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Will Overfishing and Proposed Mississippi River Diversions Imperil Louisiana Oyster Fisheries? Commentary and Review

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Two recent articles based on oyster landings have challenged the prevailing wisdom about the most important factors controlling Louisiana oyster production. One article concludes that the northern Gulf industry (principally Louisiana) will collapse based on overfishing; the second concludes that the addition of freshwater through diversions could be harmful to production. These findings are not supported by the literature or our statistical analysis of the landings data. In an effort to put into perspective the complexity of the factors affecting oyster production in the northern Gulf of Mexico, several areas of the oyster literature are reviewed, including (1) hysteresis, (2) the heterogeneous needs of different oyster ages, and (3) the geographic distribution of Gulf oyster populations (some including statistical interpretations). We conclude that Kirby's (2004) prediction of failure of the Gulf oyster fishery as a result of the danger of current levels of fishing approaching overfishing is exaggerated. We further conclude that Turner's (2006) data do not support his thesis that diversions are at least unjustified, if not harmful to overall oyster production.

INTRODUCTION

A claim of impending environmental damage in oyster reefs (Beck et al., 2009) is an example of a trend of negative prognostications related to the future of fisheries. The assessment of Beck et al. concerning the risk of shellfish reefs in the northern Gulf of Mexico did not include data from Louisiana, the single largest oyster fishery in the Gulf. This fact alone leads one to question the credibility of their conclusions. Kirby (2004) presumed that patterns of oyster overfishing predict an impending failure of the most productive Gulf of Mexico areas, principally Louisiana. Rothschild et al. (1994) concluded that intense fishing pressure was the main cause of the decline of eastern oyster production in Chesapeake Bay. In a similarly negative prediction, Turner (2006) concluded that oyster landings are inversely related to freshwater inflow and that proposed diversions of freshwater would be unjustified, if not injurious to oysters, conclusions that conflict with those long held by professional oystermen and oyster biologists (Perret and Chatry, 1988). In fact, increased oyster production with freshwater inflow was called a ''rule of thumb'' by Powell et al. (2003; and cited by Turner 2006).

The principal success of the Louisiana Eastern oyster (*Crassostrea virginica*) program has been attributed to the continuing production of seed oysters (Perret and Chatry, 1988). Utilizing the strategy of producing seed oysters to maintain and improve oyster landings, oystermen have long recognized the importance of freshwater to subsequent oyster production (Dugas et al., 1997). This view had not been previously questioned until the appearance of Turner's (2006) conclusion, based on his model of 54 yr of river discharge data and oyster landings in five major estuaries of the Gulf Coast. As Turner noted, his is a contrary view that could revolutionize the basis of our understanding oyster production.

We analyzed the Louisiana landings relative to freshwater and other factors as applied to the conclusions of two articles, those of Kirby (2004) and Turner (2006). Kirby's prediction is based on the evidence from four historic events (first oyster laws, beginning of importation of seed, harvesting peaks, and the appearance of mechanical dredging). Turner's model of an inverse relationship between landings and freshwater flow is also analyzed. While we agree that even the most established ideas should be open to revision, particularly in order to clarify ideas, we believe there should be thorough analyses of these propositions. The discussion of differing points of view can only contribute positively to the oyster literature.

Fishery landings are a source of a long-term data set that provides a reasonable basis for attempting correlations with influential factors. But in the absence of critical questions related to validity when using ex post facto methodology, conclusions can be problematic. Our conclusions are based on a review of the oyster literature relevant to (1) hysteresis, (2) the heterogeneous needs of different oyster ages, and (3) the geographic distribution of Gulf oyster populations, along with statistical interpretations of some of the effects on oyster landings.

METHODS

Data for oyster landings in the states of the northern Gulf of Mexico (Texas, Louisiana, Mississippi, Alabama, and West Florida) were obtained from the website of the National Marine Fisheries Service (http://www.st.nmfs.noaa.gov/pls/webpls/MF_ANNUAL_LANDINGS.RESULTS), with older landings from their statistical digests. The landings are measured in thousands of pounds of oysters in the shell at the dock per calendar year. Oyster landings can be measured in sacks or pounds of meat, but the measure used most consistently—pounds of whole oysters—was utilized and converted to metric tons.

River flow data (in average cubic meters per second for the calendar year) were obtained from the website of the U.S. Geological Survey (http://nwis.waterdata.usgs.gov/nwis/annual). The statistical package SPSS was used to generate graphs and most statistical analyses. The State of Louisiana was emphasized, since it boasts the largest oyster production and the greatest amount of freshwater input into the estuaries. An exhaustive review of over a century of relevant oyster literature was conducted to guide the methodology and interpretation of the results.

RESULTS AND DISCUSSION

Hysteresis.—The oyster biology paradigm has long recognized that the relationship between salinity and production is not a simple linkage and has variable delays. This linkage indicates a form of hysteresis. Examples of this are the effects of predators and diseases on oysters. One of the more important predators is the southern oyster drill (*Stramonita haemostoma*) (Butler, 1985). A disease that is important to adult oysters is Dermo (*Perkinsus marinus*) (Soniat, 1996). Drills are mostly limited by salinities below 15 psu, and Dermo has an imperfect relationship with salinity but is similarly controlled by lower salinities. Along with drills and other predators, Dermo limit the seaward spread of subtidal oysters.

Predators and diseases variably influence the life span of oysters, restrict production, and limit opportunities for harvesting from year to year. Harvest (yield) and production are not the same. Harvest is modified by regulation, market forces, and effort, all of which to varying degrees are a function of production. In addition, there is an age and size beyond which mortality overtakes growth (Owen, 1953). Early harvest of oysters is preferred, especially in higher salinities. Louisiana oysters grow rapidly and are capable of reaching commercial size (3 inches) in a year (Hopkins et al., 1954) and are often moved to higher salinity waters prior to harvest. As one example, Menzel (1951) raised a few oysters that set in May and grew to over 100 mm by the next January. These considerable effects on growth and harvest would be masked by the 3-yr running average landings used by Turner (2006) to support his claim of decreased oyster production after freshwater inflow.

Exceptional circumstances may support the use of a 3-yr running average of landings. The only environment in which older oysters (4–6 inches) can survive is in large amounts of low-salinity, disease-free water. Overwintering of seed oysters of less than 3 inches can add a significant amount of growth before disease mortality occurs the next summer. Such a Louisiana case was reported (Melancon et al., 1987). In one experiment, Menzel and Hopkins (1952) reported growth of seed oysters planted in October 1947 at a peak size of 60–70 mm reaching 80–100 mm in January 1949, roughly a growth of over 1 inch in 15 mo. Some of these oysters grew nearly an inch in less than 5 mo. The seed oysters were not aged but likely were not over 18 mo old. Menzel and Hopkins found that planted oyster size distribution did not change, because as the smaller/younger size classes grew, the older ones died. This mortality was soon understood to stem from Dermo disease, which affects the larger oysters in higher salinities and temperatures (Mackin, 1962).

St. Amant et al. (1958) reported that half of a group of Louisiana oysters raised from spat reached commercial size in 12 mo, and half grew to over 4 inches in 21 mo. Because Louisiana oysters frequently suffer extensive Dermo mortalities in their second summer (Mackin, 1962), the number of older, larger oysters harvested may be minimal. In addition, size and age at harvest are going to be confounded by both environmental and regulatory conditions. As an example of the effects of regulation, the Galveston Bay legal oyster size was once reduced, successfully improving the harvest (Hofstetter, 1977).

There seems to be much variability in age at harvest. Nevertheless, Turner (2006) cited Berrigan et al. (1991) as the authority for his 3-yr running average based on oysters reaching a marketable size in 18–24 mo, claiming ''… harvest may occur for several years thereafter.''

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For his conclusions, Berrigan et al. (1991) cited only Hofstetter (1977) and Berrigan (1990) as authorities, neither of which used data from Louisiana. The latter articles were only indirectly concerned with age at harvest, and Hofstetter's (1977) growth data indicated that commercial size was reached in 13–17 mo.

Turner's conclusion that oyster landings are inversely related to freshwater inflow is based on his linkage of the 3-yr running average of normalized landings to discharge of selected Gulf rivers [Turner's fig. 5 (2006)]. However, using running averages, similar correlations have been shown to obscure interpretation of physical events (Boger et al., 2000). Furthermore, while Turner interprets 21 of 23 peaks in landings as coincidental with lows in river discharge and 17 of 19 troughs as coinciding with peaks in major river discharge, he omits the Mississippi River, which is associated with the largest oyster fishery in the Gulf.

Heterogeneous needs of oysters.—The differing requirements for spawning, spat set, growth, and predator and disease avoidance have been studied by a small library of workers. As shown by Chatry et al. (1983), poor production on Louisiana's prime seed grounds can result from both salinities that are too high and those that are too low. The low salinities cause spat failures; the high salinities allow biological effects. The optimum salinity found was over 15 psu in January down to near 7 psu in May to around 15 psu in the fall. Similarly, in the same area, Tabony (1972) found that most larvae and spat set above 17–18 psu, a value that is higher than that which the older larvae can experimentally tolerate (Davis and Calabrese, 1964). These higher salinities then become the nemesis for the remaining life of the oyster (Mackin and Hopkins, 1962). This heterogeneity indicates a broad mosaic that is not supportable by a simple linear analysis.

Geographic distribution.—The northern Gulf geographic distribution of commercial oyster reefs is associated with the amount of freshwater. Korringa (1957) discussed the major complications of optimal salinity within the genus *Crassostrea.* While oysters thrive in estuarine salinities, it is not a compulsory relationship. Korringa states that within limits, estuaries with reduced salinities produce the most oysters. There are also estuaries with little or no production as a result of excessive freshwater (Sabine, Grand, and White Lakes, Vermilion Bay in Louisiana). In Calcasieu Lake in Southwest Louisiana production was limited to the mouth (Glaser, 1904) and, more recently, to the lower lake (White and Perret, 1974). Mobile Bay is similar, with production in the lower bay and mainly near the mouth (May, 1971). Further south along the Texas coast, bays become too salty, with significant production occurring only in certain years with extensive freshwater input (Hofstetter, 1977).

Floods have long been known to cause problems with regard to oyster mortality, reproduction, condition, and spat set failure. But floods sometimes produce benefits. Turner's (2006) analysis of the several works recording flood damage only noted these negative effects. In another important example, Butler (1952) concluded that the lowering of salinity levels in Mississippi Sound "… is not necessarily dependent on the amount of fresh water discharged from the river basins." His insight is that in addition to the Bonnet Carré spillway and the Pearl River, contribution of local rainfall could be very important.

Hofstetter (1977) reported the mortalities from Galveston Bay floods, but he also found that the 1968 flood produced a 3-yr expulsion of Dermo, which is an example of a delayed benefit. May (1972) found that Mobile Bay oyster mortalities occurred in salinities that were mainly well below 2 psu. This low salinity was rare over much of the Mississippi Sound oyster areas, even during the 1970s flood years (Eleuterius, 1977) after the Bonnet Carré spillway was opened.

Large spat sets after floods are common, as evidenced by the heavy seed abundance the years after the 1973 and 1979 Bonnet Carré spillway openings (Chatry, 1987). Similarly, relatively abundant spat sets after floods were reported in Texas, but with a lot of variation (Hofstetter, 1977). These sets often produce a reef that is too thick for harvesting, which diminishes potential landings and leads to the long-established culture techniques of separating and moving seed (Hopkins, 1955).

Louisiana oyster production is usually an order of magnitude greater than that of other states and has increased along with a long-term increase in river discharge evident in all Gulf states except Florida in Turner's figure 5. In fact, Louisiana landings from 1880 to 2003 have roughly tripled, as shown in Figure 1. When Louisiana landings are correlated with calendar year over the last 120 yr using 81 yr of available data, a Pearson's correlation shows a strong linear relation [$r(81) = 0.74$; $P < 0.01$]. This indicates that the landings have generally increased over time along with the increase in river flow. This strong correlation of year with

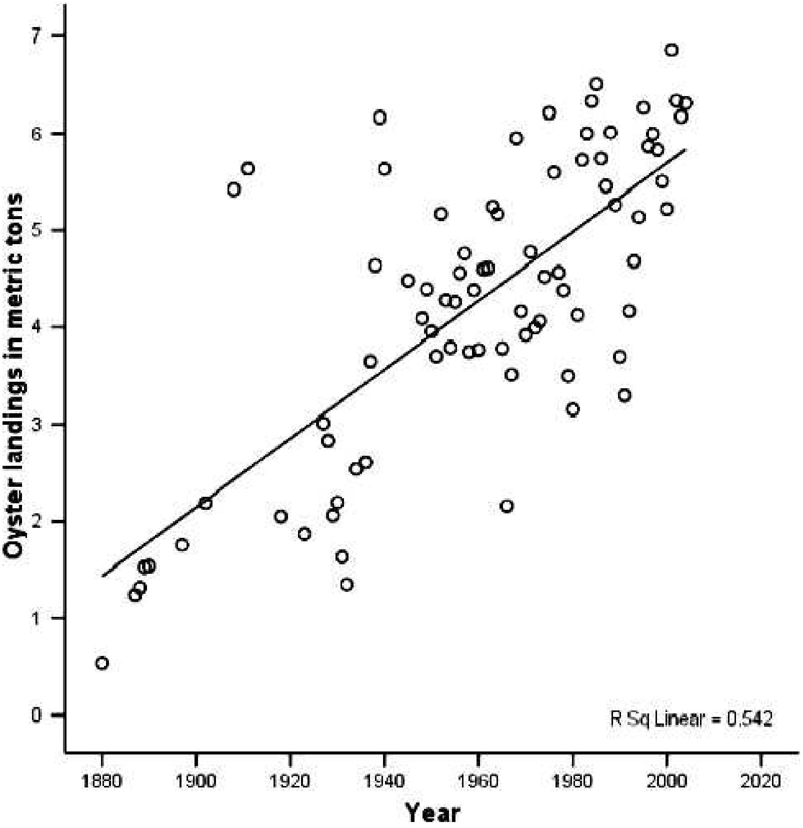

Fig. 1. Louisiana oyster landings correlated with year.

landings could confound analyses of cause and effect.

The varied effects from spillway openings must be observed over as many years as possible in order to capture the variety of outcomes. For example, the opening of the spillway in 1945 caused extensive mortality. Between the 1945 and 1950 Bonnet Carré openings a severe hurricane in 1947 killed many oysters in eastern Louisiana and Mississippi Sound, but landings still held up (Gunter, 1953). Half of the Bonnet Carré openings were in the 11 yr between 1973 and 1983, with others separated by 13 or 14 yr. Figure 2 shows the Louisiana landings for each of the 3 yr before and after four openings of the Bonnet Carré spillway. The openings selected are those that have no overlapping years before and after. These landings for these years indicate an increase following a spillway opening. Figure 3 illustrates how both landings and flow of the Mississippi River have increased over the past 70 yr.

This general increase in landings over time confounds the claim that the spillway openings increase landings in following years. Mississippi landings (Fig. 4) are much more volatile, and those in recent years, for which the records are presumably better, indicate that they produce less than a one tenth of Louisiana's catch. While it is true that Mississippi landings would be affected by spillway openings, the volatility and uncertainties of origin of production in the older data (Gunter, 1949) reduce confidence in their use as a basis for a ratio. Furthermore, spillway openings occur in wet years, which depress salinities. Pearl River flows might be better predictors, but Turner's (2006) negative correlation of landings with Pearl River flow (his fig. 6) does not agree with ours (Fig. 4), perhaps because he only used 12 of the easily available years for analysis. His use of only recent years would be more consistent with the presumed precision of records, but in our analysis we were unable to duplicate his figure 6. Our Figure 4 uses Pearl River discharge and landings. Our derived regression model with a negative slope was not statistically significant; the coefficient of determination [$r^2(43) = 0.039$, $P > 0.05$] indicates that flow of the Pearl River is not even a reasonable predictor of catch.

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Fig. 2. Mean of Louisiana landings for years surrounding the opening of the Bonne Carre Spillway (1937, 1950, 1973, and 1997).

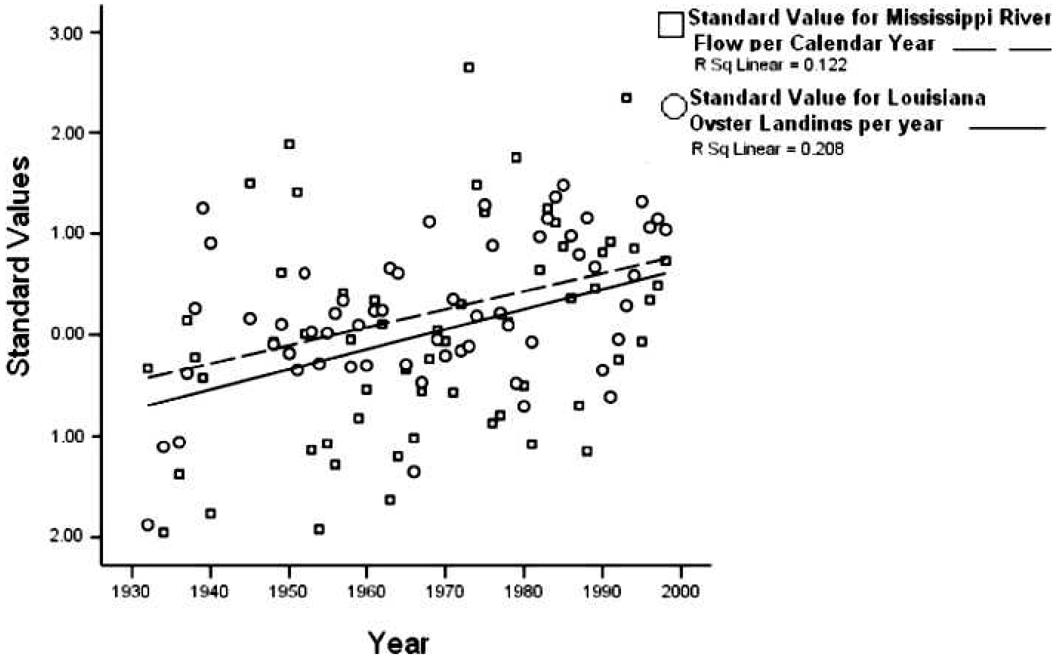

Fig. 3. Louisiana Oyster Landings and Mississippi River Flow per year.

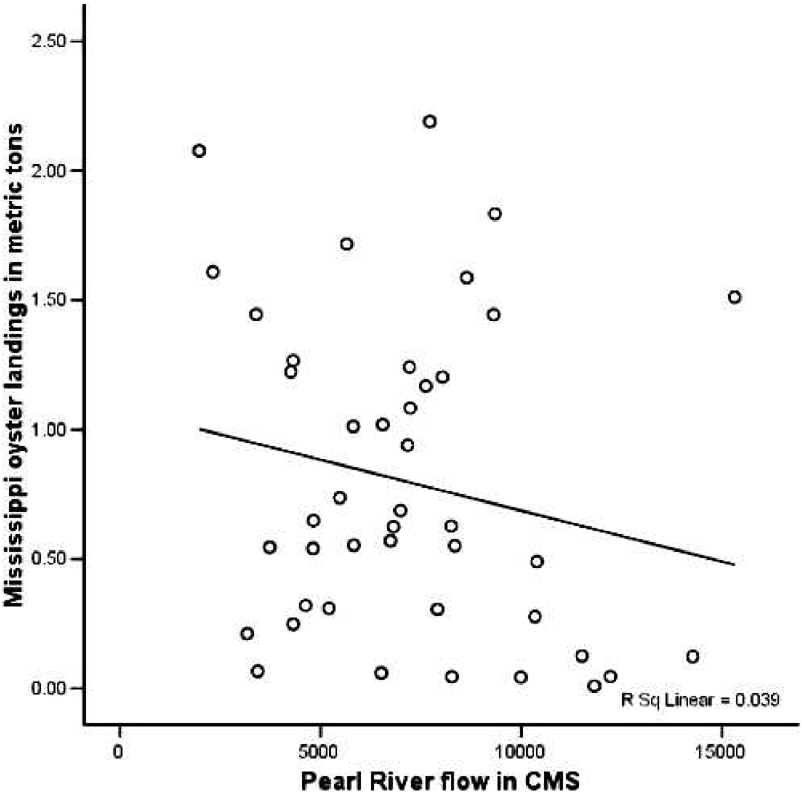

Fig. 4. Pearl River flow vs Mississippi landings (1963–2004).

Statistical interpretation.—Turner's (2006) table 2, which shows changes in ratios before and after spillway openings, is inexplicable. We reworked the landings data and computed the ratios for landings from each of four states (West Florida, Alabama, Louisiana, and Texas) to landings in Mississippi for the 7 yr of Bonnet Carré Spillway openings (1937, 1950, 1973, 1975, 1979, 1983, and 1997) and compared these to the same ratios for the second year after the opening. Turner's analysis reported that 25 of the 28 comparisons showed an increased ratio in the second year, which would indicate that the Mississippi landings were adversely affected by the openings. However, we found that only 19 of 28 comparisons showed an increased ratio, which is not statistically significant ($P = 0.145$; alpha = 0.05) using a two-tailed Wilcoxon test. Since our computed ratios did not match those shown in Turner's table 2, we recomputed the ratios using the normalized data. These ratios matched Turner's table 2 values on the first row only (1937 and 1939). The differences between the year of opening and 2 yr later were not statistically significant ($P = 0.096$).

It is true that the mean and median values of the landings ratios are greater 2 yr after the openings. However, it should be emphasized that these effects were produced by diversions during flood years averaging 6,215 ± 607 m^{3}s^{-1} maximum flow, while the proposed Bonnet Carré project is an order of magnitude smaller (McAnally and Berger, 1997; Morgan, 2000). Moreover, much of this increase in landings ratio results from the 1950 opening, when Mississippi landings had already been decreasing, probably from the preceding the very wet decade (Butler, 1952). Mississippi landings are often the most variable of any Gulf state, and since there is the possibility of combining Louisiana production landed in Mississippi, this ratio method appears suspect. For example, Mississippi landings in 1937 were over 10 million pounds, comparable to the long-term Louisiana production. Based on the area for maximum potential production in Mississippi (Kilgen and Dugas, 1989), and with recent better regulated reporting, these earlier records must have included a significant Louisiana contribution. Very high Mississippi oyster production between 1927 and 1936 (Demoran, 1972) was

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reported to be due to the ''greatest flood of all.'' Mississippi came close to Louisiana again in 1939, but landings subsequently were usually well below 4 million pounds, and in recent decades, they were usually below 1 million pounds.

In addition, harvested size may have changed as a result of the closure of canning plants in Mississippi after hurricane Betsy in 1965 (Dugas et al., 1997). Canned oysters would have been smaller, and therefore younger, with a conversion factor of 1.5 (based on the number in a sack) compared to counter oysters (Menzel and Hopkins, 1952).

Turner (2006) was inconsistent in his use of data from Louisiana. He included Louisiana landings in his ratio to those in Mississippi (his fig. 8), while claiming that it was impossible to correlate the landings with the watersheds in Louisiana. His figure 5 does not include Louisiana harvest data but uses a normalized 3-year running average of landings and discharge for all other states. He instead used older Louisiana data (1936–51) from two parishes east of the Mississippi River. This is inappropriate since 99% of Louisiana oysters have been historically produced in the main Mississippi/Atchafalaya drainages from the Pearl to the Vermilion Rivers (Keithly and Roberts, 1988). Turner's use of this older data (his fig. 7) to show the exception by which Plaquemines Parish landings increase a small amount with discharge is also inconsistent with data presented by Mackin and Hopkins (1962, their fig. 4). These data show that both St. Bernard (east of the river) and Jefferson (west of the river) Parishes steadily decreased in landings from 1943 through 1946, starting before the 1945 Bonnet Carré opening. Indeed, Gunter (1953) noted a labor shortage beginning early in World War II and did not include the years 1939, 1950, and 1951, which Turner claimed to have used for his figure 7. As a result of larger catches east of the river the effect of the labor shortage was greater there, but the decrease also apparently occurred throughout the state.

Neither article (Kirby, 2004; Turner, 2006) provided an adequate discussion of oyster biology and culture. Among several mistakes (Turner, 2006) was the citation of Pierce and Conover (1954) to show that oysters grow faster in areas with fluctuating salinities. This brief experiment in Massachusetts confounded the effects of salinity and substrate. In contrast, Menzel and Hopkins (1952) found that there was better growth in Bay Sainte Elaine, with higher and more stable salinity than is found in Bayou Bas Bleu. Two much later studies (Addison, 2006; Duke, 2008) observed better growth in oysters at ''down-estuarine sites'' (i.e., higher salinity sites). Although salinity fluctuations are proper concerns, they often seem to be overshadowed by other factors (Soniat and Brody, 1988; Soniat, 2002).

Turner (2006) cited Powell et al. (1995) regarding shifting of optimum salinity outside of the topographical reef area, which is a significant event. However, he failed to acknowledge that their model did not include the ability of the oysters to expand hard substrate, although Powell et al. had noted this phenomenon. Such examples occurred in Galveston Bay after the enlargement of the ship channel (Powell et al., 2003) and in a number of historical changes in locations of Louisiana reefs (Gunter, 1952). Turner (2006) correctly concluded (his fig. 1) that there is an optimum area away from which oyster yields decrease, but this is too much of a simplification. As one of the main attributes of the ocean, the relationship of salinity to marine organisms has too extensive a literature to consider here, so only a few salient points can be discussed. The reader is referred to Ray (1987), which still provides a current enough analysis of the subject on oysters.

The trend of Louisiana landings with Mississippi River flow is positive 2 yr and 3 yr subsequent to spillway openings, although the data are fairly scattered (Fig. 5). One could argue that the Atchafalaya flows should be included, but not only have these changed considerably with time, they also have little influence over most of the oyster grounds. Although the variability of Mississippi River flow to Louisiana landings renders the statistics not significant, it is interesting to note that the data show a consistent trend. The average landings slightly decrease the year of the opening of the spillway; they slightly increase 1 yr later; and they result in a closely matched steeper rise 2 yr and 3 yr subsequent.

As to whether the criteria used by Kirby (2004) for predicting collapse of oyster production are applicable here, it appears that there was no consideration of the long-known factors, principally sociological or economic, summarized by MacKenzie (2007). Moreover, Kirby's hypothesis is partly negated by later increased landings north of Chesapeake Bay (MacKenzie, 1981, 2007), perhaps similar to the overfishing recoveries observed by de Mutsert et al. (2008).

While we cannot analyze all the geographic areas and factors, it appears that for Louisiana, of the four criteria, only dredging is connected with ''hard'' information. For example, a typhoid epidemic in 1924 (Lumsden et al., 1925) caused serious damage to the industry, and cholera and other more recently discovered vibrios (Colwell,

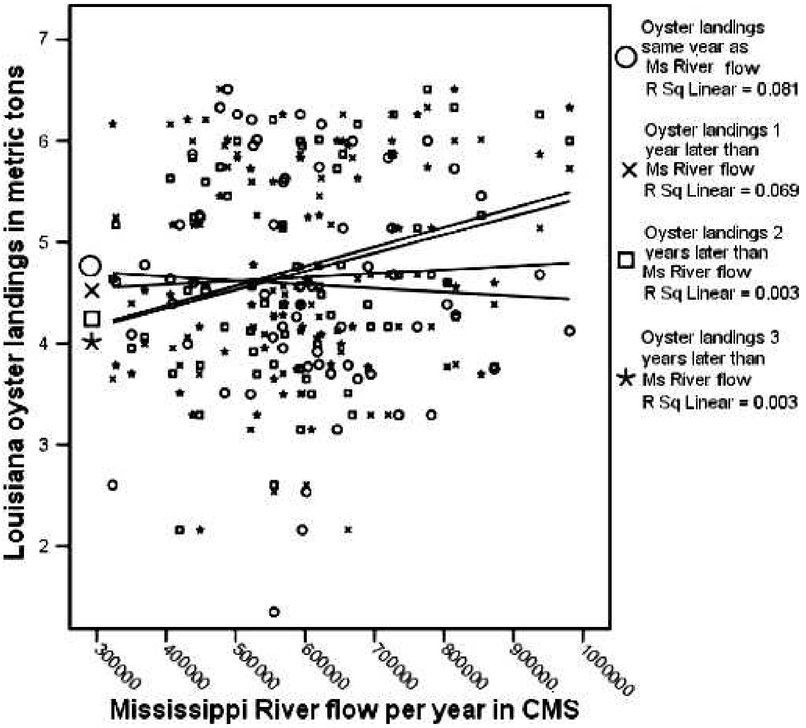

Fig. 5. Oyster landings correlated to Mississippi River flow for the same year and landings 1, 2, and 3 yr later (1932–95).

1984) are a new concern. The first appearance of laws seems an unreferenced tenuous connection to industry health. In Maryland the 1820 law was put in place when ''… the annual product of the State at that time scarcely exceeding, if it equaled, 500,000 bushels'' (Stevenson, 1894). Another 1820 law in Maryland limited nonlocal vessels, perhaps more for a territorial reason than for a concern for overfishing. However, in Louisiana the earliest laws date from the 1870s (McConnell and Kavanagh, 1941), with leasing from the state beginning in 1902 and mechanical dredging beginning shortly thereafter. Furthermore, this finding does not acknowledge that since before 1850 Louisiana has relied heavily on the farming of oysters with seed from both private and public areas (Dugas et al., 1997). As in all farms, the grounds can become barren, but production continues with the addition of new seed. Overharvesting is more of a problem on public reefs, some of which are important as seed, such as on the James River (Hargis and Haven, 1999).

In the late 1880s the importation of southern oysters into Connecticut occurred only in the New Haven area; three quarters sold immediately and the rest were used as seed oysters. At best, the total importation of southern oysters accounted for less than 30% of the state's production (Collins, 1891). So, the importation of seed oysters from southern sources to Connecticut was not significant to the state's oyster production, as concluded by Kirby. The importation of seed is not applicable in Louisiana, and there is no evidence that Louisiana production has reached a peak. As noted, dredging has been successfully used for a century with increasing production, but it changes features of the estuary of importance to other organisms (Coen et al., 2007). This is the source of a conflict between agricultural and other uses. The complexities of this situation have recently been discussed by Keiner (2009).

Kirby's (2004) suggestion that a population is degraded because it is reduced from pristine levels ignores the principle of sustained yield. One could just as easily say that the yields have been upgraded by favoring production over standing crop. To say that a peak in yield indicates a collapse in a fishery is an example of the logical error known as affirmation of the consequent. Even though many fishery collapses may be preceded by peak yields, peak yields more often may be followed by long periods of normal catches.

There are still a number of important unknowns about the relationship between river flow

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and salinity on the one hand and oyster biology on the other, mainly because of the confounding caused by other factors. Although oysters can live in lower salinities, they require mesohaline or higher salinities for reproduction. This high salinity then becomes a disadvantage to the progeny because of predators and disease limited to higher salinities. Any attempt to relate factors to oyster success must take this change in habitat requirement with age into account.

Furthermore, the formula for the Habitat Suitability Index for oysters originally used eight variables that have varying relationships to salinity and/or freshwater flow (Soniat and Brody, 1988). We have identified a dozen parameters that require consideration for an understanding of production, as from freshwater/spillway or other effects on oysters. There might well be a new paradigm that deepens our understanding, but the effect of floods on oysters is a matter of timing, the health of the oyster, and other factors, all of which are difficult to concurrently measure. It has long been accepted that good production of oysters, still a marine animal, occurs in higher salinities. But freshwater is essential to control predators and parasites. We are not suggesting that freshwater or diversions are a panacea, because mirroring habitats is difficult, but rather that they should be taken into consideration in a proper context with continuing experimentation. Diversions in some bays or parts thereof in certain years and seasons could certainly enhance oyster production. Furthermore, the comparison of controlled diversions (hundreds of m^3s^{-1} maximum) to Bonnet Carré flood control openings (thousands of centimeters maximum) is like comparing a garden hose to a fire hose for purposes of irrigating. Similarly, controlled experimental diversions move several orders of magnitude less sediment than do the historic crevasses and uncontrolled diversions (Snedden et al., 2007). It has been long recognized that floods vary in their effect (Gunter, 1953).

Finally, the premise that diversions lower salinity is questioned in that diversions are not necessarily a means of lowering of salinity, but rather provide a redistribution of freshwater. It is possible that freshwater could be ‘‘wasted’’ by poor distribution. Turner's (2006) conclusion is that most of Louisiana estuaries are so fresh that any reefs are positioned in areas that are less than optimum. This view shows a lack of understanding of the wide geographic, seasonal, and yearly variation in northern Gulf estuaries and their partitions. Currently, the Mississippi and Atchafalaya River mouths produce negligible amounts of oysters. These areas are so far below the optimum that they could only be improved by less freshwater, yet they drag down the optimum salinity average for Louisiana oyster production. Turner (2006) may be roughly correct about an inverse relationship between floods and oyster production, but this may not be causative and does not negate the well-known positive association between oyster production and greater freshwater availability. Such an inverse relationship was found in a Texas diversion project, but those authors (Wilbur and Bass, 1998) reached conclusions similar to ours. Buzan et al. (2009) also came to similar conclusions in Galveston Bay, suggesting a sometimes positive delayed effect from freshwater. This was contested by Turner (2009), who proposed alternate hypothetical causes of the exceptions that might not support the delayed model.

Additionally, many of the complications noted here were thoughtfully discussed by Meeter et al. (1979). Furthermore, Louisiana oyster production has been steadily increasing as a result of increasing demand (MacKenzie, 2007) and coincident with increasing Mississippi River flows (Fig. 3) and increasing river nutrients (Turner and Rabalais, 1991). As MacKenzie (2007) states, ‘‘Production of Gulf Coast oysters has been limited by consumer demand throughout history. For example, Louisiana oyster supplies have consistently far exceeded the capacity of US markets ....’’ As one indication, nearly half (47%) of potential Louisiana oyster acreage was unavailable in 1985 (Kilgen and Dugas, 1989).

MacKenzie's (2007) discussion of the oyster fishery from Prince Edward Island to South Carolina attributes the decline in production in the northern part of the range from 1890 to 1940 primarily to a fall in demand due to the competition of other foods and economic depression, and he attributes the decline in the 1960s in the more southern part of the range to biological and physical damage to the oyster beds due to Dermo and MSX diseases, severe storms, channel dredging, and siltation. This production decrease created a void in the market that was filled by oystermen increasing production in the northern part of the range (more recently). This contradicts prognostications by Kirby (2004) that the decline in productive oyster beds would continue on the East Coast from the northern to the southern part of the range, and it reinforces the role of market demand in oyster production. These findings indicate that Louisiana harvests are more a function of market forces than of abundance, and, therefore, oyster landings are not a valid measure of actual or potential oyster production.

Turner (2006, 2009) attempted to deal with hysteresis by integrating the effect of flooding and all of the complex environmental conditions by measuring the postflooding, 3-yr, running average of yields and showing these yields to be depressed. However, his definition of depressed is unclear and probably too generous, his data sets are selective, his analysis has many mathematical errors, and he uses flood events (large inputs) to predict the future effect of diversions (small inputs).

Freshwater is essential to sustained oyster production, and the statistical data do not support a direct negative relationship between freshwater inflow into estuaries and oyster productivity in the short term. The data do indicate a much more complex interaction of many factors difficult to subject to precise statistical analysis. Some of these factors are well understood, and some of these were misinterpreted by Kirby (2004) and Turner (2006, 2009).

Acknowledgments

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