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Polychaete assemblage as surrogate for prey availability in assessing southeastern Bering Sea flatfish habitat

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ABSTRACT

The flatfish yellowfin sole (*Limanda aspera*), northern rock sole (*Lepidopsetta polyxystra*), and Alaska plaice (*Pleuronectes quadrituberculatus*) in the southeastern Bering Sea prey mainly on infauna. Spatial correspondence between their stomach contents and infauna assemblages across habitat types was examined to identify indices of prey availability for flatfish habitat characterization and quality assessment. Benthic samples and flatfish stomachs were collected in 2009 near the Alaska Peninsula in the southeastern Bering Sea. Polychaetes and bivalves were the most dominant infauna groups, each comprising 35–60% by weight in each infauna sample. These two were also the only prey groups that frequently averaged $>50\%$ of stomach content by weight. Bivalves dominated the infauna biomass on the relatively sandy inner shelf (0–50 m depth). The muddier middle shelf (50–100 m) had the highest infauna biomass, which was dominated by polychaetes. Diet compositions of the flatfish varied spatially in correspondence with the infauna assemblage. Polychaetes were prevalent in all flatfish diets on the middle shelf, even yellowfin sole whose typical primary prey are amphipods and bivalves. Polychaete-rich habitats are potentially prime for flatfish as polychaetes are readily utilized where available and generally have high nutritional value. Flatfish did not select for specific polychaete taxa, so an index of habitat quality could be based on the biomass of aggregate polychaetes or on dominant polychaete families of the region. Under normal environmental conditions, the three flatfish have slightly-offset spatial distributions, enabling each to utilize different infauna assemblages across the shelf. However, during cold phases in the Bering Sea ecosystem, as when this study was conducted, a cold pool of <2 °C bottom water from the spring ice melt extends over the middle shelf in summer. This physiological barrier displaces all three flatfish to the inner shelf, intensifying competition for prey resources.

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1. Introduction

The southeastern Bering Sea (SEBS) continental shelf accounts for approximately half of the total US fishery production (National Research Council, 1996). The flat, shallow shelf ranges from 500 to over 800 km wide from shore to the shelf break at about the 170-m isobath, with an average cross-shelf gradient of 0.2 m km^{-1} (Kinder and Schumacher, 1981). Surficial sediment becomes finer with distance from shore and water depth (Sharma, 1979). Most of the surficial sediment can be characterized as predominantly sandy, except for nearshore areas of mixed sand and gravel, and mixed sand and mud further offshore (Smith and McConnaughey, 1999). Oceanographic fronts during the summer are defining features. The Inner Front located near the 50-m isobath and the broad Middle Front about the 100-m isobath divide the shelf into the inner, middle, and outer domains of different hydrographic conditions and productivity (Coyle et al., 2007; Kinder and Schumacher, 1981; Stabeno and Hunt, 2002). Another dominant hydrographic feature on the shelf is the "cold pool" — a tongue of cold bottom water <2 °C formed by the spring melting of sea ice that normally extends southward over the middle shelf. The extent and intensity of the cold pool are driven by the Bering Sea climate regime (Overland and Stabeno, 2004).

Flatfish are a major fishery resource in the SEBS. Yellowfin sole (*Limanda aspera*), northern rock sole (*Lepidopsetta polyxystra*), and Alaska plaice (*Pleuronectes quadrituberculatus*) are relatively small-sized species among the seven ecologically and commercially important flatfish in the SEBS (Lee et al., 2010). These benthivores have overlapping distributions in depths of ≤ 110 m. Yellowfin sole has the highest biomass among flatfish in the SEBS, and supports the largest flatfish fishery in the world (Wildebuer et al., 2005).

Understanding the ecological linkages that define suitable or essential fish habitat is crucial for ecosystem-based fishery management (Link et al., 2002; Shucksmith et al., 2006). Habitat definitions are theoretically as complex and dynamic as ecological linkages, but in fact most are simply based on observed fish distributions and environmental variables (DeLong and Collie, 2004; Norse, 2005). Environmental variables

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that are relatively easy to measure and spatially contiguous (e.g. surficial sediment type, water temperature, salinity, and water depth) have been most useful in explaining fish distributions.

On the gently-graded and mostly featureless SEBS shelf, sediment grain size distribution or substrate type is the main physical characteristic of flatfish habitat. It is often the variable with the highest correlations with flatfish distribution in soft-sediment habitats (Amezcua et al., 2003; McConnaughey and Smith, 2000; Yeung and McConnaughey, 2008). Flatfish generally prefer fine sediments for efficient burial, as demonstrated in laboratory experiments (Moles and Norcross, 1995). Granulometry also influences the availability of suitable prey (Able et al., 2005; Stoner and Ottmar, 2003). Finer sediments usually have higher organic content (Sharma, 1979) that favors higher total benthic biomass (Feder et al., 2007; Grebmeier et al., 1989), but hydrography and sea ice climatology are the principal drivers of pelagic primary production — the main supplier of organic matter to the benthos (Grebmeier et al., 1988; Overland and Stabeno, 2004; Stabeno and Hunt, 2002).

Yellowfin sole, northern rock sole, and Alaska plaice have small mouths suited for feeding on benthic infauna (Link et al., 2002; Yeung et al., 2010), particularly polychaetes, which comprise the bulk of the SEBS infauna (Haflinger, 1981; Stoker, 1981). The proportion of polychaetes in the diet by weight averaged 26% for yellowfin sole, and as high as 60% for northern rock sole and Alaska plaice (Yeung et al., 2010). Adult plaice (*Pleuronectes platessa*) abundance in the English Channel was related to the density of polychaete tubes (Shucksmith et al., 2006). The condition of adult plaice in the Irish Sea was related to the production of suitable-sized infauna (Hiddink et al., 2011). Polychaete density was found to be a significant habitat suitability variable for juvenile sole (*Solea senegalensis*) in the Tagus estuary, Portugal (Vinagre et al., 2008a). In the SEBS, the relationships of substrate to prey availability and prey demand have not been quantitatively defined. Prey availability is certainly an ecological basis for habitat selection, but is difficult and expensive to measure, particularly of the diverse infauna prey of many flatfish. In this study, we examined prey availability to the three flatfish in different SEBS habitats as defined mainly by sediment properties. We examined differences in the infauna assemblages among habitats and the spatial correspondence between flatfish diets and infauna assemblages. The ultimate goal is to identify potential quantitative indices of prey availability for flatfish habitat characterization and quality assessment.

2. Materials and methods

2.1. Benthic sampling and stomach collection

Three cross-shelf transects were surveyed with acoustic sonars on the NOAA ship *Fairweather* in July–August 2009 as part of an ongoing SEBS habitat mapping project (Yeung et al., 2010). Each transect spanned over 500 km and depths between 15 and 150 m. The transects intersected 31 of the many fixed bottom-trawl survey stations (Fig. 1a) that are sampled annually by the Alaska Fisheries Science Center (AFSC) bottom-trawl survey (Lauth, 2010). Each trawl station is located at the center of a 20 × 20 nautical mile grid cell. Standardized catches (kg ha^{-1}) by species at each trawl station are reported by the AFSC. Each transect started and ended at a survey station, with a station at approximately every 55 km in between (Fig. 1a).

A benthic grab sampler (0.1-m^2 van Veen-type) was used to collect duplicate sediment samples at the stations to characterize geochemical and biological habitat attributes. One sample was analyzed for sediment properties and the other for infauna assemblage. The average depth of penetration into the sediment by the grab was about 13 cm. The average volume of sediment sampled was about 10 L. Sediment properties analyzed included mean grain size distribution (φ), mean percentage weights (%) of gravel (grain size diameter < -1 φ), sand (-1 to 4 φ), and mud (> 4 φ), total concentrations of phosphorus (%), nitrogen (%), organic carbon (%), and chlorophyll-a (μg g^{-1}). Granulometry was often correlated to infauna community structure (Feder et al., 2007) and flatfish distributions (Yeung and McConnaughey, 2008). It was analyzed using a Malvern Mastersizer 2000 laser particle sizer. Sediment chemistry can indicate the quality and quantity of food for benthos (Grebmeier et al., 1988; Grebmeier et al., 1989). Methods of chemical analyses followed Barnes (1959), Tietjen (1968), and Naidu et al. (2000). Other habitat variables analyzed were latitude, longitude, bottom temperature (°C) and water depth (m). Infauna from grab samples were sorted and identified to the lowest taxonomic level possible. Biomass (g m^{-2}, wet weight) and abundance (ind m^{-2}) of dominant infauna taxa by station were determined (Yeung et al., 2010). Availability of resources necessitated a single infauna sample, but this sample size should not hamper our purpose of a broad classification of habitat types. Single samples per site have been effective in describing wide-scale community patterns (Gray and Elliott, 2009). We have analyzed replicate samples within grid cells collected on occasion (unpublished data), and they showed very similar community structure. Nonetheless, the spatial pattern of the infauna community in this study is a preliminary view and may be revised as more data accumulate.

During the same period, stomach contents of Alaska plaice, northern rock sole, and yellowfin sole were collected at 27 of those 31 trawl stations as part of the AFSC bottom-trawl survey (Fig. 1a). A maximum number of 15 stomachs were collected for each species per station. Stomach contents were identified to the lowest taxonomic level possible. The wet weight of each prey taxon was determined. Prey composition for a flatfish species at a station was based on the average percentage weight of each prey taxon over all non-empty stomachs of that species collected there. Prey composition in flatfish stomachs was analyzed for correspondence with the infauna assemblage to investigate the influence of prey availability on flatfish diets.

2.2. Habitat and community analyses

Standardized habitat variables (mean = 0, variance = 1) were entered into canonical correspondence analysis (CCA) with forward stepwise selection (Legendre and Legendre, 1998; ter Braak and Verdonschot, 1995) to extract the subset of variables significant to the infauna community structure as defined by the biomass and the presence–absence of polychaete families, respectively. To reduce redundancy, only one in a group of correlated habitat variables (Pearson $r \geq |\pm 0.5|$) was retained for CCA forward selection (Griffith et al., 2001). Principal coordinate analysis (PCoA) was used to analyze the relationships between habitat gradients and infauna assemblages. The CCA and PCoA analyses were conducted using the library 'vegan' in the R statistical software (R Development Core Team, 2011).

Two definitions of infauna assemblage were compared in the grouping of stations by similarity of infauna assemblages with PCoA. In one, the infauna assemblage was defined by polychaetes at the family level and the most frequently-occurring crustacean and mollusk taxa: Amphipoda, Cumacea, Bivalvia, Gastropoda, *Yoldia* spp., and Tellinidae. In the other, the infauna assemblage was defined by polychaete families only. Various measures of the assemblage were also compared in the PCoA : 1) square-root-transformed biomass, 2) square-root-transformed abundance, and 3) presence–absence, transformed into Bray–Curtis dissimilarity. Ordination results from these different measures were compared using the Procrustes test (Peres-Neto and Jackson, 2001).

Stations were assigned into a set of groups by K-means clustering of the first fifteen principal coordinate axes with random start. The appropriate number of clusters K (unrelated to prefix K in station names) was determined by evaluating the sum of squared error (SSE = sum of the squared distance between each member of a cluster and its cluster centroid) for 2 to $n-1$ clusters, where n = total number of stations. An appropriate solution is K at which the actual SSE differs the most from