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Author(s)	Trowbridge, Cynthia D.; Davenport, John; Cottrell, Dylan M.; Harman, Luke; Plowman, Caitlin Q.; Little, Colin; McAllen, Rob
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Extreme oxygen dynamics in shallow water of a fully marine Irish sea lough

Cynthia D. Trowbridge, John Davenport, Dylan M. Cottrell, Luke Harman, Caitlin Q. Plowman, Colin Little, Rob McAllen

Highlights (for review)

- Dissolved oxygen in shallow subtidal of MPA ranged from hypoxia to hyperoxia.
- Daytime conditions were hyperoxic at or near the shore and normoxic offshore.
- Shallow-water, under-rock communities were often hypoxic.
- At night, shallow water habitats were hypoxic to anoxic during calm weather.

1 **Extreme oxygen dynamics in shallow water of a fully marine Irish sea lough**

2

3 **Cynthia D. Trowbridge[a,*], John Davenport[b], Dylan M. Cottrell[a], Luke Harman[b], Caitlin Q. Plowman[a],**

4 **Colin Little[c], Rob McAllen[b]**

5

6 [a] *Oregon Institute of Marine Biology, P.O. Box 5389, Charleston, OR 97420, USA*

7 [b] *School of Biological, Earth and Environmental Sciences, University College Cork, Enterprise Centre,*

8 *Distillery Fields, North Mall, Cork, Republic of Ireland*

9 [c] *Beggars Knoll, Long River Road, Newtown, Westbury, BA13 3ED, UK*

10

11 **ABSTRACT**

12 The benthos of Lough Hyne (Europe's first marine reserve) in SW Ireland has changed dramatically in the past

13 decade with declining invertebrate communities and proliferating ephemeral macroalgae. In summer 2011 and

14 2012, we measured dissolved oxygen (DO) levels on shallow subtidal rocky shores of the lough and recorded

15 both benthic hypoxia (<2 mg O_2 L^{-1}) and hyperoxia (~10–16 mg O_2 L^{-1}). In late summer 2013, we

16 systematically characterized the spatial and temporal patterns of DO in the lough seawater. Daytime DO levels

17 were hyperoxic either at or near the rocky shore, declined with increased distance for the first 5 m offshore, then

18 stabilized at normoxic levels (~8 mg O_2 L^{-1}). DO levels above and below rocks were variable and often showed

19 large differences (max. difference of 15.6 mg O_2 L^{-1}), particularly at rocky shore sites with low current flow. At

20 night, the DO in shallow water declined, becoming hypoxic to anoxic during calm weather. These extreme

21 oxygen fluctuations (i) are amongst the first records to report severe conditions within Irish coastal waters and

22 (ii) could contribute to the known recent decline in benthic invertebrate diversity within the marine reserve.

23

24 *Keywords:* Hyperoxia • Hypoxia • Oxygen fluctuations • Lough Hyne • Ireland • Marine reserve

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26 [*]**Corresponding author:**

27 **E-mail: cdt@uoregon.edu**

28 Telephone: 001+541-574-0820

29 Mail: P.O. Box 1995, Newport, OR 97365 USA

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1. Introduction

The proliferation of (1) ephemeral macroalgae (particularly ulvoids and ectocarpoids) and (2) microalgal/cyanobacterial biofilms has been documented in aquatic systems around the world in response to increased anthropogenic nutrients (fertilizers, sewage, etc.) [1-3]. Such algal and bacterial blooms produce extremes in dissolved oxygen (DO) by their high rate of photosynthesis during the day (producing hyperoxia), and the dominance of respiration at night (causing hypoxia).

Hyperoxic conditions (oxygen concentrations higher than in air-saturated seawater) can reduce activity levels, alter behavior, and reduce growth, fecundity, and survival of invertebrates [4-13]. Hyperoxia can also cause gas bubble disease in many types of fishes and invertebrates [14-18]. Adverse effects occur at super-saturation levels as low as 108-115% [5, 6]. The Irish guidelines for bathing waters (S.I. No. 155 of 1992) are <120% air saturation. The biotic consequences of naturally occurring values of 150–200% air saturation merit ecological study, particularly in marine reserves, SACs (Special Areas of Conservation), and other ecologically or economically sensitive areas.

Hypoxic and/or anoxic conditions can be lethal for both larval and adult invertebrates and fishes (e.g., [19-28]). Although supersaturation of dissolved gases has been traditionally studied in artificial systems such as in aquaculture ponds and stream raceways, or around dams and power-plant outflows [14], both conditions (hyper- and hypoxia) may also occur in 'natural' aquatic systems such as seagrass beds or macroalgal stands.

Extreme dissolved oxygen fluctuations have been reported for freshwater lakes [29], intertidal rockpools [18, 30-31], in various cnidarian-algal symbioses [32-35], near the surface of seaweed [36-39], and in shallow marine waters [12, 24, 40-41]. Hypoxia has also been extensively reviewed for (i) stratified lakes, fiords, and sea loughs, (ii) estuaries and inlets, and (iii) the oxygen minimum zone in deep water [42-47].

Researchers from the Irish Environmental Protection Agency found no evidence of summer hypoxia to anoxia in 95 coastal water bodies surveyed in Ireland (including several sites in County Cork) between 2003 and 2007 [48], although 10 were considered oxygen-deficient (2–6 mg O_2 L^{-1}). Furthermore, a later analysis of Irish coastal and shelf waters in summer 2001 to 2009 reported the lowest seabed DO levels of about 6.3 mg O_2 L^{-1} (70% air saturation) [49]. Recently proposed Irish standards of DO in fully marine coastal waters range from about 6.3 to 10 mg O_2 L^{-1} [50]. Yet the fully marine Lough Hyne in County Cork [42-47] and the brackish Arbear Salt Lake in County Galway [51] are both known to show periodic hypoxia (<2 mg L^{-1}) and anoxia (0 mg L^{-1}). Because coastal hypoxia has not commonly been reported for Irish rocky shores and because Lough

60   Hyne is an ecologically significant and internationally outstanding marine reserve [52-59], we embarked on a

61   comprehensive program to quantify the large-scale and small-scale variations in the lough's shallow-water

62   oxygen dynamics and to consider the ecological ramifications of such fluctuations.

63   Past research has been conducted on the oxygen tolerances of several ecologically significantly species that

64   occur in the lough. For example, the embryos of the purple sea urchin (*Paracentrotus lividus*) are standardly

65   used to assess European coastal water quality [60]; although embryos, larvae, and juveniles exhibit a high

66   tolerance to low DO levels, survival and growth significantly decreases at <2 mg L^{-1} [60, Trowbridge et al.,

67   unpub. data]. Furthermore, the green urchin in Norway was 'unable to maintain high gonad growth' under DO

68   conditions of 4 and 6 mg L^{-1} [61]. Juvenile spiny starfish (*Marthasterias glacialis*) exhibit reduced movement of

69   podia, tenacity to substratum, and survival during 1-2 day exposures to hypoxia (Trowbridge et al., unpubl.

70   data). Sessile suspension feeders such as cup corals, jewel anemones, and octocorals are uncommon in Lough

71   Hyne habitats with DO values <5-6 mg L^{-1} [62, 63]. The relationship between low DO levels and species

72   mortality has already been established in Europe and elsewhere [21-22, 24, 27, 41, 44-45]; we investigated the

73   severity of the DO problems in Lough Hyne in the present study.

74   We addressed two over-arching research questions. First, do hyperoxic and/or hypoxic conditions occur

75   only along the rocky shoreline or also offshore into the body of the lough? The spatial extent of extreme DO

76   levels would indicate which organisms could be affected: benthic invertebrates, fishes, and seaweed in shallow

77   water or larvae, fishes, and other organisms in the water column offshore. Second, are shallow-water DO

78   conditions within known lethal limits of marine species, particularly ecologically significant ones such as *P.*

79   *lividus*?

80

81   **2. Material and Methods**

82   *2.1 Sea lough*

83   Lough Hyne (51°30′ N, 9°17′ W) is a semi-enclosed, fully marine sea lough in County Cork, southwest

84   Ireland. The lough is ~0.8 km long and ~0.5 km wide, has negligible freshwater input (salinity is generally 34 to

85   35), and is connected to the Atlantic Ocean by a shallow, narrow (25 m wide at high tide, 12 m at low tide)

86   channel called the Rapids (Fig. 1). The tidal range within the lough is about a meter and appreciably larger

87   outside (below the Rapids) [64]. The shallow sill in the Rapids restricts water flow into/out of the lough. The

88   estimated flushing rate ranges between 12.5 and 41 days for the seawater above the thermocline [64-65]. Recent

89   nutrient research [65] demonstrated significantly elevated nutrients relative to the 1990s [65-66]. Furthermore,

90 the mass mortality of purple urchins has released macroalgae, both perennials and ephemerals, from grazing by

91 a species previously described as a crucial and ecologically significant herbivore [53, 67].

92   The lough forms two different basins interconnected by the deep (48 m) Western Trough and shallow (1-2

93 m) eastern channel (Fig. 1). The south basin is nearest to the tidal rapids where seawater enters and exits the

94 lough, whereas the north basin is partially separated from the south by Castle Island. The Western Trough

95 becomes seasonally stratified with summer anoxia below the thermocline [42-44] and causes migration of

96 mobile megafauna [68].

97   Discrete topographical and habitat units were designated in the 1930s on the shoreline (Fig. 1). These 108

98 marked sectors within the lough are still used because handheld GPS devices have difficulty obtaining satellite

99 signals in several areas of the lough. The specific locations are designated by shore (west, south, east, north, and

100 island) and sector numbers. Monitoring sites (10-m of shoreline) were established by Ebling et al. [69] and

101 relocated and resurveyed by Little et al. [70]. Ten sites (of the original 20) have been surveyed for >30 target

102 species every year since the early 1990s [71-74]. Thus, the rocky shores of the lough have been extensively

103 studied.

104

105 *2.2 Spatial variation in dissolved oxygen*

106

107 *2.2.1 Onshore-offshore profiles*

108   To determine how spatially localized DO values were, one site was selected on each shore of the lough

109 (north, south, east, and west) and a 50-m transect was laid out perpendicular to the shore at the chosen site. This

110 procedure was repeated, with three transects being completed per day on two different occasions (27 Aug and

111 13 Sep 2013) (Fig. 1a). For the first five meters offshore, physical measurements (water temperature, dissolved

112 oxygen concentration [mg O_2 L^{-1}], and depth of the benthos) were taken every meter, using a recently calibrated

113 optical YSI ProODO™ probe, meter stick (shallow depths) and a hand-held, high-frequency digital depth

114 sounder (>1 m depths). From 5 m to 50 m offshore, the water column was generally deep enough (>0.5 m) that

115 the ephemeral algae were patchy (or absent) and physical measurements were taken every 5 m. For each

116 location, DO readings were taken at water depths of 1 cm ('surface') and 15 cm ('subsurface'). Each transect

117 took about 20 min and was done between 1400 and 1600 h.

118   To analyze these profiles, we considered how DO (dependent variable) varied with four independent

119 variables (monitoring site, distance offshore, sampling depth, and bottom depth) by using a general linear model

120 (GLM) test. The assumptions of this analysis were assessed as follows. (i) DO readings were assumed to be

121 independent given the continuous water movement within the lough. (ii) Collinearity was investigated by

122 determining which variables were strongly correlated. Because distance offshore and bottom depth were

123 significantly correlated (Pearson's correlation, $r = 0.826$, $n = 180$, $p < 0.001$), we dropped the latter variable

124 from our tested model. (iii) We inspected the residuals to ensure there was no problem with variances. Because

125 the residuals were problematic for the surface DO, subsurface DO, and the combined data, we used non-

126 parametric Spearman rank correlations to test how DO varied with distance offshore for surface and subsurface

127 sampling locations.

128 　　DO profiles were conducted on both sides of all 10 long-term monitoring sites (Fig. 1b) of Little et al. [70-

129 72]. The same methods used in the 50-m profiles (above) were repeated for the 5-m profile study, though

130 measurements were taken only from 0 to 5 m offshore. For every meter offshore, DO readings were taken at

131 depths of 1 and 15 cm, and the depth of the sea bed was recorded. Each transect took about 10 min and was

132 done between 1030 and 1630 h. To analyze these profiles, we considered the same three assumptions as above.

133 Because distance offshore and bottom depth were again significantly correlated (Pearson correlation, $r = 0.614$,

134 $n = 120$, $p < 0.001$), we removed the latter variable from our tested model. Furthermore, because DO at surface

135 and subsurface depths were highly correlated ($r = 0.954$, $n = 107$, $p < 0.001$), we simplified our model to two

136 independent variables: site and distance offshore. As before, we inspected the residuals; after confirming there

137 was no problem with variances, we conducted a 2-factor GLM with site and distance offshore as factors.

138

139 *2.2.2 Above and below rocks*

140 　　In August and September 2011, we noted that several long-term monitoring sites were becoming hypoxic to

141 anoxic, particularly under shallow subtidal rocks. Therefore, we selected two sites that had appeared most

142 oxygen-stressed, namely East Castle (sector I9) and East Goleen (W36). We measured DO concentrations

143 directly below the water surface, above the seaweed patches, in the middle of seaweed clumps, and then directly

144 above and below small slabs of rocks (10 per site) directly next to the monitoring sites. Rocks were lifted as

145 little as possible (<5 cm off the benthos) to limit water flow and, thus, changes in DO values.

146 　　In August and September 2013, oxygen levels above and under rocks were again measured, but more

147 comprehensively. We selected 5 of the 10 long-term monitoring sites (Fig. 1d): East Castle (sector I9), North

148 Labhra (I1), Codium Bay (S16), SE Labhra (I15), and Westwood South (W21/22). To avoid disturbing the

149 monitoring sites, we sampled rocks in 3-m sections directly adjacent to the sites. DO readings were taken 1 cm

5

150 above the selected rocks and then immediately under the same rocks during daytime low tides. Rocks were

151 selected to have roughly the same surface area (approx. 400 cm^2) when viewed from above and to be lying on

152 top of other rocks, thus ensuring that the oxygen probe did not penetrate benthic sediment. A minimum of 10

153 rocks were selected in the 3-m section laterally flanking each site, for a total of at least 20 rocks per site. This

154 design allowed for a comparison of small-scale variability within sites as well as large-scale variability among

155 sites. All measurements were taken at or near daytime low tide between 1030 and 1630 h to ensure that the

156 selected rocks were in the shallow subtidal region. Because cloud cover and weather was more important than

157 time of day during the late morning to late afternoon period, we did not include time of day as a factor in the

158 analysis. To analyze the resulting DO values, we used a 2-way ANOVA statistical design with site and side

159 (right vs. left) as factors and water depth as a covariate.

160

161 *2.4 Temporal variation in dissolved oxygen*

162   To document nocturnal and diurnal variation, we measured DO (in mg O$_2$ L^{-1}) with the YSI optical probe at

163 4-h intervals through a 24-h period in mid-summer (19–20 July 2012) at two sites: (a) North shore in sector N6

164 and (b) West shore at sector W6 (Fig. 1c). We also recorded surface temperature and range of depths at which

165 measurements were made (60–110 cm overall). At both sites there was patchy ulvoid seaweed, distributed down

166 to a depth of about 1 m below low tide level, thus forming a band covering the intertidal and a portion of the

167 subtidal. This green seaweed was interspersed with dead ephemeral algae and gravelly substratum. All of our

168 'tuft' measurements were in ulvoid beds. We obtained wind speed data from Met Éireann for the nearby Sherkin

169 Island for this time period as a relative measure of wind disturbance at the lough.

170   To determine whether the mid-summer oxygen extremes would persist in late summer, we deployed a

171 recently calibrated HOBO oxygen data logger (U26-001 by Onset) for 24 h. First, we set the sensor near the top

172 of the Rapids (sector S16, Fig. 1c) during 16–17 September 2013. Second, we deployed the sensor on the North

173 Shore (sector N11, Fig. 1c) during 19–20 September. In both cases, the sensor was set to record every 15 min,

174 then attached to bricks with cable ties, and placed in shallow subtidal areas (ca. 1 m deep at low tide). We again

175 obtained wind speed data from Met Éireann for the nearby Sherkin Island as a relative measure of wind

176 disturbance at the lough.

177

178 **3. Results**

179 *3.1 Spatial variation in dissolved oxygen*

6

180   *3.1.1 Onshore-offshore profiles*

181   In 2013, daytime DO levels were markedly hyperoxic (up to 14 mg O_2 L^{-1}) either at or near the shore. DO

182   levels declined with increased distance from shore in the first 5 m (Fig. 2a-b); then oxygen stabilized at

183   normoxic levels (~8 mg O_2 L^{-1}). The effect of distance offshore was highly significant (Spearman rank

184   correlation, r_s = -0.769, n = 90, p <0.001 for surface water (1 cm); r_s = -0.797, n = 84, p <0.001 for subsurface

185   water (15 cm)). We noted these results generally reflected the underlying distribution of benthic macroalgae

186   (perennial and ephemeral) in the nearshore environment although unfortunately we did not quantify the presence

187   or absence of algae at the time.

188   There was significant spatial variation in DO values measured at the 10 monitoring sites in 2013. Most of

189   the variation was among sites ($F_{(9,60)}$ = 28.5, p < 0.001) with Boundary Bay (E14), East Castle (I9) and SE

190   Labhra (I15) having the highest DO values. There were also highly significant differences in DO with distance

191   (0 to 5 m) from shore ($F_{(5,60)}$ = 10.7, p < 0.001) with maximal DO typically at 1 m from the shoreline and a

192   decline to normoxic conditions by 5 m. Site and distance from shore accounted for 85% of the variation in DO

193   values measured.

194

195   *3.1.2 Above and below rocks*

196   In 2011, the mean DO values in the water column, at the water/macroalgal interface, and on the benthos

197   were slightly hyperoxic, but <10 mg O_2 L^{-1} (Fig. 3a). In the middle of the ephemeral algal beds (mostly the

198   phaeophytes *Stilophora* and ectocarpoids), DO values were on average 13–14 mg O_2 L^{-1} with considerable

199   variation. All these values were substantially greater than those under the rocks (mean <1 mg O_2 L^{-1}) at East

200   Castle and East Goleen sites (Fig. 3a).

201   In 2013, differences in DO levels above and below rocks were variable but often large—with a maximum

202   difference for an individual rock of 15.6 mg O_2 L^{-1}. SE Labhra and Westwood South had smaller differences in

203   oxygen levels above and below rocks than East Castle, North Labhra, and Codium Bay (Fig. 3b). The former

204   two sites had higher flow rates than the latter three sites (Trowbridge, unpubl.data). There were six rocks that

205   were hypoxic (<2 mg O_2 L^{-1}) or anoxic underneath; all of these rocks were at the latter three sites. In general,

206   however, the low-oxygen conditions were not as extreme during the 2013 sampling as during the 2011 survey

207   (see East Castle in Fig. 3).

208   There were highly significant differences in DO levels above rocks among the 5 study sites (ANOVA,

209    $F_{(4,90)}$ = 76.3, p < 0.001). Although there was no significant main effect of local scale (right vs. left side of study

7

210   site, $F_{(1,90)} = 1.6$, $p = 0.210$), there was a highly significant interaction effect ($F_{(4,90)} = 6.3$, $p < 0.001$). The water

211   depth of the benthos was not a significant factor ($F_{(1,90)} = 1.9$, $p = 0.170$) explaining DO levels above rocks.

212   Below rocks, however, both site and side of site (right vs. left) were significant factors ($p = 0.001$ and 0.003,

213   respectively), whereas the interaction and water depth were not ($p = 0.276$ and 0.059, respectively).

214

215   *3.2 Temporal variation*

216   In July 2012, DO levels fluctuated widely with time of day (by up to 12 mg O_2 L^{-1}), but the results were

217   consistent between the two sites (Fig. 4). In late morning (1100 h BST), the ephemeral algae and interface above

218   them were very hyperoxic, but the surface water was close to normoxic. At 1500 h and 1900 h, the whole water

219   column was hyperoxic. An hour after sunset (2300 h) the algae had become suboxic, while the surface water

220   remained rather hyperoxic. At 0300 h, the seaweed environment was hypoxic and the water column above it

221   also exhibited reduced DO (though only slightly at the surface some 50–80 cm above). Even 1 hour after

222   sunrise, the seaweed DO was still substantially reduced on the north shore. The mean wind speed (at nearby

223   Sherkin Island) during this period was 12.7 km h^{-1}.

224   The magnitude of temporal fluctuations of DO varied with weather during our 2013 HOBO sampling (Fig.

225   5). During the 16–17 Sep. survey (Fig. 5b), diurnal-nocturnal fluctuations in DO were not very large: the water

226   was hyperoxic in the day but normoxic at night at Codium Bay on the south shore (S16). Extremely strong

227   winds developed in late afternoon and, despite the steep hills around Lough Hyne, produced large waves in the

228   lough that lasted throughout the night and next morning. The mean wind speed recorded at the nearby Sherkin

229   Island weather station was 37.5 km h^{-1}. Calmer conditions (wind speed 21.5 km h^{-1}) occurred during the 19-20

230   Sep. survey (Fig. 5a), and daytime hyperoxia (up to 16 mg O_2 L^{-1}) was recorded on the north shore (N11) and

231   hypoxia to anoxia developed at night. In the middle of the night, oxygen levels rose (during the low tide) before

232   returning to hypoxia. Even though the sensor remained submerged, the water was shallow enough (ca. 0.5 m)

233   that oxygenation may have occurred across the air-water interface. As the tide level subsequently rose, the water

234   at the benthos became hypoxic again until after sunrise (Fig. 5a). This calm-weather pattern of DO was similar

235   to our mid-summer 2012 results (Fig. 4).

236

237   **4. Discussion**

238   *4.1 Spatial patterns*

239   Extreme oxygen conditions (hyperoxia and/or hypoxia) occurred along the shoreline of Lough Hyne but not

240   offshore into the body of the lough (the epilimnion). DO levels exhibited both small-scale and large-scale

241   differences. This type of variation was expected, as the amount of ephemeral algae and benthic biofilms varied

242   within and among sites, based on physical differences among sites [63]. Shore slope (of the shallow subtidal)

243   varied among sites from 3.4° to 41.5° from the horizontal; fetch varied from 34 m to 884 m; aspect varied from

244   60° to 345° (from a north compass bearing); and four sites had tree canopy reducing light levels whereas six

245   sites did not. Furthermore, some sites were relatively similar on the two ends whereas others (such as Boundary

246   Bay) had dramatically different depth profiles and current flows at either end of the 10-m wide sites.

247   Fluctuations in local DO levels could, in turn, influence benthic community structure. If these fluctuations

248   occur with a great enough frequency and/or amplitude, the entirety of Lough Hyne's shallow subtidal

249   community could be altered (see review by Diaz and Rosenberg [24] regarding predicted biotic effects). Such

250   alteration has already started since the early 2000s: (1) unprecedented proliferation of ephemeral algae and (2)

251   massive mortality of suspension feeders (sponges, bryozoans, hydroids), and mobile invertebrates [63, Little

252   and Trowbridge, pers. obs.]. Mobile animals subjected to stressful conditions may be driven into deeper water or

253   away from the shore comparable to the habitat compression caused by seasonal anoxia below the thermocline

254   [68]. Several Atlantic and Pacific urchin species exhibit significantly reduced growth, gonad development, and

255   survival as well as abnormal embryonic and larval development under hypoxic conditions [60-61, 75]. The DO

256   levels at night on the shore as well as under shallow subtidal rocks in Lough Hyne (Fig. 3-5) were clearly low

257   enough to negatively affect purple urchins and juvenile starfish that dwell there and to have negative effects on

258   urchin reproduction, embryonic and larval development, and juvenile recruitment.

259   Habitat degradation and oxygen fluctuations within the lough may have contributed to the mass mortality of

260   urchins in the lough [71-73]as well as the demise of many sessile invertebrates. While snorkelling in late

261   summer, we have frequently seen (1) large lobsters that have emerged from their lairs onto shallow-water,

262   defaunated benches during the daytime as well as (2) rotting remains of purple urchins, large crabs, and other

263   ecologically significant consumers. These types of observations are reminiscent of the 'graveyard phenomenon'

264   described by Stachowitsch [76-77] for the mass mortalities of macro-epifaunal communities in the Gulf of

265   Trieste in the Adriatic Sea.

266   However, not all invertebrates are negatively affected by ephemeral algal blooms. For example, Waheed

267   [78] experimentally demonstrated that some species derived refuge from predators within ectocarpoid blooms.

268   How hypoxia will affect larval recruitment and energy transfer up through the food web will depend on two

9

269 factors: (1) oxygen tolerance as well as (2) prey vs predator stress tolerance. With respect to the former,

270 hypoxic-tolerant species may continue to settle and survive; our preliminary acrylic plate experiments indicated

271 that some errant polychaetes and barnacles settled more abundantly in the presence of ephemeral algae than in

272 their absence (both algal removal and unmanipulated control); bivalves and bryozoans, however, showed the

273 opposite response. With respect to the latter issue, when prey species are more vulnerable to stress than their

274 predators are, the resulting outcomes of species interactions would differ from when predators are more

275 vulnerable than prey (e.g. prey-stress vs. consumer-stress models of Menge and Olson [79]).

276   In their review of supersaturation in aquatic systems, Weitkamp and Katz [14] acknowledged that

277 photosynthesis could contribute to supersaturated water and, thus, to gas bubble disease. The DO values

278 documented in Lough Hyne substantially exceed US and Irish Environmental Protection Authority

279 supersaturation standards. Because Lough Hyne is a marine reserve with significant fish, invertebrate, and

280 seaweed communities [52-59], the frequency and magnitude of hyperoxic and hypoxic events is of considerable

281 conservation concern, particularly given the preservation objectives of the National Parks and Wildlife Service

282 [59]. Comparable oxygen problems and conservation concerns have been reported for seagrass meadows in

283 Barloge Creek (Trowbridge *et al.*, unpublished data) and elsewhere [80]. The generality of these DO results to

284 other systems depends on coastal configuration; many geographic regions have highly convoluted coastlines

285 forming semi-enclosed bays, estuaries, loughs, sloughs, etc. that would be susceptible to eutrophication-driven

286 hypoxia and hyperoxia. Diaz and Rosenberg [24] reported that >400 coastal systems in the world were dead

287 zones associated with eutrophication: it is a general phenomenon.

288

289 *4.2 Temporal patterns*

290   Diel-cycling hypoxia has been reported in several systems. In Lough Hyne, when weather conditions were

291 calm (Fig. 4 and Fig. 5b), benthic species in nearshore habitats experience extreme DO conditions that could be

292 lethal/sublethal to sessile biota. Alternatively, extreme hypoxia might drive animals out of the degraded habitats.

293 Strong winds and waves coincided with the 16–17 Sep 2013 sampling (Fig. 5a) and do not reflect normal low-

294 flow conditions of mid-summer at Lough Hyne. Winds mixed the water in the shallow subtidal, moderating the

295 hyperoxia and hypoxia. If winds and/or water currents were strong enough, DO levels which were typically

296 elevated above ephemeral algae and depressed below it could be homogenized, with likely beneficial effects on

297 the subtidal benthic communities. In other regions, Breitburg [81] reported that wind and tides influenced the

298 severity of hypoxic events, and Tyler and Targett [82] reported tidal-related variation in DO extremes. Further

299 studies are needed to gain a greater understanding of how shallow subtidal DO levels vary temporally. We

300 hypothesize that wind waves will ameliorate potential hypoxia, whereas calm spells will exacerbate the stress in

301 low-energy systems with long residence times of seawater (e.g. Lough Hyne).

302   Late summer to early autumn conditions may be extreme but what about the rest of the year? Our ongoing

303 temporal analysis of DO at several sites has indicated extreme DO fluctuations for much of the year. For

304 example, fluctuations at one site in April 2014 ranged from <1 to >20 mg O_2 L^{-1} within a 24-hour period

305 (Plowman *et al.*, unpublished data). While mobile animals (fishes and invertebrates) can move offshore to avoid

306 the stressful conditions, sessile invertebrates such as sponges, ascidians, hydroids, and bryozoans will be

307 subjected to sublethal /lethal conditions. Field experiments are ongoing to evaluate how such hypoxia and

308 hyperoxia affect larval settlement and adult survivorship (Trowbridge *et al.*, unpublished data). The primary

309 objective of the present study was to demonstrate the severity of DO problems within Ireland's only marine

310 reserve and Europe's first one.

311   Recovery from hypoxia is influenced by three factors: reduced nutrient enrichment, stratification of the

312 water, and freshwater runoff [24]. In Lough Hyne—and many other coastal systems—the nutrient enrichment is

313 apparently not autochthonous [65], so reduction is not under local control. The strength of shallow-water

314 stratification depends largely on weather. Finally, although Lough Hyne has little freshwater input, unusually

315 wet years do result in localized ulvoid blooms that exacerbate the oxygen dynamics. Potential remedial

316 measures include the restocking of purple sea urchins (*Paracentrotus lividus*) into Lough Hyne to control the

317 macroalgae. However, the efficacy of such restoration efforts would be dependent on the (i) absence of urchin

318 pathogens and (ii) effective enforcement of the "no-take" regulations of urchins and other shellfish. Without

319 intervention, the high nutrient levels and lack of effective grazers will probably continue, leading to alternating

320 hypoxia and hyperoxia in the reserve, with negative consequences for the lough's shallow-water ecosystem.

321

329 findings and conclusions or recommendations expressed in this material are those of the authors and do not

330 necessarily reflect the views of the National Science Foundation.

331

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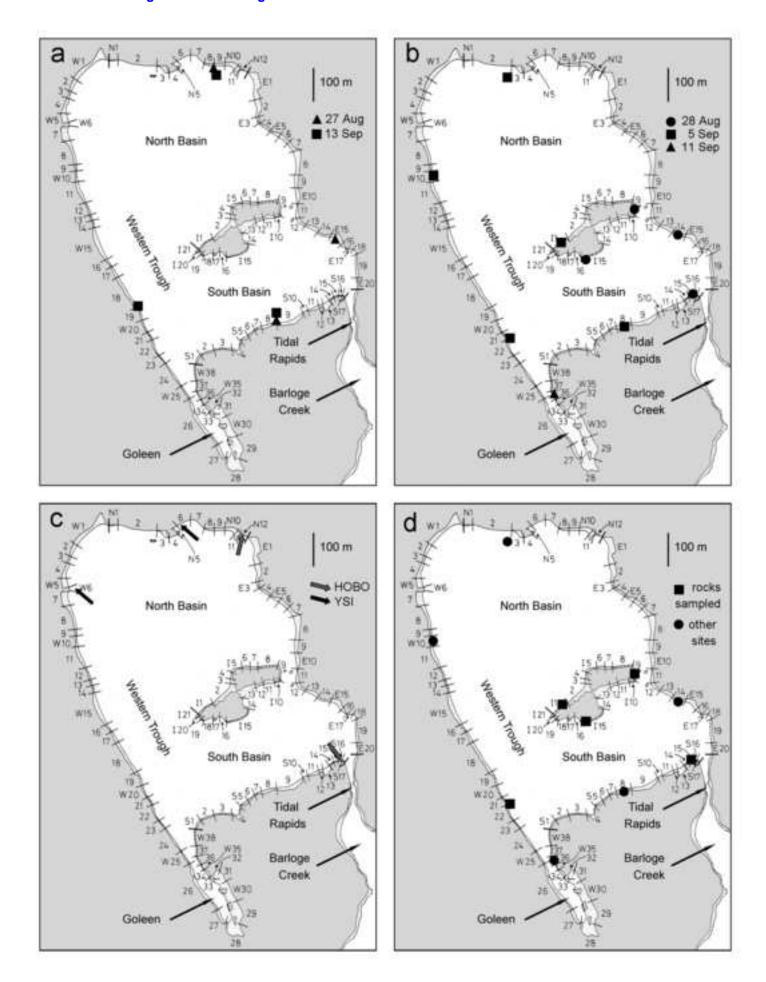479   migration of mobile benthic fauna affected by natural water column stratification. Est. Coastal Shelf Sci.

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512

513

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Figure Legends

Fig. 1. Map of Lough Hyne in SW Ireland (modified from map 4 of Myers et al. 1991). Intertidal zone (stippled) and shallow subtidal habitats are subdivided into 108 topographically discrete sectors designated by shore (W, west; S, south; E, east, N, north; I, island) and sector number. **a** Location of 50-m transects surveyed in 2013. **b** Location of 5-m transects sampled in 2013. **c** Location of temporal variation in sampling with continuously-recording HOBO sensor and a YSI hand-held sensor. **d** Location of monitoring of oxygen levels above and below rocks in 2013.

Fig. 2. Spatial variation of DO levels recorded along an onshore-offshore transect on **a** 27 Aug 2013 and **b** 13 Sep 2013 from different locations around the shore of Lough Hyne. Site codes refer to Renouf sector locations (see Fig. 1).

Fig. 3. Observed differences in dissolved oxygen concentrations above and below selected rocks in **a** Aug/Sep 2011 (n = 10 rocks/site) and **b** Aug/Sep 2013 (n = 20 rocks/site) at long-term monitoring sites in Lough Hyne, SW Ireland. Error bars represent SE and the dashed vertical line indicates oxygen saturation in air.

Fig. 4. Temporal variation in dissolved oxygen levels on 19-20 July 2012. Results are based on 6 replicate measurements per site, every 4 hours. Error bars denote ± 1 SE; in several cases, error bars are smaller than data symbol. Site codes refer to sector locations (see Fig. 1). Surface, water surface; interface, water-algal interface; tuft, inside clump of algae.

Fig. 5. Temporal variation in dissolved oxygen levels: **a** North shore (N11) on 19–20 Sep 2013 and **b** Codium Bay (S16) on 16–17 Sep 2013. Site codes refer to sector locations (see Fig. 1). Data based on HOBO data logger values recorded every 15 min. The horizontal dashed lines indicate hypoxic conditions and gray box denotes nighttime.

Figure 1

Figure 2
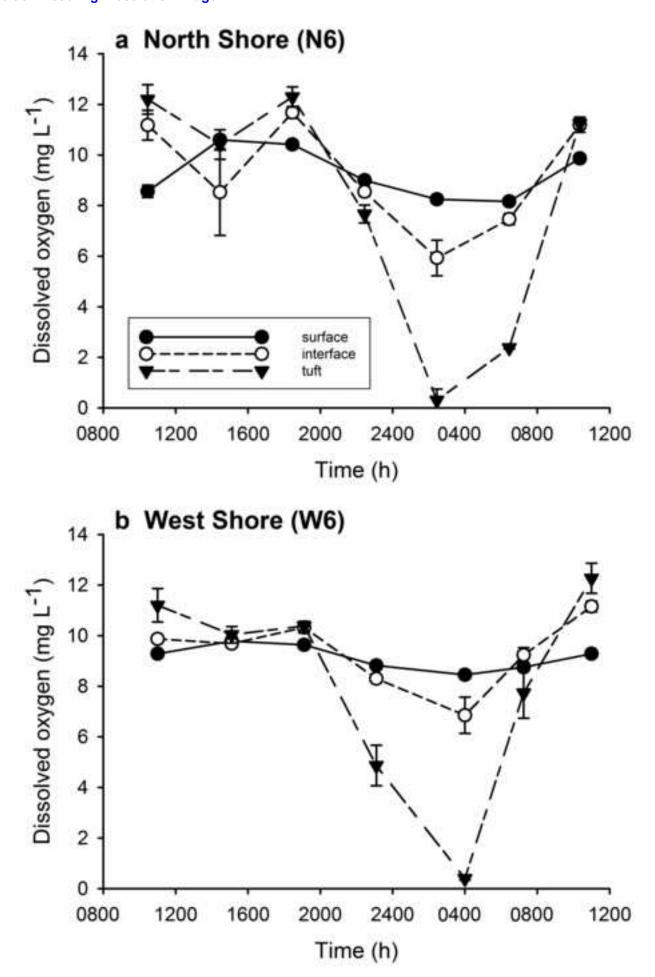
Figure 3
Click here to download high resolution image

Figure 4

a North Shore (N6)

Legend:
- surface
- interface
- tuft

b West Shore (W6)

Figure 5

a North shore (N11)

b Codium Bay (S16)

Time (h)