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Eutrophication and Fisheries: Separating the Effects of Nitrogen Loads and Hypoxia on the Pelagic-to-Demersal Ratio and Other Measures of Landings Composition

Authors: Hondorp, Darryl W., Breitburg, Denise L., and Davias, Lori A.

Eutrophication and Fisheries: Separating the Effects of Nitrogen Loads and Hypoxia on the Pelagic-to-Demersal Ratio and Other Measures of Landings Composition

Darryl W. Hondorp,*[1] Denise L. Breitburg, and Lori A. Davias

Smithsonian Environmental Research Center, Post Office Box 28, Edgewater, Maryland 21037, USA

Abstract.—Building on previous analyses suggesting that the composition of fishery landings reflects the effects of eutrophication on mobile fish and benthos, we examined landings composition in relation to nitrogen loading and the spatial extent of hypoxia in a cross-system comparison of 22 ecosystems. We hypothesized that explicit consideration of both N and hypoxia is important because nutrient enrichment has been shown to have contrasting direct and indirect effects on fisheries. Consistent with this premise, patterns in landings composition differed with respect to N load and the spatial extent of hypoxia. For example, the ratios of pelagic to benthic and demersal biomass in fishery landings (P/D) exhibited a decreasing trend across ecosystems with progressively higher N but were significantly and positively correlated with the spatial extent of hypoxia. The P/D ratios were particularly high in systems with extensive and persistent hypoxia and particularly low in several estuaries where purse seining is prohibited or not used. In analyses that considered all systems, benthic and demersal landings did not decrease at high N as predicted by previous conceptual models, and the negative association with the spatial extent of hypoxia was statistically significant only when the Black Sea was included in the analysis. Landings of pelagic planktivores did not vary with the spatial extent of hypoxia but were positively related to N for all systems combined and for semi-enclosed seas. The trophic and size composition of fishery landings were not related to N or hypoxia, perhaps because landings of large, high-trophic-level species are more influenced by fishery exploitation or practices that mask the effects of water quality. Our results suggest that the response of fisheries to eutrophication differs from prevailing paradigms, which do not clearly distinguish between nutrient and hypoxia effects on fishery landings and do not consider the important influence of fishing practices and regulations on patterns in landings data.

Declining water quality has reduced the ecological integrity and economic value of coastal and estuarine ecosystems worldwide (Boesch et al. 2001; Kennish 2002). A major cause of declining water quality in many of these systems is nutrient overenrichment, which can directly or indirectly lead to a suite of environmental changes, including reduced dissolved oxygen concentrations or hypoxia (Nixon 1995; Boesch et al. 2001; Cloern 2001; Boesch 2002; Kennish 2002; Bricker et al. 2007). Hypoxia is perceived as one of the most deleterious consequences of nutrient overenrichment because it can reduce or eliminate the ability of organisms dependent on aerobic respiration to use affected habitat (Rabalais and Turner 2001; Breitburg 2002; Diaz 2001; Levin et al. 2009). Hypoxia has significant impacts on biomass and species composition of sessile benthic macrofauna,

which are unable to escape suboptimal or lethal oxygen concentrations (Diaz and Rosenberg 1995, 2008; Rabalais et al. 2002), but population-level and system-wide effects of hypoxia on fish and mobile invertebrates have been more difficult to determine (Breitburg et al. 2009). The coincident increase in the number of ecosystems reporting hypoxia (Diaz and Rosenberg 1995, 2008; Diaz 2001) and decreases in coastal fish and fisheries (e.g., Jackson et al. 2001; Lotze et al. 2006) highlights the need to better understand the impacts of hypoxia on mobile living resources, as well as the linkages between these impacts and management control variables such as nutrient loading rates.

Previous studies suggest that the composition of fisheries landings may be an important indicator of the combined effects of nutrient enrichment and hypoxia on populations of mobile fish and invertebrates (Caddy1993, 2000; Caddy and Garibaldi 2000; de Leiva Moreno et al. 2000). Estuaries and coastal areas support many of the world's most productive fisheries, and as a consequence, landings data are available for a wide range of systems and species. Current conceptual and statistical models of the relationship between eutrophication and the abundance of upper trophic level species have relied on fisheries data because fishery-independent data at comparable spatial, tempo-

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ral, and taxonomic resolutions are less available (e.g., Caddy 2000; de Leiva Moreno et al. 2000). Furthermore, water quality effects on fisheries are important, even if landings do not mirror stock abundances.

One fishery metric thought to be sensitive to eutrophication is the pelagic-to-demersal (P/D) ratio, which is the ratio of landings (in terms of mass) of small pelagic fish to landings of benthic and demersal fish and crustaceans (Caddy 1993, 2000; Caddy et al. 1998; de Leiva Moreno et al. 2000). This index was first suggested by Caddy (1993) and Caddy and Bakun (1994), who noted the predominance of small, short-lived pelagic species (mainly planktivores) in fishery landings from upwelling zones and eutrophic coastal areas, both of which are nutrient enriched relative to open-ocean waters. From these observations, Caddy et al. (1998) argued that pelagic and benthic–demersal stocks respond differently to varying levels of nutrient enrichment. While nutrient additions to oligotrophic systems might initially increase production of both pelagic and benthic–demersal species, enrichment of mesotrophic and especially eutrophic systems was predicted to result in degradation of benthic habitats, reduced landings of benthic–demersal species, and fishery landings with elevated P/D ratios (Figure 1). The symptom of nutrient enrichment most clearly linked to declines of benthic–demersal stocks was bottom-layer hypoxia. Pelagic stocks in eutrophic ecosystems may continue to increase in spite of continued nutrient inputs because as adults they would not be expected to be directly impacted by low dissolved oxygen in benthic habitats (Figure 1). Caddy (2000) and de Leiva Moreno et al. (2000) later showed that variability in P/D ratios among 14 European and Mediterranean semi-enclosed seas was consistent with a qualitative classification of ecosystem trophic state and positively correlated with average chlorophyll *a* concentrations. These associations suggested that P/D might be considered a proxy for nutrient availability and the severity of cultural eutrophication, but it is as yet unclear how P/D and other metrics estimable from landings data are related to individual forcing variables such as nutrient loading and hypoxia.

This study builds on the work of Caddy (1993, 2000) and de Leiva Moreno et al. (2000) by examining landings composition relative to water quality across a larger and more typologically diverse set of fishery ecosystems. Our study also extends previous research in two key ways. First, trends in landings composition were examined explicitly with respect to nitrogen loading rates and to hypoxia. Consideration of each variable separately is important because nutrient enrichment can have contrasting direct and indirect effects on fisheries (Breitburg 2002; Breitburg et al.

2009). While nutrients may stimulate fish production along pelagic pathways, upper trophic level production, especially for demersal fish and mobile benthos, may decrease because of the formation of hypoxic water (Figure 1). Next, analysis of landings composition was expanded to include not only P/D, but also the trophic, size, and taxonomic structure of fishery landings. Because small, lower-trophic level species tend to predominate pelagic stocks, decreases in the size and average trophic level of species in fishery landings would be expected to accompany nutrient- and/or hypoxia-driven increases in P/D (Figure 1). Patterns in the trophic and size composition of fishery landings relative to nutrient loading and hypoxia also may provide key insight into the factors driving global trends in landings composition because both overfishing and eutrophication are predicted to result in fisheries focused on smaller, lower trophic level species (Caddy 1993, 2000).

Methods

Study systems.—We examined landings composition relative to water quality in 22 ecosystems that included estuaries, coastal seas, and semi-enclosed seas. Study systems were selected based on data availability and to represent a broad range of nitrogen loading rates and extent and severity of hypoxia. As in previous analyses (Caddy 1993, 2000; de Leiva Moreno et al. 2000), study systems were considered independent of one another but in some cases represented adjoining water bodies. Test systems included 8 semi-enclosed seas previously analyzed by de Leiva Moreno et al. (2000) (Adriatic Sea, Baltic Sea, Black Sea, Irish Sea, North Sea, Sea of Azov, Sea of Marmara, Skagerrat-Kattegat), as well as 14 new ecosystems. The new test systems represented a broader range of size and typology than did previous cross-system analyses and included both estuaries and semi-enclosed seas. Unfortunately, several Mediterranean subsystems included in de Leiva Moreno et al. (2000; Balearic Sea, Gulf of Lions, Sardinian Sea, Ionian Sea, Levant Sea) were excluded from the current study because of unavailability of water quality data at relevant spatial scales. Analyses of fishery and water quality data were restricted to the period 1990–2004 because of the availability of nutrient loading and recreational fishing data.

Fishery data sources and notes.—Fishery data reflected landings from commercial and recreational sources (Table A.1 in the appendix) but excluded aquaculture because it is less likely to reflect system-wide water quality conditions. Also excluded were bivalves and other sessile invertebrates, which are unable to behaviorally avoid hypoxia and whose
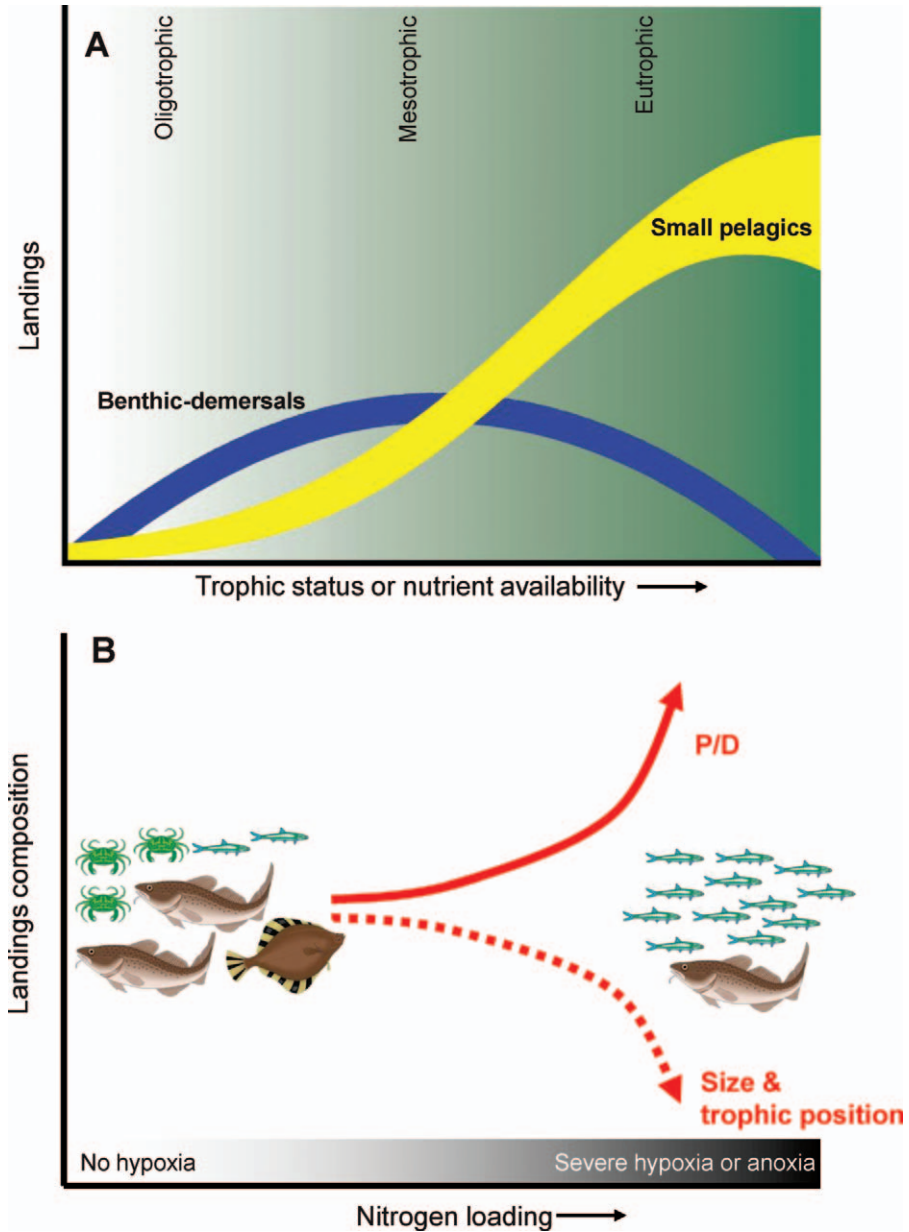
FIGURE 1.—Panel **(A)** presents a conceptual model of the response of fisheries landings to nutrient availability and/or ecosystem trophic status (adapted from Figure 5 of Caddy 2000). Seasonal hypoxia was expected to occur primarily within eutrophic systems or in systems with high nutrient availability. Panel **(B)** shows the resulting response of landings composition metrics to nutrient enrichment, assuming that severity of hypoxia is correlated with nutrient loading. The P/D ratio is the ratio of the landings (in terms of mass) of small pelagics to that of benthic and demersal fish and crustaceans.

fisheries are often sustained through hatchery supplementation.

Estimation of landings composition.—The pelagic component of the P/D ratio consisted primarily of small, planktivorous fishes in the order Clupeiformes. Mackerels in the genera *Scomber* and *Trachurus* also were included in this group because zooplankton contributes significantly to their diets (Darbyson et al. 2003; Jardas et al. 2004). The demersal component of the P/D ratio included all benthic–demersal fishes (irrespective of size) as well as mobile benthic crustaceans (shrimp, crabs, lobsters) and cephalopods

(except for ommastrephids). Herein, the demersal group is referred to as "benthic–demersal" because member species may be either obligate (e.g., flatfishes, crustaceans) or facultative (e.g., Atlantic cod) in their use of bottom habitat. In contrast to de Leiva Moreno et al. (2000), we classified sand lances as benthic–demersal. Despite being pelagic plankton feeders by day, these species make burrows and lack swim bladders (Freeman et al. 2004), factors that intrinsically link them to benthic habitats. Analyses treating this group as benthic–demersal rather than pelagic did not change any of the major conclusions of our study. Each species also was assigned a representative size and trophic position (a value between 2.0 and 4.6, representing its relative feeding position within the food web). Maximum standard length (SL; cm) was used as an index of size for each species. Trophic position and maximum standard lengths were obtained from the Fishbase (Froese and Pauly 2004) and Sea Around Us Project (2007) databases. For each ecosystem, P/D ratios, mean-weighted trophic position (with biomass as the weighting variable), and mean-weighted size of species in fishery landings were estimated annually, and then averaged across all available years within the specified period (1990–2004).

Water quality attributes and data sources.—Nitrogen loading was used as the measure of nutrient enrichment because nitrogen is the nutrient limiting primary production and eutrophication in most estuarine and coastal ecosystems (Howarth and Marino 2006). Recent analyses suggest that phosphorous may be an important nutrient limiting primary production in lower-salinity systems (Schindler et al. 2008; Bryhn and Håkanson 2009), but fisheries landings across marine and estuarine systems tend to be correlated with nitrogen (Nixon and Buckley 2002). Loading estimates included nitrogen flux from watershed sources (river discharge, runoff, point-source pollution) plus inputs from other upstream water bodies and direct nitrogen deposition from the atmosphere. Our term "basin N loading" includes most of the inputs directly or indirectly related to human activity within the drainage basin and is a measure of N loading subject to management actions. However, because N from upwelling and deep ocean currents contributes significantly to the overall nitrogen budget of several test systems, we repeated all analyses using an estimate of N loading that included fluxes from oceanic (or downstream) sources, which we refer to as "total N loading." Estimates of basin and total N loading to each test system were normalized by sea surface area and expressed as kilograms of nitrogen per square kilometer of sea surface per year (kg·km^{-2}·year^{-1}).

The Adriatic Sea and the Skagerrak-Kattegat were excluded from analyses involving total N load because estimates of downstream N loading at the appropriate spatial scale were unavailable for these systems. Nitrogen loading rates were obtained from the peer-reviewed literature and government reports (Table A.2).

Our primary measure of the severity of hypoxia was the maximum bottom area with dissolved oxygen (DO) concentrations of 3 mg/L or less. Chronic exposure to DO concentrations less than this threshold have been shown to reduce growth or reproduction in a variety of species (Breitburg 2002). Although many previous studies have used a threshold of 2 mg/L, a recent synthesis suggested that this threshold may be too low for effective conservation of marine biodiversity and fishery resources (Vaquer-Sunyer and Duarte 2008).

Test systems also differed in the frequency and duration of hypoxic events. Our data set included ecosystems in which hypoxia has never been reported in the main-stem estuary, systems in which hypoxia occurs on a periodic or seasonal basis, and, finally, systems with persistent, year-round hypoxia or anoxia (usually in the form of deep basins that remain hypoxic or anoxic for years to millennia). The persistence of hypoxic conditions is an important indicator of system susceptibility to the formation of low DO (Cloern 2001; Bricker et al. 2007). For example, the permanent stratification of the Black Sea makes this ecosystem prone to the development of hypoxic conditions even at low levels of nutrient input, whereas tidal flushing and wind-mixing may retard development of hypoxia in some systems with high nutrient loads (Breitburg et al. 2009). Consequently, relationships among nutrients, hypoxia, and fisheries may vary among groups of ecosystems that differ in their proclivity to develop low DO. Variation in ecosystem susceptibility to the symptoms of eutrophication is also critical to being able to statistically separate hypoxia and nutrient effects on fisheries.

Data analyses.—To test the conceptual models shown in Figure 1, we modeled landings composition as a function of water quality. Separate analyses were performed for each water quality variable (N loading, spatial extent of hypoxia) and landings composition metric (P/D, trophic position, and size of species in fishery landings) in order to examine individual relationships between 1) fishery characteristics and nutrients and 2) between fishery characteristics and hypoxia. The best-fit model for each pairwise relationship was determined on the basis of AICc criteria (Burnham and Anderson 2002).

To determine whether results were dependent on system diversity or system selection, we examined the

TABLE 1.—Ecosystem groupings of 14 semi-enclosed or coastal seas and 8 estuaries (bold), based on the temporal extent of hypoxic conditions.

Frequency and duration of hypoxia	Member ecosystems	n
Hypoxia absent or extremely rare in natural embayments and main-stem estuary	**Delaware Bay**, **Galveston Bay**[a], Irish Sea[b], North Sea[b]	4
Periodic or seasonally recurring hypoxia	Adriatic Sea[b], Yellow and Bohai seas, East China Sea, Seto Inland Sea, **Chesapeake Bay**, **Long Island Sound**, Skagerrak-Kattegat[b], Sound and Belt seas, Gulf of Mexico, **Neuse River estuary**, **Pamlico River**, **Tampa Bay**, Sea of Azov[b], **Corpus Christi Bay**	14
Persistent (year-round) hypoxia or anoxia	Baltic Sea[b], Black Sea[b], Sea of Marmara[b], Gulf of St. Lawrence	4

[a] Hypoxia does occur in canals and other man-made habitats with restricted circulation (Thronson and Quigg 2008).
[b] System also included in cross-system comparison performed by de Leiva Moreno et al. (2000) ($n = 8$).

relationship between fisheries and water quality within groups of systems with certain shared characteristics. First, trends in landings and landings composition were evaluated in systems with periodic or seasonal hypoxia, the systems most likely to have nutrient-driven hypoxia and to yield the patterns predicted by previous studies (Table 1). Next, systems were stratified according to size and type by classifying all systems as a "semi-enclosed or coastal sea" or an "estuary." While the inland and coastal seas used in previous cross-system analyses might be considered "megaestuaries," their large size and a variety of their physical and biological characteristics differentiate them from more typical estuaries. For example, estuarine ecosystems are more likely than semi-enclosed seas to have ichthyofauna predominated by transient species or by juvenile life stages. In our data set, 8 systems were classified as true estuaries, whereas the remaining 14 systems were considered to be semi-enclosed or coastal seas (Table 1). Finally, relationships among landings, landings composition, and water quality were reexamined after restricting analyses to the 8 semi-enclosed seas common to both the present study and previous cross-system analyses. These systems provide a snapshot view of eutrophication effects on fisheries among systems in relatively close geographic proximity that have overlapping species assemblages and pelagic and demersal stocks that are fully exploited (FAO 1997). These systems also were included in an analysis that showed that P/D ratios were positively correlated with chlorophyll *a*, a proxy for nutrient availability (de Leiva Moreno et al. 2000). Where appropriate, group comparisons were conducted using *t*-tests, analysis of variance (ANOVA), or analysis of covariance (ANCOVA). All statistical analyses were performed in SAS 9.1 and SigmaPlot 10.0.

Results

Hypoxia and Nutrient Loading

The test systems included in this analysis represented a wide range of nutrient loading rates and hypoxia (Figure 2). Basin N loading within the entire data set ranged from 664 to 25,119 $kg \cdot km^{-2} \cdot year^{-1}$, and total N loading varied between 1,345 and 57,544 $kg \cdot km^{-2} \cdot year^{-1}$. Areal extent of hypoxia ranged from 0% to 76.6% of system area.

Prior to examining relationships between fisheries and water quality, we tested our hypothesis that nutrients and hypoxia should be considered independent variables by examining the correlation between N loads and spatial extent of hypoxia. Spatial extent of hypoxia across the entire data set was not associated with basin N loading (Pearson's product-moment correlation coefficient: $r = 0.10$, $P = 0.65$, $N = 22$) or total N loading ($r = -0.12$, $P = 0.62$, $N = 20$) because some high-N systems did not have hypoxia (e.g., Delaware and Galveston bays) and some low-N systems had extensive hypoxia or anoxia (e.g., Sea of Azov, Black Sea; Figure 2A, D). Spatial extent of hypoxia across ecosystems in which low DO occurs periodically or seasonally was positively associated with basin N loading ($r = 0.45$, $P = 0.10$, $N = 14$), but the best-fit model for this relationship (not shown) still explained less than 40% of the variance in hypoxia extent ($r^2 = 0.39$). Spatial extent of hypoxia and total N loading were uncorrelated among systems with periodic or seasonal hypoxia ($r = 0.23$, $P = 0.48$, $N = 12$; Figure 2A, D). Spatial extent of hypoxia was not associated with N loading among small estuaries ($r = -0.06$, $P = 0.89$ for basin N load; $r = -0.07$, $P = 0.87$, $N = 8$ for total N load), among large semi-enclosed and coastal seas ($r = 0.20$, $P = 0.48$, $N = 14$ for basin N load; $r = -0.09$, $P = 0.79$, $N = 12$ for total N load), or among the eight test systems common to both our study and that of de Leiva Moreno et al. (2000) ($r = 0.11$, $P = 0.80$, $N = 8$ for basin N load; $r = -0.27$, $P = 0.60$, $N = 6$ total N load; Figure 2B–F).

P/D Ratios versus Nitrogen Loading

Current conceptual and statistical models predict that nutrient enrichment should increase the P/D ratio, but P/D ratios exhibited a decreasing trend with N loading
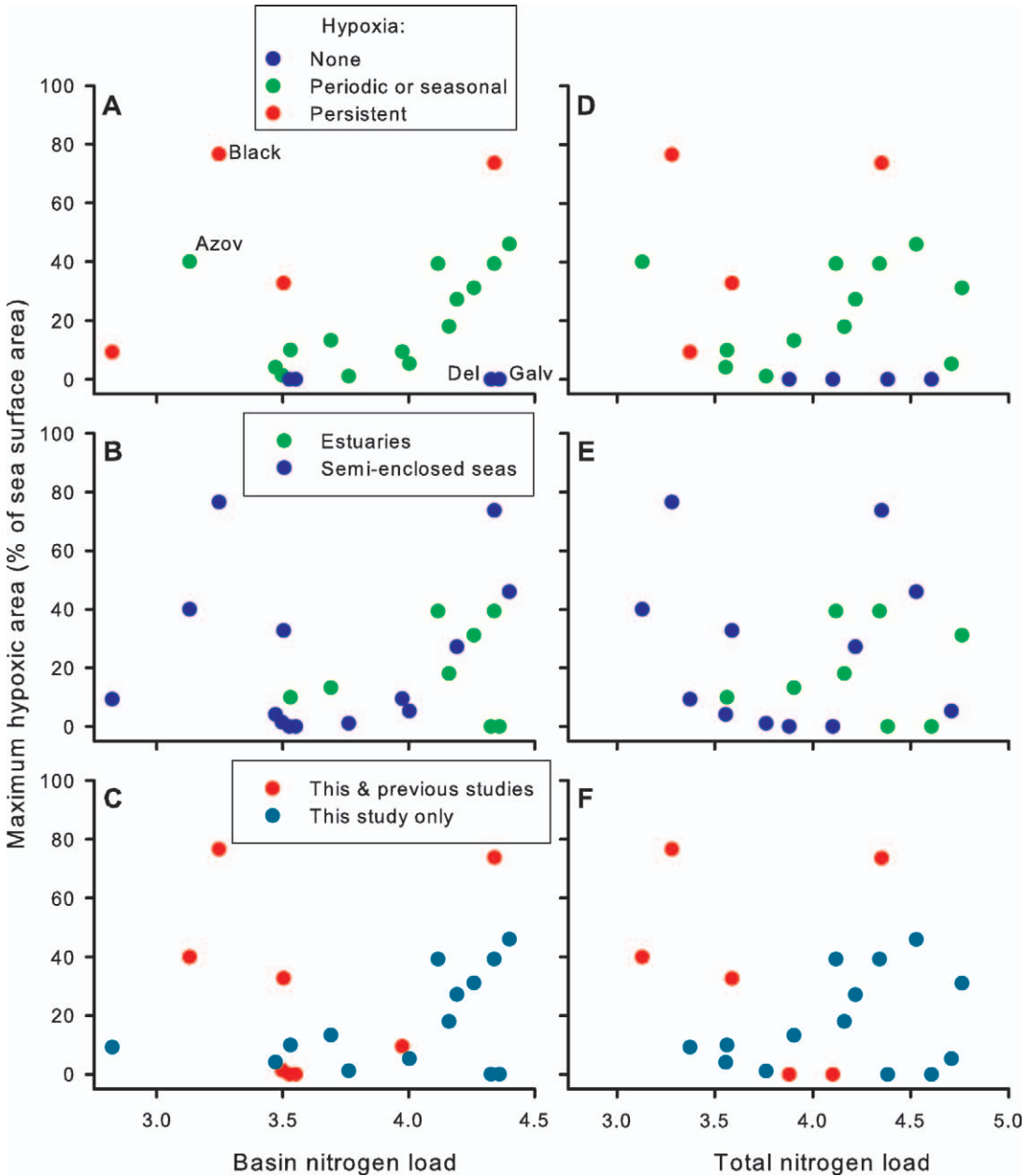
FIGURE 2.—Relationships between maximum spatial extent of hypoxia (area with dissolved oxygen < 3 mg/L expressed as a percentage of system surface area) and nitrogen loading ($\log_{10}$[kg/km^2 of sea surface per year]) from watershed sources only ("basin" nitrogen loads; left-hand panels) and estimates of total nitrogen loads that include inputs from downstream or oceanic sources (right-hand panels). Different colors distinguish systems according to (A, D) the frequency and/or duration of hypoxia, (B, E) system type or size, and (C, F) inclusion in previous cross-system analyses. Abbreviations are as follows: Black = Black Sea, Azov = Sea of Azov, Del = Delaware Bay, and Galv = Galveston Bay.
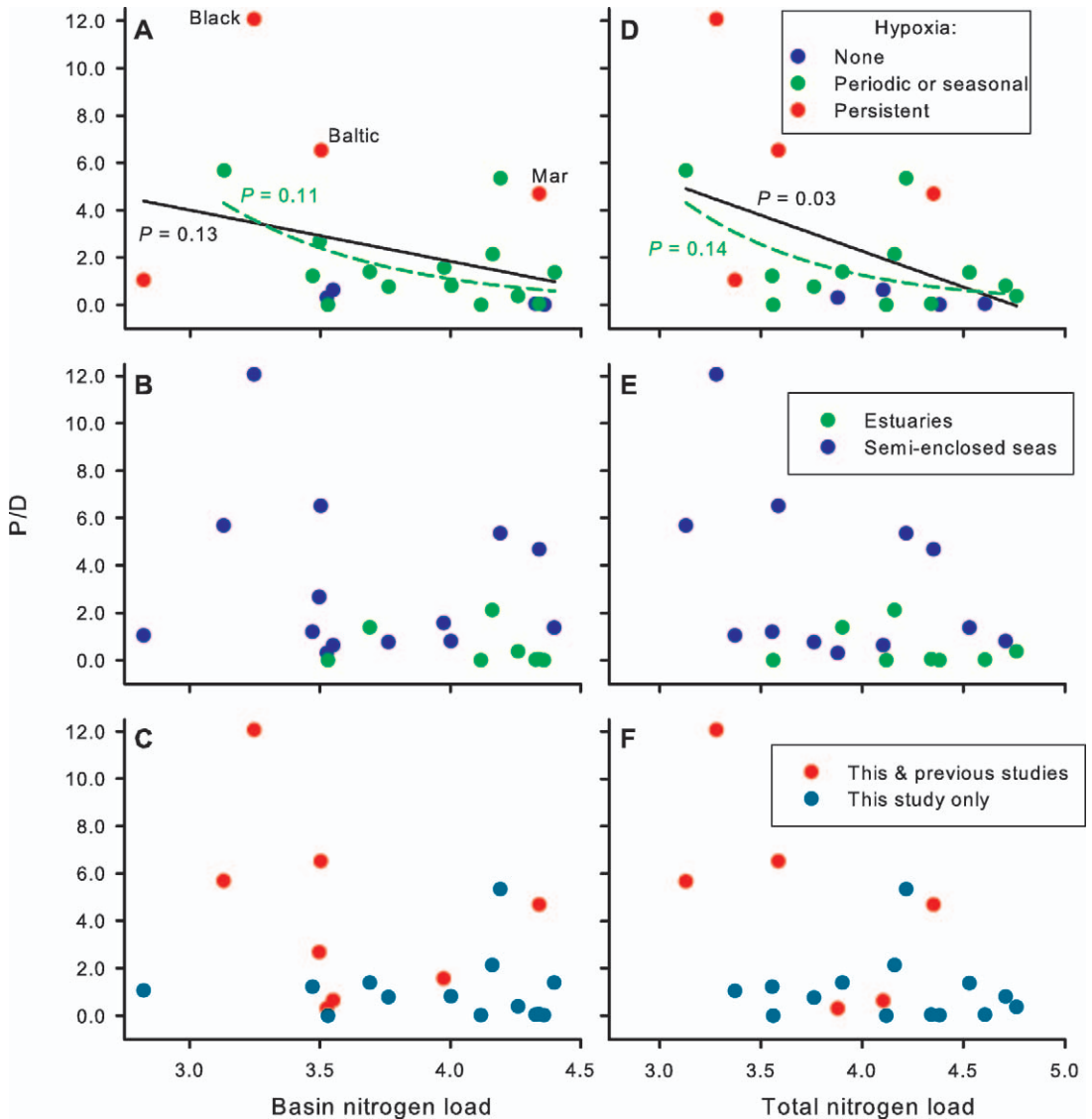
FIGURE 3.—The ratio of pelagic to benthic–demersal species biomass in fishery landings (P/D) versus nitrogen loading ($\log_{10}$[kg/km^2 of sea surface per year]) from watershed sources only ("basin" nitrogen loads; left-hand panels) and estimates of total nitrogen loading that include inputs from downstream or oceanic sources (right-hand panels). Different colors distinguish systems according to **(A, D)** the frequency and/or duration of hypoxia, **(B, E)** system type or size, and **(C, F)** inclusion in previous cross-system analyses. The lines in panels (A) and (D) represent the best-fit relationships for all systems (solid black) and for test systems with periodic or seasonal hypoxia (dashed green). For all systems, the basin N load $P/D = 10.48 - 2.16 \cdot N$ ($r^2 = 0.11$, $P = 0.13$, $N = 22$), and the total N load $P/D = 14.41 - 3.03 \cdot N$ ($r^2 = 0.23$, $P = 0.03$, $N = 14$). For systems with only periodic or seasonal hypoxia, the basin N load $P/D = 586.0 \cdot \exp(-1.57 \cdot N)$ ($r^2 = 0.20$, $P = 0.11$, $N = 14$), and the total N load $P/D = 362.6 \cdot \exp(-1.42 \cdot N)$ ($r^2 = 0.21$, $P = 0.14$, $N = 14$). Abbreviations are as follows: Black = Black Sea, Baltic = Baltic Sea, and Mar = Sea of Marmara.

when analyses included all test systems, as well as when analyses were restricted to systems with periodic or seasonal hypoxia (Figure 3A, D; Table 2). The relationships that included all test systems were not statistically significant and explained less of the variation in P/D ratios when the Black Sea—a low-N

system with a permanently anoxic central basin and a high P/D ratio—was eliminated from the analysis (Table 2). The Baltic Sea and Sea of Marmara, two additional systems with year-around hypoxic basins, also had high P/D ratios than other systems with comparable N inputs.

TABLE 2.—Fit statistics for selected models referenced in Figures 3–7, where P/D is the ratio of landings mass of small pelagic species to that of benthic–demersal species.

| Variable | | | | | | |
Dependent	Independent	Systems or system group	r^2	P	n	Figure
P/D	N load (basin)	All	0.11	0.13	22	3
	N load (basin)	Periodic or seasonal hypoxia	0.20	0.11	14	3
	N load (basin)	All excluding the Black Sea	0.04	0.41	21	3
	N load (total)	All	0.23	0.03	20	3
	N load (total)	Periodic or seasonal hypoxia	0.21	0.14	12	3
	N load (total)	All excluding the Black Sea	0.14	0.12	19	3
Pelagic landings	N load (basin)	All[a]	0.49	<0.01	17	4
	N load (basin)	Periodic or seasonal hypoxia[a]	0.68	0.01	11	4
	N load (basin)	Semi-enclosed seas	0.51	<0.01	14	4
	N load (basin)	Included in previous cross-system analyses	0.53	0.04	8	4
	N load (basin)	New to the present analysis[a]	0.39	0.07	9	4
	N load (total)	All[a]	0.32	0.03	15	4
	N load (total)	Periodic or seasonal hypoxia[a]	0.70	0.03	9	4
	N load (total)	Semi-enclosed seas	0.42	0.02	12	4
	N load (total)	New to the present analysis[a]	0.63	0.05	9	4
Benthic–demersal landings	N load (basin)	All	0.63	<0.01	22	5
	N load (basin)	Periodic or seasonal hypoxia	0.69	<0.01	14	5
	N load (basin)	Semi-enclosed seas	0.61	0.02	14	5
	N load (basin)	Included in previous cross-system analyses	0.90	0.02	8	5
	N load (basin)	New to the present analysis	0.46	0.04	14	5
	N load (total)	All	0.64	<0.01	20	5
	N load (total)	Periodic or seasonal hypoxia	0.65	<0.01	12	5
	N load (total)	Semi-enclosed seas	0.54	0.01	12	5
	N load (total)	Included in previous cross-system analyses	0.77	0.02	6	5
	N load (total)	New to the present analysis	0.31	0.04	14	5
P/D	Hypoxia extent	All	0.52	<0.01	22	6
	Hypoxia extent	All excluding the Black Sea	0.24	0.03	21	6
	Hypoxia extent	Semi-enclosed seas	0.62	<0.01	14	6
	Hypoxia extent	Semi-enclosed seas excluding the Black Sea	0.55	0.01	13	6
	Hypoxia extent	Included in previous cross-system analyses	0.69	0.01	8	6
Benthic–demersal landings	Hypoxia extent	All	0.15	0.07	22	7
	Hypoxia extent	All excluding the Black Sea	0.03	0.48	21	7
	Hypoxia extent	Semi-enclosed seas	0.31	<0.01	14	7
	Hypoxia extent	Semi-enclosed seas excluding the Black Sea	0.13	0.23	13	7

[a] Excludes the five systems in which purse seining is either prohibited or not used.

The P/D ratios (±SE) were significantly lower for small estuaries (0.50 ± 0.29, $N = 8$) than for larger coastal and semi-enclosed seas (3.19 ± 0.89, $N = 14$; t-test with unequal variances, $P = 0.01$), but were not associated with N loading for any combination of system type and N source (all $P > 0.18$; Figure 3B, E). The P/D ratios among the 14 newly included systems, which included all 8 small estuaries, were also lower (1.04 ± 0.0.50) than for the 8 semi-enclosed seas included in previous analyses (4.27 ± 1.04; t-test with unequal variances, $P = 0.05$), but were not associated with N loading in either group (Figure 3C, F) (common systems, $P > 0.19$; new systems, $P > 0.60$).

Observed patterns in P/D versus N were influenced in part by low landings of pelagic planktivores in a group of U.S. estuaries with moderate to high N in which purse seining is either prohibited or not used (Corpus Christi, Delaware, and Galveston bays and Neuse River Estuary and Pamlico River; Figure 4). These systems had the

five lowest P/D ratios (average P/D = 0.02) and included the four shallowest systems in our data set. After excluding these systems, landings of pelagic species were positively related to N among most remaining test systems and system groups (Figure 4A–E; Table 2). However, for systems with periodic or seasonal hypoxia, pelagic landings decreased slightly at basin N loads above 10,000 kg·km^{-2}·year^{-1} and at total N loads above 16,600 kg·km^{-2}·year^{-1} (Figure 4A, D). Declines in pelagic landings mass at total N loads above 16,600 kg·km^{-2}·year^{-1} also were observed for the 14 newly included systems (Figure 4F).

Patterns in P/D versus N also were influenced by the fact that benthic–demersal landings did not decrease at high N within most system groups (Figure 5). Among systems with periodic or seasonal hypoxia, among semi-enclosed and coastal seas, and among the 14 newly included systems, benthic–demersal landings did decline at basin nitrogen loads above ca. 10,000
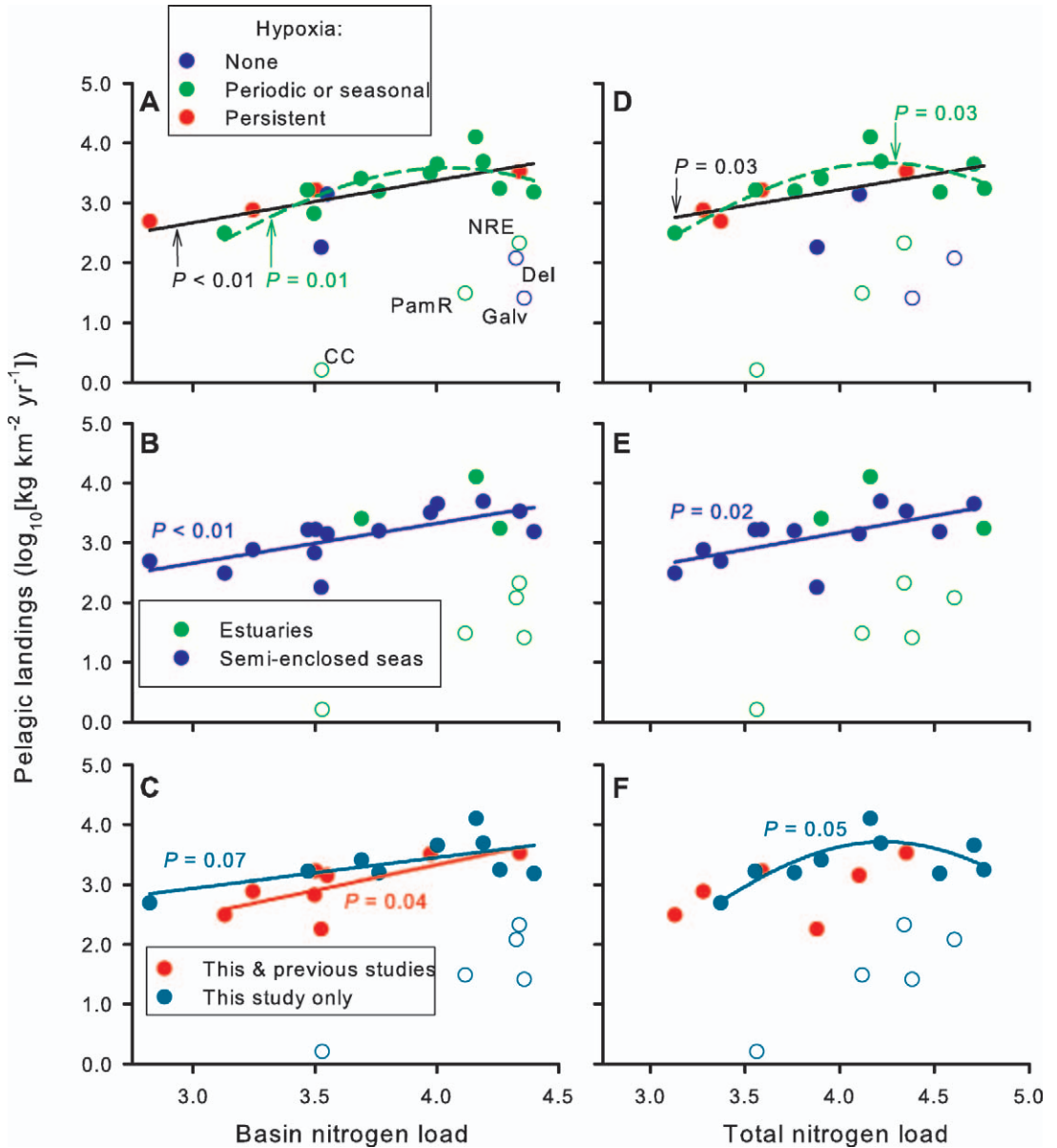
FIGURE 4.—Landings of pelagic planktivores (PEL) versus nitrogen loading from watershed sources only ("basin" nitrogen loading; left-hand panels) and estimates of total nitrogen loading that include inputs from downstream or oceanic sources (right-hand panels). Different colors distinguish systems according to (A, D) the frequency and/or duration of hypoxia, (B, E) system type or size, and (C, F) inclusion in previous cross-system analyses. The lines represent the best-fit relationships for all test systems (solid black), systems with periodic or seasonal hypoxia (dashed green), semi-enclosed and coastal seas only (solid blue), systems included in previous cross-system analyses (solid red), and the 14 systems new to the present analysis (solid cyan). All relationships exclude the five systems in which purse seining is prohibited, severely restricted, or not used (denoted by open symbols). For all systems, the basin N load PEL = $0.71 \cdot N + 0.55$ ($r^2 = 0.49$, $P < 0.01$, $N = 17$) and the total N load PEL = $0.71 \cdot N + 0.54$ ($r^2 = 0.32$, $P = 0.03$, $n = 15$). For systems with only periodic or seasonal hypoxia, the basin N load PEL = $3.56 \cdot \exp\{-0.5[(N - 4.04)/1.01]^2\}$ ($r^2 = 0.68$, $P = 0.01$, $N = 11$) and the total N load PEL = $3.67 \cdot \exp\{-0.5[(N - 4.23)/1.22]^2\}$ ($r^2 = 0.70$, $P = 0.03$, $N = 9$). For semi-enclosed and coastal seas only, the basin N load PEL = $0.67 \cdot N + 0.66$ ($r^2 = 0.51$, $P < 0.01$, $N = 14$) and the total N load PEL = $0.57 \cdot N + 0.90$ ($r^2 = 0.42$, $P = 0.02$, $N = 12$). For systems used in previous cross-system analyses, the basin N load PEL = $0.85 \cdot N - 0.07$ ($r^2 = 0.53$, $P = 0.04$, $N = 8$). For systems unique to the present study, the basin N load PEL = $0.51 \cdot N + 1.40$ ($r^2 = 0.39$, $P = 0.07$, $N = 9$) and the total N load PEL = $3.71 \cdot \exp\{-0.5[(N - 4.23)/1.10]^2\}$ ($r^2 = 0.63$, $P = 0.05$, $N = 9$). Abbreviations are as follows: CC = Corpus Christi Bay, Del = Delaware Bay, Galv = Galveston Bay, NRE = Neuse River Estuary, and PamR = Pamlico River.
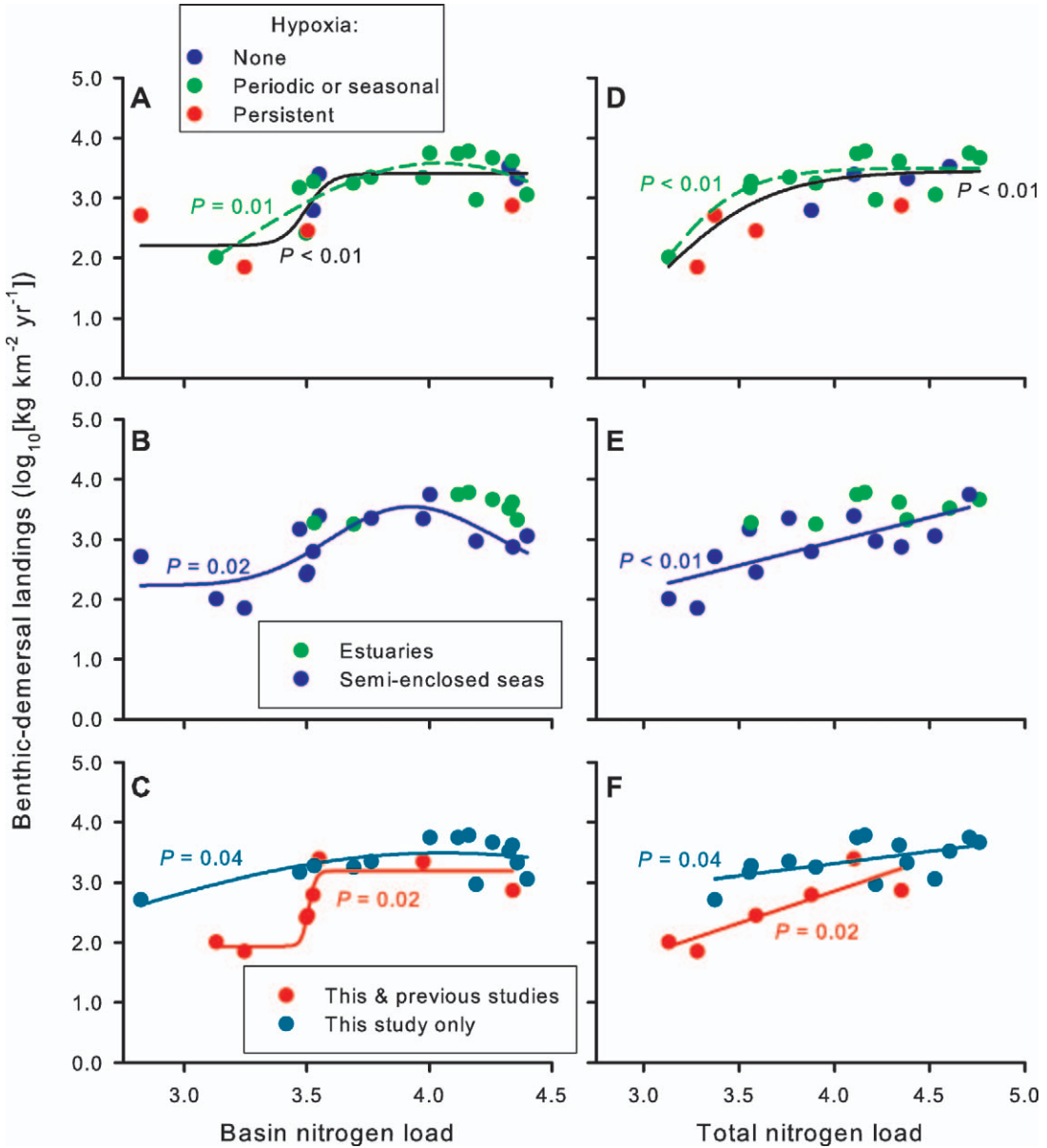
FIGURE 5.—Landings of benthic–demersal species (BD) versus nitrogen loading from watershed sources only ("basin" nitrogen loading, left-hand panels) and estimates of total nitrogen loading that include inputs from downstream or oceanic sources (right-hand panels). Different colors distinguish systems according to **(A, D)** the frequency and/or duration of hypoxia, **(B, E)** system type or size, and **(C, F)** inclusion in previous cross-system analyses. The lines represent the best-fit relationships for all test systems (solid black), systems with periodic or seasonal hypoxia (dashed green), semi-enclosed and coastal seas only (solid blue), the 8 systems included in previous cross-system analyses (solid red), and the 14 systems new to the present analysis (solid cyan). For all systems, the basin N load $BD = 2.21 + 1.20/\{1 + exp[(3.50 - N)/0.05]\}$ ($r^2 = 0.63$, $P < 0.01$, $N = 22$) and the total N load $BD = 3.45/\{1 + exp[(3.09 - N)/0.29]\}$ ($r^2 = 0.64$, $P = 0.01$, $N = 20$). For systems with periodic or seasonal hypoxia, the basin N load $BD = 3.60 \cdot exp\{-0.5[(N - 4.04)/0.85]^2\}$ ($r^2 = 0.69$, $P = < 0.01$, $N = 14$) and the total N load $BD = 3.50/\{1 + exp[(3.07 - N)/0.21]\}$ ($r^2 = 0.65$, $P < 0.01$, $N = 12$). For semi-enclosed and coastal seas, the basin N load $BD = 2.23 + 1.31 \cdot exp\{-0.5[log_e(N/3.93)/0.09]^2\}$ ($r^2 = 0.61$, $P = 0.02$, $N = 14$) and the total N load $BD = 0.80 \cdot N - 0.23$ ($r^2 = 0.54$, $P = 0.01$, $N = 12$). For systems used in previous cross-system analyses, the basin N load $BD = 1.94 + 1.25/\{1 + exp[(3.51 - N)/0.01]\}$ ($r^2 = 0.90$ $P = 0.02$, $N = 8$) and the total N load $BD = 1.06 \cdot N - 1.40$ ($r^2 = 0.77$, $P = 0.02$, $N = 6$). For systems unique to the present study, the basin N load $BD = 3.49 \cdot exp\{-0.5[(N - 4.06)/1.64]^2\}$ ($r^2 = 0.46$, $P = 0.04$, $N = 14$) and the total N load $BD = 0.40 \cdot N + 1.70$ ($r^2 = 0.31$, $P = 0.04$, $N = 14$).
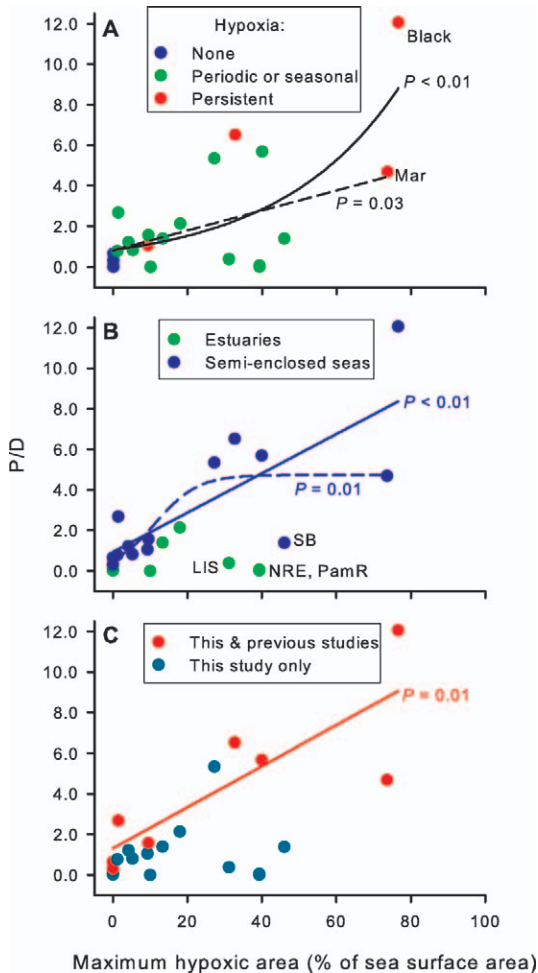
FIGURE 6.—The ratio of pelagic to benthic–demersal species biomass in fishery landings (P/D) versus the maximum spatial extent of hypoxia (area with dissolved oxygen < 3 mg/L expressed as a percentage of system surface area). Different colors distinguish systems according to (**A**) the frequency and/or duration of hypoxia, (**B**) system type or size, and (**C**) inclusion in previous cross-system analyses. The lines represent the best-fit relationships for all test systems (solid black), all test systems excluding the Black Sea (dashed black), semi-enclosed and coastal seas (solid blue), semi-enclosed and coastal seas excluding the Black Sea (dashed blue), and systems included in previous cross-system analyses (solid red). For all systems, P/D $= 0.82 \cdot \exp(0.03H)$, where H is the spatial extent of hypoxia ($r^2 = 0.52$, $P < 0.01$, $N = 22$); for all systems excluding the Black Sea, P/D $= 0.80 + 0.05H$ ($r^2 = 0.24$, $P = 0.03$, $N = 21$); for semi-enclosed and coastal seas, P/D $= 0.93 + 0.10H$ ($r^2 = 0.62$, $P < 0.01$, $N = 14$); for semi-enclosed and coastal seas excluding the Black Sea, P/D $= 4.74/\{1 + \exp[(11.52 - H)/5.68]\}$ ($r^2 = 0.63$, $P = 0.01$, $N = 13$), and for systems included in previous cross-system analyses, P/D $= 1.42 + 0.10H$ ($r^2 = 0.62$, $P = 0.01$, $N = 8$). Abbreviations are as follows: Black = Black Sea, LIS = Long Island Sound, Mar = Sea of Marmara, NRE = Neuse River Estuary, PamR = Pamlico River, and SB = Sound and Belt seas.

kg·km^{-2}·year^{-1}, but the relationship was significant and either positive or asymptotic for analyses including these same systems and N loads that included downstream or oceanic inputs (compare in Figure 5 panels A versus D, B versus E, and C versus F; Table 2).

P/D Ratios versus Hypoxia

P/D ratios increased nonlinearly with maximum spatial extent of hypoxia when analyses included all test systems (Figure 6A). This relationship was dependent on systems with persistent hypoxic basins (particularly the Black Sea and Sea of Marmara) and was not significant for systems that experience only periodic or seasonal hypoxia ($r^2 < 0.08$, $P > 0.62$ for all model fits; Table 2). The ratios also were significantly and positively related to spatial extent of hypoxia for semi-enclosed and coastal seas and for the eight systems included in previous analyses (Figure 6B, C). Removal of the Black Sea, which had a substantially higher P/D ratio than the other systems, changed the shape and reduced the explanatory power of the best-fit relationship between P/D and spatial extent of hypoxia for all systems combined and for semi-enclosed seas, although these new relationships remained statistically significant (Figure 6A, B; Table 2). The P/D ratio of fishery landings was not significantly associated with spatial extent of hypoxia among estuaries or systems unique to the study (Figure 6C; $r^2 < 0.24$, $P > 0.23$). Long Island Sound, the Neuse River Estuary, Pamlico River, and the Sound and Belt seas had low P/D ratios, despite having areas of low DO that exceeded 31% of system surface area in some years (Figure 6B).

Landings of pelagic planktivores, which as adults would not be directly impacted by bottom-layer hypoxia, were not significantly correlated with the spatial extent of hypoxia across the full data set or when test systems were stratified by the duration of hypoxia or ecosystem type or size ($r^2 < 0.20$; $P > 0.34$; Figure 7A–C).

Landings mass of benthic–demersal species were negatively correlated with spatial extent of hypoxia for all systems combined and for semi-enclosed and coastal seas, but only when the Black Sea was included in the analyses (Figure 7D, F; Table 2). Low landings of benthic–demersal species were not associated with spatial extent of hypoxia among systems with periodic or seasonal hypoxia ($r^2 < 0.11$, $P > 0.52$ for all model fits), among the 14 newly added systems ($r^2 < 0.02$, $P > 0.92$ for all model fits), or among the eight systems used in previous analyses ($r^2 < 0.35$, $P > 0.16$ for all model fits). In estuaries, landings of benthic–demersal
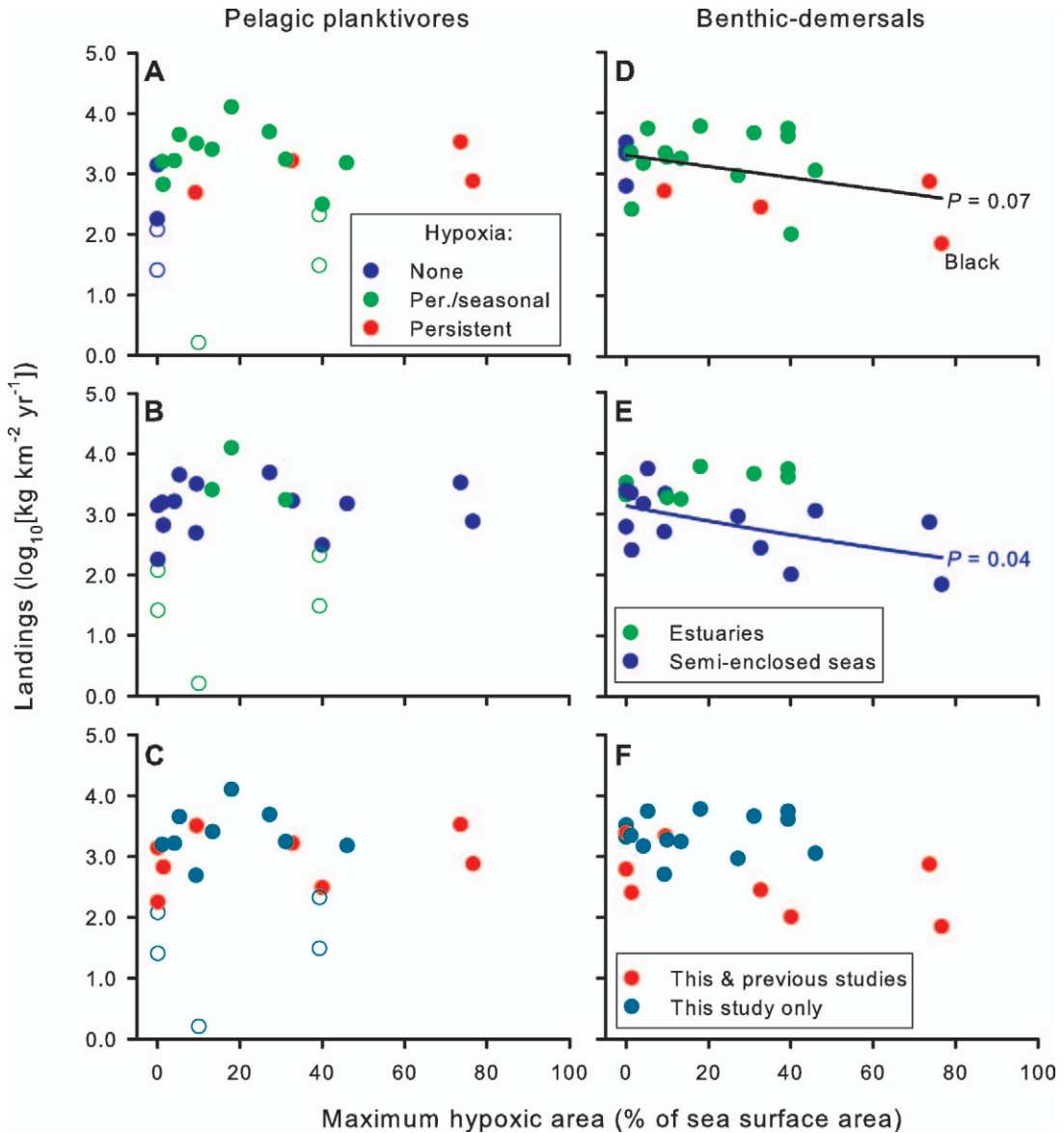
FIGURE 7.—Landings of pelagic planktivores and benthic–demersal species (BD) versus maximum spatial extent of hypoxia (area with dissolved oxygen < 3 mg/L expressed as a percentage of system surface area. Different colors distinguish systems according to **(A, D)** the frequency and/or duration of hypoxia, **(B, E)** system type or size, and **(C, F)** inclusion in previous cross-system analyses. Open symbols denote systems in which purse seining is prohibited, severely restricted, or not used. The lines represent the best-fit relationships for all test systems (solid black) and semi-enclosed and coastal seas only (solid blue). For all systems, BD = $3.30 - 0.01 \cdot H$ ($r^2 = 0.15$, $P = 0.07$, $N = 22$) and for semi-enclosed and coastal seas, BD = $3.12 - 0.01 \cdot H$ ($r^2 = 0.31$, $P = 0.04$, $N = 14$).

species (mean ± SE) were higher in the four systems with the greatest spatial extent of hypoxia ($5{,}077 \pm 432$ kg·km^{-2}·year^{-1}, $N = 4$) than in the remaining four systems ($2{,}262 \pm 351$ kg·km^{-2}·year^{-1}, $N = 4$; t-test, equal variances, $P < 0.01$; Figure 4E).

Other Landings Composition Metrics versus Nutrients and Hypoxia

Variation in the trophic and size composition of fishery landings mass was not significantly related to N loading (Figures 8A, B) or spatial extent of hypoxia
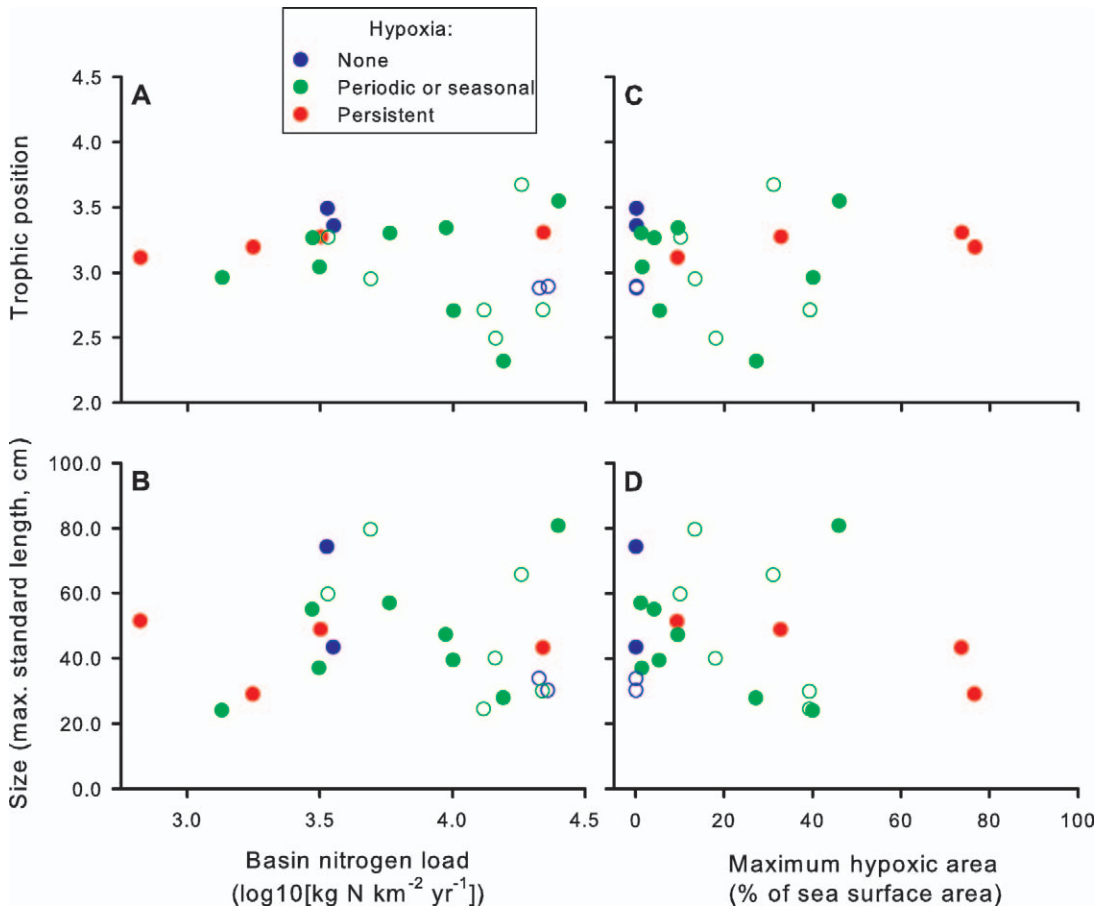
FIGURE 8.—(A) Trophic position and (B) size of species in fishery landings versus basin nitrogen loading and (C) trophic position and (D) size versus maximum spatial extent of hypoxia (area with dissolved oxygen < 3 mg/L expressed as a percentage of system surface area). Plots of trophic position and size of species in fishery landings versus total nitrogen loading did not provide any additional pertinent information and are therefore not shown. Open symbols denote estuaries; all remaining systems were classified as semi-enclosed or coastal seas.

(Figures 8C, D) within the entire data set or when test systems were stratified by the duration of hypoxia or ecosystem type or size. The average ± SE trophic position and length of landed species across all 22 test systems were 3.1 ± 0.1 and 46.5 ± 3.7 cm, respectively.

Discussion

An important difference between our study and previous cross-system comparisons is the separation of nutrient loads and hypoxia in analyses designed to better understand the relationship between eutrophication and the composition of fishery landings. Existing paradigms tend to conflate these variables under the umbrella of trophic status or nutrient availability, but our results showed that these variables are not correlated among most ecosystem groups and that patterns in landings composition differ with respect to nutrients and hypoxia. For example, the P/D ratio of fishery landings tended to be negatively correlated with N loads, but was significantly and positively correlated with the spatial extent of hypoxia. Our results also differed from the conceptual model illustrated in Figure 1A, in that the relationship between N loading and landings tended to be positive for both pelagic and benthic–demersal species. In addition, although the negative relationship between hypoxia and landings of benthic–demersal species is in agreement with the predictions of Figure 1, the statistical significance of this relationship was dependent on inclusion of a single system, the Black Sea. P/D ratios were particularly low in small estuaries where purse seining is prohibited or
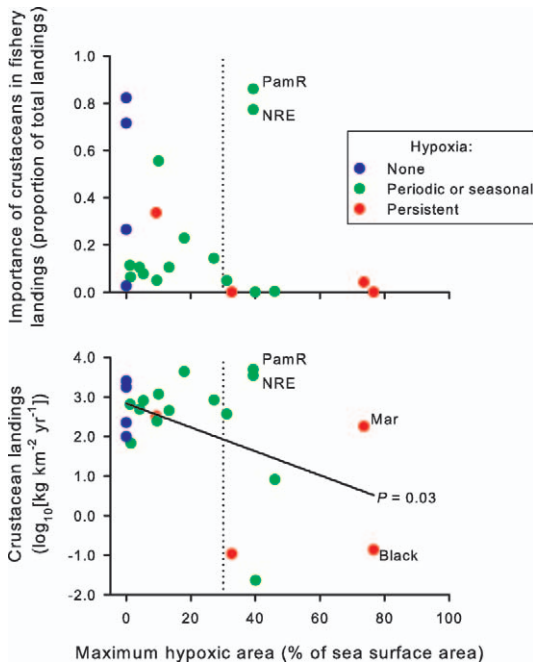
FIGURE 9.—(A) Relative importance of crustaceans in fishery landings and (B) total crustacean landings (CR) versus maximum spatial extent of hypoxia (area with dissolved oxygen < 3 mg/L expressed as a percentage of system surface area). The solid line in panel (B) represents the best-fit relationship (CR = 2.84 − 0.03·H; r^2 = 0.22, P = 0.03, N = 22). The dotted vertical lines denote a spatial extent of hypoxia equal to 30% of system surface area. Abbreviations are as follows: Black = Black Sea, Mar = Sea of Marmara, NRE = Neuse River estuary, and PamR = Pamlico River.

positively related to ecosystem-averaged chlorophyll a, a proxy variable for nutrient loads. Although several systems in that analysis were not included in our study due to the unavailability nitrogen loading data at the appropriate spatial and temporal scales, our results indicate that the combination of extensive and persistent hypoxia is more consistently associated with high P/D ratios than is high nutrient loading.

That P/D ratios did not reflect ecosystem nutrient inputs was probably attributable to several factors. First, low landings of benthic–demersal species generally were not associated with high N, as predicted by conceptual models and the conclusions of previous investigations. Among semi-enclosed and coastal seas and among systems with periodic or seasonal hypoxia in which observed patterns most closely approximated conceptual model predictions, declines in benthic–demersal annual landings above 10,000 kg/km^2 of sea surface could not clearly be attributed to symptoms of eutrophication because benthic–demersal landings were significantly and either positively or asymptotically related to N when nutrient loading estimates included downstream (or oceanic) sources. In addition, for the systems with periodic or seasonal hypoxia, spatial extent of hypoxia exceeded 31% of system area in three of the five systems with the highest benthic–demersal landings. These results suggest that increased productivity from nutrient enrichment is sufficient to offset declines in benthic habitat quality or that refuge habitat in our test systems is not limiting.

Second, the association of P/D ratios and nutrients is dramatically influenced by variability in fishery practices and regulations. An underemphasized assumption of existing conceptual models is that exploitation rates must be near maximum sustained yield effort levels in order for the P/D ratio of fishery landings to reflect relative pelagic and benthic–demersal productivity. Our data set included several small estuaries in which small pelagics were underexploited due to restrictions on the use or efficacy of certain gear types (e.g., purse seines), and consequently, these ecosystems were conspicuous outliers in the relationship between nutrients and landings of pelagic species.

Examination of fishery dynamics within individual test systems provided several additional illustrations of the importance of fishery regulations and practices on landings composition. For instance, except for the Neuse and Pamlico River estuaries, the relative importance of crustaceans in fishery landings was negligible among test systems where the spatial extent of hypoxia exceeded about 30% of system area (Figure 9A). This trend was due in part to a negative association between crustacean landings and spatial

not used, and pelagic species may not be fully exploited regardless of N loads or hypoxia extent. This observation suggests that variability in fishing practices and regulations, which can have profound effects on the relative exploitation rates of pelagic and benthic–demersal species, is an important consideration when interpreting patterns in landings data.

Differences between results of our analyses and the relationship between landings composition (particularly P/D) and nutrients predicted in Figure 1 were not wholly explained by system diversity or system selection. Separate analyses conducted after stratifying test systems into estuaries versus semi-enclosed and coastal seas, and by the occurrence and persistence of hypoxia, did not generate the predicted pattern. In fact, P/D and N loads were not positively correlated among the eight semi-enclosed seas also included in Caddy (2000) and de Leiva Moreno et al. (2000), even though P/D ratios among these and other semi-enclosed seas in Europe and the Mediterranean were shown to be
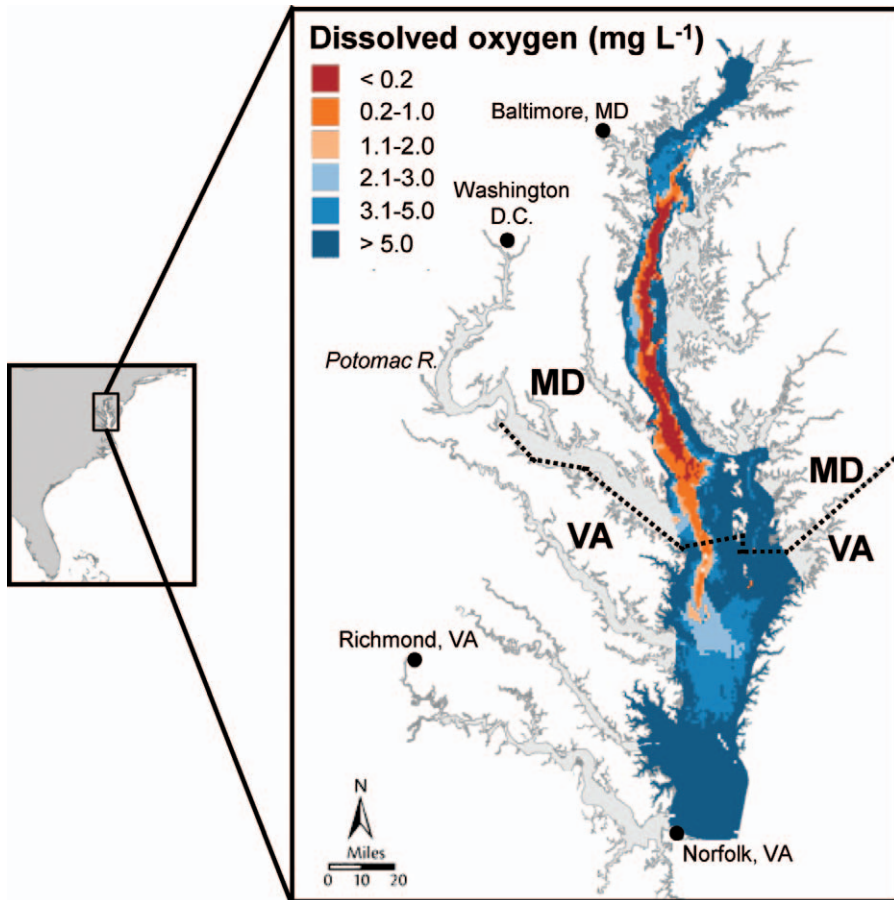
FIGURE 10.—Dissolved oxygen concentrations in Chesapeake Bay during August 2009. The dotted line represents the approximate boundary between Maryland and Virginia state waters. (Map courtesy of EcoCheck, a partnership program between the Chesapeake Bay Program Office of the National Oceanic and Atmospheric Administration and the Integration and Application Network at the University of Maryland Center for Environmental Sciences [www.eco-check.org]).

extent of hypoxia that was driven by low crustacean landings in the Black Sea (Figure 9B). However, crustacean landings in the Neuse and Pamlico river estuaries, as well as in the Sea of Marmara, were substantially higher than what would be predicted from spatial extent of hypoxia alone. In the case of the North Carolina systems, this difference is partly related to the behavior of commercial crabbers, who understand that blue crabs *Callinectes sapidus* avoid low DO and therefore focus their fishing effort on shallow refuge habitats during periods of hypoxia (Selberg et al. 2001). This spatial reallocation of fishing effort maintains crab landings in spite of severe oxygen depletion. Whether fishermen in the Sea of Marmara behave similarly is not known.

Regional and temporal variability in fishing regulations also has conspicuous effects on landings composition. For example, Chesapeake Bay supports one of the world's most productive fisheries but has been subject to intense eutrophication since the mid 20th century (Kemp et al. 2005). One symptom of nutrient overenrichment in this system is the large region of bottom-layer hypoxia that occurs along the north–south axis of the bay every summer (Figure 10). While most of the severely oxygen depleted water occurs in the Maryland portion of Chesapeake Bay, the P/D ratio of landings from Maryland during 1990–2001 (about 0.06) was lower than the P/D ratio of fishery landings from the entire Chesapeake Bay (2.13) over the same period. This difference in P/D ratios is related to industrial purse-seining operations for small pelagics (Atlantic menhaden in particular), which are permitted in Virginia state waters but not in Maryland waters.
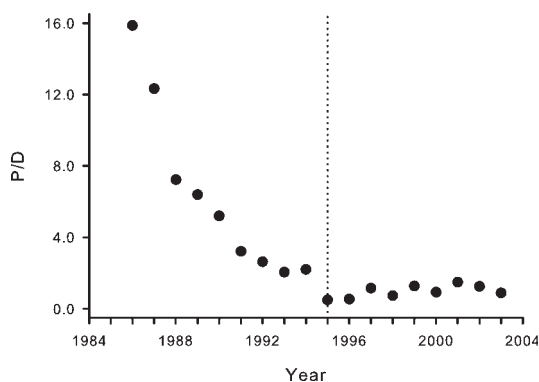
FIGURE 11.—Ratio of pelagic to benthic–demersal species' biomass in fishery landings (P/D) from Tampa Bay from 1986 to 2003. The dotted vertical line separates the time series into the years preceding and following the passage of a constitutional amendment in Florida limiting the use of large commercial trawl nets and banning gill and trammel nets.

In another example, magnitude and variability in the P/D ratios of fishery landings in Tampa Bay exhibited a conspicuous shift in 1995, even though nutrient loads to the bay had been reduced by nearly 60% by 1985 (Greening and Janicki 2006) (Figure 11). This shift perfectly coincides with the passage of a 1995 Florida constitutional amendment that limited the use of large commercial trawl nets and banned gill and trammel nets, which appeared to disproportionately reduce commercial exploitation of pelagic species (Grimes 1996). Declines in P/D ratios in Tampa Bay during 1985–1987 also were related to decreasing abundance of transient pelagics (e.g., Spanish sardines *Sardinella aurita*; personal communication, J. O'Hop, Fish and Wildlife Research Institute, Florida Fish and Wildlife Conservation Commission, St. Petersburg) whose availability in small estuaries may be controlled by factors other than estuarine productivity.

A final factor potentially affecting results of our analyses is that the timing of changes in nutrient loads and hypoxia and the rates of ecosystem decline and recovery, vary from system to system. It is difficult to evaluate the effects of these factors and of the unpredictability of ecosystem recovery trajectories (Duarte et al. 2009) on our results. Ecosystem transition between preeutrophication and posteutrophication states may depend not only on the level of nutrient enrichment but also on the timing and magnitude of other stressors, such as overfishing and the introduction of exotic species (Mee 2006). Thus, the P/D ratios of some recovering systems could reflect the legacy of past eutrophication or other ecosystem disturbances rather than current nutrient loading rates.

For example, in spite of reduced nutrient loadings to the Black Sea during the 1990s (Kideys 2002), the average P/D ratio of fishery landings from the Black Sea (about 12) during the period of our study (1990–2004) was similar to that observed during 1979–1988 (about 13), partly as a result of overfishing that resulted in the near complete extirpation of large benthic–demersal predators (Eremeev and Zuyev 2007). The slightly lower P/D ratio observed in our analysis could be a result of complex food web interactions involving an exotic ctenophore, the sea walnut *Mnemiopsis leidyi*, which preys on the eggs and larvae of small pelagics (e.g., anchovies of the genus *Engraulis*; Shiganova and Bulgakova 2000). The initial bloom of this species in the Black Sea could have contributed to lowered P/D ratios during the first few years of our time series. The Baltic Sea also may be experiencing lingering effects of higher nutrient loads and of fisheries and climate cycles, despite the efforts of European countries to limit nutrients to coastal seas. At present, the recovery of cod, historically the predominant benthic–demersal predator in the Baltic, has slowed, not so much by existing problems with eutrophication (although negative effects of hypoxia on cod egg survival was one of causes of cod declines), but rather by an overabundance of its former prey, European sprat, which feed on cod eggs (Köster and Möllmann 2000).

Variability in the trophic and size composition of fishery landings also may be influenced by factors other than water quality. These compositional indices were not clearly associated with either N loads or hypoxia in our analyses. Nutrient loading and spatial extent of hypoxia may poorly correlate with trophic and size structure of fishery landings if the abundance of large, high-trophic-level species is mainly influenced by fisheries exploitation (e.g., overfishing) or practices that mask or overwhelm any effects of deteriorating water quality (Pauly et al. 1998; Branch et al. 2005, de Mutsert et al. 2008). Similarly, variation in trophic and size structure across ecosystems may not correlate with water quality variables when the composition of fishery landings is a poor reflection of actual community composition. For example, in spite of huge decadal fluctuations in nutrient loading rates from the Mississippi–Atchafalaya River complex (Turner and Rabalais 1991), average trophic position of fishery landings from the Texas–Louisiana shelf of the Gulf of Mexico over the past 50 years have remained relatively fixed due to industry targeting of small, lower trophic level species such as shrimp of the genera *Farfantepenaeus* and *Litopenaeus* and Gulf menhaden (de Mutsert et al. 2008). Climatic and oceanic regime shifts also may mask any effects of nutrients or hypoxia

on composition of fishery landings in larger marine and coastal fishery ecosystems (Tian et al. 2006).

We do not intend to suggest that nutrient reduction and hypoxia-control strategies are not a critical step for reversing environmental degradation caused by eutrophication, or that remediation will not benefit some fisheries, especially at the local scale. Hypoxia has been shown to increase vulnerability of some demersal fish and crustacean stocks to overfishing (Baden et al. 1990; Vallin and Nissling 2000), and there are many examples of the recovery of benthic–demersal fish populations and fisheries following the implementation of primary sewage treatment (reviewed in Breitburg et al. 2009). Symptoms of eutrophication other than hypoxia also can negatively affect benthic fish (Bonsdorff et al. 2002). For example, nutrient enrichment in nursery habitats of the Swedish Skagerrak archipelago has resulted in formation of dense algal mats that may be interfering with settlement and subsequent recruitment of plaice *Pleuronectes platessa* (Pihl et al. 2005).

The pelagic-predominated landings of some severely hypoxic ecosystems also may have negative consequences for fishery stability and value. Fisheries for small pelagic fishes, which are predominated by clupeids, are difficult to manage due to the characteristically high recruitment variability associated with these taxa (Cole and McGlade 1998). Predominance of small pelagics in fishery landings also may affect fishery profits and the viability of small-scale (i.e., independent fishers) fisheries due to their comparatively low dockside value. For instance, average exvessel values of Atlantic menhaden and Atlantic herring tend to be lower than benthic–demersal species such as Atlantic cod and crustaceans (shrimps, crabs, lobsters; Sumaila et al. 2007). However, the high production per unit primary productivity of some pelagic planktivores may compensate for low annual exvessel values as in the case of the Chesapeake Bay (US$14,666/km^2) and Gulf of Mexico ($4,791/km^2; D. Hondorp, unpublished data), where fisheries include a large reduction fishery for small pelagics (mainly menhaden).

Overall, our study indicates that the relationship between eutrophication and the composition of fish and mobile benthos in fishery landings is more complex than predicted by previous conceptual models that do not clearly distinguish nutrient enrichment and hypoxia and do not differentiate between seasonally and permanently hypoxic systems. Clearly, establishing actual cause and effect will require identifying the specific mechanisms responsible for the patterns we observed. While we did not directly compare the relative effects of fishing and nutrient enrichment on fishery landings, the correspondence of specific patterns in landings composition with the use or efficacy of certain fishing methods (e.g., low P/D ratios and restricted purse seining) indicates that fishing itself has a substantial influence on global patterns of landings composition even among estuarine and coastal systems subject to intense eutrophication (see also Fulton et al. 2005; de Mutsert et al. 2008). Consequently, the effects of nutrient and hypoxia control measures on fisheries will vary and will depend, in part, on ecosystem type and market and regulatory forces that have a large impact on fishery landings independent of water quality.

helpful comments that greatly improved the manuscript.

References

Baden, S. P., L. Pihl, and R. Rosenberg. 1990. Effects of oxygen depletion on the ecology, blood physiology and fishery of the Norway lobster *Nephrops norvegicus*. Marine Ecology Progress Series 67:141–155.

Boesch, D. F. 2002. Challenges and opportunities for science in reducing nutrient overenrichment of coastal ecosystems. Estuaries 25:886–900.

Boesch, D. F., W. Dennison, E. Houde, M. Kemp, V. Kennedy, R. Newell, K. Paynter, R. Orth, and R. Ulanowicz. 2001. Factors in the decline of coastal ecosystems. Science (Washington, D.C.) 293:1589–1591.

Bonsdorff, E., C. Ronnberg, and K. Aarnio. 2002. Some ecological properties in relation to eutrophication in the Baltic Sea. Hydrobiologia 475/ 476:371–377.

Branch, T. A., R. Hilborn, and E. Bogazzi. 2005. Escaping the tyranny of the grid: a more realistic way of defining fishing opportunities. Canadian Journal of Fisheries and Aquatic Sciences 62:631–642.

Breitburg, D. L. 2002. Effects of hypoxia, and the balance between hypoxia and enrichment, on coastal fishes and fisheries. Estuaries 25:767–781.

Breitburg, D. L., D. W. Hondorp, L. A. Davias, and R. J. Diaz. 2009. Hypoxia, nitrogen, and fisheries: integrating effects across global and local landscapes. Annual Reviews of Marine Science 1:329–349.

Bricker, S., B. Longstaff, W. Dennison, A. Jones, K. Boicourt, C. Wicks, and J. Woerner. 2007. Effects of nutrient enrichment in the nation's estuaries: a decade of change. National Oceanographic and Atmospheric Administration, Decision Analysis Series 26, Silver Spring, Maryland.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd edition. Springer-Verlag, New York.

Bryhn, A. C., and L. Håkanson. 2009. Coastal eutrophication: whether N and/or P should be abated depends on the dynamic mass balance. Proceedings of the National Academy of Sciences of the USA 106:E3.

Caddy, J. F. 1993. Toward a comparative evaluation of human impacts on fishery ecosystems of enclosed and semi-enclosed seas. Reviews in Fisheries Science 1:57–95.

Caddy, J. F. 2000. Marine catchment basin effects versus impacts of fisheries on semi-enclosed seas. ICES Journal of Marine Science 57:628–640.

Caddy, J. F., and A. Bakun. 1994. A tentative classification of coastal marine ecosystems based on dominant processes of nutrient supply. Ocean & Coastal Management 23:201–211.

Caddy, J. F., F. Carocci, and S. Coppola. 1998. Have peak fishery production levels been passed in continental shelf areas? Some perspectives arising from historical trends in production per shelf area. Journal of Northwest Atlantic Fisheries Science 23:191–219.

Caddy, J. F., and L. Garibaldi. 2000. Apparent changes in the trophic composition of world marine harvests: the perspective from the FAO capture database. Ocean & Coastal Management 43:615–655.

Cloern, J. E. 2001. Our evolving conceptual model of the coastal eutrophication problem. Marine Ecology Progress Series 210:223–253.

Cole, J., and J. McGlade. 1998. Clupeoid population variability, the environment and satellite imagery in coastal upwelling systems. Reviews in Fish Biology and Fisheries 8:445–471.

Darbyson, E., D. P. Swain, D. Chabot, and M. Castonguay. 2003. Diel variation in feeding rated and prey composition of herring and mackerel in the southern Gulf of St. Lawrence. Journal of Fish Biology 63:1235–1257.

de Leiva Moreno, J. I., V. N. Agostini, J. F. Caddy, and F. Carocii. 2000. Is the pelagic-demersal ratio from fishery landings a useful proxy for nutrient availability? A preliminary data exploration for the semi-enclosed seas around Europe. ICES Journal of Marine Science 57:1091–1102.

de Mutsert, K., J. H. Cowan, Jr., T. E. Essington, and R. Hilborn. 2008. Reanalyses of Gulf of Mexico fisheries data: landings can be misleading in assessments of fisheries and fisheries ecosystems. Proceedings of the National Academy of Sciences of the USA 105:2740–2744.

Diaz, R. J. 2001. Overview of hypoxia around the world. Journal of Environmental Quality 30:275–281.

Diaz, R. J., and R. Rosenberg. 1995. Marine benthic hypoxia: a review of its ecological effects and the behavioural responses of benthic macrofauna. Oceanography and Marine Biology an Annual Review 33:245–303.

Diaz, R. J., and R. Rosenberg. 2008. Spreading dead zones and consequences for marine ecosystems. Science (Washington, D.C.) 321:926–929.

Duarte, C. M., D. J. Conley, J. Carstensen, and M. Sánchez-Camacho. 2009. Return to neverland: shifting baselines affect eutrophication restoration targets. Estuaries and Coasts 32:29–36.

Eremeev, V. N., and G. V. Zuyev. 2007. Commercial fishery impact on the modern Black Sea ecosystem: a review. Turkish Journal of Fisheries and Aquatic Sciences 7:75–82.

FAO (Food and Agriculture Organization of the United Nations). 1997. Review of the state of the world fishery resources: marine fisheries. FAO Fisheries Circular 920.

Freeman, S., S. Mackinson, and R. Flatt. 2004. Diel patterns in the habitat utilization of sandeels revealed using integrated acoustic surveys. Journal of Experimental Marine Biology and Ecology 305:141–154.

Froese, R., and D. Pauly. 2004. Fishbase. Available: fishbase.org. (September 2009).

Fulton, E. A., A. D. M. Smith, and A. E. Punt. 2005. Which ecological indicators can robustly detect effects of fishing? ICES Journal of Marine Science 62:540–551.

Greening, H., and A. Janicki. 2006. Toward reversal of eutrophic conditions in a subtropical estuary: water quality and seagrass response to nitrogen loading reductions in Tampa Bay, Florida, USA. Environmental Management 38:163–178.

Grimes, S. R. 1996. The 1994 net ban constitutional amendment: a case study of marine fisheries management

in Florida. Master's thesis. Texas A&M University, College Station.

Howarth, R. W., and R. Marino. 2006. Nitrogen as the limiting nutrient for eutrophication in coastal marine ecosystems: evolving views over three decades. Limnology and Oceanography 51:364–376.

Jackson, J. B. C., M. X. Kirby, and W. H. Berger. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science (Washington, D.C.) 293:629–638.

Jardas, I., M. Santic, and A. Pallaoro. 2004. Diet composition and feeding intensity of horse mackerel, *Trachurus mediterraneus* (Osteichthyes: Carangidae) in the eastern Adriatic. Marine Biology 144:1051–1056.

Kemp, W. M., W. R. Boynton, J. E. Adolf, D. F. Boesch, W. C. Boicourt, G. Brush, J. C. Cornwell, T. R. Fisher, P. M. Glibert, J. D. Hagy, L. W. Harding, E. D. Houde, D. G. Kimmel, W. D. Miller, R. I. E. Newell, M. R. Roman, E. M. Smith, and J. C. Stevenson. 2005. Eutrophication of Chesapeake Bay: historical trends and ecological interactions. Marine Ecology Progress Series 303:1–29.

Kennish, M. J. 2002. Environmental threats and environmental future of estuaries. Environmental Conservation 29:78–107.

Kideys, A. E. 2002. Fall and rise of the Black Sea ecosystem. Science (Washington, D.C.) 297:1482–1484.

Köster, F. W., and C. Möllmann. 2000. Trophodynamic control by clupeid predators on recruitment success in Baltic cod? ICES Journal of Marine Science 57:311–323.

Levin, L. A., W. Ekau, A. J. Gooday, F. Jorissen, J. J. Middelburg, S. W. A. Naqvi, C. Neira, N. N. Rabalais, and J. Zhang. 2009. Effects of natural and human-induced hypoxia on coastal benthos. Biogeosciences 6:2063–2098.

Lotze, H., H. S. Lenihan, B. J. Bourque, R. H. Bradbury, R. G. Cooke, M. C. Kay, S. M. Kidwell, M. X. Kirby, C. H. Peterson, and J. B. C. Jackson. 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. Science (Washington, D.C.) 312:1806–1809.

Mee, L. 2006. Reviving dead zones. Scientific American 295:79–85.

Nixon, S. W. 1995. Coastal marine eutrophication: a definition, social causes, and future concerns. Ophelia 41:199–219.

Nixon, S. W., and B. A. Buckley. 2002. "A strikingly rich zone"—nutrient enrichment and secondary production in coastal marine ecosystems. Estuaries 25:782–796.

Pauly, D., V. Christensen, J. Dalsgaard, R. Froese, and F. J. Torres. 1998. Fishing down marine food webs. Science (Washington, D.C.) 279:860–863.

Pihl, L., J. Modin, and H. Wennhage. 2005. Relating plaice (*Pleuronectes platessa*) recruitment to deteriorating habitat quality: effects of macroalgal blooms in coastal nursery grounds. Canadian Journal of Fisheries and Aquatic Sciences 62:1184–1193.

Rabalais, N. N., and R. E. Turner, editors. 2001. Coastal hypoxia: consequences of living resources and ecosystems. American Geophysical Union, Washington, D.C.

Rabalais, N. N., R. E. Turner, and W. Wiseman, Jr. 2002. The Gulf of Mexico hypoxia, a.k.a. "the dead zone." Annual Review of Ecology and Systematics 33:235–263.

Schindler, D. W., R. E. Hecky, D. L. Findlay, M. P. Stainton, B. R. Parker, M. J. Paterson, K. G. Beaty, M. Lyng, and S. E. M. Kasian. 2008. Eutrophication of lakes cannot be controlled by reducing nitrogen input: results of a 37-year whole-ecosystem experiment. Proceedings of the National Academy of Sciences of the USA 105:11254–11258.

Sea Around Us. 2007. A global database on marine fisheries and ecosystems. Fisheries Centre, University of British Columbia, Vancouver. Available: seaaroundus.org. (September 2009).

Selberg, C. D., L. A. Eby, and L. B. Crowder. 2001. Hypoxia and the Neuse River estuary: responses of blue crabs and crabbers. North American Journal of Fisheries Management 21:358–366.

Shiganova, T. A., and V. Bulgakova. 2000. Effects of gelatinous plankton on Black Sea and Sea of Azov fish and their food resources. ICES Journal of Marine Science 57:641–648.

Sumaila, U. R., A. D. Marsden, R. Watson, and D. Pauly. 2007. A global ex-vessel fish price database: construction and applications. Journal of Bioeconomics 9:39–51.

Thronson, A., and A. Quigg. 2008. Fifty-five years of fish kills in coastal Texas. Estuaries and Coasts 31:802–813.

Tian, Y., H. Kidokoro, and T. Watanabe. 2006. Long-term changes in the fish community structure from the Tsushima warm current region of the Japan/East Sea with an emphasis on the impacts of fishing and climate regime shift over the last four decades. Progress in Oceanography 68:217–237.

Turner, R. E., and N. N. Rabalais. 1991. Changes in Mississippi River water quality this century: implications for coastal food webs. Bioscience 41:140–148.

Vallin, L., and A. Nissling. 2000. Maternal effects on egg size and egg buoyancy of Baltic cod, *Gadus morhua*: implications for stock structure effects on recruitment. Fisheries Research 49:21–37.

Vaquer-Sunyer, R., and C. M. Duarte. 2008. Thresholds of hypoxia for marine biodiversity. Proceedings of the National Academy of Sciences of the USA 105:15452–15457.

Appendix: References and data sources by ecosystem and region

TABLE A.1.—Data sources used to estimate ratios of pelagic to benthic–demersal species biomass (P/D), mean trophic position, and average length of species in fishery landings. Fishery ecosystems are grouped by geographical region (alphabetically by continent). Major fisheries are the most important commercially fished species, based on total landings for the period 1990–2004.

Ecosystem	Data availability	Major fisheries	P/D	Trophic position	Length (mm)	Data source
Asia						
East China Sea	1990–2003	Yellow croaker *Laramichthys polyactis*, Japanese anchovy *Engraulis japonicus*	1.22	3.27	55	Sea Around Us (2007)
Seto Inland Sea	1990–1999	Sand eel *Ammodytes personatus*, Japanese anchovy	0.80	2.71	39	Ogawa (2001)
Yellow–Bohai seas	1990–2003	Pacific saury *Cololabis saira*, Japanese flying squid *Todarodes pacificus*	0.77	3.30	57	Sea Around Us (2007)
Europe						
Adriatic Sea	1990–2004	European pilchard *Sardina pilchardus*, European anchovy *Engraulis encrasicolus*	2.67	3.04	37	FAO-GFCM (2007)
Baltic Sea	1990–2004	European sprat *Sprattus sprattus*, Atlantic herring *Clupea harengus*	6.52	3.27	49	ICES (2007)
Black Sea	1990–2004	European anchovy, European sprat	12.06	3.19	29	FAO-GFCM (2007)
Irish Sea	1990–2004	Norway lobster *Nephrops norvegicus*, Atlantic herring	0.30	3.49	74	ICES (2007)
Sea of Marmara	1990–2004	European anchovy, blue whiting *Micromesistius poutassou*	4.69	3.31	43	FAO-GFCM (2007)
North Sea	1990–2004	Sand lances *Ammodytes* spp., Atlantic herring	0.64	3.36	43	ICES (2007)
Sea of Azov	1990–2004	Azov Sea sprat *Clupeonella cultriventris*, so-iuy mullet *Mugil soiuy*	5.68	2.96	24	FAO-GFCM (2007)
Skagerrak-Kattegat	1990–2004	Atlantic herring, European sprat	1.57	3.34	47	ICES (2007)
Sound and Belt	1990–2004	Atlantic herring, Atlantic cod *Gadus morhua*	1.38	3.55	81	ICES (2007)
North America						
Chesapeake Bay	1990–2001	Atlantic menhaden *Brevoortia tyrannus*, blue crab *Callinectes sapidus*	2.13	2.49	40	NOAA-CBO[a], Vaughan et al. (2002)
Corpus Christi Bay	1990–2001	Shrimp *Farfantepenaeus* spp., white shrimp *Litopenaeus setiferus*, blue crab	<0.01	3.27	60	Culbertson et al. (2004), Green and Campbell (2005)
Delaware Bay	1990–2000	Blue crab, horseshoe crab *Limulus polyphemus*	0.04	2.88	34	Whitmore and Cole (2002, 2003)
Galveston Bay	1990–2001	Shrimp *Farfantepenaeus* spp., white shrimp, blue crab	0.01	2.89	30	Culbertson et al. (2004), Green and Campbell (2005)
Gulf of Mexico[b]	1990–2004	Gulf menhaden *B. patronus*, shrimp *Farfantepenaeus* spp., white shrimp	5.35	2.32	28	Vaughan et al. (2007), NMFS-SEFSC[c]
Gulf of St. Lawrence	1990–2003	Atlantic herring, snow crab *Chionoecetes opilio*	1.05	3.11	51	NAFO[d]
Long Island Sound	2000, 2001	Skates *Raja* spp., Atlantic herring	0.38	3.67	66	AACSP 2006[e]; CTDEP[f]; NYSDEC[g]; NMFS[h]
Neuse River estuary	1990–2004	Blue crab, Atlantic menhaden	0.05	2.71	30	NCDMF[i]; Vogelsong and Nobles (2004)
Pamlico River	1990–2004	Blue crab, Atlantic menhaden	0.01	2.71	25	NCDMF; Vogelsong and Nobles (2004)
Tampa Bay	1991–2004	Mullet *Mugil* spp., Atlantic thread herring *Opisthonema oglinum*	1.39	2.95	80	FFWCC[j], NMFS

[a] National Oceanographic and Atmospheric Administration, Chesapeake Bay Office, personal communication.
[b] Texas–Lousiana shelf only.
[c] National Marine Fisheries Service, Southeast Fisheries Science Center, personal communication. Catch totals from statistical grids 12–19 only.
[d] North Atlantic Fisheries Organization 21A database. Available: www.nafo.int/about/.
[e] Atlantic Coastal Cooperative Statistics Program (www.accsp.org).
[f] Connecticut Department of Environmental Protection, personal communication.
[g] New York Department of Environmental Conservation, personal communication.
[h] National Marine Fisheries Service, Fisheries Statistics Division (www.st.nmfs.gov/st1).
[i] North Carolina Division of Marine Fisheries, personal communication.
[j] Florida Fish and Wildlife Conservation Commission, personal communication.

TABLE A.2.—Nitrogen loads (in metric tons $N \cdot km^{-2} \cdot year^{-1}$) and spatial extent of hypoxia data for the ecosystems examined in this analysis (NA = data not available).

Ecosystem	Basin N load	Total N load	Nitrogen load references	Hypoxic area[a]	Hypoxia references
Asia					
East China Sea	3.0	3.6	Wang and Wang (2007), Seitzinger et al. (2002)	4.1	Daoji et al. (2002)
Seto Inland Sea	10.1	51.1	Yanagi and Ishii (2004), Seitzinger et al. (2002)	5.3	Kasai et al. (2007), Suzuki (2001), Jun Shoji[b]
Yellow-Bohai Sea	5.8	5.8	Bashkin et al. (2002)	1.2	Daoji et al. (2002)
Europe					
Adriatic Sea	3.1	NA	Borysova et al. (2005), Salvetti et al. (2006), Zavatarelli et al. (2000), Seitzinger et al. (2002)	1.4	Dalla Via et al. (1994)
Baltic Sea	3.2	3.9	Savchuk (2005)	32.7	Hansen et al. (2007)
Black Sea	1.8	1.9	Teodoru et al. (2007), Borysova et al. (2005), Polat (2000), Seitzinger et al. (2002)	76.6	Mee et al. (2005), Prodanov et al. (1997)
Irish Sea	3.4	7.6	Smith et al. (2003), Seitzinger et al. (2002)	0.0	CEFAS (2006), Dickson (1987)
Sea of Marmara	21.9	22.5	Seitzinger et al. (2002), Tugrul and Polat (1995)	73.6	Baykut et al. (1987), Besiktepe et al. (1994)
North Sea	3.5	12.7	Brion et al. (2004)	0.0	Druon et al. (2004)
Sea of Azov	1.3	1.3	Borysova et al. (2005), Seitzinger et al. (2002)	40.0	Debol'skaya et al. (2005)
Skagerrak-Kattegat	9.4	NA	Savchuk (2005)	9.5	Ærtebjerg et al. (2003)
Sound and Belt	25.1	33.8	Savchuk (2005)	46.0	Ærtebjerg et al. (2003)
N. America					
Chesapeake Bay	14.5	14.5	USGS (2006), Castro et al. (2003), Cerco (1995)	18.0	David Jazinski[c], Bahner (2003)
Corpus Christi Bay	3.4	3.6	Castro et al. (2003)	10.0	Paul Montagne[d]
Delaware Bay	21.2	40.3	Castro et al. (2003)	0.0	Timothy Targett and Jonathan Sharp[e]
Galveston Bay	22.9	24.1	Armstrong and Ward (1994), Newell et al. (1992), Brock et al. (1996)	0.0	James Pinckney and Steve Johnston[f]
Gulf of Mexico[g]	15.5	16.5	Aulenbach (2006), Seitzinger et al. (2002)	27.2	Rabalais et al. (2007)
Gulf of St. Lawrence	0.7	2.4	Aulenbach (2006), Seitzinger et al. (2002), Savenkoff et al. (2001)	9.3	Gilbert et al. (2007)[h]
Long Island Sound	18.2	57.8	HydroQual (2004), CTDEP and NYSDEC (2000)	31.1	CTDEP (2007)
Neuse River estuary	21.8	21.9	Burkholder et al. (2006), Castro et al. (2003)	39.3	Breitburg et al. (2009)
Pamlico River	13.1	13.1	NEEA (2006)	39.3	Breitburg et al. (2009)
Tampa Bay	4.9	8.0	Greening and Janicki (2006)	13.3	Janicki et al. (2001)

[a] Areas with dissolved oxygen concentrations $\leq$ 3 mg/L expressed as a percentage of system surface area.
[b] Takehara Fisheries Research Station, Hiroshima University, personal communication.
[c] National Oceanic and Atmospheric Administration, Chesapeake Bay Program, personal communication.
[d] University of Texas Marine Science Institute, personal communication.
[e] University of Delaware, personal communication.
[f] University of South Carolina and Galveston Bay Estuary Program, personal communication.
[g] Texas–Lousiana shelf only.
[h] And personal communication with Denis Gilbert (Department of Fisheries and Oceans, Canada).

TABLE A.3.—Data sources.

Sources

Ærtebjerg, G., and J. Carstensen. 2003. The 2002 oxygen depletion event in the Kattegat, Belt Sea, and western Baltic, Helsinki Commission, Baltic Sea Environment Proceedings 90, Helsinki. Available: http://www2.dmu.dk/1_viden/2_publikationer/3_ovriga/rapporter/helcom2003_baltseaenvironprocno90.pdf.

Armstrong, N. E., and G. H. Ward. 1994. Point source loading characterization of Galveston Bay. Galveston Bay National Estuary Program, Publication GBNEP-36, Webster, Texas. Available: http://gbic.tamug.edu/publications.htm. (February 2008).

Aulenbach, B. T. 2006. Annual dissolved nitrite plus nitrate and total phosphorus loads for the Susquehanna, St. Lawrence, Mississippi–Atchafalaya, and Columbia River basins, 1968–2004. U.S. Geological Survey, Open-File Report 2006–1087. Available: http://pubs.usgs.gov/ofr/2006/1087/. (April 2007).

Bahner, L. 2003. User guide for the Chesapeake Bay and tidal tributary river interpolator. National Oceanic and Atmospheric Administration, Annapolis, Maryland.

Bashkin, V. N., S. U. Park, M. S. Choi, and C. B. Lee. 2002. Nitrogen budgets for the Republic of Korea and the Yellow Sea region. Biogeochemistry 57/58:387–403.

Baykut, F., A. Aydin, and M. I. Artuz. 1987. Ecological situation of Sea of Marmara. Chemosphere 16(2/3):339–350.

Besiktepe, S., H. I. Sur, E. Özsoy, M. A. Latif, T. Oğuz, and U. Ünlüata. 1994. The circulation and hydrography of the Marmara Sea. Progress in Oceanography 34:285–334.

Borysova, O., A. Kondakov, S. Paleari, E. Rautalahti-Miettinen, F. Stolberg, and V. Daler. 2005. Eutrophication in the Black Sea region: impact assessment and causal chain analysis. University of Kalmar, Kalmar, Sweden.

Breitburg, D. L., D. W. Hondorp, L. A. Davias, and R. J. Diaz. 2009. Hypoxia, nitrogen, and fisheries: integrating effects across global and local landscapes. Annual Reviews of Marine Science 1:329–349.

Brion, N., W. Baeyens, S. De Galan, M. Elskens, and R. Laane. 2004. The North Sea: source or sink for nitrogen and phosphorus to the Atlantic Ocean? Biogeochemistry 68:277–296.

Brock, D. A., R. S. Solis, and W. L. Longley, 1996. Guidelines for water resources permitting: nutrient requirements for maintenance of Galveston Bay productivity. Texas Water Development Board, Austin.

Burkholder, J. M., D. A. Dickey, C. Kinder, R. E. Reed, M. A. Mallin, M. R. McIver, L. B. Cahoon, G. Melia, C. Brownie, J. Smith, N. Deamer, J. Springer, H. B. Glasgow, and D. Toms. 2006. Comprehensive trend analysis of nutrients and related variables in a large eutrophic estuary: a decadal study of anthropogenic and climatic influences. Limnology and Oceanography 51:463–487.

CEFAS (Centre for Environment, Fisheries and Aquaculture Science). 2006. Interactive spatial explorer and administrator (iSEA). Available: http://www.cefas.co.uk/isea/ (February 2007).

Cerco, C. F. 1995. Response of Chesapeake Bay to nutrient load reductions. Journal of Environmental Engineering 121:549–557.

CTDEP (Connecticut Departemnt of Environmental Protection). 2007. Long Island Sound water quality monitoring. Available: http://www.ct.gov/dep/. (February 2007).

CTDEP and NYSDEC (Connecticut Department of Environmental Protection and New York State Department of Environmental Conservation). 2000. A total maximum daily load analysis to achieve water quality standards for dissolved oxygen in Long Island Sound. CTDEP and NYSDEC, Hartford and Albany.

Culbertson, J., L. Robinson, P. Campbell, and L. Butler. 2004. Trends in Texas commercial fishery landings, 1981–2001. Texas Parks and Wildlife Department, Management Data Series 224, Austin.

Dalla Via, J., G. van den Thillart, O. Cattani, and A. de Zwaan. 1994. Influence of long-term hypoxia exposure on the energy metabolism of *Solea solea,* II. Intermediary metabolism in blood, liver, and muscle. Marine Ecology Progress Series 111:17–27.

Daoji, L., Z. Jing, H. Daji, Y. Wu, and L. Jun. 2002. Oxygen depletion off the Changjiang (Yangtze River) estuary. Science in China (Series D) 45:1137–1146.

Debol'skaya, E. I., E. V. Yakushev, and A. I. Sukhinov. 2005. Formation of fish kills and anaerobic conditions in the Sea of Azov. Water Resources 32:151–162.

Dickson, R. R. 1987. Irish Sea status report of the Marine Pollution Monitoring Management Group. Centre for Environment, Fish, and Aquacultural Science, Lowestoft, UK.

Druon, J.-N., W. Schrimpf, S. Dobricic, and A. Stips. 2004. Comparative assessment of large-scale marine eutrophication: North Sea area and Adriatic Sea as case studies. Marine Ecology Progress Series 272:1–23.

FAO–GFCM (United Nations Food and Agriculture Organization–General Fishery Commission of the Mediterranean). 2007. United Nations Food and Agriculture Organization–General Fishery Commission of the Mediterranean capture production database. Available: www.fao.org/fishery/. (February 2007).

Gilvert, D., D. Chabot, P. Archambault, B. Rondeau, and S. Hébert. 2007. Appauvrissement en oxygène dans les eaux profondes du Saint-Laurent marin: causes possibles et impacts écologiques. [Oxygen depletion in the deep waters of the tidal Saint Lawrence: possible causes and ecological impacts.] Naturaliste Canadien 131:67–75.

Green, L. M., and P. R. Campbell. 2005. Trends in finfish landings of sport boat anglers in Texas marine waters, May 1974–May 2003. Texas Parks and Wildlife Department, Management Data Series 234, Austin.

Greening, H., and A. Janicki. 2006. Toward reversal of eutrophic conditions in a subtropical estuary: water quality and seagrass response to nitrogen loading reductions in Tampa Bay, Florida, USA. Environmental Management 38:163–178.

Hansen, I.S., N. Keul, J. T. Sørensen, A. Erichsen, and J. Andersen. 2007. Baltic Sea oxygen maps, 2000–2006. BALANCE, Interim Report 17, Copenhagen.

HydroQual. 2004. SWEM flux calculations. HydroQual, Technical Report File HRFO0013, Stamford, Connecticut.

ICES (International Council for the Exploration of the Sea). 2007. Eurostat/ICES database on catch statistics (by species, area, and year 1973–2007). Available: www.ices.dk/fish/statlant.asp. (January 2008).

Janicki, A., R. Pribble, and M. Winowitch. 2001. Examination of the spatial and temporal nature of hypoxia in Tampa Bay, Florida. Janicki Enviornmental, St. Petersburg, Florida.

Mee, L. D., J. Friedrich, and M. T. Gomoiu. 2005. Restoring the Black Sea in times of uncertainty. Oceanography 18:100–111.

NEEA (National Estuarine Eutrophication Assessment). 2006. National Estuarine Eutrophication Assessment database. Available: http://ian.umces.edu/neea/. (January 2008).

Newell, C. J., H. S. Rifai, and P. B. Bedient. 1992. Characterization of nonpoint sources and loadings to Galveston Bay. Galveston Bay National Estuary Program, GBNEP-15, Webster, Texas. Available: http://gbic.tamug.edu/publications.htm. (January 2008).

Ogawa, T. 2001. Fish landings of the Seto Inland Sea. Fisheries Research Agency of the Seto Inland Sea, Hiroshima, Japan.

TABLE A.3.—Continued.

Sources

Polat, C. 2000. An assessment of nitrogen, phosphorus, and organic carbon inputs to the Black Sea. Pages 98–103 *in* N. Cagatay, editor. IOC/ BSRC (Intergovernmental Oceanographic Commission/Black Sea Regional Committee) Workshop on Black Sea fluxes. Intergovernmental Oceanographic Commission, Report 145, Paris. Available: http://unesdoc.unesco.org/images/0012/001205/120553eo.pdf.

Prodanov, K., K. Mikhailov, G. M. Daskalov, C. Maxim, A. Chashchin, A. Arkhipov, V. Shlyakhov, and E. Ozdamar. 1997. Environmental management of fish resources in the Black Sea and their rational exploitation. United Nations Food and Agriculture Organization, Rome.

Rabalais, N. N., R. E. Turner, B. K. Sen Gupta, D. F. Boesch, P. Chapman, and M. C. Murrell. 2007. Hypoxia in the northern Gulf of Mexico: does the science support the plan to reduce, mitigate, and control hypoxia? Estuaries and Coasts 30:753–772.

Salvetti, R., A. Azzellino, and R. Vismara. 2006. Diffuse source apportionment of the Po River eutrophying load to the Adriatic Sea: assessment of Lombardy contribution to Po River nutrient load apportionment by means of an integrated modeling approach. Chemosphere 65:2168–2177.

Savchuk, O. P. 2005. Resolving the Baltic Sea into seven subbasins: N and P budgets for 1991–1999. Journal of Marine Systems 56:1–15.

Savenkoff, C., A. F. Vezina, P. C. Smith, and G. Han. 2001. Summer transports of nutrients in the Gulf of St. Lawrence estimated by inverse modeling. Estuarine, Coastal and Shelf Science 52:565–587.

Sea Around Us. 2007.

Seitzinger, S. P., C. Kroeze, A. F. Bouman, N. Caraco, F. Dentener, and R. V. Styles. 2002. Global patterns of dissolved inorganic and particulate nitrogen inputs to coastal systems: recent conditions and future projections. Estuaries 25:640–655.

Smith, S. V., D. P. Swaney, L. Talaue-Mcmanus, J. D. Bartley, P. T. Sandhei, C. J. McLaughlin, V. C. Dupra, C. J. Crossland, R. W. Buddemeier, B. A. Maxwell, and F. Wulff. 2003. Humans, hydrology, and the distribution of inorganic nutrient loading to the ocean. Bioscience 53:235–245.

Teodoru, C. R., G. Friedl, J. Friedrich, U. Roehl, M. Sturm, and B. Wehrli. 2007. Spatial distribution and recent changes in carbon, nitrogen, and phosphorus accumulation in sediments of the Black Sea. Marine Chemistry 105:52–69.

Tugrul, S., and C. Polat. 1995. Quantitative comparison of the influxes of nutrients and organic carbon into the Sea of Marmara both from anthropogenic sources and from the Black Sea. Water Science and Technology 32:115–121.

USGS (U.S. Geological Survey). 2006. Nontidal nitrogen loads and river flow to the Chesapeake Bay. Available: http://www.chesapeakebay. net/. (February 2007).

Vaughan, D. S., K. W. Shertzer, and J. W. Smith. 2007. Gulf menhaden (*Brevoortia patronus*) in the U.S. Gulf of Mexico: fishery characteristics and biological reference points for management. Fisheries Research 83:263–275.

Vaughan, D. S., J. S. Smith, and E. H. Williams. 2002. Analysis on the status of the Atlantic menhaden stock. National Oceanic and Atmospheric Administration, Center for Coastal Fisheries and Habitat Research, Beaufort, North Carolina.

Vogelsong, H., and J. Nobles. 2004. The impact of recreational crabbing on North Carolina's crab population. Pages 417–420 *in* J. Murdy, editor. Proceedings of the 2003 Northeastern Recreation Research Symposium. U.S. Forest Service General Technical Report NE-317.

Wang, B., and X. Wang. 2007. Chemical hydrography of coastal upwelling in the East China Sea. Chinese Journal of Oceanology and Limnology 25:16–26.

Whitmore, W. H. 2003. Marine recreational fishing in Delaware: a summary report of the Marine Recreational Fisheries Statistics Survey (MRFSS). Delaware Division of Fish and Wildlife, Federal Aid in Fish Restoration, Project F-33-R-22, Dover.

Whitmore, W. H., and R. W. Cole. 2002. Commercial fishing in Delaware, 2001: annual landings report. Delware Division of Fish and Wildlife, Dover.

Yanagi, T., and D. Ishii. 2004. Open-ocean originated phosphorus and nitrogen in the Seto Inland Sea. Japanese Journal of Oceanography 60:1001–1005.

Zavatarelli, M., J. W. Baretta, J. G. Baretta-Bekker, and N. Pinardi. 2000. The dynamics of the Adriatic Sea ecosystem: an idealized model study. Deep-Sea Research 47:937–970.