Ecological Applications, 23(6), 2013, pp. 1475–1487

Rising catch variability preceded historical fisheries collapses in Alaska

MICHAEL A. LITZOW,[1,2,5] FRANZ J. MUETER,[3] AND J. DANIEL URBAN[4]

[1]*Farallon Institute for Advanced Ecosystem Research, Petaluma, California 94952 USA*
[2]*Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, Tasmania 7001 Australia*
[3]*School of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Juneau, Alaska 99801 USA*
[4]*Alaska Fisheries Science Center, National Oceanic and Atmospheric Administration, Kodiak, Alaska 99615 USA*

Abstract. Statistical indicators such as rising variance and rising skewness in key system parameters may provide early warning of "regime shifts" in communities and populations. However, the utility of these indicators has rarely been tested in the large, complex ecosystems that are of most interest to managers. Crustacean fisheries in the Gulf of Alaska and Bering Sea experienced a series of collapses beginning in the 1970s, and we used spatially resolved catch data from these fisheries to test the predictions that increasing variability and skewness would precede stock collapse. Our data set consisted of catch data from 14 fisheries (12 collapsing and two non-collapsing), spanning 278 cumulative years. Our sampling unit for analysis was the Alaska Department of Fish and Game statistical reporting area (mean n for individual fisheries = 42 areas, range 7–81). We found that spatial variability in catches increased prior to stock collapse: a random-effects model estimating trend in variability across all 12 collapsing fisheries showed strong evidence of increasing variability prior to collapse. Individual trends in variability were statistically significant for only four of the 12 collapsing fisheries, suggesting that rising variability might be most effective as an indicator when information from multiple populations is available. Analyzing data across multiple fisheries allowed us to detect increasing variability 1–4 years prior to collapse, and trends in variability were significantly different for collapsing and non-collapsing fisheries. In spite of theoretical expectations, we found no evidence of pre-collapse increases in catch skewness. Further, while models generally predict that rising variability should be a transient phenomenon around collapse points, increased variability was a persistent feature of collapsed fisheries in our study. We conclude that this result is more consistent with fishing effects as the cause of increased catch variability, rather than the critical slowing down that is the driver of increased variability in regime shift models. While our results support the use of rising spatial variability as a leading indicator of regime shifts, the failure of our data to support other model-derived predictions underscores the need for empirical validation before these indicators can be used with confidence by ecosystem managers.

Key words: Alaskan fisheries; collapse; crustacean fisheries; early warning; fisheries; indicators; management; multiple stable states; regime shift; spatial variability.

INTRODUCTION

Anthropogenic stress has increased the global risk of ecological regime shifts: abrupt, difficult-to-reverse reorganizations stemming from multiple stable-state dynamics (Folke et al. 2004). Accordingly, there is much interest in developing indicators that might give managers early warning when such a shift is imminent. A promising approach comes from modeling studies suggesting that complex systems show generic statistical behaviors as resilience declines and a regime shift becomes more likely. These generic indicators include slower recovery from perturbations and increased variability, autocorrelation, and skewness (Scheffer et al. 2009). It has been proposed that these indicators should be present in many types of complex systems (ecological, social, financial, and physical; Scheffer et al. 2009), and in ecology they have been applied to sudden transitions in both ecosystems (Carpenter and Brock 2006, Guttal and Jayaprakash 2009, Donangelo et al. 2010, Carpenter et al. 2011) and populations (Oborny et al. 2005, Takimoto 2009, Drake and Griffen 2010). While these indicators have attracted much attention, a cautionary note is sounded by the observation that many ecosystem models show no early-warning signs of regime shifts (Hastings and Wysham 2010), and observations that other models show inconsistent patterns (either increases or decreases) in proposed indicators prior to shifts (Dakos et al. 2012). Additionally, regime shift indicators perform poorly in models that simulate realistic levels of ecological noise (Perretti and Munch 2012). Few empirical tests of the proposed

Manuscript received 23 April 2012; revised 17 January 2013; accepted 23 January 2013. Corresponding Editor: S. B. Baines.

[5] E-mail: Michael.Litzow@utas.edu.au

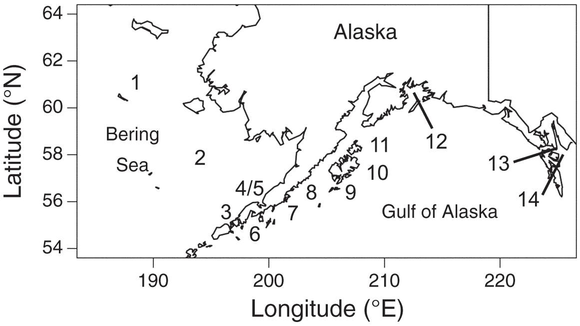

FIG. 1. Approximate location of fisheries included in this study. Fisheries (by number) are: 1, St. Matthew Island blue king crab; 2 and 3, Bering Sea snow crab and Tanner crab, respectively; 4/5, Bristol Bay red king crab; 6–8, Alaska Peninsula pink shrimp, red king crab, and Tanner crab, respectively; 9–11, Kodiak Island red king crab, Tanner crab, and pink shrimp, respectively; 12, Prince William Sound spot shrimp; 13 and 14, Southeast red king crab and spot shrimp, respectively.

indicators have been conducted to date, and most empirical work has, by necessity, taken place in laboratory microcosms or small, simple ecosystems that are amenable to experimental manipulation (e.g., Cottingham et al. 2000, Drake and Griffen 2010, Carpenter et al. 2011). As a result, the utility of these regime shift indicators in the large, complex ecosystems that are typically the concern of managers remains largely untested.

Commercial fisheries collapses are often coincident with abrupt reorganization in marine communities (e.g., Hare and Mantua 2000, Choi et al. 2004), and these events have been cited as leading examples of deleterious ecological regime shifts (e.g., Scheffer et al. 2001, Biggs et al. 2009, Carpenter et al. 2011). Better indicators of the community effects of fishing have long been sought (e.g., Duplisea and Castonguay 2006), making commercial fisheries a natural venue for testing the utility of the proposed generic regime shift indicators. Furthermore, while controlled experimental perturbation of ecosystems at very large spatial scales (i.e., many thousands of square kilometers) is never possible, commercial fisheries offer an opportunity to test ecological theory at these scales through unplanned experiments, because fisheries constitute anthropogenic perturbations to ecosystems, and are often meticulously detailed in catch records (Jensen et al. 2012). Tests of regime shift indicators with commercial fisheries data are therefore potentially valuable both for contributing to improved fisheries management and for assessing the general utility of these indicators in large ecosystems.

We analyzed historical catch records to evaluate the ability of generic regime shift indicators to predict a series of collapses in Alaskan crustacean fisheries that occurred during the 1970s, 1980s, and 1990s. These collapses occurred over very large spatial scales in the Gulf of Alaska and southeastern Bering Sea (combined shelf area ~6.7×10^5 km^2), and were part of a basin-scale community reorganization following the 1976/1977 change in sign of the Pacific Decadal Oscillation (PDO) Index (Hare and Mantua 2000). Overfishing also contributed to crustacean collapses in Alaska (Orensanz et al. 1998), and the relative importance of these two forcing mechanisms is not known for any fishery in our study. Available time series commonly may be too short for calculating meaningful trends in the temporal regime shift indicators (variance, skewness, and autocorrelation) proposed by modeling studies (Guttal and Jayaprakash 2009, Dakos et al. 2010), and this was the case with the time series in our study (mean time series length prior to collapse = 17 years). However, spatial variability and skewness are expected to show the same early-warning behavior as temporal indicators, and are suitable for use with shorter time series (Guttal and Jayaprakash 2009, Donangelo et al. 2010), so we used spatial parameters as our candidate indicators of impending collapse. Our specific goals were to test for significant increases in spatial variability and skewness of catches prior to fisheries collapses, and to test for "false positive" signals in non-collapsing fisheries. To make inferences about the mechanisms driving the changes in spatial statistics that we observed, we also tested the model-derived prediction that observed increases in regime shift indicators would be transitory, and limited to the period around the shift (e.g., Carpenter and Brock 2006, Biggs et al. 2009, Guttal and Jayaprakash 2009). To our knowledge, this study constitutes the most extensive empirical test of regime shift indicators in an actual management context to date.

MATERIALS AND METHODS

Data

The fisheries in our study included trawl fisheries for pink shrimp (*Pandalus borealis*) and pot fisheries for red king crab (*Paralithodes camtshaticus*), blue king crab (*Paralithodes platypus*; see Plate 1), snow crab (*Chionoecetes opilio*), Tanner crab (*Chionoecetes bairdi*), and spot shrimp (*Pandalus platyceros*). These fisheries were economic mainstays in coastal Alaska during the 1960s and 1970s, when groundfish and salmon catches were below long-term mean values.

Catch records were obtained from the Alaska Department of Fish and Game (ADF&G), which has collected catch data resolved by statistical area since the late 1960s. Data from fisheries managed through limited entry or individual fishing quotas (IFQs) were excluded from analysis, because statistical parameters for these fisheries were markedly different from those of the more common derby-style fisheries. Marine ecosystem indicator time series typically require at least 10 years of data to detect a trend (Nicholson and Jennings 2004), so we limited analysis to fisheries providing a minimum of 10 years of data prior to collapse ($n = 14$ total fisheries; Fig. 1). Our unit of spatial analysis was the ADF&G statistical area, which was designed to divide larger

TABLE 1. Details of Alaskan crustacean fishery catch time series used in analysis.

No.	Fishery name	Group	Scaling parameter, ß	Pre-collapse data	Post-collapse data	Mean *n* (areas)
1	St. Matthew Is. blue king crab	collapse	2.2	1986–1998	n/a	8
2	Bering Sea snow crab	collapse	1.9	1978–1999	2001–2005	61
3	Bering Sea Tanner crab	collapse	2.1	1968–1981	1983–1985, 1988–1997	35
4	Bristol Bay red king crab (a)	collapse	2.2	1966–1980	n/a	26
5	Bristol Bay red king crab (b)	non-collapse	2.0	n/a	1986–1993, 1996–2004	20
6	Alaska Peninsula pink shrimp	collapse	2.3	1968–1979	n/a	22
7	Alaska Peninsula red king crab	collapse	2.1	1966–1983	n/a	35
8	Alaska Peninsula Tanner crab	collapse	2.0	1968–1989	n/a	30
9	Kodiak Is. red king crab	collapse	2.2	1970–1982	n/a	81
10	Kodiak Is. Tanner crab	collapse	2.0	1967–1986	1989–1994	62
11	Kodiak Is. pink shrimp	collapse	2.1	1966–1978	1980–1986	34
12	Prince William Sound spot shrimp	collapse	1.8	1969–1988	n/a	7
13	Southeast red king crab	collapse	1.9	1969–1985	n/a	36
14	Southeast spot shrimp	non-collapse	2.2	n/a	1976–2009	80

Notes: Abbreviations are: Is., Island; n/a, data "not available" for fisheries designated as collapsing (for fisheries designated as non-collapsing [5 and 14], n/a indicates "not applicable").

management regions into general habitat types (inshore/offshore) and by geographic features (e.g., various bays and islands) in order to monitor the spatial distribution of fishing effort and the spatial status of stocks. The individual fisheries used in our analysis reflect independent stocks based on understanding at the time that management areas were defined, and the idea that fisheries in our study are independent is supported by observations of nonsimultaneous collapse among different fisheries for the same species (Orensanz et al. 1998). Because the spatial area exploited by fleets increases as fisheries develop, areas with zero reported catch early in time series are likely to indicate an absence of fishing effort. Additionally, available records did not always allow us to determine if zero-catch areas had actually been open to fishing in a given season. Because we could not determine if zero-catch areas reflected the absence of effort or localized depletion of stocks, we only used statistical areas with non-zero catches in our analysis. The annual average number of active statistical areas in different fisheries ranged between 7 and 81 (Table 1).

Catch per unit effort (CPUE) data were available only for a subset of fisheries in this study, so we used catch data, rather than CPUE, for analysis in order to provide consistency for hypothesis tests across multiple fisheries. We defined fishery collapse as any situation in which total catch declined 75% or more within three years or less, with no recovery to pre-collapse levels in the subsequent five years. Twelve fisheries met this definition of collapse, and one fishery (Southeast Alaska spot shrimp) never collapsed (Fig. 2A). The Bristol Bay red king crab fishery collapsed in 1981, and in the three decades since then, catches have been stable at 6–16% of peak pre-collapse levels, reflecting a successful rebuilding effort that has stabilized the stock at a fraction of its pre-collapse size (Kruse et al. 2010). We judged that this persistence and stability justified treating the post-collapse fishery as an established alternate state. We therefore treated data from 1966 (the start of the time series) to 1980 as an example of a collapsing fishery, and, after a five-year transitional period, we treated the data from 1986 to 2004 (the last year before individual fishing quotas [IFQs] were instituted) as a second example of a non-collapsing fishery (Fig. 2A). Our study therefore contained 12 collapsing and two non-collapsing fisheries. Although examples of non-collapsing salmon and groundfish fisheries are available from our study region, including these populations would have resulted in conflation of taxonomic differences with population trajectories, as our study would have compared mostly crustacean, collapsing fisheries with mostly fish, non-collapsing fisheries (Anderson and Piatt 1999, Litzow 2006). Low (or no) replication at the level of populations or ecosystems is a common feature of empirical studies of regime shift indicators at spatial scales greater than laboratory microcosms, and the population-level replication in our study compares favorably with that of previous empirical studies (e.g., Litzow et al. 2008, Carpenter et al. 2011, Lindegren et al. 2012, Seekell et al. 2012).

Analysis

The time series in our study were too short for meaningful analysis of temporal regime shift indicators (e.g., variance and autocorrelation), but large samples of spatial units for most fisheries (Fig. 2B) provided the opportunity for powerful tests of proposed spatial regime shift indicators. Although increasing spatial correlation has been proposed as a particularly informative leading indicator of regime shifts in modeling studies (Dakos et al. 2012), the irregular spacing of statistical areas in our study precluded the calculation of this metric. We therefore restricted our analysis to changes in spatial variability and skewness.

Selection of an appropriate measure of variability is a critical consideration in studies of ecological variability (Fraterrigo and Rusak 2008). Catch data in our study were highly (positively) skewed, and the coefficient of variation, one of the more common measures of variability, produces systematic errors when used with skewed data (McArdle et al. 1990). We therefore used

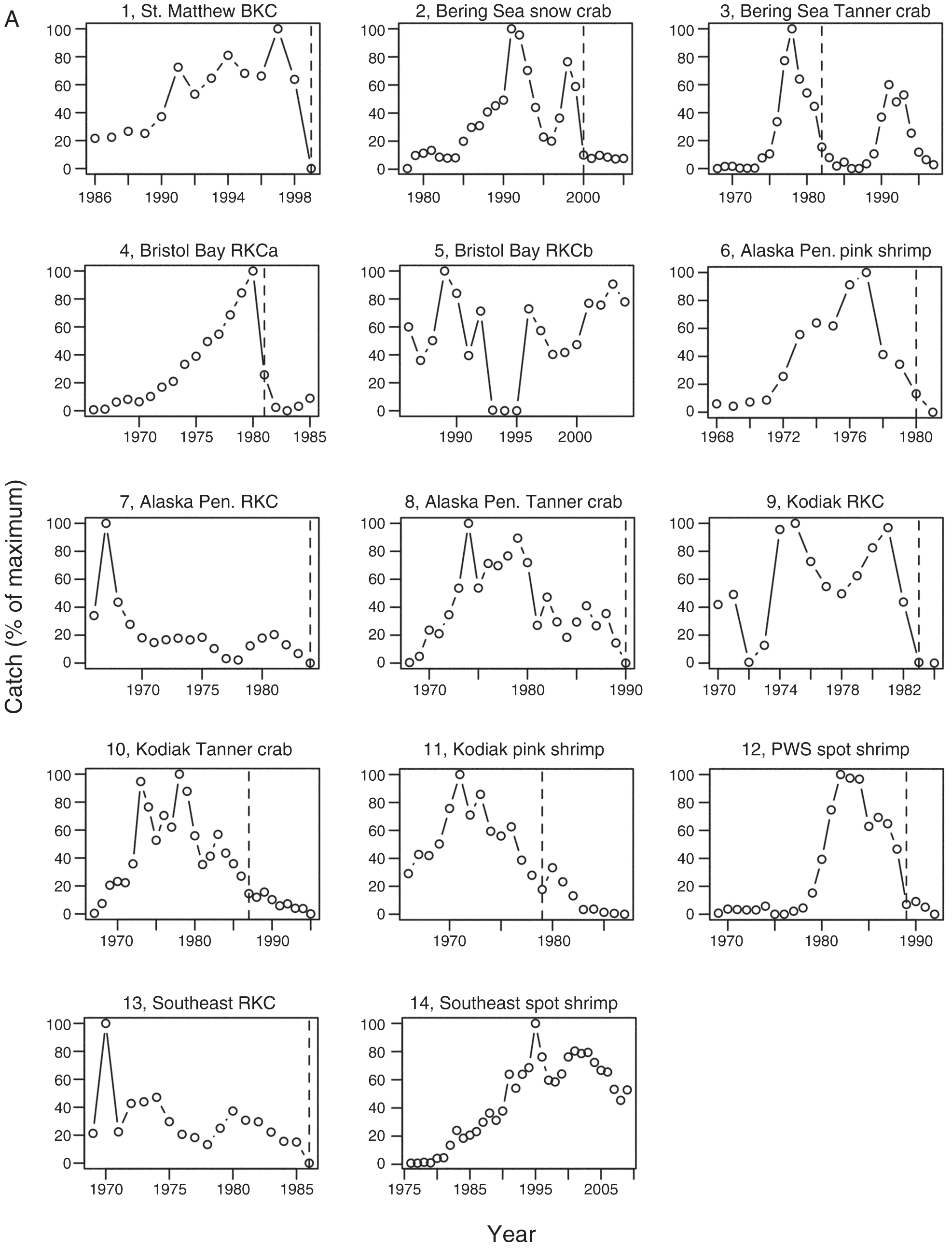

FIG. 2. (A) Catch time series included in the study, plotted as a percentage of maximum catch size for each fishery (fisheries numbers correspond to those in Fig. 1). Collapse points used in the analysis are indicated by vertical dashed lines. Note that Bristol Bay red king crab data were separated into collapsing and non-collapsing periods for analysis. (B) Sample size (number of active statistical areas) by fishery and year. Horizontal dashed lines indicate mean *n* for each fishery. Missing years within time series were either years of identified collapse, which were not used in analysis, or years with zero catch for the fishery. Abbreviations are: BKC, blue king crab; RKCa, red king crab, collapsing; RKCb, red king crab, non-collapsing.

the standard deviation of log-transformed data (hereafter "SDL"), justified by Taylor's power law, which relates the mean and variance of density (N) as

$$\mathrm{var}(N) = \alpha \bar{N}^{\beta}.$$

For populations with scaling parameter $\beta = 2$, the SD and mean of log-transformed data are independent of each other (McArdle et al. 1990). We confirmed that values of $\beta = 2$ generally described mean–variance scaling for the populations in our study ($\beta = 2.06 \pm 0.14$, mean ± SD; Table 1), suggesting that SDL was an appropriate metric for our analysis. To guard against the possibility of weak relationships between the SD and the mean of log-transformed data in situations where β

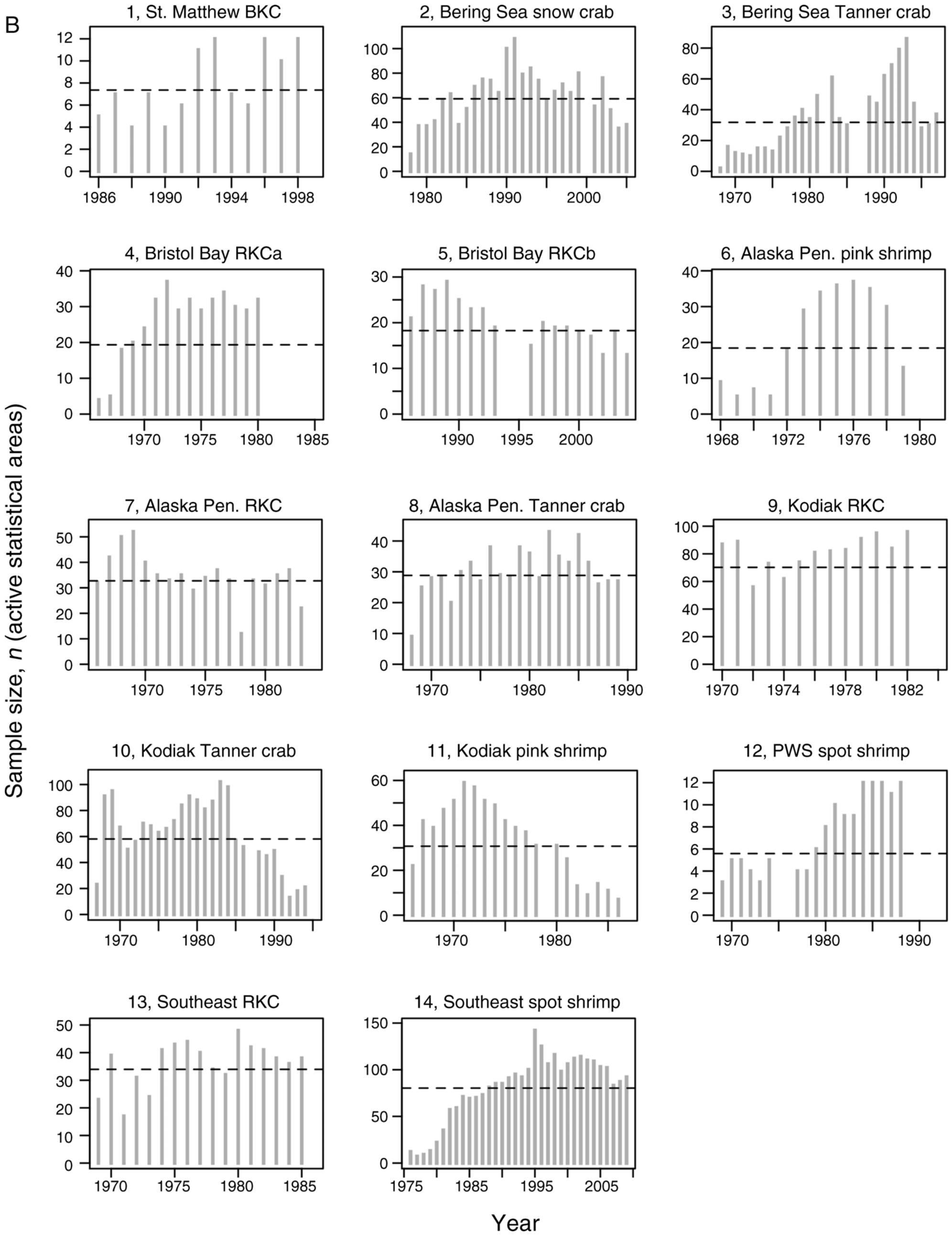

FIG. 2. Continued.

was slightly different from 2, we included the mean of log-transformed data as an explanatory variable for all hypothesis tests concerning SDL values. We also guarded against any potential effect of varying sample size on SDL or skewness by including sample size (number of active statistical areas) as an explanatory variable in all analyses.

Our analysis consisted of testing three hypotheses concerning generic spatial indicators for regime shifts: H_1, spatial variability in catch increases prior to population collapse; H_2, skewness in spatial catch distribution increases prior to population collapse; and H_3, increased variability is a transient phenomenon associated with collapse.

We began tests of H_1 and H_2 by plotting annual-scale trends in SDL and skewness (i.e., the slope of the linear trend for the parameter of interest) for each collapsing fishery. This analysis was conducted with linear regression including the sample size and the mean of log-transformed data as explanatory variables, using estimates of residual standard errors pooled across all 12 collapsing fisheries, with package "nlme" (Pinheiro and Bates 2000) in the computer language R (R Development Core Team 2010). Because the sampling unit for testing H_1 and H_2 is the individual fishery, we used global estimates of trends in the parameter of interest (i.e., the slope of the linear trend over time) across all collapsing fisheries to test our hypotheses. This analysis again used package "nlme," employing either full random-effects models (i.e., random-effect intercepts and slopes) or mixed-effects models (random-effect intercepts and fixed-effect slopes; Pinheiro and Bates 2000). Both random- and mixed-effects models estimated first-order autocorrelation in the residuals as a separate parameter, and Akaike's Information Criterion (AIC) was used to select the best model for tests of each hypothesis. We also used the best model, as determined by AIC, to test for "false positives" by comparing slopes between collapsing and non-collapsing fisheries. Trends in SDL and skewness for collapsing fisheries were calculated up to the year prior to collapse, while trends for non-collapsing fisheries were calculated across entire time series. These were one-tailed tests, because the hypotheses predict rising values of SDL and skewness (positive slopes) prior to collapse. Comparisons between collapsing and non-collapsing fisheries were also one-tailed, because H_1 and H_2 predict a stronger tendency for increasing SDL and skewness (i.e., greater slopes for linear trends) for collapsing than non-collapsing fisheries. A total of eight fishery–year combinations (i.e., 5% of the 278 cumulative years of data; Fig. 2B) had sample sizes of 3–5, and we dropped these data from analysis for H_2, because we judged that $n = 6$ was the minimum sample size capable of producing informative skewness estimates.

If either H_1 or H_2 were supported, we assessed at what point in time the indicator in question might generate a warning by curtailing the data included in analysis 1–5 years in advance of the collapse, and again using either fixed- or random-effects models (depending on AIC results) to estimate trends in spatial variability across fisheries. These estimates were again subjected to one-tailed tests, which evaluated our ability to detect trends in regime shift indicators 1–5 years prior to a collapse.

Analysis for H_3 included fisheries for which at least five years of post-collapse data were available; shorter time series were judged adequate in this case because we were estimating a single parameter (mean variability) for each time series, rather than the trend in variability over time. Pre- and post-collapse SDL estimates were compared with ANCOVA. Finally, all parameter trend estimates are presented with associated 95% confidence intervals (CI).

Results

H_1: Spatial variability in catch increases prior to population collapse

This hypothesis was supported. Best linear fits for nine of the 12 collapsing fisheries showed positive slopes for SDL over time (i.e., increases in spatial variability) prior to collapse (Fig. 3). Although only four of the 12 individual collapsing fisheries showed statistically significant increases in variability prior to collapse (one-tailed $P \leq 0.0001$), the random-effects model, accounting for the effects of sample size and mean values of log-transformed catch, showed strong evidence for increasing variability prior to collapse across all 12 fisheries (estimated mean slope of SDL, with 95% CI, over time = 0.016 ± 0.009; $t_{182} = 3.57$, one-tailed $P = 0.0002$). In this case, the random-effects model was superior to the mixed-effects model ($\Delta\text{AIC} = 2.54$). Across all collapsing fisheries, the random-effects model showed a significant negative relationship between SDL and mean values of log-transformed data (coefficient = −0.067 ± 0.060 [95% CI]; $t_{182} = 2.19$, two-tailed $P = 0.03$), and a significant positive relationship between SDL and sample size (coefficient = 0.002 ± 0.0017; $t_{182} = 2.82$, two-tailed $P = 0.005$), confirming the need to control for these effects. When trends were estimated across all collapsing fisheries, we found that statistically significant, increasing trends in spatial variability could be detected 1–4 years prior to fishery collapse (one-tailed $P \leq 0.02$; Fig. 4A). Finally, the random-effects model showed a significantly greater slope of spatial variability on year for collapsing (slope = 0.018 ± 0.008) than non-collapsing (slope = −0.003 ± 0.012) fisheries ($t_{230} = 1.81$, one-tailed $P = 0.04$; Fig. 4B).

H_2: Spatial skewness in catch increases prior to population collapse

Our data clearly did not support this hypothesis: best linear fits for only four of the 12 collapsing fisheries showed positive trends in skewness prior to collapse, and only one of these was statistically significant (Alaska Peninsula Tanner crab, one-tailed $P = 0.03$; Fig. 5). The mixed-effects model was superior to the random-effects model for estimating the trend in pre-collapse skewness across all collapsing fisheries ($\Delta\text{AIC} = 2.26$); however, this model failed to reject the null hypothesis (estimated slope of skewness on year = −1.05 ± 2.20; $t_{172} = 0.94$, one-tailed $P = 0.83$). Results of this hypothesis test were not different when the skewness of log-transformed data was analyzed (estimated slope of skewness on year = 0.59 ± 2.01; $t_{172} = 0.58$, one-tailed $P = 0.28$).

H_3: Increased variability is a transient phenomenon associated with collapse

This hypothesis also was not supported by our data. We found significantly higher spatial variability in catches in post-collapse (mean $n = 15$ years) vs. pre-collapse (mean $n = 17$ years) fisheries (ANCOVA with fishery identity, sample size, mean of log-transformed catches, and pre-or post-collapse state as explanatory variables; model $F_{7,126} = 10.33$, $P < 0.0001$; effect of pre- vs. post-collapse state, $P < 0.0001$; Fig. 6).

Discussion

Fishing effects in marine ecosystems may act synergistically with other forcing mechanisms, notably climate change, coastal eutrophication, and habitat loss

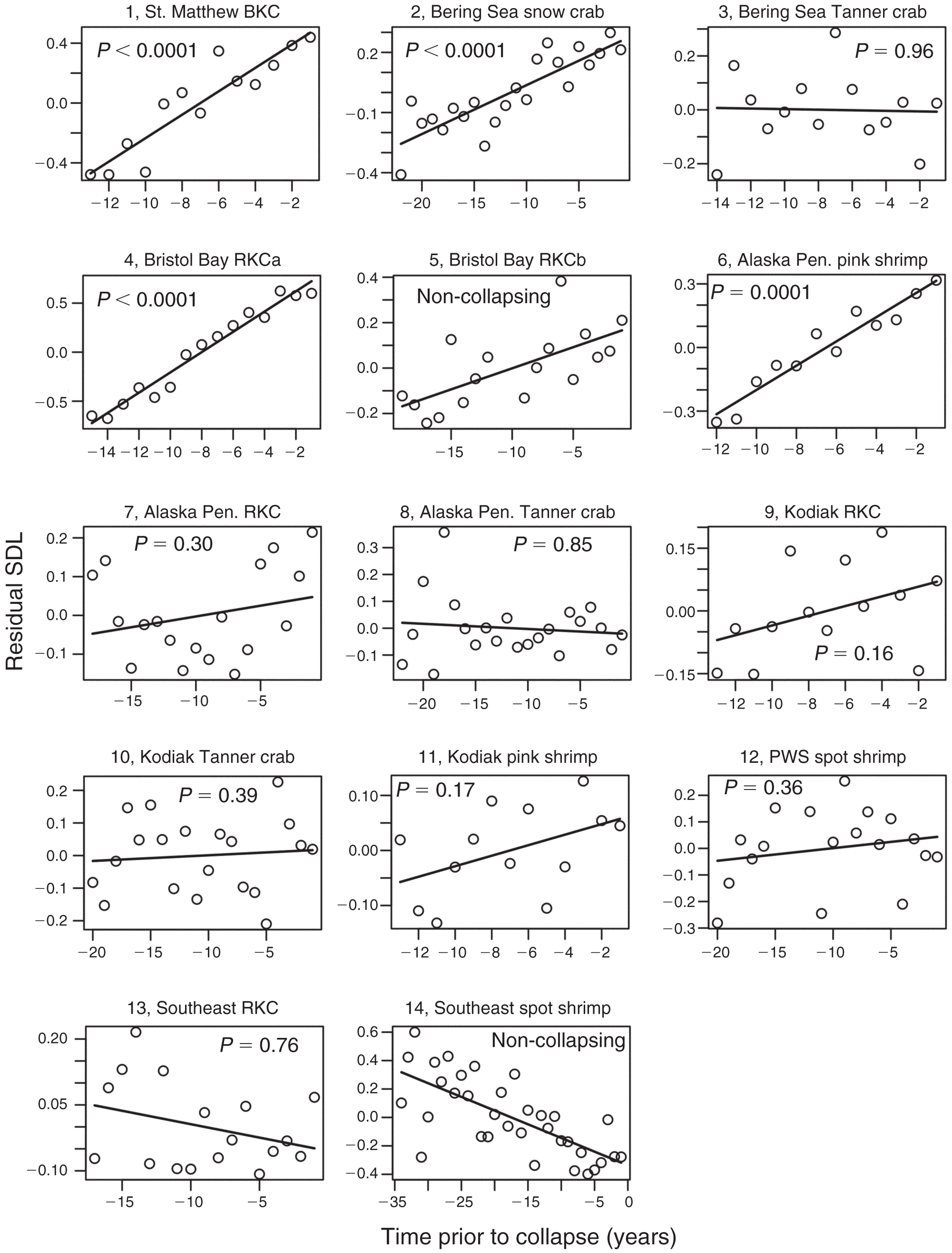

FIG. 3. Increasing spatial variability as a predictor of fisheries collapse: partial residual plots of SDL (SD of log-transformed data) vs. years prior to collapse. Plotted data are predicted SDL values after effects of mean of log-transformed data and sample size have been accounted for. Lines are best-fit linear trends, with associated one-tailed P values testing the hypothesis of increasing variability prior to collapse. The random-effects model showed strong evidence of increasing variability across all collapsing fisheries ($P = 0.0002$). Trends are indicated for non-collapsing fisheries, but P values are not plotted, as these fisheries were not included in hypothesis testing for pre-collapse behavior.

(Harley et al. 2006, Crowder et al. 2008), in a way that makes regime shifts and "ecological surprises" likely (deYoung et al. 2008). Given the poor global record of achieving fisheries sustainability (Worm et al. 2009), a tool that would provide early warning of impending nonlinear behavior in exploited stocks and communities would be an important addition to fisheries management. Our results support the use of one proposed generic regime shift indicator—increased spatial variability—to predict fisheries collapse. Although the considerable noise inherent in many marine populations creates a challenge for detecting statistically significant

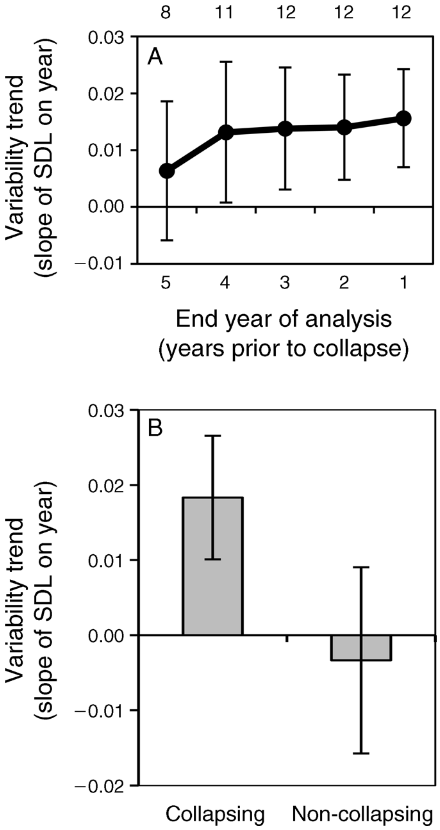

FIG. 4. (A) Length of potential warning from rising spatial variability: estimates of trend in SDL (slope on year) across all collapsing fisheries for analysis periods ending 1–5 years prior to collapse. Sample sizes (number of fisheries with $n \geq 10$ years of data for different analysis periods) are given above the panel. Random-effects models showed significant increases in variability, across all fisheries, for data ending 1–4 years prior to collapse (one-tailed $P \leq 0.02$). (B) "False positives" test: estimates of trend in variability across all collapsing and non-collapsing fisheries (random-effects model, one-tailed $P = 0.04$). Error bars in panels (A) and (B) show the 95% CI.

trends (Nicholson and Jennings 2004), and the time series in our study were quite short (mean = 17 years prior to collapse), we found evidence for increasing variability prior to collapse when an overall trend in variability was estimated across all collapsing fisheries ($P = 0.0002$). However, although sample size for most fisheries (Fig. 2B) achieved the sampling intensity ($n =$ 28–50) found necessary to detect spatial indicators of regime shifts in experimental manipulations (Carpenter et al. 2011, Seekell et al. 2012), we only detected statistically significant increases in spatial variability prior to collapse in four of 12 collapsing fisheries (Fig. 3). The considerable difference among populations in variability trends that we observed suggests that efforts to use this indicator for single populations may require levels of statistical power that are rarely available in management situations (Perretti and Munch 2012). Tests for change in variability across multiple populations, as we have presented here, may be a more realistic approach.

Although the statistical power of our test for "false positives" was severely limited by the small sample of non-collapsing fisheries ($n = 2$), we were able to reject the null hypothesis of no difference in trends of spatial variability between collapsing and non-collapsing fisheries (one-tailed $P = 0.04$; Fig. 4B). Thus, if managers of historical Alaskan crustacean fisheries had been monitoring trends in the spatial variability of catches, they would have had early warning of impending collapse, and also would have had a basis for distinguishing fisheries in danger of collapse from those that were not.

Critically, analysis across multiple fisheries was able to detect statistically significant increases in variability up to four years prior to collapse (Fig. 4A). The question of whether adequate early warning is generated for an effective management response is central to evaluations of regime shift indicators (Biggs et al. 2009, Contamin and Ellison 2009). The immediate mechanism leading to fisheries collapses may be spikes in fishing mortality 1–3 years before the collapse is reached (Myers et al. 1996), which suggests that a four-year warning might be adequate for decisive management action to stave off collapse. However, we grouped different fisheries relative to the number of years prior to collapse, which is only possible in a retrospective analysis. Because individual fisheries actually collapsed in different years (Fig. 2A), the statistical power that we gained by synchronizing fisheries relative to collapse year would not be available to managers conducting a monitoring study. This observation highlights the need to develop adequate statistical power by applying regime shift indicators to as many populations as possible when used in a fisheries context, ideally for a diverse set of species, because community reorganizations associated with fishery collapses often affect taxonomically diverse populations at multiple trophic levels (Hare and Mantua 2000, Choi et al. 2004). Furthermore, the 1976/1977 PDO shift also set into motion changes in internal community dynamics, such as the direction of trophic control (Litzow and Ciannelli 2007), that might have doomed crustacean stocks to collapse regardless of changes in exploitation rate. This is a potential problem for any early warning of a possible regime shift in complex systems, such as the Bering Sea and Gulf of Alaska continental shelf ecosystems, where the dynamics underlying nonlinear behavior are not understood. In such instances, there is little ability to provide scientific advice for an appropriate management response if declining resilience is detected by regime shift indicators. However, fisheries are typically the leading perturbation to marine ecosystems (Jackson et al. 2001), and catch rates are much more amenable to rapid management adjustment than other sources of perturbation, such as habitat loss or climate change (Biggs et al. 2009). We therefore suggest that catch reductions are an appropriate response in any situation in which evidence of an

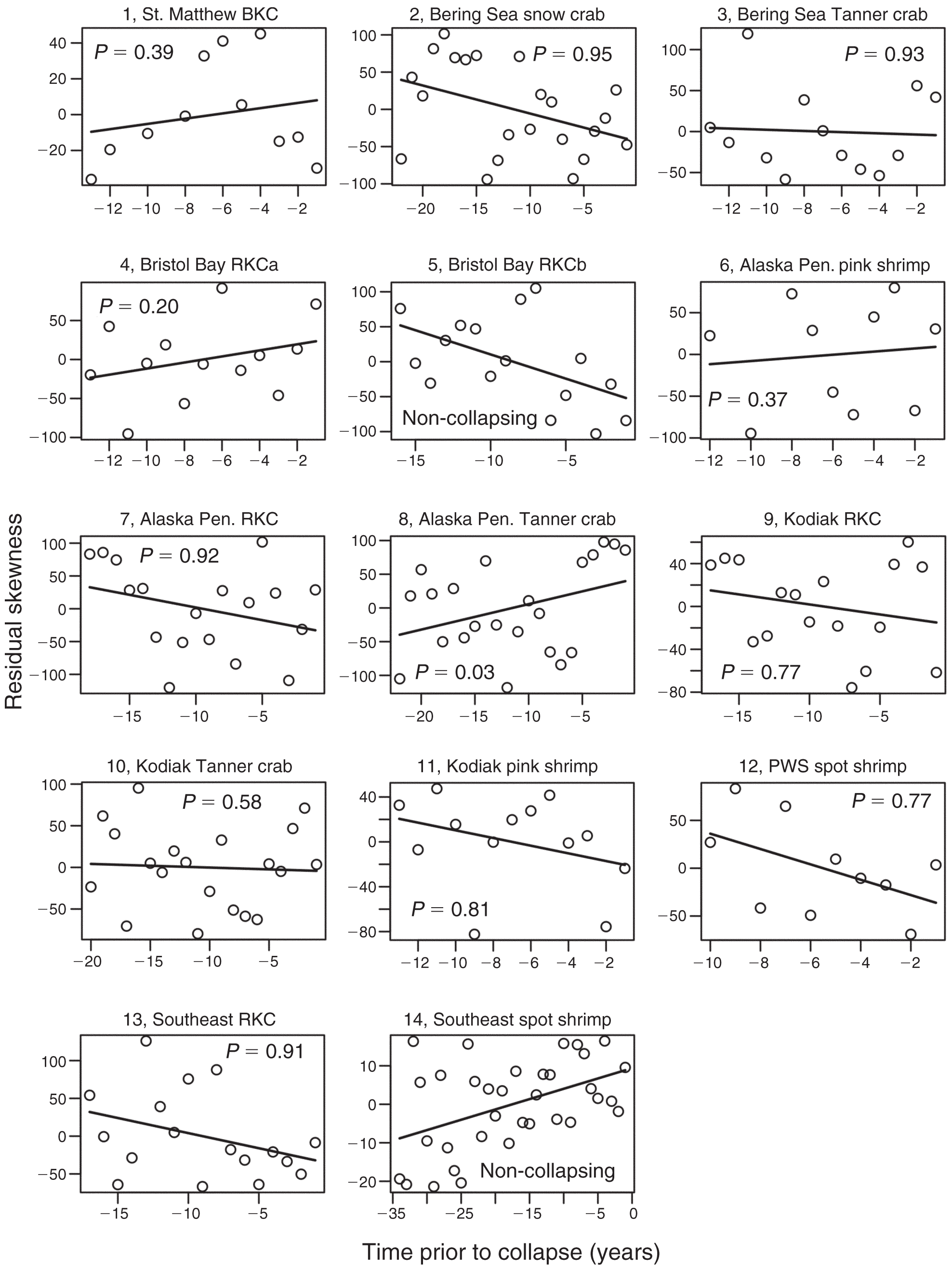

FIG. 5. Trends in spatial skewness of catch across all fisheries: partial residual plots after effects of sample size have been accounted for. Lines illustrate best-fit linear trends, with associated one-tailed P values testing the hypothesis of increasing skewness prior to collapse. Trends are indicated for non-collapsing fisheries, but P values are not plotted, as these fisheries were not included in hypothesis testing for pre-collapse behavior. The random-effects model showed no evidence of pre-collapse increases in skewness across all collapsing fisheries (one-tailed $P = 0.83$).

impending shift in exploited stocks is observed. Indeed, the ability to provide an early warning in systems where the underlying dynamics are not understood is one of the great potential benefits of generic indicators (Carpenter and Brock 2006, Guttal and Jayaprakash 2009). This contrasts with other possible spatial indicators of impending regime shifts (e.g., scale-invariant distributions of patch size), which require detailed knowledge of underlying system dynamics to be applied appropriately (Scheffer et al. 2009).

For regime shift indicators to be used by managers, reference points are needed to allow the risk of a regime shift to be inferred from the observed magnitude of change in the indicator. While a properly designed

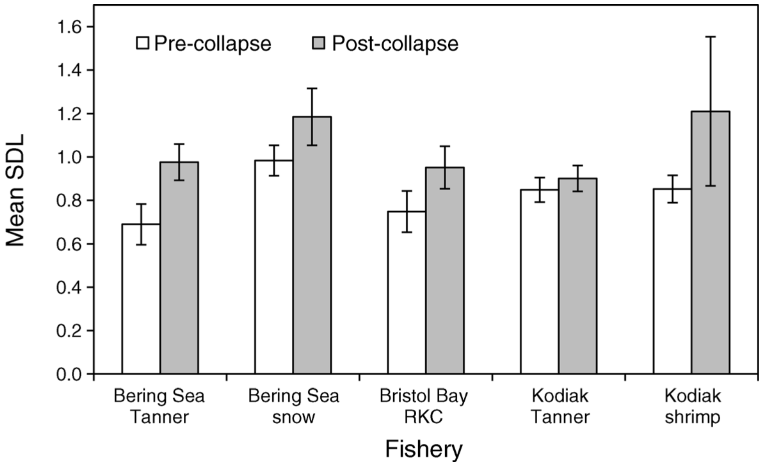

FIG. 6. Evidence of persistent increases in spatial variability in post-collapse fisheries, relative to the pre-collapse state (ANCOVA, pre- vs. post-collapse state, $P < 0.0001$). Error bars show 95% CI.

laboratory experiment can produce such reference points in terms of units of variance increase in indicators (Drake and Griffen 2010), a single observational study cannot. Aside from the question of whether the rates of increase in variability that we observed can be generalized to other fisheries or other ecosystem types, the fact that collapsing fisheries ($n = 12$) greatly outnumbered non-collapsing fisheries ($n = 2$) in our study means that our observations are greatly skewed toward the pre-collapse state, and we lack a range of observations in non-collapsing fisheries to define the full range of variability that might be observed at different levels of risk for a regime shift. Given the data available to us, the only recommendation we can make to managers is that statistically significant increases in the spatial variability of catches across multiple populations may indicate an elevated risk of collapse within 1–4 years, and may warrant precautionary reductions in harvest levels until trends in variability are stabilized. We also note a corollary: if increasing spatial variability is a characteristic of stocks that are approaching collapse (Fig. 3), and if this variability is driven by fishing, then preventing increases in variability (e.g., through spatially explicit harvest rules) suggests a management strategy for preventing collapse.

We found no support for the use of rising skewness in catch data as a leading indicator of fisheries collapses. There was no evidence of a linear increase in skewness prior to collapse, nor did time series show peaks in skewness around collapse points (Fig. 5). The average sample size for collapsing fisheries ($n = 37$; Table 1) was large enough to rule out inadequate statistical power as the cause for failing to reject the null hypothesis (Guttal and Jayaprakash 2008). Although they have a strong theoretical basis (i.e., asymmetry in the landscape picture of ecosystem dynamics near a bifurcation; Guttal and Jayaprakash 2008, Scheffer et al. 2009), increases in spatial skewness near a regime shift have to our knowledge not been demonstrated empirically. Fisheries catch data typically are highly skewed, so it may be that expectations derived from observing landscape asymmetry in minimal ecosystem models that do not assume high ambient skewness may not be applicable in fisheries systems. Another issue in empirical tests of model-generated regime shift indicators is the presence of noise in real ecological data (e.g., due to observational error) that is not captured by the stochastic dynamics of the model (Guttal and Jayaprakash 2008, Contamin and Ellison 2009). This issue is particularly important when fisheries catch data are being used, as in this study. Because catchability is nonconstant and usually unknown, the relationship between catch and abundance typically cannot be estimated (Maunder et al. 2006, Branch et al. 2011). This situation creates a recognized, but unquantifiable, source of noise between the parameter proposed for increasing variability (abundance) and the parameter tracked by managers (catch). Although inferring population collapse from catch or CPUE data is often problematic (Maunder et al. 2006, Branch et al. 2011), depressed crustacean fisheries catches in Alaska are well known to reflect persistently low levels of abundance in the underlying populations. Evidence demonstrating collapses in the populations in our study includes both abundance estimates from decadal-scale fisheries-independent surveys in the Gulf of Alaska and Bering Sea (Anderson and Piatt 1999, Loher and Armstrong 2005, Litzow 2006, Litzow and Ciannelli 2007) and model-derived estimates of demographic parameters (Zheng and Kruse 2000, Zheng et al. 2001, Zheng and Kruse 2006, Bechtol and Kruse 2009). Decadal-scale periods of reduced population size for Alaskan crustaceans are also believed to reflect large-scale ecological responses to the 1976/1977 PDO regime shift (Anderson and Piatt 1999, Hare and Mantua 2000, Litzow 2006, Litzow and Ciannelli 2007). Using management data, such as the catch data in this study,

Plate 1. Blue king crab (*Paralithodes platypus*). The fishery for this species around St. Matthew Island, Bering Sea, showed increasing spatial variability in catches before collapsing in 1999. Photo credit: J. D. Urban.

inevitably involves accepting limitations that are not present in data from a properly designed experiment. However, given the fisheries-independent support that we have outlined, we believe that it is reasonable to assume that collapsing commercial catches in this instance reflect persistent change in underlying populations.

As exploited stocks are driven to collapse, the population distribution contracts to high-quality habitat areas, such that the proportion of areas with high population density remains fairly constant, while the proportion of low- and medium-density areas falls (Hutchings 1996). This dynamic suggests a mechanism by which commercial fishing might drive the expected increase in spatial variability as collapse approaches; increases in temporal variability in exploited stocks due to fishing-induced truncation in age structures (Hsieh et al. 2006, Anderson et al. 2008) previously have been invoked as a mechanism that may induce nonlinear behavior in marine ecosystems (Scheffer et al. 2009). Fishing-driven retractions in distribution, and resulting loss of heterogeneity of habitat, may also act synergistically to increase sensitivity of exploited stocks to climate variability (Hsieh et al. 2008). We presume that the increase in spatial variability in catch data prior to collapse (Fig. 3) is driven by underlying increases in the variability of abundance. Standardized fisheries-independent surveys of crustacean stocks in Alaska generally began in the early 1980s, so pre-collapse measurements of abundance are available for few stocks. However, one available standardized survey from a single bay in the Gulf of Alaska does show rising variability in the abundance of pandalid shrimp immediately around a late-1970s community reorganization (Litzow et al. 2008), providing limited confirmation that the increased variability in catch that we observed reflected patterns of underlying abundance.

Expectations of rising variability prior to regime shifts stem from model observations of critical slowing down in system response to perturbation as a bifurcation is approached (Scheffer et al. 2009). Because critical slowing down is observed only around the bifurcation, models predict a transient increase in variability around the regime shift (Carpenter and Brock 2006, Biggs et al. 2009, Guttal and Jayaprakash 2009). This was not the case in our study. At the temporal scale of our analysis (mean $n = 17$ years pre-collapse, 15 years post-collapse), variability was significantly greater in the post-collapse than the pre-collapse state (Fig. 6). Rapid (annual-scale) change in community structure is a central feature of PDO-forced regime shifts in North Pacific ecosystems (Hare and Mantua 2000), and peak response to climate variability by continental shelf communities in Alaska is observed at lags of 2–4 years (Litzow 2006), suggesting that our observation of increased variability extended past the period of ecological transition. We interpret this persistent increase in variability as being more consistent with fishing effects on variability, rather than critical slowing down. For fisheries managers, this distinction is perhaps not very important: as long as rising spatial variability is a signal of an increasing risk of stock collapse (Fig. 3), the exact mechanisms behind the relationship are not critical. However, the suggestion that mechanisms other than multiple stable-state dynamics may have produced the elevated variability that we observed, coupled with the failure of rising skewness as an early indicator of collapse, suggest that caution is warranted when generalizing our results to other ecosystem types.

Although multiple stable-state dynamics have been formally demonstrated in marine ecosystems (e.g., Hsieh et al. 2005, Schröder et al. 2005, Hsieh and Ohman 2006), they are often simply inferred from abrupt shifts in ecological time series (Scheffer et al. 2001). However, other types of time series variability may cause these sudden shifts (Rudnick and Davis 2003). At times, ecologists have uncritically embraced multiple stable states as a conceptual model for understanding abrupt community shifts even though available evidence supports a more parsimonious explanation (Dudgeon et al. 2010). Regime shift indicators suggest a solution to one of the leading problems in applied ecology, are presented as being ubiquitous in a wide range of complex systems, and are generating much interest in high-profile journals (e.g., Biggs et al. 2009, Scheffer et al. 2009, Drake and Griffen 2010, Carpenter et al. 2011). However, our failure to detect pre-collapse increases in skewness, and, to a lesser extent, our observation of persistent post-collapse increases in variability, suggest that these indicators need to be applied cautiously in systems where nonlinear dynamics are either not formerly defined or not understood. Empirical tests are important in this context. Given the possibility of a "bandwagon" effect for such a novel and promising approach to detecting regime shifts, we suggest that studies producing negative results may be particularly useful in defining the actual utility of these indicators.

ACKNOWLEDGMENTS

We thank Paul Converse, Kim Phillips, and Gail Smith for assistance accessing data sets. We also thank Stewart Frusher and Alistair Hobday for helpful discussion, and Steve Carpenter and two anonymous reviewers for helpful comments on an earlier version of this paper. Funding was provided by the Alaska Sea Grant College Program with funds from the NOAA Office of Sea Grant, U.S. Department of Commerce, under grant NA10OAR4170097 (project R/31-22), with additional support from the Institute for Marine and Antarctic Studies, University of Tasmania.

LITERATURE CITED

Anderson, C. N. K., C. H. Hsieh, S. A. Sandin, R. Hewitt, A. Hollowed, J. Beddington, R. M. May, and G. Sugihara. 2008. Why fishing magnifies fluctuations in fish abundance. Nature 452:835–839.

Anderson, P. J., and J. F. Piatt. 1999. Community reorganization in the Gulf of Alaska following ocean climate regime shift. Marine Ecology Progress Series 189:117–123.

Bechtol, W. R., and G. H. Kruse. 2009. Reconstruction of historical abundance and recruitment of red king crab during 1960–2004 around Kodiak, Alaska. Fisheries Research 100:86–98.

Biggs, R., S. R. Carpenter, and W. A. Brock. 2009. Turning back from the brink: Detecting an impending regime shift in time to avert it. Proceedings of the National Academy of Sciences USA 106:826–831.

Branch, T. A., O. P. Jensen, D. Ricard, Y. M. Ye, and R. Hilborn. 2011. Contrasting global trends in marine fishery status obtained from catches and from stock assessments. Conservation Biology 25:777–786.

Carpenter, S. R., and W. A. Brock. 2006. Rising variance: a leading indicator of ecological transition. Ecology Letters 9:308–315.

Carpenter, S. R., et al. 2011. Early warnings of regime shifts: A whole-ecosystem experiment. Science 332:1079–1082.

Choi, J. S., K. T. Frank, W. C. Leggett, and K. Drinkwater. 2004. Transition to an alternate state in a continental shelf ecosystem. Canadian Journal of Fisheries and Aquatic Sciences 61:505–510.

Contamin, R., and A. M. Ellison. 2009. Indicators of regime shifts in ecological systems: What do we need to know and when do we need to know it? Ecological Applications 19:799–816.

Cottingham, K. L., J. A. Rusak, and P. R. Leavitt. 2000. Increased ecosystem variability and reduced predictability following fertilisation: Evidence from palaeolimnology. Ecology Letters 3:340–348.

Crowder, L. B., E. L. Hazen, N. Avissar, R. Bjorkland, C. Latanich, and M. B. Ogburn. 2008. The impacts of fisheries on marine ecosystems and the transition to ecosystem-based management. Annual Review of Ecology, Evolution, and Systematics 39:259–278.

Dakos, V., E. H. van Nes, P. D'Odorico, and M. Scheffer. 2012. Robustness of variance and autocorrelation as indicators of critical slowing down. Ecology 93:264–271.

Dakos, V., E. H. van Nes, R. Donangelo, H. Fort, and M. Scheffer. 2010. Spatial correlation as leading indicator of catastrophic shifts. Theoretical Ecology 3:163–174.

deYoung, B., M. Barange, G. Beaugrand, R. Harris, R. I. Perry, M. Scheffer, and F. Werner. 2008. Regime shifts in marine ecosystems: detection, prediction and management. Trends in Ecology and Evolution 23:402–409.

Donangelo, R., H. Fort, V. Dakos, M. Scheffer, and E. H. Van Nes. 2010. Early warnings for catastrophic shifts in ecosystems: comparison between spatial and temporal indicators. International Journal of Bifurcation and Chaos 20:315–321.

Drake, J. M., and B. D. Griffen. 2010. Early warning signals of extinction in deteriorating environments. Nature 467:456–459.

Dudgeon, S. R., R. B. Aronson, J. F. Bruno, and W. F. Precht. 2010. Phase shifts and stable states on coral reefs. Marine Ecology Progress Series 413:201–216.

Duplisea, D. E., and M. Castonguay. 2006. Comparison and utility of different size-based metrics of fish communities for detecting fishery impacts. Canadian Journal of Fisheries and Aquatic Sciences 63:810–820.

Folke, C., S. Carpenter, B. Walker, M. Scheffer, T. Elmqvist, L. Gunderson, and C. S. Holling. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. Annual Review of Ecology, Evolution, and Systematics 35:557–581.

Fraterrigo, J. M., and J. A. Rusak. 2008. Disturbance-driven changes in the variability of ecological patterns and processes. Ecology Letters 11:756–770.

Guttal, V., and C. Jayaprakash. 2008. Changing skewness: an early warning signal of regime shifts in ecosystems. Ecology Letters 11:450–460.

Guttal, V., and C. Jayaprakash. 2009. Spatial variance and spatial skewness: leading indicators of regime shifts in spatial ecological systems. Theoretical Ecology 2:3–12.

Hare, S. R., and N. J. Mantua. 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. Progress in Oceanography 47:103–145.

Harley, C. D. G., A. R. Hughes, K. M. Hultgren, B. G. Miner, C. J. B. Sorte, C. S. Thornber, L. F. Rodriguez, L. Tomanek, and S. L. Williams. 2006. The impacts of climate change in coastal marine systems. Ecology Letters 9:228–241.

Hastings, A., and D. B. Wysham. 2010. Regime shifts in ecological systems can occur with no warning. Ecology Letters 13:464–472.

Hsieh, C. H., S. M. Glaser, A. J. Lucas, and G. Sugihara. 2005. Distinguishing random environmental fluctuations from ecological catastrophes for the North Pacific Ocean. Nature 435:336–340.

Hsieh, C.-H., and M. D. Ohman. 2006. Biological responses to environmental forcing: the linear tracking window hypothesis. Ecology 87:1932–1938.

Hsieh, C.-H., C. S. Reiss, R. P. Hewitt, and G. Sugihara. 2008. Spatial analysis shows that fishing enhances the climatic sensitivity of marine fishes. Canadian Journal of Fisheries and Aquatic Sciences 65:947–961.

Hsieh, C.-H., C. S. Reiss, J. R. Hunter, J. R. Beddington, R. M. May, and G. Sugihara. 2006. Fishing elevates variability in the abundance of exploited species. Nature 443:859–862.

Hutchings, J. A. 1996. Spatial and temporal variation in the density of northern cod and a review of hypotheses for the stock's collapse. Canadian Journal of Fisheries and Aquatic Sciences 53:943–962.

Jackson, J. B. C., et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629–638.

Jensen, O. P., T. A. Branch, and R. Hilborn. 2012. Marine fisheries as ecological experiments. Theoretical Ecology 5:3–22.

Kruse, G. H., J. Zheng, and D. L. Stram. 2010. Recovery of the Bristol Bay stock of red king crabs under a rebuilding plan. ICES Journal of Marine Science 67:1866–1874.

Lindegren, M., V. Dakos, J. P. Groger, A. Gardmark, G. Kornilovs, S. A. Otto, and C. Möllmann. 2012. Early detection of ecosystem regime shifts: A multiple method evaluation for management application. PLoS One 7(7):e38410.

Litzow, M. A. 2006. Climate regime shifts and community reorganization in the Gulf of Alaska: how do recent shifts compare with 1976/1977? ICES Journal of Marine Science 63:1386–1396.

Litzow, M. A., and L. Ciannelli. 2007. Oscillating trophic control induces community reorganization in a marine ecosystem. Ecology Letters 10:1124–1134.

Litzow, M. A., J. D. Urban, and B. J. Laurel. 2008. Increased spatial variance accompanies reorganization of two continental shelf ecosystems. Ecological Applications 18:1331–1337.

Loher, T., and D. A. Armstrong. 2005. Historical changes in the abundance and distribution of ovigerous red king crabs (*Paralithodes camtschaticus*) in Bristol Bay (Alaska), and potential relationship with bottom temperature. Fisheries Oceanography 14:292–306.

Maunder, M. N., J. R. Sibert, A. Fonteneau, J. Hampton, P. Kleiber, and S. J. Harley. 2006. Interpreting catch per unit effort data to assess the status of individual stocks and communities. ICES Journal of Marine Science 63:1373–1385.

McArdle, B. H., K. J. Gaston, and J. H. Lawton. 1990. Variation in the size of animal populations—patterns, problems and artifacts. Journal of Animal Ecology 59:439–454.

Myers, R. A., J. A. Hutchings, and N. J. Barrowman. 1996. Hypotheses for the decline of cod in the North Atlantic. Marine Ecology Progress Series 138:293–308.

Nicholson, M. D., and S. Jennings. 2004. Testing candidate indicators to support ecosystem-based management: the power of monitoring surveys to detect temporal trends in fish community metrics. ICES Journal of Marine Science 61:35–42.

Oborny, B., G. Meszena, and G. Szabo. 2005. Dynamics of populations on the verge of extinction. Oikos 109:291–296.

Orensanz, J. M. L., J. Armstrong, D. Armstrong, and R. Hilborn. 1998. Crustacean resources are vulnerable to serial depletion—the multifaceted decline of crab and shrimp fisheries in the Greater Gulf of Alaska. Reviews in Fish Biology and Fisheries 8:117–176.

Perretti, C. T., and S. B. Munch. 2012. Regime shift indicators fail under noise levels commonly observed in ecological systems. Ecological Applications 22:1772–1779.

Pinheiro, J. C., and D. M. Bates. 2000. Mixed-effects models in S and S-PLUS. Springer, New York, New York, USA.

R Development Core Team. 2010. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rudnick, D. L., and R. E. Davis. 2003. Red noise and regime shifts. Deep-Sea Research Part I: Oceanographic Research Papers 50:691–699.

Scheffer, M., J. Bascompte, W. A. Brock, V. Brovkin, S. R. Carpenter, V. Dakos, H. Held, E. H. van Nes, M. Rietkerk, and G. Sugihara. 2009. Early-warning signals for critical transitions. Nature 461:53–59.

Scheffer, M., S. Carpenter, J. A. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. Nature 413:591–596.

Schröder, A., L. Persson, and A. M. De Roos. 2005. Direct experimental evidence for alternative stable states: a review. Oikos 110:3–19.

Seekell, D. A., S. R. Carpenter, T. J. Cline, and M. L. Pace. 2012. Conditional heteroskedasticity forecasts regime shift in a whole-ecosystem experiment. Ecosystems 15:741–747.

Takimoto, G. 2009. Early warning signals of demographic regime shifts in invading populations. Population Ecology 51:419–426.

Worm, B., et al. 2009. Rebuilding global fisheries. Science 325:578–585.

Zheng, J., and G. H. Kruse. 2000. Recruitment patterns of Alaskan crabs in relation to decadal shifts in climate and physical oceanography. ICES Journal of Marine Science 57:438–451.

Zheng, J., and G. H. Kruse. 2006. Recruitment variation of eastern Bering Sea crabs: Climate-forcing or top-down effects? Progress in Oceanography 68:184–204.

Zheng, J., G. H. Kruse, and D. R. Ackley. 2001. Spatial distribution and recruitment patterns of snow crabs in the Eastern Bering Sea. Pages 233–255 *in* G. H. Kruse, N. Bez, A. Booth, M. W. Dorn, S. Hills, R. N. Lipcius, D. Pelletier, C. Roy, S. J. Smith, and D. Witherell, editors. Spatial processes and management of marine populations. University of Alaska Sea Grant, Fairbanks, Alaska, USA.