Supporting Information

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SI Methods

Modeling the Extent of Suitable Flatfish Habitat. To determine the spatial extent of suitable flatfish habitat in Elkhorn Slough, we modeled the probability of flatfish presence (using logistic regression curves) as a function of hypoxia extent in the estuary. We only incorporated logistic regression curves from deep-channel habitats because they had a larger range of probabilities and DO. We did not use data from 1970 to 1988 because of a gap in water quality data from 1976 to 1988; therefore, we opted to use the dataset that was most continuously sampled [1988–2012, Elkhorn Slough National Estuarine Research Reserve (ESNERR)].

Using spatial analysis, we mapped out the probability of occurrence for English sole and speckled sanddab using DO values among sites within Elkhorn Slough. We combined Python and Numerical Python (NumPy) scripting with ArcGIS 10.2 (Environmental Systems Research Institute) to parse, prepare, and analyze tabular DO data. To calculate the 10th percentile of DO throughout Elkhorn Slough, we interpolated each monthly sample ($n = 252$) to create 25 × 25-m resolution ESRI Grid (raster) files. Within the Spatial Analyst extension of ArcGIS, we used the Spline with Barriers interpolation tool, which attempts to fit a surface among all values while minimizing the amount of curvature and respecting breaks and discontinuities imposed on the surface (1). Each resulting raster was converted into a NumPy array, and the NumPy percentile function used to determine the 10th percentile for all colocated cells, through the stack of arrays, resulting in a single array that was then converted back into a raster for further analysis (Fig. S5). The resulting raster of 10th percentile DO values was used to calculate the probability of occurrence of English sole and speckled sanddab using the logistic regression analysis described in the main text. The raster calculator function of ArcGIS was used to apply the algorithm to each raster cell based on the 10th percentile DO value for that cell.

Model Validation of Flatfish Logistic Regressions. Next, we validated our logistic regression using a directed flatfish survey within Elkhorn Slough. A 2005 survey by Ritter et al. (2) thoroughly sampled the Elkhorn Slough fish assemblage by sampling shallow margin habitats using beach seines at 16 stations strategically located less than 500 m to the nearest water quality monitoring station (Figs. S2*A* and S3). Each station was sampled in the spring and again in the summer, coinciding with periods of increased hypoxia (Fig. S6). We used each sampling date at each station as a replicate in a logistic regression analysis. The logistic regression analysis was run using presence/absence for flatfish species as the dependent variable and the 10th percentile DO calculated for the entire ESNERR dataset (1988–2012). By using the 10th percentile of DO, we were able to compare the relative degree of hypoxia for each sampling station (3). We combined all flatfish species caught in the 2005 survey: speckled sanddab, California halibut (*Paralichthys californicus*), starry flounder (*Platichthys stellatus*), fantail sole (*Xysteurys liolepis*), and California tonguefish (*Symphurus atricauda*) into one group given their similar lifestyles and because of low replication among the individual species during the survey period.

Additionally, we mapped out flatfish probabilities from the 2005 fish survey to assess similarity in the spatial distribution of flatfish probabilities between the 2005 fish survey and 1988–2012 water quality datasets.

Developing a Dissolved Oxygen Anomaly. To scale up to the estuary-wide hypoxic condition, we developed a dissolved oxygen anomaly (DOA) to identify hypoxic periods in the estuary that could be correlated with the fish assemblage. The DOA was calculated using DO samples collected monthly from the shore at 1-m depth for the entire ESNERR water quality record (3) (1988–2012) at stations ($n = 6$; Fig. S2*A*) that were sampled within the fish sampling range along the main channel of the estuary by calculating Z scores: Global Mean – Raw DO ($\mathrm{mg{\cdot}L^{-1}}$)*Global $\mathrm{SD^{-1}}$ (see *Descriptions of Data Sources* for more information on water quality data). The average monthly DOA value among all of the sampling stations was used for a single monthly value that represented the DO condition for the estuary for that month. We defined hypoxic as any negative DOA value and normoxic as any positive DOA value.

Identifying Drivers of DO. We explored the key correlates of hypoxia by using continuous water quality monitoring stations in the upper and lower estuary (Fig. S2*A*) that sample for DO, temperature, and salinity with YSI (Yellow Springs Instruments) data sondes placed in shallow water (1–2 m). The lower estuary site is closer to the mouth of the estuary and therefore more likely influenced by oceanographic processes, whereas the upper estuary site is located halfway up the estuary where residence times are higher and is more representative of mid to upper estuarine sites. We characterized hypoxia at each site by calculating the 10th percentile of DO (an indicator of the level of hypoxia) (3) for an entire water year, and then used structural equation modeling (SEM) to explore the key direct and indirect correlates of hypoxia to test for direct and indirect effects (see refs. 4 and 5 for a description of SEM). By constructing path models, we tested the hypothesis that environmental processes (i.e., El Niño and upwelling) regulate the effects of anthropogenic nutrient loading on hypoxia at both stations in the upper and lower parts of the estuary. Models were reduced to eliminate insignificant factors ($P > 0.10$). For the model, we used annual means for ENSO, Monterey Bay upwelling, nitrate, water temperature and salinity, total annual precipitation, and the annual 10th percentile of DO as an indicator of hypoxia. Nitrate data were from water samples collected and averaged monthly from three monitoring stations near the estuary mouth where the estuary receives the greatest land-based nutrient load (3, 6). We used the annual values of each factor as replicates in the SEM for the upper ($n = 15$) and lower ($n = 10$) estuary. SEMs were calculated using SPSS Amos, version 22.0 (IBM).

To determine the influence of El Niño on hypoxic conditions of northeast Pacific estuaries, we selected six sites within the NERR system that have sampled DO continuously at multiple stations since 1997 (cdmo.baruch.sc.edu). Most NERR stations use YSI data sondes to measure DO, which are set ~1 m above the bottom in <20-m depth. All stations are sampled near the shore except for Padilla Bay, which has two stations situated in channels 1–2 km from shore, including one station where the data sonde is located 0.5 m below the water surface. These estuarine sites consisted of three California sites: Tijuana River Estuary/San Diego Bay ($n = 4$ stations), Elkhorn Slough ($n = 4$ stations), San Francisco Bay ($n = 1$ station); South Slough, Oregon ($n = 4$ stations); Padilla Bay, Washington ($n = 4$ stations); and Kachemak Bay, Alaska ($n = 2$ stations). We first characterized each year as El Niño (mean annual ENSO index, >0.50; $n = 3$; 1997–1998, 2002–2003, 2004–2005) or neutral non-El Niño (mean annual ENSO index, −0.50 to 0.50; $n = 3$; 2001–2002, 2005–2006, 2008–2009).

For the purposes of this analysis, we did not include La Niña years (mean annual ENSO index, less than −0.50; 1998–2001, 2007–2008) because La Niña can produce highly variable weather and climate conditions in the northeast Pacific, and we were primarily interested in the relationship between El Niño and hypoxia. We determined the mean annual hypoxic condition (10th percentile DO) for independent monitoring stations within each estuary (one to four stations per estuary; $n = 19$). The number of stations within each NERR site varied because some sites had more established stations over the 1997–2009 time period. The main requirement for each station was that it captured at least one El Niño and one non-El Niño year for the paired analysis. We compared the mean annual hypoxic condition during El Niño vs. non-El Niño conditions at each station using a paired-samples t test.

Descriptions of Data Sources.

Characterizing the nursery fish assemblage. We used a long-term (1970–2010) fish survey dataset from the Monterey Bay National Marine Sanctuary's Sanctuary Integrated Monitoring Network (SIMoN) (sanctuarysimon.org/projects/project_info.php?projectID=100116&site=true) to determine the effects of variable environmental conditions on the structure and distribution of the fish assemblage that inhabits Elkhorn Slough. The dataset incorporates data from a number of studies, combining deep-channel surveys using otter trawls ($n = 626$) and shallow-margin surveys using beach seines ($n = 318$) to sample the fish assemblage at various sites within Elkhorn Slough (Fig. S2*A*). The dataset captures a high degree of temporal and spatial variability, which makes it ideal to test the effect of varying water quality on the fish assemblage. We limited analyses to those deep-channel ($n = 8$) and shallow-margin ($n = 10$) sites that had been consistently sampled at least 28 and 16 times, respectively, through the entire time series, and had also been sampled for water quality around the time of sampling.

Both otter trawl (deep-channel habitat) and beach seine (shallow-margin habitat) efforts were located along the entire main channel of the estuary (Fig. S2*A*). Trawl net size (4.8-m head rope, 3.8-cm stretch mesh, 1.3-cm codend liner) and sampling area (typically run at 1.5–3 kn for 10 min) was consistent throughout the entire study period. Net size of the beach seines varied from 8 to 100 m, making it difficult to standardize for abundance, so only presence/absence analyses were used for seine surveys. Beach seines were assigned to the nearest water quality station. Each fish sampling event (otter trawls and beach seines) was located <500 m and <30 d to the nearest water quality sampling event. If there were multiple sampling events within the same 30-d period at the same sampling station, we either combined them (presence/absence data) or used an average (abundance and species richness data) to ensure independence among replicates. It was assumed that the monthly water quality sample was a good indicator for the overall water quality condition for the fish sample.

Water quality parameters. We used several datasets that span from 1970 to 2012 (ref. 7, 1970–1972; ref. 8, 1974–1976; ref. 3, ESNERR water quality monitoring program, 1988–2012). These data were from water samples collected monthly from shore (∼1-m depth) at various stations around the estuary (Fig. S2*A*). The parameters we used for analyses in this study were daytime DO (in milligrams per liter), nitrate (in milligrams per liter), temperature (in degrees Celsius), and salinity (in parts per thousand), as these were factors known to affect fish presence in estuarine environments (9). We used the raw monthly values for DO, temperature, salinity, and nitrate for logistic regression analysis with the two target flatfish species. Data from the 1970s (7, 8) were collected using Winkler titrations (DO), cadmium reduction (nitrate), thermometers (temperature), and a Beckman RS-7B precision induction salinometer (salinity). Data from 1988 to 2012 (3) were collected using YSI data sondes for salinity, DO, and temperature; and nitrate was determined using a flow injection autoanalyzer from grab samples.

For offshore Monterey Bay DO and temperature, we used data collected from the Monterey Bay Aquarium Research Institute. Monterey Bay and the contiguous waters of the California Current have been sampled repeatedly since 1988 by the Monterey Bay Aquarium Research Institute (10). Conductivity, temperature, and depth (CTD) casts are made with a Seabird 911 with a 12-place rosette with Niskin bottles. Redundant temperature sensors are used and these are calibrated annually. DO from the Niskin bottles is analyzed routinely by the modified Winkler titration method (11). During the early years, samples from the 12 bottles were analyzed but after the development of reliable oxygen sensors for CTDs (i.e., Seabird 43) the number of samples was greatly reduced and used solely to calibrate the Seabird 43 oxygen sensor. We used samples collected near the bottom at a standardized depth (200 m) within English sole habitat. Samples were collected during July and August because these were the only months consistently sampled every year throughout the entire data series (1989–2011). We used the mean annual DO value for samples taken each year. There were on average seven DO samples collected each year, which we considered to accurately capture bottom DO conditions because the within-year SD was low ($\mu_{SD} = 0.67$). Preliminary regression analysis of temperature, which was consistently low throughout the dataset ($\mu_{\text{Monterey Bay}} = 8.7 \pm 0.44$ °C SD), determined that it was not an important driver of English sole and was therefore not included in the final analysis.

Climate and oceanographic indices. We used El Niño Southern Oscillation (ENSO) (www.esrl.noaa.gov/psd/enso/mei/table.html), Pacific Decadal Oscillation (PDO) (jisao.washington.edu/pdo/PDO.latest), North Pacific Gyre Oscillation (NPGO) (www.o3d.org/npgo/npgo.php), and local Monterey Bay upwelling (www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/NA/upwell_menu_NA.html) indices to investigate the relative effects of large-scale climate variation on the Elkhorn Slough water quality and fish assemblage over the past 40 y. These indices are reported as mean monthly values, so we matched the month of each fish and water quality sample to the corresponding ENSO, PDO, NPGO, and upwelling indices and used those in the statistical analyses.

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11. Carpenter JH (1965) The Chesapeake Bay Institute technique for the Winkler dissolved oxygen method. *Limnol Oceanogr* 10:141–143.

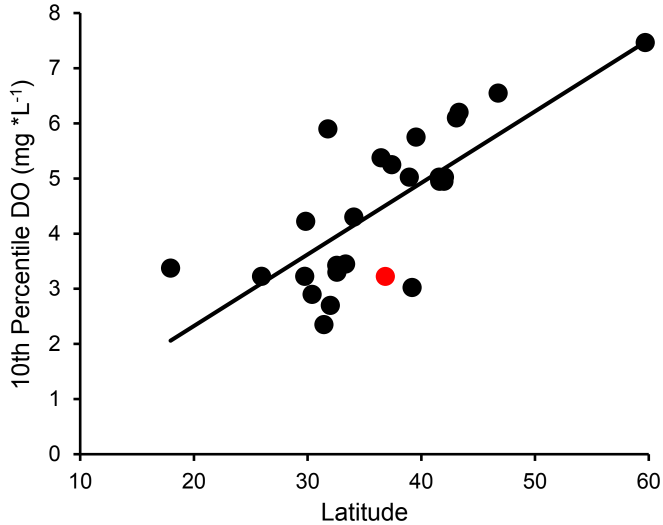

Fig. S1. Estuarine hypoxia in the United States. Relationship between latitude and hypoxia in United States estuaries [$R^2 = 0.56$, $P < 0.0005$, $F_{(1,24)} = 30.59$, $n = 27$], measured as the 10th percentile DO (in milligrams per liter) from continuously collected (15- to 30-min intervals) data from 2009–2010 (cdmo.baruch.sc.edu). Each point represents an average over the 2-y period from three to four monitoring stations within each estuary. The red point indicates Elkhorn Slough.

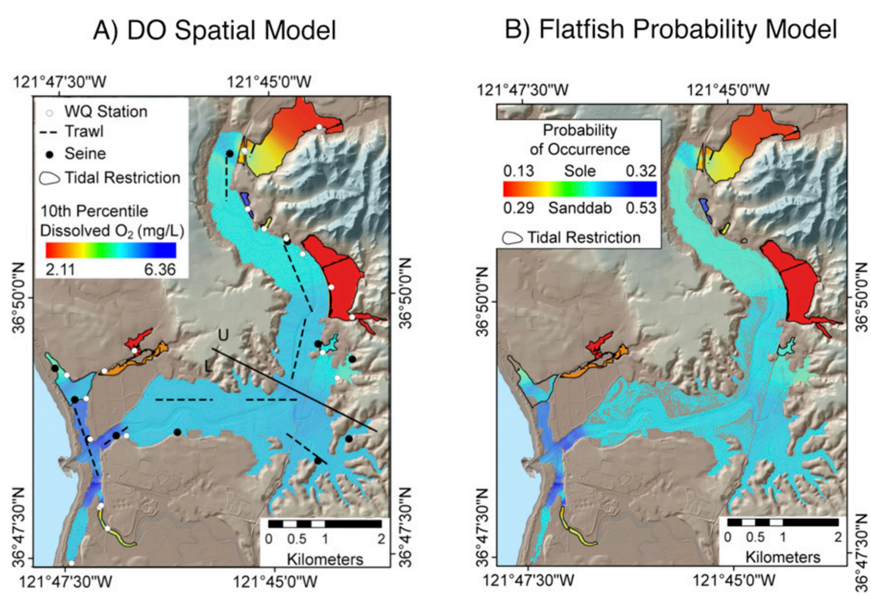

Fig. S2. (*A*) Survey locations for both water quality monitoring and fish sampling along with a spatial model of 10th percentile DO from 1988 to 2012. Tidal height is mean higher high water (MHHW) to indicate the greatest available habitat on an average day within Elkhorn Slough. Open circles (○) are the ESNERR water quality monitoring stations as well as the 2005 slough-wide sampling stations from Ritter et al. (2). Dark circles (●) indicate locations for historical shallow-margin (beach seine) surveys, dashed lines (---) indicate approximate locations of historical deep channel (otter trawl) surveys, and the solid line (—) indicates the division of upper (U) and lower (L) estuarine stations. Areas behind tidally restricted water control structures were indicated with a bold line drawn around the area. (*B*) Predicted probabilities of presence of English sole and speckled sanddab based on logistic regression analysis. Spatial probabilities were calculated based on the interpolated 10th percentile of DO (in milligrams per liter) collected monthly from the 1988–2012 ($n = 252$) ESNERR water quality database. Probability scales for each species were adjusted to conform to the interpolated DO values.

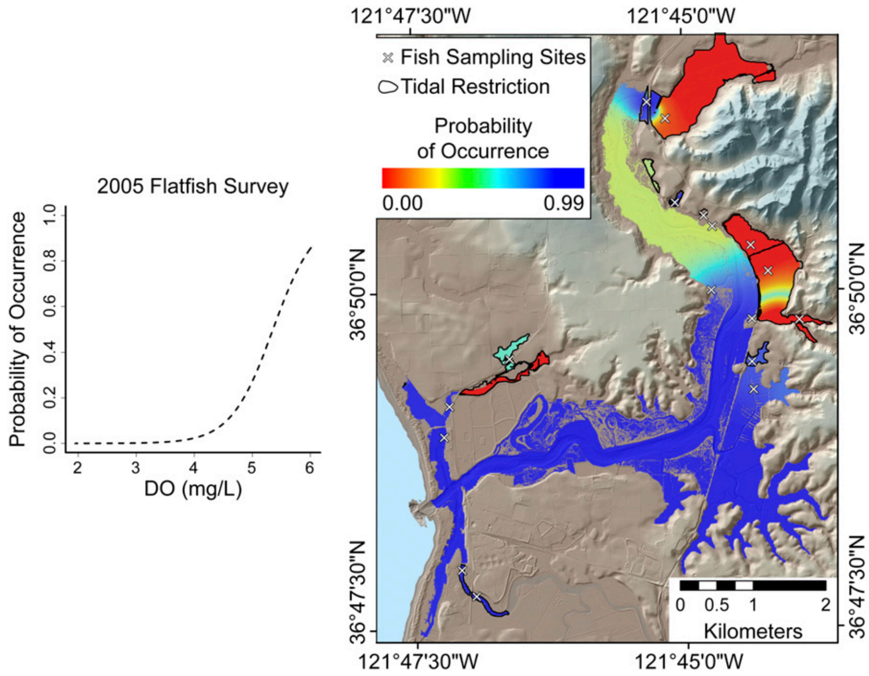

Fig. S3. Logistic regression analysis of the predicted probability of flatfish occurrence during 2005 shallow-margin surveys in Elkhorn Slough as a function of 10th percentile of DO from 1989 to 2011 ($n = 33$). Tidal height is mean higher high water (MHHW) to indicate the greatest available habitat on an average day within Elkhorn Slough. See Table S2 for statistical results. Areas behind tidally restricted water control structures were indicated with a bold line drawn around the area.

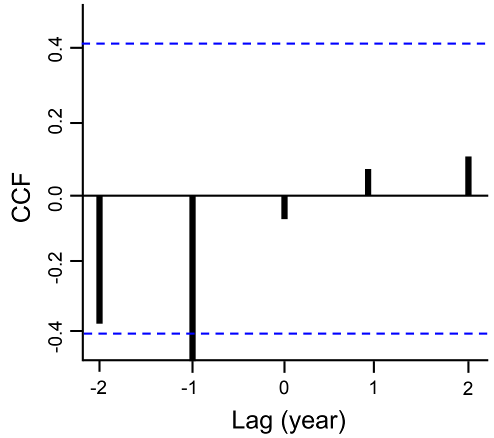

Fig. S4. Cross-correlation analysis determining the lag (years) of offshore English sole recruitment (recruits per hectare, 2003–2011, $n = 9$) with the greatest cross-correlation function (CCF) to the number of hypoxic months per year in Elkhorn Slough. The dashed blue line indicates the threshold for significant correlations based on 95% CI.

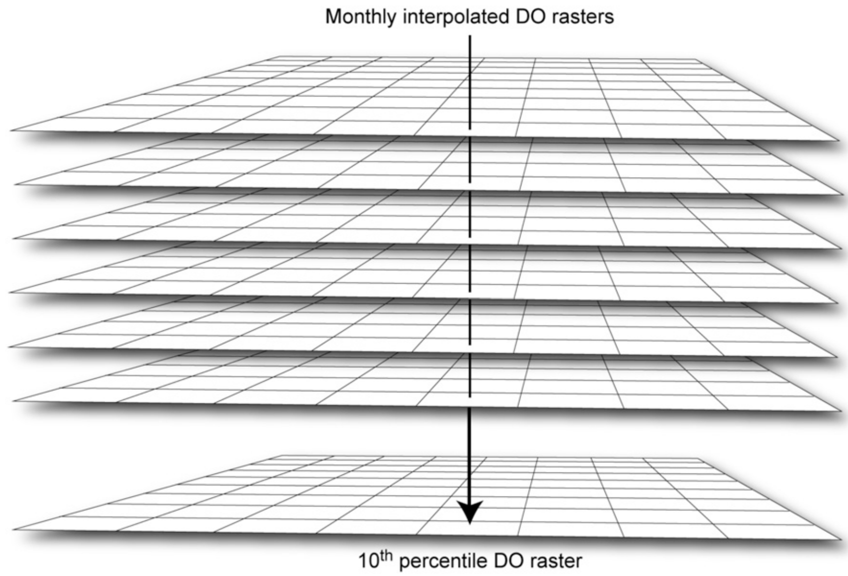

Fig. S5. Graphical representation of same-cell analysis among monthly interpolated dissolved oxygen rasters (i.e., raster stack), used to calculate 10th percentile DO for the entire sampling period.

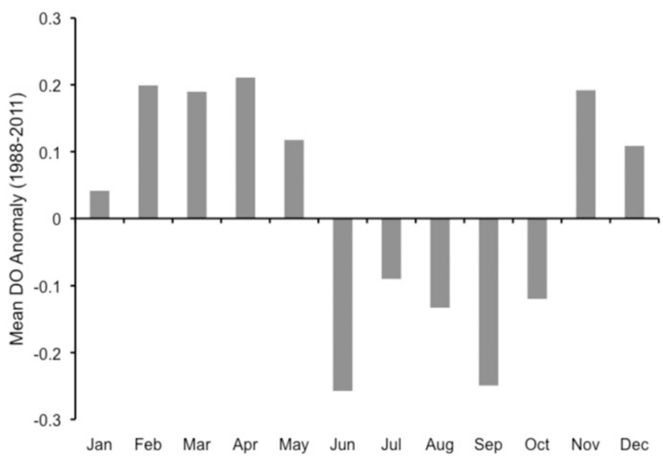

Fig. S6. The mean monthly DOA for all water quality monitoring stations in Elkhorn Slough from 1988 to 2011.

Table S1. Sequential logistic regression results testing the effects of DO, temperature, salinity, ENSO, PDO, upwelling, and daily sampling effort on presence/absence data for English sole and speckled sanddab (Fig. 1) using surveys from both deep-channel (n = 169) and shallow-margin (n = 78) habitats

Variable/habitat/model	Source	Estimate	SE	*z* value	*P*
English sole					
Deep channel					
Best-fit model	DO	0.283	0.092	3.077	**0.002**
	Temperature	0.124	0.064	1.926	**0.054**
	Upwelling	0.018	0.004	4.424	**<0.0005**
	ENSO	0.326	0.209	1.559	0.119
	AIC = 202.7				
DO model	DO	0.256	0.087	2.942	**0.003**
Shallow margin					
Best-fit model	Temperature	−0.350	0.187	−1.875	**0.061**
	Upwelling	0.020	0.008	2.692	**0.007**
	AIC = 49.55				
DO model	DO	0.409	0.215	1.906	**0.056**
Speckled sanddab					
Deep channel					
Best-fit model	DO	0.238	0.092	2.577	**0.010**
	Temperature	−0.147	0.063	−2.315	**0.021**
	ENSO	0.487	0.221	2.205	**0.027**
	AIC = 212.8				
DO model	DO	0.234	0.0917	2.551	**0.011**
Shallow margin					
Best-fit model	DO	0.403	0.197	2.049	**0.040**
	Temperature	−0.236	0.135	−1.755	**0.079**
	PDO	1.329	0.512	2.595	**0.009**
	Salinity	−0.134	0.057	−2.359	**0.018**
	Sampling effort	0.512	0.271	1.890	**0.059**
	AIC = 79.3				
DO model	DO	0.347	0.158	2.2	**0.028**

The best-fitting model was confirmed using AIC weights, and we reported the best-fitted model using multiple logistic regression. Last, the model was reduced down to using only DO as the predictor to test for generality of DO effects. Significant values ($P < 0.10$) are in bold.

Table S2. Logistic regression analysis of the presence/absence of flatfish during two 2005 shallow-margin surveys at 16 locations in Elkhorn Slough as a function of 10th percentile of DO from 1989 to 2011 (n = 33) (Fig. S3)

Source	Estimate	SE	*z* value	*P*
DO	2.751	1.339	2.054	0.040

Table S3. Deep-channel survey results from *t* tests testing for the effect of hypoxia and region on abundance of English sole and speckled sanddabs (abundance per hectare) and fish species richness (species per trawl)

Analysis type	Dependent variable	Mean difference	SE difference	t	df	P
Pooled (hypoxia vs. normoxia)*						
	English sole abundance[†]	−25.779	11.616	−2.219	29	**0.034**
	Speckled sanddab abundance	−9.810	7.125	−1.378	48	0.175
	Species richness	−1.557	0.691	−2.253	48	**0.029**
Paired (lower–upper estuary)[‡]						
Normoxia	English sole abundance	−14.032	23.511	−0.597	13	0.561
	Speckled sanddab abundance	12.834	12.092	1.061	15	0.305
	Species richness	−0.960	0.637	−1.506	15	0.153
Hypoxia	English sole abundance	7.446	2.152	3.461	5	**0.018**
	Speckled sanddab abundance	17.345	7.190	2.413	8	**0.042**
	Species richness	1.684	0.447	3.766	8	**0.005**
Partitioned (lower and upper estuary)[§]						
Lower (hypoxia vs. normoxia)	English sole abundance	−12.287	18.442	−0.666	18	0.514
	Speckled sanddab abundance	−7.562	14.187	−0.533	23	0.599
	Species richness	−0.495	0.918	−0.595	23	0.595
Upper (hypoxia vs. normoxia)	English sole abundance[†]	−39.272	19.742	−1.989	13	**0.068**
	Speckled sanddab abundance[†]	−12.074	5.814	−2.077	16	**0.054**
	Species richness	−3.139	0.894	−3.508	23	**0.002**

Significant values ($P < 0.10$) are in bold. Note: English sole had a reduced sample size because the analysis excluded sampling dates when no English sole were caught ($n = 12$ hypoxic; $n = 28$ normoxic).

*Independent-samples *t* test comparing hypoxic ($n = 18$) and normoxic ($n = 32$) periods on fish parameters (Fig. 2 *B–D*).

[†]Welch's *t* test of unequal variances.

[‡]Paired-samples *t* test testing for differences among each sampling date for fish parameters during (*i*) hypoxic periods and (*ii*) normoxic periods (Fig. 2 *E–G*).

[§]Independent-samples *t* test comparing fish parameters between hypoxic and normoxic periods for the (*i*) lower and (*ii*) upper estuary, respectively (Fig. 2 *E–G*).

Table S4. Stepwise backward regression and AIC model selection identifying the important drivers (nursery hypoxia, measured as the number of hypoxic months according to the DOA, and DO in the offshore region) of English sole recruitment in Monterey Bay (recruits per hectare; survey 1, $n = 6$; survey 2, $n = 9$) and residuals of annual English sole fishery landings (in kilograms) in Monterey Bay ($n = 23$)

Variable/survey/model	Source	Estimate	SE	t	P	AIC
English sole recruitment, Monterey Bay						
Survey 1: 1989–2004						
Best-fit model	Nursery hypoxia	−1.938	0.906	−2.139	**0.099**	**17.5**
	$R^2 = 0.534$		$F_{(1,4)} = 4.576$			**15.0** (FS)
Survey 2: 2003–2011						
Best-fit model	Nursery hypoxia	−0.845	0.404	−2.092	**0.075**	**20.9**
	$R^2 = 0.385$		$F_{(1,7)} = 4.377$			**18.5** (FS)
English sole landings, Monterey Bay						
Best-fit model	Nursery hypoxia	−12,845.2	4,212.7	−3.049	**0.006**	**508.3**
	Upwelling	−1,283.1	522.9	−2.454	**0.023**	**505.6**
	Full model $R^2 = 0.299$		$F_{(2,20)} = 5.694$		**0.011**	**501.5** (FS)

AIC values from the best-fit model are reported for each factor and for the final step (FS). Upwelling, PDO, NPGO, and ENSO were also included as predictors for the fishery model. Significant values ($P < 0.10$) are in bold.