism increases

140   their mortality. The expectations for cyclic patterns and autocorrelations are summarised in

141   Table 1. Further, fig. 2 shows an example of the development in recruitment and spawning

142   stock size of a population of fish which become cannibalistic at age 3 and spawn at age 5

143   with a weight of 1 kg which individuals then retain hereafter. The random interannual

6

144   recruitment variation multiplied with the underlying development in recruitment in each

145   hypothesis is taken from cod west of Scotland, and does not differ significantly from white

146   noise.

147   **Model input**

148   The model input used for the analyses came from approved stock assessments (Table 2:

149   recruitment, spawning stock biomass (SSB), age at 50% maturity and weight at age) and the

150   International Comprehensive Ocean-Atmosphere Data Set (NCAR, 2018). Monthly sea

151   surface temperature from February to June from 1960-2017 was downloaded from NCAR in

152   1x1 degree resolution and used to calculate the annual mean SST in each of the 21 stock

153   assessment areas. The most recent analytical assessments available were used for biological

154   data, except where substantial changes had occurred in the stock assessment and the time

155   series recently had been shortened. Recruitment was defined as the number of individuals at

156   the earliest ages recorded in the stock assessment and assigned to the year the recruits were

157   spawned (i.e. recruitment at age 2 in 2010 was taken as an indicator of recruitment at age 0 in

158   2008). We estimated the recruitment per spawning stock biomass unit (R/SSB), dividing

159   recruitment by SSB in the year the cohort was spawned. We used recruits per spawning stock

160   biomass rather than residuals from a stock-recruitment curve to ensure that the

161   autocorrelation effects of the competition or cannibalism, which seem necessary to explain

162   the curvature of most stock recruitment curves, were retained in the time series. The two last

163   years in the time series were removed to ensure that all recruitment estimates were supported

164   by more than 2 years of catch at age data. The age of recruitment used in stock assessments

165   differs across stocks, but usually corresponds to the age when the fish enter the fishery, which

166   often is after the majority of the natural mortality has acted (ICES 2017a). Substantial

167   periodicities in recruitment should however be retained until the entry of the cohort to the

168   fishery and hence the differences in recruitment age used are not expected to preclude the

7

169   analyses, although they may introduce some variability, which could reduce our ability to

170   identify common trends.

171   Weight at age was derived from the observed mean weight at age in the stock, where this was

172   available, otherwise weight at age in the catch was used (see table 2 for sources). Average

173   weight at age 4 was used as a proxy for stock specific individual growth rate, as data for this

174   age was given in all assessments (Brander 1995; Mantzouni and MacKenzie 2010). Early

175   parts of the time series for some stocks used constant weight at age, and these were removed

176   prior to analysis. Annual growth anomalies were derived as the difference between the

177   observed and the average weight of the age group divided by the standard deviation of the

178   weights in the time series for the particular age group. From these age-specific anomalies, the

179   annual growth anomaly was estimated as the average of anomalies of all age groups except

180   the youngest and two oldest to account for the lower certainty in these poorly sampled age

181   groups in line with Clausen et al. (2018). The exclusion of the second oldest age group

182   ensured that all stocks exhibited consistently increasing weight with age. As cod generally

183   spawn in winter, the annual anomalies were used as indices of growth and growth anomalies

184   in a given year were analysed for their effect on recruitment success in the following year.

185   Age at 50% maturity was estimated by linear interpolation between the age with the highest

186   average proportion mature <50% and the age with the lowest proportion mature ≥50%.

187

Analyses

189   Long term effects of e.g. the level of SSB and regime shifts were removed by de-trending the

190   time series of ln(R/SSB). The detrending was performed by fitting a polynomial to the time

191   series and conducting all analyses of autocorrelation and periodicity on the residuals. The

192   order of the polynomial was determined by the length of the time series, restricting the

193   number of parameters in the polynomial to one per 10 year of data (i.e. a stock with 45 years

8

194   of data was de-trended using a 3rd degree polynomial). The polynomials were reduced by

195   removing the highest order terms that were not significant at the 5% level. These polynomials

196   retained decadal and shorter periodicities in data and avoided the loss of years in both ends of

197   the time series as would be the case if using a moving average or smoothing functions for de-

198   trending. Examples of the resulting de-trended series of recruitment success are shown in Fig.

199   3.

200   The effect of temperature and weight at age on recruitment success was estimated by simple

201   regression as well as by testing the effect of temperature and weight at age as a linear effect

202   together with the polynomial used to de-trend recruitment success. Both variables were

203   included in the same model.

204

Periodicity in recruitment success

206   All of the time series were tested to determine if they deviated significantly from white noise

207   (Bartlett's test). To determine the wavelengths of cycles in recruitment success, we estimated

208   the dominant wavelength in the data using periodograms (Madsen 2007). Periodograms were

209   estimated from the de-trended recruitment series smoothed by a Quadratic Spectral kernel

210   (Andrews 1991). Preliminary investigations showed that the results were not particularly

211   sensitive to the choice of smoother. Periodograms integrate information from all lags in one

212   measure and were used to derive the dominant wavelength. Autocorrelations were estimated

213   and analysed for lags 1 to 10 to identify significant negative and positive autocorrelations,

214   taking the presence of other autocorrelations into account through backwards elimination. In

215   contrast to where autocorrelations are estimated within assessment models, this type of

216   external estimation is unbiased (Johnson et al. 2016).

217   Estimated dominant wavelengths of recruitment success were compared to the average

218   weight at age 4 and age at 50% maturity. All comparisons were performed using a

9

219 generalized linear model with normally distributed residuals (McCullaugh and Nelder 1989).

220 All statistical analyses were performed in SAS® version 9.4 for Windows® (SAS Institute

221 2017).

Results

No significant cyclic patterns in cod recruitment success (H1)

224 Thirteen of the 21 cod data series exhibited significant periodicity in recruitment success

225 (white noise probability less than 5%, Table 3) and 12 of the 13 stocks showed significant

226 autocorrelation at lag 1. The probability of achieving 13 significant periodicities in 21 stocks

227 by type 2 error when each periodicity has a 5% risk of type 2 error is <0.0001 (estimated

228 from the binomial distribution). The length of the time series had a significant impact on the

229 probability of rejecting the hypothesis of white noise: 4 of the 5 stocks with more than 50

230 years of data showed significant periodicity whereas only 6 of the 10 stocks with less than 40

231 years of data showed significant periodicity (P=0.0061 of the probability being the same in

232 the two cases), in line with the results of Johnson et al. (2016). Time series length had no

233 significant effect on estimated wavelength (P=0.2901). Of the eight stocks not showing

234 significant differences from white noise, one showed significant autocorrelation at one or

235 more lags. Hence, the available data did not support hypothesis 1 as a general explanation.

Recruitment success of cod is linked to climate (H2)

237 Recruitment success was significantly related to temperature in four of the 21 stocks prior to

238 detrending recruitment success: S. Gulf of St. Lawrence cod (effect of temperature=-0.46,

239 P=0.0050), Iceland cod (effect of temperature=0.37, P=0.0005), Irish Sea cod (effect of

240 temperature=-0.63, P=0.0001) and North Sea cod (effect of temperature=-0.66, P<0.0001).

241 After detrending, recruitment success of three stocks remained significantly related to

242 temperature: Irish Sea cod (effect of temperature=-0.63, P=0.0001, identical since this stock

10

243 showed no significant trend), Celtic Sea cod (effect of temperature=-0.82, P=0.0129) and

244 North Sea cod (effect of temperature=-0.41, P=0.0038). Plots of the relationships for each

245 stock are in the supplementary material (Fig. S1).

246 On average, the dominant wavelength for cod recruitment success was 5.2 years (95%

247 confidence intervals 3.7 to 6.6 years, Table 3). The confidence interval does not include 10

248 (decadal periodicity) and only two stocks show wavelengths above 10 years. If the

249 probability of obtaining wavelengths above and below 10 is equal (the mode of the

250 distribution is 10), the probability of achieving only 2 values above 10 is 0.0001. The

251 estimated wavelength differed by a factor 11 between stocks and hence, the data did not

252 support hypothesis 2 of a constant wavelength of recruitment success of around 10 years or

253 the hypothesis that a significant effect of temperature caused periodicity in recruitment

254 success.

255 ***Patterns in the somatic growth of adults generate patterns in recruitment success***

256 ***(H3)***

257 There was a significant correlation between weight anomaly and recruitment success in 6 of

258 the stocks (Fig. S2 in the supplementary material). However, three of these correlations were

259 negative and hence not in the expected direction. When analysing the effect of the weight

260 anomaly on the detrended recruitment success, the significant effect of weight anomaly was

261 retained in three of these stocks and two additional stock exhibited a significant effect of

262 weight anomaly. Three of these five effects were significantly negative. Hence, only two of

263 the 21 stocks (N Gulf of St. Lawrence and N Newfoundland) showed a consistent positive

264 effect of weight anomaly, a level not significantly different from that expected by type 2 error

265 alone (P=0.0849). Hypothesis 3 was thus not supported by the available data.

266

11

267 ***The link between recruitment and the subsequent SSB causes negative***

268 ***autocorrelations in recruitment success (H4)***

269 The dominant wavelength of recruitment success was not significantly related to age at 50%

270 maturity (P=0.1196, Fig. 4a). Hence, hypothesis 4 was not supported by the available data.

271 ***Relationship between average weight at age and recruitment periodicity (H5, H6***

272 ***and H7)***

273 Weight at age 4 was significantly linearly related to the dominant wavelength of recruitment

274 success (P=0.0068, correlation=-0.57, corresponding to an r^2 of 0.33) and a power

275 relationship between weight at age 4 and wavelength explained slightly more (39%) of the

276 total variation (r^2=0.39, P=0.0041, Fig. 4b). This is consistent with hypotheses 5 to 7. Of the

277 21 stocks, 16 showed positive autocorrelations at lag 1 consistent with hypothesis 5 whereas

278 5 showed negative autocorrelations at lag 1 (Fig. 5). Significant autocorrelation at lag 1 was

279 found in 10 out of the 21 stocks, and this autocorrelation was significantly correlated to

280 weight at age 4 (P= 0.0453, Fig. 4c). The relationship was even stronger when using an

281 exponential relationship (P=0.0025). In the autoregressive models, 10 of the 11 significant

282 effects at lag 1 were positive consistent with hypothesis 5, whereas 12 of the 14 effects

283 significant at lags greater than 1 were negative consistent with hypothesis 7 (Table 4). Hence,

284 positive effects were most likely at lag 1 and negative effects most likely at longer lags,

285 consistent with the fact that cannibalism is most prevalent in larger individuals while

286 apparent mutualism should act only at short lags. Of the 13 stocks that showed significant

287 autocorrelative effects, 12 had negative effects at one or more lags, in 11 of the cases

288 counteracting an initial positive effect at lag 1 (Fig. 5). Hence, the data do not support either

289 of the hypotheses 5 and 7 as being the only explanation, but instead point to a combination of

290 the hypotheses. Hypothesis 6 received comparatively less support as only one stock showed

291 significant negative autocorrelation at lag 1.

12

292

Discussion

294 Autocorrelation and cyclic patterns in recruitment success occurred in just above half of the

295 stocks. Slow-growing cod stocks tended to exhibit periodicities consistent with decadal

296 cycles while fast-growing cod stocks showed more rapid fluctuations. Both types exhibited

297 negative autocorrelations at one or more lags greater than lag 1. Of the seven hypotheses

298 suggested in the introduction, five are unlikely to determine recruitment patterns for more

299 than a few of the cod stocks in the present analyses. While dominant wavelengths of slow-

300 growing stocks (weight at age 4 less than 1.5 kg) seemed to correspond to the decadal

301 periodicity expected from climatic changes alone, fast-growing stocks (weight at age 4

302 greater than 1.5 kg) had significantly shorter wavelengths. Further, no consistent relationship

303 with local temperature was found, though three of the four stocks with the fastest growth

304 showed a significant decrease in recruitment success with increasing temperature. Hence, the

305 cycles in recruitment success of cod were not consistently linked to local or panregional

306 climatic changes (hypothesis 2). There was no significant correlation between recruitment

307 success and growth, indicating that patterns in somatic growth did not cause cyclic patterns in

308 offspring quality (hypothesis 3). Further, the lack of a clear link between age at 50% maturity

309 and recruitment lags meant that the hypothesis that the link between recruitment and the

310 subsequent SSB causes negative autocorrelations in recruitment success (hypothesis 4,

311 Gilbert 1997) could also be rejected. Finally, only one of the 21 stocks exhibited significant

312 negative autocorrelation at lag 1, indicating that the hypothesis that a large year class

313 decreases the growth and thereby increases the mortality of the subsequent year class

314 (hypothesis 6, inter-cohort competition) could also be rejected.

315 Our analyses estimated shorter wavelengths than those of Spencer and Collie (1997) and

316 Szuwalski et al (2015), who reported average wavelengths of 24 and 21 years, respectively.

13

317   However, their methods are expected to result in greater wavelengths in virtually all cases

318   due to differences in methods. Firstly, Spencer and Collie investigated the strongest

319   autocorrelation in total biomass (equivalent to using the lag with the highest value in table 4).

320   Total biomass integrates several recruitment events and is likely to develop slowly between

321   years except in short-lived species (Spencer and Collie 1997). Szuwalski et al. used

322   recruitment directly to determine regime length. For longer lived stocks with a close

323   relationship between recruitment and SSB in the year of spawning, recruitment should show

324   positive autocorrelation as SSB will not vary greatly from one year to the next. Further,

325   Spencer and Collie (1997) examined periodicity after linear detrending, and this removes less

326   of the long term temporal changes than the detrending method used here, leading to greater

327   expected wavelengths.

328   Interestingly, our results support the theory of cohort resonance (Bjørnstad et al. 2004;

329   Botsford et al. 2014). As this theory is based on the assumption that recruitment success is

330   constant, it should not result in changes in recruitment success over time, though the absolute

331   recruitment (not recruitment success) should show wavelengths consistent with age at 50%

332   maturity.

333   While the present analyses could not confirm hypotheses 1-4 and 6 as determining cyclic

334   recruitment patterns across all cod stocks examined, it is possible that the factors determining

335   cyclic patterns vary between stocks. For some stocks, no significant cycles existed, while for

336   others, significant cycles clearly differed from a decadal pattern. Five stocks exhibited

337   significant cycles with wavelengths compatible with climate induced decadal fluctuations

338   (wavelengths greater than 8: cod in the eastern Baltic, southern Gulf of St. Lawrence,

339   Flemish Cap, Grand banks and Eastern Scotian Shelf). Of these stocks, one exhibits negative

340   autocorrelative effect at lag 2 (eastern Baltic cod), which may indicate that recruitment in this

341   stock is controlled by combined effects of climate and cannibalism. However, this particular

14

342   stock showed no significant relationship between temperature and recruitment success, and

343   hence, other climatic factors would have to be responsible for the periodicity.

344   Positive autocorrelations at lag 1 and a decreasing wavelength with increasing weight at age

345   are consistent with large year classes diluting the predation mortality of year classes of a

346   similar weight in slow growing stocks (Table 1). All of the ten stocks, which had a weight of

347   less than 1.5 kg at age 4 showed positive autocorrelations at lag 1. Positive autocorrelations

348   may also be introduced by age reading errors because age reading bias is likely to distribute

349   individuals from strong year classes across adjacent year classes. Comparisons of Norwegian

350   and Russian cod age determinations for Northeast Arctic cod over the time period from 1992

351   to 2007 revealed disagreement in 23% of the determinations, but found more disagreement in

352   cold years than in warm years where cod growth was higher (Yaragina et al. 2011),

353   confirming that slow growing individuals are more prone to age reading bias. This effect may

354   thus contribute to the positive short term autocorrelation observed in slow growing stocks.

355   It is not possible with the current data to determine whether the positive autocorrelation of

356   slow growing stocks are a result of NAO effects or of slow growing cod exhibiting apparent

357   mutualism (hypotheses 2 and 5). Determining which of these causes are of greatest

358   importance for slow growing stocks will require a collation of information about the

359   mortality and growth in different life stages. Other local deviations from the general patterns

360   obviously also occur (for example, Iceland cod showed no significant periodicity in

361   recruitment success). Among the 21 cod stocks, there were 12 stocks with significant

362   negative autocorrelative effects at one or more lags, a pattern consistent with cannibalism

363   (hypotheses 7). However, determining whether the level of cannibalism is sufficient to induce

364   cycles of this magnitude requires modelling based on specific knowledge of diet composition,

365   food consumption and abundance of juvenile and cannibalistic fish. Whereas abundance of

366   fish is often part of standard survey designs, the investigation of consumption and diet

15

367   composition unfortunately is not, and hence the majority of stocks will not have this type of

368   information readily available.

369   The vast majority of the gadoid species include fish among the top three of reported prey

370   items. About 2/3 of all gadoid species are large enough to be potential cannibals after the

371   larval stage and another 1/6 are large enough to be potential cannibals at two trophic levels:

372   medium size fish on newly settled fish and large fish on medium sized fish (e.g. Pacific cod,

373   Atlantic cod and pollock). This means that cannibalism is a potential source of periodicity in

374   most gadoids, and as a result, simply assuming a positive autocorrelation as a prior for all

375   stocks is unlikely to provide an appropriate description (Thorson et al. 2014). Further,

376   including autocorrelation only at lag 1 may provide overly positive expectations to

377   recruitment as the initial positive autocorrelation was generally followed by subsequent

378   negative autocorrelations at greater lags. If the cycles are caused by cannibalistic effects, their

379   persistence at low stock sizes depends on the persistence of the spatial overlap of juveniles

380   and adults, and as a consequence cannibalistic cycles may occur only at high stock sizes.

381   Introducing autocorrelation in recruitment in assessment at low stock size may then introduce

382   an undesirable bias.

383   The cause and persistence of the recruitment cycles carry serious implications for

384   management. Most short-term forecasts of fishing opportunities assume that the incoming

385   yearclass will be equal to the geometric mean over a long period. However, when a year of

386   poor recruitment success is likely to be followed by several years of low recruitment success

387   in cold water stocks, and spawning stock biomass tends to change slowly, a poor recruitment

388   is likely to be followed by a similar below average recruitment. Assuming that the two are

389   uncorrelated is likely to result in overoptimistic predictions of recovery rates and as a result,

390   excessive levels of fishing after years of low recruitment success. Including autocorrelation in

391   recruitment predictions can potentially improve estimates of short-term stock development

16

392   and hence increase the quality of catch advice (Johnson et al. 2016). Autocorrelation in

393   recruitment success can make the stock either more resilient or more sensitive to fishing

394   depending on the direction it takes, an important factor to include in management strategy

395   evaluations (Punt et al. 2016) and the estimation of reference points such as the fishing

396   mortality expected to provide the maximum sustainable yield. Based on our analyses, we

397   recommend that autocorrelation and cyclic patterns are considered and if found to be

398   significant, incorporated in both short term and long term projections of recruitment.

399

Acknowledgements

References

406   Andrews, D. W. 1991. Heteroskedasticity and autocorrelation consistent covariance matrix

407   estimation. Econometrica: Journal of the Econometric Society, 817-858.

408   Beaugrand, G., Brander, K. M., Lindley, J. A., Souissi, S., & Reid, P. C. 2003. Plankton

409   effect on cod recruitment in the North Sea. Nature **426**(6967): 661.

410   Bjørnstad, O. N., Fromentin, J. M., Stenseth, N. C., and Gjøsæter, J. 1999. Cycles and trends

411   in cod populations. P. Natl. Acad. Sci. **96**(9): 5066-5071.

412   Bjørnstad, O. N., Nisbet, R. M., and Fromentin, J. M. 2004. Trends and cohort resonant

413   effects in age-structured populations. J. Anim. Ecol. **73**: 1157-1167.

414 Bogstad, B., Lilly, G. R., Mehl, S., Palsson, O. K., and Stefánsson, G. 1994. Cannibalism and

415 year-class strength in Atlantic cod (*Gadus morhua* L.) in Arcto-boreal ecosystems (Barents

416 Sea, Iceland, and eastern Newfoundland). ICES mar. Sci. Symp. **198**: 576-599.

417 Botsford, L.W., Holland, M.D., Field, J.C., and Hastings, A. 2014. Cohort resonance: a

418 significant component of fluctuations in recruitment, egg production, and catch of fished

419 populations. ICES J. Mar. Sci. **71**: 2158–2170.

420 Bradford, M. J. 1991. Effects of ageing errors on recruitment time series estimated from

421 sequential population analysis. Can. J. Fish. Aquat. Sci. **48**(4): 555-558.

422 Brander, K. 1995. The effect of temperature on growth of Atlantic cod (*Gadus morhua* L.).

423 ICES J. Mar. Sci. **52**: 1-10.

424 Brassard, C., Gauthier, J., Schwab, P., Le Bris, A., Way, M., and Collier, F. 2016. The Status

425 of the Northern Gulf of St. Lawrence (3Pn, 4RS) Cod Stock (*Gadus morhua*) in 2014. DFO

426 Can. Sci. Advis. Sec. Res. Doc 2016/010. xi + 120 p.

427 Brattey, J., Cadigan, N., Dwyer, K. S., Healey, B. P., Ings, D. W., Lee, E. M., Maddock

428 Parsons, D., Morgan, M. J., Regular, P., and Rideout, R. M. 2018. Assessment of the

429 Northern Cod (*Gadus morhua*) stock in NAFO Divisions 2J3KL in 2016. DFO Can. Sci.

430 Advis. Sec. Res. Doc. 2018/018. v + 107p

431 Casini, M., Hjelm, J., Molinero, J. C., Lövgren, J., Cardinale, M., Bartolino, V., Belgrano, A.

432 and Kornilovs, G. 2009. Trophic cascades promote threshold-like shifts in pelagic marine

433 ecosystems. P. Natl. Acad. Sci. **106**(1): 197-202.

434 Clark, D. S., and Emberley, J. 2009. Assessment of Cod in Division 4X in 2008. DFO, Can.

435 Sci. Advis. Sec. Res. Doc. 2009/018. vi + 101 p.

436 Clausen, L. W., Rindorf, A., Van Deurs, M., Dickey-Collas, M., and Hintzen, N. T. 2018.

437 Shifts in North Sea forage fish productivity and potential fisheries yield. Journal of Applied

438 Ecology, 55(3), 1092-1101.

18

439 DFO. 2016. Assessment of Atlantic cod (*Gadus morhua*) in the southern Gulf of St.

440 Lawrence (NAFO Div. 4T-4Vn (Nov. – April)) to 2014. DFO Can. Sci. Advis. Sec. Sci.

441 Advis. Rep. 2015/061.

442 Drinkwater, K. F., Miles, M., Medhaug, I., Otterå, O. H., Kristiansen, T., Sundby, S., and

443 Gao, Y. 2014. The Atlantic Multidecadal Oscillation: Its manifestations and impacts with

444 special emphasis on the Atlantic region north of 60 N. Journal of Marine Systems, 133, 117-

445 130.

446 Fogarty, M. J., Myers, R. A., and Bowen, K. G. 2001. Recruitment of cod and haddock in the

447 North Atlantic: a comparative analysis. ICES J. Mar. Sci. **58**(5): 952-961.

448 Gilbert, D. J. 1997. Towards a new recruitment paradigm for fish stocks. Can. J. Fish. Aquat.

449 Sci. **54**(4): 969-977.

450 González-Troncoso, D. 2015. Assessment of the Cod Stock in NAFO Division 3M. NAFO

451 SCR Doc. 15/033.

452 Holt, R. D., 1977. Predation, apparent competition, and the structure of prey communities.

453 Theor. Popul. Biol. **12**(2): 197-229.

454 Hurrell, J. W. 1995. Decadal trends in the North Atlantic oscillation. Science **269**: 676-679.

455 ICES 2011. Report of the Working Group on Multispecies Assessment Methods (WGSAM),

456 10–14 October 2011, Woods Hole, USA. ICES CM 2011/SSGSUE:10. Available from

457 www.ices.dk.

458 ICES. 2013a. Report of the Baltic Fisheries Assessment Working Group. ICES CM

459 2011/ACOM:10. 843 pp. Available from www.ices.dk.

460 ICES. 2013b. Report of the Arctic Fisheries Working Group. ICES CM 2013/ACOM:05.

461 733pp. Available from www.ices.dk.

462 ICES 2017a. Interim Report of the Working Group on Multispecies Assessment Methods

463 (WGSAM). ICES CM 2017/SSGEPI:20 Available from www.ices.dk.

464   ICES 2017b. Report of the Arctic Fisheries Working Group (AFWG). ICES CM

465   2017/ACOM:06. Available from www.ices.dk.

466   ICES 2017c. Report of the Working Group on Assessment of Demersal Stocks in the North

467   Sea and Skagerrak (WGNSSK). ICES CM 2017/ACOM:21. Available from www.ices.dk.

468   ICES 2017d. Report of the North Western Working Group (NWWG) ICES CM

469   2017/ACOM:08. Available from www.ices.dk.

470   ICES 2017e. Report of the Working Group on Celtic Seas Ecoregion (WGCSE) ICES CM

471   2017/ACOM:13. Available from www.ices.dk.

472   Johnson, K. F., Councill, E., Thorson, J. T., Brooks, E., Methot, R. D., and Punt, A. E. 2016.

473   Can autocorrelated recruitment be estimated using integrated assessment models and how

474   does it affect population forecasts? Fish. Res. **183**: 222-232.

475   Kikkert, A. H. 1993. Analysis of the cod samples collected in the North Sea during the 1991

476   international stomach sampling project. ICES CM 1993/G:13. Available from www.ices.dk.

477   Kjesbu, O.S., Bogstad, B., Devine, J.A., Gjøsæter, H., Howell, D., Ingvaldsen, R.B., Nash,

478   R.D.M., and Skjæraasen, J.E. 2014. Synergies between climate and management for Atlantic

479   cod fisheries at high latitudes. P. Natl. Acad. Sci. **111**(9): 3478-3483.

480   DOI:10.1073/pnas.1316342111

481   Madsen, H. 2007. Time series analysis. Chapman & Hall, pp. 400.

482   Mantzouni, I., and MacKenzie, B. R. 2010. Productivity responses of a widespread marine

483   piscivore, *Gadus morhua*, to oceanic thermal extremes and trends. P. R. Soc. Lond. B. Bio.

484   **277**(1689): 1867-1874.

485   McCullaugh, P., and Nelder, J.A. 1989. Generalized linear models. Monogr. Statist. Appl.

486   Probab. No. 37.

487 Mohn, R.K., and Rowe, S. 2012. Recovery Potential Assessment for the Laurentian South

488 Unit of Atlantic Cod (*Gadus morhua*): The Eastern Scotian Shelf Cod Stock (NAFO Div.

489 4VsW). DFO Can. Sci. Advis. Sec. Res. Doc. 2011/138: viii + 71p.

490 Morgan, M. J., and G. R. Lilly. 2006. The impact of condition on reproduction in Flemish

491 Cap cod. J. Northw. Atl. Fish. Sci. **37**: 81–86. doi: 10.2960/J.v37.m560

492 NCAR, 2018. International Comprehensive Ocean-Atmosphere Data Set (ICOADS) Release

493 3, Monthly Summaries. Research Data Archive at the National Center for Atmospheric

494 Research, Computational and Information Systems Laboratory.

495 https://doi.org/10.5065/D6V40SFD. Accessed Oct. 11 2018.

496 Northeast Fisheries Science Center. 2013. 55th Northeast Regional Stock Assessment

497 Workshop (55th SAW) Assessment Report. US Dept Commer, Northeast Fish Sci Cent Ref

498 Doc. 13-11; 845 p. Available from: National Marine Fisheries Service, 166 Water Street,

499 Woods Hole, MA 02543-1026, or online at http://www.nefsc.noaa.gov/nefsc/publications/

500 Punt, A. E., Butterworth, D. S., de Moor, C. L., De Oliveira, J. A., and Haddon, M. 2016.

501 Management strategy evaluation: best practices. Fish Fish. **17**: 303-334.

502 Rideout, R. M., Ings, D.W. and Brattey, J. 2017. An Assessment of the Cod Stock in NAFO

503 Divisions 3NO. NAFO SCR Doc. No. 17/042

504 Rideout, R.M., Ings, D.W., Healey, B.P., Brattey, J., Morgan, M.J., Maddock Parsons, D.,

505 Koen-Alonso, M., and Vigneau, J. 2016. Assessing the status of the cod (*Gadus morhua*)

506 stock in NAFO Subdivision 3Ps in 2015. DFO Can. Sci. Advis. Sec. Res. Doc. 2016/048 vi +

507 90p

508 Ricard, D., Zimmermann, F., and Heino, M. 2016. Are negative intra-specific interactions

509 important for recruitment dynamics? A case study of Atlantic fish stocks. Mar. Ecol. Progr.

510 Ser. **547**: 211-217.

511 SAS Institute Inc. 2017. SAS version 9.4 [computer program]. SAS Institute Inc., Cary,

512 North Carolina.

513 Skjæraasen, J. E., Nash, R. D., Korsbrekke, K., Fonn, M., Nilsen, T., Kennedy, J., Nedreaas,

514 K. H., Thorsen, A., Witthames, P. R., Geffen, A. J., Høie, H. and Kjesbu, O. S. 2012.

515 Frequent skipped spawning in the world's largest cod population. P. Natl. Acad. Sci. **109**(23):

516 8995-8999. doi.org/10.1073/pnas.1200223109

517 Spencer, P. D., and Collie, J. S. 1997. Patterns of population variability in marine fish stocks.

518 Fish. Oceanogr., **6**: 188-204.

519 Sundby, S. 2000. Recruitment of Atlantic cod stocks in relation to temperature and advectlon

520 of copepod populations. Sarsia, **85:** 277-298.

521 Szuwalski, C.S., Vert-Pre, K.A., Punt, A.E., Branch, T.A. and Hilborn, R., 2015. Examining

522 common assumptions about recruitment: a meta-analysis of recruitment dynamics for

523 worldwide marine fisheries. Fish Fish., **16**(4): 633-648.

524 Thorson, J. T., Jensen, O. P. and Zipkin, E. F. 2014. How variable is recruitment for

525 exploited marine fishes? A hierarchical model for testing life history theory. Can. J. Fish.

526 Aquat. Sci. **71**(7): 973-983.

527 Yaragina, N.A., Høie, H., Koloskova, V.P., Mjanger, H., Nedreaas, K.H., Senneset, H.,

528 Zuykova, N. V. and Ågotnes, P. 2011. Precision of the Northeast Arctic cod age

529 determination under variable environmental and information conditions. Marine Biology

530 Research, 7(6), 599-607.

22

531 **Tables**

532 Table 1. Summary of expected autocorrelations and cyclic patterns under each of the

533 examined hypotheses.

H	Description	Positive auto-correlation at lag 1?	Negative auto-correlations?	Cycling patterns?
1	There are no significant cyclic patterns in cod recruitment success	No	No	White noise
2	Recruitment of cod is linked to annual or decadal climatic variation	Annual effect: None after accounting for effect of temperature Decadal effect: Yes	Annual effect: None after accounting for effect of temperature Decadal effect: No	Annual effect: None after accounting for effect of temperature Decadal effect: Decadal wavelength In all stocks
3	Cyclic patterns in somatic growth causes cyclic patterns in offspring quality	None when accounting for effect of weight at age in analyses	None when accounting for effect of weight at age in analyses	Residuals from the weight-recruitment success relationship show no cyclic patterns
4	The link between recruitment and the subsequent SSB causes negative autocorrelations in recruitment success at some lags.	No	At the age corresponding to age at 50% maturity	Wavelength of 2*age at 50% maturity
5	A large year class dilutes the predation mortality of year classes of a similar weight causing positive	Yes, can occur for slow growing stocks at more	No	Significant cyclic patterns for slow growing stocks but

23

	autocorrelation in slow growing stocks	lags than fast growing stocks		not for fast growing stocks
6	A large year class reduces the resources available for the following year class causing negative autocorrelation in slow growing stocks	No	Yes	Wavelength decreases with increasing weight at a specific age
7	Cycles are introduced by cannibalism	No[*]	Yes	Wavelength decreases with increasing weight at a specific age

534   [*]Note that this hypothesis may co-occur with hypothesis 5, in which case positive correlations

535   will occur.

536

537

24

538 Table 2.

539 Summary of population data used.

Stock	Area	Years			Reference
cod-4tvn	S Gulf of St. Lawrence (4TVn)	1950	-	2014	DFO 2016
cod-3pn4rs	N Gulf of St. Lawrence (3Pn4RS)	1974	-	2015	Brassard et al. 2016
cod-2j3kl	N Newfoundland (2J3KL)	1983	-	2015	Brattey et al. 2018
cod-arct	NE Arctic (I, II)	1946	-	2016	ICES 2017b
cod-3no	Grand bank (3NO)	1959	-	2017	Rideout et al. 2017
cod-3ps	S Newfoundland (3Ps)	1983	-	2016	Rideout et al. 2016
cod-2532	E Baltic (IIId -east)	1966	-	2012	ICES 2013a
cod-4vsw	E Scotian Shelf (4VsW)	1958	-	2008	Mohn and Rowe 2012
cod-3m	Flemish Cap (3M)	1972	-	2014	González-Troncoso 2015
cod-ice	Iceland (Va)	1955	-	2016	ICES 2017d
cod-coas	Norwegian Coastal (IIa)	1984	-	2004	ICES 2013b
cod-2224	W Baltic (IIId -west)	1970	-	2005	ICES 2013a
cod-4x	W Scotian Shelf (4X)	1980	-	2007	Clark and Emberley 2009
cod-gom	Gulf of Maine (5Y)	1982	-	2010	Northeast Fisheries Science Center 2013
cod-kat	Kattegat (IIIa -east)	1971	-	2010	ICES 2013a
cod-farp	Faroe Plateau (Vb)	1961	-	2012	ICES 2017d
cod-gb	Georges Bank (5Z)	1978	-	2010	Northeast Fisheries Science Center 2013
cod-347d[*]	North Sea (IIIa-IV-VIId)	1974	-	2016	ICES 2017c
cod-6a	W Scotland (VIa)	1981	-	2016	ICES 2017e
cod-7a	Irish Sea (VIIa)	1968	-	2016	ICES 2017e
cod-7e-k	Celtic Sea (VIIe-k)	1971	-	2016	ICES 2017e

540 [*]Only the years from 1974 onwards were used as the natural mortalities for the years 1963-

541 1973 are only indicative (ICES 2011).

25

542 Table 3. Summary of results. White noise test, autocorrelation at lag 1 (without correcting for effects of other lags), estimated dominant

543 wavelength and effects of weight anomaly and temperature on detrended recruitment success. Effects are estimated in models including only one

544 of the variables weight anomaly and temperature at a time as no stock showed significant effects of both variables in combined analyses. Bold

545 indicates significant effects at the 5% level.

| Stock | Area | Weight at age 4 | Recruitment success | | | Weight anomaly | | Temperature | |
			Autocorrelation (lag 1)	P(white noise)	Wavelength	P	Effect	P	effect
cod-4tvn	S Gulf of St. Lawrence (4TVn)	0.39	**0.69 (<0.0001)**	**<0.0001**	**9.5**	0.3716	0.10	0.5462	-0.10
cod-3pn4rs	N Gulf of St. Lawrence (3Pn4RS)	0.40	**0.47 (0.0351)**	**0.0057**	**4.9**	**0.0158**	**0.04**	0.6449	-0.05
cod-2j3kl	N Newfoundland (2J3KL)	0.53	**0.80 (0.0006)**	**<0.0001**	**7.2**	**<0.0001**	**2.30**	0.6659	0.13
cod-arct	NE Arctic (I, II)	0.68	**0.40 (0.0007)**	**<0.0001**	**3.3**	**0.0003**	**-0.38**	0.1438	0.29
cod-3no	Grand bank (3NO)	0.68	**0.60 (<0.0001)**	**<0.0001**	**9.2**	0.7158	0.71	0.9185	0.02
cod-3ps	S Newfoundland (3Ps)	0.76	**0.48 (0.0116)**	**0.0274**	**4.7**	0.4401	-0.20	0.8298	0.03
cod-2532	E Baltic (IIId -east)	0.95	**0.65 (<0.0001)**	**<0.0001**	**10.7**	0.3805	0.11	0.8060	0.01
cod-4vsw	E Scotian Shelf (4VsW)	1.02	**0.59 (<0.0001)**	**0.0003**	**12.2**	0.3214	0.15	0.9167	0.01

26

cod-3m	Flemish Cap (3M)	1.34	**0.42 (0.0039)**	**0.0065**	**10.0**	0.1100	0.76	0.6736	0.13
cod-ice	Iceland (Va)	1.43	0.21 (0.0951)	0.1106	4.3	**0.0012**	**-0.33**	0.3558	-0.13
cod-2224	W Baltic (IIId -west)	1.60	-0.15 (0.4377)	0.5537	1.5	0.1435	0.33	0.1412	0.17
cod-coas	Norwegian Coastal (IIa)	1.60	**0.59 (0.0024)**	**0.0044**	**6.2**	0.4546	-0.08	0.6119	-0.10
cod-4x	W Scotian Shelf (4X)	1.82	-0.33 (0.1002)	0.3311	1.2	0.5975	-0.31	0.3313	0.12
cod-gom	Gulf of Maine (5Y)	2.03	0.09 (0.6116)	0.1827	4.5	0.9416	0.02	0.9093	-0.02
cod-kat	Kattegat (IIIa -east)	2.06	**-0.47 (0.0024)**	**0.0203**	**1.2**	0.6866	-0.05	0.3685	0.09
cod-farp	Faroe Plateau (Vb)	2.51	**0.51 (<0.0001)**	**<0.0001**	**4.0**	**<0.0001**	**-1.03**	0.8387	0.06
cod-gb	Georges Bank (5Z)	2.73	0.10 (0.4711)	**0.0317**	**5.2**	0.1167	-0.28	0.5029	-0.13
cod-347d[*]	North Sea (3a-4-7d)	3.98	-0.18 (0.2685)	0.2714	1.3[**]	0.4113	0.12	**0.0038**	**-0.41**
cod-6a	W Scotland (6a)	4.44	-0.13 (0.4223)	0.3242	1.3	0.0816	-0.26	0.8567	-0.05
cod-7a	Irish Sea (7a)	5.51	0.12 (0.4260)	0.2752	1.0[**]	0.1543	0.32	**0.0001**	**-0.63**
cod-7e-k	Celtic Sea (VIIe-k)	7.18	0.18 (0.2267)	0.2416	2.2[**]	0.9343	0.02	**0.0129**	**-0.82**

546   [*]Only the years from 1974 onwards were used as the natural mortalities for the years 1963-1973 are only indicative (ICES 2011).

547   [**]Based on residuals from the relationship with annual temperature.

548

27

549 Table 4. Parameters in reduced autoregressive model. All parameters are given so negative parameters correspond to negative autocorrelation

550 and positive parameters to positive autocorrelation.

Stock	Area	Lag 1	Lag 2	Lag 3	Lag 4	Lag 5	Lag 6	Lag 7	Lag 8	Lag 9	Lag 10
cod-4tvn	S Gulf of St. Lawrence (4TVn)	0.64								-0.20	
cod-3pn4rs	N Gulf of St. Lawrence (3Pn4RS)	0.43			*-0.39*						
cod-2j3kl	N Newfoundland (2J3KL)	1.23	*-0.54*								
cod-arct	NE Arctic (I, II)	0.34		*-0.51*				*-0.22*			
cod-3no	Grand bank (3NO)	0.62					*-0.43*	0.29			
cod-3ps	S Newfoundland (3Ps)										
cod-2532	E Baltic (IIId -east)	0.93	*-0.45*								
cod-4vsw	E Scotian Shelf (4VsW)	0.44								*-0.44*	
cod-3m	Flemish Cap (3M)	0.37									*-0.39*
cod-ice	Iceland (Va)				*-0.28*						
cod-2224	W Baltic (IIId -west)										

28

code	region										
cod-coas	Norwegian Coastal (IIa)	0.52									
cod-4x	W Scotian Shelf (4X)										
cod-gom	Gulf of Maine (5Y)										
cod-kat	Kattegat (IIIa -east)	*-0.46*									
cod-farp	Faroe Plateau (Vb)	0.80	*-0.59*								
cod-gb	Georges Bank (5Z)		0.50		*-0.56*						
cod-347d	North Sea (IIIa-IV-VIId)										
cod-6a	W Scotland (VIa)										
cod-7a	Irish Sea (VIIa)										
cod-7e-k	Celtic Sea (VIIe-k)										
	Total number of significant parameters (positive/negative autocorrelative effects)	10/1	1/3	0/1	0/3	0/0	0/1	1/1	0/0	0/2	0/1

Captions

552 **Captions**

553 Fig. 1. Examples of time series showing both long term change and shorter term cycles. Panel

554 a shows two observed time series (solid and broken black), the long term trend (dotted grey)

555 estimated by different polynomial orders corresponding to 20 (linear) and 30 (quadratic) and

556 years of data fitted to the broken line time series and the true trend (dash-dot). Panel b shows

557 the detrended time series and the wavelength defined as the number of years between

558 successive peaks (arrows on top in panel b). Panel c shows the autocorrelation at different

559 lags of the two cycles, the short wavelength (solid line in panels a and b) is shown as filled

560 columns, the long wavelength (dashed line in panels a and b) as open columns.

561

562 Fig. 2. Examples of development of recruitment (solid line, left panel) and spawning stock

563 biomass (broken line, left panel), ln(R/SSSB) (middle panel) and autocorrelation (right panel)

564 under each hypothesis 1 and 4-7. Hypotheses 2 and 3 would result in significant effects of

565 temperature (2) or growth (3) on recruitment success, but accounting for these effects in the

566 detrending of the time series would lead to periodicities in detrended ln(R/SSSB) similar to

567 results for hypothesis 1. Hypotheses 1 and 4 are not significantly different from white noise

568 (P>0.6000), though hypothesis 4 shows significant autocorrelation at lag 5 (the age at

569 maturity). Hypotheses 5 to 7 are all significantly different from white noise (P=0.0007, 0.0144

570 and 0.0015, respectively).

571

572 Fig 3. Time series of recruitment (thousands, left panel, solid line), SSB (left panel, broken

573 line), recruitment success (middle panel, solid line is observation and broken line is polynomial

574 fit) and detrended recruitment success (right panel) of selected stocks. Year indicates the year

575 the cohort was spawned. Examples of low wavelength (North Sea, cod-347d, a, b and c),

30

576   intermediate wavelength (Iceland cod, cod-ice, d, e and f), high wavelength (Grand Banks cod,

577   cod-no, g, h and I and Northern Newfoundland cod, j, k and l).

578

579   Fig 4. Relationship between the dominant wavelength of recruitment success and age at 50%

580   maturity (a), weight at age 4 (b) and between autocorrelation at lag 1 and weight at age 4 (c).

581   Lines are regressions using all periodicities (linear for a, logarithmic for c and d). Filled

582   symbols denote significant periodicity and autocorrelations.

583

584   Fig. 5. Observed autocorrelations of stocks ordered according to increasing weight at age 4.

585   Colour of bars indicate weight at age 4: white <1.5 kg, grey 1.5-3 kg, black> 3 kg. Stars indicate

586   where lags are significant at the 5% level in a reduced autoregressive model with lags up to 10.

31

1 **Figures**
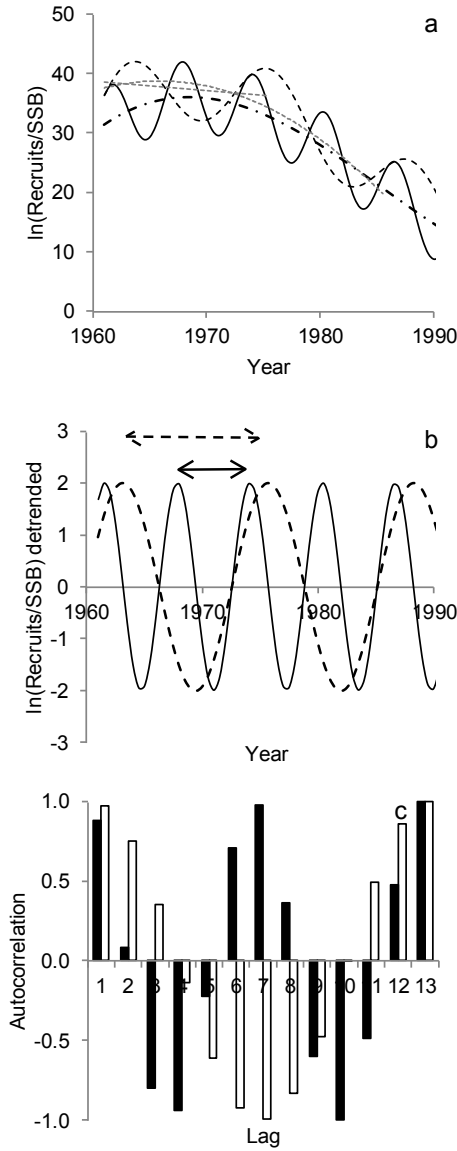
2

3   Fig. 1. Examples of time series showing both long term change and shorter term cycles. Panel a

4   shows two observed time series (solid and broken black), the long term trend (dotted grey)

5   estimated by different polynomial orders corresponding to 20 (linear) and 30 (quadratic) and years

6   of data fitted to the broken line time series and the true trend (dash-dot). Panel b shows the

1

7   detrended time series and the wavelength defined as the number of years between successive peaks

8   (arrows on top in panel b). Panel c shows the autocorrelation at different lags of the two cycles, the

9   short wavelength (solid line in panels a and b) is shown as filled columns, the long wavelength

10   (dashed line in panels a and b) as open columns.

11
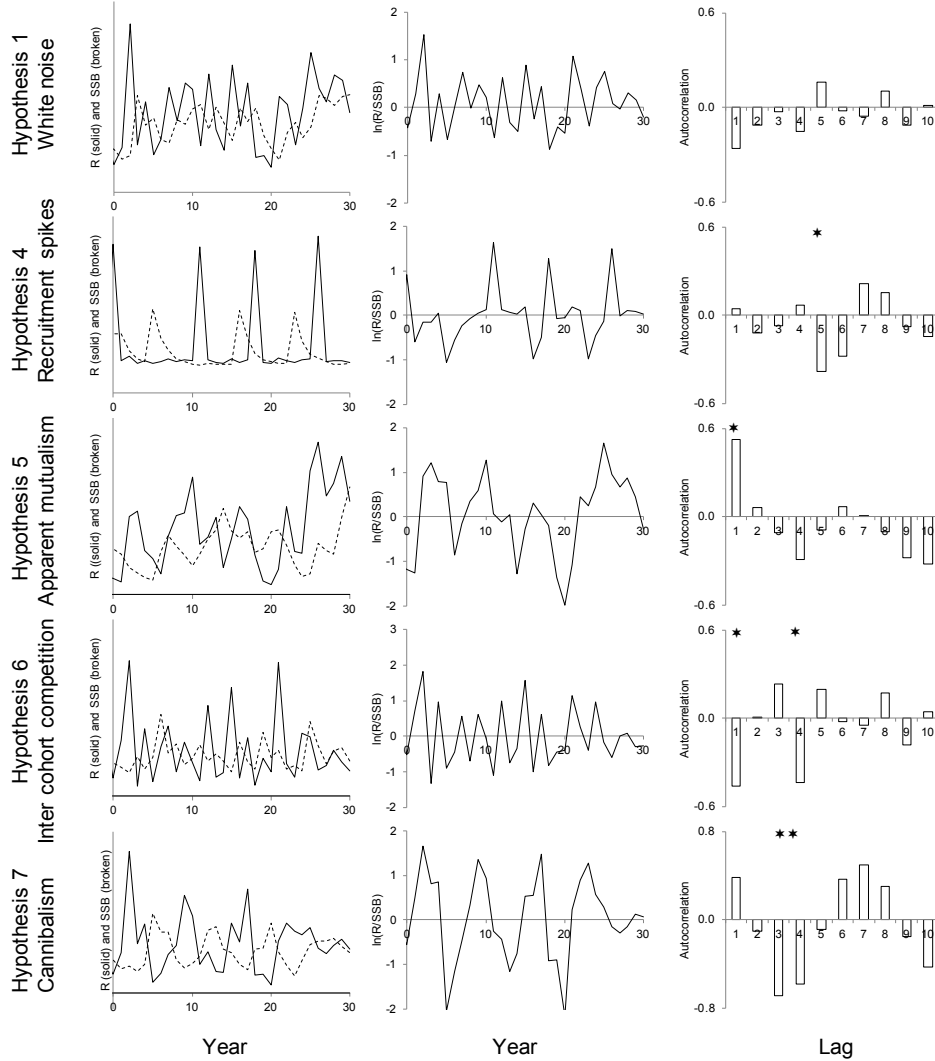
2

12

Fig. 2. Examples of development of recruitment (solid line, left panel) and spawning stock biomass

(broken line, left panel), ln(R/SSSB) (middle panel) and autocorrelation (right panel) under each

hypothesis 1 and 4-7. Hypotheses 2 and 3 would result in significant effects of temperature (2) or

growth (3) on recruitment success, but accounting for these effects in the detrending of the time series

would lead to periodicities in detrended ln(R/SSSB) similar to results for hypothesis 1. Hypotheses 1

and 4 are not significantly different from white noise (P>0.6000), though hypothesis 4 shows

3

19   significant autocorrelation at lag 5 (the age at maturity). Hypotheses 5 to 7 are all significantly different

20   from white noise (P=0.0007, 0.0144 and 0.0015, respectively).


21

22

Year
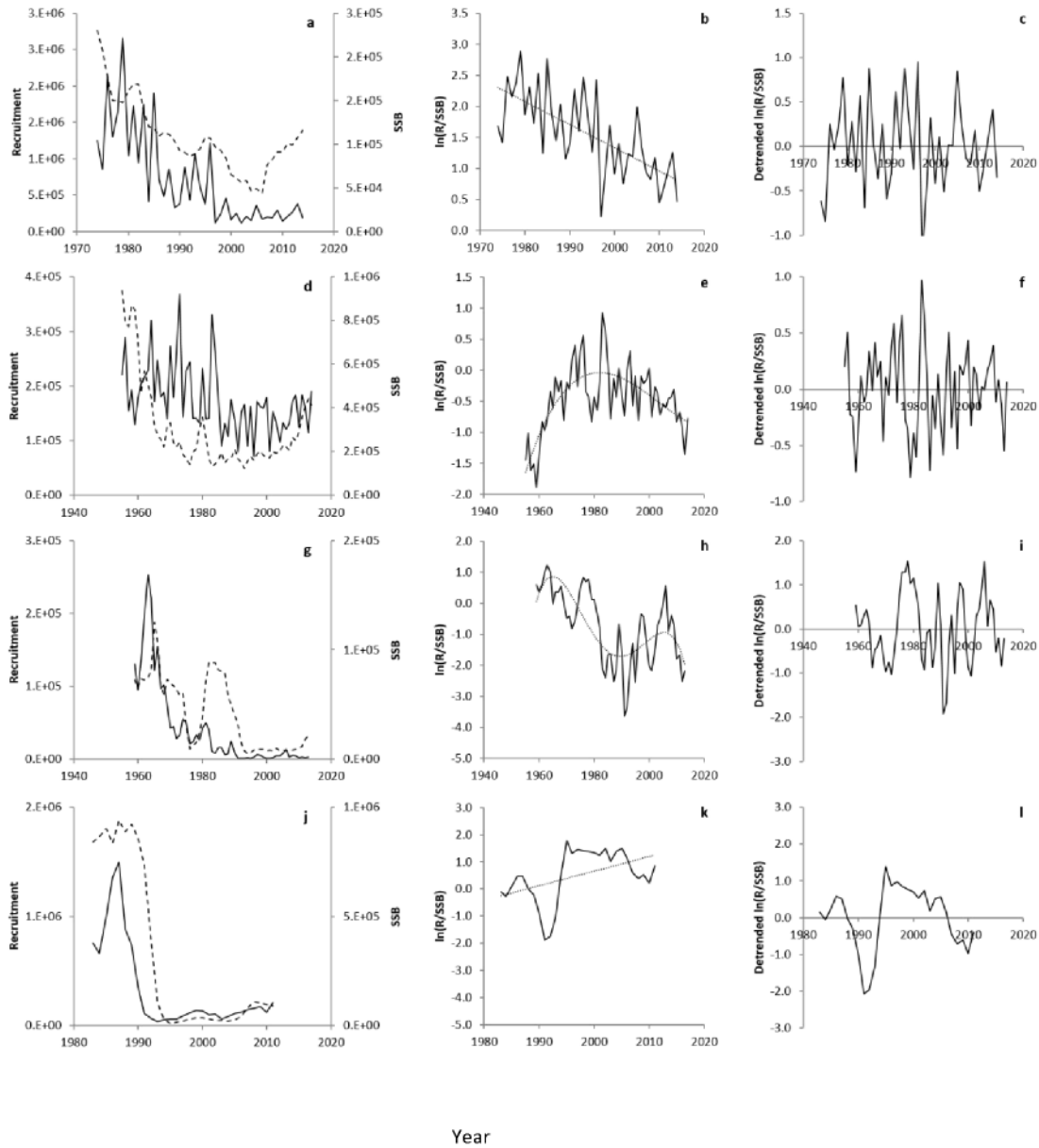
23   Fig 3. Time series of recruitment (thousands, left panel, solid line), SSB (left panel, broken line),

24   recruitment success (middle panel, solid line is observation and broken line is polynomial fit) and

4

25 detrended recruitment success (right panel) of selected stocks. Year indicates the year the cohort was

26 spawned. Examples of low wavelength (North Sea, cod-347d, a, b and c), intermediate wavelength

27 (Iceland cod, cod-ice, d, e and f), high wavelength (Grand Banks cod, cod-no, g, h and I and Northern

28 Newfoundland cod, j, k and l).

29

30
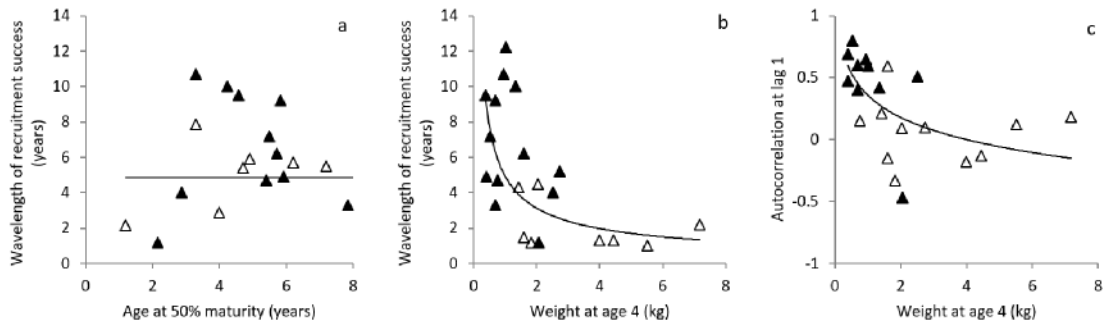
31

32 Fig 4. Relationship between the dominant wavelength of recruitment success and age at 50%

33 maturity (a), weight at age 4 (b) and between autocorrelation at lag 1 and weight at age 4 (c). Lines

34 are regressions using all periodicities (linear for a, logarithmic for c and d). Filled symbols denote

35 significant periodicity and autocorrelations.

36
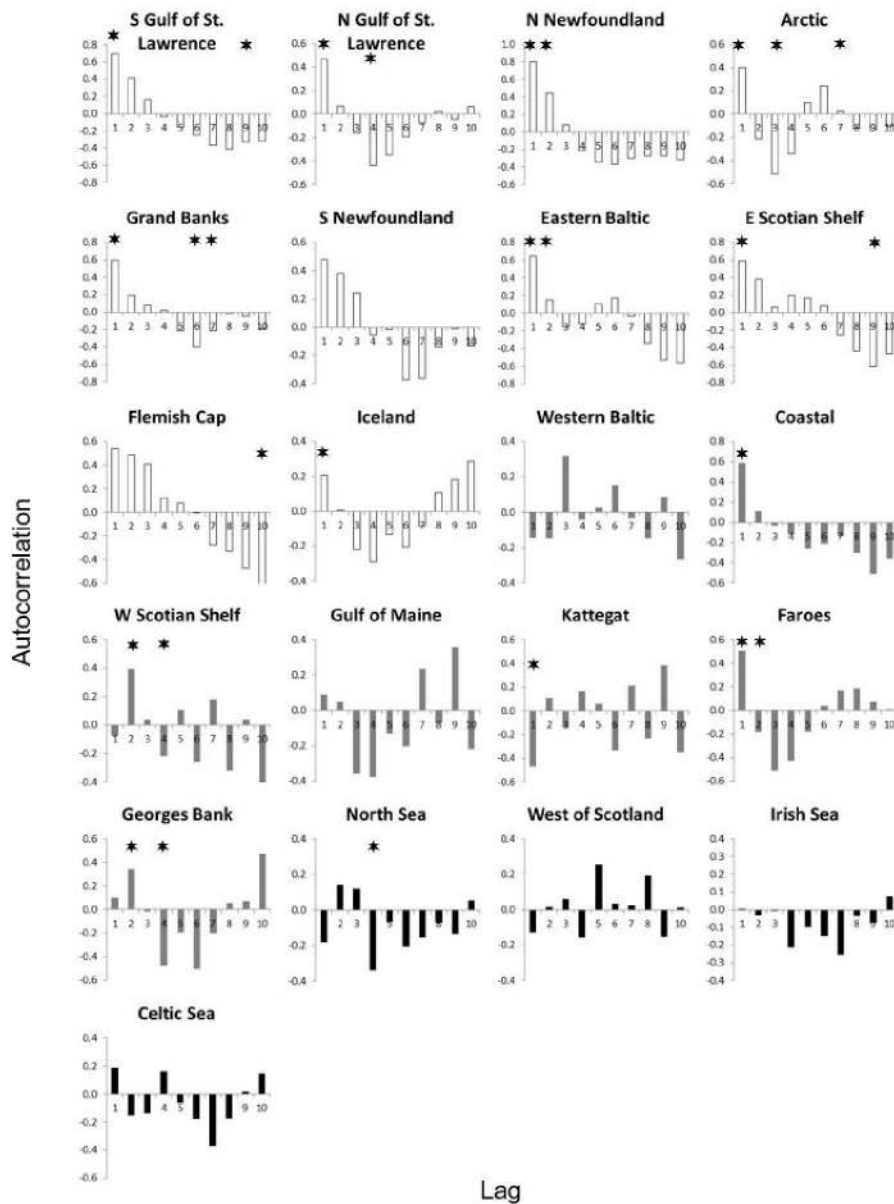
5

37

Fig. 5. Observed autocorrelations of stocks ordered according to increasing weight at age 4. Colour of

bars indicate weight at age 4: white <1.5 kg, grey 1.5-3 kg, black> 3 kg. Stars indicate where lags are

significant at the 5% level in a reduced autoregressive model with lags up to 10.

41

6