Untangling the relationships among climate, prey and top predators in an ocean ecosystem

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ABSTRACT: Successful ecosystem-based conservation of marine resources can benefit from quantitative indicators of ecosystem productivity, particularly if such indicators quantify and incorporate the relationships between physical and biological components of the ecosystem simultaneously. Despite widespread explorations of relationships between physical processes particularly important to the ocean system (e.g. wind indices, advection and retention of coastal waters, sea surface temperature, coastal sea level and the temporal aspects of these factors) and resulting biological responses, explicit understanding of mechanistic connections often remains elusive. We use path analysis and partial least squares regression to visualize and quantify links between biological and physical components in the California Current ecosystem and to predict reproductive success at 3 trophic levels. We examine the applicability of this approach using a hierarchical pattern of environmental indices, relationships previously described in the literature and quantitative measures of zooplankton, fish and seabird productivity. We show that each trophic level and community production can be described using environmental and biological data in a manner that provides a comprehensive evaluation of physical and biological connectivity and mechanisms. Importantly, our approach to modeling an ecosystem represents a practical middle ground between simple correlative methods typically employed and a perhaps unattainable complete mechanistic understanding of all physical and biological mechanisms regulating variability in reproductive success.

KEY WORDS: Common murre · Auklet · Krill · Rockfish · California Current · Climate

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INTRODUCTION

Proponents of ecosystem-based conservation approaches cite the need for unambiguous, quantifiable and predictive measures of ecosystem state and flux (Murawski 2000, deYoung et al. 2004, Pikitch et al. 2004). Along the California Current, a wide range of physical indices have been used as proxies for unspecified mechanisms that drive the production of zooplankton, fish and seabirds. These include upwelling wind indices (Croll et al. 2005), turbulence (Lasker 1981, MacKenzie 2000), advection and retention of

coastal waters (Bakun & Parrish 1982), sea surface temperature (Logerwell et al. 2003), coastal sea level (Chelton et al. 1982) and the temporal aspects of these factors (Bertram et al. 2001). Such information is increasingly applied. For example, the California sardine *Sardinops sagax* harvest guidelines are based on sea surface temperature (Jacobson & MacCall 1995), and projections of sablefish *Anoplopoma fimbria* recruitment are based, in part, on indices of coastal sea level (Schirripa & Colbert 2006). Yet, explicit understanding of causal physical processes on production has been elusive and thus the potential for relation-

ships to break down in different steady environmental states (regimes, Bond et al. 2003) threatens applications and predictive power. Here, we explore more complete sets of biotic and environmental factors related to production at various trophic levels through to top predators and provide more robust conceptual and predictive models of ecosystem state and function.

We developed data-driven models based on demonstrated relationships within the environment and between the environment and production of zooplankton, shortbelly rockfish *Sebastes jordani*, and top predators (the common murre *Uria aalge*, Cassin's auklet *Ptychoramphus aleuticus*, and the rhinoceros auklet *Cerorhinca monocerata*), which represent trophic chains within the central California Current ecosystem. By design, our approach incorporates multiple indicators of the physical and biological environment in order to both quantify and visualize how each of these variables relates to the other. For example, euphausiid and copepod (the primary components of our zooplankton data set) dynamics are expected to relate directly to environmental forcing (Marinovic et al. 2002, Brinton & Townsend 2003, Dorman et al. 2005). They also represent dominant prey for shortbelly rockfish (Chess et al. 1988), as well as a great many other *Sebastes* spp. (Brodeur & Pearcy 1984, Reilly et al. 1992). Further, juvenile shortbelly rockfish are a key prey item for many piscivores in this region (Ainley et al. 1996, Mills et al. 2007).

The coupled dynamics of rockfishes and seabirds along central California are representative of the greater food web dynamics and of the ocean condition (Miller & Sydeman 2004, Mills et al. 2007). For many resident central California piscivorous seabirds, as much as 90% of the chick diet is comprised of juvenile rockfish during the late spring and early summer breeding seasons. Shortbelly rockfish, an unfished species, generally accounts for more than two-thirds of the juvenile rockfish identified in the diets (Ainley et al. 1993, Sydeman et al. 2001, Miller & Sydeman 2004). However, there is considerable interannual and interdecadal variability in the proportion of rockfish in seabird diets. Throughout the 1990s, foraging rates on juvenile rockfish by central California seabirds declined for both exploited and unexploited rockfish species, primarily in response to changes in ocean conditions associated with poor recruitment for rockfish (Sydeman et al. 2001, Miller & Sydeman 2004, Mills et al. 2007). As an ecologically important but unfished resource, shortbelly rockfish is a natural control for assessing the interactions between environment and prey availability on their predators. Production of shortbelly rockfish also covaries with production of exploited rockfish spawned in the central California region (Field, unpubl. data); therefore, this species is

an indicator of reproductive success for a broader ecological community. Similarly, production of the seabirds we examined covary with the productivity of other breeding seabird populations in the California Current (Sydeman et al. 2001).

MATERIALS AND METHODS

We analyzed time series of biological data from the central California coastal region (Fig. 1). Spring zooplankton abundance, which was used as both an estimate of production and abundance, was estimated using geometric means of tows across daily values of small plankton volume (all plankton with a displacement of <5 ml, ml 1000 m^{-3} to 210 m depth) for March, April and May California Cooperative Oceanic Fisheries Investigations (CalCOFI, calcofi.org) surveys (Fig. 1). Geometric mean is appropriate when, like zooplankton data, variability in the data is substantial and the biological response of predators (e.g. feeding
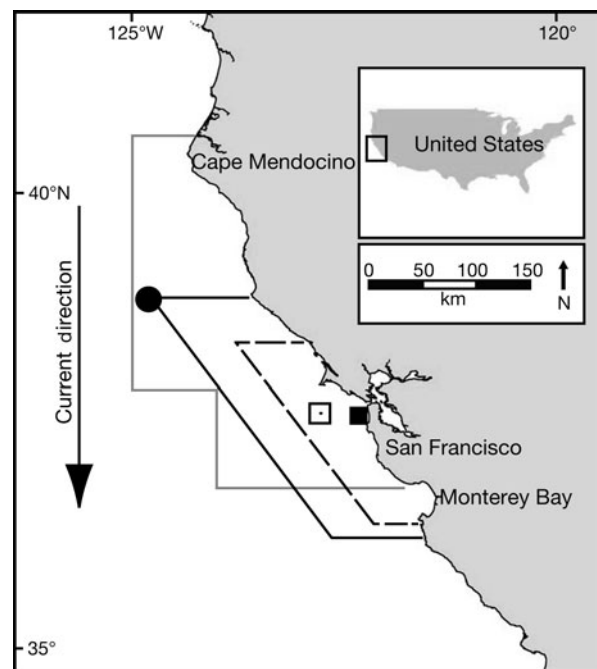

Fig. 1. Central California coast. Bounds represent areas from which California Cooperative Oceanic Fisheries Investigations (CalCOFI) (black), NOAA (dashed black) trawl survey data, and the 1° resolution International Comprehensive Ocean-Atmosphere Data Set (ICOADS) data (grey) were collected. Also shown are the Pacific Fisheries Environmental Laboratory (PFEL) shore station (●), coastal sea level gauge (■) and Southeast Farallon Island (□). Unaveraged temporal resolution of the data series—ICOADS data and PFEL shore station and coastal sea level data: monthly; CalCOFI data: daily; NOAA trawl data was an individual-estimated value for spring

behavior) is nonlinear (Thayer & Sydeman 2007). We restricted CalCOFI data to that from along the nearshore outward to ca. 100 km offshore. Zooplankton abundance data from years when the CalCOFI survey was not available in the region of central California (Fig.1, one-third of years represented) were estimated from a regression on all stations in southern California weighted by the number of stations sampled each year (1951 to 2005, $r^2 = 0.46$, $p < 0.0001$, N = 35). We used the years 1972 to 2005 for central California estimates of production and abundance (less 1973,1974, 1976 and 1977 for which there were no estimates or means by which to approximate central California values).

Juvenile shortbelly rockfish regional production variability in central California was estimated by deviations around a Beverton-Holt stock–recruitment relationship (Field et al. 2007, Fig. 1). This is equivalent to estimating the amount of variability in recruitment not accounted for by spawning stock biomass. The values we used for production were the standardized log-normally distributed residuals around an assumed spawner–recruit relationship (years used, 1975 to 2005). The residuals were free parameters that were estimated in an age- and size-structured statistical model, Stock Synthesis 2, which is the modeling framework used for most USA Pacific coast rockfish stock assessments. As shortbelly rockfish are an unfished species, most of the information regarding year-class strength was derived from a juvenile trawl survey (Sakuma et al. 2006) and from predator studies, rather than commercial size or age data, although limited size composition data from fishery-independent surveys were also incorporated into the model. Importantly,

when shortbelly rockfish was used as a prey item in our models, we focused on total abundance data rather than production variability. As the Field et al. (2007) model includes common murre food habits data as an index of Age-0 abundance, the abundance data used in the common murre analyses presented in the current work is similar to Field et al. (2007), but was based solely on the juvenile rockfish survey index of abundance from 1983 to 2005.

Production of common murre (1975 to 2005), Cassin's auklet (1972 to 2005) and rhinoceros auklet (1986 to 2005) were estimated as the average number of chicks fledged from breeding pairs in a season from observations on Southeast Farallon Island (Fig. 1). Methodology for bird observations follows Sydeman et al. (2001). Importantly, common murre continue parental care for ca. 1 mo. following fledging. Therefore, productivity, as measured here for common murre, is a scalar rather than a direct measure of productivity. Common murre and rhinoceros auklet lay only 1 egg per breeding season; therefore, production estimates are proportions and required arcsin transformation to meet the assumptions of linearity.

We used environmental data for 1972 to 2005 (1978 was removed because values for wind-stress curl were not available, Fig. 1). Table 1 shows the time series and sources of each environmental data series. The environmental variables we examined were not a subset from an exploratory statistical search but, rather, we decided upon them before analyses because together they represent various specific aspects of the system. The spring transition date, when the coastal system became dominated by wind-driven upwelling, was

Table 1. Eight environmental variables used to characterize the ocean environment of central California (Fig. 1) were collected from various sources for the years 1972 to 2005. Variables were averaged within the region and into spring (March, April and May) and summer (June, July and August) values. These seasonal values (15 variables in total) were included in season-specific path analyses, and those variables with effects were included in partial least squares regression analyses to model variation in productions. The variables, identifiers used in figures, their sources and associated noteworthy comments are listed

Variable description	Variable identifier	Source
Transition date[a]	Transition	Schwing et al. (2006)
Easterly pseudo-wind stress[b]	East stress	Worley et al. (2005)[c]
Northerly pseudo-wind stress[b]	North stress	Worley et al. (2005)[c]
Non-directional wind speed; scalar wind speed	Wind speed	Worley et al. (2005)[c]
Upwelling	Upwelling	Pacific Fisheries Environmental Laboratory station[d]
Curl[e]	Curl	Pacific Fisheries Environmental Laboratory station[d]
Sea surface temperature	SST	Worley et al. (2005)[d]
Coastal sea level height	CSL	University of Hawai'i Sea Level Center station, San Francisco, CA

[a]Used only for spring
[b]Converted to meteorological notation
[c]International Comprehensive Ocean Atmosphere Data Set using 1° resolution averages
[d]39° N, 125° W (see Fig. 1)
[e]Spring values in 1978 were unavailable

estimated based on initiation and stability of up-welling (Schwing et al. 2006). Easterly and northerly wind stresses (meteorological notation) and sea sur-face temperatures were obtained from the 1° monthly averaged values from International Comprehensive OceanAtmosphere Data Set (ICOADS, http://dss.ucar.edu/datasets/ds540.1/data/msga.form.html; Worley et al. 2005). Monthly-averaged values of upwelling and wind-stress curl, measures of production, retention along the coast and convergence near the coast were obtained from a NOAA shore station central to our region of interest (www.pfeg.noaa.gov). Finally, monthly-averaged values of coastal sea level, which relates to current strength and the concomitant effects of environmental conditions, was obtained from the University of Hawai'i Sea Level Center located cen-trally to our region of interest (http://uhslc.soest.hawaii.edu). Environmental values were averaged for spring (March, April and May) and summer (June, July and August). While many of these indices covary, each one represents a distinct feature of ocean condition and has been identified as important to the production of some element of the ecosystem. Our approach offers a comprehensive method for quantifying statistical relationships between these physical variables and the biological responses.

We used path analysis to identify correlations be-tween biotic and environmental variables, determine the direct and indirect relationships of variables to pro-duction and visualize likely mechanisms forcing pro-duction at 3 trophic levels (Wright 1934, Mitchell 1992, Petraitis et al. 1996). Importantly, not only does path analysis identify correlations between variables but each variable can have both direct and indirect effects on other variables. Therefore, we can separate the likelihood that a variable has both a positive and neg-ative effect on another variable (e.g. a variable may have a positive direct effect on production while its total effect, transferred through a series of other vari-ables to production, may be negative). Path models were built separately for spring and summer periods to better model the temporal variability in our system. The structure of path models was determined *a priori* based on our understanding of oceanographic and trophic interactions. Before analysis, the data was stan-dardized such that paths were represented as stan-dardized slope coefficients. All paths among variables were considered and stepwise regressions (or direct correlations in the case of exogenous variables) were used to determine the significance of each path.

The first stepwise regression was performed with the production variable as the dependent variable and all other variables were independent. The variable that was nearest the production variable (its position in the structural equation model) and shown to be sig-nificantly related to the production variable was then treated as the dependent variable with all variables above it in the model structure as independent. The pattern was continued until only exogenous vari-ables remained. Lastly, the significance of correlations among exogenous variables was evaluated. Fig. 2 shows how the sequence progressed. We relied on a $p < 0.10$ selection criteria for inclusion in regressions and $p < 0.05$ to consider the complete regressions sig-nificant. To evaluate the effects of collinearity in the path models, the condition indices were examined for all regressions; the overwhelming majority of values were near 1.0 and none were greater than 4.0, indicat-ing collinearity had minimal affect on interpretation of path models (Myers 1990, Petraitis et al. 1996). Also, using a goodness of fit test, we showed that all esti-mated path models were not dissimilar from the struc-ture of the observed data ($p > 0.05$, procedure CALIS, SAS Institute 2004)

Based on path results, we incorporated variables with direct and indirect relationships with production into a partial least squares regressive model to develop predictive relationships (Geladi & Kowalsky 1986, pro-cedure PLS, SAS Institute 2004). Partial least squares models combined the variables across seasons such that a single and inclusive predictive relationship could be built. Partial least squares reduces the dimen-sions of the independent data set and maximizes its relationship of the first latent variable to the dependent data set while still maintaining relationships between individual independent variables. The first latent vari-able of the independent data set resulting from partial least squares can then be used to model the biological parameter with simple linear regression (Geladi & Kowalsky 1986). The combined approach of path ana-lysis and partial least squares regression results in pre-dictive models that allow for realistic interpretation of statistically and biologically significant interactions (Wells et al. 2007). We demonstrate the capacity of the models to predict production of a trophic level in a given year using a cross-validation procedure [mean square error of prediction (MSEP) (Geladi & Kowalsky 1986)]. After appropriate transformation of the data, all assumptions of linear regression are met. The variable with the shortest time series in any analysis determines the length of the time series used in each analysis.

RESULTS

Zooplankton, shortbelly rockfish and common murre

Zooplankton was modeled significantly by the path analysis, showing that zooplankton abundance in a given year could be fit directly using sea surface tem-
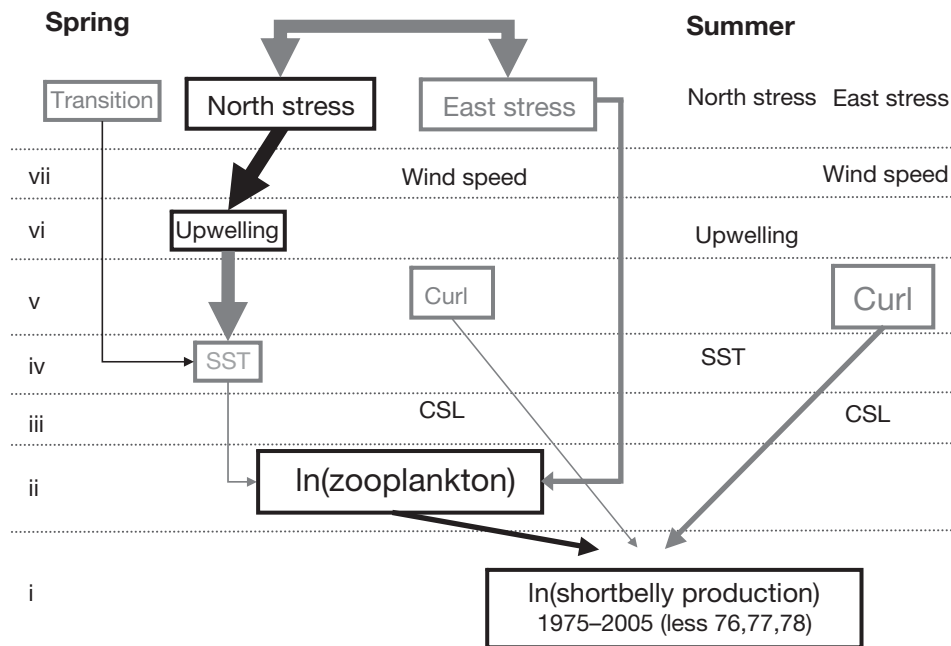
Fig. 2. Zooplankton and *Sebastes jordani.* Spring and summer path analyses on shortbelly rockfish production (log-normally distributed deviations around the spawner–recruit curve) (Field et al. 2007). Arrows indicate standardized positive (black) and negative (grey) slope coefficients shown as 3 line weights representing estimates of 0.20 to 0.40, 0.41, 0.60 and 0.61 to 0.80. Variables are shaded to represent positive (black) and negative (grey) ultimate relationships with shortbelly rockfish production (calculated by summing the cumulative slope coefficients along each direct path to shortbelly production). Three font sizes represent total correlations of 0 to 0.20, 0.21 to 0.40, and 0.41 to 0.60. We *a priori* arranged variables for path analysis to represent causation (e.g. wind drives upwelling) and/or accumulated variance (e.g. coastal sea level, CSL, represents accumulation of variation in all previous variables). Path models were built separately for spring and summer to interpret seasonal differences. Seven successive forward stepwise regressions on standardized data were performed (represented by Roman numerals). SST: sea-surface temperature
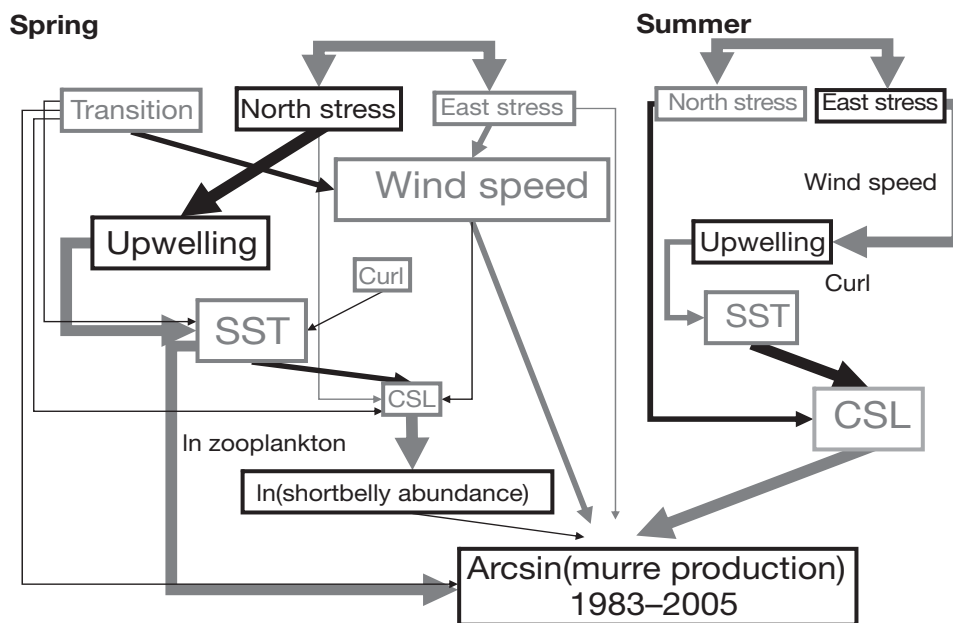

Fig. 3. Zooplankton, *Sebastes jordani*, and *Uria aalge*. Results for spring and summer path analyses for common murre production. Legend for Fig. 2 can be applied except an additional regressive step was done for shortbelly rockfish abundance, and there is an additional font size representing total effects of 0.61 to 0.80

perature and easterly wind stress. We do not present the path model for zooplankton here as it is similar to the resulting inset model in the shortbelly rockfish model (Fig. 2).

In addition to a strong direct relationship to their principal prey, zooplankton, shortbelly rockfish pro-

duction was negatively related to curl (offshore transport), suggesting that onshore transport and convergence (decrease in wind-stress curl) in both spring and summer relate to increased productivity (Fig. 2).

Production of common murre was positively related to juvenile rockfish abundance (Fig. 3). Spring scalar
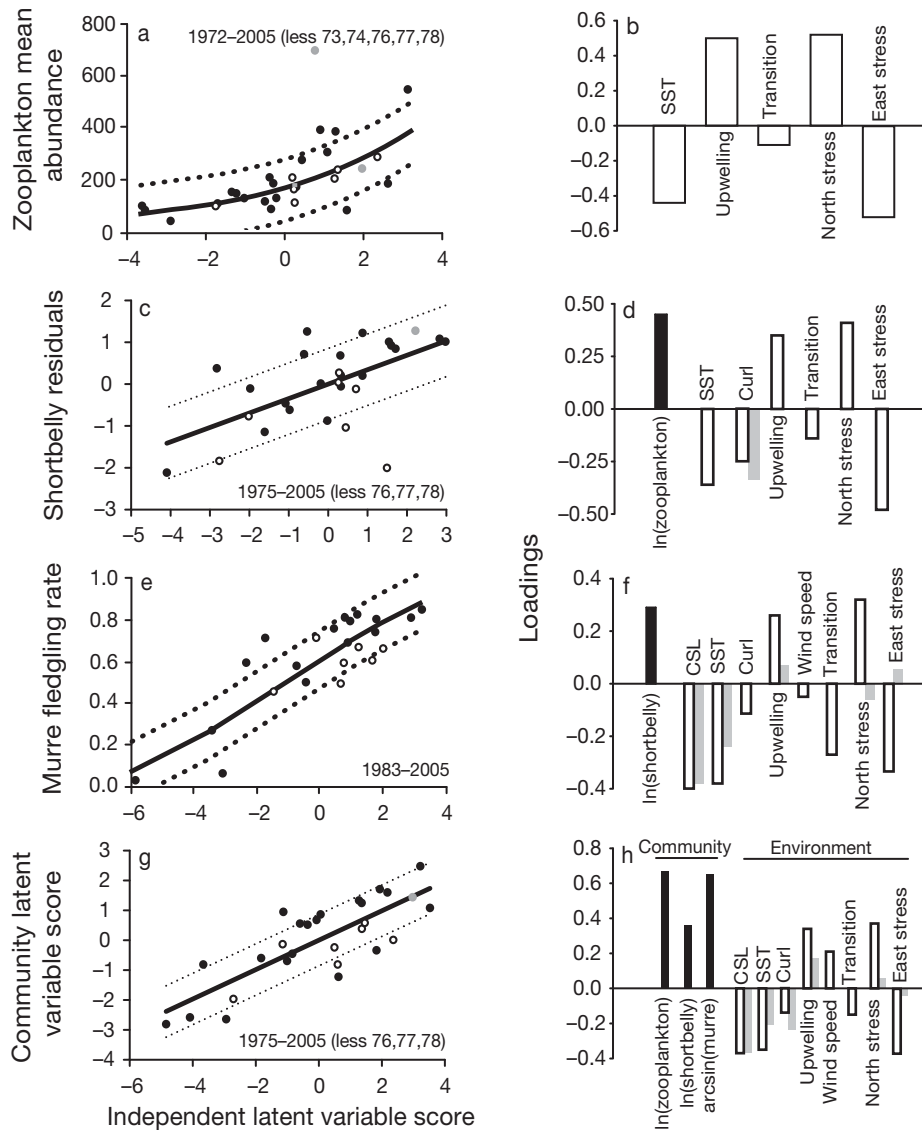

Fig. 4. Zooplankton, *Sebastes jordani*, and *Uria aalge*. (a,c,e) Model fits to geometric mean values of zooplankton abundance, log-normally distributed shortbelly production deviations and common murre fledgling rate (production). (g) Fit of first latent variable of data set made up of 3 production vectors to the first latent variable of environmental data set. Scatter plots show data from 3 reputed environmental regimes. Environmental regimes: before 1978 (●), 1978 to 1998 (●), 1999 to 2005 (○). (b,d,f) Loadings of each variable included in the partial least squares regression model to fit production of 3 trophic levels [ln(zooplankton abundance), standardized ln(shorbelly production) and arcsin(common murre production)]. Black bars: biological (prey) loading values; white bars: spring environmental loading values; grey bars: summer environmental loading values. These loadings demonstrate the influence of each variable on the prediction of the dependent variable. (h) Loadings on the environmental latent variable score as well as the loadings on the community latent variable score made up of ln(zooplankton abundance), standardized ln(shortbelly production) and arcsin(commone murre production), shown as black bars. For (a,c,e,g) solid lines indicate predicted relationships and dotted lines indicate square root of mean square error of prediction around that line. CSL: coastal sea level; SST: sea-surface temperature

winds had a direct negative relationship with murre production. Spring easterly wind stresses were negatively related to production. Sea surface temperature was negatively related to production. Possibly, as a spurious result, transition date also had a small direct positive relationship with common murre production. However, the total effect was negative. Finally, reduced summer current strength and its associated conditions (e.g. increased sea surface temperature and decreased upwelling) were associated with reduced common murre production.

When factors having relationships to production of given trophic levels were incorporated into the partial least squares regressions, they yielded significant predictive models (Fig. 4). It is worth noting that the partial least squares regressive approach is unstructured (i.e. no *a priori* arrangement of factors) and combines variables across seasons such that the pattern of loadings on the first latent variable (analogous to a principle component) provides a second evaluation of the relationships among variables deemed significant from the path analysis.

The fit of the first latent variable from the partial least squares approach to zooplankton production was significant ($r^2 = 0.49$, p < 0.0001, N = 29, Fig. 4a,b), and the loadings on the variables on the first latent variable were consistent with total effects calculated from the path analysis. Similarly, shortbelly rockfish production was significantly modeled ($r^2 = 0.35$, p = 0.0008, N = 28, Fig. 4c,d), and the loadings on the first latent variable were consistent with path analysis. Finally, common murre production fit very well to the first latent variable, likely as an integrator of all physical conditions and trophic levels beneath ($r^2 = 0.70$, p < 0.0001, N = 23, Fig. 4e,f).

The partial least squares regressive approach enables us to model the community (i.e. vectors of zooplankton production, shortbelly rockfish production and common murre production) with the environmental data set. Because the community model includes common murre, shortbelly rockfish production was estimated without common murre diet data (the Field et al. 2007 model without common murre diet included). Importantly, shortbelly rockfish production estimated with and without common murre diet were highly correlated ($r^2 = 0.66$, m = 1.1, intercept = 0, p < 0.0001). We fit all the

environmental variables that were shown to have a relationship with any of the 3 trophic levels to the community data set. The community production was fit well by the environmental data ($r^2 = 0.63$, p < 0.0001, N = 28, Fig. 4g,h). The time series of predicted production of the community demonstrated the general applicability of this approach to estimating community production (Fig. 5a).

Rhinoceros auklet

Rhinoceros auklet path models indicated that, directly, zooplankton abundance and shortbelly rockfish abundance in the spring, and coastal sea level, sea surface temperature and upwelling in the summer, could be used to model production variability (Fig. 6).

Partial least squares regression developed for rhinoceros auklet was significant ($r^2 = 0.52$, p = 0.0003,
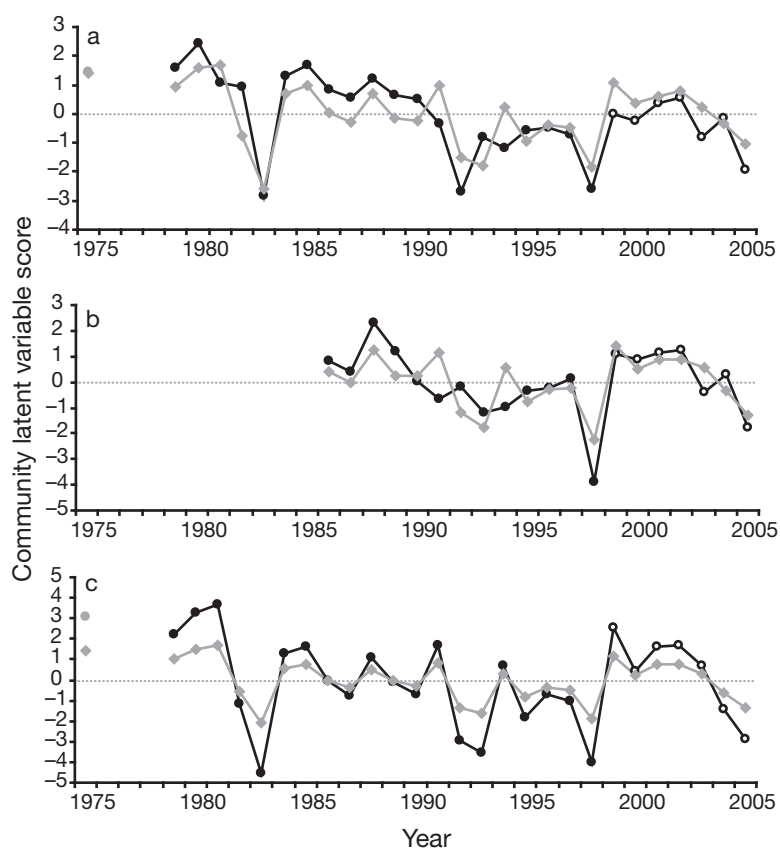

Fig. 5. Zooplankton, *Sebastes jordani*, *Uria aalge*, *Cerorhinca monocerata*, and *Ptychoramphus aleuticus*. Community latent variable scores, generated from partial least squares, plotted as time series over the years for which we have data. Data for (a) common murre, (b) rhinoceros auklet and (c) Cassin's auklet trophic chains. Black: observed community latent variable scores from partial least squares; grey: predicted scores from regression using only environmental latent variable scores as independent values. Environmental regimes: before 1978 (●); 1978 to 1998 (●); 1999 to 2005 (○)
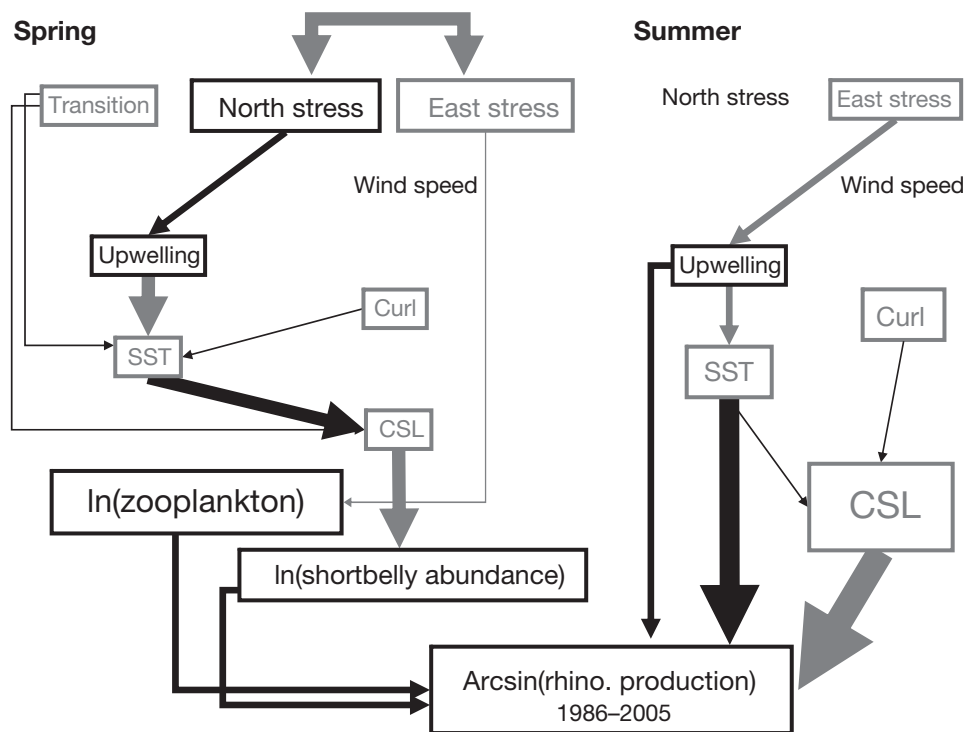
Fig. 6. Zooplankton, *Sebastes jordani*, and *Cerorhinca monocerata*. Results for spring and summer path analyses for rhinoceros auklet production. Legend for Fig. 2 can be applied, except an additional regressive step was done for shortbelly rockfish abundance, there are 2 additional arrow weights representing correlations of 0.81 to 1.00 and 1.01 to 1.20, and there is one additional font size representing total effects of 0.61 to 0.80

N = 20) and a linear model was appropriate (Fig. 7a,b). Community models built on zooplankton, shortbelly rockfish and rhinoceros auklet production vectors were significant. Specifically, using the first latent variable for the environmental data to fit the first latent variable of the 3 production vectors demonstrates that the fit is significant and linear ($r^2 = 0.58$, p = 0.0001, N = 20, Fig. 5b). The results and loadings on the first latent variable of the community matrix (Fig. 7d) are similar to the common murre community model, indicating a similarity of patterns. The time series examination shows that the environmental latent variable can be used to model community production throughout the years for which we have data (Fig. 5b).

Cassin's auklet

Cassin's auklet path models indicated that coastal sea level in spring and summer could be used to model variation in production directly (Fig. 8). Zooplankton did not vary significantly with Cassin's production.

Partial least squares regression developed for Cassin's auklet were significant ($r^2 = 0.46$, p = 0.0001, N = 29) and the fit was linear (Fig. 9a,b). Community models built on zooplankton, shortbelly rockfish and

Cassin's auklet production vectors were significant. Specifically, using the first latent variable for the environmental data to fit the first latent variable of the 3 production vectors demonstrates that the fit is significant and linear ($r^2 = 0.63$, p = 0.0001, N = 28, Fig. 9c). The results and loadings on the first latent variable of the community matrix (Fig. 9d) are similar to the common murre and rhinoceros auklet community models, indicating a similarity of patterns. The environmental latent vector could be used to predict production of the community across the years we examined (Fig. 5c).

DISCUSSION

Model statistics

In the majority of studies examining the relationships between the environment and system dynamics, bivariate or multivariable regressive techniques have been used. Such correlative analyses do not frame the environmental variables examined in the context of their mechanistic roles in the system. The path models we used allow one to interpret the effect of each variable within the structure of other and well-known mechanistic interactions (e.g. northerly wind stress drives up-
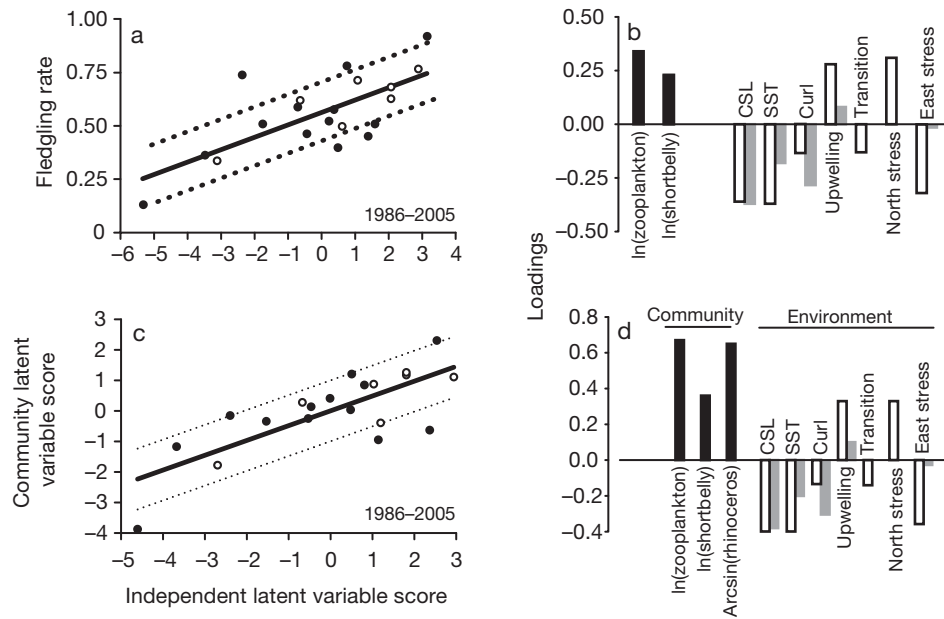
Fig. 7. Zooplankton, *Sebastes jordani*, and *Cerorhinca monocerata.* (a) Model fits of rhinoceros anklet fledgling rate (production) to the first latent variable of the independent data set; (b) loadings of each variable on the first latent variable of the independent data set. (c) Fit of first latent variable of the data set made up of 3 production vectors [ln(zooplankton abundance), standardized ln(shortbelly production) and arcsin(rhinoceros auklet production)] to the first latent variable of environmental data set. (d) Loadings of each variable on the first latent variable of the independent and dependent data sets. Scatter plots show data from reputed environmental regimes. Environmental regimes: 1978 to 1998 (●); 1999 to 2005 (○). For histograms, black bars indicate biological variables, and white and grey bars indicate spring and summer environmental values, respectively. For (a) and (c), solid lines indicate predicted relationships, and dotted lines indicate square root of mean square error of prediction around that line. CSL: coastal sea level; SST: sea-surface temperature
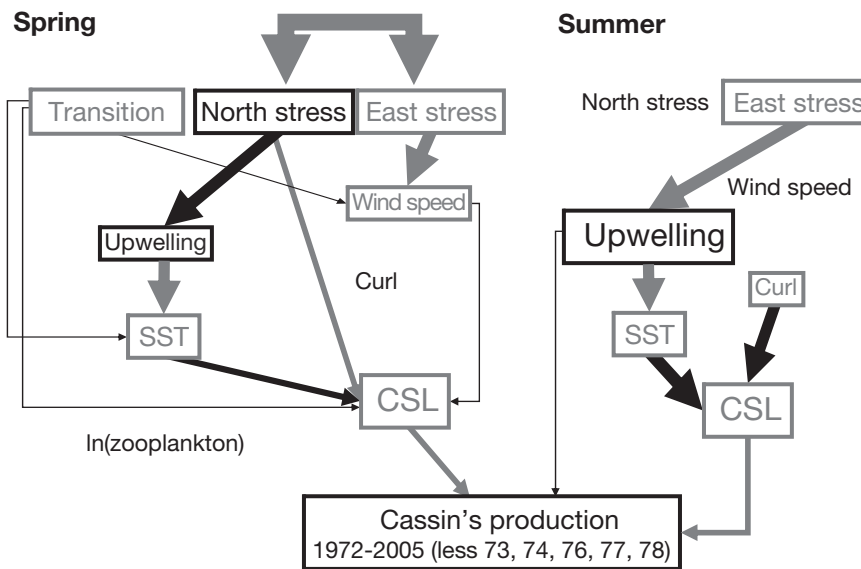

Fig. 8. Zooplankton and *Ptychoramphus aleuticus.* Spring and summer path analyses on Cassin's auklet. Legend for Fig. 2 is appropriate here except there is an additional arrow line weight to represent a standardized slope coefficient of 0.81 to 1.00
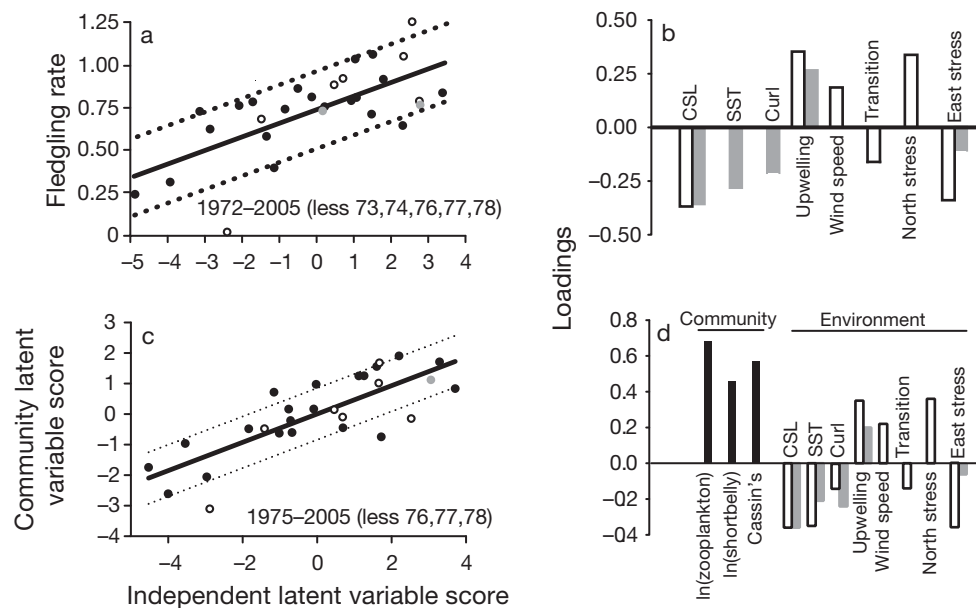
Fig. 9. Zooplankton, *Sebastes jordani*, and *Ptychoramphus aleuticus*. (a) Model fit of Cassin's fledgling rate (production) to the first latent variable of the independent data set; (b) loadings of each variable on the first latent variable of the independent data set. (c) Fit of first latent variable of data set made up of 3 production vectors [ln(zooplankton abundance), standardized ln(short-belly production) and (Cassin's auklet production)] to the first latent variable of environmental data set. (d) Loadings of each variable on the first latent variable of the independent and dependent data sets. Scatter plots show data from reputed environmental regimes. Environmental regimes: 1978 to 1998 (●); 1999 to 2005 (○). For histograms, black bars indicate biological variables, and white and grey bars indicate spring and summer environmental values respectively. For (a) and (c), solid lines indicate predicted relationships, and dotted lines indicate square root of mean square error of prediction around that line. CSL: coastal sea level; SST: sea-surface temperature

welling and both relate to coastal sea level). We chose variables and interactions *a priori* that have been shown to relate to ecosystem productivity. Our work is significant in that we then demonstrated likely causal pathways by quantifying how those variables relate to one another and to production in a lower-to-higher tropic level chain construct. Importantly, unlike previous unstructured stepwise regressions of multiple variables, path analysis forces one to define intercorrelations and, through calculation of total direct and indirect effects, facilitates interpretation of detailed statistical relationships. For instance, both easterly and northerly wind stresses affect production, but when calculating the effect of each it is paramount to consider the correlations between them. This is a significant advancement over the standard multiple regression exploratory approach.

By coupling structural path models with partial least squares regressions, we have attempted to deliver a comprehensive approach that incorporates all variables in a bio-physical and statistically appropriate fashion. As a result, we can now describe, for the first time, why and how a variable such as coastal sea level, which apparently relates to ecosystem variability on multiple trophic levels (e.g. Logerwell et al. 2003,

Schirripa & Colbert 2006), determines productivity. The final model provides what might be described as a quantitative conceptual model of how variables drive productivity.

A desired attribute of predictive models of the relationships between the marine environment and biology is that they would be robust to anomalous years and changes in system state (e.g. regime shifts). For instance, during the course of the time period we examined, there were 3 distinct environmental regimes (Bond et al. 2003, Peterson & Schwing 2003). While environmental interrelationships may vary somewhat between regimes, which would manifest itself here as variability in path model interaction strengths, the mean models we built incorporate a reasonably complete list of variables describing various aspects of the system, and are, therefore, robust to anomalous years or shifts in regime state (Fig. 5a–c). Examination of Figs. 4, 7 & 9 demonstrates that even during prolonged shifts in environmental state our models still fit the data linearly. This is consistent with the results of Hsieh et al. (2005), who demonstrated that the physical condition of the North Pacific evolves in a complicated but apparently linear manner involving the sum of many variables.

In contrast, previous bivariate analyses have failed to be robust to shifts in the environment. As a relevant example, Ainley et al. (1993) demonstrated that upwelling had a parabolic relationship with rockfish production across the years 1973 to 1990, yet with the extension to years 1975 to 2002 the relationship fell apart (Miller & Sydeman 2004). In our analysis, we have developed models in which complex environmental and biological interactions were simultaneously fit, which should diminish the possibility of loss of predictive power through time. This should bode well for management practices over the long term. As 2 examples of management application, (1) the partial least squares regression for shortbelly rockfish can be used to reduce variability around the spawner–recruit curve by incorporating the latent variable as a term in the spawner–recruit model, and (2) the environmental latent variable from the community model can be used as an index of the current state of the system. This is a clear necessity and step forward in the process of ecosystem-based fisheries management.

Zooplankton

The relationships we determined for zooplankton (mostly euphaussids and larger forms) production were consistent with the known biology for the likely species included. Cooler waters and decreased easterly wind stress corresponded with increased zooplankton biomass (Chelton et al. 1982, McGowan et al. 1998). Indirectly, factors affecting sea surface temperature such as transition date, upwelling and northerly winds also had significant effects. Specifically, those conditions that led to cooler more productive waters increased the number of zooplankton. These results demonstrate the links between conditions conducive to nutrient availability (e.g. upwelling) and zooplankton abundance and availability locally.

Rockfish

We examined variability around the spawner–recruit curve to determine the role the environment has on production of rockfish beyond the variability incurred by changes in spawning stock biomass. This was a test between the environment and production. Importantly, for rockfishes, the oceanographic conditions experienced during their pelagic phase dramatically affect recruitment, with year-class strength set by the end of the pelagic period (Ralston & Howard 1995). Therefore, our measure of productivity, while representing only a fraction of the life cycle in which adult abundance is determined, was focused on a critical

period (Ralston & Howard 1995, Tolimieri & Levin 2005).

The amount of available zooplankton prey is a significant contributor to production of juvenile rockfish. This finding is similar to that of Peterson & Schwing (2003) where environmentally-mediated copepod biomass in the northern California Current was positively related to the coho salmon *Oncorhynchus kisutch* returns in Oregon. In addition to zooplankton availability and factors determining zooplankton abundance, retention of juvenile rockfish probably determines a significant amount of variability in rockfish productivity. That is, there is a direct negative relationship to positive wind-stress curl (offshore transport). Similar findings were demonstrated for the larval hake *Merluccius productus* (Bailey 1981). That curl had a direct relationship with rockfish, yet none with zooplankton, suggests that variability in curl directly affects the distribution of the rockfish, possibly through local retention along the coast in the late spring before settlement of pelagic juveniles during summer, and through convergence, or accumulation of rockfish and their food sources as they are transported toward the coast (Farrell et al. 1991, Bjorkstedt et al. 2002).

In models of upper trohic level predators, using rockfish as prey, we used actual abundance estimates as this is what logically relates to predator production. The spawner–recruit residuals would tell us less about effects of juvenile rockfish abundance on seabird productivity because the dominant feature in this relationship is spawning stock biomass. This may also explain why some of the relationships found in our analyses of juvenile rockfish productivity were not maintained within models using rockfish as prey (Figs. 3 & 6).

With use of partial least squares regression, variables shown to be significant in the path models were used to predict rockfish productivity. In agreement with path analyses, zooplankton abundance in spring was the strongest contributor to estimating the production of rockfish.

Common murre

Male murres take their offspring to sea when only ca. one-third grown, at ~25 d of age (Tuck 1960). Male murres care for these young for a period of up to 2 mo after departing the colony. Therefore, in accordance with our interest in variables affecting productivity, be it for zooplankton, fish or seabirds, we looked at an index of murre productivity for an early stage of their life cycle. This approach is not sufficient to explore factors that regulate seabird population size.

The common murre model provided insight into many interactions with the environment. For instance,

we showed that wind speed in the spring, before chick-rearing, was negatively related to reproductive success, as we have it defined (survival to age ~25 d). As wind is related to turbulence, this suggests that turbulence may diminish reproductive success, presumably by interfering with foraging. This is not a new idea, but here we have defined how and when turbulence may be a factor. Birkhead (1976) showed that common murre foraging success is reduced during turbulent (windy) conditions. Among other reasons put forth by Birkhead (1976), turbulence in our system may relate to dispersal of shoaling forage fish, in this case juvenile rockfish schools.

We found a strong direct inverse relationship between spring sea surface temperature and murre productivity. It is possible that common murres use sea surface temperature as a cue for timing of breeding. Boekelheide et al. (1990) demonstrated that the timing of egg laying was related to sea surface temperatures. Cooler temperatures are indicative of upwelling or early onset of upwelling, which may be a contributing factor. We are cautious that sea surface temperature may simply integrate the variance of all the previous variables in the model and be solely a statistical relationship. However, if it were only a statistical relationship, the impact of sea surface temperature likely would be indirect and accounted for through the existing path from coastal sea level. Interestingly, that is exactly the case during the summer after the period of egg laying (Fig. 3).

As was expected from previous work (Ainley et al. 1995, Sydeman et al. 2001), common murre production was also driven by rockfish abundance. We did not have estimates of prey abundance during the peak of chick-rearing in June each year, but apparently the data from May reasonably reflect what is available in June. This correspondence may relate to the timing of prey switching through the seasons. Specifically, rockfish settle (sink) out of the upper water column during the summer, which relates to the timing of prey switching from rockfish to alternate prey items later in the summer (Ainley 1990, Ainley et al. 1990).

Using the variables found to be significant in the common murre path analysis and incorporating them in partial least squares regression resulted in similar findings. Prey (rockfish abundance) was a heavily weighted component of the model, along with wind stress, timing of upwelling onset, the amplitude of upwelling and integrative factors such as sea surface temperature and sea level. Interestingly, the impact of wind speed was of lesser importance in the partial least squares regression, whereas its effect was large in the path model. It is also important to acknowledge that transition date, while ultimately negatively related to murre production in the path model, had a small direct positive effect. We are unclear of the reasons behind this inconsistency.

Rhinoceros auklet

Rhinoceros auklet models give insights into the life history of this species in central California. First, it is apparent that prey (both zooplankton and rockfish) had direct positive relationships with rhinoceros auklet production; like the common murres, this may reflect a correlative relationship between spring and summer prey dynamics. While rhinoceros auklets are primarily piscivorous during breeding, and only feed their offspring fish, they have been noted to consume zooplankton prior to breeding (Ainley & Sanger 1979).

Rhinoceros auklets have a relatively long incubation and offspring-rearing period. Upwelling in the summer had a strong positive effect on production. Upwelling in the coastal system is a primary mechanism by which productivity of the system is driven. As rhinoceros auklets have a long offspring-rearing period during summer, continued upwelling would be expected to be significant, whereas, common murre, which have a shorter offspring-rearing period, would have their production less tied to specific oceanic features during summer. Partial least squares regression fit the rhinoceros auklet production data well and reaffirmed the results from path analyses, that prey abundance was the primary variable determining reproductive success.

Cassin's auklet

Surprisingly, Cassin's auklet productivity was modeled exclusively by environmental variables. Cassin's auklets are primarily planktivorous and production has been shown to vary tightly with euphausiids abundance (Abraham & Sydeman 2004). Yet, Cassin's auklets are selective foragers and there is prey switching between the 2 dominant euphausiid species in the middle of the reproductive season (Abraham & Sydeman 2004). Our estimate of zooplankton abundance certainly is dominated by euphausiids and copepods, but makes no discrimination in the actual species composition; in addition, salps, which are not eaten by the auklets, may be irregularly sampled. It is likely that the broad category of zooplankton is insufficient to capture variability between Cassin's auklet production and the abundance of their preferred prey. This may also point to the reason we did not detect any relationship between common murre and zooplankton even though they have also been shown to feed on zooplankton prior to the breeding season (Sydeman et al. 1997).

Regardless, we captured much of the variability in production of Cassin's auklet using environmental variables. Summer relationships were similar to those determined for rhinoceros auklet. Upwelling was directly implicated in the success of reproduction. Cassin's auklets have an offspring-rearing period that occurs during a significant portion of our defined summer period. Therefore, as with rhinoceros auklets, specific conditions related to general productivity of the system would be expected to relate to reproductive success. Moreover, as the response time of zooplankton to upwelling may be more rapid than that of forage fish, these summertime relationships may reflect the life history of their prey.

Trophic chain comparisons

Our data on 3 seabird species represent different, though interrelated, trophic levels. This allows us to identify generalities about trophic structure. Environmental variables that maintain effects across species may indicate generalities in relationships. By examining exogenous variables, which ultimately drive ecosystem dynamics as a whole, similarities can be noted between the 3 seabird trophic chain responses to the environment. As an example, consider transition date had an ultimate negative effect for all species, indicating that a later onset of the upwelling season relates to reduced reproductive success at multiple trophic levels. The exact mechanism is unknown, but it may relate to match–mismatch between prey resources and predator demand (Cushing 1990, Bertram et al. 2001) or simply reflect reduced food availability overall. We provide support for a match–mismatch mechanism in that an early transition to upwelling benefits zooplankton production and zooplankton abundance promotes rockfish production and ultimately the availability of rockfish to seabirds, though we have yet to align availability intraseasonally or spatially. Conversely, a later onset of upwelling negatively impacts the trophic chain as the availability of zooplankton is limited during the critical pelagic period of juvenile rockfishes. Similar findings are presented in the northern California Current where there exists a negative relationship between the timing of upwelling onset and coho salmon survival (Logerwell et al. 2003), which corresponds to the temporal availability of high-quality zooplankton prey (Peterson & Keister 2003, Hoof & Peterson 2006) that ultimately relates to coho salmon survival (Peterson & Schwing 2003).

Spring northerly wind stress was positively related to reproductive success of all of the seabirds. Generally, northerly wind stress provides the force for upwelling in the system, consistent with a positive relationship. Easterly wind stress was negatively related to reproductive success. The mechanism for easterly wind stress is unclear. However, examination of the zooplankton productivity model indicates that easterly wind stress has a direct negative effect on the production of this prey item, as well as an indirect effect on production of rockfish. Furthermore, easterly wind stress has a direct effect on zooplankton in the rhinoceros auklet model and relates directly to common murre production. In total, easterly wind stress plays a direct or indirect negative role in production across all of our models.

Easterly winds (westward and offshore) are associated with northerly Ekman transport, which may be the cause of the negative relationship we noted. These results are similar to Schirripa & Colbert (2006), wherein sablefish production along the California Current was found to be negatively correlated to northern Ekman transport at 48° N. Within central California it is possible that reduced offshore wind stress enables advection of nutrients, zooplankton and larvae into relaxed waters equatorward of upwelling jets (Strub et al. 1991, Graham et al. 1992, Wing et al. 1995). These relaxed features provide retentive, warm waters in which primary production is increased and zooplankton and larvae are retained (Wing et al. 1995, Vander Woude et al. 2006). Importantly, Vander Woude et al. (2006) further suggest that much of the overall productivity of upwelling systems is derived by these relaxed features.

The community models we built from the 3 seabird trophic chains were each significant and provided reasonably predictive fits. From the perspective of ecosystem-based fishery management, the environmental latent vector may serve as an informative index of ecosystem productivity (Fig. 5). This approach to modeling the ecosystem represents a practical middle ground between simple correlative methods and a holistic (and perhaps unattainable) understanding of all physical and biological mechanisms that regulate variability in production (de-Young et al. 2004). For example, while a simple correlation between common murre production and shortbelly rockfish abundance also resulted in a reasonable fit ($r^2 = 0.39$, $p = 0.0014$, N = 23), the approach developed here demonstrates both conceptually and quantitatively that the environment and zooplankton abundance are the proximate drivers of variable production as well. This also demonstrates from a mechanistic standpoint how higher trophic level organisms act to integrate multiple drivers of variation in the ecosystem and is consistent with the notion that seabirds can be indicators of ecosystem status and productivity.

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