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Abstract.—Although hypoxia is a threat to coastal ecosystems, policy makers have limited information about its economic impacts on fisheries. Studies using spatially and temporally aggregated data generally fail to detect statistically significant effects of hypoxia on fisheries. Limited recent work using disaggregated fishing data (microdata) has revealed modest effects of hypoxia on the catches of recreationally harvested species. These studies did not account for important spatial and temporal aspects of the system, however. For example, the effects of hypoxia on catch may not materialize instantaneously but involve a lagged process reflecting cumulative past exposure. This paper develops a differenced bioeconomic model to account for the lagged effects of hypoxia on the North Carolina fishery for brown shrimp *Farfantepenaeus aztecus*. The model integrates high-resolution oxygen monitoring data with fishery-dependent microdata from North Carolina's trip ticket program to investigate the detailed spatial and temporal relationships of hypoxia to commercial fishery harvests. The main finding is that hypoxia may have resulted in a 12.9% annual decrease in the brown shrimp harvest during the period 1999–2005. The paper also develops two alternative models—a nondifferenced model and a polynomial distributed lag model—whose results are consistent with those of the main model.

Environmental policies to address nutrient pollution require understanding both the ecological and economic consequences of hypoxia (Pew Oceans Commission 2003; U.S. Commission on Ocean Policy 2004). Although there is more to learn, the ecological dimensions of nutrient pollution have been well studied around the world (Rosenberg 1985; Colombo et al. 1992; Nixon 1995; Howarth et al. 1996; Vitousek et al. 1997, National Research Council 2000; Diaz 2001; Kemp et al. 2005; Paerl 2006; Breitburg et al. 2009a, 2009b). The effects of hypoxia on individual growth (Stierhoff et al. 2009), mortality (Miller et al. 2002), movement (Wannamaker and Rice 2000), reproduction (Thomas et al. 2007), and food web interactions (Breitburg 2002) have been documented for many species and ecosystems. Although hypoxia is becoming more frequent and widespread in coastal and estuarine systems (Diaz 2001; National Research Council 2000;

Boesch et al. 2001; Diaz and Rosenberg 2008), the economic consequences for fisheries and the implications for fisheries management are largely unknown.

Despite the documented biological consequences of hypoxia, the severity of economic effects on fisheries is unclear. Some studies simply fail to detect economic effects (Zimmerman et al. 1997; Diaz and Solow 1999). Diaz and Solow (1999) argue that a key difficulty is the lack of statistical power when analysts attempt to infer hypoxia effects from correlations between spatially and temporally aggregated fishing data (e.g., landings) and coarse indicators of hypoxia severity. Most harvested species can avoid hypoxia such that population-level effects are mostly indirect. Avoidance behavior shifts the spatial distribution of the fishery resource, which in turn, can affect trophic and fishery interactions (Breitburg et al. 2009b; Rose et al. 2009). For example, by inducing habitat shifts and altering the spatial distribution of targeted species, hypoxia can affect the behavior of fishermen and the associated catch efficiency of the fishery (Zimmerman and Nance 2001; Craig and Crowder 2005; Craig et al. 2005; Smith and Crowder 2005; Smith 2007). In addition, most harvested species occupy different

habitats during the larval, juvenile, and adult stages. As a result, hypoxia effects are typically specific to particular life history stages and habitats that may be the same or different from those subject to the fishery. This creates the potential for spatiotemporal lags in the response of the fishery that may not be obvious in aggregate harvest data.

As an alternative to aggregate data, economists have used data on individual fisherman (microdata) to quantify the economic effects of hypoxia on fisheries. The degrees of freedom for detecting effects in a statistical model dramatically increase when using microdata, such as information on fishing effort and harvest at the level of individual trips, compared with data aggregated over time (e.g., annual) and space (e.g., the distribution of the stock). Microdata also allow for the control of spatiotemporal differences in fishing effort, which often confound analyses of environmental effects on fisheries. Using microdata on recreational fishing for striped bass *Morone saxatilis*, Lipton and Hicks (2003) found modest economic effects of low dissolved oxygen in the Patuxent River, Maryland, and potentially large effects if environmental conditions were to deteriorate significantly. Massey et al. (2006) also used microdata on recreational anglers to quantify the effects of low dissolved oxygen on the fishery for summer flounder *Paralichthys dentatus* in a tributary to Chesapeake Bay. They were able to control for a larger set of environmental conditions (including dissolved oxygen, water temperature, salinity, and turbidity) than were Lipton and Hicks (2003) and found modest economic effects of hypoxia. Mistiaen et al. (2003) estimated the effects of low dissolved oxygen on commercial harvests of blue crab *Callinectes sapidus* in Chesapeake Bay tributaries. They found that reductions in dissolved oxygen led to large instantaneous declines in the population available for harvest in the tributaries, but they were unable to determine whether these effects lowered overall harvest in the Chesapeake Bay fishery.

Quantifying the economic effects of hypoxia on fisheries requires a statistical approach that can isolate the effects of hypoxia from other potentially covarying environmental factors. Further, economic effects of hypoxia occur through a complex set of ecological and behavioral pathways. Some may be instantaneous, such as when fish move to avoid low oxygen, but many unfold over time. In particular, if low oxygen affects juvenile growth, mortality, or migration, fisheries data will not reveal these effects for some time, at least until the juveniles recruit into the fishery. As such, analyzing fishing microdata requires a dynamic approach that controls for correlated factors and allows for the possibility of lagged effects. Massey et al. (2006) incorporated the dynamic effects of hypoxia in a population simulation model based on laboratory experiments, but their empirical analysis of catches only included contemporaneous effects of low dissolved oxygen. Not controlling for potential lagged effects of environmental conditions raises the possibility that inferences regarding the economic consequences to the fishery are influenced by a temporal mismatch between harvest and hypoxia.

We developed a bioeconomic model to identify the lagged effects of hypoxia on commercial harvest of brown shrimp *Farfantepenaeus aztecus* in North Carolina while also accounting for spatial aspects of shrimp life history and the fishery. Disentangling the effects of hypoxia from fishing pressure presented challenges because both are temporally dynamic and co-occur during summer and early fall in inshore estuarine waters.

Methods

Our approach to quantifying the lagged effects of hypoxia on the brown shrimp fishery proceeded in three steps. First, we developed a model to link the stock of brown shrimp, the commercial fishery harvest, and multiple environmental factors. Second, we determined how many days the system was below a dissolved oxygen threshold annually from 1999 to 2005, which we used to represent the cumulative effect of hypoxia on the fishery. We used detailed water quality data that provided a high-resolution (15 min sampling interval) record of oxygen conditions in the estuary to characterize the temporal dynamics of hypoxia. Third, we estimated model parameters empirically using available trip harvest and oxygen monitoring data. We accounted for the spatial dynamics of hypoxia and shrimp harvest by conducting parallel estimation of the model in two adjacent areas: the Neuse River and the Pamlico Sound. The Neuse River experiences severe hypoxia and low to moderate levels of shrimp harvest. The Neuse is a nursery area that supplies shrimp to the larger Pamlico Sound, which experiences little hypoxia but is where the majority of shrimp harvest occurs. We recovered the parameters of both models using a backwards selection technique to identify the best-fitting linear model. We then used a nondifferenced model and a polynomial distributed lag model to check the robustness of our findings to alternative model structures. Although our model application is to a medium-sized fishery with intermittent hypoxia, the approach we developed is general and can be applied to a number of other fisheries and environmental perturbations.

Shrimp life history and fishery.—Brown shrimp spawn in offshore shelf waters during February–

March; the larvae recruit to estuarine nursery habitats, including riverine tributaries, during March–May (Lassuy 1983; Steele 1994). As juveniles increase in size during the summer months, they gradually migrate to deeper areas of bays and sounds before returning to the shelf during the fall (September–November). The population dynamics of brown shrimp are thought to be strongly influenced by environmental factors, such as temperature, salinity, dissolved oxygen, and access to marsh habitat (Sutter and Christmas 1983; Haas et al. 2001; Li and Clarke 2005; Roth et al. 2008). Environmental effects on recruitment in conjunction with high fecundity and an annual life history cycle result in a weak stock–recruitment relationship. The weak stock–recruitment relationship simplifies our analysis because annual recruitment is unrelated or only weakly related to past recruitment and past environmental conditions. As a result, each year-class can effectively be treated as independent of prior year-classes. Because brown shrimp have a short life span, these year-classes do not overlap significantly such that each year approximately represents a single cohort.

The shrimp fishery has ranked first or second in terms of economic value among fisheries in North Carolina over the last 30 years (summarized in NCDENR–DMFFMP 2006). The North Carolina shrimp trawl fishery is unique in the South Atlantic in that most of the harvest (about 76% historically) occurs in inshore estuarine waters. The fishery harvests three penaeid shrimp species (brown shrimp, white shrimp *Litopenaeus setiferus*, and pink shrimp *Farfantepenaeus duorarum*), which are resident in estuaries for several months from May to October. Brown shrimp have historically accounted for the majority (about two-thirds) of the catch. North Carolina currently accounts for about 61% of the total landings of brown shrimp from the South Atlantic. Most of the state landings (67%) come from Pamlico Sound, a large (about 6,000 km²) drowned river valley bounded seaward by an extensive network of barrier islands and fed landward by numerous riverine tributaries (Figure 1). The fishery is also prosecuted in the tributaries, of which the Neuse River estuary is the largest, both in terms of areal extent and shrimp harvest (about 2% of the total statewide landings). About 72% of the annual shrimp harvest in inshore North Carolina waters occurs from July to October.

The Neuse River estuary is the major southern tributary to the larger Pamlico–Albemarle estuary (Figure 1). The Neuse experiences severe hypoxia during summer (May–August) due to excess nutrient loading from its 16,000 km² watershed (Paerl et al. 1998; Stow et al. 2001). Hypoxia has also been documented in other major tributaries (Stanley and Nixon 1992) and in Albemarle Sound to the north (Tuomikowski et al. 2008). Although the occurrence of hypoxia in these systems is largely driven by nutrient and freshwater inputs, typically it is highly dynamic spatially and temporally because of the shallow depths (about 3 m) that promotes episodic, wind-induced mixing (Reynolds-Fleming and Luettich 2004). Though not as well monitored as the river tributaries, hypoxia appears rare in Pamlico Sound, except under extreme climatological conditions (Paerl et al. 2001).

A differenced model.—Let C represent the average shrimp landings per trip (lb/trip) made on a particular day t of a year y; C is a nonlinear function of fishing effort, which we measured as the average number of trips (K_{yt}) and the average length of vessels (Len) that made those trips on each day of the year. Other terms in the model include month- and gear-specific catchability ($q_{ym,g}$, in which m indicates month and g indicates gear type) and shrimp biomass (X_{yt}). Catchability is a biomechanical coefficient that converts biomass and fishing effort into catch, and ε is an error term assumed to be independently and identically distributed with a normal distribution. The model is

$$C_{yt} = q_{ym,g}k_{yt}^{\alpha}\,\text{Len}_{yt}^{\beta}X_{yt}e^{\varepsilon_{yt}}. \qquad (1)$$

This form of the production function allows α and β to measure the curvature in the relationship between catch and effort (see Smith et al. 2006). Shrimp biomass (X_{yt}) can be decomposed into the total number of shrimp (z_{yt}) and individual shrimp weight (w_t), that is,

$$X_{yt} = z_{yt}w_t, \qquad (2)$$

where w_t reflects the baseline intraannual growth before accounting for environmental factors, so it is only a function of t and not specific to a particular year y. We use the standard von Bertalanffy growth function to model shrimp growth in length and an allometric function to relate length and weight. The von Bertalanffy function is

$$L(t) = L_{\infty}(1 - e^{\delta t}), \qquad (3)$$

where L denotes the total length of shrimp, and L_{∞} is the terminal length. The parameter δ captures the decay rate, or the rate at which shrimp approach asymptotic size. Shrimp weight is represented as an allometric function of shrimp length, namely,

$$w_t = \omega L(t)^{\eta}. \qquad (4)$$

The total baseline number of shrimp (z_{yt}) in equation (2) is year specific to account for recruitment
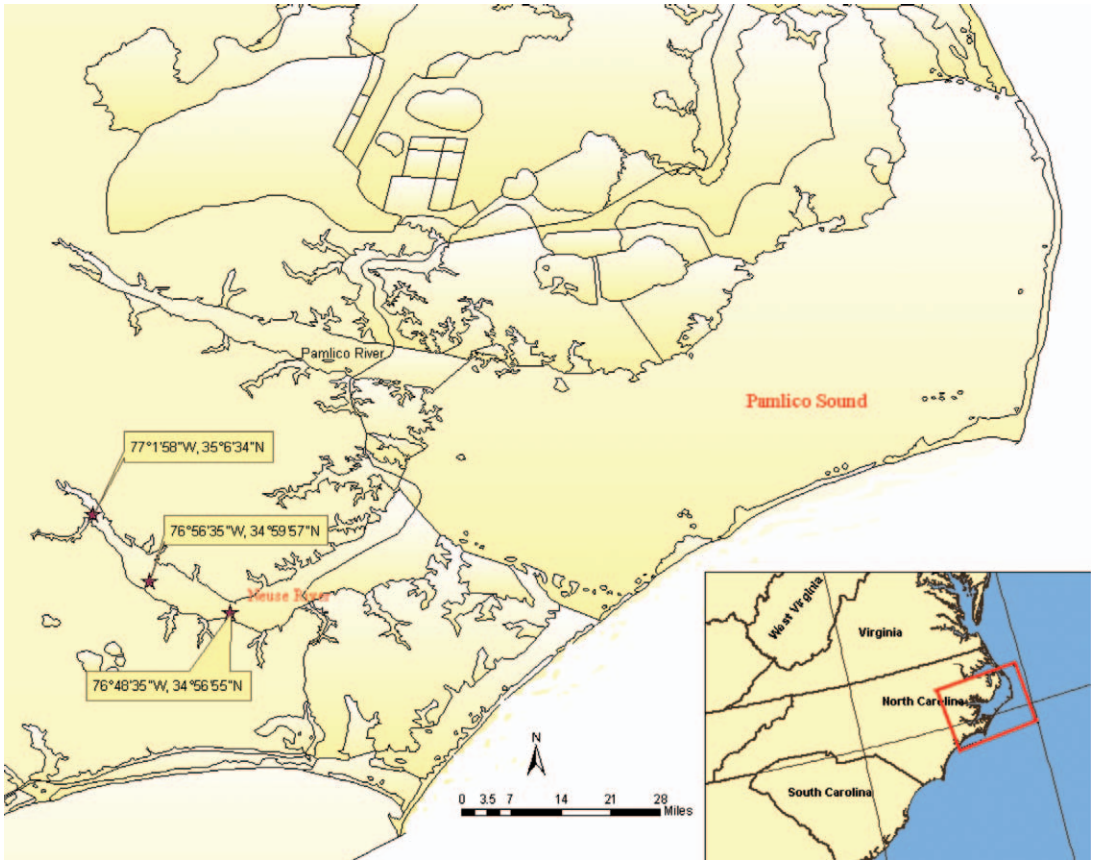
FIGURE 1.—Pamlico Sound and its major tributaries (the Neuse and Pamlico rivers), where the fishery for brown shrimp was studied. Three water quality monitoring sites are located in the Neuse River (stars).

variability and declines over the season due to natural mortality, emigration, and fishing mortality:

$$z_{yt} = z_{y(t-1)} \cdot e^{-\Delta m_{0t} - \Delta m_{1t}} \cdot e^{m_f H_{y(t-1)} / w_{t-1}}. \quad (5)$$

In the above equation, the loss rates of shrimp per day include natural mortality (Δm_{0t}), emigration from the system (Δm_{1t}), and fishing mortality (m_f). The first two factors are not year specific. To simplify the model, the fishing mortality rate is held constant over time; $H_{y(t-1)}$ is the total catch (lb) on the previous day and $H_{y(t-1)}/w_{t-1}$ converts pounds to the number of shrimp landed. Equations (1)–(5) describe the basic relationships among shrimp harvest, fishing effort, and stock dynamics. Substituting equation (1) with equations (2) (biomass) and (5) (abundance) gives the following:

$$c_{yt} = q_{ym,g} K_{yt}^{\alpha} \operatorname{Len}_{yt}^{\beta} z_{y(t-1)} \cdot e^{-\Delta m_{0t} - \Delta m_{1t}}$$
$$\cdot e^{m_f (H_{y(t-1)}/w_{t-1})} \cdot w_t e^{\varepsilon_{yt}}. \quad (6)$$

In addition to the intrinsic growth variables above, external environmental factors, including dissolved oxygen, temperature, and salinity, may affect shrimp harvest. The following equation captures the influence of various environmental factors:

$$C_{yt} = q_{ym,g} K_{yt}^{\alpha} \operatorname{Len}_{yt}^{\beta} z_{y(t-1)} \cdot e^{-\Delta m_{0t} - \Delta m_{1t}} \cdot e^{m_f (H_{y(t-1)}/w_{t-1})}$$
$$\cdot w_t \cdot e^{a_1 \operatorname{OI}_{yt} + a_2 \operatorname{TI}_{yt} + a_3 \operatorname{SI}_{yt}} e^{\varepsilon_{yt}}. \quad (7)$$

In this equation, OI (dissolved oxygen), TI (temperature), and SI (salinity) are binary indices of whether particular environmental factors are within a tolerable range based on information in the literature, a_1 to a_3 are parameters, and other terms are as defined previously. For dissolved oxygen (DO), laboratory experiments have shown that brown shrimp avoid areas with levels less than 2 mg/L (Renaud 1986). Based on field data, Eby and Crowder (2002) reported an avoidance threshold of 2.2 mg/L. Based on laboratory experiments, Wannamaker and Rice (2000) reported that

brown shrimp avoided DO of 1 mg/L but not 4 mg/L. Furthermore, Renaud (1986) reported that brown shrimp avoid 1.5 mg/L and 2.0 mg/L, but not 3.0 mg/L. Based on these empirical results we used 1.5, 2.0, and 2.5 mg/L as alternative thresholds for defining whether DO conditions were within a tolerable range. Gunter and Hildebrand (1951) found that temperatures of 4.4°C or less caused narcosis and mortality of shrimp. Kutkuhn (1966) reported that temperature over 32.2°C reduced shrimp growth and survival, which is also consistent with the findings of Zein-Eldin and Aldrich (1965). In addition, the minimum tolerated salinity has been reported as 0.8‰ (Gunter et al. 1964). In field studies, few shrimp are actually found in waters of less than 5‰ (Christmas and Langley 1973; Loesch 1976). Note that the effects of environmental factors captured by equation (7) could be due to multiple, interdependent mechanisms that influence shrimp growth, mortality, migration, or catchability to the fishery. Our model does not distinguish the particular mechanism(s) by which environmental factors influence shrimp harvest.

In equation (7), a_1 to a_3 measure the marginal daily effects of the environmental factors on shrimp catch (log transformed). Ultimately, we are interested in the cumulative effects of each environmental factor over time and the direction and magnitude of their effect on harvest. If we accumulate the effects over time, equation (7) becomes

$$C_{yt} = q_{ym,g}K_{yt}^{\alpha} \text{Len}_{yt}^{\beta} z_{y0} \cdot e^{-\Delta m_{0t} - \Delta m_{1t}} \cdot e^{m_f \Sigma_{i=0}^{t-1} H_{yi}/w_i}$$
$$\cdot w_t \cdot e^A e^{\varepsilon_{yt}}. \qquad (8)$$

where z_{y0} is the initial number of shrimp in year y, τ is the number of days over which the environmental effects are accumulated, and

$$A = a_1 \sum_{i=\tau-t+1}^{t} \text{OI}_{yi} + a_2 \sum_{i=\tau-t+1}^{t} \text{TI}_{yi} + a_3 \sum_{i=\tau-t+1}^{t} \text{SI}_{yi}.$$

For example, if $\tau = 40$, the marginal effects of environmental conditions are aggregated over 40 d before harvest (i.e., 40-d lagged effect). This means that the occurrence of one day of hypoxia (DO less than the specified threshold) has marginal effects on shrimp harvest that can extend over the following 40 d, after which there is no effect.

Although the lagged effects of low DO on shrimp production might reasonably be assumed to operate in a threshold manner (where there is no effect until conditions are below some critical level), DO as well as other environmental factors may also have contemporaneous effects on shrimp harvest over the range of conditions experienced in the estuary. For example, we expect avoidance behavior to be a function of the

severity of low DO and to appear on the same day. The effects on harvest could be negative or positive, depending on whether avoidance leads to aggregation along the edges of hypoxic areas (increases catchability) or disperses existing aggregations of shrimp (decreases catchability). Therefore, we developed the following equation to capture this broader range of potential environmental effects:

$$C_{yt} = q_{ym,g}K_{yt}^{\alpha} \text{Len}_{yt}^{\beta} z_{y0} \cdot e^{-\Delta m_{0t} - \Delta m_{1t}} \cdot e^{m_f \Sigma_{i=0}^{t-1} H_{yi}/w_i}$$
$$\cdot w_t \cdot e^A (O_{yt}^{b_1} T_{yt}^{b_2} S_{yt}^{b_3}) e^{\varepsilon_{yt}}, \qquad (9)$$

where O_{yt} is the DO concentration (mg/L), T_t, is the temperature (°C), and S_{yt} is the salinity (‰). Including both absolute values and binary indices to represent environmental effects in the model provides a flexible functional form that can capture the multiple levels over which environmental conditions may influence shrimp production and harvest.

To simplify the nonlinear estimation, we linearized equation (9) by taking the log of both sides, that is,

$$\log_e C_{yt} = \log_e q_{ym,g} + \alpha \log_e K_{yt} + \beta \log_e \text{Len}_{yt}$$
$$+ \log_e z_{y0} + (\log_e w_t - m_{0t} - m_{1t})m_f \sum_{i=0}^{t-1} \frac{H_{yi}}{w_i}$$
$$+ a_1 \sum_{i=\tau-t+1}^{t} \text{OI}_{yi} + a_2 \sum_{i=\tau-t+1}^{t} \text{TI}_{yi}$$
$$+ a_3 \sum_{i=\tau-t+1}^{t} \text{SI}_{yi} + b_1 \log_e O_{yt} + b_2 \log_e T_{yt}$$
$$+ b_3 \log_e S_{yt} + \varepsilon_{yt}. \qquad (10)$$

Note that in equation (10), the parameters w_t, m_{0t}, and m_{1t} are not year specific. Therefore, without a loss of generality, we can choose a basis year such that these non-year-specific terms cancel, obtaining the following:

$$\log_e C_{yt} - \log_e C_{bt}$$
$$= (\log_e q_{ym,g} - \log_e q_{bm,g}) + \alpha(\log_e K_{yt} - \log_e K_{bt})$$
$$+ \beta(\log_e \text{Len}_{yt} - \log_e \text{Len}_{bt}) + (\log_e z_{y0} - \log_e z_{b0})$$
$$+ m_f \left(\sum_{i=0}^{t-1} \frac{H_{yi}}{w_i} - \sum_{i=0}^{t-1} \frac{H_{bi}}{w_i} \right)$$
$$+ \sum_{i=\tau-t+1}^{t} a_1(\text{OI}_{yi} - \text{OI}_{bi})$$
$$+ \sum_{i=\tau-t+1}^{t} a_2(\text{TI}_{yi} - \text{TI}_{bi}) + \sum_{i=\tau-t+1}^{t} a_3(\text{SI}_{yi} - \text{SI}_{bi})$$
$$+ b_1(\log_e O_{yt} - \log_e O_{bt}) + b_2(\log_e T_{yt} - \log_e T_{bt})$$
$$+ b_3(\log_e S_{yt} - \log_e S_{bt})$$
$$+ (\varepsilon_{yt} - \varepsilon_{bt}), \qquad (11)$$

where b denotes the basis year. This equation provides

TABLE 1.—Parameters used to develop a differenced bioeconomic model to account for the lagged effects of hypoxia on the North Carolina fishery for brown shrimp.

Parameter	Value	Function	Parameter source
L_∞	177.7	Von Bertalanffy growth function	McCoy (1968)
δ	−0.0104	Von Bertalanffy growth function	McCoy (1968)
ϕ	1.4866	Natural mortality rate	Minello et al. (1989)
ρ	−1.1163	Natural mortality rate	Minello et al. (1989)
ω	10.52×10^{-6}	Allometric function (weight)	Fontaine and Neal (1971)
η	2.94	Allometric function (weight)	Fontaine and Neal (1971)

a complete model structure describing how the environmental factors influence stock dynamics and harvest.

Estimates of the parameters in equations (3) and (4) for brown shrimp are available in the literature, though not necessarily specific to the North Carolina population (Table 1). With these two equations, we now can apply the model (equation 11) to empirical data to test the hypothesis that environmental variables, and in particular low DO, affect shrimp harvest.

Data source.—We used harvest data from the North Carolina Division of Marine Fisheries trip ticket program (http://www.ncfisheries.net/). Each dealer reports commercial landings information for each individual fishing trip, including the gear type, trip starting, and landing date, and price and quantity of landed fish and shrimp. From 1978 to 1993, North Carolina commercial landings information was collected on a voluntary basis. In 1994, the N.C. General Assembly mandated trip-level reporting of commercially harvested species. The brown shrimp harvest data used in this paper contain complete landings in the Neuse River and Pamlico Sound from 1999 to 2005 (Table 2), the period over which water quality has been continuously monitored in the Neuse River estuary.

We used water quality monitoring data collected by the U.S. Geological Survey from the Neuse River estuary (http://nc.water.usgs.gov/). Previous studies have documented that the Neuse River estuary experiences severe and recurring hypoxia during the summer months that leads to fish kills and other ecological effects (Paerl et al. 1998; Lenihan et al. 2001; Eby et al. 2005). The data consisted of 15-min sampling intervals of surface and bottom DO, temperature, salinity and other water quality variables at three moorings in the Neuse River from 1999 to 2005 (Figure 1). These data have been the basis for several water quality modeling efforts and other studies in the system (Borsuk et al. 2001; Stow et al. 2003). We took the average of the 15-min values each day over these three moorings as a daily measure of environmental conditions. Because shrimp are demersal and strongly associated with the bottom, we used bottom values for DO, temperature, and salinity (Table 2). We quantified the severity of hypoxia by calculating the number of days during which average bottom DO concentrations were below the specified threshold in each year from 1999 to 2005 (range of <2 mg/L is reported in Table 2; we also used ranges of <1.5 mg/L and <2.5 mg/L). The average number of hypoxic days over these 7 years was 61 d/year for range of less than 2 mg/L. For temperature and salinity conditions, the intolerable temperature threshold was defined as less than 4.4°C and greater than 32.2°C, and the intolerable salinity threshold was less than 5‰.

Similar water quality data were not available for Pamlico Sound, which may experience hypoxia, particularly near the mouths of major tributaries (Paerl et al. 2001). However, harvest of brown shrimp in the sound is more likely to be influenced indirectly by DO conditions in the tributaries. Therefore, hypoxia effects on growth, mortality or emigration of brown shrimp in the Neuse River and other tributaries may have important consequences for harvest in the Pamlico Sound. We used water quality data in the Neuse River estuary as a proxy for conditions in the major tributaries supplying the sound and then quantified the effects of hypoxia on shrimp harvest in both the Neuse River and the Pamlico Sound.

To test the hypothesis that environmental factors influence shrimp harvest using equation (11), we needed an estimate of the initial number of brown shrimp in each year. The North Carolina Division of Marine Fisheries conducts annual monitoring surveys for shrimp and finfish in early May to June. The shrimp survey (program 510) samples multiple stations throughout the Albemarle and Pamlico Sound estuarine system and its tributaries during the last week of May or first week of June. The survey is designed to provide information on annual recruitment to set opening dates for the fishery. One-minute tows are conducted during daytime with a 3.2-m bottom trawl (6.4-mm mesh in the body and 3.2-mm mesh in the cod end). The estuarine trawl survey (program 120) samples about 100 fixed stations in shallow (<2 m) nursery habitats from Roanoke Island through Cape Fear River. One-

TABLE 2.—Summary of brown shrimp fishery statistics for the Neuse River and Pamlico Sound for all years of the study combined and for each year individually. Yearly Neuse River dissolved oxygen, water temperature, and salinity statistics are also provided for reference; N is the number of observations.

Variable	N	Mean	SD	Minimum	Maximum	1999	2000
Neuse River							
Catch/trip (lb)	2,245	308.4	579.1	4.0	7,985.6		
Trip days	2,245	1.9	1.3	1.0	10.0		
Vessel length (ft)	2,211	37.0	13.6	15.0	80.0		
Pamlico Sound							
Catch/trip (lb)	11,690	1,524.7	1,808.7	1.0	22,097.0		
Trip days	11,690	3.5	3.9	1.0	366.0		
Vessel Length (ft)	11,651	51.9	18.1	12.0	91.0		
Catch (lb)							
Neuse River						17,915	193,960
Pamlico Sound						1,208,294	5,096,432
Water quality							
Dissolved oxygen (mg/L)						5.28	6.03
Temperature (°C)						17.39	19.49
Salinity (‰)						8.38	8.35
Intolerable days							
Dissolved oxygen < 2 mg/L						50	38
Temperature < 4.4°C or > 32.2°C						0	0
Salinity < 5‰						78	51

minute tows are conducted during daytime with a 3.2-m otter trawl (6.4-mm mesh in the wings and body and 3.2-mm mesh in the cod end; West et al. 2006). These surveys record shrimp species, catch per unit effort (CPUE), and total length at each station. Additional details on the survey design can be found in West et al. (2006) and West and Wilson (1994). We calculated the averaged CPUE of brown shrimp from each of these surveys and then averaged across the two surveys in each year to construct an annual index of initial brown shrimp abundance for each year from 1999 to 2005.

We specified the 80th day of the calendar year as the starting point for the model, which is about the time of larval ingress and subsequent settlement into juvenile nursery habitats (Lassuy 1983; Larson et al. 1989). In the estimation, we started with a full model including all variables and then used a backwards selection procedure to eliminate statistically insignificant variables based on F-tests. In addition to the environmental (oxygen, temperature, salinity) and fishing effort (trip days, vessel length) variables, we also considered the effects of month (July to November), gear, and their interaction. We only considered two types of gear in our model (shrimp trawl, others) because 91% of the brown shrimp harvested were taken by shrimp trawl. Month and the interaction of gear and month were used to capture the effect of catchability on shrimp harvest ($q_{ym,g}$ in equation 11). The variables in the model were each differenced between the current year and a basis year. We chose 2000 as the basis year, but choosing a different basis year would not affect the statistical results. We estimated the parameters of the differenced model with a 60-d lagged hypoxia effect separately for

the Neuse River and the Pamlico Sound. We chose 60 d because this is probably the minimum period during which shrimp are present in the estuary (Larson et al. 1989). We evaluate this assumption in a later section (see Robustness of Findings).

Results

Empirical Results for the Differenced Model

The fit of our regression model (equation 11) indicated that the parameter estimates for the number of trip-days and vessel length were positive for both the Neuse River and Pamlico Sound, which is consistent with our expectation that increased fishing effort leads to increased harvest (Tables 3, 4). The parameter estimate for total harvest ("accumulated harvest" in Table 3), which represents fishing mortality, was negative in both models. This is also consistent with our expectation that fishing reduces the abundance of the stock. Average daily temperature in the estuary was never outside of the tolerable range (4.4–32.2°C; Table 2), so there was no associated parameter estimate for the binary effect of temperature. The effect of salinity was positive and significant for the Neuse River, indicating higher harvests when salinities were high; this was not true for the Pamlico Sound. For the variables representing the continuous effects of environmental factors on shrimp harvest, which describe contemporaneous conditions that are not cumulative over time, no variable was significant in either the Neuse River or the Pamlico Sound models.

The effect of dissolved oxygen on shrimp harvest (accumulated oxygen index, Table 3) was negative and significant for both the Neuse River and the Pamlico

TABLE 2.—Extended.

Variable	2001	2002	2003	2004	2005	Mean
Neuse River						
Catch/trip (lb)						
Trip days						
Vessel length (ft)						
Pamlico Sound						
Catch/trip (lb)						
Trip days						
Vessel Length (ft)						
Catch (lb)						
Neuse River	18,063	162,860	99,077	73,550	108,228	96,236
Pamlico Sound	2,495,106	4,618,086	1,991,780	1,602,778	5,475,80	2,508,579
Water quality						
Dissolved oxygen (mg/L)	5.46	5.89	5.96	5.52	6.52	5.81
Temperature (°C)	18.43	18.94	17.64	18.01	17.63	18.22
Salinity (‰)	12.21	15.29	5.25	7.94	7.70	9.30
Intolerable days						
Dissolved oxygen < 2 mg/L	80	43	69	87	57	61
Temperature < 4.4°C or > 32.2°C	0	0	0	0	0	0
Salinity < 5‰	26	2	224	100	80	80

TABLE 3.—Estimated parameters of the differenced models of the effects of hypoxia on the brown shrimp fishery in the Neuse River ($n = 297$; $R^2 = 0.3869$) and Pamlico Sound ($n = 549$; $R^2 = 0.6062$). All variables are the differences between the values for the current year and those for 2000, with a 60-d lag. The estimation used backward selection to eliminate statistically insignificant variables (ns) based on F-tests; all of the remaining variables are significant at the 2% level. See text for additional details.

	Neuse River			Pamlico Sound		
Differenced variable	Parameter estimate	SE	P	Parameter estimate	SE	P
Intercept	−0.22601	0.09228	0.0149	−0.38668	0.05173	<0.0001
Gear × month 7			ns			ns
Gear × month 8			ns			ns
Gear × month 9	−0.63218	0.23135	0.0067			ns
Gear × month 10			ns			ns
Gear × month 11			ns	1.22423	0.29705	<0.0001
Initial abundance			ns			ns
Log_e(trip days)	1.11913	0.09397	<0.0001	0.16995	0.04304	<0.0001
Log_e(vessel length)	0.94943	0.17746	<0.0001	2.61114	0.10939	<0.0001
Accumulated oxygen index	−0.01343	0.00535	0.0126	−0.01014	0.0029	0.0005
Accumulated salinity index	0.00804	0.00282	0.0047			ns
Accumulated harvest	-8.50×10^{-8}	3.05×10^{-8}	0.0056	-2.06×10^{-9}	7.69×10^{-10}	0.0077
Log_e(oxygen)			ns			ns
Log_e(temperature)			ns			ns
Log_e(salinity)			ns			ns

TABLE 4.—Actual harvests of brown shrimp in the Neuse River and Pamlico Sound and predicted reductions due to hypoxia.

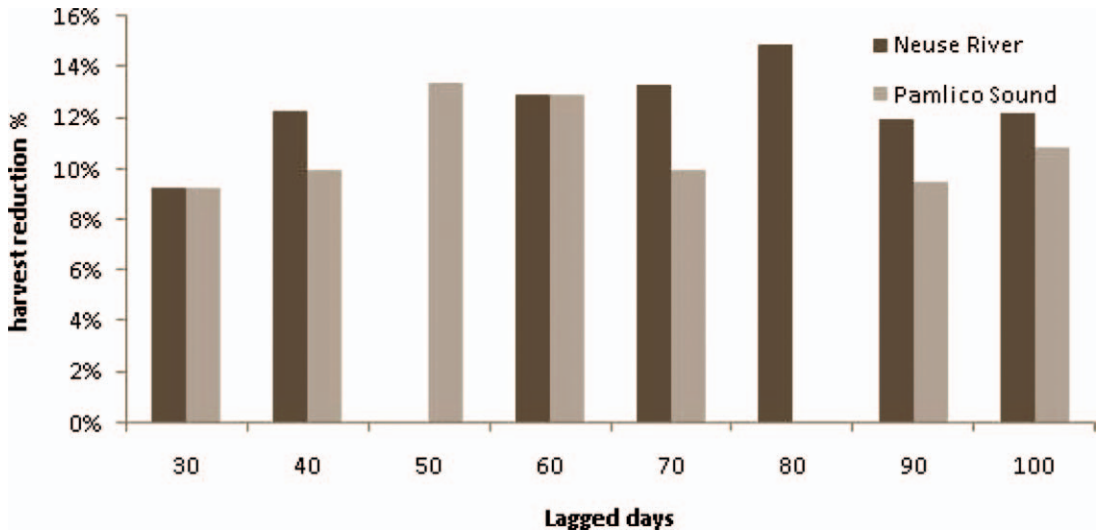|	Neuse River		Pamlico Sound	
Variable	Weight (lb)	Value ($)	Weight (lb)	Value ($)
Actual harvest				
(7 years total)	695,061	1,467,358	17,823,727	55,867,879
Predicted harvest reduction due to hypoxia				
(7 years total)	102,654	220,887	2,631,971	8,645,167
Reduced harvest due to hypoxia (%)	12.87	13.08	12.90	13.43

FIGURE 2.—Reduction in the harvest of brown shrimp in the study area attributable to hypoxia, as projected by a differenced model with different lags. In almost all cases, the hypoxia variable was negative and statistically significant.

Sound models. For the Neuse River model, the coefficient was −0.01343, which means that 1 d of hypoxia leads to a decrease of 1.343% of the total shrimp harvest in the Neuse River for each of the following 60 d. Similarly, for Pamlico Sound 1 d of hypoxia leads to a decrease in harvest of 1.01% for each of the following 60 d. Using these marginal effects, we then can measure the total annual hypoxia effects.

If we compare the observed pattern of hypoxia in the Neuse River to a system with no hypoxia, then the 1999–2005 total decrease in harvest attributable to hypoxia is 46,605 kg or 12.87% of the total harvest over the 7-year period (Table 4). We multiplied the harvested weight of shrimp by the weighted average daily price over different shrimp sizes (calculated by dividing the total shrimp value [US$] on day t by the total shrimp catch [lb] on the same day) to estimate the annual decrease in revenue to the shrimp fishery due to hypoxia. We estimate a decrease of about US$32,000, which is 13.08% of the average Neuse River revenue over the 7-year period (all the economic values in this paper were converted to 1999 U.S. dollars using the consumer price index for all urban consumers). We assume the quantity changes do not affect price because North Carolina shrimp harvest constitutes a very small percentage (roughly 0.63%) of a large global market (FAO 2007). Similarly, for the Pamlico Sound there is a decrease of 12.9% of the total catch due to hypoxia, which translates into a value of $1,240,000 or 13.43% of the average revenue from 1999 to 2005.

Robustness of Findings

The results from our differenced bioeconomic model suggest that hypoxia can have substantial economic consequences for the North Carolina brown shrimp fishery. In this section, we address the robustness of our findings by varying the lag length in the differenced bioeconomic model, which determines the time over which hypoxia effects are accumulated. To check how sensitive our 60-d differenced model results are to the hypoxia avoidance threshold (<2 mg/L), we ran models with different hypoxia thresholds. We then developed and analyzed two different model types, a nondifferenced model and a polynomial distributed lag model.

Differenced model with different day lags.—The previous results show that there is a significant effect of hypoxia on shrimp harvest in the Neuse River and the Pamlico Sound when environmental effects are accumulated over 60 d. Figure 2 reports the results from the same model but with the number of lagged days set from 30 to 100 d. There were statistically significant effects of hypoxia on shrimp harvest in the Neuse River for all but the 50-d lag. The coefficients for the hypoxia effect on shrimp harvest are all negative, suggesting a trend in the Neuse River toward decreased shrimp harvest with increasing severity of hypoxia. Similarly, there were significant negative effects of hypoxia on shrimp harvest in Pamlico Sound at all lags except for 80 d. The reduction in harvest in the Neuse River based on parameter estimates from models with different lags varied from 9.23% to 14.92%, which is
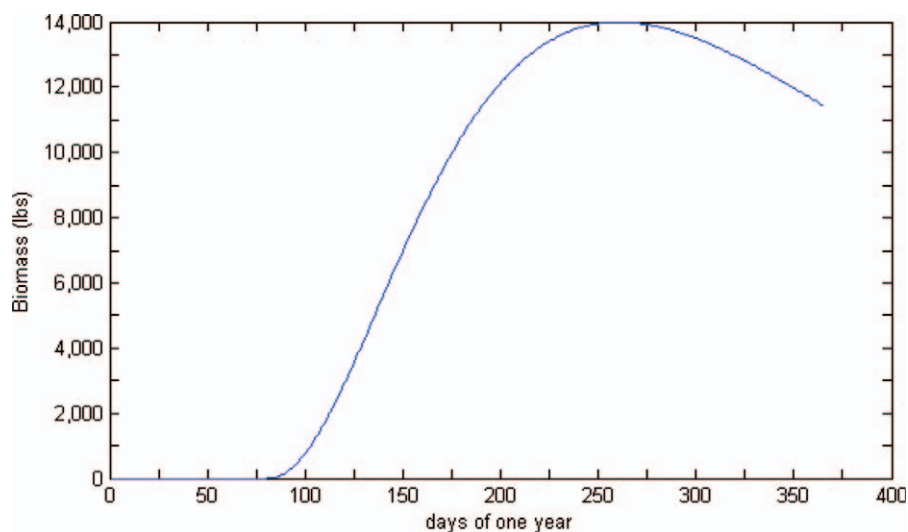
FIGURE 3.—Estimated seasonal biomass of brown shrimp in the Neuse River and Pamlico Sound with no harvest and no hypoxic effects (based on the population parameters in Table 1 and an initial population size of 1 million).

of similar magnitude to that at 60-d lag (12.87%). For the Pamlico Sound model, the reduction in harvest ranged from 9.21% to 13.41%, which again was similar to that at 60-d lag (12.90%). Therefore, hypoxia effects on shrimp harvest are robust to variation in the duration over which these effects are accumulated in the model.

Differenced model with different hypoxia thresholds.—To check the robustness of the differenced model to the hypoxia threshold, we ran models for the Neuse River and Pamlico Sound using less than 1.5 mg/L and less than 2.5 mg/L as two alternative intolerable oxygen ranges, while keeping other assumptions the same as in the 60-d differenced model. We found that for the Neuse River model, the hypoxia effect was significant with the 1.5 mg/L threshold but not significant with 2.5 mg/L threshold. For the Pamlico Sound model, the hypoxia effects were significant for both ranges. The coefficients were similar in magnitude to those from the 60-d differenced model. The reduction in harvest was also similar. We estimated an 11.43% decrease in harvest in the Neuse River with the 1.5 mg/L threshold and a decrease in harvest in the Pamlico Sound of 11.41% with the 1.5 mg/L and 13.26% for the 2.5 mg/L thresholds.

Nondifferenced model.—The differenced model (equation 11) allowed us to simplify the original model (equation 10) by omitting terms describing the shrimp growth and loss rate (mortality and emigration, which are not well known). If these biological parameters were known, then the nondifferenced version of the model (equation 10) could be fit. The advantage of the nondifferenced model is that we can use more detailed information on shrimp harvest that is specific to each trip j on day t instead of the average catch on each day. We developed a nondifferenced form of the model by using a natural mortality rate to represent shrimp loss. Thus, equation (10) can be rewritten as

$$
\begin{aligned}
\log_e C_{ytj} = {} & \log_e q_{ym,g} + \alpha \log_e K_{ytj} + \beta \log_e \text{Len}_{ytj} \\
& + \log_e z_{y0} + (\log_e w_t - m_{0t} - m_{1t}) m_f \sum_{i=0}^{t-1} \frac{H_{yi}}{w_i} \\
& + a_1 \sum_{i=\tau-1+1}^{t} \text{OI}_{yi} + a_2 \sum_{i=\tau-1+1}^{t} \text{TI}_{yi} \\
& + a_3 \sum_{i=\tau-1+1}^{t} \text{SI}_{yi} + b_1 \log_e O_{yt} \\
& + b_2 \log_e T_{yt} + b_3 \log_e S_{yt} + \varepsilon_{ytj}.
\end{aligned}
\tag{12}
$$

Equation (12) is identical to equation (10) except that the catch (C), number of trip days (K), and vessel length (Len) are specific to each fishing trip. Natural mortality can then be modeled as a function of shrimp length, that is,

$$
m_{0t} = \int_0^t \phi L(s)^\rho \, ds,
\tag{13}
$$

where $L(t)$ is shrimp length (modeled by equation 3) at time t, and ϕ and ρ are parameters. The daily instantaneous natural mortality rate of shrimp (Δm_{0t}) decreases as shrimp increase in body size ($\phi > 0$ and $\rho < 0$). Estimates of ϕ and ρ in equation (13) are taken from Minello et al. (1989; Table 1). Figure 3 shows the temporal dynamics of shrimp biomass with no hypoxia,

TABLE 5.—Estimated parameters of nondifferenced models of the effects of hypoxia on the brown shrimp fishery in the Neuse River ($n = 2,186$; $R^2 = 0.5235$) and Pamlico Sound ($n = 11,503$; $R^2 = 0.6286$). These models, which serve as checks of the robustness of those shown in Table 3, assume deterministic population dynamics based on the parameters in Table 1 and no emigration; ns = not significant.

	Neuse River			Pamlico Sound		
Variable	Parameter estimate	SE	P	Parameter estimate	SE	P
Intercept	−6.77884	2.20338	0.0021	−3.02186	0.5775	<0.0001
Month 5	1.99866	0.65568	0.0023	1.59276	0.14744	<0.0001
Month 6	2.78769	0.53748	<0.0001	2.11061	0.10331	<0.0001
Month 7	2.18377	0.54421	<0.0001	1.45981	0.26284	<0.0001
Month 8	2.06308	0.55043	0.0002	1.66689	0.09791	<0.0001
Month 9	1.33622	0.54405	0.0141	1.43574	0.10027	<0.0001
Month 10			ns	0.89198	0.10414	<0.0001
Gear × month 7	0.33852	0.10104	0.0008	0.75958	0.24524	0.0018
Gear × month 8	−0.41178	0.13199	0.0018			ns
Initial abundance	0.46926	0.12262	0.0001	0.19393	0.03343	<0.0001
$\log_e$(trip days)	0.98428	0.03638	<0.0001	0.62187	0.01484	<0.0001
$\log_e$(vessel length)	1.22298	0.05503	<0.0001	2.00255	0.02629	<0.0001
Accumulated oxygen index	−0.01682	0.0019	<0.0001	−0.02164	0.00091242	<0.0001
Accumulated salinity index	0.01223	0.0025	<0.0001			ns
Accumulated harvest	$−8.32 \times 10^{-8}$	1.49×10^{-8}	<0.0001	$−4.31 \times 10^{-9}$	2.93×10^{-10}	<0.0001
$\log_e$(oxygen)	0.21609	0.05739	0.0002			ns
$\log_e$(temperature)			ns			ns
$\log_e$(salinity)			ns			ns

no harvest, and the dynamics driven by the natural mortality rate from equation (13) and weight dynamics (equation 4).

The only remaining unknown parameter in the nondifferenced model (equation 12) is the migration rate m_{1t} (for the Neuse model, migration rate is the rate of emigration from the Neuse River to the Pamlico Sound and, for the Pamlico model, from the Pamlico Sound to the ocean). Emigration rates of shrimp from estuarine systems are not well documented and are probably highly variable across species and ecosystems. Therefore, we fit the nondifferenced model assuming the migration rate was zero. Although this assumption will induce some unknown bias in the parameter estimates, the results are still useful for making qualitative comparisons of the magnitude of hypoxia effects on shrimp harvest between the non-differenced and differenced models.

Based on the nondifferenced model, hypoxia effects on shrimp harvest in the Neuse River and the Pamlico Sound were both negative and significant (Table 5). Compared with the differenced model, the magnitude of the hypoxia effect was larger in both the Neuse and Pamlico models (−0.01682 versus −0.01343 for the Neuse River and −0.02164 versus −0.01014 for the Pamlico Sound), indicating that our initial results from the differenced model may be conservative. This difference in the magnitude of the hypoxia effect between the two models may be due to omission of the migration parameter in the nondifferenced model so that any effect of hypoxia on shrimp emigration is absorbed in part by the accumulated effect of hypoxia. Alternatively, the differenced model may underestimate the magnitude of the hypoxia effect, if hypoxia induces emigration from the system over that in the absence of hypoxia. Both models have potential sources of bias but yield qualitatively similar results.

Polynomial distributed lag model.—The differenced model assumed that the marginal effect of hypoxia on shrimp harvest was the same over each day of the chosen number of lagged days. To relax this assumption, we used a polynomial distributed lag (PDL) to model the lagged effect of hypoxia, allowing different marginal effects for each day. Equation (11) becomes

$$
\begin{aligned}
\log_e & C_{yt} - \log_e C_{bt} \\
= {} & (\log_e q_{ym,g} - \log_e q_{bm,g}) + \alpha(\log_e K_{yt} - \log_e K_{bt}) \\
& + \beta(\log_e \text{Len}_{yt} - \log_e \text{Len}_{bt}) + (\log_e z_{y0} - \log_e z_{b0}) \\
& + m_f \left(\sum_{i=0}^{t-1} \frac{H_{yi}}{w_i} - \sum_{i=0}^{t-1} \frac{H_{bi}}{w_i} \right) \\
& + \sum_{i=\tau-t+1}^{t} a_{1i}(\text{OI}_{yi} - \text{OI}_{bi}) \\
& + \sum_{i=\tau-t+1}^{t} a_{2i}(\text{TI}_{yi} - \text{TI}_{bi}) \\
& + \sum_{i=\tau-t+1}^{t} a_{3i}(\text{SI}_{yi} - \text{SI}_{bi}) + b_1(\log_e O_{yt} - \log_e O_{bt}) \\
& + b_2(\log_e T_{yt} - \log_e T_{bt}) + b_3(\log_e S_{yt} - \log_e S_{bt}) \\
& + (\varepsilon_{yt} - \varepsilon_{bt}). \quad (14)
\end{aligned}
$$

Note that now the marginal effects of each

TABLE 6.—Akaike information criterion values for polynomial distributed lag models for the Neuse River and Pamlico Sound with different degrees of the polynomial. The best model for each water body (asterisks) was used for comparison with the differenced model.

Degree of polynomial	Neuse River	Pamlico Sound
1	823.49*	1,286.57*
2	825.52	1,288.99
3	828.14	1,290.07
4	831.17	1,292.43
5	833.19	1,289.43
6	830.20	1,293.15
7	832.28	1,295.94
8	835.00	1,297.68
9	838.77	1,296.35
10	841.49	1,299.24
11	845.28	1,299.36
12	848.83	1,301.12
13	847.91	1,304.22
14	849.87	1,303.86
15	849.17	1,306.5
16	850.87	1,300.14

environmental factor on shrimp harvest can vary on each day (a_i in equation 14). The a_i can then be modeled with orthogonal polynomials as

$$a_i = \rho_0 + \sum_{k=1}^{d} \rho_k f_k(i), \qquad (15)$$

where ρ_1–ρ_d are the coefficients to be estimated, d ($\leq \tau$) is the degree of the polynomial, and $f_k(i)$ is a polynomial of degree k in the lag day i (see Judge et al. 1988 for a detailed discussion of the PDL).

To compare results from the PDL model with our earlier results we set $\tau = 60$, the number of lagged days in the differenced and nondifferenced models above. We fit the differenced PDL model with different degrees for the polynomials ($d = 1$–16) and used the Akaike information criterion (AIC) to choose the best model (Table 6). The best models for both the Neuse River and the Pamlico Sound had a polynomial of degree one ($d = 1$). We report the PDL model results in Table 7. As expected, the coefficients for trip days and vessel length were positive and significant. The marginal daily effects of hypoxia on shrimp harvest were below zero, which is consistent with our earlier result of negative effects of hypoxia on harvest in the Neuse River and the Pamlico Sound. Based on the PDL model, the average potential loss of shrimp harvest for the Neuse River that is attributable to hypoxia was 15.47% (7-year range, 6.94–35.18%). For the Pamlico Sound, the average loss was 20.56% (7-year range, 12.75–29.54%; Figure 4). The predicted effect of hypoxia from the PDL model was larger than that of the differenced model, but the estimates were of similar magnitude. The PDL model probably overestimated the hypoxia effect somewhat because some of the marginal daily effects in the PDL model were negative but not significant.

Discussion

We developed a bioeconomic model to assess the economic effect of hypoxia on the North Carolina brown shrimp fishery. In the Neuse River, a major North Carolina tributary to a larger estuarine system, model estimates indicated about a 12.87% decrease in shrimp harvest relative to a pristine system with no hypoxia. Model estimates for the Pamlico Sound, which does not experience severe hypoxia but is the primary fishing ground for shrimp that use riverine tributaries as nursery habitat, also indicated about a 12.90% decrease in harvest attributable to hypoxia. The decline in harvest due to hypoxia equates to a loss of $32,000 per year in the Neuse River fishery and about $1,240,000 per year in the Pamlico Sound fishery, the difference being due to the much larger size of the Pamlico Sound fishery (i.e., about 50.9% of the 1999–2005 statewide harvest). Our results were robust to different assumptions about the duration of temporal lags between when hypoxia effects occur and when they are expressed in the fishery, as well as several alternative model structures (differenced, nondifferenced, and polynomial distributed lags) with different underlying assumptions. In fact, permutations of the model indicated that harvest losses attributable to hypoxia range from 8% to 35%, suggesting our primary results (12.9%) are conservative.

A major contribution of this paper is the integration of trip-level catch and effort data (i.e., microdata from a commercial fishery with high resolution [daily]) and continuous water quality monitoring data to capture the complex relationships between environmental factors and their lagged effects on fishery harvests. Compared with previous approaches, our model makes use of detailed temporal and spatial information, which we argue is important for evaluating the economic effects of hypoxia, particularly in dynamic systems where environmental conditions, fishing effort, and harvest are changing through time. Hypoxia influences shrimp harvest, both through effects on processes underlying production such as growth and mortality (including effects on juveniles before they are subject to fishing mortality) and on processes influencing catchability (e.g., emigration, avoidance behavior). Therefore, it is necessary to model these bioeconomic pathways throughout the life history. Our model takes these complexities into account and, thus, is able to evaluate the economic effects of hypoxia on the fishery via a highly disaggregated fishery dataset.

Our model is only able to measure the net effect of

TABLE 7.—Estimated parameters of the first-degree-polynomial distrubted lag models of the effects of hypoxia on the brown shrimp fishery in the Neuse River ($n = 297$; $R^2 = 0.4416$) and Pamlico Sound ($n = 549$; $R^2 = 0.6232$). All variables are differenced; all environmental variables are lagged 60 d. According to these models, hypoxia reduces the harvest in the Neuse River by 15.47% in terms of weight and 15.79% in terms of value; the corresponding reductions in Pamlico Sound are 20.56% and 21.32%.

Differenced variable[a]	Neuse River			Pamlico Sound		
	Parameter estimate	SE	P	Parameter estimate	SE	P
Intercept				−1.0133	1.3998	0.4694
DO_{ind}**0	−0.1335	0.045	0.0033	−0.1464	0.0326	<0.0001
DO_{ind}**1	−0.0249	0.0557	0.6552	0.0389	0.032	0.2239
Sal_{ind}**0	0.0172	0.0684	0.802	−0.027	0.0271	0.3204
Sal_{ind}**1	0.2586	0.0655	<0.0001	0.1137	0.0378	0.0028
Gear × month 6	0.118	0.2134	0.5806	1.0273	1.417	0.4688
Gear × month 7	−0.004601	0.1801	0.9796	0.8304	1.4132	0.557
Gear × month 8	0.0259	0.1697	0.8787	0.6922	1.4118	0.6241
Gear × month 9	−0.7698	0.2426	0.0017	0.5427	1.4091	0.7003
Gear × month 10				0.3983	1.409	0.7775
Gear × month 11				1.9129	1.4388	0.1842
Initial abundance	0.1252	0.3219	0.6977	−0.425	0.1522	0.7801
Log_e(trip days)	1.078	0.0938	<0.0001	0.1645	0.0428	0.0001
Log_e(vessel length)	0.8748	0.1784	<0.0001	2.6055	0.1108	<0.0001
Accumulated harvest	-6.17×10^{-8}	3.76×10^{-8}	0.0997	-3.89×10^{-9}	1.20×10^{-9}	0.0013
Log_e(oxygen)	−0.0645	0.0238	0.0072	−0.008917	0.0159	0.5745
Log_e(temperature)	−2.7802	1.51	0.0666	−0.3519	0.6393	0.5823
Log_e(salinity)	−0.1717	0.1565	0.2738	−0.035	0.0503	0.4871

[a] **0 and **1 refer to polynomials of degrees 0 and 1, respectively.

hypoxia on the fishery and cannot distinguish among various underlying causal mechanisms. For example, hypoxia can lead to reduced growth and survival due to direct exposure to low DO (Miller et al. 2002; Stierhoff et al. 2009). Organisms that avoid hypoxia may also experience reduced growth and survival via a number of indirect mechanisms (Breitburg 2002; Eby et al. 2005). In either case, decreases in abundance and biomass due to hypoxia may influence subsequent harvest by the fishery. Hypoxia may also alter spatial distributions or emigration rates of shrimp, thus altering catchability by the fishery. For example, Craig and Crowder (2005) showed that brown shrimp aggregate at high density near the edges of hypoxic zones, and they suggested that catchability in the commercial shrimp trawl fishery may be locally enhanced in these regions. Alternatively, hypoxia may enhance dispersion leading to decreases in catchability. Although our results indicate a significant economic effect of hypoxia on the North Carolina shrimp fishery, additional research is necessary to identify the particular ecological and fishery interactions that contribute to this effect.

In this paper, we provide the first empirical dynamic bioeconomic assessment of hypoxia-induced declines in harvest and revenues in a commercial fishery using microdata. Studies that use aggregated data typically fail to detect statistically significant economic impacts of hypoxia on fisheries (Diaz and Solow 1999). Of the papers that use microdata, Massey et al. (2006) is the

most similar case to ours. They analyzed the economic consequences of hypoxia for the summer flounder recreational fishery in a tributary of Chesapeake Bay by using a bioeconomic simulation model that considered the dynamic effects of low DO. They found that recreational catches could potentially increase by approximately 2% if the number of hypoxic days was reduced by 50% in the study region (a modest amount). If the number of hypoxic days were reduced by 50% in all of Maryland's coastal bays, however, they find a potential 20% increase in harvest. Our finding—a potential 12.9% increase in brown shrimp harvest in the North Carolina commercial fishery if hypoxia in the Neuse River is eliminated—seems large. This river is just one of several major tributaries that contribute to the shrimp fishery; however, it is the largest tributary to the system, suggesting it may be an important source of recruits to the fishery, and it is morphologically similar to the other major tributary to the north, the Pamlico River, which is also known to experience hypoxia (Stanley et al. 1992). If shrimp year-class strength and the severity of hypoxia are spatially correlated across riverine tributaries (perhaps due to regional patterns in climatic conditions and freshwater and nutrient loading), then environmental conditions in the Neuse River may reflect broader patterns influencing the fishery. From this perspective, the magnitude of our results appear comparable to those of Massey et al. (2006).

It is important to note that our analysis compared the actual shrimp harvest to a scenario with no hypoxia for
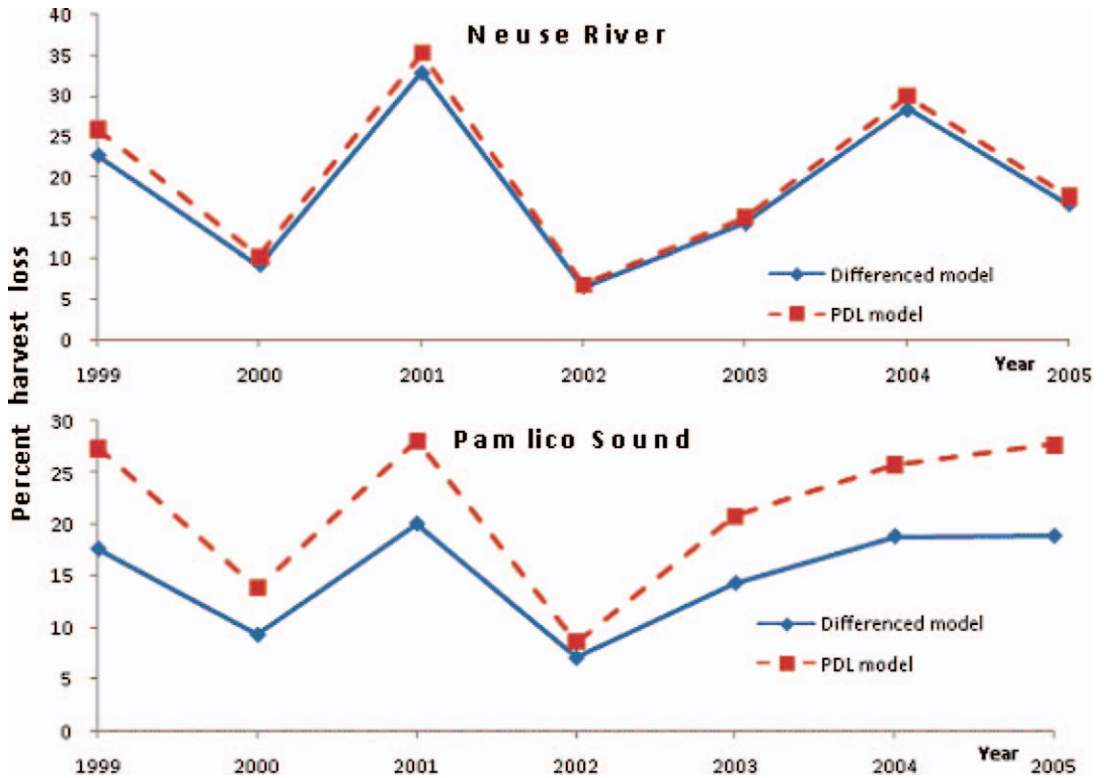
FIGURE 4.—Percentage losses in revenue due to hypoxia (relative to the baseline case of no hypoxia) in the Neuse River (upper panel) and Pamlico Sound (lower panel), 1999–2005. The differenced model is our main result, and the polynomial distributed lag (PDL) model serves as a robustness check.

one whole year (DO is at least 2 mg/L). To conduct a complete cost–benefit analysis, it would be necessary to calculate the nonfishery benefits of reduced hypoxia and benefits to other fisheries, and juxtapose those against the costs of reducing nutrient pollution to achieve improved oxygen conditions. Our result of $1,240,000 in lost annual revenues to the Pamlico Sound fishery would amount to $27,560,000 total lost revenues over time (in perpetuity), based on a 4.5% real discount rate. If we assume no behavioral changes in the fishery (a strong assumption), we can equate this revenue loss to lost fishery rents. In a simulation model, Smith (2007) found that a 30% reduction in nutrient loading to the Neuse River would lead to $700,000 to $6,400,000 present-value rent increases for the blue crab fishery. Our results are not directly comparable for a number of reasons: the biology of blue crab is different from that of brown shrimp, the industry structures are different, a 30% reduction in nutrients would not necessarily eliminate hypoxia, and the blue crab model allows for entry to the fishery. With these caveats in mind, the economic gains from reducing nutrient pollution include the gains that

accrue to both of these important commercial fisheries. By way of comparison, the perpetuity cost of reducing nutrient pollution would range from $155,000,000 to 266,000,000, a range based on converting annual 1994 dollars from Schwabe (2001) to a perpetuity value in 1999 dollars. Therefore, gains in fishery rents appear to pay for a small fraction of the costs of reducing nutrient pollution. Benefits from other sources, such as consumer gains from lower seafood prices, gains to other fisheries (direct and indirect from increased availability of shrimp for foraging), and nonmarket benefits, would need to be substantial in order to justify dramatic policy actions to reduce nutrient pollution based on cost–benefit analysis applied to individual fisheries alone.

Our model provides a road map for resolving spatiotemporal lagged effects of habitat degradation on fisheries. We calculated the economic effects of hypoxia by analyzing the dynamics of catch data in both the nursery and in the adjacent primary fishing ground, noting that many of the economic consequences result from how juvenile brown shrimp are affected in the nursery grounds before the fishing season.

Linking the nursery habitat and fishing grounds requires making some assumptions, but establishing causality via other approaches is likely to present similar challenges. Many fished species spend critical life stages in habitat that differs from where they are fished, and tracking larvae and juveniles from nursery areas to fishing grounds is notoriously difficult. Because fishing effort, fleet composition, and other environmental factors are in flux, the effects of habitat degradation will be difficult to detect given the noise inherent in aggregate fisheries data. We demonstrate that controlling for dynamic factors in finely resolved fishery microdata provides a structure for extracting this noisy signal.

On a broader level, our analysis illustrates a useful approach for providing input into ecosystem-based fishery management. Though we focus on a specific case of intermittent hypoxia in a moderate-sized fishery, our model could be adapted to study potentially more economically consequential cases, such as the effects of the Gulf of Mexico dead zone on Gulf shrimp fisheries. Beyond shrimp, adapting the model to fisheries with strong stock–recruitment relationships strengthens the case for dynamic modeling of environmental quality but introduces new challenges that require further research. In particular, the population dynamics become a function of the entire history of environmental stress. Perhaps more importantly, econometric modeling that links water quality data and fishing microdata can be used to study a wide range of ecosystem impacts on fisheries and economic consequences. A similar model to the one in our paper could analyze the economic consequences of toxic algal blooms, changes in freshwater supply to estuaries (e.g., due to drought or upstream diversions), sedimentation, or other habitat disturbances. The key ingredients in all of these cases would be (1) water quality data with sufficient temporal resolution to address lags in responses of fishery productivity to environmental changes, (2) fishing microdata that allows the analyst to control for changing fleet composition over time, such as the number of fishing trips by gear type and vessel size, and (3) a bioeconomic link that connects the two spatially. These ingredients are probably present for many managed U.S. fisheries and elsewhere, which increasingly require spatially detailed logbooks and vessel monitoring systems, trip landings tickets, and observer coverage. Econometric modeling of fishery-dependent data is not a panacea, but it offers a useful empirical approach for translating the effects of environmental degradation into economic terms that can be used to help inform policy decisions. Similar efforts to integrate water quality and fishery microdata in an econometric modeling framework could be a fruitful way to explore many other ecosystem impacts on fisheries.

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