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2014

# The Response of Lake Pontchartrain Fish Assemblages to Hurricanes Katrina and Rita

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#### Recommended Citation

Martin T. O'Connell, Ann MU O'Connell, and Christopher S. Schieble. (post print) "Response of Lake Pontchartrain Fish Assemblages to Hurricanes Katrina and Rita" Estuaries and Coasts 37.2 (2014): 461-475.

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## Introduction



 were associated with extensive habitat destruction (i.e., shell dredging) in Lake Pontchartrain (O'Connell et al. 2004). We recognize, though, that hurricane impacts may not actually be responsible for observed fish declines, especially when data are not analyzed thoroughly. A decline in species richness, total fish abundance, and abundances of select species on a coral reef in St. Croix were initially assumed to be caused by Hurricane Marilyn in 1995. On further analysis, though, these impacts were found to be unrelated to the storm and indicated that other forces (e.g., fishing pressure) were responsible (Adams 2001). As in other estuary and marine habitats, there is a need in Lake Pontchartrain to better understand the relationships between anthropogenic effects and the innate resiliency of the aquatic ecosystem to natural disturbances (Greening et al. 2006; Poirrier et al. 2008).

 Hurricanes Katrina and Rita struck southeastern Louisiana in autumn 2005 causing a unique combination of both natural and anthropogenic impacts for the Lake Pontchartrain ecosystem. Natural impacts from both storms included large storm surges (2 - 4 m) which inundated the estuary and caused extensive infauna mortality (Poirrier et al. 2008). The most prominent anthropogenic impact associated with the 2005 storms was the discharge of floodwaters from inundated New Orleans into Lake Pontchartrain (Hoe et al. 2006; Van Metre et al. 2006). These stagnant floodwaters had remained in the flooded city for three weeks after Hurricane Katrina struck and were assumed to be a highly toxic combination of biological and chemical components (Farris et al. 2007). To assess possible impacts on Lake Pontchartrain fish assemblage due either to natural or anthropogenic impacts associated with the 2005 hurricanes, we compared monthly trawl, beach seine, and gillnet collections taken at six sites before (2000- 2003, 2005) and after (2006-2009) to determine if significant assemblage changes occurred. We also tested for significant post-hurricane declines or increases in abundant or influential fish



#### Data Collection



 All three gear types were fished on a monthly basis both prior to the 2005 hurricanes (2000-2003, 2005) and after (2006-2009) at five sites in Lake Pontchartrain, with an extra mid-165 lake trawl sample also included in the analyses (Fig 1). A total of 1,674 collections were made: 787 pre-hurricane collections (410 trawls, 224 beach seines hauls, and 153 gillnet sets) and 887 post-hurricane collections (455 trawls, 252 beach seines hauls, and 180 gillnet sets; Table 1). Fishes were either counted, identified, and released in the field or anesthetized with sodium bicarbonate (UNO-IACUC Protocol # 09-016), fixed with 10% formalin, and processed back in the laboratory. For each collection, salinity, dissolved oxygen (ppm), Secchi depth (m), and 171 surface water temperature  $({}^{\circ}C)$  were measured.

## Data Analyses



 five (beach seine and gillnet) or six (trawl) sites were used such that each ANOSIM typically compared from 60 to 168 pre-2005 collections with 60 to 168 post-2005 collections, with 60 representing the shortest calculated season (beach seine collections from April to June: 3 months X 5 sites X 4 years) and 168 representing the longest calculated season (trawl collections from November to May: 7 months X 6 sites X 4 years). Seasonal data were analyzed using a two-way crossed ANOSIM design with site and pre/post 2005 as factors. If a collection contained no fishes, it was omitted from the analysis. While these omissions sometimes generated unequal sample sizes, two-way crossed ANOSIM is robust to minor amounts of missing data (Clarke and Warwick 2001). To minimize the influence of rarer species, all abundance data were square root transformed prior to analysis. If a significant difference was detected, we used the PRIMER similarity percentages routine (SIMPER) to determine which species contributed most to the observed change in species composition. We also generated MDS plots to present the relationships between pre- and post-hurricanes assemblages for each season and each gear type. To test for possible significant post-hurricane declines or increases in those fish species that were determined to contribute to assemblage dissimilarity based on the SIMPER results or those that were the top 15 most common species collected by each gear type, we used multiple Friedman's tests. To account for seasonality, we limited our analyses to the 1-7 month abundance peak for each individual species for each gear type. This peak was determined by comparing mean monthly abundances for each species and choosing the multi-month period with the highest abundances. With this non-parametric rank-based procedure, we assessed the species' data using site averages as the block (that is, the average abundance of a species at one site over the four year pre/post period) and pre/post 2005 as the factor.



 *undulatus*) were more numerous after the hurricanes, while in both seasons Gulf menhaden (*Brevoortia patronus*) were less numerous in post-hurricane trawls (Table 2). For both seasons, SIMPER analyses also revealed that *A. mitchilli* contributed most to the observed fish assemblage changes with *M. undulatus* the being the second-most influential species (Table 2). Beach seine data were more distinctly clustered into three seasonal groupings: December through March (Season I), April through June (Season II), and July through November (Season III). Inshore fish assemblages (those collected by beach seines) also exhibited significant post-248 hurricane changes in all three pre-determined seasons (ANOSIM,  $R < 0.12$ ,  $p < 0.05$ ). Again, the low global-R value suggests minor changes in species composition between periods and assemblages showed little to no multivariate separation in the MDS ordination (Fig. 3). In all three seasons, *A. mitchilli* and *M. beryllina* were less numerous after the storms and these species contributed the most to assemblage differences in two of the seasons. The change in assemblage in the remaining season (II) was attributed mostly to a decrease in *B. patronus.*  While this species and *M. undulatus* decreased in two seasons, both species experienced increases in the remaining season*.* 

 As with the trawl data, gillnet data also clustered into two less distinct seasonal groups, but these consisted of samples collected from April through October (Season I) and November through March (Season II). Gillnet collections yielded only one season (Season I) with significant assemblage differences between the two periods, again with a markedly low global R 260 value (ANOSIM,  $R = 0.045$ ,  $p = 0.004$ ) and little to no multivariate separation in the generated MDS ordination (Fig. 4). SIMPER analyses revealed that differences in this season's collected assemblages were attributed to post-hurricane decreases in *B. patronus* along with increases in

 gafftopsail catfish (*Bagre marinus*) and hardhead catfish (*Ariopsis felis*), and to a lesser extent decreases in *M. undulatus* (Table 2).

 When peak abundance periods were compared for individual fish species, *B. patronus* 266 declined significantly (Friedman's test,  $\chi^2 = 6.00$ , p = 0.014) in trawl collections after the 267 hurricanes but increased significantly (Friedman's test,  $\chi^2$ =5.00, p = 0.025) in gillnet collections (Figs. 5 and 7). Trawl data also revealed a significant increase in *A. felis* after the hurricanes 269 (Friedman's test,  $\chi^2$  = 6.00, p = 0.014; Fig. 5). In beach seine collections, three species exhibited 270 significant declines: naked gobies (*Gobiosoma bosc*; Friedman's test,  $\chi^2$ =5.00, p = 0.025), Gulf 271 pipefish (*Syngnathus scovelli*; Friedman's test,  $\chi^2$ =5.00, p = 0.025), and rough silverside 272 (*Membras martinica*; Friedman's test,  $\chi^2$ =5.00, p = 0.025; Fig. 6). In gillnet collections, three 273 other species exhibited significant declines: *M. undulatus* (Friedman's test,  $\chi^2$  = 5.00, p = 0.025), 274 Spanish mackerel (*Scomberomorus maculatus*; Friedman's test,  $\chi^2$ =4.00, p = 0.046), and sand 275 seatrout (*Cynoscion arenarius*; Friedman's test,  $\chi^2$ =4.00, p = 0.046; Fig. 7). For all remaining fish species, there were no significant differences in pre/post-hurricane abundances. Trends for some species as measured by the SIMPER analyses did not always agree with those from the Friedman analyses. For example, while *M. undulatus* was an important contributor to assemblage changes in trawl collections, there was no significant change in its abundance. Likewise, in beach seine collections none of the species that experienced significant declines were important in driving pre/post- assemblage changes based on SIMPER analyses (Table 2). For the gillnet data, there is an apparent discrepancy between an increase in *B. patronus* during its peak abundance period (April-June) and its supposed decrease during Season I (April-October). According to the SIMPER results, this latter decrease contributed greatly to the measured assemblage difference, with *B. patronus* being the most influential fish species



#### Discussion

 Our results suggest that four years after the 2005 hurricanes, Lake Pontchartrain fish assemblages have mostly recovered. Benthic assemblages (as measured by trawl sampling) exhibited changes in both seasons, but these were driven by the two most common species (*A. mitchilli* and *M. undulatus*) increasing after the storms. It is interesting to note that these same two species also increased in Chesapeake Bay after Hurricane Isabel struck in 2003 (Houde et al. 2005). Concerns exist, however, about measured post-hurricane declines in trawl-collected *B. patronus*, especially since numbers of this species had remained relatively stable in Lake Pontchartrain over a half-century of extensive disturbances (O'Connell et al. 2004). The abundance of most individual fish species remained unchanged following these disasters. The resilience of these fish assemblages is similar to that observed for other estuaries that were affected by hurricanes (Greenwood et al. 2006; Piazza and La Peyre 2009; Stevens et al. 2006; Switzer et al. 2006). In Breton Sound, an estuary southeast of Lake Pontchartrain, the 2005 hurricanes caused extensive habitat damage to tidal freshwater marshes (Piazza and La Peyre 2009). While this destruction led to a short-term change in the composition of local species, by spring 2007 the pre-hurricane nekton community had recovered despite the fact that marsh habitat remained damaged (Piazza and La Peyre 2009). Similar physical habitat damage occurred in Charlotte Harbor, Florida during the active 2004 hurricane season and again the local estuarine fish assemblage structure remained stable (Greenwood et al. 2006; Greenwood et al. 2007). It should be noted, though, that continued deterioration of mangrove root structure and the slow rate of mangrove colonization may yet affect fish assemblages on a long-term basis (Greenwood et al. 2007). One of these 2004 hurricanes also generated hypoxic conditions in Charlotte Harbor which led to local fish kills (Stevens et al. 2006). This impact was also

 temporary in that the local fish assemblages appeared to have recovered in no more than two weeks following the storm (Stevens et al. 2006). During the same hurricane season, the St. Lucie estuary in southeastern Florida also experienced extensive storm-related disturbances such as increased fresh water input and near hypoxic conditions (Switzer et al. 2006). Again, local nekton community recovery was evident after four months (Switzer et al. 2006). In most of these examples, assemblage or community recovery is attributed to the ability of adult nekton to avoid adverse conditions though their mobility (Greenwood et al. 2006; Switzer et al. 2006). Such mobility is not available to benthic or sedentary organisms and may lead to relatively higher hurricane-related mortality for these estuarine organisms (Poirrier et al. 2008). The positive effects of nekton mobility in response to disturbances may be minimized when escape corridors are reduced or eliminated in highly modified estuaries.

 In trawl collections after the 2005 hurricanes, the ecologically and economically important species *B. patronus* decreased significantly during its typical period of peak abundance (March through May). This filter-feeding species serves as a prey item for many other fishes and supports one of the top fisheries by volume in the United States (Smith 2001; Vaughan et al. 2011). The extent to which *B. patronus* influences estuarine communities in the northern Gulf of Mexico makes this species an indicator of the overall health and productivity of these aquatic systems (Vaughan et al. 2011). Trawl sampling in Lake Pontchartrain mostly collects juvenile *B. patronus*, not adults. During the spring (again, March through May) juvenile *B. patronus* typically use upper estuaries such as Lake Pontchartrain as nurseries. Higher salinities could have driven these fish to use other less saline habitats farther up the estuary such as Lake Maurepas, similar to the results of other studies of Lake Pontchartrain (Cashner et al. 2001) and elsewhere (Haley et al. 2010; VanderKooy 2011). But salinities were lower after 2005 during

 Season I (November through May) trawl collections which coincided with the period of peak abundance of *B. patronus* in the trawl (March through May), even though salinities were typically higher in other post-hurricane comparisons (Table 3). Another explanation for the decline in *B. patronus* is that significantly lower dissolved oxygen levels in both trawl seasons caused these fish to avoid portions of Lake Pontchartrain. While these lower dissolved oxygen levels were not hypoxic (lowest measurement = 4.60 mg/l), nearby 'dead zones' had been identified farther down the estuary in Chandeleur Sound during the same period (Lopez et al. 2010). In avoiding hypoxic or anoxic areas, aquatic organisms (including *B. patronus*) can become concentrated in normoxic water, thus making them more vulnerable to fishing effort (Smith 2001; Burkholder et al. 2004; Breitburg et al. 2009). Local commercial fishing pressure on *B. patronus* has actually been reduced following the 2005 hurricanes due to damage to fishery infrastructure, but fishing mortality has also increased possibly due to *B. patronus* displaced from offshore hypoxic zones being captured more effectively in near shore waters (Vaughan et al. 2007). A similar fishery response was observed in the Albemarle–Pamlico Estuarine System in North Carolina and Virginia after the active 1999 hurricane season which included three named storms impacting the region (Burkholder et al. 2004). Hurricane floodwaters displaced high numbers of blue crabs (*Callinectes sapidus*) causing them to "hyperaggregate" in areas where they were exposed to increased commercial fishing pressure (Burkholder et al. 2004). This, in turn, resulted in a 70% reduction of adult *C. sapidus* in 1999-2002 (Burkholder et al. 2004).

 One benthic species, *A. felis*, increased in trawl collections after the hurricanes. This species may have benefitted from the lack of commercial fishing pressure in Lake Pontchartrain due to hurricane damage to boats and infrastructure (Buck 2005). Benthic fin-fishes are

 consistently taken in large numbers as bycatch in trawling conducted by Louisiana commercial shrimpers (Adkins 1993). Unlike the purse seines used in the local *B. patronus* fishery, trawls not only impact benthic fishes through direct fishery mortality but also severely alter these animals' habitats (Watling and Norse 1998). The reduced trawling in eastern Lake Pontchartrain and nearby Lake Borgne likely reduced overall mortality for this species in the years following the 2005 hurricanes. Significant changes in post-hurricane environmental variables (decreased dissolved oxygen and water clarity) in trawl Season II (June through October) which coincided with the peak period of abundance for *A. felis* (June through October) likely played less of a role in explaining the increase in this species, unless this known scavenger was consuming other organisms that may have succumbed to the detrimental local conditions caused by the hurricanes. For example, *A. felis* can adjust its foraging behavior and take advantage of discarded bycatch generated during shrimping season in southeastern Louisiana (Eustis 2011). As with other estuaries, long term increases in such scavenger species may reflect an overall decline in trophic structure and general ecosystem health.

 Three small species, *G. bosc*, *S. scovelli*, and *M. martinica* declined after the hurricanes in beach seine collections. For *G. bosc*, this change may have been associated with decreases in dissolved oxygen and water clarity, while dissolved oxygen decreases during their periods of abundance may have explained the decreases in the *S. scovelli* and *M. martinica*. The 2005 hurricanes caused extensive damage to Lake Pontchartrain's benthic community, especially the ecologically dominant *Rangia cuneata* clam (Poirrier et al. 2008). Many benthic invertebrates died as a result of scouring as surge waters retreated back to the Gulf of Mexico. The decline of *R. cuneata* (a filter feeding organism) likely contributed to poorer water quality in nearshore habitats where adults of these three species occur. Scouring may have impacted *G. bosc* as it did

 benthic invertebrates because this species is a slow-moving, estuarine-resident goby that is highly associated with benthic habitats, especially bivalve shell material (Ross and Rhode 2004). Declines in *S. scovelli* and *M. martinica* may be linked to these nearshore species being commonly associated with submersed aquatic vegetation (SAV). Under normal conditions, *S. scovelli* will use SAV as refuge from predators while *M. martinica* deposits its eggs on SAV. The decline of *R. cuneata* since the storms and subsequent decrease in water clarity over time may have contributed to a decline in the amount of SAV available for *S. scovelli* and *M. martinica* (i.e., plants need light). For example, October 2005 surveys discovered major decreases in SAV aboveground biomass throughout Lake Pontchartrain (Poirrier et al. 2009). While many SAV species can eventually recover from hurricane impacts (much like estuarine nekton), the short term (3-4 years) lack of SAV after the 2005 hurricanes may have interfered with the ability of *S. scovelli* to avoid predation and with the reproductive success of *M. martinica*.

 In gillnet collections, *B. patronus* increased after the hurricanes during its peak abundance period, yet this result seemed to contradict both an assemblage-driving decrease reported by the SIMPER results (Table 2) and the significant post-hurricane decline of this 417 species in trawl collections (Fig. 7). On closer examination, the SIMPER decline represents an in-consequential decrease in mean abundance per collection from 19.42 to 19.40 individuals after the hurricanes. The discrepancy between the gillnet and trawl results likely represents a difference in response to the hurricanes by two different life stages of *B. patronus*. Adult *B. patronus* are typically only collected in gillnets while juveniles are most numerous in trawl collections. We suggest that adult *B. patronus* (age 2-4 years) fared better after the hurricanes than juveniles because of their superior swimming ability that allows them to avoid hazardous

 conditions. Not only would juvenile *B. patronus* lack this escape ability, they would also be exposed to those degraded nearshore habitat conditions described in the previous paragraph. Like the juveniles of most estuarine-dependent species, *B. patronus* occur in large numbers in nearshore habitats which they use as refugia from predator pressure. Because of the ecological and economic importance of this species, it will be necessary to monitor the recovery of *B. patronus* juveniles in this estuary.

 The declines in gillnet collections of *M. undulatus*, *S. maculatus* and *C. arenarius* may be cause for concern, although the latter two species did not contribute to the measured pre/post- assemblage change measured in April through October (gillnet Season I). In other words, although the abundance of both *S. maculatus* and *C. arenarius* declined significantly, they were not the drivers of overall assemblage change and, therefore, not representative of a truly concerning ecological perturbation (Table 2). Unlike these two species, *M. undulatus* did contribute 8.72% to the overall assemblage change measured in Season I gillnet data, with its mean abundance declining from 2.54 to 0.61 individuals after the hurricanes (Table 2). The abundances of the three species that contributed the most to assemblage change during gillnet Season I (*B. patronus*, *Bagre marinus*, and *A. felis*) either increased or did not change markedly (Table 2). However, the increase of the two catfish species (*B. marinus* and *A. felis*) and decline of two drum (family Sciaenidae) species (*M. undulatus* and *C. arenarius*) may indicate the beginning of system-wide environmental stress or trophic shifts. Similar changes in dominant fish species in other estuaries have led to the decline of targeted and desirable fishery species, that are then replaced by less desirable, lower trophic species. The alteration of the benthos by the hurricanes (as described above) may have contributed to the decline of *M. undulatus* and *C. arenarius*, both of which are associated with benthic habitats. The scouring that displaced many

 *R. cuneata,* also likely displaced many polychaete worms, a key diet item for *M. undulatus*. While *C. arenarius* feeds more on penaeid shrimp and *A. mitchilli*, this species is more benthic- oriented than its sister species *C. nebulosus* and the disruption of the benthic habitat of its prey may have led to its decline. Of the three species that declined in gillnet Season I, *S. maculatus* is the only truly marine species (compared to the two estuarine dependent drum species). This species is an uncommon late-summer visitor to the estuary, typically occurring in drier years (e.g., 2000 and 2001). It is possible that their decline is more the reflection of a lack of true drought years after the hurricanes rather than impacts from the storms themselves. After the storms, environmental variables were typical of conditions measured immediately after other hurricanes in the southeastern United States. Higher salinity, lower dissolved oxygen, and increased turbidity are common outcomes of hurricane landfalls in estuaries (Tabb and Jones 1962; Burkholder et al. 2004; Mallin and Corbett 2006; Stevens et al. 2006; Edmiston et al. 2008). A repeated theme among these studies of immediate hurricane impacts on estuaries is that conditions quickly return to normal, including the composition of local fish assemblages (Tabb and Jones 1962; Piazza and La Peyre, 2009; Rodgers et al. 2009). The changes in fish assemblages after the 2005 hurricanes were often associated with increases of influential species and in many seasons the abundances of other common species remained stable (Table 2). Though there is concern for species that consistently declined over multiple gear types (e.g., *B. patronus*) it appears that many of the hurricanes' impacts on local species are short-lived. Even though many water quality parameters were significantly different after the hurricanes, our post-hurricane period lasted four years beyond the storms, long after environmental variables should typically revert back to normal. In some cases, it is possible that

 environmental variables remained changed due to other circumstances (i.e., impacts from newly constructed hurricane protection structures, closure of the Mississippi River Gulf Outlet, etc.).

 As coastal areas in the southeastern United States become more susceptible to projected increased tropical storm activity, long term data such as we present here will allow documentation of any effects from both natural and anthropogenic disasters. While most estuarine nekton species appear resilient to storms, we did measure significant declines in important fishery species (e.g., *B. patronus*) as well as some smaller, inshore species (e.g., *S. scovelli*). Whether these changes are short or long term, can only be determined with future sampling. Beyond estuarine nekton, other organisms such as seagrasses can eventually recover after storms (Byron and Heck 2006, Poirrier et al. 2009), whereas other taxa (e.g., benthic bivalves) are more susceptible to hurricane impacts (Poirrier et al. 2008). If these organisms which have important roles in estuarine ecosystems (e.g., water filtration, prey items) cannot recover from hurricane damage, then we may expect to experience long-term impacts on other organisms which rely on them. For example, the widespread and ecologically dominant *R. cuneata* is an important prey item for blue crabs (*C. sapidus*) which, in turn, are important prey items for estuarine finfish, including most drums; as go the prey species, so go the predator species. These trophic cascades can develop in estuarine ecosystems and advance unnoticed for years because nekton species are resilient and estuaries themselves are highly variable on a year- to- year basis. To detect such impacts, it is necessary to continuously collect and evaluate long- term data to effectively measure possible changes to an ecosystem and determine their causes. These continuous data will be needed to determine long term trends in declining species or species that may indicate increasing habitat perturbation. Managers of estuarine resources need to beware of the apparent short-term recovery of estuarine nekton assemblages after disasters



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645 **Fig**. **1** Sampling sites in Lake Pontchartrain for trawl, beach seine, and gillnet collections. Mid-lake site (M) was only sampled with 646 trawls.

647 **Fig. 2** MDS plots of pre (black triangles) and post (gray triangles) 2005 hurricane trawl samples collected from Lake

- 648 Pontchartrain during Seasons I (November-May) and II (June-October).
- 649 **Fig. 3** MDS plots of pre (black triangles) and post (gray triangles) 2005 hurricane seine samples collected from Lake

650 Pontchartrain during Seasons I (December-March), II (April-June), and III (July-November).

651 **Fig. 4** MDS plots of pre (black triangles) and post (gray triangles) 2005 hurricane gillnet samples collected from Lake

652 Pontchartrain during Seasons I (April-October) and II (November-March).

- 653 **Fig. 5** Mean number of *B. patronus* and *A. felis* collected by trawls at six Lake Pontchartrain sites before and after the 2005
- 654 hurricanes. Collections were made during peak seasons for both species: *B. patronus* (March-May) and *A. felis* (June-October).
- 655 In trawl collections taken after the 2005 hurricanes, there were significantly less *B*. *patronus* (Friedman's test,  $\chi^2$  = 6.00, p =
- 656 0.014) and significantly more *A. felis* (Friedman's test,  $\chi^2 = 6.00$ , p = 0.014).

657 **Fig. 6** Mean number of *G. bosc*, *S. scovelli*, and *M. martinica* collected by beach seines at five Lake Pontchartrain sites before and

658 after the 2005 hurricanes. Collections were made during peak seasons for each species: *G. bosc* (February-May), *S. scovelli*

- 659 (April-August), and *M. martinica* (July-October). In beach seine collections taken after the 2005 hurricanes, all three species
- 660 declined significantly: *G. bosc* (Friedman's test,  $\chi^2$ =5.00, p = 0.025), *S. scovelli* (Friedman's test,  $\chi^2$ =5.00, p = 0.025), and *M*.
- 661 *martinica* (Friedman's test,  $\chi^2 = 5.00$ , p = 0.025).

 **Fig. 7** Mean number of *B. patronus*, *M. undulatus*, *S. maculatus*, and *C. arenarius* collected by gillnets at five Lake Pontchartrain sites before and after the 2005 hurricanes. Collections were made during peak seasons for each species: *B. patronus* (April-June) *M. undulatus* (May-September), *S. maculatus* (August-October), and *C. arenarius* (June-September). In gillnet collections 665 taken after the 2005 hurricanes, *B. patronus* increased significantly (Friedman's test,  $\chi^2$ =5.00, p = 0.025) while the other three 666 species decreased significantly: *M. undulatus* (Friedman's test,  $\chi^2$ =5.00, p = 0.025), *S. maculatus* (Friedman's test,  $\chi^2$ =4.00, p = 667 0.046), and *C. arenarius* (Friedman's test,  $\chi^2$ =4.00, p = 0.046). 

 **Table 1** Numbers of nekton collections made from Lake Pontchartrain 672 both pre- (2000-2003, 2005) and post-hurricanes (2005-2009) using three 673 gear types: trawls, beach seines, and gillnets.



**Table 2** Pre/post mean abundances, contribution percentages, and cumulative percentages for those species that contributed significantly to pre/post hurricane differences in assemblages from SIMPER analyses. Results are by season and gear type from trawl (2 seasons), beach seine (3 seasons), and gillnet (1 season) collections. Note that for the sake of clarity in interpretation, we here report actual mean abundances per collection whereas typical SIMPER tables reports transformed mean abundances.







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706 **Table 3** Mean values and standard errors (S.E.) for environmental variables measured pre- and post-hurricanes by gear and season.

707 Significance (p) values for the factor Pre/Post hurricanes were calculated from either MANOVA/ANOVA, ANOVA, or Friedman's

708 tests. MANOVA was performed when the test of the preliminary assumption that the covariance matrices of the dependent variables

709 are the same across groups in the population was met, as indicated by the Box's test. For those combinations of environmental

710 variables that could be tested by MANOVA, this test was performed with the environmental variables as dependent factors and

711 Pre/Post (shown), Site, and Pre/Post\*Site as the independent factors. For MANOVA, the Overall Pre/Post significance value indicates

712 the significance of the Pre/Post factor. If this was significant, subsequent ANOVAs were run for each variable, with the *post-hoc* error

713 rate adjusted to 0.025. If the Box's test was significant or the MANOVA could not be performed, an ANOVA was performed

714 individually for each variable, without the error rate adjustment. ANOVAs were performed for those variables that met the

715 homogeneity of variance test (Levene's). If ANOVA could not be performed (i.e., Levene's test was significant), then Friedman's test

716 (a non-parametric rank-based procedure; seasonally, with site averages as the block and Pre/Post as the factor) was performed.

717 Bolded values indicate significant results and Pre/Post trends in environmental variables are indicated.































trawl collection sites

Figure 5







gillnet collection sites

Figure 7 part 1



gillnet collection sites

Figure 7 part 2