

# Complexity and constraints combined in simple models of recruitment

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## Abstract

A simple model is described that uses a combination of stochastically varying mortality during early life and deterministically-driven mortality in the juvenile phase to simulate recruitment. The model is applied to data on walleye pollock *Theragra chalcogramma* in the Gulf of Alaska and Pacific hake *Merluccius productus* in the California Current region to simulate a recruitment time series for each stock. When compared with observed recruitment time series, the model simulations accurately capture the trends and characteristics of recruitment for these stocks, demonstrating the interplay of high frequency activating factors and low frequency constraining factors in the complex process of recruitment.

## Introduction

Recruitment is a complex biophysical process, but macro-ecological principles and deterministic factors put boundaries and constraints on the array of possible outcomes. The interaction of biological and environmental factors influencing larval survival is complex and noisy. For example, larval feeding success is influenced by turbulence, light levels, temperature and prey availability and their interactions. Larval feeding increases with moderate turbulence due to higher contact rates with potential prey, but reaches a maximum and declines with higher turbulence due to interference with larval feeding behavior; thus the relationship of larval feeding success with turbulence is nonlinear (MacKenzie et al. 1994). In the case of walleye pollock (*Theragra chalcogramma*), their larvae also avoid turbulence by diving, which removes them from the turbulent regime (Davis 2001), but also takes them out of more illuminated depths with higher prey densities (Kendall et al. 1994). There are other relatively high frequency environmental events that influence larval survival besides feeding conditions, such as outbursts of planktonic predators (like jellyfish),

advection, and environmentally driven shifts in spatial and temporal interactions with biota (e.g., blooms, predator-prey overlaps) and physical features (e.g., seasonal warming, fronts).

On the other hand, boundary conditions and deterministic processes constrain and dampen the oscillations generated by variability in larval survival. For example, the amount of suitable habitat area places a strong constraint on population size. A long-term buildup of large long-lived predators in a community may also constrain recruitment levels. In the Gulf of Alaska, such an increase in groundfish predators, possibly due to an environmental regime shift (Anderson and Piatt 1999), is responsible for increased mortality of juvenile pollock and decreased recruitment (Bailey 2000). Density-dependent processes also may dampen recruitment variations (van der Veer 1986).

Recruitment may be described, therefore, as the interplay of high frequency activating factors (Levin and Pacala 1997), that is, noisy environmental conditions occurring during early life, and constraining factors acting on juveniles. Changes in these constraining (and sometimes boundary or even emergent) conditions occur at relatively low frequency. In this paper, we describe some early stage "hybrid" models by which larval survival is described stochastically (but under the influence of environmental conditions), and juvenile survival is influenced deterministically by constraining factors such as predation and density-dependence. In the cases presented here for walleye pollock (*Theragra chalcogramma*) in the western Gulf of Alaska and Pacific hake (*Merluccius productus*) in the California Current system, these models fairly accurately describe the pattern and magnitude of recruitment, illustrating the concept of bio-complexity, importance of initial and boundary conditions, and interaction of high and low frequency events.

## Materials and Methods

A simple type of recruitment model was formulated that describes early life events as stochastically varying, but under the influence of environmental factors and the deterministic control of low frequency and boundary conditions. Similar models have been formulated by Stenseth et al. (1999) and Bjornstad and Grenfell (2001). The form of the survival model for walleye pollock was the standard population dynamics equation:

$$R = E * e^{-(m_1 * t_1 + m_2 * t_2 + m_3 * t_3)}$$

where R is the number of age-2 recruits, E is the initial number of eggs spawned and  $m_1$  is randomly generated mortality over the egg and larval period  $t_1$ , with a low or high range of mortality that depends on environmental conditions. Walleye pollock spawn mainly in Shelikof Strait between Kodiak Island and the Alaska Peninsula in the Alaska Coastal Current (Fig. 1A). Wind speed and sea surface temperature (SST) are two factors associated with survival of larval pollock in this region (Bailey and Macklin 1994; Bailey et al. 1996). Therefore, a low range of mortality ( $m_1 t_1 = 5$  to 6.5) was generated if SST (April-June) was above average and wind speed (May) was below average, otherwise a high range of mortality ( $m_1 t_1 = 7.5$  to 9.5) was generated. The overall range of larval mortality was determined from a life table (Bailey et al. 1996); non-overlapping high and low ranges under differing environmental conditions were estimated to reflect the "boom

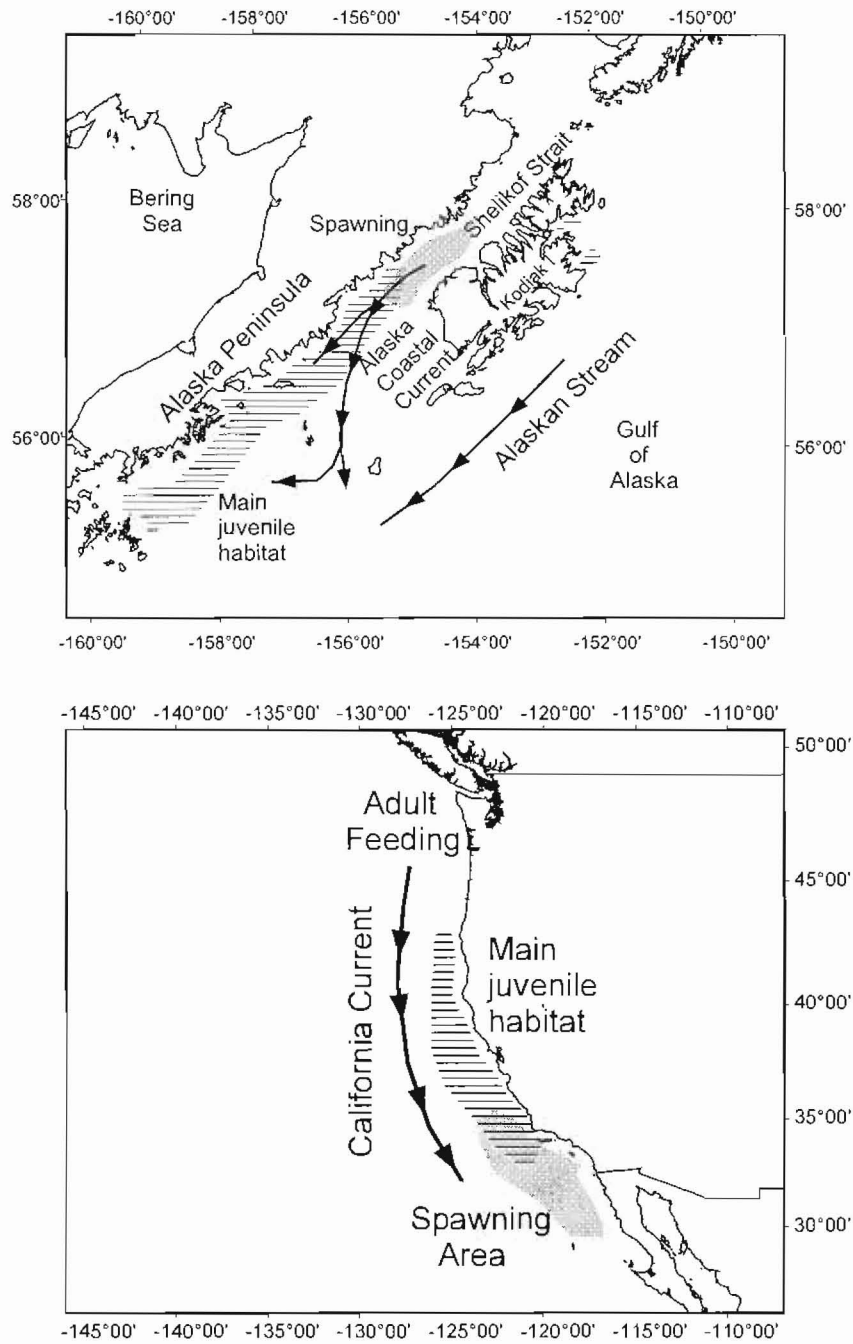


Figure 1. The area of spawning and transport scheme of eggs and larvae of a) walleye pollock *Theragra chalcogramma* and b) Pacific hake *Merluccius productus*.

or bust" nature of larval survival. Late larval mortality rate,  $m_2$ , is density dependent (Schumacher and Kendall 1991). The range of late larval mortality over the period  $t_2$  was determined from life tables (Bailey et al. 1996) and mortality was thus scaled between 1 and 5 depending on cohort density. Juvenile mortality,  $m_3$ , was assumed to depend on potential consumption by large predators over period  $t_3$ ; thus  $m_3 t_3$  was scaled between 1 and 3 against the predation potential of large piscivorous groundfishes as presented by Bailey (2000). There was no attempt to fit or optimize the model. The model was run 200 times, each with a fresh set of random numbers, to simulate variation in the early larval mortality.

For comparison of simulated and observed recruitment, a recruitment time series of age-2 pollock in the Gulf of Alaska from catch-at-age analysis was obtained from stock assessment documents (NPFMC 1997). Natality was calculated for the spawning biomass in the western Gulf of Alaska accounting for eggs  $\text{kg}^{-1}$  and sex ratios and was provided by B. Megrey (Alaska Fisheries Science Center, Seattle WA, pers. comm.). Predation pressure on juvenile pollock was taken from Bailey (2000), calculated from a model accounting for predator biomass, daily ration, overlapping of predator and prey, and percent pollock in the diet. SST was the average value over April-June and was obtained from the NCEP Reanalysis data set provided by N.A. Bond (Pacific Marine Environmental Laboratory, pers. comm.) and was centered on  $56^\circ\text{N}$   $156^\circ\text{W}$ . The average May wind mixing parameter ( $\text{m}^3 \text{s}^{-3}$ ) was derived from the surface stress from gradient winds and was provided by S.A. Macklin (Pacific Marine Environmental Laboratory, pers. comm.).

In the case of Pacific hake a similar model form was used. Pacific hake spawn in offshore waters of central to Baja California within the California Current system (Fig. 1B). As with the pollock model,  $R$  and  $E$  are the number of age-2 recruits and the number of eggs spawned. The ranges of mortality of larvae and juveniles was determined from a life table in Hollowed (1992). SST is correlated with larval survival of Pacific hake (Bailey 1981). Therefore early larval mortality,  $m_1$ , was randomly generated over the larval period  $t_1$ , with a low range ( $m_1 t_1 = 7$  to  $8.5$ ) if temperature was above average and a high range ( $m_1 t_1 = 9.5$  to  $11.5$ ) if temperature was below average. Density-dependent mortality due to cannibalism on age-0 and age-1 juvenile hake by older fishes is believed to occur (Buckley and Livingston 1997); density dependent mortality was described here by an empirical fitted relationship between the abundance of the immediately preceding three older year classes (age-1 to age-2 mortality was linearly scaled between 0.15 and 0.4 depending on the three year  $\{t, t-1$  and  $t-2\}$  running average of observed age-2 recruits). For comparison with the simulated recruitment time series, values for the observed number of recruits were from catch-at-age analysis of commercial harvests (Dorn et al. 1994; 1999). SST was the average value over January-March and was obtained from the NCEP Reanalysis data set provided by N.A. Bond (Pacific Marine Environmental Laboratory, pers. comm.) and was centered on  $33^\circ\text{N}$   $120^\circ\text{W}$ .

## Results

The time series of data on recruitment of walleye pollock in the Gulf of Alaska extends back to the late 1960s although the early years are probably not reliable. There is evidence of eight strong or moderately strong year classes in the 30 year series, occurring in 1972, 1976-79, 1984, 1988 and 1993 (Fig. 2). Since the late 1970s there has been a trend for decreasing recruitment (slope of time

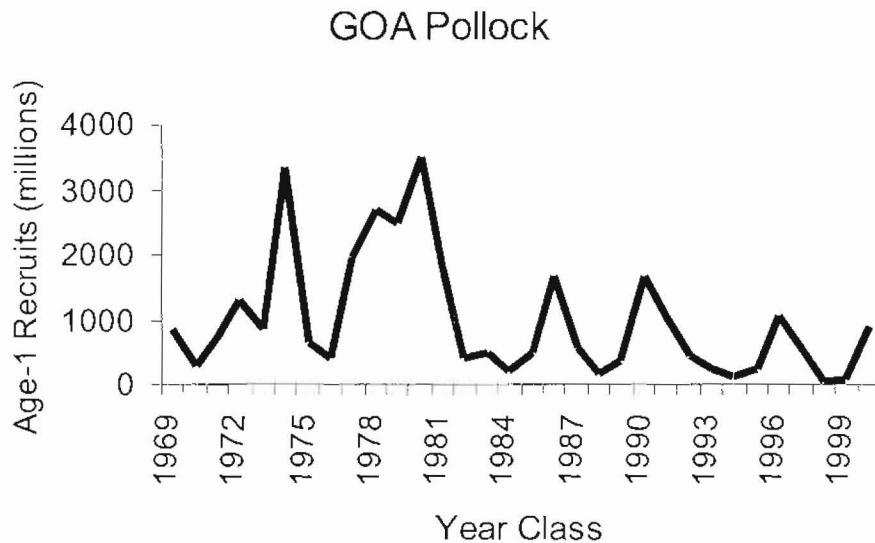


Figure 2. The time series of recruitment of walleye pollock *Theragra chalcogramma* in the western Gulf of Alaska.

trend on the log of observed recruits is  $-0.11$ ,  $p < 0.001$ ). There is a significant auto correlation coefficient (AC) at a 1 year time lag ( $r=0.48$ ), indicating that adjacent year classes tend to be either weak or strong, perhaps suggesting runs of strong or weak year classes or possibly some blending of age classes due to aging errors. ACs at other time lags were not significant.

A recruitment time series for walleye pollock was simulated with environment-scaled stochastic larval mortality, intra-cohort density-dependent late larval mortality, and predator-dependent juvenile mortality (Fig. 3). The modeled time series of recruitment is similar to the observed time series ( $R^2=0.65$ ,  $p < 0.001$ ). Comparisons of the simulated and observed means ( $1.01 \times 10^9$ ;  $1.63 \times 10^9$ ), standard deviations ( $9.73 \times 10^8$ ;  $1.38 \times 10^9$ ) and ranges ( $3.48 \times 10^9$ ;  $5.28 \times 10^9$ ) were similar. The modeled series began in 1975 because data on predator abundance were not available for earlier years. In the model, a series of strong year classes in the late 1970s was described, as well as the 1984 and 1988 year classes. The model had several moderately strong year classes that did not appear in the observed data. The declining trend in recruitment noted above in the observed series was captured by the simulation (slope of time trend on the log of modeled recruits is  $-0.09$ ,  $p < 0.001$ ).

The observed time series for Pacific hake recruitment extends back to 1960. There have been peaks in recruitment in the hake population occurring every 3-4 years (Fig. 4). There is no trend in the recruitment data (slope of time trend on the log of observed recruits is  $0.01$ ,  $p = 0.84$ ). The ACs for the hake time series were not significant, although at lags of 1 and 2 years they were negative, and at lags of 3 and 4 years they were positive.

For Pacific hake, the recruitment time series was simulated with environment-scaled stochastic larval mortality and inter-cohort density-dependent cannibalistic juvenile mortality resulting from the abundance of the three immediately preceding year classes. The modeled series describes

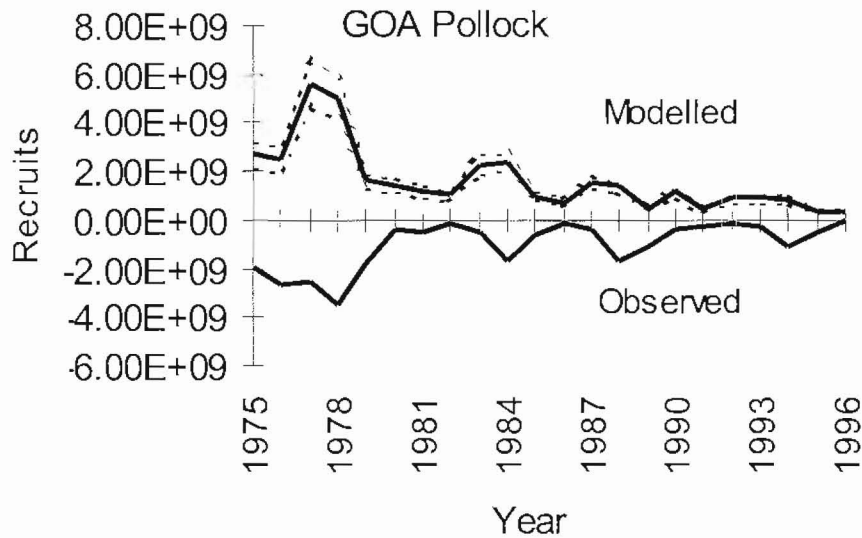


Figure 3. Comparison of observed recruitment (below axis line) to simulated recruitment of walleye pollock *Theragra chalcogramma*. The dotted lines represent  $\pm 1$  sd from 200 simulations.

the major peaks in recruitment of hake and the 3–4 year periodicity observed. Fournier analysis showed the major spectral peaks at 3.2 years for both the observed and simulated time series. The magnitude of actual recruitment varies quite a bit from the model results (Fig. 5). The simulated mean was higher than the observed ( $3.89 \times 10^9$ ;  $1.81 \times 10^9$ ) as was the standard deviation ( $3.38 \times 10^9$ ;  $2.55 \times 10^9$ ). These differences were due to the tendency of the model to identify consecutive strong year classes. There was no trend in recruitment in the model results (slope of time trend on the log of modeled recruits is 0.003,  $p < 0.90$ ), similar to the lack of trend in the observed series.

## Discussion

Our objective in working with these simple models was not to obtain “best fits”, but to capture patterns and trends in recruitment with simple models by describing recruitment as a noisy process that is constrained by boundary effects. Thus we described the high frequency recruitment processes in early life stochastically, although they are influenced by environmental proxies such as SST. Deterministic factors such as density-dependence and predation act to constrain recruitment in the models presented here.

Recruitment of walleye pollock in the Gulf of Alaska is dynamic and perhaps periodic, with an apparent downward trend in recruitment since the 1980s. The pollock model incorporated random larval mortality scaled by SST and wind speed, and was constrained by density dependence and predation pressure. The model simulated peaks in recruitment at the same frequency and usually the same years as the observed time series, and captured the long-term trend.

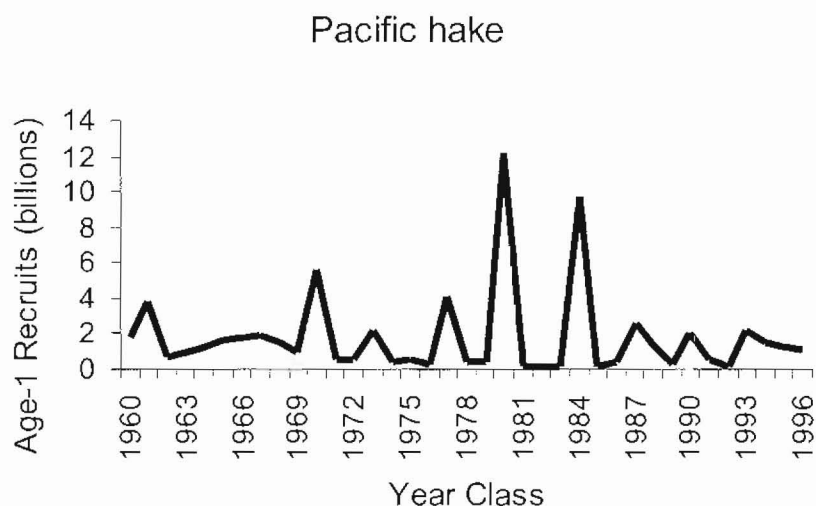


Figure 4. The time series of recruitment of Pacific hake *Merluccius productus* in the California Current region.

In the case of Pacific hake, recruitment is apparently dynamic and periodic, but without a trend. The model incorporated random larval mortality scaled by SST and constrained by cannibalism. Within the frame of the time series used in the analysis, the hake model simulated the 3-4 year periodicity of strong year classes in the population. Strong and weak year classes were accurately captured by the models, but the magnitude of strong year classes often differed from observed strengths. The model generally constructed coupled strong year classes, which did not occur in the observed time series, resulting in a poor statistical fit of modeled results to the observed time series. Although the hake model is promising, it would benefit from refinements, in particular the formulation of density dependence and cannibalism.

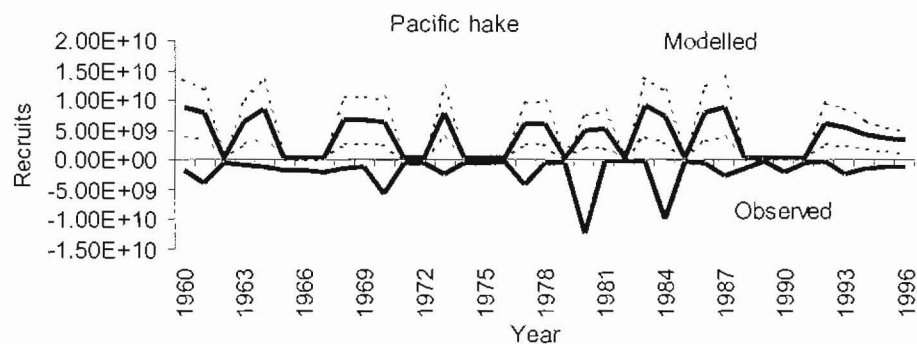


Figure 5. Comparison of observed recruitment (below axis line) to simulated recruitment of Pacific hake *Merluccius productus*. The dotted lines represent  $\pm 1$  sd from 200 simulations.

There are many sources of error and variability in the data utilized in the models, including measurement of environmental conditions, spawning biomass, egg production and predator biomass and consumption (Bailey 2000). There is probably a lot of error in the estimates of the observed time series of recruitment as well. Therefore, we stress that capturing relatively strong patterns and trends has been our main objective rather than obtaining an exact fit of simulated and observed time series; we believe that these simple models are of interest because they are successful at demonstrating the interplay of complexity and constraints underlying the patterns and trends in the recruitment time series for these species. Future work on these models might involve refinement of the biological processes represented in the models, better representation of the error structure in the models, and including the interaction of density-dependence and predation with environmental conditions.

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