From Ole: Here is an almost full draft of the first groundfish paper (abstract is missing). I’d love some other eyes to read through it, catch my logical mistakes, and make sure that I haven’t overlooked or underemphasized existing literature. Also, the methods are a bit long but that is somewhat intentional as several other papers will be citing this one for methods as they use outputs from the same models. There are a few spots that have notes to myself, still. Hope it all makes sense. Let me know if you have any questions/comments

Also, if you’d like to still be an author after reading through, please add your address on this title page. Thanks! Ole

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. Your title goes here.

**Authors – order TBD.**

Andrew Olaf Shelton1,2\*

Mary Hunsicker

Rachel Blake

Janet Duffy-Anderson

Blake Feist1

Anne Hollowed

Colette Ward  
Eric Ward1

Ben Williams

1Conservation Biology Division, Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 2725 Montlake Blvd. E, Seattle, WA 98112, U.S.A.

2Earth Resources Technology, Inc. 14401 Sweitzer Lane Suite 300 Laurel, MD 20707.

\*E-mail: ole.shelton@noaa.gov

**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 2010). 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), 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 & Ford 1996) to the gradual and indirect, including negative consequences for growth, development, and reproduction (Collier et al. 1992, Rice et al. 2001, Hicken et al. 2011, Monson et al. 2011). 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

(Peterson 2001, Peterson et al. 2003, Awkerman et al. 2016) 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, 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 (Wolfe et al. 1994, Paine et al. 1996) [confirm this number]. 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 (Wolfe et al. 1994, Short & Heintz 1997) 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; 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 (Krahn et al. 1992, Collier et al. 1993, Short & Heintz 1997, Sol et al. 2000, Peterson 2001, Marty et al. 2003). 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 nearly 30 years after the spill along shorelines (Peterson et al. 2003, Short et al. 2007).

Despite undisputed evidence that oil spills have negative consequences for marine ecosystems and that EVOS was a widely dispersed and disruptive event in the Gulf of Alaska (Peterson et al. 2003), it has been difficult to quantify ecosystem wide consequences of EVOS. Direct mortality to charismatics species such as marine mammals (Garrott et al. 1993) and birds (Piatt et al. 1990, Piatt & Ford 1996) is well documented and some longer-term signals of oil impacts have been described for some species and habitats (Short et al. 2007, Monson et al. 2011). 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 25 years later 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. 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 other, 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 ((but see Wiens et al. 1996, Rice et al. 2001, Deriso et al. 2008, Monson et al. 2011)[the but should only apply to Wiens], we assess aspects of the demersal fish community and examine available information for signals of impacts of EVOS. Our work compliments existing research focused on detailed assessments for tactical management (Hollowed 2000)[add a few other REFS]and multi-species studies exploring spatial patterns of groundfish communities and their response to climatic shifts (Mueter & Norcross 2002, Mueter & Megrey 2005, Mueter et al. 2009, Baker & Hollowed 2014, Holsman et al. 2015).

**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 & 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). 53 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 & 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 & 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 (Ward et al. 2015, Ono et al. 2016).

We estimate the model using the integrated nested Laplace approximation as implemented in the R package INLA (www.r-inla.org,(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 Markov Chain Monte Carlo (MCMC) samples from the joint approximate posterior density for each species and for each MCMC 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 MCMC 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 MCMC sample from the occurrence and positive model. Specifically, for the *g*th MCMC 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 (Fig. 1; Wolfe et al. 1994, Niebauer et al. 1994, Short & Heintz 1997). The east-most area (Area 1) was almost 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). 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 (Wolfe et al. 1994, Niebauer et al. 1994, Short & Heintz 1997). 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.

***Community metrics***

For each area, we summarized the groundfish community by constructing four community metrics from the single-species spatio-temporal models. We hypothesized the 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 MCMC 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. 2012, 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, low level toxicity, that negatively affected 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 Lingcod, *Ophiodon elongates,* and Pacific halibut, *Hippoglossus stenolepis;* Table S1*).* As the majority of EVOS oil in these habitats was thought to be present in benthic sediments, 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). We hypothesize that species with diets based heavily upon invertebrates will exhibit a greater population decline [probably need something more here]

*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; REF). 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. We hypothesize that shorter recruitment interval species will exhibit an immediate effect of EVOS while longer recruitment interval species will exhibit delayed effects.

We initially considered additional groupings based upon the reproductive characteristics of fish (e.g. oviparous versus ovoviviparous) but discovered that classification by reproductive characteristics produced groups the coincided almost identically with guilds and produced virtually identical results. Therefore we omit detailed results for reproductive traits.

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 & de Mazancourt 2008). The parameter ranges between 0 (indicating uncorrelated fluctuations) and 1 (indicating perfect synchrony; Loreau & 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.

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 (REF). 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).

Examination of linear trends revealed an association between negative linear trends in total biomass and EVOS exposure. 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. 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. 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), that 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. 5), 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 (e.g. Piatt & Ford 1996, Monson et al. 2011) that is immediately obvious, whereas subtle and chronic consequences can affect growth and development through a range of physiological pathways (e.g. Rice et al. 2001, Hicken et al. 2011, Incardona et al. 2015, 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) [missing REFS?]. We recognize that substantial oil enters the marine environment via natural seeps but natural seeps are funamdentally different (elaborate)

(National Research Council 2003, Ramseur 2010).

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.

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… appendix?).

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).

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 & Mantua 2000)[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.

**References**

Armistead CE, Nichol DG (1990) 1990 Bottom Trawl Survey of the Eastern Bering Sea Continental Shelf. NOAA Tech. Memo. NMFS-AFSC-7, 190 p.

Armstrong DA, Dinnel PA, Orensanz JM, Armstrong JL, McDonald TL, Cusimano RF, Nemeth RS, Landolt ML, Skalski JR, Lee RF, Huggett RJ (1995) Status of selected bottomfish and crustacean species in Prince William Sound following the Exxon Valdez oil spill

. In: Wells PG, Butler JN, Hughes JS (eds) Exxon Valdez Oil Spill: Fate and Effects in Alaskan Waters. ASTM International, 100 Barr Harbor Drive, PO Box C700, West Conshohocken, PA 19428-2959, p 485–547

Awkerman JA, Hammer B, Almario A, Lilavois C, Barron MG, Raimondo S (2016) Spatially explicit assessment of estuarine fish after Deepwater Horizon oil spill: tradeoffs in complexity and parsimony

. Ecological Applications

Aydin KY, Gaichas S, Ortiz I, Kinzey D, Friday N (2007) A comparison of the Bering Sea, Gulf of Alaska, and Aleutian Islands large marine ecosystems through food web modeling. US Department of Commerce, Washington, D.C. NOAA Tech. Memo. NMFS-AFSC-178

Baker MR, Hollowed AB (2014) Delineating ecological regions in marine systems: Integrating physical structure and community composition to inform spatial management in the eastern Bering Sea. Deep-Sea Research Part II 109:215–240

Camilli R, Reddy CM, Yoerger DR, Van Mooy BAS, Jakuba MV, Kinsey JC, McIntyre CP, Sylva SP, Maloney JV (2010) Tracking Hydrocarbon Plume Transport and Biodegradation at Deepwater Horizon. Science 330:201–204

Collier TK, Krahn MM, Krone CA, Johnson LL, Myers MS, Chan S-L, Varanasi U (1993) Oil exposure and effects in subtidal fish following the Exxon Valdez oil spill. http://dxdoiorg/107901/2169-3358-1993-1-301:301–305

Collier TK, Singh SV, Awasthi YC, Varanasi U (1992) Hepatic xenobiotic metabolizing enzymes in two species of benthic fish showing different prevalences of contaminant-associated liver neoplasms. Toxicology and Applied Pharmacology 113:319–324

Conan G, Dunnet GM, Crisp DJ (1982) The Long-Term Effects of the Amoco Cadiz Oil Spill [and Discussion]. Philosophical Transactions of the Royal Society B: Biological Sciences 297:323–333

Deriso R, Maunder M, Pearson W (2008) Incorporating covariates into fisheries stock assessment models with application to Pacific herring. Ecological Applications 18:1270–1286

Gaichas S, Skaret G, Falk-Petersen J, Link JS, Overholtz W, Megrey BA, Gjøsæter H, Stockhausen WT, Dommasnes A, Friedland KD, Aydin K (2009) A comparison of community and trophic structure in five marine ecosystems based on energy budgets and system metrics. Progress in Oceanography 81:47–62

Garrott RA, Eberhardt LL, Burn DM (1993) Mortality of sea otters in Prince William Sound following the Exxon Valdez oil spill. Marine Mammal Science 9:343–359

Gundlach ER, Boehm PD, Marchand M, Atlas RM, Ward DM, Wolfe DA (1983) The fate of Amoco Cadiz oil. Science 221:122–129

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

Hicken CE, Linbo TL, Baldwin DH, Willis ML, Myers MS, Holland L, Larsen M, Stekoll MS, Rice SD, Collier TK, Scholz NL, Incardona JP (2011) Sublethal exposure to crude oil during embryonic development alters cardiac morphology and reduces aerobic capacity in adult fish. Proceedings of the National Academy of Sciences 108:7086–7090

Hollowed A (2000) Are multispecies models an improvement on single-species models for measuring fishing impacts on marine ecosystems? ICES Journal of Marine Science 57:707–719

Holsman KK, Ianelli J, Aydin K, Punt AE, Moffitt EA (2015) A comparison of fisheries biological reference points estimated from temperature-specific multi-species and single-species climate-enhanced stock assessment models. Deep-Sea Research Part II

Incardona JP, Carls MG, Holland L, Linbo TL, Baldwin DH, Myers MS, Peck KA, Tagal M, Rice SD, Scholz NL (2015) Very low embryonic crude oil exposures cause lasting cardiac defects in salmon and herring. Scientific Reports 5:13499

Incardona JP, Vines CA, Anulacion BF, Baldwin DH, Day HL, French BL, Labenia JS, Linbo TL, Myers MS, Olson OP, Sloan CA, Sol S, Griffin FJ, Menard K, Morgan SG, West JE, Collier TK, Ylitalo GM, Cherr GN, Scholz NL (2012) Unexpectedly high mortality in Pacific herring embryos exposed to the 2007 Cosco Busan oil spill in San Francisco Bay. Proceedings of the National Academy of Sciences 109:E51–E58

Krahn MM, Burrows DG, Ylitalo GM, Brown DW, Wigren CA, Collier TK, Chan S-L, Varanasi U (1992) Mass spectrometric analysis for aromatic compounds in bile of fish sampled after the Exxon Valdez oil spill. Environmental Science and Technology 26:116–126

Lindgren F, Rue H, Lindström J (2011) An explicit link between Gaussian fields and Gaussian Markov random fields: the stochastic partial differential equation approach. Journal of the Royal Statistical Society B 73:423–498

Loreau M, de Mazancourt C (2008) Species synchrony and its drivers: neutral and nonneutral community dynamics in fluctuating environments. Am Nat 172:E48–66

Martins TG, Simpson D, Lindgren F, Rue H (2013) Bayesian computing with INLA: New features. Computational Statistics and Data Analysis 67:68–83

Marty GD, Hoffmann A, Okihiro MS, Hepler K, Hanes D (2003) Retrospective analysis: bile hydrocarbons and histopathology of demersal rockfish in Prince William Sound, Alaska, after the Exxon Valdez oil spill. Marine Environmental Research 56:569–584

Maunder MN, Punt AE (2004) Standardizing catch and effort data: a review of recent approaches. Fish Res 70:141–159

Monson DH, Doak DF, Ballachey BE, Bodkin JL (2011) Could residual oil from the Exxon Valdez spill create a long‐term population “sink” for sea otters in Alaska? Ecological Applications 21:2917–2932

Mueter FJ, Megrey BA (2005) Distribution of population-based indicators across multiple taxa to assess the status of Gulf of Alaska and Bering Sea groundfish communities. ICES Journal of Marine Science: Journal du Conseil 62:344–352

Mueter FJ, Norcross BL (2002) Spatial and temporal patterns in the demersal fish community on the shelf and upper slope regions of the Gulf of Alaska. Fishery Bulletin 100:559–581

Mueter FJ, Broms C, Drinkwater KF, Friedland KD, Hare JA, Hunt GL Jr., Melle W, Taylor M (2009) Ecosystem responses to recent oceanographic variability in high-latitude Northern Hemisphere ecosystems. Progress in Oceanography 81:93–110

National Research Council (2003) Oil in the Sea III. National Academies Press, Washington, D.C.

Niebauer HJ, Royer TC, Weingartner TJ (1994) Circulation of Prince William Sound, Alaska. Journal of Geophysical Research: Atmospheres 99:14113–14126

NOAA (1997) EVOS research and restoration information project CD-ROM. Alaska Deptartment of Natural Resources (ADNR) and National Oceanic and Atmospheric Administration (NOAA). Anchorage, AK, National Centers for Environmental Information, NESDIS, NOAA, U.S. Department of Commerce.

Ono K, Shelton AO, Ward EJ, Thorson JT (2016) Space-time investigation of the effects of fishing on fish populations. Ecol App 26:392–406

Paine RT, Ruesink JL, Sun A, Soulanille EL (1996) Trouble on oiled waters: lessons from the Exxon Valdez Oil Spill. Annual Review of Ecology and Systematics 27:197–235

Peterson CH (2001) The “Exxon Valdez” oil spill in Alaska: acute, indirect and chronic effects on the ecosystem. Advances in Marine Biology 39:1–103

Peterson CH, Rice SD, Short JW, Esler D, Bodkin JL, Ballachey BE, Irons DB (2003) Long-Term Ecosystem Response to the Exxon Valdez Oil Spill. Science 302:2082–2086

Piatt JF, Ford RG (1996) How many seabirds were killed by the Exxon Valdez oil spill. American Fisheries Society Symposium 18:712–719

Piatt JF, Lensink CJ, Butler W, Nysewander DR (1990) Immediate Impact of the “Exxon Valdez” Oil Spill on Marine Birds. The Auk 107:387–397

Ramseur JL (2010) Oil spills in U.S. coastal waters: background, governance and issue for congress

. Congressional Research Service -, Washington DC, USA

Rasmussen C, Williams C (2006) Gaussian processes for machine learning. MIT press

Rice SD, Thomas RE, Carls MG, Heintz RA, Wertheimer AC, Murphy ML, Short JW, Moles A (2001) Impacts to Pink Salmon Following the Exxon Valdez Oil Spill: Persistence, Toxicity, Sensitivity, and Controversy. Reviews in Fisheries Science 9:165–211

Rue H, Martino S, Chopin N (2009) Approximate Bayesian inference for latent Gaussian models by using integrated nested Laplace approximations. Journal of the Royal Statistical Society B 71 part 2:319–392

Ruiz-Cárdenas R, Krainski ET, Rue H (2012) Direct fitting of dynamic models using integrated nested Laplace approximations — INLA. Computational Statistics and Data Analysis 56:1808–1828

Shelton AO, Dick EJ, Pearson DE, Ralston S, Mangel M, Walters C (2012) Estimating species composition and quantifying uncertainty in multispecies fisheries: hierarchical Bayesian models for stratified sampling protocols with missing data. 69:231–246

Shelton AO, Thorson JT, Ward EJ, Feist BE (2014) Spatial semiparametric models improve estimates of species abundance and distribution. Can J Fish Aq Sci

Short JW, Heintz RA (1997) Identification of Exxon Valdez oil in sediments and tissues from Prince William Sound and the Northwestern Gulf of Alaska based on a PAH weathering model. Environ Sci Technol 31:2375–2384

Short JW, Irvine GV, Mann DH, Maselko JM, Pella JJ, Lindeberg MR, Payne JR, Driskell WB, Rice SD (2007) Slightly Weathered Exxon ValdezOil Persists in Gulf of Alaska Beach Sediments after 16 Years. Environ Sci Technol 41:1245–1250

Silliman BR, Dixon PM, Wobus C, He Q, Daleo P, Hughes BB, Rissing M, Willis JM, Hester MW (2016) Thresholds in marsh resilience to the Deepwater Horizon oil spill. Scientific Reports 6:32520

Sol SY, Johnson LL, Horness BH, Collier TK (2000) Relationship Between Oil Exposure and Reproductive Parameters in Fish Collected Following the Exxon Valdez Oil Spill. Marine Pollution Bulletin 40:1139–1147

Squire JL Jr (1992) Effects of the Santa Barbara, Calif., Oil Spill on the Apparent Abundance of Pelagic Fishery Resources. Marine Fisheries Review 54:7–14

Stauffer G (2004) NOAA Protocols for Groundfish Bottom Trawl Surveys of the Nation’s Fishery Resources. U.S. Dep. Commerce, NOAA Tech. Memo. NMFS-F/SPO-65, p.205

Sørhus E, Incardona JP, Karlsen Ø, Linbo T, Sørensen L, Nordtug T, van der Meeren T, Thorsen A, Thorbjørnsen M, Jentoft S, Edvardsen RB, Meier S (2016) Crude oil exposures reveal roles for intracellular calcium cycling in haddock craniofacial and cardiac development. Scientific Reports 6:31058

Tolimieri N, Shelton AO, Feist BE, Simon V (2015) Can we increase our confidence about the locations of biodiversity ‘hotspots' by using multiple diversity indices? Ecosphere 6:ar 290

Ward EJ, Jannot JE, Lee Y-W, Ono K, Shelton AO, Thorson JT (2015) Using spatiotemporal species distribution models to identify temporally evolving hotspots of species co‐occurrence. Ecological Applications 25:2198–2209

White HK, Hsing P-Y, Cho W, Shank TM, Cordes EE, Quattrini AM, Nelson RK, Camilli R, Demopoulos AWJ, German CR, Brooks JM, Roberts HH, Shedd W, Reddy CM, Fisher CR (2012) Impact of the Deepwater Horizon oil spill on a deep-water coral community in the Gulf of Mexico. Proceedings of the National Academy of Sciences 109:20303–20308

Wiens JA, Crist TO, Day RH, Murphy SM, Hayward GD (1996) Effects of the Exxon Valdez Oil Spill on Marine Bird Communities in Prince William Sound, Alaska. Ecological Applications 6:828–841

Wolfe DA, Hameedi MJ, Galt JA, Watabayashi G, Short J, O'Claire C, Rice S, Michel J, Payne JR, Braddock J, Hanna S, Sale D (1994) The Fate of the Oil Spilled from the Exxon Valdez. Environmental Science and Technology 28:560A–568A