A new model for simulating growth in fish

A real dynamic population model calculates change in population sizes independent of time. The Beverton & Holt (B&H) model commonly used in fish assessment includes the von Bertalanffy growth function which has time as an independent variable. As a result the B&H model has to assume constant fish growth. However, growth in fish is highly variable depending on food availability and environmental conditions. We propose a new growth model where the length increment of fish living under constant conditions and unlimited food supply, decreases linearly with increasing fish length until it reaches zero at a maximal fish length. The model is independent of time and includes a term which accounts for the environmental variation. It is a simplification of a second order polynomial equation that fits all ages, and can be used after the fish have past the point of maximum length increment. In the present study, the model was validated in Zebrafish held at constant conditions. There was a good fit of the model to data on observed growth in Norwegian spring spawning herring and capelin from the Barents Sea, farmed cod and cod from the North Sea, but not for cod from the Barents Sea. The last result can be explained by environmental factors and food availability for this stock. Data on length increment in mice were also fitted to the model with good results, indicating that it is valid for vertebrates other than fish. The model implicates that the efficiency of energy conversion from food decreases as the individual animal approaches its maximal length and is probably a representation of a natural law of vertebrate growth.

1   Johannes Hamre, Institute of Marine Research, Bergen, Norway

2   Espen Johnsen, Institute of Marine Research, Bergen, Norway

3   Kristin Hamre, National Institute of Nutrition and Seafood Research (NIFES), Bergen,

4   Norway

7   **Corresponding author:**

8   Kristin Hamre,

9   NIFES,

10   PO Box 2029,

11   5017 Bergen,

12   Norway

13   Phone: +47 48185034

14   E-mail: kha@nifes.no

16 Introduction

17 A main objective in fisheries management is to track the impact of fisheries on the fish stocks

18 and predict the Maximum Sustainable Yield (MSY) (Pitcher & Hart 1982). A real dynamic

19 population model calculates changes in population size and biomass independent of time. In

20 mathematical terms, such a model is often formulated with differential equations where the

21 change is initially measured as a function of time. The time factor is then removed by

22 integration, but the differential models describing increment in biomass of fish cannot be

23 integrated (Beverton & Holt 1957; Lotka 1925; Schaefer 1957; Volterra 1926). Furthermore,

24 fish growth, i.e. the size increment with time, varies greatly with food quality and availability,

25 temperature and other environmental factors and the fish will reach the different stages in

26 development more dependent on size than on age (Amara & Lagardere 1995; Aritaki & Seikai

27 2004; Sæle & Pittman 2010). A certain size or energy store is needed for metamorphosis in

28 fish larvae (Amara & Lagardere 1995; Aritaki & Seikai 2004), smoltification in salmon

29 (McCormick & Bjørnsson 1994) and sexual maturation in fish in general. Accordingly,

30 farmed cod grow faster and mature at an earlier age than wild cod (Braaten 1984; Karlsen et

31 al. 1995; Karlsen et al. 2006). If the required size is not obtained, the fish will simply

32 postpone development. Therefore, a growth function which omits time and is based on fish

33 size would be in line with real fish growth and development, and would be preferred for

34 calculation of yield in simulation models.

35

36 Population dynamic models built on the classical Beverton & Holt (B&H) model are often

37 used in fish stock assessments (Beverton & Holt 1957; Hilborn 1994). This model estimates

38 the yield per recruit by assuming that growth is a function of age, e.g. accumulated time

39 (Bertalanffy 1938). As a result, the B&H model cannot sum up the yield in all year classes in

40 the same year, but it can be used to sum up the yield in one year-class during life. The authors

41 therefore assume that the yield of all year-classes in one year is equivalent to the yield of one

42 year-class through life (Beverton & Holt 1957), e.g. the model assumes constant growth.

43

44 Another way to quantify changes in mass than using differential equations was introduced by

45 Albert Einstein, when he presented the theory of relativity. Instead of using mathematics to

46 deduce from a known physical law, he postulated that energy and mass are equivalents and

47 depend on the speed of light ($E=mc^2$) (Einstein 1905). Later experiments with particle

48 acceleration, have verified this postulate. In a similar way, we postulate that the length

49 increment (dL), which is the basis for harvesting fish stocks, is inversely proportional to the

50 length (Ls) and that dL is reduced towards a maximum length (Lmax):

51

52                      $$dL = k \cdot (Lmax - Ls) \qquad\qquad 1$$

53

54 *k* is a variable determined by environmental factors, such as food availability and temperature.

55 Eq. 1 includes only measurable factors so that dL can be summed arithmetically, either per

56 year or by year classes, using modern computer techniques. It can be applied for vertebrates,

57 only, because the dynamic term (Lmax-Ls) cannot be negative, i.e. the animal cannot shrink.

58

59 The present study aims at developing a real dynamic growth model based on an unchangeable

60 and predictable natural law which is independent of time. Eq. 1 is validated using length

61 increment in zebrafish kept at constant conditions for one generation (Gomez-Requeni et al.

62 2010). We also investigate how the model fits to the observed growth of herring, capelin and

63 cod in the North East Atlantic, the Barents Sea and the North Sea and of farmed cod, and we

64 look at growth in laboratory mice in order to extend the findings to vertebrates other than fish.

65   Later we intend to use this law to simulate the development in fish stocks, starting with

66   measurement of the state of the stocks using acoustic surveys, in accordance with Bjerknes'

67   principle of exact science (Bjerknes 1904)

68

69   **Materials and methods**

70   *Data acquisition and organisation*

71   The data on growth in zebrafish were extracted from Gomez-Requeni et al. (2010). Mean

72   lengths (L) of herring, capelin and cod were from ICES working group reports (ICES 2012a;

73   ICES 2012c). In herring, data on 1 to 9 year old fish, from 1985 until 2003 were used, while

74   fish older than 9 years were omitted from the dataset, because they had essentially no length

75   increment. The data were organized as development of length with age in different year

76   classes. Full year classes were obtained from those reaching one year of age in 1985-1995.

77   Data on capelin and cod from the Barents Sea were also organized as development of length

78   per year-class, the 1986-2001 year-classes for capelin and the 1985-1995 year-classes for cod.

79   Data on weights of North Sea cod were taken from the ICES working group report ICES

80   (2012b) and converted to length using a condition factor of 0.0104 (Daan 1974). The data on

81   farmed cod were from cod hatched and reared in pens at Austevoll aquaculture research

82   station, Instiute of Marine Research, Norway. All fish were fed in excess with commercial dry

83   pellets, and became sexually mature at age 2 years. Daily water temperature measured at 2 m

84   depth from summer 1990 to autumn 1996 had a clear seasonal pattern, with minimum and

85   maximum temperatures during spring and autumn, respectively (Hoie et al. 2004). Data on

86   growth of laboratory mice were extracted from Sagazio et al. (2007).

87

88   *Calculations and statistics*

89 Increment in length (dL) was calculated as $dL = L_{(a+1)} - L_{(a)}$, where a is fish age, using time

90 intervals of one day for zebrafish, one week for mice, 0.5years for farmed cod and one year

91 for the wild fish stocks.

92 The statistical treatment was performed with GraphPad Prism, ver. 6 for Windows (GraphPad

93 Inc., La Jolla, CA, USA). For the zebrafish data, the plot of length increment day^{-1} by length

94 was fitted to a second order polynomial equation. The points after the maximum of the

95 obtained parable were then fitted to a linear and a second order polynomial equation and the

96 results compared using the GraphPad software. For herring, capelin, and wild cod, average

97 length increment year-1 by length in the year-classes were also fitted to a linear and a second

98 order polynomial equation, and the results compared by the software.

99 For herring, length increment year^{-1} was plotted against length for 1-9 year old fish in each

100 year-class and fitted to the linear equation. In all cases, $R^2 > 0.98$ for 3-9 year old fish and

101 Lmax could be calculated from these data (average Lmax=354 mm). The slope of the line (k)

102 between length increment in 1 and 2 year old fish and the zero length increment at Lmax, was

103 compared with the slope of the data on 3-9 year old fish, using GraphPad software. The slope

104 of 1 and 2 year old fish was taken to be significant different from that of the 3-9 year old fish

105 when it was outside the mean±1 confidence interval.

106

107

108 **Results**

109 Zebrafish growth as a function of age fits a sigmoid curve (Figure 1A), and plotting length

110 increment as a function of length gave an almost perfect fit to the second order polynomial

111 $y = -0.0027x^2 + 0.078x + 0.25$ ($R^2 = 0.994$, Figure 1A). When omitting the first two points

112 corresponding to the larval and very early juvenile stages, and comparing the polynomial

113   (R^2=0.9988) and the linear equation, the second order polynomial was preferred (p=0.015),

114   but the straight line still had an R^2=0.9887 (Figure 1C). Therefore, for simplicity, growth in

115   zebrafish held at constant conditions after the juvenile stage can be formulated

116   mathematically by equation 1:

117

118   dL=k*(Lmax-Ls) = -k*Ls+k*Lmax

119

120   The slope of the curve corresponds to -k, while Lmax can be calculated from the intercept

121   with the y-axis; k*Lmax (Figure 1C).

122

123   The curve of length by age of the 1985 to the 1995 year-classes of herring from 1 until 9 years

124   of age (Fig 2A) shows rapid growth in length of young fish and a decrease in length increment

125   as the fish gets older and increase in size. The decrease in length increment starts already after

126   the second year and lasts until year 9, where-after the length increment per year is close to

127   zero (data not shown). Figure 2B shows the plot of average length increment by length in all

128   year-classes. The fit to a second order polynomial has an R^2=0.9979, while the linear fit has

129   an R^2=0.9904. Here the second order equation is again preferred (p=0.01). Figure 2C shows

130   that the plots of length increment by length differ in the different year classes. The points for 1

131   and 2 year old fish deviate from each other and from the straight line obtained for in 3-9 year

132   old fish (R^2>0.98) in the year-classes 1985, -86, -92, -93 and -94. The points in 1 year old fish

133   deviate from the straight line obtained for 2-9 year old fish (R^2>0.99) in the year-class 1987.

134   All ages fit a straight line in the 1988, -89, -90, -91 and -95 year-classes (R^2>0.98).

135   Representatives of the different groups of year-classes marked in Figure 2C are given in

136   Figure 2D-F.

137

138   Assuming that the deviations from the linear relationship are due to differences in

139   environmental conditions that can be expressed by k, k was plotted by year-class for 1 year

140   old, 2 year old and 3-9 year old herring, respectively, from 1985 to 1995 (Figure 3). K was

141   lower in the one and two year old herring, compared to the 3-9 year olds, in the year-classes

142   1985-1987 and 1992-1994 and similar for all ages in the year-classes 1988-1991. The periods

143   of high k in 1 and 2 year old fish coincided with high temperature in the Kola section,

144   although there was no significant correlation between temperature and k.

145

146   Growth in capelin given as length by age is shown in Figure 4A. As in herring, the length

147   increment decreases as the fish increase in age and size, however the number of points in the

148   regression is limited by the life span of capelin, which is only 4-5 years, since almost all fish

149   die after the first spawning. Average length increment by length in the year-classes from 1986

150   to 2001 is given in figure 4B and C, in 4B with a 2nd order polynomial fit (R^2=0.9983), in 5C

151   with a linear fit (R^2=0.9766). In this case, the linear equation was preferred (p=0.17). Most of

152   the year-classes of capelin had a similar pattern of length increment as the average (data not

153   shown).

154

155   Growth in Northeast Arctic cod of different year-classes, given as length by age, seems to fit a

156   linear equation, not a sigmoid curve as in the other fish stocks (Figure 5A). Figure 5 B-D

157   shows that length increment in this case is very variable and does not seem to follow either

158   the 2nd order (R^2=0.85-0.27) or the linear relationship (R^2=0.88-0.06) on a regular basis.

159   However, growth in North Sea cod given as length by age (Figure 6A), did follow a sigmoid

160   curve and length increment by length (Figure 6B) showed a good fit to Eq. 1 (R^2=0.98). The

161   2nd order polynomial fit was rejected (R^2=0.98, p=1.0). Furthermore, length increment by

162   length in cod kept in captivity at relatively constant conditions and fed a dry diet to satiation

163 showed a good fit to Eq. 1 (Fig 7C, R^2=0.85) and the linear function was preferred over the

164 second order one (p=0.32).

165

166 Growth in mice held at constant conditions in the laboratory, registered as mouth to anus

167 length by age, is presented in Figure 6A. The curve approaches a maximum length, as found

168 in fish, and the fit to the 2nd order equation of length increment to length has an R^2=0.92,

169 however, the fit to Eq. 1(R^2=0.87) was preferred (p=0.18).

170

Discussion

171

172 The questions asked in this study are: 1) Do fish grow according to an unchangeable natural

173 law, independent of time? 2) Can such a law be described by Eq. 1? 3) Is this law also valid

174 for other vertebrates?

175

176 Zebrafish is used as a model organism for mechanistic biological research and in this context

177 it is kept under strictly controlled and constant conditions. The Zebrafish from which the

178 present growth curve was extracted had been held at constant environmental conditions and

179 fed *Artemia* only, according to a standard feeding regime, from 15 days post fertilization until

180 the end of the experiment (Gomez-Requeni et al., 2010). This created a conventional sigmoid

181 curve of weight by age, which seems to be common in all terrestrial vertebrates (Dumas et al.

182 2010). According to Dumas et al. (2010) and references therein, there is doubt that fish

183 approach a maximum weight, since growth continues after sexual maturation.

184

185 However, the Zebrafish trial also gave a sigmoid growth curve for length by age. In order to

186 omit time from the equation, length increment was plotted as a function of length. This plot

187 had an almost perfect fit to a second order equation, showing that length increment increased

188 in small fish, approaching a maximum, and decreased gradually in larger fish, reaching zero at

189 a maximal length (Lmax). We propose that the second order equation of length increment vs

190 length describes the general law of fish growth. Length increment leads to accumulation of

191 biomass and energy. Therefore, the model implies that energy in the food is used most

192 efficiently for biomass accumulation in relatively small fish, with decreasing efficiency as the

193 fish approach Lmax. The lower growth in larvae and very young juveniles, may be caused by

194 the energy needed to develop organ systems and the immature digestive system, which may

195 prevent optimal utilization of the feed (Rønnestad et al. 2013).The linear model given in Eq. 1

196   is a simple version of the second half of the 2nd order growth function and it fits the data for

197   Zebrafish past maximum length increment well, even though it is not statistically preferred

198   over the 2nd order equation. Eq. 1 is easy to understand, it can readily be adapted in simulation

199   models and it includes the variable k, which describes changes in the environment and food

200   availability. Furthermore, the assessment of fish stocks most often only includes fish that are

201   larger than the point where maximal length increment occurs, again favoring the use of Eq. 1.

202

203   Eq. 1 also fits the length increment by length data for the year-classes of fish, one year old or

204   more, of capelin, North Sea cod and farmed cod. The data from Norwegian Spring Spawning

205   herring of 3-9 years are very well described by Eq. 1, but in some of the year-classes, one and

206   two year old fish grow slower than the prediction of Eq. 1 for 3-9 year old fish. The deviation

207   from the straight line is larger than what would be predicted by the 2nd order polynomial fit, as

208   it extends a minimum of 1 confidence interval. Therefore we have interpreted it as a

209   difference in environmental conditions, e.g. a difference in k. There was no significant

210   mathematical correlation between temperature and k. However, a high k in one and two year

211   old fish coincided with high temperature in the Kola section, which is used as an indication of

212   the general Barents Sea temperature (Ottersen et al. 1998). The young herring grow up in the

213   Barents Sea and move to the warmer Norwegian Sea when they are 20-22cm, usually about

214   three years old (Holst et al. 2004).

215

216   Length increment by length over individual year-classes in cod from the Barents Sea does not

217   fit well to Eq. 1. This may be caused by low and varying food availability, since the Northeast

218   Arctic cod stock is large and may therefore encounter food shortage (Jørgensen 1992). On the

219   other hand, North Sea cod is heavily overfished and should have ample amounts of food

220   (Cook et al. 1997). Furthermore, older and larger Northeast Arctic cod have a tendency to

221 distribute further to the west, where they encounter gradually increasing temperatures

222 (Michalsen et al. 1998). The lack of fit of individual year-classes of Northeast Arctic cod to a

223 common version of Eq. 1, may therefore be explained by increase in k from one year to the

224 next over the whole life span. Unfortunately, the data from Northeast Arctic cod cannot be

225 used to determine Lmax, so that k cannot be defined per year.

226

227 The farmed cod were held under semi-controlled conditions, in net pens with ambient

228 sea-water temperature and natural light, but were fed the same diet for one generation. The

229 measurements were taken in summer and winter and the relatively large variation is related to

230 the seasonal variation in temperature and light. When only winter measurements were

231 included, e.g. the length increment from one winter to the next was monitored, there was a

232 perfect fit of the data to Eq. 1 (R^2=1.00). Eq. 1 also fits well to data from North Sea cod.

233

234 In Eq. 1, Lmax and k are individual characteristics determined by how the fish have adapted

235 to the environmental conditions. Lmax is different from L∞ in von Bertalanffy's growth

236 function; it is a fixed value, not an asymptote, it has a variance and it is not connected to time.

237 Lmax is assumed to be genetically determined, and may change in response to long term

238 changes in the environment and harvesting strategies, as described for North West Arctic cod

239 by Borrell (2013). It differs between species, between the stocks within a species and between

240 the individuals within a stock. Clearly, there are a considerable number of variables that

241 determine the value of k, and the parameterization will demand expertise within

242 oceanography and in biological fields such as genetics and nutrition.

243

244 Eq. 1 calculates length increment, while yield in biomass is the economically important

245 variable. It has been shown that specific growth rate (SGR) in % of body weight per day has a

246 linear relationship to fish weight on a log-log scale (Bjørnsson & Steinarsson 2002; Braaten

247 1984; Brett & Shelbourn 1975; Jobling 1983), which is an alternative formulation of the

248 natural law of animal growth to Eq. 1. One reason for using length in our model is that both

249 length of individual fish and number of fish can be measured directly using acoustic trawl

250 surveys. The length increment data can then be converted to yield in weight and biomass

251 using Fulton's condition factor (Fulton 1904). Furthermore, weight can vary greatly due to

252 varying food supply and varying gonad size in relation to sexual maturation, while length is a

253 more stable and positive measure.

254

255 According to Eq. 1, harvesting of fish which are at the point of maximum size increment is

256 energetically most efficient. In the case of herring, fish of 10 cm length grow at a rate which is

257 four times higher than fish of 30 cm length (Figure 2B). Feed conversion efficiency generally

258 increases with higher growth rates in fish (Kolstad et al. 2004), so utilization of the energy

259 from plankton would be optimized by harvesting relatively small fish. The slaughter of farm

260 animals prior to sexual maturation is a common practice in meat and fish farming which also

261 takes advantage of the high growth rates in young animals. Selective fisheries on large fish

262 may therefore defeat its own end, and prevent a maximum utilization of the marine resources.

263 A similar perspective is presented by Borrell (2013). Ecological principles may also be

264 explained as optimizing the efficiency of energy utilization. An example is the seabirds along

265 the Norwegian coast, which mainly feed on 0-group fish (Dragesund et al. 2008). This

266 represents an efficient utilization of zooplankton biomass and energy.

267

Conclusion

The data presented here indicate that there is a natural law for length increment in fish, based on achieved length, which can be described by a second order polynomial. Eq. 1 is a simplification of this law that can be used when the fish are past the point of maximal length increment. Length increment by length in laboratory mice held at controlled and constant conditions (Sagazio et al. 2007) also gave a good fit to Eq. 1, indicating that the law of length increment can be generalized to vertebrates other than fish. A consequence of Eq. 1 is that the efficiency of energy conversion from food decreases as the individual animal approaches Lmax. Length increment represents yield in biomass and energy and is the way living organisms store energy from the sun. Eq. 1 enables us to quantify these processes.

Acknowledgements

We want to thank P. Gomez-Requeni P and I. Rønnestad, the University of Bergen, Norway, for providing the dataset on Zebrafish, Ø. Karlsen, The Institute of Marine Research, Bergen, Norway, for the dataset on farmed cod and Samuel J. Penglase for critical reading of the manuscript.

285 **References**

286 Amara R, and Lagardere F. 1995. Size and age at onset of metamorphosis in sole (*Solea-Solea*

287   (L)) of the Gulf of Gascogne. *Ices Journal of Marine Science* 52:247-256.

288 Aritaki M, and Seikai T. 2004. Temperature effects on early development and occurrence of

289   metamorphosis-related morphological abnormalities in hatchery-reared brown sole

290   *Pseudopleuronectes herzensteini*. *Aquaculture* 240:517-530.

291 Bertalanffy L.von 1938. A quantitative theory of organic growth. *Human Biology* 10:181-213.

292 Beverton RJH, and Holt SJ. 1957. On the dynamics of exploited fish populations. *Fisheries*

293   *Investigation, London, Series 2* 19:1-533.

294 Bjerknes V. 1904. Das problem der Wetterforhersage, betractet vom Standpunkte der Mekanik

295   und der Physik. *Meterologische Zeitschrift, Wien* 21:1-7.

296 Bjørnsson B, and Steinarsson A. 2002. The food-unlimited growth rate of Atlantic cod (*Gadus*

297   *morhua*). *Canadian Journal of Fisheries and Aquatic Sciences* 59:494-502.

298 Borrell B. 2013. A big fight over little fish. *Nature* 493:597-598.

299 Braaten B. 1984. Growth of cod in relation to fish size and ration level. In: Dahl E, Danielssen

300   DS, Moksness E, and Solemdal P, eds. *The propagation of cod (Gadus morhua L)*.

301   Arendal, Norway: Institute of Marine Research, 677-710.

302 Brett JR, and Shelbourn JE. 1975. Growth-Rate of Young Sockeye Salmon,

303   Oncorhynchus-Nerka, in Relation to Fish Size and Ration Level. *Journal of the*

304   *Fisheries Research Board of Canada* 32:2103-2110.

305 Cook RM, Sinclair A, and Stefansson G. 1997. Potential collapse of North Sea cod stocks.

306   *Nature* 385:521-522.

307 Daan N. 1974. Growth of North Sea cod, *Gadus morhua*. *Netherlands Journal of Sea*

308   *Research* 8:27-48.

309 Dragesund O, Østvedt OJ, and Toresen R. 2008. Norwegian spring spawning herring: History
310   of fisheries, biology and stock assessment. In: Nakken O, ed. *Norwegian Spring*
311   *Spawning Herring and North East Atlantic Cod*. Trondheim, Norway: Tapir Academic
312   Press, 41-82.

313 Dumas A, France J, and Bureau D. 2010. Modelling growth and body composition in fish
314   nutrition: where have we been and where are we going? *Aquaculture Research*
315   41:161-181.

316 Einstein A. 1905. Zur Electrodynamik bewegter Körper. *Randiconti del Circolo Matematico*
317   *di Palermo*.

318 Fulton TW. 1904. The rate of growth in fishes. *Fish Board Scotland, Ann Rep* 22:141-241.

319 Gomez-Requeni P, Conceicao LEC, Jordal AEO, and Ronnestad I. 2010. A reference growth
320   curve for nutritional experiments in zebrafish (*Danio rerio*) and changes in whole
321   body proteome during development. *Fish Physiology and Biochemistry* 36:1199-1215.

322 Hilborn R. 1994. Book reveiw: Beverton, R.J.H. & Holt, S.H. On the Dynamics of Exploited
323   Fish Populations. *Reviews in Fish Biology and Fisheries* 4: 259-266.

324 Hoie H, Andersson C, Folkvord A, and Karlsen O. 2004. Precision and accuracy of stable
325   isotope signals in otoliths of pen-reared cod (*Gadus morhua*) when sampled with a
326   high-resolution micromill. *Marine Biology* 144:1039-1049.

327 Holst JC, Røttingen I, and Melle W. 2004. The herring. In: Skjoldal H-R, Sætre R, Faernö A,
328   Misund OA, and Røttingen I, eds. *The Norwegian Sea ecosystem*. Trondheim: Tapir
329   Academic Press, 203-226.

330 ICES. 2012a. Report of the Arctic Fisheries Working Group 2012 (AFWG), 20 - 26 April
331   2012. Copenhagen: ICES Headquarters.

332   ICES. 2012b. Report of the Working Group on the Assessment of Demersal Stocks in the

333   North Sea and Skagerrak (WGNSSK), 27 April - 3 May 2012. Copenhagen: ICES

334   Headquarters.

335   ICES. 2012c. Report of the Working Group on Widely Distributed Stocks (WGWIDE),

336   21 - 27 August 2012. Lowestoft, United Kingdom.

337   Jobling M. 1983. Growth-studies with fish - Overcoming the problems of size variation.

338   *Journal of Fish Biology* 22:153-157.

339   Jørgensen T. 1992. Long-term changes in growth of North-east Arctic cod (*Gadus morhua*)

340   and some environmental influences. *ICES Journal of Marine Science: Journal du*

341   *Conseil* 49:263-278.

342   Karlsen O, Holm JC, and Kjesbu OS. 1995. Effects of Periodic Starvation on Reproductive

343   Investment in 1st-Time Spawning Atlantic Cod (*Gadus-Morhua* L). *Aquaculture*

344   133:159-170.

345   Karlsen O, Norberg B, Kjesbu OS, and Taranger GL. 2006. Effects of photoperiod and

346   exercise on growth, liver size, and age at puberty in farmed Atlantic cod (*Gadus*

347   *morhua* L.). *Ices Journal of Marine Science* 63:355-364.

348   Kolstad K, Grisdale-Helland B, and Gjerde B. 2004. Family differences in feed efficiency in

349   Atlantic salmon (*Salmo salar*). *Aquaculture* 241:169-177.

350   Lotka AJ. 1925. *Elements of Physical Biology*. Baltimore: Williams and Wilkins Co.

351   McCormick SD, and Bjørnsson BT. 1994. Physiological and hormonal differences among

352   Atlantic salmon parr and smolts reared in the wild, and hatchery smolts. *Aquaculture*

353   121:235-244.

354   Michalsen K, Ottersen G, and Nakken O. 1998. Growth of North-east Arctic cod (*Gadus*

355   *morhua* L.) in relation to ambient temperature. *Ices Journal of Marine Science*

356   55:863-877.

357   Ottersen G, Michalsen K, and Nakken O. 1998. Ambient temperature and distribution of

358   north-east Arctic cod. *Ices Journal of Marine Science* 55:67-85.

359   Pitcher TJ, and Hart PJB. 1982. *Fisheries Ecology*. London: Chapman and Hall.

360   Rønnestad I, Yufera M, Überschär B, Ribeiro L, Sæle Ø, and Boglione C. 2013. Feeding

361   behaviour and digestive physiology in larval fish: current knowledge and gaps and

362   bottlenecks in research. *Reviews in Aquaculture* 5:S59-S98.

363   Sæle O, and Pittman KA. 2010. Looking closer at the determining of a phenotype? Compare

364   by stages or size, not age. *Journal of Applied Ichthyology* 26:294-297.

365   Sagazio A, Piantedosi R, Alba M, Blaner WS, and Salvatori R. 2007. Vitamin A deficiency

366   does not influence longitudinal growth in mice. *Nutrition* 23:483-488.

367   Schaefer MB. 1957. Some Considerations of Population Dynamics and Economics in

368   Relation to the Management of the Commercial Marine Fisheries. *Journal of the*

369   *Fisheries Research Board of Canada* 14:669-681.

370   Volterra V. 1926. Variazioni e fluttuazioni del numero d'individui in specie animali conviventi.

371   *Mem R Accad Naz dei Lincei Ser VI* 2.

372

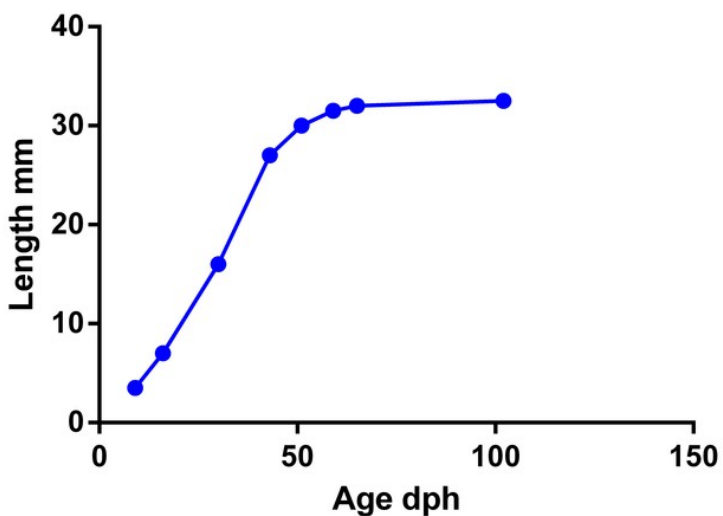
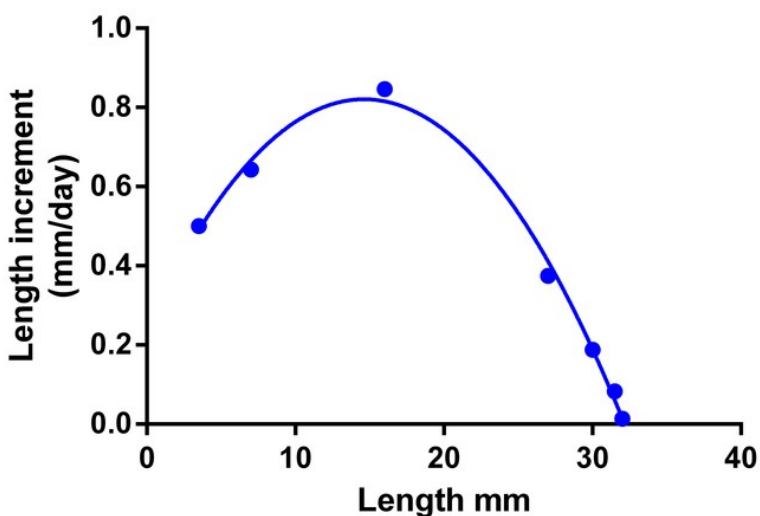
373

374

Figure 1

Growth in Zebrafish kept under constant conditions and fed *Artemia* to satiation through one generation

A. Growth in length by age (Extracted from Gomez et al., 2012). B. Length increment by length for all data-points with a second order polynomial fit. C. Points past the exponential growth phase fitted to a linear equation.

Lenghtwise growth by age

Length increment by length

Length increment after exponential phase

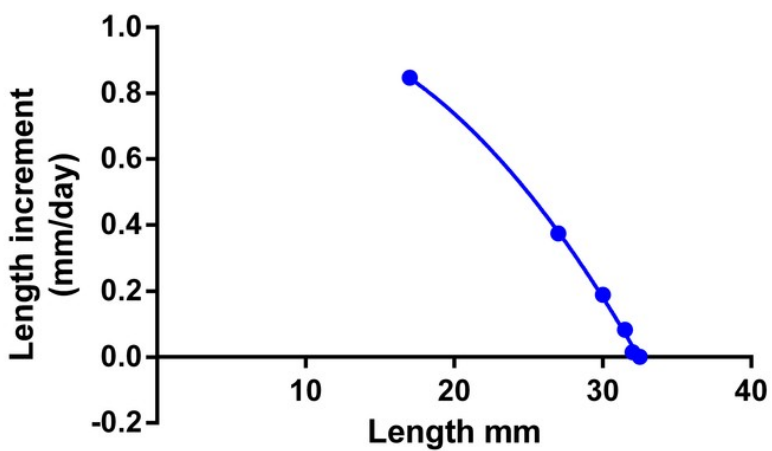



Figure 2

Growth in the year-classes 1985-1995 of Norwegian spring spawning herring

A. Growth in length with age. B. and C. Average and individual year-class length increment by length in all year-classes from 1985 until 1995. D-F. Representatives of the groups marked in C with linear fits (see text for explanation).

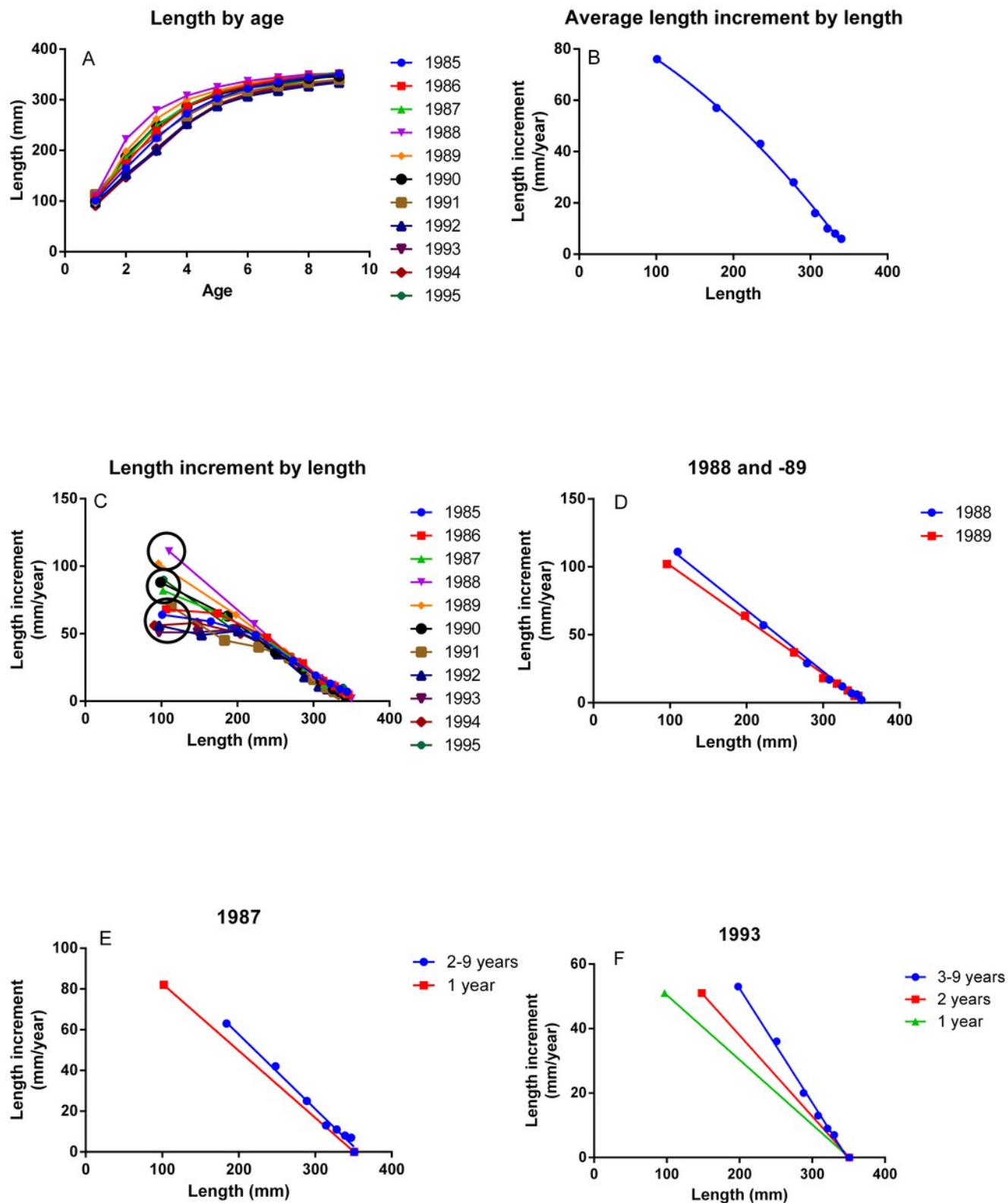



Figure 3

K in herring of different ages in the year-classes 1985-1995 and temperature in the Kola section when the fish were one year of age

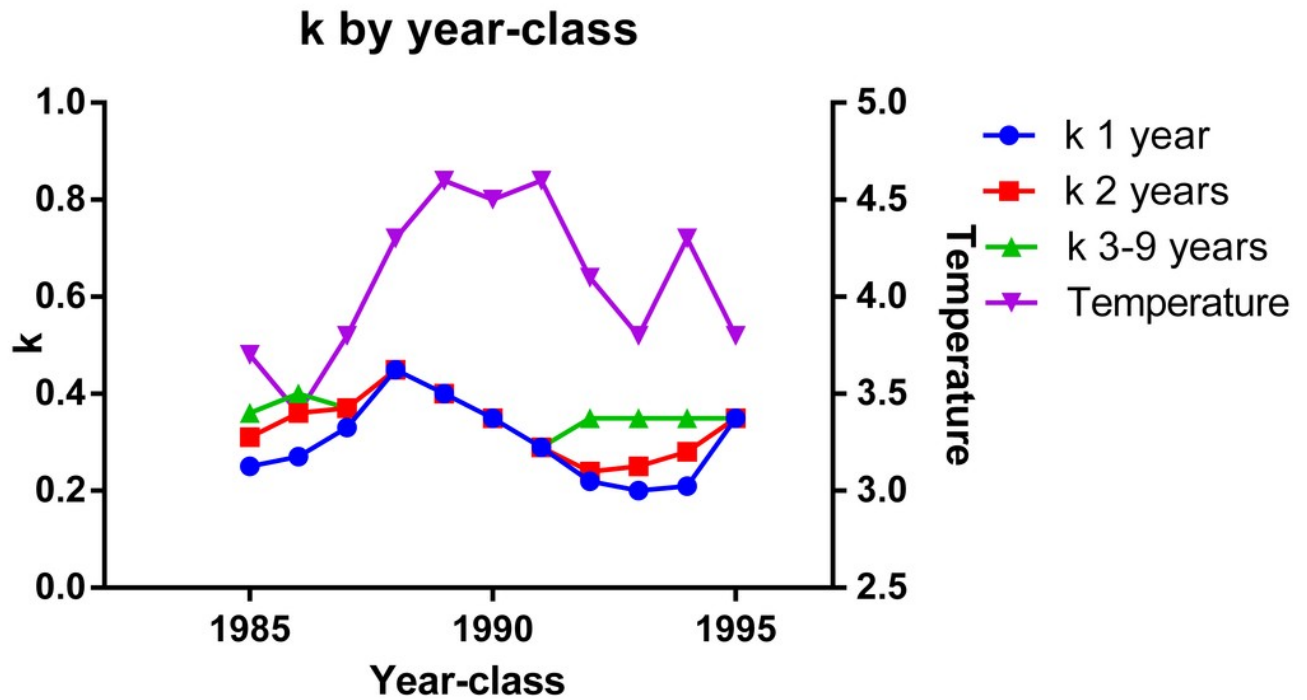



Figure 4

Growth in capelin

A. Growth as length by age. B. Second order exponetial fit and C. linear fit of length increment by length, average for all year-classes from 1986 until 2001.

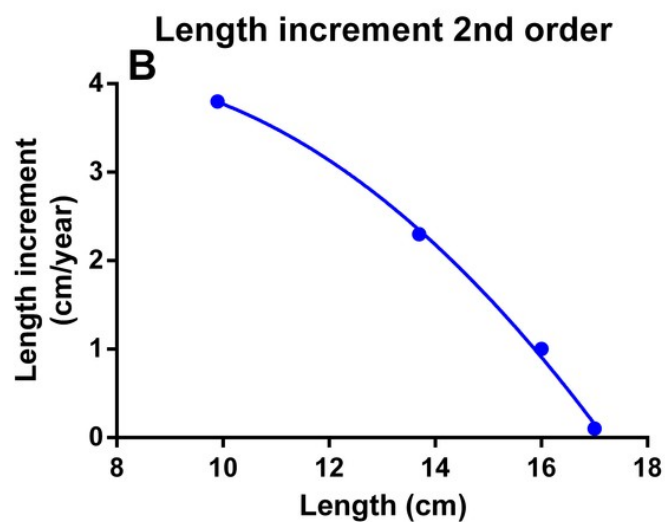
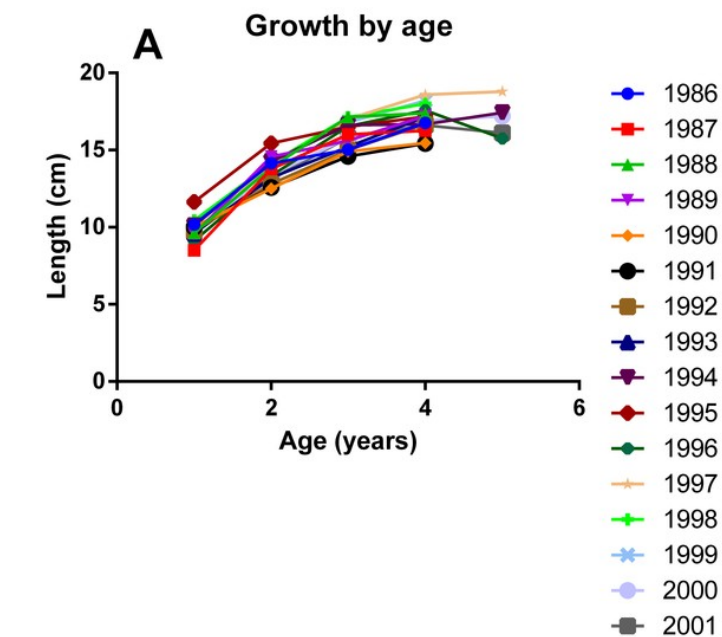



Figure 5

Growth in Northeast Arctic cod

A. Growth as length by age. B-D. Examples of length increment by length in different year-classes.

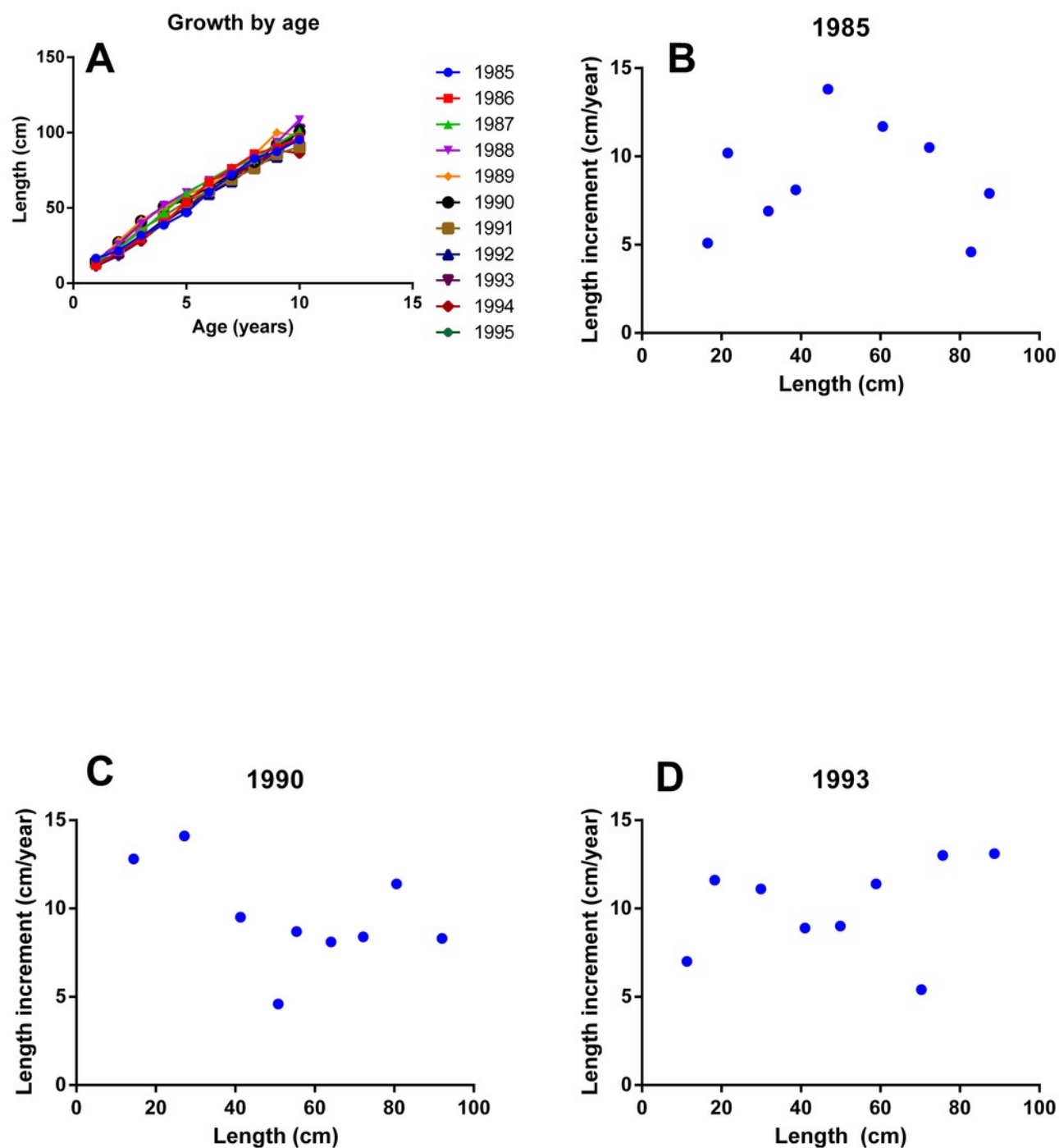
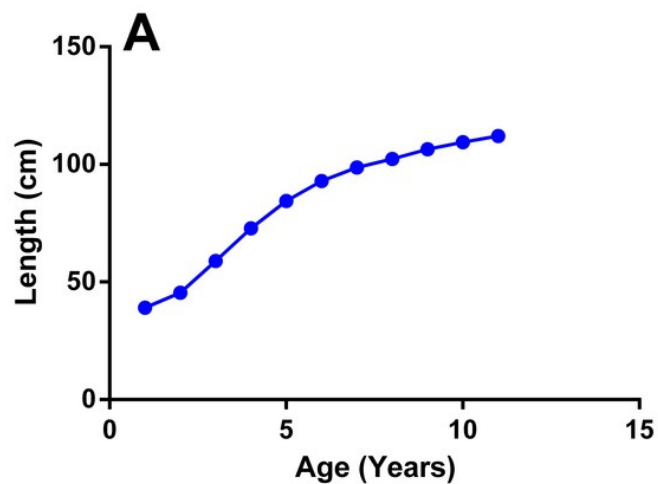
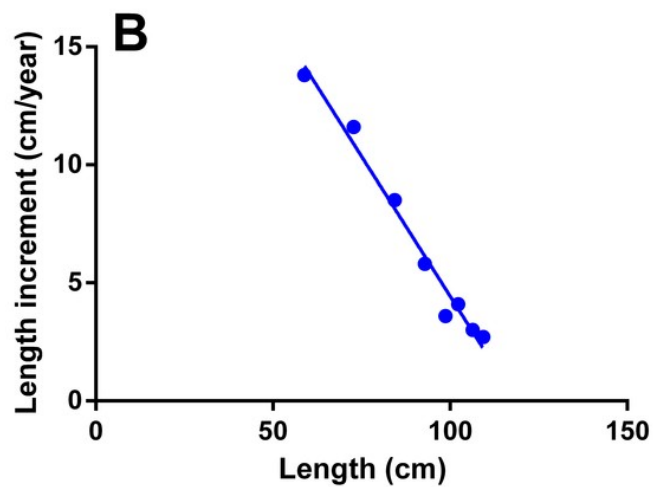



Figure 6

Growth in North Sea cod

A. Growth as length by age. B. Length increment by length with a linear fit and C. Farmed cod,

Length increment by length.

North Sea cod

North Sea cod

Captive cod

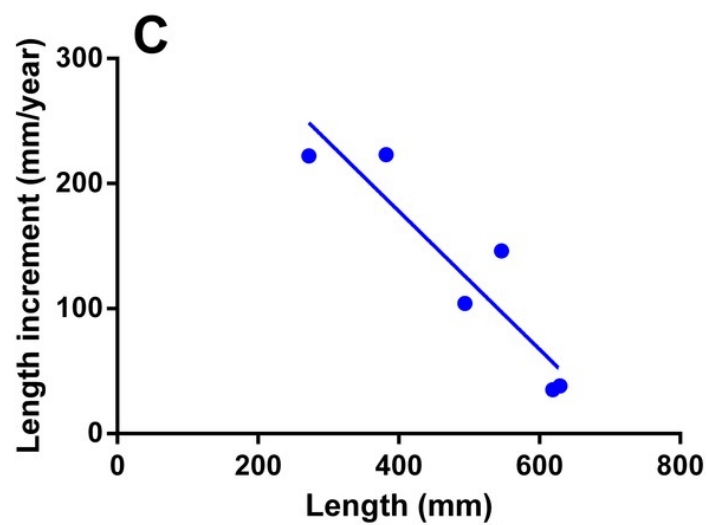



Figure 7

Growth in Laboratory mice

A. Growth as length by age. B. Length increment by length with a linear fit.

Length by age

Length increment by length