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Spatiotemporal Variability of Benthic Communities on Weathervane Scallop Beds off Alaska

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Abstract

Marine benthic communities are critical biotic components of habitat due to their roles in ecosystem function and health and as indicators of ecosystem change. Benthic communities are receiving increasing attention as institutions adopt ecosystem-oriented research approaches. We conducted a multidecadal analysis of benthic communities in areas targeted by a commercial weathervane scallop *Patinopecten caurinus* fishery on the continental shelf off Alaska. Using bycatch data collected by onboard observers during 1996–2012, we analyzed spatiotemporal patterns in community composition on weathervane scallop beds. We also explored whether spatiotemporal differences were related to environmental (sediment and depth) and anthropogenic (dredging effort) variables. Statistically significant ($P < 0.05$) temporal changes in community composition occurred during 1996–2012, with a split between 1996 and 1999 and subsequent years. Taxa contributing to temporal changes were not consistent across fishery registration areas. Significant spatial differences in community structure were detected both at the scale of registration areas (200–2,000 km) and individual scallop beds (<50 km). We also found significant correlations between benthic species composition and environmental and anthropogenic variables over space and time. Although the relationships were generally weak, the ecological associations were consistent with expected depth and sediment relationships in this region. Our results are directly relevant to the habitat objective of the scallop fishery management plan, inform essential fish habitat designations for weathervane scallops and other commercially important species, and serve as a baseline against which to compare future changes associated with fishing and climate change. Ensuing research should include the collection of environmental data at the spatial scale of individual scallop beds as well as controlled experiments on the impacts of fishing on benthic communities and their recovery.

Over the past two decades, the focus of fisheries research has shifted toward ecosystem-scale properties, including habitat characteristics, multispecies interactions, and long-term environmental change (Hare and Mantua 2000; Mueter and Megrey 2005). These global research undertakings have paralleled efforts to implement ecosystem-based management (EBM) of marine resources in many countries, including the USA (Hare and Mantua 2000; Witherell et al. 2000; Latour et al. 2003; Mueter

and Megrey 2005). Two essential components of EBM in a commercial fisheries context include maintaining (1) healthy ecosystem structure and (2) natural interactions between target and nontarget species (Cogan et al. 2009). Article 5f of the United Nations Fish Stocks Agreement states that "fishing operations should be managed to minimize their impact on the structure, productivity, function, and biological diversity of the ecosystem" (UN 1995). Protecting ecosystem structure,

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specifically habitat, is a central feature of the Food and Agriculture Organization's technical guidelines for implementing an ecosystem approach to fisheries (FAO 2003). Accordingly, requirements to consider fish habitat appear in national legislation in a number of countries. The U.S. Sustainable Fisheries Act of 1996 mandates that federal fishery management plans must describe and identify essential fish habitat (EFH), minimize adverse fishing effects on such habitats to the extent practicable, and identify other actions for habitat conservation and enhancement (NMFS 2005). In the USA, EFH is defined as "those waters and substrate necessary to fish for spawning, breeding, feeding, or growth to maturity." The European Commission adopted a similar EFH definition in an initiative to identify areas critical for the survival and health of fish populations in the Mediterranean Sea and adjacent areas (Valavanis 2008).

Marine benthic communities are recognized as critical biotic components of habitat because of their roles in ecosystem function and health (Gili and Coma 1998; Orejas et al. 2000; Austen et al. 2002; Airoldi et al. 2008) and because they serve as indicators of ecosystem change (Kennedy and Jacoby 1999; Lenihan et al. 2003; Piepenburg et al. 2011). Benthic community structure is often studied in the context of oil and gas development (Atlas et al. 1978; Blanchard et al. 2003), effects of commercial fishing (McConnaughey et al. 2000; Brown et al. 2005; Stone et al. 2005; Rooper et al. 2011), and coastal development (Feder and Jewett 1986; Jewett et al. 2009). However, in the USA, sparse information on benthic communities and habitats has hampered original EFH definitions for federally managed fisheries. For example, off the coast of Alaska, EFH definitions for federally managed groundfish, crabs, and scallops were based primarily on geographic distributions of target species' commercial catches instead of on thorough assessments of habitat requirements. Although some investigations in Alaska have characterized marine benthic fauna comprehensively (Feder and Jewett 1986; Feder et al. 2005; Piepenburg et al. 2011), most fishery-independent information on benthic communities in the North Pacific comes from bottom trawl surveys conducted in the Gulf of Alaska and Bering Sea. These surveys are designed primarily to assess the abundance and distribution of commercially important species, mainly groundfish and crabs.

The weathervane scallop *Patinopecten caurinus* has received some research focus owing to its commercial importance; however, the fishery for this species, which began in Alaska in 1967, remains data limited, with surveys only occurring in a small portion of its range (Kruse et al. 2005). The majority of weathervane scallop vessels tow two New Bedford-style dredges, which are dragged over the seafloor. These dredges are fairly efficient at catching weathervane scallops, which comprised 78% of the catch during the 2011–2012 season (Rosenkranz and Spafard 2014). However, hundreds of bycatch species are caught by this fishery, including commercially important fishes (e.g., Pacific Halibut *Hippoglossus stenolepis*, Walleye Pollock *Gadus chalcogrammus*, and many skates and flatfishes) as well as benthic

invertebrates, such as sea stars, clams, and others that form biotic habitat (e.g., Porifera and Pennatulacea; Supplementary Table S.1 available separately online with this article). Since 1993, most vessels have been required to carry observers, who record data on bycatch. Aside from simple summary statistics, bycatch data in the weathervane scallop fishery have not been analyzed to date, except for crab bycatch (Rosenkranz 2002).

The primary objective of this study was to quantify spatiotemporal patterns in benthic community composition associated with weathervane scallop beds over a 17-year period. We characterized community structure over space and time and explored correlations with routinely collected environmental variables, namely sediment and depth. In addition, because dredging for weathervane scallops occurs over a vast (>1,000-km) portion of the continental shelf off Alaska, our second objective was to look for effects of scallop dredging on benthic communities. The impacts of scallop dredging and bottom trawling have been investigated on a variety of benthic habitats in other regions of the world's oceans (Collie et al. 2000; Thrush and Dayton 2002; Kaiser et al. 2006). In many regions, dredging has had severe negative effects on marine habitats and benthic communities (Collie et al. 1997; Hall-Spencer and Moore 2000; Jenkins et al. 2001), whereas in other regions dredging impacts appear to be species specific and substrate specific (Currie and Parry 1999; Boulcott and Howell 2011; Hinz et al. 2011; Howarth et al. 2016). Quantifying fishing impacts on nontarget benthic species can have important implications for fishery management policies that utilize ecosystem-based approaches. We used scallop observer data as a proxy for benthic community composition to investigate weathervane scallop bycatch composition over space and time off the coast of Alaska.

STUDY SITE

Commercial scallop beds adjacent to Alaska's coastline are located off Yakutat, Kayak Island (southeast of Prince William Sound [PWS]), Kodiak Island, in lower Cook Inlet, along the Alaska Peninsula and Aleutian Islands, and in the southeastern Bering Sea (Figure 1). The fishery is managed across nine registration areas, some of which are subdivided into smaller districts (Figure 1; NPFMC 2016). Commercial scallop beds have been delineated by using environmental variables and data on past fishing effort (Turk 2001), and the delineations are updated by the Alaska Department of Fish and Game (ADFG) to reflect spatial changes in fishing effort (G. Rosenkranz, ADFG, personal communication). Beds consist of a variety of substrates, including clayey silt, sand, and gravely sand sediments (Turk 2001), and they tend to be spatially aligned with bottom currents and bathymetry (Masuda and Stone 2003; Kruse et al. 2005). Weathervane scallops are found at depths less than 300 m, with commercial harvests generally occurring between 38 and 182 m (Ronholt et al. 1978).

METHODS

Bycatch data.—Observer data were obtained from scallop fishing vessels during 1996–2012; sampling protocols were
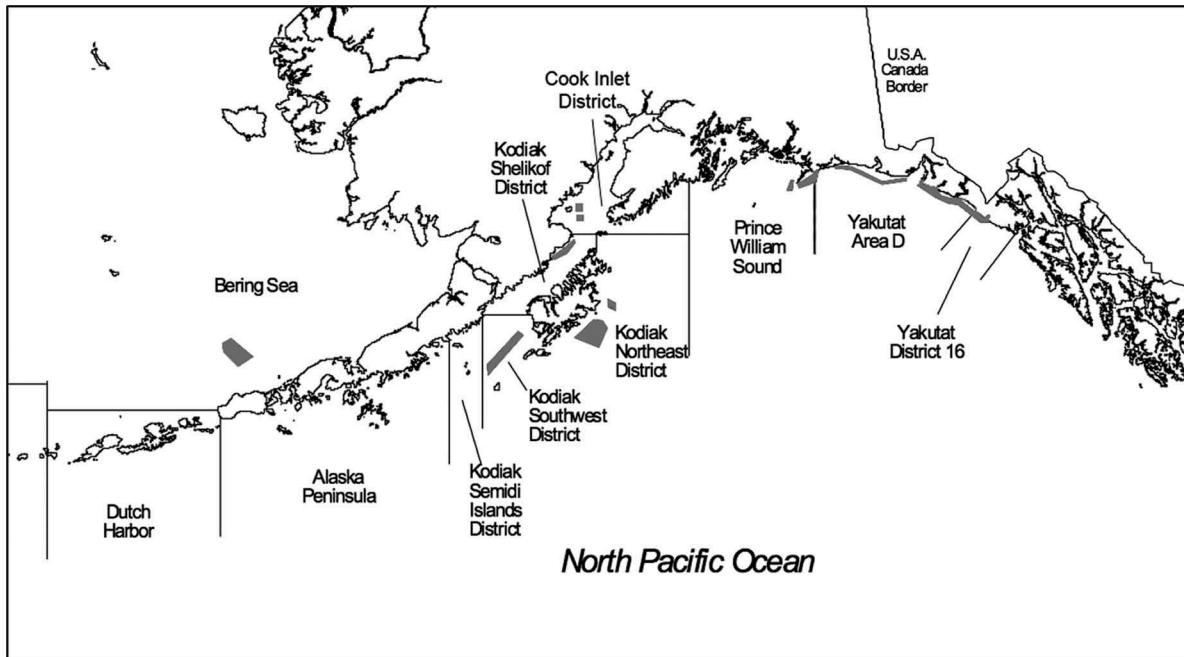
FIGURE 1. Map of the state of Alaska registration areas (labels) for the weathervane scallop fishery and the general areas of commercial effort (gray polygons). Figure is modified from Rosenkranz and Spafard (2014).

described in detail by Rosenkranz and Spafard (2014). In summary, tows were randomly selected for sampling prior to retrieval. Complete haul composition was determined for one dredge per vessel per day. Dredge contents were sorted to the lowest possible taxonomic level, placed into baskets, and weighed. Vessel operators also maintained logbooks provided by ADFG. For each tow, the operator recorded variables such as gear performance, tow duration, average depth, average speed, estimated retained weight of whole scallops, and estimated discarded scallop catch.

Sediment, depth, and dredging effort data.—Contoured surficial sediment maps of regions in the Gulf of Alaska were obtained from the U.S. Geological Survey (USGS; J. Reid, USGS, Pacific Coastal and Marine Science Center, personal communication). Data collection methods were described by Evans et al. (2000). Sediment data for the eastern Bering Sea were obtained from the National Marine Fisheries Service (NMFS), Alaska Fisheries Science Center (AFSC; R. McConnaughey, NMFS–AFSC, personal communication). Sediment collection methods in the Bering Sea and Aleutian Islands were described by Smith and McConnaughey (1999) and Zimmerman et al. (2013), respectively. Based on the sediment classification methods for each data set, we constructed numerical classifications (1–8) to reflect sediment type, ranging from the largest (bedrock) to the smallest (silty clay/mud) grain size. Sediment values were spatially overlaid with scallop haul points by using QGIS software (QGIS 2014), and a sediment value was assigned to each overlapping haul. Sediment data were not available for some fishery management areas in the Gulf of Alaska (Figure 1), including the Kodiak Semidi Islands, Kodiak Southwest, Alaska Peninsula, and Kodiak Shelikof (except for the largest Kodiak Shelikof bed, KSH 1); therefore, data for those areas were only included in bed-scale analyses (Table S.2). Haul depths were extracted from vessel logbooks for spatial analyses. Depth was excluded as a variable from temporal analyses because fishing depths were generally constant within a registration area over time. An index of dredging disturbance (hereafter, "dredging effort") was estimated by dividing the total area swept by the dredge (km^2; obtained from vessel logbooks) by the total area (km^2) of the bed, which was calculated in QGIS by using scallop bed polygons obtained from ADFG (Rosenkranz, personal communication). For scallop beds that were fished during 1996–2012, we compiled a time series of the proportion of each bed dredged. We considered short-term effects of dredging effort on benthic species composition by lagging values by 1 year.

Data organization.—We compiled two matrices using observer and logbook data. The first was a haul composition matrix that included information for each haul: haul identification (Haul ID), registration area, scallop bed code, set date, set position (latitude and longitude), and the CPUE (kg/m^2) of each taxon sampled. Haul ID numbers were unique and served as sampling units within the data set. The CPUE was calculated with a measurement of area swept (m^2) for each haul and was adjusted for differences in observed species densities as well as variances in dredging effort due to differences in tow duration and dredge widths. To address changes in observer sampling procedures over time—namely

a trend toward more detailed identification of certain taxa during later years of sampling—the CPUE of each taxon was aggregated into taxonomic groups ranging from families to phyla, with most groups aggregated to the family level (Table S.1). Separate categories were established for "roundfish," "skate egg cases," and "gastropod eggs," which were frequently recorded by observers. Because weathervane scallops are included in the aggregated family Pectinidae, we do not report specifically on spatiotemporal patterns of weathervane scallop catches. Detailed summary statistics on weathervane scallop catches are published annually by ADFG (Rosenkranz and Spafard 2014). The second matrix contained the sediment index, depth, and dredging effort (proportion of bed dredged), all of which corresponded to a haul ID.

Statistical analyses.—Multivariate analyses were conducted using PRIMER software (Clarke 1993; Clarke and Gorley 2006). We visualized all raw data in R to determine appropriate transformations (R Core Team 2017). Taxa contributing at least 5% of the total biomass of the data set were selected, and a fourth-root transformation was applied to CPUE data to downweight the right-skewness caused by the most abundant species (Clarke 1993). The CPUE of each taxon was then standardized relative to its maximum for the overall data set, so that each taxon contributed equally (Clarke and Warwick 2001). From that data matrix, we computed pairwise similarities between samples based on the Bray–Curtis similarity coefficient (Bray and Curtis 1957). We applied a square-root transformation to dredging effort to correct for right-skewness. To account for a negatively skewed distribution in sediment data, we subtracted all values from 9 (the highest value plus 1) and calculated the natural logarithm. We then standardized environmental and dredging effort data to a mean of zero and an SD of 1 to account for differences in measurement units. Similarities between environmental and anthropogenic variables were calculated using Euclidean distances.

Using various groupings (e.g., registration area, bed, and year), nonmetric multidimensional scaling (NMDS) was conducted to visualize similarities in composition between groups. To test whether haul composition differed significantly among regions at varying spatial scales and across time, analyses of similarity (ANOSIMs) were conducted using the Bray–Curtis resemblance matrices. The ANOSIM is a permutation test that is most applicable to multispecies data that do not meet standard assumptions required by multivariate ANOVA. The test statistic, Clarke's R, measures the degree to which species compositions differ between two discrete groups (e.g., locality or year) by measuring corresponding (rank) similarities in the Bray–Curtis resemblance matrices (Clarke 1993). As differences between species compositions become larger, Clarke's R approaches 1. When the ANOSIM test detected significant differences ($P <$ 0.05), a similarity percentage (SIMPER) analysis was conducted to examine the taxa that contributed most to the differences. To test whether environmental and anthropogenic variables were correlated with variations in species compositions, a bio-

environmental analysis (BIOENV; Clarke 1993; Clarke and Ainsworth 1993) was conducted. BIOENV calculates Spearman's rank correlation between the species similarity matrix and corresponding environmental similarities. Spearman's rank correlation coefficient (ρ) indicates the significance of agreement in the multivariate pattern when comparing two similarity matrices. Using CLUSTER analyses, we tested for the significance of observed splits with the similarity profile (SIMPROF) permutation test, which gives a test statistic (π) indicating whether group structure is significantly different from random structuring. We also examined patterns of seriation (continual change over time) by using the RELATE procedure, which generates a ρ value to indicate the presence of serial structure across years. Statistical significance for all tests was designated at P-values less than 0.05.

Data aggregation.—Data were aggregated in several ways to facilitate analyses at two spatial scales (scallop bed and region) and over time (Table 1). Regional-scale comparisons corresponded to fishery registration areas, which (in addition to being used for management) are representative of geographic regions across Alaska's continental shelf. Yakutat Area D, District 16 (D16), and PWS were aggregated prior to analysis (Yakutat/D16/PWS), as these beds are contiguous and characterize the northeastern Gulf of Alaska (Figure 1). We did not aggregate the three districts within the Kodiak registration area (i.e., Kodiak Shelikof, Kodiak Northeast, and Kodiak Semidi Islands) due to their distinctive oceanographic features. Kodiak Shelikof, for example, is strongly influenced by freshwater runoff associated with the Alaska Coastal Current, whereas Kodiak Northeast is influenced by exchange with offshore waters from the deep basin of the Gulf of Alaska (Stabeno et al. 2004).

For temporal analyses, hauls were aggregated by registration area or district and were limited to those continuously sampled over 1996–2012 to account for confounding changes that may have arisen due to differing fishing locations over time (Table 1). These included Kodiak Shelikof, Kodiak Northeast, Yakutat/D16/PWS, and the Bering Sea. In Kodiak Shelikof, only the KSH 1 bed was sampled consistently; thus, it was the only bed in this district that was analyzed for temporal differences. The bed Yak B in the Yakutat area was excluded because it was only sampled during 2009–2012. Because preliminary data analyses indicated differences in communities between the 1996–1999 period and subsequent years, we examined temporal patterns spanning 2000–2012 as well as the full sampling period (1996–2012) to help to identify additional changes, if any, occurring after 1999.

For registration area spatial analyses, we averaged hauls by bed code before calculating the similarity matrix to eliminate the risk of pseudoreplication (Table 1; Hurlbert 1984). After preliminary results showed evidence of temporal changes over time, we performed separate spatial analyses by taking an average CPUE for two periods: the earliest 4 years (1996–1999) and the latest 4 years (2009–2012). We chose this approach because we were interested in identifying changes associated with the

TABLE 1. Summary of spatial and temporal analyses conducted on benthic community composition in Alaskan scallop beds (D16 = District 16; PWS = Prince William Sound). Hauls were averaged by registration area for temporal analyses. Area-scale spatial analyses were averaged by scallop bed. For area-scale and bed-scale spatial analyses, we compared hauls averaged over two periods: 1996–1999 and 2009–2012. The three categories of analysis considered different combinations of areas owing to data availability.

Area	Years
Spatial analyses: area scale	
Yakutat/D16	1996–1999, 2009–2012
PWS	1996–1999, 2009–2012
Kodiak Shelikof	1996–1999, 2009–2012
Kodiak Northeast	1996–1999, 2009–2012
Kodiak Semidi Islands	1996–1999
Kodiak Southwest	2009–2012
Alaska Peninsula	1996–1999, 2009–2012
Aleutian Islands	1996–1999, 2009–2012
Bering Sea	1996–1999, 2009–2012
Spatial analyses: bed scale	
Kodiak Shelikof	1996–1999, 2009–2012
Kodiak Northeast	1996–1999, 2009–2012
Yakutat/D16/PWS	1996–1999, 2009–2012
Temporal analyses	
Kodiak Shelikof (bed KSH 1 only)	1996–2012
Kodiak Northeast	1996–2012
Yakutat/D16/PWS[a]	1996–2012
Bering Sea	1996–2012

[a]Temporal analyses excluded the bed Yak B (Yakutat area) because it was only sampled during 2009–2012.

cumulative effects of fishing over the full study period. This approach also allowed for clearer interpretation of spatial patterns that were less confounded by interannual variability. We considered utilizing a time series approach that would include all years, but this would have generated an enormous number of non-statistically independent comparisons.

Bed-scale spatial analyses were limited to those registration areas with large numbers of beds that were consistently sampled; these included Kodiak Shelikof, Kodiak Northeast, and Yakutat/D16/PWS (Table 1). Hauls for bed-scale spatial analyses were averaged by bed and year for NMDS ordinations to facilitate visual examination of patterns but were not aggregated for ANOSIM or SIMPER analysis. We also analyzed bed-scale spatial patterns during both 1996–1999 and 2009–2012 for the same reasons described above.

RESULTS

Descriptive Statistics

In total, 4,420 hauls and 79 taxa (Table S.1) from 42 individual scallop beds were included in the final data matrix. Most taxa were resolved to the family level (48 taxa), followed by class (12 taxa), order (10 taxa), phylum (4 taxa), N/A (3 taxa), subclass (1 taxon), and infraorder (1 taxon; Table S.1). The original data set included 94 taxa before we excluded those that contributed less than 5% to overall biomass. Hauls were sampled in habitats ranging from bedrock to silty clay/mud (Table S.2) at depths of 46–172 m (Table S.3). Dredging effort averaged 0.068 overall during 1996–2012 (Table S.4) and, on average, was highest on the KSH 1 bed in the Kodiak Shelikof district, ranging from 0.020 to 0.410 during 1996–2012.

Temporal Patterns

In the four districts analyzed for temporal changes, haul composition varied significantly over 1996–2012 and 2000–2012 (Table 2). A significant split was observed in all districts between 1996–1999 and subsequent years, as verified by the SIMPROF analysis and visualized by using NMDS (Figure 2a–d). Effects of seriation were present in all districts, implying that changes in community composition occurred sequentially across years, but the effects were more apparent during 1996–2012, as indicated by higher ρ values generated by the RELATE procedure (Table S.5). The greatest temporal differences in community composition were observed in the Bering Sea (Table 2). Dredging effort was significantly—although weakly—correlated with temporal changes in community composition in all districts over 1996–2012, while sediment was also significantly correlated with changes in the Yakutat/D16/PWS group (Table 2).

In all districts, a higher number of taxa contributed to haul similarity during 2009–2012 than during 1996–1999, with a large amount of overlap in community composition observed during the first 4 years and the last 4 years. In Kodiak Shelikof, a SIMPER comparison indicated higher relative abundances of Ranellidae, Aphroditidae, Goniopectinidae, Buccinidae, and Cardiidae during 2009–2012, compared to a higher prevalence of Gastropoda, Bivalvia, roundfish, and Echinoida during 1996–1999 (Table S.6). In Kodiak Northeast, taxa that contributed uniquely to haul composition over 2009–2012 included Ranellidae, Solasteridae, skate egg cases, and Lithodidae, among others (Table S.7). Clypeasteroida was the only taxon contributing uniquely to haul composition in Kodiak Northeast during 1996–1999. In the Yakutat/D16/PWS group, the second most dominant taxa after Pectinidae were Asteroidea during 1996–1999 and Aphroditidae during 2009–2012 (Table S.8). Luidiidae, Ophiuridae, Actiniaria, and Pennatulacea were prevalent only during 2009–2012. In the Bering Sea, Pectinidae, Oregoniidae, and Pleuronectiformes were dominant during both time periods, with Pennatulacea, Polychaeta, and Buccinidae becoming prominent during 2009–2012 (Table S.9).

Area-Scale Spatial Patterns

The ANOSIM test revealed statistically significant differences in CPUE among registration areas between 1996–1999

TABLE 2. Summary of test statistics from analysis of similarity (ANOSIM) and bio-environmental analysis (BIOENV), including significant BIOENV variables, for temporal and spatial analyses (D16 = District 16; PWS = Prince William Sound; NA = the analysis was not performed; NS = nonsignificant results). See the Methods for a description of the ANOSIM and BIOENV test statistics.

| Area | ANOSIM results | | BIOENV results | | |
	Clarke's R	P	ρ	P	BIOENV variable(s)
Temporal analyses (1996–2012)					
Kodiak Shelikof	0.257	0.001	0.203	0.001	Dredging effort
Kodiak Northeast	0.220	0.001	0.094	0.001	Dredging effort
Yakutat/D16/PWS	0.273	0.001	0.077	0.001	Sediment, dredging effort
Bering Sea	0.485	0.001	0.200	0.001	Dredging effort
Temporal analyses (2000–2012)					
Kodiak Shelikof	0.158	0.001	NA		NA
Kodiak Northeast	0.129	0.001	NA		NA
Yakutat/D16/PWS	0.154	0.001	NA		NA
Bering Sea	0.349	0.001	NA		NA
Spatial analyses (1996–1999)					
District scale	0.413	0.001	NS		
Kodiak Shelikof	0.185	0.001	0.168	0.001	Dredging effort
Kodiak Northeast	0.354	0.001	0.353	0.001	Depth
Yakutat/D16/PWS	0.138	0.001	0.099	0.001	Depth, sediment
Spatial analyses (2009–2012)					
District scale	0.611	0.001	0.253	0.001	Depth, dredging effort
Kodiak Shelikof	0.287	0.003	0.204	0.001	Depth, dredging effort
Kodiak Northeast	0.347	0.001	0.290	0.001	Depth, dredging effort
Yakutat/D16/PWS	0.246	0.001	0.169	0.001	Depth, dredging effort

and 2009–2012 (Table 3). Four taxa contributed most to similarities across all areas: Pectinidae, Pleuronectiformes, Rajidae, and Asteroidea. A longitudinal gradient in haul composition was apparent, with significant differences between Yakutat/D16 and all registration areas to the southwest except neighboring PWS and the Bering Sea (Table 3). However, a small sample size hampered significance testing of any comparisons involving the Bering Sea. The BIOENV indicated a weak but significant agreement between the species similarity matrix, depth, and dredging effort at the registration area scale for the years 2009–2012 only (Table 2).

The SIMPER analyses revealed that in some cases, the taxa responsible for differences between registration areas were consistent between early and late time periods. For example, during 1996–1999 and 2009–2012, Kodiak Shelikof consistently had higher relative abundances of Aphroditidae, Yakutat was distinguishable by a high relative abundance of skate egg cases, and the Bering Sea hosted a higher prevalence of Oregoniidae (Table S.10). However, in most instances, the taxa contributing to the top 50% of differences between areas were not consistent between the two periods. For instance, Porifera and Scyphozoa occurred in higher abundances in the Bering Sea than in other areas during 2009–2012 and 1996–1999, respectively. The Bering Sea and Alaska Peninsula both had comparatively higher relative abundances of Pennatulacea and Polychaeta during 2009–2012 but not during 1996–1999. High relative abundances of Gorgonocephalidae distinguished the Alaska Peninsula during 1996–1999, and Luidiidae characterized Yakutat/D16 from all other areas during 2009–2012 (Table S.10).

Bed-Scale Spatial Patterns

Significant, although subtle, spatial differences in haul composition were revealed by the ANOSIM among beds in all districts analyzed during both 1996–1999 and 2009–2012 (Table 2). These differences were significantly correlated with depth and dredging effort in all districts during 2009–2012, whereas correlations with environmental variables over 1996–1999 varied depending on the area (Table 2). Beds tended to be distinguished by differences in taxon CPUE rather than contrasts in presence or absence.

In Kodiak Shelikof, we observed much lower CPUE of taxa on bed KSH 1 than on other beds to the southwest in Shelikof Strait. This was illustrated by a comparison of beds KSH 1 and KSH 6, which displayed little overlap in taxa (Table 4). Bed KSH 1 had lower relative abundances of all taxa during both time periods except Aphroditidae and Paguridae during 2009–2012 (Table 4). Dredging effort was higher on KSH 1 than on all other beds in the Kodiak Shelikof district,
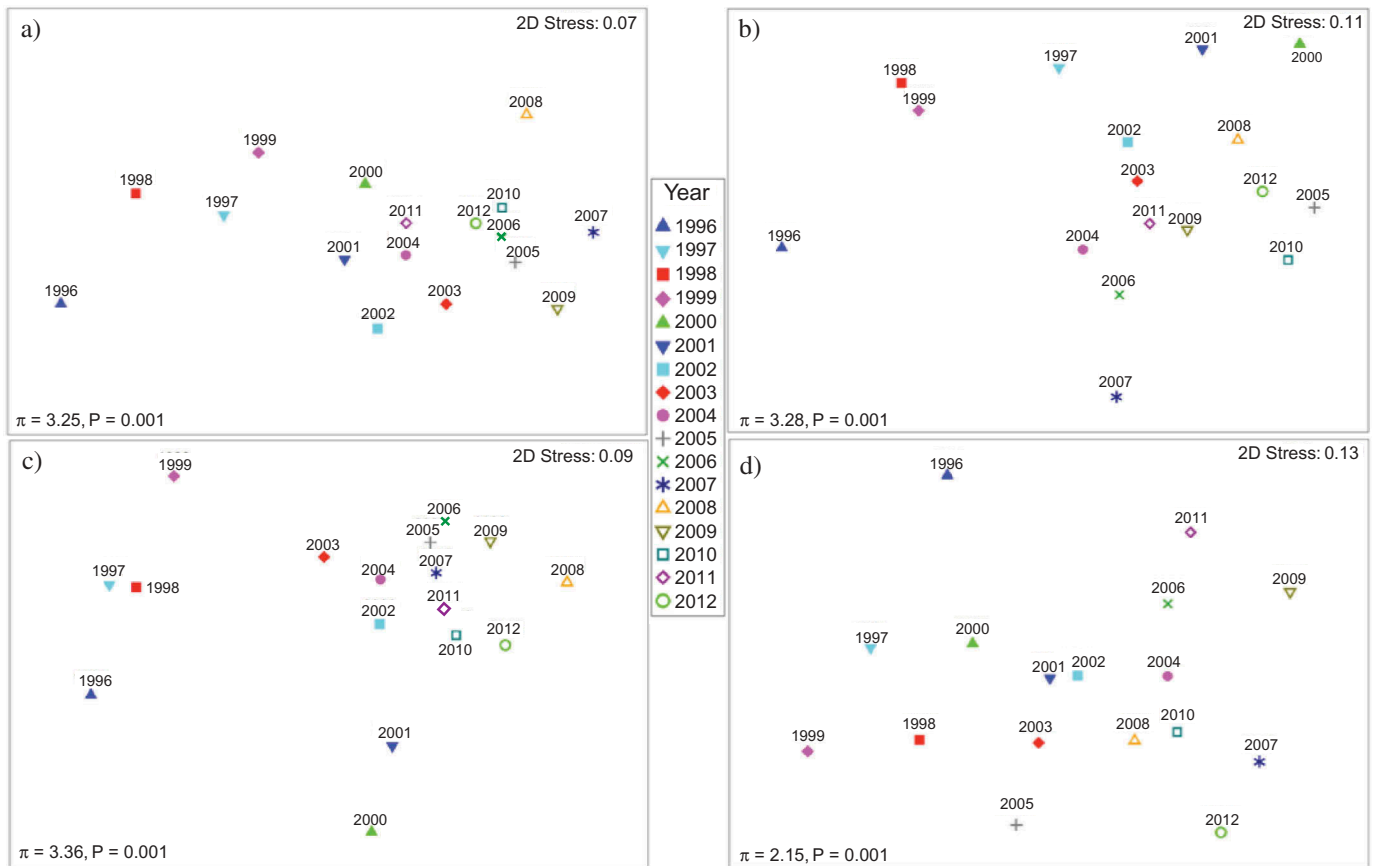
FIGURE 2. Nonmetric multidimensional scaling ordination of dredge haul composition samples aggregated by year (1996–2012) in Alaska registration areas: **(a)** Kodiak Shelikof, **(b)** Kodiak Northeast, **(c)** Yakutat/District 16/Prince William Sound, and **(d)** the Bering Sea. The similarity profile (SIMPROF) permutation test statistic (π), an indication of whether group structure is significantly nonrandom, is provided in the bottom left corner of each panel.

averaging 0.248 for 1996–2012 compared to a district average of 0.139 when excluding KSH 1. It was not possible to measure correlations with sediment type in the Kodiak Shelikof district due to a lack of available sediment data.

In Kodiak Northeast, depth was significantly correlated with bed-scale differences, whereas sediment type was not, even though sediment and depth are often closely associated (Table 2). Kodiak Northeast beds KNE 3 and KNE 6, which were both sampled consistently during the early and late time periods, serve as examples of contrasting sediment types and depth profiles in this district (Table 5). Bed KNE 3 is fairly shallow (68–88 m) and contains a mix of sand and gravel, whereas KNE 6 is deeper (80–117 m) and consists of silty sand. Bed KNE 3 had higher relative abundances of Actiniaria, Buccinidae, Clypeasteroida, and most echinoderms, reflecting the larger substrate grain size, whereas KNE 6 had a higher prevalence of crustaceans and Pennatulacea (Table 5).

The Yakutat/D16/PWS group was the only district with significant correlations between sediment type and community composition (Table 2). Scallop beds in this region span a wide range of sediment types (Table S.2) and depths (49–117 m;

Table S.3). The two beds located farthest apart (>400 km; Yak 6 and WKI) did not exhibit high dissimilarities, whereas beds Yak B and Yak 2, which are about 64 km apart, showed high dissimilarities during 2009–2012 that reflected differences in depth and sediment (Clarke's $R = 0.731$, $P = 0.001$; Table 6). Yak B is deeper (82–106 m) and consists entirely of silty clay/ mud, whereas Yak 2 (49–84 m deep) has a more heterogeneous substrate composition, including larger substrates such as gravelly mud and sandy silt. Over 2009–2012, Yak B was characterized by a higher prevalence of Buccinidae, Goniopectinidae, Gorgonocephalidae, and Goniasteridae, which tend to be found on deeper, muddy substrates (Table 6). Yak B also had a high abundance of Pennatulacea (data not shown), which provide structural support for gorgonocephalid basket stars. Yak B was not sampled during 1996–1999, so a comparison during that period was not possible.

DISCUSSION

Throughout our 17-year study period, commercial scallop dredge hauls in the Gulf of Alaska, Bering Sea, and Aleutian

TABLE 3. Clarke's *R*-values, indicating the strength of pairwise spatial differences in haul composition samples between Alaska scallop registration areas during 1996–1999 and 2009–2012 (D16 = District 16; PWS = Prince William Sound). Clarke's *R* approaches a value of 1 as differences in community composition increase. Asterisks indicate statistically significant values ($P < 0.05$).

Area	Yakutat/ D16	PWS	Kodiak Shelikof	Kodiak Northeast	Semidi Islands (1996–1999) or Kodiak Southwest (2009–2012)	Alaska Peninsula	Aleutian Islands
				1996–1999			
PWS	0.635						
Kodiak Shelikof	0.724*	0.701*					
Kodiak Northeast	0.578*	0.281	0.542*				
Semidi Islands	0.543*	0.281	0.597*	0.467*			
Alaska Peninsula	0.399*	0.188	0.558*	0.217*	0.101		
Aleutian Islands	1.000*	0.917	0.595*	0.302	0.160	–0.226	
Bering Sea	1.000	1.000	0.429	0.511	0.289	0.279	1.000
				2009–2012			
PWS	0.364						
Kodiak Shelikof	0.616*	0.302					
Kodiak Northeast	0.896*	0.875*	0.352*				
Kodiak Southwest	0.968*	1.000	0.490	0.813*			
Alaska Peninsula	0.915*	0.891*	0.507*	0.629*	0.400		
Aleutian Islands	0.916*	0.250	0.458	0.646*	0.250	0.600	
Bering Sea	1.000	1.000	0.267	0.689	0.000	–0.160	0.000

Islands were dominated by Pectinidae, Pleuronectiformes, Rajidae, and Asteroidea, while the remaining taxa differed at a regional scale across fishery registration areas (200–2,000 km) as well as among individual scallop beds within an area (<50 km). Associations with environmental and anthropogenic variables were statistically significant in all but one case, and though correlations tended to be weak, they are ecologically relevant.

Temporal Patterns

Excluding the four dominant taxa mentioned above, our observations suggest area-specific increases in richness over time rather than consistent ecosystemwide changes across the northeast Pacific study region. We considered the possibility that changes in the observer program, such as more precise taxonomic resolution over time, could be responsible for such a pattern (R. Burt, ADFG, personal communication). However, we aggregated taxonomic groupings accordingly to mediate such potential effects. Instead, the split could be associated with changes in fishing behavior after the consolidation of the fishery and formation of a weathervane scallop marketing cooperative in 2000, which resulted in concerted efforts to increase fishing efficiency and avoid crab bycatch (Brawn and Scheirer 2008; Glass et al. 2015). Alternatively, environmental fluctuations may have contributed to the observed differences between the late 1990s and subsequent years. For example, anomalous weather conditions occurred during 1997 in the North Pacific, influenced by El Niño and other decadal-scale atmospheric processes (Napp and Hunt 2001; Overland et al. 2001). This was followed by a shift from a warm regime to a cold regime in 1998, resulting in cooler sea surface temperatures and shifts in zooplankton and pelagic fish abundances (Peterson 2003).

Spatial Patterns

At a regional level, the starkest spatial differences in community composition occurred between the easternmost (Yakutat/D16) and westernmost (Alaska Peninsula, Aleutian Islands, and Bering Sea) registration areas. These spatial differences likely reflect biogeographic patterns in the distributions of species due to regional environmental influences (see the "Environmental Correlates" section below). In agreement with our temporal results, taxa contributing to spatial differences were not consistent between the first 4 years and last 4 years of sampling, with three exceptions. First, the high prevalence of Oregoniidae in the Bering Sea was expected given that scallop dredging is more restricted in the Gulf of Alaska for the specific purpose of protecting southern Tanner crab *Chionoecetes bairdi* habitat. Moreover, Tanner crabs and snow crabs *Chionoecetes opilio* have supported a larger fishery in the Bering Sea than in the Gulf of Alaska; accordingly, oregoniid bycatch in the scallop fishery is consistently highest in the Bering Sea (Rosenkranz 2002; Rosenkranz and Spafard 2014). Second, the higher CPUE of skate egg cases in the

TABLE 4. Comparison of relative contributions of each taxon to 50% of the cumulative dissimilarities between two scallop beds in the Kodiak Shelikof district (KSH 1 and KSH 6) during 1996–1999 and 2009–2012. The average CPUEs (kg/m^2) for each taxon in each bed are shown, along with the percentage that each taxon contributed to the total (Contrib %) and the cumulative percent contribution (Cumulative %).

Taxon	KSH 1 average CPUE	KSH 6 average CPUE	Contrib %	Cumulative %
1996–1999 (average dissimilarity = 60.13)				
Brachiopoda	1.65	81.98	9.35	9.35
Cancridae	3.61	50.75	5.51	14.86
Polychaeta	17.67	47.98	5.02	19.88
Ascidiacea	1.23	39.03	4.39	24.27
Holothuroidea	3.21	39.00	4.29	28.56
Gorgonocephalidae	0.65	35.34	4.04	32.60
Rajidae	43.81	48.29	4.00	36.60
Demospongiae	1.18	34.24	3.87	40.46
Onchidoridae	0.55	31.47	3.55	44.02
Gastropoda	22.75	52.24	3.52	47.54
Echinoida	14.07	34.17	3.48	51.02
2009–2012 (average dissimilarity = 53.17)				
Cancridae	2.62	72.87	10.44	10.44
Nereidae	24.55	76.38	8.13	18.57
Holothuroidea	3.14	51.35	7.17	25.74
Aphroditidae	41.63	0.00	5.88	31.62
Ascidiacea	0.59	35.38	5.15	36.76
Goniasteridae	2.68	34.65	4.77	41.53
Gastropod eggs	17.07	47.85	4.66	46.19
Paguridae	31.00	0.00	4.41	50.60

TABLE 5. Comparison of relative contributions of each taxon to 50% of the cumulative dissimilarities between two scallop beds in the Kodiak Northeast district (KNE 3 and KNE 6) during 1996–1999 and 2009–2012. Average CPUEs (kg/m^2) for each taxon in each bed are shown, along with the percentage that each taxon contributed to the total (Contrib %) and the cumulative percent contribution (Cumulative %).

Taxon	KNE 3 average CPUE	KNE 6 average CPUE	Contrib %	Cumulative %
1996–1999 (average dissimilarity = 53.74)				
Pennatulacea	16.14	42.57	7.63	7.63
Actiniaria	36.17	0.00	7.55	15.18
Clypeasteroida	28.72	0.00	6.12	21.30
Rajidae	19.58	36.63	5.79	27.09
Lithodidae	0.88	29.48	5.73	32.82
Majidae	14.40	36.41	5.00	37.82
Onchidoridae	10.47	22.58	4.59	42.41
Buccinidae	11.81	15.55	4.36	46.77
Polynoidae	3.29	20.09	4.23	51.00
2009–2012 (average dissimilarity = 54.33)				
Lithodidae	0.00	54.00	8.10	8.10
Actiniaria	40.19	2.51	5.60	13.70
Rajidae	28.51	45.30	4.80	18.49
Pennatulacea	23.10	34.73	3.68	22.17
Buccinidae	26.09	13.87	3.57	25.75
Roundfish	14.12	21.33	3.50	29.25
Ophiuridae	23.27	0.00	3.36	32.60
Goniasteridae	17.44	32.02	3.31	35.91
Luidiidae	23.20	0.00	3.31	39.22
Asteroidea	47.82	37.53	3.30	42.52
Solasteridae	29.40	10.78	3.30	45.82
Demospongiae	14.85	20.76	3.20	49.02
Goniopectinidae	2.73	20.47	3.00	52.02

Yakutat area is noteworthy given recent interest by the National Oceanic and Atmospheric Administration (NOAA) to protect skate nurseries in the Bering Sea based on the high CPUE in research surveys (Hoff 2010). The depth and substrate characteristics of beds in the Yakutat area are similar to conditions fostering skate nurseries in the Bering Sea (Hoff 2010). Third, a high prevalence of Aphroditidae (sea mice) in Kodiak Shelikof may be indicative of disturbance, as discussed below (see the "Anthropogenic Correlates" section).

Environmental Correlates

Throughout the world, attempts have been made to characterize and quantify the environmental drivers of benthic community structure by using a variety of factors, such as sediment grain size, food availability, and measures of habitat stability (Grebmeier et al. 1989; McConnaughey and Smith 2000; Herman et al. 2001; Callaway et al. 2002; Szostek et al. 2016). Off the coast of Alaska, benthic community structure is influenced by regional-scale environmental factors, such as sediment loading from glacial meltwater and the Alaska Coastal Current (Royer 1982; Feder and Jewett 1986). Our

study sites exhibited various degrees of correlation with sediment and depth over space and time. Clear differences in community structure due to varying depth and substrate at the scallop bed scale were observed in the Kodiak Northeast and Yakutat districts, and our results are congruent with previous findings of a high biomass of deposit feeders (e.g., crabs and mud stars) in Gulf of Alaska regions containing banks and troughs filled with finer sediments (Feder and Jewett 1986). Moreover, consistent with our observations for 2009–2012, the Aleutian Islands have been identified as a region dominated by filter feeders because sediment accumulation is minimal due to strong vertical mixing (Feder and Jewett 1986). In the Bering Sea, our observations of high oregoniid prevalence are in accordance with previous surveys, which attributed the taxon's success in this region to high organic carbon enrichment (Feder and Jewett 1981; Jewett and Feder 1981).

As for the remaining beds throughout the study region, sparse environmental data have been collected at a spatial

TABLE 6. Comparison of relative contributions of each taxon to 50% of the cumulative dissimilarities between two scallop beds in the Yakutat district (Yak 2 and Yak B) during 2009–2012 (average dissimilarity = 55.36). Average CPUEs (kg/m²) for each taxon in each bed are shown, along with the percentage that each taxon contributed to the total (Contrib %) and the cumulative percent contribution (Cumulative %).

Taxon	Yak 2 average CPUE	Yak B average CPUE	Contrib %	Cumulative %
Veneridae	56.62	0.00	9.38	9.38
Buccinidae	2.20	37.76	6.48	15.86
Goniopectinidae	0.90	30.01	5.27	21.13
Luidiidae	42.20	16.37	5.00	26.13
Actiniaria	28.50	0.00	4.97	31.10
Rajidae	39.43	34.11	4.72	35.83
Gorgonocephalidae	1.34	25.95	4.54	40.37
Pleuronectiformes	33.31	36.65	4.44	44.81
Goniasteridae	2.72	23.96	3.92	48.73
Roundfish	12.61	18.34	3.79	52.52

scale specific to scallop beds, making it challenging to determine whether observed correlations are ecologically meaningful. Only one study has aimed to characterize weathervane scallop beds based on physical variables, finding that they tolerate a broad spectrum of substrate types but prefer finer substrates (Turk 2001). Another study in the central Gulf of Alaska identified positive associations between adult weathervane scallops and both anemones and large sea whips and reported negative associations between adult scallops and predatory sunflower sea stars *Pycnopodia helianthoides*, but that study failed to include information on substrate type (Masuda and Stone 2003). Camera surveying tools for weathervane scallop beds have been developed by the ADFG, but associated research has focused primarily on crab habitat (Rosenkranz and Byersdorfer 2004; Rosenkranz et al. 2008).

Anthropogenic Correlates

Our results suggest that the species richness of benthic communities on weathervane scallop beds has increased over the past 17 years despite repeated disturbance. Weak correlations with dredging across a wide range of substrate types may be explained by a combination of factors, namely (1) high interannual variability in dredging effort, (2) our inclusion of both motile and sessile fauna that may respond to disturbance differently, and (3) the fact that most beds are represented by a mix of soft substrates. Although there is strong evidence that scallop dredging reduces diversity (Collie et al. 1997; NRC 2002; Alves et al. 2003), habitat type affects the level of impact and recovery rate from dredging (Collie et al. 2000; Kaiser et al. 2006). In previous work examining the effects of scallop dredging on soft-bottom habitat in the Gulf of Alaska, significant but minimal differences in epifaunal benthic

community abundance and species diversity existed between areas that were open and closed to trawling and dredging (Stone et al. 2005). Elsewhere in Alaska, motile fauna (e.g., crabs and sea stars) demonstrated mixed responses to bottom trawling based on comparisons of fished and unfished areas of sandy substrate in the Bering Sea (McConnaughey et al. 2000) and harder substrate in the Gulf of Alaska (Freese et al. 1999). Habitat complexity may also shield associated benthic species from negative dredging effects (Hinz et al. 2011; Howarth et al. 2011; Szostek et al. 2016).

Notably, we found evidence that the Bering Sea scallop bed is recovering from fishing disturbance, primarily through observed increases in the CPUE of sessile taxa that are considered highly vulnerable to dredging: such taxa include Porifera (sponges), Actiniaria (anemones), and Pennatulacea (sea pens). These observations are in accordance with previous records indicating higher abundances of anemones, sponges, and other sessile fauna at sites undisturbed by trawling compared to heavily fished areas in the Bering Sea (McConnaughey et al. 2000). Our observations coincide with decreases in scallop fishing effort in the Bering Sea prior to and during our study period, as dredging effort was substantially higher during 1990–1994. The Alaskan statewide harvest in 1992 was 737 metric tons, almost four times higher than the average annual harvest during the ensuing decade (Kruse et al. 2005). During 1993 and 1994 in the Bering Sea alone, 129 and 229 metric tons of shucked meats were harvested, respectively, compared to an average annual harvest of only 36 metric tons during our study period (Rosenkranz and Spafard 2014). Though not included in our study, a reduction in pelagic trawling as well as geographical shifts in trawling effort away from the scallop bed occurred over 2000–2012 (Zador 2013) and likely contributed to bed recovery.

In contrast with the Bering Sea, we observed negative changes in community composition in the Kodiak Shelikof district. The bed KSH 1 exhibited the lowest increase in richness (one taxon) compared to all other districts. Moreover, increases in CPUE were only seen for two taxa, Paguridae and Aphroditidae, suggesting dredging disturbance. The two most-commonly sampled pagurid genera in this study (*Pagurus* and *Elassochirus*) are known scavengers, and past studies have found beneficial impacts of dredging on pagurid species (Ramsay et al. 1996; Collie et al. 1997; Bradshaw et al. 2002). Moreover, during a previous study on polychaete assemblages in the Bering Sea, Yeung et al. (2010) attributed high abundances of Aphroditidae to an environment that was frequently disturbed by trawling and fish discards. Likewise, increased Aphroditidae abundance was observed off Portugal after 2 years of experimental dredging (Alves et al. 2003). Bed KSH 1 has consistently been the most heavily dredged scallop bed in the North Pacific and exhibited the starkest spatial differences in community composition within our study region, with lower CPUEs for all taxa except Paguridae and Aphroditidae.

Caveats

It is important to acknowledge that yearly changes in environmental or anthropogenic factors may be unlikely to translate

into one-to-one annual changes in benthic communities. For instance, given their population dynamics, significant changes in CPUE of long-lived benthic species (e.g., weathervane scallops, which live to 29 years of age) may be difficult to discern over time frames like that of our study (Hennick 1973; Renaud et al. 2007). Our observation of differences in haul composition over a 17-year period indicates that changes are indeed occurring and that monitoring should continue. Additionally, dredge haul composition depends on gear selectivity, which is relatively high for scallops but unknown for other taxa. This is currently being examined in Alaska through the implementation of underwater video technology to estimate dredge efficiency (Gustafson and Goldman 2012). We assuaged this bias by calculating CPUE, and therefore our results must be interpreted as changes in relative catch rates by scallop gear and not as changes in total abundances. Furthermore, definitive separation of dredging effects from natural disturbances is difficult without controlled experiments. Although controlled studies of this sort have been implemented in several areas of the world (e.g., Schratzberger et al. 2002; Pitcher et al. 2009; Szostek et al. 2016), only one study has applied this approach to address dredging effects in one region of Alaska (Stone et al. 2005).

Fishery Management Implications

Our results suggest that benthic communities on weathervane scallop beds in Alaska are relatively lightly disturbed, apart from the largest bed in Shelikof Strait. The direct effects of the fishery on commercially important bycatch species are minimal, as none of the taxa contributing to higher richness are targeted by commercial fisheries in Alaska, with the exception of Rajidae. Instead, bycatch taxa function primarily as prey or habitat for commercially harvested fish and crab species. To limit adverse impacts from dredging as well as to address declines in scallop CPUE over the past 15 years (NPFMC 2016), management constrains the commercial weathervane scallop fishery to a small number of participants (two to four vessels in recent years) and a small fishery footprint (~3,145 km^2; Turk 2001). Vast areas have been closed to scallop dredging to reduce impacts on sensitive habitats and benthic invertebrates (Witherell and Woodby 2005; Figure 2 in NPFMC 2014). Gear modification is unlikely to be implemented in this fishery, as the New Bedford-style dredge has remained more or less unmodified for the past 40 years (Glass et al. 2015). However, scallop fishery participants exhibit a high degree of self-regulation, which has led to successful reductions in bycatch (Brawn and Scheirer 2008; Glass et al. 2015).

By identifying spatiotemporal patterns of benthic communities on scallop beds, including important prey and habitat-forming taxa, this study informs fishery managers of the composition of biotic habitat in designated weathervane scallop EFH areas. This study also serves to inform EFH definitions for other commercially important North Pacific species

(e.g., Tanner crab, flatfishes, and Walleye Pollock) that overlap with scallop beds. An understanding of smaller-scale biotic habitat associations, which can indicate bed resilience and recovery time, would assist fishery managers because identification of spatially explicit links between benthic communities and physical and biotic variables is an important component of EBM (Fluharty 2000; Peterson et al. 2000; Howarth et al. 2011). In Australia, for example, a holistic effort was undertaken to address the role of large benthic invertebrates as habitat for finfishes in tropical off-reef environments (Pitcher et al. 2009). Although translating small-scale studies on fishing effects into regional and national management policies is challenging, recent progress has been made in this regard using a modeling framework to examine management alternatives (Ellis et al. 2014).

Research Recommendations

We offer three primary research recommendations, beginning with extensions of our benthic community analysis. Because the current EFH designation does not associate the geographic distribution of weathervane scallops with detailed habitat characteristics (NMFS 2005), bed-specific sampling of environmental variables (e.g., substrate and temperature) should be conducted. These could be used to develop habitat suitability index models for weathervane scallops (Brown et al. 2000), to define spatially explicit habitat requirements for particular life stages of scallops, and to determine the vulnerability of beds to sustained dredging (Kostylev et al. 2003). Marine habitat mapping in Alaska is currently ongoing due to efforts from NOAA and ADFG, but data for weathervane scallop beds were not publicly available at the time of publication (Greene et al. 2008). Second, controlled fishing experiments, such as those using the before–after, control–impact (BACI) design, are recommended to better quantify the effects of scallop dredging on benthic communities off the coast of Alaska (Schratzberger et al. 2002; Skilleter et al. 2006; Pitcher et al. 2009). Last, the high catches of skate egg cases and the dominance of Rajidae in haul samples off Yakutat lead us to recommend an investigation of potential skate nursery sites in the northeastern Gulf of Alaska. In 2012, the North Pacific Fishery Management Council identified six areas of skate egg concentration in the eastern Bering Sea as habitat areas of particular concern (NPFMC 2012). Skates are specifically relevant due to the vulnerability of elasmobranchs to overfishing (Musick et al. 2000) and the recent interest in retaining skate bycatch in Alaska (Gburski et al. 2007; Ebert et al. 2008).

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