



Uncertainties of natural mortality estimates for eastern Bering Sea snow crab, *Chionoecetes opilio*

Jie Zheng*

Alaska Department of Fish and Game, Division of Commercial Fisheries, P.O. Box 25526, Juneau, AK 99802-5526, USA

Abstract

Instantaneous natural mortality (M) estimates are very uncertain for eastern Bering Sea snow crab, *Chionoecetes opilio*. An M of 0.3 per year has commonly been used for the mature population, whereas a sole published study concluded that M is larger than 1.06 per year for morphometrically mature males. In this study, catch-survey models were constructed using trawl survey data from 1989 to 2000 to estimate M for the eastern Bering Sea snow crab stock under different assumptions of moulting probability of morphometrically mature males, handling mortality rate of bycatch and survey catchability. Male abundance was categorized by size (80–99, 100–119 and >119 mm carapace width), shell condition (newshell and oldshell) and morphometrically mature status. Mature female abundance was grouped by shell condition. M estimates for males vary greatly, ranging from 0 to 0.97 per year, depending on model assumptions. Moulting probability of morphometrically mature males and survey catchability for large males (>99 mm) are the two most sensitive factors. Allowing morphometrically mature males to moult resulted in a significantly better data fit than a zero moulting probability assumption, and assuming a low survey catchability for large males resulted in a high estimate of M for mature males. The F statistic test indicated that the most parsimonious model for males was the scenario of a constant M of 0.35 per year without the terminal moult assumption. Because of no retained catch, very low bycatch and no moulting after maturity, M estimates for mature females were not so sensitive to model assumptions. The M for mature females was estimated as 0.52 per year for crab south of 61.2°N latitude and 0.56 per year for all crab.

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Keywords: Bering Sea snow crab; Natural mortality; Parameter uncertainty; Length-based model

1. Introduction

Among the four factors influencing population dynamics, recruitment, growth, instantaneous natural mortality (M) and harvest, M is the least understood. M estimates are not only confounded with the other three factors, but M is also difficult to observe directly. Thus, M is usually estimated with a stock assessment model when survey data are available or with a life-history analysis. Quinn and Deriso

(1999) reviewed six common approaches for estimating natural mortality: (1) catch curve analysis, (2) length–frequency analysis, (3) mark-recapture experiments, (4) collection of dead organisms, (5) fitting population models, and (6) life-history (or meta-) analysis. M estimates from any of these approaches are likely subject to a great deal of uncertainty due to parameter confounding and data limitation.

The challenge of estimating M can be demonstrated with the eastern Bering Sea snow crab (*Chionoecetes opilio*) stock, which supports the most important crab fishery in Alaska with exvessel value peaking in 1994 at US\$ 192.4 million (Morrison, 1999). Due to lack of

* Tel.: +1-907-465-6102; fax: +1-907-465-2604.

E-mail address: jie.zheng@fishgame.state.ak.us (J. Zheng).

data, Somerton (1981) assumed M for eastern Bering Sea snow crab to be the same as those estimated for eastern Bering Sea Tanner crab, *Chionoecetes bairdi*. His estimates of M ranged from 0.13 to 0.28 per year for adult Tanner crab based on different data and models and 0.35 per year for juvenile Tanner crab. Based on Somerton's supposition, an M of 0.3 per year was assumed for eastern Bering Sea snow crab to qualitatively evaluate the fishery management plan and to establish the overfishing rate and overfished population threshold levels by the North Pacific Fishery Management Council (NPFMC, 1990, 1998). However, the only published study so far indicates that M is much higher than 0.3 per year for morphometrically mature (a differentiation based on the shape of the chela, i.e. large-clawed, on the basis of the chela height–carapace width (CW) relationship) male snow crab (Otto, 1998). Otto's estimates of M were based on trawl survey and commercial catch data and were size-dependent, ranging from 2.11 per year for crab of 50 mm CW to 1.08 per year for crab of 130 mm CW with an asymptotical M of 1.07 per year. The huge difference between the assumed M for the management plan and the estimated M in the literature shows the need to further investigate M for this stock.

In this study, catch-survey models were constructed with trawl survey and commercial catch data from 1989 to 2000 to estimate M for the eastern Bering Sea snow crab stock under different assumptions of moulting probability of morphometrically mature males, handling mortality rate of bycatch and survey catchability. For convenience, "morphometrically mature" males were referred to as "mature" and "morphometrically immature" males as "immature" in this paper.

2. Methods

2.1. Data

National marine fisheries service (NMFS) trawl survey and commercial catch data from 1989 to 2000 were used in this study because no chela height data were available before 1989. The area-swept approach was used to estimate abundance by year, sex, shell condition and size class (Stevens et al., 2000). Crab

abundance was estimated either from all survey stations or stations south of 61.2°N latitude that exclude stations north of St. Matthew Island.

The average linear relationship between the natural logarithms of CW and chela height developed by Otto (1998) and updated with survey data from 1989 to 2000 was used to classify morphometrically mature and immature male crab. The updated separation line is

$$\ln(\text{chela height in mm}) = -2.8628 + 1.2899 \ln(\text{CW in mm}) \quad (1)$$

All crab sampled from the survey for chela height measurement were identified as newshell or oldshell and proportions of small-claw (immature) and large-claw (mature) types within each shell condition were estimated for every 5 mm CW interval. These proportions were applied to the area-swept estimates of survey abundance.

Chela height data have been collected since 1996 from the commercial catch. Proportions of newshell and oldshell immature and mature male crab sampled from the commercial catch were estimated for each 5 mm CW interval each year using Eq. (1). Due to missing data points in some CW intervals, a logistic function was fit to proportion by CW data to smooth the estimates and fill in the missing data points. Because maturity proportions by CW were generally much higher for oldshell males than for newshell males (Otto, 1998), for a given CW group, the estimate of the maturity proportion for oldshell males was set to be equal to or greater than that for newshell males. These estimated proportions were applied to the commercial catch data in the corresponding years from 1996 to 2000. Estimated maturities by CW and shell condition from 1996 to 1999 were similar but quite different from those for 2000. Due to the ice condition in the Bering Sea and a small catch quota, the fishing season in 2000 started 3 months later than the previous seasons and lasted for only a few days compared to 2 months or longer in the previous years. Therefore, average maturity proportions by shell condition by 5 mm CW intervals from 1996 to 1999 were used to classify maturity status of the commercial catch from 1989 to 1995. The commercial catch data were assumed free of errors in the model due to their large sample sizes and big size classes.

2.2. Models

A catch-survey analysis (Zheng and Kruse, 2002) was modified to model morphometrically mature and immature male crab in this study. To reduce the influence of recruitment, growth and survey catchability on M estimates, only male crab ≥ 80 mm CW with a large CW group interval were modeled. Male crab abundance was divided into three CW intervals: 80–99, 100–119 and ≥ 120 mm. Each of the first two intervals consisted of four groups: newshell mature and immature and oldshell mature and immature. Because there were few oldshell crab ≥ 120 mm, the last interval was separated by maturity only. The male model links the crab abundances in year $t + 1$ to the abundances and catch in year t in three stages through natural mortality, moulting probability and a growth matrix. Abundances of newshell males are

$$\begin{aligned}
 N_{t+1,j,1} &= \sum_{i=1}^j [A_{t,i,1}mm_iG_{i,j} + A_{t,i,2}mi_i mp_i G_{i,j}] \\
 &\quad + R_{t+1}r_{t+1,j,1}, \\
 N_{t+1,j,2} &= \sum_{i=1}^j [A_{t,i,2}mi_i(1 - mp_i)G_{i,j}] + R_{t+1}r_{t+1,j,2}
 \end{aligned}
 \tag{2}$$

where $N_{t+1,j,1}$ and $N_{t+1,j,2}$ are the abundances of newshell males in year $t + 1$ and CW interval j for mature (1) and immature (2) crab, mm_j and mi_j the moulting probabilities of mature and immature males in CW interval j , mp_j the proportion of moulting males to become mature in CW interval j , $G_{i,j}$ the growth matrix containing the proportions of moulting crab growing from group i to group j , R_{t+1} the total recruitment in year $t + 1$, and $r_{t+1,j,1}$ and $r_{t+1,j,2}$ are the proportions of recruitment in year $t + 1$ to CW interval j for mature and immature males. The average growth increments per moult for 80–99 mm CW male snow crab in the Gulf of St. Lawrence ranged from 17 to 19 mm (Sainte-Marie et al., 1995). By assuming Bering Sea male snow crab have similar growth rates, recruitment to the model was defined as newshell crab entering the 80–99 mm CW interval only. Thus, $r_{t,1,1} + r_{t,1,2} = 1$ and $r_{t,j,1} = 0$ and $r_{t,j,2} = 0$ when $j > 1$. $A_{t,j,1}$ and $A_{t,j,2}$ are intermediate variables

defined as

$$\begin{aligned}
 A_{t,j,k} &= (N_{t,j,k} + O_{t,j,k})e^{-M_{j,k}} \\
 &\quad - (C_{t,j,k} + B_{t,j,k}s)e^{(y_t-1)M_{j,k}}
 \end{aligned}
 \tag{3}$$

where $O_{t,j,k}$ is the abundance of oldshell males in year t , CW interval j and maturity status k , $M_{j,k}$ the natural mortality in CW interval j and maturity status k , $C_{t,j,k}$ and $B_{t,j,k}$ the commercial catch and bycatch in year t , CW interval j and maturity status k , s the mortality rate of bycatch in the directed pot fishery, and y_t is the time lag from the survey to the midpoint of the fishery in year t . Abundance of oldshell males comes from the surviving, unmoulting crab in the previous year:

$$\begin{aligned}
 O_{t+1,j,1} &= A_{t,j,1}(1 - mm_j), \\
 O_{t+1,j,2} &= A_{t,j,2}(1 - mi_j)
 \end{aligned}
 \tag{4}$$

The model for female crab is somewhat simpler than the male model. To avoid survey catchability problems, I modeled only mature females. Because a large majority of mature females were within a CW range of 45–65 mm, mature females were grouped by shell condition only. Bycatches of female snow crab in the directed crab fisheries were very low (Moore et al., 2000) and thus ignored in this study. Because mature females do not moult, newshell mature female abundance is equal to recruitment into the model and oldshell mature females are the survivors of mature females in the previous year:

$$N_{t+1}^f = R_{t+1}^f, \quad O_{t+1}^f = (N_t^f + O_t^f)e^{-M^f}
 \tag{5}$$

where N_t^f and O_t^f are the newshell and oldshell mature female abundances in year t , R_t^f the female recruitment in year t and M^f is the female natural mortality. The male and female models are completely independent.

2.3. Parameter estimation

Survey catchabilities were used to scale absolute abundances to relative (survey) abundances for parameter estimation. For trawl surveys, the survey catchability (q_2 and q_3) of large males (≥ 100 mm CW) was assumed to be one to reduce the number of parameters and estimated the survey catchability (q_1) for males of 80–99 mm CW. Trawl survey catchabilities for mature females were assumed independent of size

and shell condition. Measurement errors of survey estimates of relative abundances were assumed to follow a log-normal distribution. A nonlinear least squares approach that minimizes the residual sum of squares (RSS) was used to estimate parameters:

$$\begin{aligned} \text{RSS} &= \sum_{t=1989}^{2000} \sum_{j=1}^3 \sum_{k=1}^2 [\ln(N_{t,j,k}q_j + 1) \\ &\quad - \ln(\widehat{N}_{t,j,k} + 1)]^2 + [\ln(O_{t,j,k}q_j + 1) \\ &\quad - \ln(\widehat{O}_{t,j,k} + 1)]^2, \\ \text{RSS}^f &= \sum_{t=1989}^{2000} [\ln(N_t^f + 1) - \ln(\widehat{N}_t^f - 1)]^2 \\ &\quad + [\ln(O_t^f + 1) - \ln(\widehat{O}_t^f + 1)]^2 \end{aligned} \quad (6)$$

where superscript f stands for females, $\widehat{N}_{t,j,k}$ and $\widehat{O}_{t,j,k}$ are the relative trawl survey (area-swept) abundances of newshell and oldshell males in year t , CW interval j and maturity status k , and \widehat{N}_t^f and \widehat{O}_t^f are the relative trawl survey (area-swept) abundances of newshell and oldshell mature females in year t .

No growth increment data are available for eastern Bering Sea snow crab. Thus, the growth matrix was estimated from growth data for snow crab in the Gulf of St. Lawrence, Canada (Sainte-Marie et al., 1995). Assuming a normal distribution of growth increments per moult, the growth matrix was derived from mean growth increment per moult and its standard deviation in each size group. Because of lack of observed growth data for pre-moulting crab >91 mm CW, mean growth increments per moult were estimated from the growth functions derived by Sainte-Marie et al. (1995) and standard deviations were estimated by applying an estimated 10% coefficient of variation to the corresponding mean growth increments per moult. Due to large size-group intervals in the model, the growth matrix was relatively insensitive to the estimated standard deviations. The first row of the growth matrix was estimated to be 0.107, 0.888 and 0.005 and the second row 0.0, 0.037 and 0.963. Both immature and mature males were assumed to have the same growth matrix.

Six scenarios based on moulting probability of mature males (zero and estimated) and different M 's for immature and mature males were compared for the

male model and two scenarios based on the mature female abundances in the total survey area and south of 61.2°N latitude were contrasted for the female model. The F statistic test (Schnute, 1981) was used to compare each pair of scenarios with different degrees of freedom and to choose the most parsimonious model. Sensitivity analyses were also conducted by varying values of M for immature males, survey catchability for males >99 mm CW and bycatch handling mortality rate for selected scenarios. All parameters except that under consideration were estimated in each sensitivity analysis.

Estimated parameters include natural mortalities, moulting probabilities, catchabilities, abundance of crab entering the models for the first time each year except the first and total abundance in the first year. Similar to the length-based model (Zheng et al., 1995), the relative frequencies of size groups from the first-year trawl survey data were assumed to approximate the true relative frequencies. Thus, size-specific abundance estimation was not needed for the first year. Parameters for male and female models were estimated separately by minimizing RSS using the quasi-Newton method. The AD Model Builder (Otter Research Ltd., 1994) was used in the parameter estimation.

3. Results

M estimates for males varied greatly, ranging from 0 to 0.97 per year depending on model assumptions (Table 1). When estimated separately, M was the lowest for immature males and highest for mature males of 80–99 mm CW. M estimates for immature and mature males without the terminal moult assumption appear to be negatively confounded among them, with the correlation coefficient being equal to -0.88 . Correlation coefficients among the M estimates for the other scenarios were within -0.1 and 0.3 . The coefficients of variation of M estimates were the smallest when a constant M was assumed for all male crab. Assuming a zero moulting probability for mature males resulted in much higher estimates of M for mature males and close to zero mortality for immature males.

Estimated moulting probabilities depended primarily on the moulting assumption of mature males (Table 1). Estimated moulting probabilities for im-

Table 1

Parameter estimates and their standard deviations (in parentheses) for male snow crab in the eastern Bering Sea with six scenarios of combinations of mature moulting probability and natural mortality^a

Parameter	Moulting probability of mature males					
	Estimated			Assumed to be zero		
	A1	B1	C1	A2	B2	C2
Natural mortality (per year)						
Matures 80–99 mm	0.701 (0.168)	0.469 (0.202)	0.347 (0.062)	0.971 (0.140)	0.816 (0.112)	0.527 (0.074)
Matures >99 mm	0.274 (0.237)	0.469 (0.202)	0.347 (0.062)	0.457 (0.161)	0.816 (0.112)	0.527 (0.074)
Immatures	0.136 (0.313)	0.064 (0.392)	0.347 (0.062)	<0.001 (0.001)	<0.001 (0.001)	0.527 (0.074)
Moulting probability						
Immatures 80–99 mm	0.930 (0.024)	0.931 (0.029)	0.911 (0.021)	0.941 (0.015)	0.936 (0.017)	0.885 (0.021)
Immatures 100–119 mm	0.766 (0.140)	0.804 (0.124)	0.712 (0.107)	0.888 (0.030)	0.893 (0.030)	0.885 (0.021)
Matures 80–99 mm	0.242 (0.094)	0.393 (0.163)	0.481 (0.063)	0	0	0
Matures >99 mm	0.241 (0.093)	0.244 (0.128)	0.298 (0.069)	0	0	0
Moulting to maturity						
80–99 mm	0.840 (0.048)	0.837 (0.071)	0.780 (0.041)	0.819 (0.024)	0.858 (0.015)	0.740 (0.013)
100–119 mm	0.891 (0.087)	0.913 (0.071)	0.859 (0.080)	0.956 (0.020)	0.958 (0.019)	0.961 (0.020)
Catchability						
80–99 mm	1.000 (0.008)	1.000 (0.004)	1.000 (0.004)	0.907 (0.179)	0.621 (0.081)	0.353 (0.053)
RSS	19.474	20.248	20.513	22.991	25.998	42.670
d.f.	88	89	90	90	91	92
P-value						
A1	–	0.065	0.102	<0.001	<0.001	<0.001
B1	–	–	0.284	<0.001	<0.001	<0.001
C1	–	–	–	–	<0.001	<0.001
A2	–	–	–	–	<0.001	<0.001
B2	–	–	–	–	–	<0.001

^a A1 and A2: different natural mortalities for immature, mature 80–99 mm and mature >99 mm CW males; B1 and B2: different natural mortalities for immature and mature males; C1 and C2: the same natural mortality for all males.

mature males of 100–119 mm CW were higher with the terminal moult assumption (zero moulting probability for mature males) than without it. Estimated moulting probabilities for mature males ranged from 0.242 to 0.481 for crab of 80–99 mm CW and from 0.241 to 0.298 for crab >99 mm CW, much lower than estimated values for immature males. Among moulting crab of 100–119 mm CW, estimated proportions of moulting to maturity were also higher with the terminal moult assumption than without it. Survey catchabilities were assumed to be one for males >99 mm CW and estimated catchabilities for males of 80–99 mm CW were also equal to one without the terminal moult assumption and ranged from 0.353 to 0.907 with the terminal moult assumption. Under the terminal moult assumption and the constant *M*

scenario, the model lowered the survey catchability for males of 80–99 mm CW to fit the relatively low survey abundance of oldshell mature males in this size group.

Estimated total male survey abundances had the same trend over time and fit the observed values well for all scenarios (Fig. 1). The highest estimated abundance occurred in 1990 and the lowest one in 2000. The estimated abundances for all three scenarios of estimating moulting probability for mature males were very close to each other and fit the observed abundance better than those scenarios with the terminal moult assumption. Like total survey abundance, three scenarios without the terminal moult assumption closely fit the male abundance by size, shell condition and maturity status (Fig. 2). Three scenarios with

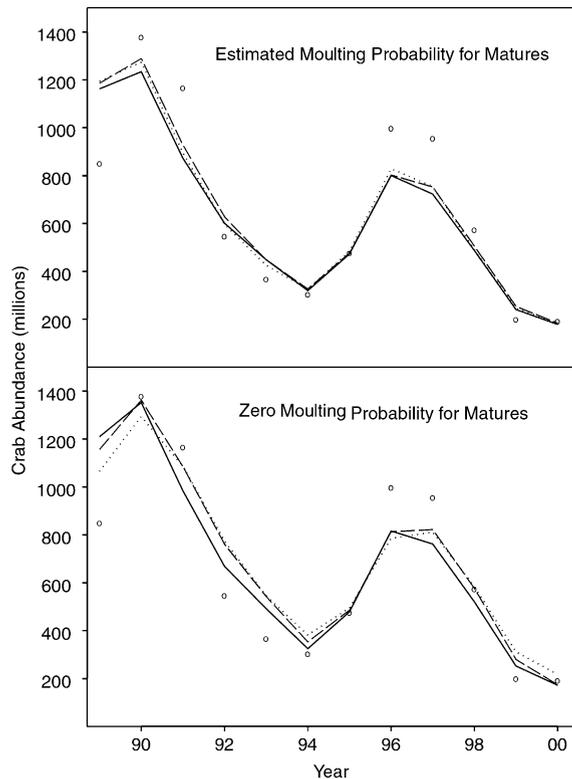


Fig. 1. Comparison of observed (letter 'o') and estimated (lines) survey male snow crab abundances in the eastern Bering Sea. Solid lines represent a scenario with different natural mortalities for immature, mature 80–99 mm CW and mature >99 mm CW crab; dashed lines denote a scenario with different natural mortalities for immature and mature males; dotted lines show a scenario with the same natural mortality for all males.

the terminal moult assumption generally fit the group abundance reasonably well, except for immature newshell abundance of 100–119 mm CW, mature oldshell abundance of 80–99 mm CW and mature newshell abundance of 100–119 mm CW (Fig. 3). Abundances estimated with these three scenarios for these three groups were generally much higher than the observed abundances, especially with the scenario of a constant M .

The F statistic test indicated that the most parsimonious model was the scenario of a constant M without the terminal moult assumption (Table 1). The P -values of paired tests among the three scenarios without the terminal moult assumption were all greater than 0.06, indicating that data fittings among these

three scenarios were statistically not significantly different ($P > 0.05$). These three scenarios fit the data better than the other three scenarios with the terminal moult assumption (Table 1). Thus, with the lowest number of parameters without the terminal moult assumption, the constant M scenario was the most parsimonious model. Among the three scenarios with the terminal moult assumption, the best fitting model was the scenario with different M 's for immature, mature 80–99 mm CW and mature >99 mm CW male crab (Table 1).

Estimated M 's were confounded with other parameters (Fig. 4). Estimated M for mature males was negatively related to M for immature males and moult probability of mature males (Fig. 4A). When the survey catchability for males >99 mm CW was assumed to be one, RSS was insensitive to M of 0–0.1 per year for immature males and slowly increased with M . Current bycatch handling mortality rate was assumed to be 0.25 and had little effect on estimated M values for male crab and RSS when it was <0.5 (Fig. 4B). Extremely high handling mortality rates of bycatch resulted in lower estimated M values for mature males and higher RSS. Estimated M for mature males was also negatively associated with survey catchability for male crab >99 mm CW (Fig. 4C). Lower survey catchability also resulted in lower moult probability for mature males and generally lower RSS. With the terminal moult assumption, estimates of M for mature males >99 mm CW were much more sensitive than those for mature males 80–99 mm CW to survey catchability of crab >99 mm CW (Fig. 4D).

The model fittings to the mature female abundance south of 61.2°N latitude and in total survey area were similar, with RSS being 2.848 and 2.846, respectively. An estimated M of 0.516 per year with a standard deviation of 0.109 in the area south of 61.2°N was slightly smaller than the estimated M of 0.564 per year (standard deviation of 0.113) in the total survey area. Both scenarios fit the data well (Fig. 5). When separate M 's were estimated for newshell and oldshell mature females, estimated M for newshell mature females was more than twice that for oldshell mature females and was biologically unreasonable. This may be caused by the confounding between estimates of recruitment and M for newshell mature females.

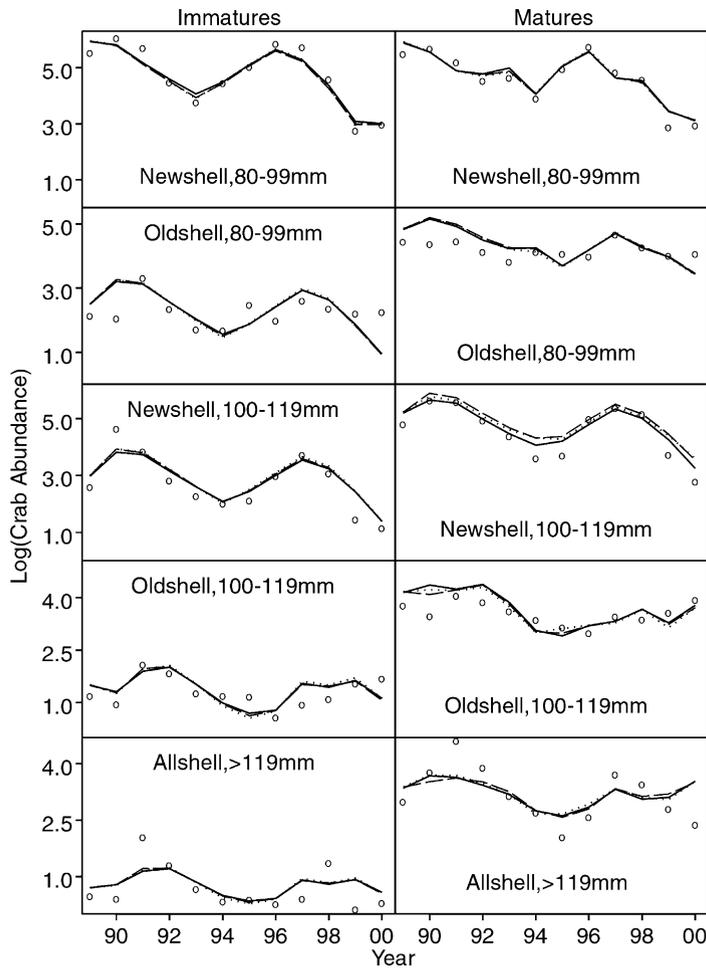


Fig. 2. Comparison of observed (letter ‘o’) and estimated (lines) logarithm of abundances by size group of eastern Bering Sea male snow crab from 1989 to 2000 with scenarios of estimated moulting probability for mature crab. Solid lines represent a scenario with different natural mortalities for immature, mature 80–99 mm CW and mature >99 mm CW crab; dashed lines denote a scenario with different natural mortalities for immature and mature males; dotted lines show a scenario with the same natural mortality for all males.

4. Discussion

4.1. Terminal moult

Among the factors influencing M estimates for male snow crab in the eastern Bering Sea, the terminal moult assumption is most sensitive. With the terminal moult assumption, newshell mature males became oldshell in the following year. Due to the relatively small proportion of oldshell crab observed in mature male abundance, estimated M for mature males had to be very high to fit the data. Estimated M for immature

males was forced to be zero to fit the observed high abundance of newshell mature males. In the scenario of estimating M separately for immature and mature males with the terminal moult assumption, estimated M increased from 0.0 per year for immatures to 0.82 per year for matures, which was biologically unlikely. In addition, scenarios without the terminal moult assumption statistically fit the data better than those with it.

The terminal moult assumption for male snow crab has been well accepted for Atlantic stocks (e.g. Conan and Comeau, 1986; Jamieson et al., 1988;

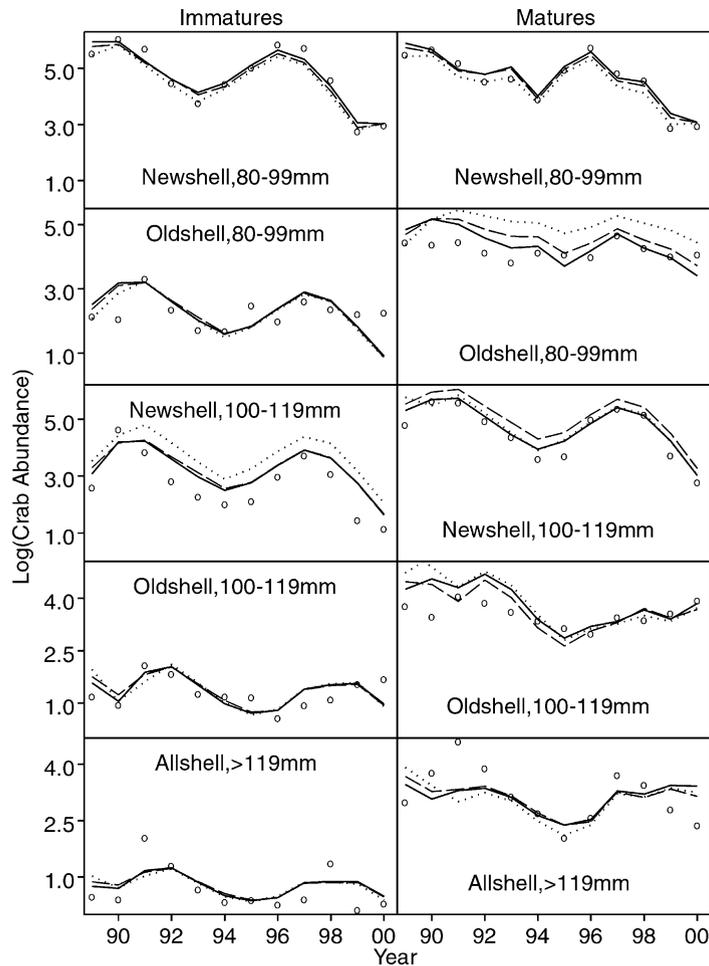


Fig. 3. Comparison of observed (letter 'o') and estimated (lines) logarithm of abundances by size group of eastern Bering Sea male snow crab from 1989 to 2000 with scenarios of zero moulting probability for mature crab. Solid lines represent a scenario with different natural mortalities for immature, mature 80–99 mm CW and mature >99 mm CW crab; dashed lines denote a scenario with different natural mortalities for immature and mature males; dotted lines show a scenario with the same natural mortality for all males.

Sainte-Marie et al., 1995). Although evidence exists that some tagged mature male snow crab moulted in Conception Bay, Newfoundland (Dawe et al., 1991), moulting rates were probably very low and the terminal moult assumption was practically accepted (Earl Dawe, Department of Fisheries and Oceans, St. John's, Nfld, Canada, pers. commun.). Based on their snow crab work in the Gulf of St. Lawrence and the literature on majid crabs, Conan and Comeau (1986) and Conan et al. (1990) suggested that *Chionoecetes* males have a terminal moult at morphometric maturity as well. This assertion led to a considerable debate

(Conan and Comeau, 1988; Donaldson and Johnson, 1988; Conan et al., 1990; Dawe et al., 1991).

Dawe et al. (1991) pointed out that the gap between body sizes of observed largest small-clawed and large-clawed snow crab from Conception Bay, Newfoundland exceeded one moult increment, which did not support the terminal-moult hypothesis. For eastern Bering Sea male snow crab, there was an abundance gap between large immature and large newshell mature males. In 8 of 11 years, the survey abundance of newshell mature males >119 mm CW exceeded the survey abundance of immature males >99 mm

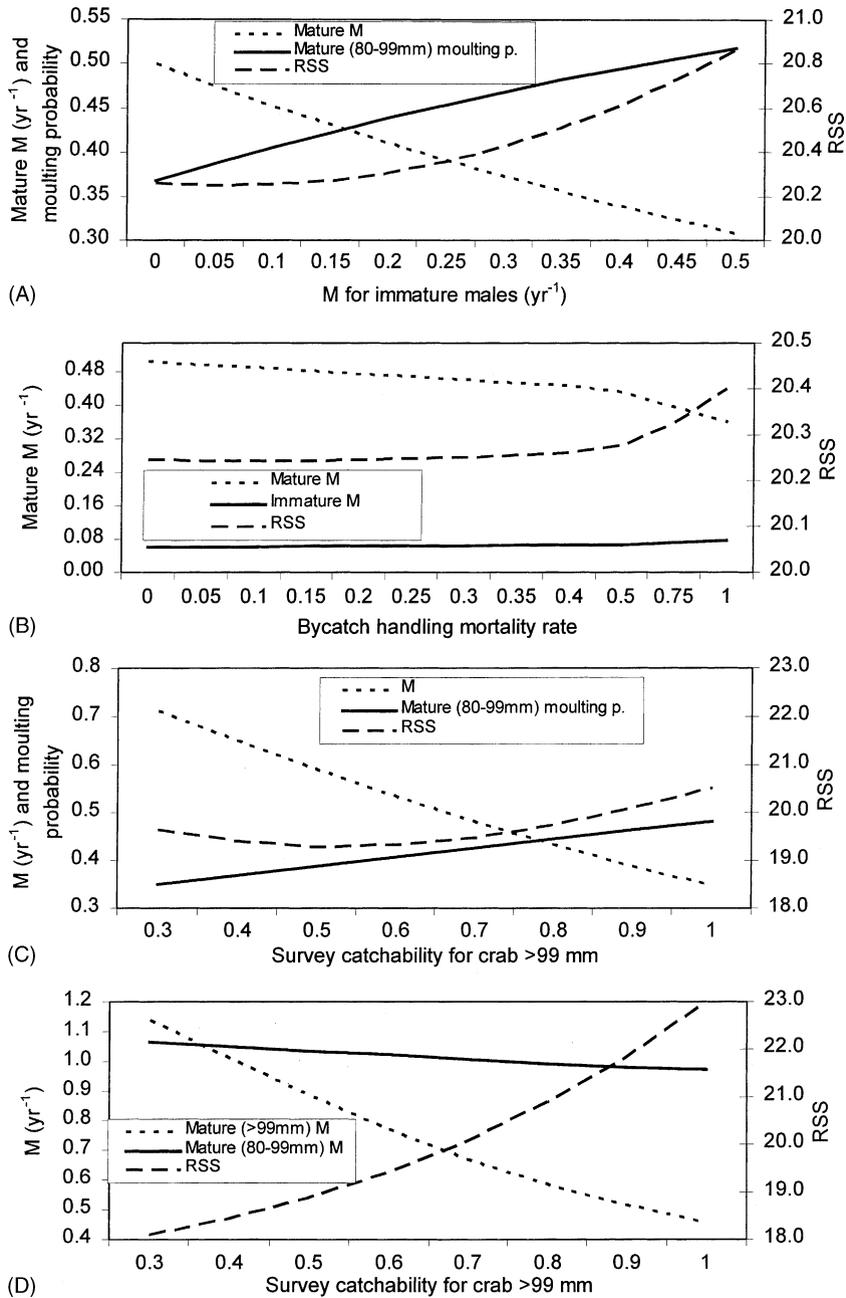


Fig. 4. Relationships among natural mortality, mature moult probability, RSS, survey catchability for male crab >99 mm CW and bycatch handling mortality rate for eastern Bering Sea male snow crab. Different natural mortalities were estimated for immature and mature males without the terminal moult assumption (panels A and B, i.e. scenario B1 in Table 1), the same natural mortality was estimated for all males without the terminal moult assumption (panel C, i.e. scenario C1 in Table 1) and different natural mortalities were estimated for immature, mature 80–99 mm and mature >99 mm CW males with the terminal moult assumption (panel D, i.e. scenario A2 in Table 1).

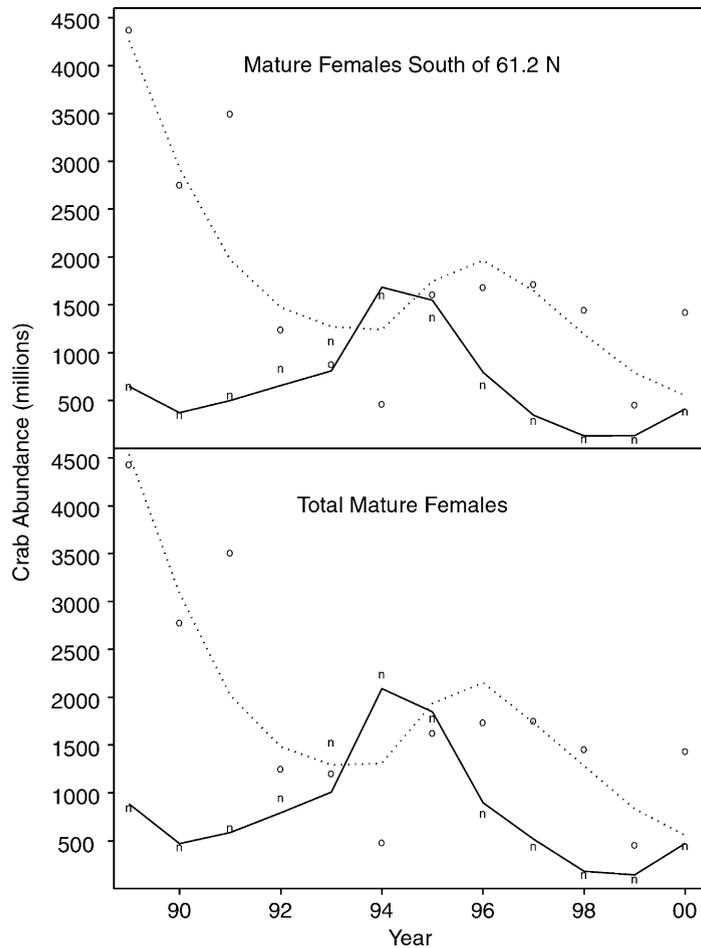


Fig. 5. Comparison of observed (letters 'n' for newshell and 'o' for oldshell) and estimated (solid line for newshell and dotted line for oldshell) abundances of eastern Bering Sea mature female snow crab from 1989 to 2000.

CW adjusted by catch but not by M a year earlier (Fig. 6). The same pattern held for survey abundance of newshell mature males >129 mm CW and survey abundance of immature males >109 mm CW (Fig. 6). Growth increment per moult data for eastern Bering Sea snow crab are not available. For Atlantic snow crab stocks, a variety of estimates of mean growth increment per moult for a male crab of 100 mm CW have been published, ranging from 11.2 mm in Conception Bay, Newfoundland (Taylor and Hoenig, 1990), 15.1 mm in the southern Gulf of St. Lawrence (Moriyasu et al., 1987), 18.4 mm in the western Gulf of St. Lawrence (Miller and Watson, 1976), 19.2 mm in Bonne Bay, Newfoundland (Comeau et al.,

1998), to 19.5 mm in Baie Sainte-Marguerite Bay, the Gulf of St. Lawrence (Sainte-Marie et al., 1995). Another study on the growth of male crab in Conception Bay, Newfoundland shows that mean growth increment per moult for a male crab of 100 mm CW could reach 20 mm (Hoenig et al., 1994). The results from Sainte-Marie et al. (1995), which are among the upper estimates, were used in this study. If mean growth increment per moult for males <100 mm CW is 20 mm or less and if the survey catchability of males >99 or 109 mm CW is close to one, the large newshell mature males in the eastern Bering Sea cannot come from immature males alone (Fig. 6). Note that some of the immature males remained immature

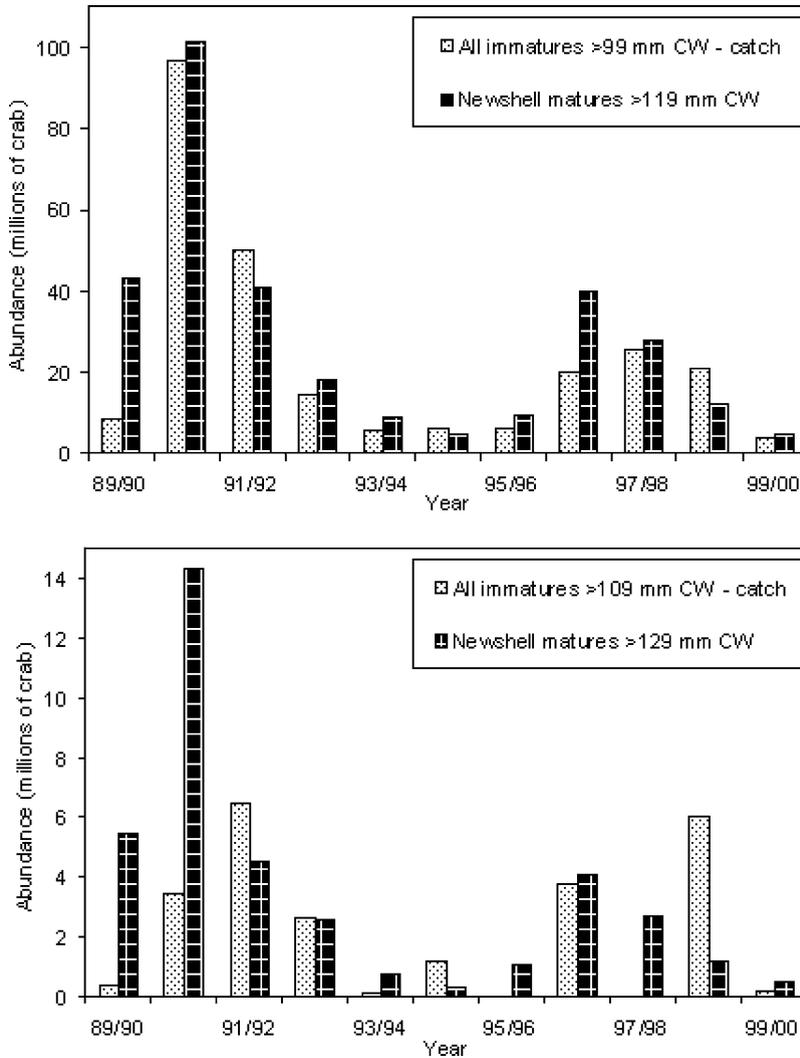


Fig. 6. Comparison of observed abundance of immature males >99 and >109 mm CW adjusted by catch and observed abundance of newshell mature males >119 and >129 mm CW in the following year in the eastern Bering Sea from 1989 to 2000. An *M* of zero was used when adjusted the corresponding catch from the immature abundance.

in the following year, either due to not moulting or not moulting into maturity. One possible explanation is that the survey catchability is smaller for the large immature than for large mature crab, as suggested by Conan and Comeau (1986). For eastern Bering Sea snow crab, the trawl survey is systematic and there have not been any studies to conclude that large immature crab avoid the trawls more than large mature crab. In contrast, because mature snow

crab tends to move to deeper water than immature crab (Zheng et al., 2001), some mature males may move out of the trawl survey area. Thus, whether mature male snow crab in the eastern Bering Sea moult or not is still an unanswered question. Given the important implications of the terminal moult assumption on natural mortality estimates and fishery management, future research is needed to address this issue.

4.2. Survey catchability

The second most important factor affecting M estimates is survey catchability. Similar to the results by Zheng et al. (1997) for eastern Bering Sea blue king crab (*Paralithodes platypus*), M and survey catchability estimates were negatively related for eastern Bering Sea snow crab. Because the harvest rate is applied to survey abundance to determine catch quota, a lower survey catchability means a smaller realized harvest rate. Given a total mortality rate, a decrease in harvest rate results in an increase in M . As female catch cannot legally be retained and female bycatch was very low, M estimates for females were not sensitive to changes in survey catchability. Little has been published on trawl survey catchability for eastern Bering Sea snow crab. Based on a limited experiment, net efficiencies (the capture probability of crab that occur between the wing-tips of the trawl net) at the midpoints of three crab groups (90, 110 and 130 mm CW) for the eastern Bering Sea snow crab survey were estimated to be 0.65, 0.79 and 0.88 (Somerton and Otto, 1999). If survey catchabilities are equal to these estimated net efficiencies, estimates of M are similar to those with survey catchability of 0.7–0.8 for crab >99 mm CW in Fig. 4C and D. These catchabilities do not change the conclusion that the constant M scenario without the terminal moult assumption is the most parsimonious model. Generally, low survey catchability would also result in low estimates of moulting probability for mature males. A survey catchability of 0.3 would result in a mature moulting probability of about 0.05 when estimating M values separately for mature and immature males and 0.35 with a constant M for both mature and immature males. The terminal moult assumption fits the data better with decreasing survey catchability.

4.3. Comparisons with other estimates

The results in this study are similar to those by Otto (1998), with the exception that present M estimates for mature males are lower. The comparable scenario in Otto's study is different M values for immature, mature 80–99 mm CW and mature >99 mm CW crab with the terminal moult assumption. M values were estimated to be 0, 0.97 and 0.46 per year for these three categories of male crab. Otto estimated M to be 1.18 per year for mature males of 90 mm CW and 1.09 per

year for mature males of 120 mm CW. Otto did not estimate M for immature males, but an M of zero for immature males resulted in the best prediction in his study. The different results obtained in the two analyses can be explained by two factors. First, Otto used data from 1989 to 1994 and data from 1989 to 2000 were used in this study. No chela height measurements from commercial catches were made before 1995, so proportions of maturity by size from the survey data were applied to commercial catches in Otto's study. Because mature males move to deep water where the commercial fishery has been concentrated, the proportion of maturity for a given size was higher from the commercial catches than from the survey data. The underestimates of fishing mortality rate of mature males would result in higher estimates of M in Otto's study. Second, different approaches to estimate M were used. Multiple years of data were modeled together to estimate M in this study, whereas about 100 M 's were estimated by pairs of data points and a logistic function of size was fit to these M 's in Otto's study. More importantly, it appears that Otto's study implied that M occurred primarily during and after the commercial fishery, which usually started about 6 months after the survey. The extremely high M estimated by Otto (1998) for large mature male snow crab in the eastern Bering Sea was partly caused by this implication.

Directed fishing mortality rates were very small or close to zero for small male snow crab in the eastern Bering Sea, so Otto's assumption cannot explain the high estimates of M for small males in Otto's study (e.g. $M = 2.11$ per year for mature male crab of 50 mm CW). I speculate that several factors could contribute to these high estimates. First, small immature and mature male crab were highly overlapping in the CW–chela height plots (Otto, 1998) and hardly any visible separation could be detected between these two groups for crab <80 mm CW for most years. Abundances of small immature males were much higher than those of small mature males. So for a given percentage (of abundance) of classification error, a greater number of immature males would be wrongly classified as mature males than mature males wrongly classified as immature males. Due to the overlap and difference in abundance, classification errors could artificially inflate estimates of small newshell mature males, which could cause higher estimates of M . Second, oldshell or large crab tended

to move to deep water (Zheng et al., 2001). If some oldshell mature males moved outside the survey area, it could inflate estimates of M . Third, because of extremely low or no directed fishing mortality, average relative ages of small males after maturity may be higher than those of large mature males, which could result in a higher M . Finally, some mature males may continue to moult. If this is true, M was overestimated with the terminal moult assumption.

It is difficult to compare estimated M 's for the eastern Bering Sea snow crab stock with those for the other stocks. Based on survey and fishery data from 1993 to 2000, M for the snow crab stock in the southwestern Gulf of St. Lawrence, Canada was estimated to be 0.11 per year for immature males, 0.63 per year for mature males with shell conditions 1 and 2, 0.22 per year with shell condition 3, 0 per year with shell condition 4 and infinite with shell condition 5 (E. Wade, Gulf Fisheries Centre, DFO, Canada, pers. commun.). Based on these M 's as a function of shell condition, overall M for all mature males for this stock should be less than 0.5 per year. Total mortality (Z) was estimated to range from 0.40 to 0.54 per year, using the size frequency data from 1985 to 1988 for legal-sized male snow crab in the western Japan Sea (Yamasaki et al., 1990). Using the size frequency data in 1989 and 1990, Yamasaki et al. (1993) derived Z to be higher than 0.84–1.05 per year for males within a year of maturity and to range from 0.34 to 0.54 per year for males that had been mature for more than 1 year for the same snow crab stock. Fishing mortality was not given for this stock but was considered to contribute to most of the deaths for males that had been mature for more than 1 year (Yamasaki et al., 1993). High mortality for males within a year of maturity was caused by fishing and high M during moulting to maturity (Yamasaki et al., 1993). Z was estimated to range from 1.15 to 1.41 per year from 1963 to 1966 from the size frequency data of mature female snow crab in the Japan Sea (Sinoda and Kobayasi, 1968). Fishing mortality may account for a large part of these high mortalities.

4.4. Implications to management strategies

With the uncertainties of M estimates, what M values should be used to manage the snow crab fishery in the eastern Bering Sea? For example, based on the assumption of $F_{MSY} = M$ used by NPFMC (1998)

to determine MSY for the eastern Bering Sea crab fisheries, should $F_{MSY} = 0.3$ (currently assumed), 1.07–2.11 (Otto, 1998), or 0.35 without the terminal moult assumption and 0.46–0.97 with the terminal moult assumption (from this study) for mature male crab? Different choices of M would influence optimal management strategies greatly. Uncertainties demand a conservative or precautionary approach (Restrepo et al., 1998). On the other hand, management strategies shall be based on the best scientific information available (NPFMC, 1998). Therefore, when developing a management strategy, all these M 's along with associated survey catchabilities and moulting probabilities should be considered and evaluated for their implications to the realization of the fishery management goals and for their biological feasibility. Before this study, the precautionary approach was to select a conservative M of 0.3 per year (NPFMC, 1998). In the future, research efforts on estimating M should be focused on reducing the uncertainty. Further understanding of the terminal moult issue, survey catchability and migration patterns between the US–Russia boundary northwest of St. Matthew Island will help reduce the uncertainty.

Acknowledgements

R.S. Otto and B.G. Stevens of NMFS provided survey data. R.S. Otto also provided chela height data for the commercial catch and maturity separation lines for male snow crab. R.S. Otto, D. Pengilly and M.S.M. Siddeek reviewed an earlier version of this manuscript. This work is funded, in part, by cooperative agreement NA97FN0129 from the National Oceanic and Atmospheric Administration (NOAA). The views expressed are those of the author and do not necessarily reflect the views of NOAA or any of its sub-agencies. Contribution PP-222 of Alaska Department of Fish and Game, Commercial Fisheries Division, Juneau.

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