

# Climate change causing phase transitions of walleye pollock (*Theragra chalcogramma*) recruitment dynamics

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In 1976 the North Pacific climate shifted, resulting in an average increase of the water temperature. In the Gulf of Alaska the climate shift was followed (i.e. early 1980s) by a gradual but dramatic increase in the abundance of groundfish species that typically prey on pre-recruitment stages of walleye pollock. In the present study we used a previously parameterized model to investigate the effect of these climate and biological changes on the recruitment dynamics of walleye pollock in the Gulf of Alaska. Simulations covered the 1970–2000 time frame and emphasized the medium-to-long temporal scale (i.e. about 5–10 years) of environmental variability. Results showed that during periods characterized by high sea surface temperature and high predation on juvenile pollock stages, recruitment variability and magnitude were below average, and recruitment control was delayed to stages older than the 0-group. Opposite dynamics (i.e. high abundance and variability, and early recruitment control) occurred during periods characterized by low temperature and predation. These results are in general agreement with empirical observations, and allowed us to formulate causal explanations for their occurrence. We interpreted the delay of recruitment control and the reduction of variability as an effect of increased constraint on the abundance of post age-0 stages, in turn imposed by high density dependence and predation mortality. On the other hand, low density-dependence and predation favoured post age-0 survival, and allowed for an unconstrained link between larval and recruitment abundance. Our findings demonstrate that the dominant mechanisms of pollock survival change over contrasting climate regimes. Such changes may in turn cause a phase transition of recruitment dynamics with profound implications for the management of the entire stock.

**Keywords:** phase transition; regime shift; climate; walleye pollock; Gulf of Alaska; recruitment

## 1. INTRODUCTION

Phase transitions are low frequency and high amplitude changes of a system attribute in relation to slow changes of forcing variables (Duffy-Anderson *et al.* in press). Examples of population or community transitions or re-organizations are fairly common in the marine ecology literature, ranging from anchovy/sardine shifts in dominance (Chavez *et al.* 2003) and changes of cod recruitment (O'Brien *et al.* 2000), to entire community restructuring (Anderson & Piatt 1999; Cury & Shannon 2004). However, the variability and the shortness of many of these time-series make it difficult to conclude whether the observed changes are occasional events due to stochasticity or actual attractions toward new states of the system (Rothschild & Shannon 2004). The distinction between a stochastic event and a change of state is not just semantics, as the dynamic properties of a system may radically change over contrasting states (Collie *et al.* 2004).

Scheffer & Carpenter (2003) argued that the positive identification of a system transition cannot be solely based on observational time-series, but it is also necessary to possess a mechanistic understanding of how internal (e.g. density dependence) and external (e.g. environmental forcing) variables affect key properties of the system. Within this context, dynamic models are very useful tools, as they are easily manipulated for the exploration of new system properties (Steele 2004). If the models are based on empirical statistical analysis they become very reflective of the actual dynamics of the system. In the present study we investigate, through simulations of an earlier parameterized model (Ciannelli *et al.* 2004), changes of the Gulf of Alaska (GOA) walleye pollock (*Theragra chalcogramma*) recruitment dynamics in relation to environmental variables linked with climate change. Our overall intent is to establish a causal link between recruitment changes and climate variability, a link that may reveal whether pollock recruitment dynamics have undergone phase transitions and that may ultimately improve the management of pollock in the face of incumbent climate change.

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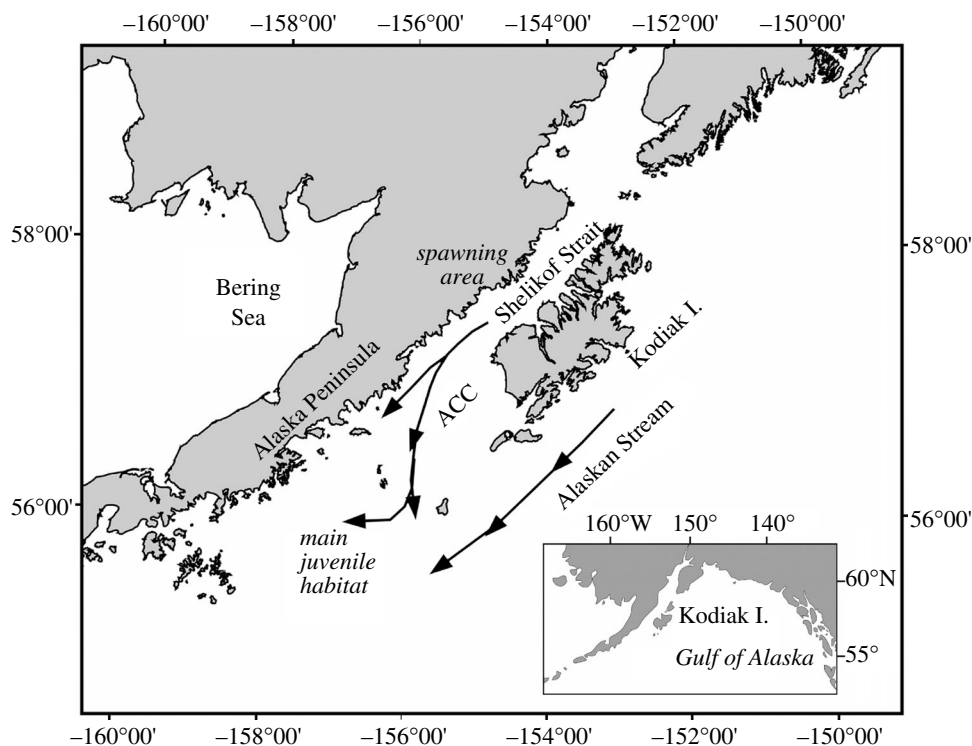


Figure 1. The Gulf of Alaska and Shelikof Strait region, where the bulk of the GOA pollock spawns during early April. ACC: Alaska Coastal Current.

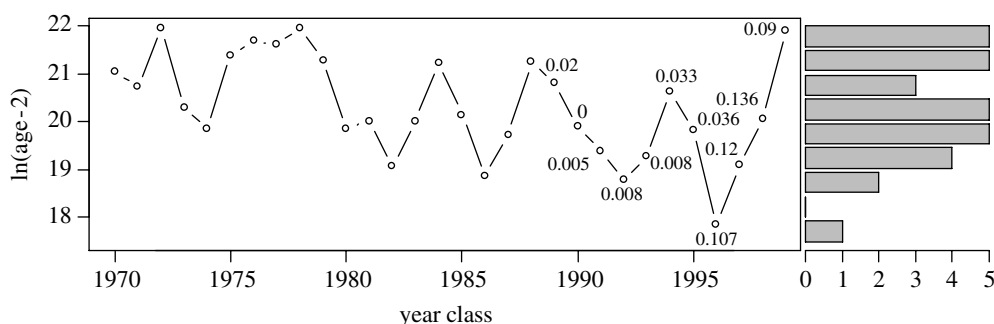


Figure 2. Walleye pollock recruitment (natural log transformed) as estimated from the National Marine Fisheries Service assessment (Dorn *et al.* 2002). Numbers next to the last 11 data points indicate the  $p$ -values of the multimodality test (null hypothesis = unimodality) applied to the time series going from its start (1970) to the year for which the  $p$ -value is shown. The null hypothesis of unimodality is rejected (at 0.05 significance level) up to the year 1995. The reported  $p$ -values were computed based on the Silverman test assuming independent and identically distributed data, with an adjustment due to Hall & York (2001) and 1000 bootstrap replications; these  $p$ -values were almost identical under the assumption that the data were generated from a first-order or second-order Markov process (Chan & Tong 2004). Also shown, on the right side of the plot, is the frequency distribution of the entire (i.e. 1970–1999) recruitment time series.

## 2. TERMINOLOGY PREAMBLE: PHASE AND REGIME

This paper refers extensively to the terms ‘phase transition’ and ‘regime shift’—words sometimes being used interchangeably in the ecological literature but with quite different meanings. We adopt the definitions presented in Duffy-Anderson *et al.* (in press) that are summarized below.

*Regime shift:* refers to changes in the forcing variables of a system. In mathematical terms a change of regime corresponds to a change of the model parameters. Unlike phases, regimes refer to a homogeneous set of ‘controlling variables’. Climate, for example, represents a set of controlling variables acting on fish populations and entire biological communities, and thus a climate change is a ‘regime shift’ when referring to population and community dynamics.

*Phase transition:* describes the change of dynamic attributes and mechanistic properties of a system, potentially caused by a regime shift. The mechanistic properties of a system indicate how its primary attributes react to external (i.e. environmental) or internal (i.e. density-dependence) forcing. Examples of system attributes include diversity in a community or recruitment in a population. From these definitions, it follows that phase transition refers to a homogeneous set of ‘observational patterns’. Examples include: recruitment phase transitions, community phase transitions, etc.

We realize that our definitions of ‘phase’ and ‘regime’ may differ from the more common usage in marine ecology. For example, ‘regime shift’ is typically used to describe large scale and abrupt changes of one or more ecosystem attributes in relation to climate change (e.g. Beamish *et al.* 1999; Beaugrand 2004). We believe that

Table 1. Models of pre-recruitment pollock survival used in the climate simulations.

(Note that from the egg to the age-0 stage and from the age-0 to the age-1 stage the models are non-additive (i.e. there is an environmental threshold over which the density-dependent function changes from  $f_1$  to  $f_2$ ). The models were previously developed and parameterized in Ciannelli *et al.* (2004). Below,  $\alpha\{T_{S,t}, W_t\}$  denotes a linear function of the covariates enclosed by the curly brackets, i.e.  $\alpha\{T_{S,t}, W_t\} = \alpha_1 T_{S,t} + \alpha_2 W_t$  where  $\alpha_1, \alpha_2$  are two coefficients.)

stages	formulation
egg to age-0	$S_t^a = b_1^a + f_1^a(X_t^a) + g_1^a(W_t) + \varepsilon_t$ if $\alpha\{T_{S,t}, W_t\} \leq r$
age-0 to age-1	$S_t^a = b_2^a + f_2^a(X_t^a) + g_1^a(W_t) + \varepsilon_t$ if $\alpha\{T_{S,t}, W_t\} > r$
age-1 to age-2	$S_t^a = b_1^a + f_1^a(X_t^a) + g_1^a(T_{F,t}) + \varepsilon_t$ if $\alpha\{T_{F,t}, P_{G,t}\} \leq r$ $S_t^a = b_2^a + f_2^a(X_t^a) + g_1^a(T_{F,t}) + \varepsilon_t$ if $\alpha\{T_{F,t}, P_{G,t}\} > r$
symbol	explanation
$X_t^a$	natural logarithm of pollock abundance at age $a$ and time $t$
$S_t^a$	pollock survival from age $a$ to age $a+1$ , at time $t$
$f$	effect of pollock density on survival
$g$	effect of environmental variable on survival
$b$	intercept
$T$	spring ( $T_S$ ) or fall ( $T_F$ ) sea surface temperature
$W$	wind speed cubed
$P_G$	groundfish predation intensity
$r$	environmental threshold
$\alpha$	row vector of coefficients
$\varepsilon$	error

this usage generates confusion as to what has actually changed in a system, since it makes no clear distinction between changes of forcing (e.g. climate) and forced (e.g. recruitment) variables. In our proposed terminology we attempt to reconcile these two facets referring to existing definitions from other scientific fields (Duffy-Anderson *et al.* in press).

### 3. MATERIAL AND METHODS

#### (a) Gulf of Alaska and walleye pollock

Walleye pollock currently constitutes the second largest single species fishery in the world (FAO 2002). Most of the landings come from the Bering sea, but a large pollock stock, at present estimated at about 200 000 metric tonnes (spawning biomass), is also present in the GOA (Dorn *et al.* 2002). Historically, the bulk of GOA pollock spawning has occurred in early April in Shelikof Strait, between Kodiak Island and the Alaska peninsula (Kendall *et al.* 1996; figure 1). During their maturation, eggs and larvae are advected southwestward by the Alaska coastal current. The egg stage lasts approximately two weeks, after which non-feeding yolk-sac larvae are hatched (duration about one week), followed by feeding larval (duration 40–60 days) and then 0-age juvenile stages. At age 1–2 (1 and 2 years old, respectively) pollock are detected by the acoustic and trawl surveys, and at age 4–5 (4 and 5 years old, respectively) they enter the fishery.

Information on pollock year-class strength is available as number of age-2 recruits and dates back to 1959. Year-class strength is estimated from an age-structured stock assessment model tuned statistically to the commercial harvests and acoustic and bottom trawl surveys (Dorn *et al.* 2002). In the present study, to ensure the data quality, we focus on the recruitment dynamics during the time frame 1970–2000 (figure 2). Early estimates may be biased due to inaccuracy of fishing and natural mortality rates during the start of the commercial fishery, non-random sampling of the commercial catch during the early years of the pollock fishery (K. Bailey,

personal observation), and the use of a common age-length key over aggregated years (Megrey *et al.* 1995). The most recent estimates may also be unreliable because the cohort has been observed only a few times in the catches. From here, we refer to the recruitment time-series estimated from the stock assessment model as ‘observed’ to differentiate from the recruitment values estimated by our model simulations, referred to as ‘simulated’ or ‘predicted’.

In the presence of sudden changes or jumps in time-series, which may be indicative of a phase transition, the frequency distribution of key population variables should be multimodal (Scheffer & Carpenter 2003). In this study, we tested whether the analysed time series of pollock recruitment followed a multimodal distribution using an extended application of the Silverman test (Chan & Tong 2004). To increase the power of the test we adopted the Hall & York (2001) adjustment under the null hypothesis of unimodality (i.e. method 1 in Hall & York). The significance level was set at 5%.

#### (b) Model simulations

In an earlier study (Ciannelli *et al.* 2004) we explored a variety of model formulations to reproduce pollock recruitment in the GOA. Using non-parametric regression techniques (i.e. generalized additive models) we modelled recruitment as a series of survival events, going from egg to age-0, from age-0 to age-1 and from age-1 to age-2. The statistically based best models for the egg to the age-0 and for the age-0 to the age-1 stages assumed a threshold non-additive effect of environmental and demographic variables on survival (table 1). In particular, it was found that the intensity of negative density-dependence (i.e. compensation) from the egg to the age-0 stage increased in the presence of high wind speed and low spring seawater temperature. Similarly, from the age-0 to the age-1 stage, compensation increased in the presence of high predator abundance and warm fall (autumn) water temperature (figure 3). The model selection criterion was based on the minimization of the generalized cross-validation (GCV).

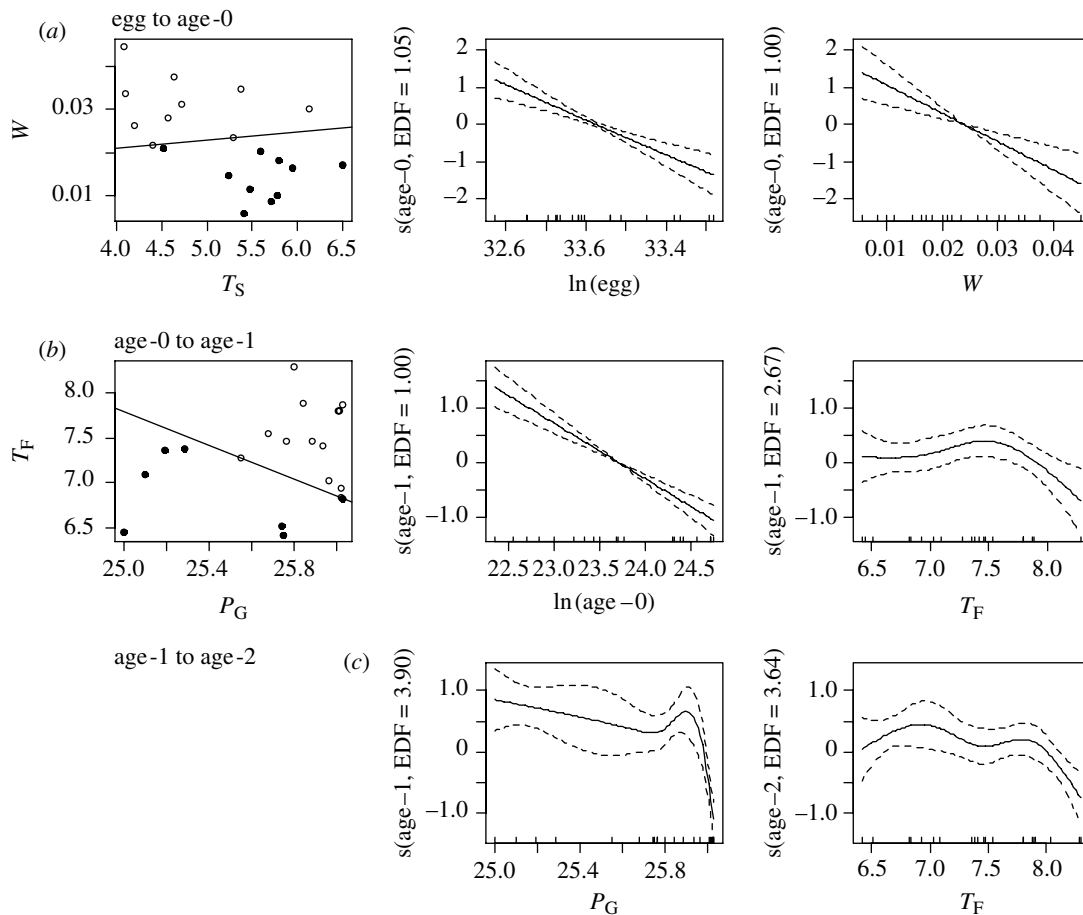


Figure 3. Factors affecting pollock pre-recruitment survival, as detected in Ciannelli *et al.* (2004). (a) The first graph of the egg to age-0 and (b) age-0 to age-1 survival, shows the environmental regimes over which the density-dependent function is partitioned. Environmental regimes identified by open circles cause the negative density-dependent effect shown in the second graph, while closed circles do not trigger any significant density-dependent effect (i.e. horizontal line between the data and survival; not shown). The threshold line, separating the two environmental regimes, was determined from the data. (c) Note that the survival from the age-1 to the age-2 stage was only affected by environmental variables and thus it does not bear partition of the density-dependent function. In panels showing a covariate effect (second and third columns), the dashed lines indicate the 95% confidence interval of the covariate effect, and the label of the  $y$ -axis also identifies the estimated degree of freedom (EDF) of the covariate effect. Other labels are as in table 1.

Briefly, the GCV is a measure of the predictive squared error of the model (Wahba 1990; Green & Silverman 1994; Wood 2000). Low values indicate the best compromise between model complexities (i.e. number of parameters) and fit to the observed data. In the case of parametric models it can be shown that the GCV and the more frequently used Akaike information criteria (AIC) are asymptotically equivalent (Stone 1977). However, the AIC cannot be directly applied to non-parametric models, like the one adopted in this study, because of the use of non-maximum likelihood estimation schemes.

In the current analysis we used the previously developed model to simulate critical pollock recruitment metrics under contrasting environmental scenarios. The simulated metrics include average magnitude, average coefficient of variation ( $CV = \text{standard deviation}/\text{mean}$ ) and relative stage of recruitment control. Here, recruitment control is assumed to provide an indication of how early (late) recruitment is set, and is therefore representative of the 'critical period' (*sensu* Hjort 1914) of pollock life history. We inferred recruitment control from the coefficient of determination ( $R^2$ ) between the abundance of the pre-recruitment (i.e. eggs, age-0 and age-1) and the recruitment (i.e. age-2) stages; the higher the  $R^2$  between two stages, the earlier the recruitment control.

Pollock recruitment metrics were predicted from a set of pre-specified initial conditions and from the average of multiple model runs. Initial conditions included egg density, sampled from within the available time series, and the environmental variables typically associated with the inspected climate regime (see the section 'Climate regimes' for a description of the initial conditions associated with each simulated regime). We first predict age-0 from the initial egg abundance and relevant environmental variables, then age-1 from the predicted age-0 and finally age-2 (the age of recruitment) from the predicted age-1 abundance. The modelling results were the average from 1000 realizations of 15 years each. Each realization was derived by adding random error (sampled from the model residuals) to a single prediction, and by sampling the environmental variables from a normal distribution with mean and standard deviation determined from the observed data.

### (c) Climate regimes

Climate regimes used to force our pollock recruitment model were characterized by a unique combination of environmental variables that are known to affect pollock early-life survival. Specifically, for the survival from egg to age-0, the environmental variables included mean May wind speed

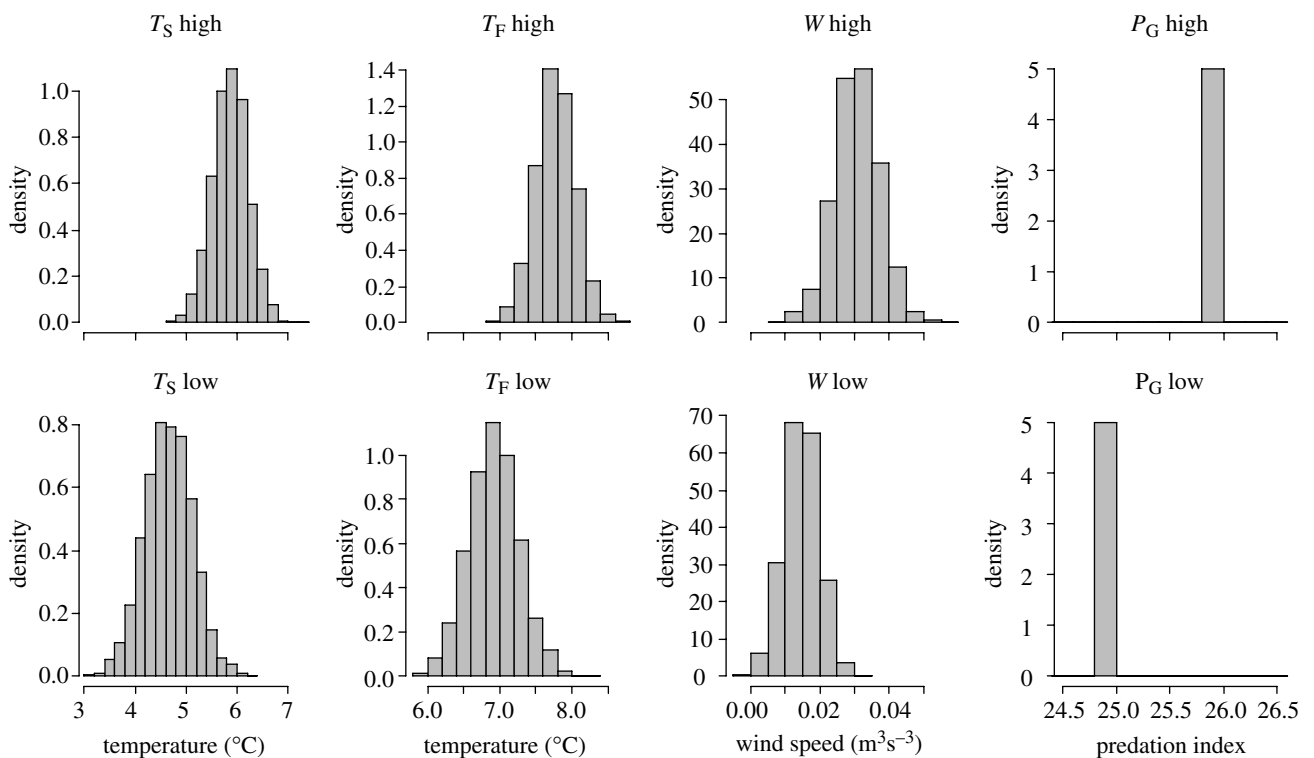


Figure 4. Distribution of the environmental variables used in the model simulations. See table 1 for a list of the distribution parameters and the labels.

cubed, and mean April–June sea surface temperature (referred to as spring water temperature). For the survival from age-0 to age-1, and from age-1 to age-2, the environmental variables included mean October–November sea surface temperature (referred to as fall water temperature), and groundfish predation intensity on the age-0 and age-1 stages. A more complete description of the variables used to characterize climate regimes can be found in Bailey (2000) and Ciannelli *et al.* (2004).

For each of the environmental variables we assumed two magnitude and variability levels: *low* if it was below the median and *high* otherwise. This type of partition was justified by the fact that climate events in the North Pacific do not appear to have a specific periodicity (Bond *et al.* 2004), thus complicating the selection of time-explicit environmental phases. Furthermore, a time-explicit selection of the environmental variables would introduce a high degree of dependence between the time series used to calibrate the models and those used in the current simulations.

The distribution parameters (i.e. mean and standard deviation (s.d.)) of all environmental variables, except predation, were estimated from the observed time-series. *Low* or *high* mean and s.d. referred to the available time series below or above the median value, respectively. The predation index was fixed at 25.0 when low or 26.0 when high, an interval approximately covering the range of the available time-series. Such selection was justified by a long life cycle (15–20 years) of the species included in the predation metrics, suggesting that this index is unlikely to significantly change within the time frame of a simulated climatic regime, but is more likely to change over different regimes. For each simulated regime, the level of wind speed (i.e. high or low) was always the opposite of the spring temperature level; as in the GOA these two variables are to some degree negatively correlated: high wind induces deeper water mixing and cooling of surface temperature. The distributions of the

environmental variables used in the model simulations are shown in figure 4.

The environmental scenarios simulated in our analysis mirrored climate and biological regimes having occurred in the GOA during the last 40 years (table 2). The pre-1976 regime was characterized by low sea surface temperature (SST) and biologically by low abundance of groundfish predators. Reversed conditions applied to the post-1976 regime. The post-1989 regime was a transitional state, characterized by opposite trends of spring and fall SST (former low, latter high; Hare & Mantua 2000) and by high groundfish biomass (Mueter & Norcross 2002). We also defined two additional transitional state which may have occurred after the 1976 regime shift: (i) ‘early-transitional’, characterized by high spring temperature, and low fall temperature and predation, and (ii) ‘late-transitional’, characterized by high spring and fall temperature, and low predation. Finally, we defined a post-1998 regime characterized by low fall and spring temperature, but still high predation. Although still debatable, such a transitional state was presumably indicative of a recent return to pre-1976 conditions of the North Pacific climate (McFarlane *et al.* 2000; Mantua & Hare 2002; Bond *et al.* 2004).

#### 4. RESULTS

The environmental variables, associated with climate regimes, greatly influenced the stage of pollock recruitment control. In general, there was a delay of recruitment control with the increasing of both fall temperature and groundfish predation, typical features of the post-1976 regime (table 2). Increasing only the water temperature (late-transitional) shifted the recruitment control from the age-0 to the age-1 stage, and increasing both fall temperature and predation (post-1976) delayed recruitment control even further, as inferred by the reduction of



Table 2. Model predictions of the stage of recruitment control as determined by the correlation coefficients between recruitment and pre-recruitment stages over different climate regimes.

(The mean and the s.d. (in parentheses) of the environmental variables characterizing a climate regime are also shown.  $P_G$  = predation,  $T_F$  = fall temperature,  $T_S$  = spring temperature,  $W$  = wind speed cubed, CD = coefficient of determination between pre-recruitment and recruitment stages (E-R = egg-recruitment, 0-R = 0-age-recruitment, 1-R = 1-age-recruitment).)

regime	climatic conditions				CD		
	$T_S$	$W$	$T_F$	$P_G$	E-R	0-R	1-R
pre-1976	4.65 (0.46)	0.031 (0.006)	6.91 (0.35)	25 (0)	0.33	0.88	0.92
early-transitional	5.86 (0.35)	0.014 (0.005)	6.91 (0.35)	25 (0)	0.33	0.83	0.89
late-transitional	5.86 (0.35)	0.014 (0.005)	7.77 (0.27)	25 (0)	0.12	0.21	0.86
post-1976	5.86 (0.35)	0.014 (0.005)	7.77 (0.27)	26 (0)	0.06	0.06	0.64
post-1989	4.65 (0.46)	0.031 (0.006)	7.77 (0.27)	26 (0)	0.07	0.07	0.63
post-1998	4.65 (0.46)	0.031 (0.006)	6.91 (0.35)	26 (0)	0.16	0.27	0.84

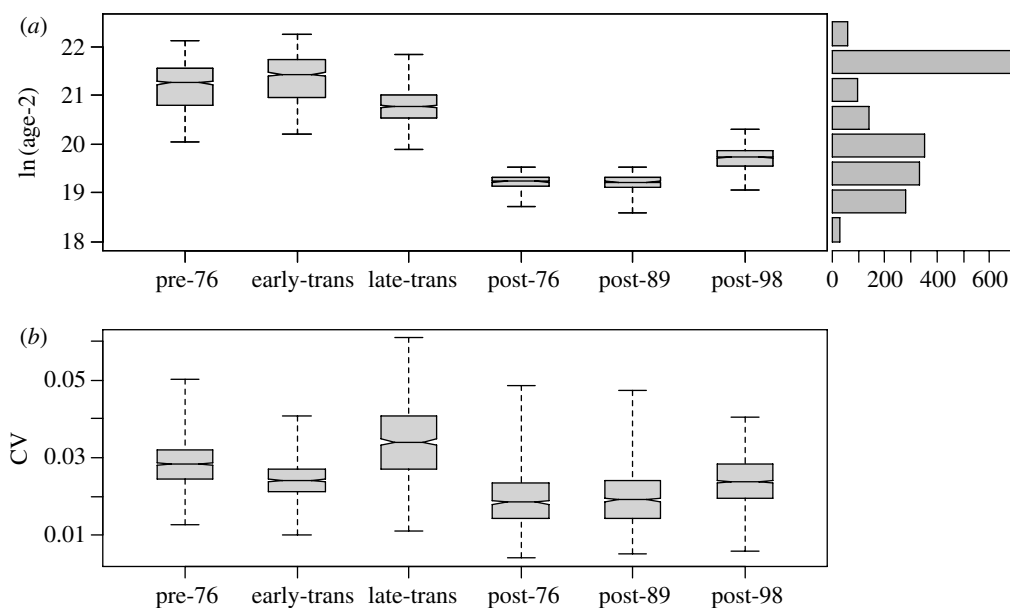


Figure 5. (a) Average recruitment magnitude and (b) coefficient of variation as predicted from the model simulations for the climatic regimes specified in the  $x$ -axis. Boxes in the magnitude panel show the distribution of 15 000 model realizations (1000 simulations of 15 years each). The lower and upper margins of the box represent the first and third quartile, respectively. The central line is the median and the notches are the 95% confidence interval around the median. Whiskers extend to the data range. Boxes in (b) show the distribution of 1000 values, each representing the variability of a 15-year realization. Also shown, on the right side of the magnitude plot (a), is the frequency distribution of a sample of 2000 realizations, weighted by the approximate duration of the climate regime; 'trans' stands for 'transitional'.

correlation between the age-1 and age-2 abundances. In contrast to all of the post-1976 regimes, in the pre-1976 regime (including the early-transitional) we estimated a high correlation between the age-0 and the age-2 stages (table 2), indicating that recruitment was already set by age-0 juvenile stage, or even earlier (larval stage).

The magnitude of pollock recruitment, as predicted by our model simulation, was highest during the pre-1976 and immediately after the 1976 regime shift (early-transitional), when spring temperature was high and both fall temperature and predation were low. It was lowest during the post-1976 regime when fall temperature and predation were high, and went up again during the post-1998 regime, when spring and fall temperatures were low, but predation was still high (figure 5). A sample of 2000 realizations of simulated pollock recruitment values, with sample probabilities weighted by the approximate regime duration (in years), had a pronounced bimodal distribution. (The weight coefficients for each climate

regime were: pre-1976 = 7, early- and late-transitional = 5, post-1976 = 8, post-1989 = 3, post-1998 = 2.)

In general, the recruitment CV decreased with the increasing predation. CV was lowest when both predation and fall temperature were high (i.e. post-1976 and post-1989 regimes) while it was highest when both spring and fall temperatures were high but predation was low (late-transitional; figure 5).

The metrics of pollock recruitment, predicted in the current analysis, were in general agreement with the empirical evidence gathered in the same study region and climate regimes covered by the simulations. With regard to stage of recruitment control, Bailey (2000) reported that during the decade following the 1976 North Pacific regime shift (i.e. our early- and late-transitional regimes), recruitment was already set at the larval stage, while in subsequent years (i.e. post-1976 regimes) it was delayed toward the juvenile stage. Similar patterns were predicted in our modelling analysis (table 2).

With regard to magnitude, the observed time-series of pollock recruitment shows a series of strong year classes during the decade 1970–80 followed by a decline of the average maximum recruitment from 1980 to the late 1990s (figure 2). During the decline there were other strong year classes, but these were not comparable in magnitude to those of the post-1976 decade. Similar patterns were predicted with our model. The management agency also estimated a strong year class in 1999 (Dorn *et al.* 2002), and so did our model in the post-1998 regime (figure 5). However, due to the partial nature of recruitment into the survey (2001), the actual magnitude of the 1999-year class is uncertain at the time of this writing. Finally, the observed time series of pollock recruitment was clearly multimodal up to the year 1995, while the applied test marginally failed to reject the null hypothesis of unimodality over the entire time series (figure 2).

## 5. DISCUSSION

### (a) Mechanisms of pollock recruitment dynamics

Our simulation analysis shows that three critical metrics of pollock recruitment dynamics (i.e. magnitude, variability and control) can markedly change over contrasting climate regimes in a way that conforms to empirical observations. Bailey (2000) showed that during the mid- and late-1980s there was an increase of juvenile pollock mortality due to a gradual build-up of groundfish predators. Ciannelli *et al.* (2004) illustrated that density-dependent mortality is high when temperature and predation are also high. Here we show that the increase of fall temperature and predation, and relative increase of density-dependent survival, imposes a constraint on the abundance of the age-1 and age-2 stages (as shown by a decrease of the recruitment magnitude and CV). We also show that the constraint on the abundance of late juvenile stages can overcome the effect of the dynamics occurring during earlier stages, thereby delaying the stage of recruitment control. In contrast, during environmental regimes characterized by low water temperature and predation, juvenile pollock stages experience a reduction of density-dependent control, which allows for a more direct link between larval and recruitment dynamics. Consequently, the ‘critical period’ (Hjort 1914) is anticipated and the magnitude of year-class strength and variability are considerably increased.

### (b) Modelling assumptions and limitations

The model parameters used in our analysis were estimated during an epoch (1975–98, Ciannelli *et al.* 2004) that is included within the periods covered by the current model simulations. However, the general agreement between the predicted and empirical recruitment patterns occurred independently from the model parameterization. First, the environmental variables used in the current simulations were drawn from statistical distributions, and for that reason were different in value from those used in the model parameterization. Second, and more importantly, with the exception of average recruitment magnitude, the patterns predicted here (i.e. stage of recruitment control and recruitment variability) are independent from the variables that were used to parameterize the model (i.e. abundance). In this respect, the newly simulated patterns should be considered as ‘emergent’ properties of pollock

pre-recruitment dynamics. Finally, a fully additive model, parameterized on the same set of environmental variables, was not as efficient in reproducing the empirical observations (unreported simulations), pointing to the fact that it was the model structure (i.e. additive versus non-additive) rather than the model parameters that caused the agreement between data and predictions.

Due to the lack of suitable data, our study does not consider a number of factors that may also affect pollock recruitment. For example, concomitant with the decrease of the pollock stock after the mid-1980s, there has been a decrease in the abundance of the Shelikof Strait spawners, while other secondary spawning aggregations (e.g. Shumagin Islands or in various locations along the shelf edge) have remained relatively stable (Dorn *et al.* 2002). The decline of spawning in historically rich locations (e.g. Shelikof Strait) may affect pollock recruitment dynamics if the environmental conditions of new or secondary locations are less than ideal.

Competitive interactions with other species may also affect pollock year-class strength in the GOA. Up to the late 1960s there was a large population of Pacific ocean perch (POP, *Sebastes alutus*) in the GOA, which was decimated by the fishery in the early 1970s. Likewise capelin (*Mallotus villosus*) were abundant in the late 1960s and early 1970s, but have since nearly disappeared (Anderson & Piatt 1999). Both POP and capelin are zooplankton feeders and their disappearance may have released walleye pollock from competitive pressure. Finally, density-dependent egg production, egg quality (Rjinsdorp 1994) and spawner age-related quality of eggs and larvae (Berkeley *et al.* 2004) are also factors where improved understanding of mechanisms may lead to more refined models.

### (c) Ecological and management implications

A change of recruitment metrics and survival mechanisms may have profound ecological and management implications. For example, recruitment control has long been considered in fisheries oceanography (Houde 1987; Sundby *et al.* 1989; Bailey & Spring 1992; Leggett & DeBolis 1994; Ellersten *et al.* 1995; Helle *et al.* 2000). Current knowledge assumes that recruitment control is partly a species-specific function of the life cycle. Pollock, for example, fall in the category of the ‘cod-like’ group, for which Houde (1987) hypothesized a control during the juvenile stage. Analogously, Myers & Caddigan (1993) suggested that recruitment control of the Atlantic cod (*Gadus morhua*) was set at the juvenile stage. Species with a short life cycle and high larval growth and mortality (e.g. anchovies) may be controlled at earlier stages, such as the larval stage (Houde 1987). Here, however, we show that environmental variables, related to climate change, may also anticipate or delay the stage of recruitment control.

Our modelling results point to the possibility that pollock recruitment dynamics have undergone a phase transition in the last 30 years. Essentially, we can divide the period 1970–2000 into two recruitment phases: the pre- and post-1976, each characterized by distinct dynamic properties, and recruitment mechanisms. The passage between the two phases may not have happened abruptly (i.e. within a year), but rather through an inter-annual transitional period with dynamic properties representative of both the pre- and post-1976 phases.

In the pre-1976 climate regime, recruitment magnitude and variability were both high and occasionally low year-classes may have simply occurred due to chance. Within this regime pollock recruitment was already set at the age-0 stage, indicating that larval dynamics were central in setting the year-class strength. In the post-1976 climate regimes, pollock recruitment magnitude and variability were low and recruitment control was delayed to the juvenile stage. Predation by groundfish became an important forcing variable, as did density dependence during the juvenile stages.

Our finding of a phase transition of pollock recruitment dynamics is in agreement with ecological theory and empirical observations of other systems. For example, Collie *et al.* (2004) illustrated that different stock-recruitment functions over different environmental regimes may, in a changing environment, give rise to abrupt changes of demographic variable (e.g. population size, recruitment). The stock-recruitment function of pollock changes over contrasting environmental regimes (Ciannelli *et al.* 2004) and here, in line with the observations of Collie *et al.* (2004), we demonstrate that the dynamic implications of these compensatory changes may give rise to recruitment phase transitions. The existence of a bimodal distribution of recruitment magnitude is also indicative of sudden changes of system properties, and therefore a phase transition (Scheffer & Carpenter 2003). Our simulated recruitment values clearly follow a bimodal distribution, while the observed time series of pollock recruitment supports a bimodal distribution up to the year 1995, but not afterwards (figure 2). However, the latest estimates of pollock recruitment are the least reliable and therefore noisier, as they are based on fewer observations of year class strength. Moreover, the latest years may correspond to a transitional phase toward a pre-1976 regime. Thus, we believe that there is support for a bimodal distribution also in the observed values of pollock year-class strength.

In the presence of phase transition driven by climate regime shifts, it becomes important to alter the reference and target metrics typically adopted in fisheries management (e.g. Hilborn & Walters 1992). For example, during periods characterized by early recruitment control, there can be a more sensitive link between the harvest and the strength of the ensuing year-class (through spawner-recruit functions). Furthermore, as we show in our analysis, recruitment becomes more responsive to short-scale environmental fluctuations and consequently more variable, when controlled during early-life stages. Lastly, a better understanding of the mechanisms regulating the stage of recruitment control can be used for monitoring purposes as the first stage that is significantly correlated with recruitment abundance also provides the first reliable estimate of the year-class strength. The emphasis of current fisheries management practices on the forecasting of the population abundance from one year to the next obscures the significance of longer time-scales, typically related to climate regimes. Hence, there is a need to formulate a new theoretical framework in fisheries science that balances short-term biocomplexity with adaptive management over medium to long time-scales in the presence of changing climate (Steele 1996; Rothschild & Shannon 2004; Duffy-Anderson *et al.* in press).

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## REFERENCES

- Anderson, P. J. & Piatt, J. F. 1999 Community reorganization in the Gulf of Alaska following ocean climate regime shift. *Mar. Ecol. Progr. Ser.* **189**, 117–123.
- Bailey, K. M. 2000 Shifting control of recruitment of walleye pollock *Theragra chalcogramma* after a major climatic and ecosystem change. *Mar. Ecol. Progr. Ser.* **198**, 215–224.
- Bailey, K. M. & Spring, S. M. 1992 Comparison of larval, age-0 juvenile and age-2 recruit abundance indexes of walleye pollock, *Theragra chalcogramma*, in the western Gulf of Alaska. *ICES J. Mar. Sci.* **49**, 297–304.
- Beamish, R. J., Noakes, D. J., McFarlane, G. A., Klayshorin, L., Ivanov, I. I. & Kurashov, V. 1999 The regime concept and natural trends in the production of Pacific salmon. *Can. J. Fish. Aquat. Sci.* **56**, 516–526.
- Baugrand, G. 2004 The North Sea regime shift: evidence, causes, mechanisms and consequences. *Progr. Oceanogr.* **60**, 245–262.
- Berkeley, S. A., Chapman, C. & Sogard, S. M. 2004 Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanops*. *Ecol.* **85**, 1258–1264.
- Bond, N. A., Overland, J. E., Spillane, M. & Stabeno, P. 2004 Recent shifts in the state of the North Pacific. *Geoph. Res. Lett.* **30**, 2183–2186.
- Chan, K. S. & Tong, H. 2004 Testing for multimodality with dependent data. *Biom.* **91**, 113–123.
- Chavez, F. P., Ryan, J., Lluch-Cota, S. E. & Niquen, M. C. 2003 From anchovies to sardines and back: multidecadal change in the Pacific Ocean. *Science* **299**, 217–222.
- Ciannelli, L., Chan, K. S., Bailey, K. M. & Stenseth, N. C. 2004 Non-additive effects of the environment on the survival of a large marine fish population. *Ecol.* **85**, 3418–3427.
- Collie, J. S., Richardson, K. & Steele, J. H. 2004 Regime shifts: can ecological theory illuminate the mechanisms? *Progr. Oceanogr.* **60**, 281–302.
- Cury, P. & Shannon, L. 2004 Regime shifts in upwelling ecosystems: observed changes and possible mechanisms in the northern and southern Benguela. *Progr. Oceanogr.* **60**, 223–243.
- Dorn, M., Barbeaux, S., Guttormsen, M., Mergrey, B., Hollowed, A., Brown, E. & Splaingier, K. 2002 Assessment of walleye pollock in the Gulf of Alaska. In *Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska*. Anchorage, AK: North Pacific Fishery Management Council.
- Duffy-Anderson, J.T., Bailey, K., Ciannelli, L., Cury, P., Belgrano, A. & Stenseth, N.C. In press. Phase transitions in marine fish recruitment processes. *Ecol. Compl.*
- Ellersten, B., Fossum, P., Solemda, P. & Sundby, S. 1995 The 'critical period' concept—a century of recruitment research. *Mar. Ecol. Progr. Ser.* **128**, 305–308.
- FAO, Food and Agricultural Organization 2002 The state of world fisheries and aquaculture. FAO, Rome. ([www.fao.org](http://www.fao.org))



- Green, P. J. & Silverman, B. W. 1994 *Nonparametric regression and generalized linear models: a roughness penalty approach*. London: Chapman and Hall.
- Hall, P. & York, M. 2001 On the calibration of Silverman's test for multimodality. *Statist. Sinica* **11**, 515–536.
- Hare, S. R. & Mantua, N. J. 2000 Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Prog. Oceanogr.* **47**, 103–145.
- Helle, K., Bogstad, B., Marshall, T., Michalsen, K., Otterresen, G. & Pennington, P. 2000 An evaluation of recruitment indices for Arcto-Norwegian cod (*Gadus morhua* L.). *Fish. Res.* **48**, 55–67.
- Hilborn, R. & Walters, C. J. 1992 *Quantitative fisheries stock assessment: choice, dynamics and uncertainty*. London: Chapman and Hall.
- Hjort, J. 1914 Fluctuations in the great fisheries of Northern Europe. Viewed in the light of biological research. *Rapp. P.-v Reun. Cons. Inst. Explor. Mer.* **20**, 1–228.
- Houde, E. D. 1987 Fish early life dynamics and recruitment variability. *Am. Fish. Soc. Symp.* **2**, 17–29.
- Kendall, A. W., Schumacher, J. D. & Kim, S. 1996 Walleye pollock recruitment in Shelikof Strait: applied fisheries oceanography. *Fish. Oceanogr.* **5**, 4–18.
- Leggett, W. C. & DeBlois, E. 1994 Recruitment in marine fishes: is it regulated by starvation and predation in the egg and larval stages? *Neth. J. Sea Res.* **32**, 119–134.
- Mantua, N. J. & Hare, S. R. 2002 The Pacific decadal oscillation. *J. Oceanogr.* **58**, 35–44.
- McFarlane, G. A., King, J. R. & Beamish, R. J. 2000 Have there been recent changes in climate? Ask the fish. *Prog. Oceanogr.* **47**, 147–169.
- Megrey, B. A., Bograd, S. J., Rugen, W. J., Hollowed, A. B., Stabeno, P., Macklin, S. A., Schumacher, J. D. & Ingraham, W. J. 1995 An exploratory analysis of associations between biotic and abiotic factors and year-class strength of Gulf of Alaska walleye pollock. *Can. J. Fish. Aquat. Sci.* **121**, 227–243.
- Mueter, F. J. & Norcross, B. L. 2002 Spatial and temporal patterns in demersal fish community on the shelf and upper slope regions of the Gulf of Alaska. *Fish. Bull.* **100**, 559–581.
- Myers, R. A. & Cadigan, N. 1993 Density-dependent juvenile mortality in marine demersal fishes. *Can. J. Fish. Aquat. Sci.* **50**, 1576–1590.
- O'Brien, C. M., Fox, C. J., Planque, B. & Casey, J. 2000 Climate variability and North Sea cod. *Nature* **4**, 142.
- Rjinsdorp, A. D. 1994 Population-regulating processes during the adult phase in flatfish. *Neth. J. Sea Res.* **32**, 207–223.
- Rothschild, B. J. & Shannon, L. J. 2004 Regime shifts and fishery management. *Prog. Oceanogr.* **60**, 397–402.
- Scheffer, M. & Carpenter, S. R. 2003 Catastrophic regime shifts in ecosystems: linking theory to observations. *Trends Ecol. Evol.* **18**, 648–656.
- Steele, J. H. 1996 Regime shifts in fisheries management. *Fish. Res.* **25**, 19–23.
- Steele, J. H. 2004 Regime shifts in the oceans: reconciling observations and theory. *Prog. Oceanogr.* **60**, 135–141.
- Stone, M. 1977 An asymptotic equivalence of choice of model by cross-validation and Akaike's criterion. *J. R. Stat. Soc. B* **39**, 44–47.
- Sundby, S., Bjorke, H., Soldal, A. V. & Olsen, S. 1989 Mortality rates during the early life stages and year-class strength of northeast Arctic cod (*Gadus morhua* L.). *Rapp. P.-v Reun. Cons. Inst. Explor. Mer.* **191**, 351–358.
- Wahba, G. 1990 Spline models for observational data. *Regl. Conf. Ser. Appl. Math.*, 59.
- Wood, S. J. R. 2000 Modelling and smoothing parameter estimation with multiple quadratic penalties. *J. R. Stat. Soc. B* **62**, 413–428.

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