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

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ABSTRACT: The natural mortality rate is a key parameter in ecology and fisheries, but it may be difficult to estimate as it is highly variable and often confounded with other factors such as fishing mortality and migration. This is especially true for crustaceans in general, as age determination is problematic, and for snow crabs *Chionoecetes opilio* in particular because density-dependent processes may lead to highly variable mortality rates across life history stages. In this context, we developed an original method to estimate the natural mortality rate of adult (i.e. terminally molted) female snow crab, and its consequences on egg production. This new method relies on shell condition, carapace width and abundance of adult females and was applied to a time series (1991–2012) of annual trawl survey data for a snow crab population in the Gulf of St. Lawrence, eastern Canada. Two natural mortality estimates were provided by the method depending on 2 distinct assumptions about the survey. Both estimates (0.66 and 0.78 yr^{-1}) were high compared to previous estimates for snow crab. These values imply that female life expectancy after terminal molt was short and that primiparous females (first-time spawners) contributed a large share (at least 81%) of the total number of eggs produced by the case-study population over the period 1992 to 2010.

KEY WORDS: *Chionoecetes opilio* · Natural mortality · Terminal molt · Body size · Egg production

INTRODUCTION

Knowledge of natural mortality is of paramount importance in ecological and fishery sciences (e.g. Defeo & Cardoso 2002, Lipcius & Stockhausen 2002). Natural mortality is a key determinant of the potential productivity of a population and, consequently, of a species' potential to resist environmental stressors or to sustain exploitation. Natural mortality rates are especially difficult to estimate because they are generally highly variable across life-history stages and because in exploited species they may be confounded with direct or indirect fishing mortality. This is especially true for several harvested crabs (Zheng 2005) in which density-dependent processes, such as

cannibalism (Sainte-Marie & Lafrance 2002), may cause mortality rates to vary through ontogeny.

Estimation of natural mortality rates usually depends on knowledge of individual age, which has never been determined directly for crabs and other crustaceans because there are no known body parts recording annual age marks (e.g. Vogt 2012). Consequently, various other methods have been proposed or used to estimate crab natural mortality rates. Tagging experiments have been widely employed (e.g. Siddeek et al. 2002, Lambert et al. 2006), but this technique is more difficult to apply to crabs than to fishes, because of molting, and is generally expensive. Indirect methods such as length-based models have also been used to provide estimates of natural

mortality rates (Zheng et al. 1995a,b, Siddeek et al. 2002), but these models generally require a large amount of data to provide reliable estimates. In the last few decades, methods have been developed and applied to assess age via the neural pigment lipofuscin — while these methods do not allow precise individual age determination, they do assign a probable age to individuals based on the average rate of lipofuscin accumulation (Puckett et al. 2008, Sheehy & Prior 2008).

In the many crab species with a terminal molt, such as those belonging to the genera *Chionoecetes* and *Maja*, natural tags (epibionts) and shell condition (Dick et al. 1998), carapace radiometry (Le Foll et al. 1989, Ernst et al. 2005) and dactyl wear (Fonseca et al. 2008, Fahy & Carroll 2009) have also been proposed as methods for determining relative age (since terminal molt) and mortality rates for the ultimate, reproductive life-history phase, called adult. However, each of these methods has its drawbacks, including uncertainty and/or cost. For example, time of epibiont settlement and subsequent growth rate are generally unknown, carapace radiometry is costly and assumes that shell composition is static from time of molt (no minerals added), and dactyls may wear differently among individuals. Recently, Kilada et al. (2012) proposed that age may be recorded in the eye-stalk of some decapod crustaceans, including snow crab, but the method must be further validated especially with regard to its application to terminally molted individuals (C. Vanier pers. comm.).

The present study examines survival of adult (i.e. terminally molted and sexually mature) female snow crabs *Chionoecetes opilio* (Oregoniidae, Majoidea) and its consequences for egg production using a new approach for determining mortality. The case-study population is located in the northwestern Gulf of St. Lawrence, eastern Canada. Fishery regulations impose a strict ban on the landing of female snow crabs in eastern Canada, so female survival after terminal molt should largely reflect natural mortality. Snow crab terminal molt can occur at variable instars, with females becoming adult on average at a smaller size (instar) and a younger age than males. In the Gulf of St. Lawrence, most females become adult in Instars IX to XI, which correspond to a post-hatching age of about 6 to 8 yr, and most males, in Instars IX to XIV at about 6 to 11 yr (Sainte-Marie et al. 1995, Alunno-Bruscia & Sainte-Marie 1998, Comeau et al. 1998). The female terminal molt to maturity occurs sometime between late December and April (Alunno-Bruscia & Sainte-Marie 1998). Females can be inseminated by males shortly after this molt and thereafter

experience a transition through 3 reproductive stages: (1) 'nulliparous' from time of terminal molt until they extrude their first egg clutch, which happens usually hours or days after molting/mating; (2) 'primiparous' after extruding their first egg clutch; and (3) 'multiparous' after extruding their second or an ulterior clutch (Sainte-Marie et al. 2008, 2010). Primiparous and multiparous females have different reproductive outputs, the former extruding eggs that are about 20% fewer per clutch but about 2% larger in diameter than those of similarly sized multipara (Sainte-Marie 1993). Eggs are brooded beneath the female's abdomen and develop and hatch out as larvae in about 1 yr in 'warm' (>0.75°C) conditions i.e. females reproduce annually, or in about 2 yr in 'cold' (<0.75°C) conditions i.e. females reproduce biennially (Moriyasu & Lanteigne 1998, Comeau et al. 1999, Sainte-Marie et al. 2008, Kuhn & Choi 2011).

Classification of adult female snow crabs into reproductive stages relies on shell condition: the exoskeleton is clean, iridescent and still soft in nullipara; clean, iridescent, but hardening in early primipara (<3 to 6 mo since terminal molt); and with additional time it progressively becomes fouled, dull and scarred. Shell fouling and scarring is more or less apparent in late primipara (about 6 mo to 2 yr since terminal molt in cold environments), depending on year and site, but it is usually obvious in multipara (Sainte-Marie 1993). Adult females have been assumed to survive mostly for 3 to 5 yr after terminal molt (Alunno-Bruscia & Sainte-Marie 1998, Comeau et al. 1998), but maximum longevities of 6 to 9 yr after terminal molt have been reported (Ernst et al. 2005, Gosselin 2009, Kon et al. 2010).

Adult females recruited to the snow crab population in a given year form a pseudo-cohort (term coined by Ernst et al. 2005), often with very distinct characteristics of abundance and mean size relative to other pseudo-cohorts. Variation in pseudo-cohort strength can be extreme (orders of magnitude), and recruitment of adult females occurs in multiyear waves or pulses (Sainte-Marie et al. 1996, 2008, Ernst et al. 2012). Waves (and intervening troughs) are thought to reflect episodic or quasi-cyclic oscillations in settlement intensity or early juvenile survival (Conan et al. 1996, Sainte-Marie et al. 1996, Ernst et al. 2012). Variation in mean body size of adult females in pseudo-cohorts may be inversely related to pseudo-cohort density and so mean body size also oscillates over time (Sainte-Marie et al. 1996, 2008, Orensanz et al. 2007, Ernst et al. 2012).

The objective of this study was to explore the combined use of shell condition (or reproductive stage),

abundance index and body size during the maturation of 2 successive recruitment waves for determining the natural mortality rate of adult female snow crab. We entertained this possibility because newly recruited adult females can, under some circumstances, be confidently recognized and the pseudo-cohort they form has distinct characteristics of abundance and mean size that could serve as tracers. Additionally, we estimated population and per capita egg production, and primipara and multipara shares of population egg production, using the estimated mortality rate under a scenario of annual or biennial female reproduction.

MATERIALS AND METHODS

Data

Every year (denoted y) from 1991 (denoted y_1) to 2012 (denoted Y), a beam trawl survey was carried out in Baie Sainte-Marguerite. This small ($\sim$400 km^2) bay is located in the northwestern Gulf of St. Lawrence, eastern Canada. A description of the survey is provided in Lovrich et al. (1995) and Sainte-Marie et al. (1996). Briefly, the survey was conducted between late April and late May, just after the end of the annual period for terminal molting of females. The survey design allocated at least 3 randomly positioned trawl sets in each of 3 depth strata: 4–20 m, 20–80 m and 80–140 m. This depth range covers essential female snow crab habitat during the spring. All sampled crabs were sexed, rated for shell condition (Sainte-Marie 1993), and females were measured for carapace width (CW, ±0.1 mm) and assigned a maturity status (pre-adult or adult) based on the relative size of their abdomen (Alunno-Bruscia & Sainte-Marie 1998).

Classification of adult females was further refined into 2 groups: newly recruited females (with a clean and soft, brittle or hard shell) denoted A0 or previous years' recruits (with a more or less fouled and scarred shell, corresponding to intermediate, dirty-hard, or dirty-soft shell conditions) denoted A1+. The distinction between new recruits and previous years' recruits was easy at the time of the survey and was confirmed post hoc each year by examination of the spermathecal content of a sample of adult females (n = 60 to 90) during routine monitoring of female reproductive success (Sainte-Marie et al. 2008). Stored ejaculates were all white in A0 females, indicating females had experienced only 1 recent mating period, whereas some or all of the ejaculates were

much darker (yellow-ochre to brown) in A1+ females due to storage for a year or more (Duluc et al. 2005). At the time of the survey, Group A0 was composed exclusively of primiparous females that had molted and oviposited sometime in the previous 4 to 5 mo, while Group A1+ was composed of all multiparous females and may have also included late primipara in their second year of egg incubation under cold conditions or late primipara close to hatching their clutch under warm conditions. Group A1+ may conceptually be subdivided into pseudo-cohorts: A1, A2, A3, etc. represent females that underwent terminal molt and became adult 1, 2, 3, etc. years, respectively, before the current survey year.

An index of abundance by 0.02 $\log_{10}$ classes of CW was calculated for each group of adult females based on the area swept by trawl sets and the area of each depth stratum. Thus, the survey provides annual abundance indices for A0 and A1+ groups (denoted $U_{A0}(y)$ and $U_{A1+}(y)$ respectively) and estimates of mean CW (denoted $\overline{CW_{A0}(y)}$ and $\overline{CW_{A1+}(y)}$, respectively) from year y_1 to Y. Standard errors for mean CW were calculated and denoted $SE_{A0}(y)$ and $SE_{A1+}(y)$. The size distribution of adult females in a given year may be approximated by a normal (Gaussian) distribution because they are mainly concentrated in 2 successive instars with largely overlapping sizes (Alunno-Bruscia & Sainte-Marie 1998, Burmeister & Sainte-Marie 2010).

Dynamic equations

If $\mu_{A0}(y)$ and $N_{A0}(y)$ denote Group A0 mean CW and abundance in the population in year y (as opposed to $\overline{CW_{A0}(y)}$ and $U_{A0}(y)$ which denote the mean carapace weight observed in survey samples and abundance indices), while $\mu_{A1+}(y)$ and $N_{A1+}(y)$ denote Group A1+ mean CW and abundance in year y, Group A1+ mean CW and abundance in the following year can easily be calculated by:

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

(expectation of the mixture of 2 Gaussian distributions) (1)

and

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

where M is the natural mortality rate that we want to estimate and Δ_p the offset in years between A0 and A1+ data. This offset will be set to either 1 or 2 yr.

Given Eqs. (1) & (2), if

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

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

Parameter estimations

The set of parameters (θ) was estimated,

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

where q is the survey catchability i.e. the ratio between abundance index and abundance, by maximizing a likelihood function. Two types of data were included in the likelihood function for both A0 and A1+ groups: (1) mean CW and (2) abundance index.

Assuming that the number of sampled crabs was sufficient, the law of large numbers implies that observed mean CW of A0 and A1+ groups follow a normal distribution of means $\mu_{A0}(y)$ and $\mu_{A1+}(y)$ and of standard errors $SE_{A0}(y)$ and $SE_{A1+}(y)$. Thus, the log-likelihood for carapace width (logL$_{CW}$) is:

$$\log L_{CW}(\mu) = \frac{1}{2}\cdot\sum_{y=y_1}^{y=Y-\Delta_p}\left[\frac{\overline{CW_{A0}(y)}-\mu_{A0}(y)}{\max(SE_{A0}(y),2.38)}\right]^2$$
$$+ \frac{1}{2}\cdot\sum_{y=y_1+\Delta_p-1}^{y=Y}\left[\frac{\overline{CW_{A1+}(y)}-\mu_{A1+}(y)}{\max(SE_{A1+}(y),2.38)}\right]^2 \quad (3)$$

In Eq. (3), 2.38 corresponds to the average CW class width (converted from log values to mm): we considered that mean standard errors could not be inferior to this width.

We assumed that the abundance indices of A0 and A1+ groups provided by the survey followed a log-normal distribution of means $qN_{A0}(y)$ and $qN_{A1+i}(y)$. Thus, from Deriso et al. (2007), the log-likelihood for abundance indices is:

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

where n is the number of observations in the dataset. Consequently, parameters are estimated by maximizing the total log-liklelihood:

$$\log L(\theta) = \log L_U(\theta)+\log L_{CW}(\theta) \quad (5)$$

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

The Bayesian information criterion (BIC; see Schwarz 1978, Burnham & Anderson 2002) was used to determine whether a 2 yr offset was more appropriate for estimating natural mortality than a 1 yr offset. The model with the smallest BIC was expected to be the best. The same approach was also used to test whether distinct natural mortality rates for A0 and A1+ groups are more appropriate than a common natural mortality rate.

Egg production

Analytical results were combined with fecundity estimates derived from equations in Sainte-Marie (1993) to calculate (1) theoretical contributions of A0 and A1+ groups to total population egg production assuming that all females reproduced annually or biennially (estimated numbers of A0 females and A1+ females multiplied by estimated fecundity at mean CW for the 2 female reproductive groups) and (2) the expected lifetime production of eggs by a female (number of eggs per clutch multiplied by the survival probability) at 1 of 2 sizes and in warm or cold conditions (i.e. annual vs. biennial reproduction). The 2 selected sizes, 45.6 and 57.3 mm CW, corresponded to the range of observed mean CW for primipara in Baie Sainte-Marguerite over the period 1991 to 2012. The number of eggs per clutch for a given body size was assumed to be independent of temperature regime, and there was no allowance in our calculations for a likely reduction in egg number per clutch among senescent multipara (e.g. Kon et al. 2010).

RESULTS

The time series of adult female abundance and body size in our case-study population are shown in Fig. 1. The primipara abundance index fluctuated inter-annually by several orders of magnitude, through one very strong (1995 to 1999) and one weak (2008 to 2010) recruitment wave, and was negatively correlated with primipara mean body size (r = −0.618, p = 0.003).

Strong positive correlations (p < 0.001) between A1+ and A0 adult female groups of snow crabs existed for mean CW and abundance index with 1 or 2 yr offsets, although for both variables the correlation was slightly weaker at an offset of 1 yr compared to
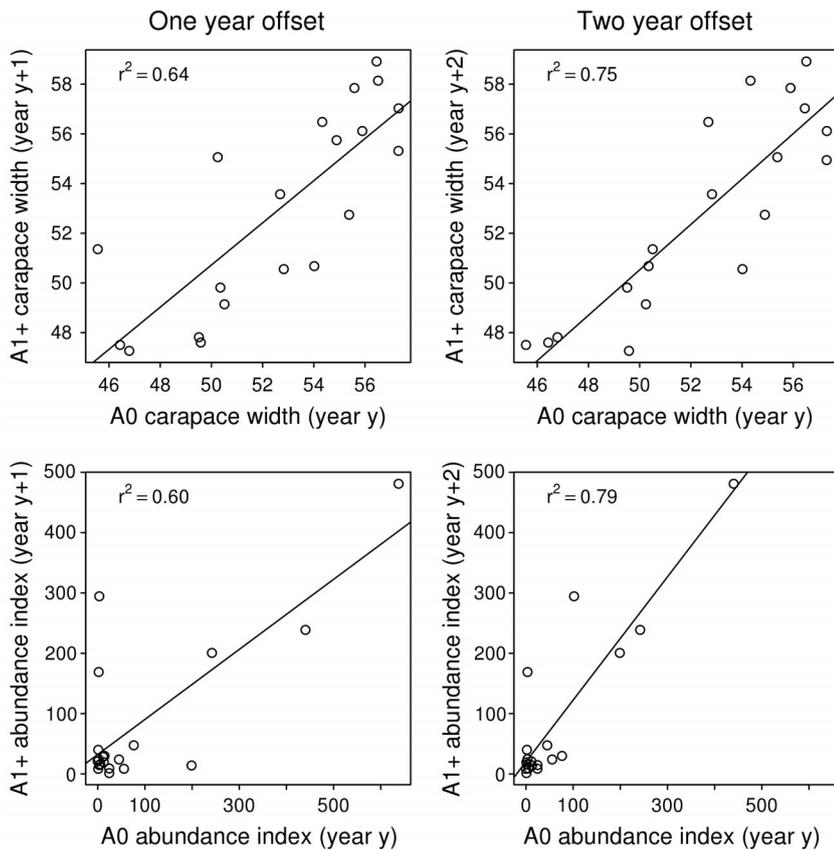
Fig. 1. *Chionoecetes opilio*. Correlation in mean carapace width (mm) and abundance index between adult female snow crabs recruited to the Baie Sainte-Marguerite population in the survey year (A0) and those recruited in previous years (A1+), over the period 1991–2012, with a 1 yr or 2 yr offset
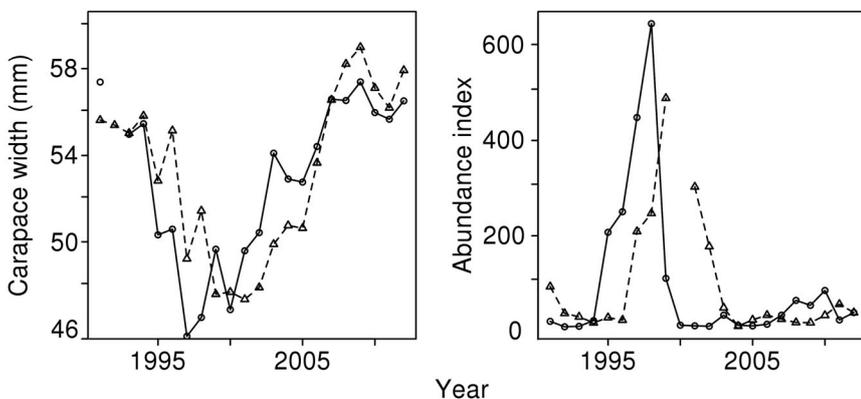

Fig. 2. *Chionoecetes opilio*. Variation of mean carapace width and abundance index of female snow crabs recruited to the Baie Sainte-Marguerite population in the survey year (A0, solid lines and circles) or in previous years (A1+, dashed lines and triangles) during the passing of 2 successive recruitment waves (1995 to 1999 and 2008 to 2010). The abundance index is standardized to A0 abundance in 1993. A1+ abundance in 2000 is not shown because it was unrealistically high (abundance = 2831)

2 yr (Fig. 2). The intensity of correlation in mean CW and abundance index between the 2 female groups progressively decreases at offsets >2 yr and becomes non-significant at an offset of 4 to 5 yr. The stronger correlation in abundance index between A0 and A1+ females at a 2 yr offset, which is particularly apparent during the period 1995 to 1999 when A0 abundance increased sharply (Fig. 1), raises a question about the trawl's efficiency at sampling A1 females (i.e. females that became adult in the year preceding the survey). This concern motivated the use of 1 or 2 yr offsets between the 2 female groups when modeling mortality rate: if A1 females are not sampled, A0 females suffer 2 yr of mortality before being detected in the A1+ group as A2 females.

Our simple model was able to fit the variation in mean CW and abundance during the passing of the 2 successive recruitment waves (Fig. 3). The variations in abundance were especially well described by the model when assuming a 1 yr offset between A0 and A1+ females; however, the model described variations in mean CW equally as well with either offset.

Estimates of natural mortality rate derived from the model were quite high: 0.78 yr^{-1} (SE = 0.07 yr^{-1}) for a 1 yr offset and 0.66 yr^{-1} (SE = 0.05 yr^{-1}) when assuming a 2 yr offset. These high values imply that only 45.8% (1 yr offset) or 51.7% (2 yr offset) of females survived >1 yr after their terminal molt and that only 21.0% or 26.7%, respectively, survived at least 2 yr, i.e. the time required for eggs to develop and hatch in cold conditions. The model was also applied assuming A0 and A1+ females have distinct mortality rates, but confidence intervals were huge and the model became over-parameterized; consequently, it was not possible to conclude whether natural mortality was different between the 2 female groups. We, therefore, focused on a model assuming a common mortality rate for both A0
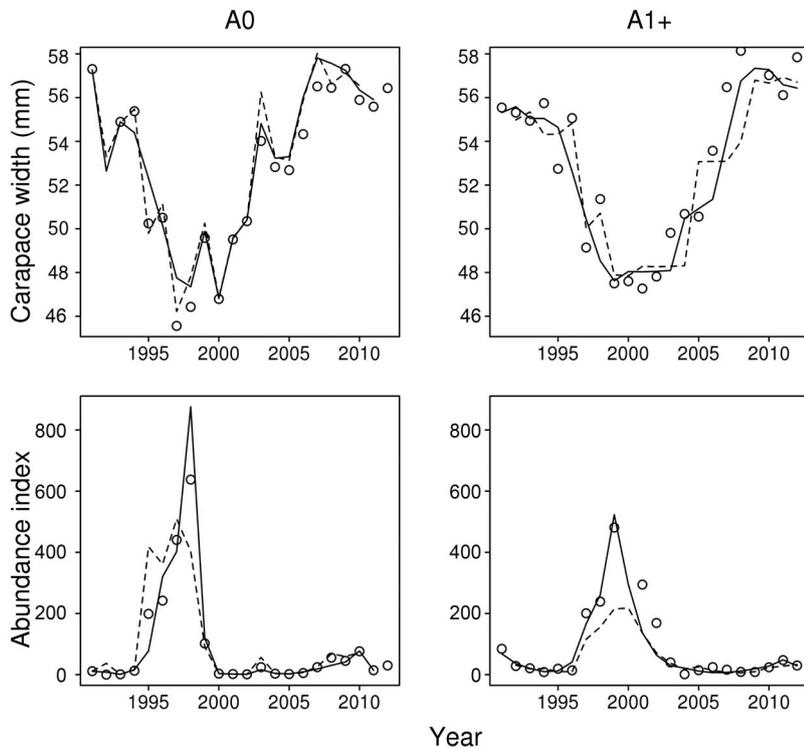
Fig. 3. *Chionoecetes opilio*. Observed (open circles) and estimated (lines) mean carapace width and abundance index for adult female snow crabs recruited to the Baie Sainte-Marguerite population in the survey year (A0) and those recruited in previous years (A1+) when assuming a 1 yr (solid line) or 2 yr (dashed line) offset between the 2 female groups

and A1+ females. The BIC value of the model was lower (i.e. preferred) with a 2 yr offset (BIC = 3880.5) than with a 1 yr offset (BIC = 4244.5) between the A0 and A1+ females. This suggests, as above, that there could be a catchability issue with A1 females. Thus, the following analyses of egg production are based on natural mortality rate estimated with a 2 yr offset.

Estimates of egg production at the individual or population level suggest strongly that primipara play a key role in snow crab reproduction and population dynamics. The first clutch represented nearly half (43.9%) of the expected lifetime egg production of an adult female in warm conditions and >69.7% in cold conditions (Fig. 4), even though primipara are about 20% less fecund at size than multipara (Sainte-Marie 1993). Estimated total annual population egg production was variable over time due to pulsed recruitment (Fig. 5), but on average would have been 1.75 times higher under annual compared to biennial reproduction. Fig. 5 shows that the relative contribution of A0 and A1+ females to estimated population egg production changed over the years in relation to the passing of the strong recruitment wave of 1995 to 1999. A0 females produced a greater share of eggs

than A1+ females at the beginning of the period of high adult female abundance, and the reverse was true at the end of that period and during the subsequent recruitment trough. The inversion of relative contribution to total egg production toward the end of a recruitment wave reflected the accumulation of older females (multipara) with greater per capita fecundity in conjunction with much reduced primipara abundance. This pattern of shifting relative shares of egg production between the 2 female reproductive stages was more striking when assuming biennial reproduction than when assuming annual reproduction. Under the scenario of biennial reproduction, which may best describe Gulf of St. Lawrence snow crabs (Sainte-Marie 1993, Moriyasu & Lanteigne 1998, Comeau et al. 1999), A0 females were responsible for >90% of population egg production in 1995 to 1998 as well as in 2008 to 2010 (Fig. 5) and for an estimated 81% over the entire period 1992 to 2010.

DISCUSSION

This paper presents an original approach for estimating natural mortality of adult female snow crabs. The method is innovative in combining classic accounting of crab numbers with the autocorrelated interannual variability of body size of recruiting adult females as a tracer for resolving mortality rates in a natural population. This approach is rather generic and can probably be applied to other crustacean populations that have a terminal molt, insofar as they are seasonally breeding, univoltine (or perhaps even bivoltine), and exhibit interannual variability of adult body size and numbers. The natural mortality estimate we obtained (0.66 yr^{-1}) was high but similar to estimates of 0.53 to 1.02 yr^{-1} for sublegal (<95 mm CW) adult male snow crabs in the southern Gulf of St. Lawrence (Wade et al. 2003) and less than estimates reported for adult females of other crab species with a terminal molt (Miller et al. 2005, Zheng 2005, Hewitt et al. 2007). For snow crabs specifically, natural mortality of adult females was estimated at 0.56 yr^{-1} in 2 distinct studies: one performed in a small (13.7 km^2)
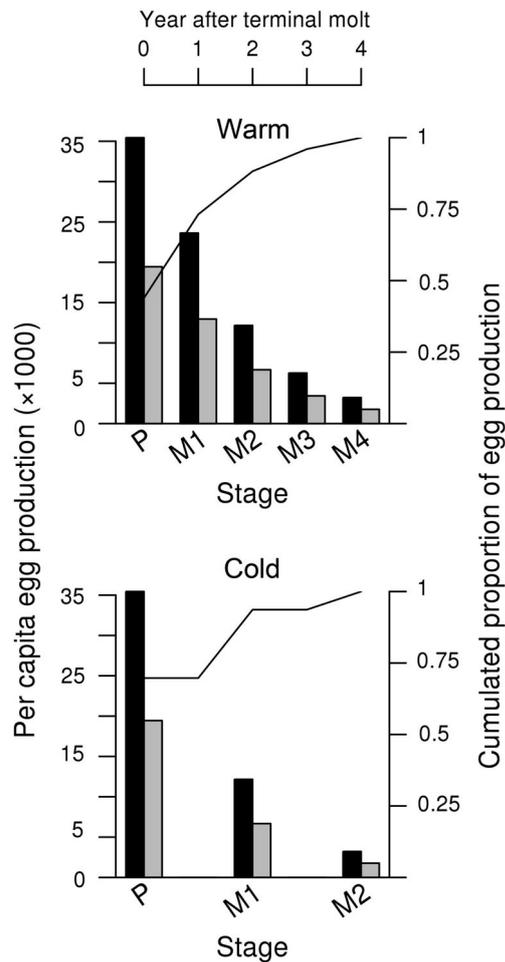
Fig. 4. *Chionoecetes opilio*. Probabilistic lifetime egg production of adult female snow crabs under warm (annual reproduction) and cold (biennial reproduction) conditions. Females of 57.3 and 45.6 mm carapace width (black and gray bars, respectively) were considered. Egg production in each successive reproductive stage was weighted by survival probability, calculated from the estimated mortality rate of 0.66 yr^{-1}. The continuous black line represents the proportional contribution of each reproductive stage to lifetime reproductive output (P: primiparous oviposition; M1: multiparous first oviposition event; M2: multiparous second oviposition event; etc.)
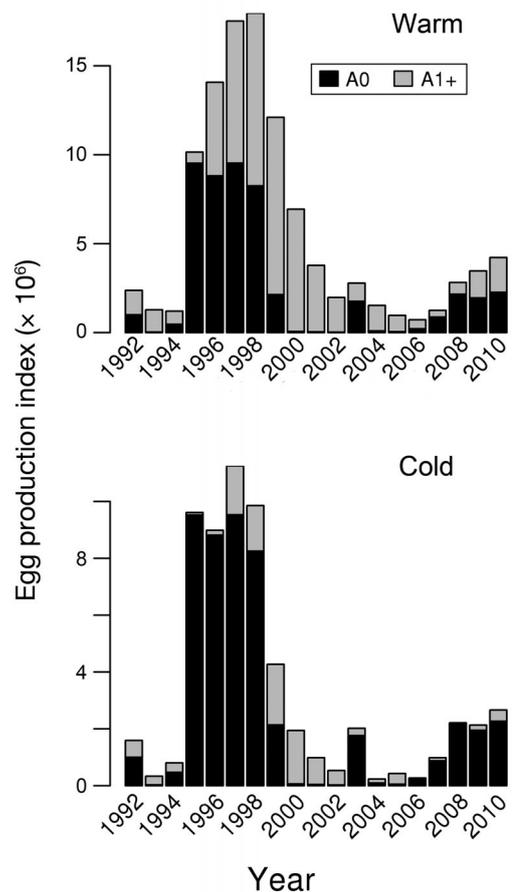

Fig. 5. *Chionoecetes opilio*. Contribution of A0 and A1+ groups to yearly egg production of the snow crab population in Baie Sainte-Marguerite, assuming that females reproduce annually (i.e. warm conditions) or bienially (i.e. cold conditions), based on estimated abundance indices and mean carapace widths

marine reserve in the Sea of Japan using tag-recapture methods (Yamasaki et al. 2001) and the other at the scale of the eastern Bering Sea using numerical accounting (Zheng 2003).

The simultaneous use of 2 different variables, mean CW and abundance index, for calculating snow crab natural mortality may provide more robust and reliable estimates than any single variable. However, we estimated natural mortality using each variable separately (assuming a 2 yr offset): the value was 0.63 yr^{-1} (SE = 0.06 yr^{-1}) when fitting the model

on abundance indices and was 0.68 yr^{-1} when only carapace widths were used. It was not possible to estimate confidence intervals in this last case because the model was overparameterized. Our best estimate using the mean CW and abundance index (0.66 yr^{-1}) was thus a compromise between those 2 values.

The method proposed herein for estimating natural mortality depends on several important assumptions. The first is that classification of A0 and A1+ females is faultless. While there is good reason to believe that the accuracy of classification is very high (see 'Materials and methods'), misclassification of A1+ females as A0 females would lead to an overestimation of natural mortality, while the reverse would lead to an underestimation. The second assumption is that adult females in all pseudo-cohorts are equally catchable. However, visual examination of trends in mean CW and abundance index and correlation

analysis suggest that catchability of A1 females may have been low relative to females in other pseudo-cohorts. This possibility was taken into account by fitting the model with 2 different offsets between A0 and A1+ females: the 1 yr offset assumed that A1 female catchability was similar to that of other adult females, while the 2 yr offset assumed that A1 females were not catchable at all. The better performance of the model with a 2 yr offset was consistent with the idea that catchability of A1 females was low. A possible reason for this is the ontogenetic migration after terminal molt from shallow molting grounds to deep multiparous female habitat (Sainte-Marie & Hazel 1992, Lovrich et al. 1995, Ernst et al. 2005). In Baie Sainte-Marguerite, this migration may occur over a period of a year or so on relatively steep slopes where our small beam trawl may not perform well. Alternatively or complementarily, A1 females might behave differently, perhaps burrowing more, than other adult females. Additionally, we assume that there is no net immigration or emigration of A0 or A1+ females into, or away from, the relatively small study area. Finally, we posit that adult female snow crabs are not subject to direct or indirect fishing mortality and that natural mortality is independent of their body size.

Hewitt & Hoenig (2005) proposed the equation 4.22 divided by maximum longevity as a rule of thumb for estimating natural mortality in various marine animal taxa. Applying this rule to adult female snow crabs, with mean age at terminal molt to adulthood set at 7 yr and subsequent maximum life expectancy ranging from 3 to 9 yr (see 'Introduction'), produces natural mortality estimates of 0.42 to 0.26 yr^{-1} (4.22/10 or 4.22/16). These estimates represent average natural mortality over the lifetime of a female and are lower than ours, which represent natural mortality of a female after terminal molt only. Prominent causes of natural mortality for pre-adult and adult females include fish predators such as skates and cod (Robichaud et al. 1991, Chabot et al. 2008) and in some areas (but not the northern Gulf of St. Lawrence) bitter crab disease (Shields et al. 2007, Mullowney et al. 2011). However, natural mortality rates of adult females may be higher on average than those of pre-adult females because of density-dependent sexual conflicts arising during the female's first mating period, which is intimately associated with terminal molt (Sainte-Marie et al. 2008; see Adler & Bondiuransky 2011 for more general considerations on sex ratio, density and the rate of ageing). When the adult snow crab sex ratio is strongly biased towards males, dominant males may forcefully take over females

from other males or coerce females into mating, sometimes inflicting immediate death or severe injuries (e.g. multiple limb loss) that will curtail female life expectancy; when the adult sex ratio is strongly biased towards females, dominant males reduce guard time and the vulnerable, newly molted females may be subject to harassment by subordinate males, as well as being exposed to predators (Sainte-Marie & Hazel 1992, Sainte-Marie et al. 2008 and references therein). Adult female mortality rates may be lower at more balanced sex ratios; it will probably be possible to include density-dependence in the model to account for this source of variability in natural mortality when the times-series becomes longer.

We have not yet attempted to estimate natural mortality for adult male snow crabs. Males also undergo a terminal molt and their abundance index and mean CW change over the years (Sainte-Marie et al. 2008), but large adult males are targeted by the fishery; consequently, it is more difficult to distinguish between natural and fishing mortality. It may, however, be possible to estimate natural mortality for sublegal (<95 mm CW) adult males using our method. Our method certainly cannot be used for determining natural mortality of pre-adult snow crabs, so additional studies by tagging or other methods (e.g. Kilada et al. 2012) will be needed to improve natural mortality estimates for snow crabs in general.

Our high estimate of natural mortality for adult females has important implications for the perception of relative contributions of primipara and multipara to population egg production. Although multipara are more fecund at size than primipara (Sainte-Marie 1993), primipara are expected to contribute a large share of population egg production in both cold and warm conditions. Note that the primipara share of population egg production may be underestimated, as we did not take into account a possible reduction in fecundity at size in senescing multipara (see Kon et al. 2010). Assuming 2 clutches per female lifetime and no brood mortality, Sainte-Marie (1993) inferred that snow crab primipara would produce >40% of total larvae produced by biennially reproducing females, which is comparable to our estimate of the primipara average share of egg production in warm conditions (43.9% over the study period), but smaller than our estimate of the primipara average share in cold conditions (69.7%). However, it is clear from our study that decadal oscillations occur in the relative contributions of primipara and multipara to annual egg production. Due to differences in size (quality) of primipara and multipara eggs (Sainte-Marie 1993) and unaccounted brood mortality, which might differ

between the 2 female reproductive stages, we cannot currently determine the respective contributions of primipara and multipara to recruitment. Nevertheless, this work and other studies (e.g. Ernst et al. 2012) suggest that snow crabs should be managed to ensure high reproductive success of primiparous females.

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