NONADDITIVE EFFECTS OF THE ENVIRONMENT ON THE SURVIVAL OF A LARGE MARINE FISH POPULATION

Lorenzo Ciannelli,[1,4] Kung-Sik Chan,[2] Kevin M. Bailey,[3] and Nils Chr. Stenseth[4,5]

[1]*University of Washington, Joint Institute for the Study of Atmosphere and Ocean, Seattle, Washington 98105 USA*
[2]*Department of Statistics and Actuarial Sciences, University of Iowa, Iowa City, Iowa 52242 USA*
[3]*Alaska Fisheries Science Center, NOAA, Seattle, Washington 98115 USA*
[4]*Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biology, University of Oslo, Oslo N-0316 Norway*

Abstract. Climate can affect population dynamics in indirect ways via nonadditive forcing by external variables on internal demographic rates. Current analytical techniques, employed in population ecology, fail to explicitly include nonadditive interactions between internal and external variables, and therefore cannot efficiently address indirect climate effects. Here, we present the results of an analysis, employing specifically developed statistical methodology, on density-dependent survival of walleye pollock (*Theragra chalcogramma*) prerecruitment stages in relation to background environmental variables in the Gulf of Alaska. We found that spring winds and water temperature mediate the intensity of density-dependent survival from the eggs to the age-0 stage. Fall water temperature and juvenile pollock predator abundance mediate density dependence from the age-0 to the age-1 stage. The inclusion of such nonadditive and nonlinear effects in a population dynamics model improved our ability to simulate pollock recruitment. Our results point to the importance of understanding nonadditive and nonlinear interactions between external (climate) and internal factors in the presence of underlying environmental variation. These topics are discussed in the context of current research priorities in population ecology and conservation biology.

Key words: density dependence; environmental change; Gulf of Alaska; nonadditivity; phase dependence; Theragra chalcogramma; *walleye pollock.*

INTRODUCTION

The ecological effects of environmental change on population dynamics have received much attention, particularly with respect to climate variation (Stenseth et al. 2002). It is well known that self-regulating and internal forces, such as density dependence (e.g., Stenseth et al. 1999), and external environmental variables, such as climate (e.g., Chavez et al. 2003), can directly affect individual survival. However, in the presence of both internal and external control, an understanding of their joint effect is less clear. A survey of the literature indicates that internal and external variables may indirectly and nonadditively influence individual survival. For example, through in situ experimental studies it was found that the coral reef fishes *Chromis cyanea* and *Thalassoma hardwicke* show different levels of density-dependent mortality in different patch reefs, each characterized by a unique set of external environmental variables (Hixon and Carr 1997, Shima and Osenberg 2003). Also, blue petrels *Halobalena caerulea* in the southern Indian Ocean exhibit sharp declines in abundance during periods of high population density

and unfavorable oceanographic conditions (Barbraud and Weimerskirch 2003).

Most analytical approaches used in population ecology assume additive effects of external variables on population demographic parameters (e.g., Grenfell et al. 1992, Cury et al. 1995, Stenseth 1999, Stenseth et al. 1999, Dennis and Otten 2000), and are therefore inadequate to address nonadditive interactions. In the present study, we focus on the structure of density-dependent survival of prerecruitment Gulf of Alaska (GOA) walleye pollock (*Theragra chalcogramma*) in relation to environmental variables known to affect pollock early life survival. We develop and test a new model approach where the shape of the density-dependent function may change according to whether some external environmental covariates are below or above a threshold value; hence our model explicitly includes nonadditive interactions. We compare the results from the threshold formulation with those from a nonadditive but continuous (rather than threshold) formulation and with those from a fully additive model. Through these comparisons, we address not only the effect of internal and external variables on pollock survival but also the type of dynamics involved (i.e., additive, nonadditive threshold, nonadditive continuous).

Walleye pollock currently constitutes the second largest single species fishery in the world (FAO 2002;

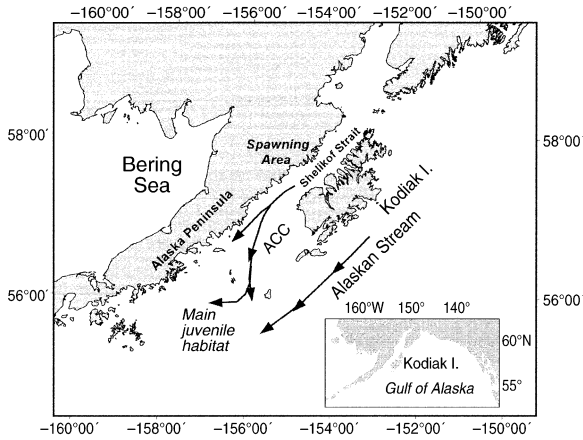[5] Corresponding author. E-mail: n.c.stenseth@bio.uio.no

FIG. 1. The Gulf of Alaska (GOA) and Shelikof Strait region, where the bulk of the GOA pollock spawns during early April. ACC stands for Alaska Coastal Current.

second only to the Peruvian anchoveta). Most of the landings come from the Bering Sea, but a large pollock stock of about 800 000 Mg (averaged over the last 20–30 yr) is also present in the GOA (Dorn et al. 2002). The GOA stock has served as a model population for research, as the early life stages are aggregated in smaller areas than in those of the Bering Sea population. Typically, the bulk of the GOA pollock population spawns at the beginning of April in Shelikof Strait, a limited area between Kodiak Island and the Alaska Peninsula (Fig. 1). After spawning, eggs and larvae are advected in the Alaska Coastal Current along the Alaska Peninsula. The egg stage lasts approximately two weeks and the larval stage lasts from 40 to 60 days,

after which larvae metamorphose into the juvenile pelagic form (age-0). Pollock recruit to the mature population and to the fishery at about age-4. In this study we focus on the prerecruitment survival (i.e., <age-2) of the GOA pollock population spawning in Shelikof Strait.

METHODS

The data

We analyzed the density-dependent structure of pollock survival in the Gulf of Alaska (GOA) during the period 1975–1996 between the following prerecruitment stages: from eggs to age-0, from age-0 to age-1, and from age-1 to age-2. The analysis was done in relation to environmental variables known to have an effect on pollock early life survival (Megrey et al. 1995, Bailey 2000). These are wind speed cubed (W; proportional to water column turbulence), spring (T_S) and fall (T_F) mean sea surface temperature, and groundfish predation intensity (P_G; Fig. 2). The time series from 1975 to 1996 was chosen to insure the quality of data for the study. Information on P_G larval and juvenile abundance is not available for earlier time periods, and estimates of recruitment strength are less reliable. In addition, more recent time series on age-specific larval abundance are not available, nor are recent estimates of age-0 abundance.

Pollock prerecruitment abundance estimates were taken from Bailey et al. (1996) and Bailey (2000). In brief, egg abundance (Fig. 2) was calculated from the spawning biomass, using fertility and sex ratio estimates. Estimates of age-0 abundance were available from late summer/autumn shrimp trawl and juvenile
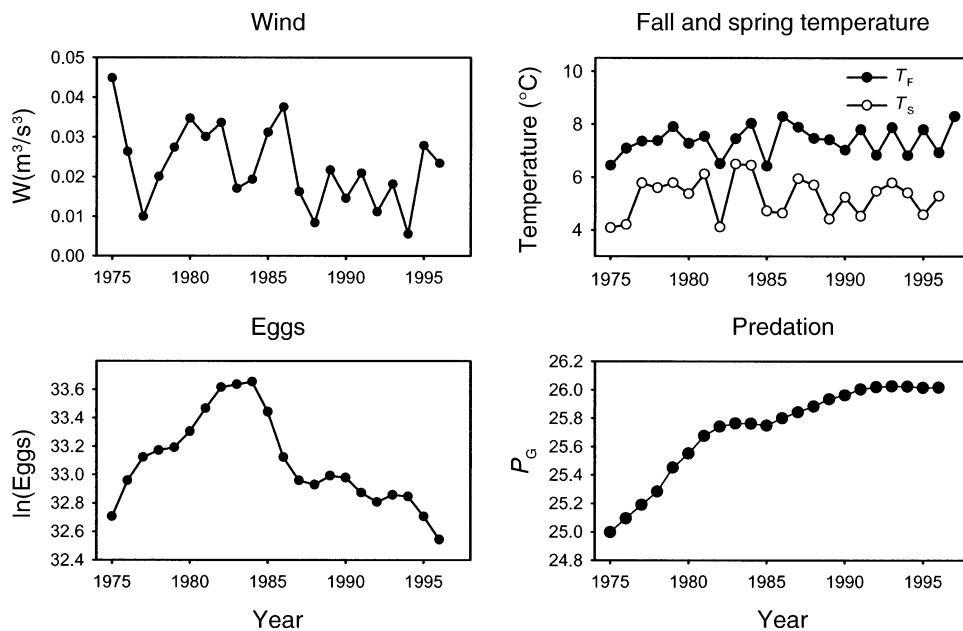

FIG. 2. Time series of the environmental and population variables used in our analysis. T_S = spring sea surface temperature; T_F = fall sea surface temperature; P_G = groundfish predation index.

pollock surveys (described in Bailey and Spring 1992), with additional data from Wilson et al. (1996). Values from years with missing data were estimated by interpolating across stages and years from a life table analysis (Bailey et al. 1996). In the total life table, 12 of 112 possible cells were filled by this interpolation method. In years when data were available, estimated values were compared to observed values, showing that the method is fairly robust ($r = 0.97$; $P < 0.001$). For the age-0 data alone, comparison of observed vs. estimated values was also robust ($r = 0.82$; $P < 0.05$). Estimates of age-1 abundance are from acoustic surveys done in early spring, as described in Bailey (2000). Since the survey covers only part of the full distribution range of the age-1 juveniles, it was considered a relative index of abundance. The estimated number of age-1 juveniles was proportional to the abundance index, scaled to fall within the range of age-0 and age-2 abundance from life tables. Age-2 recruits were available from an age-structured stock assessment model tuned statistically to the commercial harvests and acoustic and bottom trawl surveys (Dorn et al. 2002).

The environmental data were obtained from a variety of databases (Fig. 2). T_S was the mean value over the April–June early life period, and T_F was the mean value between October and November. Both were centered on 56° N, 156° W, and were obtained from reanalysis of the National Center for Environmental Prediction data set. The W variable (m^3/s^3) was derived from gradient winds and averaged over the month of May (Bailey and Macklin 1994). The groundfish predation index (P_G) is proportional to the amount eaten by the major predators of age-0 and age-1 pollock, including arrowtooth flounder (*Atherestes stomias*), adult pollock, cod (*Gadus macrocephalus*), halibut (*Hippoglossus stenolepis*), and flathead sole (*Hippoglossoides elassodon*). P_G was calculated from a model accounting for predator biomass, daily ration, overlapping of predator and prey, and percent pollock in the diet (Bailey 2000).

The models

We hypothesize that internal (i.e., demographic) and external (i.e., environmental) variables have nonadditive effects on pollock survival. Further, we hypothesize that nonadditive interactions, if present, act to change the level of density-dependent survival. To study the density-dependent survival of young pollock across different environmental conditions we used variations of generalized additive model (GAM) formulations, as implemented in the mgcv library of R (Wood 2000, Wood 2001). Specifically, let X_t^a be the natural logarithm of the abundance of the prerecruitment population stage a at time t. Let S_t^a be the survival at time t between two consecutive prerecruitment stages (calculated as the difference between the logarithmic abundances). Let $\mathbf{E}_t$ be a vector of environmental variables at time t whose single components are identified by the

superscript j; let f and g_j be nonparametric, smoothing functions, respectively, specifying the effect of population abundance (i.e., density dependence) and environmental forcing of the covariate $\mathbf{E}^j$ on the demographic variable S. By assuming no changes of density dependence across the entire modeled phase (i.e., additivity), the formulation becomes:

$$S_t^a = b + f(X_t^a) + \sum_j g_j(\mathbf{E}_t^j) + \varepsilon_t \qquad (1)$$

where b is an intercept and ε is a noise term; for the model identification, all additive function components are henceforth assumed to be centered, i.e., having zero mean over the data.

In contrast, if there is a change of density dependence across contrasting environmental phases (i.e., nonadditivity) the model assumes either a continuous (if changes of density dependence are gradual) or a threshold (if changes are abrupt) formulation. In the continuous case, Model 1 is enriched by the inclusion of second order interaction terms, whose effect is regulated by the nonparametric functions s (Hastie and Tibshirani 1990). Specifically,

$$S_t^a = b + f(X_t^a) + \sum_j g_j(\mathbf{E}_t^j) + \sum_k s_k(\hat{X}_t^a \hat{\mathbf{E}}_t^k) + \varepsilon_t. \quad (2)$$

We refer to this model as CGAM, where C stands for "continuous interaction." The variables $\hat{X}_t^a$ and $\hat{\mathbf{E}}_t^k$ are the standardized and shifted (a constant is added in order to make the variable ≥ 0) population and environmental covariates, respectively. The superscript k, uniquely identifies the interacting environmental covariates among all those present in the vector $\mathbf{E}$.

The threshold nonadditive formulation (hereon referred to as TGAM, where T stands for "threshold interaction") is composed by two additive formulations. In particular, assuming a change of density dependence (i.e., nonadditivity) as a function of a linear combination of the environmental vector ($\boldsymbol{\alpha}\mathbf{E}$; where $\boldsymbol{\alpha}$ is a row vector of coefficients) the effect of internal and external variables on pollock survival can be modeled as follows:

$$S_t^a = \begin{cases} b_1 + f_1(X_t^a) + \sum_j g_j(\mathbf{E}_t^j) + \varepsilon_t & \text{if } \boldsymbol{\alpha}\mathbf{E} \leq r \\ b_2 + f_2(X_t^a) + \sum_j g_j(\mathbf{E}_t^j) + \varepsilon_t & \text{otherwise} \end{cases} \quad (3)$$

where r is an environmental threshold across which the density-dependent function switches from f_1 to f_2, with possible changes in the intercept as well (from b_1 to b_2), with the additive environmental effects otherwise unaltered.

In the case of Model 3, if the environmental covariate is two dimensional, $\boldsymbol{\alpha}\mathbf{E} \leq r$ and $\boldsymbol{\alpha}\mathbf{E} > r$ define two half spaces between a set of two external variables, separated by a threshold straight line, $\boldsymbol{\alpha}\mathbf{E} = r$, to be estimated from the data. The estimation procedure of the threshold line for Model 3 consists of the following

steps. Each pair of distinct observed covariate vectors implicitly defines a threshold line $\alpha\mathbf{E} = r$. For a fixed threshold line, Model 3 may be written as a GAM with known multiplicative factors, as follows:

$$S_t^a = b_1 I(\alpha\mathbf{E}_t \leq r) + f_1(X_t^a)I(\alpha\mathbf{E}_t \leq r) + b_2 I(\alpha\mathbf{E}_t > r)$$

$$+ f_2(X_t^a)I(\alpha\mathbf{E}_t > r) + \sum_j g_j(\mathbf{E}_t^j) + \varepsilon_t \quad (4)$$

where the operator I designates indicator variables (1, 0). Model 4 is an extended GAM and can be estimated by the method of penalized least squares (Wahba 1990, Green and Silverman 1994; see also Appendix A for explanation of penalized least squares), with the corresponding generalized cross validation (GCV) denoted by $GCV(\alpha, r)$. We estimate α and r by minimizing $GCV(\alpha, r)$ over all lines defined by pairs of observed covariate vectors, except those lines whose associated half spaces contains <20% of the data cases; this is done to ensure adequate data for estimation. The minimum $GCV(\alpha, r)$ is then defined as the GCV of the estimated TGAM.

However, the GCV so defined has not properly accounted for the parameters defining the threshold line; hence it cannot be directly compared with that of the best fitted additive environmental-effect Model 1 or nonadditive continuous effect Model 2. To handle this problem, we compute the ''genuine'' cross-validatory squared prediction error (genuine CV), as follows. Each data case is deleted one at a time with the response of the deleted case predicted by the examined model (GAM, CGAM, or TGAM) fitted to all the remaining cases. A square prediction error is then calculated, and the same routine is repeated across all data cases. The mean of all squared prediction error is then the (genuine) cross-validatory squared prediction error for the examined model. While this procedure is rather computationally intensive, it properly accounts for the estimation of the threshold line and the estimation of the degrees of freedom for the functions appearing in all additive and nonadditive formulations (see Efron and Gong 1982, Li 1986, 1987).

Our model building strategy consisted of four steps. First, we used a TGAM formulation to assess, based on the model GCV, the effect (i.e., additive or nonadditive) of the environmental covariates under scrutiny. We only examined covariates that from previous studies were known to influence pollock recruitment. In the survival from egg to age-0 these were W and T_S, and in the survival from age-0 to age-1 (and from age-1 to age-2) the environmental covariates were P_G and T_F. T_F and P_G were not included in the analysis of egg to age-0 survival because the first refers to a time of the year (October–November) that does not include the passage from the egg (April) to the age-0 (August) stage, while the second refers to the predation on stages older than the age-0. Likewise, T_S and W were not considered in the survival analysis of the juvenile stag-

es because we assume that most of the juvenile pollock mortality, which is not accounted for by predation, occurs during fall and winter, a view largely shared in recruitment studies of marine fish populations residing in a seasonal environment (Schultz et al. 1998). The second step of the model building strategy was to include the same covariates used in the TGAM (both additive and interacting) in an additive formulation (GAM). The third step was to add a continuous interaction term to the GAM, to obtain a CGAM formulation. We only examined second order interaction terms (third order interactions are not properly addressed using the adopted scheme [Hastie and Tibshirani 1990]). One of the two covariates of the CGAM interaction term was always initial population size (X_t), and the other was one of the environmental variables found to significantly interact in the TGAM formulation. Because the TGAM formulation always had two interacting covariates (besides X), there were two second order interaction terms that could potentially be added to the CGAM formulation. Initially, we included all interacting terms; however, in the final formulation, we only retained those that minimized the model GCV. The fourth and final step of the model building strategy was to compare all inspected formulations using the genuine CV criterion.

To further assess the significance of the additive (Model 1) vs. the nonadditive (Models 2 and 3) model formulations we simulated the dynamics of pollock prerecruitment stages using the estimated survival rates from all final models. This was done for the calibration period (1975–1996), and for a set of three independent data points (1972–1974) for which we only had estimates of age-2 abundance and environmental variables. In the simulation, each model formulation was used to first predict age-0 from the observed egg abundance and environmental variables, then age-1 from the predicted age-0 (plus error), and finally age-2 from the predicted age-1 (plus error). All estimated abundances (age-0, age-1, and age-2) were the means of 1000 simulations, each resulting from the addition of an error term (randomly sampled from the model residuals) to the model estimate.

RESULTS

The survival from egg to age-0 was marginally best modeled by the nonadditive continuous (CGAM) formulation, followed by the threshold (TGAM) formulation, and lastly by the fully additive (GAM) formulations (Table 1). The survival from age-0 to age-1 was best modeled by the TGAM formulation, followed by the GAM, and finally by the CGAM formulations. In the egg to age-0 and the age-0 to age-1 survival phases, the interaction of the CGAM was best modeled (based on the GCV criteria) by a linear term (Table 1). In contrast to earlier stages, initial density in the survival from age-1 to age-2 did not enter as a significant factor in an additive model ($P = 0.11$). Based on this result

TABLE 1. Final formulations and genuine cross validation (CV) of all inspection models in the analysis of pollock pre-recruitment survival.

Model type	Stages	Formulation	CV
GAM (Model 1)	egg to age-0	$S_t^a = b + f(X_t^a) + g_1(T_{S,t}) + g_2(W_t) + \varepsilon_t$	0.728
	age-0 to age-1	$S_t^a = b + f(X_t^a) + g_1(T_{F,t}) + g_2(P_{G,t}) + \varepsilon_t$	0.627
	age-1 to age-2	$S_t^a = b + g_1(T_{F,t}) + g_2(P_{G,t}) + \varepsilon_t$	0.279
CGAM (Model 2)	egg to age-0	$S_t^a = b + f(X_t^a) + g_1(T_{S,t}) + g_2(W_t) + \alpha \hat{T}_{S,t} \hat{X}_t^a + \varepsilon_t$	0.602
	age-0 to age-1	$S_t^a = b + f(X_t^a) + g_1(T_{F,t}) + g_2(P_{G,t}) + \alpha \hat{T}_{F,t} \hat{X}_t^a + \varepsilon_t$	0.754
	age-1 to age-2	NA	NA
TGAM (Model 3)	egg to age-0	$S_t^a = b_1 + f_1(X_t^a) + g_1(W_t) + \varepsilon_t$ if $\alpha\{T_{S,t}, W_{,t}\} \le r$	0.617
		$S_t^a = b_2 + f_2(X_t^a) + g_1(W_t) + \varepsilon_t$ if $\alpha\{T_{S,t}, W_{,t}\} > r$	
	age-0 to age-1	$S_t^a = b_1 + f_1(X_t^a) + g_1(T_{F,t}) + \varepsilon_t$ if $\alpha\{T_{F,t}, P_{G,t}\} \le r$	0.329
		$S_t^a = b_2 + f_2(X_t^a) + g_1(T_{F,t}) + \varepsilon_t$ if $\alpha\{T_{F,t}, P_{G,t}\} > r$	
	age-1 to age-2	NA	NA

Notes: Initial population size was not found to significantly affect the survival from age-1 to age-2; therefore, such passage was only inspected with an additive model formulation. T_S = spring sea surface temperature; T_F = fall sea surface temperature; W = wind speed cubed; P_G = groundfish predation index on juvenile pollock; α = linear coefficient; r = environmental threshold. See Eqs. 1–3 (*Methods: The models*) for explanation of additional model parameters.

we inferred that there was no evidence of density-dependent survival from age-1 to age-2. Therefore, no conclusions could be drawn on age-1 survival, regarding nonadditivity of environmental and demographic variables.

The TGAM formulation indicated that during the egg to age-0 stage, high W, and to a lesser extent low T_S, induced negative density dependence (i.e., compensation). Under the inverse conditions there was no noticeable effect of density on survival, suggesting an overall relaxation of density-dependent effects (Fig. 3). High P_G and T_F induced compensation in pollock survival from the age-0 to the age-1 stage, while no particular density-dependent structure was detected during the opposite environmental conditions (Fig. 3).

The resulting qualitative picture obtained for the CGAM formulation was similar to that of the TGAM (Fig. 4). One exception was that water temperature, rather than wind speed, was the most important inter-acting covariate in the survival from egg to age-0 (Table 1, Fig. 4). However, in our study region, W and T_S are to some degree negatively correlated ($R^2 = 0.28$; high wind induces deeper water mixing and cooling of surface temperature; Fig. 3), so their final effect on egg

survival is also correlated. Survival from age-1 to age-2 was not significantly affected by the initial population density, while it was affected by P_G and T_F, in an additive fashion (Fig. 4).

The nonadditive threshold formulation (Model 3) was always found to best reproduce the observed abundance of pollock prerecruitment stages from initial conditions (i.e., egg density and environmental covariates; Fig. 5). At the recruitment level of age-2, for example, the TGAM captured 69% of the observed variability, while the CGAM captured 64% and the GAM captured 59%. In addition, during the independent period 1972–1974, the TGAM closely predicted two out of three age-2 abundance estimates, while both CGAM and GAM grossly over predicted all three data points (Fig. 5).

From visual inspection of normal probability plots of the model residuals, we did not observe any major departure from normality, given the constraint of the small sample size (see Appendix B for residual analysis). We also noticed the presence of a potential outlier in the CGAM formulation of the egg to age-0 survival (Year 1991) and in the TGAM formulation of the age-0 to age-1 survival (Year 1982). However, the removal of the offending case, or the addition of an outlier effect

FIG. 3. Scatter plot of the interacting environmental covariate affecting the density-dependent survival of pollock, as estimated from the TGAM formulation. Also shown are the threshold lines (detected by the GCV criteria) that divide the plot of environmental variables in two regions, one above and one below the line. Regions above the threshold line correspond to environmental regimes with negative density dependence, while no significant density-dependent structure was detected in regions below the threshold line. Plots are shown for covariates affecting egg to age-0 survival (W = wind speed cubed; T_S = spring sea surface temperature) and age-0 to age-1 (T_F = fall sea surface temperature; P_G = groundfish predation index) survival.
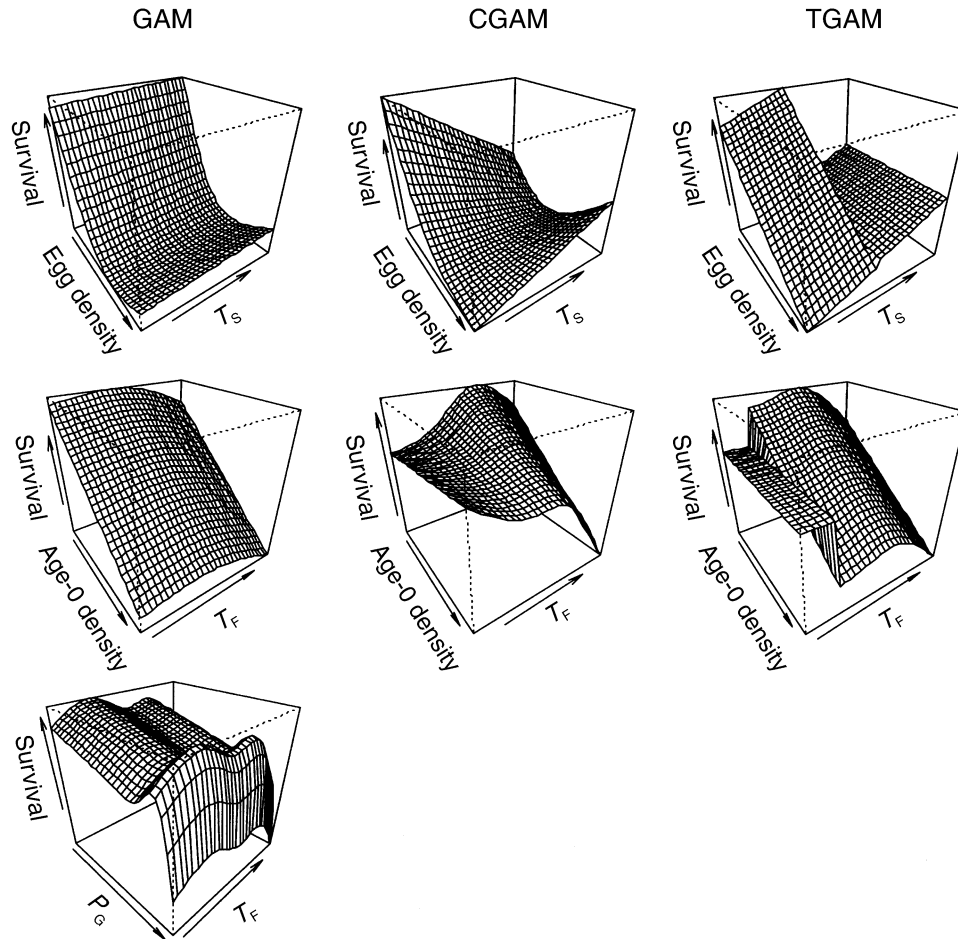
GAM CGAM TGAM
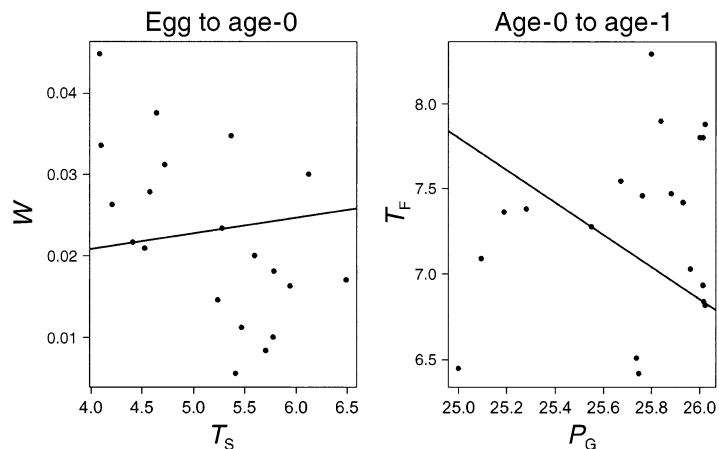
FIG. 4. Surface plots of survival for each of the inspected pollock prerecruitment stages and model formulations. For egg to age-0 survival and age-0 to age-1 survival (first and second row, respectively), the three-dimensional plots only show the effect of the variables that were significantly interacting in a CGAM formulation (see Table 1), while all covariates affecting age-1 survival (third row) were used in the surface plot (see Table 1). The three-dimensional plots were derived by predicting survival from a regular grid in which the plotted variables ranged from their minimum to maximum values, and the nonplotted variables were held constant as their average values. The only exception was for W in the egg survival plots (first row), which was varied as a function of T_S (W and T_S are negatively correlated). The environmental regimes for the contrasting phases of the TGAM formulations are identified in Fig. 3.

(indicator variable) to the model formulation, further normalized the residual plot, and did not change any of the model conclusions (see Appendix B). Residuals from a GAM formulation that only contained the demographic variable (i.e., population size), against the distance from the threshold line of the corresponding TGAM formulation (shown in Fig. 3), revealed the presence of a linear trend. This pattern was observed for both the egg to age-0 and the age-0 to age-1 survivals (see residual analysis in Appendix B). The presence of linear correlation between the GAM residuals and the interacting covariate (i.e., distance from the threshold line of Fig. 3) further supports the claim of nonadditivity.

DISCUSSION

We have demonstrated that external environmental variables can affect pollock survival in a nonadditive

and interactive fashion, and that the inclusion of these nonadditive effects in a population dynamics model improves our ability to simulate recruitment. We further demonstrate that nonadditive interactions are the result of changes in density-dependent survival in relation to background environmental variables.

Previous studies have simulated pollock recruitment in the Gulf of Alaska and eastern Bering Sea (Megrey et al. 1995, Quinn and Niebauer 1995, respectively) with linear regression models, solely based on abiotic variables. These earlier analyses have been very relevant in isolating key variables that affect pollock recruitment (e.g., air temperature and ice cover [Quinn and Neibauer 1995], and precipitation and wind mixing [Megrey et al. 1995]). However, due to the direct link between the examined covariates and the recruitment level, these studies could not provide extensive explanations for the mechanisms involved in the regulation
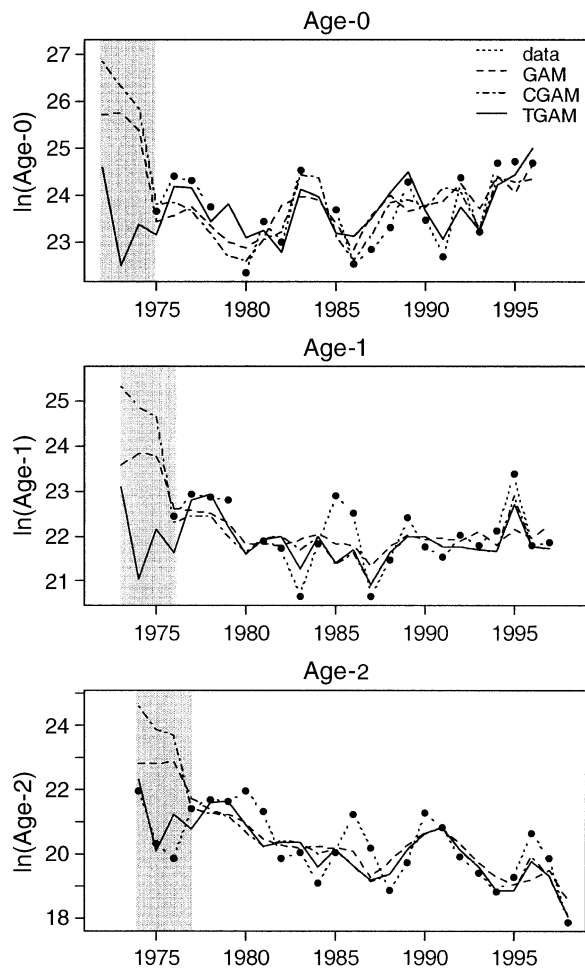
Age-0

Age-1

Age-2

FIG. 5. Observed and simulated abundances of pollock prerecruitment stages during the calibration (clear areas) and validation period (shaded areas). Correlations for the ln(age-0) simulations (R^2 values) are: GAM, 0.43; CGAM, 0.58; and TGAM, 0.65. For the ln(age-1) simulations, R^2 values are: GAM, 0.36; CGAM, 0.44; and TGAM, 0.51. For the ln(age-2) simulations, R^2 values are: GAM, 0.59; CGAM, 0.64; and TGAM, 0.69. Only the values included in the calibration period were used to calculate R^2.

of pollock survival. In our analysis, we considered density-dependent forces and biotic factors (e.g., predation index) in addition to abiotic variables, and compared a variety of contrasting survival dynamics (i.e., additive vs. nonadditive, continuous vs. threshold). Moreover, we focused on pollock stage-specific survival (i.e., from eggs to age-0, from age-0 to age-1, and from age-1 to age-2) over a longer time series than those available to earlier studies. Consequently, we also provide a more comprehensive treatment of the mechanisms involved in regulating pollock prerecruitment survival.

The threshold nonadditive statistical formulation (TGAM) that we developed can be regarded as a nonparametric generalization of the Threshold Autoregressive Models (Tong 1990). This linkage may be

helpful for investigating the probabilistic properties of the TGAM and large sample properties of the proposed estimation scheme. A continuous (CGAM) model formulation was marginally superior (in terms of genuine cross validation) to the TGAM only from egg to age-0, while survival from age-0 to age-1 was best modeled with a TGAM. However, the CGAM was not efficient in simulating three independent recruitment points (1972–1974), while the TGAM closely predicted two out of three points (Fig. 5). The out-of-sample forecast reflects the general problem of modeling interactions by product terms. A product term is of second degree and, as such, provides adequate within-sample forecast but may give a worse prediction upon extrapolation due to the stronger curvature of second degree terms. In general, piecewise linear models such as the TGAM can be expected to perform better in extrapolation. Hence, on the basis of model selection criteria (genuine CV) and out-of-sample forecast performance, we prefer the TGAM to the continuous interaction model for both egg to age-0 and the age-0 to age-1 stages. In addition, as we show in our analysis, the TGAM methodology can be easily adapted to explore interactions of order >2 (e.g., $P_G \times T_F \times X^a$), not easily addressed by CGAM formulations (Hastie and Tibshirani 1990).

The observed changes of pollock density-dependent survival are in agreement with what is expected from previous studies. Increased negative density dependence of egg and larval survival during conditions of high wind and low temperature may be partly induced by water column turbulence. For pollock it has been shown that high turbulence may reduce the foraging success of young larvae (Bailey and Macklin 1994). Strong winds can also have a direct effect on survival by increasing transport and advection of larvae and juveniles into offshore and unfavorable nursery areas (Bailey and Macklin 1994). Similar negative effects of high wind on recruitment were also observed in small pelagic fishes (e.g., sardine and anchovies) residing in Ekman-type upwelling systems (Cury and Roy 1989). The effect of T_S on egg and larval survival is not as straightforward to interpret since temperature may affect survival across multiple substages both directly (e.g., through growth) and indirectly (e.g., through food availability and competition with other species). However, in our study region, W and T_S are to some degree negatively correlated, which explains their opposite outcome on the regulation of pollock density dependence.

From age-0 to age-1, several mechanisms may explain the observed increase in compensation with increased predation and water temperature. One possibility is an increase of interspecific competition for food. In fact, groundfish predators, besides feeding on young pollock, also consume a number of zooplankton prey common in the diet of juvenile pollock (e.g., euphausiids and large copepods; see Brodeur and Wilson 1996 and references therein). In addition, interspecific

competition for food may increase during high water temperature regimes, due to increased metabolic demands of young pollock (Ciannelli et al. 1998). Another possible explanation is habitat reduction, as warm sea surface temperatures force juvenile pollock to reside in a restricted region of the water column (Brodeur and Wilson 1996). The absence of a significant effect of initial density on the survival of pollock between age-1 and age-2 may also be expected, due to a change of ecological niche between the two stages (Duffy-Anderson et al. 2003). However, care should be placed in interpreting this result, given the narrow margin by which the initial density term failed to significantly differ from zero ($P = 0.11$, rejection at $P < 0.05$), and the uncertainty of the demographic variables used in our study.

In evaluating the results of our analysis it bears noting that a great deal of uncertainty is inherent in each of the data sources, such as sampling errors or estimation of missing values (Bailey et al. 1996, Bailey 2000). Also, the application of the nonadditive models to the data in hand, while extremely interesting, is also limited by the rather brief time series. For example, we found that in the CGAM formulations, linear interaction terms were favored against nonlinear ones; however, nonlinear relationships are not easily identifiable under the constraint of a small sample size.

In fisheries science, it has long been recognized that prerecruitment dynamics are overwhelmingly important in shaping the abundance of the entire population (Hjort 1914). Recruitment of marine fishes is a complex process, being the emergent property of nonlinear interactions among external and demographic variables, as well as low frequency physical and biological events (Bailey et al. 2003). In such context, our results offer a template whereby the joint effect of demographic and external variables may be better understood. This level of comprehension is particularly relevant in studying the outcome of climate variability on the population ecology of marine species. Our study may, in fact, provide insights in understanding the effect of the mid 1970s climate change on the GOA pollock dynamics. Following the climate regime shift in the North Pacific, there was an increase in both water temperature (Mantua et al. 1997) and groundfish biomass (Anderson and Piatt 1999) in the Gulf of Alaska. Bailey (2000) showed that in concomitance with such changes, recruitment control of pollock shifted from the larval to the juvenile stage. We have demonstrated that both T_F and P_G trigger changes in pollock density dependence and notably affect survival. Therefore, it is possible that the shift in recruitment control was the result of increased density dependence during the juvenile stage.

A mechanistic understanding of the interaction between external and internal population variables is relevant to the management of renewable marine resources in the face of underlying environmental variability.

Density dependence is, in fact, widely assumed in many fisheries management models (Hilborn and Walters 1992). However, it also is one of the most elusive process to detect in marine populations (Rose et al. 2001). Failure to detect density dependence can arise in part because, as we demonstrate, its intensity can change over temporally distinct environmental phases. Hence, analyses that integrate over time, without allowing for explicit changes of density-dependent survival, will inevitably integrate across periods of contrasting population phases.

The statistical methodology developed here can be easily applied to other marine and terrestrial populations. In terrestrial ecology, for example, many studies point to the importance of understanding how internal and external variables jointly affect population abundance (Leirs et al. 1997, Lima et al. 2001, Stenseth et al. 2003). Previous efforts to model joint effects of these two forcing mechanisms include linear (Barbraud and Weimerskirch 2003), and a priori specified nonlinear formulations (e.g., parametric threshold models; Tong 1990, Stenseth et al. 1998). However, these approaches fall short in the presence of nonlinear dynamics or poorly understood functional relationships. In such a context, the phase-dependent and nonparametric nature of the TGAM and CGAM methodologies will advance our ability to address internal and external mechanisms of population control.

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APPENDIX A

A description of the method of penalized least squares is available in ESA's Electronic Data Archive: *Ecological Archives* E085-119-A1.

APPENDIX B

A description of residual analysis and figures showing normal probability plots and correlation between residuals and distance from the threshold line of Fig. 3 are available in ESA's Electronic Data Archive: *Ecological Archives* E085-119-A2.