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Estimation of mean annual natural mortality for adult male snow crab *Chionoecetes opilio* in the southern Gulf of St. Lawrence.

Estimation du taux de mortalité naturelle chez les males adultes du crabe des neiges *Chionoecetes opilio* dans le sud du Golfe Saint-Laurent.

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Abstract

A population of snow crab (*Chionoecetes opilio*). In the southern Gulf of St. Lawrence was monitored over a period of 15 years (1988-2002) using a series of trawl surveys. Historically, the estimates of legal sized adult males from these fall surveys were projected as the available fishable biomass the following spring fishing season, assuming that the mortality rate was zero. Using delay-difference models, we estimate the mean annual instantaneous natural mortality rate using three statistical approaches: Non-linear least squares regression (NLLS), simulation/NLLS, and bayesian analysis. To reduce possible bias in the estimation of the natural mortality rate, catchability coefficients and migration coefficients are added to the model. Estimates for mean annual instantaneous mortality rates (M) ranged from 0.26 to 0.48.

Résumé

La population de crabe des neiges (*Chionoecetes opilio)* du sud du golfe du Saint-Laurent a été étudiée depuis une quinzaine d'années (1988-2002) à l'aide de relevés au chalut. Historiquement, les estimés de biomasse de crabes adultes de taille légale à l'automne étaient directement projetés comme étant la biomasse exploitable au cours du printemps suivant, assumant ainsi que le taux de mortalité naturelle durant l'hiver était égal à zéro. En utilisant plusieurs modèles de 'delay-difference', ce document cherche à estimer le taux annuel moyen de mortalité naturelle instantanée en utilisant trois différentes approches statistiques: la régression non-linéaire a moindre carrés (NLLS), la simulation avec NLLS et l'analyse Bayesienne. Afin de réduire un biais possible dans l'estimation du taux de mortalité naturelle instantanée, des coefficients de capturabilité et de migration ont été ajoutés au modèle. Les estimations des taux moyens de mortalité instantané annuel (M) varient de 0,26 à 0,48.

Introduction:

A commercial trap fishery for snow crab, (*Chionoecetes opilio)*, began in the southern Gulf of St. Lawrence (sGSL) in the mid-1960s. The sGSL is divided into five crab fishing areas (CFA) (Fig. 1), and each is managed separately. The largest fishery within the sGSL is CFA 12. The fishery in CFA 12 opens in spring, generally as soon as the area is clear of ice (April-May) and lasts about 10-12 weeks. This fishery grew quickly from 1966, peaking at 31,500 t in 1982. Catches then fluctuated around 25,000 t until 1986 and then dropped to about 12,000 t in 1987-88. In 1989, the fishing season was prematurely closed with landings of 6,950 t, because of a rapid decline in catch-per-unit-of-effort (CPUE) and a growing incidence of soft-shelled crabs in the catches. New management measures were introduced in 1990, including a total allowable catch (TAC) or quota based on the biomass of adult legal sized male crab, which is estimated from the trawl survey results. Legal size is ≥ 95 mm carapace width (CW). This trawl survey was conducted for the first time in 1989. The quota was set at 7,000 t in 1990 in accordance with these new management considerations. The catches rose, reaching 19,944 t (quota of 20,000 t) in 1995. The quota was then set in accordance with the downward trends of the biomass index varying between 15,972 t and 11,125 t in 1996 and 1999 respectively. The quota was then gradually increased from 15,400 t in 1997 to 22,000 t in 2002 due to the combined effects of an increased trend in biomass and the implementation of an aggressive exploitation strategy. Over this period, a large fluctuation was observed in the survey abundance index for commercial male snow crab (Fig. 2).

In the sGSL, the molting of snow crab occurs in December-April (Watson, 1972; Conan *et al.*, 1988; Sainte-Marie *et al.*, 1995; Benhalima *et al.*, 1998; Hébert *et al.*, 2002a), prior to the fishery. Snow crabs normally molt every year until they reach a final or "terminal" molt (Conan & Comeau, 1986). Males undergo this terminal molt at sizes ranging between 40 and 160 mm CW (Conan & Comeau, 1986; Sainte-Marie & Hazel, 1992; Sainte-Marie *et al.*, 1995), while females attain terminal molt at smaller sizes, between 30 and 95 mm CW (Moriyasu & Conan, 1988; Sainte-Marie & Hazel, 1992; Sainte-Marie *et al.*, 1995). After molting, crabs have a soft shell for 8-10 months (Hébert *et al*. 2002*a*). Only mature hard-shelled males with CW ≥ 95 mm can be landed in the fishery. Terminally molted soft-shelled males with CW ≥ 95 mm will be recruited to the fishery the following year. Females mate and extrude eggs for the first time during December and April immediately after their terminal molt (primiparous stage) while the carapace is still soft (Watson, 1969; Moriyasu & Conan, 1988). The second mating season occurs from May to June before and after hatching (Conan & Comeau, 1986; Moriyasu & Conan, 1988; Sainte-Marie and Hazel 1992; Moriyasu & Comeau, 1996; Sainte-Marie *et al.*, 1999; Comeau *et al.*, 1991). Female snow crabs may also produce more than one viable brood from sperm stored in their spermathecae from the first mating, without subsequent mating (Sainte-Marie *et al.*, 1999). Larval hatching will occur approximately 2 years after mating (Moriyasu & Lanteigne, 1998; Comeau *et al.*, 1999). There is no evidence of a one-year reproductive cycle in the sGSL, as suggested by Sainte-Marie *et al.* (1995) for to females in Baie Sainte-Marguerite in the northwestern Gulf of St. Lawrence. Pubescent females are identified as being adolescent females (a non-reproductive state) with a narrow abdomen and fully developed orange gonads. These females will molt to maturity the following year as primiparous characterized by an enlarged abdomen and ripe ovaries, and mate and extrude fertilized eggs for the first time (first brood). Multiparous females are repeat spawners (second brood and onward).

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Before 1988, the biomass estimation of snow crab in the sGSL was done indirectly from catch and effort data using Leslie analysis (Leslie & Davis, 1939; Ricker, 1975). This analysis did not provide a biomass estimate for the following year and its precison is limited due to violations in underlying assumptions (Miller, 1975). In 1989, a post-fishery season trawl survey was then implemented to provide a predicted biomass index for the following year from point density estimates. However Miller (1975) and Conan and Maynard (1987) showed that the use of the conventional estimates, such as the mean, was biased with regards to snow crab abundance due to the aggregated distribution pattern of this species. To deal with this problem, kriging estimates were used to improve the snow crab abundance accuracy and distribution estimates, by dealing with spatial auto-correlation between sampling units (Conan & Maynard, 1987). However, a recent review of the snow crab assessment methodology (Anonymous, 2002) indicated that there is a systematic bias in the predicted biomass estimate resulting in a possible overestimation of the population. This may be caused by faulty underlying assumptions, such as 0% mortality (including natural mortality and migration) between the survey and fishing season, and 100% catchability of commercial sized males by the trawl net. Consequently, the estimated value generated from the trawl survey data analyses may not represent the absolute biomass or abundance. Therefore the estimation of mortality rate is urged so that an accurate estimate of the abundance and biomass can be realized.

Material and Methods

Background:

The relation between predicted abundance of commercially exploited crab (Legal sized Adult Crab, LAC,) from year *y* (A_y) to the remaining LAC abundance after the following fishing season and the abundance of LAC caught during the season (A'_{y+1} and C_{y+1}, respectively) for year *y+1* is:

$$A_y \rightarrow A'_{y+1} + C_{y+1}$$

Using delay-difference formulae we can relate groups of snow crab from adjacent years to estimate certain key population parameters. Three types of delay-difference models were used (two are special cases of the more general one) to examine three parameters of interest: 1) the mean mortality rate per unit year, 2) the catchability coefficient of the catch gear relative to the survey sampling gear (Smith & Lundy, 2002) and 3) the migration between CFA 12 and CFA 18,19 & 12F. The development of the general model stems from the relation above and under its simplest form is given by:

(1) $$A_y = A'_{y+1} + C_{y+1}$$

This equation, under various forms has been called the forward-backward check formula in past documents (Chiasson *et al*., 1995; Hébert, 2002b) and is in fact a special case of the general formula under study (2). It was noted in previous exploratory analyses that a unidirectional bias (Hilborn & Walters, 1992) was present in our data. This phenomenon could be due to a number of factors such as sampling biases in the survey or catch data, migration or natural mortality.

We generally assume that migration in the sGSL as a whole is negligeable relative to other effects based on the historical data on tag-recapture studies (M. Biron, 2003). There is evidence of some exchanges in the northern part of Cape Breton and off the Gaspé Peninsula (Watson, 1970; Watson & Wells, 1972) that are assumed to be small relative to stock fluctuations within the sGSL. However, between snow crab fishing areas within the sGSL, there is some evidence that migration exists as infered from a model applied to CFAs 12, 12E and CFAs 18,19 & 12F data.

The central interest of the present paper is to obtain a reasonable estimate of the mean annual instantaneous natural mortality rate in the sGSL (referred to as natural mortality hereafter). Our general model for the sGSL thus includes two parameters of interest. One is the mortality rate term M and the other is the catchability coefficient of the catch gear relative to the trawl, denoted q.

$$(2) \qquad A'_{y+1} = e^{-M} A_y - q C_{y+1}$$

Note that q is a proportion while M is a rate per unit time. Assuming in (2) that $M = 0$ and $q = 1$ yields (1). If the latter assumption held, we would be able to use stock abundance estimates as unbiased measures of population abundances. However, the presence of a systematic bias in our data (Fig. 2) undermines such an assumption. This is especially evident for southwestern Gulf of St. Lawrence (swGSL) and the sGSL.

Between CFA 12 and CFAs 18,19 & 12F, it has long been suspected that a migratory influx of crab from the former into the latter exists. And so to treat these two zones individually, we need to account for this migration. Treating each abundance estimate within each zone (or zone grouping) as a single data point, we generalize (2) and include an additional parameter d used in conjunction with an indicator variable I denoting the zone to which the data belongs .

$$(3) \qquad A'_{y+1} = e^{-M} A_y - q C_{y+1} + dI$$

Three statistical methods:

Thus, we have three models numbered I, II and III corresponding to equations (1), (2) and (3), respectively. The first two contain no migration term d and are applied to the sGSL dataset (Table 1a). Model III, the full model with mortality, catchability and migration terms, is applied to CFA 12 and CFAs 18,19 & 12F data sets simultaneously (Table 1b, 1c).

Our three models, with their respective data sets are then fitted via three different estimation techniques. The first will be a standard non-linear least-squares regression with error on the A_{y+1} variable. The second will be a parametric bootstrap using the error estimates on the variables from the kriging analysis used to generate them (Table 1) and performing a constrained optimization with respect to the catchability coefficient. The third will be a Bayesian approach with non-informative priors on the mortality and catchability coefficients and empirical priors on the migration term and the standard deviation parameter.

For M, we will thus have 8 estimates from various models estimated using three different statistical methods, for q, we will have 5 estimates stemming from models II and III. Finally we will have two estimates for the migration term d from the estimation methods applied to model III.

Trawl survey abundance data:

Bottom-trawl surveys have been conducted annually in the sGSL since 1988 (Moriyasu *et al*., 1998). The surveys have varied in range, with CFA 12 being covered from the beginning, and then increased to cover the whole commercial snow crab fisheries in the entire sGSL.. The abundance estimates are made using the area-swept method, (4) where the density at each station (i) is estimated by considering the performance of the trawl as measured by a SCANMAR™ or NETMIND™ system. Although catchability probably varies between stations, there is no practical measurement of this parameter to date. Lacking this information, catchability is assumed to be at 1.0.

$$(4) \qquad Density = \frac{n}{q \int_{t1}^{t2} w(t)\,dt}$$

Where,

n : Number of individuals caught by trawl net
q : Catchability coefficient
$w(t)$: Trawl width at time t.
t_1, t_2 : Trawl net's touch-down and lift-off times, respectively.

A biomass index is then calculated using a geostatistical approach, (Conan, 1985; Deutsh and Journel 1992) specifically ordinary kriging with uncertainties reflected by the kriging standard deviation (Matheron, 1971; Marcotte, 1991).

Catch abundance data:

Data on the catch and effort were obtained from fishermen's logbooks and the sales slips of processing plants. With a size-weight relation (Hebert *et al*, 2002b), and size-frequency distributions from sea-samples, conversions from landings to abundance were performed (Table 1). The error on these values was estimated using the regression error term.

Sample groupings:

The group of snow crab studied here is legal-sized (male adult >95mm CW) that is exploited commercially. Shell condition is an index to the relative age of the snow crab since the last molt (Hebert *et al*. 2002b). Index values range from 1 (newly molted) to 5 (old and mossy carapace) (Appendix I). After the terminal molt, adult males having shell

condition 1 and 2 are not exploited in the fishery since their landing is prohibited. Furthermore, individuals having shell condition 1 and 2 in year y will become individuals having shell condition 3 and 4 in year $y+1$. Therefore, the criteria for individuals to be considered for the abundance estimate (A_y) in year y are: LAC having shell condition 1 through 5. Variables in the following year $y+1$ (A'_{y+1}, C_{y+1}) have all the same criteria, except that they are of shell condition 3, 4 or 5.

Study area:

The area to be considered for the analysis covers two main fishing zones in the sGSL. The southwestern GSL (swGSL) zone, CFA 12 and CFA 12F, covers the majority of the snow crab fishery in the sGSL (Fig. 1). The area referred to as Cape Breton (CB) zone covers CFAs 18, 19, and F. The total area (two zones combined) will also be used as a study area, since as mentioned above, any migration factor will be minimized due to environmental limitations. A high water temperature in the Laurentian channel probably prevents adult crabs from mixing with other CFAs in the north of the channel, and minimal mixing is believed to take place along the narrow corridors north of the Gaspe peninsula towards the north of Cape Breton Island (Biron *et al.*, 2003).

Regression using non-linear least squares (NLLS)

Non-linear regression was performed using the Matlab™ Statistical Toolbox function *fminunc* and error estimates were obtained via the Hessian matrix for models I (1), II (2) and III (3). There were no problems with the convergence of the numerical search algorithm. Multiple starting points were used to test whether the solution was in fact a global maximum.

Simulation/NLLS model

Simulated data was produced and analyzed using Analytica™ version 2.0. Each variable (A_y, A'_{y+1}, C_y) was simulated as a normally distributed random variable. The means of the variables were those found by the methods described above and the variances were the kriging variances obtained from analysis of the survey data and the error estimates for the catch data. The variance in the population estimate variables (A_y and A'_{y+1}) are based on the kriging variance. The variance in the catch variable (C_y) was attributed to the standard deviations observed in mean weight estimates from the survey which is then used in converting catches, based on official statistics reports, from metric tons to numbers of crab. Once the probability distribution functions (pdf's) were defined, the simulation process consisted of randomly sampling from the pdf's 10000 times, and performing a regression analysis from each sample. The catchability parameter was either arbitrarily set at 1 (model I) or described as a uniform (pdf) ranging from 0 to 1 (model II).

Bayesian approach

Bayesian analysis offers several advantages in a data analysis context with respect to certain key points. It allows natural incorporation of prior information on the parameters (called the prior distribution) into the analysis, where we may be as precise or as vague as reason dictates (e.g. non-informative priors). In effect, we may constrain the

parameter space in which our solutions may be found. Furthermore, the end result is a probability distribution (called the posterior distribution) of the parameters *given the dat,* which we may then use to obtain relevant statistics (mean, variance, moments, etc…) and inference. The data model is incorporated into the analysis via the likelihood function, which is a probability distribution of the data *given the parameters* (Efron, 1986). The likelihood function is identical to that which would be used in a classical analysis though the frame of reference is shifted from the parameters to the data.

In general terms, the Bayesian approach may be summarize by the following symbolic model:

(5)
$$p(\theta \mid \overset{\omega}{x}) \propto \pi(\theta) L(\overset{\omega}{x} \mid \theta)$$

where $\pi(\theta)$ is the *prior* distribution of the parameter vector θ, $L(\overset{\omega}{x} \mid \theta)$ is the *likelihood* function and $p(\theta \mid \overset{\omega}{x})$ is the *posterior* distribution of the parameter vector θ given the data matrix $\overset{\omega}{x}$. Note that (5) is a proportionality relation and finding the normalizing constant necessary to balance the equation is frequently a more complex problem than solving the above equation. Using Monte Carlo methods one can generally obtain random samples from the posterior distribution in order to approximate statistics up to any desired degree of precision.

In this case, a Sampling-Importance-Resampling (SIR) algorithm was used to generate samples from the posterior distribution. Pragmatically, random variates are generated from the prior distribution and these are then resampled in proportion to ascribed weights in provenance from their respective likelihood values (Smith & Gelfand, 1992; Evans & Swartz, 1995).

The delay difference model used in this case is given by:

(6)
$$A'_{y+1} = e^{-M} A_y - qC_{y+1} + dI + \varepsilon, \qquad \text{where } \varepsilon \sim N(0, \sigma^2)$$

Where, A_i: Stock abundance estimate for year i.

A'_i: Remaining stock abundance estimate for year i.

C_i: Catch abundance estimate for year i.

I_i: Indicator variable (equals 1 when in zone 12 and –1 otherwise) for datum in year i.

M: Mean annual instantaneous natural mortality rate.

q: Catchability coefficient.

d: Migration term.

ε: Normally distributed error term with mean 0 and variance σ^2.

σ: Standard deviation of error term.

The likelihood function for this model is thus given by:

(7)
$$L(D \mid M, q, d, \sigma) = \prod_{i=1}^{n} \frac{1}{\sqrt{2\pi}\sigma} \exp\left[-\frac{\left(A'_{i+1} - e^{-M} A_i + qC_{i+1} - dI_i\right)^2}{2\sigma^2} \right]$$

where D is the data set $D = \{A_1,...,A_n, A_2^i,..., A_{n+1}^i C_1,...,C_n, I_1,...,I_n\}$.

We now need to specify which functional form will be used to specify the prior distributions of the parameters M, q and σ. Since M was the primary focus of our analysis, we wished to be as unrestrictive as possible in the specification of its prior. Considering that M is positive, e^{-M} ranges from 0 to 1, as desired. We may then pose that e^{-M} follows a standard uniform distribution ($e^{-M} \sim U(0,1)$) or equivalently that M follows an exponential distribution with scale parameter 1 ($M \sim Exp(1)$).

Results

Survey abundance is related to population abundance by the catchability parameter (q) of the trawl. The parameter q is correlated with M. Fu (2001) demonstrated that for their survey data, q could not be estimated with sufficient accuracy along with M, even when underlying q was constant over time. Some authors favor estimating q while assuming that M is known (Quinn & Deriso, 1999) to accommodate the potential variability in q. Zheng *et al*. (1995) suggested estimating M while keeping q fixed at a chosen value. We compared two approaches in the situation with (1) estimating M while keeping a constant q of 1.0, and (2) solving for M and q simultaneously. A variation of the second option was used whereas in the simulation approach, q was described as a pdfs ranging from either 0 to 1 or 0.5 to 1, while in the bayesian approach these same pdfs were used a priors. A chart displaying the survivorship as a function of M is shown in Fig. 3.

NLLS Regression

The regression model (2) was solved and resulted in the estimates shown in Table 2. The natural mortality (*M)* for the whole sGSL was 0.27, while assuming a catchability of 1. If catchability was not assumed to be equal to 1.0, *M* for the whole sGSL was 0.48 with a 95% confidence interval ranging from 0.15 to 0.82 and the average catchability parameter was 0.45 with a wide 95% confidence interval (CI) ranging from –0.23 to 1.13.

Simulation with NLLS

Results from the regressions based on the simulation approach are summarized in Table 3. The 95% CI for the *M* estimates in the sGSL using model I ranged from 0.15 to 0.39 with a mid value of 0.27, while assuming a constant catchability of 1. Model II results showed that for the whole sGSL, the mean M was 0.48 with a 95% CI ranging from 0.15 to 0.82, while the mean value of *q* was 0.45 with a 95% CI ranging from –0.23 to 1.13. When comparing the various realizations from the Monte-Carlo simulation, we find a high correlation (r^2=0.882) between *M* and *q*.

For model III, we find that the additional parameter *d* which represents any losses due to mixing between the swGSL and the CB zone showed that on average, the swGSL zone loses adult crab populations to the CB zone. Specifically, the mean loss from swGSL zone to CB zones is 1.6 million individuals per year. The 95% CI range for this parameter however was quite large with an upper range showing a loss of 3.4 million and a lower range showing a net gain of 0.1 million.

Bayesian analysis

The Bayesian posterior analysis for model I showed a lower mortality (0.26) than for either model II (0.48) or model III (0.48) values (Table 4) (Fig. 4). Though the rates in model II & III were almost twice as much as that for model I, these correspond to survival fractions of 62% versus 77%, respectively, a rather narrow margin considering the different assumptions and model specifications. The standard error associated with M was larger for model II (0.13) (Fig. 5) than for model I (0.07). This probably reflects the information lost when estimating three parameters instead of only two. In model III the error was intermediate between model I and II. This is probably due to the fact that we have almost twice as many data points (combining CFA 12 and CFA18,19 & 12F), which generally increases the precision of the estimate, while we have four parameters in the model, which generally decreases the precision.

As expected, increasing either the number of parameters in the model or increasing the number of data points increased the precision of the standard deviation parameter (σ) associate with the error term (ε). Though important for predictive models, σ holds little interest in the present study because of its low correlation with the main parameter of interest M.

The catchabilty parameter q in model II and III (Fig. 6.1 and Fig. 6.2) had very high standard deviations and confidence intervals which practically spanned the support from 0 to 1, with a slight modality being visible center or off-center. Unfortunatey the posteriors are much too diffuse to be able to make any valid inferences about this parameter. The role of this parameter is thus restricted to limiting the bias-effects upon the mortality rate M.

The migration term d in model III was biased towards a negative value at the mean level of $-1.7 \cdot 10^{6}$ individuals. Empirically, if the inference holds, this may be interpreted as an influx of crab into CFA18, 19 & 12F from CFA12 & 12E, and the probability, given the model and data, was estimated at 0.8. There is, however, a large degree of associated error with this parameter.

Discussion:

Three different analytical approaches were used to estimate *M* and *q* based on snow crab survey data from the sGSL. One of the main conclusions is that estimates for *q* have very high variability regardless of the approach used. However, reasonable confidence and credibility intervals for *M* were obtained. The range of the solutions for *M* is relatively wider than I would be if an independent study narrowed down the catchability parameter. (Fig. 7). Mortality estimates for sub-legal sized adult crab (SAC) were consistently higher than for legal sized adult crab (LAC), and ranged from 0.53 to 1.02. (Appendix II)

For this study, we included shell condition 5 even though it is often assumed that snow crab can only be in the shell condition 5 state for less than one year and thus shell condition 5 crabs seen in the survey will not survive until the following year's survey.

Therefore, if we were to exclude the shell condition 5 from the survey data, *M* value would probably be lower. Further study is needed to consider differential *M* relative to the carapace condition.

Based on the population indices obtained from the survey data in the sGSL, it is clear that a high variability in stock abundance has occurred since the late 1980's (Fig. 2). Local high density of crab results in a high competition for optimal grounds which in turn results in a widening of the habitat range covered by the stock (Comeau *et al*., 1998; Winters *et al*., 1985). This was evident in our survey that covered the main concentrations of commercial sized males when it was first established in 1988 during a period when the commercial population size was very low. As the biomass increased, the coverage of the survey had to be increased to accommodate an increase in the range covered by the main concentrations. If concentrations are pushed into unfavorable outlying habitat, and mortality is dependant on habitat quality, then high mortality may occur. It would be interesting to attempt to consider this density dependent mortality.

During periods of high recruitment there is a probable increase in mortality due to increased competition. In addition, it is speculated that snow crab are more vulnerable to increased mortality just after terminal molt, a stage we labeled as soft shelled. Based on observation of molting in aquaria (M. Moriyasu, pers. obs.), there is a positive relationship between the duration of molting and crab size. Furthermore, Hébert *et al*. (2002a) reported that larger crabs require a longer duration of carapace hardening time than smaller individuals. This means that the vulnerability increases for larger crabs during the critical period of their life cycle. Based on the tag-return study (M. Biron, pers. comm.), post-molt males seem to be more active in migration than hard-shelled adult males. Hard-shelled adult males tend to move toward favorable habitat when the stock is in decline (lower crab density), and when the stock increases (higher crab density), some crab tend to move towards peripheral, less favorable habitat possibly due to competition for the habitat. In addition, individuals molted to the terminal phase during winter-spring season will actively participate in mating in the following February with pubescent-mulliparous, females and also the subsequent mating in May with multiparous females. Newly molted males to the terminal phase might have invested their energy into both morphometric change in chelae and gonad development through the period between spring and fall, and face two sequences of competitive matings (Comeau *et al*., 1998). It is therefore expected under this assumption that when a high proportion of the commercial stock is composed largely of soft-shelled adult crab, the mortality would be high. Similarly, when a large proportion of the commercial stock is composed of hard shelled crab (shell condition 3 and 4), the mortality would be low. If the management of the stock is such that it is enabling most of the stock to reach a condition labeled old-shelled (shell condition 5), which is the last stage in the life of a crab, then the overall mortality rate would be very high.

To estimate absolute abundance from research trawl surveys, the catchability of snow crab to the gear must be known. By using the present assumption that the catchability is 1, this would suggest that swept-area abundance estimates were likely be underestimated. In any model containing mortality and catchability terms, there is great difficulty in resolving each from the other because of high correlation between the parameters. To remedy this, a series of depletion experiments were conducted at six different locations in the Baie des Chaleurs region during the early fall in 2002. The protocol called for the depletion type experiment to be repeated at several sites over abundant crab stocks. Problems arising from difficulties in positioning the boat within certain tolerances prevent us from deducing any catchability estimates. The experiment

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will be repeated later with provisions for a modified protocol. Although the analytical studies presented in this paper have found that the estimate of catchability was somewhat ambiguous, a future catchability study is crucial in the reconstruction of crab structure for future population or ecosystem models and as auxiliary (or prior) information for future crab stock assessments.

Zheng *et al*. (1995) estimated natural mortality among other parameters in a length-based population model for the red king crab (*Paralithodes camtschaticus)*, (RKC) in Alaska. They considered more than one scenario, one of which was calculating a constant mortality for all years. Under this scenario they showed that the minimum natural mortality of male RKC is 0.27 and crabs with carapace length greater than 125.1 mm had relatively lower natural mortality. Assuming that the carapace length of RKC for the model varies from 95 to 200 mm, they then obtained an average value of this function (using integration) as 0.41. Zeng *et al*. (1995) mentioned that under the scenario of four levels of time-dependent natural mortality factor, this mortality factor was very low in the 1970s (0.19) and could have been as high as 1.26 in the 1980s. Indeed, the overall instantaneous mortality rates may have been higher since these estimates were only the time-dependent mortality rates. They also estimated population abundance of tanner crab in a length-based model. They estimated the natural mortality for the tanner crab under two scenarios and both estimates were above 0.4. Somerton (1981) had also estimated natural mortality for the tanner crab earlier and had obtained estimates of 0.35 for pre-recruit male tanner crab and from 0.22 to 0.28 for commercial-size male tanner crab in the eastern Bering Sea. Zheng *et al*. (1995), however, argued that the low estimates obtained by Somerton (1981) were due to the rapid increase in the estimates of survey abundance form 1972 to 1975, during which time estimated natural mortality was negative.

Determination of a more accurate estimate of the natural mortality rate parameter will continue to be difficult because of the year to year variability in the population density, environment and uncertainty in the catchability of the trawl. But by agreeing on an interim catchabiliy value or range and also by introducing realistic uncertainty into estimates of both current and forecast stock sizes, we can consider a fairly narrow range of natural mortality, which in turn will result in a more realistic representation of the true snow crab population in sGSL. In this manner, we agree with Schnute and Richards (1995) who stated that realistic analyses of population structure must take into account the uncertainty of *M*.

Acknowledgments:

References:

Anonymous 2002. Zonal snow crab workshop/Atelier zonal sur le crabe des neiges. 14-18 January, 2002/ le 14-18 janvier, 2002 St. John's NF. (J. Moores, ed.). Can. Sci. Adv. Secret. Proceedings Ser. 2002/022.

Benhalima, K., Moriyasu, M. and Hébert, M., 1998. A technique for identifying the early-premolt stage in the male snow crab, *Chionoecetes opilio* (Brachyura: Majidae) in Baie des Chaleurs, southern Gulf of St. Lawrence. Can. J. Zool. 76: 609-617.

Biron, M., Savoie, L., Sabean, C., Wade, E., and Moriyasu, M. 2003. Assessment of the 2002 snow crab, *Chionoecetes opilio*, fishery off eastern Nova Scotia (CFAs 20 to 24). CSAS Res. Doc. 2003/012.

Chiasson, Y., Hébert, H., DeGrâce, P., Campbell, R., Wade, E., and Moriyasu, M. 1995. L'Évaluation du Stock de Crabe des Neiges (*Chionoecetes opilio*) dans le Sud du Golfe du Saint-Laurent (Zones 12, 18, 19 et 25/26) de 1992 a 1994. MPO Pêches Atl. Doc. Rech. 95/104.

Comeau, M., Starr, M. Conan, G.Y., Robichaud, G., Therriault, J.-C., and 1999. Fecundity and duration of egg incubation for multiparous female snow crabs (*Chionoecetes opilio*) in the fjord of Bonne Bay, Newfoundland. Can. J. Fish. Aquat. Sci. **56**: 1088-1095

Comeau, M., Conan, G.Y., Maynou, F., Robichaud, G., Therriault, J.-C., and Starr, M. 1998. Growth, spatial distribution, and abundance of benthic stages of the snow crab (*Chionoecetes opilio*) in Bonne Bay, Newfoundland, Canada. Can. J. Fish. Aquat. Sci. **55**: 262-279

Comeau, M., Robichaud, G., Starr, M., Therriault, J.-C. and Conan, G.Y. 1998. Mating of snow crab (Chionoecetes opilio) (O. Fabricius, 1788)(Decapoda, Majidae) in the fjord of Bonne Bay, Newfoundland. Crustaceana 71: 925-941.

Conan, G.Y. 1985. Assesment of shellfish stock by geostatistical techniques. ICES C.M. 1985/K;30.

Conan, G.Y. and Comeau, M. 1986. Functional maturity of male snow crab (*Chionoecetes opilio*). Can. J. Fish. Aquat. Sci. 43:1710-1719.

Conan, G. Y. and Maynard, D. R. 1987. Estimates of snow crab (*Chionoecetes opilio*) abundance by underwater television – a method for population studies on benthic fisheries resources. J. Appl. Ichtyol. 3: 158-165.

Conan, G. Y., Moriyasu, M., Comeau, M., Mallet, P., Cormier, R., Chiasson, Y. and Chiasson, H. 1988. Growth and maturation of snow crab (*Chionoecetes opilio*). P. 45-66. In: G.S. Jamieson and W.D. McKone (eds.), Proceedings of the international workshop on snow crab biology. December 8-10, 1987, Montreal Québec. Can. MS Rep. Fish. Aquat. Sci. 2005.

Deutsch, C.V. and Journel, A.G., 1992. GSLIB Geostatistical Software Library and User's Guide. Oxford University Press, Oxford.

Dufour, R., Bernier D., and Brêthes, J.C. 1997. Optimization of meat yield and mortality during snow crab (*Chionoecetes opilio*: O. Fabricius, 1788) Fishing operations in eastern Canada. Can. Tech. Rep. Fish. Aquat. Sci. 2152:1-30.

Efron, B. 1986. Why isn't everyone a Bayesian? Am. Stat. 40:1-11.

Evans, M. and Swartz, T. 1995. Methods for approximating integrals in statistics with special emphasis on Bayesian integration problems. Statist. Sci. 10(3):254-272.

Fu, C. 2001. Estimability of natural mortality and other population parameters in a length-based model: *Pandalus borealis* in Kachemak Bay, Alaska. Can. J. Fish. Aquat. Sci. **57**: 2420-2432

Hébert, M., Benhalima, K., Miron, G. and Moriyasu, M. 2002*a*. Molting and growth of male

snow crab, *Chionoecetes opilio*, (O. Fabricius, 1788) (Crustacea: Majidae) in the southern Gulf of St. Lawrence. Crustaceana 75(5):671-702.

Hébert, M., Wade, E., Surette, T., and Moriyasu, M. 2002*b*. The 2001 assessment of snow crab, *Chionoecetes opilio*, stock in the southern Gulf of St. Lawrence (Areas 12, E and F). CSAS Res. Doc. 2002/013.

Hilborn, R. and Walters, C. J. 1992. Quantitative Fisheries Stock Assessment: choice dynamics and uncertainty. Routledge, Chapman & Hall. New York, NY.

Leslie, P. H. and Davis, D. H. S. 1939. An attempt to determine the absolute number of rats on a given area. J. Anim. Ecol. 8: 94-113.

Marcotte, D. 1991. Cokriging with Matlab. Computers & Geosciences, 17**(**9), 1265-1280.

Matheron, G. 1971. The theory of regionalized variables and its applications. Les cahiers du centre de morphologie mathematique de Fontainebleau.

Miller, R.J. 1975. Density of the commercial spider crab, *Chionoecetes opilio*, and calibration of effective area fished per trap using bottom photography. J. Fish. Res. Board Can. 32: 761-768.

Moriyasu, M., and G. Y. Conan. 1988. Aquarium observation on mating behaviour of snow crab, *Chionoecetes opilio*. ICES C. M. 1988/K:9.

Moriyasu, M. and M. Comeau. 1996. Graspinf behavior of male snow crab, (*Chionoecetes opilio* O. Fabricius, 1788, Decapoda, Majidae). Crustaceana 69: 211-222.

Moriyasu, M. and C. Lanteigne. 1998. Embryo development and reproductive cycle in the snow crab, *Chionoecetes opilio* (Crustacea: Majidae), in the southern Gulf of St. Lawrence, Canada. Can. J. Zool. 76:2040-2048.

Moriyasu, M., Wade, E. Sinclair, A. and Chiasson, Y. 1998. Snow crab, (*Chionoecetes opilio*), stock assessment in the southern Gulf of St. Lawrence by bottom trawl survey. p.29-40 In; G.S. Jamieson & A. Campbell (eds.) Proceedings of the North Pacific Symposium on Invertebrate Stock Assessment and Management. Can. Spec. Publ. Fish. Aquat. Sci. 125

Quinn, T.J. and Deriso, R.B. 1999. Quatitative Fish Dynamics. Oxford University Press. New York. NY.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191.

Sainte-Marie, B. and Hazel, F. 1992. Moulting and Mating of Snow Crabs, *Chionoecetes opilio* (O. Fabricius), in Shallow Waters of the Northwestern Gulf of Saint Lawrence. Can. J. Fish. Aquat. Sci. 49:1282-1293

Sainte-Marie, B., Raymond, S. and Brêthes, J.-C. 1995. Growth and maturation of the benthic stages of male snow crab, *Chionoecetes opilio* (Brachyura: Majidae). Can. J. Fish. Aquat. Sci. 52 : 903-924.

Sainte-Marie, B., Urbani, N., Sévigny, J.-M., Hazel, F. and Kuhnlein, U. 1999. Multiple choice criteria and the dynamics of assertive mating during the first breeding season of female snow crab *Chionoecetes opilio* (Brachyura, Majidae). Mar. Ecol. Prog. Ser. 181 : 141-153.

Schnute, J.T. and Richards, L.J. 1995. The influence of error on population estimates from catch-age models. Can. J. Fish. Aquat. Sci. 52:2063-2077.

Smith, A.F.M. and Gelfand, A.E. 1992. Bayesian statistics without tears: A sampling-resampling perpective. The American Statistician. 46(2):84-88.

Smith, S. and Lundy, M. 2002. Scallop Production Area 4 in the Bay of Fundy: Stock status and forcast. CSAS Res. Doc. 2002/018.

Somerton, D. A. 1981. Contribution to the Life History of the Deep-Sea King Crab, *Lithodes couesi*, in the Gulf of Alaska. Fishery Bulletin. 79(2): 259-269

Watson, J. 1969. Biological investigation on the spider crab, *Chionoecetes opilio*, p. 23-47. In: Proceedings of the meeting on Atlantic Crab Fishery Development. Can. Fish. Rep. 13.

Watson, J. 1970. Tag recaptures and movements of adult male snow crabs *Chionoecetes opilio* (O. Fabricius) in the Gaspé region of the Gulf of St. Lawrence. Fish. Res. Board Can. Tech. Rept. 204: 10 p.

Watson, J. 1972. Mating behavior in the spider crab, *Chionoecetes opilio*. J. Fish. Res. Board Can. 29: 447-449.

Watson, J. and Wells, P. G. 1972. Recaptures and movements of tagged snow crabs (*Chionoecetes opilio*) in 1970 from the Gulf of St. Lawrence. Fish. Res. Board Can. Tech. Rept. 349: 12 p.

Winters, G. H. and Wheeler, J. P. 1985. Interaction between stock area, stock abundance, and catchability coefficient. Can. J. Fish. Aquat. Sci. 42**:** 989-998.

Zheng, J., Murphy, M.C. and Kruse, G.H. 1995. A length-based population model and stock recruitment relationaships for red king crab, *Paralithodes camtschaticus*, in Bristol Bay, Alaska. Can. J. Fish. Aquat. Sci. 52 :1229-1246.

Table 1: Abundance data for legal-sized males used for analyses

(a) Southern Gulf of St. Lawrence

Year y	$A_y\,(\times 10^6)$	$A'_{y+1}\,(\times 10^6)$	$C_{y+1}\,(\times 10^6)$
1991	76.44 +/- 11.82	57.26+/- 7.781	26.74+/- 10.16
1992	136.5 +/- 14.41	92.75 +/- 14.97	32+/- 10.28
1993	221.5 +/- 28.93	110.1 +/- 8.581	43.16+/- 14.15
1994	205.2 +/- 12.42	98.14 +/- 8.878	40.4+/- 14.44
1997	84.05 +/- 5.789	40.57 +/- 4.719	26.24+/- 12.44
1998	79.94 +/- 7.291	40.87 +/- 4.076	34.94+/- 24.13
1999	80.36 +/- 5.684	12.8 +/- 2.245	37.9+/- 17.01
2000	63.39 +/- 5.492	23.9 +/- 2.743	41.13+/- 14.48
2001	81.89 +/- 6.998	20.32 +/- 1.579	57.72+/- 21.18

(b) Southwestern Gulf of St. Lawrence

Year y	$A_y\,(\times 10^6)$	$A'_{y+1}\,(\times 10^6)$	$C_{y+1}\,(\times 10^6)$
1988	18.22+/-2.989	1.147+/-0.4048	15.54+/-5.561
1989	33.72+/-6.673	4.625+/-1.01	14.96+/-7.458
1990	71.87+/-10.51	8.744+/-2.92	20.45+/-9.318
1991	80.41+/-10.87	47.33+/-7.369	21.99+/-8.359
1992	120.1+/-11.64	86.64+/-9.832	27.4+/-8.8
1993	216.3+/-22.45	101.4+/-6.568	38.22+/-12.53
1994	193.7+/-10	100.9+/-7.43	36.91+/-13.19
1997	76.47+/-4.89	36.42+/-3.647	21.15+/-10.03
1998	71.4+/-5.498	35.63+/-3.7	26.58+/-18.36
1999	71.14+/-4.919	8.55+/-2.088	28.07+/-16.74
2000	51.79+/-4.307	18.27+/-2.435	28.68+/-10.1
2001	66.68+/-6.223	16.04+/-1.413	45.27+/-16.61

(c) Southeastern Gulf of St. Lawrence

Year y	$A_y\,(\times 10^6)$	$A'_{y+1}\,(\times 10^6)$	$C_{y+1}\,(\times 10^6)$
1991	7.281+/-2.354	10.64+/-1.385	3.4983+/-1.072
1992	16.55+/-2.314	5.902+/-2.815	3.7638+/-1.075
1993	8.88+/-4.9	8.639+/-2.006	3.6945+/-1.068
1994	11.99+/-3.252	4.937+/-2.026	3.9132+/-1.146
1995	6.76+/-2.959	4.383+/-0.6394	2.9538+/-0.8361
1996	7.711+/-1.632	2.354+/-0.9216	3.2994+/-0.9217
1997	7.683+/-2.143	3.839+/-1.558	4.1166+/-1.138
1998	9.663+/-1.773	6.094+/-0.7906	4.4667+/-1.186
1999	10.53+/-1.878	4.096+/-0.6277	6.2658+/-1.768
2000	16.02+/-1.597	5.388+/-0.8584	7.9524+/-2.012
2001	15.04+/-2.16	4.507+/-0.6237	7.9524+/-2.012

Table 2: Non-linear regression model statistics of natural mortality (M), catchability (q) and migration (d) parameter estimates:

Model	Parameter	Estimate	Confidence interval (95%)
I	M	0.27	$[0.13, 0.40]$
II	M	0.48	$[0.14, 0.82]$
	q	0.45	$[-0.23, 1.13]$
III	M	0.46	$[0.25, 0.68]$
	q	0.57	$[0.07, 1.09]$
	d	$-1.7 \cdot 10^6$	$[-7.1 \cdot 10^6, 3.8 \cdot 10^5]$

Model I : $A'_{y+1} = e^{-M} A_y + C_{y+1}$

Model II : $A'_{y+1} = e^{-M} A_y - qC_{y+1}$

Model III : $A'_{y+1} = e^{-M} A_y - qC_{y+1} + dI$

Table 3: Simulation model statistics of natural mortality (M), catchability (q) and migration (d) parameter estimates:

Model	Parameter	Estimate	Confidence interval (95%)
I	M	0.27	$[0.15, 0.39]$
II	M	0.48	$[0.15 , 0.82]$
	q	0.45	$[-0.23 , 1.13]$
III	M	0.55	$[0.35 , 0.76]$
	q	0.45	$[0.10 , 0.88]$
	d	$-1.7 \cdot 10^6$	$[-3.4 \cdot 10^6 , 1.1 \cdot 10^5]$

Model I : $A'_{y+1} = e^{-M} A_y + C_{y+1}$

Model II : $A'_{y+1} = e^{-M} A_y - qC_{y+1}$

Model III : $A'_{y+1} = e^{-M} A_y - qC_{y+1} + dI$

Table 4: Results of bayesian posterior statistics of natural mortality (*M*), catchability (*q*) and migration (*d*) parameter estimates:

Model	Parameter	Estimate	Standard deviation	Credibility interval (95%)
I	M	0.27	0.069	$[0.13 , 0.42]$
	σ	$1.9 \cdot 10^7$	$5.30 \cdot 10^6$	$[1.2 \cdot 10^7 , 3.2 \cdot 10^7]$
II	M	0.48	0.12	$[0.26 , 0.74]$
	q	0.47	0.23	$[0.049 , 0.92]$
	σ	$1.6 \cdot 10^7$	$4.5 \cdot 10^6$	$[1.01 \cdot 10^7 , 2.8 \cdot 10^7]$
III	M	0.47	0.097	$[0.30 , 0.68]$
	q	0.56	0.22	$[0.12 , 0.96]$
	d	$-1.7 \cdot 10^6$	$2.2 \cdot 10^6$	$[-6.03 \cdot 10^6 , 2.4 \cdot 10^6]$
	σ	$1.1 \cdot 10^7$	$1.7 \cdot 10^6$	$[7.9 \cdot 10^6 , 1.4 \cdot 10^7]$

Model I : $A'_{y+1} = e^{-M} \; A_y + C_{y+1} + \varepsilon$

Model II : $A'_{y+1} = e^{-M} \; A_y - qC_{y+1} + \varepsilon$

Model III : $A'_{y+1} = e^{-M} \; A_y - qC_{y+1} + dI + \varepsilon$

$\Pr iors : e^{-M} \sim U(0,1)$

$\quad\quad q \sim U(0,1)$

$\quad\quad \varepsilon \sim N(o, \sigma^2)$

$\quad\quad \sigma \sim Gam(\alpha , \beta) \; ; \; E[\sigma] = MSE$

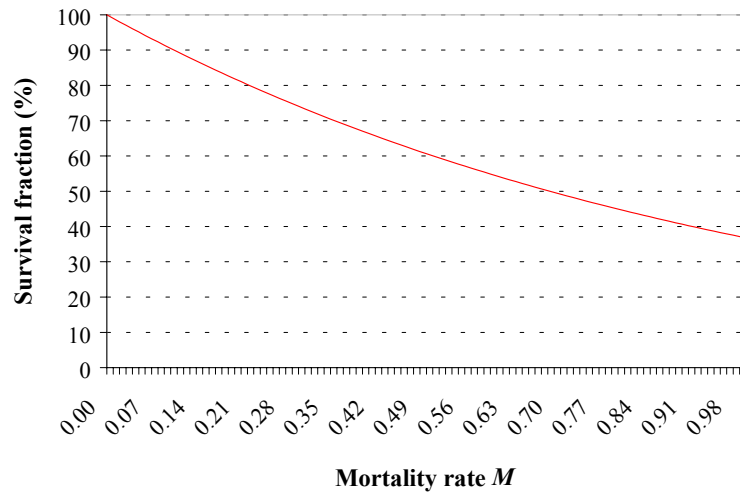$\quad\quad\quad\quad\quad\quad Var[\sigma] = var(MSE)$

$\quad\quad d \sim N(\mu_d , \sigma_d^2)$
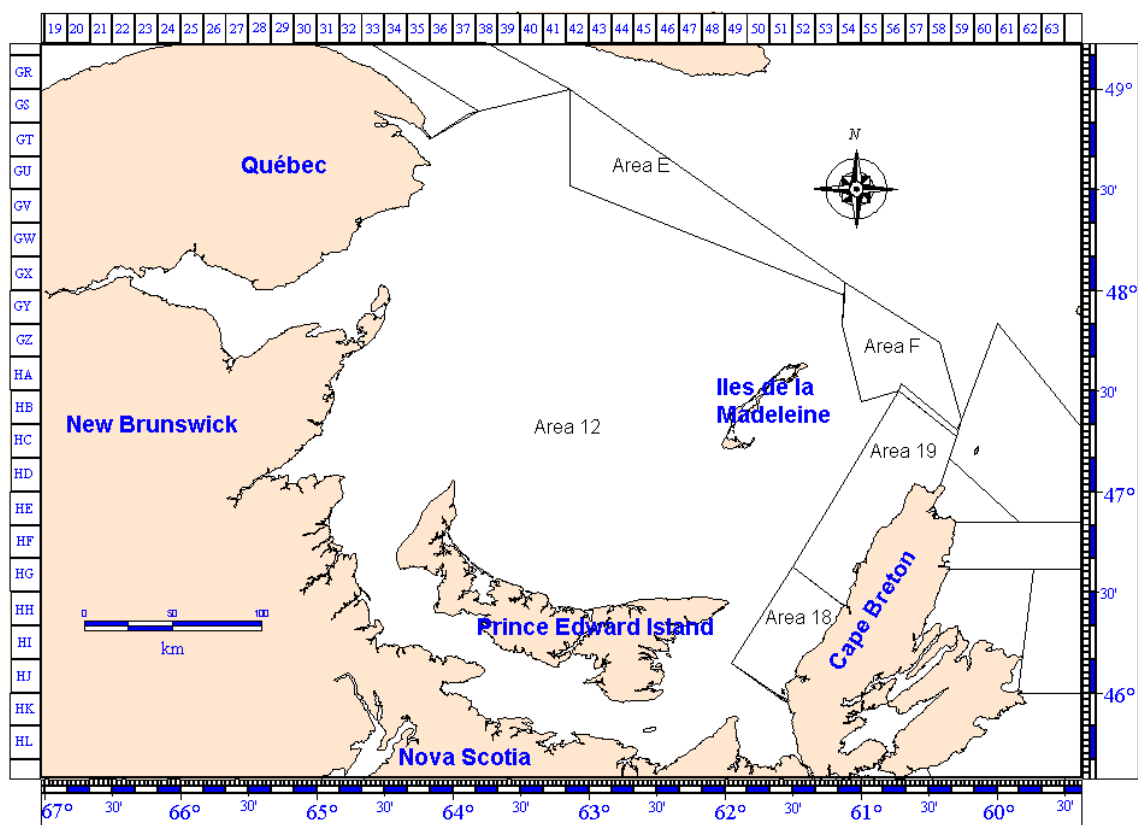
Figure 1: Snow crab fishing areas (CFA) in the southern Gulf of St. Lawrence.
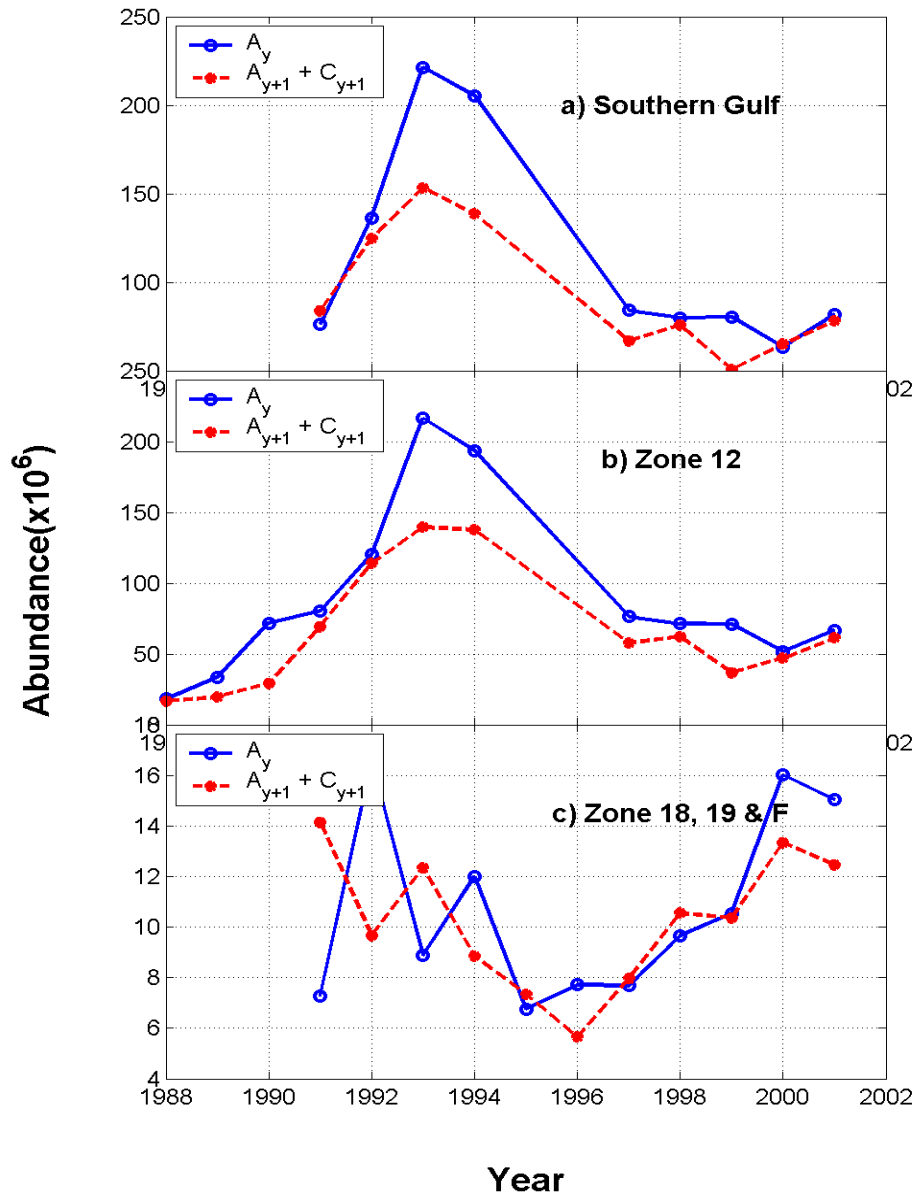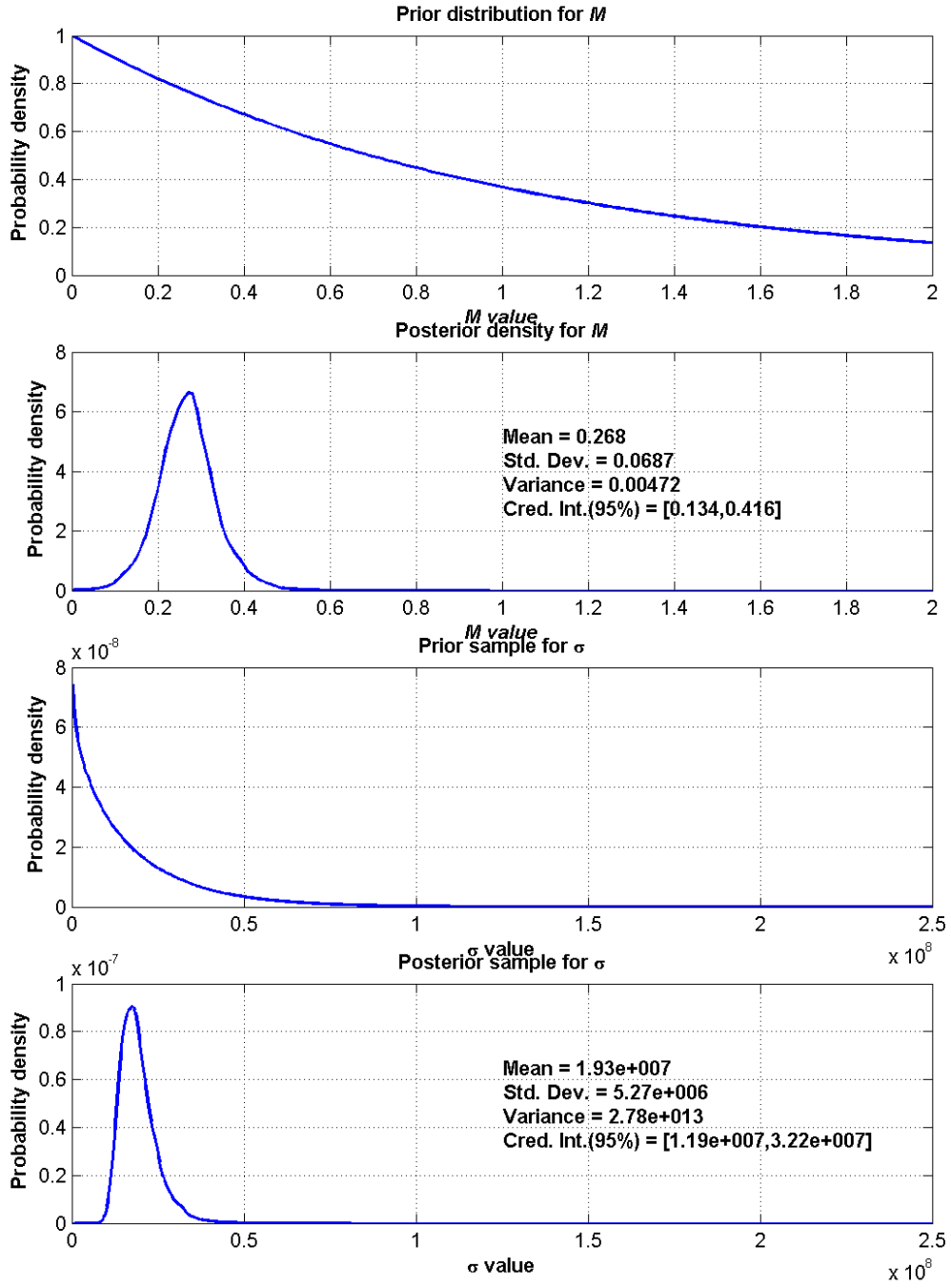
Figure 2: Pre-season abundance estimate A_y and post-season abundance estimate A'_{y+1} plus catch abundance C_{t+1} versus time for three different study zones for legal-sized males: a) southern Gulf, b) southwestern Gulf c) southeastern Gulf.
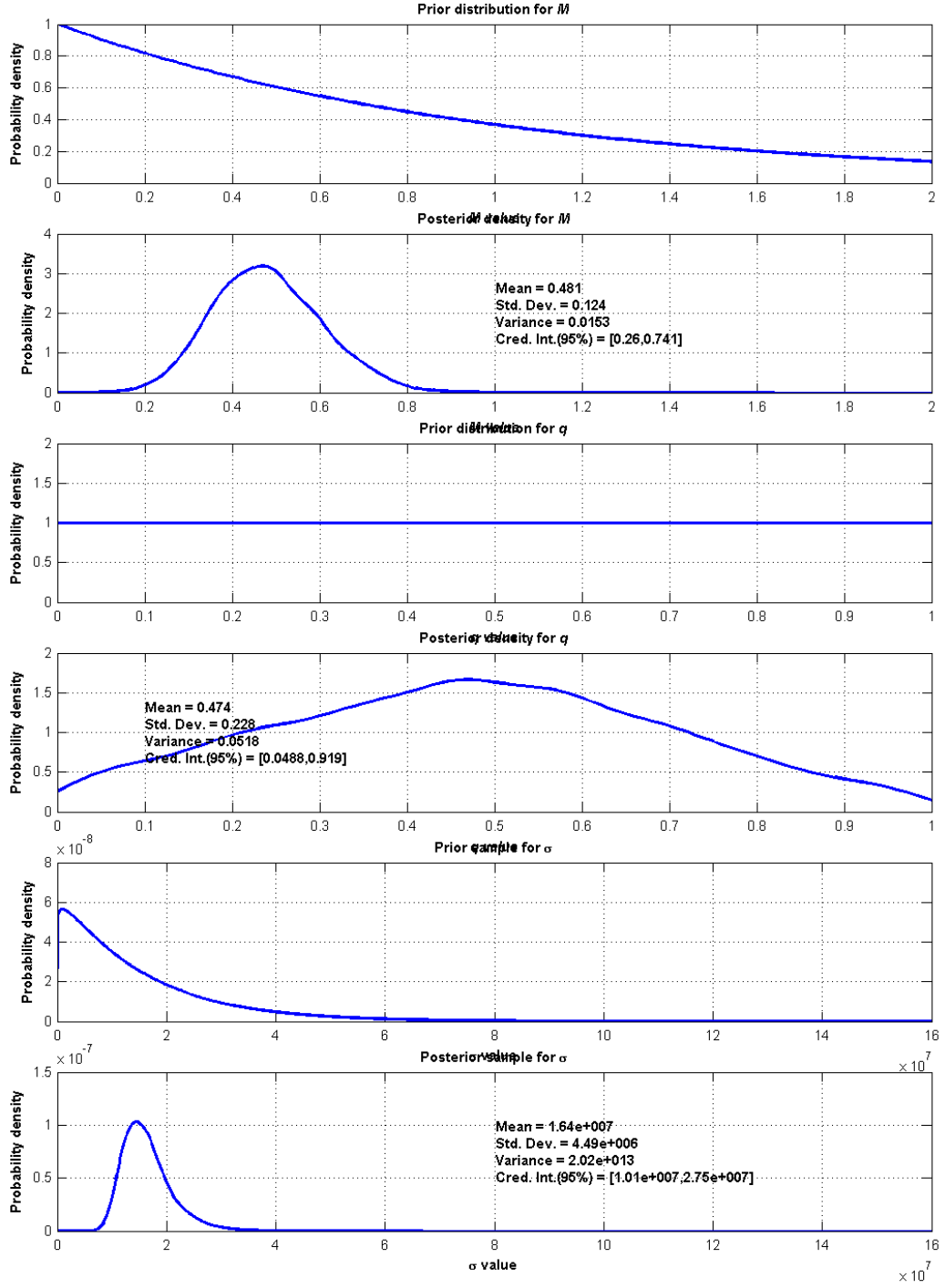
$$S = e^{-M}$$

Figure 3: Conversion graph relating the mortality rate M to the survival fraction S .
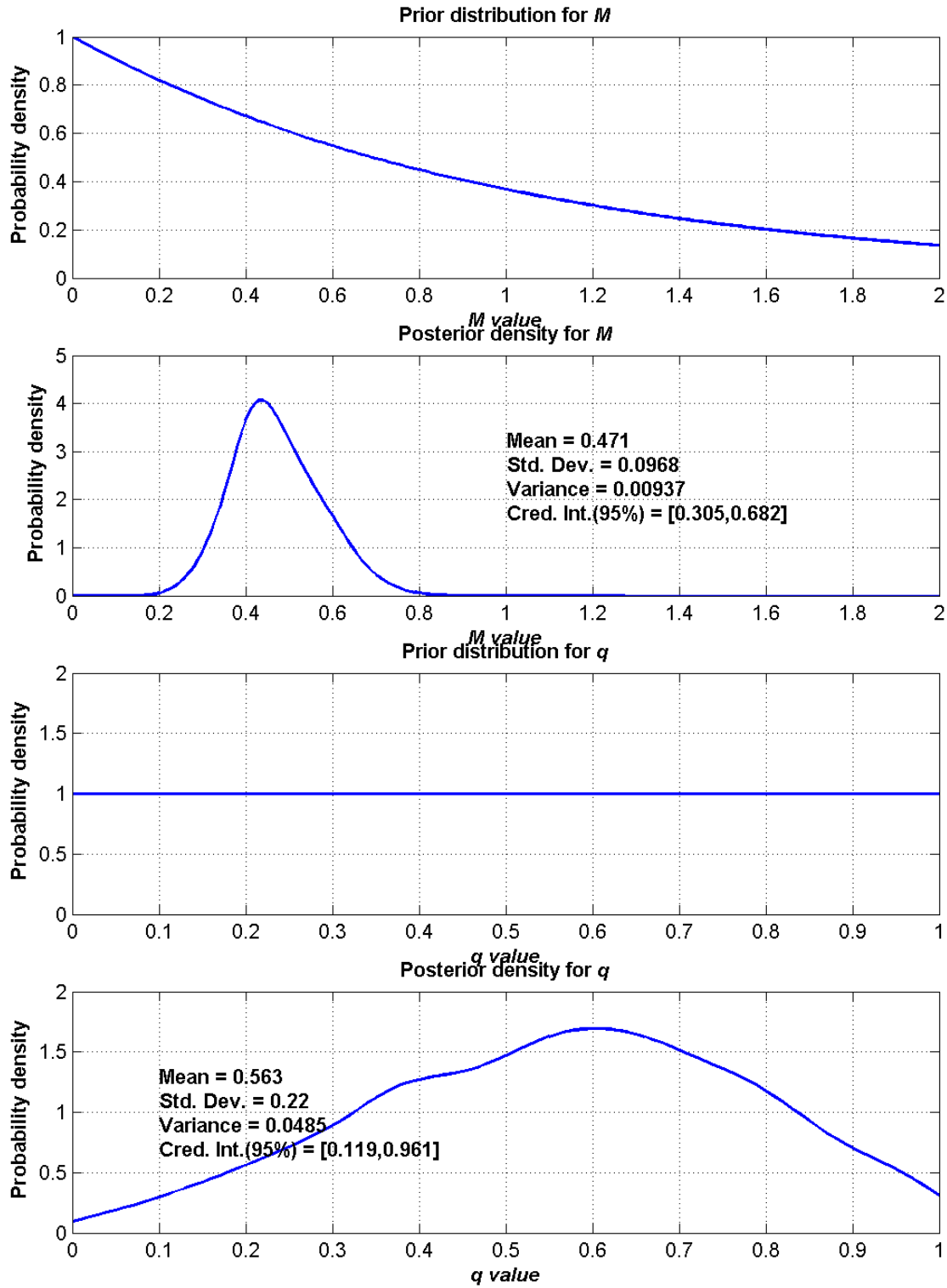
Figure 4: Prior and posterior distributions for parameters from model I ($A'_{y+1} = e^{-M} A_y + C_{y+1} + \varepsilon$).
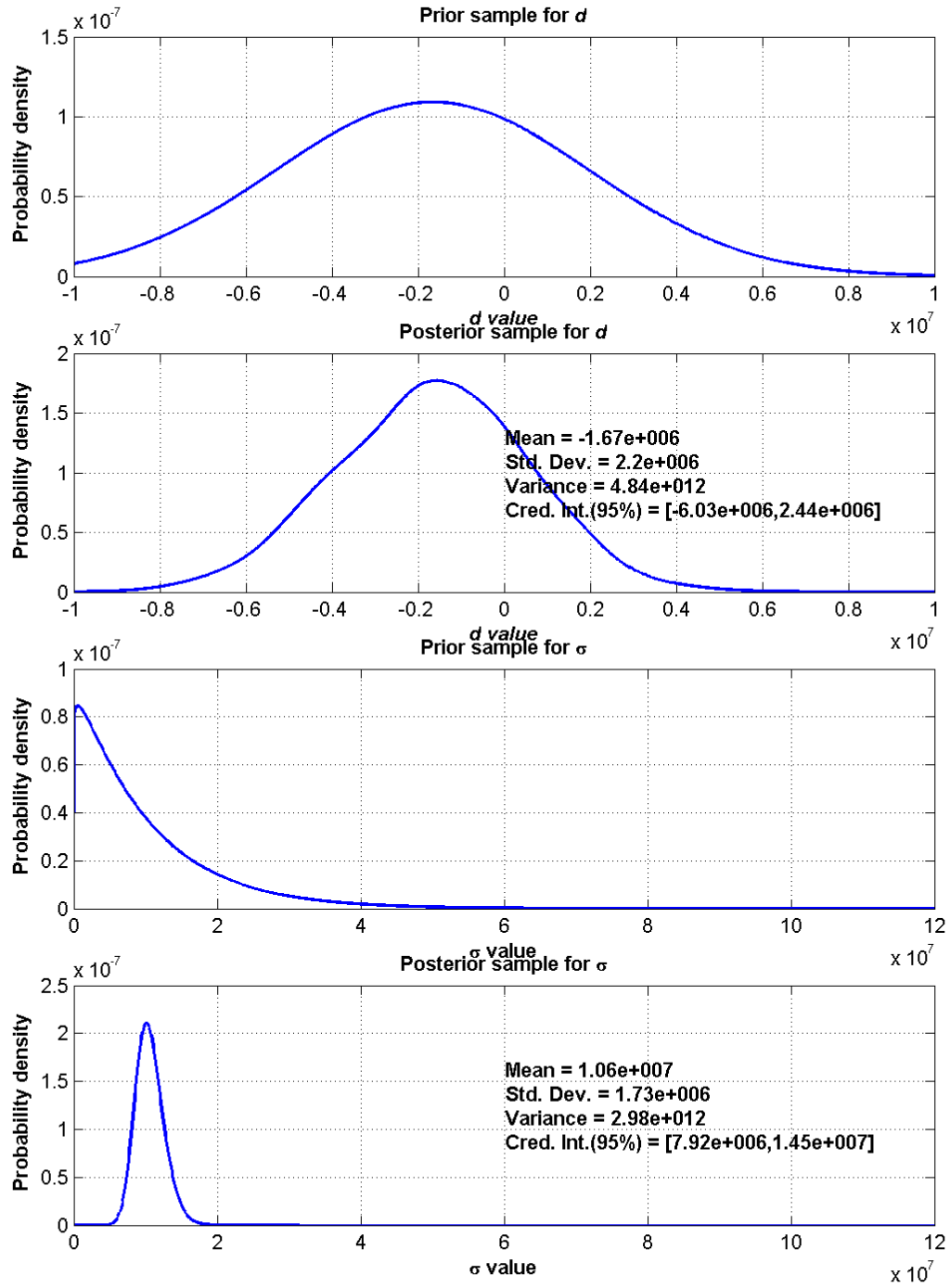
Figure 5: Prior and posterior distributions for parameters from model II ($A'_{y+1} = e^{-M} A_y - qC_{y+1} + \varepsilon$).

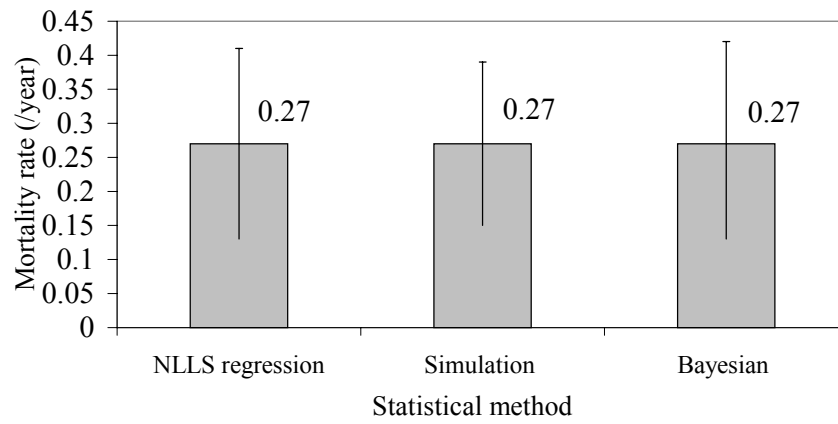**Figure 6.1**: Prior and posterior distributions for parameters M and q from model III ($A'_{y+1} = e^{-M} A_y - qC_{y+1} + dI + \varepsilon$).
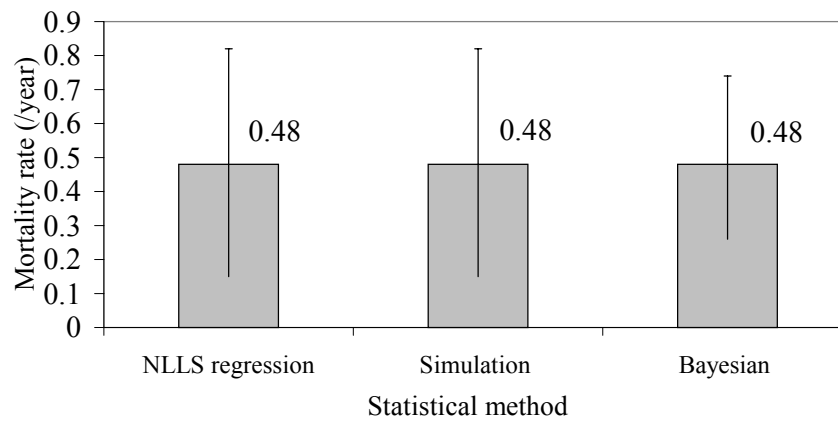
Figure 6.2: Prior and posterior distributions for parameters d and σ from model III ($A'_{y+1} = e^{-M} A_y - qC_{y+1} + dI + \varepsilon$).
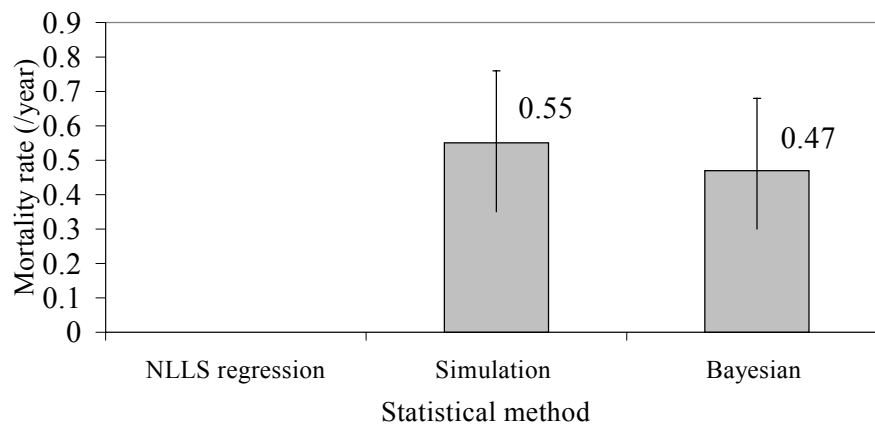
Model I

Model II

Model III

Figure 7: Comparison of mean natural morality estimates *M* for the three models used.

Appendix I

Classification of shell condition developed for the sGSL stock based on carapace condition, durometer reading and corresponding approximate age after terminal molt (modified from Moriyasu *et al.*, 1998; Anonymous 1994).

Category	Stage	Durometer reading	Carapace condition	Approximate age after terminal molt
New soft	1	< 68	brightly colored, iridescent, soft, no epibionts, chelae easily bent.	0-5 months
Clean	2	variable	brightly colored, some iridescence, may have epibionts, chelae not easily bent	5 months- 1 year
Inter-mediate	3	> 68	dull brown dorsally and yellow-brown ventrally, no irridescence, shell abrasion evident, epibionts.	8 months -3 years
Old	4	> 68	carapace very dirty but hard, decay may be present at leg joints, epibionts removable at processing plant.	2 - 5 years
Very old	5	variable	carapace very dirty and may be soft (durometer reading < 68), progression of decay may be evident, epibionts not removable at processing plant.	4-6 years

Appendix II:

Estimates of natural mortality for sublegals.

Estimates of the natural mortality for sublegal sized adult crab (SAC) can be obtained in a similar manner as described in the document. Although the SACs are not landed, they are still affected somewhat by the fishing activities. Catches for sublegal sized males are small for the time series. Estimates of catches from this non-commercial category are available from a sea sampling program which has been in place since the mid nineties. The average percentage of sublegals from those years where those numbers are available was used in estimating the portions of sublegals when no data was available. The sublegals that get into the traps are put back into the water as part of the fishermen's condition of license. However, not all of these individuals will survive. Dufour et. al. (1997) estimated that approximately 12.5% mortality occurred due to handling. So for analysis on the sublegal class, we shall consider that 12.5% of the catches projected from the sea sampling data constitutes a loss due to fishing activity.

Considering this, we can therefore attempt to estimate the natural mortality parameter for the sublegal adult component of the population in the gulf. The equation will be modified to:

(8)
$$A'_{y+1} = e^{(-M_t)} A_y + q * 0.125 * C_{y+1}$$

Where: A'_{y+1}= Abundance of adult sublegals with shell condition 3,4 or 5 at year $y+1$
A_y= Abundance of adult sublegals with shell condition 1,2,3,4 or 5 at year y
q= catchability of trawl
C_{y+1}= Catch of sublegals in traps during fishing activities from at sea observer data.

Survey population estimates for gulf male adult sublegal and projected mortality from handling.

Year y	A_y	A'_{y+1}	C_{y+1}
1988	105200000	14360000	245200
1989	102600000	39870000	230300
1990	199500000	65650000	321500
1991	141200000	125100000	341300
1992	150500000	91970000	428800
1993	107400000	73210000	598300
1994	89470000	53940000	582000
1997	101500000	23490000	344100
1998	137200000	42950000	376800
1999	230600000	106700000	466100
2000	196300000	78150000	764400
2001	188000000	108800000	255700

Results show that mortality estimates for the adult sublegal category are higher than for legal sized adult. Estimates of M for the gulf range from 0.53 to 1.02 with a mid value of 0.75 when using a simple regression approach with a constant catchability of 1. The mid value of M increases to 0.85 with a 95% C.I. range of 0.34 to 1.99 when solving for both M and q. The catchability coefficient however is widely variable from –82.18 to 116.7 with a mid value of 17.1.