

The role of sex change, growth and mortality in *Pandalus* population dynamics and management

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Fu, C., Quinn, T. J., II, and Shirley, T. C. 2001. The role of sex change, growth and mortality in *Pandalus* population dynamics and management. – ICES Journal of Marine Science, 58: 607–621.

Sex change, growth, and mortality of *Pandalus* populations are important to stock management. To investigate the importance of these life history traits in setting management strategies, we performed a variety of simulations using a length-based model. We compared three populations: a Kachemak Bay, Alaska type (K_pop); a hypothetical one with the same growth but without sex change (H_pop); and a northern Barents Sea type (B_pop). The main difference between K_pop and B_pop is growth rate; K_pop has faster growth and a shorter live span, whereas B_pop lives farther north, and therefore has slower growth and greater longevity. We found that populations with sex change were more sensitive to fishing pressure. Continuous fishing was detrimental to K_pop when instantaneous fishing mortality was above 0.3, but threshold management, i.e. closing the fishery at a low population level, greatly improved the population performance. B_pop, the slower-growing, longer-lived population required larger mesh sizes than K_pop, but increasing mesh size could not prevent collapse under high fishing mortality, and fishery closure under threshold management was necessary to sustain the population. Abrupt decrease of age one and two males caused populations with sex change to fluctuate in spawning biomass. Seasonality in growth and natural mortality is also pertinent to shrimp management. Given faster growth in summer, higher natural mortality in summer means fishing after spring hatching tends to result in higher cumulative yield than fishing after fall mating, and vice versa. In addition, fishing after hatching is in general more robust to overfishing. From the simulation analyses, we concluded that both sex change and seasonality of growth and mortality of *Pandalus* populations should be taken into account in shrimp management.

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Key words: *Pandalus*, sex change, growth, mortality, population dynamics, shrimp management.

Received 5 May 2000; accepted 26 January 2001.

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Introduction

The most prominent feature in *Pandalus* life history is protandric hermaphroditism, i.e. starting as males in early life, changing to a transitional phase, and subsequently becoming females. Females, after extruding eggs and mating in fall, carry their eggs for three to nine months. Hatching commonly occurs in late winter or early spring. Shumway *et al.* (1985) presented a comprehensive synopsis of biological information on *Pandalus*.

Despite diverse research available on biological parameters, such as growth and reproduction, the lack of age data for *Pandalus* shrimp causes difficulty in stock assessment. Consequently, the lack of basic knowledge of stock dynamics limits the scientific basis for shrimp management (Aschan and Godø, 1999).

The lack of age data for invertebrates resulted in the development of a generic length-based population model that has been applied to shrimp and prawn populations (Quinn *et al.*, 1998; Fu *et al.*, 1999). However, this model

does not explicitly deal with sex change or with seasonal growth and mortality. The ICES study group on life histories and assessment of *Pandalus* stocks in the North Atlantic identified the aspects that were pertinent to stock management in the North Atlantic as spatial distribution, sex change, growth, and natural mortality primarily caused by predation (Anon., 1994). In order to identify the roles that the life history traits, such as sex change and seasonal variations in growth and mortality, play in the dynamics of *Pandalus* populations, a population dynamics model that reflects these features explicitly is needed. Therefore, in this paper, we extended the population model by Quinn *et al.* (1998) and Fu *et al.* (1999) to account for sex change and seasonal growth and mortality.

Pandalus borealis Krøyer is one of the most abundant species of the genus *Pandalus* (Kartavtsev *et al.*, 1991), and it is commercially important in the Northern Hemispheres. We chose *P. borealis* as an example of typical *Pandalus* populations in this paper. The decline of the *P. borealis* population in Kachemak Bay, Alaska, in the early 1980s, which consequently resulted in fishery closure in 1986 after continuous high catch throughout the 1970s (Gustafson, 1994), has led to various research effort (Fu *et al.*, 1999; Fu *et al.*, 2000). However, the role of sex change in an exploited population has not been explored. Our first objective was to use the *P. borealis* population in Kachemak Bay (denoted as K_pop) as an example of how a fishery has different impacts on the K_pop with sex change and on a population without sex change. For this purpose, we created a hypothetical population (denoted as H_pop) using the same population parameters as those of the K_pop, but assuming equal maturation age for males and females with 1:1 sex ratio.

Because of the increasing concern about predation mortality of *Pandalus* species (Anon., 1994), we conducted a simple simulation with predation on young shrimp. Daan (1991) noted that young predators depended largely on juvenile shrimps (carapace length less than 10 mm). Atlantic cod (*Gadus morhua*) was also found to be an important predator on age one shrimp (10 mm) in Flemish Cap, off Newfoundland (Rodríguez-Marin and del Río, 1999). Thus, when there is strong predator recruitment, predation by young predators can greatly reduce the number of small, primarily male shrimps. Our second objective was to examine how predation impacts the K_pop with sex change and the H_pop without sex change.

Our third objective was to examine fishery impact on *P. borealis* populations with different growth rates and maturation ages. The K_pop begins transition in March or April at age two or three years, and begins to function as females at ages of 2.5 to 3.5, living up to six years old (Davis, 1982). However, geographic differences in the rate of maturation and transition from males to females

are well documented (Rasmussen, 1953; Balsiger, 1981; Teigsmark, 1983). Teigsmark (1983) reported that the population in the northern areas of the Barents Sea first functioned as females at six years old and only every second year thereafter with a life span of ten years. Teigsmark's information came from a cold period during 1979–1981 and now the population apparently spawns every year starting at age five or age six (Anon., 1994). Nevertheless, we used information from the earlier period to illustrate potential impact on the more vulnerable *Pandalus* population. We noted this northern Barents Sea population as B_pop, and made comparisons with the K_pop. Other *Pandalus* populations of various growth rates can be compared if necessary, but we believe that the general conclusion would not be altered.

The growth of *Pandalus* populations is generally better described by a modified von Bertalanffy (VB) function with seasonal oscillations (Bergström, 1992) because of the distinct feature of stepwise growth (Rasmussen, 1953; Haynes and Wigley, 1969; Shumway *et al.*, 1985). However, seasonal growth has not yet been incorporated into shrimp assessment and management. In addition, shrimp management usually assumes a constant annual natural mortality. Seasonal variations in this parameter have not yet been documented but are likely to exist (P. J. Anderson, National Marine Fisheries Service, Kodiak, Alaska, USA, pers. comm.). Thus, our fourth objective was to explore optimal fishing seasons based on seasonal variations in growth and natural mortality, because the potential seasonality in these two factors may have implications in shrimp management.

Materials and methods

Population model without seasonality

Population dynamics were simulated with a length-based stochastic population model on an annual basis (Deriso and Parma, 1988; Quinn *et al.*, 1998; Fu *et al.*, 1999). Recruitment (R) was defined as shrimp abundance at age one, and R at time *t* was simulated using a Beverton–Holt spawner–recruitment model with autocorrelation (simply called B-H in the following context) and lognormal errors, as in Fu *et al.* (2000):

$$R_t = \frac{\alpha S_{t-1}}{1 + \beta S_{t-1}} e^{\phi \varepsilon_{t-1} + v_t}$$

where $\phi \varepsilon_{t-1}$ is the first-order autocorrelated error term, and $v_t \sim N(0, \sigma_R^2)$ with $\sigma_R = 0.5$ (equivalent to a lognormal CV of 53%). Spawner biomass S_{t-1} was calculated as the biomass of reproductive females, i.e. spawning stock biomass (SSB) at time $t - 1$. Justification for this recruitment model appears in the discussion.

Table 1. Comparisons of parameters for spawner-recruit ($\alpha, \beta, \phi, \sigma_R$), growth parameters (L_∞ and κ, σ, σ_r), gear selectivity (L_{50}, γ), annual natural mortality (M), maximum age (T_{max}) and maturity between three populations: Kachemak Bay type (K_pop), hypothetical population (H_pop) and northern Barents Sea type (B_pop). N denotes abundance at age, and subscripts are for ages.

Population	K_pop	H_pop	B_pop
α	1.826	1.826	1.826
β	0.002	0.002	0.002
ϕ	0.267	0.267	0.267
σ_R	0.5	0.5	0.5
L_∞	24.70	24.70	27.44
κ	0.367	0.367	0.235
σ	0.529	0.529	0.529
σ_r	1.127	1.127	1.127
L_{50}	16.72 (13.18, 19.12)	16.72	19.12 (16.72, 20.86, 22.24)
γ	0.572	0.572	0.572
M	0.4	0.4	0.24
T_{max}	6	6	10
Male amount	$N_2 + N_3$	$0.5 \sum_{a=2}^6 N_a$	$N_4 + N_5$
Female amount	$N_4 + N_5 + N_6$	$0.5 \sum_{a=2}^6 N_a$	$0.5 \sum_{a=6}^{10} N_a$

Assuming the length frequency at recruitment is a simple discrete normal distribution, then $L_r \sim N(\mu_r, \sigma_r^2)$. Parameter μ_r is the mean length at recruitment age r ($r=1$), and σ_r is the deviation of the length frequency normal distribution at age r . The recruited shrimp and those at older ages are modeled to go through a growth and mortality process. The standard von Bertalanffy growth model is used to express the growth pattern from one age to the next, assuming that growth parameters are constant over time, but growth has random normal variation each year:

$$L_{a+1} = L_\infty(1 - \rho) + \rho L_a + \varepsilon_t^*, \quad \varepsilon_t^* \sim N(0, \sigma^2)$$

where L_∞ is the asymptotic length, ρ is the Brody coefficient with $\rho = e^{-\kappa}$, and κ is a curvature parameter, governing the speed to approach L_∞ .

Given instantaneous fishing mortality F_t at ages of full recruitment, the abundance at age $a+1$ at the start of time $t+1$, $N_{a+1,t+1}(x)$, after growth, fishing and natural mortality (M) is:

$$N_{a+1,t+1}(x) = N_{a,t}(x) e^{-(F_t s_x + M)}$$

where s_x is the gear selectivity function that follows the logistic curve:

$$s_x = \frac{1}{1 + e^{-\gamma(x - L_{50})}}$$

Parameter γ is the shape parameter, and L_{50} is the length at which 50% of the individuals are vulnerable to fishing.

One thousand replicates of 40-year simulations were initialized in year one when a virgin population was at equilibrium. In addition to the errors associated with R , parameter M was simulated as a lognormal random variable around an assumed average level with a CV of 20% ($\sigma_M = 0.2$). This level of CV was chosen based on the one estimated in *Fu et al. (1999)*. Lognormal measurement errors in SSB were imposed using a CV of 20% based on the average historical variability for survey biomass estimates (*Gustafson, 1994*). Parameter F was assumed to be implemented without error.

Fishery impact on populations with and without sex change

To examine the fishery impact on populations with and without sex change, the K_pop and H_pop were simulated. The same values of the parameters of the B-H model (α, β, ϕ), growth ($L_\infty, \kappa, \sigma, \sigma_r$), gear selectivity (γ, L_{50}), mean M , and maximum age (T_{max}) (Table 1) were assumed for the two populations. Because the estimated M values for the Kachemak Bay *P. borealis* population increased over time (*Fu et al., 1999*), we adopted a constant value of 0.4 as the mean M following *Fu et al. (2000)*. All other parameters were obtained from the estimates for the K_pop (*Fu et al., 1999*). Shrimp of the K_pop were assumed to function as males at ages two and three, and females at ages four to six as in *Fu et al. (2000)*. The H_pop was assumed to mature as males and females at age two, and function as the same type up to its maximum age of six (Table 1).

Each population was simulated with a fishery of constant F ranging from 0.0 to 1.5 for fully selected shrimp. Management of the fishery was conducted with both threshold and non-threshold management. Under threshold management, the fishery was closed the following year once the SSB was detected to be below the threshold, where it was assumed that a survey occurred annually. The threshold was defined as 20% of virgin SSB (Francis, 1993; Thompson, 1993). Virgin SSB was obtained when the simulated population reached equilibrium under no fishing. When the population SSB went below the threshold, the population was considered to be at risk of collapse.

Predation impact on populations with and without sex change

To compare predation impact on K_pop and H_pop , we assumed that there was a sudden increase in predation mortality of young shrimp at ages one and two, ten years after the fishery was initiated. The annual predation mortality was set at 0.74, a level that was at the low end of the range for a Barents Sea *P. borealis* population (Berenboim *et al.*, 1991), and it continued for one to four years.

Fishery impact on populations of different growth

To examine fishery impact on populations of different growth, we generated the B_pop for comparison with the K_pop . Growth parameters for the B_pop were taken from Teigsmark (1983) (Table 1). T_{max} for B_pop is ten years old, and females at first egg extrusion are six years old. Growth variation parameters (σ , σ_r) were assumed to be the same for the two populations. Constant mean M with annual random variation was imposed for both populations. To be comparable, constant mean M of 0.24 for B_pop was derived based on the K_pop M value of 0.4 and the assumption that maximum age is negatively correlated with annual M , i.e., $T_{max1}M_1 = T_{max2}M_2$. Recruitment was assumed to have the same parameters and the same B-H model.

Comparisons of optimal F

To provide some quantitative representation of the harvesting comparison, we defined optimal F as the value that maximized yield while minimizing the risk of population decline (Hollowed and Megrey, 1993). Therefore the following objective function (f) is employed for calculating optimal F :

$$f = \text{Max} \left\{ \frac{Y_F}{\text{Max}Y} - \text{RISK}_F \right\}$$

For each F , annual average risk RISK_F was calculated as the percentage of time over the 1000 replicates that the population fell below 20% of virgin SSB. Y_F is the cumulative yield over all years at a given F averaged over the 1000 replications and $\text{Max}Y$ is the maximum among the Y_F values. If an F produces maximum yield but always drives the population below 20% of virgin SSB, then the objective function has a value of 0.0.

Comparisons among management strategies

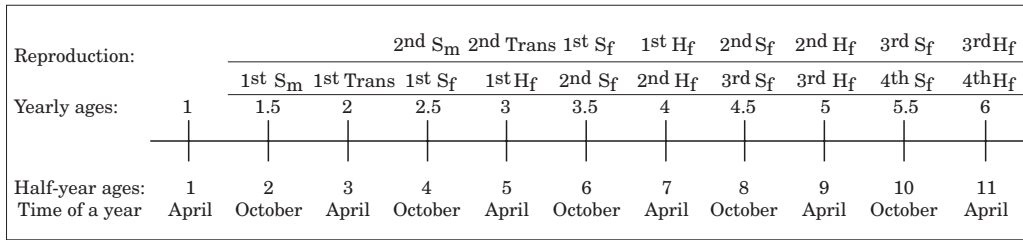
Enlarging mesh size for immature individuals to escape, protecting egg-bearing females by closing spawning grounds, and closing the fishery at low population levels (i.e. threshold management) are three major strategies in fishery management to prevent overfishing. To simulate mesh size options, we assumed that mesh size was directly related to the gear selectivity parameter L_{50} but independent of γ in the logistic curve. We derived relationships between L_{50} and maturation age for K_pop and B_pop (Appendix 1). To compare the performances of these three strategies for *Pandalus* shrimp, we compared the SSB dynamics, yield, and risk of the B_pop under three conditions: (1) enlarging selectivity parameter L_{50} from 19.12 to 22.24 (mm); (2) preserving 50% of females not to be fished while keeping L_{50} at 19.12 (mm); (3) implementing threshold management while keeping L_{50} at 19.12 (mm).

Model extension to half-year dynamics

The population model without seasonal consideration assumed a knife-edged sex change at age four for the K_pop . This approximation may not be appropriate because some age three individuals become first-egg extrusion females in Kachemak Bay. The proportion of sex change at certain ages was found to be variable, and the variability may be correlated with environmental conditions, population abundance and the proportion of females (Charnov and Anderson, 1989). To determine if the average size/age of sex change has any relevance in shrimp management, we extended the yearly population dynamics model to a half-year dynamics model with separate summer and winter periods. The extension enabled modelling of the sex change proportion and examination of its effect on population dynamics.

The extended model was applied to the K_pop . The simulated population dynamics start with recruitment in April at age one. Surviving individuals pass through a fast growing summer season. In October, the 1.5 year-old shrimp spawn as males, after which some of these survive over a slow growing and possibly high natural mortality season. In spring, some of the males change to transitionals. The transformed individuals begin their first egg extrusion at age 2.5, and hatch eggs at age three. Meanwhile, other untransformed three year-old males

(a) Cohort time frame



(b) Yearly time frame

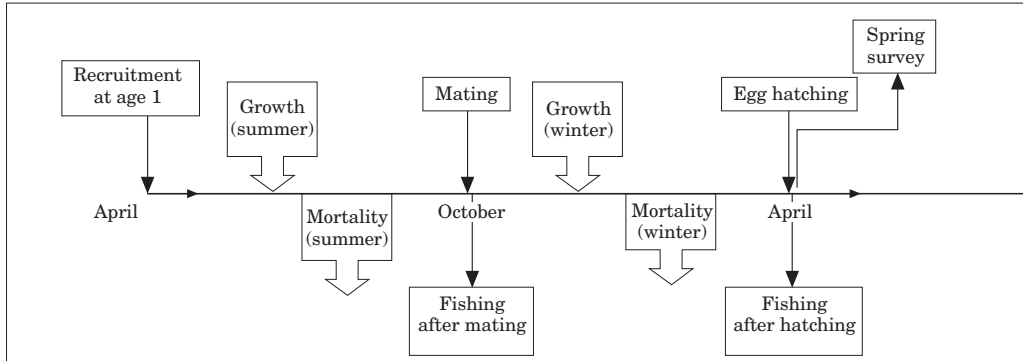


Figure 1. (a) Schematic representation of cohort life history with time lines of yearly ages along with half-year ages. H_f stands for female egg hatching, S_f for female mating, S_m for male mating and Trans. for sex transformation. (b) Schematic representation of life history processes in a one-year scheme.

begin to change sex at age three, and thereafter contribute to the population reproduction [Figure 1, (a)]. For the half-year dynamics model, subscripts for subsequent ages were incremented by one every half year. For year *t*, the time subscript for the spring is $2t - 1$, and that for the fall is $2t$. Figure 1(b) illustrates the one-year time frame for recruiting, mating and egg extrusion, hatching, and fishing.

Assume the probability of sex transformation from males to females at age two is a logistic function of length with more individuals at larger size transforming into females:

$$\psi = \frac{1}{1 + e^{-\gamma_\psi(x - L_\psi)}}$$

where γ_ψ is the shape parameter and L_ψ is the length at which half of the shrimp step into the transition stage at age two. In this paper, γ_ψ and L_ψ were set at 0.5 and 14.5 mm corresponding to a proportion of about 40% that transform sex at age two. Male abundance at age 2.5 (equivalent to four in a half-year schedule) is:

$$N_{2t,4,m}(x) = N_{2t-1,3}(x)(1 - \psi(x))e^{-(F_{2t-1} \cdot S_x + M_{2t-1})}$$

where subscript *m* stands for male, s_x is the gear selectivity function, and F_{2t-1} and M_{2t-1} are fishing

and natural mortalities. The remaining males begin to spawn as females at age 3.5.

Female abundance (with subscript *f* denoting female) is:

$$N_{2t,4,f}(x) = N_{2t-1,3}(x)\psi(x)e^{-(F_{2t-1}s_x + M_{2t-1})}$$

Abundance of females hatching eggs in the spring is:

$$N_{2t+1,f}(x) = \xi \left[N_{2t,4,f}(x)e^{-(F_{2t}s_x + M_{2t})} + \sum_x N_{2t+1,a,f}(x) \right]$$

where $a = 7, 9$ and 11 ,

from which the recruits in the following spring are produced. Parameter ξ is equal to the sex ratio (males to females) if the sex ratio is less than 1.0, and ξ is equal to 1.0 if the sex ratio is greater than 1.0. This assumption implies that all females can be fertilized if there is an equivalent number of males. This assumption is reasonable, since a sex ratio of 1.0 was considered necessary for a reproductively successful *Pandalus* population (Fox, 1972). When fishing occurs after hatching, $F_{2t} = 0$.

With seasonal consideration, growth functions for summer and winter were assumed to have the same asymptotic length L_∞ but distinct curvature parameters κ_s and κ_w and deviations σ_s and σ_w , where the subscript *s* stands for summer and *w* for winter. Therefore, the

basic VB growth model that has no seasonal variation can be converted to a form of half-year steps with odd subscripts denoting summer and even for winter:

$$L_{r+2t+1} = L_{\infty}(1 - \rho_s) + \rho_s L_{r+2t} + \varepsilon_s, \text{ where } \varepsilon_s \sim N(0, \sigma_s^2), t=1,2 \dots,$$

$$L_{r+2t} = L_{\infty}(1 - \rho_w) + \rho_w L_{r+2t-1} + \varepsilon_w, \text{ where } \varepsilon_w \sim N(0, \sigma_w^2), t=1,2 \dots,$$

with Brody coefficients $\rho_s = e^{-\kappa_s}$, $\rho_w = e^{-\kappa_w}$. We use recursive formulae to obtain the variation calculations:

$$\sigma_{r+2t+1}^2 = \rho_s^2 \sigma_{r+2t}^2 + \sigma_s^2,$$

$$\sigma_{r+2t}^2 = \rho_w^2 \sigma_{r+2t-1}^2 + \sigma_w^2$$

At $t=0$, $L_{r+1} = L_{\infty}(1 - \rho_s) + \rho_s L_r + \varepsilon_s$ and $\sigma_{r+1}^2 = \rho_s^2 \sigma_r^2$, where L_r and σ_r are the mean length at recruitment and the deviation of the length frequency normal distribution at age r , where $r=1$ in this paper.

We introduced parameters φ_{κ} and φ_{σ} to establish equivalence between the seasonal and nonseasonal models. Let $\kappa_s = \varphi_{\kappa} \kappa$, then $\kappa_w = (1 - \varphi_{\kappa}) \kappa$; further note that the units of κ_s and κ_w are half-years, while κ has units of years. Therefore φ_{κ} determines the relative growth in the summer season compared to that in the winter. Similarly, let φ_{σ} determine the relative variation in the summer season corresponding to that in the winter, then there are relationships:

$$\sigma_s^2 = \frac{\varphi_{\sigma}}{\rho_w^2} \sigma^2, \text{ and } \sigma_w^2 = (1 - \varphi_{\sigma}) \sigma^2$$

For this paper, we assumed that φ_{κ} and φ_{σ} had the same value.

Parameters for natural mortality in the summer and winter are M_s and M_w respectively. We let $M_s = \varphi_M M$, and $M_w = (1 - \varphi_M) M$, where φ_M reflects the relative difference between summer and winter mortality by using a half-year scale similar to growth parameters. Again, units of M_s and M_w are half-years, while M has units of years.

As in the nonseasonal model, uncertainties in M and R were incorporated. The annual M was imposed with lognormal errors with CV of 20%. Parameter R was generated by imposing a lognormal error upon the B-H model with CV of 53%.

Fishing season

With the K_{pop} , two types of seasonal fisheries were compared: harvesting after mating (i.e. egg extrusion and fertilization) in the fall after shrimp have experienced summer growth and M_s , and harvesting after egg

hatching in the spring by which time shrimp have had winter growth and M_w (Figure 1). A threshold of 20% of virgin SSB was imposed, so that populations were not driven to extinction under high F . When fishing occurs after mating, the number of females that are able to hatch their eggs in spring and contribute to the subsequent recruitment depends on M during summer and winter months and F after mating. If fishing occurs after egg hatching, reproductive females are only subject to M during the winter season. Survey was modelled to occur in the spring after fishing, and a decision of opening or closing the fishery for the following year was made based on the survey SSB estimate relative to the threshold level.

Results

Fishery impact on populations with and without sex change

In the K_{pop} with sex change, females are larger and more vulnerable to fishing than the H_{pop} without sex change, in that high F resulted in recruitment overfishing more often. For the H_{pop} , even a high F of 1.5 resulted in a small risk of collapse (Figure 2). However, the K_{pop} was sustained only at F of 0.3 or below. F of 0.6 had a tendency to gradually decrease the population's SSB, and F at 0.9 or higher quickly wiped out the population. The optimal F without threshold management is 1.0 with risk of 0.026 for H_{pop} , while the optimal F for K_{pop} is only 0.30 with risk of 0.052 (Table 2). Clearly, the population without sex change is much more robust to fishing pressure.

Under high F , threshold management appears to be critical to protect a population with sex change from recruitment overfishing. If the fishery was closed once SSB was detected to be below 20% of the virgin SSB, F at 0.9 or higher did not result in population extinction. Instead, K_{pop} was sustained at a low level (Figure 3). Since high F of 1.5 can still sustain H_{pop} , threshold management only slightly increased SSB. For H_{pop} there seemed to be no need to conduct threshold management.

Predation impact on populations with and without sex change

When predation on age one and two males was suddenly increased to 0.74 for only one year, the number of K_{pop} males was reduced for the first year. The reduced number of males resulted in a slight decrease in the female egg extrusion biomass. SSB continued to decline for another two years despite the relaxation of predation mortality (Figure 4). Predation on young shrimp of K_{pop} , in general, had longer and more gradual influence on the population dynamics than on that of H_{pop} .

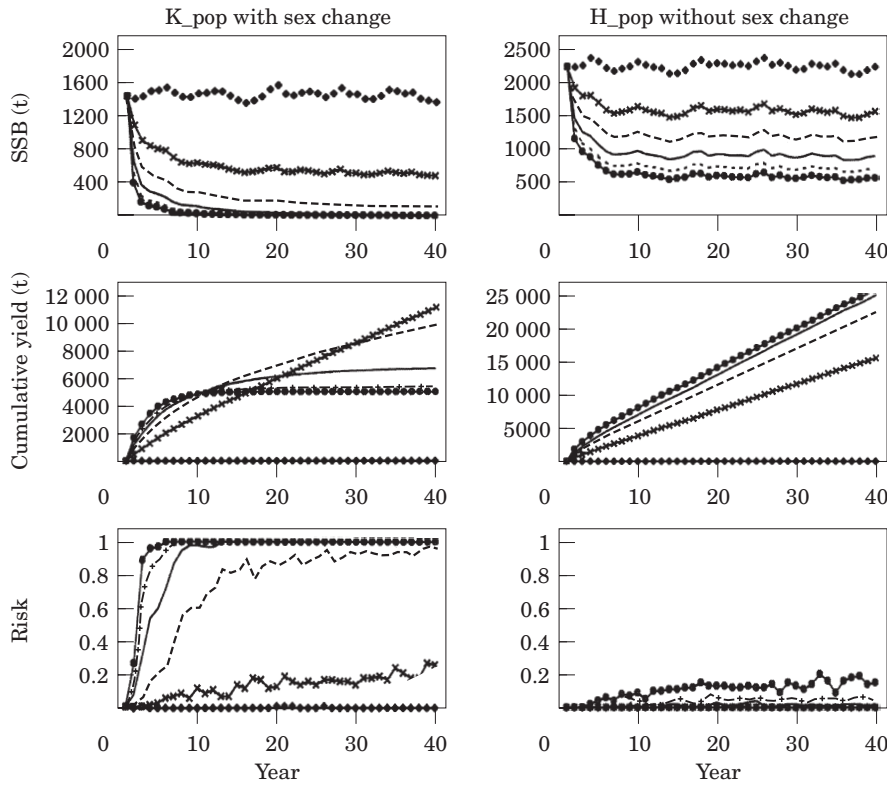


Figure 2. Comparisons of spawning stock biomass (SSB), cumulative yield, and risk over time from six levels of fishing mortality F without threshold management between the Kachemak Bay type population (K_pop) and the hypothetical population (H_pop). \blacklozenge , $F=0$; $- \times -$, $F=0.3$; $\cdots \cdots$, $F=0.6$; $—$, $F=0.9$; $+ - + -$, $F=1.2$; $- \bullet -$, $F=1.5$.

The change in SSB due to predation on the young of H_pop was more abrupt, and SSB began to climb once predation was relaxed. The results were similar when high predation mortality remained for another few years (not shown).

Fishery impact on populations of different growth

The slower the growth that a protandric, hermaphroditic shrimp population has, the longer it lives and the

Table 2. Optimal fishing mortality (F), objective function value (f), maximum cumulative yield (MaxY, units of t) and risk of population decline averaged over the entire time period under various levels of gear selectivity parameter (L_{50}) for populations H_pop , K_pop and B_pop .

Population	L_{50}	F	f	MaxY	Risk
H_pop	16.72	1.0	0.9525	26 739	0.026
K_pop	13.18	0.21	0.8956	12 672	0.064
K_pop	16.72	0.30	0.8980	11 501	0.052
K_pop	19.12	0.46	0.9014	10 797	0.063
B_pop	16.72	0.20	0.8893	17 322	0.061
B_pop	19.12	0.27	0.8912	16 473	0.052
B_pop	20.86	0.39	0.8971	16 297	0.053

later individuals transform into mature females. Correspondingly, high F generates more impact on slower growing populations. Using the same mesh size as that for K_pop (i.e., $L_{50}=16.72$ mm), B_pop had a slight declining trend even under low F of 0.3, while K_pop was able to stabilize. Increasing L_{50} to 19.12 mm, B_pop was sustained at an F level close to 0.3 (Figure 5), similar to results for K_pop under $L_{50}=16.72$ mm (Figure 3). With larger mesh size ($L_{50}=19.12$ mm), K_pop was kept at a relatively high population level even when $F=0.6$ (Figure 5). As L_{50} increased from 16.72 mm to 20.86 mm ($t - t_0=6.079$), the optimal harvest level for B_pop increased from 0.2 to 0.39, yet total yield decreased by 1025 t (Table 2). The same trend was also true for K_pop .

Comparisons among management strategies

For B_pop , increasing gear mesh size by increasing L_{50} from 19.12 mm to 22.24 mm ($t - t_0=7.079$) slowed down the speed of collapse under high F ; however, it did not change the declining trend (Column 1, Figure 6). Meanwhile, protecting 50% of females each year could not prevent the population from collapsing under F higher than 0.6 (Column 2, Figure 6). On the other hand, a

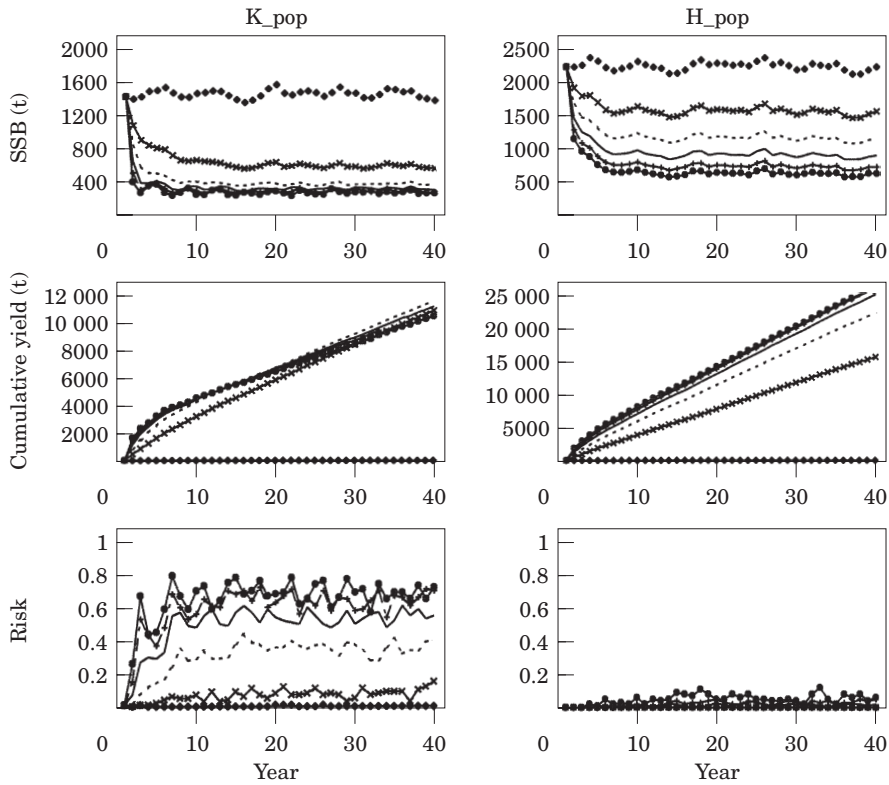


Figure 3. Comparisons between the Kachemak Bay type population (K_pop) and the hypothetical population (H_pop) of spawning stock biomass (SSB), cumulative yield, and risk over time from six levels of fishing mortality F with threshold management, threshold being 20% of the virgin SSB. \blacklozenge , $F=0$; $-\times-$, $F=0.3$; \cdots , $F=0.6$; $—$, $F=0.9$; $-\cdot-$, $F=1.2$; $-\bullet-$, $F=1.5$.

smaller mesh size along with a threshold management prevented population collapse even under the highest F (Column 3, Figure 6). The results indicated that a management policy that protects only a certain proportion of females while allowing high F on other shrimp could lead to collapse. In comparison, protecting young shrimp by increasing mesh size was more desirable, because protecting young shrimp and allowing them to grow to egg extrusion females is the only way to prevent female depletion. As a whole, threshold management strategies were most efficient to prevent a population from overfishing.

The impact of seasonal variations in growth and M

The optimal fishing season was found to be dependent on all three factors: F , and proportions of growth and M in summer (April–October) and winter (October–April) seasons. When the population was exploited at $F=0.3$, total yield from fishing after fall mating and egg extrusion was consistently higher than that from fishing after hatching if M in summer was half of the amount in

winter (i.e. $\phi_M=0.333$) (Column 1, Figure 7). This makes sense, because fishing later in the year allows yield per recruit to increase due to growth and lower M in the summer. On the other hand, the total yield was nearly identical if M was higher in summer (e.g. $\phi_M=0.667$).

When F increased to 1.2 and $\phi_M=0.333$, fishing after fall mating and egg extrusion had higher yield in the early years than fishing after hatching, but it fell below fishing after hatching as time progressed (Column 2, Figure 7). With $\phi_M=0.667$, fishing after egg hatching consistently produced higher yield than fishing after egg extrusion. This was apparently due to the compensatory effects of M and F : under high M , too few shrimp survive the half-year for shrimp biomass to grow. Under any case, fishing after hatching resulted in lower risk of population collapse, because it allowed more ovigerous females to hatch and contribute to the population reproduction. Therefore, fishing after hatching is more robust to overfishing.

Regardless of seasonal growth variations (i.e. $\phi_k=0.8$ or $\phi_k=0.5$), optimal F and corresponding risk were consistently lower for fishing after mating and egg extrusion in the fall than that after egg hatching in the

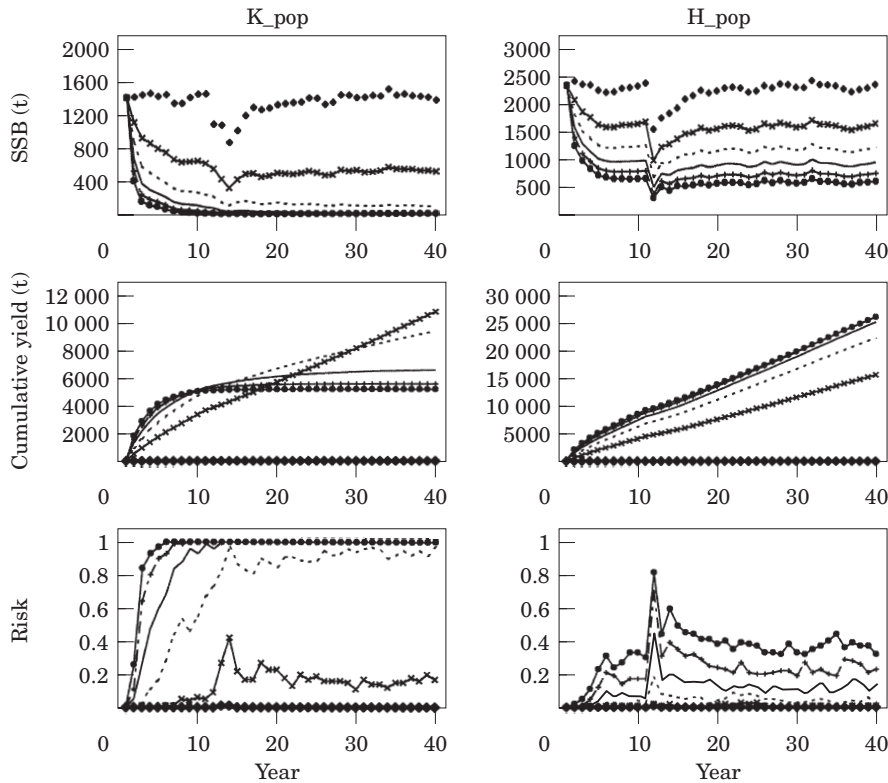


Figure 4. Comparisons of spawning stock biomass (SSB), cumulative yield, and risk over time from six levels of fishing mortality F without threshold management between the Kachemak Bay type population (K_pop) and the hypothetical population (H_pop). A sudden increase of predation mortality for individuals at ages one and two, ten years after exploitation was introduced. \blacklozenge , $F=0$; $-\times-$, $F=0.3$; \cdots , $F=0.6$; $—$, $F=0.9$; $-\+-$, $F=1.2$; $-\bullet-$, $F=1.5$.

spring (Table 3). If fishing was not tightly regulated, then actual F could be high, so that fishing after fall mating and egg extrusion could be more subject to recruitment overfishing. Fishing after egg extrusion in the fall had higher yield than fishing after egg hatching in the spring only under $\phi_M=0.333$ (Table 3).

The average risk over the simulation period was generally small, which is in agreement with the finding of Fu *et al.* (2000). That is, a population with mean M of 0.4 sustains above the threshold under optimal F . In addition, because risk was calculated as the probability of SSB going below the threshold in the spring after fishing, seasonal variations in M had no effects on the level of risk. Overall, with the population truly exploited under optimal F levels, fishing after egg hatching in the spring did not seem to be more advantageous over fishing after egg extrusion in the fall, except that the risk was higher because optimal F s were different (Table 3). However, fishing after egg hatching rendered higher yield and lower risk, when the same high F level was applied to both situations, as shown in Figure 7.

Discussion

Spawner–recruitment relationship and natural mortality

The assumption of a relationship between spawning and recruitment is a necessary factor in the simulation of population dynamics, without which an equilibrium population cannot occur. The B-H model was applied in all of the simulation scenarios given above. In the past, attempts to derive a spawner–recruitment relation for shrimp met with little success, and environmental influences were considered to be central (Geibel and Heimann, 1976; Hannah, 1993). We included autocorrelated recruitment in our model to partially account for environmental influences. Furthermore, Hannah (1995) stated that the lack of success in detecting a spawner–recruitment relationship for shrimp could also be the result of more fundamental problems with the method used. He recognized the high variability in catchability and natural mortality, which obscured an underlying relationship between spawning and recruitment, and

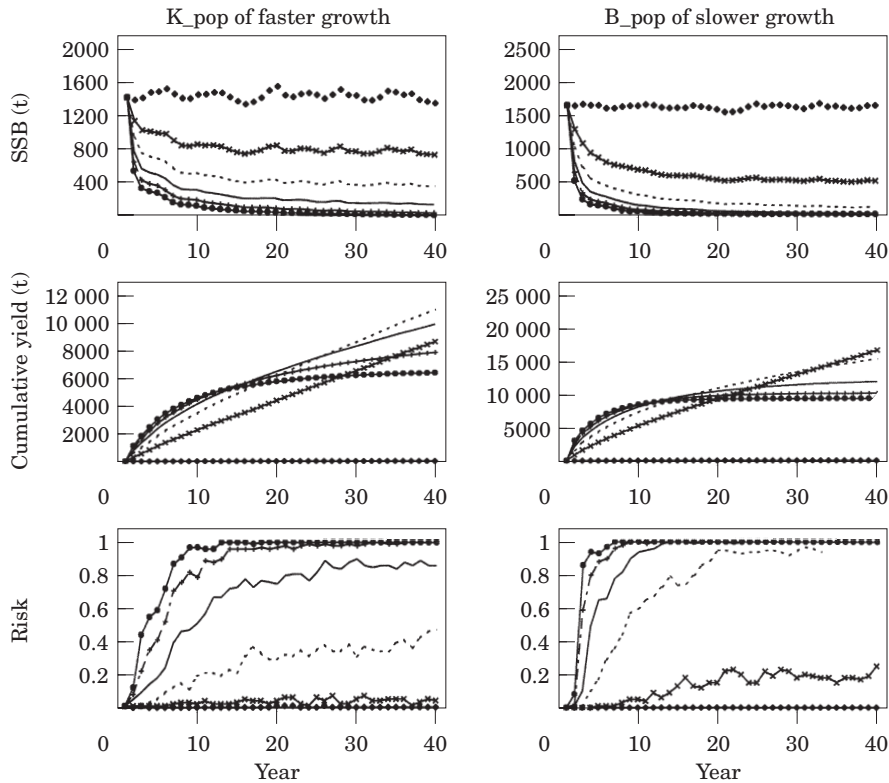


Figure 5. Comparisons of spawning stock biomass (SSB), cumulative yield, and risk over time from six levels of fishing mortality F without threshold management, between the Kachemak Bay type population (K_pop) and the northern Barents Sea population (B_pop) with $L_{50}=19.12$. \blacklozenge , $F=0$; $-X-$, $F=0.3$; \cdots , $F=0.6$; $—$, $F=0.9$; $-+—$, $F=1.2$; $—\bullet—$, $F=1.5$.

found evidence for the ascending leg of the curve in a spawner–recruitment for shrimp (Hannah, 1999). Although data in Hannah (1999) gave little indication of the shape of the right hand portion of the curve, thus leaving the proper functional form inconclusive, we considered the B-H model reasonable based on the data in Fu et al. (1999). Additional support for this relationship can be found in Livingston and Method (1998), where the authors showed recruitment of a walleye pollock population at age one was more asymptotic at high spawning stock sizes after accounting for predation on age one fish.

In this paper, we focused on the effects of fishing on *Pandalus* population dynamics, and did not incorporate a trend in natural mortality over time. However, acknowledging the possibility of a trend in M , particularly an increasing trend, is vital in shrimp management. Retrospective analyses of the Kachemak Bay *P. borealis* population suggested that increasing M rather than declining R in the 1980s may be the major factor that prevented the population from recovering (Fu et al., 1999). The increase in M reduces the optimal level of F (Fu et al., 2000). For the impact of increasing trend of M , readers are referred to Fu et al. (2000).

Fishery impact on the dynamics of *Pandalus* populations

Using the B-H model and constant mean M , we examined fishery impact on population dynamics. Commercial landings of *Pandalus* species have widely fluctuated in the Northern Hemisphere (Balsiger, 1981; Apollonio et al., 1986; Anderson and Piatt, 1999). The abundance fluctuation and frequent population decline was postulated to be closely related to environment-induced variations in year-class success (Balsiger, 1981), predation (Berenboim et al., 1991; Anon., 1994), reduction of SSB due to high exploitation (Hannah, 1995; Hannah, 1999), or a combination of various factors (Orensanz, 1998). However, how fishery affects *Pandalus* populations has rarely been investigated on the basis of population dynamic models.

Comparisons between populations with and without sex change indicated that populations with sex change are more vulnerable to fishing. Our simulation with an F level of 1.5 for the H_pop without sex change resulted in only small risk of population collapse. Nevertheless, continuous fishing at F levels of 0.6 or above on the K_pop caused the population to collapse over a period

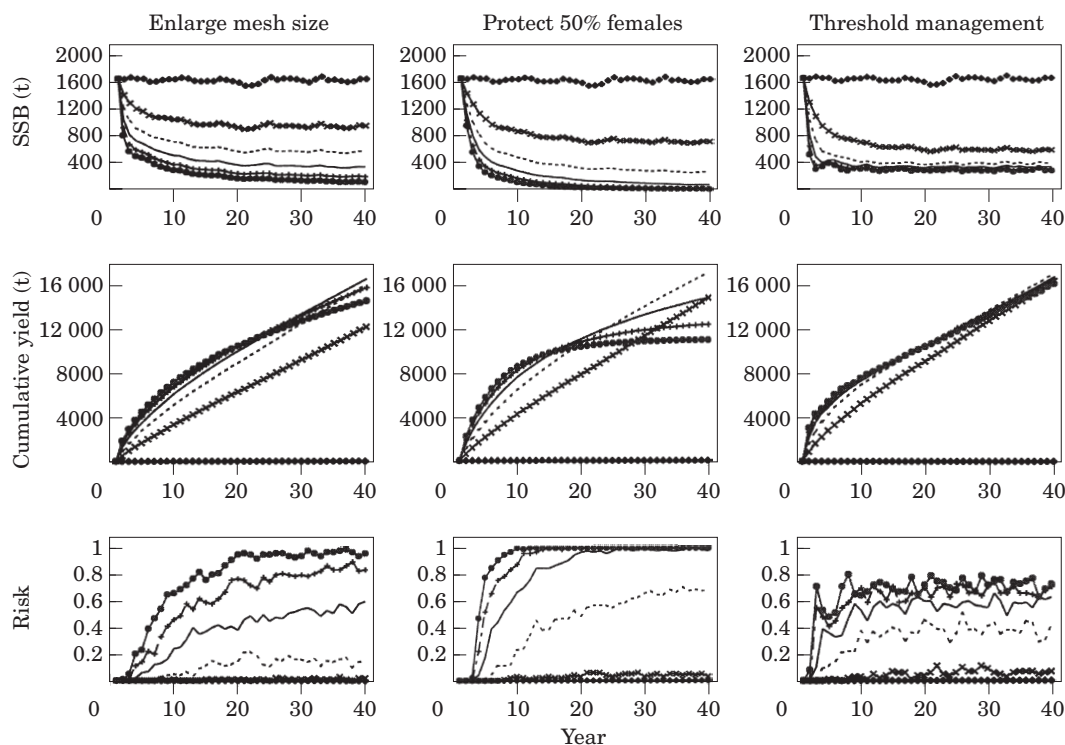


Figure 6. Comparisons of spawning stock biomass (SSB), cumulative yield, and risk over time from six levels of fishing mortality F for the B_{pop} under three scenarios: enlarge mesh size ($L_{50}=22.24$); use standard mesh size ($L_{50}=19.12$), but protect 50% of females; use standard mesh size and threshold management (20% of virgin SSB). \blacklozenge , $F=0$; $- \times -$, $F=0.3$; \cdots , $F=0.6$; $—$, $F=0.9$; $- + -$, $F=1.2$; $- \bullet -$, $F=1.5$.

of about ten years. This is an important recognition. With the Kachemak Bay *P. borealis* population, estimated F for fully selected shrimp was around 0.6 in the 1970s, and it stayed around 1.0 for years 1980–1982 (Fu *et al.*, 1999). So, it is possible that *P. borealis* in Kachemak Bay already had a tendency to decline from a long period of high F before the increasing M played its role in the 1980s.

Predation on the dynamics of *Pandalus* populations

Pandalus species are major prey items for many groundfish species, such as Atlantic cod and halibut (*Reinhardtius hippoglossoides*) (Bowering *et al.*, 1984). Thus, the dynamics of *Pandalus* populations are undoubtedly related to the abundance of their predators. Predation mortality has a different effect on a population than a fishery in that it not only affects the survival of large females, but it primarily affects the survival of small males (Daan, 1991; Rodríguez-Marín and del Río, 1999). Our simple simulation of predation of age one and two shrimps indicated that predation causes SSB of *Pandalus* species to fluctuate more than that of populations without sex change. Based on the

available data for the stocks in the Barents Sea, North Sea, West Greenland, and Iceland, predation mortality may be the major factor regulating population size, and it may be the main reason behind the high variations in the *Pandalus* populations (Anon., 1994). Quantitative modelling to account for predation has been tried with virtual population analyses (VPA) and production models (Berenboim *et al.*, 1991; Stefánsson *et al.*, 1994; Berenboim *et al.*, 2000). Because of the important role predation plays in the dynamics of *Pandalus* populations, systematic research on their predators and food consumption is necessary for leading to multi-species modelling, and thereafter achieving better understanding of their dynamics.

Fishery impact on populations of different growth

Because it takes longer for slower growing protandric, hermaphroditic shrimp to transform into mature females, high F generates more impact on the population dynamics of slower growing shrimp species. The simulation indicated that slower growing shrimp require a larger value of the gear selectivity parameter L_{50} to prevent growth overfishing. In other words, mesh size

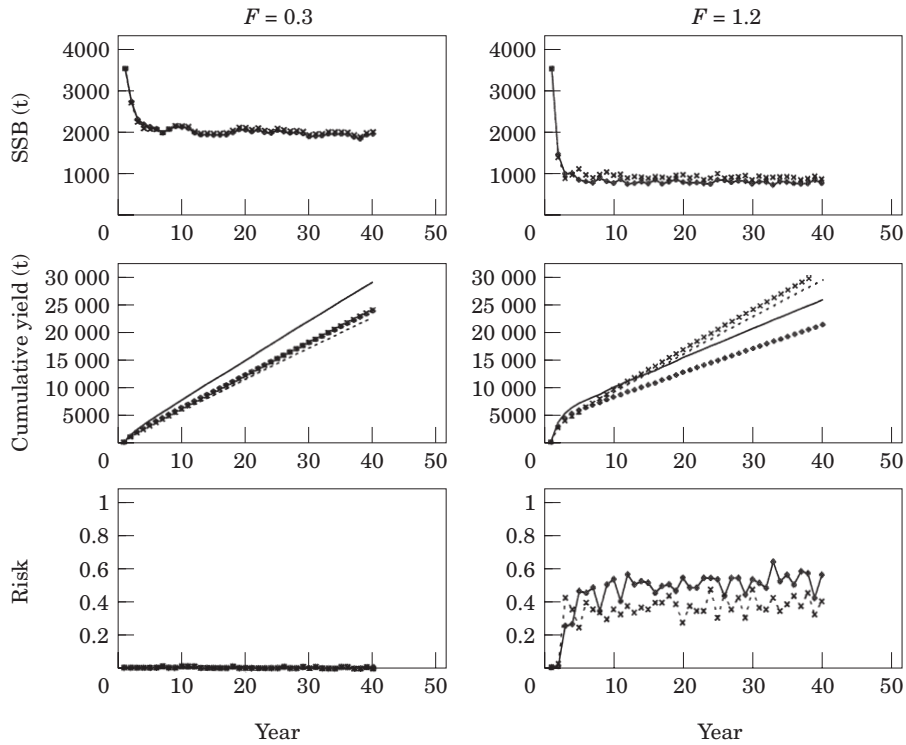


Figure 7. Within panel comparisons of spawning stock biomass (SSB), cumulative yield, and risk from a fishery after spring egg hatching (Hl: $\phi_M=0.333$; Hh: $\phi_M=0.667$) and a fishery after fall mating and egg extrusion (El: $\phi_M=0.333$; Eh: $\phi_M=0.667$) with l and h standing for low and high natural mortality M respectively; Between column comparisons of these quantities are shown under two levels of fishing mortality F. —, El; \blacklozenge , Eh; \cdots , Hl; \times , Hh.

used in the northern Barents Sea shrimp fishery should be larger than that used in Kachemak Bay. A mesh size of 38 mm was used in Icelandic fisheries and 40 mm in

Greenland waters (Anon., 1994). The Kachemak Bay shrimp fishery used 35-mm mesh size (Davis, 1982). However, the suitability of these mesh sizes has not been investigated. Because populations under a small-mesh fishery are more vulnerable to fishing, it is essential to conduct research concerning optimal mesh size and its selectivity function. Particularly, the determination of mesh size for a population should be related to individual growth and maturation rate.

Table 3. Optimal fishing mortality (F), objective function value (f), maximum cumulative yield (MaxY, units of t) and risk of population decline averaged over the entire time period under various levels of relative difference between summer and winter natural mortality (ϕ_M), and growth (ϕ_K). Fishing season=E means fishing takes place after egg extrusion, otherwise after hatching.

ϕ_M	Fishing season	ϕ_K	F	f	MaxY	Risk
0.333	E	0.8	0.40	0.9364	32 796	0.041
0.5	E	0.8	0.40	0.9361	29 702	0.041
0.667	E	0.8	0.40	0.9357	26 919	0.041
0.333	H	0.8	0.52	0.8745	29 036	0.079
0.5	H	0.8	0.52	0.8756	29 876	0.079
0.667	H	0.8	0.52	0.8760	30 852	0.079
0.333	E	0.5	0.46	0.9647	30 388	0.024
0.5	E	0.5	0.46	0.9644	27 527	0.024
0.667	E	0.5	0.46	0.9676	25 211	0.024
0.333	H	0.5	0.58	0.8991	29 797	0.078
0.5	H	0.5	0.58	0.8996	30 701	0.078
0.667	H	0.5	0.58	0.9002	31 646	0.078

Comparisons among management strategies

Protecting aggregated reproductive females is a common practice in shrimp management. However, our simulation indicated that merely protecting females was not sufficient for protandric populations. Individuals of these populations must grow and function as males before they are able to reproduce themselves. Therefore, it is essential to protect young shrimp until they function as females. Increasing mesh size is helpful to protect young shrimp and prevent growth overfishing, assuming that shrimp pass through large mesh without harm. However, survival rate of shrimp that escape is unknown, which makes this management strategy

uncertain. In comparison, threshold management is the most effective way of preventing population collapse. We suggest that fishery closures should be implemented whenever spawning stock size becomes low (say 20% relative to historic levels).

Fishing season

Fishery closures during the egg-bearing period have intuitive appeal (Fox, 1972), but the scientific basis for seasonal closures to protect ovigerous females has not been documented. Our simulation suggested that the optimal fishing season should also be related to seasonal growth and natural death. When summer growth was faster than in winter, higher M in the summer made fishing immediately after egg extrusion in the fall less desirable than that after egg hatching in the spring. Besides, fishing after hatching was more robust to overfishing. Therefore, investigating seasonal variations in M can help in comparing alternative seasonal fishing strategies.

Estimated F values for the Kachemak Bay *P. borealis* population increased to around 0.9 for years 1980–1982 (Fu and Quinn, 2000). Such high F favors fishing after egg hatching, a fishing season that is more robust to overfishing. However, nearly half of the shrimp catches were taken from November–April before egg hatching (Davis, 1982). To be more conservative, a much smaller catch quota could have been allocated to the winter season.

Using the length-based population model, we were able to estimate annual M for the Kachemak Bay *P. borealis* population (Fu *et al.*, 1999). Simulation-estimation experiments indicated that annual M could be well estimated given good survey biomass estimates (Fu and Quinn, 2000). In the same manner, seasonal variations in M have been well estimated (C.F., unpublished data). It is thus possible that the understanding of seasonal variations in M can be used in shrimp management, particularly if seasonal surveys are conducted. Furthermore, for forage species like *P. borealis*, one major source of M is predation. Relating seasonal M to the seasonal variations in the abundance of predators and their food consumption appears promising in a management context.

Acknowledgements

This publication is the result of research sponsored by Alaska Sea Grant with funds from the National Oceanic and Atmospheric Administration, Office of Sea Grant, Department of Commerce, under grant no. NA90AA-D-SG066, project numbers R/07-21 and R/31-03, and from the University of Alaska with funds

appropriated by the state. We would like to thank Gordon H. Kruse (Alaska Department of Fish and Game, USA) and Milo D. Adkison (University of Alaska Fairbanks, USA) for their comments. We are also grateful to Peter Koeller and Paul Fanning (Department of Fisheries and Oceans, Bedford Institute of Oceanography, Canada) for valuable comments and logistic support.

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Appendix 1

Derivation of the gear selectivity parameter L_{50}

Based on the basic von Bertalanffy (VB) function $\{L_a = L_\infty(1 - e^{-\kappa(t-t_0)})\}$, the age relative to t_0 (i.e., $t - t_0$) corresponding to the L_{50} , where 50% of shrimp are vulnerable to fishing gear, can be calculated for the K_{pop} as:

$$(t - t_0)_{K_{pop}} = \frac{-1}{\kappa_{K_{pop}}} \left(1 - \ln \frac{L_{50K_{pop}}}{L_{\infty K_{pop}}} \right) = 3.079$$

This value is approximately equivalent to the age when shrimp begin to change from males to females. This gear selectivity curve allows for at least half of the shrimp to change into females before being caught by fishing gear. To extend this relationship between L_{50} and age of sex transformation to the B_{pop} of slower growth, we estimated a reasonable L_{50} to be:

$$L_{50B_{pop}} = L_{\infty B_{pop}}(1 - e^{-\kappa_{B_{pop}}[(t - t_0)_{K_{pop}} + 2]}) = 19.12$$

(Carapace length: mm),

where $\{(t - t_0)_{K_{pop}} + 2\}$ indicates that shrimps are two years older for the B_{pop} when they transform into females than for the K_{pop} .

We assumed the two populations had the same shape parameter for the logistic selectivity curves. We also applied an L_{50} of 13.18 ($(t - t_0)_{K_pop} = 2.079$) and 19.12 mm to the K_pop to examine the effect of changing selectivity. For the B_pop , in addition to L_{50} of 16.72 mm, we also increased L_{50} by increasing the $(t - t_0)_{B_pop}$ by one and two, which resulted in L_{50} values of 20.86 mm and 22.24 mm.