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Appendix, audio S1). Many marine fishes are broadcast spawners and spawn at dusk and during the night, which may reduce the risk from visual predators on planktonic eggs and adults (Hobson et al. 1978; Robertson 1983; Holt et al. 1985).

Effects of Hurricane Charley on fish chorusing

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Hurricane Charley, a category 4 hurricane, passed through Charlotte Harbor, Florida, directly over an autonomous underwater acoustic datalogger used to record sound production by fishes associated with courtship and spawning. Acoustic recordings made on 9 days prior to the storm, during and 3 days after the storm provided unprecedented documentation of the hurricane's passage and its effect on fishes' calling behaviour. The hurricane did not inhibit nightly chorusing events of spawning fish. Sound levels produced by spawning fish on the night of and 3 days after the hurricane were higher and lasted longer than any of the 9 days recorded prior to the hurricane.

Keywords: hurricane; fishes' sound production; Charlotte Harbor

1. INTRODUCTION

Hurricanes are acute, catastrophic events that have the capacity to severely alter natural ecosystems (Mallin et al. 1999). Ecological impact studies following hurricane events have traditionally included an assessment of habitat alteration, consequent changes in community structure and recovery rates in areas where pre-hurricane data were available for comparison. Although insightful, such a posteriori investigations do not report on the acute responses of biota during, or on temporal scales more immediate to the time of a hurricane strike. Indeed, it is an exceedingly rare occasion for a direct hurricane strike to occur at the precise time and location of an ongoing field study (Spiller et al. 1998). However, on 13 August 2004, this is exactly what occurred in Charlotte Harbor, Florida. The passage of Hurricane Charley directly through Charlotte Harbor provided a unique opportunity to document the acoustic energy associated with the storm and to investigate whether such a major catastrophic event altered the calling behaviour of soniferous fish.

Spawning is an important part of the life history of fishes, and spawning output can influence subsequent recruitment of juvenile fishes. Males of many fishes, particularly members of the family Sciaenidae, produce species-specific courtship sounds, which can be identified with hydrophone surveys to determine when and where spawning is taking place (Mok & Gilmore 1983; Saucier et al. 1992; Saucier & Baltz 1993; Mann & Lobel 1995; Luczkovich et al. 1999; Zelick et al. 1999; Gilmore 2003; Electronic

2. MATERIAL AND METHODS

To investigate diel patterns of fish sound production, a long-term acoustic recording system (LARS) was deployed in Charlotte Harbor, Florida from 4-17 August 2004. The LARS was custom built by the University of South Florida College of Marine Science and consisted of a Persistor Microcomputer (CF2), an Oceanographic Embedded Systems 16-bit A/D board (AD16S2) and a custom built signal conditioning board that allowed signal calibration and use of anti-aliasing filters. The LARS was held in an underwater housing and connected to an external hydrophone (sensitivity: -164 dBV re 1 μPa; High-Tech, Inc. HTI: 96 min). The underwater housing was attached by chain to a tie-down anchor and remained positively buoyant some 50 cm above the bottom of the harbour at a 3.5 m depth.

Acoustic data were sampled at 3333 Hz for 10 s every 10 min and recorded to onboard Compact Flash memory. These data were processed using QLOGGER, a custom Matlab (v. 6.5) program (Mathworks, Inc.). Each 10 s file was transformed with a 3333 point fast Fourier transform (FFT) to generate a power spectrum. Data were averaged in 100 Hz bins to analyse the timing associated with chorusing. To analyse the fish sound production, the timeseries of average spectrum level sound between 500 and 600 Hz was smoothed using a 5-point moving average to reduce variability from sounds produced by boat traffic. To quantitatively characterize chorusing events, four parameters were established from the smoothed time-series, including daily chorus start times, end times, duration and maximum sound pressure level (SPL). The chorus start time was defined as the time when the SPL exceeded 90 dB. The chorus end time was defined as the time when the SPL decreased to less than 90 dB after the chorus had started. The 90 dB SPL threshold used to define chorus start and end times was calculated as three standard deviations, (12 dB) above mean (78 dB SPL) daytime (05:00-17:00 h) SPL. Although conservative, this method provides an objective way to establish parameter values. Chorus duration was the chorus end time minus the chorus start time. To investigate the potential influence of Hurricane Charley on the cyclic sound producing behaviour of fish we fit the time-series of each parameter to a fourth-order polynomial equation. Data points from the day of the hurricane were excluded from the models to allow for a comparison of predicted versus observed values.

3. RESULTS

Charley, a strong category 4 hurricane, produced wind speed in excess of 226 kph (140 mph) as it crossed Charlotte Harbor on a north-northeasterly track at an approximate speed of 35.5 kph (22 mph) on the afternoon of 13 August 2004. Charley was the strongest hurricane to hit the United States since Hurricane Andrew in 1992. The eye of the storm crossed into the harbour over the barrier islands of North Captiva and Cayo Costa south of Boca Grande Pass at approximately 16:00 h eastern daylight saving time (EDT) and departed through the Peace River corridor at approximately 17:00 h EDT (Pasch et al. 2004; figure 1).

By 14:00 h EDT on 13 August, low-frequency acoustic signals generated by Charley were received by the LARS. At this time, the outer bands were circulating over the harbour, but the eye of the storm was in the Gulf of Mexico 80 km to the southwest. The loudest received signals (raw, unsmoothed data; 118 dB, 0-100 Hz frequency bin) associated with the storm were recorded at approximately 16:00 h EDT when the hurricane's eye, approximately 8 km in diameter, was entering the harbour and the inner bands were directly over the study site (Electronic

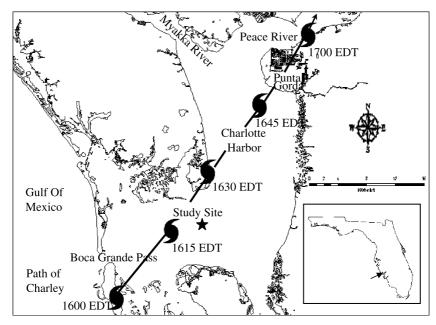


Figure 1. Map of Charlotte Harbor, Florida showing study site location and path of Hurricane Charley as it crossed the harbour.

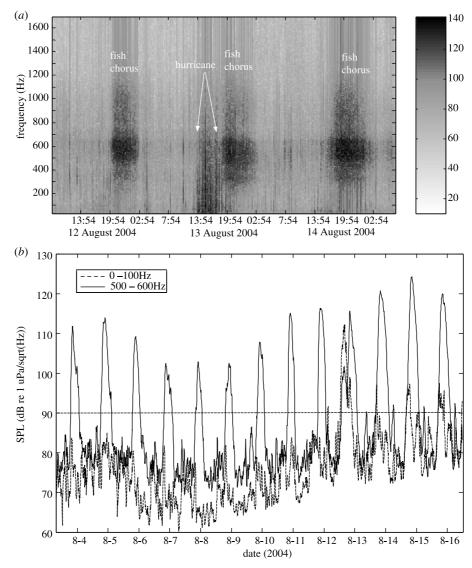


Figure 2. (a) Composite time-series of power spectra calculated with a 512-point FFT for each 10 s data file. Grey-scale bar indicates spectrum level sound (dB re 1 μ Pa Hz $^{-0.5}$). Three days from 12 August 2004 to 14 August 2004 showing nightly fishes' chorus and sounds associated with the hurricane on 13 August 2004. (b) Spectrum level time-series of 5-point smoothed data of 100 Hz wide frequency bins containing the greatest acoustic energy for fishes (500–600 Hz) and Hurricane Charley (0–100 Hz). Dashed line at 90 dB SPL indicates chorus threshold. Tick marks on the x-axis correspond to midnight.

Table 1. Parameter values for fish chorusing events.

(Hurricane Charley passed through Charlotte Harbor on 13 August (italicized) prior to the start of chorusing. SPL dB, sound pressure level in decibels (SPL dB re: 1 μ Pa Hz^{-0.5}); EDT, eastern daylight savings time.)

date 2004	chorus start time EDT	chorus end time EDT	chorus duration (h)	daily max SPL (dB)	
8/4	19:54:36	02:24:36	6.50		
8/5	19:24:36	03:44:36	8.33	113.97	
8/6	20:04:36	02:04:36	6.00	109.12	
8/7	20:34:36	02:54:36	6.33	102.46	
8/8	20:54:36	02:04:36	5.17	102.83	
8/9	20:14:36	01:04:36	5.50	102.44	
8/10	21:04:36	02:34:36	5.50	107.78	
8/11	20:44:36	02:14:36	5.50	115.07	
8/12	20:14:36	02:24:36	6.17	116.31	
8/13	18:34:36	02:24:36	7.83	115.66	
8/14	17:24:36	03:34:36	9.17	120.65	
8/15	17:04:36	02:54:36	8.83	124.34	
8/16	17:44:36	03:14:36	8.50	119.98	
mean	19:32:18	02:35:22	6.87	112.50	
s.d.	1 h 23 min	36 min	1.44	7.22	

Table 2. Polynomial models for chorus start, end, duration and maximum SPL fit to time-series data excluding the night of the hurricane.

(Predicted values were calculated for the night of the hurricane based on each model. SPL dB, sound pressure level in decibels. SPL re: $1 \mu Pa Hz^{-0.5}$.)

data	fitted polynomials	r^2	mean	s.d.	predicted	observed
chorus start	$y = 0.1595x^4 - 4.3448x^3 + 36.002x^2$ $-96.718x + 854.25$	0.93	18:37:06	1:24:46	18:41:57	18:34:36
chorus end	$y = -8 \times 10^{-05} x^4 + 0.0021 x^3 -0.0179 x^2 + 0.0497 x + 0.037$	0.49	1:39:36	0:37:32	1:03:22	1:24:36
chorus duration	$y = -0.0049x^4 + 0.1328x^3 - 1.103x^2 + 2.9326x + 4.8645$	0.88	6 h 48 min	1 h 29 min	7.69 h	7.83 h
max SPL dB	$y = -0.0128x^4 + 0.2799x^3 - 1.4011x^2 -0.7256x + 115.67$	0.91	112.2	7.5	120.20	115.66

Appendix, audio S2). Signals received from the hurricane were absent or minimal by 17:30 EDT, at which time the first discernable fish calls were recorded.

Acoustic energy related to the hurricane was mainly below 400 Hz and concentrated from 0–100 Hz, whereas most of the energy associated with the fish chorus comprised mainly of sand seatrout (*Cynoscion arenarius*) was between 500 and 600 Hz (figure 2a). An analysis of the 500–600 Hz band showed there was pronounced diel periodicity in fish sound production (figure 2b). Nightly chorusing events commenced on average at 19:32 h EDT and lasted nearly 7 h (Electronic Appendix, audio S3).

Four parameters were used to characterize chorusing events including chorus start time, chorus end time, chorus duration and maximum SPL. With the exception of chorus end time, all models provided a fit sufficient for predicting data points on the day of the hurricane within 95% confidence. Observed values were in close agreement with predicted values and were within the standard deviation of the mean for each parameter (tables 1 and 2).

4. DISCUSSION

The ability of the model to predict results well within the inherent variability of each parameter tested indicates the hurricane had no immediate deleterious effect on fish sound production. In fact, data recorded from the three nights after the hurricane showed increased calling by fish with the highest maximum sound levels and start times up to 2.5 h earlier than previous nights. The night of the hurricane was transitional from previous days to these high levels of sound production. This could be attributable to the influence of the hurricane on the distribution of fishes or the result of a longer-term cycle in chorusing behaviour that may have taken place without the occurrence of the hurricane. While this study found no immediate negative impact on populations of chorusing fishes, it is possible that a delayed onset of lowered oxygen concentrations resulting from increased freshwater inflow associated with the hurricane could impair fish chorusing and spawning activity in affected areas of Charlotte Harbor.

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The supplementary Electronic Appendix is available at http://dx. doi.org/10.1098/rsbl.2005.0309 or via http://www.journals.royalsoc.