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USING PASSIVE ACOUSTICS TO INFER SPAWNING BEHAVIOR AND PHENOLOGY: A CASE STUDY OF HADDOCK ON GEORGES BANK

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ABSTRACT

Climate change has the potential to impact many aspects of an organism's biology, including phenology, the timing of important biological events. The timing of reproduction and spawning events for commercially important fish species is a critically important area of research for fisheries management. Haddock are commercially important as well as sound-producing, which allows for monitoring via non-invasive passive acoustics. This study presents an application of passive acoustic monitoring to a multi-year dataset to increase understanding of haddock sound production, as well as trends in spawning phenology and behavior. An automatic acoustic detector was able to identify haddock calls within known spawning grounds, and identify the timing of spawning events from fish choruses and calls that have been linked to spawning behavior. When used in conjunction with traditional fisheries research methods such as boat-based surveys, passive acoustic monitoring can be a powerful tool for fisheries biology and management. This is the first study to show the application of these techniques to this commercially important fish species in its natural environment.

Using passive acoustics to infer spawning behavior and phenology: a case study of haddock on Georges Bank

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Thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Biology.

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GLOBAL IMPACTS OF CLIMATE CHANGE

Climate change is certainly one of the most pressing issues of the 21st century, as warming temperatures and more variable climate patterns around the globe impact every facet of life on earth. Scientists have long predicted that the changing of the earth's climate would have profound impacts on the distribution of species, and this is seen throughout the fossil record as the earth's temperature has fluctuated through time (Raup 1986, Davis and Shaw 2001). In fact, throughout time, climatic changes and sea level shifts have been the two biggest drivers of global extinction events (Raup 1986). In addition to extinction, climate shifts can have profound impacts on ecosystems by altering habitat ranges and behavior for organisms, which can change food web dynamics and disrupt the balance of the system (Davis and Shaw 2001). In recent years, changes to temperatures and climate patterns have been linked to increased storms, prolonged drought, and a decrease in the biodiversity of many ecosystems (O'Gorman 2015, Yilmaz et al. 2014, Bellard et al. 2012). This loss of biodiversity is especially problematic for ecosystems under climate stress, and can come from changes in organisms' ranges, shifts in phenology, or physiological impacts and extinction (Bellard et al. 2012). Marine systems are of special concern with regard to climate change because they play a critical role in the global carbon cycle, and thus directly impact the pace and extent of climate change (Hays et al. 2005, Heogh-Guldberg and Bruno 2010).

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EFFECTS OF CLIMATE CHANGE IN MARINE SYSTEMS

Primary Productivity

In marine pelagic systems, water temperature is directly linked primary productivity and growth of phytoplankton (Edwards et al. 2016; Thomas et al. 2017). Most phytoplankton species are quite sensitive to changes in temperature, with a limited temperature band for optimal growth (Edwards et al. 2016). Many phytoplankton species are also strongly limited by nitrogen and phosphorus availability, and their sensitivity to high temperatures is exacerbated in low-nutrient conditions (Thomas et al. 2017).

Phytoplankton species are particularly good indicators of the effects of climate change on the marine environment for a number of reasons. First, their physiology is temperature- and nutrient-dependent, so changes to the global climate will have impacts on the phytoplankton community (Geider 1987). Second, these organisms are short-lived, with a distinct growing season, so their abundance is directly related to environmental conditions, rather than the persistence of individuals from previous generations (Thomas et al. 2003). Third, phytoplankton are not commercially harvested, so any changes to their abundance or distribution are most likely due to climate effects. This all leads to a strong relationship between phytoplankton abundance and climate, and changes to the abundance of primary producers can often be reflected throughout the food web via trophic cascades.

Marine Biodiversity

Changes to temperature, salinity, and other physical features of the environment have the potential to cause many direct or indirect effects on marine animals. The first response for many organisms to rising temperatures is a shift in distribution, which has been seen for many fish stocks in the North Atlantic (Nye et al. 2009, Perry et al. 2005). Some species may adapt and shift their ranges more readily than others, which could leave some species more vulnerable to the effects of climate change (Perry et al. 2005). Climate change has also been linked to the decline of many marine species in recent decades, including puffins (Sandvik et al. 2005), right whales (Greene and Pershing 2004), and a number of fish species (Rjinsdorp et al. 2009). Perhaps the most dramatic example in recent years is the Atlantic cod, where rapid and extreme warming of the waters of the Gulf of Maine combined with fishing pressure led to a total collapse of the cod fishery in the early 1990's (Pershing et al. 2015). Despite a fishing moratorium since 1992, the cod fishery still shows no signs of recovery in the Gulf of Maine (Pershing et al. 2015, Budreau and McBean 2006). As the waters of the Gulf of Maine continue to warm, continued fishing pressure on other species may lead to eventual collapse if not properly managed. In addition to extinction or loss of biodiversity, these effects could lead to further consequences for the ecosystem through trophic dynamics.

Food Web Dynamics

Much of ecology is focused on understanding the relationships of organisms to each other and their environment, and understanding how large-scale processes impact

plant and animal populations. Trophic ecology aims to decipher the energetic relationships between predators and their prey in an ecosystem. We can follow the flow of energy from photosynthesizers through grazers to animal predators, in what is known as a bottom-up process; alternatively, we can investigate complementary top-down processes, where consumers impact the abundance and behavior of their prey. Insight into the trophic interactions of an ecosystem can help illuminate the complexity of the system, thus providing a fundamental basis for generating predictions for how an ecosystem may respond to extrinsic disturbances, such as climate change or exploitation.

As water temperatures produce changes to the abundance and distribution of the primary producers in marine pelagic systems, higher trophic levels begin to experience these effects as well. Previous research has shown that copepod abundance fluctuates with temperature, and because they make up the base of the marine food web as the primary prey item for many species of small fish as well as some large whales, changes in copepod abundance will be transferred through the food web to impact animals at higher trophic levels. During the last few decades of the 20th century, peak copepod abundance shifted forward by 10 days (Edwards and Richardson 2004), and distribution patterns have changed dramatically from year to year. These changes at lower trophic levels must then have consequences for the predators that feed on them.

Many fish species go through larval stages that also depend on phytoplankton and zooplankton for food in their early life stages. As changes in temperature and climate produce shifts in the phenology of plankton blooming, this could have significant

impacts on the success of larval survival and recruitment for these fish. In the North Atlantic, the successful recruitment of larval haddock has been linked to the timing of the fall phytoplankton bloom in recent years, suggesting that we are already seeing the impacts of climate change on marine food webs (Leaf and Friedland 2014).

Studies have already begun to show the impacts of climate change on predatory species due to indirect effects such as predator prey interactions (Fredericksen et al. 2013, Durant et al. 2003, Hedd et al. 2006, Meyer-Gutbrod and Greene 2018). Trophic effects (bottom-up controls) have been seen in multiple seabird populations in the North Atlantic, with hatching success being negatively correlated with sea surface temperatures (SST) from the previous year, via change in the abundance of the dominant copepod Calanus finmarchius, which forms the base of this food web (Fredericksen et al. 2013). Previous work has shown that sandeel abundance is positively correlated with copepod abundance, and bird hatching success was positively correlated with sandeel abundance, with a one-year lag (Fredericksen et al. 2006), suggesting that there is significant bottom-up control for predators in this system. Temperature-linked declines in herring availability are linked to lowered hatching success for Atlantic puffins, which depend on herring as a staple in their diet (Durant et al. 2003). Similarly, on the west coast of North America, temperature driven availability of first-year sand lance was directly related to the breeding success of the rhinoceros auklet, which depends heavily on this fish for prey (Hedd et al. 2006). Calanus copepods make up more than ninety percent of the diet for North Atlantic right whales, and due to rising temperatures, these copepods have shifted their range northward over

the past decade. If right whales continue to follow their prey northward, they will be in unprotected waters, leaving them vulnerable to increased anthropogenic mortality, which has already been seen in the past year (Meyer-Gutbrod and Greene, 2018). The continuation of these changes could have dramatic effects for the ecosystem as a whole, including for the many commercially important species in this system.

Through bottom-up processes, we expect climate-driven changes at the level of primary producers to have cascading effects through higher trophic levels. Many top predators in marine systems, such as marine mammals and seabirds, are endothermic, so climate effects on these taxa are mostly indirect, influenced primarily by habitat or prey availability (Sydeman et al. 2015).

Phenology

In temperate systems with seasonal growing cycles, another dimension must be added to our understanding of the system. In addition to changes in abundance, organisms may also display changes in phenology, which is the timing of important biological events in an organism's life, such as blooming or spawning. Temperature changes have been shown to affect the phenology of phytoplankton and zooplankton, and are expected to impact the phenology of fish and other predators as well. Phenology can alter the dynamics of trophic relationships, resulting in a "trophic mismatch," where animals at higher trophic levels reach high abundance either earlier or later than their prey species, which can change the dynamic of the ecosystem. For example, a 2004 study by Edwards and Richardson demonstrated a shift in timing of the

major annual dinoflagellate bloom between about 1960 and 2000, with the peak biomass shifting to almost 1 full month earlier in more recent years. If dinoflagellate predators had not yet adapted to this change in phenology, predator populations would likely decline as they would miss the peak abundance of their prey.

Some 14honological changes are already being observed in marine predators. Seabirds such as puffins and auks have changed their breeding and nesting phenology in response to changes in the timing of food availability (Frederikson et al. 2004, Moe et al. 2009). Some species have shifted earlier in the year, while others have shifted later, which will change the seasonal makeup of the biological community in these ecosystems (Moe et al. 2009). Fish species have shown changes in phenology too, as atlantic cod were shown to alter their spawning phenology as temperatures rise in the Gulf of Maine, shifting earlier in the year as water temperatures increased (McQueen and Marshall 2017). For marine mammals, changes in migration phenology have been seen in a temperate system in the St. Lawrence estuary, where fin and humpback whales shifted their timing of arrival on foraging grounds one month earlier over the course of 30 years (Ramp et al. 2015), which may have consequences for their feeding success or the survival of their forage fish prey.

CONCLUSIONS

As the climate continues to warm, scientists try to predict how ecosystems may respond to temperature increases in the future. Characterizing patterns and trends correlated to localized, short-term climate cycles allows us to extrapolate and predict

impacts of human activities like large-scale anthropogenic climate change on marine

ecosystems, and particularly highproductivity systems like the Gulf of Maine, which

provides critical foraging habitat for many endangered and ecologically important

species, as well as supporting many lucrative fisheries on which we depend for food. In

the next chapter, I present a case study of spawning phenology in haddock in relation to

climate and water temperature over a span of nearly a decade. This study can be used

to build predictions for the consequences of climate change on other species and other

systems in the future.

USING PASSIVE ACOUSTICS TO INFER SPAWNING BEHAVIOR AND PHENOLOGY: A CASE STUDY OF HADDOCK ON GEORGES BANK

INTRODUCTION

Understanding the reproductive biology and spawning behavior of fish species has been a critical area of research in fisheries management for decades. Traditional methods of studying spawning have involved large research vessels and net tows to identify and quantify larval fish and eggs (Ciannelli et al. 2007, Neidetcher et al. 2014, Fincham et al. 2013, Asch et al. 2015, Genner et al. 2009). When these data are collected consistently over a long period of time, they can be extremely useful for understanding the dynamics of spawning for a species. These data are used to assess spawning success and recruitment, as well as temporal and spatial variability in spawning season and location. For example, long-term ichthyoplankton sampling by the Alaska Fisheries Science Center allowed for the characterization of spawning phenology in Alaskan Pollock (*Gadus chalcogrammus*), and linked changes in spawning phenology to large-scale changes in climate (Ciannelli et al. 2007).

These traditional approaches to studying spawning have their limitations, however. They are costly, requiring a huge amount of survey effort, using expensive research vessels to collect data in each year. As mentioned in Ciannelli et al. (2007), the data collection is often inconsistent in time and space, due to constraints of funding or weather between years. Another risk to this method is if sampling begins after spawning has started, it is impossible to get accurate measurements of spawning seasonality or spawning success in that year.

Passive Acoustics

Passive acoustic monitoring has been an important tool in marine science and management for decades. Sound recorders can be deployed in the environment to collect data on acoustic communication, animal interactions, and ambient noise without disturbing the organisms. Multiple recorders can be used to collect data over large spatial areas for extended durations of time, and recordings can be made in all weather conditions (Mellinger et al. 2007). Passive acoustic techniques have been used extensively with marine mammal populations to monitor presence, movement, communication, and behavior (Sousa-Lima et al 2013, Van Parijs et al. 2009, Zimmer 2011), but only recently been more widely applied to other sound producing species.

Sound-producing fish have been known since the time of Aristotle, and they produce sounds for a variety of reasons, usually in intraspecific communication, such as coordinating spawning, attracting a mate, or defending territory. Early fish acoustic studies focused on characterization of sounds and exploration of the behavioral functions of these sounds (Myrberg 1981, Fish and Mowbray 1970, Hawkins and Chapman 1966), but the application of passive acoustics to fisheries biology has been a more recent development (Rountree et al. 2006). In recent years, the field of fisheries passive acoustics has yielded vast amounts of new data from several species, to document many different aspects of fish biology. Passive acoustic monitoring has been used to study fish presence and movement patterns (e.g. D'Spain and Batchelor 2006, Luczkovich et al. 2008, Wall et al. 2013), group and individual communication (e.g. Myrberg 1981, Fine and Thorson 2000), and spawning behavior (e.g. Lobel 2002,

Hawkins and Amorim 2000). The first group of soniferous (sound-producing) fish to be

studied extensively via passive acoustics were fish from the family *Sciaenidae*.

(Rountree at el 2006, Fish and Mobray 1970, Ramcharitar et al 2006). The sciaenids

include drums and their relatives, who have long been known to produce sounds, and

their spawning behavior has been studied acoustically to provide information about

phenology and behavior (Luczkovitch et al. 2008, Rice et al. 2016, Monczak et al.

2017). Acoustic methods have provided critical data about movement patterns, stock

composition, and spawning phenology for a number of sciaenid species

(Lowerre-Barbieri et al. 2008, Luczkovitch et al. 2008).

The sciaenids may be the best studied, but they are not the only soniferous fish.

Many fish species across multiple families produce specific sounds that serve to

coordinate spawning (Luczkovitch et al. 2008, Amorim 2006). Lab and tank-based

experiments characterized the behavioral context of these spawning calls for many

species (Hawkins and Chapman 1966), which has since allowed for the identification of

spawning grounds in situ through passive acoustic recordings (Lobel 2002, Gilmore

2002, Roundtree 2006). In 2006, a review of passive acoustic research in fisheries

proposed that an understanding of spawning phenology, or the seasonal timing of

spawning events, was an area of critical need for research for fisheries management

(Rountree et al. 2006).

Haddock as a Model System

Haddock (*Melanogrammus aeglefinus)* are abundant deep-water fish that provide

one of the most important fisheries in the North Atlantic, producing between 14,000 and 20,000 metric tons per year in the U.S. (Brooks et al. 2008, Brodziak et al. 2006). While not fished as heavily as the closely related cod (*Gadus morhua)*, the fishery has been heavily exploited since the early 1900's. Severe overfishing in the late decades of the 20th century lead to the near collapse of the fishery in the 1990s. Since then, a rigorous management plan and cooperation between U.S. and Canadian agencies has allowed a slow recovery of haddock populations in the western North Atlantic (Brooks et al. 2008).

Haddock are found on both sides of the Atlantic Ocean, and the western North Atlantic population is comprised of two separate breeding stocks, one which spawns in the Bay of Fundy, Canada and one which spawns on Georges Bank, in the Gulf of Maine off the U.S. coast. The timing of haddock spawning can vary widely from year to year, but the average spawning period in the Gulf of Maine begins in February, with a peak spawning concentrated in March and into early April (Page et al. 1999, Gulf of Maine Research Institute, Brodziak et al. 2006).

While haddock were presumed to be sound-producing fish for most of the 20th century, the first recorded sounds of haddock and hypotheses about their behavioral contexts came from Hawkins and Chapman (1966). They suggested that the knocking sounds they recorded were likely used in agonistic territorial interactions between mature males (Hawkins and Chapman 1966). Further work with captive haddock acoustics by Hawkins identified a range of sound types, and linked specific signal production to courtship and spawning in addition to the aggression signals (Hawkins et al. 1967, Hawkins et al. 2000, Casaretto and Hawkins 2002, Hawkins et al. 2012). The

work of Hawkins et al. provided a baseline for haddock call production their connection to spawning behavior.

Once the sounds of spawning haddock had been characterized in captivity, Hawkins et al. took short acoustic recordings in known haddock spawning areas to locate spawning aggregations in situ (Hawkins et al. 2002, Casaretto et al. 2014). These methods have since been applied to corroborate fisheries-based observations of spawning sites in the Northeast Atlantic (Casaretto et al. 2014). Van Parijs et al (2009) characterized examples of haddock calls recorded in situ in Massachusetts Bay, including spawning calls, and showed that these calls can be identified via automatic acoustic detectors.

Implications for Spawning Phenology

Stereotyped calls with a clear behavioral context allow for the inference of spawning behavior and phenology from acoustic recordings. Multi-year acoustic datasets can provide additional information about inter-annual variability in seasonality and phenology. These data can provide insights into the phenology of spawning activity of target sound producing species. When linked with traditional fisheries sampling methods, validation of these acoustic techniques can further the potential for applications of passive acoustic monitoring as a valuable remote sensing tool to aid in fisheries management and conservation. These data may be able to provide critical information about the spawning activity of commercially important species, which have implications for the long-term health of fish stocks and can be used to inform

management decisions. Multiple scientists have proposed that passive acoustics could be used to study the spawning seasonality of haddock (Lobel 2002, Rountree et al. 2006, Hawkins and Casaretto 2004, Casaretto et al. 2014). This study is the first to show the potential for this approach to track interannual variability in the spawning season of haddock.

METHODS

Acoustic Data Collection

Acoustic recordings used in this study were collected as part of a monitoring project for marine mammal activity in Massachusetts Bay. Nineteen bottom-mounted Marine Autonomous Recording Units (MARUs) were deployed by the Cornell University Bioacoustics Research Program in a grid within Massachusetts Bay in summer of 2007, and recorded continuously through the summer of 2013, spanning six years of haddock spawning (Calupca et al. 2000) (Figure 1).
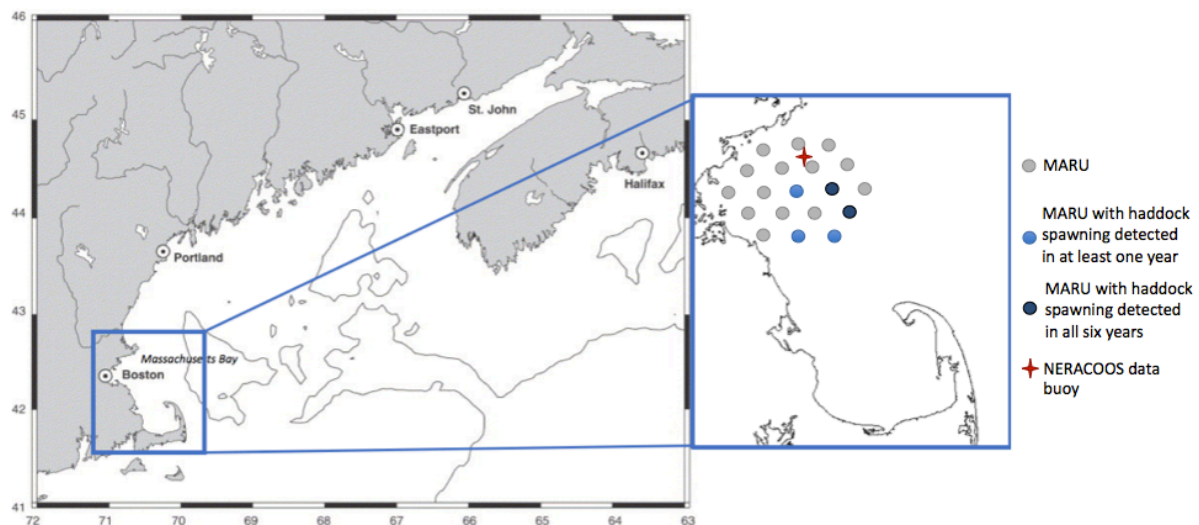
Figure 1. Map of Massachusetts Bay showing the deployment locations of all nineteen MARUs (circles) and the NERACOOS oceanographic station (red star). The initial detector run identified five locations with haddock spawning calls in at least one year, which are shown in blue. Dark blue indicates the two locations that had haddock spawning calls in all years of the study period. These locations were then used to determine annual variability in haddock spawning phenology.

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Each MARU contained an HTI-94-SSQ hydrophone (High Tech Instruments;

sensitivity: −168 dB re 1 V/μPa), connected to a pre-amplifier and A/D converter with

12-bit resolution, resulting in an effective system sensitivity of −151.7 dB re 1 V/μPa.

MARUs sampled continuously at a rate of 2000 Hz, producing an effective analysis

bandwidth of 10 to 1000 Hz, with a flat frequency response (±1 dB) between 55 and 585

Hz. The units were moored 1 to 2 m above the sea floor in depths ranging from 30 to

100 m, and approximately 3 kilometers apart. Units were deployed for approximately 3

months at a time and were recovered and redeployed throughout the study period with

minimal days in between (see Risch et al. 2013). The result is near-continuous data for

more than six years at a large spatial scale, with the exception of occasional equipment

failure or accidental trawling of the recording units that resulted in short data gaps.

Spatial Detection of Haddock

Recorders from the acoustic array were located within known haddock spawning

grounds in the Gulf of Maine (Page et al. 1999). To narrow the study location, a

template spectrogram detector (RavenPro 2.0, Cornell University Bioacoustics

Research Program) was developed to detect haddock spawning pulses. The detector

was developed and trained using haddock spawning calls found within a 24-hour period

of February 28th, 2013. This detector had a high false negative rate, meaning that it

often missed haddock signals but only one false positive for the data sample where the

detector was run (7.1% false positive rate). The detector was then run on all 19

locations for all 24 hours of March 5th in each year. This date was chosen as it has

historically been the time of peak haddock spawning activity (Brodziak et al. 2006, Brooks et al. 2008). Given the high call rate of haddock during the spawning season, the probability of missing all haddock calls in a full 24-hour recording was relatively low. The goal of the detector was to efficiently screen all 19 recorders to identify areas with consistent haddock spawning detections in all years. Haddock spawning calls were identified via detector on five of the recording units in at least one year (Figure 1). The detector identified two adjacent recorders, located within a known haddock spawning area on Georges Bank (Page et al. 1999, Brodziak et al. 2002), approximately 3 km apart, where haddock spawning pulses were consistently detected in each year, and this subset was used for further analysis to look at inter-annual variability in spawning sound activity (Table 1).

Table 1: Locations for the two MARU sites used in the spawning phenology analysis, and the NERACOOS oceanographic recording station A01.

Site	Latitude	Longitude	Depth (m)
15	42 19.29	-70 43.84	61
19	42 19.20	-70 46.52	34
NERACOOS	42 31.23	-70 33.55	65

Acoustic Signal Analysis

Van Parijs et al. (2009) provided examples of haddock calls recorded in situ in Massachusetts Bay, and identified three main species-specific call types: single knocks,

double knocks, and repetitive knocking pulse trains. The series of repeated knocks has been directly linked to spawning behavior, and was the target sound for the present study. These pulse trains are broadband, with frequency ranges from approximately 10 Hz to 350 Hz, with peak energy centered around 70-100 Hz. See figure 2 for examples of haddock spawning pulses.
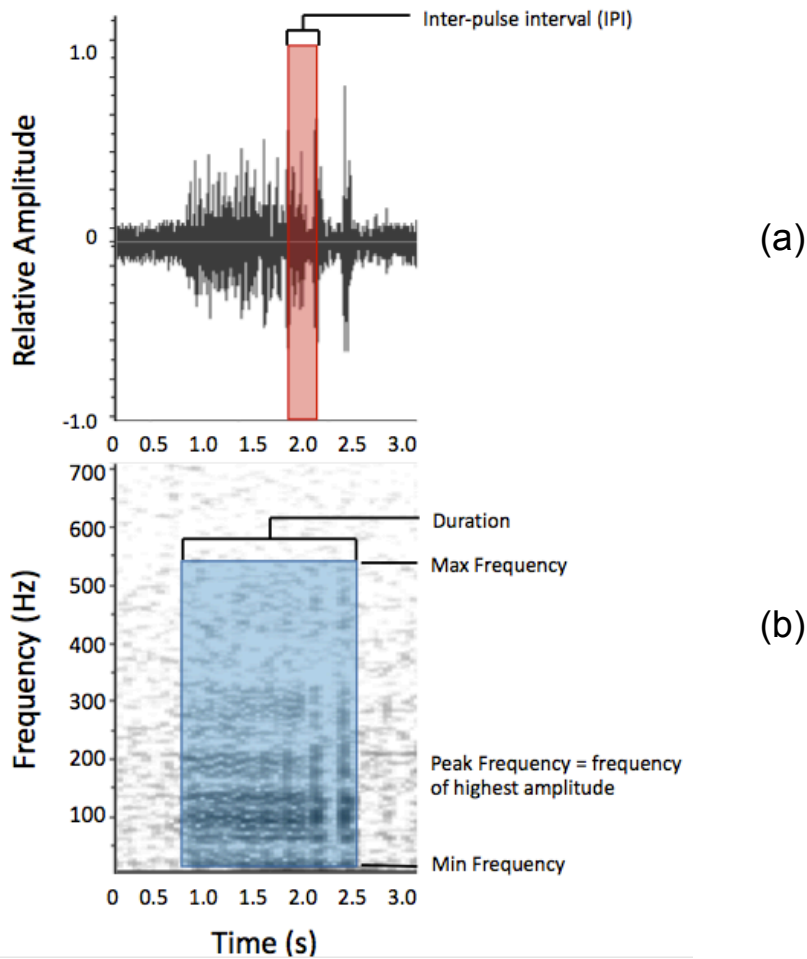
Figure 2. An example waveform (a) and spectrogram (b) showing a spawning call from a male haddock. Measurements of the call parameters were taken as shown using Raven 2.0.

For each of the six years with complete data, acoustic data from these units were browsed visually and aurally to detect the presence of haddock spawning calls. Browsing was done in RavenPro 2.0, with an FFT of 1024 and a window of 300 seconds. Eighty spawning pulses with a high signal-to-noise ratio were selected across years for detailed signal analysis. For each call, the minimum frequency, maximum frequency, duration, 1st quartile frequency, bandwidth, peak frequency, and inter-pulse interval were measured using RavenPro 2.0 (Figure 2).

Acoustic Detection of Spawning Phenology

The start of the spawning season was determined as the first day where multi-pulse haddock calls were detected, indicating spawning. The detections of these calls were documented on a daily basis until three consecutive days without haddock spawning call detections were found, and this was marked as the end of the spawning period for haddock at that location in that year. Three metrics were then used to characterize the spawning activity of haddock at this location: start of spawning, end of spawning, and total length of spawning season.

Ichthyoplankton Survey Data

Data on the abundance and distribution of haddock larvae on George's Bank have been collected from ichthyoplankton surveys conducted by the NOAA Northeast Fisheries Science Center since 1977. Since 1999, plankton sampling was conducted bi-monthly, monthly, or quarterly each year depending on the sampling program (David

Richardson, NOAA, *personal communication*). Samples were collected both day and night on cruises using a 61-cm bongo net fitted with a 333-µm mesh net. Oblique tows were a minimum of 5-minutes in duration, and fished from the surface to within 5-m of the seabed or to a maximum depth of 200-m. A mechanical flowmeter was fitted in the mouth of each net to record the volume of water sampled. The Georges Bank region was sampled each April, and this data set was compared to our acoustic results.

Adult Haddock Survey Data

Fisheries data were collected as part of the NOAA spring trawl survey, which takes place in March-May of each year. The Massachusetts Bay sites are generally sampled in late April or early May. This time period is after the peak spawning period of haddock, but these data can still be useful for assessing fish abundance and site fidelity or changes in habitat use between years. Sites are randomly selected within geographic ranges, so the same sites are not always sampled in each year.

Temperature Data

Water temperature data were collected daily from the Northeast Regional Association of Coastal and Ocean Observing Systems (NERACOOS) archive, and came from Station A01, which is located in Massachusetts Bay and records temperatures at the surface as well as at 50 meters depth (Figure 1, Table 1). While average sea surface temperature data was available for every month of the study period, the data at depth was less complete, and only included complete samples from January of each year.

RESULTS

Spatial Detection of Haddock

Preliminary use of an automatic acoustic detector identified five recorders with

haddock spawning calls present in at least one year (Figure 1). Two of these locations

contained haddock spawning calls in all years of the study period. Haddock were

generally found further offshore, at the deepest locations of the array, and were not

detected at any of the shallow near-shore locations.

Acoustic Signal Analysis

Haddock spawning calls consisted of multiple pulses in quick succession,

sometimes running together to form a continuous rumble. The average call parameters

for this call type are shown in table 2.

Table 2: Call parameters for a subset of eighty spawning calls taken across years of the study period.

	Low Freq (Hz)	High Freq (Hz)	Q1 Freq (Hz)	BW 90% (Hz)	Duration (s)	Peak Freq (Hz)	Inter-pulse interval
average	12.3	336.0	69.8	184.3	2.363	88.0	0.29
stdev	7.5	130.8	12.4	70.6	0.973	16.5	0.05
min	4.7	150.9	43.0	74.2	0.672	50.8	0.20
max	29.7	558.3	89.8	269.5	4.116	128.9	0.41

Average pulse duration was about two seconds (+/-0.97 seconds), with an average inter-pulse interval of about 0.29 seconds (+/-0.05 seconds). The peak frequency of the calls was generally between 80 and 90 kHz, but varied between 50.8 and 128.9 kHz. These parameters are similar to descriptions of spawning calls both collected in captivity (Hawkins and Amorim 2000) and in situ (Van Parijs et al. 2009). Previous studies have shown some individual variation in sound production by different fish (Hawkins and Amorim 2000, Hawkins et al. 2002), but individuality could not be assessed in this study.

Acoustic Detection of Spawning Phenology

Haddock spawning phenology was measured at two sites in the study area that had haddock spawning calls present in each year. Overall, the start of the haddock spawning seasonality was fairly consistent between years (Figure 3). The spawning season had an average start date of February 16th, and lasted for an average of 34 days. The earliest spawning start date was February 10th, and the latest start date was February 29th. The earliest spawning season end date was March 5th, and the latest spawning season end date was April 15th. The shortest spawning season spanned 6 days (2012), while the longest was 64 days (2013) (Table 3).

Data coverage and detection dates for haddock spawning calls
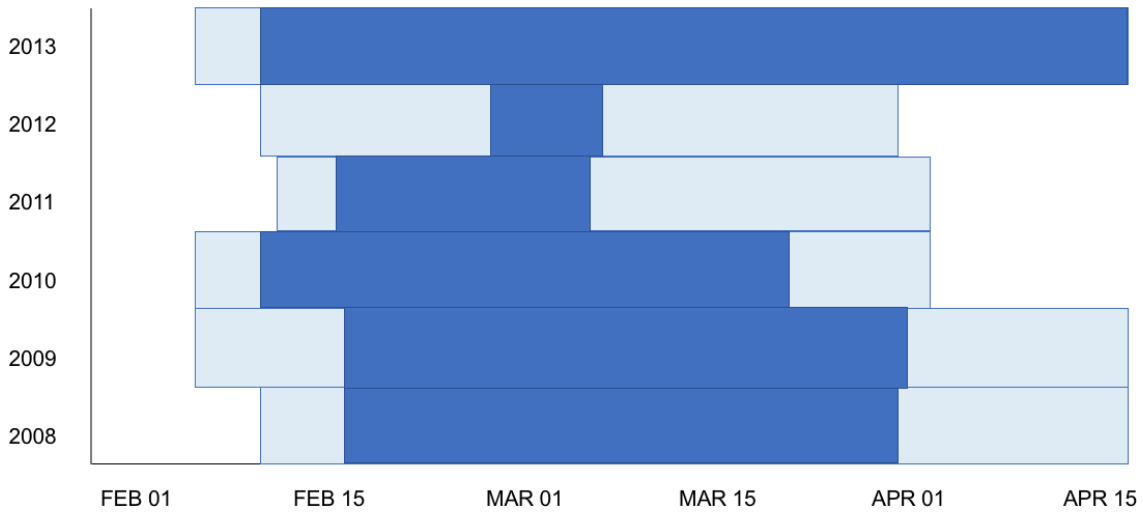
Figure 3. Annual variation in the overall recording time (light blue) and days with haddock spawning call detections (dark blue)

Table 3: Phenology measurements for the haddock spawning season in each year taken from acoustic analysis. All dates are listed as Julian day.

Year	Spawning Start Date	Spawning End Date	Spawning Season Length
2008	47	89	42
2009	47	90	43
2010	41	76	35
2011	46	63	17
2012	60	65	5
2013	41	105	64

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Ichthyoplankton Survey Analysis

The NOAA ichthyoplankton surveys covered Georges Bank and the Gulf of Maine in February and April of each year. For the purposes of this study, the April survey data is presented, since these surveys took place immediately after the peak spawning season in early March. The sampling sites varied between years, but larval haddock were present on Georges Bank in each year of the study period. The highest abundance of larval haddock was found in 2009, while the lowest abundance was found in 2012 (Table 4). The results of the haddock sampling in each years are shown in Table 4. Abundance of haddock varied by location in each year as well. Figure 4 shows the relative abundance of larval haddock at each sampling site for each year during the study period, as well as sampling locations where no larval haddock were detected in each year.

Table 4. The average abundance of haddock larvae (count per 100 cubic meters of seawater) in each year of the study period. Data were collected during NOAA cruises in April of each year, at randomly selected sampling sites across Georges Bank, Massachusetts Bay, and the Gulf of Maine.

	2008	2009	2010	2011	2012	2013
average	144.92	409.26	288.68	364.95	101.19	209.55
stdev	192.15	487.55	539.30	397.21	146.30	327.29
min	0	0	0	0	0	0
max	1145	2286	2107	1967	822	1834
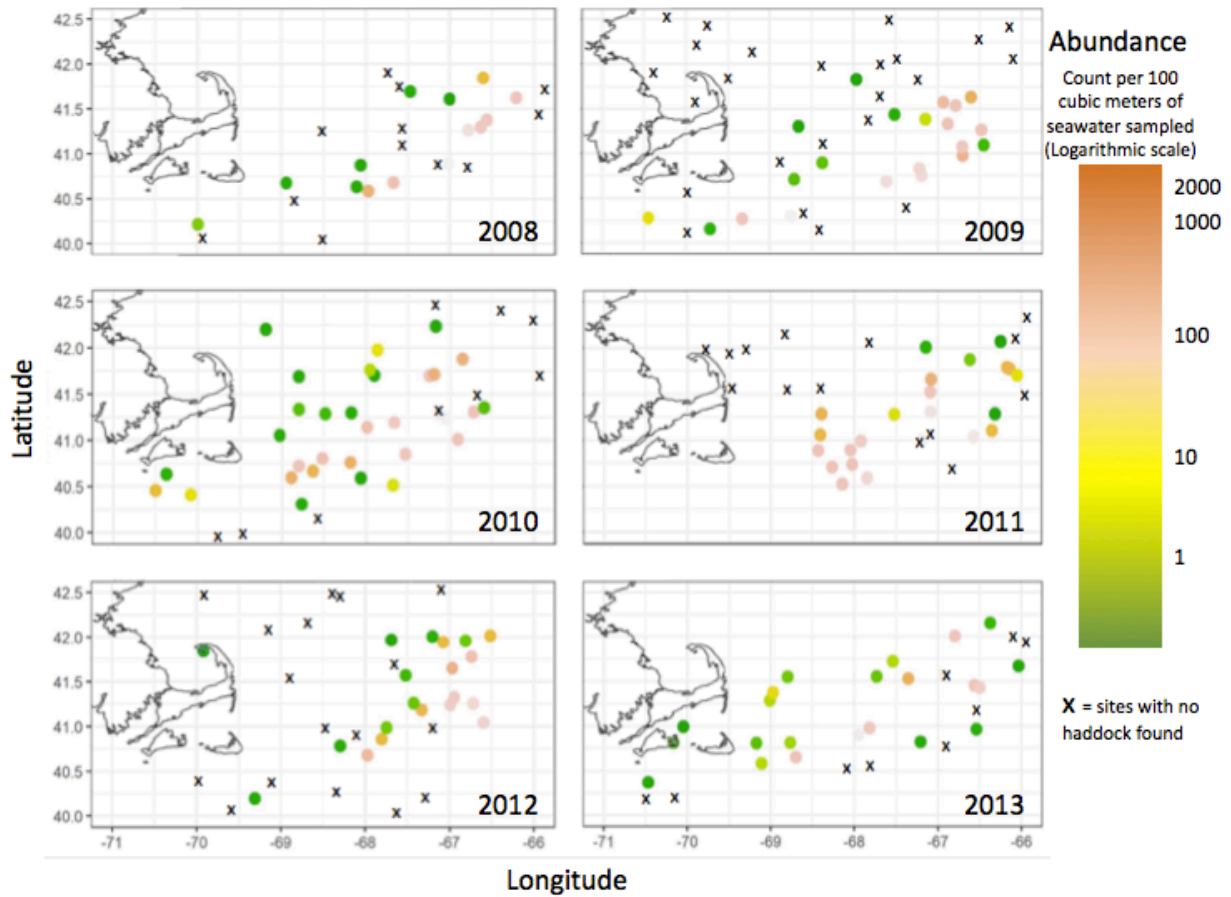
Figure 4. Abundance of larval haddock collected during ichthyoplankton surveys conducted by NOAA in April of each year. Survey sites were randomly selected in each year and trawled once to determine species composition. Circles show sites where larval haddock were collected, while X's show locations where samples were taken, but no haddock were found.

Adult Haddock Survey Analysis

The NOAA spring trawl survey of Massachusetts Bay took place in late April or early May for each year during our study period, with the earliest trawl in 2009 (April 22), and the latest trawl in 2011 (May 10). Adult haddock were present in the Massachusetts Bay study area at this time in four out of six years of the study period. The results of these trawl surveys are summarized in Table 5.

Table 5. Total counts of adult haddock collected during NOAA spring trawl surveys of Massachusetts Bay

	2008	2009	2010	2011	2012	2013
Location of trawl sample (Latitude, Longitude)	42 23.7 -70 42.4	42 24.6 -70 40.6	42 30.5 -70 41.5	42 12.9 -70 29.5	42 24.8 -70 47.5	42 23.5 -70 44.9
Total haddock count in Massachusetts Bay	109	7	9	20	0	0

Temperature Data

Temperature values varied across years, but overall showed an increasing trend, with 2012 having the highest water temperatures in all months and depths (Table 6). The beginning of the spawning period was shown to correlate positively with water temperature (Figure 5). A longer study period over a larger spatial scale is needed to evaluate the relationship of temperature and climate to long-term spawning phenology of haddock.

Table 6. Average monthly water temperatures collected at sea surface (SST) for January, February, and March in each year, and collected at 50 meters in January of each year. All data collected from the NERACOOS data station in Massachusetts Bay.

| Year	SST Jan	SST Feb	SST Mar	Depth Jan
2008	4.5	3.4	3.2	5.2
2009	4.3	3.1	3.3	4.8
2010	4.9	3.7	4.6	5.4
2011	4.7	3.3	3.9	5.5
2012	6.9	5.5	6.3	7.2
2013	6.8	5.0	4.1	7.6
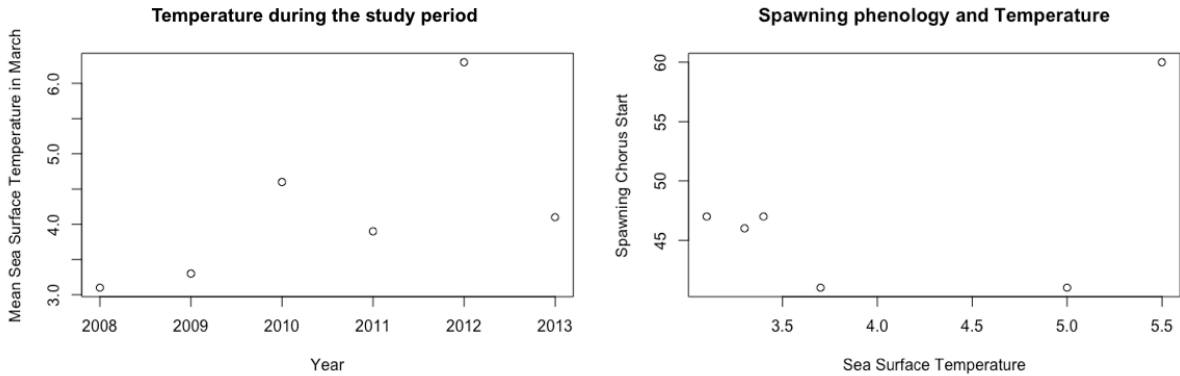
Figure 5. Average monthly sea surface temperature in March of each year (a), and the relationship between the start of the spawning season and temperature. The relationship is driven by the extremely late spawning start in 2012, which was also the warmest March temperature.

DISCUSSION

As seen in previous studies, stereotyped haddock calls were readily identified, and fell into three categories: single pulses, double pulses, and pulse trains. These findings are consistent with previous work that has characterized haddock sounds, both in captivity and in situ (Hawkins and Amorim 2000, Van Parijs et al. 2009). The pulse trains were found during the known peak spawning season and on recorders that are positioned closely to known spawning grounds, providing further support that these calls are an indication of spawning behavior. Overall, these results indicate that passive acoustic monitoring is a valid and valuable remote sensing method to monitor haddock spawning activity in situ, and improve out understanding of interannual variability in spawning which impacts the larval success and recruitment for the fishery in each year.

The spawning calls varied in frequency range, peak frequency, duration, and inter-pulse interval, with mean values similar to previously reported measurements (Hawkins et al. 2002). Recordings collected from captive haddock have found high

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levels of variability between individual fish, which may account for some of the variability in these calls. Despite this individual variation, haddock spawning calls are stereotyped enough to allow for the use of broad template detectors to locate calls automatically. This method was introduced by Van Parijs et al. (2009), who showed that haddock calls could be identified by means of an automated detection algorithm. The present study builds on this foundation to show the application of a detector over multiple locations and multiple sites to identify areas of high acoustic spawning activity. Future studies should explore passive acoustic monitoring of spawning phenology for other haddock stocks to assess variation in these signal characteristics between haddock stocks in the wild. In species with patchy distribution and small-group spawning, being able to monitor large areas simultaneously is a clear advantage of passive acoustic techniques that can be applied to fisheries of high management concern such as haddock.

Passive acoustic monitoring, thus, is a viable and valuable tool for remote sensing of spawning behavior, including variations in spatial distribution and interannual variations in phenology, in haddock. Acoustic recordings consistently detected haddock in locations that have been previously known as spawning grounds (Brodziak 2006, Perry et al. 2005). While a majority of the Georges Bank haddock spawn further offshore, the consistent presence of spawning calls at inshore locations within Massachusetts Bay support the hypothesis that haddock spawn in small groups at many different spawning sites that contribute to the overall larval population (Rountree 2017). The presence of haddock spawning calls at these recording stations each year shows spawning site fidelity, while also allowing for quantification of the timing of spawning activity.

The first four years of sampling show a remarkably stable spawning phenology at this site, with the start and end of the spawning season varying by only five days. The final two years of our study period showed different patterns. In 2012, the spawning season was dramatically different, with a start nearly three weeks after the previous years, and an extremely short spawning period, lasting only five days. In 2013, the spawning start date was consistent with previous years, but the spawning season was much longer in duration. While previous studies have shown variation in spawning success and recruitment from year to year, the reasons for these differences are not well understood (Brodziak et al. 2006).

Traditional methods of studying spawning phenology involve large research ships and many personnel, are often weather dependent, and have spatial and temporal limitations (Ciannelli et al. 2007). The nature of boat-based surveys means that sites are sampled sequentially, rather than simultaneously, which can cause inaccuracies when dealing with highly mobile study subjects over the course of surveys which can take weeks or often months to complete.

The ichthyoplankton surveys found the lowest abundance of haddock in George's Bank in 2012, which was the year with the shortest duration of spawning calls from the acoustic data. In this year, haddock larvae were also concentrated further offshore, with areas low density and no larvae inshore (Figure 4). This suggests that the haddock may have changed their spawning location or phenology during this year of abnormally high temperatures, but due to the patchy nature of sampling, and the fact that not all sites were sampled in all years, it is difficult to draw conclusions about haddock spawning behavior from these data.

Likewise, the surveys of Massachusetts Bay for adult haddock are limited by their timing, taking place well after the peak of spawning activity in haddock. Both surveys noted a decrease in haddock biomass in Massachusetts Bay during the 2012 season, which was one of the warmest winters to date, and which was mirrored by the acoustic phenology data (Mills et al. 2013). The two warmest winters during the study period, 2012 and 2013, found no adult haddock in Massachusetts Bay in late April, suggesting that they may have changed their distribution in response to temperature changes. Without broader simultaneous sampling it is impossible to determine where haddock may have moved to, and if this change in distribution corresponds to a decrease in spawning or spawning success, or simply a spatial shift in distribution. Haddock are known to be affected by water temperatures, having a fairly narrow temperature band for successful egg development, between 1 and 8 degrees C (Buckley et al. 2000). Because of this physiological constraint, localized changes to water temperatures could force haddock to change spawning grounds in order to find areas with more optimum temperature.

The North Atlantic, and the Gulf of Maine in particular, are currently being impacted by global climate change at a greater rate and magnitude than about 99% of the world's oceans (Belkin et al. 2009; Wassmann et al. 2011, Mills et al. 2013). Rising water temperatures could impact haddock physiology in multiple ways. In addition to physiological constraints of spawning and egg development, changes in water temperature have been shown to impact the timing and strength of phytoplankton blooms, which are a critical source of food for haddock larvae (Edwards and Richardson 2004). Fish species have shown changes in phenology too, as Atlantic cod were shown

to alter their spawning phenology as temperatures rise in the Gulf of Maine, shifting

earlier in the year as water temperatures increased (McQueen and Marshall 2017). As

cod are closely related to haddock, we may expect to see a similar trend in haddock

spawning as waters continue to warm. Our shortest spawning season, 2012, was also

the year with the lowest larval haddock abundance, and coincided with one of the

warmest winters on record. If haddock are responding to rising water temperatures by

moving or abandoning their traditional spawning grounds, this could have serious

implications for fisheries management.

One potential drawback to relying exclusively on acoustic data is the limited

detection range. Fish calls are in general low-amplitude, and thus do not travel far

through the water. Previous studies have estimated the detection range of haddock in

the natural environment at around 50-100 meters (Casaretto et al. 2014). Thus, while

acoustic data can provide a detailed picture of acoustic activity over a long period of

time, these data are spatially limited. Haddock are known to spawn in small clusters, so

spawning may be patchy, and a single acoustic recorder may not provide the most

accurate indication of the presence of spawning, as suggested by Rountree (2017).

However, by using an array of acoustic recorders, and complementing acoustic data

with traditional fisheries surveys, we can produce a more complete picture of fish

spawning activity over a broad scale.

Future research should aim to expand the use of passive acoustic monitoring in

areas that are thought to be important for spawning, to improve spatial resolution and

gain insight into movement and distribution of fishes within traditional spawning

grounds. This is especially critical for recovering stocks, to expand our understanding of

habitat use and site fidelity to help with conservation measures and management (Hernandez et al. 2013, Rountree et al. 2006). Additionally, acoustic surveys have the potential to expand our understanding of spawning behavior over long time scales. Long-term acoustic monitoring with an array or recorders to pick up spatial fluctuations would produce the detail necessary to determine trends in phenology and habitat use in relation to physical and biological parameters that may influence spawning, and thus allow for the implementation of management practices to conserve these stocks. The use of passive acoustic monitoring alongside traditional surveys allows for more robust data that can be used to inform management decisions and aid in conservation.

CONCLUSIONS

Passive acoustic monitoring is a powerful tool that has the potential to greatly increase our knowledge of fish behavior and biology. The relatively low cost and large sampling range, both spatially and temporally, of acoustic recordings allows for more in-depth data collection for some of the most important commercial fisheries. When used in combination with traditional fisheries surveys, passive acoustics can provide great insight into the spawning behavior of acoustically active fish. These data can be critical for fishery management, as we see changes in the distribution and abundance of many species as a result of environmental changes.

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EDUCATION
Syracuse University, Syracuse, NY. Master of Science in Biology (June 2018)
- Advisor: Dr. Susan Parks
- Concentration in Ecology
Cornell University, Ithaca, NY. B.S. Biological Sciences with Distinction in Research (January 2013)
- Concentration in Ecology and Evolutionary Biology
- Minor in Marine Biology
Duke University Marine Lab, Beaufort, NC (fall 2011)
- Semester of coursework and research

RESEARCH EXPERIENCE
Syracuse University, Syracuse, NY
  - Graduate Research Assistant, Parks Bioacoustics Lab (fall 2015–present)
  - Thesis topic: Investigating the relationship between water temperature and spawning behavior of haddock in the North Atlantic Ocean between 2007 and 2013.
  - Manuscript in preparation for publication
  - Serve as research mentor to undergraduate students pursuing Independent Research projects.
  - Member of the Graduate Student Outreach Committee, which plans events and trips to local schools and educational programs to introduce local students of all ages to science.
  - Assist with a variety of lab projects to assess conservation of acoustically active species, acoustic communication, and effects of anthropogenic noise on animals.
Duke University Marine Lab, Beaufort, NC
  - Research Technician, Marine Conservation Ecology group (February 2014–April 2015)
  - Manage acoustic monitoring program for assessing impacts of marine construction on local fauna.
  - Serve as research mentor to undergraduate students pursuing Independent Research projects.
  - Assist with a variety of other projects, including photo analysis and boat-based surveys, as needed.
  - Independent Research Student (fall 2011)
  - Analyzed photo-identification data from multiple collaborators to investigate long-term social behavior of bottlenose dolphins in Tampa Bay.
  - Undergraduate Assistant, Marine Conservation Ecology group (fall 2011)
  - Helped establish a photo-ID catalog of fin whales from the Gulf of Maine, and analyze video data of Arnoux's Beaked Whales from the Antarctic.
ABCD Research Project, Massey University, Auckland, NZ - Research Assistant (fall 2013)
  - Research team member for boat-based behavior and photo-ID surveys of local bottlenose dolphins.
Bioacoustics Research Program, Cornell Lab of Ornithology, Ithaca, NY
  - Full-time research analyst (January 2013–September 2013)
  - Acoustic Analysis Team Member for a variety of monitoring projects focusing on conservation of marine mammals around the world.
  - Undergraduate Research Intern (February 2012–December 2012)
  - Developed and carried out independent research project using acoustic behavior to assess the status of endangered sperm whales in Gulf of Mexico after the 2010 oil spill
  - Undergraduate Analyst, Elephant Listening Project (spring 2011)
  - Analyzed sound recordings of endangered African Forest Elephants to evaluate abundance and population demographics
Florida Aquarium, Tampa, FL
  - Dolphin Photo-ID Intern (summer 2011)
  - Conducted daily boat-based photo-identification surveys of resident bottlenose dolphins in Tampa Bay, Fl, and kept a photo catalog of more than 300 individuals.

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PUBLICATIONS AND PRESENTATIONS

"**Building time-budgets from bioacoustic signals to measure population-level changes in behavior: a case study with sperm whales in the Gulf of Mexico.**" Co-authors: Janelle L. Morano, Annamaria Izzi, Aaron N. Rice
  - Published in Ecological Indicators, 72, 360-364, January 2017 (online 3 September 2016)

"Changes in sperm whale (Physeter macrocephalus) acoustic behavior in the northern Gulf of Mexico following the Deepwater Horizon oil spill." co-authors: Janelle L. Morano, Annamaria Izzi, Aaron N. Rice
  - Completed Undergraduate Honors Thesis in Neurobiology and Behavior
  - Presented research poster at the 20th Biennial Conference on the Biology of Marine Mammals, Dunedin, NZ (2013)
  - Presented research poster at the Cornell Undergraduate Research Board spring forum 2013
  - Awarded best poster for Life Sciences research

"Long-term community structure of bottlenose dolphins (Tursiops truncatus) in Hillsborough Bay, Florida." co- authors: Andrew J. Read, Kim W. Urian, Paul Anderson
  - Completed Independent Study project
  - Presented research poster at the 13th American Cetacean Society conference, San Diego, CA (2012)