# Recruitment and survival of Northeast Pacific Ocean fish stocks: temporal trends, covariation, and regime shifts

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**Abstract:** Two measures of productivity for fish stocks (recruitment and stock–recruit residuals) within two large marine ecosystems (Gulf of Alaska and eastern Bering Sea – Aleutian Islands) showed significant positive covariation within several groups of species and significant negative covariation between certain others. For example, stock–recruit residuals of gadids (Gadidae) in the Bering Sea were inversely related to those of shelf flatfishes (Pleuronectidae), suggesting that environmental forcing affects these groups in opposite ways. Salmon (*Oncorhynchus* spp.), Pacific herring (*Clupea pallasii*), and groundfish stocks each showed strong patterns of covariation within these taxonomic groups and within ecosystems, and both salmon and groundfish stocks showed positive covariation between the two ecosystems. However, we found little evidence of covariation between salmon and herring stocks or between these stocks and demersal stocks. Recruitment and stock–recruit residuals in individual stocks did not show a consistent response to known climatic regime shifts. However, combined indices of productivity across stocks showed decadal-scale variability (regime-like patterns), suggesting that both pelagic productivity (mostly salmon) and demersal productivity increased in response to the well-documented 1976–1977 climatic regime shift, whereas the 1988–1989 regime shift produced inconsistent or short-lived responses.

**Résumé :** Deux mesures de la productivité des stocks de poissons (résidus du recrutement et des stocks–recrues) dans deux grands écosystèmes marins (golfe d'Alaska et est de la mer de Bering – îles Aléoutiennes) affichent une covariation positive significative chez plusieurs groupes d'espèces et une covariation négative significative chez certains autres. Par exemple, les résidus stocks–recrues des gadidés (Gadidae) de la mer de Bering sont en relation inverse avec ceux des poissons plats du plateau continental (Pleuronectidae), ce qui laisse croire que le forçage environnemental affecte ces groupes de manière inverse. Les stocks de saumons (*Oncorhynchus* spp.), de harengs (*Clupea pallasii*) et de poissons de fond montrent tous de forts patrons de covariation à l'intérieur de ces groupes taxonomiques et au sein des écosystèmes; les stocks de saumons et de poissons de fond montrent tous les deux une covariation positive entre les deux écosystèmes. Nous ne trouvons que peu d'indication de covariation entre les stocks de harengs et de saumons ou entre ces stocks et les stocks benthiques. Les résidus du recrutement et des stocks–recrues dans les stocks individuels n'offrent pas de réponse uniforme aux changements connus du régime climatique. Cependant, les indices combinés de productivité dans tous les stocks montrent une variabilité (patrons typiques d'un régime) à l'échelle de la décennie; cela indique que la productivité pélagique (surtout du saumon) et la productivité profonde ont augmenté toutes les deux en réaction au changement de régime climatique bien étudié de 1976–1977, alors que le changement de régime de 1988–1989 a produit des réactions irrégulières ou de courte durée.

[Traduit par la Rédaction]

## Introduction

The abundance and productivity of commercial fish stocks varies on interannual and interdecadal time scales as a result of environmental variations, species interactions, and fishing. Although the relative magnitude of these effects is not known, it is widely believed that environmental conditions have a dominant influence on productivity of fish populations in the Northeast Pacific Ocean through bottom-up forcing (e.g., Francis et al. 1998). Large-scale patterns of environmental variability and decadal-scale regime shifts in the Northeast Pacific appear to coincide with changes in many biological communities (Hare and Mantua 2000). For example, shifts in the mean state of the Pacific Decadal Oscillation (PDO), the dominant pattern of sea-surface temperature variability over much of the 20th century (Mantua and

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912

Can. J. Fish. Aquat. Sci. Vol. 64, 2007

Hare 2002), correspond to similar shifts in catches of several salmon species (*Oncorhynchus* spp.) aggregated across large areas (Hare and Francis 1995). Similarly, variability in recruitment of many groundfish (demersal) stocks in the Northeast Pacific is characterized by synchronous strong year classes, with timing and frequency that appear to be related to interannual and decadal-scale variations in sea-surface temperature, which is in turn related to El Niño and decadal-scale variability (Hollowed and Wooster 1995; Hollowed et al. 2001). Field and Ralston (2005) also documented substantial spatial synchrony in recruitment within each of three rockfish species (*Sebastes* spp.) across locations of up to about 1000 km in the California Current system, but they did not use environmental data to interpret the observed synchrony.

Previous studies have also found regional-scale synchronicity within species for herring and salmon stocks in the Northeast Pacific. In contrast to many recent studies that have focused on large-scale climate variability at decadal time scales, stock-specific survival rates of salmon from spawners to adults tend to be dominated by interannual variability and show positive covariation among stocks at smaller spatial scales of only a few hundred kilometres (Peterman et al. 1998; Botsford and Paulsen 2000; Pyper et al. 2001). These salmon survival rates are more strongly related to local or regional-scale variability in coastal sea-surface temperatures during early ocean life than to large-scale indices such as the PDO (Mueter et al. 2002*a*). Similarly, recruitment of Pacific herring (*Clupea pallasi*) stocks in British Columbia, southeastern Alaska coastal waters, the outer Gulf of Alaska, and the Bering Sea is positively correlated within each of these four regions but is largely uncorrelated between regions (Williams and Quinn 2000). Herring and salmon recruitment in the Bering Sea and Gulf of Alaska typically increase with increasing coastal ocean temperatures, whereas recruitment of more southern stocks from British Columbia (B.C.) and Washington is reduced by high coastal sea-surface temperatures during the early ocean life phase (Williams and Quinn 2000; Mueter et al. 2002*a*), implying that synchronous changes in coastal temperatures affect recruitment of southern and northern stocks in opposite ways.

The observation that catches, recruitment, or survival rates of numerous pelagic and demersal fish stocks are linked to local and large-scale variability in sea-surface temperature suggests that widespread covariation or synchronicity in productivity might also occur across species as a result of shared environmental forcing and its influence on productivity of lower trophic levels. Positive covariation is apparent in long-term catch trends of different Pacific salmon species (Beamish and Bouillon 1993; Hare et al. 1999) and in the appearance of synchronous strong year classes in major Northeast Pacific groundfish populations (Hollowed and Wooster 1995; Hollowed et al. 2001). However, the magnitude and spatial scale of covariation across different species in the North Pacific has rarely been quantified. Notable exceptions are Botsford and Lawrence (2002) for Dungeness crab (*Cancer magister*) and Chinook (*Oncorhynchus tshawytscha*) and coho (*O. kisutch*) salmon, Pyper et al. (2005) for sockeye (*O. nerka*), pink (*O. gorbuscha*), and

chum (*O. keta*) salmon, and Field and Ralston (2005) for three rockfish species.

To improve our understanding of how climate variability affects different fish populations within species, as well as across species, in the Northeast Pacific, we conducted a comprehensive analysis of covariation patterns among groundfish, salmon, and herring stocks off Alaska. Our goal was to quantify the spatial extent of covariation in productivity, as measured by recruitment or survival rate indices (stock–recruit residuals, which can be interpreted as survival rates adjusted for density dependence), among major commercial fish stocks in the Bering Sea – Aleutian Islands and the Gulf of Alaska ecosystems (Fig. 1). Specifically, we examined time series of recruitment and survival rate indices for the presence of either positive or negative covariation among stocks within each ecosystem and between ecosystems. In addition, we examined trends in the indices for individual stocks and across stocks within each ecosystem for evidence of decadal-scale variability and abrupt shifts in the mean state of an index. Our general hypotheses included (1) recruitment–survival of different demersal stocks within the two regional ecosystems do not vary independently; (2) recruitment–survival of demersal stocks is correlated between ecosystems; (3) recruitment–survival of salmon and herring stocks varies independently from that of demersal stocks; (4) temporal variability in recruitment–survival is dominated by decadal-scale patterns; and (5) abrupt shifts in mean recruitment or survival occur more frequently than expected by chance. Each of these hypotheses was tested against the null hypothesis of no significant correlations among time series of productivity (hypotheses 1–3) or no significant temporal trends in productivity series (hypotheses 4–5).

## Materials and methods

### Data sources

We compiled data from various agencies and researchers. Time series of spawning biomass and recruitment for 23 stocks of groundfish from the Bering Sea and Aleutian Islands region (BSAI, 11 stocks) and Gulf of Alaska (GoA, 12) were obtained from 2005 stock assessments (Table 1). Recruitment estimates for recent years were not included if deemed unreliable by management agency authors of the assessment. Spawner abundances and number of recruits by ocean-entry year were obtained for 14 regional stock groups of sockeye (4 groups), pink (5), and chum (5) salmon between northern British Columbia and western Alaska (Table 1). The number of spawners and recruits of pink and chum salmon were combined across stocks within regions for which there was strong within-species positive covariation in survival rates, as identified in Pyper et al. (2001). Spawner and recruit data for sockeye salmon stocks were similarly combined within regions as summarized in Table 1. Salmon within each of these regions were treated as a single stock (or "stock group") in the analysis. We obtained time series of spawning stock biomass and recruitment for 13 herring stocks from Williams and Quinn (2000) and used these to describe spatial covariation among herring stocks. Because these time series had little overlap with some of the salmon and groundfish stocks, we used updated time series

**Fig. 1.** Map of Northeast Pacific showing the Bering Sea – Aleutian Islands and the Gulf of Alaska ecosystems (hatched areas).
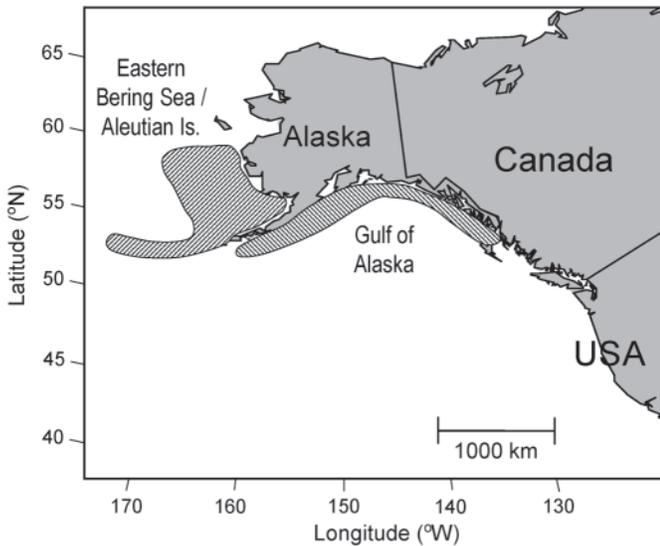


of spawning biomass and recruitment for the Togiak herring stock, for Prince William Sound herring, and for several Southeast Alaska herring stocks combined (Table 1) in the analysis of covariation. All demersal stocks included here, with the exception of sablefish and Pacific halibut, are assessed and managed as a unit stock within one of the two ecosystems. The sablefish stock ranges throughout the GoA and into the BSAI region but was assigned to the GoA ecosystem because 91% of total Alaskan sablefish catches over the last decade (1993–2002) occurred within the GoA. Pacific halibut are assessed separately within different regions, but we included only the GoA portion of the stock (International Pacific Halibut Commission regulatory areas 2B, 2C, and 3A combined) because time series in the BSAI were too short for our analysis.

### Indices of fish productivity

We used two different measures of productivity in our analyses: (i) log-transformed recruitment estimates (log $R$, using natural logarithm) and (ii) stock–recruit residuals (SR index) from the best-fit stock–recruitment model as defined below. Recruitment of groundfish and herring stocks was simply the estimated number of recruits at the youngest age that was estimated in age-structured assessment models. Age at recruitment varied from age 1 to age 6 (Table 1). Recruitment of salmon stocks was estimated as the total number of salmon from a given brood (spawning) year that survive to either be caught in the fishery or escape to spawn (for further details, see data sources in Table 1). All recruitment estimates were log-transformed to reduce the influence of exceptionally strong year classes and to obtain an index that is more appropriate in correlation analyses, which can be sensitive to outliers. The SR index was obtained for each of the stocks or stock groups listed in Table 1 by computing residuals from a stock–recruitment model that was fit to time series of recruits resulting from parental spawning in year $t$ ($R_t$) and the corresponding spawner abundance or biomass ($S_t$). Models were fit on a log scale with log(survival), i.e., log($R_t/S_t$), as the dependent variable and $S_t$ as the independ-

ent variable (see below). This has the effect of removing presumed density-dependent effects of spawner abundance on survival rates; hence, the SR index reflects unexplained variability in recruitment resulting from environmental fluctuations and measurement errors (e.g., Peterman et al. 1998).

Because the form of the stock–recruitment relationship is unknown and may vary among stocks, we fit several models to each spawner–recruit series, including the two-parameter Ricker and Beverton–Holt (BH) models. Functional forms and parameter estimation routines are described in Quinn and Deriso (1999). Models assumed a multiplicative, lognormal error structure and took the following general form:

$$\log(R_t/S_t) = f(S_t) + \varepsilon_t$$

where $f()$ denotes a function describing the stock–recruitment relationship on the log-transformed scale and $\varepsilon_t$ denotes the normally distributed residual for year $t$. Residuals were assumed to be either independent and identically distributed or first-order autocorrelated (see below), and $S_t$ was assumed to be known without error. Models were fit using linear (Ricker) or nonlinear (BH) least-squares regression.

Annual stock–recruit residuals are often not statistically independent and we tested for significant autocorrelation by fitting autoregressive models ranging from order 0 (independent observations) to order 6 (up to 6-year "memory") to each residual series. With few exceptions, residuals were independent or were best approximated by a first-order autoregressive process. Therefore, to account for time-series dependence in log(survival), we fit each of the models with and without first-order autocorrelation ($\varepsilon_t = \phi_1 \varepsilon_{t-1} + \nu_t$, where $\phi_1$ is the first-order autoregressive coefficient and $\nu_t \sim N(0, \sigma_\nu^2)$). Models with autocorrelated residuals were fit using a linear or nonlinear generalized least-squares approach as implemented in S-Plus (Pinheiro and Bates 2000). The statistically best model for each stock was selected from the set of four different models (Ricker and BH models with or without first-order autocorrelation) based on the small-sample Akaike information criterion (AIC$_c$; Hurvich and Tsai 1989). We then used residuals from the model with the lowest AIC$_c$ score as our final SR index in further analyses.

To compare recruitment and stock–recruit residuals among stocks and to estimate the magnitude of covariation, we aligned all indices (log $R$ and SR) by year class, which was defined as the larval stage (age 0) for groundfish and herring and as the year of ocean entry (outmigration) for juvenile salmon. The larval stage was used for groundfish and herring because much of the variability in survival and recruitment is generally believed to be determined during early life stages. However, by aligning stocks in this manner, the mechanisms that induce covariation among stocks may occur at any life stage, as long as they occur at the same stage in different species. Ocean-entry year was used for salmon because much of the variability in overall spawner-to-recruit survival is due to variability during the early ocean phase (Peterman 1987; Pyper et al. 2005) and because it is the only time when juvenile salmon share the coastal environment with early life stages of nonsalmonid coastal marine species. Pink and chum salmon enter the coastal ocean at age 1 year, sockeye salmon from B.C. enter the ocean at age 2, and all

914

Can. J. Fish. Aquat. Sci. Vol. 64, 2007

**Table 1.** Stocks and stock groups used in analyses by species and region (BSAI, Bering Sea – Aleutian Islands; GoA, Gulf of Alaska; cGoA, central Gulf of Alaska; wGoA, western Gulf of Alaska, etc.; PWS, Prince William Sound; SEAK, Southeast Alaska; nBC, northern British Columbia), range of year classes for which both spawner and recruitment data were available, age for recruitment as specified in age-structured assessment models, the best stock–recruitment model (BH, Beverton–Holt), the autoregressive coefficient ($\phi_1$) for residuals from the stock–recruitment model, if significant at $\alpha = 0.05$, proportion of deviance (% Dev.) explained by decadal-scale trends, associated $p$ values, and significant trends in log $R$ and SR series.

| Scientific name | Common name | Region | Year classes | Age | Model | $\phi_1$ | % Dev. | $p$ value | Linear trend log $R$ | Linear trend SR |
|---|---|---|---|---|---|---|---|---|---|---|
| *Atheresthes stomias* | Arrowtooth flounder | BSAI[a] | 1976–2001 | 2 | BH | | 40.0 | 0.053 | + | |
| | | GOA[b] | 1961–2001 | 3 | BH | 0.89 | **89.2** | **<0.001** | + | |
| *Hippoglossoides elassodon* | Flathead sole | BSAI[a] | 1977–2002 | 3 | Ricker | | 14.3 | 0.674 | – | |
| | | GOA[b] | 1984–2001 | 3 | Ricker | | 22.9 | 0.460 | | |
| *Reinhardtius hippoglossoides* | Greenland turbot | BSAI[a] | 1974–2001 | 1 | Ricker | 0.95 | **77.6** | **<0.001** | | |
| *Hippoglossus stenolepis* | Pacific halibut | GOA[c] | 1974–1999 | 6 | Ricker | | 26.3 | 0.257 | + | |
| *Limanda aspera* | Yellowfin sole | BSAI[a] | 1964–2000 | 5 | Ricker | | 36.0 | 0.052 | – | |
| *Lepidopsetta* sp. | Rock sole | BSAI[a] | 1975–1999 | 4 | Ricker | 0.51 | **56.8** | **0.004** | | |
| *Pleuronectes quadrituberculatus* | Alaska plaice | BSAI[a] | 1975–2001 | 3 | BH | | **44.4** | **0.022** | – | – |
| *Glyptocephalus zachirus* | Rex sole | GOA[b] | 1982–2001 | 3 | Ricker | | **46.7** | **0.040** | | |
| *Microstomus pacificus* | Dover sole | GOA[b] | 1984–2001 | 3 | Ricker | | 6.8 | 0.913 | | |
| *Theragra chalcogramma* | Walleye pollock | BSAI[a] | 1964–2003 | 1 | Ricker | | 19.5 | 0.476 | – | – |
| | | GOA[b] | 1969–2003 | 2 | BH | 0.56 | **51.1** | **0.004** | | |
| *Gadus macrocephalus* | Pacific cod | BSAI[a] | 1964–2003 | 0 | BH | 0.38 | **55.2** | **<0.001** | – | |
| | | GOA[b] | 1964–2003 | 0 | BH | 0.35 | **47.7** | **0.005** | | |
| *Pleurogrammus monopterygius* | Atka mackerel | BSAI[a] | 1977–2002 | 1 | Ricker | | 35.6 | 0.094 | | |
| *Anoplopoma fimbria* | Sablefish | GOA[b] | 1960–2003 | 2 | Ricker | | 16.4 | 0.668 | | |
| *Sebastes alutus* | Pacific ocean perch | BSAI[a] | 1960–1994 | 3 | BH | | **47.6** | **0.008** | + | |
| | | GOA[b] | 1961–2001 | 2 | BH | 0.56 | 31.6 | 0.085 | | |
| *Sebastes polyspinis* | Northern rockfish | BSAI[a] | 1977–1994 | 3 | Ricker | | 25.8 | 0.385 | + | |
| | | GOA[b] | 1977–1999 | 2 | Ricker | | 19.1 | 0.351 | | |
| *Sebastes variabilis* | Dusky rockfish | GOA[b] | 1977–2001 | 4 | Ricker | | **68.1** | **<0.001** | + | |
| *Sebastes aleutianus* | Rougheye rockfish | GOA[b] | 1977–2001 | 3 | Ricker | | 17.3 | 0.565 | + | |
| *Oncorhynchus nerka*[d] | Sockeye salmon | BSAI | 1959–1996 | | Ricker | 0.61 | **67.6** | **<0.001** | + | + |
| | | wGoA | 1953–1996 | | Ricker | | 17.2 | 0.550 | + | |
| | | cGoA | 1973–1994 | | Ricker | | 27.0 | 0.227 | + | – |
| | | nBC | 1969–1993 | | BH | | 23.4 | 0.364 | + | |
| *Oncorhynchus keta*[e] | Chum salmon | BSAI | 1979–1993 | | BH | | 37.6 | 0.144 | + | + |
| | | wGoA | 1963–1993 | | BH | 0.59 | **53.5** | **0.003** | + | |
| | | cGoA | 1973–1993 | | BH | | **52.5** | **0.014** | – | – |
| | | PWS | 1967–1994 | | BH | 0.56 | **66.1** | **<0.001** | | |
| | | nBC | 1966–1993 | | BH | | 17.9 | 0.605 | | |
| *Oncorhynchus gorbuscha*[f] | Pink salmon | wGoA | 1963–1996 | | BH | 0.60 | **58.8** | **0.001** | + | + |
| | | Kodiak | 1963–1997 | | Ricker | | 15.4 | 0.672 | + | |
| | | cGoA | 1972–1997 | | BH | | 27.7 | 0.224 | | |
| | | SEAK | 1961–1997 | | BH | 0.34 | **39.2** | **0.029** | + | + |
| | | nBC | 1951–1996 | | Ricker | | 20.6 | 0.406 | | |

**Table 1** (concluded).

| Scientific name | Common name | Region | Year classes | Age | Model | $\phi_1$ | % Dev. | p value | Linear trend log R | SR |
|---|---|---|---|---|---|---|---|---|---|---|
| *Clupea pallasi* | Pacific herring | BSAI[g] | 1977–2001 | 4 | BH | | **67.2** | **<0.001** | | – |
| | | PWS[h] | 1980–2002 | 3 | BH | | 20.7 | 0.512 | | |
| | | SEAK[i] | 1980–2000 | 3 | BH | | 17.8 | 0.504 | | |

**Note:** Year classes for salmon denote year of ocean entry. The percent deviance explained (% Dev.) is an estimate of the proportion of variability in stock-recruit residuals accounted for by decadal-scale trends (see text), and the associated p value denotes the significance of decadal-scale patterns relative to a constant mean model, based on an approximate $\chi^2$ test. Boldface cases are significant at the 0.05 level. Significant ($p < 0.05$) positive (+) and negative (–) linear trends in log recruitment (log R) and stock–recruit residuals (SR) are based on a generalized least-squares regression with first-order autocorrelated residuals. All *Oncorhynchus* and *Clupea* species are referred to in the text as "pelagic" stocks; all others are "demersal" stocks.

[a]Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea – Aleutian Islands regions, North Pacific Fishery Management Council, 605 W. 4th Avenue, Suite 306, Anchorage, AK 99501, USA.

[b]Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska, North Pacific Fishery Management Council, 605 W. 4th Ave., Suite 306, Anchorage, AK 99501, USA.

[c]Stephen Hare, International Pacific Halibut Commission, P.O. Box 95009, Seattle, WA 98145-2009, USA (personal communication).

[d]Individual sockeye stock data sets are from Peterman et al. (1998) and Mueter et al. (2002b). Stocks were combined within the Bering Sea (eight Bristol Bay stocks, Nuyakuk excluded because of missing years), western GoA (Black and Chignik lakes), central GoA (four stocks from Kodiak Island, Cook Inlet, and Copper River), and Northern B.C. (Skeena and Nass rivers). Outmigration was assumed to occur at age 3 for Alaska sockeye stocks and age 2 for stocks in British Columbia.

[e]Chum salmon data based on Pyper et al. (2002). Data were combined by region within the Bering Sea (Bristol Bay, Yukon, and Norton Sound stocks), western GoA (Alaska Peninsula and Chignik), central GoA (Kodiak and Cook Inlet), Prince William Sound, and northern British Columbia.

[f]Pink salmon stocks were combined within five regions based on fig. 5 in Pyper et al. (2001), excluding Norton Sound and Washington stocks.

[g]Fred West, Alaska Department of Fish and Game, Anchorage, Alaska (personal communication).

[h]Steve Moffit, Alaska Department of Fish and Game, Cordova, Alaska (personal communication).

[i]Sherri Dressel, Alaska Department of Fish and Game, Juneau, Alaska (personal communication; sum of all Southeast Alaska stocks.

sockeye salmon smolts from Alaska were assumed to enter the ocean at age 3.

## Data analysis

We describe patterns of variability and covariation in productivity of Northeast Pacific fish stocks by several methods, as detailed below: (*i*) examining the frequency distribution and temporal variability of log R and SR indices; (*ii*) quantifying the spatial scales of covariation among salmon stocks and among herring stocks, as well as between salmon and herring stocks, based on pair-wise correlations among log R or SR indices; (*iii*) testing for significant covariation between pelagic (salmon and herring) and demersal stocks within both ecosystems and among different demersal stocks within and between ecosystems (Fig. 2); (*iv*) identifying clusters of demersal stocks that showed similar patterns of variability; (*v*) developing combined indices of variability in log R and SR across all demersal stocks and across all pelagic stocks within a given ecosystem; and (*vi*) identifying significant change points (years with a significant step change) in log R and SR time series for individual stocks, stock clusters, and ecosystems.

### Frequency distribution and temporal variability

The distribution of each log R and SR series was examined for univariate outliers, which may have an undue influence in the analysis of trends. Because outliers (>2.5 standard deviation, SD, from the mean) existed in some series, we repeated the trend analyses with these outliers excluded. We examined temporal variability in log R and SR indices to quantify the extent of autocorrelation and the magnitude of interannual variability relative to long-term, decadal-scale trends. Covariation in productivity among stocks may be due to shared variability at interannual scales or at longer, e.g., decadal, scales. To quantify the magnitude of interannual- and decadal-scale variability, we fit nonparametric smoothing splines (cubic B-spline smoother) to each of the time series (Hastie and Tibshirani 1990) and computed the proportion of overall variability that was attributable to decadal-scale trends as the proportion of overall deviance explained by the smooth fit. The deviance is a likelihood ratio statistic for generalized linear and additive models that is roughly equivalent to the coefficient of determination in linear models (see, e.g., Hastie and Tibshirani 1990). Smoothing splines were constrained to have approximate degrees of freedom (df) in proportion to the length of each time series (df = 2T/10 years, where T is the number of years in the series). Although the degree of smoothing was arbitrary, the denominator (10 years) ensures that if there is a trend in the smoothed series, it will roughly correspond to the decadal-scale variability that is dominant in many biological and physical time series in the Northeast Pacific (Hare and Mantua 2000). By fixing the degree of smoothing across time series of equal length, we ensured that the proportion of variability accounted for by smooth trends was comparable across series. However, the shape of the smooth functions could vary greatly between series. For each time series, we tested whether a decadal-scale trend based on smoothing splines provided a significantly better fit than a constant mean model, using an approximate $\chi^2$ test (Wood 2000). In addition, we tested whether significant lin-

916

Can. J. Fish. Aquat. Sci. Vol. 64, 2007

**Fig. 2.** Schematic of types of comparisons among different groups of species within and between the Gulf of Alaska and Bering Sea – Aleutian Islands. Each stock is depicted by a small circle. Salmon stocks include sockeye (S), chum (M), and pink (P) salmon.
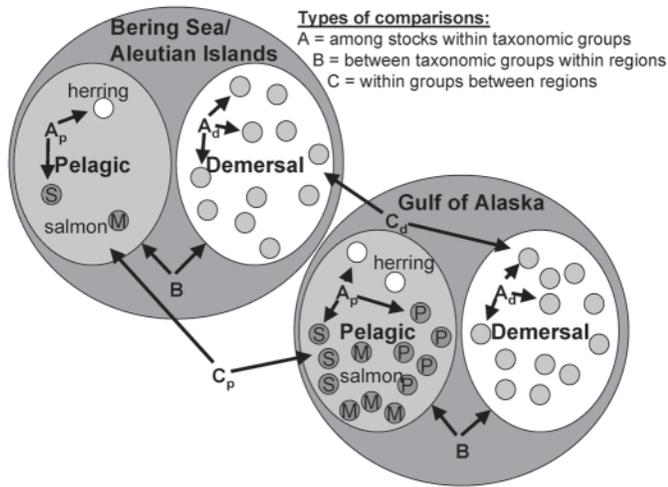


ear time trends were present in the time series by fitting generalized least squares regressions that allowed for first-order autocorrelated residuals to each log $R$ and SR series.

### Spatial scales of covariation of salmon and herring stocks

Spatial scales of covariation among different salmon species are quantified in Pyper et al. (2005). We used the same approach to quantify the spatial scale of covariation among SR indices of 13 herring stocks. We first computed Pearson's product-moment correlations between each pair of log $R$ (or SR) series based on all years that had data for both series in a given pair. Although trend removal or prewhitening is sometimes used before computing correlation to focus on covariation at interannual scales, we computed correlations among "raw" (rather than detrended) indices. Therefore, the patterns of covariation described here reflect shared variability among stocks at all time scales. Bivariate outliers may have a strong influence on pair-wise correlations and could lead to erroneous conclusions. Therefore, we used two methods to guard against such errors. First, we computed Spearman's rank correlations, which are not affected by outliers, and compared results with the analysis of Pearson's correlations. Second, we examined scatterplot matrices of all pairs of indices for potentially influential outliers. These analyses revealed several influential observations that were evident both in individual series and in bivariate scatterplots. Eliminating these observations or using rank-based correlations resulted in larger absolute correlations and would have strengthened our conclusions. Because there was no a priori reason to exclude these observations, we show results based on Pearson's product-moment correlations with all observations included.

We described the spatial extent of covariation among herring stocks by plotting pair-wise correlations between log $R$ (or SR) series of different stocks as a function of the geographical distance separating their centers of distribution. Average correlations at a given separation distance were esti-

mated by fitting a nonparametric covariance function (Bjørnstad and Falck 2000) to the observed correlations as a function of distance. Similarly, we computed pair-wise correlations between the SR indices of all salmon stocks for a given species (sockeye, pink, or chum salmon) and the SR indices of herring stocks. To estimate average correlations between SR indices of herring and salmon stocks by distance, we fit a nonparametric covariance function to the relationship between the observed pair-wise correlations and the geographical distance separating the ocean entry point of a given salmon stock from the center of distribution of a given herring stock.

### Covariation patterns of demersal and pelagic stocks

Unlike herring and salmon, which can be divided into multiple regional stocks, the demersal species examined here typically consist of a single management unit and (or) biological population (i.e., a single stock) within a given ecosystem. Therefore it was not possible to describe spatial patterns of covariation within a species as a function of distance using covariance functions. Instead, we examined covariation among different demersal stocks or species within and between ecosystems (comparisons $A_d$ and $C_d$, respectively, in Fig. 2) and between demersal and pelagic stocks within each ecosystem (comparisons B in Fig. 2). To summarize correlations among log $R$ series of demersal stocks, we plotted frequency distributions (histograms) of all pair-wise correlations within and between ecosystems. Correlations among SR series were examined similarly. The observed correlations will differ from zero because of random variability and because of true covariation between stocks (positive or negative). Because we examined multiple pair-wise correlations, univariate tests are not appropriate to detect significant covariation. Instead, we evaluated whether the frequency distribution of pair-wise correlations differed from the expected distribution under the null hypotheses ($H_0$) that stocks vary independently, i.e., that log $R$ (or SR) series for a given group of stocks (for example, all demersal stocks in the GoA) are independent of each other.

In the presence of significant covariation among stocks, the observed frequency distribution of correlations may differ from that expected under $H_0$ in at least two important ways. First, the average correlation ($\bar{r}$) may differ from zero. Second, correlations may be more dispersed than expected under $H_0$, implying both significant positive and significant negative covariation among stocks. To test whether $\bar{r}$ among a group of stocks significantly differed from zero, we used randomization tests to obtain the expected distribution of $\bar{r}$ under $H_0$. The randomization procedure was designed to account for autocorrelation in the time series and for observed within-group correlations when testing correlations between groups, as described in detail in Pyper et al. (2001). Specifically, we examined the following hypotheses with regard to covariation in productivity (as measured by log $R$ or SR indices) within and between different groups of fish stocks. First, for both ecosystems (BSAI and GoA), we tested whether the average correlation between log $R$ (or SR) indices across all pairs of demersal stocks was significantly different from zero (comparisons $A_d$ in Fig. 2). Pelagic stock groups within each system were compared in the same way

(comparisons $A_p$ in Fig. 2). Second, we tested whether average correlations between indices for pelagic stocks in a given ecosystem and indices for demersal stocks in the same ecosystem were significantly different from zero (comparisons B in Fig. 2). Third, we tested whether average correlations among indices for demersal stocks from different ecosystems (i.e., groundfish stocks in the BSAI versus those in the GoA) were significantly different from zero (comparison $C_d$ in Fig. 2). Pelagic stocks were compared between ecosystems in the same way (comparison $C_p$ in Fig. 2). If, for any groups, average correlations were not significantly different from zero, we tested for significant overdispersion in the frequency distribution of all pair-wise correlations. Overdispersion implies larger absolute correlations ($|r|$) than expected under $H_0$ or, equivalently, a larger variance of the observed correlations ($\sigma_r^2$) than expected. Therefore, we compared the observed values of $|r|$ and $\sigma_r^2$ with those expected under the null hypothesis of no significant overdispersion. The expected distribution of $|r|$ and $\sigma_r^2$ under $H_0$ was obtained as part of the same randomization procedure that was used to test average correlations as described above and in Pyper et al. (2001). The tests for overdispersion are only valid if average correlations are not significantly different from zero because such a difference implies significantly higher absolute correlations (as can be easily verified through simulations).

### Clustering of demersal stocks

To identify groups of demersal stocks that vary in similar ways within each ecosystem, we applied hierarchical clustering using Ward's minimum variance method and Euclidean distances (Kaufman and Rousseeuw 1990) to the log $R$ and, separately, to the SR index series within each system. Pairwise Euclidean distances among the standardized series were computed using all years of overlap between the two component series of a given pair. To examine the sensitivity of results to the distance measure and clustering algorithm, we also used Manhattan distances (sum of absolute differences) and average linkage clustering with both Euclidean and Manhattan distances. Results based on different clustering algorithms were examined for consistency. If consistent clusters were identified, we combined the log $R$ (or SR) series within each cluster by standardizing each series (zero mean and unit variance) and computing the mean across series to obtain a single time series of log $R$ (or SR) indices for each cluster. The resulting time series characterize variability in recruitment or survival rates of the major groups of positively covarying species. We assume that positive covariation results from shared environmental influences on recruitment or survival rates; hence combining series may provide a clearer "signal" of the underlying environmental influences than that provided by individual time series, which are more variable because of random observation errors.

### Combined indices of recruitment and survival rate

In addition to stock-specific and cluster-specific indices of productivity, we combined log $R$ and SR across all demersal and pelagic stocks within the BSAI and GoA, respectively. Each time series of log $R$ indices was first standardized and indices were averaged f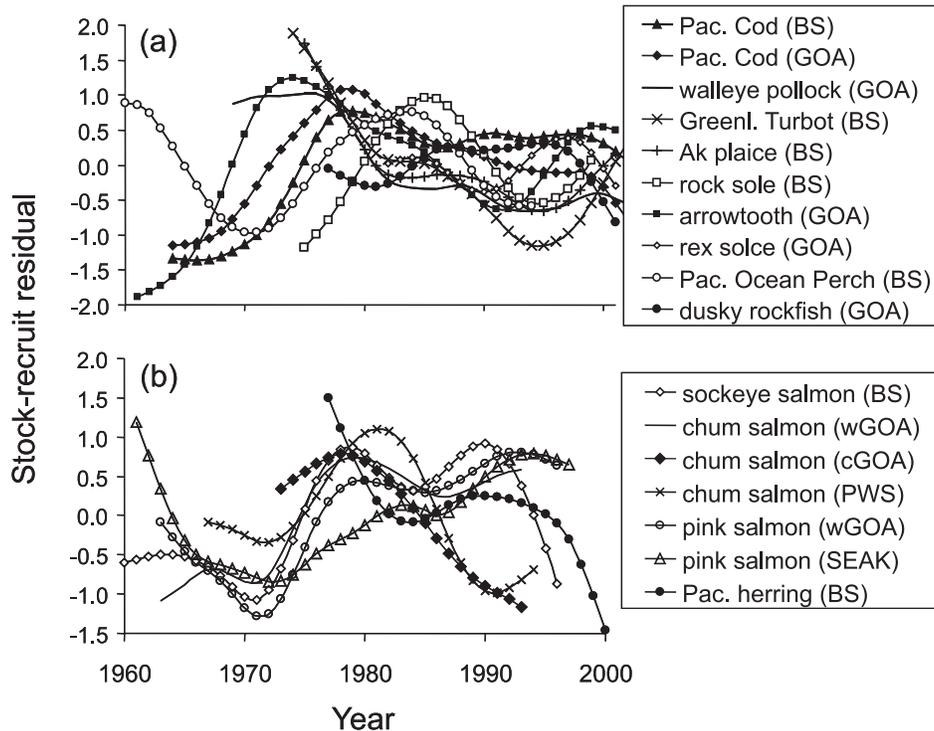or a given year class across all demersal or pelagic stocks in an ecosystem. SR indices were combined in the same way. The combined or aggregated log $R$ and SR indices thus give equal weight to each stock rather than weighting by abundance, which would have resulted in indices that are dominated by the most abundant species. We obtained four combined log $R$ indices and four combined SR indices consisting of two indices of demersal productivity (one for each ecosystem) and two indices of pelagic productivity. Although we averaged across different series that may have fluctuated independently or even in opposite ways, the combined standardized indices reflect whether recruitment and survival rates were generally above or below average across the most important commercial species. Before standardizing individual series, "missing" values at the beginning and end of each series were estimated by regression imputation, which exploits the correlation structure among series to estimate missing values and assumes that this correlation structure is the same throughout the time series (Schafer 1997). Missing values were only estimated if log $R$ or SR values were available for at least 50% of the stocks in a given year and only for year classes between 1970 and 2001. Filling in missing values adds uncertainty to the combined, or averaged, indices. To account for this uncertainty, we obtained multiple imputations through bootstrap resampling from the full distribution of imputed values (2000 replicates), averaged the stock-specific indices resulting from each imputation, and constructed 95% confidence intervals based on the frequency distribution of these averages across multiple imputations.

### Change point analysis

We examined stock-specific and ecosystem-specific time series of log $R$ and SR indices using a "sequential $t$ test analysis of regime shifts" (STARS; Rodionov and Overland 2005). The STARS method sequentially tests whether each data point in a time series is significantly different from the mean of data points representing the latest "regime". The last data point in a time series may be identified as the beginning of a new "regime", and as more data are added to the time series, this is confirmed or rejected. The STARS method requires the prior specification of a cutoff value (minimum number of years in a regime) and a $p$ value (probability level). For this analysis, we chose a cutoff value of 10 years and a $p$ value of 0.1. The analysis was completed for a range of cutoff values (5, 7, 10, 15, 20) and two $p$ values (0.05, 0.1). The results from each combination of these parameter values were compared, and we found that a cutoff value of 10 and a $p$ value of 0.1 consistently captured the majority of shifts that were captured by other combinations of parameter values. Results for other combinations of parameter values differed primarily because of shifts found near the ends of certain time series and additional shifts found in some highly variable series.

We applied the STARS analysis across all demersal stocks (Bering Sea and Gulf of Alaska combined) and across all pelagic stocks, respectively, and measured the evidence for a significant shift in any given year across all stocks based on the "regime shift index" (RSI) of Rodionov and Overland (2005). The RSI was computed for each stock and was averaged separately across demersal and pelagic stocks. There-

918

Can. J. Fish. Aquat. Sci. Vol. 64, 2007

**Fig. 3.** Smoothed trends (cubic B-spline smoother) in stock–recruit residuals (SR indices) for (*a*) six groundfish stocks and (*b*) eight pelagic stocks that had significant ($p < 0.05$) decadal-scale trends. Pac., Pacific; Ak, Alaska; BS, Bering Sea; GOA, Gulf of Alaska; wGOA, western GOA; cGOA, central GOA; PWS, Prince William Sound; SEAK, Southeast Alaska.



## Results

### Frequency distribution and temporal variability

Time series of both log $R$ and SR indices were typically close to normally distributed, but one or more outliers (>2.5 SD from the mean) were present in some series. However, the influence of these outliers on the trend analysis was generally negligible, and eliminating individual outliers did not change the overall conclusions. Therefore, all results are presented without excluding outliers.

Most of the time series of log $R$ and SR indices could be well approximated by either a white-noise series or a first-order autoregressive series. First-order autoregressive coefficients for the stock–recruit residuals were generally positive and were significant ($p < 0.05$) for 12 out of 40 stocks, with significant autoregressive coefficients ranging from 0.34 to 0.95 (Table 1). Strong autocorrelation in stock–recruit residuals was evident in several rockfish and salmon stocks and in the GoA stocks of walleye pollock and Pacific cod (but not, or to a much lesser extent, in the BSAI stocks of these species). In addition, we found strong autocorrelation in the log $R$ series of most flatfish stocks. However, after accounting for effects of spawner biomass on flatfish recruitment, autocorrelation in the SR indices was no longer significant

fore, a large average RSI may result from a pronounced shift in one or a few series or from small shifts in many individual series. In addition, we applied the STARS analysis to each of the combined, ecosystem-wide log $R$ and SR indices to test for significant shifts in these combined indices.

in most cases, except for arrowtooth flounder in the GoA and Greenland turbot and rock sole in the BSAI (Table 1).

Ten out of 23 demersal stocks and 7 out of 17 pelagic stocks showed significant evidence of decadal-scale variability in stock–recruit residuals, with most of those showing greater than 50% of the deviance accounted for by decadal-scale smoothed trends (Table 1). Although patterns of decadal-scale variability differed among species, several common trends emerged (Fig. 3). Stock–recruit residuals of the demersal stocks with significant trends typically increased in the 1970s, peaked in the late 1970s or early 1980s, and were relatively low in the 1990s. Almost all of the salmon stocks were characterized by strongly negative stock–recruit residuals, indicating unusually low survival rates, in the early 1970s, increasing to positive stock–recruit residuals in the late 1970s – early 1980s. Compared with SR indices, recruitment series showed similar patterns of variability but displayed more pronounced decadal-scale trends in some cases (e.g., flatfishes), presumably because of the effects of low-frequency variations in spawner abundance on recruitment.

An analysis of statistically significant linear time trends between 1970 (or the first year after 1970 with data) and the last year for which estimates were available suggested that recruitment and stock–recruit residuals of demersal stocks showed variable trends over this period, whereas those of salmon stocks generally increased (Table 1). Of nine demersal stocks with significant linear trends in log $R$, four stocks showed long-term decreasing trends in recruitment since 1970, whereas recruitment of five stocks increased over time (Table 1). Of 14 salmon stocks, the log $R$ of seven

stocks increased significantly from 1970 to the late 1990s, whereas only one stock (chum salmon in the central GoA) decreased significantly. Fewer SR than log $R$ series showed significant trends over time, but they generally had the same sign as trends in log $R$ for a given stock.

## Spatial covariation of salmon and herring stocks

Average correlations between pairs of SR indices for salmon stocks of the same species (Fig. 4a and Mueter et al. 2002b) and for Pacific herring stocks (Fig. 4c) show moderate to strong positive covariation at regional spatial scales of up to several hundred kilometres but no evidence of significant correlations at larger spatial scales. The covariance function by distance for herring stocks was very similar in magnitude to that observed for pink salmon. The average correlation between nearby herring stocks was about 0.6 and decreased to less than 0.2 at about 1000 km. Average correlations among herring stocks were not significantly different from zero at distances larger than 1000 km. Similarly, stocks of different salmon species with ocean-entry points separated by less than a few hundred kilometres tended to be positively correlated (Fig. 4b and Pyper et al. 2005), whereas stocks that are separated by larger distances were on average uncorrelated. The largest between-species correlations were observed between SR indices of pink and chum salmon stocks with much weaker correlations between SR indices of sockeye salmon and either pink or chum salmon. We found no evidence of either positive or negative covariation between SR indices of herring and those of any of the salmon species (Fig. 4c), suggesting that the processes that determine survival of herring and salmon (as measured by SR indices) operate independently.

## Covariation patterns of demersal and pelagic stocks

Based on average correlations among log $R$ or SR indices, groundfish stocks within the BSAI and GoA showed relatively weak coherence. We found moderate but highly significant positive covariation among both log $R$ and SR indices of the 12 demersal stocks in the GoA (Table 2) but little or no positive covariation, on average, among groundfish stocks in the BSAI. However, both the average absolute correlation and the variance across all pair-wise correlations in the 11 BSAI demersal stocks were much larger than expected by chance (hypotheses $H_2$ and $H_3$ in Table 2; Fig. 5), which implies that the magnitude of some correlations in the BSAI, both positive and negative, was higher than expected. This overdispersion resulted from two groups of species (flatfishes and gadids) with log $R$ series, as well as SR series, that were positively correlated within groups but negatively correlated between groups (see clustering results below).

There was some positive covariation between demersal stocks in the BSAI and demersal stocks in the GoA, as evident in average correlations among log $R$ indices and among SR indices that were significantly larger than zero (Table 2; Fig. 5). Positive covariation between groundfish in the two ecosystems was in part a result of covariation between stocks of the same species with log $R$ and SR indices that were typically positively correlated between ecosystems. However, the correlations were significant for Pacific cod and Pacific ocean perch only ($p < 0.05$; Table 3) and were

**Fig. 4.** Spatial correlation scales for salmon and herring stocks in the Northeast Pacific: (a) estimated average correlation between stocks of the same species as a function of the distance between ocean entry points for pink, chum, and sockeye salmon (modified from Mueter et al. 2002b); (b) estimated average correlations between stocks of different salmon species by distance (modified from Pyper et al. 2005); and (c) pair-wise correlations (circles) and average correlation by distance (heavy line) with 95% confidence interval (thin lines) for 13 herring stocks. Dotted lines in (c) denote pair-wise correlations by distance between herring stocks and sockeye, pink, and chum salmon stocks, respectively, none of which was significantly different from zero at any distance.
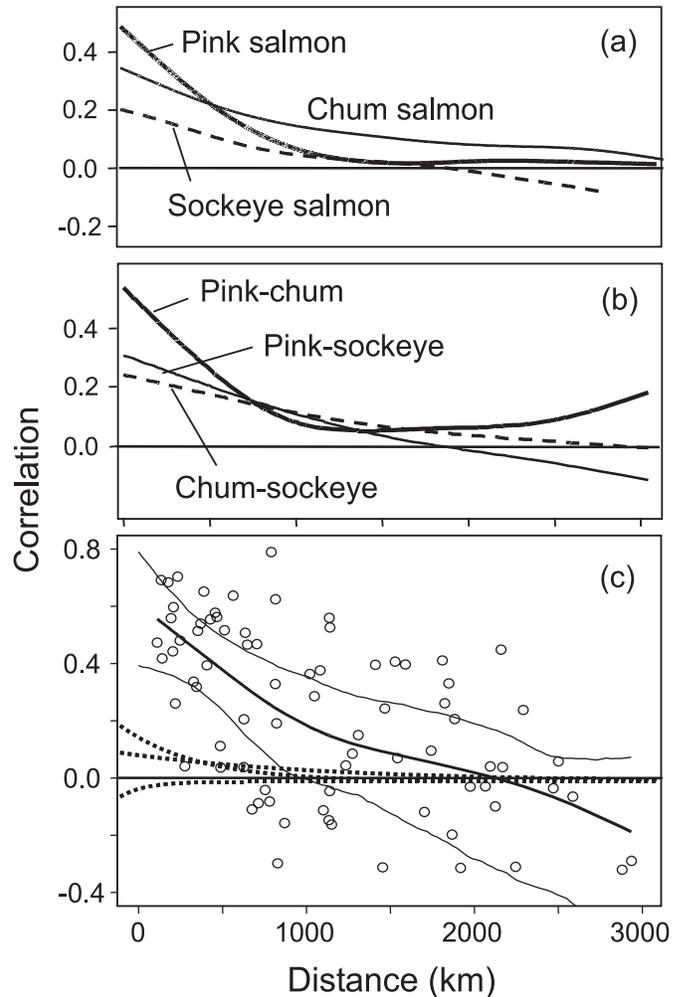


close to zero or negative for flathead sole and walleye pollock. Furthermore, there were numerous other positive correlations among specific stocks in the two systems that were significant ($p < 0.05$) but no significant negative correlations.
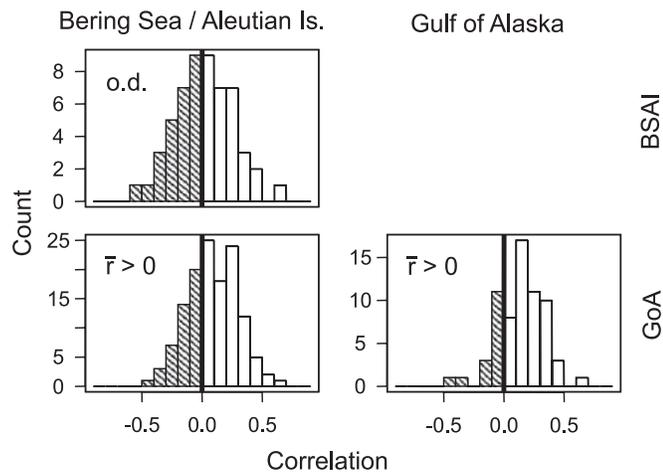
Finally, we found weak but significant positive covariation between log $R$ (as well as SR) series of demersal and pelagic stocks in the GoA but not in the BASI region (Table 2). Positive covariation among demersal and pelagic stocks in the GoA resulted from positive correlations among the recruitment series of Pacific halibut, arrowtooth flounder, and several sockeye and pink salmon stocks. Correlations among

920

Can. J. Fish. Aquat. Sci. Vol. 64, 2007

**Table 2.** Summary of results from randomization tests to test three hypotheses about within- and between-group correlations.

| | log $R$ | | | | | SR | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | $\bar{r}$ | $H_1$ ($p$ value) | $|r|$ | $H_2$ ($p$ value) | $H_3$ ($p$ value) | $\bar{r}$ | $H_1$ ($p$ value) | $|r|$ | $H_2$ ($p$ value) | $H_3$ ($p$ value) |
| **Within-group correlations** | | | | | | | | | | |
| BSAI: 11 demersal stocks | 0.029 | 0.155 | 0.22 | 0.012* | 0.013* | 0.033 | 0.132 | 0.195 | 0.088 | 0.065 |
| GOA: 12 demersal stocks | 0.176 | <0.001*** | | | | 0.203 | <0.001*** | | | |
| **Between-group correlations** | | | | | | | | | | |
| BSAI vs. GoA: demersal | 0.1 | 0.011* | | | | 0.11 | <0.001*** | | | |
| BSAI: demersal vs. pelagic | 0 | 0.662 | 0.17 | 0.742 | 0.62 | 0 | 0.541 | 0.178 | 0.658 | 0.681 |
| GoA: demersal vs. pelagic | 0.12 | 0.003** | | | | 0.1 | 0.039* | | | |

**Note:** We tested the overall hypothesis of independence of log recruitment (log $R$) or stock–recruit residuals (SR) of demersal stocks within or between each of two ecosystems and between demersal and pelagic stocks within a given ecosystem using three specific null hypotheses: $H_1$, the average correlation among stocks is zero ($\bar{r} = 0$); $H_2$, the average absolute value of correlations among stocks ($|r|$) is as expected under the assumption of independence ($|r|_{obs} = |r|_{exp}$); $H_3$, the variance of observed correlations is as expected under independence ($Var(r_{obs}) = Var(r_{exp})$). Within-group correlations were accounted for when testing correlations between groups. Significance: *, $p = 0.05$; **, $p = 0.01$; ***, $p = 0.001$.

**Fig. 5.** Histograms of all pair-wise correlations among stock–recruitment residuals (SR indices) of groundfish stocks within the Bering Sea – Aleutian Islands (BSAI, 11 stocks) and Gulf of Alaska (GoA, 12 stocks) (panels along diagonal) and between the BSAI and GoA (lower left panel). Hatched bars correspond to negative correlations. Results from randomization tests are indicated: $\bar{r} > 0$ means that average correlations are significantly larger than 0 ($p < 0.05$); o.d. means significant overdispersion.



**Table 3.** Pair-wise Pearson's correlation coefficients ($r$) between log(recruitment) (log $R$) or stock–recruit residuals (SR) of stocks of the same species from the GoA and BSAI, with $p$ values in parentheses (adjusted for autocorrelation following Pyper and Peterman (1998)); significant correlations ($p < 0.05$) are in boldface type.

| Species | log $R$ | SR |
|---|---|---|
| Arrowtooth flounder | 0.219 (0.472) | 0.145 (0.578) |
| Flathead sole | –0.156 (0.499) | 0.015 (0.961) |
| Walleye Pollock | 0.141 (0.407) | –0.012 (0.948) |
| Pacific cod | **0.639 (0.014)** | **0.487 (0.021)** |
| Pacific ocean perch | **0.471 (0.042)** | **0.549 (0.018)** |
| Northern rockfish | 0.338 (0.201) | 0.493 (0.062) |

the SR indices were weaker than among log $R$ indices but were still significantly different from zero (Table 2). Both results suggest similar patterns in environmentally driven survival rates of these demersal and pelagic stocks.

## Clustering of demersal stocks

Cluster analysis revealed several groups of demersal stocks within the BSAI ecosystem that showed similar patterns of variability in stock–recruit residuals (SR indices) over time (Fig. 6). We only show results from cluster analyses based on correlations among SR indices. Using correlations among log $R$ series often resulted in different clusters that appeared to be driven by shared long-term trends in recruitment resulting from strong trends in spawning stock biomass. Because we were primarily interested in environmentally driven variability in survival rates, we chose to fo-

cus cluster analyses on patterns in SR indices, which better reflect those environmentally driven changes because the effect of changing spawner abundance has been removed.

At least three biologically sensible clusters were evident among Bering Sea groundfishes, including a gadid cluster (walleye pollock and Pacific cod), shelf flatfishes (arrowtooth flounder, yellowfin sole, rock sole, and flathead sole), and rockfishes (Pacific ocean perch and northern rockfish, which clustered together with Atka mackerel) (Fig. 6). In addition, Greenland turbot and Alaska plaice, in spite of large differences in life history and distribution, formed another cluster because both species showed a strong decrease in their SR indices in the late 1970s. All four clustering algorithms yielded the same clusters for Bering Sea SR indices. There was remarkable synchrony in the stock–recruit residuals of walleye pollock and Pacific cod in the Bering Sea but asynchrony between SR indices of the gadid group and those of the flatfish group (Fig. 6). This asynchrony in survival was evident in a number of negative correlations between the SR indices of the four flatfish species and those of Pacific cod or walleye pollock (average correlation $r = -0.33$). Averaging the species-specific SR indices across species within the gadid and flatfish clusters, respectively, confirmed the strong negative relationship between the two groups (correlation between combined SR series, $r = -0.65$, $p = 0.0008$).

**Fig. 6.** (*a*) Time series of stock–recruit residuals (1970–2004 year classes, magnitude of SR indices reflected by diameter of circles; solid circles, positive residuals; open circles, negative residuals) and (*b*) cluster dendrograms based on group-average clustering of pairwise dissimilarities (based on Euclidean distances) among SR indices of 11 groundfish stocks in the Bering Sea – Aleutian Islands. The vertical broken line represents the chosen cutoff for identifying clusters. P., Pacific.
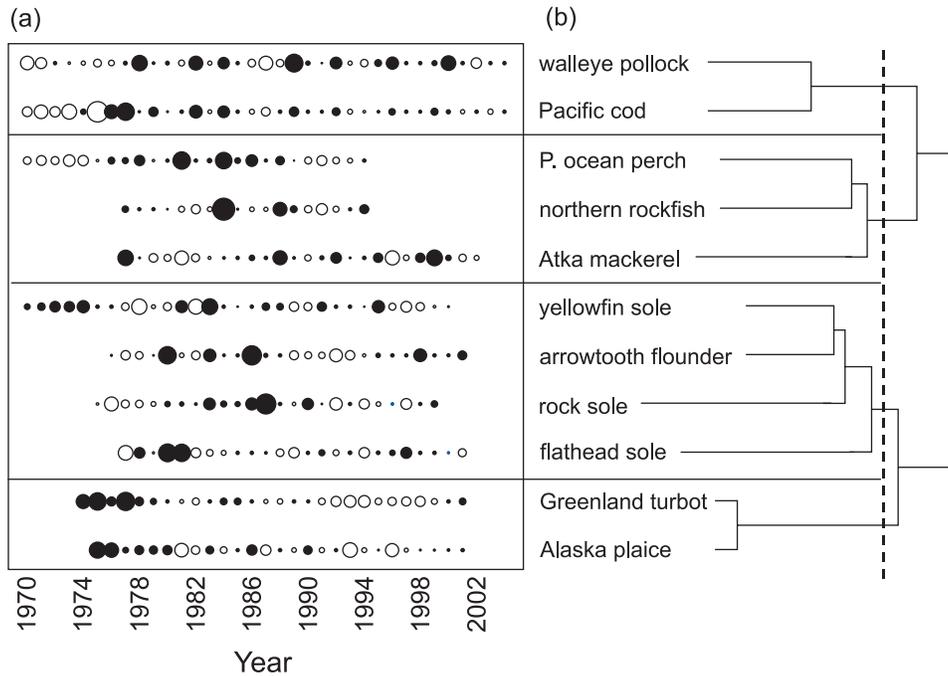


In the Gulf of Alaska we did not identify clear groupings among groundfish species (Fig. 7), and cluster composition was very sensitive to the clustering algorithm used. Only two pairs of species consistently clustered together because their SR indices were moderately positively correlated. These species pairs consisted of walleye pollock and arrowtooth flounder ($r = 0.55$, $p = 0.0008$) and Pacific ocean perch and dusky rockfish ($r = 0.43$, $p = 0.034$).

We examined the sensitivity of the clustering results to deleting the last two years of each time series because the more recent year classes are still poorly sampled owing to incomplete recruitment in many of the stocks. Clusters in the Bering Sea remained largely unchanged; however, northern rockfish SR indices (the shortest series with 16 years) no longer clustered with the rockfish group.

**Combined indices of recruitment and survival rate**

Combined indices of log $R$ and stock–recruit residuals across 11 demersal stocks in the BSAI and across 12 demersal stocks in the GoA showed significant decadal-scale trends (Table 4), with typically above-average recruitment and survival rates in the 1980s and below-average recruitment and survival rates in the early 1970s and early 1990s (Fig. 8). The combined log $R$ and SR series showed an increase from generally negative values in the late 1960s and early 1970s to mostly positive values in the late 1970s and 1980s. This increase corresponded to the well-known 1976–1977 climatic regime shift and was much less pronounced in the BSAI series. However, time series for individual demersal stocks in the BSAI were too short to adequately resolve a potential shift in the 1970s, and values of the combined indices are highly uncertain because they are based on

**Fig. 7.** Time series of stock–recruit residuals (1970–2004 year classes, magnitude of SR indices reflected by diameter of circles; solid circles, positive residuals; open circles, negative residuals) of 12 groundfish stocks in the Gulf of Alaska.
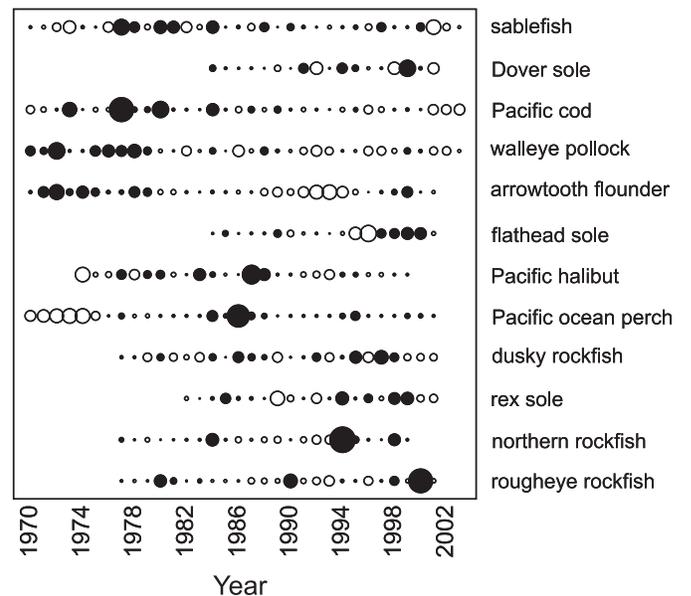


few stocks in early years. A shift from relatively high to low productivity occurred in the late 1980s to early 1990s and appeared to be more pronounced and longer-lasting in the Bering Sea than in the Gulf of Alaska, where demersal log $R$ and SR indices increased substantially in 1994 and stayed

922

Can. J. Fish. Aquat. Sci. Vol. 64, 2007

**Table 4.** Proportion of variability in combined productivity series (log recruitment (log $R$) or stock–recruit residuals (SR)) accounted for by decadal-scale trends (percent deviance explained in text) in the Bering Sea – Aleutian Islands (BSAI) and Gulf of Alaska (GoA).

| | Percent deviance ($p$ value) | | Years of regime shifts | |
| Group | log $R$ | SR | log $R$ | SR |
|---|---|---|---|---|
| BSAI demersal | 43.5 (**0.017**) | 47.8 (**0.008**) | 1976 (1991) | 1976 (1991) |
| GoA demersal | 43.7 (**0.017**) | 21.1 (0.381) | 1976, 1994 | |
| BSAI pelagic | 44.5 (**0.022**) | 64.9 (**0.001**) | 1977 | 1974 |
| GoA pelagic | 75.6 (**0.001**) | 57.8 (**0.003**) | 1977 (1986) | 1974 (1986) |

**Note:** Significant $p$ values (boldface) refer to decadal-scale patterns relative to a constant mean model, based on an approximate $\chi^2$ test. Years of regime shifts are significant change points ($p < 0.1$) in combined productivity series. Regime shifts were identified by the STARS method (Rodionov and Overland 2005). Years with significant decreases in log $R$ or SR are indicated in parentheses, all other years reflect significant increases.

**Fig. 8.** Indices of log(recruitment) (combined log $R$, left column) and log(survival rate) (combined SR, right column) averaged across all groundfish stocks within the Bering Sea – Aleutian Islands (BSAI) and Gulf of Alaska (GoA). Solid bars represent years with data for all stocks, hatched bars represent years that do not have data for all stocks (lighter hatching corresponds to fewer years with data). Missing values were estimated by imputation, and error bars reflect the uncertainty (95% point-wise confidence interval) resulting from filling in missing values before averaging across stocks.
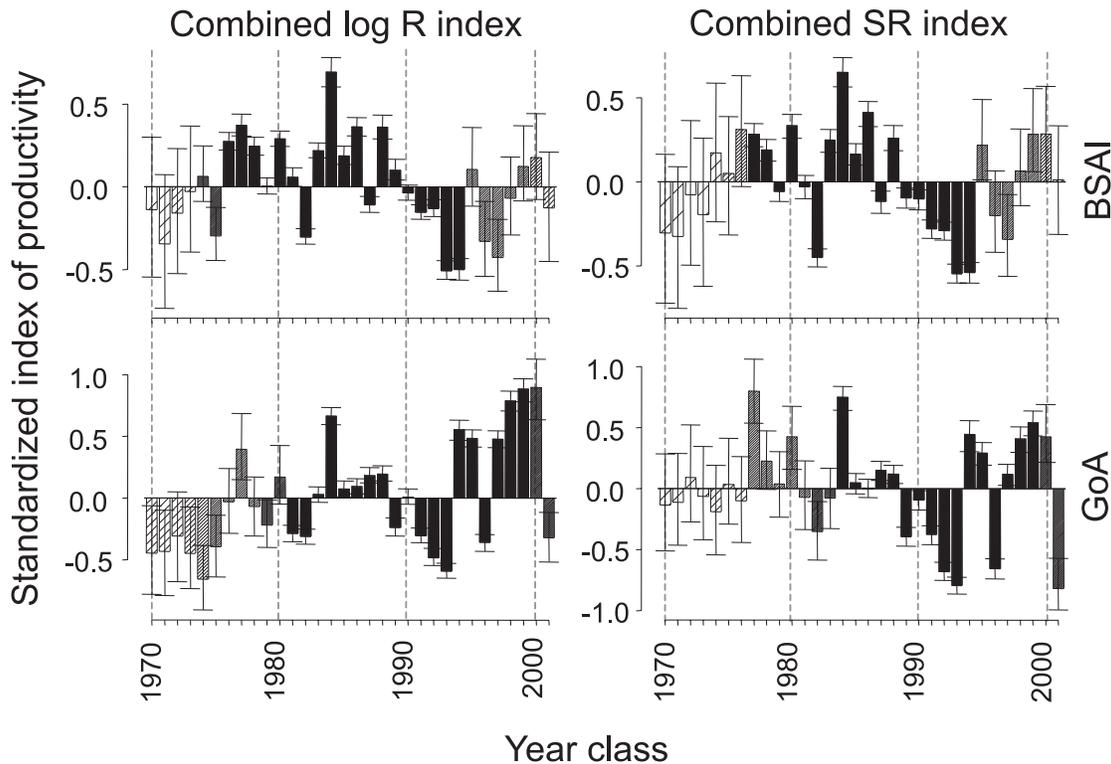


above average thereafter, with the exception of 1996 and 2001. However, as noted above, recruitment estimates for 2001 are highly uncertain.

Another notable feature of the combined demersal indices is that both log $R$ and SR series show a marked increase from 1982, which had below-average anomalies in both ecosystems, to 1984, which had the largest positive anomaly of the entire time series in both cases (Fig. 8). This suggests that 1984 was an exceptionally productive year for demersal species in the these ecosystems, with 19 out of 23 species showing above-average recruitment (log $R$) and survival (SR) relative to the 1970–2001 averages. Although values of

the indices in recent years are still highly uncertain, the numerous positive recruitment anomalies of Gulf of Alaska groundfish stocks after 1993 (Figs. 7, 8) provide some evidence that the low-productivity state of the early 1990s, in terms of recruitment and survival, gave way to higher productivity toward the end of the 1990s.

Pelagic stocks in both the Bering Sea and Gulf of Alaska showed a marked increase in recruitment and survival rates across stocks in the late 1970s corresponding to the 1976–1977 regime shift (Fig. 9). Unlike demersal stocks, pelagic stocks did not appear to respond to the documented 1988–1989 regime shift (Hare and Mantua 2000). Although the

**Fig. 9.** Indices of log(recruitment) (log $R$, left column) and log(survival rate) (SR, right column) averaged across all pelagic stocks or stock groups (salmon + herring) within the Bering Sea – Aleutian Islands (BSAI) and Gulf of Alaska (GOA). Hatching and error bars as in Fig. 8.
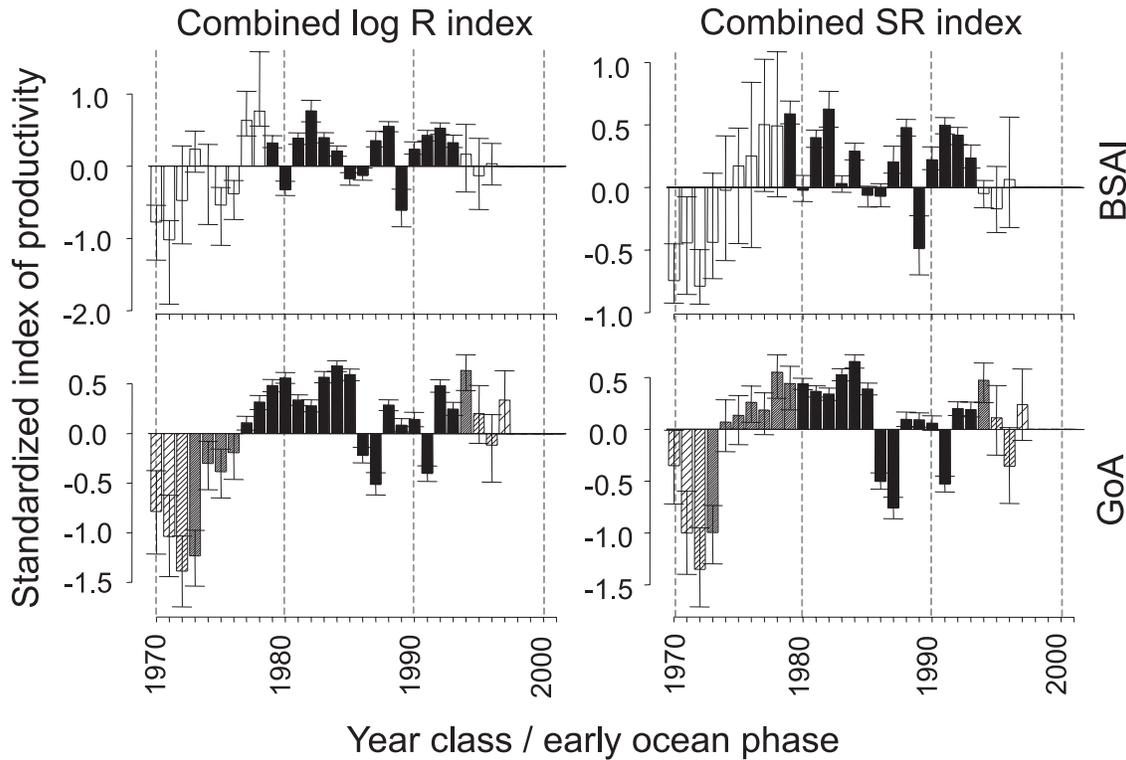


**Table 5.** Correlations (below diagonal) and corresponding $p$ values (above diagonal) between combined indices of survival rates across all demersal stocks or pelagic stocks (primarily salmon) within a given ecosystem (BSAI, Bering Sea – Aleutian Islands; GoA, Gulf of Alaska).

|  |  | Demersal stocks | | Pelagic stocks | |
|---|---|---|---|---|---|
|  |  | BSAI | GoA | BSAI | GoA |
| Demersal stocks | BSAI |  | **0** | 0.661 | 0.29 |
|  | GoA | **0.56** |  | 0.94 | 0.37 |
| Pelagic stocks | BSAI | 0.11 | 0.015 |  | **0** |
|  | GoA | 0.27 | 0.183 | **0.571** |  |

**Note:** Significant correlations ($p < 0.05$) and corresponding $p$ values are in boldface type.

combined log $R$ and SR indices for the Bering Sea were below average in 1989, they were above average in the early 1990s. In the Gulf of Alaska, log $R$ and SR indices showed a pronounced decrease between 1985 and 1986 but were generally above average again in the 1990s (Fig. 9).

Pair-wise correlations among the combined demersal indices suggest that overall demersal productivity displays similar patterns of variability in both the Bering Sea and Gulf of Alaska (Table 5). Similarly, combined indices of pelagic productivity are positively correlated between systems (Table 5). In contrast, there was no significant correlation between demersal and pelagic indices within a system or between the two systems (Table 5).

**Change-point analysis**

The change-point analysis identified apparent transition points (i.e., years when a major change occurred to a relatively persistent new "state") in the overall productivity of demersal and pelagic stocks in the Bering Sea and Gulf of Alaska based on an analysis of the combined productivity indices (log $R$ and SR). We identified significant step increases ($p < 0.1$) in the combined log $R$ and SR series for both ecosystems and for both pelagic and demersal species in 1976 or 1977 (Table 4). In addition, we found a significant step decrease in the combined log $R$ index for BSAI demersal stocks in 1991, a significant step increase in the combined log $R$ index for GoA demersal stocks in 1994, and a significant decrease in the combined indices for GoA pelagic stocks in 1986 (Table 4; Figs. 8, 9).

Significant change points for individual demersal stocks were detected throughout the available time series, with little evidence that these shifts corresponded to the known climatic regime shifts (Fig. 10). Average regime shift indices (RSI) from the STARS analysis, which average the estimated strength of shifts in a given year across all stocks with a significant shift in that year, showed no clear indication that abrupt shifts were concentrated in certain periods (Figs. 10a, 10b), although shifts in average log(recruitment) tended to occur more frequently in the late 1970s – early 1980s, as well as in the mid- to late 1990s. Shifts in recruitment or survival rates of pelagic stocks, in particular salmon, were frequently associated with the 1976–1977 climatic regime shift (Figs. 10c, 10d). Of 14 salmon stocks examined, eight showed a significant increase in log $R$ and (or) SR in-

924

Can. J. Fish. Aquat. Sci. Vol. 64, 2007

**Fig. 10.** Average regime shift indices (RSI) values (absolute values from the STARS analysis indicating strength of regime shift) for log(recruitment) indices (log $R$, left column) and stock–recruit residuals (SR, right column) by year across (*a*, *b*) 23 groundfish stocks and (*c*, *d*) 17 pelagic groups from the Gulf of Alaska and Bering Sea – Aleutian Islands. Vertical boxes indicate 1976–1977 and 1988–1989 regime shifts in climatic conditions.
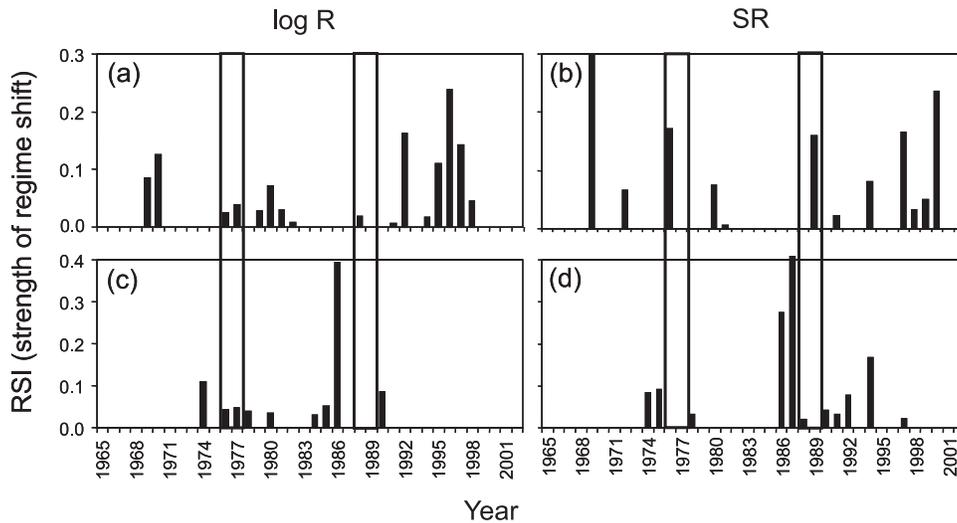


dices between 1974 and 1980, whereas none showed a significant decrease. In contrast, shifts in the mid-1980s to mid-1990s were evenly divided between increases and decreases. Pronounced step decreases in the SR indices of two chum salmon stocks (central GoA and Prince William Sound) were observed in 1986 and 1987, respectively, resulting in a high regime shift index for pelagic stocks in these years (Figs. 10*c*, 10*d*). Results from the STARS analysis were not sensitive to eliminating the last two years from each series, although some of the shifts in the late 1990s were no longer significant when the last two years were eliminated.

## Discussion

We examined variability in log $R$ and stock–recruit residuals of pelagic and demersal fish stocks in two large marine ecosystems off Alaska. We assume that both log $R$ and SR indices, at least in part, reflect real differences in productivity between years, although random variability due to uncertainties in estimation of spawner abundances and recruitment is likely to be substantial. Our SR indices, or residuals from each stock's best-fit stock–recruitment model, are preferable to abundance of recruits as indicators of productivity because they adjust for density-dependent effects of spawner abundance on productivity and are therefore more likely to reflect environmentally driven, or density-independent, components of variability (Peterman et al. 1998). However, recruitment may provide a better indicator of productivity in cases where the stock–recruitment relationship is highly uncertain and where fitting that relationship may introduce biases. Hence, we used both indices of productivity. Stock–recruit residuals, as well as recruitment, are also affected by predation; therefore, "environmental" effects on productivity include changes in abundance of important predators, regardless of whether these were caused by environmental variability, fishing, or other factors.

Within both ecosystems, we found significant between-species correlations for certain species groups that displayed

similar patterns of variability at both interannual and decadal scales. Positive covariation among survival rate series of three species of salmon at spatial scales of up to about 1000 km has been documented previously (Pyper et al. 2005). Our results suggest similar covariation among certain groups of demersal species within ecosystems that have a spatial distribution across at least 1000–2000 km. Although different salmon species tend to show only positive covariation (Hare et al. 1999; Pyper et al. 2005), the demersal stocks examined here showed evidence of both positive and negative covariation, demonstrating that certain groups of species may be affected in opposite ways by shared environmental forcing. Most notably, both log $R$ and stock–recruit residuals of flatfishes on the Bering Sea shelf were negatively correlated with those of gadids in the same region. This may be a consequence of environmental forcing that results in alternative pathways for production and favors pelagic feeders, such as pollock, during years with an early ice retreat but benthic-feeding flatfishes during years with a late ice retreat (Hunt and Stabeno 2002; Mueter et al. 2006).

Positive covariation in productivity indices of individual stocks and in the combined indices of overall productivity between the BSAI and GoA suggests that large-scale environmental influences affect the recruitment and survival of some species and overall productivity in both systems in similar ways. Likewise, positive covariation between the productivity indices for demersal and pelagic stocks within the GoA suggests that at least some of these stocks are affected in similar ways by environmental variability. In contrast, recruitment and survival rates of pelagic and demersal stocks within the BSAI appear to be determined by independent processes.

Much of the variability in recruitment and survival rates of some species and in overall productivity indices occurs at decadal time scales and suggests alternating periods of low and high productivity that correspond to the major oceanographic regime shifts observed in the Northeast Pacific (Hare and Mantua 2000). A large increase in salmon catches off

Alaska was observed in the late 1970s (Hare and Francis 1995) and was consistent with increases in productivity as measured by the Ricker *a* parameter (Adkison et al. 1996; Peterman et al. 2003). The abundance of groundfishes also increased in the late 1970s in the GoA (Anderson and Piatt 1999) and in the BSAI (Conners et al. 2002), consistent with an increase in the recruitment of numerous demersal species following the 1976–1977 regime shift (Hollowed et al. 2001) and evident in unusually large values of our indices of overall productivity in 1977. In addition to previously observed increases in both pelagic and demersal productivity after the 1976–1977 regime shift in the GoA and BSAI, our results suggest a widespread decrease in recruitment and survival rates of demersal species in both ecosystems following the 1989 regime shift, with very low values in the early 1990s. A pronounced decrease in the recruitment of several flatfish species in the Bering Sea after 1988 was previously described by Wilderbuer et al. (2002), but poor recruitment in the early 1990s was also observed in Pacific Ocean perch and northern rockfish. The pronounced increase in the combined recruitment index for the GoA in 1994 reflects above-average recruitment and survival of most flatfish and rockfish species in the GoA from 1994 to at least 2000 but does not correspond to a known regime shift. Megrey et al. (2006) reported similar increases in model-based time series of zooplankton density and herring growth in the mid-1990s in the Northeast Pacific.

The response of individual groundfish stocks to the known major environmental regime shifts was highly variable, and there was little indication that observed shifts in recruitment or survival rates were unusually pronounced or had a higher frequency during the major regime shift periods. However, shifts that were detected during these periods were generally positive in the late 1970s and mostly negative in the late 1980s and early 1990s, resulting in relatively pronounced shifts in the aggregated indices of productivity. These patterns suggest that climatic regime shifts may affect overall fish productivity by altering the frequency of high survival or recruitment across stocks in a given year. This can result in periods with overall low or high productivity across stocks, in spite of large variability among stocks in their stock-specific responses.

Long-term trends or abrupt shifts and covariation in productivity among species have important implications for the assessment and management of fish stocks. Current models and projections generally assume that variability in recruitment arises from independent stochastic processes and recruitment is typically modeled as a function of spawning stock biomass plus random white noise (e.g., North Pacific Fishery Management Council 2005). To project future biomass levels, recruitments are usually drawn from the estimated, time-invariant stock–recruitment relationship or from recently observed recruitments. Given the changes in recruitment that we have found, it is clear that this approach tends to overestimate (or underestimate) future biomasses at the beginning of a low-productivity (or high-productivity) period. Therefore, management strategies need to be robust to both short-term and decadal-scale variations in recruitment.

Optimal management strategies depend on the nature of important sources of environmental variability, the ecology

of the species of interest, and the management objectives (MacCall 2002). For a relatively short-lived species such as the sardine (*Sardinops sagax*), MacCall (2002) shows how harvest rates can be specified as a function of environmental conditions. Ideally, linking harvest policies directly to environmental variability should involve a clear understanding of the important effects of environmental factors on productivity, but that understanding is currently lacking for demersal species in the Northeast Pacific. Nevertheless, effects of regime shifts on productivity of some flatfish species in the BSAI have been estimated (for example, Wilderbuer et al. 2002) and have been incorporated into stock assessments by estimating separate stock–recruitment relationships for different regimes. However, a considerable postregime shift period (minimum of 10–15 years) is required to obtain reliable estimates of productivity for the new regime. Our results suggest that regime-like periods can be of relatively short duration and shifts may not be detected in time to incorporate their effects.

Another way to develop management strategies for fish species in regions with long-term trends or shifts in productivity is to use stock–recruitment models that assume one or more time-dependent parameters. Those parameters can be estimated annually using a Kalman filter to help track changes in productivity (e.g., Peterman et al. 2003). As long as the time lag is not too long between the environmental effects occurring and the estimate of its effect, then this method will improve management performance compared with the case in which the environment is constant or follows a white-noise pattern. Appropriate harvest policies for stocks with environmentally driven variability have also been explored under a variety of scenarios and indicate that either a constant harvest rate approach (Walters and Parma 1996) or variable harvest rate policies (Spencer 1997) can result in the best overall strategy. De Oliveira and Butterworth (2005) show that management actions can be improved by using environment-dependent stock–recruitment models, as long as these models explain about 50% or more of the total variation in recruitment. This is difficult to achieve given our current understanding, or lack thereof, of recruitment dynamics in most fish stocks.

Risks associated with the effects of environmental variability on individual stocks are magnified in the presence of covariation among stocks. Such covariation implies that a change in overall fish productivity affects the productivity of multiple stocks similarly and simultaneously, even if the effects may not be readily apparent at the stock-specific level but only at aggregate levels. Such effects are not explicitly accounted for by current single-species or multispecies models, but there are several ways in which covariation among stocks can be exploited to improve existing models. First, single-species models can take into account the effects of positive or negative covariation in productivity between species by including estimates for recruitment or survival rates of species that recruit at an early age as covariates in stock–recruitment models of species that recruit at later ages. For example, stock–recruit residuals of yellowfin sole and walleye pollock in the Bering Sea are strongly negatively correlated across year classes. Therefore, survival rate anomalies or stock–recruit residuals for a given walleye pollock

926

Can. J. Fish. Aquat. Sci. Vol. 64, 2007

year class, which can be reliably assessed at age 2, could be used to forecast yellowfin sole survival rates of the same year class, which recruits into the fishery several years later. The same approach may be applied to pink salmon, which recruit as 2-year-olds, and chum salmon, which have mainly 4- or 5-year-old recruits (Haeseker et al. 2005). Second, uncertainty in temporal trends in productivity and in the effects of environmental variability on productivity can be reduced by estimating trends and effects across covarying populations or species using appropriate multistock models such as mixed-effects or other hierarchical models (Mueter et al. 2002a). These improved estimates can then be incorporated into single-stock models as fixed effects or as prior distributions (Punt and Hilborn 1997). Third, multispecies assessment models could account for covariation among species by linking recruitment between species or modeling recruitment as a shared process with stock-specific variability.

In summary, this and other recent studies demonstrate that the recruitment and survival of different demersal and pelagic fish stocks in the Northeast Pacific does not fluctuate independently but shows significant positive or negative covariation. The covariation is strongest among certain demersal stocks sharing the same ecosystem, among salmon stocks of the same or different species sharing coastal marine areas during early ocean life, and among herring stocks that spawn within certain geographic regions. Limited spatial scales of covariation appear to result from regional environmental influences that affect survival rates of different species in similar or opposite ways (the latter for some demersal stocks). Although productivity of individual stocks primarily varies at interannual time scales, aggregate indices of overall demersal and pelagic productivity show strong decadal-scale patterns and stronger evidence of abrupt shifts such as those in the late 1970s and in the late 1980s – early 1990s. Such shifts imply changes in overall fish productivity that affect the probability and (or) magnitude of strong year classes across stocks. Rational management should account for changes in overall productivity, but methods to account for the effects of changing productivity are hampered by our ability to detect significant shifts in a timely manner. Nevertheless, the information inherent in the observed covariation among stocks can be exploited to potentially improve current single-species and multispecies models.

## Acknowledgements

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