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

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1 Title: Response of Lake Pontchartrain Fish Assemblages to Hurricanes Katrina and Rita

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45 Abstract: To assess possible impacts on Lake Pontchartrain fishes from the 2005 hurricanes, we
46 compared trawl, beach seine, and gillnet collections taken before (2000-2003, 2005) and after
47 (2006-2009) to determine if significant assemblage changes occurred. We also compared basic
48 environmental variables to test for hurricane-related changes. Significant post-hurricane changes
49 in fish assemblages occurred in trawl (ANOSIM, $R < 0.090$, $p < 0.05$) and beach seine
50 (ANOSIM, $R < 0.120$, $p < 0.05$) collections across all seasons. Gillnet assemblages exhibited
51 changes in only one season (ANOSIM, $R = 0.045$, $p < 0.05$). These consistently low global R
52 values (all $R < 0.120$) across all gears suggest only minor compositional changes in species.
53 When peak abundance periods were compared for individual species, Gulf menhaden
54 (*Brevoortia patronus*) declined in trawl collections after the hurricanes (Friedman's test, $\chi^2 =$
55 6.00 , $p = 0.014$) but increased in gillnet collections (Friedman's test, $\chi^2 = 5.00$, $p = 0.025$).
56 Hardhead catfish (*Ariopsis felis*) increased in trawl collections, but Gulf pipefish (*Syngnathus*
57 *scovelli*), naked gobies (*Gobiosoma bosc*), and rough silverside (*Membras martinica*) all
58 declined in beach seine samples and Atlantic croakers (*M. undulatus*), Spanish mackerel
59 (*Scomberomorus maculatus*), and sand seatrout (*Cynoscion arenarius*) all declined in gillnet
60 samples. In general, salinity increased and water clarity and dissolved oxygen decreased after
61 the hurricanes. While the overall composition of Lake Pontchartrain fish assemblages remains
62 stable, the significant decline of some species and changes in certain environmental variables are
63 cause for concern. Future monitoring should determine if all elements of this estuary will
64 recover from these impacts.

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68 Keywords: fish assemblages, hurricanes, Lake Pontchartrain, Hurricane Katrina, Hurricane Rita

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Introduction

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Estuarine fish assemblages typically exhibit resilience to large-scale natural disturbances such as hurricanes (Greenwood et al. 2006; Stevens et al. 2006; Switzer et al. 2006). While acute assemblage impacts may occur in the short-term due to hypoxic conditions (Stevens et al. 2006) or other immediate changes in water quality (Greening et al. 2006), for the most part estuarine fish populations recover by the following season if not sooner. Unlike less mobile estuarine organisms such as benthic infauna (Poirrier et al. 2008), adult fishes can actively swim to avoid hazardous conditions and re-colonize affected habitats soon after disturbances (Greenwood et al. 2006). More severe hurricane assemblage impacts have been observed in physically restricted estuarine habitats such as coastal streams (Van Vrancken and O'Connell 2010) and tidal freshwater marshes (Piazza and La Peyre 2009) where extensive habitat damage occurs. Fish assemblage recovery in these habitats is also slower because their hydrologically isolated nature precludes rapid recolonization.

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Although estuarine fishes in the southeastern United States have evolved resiliency to hurricanes, their ability to recover may be reduced in systems where anthropogenic disturbances occur alongside natural disturbances (Mallin and Corbett 2006). Short-term resiliency to disturbances by estuarine fishes may hide significant long-term impacts associated with artificially altered habitats. For example, in Lake Pontchartrain (a large oligohaline embayment that borders New Orleans in southeastern Louisiana) we observed little to no year-to-year fish assemblage change in a short term (three years) study (O'Connell et al. 2006). When we used a larger data set that ranged over the last half century, though, we identified marked declines in a common benthic fish species (Atlantic croaker, *Micropogonias undulatus*) and these impacts

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

114 Hurricanes Katrina and Rita struck southeastern Louisiana in autumn 2005 causing a
115 unique combination of both natural and anthropogenic impacts for the Lake Pontchartrain
116 ecosystem. Natural impacts from both storms included large storm surges (2 - 4 m) which
117 inundated the estuary and caused extensive infauna mortality (Poirrier et al. 2008). The most
118 prominent anthropogenic impact associated with the 2005 storms was the discharge of
119 floodwaters from inundated New Orleans into Lake Pontchartrain (Hoe et al. 2006; Van Metre et
120 al. 2006). These stagnant floodwaters had remained in the flooded city for three weeks after
121 Hurricane Katrina struck and were assumed to be a highly toxic combination of biological and
122 chemical components (Farris et al. 2007). To assess possible impacts on Lake Pontchartrain fish
123 assemblage due either to natural or anthropogenic impacts associated with the 2005 hurricanes,
124 we compared monthly trawl, beach seine, and gillnet collections taken at six sites before (2000-
125 2003, 2005) and after (2006-2009) to determine if significant assemblage changes occurred. We
126 also tested for significant post-hurricane declines or increases in abundant or influential fish

127 species. To better understand whether natural or anthropogenic impacts drove assemblage
128 change, we also compared pre- and post-hurricane measurements of basic water quality
129 parameters.

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Materials and Methods

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Study location

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Lake Pontchartrain is a semi-enclosed oligohaline estuary with a surface area of 1,630 km² and a mean depth of 3.7 m (Sikora and Kjerfve 1985). It experiences low tidal ranges (Swenson 1980) and receives fresh water input from Lake Maurepas to the west and numerous rivers and streams along its northern shore. During periods of extremely high discharge (e.g., 2008, 2011), Mississippi River water is diverted into the Lake via the Bonnet Carre Spillway which is located in the southwest region of the Lake. Sources of pollution include urban runoff from the Greater New Orleans Metropolitan Area (GNOMA) and agricultural runoff from rivers and streams along the northern shore (Penland et al. 2002). Much of the southern shore is armored and limited beds of submersed aquatic vegetation (SAV) still occur, mostly along shore in the northeast region of the Lake. Until recently, there was an artificial connection between Lake Pontchartrain and the Gulf of Mexico via connections with the Mississippi River Gulf Outlet (MRGO). This connection allowed higher salinity water to enter the southeastern region of the Lake. When New Orleans was pumped dry after the 2005 hurricanes, the storm water was released into the estuary through outfall canals on the southern shore.

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Data Collection

For both pre- and post-hurricane sampling, fishes were collected using three gear types: trawls, beach seines, and gillnets. Trawl sampling in demersal habitats involved using a 4.9 m otter trawl, consisting of a 16 mm bar mesh body and a 6.3 mm bar mesh tail. Since Lake Pontchartrain has an average depth of 4.27 m, the standard scope ratio of 7:1 was maintained by using 30.5 m warps connected to the standard 40 cm X 76 cm wooden doors. The tow duration was maintained at 10 minutes and the speed kept at a constant 1.83 m/s using a GPS receiver. For shallow nearshore habitats, we used a 15.25 m X 1.83 m bag seine with 0.95 cm mesh which was pulled to sample 50 m X 15.25 m of habitat at each site. In deeper pelagic habitats, we fished a 250 m X 3.66 m gillnet with different mesh sizes: bar measurement was 5.08, 6.35, 7.62, 8.89, and 10.16 cm for five equally sized panels. Gillnets were fished using the strike method which involves setting the net and circling it three times with a boat to drive fishes into the panels.

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-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 surface water temperature (°C) were measured.

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Data Analyses

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Prior to assessing possible long-term assemblage changes, we tested for short-term, acute assemblage changes immediately following the hurricanes. We pooled the data by year and for all gear types and performed non-metric multidimensional scaling (MDS) plots to determine if 2006 assemblages (those collected in the year following the hurricanes) differed from those in subsequent years. In these plots, multi-dimensional relationships are represented in a two dimensional graph and assemblages that are more similar in species composition appear closer together. The resulting MDS plots showed no evidence that 2006 assemblages were different from subsequent years for all gear types. Based on these results, we included data from 2006 in all of our analyses.

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To determine if fish assemblages changed after the 2005 hurricanes, we conducted analysis of similarity (ANOSIM) to compare species composition using PRIMER v6 software (Clarke and Warwick 2001). This multivariate method compares multiple assemblages and establishes if statistically significant differences exist among them. Because estuarine fish assemblages change seasonally (e.g., influx of marine species), we minimized this potential influence by only comparing collections made in the same time period or season. We determined seasons for each gear type by using agglomerative hierarchical clustering with group-average linking (Kaufman and Rousseeuw 1990, Clarke and Warwick 2001) to group months containing similar fish assemblages into seasonal groups (Idelberger and Greenwood 2005). After determining seasons for each gear type, we compared collections taken before 2005 in a given season with collections taken after 2005 in the same season, and so on. We repeated this for all seasons and for all three gear types. For each analysis, seasonal collections taken at either

196 five (beach seine and gillnet) or six (trawl) sites were used such that each ANOSIM typically
197 compared from 60 to 168 pre-2005 collections with 60 to 168 post-2005 collections, with 60
198 representing the shortest calculated season (beach seine collections from April to June: 3 months
199 X 5 sites X 4 years) and 168 representing the longest calculated season (trawl collections from
200 November to May: 7 months X 6 sites X 4 years). Seasonal data were analyzed using a two-way
201 crossed ANOSIM design with site and pre/post 2005 as factors. If a collection contained no
202 fishes, it was omitted from the analysis. While these omissions sometimes generated unequal
203 sample sizes, two-way crossed ANOSIM is robust to minor amounts of missing data (Clarke and
204 Warwick 2001). To minimize the influence of rarer species, all abundance data were square root
205 transformed prior to analysis. If a significant difference was detected, we used the PRIMER
206 similarity percentages routine (SIMPER) to determine which species contributed most to the
207 observed change in species composition. We also generated MDS plots to present the
208 relationships between pre- and post-hurricanes assemblages for each season and each gear type.

209 To test for possible significant post-hurricane declines or increases in those fish species
210 that were determined to contribute to assemblage dissimilarity based on the SIMPER results or
211 those that were the top 15 most common species collected by each gear type, we used multiple
212 Friedman's tests. To account for seasonality, we limited our analyses to the 1-7 month
213 abundance peak for each individual species for each gear type. This peak was determined by
214 comparing mean monthly abundances for each species and choosing the multi-month period with
215 the highest abundances. With this non-parametric rank-based procedure, we assessed the
216 species' data using site averages as the block (that is, the average abundance of a species at one
217 site over the four year pre/post period) and pre/post 2005 as the factor.

218 We compared pre- and post-hurricane measurements of salinity, dissolved oxygen,
219 Secchi depth, and surface water temperature to determine if they possibly influenced observed
220 fish assemblage changes. We used multivariate analysis of variance (MANOVA) on these
221 variables only for seasons (determined previously by agglomerative hierarchical clustering) and
222 gear types when a significant assemblage change was measured using ANOSIM. For example,
223 for a given trawl season data were compared using measurements collected from the six sites
224 before (2000-2003, 2005) and six sites after (2006-2009) the hurricanes. For each set of seasons
225 analyzed, data were organized with individual sites as factors and multiple years as replicates. If
226 tests for homogeneity of variances could not be met (even with severe transformations), then
227 those single variables causing the lack of homogeneity were removed and a MANOVA was
228 conducted on the remaining variables. If only one variable exhibited homogeneity of variances,
229 then an ANOVA was used to compare pre/post 2005 data. Those single variables that exhibited
230 no homogeneity of variances were compared using Friedman's test (as explained above).

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Results

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For trawl data, two seasons were identified by cluster analysis: November through May (Season I) and June through October (Season II). Benthic fish assemblages (those collected by trawls) exhibited significant post-hurricane changes in both seasons (ANOSIM, $R < 0.09$, $p < 0.05$). It should be noted, though, that this low global R value suggests only minor changes in species composition between periods, with pre/post- assemblages exhibiting little to no multivariate separation in the generated MDS ordination (Fig. 2). In both seasons, SIMPER analyses revealed that bay anchovies (*Anchoa mitchilli*) and Atlantic croaker (*Micropogonias*

241 *undulatus*) were more numerous after the hurricanes, while in both seasons Gulf menhaden
242 (*Brevoortia patronus*) were less numerous in post-hurricane trawls (Table 2). For both seasons,
243 SIMPER analyses also revealed that *A. mitchilli* contributed most to the observed fish
244 assemblage changes with *M. undulatus* the being the second-most influential species (Table 2).

245 Beach seine data were more distinctly clustered into three seasonal groupings: December
246 through March (Season I), April through June (Season II), and July through November (Season
247 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,
249 the low global-R value suggests minor changes in species composition between periods and
250 assemblages showed little to no multivariate separation in the MDS ordination (Fig. 3). In all
251 three seasons, *A. mitchilli* and *M. beryllina* were less numerous after the storms and these
252 species contributed the most to assemblage differences in two of the seasons. The change in
253 assemblage in the remaining season (II) was attributed mostly to a decrease in *B. patronus*.
254 While this species and *M. undulatus* decreased in two seasons, both species experienced
255 increases in the remaining season.

256 As with the trawl data, gillnet data also clustered into two less distinct seasonal groups,
257 but these consisted of samples collected from April through October (Season I) and November
258 through March (Season II). Gillnet collections yielded only one season (Season I) with
259 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
261 MDS ordination (Fig. 4). SIMPER analyses revealed that differences in this season's collected
262 assemblages were attributed to post-hurricane decreases in *B. patronus* along with increases in

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

265 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
268 (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
276 fish species, there were no significant differences in pre/post-hurricane abundances.

277 Trends for some species as measured by the SIMPER analyses did not always agree with
278 those from the Friedman analyses. For example, while *M. undulatus* was an important
279 contributor to assemblage changes in trawl collections, there was no significant change in its
280 abundance. Likewise, in beach seine collections none of the species that experienced significant
281 declines were important in driving pre/post- assemblage changes based on SIMPER analyses
282 (Table 2). For the gillnet data, there is an apparent discrepancy between an increase in *B.*
283 *patronus* during its peak abundance period (April-June) and its supposed decrease during Season
284 I (April-October). According to the SIMPER results, this latter decrease contributed greatly to
285 the measured assemblage difference, with *B. patronus* being the most influential fish species

286 (Table 2). Although the abundance of *B. patronus* in collections made this species highly
287 influential to assemblage compositions, the observed discrepancies suggest that pre/post values
288 were actually similar (pre-hurricane mean abundance per collection = 19.42 and post-hurricane
289 mean abundance per collection = 19.40; Table 2). Also, while changes in the abundance of *M.*
290 *undulatus* contributed somewhat to measured assemblage change in Season I (it was the fourth
291 most influential species), neither *S. maculatus* nor *C. arenarius* (both of which experienced
292 significant changes in abundance), contributed markedly to this assemblage change according to
293 SIMPER results (Table 2).

294 Salinity was significantly lower (ANOVA, $p = 0.042$) after the 2005 hurricanes as
295 measured during Season I trawl collections (Table 3) but was significantly higher for
296 measurements during Season II trawl collections (ANOVA, $p = 0.011$) and Seasons I
297 (Friedman's test, $p = 0.025$) and II (MANOVA, $p = 0.001$) beach seine collections. Dissolved
298 oxygen was significantly lower after the hurricanes for measurements taken during Seasons I and
299 II trawl collections (ANOVA, $p < 0.001$; Table 3), Seasons I (ANOVA, $p < 0.001$) and II
300 (MANOVA, $p = 0.008$) beach seine collections, and Season I gillnet collections (ANOVA, $p <$
301 0.001). Water clarity as measured by Secchi depth was significantly higher prior to the
302 hurricanes during Season I (ANOVA, $p < 0.001$) and II (Friedman's test, $p = 0.014$) trawl
303 collections and also during Season I (ANOVA, $p = 0.004$) seine collections (Table 3). All other
304 pre/post comparisons of these variables, along with pre/post comparisons of water temperature,
305 were non-significant (Table 3).

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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

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

343 In trawl collections after the 2005 hurricanes, the ecologically and economically
344 important species *B. patronus* decreased significantly during its typical period of peak abundance
345 (March through May). This filter-feeding species serves as a prey item for many other fishes and
346 supports one of the top fisheries by volume in the United States (Smith 2001; Vaughan et al.
347 2011). The extent to which *B. patronus* influences estuarine communities in the northern Gulf of
348 Mexico makes this species an indicator of the overall health and productivity of these aquatic
349 systems (Vaughan et al. 2011). Trawl sampling in Lake Pontchartrain mostly collects juvenile *B.*
350 *patronus*, not adults. During the spring (again, March through May) juvenile *B. patronus*
351 typically use upper estuaries such as Lake Pontchartrain as nurseries. Higher salinities could
352 have driven these fish to use other less saline habitats farther up the estuary such as Lake
353 Maurepas, similar to the results of other studies of Lake Pontchartrain (Cashner et al. 2001) and
354 elsewhere (Haley et al. 2010; VanderKooy 2011). But salinities were lower after 2005 during

355 Season I (November through May) trawl collections which coincided with the period of peak
356 abundance of *B. patronus* in the trawl (March through May), even though salinities were
357 typically higher in other post-hurricane comparisons (Table 3). Another explanation for the
358 decline in *B. patronus* is that significantly lower dissolved oxygen levels in both trawl seasons
359 caused these fish to avoid portions of Lake Pontchartrain. While these lower dissolved oxygen
360 levels were not hypoxic (lowest measurement = 4.60 mg/l), nearby ‘dead zones’ had been
361 identified farther down the estuary in Chandeleur Sound during the same period (Lopez et al.
362 2010). In avoiding hypoxic or anoxic areas, aquatic organisms (including *B. patronus*) can
363 become concentrated in normoxic water, thus making them more vulnerable to fishing effort
364 (Smith 2001; Burkholder et al. 2004; Breitburg et al. 2009). Local commercial fishing pressure
365 on *B. patronus* has actually been reduced following the 2005 hurricanes due to damage to fishery
366 infrastructure, but fishing mortality has also increased possibly due to *B. patronus* displaced
367 from offshore hypoxic zones being captured more effectively in near shore waters (Vaughan et
368 al. 2007). A similar fishery response was observed in the Albemarle–Pamlico Estuarine System
369 in North Carolina and Virginia after the active 1999 hurricane season which included three
370 named storms impacting the region (Burkholder et al. 2004). Hurricane floodwaters displaced
371 high numbers of blue crabs (*Callinectes sapidus*) causing them to “hyperaggregate” in areas
372 where they were exposed to increased commercial fishing pressure (Burkholder et al. 2004).
373 This, in turn, resulted in a 70% reduction of adult *C. sapidus* in 1999-2002 (Burkholder et al.
374 2004).

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

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

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

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

414 In gillnet collections, *B. patronus* increased after the hurricanes during its peak
415 abundance period, yet this result seemed to contradict both an assemblage-driving decrease
416 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
418 in-consequential decrease in mean abundance per collection from 19.42 to 19.40 individuals after
419 the hurricanes. The discrepancy between the gillnet and trawl results likely represents a
420 difference in response to the hurricanes by two different life stages of *B. patronus*. Adult *B.*
421 *patronus* are typically only collected in gillnets while juveniles are most numerous in trawl
422 collections. We suggest that adult *B. patronus* (age 2-4 years) fared better after the hurricanes
423 than juveniles because of their superior swimming ability that allows them to avoid hazardous

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

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

447 *R. cuneata*, also likely displaced many polychaete worms, a key diet item for *M. undulatus*.
448 While *C. arenarius* feeds more on penaeid shrimp and *A. mitchilli*, this species is more benthic-
449 oriented than its sister species *C. nebulosus* and the disruption of the benthic habitat of its prey
450 may have led to its decline. Of the three species that declined in gillnet Season I, *S. maculatus* is
451 the only truly marine species (compared to the two estuarine dependent drum species). This
452 species is an uncommon late-summer visitor to the estuary, typically occurring in drier years
453 (e.g., 2000 and 2001). It is possible that their decline is more the reflection of a lack of true
454 drought years after the hurricanes rather than impacts from the storms themselves.

455 After the storms, environmental variables were typical of conditions measured
456 immediately after other hurricanes in the southeastern United States. Higher salinity, lower
457 dissolved oxygen, and increased turbidity are common outcomes of hurricane landfalls in
458 estuaries (Tabb and Jones 1962; Burkholder et al. 2004; Mallin and Corbett 2006; Stevens et al.
459 2006; Edmiston et al. 2008). A repeated theme among these studies of immediate hurricane
460 impacts on estuaries is that conditions quickly return to normal, including the composition of
461 local fish assemblages (Tabb and Jones 1962; Piazza and La Peyre, 2009; Rodgers et al. 2009).
462 The changes in fish assemblages after the 2005 hurricanes were often associated with increases
463 of influential species and in many seasons the abundances of other common species remained
464 stable (Table 2). Though there is concern for species that consistently declined over multiple
465 gear types (e.g., *B. patronus*) it appears that many of the hurricanes' impacts on local species are
466 short-lived. Even though many water quality parameters were significantly different after the
467 hurricanes, our post-hurricane period lasted four years beyond the storms, long after
468 environmental variables should typically revert back to normal. In some cases, it is possible that

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

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

492 which may hide long-term significant declines in species, such as those we have measured in
493 Lake Pontchartrain (O'Connell et al. 2004; O'Connell et al. 2007).

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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, $\chi^2=5.00$, $p = 0.025$).

662 **Fig. 7** Mean number of *B. patronus*, *M. undulatus*, *S. maculatus*, and *C. arenarius* collected by gillnets at five Lake Pontchartrain sites
663 before and after the 2005 hurricanes. Collections were made during peak seasons for each species: *B. patronus* (April-June)
664 *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, $\chi^2=4.00$, $p = 0.046$).

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671 **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.

	Year	Trawl	Beach Seine	Gillnet
Pre-Hurricanes				
	2000	54	30	18
	2001	125	60	41
	2002	98	59	47
	2003	44	27	17
	2004	20	11	7
	2005	<u>69</u>	<u>37</u>	<u>23</u>
	Total	410	224	153
Post-Hurricanes				
	2005	5	13	0
	2006	96	59	36
	2007	113	60	47
	2008	130	60	52
	2009	<u>111</u>	<u>60</u>	<u>45</u>
	Total	455	252	180

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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.

Gear-Season	Species	Pre-hurricane mean abundance per collection	Post-hurricane mean abundance per collection	Percent contribution to assemblage change	Cumulative percent contribution to assemblage change
Trawl-Season I (Nov.-May)	<i>Anchoa mitchilli</i>	154.39	262.81	55.15	55.15
	<i>Micropogonias undulatus</i>	14.65	18.26	18.10	73.25
	<i>Brevoortia patronus</i>	20.64	4.42	13.19	86.44
	<i>Cynoscion arenarius</i>	1.12	0.78	2.89	89.93
	<i>Ictalurus furcatus</i>	0.25	0.14	1.29	90.61
Trawl-Season II (Jun.-Oct.)	<i>Anchoa mitchilli</i>	481.58	853.38	71.48	71.48
	<i>Micropogonias undulatus</i>	11.21	12.08	10.68	82.17
	<i>Cynoscion arenarius</i>	0.63	2.51	4.22	86.38
	<i>Brevoortia patronus</i>	2.20	0.73	2.41	88.79
	<i>Anchoa hepsetus</i>	0.38	0.17	1.83	90.62
Seine-Season I (Dec.-Mar.)	<i>Menidia beryllina</i>	61.12	48.60	20.00	20.00
	<i>Anchoa mitchilli</i>	72.58	17.65	16.98	36.98
	<i>Micropogonias undulatus</i>	41.07	13.18	13.78	50.76
	<i>Brevoortia patronus</i>	112.67	5.05	12.92	63.68
	<i>Mugil cephalus</i>	7.80	1.24	5.77	69.45

	<i>Mugil curema</i>	23.24	2.76	4.55	74.00
	<i>Leiostomus xanthurus</i>	33.29	4.72	3.86	77.86
	<i>Fundulus grandis</i>	0.87	2.34	3.48	81.34
	<i>Cyprinodon variegatus</i>	3.70	1.66	2.89	84.23
	<i>Gobiosoma bosc</i>	2.88	0.19	2.53	86.76
	<i>Lucania parva</i>	11.50	0.34	2.01	88.77
	<i>Fundulus similis</i>	0.17	1.96	1.99	90.76
Seine-Season II (Apr.-Jun.)	<i>Brevoortia patronus</i>	462.79	265.60	25.36	25.36
	<i>Anchoa mitchilli</i>	92.76	22.43	11.61	36.97
	<i>Menidia beryllina</i>	87.93	23.47	11.18	48.16
	<i>Micropogonias undulatus</i>	18.28	37.90	8.99	57.15
	<i>Mugil cephalus</i>	15.95	9.22	5.24	62.39
	<i>Leiostomus xanthurus</i>	20.12	5.07	4.40	66.79
	<i>Lucania parva</i>	58.41	0.63	3.40	70.19
	<i>Fundulus grandis</i>	3.40	2.02	2.60	72.79
	<i>Strongylura marina</i>	1.76	1.98	2.52	75.31
	<i>Elops saurus</i>	1.69	1.03	2.44	77.75
	<i>Cyprinodon variegatus</i>	11.26	0.72	2.25	80.00
	<i>Gobiosoma bosc</i>	2.33	0.33	2.00	82.00
	<i>Lagodon rhomboides</i>	3.24	0.45	1.89	83.89
	<i>Syngnathus scovelli</i>	2.76	0.30	1.83	85.72
	<i>Membras martinica</i>	2.00	0.27	1.65	87.37
	<i>Cynoscion arenarius</i>	1.22	0.68	1.65	89.01
	<i>Fundulus similis</i>	0.78	1.20	1.19	90.20
Seine- Season III (Jul.-Nov.)	<i>Anchoa mitchilli</i>	107.88	62.26	21.88	21.88
	<i>Menidia beryllina</i>	97.47	14.48	14.48	36.36
	<i>Mugil cephalus</i>	4.66	2.34	5.86	42.22

	<i>Elops saurus</i>	1.27	4.67	4.87	47.10
	<i>Micropogonias undulatus</i>	4.49	1.29	4.29	51.39
	<i>Brevoortia patronus</i>	3.18	16.24	4.17	55.56
	<i>Cynoscion nebulosus</i>	2.17	1.22	3.94	59.50
	<i>Strongylura marina</i>	1.24	2.42	3.67	63.17
	<i>Membras martinica</i>	2.59	1.10	3.38	66.55
	<i>Gobiosoma bosc</i>	2.99	0.06	2.25	68.80
	<i>Fundulus grandis</i>	1.12	0.92	2.12	70.92
	<i>Leiostomus xanthurus</i>	0.92	0.70	2.11	73.03
	<i>Lagodon rhomboides</i>	0.99	1.17	2.00	75.03
	<i>Syngnathus scovelli</i>	4.03	0.63	1.93	76.96
	<i>Oligoplites saurus</i>	0.48	0.79	1.90	78.85
	<i>Lucania parva</i>	5.04	0.24	1.57	80.42
	<i>Bairdiella chrysoura</i>	0.80	1.32	1.46	81.88
	<i>Anchoa hepsetus</i>	1.14	0.91	1.38	83.27
	<i>Cyprinodon variegatus</i>	4.07	0.08	1.10	84.37
	<i>Ariopsis felis</i>	0.50	0.49	1.10	85.47
	<i>Fundulus similis</i>	0.29	0.47	1.02	86.49
	<i>Mugil curema</i>	0.10	0.35	1.01	87.49
	<i>Sphoeroides parvus</i>	0.70	0.15	0.94	88.44
	<i>Sciaenops ocellatus</i>	0.09	0.66	0.88	89.32
	<i>Gobiesox strumosus</i>	0.42	0.06	0.82	90.14
Gillnet-Season I	<i>Brevoortia patronus</i>	19.42	19.40	24.92	24.92
(Apr.-Oct.)	<i>Bagre marinus</i>	2.85	3.69	18.10	43.02
	<i>Ariopsis felis</i>	1.00	1.43	8.80	51.82
	<i>Micropogonias undulatus</i>	2.54	0.61	8.72	60.54
	<i>Leiostomus xanthurus</i>	2.64	0.89	6.17	66.71

<i>Alosa chrysochloris</i>	0.67	0.51	5.45	72.16
<i>Dorosoma cepedianum</i>	1.12	0.97	5.30	77.46
<i>Cynoscion nebulosus</i>	1.22	0.45	5.23	82.69
<i>Mugil cephalus</i>	0.61	0.16	3.00	85.69
<i>Elops saurus</i>	0.15	0.17	2.65	88.34
<i>Pogonias cromis</i>	0.15	0.38	2.24	90.58

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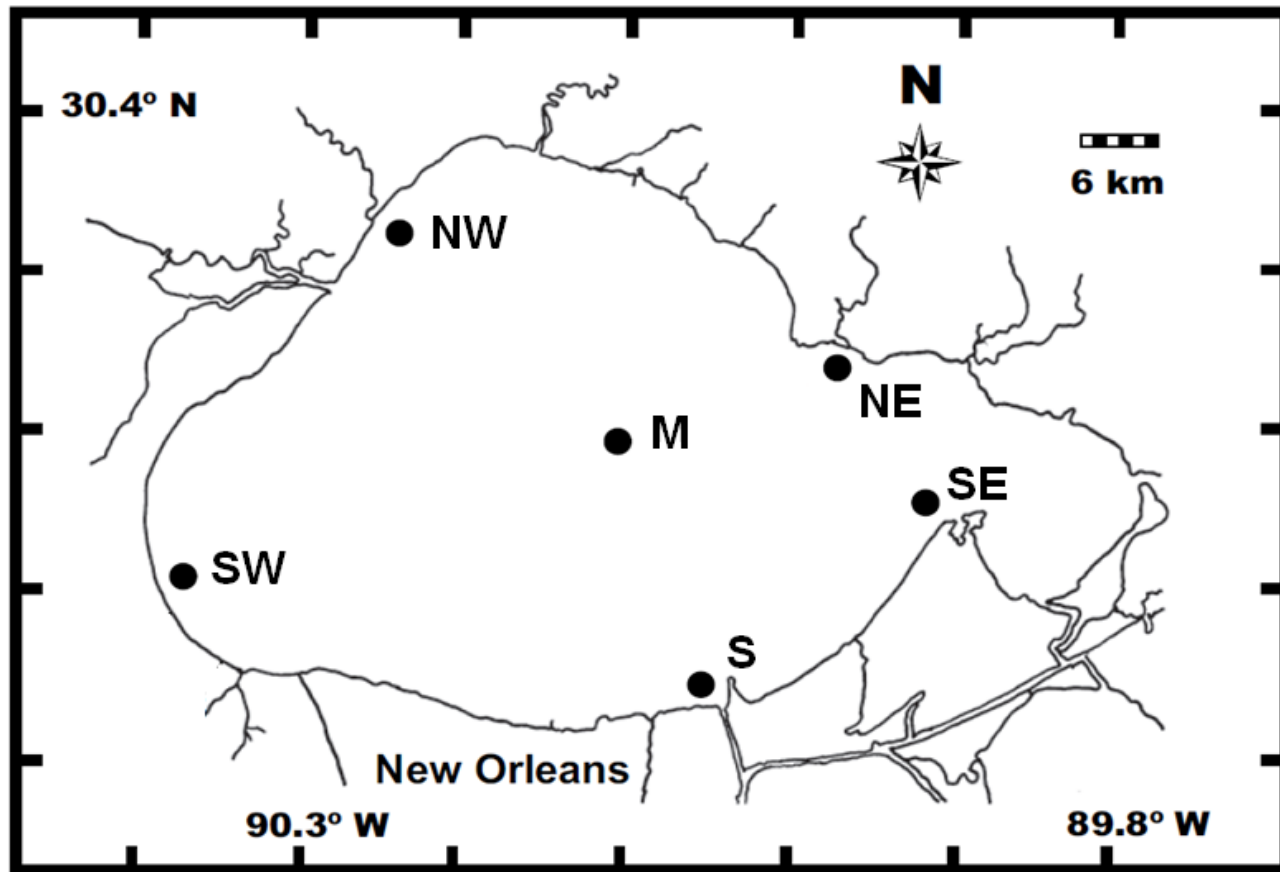
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706 **Table 3** Mean values and standard errors (S.E.) for environmental variables measured pre- and post-hurricanes by gear and season.
707 Significance (p) values for the factor Pre/Post hurricanes were calculated from either MANOVA/ANOVA, ANOVA, 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.
718

Environmental Variable	Gear / Season	Pre-Hurricanes	Post-Hurricanes	Overall MANOVA Pre/Post significance	Individual Pre/Post significance	Trend	Test Used
	Trawl/SI (Nov.-May)	Mean (S.E.)	Mean (S.E.)				
Temperature		18.48(0.36)	18.24 (0.83)		0.208		ANOVA
Water Clarity		1.33(0.04)	0.97(0.10)		0.001	pre>post	ANOVA
Salinity		4.92(0.15)	4.80(0.34)		0.042	pre>post	ANOVA
Dissolved O ₂		8.77(0.09)	8.01(0.21)		0.001	pre>post	ANOVA
	Trawl/SII (Jun.-Oct.)						
Temperature		27.76(0.27)	28.04(0.23)		0.671		ANOVA
Water Clarity		1.55(0.05)	1.34(0.04)		0.014	pre>post	Friedman's
Salinity		5.61(0.20)	5.89(0.18)		0.011	pre<post	ANOVA
Dissolved O ₂		7.04(0.09)	6.57(0.07)		0.001	pre>post	ANOVA
	Seine/SI (Dec.-Mar.)						
Temperature		13.76(0.38)	13.92(0.62)		0.655		Friedman's
Water Clarity		0.82(0.05)	0.60(0.07)		0.004	pre>post	ANOVA

Salinity		4.39(0.25)	4.57(0.42)		0.025			
Dissolved O ₂		9.45(0.16)	8.36(0.26)		0.001		pre<post	Friedman's ANOVA
	Seine/SII (Apr.-Jun.)						pre>post	
Temperature		26.12(0.54)	25.45(0.53)	0.001	0.380			MANOVA/ANOVA
Water Clarity		0.84(0.04)	0.79(0.04)	0.001	0.181			MANOVA/ANOVA
Salinity		3.51(0.22)	4.56(0.21)	0.001	0.001		pre<post	MANOVA/ANOVA
Dissolved O ₂		6.89(0.17)	6.25(0.17)	0.001	0.008		pre>post	MANOVA/ANOVA
	Seine/SIII (Jul.-Nov.)							
Temperature		25.90(0.58)	25.68(0.54)	0.053				MANOVA
Water Clarity		0.89(0.04)	0.84(0.04)		0.655			Friedman's
Salinity		5.76(0.30)	6.05(0.28)		0.180			Friedman's
Dissolved O ₂		6.62(0.15)	6.21(0.14)	0.053				MANOVA
	Gillnet/SI (Apr.-Oct.)							
Temperature		26.76(0.37)	26.47(0.33)		0.493			ANOVA
Water Clarity		1.26(0.06)	1.13(0.05)		0.180			Friedman's
Salinity		4.85(0.25)	5.34(0.23)		0.139			ANOVA
Dissolved O ₂		7.10(0.12)	6.45(0.11)		0.001		pre>post	ANOVA

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Fig. 1

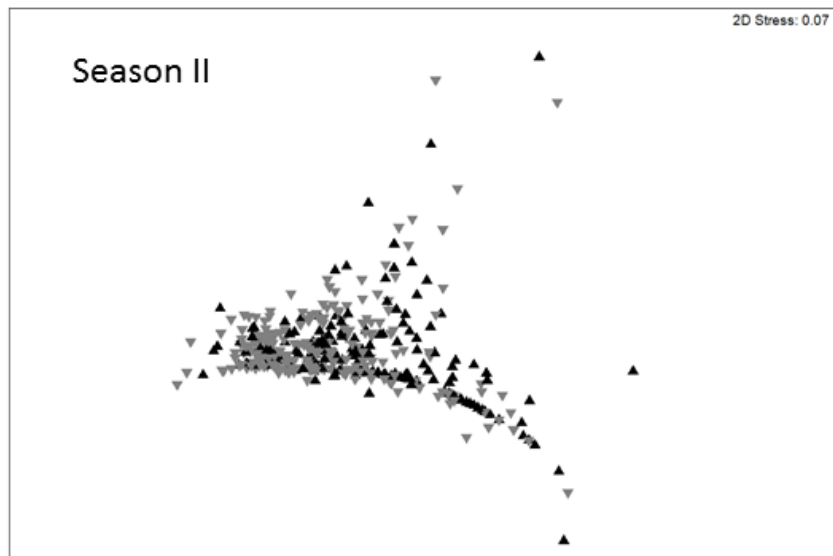
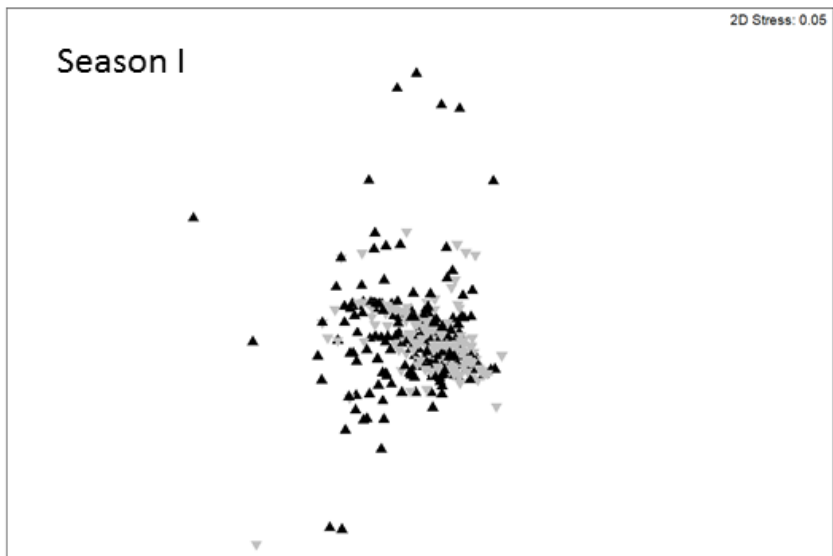


Figure 2

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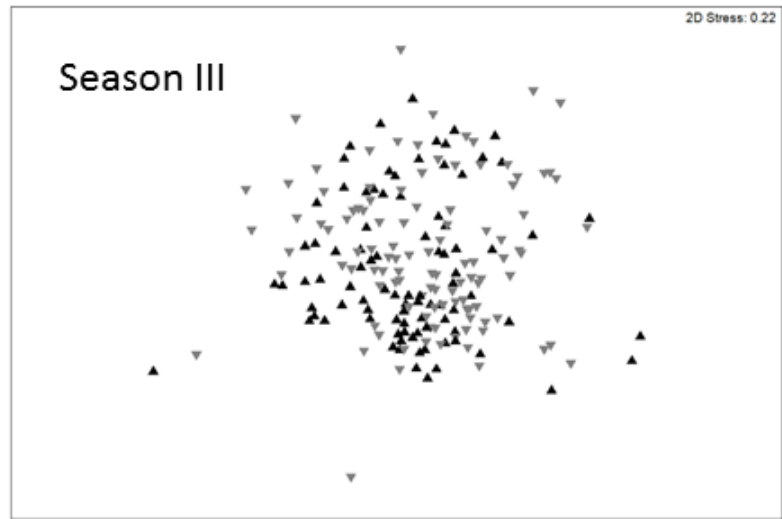
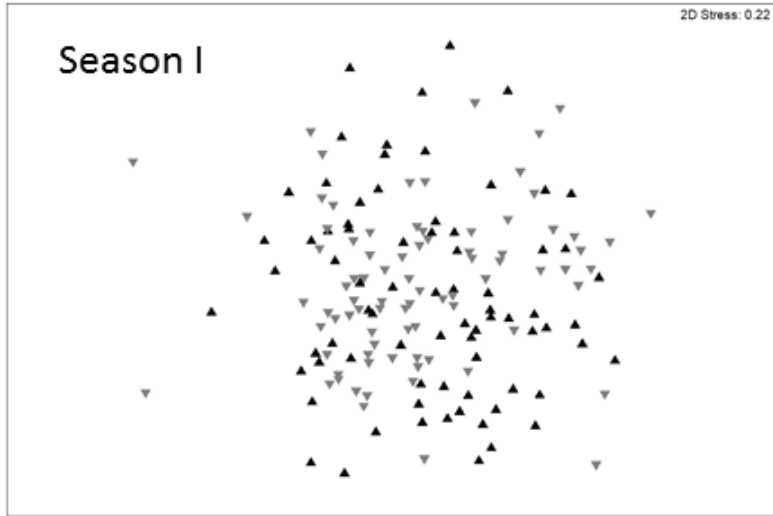


Figure 3

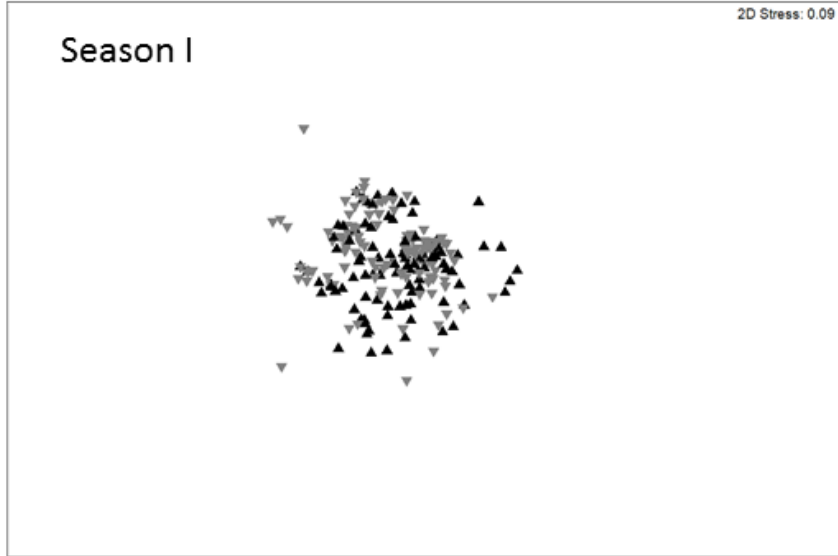


Figure 4

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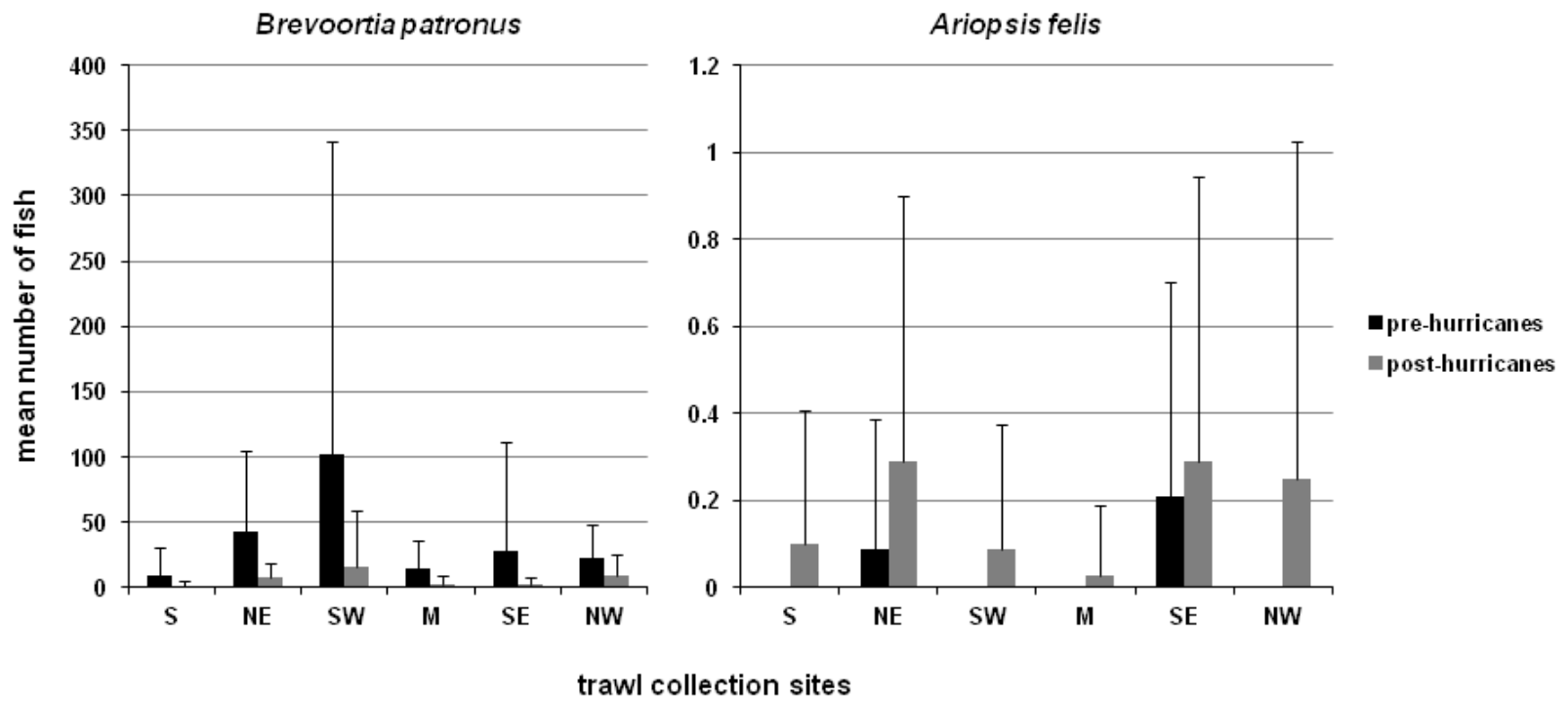


Figure 5

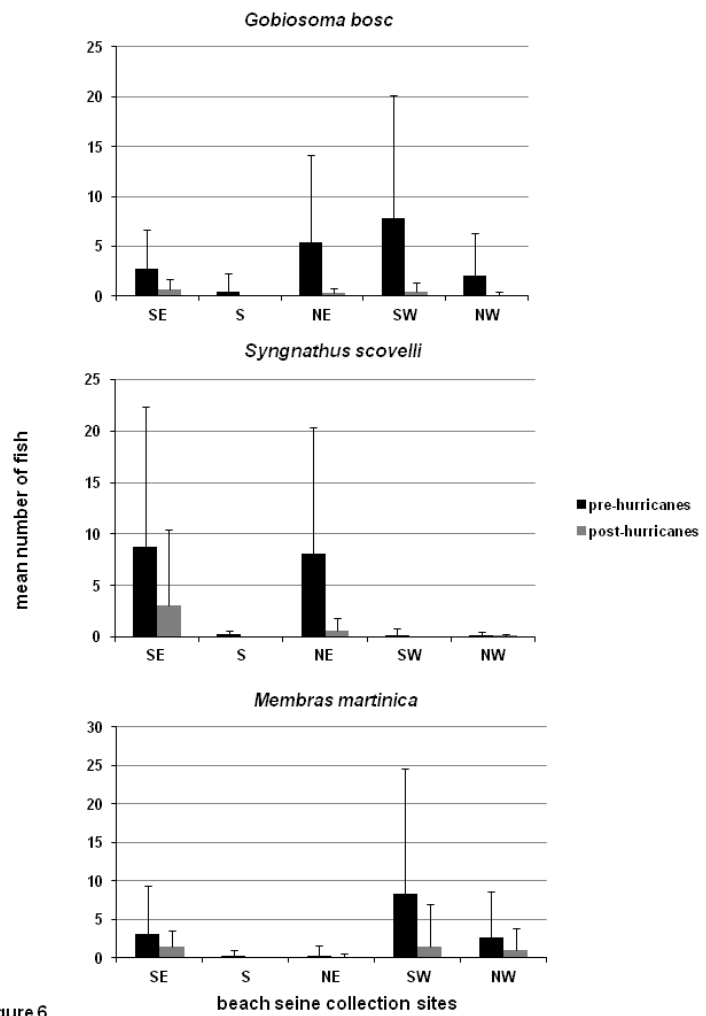


Figure 6

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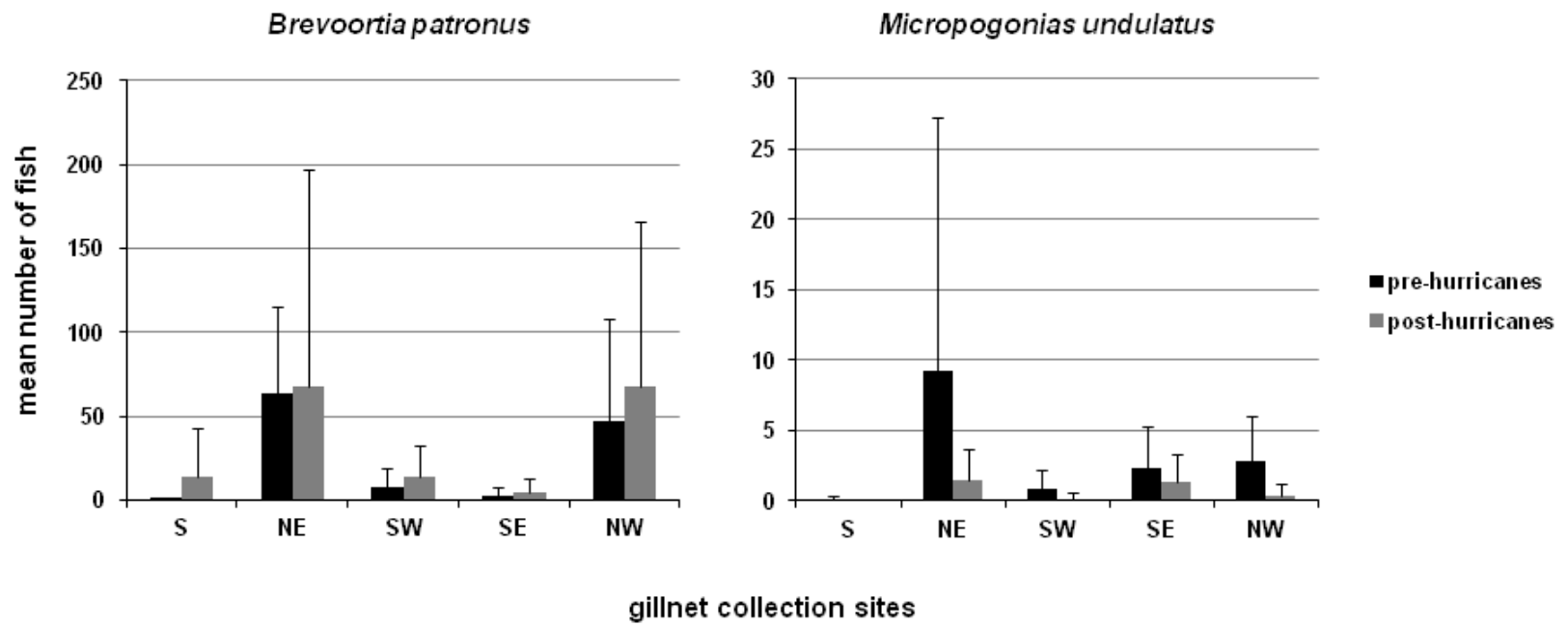


Figure 7 part 1

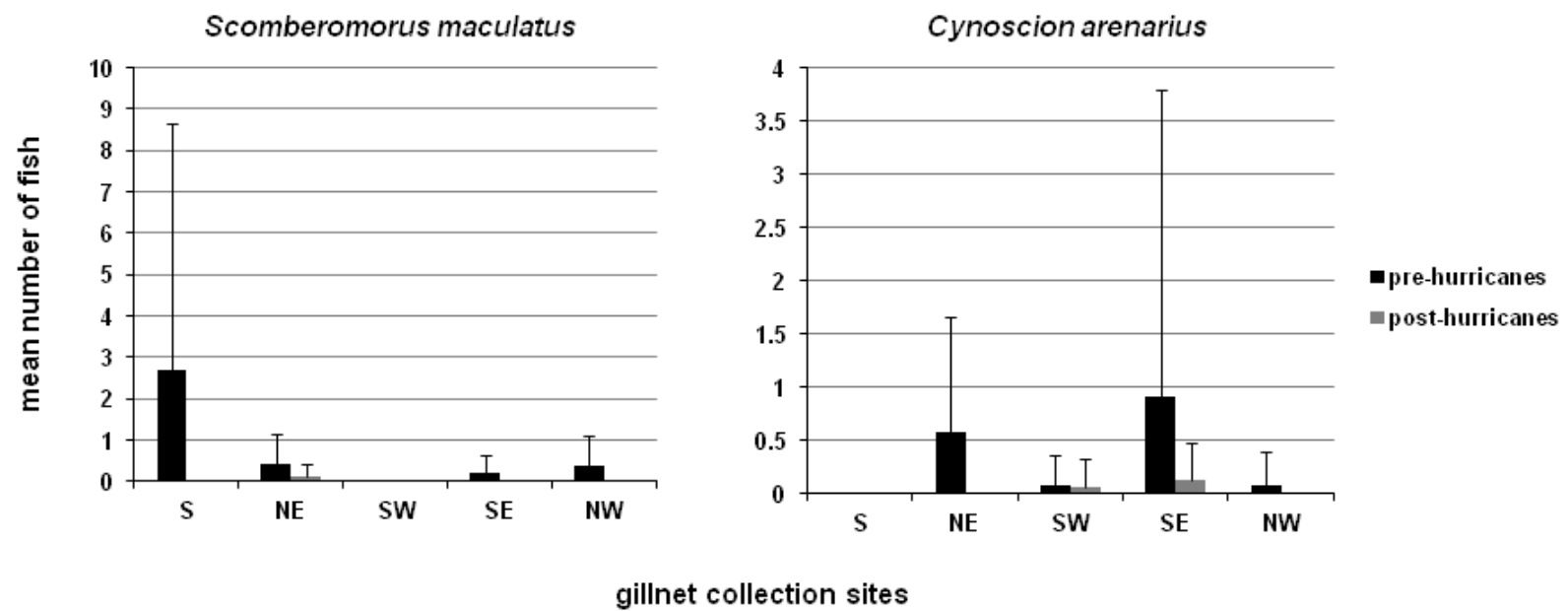


Figure 7 part 2