Titles

1. Spatial and temporal patterns in demersal fish communities following Exxon Valdez

2. Spatio-temporal models reveal subtle changes to demersal communities following the Exxon Valdez oil spill.

3. Subtle changes to demersal communities persist more than a quarter century after the Exxon Valdez oil spill

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**Keywords:**

**Abstract**

**Introduction**

Major environmental disasters such as oil spills are a persistent concern to marine ecosystems worldwide, with major oil disasters striking coastal seas throughout the past century and affecting all oceans. In United States coastal waters alone between 1973 and 2011, nearly 2.7 million m3 of oil were accidently released, though annual release rates have dropped substantially over the past 20 years

(Ramseur, 2012). Particularly well publicized spills include the Santa Barbara, CA oil spill of 1969 (Squire, 1992), the Amoco Cadiz spill off France in 1978 (Conan *et al.*, 1982; Gundlach *et al.*, 1983), the Exxon Valdez spill in 1989 (Paine *et al.*, 1996; Peterson *et al.*, 2003), and the Deepwater Horizon spill of 2010 (Camilli *et al.*, 2010; White *et al.*, 2012). Oil spills have devastating and long lasting impacts on the marine environment, spanning the spectrum of ecological systems from the intertidal to the deep sea and from plankton to fish to marine mammals (Conan *et al.*, 1982; Paine *et al.*, 1996; Peterson *et al.*, 2003; Silliman *et al.*, 2016).

The impacts of petroleum contamination on marine communities are varied and complex. Documented effects range from the acute and direct (e.g., toxicological effects that cause serious injury or immediate death (Garrott *et al.*, 1993; Piatt and Ford, 1996) to the gradual and indirect, including negative consequences for growth, development, and reproduction (Collier *et al.*, 1992; Hicken *et al.*, 2011; Monson *et al.*, 2011; Rice *et al.*, 2001). In recent years, a consensus has developed indicating that even relatively low levels of exposure can have considerable fitness consequences for individuals

(Collier *et al.*, 1993; Hicken *et al.*, 2011; Incardona *et al.*, 2015; Sørhus *et al.*, 2016). While detailed laboratory studies have repeatedly found negative consequences of petroleum related contaminants, connecting these excellent individual level studies to population or community level effect in natural populations has proven difficult (Awkerman *et al.*, 2016; Peterson, 2001; Peterson *et al.*, 2003) primarily because information on important components of the ecosystem before the spill are often lacking, natural environmental variation – both spatial and temporal - can obscure signatures of oil impacts in marine communities, spatial fishing pressures may confound oil effect, and sparse biological sampling may result in insufficient power to detect the biological effects of an oil spill (Paine *et al.*, 1996).

The Exxon Valdez oil spill (hereafter “EVOS”) in March 1989 spilled approximately 257,000 barrels (36,000 mt) of crude oil into Prince William Sound, Alaska (Paine *et al.*, 1996; Wolfe *et al.*, 1994). In the weeks and months following the spill, oil was advected by wind and currents to the southwest, spreading into the Gulf of Alaska. While the exact dispersal path and final distribution of oil in water and sediments remains uncertain, the approximate distribution and extent of surface oil is documented (Short and Heintz, 1997; Wolfe *et al.*, 1994) as are beaches that were contaminated with oil (Fig. 1; NOAA, 1997). Furthermore, multiple lines of evidence suggest that oil from EVOS reached a wide range of habitats and species; oil was observed both directly in some deep water trawls (Armstrong *et al.*, 1995) and a range of metabolites associated with petroleum exposure were detected in a wide range of invertebrate and fish species across a vast spatial area

(Collier *et al.*, 1993; Krahn *et al.*, 1992; Marty *et al.*, 2003; Peterson, 2001; Short and Heintz, 1997; Sol *et al.*, 2000). Estimates by Wolfe et al. (1994) suggest about 20% or the oil reached the sediments in Prince William Sound and the Gulf of Alaska. Furthermore, in at least some habitats EVOS oil remains in the environment to the present day: oil has been documented many years after the spill along shorelines (Peterson *et al.*, 2003; Short *et al.*, 2007) and detected through metabolites in sampled fish (Jewett *et al.*, 2002).

The EVOS occurred within a high latitude coastal shelf system that is influenced by complex topography with seasonal, interannual, and decadal variability (Stabeno *et al.*, 2004).  The region sits in an major oceanographic transition zone that partitions coincides with the boundaries of the Oregonian and Aleutian zoogeographic provinces (Allen and Smith, 1988) and the Gulf of Alaska and North American Pacific Fijordland ecoregions (Spalding *et al.*, 2007). The region is influenced by a location and intensity of the Aleutian Low, a major atmospheric feature that affect weather in the Gulf of Alaska and is influenced by large-scale atmospheric patterns (Overland *et al.*, 1999). The timing of the EVOS coincided with a well documented shift in climate conditions in 1988/89 which impacted the coastal and open ocean conditions in the GOA (Bond *et al.*, 2003; Di Lorenzo *et al.*, 2008). The region is characterized by freshwater inputs, a complex topographic system, and vigorous coastal currents that generates eddies, topographic steering, entrainment of offshore production at the heads of gullies, and complex frontal structure (Royer *et al.*, 2001; Stabeno *et al.*, 2004; 2016). Episodic storm events impact water column stability with associated effects on the timing of spring blooms and the disruption of the provisioning of nutrients to the surface in summer (Gargett, 1997; Henson, 2007; Hollowed *et al.*, 2007). These complex environmental processes influence survival and dispersal of fish across the coastal shelf via direct impacts on the availability of preferred habitats and indirect impacts on seasonal primary production, spatial patterns of the quality and quantity of zooplankton in the region, and encounter rates between predators and prey.

In addition to environmental variation, post-juvenile groundfish in the Gulf of Alaska have been exposed to spatially and temporally heterogeneous patterns in commercial fishing over the past half century. Five main events have impacted the spatial and temporal patterns of fishing: 1) foreign fisheries depleted rockfish (primarily Pacific ocean perch) populations in the late 1960s and early 1970s prior to United States harvest restrictions and populations slowly recovered throughout the 1990s (Hulson *et al.*, 2014); 2) domestication of the foreign fisheries 1985-1990 (need REF); 3) the establishment of individual fishing quotas (IFQs) in the sablefish and Pacific halibut fisheries (NPFMC and NMFS, 1992; Pautzke and Oliver, 1997); 4) a series of Bering Sea and pollock allocation and management actions culminating in the passage of the American Fisheries Act (1998; REF); 5) implementation of the Steller sea lion mitigation measures which established no trawl zones around haulouts and rookeries and implementation of seasonal quotas for sea lion prey (2001). A detailed discussion of the implications of management impacts on diversification of several fisheries can be found in (Anderson et al. NCEAS paper, Boudreau in prep n/d, and Haynie n/dxxxxx).

Quantifying the relative contribution of EVOS, natural environmental variability, and fisheries to population and community change is difficult (Peterson *et al.*, 2003). Direct negative effects of EVOS on charismatic species such as marine mammals (Garrott *et al.*, 1993) and birds (Piatt and Ford, 1996; Piatt *et al.*, 1990) are well documented. Additionally, some longer-term signals of oil impacts have been described for other species and habitats (Monson *et al.*, 2011; Short *et al.*, 2007). However, ecological systems are extraordinarily complex and theory suggests that many ecosystem level consequences of an event like EVOS are the result of indirect interactions and complex species-by-environment interactions (Peterson, 2001; Peterson *et al.*, 2003). Thus, a retrospective examination of the ecological consequences of EVOS after 25 years is warranted.

Here we focus an understudied community in the context of EVOS - demersal fish communities of the central and western Gulf of Alaska - to explore community responses to the EVOS spill over a large geographic area in the context of a dynamic ocean environment and fisheries. Demersal fish communities were exposed to EVOS as oil swept west out of Prince William Sound (Fig. 1, Collier et al. 1993, Sol et al. 2000). While the extent and exposure of fish communities to oil is almost wholly undocumented, it is clear that some areas were exposed to significant amounts of oil while similar habitats in other areas were left unexposed. We leverage this spatial gradient in exposure to contrast demersal fish communities over the past 30 years (1984-2015) and compare groundfish communities in areas across a gradient of EVOS exposure. Specifically, we develop and apply a suite of spatio-temporal models to a fishery-independent groundfish survey and calculate a range of community metrics for demersal fish communities. Then we compare both spatial and time-series patterns of areas that experienced a range of exposure to EVOS to identify any potential EVOS related signal in changes to the groundfish community. Rather than focus on a detailed analysis of individual species as has been done previously (Deriso *et al.*, 2008; Jewett *et al.*, 1999; Monson *et al.*, 2011; Rice *et al.*, 2001; but see Wiens *et al.*, 1996)[the “but” only applies to Wiens and Jewett, fix in submitted version.], we assess aspects of the demersal fish community and examine available information for signals of impacts of EVOS within the context of environmental and management change. Our work compliments existing research focused on detailed assessments for tactical management (Hollowed *et al.*, 2000)and multi-species studies exploring spatial patterns of groundfish communities and their response to climatic shifts (Baker and Hollowed, 2014; Holsman *et al.*, 2015; Mueter and Megrey, 2005; Mueter and Norcross, 2002; Mueter *et al.*, 2009).

**Methods**

*Data*

To assess spatial and temporal patterns in groundfish communities we used fisheries independent surveys conducted by the Alaska Fisheries Science Center (AFSC) between 1984 and 2015. The AFSC used the same sampling methodology and bottom trawl gear over the time series (stratified random sampling design, (Armistead and Nichol, 1990; Stauffer, 2004)). The mean latitude and longitude coordinates of each survey tow were converted to a Cartesian coordinate system (Alaska Albers equal area conic), which was compatible with existing EVOS geospatial data layers, and conserves area and distance for accurate spatial calculations. We limited our analyses to trawls set at depths shallower than 600m, which numbered 7601 individual hauls between 1984 and 2015.

We applied our models to 53 species groups. These groups represent species that were observed in at least 3% of the tows (>230 tows). 50 of these groups represent individual species and 3 represent species complexes that were not identified to species separately during field sampling throughout the survey extent (Table S1). For brevity, we refer to these species and species-groups simply as “species” subsequently.

*Statistical model*

We constructed separate models for each groundfish species to understand the spatial and temporal patterns of occurrence and abundance. We estimated a model for each species independently and subsequently combined the model outputs to generate a suite of multi-species metrics of the groundfish communities. We first present the statistical model and then describe the spatio-temporal metrics groundfish communities.

In all models, we used catch per unit effort (kg∙hectare-1) observed on each trawl as the response variable. Because most species were absent from a large number of observed trawls, we separately modeled the presence and distribution of species density, adopting a delta-GLMM approach with two sub-models (Maunder and Punt, 2004; Shelton *et al.*, 2014). Probability of occurrence, ***π****it*(***s***), of the *i*th species in year *t* for a set of locations ***s***, was modeled using a binomial GLMM with logit link,

(1)

where represents a matrix of fixed effect covariates at locations ***s*** in year *t*, represents a vector of coefficients for species *i*, and represents a vector of spatial random effects that follow a first-order autoregressive process:

(2)

where ***ρ*** represents the degree of autoregression in encounter probabilities and ***Σ*** represents spatial covariation in random effects (discussed below). Random effects were assumed to be autoregressive to account for variation not explicitly included in our model (e.g., variation due to the environment or population processes such as density dependence). Note that because trawl surveys are not conducted annually but triennially (1984-1999) or biennially (1999-2015) the autoregressive term refers to the date of the previous survey year, not the previous calendar year.

The second groundfish sub-model describes the distribution of CPUE conditional on the occurrence of at least one individual. We assumed that for this “positive” sub-model that groundfish CPUE was Gamma distributed and used a log-link,

(3)

where is a matrix of covariates corresponding to each haul location, represents the estimated species-specific coefficients, represent spatial random effects that again follow an autoregressive process (analogous to eqn 2, but with an independently derived covariance matrix). Then represents the mean and *σi* the scaleparameter of the Gamma distribution. Again this model incorporates only hauls in which the species was observed and so describes the CPUE of each species conditioned on the species presence.

For all models we used available haul level information about bottom depth (m) and included both linear and quadratic terms for log(depth) in the occurrence and positive models (Shelton *et al.*, 2014; Tolimieri *et al.*, 2015). We centered log(depth) by subtracting the mean log(depth) across all tows. We also considered two models for fixed year effects: i) we estimated a single intercept, and ii) we allowed for a distinct intercept for each year. As the intercept scales the occurrence or conditional CPUE, respectively for the entire region, models with variable intercepts allow for spatially uniform, region-wide changes in occurrence or CPUE.

Covariance for spatial random effects was modeled as a function of distance using the Matérn function in the occurrence and positive models. The covariance between location *sj* and *sk* distance in the Matérn function is

(4)

where *τ*2 is the spatial variance, *Γ*() and *Kν()* represent the Gamma and Bessel functions, respectively, *djk* is the Euclidian distance between locations *sj* and *sk*, and *κ* is an estimated scaling parameter (Lindgren *et al.*, 2011). The parameter *ν* controls the smoothness of the Matérn function and is usually fixed rather than estimated from data (when *ν*  = 0.5, the Matérn reduces to the exponential covariance function). Following previous work, we chose *ν* = 3/2; this allows the Matérn to be more flexible than the exponential, but also allows the function to be differentiable (Rasmussen and Williams, 2006; Ward *et al.*, 2015). The covariance matrices for the presence-absence and positive models for each species have separate parameters *τ*2 and *κ*, reflecting the assumptions that each model component may have a different variance or rate at which correlations decline as a function of distance. Further details can be found in previous publications (Ono *et al.*, 2016; Ward *et al.*, 2015).

We estimate the model using the integrated nested Laplace approximation as implemented in the R package INLA (Martins *et al.*, 2013). INLA approximates the inverse of the spatial variance-covariance matrix of fixed locations using three large sparse matrices using stochastic partial differential equations (Rue *et al.*, 2009; Ruiz-Cárdenas *et al.*, 2012). Estimation of the fixed effects is then done via marginal maximum likelihood using the Laplace approximation to approximate the integral across random effects, and random effects are estimated via Empirical Bayes. Using these estimates and non-informative priors on fixed effects, INLA allows Monte Carlo samples to be generated from the posterior distribution, as the Laplace approximation to the marginal likelihood.

Four models were estimated for each species: two occurrence models and two positive models. For each submodel, we estimated one model with a single intercept and one with a year-specific intercept. We compared single and year-specific models using posterior predictive plots and deviance information criterion (DIC) to then identified preferred models for each species.

***Generating predictive densities for each species***

After estimating the two sub-models for each species, we used the estimated models to generate predicted densities for Gulf of Alaska. We projected our model estimates to the centroid of each 2x2 km grid cell covering the entire Gulf of Alaska out to the 600m isobath. We generated 1,000 Monte Carlo samples from the approximate joint posterior density for the parameters of the models for each species and for each sample we predicted a density for each sub-model to the 2x2 km grid. We then combined the occurrence and positive models to generate an unconditional expectation for CPUE for each grid cell. Using samples from the full posterior distribution maintains the spatio-temporal correlation structure of the estimated parameters and random effects and properly accounts for uncertainty in these estimates. Because the occurrence and positive models are estimated independently, we can calculate the unconditional expectation for CPUE of species at time *t* and location *s* by multiplying each sample from the occurrence and positive model. Specifically, for the *g*th Monte Carlo sample, the unconditional CPUE estimate is and has units kg∙hectare-1.

***Defining areas for comparison across the Gulf of Alaska***

We identified eleven areas across the Gulf of Alaska to compare groundfish communities through time (Fig. 1). Each area represents habitat between 50 and 150 m deep divided by natural bathymetric breaks (canyons) resulting in irregularly shaped areas that range in size from 1,352 to over 8,000 km2 (Table 1). Due to the bathymetry, some focal areas are divided by narrow channels while others are separated by large distances. This is an unavoidable aspect of complex bathymetry in the Gulf of Alaska. The focal areas span a range of habitats with differing exposures to EVOS, environmental disturbance, and fishing. (Niebauer *et al.*, 1994; Short and Heintz, 1997; Fig. 1; Wolfe *et al.*, 1994). The east-most area (Area 1) was wholly unexposed to EVOS oil as currents and wind drove EVOS oil west out of Prince William Sound. Areas 3, 4, and 5 were exposed to main flow of oil, as evidenced by both direct observation of surface sheens as well as shorelines documented to be oiled during EVOS (NOAA, 1997).

Parts of areas 2 and 6 received some oil, but the majority was thought to have traveled down Shelikof Straight, inside of Kodiak Island. Areas 7 to 11 may have been slightly exposed to EVOS, but direct observations of oil and oceanographic models suggest minimal impact for these areas (Niebauer *et al.*, 1994; Short and Heintz, 1997; Wolfe *et al.*, 1994). Furthermore, west of area 5 (Fig. 1), most EVOS oil had transformed into tar balls, a less biologically available and toxic form of oil (NEED REFS FROM JEEP). Thus our comparison areas bracket the spill spatially and provide areas with more and less exposure to EVOS. We do not consider areas further east of Cape Suckling (144° W longitude) due to concerns about distinct groundfish assemblages east and west of this line.

To understand the contribution of fisheries exploitation we collated catch records for groundfish in the central Gulf of Alaska. Due to differences in catch location reporting requirements for different species and changes in reporting over our time period, we compiled catch statistics for four broad areas encompassing all of our focal areas: Prince William Sound, Cook Inlet, Kodiak, and Alaska Penninsula (Fig. 1). We obtained individual and vessel-level gross fishing catch data from the Commercial Fisheries Entry Commission (CFEC; [https://www.cfec.state.ak.us](https://www.cfec.state.ak.us" \t "_blank)) for years 1985-2014 and calculated the total groundfish mass sold from trawl and longline fisheries for each area in each year. Because harvest regions differ substantially in area, we standardized the catch to metric tons per km2 to facilitate direct comparisons among areas.

***Community metrics***

For each area, we summarized the groundfish community by constructing four community metrics from the single-species spatio-temporal models. We hypothesized that any effect of EVOS would manifest differentially across species with multiple life-history and functional attributes, so we focused on community metrics that reflected species groups with different characteristics. For each metric, we summarized the predicted CPUE for each species in each year in each region using the Monte Carol draws for each 2x2 km grid cell. We combined information across grid cells within each area to generate an index-standardized mean estimate (and uncertainty) for unconditional CPUE (Shelton *et al.*, 2014; Ward *et al.*, 2015). Thus for each metric in each area, we have a time-series for each species for 1984 to 2015. We combined these species-specific metrics to generate multi-species community metrics for each area in each year. We describe the multi-species metrics and how they map onto expected EVOS impacts in turn.

*Total biomass*. This was the simplest attribute and reflected the sum of all 53 fish species estimated by the spatio-temporal model. We hypothesized that total biomass would exhibit an overall decline if EVOS initiated a decrease in productivity as a result of persistent, sublethal effect that negatively affected recruitment, reproduction, growth, or survival at the community scale.

*Feeding Guild.* We definedguilds for Gulf of Alaska groundfish based on the categorization of species primary feeding habitat: pelagic (P) or benthic (B) foragers (Aydin *et al.*, 2007; Gaichas *et al.*, 2009). In addition, we categorized the eight largest and most voracious fish predators in the system as apex (A) predators (including e.g. Lingcod, *Ophiodon elongates,* and Pacific halibut, *Hippoglossus stenolepis;* Table S1*).* As the majority of EVOS oil in these habitats was thought to be present on the benthos, not suspended in the water column, we hypothesized that benthic feeders would be the most likely guild to exhibit a response to EVOS, though apex predators may respond indirectly via foodweb connections.

*Diet classification.* We classified species based on their published dietary preferences. We use published diet data for each species (Aydin *et al.*, 2007) to classify the dominant prey type for each species. We defined species diet as predominantly invertebrate (>80% of diet is invertebrates; I), predominantly fish (>80% of diet is fish; F), or generalist (diet is between 20 and 80% for both fish and invertebrates).

*Recruitment interval.* Hydrocarbon effects are documented to be particularly detrimental to early life-stages of fish (Hicken *et al.*, 2011; Incardona *et al.*, 2015; Sørhus *et al.*, 2016). However, as the trawl survey only catches species that are generally longer than 15cm standard length, the lag between the exposure of larvae to the oil and when juvenile fish are observed in the survey will vary among species. Therefore we divided species into three groups by the number of years expected between parturition and achieving a size of 20cm (a size at which survey capture efficiency is close to one). We categorized this interval as short (<2 years), medium (2 to 4 years), or long (>4 years). We defined the interval using published parameters for the von Bertalanffy growth curve and generated a predicted age to reach 15cm. For species with multiple estimates of *k* and *L∞* we used the median estimate. For a few species, we could not find published growth parameter. In these cases we used available estimates from similar species in the same family. Surface waters we undeniably impacted by EVOS oil in 1989 and pelagic eggs, larvae, and juvenile fish were potentially exposed. We hypothesize that shorter recruitment interval species will exhibit an immediate effect of EVOS while longer recruitment interval species will exhibit delayed effects.

For all community metrics, we present four summaries to describe their change over time. First we present the raw time-series for each focal area to visually examine the time-series for evidence of a perturbatoin provided by EVOS. Second, to compare among areas exposed to varying amounts of oil, we calculate a linear trend for each area post-spill (1990-2015). To calculate the trend, we used the mean estimated CPUE for each area and year weighted by the inverse of the variance. Ideally, we would have compared trends before and after the spill but with only two surveys occurring before EVOS, breakpoint analysis was not statistically feasible. Third, we compared the variability of each metric during the post-spill period using the coefficient of variation (CV = standard deviation/mean). We calculated the CV using the deviations from the linear trend to estimate the standard deviation and the overall mean abundance from 1990 to 2015.

Beyond trends and variability, we used two metrics of synchrony for the demersal groundfish community to compare areas classified as EVOS-affected (areas 2-6) and Control (areas 1, 7-11). We calculated community-wide synchrony, , for each area for the entire time period (Loreau and de Mazancourt, 2008). The parameter ranges between 0 (indicating uncorrelated fluctuations) and 1 (indicating perfect synchrony; Loreau and de Mazancourt, 2008). We compared among areas and used a permutation test to ask if the calculated synchrony deviated significantly from a community in which all species are fluctuating independently (using the *community.sync* function in R package *synchrony; REF).* To examine if community synchrony changed over the time-series, we use moving window approach, calculating in 9-year blocks for each area. For all of these analyses, wee use the estimated mean density of each species in each area.

Finally, to ask if focal areas fluctuated in unison over the time-series, we calculated all pairwise Person product moment correlations among areas. As with we calculated both single pairwise correlation for the entire time-series and correlations using a 9-year moving window.

**Results**

We successfully estimated spatio-temporal models for 53 species (Table S1) and generated predictions for each of the 2x2 km grid cells in the Gulf of Alaska. We then combined predicted densities into our multi-species metrics for each of the focal areas. Our analysis revealed substantial variation among areas across all community metrics (Fig. 2). For example, areas varied more than three fold in total biomass and in general the relative rank of individual areas tended to be stable through time; low biomass areas tended to remain low biomass areas and high biomass areas tend to remain high biomass areas, reflecting well-known spatial variation in productivity across the Gulf of Alaska. In general, the raw time-series from three focal areas most exposed to EVOS do not appear notably different than other areas in the GOA. This is true for total biomass as well as all guilds, diet types, and recruitment categories (Fig. 2).

Total catch from trawl and longline for each of areas also reflect substantial variation in groundfish communities among areas (Fig. 3). Kodiak and Alaska Peninsula average catches 2 to 4 times the catch in Cook Inlet or Prince William Sound on an area standardized basis and both, the magnitude and ranking of areas with respect to catch are consistent over time (Fig. 3). The initial increase in documented catches from 1985-1990 for all areas reflect, in part, the transition to an entirely U.S. based fleet, not necessarily an increase in overall catch. Regardless, there is evidence of changes in catch 1989 or 1990 in response to EVOS in any area and broadly speaking, total removals are relatively stable across the time-series from 1990.

Examination of linear trends revealed an association between negative linear trends in total biomass and EVOS exposure (Fig. 4). The three most exposed areas having strongly negative trends, the two areas classified as moderate EVOS exposure a strong negative and no trend, while control regions had zero or positive trends. The pattern among areas in total biomass trend was not driven by a single species or group (Fig. 4). Instead the negative trend in EVOS regions total biomass was associated with a negative trend in the apex predator guild (Guild A) and a lower (near zero) trend in the pelagic forager guild (Guild P) in areas most exposed to EVOS. There was not an obvious pattern in trend for diet types and the trend for recruitment categories; species with short times to recruitment and long times to recruitment showed an inclination toward more negative trends.

In contrast to the trend analysis, there were no obvious patterns of temporal variability in response to EVOS (Fig. 5). Values for CV were relatively similar across all areas in all metrics, though there were two categories, pelagic foragers (Guild P) and invertebrate consumers (Diet type I), which exhibited a general decline in CV from east to west (from area 1 to area 11).

Estimates of community-wide synchrony for the entire study region were low across all areas ( and permutation tests revealed no significant difference at any area between estimated synchrony and simulated communities in which species undergo uncorrelated fluctuations (*p* > 0.10 for all areas). Sliding window analysis of community synchrony also showed no obvious changes in synchrony across the time series. There is a suggestion of a slight decline in synchrony for EVOS areas relative to Control areas (Fig. S1), but any difference is very minor. Similarly, we found no changes in synchrony measures when analyses were applied to individual guilds, diet types, or recruitment intervals (results not shown).

Finally, we did find evidence of a time-varying signature in the cross correlation in total biomass among EVOS areas and among Control areas (Fig. 6). At the beginning and end of the time-series, correlations among EVOS, among Control, and between EVOS and Control areas, are indistinguishable. However, EVOS and Control area showed strong positive correlations during the 1990-1999 window before both declined gradually over the next 20 years. Interestingly, during this period the cross-correlation between EVOS and Control areas decreased to become negative, indicating that biomass fluctuated in opposite directions between EVOS-affected and Control areas during these periods (Fig. 6). Pairwise correlations for the entire time period were much lower than the 1990-99 span.

**Discussion**

Detecting oil spill impacts in marine ecosystems is simultaneously easy and difficult. Acute petroleum contamination can cause direct mortality (Monson *et al.*, 2011; e.g. Piatt and Ford, 1996) that is immediately obvious, whereas subtle and chronic consequences can affect growth and development through a range of physiological pathways (Hicken *et al.*, 2011; Incardona *et al.*, 2015; e.g. Rice *et al.*, 2001; Sørhus *et al.*, 2016). But how such effects translate from individuals and focal populations to full communities remains poorly understood. Here we focused on an ecologically and economically important component of the marine community, demersal groundfish, to attempt to detect a signature of EVOS using 25 years of data following the spill. EVOS contaminated substantial portions of the Gulf of Alaska as evidenced by both direct observations of oil, and evidence of exposure from sampled fish

(Collier *et al.*, 1993). Groundfish have largely been neglected in the context of EVOS following the conclusion of Armstrong et al. (1995) that EVOS did cause sufficient direct mortality to affect substantial proportions of fish populations. Since Armstrong et al. (1995), however, there has been a paradigm shift in how researchers assess the consequences of petroleum contamination (Peterson *et al.*, 2003) with increasing attention paid to the effects of low-level, sublethal consequences of oil toxicity in a range of marine fish species (Hicken *et al.*, 2011; Incardona *et al.*, 2012; Sørhus *et al.*, 2016). We recognize that substantial amounts of oil enters the marine environment via natural seeps (National Research Council, 2003; Ramseur, 2010) in addition to surface oil spills such as EVOS. However, we view natural seeps as a temporally invariant, background driver of communities across the gulf whereas EVOS was a pulse of oil that affected a specific area at a particular time providing contrast to detect a signature of EVOS.

As the signature of EVOS on demersal fish communities is expected to be indirect and complex, we adopted a community-level approach to detecting the signature of EVOS in demersal groundfish. Our approach showed that while EVOS and Control areas were indistinguishable in term of temporal variability (CV) and measures of community synchrony, we demostrated that EVOS-affected areas had a decreasing trend in total biomass relative to Control areas. This signal appears to be driven largely by declines of apex predators in the EVOS-affected areas, including important fisheries species such as Lingcod (*Ophiodon elongatus*), Pacific cod (*Gadus macrocephalus*), and Pacific halibut (*Hippoglossus stenolepis*) and reduced trend of the pelagic foragers guild such as Pacific hake *(Merluccius productus)* and multiple rockfish species in the genus *Sebastes.* In contrast to our expectations that benthic foragers would be most susceptible to any oil toxicity, we observed no clear signal between EVOS and Control regions among benthic foragers. Inspection of fisheries removals (Fig. 3) do not suggest obvious changes in removals that could drive community wide changes in the groundfish community.

We also showed a signature of increased correlation among EVOS and Control regions in that peaks coincident with the expected peak window in which EVOS effects should be apparent (1990-99). We know of no other shared driver among these areas that would be hypothesized to produce such a pattern. A similar temporal pattern is evident among the apex predator guild as well, though not as strong (not shown).

We suggest that our observed patterns in the groundfish community are consistent with a small, though generalized reduction in recruitment in EVOS areas relative to Control areas. A slight but broad based impact is consistent with our current understanding of sublethal effects of oil on pelagic eggs and larvae that can lead to reduced fish fitness (e.g. reduced growth). Such signatures would be most evident only when examined across the entire community simultaneously, rather than on a species by species basis (Fig. 3). Simply due to the longevity of many of the groundfish species any effect of reduced reproduction, recruitment, or growth, would manifest itself in the community gradually over the span of years to decades.

In the absence of data that can be brought to directly assess these proposed mechanisms (e.g., spatial time-series of recruitment or growth) the exact causes of these patterns must remain speculative. As with any large scale and long-term study, it is impossible to control all possible covariates to isolate the effects of an oil spill and we must acknowledge that the observed patterns could arise from biological processes as yet unidentified. We designed our study to make comparisons that control for as many aspects as possible. We utilized a major fishery-independent data set and identified discrete areas within a standardize depth range and divided by natural bathymetric breaks. We only include areas contained within a single biogeographic region so all areas share major oceanographic drivers such as the Pacific Decadal Oscillation (PDO; Hare and Mantua, 2000)[add other major refs]. Finally, we constructed statistical models that account for occurrence probability, density, and incorporate measurement error. Thus we feel confident that the signals detected represent real patterns.

Overall, we must echo Armstrong et al.’s (1995) conclusion that the signature of EVOS was not an obvious, major impact on groundfish communities and other drivers such as environmental variability and fishing may override other drivers. However, our analysis does suggest that low-level, long term consequences of a major environmental perturbation are detectable in natural systems and that spatial analyses conducted over broad spatial and temporal scales provide a rigorous approach for identifying such signatures.

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