

## LETTER

# Oscillating trophic control induces community reorganization in a marine ecosystem

Michael A. Litzow<sup>1</sup> and Lorenzo Ciannelli<sup>2\*</sup>

<sup>1</sup>National Oceanic and Atmospheric Administration, Alaska Fisheries Science Center, Kodiak, AK 99615, USA

<sup>2</sup>College of Oceanic and Atmospheric Sciences, Oregon State University, Corvallis, OR 97331, USA

\*Correspondence: E-mail: lciannel@coas.oregonstate.edu

## Abstract

Understanding how climate regulates trophic control may help to elucidate the causes of transitions between alternate ecosystem states following climate regime shifts. We used a 34-year time series of the abundance of Pacific cod (*Gadus macrocephalus*) and five prey species to show that the nature of trophic control in a North Pacific ecosystem depends on climate state. Rapid warming in the 1970s caused an oscillation between bottom–up and top–down control. This shift to top–down control apparently contributed to the transition from an initial, prey-rich ecosystem state to the final, prey-poor state. However, top–down control could not be detected in the final state without reference to the initial state and transition period. Complete understanding of trophic control in ecosystems capable of transitions between alternate states may therefore require observations spanning more than one state.

## Keywords

Alternate stable states, bottom–up control, climate change, community reorganization, fishery, Pacific Decadal Oscillation, phase transition, regime shift, top–down control, trophic control.

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## INTRODUCTION

Much recent research has sought to understand the relative strength of top–down (consumer-limited) and bottom–up (resource-limited) control in marine food webs, as the impact of climate change, eutrophication and overfishing in marine ecosystems depends on the nature of trophic control. This topic has often been treated as an either–or question, with studies providing evidence of the primacy of either top–down control (Worm & Myers 2003; Frank *et al.* 2005; Halpern *et al.* 2006) or bottom–up control (Ware & Thompson 2005; Bishop *et al.* 2006; Frederiksen *et al.* 2006; Greene & Pershing 2007). In the face of these conflicting results, a new synthesis has begun to emerge, in which top–down and bottom–up effects are seen to either operate simultaneously, or to show spatial and temporal variability in patterns of dominance (Scheffer *et al.* 2005; Frank *et al.* 2006; Hunt & McKinnell 2006). This new view may be particularly useful for understanding climate-forced catastrophic reorganizations in marine ecosystems.

During the 20th century, North Pacific Ocean ecosystems were subject to a series of abrupt ecological reorganizations following climate regime shifts (Chavez *et al.* 2003). These events are often proposed as an example of transitions between alternate stable ecosystem states (Scheffer *et al.*

2001; Scheffer & Carpenter 2003). Such transitions are often referred to as ‘regime shifts’, but this terminology confuses the external cause in the North Pacific case (a climate regime shift) with the ecological effect, and we follow earlier authors (Ciannelli *et al.* 2005; Duffy-Anderson *et al.* 2005) in using the term ‘phase transition’ to describe these shifts between alternate ecosystem states. The idea that climate regime shifts in the North Pacific produce ecological phase transitions has been controversial, as observational, non-experimental evidence of phase transitions is open to alternate explanations (Schröder *et al.* 2005). However, observational time series of North Pacific biological communities do exhibit the nonlinear dynamics that are characteristic of alternate states and phase transitions (Hsieh *et al.* 2005). This implies that alternate stable state theory, which has been developed in small, experimentally manipulated ecosystems (notably freshwater ponds) may be applied to understanding poorly explained dynamics in large, economically and socially important continental shelf ecosystems. Theory predicts that phase transitions are caused by interaction between sources of population variability that are external to and internal to the ecosystem in question (Scheffer & Carpenter 2003). In line with such theory, one hypothetical explanation for oceanic phase transitions invokes climate as the external mechanism and

trophic control as the internal mechanism (Hunt *et al.* 2002). However, climate regulation of trophic control has never been empirically demonstrated for an oceanic phase transition.

Here, we test for changes in trophic control during a well-documented phase transition in the Gulf of Alaska, using as a model system the dynamics between Pacific cod (*Gadus macrocephalus* Tilesius) and five species that dominated cod diets around the time of the transition: capelin (*Mallotus villosus* Müller), pink shrimp (*Pandalus borealis* Kroyer), humpy shrimp (*P. goniurus* Stimpson), coonstripe shrimp (*P. hypsinotus* Brandt) and sidestripe shrimp (*Pandalopsis dispar* Rathbun). Our data come from a small-mesh bottom trawl survey of Pavlof Bay in the Gulf of Alaska, conducted annually during 1972–2005. This time series spans a phase transition of the North Pacific following the 1976/1977 climate regime shift in the Pacific Decadal Oscillation (PDO; Mantua & Hare 2002), resulting in a switch throughout the Gulf of Alaska and south-east Bering Sea from a community dominated by decapod crustaceans and small pelagic fish to one dominated by groundfish (Anderson & Piatt 1999; Connors *et al.* 2002). Because the Pavlof Bay time series includes data on both the predator and the prey components of the community, it represents a unique opportunity to identify the underlying mechanisms leading to a change of community state following a climate perturbation. Our results show how phase transitions due to changing trophic control, a phenomenon previously known from small, experimentally manipulated ecosystems (e.g. Schmitz 2007), can be used to explain climate-forced reorganization of large, open ecosystems.

## MATERIAL AND METHODS

Our specific goals were to test two hypotheses: (i) climate regulates trophic control in Pavlof Bay and (ii) changes in trophic control were causative mechanisms in the phase transition following the 1976/1977 regime shift. We tested the first hypothesis by relating a regional climate index to the correlation coefficient ( $r$ ) between cod and prey abundance, with negative correlations providing evidence of top–down control and positive correlations providing evidence of bottom–up control (Worm & Myers 2003; Frank *et al.* 2006). Although it is difficult to assign causation by analysing correlations in observational data sets, this approach is unavoidable for understanding causative mechanisms in large, open systems that are not amenable to manipulation, and this approach has produced important advances in understanding the function of continental shelf ecosystems (e.g. Worm & Myers 2003; Frank *et al.* 2005, 2006). Accordingly, we used a two-pronged approach to test our second hypothesis with observational data. First, we tested for changes in trophic control as the community

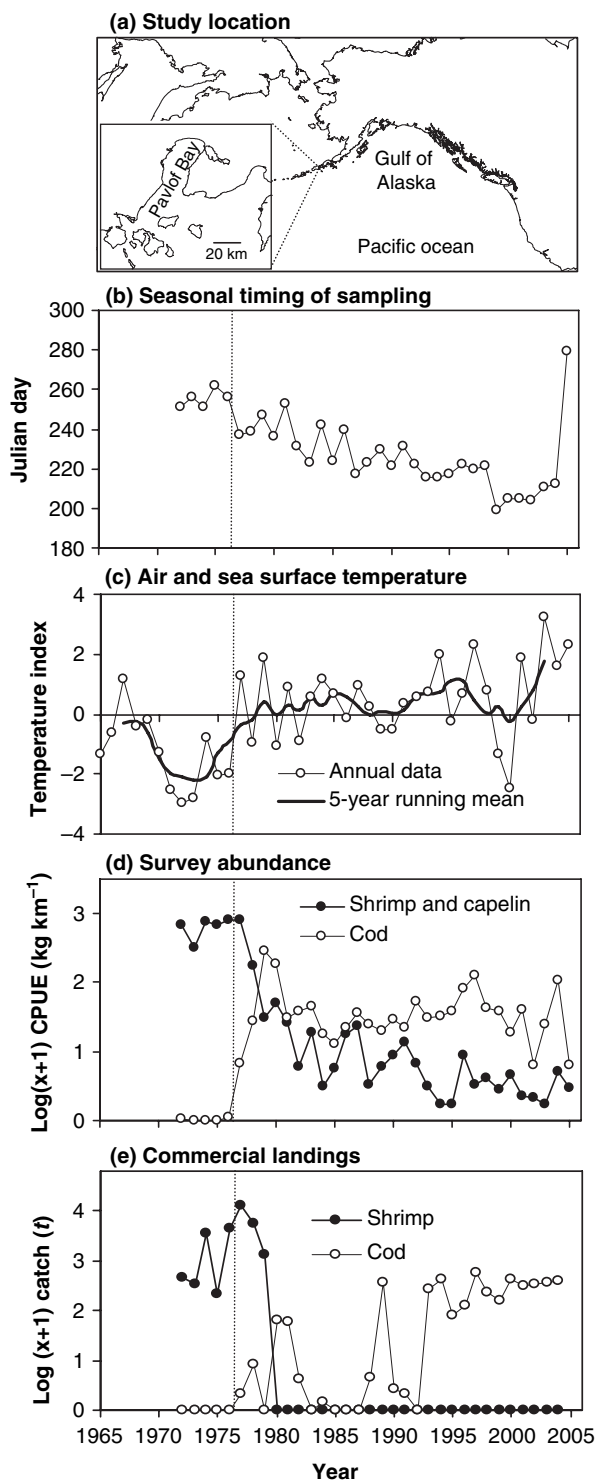
passed through the phase transition, a necessary condition for changing trophic control to act as a causative mechanism. Then, because theory predicts a change in the set of factors controlling populations during phase transitions (Scheffer & Carpenter 2003), we tested for differences in the factors controlling predator and prey populations between the two community states, using trophic control and all other independent variables for which we have data (direct climate effects, commercial fishing effects and density dependence).

## Data sources

Our biological data come from a small-mesh bottom trawl survey of Pavlof Bay, on the south side of the Alaska Peninsula (59.6°N, 161.6°W; Fig. 1a), conducted annually during 1972–2005 by the U.S. National Marine Fisheries Service and the Alaska Department of Fish and Game. Logistic constraints have resulted in seasonal variability in the timing of sampling across the time series: in September or August during 1972–1998, in July during 1999–2004 and in October in 2005 (Fig. 1b). However, ecological change in the Pavlof Bay time series has been confirmed by persistent changes in commercial fisheries (Litzow 2006) and seabird diets (Piatt & Anderson 1996) across the Gulf of Alaska, confirming that the changes we document were results of community reorganization, and not artefacts of seasonal differences in timing of sampling.

The survey utilizes a high-opening net built with 32 mm stretched mesh throughout, and we used survey catch per unit effort (CPUE; kg km hauled<sup>-1</sup>) as our measure of abundance. Pavlof Bay stations are randomly selected from a standard grid with a mean sampling depth of 99 m (range: 18–139). At least 10 hauls were made in each year (average  $n = 17 \pm 6$  SD hauls per year) except for 1973, when two hauls were made. Sidestripe shrimp were not captured in 1973, and their absence in the catch that year was judged to be an artefact of low sampling effort, so sidestripe shrimp abundance in that year was estimated as the average of CPUE in 1972 and 1974. No other attempts were made to address sampling error. Areas throughout the western Gulf of Alaska are sampled, but sampling prior to the 1976/1977 regime shift was sparse in most areas, and Pavlof Bay is the only bay that has been sampled in every year of the time series. For detailed survey methods, see Anderson & Piatt (1999).

Pacific cod were selected as the predator species for analysis because they have long been suspected as a leading agent in the decline of Gulf of Alaska shrimp populations following the 1976/1977 PDO regime shift (Albers & Anderson 1985; Anderson & Piatt 1999). Capelin and the four shrimp species were selected as the prey species for analysis because they dominated the catch (80–90% of total



**Figure 1** (a) Location of Pavlof Bay, Alaska, (b) seasonal timing of first day of sampling, and time series of (c) regional temperature index, (d) survey catches and (e) commercial fishery landings. Dotted vertical lines in (b–e) indicate 1976/1977 Pacific Decadal Oscillation climate regime shift. Temperature index is first principal component of summer and winter values from two regional time series.

biomass) prior to the regime shift and are important components of Pacific cod diet in Pavlof Bay (Albers & Anderson 1985; Anderson & Piatt 1999; Yang 2004). Commercial catch data were obtained from the Alaska Department of Fish and Game, and were calculated for the 12-month period prior to each annual survey.

We used a regional, rather than local, measure of climate in our study. This is because simple measures of local climate may fail to capture complex associations between weather and ecological processes, while regional-scale measures of climate are correlated with a wide variety of climate parameters, and so are often more successful at predicting climate effects on localized ecological processes (Hallett *et al.* 2004). However, the PDO index, which describes the dominant decadal-scale pattern in North Pacific climate during the 20th century, lost its ‘regime’ characteristics (i.e. interannual autocorrelation) in 1988/1989 (Bond *et al.* 2003), and since that time other factors (changing Arctic climate patterns, global warming) have also affected Gulf of Alaska climate (Litzow 2006). No ‘off the shelf’ climate index could therefore express Gulf of Alaska climate variability during the entire 34 years of our study. We therefore constructed a regional-scale climate index specifically for this study, using the first principal component (PC1) of winter (DJF) and summer (JJA) surface temperatures from two  $5^{\circ} \times 5^{\circ}$  squares centred over Pavlof Bay (southern square:  $50^{\circ}\text{--}55^{\circ}\text{N}$ ,  $160^{\circ}\text{--}165^{\circ}\text{W}$ ; northern square:  $55^{\circ}\text{--}60^{\circ}\text{N}$ ,  $160^{\circ}\text{--}165^{\circ}\text{W}$ ) from the HadCRUT2 combined land and marine temperature anomaly data set (Rayner *et al.* 2003, available at <http://www.cru.uea.ac.uk>). PC1 explained 57% of total variability in the four temperature variables (i.e. summer and winter temperature from the two squares) during 1965–2005, and generally reflected warming, with positive eigenvectors for all four individual temperature time series (eigenvector range: 0.46–0.56).

## Analysis

We log-transformed  $(x + 1)$  CPUE values before analysis to achieve approximate normality. To account for differences in catchability between prey species, we standardized log (CPUE) values for all species as mean zero, unit variance. We used the Modified Chelton method to adjust our estimated degrees of freedom (EDF) to account for autocorrelation in all cod–prey correlation analyses (Pyper & Peterman 1998). These results are reported with corrected sample size ( $n'$ ) and probability ( $P'$ ) values.

We used a previously published non-metric multidimensional scaling (NMDS) index of survey catch composition in Pavlof Bay to measure changes in community composition across the time series (Litzow 2006). Briefly, the NMDS analysis summarizes variability in the fourth root-

transformed CPUE of the 30 most common taxa in the time series (comprising 98.8% of the total catch) in a manner conceptually similar to principal components analysis. NMDS, however, is more appropriate to data sets, like this trawl survey, that are characterized by a large number of zero values (Mueter & Norcross 1999, 2000). The leading NMDS axis used in this analysis explains 34% of variability in small-mesh survey catches across the Alaska Peninsula and Kodiak Island (i.e. for all 30 taxa across all depths and all years), and captures the phase transition in the Gulf of Alaska community (i.e. negative values indicate dominance by shrimp and capelin, positive values indicate dominance by groundfish; Litzow 2006).

To assess the generality of Pavlof Bay results for the entire Gulf of Alaska, we compared annual mean Pavlof Bay NMDS axis 1 scores with annual mean axis 1 scores for other well-sampled bays ( $n = 1202$  hauls over 24 years, data in Litzow 2006). This analysis showed a strong correlation between Pavlof and other areas ( $r = 0.91$ ), indicating that the community dynamics that we observed in Pavlof Bay were emblematic of ecological change across the Gulf of Alaska.

Because few years of sampling occurred before the 1976/1977 regime shift, it is also important to use other data sources to assess the stability of the pre-regime shift community state. NMDS axis 1 scores from Pavlof Bay and two other well-sampled bays are highly correlated ( $r = 0.95$ ) with the leading principal component of variability in the composition of commercial fisheries catches in the Gulf of Alaska (Litzow 2006). PC1 of the commercial catch was in a state indicating negative NMDS axis 1 values (i.e. the pre-regime shift stable state) back to 1960 (Litzow 2006). Furthermore, time series of salmon catches, which are strongly correlated with overall community state (Litzow 2006), indicate that the Gulf of Alaska was likely dominated by crustaceans and small pelagic fish since shortly after the previous PDO regime shift, in the 1940s (Mantua & Hare 2002). Available evidence therefore indicates that although few years of small-mesh trawl sampling occurred before the 1976/1977 regime shift, these years are representative of a stable ecological state that had persisted for decades.

To elucidate the relationship between climate, community state and trophic control, we calculated Pearson correlation coefficients ( $r$ ) between log-transformed cod and prey abundance on a 5-year sliding window and related these to corresponding 5-year running means of climate PC1 (lagged 1 year) and our measure of community state (NMDS axis 1 scores). These analyses were conducted with Generalized Additive Models (GAMs; Hastie & Tibshirani 1990), a nonlinear regression technique that uses smoothed functions to model the relationship between dependent and independent variables. An advantage of GAM over traditional regression techniques is that GAM does not require

an *a priori* specification of the shape of the relationship between dependent and independent variables. We used natural cubic splines for our smooth functions (Wood 2006) and determined the level of complexity (roughness) of each function by minimizing the roughness penalty function, which is defined as the sum of the prediction error (sum of squares) and the roughness of the smooth function (i.e. the integral of the squared second derivative; Green & Silverman 1994).

The 5-year window length used in the cod-prey correlation analysis was set *a priori* based on statistical considerations: 5 years was judged to be long enough to give adequate power to detect annual-scale processes, but short enough to detect the rapid ecological transition following the PDO regime shift. We tested the sensitivity of our results to the selection of window size by calculating the relationships between climate and trophic control, and community state and trophic control, at windows of 3–10 years. This analysis allowed us to both assess our ability to reject the null hypothesis at various window lengths, and to test for nonlinearity in the relationships as a function of window sizes. Nonlinearity was assessed through the EDF results from GAM; EDF = 1 for linear relationships and increases with progressively more nonlinear relationships (Wood 2006).

To test for differences in the factors regulating cod and prey populations in different community states, we compared competing fully additive models (GAMs) and threshold non-additive models (TGAMs), each evaluating the strength of correlation between abundance and a suite of independent variables (trophic interaction, direct climate effects, density dependence and commercial fishing). While GAM assumes a continuous relationship between dependent and independent variables across the time series, TGAM assumes an abrupt change in these relationships (i.e. a phase transition) at a specific value of some threshold variable. This approach represents an extension of non-parametric regression techniques (Hastie & Tibshirani 1990), and was developed to test hypotheses of non-additive climate effects on demographic parameters (Ciannelli *et al.* 2004, 2005). In this case community state (NMDS axis 1) was used as the threshold variable.

The appropriate threshold value was selected by minimizing the model Generalized Cross Validation (GCV) score, a measure of the mean-squared predictive error of the model (Green & Silverman 1994). Threshold selection is achieved by running individual model formulations for each of 25 possible threshold values contained within the upper 0.8 and lower 0.2 quantile range of observed NMDS values. Limiting the threshold covariate range to the upper 0.8 and lower 0.2 quantile ensured that at least 20% of the data was left within each of the community states, an appropriate restriction given the observed timing of the phase transition

within the small-mesh survey time series (Litzow 2006). The NMDS value from the model producing the lowest GCV score was retained as the threshold value. Similar iterations were used to select appropriate time lags for analysis of temperature and density-dependent effects (from candidate lags of 0–3 and 1–3 years, respectively). Commercial fishery effects were only examined at lag 1 (i.e. for the 12 months prior to a given survey), and, following an earlier study (Worm & Myers 2003), trophic control was only examined at lag 0.

Generalized Cross Validation scores could not be used to directly compare candidate TGAM and GAM models because the GCV score does not properly account for the presence of an additional parameter (i.e. the threshold) in the TGAM, so a genuine cross-validation (gCV) score was used instead. We calculated gCV scores by excluding a single datum from the time series and using the remaining data to fit a new candidate model (including a re-estimation of the threshold in the TGAM case). The new model was then used to estimate the out-of-sample data case, and the mean-squared predictive error was recorded. The same routine was repeated for the remaining data points, with the final gCV being the average mean-squared predictive error of all runs for each candidate model (Ciannelli *et al.* 2004).

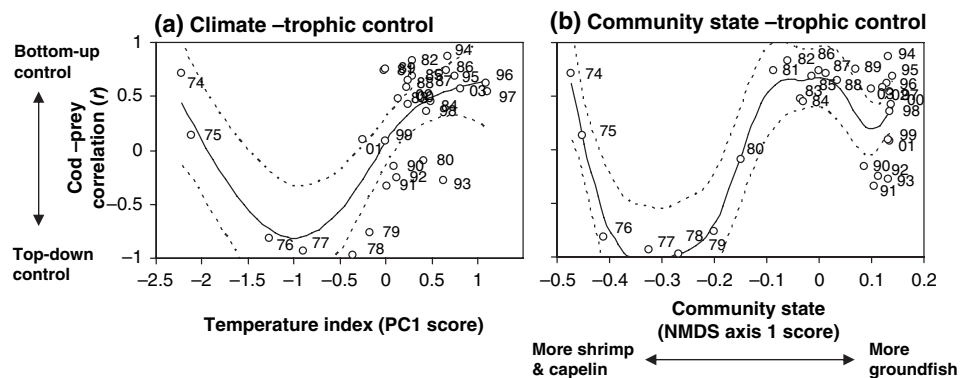
Of the five prey species in our study, four (capelin, humpy shrimp, coonstripe shrimp and sidestripe shrimp) became so scarce after the community phase transition that CPUE fell below  $0.01 \text{ kg km}^{-1}$  in some years. Thus, while cumulative abundance of the five prey species could be precisely measured throughout the time series, it was judged that measurement error for the four least dominant species was too large relative to their abundance late in the time series for individual models of abundance to be constructed.

Therefore, pink shrimp, which remained relatively common in every year ( $\text{CPUE} > 0.5 \text{ kg km}^{-1}$ ) and were the dominant prey of cod around the phase transition (Albers & Anderson 1985), were the only prey species for which detailed models of abundance were constructed.

## RESULTS

The PDO regime shift appeared as a rapid warming in our regional-scale climate index (PC1 score; Fig. 1c). This increase in temperature was followed by an increase of more than three orders of magnitude in survey CPUE of Pacific cod between 1976 and 1979 (Fig. 1d). As cod abundance in Pavlof Bay increased, the five prey species showed a three order of magnitude decrease in cumulative survey CPUE (Fig. 1d), and the collapse of shrimp populations and increase in cod abundance resulted in a rapid transition from a shrimp fishery to a cod fishery (Fig. 1e).

Across the entire Pavlof Bay time series, we found a negative correlation between log-transformed abundance of cod and the five prey species as a group ( $r = -0.70$ ,  $n' = 11.2$ ,  $P' = 0.01$ ), indicating top-down control of prey populations by cod predation. However, temporal decomposition of the time series revealed variability in trophic control that was related to temperature: the time series begins in a cold, bottom-up state (cod and other groundfish predators largely absent), followed by warming and strong top-down control, then a reversion to bottom-up or weak control with further warming (GAM,  $R^2 = 0.49$ ,  $n = 30$ ,  $\text{EDF} = 3.58$ ,  $P = 0.003$ ; Fig. 2a). These changes in trophic control were coincident to the phase transition between alternate community states in Pavlof



**Figure 2** (a) Oscillating trophic control in Pavlof Bay, Alaska in response to climate change: correlations between cod and prey abundance on a 5-year sliding window plotted against 5-year running mean climate index (first principal component of summer and winter temperatures from two regional time series) lagged 1 year. (b) Shift to top-down control during phase transition between alternate states in Pavlof Bay: cod–prey correlations on 5-year window plotted against 5-year running mean non-metric multidimensional scaling (NMDS) axis 1 score of survey catch composition. NMDS expresses the community differences before (negative values) and after (positive values) phase transition. Labels indicate midpoints of 5-year windows, solid lines depict smoothed nonparametric regressions, and dotted lines indicate 95% confidence intervals around regression lines.

Bay, as shown by a similar nonlinear relationship between community state (NMDS axis 1) and trophic control (GAM,  $R^2 = 0.68$ ,  $n = 30$ , EDF = 6.87,  $P < 0.0001$ ; Fig. 2b). These results were robust to the selection of sliding window size: across window sizes 3–10 years, both the climate–trophic control relationship and the community composition–trophic control relationship maintained EDF > 3 (indicating strongly nonlinear relationships) and  $P < 0.05$ , although increasing autocorrelation at larger window sizes indicated that the assumption of independent residuals was violated for windows > 5 years in length (Table 1).

Comparisons of competing additive (GAM) and non-additive (TGAM) models confirmed that change in trophic control contributed to a change in the set of factors controlling prey populations after the phase transition. Prey (pink shrimp) abundance was best described by a threshold model (TGAM,  $R^2 = 0.94$ , gCV = 0.103; Table 2), with differential control above and below an NMDS threshold value of  $-0.005$ , a value that was first reached in 1984 (Fig. 2b). Below the NMDS threshold, pink shrimp abundance was negatively associated with cod abundance ( $P = 0.0003$ ; Fig. 3a, for detailed results see Table 3) and temperature (temperature lagged 1 year,  $P = 0.01$ ; Fig. 3b). Above the NMDS threshold, pink shrimp abundance was explained by a nonlinear relationship with temperature ( $P = 0.0007$ ; Fig. 3c), with no significant effect of cod

abundance ( $P > 0.1$ ), supporting the previous result (Fig. 2) of bottom–up or weak control in the latter parts of the time series. Throughout the time series (i.e. above and below the NMDS threshold), there was a positive linear relationship with commercial catch in the previous year ( $P < 0.0001$ ; Fig. 3d), supporting the hypothesis that commercial fishing was not the primary driver of rapid declines in shrimp abundance, and a dome-shaped relationship with lagged shrimp abundance ( $P = 0.01$ ; Fig. 3e), suggesting negative density dependence at very high shrimp densities.

Factors affecting cod abundance differed above and below an NMDS threshold value of  $-0.102$ , a value first reached in 1981 (Fig. 2b), indicating that the mechanisms affecting cod dynamics also changed over the community phase transition (TGAM,  $R^2 = 0.83$ , gCV = 0.152; Table 2). Prey abundance showed a negative correlation with cod abundance below the threshold ( $P < 0.0001$ ; Fig. 3f, for detailed results see Table 3), but was not related to cod abundance above the threshold ( $P > 0.1$ ), again confirming a pattern of transient top–down control. Cod abundance was positively correlated with temperature below the threshold (temperature lagged 2 years,  $P = 0.05$ ; Fig. 3g), and showed a dome-shaped response to temperature above the threshold (temperature lagged 2 years,  $P = 0.01$ ; Fig. 3h). Cod abundance showed a nonlinear response to commercial catch rates across the time series ( $P = 0.02$ ; Fig. 3i), suggesting that exploitation regulated the cod population at high levels of abundance. Factors

**Table 1** Analysis of relationships between climate state, community composition and trophic control: sensitivity to duration of sliding window

| Comparison  | Window size (years) | $n$ | $R^2$ | Estimated degrees of freedom | $P$ -value | Lag 1 autocorrelation coefficient |
|---|---------------------|-----|-------|------------------------------|------------|-----------------------------------|
| Climate index (PC1) vs. cod–prey correlation ( $r$ )                  | 3                   | 31* | 0.33  | 5.09                         | 0.04       | –0.01                             |
|   | 4                   | 31  | 0.44  | 3.61                         | 0.003      | 0.57                              |
|   | 5                   | 30  | 0.49  | 3.58                         | 0.003      | 0.38                              |
|   | 6                   | 29  | 0.59  | 3.55                         | 0.0004     | 0.51                              |
|   | 7                   | 28  | 0.71  | 3.54                         | < 0.0001   | 0.62                              |
|   | 8                   | 27  | 0.72  | 3.72                         | < 0.0001   | 0.60                              |
|   | 9                   | 26  | 0.72  | 3.11                         | < 0.0001   | 0.73                              |
| Community compositions (NMDS axis 1) vs. cod–prey correlation ( $r$ ) | 10                  | 25  | 0.66  | 3.23                         | 0.0001     | 0.78                              |
|   | 3                   | 31* | 0.31  | 3.69                         | 0.04       | –0.10                             |
|   | 4                   | 31  | 0.59  | 4.93                         | 0.0002     | 0.49                              |
|   | 5                   | 30  | 0.68  | 6.87                         | < 0.0001   | 0.27                              |
|   | 6                   | 29  | 0.82  | 8.12                         | < 0.0001   | 0.34                              |
|   | 7                   | 28  | 0.83  | 7.24                         | < 0.0001   | 0.36                              |
|   | 8                   | 27  | 0.84  | 6.66                         | < 0.0001   | 0.40                              |
|   | 9                   | 26  | 0.87  | 6.33                         | < 0.0001   | 0.65                              |
|   | 10                  | 25  | 0.86  | 5.95                         | < 0.0001   | 0.64                              |

The null hypothesis for each relationship was tested at various window sizes using smoothed nonparametric regression. Estimated degrees of freedom values  $\gg 2$  indicate strongly nonlinear relationships, values  $< 2$  indicate nearly linear relationships.

\*One 3-year window contained no variability in cod abundance and was dropped from analysis.

NMDS, non-metric multidimensional scaling.

**Table 2** Results for selection of competing GAMs and TGAMs used to describe population correlates for pink shrimp and Pacific cod in the Pavlof Bay time series

| Response variable    | Model type | Formulation  | R <sup>2</sup> | gCV    |
|----------------------|------------|--|----------------|--------|
| Log pink shrimp CPUE | GAM        | $\text{Shrimp}_{t+1} = 1.020 + g_1(\text{Cod}_{t+1}) + g_2(\text{Temperature}_t) + g_3(\text{Shrimp}_t) + g_4(\text{Catch}_t) + \varepsilon_{t+1}$   | 0.83           | 0.1563 |
|                      | TGAM       | $\text{Shrimp}_{t+1} = g_1(\text{Shrimp}_t) + g_2(\text{Catch}_t) + \varepsilon_{t+1} + \begin{cases} 1.173 + g_3(\text{Cod}_{t+1}) + g_4(\text{PCT}_t), & \text{if NMDS}_t \leq -0.005 \\ 0.872 + g_5(\text{Temperature}_t), & \text{if NMDS}_t > -0.005 \end{cases}$ | 0.94           | 0.1034 |
| Log cod CPUE         | GAM        | $\text{Cod}_{t+1} = 1.296 + g_1(\text{Prey}_{t+1}) + g_2(\text{Temperature}_{t-1}) + g_3(\text{Catch}_t) + \varepsilon_{t+1}$  | 0.77           | 0.1581 |
|                      | TGAM       | $\text{Cod}_{t+1} = g_1(\text{Catch}_t) + \varepsilon_{t+1} + \begin{cases} 2.522 + g_2(\text{Prey}_{t+1}) + g_3(\text{Temperature}_{t-1}), & \text{if NMDS}_t \leq -0.102 \\ 1.371 + g_4(\text{Temperature}_{t-1}), & \text{if NMDS}_t > -0.102 \end{cases}$          | 0.83           | 0.1522 |

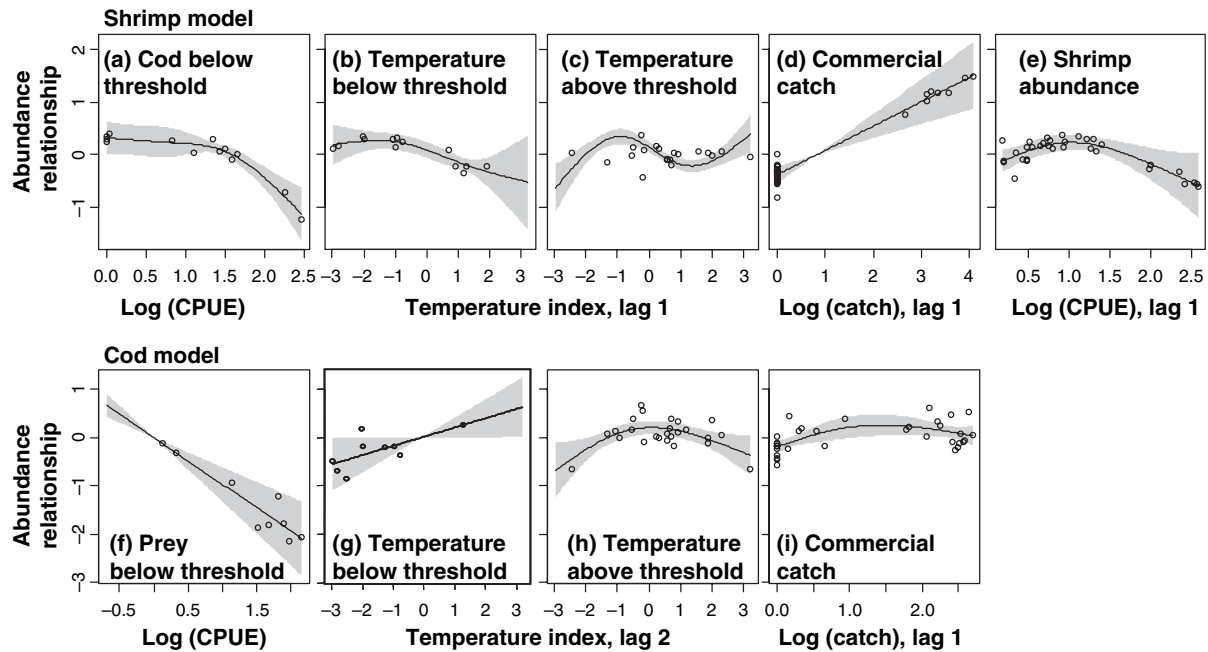
The best model for each species is indicated by the lowest gCV score, which rewards model parsimony and predictive ability. Selected models indicated with gCV values in bold. GAM, Generalized Additive Model; TGAM, Threshold Generalized Additive Model; CPUE, catch per unit effort; gCV, genuine cross-validation.

with significant, but not causal, relationships to abundance (Fig. 3d,f) were retained because these results allowed us to evaluate the effects of fishing and trophic interactions, respectively. Residuals were not autocorrelated in either TGAM, and visual inspection did not suggest deviations from normality or signs of heteroscedasticity, indicating good fits with data.

**DISCUSSION**

While coincident climate regime shifts and ecological phase transitions are well recognized in the Pacific Ocean, the ecological processes involved remain very poorly understood (Chavez *et al.* 2003). In addition to being an important issue of basic ecology, a mechanistic understanding of climate-forced phase transitions is critical for improved fisheries management, as phase transitions are economically and socially devastating to fishing communities even when productive new fisheries are created by the transition (Hamilton *et al.* 2004). The nonlinear relationship between climate state and top–down control in Pavlof Bay (Fig. 2a) is an example of a process that may lead to unexpected ecological reorganizations in response to climate change (Schmitz *et al.* 2003), so the mechanistic link between the 1976/1977 climate regime shift and ecological change that we document may serve as a case study for understanding the possibility of abrupt responses to climate change in other ecosystems. Although causation is difficult to determine in observational data sets, the simultaneous switch from bottom–up to top–down control and transition to a prey-poor state (Fig. 2b), coupled with the change in the set of factors regulating prey abundance (Fig. 3), lead us to conclude that the climate-regulated switch from bottom–up to top–down control was an important cause of the Pavlof Bay phase transition. The timing of the threshold changes in population regulation (1981 for cod and 1984 for pink shrimp) is consistent with the timing of the phase transition; community change became noticeable *c.* 2 years after the regime shift, and continued into the mid- or late-1980s (Anderson & Piatt 1999; Litzow 2006). Because the Pavlof Bay community reorganization was similar to that occurring across other areas of the Gulf of Alaska (NMDS axis 1 in Pavlof Bay and other areas correlated at  $r = 0.91$ ), we conclude that the climate-regulated oscillation in trophic control (Fig. 2) and change in the set of factors regulating predator and prey populations (Fig. 3) that we observed in Pavlof Bay were important causative mechanisms for ecological reorganization across the Gulf of Alaska.

To our knowledge, this study is the first empirical demonstration of climate-regulated trophic oscillations and community reorganization in a marine ecosystem at the scale of Pavlof Bay ( $10^3 \text{ km}^2$ ) and, by association, the Gulf



**Figure 3** Threshold models of population correlates for pink shrimp (a–e) and Pacific cod (f–i) in Pavlof Bay, Alaska, showing differential population control above and below threshold in community composition corresponding to community phase transition (non-metric multidimensional scaling axis 1). Significant negative predator–prey relationships below community threshold for shrimp (a) and cod (f) indicate top–down control early in time series, but trophic interactions were not significant in either model above threshold ( $P > 0.1$ ). Temperature effects were different for both shrimp (b and c) and cod (g and h) above and below threshold. Factors showing continuous relationships across the time series were commercial catch (d) and population size (e) for shrimp and commercial catch (i) for cod. Prey abundance in (f) is grand mean of standardized catch for five prey species. Solid lines indicate smoothed nonparametric trends, grey areas indicate 95% confidence intervals around trends. Temperature index is first principal component of summer and winter values from two regional time series.

**Table 3** Test statistics for best models of pink shrimp and cod abundance correlates: estimated significance of smoothed terms

| Response variable | Term                                   | NMDS value    | Estimated degrees of freedom | $F$   | $P$ -value |
|-------------------|--|---------------|------------------------------|-------|------------|
| Log shrimp CPUE   | Log cod CPUE                           | $\leq -0.005$ | 2.57                         | 9.82  | 0.0003     |
|                   | PC <sub>temp</sub> lag 1 year          | $\leq -0.005$ | 1.99                         | 4.59  | 0.01       |
|                   | PC <sub>temp</sub> lag 1 year          | $> -0.005$    | 2.97                         | 8.55  | 0.0007     |
|                   | Log shrimp CPUE lag 1 year             | All           | 2.46                         | 4.93  | 0.01       |
|                   | Log commercial shrimp catch lag 1 year | All           | 1.000                        | 29.74 | 0.00002    |
| Log cod CPUE      | Log prey abundance                     | $\leq -0.102$ | 1.000                        | 30.69 | 0.000008   |
|                   | PC <sub>temp</sub> lag 2 year          | $\leq -0.102$ | 1.000                        | 4.14  | 0.05       |
|                   | PC <sub>temp</sub> lag 2 year          | $> -0.102$    | 2.365                        | 4.45  | 0.01       |
|                   | Log commercial cod catch lag 1 year    | All           | 2.001                        | 3.74  | 0.02       |

NMDS value refers to threshold parameter for TGAM model.

NMDS, non-metric multidimensional scaling; TGAM, Threshold Generalized Additive Model; CPUE, catch per unit effort.

of Alaska ( $1.9 \times 10^5 \text{ km}^2$ ). Experimental manipulations have previously shown that changing trophic control can produce phase transitions in very small ( $10^{-6}$  to  $10^{-2} \text{ km}^2$ ) terrestrial ecosystems (Schmitz 2007). With regard to marine ecosystems, Hunt *et al.* (2002) have proposed the oscillating control hypothesis (OCH) as a mechanism to explain ecological reorganization in the south-east Bering Sea.

Specifically, the OCH invokes alternation between top–down and bottom–up control of juvenile groundfish survival triggered by sea ice-regulated changes in the timing of the spring bloom. The OCH remains untested, but our results support that hypothesis to the extent of demonstrating that switches in trophic control can cause sudden reorganizations of marine ecosystems. However, the specific

mechanism of the OCH is not applicable to the Gulf of Alaska, which is almost entirely ice-free.

Change in trophic control following the removal of consumers is apparently the mechanism underlying phase transitions caused by overfishing (Hughes 1994; Choi *et al.* 2004; Dulvy *et al.* 2004; Frank *et al.* 2005), so our results suggest that marine ecosystem phase transitions caused by different primary external mechanisms (overfishing and climate change) share the same internal mechanism (trophic control). These results also show how direct climate effects on cod abundance (Fig. 3g) apparently restructured the Pavlof Bay ecosystem, which underlines the ecological importance of direct climate effects on top predators (Post *et al.* 1999; Voigt *et al.* 2003). We have no information on the mechanisms behind the relationship between temperature and cod abundance. However, similar climate–abundance relationships have begun to lead to detailed mechanistic understanding of climate effects on Atlantic cod (*Gadus morhua*; Portner *et al.* 2001; Drinkwater 2005). In the Pacific, hypotheses for climate effects on cod abundance include warming-mediated shifts in the timing of peak zooplankton abundance that increased larval cod survival (Anderson & Piatt 1999) and temperature-specific cod migration on interannual and longer time scales (Ciannelli & Bailey 2005).

While climate forcing is often considered as a bottom–up mechanism in marine ecosystems (Frederiksen *et al.* 2006; Greene & Pershing 2007), our results show how climate change may act either through direct effects on populations (Fig. 3b,g), or by changing the nature of trophic control within the system (Fig. 2a). Linear analyses of spatial patterns of temperature and trophic control in the North Atlantic have previously demonstrated temperature regulation of trophic control over different areas (i.e. top–down control in colder areas and bottom–up control in warmer areas; Worm & Myers 2003; Frank *et al.* 2006). However, we believe that our observation of strongly nonlinear temporal covariation in temperature and trophic control (Fig. 2a) is novel. This type of nonlinear relationship between external forcing mechanisms and ecological processes is a necessary condition for unstable equilibria in ecosystem dynamics (Scheffer & Carpenter 2003; Hsieh *et al.* 2005), and nonlinear analyses of changing trophic control may help to elucidate the mechanisms underlying phase transitions in other ecosystems.

These results also have important implications for the debate over the relative importance of top–down and bottom–up effects in marine ecosystems. Even though top–down control apparently contributed to the transition to a prey-poor state in Pavlof Bay, strong top–down control appeared in our data only for the transition period between states (Fig. 2b). Thus, if the time series covered only the final community state, we would conclude that the system

was under bottom–up or weak trophic control, even though the predator-rich, prey-poor state was apparently established by top–down control. A similar pattern has been observed in the North Atlantic, where top–down effects were apparent only after overfishing largely removed Atlantic cod (Worm & Myers 2003; Frank *et al.* 2005). In both of these instances top–down control was, paradoxically, difficult to detect if the only data available came from an ecosystem state structured by top–down control. Thus, a full understanding of the nature of trophic control in ecosystems prone to phase transitions (e.g. kelp forests; Halpern *et al.* 2006) may require observation through a full transition from one alternate state to another. The rapid return to bottom–up control in Pavlof Bay following the top–down transition period (Fig. 2) is consistent with the view that ecosystems are fundamentally structured by bottom–up forces in the absence of strong perturbations (Strong 1992; Frank *et al.* 2006). Weaker trophic interactions later in the final community state (Fig. 2) are likely the result of cod switching to alternate prey as shrimp and capelin became scarce (Yang 2004).

Another important issue in understanding phase transitions in the Gulf of Alaska and other marine ecosystems is the nature of interaction between fishing and climate effects. Overfishing has been proposed as the major cause of collapse of Gulf of Alaska crustacean stocks in the late 1970s and early 1980s (Orensanz *et al.* 1998). However, while commercial shrimp catches were declining in some areas of the Gulf of Alaska prior to the 1976/1977 climate regime shift, indicating that overfishing was likely depressing stocks before the effects of the regime shift were felt (Orensanz *et al.* 1998), shrimp abundance in Pavlof Bay was stable until cod abundance increased (Fig. 1d). Our TGAM results show a linear positive correlation between pink shrimp abundance and commercial shrimp catches in the previous 12 months (Fig. 3d), which is not consistent with the hypothesis that overfishing was the leading cause of Pavlof Bay shrimp declines. While overfishing effects are often relatively easy to demonstrate, the mechanisms linking climate change to stock status are often purely speculative, making rigorous comparison of fishing and climate effects impossible (Orensanz *et al.* 1998). Fisheries-independent abundance data from Pavlof Bay allowed us to demonstrate empirically how trophic control may be regulated by climate (Fig. 2a), and also to assess simultaneously the importance of fishing, direct climate effects and trophic control in this ecosystem (Fig. 3). These results show that ecological change related to the climate regime shift were sufficient to produce a phase transition even in areas, such as Pavlof Bay, that were not experiencing exploitation-related stock declines. This example may provide a useful template for understanding the factors regulating

exploited stocks during transitions between alternate states in other marine ecosystems.

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