1 **Title:** Reviews and syntheses: Biological Indicators of Oxygen Stress in Water
2 Breathing Animals

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32   *ABSTRACT*

33   Anthropogenic warming and nutrient over-enrichment of our oceans have
34   resulted in significant, and often catastrophic, reductions in dissolved oxygen
35   (deoxygenation). Stress on water-breathing animals from this deoxygenation has been
36   shown to occur at all levels of biological organization: cellular; organ; individual;
37   species; population; community; and ecosystem. Most climate forecasts predict increases
38   in ocean deoxygenation, thus it is essential to develop reliable biological indicators of
39   oxygen stress that can be used by regional and global oxygen monitoring efforts to detect
40   and assess the impacts of deoxygenation on ocean life. This review focuses on indicators
41   of low-oxygen stress that are manifest at different levels of biological organization and at
42   a variety of spatial and temporal scales. We compare particular attributes of these
43   indicators to the dissolved oxygen threshold of response, time-scales of response,
44   sensitive life stages and taxa, and the ability to scale the response to oxygen stress across
45   levels of organization. Where there is available evidence, we discuss the interactions of
46   other biological and abiotic stressors on the biological indicators of oxygen stress. We
47   address the utility, confounding effects, and implementation of the biological indicators
48   of oxygen stress for both research and societal applications. Our hope is that further
49   refinement and dissemination of these oxygen stress indicators will provide more direct
50   support for environmental managers, fisheries and mariculture scientists, conservation
51   professionals, and policy makers to confront the challenges of ocean deoxygenation. An
52   improved understanding of the sensitivity of different ocean species, communities and
53   ecosystems to low oxygen stress will empower efforts to design monitoring programs,
54   assess ecosystem health, develop management guidelines, track conditions, and detect
55   low-oxygen events.

60   *INTRODUCTION*

61   Oxygen remains fundamental to the success of most marine life. As a result of
62   both a warming planet and coastal eutrophication, oxygen-depleted waters (referred to
63   here as deoxygenated), have increased in both spatial and temporal extent in our oceans
64   (Breitburg et al., 2018). Open ocean oxygen minimum zones have expanded (Stramma et
65   al., 2008; 2010) and coastal areas experiencing hypoxia (low or depleted dissolved
66   oxygen) continue to increase worldwide (Diaz and Rosenberg, 2008; Dai et al., 2023).
67   While some ocean biota have evolved to live in permanently low-oxygen environments,
68   normally oxygenated (normoxic) coastal waters are now experiencing periods of hypoxia
69   that range from diel to seasonal in time-scale and result in stress for water-breathing
70   animals. In addition, increases in ocean temperatures both gradual with climate change
71   and episodic through events like marine heat waves, have decreased the solubility of
72   oxygen across various marine ecosystems and increased organisms' metabolic demands
73   and respiration such that deoxygenated waters are becoming less tolerable for marine
74   animals (Woods et al., 2022). New anthropogenic initiatives such as the expansion of
75   aquaculture (e.g. Zhang et al., 2018) and planned large-scale mitigation measures to
76   enhance marine carbon sequestration (Levin et al., 2023) present new challenges with
77   respect to deoxygenation. These current and future challenges reinforce the critical need
78   to develop biological indicators of oxygen stress that can be used to assess and predict
79   the effects of expanding deoxygenation on ocean biota.

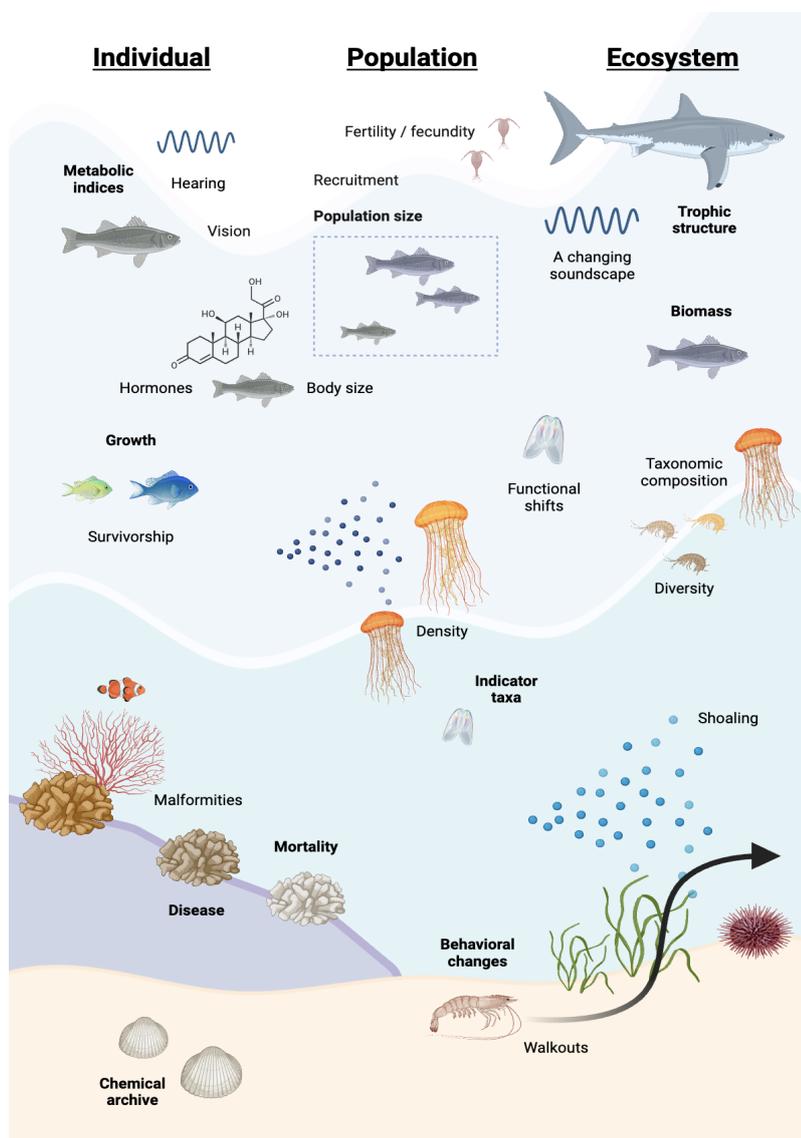
80   Oxygen content itself has been proposed as an indicator of ocean health and of
81   large-scale restoration progress; for example, we can use oxygen content to monitor
82   reduced nutrient loading (Grégoire et al., 2021). However, biotic indicators may provide
83   more direct support for environmental managers, fisheries scientists and policy makers in
84   their efforts to better assess the sensitivity of different ocean species, communities and
85   ecosystems in response to oxygen stress. Indicators enable us to use readily available and
86   measurable data to develop a variable, or set of variables, that reflects the state of some
87   aspect of the system that is important and worth monitoring. Indicators are often used
88   because they can be easier to measure than the actual aspect of the system they are
89   designed to assess. For example, observations of changes in animal behavior can
90   sometimes be used as a quick, reliable and inexpensive indicator of deoxygenation
91   whereas sensors used to measure oxygen loss might be difficult to obtain, costly, and
92   time intensive. Indicators can integrate exposure effects over space and time and they are
93   likely to reflect cause-and-effect as they tend to have a direct mechanistic link to a
94   stressor of interest.

95   Indicators have been widely used by organizations at the international level to
96   assess the state of environmental health and sustainability. However, there remains an
97   open need for the development of indicators at the international level which focus on the
98   biological effects of deoxygenation. For example, the Framework for Ocean Observing
99   (Lindstrom et al., 2012) has identified numerous Essential Ocean Variables (EOVs)
100   intended to capture the fundamental characteristics of marine ecosystems that can be

101 combined into indicators in order to represent natural complexity, track changes in the
102 environment, reflect management performance, deliver information, and assess progress
103 in achieving long-term goals (Miloslavich et al., 2018). EOVs, which are selected for
104 their societal and scientific responsiveness as well as their implementation readiness
105 include abiotic variables, such as oxygen, as well as biological variables, such as
106 biomass of phytoplankton and zooplankton, fish abundance, and coral cover. Garçon et
107 al. (2019) examined the application of EOVs to understand biotic responses to oxycline
108 changes within Oxygen Minimum Zones (OMZs) by comparing global monitoring
109 programs. The study of EOVs and similar indicator inquiries can have tangible impacts
110 on management and policy, with the potential to shape mitigation efforts and the
111 direction of associated biodiversity policies. Thus, here we examine indicators that show
112 biological and ecological responses of organisms to low dissolved oxygen (DO) in an
113 effort to help guide those international efforts as well as the efforts of local biological
114 management.

115 Low-oxygen stress has been shown to occur at all levels of biological
116 organization (cellular, organ, individual, population, community and ecosystem) with
117 varying degrees of oxygen sensitivity and time-scales of response (Woods et al., 2022;
118 Figure 1). Measurements are often made on individuals and extrapolated to higher levels
119 of biological organization, time scales and spatial extent using various scaling methods
120 that are conceptual, statistical, or simulation-based. Issues specifically related to
121 indicators of low-DO effects include: (a) differentiating lethal versus sublethal
122 responses; (b) the fact that exposure of individuals to low-DO is time-dependent because
123 DO varies spatially and temporally and mobile organisms move through dynamic DO
124 fields; (c) low-DO exposure is almost always part of a suite of abiotic stressors that
125 covary to various degrees, thus making it difficult to isolate the responses to low-DO;
126 (d) scaling beyond the measured individual response to low-DO can be challenging
127 because the responses integrate across the population, community and ecosystem levels
128 which include a complex suite of biological interactions that are themselves affected by
129 low oxygen.

130 Deoxygenation rarely acts alone as a stressor. It is frequently recognized to be a
131 result of ocean warming and a product of increased respiration (which can be induced by
132 higher temperatures or excess nutrients). Thus, it is common for hypoxia to co-occur
133 with elevated temperature, lower pH and carbonate saturation state, presence of
134 hydrogen sulfide, and /or increased food supply (Breitburg et al., 2019; Laffoley and
135 Baxter, 2019). This means that some oxygen indicators can be confounded with other
136 environmental factors and attribution to oxygen limitation specifically becomes
137 problematic. In a mixed model meta-analysis of experimental studies, Sampao et al.
138 (2021) found that relative to warming and acidification, hypoxic events tended to induce
139 stronger negative effects on survival, abundance, development, metabolism, growth and
140 reproduction across taxonomic groups (mollusks, crustaceans and fish), ontogenetic
141 stages, and climate regions studied. However, there were also clear interactions among
142 stressors in their biotic effects (both antagonistic and synergistic; Sampao et al., 2020).

143   The focus of this review is on biological indicators of oxygen stress in water-
144 breathing marine animals. We identify indicators for three levels of organization, broadly
145 defined: cellular/individual, population/species, and community/ecosystem (Figure 1).
146 We compare particular attributes of these indicators to the oxygen threshold of response,
147 time-scales of responses, sensitive life stages and taxa, and the ability to scale up the
148 response to oxygen stress to higher levels of organization.

150   Figure 1. Schematic of deoxygenation indicators discussed below for (left)
151 individuals, (middle) populations and species, and (right) communities and ecosystems.

152

153   *INDICATORS OF OXYGEN STRESS*

154   **Individual Indicators**

155   *Cellular Responses:* Hypoxia Inducible Factors (HIF) and HIF-alpha in particular
156   is a transcription factor common to most metazoans that mediates gene expression in
157   many of the pathways which regulate cellular responses to hypoxia, including metabolic
158   depression, anaerobic metabolism, and mitophagy. Hypoxia as well as Reactive Oxygen
159   Species (ROS) can inhibit the degradation of HIF-alpha, leading to HIF-alpha
160   accumulation in the cell. The response of the HIF-alpha subunit to hypoxia can be
161   measured through gene expression using RNA sequencing (e.g. Alderdice et al., 2021).
162   The relative amount of HIF-alpha and its location within a cell can be tracked using
163   fluorescent protein tagging (e.g., Kallio et al., 1998). HIF-alpha is expressed at a higher
164   rate, accumulates in the cell and is translocated into the nucleus where it accumulates and
165   is then associated with targeted metabolic responses. In responsive species, the HIF
166   expression can respond within minutes (i.e. 0.5 h) following exposure to hypoxia but can
167   take hours in less responsive species. HIFs play a pivotal role in regulating the metabolic
168   response of cells to hypoxia and a change in HIF is likely to have a number of cascading
169   physiological effects. Application of this indicator would require molecular / cellular
170   techniques to detect changes in HIF (i.e. access to specialized laboratory facilities).
171   Baseline levels and response times vary among different species, thus multiple time
172   points would be required to know whether an individual is exhibiting an elevated
173   response. HIF expression can also vary diurnally, therefore treatment controls and
174   temporal factors need to be considered for the use of this indicator.

175   HIF appears to be widespread across metazoan phyla (aside from sponges) and is
176   therefore highly conserved (Rytkonen et al., 2011). However, there are differences
177   between closely related taxa (congeners) in the timing and magnitude of the HIF
178   response (Alderdice et al., 2020). Broad control of metabolic responses by HIFs is likely
179   to mediate organismal responses to other stressors. More work is needed to determine
180   why species differ in their baseline levels of HIF and the regulation of HIF with
181   prolonged hypoxia exposure since sustained response could have negative / irreversible
182   consequences for organisms. While HIF may be more difficult to measure than responses
183   at the population or ecosystem level, it would be valuable to explain differences among
184   species in their response and tolerance to hypoxia.

185

186   *Sensory Systems:* Vision metrics which show a negative response to low-DO
187   include electroretinogram responses (McCormick et al., 2019), behavioral responses
188   (swimming, sinking response to light) and distribution responses that are based on the
189   loss / impairment of vision (McCormick et al., 2017). If some species require more light
190   in deoxygenated waters, activities such as prey capture, predator avoidance and mating
191   may be impaired. Manifestations of visual impairment by hypoxia could include changes

192 in behavior, shoaling distributions and eye abnormalities (resulting from maternal
193 hypoxia). The physical manifestations of hypoxia, such as abnormalities and growth
194 defects, may be easier to detect than changing visual responses since visual response to
195 oxygen has been quantified in very few organisms. There is a need to study how
196 deoxygenation might impact the vision of commercially harvested species, particularly
197 since the vision of several larval species is highly sensitive to deoxygenated waters.
198 Impaired vision could influence their survival (McCormick et al., 2022b) and hence be
199 useful for management in considering susceptibility to catch and possible fisheries
200 restrictions.

201   Similarly, animal perception of sound may also be impaired by the loss of
202 oxygen. For example, studies on fish show temporary losses of hearing under anoxia; a
203 lowered probability of a "fast startle" response, with an increased risk of falling prey and
204 decreased likelihood of successful foraging; and, possibly, a reduced ability to
205 communicate (Suzue et al., 1987; Sanchez-Garcia et al., 2019). While some reduction in
206 hearing response can occur rapidly with decreased oxygen (< 24 h), morphological
207 changes to fish otoliths in deoxygenated waters may occur over years. While animals'
208 perception of sound underwater is changing due to deoxygenation, we can expect to see
209 changes in the underwater soundscape itself that are associated with changes in
210 populations and ecology. Anthropogenic warming is speeding up the rate at which sound
211 travels underwater via changes in density (e.g. Affatati et al., 2022), while changes in
212 oxygen may alter what sounds animals make or the frequency of those sounds.

213   Changes in the olfactory processes / responses of some marine animals may be
214 associated with changes in oxygen. However, these changes are generally much harder to
215 study and have not been adequately explored across marine fauna to be useful as an
216 indicator at this time (Tigert and Porteus, 2023).

217

218   *Hormonal Changes Influencing Growth and Fertility:* Hypoxia exposure causes
219 physiological stress which increases endocrine cortisol levels relative to normoxic
220 conditions in fish (Léger et al., 2021). Hypoxia can also alter the levels of growth-
221 hormone-insulin-like growth factor thereby negatively affecting growth among
222 individuals, relative to normoxic conditions (Hou et al., 2020). Cortisol levels increase
223 when oxygen levels are low enough to cause a physiological stress response. Oxygen
224 thresholds that give rise to changes in cortisol and growth hormone levels are specific to
225 species and developmental life stage. Changes in cortisol levels can include rapid
226 responses to acute hypoxia exposure or chronic responses to long-term hypoxia
227 exposure. These types of changes in stress hormones can subsequently give rise to
228 reduced immune function and feeding suppression (Gregory and Wood, 1999)
229 potentially leading to reductions in growth or higher natural mortality. Measurements of
230 cortisol in fish are typically conducted using an enzyme-linked immunoassay (ELISA) in
231 blood serum. Since plasma cortisol is the most commonly used indicator of stress in fish,
232 there are ongoing efforts to develop improved protocols for cortisol measurement

233 including non-invasive methods using fish scales (Sadoul and Geffroy, 2019). Similarly,
234 immunoassays can also be used to measure levels of growth hormone in fish. This
235 indicator is not hypoxia-specific however, and changes in cortisol or growth hormone
236 levels can reflect responses to other stressors such as handling stress during sampling
237 (which can artificially elevate cortisol). Thus, this indicator would likely work best in
238 experimental or controlled settings such as aquaculture facilities. However, new
239 approaches for measuring cortisol levels in fish scales may further extend the utility of
240 this indicator to field studies / nature.

241   Hypoxia can disrupt a variety of other hormones in fish and invertebrates beyond
242 stress and growth hormones and include hormones that control gonad development,
243 sperm motility, and reproductive behaviors (Thomas and Rahman, 2009; Wu, 2009). At
244 certain low-oxygen levels, reproduction is entirely inhibited and animals will not attempt
245 to mate for reasons that are not fully understand but likely have to do with hormonal
246 triggers. For example, the egg production rate of copepods has been shown to decrease in
247 deoxygenated water (Ambler, 1985) and egg production overall is reduced in response to
248 chronic oxygen limitation during the copepods' adult life stages. Rising temperatures and
249 low-DO conditions have been linked to changes in copepod antioxidants that would
250 normally protect lipids, proteins and DNA, all of which are important building blocks for
251 meiosis (von Weissenberg et al., 2022). Laboratory experiments also indicate that
252 exposure to low-oxygen conditions can have transgenerational effects on fish
253 reproduction. For example, Wang et al. (2016) found that hypoxia exposure among male
254 medaka fish led to decreased spermatogenesis and reduced sperm motility in the F2
255 generation. Female medaka exposure led to greatly reduced hatching success in the F2
256 generation (Lai et al., 2019). In croaker fish (*Micropogonias undulates*), exposure to
257 summer-time hypoxia resulted in reduced fertility indicator values measured in the fall at
258 the start of the adult spawning season (Thomas et al., 2015). Reductions in fertility were
259 seen at DO levels above those typically associated with croakers' avoidance behavior
260 such that exposure to fertility-limiting DO levels was high and quite common among
261 individuals found within the hypoxic zone of the Gulf of Mexico (Rose et al., 2018b).
262 Reductions in fertility caused by limiting DO represent sub-lethal effects of
263 deoxygenation and can be linked to important changes in population dynamics (e.g.
264 Richmond et al. 2006; Rose et al., 2018a,b).

265   The development of the fertility indicator illustrates how, through a series of
266 coordinated laboratory experiments, field data collection and modeling, cause-and-effect
267 can be established between low-DO exposure and the resulting changes in the endocrine-
268 based indicator. Detailed laboratory experiments enabled the causal links between
269 exposure and endocrine responses within an individual female adult croaker (Thomas
270 and Rahman, 2009, Rahman and Thomas, 2017). The laboratory data were then used to
271 develop a model of the endocrine functioning of vitellogenesis of individual fish
272 (Murphy et al., 2009) to examine how the indicators measured as blood and organ
273 concentrations would vary over time and under exposures not replicated in the
274 laboratory. These results were then applied to field data from the northern Gulf of

275   Mexico and the indicators of hypoxia exposure / effects were used to assess hypoxia
276   effects at the population-level (Thomas et al., 2015; Rose et al., 2018a).

277

278   *Growth/Body Size/Condition Factor:* Growth, size and condition respond to
279   multiple biotic (i.e. food quality and quantity) and abiotic (oxygen, temperature, pH,
280   salinity) factors. The high ecological relevance of growth, size and condition is because
281   they integrate physiology over multiple sub-processes (metabolism, feeding) and are
282   influenced by multiple factors and stressors. Thus, while establishing cause-and-effect
283   linkages between low-DO and growth, size, and condition can be difficult, there is also
284   extensive information available at the individual-level regarding oxygen-induced
285   changes in these factors that are derived from laboratory and field data. This abundance
286   of data reflects the fact that body size and growth are relatively easy to measure and are
287   important determinants of individual fitness because they directly influence other
288   processes that are size- or condition-dependent (e.g., reproduction, mortality). A study
289   indicated that the sensitivity of early life growth of estuarine fish to low-DO is higher
290   than that of low pH conditions (Depasquale et al., 2015). Reduced growth is observed at
291   DO levels above lethal levels and above DO levels that trigger avoidance in zooplankton
292   and fish (Richmond et al., 2006; Stierhoff et al., 2009). In the field, proxies for animal
293   growth rates have included measurements of RNA and DNA, otoliths and weight-
294   specific egg production (e.g. for copepods) which is usually the same as weight-specific
295   somatic growth (Berggreen et al., 1988). Low-DO affects movement, metabolism,
296   feeding behavior and energy intake, all of which depend non-linearly on both DO and
297   temperature (Woods et al., 2022).

298   Both laboratory and field studies have shown that fish and invertebrate species
299   are often smaller in oxygen-limited waters (Richmond et al., 2006; Casini et al., 2016;
300   Limburg and Casini, 2018). Physiology suggests that growth rate is more sensitive to
301   oxygen than development rate, thus for crustaceans, animals grow less between molts
302   and are smaller. The environmental oxygen level below which an organism can no
303   longer obtain sufficient oxygen to support 'normal' respiration is often termed the
304   organism's critical oxygen partial pressure, P_{crit}. Respiration rate will be independent of
305   environmental oxygen above P_{crit} and will be limited by, and proportional to
306   environmental oxygen, below P_{crit}. The environmental oxygen level below which an
307   organism can no longer obtain sufficient oxygen to support a minimum survivable
308   respiration rate can be thought of as the organism's lethal oxygen partial pressure, P_{leth}.
309   Below P_{leth} there will be an increased probability of mortality due to the scarcity of
310   oxygen in the environment. When oxygen levels are $< P_{crit}$ for any particular species, a
311   reduction in growth and size is likely to occur. When oxygen levels are $< P_{leth}$ for that
312   same hypothetical species, it might be replaced by a smaller species with a lower P_{leth}.
313   Thus, dominance of smaller-sized organisms can occur as the result of oxygen limiting
314   growth among particular cohorts of individuals or through the replacement of large-
315   bodied individuals / species in an area by smaller species over a prolonged period of

hypoxia. Warmer temperature can also result in smaller body sizes among fish and invertebrates (e.g. Atkinson, 1994). Thus, lower oxygen frequently interacts with temperature to reduce organism size and can also cause a shift towards smaller bodied species (Chapelle and Peck, 1999; Gillooly et al., 2001; Rubalcaba et al., 2020; Verberk et al., 2021). For example, smaller copepods have a higher surface to volume ratio compared to larger copepods, which favors their oxygen uptake (which occurs through their body surface) over larger copepods in hypoxic waters. In laboratory experiments Stalder and Marcus (1997) showed that the smaller copepod *Acartia tonsa*, survived low oxygen conditions better than the larger *Labidocera aestiva* and *Centropages hamatus*. In similar types of laboratory experiments, Roman et al. (1993) found that the smaller copepod *Oithona colcarva* survived low oxygen conditions better than the larger *Acartia tonsa*. Small-bodied and sessile benthic taxa are often more hypoxia- tolerant than large-bodied taxa. This can lead to faunal size zonation across oxygen gradients among benthic meio-, macro- and megafauna, as observed in oxygen minimum zones of the Indian (Gooday et al., 2009a) and Pacific Oceans (Levin et al., 1991).

Condition factor is calculated from organism length and weight or by direct methods related to lipid content (e.g. Herbinger et al., 1991). Condition factor is a morphometric measurement taken on animals collected inside/outside of hypoxic areas, while estimates for growth require that multiple samples be taken over time. Condition factor of Baltic cod has been related to hypoxia exposure with worsening hypoxia in the last two decades leading to poor condition that along with other trending factors (decreasing food availability), has contributed to a long-term population decline (Casini et al., 2016; Limburg and Casini, 2019). Both individual growth and condition factor can be scaled up to the population with sufficient sampling. For example, Eby et al. (2005) assessed low-DO effects on Atlantic croaker in the Neuse River US estuary using growth rates estimated from cage experiments in the field and benthic cores used to quantify food availability. They compared summers across three years that had different hypoxia conditions and conducted field surveys (feeding, condition, growth) to assess the effects of low-DO on juvenile fish growth rate. They used a stage-within-age matrix model to ascertain the population-level effects of low-DO and found that reduced juvenile growth due to hypoxia also reduced population growth rates. As coastal hypoxia expands, more studies are needed to understand the effects of low-DO on animal growth rates.

Malformation: Low-DO conditions can result in abnormal development of marine organisms. The most sensitive life stages are larvae with malformation by hypoxia confirmed for larval stages of polychaetes, oysters, and fishes in laboratory experiments. For example, larval development of the tubeworm *Hydroides elegans* was delayed and more malformed larvae were found in low-DO conditions (Shin et al., 2013; 2014; Leueng and McAfee, 2020). High mortality and detrimental effects on development and growth were found in the oyster, *Crassostrea virginica*, under hypoxia (Baker and Mann, 1992). Exposure to moderate hypoxia for larval stages of the

European Seabass (*Dicentrarchus labrax*) induced opercular malformation (Cadiz et al., 2018). A subset of market squid (*Doryteuthis opalescence*) embryos exposed to low-DO and low pH exhibited malformations including eye dimorphism and deformities in the mantle and body (Navarro et al., 2016). Malformation caused during early life stages might induce lower survival of larvae through reduced ability to capture food and escape from predators. More research is needed to determine the carry-over effects of malformation during larval stages to the later developmental stages. Oxygen demand and food availability are both related to malformation, thus warmer temperatures and less food availability are important co-stressors.

Mortality: Mortality is the most conspicuous and common metric for hypoxia impact on aquatic organisms and is used in the development of water quality criteria in various coastal systems. Mortality at a particular oxygen level indicates that the organism's metabolic processes cannot be maintained by the ambient oxygen. While animals may tolerate short-term reductions in oxygen, mortality occurs once they deplete their anaerobic coping mechanisms. Immediate mortality may occur during extreme hypoxic events or under anoxic conditions that are accompanied by the release of hydrogen sulfide. Most low-oxygen tolerance measurements for mortality are made under laboratory conditions by manipulating oxygen partial pressure (Vaquer-Sunyer and Duarte, 2008). The lethal oxygen concentration as defined in laboratory experiments is measured over a set time period, usually 24 h. Lethal hypoxia has also been estimated from field measurements with organism presence/absence as a function of oxygen concentration (or partial pressure). Field-based estimates of mortality are less certain because of the temporal and spatial variations in oxygen as well as changes in the vertical/horizontal distribution of the organism. Temperature will affect the assessment of lethal oxygen level because of its influence on oxygen solubility as well as the animals' overall metabolic demands. Thus, if an oxygen concentration is used for estimates of lethal oxygen level, the temperature and salinity conditions should also be reported to allow for the calculation of oxygen partial pressure (Hofmann et al., 2011).

The accurate use of mortality as an indicator of deoxygenation is subject to the characteristics of an organism's life history and habitat. Larval stages with limited oxygen uptake features may have higher lethal oxygen thresholds than juvenile and adult stages. Benthic species which cannot swim out of hypoxic zones may have more physiological mechanisms to survive at low-oxygen concentrations. Low-DO that results in individual mortality can have a range of critical levels that may depend on the age/size of the organism. These variable impacts could be used in assessments of the impact of low-oxygen on the mortality rate of populations (Rose et al., 2018b). The lethal limit of oxygen for a particular species can be used for the analysis of available animal habitat (e.g. Brandt et al., 2023) and as a water quality criterion for maintaining the species in particular water bodies (Ekau et al., 2020).

398   *Chemical Archives of Hypoxia Exposure:* Dissolved manganese (Mn^{2+} and Mn^{3+})
399 becomes more abundant under low oxygen conditions in marine waters (Trouborst et al.,
400 2006). Fish otoliths take up the trace element manganese (Mn) and the Mn:Ca ratio in
401 the aragonitic otoliths can reflect the fish's presence in deoxygenated waters (Limburg et
402 al., 2015). The use of Mn:Ca in otoliths as a hypoxia indicator requires knowledge about
403 regional differences in seawater Mn concentrations which can otherwise confound or
404 complicate interpretations of otolith data in fish from different areas. Further
405 complicating the use of this metric of hypoxia exposure is the observation that
406 manganese uptake is also affected by growth rate (Limburg et al., 2015). Another otolith
407 chemical proxy for hypoxia is the ratio of Mn to the trace element magnesium (Mg),
408 which is also taken up in otoliths but is regulated by growth processes (Limburg et al.,
409 2018). These chemical ratios in otoliths were used to infer not only exposure to hypoxia
410 of cod to low oxygen waters in the Baltic but also physiological stress as indicated by
411 reduced metabolic activity as suggested by lower Mg:Ca (Limburg and Casini, 2019),
412 but see Valenza et al., (2023) for an opposite response in Gulf of Mexico. Recent
413 analysis of six fish species from 3 open ocean OMZs (Namibia, Southern California and
414 Baja California) revealed a common elemental fingerprint attributed to hypoxia
415 exposure, based on Sr:Ca, Mn:Ca, Ba:Ca, Cu:Ca and Mg:Ca and distinct from giant sea
416 bass collected in well-oxygenated shallow waters (Cavole et al., 2023). Few tests of
417 invertebrate structures exist, however Navarro et al. (2014) documented elevated U:Ca in
418 squid statoliths experimentally subjected to low-oxygen alone and low-oxygen / low pH
419 compared to normoxic conditions.

420

421   *Metabolic Indices:* The tolerance to hypoxia decreases with increasing
422 temperature as a result of reduced oxygen solubility and increased animal respiration
423 (Pörtner and Knust, 2007). The relationship of oxygen supply to oxygen demand, called
424 the Metabolic Index (MI), describes the potential of the environment to support aerobic
425 metabolism relative to basal metabolism (Deutsch et al., 2015). The MI accounts for the
426 non-linear interactions of temperature and oxygen stress to particular organisms. Deutsch
427 et al. (2020) recently updated this metabolic index to account for the effect of species-
428 specific oxygen supply capacity. This modification improves estimates for highly mobile
429 or hypoxia-tolerant species with high oxygen supply capacities. The application of both
430 metabolic indices (Penn et al., 2018; Deutsch et al., 2020) requires information on
431 experimentally derived temperature-dependent low-oxygen thresholds that are not
432 available for most marine species. Yet, these indices can still be applied when
433 experimental data are lacking, using the approach developed by Howard et al. (2020),
434 which is based on the development of different ecophysiotypes. This modeling approach
435 has been used to project species distributions in future warmer oceans (Deutsch et al.,
436 2015), past and future species extinction (Penn and Deutsch, 2022), the distribution and
437 size of species in future oceans (Deutsch et al., 2023) and the "climate velocity" of the
438 MI, which predicts how fast and in which direction an organism will need to move in
439 order to survive and maintain its metabolic niche in a future ocean (Parouffe et al.,

2023). Clarke et al. (2021) developed a comparable index, called the Aerobic Growth
Index (AGI), which integrates growth theory, metabolic theory and biogeography
(Cheung et al., 2013) to create a theoretical oxygen supply to demand ratio. AGI uses
oxygen demand at the maintenance metabolic rate, while the metabolic indices (Deutsch
et al., 2020; Penn et al., 2018) use oxygen demand at the resting metabolic rate. In AGI,
maintenance metabolic oxygen demand supports survival, feeding and movement but not
growth (Pauly and Cheung, 2018). The resting metabolic oxygen demand of the
metabolic indices (Deutsch et al., 2020; Penn et al., 2018) occurs at the onset of mortality
or anaerobic metabolism (Deutsch et al., 2015). Therefore, the difference between the
maintenance and resting metabolic rate is the scope for feeding and movement.

Note that these forecasts and hindcasts using MI include livable habitat space
estimated from temperature and oxygen and not the required food resources or predation
pressure. In addition, the forecasts of animal distributions based on MI or AGI currently
do not allow for variation in tolerances within species, adaptive responses that take days
or weeks to occur, nor adaptation to lower oxygen through evolution. Most of the
information we have on oxygen tolerance (which forms the basis of MI) is derived from
studies that focused on the adult stages of larger organisms. Few, if any of these MI
forecasts include validation with measurements of animal abundance. One validation
used the *in-situ* temperature and oxygen of Chesapeake Bay to predict the Bay volume
where oxygen supply would exceed oxygen demand for the copepod *Acartia tonsa*
(Roman and Pierson, 2019). Field measurements of copepod distributions verified that *A.
tonsa* abundance was higher in areas of the water column with a positive predicted MI
index (Roman and Pierson, 2019).

Field Metabolic Rates (FMR) have been estimated for teleost fish by analyzing
the δ^{13}C of their otoliths (Chung et al., 2019). The stable isotope composition of C in the
aragonite of fish otoliths varies with the isotopic composition of fish blood which is
determined by the DIC in ambient water and the metabolized carbon released by
respiration. Chung et al. (2019) determined that the δ^{13}C of the otoliths of Atlantic cod
(*Gadus morhua*) were related to oxygen consumption in the laboratory. The relationships
established were applied to wild cod and other deep-water fish species to infer *in situ*
FMR (Chung et al., 2019). Jones et al. (2023) applied the FMR approach to assess
warming and deoxygenation of the North Sea on both juveniles and adult European
plaice (*Pleuronectes platessa*) in time-series in the North Sea between the 1980's and
2000's to show the effect of increasing temperatures on the FMR of the fish. Like other
otolith proxies, the FMR was limited to timescales no shorter than approximately one
month (e.g., Jones et al., 2023). However recent developments of otolith microchemistry
increased the timescale for 10 days (Sakamoto et al., 2022) and possibly extends to
weekly to daily for faster growing otolith species like jack mackerel (Muto et al., 2023;
Enomoto et al., 2023). Otolith δ^{13}C and δ^{18}O can be measured simultaneously and thus
can be used to assess FMR (carbon ratios) and temperature (oxygen ratios) under model
assumptions and known salinity conditions since δ^{18}O of water has a linear relationship
with salinity. Additional laboratory work to calibrate the δ^{13}C of otoliths to respiration

482   needs to be conducted for additional fish species including both juveniles and adults over
483   a range of temperatures. Both the MI and FMR have potential to be widely used for
484   direct measurements of metabolic rate in fishes, serve as valuable input data to models
485   and, are important tools to assess fish in a future warmer ocean with less oxygen.

486

487   **Species/Population**

488

489   *Indicator Species*: Indicator species, sometimes also termed sentinel species
490   (Schwacke et al., 2013), are used to reflect present and past oxygen conditions. They
491   may reflect high sensitivity to hypoxia or they may be hypoxia-tolerant species that
492   dominate a system under severe oxygen loss as other species are eliminated. We can also
493   identify indicator taxa (higher-level groupings such as genera or families) whose
494   presence or absence may reflect hypoxia. Ligooxyphiles are low-oxygen specialists
495   meaning that they are species that select for and thrive in environments with extreme
496   hypoxic conditions (Gallo et al., 2019); their presence and abundance can be used as an
497   indicator of hypoxic conditions. Examples of macroscopic ligooxyphiles include certain
498   types of soft-bodied fishes, cnidarians (jellies) and ctenophores.

499   At the level of species, indicator response could be to oxygen availability
500   (concentration, partial pressure, percent saturation) or to extremes, duration, or temporal
501   variability of hypoxia. Loss or increase of sentinel hypoxia indicator species or taxa are
502   likely detected via community inventories as part of time series. Community-based
503   sampling through imagery taken by Remote Operated Vehicles (ROVs) or sampling by
504   trawls, multicores or grabs can detect these sentinel species. The presence of biogenic
505   materials from sentinel/indicator species (e.g. shells, scales, otoliths, environmental
506   DNA (eDNA), bones) in sediment cores could also be used to examine species response
507   to oxygenation through time and to detect hypoxia indicator taxa (e.g. Moffitt et al.,
508   2015).

509   Hypoxia tolerance is often associated with organic enrichment as is the case for
510   annelids in the genus *Capitella* (Rosenberg, 1972) although *Capitella* cannot tolerate
511   anoxia (Ogino and Toyohara, 2019). Taxa indicative of low oxygen conditions that are
512   found commonly in suboxic basins (DO <0.1 ml L^{-1}) often include the gastropod *Astyris*
513   *(Allia) permodesta* and the oligochaete *Olavius crassitunicatus* (Levin et al., 2003). In
514   the Gulf of California, the catshark *Cephalurus cephalus* and the ophidiid *Cherublemma*
515   *emmelas* select for areas with suboxic conditions (DO < 5 μmol kg^{-1}; Gallo et al. 2019).
516   The molluscs *Lucinoma heroica* and *Dacrydium pacificum* and the codlet *Bregmaceros*
517   *bathymaster* are also species indicative of the presence of extreme hypoxic conditions in
518   the Gulf of California (Zamorano et al., 2007). Certain species of benthic foraminifera
519   have been used as indicators of low-oxygen conditions in paleo-oceanographic studies
520   (Gupta and Machain-Castillo, 1993). *Uvigerina peregrina* for example, is associated
521   with oxygen minimum zones in the Pacific and Arabian Sea (e.g., Moffitt et al., 2014).

522 Members of the genera *Globobulimina* and *Chilostomella* can withstand euxinic
523 conditions and can store and respire nitrate (Glud et al., 2009; Piña-Ochoa et al., 2010).
524 The benthic foraminifera, *Globobulimina pseudospinescens*, *Stainforthia fusiformis*, and
525 *Nonionella turgida* can indicate the presence of anoxic or severely hypoxic conditions in
526 Scandinavian fjords and these species can survive these conditions by storing and
527 respiring intracellular nitrate (Risgaard-Petersen et al., 2006). For hypoxia-tolerant
528 species that take over a system via successful reproduction this may be related to life-
529 cycle duration and could take months to years. Long-term seasonal presence of bottom
530 water hypoxia may favor pelagic copepod species which brood their eggs as compared to
531 broadcast spawners whose eggs would sink into anoxic/hypoxic bottom waters. For
532 example, increased eutrophication and low-oxygen bottom waters have resulted in an
533 increase in the abundance of the small, egg-carrying copepod *Oithona davisae* in Tokyo
534 Bay and decline in the occurrence of *Acartia omorii* and *Paracalanus sp.*, copepods that
535 release their eggs into the water column (Uye, 1994).

536 Indicator species presence may be a straightforward way to detect oxygen
537 changes and is easy to interpret. Hypoxia thresholds have been demonstrated for many
538 taxa (Vaquer-Sunyer and Duarte, 2008) and highly sensitive species have been
539 identified. However, indicator species or taxa may vary regionally as species evolve
540 different oxygen tolerances in different settings or geographic regions that vary in the
541 intensity and temporal variability of hypoxia (Chu and Gale, 2017). Mobile species tend
542 to function as hypoxia-sensitive sentinels whereas sessile taxa may be better tolerant
543 sentinels. A species utility as a sentinel may be determined by accessibility, interest, and
544 response time. If the sentinel species is dominant and lost under increasing hypoxia or if
545 the sentinel species is rare and increasing under hypoxia, it can alter the structure and
546 diversity of communities (or catch). Hypoxia-tolerant and hypoxia-sensitive species may
547 also have different trophic strategies giving rise to food web shifts that accompany the
548 loss or gain of certain indicator taxa.

549

550 *Disease/Parasites:* Under low oxygen conditions, some parasitic and microbial
551 infections can become more common or severe, affecting both individuals and
552 populations. Certain types of pathogenic bacteria start to grow under low-oxygen
553 conditions, increasing organisms' likelihood of exposure (Guo et al., 2022). In addition,
554 low-oxygen effects on host immune responses are common. For instance, low-oxygen
555 disrupts endocrine function and can alter organisms' abilities to buffer against parasitic,
556 bacterial and viral infections at the hormone level (Overstreet, 2021). Reduced
557 hemocyte function and reactive oxygen species production have been found in fish,
558 molluscs and crustaceans exposed to hypoxia (Mydarz et al., 2006; Breitburg et al.,
559 2019; Burnett and Burnett, 2022). The exposure to hypoxia can alter individuals'
560 immune responses on time scales of minutes to hours as well as through longer-duration
561 chronic exposure. At the population level, low-oxygen can increase the prevalence, mean
562 intensity and spatial distribution of infections. For example, diel-cycling hypoxia

563   increased acquisition and progression of the pathogen *Perkinsus marinus* (Dermo)
564   infections in oysters (*Crassostrea virginica*), with stronger effects on younger (1 y)
565   oysters and spatial patterns of prevalence and mean intensity of infections varying with
566   spatial patterns of the frequency and intensity of diel cycling hypoxia (Breitburg et al.,
567   2015). Understanding disease as an indicator of low-oxygen conditions may be
568   especially important in an aquaculture context, as steps can be taken to improve oxygen
569   conditions for the organisms or to move the organisms to well oxygenated waters. The
570   concentration or partial pressure of oxygen that induces disease is a potentially
571   significant non-lethal oxygen threshold that may be useful in setting water quality goals.
572   However, elevated infection prevalence and intensity can be influenced by a wide variety
573   of factors, including co-occurring stressors such as elevated $p\text{CO}_2$. Disease metrics may
574   therefore serve as better indicators of past hypoxia (and the biological changes caused by
575   hypoxia) than as indicators that hypoxia is currently occurring.

576

577   *Behavioral Responses:* Avoidance is a near-universal response of mobile species
578   to encountering low-oxygen conditions. Tolerances vary among species and life stages,
579   and because species vary in how they respond to near lethal levels of hypoxia, avoidance
580   behaviors have broad implications for functional habitat availability and can alter spatial
581   and temporal overlap between predators and prey, potential competitors and
582   conspecifics.

583   Fish are among the most hypoxia-sensitive and most mobile aquatic species who
584   shoal towards the surface, into shallow areas, or away towards open/oxygenated water as
585   oxygen concentrations decline (Eby and Crowder, 2002; Wu et al., 2002). For example,
586   avoidance of low-oxygen has been demonstrated by billfish (Stramma et al., 2012), tuna
587   (Ingham et al. 1977) and sharks (Vedor et al., 2021). Skipjack tuna in particular exhibit
588   an alarm threshold of 3.5 ml L^{-1} DO which helps them avoid conditions representing
589   their median tolerance of 2.4-2.8 ml L^{-1} DO (Ingham et al., 1977). These various
590   behavioral responses to evade hypoxia can lead to habitat compression in which a
591   portion of an organism's range becomes unusable (Kim et al., 2023) and the absence of
592   an organism from where it is normally found. In extreme situations, such an escape
593   response may fail when fish are trapped by land, the entire water column goes hypoxic
594   and/or fish are encircled by hypoxic water, resulting in fish kills which are among the
595   most conspicuous signs of hypoxia. Few studies have examined the response time of
596   avoidance behaviors of mobile taxa which appear to vary for sensitive versus tolerant
597   species from minutes to days.

598   Hypoxia may force organisms into subpar habitat with fitness consequences such
599   as striped bass that are pushed from deeper hypoxic waters in shallows where they are
600   confronted with thermal stress (Kraus et al., 2015; Itakura et al., 2021). Many shallow-
601   water fish species also utilize aquatic surface respiration, ventilating more highly
602   oxygenated water at the air water interface. While this avoidance behavior of 'last resort'
603   may enhance survival, there are associated risks of increased vulnerability to aerial and

surface predators (Dominici et al., 2007). This phenomenon is apparent in the "Jubilees"
in Mobile Bay, Alabama, USA (May, 1973), and "Lobster walkouts" in St. Helena Bay,
South Africa (Cockcroft, 2002) which are among the most widely recognized of such
events that have achieved culturally iconic status. In these cases, commercially important
species including crustaceans and fish, flee hypoxic bottom waters and move into
shallows, or even onto shore, searching for more oxygenated water where they are
vulnerable to harvest in their lethargic and moribund state. Often mobile organisms
emerging from their burrow or crevice habitats become more vulnerable to predation,
and so an ancillary indicator of hypoxia may be predators gorging on dead and moribund
organisms where those predators are adept at tracking the edge of fluctuating hypoxia
areas and/or at making brief forays into hypoxic areas (Seitz et al., 2003). However,
these top predators with high mobility are facing a tradeoff between low-oxygen and
increased prey availability. In other cases, predators that track more oxygenated water
masses may be able to exploit prey that have done the same, such as tuna species in the
mid-latitudes that aggregate in the warm core eddies with high oxygen concentration in
the subsurface which allows them to feed on mesopelagic species for a longer time (Xing
et al., 2023).

Soft-bottom infaunal species also exhibit escape responses emerging from
burrows and buried positions to the sediment surface to seek higher oxygen (and possibly
evading hydrogen sulfide). This includes *Nephrops* lobsters normally tucked away in
burrows that suddenly appear in bottom trawls during hypoxic events, infaunal worms
atypically exposed on the sediment surface and amphipods that extend their tubes above
the sediment surface to reach higher into the water columns (Diaz and Rosenberg, 1995).
Zooplankton can also change their vertical position in the water column to avoid low-DO
bottom waters. In general, depth-stratified zooplankton sampling has shown that copepod
abundances are higher in the surface mixed layer and within the pycnocline compared to
hypoxic bottom water in coastal environments (Roman et al., 1993;2012; Keister et al.,
2000; Pierson et al., 2009; Keister and Tuttle, 2013). However, the vertical compression
of their distribution to the upper water column can increase their vulnerability to
predation by visually feeding fish, and thus alter food-web processes (e.g. Pothoven et
al., 2012; Roman et al., 2012).

Population Size: A reduction in population size in response to deoxygenation can
be the result of reduced reproduction and recruitment, increased mortality as a direct
response to oxygen stress or indirect response through less food availability or increased
predation. Depending on the generation time of the species, both short-term episodic as
well as longer-term chronic deoxygenation can reduce population size (Adamack et al.,
2017; Roman and Pierson, 2019; Pierson et al., 2022; 2023; Duskey, 2023). The limiting
and lethal oxygen partial pressure for impacts on the various developmental stages of the
species would allow the assessment of the impact of *in-situ* oxygen partial pressures on
the population. Limits of this approach include the need to know the P_{crit} and P_{leth} oxygen
levels of the various life stages, unknown genetic adaptations to low oxygen and other
abiotic/biotic factors that complicate the interpretations. It usually is not possible to have

646 the oxygen tolerance information for all species of interest so comparisons/modeling will
647 be necessary to broaden applications to guilds, functional groups and body size scaling.
648 Impacts of low-oxygen are taken into consideration for population models for
649 commercial fisheries and predictions of essential habitat for restoration and protection.

650

651 *Population Growth Rate:* Population growth rate integrates growth, survival, and
652 reproduction of individuals and expresses the net effect of these vital rates at the
653 population-level. Population growth rate therefore reflects multiple pathways of low-DO
654 effects. Population level growth rate is also the basis of management of harvested species
655 and regulatory actions. Like mortality, measuring population growth rate directly in the
656 field is challenging but there is a long history of using statistics and modeling to scale
657 population growth from the available data on growth, mortality, and reproduction (Doak
658 et al., 2021).

659 Population growth rates integrate across effects and life stages and are used for
660 fisheries management and species conservation. Logistic population models have a long
661 history in ecology and directly use population growth rate (r) and carrying capacity (K).
662 Maximum Sustainable Yield (MSY) is traditionally estimated as 1/4th of K times r.
663 Fisheries stock assessments and population modeling for conservation often use more
664 complicated matrix projection models with the population divided into classes (age,
665 stage, or size) that use survival, growth, and reproduction rates specific to classes to
666 generate r and K, in addition to other population-level metrics (Doak et al., 2021). The
667 link to hypoxia indicators is how exposure to low-DO affects the survival, growth, and
668 reproduction rates, either of the total population or by age-class (Rose et al., 2001).
669 Smith and Crowder (2011) used a logistic growth model for blue crabs (*Callinectes*
670 *sapidus)* and included hypoxia effects via changes in predation mortality which affects r
671 and K. Eby et al. (2005) demonstrated how a traditional stage-based matrix model can
672 be used to combine reduced juvenile stage growth rate due to hypoxia to finite
673 population growth rate λ, which is equal to e^r. There are many examples of hypoxia
674 causing reduced habitat availability (e.g., Zhang et al., 2010; Gallo and Levin, 2016;
675 Franco et al., 2022) that can limit the production of a particular life stage within the life
676 history, translating into reduced local productivity (related to r) and reduced carrying
677 capacity. Long et al. (2014) used an age-structured matrix model for the clam *Macoma*
678 *balthica* in two regions with varying DO (permanently normoxic and occasionally
679 hypoxic) and found that hypoxia affected mortality via altered predation pressure,
680 fecundity, and maturity. They reported the response of λ as a function of the proportion
681 of area extent of the hypoxic zone and the duration of the hypoxia.

682 Low-DO has direct and indirect effects that affect survival and reproduction
683 (maturity, fecundity), all of which determine population growth rate, r. There are few
684 examples of direct calculation of growth rate of the population from field data, but it is
685 more common to use a model to scale these parameters to population growth rates. An

686 example is Eby et al. (2005) who used a stage-within-age matrix projection model and
687 converted low-DO effects on growth rate of individuals into extended stage duration for
688 juvenile croaker.

689

690 *Recruitment Rate:* We use the term recruitment here in the fisheries sense of the
691 number of individuals that survive to the stage or age after which natural mortality rate is
692 relatively constant. Note that recruitment is also used (often with benthos and some
693 invertebrates) as the number of larvae that settle and enter their sessile stage. Fisheries
694 recruitment as an indicator of low-DO is of direct ecological and management relevance
695 as it is a driver of population dynamics and forms the basis of most fisheries
696 management plans. However, examples of empirically-based DO effects on fisheries
697 recruitment are rare because recruitment is highly variable, logistically difficult to study,
698 and influenced by many factors and stressors (Houde, 1997), making isolation of the
699 effects of low-DO challenging.

700 Ariyama and Secor (2010) analyzed dredge catch data and showed that the
701 recruitment of Gazami crab (*Portuans trituberculatus)* is related to DO levels. Jung and
702 Houde (2004) examined bay anchovy (*Anchoa mitchilli*) in Chesapeake Bay and found
703 that recruitment of young of the year (YOY) in October was related to DO
704 concentrations and standing stock biomass in the previous summer. They used anchovy
705 length rather than DO directly as a proxy for low-DO effects on growth in a Ricker
706 spawner-recruitment model. Similarly based on analysis of survey data, Boyer et al.
707 (2001) also implicate hypoxia in reduction of the northern Benguela sardine (*Sardinops*
708 *sagax)* recruitment. Population recruitment is thus a valuable index of deoxygenation
709 that has a direct application to fisheries management.

710

711 **Ecosystem Indicators**

712

713 *Diversity:* Diversity metrics reflect the number of species present and how
714 individuals are distributed among the species. This information represents an aggregated
715 outcome of biotic responses manifesting at the individual and population level that are
716 discussed earlier in this paper. Diversity metrics may include components of species
717 richness, evenness, dominance, rarity, or a combination of these metrics. Common
718 indices include species richness (*S*), Shannon Wiener (*H'*), Pielou's *J*, Rarefaction (*ESx*),
719 Hill numbers (*�q D*), and Rank 1 dominance (*R1D*). Diversity indicator metrics can be
720 applied to counts of individuals categorized by species, family or even phyla, but can
721 also be applied to Operational Taxonomic Units (OTUs) or Amplicon Sequence Variants
722 (ASVs), even when species associated with genetic sequences are not known. Diversity,
723 as well as evenness and dominance, are calculated from count data based on field
724 samples or imagery, that are often generated by extensive processing or analysis in the

725 laboratory. Diversity of eukaryotes typically declines with decreasing DO concentration
726 below a threshold that varies with guild and assemblage body size (e.g., mega, macro,
727 meiofauna; Breitburg, 2002; Levin, 2003; Gooday et al., 2010). Examples of species-
728 richness declines under low-oxygen exist for many different systems, including bivalves
729 in temperate estuaries (Ducrotoy et al., 2019), corals in tropical reefs (Altieri et al. 2017),
730 benthos and plankton on seamounts (Wishner et al., 1995), demersal fish in oxygen
731 minimum zone regions (Gallo and Levin, 2016) and fauna of continental slopes (Gooday
732 et al., 2010; Hunter et al., 2012). Dramatic diversity declines are often accompanied by
733 declines in evenness and increased dominance by one or a few species (Levin, 2003;
734 Jeffreys et al., 2012; Yasuhara et al., 2012). Dominance by species may reflect high
735 physiological tolerance to low-oxygen, better competitive abilities under low-oxygen
736 (relative to other species), high food supply or a combination of these factors.

737 Diversity thresholds are influenced by the duration of exposure and temporal
738 variability of low-oxygen stress such that diversity responses differ in coastal versus
739 bathyal OMZ settings in different ocean basins and for mobile versus sessile fauna
740 (Levin et al., 2010; Chu and Gale, 2016; Chu et al., 2018). Diversity (and evenness and
741 dominance) response to oxygen declines or increases have been documented over
742 seasonal cycles, inter annually (e.g. ENSO) and over historical and geological time
743 scales (Arntz et al., 2006; Rabalais and Baustian, 2020; Zarikian et al., 2022). In East
744 Pacific OMZs where oxygen stress is persistent, diversity thresholds for benthic
745 macroinvertebrates and demersal fish occur around 7 µmol kg^{-1} DO (Sperling et al.,
746 2016; Gallo et al., 2020). In coastal waters with seasonal hypoxia, diversity thresholds
747 (assumed to be reflected in species thresholds) may average around 63 µmol kg^{-1} DO, but
748 for crustaceans can be 25-42 µmol kg^{-1} DO in the East Pacific, and 43-77 µmol kg^{-1} DO
749 in the Atlantic Ocean (Chu and Gale, 2016).

750 Advantages of diversity (and evenness and dominance) as an indicator of low
751 oxygen stress include integration of response across species with a clear linkage to
752 ecosystem function and health. Changes in dominance are easy to detect via monitoring
753 programs. Thus, when the community shifts to a dominant that is a hypoxia-tolerant
754 species, it can be a good indicator of oxygen stress at the ecosystem level. Diversity
755 assessment often requires painstaking inventory of species and counts of individuals,
756 requiring both time and resources. Quantitative multiplex PCR (e.g. Wong et al., 2022)
757 can measure eDNA for several target species, small species, and even cryptic species,
758 but is limited for quantitative assessment (e.g., Shelton et al., 2023). Diversity, evenness
759 and dominance can also be influenced by other factors such as food availability or
760 contamination, independently or synergistically with deoxygenation (Rozenzweig and
761 Abramsky, 1993; Levin and Gage, 1998; Pilo et al., 2015).

762 Local (alpha) diversity responses to low-oxygen stress are well documented for
763 benthic metazoan invertebrates (Gooday et al., 2010), benthic foraminifera (Tsujimoto et
764 al., 2006) and demersal fish (Gallo et al., 2020), with the paleo literature replete with
765 examples for fossil forming biota (e.g., Tsujimoto et al., 2008; Yasuhara et al., 2012;

766   Moffit et al., 2014; 2015; Singh et al., 2015). Alpha diversity can be scaled up to beta
767   diversity across gradients or gamma diversity at larger geographic scales. Annelid,
768   nematode and calcareous foraminifera species show high dominance among benthic
769   sediment fauna subject to severe hypoxia. In extreme OMZs, a single species may
770   comprise 40-100% of the macrofauna (Levin, 2003; Jeffries et al., 2012) and
771   foraminifera (Gooday et al., 2000). Metazoan examples include *Linopherus* sp. on the
772   Pakistan Margin at 800m (100% of macrofaunal individuals); *Olavius crassitunicatus* on
773   the Peru margin (86%) and *Diaphorosoma* sp. on the Chile margin (73%). Protozoan
774   examples include the foraminifera *Bolivina seminuda on* the Oman margin (43%)
775   (Gooday et al. 2000). In coastal waters of Chesapeake Bay, paleo dominance (60-90%)
776   by *Ammonia parkinsoniana* is associated with hypoxia (Karlson et al., 2000).

777   Because hypoxia can favor some species, including invasives, hypoxia may lead
778   to higher regional beta or gamma diversity in an ecosystem, even while suppressing
779   alpha diversity at a given impacted site. Given that recovery of diversity following a
780   hypoxic event may take far longer than the initial decline, the fingerprint of diversity as a
781   hypoxia indicator may be apparent for years or decades, allowing for 'detection' of a
782   hypoxic event long after oxygenated conditions have returned.

783   A more mechanistic community-level indicator of the intensity of effects caused
784   by eutrophication-induced hypoxia, focused on species loss, is the Effect Factor (EF)
785   (Cosme and Hauschild, 2016). EF is designed to evaluate impacts of anthropogenic
786   nitrogen and organic inputs on demersal communities by assessing the fraction of species
787   that will be affected by hypoxia based on their individual thresholds. It requires
788   knowledge of species in the community, their hypoxia sensitivities, their geographic
789   distributions and environmental conditions. A species sensitivity distribution
790   methodology is used to combine species distribution and lowest-observed-effect-
791   concentrations for species to estimate the DO concentration at which half of the
792   community's species are affected. This metric, which extends the concept of diversity to
793   include species sensitivity to hypoxia can function as a hypoxia stress or ecosystem
794   health index; it has been applied at large spatial scales for 5 climate zones (Cosme and
795   Hauschild 2016) and to 66 Large Marine Ecosystems (Cosme et al. 2017). Modifications
796   involving species density distributions have generated additional indices including a
797   Potentially Affected Fraction and Potentially Disappeared Fraction (Cosme et al. 2017).
798

799   *Abundance and Biomass:* Changes to community-level measures of abundance
800   and biomass can occur in response to hypoxia. Animal abundance and biomass
801   collections are typically made using community-sampling methods, including trawls,
802   sediment cores, net tows or pumps and visual surveys, or are quantified from video and
803   still imaging by ROVs, submersibles, photo-sleds or autonomous landers. Changes in
804   these indicators can be seen when sampling across oxygen gradients in space or in a time
805   series as abundance and biomass respond to oxygen changes seasonally, as well as over
806   interannual, historical and geologic time scales (Seitz et al., 2009; Moffitt et al., 2014;

807 2015). Species abundance and biomass reflect important biological processes such as
808 recruitment, growth, avoidance, mortality and local extinctions. These indicators broadly
809 integrate responses across species and changes related to the productivity of a system,
810 which is important from a fisheries and ecosystem management perspective (Breitburg,
811 2002). However, because abundance and biomass are closely linked to productivity and
812 food availability, they are often confounded with nutrient input and eutrophication,
813 which gives rise to opposing responses (i.e. abundance will increase with eutrophication
814 but decrease with deoxygenation; Breitburg et al., 2009).

815 The abundance of vulnerable taxa or size groups will typically decrease once
816 oxygen levels fall below a certain oxygen threshold and they may first rapidly increase to
817 higher than baseline levels prior to or at this threshold due to 'edge effects' (Wishner et
818 al., 1995; 2013; Levin, 2003; Yasuhara et al., 2007; 2012; Gooday et al., 2010). Edge
819 effects can result from: (a) different taxa aggregating in a smaller area due to avoidance
820 of a hypoxic zone as described for certain fisheries species in the Gulf of Mexico (Craig,
821 2012); (b) plentiful food (e.g., phytodetritus and meiofauna) combined with absence of
822 predators in a specific oxygen zone as described for OMZs (Gallo and Levin, 2016); or
823 (c) can be related to dominant taxa that thrive at high abundances at a specific low-
824 oxygen threshold, for example ophiuroids bands that form on seamounts and continental
825 margins (Levin, 2003; Vlach, 2022), cusk eels in Narragansett Bay (Hale et al., 2016),
826 and the cusk eel *Cherublemma emmelas* in the Gulf of California (Gallo et al., 2018;
827 2020).

828 The degree of abundance and biomass limitation due to low-DO is dependent on
829 the severity, extent and duration of hypoxia. Oxygen thresholds are taxon-specific, body-
830 size specific, and region-specific. For example, on the US Pacific Coast (Keller et al.,
831 2015) and off Peru (Rosenberg et al., 1983) the catch per unit effort (CPUE) of demersal
832 fish decreases below a specific oxygen threshold, however the thresholds differ between
833 the two systems, with the oxygen threshold being lower off the coast of Peru. DO has
834 also been shown to be an important covariate in explaining demersal fish CPUE in the
835 Chesapeake Bay (Bucheister et al., 2013). However, in general fish landings can be poor
836 indicators of hypoxia due to the effects of shoaling and aggregation (Rose et al., 2019;
837 Chesney et al., 2020).

838 At the community level, changes in animal abundances typically occur at a lower
839 oxygen threshold than that required to see changes in diversity. For demersal fish in the
840 Gulf of California, for instance, DO 3 +/- 1 μmol kg^{-1} was identified as the threshold
841 below which fish abundance decreased (Gallo et al., 2020), compared to a threshold of
842 DO 7 μmol kg^{-1} for diversity. Reductions in abundance of sensitive, less-mobile fish
843 species may occur due to fish kills (Graham et al., 2004; Thronson and Quigg, 2008).
844 Effects may be direct via increased mortality, through prolonged exposure to low-DO
845 (Breitburg et al., 1999; 2003; Turner, 2001; Diaz and Breitburg, 2009) or indirect via
846 reduction of habitat availability in the benthos (Turner, 2001), water column (Wang,
847 1998; Breitburg et al., 1999; Chesney et al., 2000; Turner, 2001) or through alterations to

848 food web structure (Graham, 2001). The general observation of reduced coastal copepod
849 abundances (Roman et al.,1993; Keister et al., 2000; Kimmel et al., 2012) suggests they
850 have lower population growth, greater mortality, predation and/or emigration in water
851 columns with hypoxic bottom waters.

852

853   *Taxonomic Shifts and Ratios:* Taxonomic shifts in community composition and
854 resulting ratios of specific taxa are sometimes considered as hypoxia indicators. These
855 typically reflect differential tolerance of taxa at the species or higher level. As with other
856 indicators the intensity, persistence, duration and temporal sequence of hypoxia will
857 influence taxonomic responses. Taxonomic responses are detected by sampling and
858 counting the entire community or by sampling and counting targeted taxa. Thresholds for
859 taxonomic response differ between seasonally hypoxic/coastal systems and permanently
860 hypoxic systems and with species ontogenetic stage, mobility and body size.

861   It is generally thought that larger-bodied animals that can swim will be most
862 sensitive to low-oxygen conditions and will avoid areas of hypoxia when possible. For
863 example, in a meta-analysis of Atlantic species, fish and crustaceans exhibited less
864 hypoxia tolerance (i.e., higher sublethal and lethal thresholds) than priapulids and
865 molluscs (Vaquer-Sunyer and Duarte, 2008), presumably because of their high metabolic
866 demands and their high mobility. In pelagic systems, specific copepod and krill genera
867 specialize in low-oxygen conditions (Wishner et al., 2013; Tremblay et al., 2020). In
868 coastal waters the dominance of gelatinous zooplankton (ctenophores, jellyfish,
869 siphonophores, salps) over crustaceans in hypoxic waters reflects their tolerance to
870 hypoxia (Breitburg et al., 1997; Ekau et al., 2010; Miller et al., 2012; Purcell, 2012).
871 Note however, that cusk eels and cat sharks (Gallo et al., 2018) and tuna crabs (Pineda et
872 al., 2016) at bathyal depths in the Eastern Pacific can be extraordinarily abundant at DO
873 concentrations < 2 μmol kg^{-1}.

874   Within OMZs and other hypoxic areas, echinoderms often avoid the lowest
875 oxygen concentrations but form dense bands at OMZ edges (discussed earlier). Sponges
876 with high hypoxia tolerance often replace stony corals (Chu et al., 2019) and annelids
877 and nematodes often dominate over other major taxa in both coastal and deep sediments
878 subject to hypoxia (Levin, 2003; Levin et al., 2009; Rabalais and Basutian, 2020).
879 However, there are locations such as the Namibian shelf where molluscs or crustaceans
880 dominate the infauna at very low oxygen concentrations and the longer-lived, hard
881 shelled gastropod and bivalve taxa have been proposed as indicators of oxygen change
882 (Zettler et al., 2009; 2013). Among foraminifera, the rotaliids and buliminids with small,
883 thin walled calcareous tests dominate in severe hypoxia over forams with agglutinated
884 tests (Gooday et al., 2009). On the Louisiana shelf *Pseudononion atlanticum,*
885 *Epistominella vitrea* and *Buliminella morgani* have been used as indicators of
886 historically low-oxygen in sediment core records (Osterman et al., 2003). Similarly,
887 some ostracod species (e.g., *Bicornucythere bisanensis* in Japan; Irizuki et al., 2003;
888 Yasuhara et al., 2003; 2007; *Loxoconcha* sp. in the eastern coast of USA; Alvarez

889   Zarikian et al., 2000, Cronin and Vann, 2003) have been used as low-oxygen indicators
890   (Yasuhara et al., 2012; 2019).

891   Assessing taxonomic shifts and ratios is an important objective of most long-term
892   ecological time series, however it can be difficult to assess these indicators across
893   ecosystems due to methodological artifacts and limitations. For instance, the temporal
894   and spatial scales of response by the zooplankton community to low-oxygen can be very
895   small and sometimes go undetected due to the coarsely integrated sampling approach of
896   most extended net tows (Wishner et al., 2020). For metazoan meiofaunal communities,
897   the nematode:copepod ratio is often cited as an indicator of contaminant stress
898   (Warwick, 1981) but is also seen to change along oxygen gradients in space and time
899   (Levin et al., 2009). Nematode counts increase relative to copepod counts as oxygen
900   declines, reflecting strong tolerance of nematodes to severe hypoxia. The ratio emerges
901   easily from quantitative surveys of meiofaunal taxa, but can be time consuming and
902   difficult to compute when done manually. Changes in nematode:copepod ratios have
903   been observed along OMZ gradients in the Eastern Pacific on a seamount off Mexico
904   (Levin et al., 1991) and on the Costa Rica (Neira et al., 2018), Chile (Neira et al., 2001),
905   and Peru (Levin et al., 2002) margins. Interannual changes in nematode dominance are
906   associated with ENSO cycles off Peru and Chile (Gutierrez et al., 2008; Levin et al.
907   2009). The ratio affects the next trophic level – potentially selecting for consumers with
908   different food preferences and can indicate functional change. Among protozoa, the ratio
909   of *Ammonia* to *Elphidium* (both benthic foraminifera genera) is a common
910   oxygen/eutrophication proxy, with *Ammonia* species much more tolerant to hypoxia (Sen
911   Gupta et al., 1993).

912   Recovery following hypoxia may follow a predictable pattern of species
913   accumulation and replacements (Lim et al., 2006; Steckbauer et al. 2011) and thus
914   taxonomic characterization of communities in a well-studied system may indicate the
915   timing of a prior hypoxic event. As a consequence of variation among species in their
916   tolerance to hypoxia and their ability to recolonize habitat following a low-oxygen event,
917   community composition will be a product of not only the severity of hypoxia, but also
918   the interval between such events (i.e., persistent, seasonal, episodic, or periodic). In areas
919   where hypoxia is persistent, frequent, or recently occurred, we might expect to see the
920   simplest types of communities made up of a limited number of hypoxia-tolerant and/or
921   opportunistic species. While hypoxia is typically thought of as an agent of species
922   elimination, it can have positive effects at the local scale on the presence or abundance of
923   some animals, by freeing up resources through elimination of competitively dominant
924   species, or by excluding less tolerant predators and creating a predation refuge for more
925   hypoxia tolerant prey. Moreover, these potential benefits can extend to invasive species,
926   and as a consequence, hypoxia may lead to higher beta or gamma diversity in an
927   ecosystem, even while suppressing alpha diversity at a given impacted site.

928

Functional Shifts: In areas subject to episodic or seasonal hypoxia, infaunal
animals may exhibit changes in dwelling habit and depth within sediments. Behavioral
responses to hypoxia include tube lengthening or body extension into the water column
by polychaetes and amphipods, shallower burial, emergence from sediment or aggregate
formation to raise animals up into the water column (reviewed in Diaz and Rosenberg,
1995; Levin et al., 2009). Although these are rarely monitored as indicators, they
generally reflect oxygen declines. These changes along with replacement of large, deep
dwellers and suspension feeders by taxa that are smaller, near-surface dwelling and
surface-deposit-feeding lead to declines in bioturbation and bio-irrigation under hypoxia
(Diaz and Rosenberg, 1995; Middelburg and Levin, 2009). However, under persistent,
stable hypoxia some tolerant species deepen their vertical distributions as long as some
oxygen is present (Levin et al., 2009a).

Thresholds for the changes outlined above often occur around 2 ml L^{-1} DO for
shallow water taxa and at 0.4 ml L^{-1} DO (or less) for OMZ species. Sediments on the
Pakistan margin shift from laminated (no bioturbation) to fully bioturbated across
gradients from DO 0.1 to 0.2 ml L^{-1} (Levin et al. 2009b). Because nutrient and organic
matter additions often drive oxygen depletion the hypoxia indicators described above
also reflect organic matter enrichment (Pearson and Rosenberg, 1978). Other functional
changes can include altered rates of colonization (DO between 0.05 and 0.5 ml L^{-1};
Levin et al. 2013) and altered carbon cycling pathways (Woulds et al., 2007) with
protozoans dominating carbon uptake over metazoans under severe hypoxia. These
functional responses tend to occur on seasonal or longer time scales and may therefore
prove most useful as an indicator of long-term oxygen loss.

Food Web Structure: Deoxygenation can result in changes in the presence,
abundance, and behavior of interacting species in marine food webs. The severity and
distribution of oxygen concentrations (or partial pressures) can affect relevant behaviors
and alter encounter rates. As discussed previously, the presence, distribution, and
behaviors of individual species can change in response to both oxygen distribution and
its effects on organisms at low levels. Under low-oxygen conditions, tolerant species can
become more dominant throughout the food web because their: abundance is privileged
by low-oxygen; consumer / predatory strategies are less affected or; escape behavior is
less impaired relative to other species with which they interact (Breitburg et al., 1997;
1999). Certain feeding modes such as carnivory can become less common or even absent
under severely hypoxic conditions (Sperling et al., 2013). Food chain length can also be
impacted by hypoxia, becoming longer and supporting fewer top predators, with more
energy flow-dominated by microbial pathways (such a shift from carbon fixation to
chemosynthesis). This change in food web structure results in less trophic transfer
upward and the presence of conspicuous microbial mats that are themselves an indicator
of hypoxic conditions (Levin, 2003; Woulds et al., 2007; Levin et al., 2009a). This
relationship between food chain length and low-oxygen was apparent during the early

970   Cenozoic warm period (50 mya), when the warmer, less oxygenated ocean supported
971   longer food chains and a lower abundance of top predators (Norris et al., 2013).

972   Shifts in the distribution of species from an area subject to oxygen loss to areas
973   nearby (where oxygen levels may vary) could alter surrounding food webs. Certain
974   ecological guilds that were once underrepresented may become more abundant in an
975   ecosystem as they escape deoxygenation elsewhere or track prey that have migrated to
976   find better oxygenated waters.

977   As with other metrics, thresholds for trophic changes will depend on differences
978   in tolerance of the various interacting species. Tolerance thresholds will vary among
979   species (e.g. finfish versus gelatinous zooplankton), habitats (e.g. estuaries vs OMZs),
980   geography and temperatures. In estuaries, gelatinous zooplankton (scyphozoans and
981   ctenophores) tend to be more tolerant of low-oxygen exposure than their copepod and
982   larval fish prey and more tolerant than juvenile or adult fishes competing for the same
983   prey (Breitburg et al., 1997). Conversely, sessile or relatively sedentary organisms are
984   often more hypoxia-tolerant than their predators and may gain a refuge. This is the case
985   for estuarine hard clams that reach their highest abundance in low-DO areas where their
986   predators are excluded (Altieri. 2008) and in kelp forests where hypoxia reduces grazing
987   pressure, thereby increasing kelp survival (Ng and Micheli, 2020).

988   Shifts in consumer interactions associated with hypoxia result in altered food web
989   structure and trophic function. Lower proportions of carnivory in the polychaete
990   community have been found under low-oxygen conditions (Sperling et al., 2013). Under
991   hypoxic conditions demersal fish on continental slopes shift from feeding in the water
992   column (on vertically migrating zooplankton and fish) to consuming largely benthic
993   prey, yielding longer, less efficient food chains (Gallo, 2018). Hypoxia-induced changes
994   in food webs may result from changes in the abundances of some species and/or the
995   distributional overlap of predators and prey (Breitburg et al., 1997; Ekau et al., 2010).
996   Diets of fishes can differ in hypoxic water as shown for Atlantic bumper
997   (*Chloroscombrus chrysurus*) in the Gulf of Mexico (Glaspie et al., 2018). Some fishes
998   may even benefit from hypoxia if their prey are forced into more vulnerable predatory
999   habitats as suggested for Chesapeake Bay where striped bass may benefit from
1000 concentration of bay anchovy prey in the well-oxygenated mixed layer (Costantini et al.,
1001 2008). Whether effects of hypoxia on fish populations are positive or negative is likely to
1002 be species-specific and ecosystem-dependent (Breitburg et al., 1997; 2002; Costantini et
1003 al., 2008) and also dependent on the severity of low-oxygen coupled to the prevailing
1004 temperatures and the relative tolerances of predators and prey.

1005   Shifts in trophic structure are detected with field measures of encounter rates, gut
1006 contents analysis and stable isotopes that detect changes in the base of the food chain (δ
1007 ^{13}C) or trophic level (δ ^{15}N). Models such as ECOPATH/ECOSIM (Christensen and
1008 Walters, 2004) are useful to combine field and experimental data to achieve a more
1009 comprehensive understanding of changes to food webs (e.g. de Mutsert et al., 2017).

1010 Similarly, biomass, abundance or catch trophic spectra can offer a high-level indicator of
1011 changes to food webs (e.g. Gascuel et al., 2005).

1012 Trophic indicators offer a holistic measure that synthesize a variety of responses
1013 of individual species. As with many indicators discussed here, time and resources are
1014 required for fieldwork and experiments. Changes in food web structure can be driven by
1015 other co-occurring environmental stressors in addition to hypoxia such as changes in
1016 nutrient input, introduction of an invasive species and species distribution changes due to
1017 climate change.

1018

1019 *DISCUSSION*

1020 I. *Scaling of Indicators*

1021 Scaling of indicators is often necessary to enable the observed values of the
1022 indicator to be interpreted as representing the state of the system and for results to be
1023 expressed on spatial and temporal scales that are ecologically or societally meaningful.
1024 Consideration of what types and to what extent scaling is needed is important when
1025 selecting an indicator, designing a sampling plan and interpreting and communicating the
1026 results of an indicator. Scaling often determines what species and life stages to measure,
1027 the specific indicator(s) needed and how to allocate effort to sampling locations and
1028 frequency of sampling.

1029 The first type of scaling typically employs graphical or statistical analyses to
1030 examine trends in time and space to help attribute variability of the measured indicator to
1031 underlying causative factors. These types of statistical analyses focus on the measured
1032 values of the indicator and possibly covariates. The extrapolation or inference level is
1033 derived from the measured conditions of the individuals and applied to broader areas
1034 than those locations sampled (e.g. sub-regions, basin-wide) or to more generalized
1035 timescales than those captured by the data (e.g. month, season, years). This scaling
1036 employs the statistical concept of looking for patterns in the data collected at different
1037 locations and/or over time and subsequently making key assumptions about how these
1038 data reflect broader conditions to infer the population of indicator values. For example,
1039 Duskey et al. (2023) used a size-spectrum food web model of the central Baltic Sea and
1040 incorporated how P_{crit} affected a suite of indicators: benthic resource carrying capacity,
1041 occupancy in benthic habitat, maximum consumption rate, fish search rate for prey,
1042 assimilation efficiency and fish egg survival.

1043 The second major type of scaling analysis used with indicators employs a
1044 mechanistic understanding of how the indicator logically and causally relates to the state
1045 of the system. For example, low-DO impaired vision affects detecting prey that
1046 determines feeding and growth that affects vulnerability to predator (mortality) and
1047 fecundity, which affect population abundance. This integration and scaling across levels
1048 of biological organization from the organismal to ecosystem level can be represented in a

1049   conceptual diagram (Altieri and Witman, 2006), where low-oxygen stress reduced
1050   survivorship and growth of individual mussels, and impacted the density and spatial
1051   extent of mussel populations. Individuals of a single species could be used to infer the
1052   state of the population while observations on multiple species can be leveraged to
1053   community (e.g. diversity) and food web levels (e.g. energy pathways). The condition of
1054   individuals as indicated by lipid content (e.g. Herbinger et al.,1991) suggests sufficient
1055   exposure to low-DO can elicit a response of the bioenergetics and physiology of the
1056   individual. Reduced animal condition can be related to the oxygen state of the system
1057   and can lead to higher mortality, lowered fecundity and other responses that can be
1058   directly related to population, community or food web levels. While values of indicators
1059   on subsets of individuals can stand alone to show exposure and responses of individuals,
1060   scaling translates indicator observations into potentially more-relevant levels of
1061   biological organization and scales of time and space. This mechanistic scaling approach
1062   was used by Rose et al. (2018a, b) to examine how reduced growth, increased mortality,
1063   and reduced fecundity due to low-DO exposure affected croaker (*Micropogonias*
1064   *undulatus*) population dynamics in the Gulf of Mexico. By using an agent-based model
1065   with a 2-D grid that included dynamic DO field, the time-dependent exposures of
1066   individuals were simulated and avoidance behavior was projected.

1067   The third general approach for scaling of indicators involves examining the
1068   causality of deoxygenation through ecological models that provide a quantitative basis
1069   for scaling indicators. Numerical models provide a quantitative translation of the
1070   indicator into variables that might be more relevant to management and society.
1071   Modeling involves significant effort beyond the conceptual modeling that is thus done in
1072   scaling of indicators when quantitative links from the indicator to the system state are
1073   needed. Common situations requiring such modeling are when multiple stressors covary
1074   and DO effects need to be isolated or when expressing indicators in units explicitly
1075   chosen to inform policy (e.g. economic impacts of reduced biodiversity) and
1076   management decisions (e.g. fisheries yield). For instance, Franco et al. (2022) scaled
1077   low-DO effects to habitat changes of Pacific halibut (*Hippoglossus stenolepis*) in the
1078   Northeastern Pacific. They used fisheries-independent data and model predictions from
1079   ROMS-BEC of oxygen and a metabolic index was used to map suitable aerobic habitat.

1080   *II.   Application of Indicators*

1081   The suite of indicators discussed differ in the time and space scales of oxygen
1082   influence which are reflected in the types of settings where it is most applicable, in
1083   possible confounding factors and in the expertise and resources required for application.
1084   These differences are summarized in Table 1. All of these aspects together influence
1085   the potential applications of the different indicators of oxygen stress.

Table 1. Summary considerations for application of hypoxia indicators including settings, confounding factors, expertise, resource requirements and utility.

Indicator Category	Indicator	Useful & Relevant Settings	Confounding Factors	Expertise Required	Resources/Accessibility	Overall Utility/Application
Individual - Cellular Responses	HIF	Field, Aquaculture, Lab Expt	species differences	Physiology	access to specialized laboratory facilities	Specialized
Individual - Sensory Systems	Vision	Lab Expt.	Acidification	Physiology	Requires specialized tools for Ex	Management of fishery stocks (catch limits, closures) or endangered species
	Hearing	Field, Laboratory Expt	Acidification	Physiology/acoustics	access to specialized laboratory	Not clear at this time
Individual - Hormonal Responses	endocrine, cortisol levels	Laboratory	Handling stress	Physiology	Immunoassay facility	Experimental/aquaculture
	growth hormone	Field, Aquaculture, Lab Expt	endocrine disruptors	Physiology	Access to specialized laboratory	Management of fisheries stocks
	reproduction/fertility	Field, Aquaculture, Lab Expt	Size, temperature, food supply	Physiology	Access to specialized laboratory	Fisheries management, conservation, aquaculture
Individual - Growth and condition	body size	Field, Aquaculture, Lab Expt	Temperature, Food supply	Ecological	facilities, sampling gear, calipers, microscopes,	Fisheries management, conservation of endangered species, aquaculture
	malformation	Field, Aquaculture, Laboratory	Acidity, food supply, temperature	Basic?	facilities, sampling gear, calipers, microscopes,	Diagnostic for habitat suitability
	mortality	Field, Laboratory Expt.	Temperature, disease	Basic?	facilities, sampling gear, calipers, microscopes,	Establishing oxygen thresholds, improving aquaculture conditions, remediation
Individual - Immune response	disease	Field Aquaculture collection	pCO2, temperature, crowding	Pathology	facilities, sampling gear, calipers, microscopes,	Diagnostic for habitat suitability
	chemical archive of hypoxia exp	Field exposures		Trace element fingerprinting	LA-ICPMS, Synchrotron	Hindcasting exposures
Individual - physiology	Metabolic indices	Past, present and future ocean	Temperature	Ecological/Modeling	Computer	Diagnostic for habitat suitability
Species/Population - Abundance re	Population Size	Field	Food supply	Ecological	Boats, ships, transects, sampling gear, personnel	Management of fishery stocks (catch limits, closures) or endangered species
	Growth Rate	Field, Aquaculture, Lab Expt	Temperature, Food supply	Ecological/Modeling	Boats, ships, or lab rearing facilities, sampling gear, calipers, personnel	Establishing oxygen thresholds, improving aquaculture conditions, remediation
	Fertility	Field, Aquaculture, Lab Expt	Temperature, Food supply	Reproductive physiology	facilities, sampling gear, calipers, computer, personnel	Stock assessment models, improving aquaculture conditions
	Survivorship	Field, Aquaculture, Lab Expt	Temperature, Food supply	Ecological	facilities, sampling gear, calipers, microscopes,	Stock assessment models, improving aquaculture conditions
	Recruitment rate	Field	Temperature, Food supply	Modeling	Computer	Stock assessment models, improving aquaculture conditions, conservation priorities
	Indicator species/taxa	Field	predation, food supply	Taxonomic	Boats, ships, diving, sampling gear	Early warning of hypoxia hazard, remediation success,
Species/Population - Behavior	Avoidance/Walkouts	Field	temperature	Field ecology, Citizen science	imaging/photography,	Hypoxia event indicator, species-specific management (fisheries, aquaculture)
	Aquatic surface respiration	Field		Citizen Science	can be observed from piers or boat	very specific to low oxygen conditions; high utility as hypoxia event indicator, aquaculture management
	Shoaling distributions	Field	Temperature	Field ecology	Boats, ships, depth-stratified field	Ecosystem based management, Fisheries implications
	Benthic emergence	Field, Aquaculture, Lab Expt	H2S	Field ecology	Scuba gear, imaging systems	Hypoxia event indicator, benthic species-specific management (fisheries, aquaculture)
Community/Ecosystems	Diversity	Field system, Mesocosms	Food supply, disturbance		imaging gear, balances, personnel	Water quality/waste management, deoxygenation detection; co-management of cumulative disturbances
	Dominance	Field system, Mesocosms	Food supply	Taxonomic expertise	imaging gear, microscopes, personnel	Water quality/waste management, deoxygenation detection, co-management of cumulative disturbances
	Density	Field system, Mesocosms	Food supply, H2S	Taxonomic expertise	imaging gear, microscopes, personnel	Water quality/waste management, deoxygenation detection, co-management of cumulative disturbances
	Biomass	Field, Aquaculture, Lab Expt	Food supply	Ecological	imaging gear, balances, calipers, personnel	Water quality/waste management, deoxygenation detection, co-management of cumulative disturbances
	Taxonomic composition	Field system, Mesocosm	Contaminants	Ecological and/or molecular expertise	Microscopes, Image analysis, eD	Water quality/waste management, hypoxia/deoxygenation detection, co-management of cumulative disturbances
	Taxonomic ratios	Field system, Mesocosm	Contaminants	Low-level taxonomic expertise	Microscopes, Image analysis, cD	Hypoxia/deoxygenation detection, co-management of cumulative disturbances
	Functional Shifts	Field system	Food supply	Low-level taxonomic expertise	Microscopes, Image analysis, eDNA, literature access	Fisheries management, deoxygenation detection, co-management of cumulative disturbances
	Trophic Structure	Field system	Food supply	Isotopic, Gut, Modeling	microscopes, dissecting tools for gut contents, computer	Fisheries management, co management of cumulative disturbances

Fisheries and Aquaculture - Coastal areas where natural and anthropogenic nutrient inputs can result in deoxygenation of bottom waters include regions of enhanced fisheries and aquaculture (Nixon and Buckley, 2002; Breitburg et al., 2018; Zhan et al., 2023). While deoxygenation impacts on fisheries catch can be difficult to ascertain because of fish movement, adaptations and changes in fishing effort and techniques, laboratory experiments have demonstrated deleterious impacts on species that are commercially harvested (Roman et al., 2019; Rose et al., 2018b; Laffoley and Baxter, 2019; Zhan et al. 2023). Deoxygenation impacts on fisheries may be most impactful on artisanal fisheries and aquaculture facilities which often have little capacity to relocate as hypoxia grows in space and time. Aquaculture can contribute to deoxygenation through the organic input to bottom waters (Rice, 2014) and animals restrained in nets and cages are unable to escape harmful oxygen conditions. Research is needed to develop aquaculture species with strong hypoxia tolerance and economic potential (see Zhan et al., 2023).

Water Quality Management - Environmental management agencies in many countries have established goals to protect and expand essential habitat for aquatic organisms using oxygen concentration as an indicator to estimate *in-situ* physiological stress. In Chesapeake Bay, U.S., this approach has been taken to develop estimated habitat space for different animal groups based on oxygen concentrations and low-oxygen tolerance (e.g. Batiuk et al., 2009; Zhang et al., 2018). In the Gulf of Mexico, nutrient management targets aim to reduce the area of the hypoxic zone to achieve similar habitat improvements (Scavia and Donnely, 2007). The Baltic Marine Environment Protection Commission (HELCOM) considers "oxygen debt" as a metric for ecosystem health (e.g. Stoicescu et al., 2019). This is consistent with the EU Marine Strategy Framework Directive aimed at improving marine waters, which considers the concentration of oxygen in near-bottom waters as an indicator (Friedland et al., 2021). In all of these cases, low-oxygen conditions are prioritized because they are considered to have negative consequences for a broad range of harvestable marine organisms as well as their pelagic and benthic prey. Generally, these minimum oxygen concentrations are based on mortality estimates and sometimes non-sublethal effects. The partial pressure of oxygen rather than oxygen concentration may be the more relevant measure of DO availability (Hofmann et al. 2011) because it integrates the effects of temperature and salinity on oxygen availability.

Climate and the Carbon Cycle - Biotic changes associated with deoxygenation can alter processes of carbon and nutrient mixing, remineralization, nitrification and denitrification, carbon transport, accumulation and sequestration, or climate feedbacks from nitrous oxide or methane release (Breitburg et al., 2018). Use of biotic indicators can identify times, places or conditions where these climate-relevant changes to the carbon or nutrient cycles or feedbacks may occur. The Intergovernmental Panel on Climate Change (IPCC) reports and World Ocean Assessments mention oxygen in the context of climate change far more than IPBES, but even these suffer from low confidence of oxygen observations or models and limited-to-no attention in summaries

1130   for policy makers (Levin, 2022). Ideally oxygen sensitivity and indicators discussed in
1131   this review could become a central part of climate change and biodiversity policy, for
1132   example: in the United Nations Framework Convention on Climate Change (UNFCCC)
1133   global stock take; Ocean Dialogue; Nationally Determined Contributions and National
1134   Adaptations Plans; as well as in the research and systematic observations discussions in
1135   UNFCCC Subsidiary Body for Scientific and Technological Advice (SBSTA).

1136   **Biodiversity and Conservation** - Deoxygenation is recognized as a threat to
1137   biodiversity, particularly for larger taxa or those adapted to highly oxygenated waters.
1138   However, the extent to which deoxygenation is recognized and addressed in global
1139   assessments of marine threats and in policies that conserve biodiversity varies greatly.
1140   The Convention on Biological Diversity Framework 2030 does not mention oxygen, but
1141   is developing diversity indicators that could readily incorporate oxygen-sensitive taxa or
1142   guilds (Hughes and Grumbine, 2023). The new Biodiversity Beyond National
1143   Jurisdiction (BBNJ) Agreement to protect biodiversity and enable its sustainable use in
1144   international waters mentions deoxygenation only in its preamble and in the context of
1145   types of capacity development and technology transfer, but climate and specifically
1146   oxygen vulnerability is not included in a list of criteria for marine protected areas or
1147   environmental impact assessment. Projected changes in oxygen availability and habitat
1148   suitability for sensitive species can be applied to the designation of protected areas,
1149   fisheries regulations and evaluation of cumulative impacts in environmental impact
1150   assessment (Dunn et al., 2018; Levin et al., 2020).

1151   **Tourism, Recreation and other Livelihoods** - Biological indicators of low-
1152   oxygen in coral reefs or recreational fishing habitats as well as mass mortality events
1153   washing up on beaches represent important sentinels of oxygen effects on tourism and
1154   recreation. Having early warning signs of impending or existing hypoxic events can
1155   permit various forms of adaptation among those dependent on a healthy ocean, resilient
1156   fish populations and clean beaches for income.

1157   *III. Research Needs and Opportunities*

1158   Recent reviews on deoxygenation have suggested research needs to improve our
1159   understanding and prediction of impacts on marine organisms (e.g. Breitburg et al.,
1160   2018; Woods et al., 2022; Zhan et al., 2023). There needs to be more research on the
1161   impacts of low oxygen and relevant stressors (especially temperature) on the various life
1162   stages of commercially-harvested species. Studies on important commercial and
1163   keystone species should include the relevant time scales to assess the impacts of
1164   episodic, seasonal, annual and inter-annual fluctuations of low-DO waters on individuals
1165   and populations. Research on the impacts of low oxygen waters on marine organisms
1166   should include more studies that integrate the effects that cascade through the organism
1167   to population, community and ecosystem levels. Similarly, when addressing the impacts
1168   of deoxygenation on a commercially harvested species, low-DO should be included in an
1169   Ecosystem Based Management (EBM) approach that includes predators, prey and human
1170   influences. Investigators need to consider that oxygen concentration alone is not a

1171   predictor of organisms' fitness. While oxygen partial pressure is the relevant physiology
1172   measure, knowledge of exposure histories, life-stage sensitivity and cumulative stressors
1173   is essential for holistic understanding.

1174   Opportunities for national and international research on the impacts of
1175   deoxygenation include the IOC-UNESCO's Global Ocean Oxygen Network (GO2NE),
1176   UN Decade of Ocean Science for Sustainable Development program and Global Ocean
1177   Oxygen Decade (GOOD). GO2NE is committed to providing a global and
1178   multidisciplinary view of deoxygenation, with a focus on understanding the multiple
1179   aspects and impacts. From 2021-2030 the Ocean Decade program GOOD will raise
1180   global awareness about ocean deoxygenation, provide knowledge for action and develop
1181   mitigation and adaptation strategies to ensure continued provision of ecosystem services
1182   and minimize impacts on the ocean economy through local, regional, and global efforts.
1183   A GOOD programmatic focus on development and application of biological indicators of
1184   hypoxia, possibly tied to the Global Ocean Oxygen Database and ATlas (GO2DAT;
1185   Grégoire et al., 2021) would facilitate the integration of deoxygenation more broadly into
1186   ocean management. Many of the biological indicators of oxygen stress described in this
1187   paper, if tied to specific DO response thresholds, can be used in monitoring and applied
1188   to management of water quality, biodiversity and fisheries.

1189   *IV. A Global Endeavor: Challenges for Equitable Application of Indicators*
1190
1191   The ability to apply oxygen indicators across the global ocean in both coastal and
1192   open ocean waters will depend on: (a) improved oxygen literacy across various
1193   stakeholders, including managers, funders and academics; (b) expanded technical
1194   capacity, such as instrumentation, associated infrastructure and technical expertise; (c)
1195   improved data access according to Findability, Accessibility, Interoperability and
1196   Reusability (FAIR) implementation principles (Jacobsen et al., 2020); and, (d) inclusive
1197   training and empowerment of the next generation of scientists and practitioners. Each of
1198   these represents a challenge that can be addressed by different elements of the Global
1199   Ocean Oxygen Decade program and other regional and international networks. One goal
1200   would be to enable small island developing states, least developed countries and the
1201   global south more generally to join wealthier nations in having the knowledge,
1202   instruments, funding and expertise to apply oxygen indicators for science and
1203   management. Training opportunities such as the recent summer schools generated by
1204   GO2NE represent a valuable mechanism for achieving these goals.
1205
1206   *DATA AVAILABILITY*
1207
1208   Data included in the manuscript can be found in the referenced citation.
1209
1210   *AUTHOR CONTRIBUTIONS*
1211

MRR and LAL contributed equally to developing the concept and lead writing of the manuscript. The other authors contributed essential scientific sections of the manuscript.

COMPETING INTERESTS

The contact author has declared that none of the authors has any competing interests.

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