



# Linking Northeast Pacific recruitment synchrony to environmental variability

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## ABSTRACT

We investigated the hypothesis that synchronous recruitment is due to a shared susceptibility to environmental processes using stock–recruitment residuals for 52 marine fish stocks within three Northeast Pacific large marine ecosystems: the Eastern Bering Sea and Aleutian Islands, Gulf of Alaska, and California Current. There was moderate coherence in exceptionally strong and weak year-classes and correlations across stocks. Based on evidence of synchrony from these analyses, we used Bayesian hierarchical models to relate recruitment to environmental covariates for groups of stocks that may be similarly influenced by environmental processes based on their life histories. There were consistent relationships among stocks to the covariates, especially within the Gulf of Alaska and California Current. The best Gulf of Alaska model included Northeast Pacific sea surface height as a predictor of recruitment, and was particularly strong for

stocks dependent on cross-shelf transport during the larval phase for recruitment. In the California Current the best-fit model included San Francisco coastal sea level height as a predictor, with higher recruitment for many stocks corresponding to anomalously high sea level the year before spawning and low sea level the year of spawning. The best Eastern Bering Sea and Aleutian Islands model included several environmental variables as covariates and there was some consistent response across stocks to these variables. Future research may be able to utilize these across-stock environmental influences, in conjunction with an understanding of ecological processes important across early life history stages, to improve identification of environmental drivers of recruitment.

**Key words:** Bayesian hierarchical models, environment, fish recruitment, Northeast Pacific Ocean, synchrony

## INTRODUCTION

Fishing and environmental conditions can both influence the abundance and productivity of marine fish stocks. Recruitment to fisheries (a measure of year-class strength) is especially variable and is impacted by fluctuations in spawner abundance, egg production, and survival during early life stages (Hjort, 1914; Cushing, 1982). Spawner abundance often accounts for only a small portion of the variability in recruitment (Myers *et al.*, 1994; Gilbert, 1997; Vert-pre, 2013). Investigations of environmental influences on egg and early life stage survival may be needed to identify the mechanisms governing variations in survival rate for stocks that have a large fraction of unexplained variability in recruitment (Mueter *et al.*, 2011).

Environmental relationships have been incorporated into some fish stock assessments to quantify the amount of recruitment variability that can be attributed to environmental covariates (e.g., Schirripa *et al.*, 2009). However, many identified environmental–recruitment correlations have not remained robust over time, which makes understanding and forecasting recruitment dynamics especially challenging (Myers, 1998; Deyle *et al.*, 2013). Recent research has

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concentrated on incorporating environmental covariates into fisheries stock projection models to account for both interannual variability around a mean level of productivity and regime-like shifts in the mean level of productivity (Maunder and Watters, 2003; Deriso *et al.*, 2008; A'mar *et al.*, 2009; Haltuch and Punt, 2011). Identification of environmental influences that explain a large portion (50% or more) of the variability in recruitment and are reliably measurable and predictable may contribute to improved resource management through improved stock projections that incorporate these factors (Basson, 1999; De Oliveira and Butterworth, 2005; Brunel *et al.*, 2010). Environmental correlations can also be used to evaluate climate change impacts on fish stocks and fisheries in management strategy evaluations (Punt *et al.*, in press). However, such in-depth analyses remain to be done for many fish stocks. An analysis that includes many populations may be especially valuable for testing general hypotheses of environmental–recruitment relationships (Myers, 1998).

Ecosystem-wide associations between environmental conditions and biological communities have been documented in the Northeast Pacific (Hare and Mantua, 2000). These relationships may be exhibited through productivity shifts in the biological community (Hare and Mantua, 2000) or synchrony in productivity dynamics across multiple stocks (Hollowed *et al.*, 1987; Mueter *et al.*, 2007; Ralston *et al.*, 2013). Previous studies have identified common taxonomic and life history characteristics across stocks exhibiting recruitment synchrony (Hollowed *et al.*, 1987; Mueter *et al.*, 2007). Such studies suggest that knowledge of the early life history of a stock may aid in identifying how recruitment responds to environmental

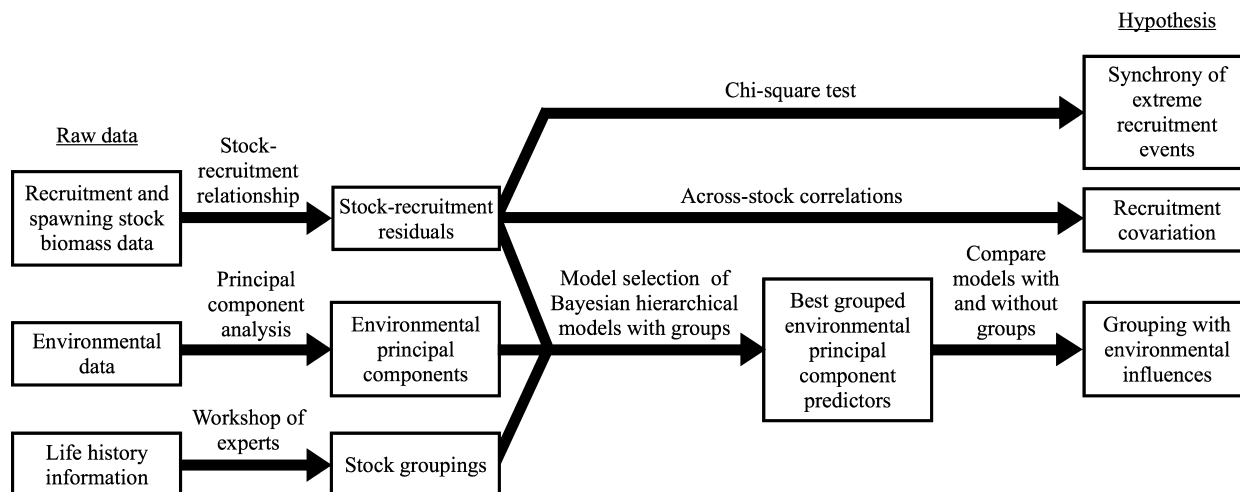
variability, and how different stocks with similar life history features may be similarly influenced (Doyle and Mier, 2012). We test *a priori* hypotheses about the common vulnerability of groups of stocks to environmental influences during their early lives to determine whether there is evidence for recruitment synchrony driven by common environmental influences. If recruitment synchrony is related to identifiable common susceptibilities, we can use knowledge of the well-studied Northeast Pacific fish stocks to aid in understanding environmental influences on recruitment dynamics for other stocks for which information is limited but estimates of recruitment and life history information are available.

We investigate whether recruitment synchrony might be related to shared sensitivity to broad-scale environmental drivers. Specifically, we investigate recruitment synchrony and evaluate the relationships between recruitment and environmental covariates for groups of marine fish stocks within three Northeast Pacific large marine ecosystems: the Eastern Bering Sea and Aleutian Islands, Gulf of Alaska, and California Current. Groups of stocks are defined based on hypothesized similar susceptibility to environmental variability based on their early life histories and previous studies of environmental influences on recruitment for these stocks. Using hierarchical models, we test whether synchrony can be predicted based on this prior classification of stocks on the basis of putative sensitivity to processes affecting early life history stages.

## METHODS

Our methods are summarized in Figure 1. We model environmental effects on recruitment for each

Figure 1. Summary of the methods.



ecosystem independently based on previous analyses that have found differing responses of groundfish recruitment by ecosystem (Hollowed *et al.*, 1987; Mueter *et al.*, 2007). The stocks investigated have varied histories of exploitation so we also account for the effects of spawning stock biomass on recruitment, although productivity shifts may often be unrelated to abundance (Vert-pre *et al.*, 2013).

#### Recruitment data

Recruitment represents the number of fish surviving to a specified age, typically the age at which they enter the fishery, and were aligned by their year of birth (year-class). We compiled recruitment and spawning stock biomass estimates from stock assessments for marine fish across the Northeast Pacific from the RAM Legacy Stock Assessment Database (Ricard *et al.*, 2012). We also compiled recruitment and spawning stock biomass estimates for Pacific herring stocks that were not available in this database (G. Buck, Alaska Department of Fish and Game, U.S.A., pers. comm.; S. Dressel, Alaska Department of Fish and Game, U.S.A., pers. comm.). Our data set did not include anadromous salmon stocks, and we only used stocks and years for which recruitment was estimated (not assumed to perfectly follow a specified stock–recruitment relationship without error) in the analysis. We did not account for uncertainty in estimates of these data. The analysis included 14 Eastern Bering Sea and Aleutian Islands stocks, 14 Gulf of Alaska stocks, and 24 California Current stocks (Table 1).

We accounted for the potential effect of spawning biomass on recruitment levels for stock assessments that did not include a stock–recruitment relationship in recruitment estimation by testing three recruitment models: Ricker, Beverton–Holt and a constant recruitment model (Appendix S1). These three models were fit using maximum likelihood estimation, assuming log-normal error, and the statistically best model was chosen based on the small-sample Akaike information criterion (AICc; Hurvich and Tsai, 1989). The residuals, in log space ( $\ln(\text{observed}/\text{predicted})$ ), from the best model were used in this analysis as an index of recruitment variability. Of the 24 stocks that were fitted to the stock–recruitment models, the Ricker model was chosen for seven stocks, the Beverton–Holt model for four stocks, and the mean model for 13 stocks (Table 1). When stock assessment models estimated recruitment as residuals from a stock–recruitment relationship, these residuals, in log space, were used as a spawning-biomass-adjusted estimate of recruitment.

#### Stock grouping

To identify groups of stocks within an ecosystem with overlapping susceptibility to environmental influences, we compiled data on their life history and ecological characteristics. Life history and ecological information collected included spawning or parturition time, spawning mode, egg size, larval size at hatching or release, pelagic stage duration, and juvenile habitat area (Table S1). We also compiled information from previous studies documenting environmental influences on recruitment for these stocks. We obtained information from scientists familiar with the stocks when it was not available in the literature.

Using the compiled information, we identified groups of stocks with similar susceptibility to environmental variability. We defined the groups *a priori*, based on expert opinion that was solicited during a 1-day workshop. The three Eastern Bering Sea and Aleutian Islands and four Gulf of Alaska groups we identified were primarily related to the stock susceptibility to transport variability based on spawning and juvenile areas and susceptibility to variability in prey available for larvae based on larval size (Table 1). The Eastern Bering Sea and Aleutian Islands groups were identified as the ‘cross-shelf transport’, ‘retention’, and ‘parental investment’ groups. The Gulf of Alaska included the same groups as the Eastern Bering Sea and Aleutian Islands in addition to the ‘coastal’ group. We identified two California Current groups primarily related to stocks’ susceptibility to upwelling and transport variability based on spawning and juvenile areas. The California Current groups were identified as ‘cross-shelf transport’ and ‘moderate upwelling’ groups.

#### Synchrony

To examine the synchrony in extreme recruitment events across stocks within each ecosystem, we identified the years corresponding to the weakest (<25th percentile), average (middle 50th percentile), and strongest (>75th percentile) stock–recruitment residuals for each stock. The observed distributions of strong, weak, and average year-classes in each year across stocks were compared with the expected distribution using a chi-square test at a significance level of  $\alpha = 0.10$  for years with stock–recruitment data for at least half of the stocks in the ecosystem. We used a Holm–Bonferroni correction to correct for the large number of comparisons.

We also examined the correlation in stock–recruitment residuals between stocks within each ecosystem to evaluate evidence for within-ecosystem recruitment

**Table 1.** The stock groups identified for the Eastern Bering Sea and Aleutian Islands (BSAI), Gulf of Alaska (GOA), and California Current (CC) ecosystems based on the characteristics of stocks in the groups, the processes thought to be important to recruitment, the stocks within the groups, and the stock–recruitment model chosen for each stock (SR: R, Ricker; BH, Beverton–Holt; M, Mean; SA, stock assessment stock–recruitment model).

Eco.	Group	Group characteristics	Important process	Stock name	Scientific name	SR
BSAI	Cross-shelf transport	Spawn on the outer continental shelf/slope; inshore juvenile nurseries	Inshore transport to juvenile nursery grounds	Arrowtooth flounder	<i>Atheresthes stomias</i>	BH
				Greenland turbot	<i>Reinhardtius hippoglossoides</i>	M
	Retention	Spawn on the continental shelf	Inshore retention; shelf productivity level and timing (related to timing of ice retreat); inshore transport away from adults (EBS walleye pollock)	Alaska plaice	<i>Pleuronectes quadrituberculatus</i>	R
				Yellowfin sole	<i>Limanda aspera</i>	M
				Flathead sole	<i>Hippoglossoides elassodon</i>	M
				Northern rock sole	<i>Lepidopsetta polyxystra</i>	BH
				Pacific cod	<i>Gadus macrocephalus</i>	M
				Togiak Pacific herring	<i>Clupea pallasii</i>	M
	Parental investment	High parental investment in young; large larval size to withstand low primary production	Parental condition; environmental conditions in the period before parturition	AI walleye pollock	<i>Gadus chalcogrammus</i>	SA
				EBS walleye pollock	<i>Gadus chalcogrammus</i>	SA
Atka mackerel				<i>Pleuragrammus monoptyerygius</i>	M	
Northern rockfish				<i>Sebastes polyspinis</i>	M	
GOA	Cross-shelf transport	Spawn on the outer continental shelf/slope; inshore juvenile nurseries	Inshore transport to juvenile nursery grounds	Rougheye & blackspotted rockfish	<i>Sebastes aleutianus</i> , <i>S. melanostictus</i>	R
				Arrowtooth flounder	<i>Atheresthes stomias</i>	R
	Retention	Spawn on the continental shelf; small egg size (Pacific cod and walleye pollock)	Inshore retention; shelf productivity level and timing	Dover sole	<i>Microstomus pacificus</i>	R
				Pacific halibut	<i>Hippoglossus stenolepis</i>	BH
				Rex sole	<i>Glyptocephalus zachirus</i>	R
				Sablefish	<i>Anoplopoma fimbria</i>	M
				Flathead sole	<i>Hippoglossoides elassodon</i>	M
				Pacific cod	<i>Gadus macrocephalus</i>	M
	Coastal	Spawn near shore	Coastal processes	Walleye pollock	<i>Gadus chalcogrammus</i>	R
				Seymour Canal Pacific herring	<i>Clupea pallasii</i>	SA
Sitka Sound Pacific herring				<i>Clupea pallasii</i>	SA	
Dusky rockfish				<i>Sebastes variabilis</i>	M	
Parental investment	High parental investment in young; large larval size to withstand low primary production	Parental condition; environmental conditions in the period before parturition	Northern rockfish	<i>Sebastes polyspinis</i>	R	
			Pacific ocean perch	<i>Sebastes alutus</i>	BH	
			Rougheye & blackspotted rockfish	<i>Sebastes aleutianus</i> , <i>S. melanostictus</i>	M	



covariation. We evaluated whether the observed distribution of correlations differed from the expected distribution under the null hypothesis that stock–recruitment residuals for stocks within each ecosystem vary independently. If there was significant covariation, the distribution of correlations could have differed from the null distribution in two ways: the mean correlation ( $\bar{r}$ ) could have differed from zero or there could have been significant overdispersion with a greater variance in the observed correlations ( $\sigma_r^2$ ) than expected (Mueter *et al.*, 2007). We used a randomization procedure to obtain the expected distributions of the correlations within each ecosystem, accounting for the effects of autocorrelation (Pyper *et al.*, 2001; Mueter *et al.*, 2007). We first evaluated  $\bar{r}$  to determine whether it differed from zero. If this was not significant, we evaluated  $\sigma_r^2$  to determine whether it differed from the expected distribution, because tests for overdispersion are only valid if average correlations are not different from zero (Mueter *et al.*, 2007).

#### *Environmental variables*

We compiled regional environmental variables hypothesized to affect recruitment for the marine fish stocks analyzed (Tables S2–S4). We chose several categories of physical variables within each ecosystem to investigate. We investigated five for the Eastern Bering Sea and Aleutian Island, four for the Gulf of Alaska, and five for the California Current. Since these variables were examined, in some cases, over several seasons and geographic locations, there were often many variables included within each category of physical covariates. To capture environmental effects on spawner condition and ecosystem productivity during the pre-spawning period, and on productivity and transport during the larval and early juvenile stages, we included all seasonal variables corresponding to the year of spawning and the year before spawning (same variables lagged by 1 year). Within all three ecosystems we included sea surface temperature (SST) data from coordinates within the ecosystems to capture environmental influences on primary production and metabolic rate, regional sea surface height (SSH) data for the ecosystem areas as a proxy for variability in currents, nutrients and primary productivity, and freshwater discharge data for major rivers within the ecosystems as a proxy for variability in coastal nutrients, fronts, and circulation.

Within the Eastern Bering Sea and Aleutian Islands we also included sea ice data as a proxy for variability in the timing of the spring bloom and the transfer of primary production up the food web (Hunt *et al.*, 2011), and wind data to capture variability in

circulation and the transport of nutrients and larvae (Danielson *et al.*, 2012a; Table S2). Across the five categories of Eastern Bering Sea and Aleutian Islands environmental variables included, a total of 20 environmental variables were considered.

Within the Gulf of Alaska we also considered Bakun upwelling indices (Bakun, 1973) because upwelling can affect the transport of nutrients and larvae (Table S3). We used a total of 26 environmental variables for the Gulf of Alaska across the four categories of environmental variables.

Within the California Current we also included coastal sea level data, which relates to alongshore geostrophic flow, upwelling, and several other physical environmental variables in this ecosystem (Chelton *et al.*, 1982; Kruse and Huyer, 1983; Sydeman and Thompson, 2010; Table S4). We chose to include sea level data from San Francisco because this has been shown to represent an integrated measure of regional and large-scale climate forcing for the California Current (Bromirski *et al.*, 2011) and has been related to biological variability in this ecosystem (Koslow *et al.*, 2013; Ralston *et al.*, 2013). We also included upwelling phenology indices, calculated using daily averages of Bakun upwelling indices (Bakun, 1973), based on the five indices of the phenology of coastal upwelling defined by Bograd *et al.* (2009), to capture influences on transport and primary productivity. In the California Current there were 66 environmental variables across the five categories of environmental variables.

We used principal component analysis (PCA) to reduce the environmental variables into a smaller number of uncorrelated variables for use as predictors in the hierarchical models. We used two approaches to select ordinated environmental variables for model comparison. We used PCA to identify covariations within each category of data separately (SST, SSH, upwelling, wind, freshwater discharge, ice or sea level) for each ecosystem. The first two principal components (PCs) explained greater than 50% of the variance for most (10 of 14) of the categories by ecosystem, and these PCs were used as predictors in the hierarchical models that included a single category of environmental data. We also used a single PCA to identify covariations across all environmental variable categories within each ecosystem. The variables were weighted so that each category had equal weight because some had a disproportionately large number of time series due to the nature of the data. Models with all environmental variable categories required more PCs to describe the environmental variability; we tested models with the first two to five PCs as predictors. PCA was conducted in R (R Development Core

Team, 2012) without weighting of variables using the 'stats' package (R Development Core Team, 2012) and with weighting of variables using the 'ade4' package (Chessel *et al.*, 2009).

#### Bayesian hierarchical models

Bayesian hierarchical modeling is advantageous for this analysis because it can utilize information from all stocks within a group to improve the parameter estimation for stocks with weaker data, generally providing more reliable parameter estimates with lower response variability (Gelman and Hill, 2007; Helser *et al.*, 2007). Moreover, it allows us to specifically test whether the *a priori* stock grouping structure is supported by data on recruitment dynamics and dependency on environmental variables by comparing models with and without the hierarchical structure. In the hierarchical structure, coefficients are estimated for individual stocks but assumed to be drawn from a distribution described by a group-level mean and variance. Bayesian hierarchical modeling allows for dependence among parameters at all levels that are estimated simultaneously so that they can inform each other. This technique has been used in several fisheries applications, including estimation of the stock–recruitment relationship for Northeast Pacific rockfish (*Sebastes* spp.) (Dorn, 2002; Forrest *et al.*, 2010) and Atlantic salmon (*Salmo salar*) stocks (Michielsens and McAllister, 2004), modeling pink salmon (*Oncorhynchus gorbuscha*) escapement abundance and timing (Su *et al.*, 2001), and in an analysis of growth variability and biological covariates for Northeast Pacific rockfish (Helsler *et al.*, 2007).

We used Bayesian hierarchical models to model the stock–recruitment residuals as a linear function of the environmental variable PCs. We assumed linear influences of these environmental variables on the stock–recruitment residuals to allow for other complexities in the model, and the limitations of this assumption are discussed further in the *Discussion* section. The models covered the time periods for which stock–recruitment residual data were available for at least one stock within the ecosystem and all of the environmental variables were available or estimated (Eastern Bering Sea and Aleutian Islands: 1953–2008; Gulf of Alaska: 1958–2008; California Current: 1968–2008). Bayesian posterior probabilities were estimated using a Markov chain Monte Carlo (MCMC) routine, implemented in Just Another Gibbs Sampler (JAGS; Plummer, 2011). Appendix S2 includes additional details on the model parameterization. We used deviance information criterion (DIC) to choose the best model in each ecosystem of those tested (nine in the Eastern

Bering Sea and Aleutian Islands and California Current, eight in the Gulf of Alaska) (Spiegelhalter *et al.*, 2002). Model fits and residuals were also used as diagnostic tools.

We also tested the hypothesis that groups of stocks with similar susceptibility to environmental processes during early life respond similarly to environmental forces and distinct from the other groups within the ecosystem. To test this hypothesis, we fit hierarchical models with no distinct groups so that all species parameters within an ecosystem were drawn from a shared distribution. We used the environmental covariates in the best model chosen with multiple groups as the covariates for these models with no distinct groups. Support for the grouping structure within each ecosystem was evaluated by comparing the DIC values.

We also investigated how well the models fit the stock–recruitment residual estimates for each individual stock. We calculated the Pearson correlation coefficients between the median predicted and observed stock–recruitment residuals for each stock, and we deemed correlations  $>0.5$  to be good model fits.

We did not account for autocorrelation within the Bayesian hierarchical models because of constraints on the ability to numerically estimate parameters; generally Bayesian or maximum likelihood methods struggled when there were both autocorrelation and hierarchical structures in the model. We therefore considered each autocorrelation separately, without considering hierarchical structure by investigating autocorrelation in the model residuals. We calculated the lag-1 autocorrelation coefficient for the residuals of the predicted stock–recruitment residuals from the best model from the observed stock–recruitment residuals to determine whether there was evidence for autocorrelation in the residuals.

## RESULTS

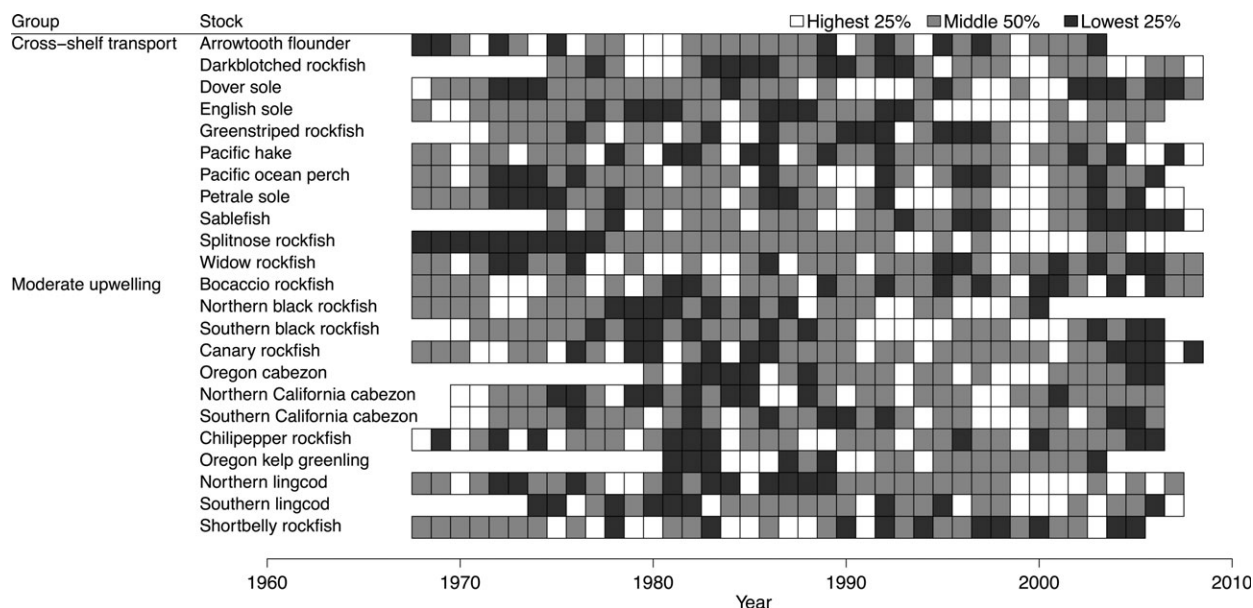
### Synchrony

There was low to moderate synchrony in exceptional (strong or weak) year-classes within each of the ecosystem. In the Eastern Bering Sea and Aleutian Islands there were no significant deviations from the expected distribution of strong, weak, and average year-classes under the null hypothesis that stocks vary independently. Although non-significant, there were eight stocks with high recruitment in 1977, eight stocks with low recruitment in 1982 and 1994, and seven stocks with low recruitment in 2004 (Fig. 2). In the Gulf of Alaska, nine stocks across the identified groups had strong year-classes in 1998 and 2000 ( $P = 0.086$ ;





Figure 4. Annual occurrence of extreme stock–recruitment residuals for the California Current stocks.



Bayesian hierarchical models

*Eastern Bering Sea and Aleutian Islands.* The best model for Eastern Bering Sea and Aleutian Islands stocks included the five ordinated environmental variables across all variable categories (Table 2). The first five PCs explained a total of 68% of the variability across all the environmental categories (Table 3). The first PC explained 31% of the variance and was strongly associated with ice cover and spring SST the year of and the year before spawning. The second PC explained 12% of the variance and was strongly associated with SSH PC1. The third PC explained 12% of the variance and was associated with winter cross-shelf wind the year of spawning. The fourth PC explained 6.8% of the variance and was associated with winter cross-shelf wind the year before spawning. The fifth PC explained 5.7% of the variance and was associated with winter along-shelf wind the year before spawning.

Greenland turbot, Pacific cod, and Eastern Bering Sea walleye pollock had a negative relationship with PC1, which relates to higher recruitment in years of increased ice cover and colder spring SST the year before and the year of spawning (Fig. 6). Several stocks within the ‘retention’ group, including flathead sole, Togiak herring, and AI walleye pollock, had a positive relationship with PC3. This relates to higher recruitment in years of stronger northeasterly cross-shelf wind, or along-shelf Ekman transport to the northwest, during the winter of spawning. These

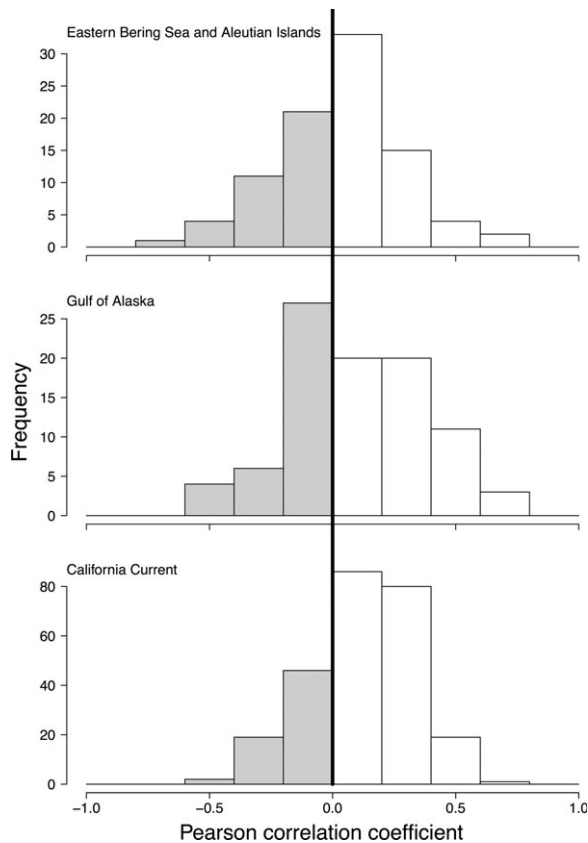
conditions during the winter before spawning were related to higher recruitment of Greenland turbot, which had a negative relationship with PC4. Both stocks in the ‘cross-shelf transport’ group, arrowtooth flounder and Greenland turbot, had a positive relationship with PC5, which relates to higher recruitment in years of stronger southeasterly along-shelf wind, or onshore cross-shelf Ekman transport, during the winter before spawning. Several of the stocks had good model fits ( $r > 0.5$ ), including arrowtooth flounder, Greenland turbot, northern rock sole, Pacific cod, and Togiak Pacific herring (Fig. S1). However, all of the stocks within the ‘parental investment’ group had poor fits.

There was significant autocorrelation in the model residuals for several of the stocks, especially northern rock sole and roughey & blackspotted rockfish (Table S5).

We found evidence that the effect of environmental variables varied across groups. The model without separate groups was 11.6 DIC units higher (worse) than that of the grouped model (Table 2).

*Gulf of Alaska.* The best Gulf of Alaska model included ordinated SSH as predictor variables (Table 2). The first two PCs accounted for 17% and 12% of the total variance across the gridded Northeast Pacific SSH data. The loadings indicated that PC1 was related to positive SSH anomalies in the coastal waters of the Northeast Pacific and negative SSH anomalies

**Figure 5.** Frequency of Pearson correlation coefficients between stock–recruitment residuals for all stocks within each ecosystem.



in offshore waters (Fig. 7). PC2 was related to negative SSH anomalies in northern offshore waters of the Northeast Pacific.

Many stocks within the ‘cross-shelf transport’ group had a positive correlation with PC1, corresponding to greater recruitment during periods of positive coastal Gulf of Alaska SSH anomalies, and a positive relationship with PC2, corresponding to greater recruitment during periods of negative offshore Gulf of Alaska SSH anomalies (Fig. 8). However, the model fits were good for only a few stocks (Pacific halibut in the cross-shelf transport group and flathead sole in the retention group), and the 95% credible intervals for estimated effect sizes spanned 0 for most stocks (Fig. S2).

There was significant autocorrelation in the model residuals for several of the stocks, especially arrowtooth flounder and Pacific ocean perch (Table S5).

There was little evidence that the effect of environmental variables varied across the identified groups. The model without separate groups had a DIC value only 1.7 DIC units greater than that of the grouped model (Table 2).

*California Current.* The model with two San Francisco sea level PCs had the lowest DIC value by at least 5.7 DIC units (Table 2). The first two San Francisco sea level PCs explained a large portion of the total variance in the sea level data, accounting for 46% and 24%, respectively (Table 4). PC1 was strongly positively associated with sea level in the spring and summer the year of spawning and the spring, summer, and fall the year before spawning. PC2 was positively associated with seasonal values for the year before spawning and negatively associated with seasonal values for the year of spawning.

Many (13) of the California Current stocks, across both groups, had a positive correlation with PC2, with greater recruitment during periods of positive sea level anomalies the year before spawning and negative sea level anomalies the year of spawning (Fig. 9). This model provided good fits for a few of the California Current stocks, including petrale sole, splitnose rockfish, and chilipepper rockfish (Fig. S3).

There was significant autocorrelation in the model residuals for several of the stocks, especially splitnose rockfish, English sole, Dover sole, and southern black rockfish (Table S5).

There was moderate evidence that the effect of environmental variables varied across groups. The model without separate groups had a DIC value 5.5 greater than that of the grouped model (Table 2).

## DISCUSSION

We examined recruitment synchrony in marine fish stocks within three large marine ecosystems of the Northeast Pacific and examined environmental variables that may drive this synchrony within these ecosystems by similarly influencing several stocks. In agreement with previous studies, we found evidence for synchrony within these ecosystems, both in the correlation of recruitment time series and in the timing of extreme recruitment events (Hollowed *et al.*, 1987; Mueter *et al.*, 2007). We found coherence within several of the defined groups in the response of the stock–recruitment residuals to the regional environmental variables investigated, providing moderate support for our hypothesis that stocks within these groups would have a similar sensitivity to environmental variables.

### *Environmental drivers of recruitment*

The best Eastern Bering Sea and Aleutian Islands model included PCs across all categories of environmental variables tested, which indicates the importance of multiple environmental processes for

**Table 2.** Model selection results for the Eastern Bering Sea and Aleutian Islands (BSAI), Gulf of Alaska (GOA), and California Current (CC) ecosystems. Results are shown as the posterior mean deviance ( $\bar{D}$ ), the effective number of parameters ( $p_D$ ), the deviance information criterion (DIC), and the increase in DIC from the lowest value within each ecosystem ( $\Delta$ DIC). The values for the best model chosen within each ecosystem are in bold. The model names correspond to the principal component (PC) model covariate type (Tables S2–S4) and ‘All’ indicates PCs across all variable types for the first two to five PCs. The best model within each ecosystem was also tested with all stocks in one group (no grouping).

Eco.	Model	$\bar{D}$	$p_D$	DIC	$\Delta$ DIC
BSAI	<b>All 5</b>	<b>842.7</b>	<b>39.4</b>	<b>882.1</b>	<b>0.0</b>
	All 5 no grouping	860.6	33.1	893.7	11.6
	All 3	863.8	31.1	894.9	12.8
	All 4	860.2	34.9	895.1	13.0
	Freshwater discharge	876.5	25.0	901.6	19.4
	SST	879.8	25.2	905.0	22.9
	All 2	880.0	25.9	905.8	23.7
	SSH	884.4	26.7	911.1	29.0
	Ice	894.5	25.2	919.6	37.5
	Wind	901.4	23.7	925.1	42.9
GOA	<b>SSH</b>	<b>786.9</b>	<b>27.6</b>	<b>814.6</b>	<b>0.0</b>
	SSH no grouping	791.8	24.5	816.3	1.7
	All 2	803.5	27.3	830.8	16.3
	All 3	799.9	31.9	831.9	17.3
	All 5	793.1	40.4	833.6	19.0
	All 4	798.8	36.4	835.2	20.6
	SST	819.3	25.0	844.3	29.7
	Freshwater discharge	820.2	25.3	845.5	30.9
	Upwelling	834.0	23.4	857.4	42.9
	CC	<b>Sea level</b>	<b>1506.8</b>	<b>40.7</b>	<b>1547.5</b>
Sea level no grouping		1514.0	39.1	1553.0	5.5
All 5		1498.4	54.9	1553.2	5.7
All 4		1509.2	50.3	1559.5	12.0
All 3		1546.1	42.0	1588.1	40.6
SST		1553.1	38.1	1591.2	43.7
SSH		1574.2	35.5	1609.7	62.2
Upwelling		1603.4	32.8	1636.2	88.7
All 2		1604.6	33.3	1637.9	90.4
Freshwater discharge		1616.0	31.2	1647.1	99.6

recruitment of the Eastern Bering Sea and Aleutian Islands fish stocks examined and/or the correlation of several of these variables that may make it difficult to identify the processes affecting recruitment. The increased ice cover and colder spring SST the year before and the year of spawning that was associated with higher recruitment for Greenland turbot, Pacific cod, and Eastern Bering Sea walleye pollock is also associated with increased production of large lipid-rich copepods that may serve as prey for these fish during early life stages and alternative prey for predators of larvae (Hunt *et al.*, 2011). Sea ice and temperature have similarly been found to be important drivers of ecosystem dynamics in many high-latitude ecosystems, but the mechanisms that relate climate to recruitment are often complex and distinct (Drinkwater *et al.*, 2010). The increased northeasterly cross-shelf wind, or

along-shelf Ekman transport to the northwest, during the winter of spawning that was associated with greater recruitment for several stocks in the ‘retention’ group, may relate to the transport of larvae to nursery grounds (Wilderbuer *et al.*, 2002, 2013) and/or reduced cannibalism when strong northward advection separates juveniles from cannibalistic adults (Mueter *et al.*, 2006). The increased southeasterly along-shelf wind, or onshore cross-shelf Ekman transport, during the winter before spawning that was associated with greater recruitment for arrowtooth flounder and Greenland turbot increases larval retention on the Eastern Bering Sea shelf and on-shelf nutrient fluxes over the southern Bering Sea shelf (Danielson *et al.*, 2012a,b). This combination may promote elevated primary production and larval feeding success on the shelf. These PCs are also related to

**Table 3.** Loading of the Eastern Bering Sea and Aleutian Islands environmental variables on the principal components (PCs) from principal component analysis, calculated as the correlation between the original variables and the PCs. Variables for the year before spawning ( $t-1$ ) and the year of spawning ( $t$ ) were included (SST, sea surface temperature; SSH, sea surface height). Strong loadings ( $|r| > 0.4$ ) are in bold. Also shown is the variance explained by the PCs.

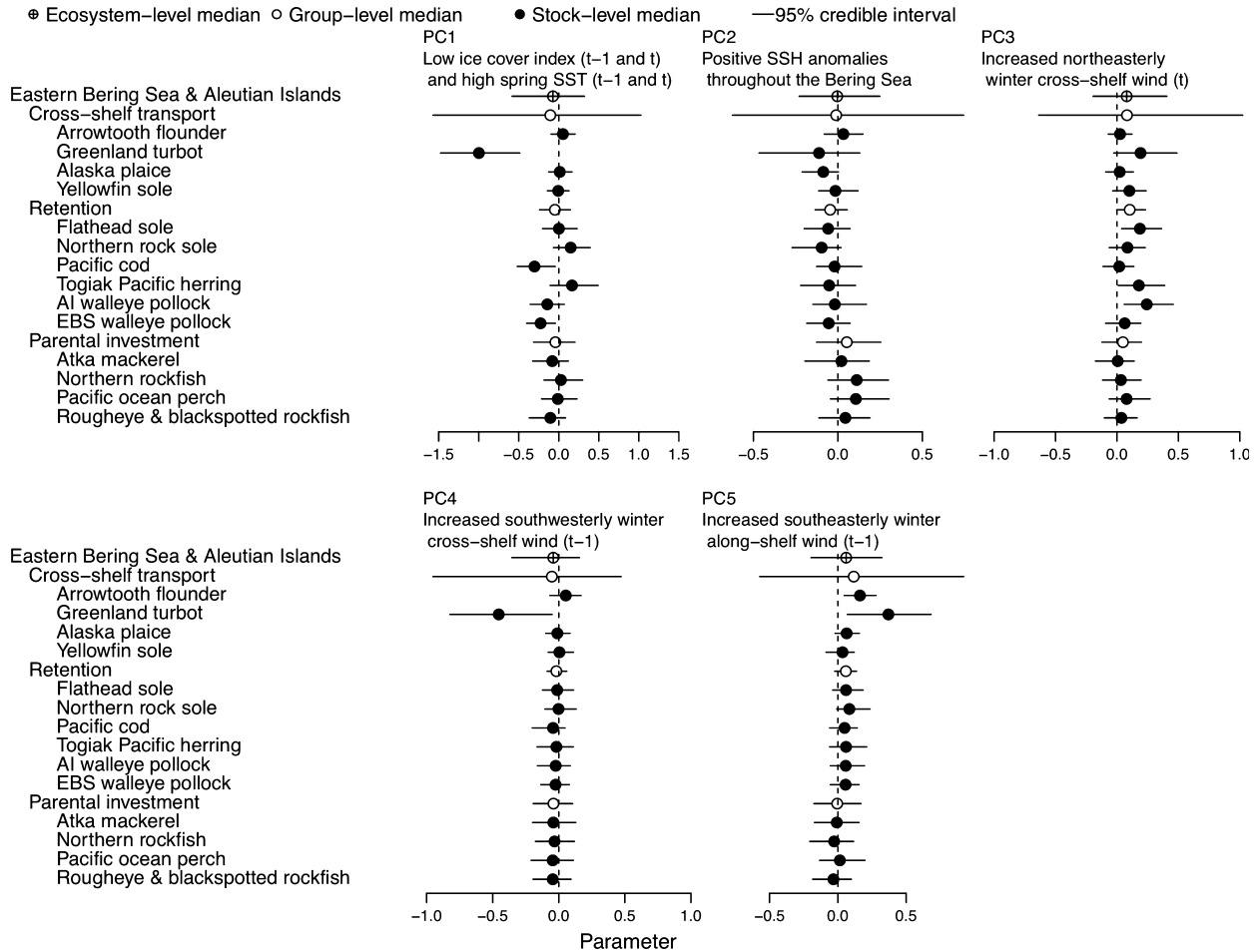
Variable	PC1 (31%)	PC2 (12%)	PC3 (12%)	PC4 (6.8%)	PC5 (5.7%)
Ice cover index ( $t-1$ )	<b>-0.76</b>	-0.31	<b>0.49</b>	0.07	-0.15
Ice cover index ( $t$ )	<b>-0.86</b>	0.19	-0.21	-0.07	0.23
Winter Kuskokwim River discharge ( $t-1$ )	0.35	0.21	-0.38	0.17	-0.20
Summer Kuskokwim River discharge ( $t-1$ )	-0.22	-0.21	-0.17	<b>0.62</b>	-0.24
Winter Kuskokwim River discharge ( $t$ )	<b>0.46</b>	-0.26	-0.16	0.05	-0.37
Summer Kuskokwim River discharge ( $t$ )	-0.20	<b>-0.44</b>	-0.23	-0.03	0.09
Winter cross-shelf wind ( $t$ )	-0.19	-0.25	<b>-0.60</b>	-0.38	-0.34
Winter along-shelf wind ( $t$ )	<b>0.58</b>	-0.34	0.24	-0.29	-0.11
Winter cross-shelf wind $t-1$ )	-0.23	-0.10	-0.20	<b>0.70</b>	-0.20
Winter along-shelf wind ( $t-1$ )	<b>0.53</b>	0.05	-0.35	0.32	<b>0.55</b>
Winter SST ( $t-1$ )	<b>0.54</b>	0.23	<b>-0.46</b>	0.18	0.24
Spring SST ( $t-1$ )	<b>0.69</b>	0.18	-0.40	-0.16	0.04
Summer SST ( $t-1$ )	<b>0.51</b>	0.16	-0.34	-0.16	-0.17
Fall SST ( $t-1$ )	<b>0.67</b>	0.19	-0.21	-0.06	-0.16
Winter SST ( $t$ )	<b>0.67</b>	-0.13	-0.03	-0.27	-0.31
Spring SST ( $t$ )	<b>0.78</b>	-0.18	0.23	0.16	-0.04
Summer SST ( $t$ )	<b>0.57</b>	-0.19	-0.08	0.23	-0.12
Fall SST ( $t$ )	<b>0.64</b>	0.06	-0.03	0.11	-0.22
SSH PC1	-0.14	<b>-0.83</b>	<b>-0.41</b>	-0.07	0.18
SSH PC2	<b>0.67</b>	-0.33	<b>0.47</b>	0.08	0.24

variation in several other environmental variables, so further investigation into environmental processes driving recruitment may provide additional insights.

Recruitment for many Gulf of Alaska stocks, especially those within the 'cross-shelf transport' group, was strongly related to the first two PCs of SSH variability. There was high coherence in the recruitment–environment relationship within the 'cross-shelf transport' group despite variation across stocks in their early life history, with distinct timing of larval production, larval duration, and drift patterns. Flathead sole was not included in the 'cross-shelf transport' group, but it showed a positive relationship with SSH PC2 similar to the 'cross-shelf transport' group stocks and may be similarly susceptible to transport processes. Higher recruitment for these stocks was associated with negative offshore and positive coastal Gulf of Alaska SSH anomalies, which relate to upwelling and enrichment in the offshore Gulf of Alaska, onshore Ekman surface layer transport, coastal downwelling, and an accelerated Alaska Coastal Current (Bakun, 1996). These conditions may reflect enhanced onshore transport of larvae and nutrients from offshore onto the continental shelf, and may also be a precursor to enhanced mesoscale eddy activity in the Alaska Coastal Current that increases cross-shelf exchange and advects deep, nitrate-rich waters onto the shelf (Thomson and

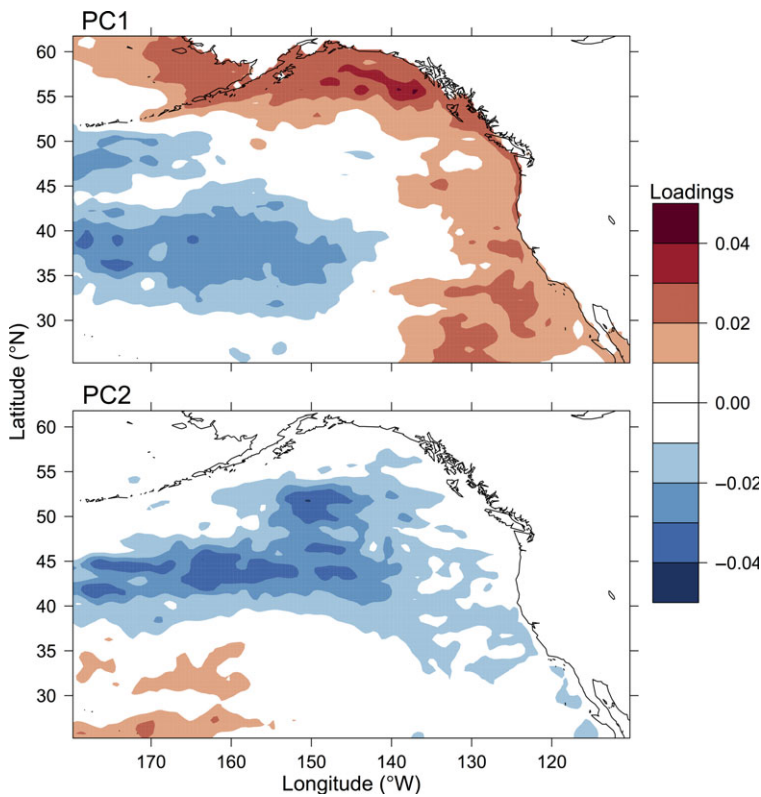
Gower, 1998; Stabeno *et al.*, 2004; Combes and Di Lorenzo, 2007). Although there have been few studies of the impacts of mesoscale eddies on marine fish, they have been found to entrain larval fish, possibly contributing to greater survival through enhanced feeding conditions within the eddies and cross-shelf transport of larvae (Atwood *et al.*, 2010; Shotwell *et al.*, in press). This SSH pattern may also relate to large-scale climate patterns such as the El Niño–Southern Oscillation (ENSO), which is often expressed in the Gulf of Alaska through positive coastal SSH anomalies during warm ENSO events (El Niño) and has been related to Pacific halibut recruitment (Melsom *et al.*, 1999; Bailey and Picquelle, 2002). Furthermore, the first SSH PC is highly correlated with the Pacific Decadal Oscillation, the dominant pattern of SST in the North Pacific, which has been linked to North Pacific productivity (Hare *et al.*, 1999). The second SSH PC is highly correlated with the North Pacific Gyre Oscillation, the second dominant pattern of Northeast Pacific SSH variability, which has been linked to nutrients and productivity in the Northeast Pacific (Di Lorenzo *et al.*, 2008; Cloern *et al.*, 2010). The coherent response of these Gulf of Alaska stocks indicates they may be similarly affected by environmental processes linked to the two dominant modes of SSH variability and may warrant further investigation.

**Figure 6.** Ecosystem-level, group-level, and stock-level parameter distribution medians and 95% credible intervals for the coefficients of the five principal components (PCs) from principal component analysis of all the environmental data for the Eastern Bering Sea and Aleutian Islands stocks. The descriptions below the PC labels indicate the environmental variables with the strongest loadings on the PCs and the sign associated with positive values of the PCs (SST, sea surface temperature; SSH, sea surface height). The environmental variables correspond to the year before spawning ( $t-1$ ) and the year of spawning ( $t$ ).



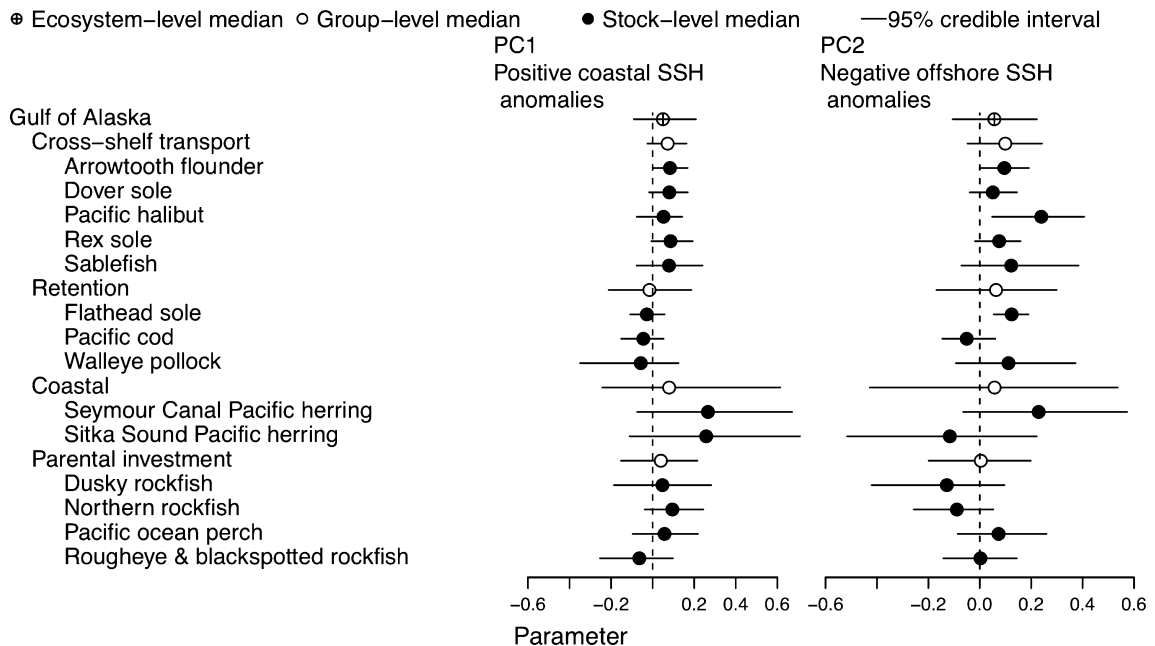
Recruitment for many California Current stocks was strongly associated with coastal sea level data, which relates to alongshore geostrophic flow, coastal upwelling, and several other physical environmental variables in this ecosystem (Chelton *et al.*, 1982; Kruse and Huyer, 1983; Sydeman and Thompson, 2010). Anomalously high sea levels the year prior to spawning and low sea levels the year of spawning were related to high recruitment for many stocks. Negative sea level anomalies during the larval stage have been found to coincide with increased recruitment for several species of rockfish (Laidig *et al.*, 2007; Ralston *et al.*, 2013) and sablefish (Schirripa and Colbert, 2006) in the California Current. Negative sea level anomalies relate to increased equatorward flows that may enhance primary and secondary production and the occurrence of large, lipid-rich cold-water copepods

(Chelton *et al.*, 1982; Keister *et al.*, 2011; King *et al.*, 2011). Positive sea level anomalies relate to increased poleward flows that may reduce productivity the year before spawning. These conditions may relate to a lower abundance of fish 1 yr older and reduced competition and cannibalism, which have been suggested to be important for Pacific hake recruitment (Buckley and Livingston, 1997). Rockfish may also have low investment in reproduction, and even skip spawning, during years of low productivity but in subsequent years invest additional energy in reproduction (Rideout *et al.*, 2005; Hannah and Parker, 2007). Similarly, sea level height has been found to affect fish recruitment in other ecosystems. For example, sea level variability in the Leeuwin Current ecosystem, related to ENSO events, has been linked to recruitment of fish and invertebrate species (Pearce and Phillips, 1988;



**Figure 7.** Loading of the annual (July–June, for year corresponding to January) Northeast Pacific sea surface height data on the principal components (PCs) from principal components analysis of these data.

**Figure 8.** Ecosystem-level, group-level, and stock-level parameter distribution medians and 95% credible intervals for the coefficients of the two principal components (PCs) from principal component analysis of Northeast Pacific sea surface height data for the Gulf of Alaska stocks. The descriptions below the PC labels indicate the sea surface height (SSH) pattern associated with positive values of the PCs.



**Table 4.** Loading of the California Current San Francisco sea level data on the principal components (PCs) from principal component analysis, calculated as the correlation between the original variables and the PCs. Variables for the year before spawning ( $t-1$ ) and the year of spawning ( $t$ ) were included. Strong loadings ( $|r| > 0.4$ ) are in bold. Also shown is the variance explained by the PCs.

Season	PC1 (46%)	PC2 (24%)
Winter ( $t-1$ )	<b>0.53</b>	<b>0.57</b>
Spring ( $t-1$ )	<b>0.70</b>	<b>0.59</b>
Summer ( $t-1$ )	<b>0.73</b>	<b>0.52</b>
Fall ( $t-1$ )	<b>0.75</b>	0.15
Winter ( $t$ )	<b>0.64</b>	-0.41
Spring ( $t$ )	<b>0.74</b>	-0.50
Summer ( $t$ )	<b>0.80</b>	-0.38
Fall ( $t$ )	<b>0.44</b>	-0.62

Caputi *et al.*, 1996). We also tested a model with Northeast Pacific SSH PCs as predictors, but this model performed worse than a model with San Francisco sea level PCs as predictors, suggesting that near-shore, rather than regional scale, processes may be more important for recruitment variations of the California Current stocks examined here.

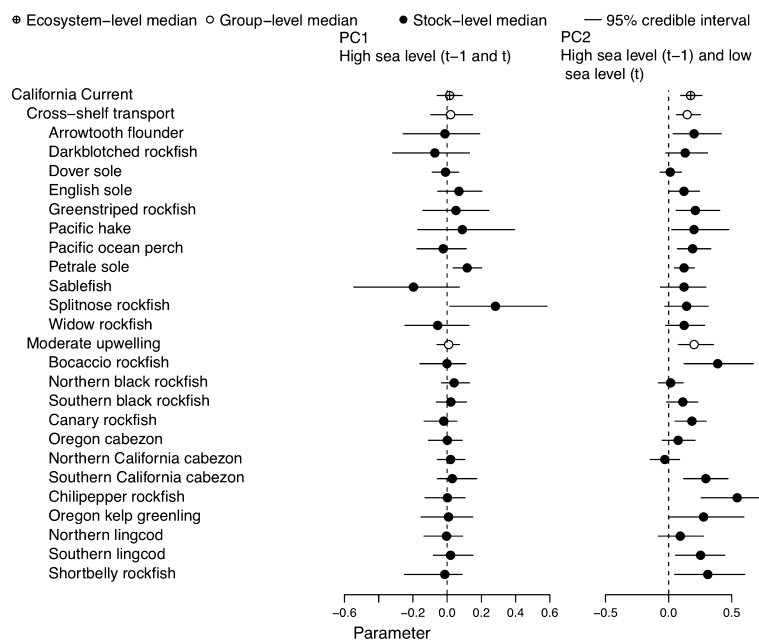
Environmental drivers associated with advective processes were important to recruitment in each of the three ecosystems we studied. The cross-shelf and along-shelf winds that were important in the Eastern Bering Sea and Aleutian Islands, SSH in the Gulf of Alaska, and coastal sea level in the California Current are all

related to advective processes in these ecosystems. Previous research has found the importance of advection for recruitment success across many species and ecosystems (Drinkwater *et al.*, 2010). For example, dispersion of eggs and larvae from spawning grounds to favorable nursery areas is important for successful recruitment, so advective processes that allow for these connections are critical (Bakun, 2010; Drinkwater *et al.*, 2010; Ottersen *et al.*, 2010). Transport of nutrients and important planktonic prey species may also affect the feeding success of larval fish (Drinkwater *et al.*, 2010; Ottersen *et al.*, 2010). Because advective processes are important for many aspects of recruitment success, these processes may be a good basis for further research to understand synchrony in recruitment dynamics among stocks within ecosystems.

*Benefits and challenges of approach*

Our analysis of environmental influences on recruitment using Bayesian hierarchical models revealed weak recruitment–environment relationships for many of the stocks, but there was coherence in the recruitment–environment relationships among stocks within several of the defined groups. Although there was only moderate evidence supporting our hypothesis that recruitment synchrony is related to shared sensitivity to broad scale environmental drivers, the use of Bayesian hierarchical models may aid in future identification of recruitment–environment relationships. Comprehensive knowledge of environmental links across early life stages is not available for most species,

**Figure 9.** Ecosystem-level, group-level, and stock-level parameter distribution medians and 95% credible intervals for the coefficients of the two principal components (PCs) from principal component analysis of the San Francisco sea level data for the California Current stocks. The descriptions below the PC labels indicate the sea level pattern associated with positive values of the PCs for data corresponding to the year before spawning ( $t-1$ ) and the year of spawning ( $t$ ).



so this method utilizing available recruitment–environmental information across ecosystems is beneficial. Multispecies synthesis of Gulf of Alaska species early life history characteristics and abundance trends has proven useful in identifying species groups that are predisposed to respond to the pelagic environment in similar ways, as well as key environmental variables that are critical to early ontogeny aspects of recruitment processes within these groups (Doyle *et al.*, 2009; Doyle and Mier, 2012). The posterior distributions may also be used to inform the recruitment–environment relationship for stocks not included in this analysis, although the wide credible intervals of these distributions in our study limit their use. Future estimation of more precise recruitment–environmental relationships within groups may be beneficial to informing these relationships for stocks where less data are available.

We also encountered several challenges in conducting this research. One of the major challenges in this analysis was in developing *a priori* hypotheses to use in grouping the stocks. In our analysis, the grouped models were slightly superior to the models with a single group for all ecosystems, especially in the Eastern Bering Sea and Aleutian Islands, indicating the grouping structure provided some improvement in model fits. Limited early life history and ecological information was available for many of the stocks, especially regarding the juvenile stage, and from the information that was available it was challenging to identify the important common exposures across stocks with many unique life history and ecological characteristics. The use of Bayesian hierarchical models to identify recruitment–environmental relationships may be more useful with the availability of additional early life history and ecological information that may aid in the development of more optimal species grouping structures. In particular, there needs to be a better understanding of ecological processes across species, ontogenetic stages, and early life history habitat for these stocks to effectively identify shared susceptibilities of stocks to environmental influences.

Another challenge was in identifying environmental variables to use as predictors within the models. The complex early life history processes can generate a diversity of responses to the pelagic environment across species, based on varieties of exposure patterns (Doyle and Mier, 2012). Therefore, the spatial and temporal scales of environmental variability most critical for recruitment success vary across species, and the utilization of ocean-basin-scale physical environmental covariates may capture only in a very limited way the ecological reality in the system at the

level of species' early life intervals and habitats. The marginal to poor fits for many of the stocks across all of the models tested in this study may therefore represent a mismatch between the regional environmental covariates and the temporal and spatial scale of exposure and response to the pelagic environment during early life.

Other limitations of the methods used may also have reduced the identification of strong recruitment–environment relationships. We used linear models to identify the recruitment–environmental relationship, so we ignored non-linear influences on recruitment. Regime shifts in the North Pacific have been widely recognized and with these ecosystem shifts the relationship between recruitment and environmental variables may not be constant over time (Bailey, 2000; Hare and Mantua, 2000; Deyle *et al.*, 2013; Stige *et al.*, 2013). Future study of recruitment–environmental relationships may benefit from testing for non-linearities and shifts in these relationships for stocks for which adequate data are available. Although we were not able to explicitly account for autocorrelation in the Bayesian hierarchical models, there was strong autocorrelation in the model residuals. Future analyses that are able to account for autocorrelation in the model fitting may allow for better identification of significant environmental drivers of recruitment. Also, the recruitment and spawning stock biomass values used were estimates from stock assessment models and we did not account for the uncertainty in these estimates. Recruitment estimates may be affected by assumptions made within the stock assessment model, such as the standard deviation of the recruitment deviations, and poor estimates of recruitment may limit our ability to relate this variability to environmental variables. Furthermore, the data representing recruitment are at a wide range of ages (e.g., age-1 for Eastern Bering Sea walleye pollock, age-5 for Eastern Bering Sea and Aleutian Islands yellowfin sole), so recruitment variability for stocks with a later age at recruitment may be largely influenced by processes during later juvenile stages.

## CONCLUSIONS

There was support for our hypothesis that species with shared sensitivity to environmental drivers would have synchronous recruitment and that groups defined *a priori* could enhance estimation of the effects of the environment on recruitment. However, the strength of evidence was often marginal, indicating that the strength of recruitment synchrony in these ecosystems is highly variable or the quality of recruitment



estimation in stock assessment models is highly variable, and that there are limits in using regional-scale environmental covariates to predict recruitment. We suggest that a promising approach is to combine focused species-level studies at fine temporal-spatial scales with the meta-analytic approach that we used here. In this way, results from species-level analyses can be used to refine group structures and selection of variables, and potentially lead to better fitting models. These models could then be used to anticipate recruitment trends of less well-studied stocks based on life history traits and knowledge of environmental dynamics. If robust recruitment–environmental relationships remain elusive, it is wise to consider the development and implementation of management policies that are robust to high levels of recruitment uncertainty (Punt *et al.*, in press).

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Stock-recruitment models.

**Appendix S2.** Bayesian hierarchical modeling.

**Table S1.** Life history and ecological information compiled for stocks from the Eastern Bering Sea and Aleutian Islands, Gulf of Alaska, and California Current ecosystems, including the peak spawning or parturition months, spawning mode, spawning habitat area, egg size, larval size at hatching/parturition, larval size at transformation to juvenile stage, pelagic duration, and juvenile habitat area. Also listed are references identifying processes important to recruitment and the source of recruitment data used in analysis.

**Table S2.** Eastern Bering Sea and Aleutian Islands physical variables included in the analysis.

**Table S3.** Gulf of Alaska physical variables included in the analysis.

**Table S4.** California Current physical variables included in the analysis.

**Table S5.** Lag-1 autocorrelation coefficient of the residuals of the median predicted stock-recruitment residuals from the observed stock-recruitment residuals. Significant ( $\alpha = 0.05$ ) autocorrelations are indicated with an asterisk (\*).

**Figure S1.** Observed and median model predicted stock-recruitment residuals for the Eastern Bering Sea and Aleutian Islands stocks for the model with five principal components from principal component analysis of all environmental data included as the predictors.

**Figure S2.** Observed and median model predicted stock-recruitment residuals for the Gulf of Alaska stocks for the model with the first two axes from principal component analysis of sea surface height data as the predictors.

**Figure S3.** Observed and median model predicted stock-recruitment residuals for the California Current stocks for the model with the first two axes from principal component analysis of sea surface height data as the predictors.