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Bluebills and bayou bivalves: Hurricane-driven trophic cascades affect wintering abundance of Lesser Scaup in Louisiana

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Abstract. The estuaries of coastal Louisiana overwinter a continentally significant proportion of Lesser Scaup (*Aythya affinis*; colloquially, "bluebills"), a migratory bird species of conservation concern since population declines began in the 1980s. Thirty-eight years of aerial waterfowl surveys of Lake Pontchartrain—an oligohaline estuarine lagoon in southeast Louisiana—show that scaup abundance fluctuates between 0 and 1,194,907 birds, though the mechanisms driving this variation are unknown. Previous studies have shown that scaup feed primarily on mollusks, and so changes in the benthic prey community have the potential to strongly influence scaup dynamics on the Lake. Benthic communities are in turn shaped by both natural and anthropogenic disturbances (e.g., hurricanes and spillway openings), potentially creating a lagged bottom-up trophic cascade that ultimately affects scaup abundance. Using 22 yr of paired benthic invertebrate and aerial waterfowl survey data, we found scaup populations increased with the abundance of medium-sized Rangia clams (*Rangia cuneata*) and Dwarf Surf Clams (*Mulinia lateralis*). Those prey species declined in years when the Lake was hit by a hurricane, but medium-sized Rangia rebounded strongly the year after, likely because storm-surge salinity induces spawning. Using long-term aerial survey data for scaup, we indeed found strong declines on the Lake in years when a hurricane made landfall, but scaup abundance increased the following year, presumably responding to large numbers of medium-sized Rangia. Our three-part analysis makes a strong case for a hurricane-driven bottom-up trophic cascade that affects scaup populations on Lake Pontchartrain. This study adds to a growing literature demonstrating not only that estuaries are tidally and seasonally dynamic, but that punctuated disturbance events can be important for maintaining ecosystem function.

Key words: aerial survey; duck; estuary; Lake Pontchartrain; *Mulinia; Rangia;* trophic cascade; waterfowl.

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Introduction

The estuaries of the Gulf Coast of the southern United States provide critical stopover habitat for neotropical migrants and overwinter millions of waterbirds annually (Wilson et al. 2002). These habitats are particularly imperiled because they suffer from both altered freshwater hydrology (e.g., increased channelization, reduced water and sediment flows) and relative sea-level rise caused by factors like subsidence and climate change (Blum and Roberts 2009). For example, Louisiana alone lost 4877 km^2 of coastal wetlands between 1932 and 2010 (Couvillion et al. 2011), and without substantive intervention, rates of absolute loss and habitat migration are forecast to increase (Couvillion et al. 2013). Estuarine ecosystems are structured strongly by salinity, and so as fresh, brackish, and intermediate estuarine zones become more saline, corresponding shifts in vegetation (DeMarco 2018) and benthic communities (Lowe et al. 2017) are anticipated. Bottom-up trophic effects on fish and wildlife populations seem inevitable (Nyman et al. 2013, Yaukey 2018).

One flagship bird species that uses estuarine habitats in vast numbers during winter is the Lesser Scaup (*Aythya affinis*; colloquially, "bluebills" but hereafter, "scaup"), which has been a species of conservation concern since populations began declining in the mid-1980s (Austin et al. 2000, Anteau et al. 2014). The Mississippi Flyway winters ~40% of the continental scaup population, of which >90% are found in Louisiana (Afton and Anderson 2001). In Louisiana, Lake Pontchartrain—an oligohaline estuarine lagoon—provides habitat for enormous numbers of scaup in some years (1,194,907 counted in a December 2006 aerial survey), but not others (zero birds counted 11 months before January 2006). One potential source for this variation in scaup abundance is coincident variation in food availability on Lake Pontchartrain.

Mollusks are an important food source for scaup throughout their range (Hoppe et al. 1986, Custer and Custer 1996, Perry et al. 2007), and both Bowman (1973) and Stroud (2018) found that clams, mussels, and snails were consumed by scaup wintering on Lake Pontchartrain. However, linking scaup abundance to mollusk abundance is not straightforward. Stroud (2018) found that scaup consumed all sizes of Rangia clams (*Rangia cuneata*) <21 mm, but only preferred medium size classes (6–16 mm), presumably for reasons of relative digestibility and profitability (Richman and Lovvorn 2004, Anteau and Afton 2006). More saline species, such as the Dwarf Surf Clam (*Mulinia lateralis*), were preferentially consumed by scaup but were not common in the benthos during the period of relatively low salinity when their sampling occurred (Stroud 2018).

The benthic invertebrate community on Lake Pontchartrain exhibits extreme fluctuations in overall abundance, biomass, and species and size diversity among years (Poirrier et al. 2009, Poirrier and Caputo 2015). This variation is in turn tied to salinity, which increases during La Niña drought periods and rapidly declines when Mississippi River floodwaters are diverted into the Lake from the Bonnet Carré Spillway (Brammer et al. 2007, Poirrier and Caputo 2015). For example, Rangia clams are generally abundant in the oligohaline waters of Lake Pontchartrain (salinity 0.5–5.0‰) where low species diversity protects them from competition and predation. However, prolonged periods of higher salinity increase species diversity, and the associated competition and predation effectively truncates the size distribution of Rangia to only large clams (Poirrier and Caputo 2015). Hurricanes have the potential to periodically reset the structure of the benthic invertebrate community. Flocks et al. (2009) found that the top 1 m of sediment is fundamentally reworked during major storm events, and because flushing rates are low (Flowers and Isphording 1990), the sediment settles on top of mollusks and causes widespread mortality (Poirrier et al. 2008). In addition, hurricane-driven storm surges create salinity stratification and low dissolved oxygen along the estuary bottom which has the potential to wipe out entire communities; Hurricane Katrina caused mortality in all dominant benthic species at depths greater than 3.7 m, which accounts for approximately half the estuary (Poirrier et al. 2008). However, widespread mortality opens niche space in the Lake, and because Rangia spawning is triggered by salinity shifts of ±5‰ at temperatures >15°C (Cain 1973), hurricanes increase recruitment of Rangia, which is otherwise stifled by intra- and interspecific competition.

Given the dramatic boom-and-bust cycles of mollusks on Lake Pontchartrain, there is clearly the potential for bottom-up trophic effects on annual scaup abundance. Here, we leveraged long-term datasets for mollusk (1996–2017) and scaup abundance (1977–2017) on Lake Pontchartrain to evaluate trophic linkages between scaup and the benthic invertebrate community. We also evaluated the role of environmental disturbances in mediating bottom-up cascades in the estuary. By identifying the drivers of scaup abundance on Lake Pontchartrain, we can begin to address the effects of food variability on wintering waterfowl distributions, which is poorly known for most species and geographies. In addition, identification of the proximate drivers of scaup abundance also should increase our capacity to predict scaup distributions over short-term and long-term scales.

Methods

Study area

Located in southeastern Louisiana (30°11′ N 90°05′ W), Lake Pontchartrain is a 1630 km^2 oligohaline estuarine lagoon with an average salinity of 3.9‰, an average depth of 3.7 m, and a maximum depth of 5 m (Sikora and Kjerfve 1985). From the northwest, Lake Pontchartrain receives freshwater from the Tchefuncte River, Tangipahoa River, and Pass Manchac which opens to Lake Maurepas. There are two natural tidal passes on the eastern portion of the estuary that allow higher salinity water to enter from Lake Borgne and the western Mississippi Sound. The directional combination of freshwater inputs and saltwater influxes creates a salinity gradient that increases from west to east (Sikora and Kjerfve 1985).

Benthic surveys

To estimate benthic invertebrate abundance, we used data from 1996 to 2017 collected along fixed transects. We collected seven benthic samples each year from five locations along a centerline east–west transect spanning the lake and two locations along a north–south centerline transect running from the north shore to center of the lake (Fig. 1). Data from the two north–south locations were unavailable for 1996 and 2007. Samples were collected between 1 October and 31 December each year, except in 2000, 2001, 2002, and 2007 when collections occurred between 1 April and 31 August. Using much of the same data, Poirrier and Caputo (2015) found no difference between monthly estimates and average yearly estimates of Rangia, so we opted to include those four years of summer sampling here.

At each sampling location, we collected three replicate dredge samples using a 15-cm^2 petite Ponar dredge (Wildco, Yulee, Florida, USA; Abadie and Poirrier 2000). Samples were rinsed and sieved using a 12-L 0.6-mm sieve bucket (Wildco) and then preserved in 10% borax-buffered formalin with rose bengal stain (Carolina Biological Supply, Burlington, North Carolina, USA). In the laboratory, we rinsed samples in a 0.5 mm sieve and used a dissecting scope to enumerate benthic invertebrates and sort them into species and 5 mm size classes (Abadie and Poirrier 2000). We then estimated the number of individuals/m^2 by extrapolating from the surface area sampled by the dredge (225 cm^2) and averaged density estimates across the three replicate samples (Abadie and Poirrier 2000) and seven sites.

We included 8 benthic invertebrate species in our analysis: two species of snails (*Texadina sphinctostoma* and *Probythinella protera*), five species of bivalves (Matagorda macoma [*Macoma mitchelli*], Dark False Mussel [*Mytilopsis leucophaeata*], Dwarf Surf Clam, Hooked Mussel [*Ischadium recurvum*], and Rangia), and insects in the family Chironomidae. Stroud (2018) found that scaup consumed all species except *M. mitchelli*, which was rare during the period they sampled. They found that Dark False Mussels and Dwarf Surf Clams were both preferred relative their availability in the benthos, but only medium size classes of Rangia (6–16 mm) were preferred, although Rangia in general was the most consumed prey item (Stroud 2018). Here, we broke Rangia into four size classes for our analysis: 0 to <6, ≥6 to <11, ≥11 to <16, and ≥16 to <21 mm.

Aerial surveys

Biologists from the Louisiana Department of Wildlife and Fisheries conducted aerial surveys along 6 fixed transects from 1977 to 2017 to estimate scaup abundance on Lake Pontchartrain. Two observers (pilot not included as an observer) flew 38 m above the water and counted and recorded all scaup within 100 m of both sides of the aircraft for each transect. The total area surveyed was 4.5% of lake area. Densities of scaup (scaup/km^2) along the six transects were multiplied by the total area of Lake Pontchartrain to obtain scaup estimates for the entire estuary. These surveys were generally conducted in both December and January each winter. However, because scaup are among the last waterfowl species to migrate south (Baldassarre 2014), we only included January surveys in our analysis. No January data were available for 1980 or 1988, so we estimated January counts using a regression built with years when both December and January data existed. No surveys were flown in 1982, 1989, or 1990.

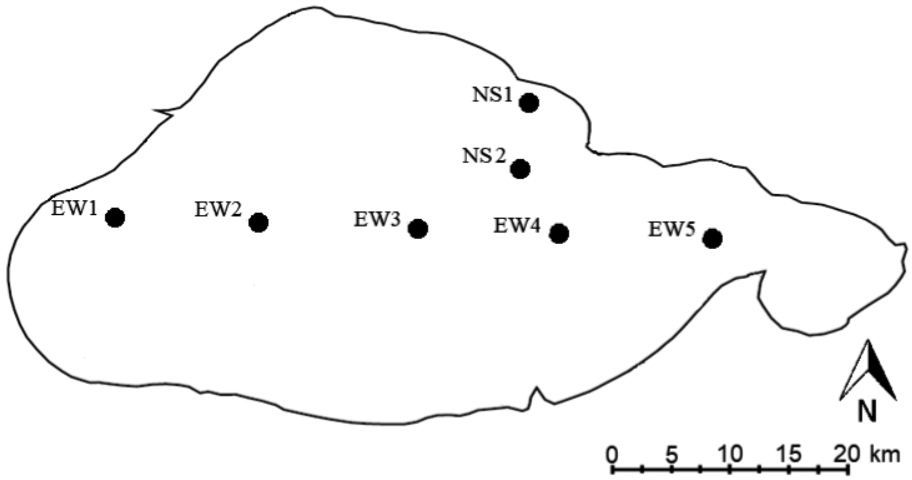

Fig. 1. Map of benthic invertebrate sampling locations (1996–2017) along the east–west (EW) and north–south (NS) transects on Lake Pontchartrain, Louisiana, USA.

Statistical analyses

We used generalized linear regression to model the effects of prey abundance on January scaup populations on Lake Pontchartrain. Because all food items are potentially important drivers of scaup abundance, we first built a fully saturated model containing all 11 prey classifications and used the dredge procedure in the MuMIn package in program R to evaluate all additive combinations of parameters. We ranked models by Akaike's information criterion corrected for sample sizes (AIC_c) score (Burnham and Anderson 2002) and used conditional model averaging of a reduced model set (see *Results*) to calculate parameter coefficients.

We also used regression to test the effects of environmental disturbance—named storms and Bonnet Carré Spillway openings—on prey abundance from 1996 to 2017. Here, we focused only on the mollusk species that our first analysis demonstrated to have an influence on scaup populations. Preliminary analyses of disturbance data included storms parsed by wind speed, but results were similar, so to ease interpretation we only present data from hurricane-force storms (all storms with winds >119 kph). We only included hurricanes that made landfall within 150 km from the center of Lake Pontchartrain (Fearnley et al. 2009) and used a binary variable to assign each year (the summer before fall scaup migration) as having experienced a storm or not. Finally, we investigated lag effects of these disturbances by modeling mollusk abundance as a function of how many years since a disturbance took place; because lag effects may not be continuous, we modeled years since disturbance as a factor variable. Preliminary investigation found no evidence of long-term lag effects that persisted for many years, so we only present coefficients for one year post-disturbance, which is biologically a relevant timescale for invertebrate variation in the estuary (Poirrier and Caputo 2015). Year-of disturbances and lag effects could not be included in the same model, because the presence of a hurricane automatically issues a value of zero for the lag effect variable. Therefore, we built four univariate regression models to estimate parameters: a year-of hurricane model, a lagged hurricane model, a year-of spillway model, and a lagged spillway model.

We also directly tested the effects of environmental disturbances (and lag effects) on scaup abundance over a longer interval that used aerial survey and disturbance data from all available years (1977–2017). Because scaup abundance on Lake Pontchartrain could ultimately be driven by annual variation in the continental population of scaup, we also tested for correlations between the Lake Pontchartrain survey and the North American breeding population data (U.S. Fish and Wildlife Service 2018). For all analyses, while Poisson or negative binomial error structures are commonly used for analyses of count data (Zar 2009), our data were so highly variable that each year effectively became a leverage point. After examining regression diagnostic plots, we selected a Gaussian error structure for all regressions because it provided the best fit to the data. All data were analyzed in Program R, and we present mean ± standard error and 85% confidence intervals commensurate with an Akaike's information criterion (AIC)-based modeling approach (Arnold 2010).

Results

Between 1977 and 2017, the mean scaup abundance on Lake Pontchartrain in January was 137,347 ± 23,919 individuals (range: 0–669,463). Hurricanes struck the Lake Pontchartrain region in 11 of 38 years for which we had scaup population data, and the Bonnet Carré Spillway was opened for flood control in 6 of 38 yr (overlapped with hurricane years in 1979, 1997, and 2008). The most abundant potential food sources on Lake Pontchartrain 1996–2017 were *T. sphinctostoma* (275 ± 68/m^2) and *P. protera* snails (124 ± 70/m^2), Hooked Mussels which were highly variable (167 ± 90/m^2), and Rangia clams 0 to <6 mm (122 ± 29/m^2) and ≥6 to <11 mm (143 ± 42/m^2).

Scaup responses to mollusk availability

Scaup abundance on Lake Pontchartrain 1996–2017 was significantly affected by food availability. However, there was considerable model uncertainty, with 33 models from the global dredge within five AIC units of the top model. Our top model included abundance of Dwarf Surf Clams and two size classes of Rangia (≥11 to <16 and ≥16 to <21 mm). To pare down our final model set for ease of interpretation, we next constructed a candidate set containing all permutations of these three important food variables and then also sequentially added other prey items to the top model to determine their individual effects (Table 1). Conditional model-averaged coefficients (Table 2) indicated that scaup populations increased in years when medium Rangia (≥11 to <16 mm; β = 3418 ± 548) and Dwarf Surf Clams (β = 191 ± 77) were abundant (Fig. 2). There was equivocal support for a model including larger Rangia (≥16 to <21 mm; $\Delta AIC_c < 2.0$), and scaup populations tended to be less numerous when large clams were present on the estuary (β = −2235 ± 1089). No other food items had a significant effect on scaup abundance (Table 2).

Mollusk responses to disturbance

Having identified three important prey items whose abundance predicts scaup populations

Table 1. Akaike's information criterion corrected for sample sizes (AIC_c) model selection for factors influencing scaup abundance on Lake Pontchartrain.

Model	Adj. R^2	AIC_c	ΔAIC_c	Weight
Dwarf Surf Clam + Rangia 10–15 + Rangia 15–20	0.82	566.0	0.0	0.26
Dwarf Surf Clam + Rangia 10–15 + Rangia 15–20 + Hooked Mussel	0.83	566.7	0.7	0.19
Dwarf Surf Clam + Rangia 10–15	0.78	567.7	1.7	0.11
Dwarf Surf Clam + Rangia 10–15 + Rangia 15–20 + Matagorda macoma	0.82	568.4	2.4	0.08
Rangia 10–15	0.74	569.1	3.0	0.06
Dwarf Surf Clam + Rangia 10–15 + Rangia 15–20 + Chironomidae	0.81	569.4	3.4	0.05
Dwarf Surf Clam + Rangia 10–15 + Rangia 15–20 + Rangia 0–5	0.81	569.4	3.4	0.05
Dwarf Surf Clam + Rangia 10–15 + Rangia 15–20 + *Probythinella protera*	0.81	569.4	3.4	0.05
Rangia 10–15 + Rangia 15–20	0.76	569.6	3.5	0.04
Dwarf Surf Clam + Rangia 10–15 + Rangia 15–20 + *Texadina sphinctostoma*	0.81	569.6	3.6	0.04
Dwarf Surf Clam + Rangia 10–15 + Rangia 15–20 + Dark False Mussel	0.81	569.7	3.7	0.04
Dwarf Surf Clam + Rangia 10–15 + Rangia 15–20 + Rangia 5–10	0.80	569.8	3.8	0.04
Rangia 15–20	0.21	593.9	27.9	0.00
Dwarf Surf Clam + Rangia 15–20	0.20	596.1	30.1	0.00
[NULL]		597.5	31.5	0.00
Dwarf Surf Clam	0.01	598.8	32.8	0.00

Note: True Rangia size classes are 0 to <6, ≥6 to <11, ≥11 to <16, and ≥16 to <21 mm.

Table 2. Conditional model-averaged parameter estimates and 85% confidence intervals for the effect of prey items on scaup abundance.

Parameter	Estimate	Lower 85% CI	Upper 85% CI
Dwarf Surf Clam	**191.26**	**79.80**	**302.72**
Rangia 10–15	**3418.31**	**2628.48**	**4208.14**
Rangia 15–20	**−2235.03**	**−3803.51**	**−666.55**
Hooked Mussel	62.69	7.22	118.16
Matagorda macoma	291.17	−99.34	681.68
Chironomidae	−175.07	−578.41	228.27
Rangia 0–5	−104.79	−351.06	141.48
Probythinella protera	−31.16	−105.97	43.65
Texadina sphinctostoma	26.51	−62.01	115.03
Dark False Mussel	−64.31	−354.67	226.05
Rangia 5–10	−23.97	−362.15	314.21

Notes: True Rangia size classes are 0 to <6, ≥6 to <11, ≥11 to <16, and ≥16 to <21 mm. Effects whose confidence interval does not include zero are shown in bold.

on Lake Pontchartrain, we then evaluated how hurricanes and the opening of the Bonnet Carré Spillway influenced those mollusk species. All species tended to decline when a hurricane struck the region, although the 85% confidence interval narrowly bounded zero for large Rangia ≥16 to <21 mm (Table 3). Medium Rangia ≥11 to <16 mm populations strongly rebounded the following year ($\beta = 69 \pm 27$), but the other two species showed little response. The opening of the Bonnet Carré Spillway had no immediate or lagged effects on any of the three mollusk species (Table 3).

Scaup population trends in relation to disturbance

Our first two analyses established the relationship between scaup and mollusk populations, and evaluated the impact of disturbance on important mollusk prey types. Here, we leveraged both longer-term datasets on scaup populations and environmental disturbance to help cement that linkage. Although numbers on Lake Pontchartrain appeared to track the 20-yr continental decline of scaup between 1980 and 2000, we found no correlation (correlation = 0.09, $P = 0.58$) between the two population indices because of highly variable scaup numbers on the Lake (Fig. 3). Wintering scaup populations on Lake Pontchartrain declined precipitously ($\beta = -136{,}151 \pm 48{,}414$) in years when a hurricane made landfall, but rebounded strongly the

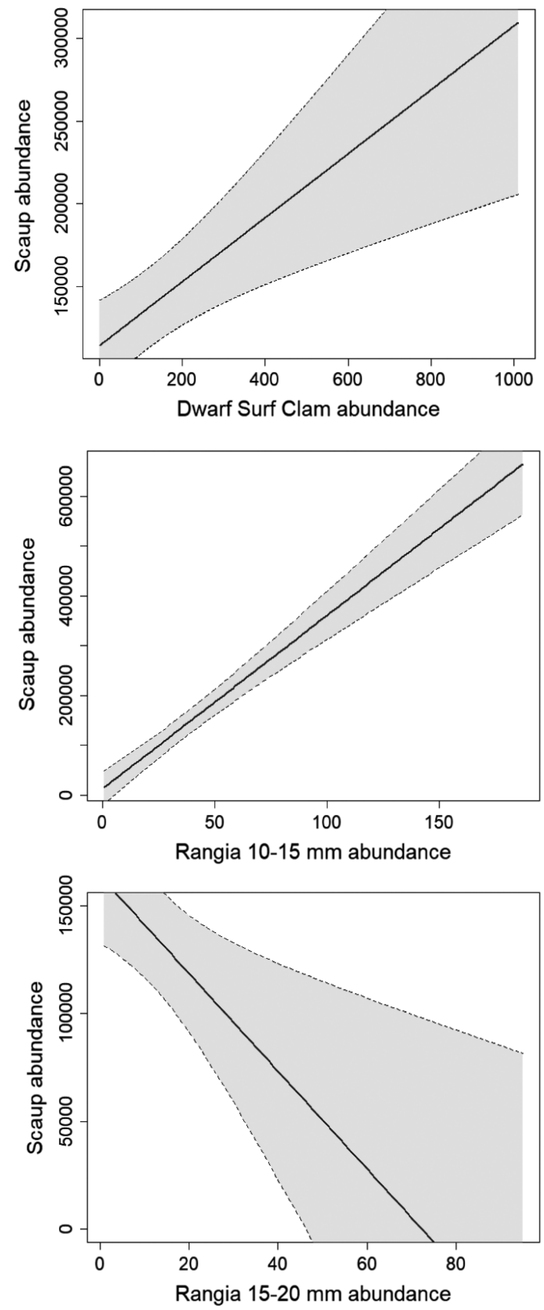

Fig. 2. Effects of prey availability on the abundance of Lesser Scaup (*Aythya affinis*) on Lake Pontchartrain, Louisiana, USA, 1996–2017. Regressions are taken from the best-fitting model where scaup abundance is distributed as an additive function of Dwarf Surf Clams (*Mulinia lateralis*), Rangia clams (*Rangia cuneata*) ≥11 to <16 mm, Rangia ≥16 to <21 mm. Regressions were constructed holding other variables at the mean and are shown with 85% confidence intervals.

following year (β = 177,005 ± 64,284; Table 4). The opening of the Bonnet Carré Spillway had no immediate or lagged effect on scaup populations (Table 4).

Table 3. Parameter estimates for the effect disturbance (hurricanes and spillway openings) and 85% confidence intervals (CIs) on important scaup food items.

Prey item	Parameter	Estimate	Lower 85% CI	Upper 85% CI
Dwarf Surf Clams	Hurricane	**−152.05**	**−302.41**	**−1.69**
	Hurricane-1	24.09	−186.22	234.39
	Spillway	−2.37	−184.96	180.22
	Spillway-1	−92.25	−377.99	193.50
Rangia 10–15	Hurricane	**−46.18**	**−80.95**	**−11.42**
	Hurricane-1	**68.58**	**29.39**	**107.77**
	Spillway	−24.18	−67.14	18.78
	Spillway-1	−9.19	−56.18	37.81
Rangia 15–20	Hurricane	−13.19	−28.42	2.04
	Hurricane-1	7.00	−5.28	19.27
	Spillway	3.08	−15.15	21.32
	Spillway-1	−12.29	−28.39	3.82

Notes: 1-yr lag effects are also shown. True Rangia size classes are ≥11 to <16 and ≥16 to <21 mm. Effects whose confidence interval does not include zero are shown in bold.

Discussion

We found that the abundance of Lesser Scaup on Lake Pontchartrain was closely associated with mollusk food sources, especially Rangia clams. However, that relationship depended on the size class of clam: Scaup populations increased when Rangia ≥11 to <16 mm were abundant, but decreased when larger Rangia ≥16 to <21 mm were prevalent. These results are largely supported by the recent work of Stroud (2018) who demonstrated that scaup preferred Rangia ≥11 to <16 mm, but avoided Rangia ≥16 to <21 mm. Stroud (2018) also found that scaup preferred smaller Rangia ≥6 to <11 mm, but our results suggest that Rangia ≥11 to <16 mm are driving scaup use of the lake, possibly because they have a higher meat-to-shell ratio and provide more nutrition per unit handling time (Richman and Lovvorn 2004, Anteau and Afton 2006). The feeding preference for clams ≥6 to <11 mm observed by Stroud (2018) could be explained by either (1) the inability of scaup to discriminate food types at millimeter scales or (2) arbitrary 5-mm bin widths which may not perfectly align with scaup food preferences. We also found that

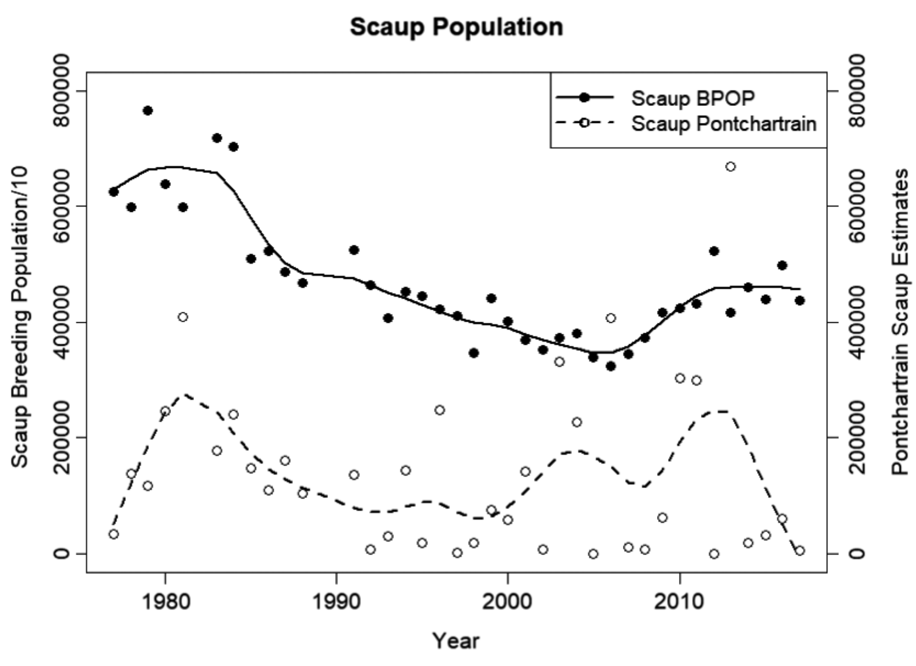

Fig. 3. Annual Lesser Scaup (*Aythya affinis*) estimates of the continental breeding population (BPOP; solid spline), and wintering Lake Pontchartrain population (dashed spline) from 1977 to 2017.

Table 4. Parameter estimates for the effect disturbance (hurricanes and spillway openings) and 85% confidence intervals on scaup populations on Lake Pontchartrain.

Parameter	Estimate	Lower 85% CI	Upper 85% CI
Hurricane	**−136,151**	**−205,868**	**−66,434**
Hurricane-1	**177,005**	**84,436**	**269,574**
Spillway	−31,245	−126,712	64,222
Spillway-1	−14,778	−222,856	193,300

Note: 1-yr lag effects are also shown. Effects whose confidence interval does not include zero are shown in bold.

scaup populations increase when more Dwarf Surf Clams were present in the Lake, but the biological effect size was an order of magnitude less than it was for either size class of Rangia.

Populations of these three mollusk species declined during the year of a hurricane (although the confidence interval for Rangia ≥16 to <21 mm narrowly bounded zero), which is consistent with Poirrier et al. (2008) who found severe bivalve mortality following Hurricane Katrina in 2005. However, Rangia clams in the ≥11 to <16 mm size class increased the following year. In a post hoc analysis, we also found similar increases in both smaller size classes of Rangia (0 to <6 mm; $\beta = 319.34 \pm 90.69$ and ≥6 to <11 mm; $\beta = 240.16 \pm 73.90$) in years following a hurricane. This makes sense. Hurricane-driven storm surges cause both direct mortality to clams through sedimentation (Flocks et al. 2009) and low dissolved oxygen, but also increase salinity which triggers Rangia to spawn and eventually produce small- to medium-sized clams the following year (Poirrier et al. 2008). Brammer et al. (2007) and Poirrier et al. (2009) found a significant decline in Rangia clams from April 1997 to January 1998 as a result of the Bonnet Carré Spillway being opened. However, our longer-term data did not reveal consistent changes in the Rangia clam sizes or Dwarf Surf Clams that are preferred by scaup, and no lag effects were observed. We conclude that hurricanes are a more important source of disturbance that affects populations of mollusks that are consumed by scaup.

Although benthic invertebrate data only exist through 1996, we used longer-term data on scaup abundance and environmental disturbance to further diagnose how ducks respond to hurricanes and spillway openings. In concordance with our analysis of disturbance and preferred prey populations, scaup numbers decreased dramatically on Lake Pontchartrain in years of a

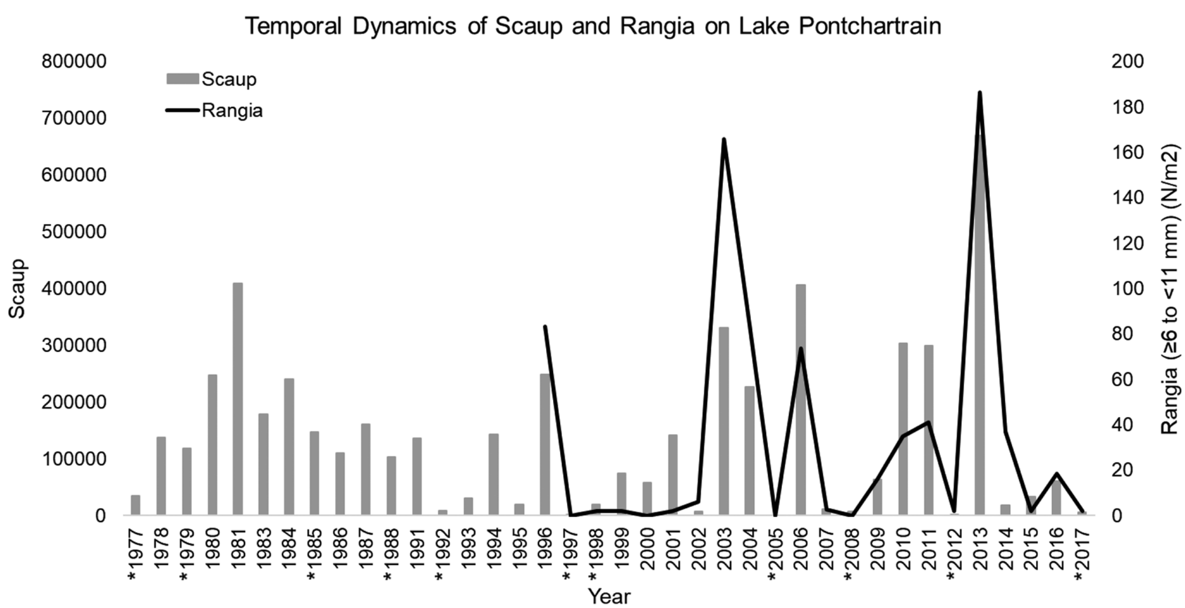

Fig. 4. Population trends for Lesser Scaup (*Aythya affinis*) and Rangia clams (*Rangia cuneata*) ≥11 to <16 mm on Lake Pontchartrain, Louisiana, USA, 1977–2017. Rangia data were unavailable before 1996. Years where a hurricane made landfall within 150 km of the Lake are marked with an asterisk.

hurricane, but rebounded the following year, presumably after the medium-sized Rangia clam population recovered. Our three-part analysis makes a strong case for a bottom-up trophic cascade that affects scaup populations. Disturbance and sedimentation from hurricanes reset the size distribution of Rangia clams by causing mortality of large clams (Poirrier et al. 2008, Flocks et al. 2009), and triggering spawning and promoting larval growth through increased salinities (Cain 1973). Thus, the year after a hurricane, Lake Pontchartrain is rife with medium-sized clams that are preferred by scaup, and duck numbers soar into the hundreds of thousands (Fig. 4).

Lesser Scaup are generalist diving ducks exploiting a diversity of prey types throughout their range (Rogers and Korshgen 1966, Afton et al. 1991, Anteau and Afton 2006, Anteau et al. 2014). It is therefore surprising that their use of Lake Pontchartrain is so tightly linked to not only a single species of bivalve, but of a particular 5 mm size class. When the clamming is good, the ducks are there. But in years of a hurricane, scaup are concentrated elsewhere in southeastern Louisiana like the Biloxi State Wildlife Management Area (Louisiana Department of Wildlife and Fisheries, *unpublished data*), where they may be exploiting saline-tolerant preferred prey like Dwarf Surf Clams.

Our results point to several important implications for scaup populations in Louisiana. First, the frequency of Atlantic hurricanes is forecast to decrease, but storm severity is expected to increase with climate change (Knutson et al. 2013, 2015). This potentially means more devastating mollusk mortality events on Lake Pontchartrain when hurricanes do strike, as well as less frequent booms of medium-sized Rangia clams, which may disperse scaup to other places in coastal Louisiana. On the other hand, sea-level rise and subsidence are causing Louisiana to lose coastal marsh faster than anywhere else in the United States (Couvillion et al. 2011), which may lead to increased use of the Lake by scaup and other waterfowl. The relative costs and benefits of scaup winter habitat selection are beyond the scope of this study, but in recent local memory, scaup would be subject to at least one additional risk in coastal Louisiana. Between 20 April and 15 July 2010, the Deepwater Horizon (DWH) oil spill released an approximate 4.9 million barrels of crude oil into the northern Gulf of Mexico and impacted ecosystems along the Louisiana, Mississippi, Florida, and Alabama coastlines (Reddy et al. 2012). Knowing full well that millions of waterbirds were headed south toward a contaminated coast, the Natural Resources Conservation Service established ~190,000 ha of inshore wetland and agricultural habitats in an attempt to prevent waterbirds from reaching the contaminated coast (Davis et al. 2014). Lesser Scaup largely overflew these areas (Tapp 2013) for the coast, and thankfully, Lake Pontchartrain had healthy Rangia populations that year and attracted large numbers of ducks. It is not clear what management actions could be taken to short-stop scaup in a future crisis scenario, but the ability to forecast their distributions is an important first step.

In a broader ecological sense, our results add to a growing literature demonstrating that estuaries are not only tidally and seasonally dynamic, but punctuated disturbance events can help maintain ecosystem function and create landscape heterogeneity (Morton and Barras 2011). Indeed, the heavy rain from hurricanes provides an influx of freshwater, sediment, and nutrients (Conner et al. 1989), as well as wave-driven sediment deposition (Williams and Flanagan 2009). While many effects of hurricanes are acute, our long-term survey of benthic invertebrate communities and diving duck populations also provides evidence for bottom-up lagged trophic effects that can redistribute hundreds of thousands of birds on the landscape.

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