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1 Estimating natural mortality and egg production of snow crab (*Chionoecetes*
2 *opilio*) adult females

3

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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" ($> 0.75^{\circ}\text{C}$) conditions so females reproduce
86 annually, or in about two years in "cold" ($< 0.75^{\circ}\text{C}$) 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. 2012). 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 ($\sim 400 \text{ km}^2$) 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 $SE_{A0}^2(y)$ and $SE_{A1+}^2(y)$.

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

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

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

170

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

172 $\theta = \{N_{A0}(y_1), \dots, N_{A0}(Y - \Delta_p), \mu_{A0}(y_1), \dots, \mu_{A0}(Y - \Delta_p), N_{A1+}(y_1 + \Delta_p - 1), \mu_{A1+}(y_1 + \Delta_p - 1), q, M\}$ 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)
$$\log L_{cw}(\theta) = \frac{1}{2} \cdot \sum_{y=y_1}^{y=Y-\Delta_p} \left[\frac{cw_{A0}(y) - \mu_{A0}(y)}{\max(SE_{A0}(y), 2.38)} \right]^2 + \frac{1}{2} \cdot \sum_{y=y_1+\Delta_p-1}^{y=Y} \left[\frac{cw_{A1+}(y) - \mu_{A1+}(y)}{\max(SE_{A1+}(y), 2.38)} \right]^2$$

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

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

187 maximising:

188 5)
$$\log L(\theta) = \log L_c(\theta) + \log L_{cw}(\theta)$$

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 $0.53\text{--}1.02 \text{ year}^{-1}$ for sublegal ($< 95 \text{ mm CW}$) 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, Mullaney 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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360

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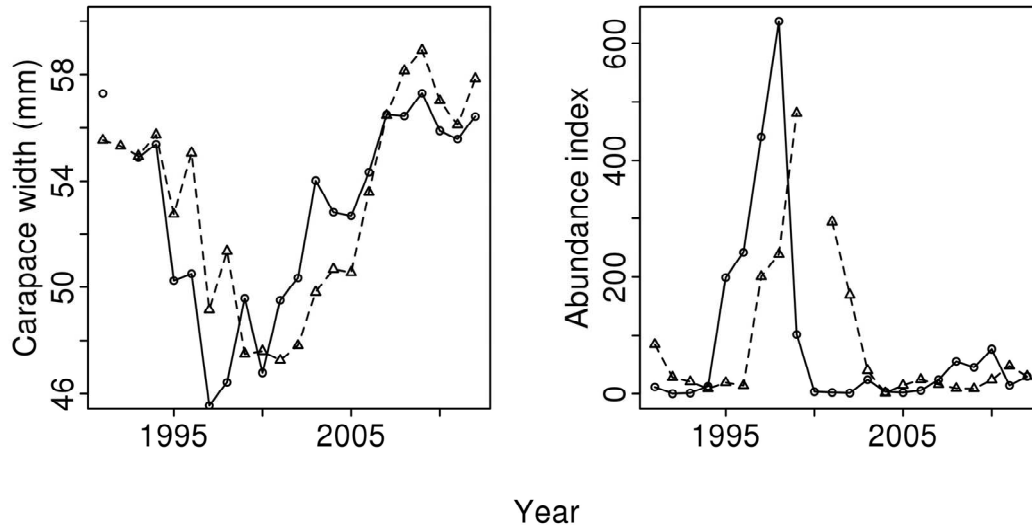
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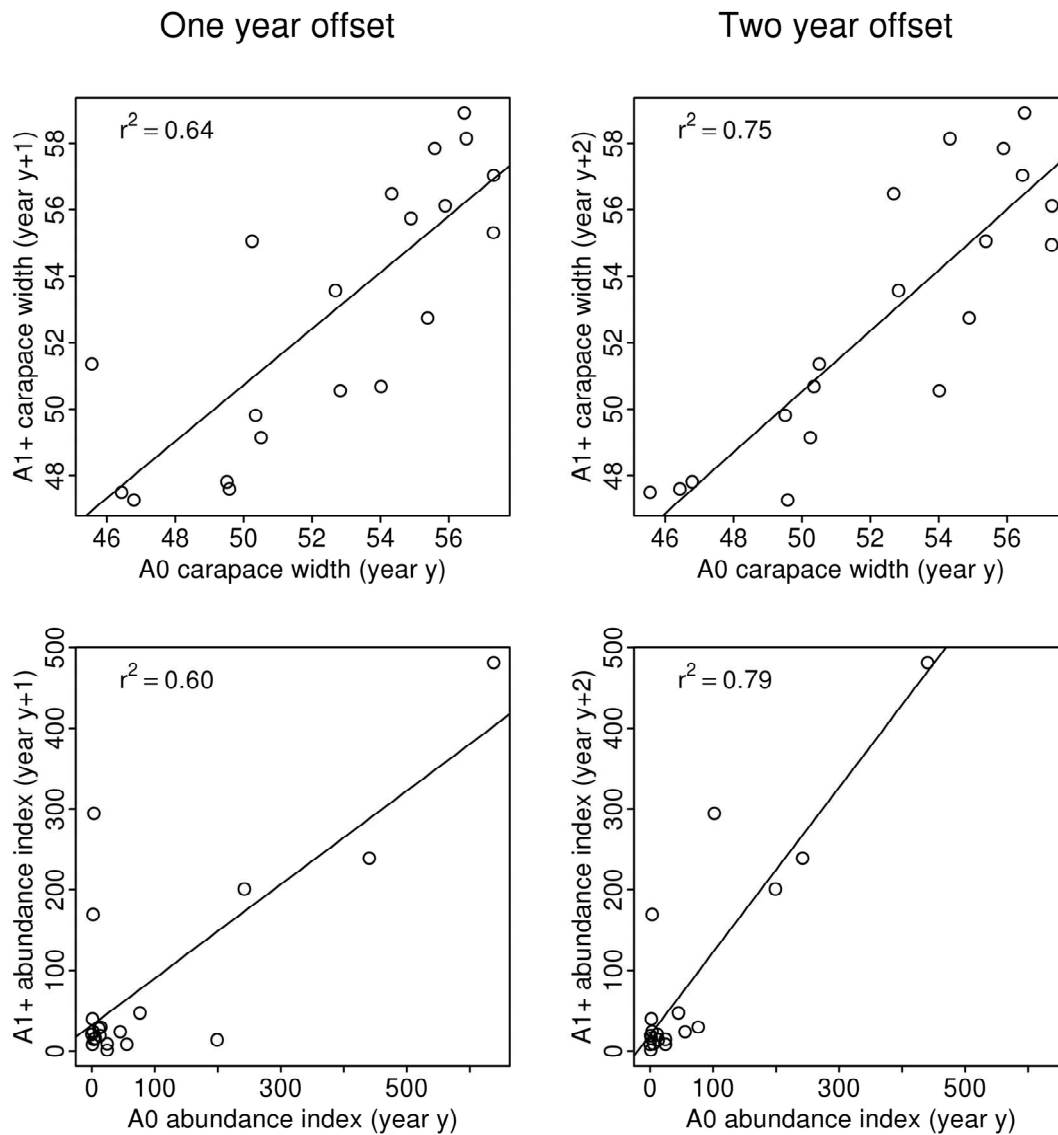
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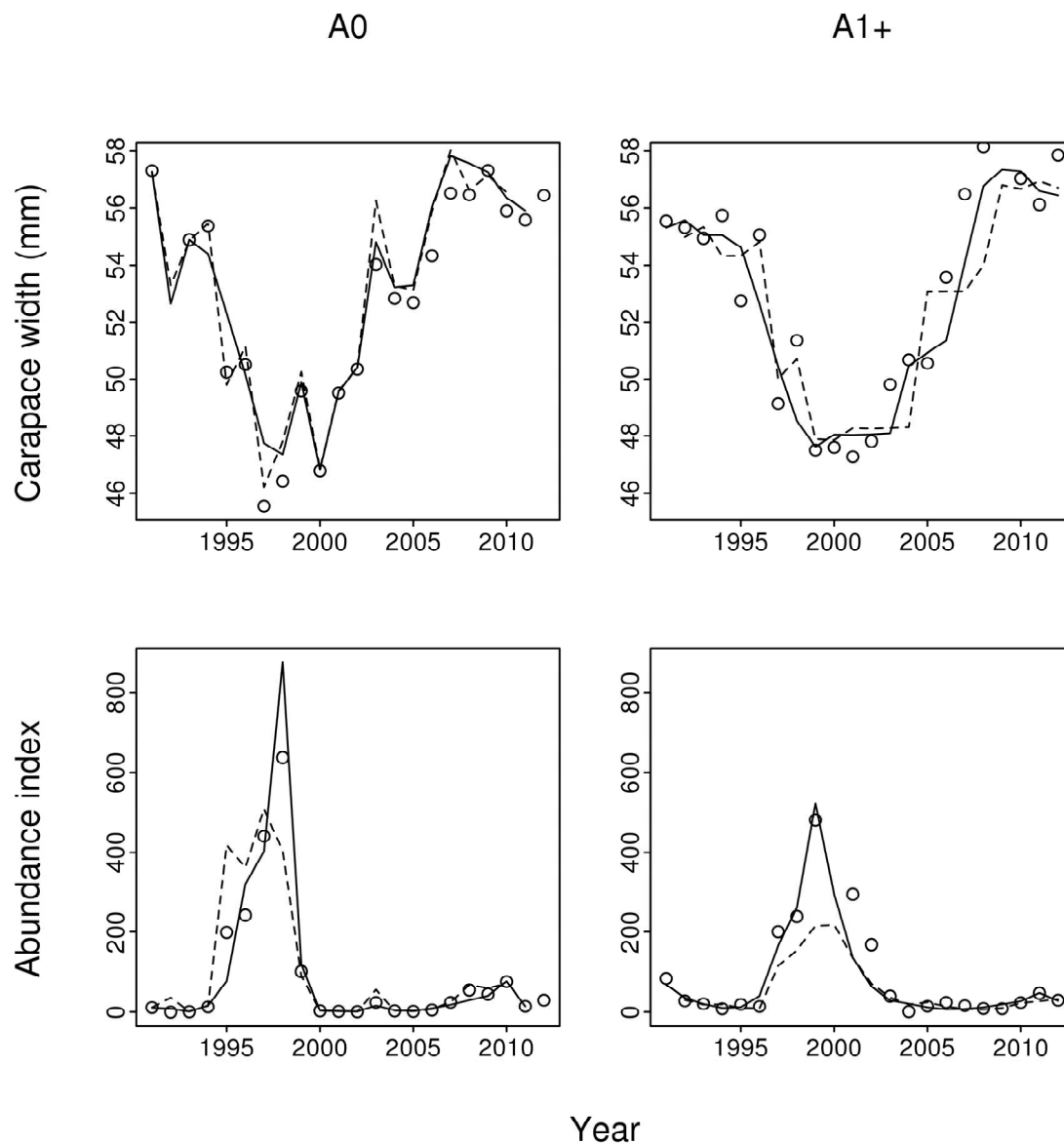


361 Fig. 1. Variation of mean carapace width (left) and abundance index (right) of snow crab females
362 recruited to the Baie Sainte-Marguerite population in the survey year (A0, solid lines and circles)
363 or in previous years (A1+, dashed lines and triangles) during the passing of two successive
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).



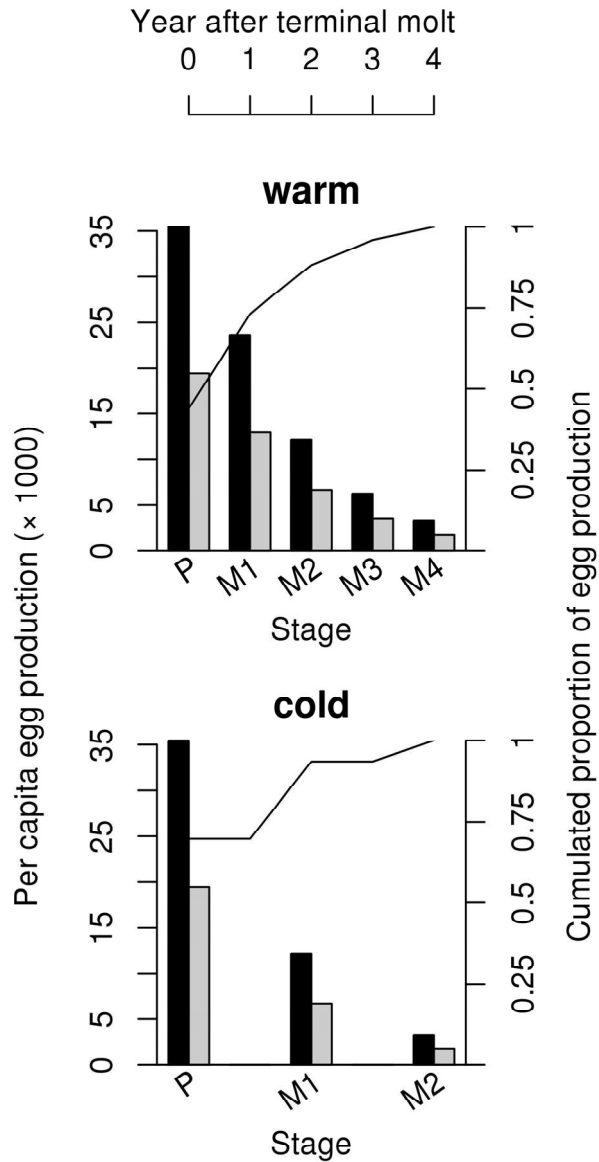
367

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

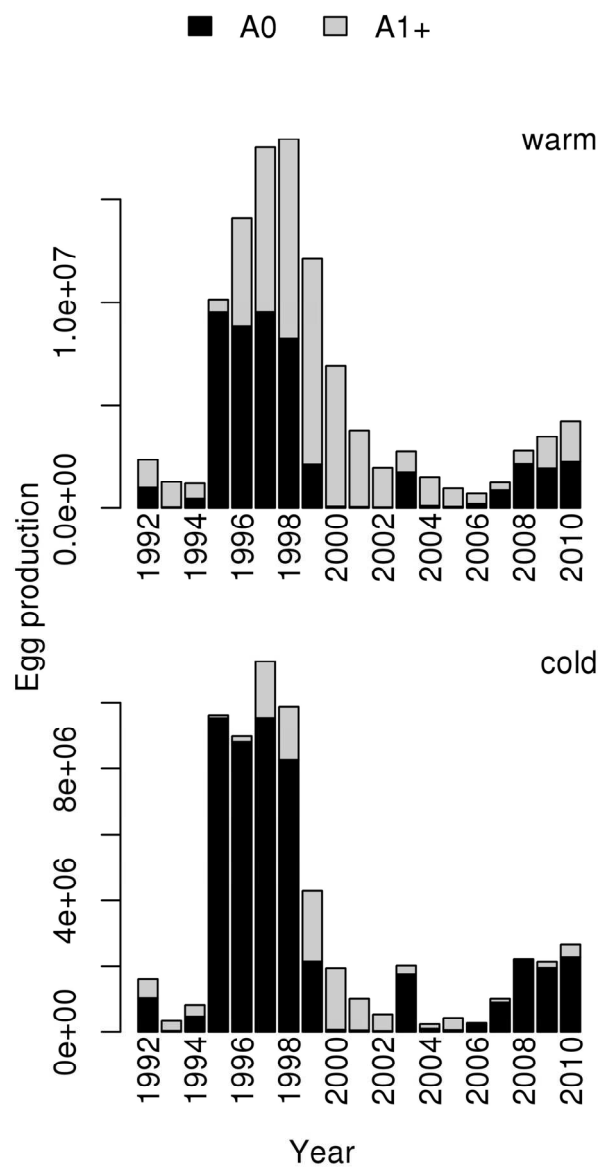
373 Fig. 3. Observed (open circles) and estimated (lines) mean carapace width (top) and abundance
374 index (bottom) for snow crab adult females recruited to the Baie Sainte-Marguerite population in
375 the survey year (A0) and those recruited in previous years (A1+) when assuming a one-year
376 (solid 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

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 biennially (i.e. cold conditions, bottom), based on estimated abundance indices

389 and mean carapace widths.