Distribution and Abundance of Juvenile Demersal Fishes in Relation to Summer Hypoxia and Other Environmental Variables in Coastal Oregon, USA

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Abstract

The juvenile demersal fish assemblage along the Pacific Northwest coast has received little attention relative to adult life history stages since pioneering work in the 1970s. Increasing severity of hypoxia along the Oregon coast in recent years has prompted investigations into the response of biota in this region. We used summer data (2008 to 2013) from a beam trawl survey targeting juvenile demersal fishes in soft-bottom habitats along the Oregon coast to describe patterns of distribution and abundance at fixed sampling stations (from 30m to 100m depth). We relate the assemblage and abundance of the common species to environmental variables and analyze condition of recently settled fish (<50 mm SL). Most of the captured fishes were young-of-the-year flatfishes, dominated by Butter Sole (*Isopsetta isolepis*), English Sole (*Parophrys vetulus*), Speckled Sanddab (*Citharichthys stigmaeus*), and Pacific Sanddab (*Citharichthys sordidus*). Community analysis of the full dataset showed some variation in species richness among years and high evenness across all sampling sites and years. Depth was a structuring variable for the community, indicated by multivariate nonmetric multidimensional scaling analysis. Generalized additive models for common flatfish species abundances during the summer months indicated depth preferences, with Butter Sole, English Sole, and Speckled Sanddab at shallower locations and Pacific Sanddab occurring at deeper locations farther offshore. Additionally, while most common species were collected in high abundances in hypoxic conditions, dissolved oxygen was a significant factor in determining flatfish abundance. Condition factor was weakly negatively impacted by low dissolved oxygen for the species assessed, but the strength of the relationship varied by species. Increased sampling frequency and spatial coverage would improve our understanding of this community, especially in light of changing environmental drivers such as decreasing pH, warming water, and episodic periods of low dissolved oxygen coinciding with settlement for many species.

Keywords:

Demersal fishes, hypoxia, flatfishes, nearshore, dissolved oxygen, condition factor, Oregon

1. Introduction

Shallow, coastal waters are nursery areas for many fish and invertebrate species. The use of nursery habitats—those that afford favorable physiological conditions, ample food supply, and protection from predators—optimizes the trade-off between growth and mortality for juvenile fishes (Sogard, 1997; Beck et al., 2001). Along the Pacific Northwest coast, nursery habitats for many fish species tend to be associated with the coastal shelf, in depths of less than 100m. While some species along this coast use estuaries as juvenile habitats (Krygier and Pearcy, 1986; Gunderson et al., 1990; Rooper et al., 2003; Hughes et al. 2015), many other species remain in coastal waters where they settle, some changing depth with ontogeny (Gunderson et al., 1990). Understanding distribution and abundance patterns, movement across habitats, and juvenile fish response to environmental conditions is important for management of these species, especially within an ecosystem context (Pikitch at al., 2004; NMFS 2013). Also, because year-class strength can be determined by environmental factors (Houde, 2002; Thannesekos et al., 2016) understanding early life histories of fishes can aid in population assessment and management. In this study, we evaluate the depth distribution and response to environmental variables, specifically dissolved oxygen, for a community of fishes in near-coastal soft-bottom nursery grounds.

The dominant geomorphology along the Oregon coastal shelf is unconsolidated soft-sediments (Romsos et al., 2007). While lesser studied than rocky reef habitats, which are also important features in this region (Pearcy et al., 1989; Tissot et al., 2007; 2008; Donnellan et al., 2009), this substratum provides habitat for a number of demersal fish and invertebrate species (Jay, 1996; Keller et al., 2010; Toole et al., 2011), many of which are of commercial importance (Miller et al., 2006; Yoklavich and Wakefield, 2015; NOAA Commercial Landings Database[1]). A predominant component of the demersal fish community is flatfishes of the families Pleuronectidae and Paralichthyidae (Toole et al., 2011). Despite an abundance of juvenile flatfishes in Oregon coastal waters and the importance of these species to commercial fisheries, little attention has been paid to early life history of these fishes on the open coast since pioneering work in the 1960s and 1970s (but see Toole et al., 2011; in addition to Pearcy, 1964; Pearcy et al., 1977; Richardson and Pearcy, 1977; Pearcy, 1978). In addition to seeking greater understanding of early life history of fishes in this region, juvenile fishes are often vulnerable to variable environmental conditions and predation, and may be good indicators of environmental change in this region.

Demersal marine fishes off the Oregon coast spawn primarily during winter months (Shanks and Eckert, 2005; Brodeur et al., 2008) with pelagic larvae captured from February to July (Richardson and Pearcy, 1977; Gadomski and Boehlert, 1984), although there is variation in timing by species, spawning mode, and depth of occurrence (Shanks and Eckert, 2005). Settlement of juvenile flatfishes to benthic habitats occurs primarily during the summer months (Pearcy et al., 1977), although variation exists among species (Krygier and Pearcy, 1986). The current study focuses on newly settled individuals over soft-sediments during the summer months from 2008-2013.

In recent years, periodic hypoxia events (dissolved oxygen <1.4 mL L^{-1}, Grantham et al., 2004) have occurred during the summer months along the Oregon coast (Grantham et

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[1] https://www.st.nmfs.noaa.gov/commercial-fisheries/commercial-landings/index

al., 2004; Chan et al., 2008; Adams et al., 2013; Peterson et al., 2013). Particularly severe events occurred in 2002 and 2006, with as much as 60% of the shelf affected by hypoxia (Peterson et al., 2013). These events occur when surface waters are driven offshore by the prevailing northwesterly summer winds, resulting in upwelling of low-oxygen, nutrient-rich waters (Chan et al., 2008; Peterson et al., 2013). If the upwelling-producing conditions are strong but interspersed with periods of upwelling relaxation, low-oxygen zones can form in the water column of the coastal shelf, resulting in die-offs of fauna that are not adapted to prolonged periods of hypoxia (Chan et al., 2008). These periodic events appear to be occurring more frequently in recent years (Chan et al., 2008; Peterson et al., 2013) and are of concern for the management of valuable marine fisheries in the region. How early life stages—which are less motile than adults, and thus, more susceptible to *in situ* conditions—are affected by periodic low-oxygen events remains unclear.

The ephemeral nature of hypoxic events, occurring with varying intensity and extent during summer months (Peterson et al., 2013), makes describing causal relationships for fauna challenging. However, Keller et al. (2010; 2015) linked decreased fish and invertebrate biomass and species diversity to depressed oxygen levels using data from a regularly-conducted NOAA-Fisheries bottom trawl survey targeting adults in this region. While the NOAA survey has a time series of catch across the shelf from Washington to California, our understanding of the juvenile fish community in this same region is limited in both time and space. To better understand the impacts of hypoxic events on young-of-the-year (YOY) fishes, a beam trawl sampling program was initiated in 2008. This survey targets nearshore soft-sediment areas where hypoxic events have been identified during the summer months (Stinton et al., 2014) and aimed to collect juvenile life stages. In recent years, the survey has expanded temporally, with year-round monthly sampling to better understand flatfish communities in nearshore waters in general (see Yergey et al., in review). The objectives of the current study were to 1.) describe the soft-bottom benthic species assemblage 2.) relate summer distribution and abundance of common species to environmental variables (specifically depth, temperature, and dissolved oxygen), and 3.) investigate linkages between flatfish condition and environmental variables, especially low dissolved oxygen. Juvenile demersal fishes may be especially susceptible to changing ocean conditions along the Oregon coast due to their limited motility. This study draws connections between dissolved oxygen and individual fish condition, abundance of common species, and the fish assemblage in an under-sampled habitat.

2. Methods

2.1 Fish Sampling

Demersal fishes were collected during the summer months from 2008-2013 at fixed stations ranging from 30-100 m along a transect extending from Yaquina Head to the west (known as the Newport Hydrographic Line, or NH Line, ~ 44.66°N). An effort was made to sample all depth strata on each cruise; however, weather and gear did not always allow for complete transects. Fishes were collected using a 2.0 m-wide, 0.5 m-tall beam trawl constructed of 38-mm mesh and lined throughout with 2.5 x 3-mm mesh; a tickler chain was attached to the beam trawl skids forward of the trawl footrope to disturb the substrate and flush fishes into the net. Tows were generally 10-min. in duration, from cable out to the start of the retrieval (assumed to be bottom contact time) and actual time of the tow was noted. The trawl was equipped with a paired odometer wheel system that measured distance sampled. The distance measured on the wheel was converted to meters and used as the distance towed. For tows lacking a distance measure (~30%), we generated a linear model including depth and time towed from other samples collected and imputed the missing values so that all catch could be standardized to area swept. Vessel speed over ground was maintained at approximately 1.0 kt for all trawls.

Catch was sorted on deck, with fishes ≥150 mm (standard length, SL) being identified and measured onboard before being released and fishes <150 mm SL placed in storage bags and flash frozen on dry ice for later processing. Samples were stored in a -80°C freezer until processed. In the lab, thawed fish were identified, and lengths and damp weights were taken. All data were entered into a database containing vessel, trip, and sample data. For all analyses, a sample was defined as one net tow at any of the set stations, with correlating fish abundances and environmental variables; the catch within this net tow was standardized to density (# m^{-2}) based upon area swept (distance towed x 2 m for the width of the beam trawl).

A CTD cast (Conductivity-Temperature-Depth, Seabird Model 25 or SBE 19 with flow-through dissolved oxygen sensor) was made at the starting point of each tow to measure the salinity, temperature, and bottom dissolved oxygen at each station. Where casts were not made (<25% of all samples), available data on environmental parameters from nearby buoys or other sampling efforts were used to populate the data set.

2.2 Data Analysis

The dataset was analyzed to address multiple objectives, using both univariate and multivariate statistical methods. We conducted all analyses in R (R Core Team, 2016). To describe the benthic fish community (including multivariate analysis and description of species richness, diversity, and evenness) the full dataset was retained. Reduced datasets were used for univariate analyses relating individual species abundances to environmental variables and for condition factor analysis (see below). Specifically, "YOY" included all young-of-the-year fishes (<100 mm SL) and "recently settled" included all newly settled juvenile flatfish (typically <50 mm SL, e.g., Van Cleve and El-Sayed, 1969; Rosenberg, 1982, for *Parophrys vetulu;* and Rackowski and Pikitch, 1989, for *Citharichthys sordidus* and *C. stigmaeus*).

2.2.1 Community

To characterize the fish community, we used two approaches. The first was to model ecological response (species richness, diversity, and evenness) as a function of year, month, station/depth, dissolved oxygen, and temperature at the bottom depth using general linear models (function *lm* in R). Species richness (*SR*) was defined as the number of species in a sample, species diversity (*H'*) was defined as the Shannon–Wiener index, $H' = -sum\ p_i\ ln\ p_i$, where p_i is the proportional abundance of species *i,* and higher H' values indicate greater diversity (Whittaker, 1972). Sample evenness (*J*) was defined as Pielou's evenness, where $J = H'/SR$, where *H'* is species diversity as defined above and *SR* is species richness. Evenness values ranged from 0 to 1, with larger values indicating that all occurring taxa were present in the same relative concentrations (Pielou, 1969). We calculated rarefied values of species richness (Heck et al., 1975) to account for differences in sampling effort and used these in addition to species richness values in our models. These responses were normally distributed and as such, general linear models were suitable. Month, station, and year were all treated as factors, while all other variables were continuous. Since depth and station are highly correlated, we only included the factor with the best model fit. All model selection was done using Akaike's Information Criterion (AIC, Burnham and Anderson, 2002; Zuur et al., 2009).

Secondly, we used nonmetric multidimensional scaling (NMDS) to analyze drivers of community structure across the sampling locations and suite of environmental variables. The dataset was comprised of species densities, standardized by area swept. NMDS is an unconstrained ordination technique that maps multidimensional data in reduced dimensional space (2d or 3d) using the rank order of dissimilarity values among samples. A Bray-Curtis distance measure was used to generate the rank order of samples on square root transformed data (Clarke and Warwick, 2001). NMDS solutions were determined in two and three dimensions using multiple random starts to maximize the likelihood of reaching a global minimum stress value. Stress, a goodness-of-fit criterion that measures the discrepancy between the distance in ordination space and the distances of the original data set, was used to determine model fit. Stress values were plotted against the number of dimensions (scree plot), to determine how increased dimensionality and stress interacted; the greatest reduction in stress occurred at 3 dimensions, but 2d solutions are presented here for ease of interpretation. To determine differences in factors of interest (year, month, depth, and dissolved oxygen and temperature at bottom depth), we conducted permutational multivariate analyses of variance (PERMANOVA), a procedure that does not require multivariate normality (Anderson, 2001). We used library "vegan" with function *metaMDS* for NMDS and function *adonis* for PERMANOVA analyses (Oksanen et al., 2015). Within significant groups (e.g., site/depth), we used the indicator species analysis package "indicspecies" to identify important species within each group (De Caceres and Legendre, 2009).

2.2.2 Abundance

For total fish abundance and for each of the most abundant flatfish species, we modeled YOY fish abundance (CPUE, catch per unit effort) over the summer season using Generalized Additive Models (GAMs). GAMs allow for nonlinearities in the relationships between response and explanatory variables. Responses (abundance, in this case) can be modeled with both a parametric component (equivalent to generalized linear modeling) and also with a non-parametric component, which relies on smoothing functions for covariates (Wood, 2006; Zuur et al., 2009; Zuur, 2013). The *gam* function in "mgcv" package in R (R Core Team, 2016) was used for all GAM modeling. The *gam* function estimates the optimal smoothed relationship in model fitting. Effective degrees of freedom (edf) is a calibration tool to determine the shape of the curve, where a value of 1 indicates a straight line and higher values a progressively non-linear pattern (Zuur, 2013). The smoothers used in this application were thin plate regression splines for all parameters. The models were fitted using the "GCV.Cp" method (Generalized Cross Validation with an unknown scale parameter) and best models were re-estimated by Restricted Maximum Likelihood (REML) to check for stability.

For all abundance models, the response variable was count of a fish species (number per tow) and the predictor variables of interest were: year (2008-2013), bottom depth (m, from ~30m-120m), the hydrographic parameters temperature and dissolved oxygen (DO) at the bottom, and monthly upwelling index. For the upwelling index, we took the average of the monthly value in which sampling occurred from the three closest index stations (42°, 45°, and 48° N, Pacific Fisheries Environmental Laboratory http://www.pfeg.noaa.gov) as an indicator of larger oceanic processes that may influence recruitment and/or distribution of fishes. We used a negative binomial distribution with natural log link in the models to account for the overdispersed nature of the abundance data and we included the natural log of area swept (m^{-2}) as an offset to account for variation in tow distance. We also considered the interaction between depth and dissolved oxygen, as exploratory plots showed possible collinearity, although it should be noted that at deeper stations dissolved oxygen was always low (<3 ml/L) with no higher measurements observed during our summer sampling periods. Collinearity among the predictors was assessed with coplots, by plotting Pearson residuals (Zuur, 2013), and by analyzing variance inflation factors (VIF) using the *aed* function (Zuur et al., 2009); all variables had VIF scores <4, suggesting collinearity was not strong. The full model form was:

$$
\begin{aligned}
&\mathit{Abundance} = \mathit{offset}(\ln(\mathit{distance\ towed})) + \mathit{Year} + s(\mathit{Depth}) + s(\mathit{DO}) + s(\mathit{Temp}) \\
&\qquad + s(\mathit{Upwell.Index}) + \varepsilon \qquad\qquad \text{(Equation 1)}
\end{aligned}
$$

All variables except year, which was treated as a factor, were smoothed (s). We constrained the wiggliness of the smoothed terms by setting the knots, k, equal to 4, which sets upper limits for degrees of freedom and aids in preventing model overparameterization. The error term (ε) is assumed to be independent and identically distributed (Zuur et al., 2009). The output of all models was assessed using the function *gam.check*, which plots residuals and presents other diagnostic measures. We used AIC for model selection and an assessment of residuals, deviance explained, and the Unbiased Risk Estimator (UBRE), a procedure designed to measure error, provided an additional evaluation of model fit and validity (Zuur 2009; 2013). We present model forms, the amount of deviance explained, and significance levels for variables for the models.

2.2.3 Condition Factor

For three of the most common species, Butter Sole (*Isopsetta isolepis*), English Sole (*Parophrys vetulus*), Speckled Sanddab (*Citharichthys stigmaeus*), we evaluated condition of newly recruited individuals as a function of environmental variables, to determine specifically whether low dissolved oxygen resulted in reduced fitness. Individual condition was evaluated through the use of both Fulton's K and residuals from a length-weight relationship. Fulton's K is a commonly used metric of fish condition (Gilliers et al., 2004; Amara et al., 2007; De Raedemaecker et al., 2012):

$$K=100*(W/L^3) \qquad \text{(Equation 2)}$$

where: W=fish blotted wet weight and L=length in cm. This metric was calculated for each individual fish for which both length and weight data were available (N=2400, 1426, and 1041 for Butter Sole, English Sole, and Speckled Sanddab, respectively). Fulton's K was then used as the response variable in our models.

Similarly, we used the residuals from a L-W relationship as a response (Schulte-Hostedde et al., 2005). To derive the residuals, we constructed GAMs for each of the three species with *Weight~s(Length),* where the length component was smoothed to allow for non-linear response. Residuals from model fits were extracted and used in multivariable model analysis. For both condition metrics, larger values indicated fish that had higher weight for their length class, suggesting better individual condition. A similar study on offshore adult demersal fishes, found that for several species, body condition was positively correlated with the dissolved oxygen concentration; however, this was a not a universal response (Keller et al., 2010). In our analysis, we selected newly settled (<50 mm SL) individuals on the premise that these organisms would be most responsive to changes in habitat condition, such as with hypoxia, because they are less motile than their larger conspecifics, and would therefore have limited means to avoid unfavorable environmental conditions.

To relate the response variables (Fulton's K and L-W Residuals) to the explanatory variables (year, temperature, dissolved oxygen, depth, and depth*dissolved oxygen interaction), we used general linear mixed models using the function *lme* in R. We included tow as a random factor in the models to account for similarity of individuals captured at the same time and location. Models were fit using restricted maximum likelihood (REML). AIC was used for model selection and model fit (R^2) for both the fixed and random components were estimated with the function *r.squaredGLMM* using the methods of Nakagawa and Schielzeth (2013).

3. Results

We made a total of 135 tows from 2008-2013, although effort was not divided equally among years and not all months/stations were sampled each year due to weather and vessel availability (Table 1). We collected over 80 species of fish from 23 families, in depths from 30 m to 120 m across the six summers of the survey (Table 2 shows species occurring in >1% of tows).

3.1 Environmental Parameters

Bottom water temperature ranged from 6.8 -11.8°C, with a mean of 7.8°C, and with deeper sampling sites being the coldest (Figure 1, Table 1). While some variability in temperature existed among years and by month (Figure 2), depth had the most influence on temperature. Similarly, bottom dissolved oxygen decreased with depth, with highest values (5.2 ml/L) in the shallowest sites and lower values (<2 ml/L) observed at all depths, but with deeper sites generally having lower values (Figure 1, Table 1). Both temperature and dissolved oxygen were most variable at shallow depths. Unlike temperature, dissolved oxygen levels decreased through the summer months (Figure 2), suggesting that while temperature and dissolved oxygen may be correlated, these variables vary according to different processes.

Mean dissolved oxygen across all sampling periods was 2.4 ml/L with 22 of 135 measurements below the 1.4 ml/L hypoxia threshold. Hypoxia occurred at depths from 30 m-125 m and in all summer months, except May. Hypoxic measurements were most numerous (and broadest in depth distribution) in 2012, but were also observed in 2008, 2010, and 2013. Salinity ranged from 32.8 to 33.9 (practical salinity units), with a mean of 33.8. Because of the narrow range of salinities observed, we did not include this variable as a factor in our analyses.

3.2 Juvenile Fishes

Pleuronectidae and Paralichthyidae (flatfishes) were the two most frequently occurring and abundant families and made up over 88% of the overall catch, with over 11,000 individuals collected. The most abundant species were the flatfishes: Butter Sole, English Sole, Speckled Sanddab, Pacific Sanddab (*Citharichthys sordidus*) and Slender Sole (*Lyopsetta exilis*). Other abundant species included: Pacific Tomcod (*Microgadus proximus*), Pacific Sandlance (*Ammodytes hexapterus*), Warty Poacher (*Occella verrucosa*), and Pacific Staghorn Sculpin (*Leptocottus armatus*), although these were much less frequently occurring and were collected in <20% of the tows (Table 2). Many species (>50%) were rare, occurring in low abundances and in less than 10% of the samples collected.

Over half the fishes collected were <50 mm (53.8%), with 22.7% sized 50-100 mm, and 23.5% >100 mm, demonstrating that the catch was comprised mostly of recently settled and juvenile individuals, as targeted by the gear type (Figure 3). Among the common flatfish species, Butter Sole ~35 mm SL were the most abundant (Figure 4). Recently settled (<50 mm SL) English Sole, Speckled Sanddab, and Slender Sole were also captured in high abundance, although Slender Sole were only abundant in 2011 and 2012. Pacific Sanddab collected by the beam trawl were slightly larger, around 60 mm SL. Minimum size of fish captured varied by year; however, not all months were sampled in all years, so comparisons of timing and size differences from year to year should be made with caution.

3.3 Community Analysis

Mean species richness was 7 (min=1, max=21) and was variable among years, with the greatest variance in 2013. Evenness and species diversity were less variable among years (Figure 5), and in general, evenness was high, showing the dominance of a few common species. General linear models showed species richness (SR) and evenness (J) to be influenced by year and station; temperature was also a significant variable for SR (these results were the same for raw and rarefied SR values and we present raw values here). For species diversity (H'), year was not a significant predictor, but month and station were, showing the importance of station for all three metrics (Table 3). Station proved to be a better predictor for all metrics than depth (by AIC), although the two are highly collinear and station can be seen as a categorical proxy for depth. Species richness, evenness, and diversity were highest at moderate depths (Stations NH3, MB40, and NH5, from 30-60 m).

To better understand assemblage associations with environmental parameters, we used nonmetric multidimensional scaling (NMDS). The two-dimensional model solution had a final stress=0.17 and the three-dimensional model had stress=0.13 (stress <0.20 has been indicated as an interpretable result, with lower values indicating better fit (Clark 1993)). Visual inspection of the Shepherd plot, an indicator of model fit, showed the predicted distances to be representative of the observed distances. Using PERMANOVA, with possible explanatory factors including: year, month, depth, temperature and dissolved oxygen, only year was not a significant predictor. Depth was the strongest predictor of community, with assemblages at greater depths being distinct from assemblages at shallower depths (Stations MB30 and MB40) (Figure 6). We repeated this analysis for the subset of data with juveniles only (<100 mm SL) and found similar results with improved model fit (two-dimensional model stress=0.12): depth was the strongest predictor, but month, temperature and dissolved oxygen were also significant predictors when tested using PERMANOVA. Because depth was the strongest structuring variable, we used indicator species analysis for each station (a categorical surrogate for depth). Indicator species analysis showed that the species driving the depth associations were Slender Sole, Rex Sole (*Glyptocephalus zachirus*), and several uncommon poacher (family Agonidae) and eelpout species (family Zoarcidae) at the deepest sites and the common flatfishes (English Sole, Butter Sole, and Speckled Sanddab) at shallow-water sites. Pacific Sanddab was characteristic of intermediate sites (50m-90m in depth).

3.4 Juvenile Flatfishes and Environmental Variables

We analyzed abundance (CPUE) of YOY related to environmental variables of the four most common flatfish species: Butter Sole, English Sole, Speckled Sanddab, Pacific

Sanddab, all of which occurred in high abundances and in a large proportion of the tows (YOY of each species were in 75%, 54%, 79%, and 43% of tows, respectively). We explored relationships for Slender Sole as well, but this species was not commonly occurring (YOY found in <20% of the tows) and was found in high abundance only in 2012, indicating that a zero-inflated modeling approach would be a better fit and it was dropped from further analysis. Exploratory plots revealed few obvious patterns in abundance as a function of the environmental variables. Depth, however, was the primary driver of abundance, with English Sole, Butter Sole, and Speckled Sanddab found at shallower depths (<70 m) and Pacific Sanddab being more abundant at mid- to deep depths (50-100m).

We explored two general model formulations in our GAM analysis: models with each factor considered independently and models that included a depth*dissolved oxygen interaction. In all cases, the best model fit was:

$$\text{Species count} \sim \text{offset}(\ln(\text{distance towed})) + s(\text{Depth}) + s(\text{DO}) + s(\text{Temp}) + s(\text{Avg.Upwelling.Index}) + \text{factor}(\text{Year}) \qquad \text{(Equation 3)}$$

where all terms were significantly different from zero in at least one level or interval within their respective range. This was consistent with our analysis of variance inflation factors, which showed weak collinearity; however, our understanding of local oceanographic processes and interest in fish response to dissolved oxygen led us to investigate the interaction. For all species (including total abundance of all species) model fits had 41-73% of deviance explained, with normal residuals (Table 4). When plots of smoothed terms of each factor were evaluated (Figure 7), the effect of upwelling index appeared neutral (not shown in figure) and abundances appeared positively correlated with temperature and negatively correlated with dissolved oxygen for all species and total fish abundance. The effects of depth varied by species, but in most cases this variable was the strongest predictor. When predicted abundances were plotted as a function of dissolved oxygen and depth, we found high concordance between the predictions and our raw catch data (Figure 8). While all species were found across a range of dissolved oxygen measurements, depth appeared to be the stronger structuring variable. Trends in annual summer abundance (Figure 9, plotted as log density by year) varied by species, with Butter Sole and Pacific Sanddab showing variation among all years, English Sole having a slight downward trend across the time series, and Speckled Sanddab having highest densities in the middle of the time series.

3.5 Juvenile Flatfish Condition

We evaluated both Fulton's K and residuals from length-weight regression models (L-W Residuals) for indications of variable fitness within newly settled individuals of Butter Sole, English Sole, and Speckled Sanddab. While Pacific Sanddab was also abundant, we collected fewer new recruits of this species and did not include this species in the analysis. There was a slight positive and non-linear correlation between Fulton's K and L-W Residuals for all three species, as both are weight-based measures of condition. Fulton's K for all three species ranged from 0.13 to 4.49, with a mean of 1.37 (50% of the values were between 1.22-1.50); these values are similar to those found for other flatfishes in this size range (De Raedemaecker et al., 2012). Fulton's K varied among the three species (ANOVA, f= 354.6, p<.001), with mean values for English Sole (1.52) significantly higher than Butter Sole (1.32) and Speckled Sanddab (1.40). Summary plots showed few clear trends among species and within the two condition metrics with regard to environmental variables. However, for both Butter Sole and English Sole, condition as measured by Fulton's K and L-

W Residuals appeared lower in 2013 than in other years; this same observation was not made for Speckled Sanddab (Fig. 10) and our mixed models only indicated year as an important explanatory variable for Butter Sole (see below, Table 5).

When analyzed with general linear mixed models, three of the six condition models had low explanatory power (R^2 ranging from 0.026 to 0.136), with slightly higher values for the other three (R^2 ranging from 0.208 to 0.384). The random effect (tow) contributed marginally to model fit (Table 5). For all three species and both metrics of condition, dissolved oxygen was included in all best models selected through AIC (lowest scores) with a slight positive relationship between condition and dissolved oxygen. However, coefficients for dissolved oxygen were very close to zero and effect sizes were small.

4. Discussion

4.1 Depth is a Primary Structuring Variable

The beam trawl was effective at collecting juvenile demersal fishes along a depth gradient on the Oregon coast. While the overall fish diversity was high, with over 80 species collected in 135 tows made over the summer months, the samples were dominated by juvenile flatfishes, which became the focus of our study. Species richness within a tow was low (mean=7), but with high overall diversity, the soft-bottom regions of the near-coastal shelf serve as habitat for many species, and appear to be critical rearing areas for young-of-the-year flatfishes (Laroche and Holton, 1979; Kryger and Pearcy ,1986). Toole et al. (2011) sampled deeper habitats (50m-400m) and found similar dominance by juvenile flatfishes. Pacific Sanddab and Slender Sole were common in that study, as at deeper sampling sites in this study; however, other species (Rex Sole and Dover sole, *Microstomus* *pacificus*), which were rare in our study, were more common. This difference likely reflects the deeper waters sampled in the Toole et al. (2011) study and preference for different depths among species, but also could be a result of differing gear types and methods (larger net opening and 6.4 mm cod end mesh in the Toole et al. gear). The species we sampled also differ from those collected in the NOAA groundfish survey, which targets adults using a larger mesh net (~14 cm) and cod-end (3.8 cm) (Keller 2010; 2015, and A. Keller, NOAA-NWFSC, Seattle, WA, personal communication). Without being duplicative, this study offers insight into the variables structuring the juvenile demersal fish community and the response of species, and individuals within species, to environmental variables such as low dissolved oxygen and temperature.

Depth was the strongest structuring variable in our analysis of community and species abundance. In analyses where we considered hydrography (bottom temperature and dissolved oxygen) as well, depth was a stronger predictor. The NMDS and PERMANOVA analyses showed modest segregation of community by depth (station). Similar results were also found by Stinton et al. (2014) on a subset of data from this study. We note that heterogeneity within assemblage groups (Anderson and Walsh, 2013) and uneven sample size (fewer samples collected at deep sites) may leave the community underrepresented at those depths.

In our community analysis and generalized additive models of abundance, English Sole and Butter Sole juveniles were collected at depths <50 m, while Speckled Sanddab were evenly distributed within the sampled depth range and Pacific Sanddab were found at the deeper stations. As adults, English Sole are mostly found in water deeper than 50m, but decrease in abundance with increasing depth across the shelf (Bradburn et al., 2011), while

Butter Sole remain in shallow habitats and are caught only in low numbers in the shallowest stratum (<184 m) by the NOAA West Coast Groundfish Survey (Bradburn et al., 2011, A. Keller, NOAA-NWFSC, Seattle, WA, personal communication). The patterns we observed, in addition to known estuarine residence (Krygier and Pearcy, 1986; Da Ben et al. 1990), suggest that English Sole use a variety of habitats during their life cycle. Butter Sole and Speckled Sanddab, which were abundant in this nearshore juvenile survey, appear confined to shallower areas throughout their life cycle, as they are not commonly collected as adults further offshore (and Butter Sole are largely absent in coastal estuaries as well, Gunderson et al., 1990). Pacific Sanddab, which we found occupying the deeper regions in our survey, appear to shift habitats as they mature, being found at even deeper sites as adults (Bradburn et al., 2011). Rooper et al. (2006) showed that among four species of flatfish in a Pacific estuary, the species were spatially segregated based upon physical habitat characteristics, even in a relatively shallow environment. Similarly, the observed depth preferences among species in our study may serve as a means of niche partitioning, especially during juvenile life stages, when densities are high and rapid growth may help mitigate predation mortality.

While depth was a strong predictor of distribution, many other environmental variables, some of which were not measured explicitly in this study, correlate with depth: temperature, dissolved oxygen, sediment grain size, wave stress, biogenic and physical features of the benthic/sedimentary environment, etc. Additionally, food availability driven by upwelling-induced nutrient delivery, subsequent primary and secondary production, and the flux of organic carbon can be depth-related in this region (Hill and Wheeler, 2002). While these factors may all play a role in structuring the fish community, our results, combined with those of Keller et al. (2010), Toole et al. (2011) and other work in this region, suggest strong depth preferences among species. Similarly, in the Baltic Sea, flatfish distribution was dictated by physical habitat variables rather than by prey availability (Florin et al., 2009), and in estuaries, spatial segregation among competitors has been observed in the presence of abundant prey (Rooper et al., 2006).

4.2 Response to Hypoxia

The initial phase of this survey was designed to collect fishes during episodic summer hypoxic events to better understand biotic response to these disturbances. Therefore, sampling effort was highest in July and August, when these events are typically strongest and most widely distributed, covering a broad expanse of the shelf area (Peterson et al., 2013). But because our sampling effort was not allocated evenly across years and months, temporal comparisons of biotic response should be made with caution. In most years we did not have before/after comparisons to know which species were present before hypoxic events occurred, and there are likely differences in recruitment timing irrespective of environmental disturbance (Shanks and Eckert, 2005). The phenology of settlement for the common species is of interest, but without sampling at a higher temporal resolution, this question remains unresolved. Continuation of the beam trawl study with monthly sampling, as has been implemented in recent years, will improve our understanding of recruitment timing (Yergey et al., in review), and potentially, movement across the shelf in response to hypoxia for sensitive species.

While our study did not encompass the years of most severe hypoxia along the Oregon coast (2002 and 2006), sampling in several years occurred during periods of moderate hypoxia, which covered as much as 40% of the shelf by area (Peterson et al., 2013). The hypoxic events in this region result from upwelling and other advective processes carrying low dissolved oxygen waters into the shallow regions sampled as part of our study (Grantham et al., 2004; Pierce et al., 2012). Climate-related changes and decreases in dissolved oxygen of source waters may further exacerbate these events (Peterson et al., 2013).

Despite collecting a number of samples in hypoxic conditions, dissolved oxygen was not observed to be the primary driver in structuring the fish assemblage nor in influencing abundances of the common flatfish species in this region. However, it was a significant covariate in all of the metrics that were statistically assessed in this study (community composition, species abundance, and fish condition). Because hypoxic events are initiated at depth from oxygen-depleted upwelled water along this coast, organisms associated with the benthos in deeper habitats would be most likely to be negatively affected. However, we caught high abundances of the flatfish species over a range of dissolved oxygen, including at depth. Increased sampling at deeper stations could improve balance within the dataset and potentially yield different results, especially since our dataset did not include any normoxic (DO>2.0 ml/L) conditions at deeper sites.

In recently settled fishes, which we assumed to be most susceptible to environmental stresses, we expected to see some correlation between low dissolved oxygen and negative fish condition based upon the work of Keller et al. (2010, 2015) with adults. However, models were poorly fitting with high unexplained variance. The Fulton's K values we observed were similar to those reported for other YOY flatfishes (Gilliers et al., 2004, De Raedemaecker et al., 2012), but this metric has been shown to be less sensitive than others (e.g., RNA:DNA ratio, hepatosomatic index, lipid content) to environmental variation (Gilliers et al., 2004; Steirhoff et al., 2009; Schloesser and Fabrizio, 2015). While relationships between condition and dissolved oxygen were not strong, there are a number of factors which were not sampled as part of this effort but which may be better predictors for condition. For example, we have no record of the prey field to which these recently settled fishes were exposed. Weight-based condition factors would be highly influenced by prey availability (De Raedemaecker et al., 2012) and with an absence of gut data, we could not directly evaluate stomach fullness or other diet-based attributes. Additionally, the hypoxic events that we captured may have been too limited in persistence to understand the sub-lethal impacts of hypoxia, such as compromised foraging ability, on recently settled fishes.

One common immediate response to hypoxia in fishes is change in behavior. Behavioral response to hypoxia can include changes in activity, increased use of air breathing, increased use of aquatic surface respiration, and vertical or horizontal movement (Kramer, 1987; Hughes et al., 2015). While increased air breathing, and increased use of surface respiration are unlikely for demersally-associated fishes, changes in behavior related to movement or change in activity are plausible, although were not directly measured in this study. Consistency in depth preference among years and at varying dissolved oxygen conditions in our study suggests that, at the dissolved oxygen levels experienced, species generally prefer the same depth range during this juvenile stage even when dissolved oxygen levels are lower.

It is also possible that the dominant species are tolerant of, or have adapted to, low oxygen. Recent work with English Sole in a lab setting on the Oregon coast showed English Sole growth to be negatively impacted at the lowest oxygen levels (1.3 ml/L) only when temperature was high (10°C and 13°C treatments) but not impacted when temperature was nearer the ambient conditions we observed in this study (7°C, Bancroft, 2015). In our study, temperature and dissolved oxygen were correlated, with low oxygen values occurring in areas of colder (upwelled) water; however, with recent warming along the Pacific Coast (Bond et al., 2015) warmer temperatures may adversely affect fishes in low oxygen areas. With the availability of modern respirometry equipment, lab studies evaluating animal response to low oxygen are illuminating some capacity for tolerance of these events (Brill et al., 2015), especially when fishes are at rest (Nelson and Lipkey, 2015). Laboratory studies would provide a mechanistic link between hypoxia and fish response and may illustrate a range of responses fishes in the wild could exhibit under unfavorable environmental conditions.

5. Conclusions

While we found weak evidence for juvenile flatfish response to low dissolved oxygen, we observed a stronger relationship between fish distribution and depth. We also observed that the inshore juvenile soft-sediment community is different than the community found further offshore in deeper waters, both juveniles and adults, when we compared our findings to those of other researchers in this region. Thus, the inshore community may provide a trophic connection between coastal waters, including estuaries, and offshore demersal fish habitats. Additionally, with ocean conditions in this region changing rapidly, understanding this nearshore community will afford better understanding of the impacts to biota across the coastal shelf. This study contributes to our understanding of newly settled demersal fishes, which may be important for determining year-class strength, in soft-bottom near-coastal habitats.

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Table 1. Physical properties and number of samples collected by year and month for each station with the beam trawl, summers 2008-2013. Temperature and dissolved oxygen are mean bottom water values.

		Station									
		MB30	***MB40***	***MB50***	***NH03***	***NH05***	***NH07***	***NH10***	***NH15***	***NH20***	
Physical Properties	Mean Depth (m)	31.2	41.0	50.7	43.7	58.5	73.2	79.8	110.9	120.0	
	Temperature (°C)	8.2	7.9	7.5	7.7	7.5	7.5	7.3	7.3	7.3	
	Dissolved Oxygen (mL/L)	2.8	2.3	1.8	1.9	1.9	1.2	1.6	1.4	1.2	
Samples Collected											Total
2008	July	1	1			1		1			4
	August	2	4			4	1	4			15
		3	*5*			*5*	*1*	*5*			*19*
2009	July	1	1			1					3
	August	1	1			1		1			4
		2	*2*			*2*		*1*			*7*
2010	June	3	3	3							9
	July	1	1	1		1		1			5
	August	4	4	3		1		1			13
		8	*8*	*7*		*2*		*2*			*27*
2011	May	3	3	3							9
	June	5	3	1							9
	July	8	8								16
	August	3	3	3							9
		19	*17*	*7*							*43*
2012	July	3	3		3	3		3			15
	August	1	1		1	1		1	1	1	7
	September	1	1			1		1	1		5
		5	*5*		*4*	*5*		*5*	*2*	*1*	*27*
2013	June	1	1		1	1		1	1		6
	August	1	1		1	1		1	1		6
		2	*2*		*2*	*2*		*2*	*2*		*12*
	Grand Total	***39***	***39***	***14***	***6***	***16***	***1***	***15***	***4***	***1***	***135***

Table 2. Fish species collected and total abundance by year for the six sampling years for species occurring in >1% of all tows. Overall abundance (Total) and frequency of occurrence (Freq.) are also shown. Frequency of occurrence refers to the proportion of tows out of the total number of tows (135) in which the species was present. This table omits 40+ species which occurred in <1% of the tows, as well as 33 unidentified specimens.

		Total Abundance							
Common Name	*Scientific Name*	*2008*	*2009*	*2010*	*2011*	*2012*	*2013*	*Total*	*Freq.*
Butter Sole	*Isopsetta isolepis*	305	80	347	861	1216	316	3125	0.84
Speckled Sanddab	*Citharichthys stigmaeus*	226	68	1072	811	413	104	2694	0.83
English Sole	*Parophrys vetulus*	632	200	444	333	634	103	2346	0.85
Pacific Sanddab	*Citharichthys sordidus*	387	120	365	68	417	208	1565	0.58
Slender Sole	*Lyopsetta exilis*	8	5	10	0	761	8	792	0.21
Sanddab spp.	*Citharichthys* spp.	0	0	76	270	68	10	424	0.27
Pacific Tomcod	*Microgadus proximus*	70	6	1	4	25	186	292	0.17
Smelt spp.	Osmeridae spp.	1	0	21	135	1	10	168	0.09
Sand Sole	*Psettichthys melanostictus*	2	2	27	91	23	10	155	0.40
Pacific Sandlance	*Ammodytes hexapterus*	111	0	16	2	2	17	148	0.16
Warty Poacher	*Occella verrucosa*	12	4	76	18	8	16	134	0.30
Righteye Flounder	Pleuronectidae spp.	0	0	0	7	54	41	102	0.11
Pacific Staghorn Sculpin	*Leptocottus armatus*	24	8	3	28	6	20	89	0.24
Slim Sculpin	*Radulinus asprellus*	10	0	0	0	60	1	71	0.05
Rex Sole	*Glyptocephalus zachirus*	1	0	0	21	43	1	66	0.10
Snailfish spp.	Liparidae spp.	1	0	0	24	22	4	51	0.17
Roughback Sculpin	*Chitonotus pugetensis*	9	9	5	7	8	8	46	0.13
Dover Sole	*Microstomus pacificus*	11	3	7	7	14	2	44	0.21
Dungeness Crab	*Metacarcinus magister*	0	0	0	0	13	23	36	0.09
Black Rockfish	*Sebastes melanops*	0	0	28	1	0	0	29	0.05
Tubenose Poacher	*Pallasina barbata*	6	2	9	1	2	1	21	0.09
Lingcod	*Ophiodon elongatus*	7	1	0	5	0	6	19	0.08
Night Smelt	*Spirinchus starksi*	0	0	0	0	16	1	17	0.03
Sculpin spp.	*Artedius* spp.	5	0	1	1	7	1	15	0.05
Pertrale Sole	*Eopsetta jordani*	2	0	1	1	3	5	12	0.07
Canary Rockfish	*Sebastes pinniger*	1	0	2	5	1	3	12	0.06
Big Skate	*Beringraja binoculata*	2	0	0	5	3	0	10	0.06
Brown Irish Lord	*Hemilepidotus spinosus*	1	0	1	0	1	7	10	0.03
Northern Ronquil	*Ronquilus jordani*	0	0	0	0	8	1	9	0.03
Poacher spp.	Agonidae spp.	7	0	1	1	0	0	9	0.03
Bluebarred Prickleback	*Plectobranchus evides*	0	0	0	0	8	0	8	0.02
Smooth Alligatorfish	*Anoplagonus inermis*	0	0	3	1	2	0	6	0.04
Northern Spearnose Poacher	*Agonopsis vulsa*	0	1	0	0	4	0	5	0.04
Pygmy Poacher	*Odontopyxis trispinosa*	0	0	2	3	0	0	5	0.04
Rockfish spp.	*Sebastes* spp.	2	0	1	1	0	1	5	0.03
Flathead Sole	*Hippoglossoides elassodon*	1	1	0	0	0	2	4	0.02
Thornback Sculpin	*Paricelinus hopliticus*	1	0	2	0	0	0	3	0.02

Table 3. Linear model output for diversity metrics, Species Richness (SR), Evenness (J), and Diversity (H') for the beam trawl community. The full model evaluated for each metric was: *Response ~ Year + Month + Station + Dissolved Oxygen + Temperature.* The best fitting models were: *SR ~ Year + Station + Temperature, J ~ Year + Station*, and *H' ~ Month + Station.* Coefficient values for significant factors are shown for each explanatory variable and for each level for categorical variables; for categorical variables, the coefficient is relative to the first level of the factor. NS=Not a significant factor and - = reference level.

Explanatory Variable	*Levels*	Species Richness (SR)	Evenness (J)	Diversity (H')
Intercept		3.69	0.64	1.39
Dissolved Oxygen		NS	NS	NS
Temperature		0.59	NS	NS
Year	2008	-	-	NS
	2009	-0.43	-0.02	NS
	2010	-1.12	-0.02	NS
	2011	-2.36	0.06	NS
	2012	1.06	-0.06	NS
	2013	1.70	0.07	NS
Month	May	NS	NS	-
	June	NS	NS	-0.13
	July	NS	NS	-0.23
	August	NS	NS	-0.03
	September	NS	NS	-0.34
Station	MB30	-	-	-
	MB40	0.41	0.07	0.16
	MB50	0.30	0.06	0.02
	NH03	-1.13	-0.06	-0.08
	NH05	-1.64	0.06	0.02
	NH07	-4.05	-0.31	-0.90
	NH10	-3.46	0.02	-0.29
	NH15	-2.60	-0.05	-0.27
	NH20	1.97	-0.04	-0.34

Table 4. GAM output for the four most common flatfish species. The best model for all species (and total abundance) was Y ~ s(Depth) + s(DO) + s(Temp) + s(Avg.Upwelling.Index) + factor(Year). For all models, all explanatory variables were significant ($p<0.001$ in all cases). The delta AIC indicates the difference in AIC between the model with and without the Depth*DO interaction term.

Species	*Deviance Explained*	*Δ AIC (difference from model with interaction)*
Total Abundance (all species)	41.3%	22.5
Butter Sole	52.1%	12.5
English Sole	73.5%	183.6
Speckled Sanddab	55.6%	118.6
Pacific Sanddab	50.1%	113.4

Table 5. Best fitting models for two metrics of condition factor for the three most abundant species of juvenile flatfish. The full model for each response was: Response ~ *Year + Depth + Dissolved Oxygen + Temperature + Dissolved Oxygen:Depth (interaction term)*. The coefficient for the dissolved oxygen parameter (the main factor of interest) and R^2 for both the fixed and random effects are provided for the best fitting model. Effect size refers to the change in condition for one unit change is dissolved oxygen. *For the models for English Sole and Speckled Sanddab, the model form only including dissolved oxygen had the lowest AIC score; however, dissolved oxygen was not a significant explanatory variable, as evidenced by coefficients near zero and low explanatory power.

Species	*Metric*	*Best Fitting Model*	*Dissolved Oxygen Coefficient*	*Effect Size*	*R2 (random)*	*R2 (fixed)*
Butter Sole (n=2400)	Residuals	Response ~ Year + DO	0.007	0.9%	0.052	0.384
	Fulton's K	Response ~ Year + DO	0.035	1.0%	0.067	0.271
English Sole (n=1426)	Residuals	Response ~ DO*	0.005	0.6%	0.002	0.208
	Fulton's K	Response ~ DO*	0.001	0.04%	0.001	0.026
Speckled Sanddab (n=1041)	Residuals	Response ~ DO*	0.007	0.4%	0.003	0.136
	Fulton's K	Response ~ DO*	0.007	0.2%	0.001	0.119

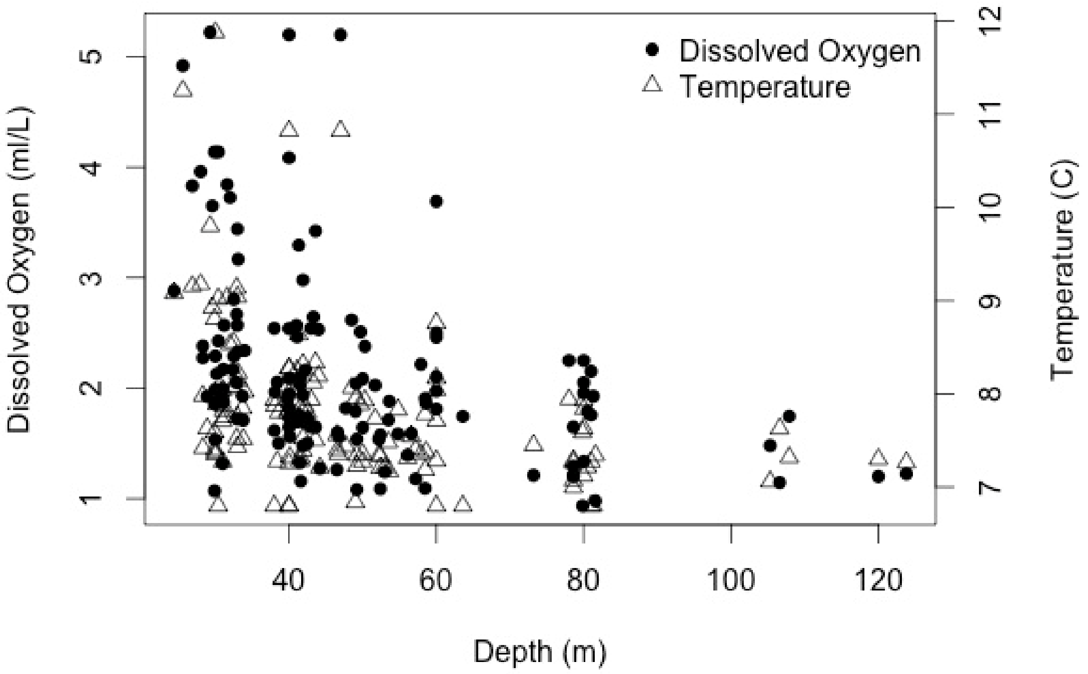

Figure 1. Dissolved oxygen (mL/L) and temperature (°C) as a function of depth as measured concurrently with beam trawl sampling.

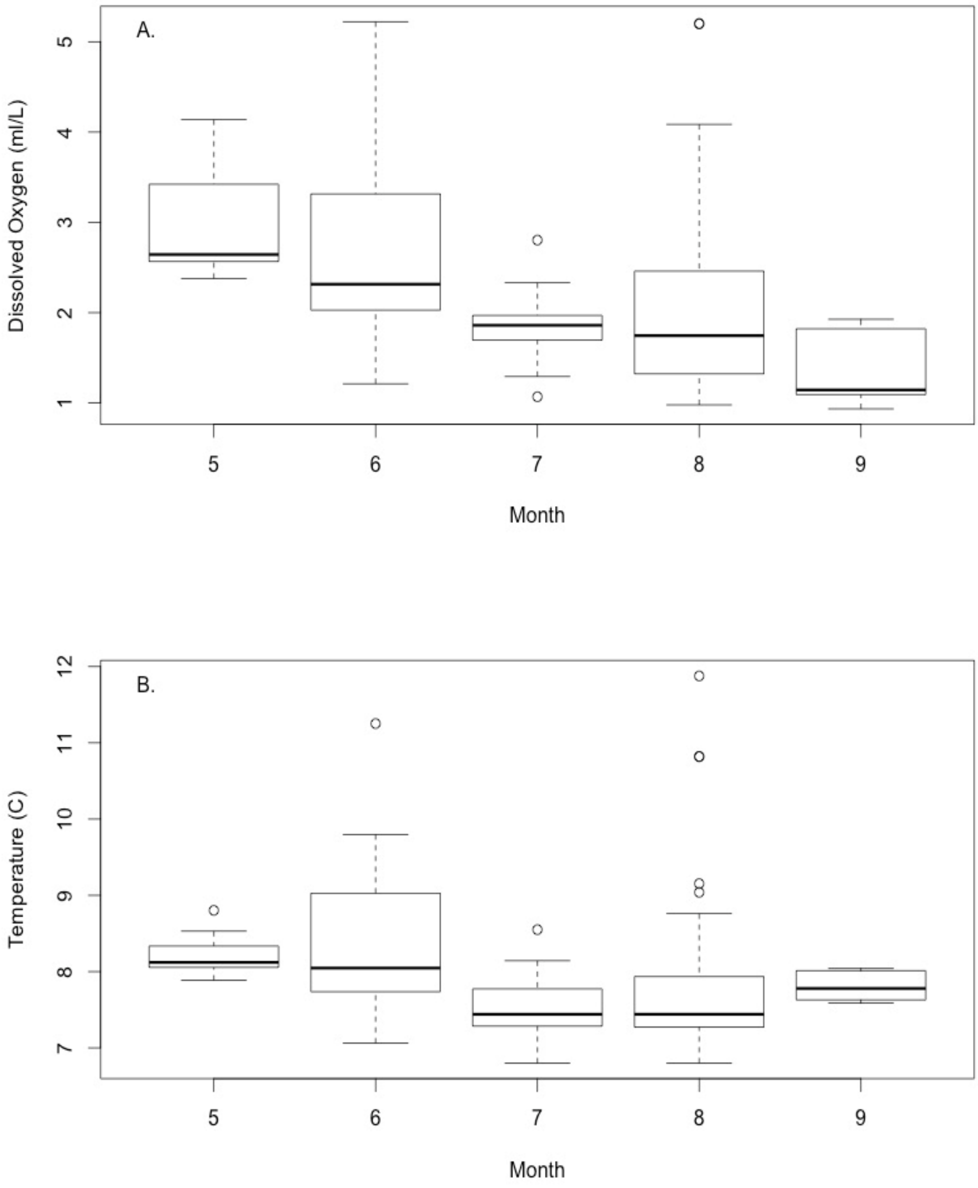

Figure 2. Dissolved oxygen (A., ml/L) and Temperature (B., °C) across all sampling sites by month, from May (5) to September (9). Dark lines show median values with boxes representing first and third quartiles.

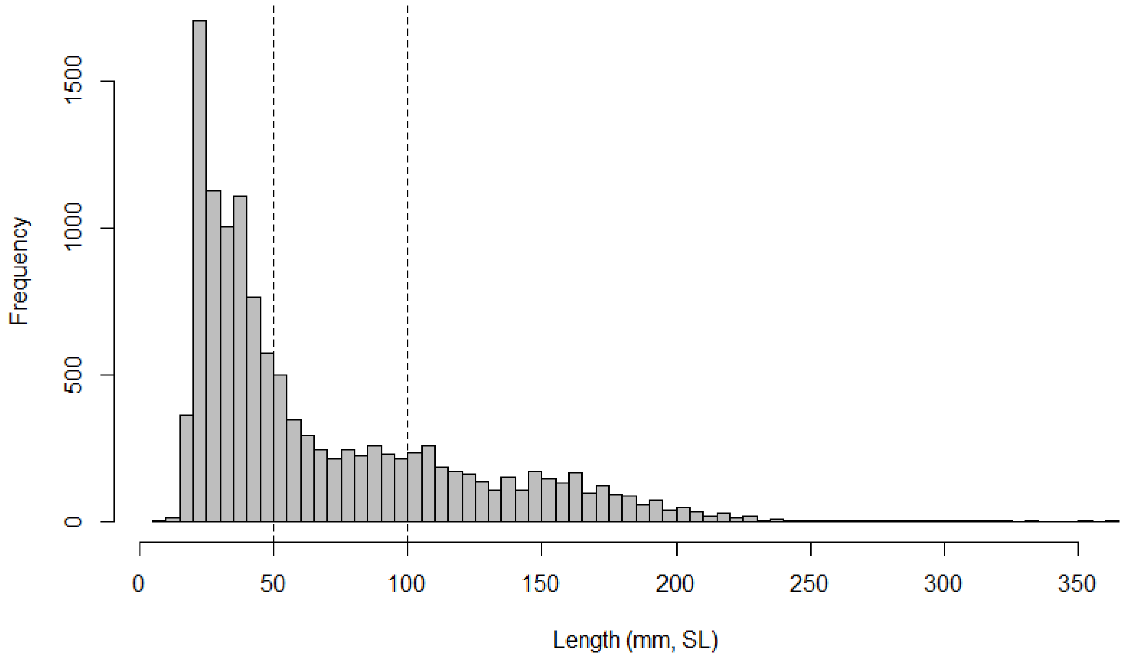

Figure 3. Length frequency of all fishes collected in the beam trawl survey. Vertical lines denote newly settled (<50 mm) and young-of-the-year (<100 mm) individuals.

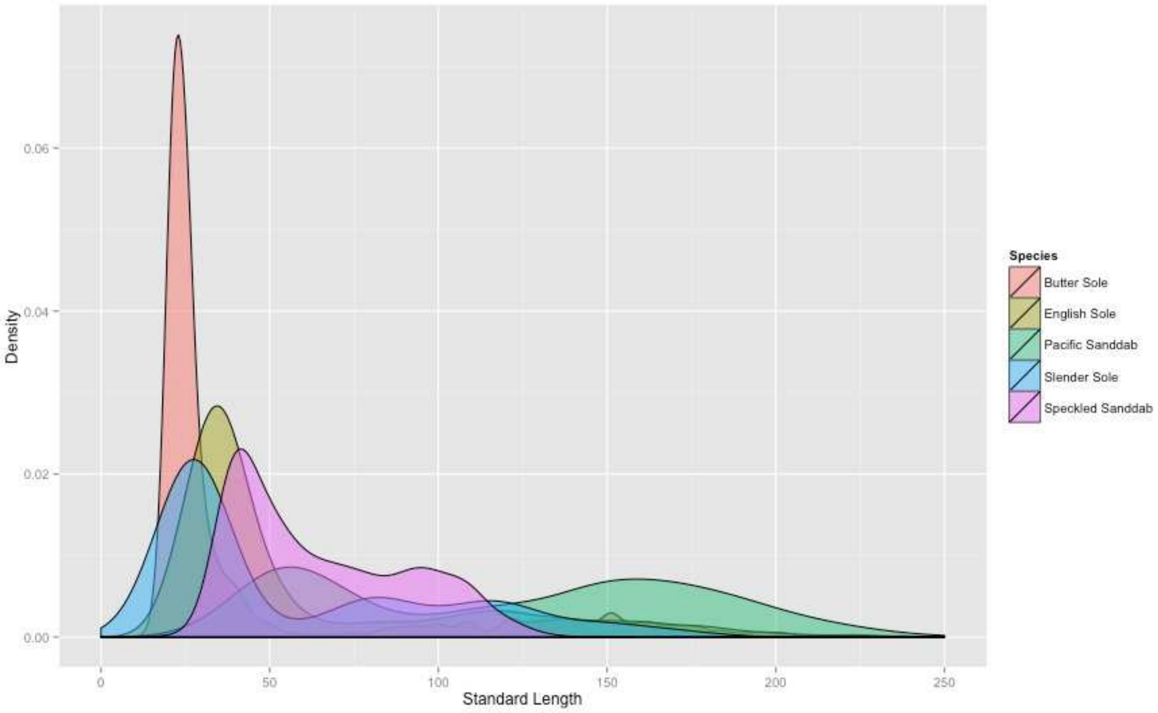

Figure 4. Probability density function of length-frequency for the five most abundant flatfish species. Young-of–the-year fishes dominated the catch, with Butter Sole (*Isopsetta isolepis*) being the most abundant and captured in highest abundance when recently settled (~35 mm SL).

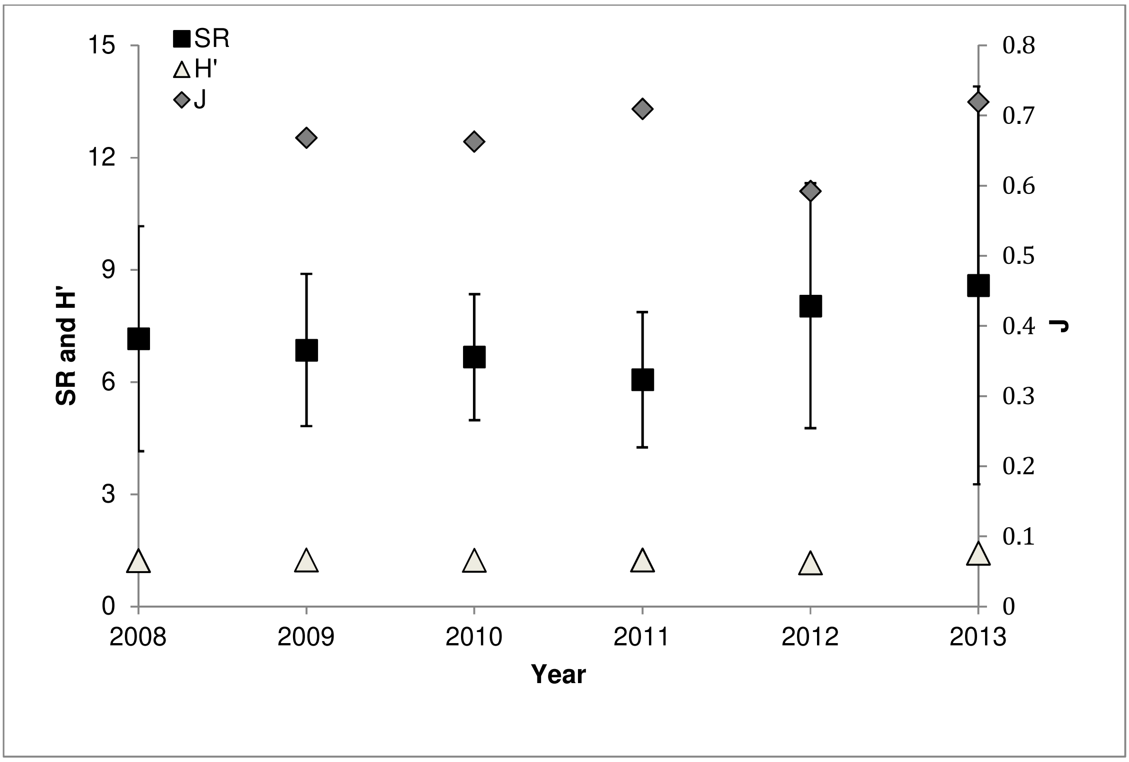

Figure 5. Species richness (SR, black squares), diversity (H', triangles) and evenness (J, gray diamonds, secondary y-axis), for all stations across the six sampling years. Error bars on species richness represent standard deviation of the mean.

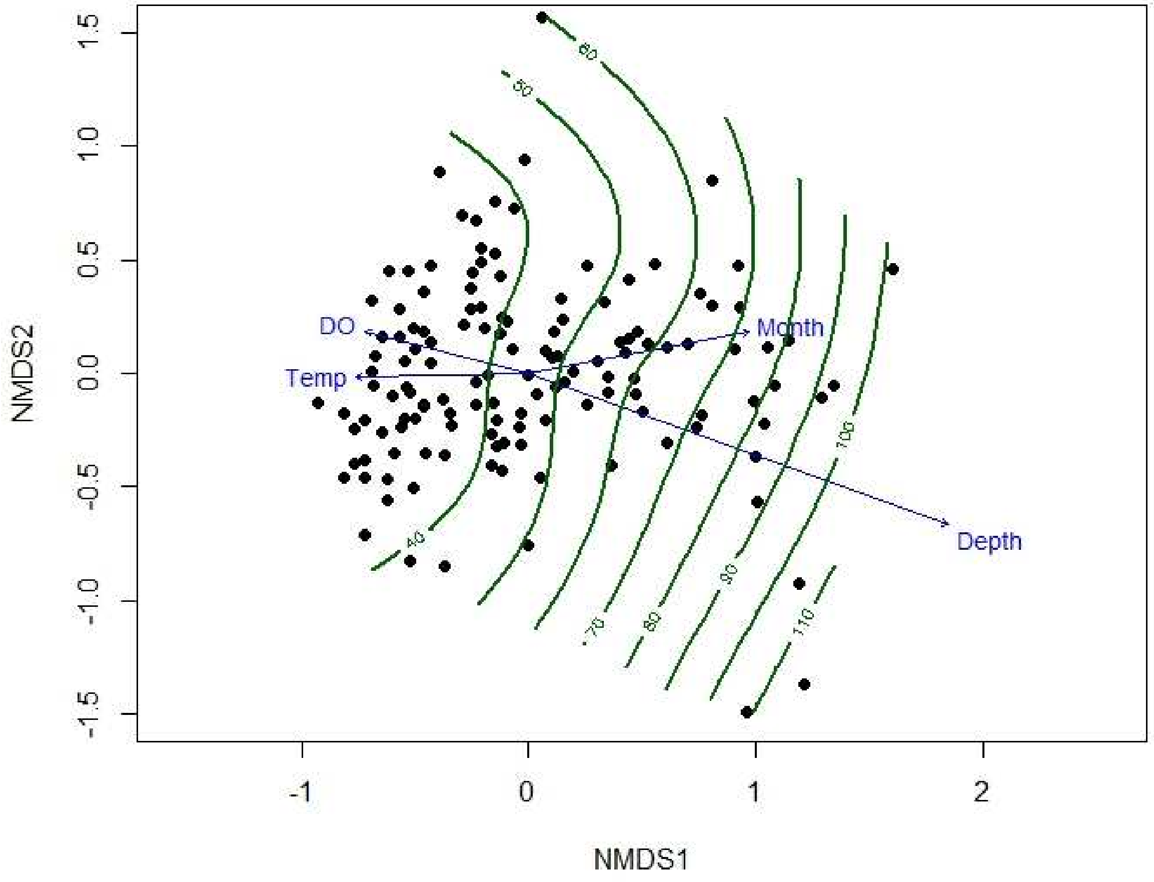

Figure 6. NMDS plot showing assemblage structure with significant explanatory variables shown as vectors. Sampled depth is represented by contour lines, with increasing depth to the right side of the plot. Depth was the strongest predictor of community structure as shown by the vector arrow across the depth contours. 2-dimensional stress for the model was 0.17.

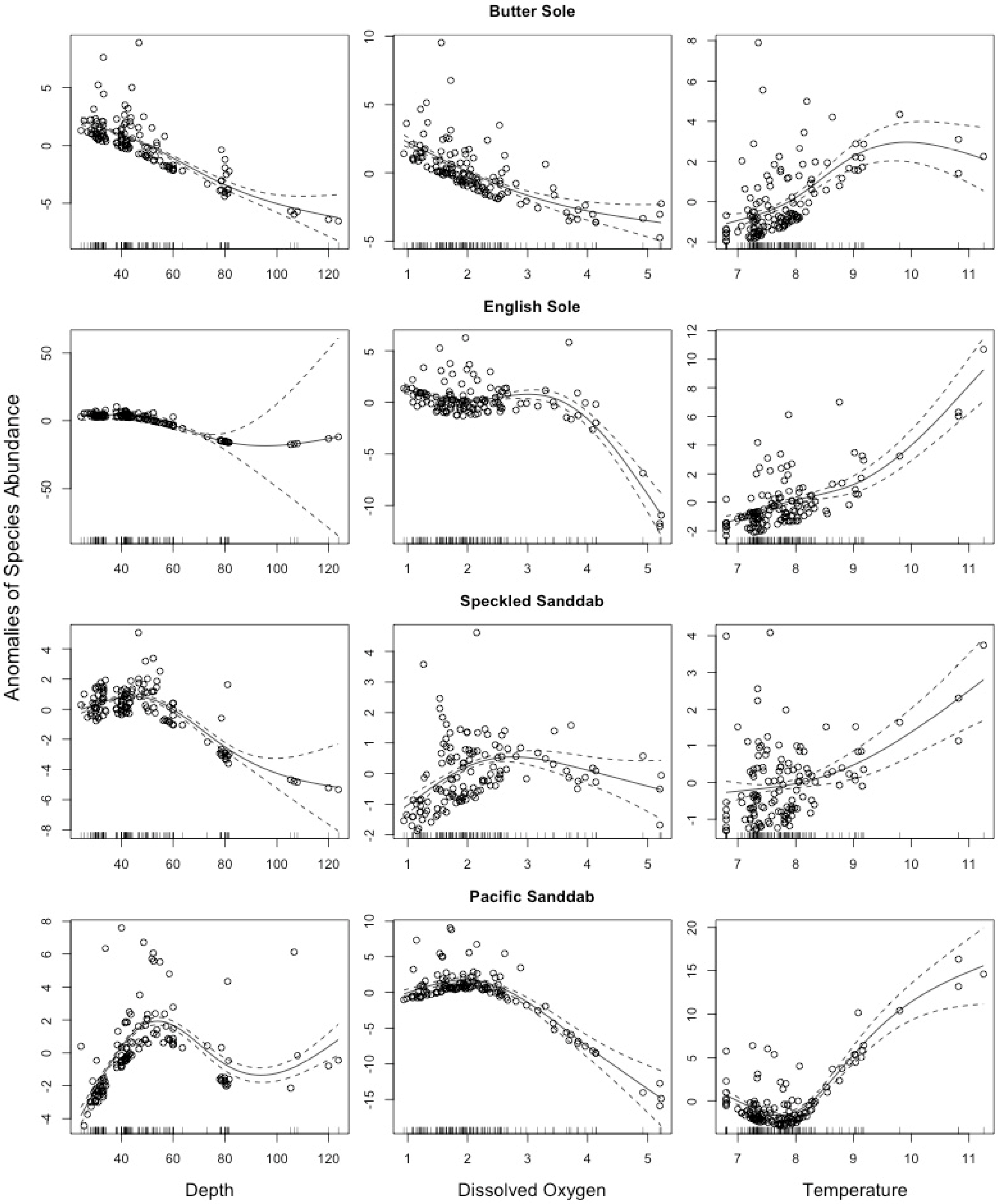

Figure 7. GAM output for species abundance anomalies for four species (rows) showing smoothed terms for each of three predictors: Depth (left column), Dissolved Oxygen (center column), and Temperature (right column). Upwelling index was included in the model, but is not shown because its effect on mean fish abundance was small and predominantly flat throughout the examined range for all species. Note that the scale of the effect size (y-axis) varies by species and predictor.

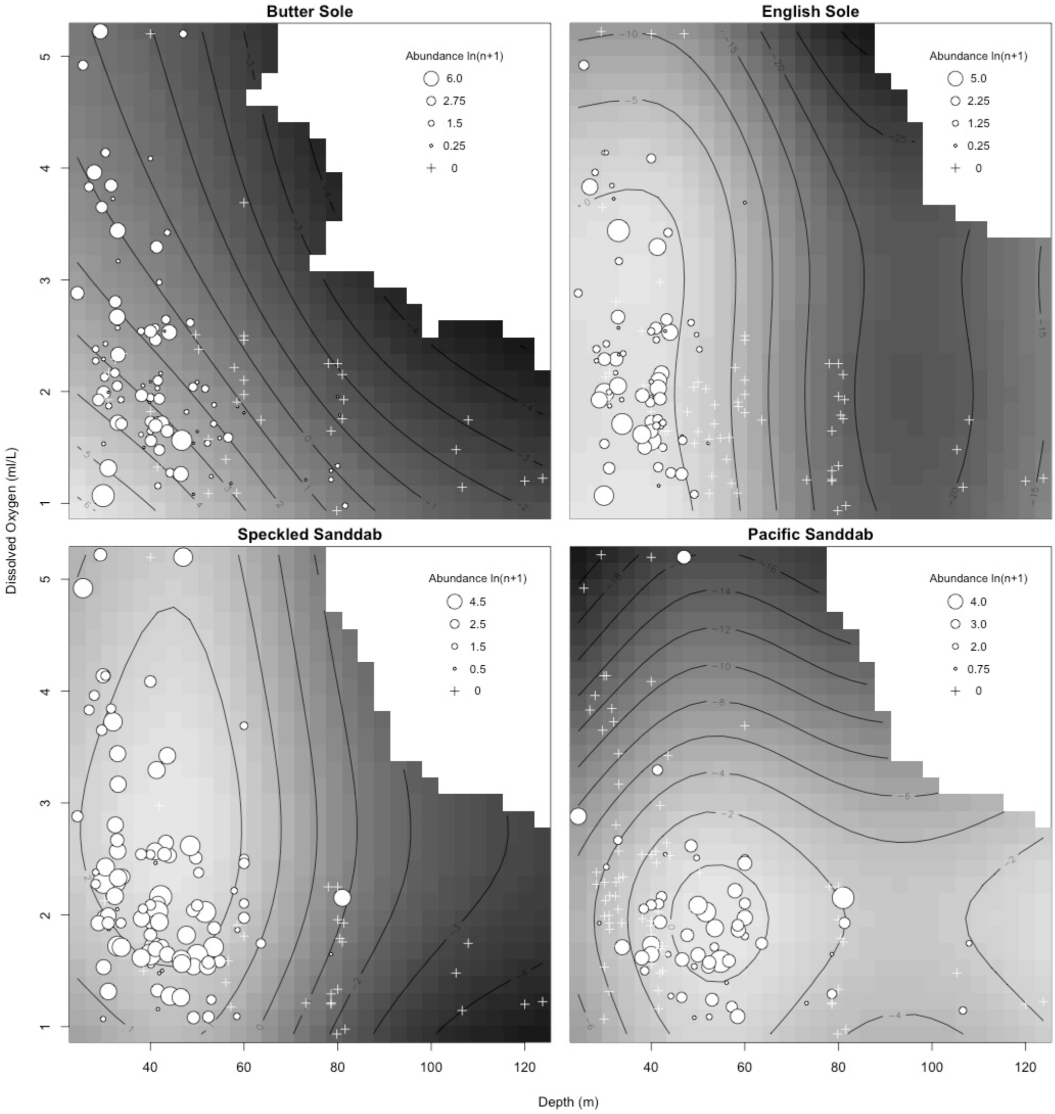

Figure 8. Model output for the most common flatfish species from GAM. Bubbles represent abundance data from the beam trawl, scaled by count (log scale, as per legend for each species). Tows with zero catches of the species are indicated by (+). Shading indicates the predicted abundance of each species based upon depth (x-axis) and dissolved oxygen (y-axis), with lighter shading indicating greater predicted abundance and darker areas indicating less predicted abundance.

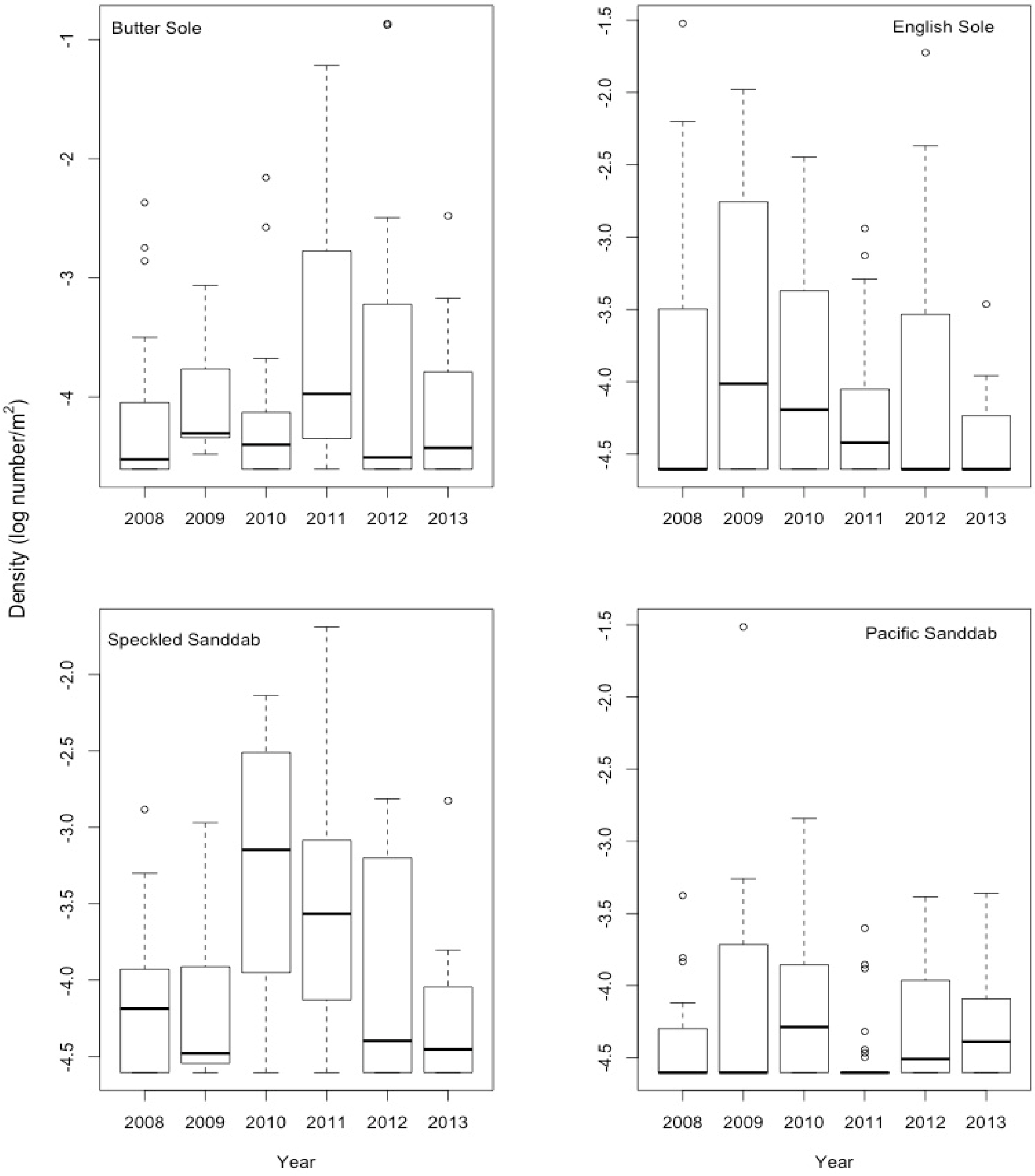

Figure 9. Density by year for four species from the beam trawl survey. Density is shown as log(n+0.01) for best resolution. Black bars within boxes show median values.

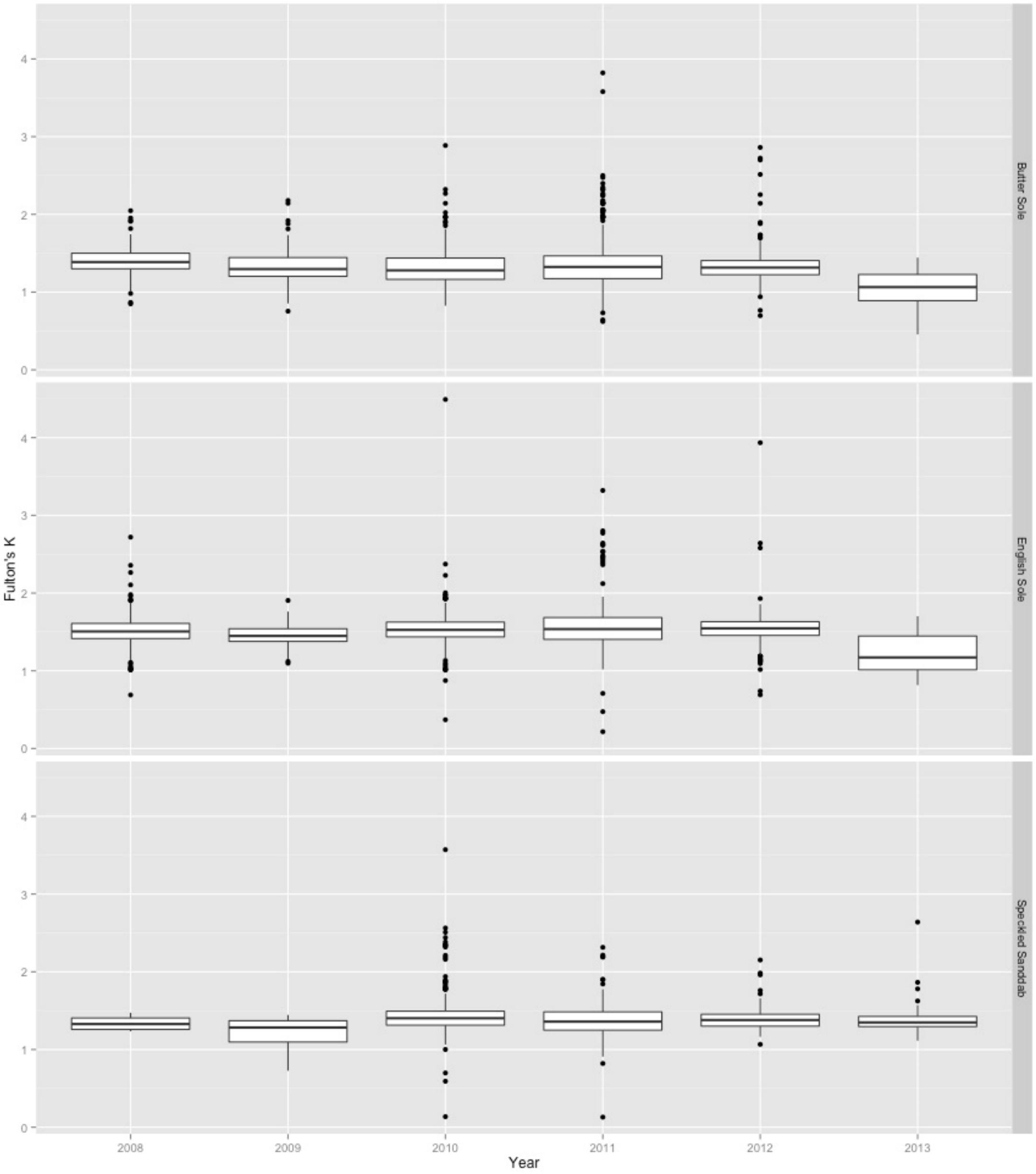

Figure 10. Fish condition, Fulton's K, across the sampling years for three common species, Butter Sole, English Sole, and Speckled Sanddab. Dark lines in the center of boxes show medians with boxes showing first and third quartiles. Black dots indicate outliers.