Estimating natural mortality and egg production of snow crab Chionoecetes opilio adult females

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13   ABSTRACT: Natural mortality rate is a key parameter in ecology and fisheries, but it may be

14   difficult to estimate for methodological reasons and because it is highly variable and often

15   confounded with other factors such as fishing mortality and migration. This is especially true for

16   crustaceans in general, because age determination is problematic, and for snow crab

17   (*Chionoecetes opilio*) in particular because density-dependent processes may lead to highly

18   variable mortality rates across life history stages. In this context, we developed an original

19   method to estimate the natural mortality rate of adult (i.e. terminally molted) female snow crab,

20   and its consequences on egg production. This new method relies on shell condition, carapace

21   width and abundance of adult females and was applied to a time series (1991–2012) of annual

22   trawl survey data for a snow crab population in the Gulf of St. Lawrence, eastern Canada. Two

23   natural mortality estimates were provided by the method depending on two distinct assumptions

24   about the survey. Both estimates (0.66 and 0.78 year^{-1}) were high compared to previous

25   estimates for snow crab. These values imply that female life expectancy after terminal molt was

26   short and that primiparous females (first-time spawners) contributed a large share (at least 81%)

27   of the total number of eggs produced by the case-study population over the period 1992–2010.

28

29   KEY WORDS: *Chionoecetes opilio*, natural mortality, terminal molt, body size, egg production

30

31   **INTRODUCTION**

32   Knowledge of natural mortality is of paramount importance in ecological and fishery sciences

33   (e.g. Defeo & Cardoso 2002, Lipcius & Stockhausen 2002). Natural mortality is a key

34   determinant of the potential productivity of a population, and consequently of a species' potential

35   to resist environmental stressors or to sustain exploitation. Natural mortality rates are especially

36   difficult to estimate because they are generally highly variable across life history stages and

37   because in exploited species they may be confounded with direct or indirect fishing mortality.

38   This is especially true for several harvested crabs (Zheng 2005) in which density-dependent

39   processes, such as cannibalism (Sainte-Marie & Lafrance 2002), may cause mortality rates to

40   vary through ontogeny.

41   Estimation of natural mortality rates usually depends on knowledge of individual age, which

42   has never been determined directly for crabs and other crustaceans because no bodypart

43   recording annual age marks was known (e.g. Vogt 2012). Consequently, various other methods

44   have been proposed or used to estimate crab natural mortality rates. Tagging experiments have

45   been widely employed (e.g. Siddeek et al. 2002, Lambert et al. 2006) but this technique is more

46   difficult to apply to crabs than to fishes, because of molting, and is generally expensive. Indirect

47   methods such as length-based models have also been used to provide estimates of natural

48   mortality rates (Siddeek et al. 2002, Zheng et al. 1995a, 1995b), but these models generally

49   require a large amount of data to provide reliable estimates. In the last few decades, methods

50   have been developed and applied to assess age via the neural pigment lipofuscin — while these

51   methods do not allow precise individual age determination, they do assign a probable age to

52   individuals based on the average rate of lipofuscin accumulation (Puckett et al. 2008, Sheehy &

53   Prior 2008).

54   In the many crab species with a terminal molt, such as those belonging to the genera

55   *Chionoecetes* and *Maja*, natural tags (epibionts) and shell condition (Dick et al. 1998), carapace

56   radiometry (Le Foll et al. 1989, Ernst et al. 2005) and dactyl wear (Fonseca et al. 2008, Fahy &

57   Carroll 2009) have also been proposed as methods for determining relative age (since terminal

58   molt) and mortality rates for the ultimate, reproductive life history phase, called adult. However,

59   each of these last methods has its drawbacks including uncertainty and/or cost. For example,

60   time of epibiont settlement and subsequent growth rate are generally unknown, carapace

61   radiometry is costly and assumes that shell composition is static from time of molt (no minerals

62   added), and dactyls may wear differently among individuals. Recently, Kilada et al. (2012)

63   proposed that age may be recorded in the eyestalk of some decapod crustaceans, including snow

64   crab, but the method must be further validated especially with regard to its application to

65   terminally molted individuals (C. Vanier, Univ. Québec à Rimouski, pers. comm.).

66   This study examines survival of adult (i.e. terminally-molted and sexually mature) female

67   snow crab (*Chionoecetes opilio*; Oregoniidae, Majoidea) and its consequences for egg

68   production using a new approach for determining mortality. The case-study population is located

69   in the northwestern Gulf of St. Lawrence, eastern Canada. Fishery regulations impose a strict ban

70   on the landing of female snow crab in eastern Canada, so female survival after terminal molt

71   should largely reflect natural mortality. Snow crab terminal molt can occur at variable instars,

72   with females becoming adult on average at a smaller size (instar) and a younger age than males.

73   In the Gulf of St. Lawrence, most females become adult in either of instars IX to XI which

74   corresponds to a post-hatching age of about 6−8 years and most males in instars IX to XIV at

75   about 6−11 years (Sainte-Marie et al. 1995, Alunno-Bruscia & Sainte-Marie 1998, Comeau et al.

76   1998). The female terminal molt to maturity occurs sometime between late December and April

77   (Alunno-Bruscia & Sainte-Marie 1998). Females can be inseminated by males shortly after this

78   molt and thereafter transition through three reproductive stages: (1) 'nulliparous' from time of

79   terminal molt until they extrude their first egg clutch, which happens usually hours or days after

80   molting/mating; (2) 'primiparous' after extruding their first egg clutch; and (3) 'multiparous'

81   after extruding their second or an ulterior clutch (Sainte-Marie et al. 2008, 2010). Primiparous

82   and multiparous females have different reproductive outputs, the former extruding eggs that are

83   about 20% fewer per clutch but about 2% bigger in diameter than those of similarly-sized

84   multipara (Sainte-Marie 1993). Eggs are brooded beneath the female's abdomen and develop and

85   hatch out as larvae in about one year in "warm" (> 0.75°C) conditions so females reproduce

86   annually, or in about two years in "cold" (< 0.75°C) conditions so females reproduce biennially

87   (Moriyasu & Lanteigne 1998, Comeau et al. 1999, Sainte-Marie et al. 2008, Kuhn & Choi 2011).

88   Classification of adult female snow crab into reproductive stages relies on shell condition: the

89   exoskeleton is clean, iridescent and still soft in nullipara; clean, iridescent but hardening in early

90   primipara (<3−6 mo since terminal molt), and with additional time it progressively becomes

91   fouled, dull and scarred. Shell fouling and scarring is more or less apparent in late primipara

92   (about 6 mo to up to 2 yr since terminal molt in cold environments), depending on year and site,

93   but it is usually obvious in multipara (Sainte-Marie 1993). Adult females have been assumed to

94   survive mostly for 3 to 5 years after terminal molt (Alunno-Bruscia & Sainte-Marie 1998,

95   Comeau et al. 1998), but maximum longevities of 6–9 years after terminal molt are reported

96   (Ernst et al. 2005, Gosselin 2009, Kon et al. 2010).

97   Adult females recruited to the snow crab population in a given year form a pseudo-cohort

98   (term coined by Ernst et al. 2005) with often very distinct characteristics of abundance and mean

99   size relative to other pseudo-cohorts. Variation in pseudo-cohort strength can be extreme (orders

100   of magnitude) and recruitment of adult females occurs in multiyear waves or pulses (Sainte-

101   Marie et al. 1996, 2008, Ernst et al. 2012). Waves (and intervening troughs) are thought to reflect

102   episodic or quasi-cyclic oscillations in settlement intensity or early juvenile survival (Conan et

103   al. 1996, Sainte-Marie et al. 1996, Ernst et al. 2102). Variation in mean body size of adult

104   females in pseudo-cohorts may be inversely related to pseudo-cohort density and so also

105   oscillates over time (Sainte-Marie et al. 1996, 2008, Orensanz et al. 2007, Ernst et al. 2012).

106   These features are well illustrated by the time series of adult female abundance and body size in

107   our case-study population (Fig. 1), where the primipara abundance index has fluctuated inter-

108   annually by several orders of magnitude, through one very strong (1995–1999) and one weak

109   (2008–2010) recruitment wave, and was negatively correlated with primipara mean body size

110   ($r = –0.618$, $p = 0.003$).

111   The objective of this study is to explore the combined use of shell condition (or reproductive

112   stage), abundance index and body size during the maturation of two successive recruitment

113   waves for determining the natural mortality rate of adult female snow crab. We entertain this

114   possibility because newly-recruited adult females can under some circumstances be confidently

115   recognized and the pseudo-cohort they form has distinct characteristics of abundance and mean

116   size that could serve as tracers. Additionally, we estimate population and per capita egg

117   production, and primipara and multipara shares of population egg production, using the

118   estimated mortality rate under a scenario of annual or biennial female reproduction.

119

120   **MATERIALS AND METHODS**

121   **Data.** Every year (denoted y) from 1991 (denoted y_1) to 2012 (denoted Y), a beam trawl

122   survey was carried out in Baie Sainte-Marguerite. This small ($\sim$ 400 km²) bay is located in the

123   northwest Gulf of St. Lawrence, eastern Canada. A description of the survey is provided in

124   Lovrich et al. (1995) and Sainte-Marie et al. (1996). Briefly, the survey was conducted between

125   late-April and late-May, just after the end of the annual period for terminal molting of females.

126   The survey design allocated at least 3 randomly positioned trawlsets in each of 3 depth strata:

127   4−20 m, 20−80 m, and 80−140 m. This depth range covers essential female snow crab habitat

128   during the spring. All sampled crabs were sexed, rated for shell condition (Sainte-Marie 1993),

129   and females were measured in carapace width (CW, ± 0.1 mm) and assigned a maturity status

130   (pre-adult or adult) based on the relative size of their abdomen (Alunno-Bruscia & Sainte-Marie

131   1998).

132   Classification of adult females was further refined into two groups: newly-recruited females

133   (with a clean and soft, brittle or hard shell) denoted A0; or previous years' recruits (with a more

134   or less fouled and scarred shell, corresponding to intermediate, dirty-hard or dirty-soft shell

135   conditions) denoted A1+. The distinction between new recruits and previous years' recruits is

136   easy at the time of the survey and is confirmed post hoc each year by examination of the

137   spermathecal content of a sample of adult females (n = 60–90) during routine monitoring of

138   female reproductive success (Sainte-Marie et al. 2008). Stored ejaculates are all white in A0

139   females, indicating females have experienced only one recent mating period, whereas some or all

140   of the ejaculates are much darker (yellow-ocre to brown) in A1+ females due to storage for a

141   year or more (Duluc et al. 2005). At the time of the survey, group A0 is composed exclusively of

142   primiparous females that molted and oviposited sometime in the previous 4–5 months, while

143   group A1+ is composed of all the multiparous females and may also include late primipara in

144   their second year of egg incubation under cold conditions or late primipara close to hatching

145   their clutch under warm conditions. Group A1+ may conceptually be subdivided into pseudo-

146   cohorts: A1, A2, A3, etc represent females that underwent terminal molt and became adult

147   respectively 1, 2, 3,etc years before the current survey year.

148   An index of abundance by 0.02 $\log_{10}$ classes of CW was calculated for each group of adult

149   females based on swept area by trawlset and area of each depth stratum. Thus, the survey

150   provides annual abundance indices for A0 and A1+ groups (denoted respectively $U_{A0}(y)$ and

151    $U_{A1+}(y)$) and estimates of mean CW (denoted respectively $\overline{cw_{A0}(y)}$ and $\overline{cw_{A1+}(y)}$ from

152   year y_1 to Y. Standard errors for mean CW are calculated and denoted $SE^2_{A0}(y)$ and $SE^2_{A1+}(y)$.

153   The size distribution of adult females in a given year may be approximated by a normal

154   (Gaussian) distribution because they are mainly concentrated in two successive instars with

155   largely overlapping sizes (Alunno-Bruscia & Sainte-Marie 1998, Burmeister & Sainte-Marie

156   2010).

157

158   **Dynamic equations.** If $\mu_{A0}(y)$ and $N_{A0}(y)$ respectively denote group A0 mean CW and

159   abundance in the population in year y, while $\mu_{A1+}(y)$ and $N_{A1+}(y)$ respectively denote group

160   A1+ mean CW and abundance in year y, group A1+ mean CW and abundance in the following

161   year can easily be calculated:

162   1) $$\mu_{A1+}(y) = \frac{N_{A0}(y-\Delta_p)\,\mu_{A0}(y-\Delta_p)\,e^{-\Delta_p \cdot M} + N_{A1+}(y-1)\cdot \mu_{A1+}(y-1)\cdot e^{-M}}{N_{A0}(y-\Delta_p)\,e^{-\Delta_p \cdot M} + N_{A1+}(y-1)\cdot e^{-M}}$$ (expectation

163   of the mixture of two Gaussian distributions),

164   2) $$N_{A1+}(y) = N_{A0}(y-\Delta_p)\,e^{-M \cdot \Delta_p} + N_{A1+}(y-1)\cdot e^{-M}$$

165   with M the natural mortality rate that we want to estimate, and Δ_p the offset in years between A0

166   and A1+ data. This offset will be set to either one or two years.

167   Given equations 1 and 2, if

168    $\{\mu_{A0}(y_1)...,\mu_{A0}(Y-\Delta_p)\,N_{A0}(y_1)...,N_{A0}(Y-\Delta_p)\,\mu_{A1+}(y_1+\Delta_p-1)\,N_{A1+}(y_1+\Delta_p-1)\,M\}$ are

169   known, A1+ mean CW and abundance can be estimated for years y_1+1 to Y.

170

171   **Parameter estimations.** The set of parameters

172      $\theta = \{N_{A0}(y_1)...,N_{A0}(Y-\Delta_p) \quad \mu_{A0}(y_1)...,\mu_{A0}(Y-\Delta_p)N_{A1+}(y_1+\Delta_p-1)\mu_{A1+}(y_1+\Delta_p-1)q,M\}$ is

173   estimated (with q the survey catchability, i.e. the ratio between abundance index and abundance)

174   by maximising a likelihood function. Two types of data were included in the likelihood function

175   for both A0 and A1+ groups: (i) mean CW and (ii) abundance index.

176   Assuming that the number of sampled crabs was sufficient, the law of large numbers implies

177   that observed mean CW of A0 and A1+ groups follow a normal distribution of means $\mu_{A0}(y)$ and

178      $\mu_{A1+}(y)$, and of standard errors $SE_{A0}(y)$ and $SE_{A1+}(y)$. Thus, the log-likelihood for CW is:

179   3) $logL_{cw}(\theta) = \frac{1}{2} \cdot \sum_{y=y_1}^{y=Y-\Delta_p} \left[\frac{\overline{cw_{A0}(y)} - \mu_{A0}(y)}{\max(SE_{A0}(y),2.38)} \right]^2 + \frac{1}{2} \cdot \sum_{y=y_1+\Delta_p-1}^{y=Y} \left[\frac{\overline{cw_{A1+}(y)} - \mu_{A1+}(y)}{\max(SE_{A1+}(y),2.38)} \right]^2$

180   In equation 3, 2.38 corresponds to average CW class width (converted from log values to mm):

181   we considered that mean standard errors could not be inferior to this width.

182   We assumed that the abundance indices of A0 and A1+ groups provided by the survey

183   followed a lognormal distribution of means $q\,N_{A0}(y)$ and $q\,N_{A1+i}(y)$. Thus, from Deriso et al.

184   (2007), the log-likelihood for abundance indices is:

185   4) $logL_C(\theta) = -\frac{1}{2} \cdot n \cdot \log \left[\sum_{y=y_1}^{y=Y-\Delta_p} \left(\log(q \cdot N_{A0}(y)) - \log(U_{A0}(y)) \right)^2 + \sum_{y=y_1+\Delta_p-1}^{y=Y} \left(\log(q \cdot N_{A1+}(y)) - \log(U_{A1+}(y)) \right)^2 \right]$,

186   with n the number of observations in the dataset. Consequently, parameters are estimated by

187   maximising:

188   5) $logL(\theta) = logL_C(\theta) + logL_{cw}(\theta)$

189   The model was also fitted assuming distinct natural mortality for A0 and A1+ groups.

190   The Bayesian Information Criterion (BIC; see Schwarz 1978, Burnham & Anderson 2002)

191   was used to determine whether a two-year offset was more appropriate for estimating natural

192   mortality than a one-year offset. The model with the smallest BIC was expected to be the best.

193   The same approach was also used to test whether distinct natural mortality rates for A0 and A1+

194   groups are more appropriate than a common natural mortality rate.

195

196   **Egg production.** Analytical results were combined with fecundity estimates derived from

197   equations in Sainte-Marie (1993) to calculate (i) theoretical contributions of A0 and A1+ groups

198   to total population egg production assuming that all females reproduced annually or biennially

199   (estimated numbers of A0 females and A1+ females multiplied by estimated fecundity at mean

200   CW for the two female reproductive groups) and (ii) the expected lifetime production of eggs by

201   a female (number of eggs per clutch multiplied by the survival probability) at one of two sizes

202   and in warm or cold conditions (i.e. annual vs biennial reproduction). The two selected sizes,

203   45.6 and 57.3 mm CW, correspond to the range of observed mean CW for primipara in Baie

204   Sainte-Marguerite over the period 1991–2012. The number of eggs per clutch for a given body

205   size is assumed to be independent of temperature regime, and there is no allowance in our

206   calculations for a likely reduction in egg number per clutch among senescent multipara (e.g. Kon

207   et al. 2010).

208

209   **RESULTS**

210   Strong positive correlations (p < 0.001) between A1+ and A0 adult female groups existed for

211   mean CW and abundance index with one-year or two-year offsets, although for both variables

212   the correlation was slightly weaker at an offset of one year compared to two years (Fig. 2). The

213   intensity of correlation in mean CW and abundance index between the two female groups

214   progressively decreases at offsets greater than two years and becomes non-significant at an offset

215   of 4 to 5 years. The stronger correlation in abundance index between A0 and A1+ females at a

216   two-year offset, which is particularly apparent during the period 1995–1999 when A0 abundance

217   increased sharply (Fig. 1), can raise a question about the trawl's efficiency at sampling A1

218   females (i.e. females that became adult in the year preceding the survey). This concern motivated

219   the use of one or two-year offsets between the two female groups when modelling mortality rate:

220   if A1 females are not sampled, A0 females suffer two years of mortality before being detected in

221   the A1+ group as A2 females.

222   Our simple model was able to fit the variation in mean CW and abundance during the passing

223   of the two successive recruitment waves (Fig. 3). The variations in abundance were especially

224   well described by the model when assuming a one-year offset between A0 and A1+ females;

225   however, the model described variations in mean CW equally as well with either offset.

226   Estimates of natural mortality rate derived from the model were quite high: 0.78 year^{-1} (s.e.

227   0.07 year^{-1}) for a one-year offset and 0.66 year^{-1} (s.e. 0.05 year^{-1}) when assuming a two-year

228   offset. These high values imply that only 45.8% (one-year offset) or 51.7% (two-year offset) of

229   females survived more than one year after their terminal molt and that only 21.0% or 26.7%

230   respectively survived at least two years, i.e. the time required for eggs to develop and hatch in

231   cold conditions. The model was also applied assuming A0 and A1+ females have distinct

232   mortality rates, but confidence intervals were huge and the model became over-parameterized;

233   consequently, it was not possible to conclude whether natural mortality was different between the

234   two female groups. We, therefore, focused on a model assuming a common mortality rate for

235   both A0 and A1+ females. The BIC value of the model was lower (i.e. preferred) with a two-year

236   offset (BIC = 3880.5) than with a one-year offset (BIC = 4244.5) between the A0 and A1+

237   females. This suggests, as above, that there could be a catchability issue with A1 females. Thus,

238   the following analyses of egg production are based on natural mortality rate estimated with a

239   two-year offset.

240   Estimates of egg production at the individual or population level suggest strongly that

241   primipara play a key role in snow crab reproduction and population dynamics. The first clutch

242   represents nearly half (43.9%) of the expected lifetime egg production of an adult female in

243   warm conditions and >69.7% in cold conditions (Fig. 4), even though primipara are about 20%

244   less fecund at size than multipara (Sainte-Marie 1993). Estimated total annual population egg

245   production was variable over time due to pulsed recruitment (Fig. 5), but on average would have

246   been 1.75 times higher under annual compared to biennial reproduction. Figure 5 shows that the

247   relative contribution of A0 and A1+ females to estimated population egg production changed

248   over the years in relation to the passing of the strong recruitment wave of 1995–1999. A0

249   females produced a greater share of eggs than A1+ females at the beginning of the period of high

250   adult female abundance, and the reverse was true at the end of that period and during the

251   subsequent recruitment trough. The inversion of relative contribution to total egg production

252   toward the end of a recruitment wave reflects the accumulation of older females (multipara) with

253   greater per capita fecundity in conjunction with much reduced primipara abundance. This pattern

254   of shifting relative shares of egg production between the two female reproductive stages was

255   more striking when assuming biennial reproduction than when assuming annual reproduction.

256   Under the scenario of biennial reproduction, which may best describe Gulf of St. Lawrence snow

257   crab (Sainte-Marie 1993, Moriyasu & Lanteigne 1998, Comeau et al. 1999), A0 females were

258   responsible for more than 90% of population egg production in 1995–1998 as well as in 2008–

259   2010 (Fig. 5) and for an estimated 81% over all of the period 1992–2010.

260

261 **DISCUSSION**

262   This paper presents an original approach for estimating natural mortality of snow crab adult

263 females. The method innovates in combining classic accounting of crab numbers with the

264 autocorrelated interannual variability of body size of recruiting adult females as a tracer for

265 resolving mortality rates in a natural population. This approach is rather generic and may

266 probably be applied to other crustacean populations with a terminal molt, insofar as they are

267 seasonally-breeding, univoltine (or perhaps even bivoltine), and exhibit interannual variability of

268 adult body size and numbers. The natural mortality estimate we obtained (0.66 year^{-1}) is high but

269 similar to estimates of 0.53–1.02 year^{-1} for sublegal (< 95 mm CW) snow crab adult males in the

270 southern Gulf of St. Lawrence (Wade et al. 2003) and less than estimates reported for adult

271 females of other crab species with a terminal molt (Miller et al. 2005, Hewitt et al. 2007, Zheng

272 2005). For snow crab specifically, natural mortality of adult females was estimated at 0.56 year^{-1}

273 in two distinct studies: one performed in a small (13.7 km^2) marine reserve in the Sea of Japan

274 using tag-recapture methods (Yamasaki et al. 2001) and the other at the scale of the eastern

275 Bering Sea using numerical accounting (Zheng 2003).

276   The simultaneous use of two different variables, mean CW and abundance index, for

277 calculating snow crab natural mortality may provide more robust and reliable estimates than any

278 single variable. However, we estimated natural mortality using each variable separately

279 (assuming a two-year offset): the value was 0.63 year^{-1} (s.e. 0.06 year^{-1}) when fitting the model

280 on abundance indices and was 0.68 year^{-1} when only carapace widths were used. It was not

281 possible to estimate confidence intervals in this last case because the model was

282 overparameterized. Our best estimate using the mean CW and abundance index (0.66 year^{-1}) is

283 thus a compromise between those two values.

284   The method proposed herein for estimating natural mortality depends on several important

285   assumptions. The first is that classification of A0 and A1+ females is faultless. While there is

286   good reason to believe that the accuracy of classification is very high (see methods),

287   misclassification of A1+ females as A0 females would lead to an overestimation of natural

288   mortality while the reverse would lead to an underestimation. The second assumption is that

289   adult females in all pseudo-cohorts are equally catchable. However, visual examination of trends

290   in mean CW and abundance index and correlation analysis suggest that catchability of A1

291   females may have been low relative to females in other pseudo-cohorts. This possibility was

292   taken into account by fitting the model with two different offsets between A0 and A1+ females:

293   the one-year offset assumes that A1 female catchability is similar to that of other adult females,

294   while the two-year offset assumes that A1 females are not catchable at all. The better

295   performance of the model with a two-year offset is consistent with the idea that catchability of

296   A1 females is low. A possible reason for this is the ontogenetic migration after terminal molt

297   from shallow molting grounds to deep multiparous female habitat (Sainte-Marie & Hazel 1992,

298   Lovrich et al. 1995, Ernst et al. 2005). In Baie Sainte-Marguerite, this migration may occur over

299   a period of a year or so on relatively steep slopes where our small beam trawl may not perform

300   well. Alternatively or complementarily, A1 females might behave differently, perhaps burying

301   more, than other adult females. Additionally, we assume that there is no net immigration or

302   emigration of A0 or A1+ females into, or away from, the relatively small study area. Finally, we

303   posit that snow crab adult females are not subject to direct or indirect fishing mortality ($F = 0$)

304   and that natural mortality is independent of their body size.

305   Hewitt & Hoening (2005) proposed the equation 4.22 divided by maximum longevity as a

306   rule of thumb for estimating natural mortality in various marine animal taxa. Applying this rule

307 to snow crab adult females, with mean age at terminal molt to adulthood set at 7 years and

308 subsequent maximum life expectancy ranging from 3 to 9 years (see introduction) produces

309 natural mortality estimates of 0.42 to 0.26 year^{-1} (4.22/10 or 4.22/16). These estimates represent

310 average natural mortality over the lifetime of a female and are lower than ours, which represent

311 natural mortality of a female after terminal molt only. Prominent causes of natural mortality for

312 pre-adult and adult females include fish predators such as skates and cod (Robichaud et al. 1991,

313 Chabot et al. 2008) and in some areas (but not the northern Gulf of St. Lawrence) bitter crab

314 disease (Shields et al. 2007, Mullowney et al. 2011). However, natural mortality rates of adult

315 females may be higher on average than those of pre-adult females because of density-dependent

316 sexual conflicts arising during the female's first mating period, which is intimately associated

317 with terminal molt (Sainte-Marie et al. 2008; see Adler & Bonduriansky 2011 for more general

318 considerations on sex ratio, density and the rate of ageing). When the snow crab adult sex ratio is

319 strongly biased towards males, dominant males may forcefully take over females from other

320 males or coerce females into mating, sometimes inflicting immediate death or severe injuries

321 (e.g. multiple limb loss) that will curtail female life expectancy; when the adult sex ratio is

322 strongly biased towards females, dominant males reduce guard time and the vulnerable, newly-

323 molted females may be subject to harassment by subordinate males and exposed to predators

324 (Sainte-Marie & Hazel 1992, Sainte-Marie et al. 2008 and references therein). Adult female

325 mortality rates may be less at more balanced sex ratios: it will probably be possible to include

326 density-dependence in the model to account for this source of variability in natural mortality

327 when the times-series becomes longer.

328 　　We have not yet attempted to estimate natural mortality for adult male snow crab. Males also

329 undergo a terminal molt and their abundance index and mean CW change over the years (Sainte-

330   Marie et al. 2008), but large adult males are targeted by the fishery and consequently it is more

331   difficult to distinguish between natural and fishing mortality. It may, however, be possible to

332   estimate natural mortality for sublegal (< 95 mm CW) adult males using our method. Our

333   method certainly cannot be used for determining natural mortality of pre-adult snow crab, so

334   additional studies by tagging or other methods (e.g. Kilada et al. 2012) will be needed to improve

335   natural mortality estimates for snow crab in general.

336   Our high estimate of natural mortality for adult females has important implications for the

337   perception of relative contributions of primipara and multipara to population egg production.

338   Although multipara are more fecund at size than primipara (Sainte-Marie 1993), primipara are

339   expected to contribute a large share of population egg production in both cold and warm

340   conditions. Note that the primipara share of population egg production may be underestimated,

341   as we did not take into account a possible reduction in fecundity at size in senescing multipara

342   (see Kon et al. 2010). Assuming no brood mortality, Sainte-Marie (1993) inferred that snow crab

343   primipara would produce > 40% of total larvae produced by biennially-reproducing females,

344   which is comparable to our estimate of the primipara average share of egg production in warm

345   conditions (43.9% over the study period) but smaller than our estimate of primipara average

346   share in cold conditions (69.7%). However, it is clear from our study that decadal oscillations

347   occur in the relative contributions of primipara and multipara to annual egg production. Due to

348   differences in size (quality) of primipara and multipara eggs (Sainte-Marie 1993) and

349   unaccounted brood mortality, which might differ between the two female reproductive stages, we

350   cannot currently determine the respective contributions of primipara and multipara to

351   recruitment. Nevertheless, this and other studies (e.g Ernst et al. 2012) can suggest that snow

352   crab should be managed to ensure high reproductive success of primiparous females.

353

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359   Collaborative Program to HD.

360

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List of figures
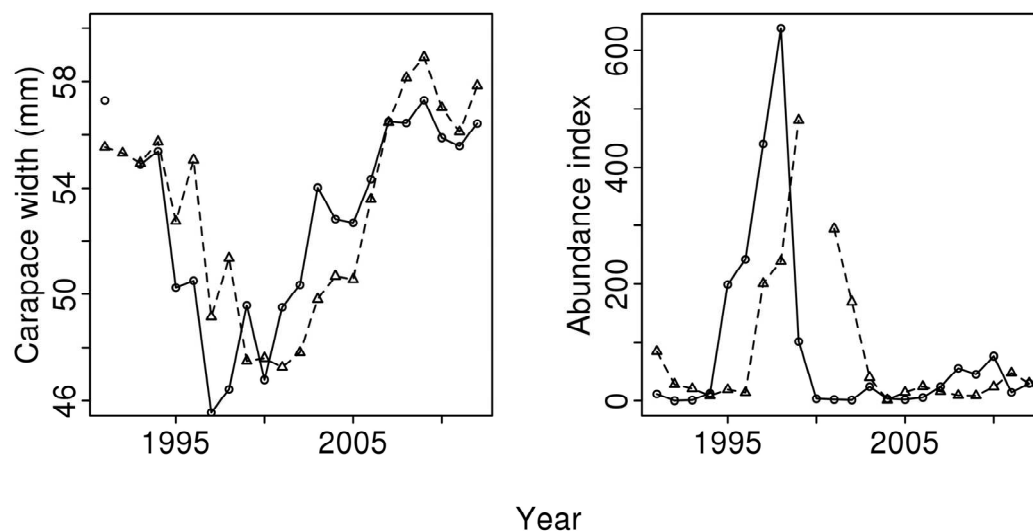
Year

361   Fig. 1. Variation of mean carapace width (left) and abundance index (right) of snow crab females

362   recruited to the Baie Sainte-Marguerite population in the survey year (A0, solid lines and circles)

363   or in previous years (A1+, dashed lines and triangles) during the passing of two successive

364   recruitment waves (1995–1999 and 2008–2010). Abundance index is standardized to A0

365   abundance in 1993. A1+ abundance in 2000 is not shown because it is unrealistically high

366   (abundance = 2,831).
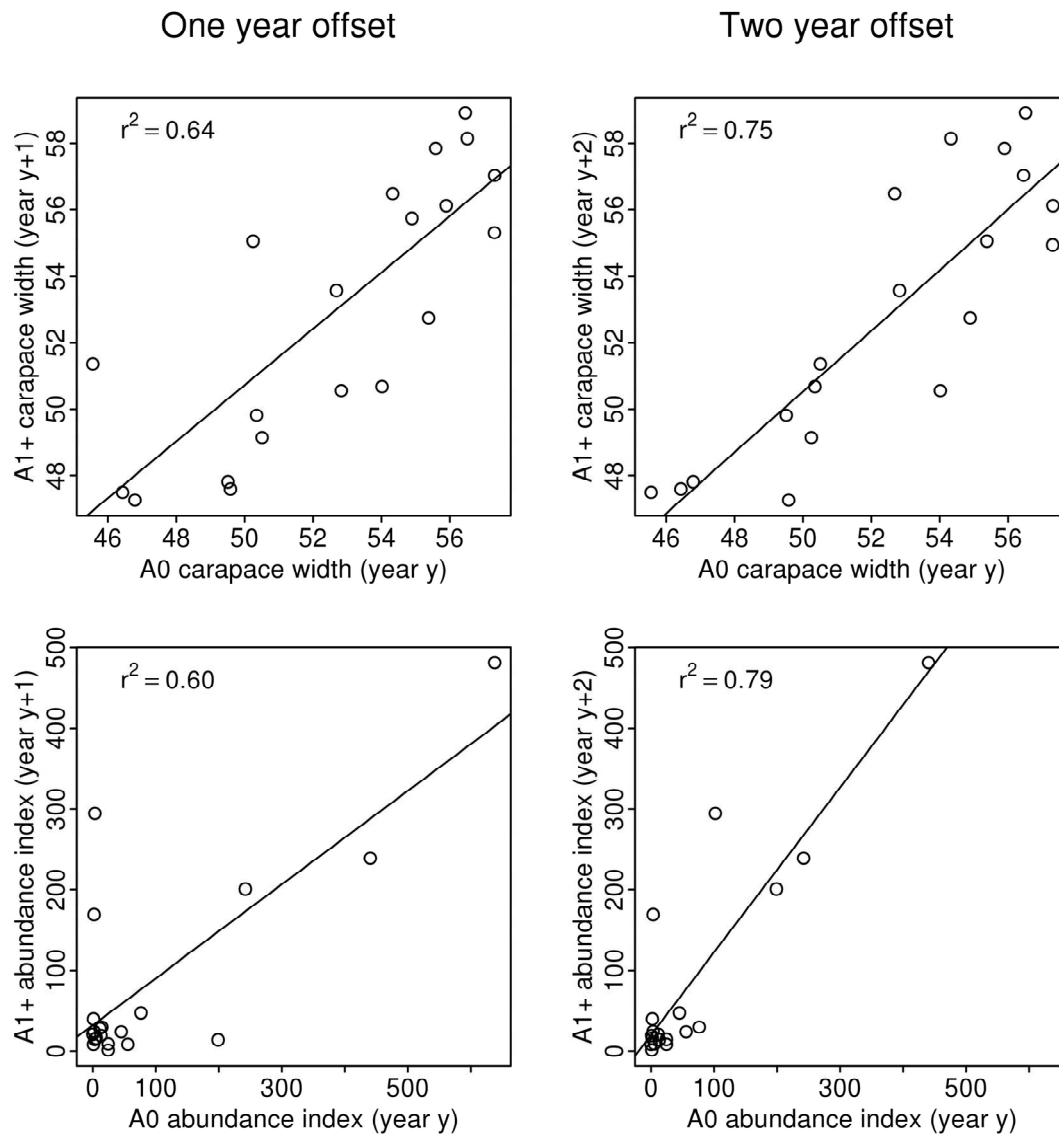
367

368   Fig. 2. Correlation in mean carapace width (top, measured in mm) and abundance index (bottom)

369   between snow crab adult females recruited to the Baie Sainte-Marguerite population in the

370   survey year (A0) and those recruited in previous years (A1+), over the period 1991–2012, with a

371   one-year (left) or two-year (right) offset.

372
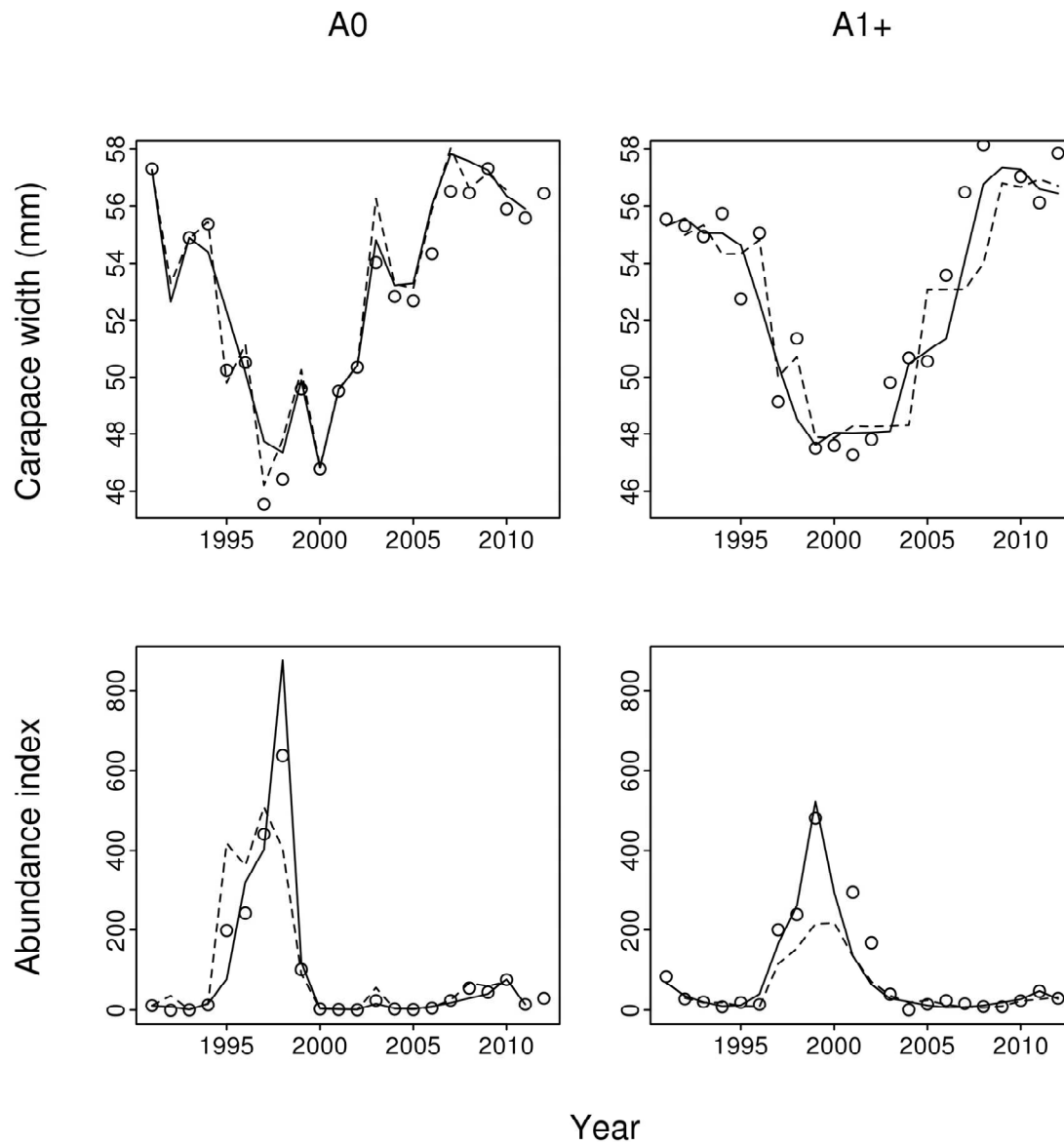
373   Fig. 3. Observed (open circles) and estimated (lines) mean carapace width (top) and abundance

374   index (bottom) for snow crab adult females recruited to the Baie Sainte-Marguerite population in

375   the survey year (A0) and those recruited in previous years (A1+) when assuming a one-year

376   (solid line) or two-year (dashed line) offset between the two female groups.
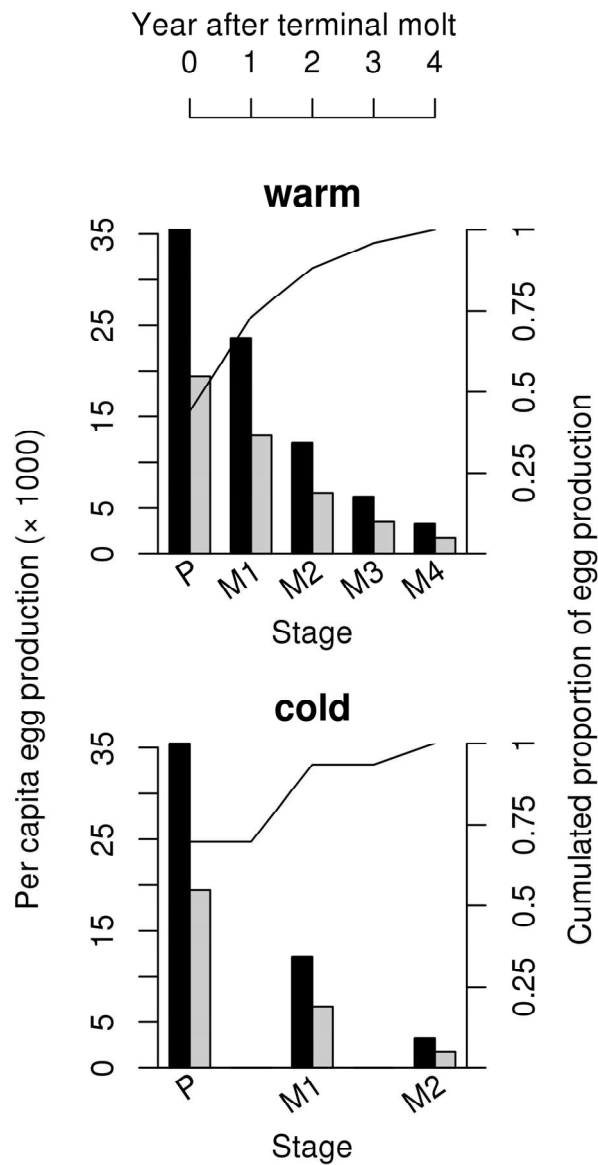
377

378   Fig. 4. Probabilistic lifetime egg production of snow crab adult females under warm (annual

379   reproduction) and cold (biennial reproduction) conditions. Females of 57.3 and 45.6 mm

380   carapace width (black and gray bars, respectively) are considered. Egg production in each

381   successive reproductive stage is weighted by survival probability, calculated from the estimated

382   mortality rate of 0.66 year^{-1}. The full black line represents proportional contribution of each

383   reproductive stage to lifetime reproductive output (P=primiparous oviposition, M1=multiparous

384   first oviposition event, M2=multiparous second oviposition event, etc).

385   Year
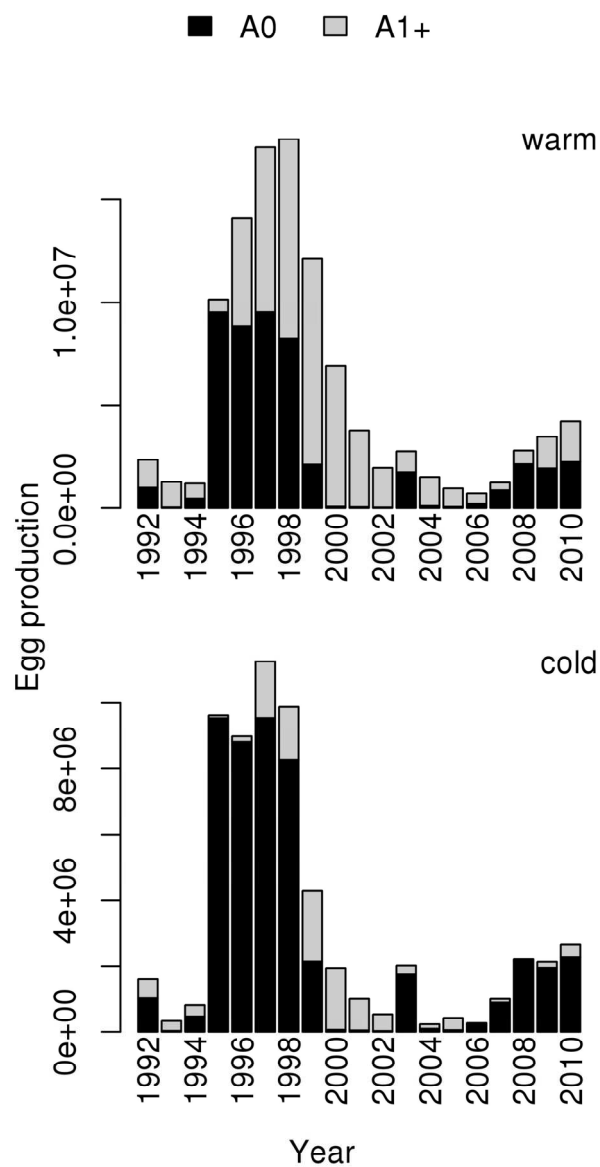
386   Fig. 5. Contribution of A0 (black) and A1+ (grey) to yearly egg production of the snow crab

387   population in Baie Sainte-Marguerite assuming that females reproduce annually (i.e. warm

388   conditions, top) or bienially (i.e. cold conditions, bottom), based on estimated abundance indices

389   and mean carapace widths.