

Interplay of temperature and hypoxia in habitat quality for a juvenile demersal fish in a coastal upwelling system

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Abstract

Coastal hypoxia around the world has raised concerns about its sublethal effects on juvenile demersal fishes. We examined the growth rate of juvenile English sole (*Parophrys vetulus*) under 15 combinations of temperature and dissolved oxygen levels. We found interactive effects of temperature and hypoxia on fish growth. Fish exposed to moderate hypoxia and normoxia exhibited similar growth responses to increasing temperature; however, a threshold effect was evident under severe hypoxia, which caused a significant reduction in growth. Further, a generalized additive mixed model was applied to simulate fish growth off the Oregon coast during a climate transition from the 2009 El Niño to the 2010–2011 La Niña. Model simulations indicated that habitat quality varied significantly between estuarine (high quality) and coastal (low quality) nurseries. Coastal habitats may remain moderately suitable during El Niño years, while estuarine refuges are more preferred during La Niña years. This study contributes to the assessment of climate change and hypoxic disturbance on demersal fisheries by providing an analytical framework to evaluate synergistic temperature–hypoxia interactions on juveniles in their nursery habitats.

Résumé

L'hypoxie littorale partout sur terre suscite des inquiétudes quant à ses effets sublétaux sur les poissons démersaux juvéniles. Nous examinons les taux de croissance de carlottins anglais (*Parophrys vetulus*) juvéniles exposés à 15 combinaisons de température et de teneurs en oxygène dissous. Nous relevons des effets interactifs de la température et de l'hypoxie sur la croissance des poissons. La croissance de poissons exposés à une hypoxie modérée et à une normoxie réagit de manière similaire à une hausse de température; un effet de seuil est toutefois évident en situation de forte hypoxie, qui entraîne une baisse significative de la croissance. Un modèle additif généralisé mixte est en outre utilisé pour simuler la croissance des poissons au large des côtes de l'Oregon durant la transition climatique de l'épisode El Niño de 2009 à l'épisode La Niña de 2010–2011. Des simulations du modèle indiquent des différences significatives de qualité de l'habitat entre les aires de croissance estuariennes (de bonne qualité) et côtières (de faible qualité). Les habitats côtiers pourraient demeurer modérément convenables durant les années El Niño, alors qu'il y a une préférence accrue pour des refuges estuariens durant les années La Niña. L'étude est utile pour l'évaluation des effets des changements climatiques et des perturbations hypoxiques sur les ressources halieutiques démersales, car elle fournit un cadre analytique pour l'évaluation des effets d'interactions synergistes de la température et de l'hypoxie sur les poissons juvéniles dans leurs habitats de croissance. [Traduit par la Rédaction]

Introduction

Global expansion of coastal hypoxia (dissolved oxygen (DO) < 1.4 mL O₂·L⁻¹) has resulted in deleterious consequences to ecosystem functions and services (Chan et al. 2008; Ekau et al. 2010). Aside from coastal eutrophication, seasonal wind-driven upwelling is responsible for hypoxia off the Oregon coast (Diaz and Rosenberg 1995, 2008). The shoreward transport of upwelled nutrient-rich water enhances primary production along the Oregon shelf (Checkley and Barth 2009); however, upwelled low-DO water coupled with increased respiration at depth from the sinking of organic matter often

exacerbates oxygen deficiency in this region (Grantham et al. 2004). Seasonal development of inner-shelf (<70 m) hypoxia has led to mass mortality and habitat degradation (Grantham et al. 2004; Chan et al. 2008). Hence, increasing attention has been paid to hypoxia disturbance on fisheries off the Oregon coast (Keller et al. 2017; Sobocinski et al. 2018).

Apart from direct hypoxia-induced mortality, low DO can alter the behavior and physiology of fishes, thereby acting as a stressor that negatively affects growth, development, survival, and reproduction (Burnett and Stickle 2001; Wu 2009). Hypoxia also indirectly affects species distribution, trophic

interaction, and community structure (Breitburg 2002; Jung and Houde 2003). When exposed to low DO waters, many fishes can sense, acclimate, and avoid hypoxia (Eby and Crowder 2002; Bell and Eggleston 2005; Craig 2012). Nevertheless, avoidance responses by fishes are commonly dependent on their life stages (Breitburg 1992; Diaz and Rosenberg 1995). For instance, juvenile fishes are often more vulnerable to hypoxia due to reduced feeding and growth rates (Pichavant et al. 2001) and habitat compression (Eby and Crowder 2002). Reduced growth and survival in juveniles have cascading effects on recruitment to adult populations and fisheries yields (Campana 1996).

The present study aims to assess hypoxia disturbance on fish growth by using juvenile English sole (*Parophrys vetulus*), a common flatfish in the northeast Pacific as a model species. Off the Oregon coast, dense aggregations of juvenile English sole are normally found in estuarine and nearshore habitats (Krygier and Percy 1986). Empirical evidence indicates that shoreward transport of upwelled source water and the following increase in primary production and respirations may cause severe hypoxia along the mid-shelf (<70 m deep, Grantham et al. 2004), inner-shelf (~15 m deep, Adams et al. 2013), and estuarine areas (Brown and Power 2011), which overlap with nursery habitats of English sole (Krygier and Percy 1986; Sobocinski et al. 2018). During hypoxia, estuarine and nearshore habitats may exhibit different hydrographic conditions available for juvenile growth of the species. For example, estuarine waters are typically warmer and less hypoxic due to increased mixing throughout the water column, while coastal waters are colder and more hypoxic, due to the onset of stratification. While hypoxia exposure and water temperature together are known to influence the growth rate of English sole (Kreuz et al. 1982; Kruse and Tyler 1983), effects of their interaction are not fully understood. Typically, fish metabolic demand for DO increases with increasing temperature with hypoxia acting to reduce DO supply (McBryan et al. 2013). Water temperature and hypoxia tend to synergistically affect fish life history (Pörtner and Peck 2010), by shifting thermal optimum and limits for fish growth (Fry 1971).

Off the Oregon coast, upwelling strength and hypoxia are linked to large-scale climatic variability (Nam et al. 2011; Jacox et al. 2015). During El Niño events, the strengthened northerly flow from tropical regions interacting with the lessened seasonal southerly flow further reduces upwelling intensity and results in positive temperature anomalies and weakened hypoxia, while the opposite phenomenon is indicative of La Niña events (Nam et al. 2011; Jacox et al. 2015). Previous studies have demonstrated the downscaling effects of climatic forcing on Oregon coastal hydrography and hence biological communities (Peterson et al. 2002; Bi et al. 2008; Liu et al. 2015). One example is the 1997–1999 El Niño/La Niña events that may have interacted with coastal upwelling to structure zooplankton communities (Peterson et al. 2002). The 2009–2011 El Niño to La Niña transition also caused dramatic changes in ichthyoplankton communities (Auth et al. 2015).

Understanding biological responses to climate and environmental change is of great interest to fisheries manage-

ment. In the present study, we conducted a series of laboratory experiments (hereinafter Expt) to investigate the effects of temperature and hypoxia on the growth rate of juvenile English sole (Bancroft 2015). Based on field measures of water temperature and DO, we applied an experimentally derived model to estimate the growth rates of juvenile English sole in estuarine and nearshore habitats off the Oregon coast during the 2009–2011 El Niño to La Niña hydrographical transition. Assessing habitat quality requires the integration of many ecosystem properties, but juvenile growth rate is considered an important indicator of habitat quality (Meng et al. 2000; Amara et al. 2009). Thus, our model simulation will explore habitat quality (indicated by growth rate) of estuarine and nearshore nurseries with regard to juvenile English sole under environmental change. Overall, the findings of this study contribute to assessments of hypoxia disturbance on recruitment and production of English sole by providing an analytical framework to evaluate temperature–hypoxia interactions of demersal fishes in light of climate-driven intensified hypoxia.

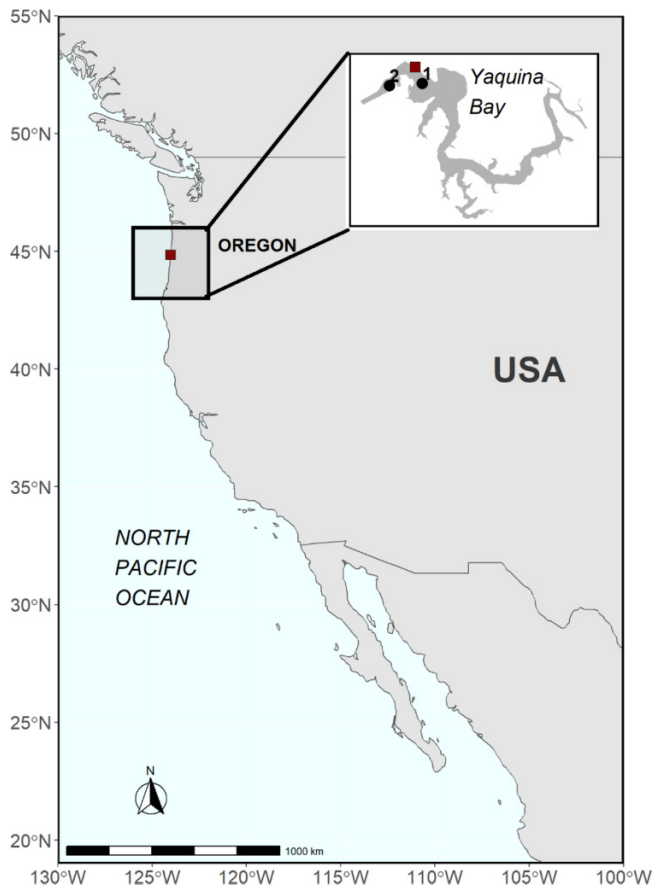
Methods

Juvenile fish collection and maintenance

Sampling was conducted within the Yaquina Bay estuary, Oregon (44.62°N, 124.03°W; Fig. 1), a drowned-river estuary located on the central Oregon coast. The upwelling off Yaquina Bay is mainly driven by the alongshore wind stress (Austin and Barth 2002). The intrusion of upwelled water appears to affect the estuarine hydrodynamics causing seasonal hypoxia in Yaquina Bay (Brown and Power 2011). On the other hand, the bay receives deep-water productivity providing important nursery functions for many juvenile fishes and invertebrates (Schwartzkopf et al. 2020).

Young-of-the-year English sole (<70 mm standard length; hereinafter juveniles) were caught near the mouth of Yaquina Bay (see Fig. 1) using otter trawls (3 mm mesh) for Expt 1 (May–June 2012) and Expt 2 (May–June 2013) and beach seines (5 mm mesh) for Expt 3 (July 2013). In each experiment, all fish captured were first transferred into 1 m × 2 m × 1 m holding tanks (with sand layers) and maintained at 9 °C (±1 °C) with continuously circulated seawater and a 12 h / 12 h light/dark light regime at the Hatfield Marine Science Center in Newport, Oregon. Prior to the treatments, fish were allowed to acclimate to the lab conditions for a minimum of 3 days. After acclimation, and for the remaining 3 days prior to the experimental treatments, fish were treated once per day, with a 1 h, 1:5500 dilution of formalin dip to remove potential parasitic trematodes. All English sole were kept for at least a month under acclimation conditions before being treated with formalin. Meanwhile, a limited ration (once or twice per week) of gel food (squid, herring, krill, amino acid supplements, and vitamins) was given to fish (Ryer et al. 2012). Trial fish were then each tagged with visible implant elastomer (Northwest Marine Technology). All fish were allowed 5 days to recover before being transferred into cleaned experimental tanks.

Fig. 1. Map of two sampling sites (Station 1 and Station 2, black dots) in Yaquina Bay, Oregon, USA. Fish samples collected from Station 1 and Station 2 were used for Expts 1 and 2 and Expt 3, respectively. Buoy locations for the estuarine station near the mouth of Yaquina Bay (Land/Ocean Biogeochemical Observatory (LOBO)) and coastal station north of Yaquina Bay at Lincoln Beach (LB15) are marked in red squares. [Colour online.]



Treatment and measurement of fish growth

The experimental set-up was a standard factorial design with two replicates for each temperature–DO combination (Fig. 2). Expt 1 and Expt 2 included three temperatures (7, 10, and 13 °C), and Expt 3 included a wider range of temperatures (5, 10, and 15 °C). In marine environments, the level of oxygen is typically categorized as hypoxia (1.4 mL O₂·L⁻¹), moderate hypoxia (2 mL O₂·L⁻¹), and normoxia (6 mL O₂·L⁻¹). Consistently, fish were exposed to three DO treatments: hypoxia (1.4 mL O₂·L⁻¹), moderate hypoxia (2 mL O₂·L⁻¹), and normoxia (6 mL O₂·L⁻¹). Laboratory temperatures and DO concentrations encompassed the range experienced by English sole off the Oregon coast (Grantham et al. 2004; Chan et al. 2008). Overall, there were 18 rearing units (3 temperatures × 3 DO concentrations × 2 replicates) in each experiment. Before the start of the experiment, 10 laboratory-held fish were randomly assigned to identical seawater tanks (walls 44 cm in height, a diameter of 56 cm, and a maximum volume of 90 L). Five hundred and forty fish were used in all experiments combined (10 fish × 18 tanks × 3 experiments) at the start of

the experiments. Experimental flow rates were maintained constant at 35 mL·s⁻¹. Water temperature was heated by an in-line heater (HTI-4–220 Electro Titanium Heater) for high-temperature treatments, while low-temperature levels were achieved by mixing cold water (~4 °C) with ambient seawater (~9 °C). The treated water was later fed into a countercurrent mixing column (filled with bio-balls) after which the oxygen depletion was regulated by the addition of nitrogen gas from a 160 L liquid nitrogen Dewar through an air diffuser on the bottom of the tank. The DO concentration in each tank was monitored daily by using a YSI DO meter.

Fish exposed to the treatments were fed ad libitum every 1 or 2 days, and excess food and animal wastes were removed from rearing tanks before the next feeding. Fish that died during experiments were immediately removed from the rearing tank and replaced to maintain a constant fish density. The replacements were excluded from analyses. In Expt 1, we excluded data from an experimental tank at 13 °C and 1.4 mL O₂·L⁻¹ because none of the fish survived. Fish wet weight, standard length, and total length were measured at the beginning of experiments (Day 0), week 2 (Day 9 to Day 18), and week 4 (Day 27 to Day 36). During the measurements, each fish was collected by a dip net and placed into a container filled with treatment water, then the length and weight were measured for the fish out of water.

Statistical analysis

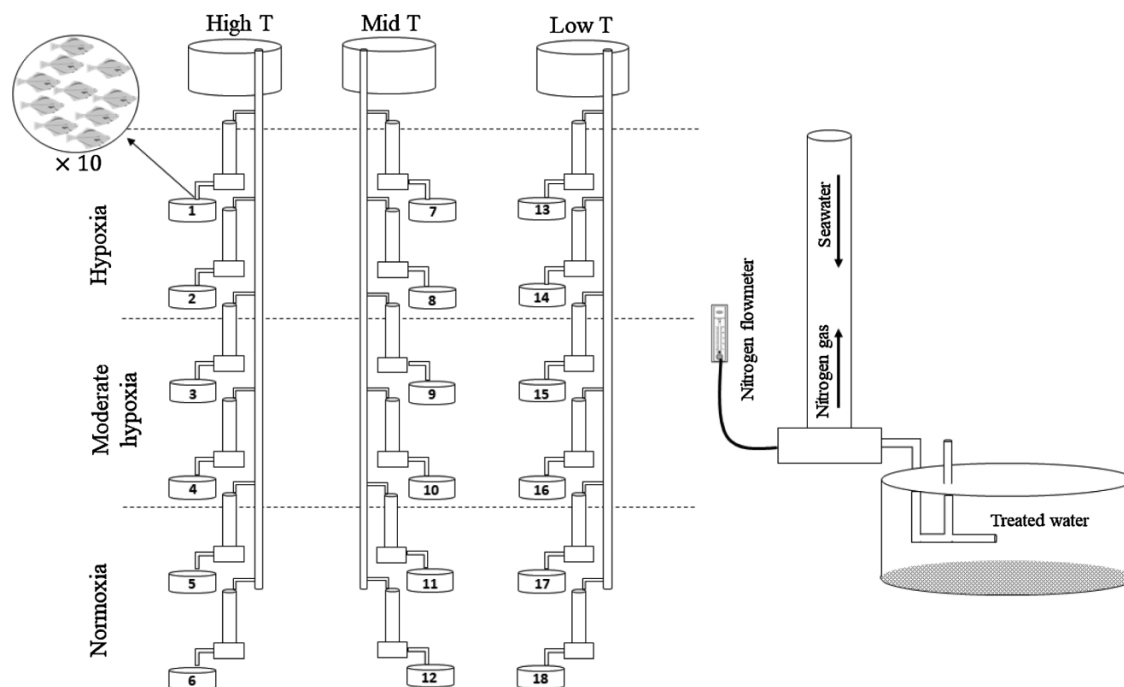
Growth of juvenile English sole was expressed by daily SGR (% mass·day⁻¹) as

$$(1) \quad \text{SGR} = \frac{\log W_2 - \log W_1}{t_2 - t_1} \times 100\%$$

where W_1 and W_2 represent the weight of fish at initial (at t_1) and final (at t_2) time. SGR was calculated for the first 2-week period and the entire 4-week period, respectively.

For growth experiments, all fish were subject to the random effects from the tank independent of treatment effects (Thorarensen et al. 2015). To account for the violation of data independence, we applied a linear mixed-effects model (LMM) in the data analysis including fixed (temperature, DO, and their interaction) and random factors (tank nested within an experiment). Compared to the conventional analysis of variance (ANOVA), LMMs accommodate unbalanced data resulting from mortality. Preliminary results showed similar patterns of fish growth between the 2-week period and 4-week period; thus, only the results over the entire 4-week period were included in data analyses. For the selection of the random-effects term, we compared the Akaike information criterion (AIC) of candidate models fitted with restricted maximum likelihood (REML). A lower AIC indicates a better model fit. Maximum likelihood (ML) is unbiased for fixed effects (Zuur et al. 2009); thus, backward elimination of fixed-effect terms was then conducted by using a chi-square test of the log-likelihood ratio for the full and reduced models fitted with ML. To consider the heterogeneity of residual variation (Breusch–Pagan test, $p > 0.05$), variance structure was expressed by a function of Expt ($\sigma^2 \times \sigma_{\text{Expt}}^2$, a different variance for each experiment). A two-way mixed-effects ANOVA

Fig. 2. Experimental setup (left panel) and countercurrent mixing tower connected with the experimental tank (right panel). A narrow range of water temperature (7, 10, and 13 °C) was tested in Expts 1 and 2, and a wide range of water temperature (5, 10, and 15 °C) was tested in Expt 3. The dissolved oxygen (DO) level was consistent across the three experiments: hypoxia (1.4 mL O₂·L⁻¹), moderate hypoxia (2 mL O₂·L⁻¹), and normoxia (6 mL O₂·L⁻¹). Each experiment consisted of 3 temperatures × 3 DO concentrations × 2 replicates = 18 rearing units.



(if the interaction term was not significant) or a separate one-way mixed-effects ANOVA for each DO concentration (if the interaction term was significant) was undertaken, followed by post hoc multiple comparisons (Shaffer's test) to determine growth differences among all treatments. Given the unbalance experimental design, we considered Type III sums of squares to evaluate multiple ANOVA hypothesis tests. We performed variance components analysis to estimate the relative contribution of fixed and random factors to the variability in the response variable under an unbalanced design. All statistical results were based on a significance level of $\alpha = 0.05$.

Semiparametric model fitting

To assess estuarine and coastal habitat quality (indicated by growth rate), based on field measures of temperature and DO, we implemented model predictions that account for possible nonlinear effects of temperature and interactions between temperature and DO on fish growth. A generalized additive mixed model (GAMM) with fish growth as the dependent variable was developed using the *gamm* function in the "mgcv" package in R (Wood 2020). GAMMs allow a combination of nonlinear forms for predictor variables and random effects. The nonlinear effects are captured by smooth curves with semiparametric functions using the thin-plate regression spline approach. Here, temperature was converted into a continuous covariate to explore a separate nonlinear regression at each DO concentration, given the temperature–DO interaction. When using "factor-by-continuous" interactions, it is often recommended to also include the factor itself as a

parametric term in the GAMM (Wood 2020). Therefore, the full GAMM was fitted including a categorical variable of DO, a nonlinear effect of temperature interacting with DO, and nested random effects:

$$(2) \quad \text{SGR}_{ij} \sim \alpha + \beta \times \text{DO} + f(\text{Temp}) \times \text{DO} + b_{ij} + \varepsilon_{ij}$$

where SGR_{ij} is the expected SGR of fish from the *i*th tank and *j*th experiment given the random effect b_{ij} , α is an overall intercept, β is the coefficient for linear predictor DO (in mL·L⁻¹), $f(\cdot)$ is a semiparametric term in which different functions of the temperature covariate (Temp, in °C) are required for each DO concentration, and ε_{ij} is a normally distributed residual error with mean 0 and variance $\sigma^2 \times \sigma_{\text{Expt}}^2$.

The maximum degrees of freedom (i.e., the basis dimension) for the smooth term is restricted to 2 to avoid overfitting problems. Model selection was evaluated in terms of the AIC of candidate REML models (for random terms only) and ML models (for fixed terms only). The effective degrees of freedom (EDF) for the smoother, indicating its relative nonlinearity, was given by the best model with minimized AIC, and the lower the EDF the more linear the relationship. The final GAMM was used for the simulation of habitat quality.

Regional and local environmental variables

Off the central Oregon coast, equatorward winds associated with strong upwelling normally peak in July (Schwing et al. 2006). Thus, we assembled large-scale climatic variables and local environmental data for the summer months (May–

September). The Oceanic Niño Index (ONI) was selected as an index of global scale El Niño-Southern Oscillation. Data are available at https://origin.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ONI_v5.php. The ONI is calculated by the 3-month running mean of sea surface temperature (SST) anomalies in the Niño 3.4 region (5°N–5°S, 120°W–170°W), based on centered 30-year base period. Positive and negative ONI values represent El Niño and La Niña episodes, respectively. The Pacific Decadal Oscillation (PDO) index was selected to represent regional-scale climatic variability. Data are available at <http://research.jisao.washington.edu/pdo/>. The PDO is defined as the leading principal component of monthly SST anomalies in the North Pacific (Mantua et al. 1997). Positive and negative PDO signals represent warm and cold phases, respectively. The Coastal Upwelling Transport Index (CUTI), referred to as the vertical rate of water transport ($\text{m}^2 \cdot \text{s}^{-1}$), was used as a reliable proxy of upwelling intensity (Jacox et al. 2018). Data are available at <https://mjacox.com/upwelling-indices/>. Daily CUTI values were averaged over the 44°N–45°N region.

Daily water temperature and DO measurements in the summer months were compiled for the Yaquina Bay estuary and its nearby coastal site for 2009–2011. Estuarine data were collected from a buoy station (44.63°N, 124.04°W; Fig. 1), operated by the Land/Ocean Biogeochemical Observatory (LOBO) (data available at <http://yaquina.loboviz.com/loboviz.shtml>). Coastal data were extracted from a mooring station along 15 m isobaths located north of Yaquina Bay at Lincoln Beach, Oregon (LB15, 44.85°N, 124.09°W; Fig. 1), operated by the Partnership for International Studies of the Coastal Ocean (PISCO) (data available at <http://www.piscoweb.org/access-data>).

Cross-correlation analyses were performed in the present study. First, we tested the correlation between estuarine and coastal environmental variables. Second, correlation analysis with lags ranging from 0 to 3 months was conducted to examine the downscaling effect of ONI and PDO on local hydrography. Correlation between daily CUTI and local hydrography was also tested.

GAMM simulations

We used *predict.gam* function in the “mgcv” package in R for the GAMM simulation (Wood 2020). We simulated the SGR of juvenile English sole at a daily time step by using temperature and DO measurements during the summer of 2009–2011. Before the simulation, DO values were aggregated into three categories: hypoxia ($<2 \text{ mL O}_2 \cdot \text{L}^{-1}$), moderate hypoxia ($2\text{--}6 \text{ mL O}_2 \cdot \text{L}^{-1}$), and normoxia ($>6 \text{ mL O}_2 \cdot \text{L}^{-1}$). Specifically, the model simulation was run k times for a month ($k = \text{number of days in a month}$), and each simulation only included environmental data from day_i ($i = 1, 2, 3, \dots, k$). Random effects are of less interest when the prediction of average levels is the goal, so they were excluded from the model prediction. Simulated values from the GAMM fits were aggregated on a monthly basis for comparison. A nonparametric Mann–Whitney U -test was applied for multiple pairwise comparisons of SGR between the two sites over the 2009–2011 period.

Results

Growth

Nearly 90% of the juvenile English sole survived the experimental treatments ($n = 481$) and were used to determine the combined effects of temperature and DO on fish SGR. Growth rates ranged from $0.18\% \pm 0.30\% \text{ mass} \cdot \text{day}^{-1}$ (at $6 \text{ mL O}_2 \cdot \text{L}^{-1}$ and $5 \text{ }^\circ\text{C}$) to $1.23\% \pm 0.58\% \text{ mass} \cdot \text{day}^{-1}$ (at $2 \text{ mL O}_2 \cdot \text{L}^{-1}$ and $15 \text{ }^\circ\text{C}$) (Table 1). Poor growth was observed at lower temperature treatments with SGR reduced by 62%–83% at $5 \text{ }^\circ\text{C}$ compared to $15 \text{ }^\circ\text{C}$ regardless of DO concentration (Table 1). Compared to growth rates at higher DO concentrations (2 and $6 \text{ mL O}_2 \cdot \text{L}^{-1}$), fish exposed to hypoxia exhibited reduction of 55% and 62%–68% in SGR at 10 and $13 \text{ }^\circ\text{C}$, respectively. However, SGR at $15 \text{ }^\circ\text{C}$ remained relatively high, even under hypoxic conditions (Table 1). Interestingly, fish exposed to moderate hypoxia and normoxia exhibited similar SGR responses to increasing temperature (Fig. 3).

Mixed-effects ANOVAs with REML highlighted the random effects of tank nested within experiments (hereinafter referred to as Expt/Tank) based on AIC values (AIC = 777.2; Table 2). A chi-square test and AIC values for mixed-effects ANOVAs with ML indicated the model with fixed effects of temperature, DO, and their interaction was better ($p = 0.016$, AIC = 739.2; Table 2). Statistical analysis indicated SGR of juvenile English sole was significantly affected by water temperature (ANOVA, $F_{[4, 46]} = 18.22$, $p < 0.001$), DO ($F_{[8, 418]} = 8.22$, $p < 0.001$), and their interaction ($F_{[2, 418]} = 2.01$, $p < 0.05$). Variance associated with temperature, DO, and their interaction accounted for 8.3%, 1.7%, and 1.9% of total variance, respectively. Note that 8.1% of total variation was attributed to the random effects of Expt/Tank.

Nonlinear effects in GAMM

A GAMM with the random effects of Expt/Tank was the preferred option based on AIC values (AIC = 820.1; Table 3). In addition, a GAMM with a separate smooth function for water temperature at each level of DO and a linear term for DO was supported as the most parsimonious model with the lowest AIC (AIC = 800.4; Table 3). The EDF for the smoother indicated a nonlinear response with respect to temperature under three DO concentrations (Fig. 4). There was a general positive trend in response curves with increasing temperature for all three DO conditions (Fig. 4). Compared to other DO levels, growth responses to water temperature appeared to be more variable under hypoxic conditions (Fig. 4a).

Climate variability and local hydrography

A significant correlation between water temperature at estuarine (LOBO) and coastal (LB15) stations was detected ($r = 0.834$, $p < 0.001$, Pearson correlation). Water temperature at the estuarine station was higher than that at the coastal station (Fig. 5a). DO concentrations at the estuarine station were also correlated with that at the coastal station, although to a lesser extent ($r = 0.388$, $p < 0.001$). Intermittent hypoxia occurred more frequently at the coastal station than at the estuarine station (Fig. 5b).

Table 1. Summary (mean ± SD) of fish initial standard length (SL, mm), final standard length (SL, mm), initial weight (wt., g), final weight (wt., g), specific growth rate (SGR, % mass·day⁻¹), and mortality over the entire 4-week period.

Treatment	Temp. (°C)	Initial SL (mm)	Final SL (mm)	Initial wt. (g)	Final wt. (g)	SGR (% mass·day ⁻¹)	Mortality (no. of fish)
Hypoxia (1.4 mL O ₂ ·L ⁻¹)	5	52 ± 10	55 ± 10	2.11 ± 0.87	2.39 ± 1.01	0.36 ± 0.23	5
	7	49 ± 8	51 ± 8	1.64 ± 0.82	1.98 ± 0.96	0.56 ± 0.45	3
	10	50 ± 9	52 ± 10	1.79 ± 0.90	2.05 ± 1.09	0.38 ± 0.55	1
	13	52 ± 8	54 ± 7	1.88 ± 0.77	2.09 ± 0.84	0.30 ± 0.71	18
	15	45 ± 7	51 ± 10	1.28 ± 0.62	1.83 ± 1.14	0.95 ± 0.54	3
Moderate hypoxia (2 mL O ₂ ·L ⁻¹)	5	52 ± 8	54 ± 8	1.83 ± 0.70	1.97 ± 0.78	0.21 ± 0.31	5
	7	49 ± 8	51 ± 8	1.63 ± 0.84	1.97 ± 0.93	0.59 ± 0.49	0
	10	49 ± 9	54 ± 11	1.69 ± 0.90	2.29 ± 1.25	0.84 ± 0.59	0
	13	49 ± 9	54 ± 10	1.65 ± 0.76	2.32 ± 1.13	0.93 ± 0.81	3
	15	43 ± 11	51 ± 11	1.31 ± 0.83	1.94 ± 1.15	1.23 ± 0.58	2
Normoxia (6 mL O ₂ ·L ⁻¹)	5	47 ± 8	49 ± 8	1.48 ± 0.63	1.59 ± 0.74	0.18 ± 0.30	1
	7	50 ± 9	52 ± 9	1.69 ± 0.95	2.12 ± 1.20	0.67 ± 0.48	5
	10	51 ± 9	55 ± 9	1.83 ± 0.91	2.43 ± 1.19	0.84 ± 0.62	4
	13	51 ± 9	54 ± 10	1.73 ± 0.95	2.27 ± 1.31	0.78 ± 0.69	7
	15	47 ± 11	54 ± 10	1.43 ± 0.76	2.03 ± 1.06	1.08 ± 0.45	2

Fig. 3. Bar graphs displaying one-way mixed-effects ANOVA results for specific growth rate (SGR) of juvenile English sole at different temperature treatments under: (a) hypoxia (1.4 mL O₂·L⁻¹), (b) moderate hypoxia (2 mL O₂·L⁻¹), and (c) normoxia (6 mL O₂·L⁻¹). The error bar represents the standard error. Asterisks indicates significant difference: *, *p* < 0.05; **, *p* < 0.01; ***, *p* < 0.001.

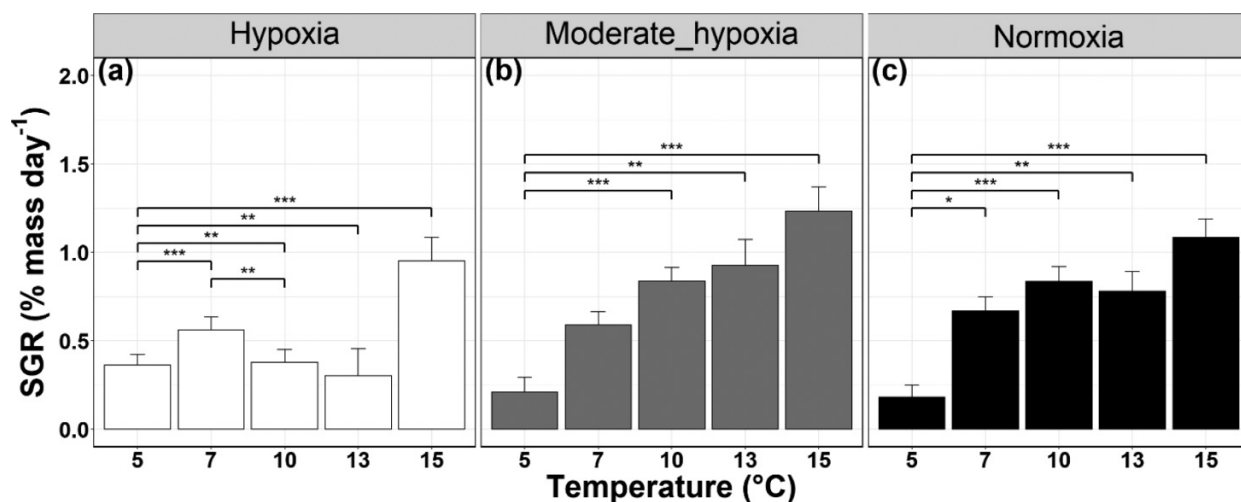


Table 2. Summary of candidate mixed-effects ANOVA models with different fixed and random effects.

Method	Model	Fixed effects	Random effects	Variance function	df	AIC	Chi-square	<i>p</i> -value
REML	1	Temp, DO, Temp × DO	—	$\sigma_{\epsilon}^2 \times \sigma_{\text{Expt}}^2$	18	838.2		
	2	Temp, DO, Temp × DO	Expt	$\sigma_{\epsilon}^2 \times \sigma_{\text{Expt}}^2$	19	777.8		
	3	Temp, DO, Temp × DO	Tank	$\sigma_{\epsilon}^2 \times \sigma_{\text{Expt}}^2$	19	840.1		
	4	Temp, DO, Temp × DO	Expt/Tank	$\sigma_{\epsilon}^2 \times \sigma_{\text{Expt}}^2$	20	777.2		
ML	1	Temp, DO, Temp × DO	Expt/Tank	$\sigma_{\epsilon}^2 \times \sigma_{\text{Expt}}^2$	20	739.2		
	2	Temp, DO	Expt/Tank	$\sigma_{\epsilon}^2 \times \sigma_{\text{Expt}}^2$	12	742.0	18.81	0.016

Note: Random intercept for Expt, random intercept for Tank, and random intercept varying among Expt and Tank within Expt were considered in model selection. σ_{ϵ}^2 defines the variance of residuals. σ_{Expt}^2 defines an adjustment of variance made for the *i*th experiment. Restricted maximum likelihood (REML) was applied to the mixed-effects ANOVA models that only differ in random terms. The model fit was evaluated based on the Akaike information criterion (AIC), and the model with the lowest AIC score (**bold**) is considered the best model. The backward elimination of fixed terms was performed on the mixed-effects ANOVA models fitted with maximum likelihood (ML) by using the log-likelihood ratio test. A significant result (**bold**) indicates the full model is better than the reduced model.

Table 3. Summary of candidate generalized additive mixed models (GAMMs).

Method	Model	Linear term	Smooth term	Random effect	Variance function	AIC
REML	1	DO	s(Temp, by = factor(DO))	Expt	$\sigma_\epsilon^2 \times \sigma_{\text{Expt}}^2$	839.6
	2	DO	s(Temp, by = factor(DO))	Tank	$\sigma_\epsilon^2 \times \sigma_{\text{Expt}}^2$	884.6
	3	DO	s(Temp, by = factor(DO))	Expt/Tank	$\sigma_\epsilon^2 \times \sigma_{\text{Expt}}^2$	820.1
ML	1	DO	s(Temp, by = factor(DO))	Expt/Tank	$\sigma_\epsilon^2 \times \sigma_{\text{Expt}}^2$	800.4
	2	—	s(Temp, by = factor(DO))	Expt/Tank	$\sigma_\epsilon^2 \times \sigma_{\text{Expt}}^2$	802.4

Note: The model fit was evaluated based on the AIC, and the model with the lowest AIC score (**bold**) is considered the best model. Note that the REML method was used for the selection of random effects and the ML method was used for the selection of fixed effects. The term “by” within the smooth function indicates factor-by-continuous interactions.

Fig. 4. Additive effects of water temperature on SGR of juvenile English sole under: (a) hypoxia (1.4 mL O₂·L⁻¹), (b) moderate hypoxia (2 mL O₂·L⁻¹), and (c) normoxia (6 mL O₂·L⁻¹). These relationships were determined from the generalized additive mixed effect (GAMM) model in eq. 2. Gray shade is estimated 95% confidence intervals. Effective degrees of freedom (EDF) are given in parentheses.

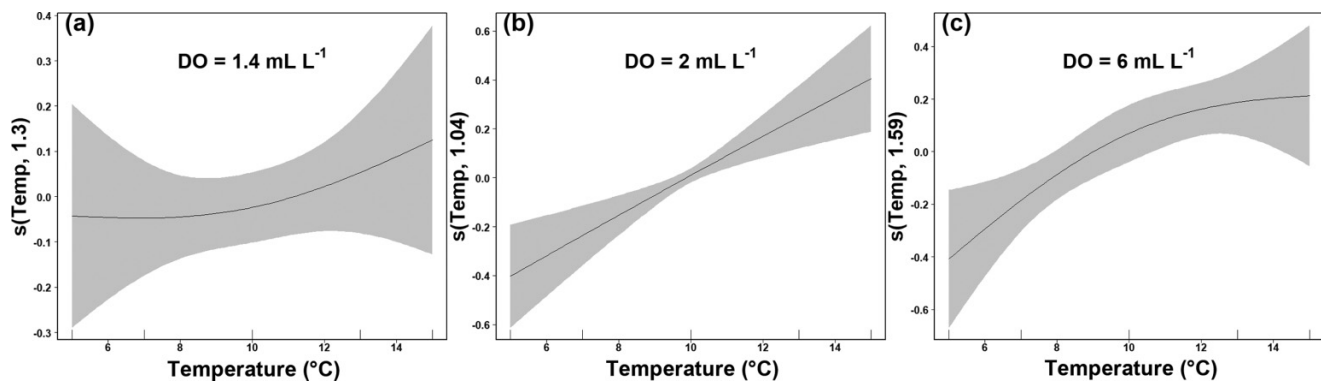
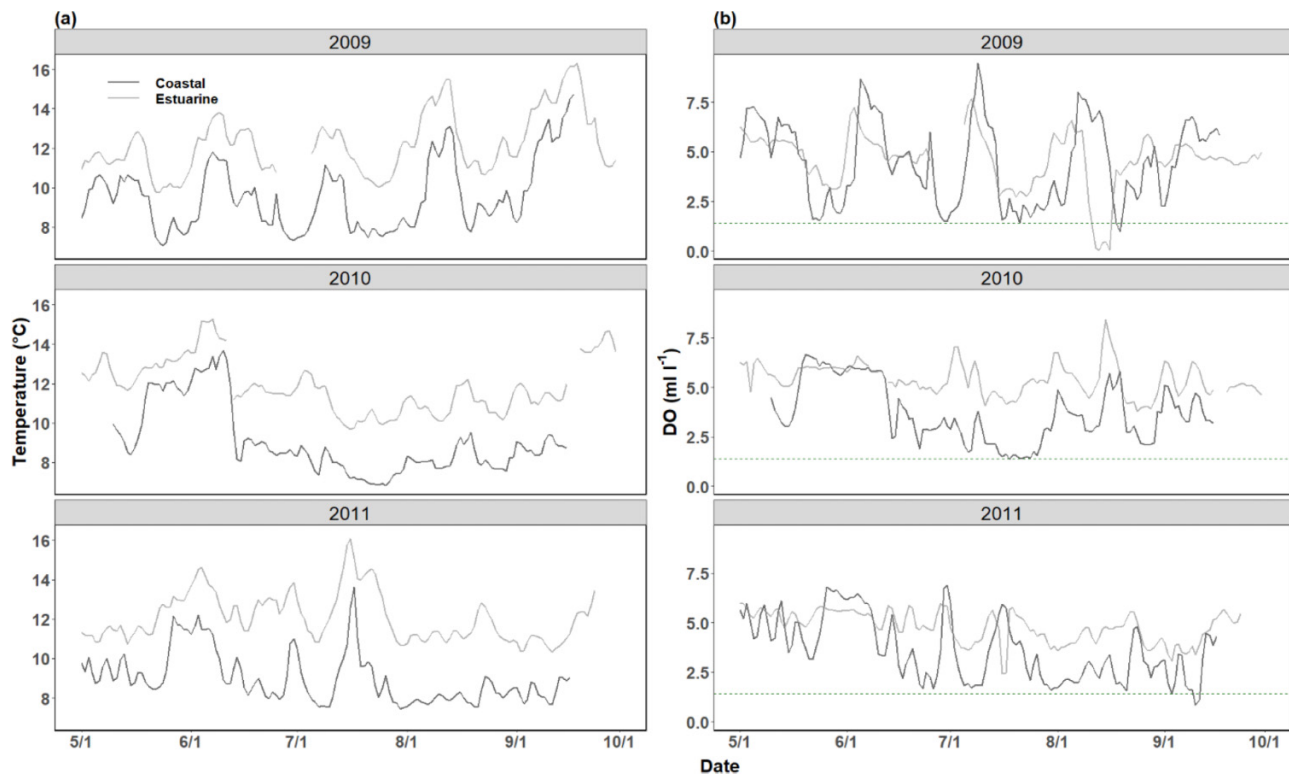


Fig. 5. Daily average values of (a) water temperature and (b) DO measured at coastal (LB15, black) and estuarine stations (LOBO, gray) in the summer months (May–September) from 2009 to 2011. The green dashed line represents the hypoxic level (1.4 mL O₂·L⁻¹). [Colour online.]



The PDO index with no lag was significantly and positively correlated with water temperature at the coastal station ($r = 0.8$, $p < 0.001$, Fig. 6a). A 1-month lag correlation was found between the PDO index and water temperature at the estuarine station ($r = 0.52$, $p < 0.05$; Fig. 6b). Correlation between ONI and water temperature was significant at the coastal station with 1-month lag ($r = 0.59$, $p < 0.05$; Fig. 6c) but not significant at the estuarine station ($r = 0.4$, $p = 0.14$; Fig. 6d). CUTI was significantly and negatively correlated with daily DO concentrations at coastal station ($r = -0.49$, $p < 0.001$; Fig. 6e) and the estuarine station ($r = 0.4$, $p < 0.001$; Fig. 6f).

Growth simulations during 2009–2011

Simulation results showed growth was consistently higher for individuals exposed to estuarine conditions (Mann–Whitney U -test, $p < 0.05$). In coastal habitats, SGR of juvenile English sole was much higher during the 2009 El Niño than during the 2010–2011 La Niña (Fig. 7). SGR in estuarine habitats remained high during the 2010–2011 La Niña (Fig. 7). Overall, monthly mean SGR ranged from 0.72% to 0.93% mass-day⁻¹ in estuarine waters and ranged from 0.48% to 0.81% mass-day⁻¹ in coastal waters. The mean difference in SGR between estuarine and coastal conditions is 0.19% mass-day⁻¹.

Discussion

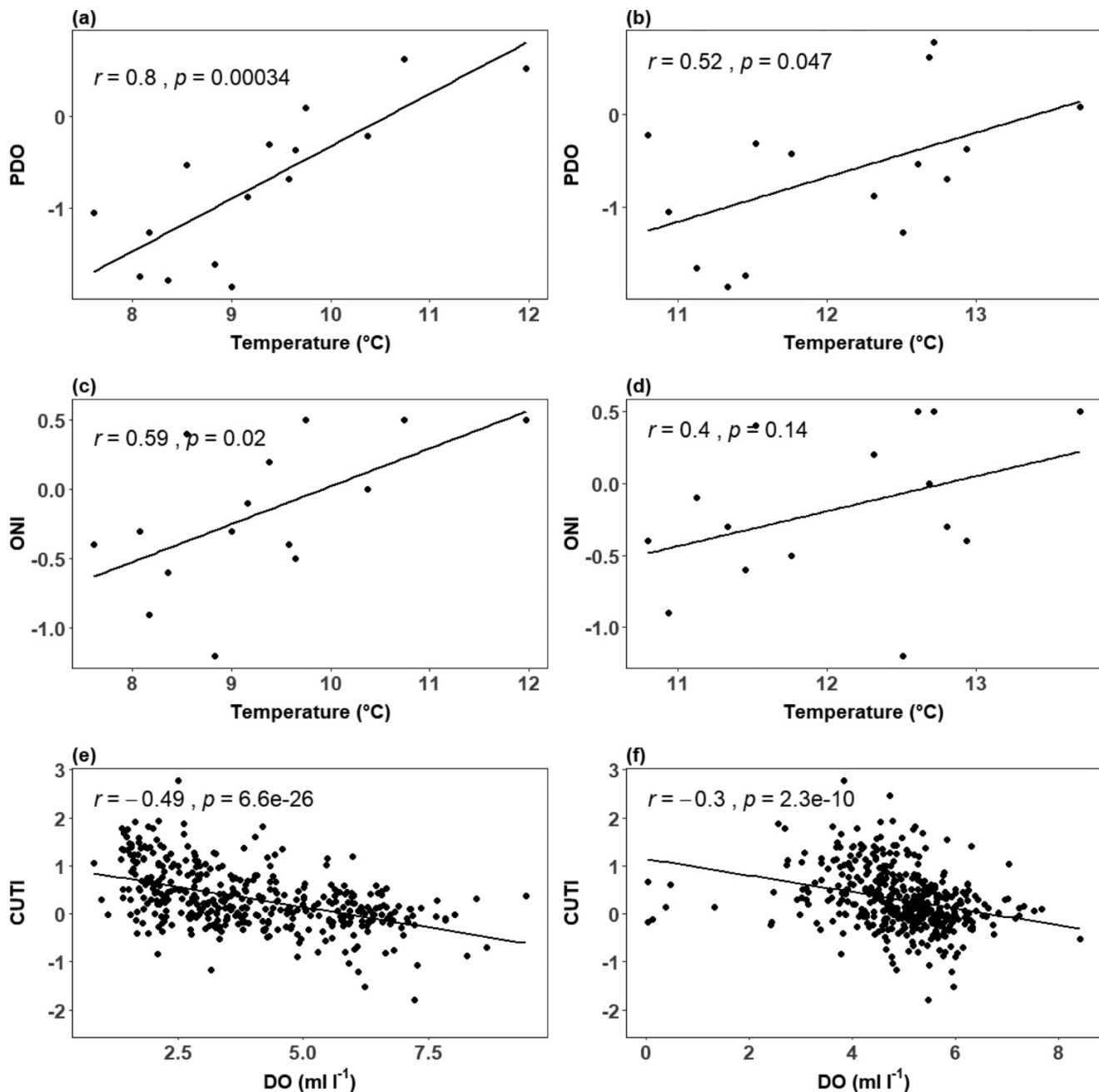
Hypoxia can affect fish through a variety of pathways. Existing literature reveals that eutrophication-driven bottom hypoxia in Chesapeake Bay restricts planktivorous fishes to the surface water, while their zooplankton prey tend to use hypoxic zones as refuges (Ludsin et al. 2009). In this way, demersal fishes with strong hypoxia tolerance may benefit from increased prey availability (Ludsin et al. 2009) and choose to dwell in hypoxic bottom waters as seen in hypoxic regions in the northern Gulf of Mexico (Switzer et al. 2009) and the inner-shelf off Oregon (Sobocinski et al. 2018). Physical processes along the northeast Pacific Ocean in response to climate variability have profound effects on multiple trophic levels from primary production (McGowan et al. 1998) to secondary production (Peterson et al. 2002; Liu and Peterson 2010; Keister et al. 2011) and fisheries yields (Auth et al. 2015). There are many studies on the disruption of fish recruitment by hypoxia in naturally eutrophic systems (e.g., Chesapeake Bay; Breitburg 1992; Ludsin et al. 2009). Off the Oregon coast, recruitment dynamics of fishes during upwelling-driven hypoxia remain understudied and hampered by complex climate-induced physical, chemical, and biological perturbations. Our study provides a gateway connecting experimental studies to modeling research with field observations to better understand how climate-driven hydrological changes affect the growth of demersal fishes off the Oregon coast. The findings provide some valuable information to assess the state of demersal fishes in support of ecosystem-based fisheries management in the region.

Growth responses to hypoxia and temperature

Fish typically exhibit metabolic depression to lower energy demand as a survival strategy when a critical hypoxia threshold is met (Dalla Via et al. 1994). Decreased growth is thus expected due to reduced feed conversion efficiency (Brett 1979). Likewise, our results showed that growth rates of juvenile English sole decreased by over 55% under moderately warm (10 and 13 °C), hypoxic (1.4 mL O₂·L⁻¹) conditions. Potential limitations on growth due to DO deficiency may change fish behavioral strategy. Prior evidence suggests that severe hypoxia may also trigger movements of demersal fishes including English sole away from Oregon coastal habitats (Keller et al. 2017). Sublethal effects of hypoxia (1.4 mL O₂·L⁻¹) on the growth of demersal fishes have been examined empirically for a wide range of species including flatfishes, with low DO consistently linked to reduced growth rates (Bejda et al. 1992; Stierhoff et al. 2006). For example, at 20 °C, winter flounder (*Pseudopleuronectes americanus*) growth was reduced 55% at 1.5 mL O₂·L⁻¹, compared to growth at 4.7 mL O₂·L⁻¹ (Bejda et al. 1992). Different from severe hypoxia curtailing growth, the effect of moderate hypoxia (2 mL O₂·L⁻¹) on fish growth is species-specific. Although many flatfishes show increased vulnerability to moderate hypoxia (Petersen and Pihl 1995; Taylor and Miller 2001), the growth of juvenile English sole was still maintained when DO concentrations dropped from 6 to 2 mL O₂·L⁻¹. This likely indicates a relatively strong hypoxia tolerance of English sole, which may explain in part the occurrence of this species in hypoxic waters off the coast of Oregon during upwelling events (Froehlich et al. 2014; Sobocinski et al. 2018). In general, demersal fishes routinely exposed to naturally occurring hypoxia are considered to have decreased sensitivity to low DO (McNatt and Rice 2004). One example is the growth reduction of juvenile spot (*Leiostomus xanthurus*) and Atlantic menhaden (*Brevoortia tyrannus*) that only occurs under severe hypoxia (1 mL O₂·L⁻¹) (McNatt and Rice 2004). Under hypoxia, the oxygen pressure can be mediated by fish physiological mechanisms associated with acclimation, including reducing oxygen demand for routine metabolism, as well as increasing ventilation rates and hematocrit levels (Taylor and Miller 2001). On the other hand, despite metabolic limitations, demersal fishes may benefit from short-lived hypoxia through predation upon hypoxia-stressed infauna (Pihl et al. 1991), concurrent with relaxed predation from predators (Craig et al. 2010). Therefore, these life history strategies of English sole during seasonal hypoxia mirror a trade-off between physiological tolerance and trophic interactions.

Temperature is characterized as a rate-governing factor for fish metabolism (Brett 1979), whereas DO acts as a limiting factor strongly depressing growth at critical levels (Cuenco et al. 1985). As DO concentration increases, growth rate may be mainly driven by temperature. Our experimental results confirmed that temperature has a profound effect on growth in English sole with SGR positively correlated with water temperature in the two DO treatments above the 1.4 mL O₂·L⁻¹ hypoxia threshold. Typically, increasing temperature promotes increase in feeding activity and metabolic rates, and

Fig. 6. Correlations between (a) coastal (at LB15) water temperature and Pacific Decadal Oscillation (PDO) (no lag), (b) estuarine (at LOBO) water temperature and PDO (1-month lag), (c) coastal water temperature and Oceanic Niño Index (ONI) (no lag), (d) estuarine water temperature and ONI (1-month lag), (e) coastal DO concentrations and Coastal Upwelling Transport Index (CUTI), and (f) estuarine DO concentrations and CUTI.

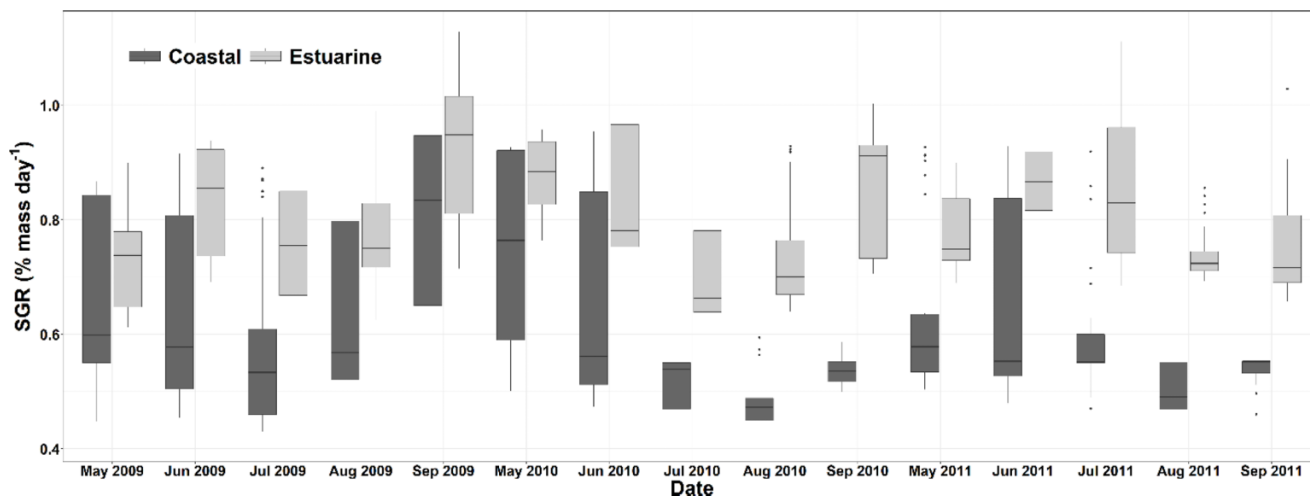


hence growth rates. Similarly, increased growth rates of juvenile English sole were observed at higher water temperatures in a previous study by Ryer et al. (2012), suggesting a positive relationship between growth and temperature. It should be noted that SGR of juvenile English sole in our study were lower than rates reported by Ryer et al. (2012). We speculate the low growth rates are related to density dependence, given the higher fish density (compared to seven fish per tank) and smaller size of the tank (compared to 1 m diameter tank) in our study. Although peak growth rates of juvenile English sole in our study occurred at 15 °C, the thermal optima for

the growth of this species may be higher than our 15 °C temperature treatment given the upper lethal threshold ranging from 21 to 27 °C (Ames et al. 1978). On the other hand, regardless of DO concentrations, at 5 °C the somatic growth of juvenile English sole was substantially suppressed in the present study, which likely indicates the bottom thermal tolerance for this species.

Research has demonstrated that lower temperatures are preferred for fish growth under hypoxic stress (Cuenco et al. 1985). Given the loss of aerobic scope at high temperatures (Pörtner and Peck 2010), high temperature combined with

Fig. 7. Box and whisker plots showing the simulation results from the generalized additive mixed model (GAMM) for SGR of juvenile English sole. The model simulation was performed for coastal (LB15, black) and the estuarine stations (LOBO, gray) using daily temperature and DO measurements in the summer months (May–September) from 2009 to 2011. Daily predictions were aggregated on a monthly basis for comparison. The box denotes the interquartile range with the upper and lower edges representing the 25th and 75th quartiles, respectively. The horizontal line inside the box represents the median. Whiskers represent the range of points within 1.5 times the interquartile range. Data points exceeding 1.5 times the interquartile range are shown with dots.



hypoxia may act synergistically upon fish and results in a narrower thermal breadth and a reduced upper critical temperature (McBryan et al. 2013). Laboratory work on juvenile southern flounder (*Paralichthys lethostigma*) showed that hypoxia at 29 °C caused the greatest reduction in growth and the temperature optimum for growth at normoxia (Del Toro-Silva et al. 2008). In the present study, we noticed that temperature and DO have a profound synergistic effect on fish growth at 10 and 13 °C, but did not find a clear pattern supporting a downshift in growth optimum under hypoxia. Instead, inconsistent temperature effects on hypoxic fish are presumably attributed to individual variations in fish behavior and physiology (Pang et al. 2015). Moreover, different fish cohorts were used in three experiments, and thus cohort-related phenotypic plasticity may also contribute to variable growth responses observed in our study (Sinclair et al. 2002).

We note that data availability from controlled experiments may limit the model utility when the sample size is small. To compensate for this constraint, DO was treated as a conditioning factor nested in the factor–smooth interaction term in the GAMM when producing smooth functions for the temperature covariate. Since the thermal sensitivity of fish growth (thermal breadth, optimum, and limits) varies depending upon oxygen supply (Pörtner and Peck 2010; McBryan et al. 2013), we anticipate that a wide range of temperature levels should enable us to capture the nonlinear signal and provide a better estimation of the parameters in the model.

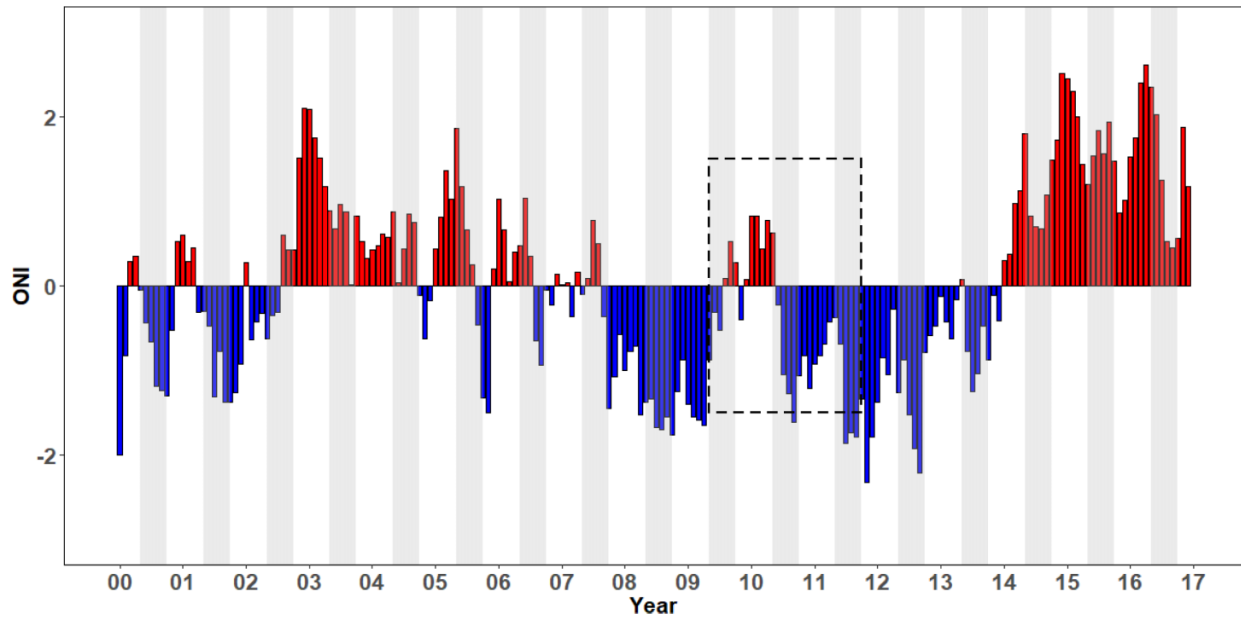
Juvenile habitats under climate variability

Our findings confirm that hydrographic processes off the Oregon coast have a 1-month lagged response to tropical El Niño/La Niña signals through atmospheric teleconnections

(Jacox et al. 2015). Evidence has indicated the propagation of El Niño signals in the northeast Pacific estuaries (Hughes et al. 2015). However, we found little evidence of the downscaling effects of the El Niño/La Niña cycle on Oregon estuaries such as Yaquina Bay. One possible explanation is that La Niña can produce highly variable weather/climate conditions (Hughes et al. 2015), leading to a weakening correlation between La Niña signals and estuarine hydrology. Regional climate indices such as PDO appear indicative of estuarine processes along the northeast Pacific (O’Higgins and Rumrill 2007), which is echoed in the present study as seen a 1-month lagged response of water temperature in Yaquina Bay in relation to the PDO index. We speculate that the hydrography off the Oregon coast is subject to PDO variations and under the remote influence of the large-scale El Niño/La Niña cycle. Negative associations between CUTI and coastal DO concentrations demonstrate that hypoxia off Oregon is likely dominated by onshore transport of upwelling and subsequent respiration of organic matter. This hypothesis is also supported by the strong correlation in environmental variables between estuarine and coastal stations.

The 2009–2011 study period is categorized as a phase transition between the 2009 El Niño and the 2010–2011 La Niña events (Fig. 8). Our simulation suggests that in summer 2009, coastal habitats were comparably suitable for juvenile English sole, while in summer 2010–2011, coastal habitats became unfavorable due to La Niña-driven strong upwelling. In addition, high habitat quality in Yaquina Bay during the summer 2010–2011 implies that the bay may provide a refuge from low temperature and hypoxia for juvenile English sole during La Niña years. The linkage between El Niño events and year class strength has been evidenced in a number of groundfish stocks (Hollowed and Wooster 1992; Hollowed

Fig. 8. Seasonal and inter-annual variations of ONI from 2000 to 2016. The gray area indicates the summer months (May–September). Note that the years within the box (2009–2011) were included in our case study. [Colour online.]



et al. 2001). A previous study also indicates that El Niño warming can mediate hypoxia in northeast Pacific estuaries, making estuarine conditions favorable for juvenile English sole (Hughes et al. 2015). Brodeur et al. (2008) reported that English sole dominates the larval fish assemblage off the Oregon coast during warm PDO years. Coastal waters off Oregon are typically colder and more hypoxic during La Niña years than during El Niño years due to increased upwelling (Jacox et al. 2015). We therefore infer that during El Niño years with weak upwelling, coastal habitats may remain moderately suitable, while during La Niña years with strong upwelling, estuarine refuges are preferred. It must be noted that cascading effects of climate change on biotic conditions can also influence habitat quality for juvenile fishes (Liu et al. 2015). For example, Keller et al. (2013) found that the feeding conditions for English sole may be greatly improved during La Niña years. El Niño-driven weakened upwelling may reduce food availability in coastal waters, which offsets the beneficial effects of El Niño on physical conditions for juvenile fishes. This explains in part why English sole recruitment was not strongly affected by El Niño events in 1982–1983, 1987–1988, and 1997–1998 (Rooper 2002). Thus, further study is needed to confirm the relationship between climate forcing and habitat quality for juvenile English sole in Oregon coastal waters.

Estuarine and coastal habitats are of importance to juvenile English sole. Physiologically, warm and less hypoxic waters (i.e., estuarine waters) enhance fish growth, whereas cold and more hypoxic waters (i.e., coastal waters), in turn, help fish undergo oxygen deprivation by lowering oxygen demand. The life-history strategy of utilizing these two habitats enables juvenile English sole to prosper in one habitat when the other becomes less favorable. Evidence suggests that density dependence may modulate fish growth translating to similar growth conditions between estuarine and coastal habi-

tats (Rosenberg 1982). Even within Yaquina Bay, growth can be highly variable between upriver and downriver locations due to varying temperature and food conditions (Stowell et al. 2019). Hence, understanding the role of estuarine and coastal habitats that play in juvenile recruitment of English sole requires a holistic consideration of biotic and abiotic environments.

Climate-driven intensified hypoxia has threatened coastal ecosystems over recent decades (Howard et al. 2020). Being less mobile, demersal fishes are particularly vulnerable to near-bottom hypoxia and other changes in habitat conditions. Our study presents an analytical framework based on a series of controlled experiments to quantify the combined effects of temperature and hypoxia on the growth of juvenile English sole. Our general findings may be applicable to other demersal fishes with similar life-history traits in response to these two climate-related stressors. By applying an experimentally derived model to different climate scenarios, our results shed light on the assessment of habitat quality for demersal fishes associated with the hypoxic zone off the Oregon coast.

Conclusions

We used a series of laboratory experiments to examine the growth rate of juvenile English sole in response to the temperature–hypoxia interaction. We applied an experimentally derived model to simulate summertime habitat quality (indicated by growth rate) for juvenile English sole under climate variability. The conclusions of this study are as follows: (1) English sole are tolerant to moderate hypoxia ($2 \text{ mL O}_2 \cdot \text{L}^{-1}$); (2) water temperature has profound effects on fish growth; (3) a threshold effect on fish growth occurs under severe hypoxia ($1.4 \text{ mL O}_2 \cdot \text{L}^{-1}$); (4) climate variability

has downscaling effects on hydrography off the Oregon coast; (5) estuarine and coastal waters may together provide suitable juvenile habitats during El Niño years, while estuarine refuges may be more preferred during La Niña years.

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Data availability

Data are available upon reasonable request.

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Hui Liu served as an Associate Editor at the time of manuscript review and acceptance; peer review and editorial decisions regarding this manuscript were handled by Sean Anderson.

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Competing interests

The authors declare no conflict of interest.

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