Vol. 484: 173–188, 2013
doi: 10.3354/meps10268

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published June 12

Large-scale passive acoustic monitoring of fish sound production on the West Florida Shelf

Carrie C. Wall[1,*], Peter Simard[1], Chad Lembke[2], David A. Mann[1]

[1]College of Marine Science, and [2]Center for Ocean Technology, University of South Florida, St. Petersburg, Florida 33701, USA

ABSTRACT: Sounds from toadfish *Opsanus* sp., and 4 other suspected fish sounds were identified in passive acoustic recordings from fixed recorders and autonomous underwater vehicles in the eastern Gulf of Mexico between 2008 and 2011. Data were collected in depths ranging from 4 to 984 m covering approximately 39000 km^2. The goals of this research were to map the spatial and temporal occurrence of these sounds. Sound production was correlated to environmental parameters (water depth, lunar cycle, and dawn and dusk) to understand the variability in seasonal calling. Toadfish 'boatwhistles' were recorded throughout the diel period, with peaks observed between 15:00 and 04:00 h. Annual peaks coincided with the spawning period in the late spring to early summer. The 4 unknown sounds were termed: '100 Hz Pulsing', '6 kHz Sound', '300 Hz FM Harmonic', and '365 Hz Harmonic'. The 100 Hz Pulsing had the temporal characteristics of a cusk-eel call with frequencies below 500 Hz. Sound production was observed mainly at night with annual peaks in the spring and fall. The 6 kHz Sound was observed exclusively at night between 15 and 50 m bottom depths; occurrence decreased significantly in the winter. The 6 kHz Sound peak frequencies correlated positively to satellite-derived sea surface temperature (SST) and negatively to chlorophyll concentration. The 300 Hz FM Harmonic was observed largely (89%) at night and appeared offshore (40–200 m depth). The 365 Hz Harmonic was observed 98% of the time at night, inshore (<40 m depth). The fundamental frequency of the 365 Hz Harmonic was positively correlated with SST, reflecting a temperature-driven increase in sonic muscle contraction rate; conversely, call duration was negatively correlated. The ubiquity of these 4 unknown sounds illustrates how little is known about biological communication in the marine environment.

KEY WORDS: Passive acoustics · Sound production · Gulf of Mexico · Toadfish · *Opsanus* · Cusk-eel · Ophidiformes

INTRODUCTION

Soniferous fishes use sound for communication associated with parental, courtship, spawning, aggressive and territorial behavior (Lobel et al. 2010). Most fish calls are species-specific and repetitive, enabling sound production to be used by researchers for identifying species distribution and behavior. Recent developments in passive acoustic technologies have facilitated marine bioacoustics studies to effectively monitor soniferous fishes over a wide range of habitat, depths and time periods (Mann & Lobel 1995, Lobel 2002, Luczkovich et al. 2008, Van Parijs et al. 2009, Lobel et al. 2010, Locascio & Mann 2011). Passive acoustic monitoring (PAM) of fishes has been successfully demonstrated using moored devices (e.g. Locascio & Mann 2008, Nelson et al. 2011) and autonomous vehicles (Wall et al. 2012). Because acoustic data can be collected at any depth and for long periods of time, using PAM to map and monitor marine species can efficiently provide year-round information on fish distribution, with minimal effects from the typical survey problems associated with weather and data collection at night.

We examined the large-scale, long-term sound production of one known fish (toadfish *Opsanus* sp.) and 4 unknown suspected fish sounds that were commonly recorded in acoustic data collected by

*Email: cwall@mail.usf.edu

hydrophone-integrated Slocum gliders (Teledyne Webb Research). This paper expands on a pilot study of glider-collected acoustic data, which demonstrated the utility of this technology as a platform for passive acoustic monitoring (Wall et al. 2012). In the pilot study, the glider was deployed off Tampa Bay for one week, during which time sounds from numerous identifiable fishes (including red grouper *Epinephelus morio*, and toadfish *Opsanus* sp.) were recorded. In addition, at least 3 unknown biological sounds suspected to be produced by fishes were also recorded. Since the initial study, multiple glider deployments and several deployments of stationary acoustic recorders have been conducted for the purpose of mapping the spatial and temporal patterns of red grouper and marine mammals.

As described in Wall et al. (2012), toadfish sounds recorded off Florida are suspected to be produced by 2 species: *Opsanus beta* in nearshore (>10 m depth) habitats and *O. pardus* in offshore (<10 m depth) habitats. The sounds produced by these 2 species are similar in that they are typical to toadfish 'boatwhistles', but they do have distinct features (Wall et al. 2012). Three of the unknown sounds presented here have been previously described. They consist of: (1) a 200–500 Hz wide band around 6 kHz ('6 kHz Sound') that appears continuously between sunset and sunrise; (2) a frequency modulated harmonic with an average peak frequency of 300 Hz ('300 Hz FM Harmonic') approximately 2.25 s in length and typically containing 4 abrupt changes in frequency, and (3) a tonal harmonic with a peak frequency of 365 Hz ('365 Hz Harmonic') and 0.51 s in length (Wall et al. 2012). All 3 sounds were observed only at night. The fourth unknown sound, termed '100 Hz Pulsing', was not documented in Wall et al. (2012). Examples of these 4 sounds can be found at www.int-res.com/articles/suppl/m484p173_supp/.

Sounds produced by fishes are low frequency (<3 kHz), repetitive, and species-specific (Luczkovich et al. 2008, Mann et al. 2008). Typical calls used for communication occur as short (~<5 s), tonal sounds with multiple harmonics or as broadband pulses (Fish & Mowbray 1970). The repetitiveness of the calls allow them to be easily recorded over time and can occur exclusively at night, peak at dawn and dusk, or occur throughout the diel period depending on the behavioral characteristics of the fish (Mann et al. 2008, Lobel et al. 2010). Each of these characteristics is markedly different from sounds produced by marine mammals, which are infrequent, range up to 200 kHz, and can be long in duration (>10 s) (Mellinger et al. 2007, Au & Hastings 2008). The correspondence of the characteristics of the 4 unknown sounds presented here to typical fish sounds leads us to hypothesize that the unknown sounds are produced by fishes.

The goals of this research were to identify habitat ranges for the 5 sounds by mapping sound production, and to determine the daily and seasonal patterns in calling. Sound occurrence was compared to environmental data to understand the variability in seasonal calling, and to help discern the sources of the 4 unknown fish sounds.

MATERIALS AND METHODS

Data collection

Acoustic data. Acoustic data were collected across the West Florida Shelf (WFS) off west-central Florida in the eastern Gulf of Mexico. All acoustic data were recorded using the digital acoustic recording system, Digital Spectrogram Recorder (DSG; Loggerhead Instruments; disclosure: D. Mann is President of Loggerhead Instruments). The DSG is a low-power acoustic recorder controlled by script files stored on a secure digital (SD) memory card (16 or 32 GB) and an on-board real-time clock. The DSG clock is highly accurate with temperature compensated drift. The DSG file system is a data file structure that stores embedded time stamps with the raw data, allowing each file to remain in synchrony with other glider or mooring data. Hydrophone (HTI-96-MIN, sensitivity −186 dBV [June and July 2008] or −170 dBV [June 2009 and Glider], ± 3 dB from 2 Hz–37 kHz, High Tech) signals were digitized with 16-bit resolution by the DSG recorders.

Stationary acoustic DSGs were deployed in June 2008 for 1 mo, in July 2008 for 2 to 5 mo, and in June 2009 for approximately 1 yr (n = 5, 18, and 63 recorders, respectively). Additional recorders were deployed in the Steamboat Lumps Marine Reserve ('Steamboat Lumps'; n = 7, 71–73 m depth) and at nearshore sites to specifically target red grouper ('RG'; n = 6, 15–40 m depth) between April 2009 and May 2010. DSGs recorded sound for 6 to 10 s every hour at a rate of 36.4 kHz or 50 kHz. Sample rate and frequency varied slightly among sites in an attempt to optimize the recording longevity and storage capacity of the SD card. In addition, a hydrophone was integrated into the aft cowling of 4 Slocum electric underwater gliders to record sound while concurrently collecting a suite of environmental (water temperature, salinity, dissolved oxygen, glider depth, and bottom depth) and optical (chlorophyll, backscatter, and irradiance) parameters. Glider DSGs recorded sound for 25 s every 5 min at a sample rate of 70 kHz. Fifteen glider missions 1 to 4 wk in duration were conducted on the WFS between April 2009 and April 2011. Mission paths, covering a range of depths up to 984 m, were opportunistic, exploratory, and in part dictated by collaborating scientists. Gliders were run and maintained at the University of South Florida, Center for Ocean Technology.

Environmental data. Satellite-derived sea surface temperature (SST) and chlorophyll *a* concentration (chl *a*) data were collected for periods and areas in which acoustic data were recorded. SST was derived from infrared data collected by NASA's Moderate Resolution Imaging Spectroradiometer (MODIS) onboard satellites Aqua and Terra. Chl *a* levels were calculated from visible data collected by ORBIMAGE's Sea-viewing Wide Field-of-View Sensor (SeaWiFS) using standard SeaDas processing. Time series data were calculated for each stationary site. These parameters were chosen because temperature can influence sonic characteristics; and the timing of some behaviors of fishes, such as spawning, and visibility, food availability, and abundance are influenced by the level of primary productivity (i.e. chl *a*). All satellite data processing was performed using IDL programs (Research Systems). Sunrise and sunset, and lunar cycle data were obtained from the United States Naval Observatory (USNO) database for June 2008 to April 2011 (Phases of the Moon: available at aa.usno.navy.mil/data/docs/MoonPhase.php, accessed January 2012; Sun or Moon Rise/Set Table: available at aa.usno.navy.mil/data/docs/RS_OneYear.php, accessed January 2012). Sunrise and sunset times were compared to the hourly peaks in calling for all 5 sounds. Daily counts of files containing each sound were extracted. A Fast Fourier Transform (FFT) was applied to the time series of daily counts to determine whether there were cyclical peaks in calling. These peaks were then compared to the cyclical pattern of moon phases (occurring at 7, 15, and 29 d) to determine if calling was influenced by lunar phase. Analyses were completed in MATLAB (Mathworks).

Data analysis

Acoustic files collected at the stationary sites were analyzed manually as spectrograms to visually identify fish sounds. Spectrograms were created in MATLAB using 2048 point Hanning-windowed FFTs with 50% overlap. The diel timing of sound production was determined from a subset of files randomly selected from fixed location recorders where each sound was commonly found. Based on the results of that analysis and a previous study (Wall et al. 2012), all files recorded between 16:00 h and 22:00 h (local time, corrected for daylight saving time) were reviewed to determine the spatial and seasonal distribution of sound occurrence. All acoustic files recorded during the glider missions were analyzed visually and audibly. Files in which sounds of interest were identified were binned into 1 h intervals over the glider track.

All sounds identified in the acoustic files were binned by hour and month and normalized by the total number of files analyzed per hour and per month ('call per unit effort') to show diel and seasonal patterns without a sampling bias. For the fixed recorders, only sites where at least one sound was detected were included in the normalization. To better understand how hourly calling patterns changed throughout the year, a matrix of the number of calls detected per hour for each month was created for the stationary data and the glider data. Separating these 2 datasets for this analysis shows where gaps in data collection exist and helps to better understand relative increases and decreases in calling. Call characteristics (peak frequency, fundamental frequency, amplitude, and duration) and timing were correlated to time series of environmental data (SST, chl *a* and lunar phase). These analyses were completed using MATLAB. Spatial maps of the data were created using ArcGIS (ESRI).

Visual analysis of the stationary recorder dataset indicated that the peak frequency and amplitude of the 6 kHz Sound and the fundamental frequency and duration of the 365 Hz Harmonic changed over time. To quantify these changes, the peak frequency of the 6 kHz Sound was estimated from FFTs with 100 Hz resolution applied to files in which the sound was present without interfering noise (e.g. boat or mechanical noise), which had been noted during the visual analysis of all acoustic files. The frequency between 3–7 kHz with the highest amplitude was extracted from each file, along with the associated amplitude. To reduce error from noise in the frequency and amplitude data, outliers (3 standard deviations away from the mean) were removed, a non-linear interpolation was applied and the data were then smoothed using a 20-point moving average. Only stationary sites that recorded sound for over 6 mo were included to ensure seasonal variation was incorporated. Long-term sound production is

Table 1. Recovered stationary recorder deployment information: recorder station number, recorder deployment and recovery dates, number of days recording, and water depth at the site. Digital spectrogram recorders (DSGs) recorded for the duration of the deployment (–) unless otherwise reported in 'End recording'. nd: recorder stopped working before deployment or only collected 'stuttered files' (a recording format not incorporated in this study). Dates given as mm/dd/yyyy

Station	Deployed	Recovered	End recording	Days recorded	Depth (m)
June 2008					
1	6/11/2008	9/16/2008	–	98	4
9	6/10/2008	6/26/2008	–	17	11
13	6/10/2008	6/26/2008	–	17	13
14	6/10/2008	6/26/2008	–	17	24
17	6/10/2008	6/26/2008	–	17	31
July 2008					
2	7/23/2008	11/13/2008	9/26/2008	66	4
3	7/23/2008	11/13/2008	8/15/2008	24	21
4	7/23/2008	12/5/2008	9/27/2008	67	12
5	7/28/2008	12/5/2008	9/4/2008	39	22
6	7/23/2008	12/5/2008	9/3/2008	43	9
8	7/28/2008	12/31/2008	–	157	27
9	7/21/2008	12/31/2008	nd	0	9
12	7/21/2008	12/31/2008	nd	0	10
14	7/21/2008	12/31/2008	nd	0	26
15	7/29/2008	12/31/2008	10/28/2008	92	14
16	7/21/2008	12/31/2008	nd	0	24
17	7/21/2008	12/31/2008	nd	0	31
19	7/29/2008	12/31/2008	nd	0	18
20	7/29/2008	9/15/2008	–	49	29
June 2009					
B2b	10/13/2009	6/10/2010	–	241	72
B3	6/1/2009	10/13/2009	7/15/2009	45	59
B4	6/1/2009	10/13/2009	8/23/2009	84	46
B5	6/1/2009	9/3/2009	8/13/2009	74	42
B5b	9/3/2009	5/20/2010	–	260	42
B6	6/1/2009	9/3/2009	nd	0	35
B6b	9/3/2009	5/20/2010	5/1/2010	235	35
B7	6/1/2009	9/3/2009	nd	0	28
B7b	8/27/2009	5/18/2010	3/28/2010	214	28
B8	6/1/2009	8/3/2009	–	64	24
B8b	8/27/2009	5/18/2010	–	265	24
B9	6/1/2009	9/3/2009	–	95	15
B9b	8/27/2009	5/18/2010	5/8/2010	255	15
B13	6/3/2009	5/25/2010	2/14/2010	257	49
B15	6/4/2009	8/1/2009	–	59	35
B17	6/5/2009	5/18/2010	3/3/2010	244	24
B33	6/4/2009	4/21/2010	2/21/2010	263	36
B33b	6/4/2009	4/21/2010	nd	0	36
B40	6/3/2009	6/2/2010	–	365	40
B42	6/4/2009	6/2/2010	3/3/2010	273	35
B44	6/5/2009	11/24/2009	6/30/2009	26	13
B49	6/3/2009	4/22/2010	–	324	49
B50	6/4/2009	4/22/2010	–	325	44
B51	6/4/2009	9/23/2009	–	112	33
B52	10/13/2009	5/20/2010	–	220	24
B53	6/5/2009	11/24/2009	10/3/2009	121	13
B58	6/3/2009	4/22/2010	9/22/2009	112	49
B61	6/4/2009	5/6/2010	7/9/2009	36	23
B62	6/4/2009	11/24/2009	–	174	15
RG					
RG1	4/23/2009	8/18/2009	–	118	16
RG2	4/11/2009	8/18/2009	–	130	30
RG3	4/23/2009	8/18/2009	–	118	39
RG4	4/23/2009	8/25/2009	nd	0	39
Steamboat Lumps					
RG 7	4/23/2009	10/12/2010	9/20/2009	163	72
RG 7b	11/17/2009	10/12/2010	5/20/2010	185	72
RG 8	4/23/2009	10/12/2010	9/20/2009	163	73
RG 8b	11/17/2009	10/12/2010	5/16/2010	181	72

displayed as a composite spectrogram in which 100 Hz resolution FFTs are applied to each file and then placed together chronologically to create an image comprising the duration of each DSG's recording period. The duration and fundamental frequency of 365 Hz Harmonic calls, with signal to noise ratios of at least 6 dB, were measured in the frequency domain. These analyses were completed using MATLAB.

RESULTS

Data collection

The acoustic library collected from stationary recorders deployed at various periods between 2008 and 2010 consisted of 377 728 files. In addition, 25 760 files were recorded throughout the 15 glider missions conducted between April 2009 and April 2011. Fig. 1 illustrates the location of recovered and unrecovered stationary recorders and tracks for the glider missions. The recording duration of each recorder is given in Table 1. Acoustic data were collected by the stationary recorders during all months and all hours. All deployed gliders were successfully retrieved; however, acoustic recordings stopped before recovery due to filled storage space on the SD card for some of the longer missions (Table 2). Gliders recorded acoustic files during all hours but not in the months of May, August, November and December.

Data analysis

Toadfish. A spectrogram of an *Opsanus pardus* boatwhistle is illustrated in Fig. 2a. Both *O. pardus* and *O. beta* were recorded with *O. beta* only present near shore (<10 m) (Wall et al. 2012), however the analysis does not differentiate between the calls and therefore the general term 'toadfish' is used to indicate both species. The hourly and monthly distribution of toadfish sound production

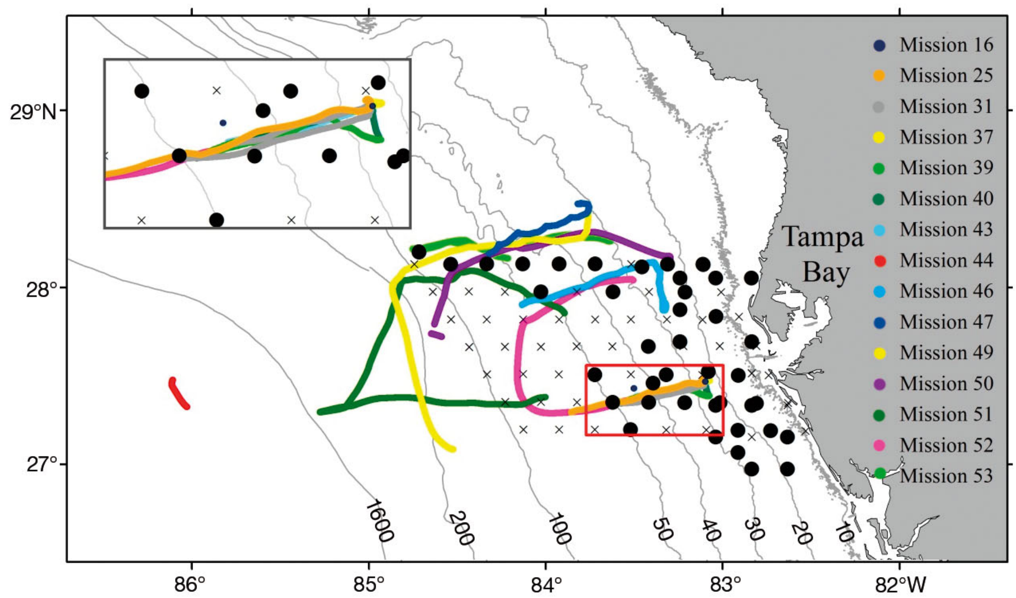


Fig. 1. Recovered stationary recorders (•), unrecovered stationary recorders (×), and interpolated tracks for hydrophone-integrated glider missions between 2008 and 2011. Red box indicates the area highlighted in the inset (Missions 16 to 43 and part of Mission 52). Depth contours (m) are also shown

show calling occurred throughout the diel period, decreasing in the early morning (06:00 h to 09:00 h), with annual peaks observed between April and June (Fig 2b–e). Calling became rare (<0.01 CPUE) from September to February. Toadfish sound production is slightly variable on the WFS, with higher densities in the northern and central part of the study area between 30 to 50 m depths (56% of observations; Fig. 2f). Toadfish were not detected in acoustic files recorded in depths greater than 83 m. The cyclical calling peak calculated from FFTs appears at 4 d cycle^{-1} for toadfish, and thus does not correspond to any lunar phase (which occur at 7, 15, and 29 d).

Table 2. Hydrophone-integrated glider deployment information: mission number, glider deployment and recovery dates, number of days acoustic data were recorded, distance the glider traveled and maximum water depth reached during the deployment. All DSGs recorded for the duration of the mission (–) unless otherwise noted in 'End recording'. Dates given as mm/dd/yyyy

Mission	Deployed	Recovered	End recording	Days recorded	Distance (km)	Max. depth (m)
16	4/9/2009	4/12/2009	–	4	51	45.1
25	6/2/2009	6/15/2009	6/7/2009	6	238	78.3
31	7/14/2009	7/21/2009	–	8	136	50.2
37	9/22/2009	9/24/2009	–	2	11	28.2
39	10/8/2009	10/14/2009	–	7	106	45.4
40	10/8/2009	10/21/2009	10/12/2009	5	209	95.4
43	4/20/2010	5/4/2010	4/23/2010	4	230	76.7
44	5/23/2010	5/25/2010	–	3	138	182.5
46	5/27/2010	6/8/2010	–	13	237	183.6
47	6/8/2010	6/14/2010	6/11/2010	4	98	57.5
49	7/13/2010	8/10/2010	7/29/2010	17	467	181.1
50	9/27/2010	10/9/2010	–	12	205	162.6
51	10/12/2010	10/30/2010	10/21/2010	10	384	984.1
52	1/31/2001	2/12/2011	–	13	225	92.4
53	3/29/2011	4/15/2011	4/14/2011	17	228	86.1

100 Hz Pulsing. The 100 Hz Pulsing consists of a series of pulses with a fundamental frequency of approximately 100 Hz (Fig. 3). Average call duration is 4.5 s (1.5 s SD, n = 27) and harmonics are present up to approximately 650 Hz. Pulse trains typically consist of 5 pulses, however, 4 pulses were observed in some recordings. This sound was observed largely at night (94% occurrence between 18:00 h and 05:00 h) and in early spring (March–April), with a secondary peak in October (Fig. 4a–d). 100 Hz Pulsing sound production was widespread throughout the study area, with calling recorded in depths ranging from 5 to 193 m (Fig. 4e). Higher numbers of glider acoustic files containing this sound were observed in the northern part of the study area. The cyclical calling peak calculated from FFTs appears at 17 d cycle^{-1} for 100 Hz Pulsing, and thus does not correspond to any lunar phase.

6 kHz Sound. A spectrogram of the 6 kHz Sound is illustrated in Fig. 5a. This sound was observed exclusively at night (100% occurrence between 18:00 h and 06:00 h) with less than 2% of the observations occurring in the winter (December to February; Fig. 5b–e). The majority of 6 kHz Sound was observed between 15 and 50 m bottom depths (94% of

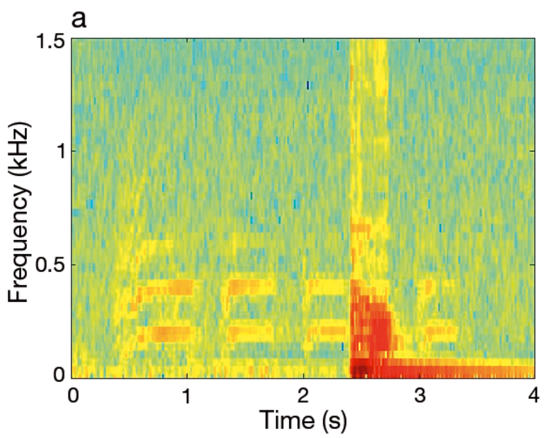
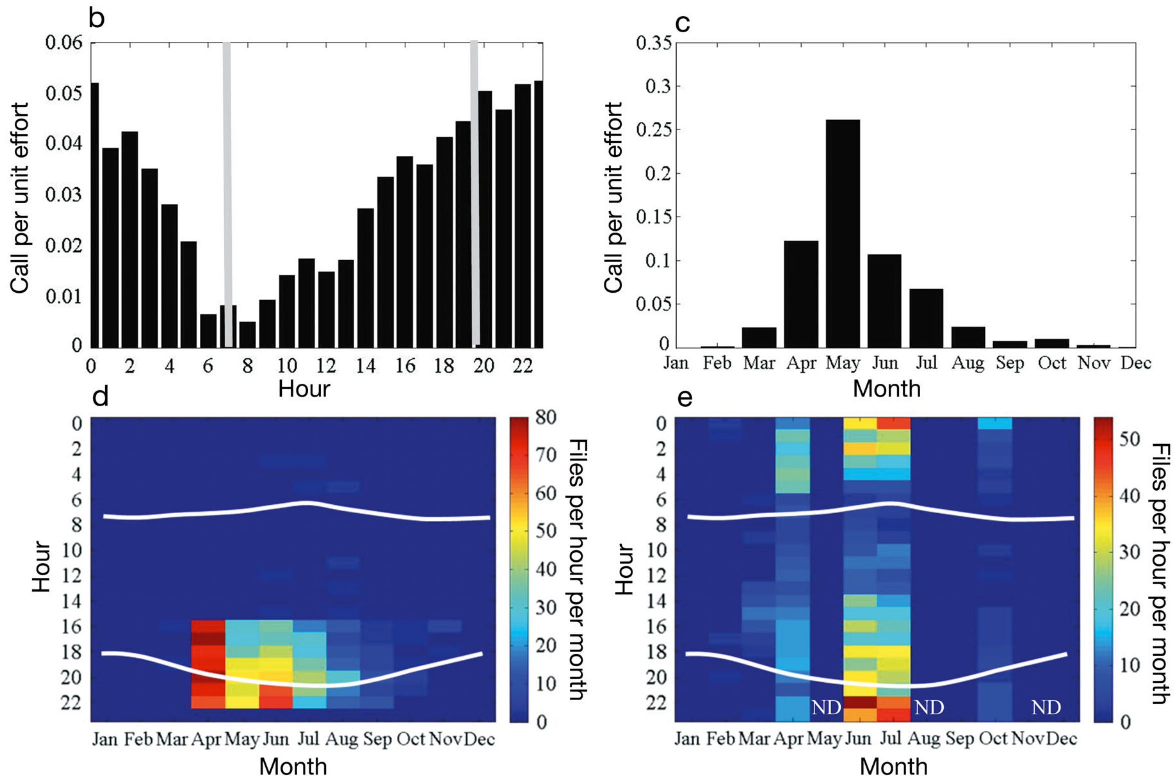
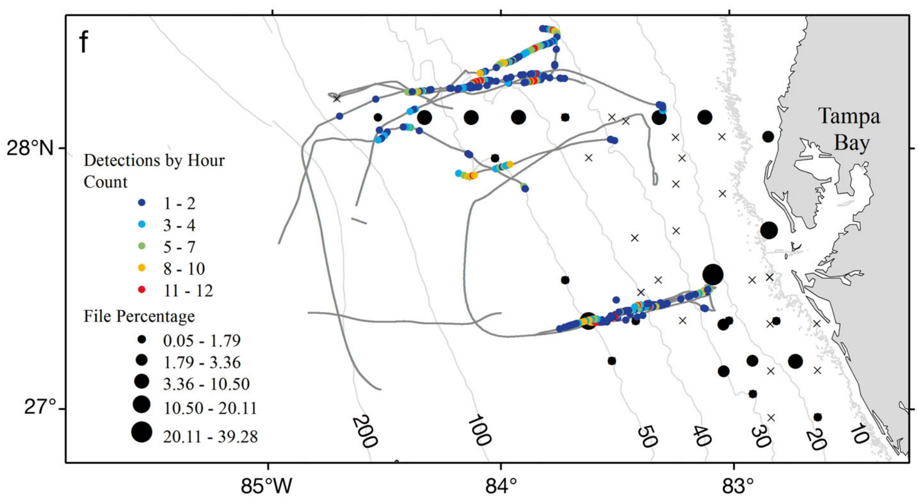


Fig. 2. Toadfish *Opsanus* sp. sound. (a) Spectrogram of this sound (broadband noise from the glider's mechanics is present between seconds 2.5 and 3). (b,c) Normalized (b) hourly and (c) monthly bins of the number of files that contained this sound, normalized by the total number of files analyzed per hour and per month, respectively, for both the stationary recorders and glider missions. Grey lines: mean sunrise (07:05 h) and sunset (19:40 h) throughout the year. (d,e) Matrix of the number of files per hour per month that contained toadfish sounds identified from (d) stationary recorders (from 16:00–22:00 h) and (e) glider missions. Color bar: number of files in which this sound was present, per hour, for each month. White lines: sunrise (top) and sunset (bottom) times. No acoustic data (ND) were collected by gliders in May, August, November or December. (Fig. 2 legend continues below)





(Fig. 2 continued.) (f) Spatial map of sound production. Stationary recorders where this sound was observed (•); symbol size is proportional to the percent of files that contained this sound from the recorder files analyzed. Stationary recorders where this sound was not observed (×). Colored dots: number of files per hour collected by the gliders that contained this sound overlaid on the interpolated glider tracks observations; Fig. 5f). The glider track within this range in which no 6 kHz Sound was detected was deployed in the winter (Mission 52: 31 Jan–12 Feb 2011). The cyclical calling peak calculated from FFTs appears at 23 d cycle^{-1} for 6 kHz Sound, and thus does not correspond to any lunar phase.

The frequency and amplitude associated with the 6 kHz Sound were significantly correlated to SST and chl *a* values (Table 3). Only 10 stationary sites recorded sound for over 6 mo (B5, B6, B7, B9, B17, B33, B42, B52, B61, and B62). SST was positively correlated to frequency and amplitude while chl *a* was mostly negatively correlated. Seasonally, as SST decreased, the frequency of the 6 kHz Sound also decreased (Fig. 6). The increase in amplitude from 130 to 134 dB with decreasing temperature in November is likely associated with increased broadband background noise and not a direct result of changes in 6 kHz Sound amplitude.

300 Hz FM Harmonic. A spectrogram of the 300 Hz FM Harmonic is illustrated in Fig. 7a. This sound appeared largely at night (89% occurrence between 18:00 h and 06:00 h), with a secondary peak at midday (12:00 h–13:00 h; Fig. 7b). Annual peaks were observed in February, April and October with an abrupt decrease in March (Fig. 7c). The stationary data identified peaks in calling in June and July; however, peaks in February, April and October were identified from the glider data (Fig. 7d,e). This discrepancy is attributed to the diel range in which glider data were analyzed compared to the subset of evening hours in which the stationary recorder data were analyzed, and is supported by the daytime calling observed only in February and April. The 300 Hz FM Harmonic appears almost exclusively offshore, in the 40 to 200 m depth range (91% of observations; Fig. 7f). The cyclical calling peak calculated from FFTs appears at 20 d cycle^{-1} for 300 Hz FM Harmonic, and thus does not correspond to any lunar phase.

365 Hz Harmonic. A spectrogram of the 365 Hz Harmonic is illustrated in Fig. 8a. This sound was observed almost exclusively at night (98% occurrence between 19:00 h and 06:00 h) and calling was largely consistent throughout the year with a small peak in the summer (June–September; Fig. 8b–e). The majority of the 365 Hz Harmonic sound was detected inshore (92% of observations occurred in waters less than 40 m deep; Fig. 8f). The cyclical calling peak calculated from FFTs appears at 19 d cycle^{-1}

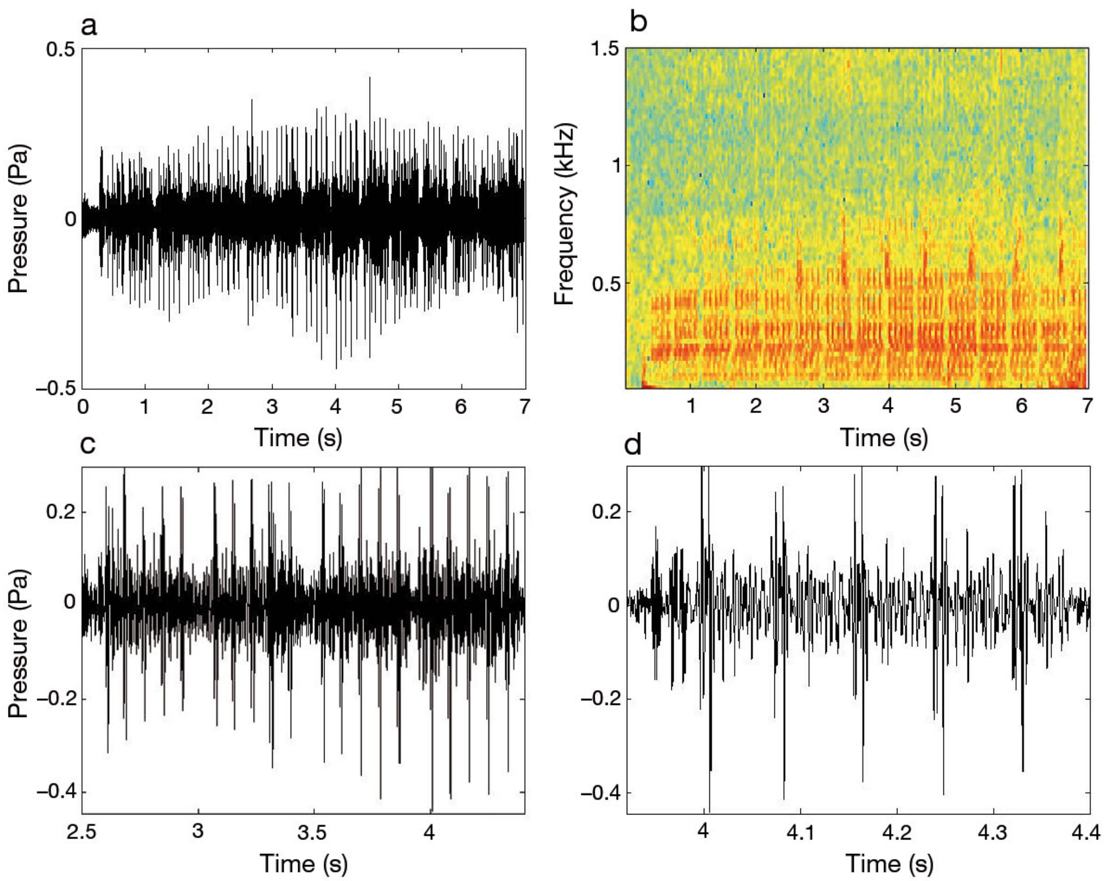


Fig. 3. 100 Hz Pulsing sound. (a) Waveform and (b) spectrogram of the full signal. Close up of the waveform shows (c) repeated 5 pulse trains and (d) the detail of a single 5 pulse train. The spectrogram was created using a 2048 point Hanning-windowed fast Fourier transform with 50% overlap

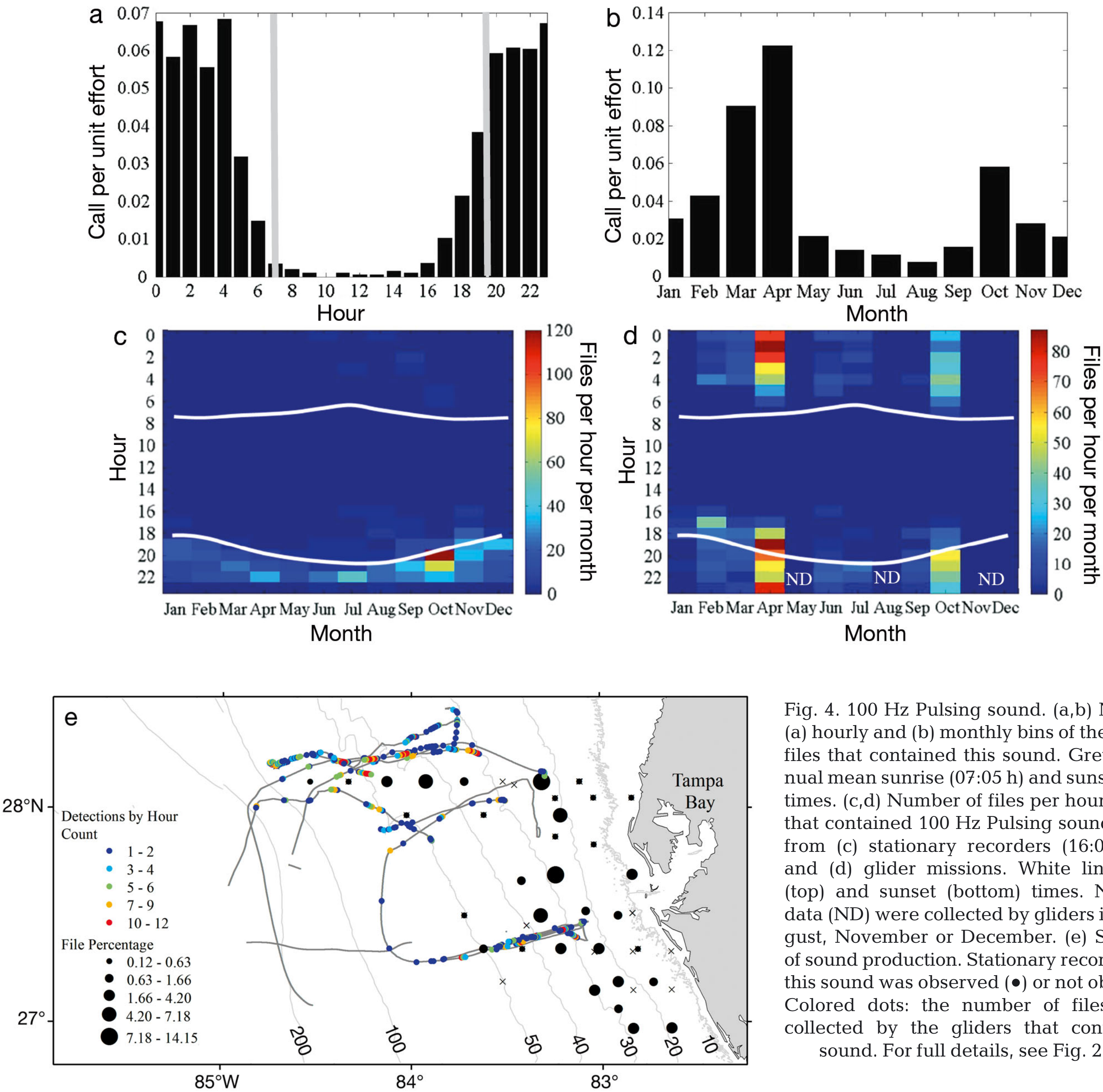


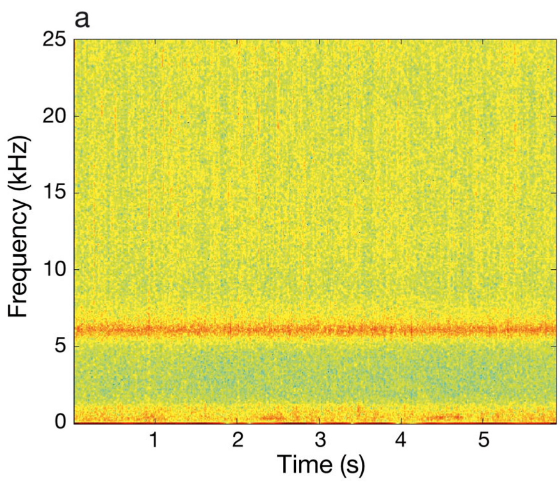
Fig. 4. 100 Hz Pulsing sound. (a,b) Normalized (a) hourly and (b) monthly bins of the number of files that contained this sound. Grey lines: annual mean sunrise (07:05 h) and sunset (19:40 h) times. (c,d) Number of files per hour per month that contained 100 Hz Pulsing sound identified from (c) stationary recorders (16:00–22:00 h) and (d) glider missions. White lines: sunrise (top) and sunset (bottom) times. No acoustic data (ND) were collected by gliders in May, August, November or December. (e) Spatial map of sound production. Stationary recorders where this sound was observed (•) or not observed (×). Colored dots: the number of files per hour collected by the gliders that contained this sound. For full details, see Fig. 2 legend

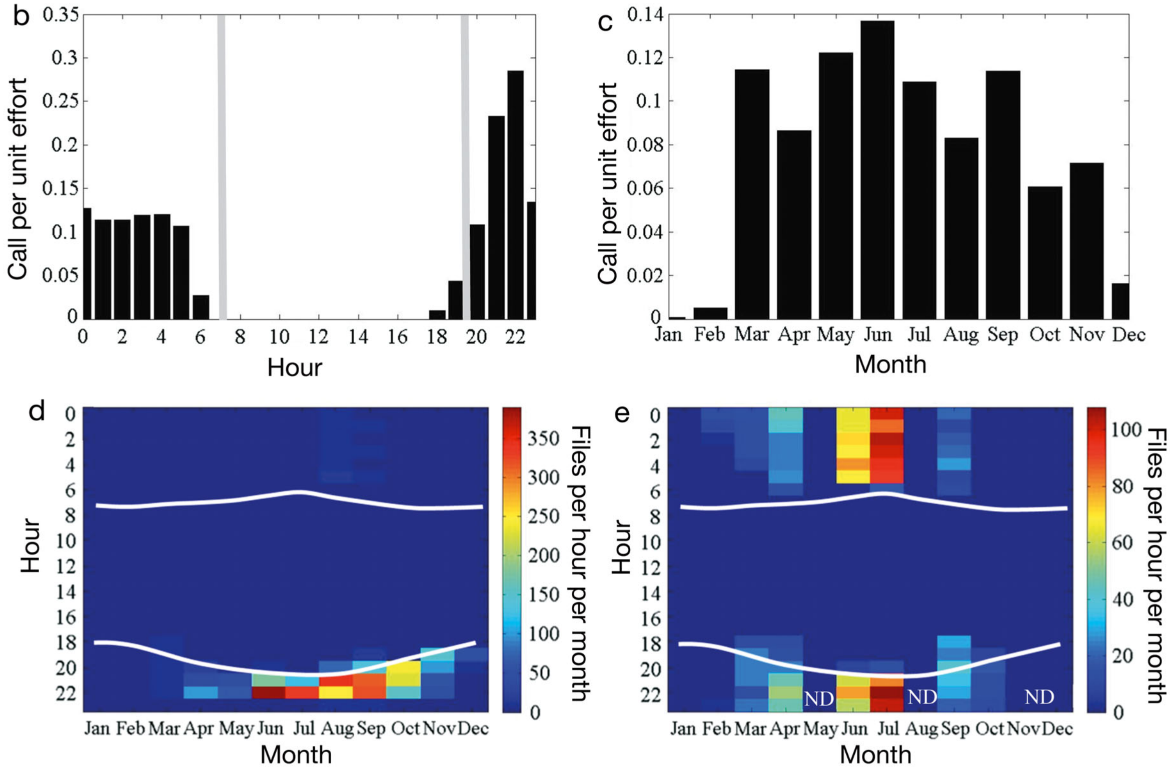
for 365 Hz Harmonic, and thus does not correspond to any lunar phase.

SST and chl *a* data were compared to the duration and fundamental frequency of the 156 examples of 365 Hz Harmonic calls selected for high signal to noise ratios (at least 6 dB) from 3 stationary recorders (Fig. 9). Call duration decreased and fundamental frequency increased with increasing SST, while call duration increased and fundamental frequency decreased with increasing chl *a*. The regression slopes are shown for each recorder, and from all recorders combined (thick black line in Fig. 9). The fit of the regression (R^2) and the slope were calculated using data from all 3 recorders. The R^2 values for call duration and fundamental frequency in relation to SST are 0.65 and 0.16, respectively, and the chl *a* are 0.21 and 0.20, respectively. An *F*-test determined that the regression was significantly different from 0 for all parameters: fundamental frequency ($F_{2,153}$ = 8.89, $p < 0.01$) and duration ($F_{2,153}$ = 31.28, $p < 0.001$) in relation to SST; fundamental frequency ($F_{2,153}$ = 8.87, $p < 0.01$) and duration ($F_{2,153}$ = 43.78, $p < 0.001$) in relation to chl *a*.

DISCUSSION

We used passive acoustic technology to determine the diel and seasonal calling patterns of 5 sounds that are suspected to be produced by fishes, in addition to outlining the spatial distribution of each acoustic signal. The sounds originated from toadfish and 4 unknown (100 Hz Pulsing, 6 kHz Sound, 300 Hz FM Harmonic, and 365 Hz Harmonic) fish-related sources. The results of this research provide insight into the habitat ranges and potential spawning patterns of several fish species in addition to determining the influence of environmental data on sound pro-





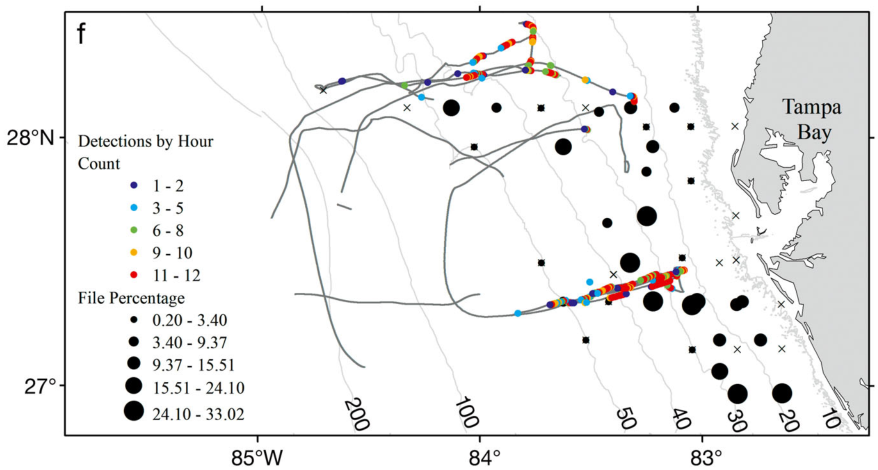


Fig. 5. 6 kHz Sound. (a) Spectrogram of this sound. (b,c) Normalized (b) hourly and (c) monthly bins of the number of files that contained this sound. Grey lines: annual mean sunrise (07:05 h) and sunset (19:40 h) times. (d,e) Number of files per hour per month that contained 6 Hz Sound identified from (d) stationary recorders (16:00–22:00 h) and (e) glider missions. White lines: sunrise (top) and sunset (bottom) times. No acoustic data (ND) were collected by gliders in May, August, November or December. (f) Spatial map of sound production. Stationary recorders where this sound was observed (●) or not observed (×). Colored dots: the number of files per hour collected by the gliders that contained this sound. For full details, see Fig. 2 legend

Table 3. 6 kHz Sound frequency and amplitude correlation to environmental data. Station sites, number of files examined (n), and mean and SD of each site's frequency and amplitude are given. Pairwise linear correlation coefficients of frequency and amplitude values to associated sea surface temperature (SST) and chl *a* were calculated for each site. Coefficients that were significantly correlated are in bold ($p < 0.05$). Only stationary recorders that collected data for over 6 mo are shown

Station	n	Frequency (Hz)				Amplitude (dB)			
		Mean	SD	SST	Chl *a*	Mean	SD	SST	Chl *a*
B5	126	4268	571	**0.30**	0.11	137	571	**0.27**	−0.02
B6	87	4642	1047	**0.93**	**0.21**	125	105	**−0.59**	−0.10
B7	135	5516	341	**0.90**	**−0.48**	144	341	**0.83**	**−0.45**
B9	123	5392	462	**0.95**	**−0.49**	149	462	**0.61**	**−0.34**
B17	244	5628	278	**0.85**	**−0.56**	128	278	**0.33**	**−0.46**
B33	266	5357	392	**0.76**	**−0.57**	128	392	**0.58**	**−0.37**
B42	340	5483	335	**0.65**	**−0.54**	129	335	**0.62**	**−0.49**
B52	402	5527	430	**0.92**	**−0.75**	131	430	**0.68**	**−0.56**
B61	237	5665	312	**0.83**	**−0.60**	131	312	**0.42**	0.03
B62	174	5721	291	**0.80**	**−0.44**	135	291	**0.68**	0.00

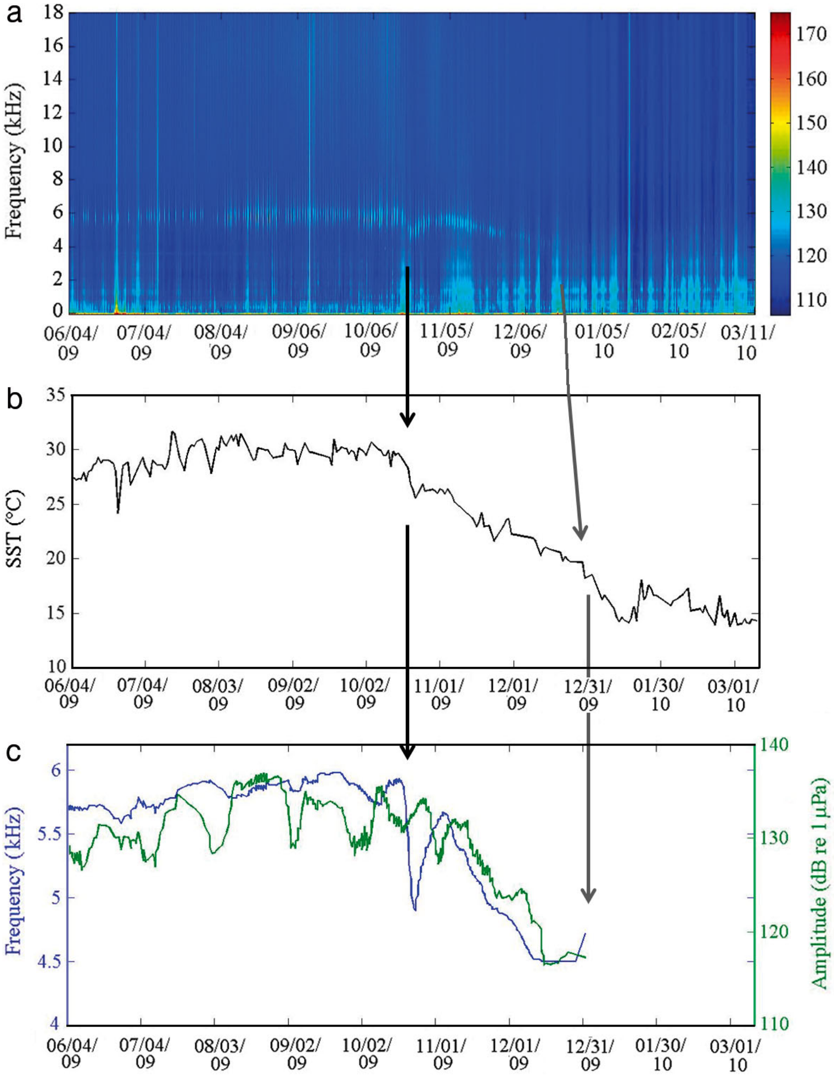
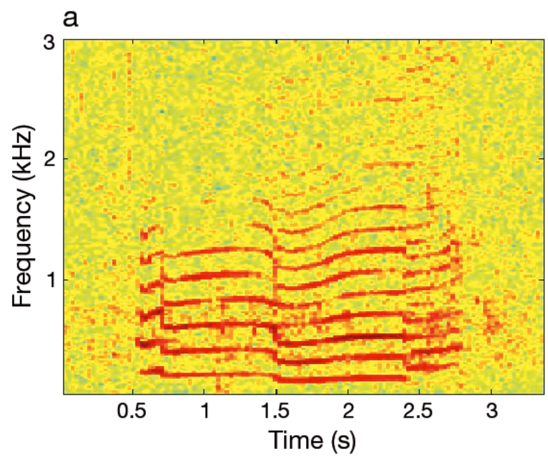


Fig. 6. Time series of the 6 kHz Sound and sea surface temperature (SST) for one stationary recorder. (a) Composite spectrogram, (b) associated SST and (c) frequency and amplitude of the 6 kHz Sound derived from the composite spectrogram. Increases in amplitude between 5 and 6 kHz represent the 6 kHz Sound. Black arrow indicates a decrease in frequency and an increase in amplitude of the 6 kHz Sound and concurrent drop in SST. Grey arrow indicates the last day the 6 kHz Sound was detected (1 January 2010). Dates given as mm/dd/yy

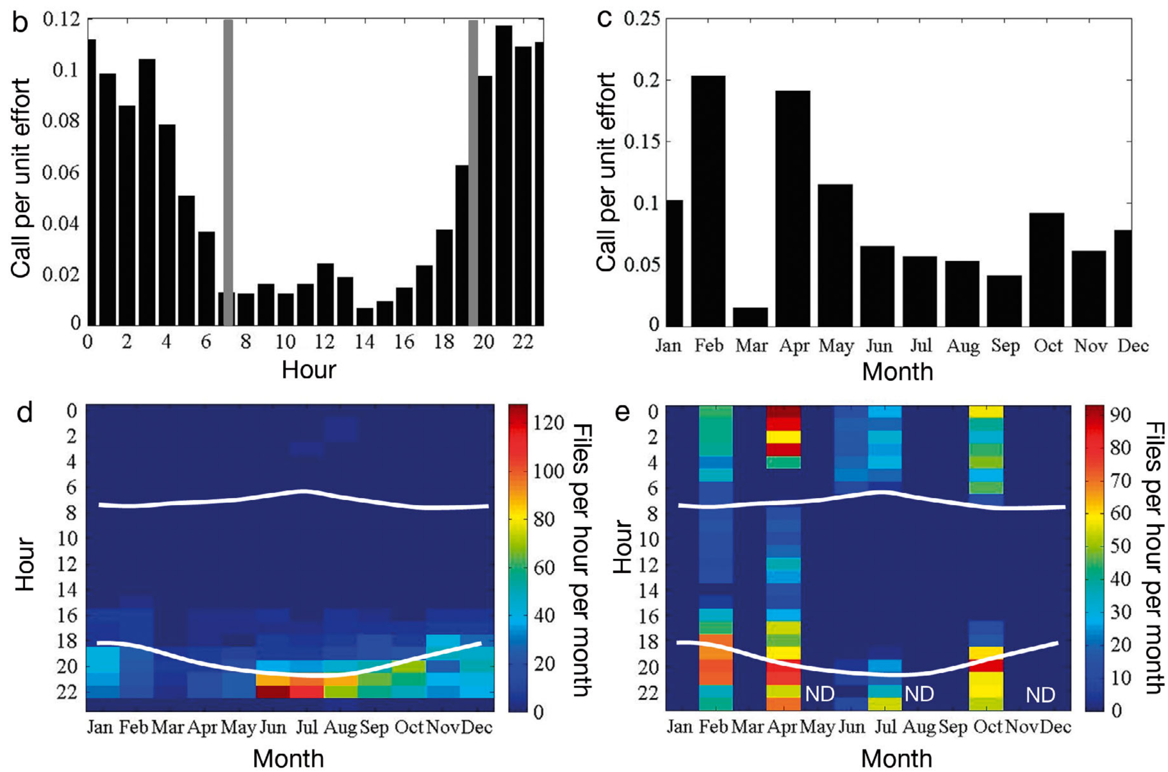
duction (detailed in the following paragraphs). Some changes in call characteristics were noted as the seasons changed, namely as temperature decreased in the winter. Since all data were visually analyzed, sounds were more likely to be identified correctly throughout the seasons as a human eye can account for slight variances in frequency or duration whereas a computer program may not.

The boatwhistle of the male toadfish is a courtship call to attract mates (Gray & Winn 1961, Breder 1968, Fine 1978, Hoñman & Robertson 1983, Barimo et al. 2007). Toadfish boatwhistles were recorded throughout all hours of the day with the majority of calls observed between 15:00 h and 04:00 h. This is consistent with Gulf toadfish *Opsanus beta* calling patterns (Breder 1968). Sound production was predominately observed from late spring to early summer (April–July); this coincides with the spawning season of oyster toadfish, *O. tau*, which are found off the east coast of Florida (May to July in 17.5–27°C, with maximum reproductive activity throughout June and early July) (Gray & Winn 1961, Fine 1978). In Biscayne Bay, FL, gonadosomatic index (GSI) data indicate that *O. beta* spawning peaks from February to April (Malca et al. 2009). Increased water temperatures associated with the more southern latitude of Biscayne Bay is likely responsible for the earlier spawning season of *O. beta* (Gray & Winn 1961). The single



peak in toadfish sound production presented here provides further evidence that *Opsanus* sp. spawn once per year instead of twice as reported in Breder (1941).

Boatwhistle sounds detected inshore (<10 m depth) may be produced by the inshore Gulf toadfish, *Opsanus beta*, found in shallow waters on the east coast of southern Florida and the Gulf of Mexico (Thorson & Fine 2002). Conversely, those detected offshore (>10 m) are likely from the offshore leopard toadfish, *O. pardus*, whose call characteristics were first described in Wall et al. (2012). Further analysis is



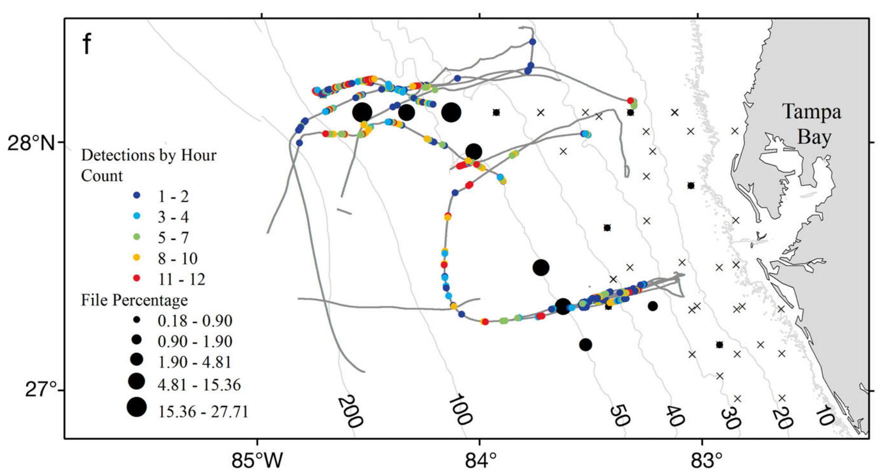
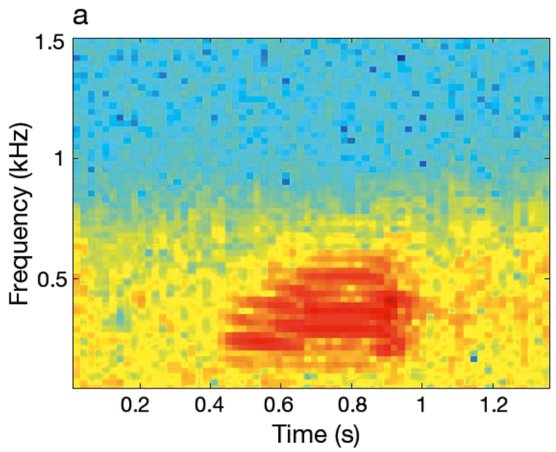
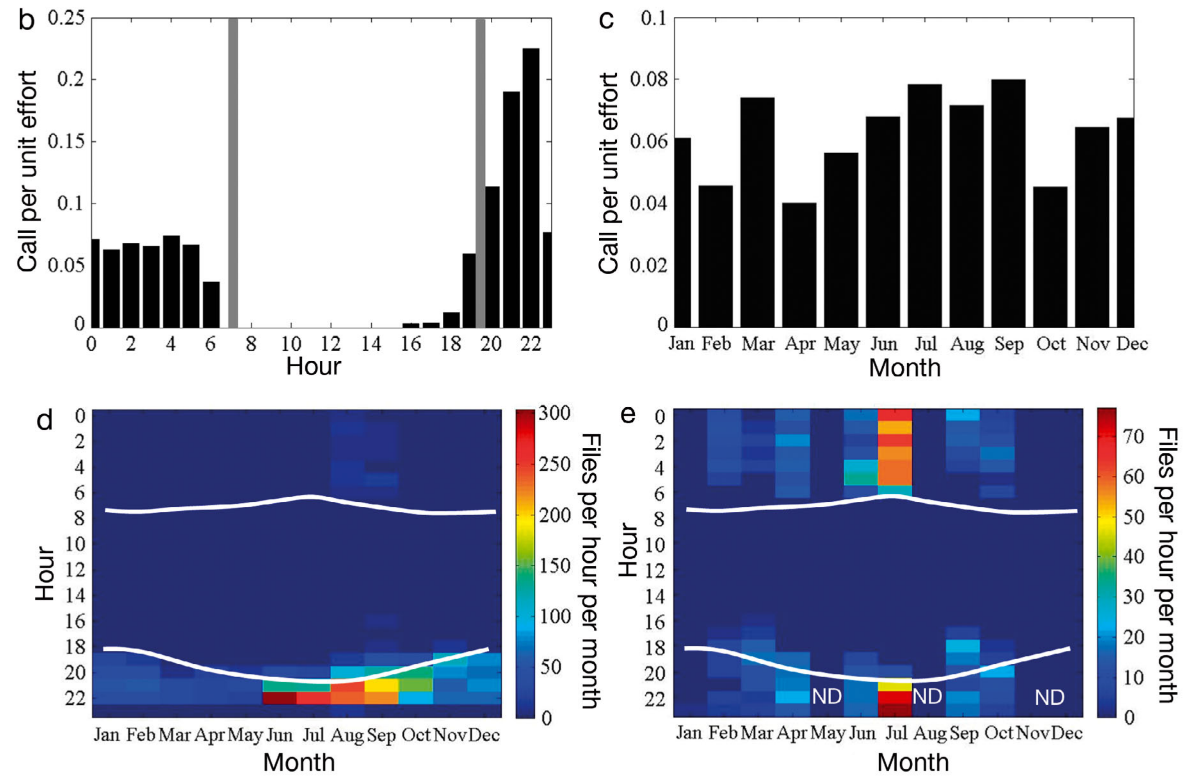


Fig. 7. 300 Hz FM Harmonic sound. (a) Spectrogram of this sound. (b,c) Normalized (b) hourly and (c) monthly bins of the number of files that contained this. Grey lines: annual mean sunrise (07:05 h) and sunset (19:40 h) times. (d,e) Number of files per hour per month that contained 300 Hz FM Harmonic sounds identified from (d) stationary recorders (16:00–22:00 h) and (e) glider missions. White lines: sunrise (top) and sunset (bottom) times. No acoustic data (ND) were collected by gliders in May, August, November or December. (f) Spatial map of sound production. Stationary recorders where this sound was observed (•) or not observed (×). Colored dots: the number of files per hour collected by the gliders that contained this sound. For full details, see Fig. 2 legend



needed to discern the exact transition of habitat range between Gulf toadfish to leopard toadfish with increasing depth.

The characteristics of the 100 Hz Pulsing are similar to the pattern of striped cusk-eel *Ophidion marginatum* sound production (Mann et al. 1997). It occured largely at night and in the same frequency range (100–600 Hz) as calls of *O. rochei*, which contain most of their energy below 500 Hz (Parmentier et al. 2010), but lower than *O. marginatum* whose calls have a peak frequency of 1200 Hz (Mann et al. 1997). The similarity in waveforms and frequency range,



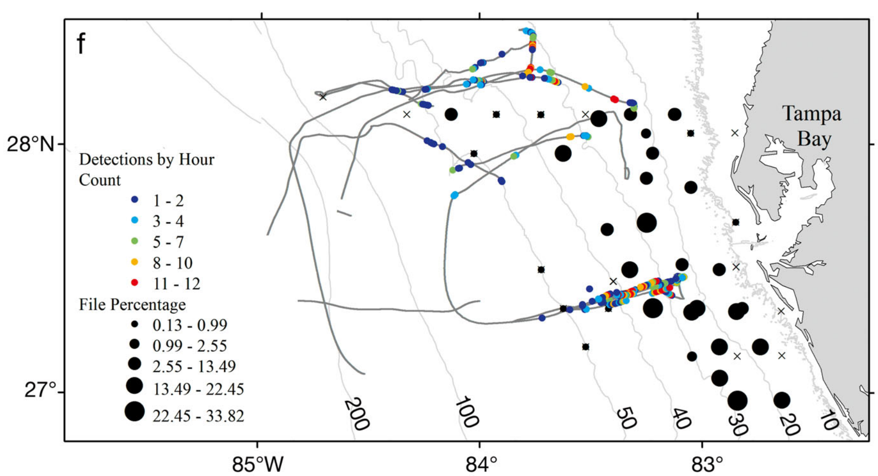


Fig. 8. 365 Hz Harmonic sound. (a) Spectrogram of this sound. (b.c) Normalized (b) hourly and (c) monthly bins of the number of files that contained this sound. Grey lines: annual mean sunrise (07:05 h) and sunset (19:40 h) times. (d,e) Number of files per hour per month that contained 365 Hz Harmonic sounds identified from (d) stationary recorders (16:00–22:00 h) and (e) glider missions. White lines: sunrise (top) and sunset (bottom) times. No acoustic data (ND) were collected by gliders in May, August, November or December. (f) Spatial map of sound production. Stationary recorders where this sound was observed (•) or not observed (×). Colored dots: the number of files per hour collected by the gliders that contained this sound. For full details, see Fig. 2 legend

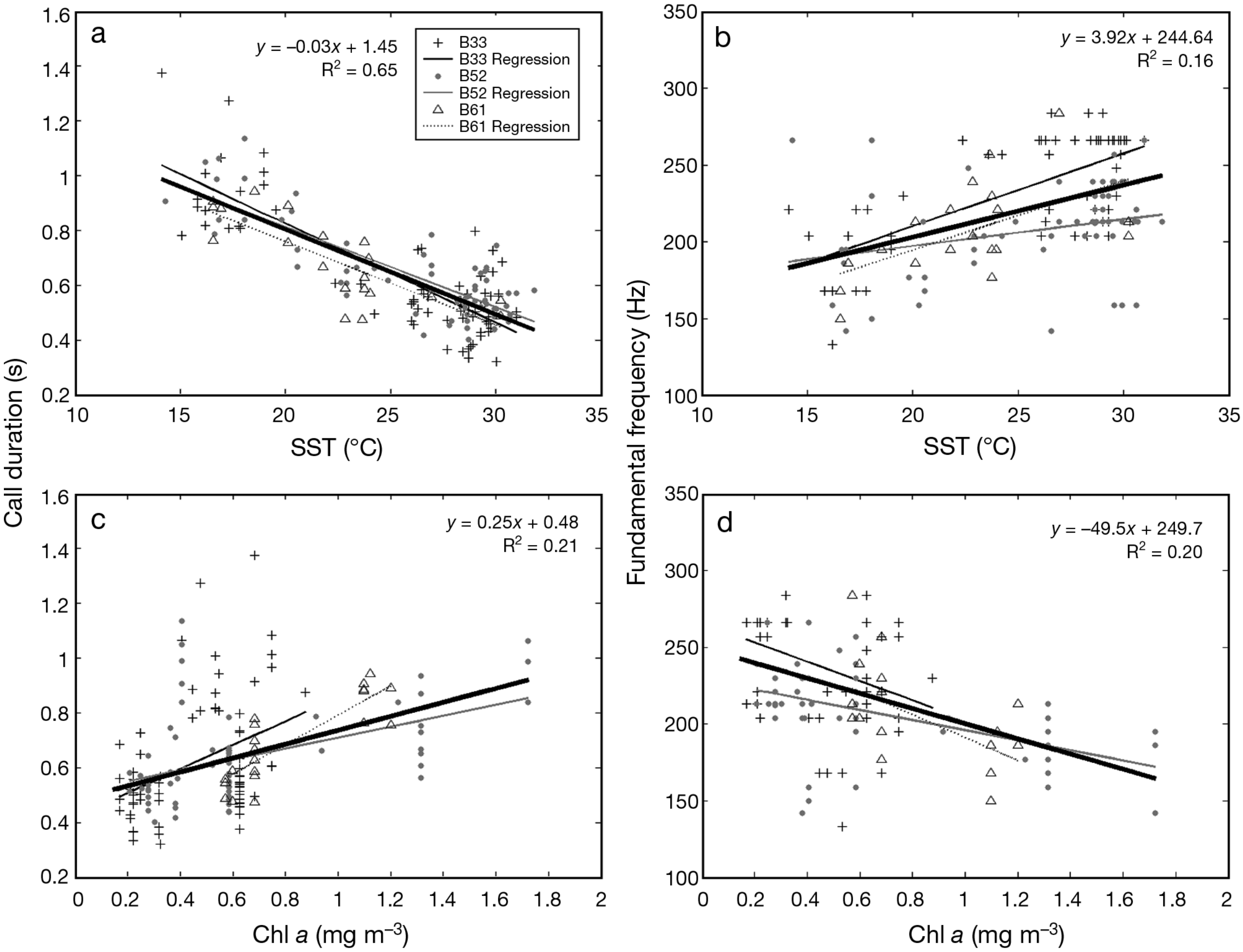


Fig. 9. Sea surface temperature (SST) and chl a associated with the 365 Hz Harmonic sound call parameters. SST and (a) call duration and (b) fundamental frequency, and chl a and (c) call duration and (d) fundamental frequency were calculated from 3 stationary recorders: B33, B52 and B61 (n = 71, 65, and 20, respectively). Regression coefficients and R^2 values are shown for the slope calculated from all data points (thick black line; n =156)

specifically with respect to *O. rochei*, suggests that the source of the 100 Hz Pulsing is likely a cusk-eel species. Fish assemblage data collected in the summer and fall of 2008 to 2010 by the Southeast Area Monitoring Assessment Program (SEAMAP; seamap.gsmfc.org/) identified *O. holbrooki*, *O. beani*, and *Lepophidium jeannae* to be common off west-central Florida.

Cusk-eel sound production is associated with courtship and spawning, and may be important for communication since spawning occurs at night (Mann et al. 1997, Sprague et al. 2001, Mann & Grothues 2009). Annual peaks in 100 Hz Pulsing sound production indicate that, if the sound is produced by cusk-eels, reproductive activity is potentially highest in the spring and fall. This is consistent with overall spawning periods (March to July or August and October to late November) identified in 4 cusk-eel species found off Texas (Retzer 1991). Retzer (1991) noted wider depth ranges and longer spawning periods for the strictly nocturnal *Lepophidium* species compared to the nocturnal and diurnal *Ophidion* species. The wide depth distribution and largely nocturnal calling of the 100 Hz Pulsing suggest *L. jeannae* is a likely source. The infrequent daytime calling observed suggests *Ophidion* species may also contribute to the overall sound production.

Wall et al. (2012) identified potential candidates for 3 of the unknown sounds. The 6 kHz Sound source was suspected to be related to gas release from clupeid schools (Nøttestad 1998, Wahlberg & Westerberg 2003, Wilson et al. 2004, Doksæter et al. 2009, Knudsen et al. 2009), the 300 Hz FM Harmonic is potentially produced by Atlantic midshipman *Porichthys plectrodon* (which is similar to *P. notatus* recorded by Brantley & Bass 1994), and the 365 Hz Harmonic (which is similar to *Prionotus carolinus* recorded by Connaughton 2004) is possibly from a searobin species, such as blackwing searobin *P. rubio*.

If the 6 kHz Sound does result from clupeid gas release, round sardine *Sardinella aurita*, scaled sardine *Harengula jaguana*, and Atlantic thread herring *Opisthonema oglinum* are common species present on the inner WFS, with Atlantic thread herring most common offshore (Pierce & Mahmoudi 2001, SEAMAP 2012). Buoyancy in physostome fishes (such as clupeids) is controlled by adjusting swim bladder pressure through the exchange of gas in the blood and the capture and release of gas through the pneumatic duct (known as the 'gasspuckerreflex') (Fänge 1976).

As fishes are ectothermic organisms, ambient temperature alters the rate swim bladder-associated muscles are innervated in some species, with decreasing temperature decreasing the rate of neuron synapsis, and thus frequency of muscle contractions (Fine 1978, Connaughton et al. 1997, 2000, 2002, McKibben & Bass 1998). This supports the positive correlation between the presence, peak frequency and amplitude of the 6 kHz Sound to SST. The approximately 2 kHz range over which the peak frequency of this sound was observed suggests that a change in nomenclature is imperative and that temperature directly affects the mechanism of sound production. Therefore, changes in the contraction rates of buoyancy-regulating muscles and size of the sphincter may play a role in altering the frequency and/or amplitude of the 6 kHz Sound. It should be noted that clupeid gas release is just one plausible hypothesis and further research is needed to determine the source of this sound with any certainty.

The acoustic distribution of the 300 Hz FM Harmonic was noted mainly offshore (>40 m depth) with the greatest abundance in the northwest corner of the study area. This spatial range is consistent with Atlantic midshipman collected off west-central Florida from 2008 to 2010 (SEAMAP; seamap.gsmfc.org/). Plainfin midshipman *Porichthys notatus* produce several sounds directly and indirectly associated with courtship and spawning (Brantley & Bass 1994, Bass et al. 1999, Sisneros 2009). One sound — a growl — is a multiharmonic, long duration (>1 s) sound with gradual changes in fundamental frequency (Sisneros 2009). This call most closely describes the 300 Hz FM Harmonic. The plainfin midshipman breeding season occurs from late spring to summer (April to August), which supports the seasonal peaks in 300 Hz FM Harmonic sound production in February, April, June and July.

The 365 Hz Harmonic sound was present mainly inshore (<40 m depth) and in the northern portion of the study area. This spatial range is consistent with blackwing searobin, barred searobin *Prionotus martis* and bighead searobin *P. tribulus* collected off west-central Florida from 2008 to 2010 (SEAMAP; seamap.gsmfc.org/). Connaughton (2004) described the sound production mechanism of northern searobin *P. carolinus* as alternating contractions of paired sonic muscles. The fundamental frequency of northern searobin (200–280 Hz) is comparable to that of the 365 Hz Harmonic (mean ± SD fundamental frequency: 223 ± 36 Hz) and both species show an increase in fundamental frequency with increasing temperature (Connaughton 2004). Variability between SST and call duration, especially among the different sites, is likely due to the temperature measurement reflecting only the ocean surface and not the bottom (ambient) temperature. The effect of temperature on call characteristics has also been observed in weakfish *Cynosion regalis* (Connaughton et al. 1997), oyster toadfish (Fine 1978, Connaughton et al. 2000, 2002) and plainfin midshipman (McKibben & Bass 1998). In both species, fundamental frequency increases with increasing temperature. Similar to the 365 Hz Harmonic, weakfish pulse duration is inversely proportional to temperature (Connaughton et al. 1997).

Peak spawning for northern searobin and striped searobin *Prionotus evolans*, in the mid-Atlantic Ocean extends from May to July (Richards et al. 1979) or May to September in offshore waters (McBride 2002, McBride et al. 2002). Leopard searobin *P. scitulus*, bluespotted searobin *P. roseus*, and barred searobin spawn on the WFS during spring and late summer (Ross 1980, 1983). These spawning periods are consistent with the 365 Hz Harmonic summer peak in sound production (June–September) observed in the stationary recorder files. In addition, bighead searobin spawn on the inner (<42 m) WFS from fall to early spring (Ross 1983), which could account for the secondary peaks in 365 Hz Harmonic sound production in March and late fall (November and December).

Atlantic midshipman and blackwing searobin are just a few sound-producing species present on the WFS. A preliminary analysis of families of soniferous fishes in the Gulf of Mexico using published literature (Fish & Mowbray 1970, Hoese & Moore 1998) and unpublished sound recordings identified nearly

90 genera that are likely to make sound based on anatomy (C. Wall unpubl. data). This leaves the list of potential sources of sound described in the present study rather vast. SEAMAP (seamap.gsmfc.org/) data show Jackknife fish *Equetus lanceolatus*, cubbyu *Equetus umbrosus*, and bluespotted searobin are all common on the WFS, with bluespotted searobin extending furthest offshore (~100 m depth). It was determined that these species are possibly soniferous via a dissection that showed both *Equetus* species have extrinsic sonic muscles and bluespotted searobin have intrinsic sonic muscles.

Passive acoustic monitoring systems record acoustic data over large spatial and temporal scales. Since sound is associated with reproduction in many species, an important application of PAM is to determine when and where reproductive activities occur for fishes (Mann & Lobel 1995, Lobel 2002, Gannon 2008, Van Parijs et al. 2009, Lobel et al. 2010). The employment of stationary and autonomous PAMs resulted in acoustic data for not only the original target species (red grouper and cetaceans) but incidental low-frequency sounds as well, which provided valuable information about the broader acoustic scene. From these data, a greater understanding of the spatial and temporal patterns of sound associated with 5 fish-related sources (toadfish, 100 Hz Pulsing, 6 kHz Sound, 300 Hz FM Harmonic, and 365 Hz Harmonic) was developed. These data can then be useful for more directed studies to verify the sound producers. Five additional unknown, suspected fish sounds were observed in the acoustic files but are not presented here (e.g. 'grunts' and 'pulses'). Further research in identifying the source of all unknown sounds is essential to advancing the field of fish bioacoustics and communication.

Acknowledgements. We thank the captains and crew of the RV 'Weatherbird II', RV 'Fish Hawk', RV 'AliCat', RV 'Eugenie Clark' and RV 'Narcosis' for their assistance in deploying and recovering acoustic recorders. We thank the University of South Florida, Center for Ocean Technology glider staff, namely M. Lindemuth, D. Edwards, A. Warren, S. Butcher and A. Farmer. Deployment and recovery efforts were aided by the assistance of Captains G. Byrd, D. Dougherty and M. Palmer, and field crew Dr. J. Locascio, C. Murphy, M. Elliot, J. Law, B. Donahue, A. Hibbard, K. McCallister, J. Isaac-Lowry, G. Barnacle and C. Richwine. We also thank G. Gonzalez for housing and mooring design, B. Barnes and Dr. C. Hu for providing the satellite data, and J. Rester, T. Switzer, S. Keenan, and K. Fischer for discussions and data regarding SEAMAP fish assemblages. This research was funded by NOPP (OCE-0741705) awarded to D.A.M. (USF CMS), Office of Naval Research (N00014-04-1-0573 and N00014-10-1-0784) awarded to C.L. (USF COT), and the USF/USGS Graduate Assistantship awarded to C.C.W. (USF CMS).

LITERATURE CITED

Au WWL, Hastings MC (2008) Principles of marine bioacoustics, Vol 1. Springer, New York, NY

Barimo JF, Serafy JE, Frezza PE, Walsh PJ (2007) Habitat use, urea production and spawning in the gulf toadfish *Opsanus beta.* Mar Biol 150:497–508

Bass A, Bodnar D, Marchaterre M (1999) Complementary explanations for existing phenotypes in an acoustic communication system. In: Hauser MD, Konishi M (eds) The design of animal communication. MIT Press, Cambridge, p 493–514

Brantley RK, Bass AH (1994) Alternative male spawning tactics and acoustic signals in the plainfin midshipman fish *Porichthys notatus* Girard (Teleostei, Batrachoididae). Ethology 96:213–232

Breder CM (1941) On the reproduction of *Opsanus beta* Goode and Bean. Zoologica 26:229–232

Breder CM (1968) Seasonal and diurnal occurrences of fish sounds in a small Florida bay. Bull Am Mus Nat Hist 138: 327–378

Connaughton MA (2004) Sound generation in the searobin (*Prionotus carolinus*), a fish with alternate sonic muscle contraction. J Exp Biol 207:1643–1654

Connaughton MA, Fine ML, Taylor MH (1997) The effects of seasonal hypertrophy and atrophy on fiber morphology, metabolic substrate concentration and sound characteristics of the weakfish sonic muscle. J Exp Biol 200:2449–2457

Connaughton MA, Taylor MH, Fine ML (2000) Effects of fish size and temperature on weakfish disturbance calls: implications for the mechanism of sound generation. J Exp Biol 203:1503–1512

Connaughton MA, Fine ML, Taylor MH (2002) Weakfish sonic muscle: influence of size, temperature and season. J Exp Biol 205:2183–2188

Doksæter L, Godø OR, Handegard NO, Kvadsheim PH, Lam FPA, Donovan C, Miller PJO (2009) Behavioral responses of herring (*Clupea harengus*) to 1–2 and 6–7 kHz sonar signals and killer whale feeding sounds. J Acoust Soc Am 125:554–564

Fänge R (1976) Gas exchange in the swimbladder. In: Hughes GM (ed) Respiration of amphibious vertebrates. Academic Press, London, p 189–211

Fine ML (1978) Seasonal and geographical variation of the mating call of the oyster toadfish *Opsanus tau* L. Oecologia 36:45–57

Fish MP, Mowbray WH (1970) Sounds of western North Atlantic fishes. A reference file of biological underwater sounds, Vol 1. The Johns Hopkins Press, Baltimore, MD

Gannon DP (2008) Passive acoustic techniques in fisheries science: a review and prospectus. Trans Am Fish Soc 137:638–656

Gray GA, Winn HE (1961) Reproductive ecology and sound production of the toadfish, *Opsanus tau.* Ecology 42: 274–282

Hoese HD, Moore RH (1998) Fishes of the Gulf of Mexico, Texas, Louisiana, and adjacent waters, Vol 2. Texas A&M University Press, College Station, TX

Hoñman SG, Robertson DR (1983) Foraging and reproduction of two Caribbean reef toadfishes (Batrachoididae). Bull Mar Sci 13:919–927

Knudsen FR, Hawkins A, McAllen R, Sand O (2009) Diel interactions between sprat and mackerel in a marine lough and their effects upon acoustic measurements of fish abundance. Fish Res 100:140–147

Lobel P (2002) Diversity of fish spawning sounds and the application of passive acoustic monitoring. Bioacoustics 12:286–288

Lobel PS, Kaatz IM, Rice AN (2010) Acoustical behavior of coral reef fishes. In: Cole KS (ed) Reproduction and sexuality in marine fishes: patterns and processes. University of California Press, Berkeley, CA, p 307–333

Locascio JV, Mann DA (2008) Diel periodicity of fish sound production in Charlotte Harbor, Florida. Trans Am Fish Soc 137:606–615

Locascio JV, Mann DA (2011) Diel and seasonal timing of sound production by black drum (*Pogonias cromis*). Fish Bull 109:327–338

Luczkovich JJ, Mann DA, Rountree RA (2008) Passive acoustics as a tool in fisheries science. Trans Am Fish Soc 137:533–541

Malca E, Barimo J, Serafy J, Walsh P (2009) Age and growth of the gulf toadfish *Opsanus beta* based on otolith increment analysis. J Fish Biol 75:1750–1761

Mann DA, Grothues T (2009) Short-term upwelling events modulate fish sound production at a mid-Atlantic Ocean observatory. Mar Ecol Prog Ser 375:65–71

Mann DA, Lobel PS (1995) Passive acoustic detection of sounds produced by the damselfish, *Dascyllus albisella* (Pomacentridae). Bioacoustics 6:199–213

Mann DA, Bowers-Altman J, Rountree RA (1997) Sounds produced by the striped cusk-eel *Ophidion marginatum* (Ophidiidae) during courtship and spawning. Copeia 1997:610–612

Mann DA, Hawkins AD, Jech JM (2008) Active and passive acoustics to locate and study fish. In: Webb JF, Fay RR, Popper AN (eds) Fish bioacoustics. Springer handbook of auditory research, Vol 32. Springer, New York, NY, p 279–309

McBride RS (2002) Spawning, growth, and overwintering size of searobins (Triglidae: *Prionotus carolinus* and *P. evolans*). Fish Bull 100:641–647

McBride R, Fahay M, Able K (2002) Larval and settlement periods of the northern searobin (*Prionotus carolinus*) and the striped searobin (*P. evolans*). Fish Bull 100:63–73

McKibben JR, Bass AH (1998) Behavioral assessment of acoustic parameters relevant to signal recognition and preference in a vocal fish. J Acoust Soc Am 104: 3520–3533

Mellinger DK, Stafford KM, Moore SE, Dziak RP, Matsumoto H (2007) An overview of fixed passive acoustic observation methods for cetaceans. Oceanography 20: 36–46

Nelson MD, Koenig CC, Coleman FC, Mann DA (2011) Sound production by red grouper *Epinephelus morio* on the West Florida Shelf. Aquat Biol 12:97–108

Nøttestad L (1998) Extensive gas bubble release in Norwegian spring-spawning herring (*Clupea harengus*) during predator avoidance. ICES J Mar Sci 55:1133–1140

Parmentier E, Bouillac G, Dragičević B, Dulčić J, Fine M (2010) Call properties and morphology of the sound-producing organ in *Ophidion rochei* (Ophidiidae). J Exp Biol 213:3230–3236

Pierce DJ, Mahmoudi B (2001) Nearshore fish assemblages along the central west coast of Florida. Bull Mar Sci 68: 243–270

Retzer ME (1991) Life-history aspects of four species of cusk-eels (Ophidiidae: Ophidiiformes) from the northern Gulf of Mexico. Copeia 1991:703–710

Richards SW, Mann JM, Walker JA (1979) Comparison of spawning seasons, age, growth rates, and food of two sympatric species of searobins, *Prionotus carolinus* and *Prionotus evolans*, from Long Island Sound. Estuaries Coasts 2:255–268

Ross ST (1980) Sexual and developmental changes in swimbladder size of the leopard searobin, *Prionotus scitulus* (Pisces: Triglidae). Copeia 1980:611–615

Ross ST (1983) Searobins (Pisces: Triglidae). In: Memoirs of the hourglass cruise, Book 6. Florida Department of Natural Resource, St. Petersburg, FL

Sisneros JA (2009) Adaptive hearing in the vocal plainfin midshipman fish: getting in tune for the breeding season and implications for acoustic communication. Integr Zool 4:33–42

Sprague MW, Luczkovich JJ, Schaefer S (2001) Do striped cusk-eels *Ophidion marginatum* (Ophidiidae) produce the 'chatter' sound attributed to weakfish *Cynoscion regalis* (Sciaenidae)? Copeia 2001:854–859

Thorson RF, Fine ML (2002) Crepuscular changes in emission rate and parameters of the boatwhistle advertisement call of the gulf toadfish, *Opsanus beta*. Environ Biol Fishes 63:321–331

Van Parijs SM, Clark CW, Sousa-Lima RS, Parks SE, Rankin S, Risch D, Van Opzeeland IC (2009) Management and research applications of real-time and archival passive acoustic sensors over varying temporal and spatial scales. Mar Ecol Prog Ser 395:21–36

Wahlberg M, Westerberg H (2003) Sounds produced by herring (*Clupea harengus*) bubble release. Aquat Living Resour 16:271–275

Wall CC, Lembke C, Mann DA (2012) Shelf-scale mapping of sound production by fishes in the eastern Gulf of Mexico using autonomous glider technology. Mar Ecol Prog Ser 449:55–64

Wilson B, Batty RS, Dill LM (2004) Pacific and Atlantic herring produce burst pulse sounds. Proc R Soc Lond B Biol Sci 271:S95–S97

Editorial responsibility: Peter Corkeron, Woods Hole, Massachusetts, USA

Submitted: September 18, 2012; Accepted: January 18, 2013
Proofs received from author(s): May 2, 2013