



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

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Toxic pollutants such as crude oil have direct negative effects for a wide array of marine life. While mortality from acute exposure to oil is obvious, sub-lethal consequences of exposure to petroleum derivatives for growth and reproduction are less evident and sub-lethal effects in fish populations are obscured by natural environmental variation, fishing, and measurement error. We use fisheries independent surveys in the Gulf of Alaska to examine the consequences of the 1989 Exxon Valdez oil spill (EVOS) for demersal fish. We delineate areas across a range of exposure to EVOS and use spatio-temporal models to quantify the abundance of 53 species-groups over 31 years. We compare multiple community metrics for demersal fish in EVOS and Control areas. We find that areas more exposed to EVOS have more negative trends in total groundfish biomass than non-EVOS areas, and that this change is driven primarily by reductions in the abundance of the apex predator guild. We show no signature of increased variability or increased levels of synchrony within EVOS areas. Our analysis supports mild consequences of EVOS for groundfish communities, but suggests that long time-series and assessments of changes at the community level may reveal sub-lethal effects in marine communities.

Keywords: Exxon Valdez, groundfish, spatio-temporal models, community analysis.

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 accidentally 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), 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). Oil spills can have long-lasting impacts on marine 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).

The effects 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 (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 laboratory studies have found negative consequences of petroleum related contaminants, connecting individual level studies to population or community level effects in natural populations has proved difficult (Peterson, 2001; Peterson et al., 2003; Awkerman et al., 2016; but see Fodrie et al., 2014) primarily because information on important components of the ecosystem before the spill are often lacking. Additionally, natural environmental variation—both spatial and temporal—can obscure signatures of oil impacts in marine communities, spatial-temporal heterogeneity of fishing pressures may confound oil effects, 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 ~257 000 barrels (36 000 t) of crude oil into Prince William Sound, Alaska (Paine et al., 1996; Wolfe et al., 1994). In the months following the spill, oil was advected by wind and currents to the southwest, spreading into the Gulf of Alaska (GOA). While the dispersal path and distribution of oil in the water column and sediments remains uncertain, the approximate distribution and extent of surface oil (Short and Heintz, 1997; Wolfe et al., 1994) and oiled beaches are documented (Figure 1; NOAA, 1997). Furthermore, 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 metabolites associated with petroleum exposure were detected in invertebrate and fish species across a vast spatial area (Collier et al., 1993; Short and Heintz, 1997; Sol et al., 2000; Marty et al., 2003;). Estimates by Wolfe et al. (1994) suggest ~20% of the oil reached the sediments in Prince William Sound and the GOA. Also, 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).

Quantifying the consequences of EVOS requires consideration of both environmental variability and other human impacts on the GOA. The EVOS occurred within a high latitude coastal shelf system that is influenced by complex bathymetry with seasonal, interannual, and decadal variability (Stabeno et al., 2016). The region is influenced by substantial freshwater inputs, vigorous coastal currents that generate eddies, topographic steering,

entrainment of offshore production at the heads of gullies, and complex frontal structure (Royer et al., 2001; Stabeno et al., 2016). While major atmospheric forces such as the Pacific Decadal Oscillation (PDO) substantially affect GOA, the timing of the EVOS coincided with a well-documented shift in climate conditions in 1988/1989 which broadly affected the Alaskan ocean conditions (Bond et al., 2003; Di Lorenzo et al., 2008). At smaller spatial scales, episodic storm events impact water column stability which affects the timing of spring blooms and the disruption of the provisioning of nutrients to the surface in summer (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 GOA 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: (i) foreign fisheries depleted rockfish (primarily Pacific ocean perch, *Sebastes alutus*) 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); (ii) domestication of the fisheries and exclusion of the foreign fleet between 1985 and 1990 (Megrey and Wespestad, 1990); (iii) the establishment of individual fishing quotas (IFQs) in the sablefish (*Anoplopoma fimbria*) and Pacific halibut (*Hippoglossus stenolepis*) fisheries in 1995 (NPFMC and NMFS, 1992; Pautzke and Oliver, 1997); (iv) a series of Bering Sea and pollock (*Gadus chalcogrammus*) allocation and management actions culminating in the passage of the American Fisheries Act (Felthoven, 2002; North Pacific Fishery Management Council (NPFMC), 2001); and (v) implementation of the Steller sea lion (*Eumetopias jubatus*) mitigation measures which established no trawl zones around haulouts and rookeries and implementation of seasonal quotas for sea lion prey (2001; McBeath, 2004).

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) 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 examine an understudied community in the context of EVOS—demersal fish communities of the central and western GOA—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 (Figure 1, Collier et al., 1993, Sol et al., 2000). While the extent and exposure of fish communities to oil is somewhat uncertain, it is clear that some areas were exposed to significant amounts of oil while

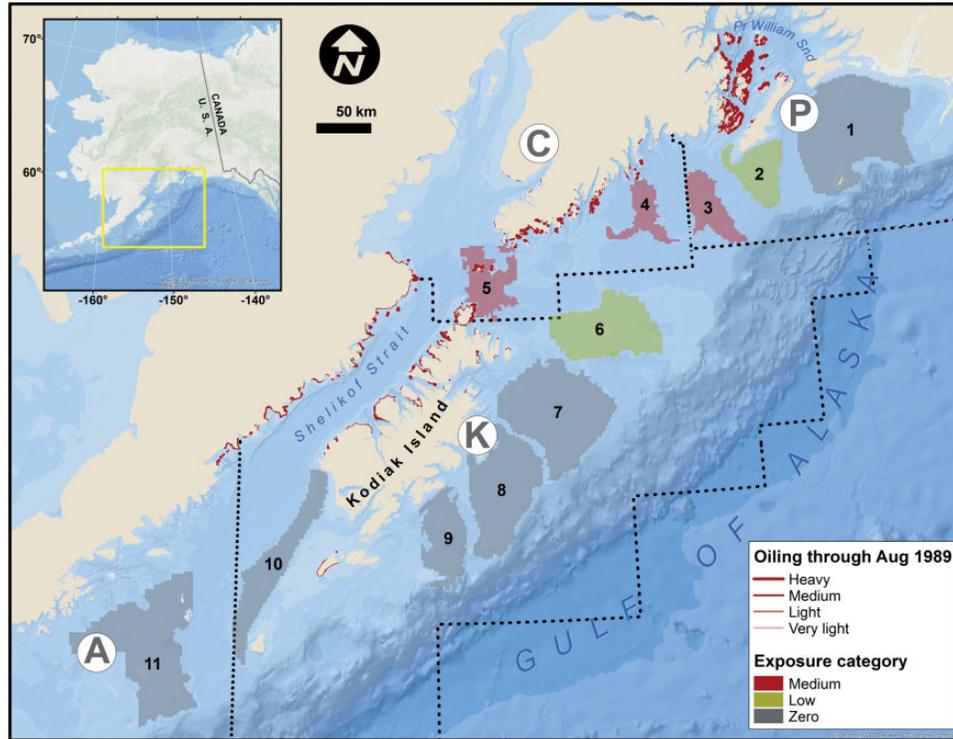


Figure 1. Map of study region with discrete areas for comparison of demersal groundfish communities. Shorelines with documented oiling from EVOS are highlighted in red. Numbered areas designate focal areas in the 50–150 m depth range and are coloured based on their categorical exposure to EVOS. Dashed lines delineate four areas used to collate groundfish catch statistics with circled letters defined as: P = Prince William Sound, C = Cook Inlet, K = Kodiak, and A = Alaska Peninsula.

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 (Rice *et al.*, 2001; Deriso *et al.*, 2008; Monson *et al.*, 2011; but see Wiens *et al.*, 1996; Jewett *et al.*, 1999), we assess aspects of the demersal fish community and analyse available information for signals of EVOS impacts within the context of environmental and management change. Our work complements 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 (Mueter and Norcross, 2002; Mueter and Megrey, 2005; Mueter *et al.*, 2009; Holsman *et al.*, 2016).

Material and 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 600 m because that depth was consistently surveyed throughout the time-series and because we focus on shallow demersal groundfish communities (see below). We used 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 three represent species complexes that were not identified to species separately during field sampling throughout the survey extent (Supplementary Table S1). For brevity, we subsequently refer to these species and species-groups collectively as “species”.

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 of groundfish communities.

In all models, we used catch per unit effort (CPUE; kg ha^{-1}) observed on each trawl as the response variable. Because most

species were absent from a large number of observed trawls, we separately modelled 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, $\pi_{it}(\mathbf{s})$, of the i th species in year t for a set of locations \mathbf{s} , was modelled using a binomial GLMM with logit link,

$$\log \text{it}[\pi_{it}(\mathbf{s})] = \mathbf{X}_t(\mathbf{s})\boldsymbol{\beta}_i + \varepsilon_{it}(\mathbf{s}) \quad (1)$$

where $\mathbf{X}_t(\mathbf{s})$ represents a matrix of fixed effect covariates at locations \mathbf{s} in year t , $\boldsymbol{\beta}_i$ represents a vector of coefficients for species i , and $\varepsilon_{it}(\mathbf{s})$ represents a vector of spatial random effects that follow a first-order autoregressive process:

$$\varepsilon_{it}(\mathbf{s}) \sim \text{MVNormal}[\rho_i \varepsilon_{it-1}(\mathbf{s}), \boldsymbol{\Phi}_i(\mathbf{s})] \quad (2)$$

where ρ represents the degree of autoregression in encounter probabilities and $\boldsymbol{\Phi}$ represents spatial covariation in random effects (discussed below). Throughout the methods, we use bold lowercase symbols to represent vectors and bold uppercase to indicate matrices. 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 were 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. We constructed an analogous model to describe the distribution of CPUE conditional on the catch of at least one individual and describe this “positive” model in Supplementary Material S1.

For all models we used available haul-level information about bottom depth(m) and included both linear and quadratic terms for $\log(\text{depth})$ in the occurrence and positive models (Shelton *et al.*, 2014; Tolimieri *et al.*, 2015). We centred $\log(\text{depth})$ by subtracting the mean $\log(\text{depth})$ 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, the single intercept model treats the spatial field as being the same across all years, whereas models with variable intercepts allow the spatial field to have the same shape, but increase or decrease by a constant intercept in each year (translating to increases or decreases in occurrence or density). For brevity, we provide technical details of the spatio-temporal random effects and estimation in the online supplementary (Supplementary Material S1).

We fit a total of four models for each species: two occurrence models and two positive models. For each submodel (occurrence, positive), we estimated one model with a single intercept and one with a year-specific intercept. Models were compared using posterior predictive plots and deviance information criterion (DIC) to select models for each species. Data, code, and additional output from this modelling is publicly available on Dryad, doi:10.5061/dryad.j3t86.

Generating predictive densities for each species

Predictions for the two sub-models for each species were used to project densities for each species for the GOA. We projected model estimates to the centroid of each 2×2 km grid cell covering the entire GOA out to the 600 m isobath from 1000 Monte

Table 1. Attributes for 11 focal areas.

Focal area	km ²	Qualitative exposure to EVOS	Catch region
1	8 364	Zero	Prince William Sound
2	2 136	Low	Prince William Sound
3	1 820	Medium	Prince William Sound
4	1 352	Medium	Cook Inlet
5	2 100	Medium	Cook Inlet
6	4 572	Low	Kodiak
7	7 064	Zero	Kodiak
8	5 280	Zero	Kodiak
9	2 792	Zero	Kodiak
10	3 732	Zero	Kodiak
11	7 840	Zero	Alaska Peninsula

All areas bounded by 50 and 150 m bathymetric isopleths and by natural bathymetric breaks (canyons). Catch regions were illustrated in Figure 1 and correspond to statistical catch areas for longline and trawl fisheries used to document fishery removals.

Carlo samples for each species. We then combined the occurrence and positive models to generate an unconditional expectation for CPUE for each grid cell. Such sampling from the joint posterior distribution properly accounts for uncertainty in these estimates. We then calculate the unconditional expectation for CPUE of species i at time t and location \mathbf{s} by multiplying each sample from the independent occurrence and positive models. Specifically, for the g th Monte Carlo sample, the unconditional CPUE estimate is $\pi_{it}^g(\mathbf{s}) \cdot \mu_{it}^g(\mathbf{s})$ and has units kg ha^{-1} .

Defining areas for comparison across the Gulf of Alaska

We identified eleven areas across the GOA to compare groundfish communities through time (Figure 1). Each area was bounded by the 50 and 150 m bathymetric isopleths, and by natural bathymetric breaks (canyons) resulting in irregularly shaped areas that ranged in size from 1352 km² to over 8000 km² (Table 1, Figure 1). Because of the bathymetry, some focal areas were divided by narrow channels while others are separated by large distances. The focal areas span a range of habitats with differing exposures to EVOS, environmental disturbance, and fishing effort (Figure 1; Wolfe *et al.*, 1994; Short and Heintz, 1997). While there is evidence from both direct observation of surface oil as well as shorelines documented to be oiled that GOA areas were exposed to oil (NOAA, 1997), most EVOS oil had weathered significantly by the time it entered the GOA (e.g. evaporation of the acutely toxic monoaromatics; decreased bioavailability because of increased tar ball formation from weathering) meaning the acute toxicity of EVOS in GOA water was reduced relative to Prince William Sound (Short and Harris, 1996; Rice *et al.*, 2007). In GOA, weathered oil accumulated into wind rows, ultimately transitioning to tar balls through continued weathering, resulting in reduced bioavailability to embryos and larval fish in the upper water column (Rice *et al.*, 2007; Short and Harris, 1996). Of the estimated 30% of the spilled oil entering the gulf, most transitioned to tar balls, while about a fifth weathered and sank as particles to the bottom sediments, over a large area (Wolfe *et al.*, 1994).

For our focal areas, 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 the main flow of weathered oil that escaped Prince William

Sound. Parts of areas 2 and 6 received some exposure, but the majority was thought to have travelled down Shelikof Strait, inside of Kodiak Island. Areas 7–11 may have been slightly exposed to EVOS, but direct observations of oil and oceanographic models suggest minimal or no impact for these areas (Short and Heintz, 1997; Wolfe *et al.*, 1994). Thus our comparison areas bracket the spill spatially and provide areas with more and less exposure to EVOS.

To understand the contribution of fisheries exploitation to changes in groundfish communities, we collated catch records for groundfish in the central GOA. Because of differences in catch location reporting requirements among species and across time, we compiled catch statistics for four broad areas encompassing all of our focal areas: Prince William Sound, Cook Inlet, Kodiak, and Alaska Peninsula (Figure 1). We obtained vessel-level total fishing catch data from the Commercial Fisheries Entry Commission (CFEC; <https://www.cfec.state.ak.us>, last accessed 5 May 2017) 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.

To examine environmental variation we calculated summaries for bottom temperature each area in survey years between 1990 and 2015. We used observed bottom temperatures from the trawl survey locations as the response variable and used a generalized additive model (GAM) to predict bottom temperature. We used a smooth of log(water depth) and an independent tensor product smooth of Cartesian coordinates (Alaska Albers equal area conic) to predict bottom temperature in each year. Changes in the within year timing of the survey are not thought to be a major driver of temperature variation (Armistead and Nichol, 1990; Stauffer, 2004). We then calculated the average temperature in each area for each year and an across-year mean bottom temperature. We examined deviations from the across-year mean to look for area-specific trends in bottom temperature. Ideally, we would have data on a wide range of potential environmental covariates for our analyses but environmental covariates that are variable among our focal areas are very limited; broad scale environmental indices like the Pacific Decadal Oscillation are constant across our focal areas.

Community metrics

For each area, we summarized the groundfish community by constructing four community metrics from the single-species spatio-temporal models (individual metrics are described below). 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 1000 Monte Carlo draws for each 2 × 2 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, Ono *et al.*, 2016). Thus for each metric in each area, we have a time-series of predictions for each species for 1984–2015. 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 chronic, sublethal effects that negatively affect recruitment, reproduction, growth, or survival at the community scale.

Feeding guild. We defined guilds for GOA 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; Supplementary Table S1). As the majority of EVOS oil in these habitats was thought to be weathered tar balls 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), pre-dominantly 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 individuals that are generally longer than 15 cm 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 20 cm (a size at which survey capture efficiency is close to one). We categorized this interval as short (<2 years), medium (2–4 years), or long (>4 years). We defined the interval using published parameters for the von Bertalanffy growth curve (retrieved from www.fishbase.org) and generated a predicted age to reach 20 cm. For species with multiple estimates of k and L_{∞} we used the median estimate. For a few species, we could not find published growth parameters. In these cases we used available estimates from similar species in the same family. Surface waters were 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 for evidence of a perturbation 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 value of the metric derived from MCMC sampling for each area and year and weighted by the inverse of the variance derived from MCMC. Weights represent the uncertainty in the value of each metric in each year-area combination. Third, we compared the variability of each metric during the post-spill period using the coefficient of variation (CV). 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 groundfish community to compare areas classified as EVOS-affected (areas 2–6) and Control (areas 1, 7–11). We calculated community-wide synchrony, ϕ , for each area for the entire time period (Loreau and de Mazancourt, 2008). The parameter ϕ ranges between 0 (indicating uncorrelated fluctuations) and 1 indicating perfect synchrony. We compared ϕ among areas and used a permutation test to examine whether the calculated synchrony deviated significantly from a community in which all species are fluctuating independently (using the community.sync function in R package synchrony; Gouhier and Guichard, 2014). To examine if community synchrony changed over the time-series, we used a moving window approach, calculating ϕ in 9-year blocks for each area. A 9-year window ensures at least four survey points are included in each correlation calculation. For all of these analyses, we use the estimated mean density of each species in each area.

Final, to ask if focal areas fluctuated in unison over the time-series, we calculated all pairwise Pearson product moment correlations among areas. As with ϕ 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 (Supplementary Table S1) and generated predictions for each of the 2×2 km grid cells in the GOA. 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 (Supplementary Figure S1). For example, focal areas varied more than threefold in total biomass and the relative rank of individual areas tended to be stable through time; low biomass areas remained low biomass areas and high biomass areas remained high biomass areas, reflecting the well-known spatial variation in productivity across the GOA. In general, the raw time-series from three focal areas most exposed to EVOS do not appear visually different than other areas in the GOA. This is true for total biomass as well as all guilds, diet types, and recruitment categories (Supplementary Figure S1).

Total catch from trawl and longline gear types also had substantial variation in groundfish communities among the four catch regions (Figure 2). Kodiak and Alaska Peninsula average catches were 2–4 times the catch in Cook Inlet or Prince William Sound per km^2 , and both the magnitude and ranking of regions with respect to catch were consistent over time (Figure 2). The initial increase in documented catches from 1985 to 1990 for all regions reflect, in part, the transition to an entirely U.S.-based fleet, not necessarily an increase in overall catch. Regardless, there is no evidence of changes in catch 1989 or 1990 in response to EVOS in any region and broadly speaking, total removals were relatively stable across the time-series after 1990.

Estimates of bottom temperature derived from the trawl survey show substantial temporal variation but there was no indication that any of the focal areas systematically differed from a broader shared pattern (Figure 2). In particular, none of the EVOS focal areas stand out as notably different from the remaining areas (Figure 2).

Examination of trends revealed negative linear trends in total biomass in EVOS exposed areas (Figure 3). The three most exposed areas had negative trends, the two areas classified as moderate EVOS exposure showed a negative and no trend,

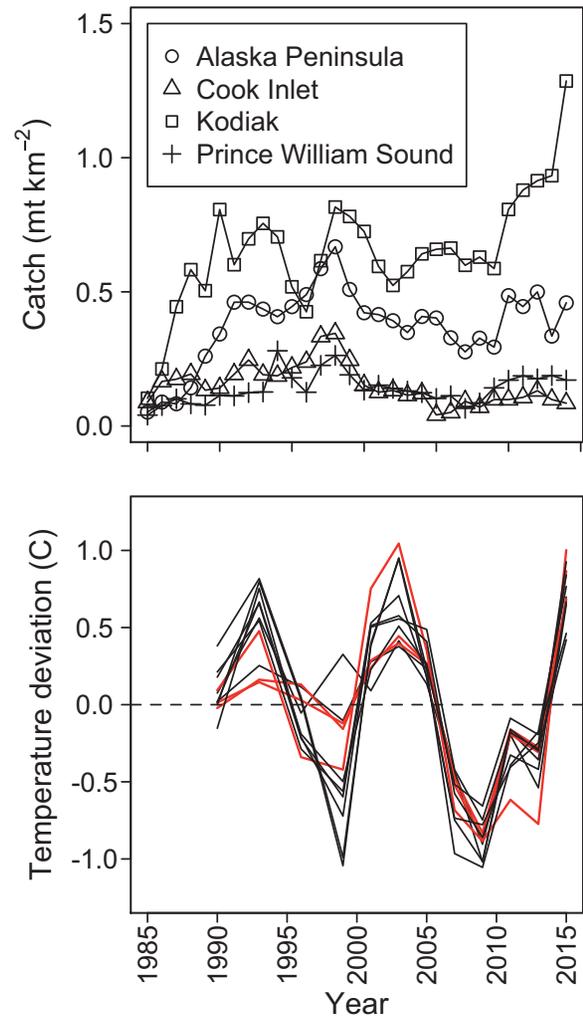


Figure 2. Top: Annual, area standardized groundfish catches for four major areas in the Gulf of Alaska. See Figure 1 for area definitions. Bottom: Bottom temperature deviations from long-term mean for each of the 11 focal areas. Focal EVOS areas are in red (areas 3, 4, and 5; Figure 1), remaining areas are in black.

respectively, while Control areas had zero or positive trends. The pattern among areas in total biomass trend was not driven by a single group (Figure 3). 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 (Short) generally had more negative trends.

In contrast to the trend analysis, there were no obvious patterns of temporal variability in response to EVOS (Figure 4). 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 ($\phi \leq 0.21$ for all sites) and permutation tests revealed no significant difference at any area between estimated synchrony and simulated communities in

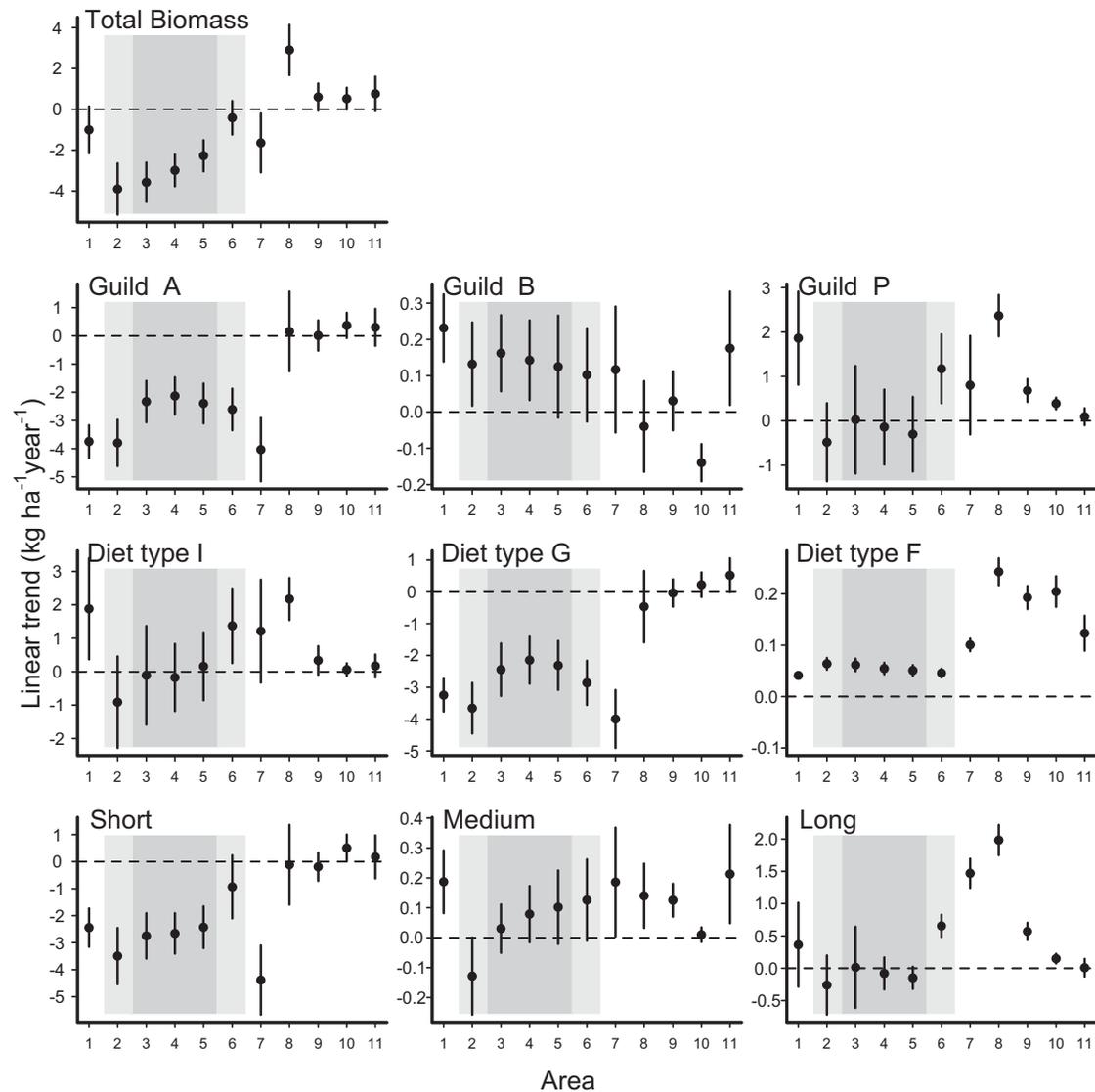


Figure 3. Estimated linear trend for the 11 groundfish regions. Areas hypothesized to be most affected by EVOS are shaded darkly, the marginal areas of EVOS exposure have lighter shading. Each row shows the community broken up based on guild, diet category, or recruitment interval. Note that the values of the y-axis vary among panels. Vertical bars represent ± 1 standard error.

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 (Supplementary Figure S2), 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).

Final, we found evidence of a time-varying signature in the cross-correlation between total biomass among EVOS areas and among Control areas (Figure 5). At the beginning and end of the time-series, correlations among EVOS, among Control, and between EVOS and Control areas, were indistinguishable. However, EVOS and Control area had 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 (Figure 5). Pairwise correlations for the entire time period were much lower than for the 1990–1999 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 (e.g. Rice *et al.*, 2001; Hicken *et al.*, 2011; Incardona *et al.*, 2015). But how such effects translate from individuals to communities remains poorly understood (Fodrie *et al.*, 2014). Here we focused on an ecologically and economically

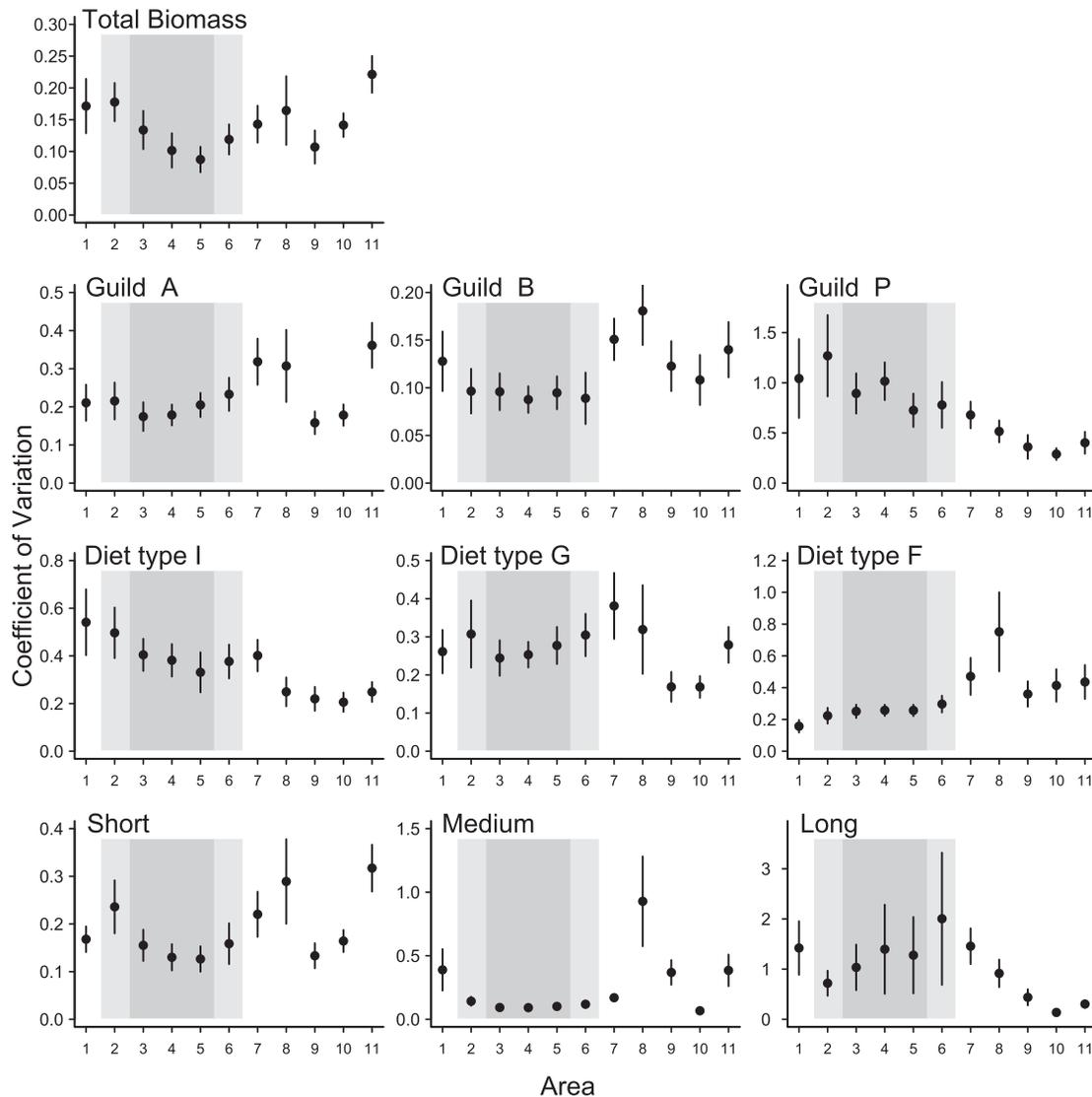


Figure 4. Estimated coefficient of variation (CV) for each of the 11 areas. Areas hypothesized to be most affected by EVOS are shaded darkly, the marginal areas of EVOS exposure have lighter shading. Each row shows the community broken up based on guild, diet category, or recruitment interval. Note that the values of the y-axis vary among panels.

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 portions of the GOA 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 not 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 enter 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 temporally invariant, background drivers of communities across the GOA 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 examining the signature of EVOS in groundfish. Our approach showed that while EVOS and Control areas were indistinguishable in terms of temporal variability (CV) and measures of community synchrony, we demonstrated 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, Pacific cod (*Gadus macrocephalus*), and Pacific halibut and reduced trend of the pelagic foragers guild which includes, for example, Pacific hake (*Merluccius productus*) and multiple rockfish species (*Sebastes*

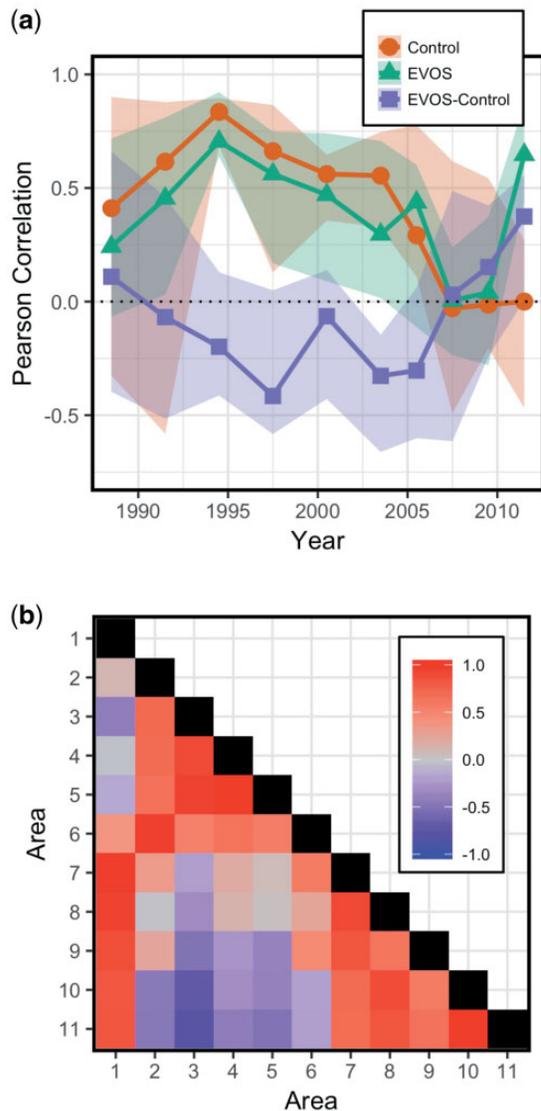


Figure 5. (a) Time-series of cross-correlations for total biomass using a nine-year moving window. Red line shows median cross-correlation among areas outside of the main EVOS spill (“Control”; areas 1 and 7–11). Green line shows median cross-correlation of all pairwise correlations in areas within the EVOS zone (“EVOS”, areas 2–6). Blue line shows median cross-correlation between areas within EVOS and the Control areas (“EVOS-Control”). Shaded regions indicate the inter-quartile range. (b) Pairwise Pearson correlations between focal locations for total biomass for the period 1990–1999.

spp.). In contrast to our expectations that benthic foragers would be most exposed to weathered oil, we observed no clear signal between EVOS and Control areas among benthic foragers. Inspection of fisheries removals (Figure 2) does not suggest obvious changes of a magnitude that could drive community wide changes in the groundfish community. Similarly, available bottom temperature data do not suggest variation among focal areas (Figure 2).

We also found an increased correlation among EVOS and Control areas coincident with the expected time interval of

maximum EVOS effects (1990–1999). We are not aware of any other shared driver among areas that would be hypothesized to produce such a pattern, though other unidentified potential drivers could exist.

We suggest that our observed patterns in the groundfish community are consistent with a small reduction in the productivity of EVOS areas relative to Control areas. Estimates of overall biomass trend suggest a decline on the order of 1–2% per year (Figure 3) for EVOS 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 (Figure 3). Because of 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 unidentified processes. However, we control for as many aspects as possible. In some ways, our ability to detect strong EVOS effects may be a function of the data in hand; if the Alaska groundfish trawl survey were done annually, for example, perhaps estimates of observation error and other uncertainties would be reduced. We constrained our analysis to only include areas contained within a single biogeographic region so all areas share major oceanographic features (e.g. PDO). Our analysis of bottom temperature supports this interpretation. Oceanographic drivers outlined in the introduction contribute to variation in groundfish abundance and productivity but how intra-regional oceanographic forces impact our results is unclear. Final, 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 a major impact on groundfish communities and other drivers such as environmental variability and fishing may mask any EVOS signal. 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.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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References

- Armistead, C. E., and Nichol, D. G. 1990. 1990 Bottom trawl survey of the eastern Bering Sea continental shelf. NOAA Tech. Memo. NMFS-AFSC-7, 190 p.
- Armstrong, D. A., Dinnel, P. A., Orensanz, J. M., Armstrong, J. L., McDonald, T. L., Cusimano, R. F., Nemeth, R. S., et al. 1995. Status of selected bottomfish and crustacean species in Prince William Sound following the Exxon Valdez oil spill. *In* Exxon Valdez Oil Spill: Fate and Effects in Alaskan Waters, pp. 485–547. Ed. by P. G. Wells, J. N. Butler, and J. S. Hughes. ASTM International, 100 Barr Harbor Drive, PO Box C700, West Conshohocken, PA 19428-2959.
- Awkerman, J. A., Hemmer, B., Almario, A., Lilavois, C., Barron, M. G., and Raimondo, S. 2016. Spatially explicit assessment of estuarine fish after Deepwater Horizon oil spill: tradeoffs in complexity and parsimony. *Ecological Applications*, 26: 1708–1720.
- Aydin, K. Y., Gaichas, S., Ortiz, I., Kinzey, D., and 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.
- Bond, N. A., Overland, J. E., Spillane, M., and Stabeno, P. 2003. Recent shifts in the state of the North Pacific. *Geophysical Research Letters*, 30: 2183.
- Camilli, R., Reddy, C. M., Yoerger, D. R., Van Mooy, B. A. S., Jakuba, M. V., Kinsey, J. C., McIntyre, C. P., et al. 2010. Tracking hydrocarbon plume transport and biodegradation at Deepwater Horizon. *Science*, 330: 201–204.
- Collier, T. K., Krahn, M. M., Krone, C. A., Johnson, L. L., Myers, M. S., Chan, S.-L., and Varanasi, U. 1993. Oil exposure and effects in subtidal fish following the Exxon Valdez oil spill. *In* Proceedings, International Oil Spill Conference, pp. 301–305. American Petroleum Institute, Tampa Bay, FL.
- Conan, G., Dunnet, G. M., and Crisp, D. J. 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., and Pearson, W. 2008. Incorporating covariates into fisheries stock assessment models with application to Pacific herring. *Ecological Applications*, 18: 1270–1286.
- Di Lorenzo, E., Schneider, N., Cobb, K. M., Franks, P. J. S., Chhak, K., Miller, A. J., McWilliams, J. C., et al. 2008. North Pacific gyre oscillation links ocean climate and ecosystem change. *Geophysical Research Letters*, 35: L08607.
- Felthoven, R. G. 2002. Effects of the American Fisheries Act on capacity, utilization and technical efficiency. *Marine Resource Economics*, 17: 181–205.
- Fodrie, F. J., Able, K. W., Galvez, F., Heck, K. L., Jensen, O. P., López-Duarte, P. C., Martin, C. W., et al. 2014. Integrating organismal and population responses of estuarine fishes in Macondo spill research. *BioScience*, 64: 778–788.
- Gaichas, S., Skaret, G., Falk-Petersen, J., Link, J. S., Overholtz, W., Megrey, B. A., Gjøsæter, H., et al. 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, R. A., Eberhardt, L. L., and Burn, D. M. 1993. Mortality of sea otters in Prince William Sound following the Exxon Valdez oil spill. *Marine Mammal Science*, 9: 343–359.
- Gouhier, T. C., and Guichard, F. 2014. Synchrony: quantifying variability in space and time. *Methods in Ecology and Evolution*, 5: 524–533.
- Henson, S. A. 2007. Water column stability and spring bloom dynamics in the Gulf of Alaska. *Journal of Marine Research*, 65: 715–736.
- Hicken, C. E., Linbo, T. L., Baldwin, D. H., Willis, M. L., Myers, M. S., Holland, L., Larsen, M., et al. 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. B., Wilson, C. D., Stabeno, P. J., and Salo, S. A. 2007. Effect of ocean conditions on the cross-shelf distribution of wall-eye pollock (*Theragra chalcogramma*) and capelin (*Mallotus villosus*). *Fisheries Oceanography*, 16: 142–154.
- Hollowed, A., Bax, N., Beamish, R., Collie, J., Fogarty, M., Livingston, P., Pope, J., et al. 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, K. K., Ianelli, J., Aydin, K., Punt, A. E., and Moffitt, E. A. 2016. 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: Topical Studies in Oceanography*, 134: 360–378.
- Hulson, P., Hanselman, D. H., Shotwell, S. K., Lunsford, C. R., and Ianelli, J. 2014. Assessment of the Pacific Ocean perch stock in the Gulf of Alaska. *In* Stock Assessment and Fishery Evaluation Report for the Groundfish Resources of the Gulf of Alaska, pp. 547–638.
- Incardona, J. P., Carls, M. G., Holland, L., Linbo, T. L., Baldwin, D. H., Myers, M. S., Peck, K. A., et al. 2015. Very low embryonic crude oil exposures cause lasting cardiac defects in salmon and herring. *Scientific Reports*, 5: 13499.
- Incardona, J. P., Vines, C. A., Anulacion, B. F., Baldwin, D. H., Day, H. L., French, B. L., Labenia, J. S., et al. 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.
- Jewett, S. C., Dean, T. A., Smith, R. O., and Blanchard, A. 1999. 'Exxon Valdez' oil spill: impacts and recovery in the soft-bottom benthic community in and adjacent to eelgrass beds. *Marine Ecology Progress Series*, 185: 59–83.
- Jewett, S. C., Dean, T. A., Woodin, B. R., Hoberg, M. K., and Stegeman, J. J. 2002. Exposure to hydrocarbons 10 years after the Exxon Valdez oil spill: evidence from cytochrome P4501A expression and biliary FACs in nearshore demersal fishes. *Marine Environmental Research*, 54: 21–48.
- Loreau, M., and de Mazancourt, C. 2008. Species synchrony and its drivers: neutral and nonneutral community dynamics in fluctuating environments. *The American Naturalist*, 172: E48–E66.
- Marty, G. D., Hoffmann, A., Okihiro, M. S., Hepler, K., and 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, M. N., and Punt, A. E. 2004. Standardizing catch and effort data: a review of recent approaches. *Fisheries Research*, 70: 141–159.
- McBeath, J. 2004. Greenpeace v. national marine fisheries service: Steller sea lions and commercial fisheries in the north Pacific. *Alaska Law Review*, 21: 1–42.
- Megrey, B. A., and Weststad, V. G. 1990. Alaskan groundfish resources: 10 years of management under the Magnuson fishery

- conservation and management act. *North American Journal of Fisheries Management*, 10: 125–143.
- Monson, D. H., Doak, D. F., Ballachey, B. E., and Bodkin, J. L. 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, F. J., and Megrey, B. A. 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*, 62: 344–352.
- Mueter, F. J., and Norcross, B. L. 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, F. J., Broms, C., Drinkwater, K. F., Friedland, K. D., Hare, J. A., Hunt, Jr, G. L., Melle, W., et al. 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.
- NOAA. 1997. EVOS research and restoration information project CD-ROM. Alaska Department 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.
- North Pacific Fishery Management Council (NPFMC). 2001. Impacts of the American Fisheries Act. Report to Congress and the Secretary of Commerce. North Pacific Fishery Management Council, Anchorage, AK.
- NPFMC and NMFS. 1992. Final supplemental environmental impact statement/environmental impact statement for the individual fishing quota management alternative for fixed gear sablefish and halibut fisheries: Gulf of Alaska and Bering Sea/Aleutian Islands. NPFMC, Anchorage, AK. https://alaskafisheries.noaa.gov/sites/default/files/analyses/amd_15_20_seis_0992.pdf.
- Ono, K., Shelton, A. O., Ward, E. J., and Thorson, J. T. 2016. Space-time investigation of the effects of fishing on fish populations. *Ecological Applications*, 26: 392–406.
- Paine, R. T., Ruesink, J. L., Sun, A., and Soulanille, E. L. 1996. Trouble on oiled waters: lessons from the Exxon Valdez Oil Spill. *Annual Review of Ecology and Systematics*, 27: 197–235.
- Pautzke, C. G., and Oliver, C. W. 1997. Development of the individual fishing quota program for sablefish and halibut longline fisheries off Alaska. North Pacific Management Council, Anchorage.
- Peterson, C. H. 2001. The 'Exxon Valdez' oil spill in Alaska: acute, indirect and chronic effects on the ecosystem. *Advances in Marine Biology*, 39: 1–103. Elsevier.
- Peterson, C. H., Rice, S. D., Short, J. W., Esler, D., Bodkin, J. L., Ballachey, B. E., and Irons, D. B. 2003. Long-term ecosystem response to the Exxon Valdez oil spill. *Science*, 302: 2082–2086.
- Piatt, J. F., and Ford, R. G. 1996. How many seabirds were killed by the Exxon Valdez oil spill. *American Fisheries Society Symposium*, 18: 712–719.
- Ramseur, J. L. 2010. *Oil Spills in U.S. Coastal Waters: Background, Governance and Issue for Congress*. Congressional Research Service, Washington D.C., USA, pp. 34.
- Rice, S. D., Spies, R. B., Short, J. W., Carls, M. G., and Moles, A. 2007. The Exxon Valdez oil spill. *In* Long-term Ecological Change in the Northern Gulf of Alaska, pp. 413–514. Ed. by R. B. Spies, T. Cooney, A. M. Springer, T. Weingartner, and G. Kruse. Elsevier, Amsterdam, Netherlands. 102 pp.
- Rice, S. D., Thomas, R. E., Carls, M. G., Heintz, R. A., Wertheimer, A. C., Murphy, M. L., Short, J. W., et al. 2001. Impacts to pink salmon following the Exxon Valdez oil spill: persistence, toxicity, sensitivity, and controversy. *Reviews in Fisheries Science*, 9: 165–211.
- Royer, T. C., Grosch, C. E., and Mysak, L. A. 2001. Interdecadal variability of Northeast Pacific coastal freshwater and its implications on biological productivity. *Progress in Oceanography*, 49: 95–111.
- Shelton, A. O., Thorson, J. T., Ward, E. J., and Feist, B. E. 2014. Spatial semiparametric models improve estimates of species abundance and distribution. *Canadian Journal of Fisheries and Aquatic Sciences*, 71: 1655–1666.
- Short, J. W., and Harris, P. M. 1996. Chemical sampling and analysis of petroleum hydrocarbons in near-surface seawater of Prince William Sound after the Exxon Valdez oil spill. *In* Proceedings of the Exxon Valdez Oil Spill Symposium. American Fisheries Society Symposium. American Fisheries Society, Bethesda, Maryland, pp. 17–28.
- Short, J. W., and Heintz, R. A. 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. *Environmental Science and Technology*, 31: 2375–2384.
- Short, J. W., Irvine, G. V., Mann, D. H., Maselko, J. M., Pella, J. J., Lindeberg, M. R., Payne, J. R., et al. 2007. Slightly weathered Exxon Valdez oil persists in Gulf of Alaska beach sediments after 16 years. *Environmental Science and Technology*, 41: 1245–1250.
- Sol, S. Y., Johnson, L. L., Horness, B. H., and Collier, T. K. 2000. Relationship between oil exposure and reproductive parameters in fish collected following the Exxon Valdez oil spill. *Marine Pollution Bulletin*, 40: 1139–1147.
- Squire, Jr, J. L. 1992. Effects of the Santa Barbara, Calif., Oil Spill on the apparent abundance of pelagic fishery resources. *Marine Fisheries Review*, 54: 7–14.
- Stabeno, P. J., Bell, S., Cheng, W., Danielson, S., Kachel, N. B., and Mordy, C. W. 2016. Long-term observations of Alaska Coastal Current in the northern Gulf of Alaska. *Deep Sea Research Part II: Topical Studies in Oceanography*, 132: 24–40.
- 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, J. P., Karlsen, Ø., Linbo, T., Sørensen, L., Nordtug, T., van der Meeren, T., et al. 2016. Crude oil exposures reveal roles for intracellular calcium cycling in haddock craniofacial and cardiac development. *Scientific Reports*, 6: 31058.
- Tolimieri, N., Shelton, A. O., Feist, B. E., and Simon, V. 2015. Can we increase our confidence about the locations of biodiversity 'hotspots' by using multiple diversity indices? *Ecosphere*, 6: ar 290.
- Ward, E. J., Jannot, J. E., Lee, Y.-W., Ono, K., Shelton, A. O., and Thorson, J. T. 2015. Using spatiotemporal species distribution models to identify temporally evolving hotspots of species co-occurrence. *Ecological Applications*, 25: 2198–2209.
- Wiens, J. A., Crist, T. O., Day, R. H., Murphy, S. M., and Hayward, G. D. 1996. Effects of the Exxon Valdez Oil Spill on marine bird communities in Prince William Sound, Alaska. *Ecological Applications*, 6: 828–841.
- Wolfe, D. A., Hameedi, M. J., Galt, J. A., Watabayashi, G., Short, J., O'Claire, C., Rice, S., et al. 1994. The fate of the oil spilled from the Exxon Valdez. *Environmental Science and Technology*, 28: 560A–568A.