

A RECURSIVE AGE-STRUCTURED MODEL
OF ALASKAN RED KING CRAB

by

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Fishery Research Bulletin No. 88-06

Alaska Department of Fish and Game
Division of Commercial Fisheries
Juneau, Alaska

July 1988

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ACKNOWLEDGMENTS

Special thanks are due to Rich Marasco, Jerry Reeves, Joe Terry, Bob Otto of the National Marine Fisheries Service and Don Collinsworth and Gordon Kruse of the Alaska Department of Fish and Game.

PROJECT SPONSORSHIP

Support for this research was provided in part by the National Marine Fisheries Service, REFM, Northwest and Alaska Fisheries Center; the Alaska Department of Fish and Game; and the Agricultural Research Center, College of Agriculture and Home Economics, Washington State University (project no. 0691).

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ABSTRACT

The biological response model for red king crab (*Paralithodes camtschatica*) consists of seven estimated recruitment/growth functions and several definitional identities. The recruitment/growth formulations were derived from variations of Ricker's spawner-recruit framework and Deriso's compound growth technique. The seven behavioral relationships combine to form a recursive, age-structured growth model for sexually mature male and female king crab. The sexes are modeled separately to reflect the impact of males-only harvest regulations on population abundance. Primary research emphasis was given to the male equations because of this regulation. Individual single age class equations are derived for beginning stocks of 5-, 6-, 7-, and 8-year-old males, and for 5-year-old females; aggregate age class equations are derived for 9-to-14-year-old males, and for 6-to-14-year-old females. Statistical significance, overall fit and ability of these equations to predict history are very good.

KEY WORDS: Alaska king crab, recruitment, growth, trajectory adjusted intrinsic recruitment, biological response, population dynamics, age class

INTRODUCTION

The Alaskan king crab industry is in a transition period, recovering from a dramatic boom-bust cycle. "King crab" is the common name given to some crustaceans in the family of stone crabs, Lithodidae. Three species are commercially significant, including the red king crab (*Paralithodes camtschatica*), the blue king crab (*Paralithodes platypus*), and the brown or golden king crab (*Lithodes aequispina*). All three species inhabit waters of the north Pacific Ocean. They are similar in appearance though noticeably varied in shell color. The red king crab has been the cornerstone of the Alaskan king crab industry because of its large size; shallow, inshore distribution; and historically greater abundance. The other two king crab species, though harvested commercially, have been much less abundant and restricted to more localized and remote habitats. Harvest pressure and commercial importance of these two species has increased during the past 6 years principally because red king crab stocks have declined; only limited (primarily incidental) catches were made prior to 1981.

Statewide harvests of red king crab began an unprecedented period of growth in 1969 that continued through 1980. Harvests more than tripled, culminating in record catches of 185.7 million lb. Growth in the Bristol Bay fishery management area was largely responsible for the boom; Bristol Bay harvests rose from 8.6 million lb in 1970 to the record catch of 130 million lb in 1980. Within 3 years, however, the industry collapsed. King crab stocks were so scarce that the Alaska Department of Fish and Game (ADF&G) ordered complete closure of the Bristol Bay fishery in 1983. Statewide harvests plummeted to 26.9 million lb. Catch dropped an additional 10 million lb by 1985 (U.S. Department of Interior 1947-1975; ADF&G 1969-1983, 1970-1985). Depressed stock conditions persist today. The economic wake of this collapse has been extensive, involving virtually every participant in the fishery. Between 1980 and 1983, ex-vessel revenues to fishermen fell by more than 50%, dropping by \$93.2 million. Processor sales dropped \$178.0 million (a 60% reduction), while sales from wholesalers declined by \$304.2 million (a 66% reduction). Multimillion dollar fishing vessels were idled, others shifted into different fisheries, processing plants closed and an industry-wide restructuring commenced.

The significance of the collapse may be placed in perspective by considering the fact that the king crab fishery was the second most valuable Alaska seafood industry between 1968 and 1983. Only the combined ex-vessel value of all six salmonid species harvested in Alaska exceeded that of king crab (ADF&G 1969-1983). Yet, the statewide king crab catch rarely exceeded one-third the total catch of salmon, by weight.

The impact of the collapse extends well beyond the Alaskan economy. Butcher et al. (1981) identified direct linkages between the shellfish sector and the economy of the Puget Sound area in western Washington. Only 32% of total shellfish revenues were returned to the Alaskan economy in direct purchases of goods and services. Much of the remaining 68% were spent in the Seattle area for vessel maintenance and construction, gear and supplies, and general consumer goods. Moreover, most of the processing and cold storage firms were based in the Seattle area. The diminished flow of processed king crab

products to domestic and foreign markets also caused a tripling of nominal wholesale and retail prices between 1980 and 1986 (NMFS, 1969-1984).

Short of blaming the open-access milieu of this common property fishery, specific causes or contributing factors to the collapse must be identified if policymakers are to contribute to a recovery. Resolution of the underlying bioeconomics is essential. This report is one in a series of three that collectively comprise a bioeconomic analysis of the Alaskan king crab industry; it addresses the biological response submodels. A second report details the economic/market submodels, from initial harvest to final consumption (Matulich, Hanson and Mittelhammer, 1988a). The biological and economic submodels are then integrated in the final report to simulate industry responses/behavior under a variety of historical and potential future policy scenarios (Matulich, Hanson and Mittelhammer, 1988b). The research findings contained in these three reports are intended to provide insight into future management of the fishery.

This report presents a recursive, age-structured growth model for sexually mature male and female king crab. Individual age class equations are estimated statistically from National Marine Fisheries Service (NMFS) Bristol Bay Trawl Survey Data for red king crab. Recruitment/growth model specifications are derived from variations on Ricker's (1954) spawner-recruit framework and Deriso's (1980) compound growth model. The analysis presented here should be regarded as preliminary, in part, due to the short time series; only 18 years of data are available for analysis. Moreover, it represents a first attempt at formulating such a model in the context of an integrated bioeconomic analysis of the industry.

THEORETICAL ISSUES AND THE ANALYTICAL FRAMEWORK

Total harvest each season is a function of several factors, one of which is the abundance of legally harvestable king crab. Consequently, the biological submodel must quantify legal king crab biomass. The literature on king crab is extensive. Most studies, however, have focused on singular dimensions of crab life history, e.g., morphology, taxonomy, physiology, rather than providing systemic population models capable of estimating stock abundance. One exception is Balsiger's (1974) computer simulation model of the eastern Bering Sea king crab population. Using data from a series of tagging experiments conducted in 1954 through 1961 and 1966 through 1968, he estimated growth, age, natural mortality, and fishing exploitation rates. These results were used to develop a model simulating king crab population response to various management strategies.

Balsiger's work provides valuable information on the correlation between growth and age structure characteristics. It is not, however, amenable to use in general bioeconomic analysis of the industry because it cannot be updated easily; no Bering Sea tagging studies have been done in recent years. Population abundance data are available from biomass estimates generated from the annual NMFS summer trawl surveys. NMFS has related these size-frequency data as measured by carapace length, to age-frequency classifications of red king crab. These data represent only an approximation of age, not knife-edge recruitment into any given age class.

A principal objective of the biological model presented in this report is to link king crab life history characteristics with the impact of harvest in order to estimate legal crab abundance. In general, abundance of legally harvestable fish populations is influenced by the combined effects of growth, natural mortality, and harvest mortality on the exploited stocks (collectively referred to as escapement), and recruitment of new individuals into the legal population. Fluctuating recruitment clearly has affected population abundance and age structure in the southeastern Bering Sea king crab fishery. Accordingly, a dynamic framework is needed that incorporates changes in both growth and natural/harvest mortality.

Choosing a suitable analytical framework was complicated by the notion of recruitment as it pertains to king crab. Recruitment typically refers to simultaneous entry of juvenile fish into both the sexually mature and legally harvestable population. King crab are an exception. Male and female king crab appear to recruit into the sexually mature population around age 5 (when males average 4.0 in length). Females are somewhat smaller, may take longer to mature, but should be sexually mature by age 7 (4.3 in. in length). Recruitment into the harvestable population (harvest recruitment), however, does not occur until age 8, and is restricted to males; females never recruit into the harvestable population. Minimum size limits and a males-only harvest regulation restrict commercial harvest to male king crab at least 8 years old. Male king crab recruit into the commercial fishery an average of 3 yr after recruitment into the sexually mature population. Lack of coincidence between these two facets of recruitment underscores the need for an age-structured model. The biological response model must be able to predict the abundance of 5-year-old male recruits as a function of their parent spawning stock, and trace the movement of these newly matured males into the legally harvestable population 3 yr later and beyond. Female recruitment into the adult spawning stock must be modeled as well. Since females cannot be harvested, less attention is given to the age structure of female recruitment.

The age-structured biological model can be conceptualized as a recursive system consisting of seven stochastic response functions and several identities. The identities are defined with the empirical results in the next subsection. The general recursive structure is illustrated in Table 1. All biological variables represent total biomass of the specified age cohort in millions of live weight pounds at the start of the regulation harvest year (July 1). As such, they define beginning stocks of the given age cohort. Beginning stocks of the single age class cohorts (i.e., MALE5, MALE6, MALE7, MALE8, and FEM5) are comprised solely of new recruits from the previous age class. The aggregate cohorts (MALE914 and FEM614) include both new recruitment and net survival of the aggregate stocks from the previous period. The 9-to-14-year-old males (MALE914) can be pooled because they all are fully recruited into the harvestable population and generally managed as a single stock. Though information on specific age structure of the legal stocks might aid harvest management, incomplete age class catch statistics prevent modeling the classes independent of one another. The 6-to-14-year-old females (FEM614) can be aggregated to simplify model structure since they also are managed as a single cohort.

In general, individual age class abundance in period t may be conceived as some function of the previous age group in period $t-1$ (i.e., the prerecruit

Table 1. Hypothesized recursive structure of the king crab submodel.

Dependent Variable ^a	Potential Explanatory Population Variables ^a
5-year-old male biomass: MALE5	ADULT _{t-6}
6-year-old male biomass: MALE6	MALE5 _{t-1} , ADULT _{t-7}
7-year-old male biomass: MALE7	MALE6 _{t-1} , ADULT _{t-8}
8-year-old male biomass: MALE8	MALE7 _{t-1} , ADULT _{t-9}
9-to-14-year-old male biomass: MALE914	MALE8 _{t-1} , MALE914 _{t-1} , QHARVT _{t-1}
5-year-old female biomass: FEM5	ADULT _{t-6}
6-to-14-year-old female biomass: FEM614	FEM5 _{t-1} , FEM614 _{t-1}

^aAll biological variables are measured at the start of the harvest season (July 1) in millions of live weight pounds and represent new recruitment into the age class. ADULT_{t-i} is defined as total male and female spawning stock biomass ages 5 to 14 lagged i periods. QHARVT_{t-1} is total king crab harvest from the southeastern Bering Sea lagged one period.

cohort), and/or by the parent spawning stock that created it. This is the general hypothesis for MALE6, MALE7 and MALE8. Although current ADF&G size limit regulations permit harvesting a portion of 8-year-old males once the season opens, the beginning stock of MALE8 is not influenced directly by the exploitation. The potential influence of prerecruits on MALE5 and FEM5 king crab cannot be included explicitly in an analytical framework because no reliable population estimates are available for the 4-year-old age class. Current abundance of the aggregate 9-to-14-year-old male cohort ($MALE914_t$) potentially can be influenced by growth, recruitment and natural survival (i.e., $MALE8_{t-1}$ and $MALE914_{t-1}$, respectively), but also by harvest during the previous period ($QHARVT_{t-1}$). The aggregate female cohort ($FEM614_t$), may be conceptualized similarly, except that females cannot be harvested. The influence of recruitment and natural survival may be captured by $FEM5_{t-1}$ and $FEM614_{t-1}$, respectively. Neither of the aggregate cohorts can be explained by a single, parental spawning stock, therefore, no $ADULT_{t-1}$ term is included in either hypothesized relationship.

Representation of these seven relations in a specific analytical framework is derived from various theoretical and analytical approaches recorded in the literature (see Clark 1976, 1985; Cushing 1973; Ricker 1975; Schaefer 1968; Walters 1986; Waugh 1984).

The well-known Gordon-Schaefer surplus yield model could be used to represent the general relationship between harvest, effort, and legal stock abundance in the king crab fishery. However, Schaefer's use of a logistic equation to model stock abundance is too simplistic to be applied here (see Schaefer 1957, 1959). The logistic model treats total stock as a single unit based on aggregate abundance in the previous time period, independent of age structure. No effort is made to separate recruitment from general population growth.

Two commonly used alternatives to the logistic growth model are the Beverton-Holt dynamic pool framework (Beverton-Holt 1957) and the Ricker stock/recruitment relationship (Ricker 1954). The Beverton-Holt model actually is a harvest yield model, having been developed as an age-structured alternative to the Gordon-Schaefer surplus yield framework. Although Beverton and Holt segregated recruitment from total harvest in their model, the approach is inadequate to use here. Beverton and Holt assumed that individuals recruited into the fishery at a constant rate, tempered only by natural mortality and the age of recruitment. They had no explicit linkage between spawning stock density and recruit abundance. A variety of density dependent recruit functions have been fit to the Beverton-Holt model, but environmental fluctuations have, in practice, made it difficult to empirically estimate the relationship between spawning stock and recruitment (Waugh 1984).

Ricker, on the other hand, developed a specific stock-recruitment relationship that directly relates recruitment of a given age class to its parent population. The Ricker model is not a harvest yield framework; it focuses only on biological response of the exploited species. Though the Ricker method is not defined explicitly as an age-structured approach, it can be modified to model individual age classes in a recursive equation system. Thus, it provides a potential framework for modeling king crab recruitment and legal stock abundance.

Ricker originally modeled the number of recruits in time period t (R_t) as a nonlinear function of parental stock abundance $n+1$ periods earlier ($P_{t-(n+1)}$) and two estimated parameters (a , b) as shown in equation (1).

$$R_t = aP_{t-(n+1)} e^{-bP_{t-(n+1)}} \quad (1)$$

Both a and b are assumed to be positive, creating a dome-shaped, density dependent relationship between spawning stock abundance and recruitment. Ricker was investigating salmon population dynamics in which there is a single adult spawning cohort. The model originally was intended for species that reproduce only once before experiencing complete mortality. Furthermore, Ricker assumed that entry into the sexually mature population occurs simultaneously with harvest recruitment.

The Ricker framework need not be restricted to modeling adult and harvest recruitment. Any age class can be modeled so long as the assumption of a single age cohort is maintained. In this more general case (equation 2), recruitment can be viewed as entry into a specific age class, e.g., recruitment into the 6-year-old population.

$$R_{n,t} = a_n P_{t-(n+1)} e^{-b_n P_{t-(n+1)}} \quad (2)$$

Recruitment into the n^{th} age class in period t ($R_{n,t}$) is shown to be a function of properly lagged ($t-(n+1)$) parental spawning stock, reflecting the time period required for gestation and growth of the progeny into the given age/size class. The parameters a and b are denoted by subscript because they are unique to the age class being modeled.

Equation (2) provides an expectation of the recruitment that would occur if normal, average conditions prevail throughout the development of an age cohort, changing only as the age class develops. These rates also are expected to follow the same trajectory from one generation to the next.

This generalized Ricker framework predicts age class recruitment based on an underlying expected natural propensity to recruit. However, observed age class growth may fluctuate up or down from intrinsic tendencies. A Ricker approach ignores a variety of potential sources of predictive error including the effects of cyclic variations, environmental perturbations, structural changes in survival or mortality, measurement errors of previous age class stocks that are used to predict the abundance of some subsequent age class, and even errors inherent in using carapace size to estimate age classes of king crab. The longer the lag required for age class prediction, i.e., the further a particular age class is removed from the parental spawning stock estimates, the greater the potential for cumulative predictive error.

Species characterized by multiple age class spawning (hereafter referred to as multicohort species), like king crab, afford opportunities to adjust

estimates of the expected age class trajectory with intermediate observations of age class abundance. Observed deviations from the intrinsic recruitment trajectory prior to actual recruitment can be incorporated to improve the estimate of actual age class development. Such adjustment is not possible in the context of single spawning cohort species, like salmon, because intermediate observations of a particular cohort are not possible.

A Trajectory Adjusted Intrinsic Recruitment (TAIR) model is developed here to proxy the cumulative effects of predictive error on intrinsic recruitment tendencies. Specifically, an intermediate observation of age class abundance is used to adjust the intrinsic recruitment trajectory formed by a Ricker model. This TAIR framework is theoretically based, empirically flexible and it improves the predictive accuracy of observed age class development.

The TAIR specification initially hypothesized is given in equation (3) for 6-year-old male recruits.

$$\text{MALE6}_t = (\text{MALE6}_t^*)^{w_1} (c_6 \text{MALE5}_{t-1})^{w_2} \quad (3)$$

Recruitment of 6-year-old male king crab is hypothesized as a geometric weighted average of two expectations. The initial expectation, (MALE6_t) is formed as a Ricker spawner-recruit model in equation (6).

$$\text{MALE6}_t^* = (a_6 \text{ADULT}_{t-7})^{e^{-b_6 \text{ADULT}_{t-7}}} \quad (4)$$

The intrinsic recruitment trajectory is formed 7 yr earlier based solely upon spawning stock biomass. Total spawning stock biomass (ADULT_{t-7}) is aggregated for pedagogical exposition. It is disaggregated by sex later in the empirical section.

The adjustment to this trajectory involves two components: (1) the second expectation $(c_6 \text{MALE5}_{t-1})$, formed as the growth and survival of an intermediate observation of prerecruit biomass, and (2) geometric weights $(w_1$ and $w_2)$ that measure the relative importance of each expectation. These components adjust the intrinsic recruitment trajectory to more accurately reflect actual spawning, growth and survival. Accordingly, this weighted adjustment process proxies the cumulative effects of predictive error that cannot be modeled at the time of spawning. The parameter c_6 is an age specific growth and survival rate. The adjustment term is incorporated multiplicatively because Ricker (1954, p. 573) argued that inclusion of ". . . environmentally caused deviations from the reproductive norm must be multiplicative rather than additive."

The TAIR specification is empirically flexible, permitting the data to determine the tendency toward intrinsic recruitment. If $w_2 = 0$ and $w_1 = -1.0$, then the Ricker specification given in equation (4) predicts observed

recruitment. If $w_2 = 1.0$ and $w_1 = 0$, growth and survival of observed prerecruit biomass is sufficient to explain age class recruitment. When neither of these parameters are zero, then the TAIR specification predicts recruitment through an adjustment to the intrinsic recruitment rate.

Equations (3) and (4) are combined in (5) to model current abundance of 6-year-old male king crab.

$$\text{MALE6}_t = (a_6 \text{ADULT}_{t-7} e^{-b_6 \text{ADULT}_{t-7}})^{w_1} (c_6 \text{MALE5}_{t-1})^{w_2} \quad (5)$$

Two parameters (a_6 and c_6) cannot be identified statistically as separate parameters in this specification. An estimable but more aggregate form of (5) that combines the influence of these parameters is given by equation (6).

$$\text{MALE6}_t = j_6 \text{ADULT}_{t-7}^{w_1} e^{-B_6 \text{ADULT}_{t-7}} \text{MALES}_{t-1}^{w_2} \quad (6)$$

$$\text{where } j_6 = a_6^{w_1} c_6^{w_2}$$

$$B_6 = b_6 w_1$$

The null hypothesis that $H_0: (w_1 + w_2) = 1.0$ can be tested with a t-statistic given by $((\hat{w}_1 + \hat{w}_2) - 1) / (\hat{\sigma}_{w_1}^2 + \hat{\sigma}_{w_2}^2 + \hat{\text{COV}}_{w_1 w_2})^{-1/2}$, where $\hat{\sigma}_{w_i}^2$ refers to the estimated variance of \hat{w}_i , and $\hat{\text{COV}}_{w_1 w_2}$ is the estimated covariance between \hat{w}_1 and \hat{w}_2 .

Rejection of the null hypothesis implies a slightly different functional form given in equation (7) that is consistent with the concept of a geometric weighted average of expectations and is statistically indistinguishable from equation (6).

$$\text{MALE6}_t = c_6 \text{ADULT}_{t-7}^{x_1} e^{-B_6 \text{ADULT}_{t-7}} (c_6 \text{MALE5}_{t-1}^{x_2})^{w_2} \quad (7)$$

The parameters x_1 and x_2 add additional flexibility to the underlying functional forms that represent both the Ricker spawner-recruit model and the adjustment component. The implied estimated equation becomes equation (8).

$$\text{MALE6}_t = j_6^{\text{ADULT}_{t-7}} e^{w_1^* - B_6^{\text{ADULT}_{t-7}}} \text{MALE5}_{t-1}^{w_2^*} \quad (8)$$

$$\text{where } j_6 = a_6^{w_1} c_6^{w_2},$$

$$B_6 = b_6 w_1,$$

$$w_i^* = x_i w_i, \quad i = 1, 2$$

The estimated geometric weights w_1^* and w_2^* now take on a composite meaning. In conclusion, the TAIR framework provides a flexible functional relationship that utilizes two pieces of information to estimate age class recruitment. Prerecruit data concerning observed age class abundance may be used to adjust the original expectation formed from spawning stock data. This adjustment process is possible because the NMFS population surveys provide annual estimates of abundance at age.

The TAIR framework is empirically applicable to only two of the seven king crab cohort equations: 6- and 7-year-old males. Inaccurate data on 4-year-old male and female crab abundance, coupled with limited time series observations and the large number of parameters, foreclose empirical application of this framework in modeling the other adult age classes.

The beginning biomass of 5-year-old king crab is modeled separately for males and females because sex specific growth rates begin to differ at this age. In general, 5-year-olds recruit from the previous period's 4-year-old population. Inaccurate biomass estimates of 4-year-old king crab require that 5-year-old male and female biomass be predicted solely from the observed spawning stock that created it 6 yr before. A variation of the lagged Ricker stock/recruitment framework specified in equation (2) can be used in this case. Nonlinear least squares may be used to estimate the gender-specific parameters.

Data limitations prevent using the TAIR framework to model male crab biomass in the 8- and 9-to-14-year-old age cohorts. The recursive structure of TAIR reduces degrees of freedom in the 8-year-old class equation below three. This is considered unsuitable for adequate hypothesis testing. The problem is even more pronounced in the 9-to-14-year-old aggregate relationship.

Fortunately, Deriso (1980) developed an approach to model composite fish stocks that only requires a three-period recursive structure rather than the $n+1$ period delay used in the TAIR approach. Deriso hypothesized that total harvestable biomass in the current period (H_t) is a function of three factors: (1) growth and survival of the harvestable stock from the previous period (H_{t-1}), (2) a "correction" for growth and age structure changes in the legal population based on variations observed between the previous two periods (H_{t-1} and H_{t-2}), and (3) the biomass of new recruits (R_t). This delay difference equation takes the general form:

$$H_t = m_t H_{t-1} - n_t H_{t-2} + p_t R_t \quad (9)$$

where m_t , n_t and P_t are parameters.

Detailed derivation of equation (9) can be found in Deriso (1980, 1983) and Walters (1986).

The Deriso framework reduces to the recruitment component ($p_t R_t$) when modeling growth of a single age class. For example, the stock of 8-year-old males at the beginning of period t ($MALE8_t$) depends only upon the recruitment of 7-year-olds from period $t-1$ ($MALE7_{t-1}$). Eight-year-old males in period $t-1$ are assumed to become 9-year-olds at the beginning of period t . Thus, the stock of 8-year-olds in $t-1$ does not influence the abundance of 8-year-olds in t , and no H_{t-1} or H_{t-2} terms are required. Nonetheless, Deriso's concept of "correcting" the growth path can be incorporated, providing it enters as an adjustment to the recruitment relationship ($p_t R_t$), rather than as a delay difference correction. Time series data of male 8-year-olds suggest such an adjustment may be appropriate. There is some evidence inherent in the Bristol Bay red king crab trawl survey data and in the catch history of other fishery areas, that an underlying cyclic phenomenon periodically may alter the intrinsic rate of recruitment. Accordingly, beginning stocks of 8-year-old males may be conceptualized as a composite, nonlinear cyclic function of 7-year-old males from the previous period, i.e., equation (10).

$$MALE8_t = [q_8 + z_1 \cos(z_2 \text{TIME}70 - z_3)] MALE7_{t-1} \quad (10)$$

The first parameter (q_8) measures average recruitment of 7-year-old males into the 8-year-old population. The second composite term is a periodic correction factor based on the cosine function (\cos), time, and prerecruit biomass. It shifts the slope of the recruitment function, incorporating the influence of possible periodic fluctuations which would be accounted for implicitly in the TAIR framework. There are three estimated parameters associated with the composite correction component (z_1 , z_2 , z_3). The first parameter (z_1) measures the amplitude of the periodic trend, the second (z_2) is the period of the trend, and the third (z_3) represents the phase. The

TIME70 variable is a linear counter that begins with 1.0 in 1970, increasing in unit increments each year. Use of the cosine function in equation (10) requires employing nonlinear least squares to estimate the model parameters. Partial differentiation of equation (10) with respect to $MALE7_{t-1}$ reveals the hypothesized average and periodic impacts of 7-year-old biomass in $t-1$ on 8-year-old recruitment (equation 11).

$$\frac{\partial MALE8_t}{\partial MALE7_{t-1}} = q_8 + z_1 \cos((z_2 \text{ TIME70}) - z_3) \quad (11)$$

The hypothesized 9-to-14-year-old relationship more closely follows Deriso's framework because several harvestable age classes are aggregated together. Beginning stock abundance in the current period ($MALE914_t$) conceivably depends on survival of existing 9-to-14-year-old males from the previous two periods ($MALE914_{t-1}$ and $MALE914_{t-2}$, respectively) and recruitment of 8-year-olds into the current population ($MALE8_{t-1}$). The general relationship takes the form of equation (12).

$$MALE914_t = s_{t-1} MALE914_{t-1} - s_{t-2} MALE914_{t-2} + r_9 MALE8_{t-1} \quad (12)$$

Equation (12) is inadequate because it does not explicitly incorporate harvest mortality into the biological submodel. Harvest must be included directly so that exploitation impacts on king crab stocks are accounted. These impacts can be included through the survival coefficients (s_{t-1} , s_{t-2}). Net survival from the previous period (s_{t-1}) can be defined as the difference between average natural survival rate over the period (u_{t-1}) and the impact of harvest on natural survival ($u_{t-1} v_{t-1}$), where harvest impacts are measured by the proportionate harvest rate (v_{t-1}). Explicit representation of s_{t-1} is given by (13).

$$s_{t-1} = (1 - v_{t-1}) u_{t-1} \quad (13)$$

The relationship for s_{t-2} can be represented in a similar fashion. Harvest rate (v_{t-1}) is the proportion of legal king crab stocks at the beginning of $t-1$ ($LEGALS_{t-1}$) that were caught in $t-1$ ($QHARVEST_{t-1}$), i.e., equation (14).

$$v_{t-1} = QHARVEST_{t-1} / LEGALS_{t-1} \quad (14)$$

Substituting the right-hand side of equation (14) into (13) disaggregates the influence of harvest mortality and natural survival in the net survival parameter (equation 15).

$$s_{t-1} = (1 - QHARVEST_{t-1} / LEGALS_{t-1}) u_{t-1} \quad (15)$$

Replacing s_{t-1} and s_{t-2} in equation (12) with the appropriate form of equation (15) gives the Deriso-type model initially estimated for the 9-to-14-year-old aggregate cohort (equation 16).

$$\begin{aligned} \text{MALE914}_t = & [(1 - (\text{QHARVEST}_{t-1} / \text{LEGAL}_{t-1})) u_{t-1}] \text{MALE914}_{t-1} \quad (16) \\ & - [(1 - (\text{QHARVEST}_{t-2} / \text{LEGAL}_{t-2})) u_{t-2}] \text{MALE914}_{t-2} + r_g \text{MALE8}_{t-1} \end{aligned}$$

Cyclic perturbations can be accommodated in equation (16) by hypothesizing the recruitment component ($r_g \text{MALE8}_{t-1}$) is similar to its 8-year-old counterpart specified as equation (10). The nonlinear form of equation (16) requires using nonlinear least squares to estimate the survival and recruitment parameters (u_{t-1} , u_{t-2} , r_g).

All equations in the biological submodel are functions of strictly predetermined variables (either exogenous or lagged endogenous). Thus, the equations can be estimated without using a simultaneous systems approach, and are segmentable from statistical analysis of king crab input and output markets. The segmentable character of the biological submodel does not imply, however, that policy analysis or management of crab stocks can and/or should be independent of market consequences. Dynamic feedback effects among the age-structured crab stocks, market price signals and industry well-being can only be studied in the context of the composite bioeconomic framework. See Matulich, Hanson and Mittelhammer (1988b) for integration of biological and market models into a composite bioeconomic analysis of the Alaska King crab industry.

EMPIRICAL RESULTS OF THE BIOLOGICAL SUBMODEL

King crab population estimates for the southeastern Bering Sea developed by the NMFS were used to estimate the parameters of the biological response submodel. Observations were available for the period from 1968 to 1985. Four criteria collectively were used to judge the goodness of statistical fit and to refine the empirical regression specifications: (1) sign and magnitude consistency of the parameter estimate with a priori reasoning and previous studies; (2) statistical significance of the estimates, as measured by the t-test reported parenthetically below the corresponding coefficient; (3) explanatory power of the estimated equations as measured by the coefficient of determination (R^2); and (4) the relationship's ability to predict historical observations and turning points of the dependent variable, as indicated by graphical comparison of observed versus predicted age class recruitment. All four of these criteria need to be considered because of the limited data set.

Estimates of the behavioral biological response equations are presented chronologically by sex. The beginning biomass of 5-year-old males is reported first, followed by male 6-, 7-, 8-, and 9-to-14-year-old male cohorts. The empirical results for 5- and 6-to-14-year-old females completes the

discussion. Deviations between empirical and conceptual specifications are discussed. All equations were estimated using the "SYSNLIN" nonlinear least squares procedure developed by SAS Institute (1984). Presence of heteroscedasticity in the 7- and 8-year-old equations required the use of weighted nonlinear least squares. The variance of the dependent variable was specified to be proportional to the square of the prerecruit stock; weights were equal to the inverse of the prerecruit stock.

Numerous attempts were made to incorporate the influence of handling mortality on nonlegal crab. Female and sublegal male king crab frequently are caught along with legal males during the fishing season. Though nonlegal crab are returned immediately to the water, unintentional harvest and handling were hypothesized to create added stress and increase overall mortality. Both total harvest in the southeastern Bering Sea and the number of potlifts made during a season were tested as proxies for handling mortality in each of the nonlegal response equations. No statistical evidence of handling stress was found from this preliminary evaluation. Parameter estimates for each of these handling stress measures lacked statistical significance.

Five-Year-Old Males (MALE5_t)

The nonlinear least squares estimate of the relationship predicting beginning 5-year-old male biomass in period t (MALE5_t) is given by equation (17).

$$\begin{aligned}
 & \qquad \qquad \qquad (-0.03458 \text{ FEM514}_{t-6}) \\
 \text{MALE5}_t &= 4.1775 \text{ FEM514}_{t-6}^e \\
 & \qquad (4.98) \qquad \qquad (-9.74) \qquad \qquad (17) \\
 & + 0.00004497 \text{ FM514}_{t-6} - 0.001696 \text{ MALE514}_{t-6} + 0.70734 \text{ IND77}) \\
 & \qquad (6.27) \qquad \qquad (-1.53) \qquad \qquad (6.20) \\
 \\
 R^2 &= 0.9402 \qquad df = 7
 \end{aligned}$$

Abundance of 5-year-old males (MALE5_t) is estimated as a variation of the basic Ricker stock/recruitment relationship specified in equation (2). The influence of adult breeding stock 6 yr earlier provided the best statistical fit when disaggregated by sex. Alternative specification of adult spawning stock abundance in the exponential term and the leading, density independent term included combined male and female biomass (ADULT_{t-6}), elimination of the male variable (MALE514_{t-6}), and several variations of the interaction term (FM514_{t-6}). Comparable specifications were evaluated for MALE6_t and MALE7_t equations. MALE5_t is shown to be a function of: the lagged, sexually mature female biomass (FEM514_{t-6}) measured in millions of pounds; lagged adult male

biomass ($MALE514_{t-6}$) also measured in millions of pounds; and of the interaction (product) between males and females ($FEM514_{t-6}$) measured in billions of pounds. An indicator variable, IND77, marks 1977 as an outlier observation that suffers from sampling error. The 1977 observation of 5-year-old males is nearly double that of adjacent years; IND77 forces the regression through the observed data point.

The statistical goodness of fit measures in conjunction with Figure 1 illustrate the predictive accuracy of equation (17) for the period 1974 to 1985. The estimated male 5-year-old crab stocks ($MALE5HAT$) predict the historical data ($MALE5$) with excellent precision. Conventional t-statistics reported in parentheses below the parameter estimates test whether a particular parameter is significantly different from zero. The exception here and in subsequent equations involves the t-statistic on the multiplicative constant term. That test is based upon the null hypothesis that the estimated parameter equals 1.0, rather than zero. It would be inappropriate to test the zero value because such a test implicitly refers to a model which is statistically unidentified in all of the remaining parameters.

The specific functional form of this Ricker model in which adult spawning stock is disaggregated by sex, characterizes a saddle function that implicates two density dependent characteristics, as illustrated by Figure 2. Density dependence in the female direction is a prominent feature of this graph. For any given level of adult male abundance ($MALE514_{t-6}$), recruitment of 5-year-old males ($MALE5_t$) rises and then declines with increasing female density ($FEM514_{t-6}$). The second concept of density dependence concerns maximal levels of recruitment shown to occur along the ridge of the saddle function portrayed in Figure 2. Following this ridge in the direction of increasing adult males draws attention to the notion of a density dependent reproduction efficiency frontier, where optimal abundance of adult females increases at an increasing rate as adult male biomass expands.

The reproductive efficiency relationship also is evident by taking the partial derivative of equation (17) with respect to adult females, yielding:

$$\begin{aligned} \partial MALE5_t / \partial FEM514_{t-6} &= 4.1775 e(.) + 4.1775 FEM514_{t-6} \\ e(.) &(-0.03458 + 0.00004497 MALE514_{t-6}) , \end{aligned} \tag{18}$$

where: $e(.)$ represents the exponential term in equation (19).

Setting equation (18) to zero and solving for the conditional, optimal level of adult females as a function of males yields the implied optimal correspondence between adult males and females (equation 19).

$$FEM514_{t-6} = 1 / (0.03458 - 0.00004497 MALE514_{t-6}) \tag{19}$$

The notion of a reproduction efficiency frontier can be grafted from Figure 2 and equation (19) into a two-dimensional illustration, Figure 3. Let adult

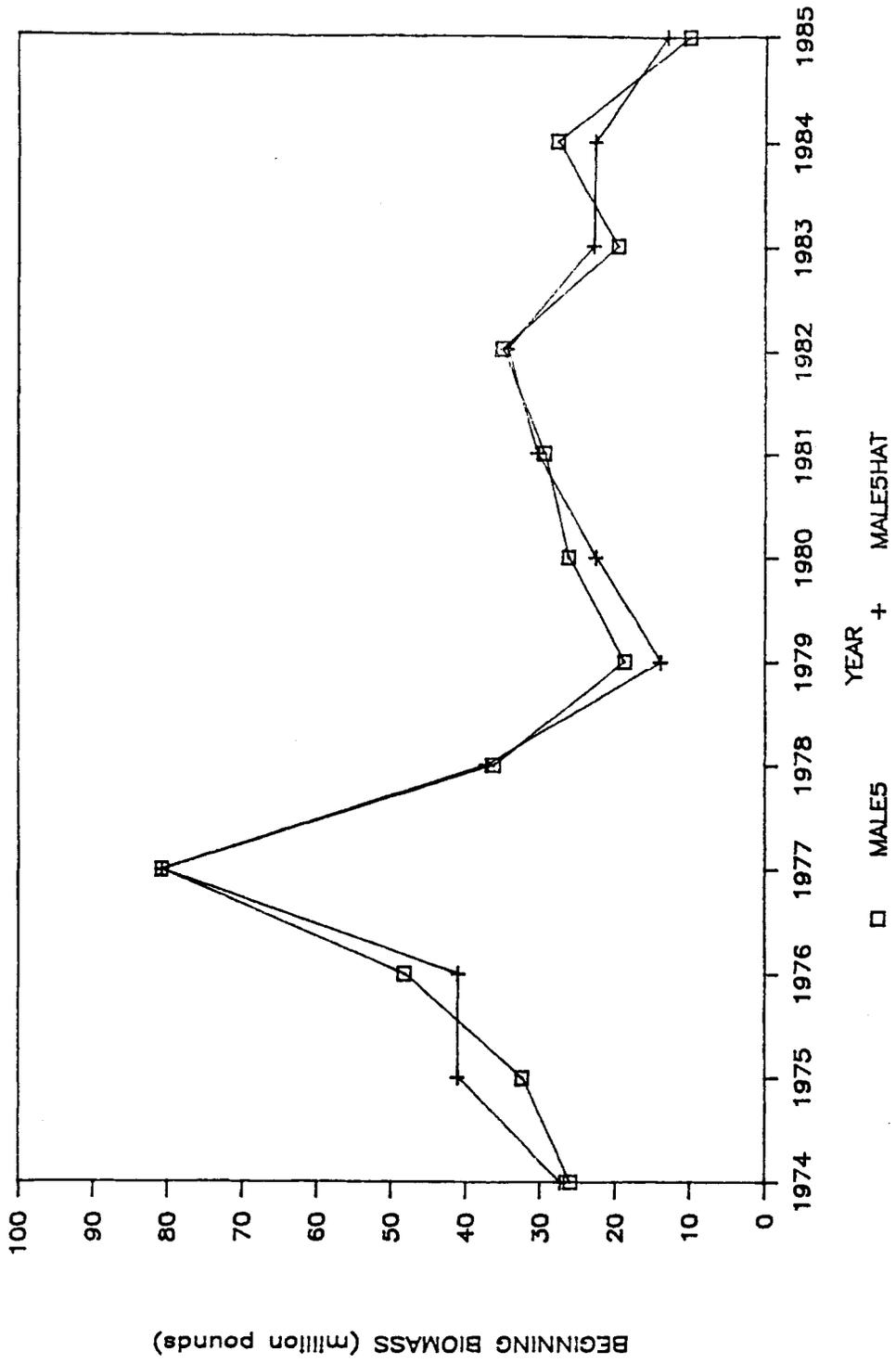


Figure 1. Actual versus predicted population levels of 5-year-old male king crab (MALE5 and MALE5HAT, respectively), 1974-1985.

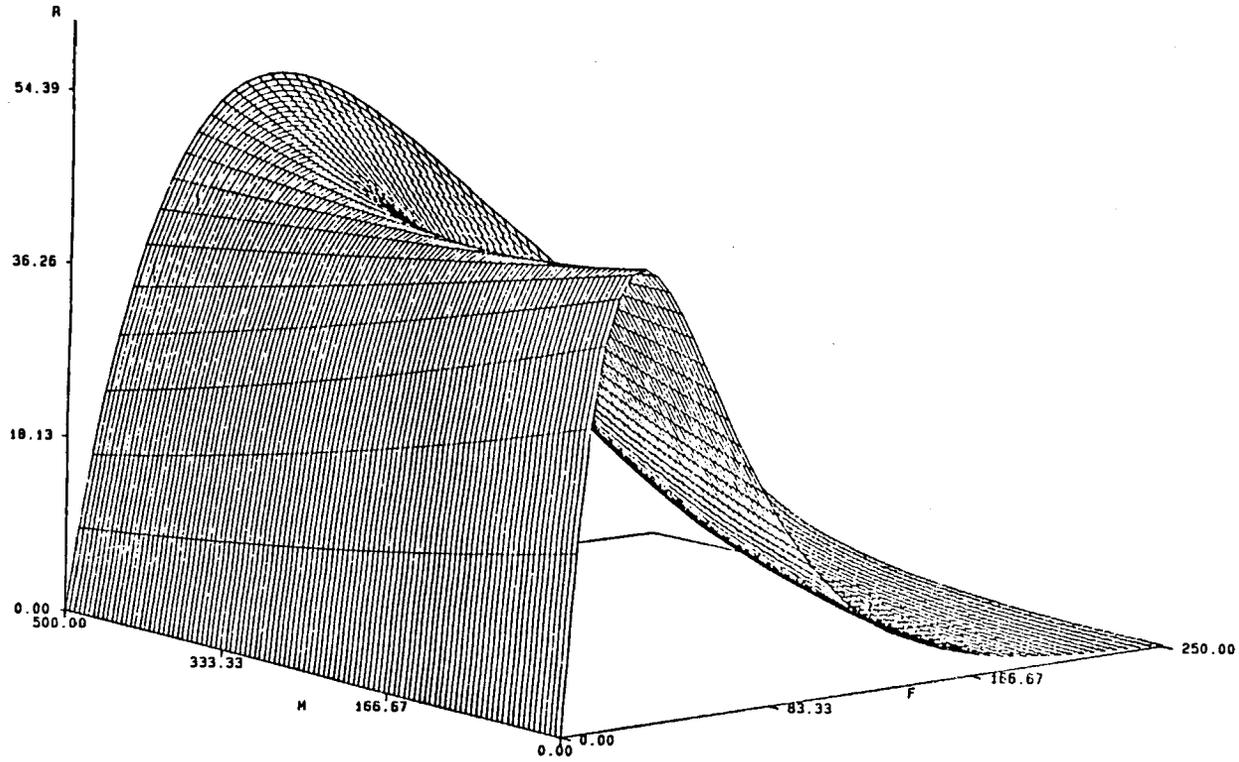


Figure 2. Three dimensional perspective of 5-year-old male king crab recruitment (R) based on male (M) and female (F) spawning stock abundance in t-6.

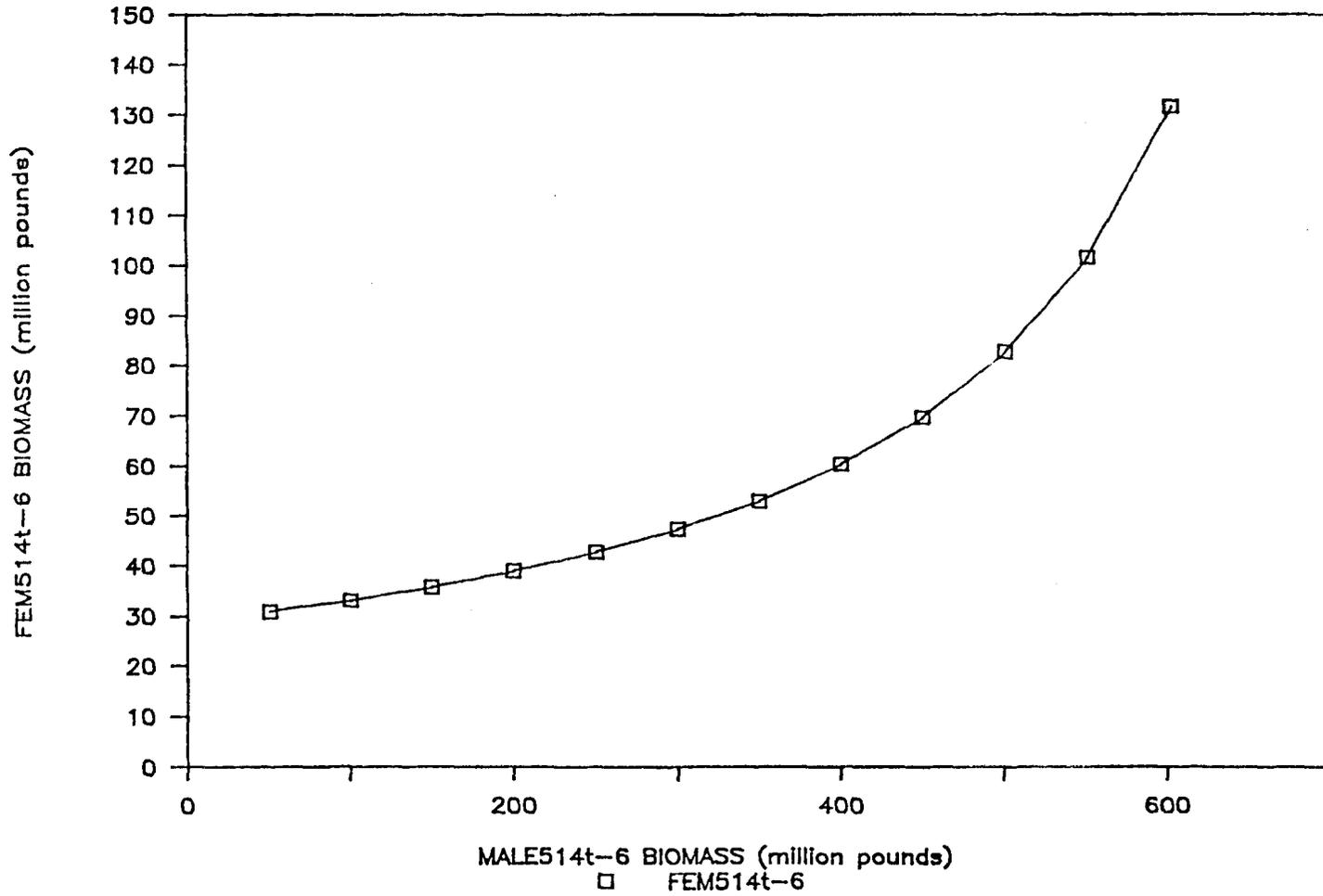


Figure 3. Optimal male and female spawning stock levels ($MALE_{514_{t-6}}$, $FEM_{514_{t-6}}$, respectively) implied by the 5-year-old male king crab ($MALE_t$) recruitment function.

male brood stock equal 300 million lb. Solution of equation (19) results in the corresponding optimal adult female biomass of 47.418 million lb. Substituting this combination of male and female density into equation (17) produces a maximum expected recruitment of 43.813 million lb of 5-year-old males. Female stocks can be varied, holding male abundance constant at 300 million lb, to verify that $MALE5_t$ recruitment declines, i.e., consider points above or below this curve. Suppose $FEM514_{t-6}$ increases 20 million lb to 67.418 million lb. Estimated recruitment would fall to 40.856 million lb. Similarly, a reduction of adult female biomass to 27.418 million lb would result in only 38.625 million lb of $MALE5_t$ recruits.

The reproduction efficiency frontier shown in Figure 3 also may be viewed as an expansion path--the path that should be followed to optimally increase $MALE5_t$ recruitment. Recruitment not only increases as one moves out the expansion path, but the optimal ratio of male to female biomass changes as well. This can be seen more clearly in Figure 4 in which the sex ratio (by weight) is related to adult male biomass. The optimal ratio of adult male to female biomass increases as $MALE514_{t-6}$ expands, reaching a maximum of 6.7:1 when adult males equal 384.5 million lb $MALE514_{t-6}$ abundance beyond 384.5 million lb, in turn, corresponds to a falling ratio.

A variety of factors observed in other species may support the notion of an optimal sex ratio implied by this density dependent reproductive relationship--these include searching efficiency, competition among males and fecundity. One might expect searching efficiency to increase nonlinearly as both male and female abundance levels rise. By itself, this phenomenon would seem to contradict the dome shape of Figure 4. Instead, it implies a density dependent sex ratio that declines throughout as adult male biomass grows.

However, for low female stocks, competition among males presumably intensifies in a nonlinear fashion as male abundance rises. Within this context, the shape of Figure 4 would suggest that up to modest levels of males and females, the rate of competition among males rises faster than the associated increased searching efficiency. Despite the evidence that a sexually mature male can successfully fertilize up to seven females in a given season, only a fraction of the adult males appear to be sexually active. That fraction of sexually active males decreases with heightened competition, and then begins to rise once a threshold of female biomass is achieved. Figure 4 shows this to occur at about 58 million lb $FEM514_{t-6}$.

Density dependent fecundity might also contribute to the general shapes of Figures 2 through 4. Fecundity in many species is believed to be a self-regulating reproduction mechanism that dampens as the breeding population grows. If this is the case with king crab, it may partially explain: (a) why the optimal sex ratio changes, and (b) why female abundance ultimately must expand at an increasing rate relative to males if recruitment is to grow. Inclusion of clutch size data in the spawner-recruit framework may lend insight into the explicit role of fecundity.

Like any Ricker function, equation (17) should be viewed as an approximation, representative of recruitment behavior only over some relevant range of data. For example, suppose $MALE514_{t-6}$ equals zero. By equation (19), $FEM514_{t-6}$ is positive and thus, according to equation (17), recruitment into the 5-year-old cohort will be positive. This clearly is a biological

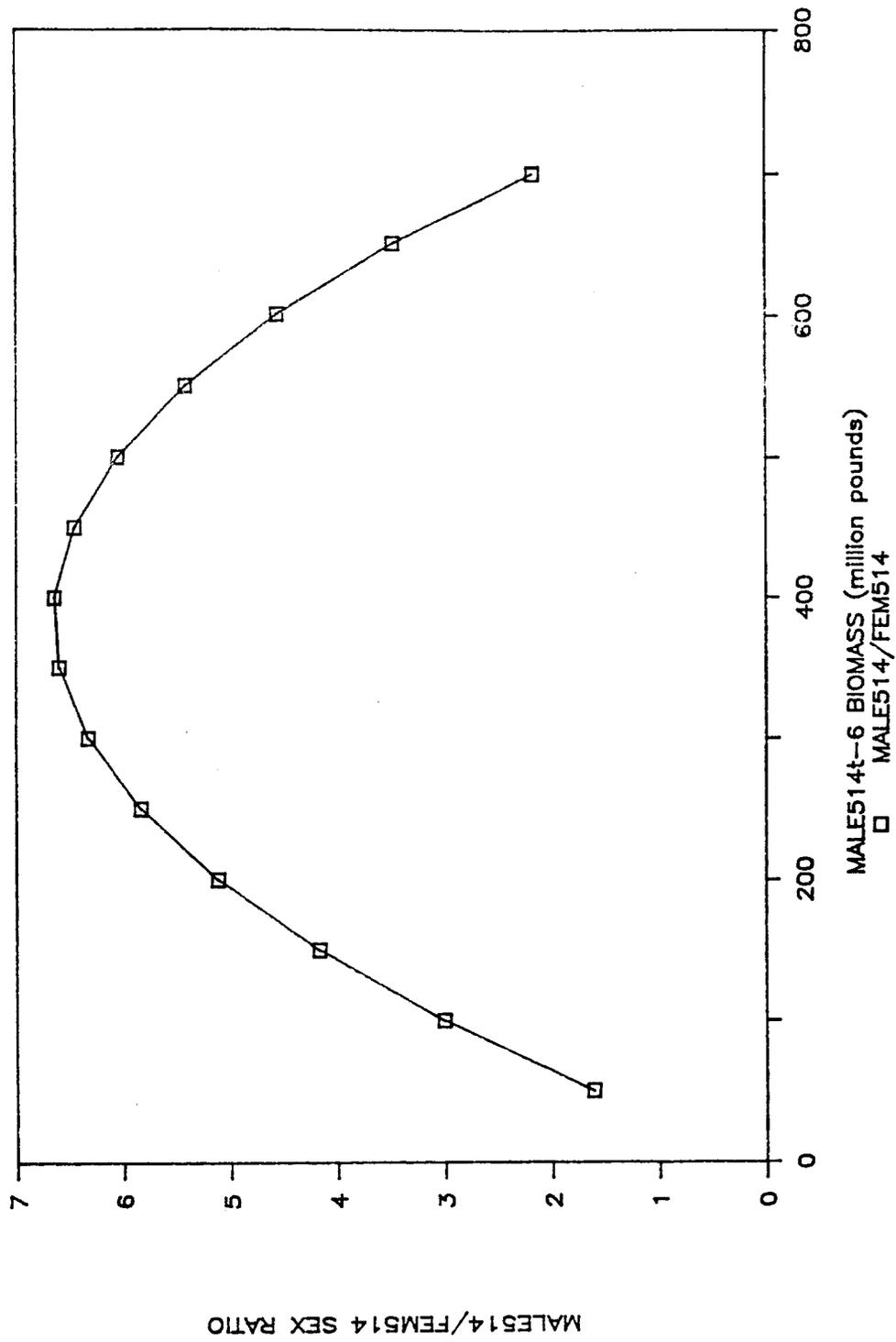


Figure 4. Optimal male to female spawning stock ratio ($MALE514_{t-6}/FEM514_{t-6}$) implied by the 5-year-old male king crab ($MALE5_t$) recruitment function.

impossibility. Future research is needed to impose concavity on the underlying functional form. Similarly, a vertical asymptote is reached in Figure 2 at 768 million lb of adult male biomass. The implied optimal female stocks would be infinitely large. Both abundance levels are equally implausible. However, the deficiency associated with extremely large parent stocks is not particularly troublesome since harvest pressures will prevent such an occurrence.

The historically observed ratios of male to female brood stock densities are above and below the implied optimal sex ratio given by equation (17). The implication is that recruitment may have been less than possible. In future seasons, when the female spawning stock biomass exceeds that implied to be optimum by equation (17), harvesting some adult females may be desirable. Whether females should be harvested even under these conditions, depends upon managerial objectives of the fishery, price feedback effects and time horizon. Future research is needed to better define the notion or existence of a density dependent optimal sex ratio, and its implication for management. Since this is the first research to find the possibility of an optimal sex ratio in red king crab, and since stock conditions are severely depressed, the risk of altering the long-standing policy of male-only harvest outweighs the possible short-term benefits. Additional research is needed before a recommendation to change this policy could be regarded prudent.

Six-Year-Old Males (MALE6_t)

The nonlinear least squares estimate of the TAIR model characterizing beginning biomass of 6-year-old males is represented by equation (20).

$$\begin{aligned}
 \text{MALE6}_t = & 0.51185 \quad [\text{FEM514}_{t-7}^{1.50104} \quad e^{(-0.03458 \text{ FEM514}_{t-7})} \quad (20) \\
 & (0.44) \quad (2.35) \quad (-2.20) \\
 & + 0.00005303 \text{ FM514}_{t-7} - 0.00714 \text{ MALE514}_{t-7} \\
 & (2.09) \quad (-2.63) \\
 & + 0.56673 \text{ IND77) } \quad 0.22434 \\
 & \quad \quad \quad] \text{ MALE5}_{t-1} \\
 & \quad \quad \quad (0.80) \\
 R^2 = & 0.9486 \quad \quad \quad df = 4
 \end{aligned}$$

The statistical goodness of fit measures in conjunction with Figure 5 illustrate good predictive accuracy. All t-statistics test the null hypothesis around zero except for the multiplicative constant term which tests 1.0.

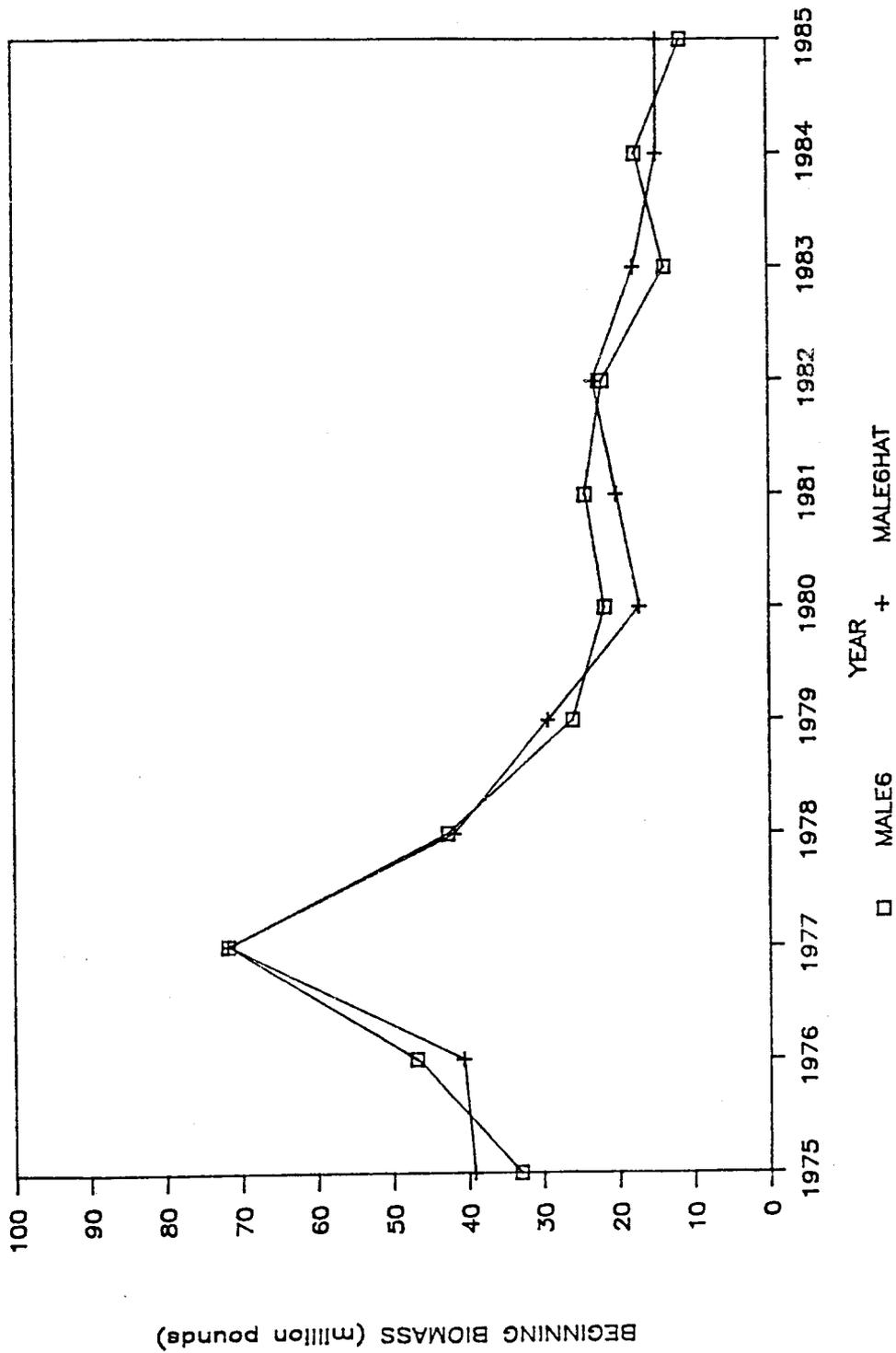


Figure 5. Actual versus predicted population levels of 6-year-old male king crab (MALE6 and MALE6HAT, respectively), 1975-1985.

Conceptually, equation (20) is equivalent to the analytical approach hypothesized in equation (6), given the disaggregation of adult spawning stocks discussed for equation (17). Density dependence is similar to the 5-year-old male cohort. An indicator variable, IND77, marks 1977 as an apparent outlier observation suffering from the same sampling error problem hypothesized in the MALE5_t relationship.

Recall from the discussion of equation (3) that w_1 and w_2 embody the adjustment to intrinsic recruitment in the TAIR framework. If $w_2 = 0$ and $w_1 = 1.0$, recruitment can be explained solely on the basis of spawning stock abundance. The appropriate functional form is an empirical issue. The point estimate for w_1 is 1.50104, while w_2 is 0.22434. The 95% confidence interval around the w_2 parameter does include zero, though the point estimate would suggest there may be some adjustment to the intrinsic recruitment trajectory. Assuming w_2 equals zero, the w_1 exponent on FEM514_{t-7} is not statistically different from 1.0. The implied intrinsic recruitment expectation would appear to be that of a pure Ricker specification.

Comparison of equation (20) with a pure, unadjusted Ricker specification reveals the importance of adjustment. The Ricker specification of intrinsic recruitment provided poor predictions for 1981-1985. Inclusion of prerecruit abundance as part of the adjustment mechanism seems to be picking up changes in natural mortality, possibly due to unmeasured environmental factors, catch of sublegal crabs in the directed fishery, bycatch in the ground fishery, disease or measurement errors in the data. The low t-statistic on the MALE5_{t-1} exponent (w_2) is suspected to be a consequence of multicollinearity in this abbreviated data set.

Seven-Year-Old Males (MALE7_t)

The weighted nonlinear least squares estimate of the male 7-year-old TAIR model is given in equation (21). A weighted estimation procedure was used to treat the presence of heteroscedasticity, as discussed earlier.

$$\begin{aligned}
 & \qquad \qquad \qquad 2.42368 \quad (-0.05442 \text{ FEM514}_{t-8}) \\
 \text{MALE7}_t &= 0.05833 [\text{FEM514}_{t-8} \quad e \quad (21) \\
 & \qquad \qquad \qquad (18.32) \quad (5.76) \quad (-5.07) \\
 & + 0.00008292 \text{ FM514}_{t-8} - 0.01132 \text{ MALE514}_{t-8} - 0.70835 \text{ IND83} \quad] \\
 & \qquad \qquad \qquad (4.77) \quad (-5.62) \quad (-2.40) \\
 & \qquad \qquad \qquad 0.33399 \\
 \text{MALE6}_{t-1} & \qquad \qquad \qquad (1.70) \\
 R^2 &= 0.9864 \quad \text{df} = 3
 \end{aligned}$$

The statistical goodness of fit measures in combination with Figure 6 illustrate the predictive accuracy of equation (21) over the period 1976 to 1985. The t-statistic for the parameter premultiplying the bracketed function tests the null hypothesis around 1.0. All other t-statistics refer to tests around zero.

The estimated MALE7_t relationship parallels that of the MALE6_t equation, differing only by the actual parameter estimates, and the inclusion of a different indicator variable (IND83). IND83 indicates a situation in which observed prerecruit population declined in 1982 while age class recruitment increased in 1983. This situation corresponds either to: favorable growth conditions, in which crab grew across more than a single age class; immigration of crab from other areas; or an unusually large sampling error.

Like the 6-year-old cohort, equation (21) reveals modest adjustment to the expected 7-year-old recruitment trajectory. The w₂ parameter was estimated to be 0.33399, suggesting that 7-year-old recruitment is adjusted even more by prerecruit biomass than is 6-year-old recruitment. The value of w₁ is 2.42368. The null hypothesis that w₁ + w₂ = 1.0 is rejected suggesting that equation (8) is the appropriate specification of TAIR.

Eight-Year-Old Males (MALE8_t)

The Deriso framework hypothesized in equation (10) to predict beginning 8-year-old male biomass proved to have empirical merit. The estimated MALE8_t relationship is given by equation (22).

$$\begin{aligned} \text{MALE8}_t &= 1.16117 \text{ MALE7}_{t-1} + [0.40034 \cos(5.83152 \text{ TIME70} & (22) \\ & \quad (16.77) \quad (3.54) \quad (595.18) \\ & - 3.52198] \text{ MALE7}_{t-1} - 8.99610 \text{ IND83} \\ & \quad (-23.80) \quad (-3.05) \\ R^2 &= 0.7921 \quad df = 12 \end{aligned}$$

Equation (24) was estimated with a weighted, nonlinear seemingly unrelated regressors technique (SUR). The weighting procedure discussed earlier was used as a correction for heteroscedasticity. Parameter values in the cosine component of MALE8_t were shared with corresponding parameters in the MALE914_t equations, necessitating a systems approach of seemingly unrelated regressors. The MALE8_t and MALE914_t equations were estimated simultaneously, incorporating cross-equation parameter restrictions. The period and phase of the cosine cycle were assumed to be invariant parameters across cohorts, while the amplitude was allowed to vary across age classes. All t-test values are significant and the accuracy of equation (22) in predicting observed MALE8_t data is quite good, as shown in Figure 7.

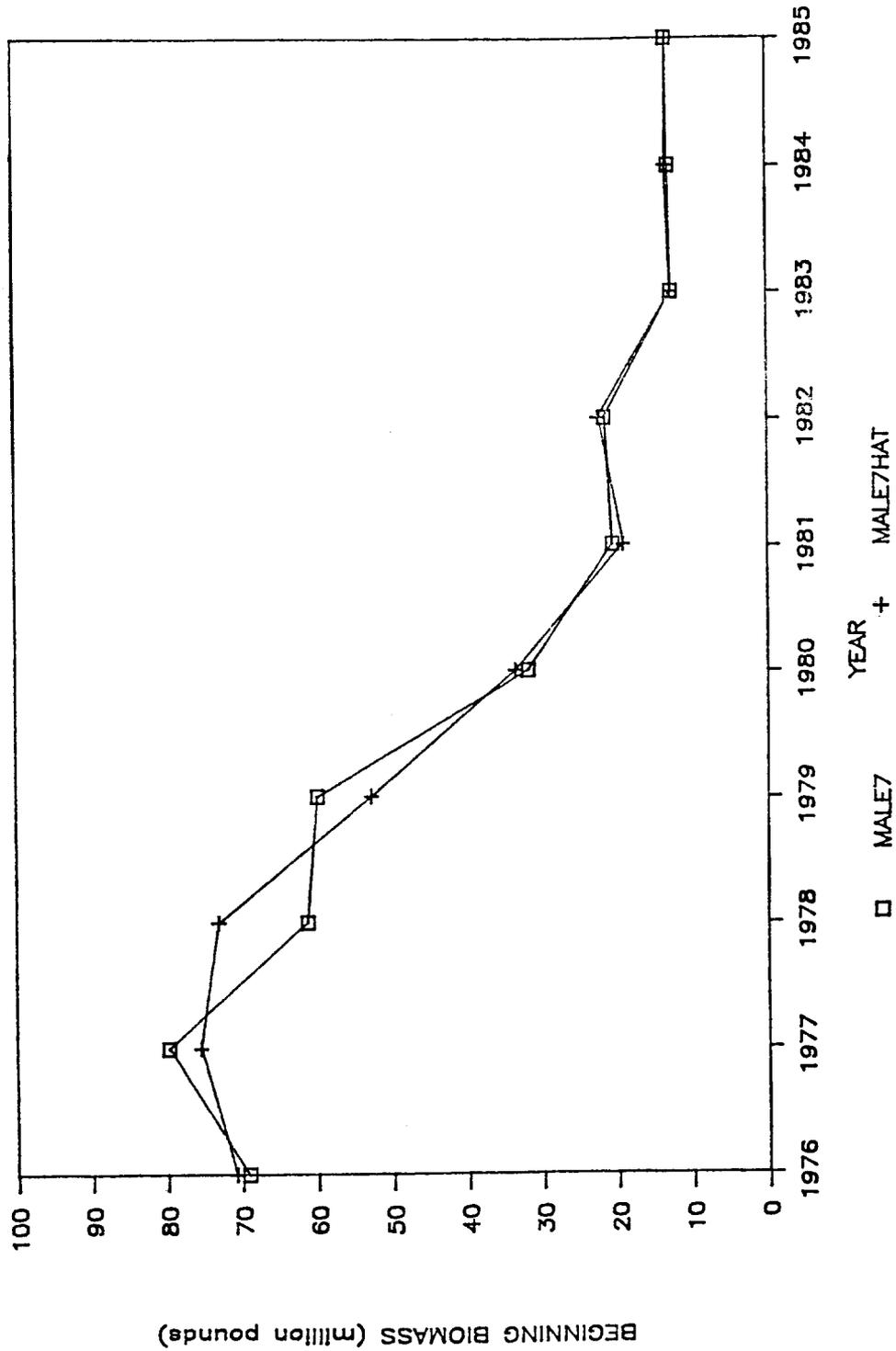


Figure 6. Actual versus predicted population levels of 7-year-old male king crab (MALE7 and MALE7HAT, respectively), 1976-1985.

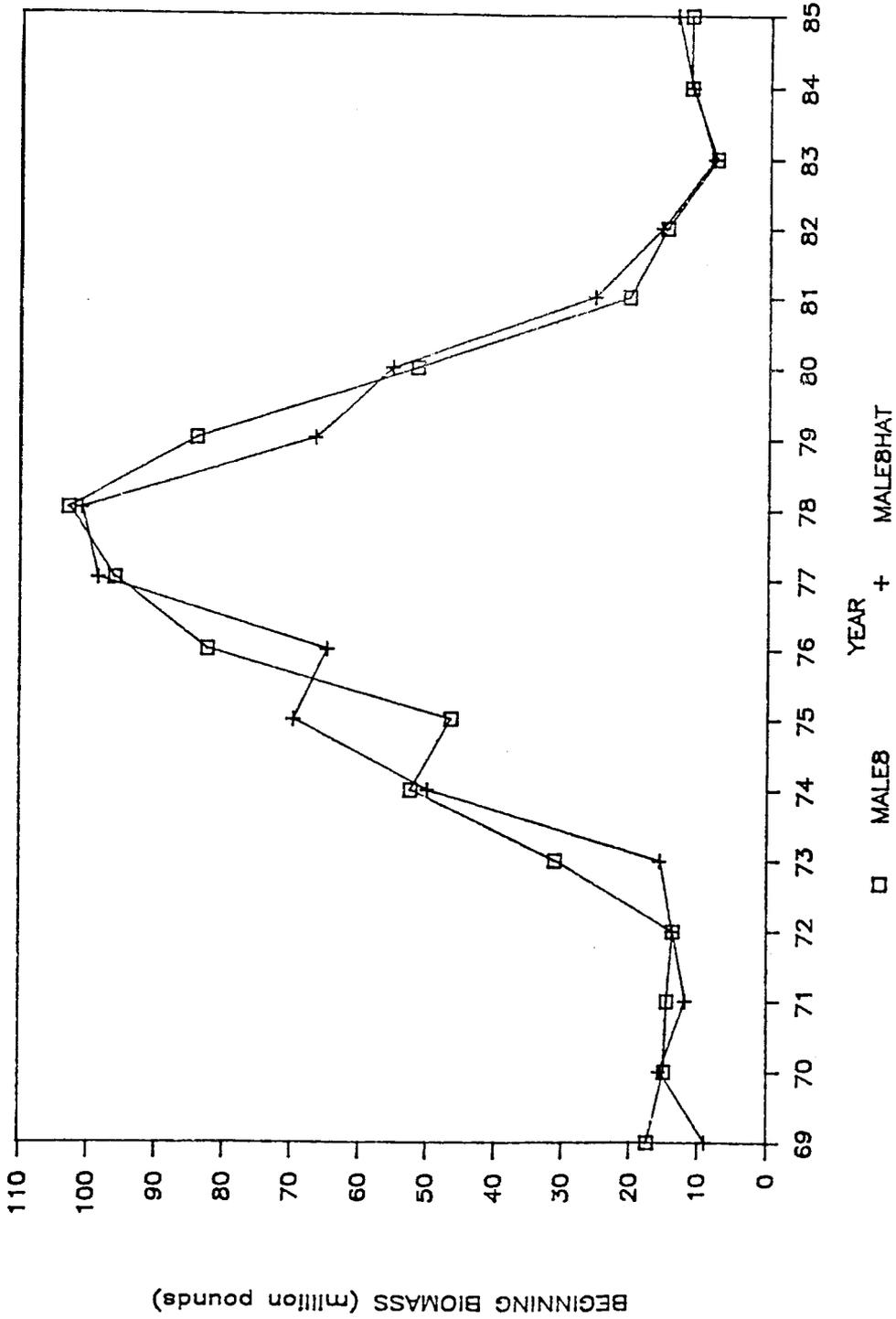


Figure 7. Actual versus predicted population levels of 8-year-old male king crab (MALE8 and MALE8HAT, respectively), 1959-1985.

The estimated intrinsic growth of 7-year-old males into the 8-year-old population, as measured by the first term in equation (22), conforms to the earlier hypothesis: $MALE7_{t-1}$ experience a net weight gain as they recruit into the $MALE8_t$ cohort. Stated differently, biomass growth exceeds natural mortality, on average.

Incorporation of the cosine function serves to perturb the intrinsic recruitment rate in a systematic fashion. The cyclic variation is dependent on time increments calibrated to zero in 1970 and increasing in single units each subsequent year ($TIME70$). The first parameter measures the amplitude of the periodic function, i.e., 0.40034. The amplitude represents the maximum deviation from the intrinsic recruitment rate that is estimated to occur. The second parameter in the bracketed component is the period of the cyclic time trend (measured in radians). The estimated period translates into a 14-yr cycle which happens to coincide with the maximum life expectancy of red king crab. The final parameter in the bracketed term is the phase of the cycle (also estimated in radians). Phase measures the distance between the nearest peak and the origin in time. In this case, the estimated peak in the cycle occurs in 1975. Thus, observed recruitment periodically fluctuates about the mean rate of 1.1617--ranging from 0.76 to 1.56 during a 14-yr period. However, these results are tentative because there is insufficient data to model more than one apparent cycle.

An indicator variable marks the 1983 $MALE8$ observation ($IND83$). $IND83$ is employed in the $MALE8_t$ equation for the same reason it is used in the estimated $MALE7_t$ relationship.

Although the $MALE8_t$ relationship could not be estimated directly as a spawner-recruit relationship, the recursive structure of the biological response submodel facilitates algebraic solution of 8-year-old male recruitment in terms of male and female breeding stocks nine periods before (i.e., $MALE514_{t-9}$ and $FEM514_{t-9}$). Recall that there were insufficient historical data to provide adequate degrees of freedom for empirical estimation of a spawner-recruit $MALE8_t$ relationship. Successive back substitutions using the estimated equations for $MALE5_t$, $MALE6_t$ and $MALE7_t$ (excluding $IND77$ and $IND83$) yields equation (23).

$$\begin{aligned}
 MALE8_t = & [1.16117 - 0.40034 \cos(5.83152 \text{ TIME70} - 3.52198)] & (23) \\
 & [0.051913 FEM514_{t-9} & e \\
 & \quad 2.99994 & (-0.06856 FEM514_{t-9} \\
 & + 0.000104 (FEM514_{t-9} MALE514_{t-9}) - 0.01383 MALE514_{t-9}) &] .
 \end{aligned}$$

This expression includes the periodic time trend used in both the $MALE8_t$ and $MALE914_t$ equations, and for purposes of illustration, is referenced to $TIME70$ equals 7.0. Equation (23) also incorporates the compound growth and modified Ricker frameworks developed for the $MALE5_t$, $MALE6_t$ and $MALE7_t$ relationships. Detailed derivation of equation (23) from the estimated equations for $MALE5_t$, $MALE6_t$, $MALE7_t$ and $MALE8_t$ can be found in Appendix A.

Figure 8 is a mapping of the production surface corresponding to equation (23) for specified ranges of $\text{MALE}_{514_{t-g}}$ and $\text{FEM}_{514_{t-g}}$ (0 to 600 and 0 to 500 million lb, respectively). The generalized saddle shape of the surface reflects the density dependent relationships characteristic of a Ricker specification in which lagged adult male and female abundance are used to predict recruitment.

One would expect the surface to be concave with respect to the $\text{FEM}_{514_{t-g}}$ plane (the density dependent influence). However, the large recruitment predicted at low adult brood stock densities are counterintuitive. Large recruitment (exceeding 200 million lb) at extremely low $\text{FEM}_{514_{t-g}}$ and $\text{MALE}_{514_{t-g}}$ levels is unrealistic. A more reasonable expectation is that recruitment will be proportionately lower at small brood stock densities, increasing only as $\text{MALE}_{514_{t-g}}$ and $\text{FEM}_{514_{t-g}}$ expand (assuming a near optimal sex ratio). In fact, one would expect recruitment to resemble that of MALE_{5_t} , as given by the production surface illustrated in Figure 2. It is doubtful that Figure 8 accurately portrays the true recruitment relationship at low levels of male and female spawners, even though the pronounced peak accurately reflects the underlying biological data.

The NMFS observed record 8-year-old recruitment in 1978 and near record recruitment in 1979 despite the apparent existence of depressed brood stock conditions 9 yr before. Eight-year-old male biomass was estimated to be 102.9 and 84.1 million lb, respectively. Corresponding total adult male biomass was only 118.8 million lb in 1969 and 60.7 million lb in 1970. Similarly, sexually mature female abundance was 45.5 and 21.8 million lb in each of these 2 years. Lack of conformity to a priori expectations, coupled with excellent predictive power, suggests the possibility of sampling error back in 1969 and 1970. Accordingly, the relevance of Figure 8 below 150 million lb of adult females or below 115 million lb of adult males is questionable.

Figure 9 is a truncated version of Figure 8. It illustrates the production surface given by equation (23) for $\text{MALE}_{514_{t-g}}$ and $\text{FEM}_{514_{t-g}}$ values ranging from 150 to 500 and 115 to 235 million lb, respectively. Most of the historical observations fall within these ranges. In this context, the estimated MALE_{8_t} relationship does conform to a priori expectations. However, additional research is needed to impose concavity at low male and female abundance levels.

Aggregate 9-to-14-Year-Old Male Biomass (MALE_{914_t})

The analytical framework hypothesized in equation (16) generated poor empirical results when estimated for the period from 1968 to 1984. Although the estimated relationship had an R^2 of 0.9108, the estimated natural survival parameter (u_j) was insignificant and the equation predicted negative MALE_{914} biomass in 1983.

Three general alternatives were evaluated as replacements for the Deriso approach given by equation (16). These alternatives included: a linear, two-period recursive function of lagged MALE_{914} abundance; a linear production model with and without periodic adjustment (i.e., with and without a cosine time trend as used in the MALE_{8_t} equation); and a net survival

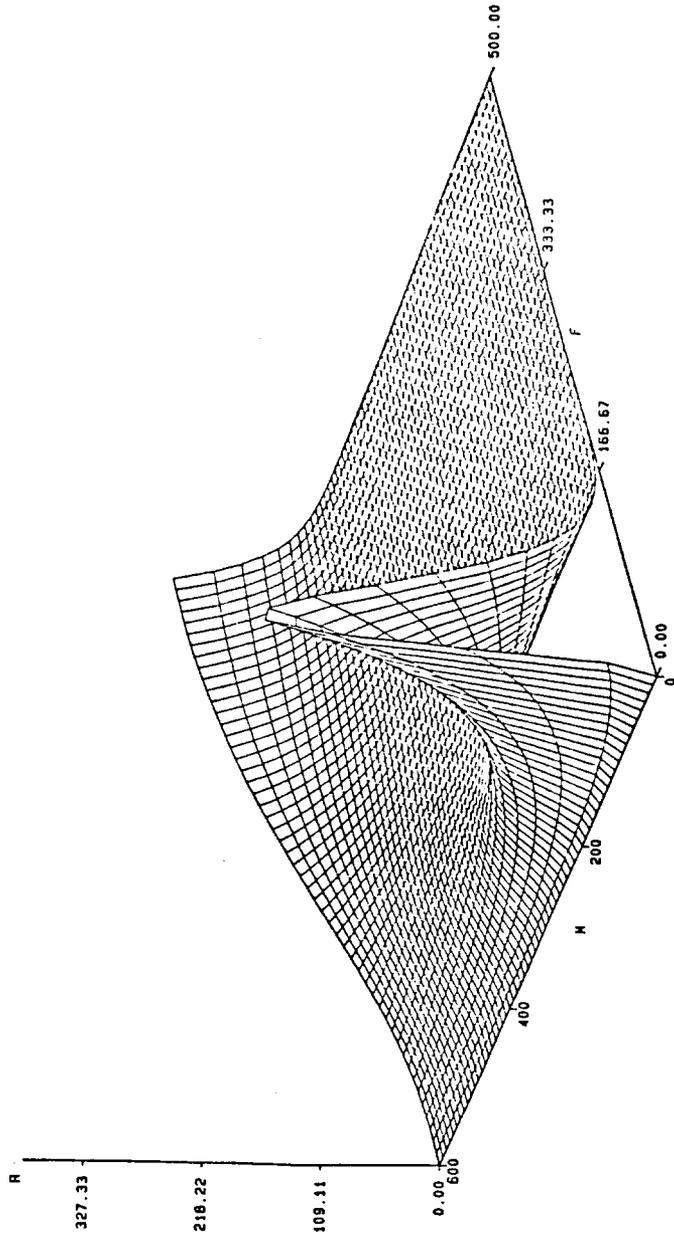


Figure 8. Three dimensional perspective of 8-year-old male king crab recruitment (R) based on reduced form equation involving male (M) and female (F) spawning stock abundance in t-9.

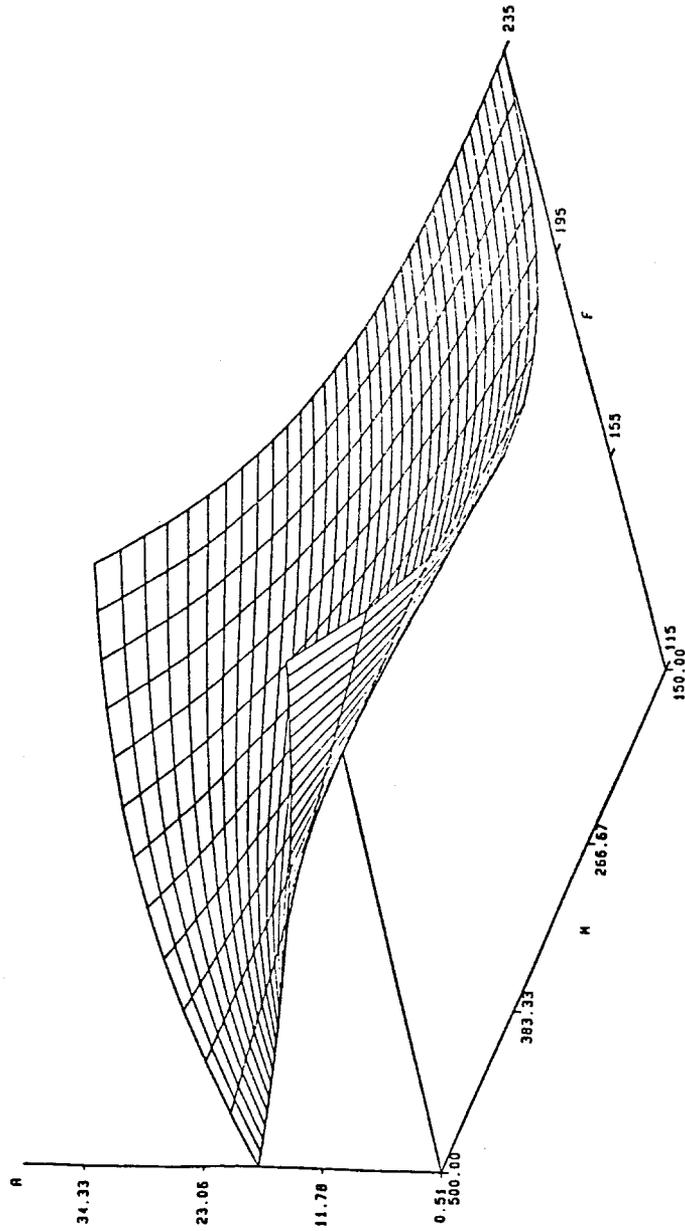


Figure 9. Truncated three dimensional perspective of 8-year-old male king crab recruitment (R) based on reduced form equation involving male (M) and female (F) spawning stock abundance in t-9.

approach with periodic adjustment. Forecasting potential of the estimated relationship strongly influenced choice of the final empirical model.

The net survival approach with periodic adjustment generated the best results. This approach may be viewed as an adaptation of the original Deriso framework, where the separate influences of recruitment, natural survival and harvest mortality are evaluated in aggregate. The aggregate term can be described as a measure of potential net survival (equation 24).

$$\text{Potential Net Survival} = \text{MALE8}_{t-1} + (\text{MALE914}_{t-1} - \text{QHARVT}_{t-1}) \quad (24)$$

Equation (24) represents the stock of male king crab in period t-1 that potentially will form the aggregate 9-to-14-year old male population in period t. The first term in equation (24) is potential recruitment; the second parenthetical term quantifies possible escapement.

Combining the right-hand side of equation (24) with a cyclic adjustment factor similar to that used in equation (22) provides the following weighted, nonlinear, seemingly unrelated regression estimates as in equation (25).

$$\text{MALE914}_t = 1.03582(\text{MALE8}_{t-1} + (\text{MALE914}_{t-1} - \text{QHARVT}_{t-1})) \quad (25)$$

(15.34)

$$+ (26.48835 \cos(5.83152 \text{ TIME70} - 3.52198)) - 33.24420 \text{ IND81}$$

$$(8.26) \quad (595.18) \quad (-23.80) \quad (-0.97)$$

$$+ 13.46790 \text{ IND84}$$

(7.52)

$$R^2 = 0.9431 \quad \text{df} = 11$$

The estimated parameter values in equation (25) agree with a priori expectations and are effective in modeling MALE914 biomass. Abundance of beginning stocks of 9-to-14-year-old male crab involves a slight (1.03582) compounding of net crab survival from period t-1 (as defined by equation (24)), plus or minus the cyclic adjustment factor. Figure 10 illustrates the predictive accuracy of equation (25).

This composite cohort equation (25) differs significantly from the Deriso model hypothesized in equation (16), though it maintains the underlying dynamics of population growth that Deriso was attempting to model. That is, age classes grow as a result of the combined influences of recruitment and escapement, "corrected" by some measure of abundance in a previous period(s). Equation (25) is similar to the relationship estimated for MALE8_t in equation (22). Differences between equations (22) and (25) include: the use of different indicator variables, and incorporation of the periodic adjustment factor as an intercept shifter rather than a slope shifting relationship.

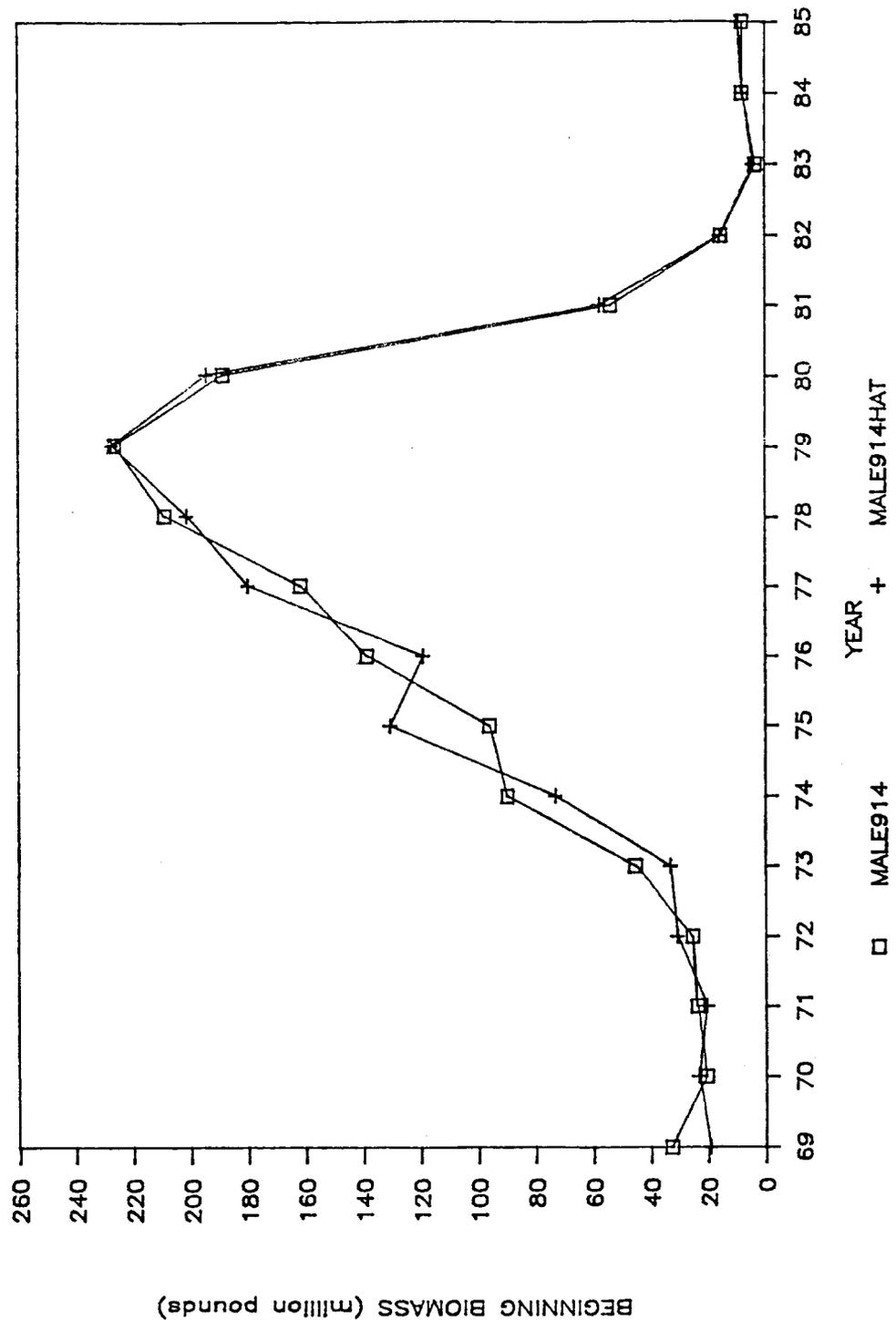


Figure 10. Actual versus predicted population levels of 9-to-14-year-old male king crab (MALE914 and MALE914HAT, respectively), 1969-1985.

Indicator variables marking the 1981 and 1984 observations (IND81 and IND84, respectively) were included in the specification. The 1981 observation was included to represent a one-time, structural change in natural mortality. It was included despite the low t-statistic because of improved predictive power. The IND84 variable incorporates the influence of no harvest in 1983. The coefficient of IND84 can be interpreted as the impact of fishery closure on age class growth, i.e., $MALE914_t$ is estimated to have increased by 13.4679 million lb during the closure.

As with the 8-year-old cohort, three forms of periodic adjustment were examined: a slope shifting form that is proportional to prerecruit abundance, an intercept form, and a combination of both. When modeled as a slope shifter (as in the $MALE8_t$ equation), periodic adjustment represents a marginal change in the intrinsic rate of biomass growth (or recruitment) and is proportional to prerecruit stock levels. If periodic changes shift only the intercept term in the growth model, adjustment is constant and additive, though its relative effect is inversely proportional to prerecruit density. The effect of periodic adjustment will diminish as prerecruit abundance increases. The best empirical estimate and historical predictions were generated with the intercept form (i.e., the cosine relationship was not multiplied by lagged $MALE914$ abundance).

Relative magnitude differences between the amplitude estimates in equations (22) and (25) reflect the dissimilar forms of adjustment used. The amplitude estimated in equation (25) is larger than that predicted in equation (22) because it measures anticipated biomass deviations by actual weight rather than as a marginal rate. Periodic adjustment is estimated to cause a maximum variation of 26.5 million lb in average net survival among the $MALE914_t$ cohort, whereas $MALE8_t$ recruitment conceivably will deviate by plus or minus 0.4 about its intrinsic rate of 1.16117. The period and phase parameters were shared between $MALE914_t$ and $MALE8_t$ equations.

Five-Year-Old Female Biomass ($FEM5_t$)

A lagged stock/recruitment framework similar to that estimated for $MALE5_t$ in equation (17) generated a suitable model to predict the beginning biomass of 5-year-old female king crab. The nonlinear least squares estimate is given by equation (26).

$$\begin{aligned}
 FEM5_t = & 2.57521 FEM514_{t-6} e^{(-0.02328 FEM514_{t-6} + 0.01578 FM514_{t-6})} & (26) \\
 & (2.40) & (-8.57) & (1.03) \\
 & - 0.0016988 MALE514_{t-6} + 1.04231 IND7779) \\
 & (-0.69) & (7.05)
 \end{aligned}$$

$$R^2 = 0.9415 \quad df = 7$$

All t-statistics test the null hypothesis around zero except for the multiplicative constant term which tests 1.0. Accuracy of equation (26) in predicting historical FEM5_t observations is illustrated by Figure 11. Overall explanatory/prediction power of equation (26) is acceptable, though the estimated model predicts a turning point in population biomass 1 yr before it is observed (1977-78). It also predicts two slight biomass increases that were not observed (1975, 1981). General sampling error of females is suspected to underpin the minor deficiencies of equation (26).

Unlike the MALE5_t equation in which a single observation is marked due to possible sampling error (i.e., 1977), a 3-yr. period beginning in 1977 is marked in the female relationship using IND7779. It is hypothesized that the same general sampling problem affected female biomass estimates in 1977, but subsequently was repeated in 1978 and 1979.

The relative magnitude differences between parameter estimates in equations (26) and (17) stem from gender specific size variations observed in male and female king crab. Five-year-old males tend to be larger than 5-year-old females. Thus, one would expect higher male intrinsic recruitment rates based on biomass. Comparison of parameter estimates in the two equations supports this fact.

Aggregate 6-to-14-Year-Old Female Biomass (FEM614_t)

Absence of harvest pressure on adult female stocks motivated a deviation in modeling philosophy. The explicit, recursive structure employed in MALE6_t through MALE914_t equations was regarded unnecessary. Instead, 6-to-14-year-old female king crab were aggregated into a single composite cohort. The nonlinear least squares estimates presented in equation (27) represent a compromise specification that serves the primary need of accurate prediction, short of making FEM614_t exogenous. In fact, FEM614_t could have been exogenized were it not for the ultimate usage in simulating future scenarios through 1992. Had FEM614_t been treated as exogenous in the biological submodel, there would have been no means to specify this data in future periods.

$$\begin{aligned}
 \text{FEM614}_t = & [7.83914 \text{ FEM514}_{t-7} e^{(-0.03939 \text{ FEM514}_{t-7})} & (27) \\
 & (6.95) & (-25.06) \\
 & + 0.00004421 \text{ FM514}_{t-7} - 0.0038566 \text{ MALE514}_{t-7} & (0.01061 \text{ FEM614}_{t-1}) \\
 & (3.97) & (-3.34) & (13.63) \\
 & e^{(-1.04467 \text{ IND78} + 1.17412 \text{ IND81} - 1.52166 \text{ IND83})} \\
 & (-15.56) & (12.43) & (-1.99)
 \end{aligned}$$

$$R^2 = 0.9979 \quad df = 4$$

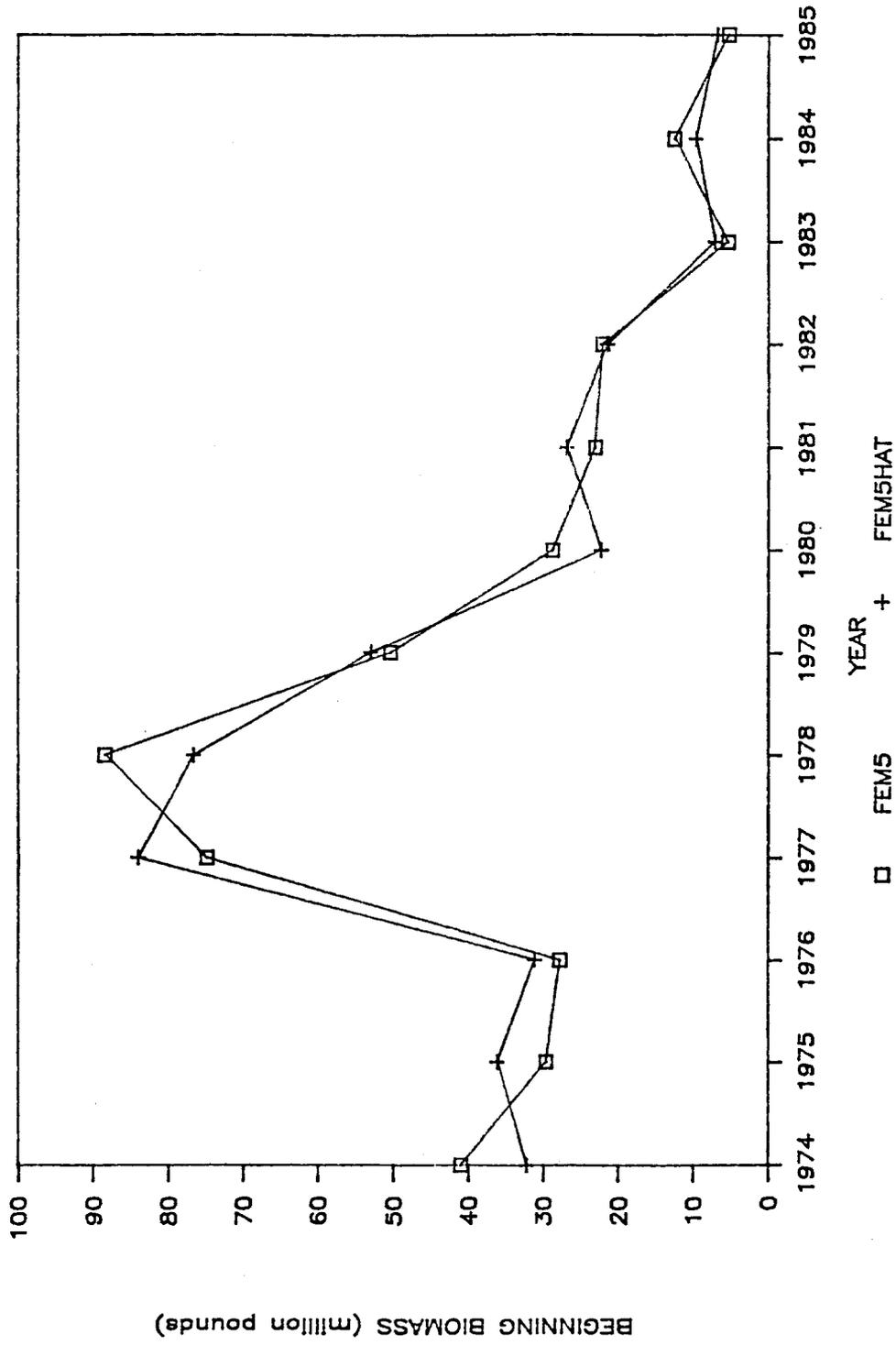


Figure 11. Actual versus predicted population levels of 5-year-old female king crab (FEM5 and FEM5HAT, respectively), 1974-1985.

All t-statistics test the null hypothesis at zero, except for that of the multiplicative constant, which tests 1.0. Figure 12 illustrates accurate prediction of FEM614_t biomass data. Though overfit, equation (27) minimally meets the needs of this research. One should not regard this specification as an adequate behavioral relation.

The combined recruitment/escapement model represented by equation (27) has three major components: (1) a lagged Ricker stock-recruitment relationship, (2) a net survival component based on compounded growth of FEM614_{t-1}, and (3) indicator variables to mark three specific observations. The first bracketed component has the same interpretation as that presented for the MALE5_t, MALE6_t, MALE7_t, and FEM5_t relationships. It represents density dependent recruitment of 6-year-old females based on the spawning stock that created them 7 yr before. The second exponential component quantifies survival and growth of FEM614 stocks from period t-1 by simple compounding. The third exponential term incorporates three indicator variables into the framework: IND78, IND81, and IND83. IND78 and IND81 are included to mark outlier observations assumed to suffer from sampling error. The third indicator variable (IND83) marks the hypothesized, one--time, structural change in mortality observed in this and other male age classes. All three major components have a multiplicative effect on one another; an additive relationship between recruitment and escapement was evaluated, but produced unacceptable empirical results. Future research is needed to explain the behavioral process of female age class recruitment.

Definitional Identities

The biological response submodel is fully defined with the addition of several identities (equations 28, 29, and 30) defining adult spawning stock abundance and legal and nonlegal crab stocks.

$$FEM514_t = FEM5_t + FEM614_t \quad (28)$$

$$MALE514_t = MALE5_t + MALE6_t + MALE7_t + MALE8_t + MALE914_t \quad (29)$$

$$FM514_t = FEM514_t MALE514_t \quad (30)$$

These three equations quantify the beginning biomass of all adult females, adult males, and the product of both sexually mature female and male king crab, respectively.

The legal king crab population is defined by minimum size limit and males-only harvest regulations imposed by ADF&G. Only that portion of the adult male population greater than or equal to the minimum size requirement can be legally harvested. Legal biomass at the start of period t (LEGALS_t) is given by the identity specified in equation (31).

$$LEGALS_t = (SIZELIM_t MALE8_t) + MALE914_t \quad (31)$$

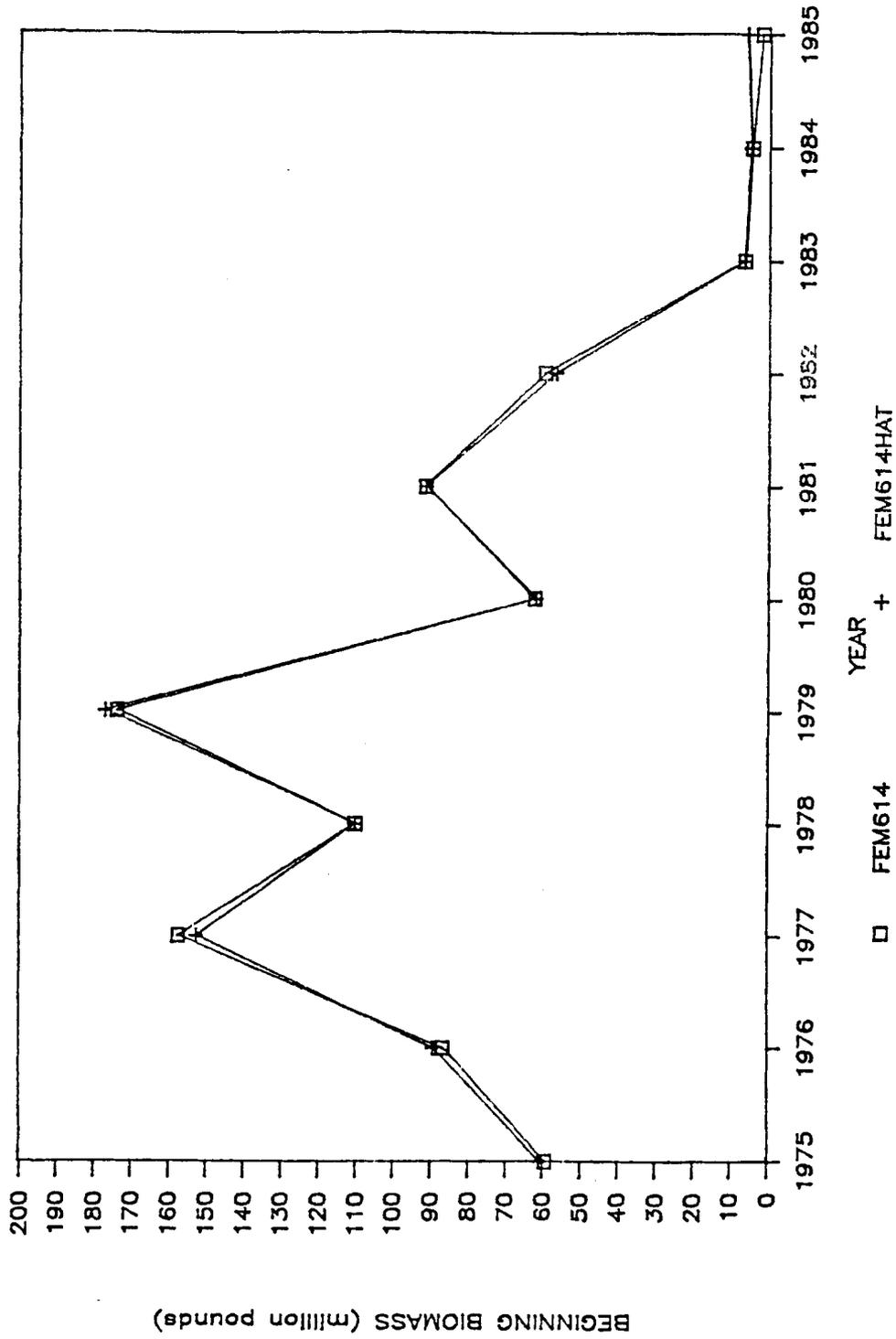


Figure 12. Actual versus predicted population levels of 6-to-14-year-old female king crab (FEM614 and FEM614HAT, respectively), 1975-1985.

$SIZELIM_t$ is a numerically equivalent translation of the regulated size limit (defined in inches) into a percentage value. This percentage corresponds to the proportion of 8-year-old males at the start of period t ($MALE8_t$) that legally can be caught during the fishing season (see Appendix B for further discussion and derivation of $SIZELIM_t$).

The beginning stock of nonlegal crab in period t ($NONLEGALSt$) includes all 5-to-14-year-old female king crab ($FEM514_t$) and sublegal 5-to 8-year-old males. Utilizing equations (28), (29) and (31), $NONLEGALSt$ is defined in equation (32).

$$NONLEGALSt = (FEM514_t + MALE514_t) - LEGALSt \quad (32)$$

The complete biological response submodel is illustrated in matrix form in Table 2. This illustration highlights the recursive aspects of the age-structured submodel. Biological response of the fishery can be linked to a market submodel through the lagged harvest variable ($QHARVT_{t-1}$). It is because of this lagged interaction that the response framework is segmentable from the market submodel, Matulich, Hanson and Mittelhammer (1988a). It does not follow, however, that king crab stocks should be managed in isolation of market forces and the associated dynamic feedback effects. See Matulich, Hanson and Mittelhammer (1988b) for an integration of this recursive age-structured model with the Alaskan king crab industry market submodels.

Table 2. Summary of biological response submodel.

Dependent Variable	Explanatory Variables											
	M A L E 5	M A L E 6	M A L E 7	M A L E 8	M A L E 9 4	M A L E 5 4	F E M 5 5	F E M 6 4	F E M 5 4	F E M 5 4	Q H A R V T	T I M E O
MALE5						L		L	L			
MALE6	L					L		L	L			
MALE7		L				L		L	L			
MALE8			L									X
MALE914				L	L					L	X	
FEM5						L		L	L			
FEM614						L	L	L	L			
MALE514	X	X	X	X	X							
FEM514							X	X				
FM514						X		X				
LEGALS				X	X							
NONLEGALS				X	X	X		X				

X denotes current value of explanatory variable.

L denotes lagged value of explanatory variable.

Indicator variables are not included in this summary.

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APPENDICES

$$\text{MALE8}_t = [a + b \cos(c\text{TIME70}-d)] f [\text{FEM514}_{t-9}^g e^{(h\text{FEM514}_{t-9})} + i\text{FM514}_{t-9} + j\text{MALE514}_{t-9}] \text{MALE6}_{t-2}^k \quad (\text{A.6})$$

The expression for MALE6_t , in turn, can be lagged two periods and substituted into equation A.6.

$$\text{MALE8}_t = [a + b \cos(c\text{TIME70}-d)] f [\text{FEM514}_{t-9}^g e^{(h\text{FEM514}_{t-9})} + i\text{FM514}_{t-9} + j\text{MALE514}_{t-9}] \{m[\text{FEM514}_{t-9}^n e^{(p\text{FEM514}_{t-9})} + q\text{FM514}_{t-9} + r\text{MALE514}_{t-9}] \text{MALE5}_{t-3}^s\}^k \quad (\text{A.7})$$

Equation (A.4) can be used to make the final substitution in the MALE8_t equation. The right-hand expression for MALE5_t must be lagged three periods. The resulting expression is given by equation (A.8).

$$\text{MALE8}_t = [a + b \cos(c\text{TIME70}-d)] f [\text{FEM514}_{t-9}^g e^{(h\text{FEM514}_{t-9} + i\text{FM514}_{t-9})} + j\text{MALE514}_{t-9}] \{m[\text{FEM514}_{t-9}^n e^{(p\text{FEM514}_{t-9} + q\text{FM514}_{t-9} + r\text{MALE514}_{t-9})} + u\text{FEM514}_{t-9} e^{(v\text{FEM514}_{t-9} + w\text{FM514}_{t-9} + x\text{MALE514}_{t-9})}]\}^s \text{MALE5}_{t-3}^k \quad (\text{A.8})$$

Distributing the exponents over the bracketed relationships and combining like terms yields the desired partially reduced form in functional notation.

$$\text{MALE8}_t = [a + b \cos(c\text{TIME70}-d)] f m^k u^{sk} \{ \text{FEM514}_{t-9}^g + nk + sk \} \{ [(h + pk + vsk) \text{FEM514}_{t-9} + (i + qk + wsk) \text{FM514}_{t-9}] + (j + rk + xsk) \text{MALE514}_{t-9} \} \quad (\text{A.9})$$

Each of the parameters specified in (A.9) can be replaced by their estimated values.

from Equation (25):

a = 1.16117
b = 0.40034
c = 5.83152
d = 3.52198

from Equation (23):

m = 0.51185
n = 1.50104
p = -0.03458
q = 0.00005303
r = -0.00714
s = 0.22434

from Equation (24):

f = 0.05833
g = 2.42368
h = -0.05442
i = 0.00008292
j = -0.01132
k = 0.33399

from Equation (20):

u = 4.1775
v = -0.03458
w = 0.00004497
x = -0.001696

Substitution and simplification of equation (A.9) using these parameter estimates generates the spawner-recruit relationship for MALE8_t implied by this partially reduced form of the biological response submodel.

$$\text{MALE8}_t = [1.16117 + 0.40034 \cos(5.83152 \text{ TIME70} - 3.52198)] \quad (\text{A.10})$$

$$\begin{aligned} & [0.051913 \text{ FEM514}_{t-9} \\ & \quad e^{2.99994 (-0.06856 \text{ FEM514}_{t-9} + 0.000104 \text{ FM514}_{t-9})} \\ & - 0.01383 \text{ MALE514}_{t-9}] \end{aligned}$$

Appendix B. Explanation and Derivation of the $SIZELIM_t$ Variable

The $SIZELIM_t$ variable incorporates minimum size limit restrictions into the equation defining legally harvestable biomass. Size limit regulations are established according to carapace width measurements. Regulations historically have allowed all 9-to-14-year-old males and some portion of the 8-year-olds to be harvested. Estimation of legal biomass requires that the minimum width regulation be transformed into a percentage value. This transformation uses a probability distribution based on a standard normal density function. $SIZELIM_t$ represents the probability that 8-year-old males will have shells no smaller than that required by the size limit regulation.

$SIZELIM_t$ is calculated assuming that individual 8-year-old males are normally distributed by width about the midpoint of the cohort's size range, with three standard deviations from the midpoint defining upper and lower bounds of the distribution. NMFS biologists estimate that 8-year-old males range in width from 6.18 to 6.63 inches (157.1 to 168.3 mm, respectively), having a midpoint of 6.405 inches. Given the assumptions and size ranges, the cumulative probability of an 8-year-old male having a carapace at least 6.5 inches wide (the current minimum width) is 0.1271. Therefore, the largest 12.71 percent of $MALE8_t$ crab are assumed to be legally harvestable.