Spatial variability in rockfish (*Sebastes* spp.) recruitment events in the California Current System

John C. Field and Stephen Ralston

Abstract: A general assumption regarding spatial patterns of recruitment variability is that species with similar early life history characteristics tend to covary in reproductive success over scales of 500–1000 km. These assumptions are based on evaluation of recruitments from independent stocks, as few studies have assessed synchrony in recruitment within broadly dispersed stocks over finer spatial scales. We used data on age composition and landings to generate regional time series of recruitment deviations for three species of rockfish in the California Current System (*Sebastes goodei*, *Sebastes entomelas*, and *Sebastes flavidus*). We then used correlation analysis, principal components analysis, and other methods to evaluate the degree of synchrony among recruitment events in these regions. Results show that 51%–72% of the year-to-year variability in recruitment is shared coastwide within these species, while a lesser but significant fraction of the variability is associated with finer scale geographic features.

Résumé : En ce qui a trait à la structure spatiale de la variabilité du recrutement, on assume généralement que les espèces qui ont des caractéristiques semblables au début de leur cycle biologique ont tendance à avoir une covariance dans leur succès reproductif sur des échelles de 500–1000 km. Ces présuppositions sont basées sur des évaluations du recrutement à partir de stocks indépendants, puisque peu d'études ont évalué conjointement le synchronisme du recrutement chez des stocks à vaste répartition à des échelles spatiales plus fines. Nous avons utilisé des données de composition en âge et de débarquements pour générer des séries chronologiques régionales des déviations du recrutement chez trois espèces de sébastes habitant le courant de Californie (*Sebastes goodei, Sebastes entomelas* et *Sebastes flavidus*). Des analyses de corrélation, des analyses des composantes principales et d'autres méthodes nous ont servi à évaluer le degré de synchronisme ente les épisodes de recrutement dans ces régions. Les résultats indiquent que 51–72 % de la variabilité inter-annuelle dans le recrutement est commune à ces espèces sur toute la côte, alors qu'une fraction moins importante, mais significative de la variabilité est associée à des caractéristiques géographiques à échelle plus fine.

[Traduit par la Rédaction]

Introduction

Quantifying the physical and biological mechanisms responsible for spatial and temporal variability in recruitment remains a principal focus of fisheries biologists and oceanographers. To date, the majority of compelling hypotheses regarding density-independent processes are based on a consideration of physical forcing on both abiotic and biotic environmental conditions of early life history stages of marine fishes (Lasker 1978; Sinclair 1988; Bakun 1996). Houde (1989) demonstrated that as a result of declining mortality with increasing size for most larval fishes, the lower growth rates observed in cooler water species are usually associated with longer stage durations and higher cumulative mortality rates. Consequently, the importance of physical processes in determining year-class strength tends to be greater for species in the temperate and subarctic zones, where the influence of seasonality and variability in the physical and biological environment is potentially greater. This observation is echoed by Longhurst (2002), who found that longevity tends to be related to recruitment variability for many temperate and subarctic species of marine fish.

In general, the assumption has been that there tends to be synchrony in year-class strength (and marine survival for anadromous species) across fairly broad regions for populations with similar early life history characteristics and exposure to environmental variability. Botsford and Lawrence (2002) showed considerable spatial and temporal synchrony in coho salmon (*Oncorhynchus kisutch*) and Dungeness crab (*Cancer magister*) catches among ports and regions in the California Current System (CCS) between 1950 and 1990; however, they found that Chinook salmon (*Oncorhynchus tshawytscha*) landings did not covary over space and time. Similarly, Peterman et al. (1998) explored patterns of covariation in marine survival for sockeye salmon (*Oncorhynchus nerka*), and Pyper et al. (2001) examined the same for pink

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salmon (*Oncorhynchus gorbuscha*) throughout a large portion of their range in the northeast Pacific Ocean. Both studies showed moderate to strong covariation within regions, yet these patterns broke down among stocks separated by more than several hundred kilometres. Mueter et al. (2002) expanded on these studies by reevaluating correlations in spatial patterns of marine survival in sockeye and pink salmon and estimating the same for both chum salmon (*Oncorhynchus keta*) and the physical environment. They found that spatial correlations were greater for chum salmon than for other species, and tended to be fairly large for several important physical ocean properties. Upwelling indices had the strongest spatial correlation (on the order of 1000 km), with sea-surface temperature (SST) having intermediate spatial consistency (on the order of 400–800 km) and sea-surface salinity showing the weakest patterns (less than 400 km); importantly, these correlations tended to be stronger during the winter. Chelton (1981) and Chelton and Davis (1982) had similarly found that sea level, upwelling winds, ocean temperatures, and salinity tended to covary throughout much of the CCS, with subsurface temperatures and transport showing stronger spatial synchrony than surface temperatures and salinity.

Hollowed et al. (1987) and Hollowed and Wooster (1995) demonstrated synchrony of extreme year classes among a variety of stocks in different regions of the northeast Pacific Ocean, with stocks tending to be in phase within regions and out of phase between regions. Williams and Quinn (2000) also showed that recruitment in Pacific herring (*Clupea pallasii*) populations was correlated over fairly large spatial scales, although there was some separation between Alaskan and British Columbian stocks. In the North Atlantic Ocean, Koslow (1984) and Koslow et al. (1987) demonstrated spatial synchrony in year-class strengths of Atlantic groundfish stocks with similar early life history characteristics, and linked this variability to environmental forcing. Myers et al. (1997) further quantified this synchrony for a range of fishes, based on an exponential-decay model, and found that spatial scales of correlation in recruitment between marine fish stocks were typically on the order of 500 km. Finally, Schwartzlose et al. (1999) have shown basin-scale (>1000 km) synchrony in the recruitment of many coastal pelagic species in boundary current ecosystems, presumably linked to basin-scale or global climate forcing.

This study extends the analysis by the above authors by explicitly evaluating the degree of spatial synchrony in recruitment over finer geographic scales. To do this, we use port-specific catch-at-age data to generate regional, independent assessment models from which we derive time series of local recruitment deviations for chilipepper, widow, and yellowtail rockfish (*Sebastes goodei*, *Sebastes entomelas*, and *Sebastes flavidus*, respectively) in the CCS. These three species are reasonably data-rich, commercially important (they collectively represent over 55% of US landings of *Sebastes* spp. coastwide between 1981 and 2003), and are winter spawners that spend between 130 and 160 days in the pelagic environment following extrusion (Wyllie-Echeverria 1987; Woodbury and Ralston 1991). We evaluate the degree of geographic synchrony by several means, including the use of pairwise correlations between port groups, evaluation of shared variability with principal

components analysis (PCA), and use of the exponential relationship between covariance and space as modeled by Myers et al. (1997). Interest in understanding temporal and spatial variability in recruitment and production has increased in recent years, fueled in part by a growing recognition of the importance of dispersal both in quantifying population dynamics and in considering the feasibility and design of spatially based management measures (Warner et al. 2000; Botsford et al. 2003).

It is not the intention in this work to draw inferences regarding stock structure or movement patterns. Widow and chilipepper rockfish have historically been managed as a single stock in the US portion of their range (Ralston et al. 1998; He et al. 2003), and widow rockfish in Canada are similarly treated as a single coastwide stock (Stanley and Haist 1997). Although Tagart (1991) found some evidence for stock differentiation in yellowtail rockfish, US stock assessments and management recommendations typically assume a coastwide stock stretching from Cape Mendocino to Vancouver Island, and Canadian assessments and management recommendations use that stock boundary along with a stock from Vancouver Island through the Queen Charlotte Islands (Stanley and Haist 1997). We have assumed that movement for all three species is minimal, which is consistent with what little is known of movement patterns for most *Sebastes* species. Stanley et al. (1994) report on 36 recoveries of yellowtail rockfish with recapture locations (from 14 000 tagged fish) from a Canadian tagging program off British Columbia and northern Washington, in which most moved less than 25 km before being recaptured, with a minority moving between 100 and 400 km. Pearcy (1992) found very little movement of adult yellowtail rockfish, based on acoustic tagging of 19 fish on Heceta Bank. Gunderson (1997) found that changes in the abundance and age composition of Pacific Ocean perch (*Sebastes alutus*) in response to fishing were highly localized, even decades after fisheries impacts, suggesting little to no migration of adults between areas of suitable habitat as close as 30 km. With regard to dispersal, we assume that pelagic larvae and juveniles are likely to be widely dispersed from their origin and that there is little latitudinal movement following settlement, such that the age structure of fish in different regions will tend to reflect the historical patterns of settlement by juveniles.

Materials and methods

Our general approach was to use regional landings and age-composition data to generate port- and region-specific age-structured models for chilipepper, widow, and yellowtail rockfish. References to port groups in the USA are consistent with the Pacific Coast Fisheries Information Network (PacFIN) hierarchical port-group structure, with the following exceptions; Eureka includes ports in the Crescent City and Brookings areas and Astoria includes both northern Oregon and all Washington ports in the Columbia International North Pacific Fisheries Commission area. Data on catch at age and landings were provided by the California Department of Fish and Game, the Oregon Department of Fish and Wildlife, the Washington Department of Fish and Wildlife, PacFIN, and the British Columbia Department of Fisheries

Table 1. Number of subsamples and number of aged fish available by port group for chilipepper (*Sebastes goodei*), widow (*Sebastes entomelas*), and yellowtail (*Sebastes flavidus*) rockfish.

Port group	Latitude (°N)	Chilipepper rockfish No. of subsamples	No. of aged fish	Widow rockfish No. of subsamples	No. of aged fish	Yellowtail rockfish No. of subsamples	No. of aged fish
Morro Bay (MRO)	35°20′	601	9 556	165	1 810	33	466
Monterey (MNT)	36°40′	922	13 309	517	4 935	129	1 136
San Francisco (SF)	37°50′	267	5 435	157	2 835	43	654
Bodega Bay (BDG)	38°20′	248	4 406	118	3 258	15	404
Fort Bragg (BRG)	39°30′	620	8 513	309	5 924	107	1 104
Eureka/CRS (ERK)	40°50′	372	3 013	732	16 640	352	5 737
Coos Bay (COOS)	43°20′			280	7 001	231	9 724
Newport (NEWP)	44°40′			730	18 869	360	12 949
Astoria (AST)	46°10′			801	34 810	855	59 561
Greys Harbor (US VN)	48°			313	19 120	579	33 833
Vancouver Island (CN VN)	49°			139	5 751	224	13 251
Queen Charlotte Islands (CHAR)	51°					251	16 544
Total		3030	44 232	4261	120 953	3179	155 363

Note: Boxes indicate port-group aggregations by species for each model.

and Oceans. Data-collection procedures for commercial fisheries for California, Oregon, and Washington are summarized in Sampson and Crone (1987) and for British Columbia in Stanley and Haist (1997). Where possible, annual-sample catch-at-age data were expanded to the total number of fish caught at age to arrive at the age composition of the catch. Where the associated catch data were not available, sampled fish were weighted equally in the age-composition data. As sampling generally occurred across a range of gear types, age data from different gears were pooled when cumulative catch-at-age curves showed no noticeable difference in selectivity. Where substantial differences in selectivity were evident, either gears were modeled as separate fisheries or data from minor gear types were excluded.

We developed data sets of catch at age and landings specific to port groups or regions from Point Conception, California, to the Queen Charlotte Islands off the British Columbia mainland. The number of sampled landings and aged fish available for each region are provided in Table 1. Boxes indicate the groupings of ports in aggregated models. For example, data for chilipepper rockfish were sufficient to have one model per port group between Morro Bay and Eureka, but there were not enough age data to model chilipepper rockfish north of Cape Blanco (the nominal boundary of the stock). By contrast, all ages and landings of yellowtail rockfish south of Cape Mendocino were included in one regional model, owing to the paucity of data for this region. The spatial extent of the study area, together with representative ports from most of the regions included in it, is shown in Fig. 1 (Fig. 1). Although the available data for this study included over 320 000 aged fish, for some early years only surface ages (i.e., whole otolith readings) were available. For example, most Oregon widow rockfish were aged with whole-otolith methods from 1979 through 1989 and by break-and-burn (Chilton and Beamish 1982) methods thereafter. Clark et al. (1987) found that surface age readings for yellowtail rockfish compared favorably with break-and-burn readings through age 15, but diverged significantly for older ages. To minimize any recruitment error associated with using surface

Fig. 1. Sampling region, with representative ports associated with the models listed in Table 1.
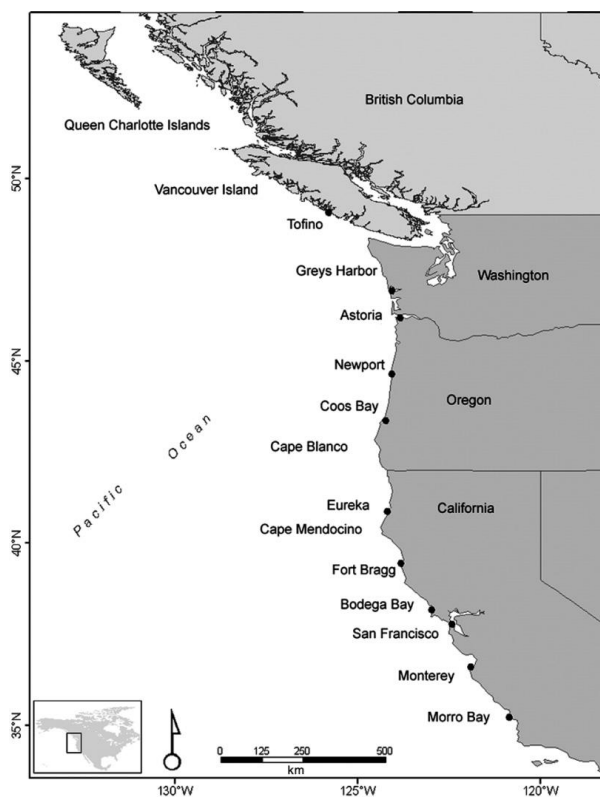
ages for older fish, while maintaining as much consistency as possible with the coastwide assessments (which typically include up to 25 age classes), we modeled age groups only between the age of recruitment to the fishery (as estimated by the coastwide assessment) up to a maximum age of 20 years, with a plus group representing older fish.

For building the regional models we used Coleraine, a generalized age-structured stock-assessment model developed by Hilborn et al. (2003). Coleraine is a spreadsheet template interfaced with AD Model Builder (Otter Research Ltd. 2000), in which parameter estimation is performed using maximum likelihood in the first step and a Bayesian approach in a second. This allows uncertainty around parameter estimates to be assessed from posteriors, although this generally was unnecessary for the purposes of this study. The model itself is a general structure for statistical age- and sex-structured models that allows for multiple fisheries, surveys, or other indices. Growth was modeled by the von Bertalanffy model, and as latitudinal gradients in size at age have been demonstrated for both widow and yellowtail rockfish (Pearson and Hightower 1991; Tagart 1991), estimates of the asymptotic length at age (L_∞), the Brody growth parameter (k), and the age at length 0 (t_0) were generated independently for each region. We found significant differences in size at age, with L_∞ increasing noticeably in more northerly regions, for all three species.

Recruitment in the model is estimated with a Beverton–Holt stock–recruit relationship:

$$(1) \qquad N_{1,t+1}^s = 0.5 \frac{S_t}{\alpha + \beta S_t} e^{\left(R\varepsilon_t - \frac{R\sigma^2}{2} \right)}$$

where is the number of age-1 fish at time $t + 1$ by sex (0.5 assumes a 50:50 sex ratio), α and β are the Beverton–Holt stock–recruit relationship parameters (derived from the parameters for the steepness of the spawner–recruit curve, h, and the recruitment at equilibrium in the absence of fishing, R_0), $R\varepsilon_t$ is the recruitment residual for year t (lognormally distributed with a mean of 0 and a prior on the standard deviation (σ) set by the user, we used a value of 1), and S_t is the spawning biomass in year t. The recruitment residuals, as they deviate from the expected recruitment, are the parameters of interest in this study because they represent the variations in year-class strength to be evaluated.

A realistic accounting of ageing error is critically important in estimating variability in year-class strength, especially when the majority of the landings are composed of older individuals and ageing error is significant (Tyler et al. 1989; Richards et al. 1997). Ageing-error matrices were generated directly from the most recent stock assessments for all three species by assuming a normal distribution of measured age for each true age based on the between-reader agreements reported in stock assessments. The percent agreement for chilipepper rockfish is estimated at 90% for age-1 fish, decreasing linearly to 30% agreement for age-21 fish (Ralston et al. 1998). Widow rockfish have 75% agreement for age-5 fish and 66% agreement for age-20 fish (He et al. 2003). Yellowtail rockfish are the most imprecise, with roughly 52% agreement for age-5 fish and just over 25% agreement for age-20 fish (Tagart et al. 2000). The predicted age composition is estimated by Coleraine in proportions of the catch by year, age, sex, and gear. For fitting to the observed age-composition data, Coleraine uses a robust likelihood formulation based on Fournier et al. (1998). The sample sizes used with the age-composition data (which scales the variance) were the number of subsamples (landings in which fish were sampled and aged) rather than the number of aged fish as in He et al. (2003) and Lai et al. (2003).

Estimates of maturity, sex-specific natural mortality, and length–weight relationships were taken directly from the most recent stock assessments as well. We did not, however, incorporate the increasing natural mortality rate for female yellowtail rockfish that has been modeled in past assessments. Although there is evidence to suggest that differences in natural mortality rate in older females of some species are significant (Leaman 1991; Tagart 1991), the use of sex-specific dome-shaped selectivity curves in assessment models should lead to similar results when they are fitted to catch curves (MacCall 1999). Moreover, different potential assumptions regarding varying natural mortality rates for older females would presumably be of greater consequence to estimates of stock status, not recruitment variability. Finally, we used the biomass estimates from the most recent coastwide assessments of each species as survey indices in each of the regional models (with the survey catchability coefficient set as a free parameter) in order to guide the biomass trajectories in the direction of those in the coastwide assessment. For these indices we assumed a coefficient of variation (CV) of 0.2 and used a range of sensitivity tests, such as replacing the trend from the coastwide assessment with a flat line, or inverting the trend entirely, to demonstrate that these indices were neither driving strong year classes nor dominating the trajectory of the model-estimated biomass.

A key objective throughout this effort was to be as consistent as possible with the most recent coastwide assessments. However, in evaluating the results, we use a range of model complexities in order to test the robustness of our results to differences in model structure. Coleraine uses nonlinear estimation procedures to fit the model to the available data in phases; consequently, we ran a suite of models with increasing complexity for each region and compared the results among models that were similar in structure. The first set of models included the estimation of the catchability coefficient, the equilibrium recruitment, the age at full selectivity (sex-specific), and the recruitment deviations by year. The second set of models included freeing up the left and right sides of the selectivity curve, implemented as a double half-Gaussian function of age (Hilborn et al. 2003), which generally improved the model fit significantly. The third set of models was the least parsimonious, wherein the parameters estimated included steepness, initial exploitation rates, natural mortality rate by sex, and error around the age at full selectivity. While implausible results were excluded, considerable latitude was granted to this set of models in order to evaluate what might be the best fitting model relative to model structure, and Akaike's Information Criterion was used as a measure of model improvement (Akaike 1992). In many cases, freeing up these additional parameters did not substantially improve model fit. Most importantly, the ultimate results varied little among these three sets of models. Consequently, we focus our discussion on the results from the second set of models (i.e., those with the left and right sides of the selectivity curve freely estimated).

We used both correlation methods and PCA to evaluate how much variability in the recruitment estimates within each species was shared coastwide. PCA has a long history

Fig. 2. Log recruitment deviations plotted over space and time for (*a*) chilipepper rockfish (*Sebastes goodei*), (*b*) widow rockfish (*Sebastes entomelas*), and (*c*) yellowtail rockfish (*Sebastes flavidus*) in the California Current System. Space corresponds to the latitude (*y* axis) of the ports or regional model as listed in Table 1.
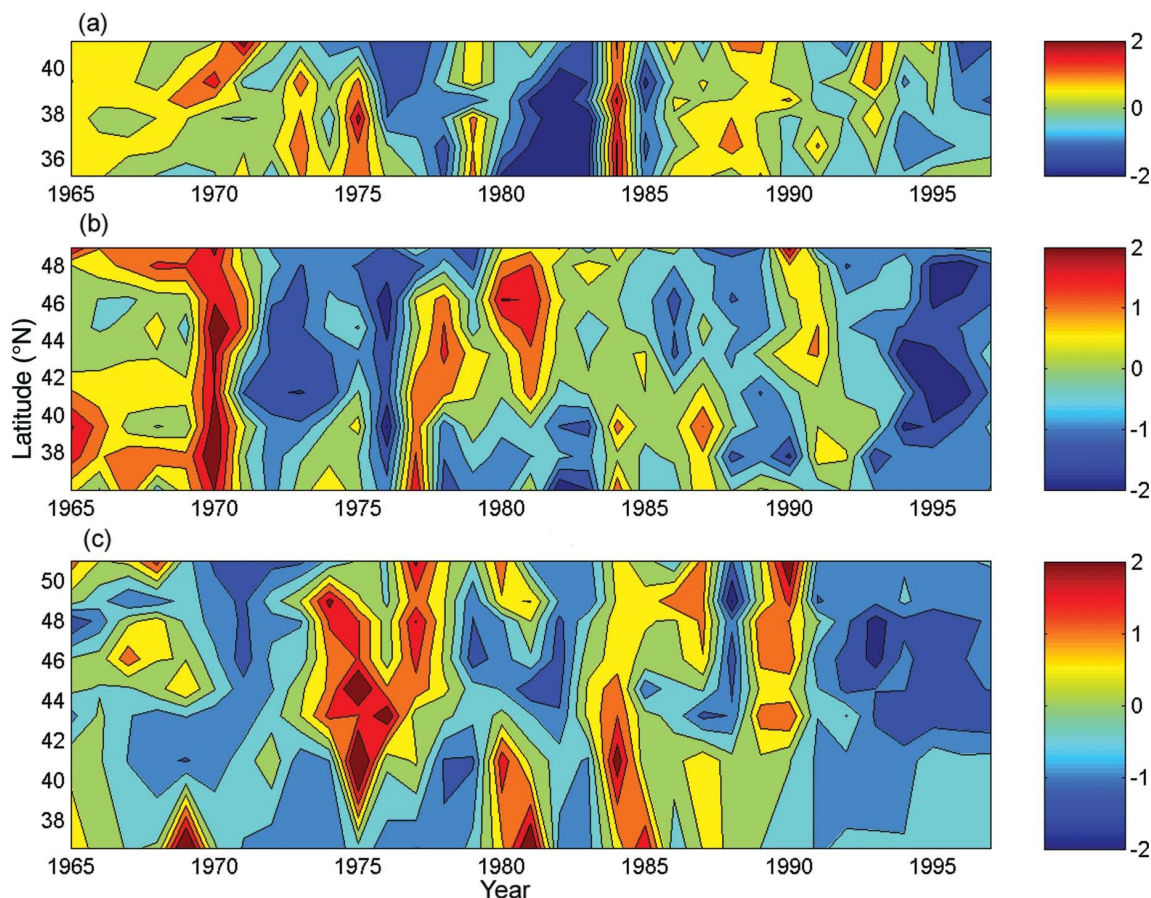
of use in climatology, and is increasingly used in fisheries and oceanography to identify common modes of variability in data sets (Mantua et al. 1997; Hare and Mantua 2000; Botsford and Lawrence 2002). The method takes a covariance matrix consisting of spatially and temporally defined data and uses eigenanalysis to generate sets of principal components (PCs, or scores), in which each is an orthogonal linear combination of the original variables. The amount of variability in the raw data that each PC explains is a function of the eigenvectors (loadings) in which positive values represent positive correlations with the PC. The eigenvalues associated with each PC determine the fraction of the total variance explained by that particular PC. To estimate standard error and evaluate significance, we followed North et al. (1982), who showed that eigenvalues that did not overlap (when bounded by standard error) were likely to be significant, while those that did overlap were not. The modeled time periods were 1968 and 1997 for chilipepper rockfish and 1966 and 1995 for both widow and yellowtail rockfish, based on the availability and resolution of the age-composition data and the age of recruitment to the fishery. Pearson's correlation coefficients were simply estimated directly from raw time series for the time periods described above.

We calculated a third statistic to measure spatial synchrony in time series of recruitment, based on Myers et al.

(1997). Those authors used available stock-assessment results for a wide range of species and assessed the spatial scale of recruitment variability by estimating the distance over which pairwise correlations between time series decayed with the equation

$$(2) \qquad \rho(d) = \rho_0 \, e^{-\frac{d}{v}}$$

where ρ_0 is the correlation between two stocks at zero separation, v is the exponential decay rate (or e-folding scale), and d is the distance between spawning locations of each population. The model is fit with nonlinear least squares and, because they found that it model was rarely improved by estimating ρ_0 independently, we evaluated this model both with ρ_0 free and with ρ_0 constrained to be 1.

Results

The recruitment time series from the regional catch-at-age models appeared to be fairly sensitive to sample sizes, with higher estimated CVs in recruitment time series for models with small sample sizes and lower CVs for models with larger sample sizes. The models with the highest recruitment CVs included chilipepper rockfish in Eureka (1.5), yellowtail rockfish south of Mendocino (1.4), yellowtail rockfish in the Eureka area (1.3), and widow rockfish in San Francisco –

Table 2. Correlation coefficients between log recruitment deviations by port-group model as defined in Table 1.

(A) Chilipepper rockfish

	MNT	SF	BDG	BRG	ERK
MRO	0.83	0.77	0.60	0.59	0.34
MNT		0.88	0.74	0.72	0.41
SF			0.77	0.85	0.44
BDG				0.79	0.48
BRG					0.49

(B) Widow rockfish

	SF	BRG	ERK	COOS	NEWP	AST	US VN	CN VN
MNT	0.62	0.70	0.33	0.26	0.27	0.16	0.17	0.33
SF		0.71	0.57	0.35	0.43	0.30	0.37	0.43
BRG			0.61	0.51	0.51	0.36	0.23	0.32
ERK				0.76	0.69	0.63	0.53	0.45
COOS					0.83	0.76	0.56	0.49
NEWP						0.90	0.63	0.51
AST							0.70	0.53
US VN								0.75

(C) Yellowtail rockfish

	ERK	COOS	NEWP	AST	US VN	CN VN	CHAR
MNT	0.15	–0.15	–0.14	0.08	0.06	0.08	0.05
ERK		0.38	0.40	0.35	0.40	0.39	0.31
COOS			0.70	0.59	0.58	0.52	0.30
NEWP				0.75	0.70	0.41	0.40
AST					0.91	0.64	0.65
US VN						0.69	0.62
CN VN							0.49

Note: Port groups are arranged south to north. A white font on black denotes a p value less than 0.01, a white font on dark grey denotes a p value between 0.01 and 0.05, and a black font on light grey denotes a p value between 0.05 and 0.10.

Bodega Bay (1.2), all of which had sample sizes between 3000 and 5000 aged fish. By contrast, recruitment time series for regions with over 10 000 aged fish typically had CVs between 0.6 and 1.0. Whether such differences in variability resulted from differences in sample size or were a consequence of some other mechanism altogether is unclear; however, we made no effort to correct for this effect. The average CV of all of the port-specific models was 0.9, which was not appreciably higher than the CVs from the most recent assessments of 0.8, 0.7, and 0.6 for chilipepper, widow and yellowtail rockfish, respectively.

For the sake of brevity, we do not report all of the resulting recruitment estimates by species, area, and model. Instead, we present the results graphically (Fig. 2) as standardized anomalies of the log-transformed recruitments plotted as contours over space and time, and one can appreciate visually the nature of spatial synchrony in recruitment anomalies by species. For example, chilipepper rockfish recruitment was strong coastwide in 1973, 1975, 1984, and 1989. Weak years were apparent in 1976–1977, 1980–1983, and 1993–1997. Recruitment of widow rockfish was very strong along their entire latitudinal range in 1970 and most of their range in 1977, with poor recruitment between 1972 and 1976 and between 1993 and 1997. There appeared to be more spatial variability in several years, with the 1980 year class stronger north of 42°N and the 1984 and 1987 year classes stronger south of 42°N (Cape Blanco). Yellowtail rockfish exhibited the greatest spatial distribution of the three species, and showed synchrony throughout most of their range in several years, such as 1976–1978, 1984–1985, and 1989. Weak recruitment is suggested for the early 1970s, 1983, and nearly all of the 1990s. It is possible that ageing error contributed to some of the slight offsets in strong year classes between regions. However, there is clearly a pattern of synchrony in year-class deviations for this population, with either more error or more spatial variation than in the other two species.

We show all possible pairwise correlation coefficients for the time series of the logarithm of annual recruitment estimates by port group (Table 2). These results also demonstrate a high degree of correlation among most "stocks" by species, particularly between adjacent port groups. The most notable exception is yellowtail rockfish for the Monterey region, which includes all catch and age data collected between Morro Bay and Fort Bragg. Recruitment in this region was essentially uncorrelated with that in all other yellowtail rockfish regions. The weakest correlations in both widow and chilipepper rockfish regions also seem to be associated with differences between the areas north and south of Cape Mendocino.

The results of the PCA also demonstrate a high degree of spatial synchrony between the ports and regions modeled. The first PCs explained approximately 72%, 57%, and 51% of the variability in recruitment over time for chilipepper, widow, and yellowtail rockfish, respectively. Loadings were quite even across the spatial variables (Fig. 3), and were

Fig. 3. The first six eigenvalues (left-hand panels) and loadings of the first (solid bars) and second (shaded bars) empirical orthogonal functions (EOFs) over port groups (right-hand panels) for (*a*) chilipepper, (*b*) widow, and (*c*) yellowtail rockfish. Port groups are as follows: Morro Bay (MRO), Monterey (MNT), San Francisco (SF), Bodega Bay (BDG), Fort Bragg (BRG), Eureka and Crescent City (ERK), Coos Bay (COOS), Newport (NEW), Astoria (AST), Greys Harbor (US VN), Vancouver Island (CN VN), and Queen Charlotte Islands (CHAR).
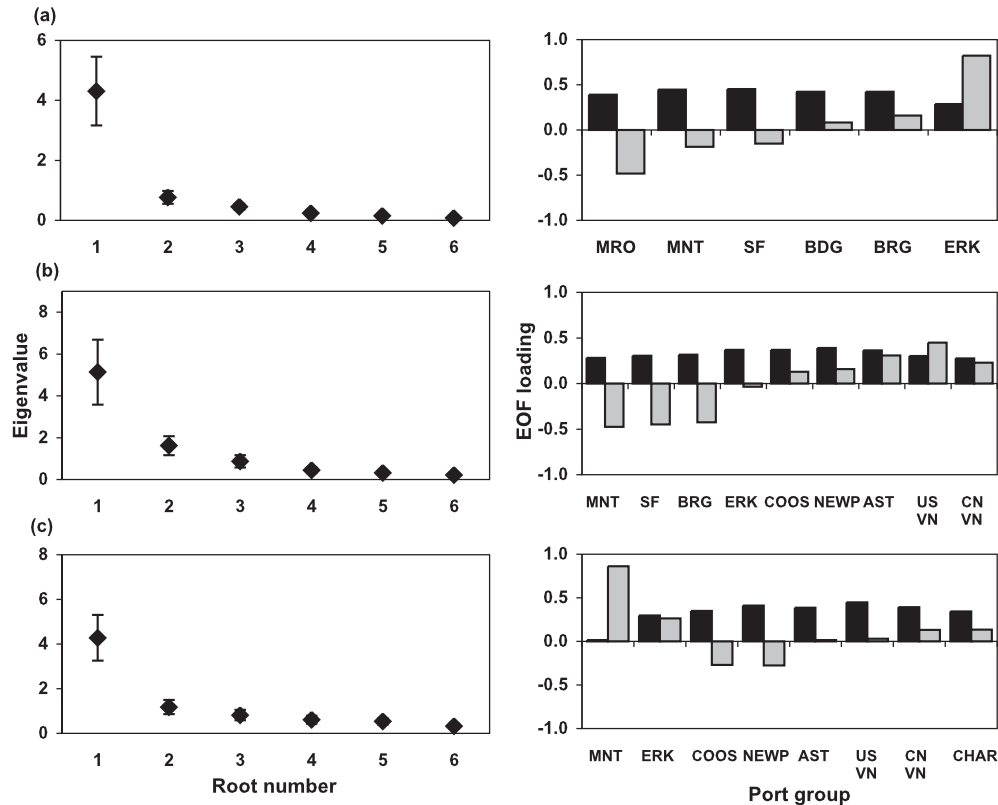
highly significant for all three species. Interestingly, the loadings on the second PC for both chilipepper and widow rockfish seem to explain major regional differences in year-class strength. The signs of the loadings on these PCs reverse from south to north, with the greatest differences again occurring between stocks separated by Cape Mendocino (Fig. 3). This was especially apparent in yellowtail rockfish, where the Monterey stock had virtually no relationship to the first PC but had the greatest loading on the second. Interestingly, if the Monterey time series is excluded from the PCA for yellowtail rockfish, the first PC explains 61% of the variability, with even loadings among locations. The first two PCs, or scores, for each of the three species over time are also shown (Fig. 4).

We tested the sensitivity of the results both to changes in model structure and to the nature of the data used in the PCA (normalized log recruitments, residuals from the spawner–recruit curve, or linearly detrended recruitments). We found that the results changed very little with regard to the analysis when accounting for any of these potential factors. For example, the eigenvalues, loadings, and PCs presented here were based on the logarithm of the resulting recruitments from the suite of models in which the left and right sides of the selectivity curves were freely fit. When only the age at full selectivity was free (simple models) the first PCs explained 73%, 57%, and 49% of the variability for

chilipepper, widow, and yellowtail rockfish, respectively. When all parameters that improved the negative log likelihood (while meeting Akaike's Information Criterion) were free, the first PC of the resulting recruitments explained 72%, 52%, and 53% of the variability, respectively. When the effects of spawning-stock biomass were explicitly removed, by using the recruitment residuals rather than the estimated recruitments, the first PC explained 70%, 55%, and 51% of the variability, respectively. Similarly, when detrended time series of recruitments were used, the first PC explained 72%, 54%, and 51% of the variance, respectively. Finally, we obtained very similar results using both longer (35 years) and truncated (20 years) time series for each of the three species. In all instances, the trajectories of the PCs, or scores, and the loadings on the spatial variables changed very little.

We also evaluated our results with the exponential-decay model with ρ_0 both free and fixed at 1 (Fig. 5). With ρ_0 free, the estimate of ρ_0 was 0.90, and the e-folding scale, v, for all three species was estimated at 800 km, somewhat greater than the average of 500 km for all of the marine stocks estimated by Myers et al. (1997). With ρ_0 constrained to be 1, the estimate of v was 670 km. Although model fit was improved by freeing ρ_0, the improvement was modest, and was not significant based on Akaike's Information Criteria when likelihoods were used to fit the model. If we fit species-

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Fig. 4. Time series of loading values for first (solid symbols and lines) and second (shaded symbols and lines) principal components of recruitment for (*a*) chilipepper, (*b*) widow, and (*c*) yellowtail rockfish.
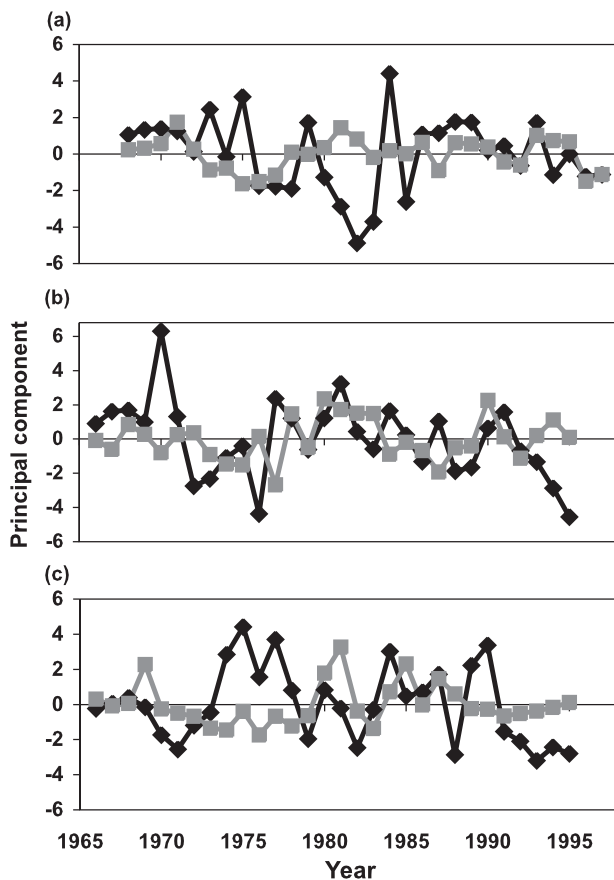
specific curves, the estimated *v* values were 720 (710), 990 (820), and 620 (550) km with ρ_0 free (fixed) for chilipepper, widow, and yellowtail rockfish, respectively. Myers et al. (1997) had previously estimated e-folding rates for North Atlantic *Sebastes* species as well as Pacific Ocean perch, a species for which Gunderson (1977) had earlier noted apparent synchrony over large spatial scales. They estimated a *v* value of 930 km for Pacific Ocean perch and 670 km for North Atlantic *Sebastes* species (both estimates made with ρ_0 fixed at 1), which suggested that *Sebastes* spp. stocks tended to show more synchrony than the overall average. The fact that our results are very similar to those of Myers et al. (1997) for *Sebastes* species in particular reinforces the notion that recruitment within this genus tends to be largely synchronous over broad spatial scales.

Discussion

Our results clearly demonstrate that there is substantial spatial synchrony in year-class strength over scales on the order of 500–1000 km for these, and possibly other, winter-spawning *Sebastes* spp. in the CCS. Intuitively, much of the spatial variability in year-class strength that does exist is associated with major geographic features such as Cape Mendocino and Cape Blanco, both of which have long been

characterized as important physical and biological transitional zones in the CCS (Parrish et al. 1981; Connolly et al. 2001). Cape Mendocino would appear to be a more significant feature based on these results, although the limitations of the data are such that the actual location of catches is somewhat uncertain. Williams and Ralston (2002) also found that Cape Mendocino (and the Mendocino Escarpment) was one of the most noteworthy barriers to the latitudinal distribution of rockfish species.

These observations suggest that large-scale physical forcing mechanisms (1000s of kilometres) may be more important than regional (10s of kilometres) or mesoscale (100s of kilometres) processes in controlling recruitment (at least for the winter-spawning *Sebastes* spp. and at the spatial scales resolvable by this study), despite notable and important spatial differences between north and south of Cape Mendocino. Moreover, these results are consistent with other estimates of spatial scales of recruitment variability by Hollowed and Wooster (1995), as well as variability in landings of Dungeness crab and coho salmon estimated by Botsford and Lawrence (2002). Hannah (1995) also suggested that ocean shrimp (*Pandalus jordani*) recruitment events seem to be synchronous throughout the northern part of the CCS, and linked recruitment variability to large-scale physical forcing. Genetic evidence also suggests high homogeneity for many shelf rockfish species in the CCS. Hedgecock (1994) found that fish and invertebrates with planktonic larvae generally maintain low spatial genetic variance over large (500–2000 km) regions in the CCS, and analysis of a range of *Sebastes* species also suggests little genetic differentiation within the CCS region (Wishard et al. 1980; McGauley and Mulligan 1995; Rocha-Olivares and Vetter 1999).

One unresolved issue in this investigation is the apparent lack of synchrony in year-class strength among these three populations. Although occasional stronger or weaker year classes are shared among the three species, there are no significant correlations among the first PCs for any of the three species, nor among the recruitment deviations for these three stocks, based on the most recent coastwide stock assessments. However, there are strong correlations among these and other stocks, and a PCA of recruitment deviations among seven of the major coastwide stocks (based on stock-assessment results) suggests that some 33%–37% of the variance is shared in the first PC, with even loading across species (J. Field, unpublished data). Similarly, covariance among species is high in 21 years of midwater trawl estimates of pelagic juvenile rockfish abundance, with the 10 most abundant species sharing on the order of 80% of their variance over the 21-year time series (S. Ralston, unpublished data). Different exploitation histories may account for part of these discrepancies, since most of the recent estimates suggest that these stocks range from less than 10% to over 50% of their unexploited biomass, as might a wide range of other physical and biological factors.

Year-class strength in winter-spawning rockfish is thought to be set prior to the late pelagic juvenile stage, because there is strong coherence between the abundance of pelagic juveniles, estimated by midwater trawl surveys, and the abundance of settled (benthic) juveniles over spatial scales of 50–350 km (Ralston and Howard 1995). The abundance

Fig. 5. Predicted correlation values across for the exponential-decay model with ρ_0 (the correlation at a distance of 0) both free (solid line) and fixed at 1 (shaded line). Points are the observed correlations between pairs of regional recruitment time series plotted against the distance between regions.
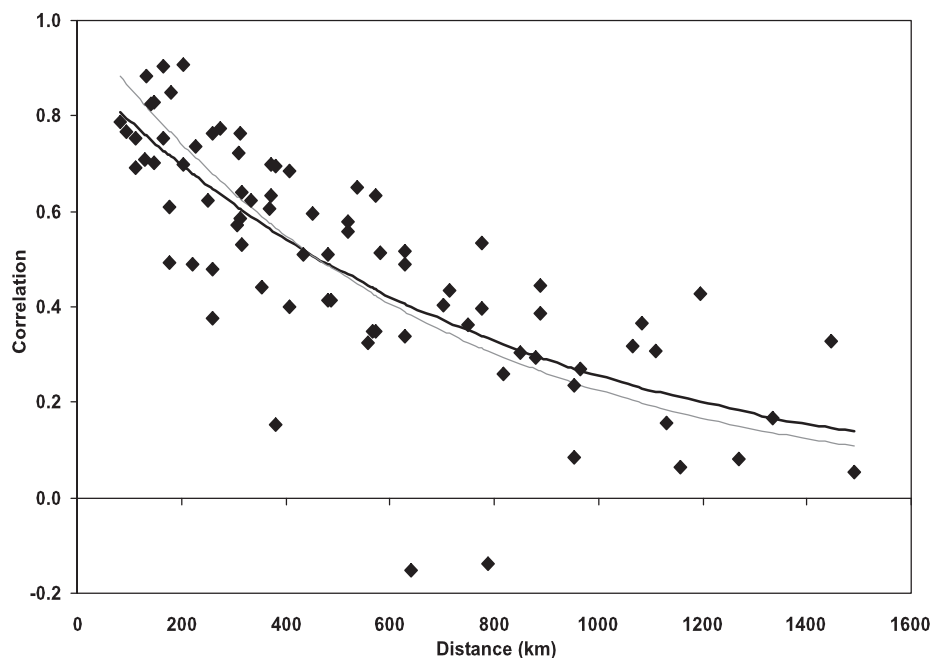
of pelagic juveniles also appears to be strongly correlated with the magnitude of winter (December–February) southward transport in the CCS (S. Ralston, unpublished data). This in turn also seems to have a strong pattern of spatial coherence, which is also reflected by the observation that coastal sea levels vary in phase along the entire west coast (Chelton and Davis 1982; Parrish et al. 2000). If year-class strength is set in the winter (post-extrusion) period, the large spatial covariance in year-class strength would also be consistent with the greater coherence in the physical ocean conditions (wind-derived upwelling, SST, and salinity) described by Mueter et al. (2002) for the winter (as opposed to spring and summer) seasons. By contrast, the salmon survival covariance patterns described by Mueter et al. (2002) and others (Peterman et al. 1998; Pyper et al. 2001) were on smaller spatial scales, perhaps because juvenile salmon survival primarily reflects ocean conditions in spring and summer, when moderate correlations at short distances declined much more rapidly over space than in winter.

An abundance of research has linked the productivity of commercially and ecologically important species throughout the northeast Pacific Ocean with large-scale climate variability, particularly interannual (El Niño/Southern Oscillation scale) and interdecadal (Pacific Decadal Oscillation (PDO) scale) climate forcing (Chelton et al. 1982; MacCall 1996; Francis et al. 1998). The PDO index, which is the leading PC of monthly North Pacific SSTs above 20°N, tracks the dominant patterns of SST variability in the North Pacific Ocean (Mantua et al. 1997). The PDO is closely associated with variations in the Aleutian Low pressure cell, which itself is the leading pattern of atmospheric variability in the North Pacific Ocean (Trenberth and Hurrell 1994). During positive phases of the PDO (which include the period be-

tween 1977 and 1998), coastal SSTs in both the Gulf of Alaska and the CCS tend to be higher, while those in the North Pacific Gyre tend to be lower; the converse is true in negative phases. Although this was first characterized with regard to changes in the productivity of salmon stocks, subsequent studies have identified links with many other marine populations, potentially including many of the west-coast rockfish that seem to have experienced poor reproductive success throughout the 1980s and 1990s (Hare and Mantua 2000; Sydeman et al. 2001; S. Ralston, unpublished data). From 1999 to 2002, ocean conditions seem to have improved for many populations, in association with lower coastal ocean temperatures, high rates of equatorward transport, and enhanced productivity of zooplankton and forage fish throughout the CCS. Such changes have been described as indicative of a possible 1999 phase shift in the PDO (Brodeur et al. 2003; Peterson and Schwing 2003). However, while the spatial patterns of warming and cooling over the last 4 years have been similar to those observed prior to 1977 for the CCS and other areas, they have been extremely different in others (Bond et al. 2003), and as the PDO index was mostly positive from 2003 through 2004, there are substantial uncertainties regarding future climate trends.

Juvenile-recruitment indices from the midwater trawl surveys have related well to recruitments estimated from coastwide stock assessments for several species, including chilipepper rockfish (Ralston et al. 1998), widow rockfish (Williams et al. 2000), and Pacific hake, *Merluccius productus* (Sakuma and Ralston 1997; Helser et al. 2002). Consequently, these recruitment indices have been incorporated into assessments as an index of year-class strength for these species. As Adams and Howard (1996) document density-dependent variability in natural mortality rates of newly

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settled juvenile blue rockfish (*Sebastes mystinus*), such that greater juvenile abundance is associated with a higher mortality rate, these indices are transformed prior to inclusion in the assessments. Given that recent surveys of juveniles cover a relatively modest (approximately 200 km) section of coastline, the evidence of spatial synchrony presented here supports the contention that these surveys are representative of larger scale trends in recruitment. The results may also have implications regarding larval dispersal and population connectivity, which might be particularly relevant to future spatially based management efforts. While marine protected areas and other spatial management measures are widely acknowledged to be an effective tool for protecting habitat and biodiversity, there remain questions regarding their impacts on future yield, many of which are centered on unanswered questions regarding the degree of connectedness and dispersal within populations (Warner et al. 2000; Hilborn et al. 2004). For example, Botsford et al. (2003) demonstrate that species with greater dispersal will likely require larger fractions of coastline in reserves if reserves are to function comparably to conventional fisheries management. While the results reported in this paper, taken alone, are not evidence of high rates of dispersal of rockfish larvae and juveniles, they do demonstrate that one reasonable expectation for high dispersal rates, synchrony in year-class strength over large spatial scales, is met for these (and presumably other) winter-spawning species.

It is increasingly evident that the low productivity, extreme longevity, and highly variable recruitment that characterize most rockfish populations are crucial life-history adaptations to their highly dynamic environment, adaptations that concurrently make such species vulnerable to overexploitation (Leaman and Beamish 1984; Parker et al. 2000; Longhurst 2002). The ability to directly and indirectly estimate year-class strengths from surveys and other sources, as well as to better understand the relationship between environmental conditions in the CCS, should improve short-term forecasts of productivity, biomass levels, and allowable catches from stock assessments. This in turn should lead to better long-term understanding and prediction of both production trends and rebuilding trajectories for overfished and depleted species.

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