2004

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Recommended Citation

Diaz, Robert J.; Nestlerode, Janet; and Diaz, Minnie L., "A Global Perspective On The Effects Of Eutrophication And Hypoxia On Aquatic Biota And Water Quality" (2004). *VIMS Books and Book Chapters*. 14.
https://scholarworks.wm.edu/vimsbooks/14

EPA/600/R-04/049

FISH PHYSIOLOGY, TOXICOLOGY, AND WATER QUALITY

Proceedings of the Seventh International Symposium, Tallinn, Estonia May 12-15, 2003

Edited By

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Published by

Ecosystems Research Division
Athens, Georgia 30605

National Exposure Research Laboratory
Office of Research and Development
U.S. Environmental Protection Agency
Research Triangle Park, North Carolina 27711

A GLOBAL PERSPECTIVE ON THE EFFECTS OF EUTROPHICATION AND HYPOXIA ON AQUATIC BIOTA

Robert J. Diaz[1], Janet Nestlerode[1], Minnie L. Diaz[2]

ABSTRACT

Development associated with human populations has led to the globalization of many environmental problems. In marine systems, the most serious of these problems are directly related to the process of eutrophication. The increased production of organic matter in these marine systems associated with eutrophication is the primary factor impacting species abundance and composition and dissolved oxygen budgets. Oxygen, which is essential to maintaining balance in ecosystem processes through its role in mediating microbial and metazoan activities, has declined to critically low levels in many systems, which has led to the development of hypoxia (<2 ml O_2/l) and anoxia (0 ml O_2/l). Currently, most oxygen depletion events are seasonal, but trends toward longer periods that could eventually lead to persistent hypoxic or anoxic conditions are emerging. Over the last 50 years, there has been an increase in the number of systems reporting problems associated with low dissolved oxygen. Currently there are over 100 hypoxic/anoxic areas around the globe, ranging in size from <1 km^2 to 70000 km^2, that exhibit a graded series of responses to oxygen depletion, ranging from no obvious change to mass mortality of bottom fauna. Ecosystems currently severely stressed by eutrophication-induced hypoxia continue to be threatened with the loss of fisheries, loss of biodiversity, alteration of food webs, and simplification of energy flows.

INTRODUCTION

Cloern (2001) succinctly summarized current understanding of coastal eutrophication, indicating that the long-term records of nutrient discharges over the past 50 years provide compelling evidence of a rapid increase in the fertility of many temperate coastal ecosystems (for example, Baltic and adjoining seas – Karlson *et al.* 2002; Northwest Black Sea – Mee 1992; Northern Adriatic Sea – Solic *et al.* 1997; North Sea rivers – Howarth *et al.* 2002; United States bays and estuaries - Jaworski *et al.* 1997, Howarth *et al.* 1996; Northern Gulf of Mexico – Rabalais *et al*. 1996, Rabalais and Turner 2001; Japan – Suzuki 2001). In each of these systems, the fertilization is directly related to an expanding human population, which recently passed 6 billion and will likely exceed 8 to 10 billion by the year 2050 (Wilson 2002). Seitzinger *et al.* (2002) found that at scales of regions and continents, human population was a good predictor of

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dissolved inorganic nitrogen (DIN) exported to coastal systems. By 2050, projections indicate that a 2.4 to 2.7-fold increase in nitrogen and phosphorus driven eutrophication will result from this population expansion (Tilman *et al.* 2001), with serious consequences for coastal ecosystems.

Fertilization of marine systems, mainly from excess nitrogen, has been linked in a complicated way to many ecosystem-level changes associated with eutrophication, or more precisely, cultural eutrophication. Cultural eutrophication is specific to impacts related to human populations on the environment and separates the conditions in these coastal systems from natural processes that can also lead to eutrophic-like conditions, such as those associated with coastal upwelling zones and oxygen minimum zones (OMZ) where oxygen consumption exceeds resupply. Oxygen depletion associated with upwelling events tends to be episodic, severe, short-lived (less than a year), and associated with the western boundaries of continental landmasses (Brongersma-Sanders 1957, Rosenberg *et al.* 1983). OMZs are unusual oxygen-depleted areas that are widespread and stable oceanic features occurring at intermediate depths (typically 400 to 1000 m), persisting for long periods of time (at greater than decadal scales), and are completely controlled by natural processes and cycles (Wyrtki 1966, Kamykowski and Zentara 1990, Olson *et al.* 1993, Childress and Seibel 1998).

While eutrophication can be defined simply as the production of organic matter in excess of what an ecosystem is normally adapted to processing (Nixon 1995), it is actually only part of a complex web of stressors that interact to shape and direct ecosystem-level processes (Breitburg *et al.* 1998, Cloern 2001) (Figure 1). From Figure 1, the most visible ecosystem response to this set of multiple stressors is the greening of the water column as primary production increases in direct response to nutrient enrichment. However, the unseen is most dangerous. For nutrient enrichment, which leads to increased organic matter production (eutrophication), the unseen decrease in dissolved oxygen in bottom waters created by the increased flux of particulate organic matter to the bottom is most threatening. The degree to which an ecosystem responds to any of the multiple stressors is dependent upon physical, chemical, and biological characteristics that act to filter and modulate the response (Cloern 2001).

Human impacts are accelerating the rate and magnitude of change within an ecosystem as more and more ecosystem level processes are affected (Jackson *et al.* 2001). The history and pattern of human disturbance in terrestrial, aquatic, coastal, and oceanic ecosystems have brought us to a point at which oxygen depletion is likely to become the keystone impact for the 21st century, replacing the 20th century keystone of overfishing (Jackson *et al.* 2001). A mounting volume of literature documenting change in marine ecosystems indicates oxygen depletion as a major phenomenon that is a tertiary manifestation of the severe levels of stress experienced by many ecosystems. The primary stress is nutrient enrichment, which regulates the secondary response of eutrophication. See reviews and summaries by Gray (1992), Nixon (1995), Diaz and Rosenberg (1995), Cloern (2001), Turner (2001), and Karlson *et al.* (2002) for examples of ecosystem responses. The correlation between human activities and declining dissolved oxygen is strong, with the oxygen budgets of many marine ecosystems around the world adversely affected by eutrophication.

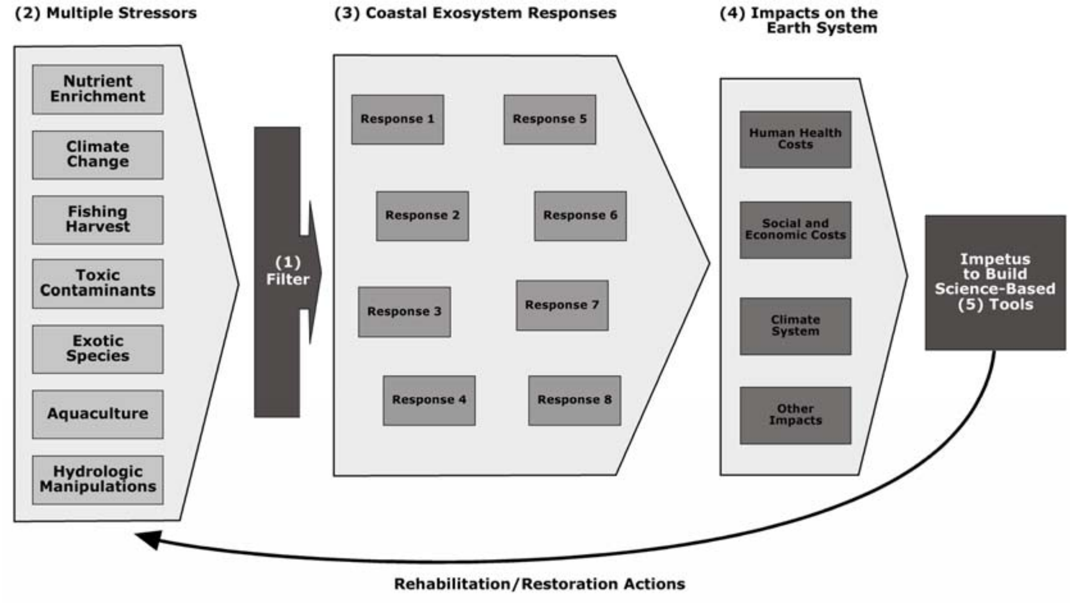

Figure 1. Conceptual model of coastal eutrophication modified from Cloern (2001). (1) system attributes that determine responses to nutrient enrichment; (2) nutrient enrichment as one of many stressors; (3) complex linkage between responses to multiple stressors; (4) change in coastal ecosystems; (5) application of scientific understanding of eutrophication with the goal of building rational management strategies for ecosystem rehabilitation/restoration.

The emphasis of this paper is ecosystem response to oxygen depletion resulting directly from eutrophication. The emphasis on dissolved oxygen is warranted given the importance of oxygen for sustaining life for all fishes and invertebrates. Metaphorically speaking, the American Lung Association motto could be adopted for this situation. "When you can't breathe, nothing else matters." When the supply of dissolved oxygen in aquatic environments is cut off or the consumption rate exceeds resupply, oxygen concentrations quickly decline beyond the point that sustains most animal life. Two factors are required for the development of hypoxia, and at times anoxia; one is water column stratification that isolates the bottom water from oxygen-rich surface water, and the second is decomposition of organic matter that reduces oxygen levels in the isolated bottom water. The first factor is generated primarily by salinity stratification and the second by microbial metabolism. Both factors must be at work for hypoxia to develop and persist. In fact, the reaction of microbial populations to eutrophication has been explosive, particularly in systems with the greatest oxygen depletion problems (Jackson *et al.* 2001).

The terms used to describe low dissolved oxygen or oxygen depletion are hypoxia and anoxia. Hypoxia is defined by dissolved oxygen concentrations <2 ml O_2/l or <2.8 mg O_2/l; for seawater this is about 18% of air saturation (Tyson and Pearson 1991). Anoxia is the complete absence of dissolved oxygen (0 ml O_2/l). The point at which various animals suffocate varies, but effects generally appear when oxygen drops below 2 ml O_2/l (Diaz and Rosenberg 1995, Breitburg *et al.* 2001, Karlson *et al.* 2002). The relationship between declining oxygen and animal response are graded and follow a predictable path, good examples of which are given by Diaz and Rosenberg (1995) and Rabalais *et al.* (2001b). This paper presents a brief overview and update of hypoxic conditions in estuarine and marine systems around the world.

OXYGEN DEPLETION AROUND THE WORLD

On a geological time scale, low-dissolved-oxygen environments (hypoxia and anoxia) have been major factors in shaping the evolution of life (Caplan and Bustin 1999). Today, the vestiges of naturally occurring oxygen depletion are the oceanic OMZs, the largest pools of hypoxic water in world oceans, particularly in the Pacific and Indian Oceans and the Arabian Sea (Olsen *et al.* 1993). The largest pool of naturally occurring anoxic water is the Black Sea (Kideys 2002). The Black Sea anoxic zone does not support any eukaryotic life, which is typical of all areas experiencing extended periods of anoxia, whether natural or anthropogenic. However, the temporal and spatial stability of OMZs has allowed the development of species aerobically adapted to dissolved oxygen concentrations from 0.5 ml O_2/l to about 0.1 ml O_2/l (Levin *et al.*1991, Childress and Seibel 1998). This is in stark contrast to the faunal response to cultural-eutrophication-induced hypoxia in shallow coastal and estuarine areas, where oxygen concentrations of <0.5 ml O_2/l lead to mass mortality of individuals and major change in community structure.

The worldwide distribution of coastal oxygen depletion is either centered on major population concentrations, or closely associated with developed watersheds that deliver large quantities of nutrients (Figure 2, Table 1). The historical perspective indicates that many of these currently hypoxic systems were not so when they were first studied. Since at least the 1950s and 1960s, dissolved oxygen concentrations of many major coastal ecosystems around the world have been adversely affected by eutrophication. Most of these coastal systems have documented declines in dissolved oxygen through time, starting in most cases from their initial oxygen measurements (Rosenberg 1990). The declining trend in dissolved oxygen seems to have lagged about 10 to 20 years behind the increased use of chemical fertilizer that began in the 1940s (Howarth *et al.*2002). For systems with historical data from the first half of the 20th century, declines in oxygen concentrations started in the 1950s and 1960s for the northern Adriatic Sea (Justic 1987), between the 1940s and 1960s for the northwest continental shelf of the Black Sea (Mee 1992, Kideys 2002), and in the 1970s for the Kattegat (Baden *et al.*1990a). Declining dissolved oxygen levels were noted in the Baltic Sea as early as the 1930s (Fonselius 1969), but it was in the 1950s that hypoxia became widespread (Karlson *et al.* 2002). Other systems have experienced hypoxia since the beginning of oxygen data collection, for example, in the 1930s for the Chesapeake Bay (Officer *et al.* 1984), and the 1970s for the northern Gulf of Mexico (Rabalais and Turner 2001) and many Scandinavian fjord systems (Karlson *et al.* 2002). However, the longer-term geochronological records indicate that hypoxia was not always present in these particular ecosystems (Sen Gupta *et al.* 1996; Karlson *et al.* 2002; Zimmerman and Canuel 2002). Not all nutrient-enriched systems have developed eutrophic conditions and related oxygen depletion problems. San Francisco Bay receives higher levels of nutrients than the Chesapeake Bay, but has lower primary production and oxygen depletion due to strong tidal mixing and turbid water (Cloern 2001).

Table 1. Eutrophication-associated hypoxic areas around the world with an emphasis on benthic and fisheries responses. Several of these systems also experience anoxia. Hypoxia is characterized as Episodic: events occurring at irregular intervals greater than one year; Periodic: events occurring at regular intervals shorter than one year; Annual: yearly events related to summer or autumnal stratification; Persistent: year-round hypoxia. Benthic faunal response is categorized as None: communities appear similar before and after hypoxic event; Mortality: moderate reductions of populations, many species survive; Mass Mortality: drastic reduction or elimination of the benthos. Benthic recovery is described by No Change: dynamics appear unrelated to hypoxia; Reduced: recolonization occurs but community does not return to prehypoxic structure; Multi-year: gradual return of community structure; Annual: return of similar community structure in a year. First observed is usually first documentation in literature and in most cases not the first occurrence of oxygen depletion.

System	Country/State	First Observations	Recent Observations	Area (km^2)	Fisheries Response	Benthic Response	Benthic Recovery	Reference
Annual Oxygen Depletion								
Åland archipelago	Finland	1990		10		Mortality	Reduced	Norkko and Bonsdorff 1996
Aquaculture	Taiwan	2000			Mortality of prawns	Mortality		Cheng *et al*. 2002
Århus Bay	Denmark	1980		1300		Mass Mortality	Multi-year	Fallesen and Jorgensen 1991
Barnegatt Inlet	New Jersey	1990				Mass Mortality	Annual	Moser 1998
Belt Sea	Denmark	1970		2150				Karlson *et al*. 2002
Bilbao Estuary	Spain	1990				Mortality		Gonzales-Oreja and Saiz-Salinas 1998; Saiz-Salinas and Frances-Zubillaga 1997
Bornholm Basin	Baltic Sea	1950		2500		Mass Mortality	Multi-year	Tulkki 1965; Leppakoski 1969
Cabbage Tree Basin	Australia	1980				Mortality	Annual	Rainer and Fitzhardinge 1981
Chesapeake Bay Mainstem	Maryland	1930		2750	Avoidance, some mortality	Mortality	Annual	Holland *et al*. 1987; Boesch *et al*. 2001; Seliger and Boggs 1988
Corpus Christi Bay	Texas	1980		15		Reduced	Reduced	Ritter and Montagna 1999
Dead-end canals	Maryland, Delaware	1990		5				Maxted *et al*. 1997
Delaware River, Lower	Delaware	1910	Improved		Recovery American shad/striped bass fishery	Mass Mortality	Increasing	Weisberg *et al*. 1996
Delaware River, Upper	Delaware	1910	Improved					Patrick 1988
Eckernforde Bay	Germany	1990				Mortality	Annual	D'Andrea *et al*. 1996
Elbe Estuary	Germany	1980	Improved		Stressed			Thiel *et al*. 1995
Elefsis Bay, Aegean Sea	Greece	1980				Mass Mortality	Annual	Friligos and Zenetos 1988; Theodorou 1996
Fjords of Skagerrak coast	Sweden	1950						Rosenberg 1990
Flushing Bay	New York	1990				Mortality		Diaz, unpublished data
German Bight	Germany	1980			Mortality	Mortality	Reduced	Brockmann *et al*. 1988; Niermann *et al*. 1990
Gialova Lagoon	Ionian Sea, Greece	1990		2500		Mortality	Annual	Arvanitidis *et al*. 1999
Goro Lagoon	Italy	1990				Mortality	Annual	Reizopoulou *et al*. 1996
Great Egg Harbor River	New Jersey	1990						Glenn *et al*. 1996
Guanabara Bay	Brazil	1990			Tropical	Mortality		Valentin *et al*. 1999
Gulf of Mexico	Louisiana	1970		17000	Avoidance	Mortality/avoidance	Reduced	Rabalais and Turner 2001
Gulf of Trieste	Adriatic Sea	1960			Stressed	Mass Mortality	Multi-year	Stachowitsch 1984, 1991; Simunovic *et al*. 1999; Justic *et al*. 1987
Gullmarsfjord	Sweden	1980			Stressed	Mass Mortality	Reduced	Nilsson and Rosenberg 2000; Josefson and Widbom 1988
Hakata Bay	Japan	1970		120		Mortality	Annual	Karim *et al*. 2002
Havstens Fjord	Sweden	1990						Gustafsson and Nordberg 2000
Herring River	Massachusetts	1980			Fish kills, decline of alewife fishery			Portnoy 1991
Hillsborough Bay	Florida	1980				Mass Mortality	Annual	Santos and Simon 1980

System	Country/State	Observations		(km^2)	Fisheries Response	Response	Recovery	Reference
Hiuchi Sound	Japan	1970				Mass Mortality		Sanukida *et al.* 1984
Hood Canal	Washington	1980						Paulson *et al.* 1993
Horseshoe Lagoon	Australia	1990						Donnelly *et al*. 1999
Hudson River	New York	1960	Improved					Bronsnan and O'Shea 1996
Inre Verkviken	Finland	1970		0.5				Lindholm 1996
Ise Bay	Japan	1990			Stressed	Mortality		Nakata *et al.* 1997
Kattegat	Sweden, Denmark	1980		3850	Collapse of Norway lobster	Mass Mortality	Multi-year	Baden *et al.* 1990a; Josefson and Jensen 1992; Rosenberg *et al.* 1992
Kiel Bay	Germany	1960		890	Stressed	Mass Mortality	Annual	Arntz 1981; Rumohr 1986; Weigelt 1990, 1991; Oeschger and Storey 1990
La Coruna Bay	Spain	1990						Lopez-Jamar *et al*. 1995
		First	Recent	Area		Benthic	Benthic	
Laholm Bay	Sweden	1980			Mortality	Mortality	Annual	Baden *et al.* 1990b; Rosenberg and Loo 1988
Lake Nakaumi	Japan	1990			Mortality/avoidance			Ishitobi *et al*. 2000
Lake Shinji	Japan	1990				Mass Mortality		Yamamuro *et al.* 1998
Limfjord	Denmark	1980		440	Demersal fisheries gone	Mass Mortality	Annual	Jorgensen 1980; Hylleberg 1993
Loire Estrary	France	1990			Mortality of migratory species			Thouvenin *et al*. 1994
Long Island Sound	New York	1980		232	Avoidance, some mortality	Mortality		Howell and Simpson 1994; Welsh *et al.* 1994; Schimmel *et al.* 1999; NOAA 1997
Los Angeles Harbor	California	1950	Improved			Mass Mortality	Reduced	Reish 1955, 2000
Lough Ine	Ireland	1970				Mass Mortality	Annual	Kitching *et al.* 1976
Mecklenburg Bay	Germany	1980		1860				Weigelt and Rumohr 1986
Mikawa & Ise Bays	Japan	1980				Mortality/avoidance		Suzuki and Matsukawa 1987
Mobile Bay	Alabama	1880		1060	Mortality	Mass Mortality		May 1973; Engle and Summers 1999; Pennock *et al.* 1994
Mullica River Estuary	New Jersey	1990						Glenn *et al*. 1996
Neuse River Estuary	North Carolina	1990			Fish kills, mortality of oyster	Mortality/avoidance	Annual	Paerl *et al.* 1995, 1998; Lenihan and Peterson 1998; Lenihan 1999
New York City Harbor	New York	1990				Mass Mortality	Annual	Diaz, unpublished data
Nichupti Lagoon	Mexico	1980						Diaz, unpublished data
Northern Adriatic Sea	Italy	1970		3750				Barmawidjaja *et al*. 1995; Justic *et al.* 1987, 1993
NW Gulf of Mexico	Louisiana	1980				Mortality	Annual	Gaston 1985
NW Shelf Black Sea	Ukraine, Romania	1960		40000	Reduced	Mass Mortality	Annual	Zaitsev 1993; Bakan and Buyukgungor 2000
Oder Lagoon	Germany	1990						Pohl *et al.* 1998
Omura Bay	Japan	1980						Iizuka and Min 1989
Osaka Bay	Japan	1980						Tanimoto and Hoshika 1997
Oslofjord	Norway	1910		150	Reduced	Mortality	Annual	Petersen 1915; Mirza and Gray 1981; Rosenberg *et al*. 1987
Palude della Rosa	Italy	1990				Mortality	Annual	Tagliapietra *et al.* 1998
Pamlico River	North Carolina	1960			Mortality	Mass Mortality	Annual	Tenore 1972; Hobbie *et al.* 1975; Stanley and Nixon, 1992
Patuxent Piver	Maryland	1990			Avoidance, low egg hatching/larval mortality	Avoidance/mortality	Annual	Keister *et al*. 2000, Breitburg *et al*. 1997
Perdido Bay	Florida	1990						Flemer *et al.* 1999
Pomeranian Bay	Germany	1990		170		Mass Mortality	Reduced	Powilleit and Kube 1999
Potomac River	Maryland	1990		264		Mortality	Annual	NOAA 1997
Raritan Bay	New York, New Jersey	1970						Christensen and Packard 1976
SE Kattegat	Sweden	1980			Reduced demersal fishes	Avoidance/mortality	Multi-year	Peterson and Pihl 1995
Seine Estuary	France	1990						Michel *et al.* 2000
Seto Inland Sea	Japan	1980				Mortality	Annual	Imabayashi 1986
St. Johns River	Florida	1990				Mortality	Annual	Mason 1998
Swedish West Coast Fjords	Sweden	1980			Stressed	Mortality	Reduced	Josefsen and Rosenberg 1988

System	Country/State	Observations		(km^2)	Fisheries Response	Response	Recovery	Reference
Thau	France	1990			Mortality/Reduced shellfish production	Mass Mortality		Souchu *et al*. 1998; Mazouni *et al*. 1996; Chapelle *et al*. 2000
Tolo Harbor	Hong Kong	1980				Mass Mortality	Annual	Wu 1982
Tome Cove	Japan	1980				Mortality	Annual	Tsutsumi 1987
Townsend-Hereford Inlet	New Jersey	1990						Glenn *et al.* 1996
Western Gulf of St. Lawrence	Canada	1990				No response		Comeau *et al* 2002
Episodic Oxygen Depletion								
Baie de Somme	France	1990			Collapse of cockle industry	Mass Mortality		Rybarczyk *et al*. 1996
Beacon Key, Biscane Bay	Florida	1990						Leverone 1995
Bude Bay	SW England	1990		12		Mortality		Gibbs *et al.* 1999
Buzzard Bay	Massachusetts	1990		2				NOAA 1997
Cape Fear River	North Carolina	1990			Fish kills	Reduced	Annual	Mallin *et al.* 1999; Posey *et al.* 1999
Chester River	Maryland	1990		24				NOAA 1997
Choptank River	Maryland	1990		48				NOAA 1997
		First	Recent	Area		Benthic	Benthic	
Connecticut River	Connecticut	1990		9				NOAA 1997
East Frisian, Wadden Sea	Netherlands	1990						Kaiser and Lutter 1998
Finnish Archipelago	Finland	1970						Karlson *et a*l. 2002
German Bight	Germany	1980		15000		Mass Mortality	Annual	Dethlefsen and Westernhagen 1983 Brockmann *et al.* 1988
Gulf of Mexico, off Freeport	Texas	1970		50	Mortality	Avoidance/mortality	2 years	Harper and Rabalais 1995
Krka, Adriatic Sea	Yugoslavia	1980				Mortality	Annual	Legovic *et al*. 1991
Lake Pontchartrain	Louisiana	1990			Loss of large clams	Reduced		Abadie and Poirrier 2000
Loch Ailort	Scotland	1990			Salmon farms in the system	Reduced		Gillibrand *et al.* 1996
New York Bight	New York, New Jersey	1970		987	Surf clam/finfish mortality, Avoidance	Mass Mortality	Multi-year	Garlo *et al.* 1979; Sindermann and Swanson 1980
North Sea coast	Germany	1980		25		Mortality	Reduced	Koenig 1996
Off Cape Rodney	New Zealand	1980			Mortality			Taylor *et al.* 1985
Pamlico Sound	North Carolina	1990			Mortality	Mortality		Paerl *et al.* 2000
Salts Hole	United Kingdom	1990		6		Mortality		McArthur 1998
SE North Sea	Denmark	1980			Stressed	Mortality	Annual	Dyer *et al.* 1983; Westernhangen and Dethlefson 1983
Sommone Bay	France	1980		3	Collapse of cockle fishery	Mass Mortality	Multi-year	Desprez *et al.* 1992
Texas Shelf, Deep	Texas	1980			Stressed	Mortality	Annual	Harper *et al.* 1981, 1991
Texas Shelf, Shallow	Texas	1980			Stressed	Mass Mortality	Multi-year	Harper *et al.* 1981, 1991
Wadden Sea	Wadden Sea	1990		3000	Stressed	Mortality		deJonge *et a*l. 1994
Wismar Bay	Baltic Sea	1980			Stressed	Mortality	Reduced	Prena 1995a, 1995b
Vestfjord		1970						Karlson *et a*l. 2002
Periodic Oxygen Depletion (>1 event per year)								
Bon Secour Bay	Alabama	2000			Loss of oyster	Mortality		Rikard *et al*. 2000
Florida Keys	Florida	1990				Mortality		Lapointe and Matzie 1996
Gironde Estuary	France	1990						Abril *et al.* 1999
Great South Bay	New York	1990		15				NOAA 1997
Gullmarsfjord, Alsback Deep	Sweden	1990				Mortality		Gustafsson and Nordberg 2001
Jamaica Bay	New York	1990		26				NOAA 1997
James Island Creek	South Carolina	1990			Avoidance	Avoidance		Cochran and Burnett 1995
Koljo Fjord	Sweden	1990				Mortality	Annual	Gustafsson and Nordberg 1999; Rosenberg *et al*. 2001
Narragansett Bay	Rhode Island	1990		11				NOAA 1997
Prevost Lagoon	France	1990			Reduced aquaculture production	Mass Mortality	Annual	Guyoneaud *et al.* 1998

System	Country/State	Observations		(km^2)	Fisheries Response	Response	Recovery	Reference
Rappahannock River	Virginia	1990		55	Avoidance	Mortality	Annual	Llanso 1992; NOAA 1997
St. Joseph Bay	Florida	1990			Avoidance			Leonard and McClintock 1999
St. Lucie River	Florida	1990						Chamberlain and Hayward 1996
York River	Virginia	1980		30	Avoidance	No response	No Change	Pihl *et al.* 1991; Diaz *et a*l. 1992; Sagasti *et al*. 2001
Persistent Oxygen Depletion								
Arkona Basin	Sweden	1980		1000				Karlson *et al* 2002
Baltic proper	Baltic Sea	1960		70000	Avoidance, mortality/low hatch cod eggs	Mortality/avoidance		deJonge *et al.* 1994
Big Glory Bay	New Zealand	2000			Caused by salmon farming	Mass Mortality		Morrisey 2000
Byfjord	Sweden	1970			Pelagic only	Mortality	Reduced	Rosenberg 1990, Rosenberg *et al.* 1977
Caspian Sea	Caspian Sea	1990				Mortality	Some?	Dumont 1998
Gdansk Basin	Poland	1960		1200				Karlson *et a*l. 2002
Gotland Basin	Sweden	1960			Avoidance, mortality/low hatch cod eggs	Mortality	Reduced	Laine *et al.* 1997
Gulf of Finland, Deep	Gulf of Finland, Deep	1960	Improved	2330		Reduced	Increasing	Laine *et al.* 1997; Andersin and Sandler 1991
Himmerfjord	Sweden	1970	Improved	11				Karlson *et al.* 2002
Idefjord	Sweden, Norway	1960	Improved	80		Mortality	Reduced	Rosenberg 1980
Loch Carron	Scotland	1970				Mass Mortality	No Change	
Scheldt Estuary	Belgium	1990						Verlaan *et al.* 1998
Sea of Azov	Russia-Ukraine	1990			Lower production	Mortality	Reduced	Balkas *et al.* 1991; Chechum 1998
		First	Recent	Area		Benthic	Benthic	
Skagerrak Coast Fjords	Sweden, Norway	1920		54	Stressed	Mortality		AnnualJohannessen and Dahl 1996a,b
St. Anna Archipelago	Sweden	1970		25				Karlson *et al.* 2002
Stockholm Inner Archipelago	Sweden	1970		60		No Benthos	No Change	Rosenberg and Diaz 1993
Sullom Voe	Shetland	1980				Mass Mortality	No Change	Pearson and Eleftheriou 1981
Tan Shui Estuary	Taiwan	1990						Jeng and Han 1996
Unknown Oxygen Depletion Cause								
Etang de Berre	France	1970		132				Stora and Arnoux 1983
Kilviken Fjord	Sweden	1970				Reduced		Hendelberg and Jensen 1993
Marmara Sea	Marmara Sea	1990			Mass Mortality	Mass Mortality		Orhon and Yuksek, unpublished data
Mauritius Island	Mauritius Island	1990			Coral reef affected			Thomassin *et al*. 1998
Mondego River	Portugal	1990						Kamp-Nielsen *et al.* 1997
Pettaquamscutt River	Rhode Island	1990						Wilkin and Barnes 1997
Roskilde Fjord	Denmark	1990						Kamp-Nielsen *et al.* 1998
Waquoit Bay	Massachusetts	1990						Fritz *et al*. 1996

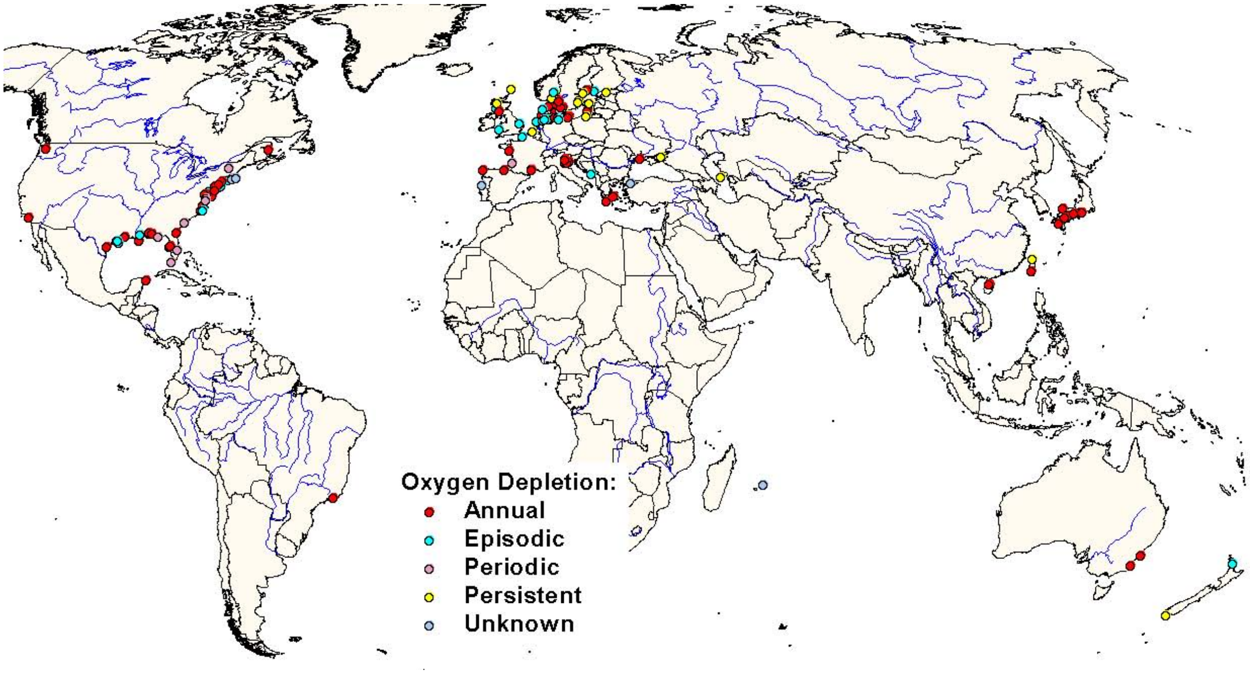

Figure 2. Global distribution of the 146 oxygen depletion zones related to cultural eutrophication listed in Table 1. Systems are categorized by type of hypoxia (see Table 1 for details).

The most common form of hypoxia is one annual event, occurring at 54% of the 146 oxygen-depleted systems. The most common response to annual oxygen depletion was mortality of benthos followed by some level of recolonization with the return of normal oxygen conditions (Table 1). In essence, annual hypoxia forces an annual pulsing of energy over the shortened interval of normal dissolved oxygen conditions (Diaz and Rosenberg 1995). The second most common form of oxygen depletion is episodic, occurring 18% of the time in the 146 systems. It appeared that episodic oxygen depletion was the first signal that a system had reached a critical point. Many systems, such as the Kattegat, first experienced episodic events that initially caused mass mortality of benthic organisms, but now experience annual oxygen depletion (Karlson *et al.* 2002).

Since the 1960s, the number of oxygen-depleted ecosystems has doubled every ten years (Figure 3). Prior to 1960, we found nine systems with cultural eutrophication-related oxygen depletion. During the 1960s, another ten systems were added, but by the 1970s estuarine and coastal ecosystems around the world were becoming over enriched with organic matter (Nixon 1995) and the number of oxygen-depleted ecosystems had doubled (Figure 3). After this point, hypoxia quickly became an annual event and a prominent feature affecting energy flow processes in marine ecosystems (Elmgren 1989, Pearson and Rosenberg 1992). During the 1980s, 37 systems were added, and in the 1990s 68 more were added (Table 1). By the end of the 20th century, oxygen depletion had become a major, worldwide environmental problem with only a small fraction of systems (6%) showing signs of improvement.

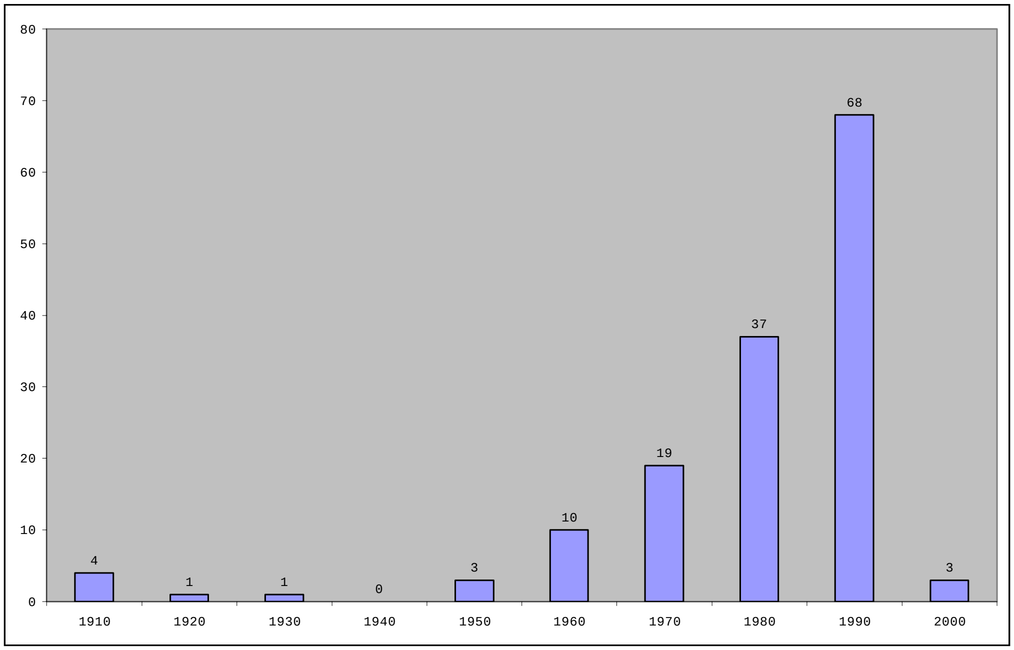

Figure 3. Histogram of the number of ecosystems reporting oxygen depletion by decade. The decade was determined either from the first time hypoxia was seen in historical data or the first year a published account appeared in the literature. Data from Table 1.

The largest systems with improved dissolved oxygen conditions were the northwest Black Sea and the Gulf of Finland. In the Black Sea, a reduction in nutrients and possibly a balancing of exotic species led to an improvement in ecosystem function and reduction in hypoxia (Kidey 2002). In the Gulf of Finland, a decrease in water column stratification led to improved dissolved-oxygen conditions and the return of benthic fauna (Karlson *et al.* 2002). Conditions have also improved in some systems that have experienced intensive regulation of nutrient or carbon inputs, such as the Hudson River, New York, and the Delaware River in Pennsylvania and New Jersey. In others, such as the Chesapeake Bay, improvements in dissolved oxygen await the 'burn off' of nitrogen that has accumulated within the system's sediments. Many examples of small-scale reversals in hypoxia associated with improvements in treatment of sewage and pulp mill effluents as early as the 1970s (Rosenberg 1972, 1976) also exist. In the northern Gulf of Mexico, the hypoxic zone is very tightly coupled with runoff from the Mississippi River. During low flow years, the area of hypoxia is greatly reduced, only to increase when river flow increases (Rabalais *et al.* 2001a, unpublished data). Similarly, the Baltic Sea can experience temporary dissolved oxygen increases associated with episodic water exchanges across the belt seas. Even though the exchange of deep water in the Baltic is episodic, there is convincing evidence that eutrophication accelerates oxygen consumption in its bottom waters (Karlson *et al.* 2002).

In general, coastal hypoxia is not a natural condition. Only hypoxia and anoxia associated with naturally-occurring events have a historical context dating back 100 to 150 years.

This includes: areas of natural upwelling, such as those off Peru and Central America (Tarazona *et al.* 1988) or West Africa's Namibian shelf (Hamukuaya *et al.* 1998); oceanic OMZ, such as in the Arabian Sea (Gooday *et al.* 2000); and stagnant basins, such as Santa Barbara Basin off California (Bernhard and Reimers 1991). Methodologies for measuring dissolved oxygen were not developed until the 1880s (Winkler 1888). Accounts in the historical literature do imply the occurrence of oxygen depletion prior to development of Winkler's method, and were generally in water bodies associated with human development. For example, in 1884 the Mobile Register (Alabama, USA) described what was very likely a hypoxic/anoxic event in Mobile Bay, with fishes congregating in shallow water where they were easily caught by hand (J. Pennock, University of Alabama, personal communication). Mobile Bay has a well-documented history of oxygen depletion that extends back to at least the 1960s, with descriptions of similar attempts by fish to escape oxygen-depleted waters (May 1973). A detailed review of the historical literature will likely find hundreds of such accounts, and we predict that most of them can be associated with some sort of human development.

The most serious effects of the combined problems associated with eutrophication and hypoxia are seen in the Black Sea and Baltic Sea, where demersal trawl fisheries have either been eliminated or severely stressed (Elmgren 1989, Mee 1992). Karlson *et al.* (2002) provide a detailed summary of the development of oxygen depletion in the Baltic and surrounding seas. The Black Sea, in particular, provides an excellent example of how multiple stressors conspired to alter an entire system. In the 1980s and early 1990s, the northwest coastal shelf of the Black Sea was in a severe state of deterioration from stress exerted by multiple factors, including over-fishing, exotic species introduction (the ctenophore *Mnemiopsis* spp.), pollution, altered hydrology and nutrient enrichment that led to eutrophication-induced hypoxia (Mee 1992, Kideys 1994, 2002). Historical data show that in the 1940s, the northwest Black Sea was considered to be oligotrophic. However, by the 1970s nutrient enrichment had led to a highly eutrophic condition that, in turn, led to alterations in the composition and quality of phytoplankton production, including harmful algal blooms (HAB). In the 1970s prior to the introduction of the ctenophore, and in the 1980s before ctenophore populations exploded, eutrophication resulted in increased anchovy (*Engraulis encrasicolus*) production and widespread hypoxia. Through the 1970s and 1980s hypoxia and anoxia became more prevalent and were the primary cause of mass mortality of the benthos, including demersal fish. Other complex changes that occurred and were likely a response to the multiple stressors included increased turbidity, decrease in nongelatinous zooplankton, decline in biodiversity, and replacement of highly-valued demersal fish species with less desirable planktonic omnivores (Mee 1992, Kideys 2002). Of the 26 commercial species fished in the 1960s, only six still supported a fishery in the early 1990s (Mee 1992). In 1989, the ctenophore populations exploded and caused a crash in the pelagic anchovy and nongelatinous zooplankton communities that was not oxygen-related. This event indicates that the combination of stressors affecting the Black Sea needs to be examined in order to understand ecosystem response. The resilience of the Black Sea ecosystem was observed in the 1990s when nutrient loads declined between 1991 and 1997. Primary production declined, there was a species shift back to diatoms, harmful algal blooms decreased, nongelatinous zooplankton increased, and pelagic fish reappeared (Kideys 2002). The introduction of the ctenophore *Beroe* spp., a predator of *Mnemiopsis* spp., further improved the Black Sea ecosystem.

The eutrophication-related oxygen depletion zone in the northwest Black Sea is not related to the central Black Sea anoxic zone, which over the last 5000 years has evolved an oxic/anoxic ecosystem in a precise redox balance (Konovalov and Murray 2001). However, there is now evidence that even the central Black Sea anoxic zone is showing the signs of eutrophication due to an increased flux of organic matter. This, in turn, has increased the rate of sulfate reduction and created an imbalance in the sulfide budget. As a result, sulfide concentrations have increased in the anoxic zone over the past 20 to 25 years (Konovalov and Murray 2001).

As early as the 1980s, the occurrence of hypoxia in coastal systems was closely linked to eutrophication. In the German Bight, van Pagee *et al*. (1983) found that from 1930 to 1983 an increase in nutrients corresponded with an increase in the duration and severity of hypoxia. In all recent cases, (listed in Table 1), hypoxia appears to be a result of general ecosystem eutrophication, with other stressors acting to complicate ecosystem response. It is difficult or impossible to separate the response of an ecosystem to eutrophication-induced hypoxia from the other multiple stressors on ecosystem functioning; the Black Sea provides a good example. However, some level of eutrophication appears to be a positive force in enhancing a system's secondary productivity (Nixon and Buckley 2002), and to a point enhances fisheries yield (Caddy 1993, 2001). The critical point in the ecosystem response trajectory to eutrophication is the appearance of severe hypoxia or anoxia, either of which can potentially cause mass mortality of both benthic and pelagic species. The general effect of eutrophication and hypoxia to favor benthic macrofaunal communities and species with opportunistic life histories, shorter life spans, and smaller body size is well characterized by the Pearson and Rosenberg (1978) organic gradient response model. However, eutrophication has a preconditioning effect on benthic fauna by eliminating sensitive species, which tends to lessen the acute response of the system to hypoxia when it does occur. This is the reason some systems that experience mild hypoxia show no acute effect, such as the York River, in Virginia (Neubauer 1993, Sagastie *et al.* 2001).

Climate change, whether from global warming or from microclimate variation, will have direct consequences for eutrophication-related oxygen depletion. The form of climate change effect will depend primarily upon how the strength of water column stratification is affected, and secondarily on factors that affect organic matter production such as nutrient supplies. At a global scale, general circulation models predict large changes in rainfall patterns under a CO_2 doubling scenario. If these changes in rainfall lead to increased discharges of freshwater to coastal ecosystems, stratification is likely to increase and oxygen depletion will expand in those systems already affected, and may begin in other systems. Conversely, if stratification decreases, oxygen depletion or the chances for depletion will decrease. For that part of the Mississippi River basin associated with the northern Gulf of Mexico annual oxygen depletion, a doubling of CO_2 would increase river discharge by 20% and temperature by 2^oC to 4^oC (Miller and Russell 1992). Justic *et al.* (1996) predicted that these changes would lead to a 50% increase in primary production, a 30% to 60% decrease in subpycnocline dissolved oxygen, and expansion of the oxygen-depleted area. Smaller-scale climate variation, such as the North Atlantic Oscillation (NAO) index, may have similar effects on dissolved oxygen budgets. Nordberg *et al.* (2000, 2001) found that the NAO index was correlated to hydrographic conditions in Swedish west coast fords, and may in part be responsible for changes in dissolved oxygen budgets, particularly in fjords not subjected to significant human pollution.

SUMMARY

Hypoxia related to anthropogenic activities appears to develop within a system as a result of the cumulative effects of eutrophication in combination with other stressors. Many times hypoxia is not noticed until higher-level ecosystem effects are manifested. For example, hypoxia did not become a prominent environmental issue in the Kattegat until the collapse of a Norway lobster fishery several years after hypoxic bottom waters were first reported (Baden *et al.* 1990b). The northern Gulf of Mexico is representative of severely stressed coastal ecosystems that currently experience seasonal hypoxia, but have not experienced hypoxia-related loss of fisheries. Although hypoxia in the northern Gulf of Mexico has affected benthic invertebrate communities over the last several decades, there is no clear signal of hypoxia in fisheries landings statistics (Rabalais *et al.* 2001a, Chesney and Baltz 2001). However, ecosystem level change is rarely the result of a single factor, and several forms of stress typically act in concert to cause change within an ecosystem. The critical point for fisheries losses in the northern Gulf of Mexico may be potential effects from global warming. The shallow, northwest continental shelf of the Black Sea (not part of the deep central basin anoxia) is another example of a system that was stressed by eutrophication-driven hypoxia in combination with other stressors that led to drastic reductions in bottom fisheries (Mee 1992, Kideys 1994, 2002).

Until the 1950s, reports of mass mortality of marine animals caused by lack of oxygen were limited to small systems that had histories of oxygen stress (Brongersma-Sanders 1957). In the 1960s, the number of systems with reports of hypoxia-related problems started to increase, but it was in the 1970s and 1980s when most initial reports of hypoxia occurred. By the 1990s, most estuarine and marine systems in close proximity to population centers had reports of hypoxia or anoxia. It does not appear that reports of oxygen depletion have leveled off, and the number of systems affected by hypoxia/anoxia continues to rise. There is encouraging news since 2000 that some large systems such as the Black Sea and Gulf of Finland have responded positively to a decrease in stressors.

Coastal and estuarine hypoxia does not appear to be a natural condition, except in areas influenced by OMZs, upwelling, or some enclosed fjord systems. The main factor in development of hypoxia in coastal and estuarine systems has been the input of excess nutrients leading to eutrophication. The determination of population or ecosystem level effects from hypoxia is complicated by many factors, including inadequate data on historic trends of species populations and dissolved oxygen concentrations and the interaction and synergistic effects of multiple stressors such as fishing pressure, habitat loss, etc. (Figure 1). Hypoxia and anoxia are among the most widespread deleterious anthropogenic effects in estuarine and marine environments. The effects of hypoxia may be reversed by the reduction of nutrient or organic inputs to a system that lead to a reduction or elimination of the hypoxia.

ACKNOWLEDGEMENTS

We thank Vance Thurston for his leadership in planning the 7th International Symposium on Fish Physiology, Toxicology, and Water Quality held in Tallinn, Estonia, as well as Gretchen Rupp and Michelle White. Kendall Watkins provided an excellent review of our manuscript.

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