1 **Interplay of temperature and hypoxia in habitat quality for a juvenile demersal fish in a**

2 **coastal upwelling system**

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23 Abstract: Coastal hypoxia around the world has raised concerns about its sub-lethal effects on

24 juvenile demersal fishes. We examined the growth rate of juvenile English sole *Parophrys vetulus*

25 under 15 combinations of temperature and dissolved oxygen levels. We found interactive effects

26 of temperature and hypoxia on fish growth. Fish exposed to moderate hypoxia and normoxia

27 exhibited similar growth responses to increasing temperature; however, a threshold effect was

28 evident under severe hypoxia, which caused a significant reduction in growth. Further, a

29 generalized additive mixed model was applied to simulate fish growth off the Oregon coast during

30 a climate transition from the 2009 El Niño to the 2010–2011 La Niña. Model simulations indicated

31 that habitat quality varied significantly between estuarine (high quality) and coastal (low quality)

32 nurseries. Coastal habitats may remain moderately suitable during El Niño years, while estuarine

33 refuges are more preferred during La Niña years. This study contributes to the assessment of

34 climate change and hypoxic disturbance on demersal fisheries by providing an analytical

35 framework to evaluate synergistic temperature-hypoxia interactions on juveniles in their nursery

36 habitats.

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Introduction

44 **Introduction**

45   Global expansion of coastal hypoxia (dissolved oxygen (DO) < 1.4 ml O_2 l^{-1}) has resulted in

46 deleterious consequences to ecosystem functions and services (Chan et al. 2008; Ekau et al. 2010).

47 Aside from coastal eutrophication, seasonal wind-driven upwelling is responsible for hypoxia off

48 the Oregon coast (Diaz and Rosenberg 1995, 2008). The shoreward transport of upwelled nutrient-

49 rich water enhances primary production along the Oregon shelf (Checkley and Barth 2009);

50 however, upwelled low-DO water coupled with increased respiration at depth from the sinking of

51 organic matter often exacerbates oxygen deficiency in this region (Grantham et al. 2004). Seasonal

52 development of inner-shelf (<70 m) hypoxia has led to mass mortality and habitat degradation

53 (Grantham et al. 2004; Chan et al. 2008). Hence, increasing attention has been paid to hypoxia

54 disturbance on fisheries off the Oregon coast (Keller et al. 2017; Sobocinski et al. 2018).

55   Apart from direct hypoxia-induced mortality, low DO can alter the behavior and physiology of

56 fishes, thereby acting as a stressor that negatively affects growth, development, survival, and

57 reproduction (Burnett and Stickle 2001; Wu 2009). Hypoxia also indirectly affects species

58 distribution, trophic interaction, and community structure (Breitburg 2002; Jung and Houde 2003).

59 When exposed to low DO waters, many fishes can sense, acclimate, and avoid hypoxia (Eby and

60 Crowder 2002; Bell and Eggleston 2005; Craig 2012). Nevertheless, avoidance responses by fishes

61 are commonly dependent on their life stages (Breitburg 1992; Diaz and Rosenberg 1995). For

62 instance, juvenile fishes are often more vulnerable to hypoxia due to reduced feeding and growth

63 rates (Pichavant et al. 2001) and habitat compression (Eby and Crowder 2002). Reduced growth

64 and survival in juveniles have cascading effects on recruitment to adult populations and fisheries

65 yields (Campana 1996).

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66   The present study aims to assess hypoxia disturbance on fish growth by using juvenile English

67   sole *Parophrys vetulus*, a common flatfish in the northeast Pacific as a model species. Off the

68   Oregon coast, dense aggregations of juvenile English sole are normally found in estuarine and

69   nearshore habitats (Krygier and Pearcy 1986). Empirical evidence indicates that shoreward

70   transport of upwelled source water and the following increase in primary production and

71   respirations may cause severe hypoxia along the mid-shelf (<70 m deep, Grantham et al. 2004),

72   inner-shelf (~15 m deep, Adams et al. 2013), and estuarine areas (Brown and Power 2011), which

73   overlap with nursery habitats of English sole (Krygier and Pearcy 1986; Sobocinski et al. 2018).

74   During hypoxia, estuarine and nearshore habitats may exhibit different hydrographic conditions

75   available for juvenile growth of the species. For example, estuarine waters are typically warmer

76   and less hypoxic due to increased mixing throughout the water column, while coastal waters are

77   colder and more hypoxic, due to the onset of stratification. While hypoxia exposure and water

78   temperature together are known to influence the growth rate of English sole (Kreuz et al. 1982;

79   Kruse and Tyler 1983), effects of their interaction are not fully understood. Typically, fish

80   metabolic demand for DO increases with increasing temperature with hypoxia acting to reduce

81   DO supply (McBryan et al. 2013). Water temperature and hypoxia tend to synergistically affect

82   fish life history (Pörtner and Peck 2010), by shifting thermal optimum and limits for fish growth

83   (Fry 1971).

84   Off the Oregon coast, upwelling strength and hypoxia are linked to large-scale climatic

85   variability (Nam et al. 2011; Jacox et al. 2015). During El Niño events, the strengthened northerly

86   flow from tropical regions interacting with the lessened seasonal southerly flow further reduces

87   upwelling intensity and results positive temperature anomalies and weakened hypoxia, while the

88   opposite phenomenon is indicative of La Niña events (Nam et al. 2011; Jacox et al. 2015). Previous

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89 studies have demonstrated the downscaling effects of climatic forcing on Oregon coastal

90 hydrography and hence biological communities (Peterson et al. 2002; Bi et al. 2007; Liu et al.

91 2015). One example is the 1997-1999 El Niño/La Niña events that may have interacted with coastal

92 upwelling to structure zooplankton communities (Peterson et al. 2002). The 2009-2011 El Niño to

93 La Niña transition also caused dramatic changes in ichthyoplankton communities (Auth et al.

94 2015).

95 Understanding biological responses to climate and environmental change is of great interest to

96 fisheries management. In the present study, we conducted a series of laboratory experiments

97 (hereafter Expt) to investigate the effects of temperature and hypoxia on the growth rate of juvenile

98 English sole (Bancroft 2015). Based on field measures of water temperature and DO, we applied

99 an experimentally derived model to estimate the growth rates of juvenile English sole in estuarine

100 and nearshore habitats off the Oregon coast during the 2009–2011 El Niño to La Niña

101 hydrographical transition. Assessing habitat quality requires the integration of many ecosystem

102 properties, but juvenile growth rate is considered an important indicator of habitat quality (Meng

103 et al. 2000; Amara et al. 2009). Thus, our model simulation will explore habitat quality (indicated

104 by growth rate) of estuarine and nearshore nurseries with regard to juvenile English sole under

105 environmental change. Overall, the findings of this study contribute to assessments of hypoxia

106 disturbance on recruitment and production of English sole by providing an analytical framework

107 to evaluate temperature-hypoxia interactions of demersal fishes in light of climate-driven

108 intensified hypoxia.

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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; hereafter 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 1×2×1 m holding tanks (with sand layers) and maintained at 9°C (± 1°C) with continuously circulated seawater and a 12/12 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 one-hour 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.

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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°C, 10°C, and 13°C), and Expt 3 included a wider range of temperatures (5°C, 10°C, and 15°C). In marine environments, the level of oxygen is typically categorized as hypoxia (1.4 ml O_2 l^{-1}), moderate hypoxia (2 ml O_2 l^{-1}), and normoxia (6 ml O_2 l^{-1}). Consistently, fish were exposed to three DO treatments: hypoxia (1.4 ml O_2 l^{-1}), moderate hypoxia (2 ml O_2 l^{-1}), and normoxia (6 ml O_2 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 Elecro Titanium Heater) for the 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 counter-current 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 dissolved oxygen meter.

Fish exposed to the treatments were fed ad libitum every one or two 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

154   fish density. The replacements were excluded from analyses. In Expt 1, we excluded data from an

155   experimental tank at 13ºC and 1.4 ml O_2 l^{-1} because none of the fish survived. Fish wet weight,

156   standard length, and total length were measured at the beginning of experiments (Day 0), week 2

157   (Day 9 to Day 18), and week 4 (Day 27 to Day 36). During the measurements, each fish was

158   collected by a dip net and placed into a container filled with treatment water, then the length and

159   weight were measured for the fish out of water.

160   **Statistical analysis**

161   Growth of juvenile English sole was expressed by daily specific growth rate (SGR, % mass day

162    $^{-1}$) as:

163    $SGR = \frac{\log W_2 - \log W_1}{t_2 - t_1} \times 100\%$ *Eq 1*

164   where W_1 and W_2 represent the weight of fish at initial (at t_1) and final (at t_2) time. SGR was

165   calculated for the first 2-week period and the entire 4-week period, respectively.

166   For growth experiments, all fish were subject to the random effects from the tank independent

167   of treatment effects (Thorarensen et al. 2015). To account for the violation of data independence,

168   we applied a linear mixed-effects model (LMM) in the data analysis including fixed (temperature,

169   DO, and their interaction) and random factors (tank nested within an experiment). Compared to

170   the conventional analysis of variance (ANOVA), LMMs accommodate unbalanced data resulting

171   from mortality. Preliminary results showed similar patterns of fish growth between the 2-week

172   period and 4-week period, thus only the results over the entire 4-week period were included in data

173   analyses. For the selection of the random-effects term, we compared the Akaike Information

174   Criterion (AIC) of candidate models fitted with restricted maximum likelihood (REML). A lower

175   AIC indicates a better model fit. Maximum likelihood (ML) is unbiased for fixed effects (Zuur et

176   al. 2009); thus, backward elimination of fixed-effect terms was then conducted by using a Chi-

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177   square test of the log-likelihood ratio for the full and reduced models fitted with ML. To consider

178   the heterogeneity of residual variation (Breusch-Pagan test, $p > 0.05$), variance structure was

179   expressed by a function of Expt ($\sigma^2 \times \sigma_{Expt}^2$, a different variance for each experiment). A two-

180   way mixed-effects ANOVA (if the interaction term was not significant) or a separate one-way

181   mixed-effects ANOVA for each DO concentration (if the interaction term was significant) was

182   undertaken, followed by *post hoc* multiple comparisons (Shaffer's test) to determine growth

183   differences among all treatments. Given the unbalance experimental design, we considered Type

184   III sums of squares to evaluate multiple ANOVA hypothesis tests. We performed variance

185   components analysis to estimate the relative contribution of fixed and random factors to the

186   variability in the response variable under an unbalanced design. All statistical results were based

187   on a significance level of $\alpha = 0.05$.

188   **Semi-parametric model fitting**

189   To assess estuarine and coastal habitat quality (indicated by growth rate), based on field

190   measures of temperature and DO, we implemented model predictions that account for possible

191   nonlinear effects of temperature and interactions between temperature and DO on fish growth. A

192   generalized additive mixed model (GAMM) with fish growth as the dependent variable was

193   developed using the *gamm* function in the "mgcv" package in R (Wood 2020). GAMMs allow a

194   combination of nonlinear forms for predictor variables and random effects. The nonlinear effects

195   are captured by smooth curves with semiparametric functions using the thin-plate regression spline

196   approach. Here, temperature was converted into a continuous covariate to explore a separate

197   nonlinear regression at each DO concentration, given the temperature-DO interaction. When using

198   "factor-by-continuous" interactions, it is often recommended to also include the factor itself as a

199   parametric term in the GAMM (Wood 2020). Therefore, the full GAMM was fitted including a

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200   categorical variable of DO, a nonlinear effect of temperature interacting with DO, and nested

201   random effects:

202    $SGR_{ij} \sim \alpha + \beta \times DO + f(Temp) \times DO + b_{ij} + \varepsilon_{ij}$ *Eq 2*

203   where SGR_{ij} is the expected SGR of fish from the *i*th tank and *j*th experiment given the random

204   effect b_{ij}, α is an overall intercept, β is the coefficient for linear predictor *DO* (in ml l^{-1}), $f(.)$ is

205   a semi-parametric term in which different functions of the temperature covariate (*Temp*, in °C) are

206   required for each DO concentration, and ε_{ij} is a normally distributed residual error with mean 0

207   and variance $\sigma^2 \times \sigma_{Expt}^2$.

208   The maximum degrees of freedom (i.e., the basis dimension) for the smooth term is restricted

209   to 2 to avoid over-fitting problems. Model selection was evaluated in terms of the AIC of candidate

210   REML models (for random terms only) and ML models (for fixed terms only). The effective

211   degrees of freedom (EDF) for the smoother, indicating its relative nonlinearity, was given by the

212   best model with minimized AIC, and the lower the EDF the more linear the relationship. The final

213   GAMM was used for the simulation of habitat quality.

214   **Regional and local environmental variables**

215   Off the central Oregon coast, equatorward winds associated with strong upwelling normally

216   peak in July (Schwing et al. 2006). Thus, we assembled large-scale climatic variables and local

217   environmental data for the summer months (May–September). The Oceanic Niño Index (ONI) was

218   selected as an index of global scale El Niño-Southern Oscillation. Data are available at

219   https://origin.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ONI_v5.php. The ONI

220   is calculated by the 3-month running mean of sea surface temperature (SST) anomalies in the Niño

221   3.4 region (5°N–5°S, 120°W–170°W), based on centered 30-year base period. Positive and

222   negative ONI values represent El Niño and La Niña episodes, respectively. The Pacific Decadal

223   Oscillation (PDO) index was selected to represent regional-scale climatic variability. Data are

224   available at http://research.jisao.washington.edu/pdo/. The PDO is defined as the leading principal

225   component of monthly SST anomalies in the North Pacific (Mantua et al. 1997). Positive and

226   negative PDO signals represent warm and cold phases, respectively. The Coastal Upwelling

227   Transport Index (CUTI), referred to as the vertical rate of water transport ($m^2\ s^{-1}$), was used as a

228   reliable proxy of upwelling intensity (Jacox et al. 2018). Data are available at

229   https://mjacox.com/upwelling-indices/. Daily CUTI values were averaged over the 44º–45ºN

230   region.

231   Daily water temperature and DO measurements in the summer months were compiled for the

232   Yaquina Bay estuary and its nearby coastal site for 2009–2011. Estuarine data were collected from

233   a buoy station (44.63°N, 124.04°W, Fig. 1), operated by the Land/Ocean Biogeochemical

234   Observatory (LOBO) (data available at http://yaquina.loboviz.com/loboviz.shtml). Coastal data

235   were extracted from a mooring station along 15-m isobaths located north of Yaquina Bay at

236   Lincoln Beach, Oregon (LB15, 44.85°N, 124.09°W, Fig. 1), operated by the Partnership for

237   International Studies of the Coastal Ocean (PISCO) (data available at

238   http://www.piscoweb.org/access-data).

239   Cross-correlation analyses were performed in the present study. First, we tested the correlation

240   between estuarine and coastal environmental variables. Second, correlation analysis with lags

241   ranging from 0 to 3 months was conducted to examine the downscaling effect of ONI, and PDO

242   on local hydrography. Correlation between daily CUTI and local hydrography was also tested.

243   **GAMM simulations**

244   We used *predict.gam* function in the "mgcv" package in R for the GAMM simulation (Wood

245   2020). We simulated the specific growth rate (SGR) of juvenile English sole at a daily time step

246   by using temperature and DO measurements during the summer of 2009–2011. Before the

247   simulation, DO values were aggregated into three categories: hypoxia (< 2 ml O_2 l^{-1}), moderate

248   hypoxia (2–6 ml O_2 l^{-1}), and normoxia (> 6 ml O_2 l^{-1}). Specifically, the model simulation was run

249   k times for a month (k = number of days in a month), and each simulation only included

250   environmental data from day_i (i = 1, 2, 3, …, k). Random effects are of less interest when the

251   prediction of average levels is the goal, so they were excluded from the model prediction.

252   Simulated values from the GAMM fits were aggregated on a monthly basis for comparison. A

253   nonparametric Mann-Whitney U-test was applied for multiple pairwise comparisons of SGR

254   between the two sites over the 2009–2011 period.

255   **Results**

256   **Growth**

257   Nearly 90% of the juvenile English sole survived the experimental treatments (n = 481) and

258   were used to determine the combined effects of temperature and DO on fish specific growth rate

259   (SGR). Growth rates ranged from 0.18 ± 0.30 % mass day^{-1} (at 6 ml O_2 l^{-1} and 5ºC) to 1.23 ± 0.58 %

260   mass day^{-1} (at 2 ml O_2 l^{-1} and 15ºC) (Table 1). Poor growth was observed at lower temperature

261   treatments with SGR reduced by 62%–83% at 5ºC compared to 15ºC regardless of DO

262   concentration (Table 1). Compared to growth rates at higher DO concentrations (2 and 6 ml O_2 l^{-}

263   ^{1}), fish exposed to hypoxia exhibited reduction of 55% and 62–68% in SGR at 10ºC and 13ºC,

264   respectively. However, SGR at 15ºC remained relatively high, even under hypoxic conditions

265   (Table 1). Interestingly, fish exposed to moderate hypoxia and normoxia exhibited similar SGR

266   responses to increasing temperature (Fig. 3).

267   Mixed-effects ANOVAs with REML highlighted the random effects of tank nested within

268   experiments (hereinafter referred to as Expt/Tank) based on AIC values (AIC = 777.2, Table 2).

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269 A Chi-square test and AIC values for mixed-effects ANOVAs with ML indicated the model with

270 fixed effects of temperature, DO, and their interaction was better ($p = 0.016$, AIC = 739.2, Table

271 2). Statistical analysis indicated SGR of juvenile English sole was significantly affected by water

272 temperature (ANOVA, $F_{[4, 46]} = 18.22$, $p < 0.001$), DO ($F_{[8, 418]} = 8.22$, $p < 0.001$), and their

273 interaction ($F_{[2, 418]} = 2.01$, $p < 0.05$). Variance associated with temperature, DO, and their

274 interaction accounted for 8.3%, 1.7%, and 1.9% of total variance, respectively. Note that 8.1% of

275 total variation was attributed to the random effects of Expt/Tank.

276 **Nonlinear effects in GAMM**

277 A GAMM with the random effects of Expt/Tank was the preferred option based on AIC values

278 (AIC = 820.1, Table 3). In addition, a GAMM with a separate smooth function for water

279 temperature at each level of DO and a linear term for DO was supported as the most parsimonious

280 model with the lowest AIC (AIC = 800.4, Table 3). The EDF for the smoother indicated a nonlinear

281 response with respect to temperature under three DO concentrations (Fig. 4). There was a general

282 positive trend in response curves with increasing temperature for all three DO conditions (Fig. 4).

283 Compared to other DO levels, growth responses to water temperature appeared to be more variable

284 under hypoxic conditions (Fig. 4a).

285 **Climate variability and local hydrography**

286 A significant correlation between water temperature at estuarine (LOBO) and coastal (LB15)

287 stations was detected ($r = 0.834$, $p < 0.001$, Pearson correlation). Water temperature at the estuarine

288 station was higher than that at the coastal station (Fig. 5a). DO concentrations at the estuarine

289 station were also correlated with that at the coastal station, although to a lesser extent ($r = 0.388$,

290 $p < 0.001$). Intermittent hypoxia occurred more frequently at the coastal station than at the estuarine

291 station (Fig. 5b).

292   The PDO index with no lag was significantly and positively correlated with water temperature

293   at the coastal station (r = 0.8, $p < 0.001$, Fig. 6a). A one-month lag correlation was found between

294   the PDO index and water temperature at the estuarine station (r = 0.52, $p < 0.05$, Fig. 6b).

295   Correlation between ONI and water temperature was significant at the coastal station with one-

296   month lag (r = 0.59, $p < 0.05$, Fig. 6c) but not significant at the estuarine station (r = 0.4, $p = 0.14$,

297   Fig. 6d). CUTI was significantly and negatively correlated with daily DO concentrations at coastal

298   station (r = -0.49, $p < 0.001$, Fig. 6e) and the estuarine station (r = 0.4, $p < 0.001$, Fig. 6f).

299   **Growth simulations during 2009-2011**

300   Simulation results showed growth was consistently higher for individuals exposed to estuarine

301   conditions (Mann-Whitney U-test, $p < 0.05$). In coastal habitats, SGR of juvenile English sole was

302   much higher during the 2009 El Niño than during the 2010–2011 La Niña (Fig. 7). SGR in

303   estuarine habitats remained high during the 2010–2011 La Niña (Fig. 7). Overall, monthly mean

304   SGR ranged from 0.72 to 0.93% mass day $^{-1}$ in estuarine waters and ranged from 0.48 to 0.81%

305   mass day $^{-1}$ in coastal waters. The mean difference in SGR between estuarine and coastal conditions

306   is 0.19% mass day $^{-1}$.

307   **Discussion**

308   Hypoxia can affect fish through a variety of pathways. Existing literature reveals that

309   eutrophication-driven bottom hypoxia in Chesapeake Bay restricts planktivorous fishes to the

310   surface water, while their zooplankton prey tend to use hypoxic zones as refuges (Ludsin et al.

311   2009). In this way, demersal fishes with strong hypoxia tolerance may benefit from increased prey

312   availability (Ludsin et al. 2009) and choose to dwell in hypoxic bottom waters as seen in hypoxic

313   regions in the northern Gulf of Mexico (Switzer et al. 2009) and the inner-shelf off Oregon

314   (Sobocinski et al. 2018). Physical processes along the northeast Pacific Ocean in response to

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315   climate variability have profound effects on multiple trophic levels from primary production

316   (McGowan et al., 1998), to secondary production (Peterson et al. 2002; Keister et al. 2011; Liu

317   and Peterson 2010), and fisheries yields (Auth et al. 2015). There are many studies on the

318   disruption of fish recruitment by hypoxia in naturally eutrophic systems (e.g. Chesapeake Bay,

319   Breitburg 1992; Ludsin et al. 2009). Off the Oregon coast, recruitment dynamics of fishes during

320   upwelling-driven hypoxia remain understudied and hampered by complex climate-induced

321   physical, chemical, and biological perturbations. Our study provides a gateway connecting

322   experimental studies to modeling research with field observations, to better understand how

323   climate-driven hydrological changes affect the growth of demersal fishes off the Oregon coast.

324   The findings provide some valuable information to assess the state of demersal fishes in support

325   of ecosystem-based fisheries management in the region.

326   **Growth responses to hypoxia and temperature**

327   Fish typically exhibit metabolic depression to lower energy demand as a survival strategy when

328   a critical hypoxia threshold is met (Dalla Via et al. 1994). Decreased growth is thus expected due

329   to reduced feed conversion efficiency (Brett 1979). Likewise, our results showed that growth rates

330   of juvenile English sole decreased by over 55% under moderately warm (10ºC and 13ºC), hypoxic

331   (1.4 ml O_2 l^{-1}) conditions. Potential limitations on growth due to DO deficiency may change fish

332   behavioral strategy. Prior evidence suggests that severe hypoxia may also trigger movements of

333   demersal fishes including English sole away from Oregon coastal habitats (Keller et al. 2017).

334   Sub-lethal effects of hypoxia (1.4 ml O_2 l^{-1}) on the growth of demersal fishes have been examined

335   empirically for a wide range of species including flatfishes, with low DO consistently linked to

336   reduced growth rates (Bejda et al. 1992; Stierhoff et al. 2006). For example, at 20ºC, winter

337   flounder *Pseudopleuronectes americanus* growth was reduced 55% at 1.5 ml O_2 l^{-1}, compared to

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338   growth at 4.7 ml O_2 l^{-1} (Bejda et al. 1992). Different from severe hypoxia curtailing growth, the

339   effect of moderate hypoxia (2 ml O_2 l^{-1}) on fish growth is species-specific. Although many

340   flatfishes show increased vulnerability to moderate hypoxia (Petersen and Pihl 1995; Taylor and

341   Miller 2001), the growth of juvenile English sole was still maintained when DO concentrations

342   dropped from 6 ml O_2 l^{-1} to 2 ml O_2 l^{-1}. This likely indicates a relatively strong hypoxia tolerance

343   of English sole, which may explain in part the occurrence of this species in hypoxic waters off the

344   coast of Oregon during upwelling events (Froehlich et al. 2014; Sobocinski et al. 2018). In general,

345   demersal fishes routinely exposed to naturally occurring hypoxia are considered to have decreased

346   sensitivity to low DO (McNatt and Rice 2004). One example is the growth reduction of juvenile

347   spot *Leiostomus xanthurus* and Atlantic menhadenn *Brevoortia tyrannus* only occurs under severe

348   hypoxia (1 ml O_2 l^{-1}) (McNatt and Rice 2004). Under hypoxia, the oxygen pressure can be mediated

349   by fish physiological mechanisms associated with acclimation, including reducing oxygen demand

350   for routine metabolism, as well as increasing ventilation rates and hematocrit levels (Taylor and

351   Miller 2001). On the other hand, despite metabolic limitations, demersal fishes may benefit from

352   short-lived hypoxia through predation upon hypoxia-stressed infauna (Pihl et al. 1991), concurrent

353   with relaxed predation from predators (Craig et al. 2010). Therefore, these life history strategies

354   of English sole during seasonal hypoxia mirror a trade-off between physiological tolerance and

355   trophic interactions.

356   Temperature is characterized as a rate-governing factor for fish metabolism (Brett 1979),

357   whereas DO acts as a limiting factor strongly depressing growth at critical levels (Cuenco et al.

358   1985). As DO concentration increases, growth rate may be mainly driven by temperature. Our

359   experimental results confirmed that temperature has a profound effect on growth in English sole

360   with SGR positively correlated with water temperature in the two DO treatments above the 1.4 ml

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361     $O_2\,l^{-1}$ hypoxia threshold. Typically, increasing temperature promotes increases in feeding activity

362   and metabolic rates, and hence growth rates. Similarly, increased growth rates of juvenile English

363   sole were observed at higher water temperatures in a previous study by Ryer et al. (2012),

364   suggesting a positive relationship between growth and temperature. It should be noted that SGR

365   of juvenile English sole in our study were lower than rates reported by Ryer et al. (2012). We

366   speculate the low growth rates are related to density dependence, given the higher fish density

367   (compared to 7 fish per tank) and smaller size of the tank (compared to 1 m diameter tank) in our

368   study. Although peak growth rates of juvenile English sole in our study occurred at 15°C, the

369   thermal optima for the growth of this species may be higher than our 15°C temperature treatment

370   given the upper lethal threshold ranging from 21°C to 27°C (Ames et al. 1978). On the other hand,

371   regardless of DO concentrations, at 5°C the somatic growth of juvenile English sole was

372   substantially suppressed in the present study, which likely indicates the bottom thermal tolerance

373   for this species.

374   Research has demonstrated that lower temperatures are preferred for fish growth under hypoxic

375   stress (Cuenco et al. 1985). Given the loss of aerobic scope at high temperatures (Pörtner and Peck

376   2010), high-temperature combined with hypoxia may act synergistically upon fish and result in a

377   narrower thermal breadth and a reduced upper critical temperature (McBryan et al. 2013).

378   Laboratory work on juvenile southern flounder (*Paralichthys lethostigma*) showed hypoxia at

379   29°C caused the greatest reduction in growth, and the temperature optimum for growth at normoxia

380   (Del Toro-Silva et al. 2008). In the present study, we noticed that temperature and DO have a

381   profound, synergistic effect on fish growth at 10ºC and 13ºC, but did not find a clear pattern

382   supporting a downshift in growth optimum under hypoxia. Instead, inconsistent temperature

383   effects on hypoxic fish are presumably attributed to individual variations in fish behavior and

384   physiology (Pang et al. 2015). Moreover, different fish cohorts were used in three experiments,

385   and thus cohort-related phenotypic plasticity may also contribute to variable growth responses

386   observed in our study (Sinclair et al. 2002).

387   We note that data availability from controlled experiments may limit the model utility when

388   the sample size is small. To compensate for this constraint, DO was treated as a conditioning factor

389   nested in the factor-smooth interaction term in the GAMM when producing smooth functions for

390   the temperature covariate. Since the thermal sensitivity of fish growth (thermal breadth, optimum,

391   and limits) varies depending upon oxygen supply (Pörtner and Peck 2010; McBryan et al., 2013),

392   we anticipate that a wide range of temperature levels should enable us to capture the nonlinear

393   signal and provide a better estimation of the parameters in the model.

394   **Juvenile habitats under climate variability**

395   Our findings confirm that hydrographic processes off the Oregon coast have a one-month

396   lagged response to tropical El Niño/La Niña signals through atmospheric teleconnections (Jacox

397   et al. 2015). Evidence has indicated the propagation of El Niño signals in the northeast Pacific

398   estuaries (Hughes et al. 2015). However, we found little evidence of the downscaling effects of

399   the El Niño/La Niña cycle on Oregon estuaries such as Yaquina Bay. One possible explanation is

400   that La Niña can produce highly variable weather/climate conditions (Hughes et al. 2015), leading

401   to a weakening correlation between La Niña signals and estuarine hydrology. Regional climate

402   indices such as PDO appear indicative of estuarine processes along the northeast Pacific

403   (O'Higgins and Rumrill 2007), which is echoed in the present study as seen a one-month lagged

404   response of water temperature in Yaquina Bay in relation to the PDO index. We speculate that the

405   hydrography off the Oregon coast is subject to PDO variations and under the remote influence of

406   the large-scale El Niño/La Niña cycle. Negative associations between CUTI and coastal DO

407 concentrations demonstrate that hypoxia off Oregon is likely dominated by onshore transport of

408 upwelling and subsequent respiration of organic matter. This hypothesis is also supported by the

409 strong correlation in environmental variables between estuarine and coastal stations.

410 The 2009–2011 study period is categorized as a phase transition between the 2009 El Niño and

411 the 2010–2011 La Niña events (Fig. 8). Our simulation suggests that in summer 2009, coastal

412 habitats are comparably suitable for juvenile English sole, while in summer 2010-2011, coastal

413 habitats become unfavorable due to La Niña-driven strong upwelling. In addition, high habitat

414 quality in Yaquina Bay during the summer 2010–2011 implies that the bay may provide a refuge

415 from low temperature and hypoxia, for juvenile English sole during La Niña years. The linkage

416 between El Niño events and year classes strength has been evidenced in a number of groundfish

417 stocks (Hollowed and Wooster 1992, Hollowed et al. 2001). A previous study also indicates that

418 El Niño warming can mediate hypoxia in northeast Pacific estuaries, making estuarine conditions

419 favorable for juvenile English sole (Hughes et al. 2015). Brodeur et al. (2008) reported that English

420 sole dominate the larval fish assemblage off the Oregon coast during warm PDO years. Coastal

421 waters off Oregon are typically colder and more hypoxic during La Niña years than during El Niño

422 years, due to increased upwelling (Jacox et al. 2015). We therefore infer that during El Niño years

423 with weak upwelling, coastal habitats may remain moderately suitable, while during La Niña years

424 with strong upwelling, estuarine refuges are preferred. It must be noted that cascading effects of

425 climate change on biotic conditions can also influence habitat quality for juvenile fishes (Liu et al.

426 2015). For example, Keller et al. (2013) found that the feeding conditions for English sole may be

427 greatly improved during La Niña years. El Niño-driven weakened upwelling may reduce food

428 availability in coastal waters, which offset the beneficial effects of El Niño on physical conditions

429 for juvenile fishes. This explains in part why English sole recruitment was not strongly affected

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430   by El Niño events in 1982-83, 1987-88 and 1997-98 (Rooper 2002). Thus, further study is needed

431   to confirm the relationship between climate forcing and habitat quality for juvenile English sole in

432   Oregon coastal waters.

433   Estuarine and coastal habitats are of importance to juvenile English sole. Physiologically, warm

434   and less hypoxic waters (i.e. estuarine waters) enhance fish growth, whereas cold and more

435   hypoxic waters (i.e. coastal waters) in turn help fish undergo oxygen deprivation by lowering

436   oxygen demand. The life-history strategy of utilizing these two habitats enables juvenile English

437   sole to prosper in one habitat when the other becomes less favorable. Evidence suggests that

438   density-dependence may modulate fish growth translating to similar growth conditions between

439   estuarine and coastal habitats (Rosenberg 1982). Even within Yaquina Bay, growth can be highly

440   variable between upriver and downriver locations due to varying temperature and food conditions

441   (Stowell et al. 2019). Hence, understanding the role of estuarine and coastal habitats that play in

442   juvenile recruitment of English sole requires a holistic consideration of biotic and abiotic

443   environments.

444   Climate-driven intensified hypoxia has threatened coastal ecosystems over recent decades

445   (Howard et al. 2020). Being less mobile, demersal fishes are particularly vulnerable to near-bottom

446   hypoxia and other changes in habitat conditions. Our study presents an analytical framework based

447   on a series of controlled experiments to quantify the combined effects of temperature and hypoxia

448   on the growth of juvenile English sole. Our general findings may be applicable to other demersal

449   fishes with similar life-history traits in response to these two climate-related stressors. By applying

450   an experimentally derived model to different climate scenarios, our results shed light on the

451   assessment of habitat quality for demersal fishes associated with the hypoxic zone off the Oregon

452   coast.

20

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: (1) English sole are tolerant to moderate hypoxia (2 ml O_2 l^{-1}); (2) water temperature has profound effects on fish growth; (3) a threshold effect on fish growth occurs under severe hypoxia (1.4 ml O_2 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.

Declaration of Competing Interest

The authors declare no conflict of interest.

Author Contribution Statement

Chengxue Li: Conceptualization, Methodology, Software, Formal analysis, Writing - Original Draft, Visualization. **Lorenzo Ciannelli**: Conceptualization, Methodology, Funding Acquisition, Writing - Review & Editing. **Morgan Bancroft**: Investigation, Data Curation, Funding Acquisition. **Jay Rooker**: Writing - Review & Editing. **Clifford Ryer**: Methodology. **Hui Liu**: Writing - Review & Editing.

480   **Data availability statement**

481   Data are available upon reasonable request.

482   **References**

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685 **Figure Captions**

686 Figure 1 Map of two sampling sites (Station 1 and Station 2, black dots) in Yaquina Bay, Oregon,

687 USA. Fish samples collected from Stations 1 and Stations 2 were used for Expt 1 & 2 and Expt 3,

688 respectively. Buoy locations for the estuarine station near the mouth of Yaquina Bay (LOBO) and

689 coastal station north of Yaquina Bay at Lincoln Beach (LB15) are marked in red squares.

690

691 Figure 2 Experimental setup (left panel) and counter-current mixing tower connected with the

692 experimental tank (right panel). A narrow range of water temperature (7°C, 10°C, and 13°C) was

693 tested in Expt 1 & 2, and a wide range of water temperature (5°C, 10°C, and 15°C) was tested in

694 Expt 3. The dissolved oxygen (DO) level was consistent across the three experiments: hypoxia

695 (1.4 ml O_2 l^{-1}), moderate hypoxia (2 ml O_2 l^{-1}), and normoxia (6 ml O_2 l^{-1}). Each experiment

696 consisted of 3 temperatures $\times$ 3 DO concentrations $\times$ 2 replicates = 18 rearing units.

697

698 Figure 3 Bar graphs displaying one-way mixed-effects ANOVA results for specific growth rate

699 (SGR) of juvenile English sole at different temperature treatments under: (a) hypoxia (1.4 ml O_2

700 l^{-1}); (b) moderate hypoxia (2 ml O_2 l^{-1}); and (c) normoxia (6 ml O_2 l^{-1}). The error bar represents the

701 standard error. Asterisk indicates significant difference: $* = p < 0.05$, $** = p < 0.01$, $*** = p <$

702 0 .001.

703

704 Figure 4 Additive effects of water temperature on specific growth rate (SGR) of juvenile English

705 sole under: (a) hypoxia (1.4 ml O_2 l^{-1}); (b) moderate hypoxia (2 ml O_2 l^{-1}); and (c) normoxia (6 ml

706 O_2 l^{-1}). These relationships were determined from the Generalized Additive Mixed Effect (GAMM)

707 model in Eq. 2. Grey shade is estimated 95% confidence intervals. Effective degrees of freedom

708 (EDF) are given in parentheses.

709

710 Figure 5 Daily average values of (a) water temperature and (b) dissolved oxygen (DO) measured

711 at coastal (LB15, black) and estuarine stations (LOBO, grey) in the summer months (May-

712 September) from 2009 to 2011. The green dashed line represents the hypoxic level (1.4 ml $O_2\,l^{-1}$).

713

714 Figure 6 Correlations between (a) coastal (at LB15) water temperature and Pacific Decadal

715 Oscillation (PDO) (no lag); (b) estuarine (at LOBO) water temperature and PDO (one-month lag);

716 (c) coastal water temperature and Oceanic Niño Index (ONI) (no lag); (d) estuarine water

717 temperature and ONI (one-month lag); (e) coastal dissolved oxygen concentrations and Coastal

718 Upwelling Transport Index (CUTI); (f) estuarine dissolved oxygen concentrations and CUTI.

719

720 Figure 7 Box and whisker plots showing the simulation results from the generalized additive mixed

721 model (GAMM) for specific growth rate (SGR) of juvenile English sole. The model simulation

722 was performed for coastal (LB15, black) and the estuarine stations (LOBO, grey) using daily

723 temperature and dissolved oxygen measurements in the summer months (May–September) from

724 2009 to 201. Daily predictions were aggregated on a monthly basis for comparison. The box denote

725 the interquartile range with the upper and lower edges representing the 25th and 75th quartiles,

726 respectively. The horizontal line inside the box represents the median. Whiskers represent the

727 range of points within 1.5 times the interquartile range. Data points exceeds 1.5 times the

728 interquartile range are shown with dots.

729

33

730 Figure 8 Seasonal and inter-annual variations of Oceanic Niño Index (ONI) from 2000 to 2016.

731 The grey area indicates the summer months (May–September). Note that the years within the box

732 (2009–2011) were included in our case study.

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735

Tables

Table 1 Summary of fish initial standard length (mm), final standard length (mm), initial weight (g), final weight (g), specific growth rate (SGR, % mass day^{-1}), and mortality over the entire 4-week period.

Treatment	T (ºC)	Initial SL (mm) mean ± SD	Final SL (mm) mean ± SD	Initial W_t (g) mean ± SD	Final W_t (g) mean ± SD	SGR (% mass day^{-1}) mean ± SD	Mortality (no. fish)
Hypoxia	5	52 ± 10	55 ± 10	2.11 ± 0.87	2.39 ± 1.01	0.36 ± 0.23	5
(1.4 ml O_2 l^{-1})	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	5	52 ± 8	54 ± 8	1.83 ± 0.70	1.97 ± 0.78	0.21 ± 0.31	5
(2 ml O_2 l^{-1})	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	5	47 ± 8	49 ± 8	1.48 ± 0.63	1.59 ± 0.74	0.18 ± 0.30	1
(6 ml O_2 l^{-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

35

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

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

Table 3. Summary of candidate generalized additive mixed models (GAMMs). 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. Note that the restricted maximum likelihood (REML) method was used for the selection of random effects and the maximum likelihood (ML) method was used for the selection of fixed effects. The term "by" within the smooth function indicates factor-by-continuous interactions.

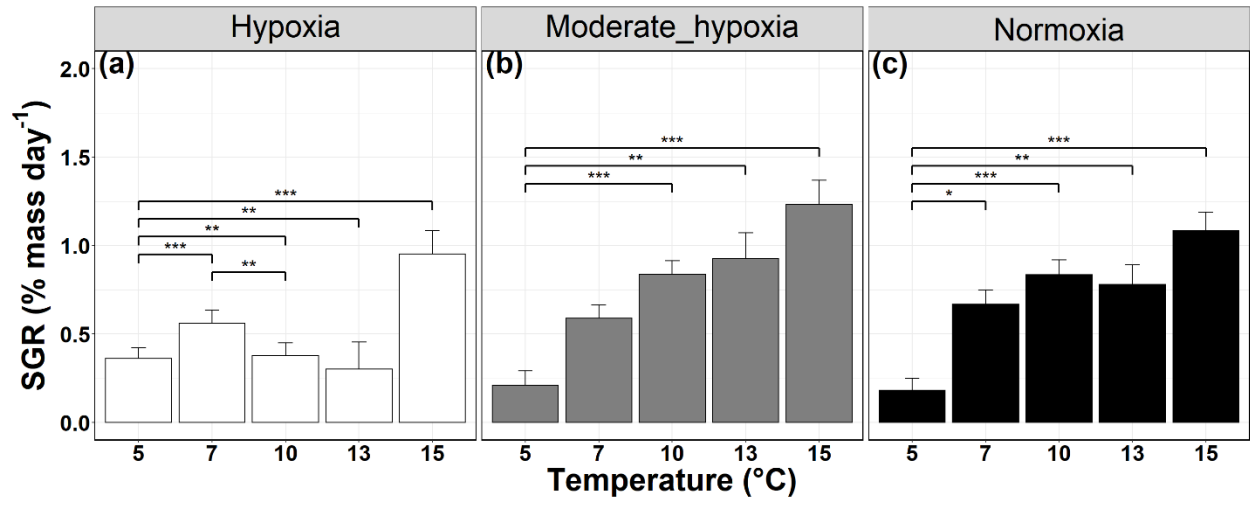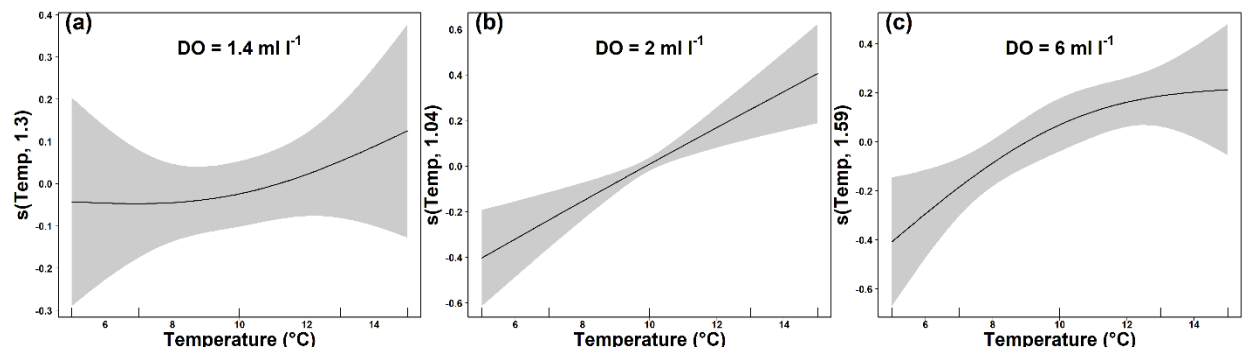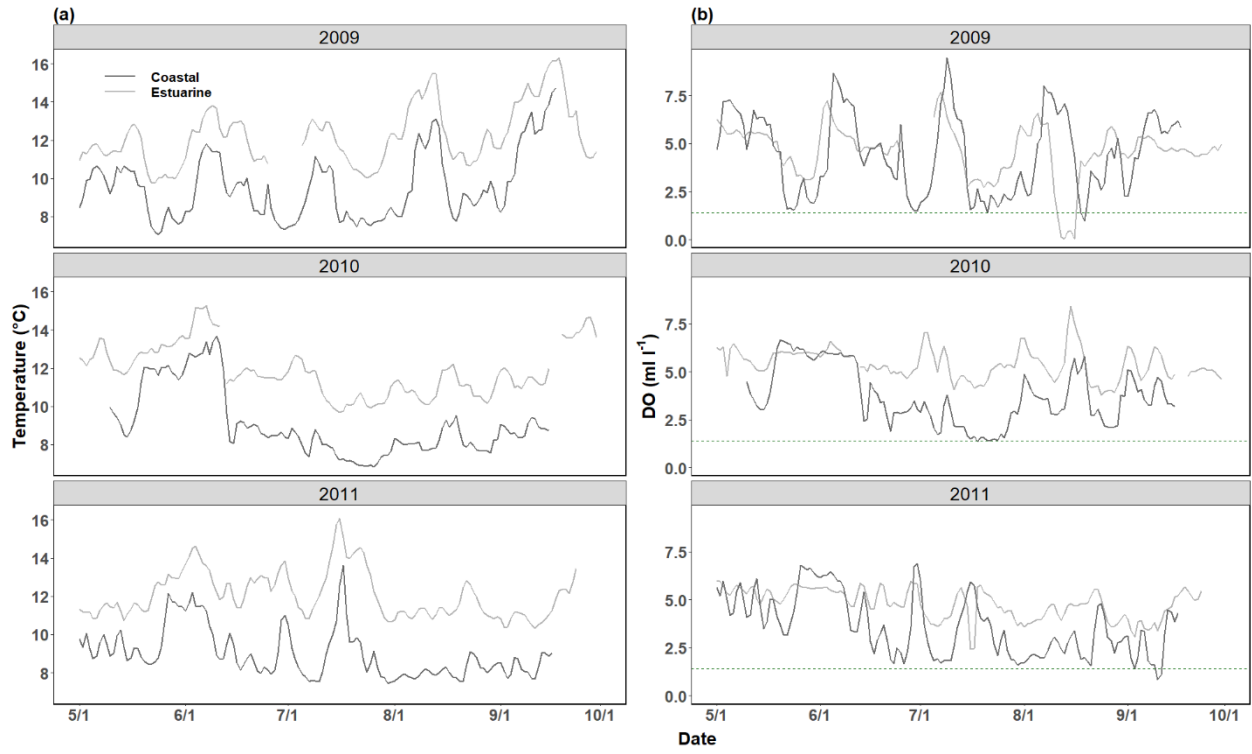| Method	Model	Linear term	Smooth term	Random effect	Variance function	AIC
REML	1	DO	s(Temp, by = factor(DO))	Expt	$\sigma_\epsilon^2 \times \sigma_{Expt}^2$	839.6
	2	DO	s(Temp, by = factor(DO))	Tank	$\sigma_\epsilon^2 \times \sigma_{Expt}^2$	884.6
	3	DO	s(Temp, by = factor(DO))	Expt/Tank	$\sigma_\epsilon^2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

Fig. 1

Fig. 2

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Fig. 3

Fig. 4

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Fig. 5.

Fig. 6.

Fig. 7.

Fig. 8