

Effects of Hypoxia, and the Balance between Hypoxia and Enrichment, on Coastal Fishes and Fisheries

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ABSTRACT: A reduction in dissolved oxygen concentration is one of the most important direct effects of nutrient over-enrichment of coastal waters on fishes. Because hypoxia can cause mortality, reduced growth rates, and altered distributions and behaviors of fishes, as well as changes in the relative importance of organisms and pathways of carbon flow within food webs, hypoxia and anoxia can lead to large reductions in the abundance, diversity, and harvest of fishes within affected waters. Nutrient enrichment, however, typically increases prey abundance in more highly oxygenated surface waters and beyond the boundaries of the hypoxic zone. Because of this mosaic of high and low oxygen areas within a system, not only the actual oxygen concentration of bottom waters, but the spatial arrangement, predictability, and persistence of highly oxygenated, high productivity habitats, and the ability of fishes to locate and use those favorable habitats, will determine the ultimate effect of low oxygen on fish populations. Negative effects of hypoxia on fish, habitat, and food webs potentially make both fish populations and entire systems more susceptible to additional anthropogenic and natural stressors.

Introduction

The effects of nutrient enrichment of coastal waters on fish populations and fisheries harvests present a contradictory picture. On one hand, fish kills affecting thousands to millions of fish have been associated with nutrient-related low oxygen events in coastal areas on each of the world's continents, except Antarctica. On the other hand, a comparison of systems ranging from coral reefs to severely eutrophic temperate estuaries indicates that there is a positive relationship between nitrogen loading and fisheries yields in coastal waters (Nixon et al. 1986). Included in the analysis by Nixon et al. are estuaries and other semi-enclosed seas that are characterized by seasonal oxygen depletion. Comparison of 14 European estuaries and other semi-enclosed European seas found higher landings of both planktivorous and demersal fishes in eutrophic systems characterized by seasonal hypoxia than in oligotrophic systems (de Leiva Moreno et al. 2000). I explore the reasons for this seeming contradiction by asking what are the predominant effects of hypoxia on estuarine fishes in nutrient-enriched systems, how and where does hypoxia negatively affect fish populations and fisheries harvests, and why are effects of hypoxia difficult to detect on a system-wide basis. Although ecological functions and fisheries harvests can be severely disrupted within hypoxic waters, increases in finfish abundance on larger spatial scales re-

sulting from the high productivity in nutrient-enriched systems are often greater than losses due to oxygen depletion. I will focus primarily on estuaries and other semi-enclosed seas, the marine systems most severely affected by nutrient over-enrichment and resultant oxygen depletion, and on finfish rather than crustacean or molluscan fisheries species. Throughout this paper, I use a much higher threshold for hypoxia than the 2 mg l^{-1} (= 24% saturation at 20°C and 15 psu) or 2 ml l^{-1} (= 34% saturation at 20°C and 15 psu) common in the scientific literature. Instead, waters with dissolved oxygen concentrations $< 50\%$ saturation will be considered hypoxic because, as discussed below, sensitive fish show avoidance, reduced growth, and other signs of physiological stress at or near such levels.

The Relationships among Nutrient Enrichment, Physical Features and Hypoxia

Hypoxia or anoxia occurs throughout the world in coastal waters that receive high loadings of nutrients from anthropogenic sources (Diaz and Rosenberg 1995). In addition to high nutrient loadings, systems most susceptible to oxygen depletion are typically characterized by strong density stratification during the season in which low oxygen is severe, long residence times, low tidal energy, and a high watershed area to estuary volume ratio (Nixon 1988; Caddy 1993; Cloern 2001). The most severe oxygen depletion occurs in subpycnocline waters, which are isolated from mixing that re-aerates surface waters with atmospheric oxygen. Wind and

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tidal forcing can periodically advect bottom waters into shallower, nearshore habitats (Loesch 1960; Schroeder and Wiseman 1988; Breitburg 1990; Sanford et al. 1990). Some systems, such as the Kattgat and Waquiot Bay, also experience near-shore, surface-layer oxygen depletion typically associated with high macroalgal biomass and periods of calm weather with little wind mixing of the water column and cloud cover (D'Avanzo and Kremer 1994; Pihl et al. 1998). In most estuaries, hypoxia is a seasonal phenomenon, coinciding with high surface temperatures and strong density stratification.

A view of low oxygen as a factor that adds physical structure and both spatial and temporal heterogeneity to the water column is especially important to understanding the effects of hypoxia on fishes. Although extreme events can occur, no coastal system is characterized by continuous, surface to bottom uniform low oxygen concentrations. Even systems characterized by severe bottom layer oxygen depletion that would eliminate large expanses of the bottom water layer and benthic habitat from use by fish have areas within the surface layer, and at least portions of shallow benthic habitat, that retain oxygen concentrations above 50% saturation. Because of this mosaic of high and low oxygen areas within a system, not only the actual oxygen concentration of bottom waters, but the spatial arrangement, predictability, and persistence of highly oxygenated areas, and the ability of fishes to locate and use those highly oxygenated areas, will determine the ultimate effect of low oxygen on fish populations (Fig. 1).

Local Effects of Hypoxia

FISH KILLS AND OTHER DIRECT MORTALITY

Fish kills, in which large numbers of dead and dying fish float to the surface or wash onto shore, are probably the most dramatic and publicly visible manifestation of hypoxia and nutrient over-enrichment of coastal waters. In addition to mass mortalities that are easily observed, high mortality of demersal fishes lacking a swim bladder can occur leaving little or no visible evidence of fish at the surface or littering beaches (e.g., Breitburg 1992). Mortality of adults, even when large in absolute numbers, typically affects only a small fraction of the total population within a water body. Habitat loss (discussed below) and mortality of early life stages are more likely to contribute to local reductions of fish populations than is direct mortality of adults and older juvenile fishes.

Low oxygen fish kills most often occur when dissolved oxygen concentrations change rapidly, when fish are concentrated in embayments, or

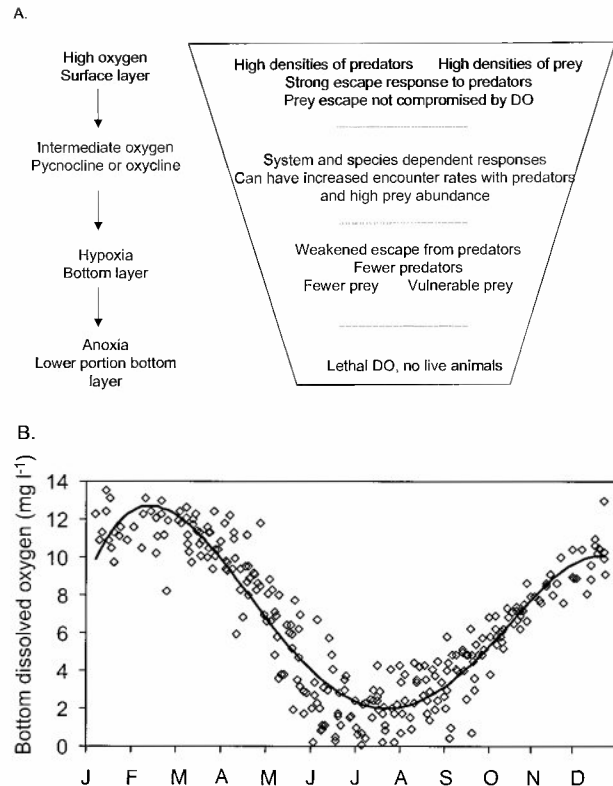


Fig. 1. Examples of spatial structure and temporal variability created by low dissolved oxygen in a temperate estuary. a) Vertical spatial structure and resultant spatial variation in direct and indirect effects of oxygen depletion. The figure shows the effect of oxygen concentration on various aspects of predator-prey interactions and abundances in different portions of a stratified water column with bottom-layer hypoxia. b) Variation in day-time bottom layer dissolved oxygen at a mesohaline site in the Patuxent River. Data show dissolved oxygen concentrations mid-channel near Broomes Island, Maryland. Variation around the fitted trend line (4th order polynomial, $r^2 = 0.87$) represent both within and among year variability in the 15-yr data set. Bottom dissolved oxygen concentrations can change rapidly as stratification is disrupted by storm-associated wind mixing. Data are from the Chesapeake Bay Program monitoring program (www.chesapeake.net).

when other conditions occur that limit or confuse appropriate escape behavior. For example, large numbers of fish and crabs can die when severely hypoxic (e.g., $< 0.5 \text{ mg l}^{-1}$) bottom water is rapidly advected towards shore by a combination of wind forcing and internal lateral tides (Breitburg 1992). Diver observations towards the end of an 18-h event at an oyster reef along the western shore of a Chesapeake Bay reef revealed a bottom littered with dead fish (especially benthic oyster reef fishes such as gobies and blennies) and crabs. During a similar event in 1987, average densities of adult and juvenile naked gobies (*Gobiosoma bosc*) in deep and mid-depth areas of the oyster reef dropped from 40 ind m^{-2} to near zero. Highest mortality of

naked gobies was of newly settled juveniles; increased densities in less severely affected shallow reef sites indicated that older juveniles and adults likely had higher rates of successful shoreward emigration. Calculations of swimming speeds, stage-specific lethal oxygen concentrations, and the predictability of oxygen declines reaching lethal levels, indicate that the environment may be less predictable to small, slower swimming fish. In a habitat with fluctuating oxygen concentrations, such individuals are less able to initiate a successful escape response without unnecessarily exposing themselves to predation risk at times when oxygen concentrations remain above lethal levels.

Die-offs of extensive algal blooms can also rapidly deplete dissolved oxygen. During extreme events, oxygen depletion can affect the entire water column, resulting in an exception to the more typical pattern in these and other systems in which surface water serves as a refuge from persistent bottom-layer hypoxia. The collapse of a massive *Prorocentrum minimum* (dinoflagellate) bloom, and warm, calm conditions that had already led to severe oxygen depletion extending into shallow waters, rapidly led to anoxia throughout the water column of the Mariager Fjord in northern Denmark during 1997 (Fallesen et al. 2000). Extensive mortality of both fish and invertebrates occurred as the Inner Fjord became anoxic and sulphidic to the surface over a 25 km long area for 2 wk.

The severity and duration of low oxygen concentrations, as well as water temperatures, strongly affect the likelihood of mortality when avoidance is ineffective. Oxygen concentrations below those that result in the standard calculated 50% mortality in 24-h to 96-h exposure tests can lead to mortality in minutes to a few hours. As exposure time increases, the oxygen saturation that causes death approaches the saturation level that results in reduced respiration, typically a saturation level 2 to 3 times higher than found to be lethal in 24-h tests (Magnusson et al. 1998).

Temperature is often an important co-factor determining when lethal conditions are reached, because high temperatures decrease amount of oxygen that can dissolve in water and can increase the metabolic requirements of fish. 50% mortality of 80–200 g Atlantic cod (*Gadus morhua*) was reached at 5, 11, 14, 15.5, 16.5, and 29% oxygen saturation, or 0.5, 1.0, 1.3, 1.4, 1.4, and 2.3 mg l⁻¹ dissolved oxygen at 5, 9, 10, 11, 15, and 17°C, respectively, in laboratory experiments with gradually declining oxygen saturations (Schurmann and Steffensen 1992). Similarly, juvenile Atlantic sturgeon (*Acipenser oxyrinchus*) held for 10 d at 3 mg l⁻¹ experienced 92% mortality at 26°C but only 22% mortality at 19°C (Secor and Gunderson 1998). The

effects of exposure duration and temperature are therefore very important to consider in setting water quality standards for dissolved oxygen concentrations, highlighting the need to set absolute minima, instead of time-averaged minima, and the need to consider geographic variation in maximum water temperatures.

Taxonomic, behavioral, and anatomical characteristics of species also appear to affect the likelihood of mortality from exposure to low oxygen in the field. Although they tend to tolerate lower oxygen concentrations than many species that actively swim throughout the water column, benthic species such as flatfish and gobies that lack a functional swim bladder cannot easily use the upper, oxygenated portions of the water column and have limited swimming speeds and ranges. Because of these constraints, they may be among the most susceptible fishes when oxygen concentrations rapidly decline.

Fish eggs and larvae may be particularly vulnerable to low oxygen because of limitations in behavioral avoidance and, in some cases, higher oxygen requirements than adults. Mortality of these early life stages is not typically considered in fish kills. Adults are unlikely to deposit eggs in areas that are at lethal or highly stressful dissolved oxygen concentrations at the time of spawning. Nevertheless, extensive mortality of benthic fish eggs can result from exposure to low dissolved oxygen concentrations during movement of a hypoxic water mass and during calm periods in areas with high macrophyte or macroalgal production. In some areas of Chesapeake Bay, benthic eggs of oyster reef fishes, including gobies, blennies, and clingfish, periodically suffer substantial mortality in shallow waters because of direct exposure to low dissolved oxygen concentrations and because males abandon the nests they are guarding (Breitburg 1992). Abandoned nests are exposed to predation as both higher oxygen concentrations and predators return, and do not receive the parental care required for embryo development and hatching. In the Baltic-Kattegat system, herring reproduce along the coasts and spawn on littoral vegetation. Low oxygen concentrations may develop for short periods of time, especially during night in areas with dense vegetation. Low oxygen together with exudates released from the algae, decreases survival of herring eggs in these areas (Aneer 1987; Larson 1997).

Planktonic eggs can sink into hypoxic or anoxic bottom layers even if spawned in highly oxygenated surface waters. Spawning locations as well as characteristics of the eggs such as oxygen tolerance, sinking rate, and time to hatch, strongly influence the extent of mortality. Considerable atten-

tion has been focused on the issue of eggs sinking into hypoxic bottom water in the Baltic-Kattegat system because of the particular vulnerability and fisheries importance of Baltic cod. The vertical range of habitat suitable for development of cod eggs in the Baltic Sea is limited, and bounded on the top by low salinity and on the bottom by low oxygen. Cod eggs are neutrally buoyant at salinities that occur only in the deepest basins of the Baltic below the halocline (50–80 m; Nissling et al. 1994; Nissling and Vallin 1996). The stratified nature of the Baltic Sea is such that these deep basins experience extensive areas of low oxygen that are unsuitable for egg survival and development. Oxygen depletion, and physical and biological factors that influence the sinking of eggs into water layers with lethal oxygen concentrations during their approximately 12–14 d development, may be some of the most important factors limiting reproductive success and influencing variation in year-class strength of Baltic cod in the central Baltic (Wieland and Zuzarte 1991; Plikshs et al. 1993; Wieland et al. 1994). Field surveys of the Baltic from 1987 to 1990 indicated that 50–95% of the Baltic cod eggs were below the lower oxygen limit required for embryo survival and successful hatching (Ohldag et al. 1991; Wieland et al. 1994). The proportion of eggs sinking into hypoxic layers will depend on variation among individuals and clutches in chorion thickness, yolk osmolality, individual female, batch number, egg quality, and egg size, as well as geographic and interannual variability in salinity (Nissling et al. 1994; Nissling and Valin 1996).

Data on the vertical distributions of bay anchovy (*Anchoa mitchilli*) eggs in Chesapeake Bay and one of its major tributaries, the Patuxent River, illustrate the potential for strong geographic variation in mortality caused by planktonic eggs sinking into hypoxic or anoxic bottom waters. Areas with the most severe and persistent levels of oxygen depletion are not necessarily those in which direct mortality will be the highest. Bay anchovy eggs suffer approximately 50% mortality during 12-h exposures to dissolved oxygen concentrations of 2.8 mg l⁻¹ (Chesney and Houde 1989). Because density stratification in the mesohaline Patuxent water column is relatively weak (generally only 1–2°C and 1–2 psu difference between surface and bottom waters during summer when oxygen depletion occurs), and eggs are distributed throughout the water column regardless of bottom oxygen concentrations (Keister et al. 2000; Breitburg unpublished data) substantial numbers of developing embryos probably die as a result of direct exposure to low oxygen. Additional mortality may result if eggs that hatch in severely hypoxic bottom waters result in yolk-sac larvae that are weakened and unable to

swim up into the oxygenated surface layer. In the Maryland portion of the mainstem Chesapeake Bay, salinity stratification is substantially stronger, the surface layer is thicker, and eggs are retained in the surface and pycnocline layers where oxygen concentrations are sufficient and typically at or above 50% saturation (North 2001; Breitburg unpublished data). Although oxygen depletion in the Maryland mainstem Chesapeake is more severe, it is less likely to cause extensive mortality of bay anchovy eggs than is the weaker oxygen depletion of the tributaries.

Just as there is likely to be variation among sites (even within a system), the effects of any given combination of oxygen depletion and stratification intensity vary among potentially exposed species. Unlike bay anchovy eggs, sciaenid eggs in the mesohaline mainstem Chesapeake are mostly found in the bottom layer (North 2001; Breitburg unpublished data) where oxygen concentrations of a few tenths of a mg l⁻¹ or less are likely to cause near total mortality. Cod and sprat (*Sprattus sprattus*) egg mortalities differ within a single location: in the deep Bornholm Basin of the Baltic where high cod egg mortality is found, sprat eggs are primarily found in the surface layer at dissolved oxygen concentrations > 5.7 mg l⁻¹ (Wieland and Zuzarte 1991).

Certain key ontogenetic transitions may require high oxygen concentrations relative to that simply required for survival of either embryos or larvae. In tests of seven species of marine fish larvae, Brownell (1980) found that initiation of first feeding required oxygen concentrations 1.7 times higher than those required for survival (mean of LC₅₀/EC₅₀ for seven species, where EC₅₀ is the oxygen concentration required for 50% of larvae, normed for controls, to initiate first feeding). Serigstad (1987) found that respiration of Baltic cod larvae also peaked at 6–8 d posthatch, at about the time the larvae require exogenous prey.

HABITAT LOSS AND AVOIDANCE OF LOW OXYGEN WATERS

The major effect of low oxygen in coastal waters and semi-enclosed seas is a loss of habitat that would otherwise be used by fishes for activities such as feeding, reproduction, and shelter from predators. The extent of habitat loss will depend on bathymetry of the system, the severity of oxygen depletion, and the physiological tolerances and behaviors of affected fish species. Field studies have repeatedly shown that as oxygen concentrations decline, the abundance and diversity of demersal fishes decrease (Fig. 2; e.g., Baden and Pihl 1996; Howell and Simpson 1994; Breitburg et al. 2001; Eby 2001). Bottom waters below approximately 2

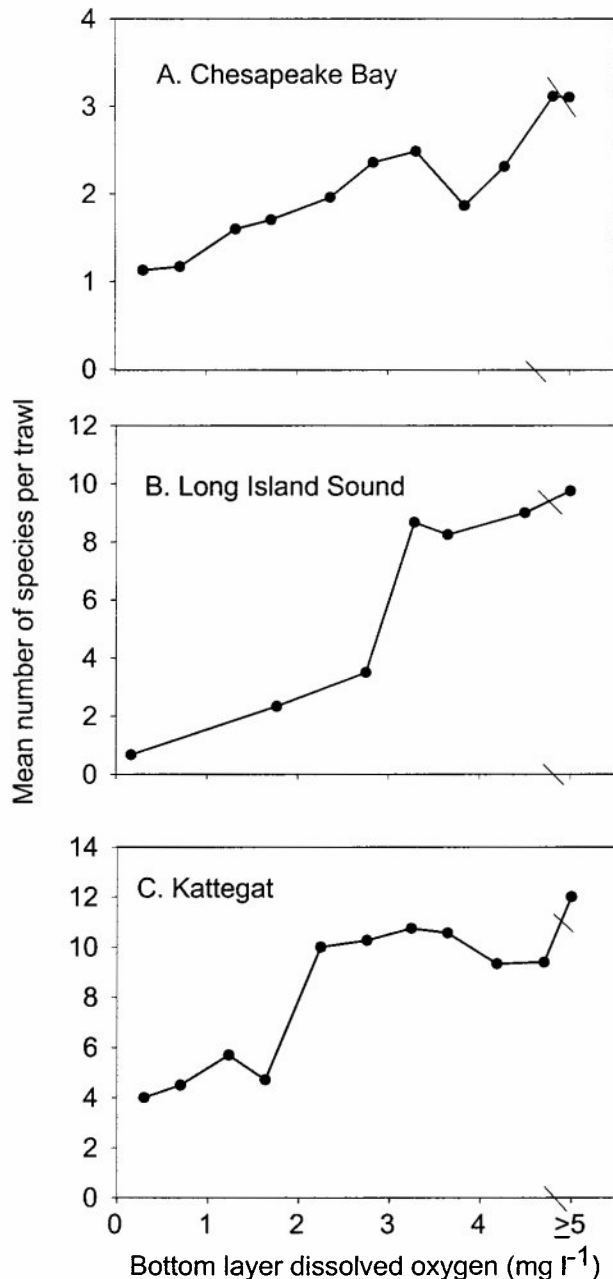


Fig. 2. Average number of species per trawl at a range of dissolved oxygen concentrations A) along the western shore of Chesapeake Bay near the Calvert Cliffs Nuclear Power Plant (Breitburg et al. 2001), B) Long Island Sound (redrawn from Howell and Simpson 1994), and C) the Kattegat (Baden et al. 1990b; Baden and Pihl 1996; redrawn from Breitburg et al. 2001). Data are averaged in approximately 0.5 mg l⁻¹ intervals and for all data ≥ 5 mg l⁻¹. Note variation in scale of the vertical axes. The number of species collected per trawl increased with increasing dissolved oxygen in all three studies.

mg l⁻¹ have extremely depauperate fish populations. Some individual species appear to have threshold concentrations, below which their densities decline precipitously (Baden and Pihl 1994; Howell and Simpson 1994; Eby 2001). Because fish species vary in both physiological tolerance and behavior, however, total fish abundance and fish species richness tend to decline gradually with declining oxygen concentrations.

The initial response of fishes to low oxygen is typically an increase in ventilatory rate. This behavior increases energy consumption, however, narrowing the scope for other responses to hypoxia and other activities (Kramer 1987; Dalla Via et al. 1994). Some degree of acclimation to low oxygen may be achieved through increased hemoglobin concentration (Petersen and Petersen 1990), altered oxygen affinity of hemoglobin, increased red cell pH, or reduced cellular ATP or GTP (Jensen et al. 1993). Such physiological adaptations vary widely among fish species (Jensen et al. 1993). Dalla Via et al. (1994) suggest that metabolic depression is a more effective survival strategy for fishes exposed to low dissolved oxygen than is the induction of anaerobic metabolism. Decreased activity levels and decreased feeding reduce oxygen requirements and may allow fish to avoid dependence on anaerobic metabolism (Chabot and Dutil 1999), but also reduce growth and potentially increase size-related mortality.

Longer duration exposures to low oxygen and more severe hypoxia lead to avoidance of and emigration from affected habitat. All larval, juvenile, and adult fishes that have been tested respond to oxygen gradients by moving upwards or laterally away from waters with physiologically stressful or potentially lethal dissolved oxygen towards higher oxygen concentrations (e.g., Deubler and Posner 1963; Stott and Buckley 1979; Breitburg 1994; Wannamaker and Rice 2000). Mortality from direct exposure to hypoxic and anoxic conditions is less than might otherwise occur because of this potential capacity for behavioral avoidance.

Habitat loss due to hypoxia in coastal waters is far greater than would be calculated based on the spatial extent of lethal conditions because most fish avoid not only lethal oxygen concentrations, but also those that would reduce growth and require greatly increased energy expenditures for ventilation. Field sampling and laboratory experiments indicate that oxygen concentrations that are avoided tend to be 2–3 times higher than those that lead to 50% mortality in 24-h to 96-h exposures, and approximately equal to concentrations that have been shown to reduce growth rates in laboratory experiments (Fig. 3).

The net result of emigration and mortality is re-

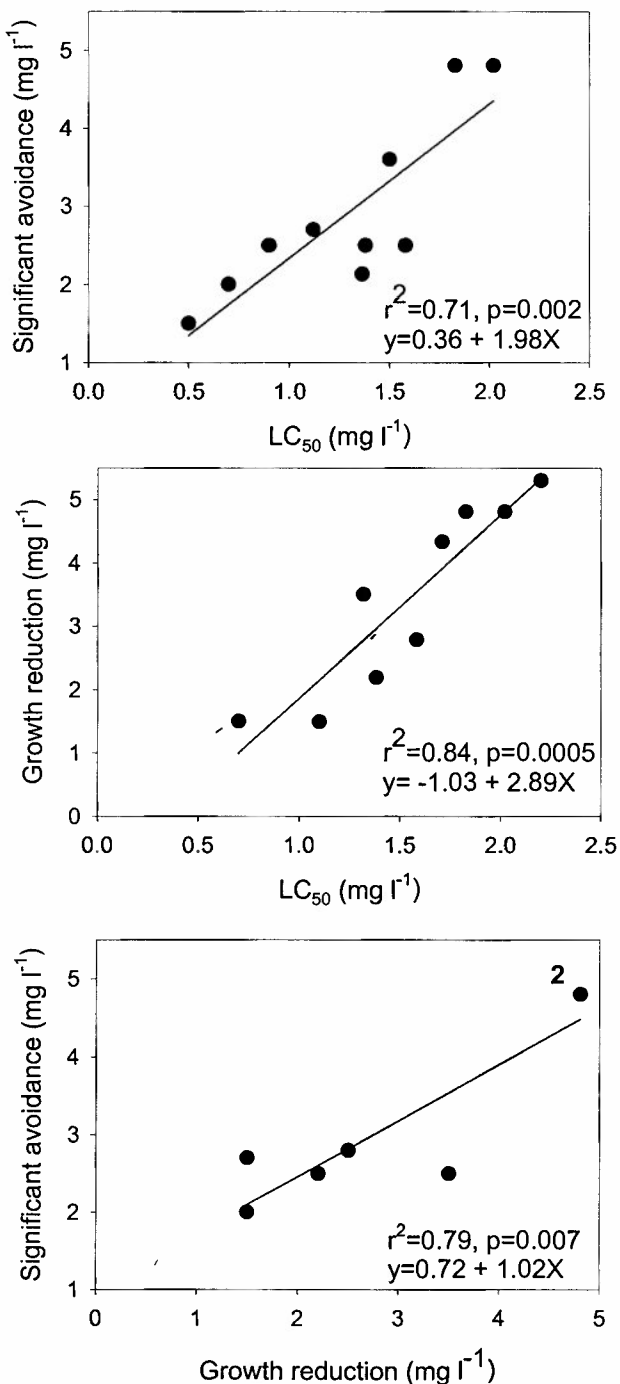


Fig. 3. Relationship between lethal dissolved oxygen concentrations and those resulting in reduced growth and behavioral avoidance of affected habitat. Top) LC₅₀ versus avoidance behavior, middle) LC₅₀ versus growth reduction, and bottom) growth versus avoidance behavior. Two identical points in bottom panel are indicated by the number 2 next to the data point. Data sources are as follows. Avoidance versus mortality: Burton et al. 1980; Coutant 1985; Petersen and Petersen 1990; Pihl et al. 1991a,b; Scholz and Waller 1992; Schurman and Steffensen 1992; Howell and Simpson 1994; Petersen and Pihl 1995; Wanamaker and Rice 2000; U.S. Environmental Protection Agency

duced diversity, abundance, and production of fishes within the portion of the water column affected by low dissolved oxygen concentrations. Variation among systems in oxygen concentrations at which abundances and diversity of fishes decline, likely reflects both the methods used for field sampling (especially how specifically the issue of low oxygen effects was targeted in the study design), as well as variation in the sensitivity of resident species. An analysis of bottom trawl data by Craig et al. (2001) indicated that demersal species in the Gulf of Mexico move from hypoxic areas with dissolved oxygen concentrations ≤ 2 mg l⁻¹ to adjacent areas with somewhat higher oxygen concentrations in the range of 2–5 mg l⁻¹. Gray (1992) suggested emigration by sensitive demersals such as cod and whiting at 25–40% saturation, and by benthic flatfishes such as dab and flounder at 15% saturation. Emigration leading to reduced densities of fishes even at oxygen concentrations approaching 40–50% saturation (3–4 mg l⁻¹) is supported by the pattern of increasing number of species in trawl samples with increasing dissolved oxygen concentrations in Long Island Sound (Howell and Simpson 1994) and Chesapeake Bay (Breitburg et al. 2001; Fig. 2), and the increasing number of finfish individuals caught per trawl hour with increasing bottom dissolved oxygen off the Louisiana Coast in the Gulf of Mexico (Diaz and Solow 1999). The mean number of finfish, squid, and lobsters north of Hempstead Harbor, Long Island Sound, predicted by correlations of catch and bottom dissolved oxygen was approximately 400 ind tow⁻¹ at 4 mg l⁻¹, 30 ind tow⁻¹ at 2 mg l⁻¹, and 5 ind tow⁻¹ at 0.5 mg l⁻¹ during 1988 through 1990 (estimated from Fig. 4 in Howell and Simpson 1994).

Shoreward migration of finfish and decapod crustaceans as a response to low dissolved oxygen has long been recognized. Loesch (1960) described how wind from the north or east causes upwelling of oxygen-depleted bottom waters in Mobile Bay, and the resultant jubilees in which

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2000; Eby 2001; Miller et al. 2002. Growth versus mortality: Burton et al. 1980; Petersen and Petersen 1990; Pihl et al. 1991; Scholz and Waller 1992; Schurman and Steffensen 1992; Petersen and Pihl 1995; Plante et al. 1998; Chabot and Dutil 1999; U.S. Environmental Protection Agency 2000; McNatt 2002. Avoidance versus growth: Coutant 1985; Pihl et al. 1991b; Scholz and Waller 1992; Howell and Simpson 1994; Petersen and Pihl 1995; U.S. Environmental Protection Agency 2000; Eby 2001; McNatt 2002; Miller et al. 2002. Only studies using a range of dissolved oxygen concentrations are included in figures. Data from multiple studies on the same species were averaged. Data from multiple studies on the same species were averaged. If responses were tested at several temperatures, the temperature with the most dissolved oxygen effects tested was selected.

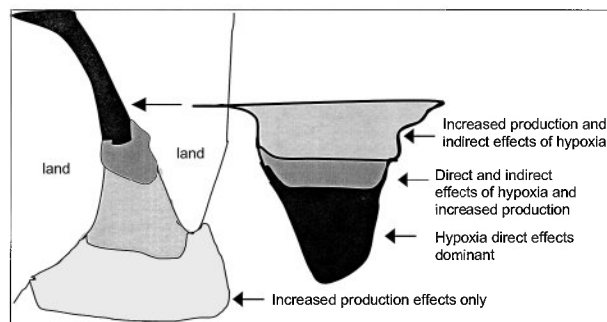


Fig. 4. Contrasting zones of positive and negative effects of nutrient enrichment on fish growth and abundance. The top-down view of the estuary depicts bottom dissolved oxygen concentrations; the cross-section indicates the vertical distribution of nutrient and hypoxia effects within an estuary segment with severely hypoxic bottom water. The relative importance of increased prey production, habitat avoidance, altered predator-prey interactions, and mortality vary both vertically and horizontally within affected water bodies.

crabs, shrimp, and demersal fishes aggregate at the water's edge. These jubilees have been recorded in local papers near Mobile Bay since 1867 (Schroeder and Wiseman 1988). Similar events have been recorded in areas such as the Brittany Coast (Rossignol-Strick 1985) and Chesapeake Bay (Officer et al. 1984). In addition to moving towards the air-water interface at the shoreline, fish are often observed at the surface of the water employing aquatic surface respiration when oxygen concentrations within the water column decline (Kramer 1987; Gee and Gee 1995). This behavior is energetically costly, especially for benthic fishes lacking a functional swim bladder, and can expose fish to increased predation by birds (Poulin et al. 1987; Kersten et al. 1991).

The oxygen concentrations at which fish will initiate an escape response or avoid affected habitat, relative to oxygen concentrations that are lethal, will likely be influenced by the energetic cost of such responses, and tradeoffs between risk of mortality due to low oxygen, risk of mortality due to predation, and loss of reproductive or feeding opportunities. Fish may also use waters with lower oxygen concentrations as the percent of the habitat affected by low oxygen increases (Eby 2001). Oxygen concentrations avoided vary considerably among species and life stages, reflecting the wide range of tolerances to low oxygen among marine and estuarine fishes.

Oxygen concentrations at which site-attached fishes will abandon nest sites or at which small cryptic species will abandon nest shelter from predators may be lower, and closer to lethal concentrations, than levels at which more highly mobile species avoid or move out of hypoxic habitat. In laboratory

tests, male naked gobies guarding either clutches of eggs attached to the inside of nesting tubes or nesting tubes without eggs, abandoned the nesting tubes at only 0.1 mg l^{-1} above the 0.25 mg l^{-1} dissolved oxygen concentration found to be lethal during short-term exposures to declining dissolved oxygen levels (Breitburg 1992). In the field, naked gobies abandoned nests and shelters at sites where oxygen concentrations dropped to lethal levels, but densities of adults and juveniles actually increased (presumably from emigration from more severely affected depths), and no egg clutches were abandoned at a slightly shallower site where oxygen concentrations remained only a few tenths of a mg l^{-1} higher. Adult toadfish (*Opsanus tau*) remained at their burrows even at depths at which oxygen concentrations had dropped to only 0.2 mg l^{-1} , although they were lethargic and most were partially outside of their burrows. In contrast to the behavior of these cryptic, site-attached benthic species, laboratory and field studies indicate avoidance, and likely abandonment of habitat by more widely ranging demersal and water column species at dissolved oxygen concentrations at which growth is reduced, rather than those that are lethal (Fig. 3). For species that rely on cryptic behavior to avoid predation, initiating escape behavior carries with it the potential for increased risk of predation.

GROWTH, DEVELOPMENT, AND REPRODUCTIVE BEHAVIOR

Extended or repeated exposure to sublethal hypoxia in laboratory experiments results in reduced growth or development rates of all life stages of fishes (summarized in Magnusson et al. 1998; U.S. Environmental Protection Agency 2000; Breitburg et al. 2001). Caging experiments and comparisons among years with varying numbers of hypoxic days in the Neuse River also indicate the potential for exposure to low oxygen concentrations to reduce fish growth in the field (Eby 2001). Reduced growth rates of juvenile fishes occurs at approximately 2.2 times the oxygen concentration found for 50% mortality during 24-h to 96-h exposures (Fig. 3). Howell and Simpson (1994) suggest that the smaller average size of winter flounder at hypoxic sites than at sites with higher oxygen concentrations may have resulted from exposure to low oxygen. Assessing the likelihood of reduced growth in the field, outside of experimental enclosures, is complicated by the mobility of fishes and the possibility of differential avoidance behavior of smaller, slower growing individuals and larger or faster growing individuals within a population or age class. Field estimates of effects are still important because laboratory experiments conducted under conditions that require minimal energy ex-

penditures to find and capture food and eliminate energy requirements of avoiding predators and swimming against currents likely underestimate the effect of low oxygen on growth of fishes in the field.

For species that provide parental care, hypoxia can also increase the energetic cost of reproduction per offspring during the egg deposition through hatch stage because of increased fanning required to supply oxygen to demersal eggs (Jones and Reynolds 1999), and increased embryonic development time (Breitburg 1992; Jones and Reynolds 1999). Increased weight loss associated with tending of eggs under hypoxic conditions may lead to increased abandonment of successive clutches even when the survival rate within tended clutches is not affected by the level of hypoxia leading to nest abandonment (Jones and Reynolds 1999).

Altered Food Webs and Trophic Interactions

The net result of altered behaviors and distributions of animals, and the spatial structure imposed on stratified water bodies by low dissolved oxygen, includes major changes in the overall food web and in trophic interactions among species. Because behavioral avoidance of low dissolved oxygen alters densities both within and surrounding waters with low oxygen concentrations, the spatial scale of low oxygen effects can extend considerably beyond the borders of the hypoxia and into highly oxygenated surface and surrounding waters. Evidence from both the Chesapeake and Baltic-Kattegat systems also highlights the importance of variation among species in behavioral responses and physiological tolerances in shaping the ultimate effects of low oxygen.

Low dissolved oxygen concentrations potentially alter all aspects of predator-prey interactions including encounter rates, attack rates, and capture success (Kramer 1987; Rahel and Nutzman 1994; Breitburg et al. 1997). The net balance of changes can lead to strong effects of bottom-layer oxygen depletion on predation mortality of early life stages of fishes throughout the water column and not only within the oxygen-depleted bottom layer (Breitburg et al. 1999). Predation mortality of eggs and larvae can either increase or decrease depending on whether bottom oxygen concentrations are sufficiently severe to compress predator-prey encounters into the oxygenated pycnocline and surface layers, or are mild (relative to egg and larval tolerances) and can serve as a refuge from highly sensitive predators. In some systems, hypoxia may favor highly tolerant gelatinous zooplankton such as scyphomedusae and ctenophores, relative to planktivorous fishes, because they can use hypoxic waters and have high capture rates of hypoxia-

stressed prey (Breitburg et al. 1997, 1999; Purcell et al. 2001). The net result can be changes in the relative importance of various trophic pathways within coastal systems (Breitburg et al. 1999).

Bottom feeding fishes that briefly enter hypoxic layers or return to sites during rising oxygen concentrations can capture stressed benthic invertebrates that lie exposed on the surface or have compromised escape behaviors (Pihl et al. 1991a). Such opportunistic feeding can increase consumption, and alter both taxonomic and size composition of prey as species normally buried deep in the sediment become available. Reliance on small, short-lived benthic invertebrates may increase in areas stressed by hypoxia where larger, longer-lived species are eliminated (Pihl 1994). In addition to changes in the relative importance of alternative trophic pathways, total biomass of prey available for fishes may be lower than in highly oxygenated environments. Eby (2001) has suggested three indirect mechanisms by which low oxygen can affect growth of juvenile fishes: restricting feeding to areas with low prey abundance, increasing crowding and density-dependent effects on growth within areas with suitable oxygen concentrations, and reducing prey abundance in areas intermittently affected by low dissolved oxygen. The spatial patchwork of enrichment and depletion created by the direct and indirect effects of high nutrient loadings can alter major features of ecosystems such as the ratio of pelagic to demersal biomass (Caddy 2000; de Leiva Moreno et al. 2000).

Larger Spatial Scales and Broader Perspectives

Given the long list of negative effects of low oxygen described above, it is appropriate to ask whether and under what circumstances hypoxia leads to decreased harvests of fish, and decreased abundances that extend beyond the immediate volume of hypoxic water. As discussed in the remainder of the paper, the answer depends on whether we try to isolate hypoxia from its nutrient over-enrichment cause, whether the question is asked from a conservation or fisheries harvest perspective, and the spatial scale of concern. The answer also depends on whether hypoxia and nutrient over-enrichment occur in isolation from other anthropogenic stressors of fish populations including overfishing and habitat degradation.

WHEN ARE FISH POPULATIONS AND FISHERIES HARVESTS MOST SEVERELY AND DIRECTLY AFFECTED BY LOW OXYGEN?

Hypoxia and anoxia strongly affect fishery landings and fishing practices on a local scale, i.e., within oxygen-depleted waters during seasons in which severe oxygen depletion occurs. Severe declines in

harvests are sometimes briefly preceded by increased catches as animals initiate behavioral responses to decreasing dissolved oxygen, but once severe hypoxia or anoxia become established, fish yields and abundances plummet. Several days of unusually large catches of sole preceded a period of zero catches as severe hypoxia developed on the Brittany coast between the Vilaine and Loire estuaries following release of freshwater from the Arzal Dam (Rossignol-Strick 1985).

Even when local in spatial extent, displacement of fishing efforts potentially leads to important economic and social costs. It is not in the economic interest of fishers to persist in behaviors that lead to extremely low or no catch when alternative fishing locations or target species are available. Once local conditions result in severely decreased catches or empty nets, local fishing efforts decline. It is not surprising that fishers do not conduct bottom trawling for epibenthic fish and crustaceans, or set traps, in the bottom layer of the Baltic, the subpycnocline mesohaline Chesapeake Bay, or the dead zone in the Gulf of Mexico during periods of the most severe oxygen depletion. Fishers may need to travel farther from their home port to reach productive fishing grounds. Increased travel distance potentially increases both costs (thus reducing profits) and risk of fishing efforts, and compromises both local economies and human health. Displacement and reductions in recreational fishing activity can also lead to reduced revenues of businesses that provide related equipment or services, or that rely on tourism.

Low dissolved oxygen appears to have been an important factor directly influencing large-scale (i.e., extending beyond the borders of the hypoxic volume of water) population declines or interannual variation in population levels of a small number of important fisheries stocks in spite of the potential for mitigating behaviors and the potential increase in prey abundance for fish. Some of the strongest evidence for effects that extend beyond the actual hypoxic volume include Baltic cod in the Baltic-Kattegat system (Plikshs et al. 1993; Mackenzie et al. 1996) and smelt (*Osmerus eperlanus*) in the Elbe estuary (reviewed in Thiel et al. 1995). In both cases, hypoxia has been suggested to have led to decreased recruitment.

The severity of the effects of low oxygen on population size of fishes appears to depend on the convergence of a number of factors, including life history characteristics, habitat use, and physical characteristics of the system that put some species at particularly high risk. Especially important is the presence of early life stages at times and in places with severe oxygen depletion and blocked migration routes. The potential for mortality of Baltic

cod eggs sinking into hypoxic bottom waters to lead to measurable population-level effects is supported by the positive correlation between the thickness of the water column with salinity > 11 psu, dissolved oxygen > 2 ml l⁻¹, and temperature $> 1.5^{\circ}\text{C}$ and the estimated number of 1 and 2 year old Baltic cod 1 and 2 years later, respectively (Bagge 1993). High mortality of smelt larvae unable to escape areas in which low dissolved oxygen develops is thought to have resulted in high mortality of larvae and recruitment failure in some years in the Elbe estuary (Thiel et al. 1995). Chittenden (1974) and Weisberg et al. (1996) also suggested that low oxygen in Delaware Bay blocked spawning migrations and seaward movement of anadromous fishes, contributing to the decline of American shad (*Alosa sapidissima*) in the Delaware basin.

MULTIPLE STRESSORS

The brief list of fisheries and fish populations with clear evidence for large-scale declines due to hypoxia is, in part, a reflection of the difficulty of disentangling low oxygen effects from effects of additional anthropogenic stressors in human-influenced systems and the potential for other stressors to exacerbate the effects of low oxygen (Breitburg et al. 1998; Breitburg and Riedel in press). Low dissolved oxygen does not occur in isolation from other human influences and natural features of the marine environment that have potential negative effects on fish abundance and harvests. High nutrient loadings are associated with loss of aquatic vegetation, decreased water clarity, changes in the zooplankton assemblage thought to encourage gelatinous predators and competitors of early life stages of fishes, and harmful algal blooms (reviewed in Nixon 1988; Cloern 2001). Waters near centers of dense human habitation are often subjected to introductions of exotic species including pathogens (Ruiz et al. 2000), intense fishing pressure, increased sediment loads, and altered hydrodynamic regimes. Increased temperatures due to human influence (National Research Council 2000) will potentially exacerbate the effects and extent of oxygen depletion. As the number and severity of stressors increase, the potential for serious cumulative and interactive effects also increases.

High nutrient loadings can be associated with and contribute to the formation of harmful algal blooms as well as hypoxia (Paerl et al. 1998). Some of these bloom-forming species are toxic to fishes, and the potential for interacting effects of hypoxia and harmful algal blooms can increase the risk to fish populations as well as make it difficult to definitively identify causative agents of fish kills. Other cases in which either multiple effects of nutrient over-enrichment or other combinations of multi-

ple stressors make it difficult to determine the role hypoxia plays in fish declines are common. Both plaice harvests and bottom dissolved oxygen have declined in the southern Kattegat during the past two decades (Christensen et al. 1998). A system-wide negative effect of hypoxia on bottom fish abundances seems unlikely since catches of dab have increased over the same time period. There appears instead to be a significant interaction between exudates of the green alga *Enteromorpha* and low dissolved oxygen (both of which have increased with eutrophication) that increases mortality of plaice larvae using shallow water habitat (Larson 1997).

Summer surface temperatures in some estuaries are above optimal levels for growth. High temperatures can result from natural features of estuaries and their watersheds, as well as from anthropogenic activities that influence freshwater inflow and global climate. Whether natural or anthropogenic, high surface temperatures interact with low dissolved oxygen in two ways: by creating a "temperature-oxygen squeeze" which reduces habitat suitable for growth more than would either stressor alone (sensu Coutant 1985; Coutant and Benson 1990) and by leading to higher oxygen requirements for growth in warmer rather than cooler waters. The potential for the combined effects of warm surface waters and cooler but hypoxic bottom waters to greatly reduce summer habitat availability and suitability to currently or previously important fisheries species has been suggested to have negatively affected populations of both striped bass (*Morone saxatilis*; Coutant 1985; Coutant and Benson 1990) and two sturgeon species (Atlantic sturgeon, *Acipenser oxyrinchus*, and shortnose sturgeon, *Acipenser brevirostrum*; Niklitschek 2001) in Chesapeake Bay. Yet all of these fishes are, or have been, the target of intense fishing pressure, and a moratorium on striped bass harvests during the late 1980s–early 1990s was followed by a resurgence of the Chesapeake population of this species. We do not know how much higher fishing pressure striped bass or sturgeon populations would have been able to withstand in the absence of hypoxia or the magnitude of the contribution that high bottom-layer oxygen concentrations could make to efforts to restore Chesapeake sturgeon populations. Harvest limits that are sustainable in the absence of hypoxia may lead to population declines in its presence. The effects of overfishing and eutrophication on fish harvests and total fish biomass are particularly difficult to disentangle because they both tend to result in increased ratios of planktivore:demersal fish biomass (Caddy 2000).

Low dissolved oxygen also has the potential to

increase the susceptibility of finfish to fishing effort because of altered behavior. The most clear-cut example comes from a crustacean fishery. Catch per unit effort of Norway lobster more than doubled in the southern Kattegat when oxygen concentrations declined to 40% saturation (Bagge and Munch-Petersen 1979 cited in Baden et al. 1990a). Lobsters emerge from their burrows at low oxygen concentrations, making them more susceptible to fishing gear (Baden et al. 1990a). Shifts in distributions in response to hypoxia can also increase the abundance of non-targeted species in bycatch by increasing their spatial overlap with species targeted by fisheries (Craig et al. 2001).

High fishing pressure can exacerbate effects of low dissolved oxygen in another way: by removing structural species that provide shallow water refuges during periods of low oxygen. Studies in both the Chesapeake Bay (Breitburg 1992) and Neuse River (Lenihan et al. 2001) have found that oyster reefs that extend vertically or shoreward into shallow water provide an important refuge for fishes and crustaceans when bottom waters are hypoxic. Loss of oyster reef habitat due to destructive fishing practices and disease can reduce or eliminate this refuge, potentially increasing mortality from exposure to lethal oxygen concentrations (Lenihan et al. 2001).

Exposure to low dissolved oxygen concentrations also appears to have an immune suppression effect. The incidence of diseases such as lymphocystis, epidermal hyperplasias, and papillomas in dab (*Limanda limanda*) in the eastern North Sea and southern Kattegat increased in the year following hypoxia and remained elevated for 3–4 yr at stations experiencing oxygen concentrations < 3 mg l⁻¹ (Møllgaard and Nielsen 1987).

CONSIDERING LARGER SPATIAL SCALES

The brevity of the list of clear examples of large-scale, hypoxia-induced population declines likely also reflects the conflicting effects of decreased habitat extent and suitability, and increased prey production, evident at expanded spatial scales that include both the volume of hypoxic water and the volume of enriched but sufficiently oxygenated habitat (Fig. 4). The surface layer, shallow benthic habitat within surface layer depths, and areas adjacent to those affected by oxygen depletion but farther from the source of nutrients are typically high in oxygen even in highly enriched coastal systems and semi-enclosed seas with oxygen-depleted bottom waters.

Whether the presence of bottom-layer hypoxia results in declines in overall fish production depends on the balance between positive and negative effects of nutrient enrichment in the full range

of habitats within a system. On the negative side are lost demersal and benthic production in sub-pycnocline waters during affected seasons due to emigration, mortality, and reduced growth, as well as altered abundances and trophic interactions outside the hypoxic volume that may increase predation mortality. Countering these negative effects are factors that can increase fisheries production such as an increase in prey in above-pycnocline and adjacent waters throughout the year, as well as potentially increased production in bottom waters in seasons without hypoxia. Thus, nutrient enrichment can lead to increased fisheries yields (Nixon et al. 1986; Caddy 2000; Grimes 2001) even while causing oxygen depletion in some portions of a system.

Growth rates as well as abundance of fishes can be increased in portions of systems experiencing positive effects of nutrient enrichment without the negative effects of hypoxia. Boddeke and Hagel (1991) suggest increases followed by decreases in the size of 4-yr old sole and plaice during 1946–1990 may have been related to changes in phosphate loading, some of which is supplied through upstream bodies of water characterized by low dissolved oxygen. This pattern contrasts sharply with decreased growth and abundance of dab and plaice within Aarhus Bay, and decreased growth of dab in the Kattegat as hypoxia has worsened within these systems (Bagge and Nielsen 1989; Bagge et al. 1994).

An interesting analysis by de Leiva Moreno et al. (2000) suggests a 30-fold increase in landings of pelagic planktivorous fishes as one moves from oligotrophic to mesotrophic to eutrophic semi-enclosed seas in Europe, but only a 2-fold increase in demersal landings per unit area. The increase in planktivores reflects the general increase in production in surface waters accompanying high nutrient loadings. The more modest increase in demersal production likely reflects the balance between habitat loss in deep waters affected by hypoxia and increased production in shallow benthic habitats and highly oxygenated deep habitats. Replotting data for demersal fishes from 14 semi-enclosed European seas (ICES 1996; de Leiva Moreno et al. 2000; data provided by de Leiva Moreno) against a hypoxic index, which ranks systems by the occurrence, persistence, and spatial extent of hypoxia, indicates only a limited negative influence on system-wide fish harvests (Fig. 5). Systems with year-round severe hypoxia and anoxia in bottom waters (the Black and Baltic Seas) averaged somewhat lower than eutrophic systems with seasonal, but widespread hypoxia. Only the Black Sea and the adjacent Sea of Azov had substantially lower demersal harvests per unit area than the average

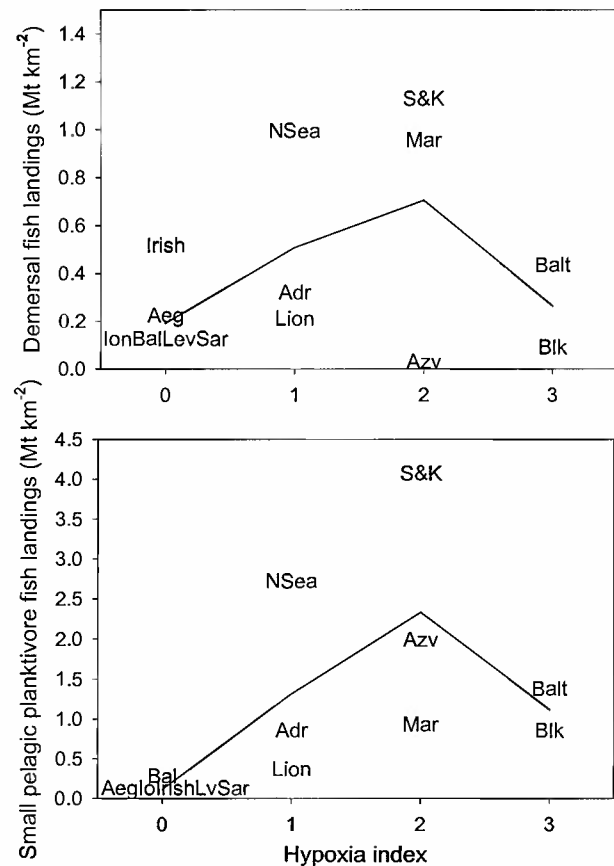


Fig. 5. Relationship between demersal fish harvests and the extent and severity of hypoxia in 14 semi-enclosed European seas. Data are from ICES (1996). The hypoxic index is as follows: 0 = hypoxia rare or does not occur, 1 = hypoxia occasional but not widespread, 2 = hypoxia occurs on a regular seasonal basis and is widespread, and 3 = persistent, year-round hypoxia or anoxia in bottom waters. Seas plotted are the Irish Sea (Irish), Aegean (Aeg), Ionian, Balearic, Levant, and Sardinia (IonBallLevSar; demersal landings ranging from 0.08 to 0.13 Mt km⁻²), North Sea (Nsea), Adriatic (Adr), Gulf of Lions (Lion), combined data for the Skagerrak and Kattegat (S&K), Sea of Marmara (Mar), Azov (Azv), Baltic (Balt), and Black Sea (Blk). AegIoIrishLvSar = Aegean, Ionian, Irish, Levant, and Sardinia Seas, which have similar landings of small pelagic planktivores. Data are the average of 1986–1995, the most recent 10 years of the data set used in ICES (1996) and de Leiva Moreno et al. (2000).

calculated for systems in which hypoxia is rare or does not occur, or systems in which hypoxia occurs only occasionally and is not typically widespread. Approximately 95% of the volume of the Black Sea is permanently anoxic. Much of the anoxic volume is a result of system depth, strong salinity stratification, and limited exchange of bottom waters with more highly oxygenated systems. The Sea of Azov is characterized by chlorophyll levels four times higher than any other system examined by de Lei-

va Moreno et al. (2000), and has experienced massive fish kills resulting from chemical pollutants.

Whether using spatial averaging to determine nutrient effects on coastal systems is appropriate depends on the objectives of both research and management. From a conservation perspective, causing large areas of a system to become seasonally unsuitable for fish and macrofauna is clearly an unacceptable consequence of nutrient over-enrichment of coastal waters. In addition to the immediate issue of environmental degradation, such habitat loss and sublethal effects of hypoxia may make populations and ecosystems more susceptible to negative effects of other stressors. The fact that massive mortality of fishes in the Gulf of Trieste (Stachowitsch 1984) appears less severe when averaged with the rest of the Adriatic or the Mediterranean as a whole, or that fish mortality in the Mariager Fjord (Fallesen et al. 2000) is not reflective of the whole of the Baltic-Kattegat system is not sufficient to justify local habitat degradation.

From a fisheries production and human food supply perspective, it is important to recognize that reducing nutrient inputs sufficiently to eliminate hypoxia will likely reduce system-wide production of pelagic planktivores, and, except in the most severely affected systems, may have minor negative effects on system-wide production of demersal fishes as well. Although the analyses in Fig. 5 and de Leiva Moreno et al. (2000) are across-system comparisons, it is likely that the time-course of nutrient enrichment and reduction effects will parallel the across-system effects. The local effects of nutrient reduction strategies should benefit harvest of demersal fishes in areas currently experiencing seasonal oxygen depletion. The larger-scale effect will depend on the diet and lifestyle of species harvested for human consumption in each system and the current severity of oxygen depletion. This caveat is not intended to provide an argument against improving environmental quality by reducing nutrient loadings from anthropogenic sources, but is a caution about what benefits can realistically be expected from such efforts. High harvest levels associated with highly enriched systems may not be sustainable. Dramatic reductions in nutrient loadings are clearly needed in many coastal systems.

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