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LENGTH-BASED MODELS AND POPULATION ANALYSES FOR NORTHERN SHRIMP *PANDALUS BOREALIS* KRØYER

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LENGTH-BASED MODELS AND POPULATION ANALYSES FOR NORTHERN SHRIMP *PANDALUS BOREALIS* KRØYER

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Abstract

The lack of basic knowledge on stock dynamics of northern shrimp *Pandalus borealis*, a protandric hermaphrodite, has caused difficulty in regulating fishing effort on a scientific basis and in understanding potential causes behind population fluctuations and collapses. Previous length-based population models (LBMs), developed for other species, are undesirable primarily for two reasons: (1) individual cohort dynamics are masked; (2) variations in annual natural mortality (M) are ignored. This research was primarily aimed at developing a more advanced LBM that provides estimates of parameters such as recruitment (R), fishing mortality (F) and especially annual M. Simulation-estimation experiments were conducted to evaluate model performance. Despite model complexity, annual M can be well estimated provided measurement errors in survey biomass estimates are low. The common assumption of constant M created biased parameter estimates. Estimated M of *P. borealis* in Kachemak Bay, Alaska increased steadily in the 1980s. Retrospective projections showed that the increasing trend in M in the 1980s resulted in the population collapse.

The ultimate goal of stock assessment is to develop sound harvest strategies. With the widely observed abundance fluctuations in shrimp populations, it is impossible to manage solely based on conventional methods, such as maximum sustainable yield (MSY). Thus, harvest strategies were compared under various situations of M and R. With M increasing over time, it is important to execute threshold management, i.e., closing the fishery at population levels below a threshold value. Simulations indicated that overfishing caused by underestimated M or overestimated R can be greatly alleviated if the population is sampled once every year. Life history aspects of sex change, growth, M, and their seasonal variations were also incorporated into the LBM. Populations with protandrous animals are likely to be subject to recruitment overfishing; merely protecting older females while allowing high exploitation on younger males can lead to population collapse. Fishing after spring egg hatching is superior to fishing after mating and egg extrusion in fall when F is high. In summary, the length-based model developed here provided a convenient framework for understanding population processes and harvest strategies and should be useful for a variety of hard-to-age species.

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Chapter 1 Introduction and overview

1.1 DISTRIBUTION AND FISHERIES WORLDWIDE

1.1.1 Distribution

Pandalus borealis Krøyer, commonly called northern or pink shrimp, is a discontinuous circumboreal species, occurring in both the Pacific and Atlantic Oceans (Allen 1959; Shumway et al. 1985). It is one of the most abundant species of the family Pandalidae (Kartavtsev et al. 1991). Some systematists recognize *P. eous* Makarov as a Pacific species of *P. borealis* Krøyer (Squires, 1992). *P. borealis* is common off the coast of Alaska and in the eastern Bering Sea, as well. It is distributed as far south as the Columbia River (latitude 46°N) (Butler 1964). In the western Pacific, it is less common but was reported from Japanese waters as far south as latitude 45°N. In the western Atlantic, *P. borealis* occurs in large numbers in the Gulf of Maine, Newfoundland, Labrador and off Cape Cod. There are also large populations of *P. borealis* off the coasts of Greenland, Norway and Iceland, and in the North Sea (Figure 1.1).

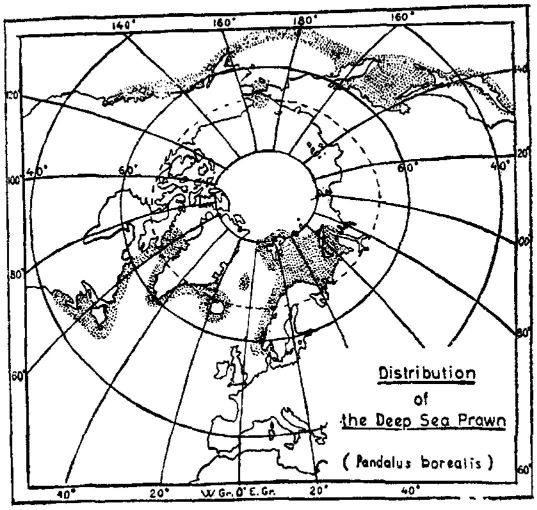

Figure 1.1. Worldwide distribution of *Pandalus borealis* (Rasmussen 1967)

1.1.2 Fisheries worldwide

The Bering Sea *Pandalus* fishery obtained large catches in the early 1960s but small catches throughout the 1970s (Shumway et al. 1985). In contrast, landings of *Pandalus* shrimp, primarily *P. borealis*, in the Gulf of Alaska (GOF) had significant increases during the first half of the 1970s, and the record high catch of 58600 metric tons (t) was achieved in 1976. However, landings declined dramatically thereafter, with harvest totalling 12800 t in 1981 (Davis 1982). The Westward Region *Pandalus* fishery contributed the most significant landings to the Alaskan shrimp industry. This fishery was initiated at Kodiak in 1957 with exploratory tows by local vessels; annual catches increased progressively from 1318 t in 1959 to 16682 t in 1967 (Jackson et al. 1983). After that, the fishery expanded from the Kodiak District to the South Peninsula, Chignik, and the Aleutian Districts, with landings peaking at 54227 t in 1976 and reducing abruptly to 9864 t in 1981 (Jackson et al. 1983). No catch was reported from the Alaska Peninsula district after 1981 (Anderson 1999). Since 1989, no landings were taken around Kodiak Island for one decade with an exception of 0.77 t in 1993; however, in 1998 pandalid shrimp landings of 5.4 t were recorded (Anderson 1999).

In comparison, the *Pandalus* fishery in Kachemak Bay, though locally important, contributed a relatively small percentage to the Alaskan shrimp industry. This fishery began with intermittent harvests of small landings in the 1950s and 1960s, targeting mainly *P. borealis* (Davis 1982). In 1970, the catch dramatically increased to 2637 t and remained near that level through the early 1980s. Since 1971, guideline harvest levels have been established from survey estimates of pandalid biomass (Davis 1982). By 1984 catch decreased to almost one tenth of that in 1980 due to reduced population abundance. The fishery was closed in fall 1986 due to continued low stock size (Gustafson 1994) and has not been reopened.

The *Pandalus* fishery in the Gulf of Maine in the eastern Atlantic began in the late 1930s. It peaked at 255 t in 1945, and declined thereafter, with no landings during 1954-57. The population revived after 1958 with a maximum catch of 12,800 t in 1969 but a rapid decline commenced in the mid-1970s which resulted in the closure of the fishery in 1978 (Apollonio et al. 1986). In the 1980s, the fishery increased again to about 5000 t in 1987, and the annual landings remained about 3500 t in the early 1990s (Anon. 1994). The fishing season usually lasts from December to May with an offshore fishery occurring mainly in December, April and May, and an inshore fishery during January, February and March.

The *Pandalus* fishery in Greenland waters began in 1935 as a local fishery in a fjord in West Greenland (Anon. 1994). The inshore fishery expanded rapidly after 1950, and total catch increased to more than 21000 t in 1992 (Anon. 1994). An offshore shrimp fishery in the Denmark Strait yielded landings of about 11000 t in 1988, but has since decreased to about 5800 t in 1992. These fisheries usually had highest catches in spring, exploiting concentrations of egg bearing females. The inshore fishery was regulated by effort limitations, while the offshore fishery was regulated by total allowable catch (TAC).

Norwegian *Pandalus* fisheries in the Barents Sea began in the early 1970s, while Russian (formerly USSR) fisheries began in 1977 (Anon. 1994). Total catch increased to about 130000 t in 1984, and it peaked again in 1990 followed by a slight decline (Anon. 1994). Landings from a *Pandalus* fishery in Icelandic waters increased from approximately 10000 t in 1980 to almost 50000 t in 1992. The *Pandalus* stock in the North Sea is exploited by several countries including Denmark, Norway, Sweden and the United Kingdom. Total landings have been stable since 1980 at levels of 10000 to 12000 t (Anon. 1994).

1.2 REVIEW OF STOCK ASSESSMENT

P. borealis stocks in Fladen, Skagerrak and Iceland were assessed using the Beverton and Holt dynamic pool yield model in the 1970s (Anon. 1977). The growth parameters of the von Bertalanffy growth equation (VB) were obtained by analyzing size composition data. The differences in length between modes of length frequency distributions were used to calculate the annual growth rate. Cassie's (1954) modal separation technique or Skúladóttir's (1981) deviation method was used to identify the modes for various year classes in length frequency distributions. Natural mortality (*M*) was usually obtained from catch-curve analysis, with estimates ranging from 0.2 to 0.5 for various stocks in Icelandic waters. With this assessment method, the maximum yield-per-recruit is very sensitive to the estimated *M* level. It was recommended that studies of *M*, age determination, and growth rates be done with high priority (Anon. 1977). It was also considered necessary to work on stock identity and the origin of recruitment, particularly in relation to larval distribution.

The traditional age based virtual population analysis (VPA, Quinn and Deriso 1999) has been applied annually to two stocks for the North Sea area (in the Skagerrak and Norwegian Deeps), and another stock in the Fladen Ground. However, since *M* is assumed to be high compared to fishing mortality (*F*), population parameter estimates are sensitive to terminal *F*, and catch predictions can be misleading (Anon. 1994). A length-based VPA (Jones 1974) was applied to the Fladen Ground stock in the North Sea (Anon. 1988). The model converts length to age by the VB growth equation. However, since recruitment (*R*), mortality, and growth are assumed constant, the method has not been considered useful (Anon. 1994).

Due to high natural mortality from predation, suggested to be one of two reasons behind frequent fluctuations of *P. borealis* abundance, a multispecies VPA (MSVPA) has been regularly used for the *P. borealis* stock in the Barents Sea by Russian researchers (Berenboim et al. 1991). The model takes into account the trophic relations between cod and shrimp. Instantaneous natural mortality from cod predation was estimated to be from 0.74 to 1.04 for all age groups in years 1984 to 1987. However, since it is impossible to distinguish age groups, only four age groups were obtained based on the analysis of length-sex composition. The absence of complete age structure may have obscured the underlying population dynamics.

A more sophisticated model called synthetic age population analysis (SAPA) was developed and applied to the *P. borealis* stock in the Gulf of St. Lawrence (Mohn and Savard 1989). The model deals simultaneously with length and age distributions using a non-linear least squares technique to optimally fit the model to the data. Similar to VPA, the model requires inputs of *M* and terminal *F*. In addition, a template of the size distributions at each age was required to act as a basis for converting catch at length into catch at age. The modes of males and females in the distributions were given subjectively with the distribution means and constant standard deviations of 1 mm (carapace length). The arbitrary definition of the length at age template is a major limitation, in addition to the common assumptions of constant M and terminal F.

Fox (1973) developed a population simulation model that allowed additionally for the life history pattern of many crustaceans and some fishes that require copulation in reproduction and a sex-differentiated maturation schedule. The simulation model was applied to a pandalid shrimp population to examine closed season management strategies. Nevertheless, with R investigated deterministically, this model was also not successful in application (Shumway et al. 1985).

1.3 OVERVIEW OF BIOLOGICAL DATA PERTINENT TO ASSESSMENT *OF P. BOREALIS*

Many biological studies have been conducted on *P. borealis*, not only because of its commercial importance, but also because of its unique life history feature of sex change. A study group (ICES) on life history and assessment of *Pandalus* stocks in the north Atlantic identified the biological data that are believed to be pertinent to stock management (Anon. 1994). These important biological data are spatial distribution/stock definition, growth, sex change and predation/natural mortality. To this list, I add recruitment, i.e., the process propagating from parents to young, because the recruiting process is also a major factor regulating population dynamics.

1.3.1 Stock definition

Spatial distribution and stock definition of *P. borealis* are least well understood, because one of the major tools, i.e., mark-recapture research, is largely unavailable or inconclusive due to frequent shedding of the exoskeleton (Skúladóttir 1985). Little genetic research on stock identification was carried out until the late 1980s (Kartavtsev et al. 1991). Morphological differences have been identified for populations from different areas, or specifically from different seas. Based on some morphological differences between *P. borealis* of the Atlantic and Pacific, Makarov proposed a new genus, *eous*, for the Pacific *P. borealis* (Squires 1992). Genetic differentiation within the Barents Sea shrimp and among the populations from the Bering Sea, the Sea of Japan and the Barents Sea was examined, and it was concluded that *P. borealis* from the three waters are self-reproducing and appear to be panmictic units (Kartavtsev et al. 1991, 1993). Meanwhile, the population genetic differentiation was least apparent between shrimp from the Barents Sea and those from the Bering Sea. Shrimp from the Barents Sea are generally homogeneous and are parts of one Mendelian population (Kartavtsev et al. 1993). However, significant genetic differences were found among shrimp inhabiting inshore and offshore areas in Icelandic waters and Dohrnbank in the Denmark Strait, and three distinct stocks were suggested (Jónsdóttir et al. 1998). Furthermore, despite weak differentiation found in shrimp populations, Kartavtsev et al. (1993) insisted that morphological differentiation within the sea basin should be taken into consideration in fishing of the *P. borealis* populations.

1.3.2 Recruitment

Recruitment has also been evaluated for several *Pandalus* populations by examining sampling methodology and results. In a review by Shumway et al. (1985), R in several populations varied widely from year to year for unknown or poorly understood reasons. By using correlation and multiple regression, Hannah (1993) found that mean sea level in April when larvae were released explained 58% of the variation in R expressed in logarithms of the *P. jordani* populations in California and Oregon waters, and a relationship between spawning stock and R was not discernible. A similar conclusion of no spawner-recruit relationship was also reached by Abramson and Tomlinson (1972). Geibel and Heimann (1976) concluded that *P. borealis* populations fluctuate with dominant environmental influences, and that it may not be possible to demonstrate a spawner-recruit relationship.

1.3.3 Growth and age determination

Growth of *P. borealis* has been extensively investigated throughout its range (Rasmussen 1953; Allen 1959; Butler 1964; Haynes and Wigley 1969; Ivanov 1969; Parsons and

Lolly 1986; Bergström 1989; Bergström 1992). Growth was found to be highly variable from location to location (Rasmussen 1953; Allen 1959), and from year to year (Skúladóttir 1981; Anderson 1991). Commonly the VB growth equation with and without modification for seasonal oscillations is employed to model growth (Fréchette and Parsons 1983; Bergström 1992). Table 1.1 lists growth parameter estimates for *P. borealis* stocks in various areas, and Figure 1.2 presents growth curves for some stocks. Temperature was found to be an important factor affecting growth (Nunes 1984), while population density may limit growth (Anderson 1991).

Since there are no known anatomical structures for aging *P. borealis,* and mark-recapture studies have been inconclusive so far (Skúladóttir 1985), reasonably accurate age records are not available for *P. borealis*. The lack of age records for pandalid shrimp creates great difficulty in stock assessment. Because of the importance of age determination, a workshop was held in 1981 in Canada, and another meeting was held in 1989 to review the progress made in age determination of *Pandalus* since 1981 (Parsons 1989). Five methods were presented with regard to their application to shrimp length frequency data to determine the age structure of *P. borealis* populations.

The program MIX (MacDonald and Pitcher 1979) was applied to length frequency samples for male *P. borealis* from Davis Strait, west coast of Greenland, to obtain estimates of the mean, proportion, and standard deviation of each normal component (Savard et al. 1989). With this method of using a single set of data and a given number of components, it is difficult to produce reliable catch-at-age data given the sensitivity to the input parameters. The program MULTIFAN (Fournier et al. 1990), that simultaneously analyzes length frequency data sets across time was applied to a *P. jordani* stock (Boutillier et al. 1989). In this program, age compositions and the parameters of the VB growth equation are estimated objectively using a robust maximum likelihood method. Shepherd's length composition analysis (LCA) assumes a VB growth function and compares the observed length frequency distributions from research trawl survey catches with those expected from the growth function using a goodness-of-fit method (Terceiro and Idoine 1990). It was applied to the *P. borealis* stock in the Gulf of Maine, and

Table 1.1. Estimates of von Bertalanffy (VB) growth parameters L_∞, κ, t_0 for *P. borealis* stocks in various waters. Numbers in parentheses are standard errors.

Area / Author	L_∞	κ	t_0
Kachemak Bay, Alaska			
(Fu and Quinn, in review)	23.80 (±0.36)	0.39 (±0.02)	—
Pavlof Bay, Alaska (Anderson 1991)			
1971 year class	29.4	0.16	-1.3
1975 year class	26.31	0.29	-0.47
The Gulf of Maine			
(Terceiro and Idoine 1990)	33.0	0.32	—
Balsfjord, Northern Norway			
(Hopkins and Nilssen 1990)			
VB no seasonality	28.0	0.35	-0.09
VB modified for seasonal growth	29.43	0.31	-0.12
Gullmarsfjorden (1985 year-class)			
Sweden (Bergström 1992)			
VB, Female	31.15	0.46	—
VB, Male	24.98	0.65	—
VBsig (VB+sigmoid), Female	26.51	0.64	—
VBsig, Male	23.31	0.76	—
Barents Sea (Teigsmark 1983)			
Southwestern part	25.61 (±0.22)	0.37 (±0.01)	-0.24 (±0.06)
Central part	26.70 (±0.14)	0.28 (±0.01)	-0.19 (±0.03)
Northern part	27.44 (±0.21)	0.24 (±0.01)	-0.10 (±0.06)

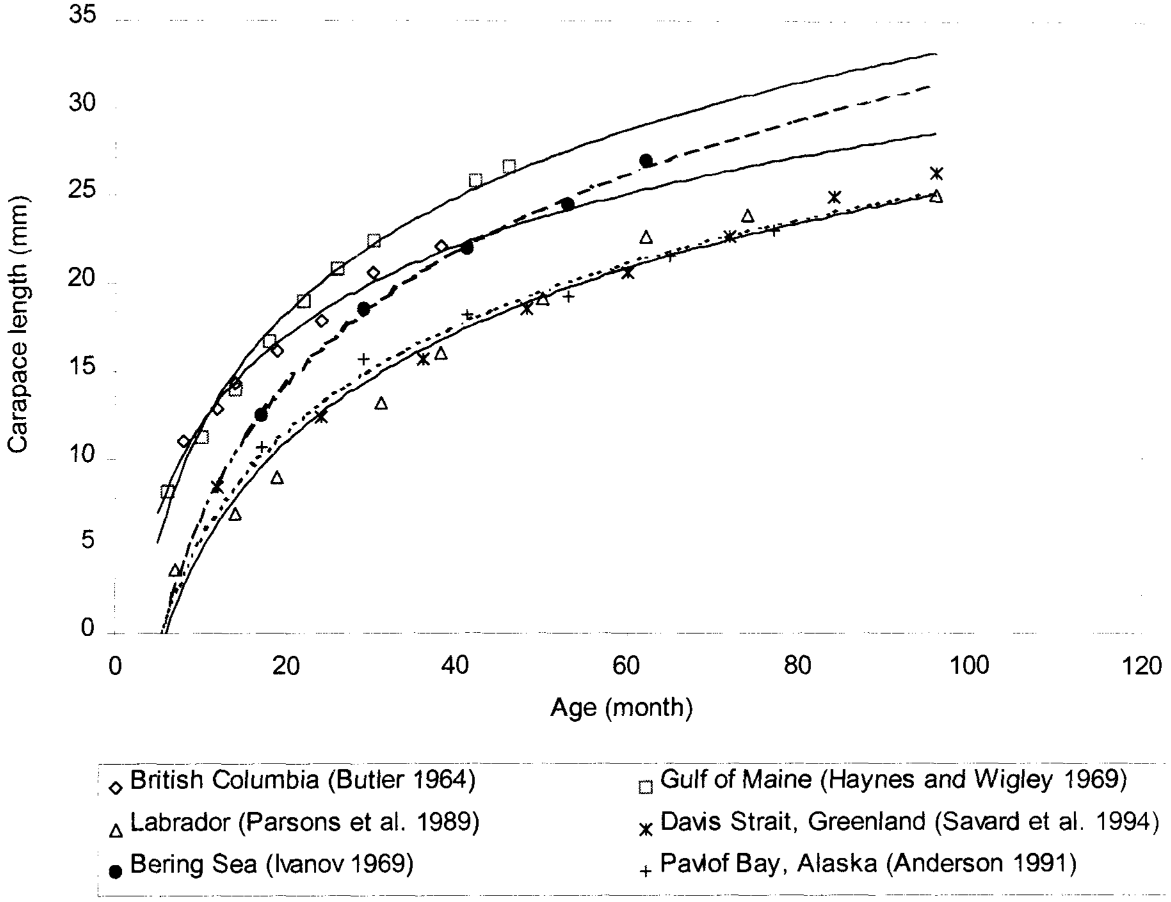

Figure 1.2. Observations of carapace length and fitted growth curves for *P. borealis* stocks in various waters.

provided an interpretation of the data close to a priori assumptions despite variable growth and recruitment in the stock (Terceiro and Idoine 1990). In addition, VPA and SAPA were also applied to obtain age composition data (Parsons 1989). In spite of all these modeling efforts in age determination, accurate age identification remains impossible for various reasons, particularly frequent growth variations.

1.3.4 Maturity and sex change

The most prominent feature in *Pandalus* life history is protandric hermaphroditism, i.e., males in early life, a transitional phase, and subsequently females. Geographic differences and temporal variations in the rate of maturation and transition from male to female have been well documented (Rasmussen 1953, 1969; Horsted and Smidt 1956; Allen 1959; Ivanov 1969; Balsiger 1981; Anderson 1991). Rasmussen reported that shrimp became ovigerous for the first time at age 5 years at Spitsbergen, northern Norway, while ovigerity occurs at ages of 2.5 to 3.5 years at more southern localities. *P. borealis* in Kachemak Bay begin transformation in March or April at an age of 2 or 3 years, and transformation may be complete in August or September (Davis 1982), such that shrimp begin to function as females at ages of 2.5 or 3.5. Females may produce 1 to 3 broods in their life.

The age/size of sex change was also suggested to vary in response to population status, i.e., sex change occurred at younger age and smaller size when mortality increased (Charnov 1982). Charnov and Anderson (1989) developed empirical relationships between percentages of sex change at ages and the proportions of females for various stocks.

1.3.5 Predation mortality

Total mortality has been estimated often by means of catch-curve analysis (Anon. 1994). Predation mortality probably accounts for a major part of *Pandalus* natural mortality (Anon. 1994). For the Barents Sea stock Berenboim et al. (1991), using a MSVPA, estimated predation mortality by Atlantic cod (*Gadus morhua*) averaged over all length groups to be 0.74 to 1.04. Predation was consistently more significant than fishing mortality that ranged from 0.1 to 0.6. In Icelandic waters, Atlantic cod, Greenland halibut (*Reinhardtius hippoglossoides*), and occasionally haddock (*Melanogrammus aeglefinus*) are important predators of *Pandalus* (Anon. 1994). In the North Sea, the annual consumption of *P. borealis* by four major predators (Atlantic cod, saithe *Pollachius virens*, haddock and whiting *Merlangius merlangus*) was estimated to be in the order of

40000 t, among which cod and saithe were responsible for 30% each (Daan 1991). Fish stomach samplings on the West Greenland shrimp grounds from 1990 to 1992 indicated that shrimp was an important part of diet for redfish (Sebastes spp.) and Greenland halibut (Anon. 1994). Consumption of the estimated trawlable shrimp biomass in the area by these two predators was estimated to be 34900 t for 1990 and 9800 t for 1991, corresponding to 26% and 10% respectively.

In the North Pacific, consumption by Pacific cod (*Gadus macrocephalus*) is considered by some scientists to be the main reason that *Pandalus* stocks in Alaska waters were prevented from recovering in the 1980s after fishery closures in various areas (Albers and Anderson 1985). In Pavlof Bay, Alaska, it was estimated that Pacific cod consumed between 142 and 875 t of *P. borealis* from May to September of 1981; cod predation was responsible for at least part of the estimated biomass reduction of 1501 t during the same period (Albers and Anderson 1985). In other westward regions of the Gulf of Alaska, particularly the Chignik District, simultaneous declines in the abundance of each cohort of *Pandalus* shrimp were observed in 1981, and the declines have coincided with an increasing abundance of Pacific cod and walleye pollock (*Theragra chalcogramma*) (Jackson et al. 1983). Based on trawl surveys conducted in summer and fall of 1982 to 1988, Pacific cod and walleye pollock annually consumed hundreds of thousands of tons of *Pandalus* shrimps in the western Bering Sea (Zgurovsky et al. 1990). Predation can significantly influence the *Pandalus* stocks in that region.

1.4 EXISTING PERPLEXITIES AND RESEARCH OBJECTIVES

1.4.1 Why a new length-based model?

The lack of age data for *Pandalus* shrimp causes difficulty in stock assessment. Interpretation of age and growth from various existing models of catch data that are solely based on length frequency distributions that assume normality is subjective due to the lack of pre-recruits in samples and overlapping modes for old ages. Consequently, the lack of basic knowledge of stock dynamics has caused severe difficulties to regulate the fishing effort on a scientific basis (Aschan and Godø 1997). Balsiger (1981) also pointed out that problems arise in the shrimp fisheries management because basic population parameters are not precisely known. Therefore, the first objective of my research was to develop a length-based model that estimates important population parameters such as R and M. This issue is addressed in chapter 2.

Since the development of length-cohort analysis by Jones (1974), length-based stock assessment approaches have been improved. Sullivan et al. (1990) presented one important length-based approach that relaxes three common assumptions of length-based methods: (1) steady-state length-distributions over time; (2) knife-edged and constant recruitment to fishery; (3) deterministic growth with length-at-age being well defined. The model proposed by Sullivan et al. (1990) was modified and applied to a red king crab (*Paralithodes camtschaticus*) population in Bristol Bay, Alaska (Zheng et al. 1995). These length-based models have the ability to estimate important population parameters such as growth, mortality, fishing selectivity and initial population abundance. Nevertheless, these length-based models are not applicable to *P. borealis* when life history traits, especially sex change, are to be incorporated. Since in these models individual cohorts are not followed through time, individual cohort dynamics are masked.

Another important age-structured, length-based model was developed which incorporates stochastic variation in growth (Deriso and Parma 1988; Parma and Deriso 1990). This stochastic model uses a recurrence relationship (developed by Cohen and Fishman 1980) to generate growth at age using a standard growth curve and an underlying normal or lognormal distribution for statistical variability. Probability distributions of length at age for abundance and catch are also generated based on stochastic growth. By approximating the size-selective function as a quadratic polynomial of size, Deriso and Parma (1988) obtained closed-form solutions for these recursive distributions along the life-span. Because the model confines the length frequency distributions at ages to be normal or lognormal, generality of mortality and particularly the fishing selectivity formulation are lost, and therefore model flexibility is compromised. Based on the Deriso and Parma model, Quinn et al. (1998) developed another model, relaxing the normal recurrence and assuming more general selectivity and natural mortality functions of length. By doing so, it is better for estimating population parameters and in understanding the fishing selectivity and natural mortality mechanisms.

In this thesis, a new length-based model for *P. borealis* populations was developed based on the framework from Quinn et al. (1998). A major extension is to estimate annual variations in *M*, a parameter that has previously been assumed to be constant in most all stock assessments. In addition, chapter 2 also addresses the evaluation of the new model and its application to the *P. borealis* stock in Kachemak Bay, Alaska.

1.4.2 Why do *Pandalus* stocks fluctuate/collapse?

Historical commercial landings of *Pandalus* shrimp fluctuated widely. Some populations, like that in the Gulf of Maine, exhibit a cyclic pattern of abundance, while some others never rebounded after a decline (Balsiger 1981). The Pribilof Island fishery started in the late 1950s, peaked at 30000 t in 1963 and then quickly declined in the early 1970s without any recovery (Shumway et al. 1985). Meanwhile, many crustacean fisheries in Alaskan waters, including that in Kachemak Bay, collapsed synchronously after peaks in the 1970s (Orensanz et al. 1998). The widespread tendency of shrimp stocks to produce very high levels of abundance in certain years and then to precipitously decline imposes great management difficulties. Shumway et al. (1985) pointed out that the concept of maximum equilibrium yield is difficult to embrace for stocks of wide fluctuations in abundance.

Abundance fluctuations in general are not well understood, but are postulated to be closely related to variations in year-class success with variations related to environmental factors (Balsiger 1981). Findings about the effects of fisheries on *Pandalus* populations are contradictory. While some research suggested that increasing fishing mortality contributed to stock collapse (Shumway et al. 1985), Hannah and Jones (1991) concluded that intensified harvest reduced the abundance of *P. jordani* stocks off the coasts of Oregon and northern California, improved density-dependent growth, accelerated the sex change process, so that the shrimp stocks were resistant to over-harvest.

As for the *P. borealis* stock in Kachemak Bay, intensified harvest was accompanied by a climate regime shift that happened around 1977. A question was naturally raised by fishermen and fishery researchers: what caused the dramatic population decline in the early 1980s? The second objective of this research was directed to answer this question, which is addressed in chapter 3.

1.4.3 What management strategies should be used with *Pandalus* populations?

With population abundance fluctuating frequently, it is unrealistic to manage *Pandalus* populations based on maximum sustainable yield (MSY). Generally *Pandalus* stocks are managed based on TACs that are estimated from research survey results (Anon. 1994). I found no documents on optimal harvesting for *Pandalus* stocks in the literature. Because the ultimate goal of stock assessment is to manage fisheries based on a sound scientific rationale, chapter 4 aims at analyzing harvest strategies and suggesting optimal management policies for *Pandalus* stocks.

1.4.4 What life history traits matter in population dynamics and fishery management?

What roles do the life history traits, such as sex change, seasonal variations in growth, and mortality, play in the dynamics of *Pandalus* populations? It is not possible to answer this question without a population dynamics model that reflects these features explicitly. Yet, answering this question is essential for sound management. Therefore, in chapter 5, a more sophisticated population model is developed that incorporates seasonal variations in growth and natural mortality.

Finally, all work in this dissertation is summarized in chapter 6 with a brief description of the future directions that I believe are necessary for successful understanding and management of *Pandalus* populations.

Chapter 2 Estimability of natural mortality and other population parameters in a length-based model: *Pandalus borealis* Krøyer in Kachemak Bay, Alaska[1]

ABSTRACT

As stock assessment models have become more complex, the question of estimability of population parameters is important. We conducted simulation-estimation experiments with a length-based model of the northern shrimp, *Pandalus borealis* Krøyer, population in Kachemak Bay, Alaska, to evaluate estimability under different assumptions about natural mortality and levels of data imprecision. Our goal was determine which population parameters, including annual recruitment, natural mortality and fishing mortality, could be estimated with confidence to achieve better understanding of the population dynamics and the apparent causes of population decline. The assumption of constant natural mortality over time created biased parameter estimates. Natural mortality was sensitive to measurement error in survey biomass estimates, but robust to errors in length frequency and yield data. Accuracy of recruitment estimates was determined mainly by measurement errors in biomass and length frequency data, and fishing mortality estimates were most affected by measurement errors in yield data. Estimated natural mortality of *P. borealis* increased in the 1980s, perhaps owing to increased predation mortality by groundfish. The ability to estimate natural mortality and its trend in this case is probably due to a strong contrast in data sources that could not be explained by adjusting other model parameters.

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[1] Fu, C., and T.J. Quinn, II. In review. Estimability of natural mortality and other population parameters in a length-based model: *Pandalus borealis* Krøyer in Kachemak Bay, Alaska. Canadian Journal of Fisheries and Aquatic Sciences.

2.1 INTRODUCTION

Stock assessment models have become increasingly complex to accommodate a variety of information on the stock (Quinn and Deriso 1999). Current models are most often age- or length-based or both and integrate frequency data from fisheries and surveys, independent estimates of relative or absolute abundance or biomass, and catch data. Increasingly, models are including additional parameters for autocorrelation, and for temporal, spatial, and environmental effects, using the ADMB methodology (Fournier 1996). For example, the age-based stock assessment model for walleye pollock in the eastern Bering Sea contains thousands of observations and 637 parameters (Ianelli et al. 1999).

Consequently, the question of estimability, or equivalently, optimal model complexity, in these models is one that is only now receiving serious attention. Ideally, adding parameters to a model should at first reduce bias by more correctly conforming to the true underlying model structure (Burnham and Anderson 1999). The tradeoff is that variance or uncertainty in the parameter estimates increases by attempting to obtain more estimates from the same amount of information. At some point, additional parameters and/or model structure are either redundant or misspecify the true structure, creating an increase in bias and uncertainty.

In this paper, we generate simulated data and employ simulation-estimation experiments to explore the sensitivity of a length-based assessment model to the specification of population parameters. In particular, we examine the specification of natural mortality, in conjunction with uncertainty in the data. Model performance is also evaluated with regard to a calibration coefficient for a biomass-based survey of the population, and ways of dealing with initial period parameters.

In stock assessment, several length-based models have been available. They can be categorized into non-age-structured types (e.g., Sullivan et al. 1990; Zheng et al. 1995) and age-structured types (e.g., Parma and Deriso 1990; Quinn et al. 1998). However, natural mortality is usually assumed to be known from other sources or is estimated as a constant value in stock assessment due to confounding with other parameters, such as fishing mortality, recruitment and catchability (Schnute and Richards 1995). Given salient interannual, and particularly directional, variations in natural mortality, the assumption of constant natural mortality can greatly bias other parameter estimates.

Pandalus borealis Krøyer, commonly called northern or pink shrimp, an important circumboreal species, occurs in both the Pacific and Atlantic Oceans. Due to the lack of age structures, great efforts have been made to interpret age, growth, and mortality from length frequency distribution data (Abramson and Tomlinson 1972; Parsons et al. 1989; Terceiro and Idoine 1990; Fournier et al. 1991). Nevertheless, analyses of population dynamics are hindered by the lack of comprehensive knowledge of fundamental population processes, including recruitment, natural mortality, and sex change. These uncertainties caused severe difficulties in regulating fishing effort on a scientific basis. One step to improve population assessments is to develop length-based models to incorporate these processes. The length-based model in Quinn et al. (1998) is desirable for investigating the dynamics of *P. borealis* populations, because it provides flexibility in considering specific life features in recruitment, growth, and death.

We used extensive data from the *P. borealis* population in Kachemak Bay, Alaska, as the basis of the modeling. This population was harvested intermittently with small landings in the 1950s and 1960s. Since 1971, trawl surveys were carried out to obtain population biomass estimates, and the fishery was managed according to a catch quota. The catch increased to 2600 *t* in 1970 and remained near that level until the early 1980s (Davis 1982). Catch in 1983 decreased by almost an order of magnitude due to reduced population abundance, and the fishery was closed after 1986 due to continued low stock size (Gustafson 1994).

Along with the *P. borealis* population in Kachemak Bay, many other crustacean stocks in Alaskan waters, for example, red king crab on the shelf around Kodiak Island, were depleted around the same period (Orensanz et al. 1998). The serial depletion of Alaskan crustacean stocks cannot be explained simply as a result of overfishing, because some lightly or seldom fished *P. borealis* populations experienced similar declines (Anderson 1991). A simulation study with the Kachemak Bay stock indicated that no alternative harvest strategies could have changed the population's fate of collapse (Chapter 3; Fu et al.

1999). Rather, the simulation suggested that natural mortality was the most important factor controlling population dynamics, and high natural mortality may have resulted in the population collapse in the 1980s.

The final goal of this paper is to produce the most reliable parameter estimates for the *P. borealis* population in Kachemak Bay, such as recruitment and natural mortality, so that population dynamics and stock decline can be better understood. Using results from the simulation-estimation study, we specify the optimal population model and estimate its parameters.

2.2 METHODS

2.2.1 Data and population model

Data from the Kachemak Bay *P. borealis* population were provided by the Alaska Department of Fish and Game (ADF&G). They include biomass estimates and carapace length frequency data from spring surveys from 1978 to 1991, and commercial yield from 1978 to 1986.

The length-based model of Quinn et al. (1998) follows each cohort from recruiting age r to maximum age A. Since detectable amounts of shrimp in Kachemak Bay become available to trawl gear at age one, $r = 1$. In this paper, A is set equal to 6, corresponding to that for the *P. borealis* population in Kachemak Bay (Davis 1982). During the initial period (labeled as years $1, \cdots, A$), when no observations are available, there are A initial recruitment parameters (R'), and A–1 initial natural mortality (M') and fishing mortality (F') parameters. Simulation experiments described below indicate that M' and F' can be specified at some constant and reasonable values. Other parameters during the initial period are assumed identical to those in the subsequent years of the model.

Observations are made starting at time A+1. Somatic growth is assumed to be time-independent with parameters including von Bertalanffy L_∞ (the asymptotic length), κ (a cruvature parameter governing the speed to approach the asymptote L_∞), σ (the deviation from the growth model) and σ_r (the deviation of the length frequency normal distribution at age r). Parameters of a logistic gear selectivity function, γ (the shape parameter) and L_{50} (the length at which 50% of the individuals are vulnerable to fishing), are estimated in the model. Other parameter estimates include time-dependent annual recruitment R_t, natural mortality M_t, full recruitment fishing mortality F_t and mean length at recruitment $\mu_{r,t}$. The overall estimation is improved significantly when $\mu_{r,\,t}$ varies over time, but no results on $\mu_{r,\,t}$ are given in this paper. Detailed descriptions of model specifications are given in Appendix 1.

Parameter estimation was accomplished by using the software Autodif Model Builder (ADMB) which estimates parameters in a step by step fashion, known as a multi-phase procedure (Fournier 1996). Specifically, interannual variation of the logarithm of M_t was modeled as the time series structure of a random walk: $\ln(M_{t+1}) = \ln(M_t) + \delta_t$, where δ_t is the deviation term.

Parameters were estimated by minimizing the objective function:

$$f = \lambda_B \sum_t (\sqrt{B'_t} - \sqrt{B_t})^2 + \lambda_L \sum_t \sum_l (\sqrt{LF'_{t,l}} - \sqrt{LF_{t,l}})^2 + \lambda_Y \sum_t (\sqrt{Y'_t} - \sqrt{Y_t})^2 + \lambda_M \sum_t \delta_t^2,$$

where the λ's are weighting factors and variables B'_t, LF'_t and Y'_t denote observed values of population biomass, population length frequency, and commercial yield, respectively, while those without primes denote corresponding predicted values. A square root transformation is desirable to reduce the contrast in the magnitude of different data sources (Quinn et al. 1998). A logarithmic transformation was also investigated, but results were qualitatively similar and so are not presented. The weighting factors λ_B, λ_L , and λ_Y for the observations were set to be proportional to the inverse of the empirical variances of transformed data sets without regard to the model deviation. A better approach is to derive the variance from the sampling, which is beyond the scope of this paper. These weighting factors were scaled so that $\lambda_B = 1.0$. We name the variance of biomass data "scaling data variance".

The term $\lambda_M \sum_t \delta_t^2$ is a penalty term controlling the degree of variability in the time series of natural mortality estimates from year to year. A large value of λ_M makes the interannual deviations of natural mortality small and vice versa. The determination of the λ_M value is described individually in the following two sections.

2.2.2 Simulation-estimation experiments

Simulation-estimation experiments were conducted to evaluate model performance under various circumstances. Uncertainties in annual natural mortality and recruitment were incorporated to generate simulated data with 14 years of survey and catch data in accord with the actual observations analyzed later. For the purpose of examining the ability of the model to estimate interannual variations in M, M values for the 14 years were obtained by drawing randomly between 0.2 and 1.2, a range within which M values are most likely to fall. Each recruitment was generated by imposing a log-normal error with coefficient of variation of 50% upon a Beverton-Holt spawner-recruit relationship, $R = \alpha S/(1+\beta S)$.

Instantaneous fishing mortality was set as constant over time (0.3). Other levels of constant F or varying F over time were also used, and there were no significant differences in the parameter estimates; rather, as F values increased, M appeared to be better estimated.

The calibration coefficient (q) for the survey usually is an unknown parameter. Thus, survey abundance estimates (or precisely called indices) using area-swept techniques generally are relative measures of total population abundance. The calibration coefficient is often set to 1.0 in calculating abundance indices (e.g., Gustafson 1994). In this case, the indices are likely to be lower than the actual stock abundance due to the fact that some shrimp, especially smaller individuals, escape through the meshes and sometimes shrimp distribute below or above the trawl range (Jackson et al. 1983). When this is the case, a value less than 1.0 should be applied to q to calibrate the abundance indices. On the other hand, it is also possible that the abundance indices are greater than the absolute abundance ($q > 1.0$) due to reasons such as herding; however, this case has not been documented to my knowledge. Therefore, three q levels (0.5, 0.8 and 1.0) were tried individually in the generation of the simulated data. Since the results with respect to parameter biases were nearly identical, only the case with $q = 1.0$ was presented below. Values of other deterministic parameters for constructing simulated data (Table 2.1) were taken from Fu et al. (1999).

For each scenario, 50 sets of simulated data were generated corresponding to 50 sets of random M and R. The same random seeds were used for each scenario, so that they were comparable when certain conditions were changed. Each generated data set was input into the parameter estimation procedure.

Experiments with different M trends including constant M over time indicated that the most appropriate λ_M value was independent of the intrinsic variations in M, but was directly related to the measurement error in biomass data. For scenarios with no measurement error in biomass data, the λ_M value can be set at 0, because annual natural mortality values can be estimated without significant errors. As measurement error in biomass gets larger, the λ_M value should increase correspondingly, so that the deviations of estimated natural mortality from their true values caused by measurement error in biomass can be alleviated. Our empirical λ_M value that provides parameter estimates with the least chance of bias was calculated as the product of the scaling data variance, which is the empirical variance of biomass data ($\hat{\mathrm{var}}(B) \approx 100.0$), and half of the coefficient of variation (CV) for biomass data. For example, when the CV for biomass data is 20%, then the most appropriate λ_M value can be calculated as $0.1 * \hat{\mathrm{var}}(B) = 10.0$. For demonstration, varying levels of λ_M (0.0, 5.0, 10.0, 20.0) were used.

Estimation results of various scenarios were compared in terms of bias ratios, i.e., the ratios of estimated to true parameter values on $\log_2$ scale, such that a value of 0.0 indicates perfect fit, and a value of 1.0 stands for two-fold overestimation (Schnute and Richards 1995). Parameter bias ratios from the 50 runs were displayed using box-plots, and the spread of a box represents variability in parameter estimation.

2.2.3 Parameter estimation for *P. borealis*

With the actual data from the *P. borealis* population, variances in square-rooted biomass, length frequency and yield data were 269.0, 63.0 and 238.0 respectively, therefore, weights λ_B, λ_L and λ_Y were assigned as 1.0, 4.3 and 1.1, proportional to the inverse of their empirical variances. The estimated CV for survey biomass estimates averaged 23% from 1977 to 1990 (Gustafson 1994), so we approximated it as 20% and set the value of λ_M to 26.9.

A bootstrap method (Efron and Tibshirani 1993) was used to estimate standard errors for the parameter estimates and the predicted biomass and yield. Bootstrap data were calculated as $O_t^B = (r_{t'}^{sqrt} + \sqrt{P_t})^2$, where $r_{t'}^{sqrt}$ denotes sampled residuals, and P_t predicted values. Due to extremely lengthy calculations, only 500 replicates were conducted, and standard errors were calculated as the standard deviations of the 500 replicates.

Retrospective analysis was employed to evaluate the ability of the model to estimate parameters for the terminal year. We carried out the analysis by leaving out one year's data at a time. Weights (λ's) were obtained using the same rule described above.

2.3 RESULTS

2.3.1 Simulation-estimation experiments

2.3.1.1 Natural mortality

Understanding the estimability of M was our primary goal. Three scenarios were compared: (1) assuming one constant known M; (2) estimating one constant M value; (3) estimating interannual variations in M. To exclude effects from other uncertainties, no measurement error (ME) was initially imposed upon any observation. Initial period parameters R', M' and F' were fixed at assumed and constant values ($e^{6.0}$, 0.2 and 0.4). Other arbitrary values were also used for R' and M' later in structuring the estimation for initial parameters.

When M was fixed at 0.6 (the average value) for each year in the first scenario, estimated F, R and other scalar parameters were highly variable (Figure 2.1). Estimating one constant M in the second scenario resulted in some improvement in the estimation of scalar parameters; nevertheless, the estimates of M, F and R were highly variable, which indicated that it was insufficient to estimate only one constant M. In contrast, when interannual variations in M were estimated, shown in the third column, all parameter estimates were nearly unbiased regardless of the intrinsic variations in M and R. In addition, linearly increasing or decreasing trend in M produced no difference with regard to estimation biases. The results indicated that it was not only possible but also desirable to estimate annual variations in M.

2.3.1.2 Measurement error

Measurement error is an important issue in any stock assessment. To investigate the relative impact of ME in biomass and yield data, three scenarios were compared: (1) no ME in biomass and 20% CV for yield data; (2) 10% CV for both biomass and yield data; (3) 20% CV for biomass and 0% for yield. Four levels of CV from 0 to 20% were tried for length frequency data, and they rendered no big difference in parameter estimates. In comparison, recruitment estimates were more sensitive to ME in length data. In order not to obscure the effects from ME in biomass and yield data, each scenario adopted a CV of a relatively lower level (5%) for the length frequency data. The highest level of CV (20%) for biomass and yield data was chosen to approximate the potential uncertainty in the data sources. This level of ME (CV = 20%) might be underestimated and too optimistic compared to most other observations, but we considered it minor, because our goal was not to discuss the ME impact in general, but to examine relative sensitivities of parameter estimation to ME in different data sources.

When there was no ME in biomass and R', M' and F' were fixed at true values, a λ_M value of 0.0 produced the least variable estimates for M (Figure 2.2). As λ_M increased to 5.0, a value that would be appropriate if the CV of biomass data is 10%, there were more occurrences of overestimating M. The tendency to overestimate became more severe when λ_M increased to 10.0, a value that would be appropriate if CV of biomass data is 20%. In addition, as λ_M increased, *R* estimates became more variable and the medians of their bias ratios moved further above zero, which implied that *R* tended to be overestimated. When biomass data had a CV of 10%, a λ_M value of 0.0 resulted in severe underestimation of *M* on some occasions (Figure 2.3), which however was alleviated when λ_M increased to 5.0. As above, there was a greater chance of overestimating *R* as λ_M increased. Only small differences in parameter estimates were produced as the λ_M value further increased to 10.0. With CV of 20% for biomass data (Figure 2.4), there was some improvement in *M*, but not in *R* estimates, when λ_M increased from 5.0 to 10.0. However, when λ_M value further increased to 20.0 (twice our empirical λ_M value), there was no significant improvement in *M* estimates. Because *R* tended to be overestimated as λ_M increased above 0.0, the choice of λ_M is a tradeoff between a greater chance of underestimation of *M* and a greater tendency of overestimation of *R*, when there is ME in biomass data. When there is no ME in biomass, λ_M should be set to 0.0.

By comparing the results (Column 1 in Figure 2.2, Column 2 in Figure 2.3, and Column 2 in Figure 2.4) from the three sets of ME, it was clear that higher ME in biomass data increased the variability of the *M* and *R* estimates. *F* estimates were robust to ME in biomass, and increased ME in yield slightly increased chances of getting bias.

To examine the effects of ME in length frequency data, two levels of CV (0 and 20%) were used with the CV for both biomass and yield data set at 10% (Figure 2.5). When the CV of length frequency data was 20%, a λ_M value of 5.0 resulted in less variable parameter estimates (shown in Columns 1 and 2), which further demonstrated that the determination of an appropriate λ_M should be dependent on ME in biomass data. Again, there were more chances that *R* was overestimated, as λ_M increased. When CV of the length frequency data was reduced to 0%, there was only slight change in the *M* and *F* estimates (shown in Columns 2 and 3). Thus, estimation of these parameters is robust to ME in length frequency data. The variabilities in annual recruitment, growth and selectivity parameter estimates, on the other hand, were reduced to some extent, as the CV of the length frequency data was reduced to 0%.

2.3.1.3 Calibration coefficient

Because it is important to examine how our perception about q affects the parameter estimation, three scenarios were compared: (1) q was fixed at true value; (2) q was estimated; (3) q was specified at 50% higher. Because it is more conservative to assume q at a higher level than the true one, we were interested in examining the scenario where q was specified at 50% higher. For examining the influence of q on parameter estimation, no ME was imposed, and R', M' and F' were fixed at values used in the generation of simulated data.

When q was estimated in scenario 2, R, M and F estimates on some occasions deviated greatly from their true values (Figure 2.6). Although on other occasions unbiased estimates were obtained, estimating q along with other parameters is not recommended, because the inability to estimate q would get more severe when there is ME. When q was specified at 50% higher than the true value, R and F estimates had the same amount of variability as in scenario 1, but the medians shifted down and upward, respectively. M estimates became more variable, but compared with R and F, their medians were much closer to zero. Except for the first year, all M estimates were consistently lower than their true values. Overall, specifying q at some value equal to or higher than the perceived true q is necessary to produce stable estimation behavior while maintaining conservatism in the assessment results.

2.3.1.4 Initial period parameters

In the previous investigations, initial period parameters R', M' and F' were fixed at the assumed and constant values. However, in reality, these parameters are always unknown. To search for a best way of dealing with these parameters, four scenarios with no ME were compared (Figure 2.7). Scenarios with ME were also examined, and they resulted in similar conclusions. To be more realistic, varying R' ($e^{7.0}, e^{6.5}, e^{5.0}, e^{5.5}, e^{6.5}, e^{7.0}$) and M' (0.5, 0.4, 0.2, 0.7, 0.3) with the values arbitrarily specified, were used for generating simulated data.

The first scenario attempted to estimate each R' and M'. Despite the variability in R' and M', and the lack of data during the initial period, *R*, *M* and *F* parameters were well estimated except for the first year, and the results were not different from those for the first scenario in Figure 2.6, where R', M' and F' were fixed at true constant values.

In scenario 2, only values of R' were estimated; M' for each year was specified at 0.2 (lower than the average value of 0.42) and F' was fixed at the true value (0.4). The estimation results had no detectable difference from the first scenario, which implied that it was impossible to estimate M'. The chance of bias in the first year estimates was greatly reduced when each M' was fixed at its true value; the results are not shown here. This is because the abundance at length for the last year of the initial period, on which the estimations of the first year *M* and *F* are based, are directly influenced by the mortality values of M'_{A-1} and F'_{A-1}. A close guess of M' in actual application would help increase the accuracy of the first year estimates of *M* and *F*. Another source for this inability in estimating the first *M* and *F* lies in the fact that R' parameters could not be estimated accurately because of the lack of data during the initial period. More specifically, the inaccuracy of the R'_A estimate, with which the first *M* and *F* are directly correlated, contributed to the failure in the first year.

Scenario 3 was the same as scenario 2, except that F' values were specified at 0.0 (incorrectly). As a result, there was more chance of getting biased estimates for *R*, *M* and *F*, but the differences were rather minor. Therefore, it would be adequate if F' is specified at some reasonable level. Scenario 4 is the case when each M' was estimated, while each R' was arbitrarily specified at $e^{6.0}$, and each F' was fixed at the true value. The estimates of *R* and *M* became very variable and all tended to be underestimated. *F* estimates were overestimated during the first few years and became stabilized in the later years.

In conclusion, it is crucial to estimate each of the initial recruitments R'. In contrast, M' and F' are not estimable, and they can be assumed constant over time and can be specified at any reasonable value without generating much bias on the overall parameter estimation.

2.3.1.5 Weights for different data categories

For the previous simulation runs, weights λ_B, λ_Y and λ_L were assigned as 1.0, 5.3 and 3.4 respectively, which were calculated from the variance ratios of the first set of simulated data. In fact, there was very little difference in the variance ratios among the 50 sets of simulated data. To examine possible effects of data-weighting, three other sets of weights (λ_B, λ_Y and λ_L) were used: (0.1, 1.0, 10.0), (1.0, 1.0, 1.0) and (5.0, 1.0, 0.5). Results indicated that there were only slight differences among different weightings. F estimates were more robust to different weights than those of R and M. In general, it seemed appropriate to weight different data categories based on their actual variance ratios.

2.3.2 Parameter estimation for *P. borealis*

The results from simulation experiments indicated that it was desirable to estimate interannual variations in M particularly when there was no ME in biomass data. ME in biomass data obscures the estimation of interannual M variations, but increasing the weighting factor λ_m to be proportional to half of the CV for biomass data can reduce the occurrence of biased M estimates. To account for the uncertainties in biomass data accuracy, natural mortality for the *P. borealis* population was estimated for each year with a relatively high λ_m value (26.9).

Because it is essential to estimate the values of R' in the initial period when they are unknown for getting less biased parameter estimates, we estimated 6 values of R' while leaving M' and F' specified at 0.2 and 0.4 respectively for each year. Accurate specification of M' and F' helps with the first year parameter estimates, but has little effect for the following years. The values of 0.2 and 0.4 were arbitrarily set close to the estimated M and F in the early years. Because of the greater uncertainties in the first M and F estimates, we chose not to specify M' and F' at those levels. In addition, because of the inability to estimate q when ME is present, which has been indicated by the simulation, we specified q at 1.0 to avoid possible large biases in parameter estimates.

The value of 1.0 was chosen with the assumption that the trawl surveys conducted by ADF&G have 100% net efficiency (Gustafson 1994).

The estimates of *R*, *M* and *F* parameters and their standard errors (SEs), obtained from the bootstrap procedure, are shown in Figure 2.8. Predicted length frequencies seem to fit the observations well (Figure 2.9). The growth and selectivity parameter estimates and their SEs are given in Table 2.2 (the first row).

The estimated *M* had a strong increasing trend during the 1980s which almost parallels that of cod abundance obtained during the same surveys (Bechtol 1997) (Figure 2.8). We suspect that the decline of *P. borealis* abundance may have resulted from the intensified predation mortality by Pacific cod (*Gadus macrocephalus*) and other groundfish species. The estimated *R* had a small peak in 1979 and a larger peak in the years of 1984 and 1985. Field observations indicated a rebound of biomass in 1985 and 1986, but mainly with small male shrimp (Gustafson 1994). These observations agree with the estimated recruitment peaks in 1984 and 1985, given a one year lag from recruiting to the population at age 1 to being largely available to the fishing gear at age 2. Furthermore, despite the two years' rebound in recruitment, the shrimp population was not able to rebuild, which could be well explained by the high consumption by predators. Albers and Anderson (1985) also concluded, after studying the diet of Pacific cod in Pavlof Bay, Alaska, that the high consumption of shrimp by cod may have prevented that shrimp population from rebuilding.

In general, the retrospective analysis showed that the model was able to estimate the terminal parameters well. For instance, the removal of data from 1 or 2 years (Data 90 or Data 91) had small effect on the estimates of *R* and *M* (Figure 2.10). However, when data were available only until 1987 or 1986, the estimates of terminal *R* tended to be lower than with more data. The dramatic decline of *R* in 1986 may have contributed to the discrepancies in terminal *R* estimation. In contrast, the terminal estimates of *M* and *F* tended to follow the actual trend well, and so they were likely to be reliable. We could also anticipate that the estimation of terminal *R* would be reasonable if there was no abrupt shift in recruitment one or two years before. Growth and selectivity parameter estimates from the reduced data sets are also given in Table 2.2. The estimates show only little variation across different data sizes.

2.4 DISCUSSION

Pandalid shrimps are well known to have large fluctuations in population abundance. The large fluctuations were postulated as closely related to variations in recruitment (Balsiger 1981). As a result, recruitment variations became the research focus, and natural mortality was often assumed constant over time, even when doing population simulations (e.g., Fox 1972). However, our previous research on retrospective projection concluded that M was a relatively more important factor than R in controlling shrimp population dynamics (Fu et al. 1999). The major shift of species composition from shrimp-dominant to groundfish-dominant in Kachemak Bay (Bechtol 1997) motivated us to direct our research effort toward estimating annual variations in M.

So far there has not been any work published in stock assessment targeted at estimating interannual variations in M. Based on simulation studies with constant M, Schnute and Richards (1995) stated, "our results confirm a high correlation between M and other model parameters, consistent with the usual requirement for a prescribed M." However they also argued that realistic analyses must take account of uncertainty in M.

The simulation-estimation experiments conducted in this paper showed that it was not only possible but also desirable to estimate annual variations in M, given survey biomass estimates, length frequency distributions and commercial yield data. This new way of dealing with natural mortality in stock assessment has ultimate advantage over the common one of assuming or estimating one constant M. In addition, experiments with different patterns of F variations over time have also been conducted (not presented here), and results indicated that the parameter estimation was robust to various F levels. Therefore, research on variations in M should be encouraged when investigating population dynamics of other pandalid shrimps and fish species that are major prey. Furthermore, as more powerful parameter estimation software such as ADMB and more flexible population models become available, estimating interannual variations in *M* will find greater application in fish stock assessment.

Nevertheless, simulation-estimation experiments illustrated that the estimation of *M* was sensitive to ME in biomass data, but it was robust to ME in yield and length frequency data. When large ME was embedded in biomass data, the estimates of *M* could deviate highly from their true values. Therefore, it could be difficult, if not impossible, to estimate *M* if no biomass data are available, as some research has concluded (Quinn and Deriso 1999). Bias in estimated *M* caused by ME in biomass data can be alleviated by using the penalty term in the objective function.

The determination of an appropriate λ_M value would naturally be connected with the interannual variations in natural mortality. Yet we discovered that the best λ_M value was independent of *M* variations, and solely dependent on the amount of ME in biomass data. When there is no ME in biomass data (an unlikely situation), λ_M value should be set to 0.0. As ME in biomass data increases, the λ_M value should increase correspondingly. Experiments with different sets of scaling data variance (for example, using the variance of yield data as scaling data variance) and with different levels of empirical variances for the generated data indicated that it would be sufficient to use half of the CV of biomass data and multiply it by the scaling data variance.

Assessment scientists often propose that the calibration coefficient be estimated (Quinn and Deriso 1999). However, simulation results in this paper indicated that it was really difficult to estimate *q* when *M* was variable. Unexpected large biases in all parameter estimates can occur, and high ME will further worsen the situation. With the *P. borealis* population in Kachemak Bay, it is likely that the actual *q* was smaller than the value (1.0) we assumed. The consequence would be an underestimation of *R* and *M*, and overestimation of *F*, as demonstrated from the third scenario with regard to *q*. We have no way to verify possible shifts in magnitude of the parameter estimates. Fortunately, the overall shifts are of less concern than the annual variations that the model was able to uncover, given *q* remained constant over time. However, if the specified *q* were smaller than the true *q*, then overestimation of *R* and *M* and underestimation of *F* would occur.

This would lead to overestimation of population abundance and increase the risk of overfishing.

The estimated *M* values from 1977 to 1982 for the *P. borealis* population were below 0.2, which seems too low for a shrimp population of only six age classes. One possible interpretation for the low *M* estimates lies in the spatial distribution change after the regime shift in 1977 that caused quick warming of the water column. *P. borealis* are less tolerant of warmer temperatures after they become females (Apollonio et al. 1986). From approximately 1979 through 1981, there were high concentrations of *P. borealis*, especially of large, mature females in the offshore sampling area west of the Homer Spit. Although there are no reliable historical records of temperature in Kachemak Bay to verify the relationship between temperature and female concentrations, we suspect that the temporary redistribution of older shrimp in the area west of the Homer Spit might have resulted in the overestimation of their survey abundance relative to young shrimp. If so, this would cause low estimates of *M*. Catches west of the spit declined quickly after the period of high concentration, which is reflected in the increasing *M* estimates afterwards.

The question of optimal model complexity is a complicated one. For estimation models with a single data source, the Akaike and Bayesian Information Criteria (Burnham and Anderson 1998, Quinn and Deriso 1999) offer a straightforward approach involving the likelihood of the data, the number of parameters, and the number of observations. However, our results showed that in more complicated problems with several data sources, the optimal model structure depends on the true dynamic processes and the amount of measurement error in the data sources. An additional complication is the choice of weighting of data sources, when the true variances are unknown (the usual case). Nevertheless, the use of simulation-estimation exercises as done in this paper is probably the best means for determining optimal model complexity, until more general theoretical principles can be obtained.

Table 2.1. Parameter values estimated from Fu et al. (1999) for constructing simulated data, including spawner-recruitment parameters (α, β, ϕ), growth parameters (L_∞, κ, σ, σ_r), and selectivity parameters (L_{50}, γ).

Parameters	Values
α	1.826
β	0.002
ϕ	0.267
L_∞	24.698
κ	0.367
σ	0.529
σ_r	1.127
L_{50}	16.720
γ	0.572

Table 2.2. Estimates of growth parameters (L_∞, κ, σ, σ_r), and selectivity parameters (L_{50}, γ) from the full and reduced data sets. Data 91 indicates the use of data for 1978-1991.

	L_∞	κ	σ	σ_R	L_{50}	γ
Data 91	23.80±0.36	0.39±0.02	0.62±0.06	1.12±0.06	15.50±0.33	0.61±0.02
Data 90	23.98	0.38	0.60	1.12	15.50	0.61
Data 89	24.18	0.37	0.59	1.08	15.46	0.61
Data 88	24.22	0.36	0.61	1.01	15.27	0.61
Data 87	24.42	0.35	0.58	1.01	15.54	0.58
Data 86	24.56	0.35	0.55	1.02	15.84	0.57
Data 85	24.51	0.36	0.56	1.02	15.80	0.580
Data 84	23.95	0.40	0.63	0.98	15.97	0.55
Data 83	24.25	0.39	0.61	0.98	16.01	0.57

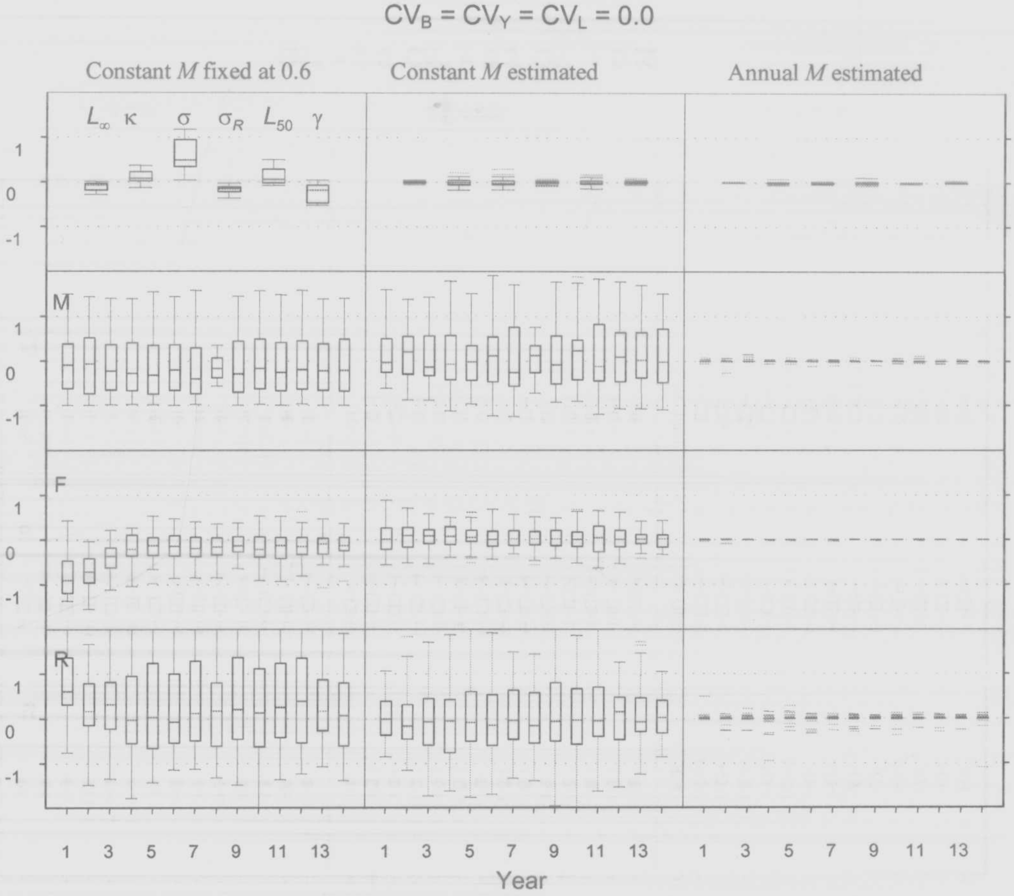

Figure 2.1. Boxplots of bias ratios of estimated to true values for the specified parameters (L_∞, κ, σ, σ_R, γ , L_{50}, *M*, *F* and *R*) on a $\log_2$ scale for 3 *M* estimation approaches. Boxes illustrate the interquartile range (25 to 75% quantiles) of the ratios, lines outside the whiskers represent extreme individual ratios. Each column represents results from a different scenario. Rows 2 to 4 represent bias ratios for annual *M*, *F* and *R* estimates. There was no measurement errors for all three scenarios, and initial period parameters R', M' and F' were fixed at true constant values. Scenario 1 assumes one constant known *M* (0.6); scenario 2 estimates one constant *M*; scenario 3 estimates annual variations in *M*.

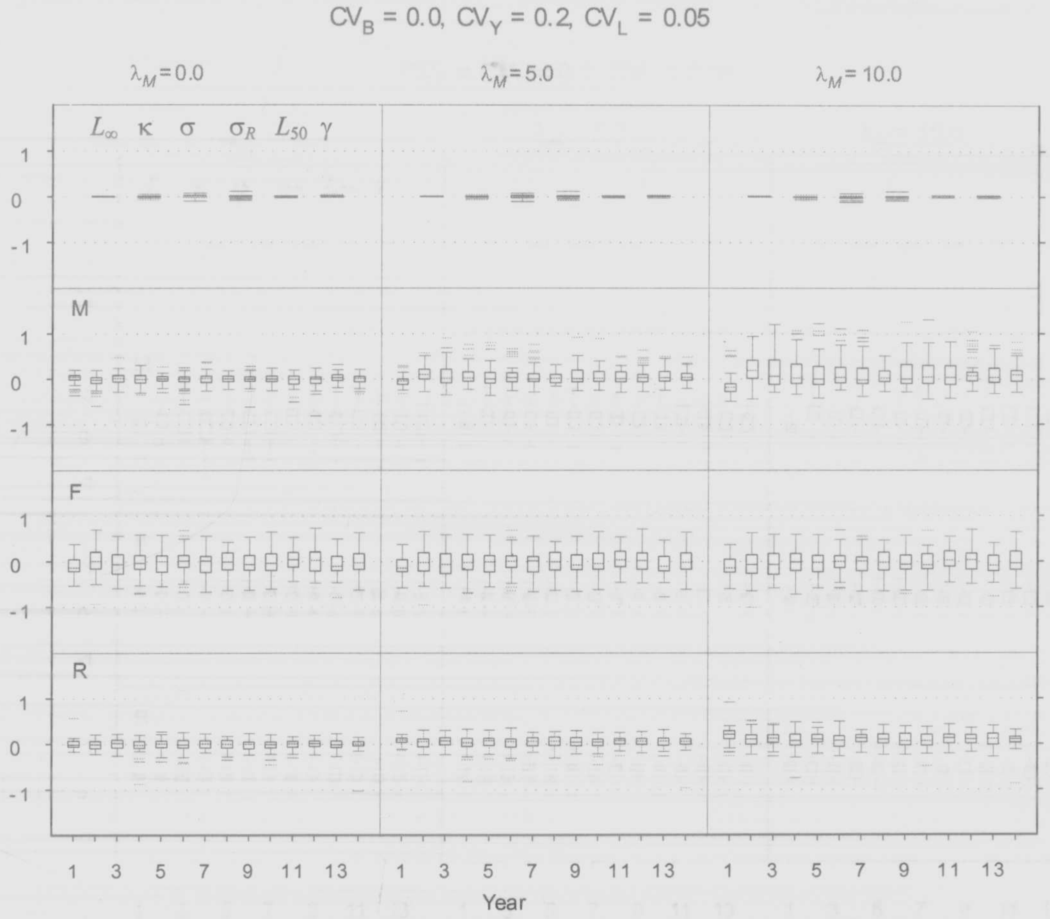

Figure 2.2. Boxplots of bias ratios for 3 λ_M weightings with no measurement error in biomass data. R', M' and F' were fixed at true constant values. CV for yield and length frequency data was 0.2 and 0.05, respectively. Scenarios 1, 2 and 3 used λ_M (penalty term for natural mortality variations) values of 0.0, 5.0 and 10.0, respectively.

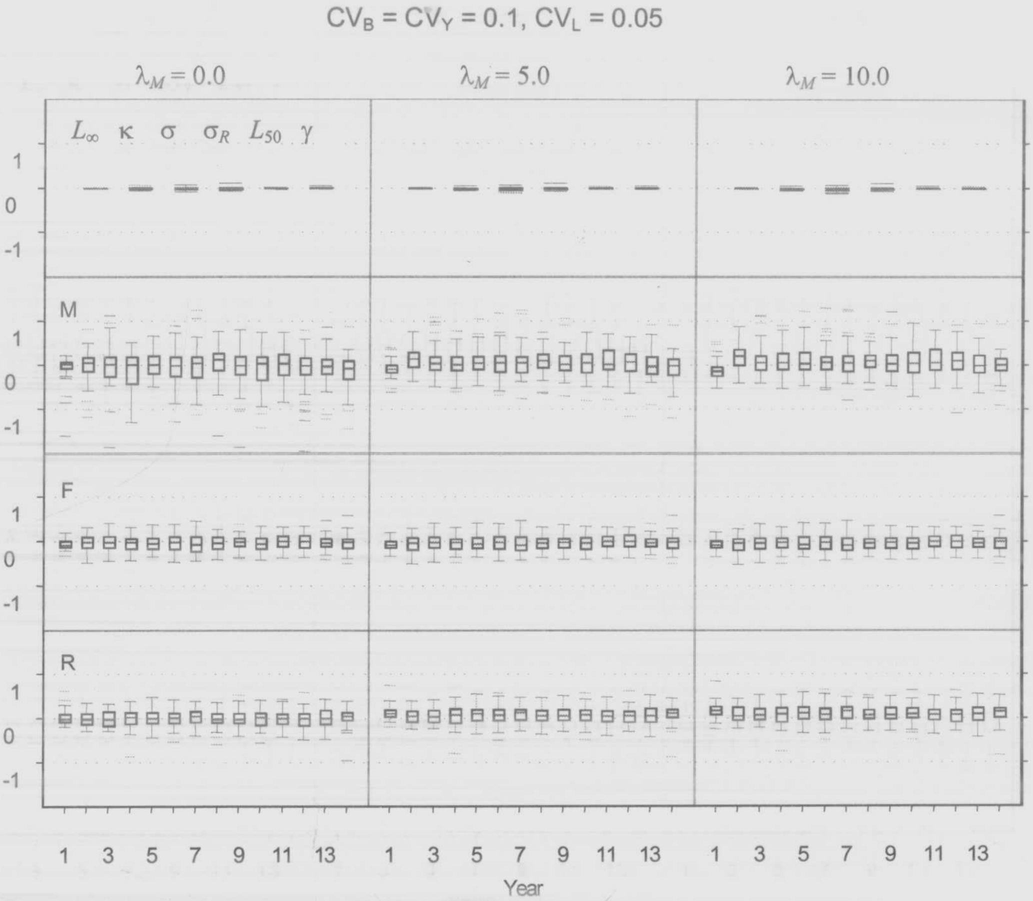

Figure 2.3. Boxplots of bias ratios for 3 λ_M weightings with measurement error in biomass data. R', M' and F' were fixed at true constant values. CVs for biomass, yield and length frequency data were 0.1, 0.1 and 0.05, respectively. Scenarios 1, 2 and 3 used λ_M (penalty term for natural mortality variations) values of 0.0, 5.0 and 10.0, respectively.

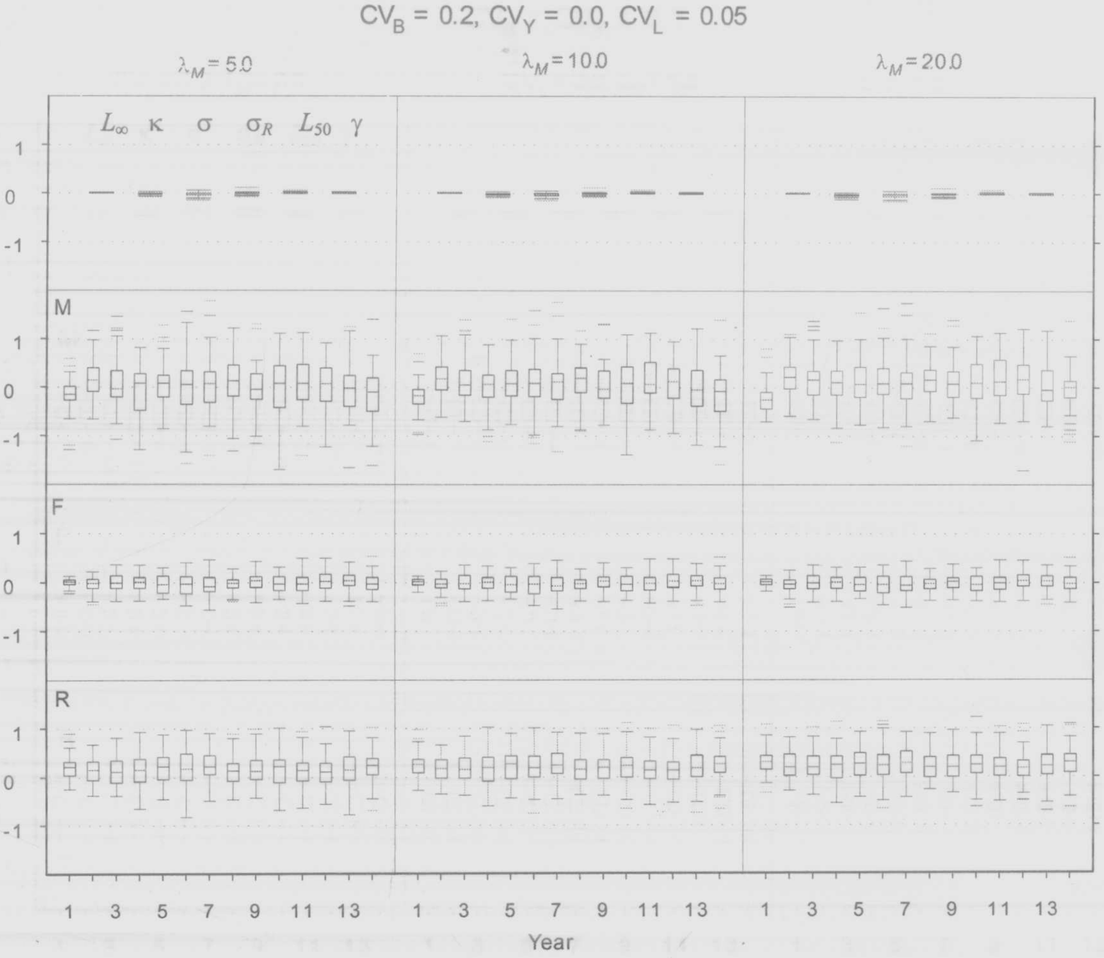

Figure 2.4. Boxplots of bias ratios for 3 λ_M weightings with no error in yield data. R', M' and F' were fixed at true constant values. CVs for biomass, yield and length frequency data were 0.2, 0.0 and 0.05, respectively. Scenarios 1, 2 and 3 used λ_M (penalty term for natural mortality variations) values of 5.0, 10.0 and 20.0, respectively.

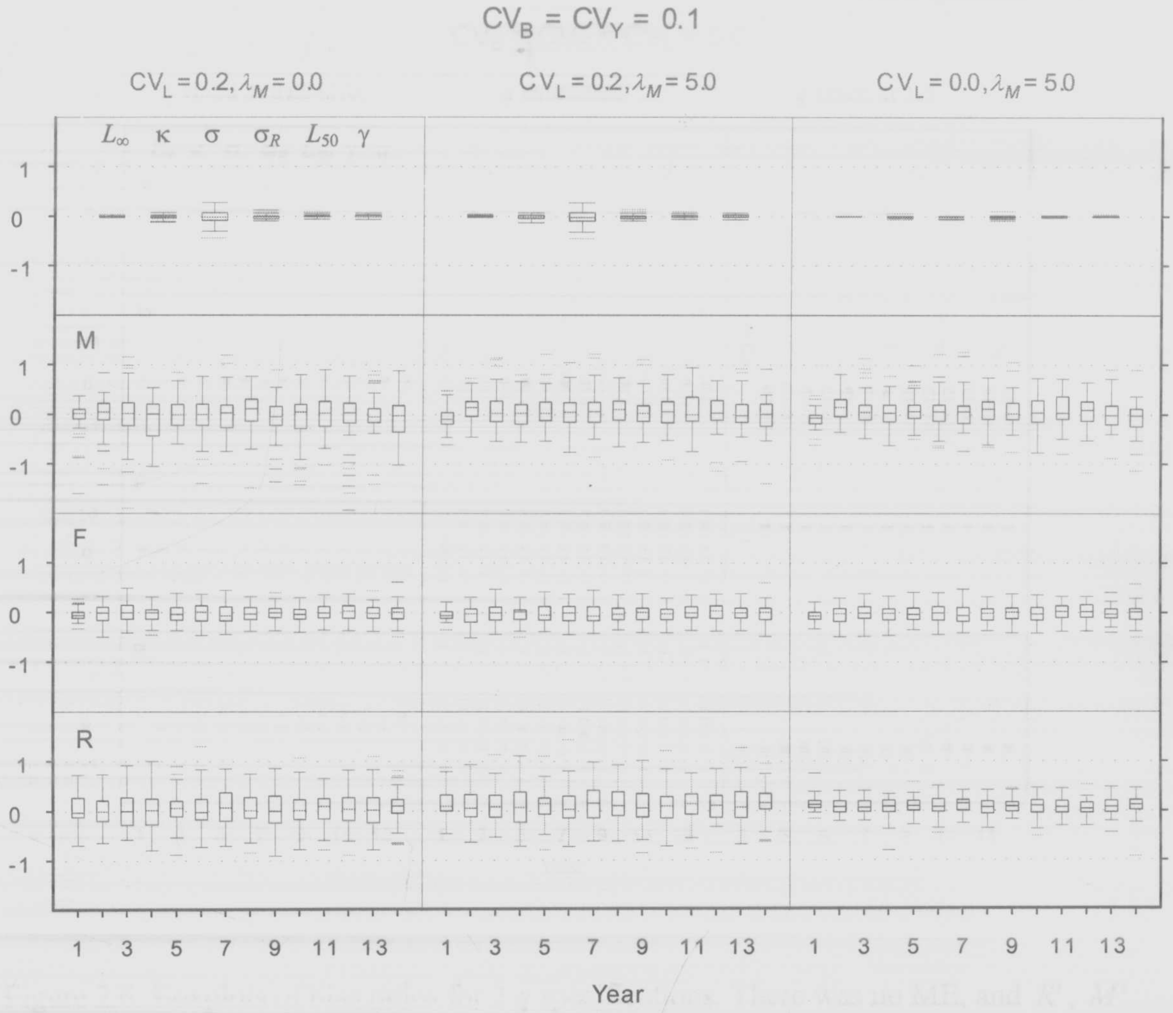

Figure 2.5. Boxplots of bias ratios for 3 combinations of CV for length frequency data and λ_M values. R', M' and F' were fixed at true constant values. CVs for biomass and yield were 0.1. CV for length frequency data was 0.2 for the first two scenarios with λ_M (penalty term for natural mortality variations) values of 0.0 and 5.0, respectively. Scenario 3 had no measurement error in length frequency data, and λ_M was 5.0.

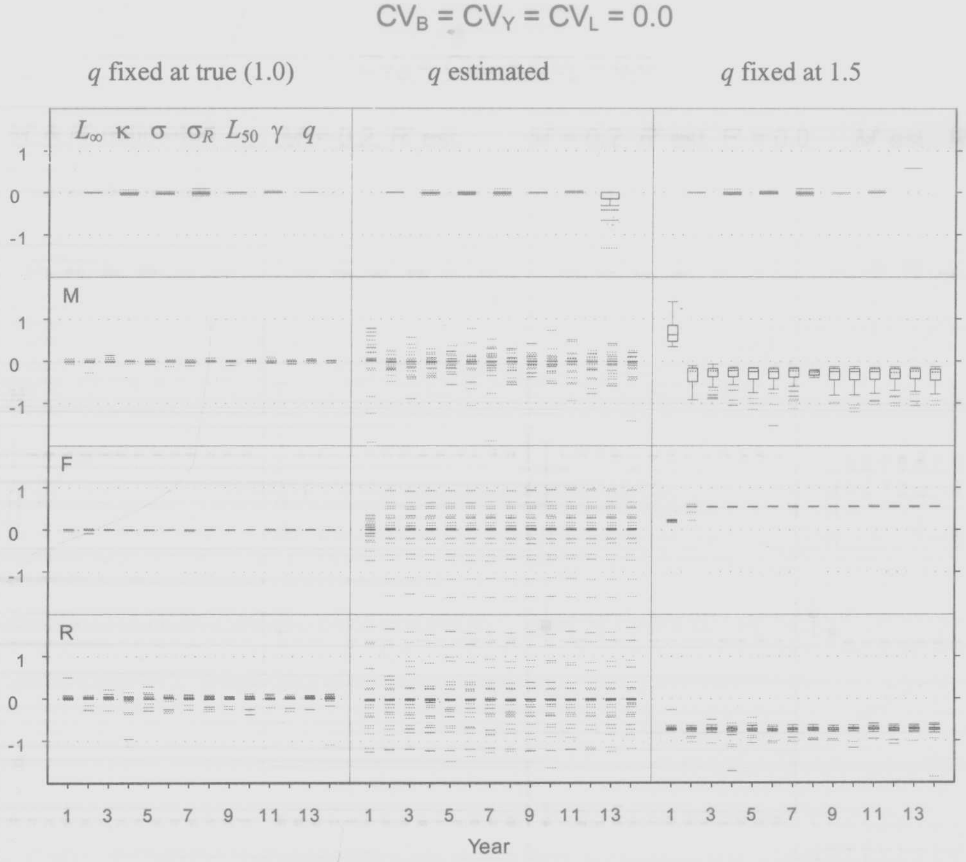

Figure 2.6. Boxplots of bias ratios for 3 q specifications. There was no ME, and R', M' and F' were fixed at true constant values. Scenario 1 fixed q at its true value (1.0); scenario 2 estimated q; scenario 3 specified q at 1.5.

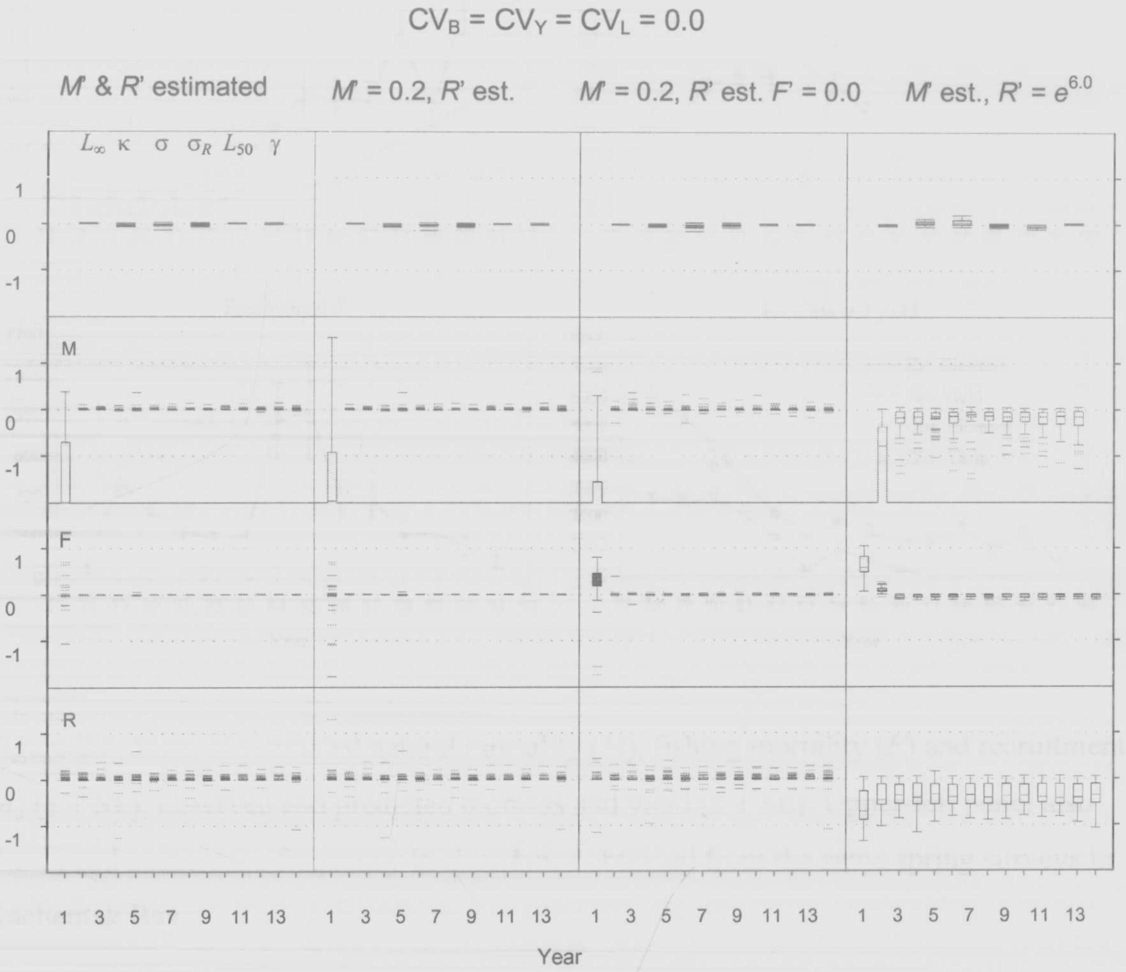

Figure 2.7. Boxplots of bias ratios for 4 specifications of *M* and *R* prior to data collection. There was no measurement error, and R' and M' varied over time, and F' was fixed at true constant value. Scenario 1 estimated each R' and M'; scenario 2 estimated each R', but fixed M' at 0.2; scenario 3 was the same as scenario 2, except that F' was specified at 0.0; scenario 4 estimated each M', but fixed R' at $e^{6.0}$.

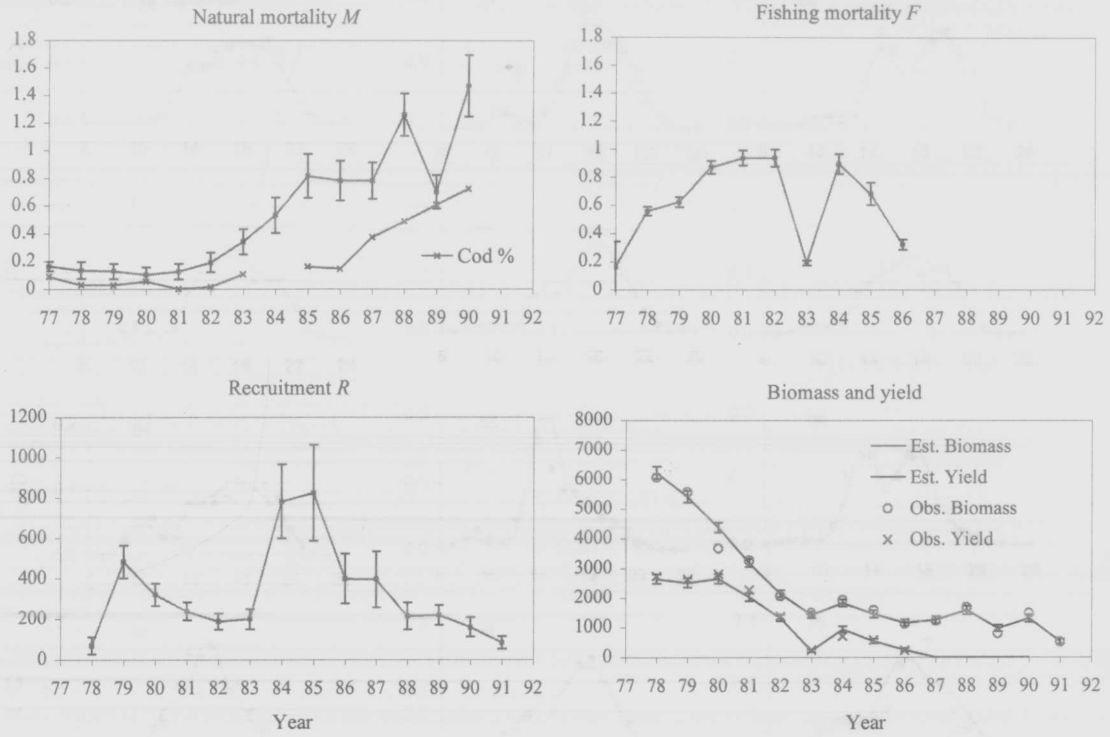

Figure 2.8. Plots of estimated natural mortality (*M*), fishing mortality (*F*) and recruitment (*R*) (± 1 SE), observed and predicted biomass and yield (± 1 SE). Upper-left panel also shows cod occurrence frequency in abundance obtained from the same spring surveys in Kachemak Bay.

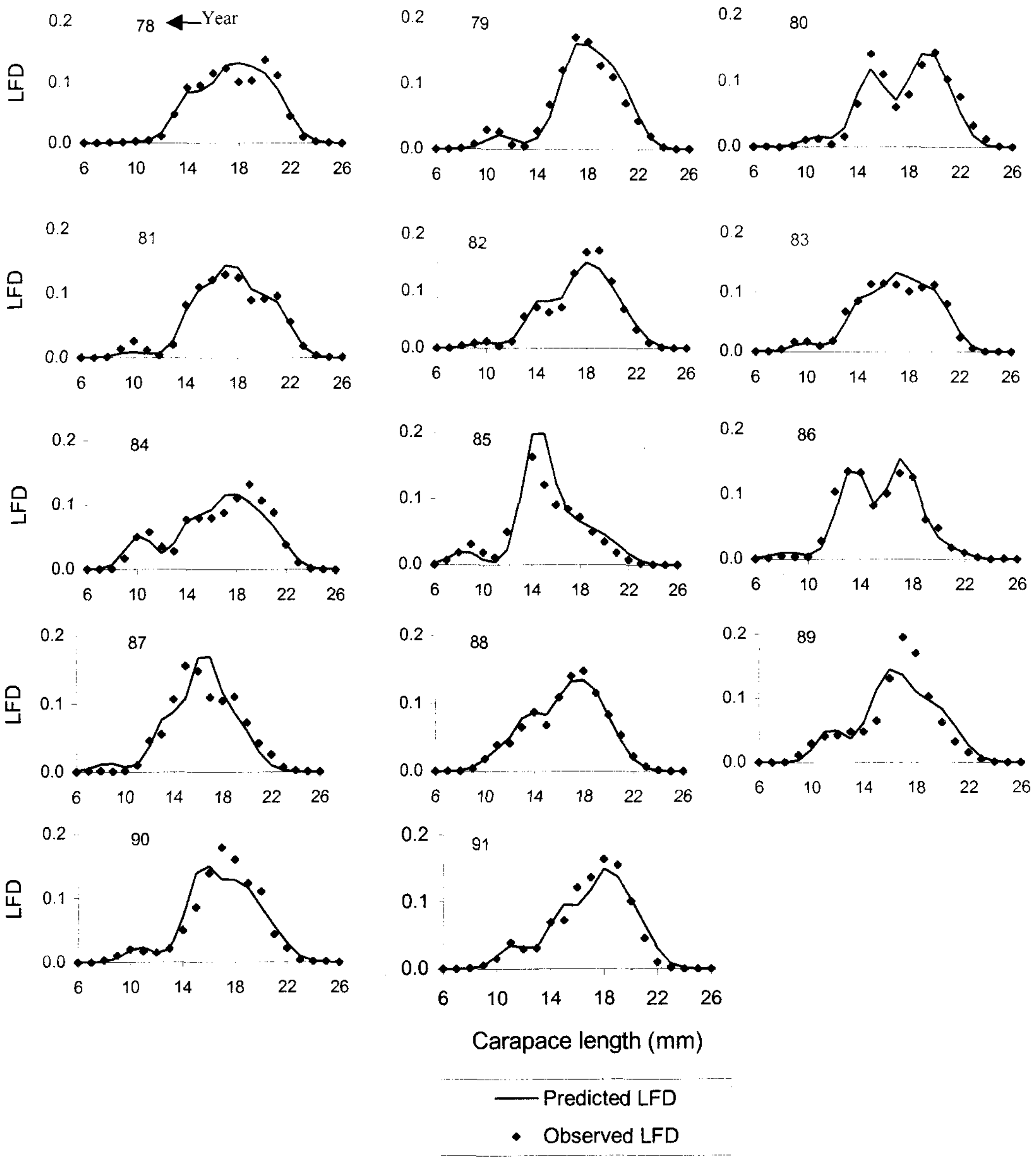

Figure 2.9. Comparisons of observed and predicted length frequency distributions (LFDs).

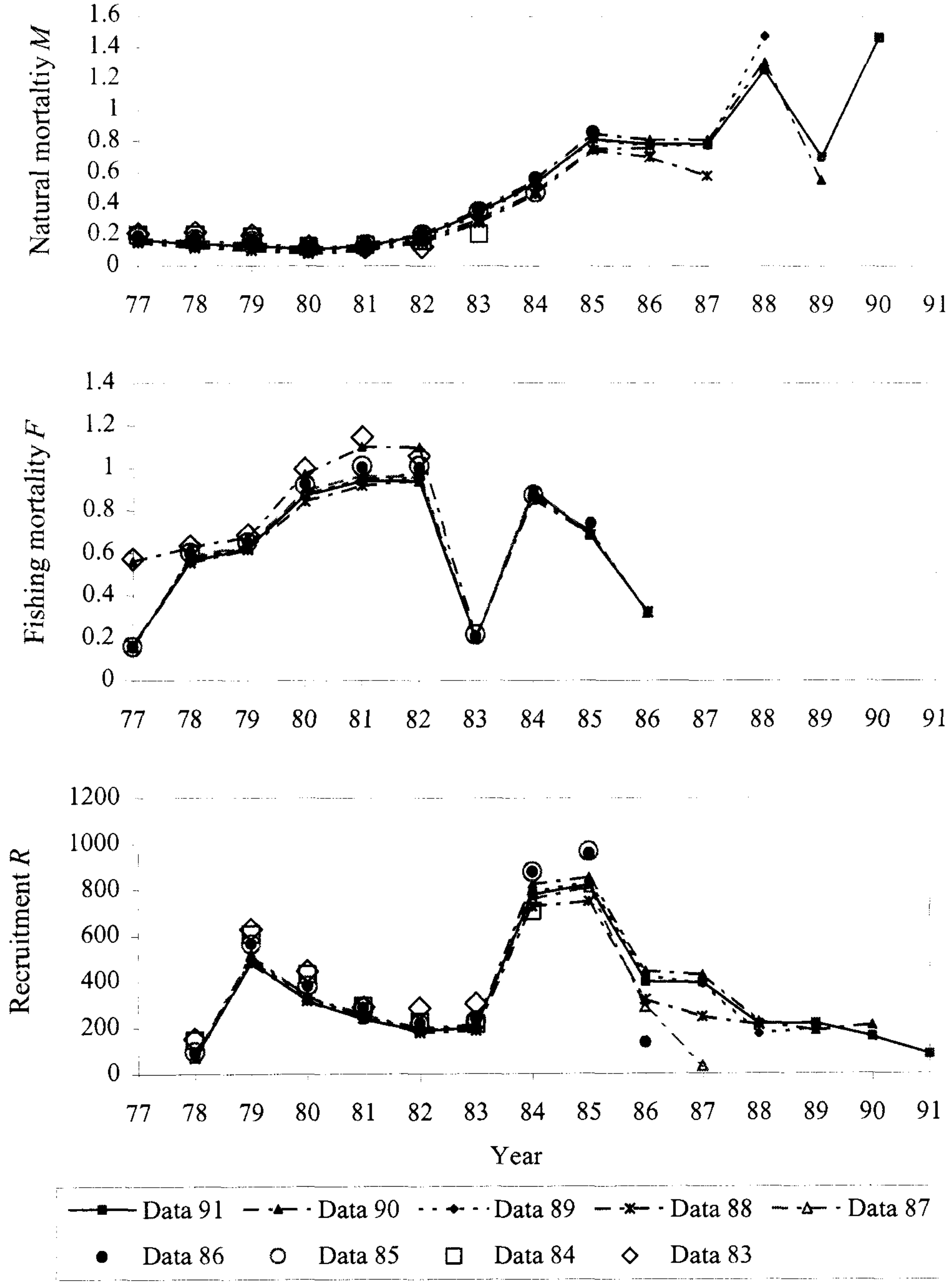

Figure 2.10. Comparisons of recruitment (*R*), natural mortality (*M*), and fishing mortality (*F*) estimates from the full data set and those with the last 1, 2, ···, 8 years' data removed, denoted respectively by data 91, data 90, data 89, ··· , data 83.

Chapter 3 Retrospective projection using Monte Carlo simulation: An application of a length-based model to Kachemak Bay northern shrimp[2]

ABSTRACT

Northern shrimp (*Pandalis borealis* Krøyer), the formerly abundant and commercially important species in Kachemak Bay, Alaska, declined in population abundance since the mid-1980's. No sign of population recovery has been detected in recent years. This paper is a retrospective look at what the risk to a population would have been under various levels of harvest rate, incorporating uncertainty in natural mortality and recruitment. A length-based population dynamics model was employed and Monte Carlo simulation was conducted to estimate the probabilities that various harvest strategies would have caused the shrimp population to fall below a threshold. Our results indicated that natural mortality was the most important factor controlling population dynamics, and the increasing trend in natural mortality in the 1980s resulted in the population collapse. Because the northern shrimp population had a very high background risk of extinction, all harvest strategies led to a similar population decline. More effort should be expended in studying the relationship between northern shrimp and its predators. The common assumption of constant natural mortality in stock assessment and population projection should be revisited for forage species like northern shrimp.

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[2] Fu, C., T. J. Quinn II, and M.D. Adkison. 1999. Retrospective projection using Monte Carlo simulation: An application of a length-based model to Kachemak Bay northern shrimp. *In* Ecosystem approaches for fisheries management. Alaska Sea Grant College Program Rep. No. 99-01, University of Alaska Fairbanks. pp. 59-77.

3.1 INTRODUCTION

Traditional fish stock assessment focuses on point estimates of population parameters such as recruitment and fishing intensity with a common assumption of constant and known natural mortality (Quinn and Deriso 1999). This assumption deserves greater attention in that it often leads to underestimation of uncertainty in population dynamics, and most importantly, in the risk of population collapse. Risk, according to Burgman et al. (1993), is the potential or probability of an adverse event, e. g., population abundance going below some defined level. For many fish populations there exist threshold levels below which the population will have difficulty to recover (Quinn et al. 1990, Zheng et al. 1993). This is especially true for some crustaceans such as northern shrimp, in which copulation is necessary in the reproduction process. Animal populations that live in a highly variable and unpredictable environment can go extinct even in the absence of human disturbance. This is termed the "Background Risk of Extinction" (Burgman et al. 1993). Human activities such as harvesting can increase this risk of extinction. The impacts on population dynamics from natural and fishing mortality should be translated into the language of risk for proper understanding.

Northern shrimp (*Pandalus borealis* Krøyer), also known as pink shrimp, was once a commercially important species in Kachemak Bay, constituting more than half of the harvests in the pandalid fishery (Davis 1982). While landings of pandalid shrimp from the otter trawl fisheries in Alaska have declined dramatically since the record high yield of 58600 metric tons (t) in 1976, trawl catches in Kachemak Bay were relatively constant from 1970 to 1983. However, the catch during 1983 decreased by almost 10 times from that in 1980 due to reduced population abundance. The fishery was closed after 1986 due to continued low stock size (Gustafson 1994) and has not reopened.

The depletion of pandalid shrimp populations in Alaska was synchronous with the collapses of many other crustacean stocks. After simultaneously examining historical data from several populations, Orensanz et al. (1998) concluded that the sequential patterns of rise-peak-demise in total catch shown by many crustacean fisheries in Alaska represented a serial depletion of resources. The serial depletion cannot be simply explained as a result of overfishing. Some lightly or seldom fished northern shrimp populations experienced similar population declines (Anderson 1991). As proposed in Orensanz et al. (1998), climate change may have reduced reproductive success and increased natural mortality.

The serial depletion of crustacean populations in Alaska regardless of fishing pressure underlines the necessity of seriously considering temporal variations in both recruitment and natural mortality. One of the purposes in this study is to understand what roles recruitment and natural mortality played in the collapse of northern shrimp population in Kachemak Bay using estimates of recruitment and natural mortality trends from a length-based model (Quinn et al. 1998) in conjunction with other assumptions. We also use retrospective analysis to examine how different harvest rates might have altered the population's fate. Monte Carlo simulation together with probabilistic risk analysis provide the essential tools for accomplishing these goals. This approach not only captures variability present in real population fluctuations but also presents results in terms of risks, which are useful in decision-making. Finally, we discuss the possibility of incorporating major environmental factors such as predator abundance into population projection and harvest recommendations.

3.2 METHODS

3.2.1 Data

For doing retrospective simulations, two components are important: i.e., parameters, some of which are random variables, and a model to describe the population in a mathematical language. To obtain population parameters, historical data need to be analyzed. Data utilized in this study come from the commercial fishery and research surveys. Annual commercial yield data from the shrimp fishery in Kachemak Bay between 1971 and 1986 were provided by the Alaska Department of Fish and Game (ADF&G). A trawl survey for pandalid shrimp in Kachemak Bay was initiated by the National Marine Fisheries Service (NMFS) in 1971, and continued once every year in May until 1974 using a 66-foot Nordby trawl net with assumed 50 percent net efficiency. From 1975 to 1990, the trawl survey was conducted twice every year (October and May) by ADF&G using 61-foot NMFS-designed net with assumed 100 percent net efficiency. Since 1991, the survey has been conducted only once every two years in May due to a depressed shrimp population. Data available from spring surveys include biomass estimates from 1971 to 1991 and length frequency data during the same period, with data missing from 1975 to 1977. For the purpose of doing simulations, we arbitrarily filled in length frequencies from 1975 to 1977 using those observed from 1971 to 1973, respectively, simply to stabilize the parameter estimation. Survey data after 1991 are not yet available due to processing lags. During fall surveys (mid-October), females are nearly 100% ovigerous, which makes identifying sex easy. Female proportion at length was therefore calculated from length frequency data obtained in fall surveys.

3.2.2 Model and parameter estimation

A length-based age-structured population model (Quinn et al. 1998) was applied to the population to obtain parameter estimates. This model follows individual cohorts through time and has flexibility to incorporate general forms of selectivity and natural mortality (Appendix 2). Parameter estimation was accomplished by using the software Autodif Model Builder (ADMB) which estimates parameters in a step by step fashion, known as a multi-phase procedure (Fournier 1996). Parameters estimated include growth parameters: L_∞, κ, σ, σ_r and mean length at recruitment $\mu_{r,t}$; annual recruitment to the population R_t at age r, and α, β and ϕ in the spawner-recruitment (S-R) relationship (described in Appendix 2); full recruitment fishing mortality F_t and selectivity parameters γ and L_{50}; and natural mortality M_t. Interannual variation of M_t was modeled as a time series structure of a random walk: $\ln(M_t) = \ln(M_{t-1}) + \delta_t$, where δ_t is a normal error term. The initial value of natural mortality was set at 0.2 per year for 1970, which gives a better fit than larger values. Parameters were estimated by minimizing an objective function (Appendix 2).

3.2.3 Retrospective projection procedure

3.2.3.1 Examining the impact of M and R

To reduce the complexity of the retrospective projection procedure, we only took account of the uncertainties in recruitment and post-recruitment natural death. All other parameters were fixed at the estimated values from the parameter estimation procedure. Temporal variations in both recruitment (R) and natural mortality (M) were simulated with log-normal error: $\Theta' = \Theta \cdot e^{cv(\Theta) \cdot Z}$, where Θ' is the random value of M or R, Θ is the deterministic value, and $Z \sim N(0,1)$.

To carry out the projection, we employed three ways of generating a deterministic M for each year. First, because traditional methods of stock assessment and population projection often make the assumption of a constant and known survival rate over time, we first investigated the validity of this assumption and its effect on the population analyses. The constant mean was assumed to be 0.2 per year. Second, the estimates of M from the model were simulated using lognormal errors with the same coefficient of variation (CV) across years of 30%. Third, a linearly increasing trend in M was also imposed for years between 1980 and 1990 together with a constant M of 0.2 per year for the years before 1980. Parameters for this linear function were obtained from a linear regression of estimated M for years between 1980 and 1990 versus year so that the linear function would approximate the estimated M. The intercept and slope were -10.559 and 0.134, respectively.

Temporal variation in R has been the focus of considering uncertainties in population projections (Francis 1992). Four ways were used to generate deterministic recruitment for the projections. Because the Beverton-Holt (B-H) model with autocorrelated errors fitted the estimated recruitment best, this relationship was first considered for projecting. The S-R parameters were obtained from the parameter estimation procedure (Table 3.1). Second, because density independent S-R models are more conservative and therefore desirable when the population level is low (Ferson 1993), a linear increasing function of spawners and recruitment with autocorrelation ($\phi = 0.35$) was also applied. The slope for the linear *S-R* function was estimated to be 0.228 by linearly regressing the estimated *R* versus *S* through the origin. Third, the common assumption of constant *R* was considered with the constant mean calculated as the average value of the estimated *R*. Fourth, for gaining a better understanding of recruitment impact on population dynamics, the estimated values of *R* were utilized. The CV for *R* was chosen as 20%, which was close to the average CV of 12% estimated from the model.

Combinations of each *M* and *R* model gave rise to 12 scenarios. For these 12 scenarios, annual *F* was fixed at the estimated values from the model in order to examine the effects on projection of uncertainties in *M* and recruitment *R*. Each scenario used the same random seeds, and 5000 replicates were implemented.

Projection was initiated using the estimated abundance at ages and lengths in 1971 from the parameter estimation procedure and continued through 1991, covering the period when historical survey indices for biomass were available. The projection procedure produced estimates of population biomass, yield, and probabilities of going below the quasi-extinction threshold level (Ferson et al. 1989) over years. The quasi-extinction threshold level was arbitrarily defined as 10% of the maximum historical biomass from the surveys.

3.2.3.2 Evaluating harvest strategies

To examine how alternative fishery management actions might have affected on the northern shrimp population, nine different harvest strategies relative to the estimated instantaneous fishing mortality (F_{est}) for each year were investigated. They were 0, $0.25F_{est}$, $0.5F_{est}$, $0.75F_{est}$, F_{est}, $1.5F_{est}$, and F_{est} with earlier fishery closures in 1980, 1982 and 1984.

For these analyses, the scenario with the estimated *M* and a B-H spawner-recruitment relationship was employed. The comparison criteria among various harvest strategies were cumulative yield over the entire fishing period and the risk of quasi-extinction in years 1987, when fishery was closed, and 1991, the last year when survey data were available.

3.3 RESULTS

3.3.1 Model parameter estimation

Estimated scalar parameters had relatively small CVs except for the *S-R* relationship parameters (Table 3.1). Estimated recruitment displayed a dramatic drop in 1978 and stayed relatively low until a peak occurred in years 1984 and 1985 (Figure 3.1). Field observations indicated a rebound of biomass in 1985 and 1986, but mainly with small male shrimp (Gustafson 1994) which is in concordance with our recruitment estimates. No strong spawner-recruitment relationship was discernable (Figure 3.2). In some years, low spawner biomass resulted in high recruitment, for instance, 1984 and 1985, while in some other years, such as 1978 and 1981, spawner biomass of median size produced low recruitment. Anderson (1991) found with a northern shrimp population in Pavlof Bay that a relatively small spawning stock may give rise to a outstandingly large year-class in some years with the majority of years conforming to a Ricker relationship. For our estimated spawners and recruitment, the B-H model with autocorrelation resulted in a better fit.

The estimates of M displayed an increasing trend, which started in 1980 (Figure 3.3). In accord with the change in M over time, there was an increasing trend in the relative abundance of Pacific cod, considered to be the major predator, in the late 1980s and through the 1990s (Bechtol 1997). The mean frequencies of occurrence for Pacific cod, calculated as the percentage of tows containing this species, were obtained during the shrimp trawl surveys in Kachemak Bay (Bechtol 1997). In contrast, estimated F was relatively stable except for that in 1983, when the fishery was partially closed, and in 1986, the last year with a fishery operation.

The overall fit of biomass and yield from the parameter estimation procedure was good after 1979. However, there were some discrepancies between the predicted and observed values in the 1970s (Figure 3.4), which might partially be due to the missing length frequency data from 1975 to 1977.

3.3.2 Comparison of projections with different models of *M* and *R*

Monte Carlo simulations produced 5000 replicates from which statistical summaries and the probabilities of extreme events were drawn. We used the scenario with the estimated *M* and *R* to illustrate the possible ways of summarizing results. Although each individual trajectory from the 5000 replicates has a different path, 50% of the projected biomass values fall into the range between the 25th and 75th percentiles (Figure 3.5). This range followed the pattern of the observed biomass trend. The mean line of the trajectories appeared to be a good representation of observed biomass. Therefore, we chose the trajectory mean to demonstrate the impact of *M* and *R* models on population projections.

Comparisons were made among the *R* models with each set of *M*. With constant *M,* the trajectory means were driven by the fluctuations in *R* and *F*. No matter what recruitment scenario was examined, there were big discrepancies between the projections and the observations after 1983 when *F* began to decrease, and they got particularly larger after 1986, when the fishery was completely closed (Figure 3.6). This discrepancy between the observed decline in biomass and a projected increasing trend in biomass indicated that *M* was greatly understated in the 1980s with the constant *M* model. Additionally, there was one biomass peak in 1976 when the estimated *R* was used. The estimated positive *R* anomalies in 1972, 1973 and 1975 created this large biomass peak that had not been counteracted by the higher *M* values throughout the early 1970s in the estimation.

In contrast, when we used the estimated *M* values as the deterministic mean, all *R* models resulted in a population decline similar to what was actually observed (Figure 3.7). The best projection came from the scenario with the estimated *R*. Once again the underestimation of biomass for years with peak biomass may have resulted from high recruitment anomalies. One prominent result from this exercise was that a constant *R* did not project the population any worse than the B-H or linear model did. Precise prediction of recruitment anomalies would help the projection, but for most years, recruitment predicted from general models is likely to be adequate.

The approximation of M to the estimated values by using a linearly increasing function resulted in projections consistent with the observed biomass values in the 1980s, similar to what were obtained from the scenario with the estimated M (Figure 3.8). The use of constant M before 1980 resulted in a similar biomass peak in 1975 that occurred in the constant M scenario. This also implies that the natural mortality must have had some increasing trend in the 1980s in order for the northern shrimp population to collapse. In conclusion, an increasing trend in M appears to be the most likely explanation of the decline of the northern shrimp population in Kachemak Bay. Recruitment did not seem to be as critical in this case.

3.3.3 Comparison of harvest strategies

Harvest strategies are commonly evaluated in terms of fishery or economic gain and their impact on the exploited populations as well. We compared the consequences of different harvest strategies based on the scenario with the estimated M and B-H R. The best harvest level was 75% of the F_{est}, which resulted in not only the highest cumulative yield, but also a lower risk of quasi-extinction (dropping below 10% of the historical maximum biomass) compared with those under harvest levels of F_{est} or 1.5 F_{est} (Table 3.2).

The population had a high background risk of quasi-extinction in 1991 (56%). The risk of quasi-extinction in 1991 became larger as fishing mortality got higher or the fishery closure was implemented later. Nevertheless, the difference among the different harvest strategies was not large in terms of the risk of quasi-extinction. The risk curves of going below various biomass levels under fishing mortality of F_{est} and no fishing mortality had great similarity (Figure 3.9), which implies that the population decline was unavoidable.

The projected mean biomass under no fishing mortality got extremely high during the early 1980s (Figure 3.10). However, there was a dramatic decline after that peak, which brought the population down to a similar level as that observed. A fishery closure in 1980 temporarily brought the population to a very high level (Figure 3.11), which was also followed by a dramatic decline. Overall, it appears that the fate of the northern shrimp population to collapse could not have been altered by lessening fishing or executing earlier fishery closures.

3.4 DISCUSSION

There is an obvious increasing trend in the estimated M values for the 1980s. A major part of M for forage species may come from predation mortality. The dramatic increase in the abundance of shrimp predators, such as Pacific cod (*Gadus macrocephalus*) and walleye pollock (*Theragra chalcogramma*), may have directly resulted in the increase in shrimp natural death in Kachemak Bay. Owing to the high correlation between natural mortality of forage species and their predator abundance, the temporal variation in M is likely to be more visible and therefore easier to study than that in R, which is generally driven by many physical environmental factors. This study leads us to conclude that more effort is desirable to investigate dynamics of predator populations to obtain more realistic population analyses and projections for forage species. Applying this conclusion to other northern shrimp populations, particularly those that are still under commercial fishing, study of M is important. Models incorporating the relationship between M and the abundance of predators should be helpful for projecting the dynamics of forage species.

In addition to predation, temperature was found to be closely related to the dynamics of several pandalid shrimp populations (e.g., Apollonio et al. 1986; Anderson 1999). The rapid increase in population size in the mid-1960s in the Gulf of Maine was preceded by a drop of 3^0C in mean annual sea surface temperatures in the late 1950s (Apollonio et al. 1986). The association between northern shrimp abundance and seawater temperature was used for abundance forecasting in the Gulf of Maine (e.g., Dow 1966). Pandalid shrimp surveys conducted from 1953 to 1999 in the Gulf of Alaska in conjunction with the record of local environmental changes showed that proportion of shrimp in survey catches was negatively correlated with water column temperature (Anderson 1999). Temperature affects northern shrimp embryonic development (Nunes 1984; Bergström 1991), larval growth and mortality (Nunes 1984; Rasmussen and Tande 1995), and adult general biology, such as growth, distribution, reproduction and mortality (Apollonio et al.

1986). Modeling the linkage between physical factors such as temperature and *M* or *R* will also be beneficial for projecting the population dynamics.

Comparing the dynamics of northern shrimp stocks in the Gulf of Maine, on the Scotian and Newfoundland Shelves (Canada), Koeller (1999) hypothesized that temperatures were more important than predators in regulating southern shrimp stocks, and vice versa in northern stocks. Later, Koeller (1999) concluded that stock assessments should flag any concurrent increase in predation, temperatures and fishing effort since they could lead to rapid population decrease and stock collapse. Similarly, the dynamics of pandalid shrimp stocks in the Gulf of Alaska were regulated by both bottom-up temperature and top-down predator effects (Anderson and Piatt 1999). Anderson (1991) expressed the view that the dynamics of northern shrimp was predominantly controlled by strong year-classes.

Further retrospective simulations will also be needed with respect to sensitivity of results to data uncertainty. The missing length frequency data for years 1975 to 1977, data that were filled arbitrarily with those from 1971 to 1973 may have biased the parameter estimates and consequently the simulations. Another important uncertainty lies in the assumed survey calibration coefficient (q) of 1.0 in the parameter estimation. Since q is negatively correlated with the estimates of *M* and *R* (Fu and Quinn in review; Chapter 2), overestimation of q could have resulted in underestimation of *M* and *R*. There may also exist potential bias related to the NMFS survey assuming 50% net efficiency and that of the ADF&G assuming 100%. Fortunately, it would not affect biomass estimates in the 1980s that were of interest. In addition, the major distribution of northern shrimp, particularly that of young shrimp, shifted from all of Kachemak Bay to east of Homer Spit only as the population declined (Gustafson 1994). Change in spatial distribution may have induced changes in q and availability of shrimp over time, which may also have biased the estimates of *M* and *R*. We propose a hypothesis that the redistribution of young shrimp in the east of Homer Spit increased the relative proportion of young shrimp in the survey, which consequently overestimated *R* and *M* in the late 1980s. Therefore, it is also possible that recruitment failure also played an important role in the population collapse, as proposed by Anderson (1999) for the pandalid shrimp stocks in the Gulf of Alaska. Overall, retrospective simulations with these uncertainties incorporated could provide more insight into the collapse of the northern shrimp population in Kachemak Bay.

Table 3.1. Estimates and coefficients of variation (CVs) of scalar parameters of spawner-recruitment relationship (α, β, ϕ), growth function (L_∞, κ, σ, σ_r), and selectivity curve (L_{50}, γ).

Parameters	Estimates	CV
α	1.826	73.87%
β	0.002	90.11%
ϕ	0.267	34.15%
L_∞	24.698	0.36%
κ	0.367	1.06%
σ	0.529	2.20%
σ_r	1.127	0.88%
L_{50}	16.720	0.58%
γ	0.572	0.66%

Table 3.2. Projected total yield and risk of quasi-extinction using estimated M and B-H R.

Scenario	F	Total Yield	1987 Risk[1]	1991 Risk
1	0	0.0	5.38%	56.02%
2	0.25 F_{est}	31.66	11.90%	60.22%
3	0.5 F_{est}	43.14	24.58%	75.26%
4	0.75 F_{est}	45.90	43.04%	71.68%
5	F_{est}	44.86	66.40%	78.34%
6	1.5 F_{est}	38.95	96.68%	89.84%
7	Closure 1980	31.60	6.90%	57.08%
8	Closure 1982	39.64	11.32%	60.88%
9	Closure 1984	43.19	25.08%	67.74%

[1] Risk is measured by the percentage of simulations in which biomass is less than 10% of the historical maximum.

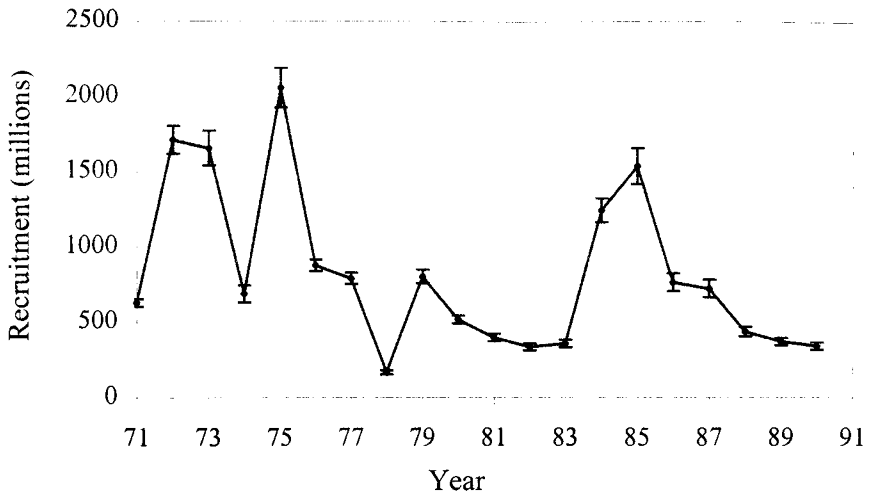

Figure 3.1. Estimated recruitment in number (± 1 SE) to the *P. borealis* population in Kachemak Bay at age 1.

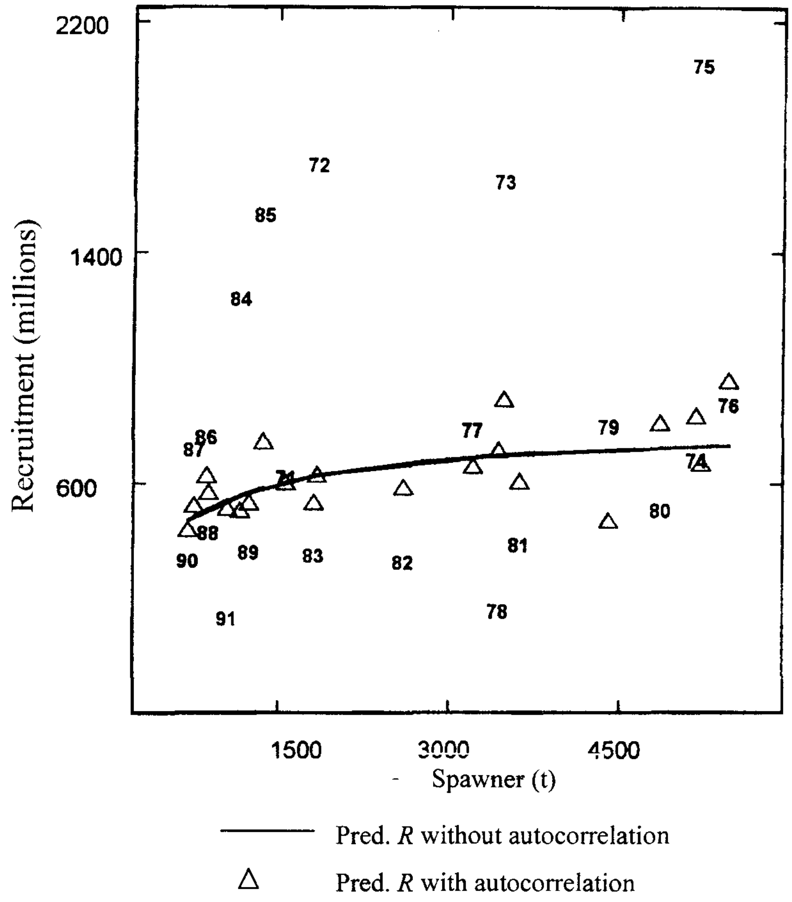

Figure 3.2. Fits of estimated recruitment in number versus spawner biomass using the Beverton-Holt (B-H) S-R model with and without autocorrelation.

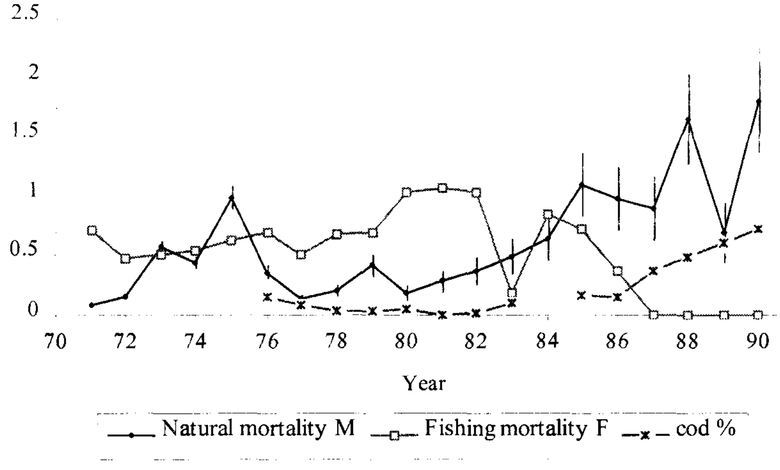

Figure 3.3. Estimated instantaneous natural mortality (± 1 SE) from 1970 to 1990, fishing mortality estimates from 1970 to 1986 from the length-based model, and relative frequencies of occurrence of Pacific cod obtained from the same shrimp trawl surveys.

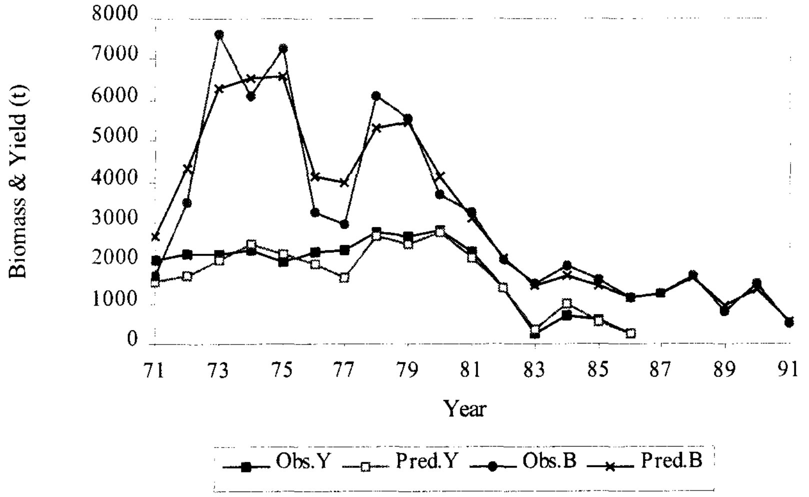

Figure 3.4. Comparisons between observed and predicted biomass and yield from the length-based model.

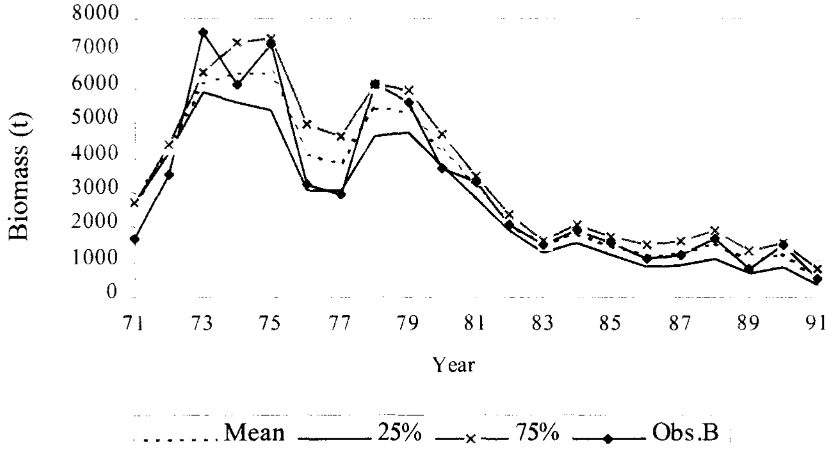

Figure 3.5. Projected biomass at the mean level, 25th and 75th percentile from the scenario with estimated instantaneous natural mortality and recruitment along with observed biomass estimates.

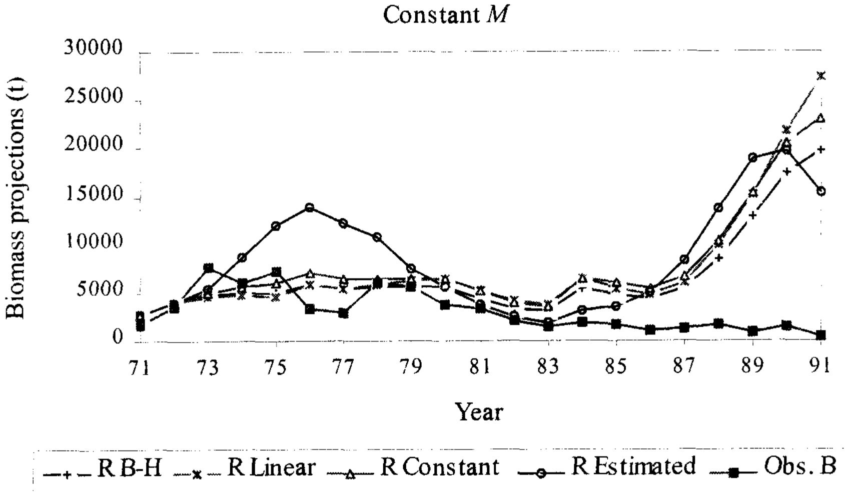

Figure 3.6. Comparisons of biomass projections among four recruitment models: B-H R, linear R, constant R and estimated R using constant natural mortality.

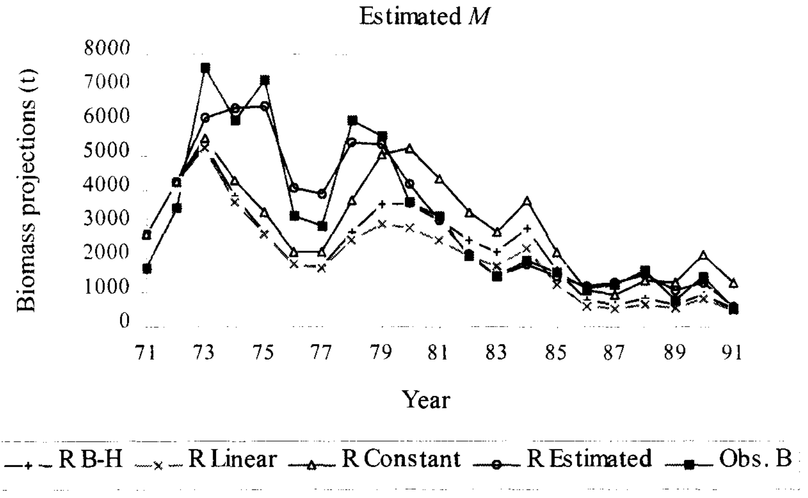

Figure 3.7. Comparisons of biomass projections among four recruitment models: B-H *R*, linear *R*, constant *R* and estimated *R* using estimated natural mortality.

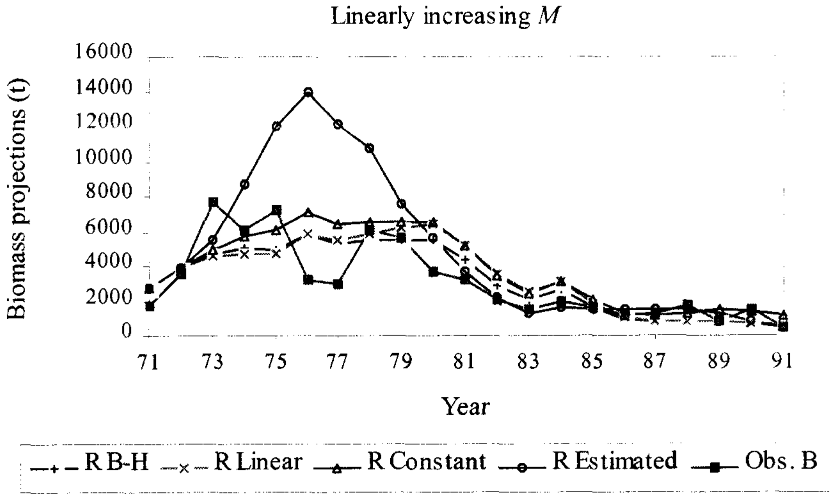

Figure 3.8. Comparisons of biomass projections among four recruitment models: B-H *R*, linear *R*, constant *R* and estimated *R* using constant natural mortality before 1980, and a linearly increasing function for years after 1980.

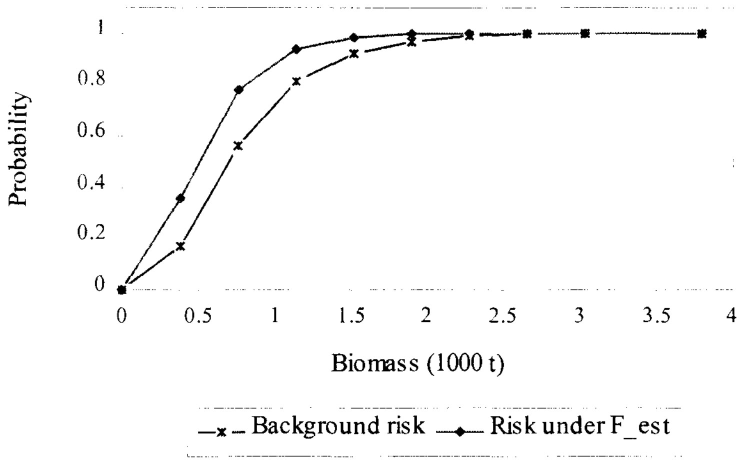

Figure 3.9. Comparisons between the background risk of biomass going below various levels and the risk when fishing at level F_{est}, using the scenario with the estimated M and predicted recruitment from B-H model with autocorrelation in 1991.

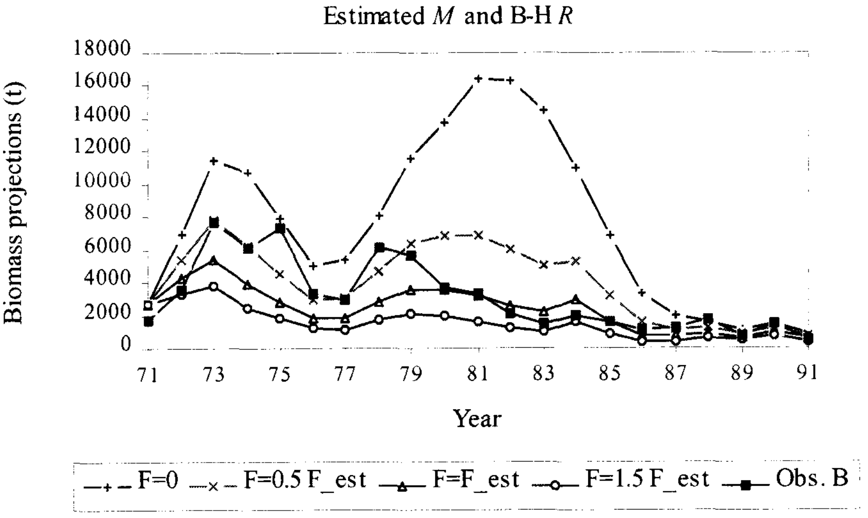

Figure 3.10. Comparisons of biomass projections under fishing mortality $F = 0$, 0.5 F_{est}, F_{est}, and 1.5 F_{est} using the scenario with estimated natural mortality and predicted recruitment from B-H model with autocorrelation.

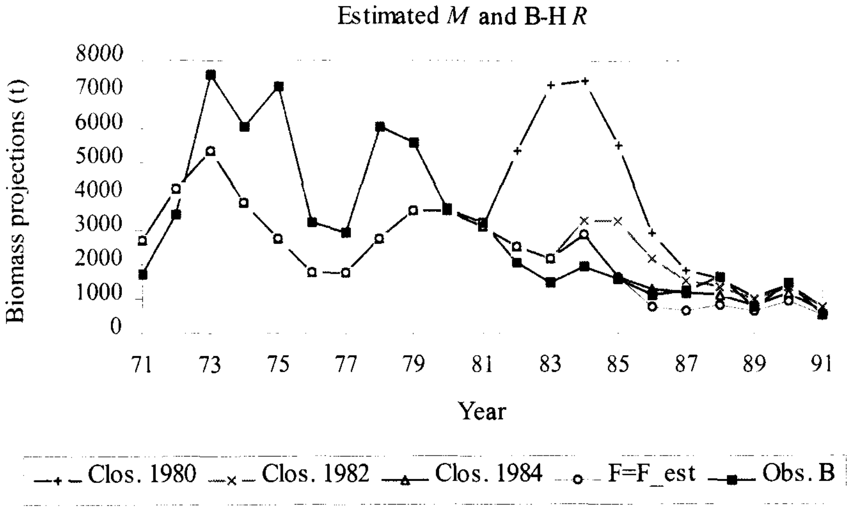

Figure 3.11. Comparisons of biomass projections under fishery closure in years 1980, 1982 and 1984 using the scenario with estimated natural mortality and predicted recruitment from B-H model with autocorrelation.

Chapter 4 Analyses of harvest strategies for pandalid shrimp populations[3]

ABSTRACT

In general, dynamics of a population are governed by natural mortality (*M*) and a spawner-recruit (S-R) relationship, yet conventional fisheries management is often based on the assumptions of constant *M* and recruitment (*R*). To compare the performance of several harvest strategies under conditions similar to the northern shrimp population in Kachemak Bay, increasing *M* and Beverton-Holt (B-H) *R* were simulated in addition to the scenarios of constant *M* or *R*. Harvest was simulated with 6 levels of constant instantaneous fishing mortality (0.0 to 1.5) and 3 levels of threshold (0 to 40% of virgin spawning stock biomass, SSB_0). With constant $M \leq 0.4$ or constant *R*, threshold management, i.e., closing the fishery at a low population level, was unnecessary under optimal harvesting. However, for a population with B-H *R*, threshold management was essential to reduce the risk of population extinction.

In light of the importance of the *M* and S-R relationships, guideline harvest levels were set in simulations with *M* and *R* thought to be higher than, lower than, or equal to their true levels. Survey sampling was assumed to occur once every 1 to 3 years. Specification of *M* too low resulted in higher cumulative yield and risk of falling below threshold regardless of sampling frequency. But more frequent sampling helped reduce this risk. On the other hand, misspecification of *R* had very little effect on forecasting population abundance if the population was sampled annually. Less frequent sampling induced higher risk of falling below threshold if *R* was specified too high, but it had little effect if *R* was specified too low. In conclusion, frequent sampling and good understanding of *M* are most important for sound management of shrimp fisheries.

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[3] Fu, C., T.J. Quinn, II, and G.H.Kruse. In review. Analyses of harvest strategies for pandalid shrimp populations. Journal of Northwest Atlantic Fishery Science.

4.1 INTRODUCTION

Patterns of recruitment, maturity and growth affect optimal harvest strategies (Clark 1991), and harvest strategies should be explored on a species basis rather than relying on general results (Sigler and Fujioka 1993). Therefore, in this paper, we examined harvest strategies for northern shrimp (*Pandalus borealis* Krøyer) based on population parameters and features of recruitment and natural mortality obtained for the Kachemak Bay, Alaska population (Chapter 3; Fu et al. 1999). Monte Carlo simulations with a length-based population model modified from Quinn et al. (1998) were employed to evaluate harvest strategies.

Northern shrimp in Kachemak Bay were harvested intermittently with small landings in the 1950s and 1960s (Davis 1982). Since 1971, annual trawl surveys have been carried out to obtain population biomass indices. Based on historic catch information and biomass surveys, a guideline harvest level (GHL) was set at 2270 t for years from 1971 to 1977 with an exception of 2500 t for the year 1972; the GHL increased to about 2700 t during the next three years (Davis 1982). Close to the guideline, catch in 1971 reached about 2000 t, and catches during the next few years remained near that level (Figure 4.1). There were significant increases in catches from 1978 to 1980 corresponding to the increases in GHLs. Ironically, catch declined sharply in 1982 despite the Alaska Board of Fisheries's conclusion that the stock appeared to be able to sustain the annual catch of 2270 t (Davis 1982). A low population biomass estimate from the survey resulted in partial closure of the fishery in 1983. The fishery was totally closed in the fall of 1986 due to continued low stock size (Gustafson 1994), and since then surveys have not indicated any stock recovery.

The decline of the northern shrimp population in Kachemak Bay seemed to be part of the serial depletion experienced by many other crustacean populations in Alaskan waters in the early 1980s, for instance red king crab on the continental shelf around Kodiak Island (Orensanz et al. 1998). Northern shrimp is a major diet source for Pacific cod (*Gadus macrocephalus*) (Albers and Anderson 1985). The consistently high level of cod and other groundfish populations since the early 1980s has probably prevented the northern shrimp population from recovering (Bechtol 1997). Annual recruitment (defined as age 1 shrimp) estimates from a length-based population were low during the late 1970s and early 1980s, but there was some rebound in the mid-1980s (Fu et al. 1999, Figure 4.1). On the other hand, estimated natural mortality from the same model displayed a sharp increasing trend since the early 1980s. Simulation of this population indicated that no alternative harvest policies could have altered the population's fate of collapse (Chapter 3; Fu et al. 1999).

However, natural mortality is commonly assumed constant over time when evaluating harvest strategies. In this paper, we specifically compared optimal harvest strategies under different assumptions about natural mortality to assess the potential impact of natural mortality on the population's response to exploitation. In addition, we also examined two types of recruitment variability in regard to management strategies.

The ultimate goal of analyzing harvest strategies is to define an optimal GHL to be established in advance of the fishery. The determination of optimal GHL is dependent on three major factors: recruitment, natural mortality, and present population status. The first two factors are beyond human control and are usually subject to high variation and uncertainty. Present population status can be assessed through a survey. Using simulations, we examined the effects of the mis-specification of natural mortality and recruitment on average yield and population sustainability under the assumption of perfect measure of population status. Our objective was not to develop optimal exploitation for specific situations, but rather to seek ways that the establishment of GHLs can be robust to uncertainties about natural mortality and recruitment.

4.2 METHODS

4.2.1 Length-based population model

The simulation for evaluating harvest strategies for pandalid shrimp is based on a length-based population model that follows each cohort throughout its life history (Quinn et al. 1998). The model follows the population from recruitment age, assuming that the length frequency at recruitment is a simple discrete normal distribution (N_D). The probability density function for the lengths x at recruiting age r and at the start of time t is:

$$f_{r,t}(x) \sim N_D(\mu_{r,t}, \sigma_r^2) = e^{-\frac{1}{2\sigma_r^2}(x-\mu_{r,t})^2} \Big/ \xi_{r,t}, \text{ where } \xi_{r,t} = \sum_x e^{-\frac{1}{2\sigma_r^2}(x-\mu_{r,t})^2}.$$

$\mu_{r,t}$ is the mean length at age r and time t, and σ_r is the deviation of the length frequency normal distribution at age r. The abundance of the newly recruited shrimp at length x is:

$$N_{r,t}(x) = N_{r,t} \cdot f_{r,t}(x).$$

The recruited shrimp and those at older ages are modeled to go through a growth and natural death process before they are subject to fishing. The standard von Bertalanffy growth model was used to express the growth pattern from one age to the next, assuming that growth is constant over time:

$$L_{a'} = L_\infty(1-\rho) + \rho L_a + \varepsilon,$$

where $\rho = e^{-\kappa}$ is the Brody coefficient, and $\varepsilon \sim N(0, \sigma^2)$. L_∞ is the asymptotic length, and κ is a curvature parameter, governing the speed to approach L_∞. Expected length after growth is then $\mu_{a',t+1} = L_\infty(1-\rho) + \rho\mu_{a,t}$, and the expected variance after growth is:

$$\sigma_{a'}^2 = \rho^2\sigma_a^2 + \sigma^2.$$

After growth, the relative distribution of lengths $p_{a',t'}(L)$ is:

$$p_{a',t'}(L) = \sum_x f_{a,t}(x) e^{-\frac{1}{2\sigma_{a'}^2}(L-\mu_{a',t+1}(x))^2}.$$

After growth and natural death during the specific time t period, the abundance $N_{a,t}(x)$ of age a shrimp at length x and at time t (starting at age r) becomes $N_{a',t'}(x)$:

$$N_{a',t'}(x) = N_{a,t}\, p_{a',t'}(x) e^{-M_t}.$$

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, natural death and fishing mortality is:

$$N_{a+1,t+1}(x) = N_{a',t'}(x) e^{-F_t s_x},$$

where s_x is the 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.

Catch at age a and during time t is: $C_{a,t}(x) = N_{a',t'}(x)(1-e^{-F_t s_x})$.

Population biomass and yield are obtained from the sum of abundance and catches across all ages multiplied by weight at length, which has a relation of $W_x = a_w x^{b_w}$. Exploitable biomass and yield are expressed as:

$$B_{t,x} = \sum_x \sum_a N_{a,t}(x) W_x S_x,$$

$$Y_{t,x} = \sum_x \sum_a C_{a,t}(x) W_x.$$

For simplicity, maturity is assumed as length-independent within the same age. Female spawning stock biomass (SSB) at time t is defined as:

$SSB_t = \omega_t \sum_x \sum_a \lambda_a N_{a,t}(x) W_x$, where ω_t is equal to 1.0 if the number of males exceeds that of females, otherwise ω_t is the sex ratio (male to female) in year t:

$$\omega_t = \frac{\sum_x \sum_{a=2} (1-\lambda_a) N_{a,t}(x) W_x}{\sum_x \sum_{a=2} \lambda_a N_{a,t}(x) W_x,}.$$

λ_a is the proportion of females at age a. Technically, northern shrimp do not "spawn" by dispersing reproductive products in the water, but instead they copulate and females carry embryos until hatching occurs. However, we liberally use the term SSB as a matter of convenience and convention with fish population dynamic models. We assume northern shrimp in Kachemak Bay are males at ages 2 to 3 and transform into females afterwards, i.e., $\lambda_2 = \lambda_3 = 0.0$ and $\lambda_4 = \lambda_5 = \lambda_6 = 1.0$.

4.2.2 Stochastic simulation

A population with a maximum age of 6 was simulated with parameters for a spawner-recruit relationship, growth, gear selectivity and the weight-at-length relationship being the same as those estimated for the northern shrimp population in Kachemak Bay, Alaska (Fu et al. 1999, Table 4.1). The simulation (1000 replications) started with an unexploited population at equilibrium that is harvested for the next 23 years, a period length equivalent to the period from 1978, when there was a climate regime shift (Albers and Anderson 1985), to 2000, the present year. The simulation model incorporated process errors associated with recruitment (*R*), natural mortality (*M*), and growth variability. Measurement errors in SSB were also incorporated, and the fishery was closed when the estimated SSB dropped below a threshold level (see Section 4.2.3). These errors were assumed to have a coefficient of variation (CV) of 20% based on the average historical variability for survey biomass estimates (Gustafson 1994). Fishing mortality was assumed to be implemented without error, so that the effects of misspecification in *R* and *M* could be better evaluated.

To investigate effects of harvest strategies on populations with different features, two models of *R* were examined: (1) constant expected *R* at the historical average value (608 million) and (2) a Beverton-Holt model with autocorrelated errors (simply called B-H):

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

where $\phi\varepsilon_{t-1}$ is the first-order autocorrelated error term, and $\upsilon_t \sim N(0,\sigma^2)$. Both *R* models included lognormal process errors with CV (= σ) of 50% (Figure 4.2). Growth variability is reflected in the mean length at recruitment ($\mu_{r,t}$), which has a normal distribution with mean of 9.0 mm and standard deviation of 1.0 mm. Similarly, two sets of *M* were used. Because *M* is commonly assumed to be constant for stock assessments and evaluations of management strategies, annual *M* was set at 0.4 with a lognormal variation (CV = 20%). To align with the actual *M* estimates from the Kachemak Bay northern shrimp stock, a second *M* model with a steadily increasing annual rate of 0.03 was employed (Figure 4.2), a rate that gave an average *M* level equal to that of the Kachemak Bay stock. Similarly, variation with a CV of 20% was imposed.

4.2.3 Comparisons of harvest and threshold levels

SSB has been used frequently as an indicator of stock size and population health. A level of 20% of pristine SSB (SSB_0) has been considered as a threshold for recruitment overfishing (Beddington and Cooke 1983; Quinn et al. 1990; Francis 1993; Thompson 1993). In addition to the common threshold of 20% of SSB_0, threshold levels of 0% (no threshold) and 40% of SSB_0 were also explored. Under threshold management, the fishery is closed when population level goes below its threshold.

We applied constant F ranging from 0.0 to 1.5. For each F level, annual average risk was calculated as the percentage of 1000 replicates in which the population fell below 20% of SSB_0. The optimal F was defined as the value that maximized yield while minimizing the risk of population decline, two contradictory objectives (Hollowed and Megrey 1993). Therefore the following objective function f was employed for obtaining the optimal F:

$$f = Max\left\{\frac{Y_F}{MaxY} - RISK_F\right\},$$

where Y_F is the cumulative yield over the 23 year simulation at a given F level averaged over the 1000 replicates; MaxY is the maximum among Y_F; and $RISK_F$ equals the average risk over the entire time period at a given F level. If a strategy produces maximum yield but always drives the population below 20% of SSB_0, then the objective function has a value of 0.0. The worst case has a value approaching -1.0 and the best case has a value approaching 1.0.

4.2.4 Sensitivity analyses

Simple sensitivity analyses with regard to gear selectivity parameters (L_{50} and γ) and female maturity at age 4 were conducted to examine their effect on the simulated population. The lowest and highest L_{50} values were set around the mean carapace length (mm) of shrimp at ages 2 and 4, respectively. The value of γ ranged from 0.4 to 1.2, representing a logistic curve with a flat to a deep slope. In these sensitivity analyses, the population was assumed to have random variable M with mean of 0.4 and lognormal error with CV of 20%. To allow the population to decline at low SSB levels, the B-H *R* model with lognormal error of CV of 50% was used. The sensitivity was inspected with respect to the assessment of optimal harvest without threshold management.

4.2.5 Establishment of guideline harvest levels

The analysis of harvest strategies is usually undertaken to advise fishery management about GHLs in advance of the fishery each year. The establishment of GHL is dependent on our knowledge about *R* and annual *M* during the coming year and present population abundance. The annual length-based population assessment model was applied with the same objective function to determine a guideline for fishing mortality (F_{GHL}). A flow chart illustrates the processes of population dynamics and the estimation of F_{GHL} (Figure 4.3).

The flow chart shows two lines in the estimation of F_{GHL} starting with the survey. For simplicity, no measurement errors in survey biomass estimates were imposed. Therefore, if the survey takes place, our knowledge about the present population abundance status will be updated to the true one. If not, then the population status will be estimated based on previously specified *R* and *M*. Therefore, the results from the simulation are the most optimistic possible. Based on the present population status and specified *R* and *M* for the following year, we calculate and implement F_{GHL}, and the population reaches a new level. The second line gives the true population abundance status and true parameters of *R* and *M* (R_{true} and M_{true}), from where true yield and risk are obtained after implementing the F_{GHL}. Values of R_{true} and M_{true} are generated in the same way as above: B-H *R* with CV of 50% and constant *M* (mean = 0.4, CV = 20%). The population was simulated within a 100-year time frame.

To examine the robustness of F_{GHL} calculation to the uncertainties in *R* and *M*, two sets of *R* were specified with two constant means of $e^{5.0}$, below the true average, and $e^{8.0}$, above the true average, and lognormal errors (CV = 50%). In addition, the specified *R* was set to 0.0 if SSB was less than 1% of SSB_0 as a precautionary approach. For annual *M*, three sets of values were specified: 0.2 less than each annual M_{true} (M_{true} - 0.2); a constant value of 0.4 with no variation (CV = 0%); and 0.2 more than each annual M_{true} (M_{true}+ 0.2). The simulated population was surveyed once every 1 to 3 years for comparisons.

4.3 RESULTS

4.3.1 Effects of constant fishing mortality

With the constant *R* and *M* model, SSB trended to a stable level for each *F* level when no threshold was imposed upon management (Figure 4.4). Cumulative yield steadily increased, and the risk of the spawning biomass going below the threshold level (20% SSB_0) was high for *F* at 0.9 and above. With a threshold of 20% SSB_0, SSB sustained around the threshold at *F* above 0.6 due to fishery closures, and risk was reduced for *F* levels above 0.3. A higher threshold level (40% of SSB_0) helped the population to sustain at a higher biomass level and to further reduce risk (not shown graphically). On the other hand, as *M* increased steadily from 0.4 to 0.9, SSB dropped to low levels even with no exploitation (Figure 4.5). Threshold management helped sustain SSB around the levels without exploitation and reduce the risk of collapse, but the resultant fishery closures greatly reduced the total yield. Under either constant *M* or increasing *M*, cumulative yield curves for *F* = 0.3 were distinctively below other yield curves. This low level of exploitation did not seem to be profitable under any case in terms of fishery yield, and it did not stop population from collapsing when *M* was high.

When recruitment was a function of SSB (with the B-H model), high *F* such as 1.2 and 1.5 without a threshold wiped out the population completely even under constant *M* (Figure 4.6). Under such conditions, management with a threshold is critical to keep the population from extinction. At a low *F* of 0.3 and constant *M*, SSB was stable at a high level and there was no need for threshold management (Figure 4.6). By the end of the 23 years, cumulative yield surpassed yields from scenarios of high $F > 0.9$. Threshold management helped increase cumulative yield under high values of *F*; but it appeared to be undesirable under $F \leq 0.3$. As *M* increased over time, SSB declined to below the threshold level under any exploitation rate. Threshold management prevented complete extinction under high exploitation (Figure 4.7). With increasing *M*, low *F* led to low levels of cumulative yield and it could not prevent a collapse when the *M* level was high.

4.3.2 Optimal constant fishing mortality

In any one year, optimal harvest is not only related to the natural process of recruitment and death, but it is also related to previous management actions, such as harvest level and management threshold. Table 4.2 shows the results for optimal *F* as a function of the S-R model, *M*, and the threshold level. Under the constant *M* and *R* model, cessation of fishing when SSB was below 20% of SSB_0 slightly increased the cumulative yield and reduced the average risk. Under increasing *M*, high *F* was preferred, and the average risk was high even with a threshold of 40% of SSB_0. Threshold management reduced risk but at the cost of greatly reduced yield.

With the B-H *R* model, as constant *M* increased from 0.2 to 0.4, optimal *F* decreased under a threshold of 0 or 20% of SSB_0 (Table 4.2). When *M* was 0.6, optimal *F* tended to be high, and the average risk was also very high in comparison. The model of increasing *M* resulted in high average risk of population collapse (0.31) under continual harvesting at *F* of 0.52 with no threshold, and threshold management reduced the risk only slightly. The high risk of population collapse under increasing *M* suggested that there is no way of protecting the population if *M* truly increased over time. Optimal *F* increased with threshold levels that were examined. However, no general rules regarding the trend in cumulative yield and risk were found.

4.3.3 Sensitivity of optimal *F* to selectivity and maturity

When the selectivity curve shape parameter γ was fixed at the estimated value of 0.572, the optimal *F* increased steadily from 0.24 to 0.54 as L_{50} increased from 13.0 to 19.0, but the resultant total yield decreased steadily from 8482 to 7313 (Table 4.3). However, corresponding risk of collapse was about the same. When L_{50} was set at the estimated value of 16.720 and γ increased from 0.4 to 1.2, total yield also decreased gradually.

Except for $\gamma = 0.4$, optimal F stayed at 0.34 for all γ levels. Average risk was about the same across the γ levels, which could be due to the fact that the population was under favorable conditions of moderate M. With the assumed logistic selectivity model, optimal harvesting was robust to changes in selectivity parameter γ when L_{50} was fixed at the estimated value. However, a combination of low L_{50} and high γ could lead to danger of growth overfishing.

Population reproduction is closely related to female abundance at age. With $M = 0.4$ and the B-H recruitment model, increasing the female proportion λ_4 at age 4 from 0.2 to 0.8 resulted in a higher population level and cumulative yield (Table 4.3). The optimal F increased also from 0.26 to 0.34. Average risk was more variable then before, but no general trends were evident.

4.3.4 Establishment of guideline harvest levels

Under the scenario of a true spawner-recruitment relationship, the effectiveness of prescribing annual GHL is determined by the level of M specified (thought to occur by the manager) and the frequency of survey sampling as well (Figure 4.8). When annual M was specified at 0.2 lower than M_{true} (underestimated), and the population was sampled once every year, the cumulative yield was consistently higher than those obtained from scenarios with levels of M equal to M_{true} or $M_{\text{true}}+0.2$. Nevertheless, cumulative risk was also consistently higher. Despite the danger of falling below threshold, the SSB did not show any declining trend. When annual M was fixed at the constant value of 0.4 without annual variations, cumulative yield was very close to that from the scenario of M_{true}; however, risk was much higher in comparison. Risk from the scenario of M_{true} was 0.0. On the other hand, specifying M by a value of 0.2 higher than the true value (overestimation) reduced the cumulative yield, but kept the population under very low or no risk of collapse.

Sampling frequency had no effect on management and population response to exploitation if M is accurately known, but it played an important role when M was misspecified, and especially when M was specified too low. Under the scenario in which

M was 0.2 lower than the true value, the risk of population collapse greatly increased when the population was sampled only once every 2 or 3 years. Compared with sampling once every 2 years, sampling once every 3 years resulted in lower yield as well as higher risk. The population was gradually wiped out as time progressed.

Under the situation of M_{true}, the accuracy of prescribing optimal *F* is more dependent on the survey sampling frequency than on the *R* levels assumed (Figure 4.9). If the population was sampled once every year, setting recruitment at either $e^{5.0}$ or $e^{8.0}$ resulted in similar yield and risk levels. However, when population was sampled once every 3 years, specifying *R* too high produced much higher yield and risk, as well. SSB was quickly depleted and remained at a very low level for several decades. Nevertheless, fishery closures and a period of favorable recruitment (despite low SSB) brought the population back to relatively high levels for a few years (years 70 to 85). In contrast, when *R* was at $e^{5.0}$ level, sampling once every 3 years did not produce a bad effect on yield and risk, although the SSB became quite variable.

4.4 DISCUSSION

Based on examinations of biological reference points using various levels of mean annual *M* with random variation, steepness of the B-H relationship (the mean recruitment at SSB = 20% SSB_0) and recruitment variability, Francis (1993) demonstrated that acceptable harvesting levels depended strongly on the steepness of the S-R relationship, and less strongly on *M*. However, constant natural mortality may not be adequate to describe *M* for some populations, for instance, the red king crab population in Bristol Bay, Alaska (Zheng et al. 1997), whose mortality rate increased sharply for a few years in the early 1980s. In this paper, we showed that with a constant mean *M* of 0.4 the northern shrimp population would be sustained under the optimal harvesting level, but with an increasing trend in *M*, high risk of collapse resulted under the B-H S-R relationship. Under the assumption of constant *M*, the importance of *M* in stock assessment was concealed.

A threshold is a level of female spawning biomass (or total biomass), below which there may not be enough recruitment to sustain a population. Except for the unrealistic scenario with constant *M* and *R*, all scenarios require threshold management to prevent complete population collapse under high exploitation. However, the stock level at which recruitment to a population will decline rapidly is not known until it happens (Botsford et al. 1997). Some arbitrary measure of threshold, such as 20% of SSB_0 or more conservative level, is necessary to implement threshold management.

With the B-H *R* model and constant *M*, the shrimp population is sustained above its threshold when fished at an optimal harvesting level, so no threshold may be necessary. Zheng et al. (1997) illustrated that a threshold had little effect on yield and spawning biomass variability when a fishery had small handling mortality of 20% or less, but a threshold was important to protect the population when handling mortality rate was 50%. Haist et al. (1993) also concluded from simulation studies that there was no requirement for a threshold spawning stock biomass for exploitation rates below 0.4 under the assumption of constant *M*. Nevertheless, under increasing *M* or low *R*, threshold management helps prevent the population from complete extinction, so threshold management is desirable when unknown changes in the ecosystem occur.

Under S-R *R* model and mean *M* levels of 0.2 and 0.4, the population sustains under an average *F* of 0.56 and 0.36, respectively. However, our results of optimal constant *F* under the situations of increasing *M* or mean *M* level of 0.6 need to be taken with great caution, because essentially there is no feedback in the analyses. Under these situations, optimal harvest level should be determined annually based on population monitoring results. Estimated *F* values for the Kachemak Bay northern shrimp population were very high for years 1980 to 1982 (around 0.9) (Chapter 2; Fu and Quinn in review), much higher than the optimal *F* level under $M = 0.2$. It is likely that the shrimp population was overfished during those years. With the displayed increasing *M* in the 1980s, fishery closure was necessary to reduce the risk of population extinction.

The establishment of GHLs is an essential ingredient of an optimal harvest policy. Its validity is dependent upon the estimation of present population status and that of *M* and *R* in the following year. When population abundance is estimated every year without measurement error, misspecification of *R* has very little effect on the forecast, but underestimation of *M* can increase population risk of collapse. Therefore, good understanding of *M* is more important than that of *R*. When sampling occurs only once every 2 or 3 years, overestimation of *R* or underestimation of *M* deteriorates the harvest management in terms of conservation. Therefore, we emphasize the need for routine annual research surveys to obtain estimates of population abundance and parameters, at least during periods when the fishery is being prosecuted. However, the results here had no measurement error in them, consequently the performance under measurement error would be reduced. Therefore, data accuracy is also essential for forecasting a stock and managing a fishery.

Table 4.1. Parameters of spawner-recruit relationship (α, β, ϕ), growth (L_{∞}, κ, σ,σ_r), selectivity (L_{50}, γ) and weight-at-length relationship (a_W, b_W) for the simulations.

Parameters	Estimates
α	1.826
β	0.002
ϕ	0.267
L_{∞}	24.698
κ	0.367
σ	0.529
σ_r	1.127
L_{50}	16.720
γ	0.572
a_W	0.00055
b_W	3.06818

Table 4.2. Optimal fishing mortality (*F*), objective function value (*f*), maximum yield (MaxY, units of t) and risk of population decline averaged over the entire time period corresponding to different *R* and *M* models and threshold levels (T) under constant *F*.

S-R	*M*	T(%)	*F*	*f*	MaxY	Risk
Constant *R*	$M = 0.4$	0	0.65	0.59	12587	0.092
Constant *R*	$M = 0.4$	20	0.80	0.80	12655	0.087
Constant *R*	$M = 0.4$	40	1.5	0.90	11771	0.096
Constant *R*	Increasing *M*	0	1.5	0.57	13203	0.431
Constant *R*	Increasing *M*	20	1.5	0.71	8602	0.293
Constant *R*	Increasing *M*	40	1.5	0.83	6404	0.173
B-H *R*	$M = 0.2$	0	0.56	0.995	21489	0.003
B-H *R*	$M = 0.2$	20	0.58	0.996	21510	0.004
B-H *R*	$M = 0.2$	40	0.80	0.999	21393	0.001
B-H *R*	$M = 0.4$	0	0.36	0.88	7623	0.054
B-H *R*	$M = 0.4$	20	0.42	0.91	7722	0.044
B-H *R*	$M = 0.4$	40	0.80	0.95	7887	0.051
B-H *R*	$M = 0.6$	0	0.44	0.599	2698	0.394
B-H *R*	$M = 0.6$	20	1.5	0.619	2620	0.381
B-H *R*	$M = 0.6$	40	1.5	0.780	1747	0.220
B-H *R*	Increasing *M*	0	0.52	0.66	5506	0.305
B-H *R*	Increasing *M*	20	0.52	0.67	4931	0.288
B-H *R*	Increasing *M*	40	1.0	0.76	4373	0.194

Table 4.3. Optimal fishing mortality (F), objective function value (f), maximum yield (MaxY, units of t) and risk of population decline averaged over the entire period corresponding to different selectivity parameters (L_{50} and γ), and different female proportions at age 4 (λ_4) under the assumptions of B-H spawner-recruitment relationship and constant M of 0.4.

	L_{50}	F	f	MaxY	Risk
$\gamma = 0.572$	13.0	0.24	0.87	8482	0.060
	14.0	0.26	0.88	8313	0.062
	15.0	0.28	0.88	8047	0.058
	16.0	0.32	0.88	7877	0.061
	17.0	0.36	0.88	7605	0.058
	18.0	0.44	0.88	7485	0.064
	19.0	0.54	0.88	7313	0.063
$L_{50} = 16.720$	γ				
	0.4	0.36	0.88	7964	0.061
	0.6	0.34	0.88	7598	0.055
	0.8	0.34	0.88	7459	0.059
	1.0	0.34	0.88	7367	0.061
	1.2	0.34	0.88	7306	0.063
$\gamma = 0.572$,	λ_4				
$L_{50} = 16.720$	0.2	0.26	0.85	4483	0.091
	0.4	0.28	0.87	5397	0.064
	0.6	0.30	0.87	6217	0.058
	0.8	0.34	0.88	7092	0.070

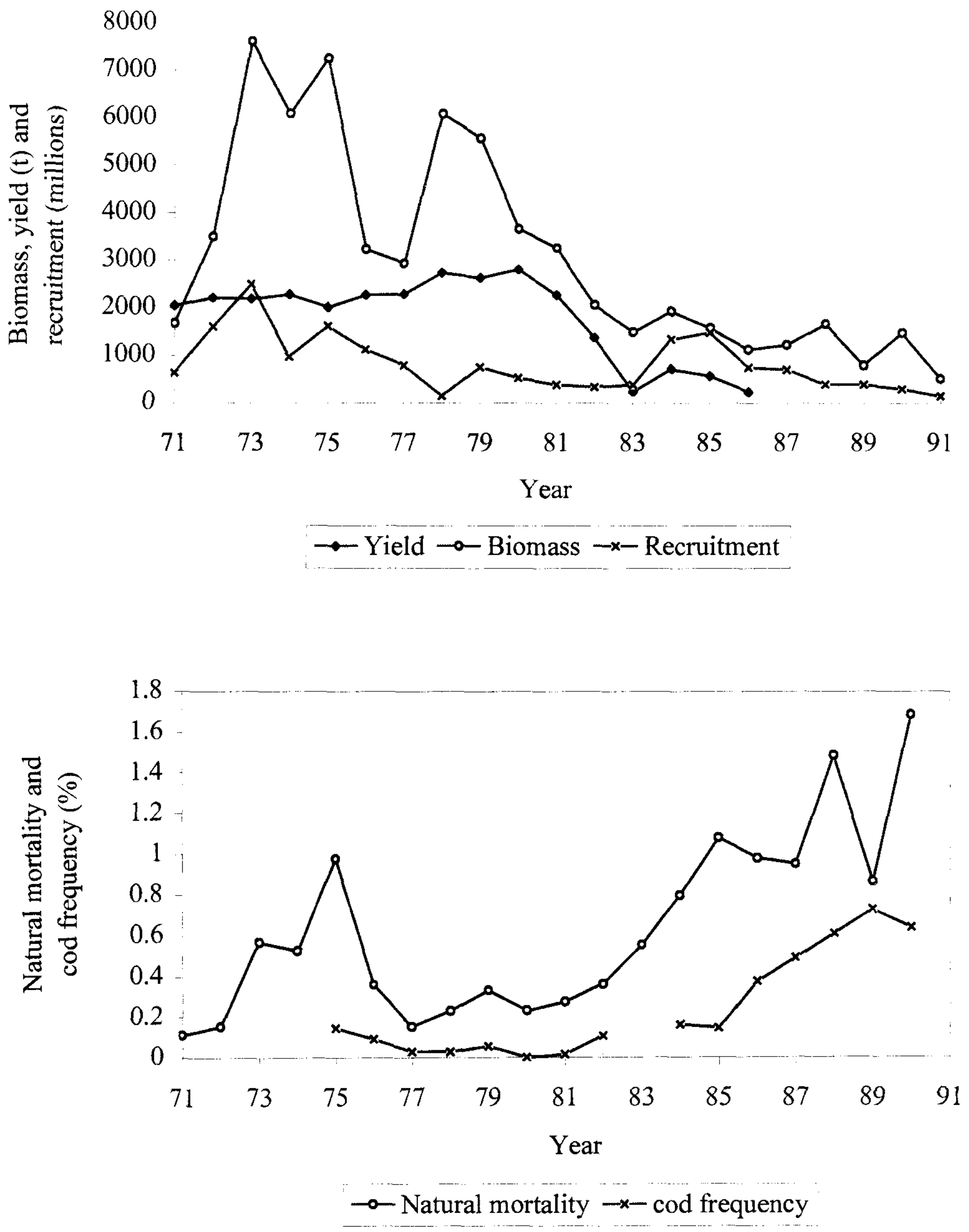

Figure 4.1. Observed yield, survey biomass estimates and estimated recruitment for the northern shrimp population in Kachemak Bay (upper panel); estimated instantaneous natural mortality and frequency of cod occurrence in numbers obtained from the same surveys (lower panel).

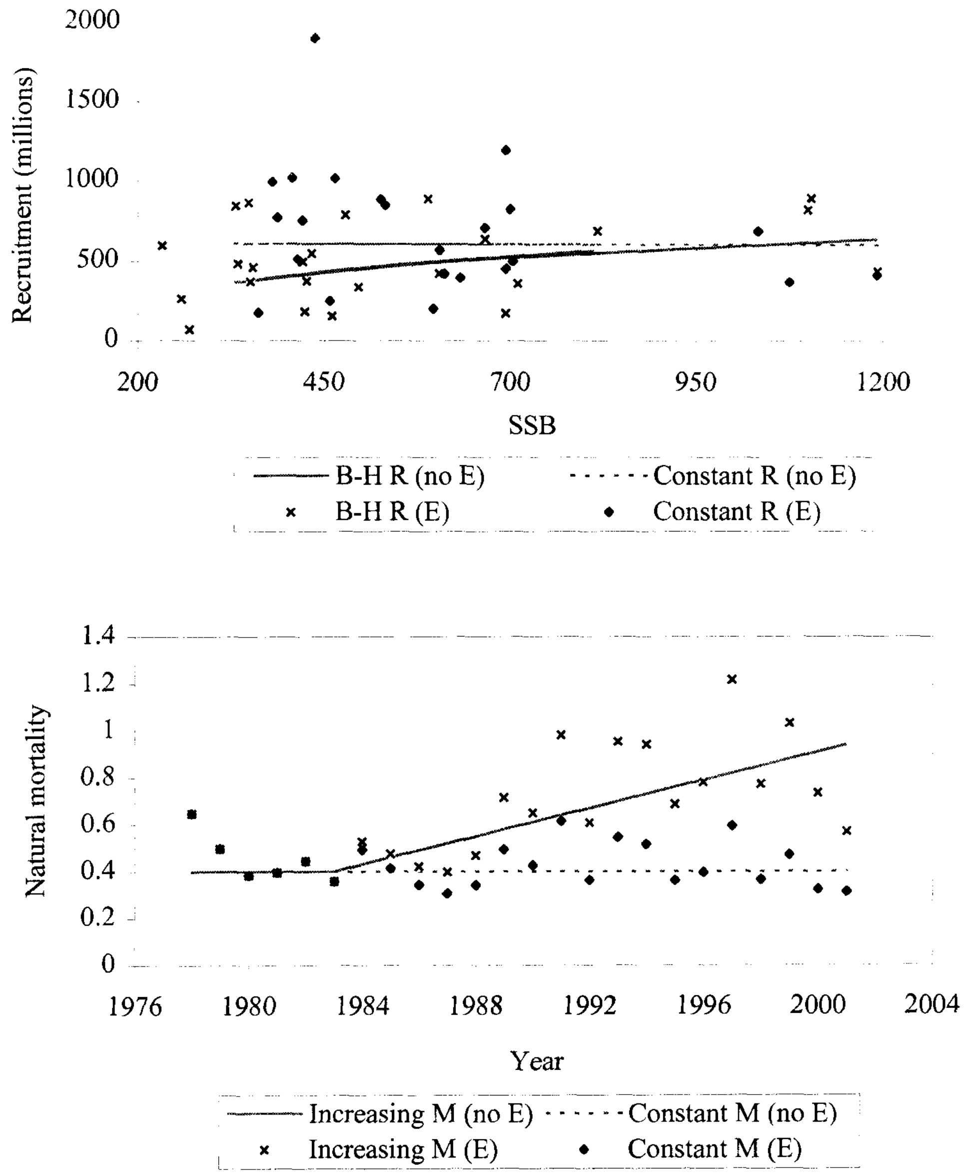

Figure 4.2. Constant (608 million) and B-H recruitment (*R*) without lognormal errors ("no E"), and one random realization of constant and B-H *R* with lognormal errors ("E", CV = 50%) (upper panel). Constant and increasing natural mortality (*M*) without lognormal errors ("no E"), and one random realization of constant and increasing *M* with lognormal errors ("E", CV = 20%) (lower panel).

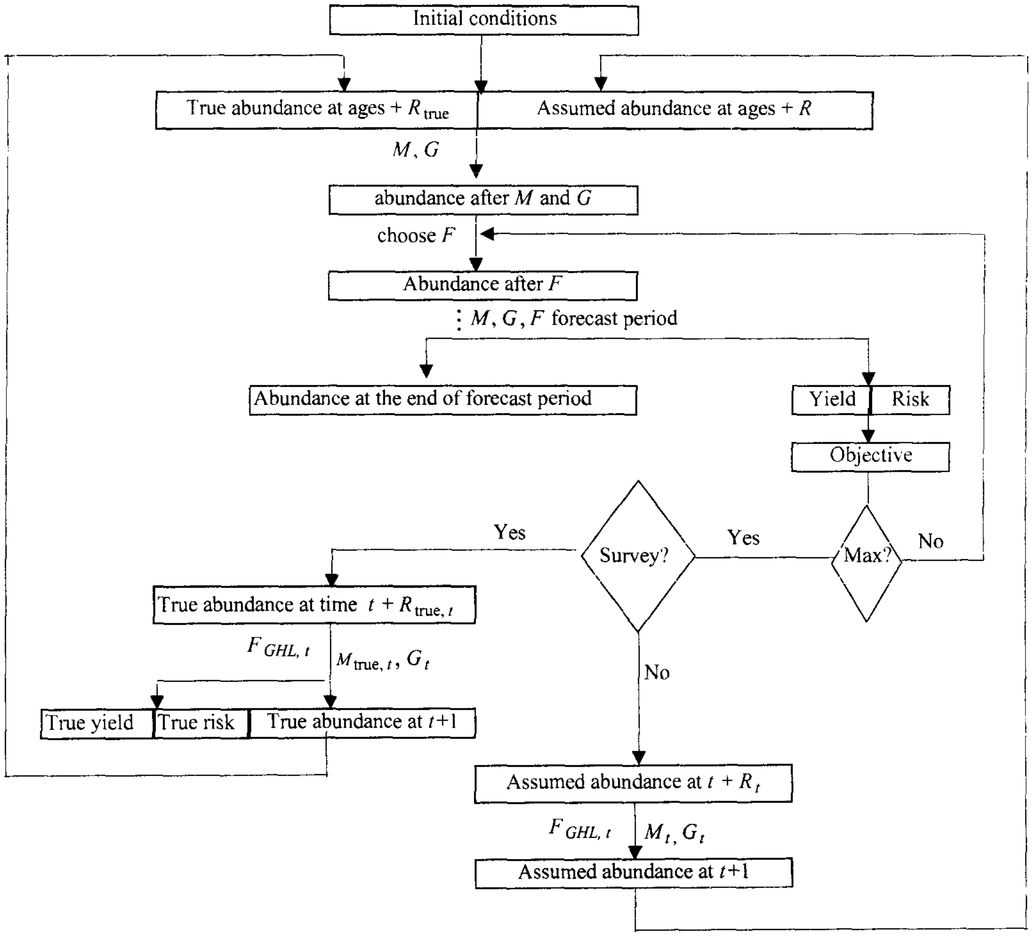

Figure 4.3. Flow chart illustrating the annual setting process for guideline harvest level (GHL); growth G was assumed to be true; R, M and F denote assumed annual recruitment, natural mortality and fishing mortality, respectively; $F_{\text{GHL},t}$ is the guideline instantaneous fishing mortality for year t, and R_{true} and M_{true} are the true R and M levels.

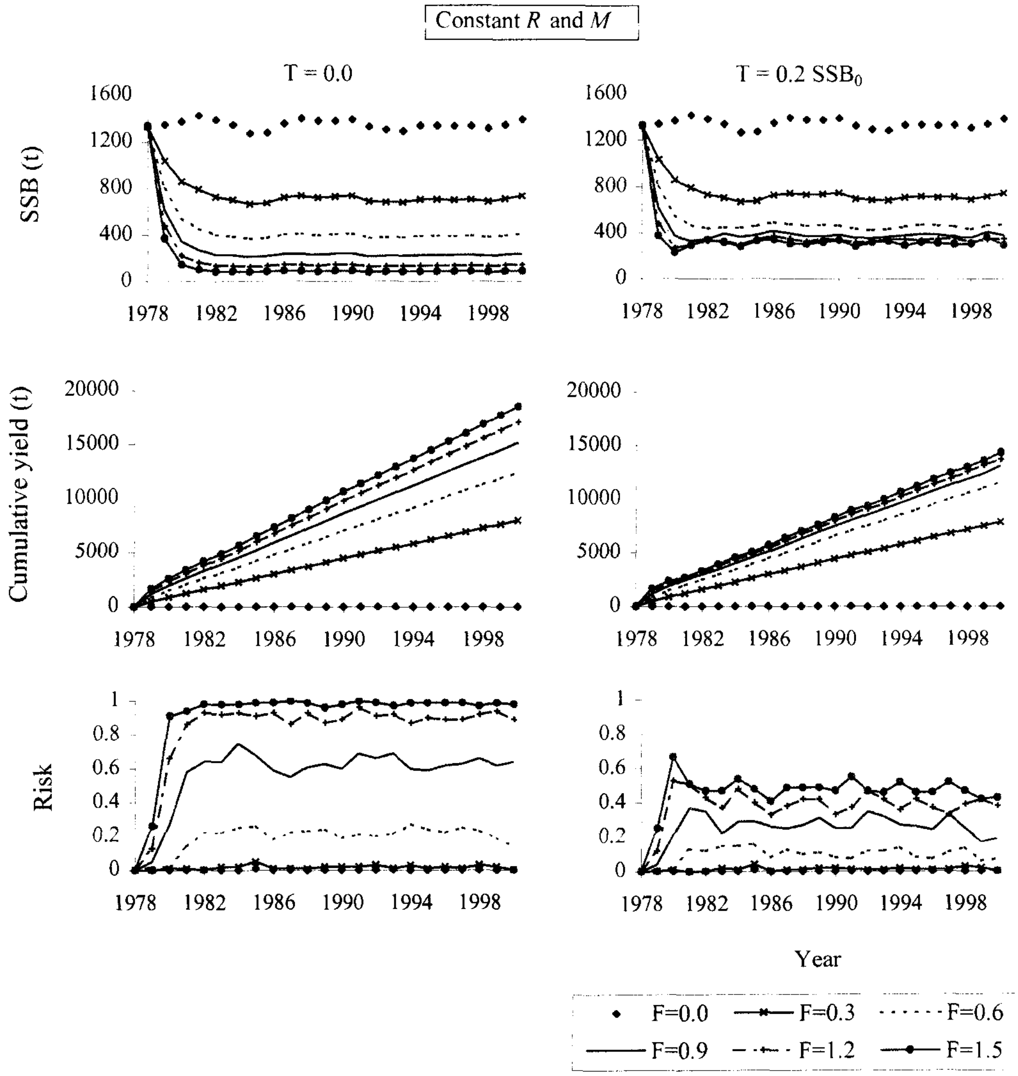

Figure 4.4. Comparisons of spawning stock biomass (SSB), cumulative yield and risk over time from 6 levels of fishing mortality (*F*) (within panel) and 2 levels of mean threshold (T = 0.0 and 260.0) (between columns) under the situation of constant recruitment (*R*) and natural mortality (*M*).

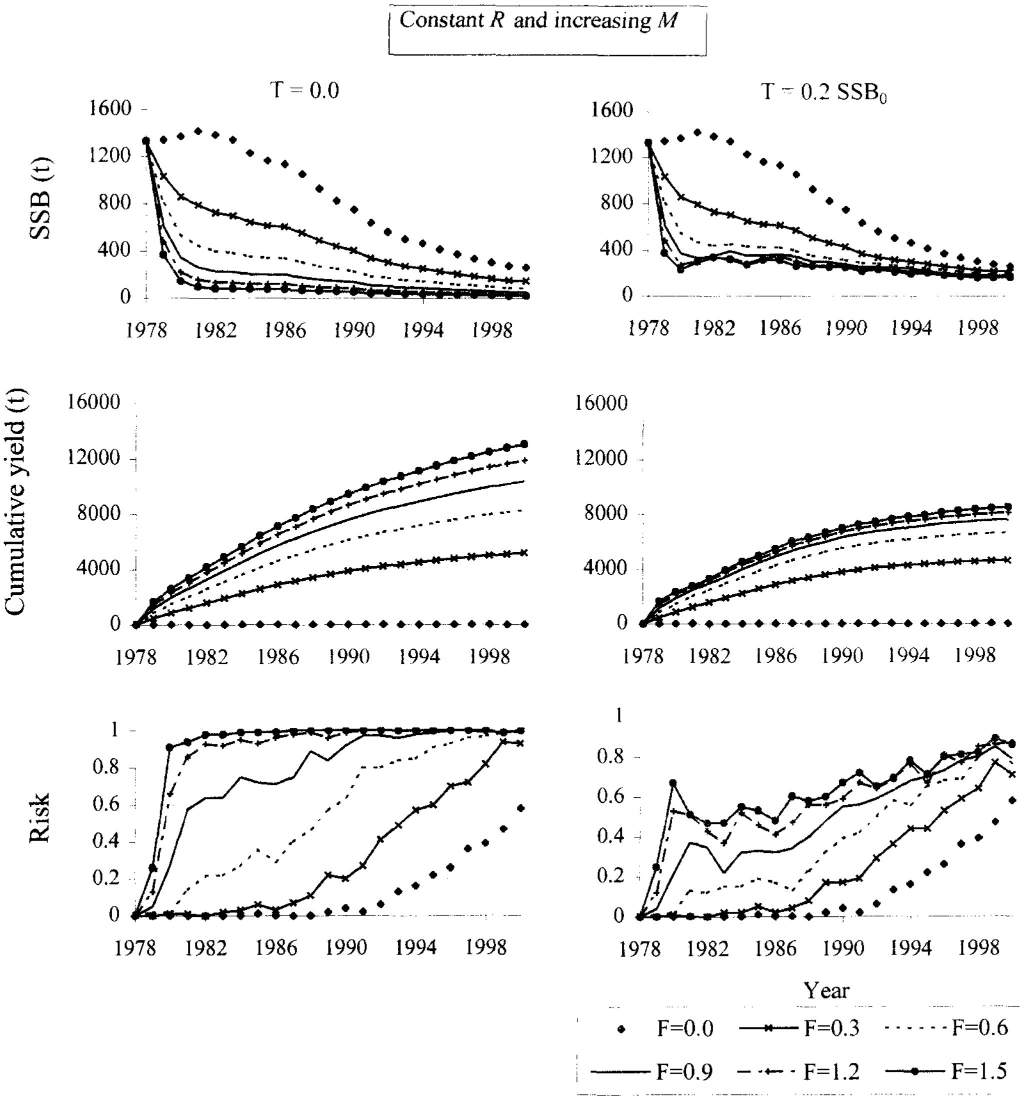

Figure 4.5. Comparisons of spawning stock biomass (SSB), cumulative yield and risk over time from 6 levels of fishing mortality (*F*) (within panel) and 2 levels of mear threshold (T = 0.0 and 260.0) (between columns) under the situation of constant recruitment (*R*) and increasing natural mortality (*M*).

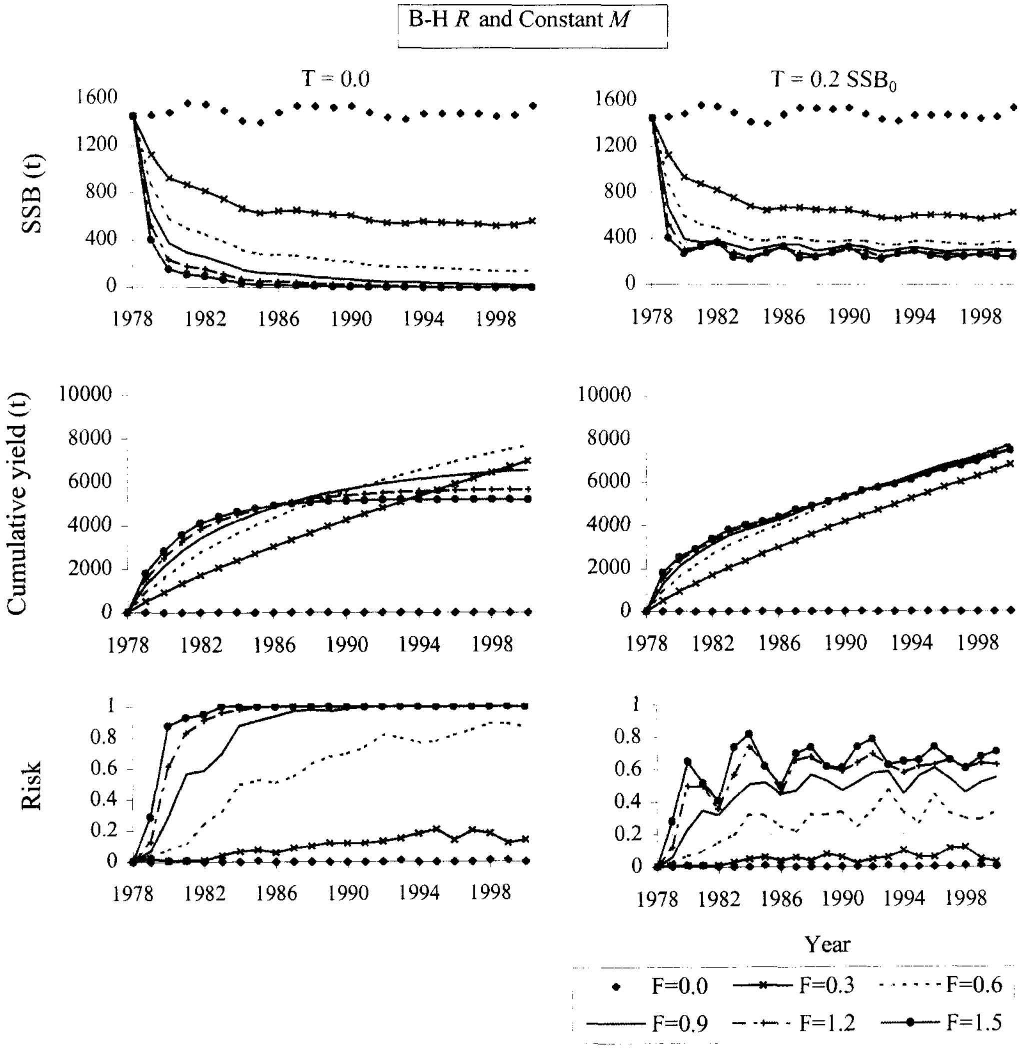

Figure 4.6. Comparisons of spawning stock biomass (SSB), cumulative yield and risk over time from 6 levels of fishing mortality (*F*) (within panel) and 2 levels of mean threshold (T = 0.0 and 290.0) (between columns) under the situation of B-H recruitment (*R*) and constant natural mortality (*M*).

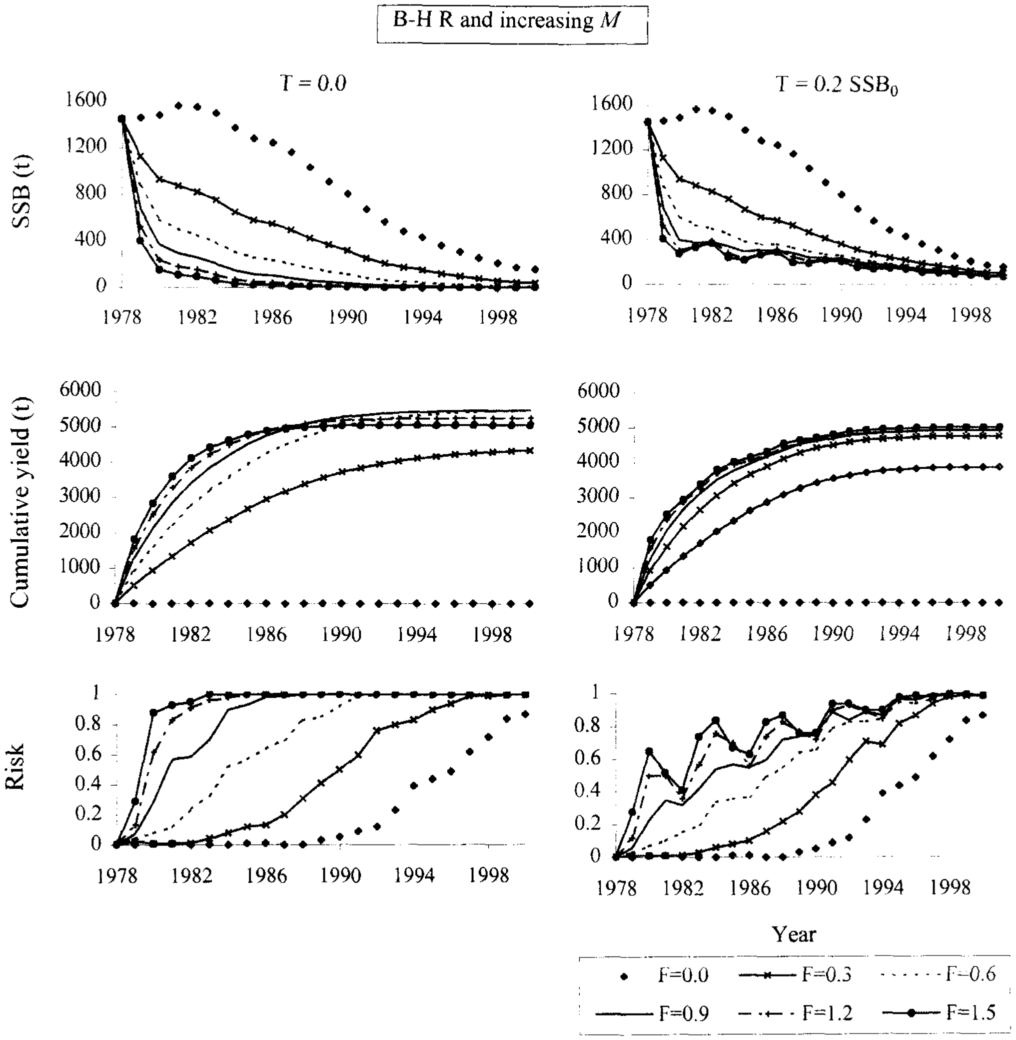

Figure 4.7. Comparisons of spawning stock biomass (SSB), cumulative yield and risk over time from 6 levels of fishing mortality (F) (within panel) and 2 levels of mean threshold (T = 0.0 and 290.0) (between columns) under the situation of B-H recruitment (R) and increasing natural mortality (M).

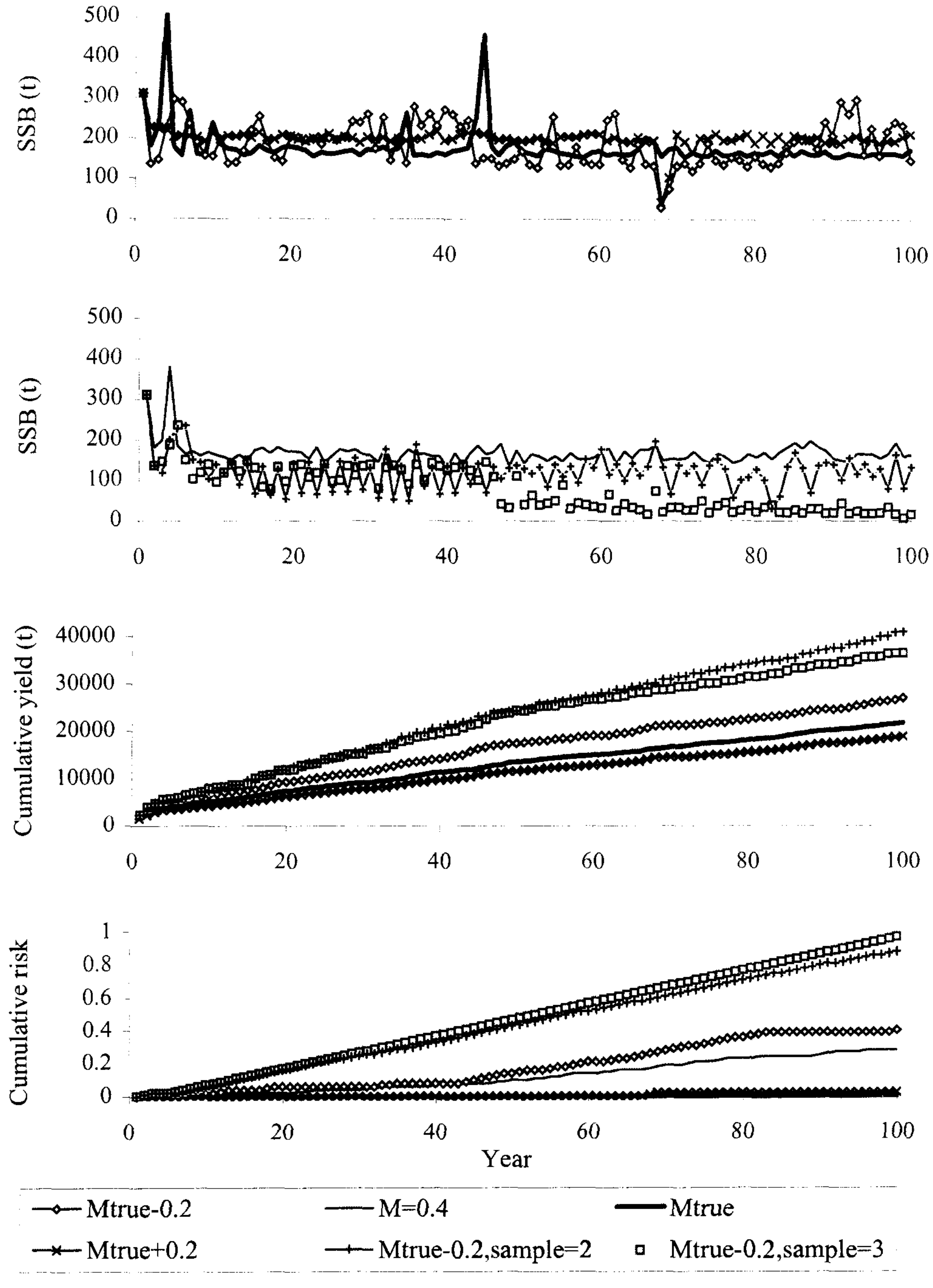

Figure 4.8. Comparisons of spawning stock biomass (SSB) (Panels 1 and 2), cumulative yield and risk from guideline harvest levels obtained under R_{true}, four levels of M (0.2 less than M_{true}, constant at 0.4, M_{true}, 0.2 more than M_{true}) and two additional sampling frequencies (sampling once every 2 and 3 years) with M_{true} - 0.2.

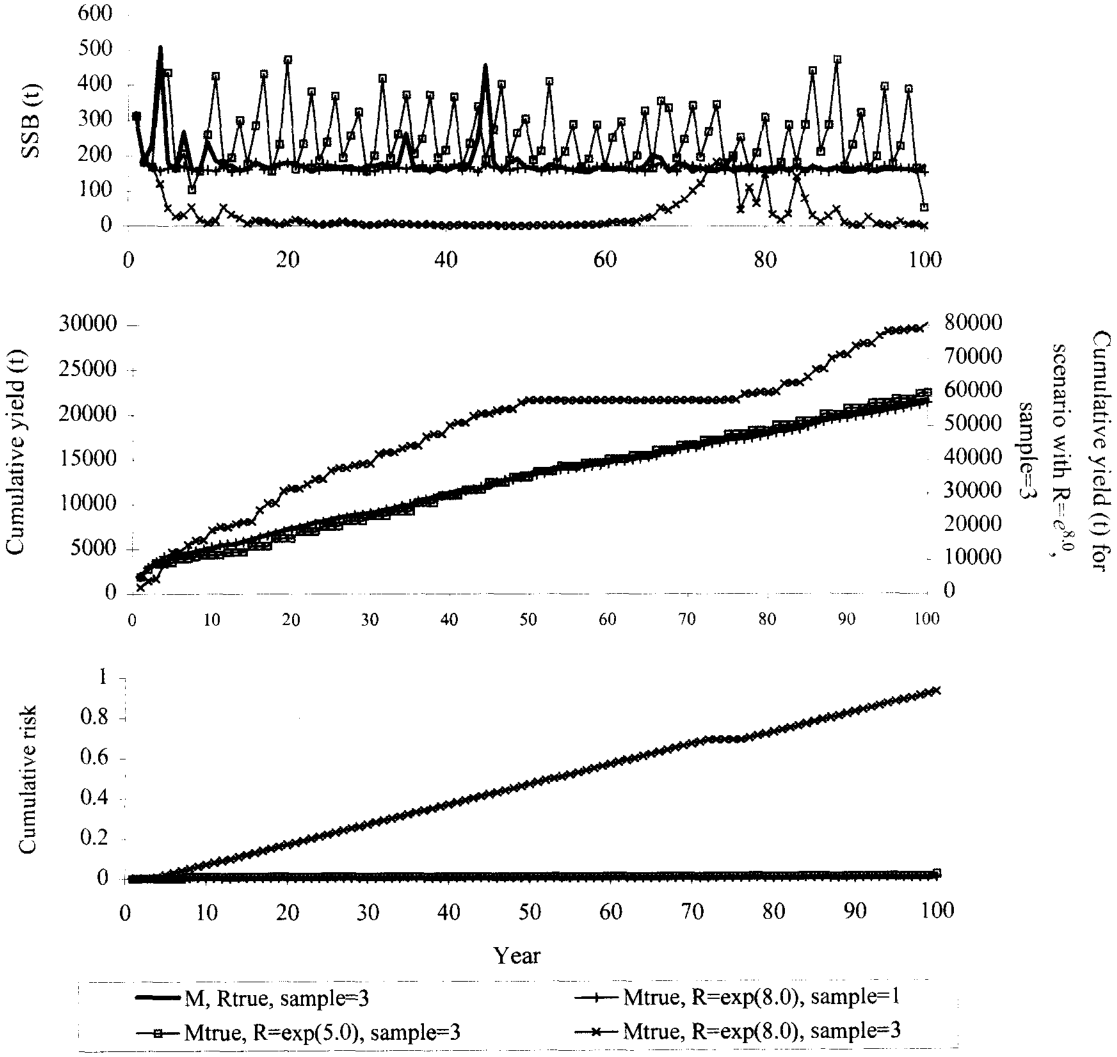

Figure 4.9. Comparisons of spawning stock biomass (SSB), cumulative yield and risk from guideline harvest levels obtained under M_{true} and sampling every 3 years, three levels of R ($e^{5.0}$, R_{true}, $e^{8.0}$), and one additional sampling frequency (sampling every year) with R of $e^{8.0}$.

Chapter 5 The role of sex change, growth and mortality in *Pandalus* population dynamics and management[4]

ABSTRACT

Sex change, growth, and mortality of *Pandalus* spp. 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 1 and 2 males caused populations with sex change to fluctuate in spawning biomass. Seasonality in growth and natural mortality is also pertinent to fishery 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 fishery management.

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[4] Fu, C., T.J. Quinn, II, and T.C. Shirley. Submitted. The role of sex change, growth and mortality in *Pandalus* population dynamics and management. ICES Journal of Marine Science.

5.1 INTRODUCTION

The biological aspects of *Pandalus* spp. shrimp, especially *Pandalus borealis* (=*P. eous*), in the Northern Hemisphere have been extensively studied, not only because of their commercial importance, but also because of their unique life history trait of protandry. Namely, the pandalids reproduce first as males, and after passing through a transitional phase, function as females for the rest of their life. Female pandalid shrimp, 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*. The study group (ICES) 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, growth, sex change, and predation/natural mortality (Anon. 1994). Despite diverse research available on biological parameters, such as growth and reproduction, the lack of basic knowledge of shrimp stock dynamics limits the scientific basis for fishery management (Aschan and Godø 1997).

The lack of age data for invertebrates resulted in the development of a length-based population model, which has been applied to shrimp and prawn populations (Quinn et al. 1998; Fu et al. 1999). Monte Carlo simulation of the *P. borealis* population in Kachemak Bay, Alaska suggested that an increasing trend in natural mortality contributed to the population decline in the 1980s (Chapter 3; Fu et al. 1999). Simulation analyses of harvest strategies for the Kachemak Bay population also highlighted the importance of understanding natural mortality in fisheries management (Chapter 4; Fu et al. in review).

In this paper, we focused on evaluating fishery impacts on populations of different growth and maturity patterns. The most prominent feature in *Pandalus* life history is sex change and our first objective was to compare the dynamics of populations with and without sex change. 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). 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 the impact of different growth rates on population dynamics. Geographic differences in the rate of maturation and transition from males to females have been well documented (Rasmussen 1953, 1969; Balsiger 1981; Teigsmark 1983). *P. borealis* in Kachemak Bay begin transition in March or April at age 2 or 3 years, and begin to function as females at ages of 2.5 or 3.5 (Davis 1982). Teigsmark (1983) reported that the population in the southern and central areas of the Barents Sea first functioned as females at 4 years and annually thereafter, but the northern population first functioned as females at 6 years old and only every second year thereafter. The former population, similar to that in Kachemak Bay, had faster growth, higher total mortality and a shorter life span of 6 years, whereas the latter had slower growth, lower mortality and a longer life span of 10 years. Our simulation comparisons emulate the Kachemak Bay and the northern Barents Sea populations as examples of typical *Pandalus* populations.

The third objective was to explore optimal fishing seasons based on seasonal variations in natural mortality and growth. Seasonal closures are enforced for some pandalid shrimp fisheries, with openings after hatching and closure during the breeding and ovigerous period (Fox 1972). However, due to the lack of knowledge on seasonal population dynamics, this management practice lacks a scientific basis.

Commonly, shrimp fisheries management assumes a constant annual natural mortality. Seasonal variations in this parameter have not yet been documented but are likely to exist (P. Anderson, NMFS, Kodiak, Alaska, pers. comm.). The potential seasonality in natural mortality may have implications in fisheries management. Bergström (1992) suggested that growth models should incorporate seasonal variations because of the distinct feature of stepwise growth (Rasmussen 1953; Haynes and Wigley 1969; Shumway et al. 1985). Growth of pandalids is generally better described by a modified von Bertalanffy (VB) function with seasonal oscillations. However, seasonal growth has not yet been incorporated into fisheries assessment and management. We incorporated seasonal variation in growth into our population model to investigate its potential effects on population dynamics and management.

5.2 METHODS

5.2.1 Stochastic simulation

Population dynamics were simulated with a length-based stochastic population model (Quinn et al. 1998; Fu et al. in review). One thousand replicates of 40-year simulations were initialized in year 1 when a virgin population was at equilibrium. The simulation model incorporated process errors associated with recruitment (*R*) and instantaneous natural mortality (*M*). *R* was simulated using a Beverton-Holt model with autocorrelation (simply called B-H) and lognormal errors with coefficient of variation (CV) of 50%. *M* was modeled as a lognormal distribution with CV of 20%, a level that was similar to the average of the estimated levels in Fu et al. (1999). Measurement errors in spawning stock biomass (SSB) were imposed using a CV of 20% based on the average historical variability for survey biomass estimates (Gustafson 1994). Fishing mortality (*F*) was assumed to be implemented without error.

5.2.2 Comparison with a hypothetical population

5.2.2.1 Effect of sex change

To examine the different impacts of a fishery and predation on populations with and without sex change, two populations were simulated with the same parameters of the spawner-recruitment (S-R) relationship (α, β, ϕ), growth (L_∞, κ, σ, σ_r), gear selectivity (γ, L_{50}), mean *M*, and maximum age (T_{max}) (Table 5.1). Except for the mean *M* that was set at 0.4 following Fu et al. (in review), all other parameters were obtained from the estimates for the Kachemak Bay *P. borealis* population (Fu et al. 1999). The protandric population was modeled after the Kachemak Bay *P. borealis* population, identified as

K_pop. Shrimp were assumed to function as males at age 2 and 3, and females at ages 4 to 6 as in Fu et al. (in review). The hypothetical population (H_pop) was assumed to mature as males and females at age 2, and function as the same type up to its maximum age of 6.

5.2.2.2 Effect of threshold management

Each population was modeled with a fishery of constant instantaneous fishing mortality 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. 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.

5.2.2.3 Effect of predation

To compare the effect of predation on K_pop and H_pop, we also assumed that there was sudden increase in predation mortality of young shrimp at age 1 and 2, 10 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 1 to 4 years.

5.2.3 Comparison with a population of different growth

To examine the impact of the fishery on populations of different growth, we generated a population of slower growth based on the growth parameters for a northern Barents Sea population (B_pop). Growth parameters were taken from Teigsmark (1983) (Table 5.1). T_{max} for B_pop is 10 years old, and females at first egg extrusion are 6 years old. Growth variation parameters (σ, σ_r) were assumed to be the same for the two populations. Constant M with annual random variation was imposed for both populations. To be comparable, constant 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., $e^{-T_{\max 1}M_1} = e^{-T_{\max 2}M_2}$. Recruitment was assumed to have the same parameters and the same B-H spawner-recruitment relationship, and again spawner was calculated as the biomass of reproductive females.

Gear selectivity parameters of a logistic curve (Fu et al. 1999) are closely related to the optimal harvest rate. 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:

$$L_{50B\_pop} = L_{\infty B\_pop}(1-e^{-\kappa_{B\_pop}[(t-t_0)_{K\_pop}+2]}) = 19.12 \text{ (Carapace length: mm)},$$

where $\{(t-t_0)_{K\_pop}+2\}$ indicates that shrimps are 2 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 to the K_pop to examine the effect of changing selectivity. For the B_pop, in addition to L_{50} of 16.72, 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 and 22.24.

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 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) increasing selectivity parameter L_{50} from 19.12 to 22.24; (2) preserving 50% of females not to be fished; (3) implementing threshold management.

5.2.4 Comparison 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), i.e., $Max\left\{\frac{Y_F}{MaxY} - RISK_F\right\}$. For each *F*, annual average risk was calculated as the percentage out of 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; MaxY is the maximum among Y_F; and $RISK_F$ equals the average risk over the entire time period at a given level of *F*. If an *F* produces maximum yield but always drives the population below 20% of SB_0, then the objective function has a value of 0.0.

5.2.5 Model extension to half-year dynamics

For simplicity, we initially modeled population dynamics on an annual basis, and fixed the female proportions at age at 0.0 for ages younger than 4 and 1.0 for ages 4 and above. This approximation may not be appropriate because some age 3 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 fisheries management, we extended the yearly population dynamics model to a half-year dynamics model with separate summer and winter periods. The extension enabled modeling of the sex change proportion and examination of its effect on population dynamics.

As in the general model, the extended model follows each cohort throughout its life history. The model corresponds to the *P. borealis* population in Kachemak Bay. The simulated population dynamics start with recruitment in April at age 1. 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 3. Meanwhile, other untransformed 3 year-old males begin to change sex at age 3, and thereafter contribute to the population reproduction (Figure 5.1, Part 1). 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 $2t$. Part 2 of Figure 5.1 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 2 is a logistic function of length with more individuals at larger size transforming into females:

$$\chi = \frac{1}{1+e^{-\gamma_\chi (L-L_\chi)}},$$

where γ_χ is the shape parameter and L_χ is the length at which half of the shrimp step into the transition stage at age 2. In this paper, γ_χ and L_χ were set at 0.5 and 14.5 mm corresponding to a proportion of about 40% that transform sex at age 2. Male abundance at age 2.5 (equivalent to 4 in a half-year schedule) is:

$$N_{2t,4,m}(L) = N_{2t-1,3}(L)(1-\chi(L))e^{-(F_{2t-1}S_L+M_{2t-1})},$$

where subscript m stands for male, L is length, S_L is length-dependent logistic selectivity function (Chapter 3; Fu et al. 1999), 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:

$$N_{2t,4,f}(L) = N_{2t-1,3}(L)\chi(L)e^{-(F_{2t-1}S_L+M_{2t-1})}.$$

Abundance of females hatching eggs in the spring is:

$$N_{2t+1,f}(L) = \xi\left[N_{2t,4,f}(L)e^{-(F_{2t}S_L+M_{2t})} + \sum_x N_{2t+1,x,f}(L)\right], \text{ where } x = 7, 9 \text{ and } 11,$$

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. When fishing occurs after hatching, $F_{2t} = 0$.

Growth was modeled following the basic VB function,

$$L_{a+1} = L_\infty(1-\rho) + \rho L_a + \varepsilon, \text{ where } \rho = e^{-\kappa} \text{ is the Brody coefficient, and } \varepsilon \sim N(0,\sigma^2).$$

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:

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

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

with Brody parameters $\rho_s = e^{-\kappa_s}, \rho_w = e^{-\kappa_w}$. 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 $\sigma_{r+1}^2 = \rho_s^2\sigma_r^2 + \sigma_s^2$, 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 $\kappa_s = \phi_\kappa \kappa$, then $\kappa_w = (1-\phi_\kappa)\kappa$; 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:

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

For this paper, we assumed that ϕ_κ and ϕ_σ had the same value.

Natural mortality in the summer and winter are M_s and M_w respectively. We let $M_s = \phi_M M$, and $M_w = (1-\phi_M)M$, 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 the processes of natural mortality and recruitment were incorporated. The annual M was imposed with lognormal errors with CV of 20%. Recruitment was generated by imposing a lognormal error upon a B-H spawner-recruit model with CV of 50%.

5.2.6 Fishery management

Two seasonal types of fisheries were compared: harvesting after mating (i.e., egg extrusion and fertilization) in the fall after shrimp have experienced summer growth and natural mortality, and harvesting after egg hatching in the spring by which time shrimp have had winter growth and death (Figure 5.1). A threshold of 20% of virgin SSB was imposed, so that populations are not driven to extinction under high fishing mortality rates. 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 the natural mortality during summer and winter months and fishing mortality after mating. If fishing occurs after egg hatching, reproductive females are only subject to natural mortality during the winter season. The single survey was modeled 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.

5.3 RESULTS

5.3.1 The role of sex change

5.3.1.1 Effect of sex change

In populations with sex change (K_pop), females are larger and more vulnerable to fishing. Thus, high exploitation resulted in recruitment overfishing more often than for populations with no sex change (H_pop). For H_pop, a high exploitation (*F* = 1.5) still results in a small risk of the population going below the threshold (Figure 5.2). However, only values of *F* of 0.3 or below were able to sustain K_pop. *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 5.2). Clearly, the population without sex change is much more robust to fishing pressure.

5.3.1.2 Effect of threshold management

Under high exploitation, 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 5.3). 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.

5.3.1.3 Effect of predation

When predation on age 1 and 2 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 2 years despite the relaxation of predation mortality (Figure 5.4). 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. 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).

5.3.2 The role of growth

The slower the growth that a protandric, hermaphroditic shrimp population has, the longer it lives and the later individuals transform into mature females. Correspondingly, high exploitation generates more impact on slower growing populations. Using the same mesh size as that for K_pop (i.e., $L_{50} = 16.72$), 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, B_pop sustained at an F level close to 0.3 (Figure 5.5), similar to results for K_pop under $L_{50} = 16.72$ (Figure 5.3). With larger mesh size ($L_{50} = 19.12$), K_pop was kept at a relatively high population level even when $F = 0.6$ (Figure 5.5). As L_{50} increased from 16.72 to 20.86 (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 (Table 5.2). The same trend is also true for K_pop.

For B_pop, further increasing L_{50} to 22.24 (t-$t_0 = 7.079$) slowed down the speed of collapse under high exploitation; however, it did not change the declining trend (Column 1, Figure 5.6). Meanwhile, protecting 50% of females each year could not prevent the population from collapsing under F higher than 0.6 (Column 2, Figure 5.6). On the other hand, a smaller mesh size along with a threshold management can prevent population collapse even under the highest exploitation (Column 3, Figure 5.6). The results indicated that a management policy that protects only a certain proportion of females while allowing high exploitation of other shrimp can 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.

5.3.3 The role of seasonal variations in growth and natural mortality

The optimal fishing season was found to be dependent on all three factors: exploitation level, and proportions of growth and natural mortality in summer (April to October) and winter (October to 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 5.7). This makes sense, because fishing later in the year allows yield per recruit to increase due to growth and lower mortality 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 5.7). 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 natural and fishing mortality: under high mortality, too few shrimp survive the half-year to wait for the growth increase. 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.

Despite 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 spring (Table 5.3). 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 5.3).

The average risk over the simulation period was generally small, which is in agreement with the finding of Fu et al. (in review; Chapter 4). 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 effect 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 5.3). However, fishing after egg hatching renders higher yield and lower risk, when the same high F level is applied to both situations, as shown in Figure 5.7.

5.4 DISCUSSION

5.4.1 Fishery impact on the dynamics of *Pandalus* species

Pandalus species, especially *P. borealis*, support sizeable fisheries throughout much of their range within boreal and sub-arctic waters of the Northern Hemisphere (Apollonio et al. 1986), but historical commercial landings have fluctuated widely. Some populations exhibit a cyclic pattern of abundance, while some others have not rebounded after a decline (Balsiger 1981). Balsiger (1981) postulated that the abundance fluctuation and frequent population decline are closely related to variations in year-class success, and these variations may result primarily from environmental factors. However, fishery effects on *Pandalus* populations have rarely been investigated on the basis of population dynamic models. Retrospective analyses of the Kachemak Bay *P. borealis* population with different trends in M and R suggested that increasing M in the 1980s may be the major factor that resulted in the population decline, rather than declining recruitment (Chapter 3; Fu et al. 1999). The increase in estimated M coincided with large increases in fish predator populations, such as Pacific cod (*Gadus macrocephalus*) and walleye pollock (*Theragra chalcogramma*). In this paper our examinations with various levels of harvesting over a fishing period of 40 years indicated that continuous fishing at F levels of 0.6 or above can cause a population to collapse over a period of about 10 years. With the Kachemak Bay *P. borealis* population, instantaneous fishing mortality for fully selected shrimp was estimated to be around 0.6 in the 1970s, and it stayed around 1.0 for years 1980 to 1982 (Chapter 3; 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 exploitation before the increasing M played its role in the early 1980s. Fishery closures might have helped to recover the *P. borealis* stock in Kachemak Bay, provided M was reasonably low. Apparently, the increase in M has prevented the population from recovering.

5.4.2 Predation effects on *Pandalus* dynamics

We focused on the effects of fishing on *Pandalus* population dynamics in this paper and did not incorporate a significant M trend as in Chapter 3 and Fu et al. (1999). However, the dynamics of *Pandalus* populations are undoubtedly related to the abundance of their predators. *Pandalus* species are major prey items for many groundfish species, such as cod (*Gadus* spp.) and halibut (*Reinhardtius* spp.) (Bowering et al. 1984). Based on the available data for the stocks in the Barents Sea, North Sea and West Greenland, predation mortality may be the major factor regulating stock size, and it may be the main reason behind the high variations in the *Pandalus* stocks (Anon. 1994). Improved determination of predation mortality will improve the assessment of *Pandalus* spp.

Predation data from the Barents Sea have been transformed into estimates of predation mortality (between 0.74 to 1.04) and put into a multispecies management context (Berenboim et al. 1991). 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 also affects the survival of small males. Abundance projection of a population based on single species models often fails, partially due to the uncertainty in the S-R relationship. By adding predation, and particularly cannibalism on pre-recruiting young, into a walleye pollock population assessment model, Livingston and Methot (1998) were able to improve the fit of the stock recruitment relationship at age 1. As a result, the relationship was changed from one with declining recruitment at high spawning stock sizes to one where recruitment is more asymptotic at high spawning stock sizes.

Our simple simulation of predation on age 1 and 2 shrimps indicated that predation caused SSB of *Pandalus* species to fluctuate more than that of populations without sex change. Further simulations on the effect of predation on *Pandalus* population dynamics may provide insight into understanding population dynamics. In addition, since *Pandalus* species are subject to predation by many fish species, systematic research on their predators and food consumption is necessary for leading to multispecies modeling, and thereafter achieving better understanding of their dynamics.

5.4.3 Management strategies

Protecting aggregated reproductive females is a common practice in fishery 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. A mesh size of 38 mm was used in Icelandic fisheries and 40 mm in Greenland waters (Anon. 1994). The Kachemak Bay pandalid fishery used 35 mm mesh size (Davis 1982). Because populations under a small-mesh fisheries are more vulnerable to high exploitation, it is essential to conduct research concerning optimal mesh size, and its selectivity function. The determination of mesh size for a population should be related to individual growth and maturity rate. In addition, since 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.

5.4.4 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 simulations 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 is 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 to 1982 (Chapter 2; Fu and Quinn in review). 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 to 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 (Chapter 3; Fu et al. 1999). Simulation-estimation experiments indicated that annual *M* could be well estimated given good survey biomass estimates (Chapter 2; Fu and Quinn in review). In the same manner, seasonal variations in *M* have been well estimated (C. Fu, unpubl. data). It is thus possible that the understanding of seasonal variations in *M* can be used in fishery management, particularly if seasonal surveys are conducted. Furthermore, for forage species like *P. borealis*, one major source of natural death is predation. Relating seasonal *M* to the seasonal variations in the abundance of predators and their food consumption appears promising in a management context.

Table 5.1. Comparisons of parameters for spawner-recruit[1] (α, β, ϕ, σ_R), growth[2] parameters (L_∞ and κ, σ, σ_r), gear selectivity[3] (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	$N_4 + N_5 + N_6$	$0.5\sum_{a=2}^{6} N_a$	$0.5\sum_{a=6}^{10} N_a$

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[1] $R_t = \alpha S_{t-r}/(1+\beta S_{t-r})e^{\varepsilon_t}, \varepsilon_t = \phi\varepsilon_{t-1} + a_t, a_t \sim N(0,\sigma_R^{\ 2})$

[2] $L_{t+1} = L_\infty(1-e^{-\kappa}) + e^{-\kappa}L_t + \varepsilon_t^*, \varepsilon_t^* \sim N(0,\sigma^2), L_r \sim N(\mu_r,\sigma_r^2), r = 1$

[3] $s_l = 1/(1+e^{-\gamma(l-L_{50})})$

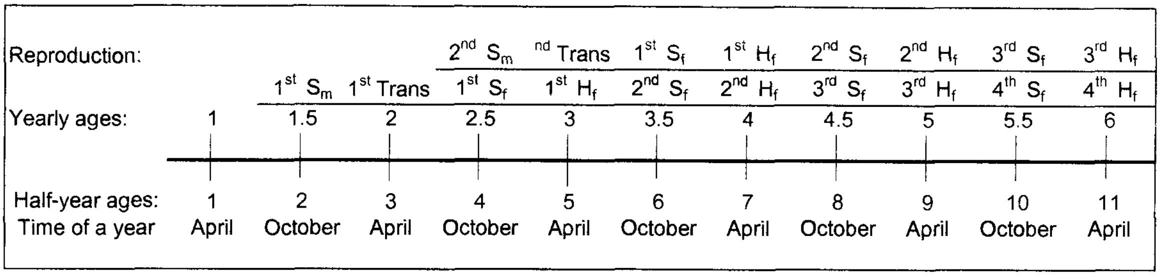
Table 5.2. Optimal fishing mortality (*F*), objective function value (*f*), maximum cumulative yield (MaxY, units of t) and risk of population decline averaged over the entire time period under various levels of gear selectivity parameter L_{50} for populations H_pop, K_pop and B_pop.

Population	L_{50}	F	f	MaxY	Risk
H_pop	16.72	1.0	0.9525	26739	0.026
K_pop	13.18	0.21	0.8956	12672	0.064
K_pop	16.72	0.30	0.8980	11501	0.052
K_pop	19.12	0.46	0.9014	10797	0.063
B_pop	16.72	0.20	0.8893	17322	0.061
B_pop	19.12	0.27	0.8912	16473	0.052
B_pop	20.86	0.39	0.8971	16297	0.053

Table 5.3. 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 seasonal natural mortality, growth and exploitation. 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	32796	0.041
0.5	E	0.8	0.40	0.9361	29702	0.041
0.667	E	0.8	0.40	0.9357	26919	0.041
0.333	H	0.8	0.52	0.8745	29036	0.079
0.5	H	0.8	0.52	0.8756	29876	0.079
0.667	H	0.8	0.52	0.8760	30852	0.079
0.333	E	0.5	0.46	0.9647	30388	0.024
0.5	E	0.5	0.46	0.9644	27527	0.024
0.667	E	0.5	0.46	0.9676	25211	0.024
0.333	H	0.5	0.58	0.8991	29797	0.078
0.5	H	0.5	0.58	0.8996	30701	0.078
0.667	H	0.5	0.58	0.9002	31646	0.078

Part 1: Cohort time frame



Part 2: Yearly time frame

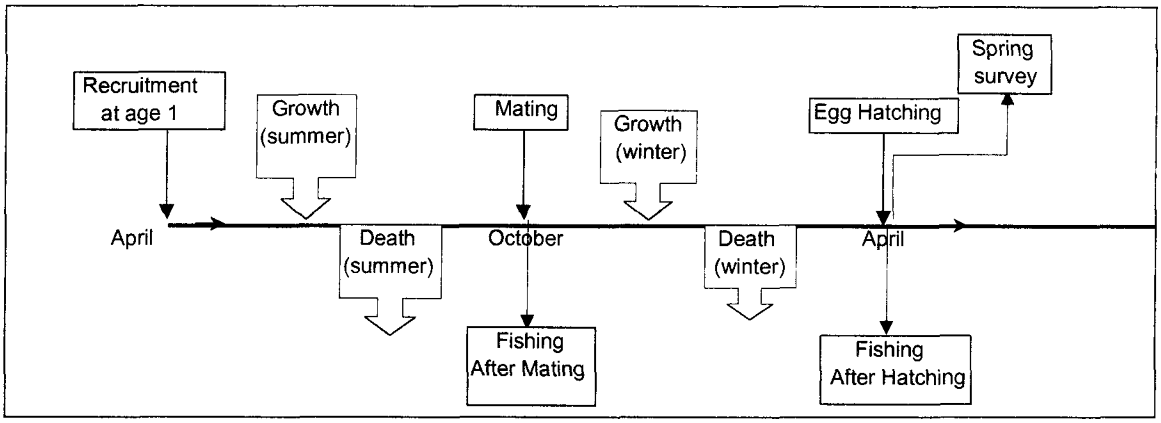


Figure 5.1. Part 1: Schematic representation of cohort life history with time lines of yearly ages along with half-year ages. H_f stands for female egg hatching, S_f for female mating, S_m for male mating and Trans. for sex transformation. Part 2: Schematic representation of life history processes in a one-year scheme.

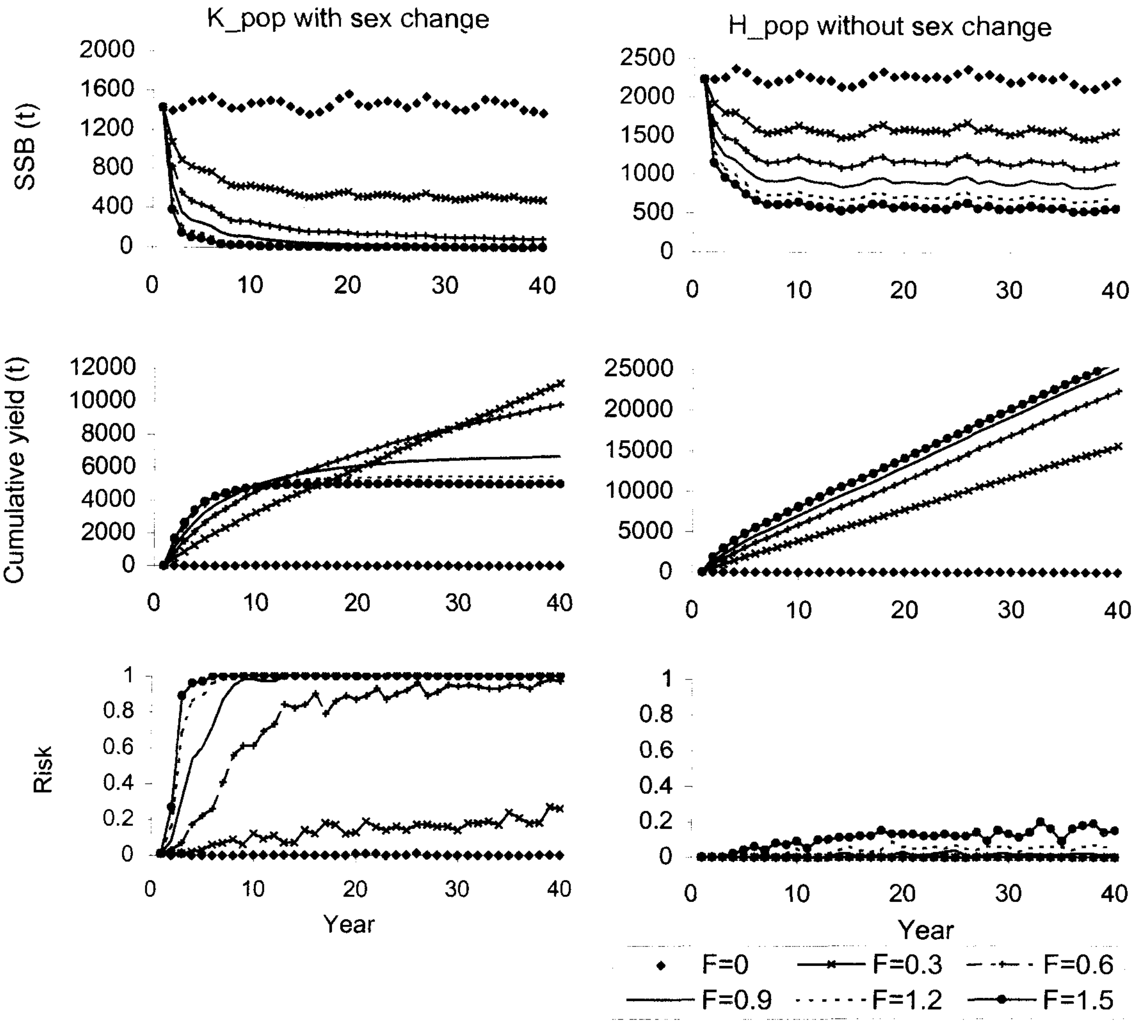


Figure 5.2. Comparisons of spawning stock biomass (SSB), cumulative yield, and risk over time from 6 levels of fishing mortality *F* without threshold management between the Kachemak Bay type population (K_pop) and the hypothetical population (H_pop).

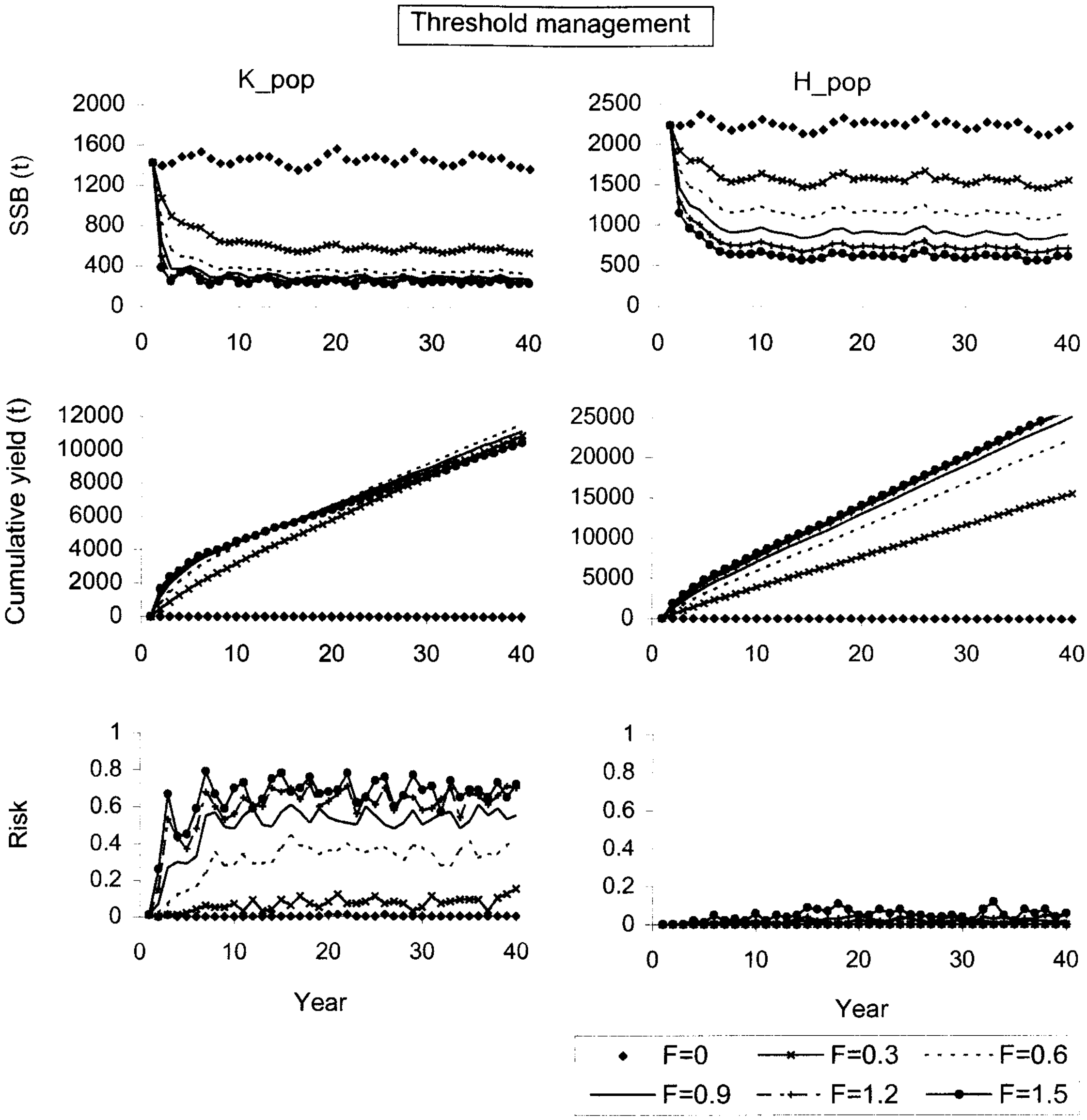


Figure 5.3. Comparisons between the Kachemak Bay type population (K_pop) and the hypothetical population (H_pop) of spawning stock biomass (SSB), cumulative yield, and risk over time from 6 levels of fishing mortality *F* with threshold being 20% of the virgin spawning stock biomass.

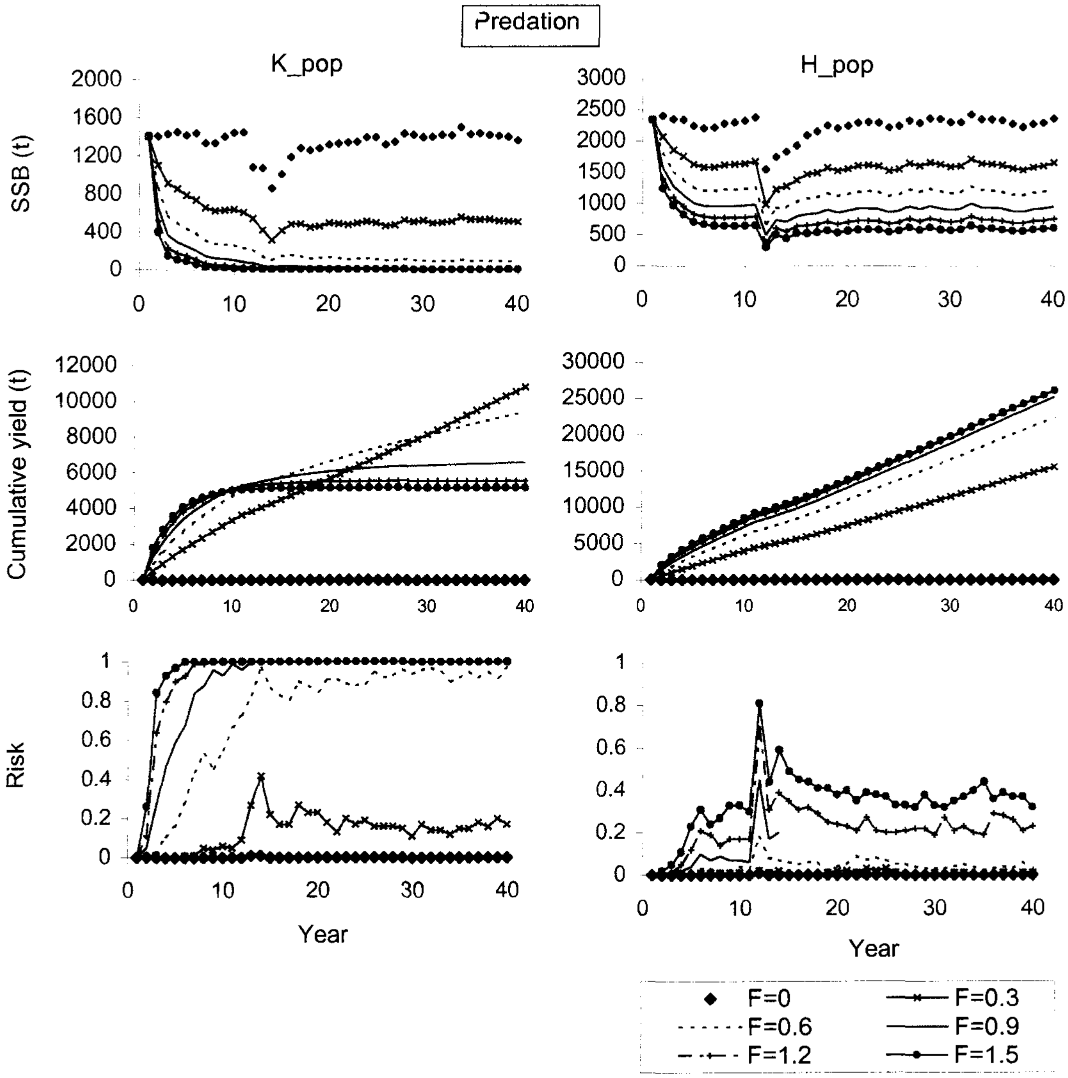


Figure 5.4. Comparisons of spawning stock biomass (SSB), cumulative yield, and risk over time from 6 levels of fishing mortality *F* without threshold management between the Kachemak Bay type population (K_pop) and the hypothetical population (H_pop). There was a sudden increase of predation mortality for individuals at ages 1 and 2, 10 years after exploitation.

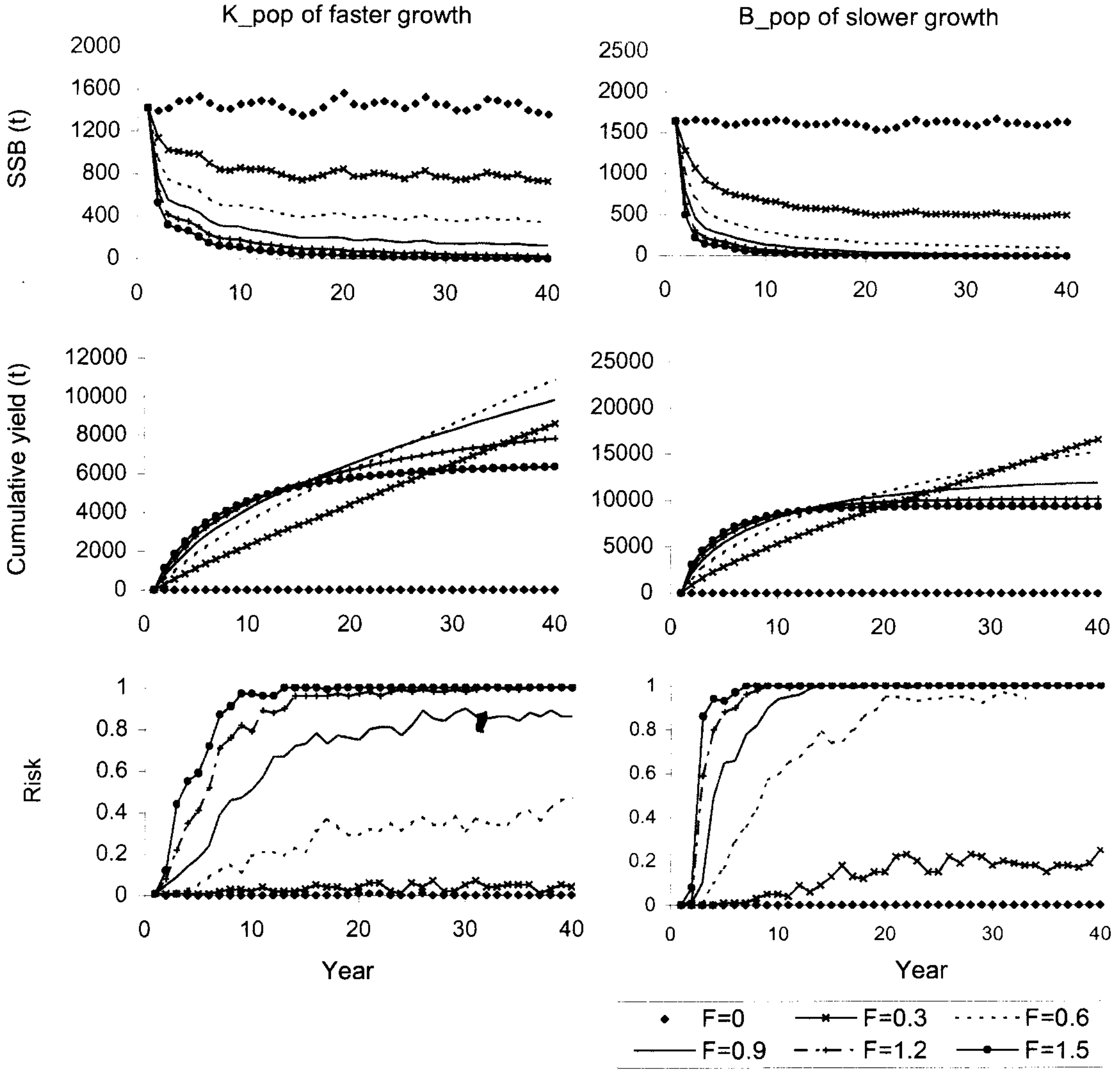


Figure 5.5. Comparisons of spawning stock biomass (SSB), cumulative yield, and risk over time from 6 levels of fishing mortality *F* without threshold management between the Kachemak Bay type population (K_pop) and the northern Barents Sea population (B_pop) with $L_{50} = 19.12$.

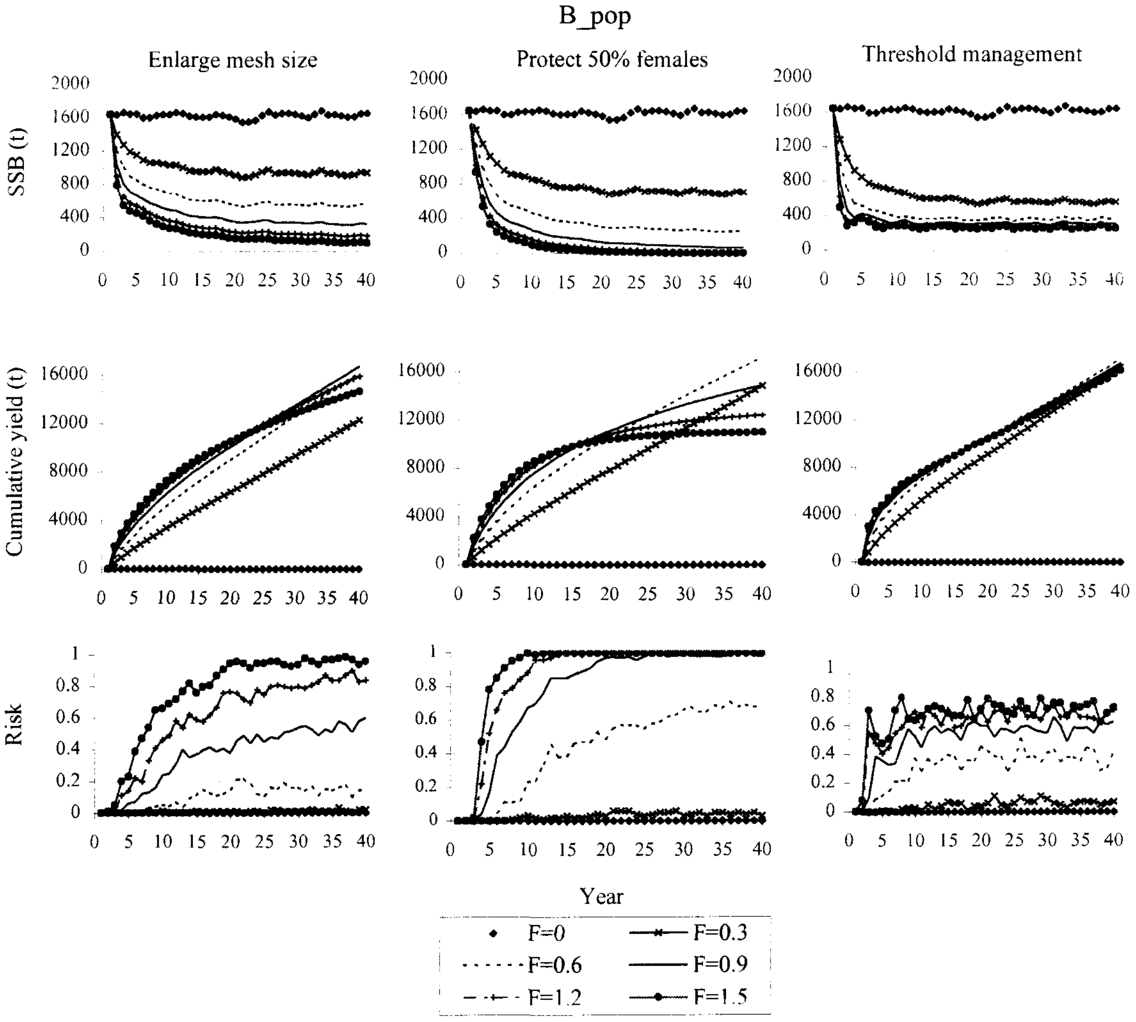


Figure 5.6. Comparisons of spawning stock biomass (SSB), cumulative yield, and risk over time from 6 levels of fishing mortality *F* for the B_pop under three scenarios: enlarge mesh size (L_{50} = 22.24); use standard mesh size (L_{50} = 19.12), but protect 50% of females; use standard mesh size and threshold management (20% of virgin SSB).

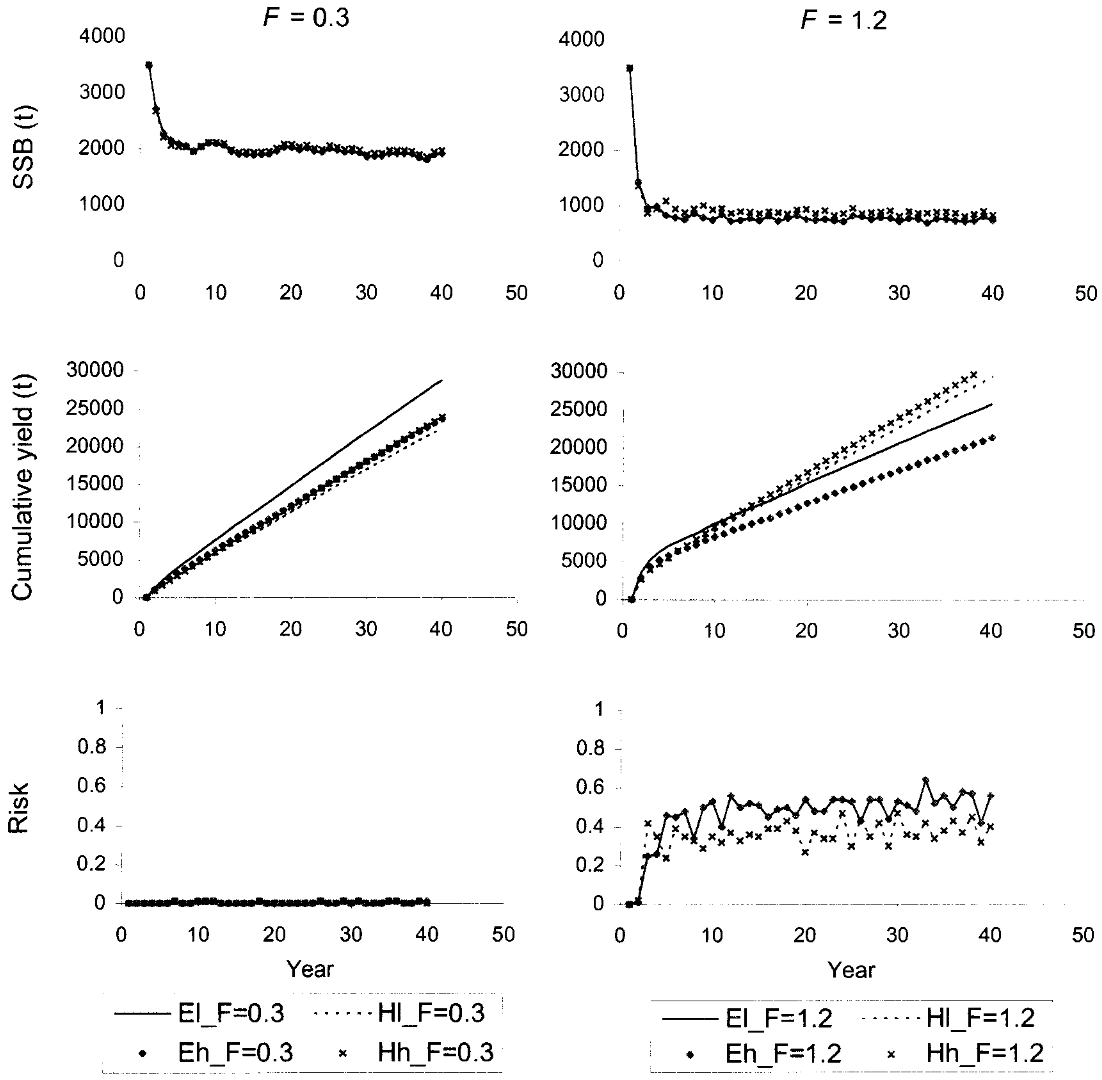


Figure 5.7. Within panel comparisons of spawning stock biomass (SSB), cumulative yield, and risk from a fishery after spring egg hatching (Hl: $\phi_M = 0.333$; Hh: $\phi_M = 0.667$) and a fishery after fall mating and egg extrusion (El: $\phi_M = 0.333$; Eh: $\phi_M = 0.667$); Between column comparisons of these quantities are shown under two levels of fishing mortality *F*.

Chapter 6 Summary

6.1 ESTIMATING NATURAL MORTALITY AND OTHER POPULATION PARAMETERS

Chapter 2 describes a length-based model designed for investigating dynamics of *Pandalus* populations. The model estimates growth parameters including those in the von Bertalanffy function (VB) (L_∞, κ), the standard deviation of each growth increment (σ), the standard deviation of length frequency at recruitment age r (σ_r) and time variable mean length at recruitment ($\mu_{r,t}$). The model also estimates annual recruitment to the population at age r (R_t), instantaneous fishing mortality for fully selected individuals (F_t) and gear selectivity parameters (L_{50}, γ). More importantly, motivated by the great need to understand natural mortality (M) level, I relaxed the common assumption of constant M to allow annual variations. Because the model becomes so complex, the question of estimability of these parameters is important.

To answer the question regarding estimability, simulation-estimation experiments were conducted. The first step was to generate data using the model along with known parameters, among which M_t, R_t and $\mu_{r,t}$ were given random variations. Observation errors were also incorporated into the generated data. The second step was to estimate parameters based on the generated data. The last step was to compare the true parameter values with those estimated and obtain biases for the parameter estimates. With the simulation-estimation experiments, the effect of measurement errors was examined. In addition, with underlying variable M for each year, model misspecification of assuming constant M was examined, and model sensitivity to calibration coefficient q was examined.

The results from the experiments are encouraging and instructive. With underlying varying *M*, estimating annual variations in *M* is not only possible but also desirable. Assuming no model misspecification, measurement error (ME) is the most significant factor affecting parameter estimation. More specifically, *M* estimates are primarily affected by ME in survey biomass data. Absence of ME in biomass can lead to rather accurate *M* estimates. However, high ME in survey biomass increases the variability of the *M* and *R* estimates. *F* estimates are robust to ME in biomass, and primarily controlled by the ME in yield data. Sensitivity of *q* demonstrated that *q* was not estimable and should be specified at some credible level. On the other hand, with selectivity parameters assumed constant over time, they were generally well estimated.

In addition, this chapter also explored aspects intrinsic to the model design, such as initial parameters and data weighting. Essentially, initial *M* and *F* can be specified at realistic levels, but initial *R* should be estimated in order to get good parameter estimates for the following years. Under the same estimation model, both varying and constant *R* and *M* for each of the initial years, where data were not available, produced the same bias ratios of the parameter estimates, which implied that the model was robust to parameter variation in the initial period. Different data weightings produced only slight differences in parameter estimates, and it would be appropriate to weight various data categories based on their variance ratios. In addition, *F* estimates tended to be more robust to different weight than those of *R* and *M*.

Finally, the model was applied to the *P. borealis* population in Kachemak Bay. Parameter estimates were obtained based on data of yield, survey biomass and length frequency distributions from 1978 to 1991. The ability of estimating terminal parameters of the model was examined using retrospective analysis, and it showed great consistency in parameter estimates from data of various sizes. The implications from this chapter are that accounting for parameter uncertainties is important, and a good measure of survey biomass is desirable.

6.2 HIGH NATURAL MORTALITY DETERMINED POPULATION FAILURE

Chapter 3 is the first manuscript written to respond to the question, "What caused the collapse of the *P. borealis* population in Kachemak Bay?" To have a longer time series, survey length frequency data from 1971 to 1974 were obtained from a different source (NMFS) and incorporated into population analysis. The missing length frequencies for years from 1975 to 1977 were filled arbitrarily by observations from 1971 to 1973 respectively, to stabilize the parameter estimation. Both survey biomass and commercial yield have complete data back to 1971. In addition, weighting factors on the various data and the M penalty term (λ_M) are different from those used in chapter 2; therefore, the parameter estimates from this chapter are slightly different from those in chapter 2. Nevertheless, with the purpose of performing retrospective projections, no accurate parameter values are necessary, and only the trend in the parameter time series is important.

The *P. borealis* population was retrospectively projected with the F levels equivalent to the presently estimated ones but under different assumptions on M and R. The most prominent conclusion from these exercises was that an increasing trend in M appeared to be the most likely explanation of the decline of the *P. borealis* population in Kachemak Bay; recruitment did not seem to be as crucial in this case. In addition, when the estimated M values were used in the projections, the population had a high background (no fishing) risk of quasi-extinction in 1991 (56%). It appears that the fate of the *P. borealis* population to collapse could not have been altered by lessening fishing or executing early fishery closure. This realization further calls for attention to research on mechanism of natural death. Additional research is also needed on the sensitivity of these results to the historical data.

As forage species, *Pandalus* shrimps are subject to consumption by several predators, such as cod (*Gadus* spp.), halibut (*Reinhardtius* spp.) and walleye pollock (*Theragra chalcogramma*) (e.g., Jackson et al. 1983; Albers and Anderson 1985; Zgurovsky et al. 1990). Unfortunately, the common assumption of constant M may have veiled the potential truth that high *M* has resulted in the collapse of many *Pandalus* fisheries. Therefore, it might be necessary to revisit the assessments of many *Pandalus* populations using length-based models that estimate annual variations in *M* along with those in *R* as in this chapter. In addition, developing population models that incorporate the relationship between *M* and the abundance of predators will be helpful for predicting the dynamics of forage *Pandalus* species.

6.3 OPTIMIZING HARVESTING AND MANAGEMENT

The significance of chapter 4 is that it compares the consequences of various levels of harvesting under various *M* and *R* situations. Under the scenario of constant *M* and *R*, a population can be sustained at any level of *F*, although the risk of going below the threshold could be high under high *F*. On the other hand, despite constant *M*, a population under a Beverton-Holt (B-H) recruitment model will be driven below its threshold in only a few years under continuous exploitation higher than *F* of 0.6, and to completely collapse under *F* higher than 0.9. Threshold management can prevent overfishing and population collapse. This exercise highlights the importance of executing threshold management, i.e., closing the fishery when population levels go below its threshold. Under the scenarios of constant *M* and *R* or increasing *M*, harvesting at a level lower than the optimal one is not desirable; instead, a reasonably high harvest level in conjunction with fishery closure provides the most benefit. In reality, *Pandalus* populations in Greenland, Icelandic and North Sea waters are managed precautionarily based on surveys, and fishery closures are enforced when population levels were low (Anon. 1994). Neither the Norwegian nor Russian *Pandalus* shrimp fisheries are managed in the Barents Sea, but it was proposed that the management strategies must be based on good knowledge of prey-predator relationships (shrimp/cod) (Anon. 1994). The simulations in this chapter have manifested the need to understand the processes of *M* and *R* before optimal harvesting can be determined.

Another significant aspect that this chapter explored is the establishment of guideline harvest levels (GHLs). Establishing GHLs is essential to fishery management. GHL is estimated annually based on existing knowledge about the present population abundance, *M* and *R* levels. The management effectiveness can be affected by available knowledge on either of these three factors. When *M* is specified 0.2 lower than the true values, the population tends to be overfished, and thus exposed to high risk of collapse. Nevertheless, the management can be greatly improved if the population is sampled once every year given the sampling provides good estimates of the population abundance levels. Under the situation of knowing the true *M*, misspecifying *R* results in very small differences as long as the population is sampled once every year without error. While accurate measurement of biomass may be unrealistic, I speculate that the general direction of these conclusions would be the same. On the other hand, overspecified *R* can be disastrous if sampling occurs once every three or more years. Based on the simulation results, research effort should be more directed to understanding the natural mortality process and to conduct frequent research surveys.

6.4 FURTHER IMPROVING *PANDALUS* FISHERY MANAGEMENT

Life history aspects such as growth, mortality and particularly sex change for *Pandalus* species are pertinent to fishery management. Taking these factors into account is needed for sound management. *P. borealis* stocks differ broadly in growth, death rate and age/size at maturity throughout its distribution (e.g., Rasmussen 1953). Chapter 5 compares 3 populations, a hypothetical one without sex change and two with protandric hermaphroditism differing in growth rate and life-span, with repect to their response to harvest levels. Populations with protandry are more subject to recruitment overfishing. Protecting protandric females, as commonly proposed, while allowing high exploitation on other size-category shrimps, can lead to population collapse. Increasing mesh size slows down the speed of collapse under high exploitation, but it cannot change the potential declining trend. On the other hand, threshold management is most efficient in protecting a population from overfishing (at least if a spawner-recruit relationship exists).

In addition, chapter 5 also explores an important issue of optimal fishing season. Due to lack of knowledge on seasonal population dynamics, proposed or practiced seasonal fishing strategies, such as fishery closure during the breeding and ovigerous period to protect egg-bearing females, often lack a strong scientific basis. Through simulation analyses in chapter 5, the optimal fishing season was found to be primarily dependent on three factors: exploitation level, patterns of seasonal growth and natural death. When harvest level is high, sooner or later depending on the relative level of natural mortality in winter and summer, fishing after spring egg hatching produces higher yield and lower risk of population collapse. Under low fishing mortality, assuming growth in summer is faster than in winter, fishing immediately after fall mating and egg extrusion produced higher yield if M in summer is less than or equal to that in winter. However, if M in summer is greater than in winter, fishing after egg hatching is superior to fishing after fall mating and egg extrusion not only in terms of higher yield but also lower risk of population collapse. On the other hand, if there is no growth difference in summer and in winter, fishing after fall mating and egg extrusion had higher yield only if M in summer is smaller than that in winter. On the whole, better understanding of seasonal difference in M is the key to optimizing fishing season. Proper population analysis of estimating seasonal M in conjunction with biennual survey will make the optimization in fishing season possible. Again, due to the close relationship between predation mortality and *Pandalus* abundance, monitoring the seasonal distribution and abundance of predators will be helpful for estimating seasonal M. However, due to the lack of seasonal data on growth and sex transformation, an explicit seasonal estimation model was not constructed for the Kachemak Bay *P. borealis* population.

6.5 FUTURE DIRECTIONS

From the *Pandalus* stocks in the north Pacific to those in the north Atlantic, all have been subject to fluctuation or collapse, intensive interaction with predators, or strong perturbation from human activities. Advice for management is either not given due to the equal or stronger impact from fishery-independent factors such as predation and recruitment than from the fishery, or ineffective because the agreed TACs have not made any restrictions of the fishery necessary (Anon. 1994). These unwelcome or undesirable results are partially due to the lack of comprehensive knowledge on population dynamics and assessment.

Pandalus populations living in different areas or different periods, or any other population in general, may have varying patterns of growth, maturity, recruitment and particularly natural mortality processes. This results in diverse population dynamics and requires different actions for management. Therefore, it would be constructive to conduct a worldwide synthesis of *Pandalus* population parameters in a meta-analysis. Eventually, this would be particularly useful for stocks for which only limited length frequency or survey information is available.

The next promising step in assessment would be to move toward Bayesian analyses with length-based models by judiciously using the results of the meta-analysis. Bayesian analyses allow direct computation of posterior distributions related to population size and the probability of collapse, expressions that are straightforward and understandable to fishery managers and fishermen.

Management for *Pandalus* populations based on single-species considerations will undoubtedly benefit from the comprehension of population parameters and dynamics. However, due to the broad existence of intensive predation, management based on ecosystem considerations would be more desirable and promising. For largely isolated stocks, such as those in fjords, adaptive management experiments can be designed to test hypotheses and to develop optimal ecosystem-based management strategies. For instance, active cropping of predators in closed waters may lead to direct testing of the hypothesis that predators control shrimp population levels. In addition, consequences regarding ecosystem health and economic profit could also be evaluated. Kachemak Bay may be one place where such a program could be attempted. A deliberate cropping of predators could be attempted in selected portions of the bay without much cost by enlisting the aid of industry. Some other areas would be closed to fishing year-round. The early 2000s may be an ideal time for this experiment as there is speculation that a cool period favorable to shrimps may be occurring (Anderson and Piatt 1999). However, due to the migratory nature of cod and other predators, the implementation of such a strategy might be difficult to achieve with success in open waters.

Spatial structure is an important aspect for populations with meroplanktonic larvae, yet it has received comparatively little attention in population theory and in its application to fisheries (Orensanz and Jamieson 1998). *P. borealis* was found to be distributed continuously in deep waters off Labrador and northeastern Newfoundland with discrete areas of high densities (Lilly et al. 1998). In contrast, the distribution of *P. borealis* on the eastern Scotian Shelf (northwest Atlantic) south of Labrador and Newfoundland is very patchy, and the northeasterly Nova Scotia current will carry larvae into unsuitable areas only a few miles to the west (Koeller 1999). Stock assessment and fishery management relies heavily on survey data, however, an aggregated distribution can result in lower survey biomass estimates if the survey misses more productive areas, or it can overestimate the biomass when encountering these productive areas (Orensanz and Jamieson 1998). Thus, it is necessary to develop or apply more efficient sampling methods, such as adaptive sampling designs (Thompson and Seber 1996), which was pioneered by Woodby (1998) in shellfish research.

Spatial distribution of *Pandalus* populations is closely related to depth, habitat and especially water column temperature (e.g., Apollonio et al. 1986; Koeller 1999). Thus, environmental factors, especially temperature, should be collected and can be used as ancillary information to increase precision in abundance estimates. Mapping surface sediment type facilitated research surveys of George Bank scallops (Smith and Robert 1998). In Kachemak Bay, the distribution of *P. borealis* shifted significantly from all over the bay to east of the Homer Spit only after the 1977 climate warm regime (Gustafson 1994). This implied that temperature might have contributed much to the spatial structure of *P. borealis* populations. Stock assessment and fishery management should explicitly take spatial processes into consideration.

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Appendix 1. Detailed descriptions of the length-based population model for chapter 2

We assumed that the length frequency of shrimp population at recruitment is a simple discrete normal distribution (N$_D$). The probability density function for the lengths x at recruiting age r and at the start of time t is:

$$f_{r,t}(x) \sim N_D(\mu_{r,t}, \sigma_r^2) = e^{-\frac{1}{2\sigma_r^2}(x-\mu_{r,t})^2} \Big/ \xi_{r,t}, \text{ where } \xi_{r,t} = \sum_x e^{-\frac{1}{2\sigma_r^2}(x-\mu_{r,t})^2}.$$

The abundance of the newly recruited shrimp at length x is: $N_{r,t}(x) = N_{r,t} \cdot f_{r,t}(x)$. To obtain abundance $N_{a+1,\,t+1}(x)$ at age a+1 and at the start of time t+1 from abundance $N_{a,t}(x)$ (starting at age r), the process of growth was accounted for first, followed by natural mortality, and then fishing mortality.

The standard von Bertalanffy growth model is utilized to express the growth pattern from one age to next, assuming that growth is constant over time:

$L_{a'} = L_\infty(1-\rho) + \rho L_a + \varepsilon$, where $\rho = e^{-\kappa}$ is the Brody coefficient, and $\varepsilon \sim N(0, \sigma^2)$. The expected length and variance at age $a+$ after growth for an individual of length x at age a from Cohen and Fishman (1980) are:

$$\mu_{a',t+1} = L_\infty(1-\rho) + \rho\mu_{a,t}, \text{ and } \sigma_{a'} = \sigma^2 \frac{1-\rho^{2(a+1-r)}}{1-\rho^2} + \rho^{2(a+1-r)}\sigma_r^2.$$

After one growth increment, the relative distribution of lengths $p_{a',t'}(L)$ is:

$$p_{a',t'}(L) = \sum_x f_{a,t}(x) e^{-\frac{1}{2\sigma_{a'}^2}(L-\mu_{a',t+1}(x))^2}.$$

The absolute abundance, $N_{a+1,\,t+1}(x)$, at the start of time t+1 after and time-dependent natural mortality M_t and fishing mortality $F_t s_x$ during time period t is:

$$N_{a+1,t+1}(x) = N_{a,t}\, p_{a',t'}(x) e^{-(M_t+F_t s_x)}.$$

The term s_x is the selectivity function that follows the common logistic curve:

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

Natural mortality is assumed constant over length and age. We assume that survey takes place at the start of time t+1, after shrimp recruit to the population. The abundances over all ages including recruitment $N_{r,t+1}(x)$ and $N_{a+1,t+1}(x)$, where a is less than maximum age A, are summed to obtain the length distributions of the population at the start of time t+1:

$$N_{t+1}(x) = N_{r,t+1} + \sum_{a=r}^{A-1} N_{a+1,t+1}(x).$$

Therefore, the expected survey biomass at time t+1 can be calculated as:

$$B_{t+1} = \sum_x qN_{t+1}(x)s_x W_x,$$

where q is a constant calibration coefficient for the survey. Weight at length is modeled as the allometric relationship: $W_x = \alpha^* x^{\beta^*}$. The parameters α^* (0.000549) and β^* (3.067179) were obtained independently from the survey conducted in spring 1997, the same time of a year when survey biomass indices and length frequency distributions were collected. The expected length frequency distributions in survey samples at time t+1 are:

$$LF_{t+1}(x) = n_{t+1}\frac{N_{t+1}(x)s_x}{\sum_x N_{t+1}(x)s_x},$$ where n_{t+1} is the sample size for measuring length.

Commercial yield is summed over the whole time period t until the start of time t+1 and denoted as Y_{t+1} so that each yield has the same subscript as survey data. Therefore, the estimated yield from the model at the start of time t+1 is:

$$Y_{t+1} = \sum_x N_{t'}(x)(1-e^{-F_{t,x}})W_x.$$

For stability and easy convergence in estimating parameters, F_t is calculated as the product of its approximation $\left(\frac{Y_{t+1}^{obs}}{B_{t+1}^{obs}+Y_{t+1}^{obs}}\right)$ and an exponential deviation term (e^{υ_t}), i.e.,

$$F_t = \frac{Y_{t+1}^{obs}}{B_{t+1}^{obs}+Y_{t+1}^{obs}} e^{\upsilon_t}.$$

Appendix 2. Details of the length-based model for chapter 3

Assume that the length frequency distribution of shrimp population at recruitment, before entering the fishery, is a simple discrete normal distribution. The probability density function for the lengths x at recruiting age r and time t is:

$$f_{r,t}(x) \sim N_D(\mu_{r,t}, \sigma_r^2) = e^{-\frac{1}{2\sigma_r^2}(x-\mu_{r,t})^2} \Big/ \xi_{r,t}, \text{ where } \xi_{r,t} = \sum_x e^{-\frac{1}{2\sigma_r^2}(x-\mu_{r,t})^2}.$$

The abundance of the newly recruited shrimp at length x is: $N_{r,t}(x) = N_{r,t} \cdot f_{r,t}(x)$. To obtain abundance $N_{a+1,t+1}(x)$ from abundance $N_{a,t}(x)$ at age a (starting at age r) and time t, the process of growth was modeled first followed by mortality. The standard von Bertalanffy growth model is utilized to express the growth pattern from one age to next, assuming that growth is constant over time:

$L_{a'} = L_\infty(1-\rho) + \rho L_a + \varepsilon$, where $\rho = e^{-\kappa}$ is the Brody coefficient, and $\varepsilon \sim N(0, \sigma^2)$. The expected length and variance at age $a+1$ for an individual of length x at age a are from Cohen and Fishman (1980):

$$\mu_{a',t+1}(x) = L_\infty(1-\rho) + \rho\mu_{a,t}, \text{ and } \sigma_{a'} = \sigma^2 \frac{1-\rho^{2(a+1-r)}}{1-\rho^2} + \rho^{2(a+1-r)}\sigma_r^2.$$

After one growth increment, the relative distribution of lengths $p_{a',t'}(L)$ is:

$$p_{a',t'}(L) = \sum_x f_{a,t}(x) e^{-\frac{1}{2\sigma_{a'}^2}(L-\mu_{a',t+1}(x))^2}.$$

Assume full recruitment fishing mortality at time t is proportional to the ratio of observed yield and estimated biomass from the survey at time t with a deviation term e^{υ_t}:

$F_t = \frac{Y_t^{obs}}{B_t^{obs}} e^{\upsilon_t}$. The selectivity function follows the common assumption of a logistic curve: $s_x = \frac{1}{1+e^{-\gamma(x-L_{50})}}$, where γ is the shape parameter and $L_{50\%}$ is the length at which 50% of the individuals are vulnerable to fishing.

Absolute abundance, $N_{a+1,\,t+1}(L)$, at the start of time t+1 after fishing mortality $F_t s_x$ and natural mortality M_t is: $N_{a+1,t+1}(L) = N_{a,t}\, p_{a',t'}(L) e^{-(M_t + F_t s_x)}$, where $M_t + F_t s_x = Z_{t,x}$ is the total mortality at time t, and natural mortality M_t is assumed to be constant for all length intervals after recruitment.

Abundance is summed over all ages for length L at time t to get length distributions of the population at time t: $N_{t,x} = \sum_a N_{a,t,x}$. Length frequency distributions in the sample at time t are: $LF_{t,x} = n \dfrac{N_{t,x} s_x}{\sum_x N_{t,x} s_x}$, where n is the sample size for measuring length.

The expected survey biomass at time t is: $B_t = \sum_x N_{t,x} s_x W_x$, where weight at length is modeled as the allometric relationship: $W_x = \alpha^* x^{\beta^*}$. The parameters α^* and β^* were obtained independently from the survey conducted in spring 1997, the same time of year when survey biomass indices and length frequency distributions were collected. We assume the length-weight relationship has no interannual variation. Estimated yield from the model at time t is:

$$Y_t = \sum_x N_{t,x} \frac{F_{t,x}}{Z_{t,x}} (1 - e^{-Z_{t,x}}) W_x .$$

Expected female abundance at time t and length x is: $FN_{t,x} = N_{t,x} \chi_{t,x}$, where $\chi_{t,x}$ is the female proportion at length x and time t. This proportion is modeled as a logistic function: $\chi_x = \dfrac{1}{1 + e^{-\delta (x - P_{50\%})}}$, where $P_{50\%}$ is the length at which 50% individuals are composed of females. Note that the female proportion parameters were estimated from the survey data outside the model to avoid complications.

Parameters were estimated by minimizing the objective function:

$$f = \lambda_B \sum_t (\sqrt{B'_t} - \sqrt{B_t})^2 + \lambda_L \sum_t \sum_l (\sqrt{LF'_{t,l}} - \sqrt{LF_{t,l}})^2 + \lambda_Y \sum_t (\sqrt{Y'_t} - \sqrt{Y_t})^2$$
$$+ \lambda_R \sum_t [\ln(R'_t) - \ln(R_t)]^2 + \lambda_M \sum_t \delta_t^2,$$

where variables B'_t, LF'_t and Y'_t denote observed values, while those without primes denote corresponding predicted values. The component $\lambda_R \sum_t [\ln(R'_t) - \ln(R_t)]^2$ is for estimating the spawner-recruitment parameters α, β and ϕ in the Beverton-Holt (B-H) *S-R* relationship with first-order autocorrelation, which fitted the recruitment estimates best:

$$\ln(R'_t) = \ln(\alpha S_{t-1}) - \ln(1 + \beta S_{t-1}) + \phi\varepsilon_{t-1} + \upsilon_t = \ln(R_t) + \upsilon_t,$$

where R'_t are observed values, $\phi\varepsilon_{t-1}$ is the first-order autocorrelated error term, and $\upsilon_t \sim N(0,\sigma^2)$. The last part of the objective function, $\lambda_M \sum_t \delta_t^2$, is a penalty term controlling the degree of variability in the time series of *M* from year to year.

The weighting factors λ's for the observations were determined based on their accuracy and variance ratio ($\lambda_B = \lambda_Y = 1.0$, λ_L (1971 to 1974 and 1978 to 1991) = 4.0, and λ_L (1975 to 1977) = 1.0). Weights λ_R and λ_M were determined based on the assumptions on the variation in the spawner-recruitment parameters and *M* (λ_R=5.0, and λ_M=10.0).