

Title	Extreme oxygen dynamics in shallow water of a fully marine Irish sea lough
Authors	Trowbridge, Cynthia D.;Davenport, John;Cottrell, Dylan M.;Harman, Luke;Plowman, Caitlin Q.;Little, Colin;McAllen, Rob
Publication date	2017-02-02
Original Citation	Trowbridge, C. D., Davenport, J., Cottrell, D. M., Harman, L., Plowman, C. Q., Little, C. and McAllen, R. (2017) 'Extreme oxygen dynamics in shallow water of a fully marine Irish sea lough', Regional Studies in Marine Science, 11, pp. 9-16. doi:10.1016/j.rsma.2017.01.008
Type of publication	Article (peer-reviewed)
Link to publisher's version	10.1016/j.rsma.2017.01.008
Rights	© 2017 Elsevier B.V. All rights reserved. This manuscript version is made available under the CC-BY-NC-ND 4.0 license. - https://creativecommons.org/licenses/by/4.0/
Download date	2024-12-05 22:59:43
Item downloaded from	https://hdl.handle.net/10468/4466

Accepted Manuscript

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

PII: S2352-4855(17)30024-5

DOI: <http://dx.doi.org/10.1016/j.rsma.2017.01.008>

Reference: RSMA 218

To appear in: *Regional Studies in Marine Science*

Received date: 18 April 2016

Revised date: 29 January 2017

Accepted date: 29 January 2017

Please cite this article as: Trowbridge, C.D., Davenport, J., Cottrell, D.M., Harman, L., Plowman, C.Q., Little, C., McAllen, R., Extreme oxygen dynamics in shallow water of a fully marine Irish sea lough. *Regional Studies in Marine Science* (2017), <http://dx.doi.org/10.1016/j.rsma.2017.01.008>

This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.



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 O₂ L⁻¹) and hyperoxia (~10–16 mg O₂ 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 O₂ L⁻¹). DO levels above and below rocks were variable and often showed
19 large differences (max. difference of 15.6 mg O₂ 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

25

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

30

31 **1. Introduction**

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

37 Hyperoxic conditions (oxygen concentrations higher than in air-saturated seawater) can reduce activity
38 levels, alter behavior, and reduce growth, fecundity, and survival of invertebrates [4-13]. Hyperoxia can also
39 cause gas bubble disease in many types of fishes and invertebrates [14-18]. Adverse effects occur at super-
40 saturation levels as low as 108-115% [5, 6]. The Irish guidelines for bathing waters (S.I. No. 155 of 1992) are
41 <120% air saturation. The biotic consequences of naturally occurring values of 150–200% air saturation merit
42 ecological study, particularly in marine reserves, SACs (Special Areas of Conservation), and other ecologically
43 or economically sensitive areas.

44 Hypoxic and/or anoxic conditions can be lethal for both larval and adult invertebrates and fishes (e.g., [19-
45 28]). Although supersaturation of dissolved gases has been traditionally studied in artificial systems such as in
46 aquaculture ponds and stream raceways, or around dams and power-plant outflows [14], both conditions (hyper-
47 and hypoxia) may also occur in 'natural' aquatic systems such as seagrass beds or macroalgal stands.

48 Extreme dissolved oxygen fluctuations have been reported for freshwater lakes [29], intertidal rockpools
49 [18, 30-31], in various cnidarian-algal symbioses [32-35], near the surface of seaweed [36-39], and in shallow
50 marine waters [12, 24, 40-41]. Hypoxia has also been extensively reviewed for (i) stratified lakes, fiords, and
51 sea loughs, (ii) estuaries and inlets, and (iii) the oxygen minimum zone in deep water [42-47].

52 Researchers from the Irish Environmental Protection Agency found no evidence of summer hypoxia to
53 anoxia in 95 coastal water bodies surveyed in Ireland (including several sites in County Cork) between 2003 and
54 2007 [48], although 10 were considered oxygen-deficient ($2-6 \text{ mg O}_2 \text{ L}^{-1}$). Furthermore, a later analysis of Irish
55 coastal and shelf waters in summer 2001 to 2009 reported the lowest seabed DO levels of about $6.3 \text{ mg O}_2 \text{ L}^{-1}$
56 (70% air saturation) [49]. Recently proposed Irish standards of DO in fully marine coastal waters range from
57 about 6.3 to $10 \text{ mg O}_2 \text{ L}^{-1}$ [50]. Yet the fully marine Lough Hyne in County Cork [42-47] and the brackish
58 Arbear Salt Lake in County Galway [51] are both known to show periodic hypoxia ($<2 \text{ mg L}^{-1}$) and anoxia (0
59 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 significant 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 $<2 \text{ mg L}^{-1}$ [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 $<5\text{-}6 \text{ mg L}^{-1}$ [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*?

81 **2. Material and Methods**

82 *2.1 Sea lough*

83 Lough Hyne ($51^{\circ}30' \text{ N}$, $9^{\circ}17' \text{ W}$) is a semi-enclosed, fully marine sea lough in County Cork, southwest
84 Ireland. The lough is $\sim 0.8 \text{ km}$ long and $\sim 0.5 \text{ km}$ 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 [$\text{mg O}_2 \text{L}^{-1}$], 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

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 cm²) 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 O₂ 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*

180 3.1.1 Onshore-offshore profiles

181 In 2013, daytime DO levels were markedly hyperoxic (up to 14 mg O₂ 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 O₂ 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 O₂ 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 O₂ L⁻¹ with considerable
199 variation. All these values were substantially greater than those under the rocks (mean <1 mg O₂ 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 O₂ 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 O₂ 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

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 $12 \text{ mg O}_2 \text{ L}^{-1}$), 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 $16 \text{ mg O}_2 \text{ L}^{-1}$) 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

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 O₂ 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

322 **Acknowledgments**

323 We are grateful to D. O'Donnell and P. Graham of the National Parks and Wildlife Service for permission to
324 carry out scientific research in the Lough Hyne Marine Reserve. We thank P. Stirling, T. Kearney, B. Dlouhy-
325 Massengale, M. Pauling, S. Phillips and C. Zucker for assistance in the field and extensive discussions in the
326 lab. B. Bingham (WWU) kindly advised us about the statistics. We thank the 2013 IRES team for their help and
327 support. The paper was substantially improved by comments and suggestions of anonymous reviewers. CDT,
328 RM, DC, CQP, and CL were supported in part by NSF grant INT-1130978 awarded to CDT. Any opinions,

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

332 References

- 333 [1] Valiela, I., McClelland, J., Hauxwell, J., Behr, P.J., Hersh, D., Foreman, K. 1997. Macroalgal blooms in
334 shallow estuaries: controls and ecophysiological and ecosystem consequences. *Limnol. Oceanogr.* 42,
335 1105–1118.
- 336 [2] Nelson, T.A., Nelson, A.V., Tjoelker, M. 2003. Seasonal and spatial patterns of “green tides” (ulvoid algal
337 blooms) and related water quality parameters in the coastal waters of Washington State, USA. *Bot. Mar.* 46,
338 263–275.
- 339 [3] Lyons, D.A., Arvanitidis, C., Blight, A.J., Chatzinikolaou, E., Guy-Haim, T., Kotta, J., Orav-Kotta, H.,
340 Queir, A.M., Rilov, G., Somerfield, P.J., Crowe, T.P. 2014. Macroalgal blooms alter community structure
341 and primary productivity in marine ecosystems. *Glob. Change Biol.* 20, 2712–2724.
- 342 [4] Torres, J.J., Mangum, C.P. 1974. Effects of hyperoxia on survival of benthic marine invertebrates. *Comp.*
343 *Biochem. Physiol.* 47A,17–22.
- 344 [5] Bisker, R., Castagna, M. 1985. The effect of various levels of air-supersaturated seawater on *Mercenaria*
345 *mercenaria* (Linné), *Mulinia lateralis* (Say), and *Mya arenaria* Linné, with reference to gas-bubble disease.
346 *J. Shellfish Res.* 5, 97–102.
- 347 [6] Bisker, R., Castagna, M. 1987. Effect of air-supersaturated seawater on *Argopecten irradians concentricus*
348 (Say) and *Crassostrea virginica* (Gmelin). *J. Shellfish Res.* 6, 79–83.
- 349 [7] Bisker, R., Castagna, M. 1988. The effect of air-supersaturated sea-water on *Argopecten irradians*
350 (Lamarck) and *Crassostrea virginica* (Gmelin) with reference to gas bubble trauma. *J. Shellfish Res.* 7, 150.
- 351 [8] Huntington, K.M., Miller, D.C. 1989. Effects of suspended sediment, hypoxia, and hyperoxia on larval
352 *Mercenaria mercenaria* (Linnaeus, 1758). *J. Shellfish Res.* 8, 37–42.
- 353 [9] Abele-Oeschger, D., Oeschger, R. 1995. Enzymatic antioxidant protection in spawn, larvae and adult worms
354 of *Phyllodoce mucosa* (Polychaeta). *Ophelia* 43, 101–110.
- 355 [10] Timmins, G.S., Penatti, C.A.A., Bechara, E.J.H., Swartz, H.M. 1999. Measurement of oxygen partial
356 pressure, its control during hypoxia and hyperoxia, and its effect upon light emission in a bioluminescent
357 elaterid larva. *J. Exp. Biol.* 202, 2631–2638.

- 358 [11] Harris, J.O., Burke, C.M., Edwards, S.J., Johns, D.R. 2000. Effect of oxygen supersaturation and
359 temperature on juvenile greenlip, *Haliotis laevis*, and blacklip, *Haliotis rubra*, abalone. J. Shellfish Res.
360 19, 518.
- 361 [12] da Rosa, C.E., de Souza, M.S., Yunes, J.S., Proença, L.A.O., Nery, L.E.M., Monserrat, J.M. 2005.
362 Cyanobacterial blooms in estuarine ecosystems: Characteristics and effects on *Laeonereis acuta*
363 (Polychaeta, Nereididae). Mar. Biol. Poll. 50, 956–964.
- 364 [13] Lardies, M.A., Fernández, M. 2002. Effect of oxygen availability in determining clutch size in *Acanthina*
365 *monodon*. Mar. Ecol. Prog. Ser. 239, 139–146.
- 366 [14] Weitkamp, D.E., Katz, M. 1980. A review of dissolved gas supersaturation literature. Trans. Amer. Fish.
367 Soc. 109, 659–702.
- 368 [15] Edsall, D.A., Smith, C.E. 1991. Performance of rainbow trout and Snake River cutthroat trout reared in
369 oxygen super-saturated water. Aquaculture 90, 251–259.
- 370 [16] Lygren, B., Hamre, K., Waagbø, R. 2000. Effect of induced hyperoxia on the antioxidant status of Atlantic
371 salmon *Salmo salar* L. fed three different levels of dietary vitamin E. Aquacult. Res. 31, 401–407.
- 372 [17] Espmark, A.M., Hjelde, K., Baeverfjord, G. 2010. Development of gas bubble disease in juvenile Atlantic
373 salmon exposed to water supersaturated with oxygen. Aquaculture 306, 198–204.
- 374 [18] Phillips, N.E., Moran, A.L. 2015. Oxygen production from macrophytes decreases development time in
375 benthic egg masses of a marine gastropod. Hydrobiologia 757, 251–259. doi:10.1007/s10750-015-2256-7.
- 376 [19] Baker, S.M., Mann, R. 1992. Effects of hypoxia and anoxia on larval settlement, juvenile growth, and
377 juvenile survival of the oyster *Crassostrea virginica*. Bio. Bull. 182, 265–269.
- 378 [20] Levin, L.A., Gage, J.D., Martin, C., Lamont, P.A. 2000. Macrobenthic community structure associated with
379 the oxygen minimum zone, NW Arabian Sea. Deep-Sea Res. Part II 47, 189–226.
- 380 [21] Levin, L.A., Ekau, W., Gooday, A.J., Jorissen, F., Middelburg, J.J., Naqvi, S.W.A., Neira, C., Rabalais,
381 N.N., Zhang, J. 2009. Effects of natural and human-induced hypoxia on coastal benthos. Biogeosciences 6,
382 2063–2098.
- 383 [22] Gray, J.S., Wu, R.S., Or, Y.Y. 2002. Effects of hypoxia and organic enrichment on the coastal marine
384 environment. Mar. Ecol. Prog. Ser. 238, 249–279.
- 385 [23] Cheung, S.G., Chan, H.Y., Liu, C.C., Shin, P.K.S. 2008. Effect of prolonged hypoxia on food consumption,
386 respiration, growth and reproduction in the marine scavenging gastropod *Nassarius festivus*. Mar. Poll.
387 Bull. 57, 280–286.

- 388 [24] Diaz, R.J., Rosenberg, R. 2008. Spreading dead zones and consequences for marine ecosystems. *Science*
389 321, 926–929.
- 390 [25] Ekau, W., Auel, H., Pörtner, H.-O., Gilbert, D. 2010. Impacts of hypoxia on the structure and processes in
391 pelagic communities (zooplankton, macro-invertebrates and fish). *Biogeosciences* 7, 1669–1699.
- 392 [26] Matabos, M., Tunnicliffe, V., Juniper, S.K., Dean, C. 2012. A year in hypoxia: epibenthic community
393 responses to severe oxygen deficit at a subsea observatory in a coastal inlet. *PLoS ONE* 7: e45626.
394 doi:10.1371/journal.pone.0045626
- 395 [27] Riedel, B., Padas, T., Pretterebner, K., Schiemer, L., Steckbauer, A., Haselmair, A., Zuschin, M.,
396 Stachowitsch, M. 2014. Effect of hypoxia and anoxia on invertebrate behaviour: ecological perspectives
397 from species to community level. *Biogeosciences* 11, 1491–1518.
- 398 [28] Riedel, B., Zuschin, M., Stachowitsch, M. 2012. Tolerance of benthic macrofauna to hypoxia and anoxia in
399 shallow coastal seas: a realistic scenario. *Mar. Ecol. Prog. Ser.* 458, 39–52.
- 400 [29] Seki, H., Takahashi, M., Hara, Y., Ichimura, S. 1980. Dynamics of dissolved oxygen during algal bloom in
401 Lake Kasumigaura, Japan. *Water Res.* 14, 179–183.
- 402 [30] Stephenson, T.A., Zoond, A., Eyre, J. 1934. The liberation and utilisation of oxygen by the population of
403 rock-pools. *J. Exp. Biol.* 11, 162–172.
- 404 [31] Truchot, J.-P., Duhamel-Jouve, A. 1980. Oxygen and carbon dioxide in the marine intertidal environment:
405 diurnal and tidal changes in rockpools. *Resp. Physiol.* 39, 241–254.
- 406 [32] Dykens, J.A., Shick, J.M. 1982. Oxygen production by endosymbiotic algae controls superoxide dismutase
407 activity in their animal host. *Nature* 297, 579–580.
- 408 [33] Dykens, J.A. 1984. Enzymic defenses against oxygen toxicity in marine cnidarians containing
409 endosymbiotic algae. *Mar. Biol. Lett.* 5, 291–301.
- 410 [34] Richier, S., Merle, P.-L., Furla, P., Pigozzi, D., Sola, F., Allemand, D. 2003. Characterization of superoxide
411 dismutases in anoxia- and hyperoxia-tolerant symbiotic cnidarians. *Biochim. Biophys. Acta* 1621, 84–91.
- 412 [35] Richier, S., Furla, P., Plantivaux, A., Merle, P.-L., Allemand, D. 2005. Symbiosis-induced adaptation to
413 oxidative stress. *J. Exp. Biol.* 208, 277–285.
- 414 [36] Kaspar, H.F. 1992. Oxygen conditions on surfaces of coralline red algae. *Mar. Ecol. Prog. Ser.* 81, 97–100.
- 415 [37] Collén, J., Davison, I.R. 1999. Reactive oxygen production and damage in intertidal *Fucus* spp.
416 (Phaeophyceae). *J. Phycol.* 35, 54–61.

- 417 [38] Irwin, S., Davenport, J. 2002. Hyperoxic boundary layers inhabited by the epiphytic meiofauna of *Fucus*
418 *serratus*. Mar. Ecol. Prog. Ser. 244, 73–79.
- 419 [39] Irwin, S., Davenport, J. 2010. Oxygen microenvironment of coralline algal tufts and their associated
420 epiphytic animals. Biology and environment. Proc. Roy. Ir. Acad. 110B, 185–193.
- 421 [40] Tunnicliffe, V. 1981. High species diversity and abundance of the epibenthic community in an oxygen-
422 deficient basin. Nature 294, 354–356.
- 423 [41] Vaquer-Sunyer, R., Duarte, C.M. 2008. Thresholds of hypoxia for marine biodiversity. Proc. Natl. Acad.
424 Sci. 105, 15452–15457.
- 425 [42] Kitching, J.A., Ebling, F.J., Gamble, J.C., Hoare, R., McLeod, A.A.Q.R., Norton, T.A. 1976. The ecology
426 of Lough Ine. XIX. Seasonal changes in the Western Trough. J. Anim. Ecol. 45, 731–758.
- 427 [43] Thain, V.M., Jones, J., Kitching, J.A. 1981. Distribution of zooplankton in relation to the thermocline and
428 oxycline in Lough Ine, County Cork. Ir. Nat. J. 20, 292–295.
- 429 [44] McAllen, R., Davenport, J., Bredendieck, K., Dunne, D. 2009. Seasonal structuring of a benthic community
430 exposed to regular hypoxic events. J. Exp. Mar. Biol. Ecol. 368, 67–74.
- 431 [45] Rabalais, N.N., Díaz, R.J., Levin, L.A., Turner, R.E., Gilbert, D., Zhang, J. 2010. Dynamics and
432 distribution of natural and human-caused hypoxia. Biogeosciences 7, 585–619.
- 433 [46] Sullivan, T., Broszeit, S., O’Sullivan K.P.A., McAllen, R., Davenport, J., Regan, F. 2013. High resolution
434 monitoring of episodic stratification events in an enclosed marine system. Est. Coast. Shelf Sci. 123, 26–33.
- 435 [47] Sullivan, T., Byrne, C., Harman, L., Davenport, J., McAllen, R., Regan, F. 2014. Determination of spatial
436 and temporal variability of pH and dissolved oxygen concentrations in a seasonally hypoxic semi-enclosed
437 marine basin using continuous monitoring. Anal. Methods 6, 5489–5497.
- 438 [48] O’Boyle, S., McDermott, G., Wilkes, R. 2009. Dissolved oxygen levels in estuarine and coastal waters
439 around Ireland. Mar. Poll. Bull. 58, 1657–1663.
- 440 [49] O’Boyle, S., Nolan, G. 2010. The influence of water column stratification on dissolved oxygen levels in
441 coastal and shelf waters around Ireland. Proc. Roy. Irish Acad. 110B, 195–209.
- 442 [50] EPA. 2007. Water Framework Directive. Proposed quality standards for surface water classification: a
443 discussion document for public consultation. Wexford, Environmental Protection Agency.
- 444 [51] Henry, L.M., Kennedy, R., Keegan, B.F. (2008) An investigation of periodic hypoxia at Ardbear Salt Lake.
445 J. Mar. Biol. Assoc. U.K. 88, 1297–1307.
- 446 [52] Kitching, J.A. 1975. The importance of Lough Ine as a site for marine conservation. An Taisce, Cork.

- 447 [53] Kitching, J.A. 1987a. Ecological studies at Lough Hyne. *Adv. Ecol. Res.* 17, 115–186.
- 448 [54] Kitching, J.A. 1987b. Lough Ine - Classic sites. *Biologist* 34, 235–239.
- 449 [55] Minchin, D. 1987. Fishes of the Lough Hyne marine reserve. *J. Fish Biol.* 31, 343–352.
- 450 [56] Myers, A.A., Little, C., Costello, M.J., Partridge, J.C. 1991. The ecology of Lough Hyne. *R. Irish Acad.*,
451 Dublin.
- 452 [57] Bell, J.J., Shaw, C. 2001. Lough Hyne: a marine biodiversity hotspot? In: Nunn JD (ed) *Marine*
453 *biodiversity in Ireland and adjacent waters.* pp 35–43.
- 454 [58] Kearney, T. 2013. *Lough Hyne: From Pre-History to the Present.* Macalla Publishing, Ireland.
- 455 [59] NPWS. 2014. Conservation objectives: Lough Hyne Nature Reserve and environs SAC 000097. Ver. 1.
456 National Parks and Wildlife Service, Dublin.
- 457 [60] Saco-Álvarez, L., Durán, I., Lorenzo, J.I., Beira, R. 2010. Methodological basis for the optimization of a
458 marine sea-urchin embryo test (SET) for the ecological assessment of coastal water quality. *Ecotoxic.*
459 *Environ. Saf.* 73, 491–499.
- 460 [61] Siikavuopio, S.I., Dale, T., Mortensen, A., Foss, A. 2007. Effects of hypoxia on feed intake and gonad
461 growth in the green sea urchin, *Strongylocentrotus droebachiensis*. *Aquaculture* 266, 112–116.
- 462 [62] Trowbridge, C.D., Little, C., Ferrenburg, L.S., Resk, H.M., Kachmarik, K., Plowman, C.Q., Stirling, P., &
463 McAllen, R. 2016. Shallow subtidal octocorals in an Irish marine reserve. *Mar. Biodivers.* 46, 879–887.
- 464 [63] Trowbridge, C.D., Kachmarik, K., Plowman, C.Q., Little, C., Stirling, P., McAllen, R. 2017. Biodiversity
465 of shallow subtidal, under-rock invertebrates in Europe's first marine reserve: Effects of physical factors
466 and scientific sampling. *Est. Coast. Shelf Sci.* 187, 43–52.
- 467 [64] Bassindale, R., Davenport, E., Ebling, F.J., Kitching, J.A., Sleigh, M.A., Sloane, J.F. 1957. The ecology of
468 the Lough Ine Rapids with special reference to water currents: VI. Effects of the Rapids on the hydrography
469 of the South Basin. *J. Ecol.* 45, 879–900.
- 470 [65] Jessopp, M., McAllen, R., O'Halloran, J., Kelly, T.C. 2011. Nutrient and ecosystem dynamics in Ireland's
471 only marine nature reserve (NEIDIN). STRIVE Report Series 66. Environmental Protection Agency,
472 Ireland. http://www.epa.ie/downloads/pubs/research/biodiversity/-STRIVE_66_Jessopp_NEIDIN_web.pdf.
473 [Accessed 14 Apr 2015.](#)
- 474 [66] Johnson, M.P., Costello, M.J., O'Donnell, D. 1995. The nutrient economy of a marine inlet: Lough Hyne,
475 south west Ireland. *Ophelia* 41, 137–151.

- 476 [67] Kitching, J.A., Ebling, F.J. 1961. The ecology of Lough Ine. XI. The control of algae by *Paracentrotus*
477 *lividus* (Echinoidea). J. Anim. Ecol. 30, 373–383.
- 478 [68] Broszeit, S., Davenport, J., Bredendieck, K., Harman, L., McAllen, R. 2013. Seasonal oxygen-driven
479 migration of mobile benthic fauna affected by natural water column stratification. Est. Coastal Shelf Sci.
480 125, 36–42.
- 481 [69] Ebling, F.J., Sleight, M.A., Sloane, J.F., Kitching, J.A. 1960. The ecology of Lough Ine: VII. Distribution of
482 some common plants and animals of the littoral and shallow sublittoral regions. J. Ecol. 48, 29–53.
- 483 [70] Little, C., Morrill, D., Stirling, P. 1992. Changes in the shore fauna and flora of Lough Hyne. Ir. Nat. J. 24,
484 87–95.
- 485 [71] Little, C. 2011. Dabbling in the waters: 55 years in Lough Hyne's intertidal and shall subtidal. In:
486 Davenport J, McAllen R (eds) Lough Hyne Marine Reserve @ 30. A conference reflecting on the past,
487 present and future directions of research at the lough. School of BEES, University College Cork, p. 12.
- 488 [72] Little, C., Trowbridge, C.D. 2014. Lough Hyne 2014. Twenty years of intertidal and shallow subtidal
489 monitoring. Report to the National Parks and Wildlife Service, Ireland.
- 490 [73] Trowbridge, C.D., Little, C., Pilling, G.M., Stirling, P., Miles, A. 2011. Decadal-scale changes in the
491 shallow subtidal benthos of an Irish marine reserve. Bot. Mar. 54, 497–506.
- 492 [74] Trowbridge, C.D., Little, C., Dlouhy-Massengale, B., Stirling, P., Pilling, G.M. 2013. Changes in brown
493 seaweed distributions in Lough Hyne, SW Ireland: a long-term perspective. Bot. Mar. 56, 323–338.
- 494 [75] Lee, G., Hwang, J., Chung, Y., Kim, D., Moh, S.H., Chang, M., Lee, T.-K. 2012. Effects of hypoxia on the
495 fertilization and early development of sea urchin, *Strongylocentrotus nudus*. J. Korea Acad.-Industrial
496 Coop. Soc. 13, 3785–3791.
- 497 [76] Stachowitsch, M. 1984. Mass mortality in the Gulf of Trieste: the course of community destruction.
498 P.S.Z.N.I. Mar. Ecol. 5, 243–264.
- 499 [77] Stachowitsch, M. 1991. Anoxia in the Northern Adriatic Sea: rapid death, slow recovery. Pp. 119-129. In
500 *Modern and Ancient Continental Shelf Anoxia*. Tyson, R.V. and Pearson, T.H. (eds.). Geological Soc. Spec.
501 Pub. 58, London.
- 502 [78] Waheed, S. 2014. Investigation of the effect of *Ectocarpus* sp. on mortality and behaviour of a number of
503 marine invertebrate species at Lough Hyne, Ireland. Dissertation, University College Cork.
- 504 [79] Menge, B.A., Olson, A.M. 1990. Role of scale and environmental factors in regulation of community
505 structure. Trends Ecol. Evol. 5, 52–57.

- 506 [80] Burkholder, J.M., Tomasko, D.A., Touchette, B.W. 2007. Seagrasses and eutrophication, J. Exp. Mar. Biol.
507 Ecol. 350, 46–72.
- 508 [81] Breitburg, D. 2002. Effects of hypoxia, and the balance between hypoxia and enrichment, on coastal fishes
509 and fisheries. Estuaries 25, 767–781.
- 510 [82] Tyler, R.M., Targett, T.E. 2007. Juvenile weakfish *Cynoscion regalis* distribution in relation to diel-cycling
511 dissolved oxygen in an estuarine tributary. Mar. Ecol. Prog. Ser. 333, 257–269.
- 512
- 513

514

515

Figure Legends

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

522

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

526

527 **Fig. 3.** Observed differences in dissolved oxygen concentrations above and below selected rocks in **a** Aug/Sep
528 2011 (n = 10 rocks/site) and **b** Aug/Sep 2013 (n = 20 rocks/site) at long-term monitoring sites in Lough Hyne,
529 SW Ireland. Error bars represent SE and the dashed vertical line indicates oxygen saturation in air.

530

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

535

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

Figure 1
[Click here to download high resolution image](#)

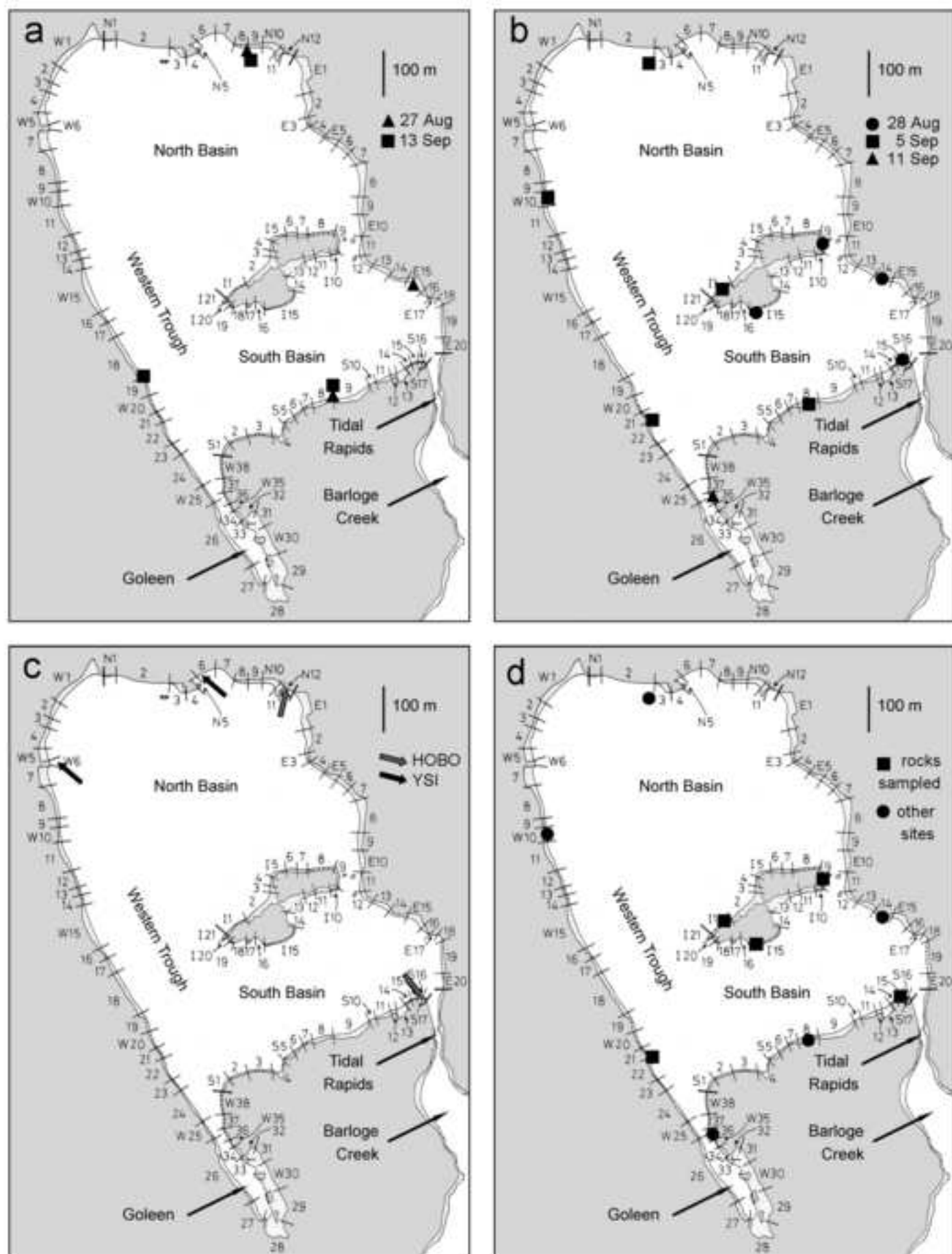


Figure 2

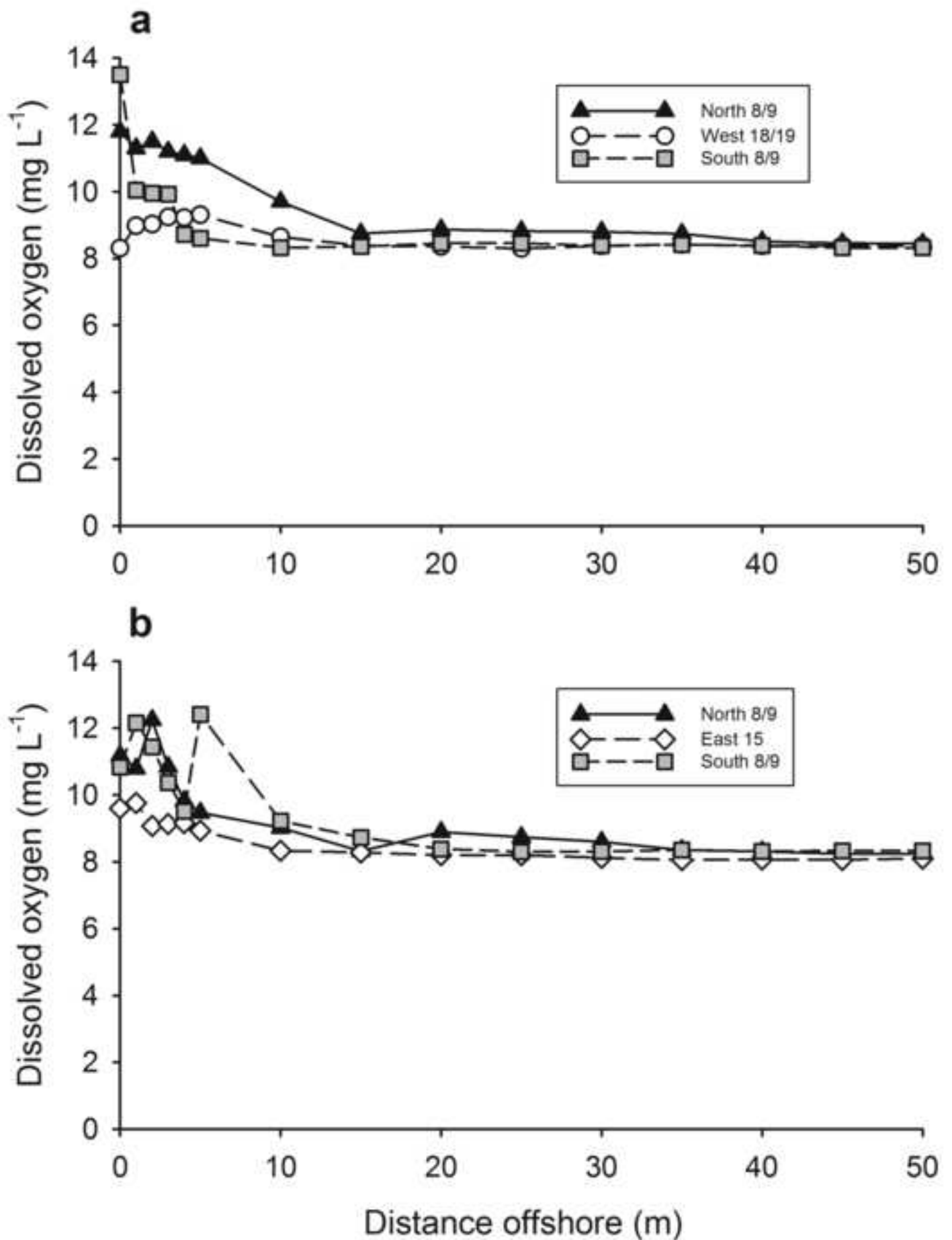
[Click here to download high resolution image](#)

Figure 3
[Click here to download high resolution image](#)

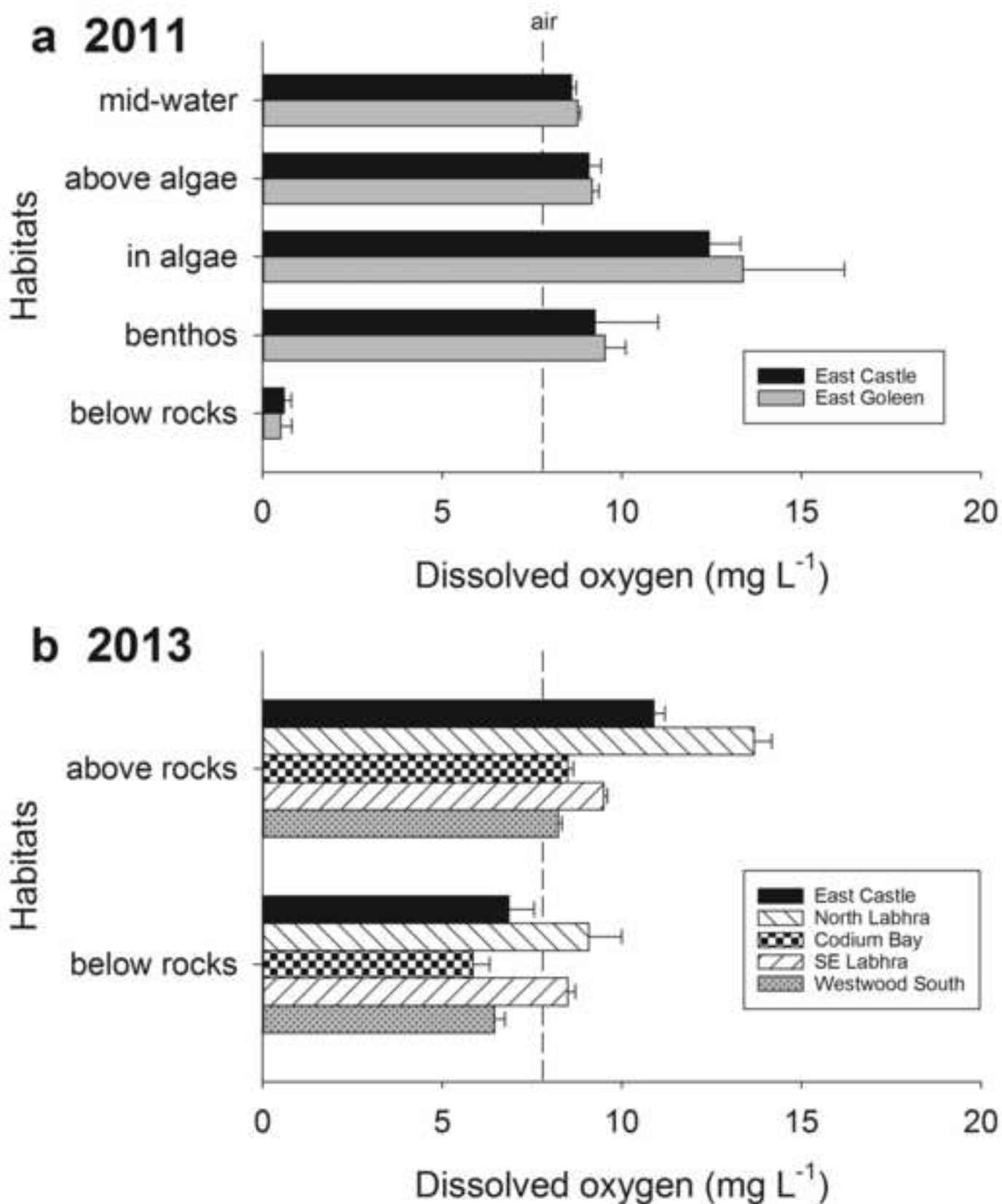


Figure 4

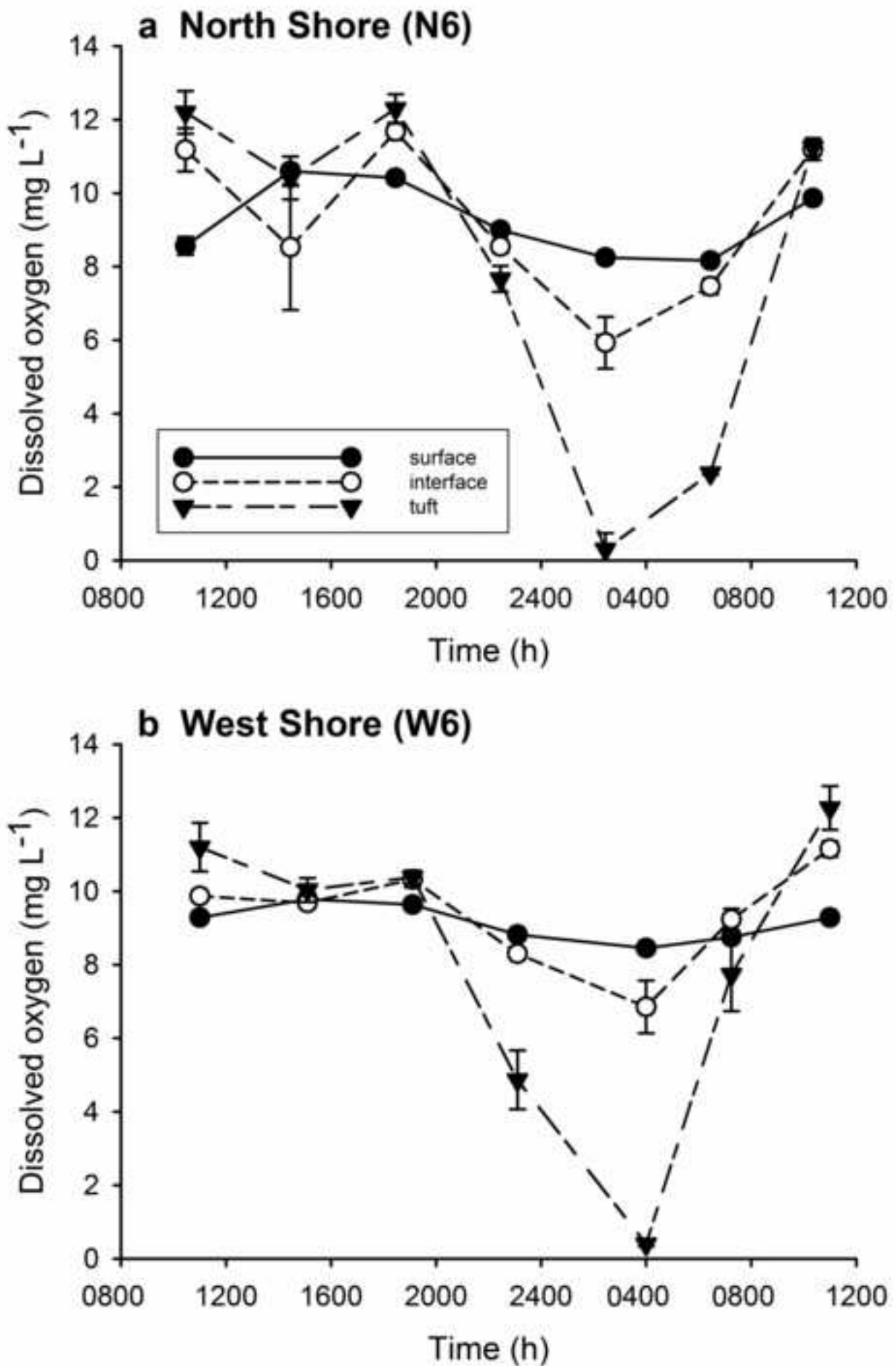
[Click here to download high resolution image](#)

Figure 5
[Click here to download high resolution image](#)

