Vol. 198: 215-224, 2000

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published June 5

Shifting control of recruitment of walleye pollock *Theragra chalcogramma* after a major climatic and ecosystem change

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ABSTRACT: The critical stage in the life history of walleye pollock *Theragra chalcogramma* at which recruitment is largely determined has shifted in the Gulf of Alaska population. This change follows a major environmental regime-shift in the late 1970s and subsequent dominance of the ecosystem by long-lived predatory flatfishes and cod. An exploratory life table of data on stage-specific abundances was constructed to analyze decadal-scale changes in population demographics. Prior to the mid-1980s, recruitment was correlated with larval mortality, which was largely influenced by environmental conditions. After the mid-1980s, the larval mortality/recruitment relationship eroded, and there was a trend for greater juvenile mortality coinciding with an increase in the abundance of predatory flatfishes and cod. Control of recruitment appears to have shifted in recent years from environmental effects on larvae to biological control of juveniles. Ecosystem change and regime status need to be considered when evaluating mechanisms underlying fish-population dynamics.

KEY WORDS: Climate change · Recruitment · Regime shift · Ecosystem · Gulf of Alaska · Population dynamics

INTRODUCTION

Recruitment is one of the major research themes in marine ecology and fisheries science (Cushing 1972, Sissenwine 1984). Variability in the level of recruitment of marine fishes is sometimes attributed to effects of environmental conditions on larval supply, while in other cases the recruitment level is determined during the juvenile phase as a result of biological processes (for examples see Victor 1986, Houde 1987, Peterman et al. 1988, van der Veer et al. 1990, Leggett & Deblois 1994, Carr & Hixon 1995). While major environmental-regime shifts are known to have dramatic effects on marine community structure (Southward 1980, Steele & Henderson 1984, Dickson et al. 1988, Southward et al. 1988, Aebisher et al. 1990), the mechanisms by which climate change influences dynamics of fish populations is not well understood, and in particular it is not known how environmental shifts affect critical demographic processes such as variability in cohort strength of marine organisms and the stage at which it is determined.

In the late 1970s, a 'regime shift' occurred in the North Pacific Ocean, with well-documented effects on the atmosphere, currents, temperature, zooplankton and fish communities (Trenberth 1990, Brodeur & Ware 1992, Hollowed & Wooster 1995, Sugimoto & Tadokoro 1997, Francis et al. 1998, McGowan et al. 1998, Anderson & Piatt 1999). The trends in physical and biological data series have been persistent (Beamish et al. 1999), and include warming of the North Pacific and an increase in the springtime zooplankton abundance. Margalef (1963, 1988) hypothesized that the ecosystem effect of a strong, prolonged external disturbance would be to reset, or trigger reorganization of community structure and succession. In theory, ecosystem maturity is defined by the importance of internal linkages in the community. After a prolonged environmental disturbance like a regime shift, community structure can change, and immature or less-structured ecosystems may be more subject to influ-

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ence from environmental input acting on planktonic processes. During later ecosystem maturation, biological control may emerge as a dominant influence. Other investigations of fish populations have indicated that climate-shifts from cold to warm periods are associated with strong year classes immediately after the change (Saetersdal & Loeng 1987, Beamish 1993), suggesting the influence of planktonic processes. Prior to the late-1970s regime-shift in the Gulf of Alaska, the nekton community was dominated by forage species such as capelin and shrimps. This period was characterized by cold-ocean conditions, perhaps reflecting unstable conditions that favored *r*-selected species. The sudden shift to warm-ocean conditions may have triggered a reorganization of the ecosystem structure, as evidenced by a dramatic decline in forage-fishes and shrimps, an initial increase in gadids, and a gradual build-up of long-lived flatfishes over the ensuing decade (Anderson et al. 1997, Anderson & Piatt 1999).

Walleye pollock *Theragra chalcogramma* is widely distributed across the North Pacific Ocean, but its spawning is relatively localized at specific spawning grounds and during restricted periods. In the Gulf of Alaska, the majority of spawning occurs in a deep sea valley, Shelikof Strait (Fig. 1), during the first 2 wk in April (Kendall et al. 1996). Larvae drift downstream in the Alaska Coastal Current, where they may be retained by eddies, transported onto the continental shelf, or swept offshore into the swift-flowing Alaskan Stream where they are presumably expatriated and perish. Shelikof Strait is at the center of storm activity in the Gulf of Alaska, and considerable year-to-year variability of environmental conditions is experienced there. Studies of population structure indicate that there is limited exchange via immigration/emigration of this local population with neighboring populations in the Bering Sea and Prince William Sound (Bailey et al. 1999). These characteristics make pollock in Shelikof Strait a good model for studies of oceanic fish-

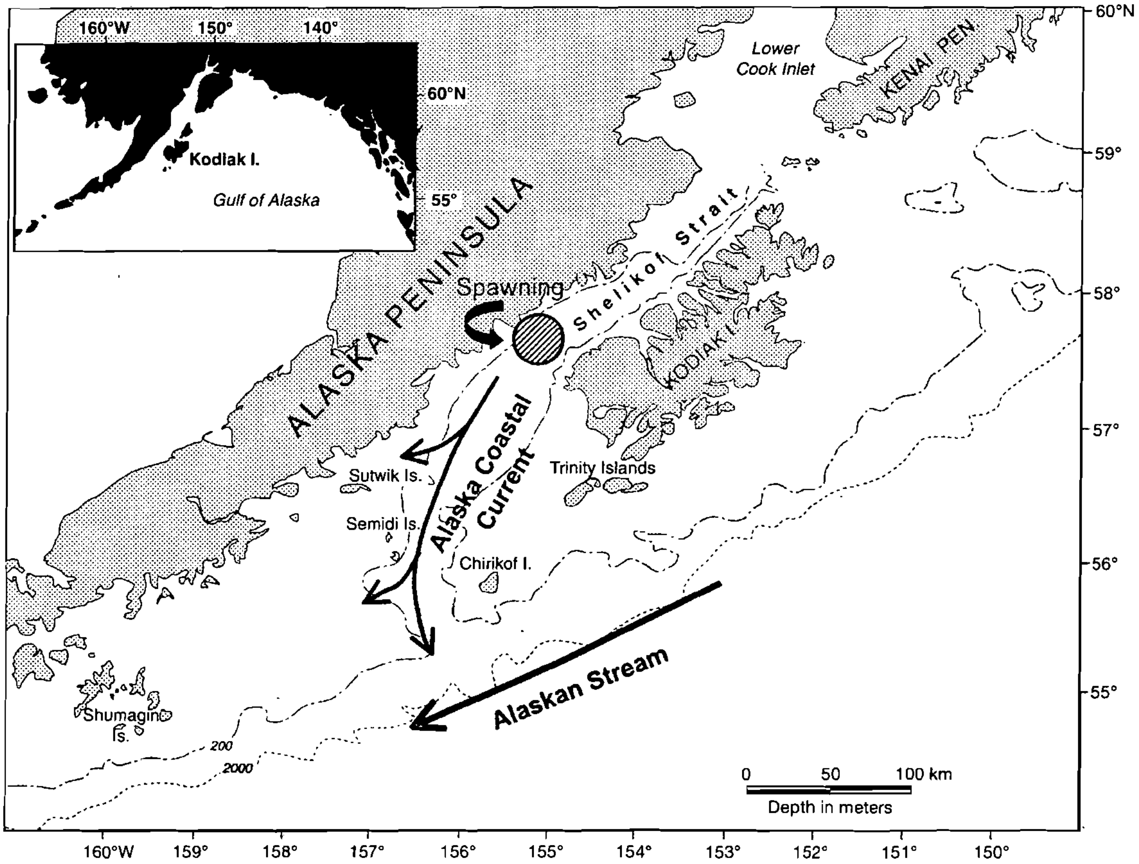

Fig. 1. Shelikof Strait region and major currents of Gulf of Alaska. Walleye pollock *Theragra chalcogramma* spawn in a restricted area of the strait near southwest end of Kodiak Island during first 2 wk in April. The eggs lie deep in water column at ~200 to 250 m and experience little water transport. Hatched larvae rise toward surface, where they develop and feed in Alaska Coastal Current. By the end of May, larvae are found in the area from southern end of Kodiak Island to as far west as continental shelf midway between Semidi and Shumagin Islands; juveniles are found around Kodiak Island and westward to Shumagin Islands

population dynamics. Several strong year classes of pollock, including 1977 and 1978, were spawned during the apparent regime-shift.

Ecosystem changes subsequent to the late 1970s regime-shift were examined for their effects on the population demography of walleye pollock. These effects included a shift in the period when year-class strength is determined, and the processes involved. An exploratory stage-specific life table was constructed using data from ichthyoplankton surveys, hydroacoustic surveys, juvenile fish surveys and commercial fisheries data. Trends in larval and juvenile mortality were compared to environmental conditions and changes in abundances of major predators; the potential impact of predators on juvenile mortality and recruitment was examined with a simple predation model.

METHODS

An estimate of the number of *Theragra chalcogramma* larvae surviving the egg and yolk-sac larval stages was made from the egg-mortality rates given in Brodeur et al. (1996b) and population fecundity over an assumed 19 d egg and yolk-sac period. Missing data on egg mortality were replaced by the mean across years, and likewise the mean was used for 1986, which had a suspect egg mortality estimate (Brodeur et al. 1996b). The use of an average value probably is appropriate in this circumstance, because the variability around egg mortality is rather low. The sensitivity of the analysis to using the mean egg mortality in missing cells was tested by Monte Carlo simulation, with random numbers replacing mean egg mortality. The random egg-mortality values were generated to fall within a normal distribution with the observed across-year mean and variance. In 1000 simulations, the effect of randomly varying egg mortality had only a small effect on significant regressions where egg mortality was a factor in calculation of other variables used in regression analyses in this study. Only 3% of simulations showed regression p-values increasing over the significance level of 0.05, and all of these were <0.10.

The number of larvae that survived the early feeding period was calculated from the estimated number surviving the egg and yolk-sac stage and their mortality. Mortality rates of early-feeding larvae were from Bailey et al. (1996a), except 1981 (from Kim & Gunderson 1989), 1985 (from Incze et al. 1989), and 1986 (from Incze & Campbell 1989). These mortality rates were assumed to apply to first-feeding larvae for a period of 10 d. Late-larval abundance estimates are from Bailey & Spring (1992) except for those in 1989 to 1996, which were calculated using the same method. This method uses size-specific abundance data from surveys of late-stage larvae; it standardizes for differences in timing of the surveys and spawning by applying assumed growth and mortality rates to the larvae in each size category and then calculating the number of larvae surviving to 15 mm in length. The standardization is necessary because a wide age range of larvae is caught in late spring, and the young larvae in the samples have not been exposed to mortality risks for as long as older larvae, who have passed through the period of high mortality risk; thus, the number of young larvae may bias the overall abundance as a population index.

The observed number of Age 0 juveniles was taken from Bailey & Spring (1992), except for the 1990 and 1991 data, which were taken from Brodeur et al. (1996a) and Wilson et al. (1996). The number of Age 1 juveniles was modified from data presented in McKelvey (1996). Since the number of Age 1 juveniles was sometimes lower than the number of Age 2s observed the following year (because the area surveyed does not encompass the overall distribution of Age 1 pollock) the number of Age 1s was used as an index. The index was scaled up to the appropriate range to obtain an estimate of Age 1 abundance based on the ranges observed for Age 0 and Age 2 (previous and subsequent life stages) abundances.

Information on adult pollock abundance, Age 2 recruits and population fecundity was available from the virtual population analysis (VPA) of commerical harvests since 1972 (NPFMC 1997). Natality was calculated from the spawning biomass of walleye pollock in the western Gulf of Alaska, the number of eggs per kilogram, and sex ratios (Picquelle & Megrey 1993, Brodeur et al. 1996b), and was obtained from B. Megrey (pers. comm.). VPA estimates of Age 2 abundance may include fish from other stocks within the western Gulf of Alaska, but it is assumed that the Shelikof population dominated the population over the time period of this study. VPA and acoustic-survey estimates of the abundance of Age 2 pollock in the Shelikof region are strongly correlated ($r = 0.86$, $p < 0.001$). k-values, the product of stage (i) duration (t_i) and stage instantaneous mortality rate (m_i), were calculated after Varley & Gradwell (1960) as:

$$k_i = \log N_i - \log N_{i+1}$$

For example, k_1 represents mortality from egg to early feeding, k_2 from early feeding to mid-stage larvae (10 d later), k_3 from mid-stage larvae to late-stage larvae (15 mm), k_4 from late-stage larvae to Age 0 juveniles in late summer, k_5 from Age 0 juveniles to Age 1 the following spring, and k_6 from Age 1 to Age 2 recruits.

Data sources, manipulation and assumptions have been discussed more thoroughly in Bailey et al. (1996c). The same data are used here, but they have been updated to include data collected in 1992 to 1996, and include modifications to some of the original data.

Not all data were available for all years, and where data-cells on a specific life stage were empty, ANOVA (Sokal & Rohlf 1981) was used to interpolate the value from adjacent cells, when both adjacent cells contained values (12 of 112 possible cells were filled in by interpolation). A form of jack-knifing, comparing the results of this estimation technique with years in which such cell values were present, showed that the technique was robust ($r = 0.97$, $p < 0.001$).

The instantaneous rates of larval mortality used here were calculated by tracking larval cohorts with consecutive ichthyoplankton surveys in early and late May. Pollock larvae were sampled with 60 cm bongo nets. In the early-season cruises, a 0.3 mm mesh net was used; later in the season, when larvae were larger and when the small mesh clogged with algae, a 0.5 mm mesh net was used. Bongo nets sample pollock larvae effectively up to a length of ~18 mm (Shima & Bailey 1994). Given a mean growth rate of ~0.2 mm d^{-1} (Yoklavich & Bailey 1990), a 5.5 mm larvae sampled in early May would be ~10 mm in length 20 d later. Bongo tows were oblique to 100 m (or 10 m off-bottom in shallow stations). For standard bongo tows, the contents of one codend were fixed in 5% formalin for quantitative sorting in the laboratory, and the contents of the other codend were quickly sorted over ice and the larvae put in 95% ethanol. All samples in formalin were sorted at the Polish Plankton Sorting Center, Szczecin, Poland. Walleye pollock larvae were identified, enumerated and a subsample of 50 larvae (or the total number caught, whichever was smaller) measured for standard length. Identifications were verified in the laboratory of the Alaska Fisheries Science Center.

Mortality of larvae was calculated according to the methods in Bailey et al. (1996a). Briefly, larval abundances were estimated from the first and last cruises under the assumption that the same cohort of larvae, determined from the hatchdate distributions, was sampled during both cruises. Satellite-tracked drifters drogued ('holey-sock' type) at 40 m were released in areas of high larval pollock abundance, with the object of tracking the larvae as they drifted with the currents. The extent of the survey grids was adjusted to account for the movement of the drifters. The lengths of larvae caught in the nets were adjusted for preservation effects. Larvae were aged using standard otolith-ageing techniques (Yoklavich & Bailey 1990). Abundances of each 3 d cohort were estimated for each survey, and mortalities were computed from the abundance-at-age for each cohort from the 2 surveys. Further details on collection, processing and analysis of data can be found in Bailey et al. (1996a). Data published previously are updated here to include ichthyoplankton surveys from 1992 to 1996.

A predation model was formulated to examine the potential impact of predators. The model was:

$$\mathrm{NC} = \sum_{i=1}^{n}\sum_{j=0}^{1}(\mathrm{PB}_i \cdot \mathrm{DR}_i \cdot \mathrm{PP}_{ij} \cdot \mathrm{FP}_i \cdot \mathrm{OL}_{ij} / \mathrm{WT}_{ij})$$

where NC = number of Age 0 and Age 1 pollock consumed by all predators, i = predator species, j = age class, PB = predator biomass, DR = daily ration consumed d^{-1}, PP = % age class pollock in diet, FP = feeding period in days, OL = % overlap of predator and prey populations, and WT = weight of pollock prey. The importance of the different predators included in the model and their daily ration was evaluated from data in Livingston & deReynier (1996) and Yang (1993). Predator-prey overlap was approximated from distribution maps. The percentage of pollock in the diet, besides being estimated as a constant proportion of the diet, was also modeled as a Type III functional response (s-shaped function of prey density) with a logistic equation using SYSTAT. Percentage survival was calculated as the ratio of the observed number of Age 1 pollock surviving and the number consumed, as calculated from the predation model. The abundance of Age 0 juveniles in August was interpolated from values in the life table for the number of juveniles in September and the mortality between June and September for each year. Late summer appears to be the period when Age 0 juvenile pollock become vulnerable to groundfish predators (Bailey 1989).

RESULTS

The instantaneous rate of mortality during the early life stages of *Theragra chalcogramma* (calculated by tracking larval cohorts with consecutive ichthyoplankton surveys ~20 d apart) was high for several days after first-feeding had been initiated (Fig. 2A). Subsequently, there was a marked decline in mortality rates with increasing age. The regression of the natural log of larval mortality (lnM) against age (a) was significant ($\ln M = -0.60 - 0.14a$, $r = 0.62$, $p = 0.0006$).

The mortality rate of early-feeding larval pollock was inversely correlated with sea-surface temperature (SST) (Fig. 2B). Sea-surface temperature data were monthly means for the survey area. The regressions of natural log of mortality against SST were significant for cohorts with initial ages of 7 and 10 d ($\ln M = 0.99 - 0.57\,\mathrm{SST}$, $r = 0.87$, $n = 9$, $p = 0.002$ and $\ln M = -0.68 - 0.33\,\mathrm{SST}$, $r = 0.63$, $n = 10$, $p = 0.049$, respectively). This relationship had disappeared by

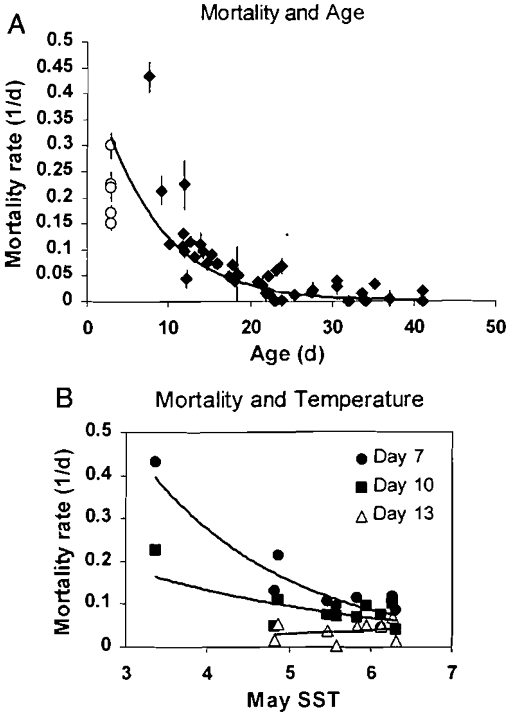

Fig. 2. (A) Instantaneous mortality rates of larvae as a function of mean age (weighted for density) in ichthyoplankton surveys from 1987 to 1996. ○ = egg mortalities; vertical lines = SD. (B) Instantaneous mortality rates for cohorts with initial ages of 7, 10 and 13 d as a function of sea-surface temperature, SST (°C). Mortality rates were estimated by tracking cohorts of larvae between 2 consecutive ichthyoplankton surveys, approximately 20 d apart, from 1987 to 1996

the time larvae were ~2 wk old. The trend for the cohort with an initial age of 13 d was not significant (r = 0.24, n = 9, p = 0.54).

In the years immediately following the late-1970s regime-shift, larval mortality, estimated from the stage-specific abundances in the life table, was inversely correlated with the subsequent year-class strength of the cohort (Fig. 3A). The period from 1981 to 1988 had a significant linear relationship ($y = 21.04 - 0.41x$; r = 0.86, p = 0.014). However, it is noticeable that in the late 1980s a prevalent high abundance of late-stage larvae resulted in a low frequency of strong year classes. In fact, the association between larval mortality and recruitment has ceased to exist since about 1989 (Fig. 3A); the relationship over the period from 1989 to 1996 was not significant (r = 0.21; p = 0.61). This non-significant relationship was not dependent on the one apparent outlying point with very low recruitment (1992), as a regression line excluding this point was still not significant (p = 0.41).

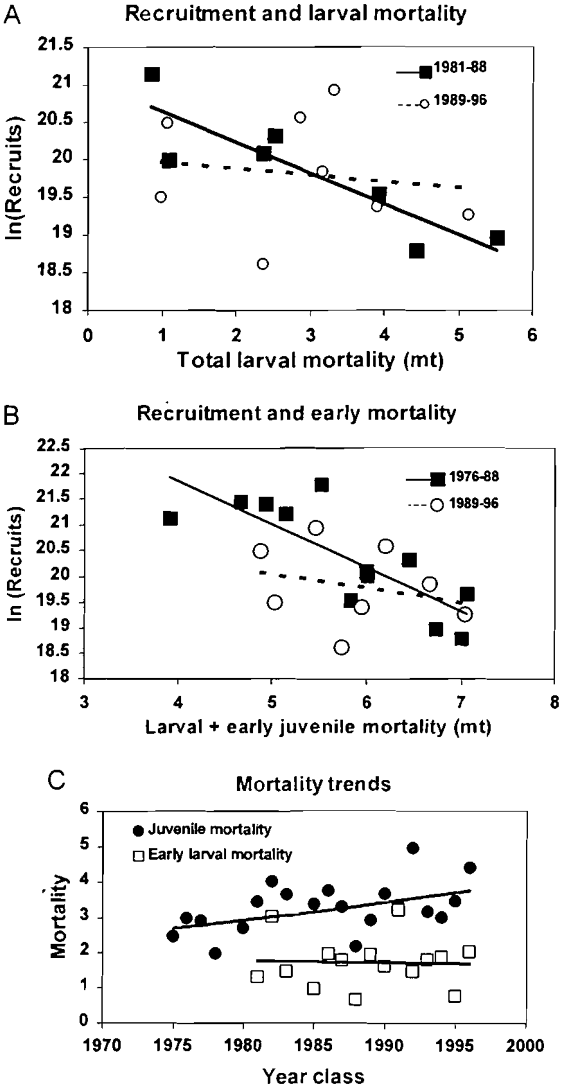

Fig. 3. (A) Natural log of number of Age 2 recruits versus stage-specific larval mortality (product of instantaneous mortality and stage duration, $m \times t$) calculated from life table for 2 periods, 1981 to 1988 and 1989 to 1996. (B) Natural log of number of Age 2 recruits versus stage-specific larval and early juvenile cumulative mortality ($m \times t$) calculated from life table for 2 periods, 1976 to 1988 and 1989 to 1996. (C) Trends in juvenile and larval cumulative mortality, calculated from stage specific life table, over time

Although there were no larval mortality estimates available prior to 1981, it was possible to examine the mortality occurring between the beginning of the larval period (given the total number of eggs produced and an annual estimate of egg mortality) and the early juvenile stage (in August/September of the first year of life) back to 1975. The relationship between early-life mortality and recruitment was independently confirmed with these data, again showing a significant relationship between mortality and recruitment from the period 1976 to 1988 ($y = 25.25 - 0.86x$; r = 0.80, n = 12, p = 0.002). The relationship disintegrated over the period from 1989 to 1996 (r = 0.30, p = 0.47; Fig. 3B).

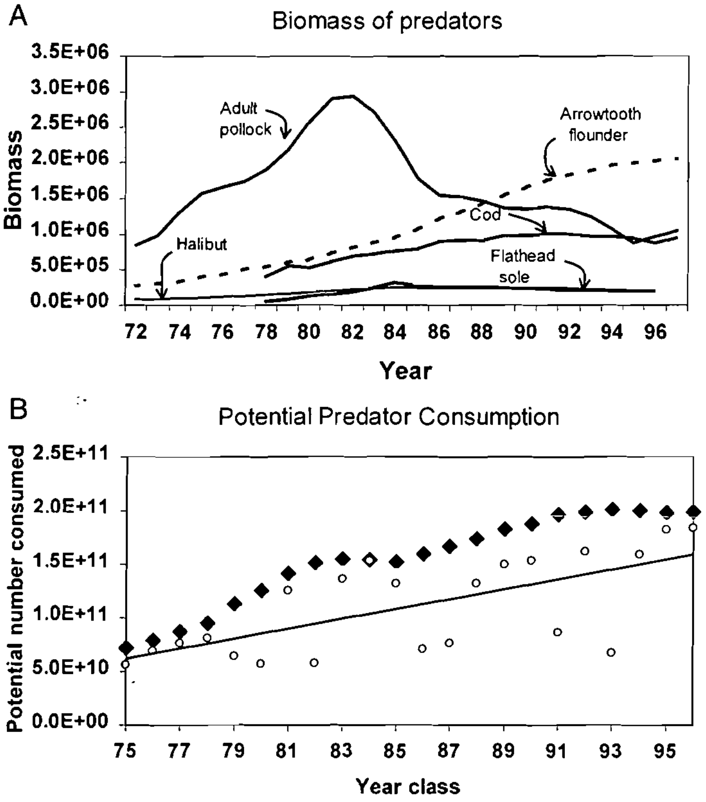

Fig. 4. (A) Changes in biomass of predators in Gulf of Alaska from 1972 to 1996; estimates of flathead sole and cod prior to 1978 are not available. (B) *Theragra chalcogramma*: sum of potential number of Age 0 and Age 1 pollock consumed from each year-class, estimated from predation model incorporating predator and prey overlap, predator ration, and diet composition; predators in model were: adult pollock, arrowtooth flounder, cod, flathead sole and halibut. ◆: model run, assuming constant percent of prey pollock in predator diets; o and trend line: varying percentage of prey pollock in predator diets, modeled as sigmoid density-dependent relationship

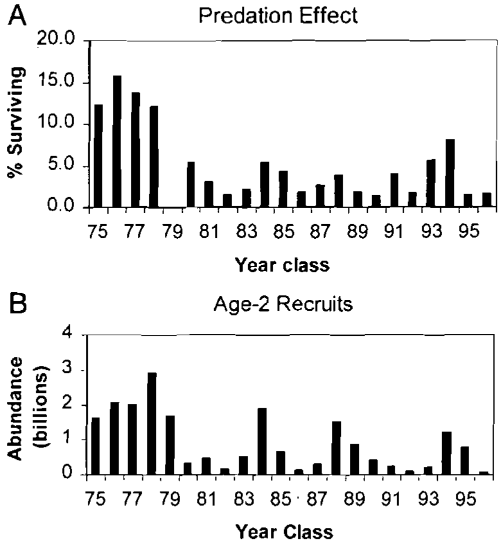

Fig. 5. (A) Potential cohort surviving predation at recruitment at Age 2, estimated from numbers of Age 0 juveniles available to predators in August of first year and numbers removed by predators. (B) Estimated abundance of Age 2 recruits in population (for comparison with number potentially remaining after predation in A)

Excluding one outlying point with low recruitment (1992) did not affect the non-significance of the regression line ($p = 0.41$).

Over the available time series, there was no significant trend in larval mortality; however, juvenile mortality, between the beginning of the juvenile phase in late summer and recruitment at Age 2, increased significantly ($y = -98.66 + 0.051x$; $r = 0.48$, $n = 20$, $p = 0.03$) over the period from 1975 to 1996 (Fig. 3C).

Across the same 1975 to 1996 period, there was an increase in the biomass of many long-lived predatory flatfish species and cod (Fig. 4A). An estimate of the potential number of Age 0 and Age 1 pollock eaten by key predators (Pacific halibut *Hippoglossus stenolepsis*, arrowtooth flounder *Atheresthes stomias*, flathead sole *Hippoglossoides elassodon*, Pacific cod *Gadus macrocephalus*, and adult pollock) from each pollock year-class was calculated from a simple model incorporating the percent and age composition of pollock in predator diets, the daily ration of predators, and the degree of spatial and temporal overlap of predators and prey. The simulations assumed a constant percent of prey pollock in predator diets and a density-dependent, sigmoid, feeding relationship. The results reveal an increasing trend in the potential consumption of juvenile pollock over a period marked by changes in the nature of the community (Fig. 4B). The trend line was significantly positive for the density-dependent consumption version ($r = 0.59$, $n = 22$, $p = 0.04$).

The percentage of the population surviving predation pressure to Age 2 recruitment was calculated from the estimated number consumed as juveniles and the number surviving (Fig. 5A). Comparison of the simulated percentage of pollock surviving predation with the number of Age 2 recruits (Fig. 5B) revealed 2 trends: (1) a relatively high percentage of juvenile pollock survived the juvenile predation period in the late 1970s and this percentage declined considerably in the 1980s through 1996; (2) the percent surviving juvenile predation pressure represents the number eventually recruited to the fishery.

DISCUSSION

Analysis of tree rings and other historical data indicate that climate regime-shifts in the North Pacific

Ocean have occurred on the average every 15 yr since the time of Columbus (Ingraham et al. 1998) or longer. Not all changes have been as strong as the late-1970s shift, but comparable events have occurred many times over the past several centuries (Wiles et al. 1998).

The exploratory life-table analysis presented here for *Theragra chalcogramma* suggests that the critical factors and life stage at which recruitment success is determined for walleye pollock depend on large-scale changes in the environment and shifts in the state of the ecosystem. During the period immediately following the regime-shift, recruitment was correlated with larval mortality. During (and after) the regime-shift, there was an increase in the springtime abundance of zooplankton in the Gulf of Alaska, presumably due to regime-shift effects on planktonic processes, which may be favorable to the survival of pollock larvae. After a 5 to 10 yr lag, as the ecosystem matured and the abundance of large predators built up, predation on juvenile pollocks had an increasing effect on recruitment.

The instantaneous rates of mortality during the early life stages of walleye pollock are very high during several days after first-feeding has been initiated (short-term instantaneous rates may actually be underestimated as they are calculated over about a 20 d period). As pollock larvae grow and age, mortality declines markedly. These results are consistent with independent observations of high percentages of walleye pollock larvae in poor nutritional condition up to a length of ~6 to 7 mm (larvae hatch at ~4 to 5 mm and take ~10 to 15 d to reach 6 to 7 mm), and a dramatic decline in the percentage of 'starved' individuals among older and larger larvae (Fig. 6; plotted from data in Theilacker et al. 1996). Furthermore, early-stage pollock larvae have a poorly developed escape-response, which improves markedly over the 10 d subsequent to initation of feeding (H. Sugisaki, K. M. Bailey & R. D. Brodeur unpubl. data). The instantaneous mortality rate of larval pollock is inversely correlated with sea-surface temperature (SST) during the early feeding period. Presumably, SST is related to the development of the zooplankton community eaten by larval pollock, as warm temperatures have been shown to favor larval condition and growth (Bailey et al. 1995, 1996b). SST may also reflect other environmental factors that could influence larval survival, such as storms and turbulence. These results are broadly indicative of the importance of environmental conditions in the process of early larval survival. Houde (1997) also re-analyzed the larval pollock data from 1985 to 1991 and found early-larvae mortality and the ratio of instantaneous rates of larval mortality to growth (M/G) to be concordant with recruitment patterns. Houde did not have the benefit of data from 1992 to 1996 to detect the effects of the changing ecosystem.

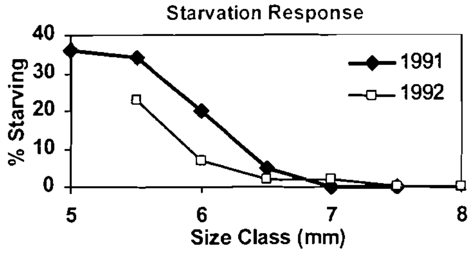

Fig. 6. Percentage of larvae in starving condition (determined from midgut cell height) as a function of standard length (data from Theilacker et al. 1996). Larvae were collected in Gulf of Alaska in May 1991 and 1992

There was no consistent temporal trend in larval mortality over the whole time-series. In the years 1981 to 1988 following the regime-shift, cumulative larval mortality, estimated from the stage-specific abundances in the life table, was inversely correlated with the subsequent year-class strength of the cohort. However, from 1989 to 1996, there was no significant association between larval mortality and recruitment. In general, the dependence of recruitment on environmental conditions that favor high larval survival may have decreased in recent years.

Although there was no significant trend in larval mortality over the available time-series as a whole, there was a significant upward trend in cumulative juvenile mortality between the beginning of the juvenile phase in late summer and recruitment at Age 2 from 1975 to 1996. Over the same time-period, there was an increase in the biomass of many long-lived predatory flatfish species and cod. Simulations using a simple model of predation by Pacific halibut, arrowtooth flounder, flathead sole, Pacific cod, and adult pollock showed an increasing trend in the potential consumption of juvenile pollock over a period marked by the maturing nature of the predator community. Aquiring a more realistic estimate of the impact of these predators is an imposing task because of the many predators involved, their complex feeding behaviors and rations under varying conditions, the importance of the spatial and temporal overlap in their interactions (necessitating detailed seasonal distribution data), and the different types of gear needed to sample and estimate abundances of each species adequately. However, this rudimentary model did illustrate the potential impact of an increasing number of predators, and the results paralleled the trend in juvenile mortality. From the late 1970s to the early 1990s, there was an approximate doubling of the number of juvenile pollock potentially consumed by flatfishes and cod, and a 25% increase from the mid-1980s onwards.

Comparison of the potential number of juvenile pollock surviving juvenile predation-pressure with the number of Age 2 recruits estimated from VPA revealed several important points. The survival of juveniles and their eventual recruitment correspond fairly well, but other important sources of juvenile mortality are not accounted for by the predators included in the model, notably at the beginning of the time series. For example, halibut in the region between Kodiak Island and Unimak Pass was not included in the predator biomass of the simulation model because it is not included in halibut stock-assessments. Other fishes, birds and mammals are also likely to be sources of mortality that varied in importance across this time series.

The model results emphasize that, since the early 1980s, mortality induced by the key predators included in the model was capable of diminishing the larval supply; however, in spite of the strong potential predation pressure, relatively strong year-classes still appeared in the population; for example, the 1994 cohort. I offer 2 explanations for this: (1) surveys of the abundance of late-larvae may underestimate the abundance of strong year-classes, which may expand their distribution range or otherwise overflow from the survey region, or may have atypical distribution patterns outside the survey region, e.g. in shallow water; (2) environmental conditions, such as bottom temperatures, or patterns of larval transport may influence the overlap of predators and prey. When the overlap is minimized, a cohort may escape the pressure of potential predators.

Although the best available information was sought and utilized for this study, it bears noting that the life table results are exploratory. Many inaccuracies in the data may be small relative to dynamics in the population abundance (10- to 30-fold variation in recruitment). Among the potential errors in these data sets are surveys that do not cover the total distribution of the population. Another potential source of error is the use of catch-at-age analysis for Age 2 recruits, and the effect of errors in parameter estimation and in assigning ages to older fish (which propagate to errors in back-calculated numbers of Age 2 recruits). Aging error may be of particular concern after a strong year class appears in the population and if there are density-dependent effects on otolith appearance. It is somewhat re-assuring that estimates of Age 2 abundance from hydroacoustic surveys of the Shelikof region and from catch-at-age analysis for the western Gulf of Alaska are significantly correlated ($r = 0.83$, $p = 0.0002$); however, there are some obvious differences in the magnitude of strong year classes and those immediately following them. The results of this study also rely on assumptions made to fill missing cells and adjust relative numbers; where possible, the effects of these assumptions were tested.

Alternative causes for increasing 'mortality' of juveniles should be considered. One potential scenario is that in recent years, juveniles spawned in the Shelikof area have increasingly recruited to another spawning region, such as the Shumagin Islands. However, spawning times inferred from hatchdate frequencies of juveniles collected in late summer in the Shumagin region coincide with the local spawning time, and differ significantly from the Shelikof spawning period (K. M. Bailey & A. Brown unpubl. data). This result is inconsistent with a supposition of emigration at the early juvenile stage. Moreover, comparison of Age 2 abundances from hydroacoustic surveys in the Shelikof region and catch-at-age analysis from the larger western Gulf of Alaska area do not indicate any large-scale shifts of recruits from the Shelikof area occurring in the period of interest from 1989 to 1996 (concluded from no significant trend in the residual difference in the 2 estimates; $r = 0.33$, $p = 0.25$). Emigration of juveniles is currently undergoing further study using other otolith characteristics as natural markers. Another explanation might be that environmental conditions changed beginning in 1989; however, this was not reflected by a trend in larval pollock mortality, nor did it affect the longer-term trend in juvenile mortality.

Margalef's (1963, 1988) concept of environmental disturbance resetting community structure, and the increased role of biological control when ecosystems mature, merit further consideration in studies of the recruitment of marine fishes. Environmental effects on planktonic stages appear to have dominated the recruitment process of walleye pollock in the years immediately succeeding the late-1970s regime-shift. As the coastal Gulf of Alaska ecosystem changed in the 1980s, and abundances of long-lived flatfishes and cod increased, the importance of predation-mediated juvenile mortality also increased. In this latter situation, a high rate of larval survival was not sufficient to ensure a strong year-class. Experimental studies on coral reef fishes have shown the impact of a changing predator community on population regulation (Hixon & Carr 1997). In the case of walleye pollock, the importance of various factors influencing recruitment varies from year to year, and it appears that longer decadal scales should also be taken into consideration. Studies on the factors that influence recruitment, the life stage at which recruitment success is determined, and the importance of larval supply must take into account long-term environmental change and changing community structure.

Acknowledgements. I thank C. Wilson, B. Megrey and A. Hollowed for providing data on Age 1 and Age 2 and adult abundances, S. Picquelle and A. Brown for collaboration on calculating larval abundances and mortality, and A. Kendall

Jr, R. Brodeur, S. Sogard, R. Beamish, M. Hixon, S. Picquelle and anonymous reviewers for comments on earlier versions of the manuscript.

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Editorial responsibility: Otto Kinne (Editor),
Oldendorf/Luhe, Germany

Submitted: October 6, 1999; Accepted: December 23, 1999
Proofs received from author(s): May 9, 2000