LINKING JELLYFISH AND LEATHERBACK SEA TURTLE DISTRIBUTIONS IN ATLANTIC CANADA

by

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Abstract

Every year, endangered leatherback sea turtles (*Dermochelys coriacea*) migrate to Atlantic Canadian waters to feed on gelatinous zooplankton (‘jellyfish’). This thesis examined spatio-temporal patterns, and environmental drivers of jellyfish occurrence, and how this dynamic prey field shapes leatherback distribution in Atlantic Canada. Citizen science and scientific trawl survey data were used to describe jellyfish phenology. *Cyanea capillata* was the most common species, with peak occurrence in July, and in the Gulf of St. Lawrence. Sea surface temperature and observer effort were significant predictors of *C. capillata* observations by citizen observers. When jellyfish and leatherback occurrence was compared regionally, the turtles lagged jellyfish presence by two weeks on the Scotian Shelf, while the Gulf of St. Lawrence showed a less clear pattern in timing. These findings suggest observations by the general public can help track jellyfish distribution, and provide useful information for defining dynamic habitat for endangered leatherbacks in Atlantic Canada.

List of Abbreviations Used

AIC	Akaike information criterion
AVHRR	Advanced very high resolution radiometer
BOF	Bay of Fundy
Chl-a	Chlorophyll-a
COSEWIC	Committee on the Status of Endangered Wildlife in Canada
CSTN	Canadian Sea Turtle Network
DC	*Dermochelys coriacea* (leatherback sea turtle)
DFO	Fisheries and Oceans Canada
GIS	Geographic Information System
GLM	Generalized linear model
GSL	Gulf of St. Lawrence
LME	Large marine ecosystems
NAFO	Northwest Atlantic Fisheries Organization
QGIS	Quantum Geographic Information System
SARA	Species at Risk Act
SS	Scotian Shelf
SST	Sea surface temperature
VIIRS	Visible infrared imaging radiometer suite

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Chapter 1 - Introduction

1.1 Leatherback sea turtles and jellyfish

The leatherback sea turtle (*Dermochelys coriacea*) is the largest species of marine turtle, growing up to two metres in length and weighing up to 700 kg (James et al. 2007). They are the only extant species of the family *Dermochelyidae* – which branched from other marine turtles over 100 million years ago (Zangerl 1980). With the most widespread distribution of all sea turtles, leatherbacks can be found in the Atlantic, Pacific and Indian Oceans, in temperature and tropical waters. They are a highly migratory species, travelling thousands of kilometers between temperate foraging and tropical nesting grounds (Pritchard 1976; Hays et al. 2004; Eckert 2006;). Leatherbacks show fidelity to both nesting and foraging grounds (Bleakney 1965; James et al, 2005a; James et al. 2005b), returning to the same areas in tropical nesting waters to nest, and temperate waters to seasonally feed.

The leatherback turtle is listed globally as vulnerable to extinction by the IUCN Red List (Wallace et al. 2013), and is recognized as an endangered species in Canada (COSEWIC 2012). Leatherback turtles face several threats globally, including: bycatch in fisheries, poaching, marine debris (e.g. a floating plastic bag resembles a jellyfish in the water column (Schuyler et al. 2014), coastal development and beach erosion, ship strikes, and impacts of climate change (COSEWIC 2012). In Canadian waters, interaction with fisheries are the greatest threat to leatherbacks – including accidental capture and entanglements in fishing gear (COSEWIC 2012; Hamelin et al. 2017).

While the overall global population trend of leatherback sea turtles is decreasing (Wallace et al. 2013), the subpopulation in the Northwest Atlantic Ocean is considered of least concern as there has been an increase in population size of 20% over the last three generations (Tiwari et al. 2013). Recent estimates suggest there are between 34,000 and 94,000 adult leatherback turtles in the North Atlantic Ocean (TEWG 2007). Future success of this subpopulation depends on continuation of conservation in breeding and foraging areas (Tiwari et al. 2013).

A seasonal aggregation of leatherbacks can be found annually in the temperate waters of Atlantic Canada, with turtles arriving from low latitude foraging and breeding areas in late spring through summer, and initiating southward migration in the fall (James et al. 2005b). Leatherback turtles make the annual migration to Canadian waters primarily to feed on their preferred prey items, large cnidarians and other gelatinous zooplankton, collectively referred to here as 'jellyfish' (Den Hartog and Van Nierop 1984; Dodge et al. 2014) (Figure 1.1). Thus, within the context of this thesis, the term 'jellyfish' is used to collectively describe all gelatinous zooplankton species, irrespective of taxonomy. While jellyfish represent a prey source for a range of species, including fish, seabirds, and other organisms (Arai 2005; Pauly et al. 2009; Lamb et al. 2017), leatherback turtles are unique in that they appear to be one of few known obligate jellyfish predators (Bleakney 1965; James and Herman 2001; COSEWIC 2012). Recent estimates suggest leatherback turtles may consume roughly 330 kg of jellyfish per day while foraging in Atlantic Canada (Heaslip et al. 2012). The highly productive waters off the Atlantic coast of Canada have been described as critical foraging habitat, and host one of the largest seasonal aggregations of leatherback turtles in the Atlantic Ocean (James et al. 2006). However, phenology of jellyfish is not well understood, nor is it known how it relates to the distribution of leatherback turtles in Atlantic Canadian waters.

Figure 1.1 - Leatherback sea turtle (*Dermochelys coriacea*) feeding on a lion's mane jellyfish (*Cyanea capillata*). Photograph credit: Canadian Sea Turtle Network

Jellyfish distributions have been assessed in other temperate regions, both individually and in relation to leatherback turtle distribution. In Chesapeake Bay, distributions of the scyphomedusae *Chrysaora quinquecirrha* were found to occur between relatively narrow temperature and salinity ranges (Decker et al. 2007). Shoreline surveys and surface counts of jellyfish from ships of opportunity indicated that jellyfish displayed species-specific distributions in the Irish and Celtic Seas, and that these distributions were driven by major hydrographic regimes (Doyle et al. 2007). Houghton et al. (2006) used aerial surveys to identify jellyfish aggregations in the Irish Sea, and then compared historical sightings of leatherbacks to these aggregations, finding that 22% of leatherback spatial variation could be explained by *Rhizostoma octopus* occurrence. Jellyfish landscapes were mapped using continuous plankton recorder survey data along with sea surface temperature, which were used to infer potential leatherback foraging habitat in the Northeast Atlantic (Witt et al. 2007). Witt et al. (2007) found acceptable thermal ranges and high prey abundances along the European continental shelf, which would be able to support foraging leatherback turtles.

The limited understanding between leatherback turtles and leatherback prey distribution is a fundamental knowledge gap identified in the ‘Recovery Strategy for the Leatherback Turtle (*Dermochelys coriacea*) in Atlantic Canada’ (Atlantic Leatherback Turtle Recovery Team 2006). One of the objectives explicitly listed in the Recovery Strategy is “habitat identification and protection” (Atlantic Leatherback Turtle Recovery Team 2006). Evaluating the distribution and abundance of leatherback turtle prey is one of strategies listed to meet this objective (Atlantic Leatherback Turtle Recovery Team 2006). However, to date, this objective has been primarily addressed by analysing leatherback movement patterns from satellite tags, thereby inferring critical and important habitat areas. Leatherback foraging in Atlantic Canada has been studied via animal-borne cameras (Heaslip et al. 2012; Wallace et al. 2014), and visual observations (James and Herman 2001). In fact, footage from animal-borne cameras suggests seasonal foraging in Atlantic Canadian waters provides non-breeding leatherbacks with over 50% of their annual energy requirements (29% for a female on 2- year reproductive cycle) (Wallace et al. 2018), highlighting the importance of this temperate foraging ground.

Although Atlantic Canadian waters (Figure 1.2) have been described as critical foraging habitat for leatherback sea turtles (James et al. 2006), the latest Committee on the Status of Endangered Wildlife in Canada (COSEWIC) status report on leatherback turtles states a precise delineation of critical habitat areas in Canadian waters had not been identified (COSEWIC 2012). A 2011 Fisheries and Oceans zonal advisory process document describes three primary important leatherback habitat areas based on movement patterns of 70 satellite tagged turtles (DFO 2011). These areas are: 1) waters east and southeast of George’s Bank; 2) the southeastern Gulf of St. Lawrence and waters off eastern Cape Breton Island, portions of the Magdalen Shallows and adjacent portions of the Laurentian Channel; and 3) waters south and east of the Burin Peninsula, Newfoundland (DFO 2011). It is then stated that “these areas are likely important for leatherback turtles because they serve as foraging habitat” (DFO 2011), however, there is no information on the jellyfish they forage upon. Without a review of prey characteristics, the functional components of critical habitat will not be complete (DFO 2011; Gregr et al. 2015). In order to refine the understanding of leatherback turtle critical habitat in Atlantic Canada, there needs to be a better understanding of the jellyfish prey field itself. This knowledge gap motivated the present thesis, which attempts to answer the following questions: what are the spatio-temporal distributions of large jellyfish occurring in Atlantic Canada? Are there any environmental drivers of jellyfish populations? And how does this dynamic prey field shape leatherback sea turtle distribution in Atlantic Canada?

Figure 1.2 - Study area (Atlantic Canadian waters), including circulation pattern and main currents (in red).

1.2 Limitations studying jellyfish

Many jellyfish species (including the scyphozoan species addressed in this thesis) have a biphasic life cycle (Brotz et al. 2012; Holstein and Laudet 2014). Planula larva settle and develop into asexually reproducing sessile benthic polyps. Through a process called strobilation, the polyp releases free-swimming ephyrae (or juvenile jellyfish). These ephyrae mature into pelagic medusa. The medusa stage if often what is described as a ‘jellyfish’, and is considered the adult stage of the life cycle. The medusa have distinguishable gonads and reproduce sexually. Sperm and eggs are released into the water, and fertilization occurs, producing planula larva that begin the cycle again (Arai 1997; Holstein and Laudet 2014). Jellyfish populations in temperate waters are thought to consist of a single cohort that grows and matures synchronously (Gröndahl 1988; Brewer 1989; Lucas 2001; Lucas et al. 2012).

What drives the strobilation process is still not well understood, and varies between species (Arai 1997; Fautin, 2002; Lucas et al. 2012). Factors including temperature, salinity, and light levels have been shown to effect strobilation in jellyfish (Lucas et al. 2012), with some species being able to withstand wider ranges of environmental conditions than others. While the pelagic medusae stage typically only survives one year in temperate waters (Gregr et al. 2015), there are recorded circumstances of medusae overwintering (Ceh et al. 2015). For example, medusae of *Cyanea capillata* have been documented in offshore waters of the North Sea in winter months, when they would otherwise have been expected to senesce (Hay et al. 1990). Polyp colonies, on the other hand, may survive several generations (Lucas et al. 2012).

Jellyfish can be ephemeral in both time and space (Pitt et al. 2009; Sweetman and Chapman 2015). Aggregations of individual jellyfish make up patches, and they are influenced by active influences (swimming), and passive influences (such as advection and currents) (Magome et al. 2007). Jellyfish aggregations, or blooms, are sporadic and unpredictable, largely in due to a lack in understanding of both the sessile benthic polyp stage of their life cycle, and environmental cues that drive strobilation, which forms the pelagic medusae stage associated with the water column (Barz and Hirche 2007). Jellyfish aggregations can fluctuate year to year, making them difficult to assess comprehensively.

Surveying and quantifying jellyfish via traditional plankton sampling methods has proven to be problematic (Graham et al. 2010). Research cruises typically require months in advance of planning, and are often limited in spatial and temporal coverage. While net tows can provide information on jellyfish presence and identification, they often damage these fragile organisms, and are limited in their utility to quantify patterns of density and abundance (Brierley et al. 2005; Colombo et al. 2009; Graham et al. 2010). Net tows also often only cover small areas, and therefore do not provide information on regional or ocean basin-wide spatial distribution (Doyle et al. 2007). Aerial observations can only detect jellyfish visible in the top few meters of the water column, and cannot account for species density at depth (Houghton et al. 2006; Benson et al. 2007; Magome et al. 2007). This is an important issue in areas such as Atlantic Canadian waters, as jellyfish are not always found at the surface, even when leatherbacks are observed handling prey at the surface (James and Mrosovsky 2004; James et al. 2005b; Hamelin et al. 2014). Recent research has suggested that species such as *C. capillata* are often associated with the thermocline (Barz and Hirche 2005; Bailey et al. 2012; Wallace et al. 2014; Hamelin et al. 2014).

Visual underwater census by cameras are often hindered by turbidity (resulting in low visibility), low light, and reduced field of view (Graham et al. 2010). For this thesis I initially attempted to survey large scyphozoan jellyfish (*C. capillata*) via underwater camera transects (horizontal and vertical) in a well-studied leatherback foraging ground off the coast of Cape Breton, Nova Scotia (James et al. 2006; Wallace et al. 2015). While the presence of feeding leatherback sea turtles was confirmed, the camera systems were unsuccessful at capturing recordings of jellyfish. The main issues included low visibility, lack of lighting on the camera, and inability to reach appropriate depths while towing behind the turtle observation platform (see Appendix A.1 for details).

Acoustic methods are frequently used to determine the distribution and abundance of both fish and zooplankton (Brierley et al. 2001, 2005). While it was originally thought jellyfish were not suitable for acoustic surveying due to the high fluid body composition (Stanton et al. 1996; Warren and Smith 2007; Colombo et al. 2009), recent studies have shown that jellyfish do produce sufficient amounts of sound scattering, and they have been successfully surveyed using acoustic echosounders (Brierley et al. 2001, 2005; Colombo et al. 2009; Purcell 2009; Graham et al. 2010; Crawford 2016). Acoustic methods can cover large areas efficiently, provide enhanced vertical and horizontal resolution, and even taxonomic information (Warren and Smith 2007; Graham et al. 2010). This thesis also attempted to survey large scyphozoans (*C. capillata*) in a known leatherback foraging area (Cape Breton, Nova Scotia) using an acoustic system. This was unsuccessful, however, as there were complications with the equipment setup, and possible modal interference (Yang et al. 2017) (see Appendix A.2 for more details).

These limitations and difficulties of previously used survey methods suggest the need for alternative approaches/methods for determining spatio-temporal distribution of jellyfish over broader scales relevant to leatherback turtles – such as Atlantic Canadian coastal waters.

1.3 Goals and objectives of thesis

The primary goal of this thesis is to better understand the spatio-temporal distribution, seasonal occurrence (‘phenology’), species composition, and environmental drivers of populations of large species of jellyfish occurring in Atlantic Canada, that are the principal prey for foraging leatherback turtles, and to predict how the dynamic prey field may shape leatherback turtle distribution in this globally important leatherback foraging area. This information is important to further clarify critical habitat for this endangered species in Eastern Canadian waters. To answer these questions in sequence, this thesis is structured into two main chapters (Chapter 2 and 3).

Chapter 2 explores the phenology of jellyfish in Atlantic Canada, by combining several data sources, including: citizen science jellyfish beach surveys, opportunistic sightings of jellyfish by volunteer observers, and Fisheries and Oceans Canada (DFO) ground fish survey by-catch data. Citizen science data provides a description of jellyfish seasonality, species composition and regional distribution patterns. Jellyfish occurrence 'hotspots' were determined using DFO by-catch records, and possible environmental predictors of jellyfish presence were analysed.

Chapter 3 considers how jellyfish distribution patterns from Chapter 2 may affect foraging leatherback sea turtles in Atlantic Canada. Jellyfish seasonality is compared to leatherback residency in Atlantic Canadian waters using data sources from Chapter 2. A lag-correlation analysis was used to estimate the temporal correlation between high jellyfish and leatherback presence.

The thesis concludes with Chapter 4, a discussion of the overall findings, limitations, management implications, and future research directions.

Chapter 2 - Phenology of jellyfish in Atlantic Canada

2.1 Introduction

2.1.1 Background: Jellyfish in Atlantic Canada

The productive waters of the Northwest Atlantic are home to several varieties of gelatinous zooplankton, including ctenophores, salps, and scyphozoan species such as *Cyanea capillata* (lion's mane jellyfish) and *Aurelia aurita* (moon jellyfish) (Sipos and Ackman 1968; James and Herman 2001; Heaslip et al. 2012). These species are seasonally abundant and likely important trophic components of the ecosystem, yet studies of jellyfish distribution and abundance are lacking in otherwise well-studied Atlantic Canadian waters (Heaslip et al. 2012; Hamelin et al. 2014; Wallace et al. 2014), as well as globally (Doyle et al. 2007; Purcell 2009; Bastian et al. 2011; Moriarty et al. 2012). Only one comprehensive global study (Brotz et al. 2012) describing jellyfish trends in large marine ecosystems (LME), includes the Canadian Maritimes (specifically the Scotian Shelf and Newfoundland/Labrador Shelf). Neither the Scotian Shelf, nor the Newfoundland/Labrador Shelf have dedicated jellyfish surveys, and information on jellyfish trends for the LME study came from zooplankton surveys (Brotz 2011). Brotz et al. (2012) concluded that there were no obvious trends of jellyfish abundance in either of these regions. A lack of long time series data for jellyfish in Atlantic Canada makes it difficult to determine basic phenology and abundance trends.

In the context of this thesis, I focused on the scyphozoans *C. capillata*, and *A. aurita*, which are known to be important prey items for leatherback turtles (James and Herman 2001). Research on both species derives from other parts of the Atlantic (Lucas 2001), including the Irish Sea (Bastian et al. 2011), and the North Sea (Lynam et al.

2005), or from the Bering Sea in the Pacific (Brodeur et al. 2002). It has been demonstrated that leading climate indices often predict the abundance of scyphozoan jellyfish, but the responses vary greatly across different regions (Lynam et al. 2005; Brodeur et al. 2008).

C. capillata is the largest species of jellyfish in the world, and is described as a ‘cold-water species’ (Lucas et al. 2012) found in cool temperate regions of the Atlantic and Pacific Ocean, in both coastal and offshore waters (Bämstedt et al. 1994). While *C. capillata* has a wide geographic range, it does not usually form dense surface aggregations typical of some other large species, making them more difficult to study (Purcell 2003). Strobilation is thought to occur at lower temperatures (Gröndahl 1988; Brewer and Feingold 1991; Lucas et al. 2012). In the North Sea, the majority of *C. capillata* ephyrae were released between 5 and 8°C (Verwey 1942; Holst 2012). Benthic stages of *C. capillata* are negatively impacted by low salinity levels, suggesting they do not tolerate wide salinity ranges (Holst and Jarms 2010). While scyphozoan medusae typically only survive one season, there have been documented cases of *C. capillata* overwintering in offshore waters of the North Sea (Hay et al. 1990). *C. capillata* feeds on zooplankton, ichthyoplankton and other jellyfish (Brewer 1989; Bämstedt et al. 1994; Purcell 2003)).

A. aurita is a wide spread and abundant species, found in coastal waters of the Atlantic, Pacific, and Indian Oceans. *A. aurita* is perhaps the most studied species of jellyfish in the world, thanks in part to their wide distribution, and their tendency to form dense aggregations, or blooms (Purcell 2003). They are found in temperate and tropical waters, occurring between 70°N and 40°S (Russell 1970; Lucas 2001; Dawson et al. 2005), and are characterized by their ability to survive a wide range of environmental conditions (Lucas 2001). *A. aurita* is able to withstand low salinity environments, including brackish waters (Holst and Jarms 2010; Lucas et al. 2012). Temperature effects on benthic stages of *A. aurita* are quite variable, with some populations tolerating wider temperature ranges than others (Lucas 2001; Purcell et al. 2007; Lucas et al. 2012; Purcell 2012). *A. aurita* are known to consume zooplankton and ichthyoplankton (Bämstedt et al. 1994).

It has been well documented that leatherback turtles return annually to productive northwest Atlantic coastal waters to feed on large scyphozoan jellyfish (such as *C. capillata* and *A. aurita*) (James and Herman 2001; James et al. 2005b) , however we still do not understand the basic characteristics of the prey field (Hamelin et al. 2014; Wallace et al. 2015). There is limited information about seasonality, relative abundance, spatial distribution and species composition for jellyfish found in Atlantic Canadian waters. It is broadly generalized that in temperate waters, jellyfish populations are made up of a single cohort that matures concurrently, sexually reproducing in warmer summer months (Brewer 1989; Lucas 2001; Lucas et al. 2012), however, there are cases that illustrate protracted ephyrae release in temperate regions (Kawahara et al. 2006). While the dynamics that drive the timing and size of jellyfish aggregations in Northwest Atlantic waters have not been studied in detail, it is likely that major hydrographic regimes/physical oceanographic processes are important in shaping the distribution of jellyfish seasonally and spatially (James et al. 2005b; Doyle et al. 2007; Houghton et al. 2007).

2.1.2 Citizen science

Due to limitations in other methods previously used to study jellyfish (see Chapter 1), this thesis took an alternative approach, building on development of a citizen science model originally initiated by the Canadian Sea Turtle Network (hereafter CSTN), a Halifax, Nova Scotia based NGO focused on marine turtle conservation, research and education.

Citizen science can be defined as "partnerships between those involved with science and the public in which authentic data are collected, shared, and analyzed" (Jordan et al. 2015). Citizen science is increasing in popularity as a research method (Bonney et al. 2014), as it represents a versatile tool that can be applied with varying levels of participation (from formulating of research questions, to data collection and analysis of data), and at varying scales, spatially (local, regional, global) and temporally (short vs. long term). One of the most appealing aspects of citizen science, is its ability to expand the range (both spatially and temporally) of a study (Freitag and Pfeffer 2013) at low cost. Citizen science is also beneficial to researchers as it provides an opportunity to engage the general public in scientific inquiry (Dickinson et al. 2012), hence most citizen science projects include education and public outreach goals and objectives in their mandate (Jordan et al. 2011; Dickinson et al. 2012; Jordan et al. 2015).

While jellyfish stranding surveys have proven useful in helping determine seasonal distribution of jellyfish in other parts of the world (Doyle et al. 2007; Houghton et al. 2007; Pikesley et al. 2014), this will be the first regional attempt utilizing a systematic citizen network. Following success with implementing a citizen-science approach for collecting data on sea turtle sightings in Atlantic Canada (Martin and James

2005; James et al. 2006), a pilot study on jellyfish strandings using citizen scientists was conducted by the CSTN 2007-2010, however sample size was quite small, and data was not published. The CSTN has contributed this data to this thesis.

2.1.3 Goals and objectives of Chapter 2

This chapter will attempt to describe phenology characteristics of the jellyfish species *C. capillata* and *A. aurita*, which are important to leatherback diet in Atlantic Canada (James and Herman 2001). It will do so by addressing the following questions:

1) What are the spatial and temporal distributions of jellyfish in Atlantic Canada?
2) Can major oceanographic variables (sea surface temperature, chlorophyll a) help predict jellyfish presence?
3) Is there one, or several reproductive cohorts of major jellyfish species throughout the season?

2.2 Methods

2.2.1 Citizen science

A pilot study on jellyfish strandings observed by citizen scientists was conducted by the Canadian Sea Turtle Network (CSTN) 2007-2010, however sample size was quite small, coverage was restricted, and data was not published. The CSTN has contributed this data, which will be compared with results from the 2016 and 2017 citizen science surveys conducted as part of this thesis.

A citizen science network was established in February of 2016, and run through 2016 and 2017 to help determine jellyfish seasonality in Atlantic Canada through regular beach surveys. Members of the citizen science network were recruited through advertising in the media (radio and television interviews and online articles), and social media posts (Facebook). A Dalhousie University email address (jellyfish@dal.ca) was established to allow for easy communication between the project lead and interested members of the public. Participating was open to everyone (no age limitation). There were only two requirements for participants: the participant must have access to the same stretch of beach for the entirety of the survey season (April – October), and the participant should be able to commit to weekly surveys. Rocky and sandy beaches were both permitted. Each participant within the citizen science network was responsible for surveying a section of beach once a week from April to October 2016 (repeated April to October 2017). The surveys coincided with low tide whenever possible, and required participants to record any sightings of stranded jellyfish by species, along with measurements of bell diameter. During mass stranding events, only the first 50 specimens encountered during a weekly survey were sampled for bell diameter. Bell diameters were measured by placing a measuring tape on the outer edge of the bell and extending it to the other side (tentacles were not included in the measurement).

Each member of the citizen science network was mailed a survey kit which was comprised of: weekly survey sheets, survey guidelines, jellyfish identification key (see Appendix B), a ruler/tape measure, gloves, and an envelope with return postage. At the end of the survey season, citizen scientists mailed the survey sheets back to Dalhousie University, where the data was manually entered into spreadsheets. The email address jellyfish@dal.ca was regularly monitored such that questions from volunteers could be frequently answered and survey progress could be routinely reported. Emails reminding network volunteers to maintain a schedule of survey effort were sent at regular intervals. The citizen science network results were summarized once all surveys were returned, and a summary was sent to the citizen scientists to keep them informed on evolving results, and allowing them to recognize the value of their individual contributions.

Opportunistic jellyfish observations were also reported to jellyfish@dal.ca. Any observations of jellyfish spotted in Atlantic Canada were welcomed. This was communicated to the general public via television and radio interviews, news articles, and social media. It was requested that each observation be accompanied by: species (if possible, if not a description including colour/shape, distinguishing factors), abundance, location (latitude and longitude), date, and pictures if possible. Each email observation was responded to with either follow up question to determine missing information, or a simple thank you message. These observations were manually entered into a spreadsheet as positive presence counts for later analysis.

Data from the citizen science network was summarized using simple statistics such as means, proportions, and was organized to show spatial and temporal distribution. A summary comparison between CSTN and Dalhousie citizen science networks was also completed. Catch per unit effort was calculated per citizen scientist over the six total years; both by distance, and by jellyfish observations per kilometer of surveyed beach.

Citizen science survey data also included measurements of diameter of stranded jellyfish. The diameter of each jellyfish was binned into size classes with 5 cm increments (ex. 1 – 5cm, 6 – 10cm, 11 – 15cm, etc.) to describe the size distribution of each species. Each jellyfish diameter was also measured against the day of year it was observed, to try to determine whether there was one reproductive cohort of jellyfish, or protracted ephyrae release. A loess curve was fit on the diameter data, separately for *C. capillata* and *A. aurita*, first across all diameter measurements, and then broken up into regions. The study area (Maritimes region of Atlantic Canada) was broken up into six main regions based on differing oceanographic features: Bay of Fundy, South Shore, Eastern Shore, Cape Breton, Gulf of St. Lawrence, and Northumberland Strait (Figure 2.1). The Bay of Fundy region has extreme tides, ranging between 6 and 16 m, with strong tidal currents. The South Shore and Eastern Shore are exposed to the Atlantic Ocean. The coastal waters of the South Shore are generally warmer, and more seasonally and spatially dynamic than the Eastern Shore (due in part to greater influence of the Gulf Stream, and increased vertical mixing on the western Scotian Shelf) (Breeze et al. 2002). The Cape Breton region consists of the eastern side of Cape Breton Island, including Sydney Bight and the southern part of the Cabot Strait. It represents an outlet for the Gulf of St. Lawrence into the Atlantic Ocean (Davies and Brown 1996). The Gulf of St. Lawrence region includes coastal waters from along the Northern side of Prince Edward Island, extending into the southern Gulf of St. Lawrence. The southern Gulf of St. Lawrence (Magdalen Shallows) is shallow (<100m) and generally warmer than the rest of the Gulf of St. Lawrence in the summer (Davis and Browne 1996). Northumberland Strait is found within the Gulf of St. Lawrence, however it is sheltered by Prince Edward Island. The Northumberland Strait is shallow (between 17 and 65 m), resulting in high water temperatures in the summer months (as high as 25°C) (Bosman et al. 2011).

Pearson's correlation coefficient was calculated to determine the strength of association between the day of year the jellyfish was observed, and its diameter. The bell diameter of *C. capillata* for individual regions (South Shore, Eastern Shore, Cape Breton, Northumberland Strait, and Gulf of St. Lawrence) was also measured against the day of year in 2016 and 2017, and Pearson's correlation coefficient was calculated for each region. Bay of Fundy region was excluded as there were no, or very few *C. capillata* observed (2016 = 0 and 2017 = 3). This individual region analysis was not completed for *A. aurita* due to fewer observations.

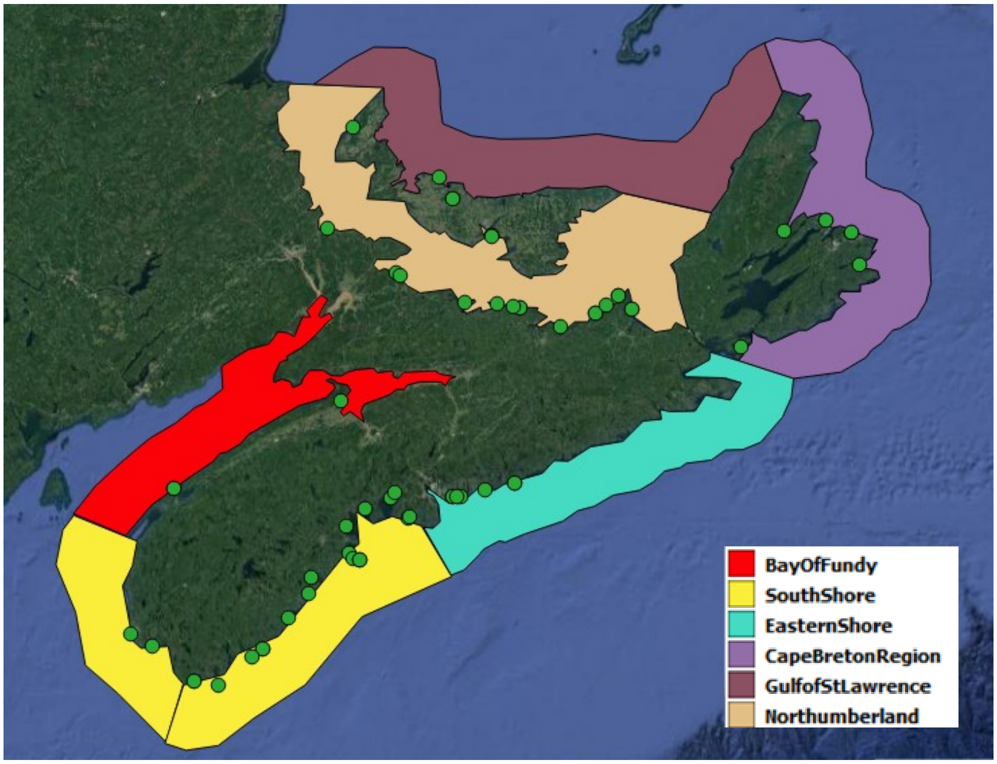

Figure 2.1 - Coloured polygons represent citizen science sampling regions. Green circles represent citizen scientist locations in 2016 and 2017.

2.2.2 Modelling environmental parameters

The *C. capillata* data from the Dalhousie University citizen science network was used to model environmental parameters. Only *C. capillata* was chosen for this analysis as it represented the majority of jellyfish sightings reported over the two year survey period (>90%). To facilitate comparisons, the study area (Maritimes region of Atlantic Canada) was broken up into six main regions based on differing oceanographic features: Bay of Fundy, South Shore, Eastern Shore, Cape Breton, Gulf of St. Lawrence, and Northumberland Strait (Figure 2.1). These regions were represented by polygons that stretched from the coastline to 25 km offshore, to represent coastal waters. Individual citizen scientist locations (latitude and longitude) were then binned into each corresponding region (Figure 2.1).

Sea surface temperature (SST) and chlorophyll-a (Chl-a) were chosen as environmental parameters to be included in the modelling (to determine whether jellyfish presence can be predicted by environmental parameters). Water temperature has been shown to impact *C. capillata* strobilation (Gröndahl 1988; Brewer and Feingold 1991; Holst 2012; Lucas et al. 2012) and other aspects of their life cycle (Mangum et al. 1972). Previous studies have shown temperature to be an important driver of jellyfish distribution more generally (Decker et al 2007; Purcell 2012; Lucas et al. 2014; Greer et al. 2015; Aleksa 2017). Chlorophyll-a concentrations can serve as a proxy of primary production (Longhurst 2007). A connection between chlorophyll-a concentrations and zooplankton in the water column has been illustrated by several studies (Benson et al. 2007; Greer et al. 2015; Greer and Woodson 2016), suggesting these areas could offer prey resources to jellyfish. All sea surface temperature and chlorophyll-a data was provided by Fisheries and Oceans Canada (AVHRR SST Dataset, Remote Sensing Group, Bedford Institute of Oceanography (BIO); VIIRS chl-a (R2014): data courtesy NASA Goddard Space Flight Center, Ocean Ecology Laboratory, Ocean Biology

Processing Group – composites created by the Remote Sensing Group at BIO). Satellite derived SST (AVHRR) and Chl-a (VIIRS) geotiff files were downloaded in bi-weekly intervals. Bi-weekly was the chosen temporal scale as it would give a finer resolution than monthly, but wouldn't be too compromised by the small spatial scales of the regions (i.e. if used daily to weekly averages).

Each bi-weekly geotiff file for SST and Chl-a downloaded covered the entire Maritimes area, and therefore each of the six above mentioned region's polygon (which contain the citizen scientist location and *C. capillata* data) needed to be clipped from that original file. The data for SST and Chl-a for each region and each bi-weekly interval was then converted (from tif file to ASCII Gridded XYZ or *.xyz file) and extracted using QGIS (version QGIS 2.18.10). The mean value was extracted for each region over each time period, for both SST and Chl-a.

All statistical modelling was done in R (version 3.4.2; R Development Core Team 2017). To measure whether *C. capillata* presence/absence was driven by environmental parameters, a generalized linear model (GLM) with a binomial distribution was fit to the data. A penalized log-likelihood approach was applied to account for linear separation in the data (package brglm, (Kosmidis 2017)).

Citizen science network results were organized with the environmental parameters SST and Chl-a, temporally into bi-weekly intervals, and spatially into the same six regions as above. Presence (or absence) of *C. capillata* was the dependent variable in the binomial GLM (*C. capillata* present = 1, *C. capillata* absent = 0). Independent variables included: SST, Chl-a, effort (number of citizen scientists), effort (total number of survey weeks in bi-weekly period), date (bi-weekly intervals), region, and year. Region was analysed separately instead of as a nested random effect to compare jellyfish presence from the different regions. Collinearity between model variables was tested using Pearson's correlation coefficients (r). Date (temporal aspect, measured in bi-weekly intervals) and sea surface temperature (SST) were collinear (r = 0.84). Since environmental parameters, including SST, were of most interest for this analysis, and SST has proven to be an important driver of jellyfish in other modelling studies (Decker et al. 2007; Purcell 2012; Lucas et al. 2014; Greer et al. 2015; Aleksa 2017), date was dropped from the model, and not included in the analysis.

The relationship between SST and *C. capillata* presence was not linear (the structure of this data can be seen in Figure 2.2), this prompted the use of a third order polynomial term applied to SST in the model.

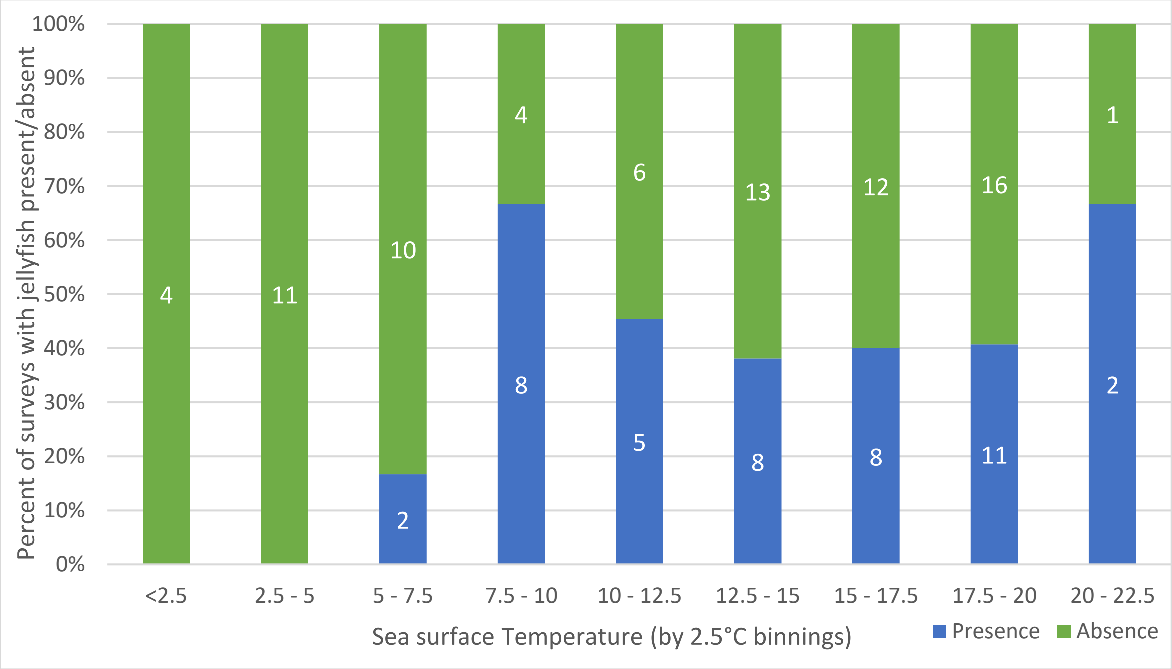

Figure 2.2 - Visual representation of *C. capillata* presence by temperature binning. The structure of the data prompted the use of a third order polynomial term in the GLM.

Model selection was done by comparing all possible subsets of the full model using Akaike's information criterion (AIC). Differences in AIC of less than two indicate there is not substantial difference between the models (Burnham and Anderson 2002). While this occurred – the model with fewest variables was chosen.

2.2.3 Ground fish survey bycatch data analysis

Fisheries and Oceans Canada (DFO) performs annual scientific groundfish trawl surveys in Atlantic Canadian waters. The primary objective of the trawl surveys is to provide information on trends in biomass and abundance for groundfish species (such as Atlantic cod (*Gadus morhua*), Atlantic Halibut (*Hippoglossus hippoglossus*), winter flounder (*Pseudopleuronectes americanus*), spiny dogfish (*Squalus acanthias*), etc.) in the Maritimes Region (DFO 2016a; 2016b). Although these are bottom trawls, targeting groundfish species, they record all other species caught as bycatch – including jellyfish.

Data was collected for the following Maritimes Region, Northwest Atlantic Fisheries Organization (NAFO) Divisions: 4VWX and a small portion of 5Y (Scotian Shelf/Bay of Fundy); 4T (Southern Gulf of St. Lawrence; and 4R, 4S, and northern part of 4T (Northern Gulf of St. Lawrence/Estuary). All data was collected from DFO, with the intent of analyzing jellyfish bycatch. In most cases, species were not recorded, but rather lumped under 'scyphozoan'. This practise made it impossible to estimate species distribution or composition. Wet weight (kg), and occasionally abundance (however rare) of jellyfish are reported for each trawl. Data was collected as far back as jellyfish were recorded in each region: Scotian Shelf: 2006 – 2017, Southern Gulf of St. Lawrence: 1985 – 2017, and Northern Gulf of St. Lawrence: 2004 – 2017.

The DFO groundfish surveys occur at different times of the year in different regions. The groundfish surveys on the Scotian Shelf occur for four to five weeks, in the month of July (sometimes including the end of June and beginning of August). The surveys in the Southern Gulf of St. Lawrence occur through the month of August (sentinel surveys, with observers on commercial fishing vessels) and the month of September (research vessel). The groundfish surveys in the Northern Gulf of St. Lawrence occurs annually during the month of September. The groundfish surveys that take place on DFO research vessels (most frequently on the CCGS Alfred Needler) use a Western IIA trawl system, which has a codend mesh of 19mm, headline height of 3.5m and wingspread of 12m (Carrothers 1988; Pers. Comm. 2018). However, the research vessel and gear type may differ if there is required maintenance in that particular year.

It is important to note that these trawl surveys do not target jellyfish species, and jellyfish are caught incidentally as bycatch species. There are currently no dedicated DFO surveys to determine jellyfish distribution, abundance, or biomass in the Maritimes Region. As many jellyfish species are pelagic or occur throughout the water column, it is most likely that jellyfish were caught during net ascent and descent. Although wet weights were recorded for jellyfish bycatch, this may not be an accurate representation of jellyfish abundance at specific trawl locations. Therefore, when examining the spatial clustering of jellyfish from the DFO groundfish surveys, records of presence and absence of jellyfish in the surveys was used instead of wet weight or abundance.

Data was grouped into three bins, based on year: 2006 – 2009, 2010 – 2013, and 2014 – 2017. A hot-spot analysis based on the Getis-Ord Gi* statistic (executed in ArcGIS 10.5) was used to analyse spatial clustering of jellyfish bycatch presence observations during each time period (from the DFO groundfish surveys). This optimized hot spot analysis tests the null hypothesis that the spatial relationship between neighbouring hotspots (high values) and coldspots (low values) is due to random clustering and is given as:

$$G_i^* = \frac{\sum_{j=1}^{n} w_{i,j} x_j - \bar{x} \sum_{j=1}^{n} w_{i,j}}{S \sqrt{\frac{n \sum_{j=1}^{n} w_{i,j}^2 - \left(\sum_{j=1}^{n} w_{i,j}\right)^2}{n-1}}}$$

where x_j is the attribute value for feature *j,* $w_{i,j}$ is the spatial weight between the feature *i* and *j, n* is equal to the total number of features, and:

$$\bar{x} = \frac{\sum_{j=1}^{n} x_j}{n}$$

and:

$$S = \sqrt{\frac{\sum_{j=1}^{n} x_j^2}{n}}$$

Local patterns of jellyfish bycatch occurrence were identified using a nearest-neighbour approach, and compared to the whole study area (Maritimes Region NAFO Divisions: 4VWX, 5Y, 4R, 4S, 4T). The Getis Ord Gi* statistics produces z-scores, which are represented numerically. Z-scores return a number, that informs if the clustering of neighbouring points is attributed to random spatial processes (given their distance and value relative to the mean). A z-score greater than 1.65 represents a 'hotspot' – a statistically significant spatial clustering of high positive values. A z-score less than -1.65 represents a 'coldspot' – a statistically significant spatial clustering of low negative values. No apparent clustering (not significant) is attributed by a near zero z-score. Confidence levels are associated with z-score, where: z-score >2.58 = hot spot with 99% confidence; z-score 1.96 to 2.58 = hotspot with 95% confidence; z-score 1.65 to 1.96 = hotspot with 90% confidence; z-score (-1.65) to 1.65 = not significant; z-score (-1.65) to (-1.96) = cold spot with 90% confidence; z-score (-1.96) to (-2.58) = cold spot with 95% confidence; and z-score < (-2.58) = cold spot with 99% confidence. The hot spot analysis corrects for both multiple testing and spatial dependence using the False Discovery Rate (FDR).

The output of the hot spot analysis was rasterized into 20km by 20km cells. Each trawl survey was assigned a hot spot confidence interval, and the most frequent hot spot confidence level throughout the 20km by 20km cell was assigned to the cell.

2.3 Results

2.3.1 Citizen science

The CSTN citizen science program was run for the years 2007 (n = 10 citizen scientists), 2008 (n = 11 citizen scientists), 2009 (n = 12 citizen scientists), and 2010 (n = 5 citizen scientists). The Dalhousie University citizen science program was run in 2016 (n = 29 citizen scientists), and 2017 (n = 37 citizen scientists) (see citizen scientist locations in Figure 2.3). A detailed summary of the two programs can be seen in Table 1. Over 500 photographs of jellyfish were submitted to jellyfish@dal.ca by participants of Dalhousie University citizen science program, and opportunistic jellyfish reporting (Figure 2.4).

The lowest observer effort occurred in 2010 with five participants and 77 survey weeks (CSTN) and the largest group of citizen scientists was in 2017 with 37 participants and 515 survey weeks (Table 2.1). With higher participation in the Dalhousie University citizen science program, came broader spatial coverage (Figure 2.3). The CSTN pilot project coverage was generally restricted to the South and Eastern Shore, with limited coverage elsewhere (i.e. Cape Breton coast, Northumberland Strait (exception of 2009 – Figure 2.3C)).

As large jellyfish are not usually seen in the winter, the citizen science surveys started in spring, as early as April 12th (2016) and ran as late as November 3rd (2008) (Table 2.1). There were variable jellyfish reported each year, 2008 had the fewest jellyfish observed with 1218, while 2017 citizen scientists reported the most jellyfish, with 8545. The 2017 survey season saw the most *C. capillata* with 8092 individuals identified, the 2008 survey season reported the most *A. aurita* with 303, and the 2010 survey season reported the most ctenophores with 1963 (Table 2.1).

The highest abundance, or peak seasonality, of *C. capillata* was in the month of July for all six survey seasons. Four of the survey years had the most observations in the second half of July (2007, 2009, 2016, and 2017), while the other two survey years had highest abundances of *C. capillata* the first half of July (Table 2.1, Figure 2.6). Peak seasonality was more variable for *A. aurita* – ranging between the first half of July (2017) and the first half of September (2010) (note: in the 2010 survey season, only 25 *A. aurita* were observed) (Table 2.1, Figure 2.7).

Table 2.1- Summary results Canadian Sea Turtle Network (CSTN) and Dalhousie University citizen science jellyfish surveys. For peak seasonality, jellyfish observations were binned into the first half of the month, and the second half of the month. For example, if the highest proportion of jellyfish were observed in the first half of July, it would be represented by the month number, followed by .1 (7.1). Second half of July = 7.2, First half of August = 8.1, etc.

	CSTN cit. sci. program				**Dalhousie cit. sci. program**	
	2007	**2008**	**2009**	**2010**	**2016**	**2017**
Citizen scientists	10	11	12	5	29	37
Survey weeks	77	92	105	70	494	515
Distance (m)	13,335 (8CS)	14,475 (8CS)	12,924 (10CS)	3848 (2CS)	23,144 (29CS)	34,856 (36CS)
Survey duration	May 4 - Oct. 3	June 7 - Nov. 3	May 25 - Oct. 5	Apr. 22 - Oct. 4	Apr. 12 - Oct. 6	May 4 - Oct 19
Total 'Jellies'	1241	1218	6283	2567	3757	8545
Total *C. capillata*	1065	328	4414	579	3359	8092
Total *A. aurita*	67	303	183	25	168	131
Total ctenophore	87	587	1686	1963	183	309
Total unknown	22	0	0	0	47	13
First *C. capillata*	July 14	June 8	June 30	May 27	May 5	May 29
Peak *C. capillata* seasonality	7.2 (45%)	7.1 (53%)	7.2 (54%)	7.1 (48%)	7.2 (80%)	7.2 (67%)
	8.1 (37%)	7.2 (43%)	8.1 (34%)	7.2 (25%)	6.2 (9%)	7.1 (17%)
	8.2 (18%)	6.2 (2%)	7.1 (11%)	8.1 (22%)	7.1 (8%)	8.1 (12%)
Last *C. capillata*	Sept. 10	Aug. 22	Sept. 7	Aug. 18	Sept. 1	Sept. 28
First *A. aurita*	July 27	July 16	June 19	June 10	June 11	June 5
Peak *A. aurita* seasonality	8.2 (42%)	8.2 (99.7%)	8.1 (50%)	9.1 (84%)	7.2 (62%)	7.1 (33%)
	8.1 (40%)	7.2 (0.3%)	7.2 (46%)	6.1 (12%)	8.2 (13%)	8.1 (33%)
	7.2 (18%)	-	7.1 (2%)	8.1 (4%)	8.1 (10%)	7.2 (20%)
Last *A. aurita*	Aug. 29	Aug. 24	Sept. 14	Sept. 14	Aug 17	Aug. 20
Diameters msr'd (total)	844	440	2149	584	705	1770
***C. capillata* diameter msr'd**	788	360	1988	559	640	1649
***A. aurita* diameter msr'd**	56	80	161	25	65	121
Size range *C. capillata*	3 - 34 (cm)	2 - 60 (cm)	3 - 30 (cm)	4 - 61 (cm)	3 - 34 (cm)	2 - 44 (cm)
Most common size *C. capillata*	11 - 15 cm (38%)	6 - 10 cm (30%)	6 - 10 cm (45%)	16 - 20 cm (25%)	11 - 15 cm (33%)	6 - 10 cm (41%)
	6 - 10 cm (32%)	11 - 15 cm (22%)	11 - 15 cm (35%)	11 - 15 cm (18%)	16 - 20 (cm) (26%)	11 - 15 cm (24%)
Size range *A. aurita*	4 - 24 (cm)	3 - 25 (cm)	3 - 54 (cm)	5 - 10 (cm)	5 - 32 (cm)	4 - 30 (cm)
Most common size *A. aurita*	11 - 15 cm (39%)	11 - 15 cm (44%)	6 - 10 cm (65%)	6 - 10 cm (96%)	16 - 20 cm (39%)	11 - 15 cm (33%)
	6 - 10 cm (30%)	16 - 20 cm (36%)	1 - 5 cm (17%)	1 - 5 cm (4%)	26 - 30 cm (19%)	16 - 20 cm (26%)

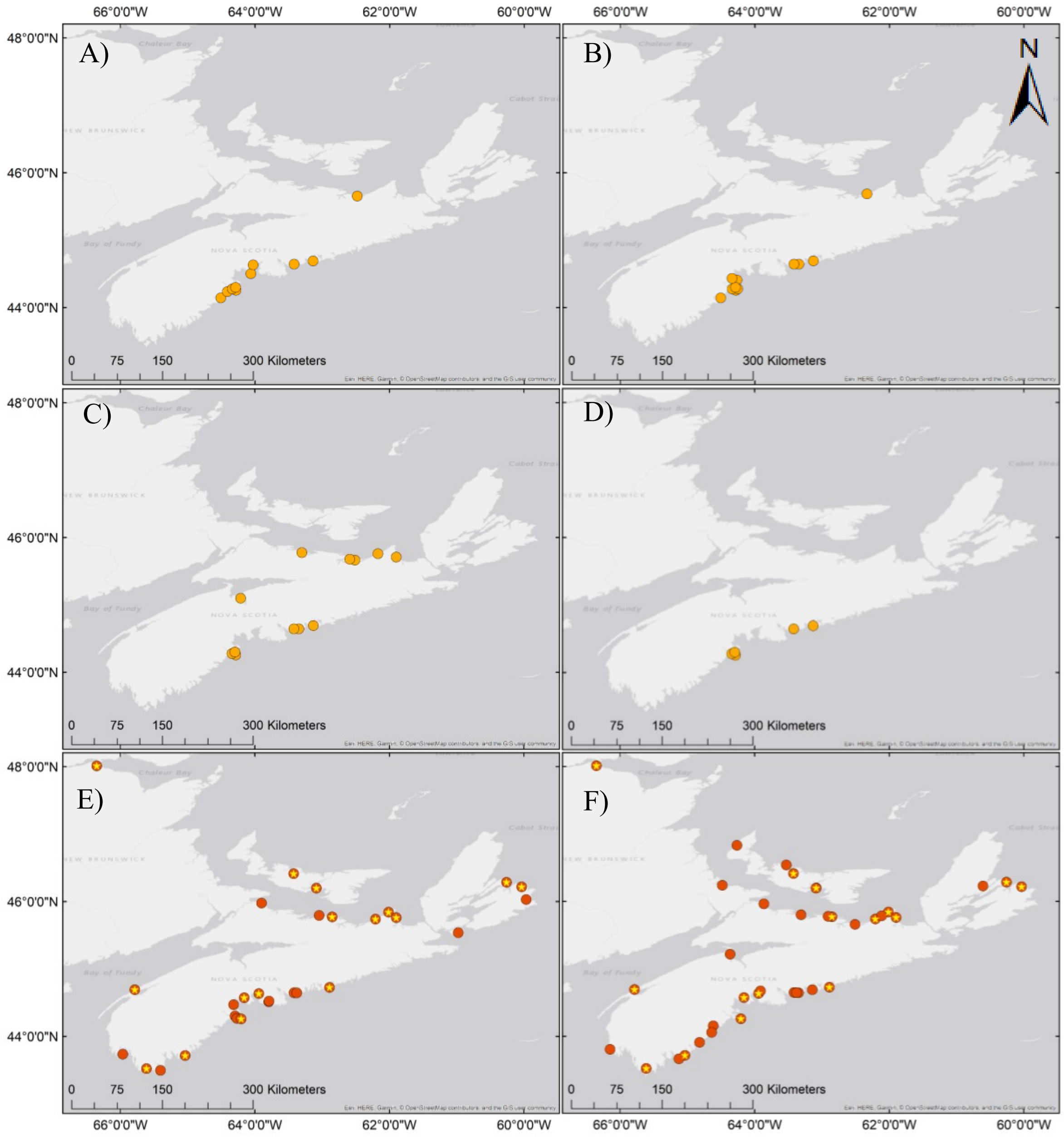

Figure 2.3 - Citizen Scientist locations for all years (CSTN data and Dalhousie data). A) 2007 with 10 citizen scientists; B) 2008 with 11 citizen scientists; C) 2009 with 12 citizen scientists; D) 2010 with 5 citizen scientists; E) 2016 with 29 citizen scientists; F) 2017 with 37 citizen scientists. Yellow stars in panel E) and F) represent repeat surveyors (those who monitored beaches in both years).

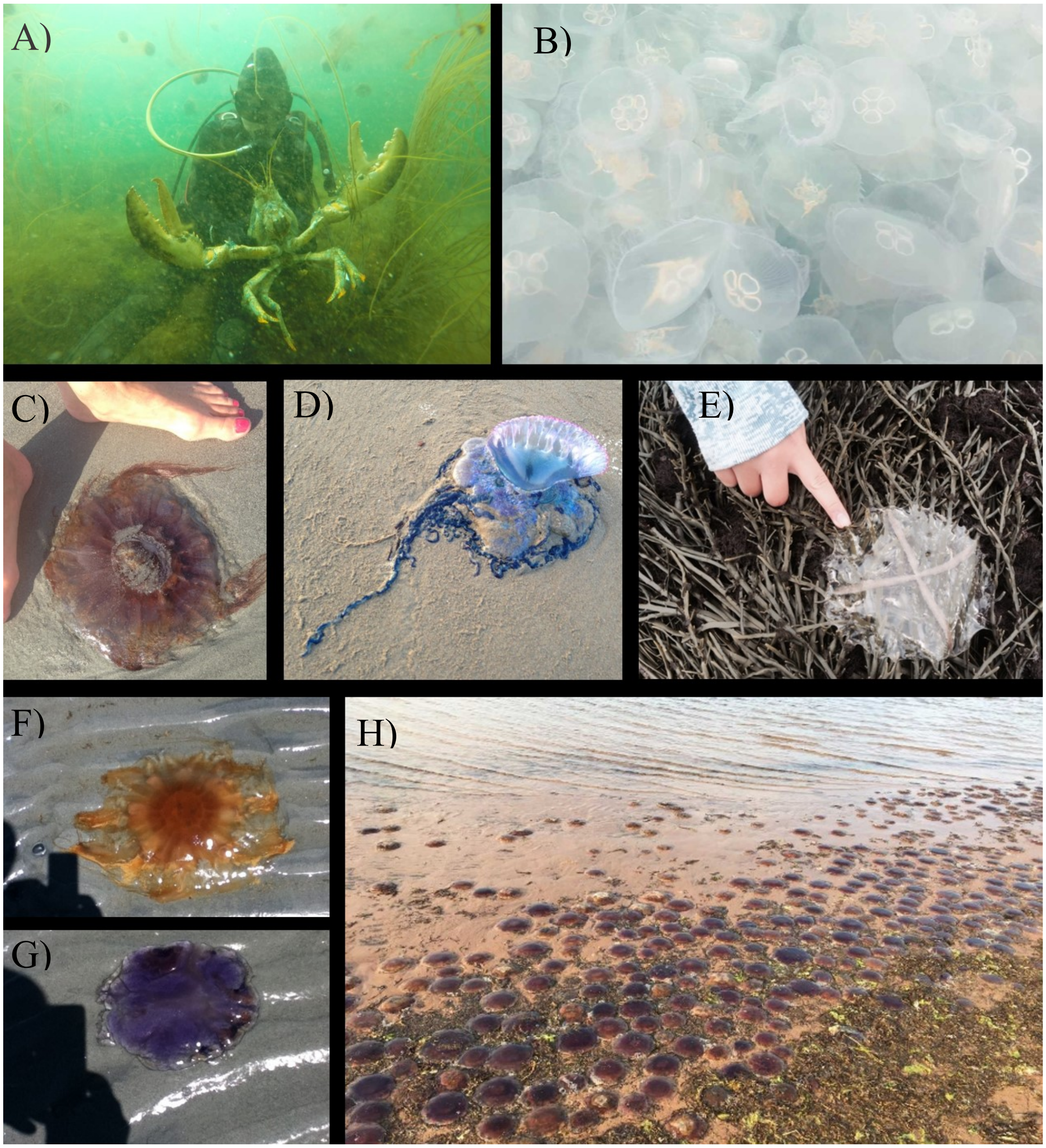

Figure 2.4 - A selection of the over 500 photos submitted through either the Dalhousie Citizen Science surveys, or opportunistic sightings. A) Photo submitted by J. Richard (Magdalen Islands, August, 2015): a scuba-diver holding a lobster in a sea of *C. capillata*; B) photo submitted by E. Burkes (Bras D'Or Lakes, NS, July 29th, 2017): a bloom of *A. aurita*; C) photo submitted by K. Goudey (White Point Beach, NS, July 22, 2016): a beached *C. capillata*; D) photo submitted by S. Vaidya (Conrad's Beach, Nova Scotia, Aug. 6th, 2017): a beached Portuguese man-o-war (*Physalia physalis*) (uncommon in Atlantic Canadian waters); E) photo submitted by G. Turner (Point Prim, Nova Scotia, June 9, 2015): white-cross jellyfish (*Staurophora mertensii*); F) photo submitted by J. Bower (Shelburne, NS, July4th, 2016): stranded *C. capillata* showing colour variation of orange; G) photo submitted J. Bower (Shelburne, NS, July4th, 2016): *C. capillata* showing colour variation of purple; H) photo submitted by A. Howatt (Tracadie Bay, PEI, July 20th, 2017): mass stranding of *C. capillata*.

The most common size range of *C. capillata* was 6 to 15 cm for five of the six survey seasons, in 2010, the most common size range was between 16 and 20 cm. The results are similar for *A. aurita*, with a size range of 6 to 15cm for five of the six survey seasons, however in 2016 the most common size range was 16 to 20cm (Table 2.1).

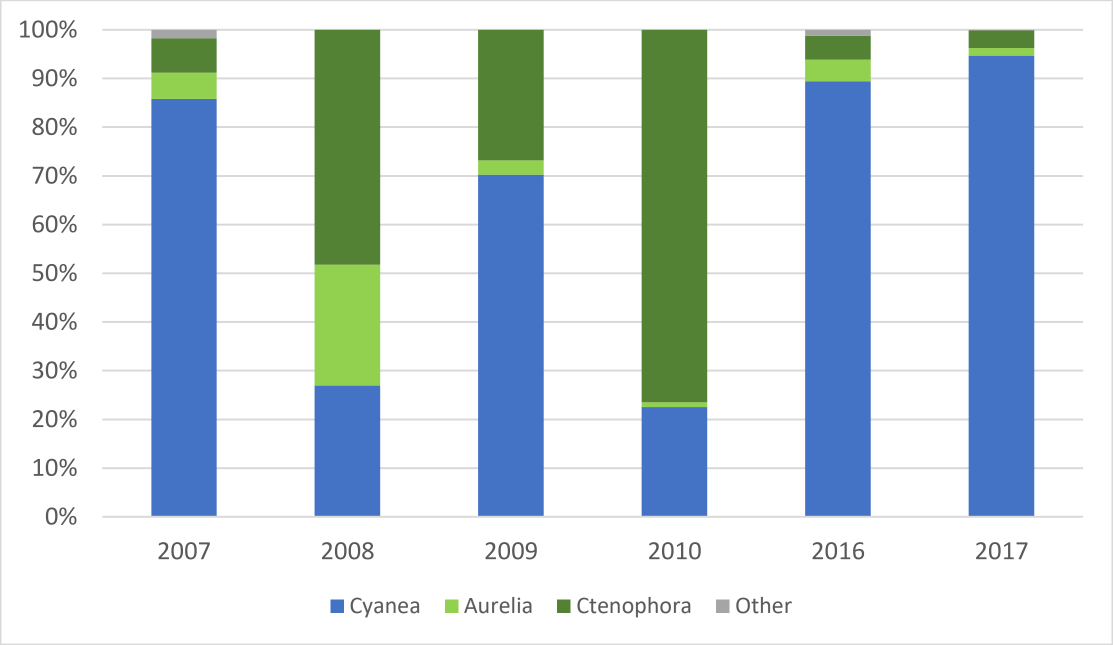

Figure 2.5 - Jellyfish composition for all years of the citizen science monitoring program (CSTN and Dalhousie).

C. capillata was the most dominant species of jellyfish identified over the six survey seasons (75.5% of total observations), ctenophores made up 20.4% of the observations, 3.7% *A. aurita*, and 0.3% were 'other' jellyfish species (i.e. *Staurophora mertensii*, 'unknown' or unidentified jellyfish). *C. capillata* was the dominant species observed in 2007, 2009, 2016, and 2017 – making up over 70% of observations in each of those years (Table 2.1, Figure 2.5). 2008 and 2010 had higher observations of ctenophores than any other species (Figure 2.5).

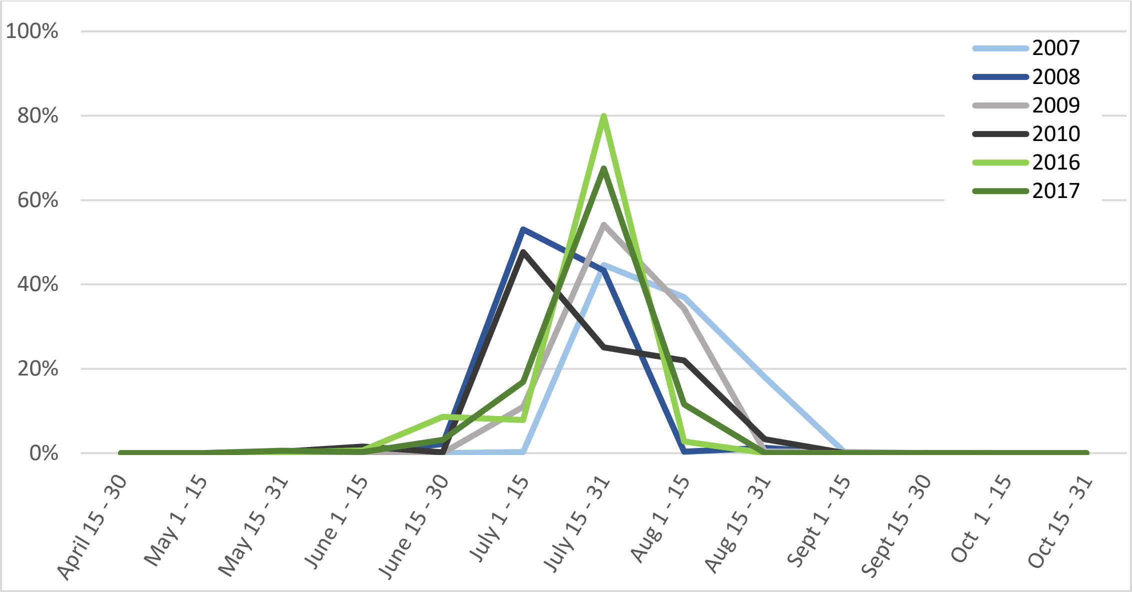

Figure 2.6 – Proportion of *C. capillata* observed through the survey period - for all years of citizen science monitoring. Note: this plot does not account for different survey start and end dates in each year.

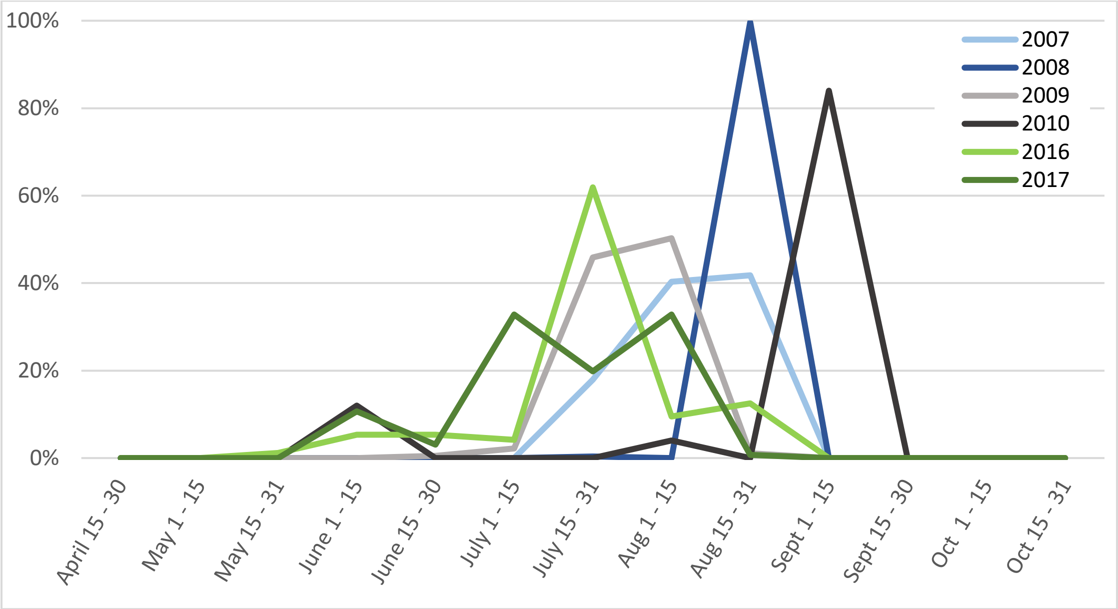

Figure 2.7 – Proportion of *A. aurita* observed through the survey period - for all years of citizen science monitoring. Note: this plot does not account for different survey start and end dates in each year.

Catch per unit effort (CPUE) was calculated for each year of the citizen science programs (Table 2.2). 2008 had the lowest CPUE of *C. capillata* per citizen scientist

(29.8) and *C. capillata* per citizen scientist per kilometer of beach surveyed (16.48). CPUE was highest in 2009 with 367.8 *C. capillata* per citizen scientist, and 284.61 *C. capillata* per citizen scientist per kilometer surveys. 2016 and 2017 had high CPUE per kilometer, with 225.88 and 145.13 *C. capillata* per citizen scientist per kilometer of beach surveyed respectively (Table 2.2).

Table 2.2 - Jellyfish catch per unit effort (CPUE) for each year of citizen science network surveys (CSTN and Dalhousie programs). CPUE is represented by *C. capillata* (CC) per citizen scientist (CS), and *C. capillata* per citizen scientist per km of beach surveyed.

Year	**Citizen Scientists (CS)**			**Distance Surveyed**	**km/CS**	**Total *Cyanea***	**CPUE**	
	(group)	(n)	(n)	(km)		(CC)	(CC/CS)	(CC/CS/KM)
2007	CSTN	10	8	13.3	1.67	1065	106.50	63.89
2008	CSTN	11	8	14.5	1.81	328	29.82	16.48
2009	CSTN	12	10	12.9	1.30	4414	367.83	284.61
2010	CSTN	5	2	3.8	1.92	579	115.80	60.19
2016	Dal	29	29	23.1	0.80	3359	115.83	145.13
2017	Dal	37	36	34.9	0.97	8092	218.70	225.88
						Average:	159.08	132.70

Due to higher spatial coverage and more volunteer participation, the Dalhousie citizen science program (2016 and 2017) was examined in more detail. *C. capillata* made up 93% of all jellyfish stranding observations in the 2016 and 2017 beach surveys. The second half of July had the most reports of stranded *C. capillata* in both years, accounting for 71% of all *C. capillata* reported over the two survey years (Figure 2.8). In each region, the majority of *C. capillata* were observed in the month of July (Figure 2.9). Spatial distribution of *C. capillata* was also examined (Figure 2.10). In 2016, the highest abundance of *C. capillata* was reported in the Northumberland Strait (n = 2896), followed by the South Shore (n = 333) and Eastern Shore (n = 114). In 2017, the Gulf of St. Lawrence had the highest abundance of *C. capillata* (n = 3819), followed by the Northumberland Strait (n = 2957) and the South Shore (n = 2957) (Figure 2.10A). Spatial distribution of *C. capillata* CPUE showed similar regional patterns as abundance (Figure 2.10B), however, Figure 2.10C illustrates that the citizen science effort was very low in the Gulf of St. Lawrence in 2017, resulting in a very high CPUE (Table 2.3).

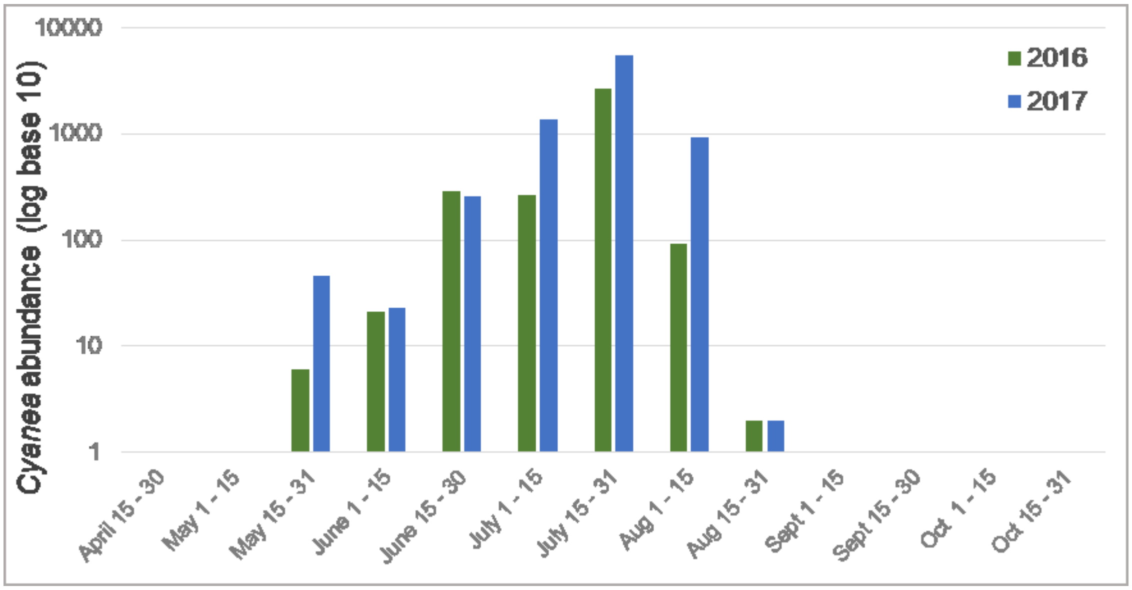

Figure 2.8 - Temporal distribution of *C. capillata* for Dalhousie citizen science network (2016 in green and 2017 in blue).

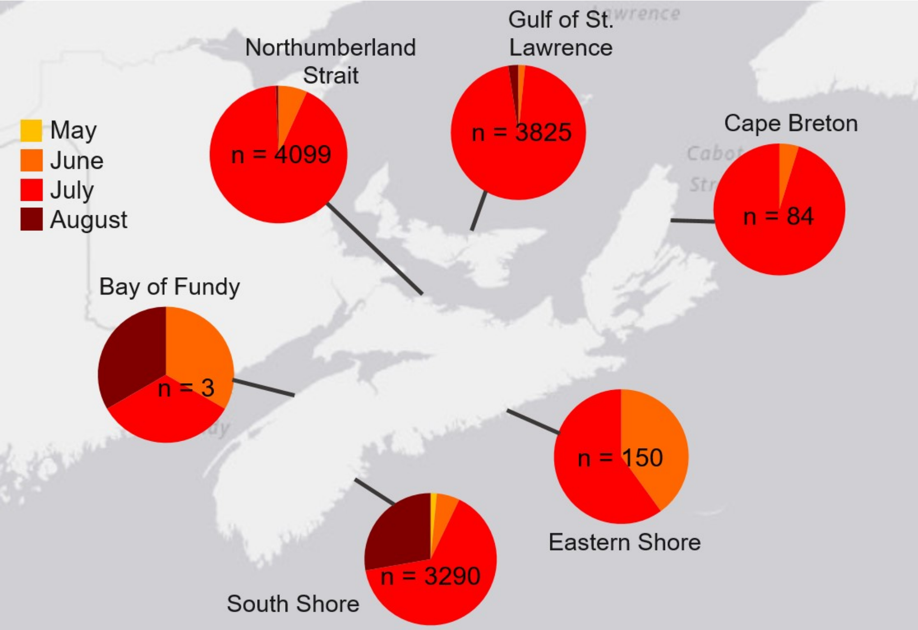

Figure 2.9 - Monthly distribution of *C. capillata* for Dalhousie citizen science network in each region (2016 and 2017 combined).

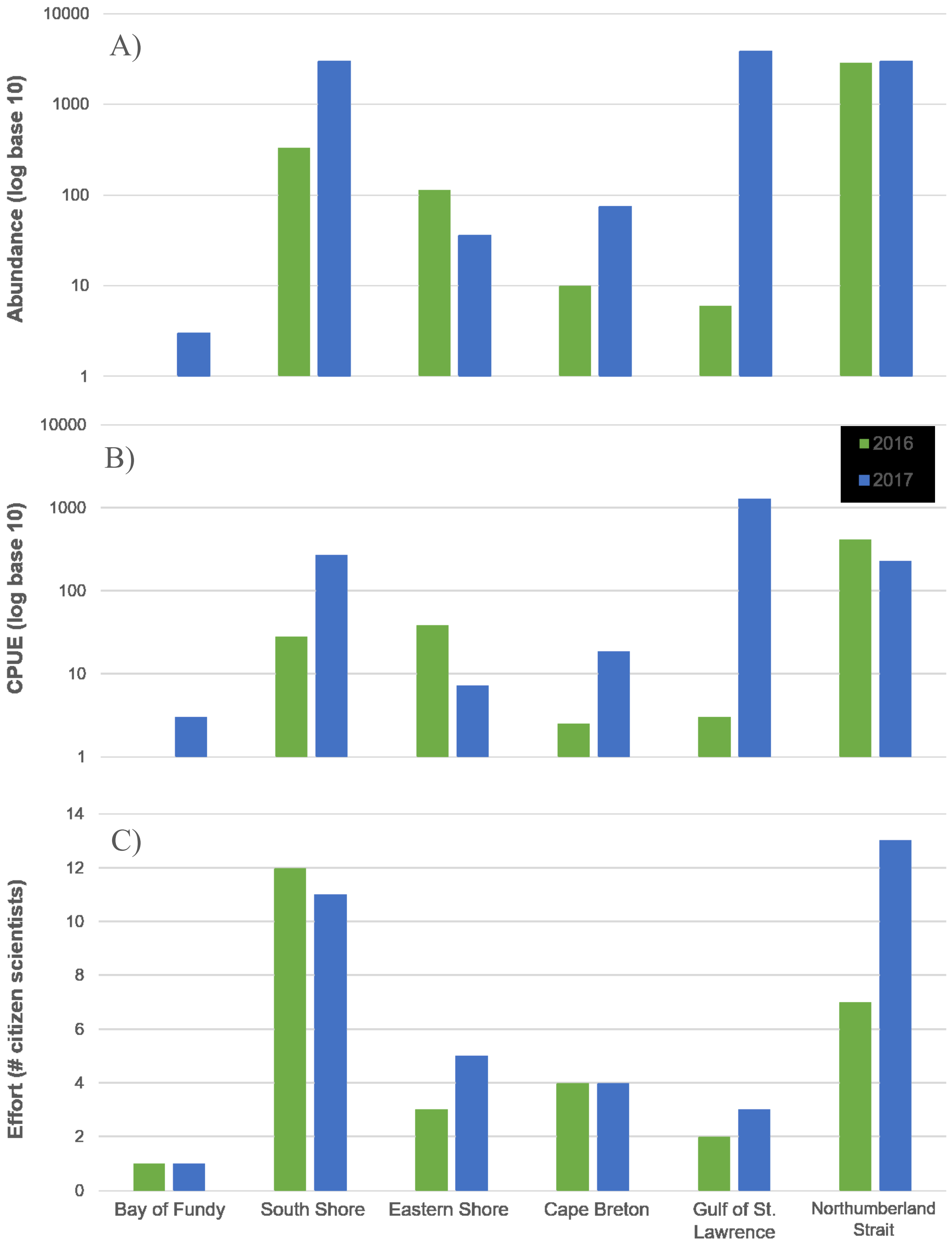

Figure 2.10 – Spatial distribution of A) abundance of *C. capillata* in each region; B) catch per unit effort (number of jellyfish per citizen scientist) in each region; and C) effort, represented by the number of citizen scientists in each region. 2016 in green, and 2017 in blue.

Table 2.3 - Catch per unit effort (CPUE) of *C. capillata* per citizen scientists for each region in 2016 and 2017. Bold italicized rows show high *C. capillata* abundance and/or CPUE.

Year	Region	Citizen scientists (CS)	Total *Cyanea* (CC)	CPUE (CC/CS)
2016	Bay of Fundy	1	0	0.00
2016	South Shore	12	333	27.75
2016	Eastern Shore	3	114	38.00
2016	Cape Breton	4	10	2.50
2016	Gulf of St. Lawrence	2	6	3.00
2016	***Northumberland Strait***	***7***	***2869***	***409.86***
2017	Bay of Fundy	1	3	3.00
2017	***South Shore***	***11***	***2957***	***268.82***
2017	Eastern Shore	5	36	7.20
2017	Cape Breton	4	74	18.50
2017	***Gulf of St. Lawrence***	***3***	***3819***	***1273.00***
2017	***Northumberland Strait***	***13***	***2957***	***227.46***

Opportunistic jellyfish sightings were also collected through jellyfish@dal.ca. In 2016, a total of 404 observations were submitted, with 83% of those sightings being *C. capillata* (Figure 2.11A, Table 2.4). In 2017, there were fewer observations submitted, 224, with 75% of those being *C. capillata* (Figure 2.11B, Table 2.4). The majority of observations of *C. capillata* were found along the Nova Scotia coastline, with gaps in sightings along the Bay of Fundy Coast, and the Eastern Shore in both 2016 and 2017 (Figure 2.11). The opportunistic jellyfish sightings showed similar temporal patterns as the citizen science survey network, with the majority of observations occurring in July (2016 = 48%, and 2017 = 51%) (Figure 2.12).

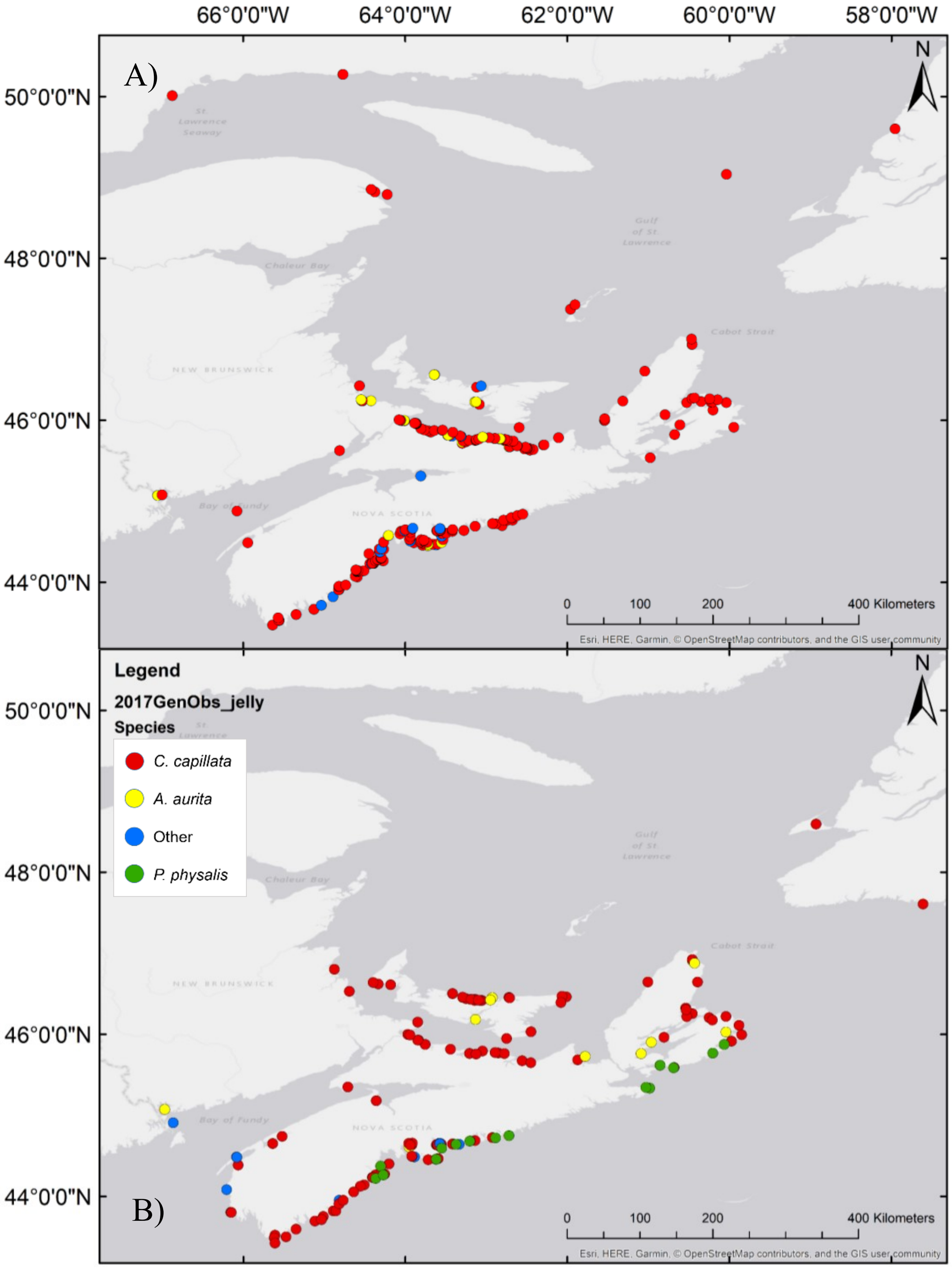

Figure 2.11 - Locations of 2016 (A) and 2017 (B) opportunistic email jellyfish reports. Note: these numbers do not represent abundance, but rather the number of observations submitted for each species. Red = *C. capillata*; yellow = *A. aurita*; green = *P. physalis*; blue = other (Ctenophores, *Staurostoma mertensii*, and unidentified jellyfish).

Table 2.4 - Species composition from the opportunistic email jellyfish reports. Note: these numbers do not represent abundance, but rather the number of observations submitted for each species. Inconsistencies in reporting made abundance counts not possible.

	2016		**2017**	
	# observations		**# observations**	
C. capillata	337	83.4%	168	75.0%
A. aurita	45	11.1%	15	6.7%
Ctenophore	14	3.5%	10	4.5%
P. physalis	0	0%	24	10.7%
S. mertensii	4	1.0%	2	0.9%
Other	4	1.0%	5	2.2%
Total	**404**		**224**	

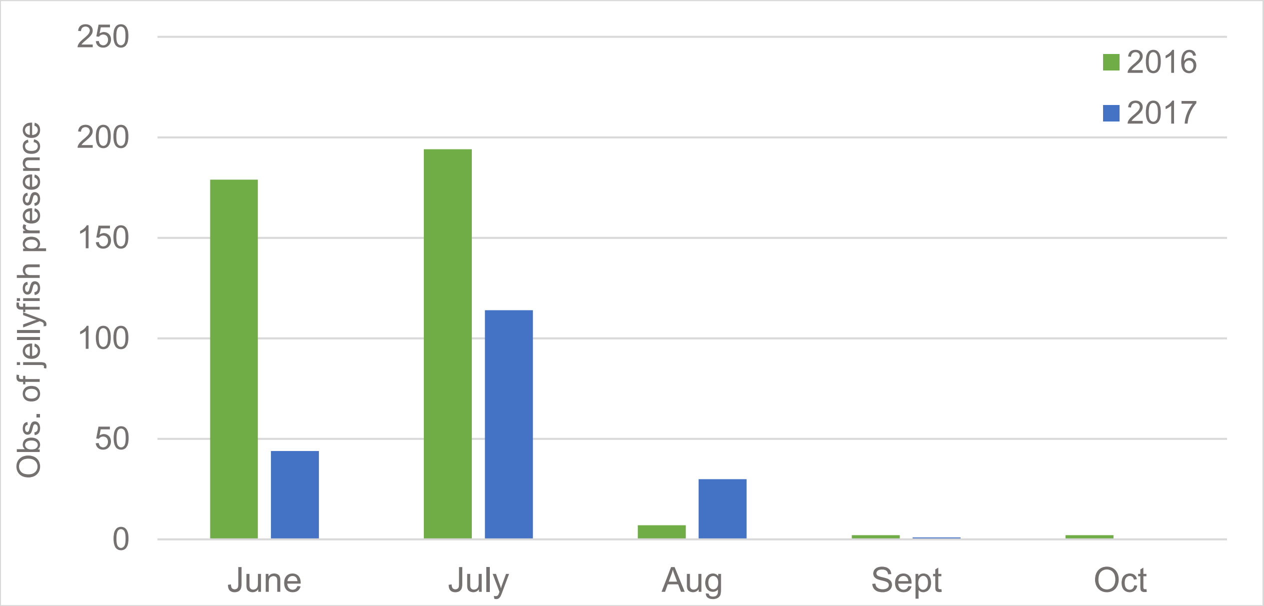

Figure 2.12 - Temporal distribution of the opportunistic email jellyfish reports. Note: these numbers do not represent abundance, but rather the number of observations submitted for each species. Inconsistencies in reporting made abundance counts not possible.

In 2017, 10.7% of the jellyfish observations were of Portuguese man-o-war (*Physalia physalis*) (see Figure 2.4D for visual reference, Table 2.4) – which is not a true jellyfish, but rather a hydrozoan. However, it shares similar characteristics to true jellyfish (scyphozoans), such as a gelatinous consistency, planktonic life cycle, inactive swimmer, etc. All of the Portuguese man-o-wars reported were observed along the

Scotian Shelf coast (South and Eastern Shore) (Figure 2.11B). There were no Portuguese man-o-war observed in 2016.

Between April and October of 2016, the bell diameter of 705 stranded jellyfish (640 *C. capillata* and 65 *A. aurita*) were measured between the 29 citizen scientist locations over 494 survey weeks. Between May and October of 2017, the bell diameter of 1770 stranded jellyfish (1649 *C. capillata* and 121 *A. aurita*) were measured between the 37 citizen scientist locations over 515 survey weeks (Table 2.5). The size range of *C. capillata* was larger in both years than *A. aurita*, but the mean bell diameter of *A. aurita* was slightly larger in 2016 and 2017 (Table 2.5).

Table 2.5 - Bell diameter for the stranded medusae of *C. capillata* (CC) and *A. aurita* (AA) for the Dalhousie citizen science program.

Year	Species	n	Mean bell diameter (cm) (SD)	Max-min (cm)
2016	CC	640	14.52 (5.69)	34 - 3
2016	AA	65	17.88 (6.52)	32 - 5
2017	CC	1649	11.60 (6.76)	44 - 2
2017	AA	121	12.88 (5.23)	30 - 4

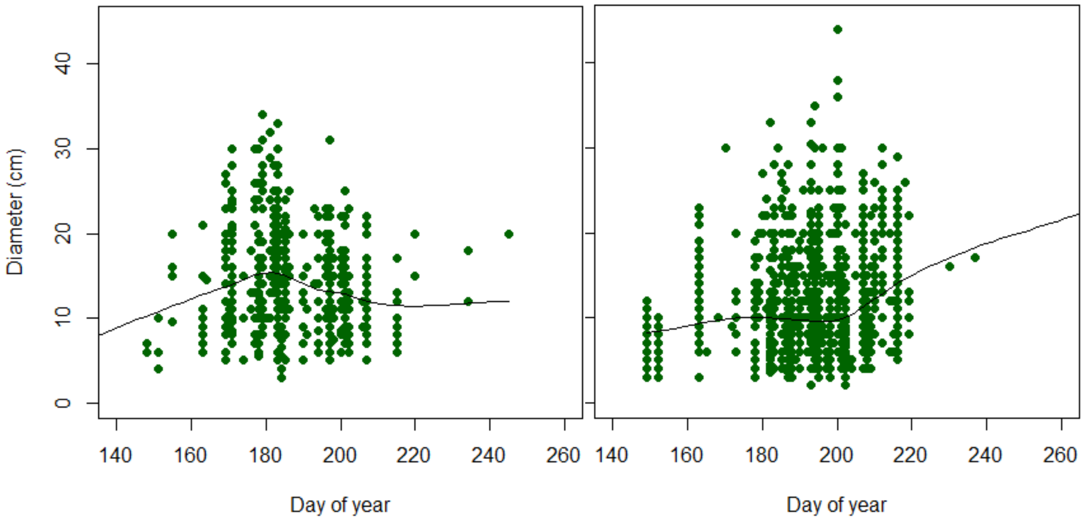

Figure 2.13 - *C. capillata* diameter measurements (cm) and the day of year (2016 on the left, 2017 on the right), fit with a LOESS curve (2016 r = -0.0919, 2017 r = 0.1405).

Diameter of all *C. capillata* measured in 2016 and 2017 were plotted against the day of year in Figure 2.13. Loess curves fit to size data revealed that there is no obvious linear relationship between diameter of *C. capillata* and day of year. Pearson's correlation coefficient did not reveal strong associations between *C. capillata* and day of year in either 2016 (r = -0.0919) or 2017 (r = 0.1405) (Figure 2.13).

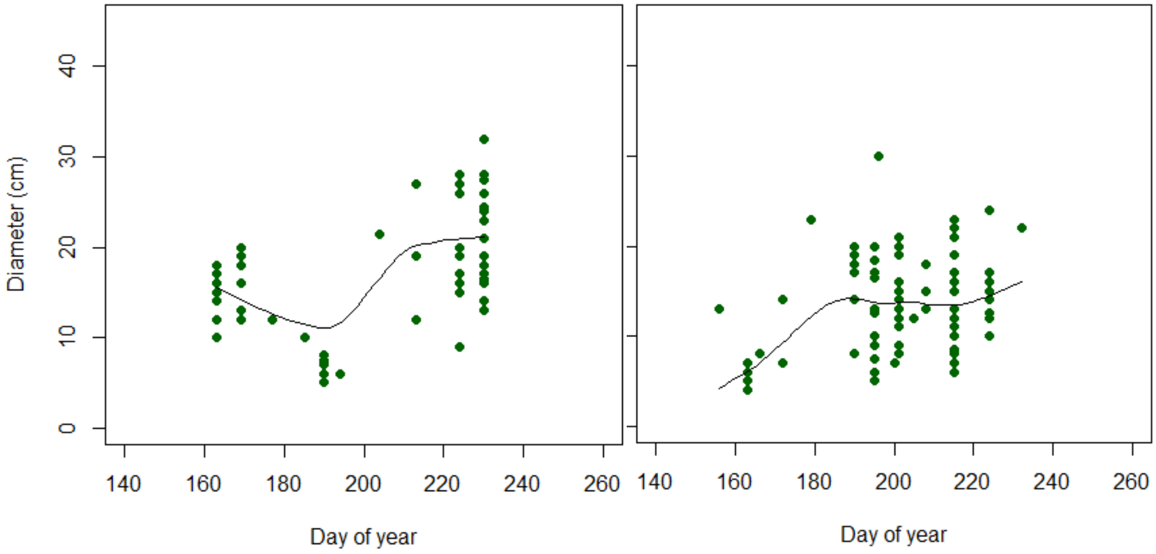

Figure 2.14- *A. aurita* diameter measurements (cm) and the day of year (2016 on the left, 2017 on the right), fit with a LOESS curve (2016 r = 0.4965, 2017 r = 0.4047)

Diameter of all *A. aurita* measured in 2016 and 2017 were measured against day of the year in Figure 2.14. Similarly to the *C. capillata* results, loess curves fit to *A. aurita* size data revealed no obvious linear relationship between diameter of *A. aurita* and day of the year. Pearson's correlation coefficient did not reveal strong associations between *A. aurita* and day of the year in either 2016 (r = 0.4965) or 2017 (r = 0.4047) (Figure 2.14).

Likewise, within individual regions, none showed an obvious linear relationship from the loess curve in either year (see Appendix C). Pearson's correlation coefficient did not reveal strong associations between *C. capillata* diameter and day of year for any of the regions in either 2016 or 2017 (Table 2.6).

Table 2.6 - Collinearity tested for each region, using Pearson's correlation.

Region	**2016**		**2017**	
	Diameters measured	Pearson's correlation r value	Diameters measured	Pearson's correlation r value
Scotian Shelf	241	-0.1757	423	0.3148
Eastern Shore	107	-0.1848	33	0.2466
Cape Breton	24	-0.0784	101	-0.3111
Gulf of St. Lawrence	6	0.3542	222	0.1481
Northumberland Strait	262	-0.0493	867	-0.2123

2.3.2 Modelling environmental parameters

Among six candidate models testing for possible linkages between jellyfish present to environmental parameters, model **polyS2** was selected based on AIC. It included the variables sea surface temperature (third order polynomial), chlorophyll-a, region, and effort (survey weeks) (Table 2.7). Although model polyS3 had a slightly lower AIC, and an AIC value that differed by less than two – model **polyS2** was selected as it included an effect for Region, which was of particular interest for this modeling exercise (Table 2.8). When there was no polynomial term applied to SST in the same model as **polyS2**, it had an AIC of 132.67, and when a second order polynomial was applied to SST in model **polyS2**, it had an AIC of 126.34, which are both higher than the AIC of the third polynomial on sea surface temperature (120.8).

Table 2.7 – *C. capillata* presence model comparison. Model selection shown in bold. SST = sea surface temperature, Effort_wks = total survey weeks, Effort_CS = number of citizen scientists surveying.

Model	Variables	AIC	Resid. Df	Resid. Dev.	dAIC	Weight
polyS	Year, poly(SST_C,3), Chl, Region, Effort_wks, Effort_CS	123.8	108	97.8	3.2	0.06
polyS1	poly(SST_C,3), Chl, Region, Effort_wks, Effort_CS	121.8	109	97.8	1.2	0.18
polyS2	**poly(SST_C,3), Chl, Region, Effort_wks**	**120.8**	**110**	**98.8**	**0.2**	**0.29**
polyS3	poly(SST_C,3), Chl, Effort_wks	120.6	115	108.6	0.0	0.32
polyS4	poly(SST_C,3), Region, Effort_wks	123.2	111	103.2	2.5	0.09
polyS5	Year, poly(SST_C,3), Region, Effort_wks, Effort_CS	123.8	109	99.8	3.1	0.07

Table 2.8 - Model output for polyS2. Significant variables are bolded.

Variable	Coefficient	SE	z-value	P
Intercept	-21.95	8.64	-2.54	0.01108
Sea surface temperature	**5.277**	**2.15**	**2.46**	**0.0141***
(SST)2	**-0.400**	**0.17**	**-2.36**	**0.01825***
(SST)3	**0.009**	**0.004**	**2.23**	**0.02570***
Chlorophyll-a	-0.497	0.29	-1.74	0.08169
Region2 – South Shore	-1.561	1.55	-1.01	0.31490
Region3 – Eastern Shore	-0.491	1.19	-0.41	0.67946
Region4 – Cape Breton	-0.634	1.15	-0.55	0.58243
Region5 – Gulf of St. Lawrence	0.636	0.99	0.64	0.51949
Region6 – Northumberland Strait	1.689	0.98	1.73	0.0841
Effort (survey weeks)	**0.184**	**0.06**	**3.05**	**0.00227***

Observer effort clearly emerged as the strongest predictor of jellyfish presence (Table 2.8, Figure 2.15), showing a positive correlation until about 20 survey weeks, where the correlation flattens out. Sea surface temperature was also a significant predictor of jellyfish presence, however slightly weaker than effort (Table 2.8, Figure 2.16). Sea surface temperature shows a positive correlation between 5°C and 11°C, a negative trend from 11°C to 18°C, and back to a positive trend from 18°C onward (Figure 2.16). Two variables that were not statistically significant, but had p-values below 0.1, were chlorophyll-a and Region 6 (Northumberland Strait). Note – the large confidence bands in Figure 2.15 and 2.16 are most likely a result of sparseness of the data.

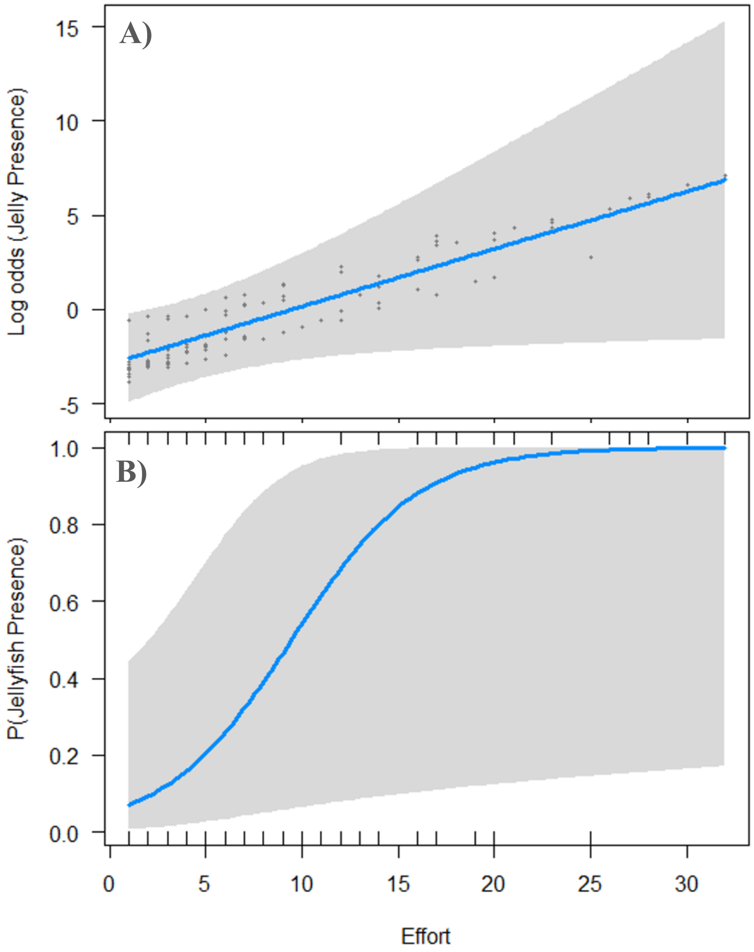

Figure 2.15 - Visualization of the significant variable effort (number of survey weeks) from the polyS2 model. A) Effort on jellyfish presence (logs odds), B) Effort on jellyfish presence (probability scale). Grey area represents 95% confidence intervals. Tick marks on x-axis represent each data point, whether *C. capillata* were observed or not at that level of effort.

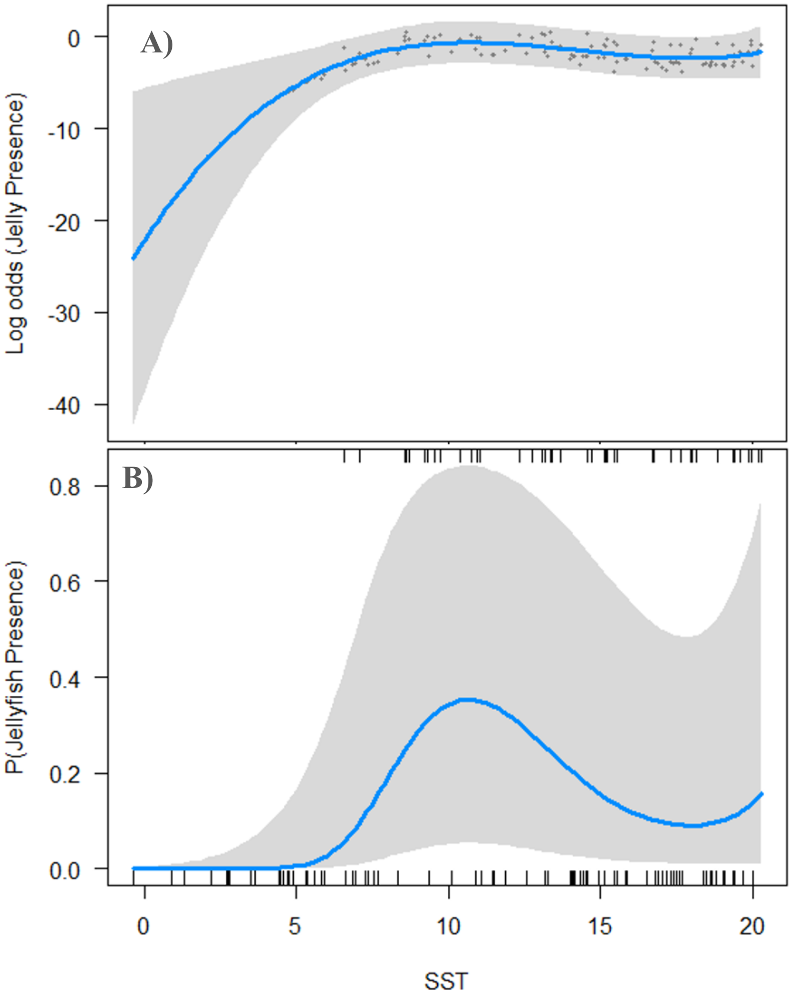

Figure 2.16 - Visualization of the significant variable sea surface temperature (SST) from the polyS2 model. A) SST on jellyfish presence (logs odds), B) SST on jellyfish presence (probability scale). Grey area represents 95% confidence intervals. Tick marks on x-axis represent each data point, whether *C. capillata* were observed or not at that specific temperature.

2.3.3 Ground fish survey bycatch data analysis

The optimized hot spot analysis highlighted hot spots within the Gulf of St. Lawrence, and in particular, the areas east and north of the Magdalen Islands as hotspots of jellyfish bycatch in the DFO ground fish surveys. These areas were classified as statistically significant spatial clusters, with 99% confidence (Figure 2.17)

Statistically significant clusters of 20km by 20km cells of jellyfish bycatch were identified for the periods 2006 – 2009, 2010 – 2013, and 2014 – 2017 (Figure 2.17; hotspots > 90% [z-scores > 1.65]). The clusters of jellyfish hotspots shift slightly between each time period. From 2006 to 2010, the hotspot completely surround the Magdalen Islands, extending to the south and north (Figure 2.17A). From 2010 to 2013, the significant hotspot cluster covers a larger area (Figure 2.17B), stretching further north along the western coast of Newfoundland. From 2014 to 2017, the Magdalen Islands are no longer a significant hotspot (Figure 2.17C), but the west coast of Newfoundland, Cabot Strait/Sydney Bight region, and the mouth of the St. Lawrence River are.

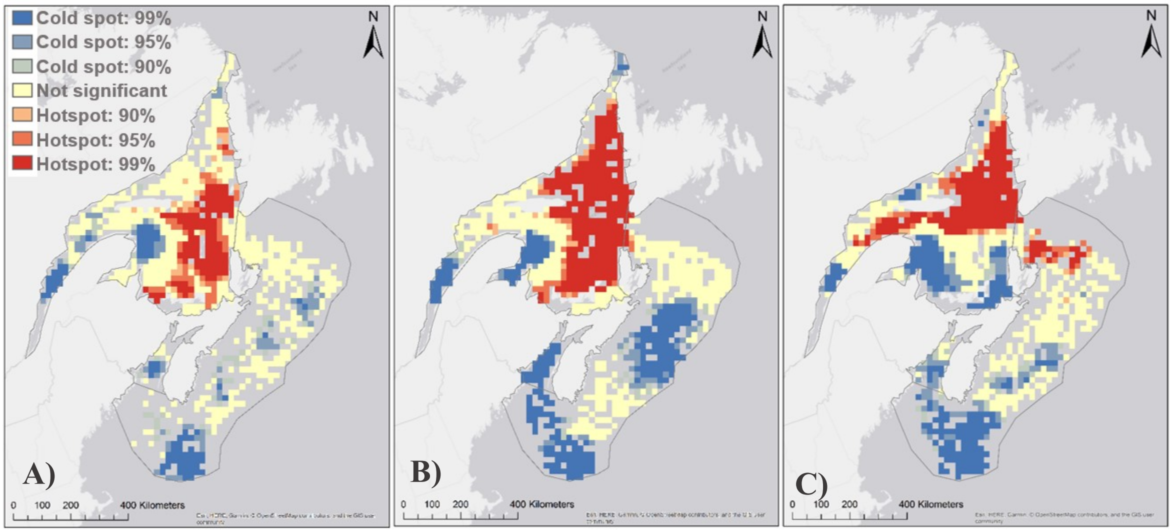

Figure 2.17 - Optimized hot spot analysis of jellyfish occurrence sightings from DFO groundfish surveys. A) 2006 – 2009; B) 2010 – 2013; and C) 2014 - 2017

Statistically significant jellyfish occurrence cold spots are highlighted in similar regions across all time periods: in the Bay of Fundy and around the Yarmouth coast, the southwestern side of Gulf of St. Lawrence, and deep into the St. Lawrence River Estuary

(Figure 2.17). Although it is represented as a hotspot in Figure 2.17 A) and B), the west side of Cape Breton for the time period 2014 to 2017 is represented as a cold spot.

2.4 Discussion

The primary objective of this chapter was to determine spatio-temporal patterns, and environmental drivers of jellyfish occurrence in Atlantic Canada. This was assessed using citizen science, DFO groundfish bycatch data, and generalized linear models.

Clear spatial and temporal patterns of jellyfish were detected from the citizen science networks. The month of July had the highest number of *C. capillata* reported each year of the citizen science programs. Temporal patterns were more variable for *A. aurita*, with observations peaking at different times in different years. The modelling results suggested sea surface temperature, but not chlorophyll, as a significant predictor jellyfish presence. Notwithstanding strong seasonal trends in jellyfish abundance. There was no significant correlation between day of the year and bell diameter for either *C. capillata* or *A. aurita.*

Spatially, the Gulf of St. Lawrence, Northumberland Strait, and South Shore regions had the most *C. capillata* observations. The hot-spot analysis revealed important spatial areas of jellyfish presence from bycatch in the DFO groundfish surveys to be within the Eastern Gulf of St. Lawrence, with northward shifts over time.

2.4.1 Citizen science

The Dalhousie citizen science network (2016 and 2017), and CSTN citizen science network (2007, 2008, 2009, and 2010) yielded broadly similar results for jellyfish species composition. Four of six survey years (2007, 2009, 2016, and 2017) revealed a dominant presence of *C. capillata*. Across all six years of the citizen science jellyfish monitoring project, the two most common scyphozoans species were *C. capillata* and *A. aurita*. This is consistent with the previous literature describing these as the primary identifiable species of foraging leatherbacks in the Maritimes Region (James and Herman 2001; Heaslip et al. 2012).

The two citizen science programs differed in effort - in the number of citizen scientists participating, distribution of citizen scientists, and total distance surveyed (Table 2.1, Figure 2.3). The CSTN citizen science network involved fewer volunteers, who primarily surveyed locations along the South Shore and Eastern Shore of Nova Scotia (Figure 2.3). Despite differences in effort between the two survey programs, temporal patterns of *C. capillata* were similar with peak observations during the last two weeks of July (Table 2.1, Figure 2.6). The opportunistic jellyfish sightings reported to jellyfish@dal.ca also corroborated these temporal trends, with the majority of observations coming in the month of July. This was the first attempt to determine baseline temporal trends of *C. capillata* in Atlantic Canadian waters, and the results are consistent with studies of jellyfish beach stranding in Europe. Doyle et al. (2007) found maximum abundance of *C. capillata* to occur late July in the Celtic and Irish Seas, and Pikesley et al. (2014) described the majority of *C. capillata* strandings to occur in the month of July in coastal United Kingdom waters. Stranding surveys conducted on the Isle of Anglesey found *C. capillata* most abundantly in July (Ionescu et al. 2016). This suggests that even with lower participant numbers in the citizen science beach surveys, useful baseline information on jellyfish seasonality can be obtained.

Discussion on jellyfish distribution will focus on the Dalhousie citizen science program, as it had the broadest spatial coverage across the six major study regions. It is important to recognize the caveats in citizen science coverage. The Dalhousie citizen science program, although it had more extensive coverage than the CSTN program, did not establish index monitoring effort in all areas (e.g. the Eastern shore, west side of Cape Breton, Gulf of St. Lawrence side of PEI, and the Bay of Fundy all had low survey coverage). The extent of survey effort can affect jellyfish detection, as higher coverage can increase detection probability (Houghton et al. 2007; Kéry et al. 2010). Some areas of Atlantic Canada have sparsely populated coastlines contributing to varying rates of volunteerism. This is one of the biggest limitations of citizen science, it is largely limited to regions where people reside, and areas that are easily accessible (Tulloch et al. 2013; Tiago et al. 2017). It is also possible that participants were more likely to sign up for the jellyfish monitoring project if they are located in an areas where the phenomenon of jellyfish strandings on local beaches is well known, or an area where observations are expected (Kéry et al. 2010; Tulloch et al. 2013). Although it was communicated when recruiting citizen scientists that areas where jellyfish are not normally seen were also important to the study, it is possible that people perceived they would not be contributing as much to the project if they did not report jellyfish through the survey season. This is evidenced by receipt of multiple personal communications with citizen scientists where they apologized for not seeing jellyfish, and expressed concern and discouragement about not seeing them.

Generally, the regions with the highest citizen science effort also observed the highest abundances of jellyfish. For example, in 2016 the South Shore region had 12 citizen scientists, and the second highest *C. capillata* abundance (n = 333), and the Northumberland Strait had the second highest number of surveyors with seven, and had the highest jellyfish abundance (n = 2869). In 2017, again the Northumberland Strait and South Shore had high effort (13 and 11 respectively) and high records of *C. capillata* abundance (2957 in both regions). However, in 2017 the Gulf of St. Lawrence region had the highest abundance of *C. capillata* reported (3819) with relatively low effort of three citizen scientists. This illustrates the need for other indices or measurements than abundance or number of participants. Catch per unit effort (CPUE) was also used to describe the effort in a more standardized way. In 2017, the Gulf of St. Lawrence region had a CPUE of 1273 *C. capillata* per citizen scientist, while the South Shore and Northumberland Strait had lower CPUEs of 269 and 227 respectively. It is possible that the Gulf of St. Lawrence region, even though it had lower effort and therefore possibly lowered detection probability (Kéry et al. 2010), is important for *C. capillata* spatial distribution. The Northumberland Strait, which was high in *C. capillata* abundance, effort, and CPUE, along with its general proximity to the Gulf of St. Lawrence region is also most likely important spatially for *C. capillata*.

Another common issue with citizen science projects can be the accuracy of species identification (Dickinson et al. 2010; Conrad and Hilchey 2011; Tiago et al. 2017). Unless photographs were provided, it was difficult to verify volunteer assigned species identification. To minimize misidentifications, jellyfish identification sheets were provided to all participants, and related questions posed by volunteers – normally via email - were promptly answered. The two most common scyphozoan jellyfish species recorded in this project, *C. capillata* and *A. aurita,* are physically quite different (Figure

2.4), therefore species misidentification is likely quite low. However, a stranded *C. capillata* that has been washed up for a number of days may have lost distinguishing tentacles and oral arms, and be discoloured by the sun, and could be mistaken for a normally transparent *A. aurita.*

There are several environmental factors that could influence if jellyfish are stranded on a beach, and if so, the magnitude of the stranding. Local factors at each citizen scientist location including wind direction and speed, local currents, tide strength, and physical characteristics of the location (ex. semi-enclosed systems versus open coastline) may all play a role in jellyfish strandings (Doyle et al. 2007; Pikesley et al. 2014; Keesing et al. 2016). Keesing et al. (2016) found that mass strandings of scyphozoan *Crambione mastigophora* on the Western coast of Australia occurred under three conditions: when winds were blowing onshore, when currents were flowing onshore, and when tides were smaller than average. The magnitude of the stranding would depend on the combination of the three factors, and the intensity of each (Keesing et al. 2016). One way this thesis tried to overcome environmental factors at individual survey locations, was by grouping them into larger regions. It is possible that this dampened the affects at each specific location, and provided a better average representation over the region.

There are large differences between the regions examined in this thesis. The Gulf of St. Lawrence and Northumberland Strait are semi-enclosed systems, the Bay of Fundy has extreme tides, and the Scotian Shelf is an open system exposed to the Atlantic Ocean. One might expect the strong tides of the Bay of Fundy to create enough significant advection away from beaches, that jellyfish are less likely to strand there and would therefore be less likely to be encountered (Keesing et al. 2016). This could partially explain the low numbers of jellyfish observed along the Bay of Fundy in the citizen science programs, along with low survey effort. In a semi-enclosed system such as the Gulf of St. Lawrence with general westward flow and counter clockwise circulation, shoreline strandings of jellyfish may be more likely to happen. In the summer months, currents sweep down the western Gulf of St. Lawrence and along Prince Edward Island before moving up the western side of Cape Breton and out through the Cabot Strait (Figure 1.2) (Galbraith et al. 2016). This presents opportunity for jellyfish within the Gulf of St. Lawrence to be advected in close proximity to the coast. On the other hand, the Scotian Shelf is open system, exposed to the Atlantic Ocean. Water from the Gulf of St. Lawrence flow into the Scotian Shelf via the Cape Breton current through the Cabot Strait. The Nova Scotia Current has a general coastal southwestern movement along the Scotia Shelf (Figure 1.2) (Sutcliffe Jr. et al.1976). Jellyfish could be transported out of the Gulf of St. Lawrence along the Nova Scotia Current and moved down the coast of Nova Scotia, with strandings occurring along the way.

The citizen science jellyfish surveys helped extend the spatial and temporal coverage of this project, and also offered other benefits including: low cost, and engaging and communicating with the general public about science and research. The results of the surveys allowed for identification of temporal peaks of jellyfish strandings at regional scales, and a broader Atlantic Canadian scale. Opportunistic sightings of jellyfish were also collected through email. In 2017, there were 24 sightings of Portuguese man o' war (*P. physalis*), which are a tropical and subtropical hydrozoan (Lane 1960) not native to Atlantic Canadian waters. All of these sightings occurred along the Atlantic coast of

Nova Scotia. Portuguese man o' war are often associated with the Gulf Stream, and strong north and northeast winds can push them as far north as Canadian waters (Johnson and Allen 2012). This highlights the capability of citizen science to capture episodic events, such as Portuguese man o' war sightings.

Citizen scientists also measured the diameter of jellyfish encountered on beach surveys. The diameter results were surprising in that *C. capillata* is the largest species of jellyfish in the world, however the diameters measured by citizen scientists were quite small with average bell diameter of 14.52 cm (±5.69) and 11.60 cm (±6.76) in 2016 and 2017 respectively. In fact, 60% of *C. capillata* measured in 2016 were between 10 and 20cm, and 65% were between 5 and 15cm in 2017. *C. capillata* captured by leatherbacks off Cape Breton, Nova Scotia, averaged a contracted bell diameter was 11.2 ± 4.4 cm (Heaslip et al. 2012), which may be representative of the sizes in this study. However, Houghton et al. (2007) measured diameter of stranded *C. capillata* in the Irish and Celtic Seas, which had an average bell diameter measurement of 49.6 cm, and a maximum size of 130 cm.

There was no obvious single reproduction event, which might have produced a visible relationship between day of year and diameter of jellyfish observed, for either *C. capillata* or *A. aurita.* This could indicate possible protracted ephyrae release of both species, as the bell diameter range remained broad throughout the survey period. Assuming growth rate was relatively constant, protracted ephyrae release is supported by the fact that there are small jellyfish size classes (5 cm diameter and under) and larger size jellyfish classes (> 20 cm diameter) at the same time. These findings are consistent with a study conducted in the Irish and Celtic Seas, where three species of jellyfish (including *C. capillata*) were all found to have broad size and weight ranges through the survey period (Houghton et al. 2007). Ceh et al. (2015) also found various sized *Chrysaora plocamia* medusa throughout medusa-season, and attributed that to multiple cohorts of ephyrae. However, this goes against previous research which suggests temperate jellyfish species populations consist of a single cohort that grows and mature together (Grondahl 1988; Brewer 1989; Lucas 2001; Lucas et al. 2012).

C. capillata are described as a cold water species, and strobilation (ephyrae release) is thought to occur at temperatures below 10°C (Verwey 1942; Grondahl 1988; Brewer and Feingold 1991; Holst 2012). While it is difficult to accurately define strobilation periods and reproductive cohorts without knowledge on polyp bed location, results on bell diameter provided in this thesis suggest there may be protracted ephyrae release. Based on bottom temperature, salinity ranges, and circulations patterns, areas that could support *C. capillata* polyp beds in Atlantic Canadian waters can be hypothesized. *C. capillata* planula larvae settle on the underside of hard substrates (both natural and artificial substrates) in protected coastal waters (Ostman 1997; Holst and Jarms 2007; Lucas et al. 2012), however preferred depth and flow rate are not known (Hay et al. 1990; van Walraven et al. 2016). The southern Gulf of St. Lawrence (Magdalen Shallows) is a semi-enclosed area, less than 100 m in depth, with bottom temperatures that stay below 8°C all year round (excluding the Northumberland Strait, which is warmer). Surface temperatures on the Magdalen Shelf usually do not surpass 10°C until end of May or early June (Galbraith et al. 2016). These temperature profiles may allow protracted *C. capillata* strobilation, which could account for the variable sizes of *C. capillata* observed throughout the survey season. Coastal areas with natural and artificial substrates (including stones, shells, concrete, wood, shells, ceramics, glass, and polyethylene terephthalate (PET) plastic) within the southern Gulf of St. Lawrence present environmental conditions that may favour the settlement of *C. capillata* planula larvae, and the development of polyp beds. While knowledge of *C. capillata* polyp beds is rare, the planula larvae of other scyphozoan jellyfish, including *A. aurita,* are known to settle and develop into polyps on marinas, wharfs and ship wreck sites (van Walraven et al. 2016). Citizen science survey results indicate *C. capillata* medusae are present in the southern Gulf of St. Lawrence. Polyp beds within the Gulf of St. Lawrence are plausible due to environmental conditions, and circulation patterns within the Gulf of St. Lawrence. The Nova Scotia Current could transport medusae through the Cabot Strait and along the Nova Scotia coastline. This could help explain the seeming absence of *C. capillata* from the Bay of Fundy in the citizen science data, as they would most likely move through advection from the location of polyp beds.

2.4.2 Modelling environmental parameters

The generalized linear modelling suggested that sea surface temperature, and the number of survey weeks (effort) were statistically significant predictors of *C. capillata* stranding in the citizen science data. For many jellyfish species, including *C. capillata,* ephyrae release occurs at a specific thermal range (Verwey 1942; Gröndahl 1988; Brewer and Feingold 1991; Holst 2012). As discussed earlier, *C. capillata* is described as a cold water species that thrives in temperate waters, and is not commonly found below certain latitudes (depending on the population). It seems intuitive that temperature would be a significant driving factor of *C. capillata*. The trends of sea surface temperature on *C.*

capillata presence observed in Figure 2.16B can possibly be explained by thermal ranges and senescence of *C. capillata* medusae. Figure 2.16B shows a positive correlation for jellyfish presence between 5 and 11°C, then a negative correlation, followed by a positive trend from 18°C onwards. The upper thermal limit where deterioration of *C. capillata* medusae starts to occur was identified to be 19.1°C (±2.3) in Connecticut waters (Brewer 1989). When sea surface temperature reached 18°C along coastal regions examined in this study, there is a positive trend and increased probability of detecting *C. capillata* on beaches. Sea surface temperatures reach values between 15 and 20°C in August in the Gulf of St. Lawrence, and can reach higher temperatures in the Northumberland Strait (Galbraith et al. 2016).

The modelling in this thesis only considered *C. capillata* that had been stranded on coastlines. It is unknown whether relative jellyfish occurrence on beaches reflects relative occurrence in adjacent waters (Fleming et al. 2013). This is important to consider with species such as *C. capillata*, as they have been observed offshore at depths associated with the thermocline, and therefore temperatures differing from surface temperature (Bailey et al. 2012; Wallace et al. 2014; Hamelin et al. 2014). Many of the *C. capillata* reported in the citizen science data were most likely dead when they were washed ashore (this can be assumed by lack of oral arms and tentacles). Development of blastulae on oral arms has been attributed to the degeneration of *C. capillata*, as once this process begins, the jellyfish is unable to feed (Brewer 1989, Hosia et al. 2015). Advection of senescing *C. capillata* from deeper, cooler waters to coastal waters may occur while healthier medusae remain. In fact, the citizen science data indicated the last *C. capillata* stranding in September in both 2016 and 2017 (which can also be partially attributed to lower survey effort at the end of the season), however leatherback sea turtles have been observed feeding on *C. capillata* in September and October (James 2005a, b; James et al. 2006), suggesting while jellyfish strandings are not being observed, there may still be *C. capillata* in adjacent waters.

Survey effort was also significant in predicting *C. capillata* presence on beaches, which is supported by the idea that increased survey effort can increase detection probability of an organism through in citizen science programs (Houghton et al. 2007; Kéry et al. 2010)

Chlorophyll-a was not a statistically significant variable in the model, and had a negative trend with jellyfish presence. One may expect that productivity would be a driving factor of jellyfish presence, as connections between chlorophyll-a concentrations and zooplankton in the water column have been made before (Benson et al. 2007; Greer et al. 2015; Greer and Woodson 2016), suggesting these areas could offer prey resources to jellyfish. However, satellite derived chlorophyll-a estimates may be unreliable if they are too close to the coast, which may have been an issue with this data set as areas only reaching 25 km from the coastline were analyzed. It is also possible that trophic interactions with zooplankton could suppress chlorophyll-a values (Aleksa 2017). Several studies have used satellite derived chlorophyll-a concentrations to infer areas of high jellyfish abundance (Fossette et al. 2010; Bailey et al. 2012). Sample size for the modelling done in this thesis was relatively small, and it is possible that chlorophyll-a values were skewed by closeness to the shore.

While the modelling results in this chapter suggest sea surface temperature is a primary driver of jellyfish presence, there may be other missing important variables.

Density driven currents, frontal systems and other factors affecting movement and mixing were not considered here, but have been suggested as important predictors for jellyfish presence and distribution (Hay et al. 1990; Doyle et al. 2007). Other environmental factors, such as salinity have been shown to be significant drivers in medusae (not specifically *C. capillata*) occurrence (Decker et al. 2007; Aleksa 2017). Lower salinity ranges were originally thought to inhibit strobilation of *C. capillata*, but recent research has shown that strobilation can occur at lower salinity than previously though (Holst and Jarms 2007; Holst 2012). Including salinity in future modelling could reveal insight into the effects of salinity on the medusae stage of *C. capillata*.

2.4.3 Ground fish survey bycatch data analysis

While DFO groundfish trawl surveys are not directly targeting jellyfish, they often catch jellyfish as bycatch. Completed every year over the same time period, they provide a consistent view of jellyfish occurrence in different regions across Atlantic Canadian waters. This provided an opportunity to develop baseline knowledge on spatial jellyfish distributions in an area that has no dedicated jellyfish surveys. The ground fish surveys occur in 3 different regions: Scotian Shelf (including the Bay of Fundy), southern Gulf of St. Lawrence, and northern Gulf of St. Lawrence. Each of these surveys occur at slightly different times, as they often use the same research vessel and trawl gear. Scotian Shelf surveys take place in July, and the surveys on the Gulf of St. Lawrence occur in August and September. All surveys have similar objectives and regional protocols, however constraints such as different timing need to be considered when conducting analysis of combined regional data-set (Chadwick et al. 2007). These biases are considered when discussing where and when jellyfish may be most prominent in the broader Atlantic Canadian zone.

The hotspot analysis highlighted areas within the eastern Gulf of St. Lawrence, and in particular, the areas east and north of the Magdalen Islands as hotspots of jellyfish bycatch in the DFO ground fish surveys (Figure 2.17). These spatial findings are generally consistent with the citizen science spatial distribution results, which had highest *C. capillata* abundance and catch per unit effort along the Northumberland Strait and Gulf of St. Lawrence coast. The Gulf of St. Lawrence is described as a highly productive marine ecosystems with areas of upwelling (Gilbert and Dufour 2008; Devine et al. 2017), thanks in part to warm Atlantic waters entering via the Cabot Strait, cold Labrador Current water entering through the Belle Isle Strait, and freshwater input from the St. Lawrence River (Figure 1.2) (Dunbar et al. 1980). Jellyfish are often associated with areas of upwelling and other oceanographic features (Benson et al. 2007). There are high abundances of phytoplankton (diatoms, dinoflagellates), zooplankton (copepods), and ichthyoplankton that vary seasonally and spatially throughout the Gulf (Dufour and Ouellet 2007). These are all known food sources of scyphozoan jellyfish such as *C. capillata* and *A. aurita* (Dufour and Ouellet 2007). Jellyfish hotspots identified in the Gulf of St. Lawrence are supported by prey availability, along with previous literature that suggests jellyfish contribute to a large fraction of zooplankton biomass in the Gulf of St. Lawrence (de Lafonatine et al. 1991; Locke 2002).

Figure 2.17 revealed a spatial shift in jellyfish hotspots through time. From 2006 to 2009 hotspots of jellyfish occurrence surrounded the Magdalen Islands. For the time period 2010 to 2013, hotspots extended north to the western coast of Newfoundland.

From 2014 to 2017, jellyfish occurrence hotspots covered almost the entire northern Gulf of St. Lawrence, and extended further into the Cabot Strait. Recent years, including 2014, 2015 and 2016, have seen warmer than usual water temperatures in the Maritimes Region (Galbraith et al. 2016; Hebert et al. 2016; Hebert et al. 2018). Environmental changes, such as increases in water temperature, can alter phytoplankton and zooplankton community structure (Li and Harrison 2008; Johnson et al. 2016), therefore altering jellyfish populations that depend on them (Lynam et al. 2004). Cold water jellyfish, such as *C. capillata,* may also be negatively impacted by warming waters (Holst 2012; Goldstein et al. 2017)). The northern Gulf of St. Lawrence has cooler sea surface temperatures than the Magdalen Shallows in the summer months (Galbraith et al. 2016), and may provide temperature ranges where *C. capillata* are more successful. While often predictable at oceanographic scales in space and time (Heaslip et al. 2012), spatial and temporal variations of jellyfish patches can vary at smaller scales, such as a within the Gulf of St. Lawrence. Jellyfish populations are known to be ephemeral in space and time, and can vary year to year depending on local environmental parameters.

The temporal patterns from the citizen science network differ slightly from the DFO groundfish survey bycatch hotspot analysis. High abundances of *C. capillata* were reported in July, and more specifically towards the end of July with the citizen science network. Even though the groundfish surveys on the Scotian Shelf take place throughout July, jellyfish occurrence hotspots were not detected. Instead, hotspots were detected throughout the Gulf of St. Lawrence, where surveys occurred in August and September. The citizen science network results indicate a decrease of jellyfish sightings in August and a disappearance of them in September. These results suggest stranded coastal jellyfish may not represent jellyfish in adjacent waters (Fleming et al. 2013; Ionescu et al. 2016). It is possible that jellyfish (such as *C. capillata*) are persisting in the water column longer than what would be seen washing up on beaches (Ionescu et al. 2016). In Norway, *C. capillata* occurrence peaks in June, but persist in the water column through November and early December (Hosia et al. 2014).

Net tows often inflict damage to jellyfish (Brierley et al. 2005; Colombo et al. 2009; Graham et al. 2010), making it hard or impossible to identify to species. In the case of the groundfish surveys, there were large quantities of other groups of organisms (fish, crustaceans, etc.) present in the trawls, and thereby decrease the structural integrity of a jellyfish, possibly rendering them un-identifiable to species. Inconsistencies in detail identifying jellyfish was a limitation of this dataset. Each region approaches recording jellyfish differently, and there appears to be more emphasis placed on identifying jellyfish down to species level in the Gulf of St. Lawrence regions. Not only did they begin recording jellyfish earlier than the Scotian Shelf (Scotian Shelf began recording jellyfish in 2006 versus 1985 in the Gulf of St. Lawrence), but they also have a higher diversity of species recorded. In the Scotian Shelf dataset, 97.6% of jellyfish were identified simply as 'scyphozoa'. The other 2.4% was made up of *C. capillata* and *Pelagia noctiluca*. In the northern Gulf of St. Lawrence dataset, 43.5% of jellyfish were identified as 'scyphozoa', and the remaining 56.5% were identified down to species (26.1% *C. capillata*, 19.7% *Periphylla periphylla*, 8.9% *A. aurita*, 1.8% *Atolla wyvillei*). Interestingly, there were species identified in the DFO groundfish surveys that were not observed in the citizen science surveys. *P. noctiluca* is a scyphozoan jellyfish species that was identified on the Scotian Shelf. It is described as an offshore species, but has been noted in stranding studies in other areas (Doyle et al. 2008; Fleming et al. 2013). *P. periphylla* and *A. wyvillei* were both identified in northern Gulf of St. Lawrence groundfish surveys. They are both deep water jellyfish species (Youngbluth and Bämstedt 2001; Herring and Widder 2004).

2.5 Conclusion

Knowledge on patterns of jellyfish occurrence and spatio-temporal patters in Atlantic Canadian waters is limited (Heaslip et al. 2012; Hamelin et al. 2014; Wallace et al. 2014). This chapter exemplified how citizen science can help track the seasonal and spatial distribution of jellyfish. It provided important insights on the basic phenology of large jellyfish in Atlantic Canada, which had not been documented previously. The results of two avenues of citizen science (weekly beach surveys and opportunistic sightings) corroborated each other, showing similar patterns in species composition, and seasonality. The most common species reported through citizen science efforts, was overwhelming *C. capillata.* Strandings of jellyfish (both *C. capillata* and *A. aurita*) occurred most frequently in the month of July. These findings are consistent with other stranding surveys from other parts of the Atlantic (notably the Irish and Celtic Seas) (Doyle et al 2007; Pikesley et al. 2014). It is possible that these temporal patterns are driven by ocean temperature (Holst 2012). Jellyfish occurrence 'hotspots' in Atlantic Canadian waters were found within the Gulf of St. Lawrence, using DFO bycatch data. These results were supported by the spatial patterns determined from the citizen science jellyfish stranding surveys. While each of the methods used in this Chapter have their biases and caveats, results from this Chapter reveal that using multiple sources of data can help determine baseline information of jellyfish in Atlantic Canadian waters.

Chapter 3 - Seasonal overlap of jellyfish and leatherback turtles in Atlantic Canada

3.1 Introduction

Determining the relationship between a field of prey species and their predator is an important challenge in ecosystem ecology (Bedford et al. 2015). Identifying the seasonal usage of different foraging habitat adds a spatial and temporal dimension to this line of inquiry (Heaslip et al. 2012). From an applied perspective, understanding the seasonal characteristics of foraging habitat can play a critical role in developing conservation and management measures for threatened species, such as time-area closures of critical habitat designations (Heaslip et al. 2012; Graham et al. 2010).

Leatherback sea turtles undertake seasonal south-north migrations from tropical nesting beaches, to productive seasonal temperate foraging grounds. These long distance migrations are believed to be driven by prey availability (James et al. 2006; Houghton et al. 2007). It has been estimated that adult leatherback turtles can consume 330kg of jellyfish per day while foraging in Atlantic Canadian waters (Heaslip et al. 2012). Leatherbacks in eastern Canada weigh 33% more than nesting turtles with the same carapace length (Eckert et al. 1989; James et al. 2005a), illustrating the importance of summer foraging grounds for building energy reserves (Heaslip et al. 2012). The spatio-temporal connection between predator foraging and prey-field dynamics in Atlantic Canada has not been well studied (Graham et al. 2003). While several studies elude to the fact that leatherback timing is driven by the prey field (James et al. 2006; Heaslip et al. 2012; Gregr et al. 2015), none of them have characterized predator-prey overlap. Understanding the association of predator and prey, especially for species at risk, and how their timing impacts one another is critical to developing appropriate management measures (space and time specific). In this Chapter, spatiotemporal data on jellyfish occurrence (see Chapter 2) is used to predict leatherback habitat use in Atlantic Canada.

The most recent SARA assessment of the Atlantic Canadian leatherback sea turtle population has not yet designated critical habitat (COSEWIC 2012), however, areas of important habitat have been identified in a recent zonal advisory process (DFO 2011). Based on satellite telemetry data of 70 leatherback sea turtle, three regions in Atlantic Canadian waters were described as important habitat: (1) the waters east and southeast of Georges Bank, including the Northeast Channel near the southwestern boundary of the Canadian Exclusive Economic Zone; (2) the southeastern Gulf of St. Lawrence and waters off eastern Cape Breton Island, including Sydney Bight, the Cabot Strait, portions of the Magdalen Shallows and adjacent portions of the Laurentian Channel; and (3) the waters south and east of the Burin Peninsula, Newfoundland, including parts of Placentia Bay (DFO 2011). While these areas are hypothesized to provide foraging opportunities for observed leatherbacks (DFO 2011), this hypothesis has not been tested directly using temporal and regional prey data.

3.1.2 Goals and objectives of Chapter 3

It has been hypothesized that the spatial and temporal distribution of jellyfish may influence the seasonal residency of leatherback sea turtle occurrence in Atlantic Canadian waters (James et al. 2005b; Houghton et al. 2007). This Chapter will address this hypothesis by using data from Chapter 2 (citizen science network data, Fisheries and Oceans ground fish survey bycatch data) to determine to which degree to jellyfish and leatherback seasonality overlap. Furthermore, consistency between seasonal peak abundances of jellyfish and leatherback turtles across data sources will be examined. Finally, cross-correlation analysis will be used to determine whether jellyfish sightings can predict leatherback turtle presence in the study area at various time lags.

3.2 Methods

3.2.1 Overlay analysis

To determine whether leatherback occurrence is driven by jellyfish seasonality, the jellyfish data from Chapter 2 was compared to two leatherback data sources. The jellyfish data sources used in this Chapter were all discussed in Chapter 2. They were either designed or collected with the purpose of this thesis (Dalhousie citizen science network data, opportunistic email data), or they were shared to support this project (DFO groundfish survey data, CSTN citizen science data). Corresponding data collection methods are detailed in Chapter 2.

The leatherback turtle data sources included residency time of satellite tagged leatherbacks binned into three oceanographically distinct regions: Bay of Fundy, Scotian Shelf, and the Gulf of St. Lawrence between 2004 and 2017 (data provided by Dr. M. James, Fisheries and Oceans Canada). Residency time in days was calculated from entry and exit dates provided for leatherbacks in each region. These turtles were all return tags, meaning they had been tagged the year before, either in Atlantic Canadian waters, or on their nesting beach, and had returned the following foraging season

As a second data source, opportunistic sightings of leatherback turtles from citizen scientists made between year 2007 to 2017 (n = 338) were provided by the Canadian Sea Turtle Network. These sightings were submitted to the CSTN by the public. All sightings were of free-swimming turtles (no stranded or entangled turtles included), and included associated latitude and longitude, date observed, and any specific notes related to the observation.

The six data sources (two leatherback data sources: satellite residency, and opportunistic sightings from the CSTN; four jellyfish data sources: DFO ground fish survey by catch, Dalhousie citizen science network, CSTN citizen science network, and general opportunistic sightings submitted through email) were expressed as proportional occurrence and binned into weekly intervals for the two main regions of interest: the Scotian Shelf, and the Gulf of St. Lawrence. The Bay of Fundy was not included as there were zero satellite tagged turtles in that region, and very few jellyfish reported there. Proportional occurrences were derived by assigning each observation to its corresponding week, and then dividing that number by the total number of occurrences. Zeros were included when there was observation effort, but no leatherbacks or jellyfish were recorded. Weeks without observer effort were recorded as missing values. Total sample size (*n*) represented the number of observations made throughout the year (either present or absent). Missing data and values are represented throughout these datasets. For example, the Dalhousie run citizen science network, surveys were only completed for 26 weeks out of the year (in 2016 and 2017), leaving 26 missing values.

The peak of highest jellyfish occurrence for each data source was then compared against each leatherback data source (satellite residency and CSTN general opportunistic sightings), in each region (Scotian Shelf and Gulf of St. Lawrence).

3.2.2 Cross-correlation function (lag)

The six data sources (two leatherback and four jellyfish) were analysed as six separate time series. Cross-correlation was used to address whether there were significant correlations at a variety of time lags between each leatherback and jellyfish source, in each region (two leatherback time series, four jellyfish time series, two region, resulting in 16 different cross-correlations). Time-series must be stationary before a cross-correlation can be applied, that is a time-series must show constant mean and equal variance over time (Cryer and Chan 2008; Groger and Fogarty 2011; Probst et al. 2012). All cross-correlation analysis was completed in R 3.4.2 (cross-correlation function (ccf)).

Of the six data sources, only the satellite residency times of leatherbacks had effort throughout the duration of the year. The other five sources had missing values, which were excluded from analysis. Cross-correlation analysis returns the correlation associated with each lag interval (in this case, for each week).

3.3 Results

3.3.1 Overlay analysis

In total, there were 19 individual entry/exit records for 11 leatherback sea turtles between 2004 and 2017– zero in the Bay of Fundy, 14 on the Scotian Shelf, and five in the Gulf of St. Lawrence. The average time spent on the Scotian Shelf was 24 days (± 27 days), and the mean time spent in the Gulf of St. Lawrence was 48 days (± 11 days) (Table 3.1).

Table 3.1 – Details of leatherback residency on the Scotian Shelf and Gulf of St. Lawrence, from satellite tagged turtles.

Scotian Shelf				**Gulf of St. Lawrence**			
Year	**Enter date**	**Exit date**	**Residency (d)**	**Year**	**Enter date**	**Exit date**	**Residency (d)**
2004	Oct. 18	Oct. 28	10	2004	Aug. 12	Oct. 18	67
2004	Jun. 21	Sep. 27	98	2010	Aug. 15	Sep. 23	39
2004	Aug. 2	Sep. 9	38	2016	Aug. 15	Oct. 6	52
2010	Jun. 17	Aug.15	59	2017	Aug. 10	Sep. 15	36
2010	Aug. 29	Oct. 19	51	2017	Aug. 14	Oct. 1	48
2016	Aug. 7	Aug. 15	8			**Mean:**	**48.40**
2016	Oct. 6	Oct. 16	10			**St. Dev:**	**10.97**
2015	Sep. 20	Sep. 22	2				
2015	Oct. 5	Oct. 9	4				
2017	Aug. 2	Aug. 9	7				
2017	Sep. 21	Oct. 1	10				
2017	Jul. 30	Aug. 14	15				
2017	Aug. 12	Aug. 21	9				
2017	Oct. 24	Nov. 2	9				
		Mean:	**23.57**				
		St. Dev:	**26.95**				

Opportunistic leatherback turtle observations were analysed separately for three oceanographically distinct regions – Bay of Fundy, Scotian Shelf, and the Gulf of St. Lawrence (Figure 3.1). While there were eight leatherback turtle observations in the Bay of Fundy, they were very close to the boundary with the Scotian Shelf (Figure 3.1). There were no turtle observations further inside the Bay of Fundy. Leatherbacks were observed most frequently along the Scotian Shelf in July (46% observations) and August (46%

observations) (Table 3.2). Spatially, most of the leatherback observations in August were very close to the Scotian Shelf/Gulf of St. Lawrence boundary (Figure 3.1). Observations in the Gulf of St. Lawrence were most frequent in August (41.7%) and September (27.8%) (Table 3.2).

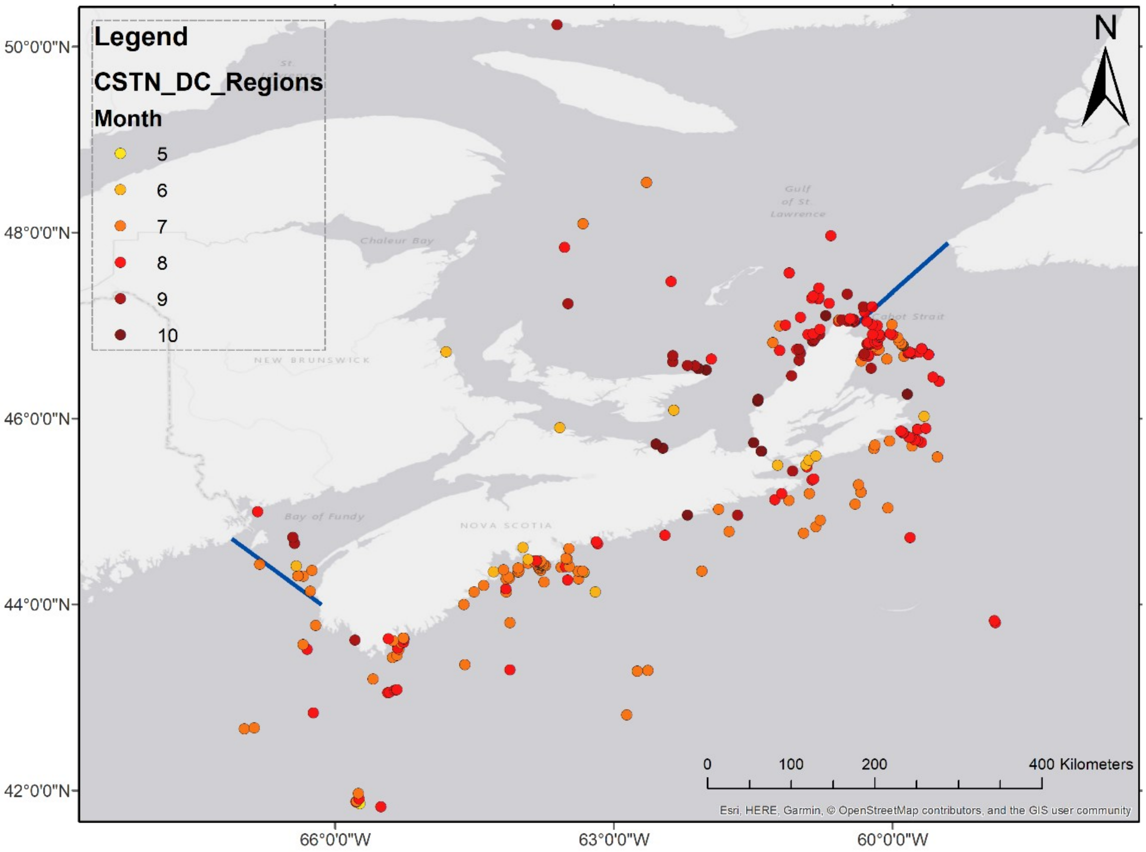

Figure 3.1 – Opportunistic leatherback turtle sightings (provided by the Canadian Sea Turtle Network) from 2006 to 2017. In the legend, the numerical value is the month of the year (5 = May, 6 = June, 7 = July, 8 = August, 9 = September, 10 = October)

Peak proportions of observations in weekly intervals are shown for all data sources and all years in Figure 3.2. Peak timing of leatherback satellite residency occurs earlier on the Scotian Shelf than on the Gulf of St. Lawrence (Figure 3.2A). This pattern is repeated for opportunistic sightings of leatherback turtles (Figure 3.2B), jellyfish as bycatch in the DFO groundfish surveys (Figure 3.2C), and the CSTN citizen science jellyfish observations (Figure 3.2D). This pattern is reversed for the Dalhousie run citizen science jellyfish observations (Figure 3.2E), and opportunistic jellyfish sightings (Figure 3.2F), with observations peaking in the Gulf of St. Lawrence before the Scotian Shelf.

Table 3.2 - Temporal summary of CSTN opportunistic leatherback sea turtle sightings for each region.

Month:	**Bay of Fundy**		**Scotian Shelf**		**Gulf of St. Lawrence**	
May	-	-	1	0.4%	-	-
June	1	10.0%	10	3.9%	4	5.6%
July	6	60.0%	118	46.1%	8	11.1%
August	1	10.0%	118	46.1%	30	41.7%
September	2	20.0%	7	2.7%	20	27.8%
October	-	-	2	0.8%	10	13.9%
Total:	10		256		72	

Year:	**Bay of Fundy**		**Scotian Shelf**		**Gulf of St. Lawrence**	
2007	-	-	17	6.6%	7	9.7%
2008	-	-	14	5.5%	12	16.7%
2009	-	-	40	15.6%	5	6.9%
2010	-	-	4	1.6%	2	2.8%
2011	2	20.0%	8	3.1%	1	1.4%
2012	3	30.0%	26	10.2%	5	6.9%
2013	-	-	20	7.8%	8	11.1%
2014	1	10.0%	17	6.6%	1	1.4%
2015	4	40.0%	27	10.5%	-	-
2016	-	-	49	19.1%	12	16.7%
2017	-	-	34	13.3%	19	26.4%
Total:	10		256		72	

Peak proportion of observations in weekly intervals for 2016 and 2017 was also comparatively analyzed (Figure 3.3). There are similar patterns in each panel of Figure

3.3 as there are in Figure 3.2. Sightings peaked earlier on the Scotian Shelf for leatherback residency as detected by satellite-tagged turtles, opportunistic leatherback sightings, and DFO jellyfish bycatch records (Figure 3.3A, B, and C). There were no observations from the CSTN citizen science network, as that program was only active from 2007 to 2010 (Figure 3.3D). The seasonal jellyfish peaks for the Dalhousie run programs (Figure 3.3E, F), occurred earlier in the Gulf of St. Lawrence than on the Scotian Shelf.

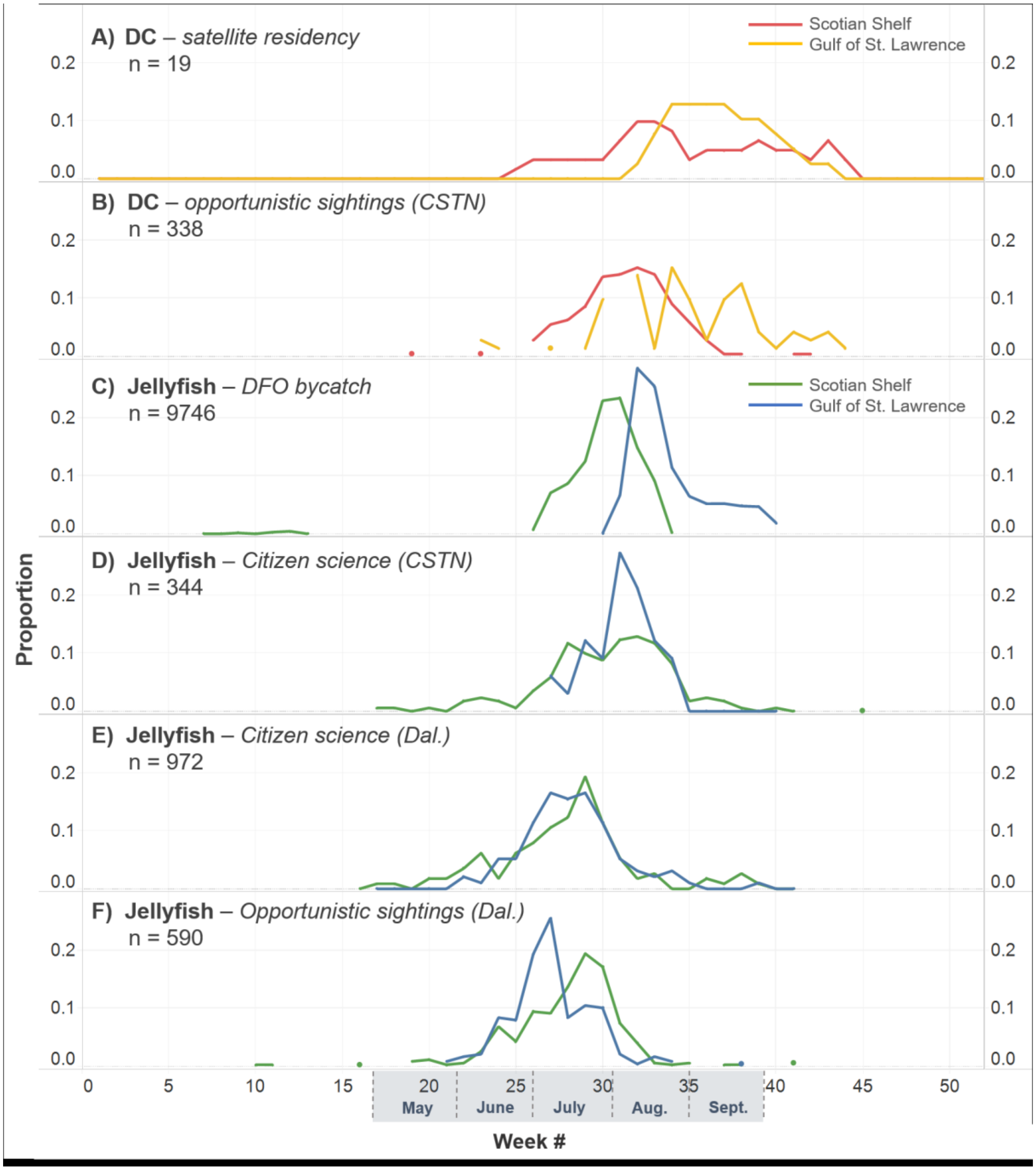

Figure 3.2 - Leatherback turtle (DC) and jellyfish data sources for all available years. Proportion of leatherback turtles (panel A) and B)) and jellyfish (panel C), D), E), and F)) observed in weekly intervals. Effort (n) includes zeros. A) DC – satellite residency: leatherback residency time in the region (Scotian Shelf or Gulf of St. Lawrence), between 2004 and 2017. B) DC – opportunistic sightings (CSTN): leatherback sightings reported to the Canadian Sea Turtle Network (CSTN) between 2007 and 2017). C) Jellyfish – DFO bycatch: jellyfish presence/absence reported in Fisheries and Oceans ground fish surveys, between 2006 – 2017. D) Jellyfish – citizen science (CSTN): jellyfish presence/absence reported in weekly beach monitoring program, run by CSTN from 2007 to 2010. E) Jellyfish – citizen science (Dal.): jellyfish presence/absence reported in weekly beach monitoring program, run by Dalhousie University in 2016 and 2017. F) Jellyfish – Opportunistic sightings (Dal.): jellyfish sightings reported via jellyfish@dal.ca by general public in 2016 and 2017.

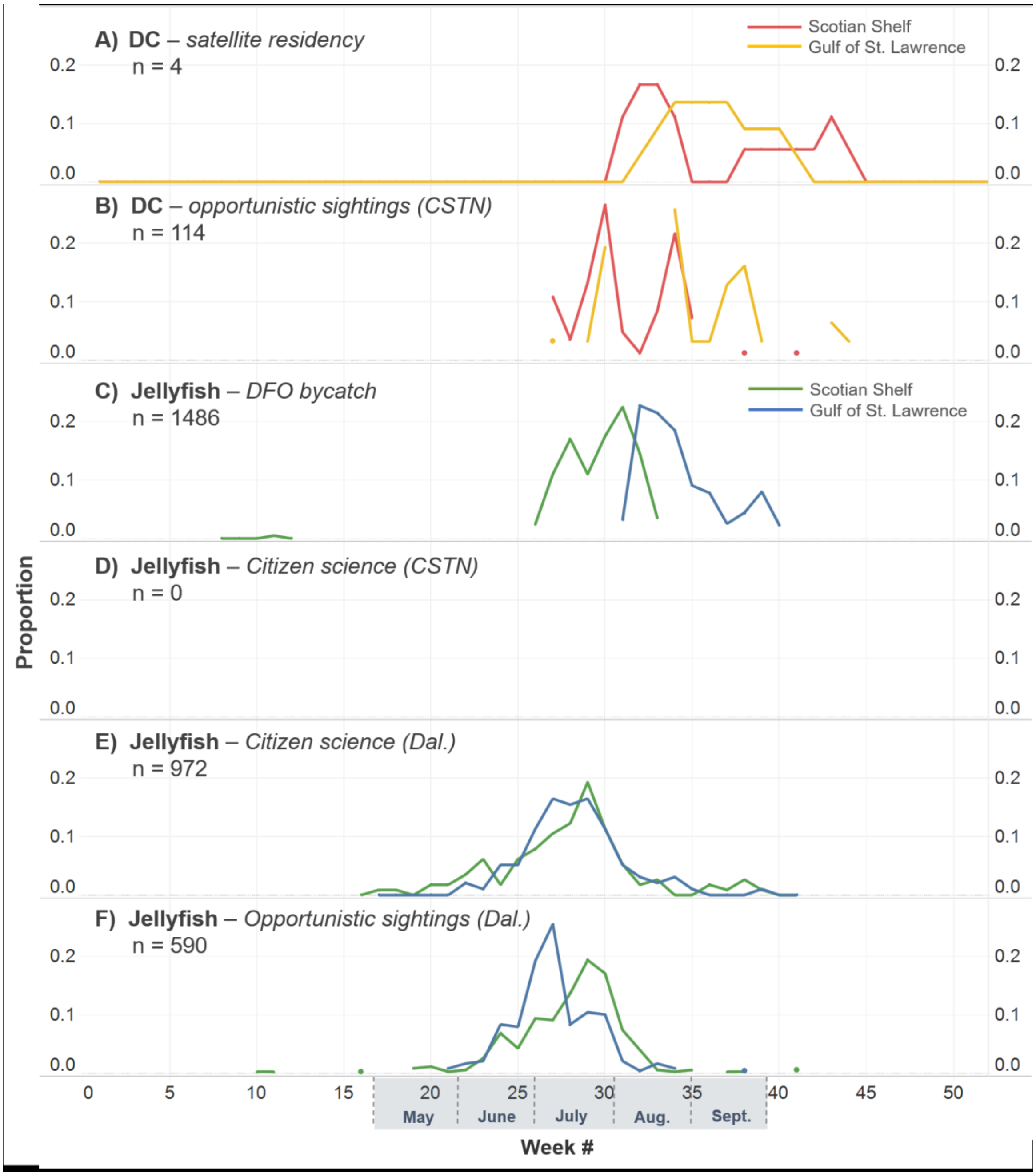

Figure 3.3 - Leatherback turtle (DC) and jellyfish data sources for 2016 and 2017 only. Proportion of leatherback turtles (panel A) and B)) and jellyfish (panel C), D), E), and F)) observed in weekly intervals. Effort (n) includes zeros. A) DC – satellite residency: leatherback residency time in the region (Scotian Shelf or Gulf of St. Lawrence). B) DC – opportunistic sightings (CSTN): leatherback sightings reported to the Canadian Sea Turtle Network (CSTN). C) Jellyfish – DFO bycatch: jellyfish presence/absence reported in Fisheries and Oceans ground fish surveys. D) Jellyfish – citizen science (CSTN): program did not run in 2016 and 2017. E) Jellyfish – citizen science (Dal.): jellyfish presence/absence reported in weekly beach monitoring program, run by Dalhousie University. F) Jellyfish – Opportunistic sightings (Dal.): jellyfish sightings reported via jellyfish@dal.ca by general public.

Table 3.3 - Data sources (from Figure 3.3) and weeks with highest proportion and numbers of observed leatherback (DC) and jellyfish respectively.

Data Source (from Figure 3.3)		Week with proportion of observation (top 3 weeks)			Total % in top 3 weeks
		1	2	3	
A.1) DC – satellite residency – SS	Week #	32	33	34	27.9%
	Proportion	0.098	0.098	0.082	
	Observations	6	6	5	
A.2) DC – satellite residency - GSL	Week #	34	35	36	51.3%
	Proportion	0.128	0.128	0.128	
	Observations	5	5	5	
B.1) DC - Opport. Sightings (CSTN) – SS	Week #	32	33	31	43.4%
	Proportion	0.152	0.141	0.141	
	Observations	39	36	36	
B.2) DC - Opport. Sightings (CSTN) – GSL	Week #	34	32	38	41.7%
	Proportion	0.153	0.139	0.125	
	Observations	11	10	9	
C.1) Jellyfish – DFO bycatch – SS	Week #	31	30	32	61.0%
	Proportion	0.233	0.229	0.148	
	Observations	159	156	101	
C.2) Jellyfish – DFO bycatch – GSL	Week #	32	33	34	65.2%
	Proportion	0.285	0.253	0.114	
	Observations	1024	912	409	
D.1) Jellyfish – Cit. Sci. (CSTN) – SS	Week #	32	31	33	48.5%
	Proportion	0.129	0.123	0.117	
	Observations	22	21	20	
D.2) Jellyfish – Cit. Sci. (CSTN) – GSL	Week #	31	32	33	72.7%
	Proportion	0.273	0.212	0.121	
	Observations	9	7	4	
E.1) Jellyfish - Cit. Sci. (Dal.) – SS	Week #	29	28	30	43.0%
	Proportion	0.193	0.123	0.114	
	Observations	22	14	13	
E.2) Jellyfish - Cit. Sci. (Dal.) - GSL	Week #	27	29	28	48.5%
	Proportion	0.165	0.165	0.155	
	Observations	16	16	15	
F.1) Jellyfish – Opport. Sightings (Dal.) – SS	Week #	29	30	28	50.1%
	Proportion	0.194	0.171	0.137	
	Observations	68	60	48	
F.2) Jellyfish – Opport. Sightings (Dal.) – GSL	Week #	27	26	29	65.7%
	Proportion	0.255	0.192	0.105	
	Observations	61	46	25	

3.3.2 Cross-correlation function

Cross-correlation analyses were completed for both sources of leatherback data with each of the four jellyfish sources, for both the Scotian Shelf and the Gulf of St. Lawrence to test whether jellyfish presence can predict seasonal leatherback sightings or vice versa.

Cross correlations of leatherback residency with each of the four jellyfish sources on the Scotian Shelf are illustrated in Figure 3.4. Leatherback residency and DFO jellyfish bycatch were significantly correlated from week -3 to 0; with the highest correlation at week -2 (ACF = 8.59), indicating a two to three week lag behind the DFO jellyfish bycatch (Figure 3.4A). Leatherback residency and the Dalhousie citizen science jellyfish observations had significant correlations from week -6 to -3; with the highest correlation at -4 weeks (ACF = 0.625), indicating a lag of leatherback behind the Dalhousie citizen science jellyfish observations (Figure 3.4B). Leatherback residency and CSTN citizen science jellyfish observations had significant correlations from week -5 to 0; with the greatest correlation at week -1 (ACF = 0.624) (Figure 3.4C). And finally, leatherback residency and opportunistic jellyfish email reports had significant correlations from week -6 to -2; with the greatest correlation at -4 weeks (ACF = 0.724), indicating a lag of leatherback presence behind the jellyfish email reports (Figure 3.4D). Across these data sources, the average lag of leatherback presence behind jellyfish is -2 weeks, indicating peak leatherback turtle presence may lag behind jellyfish presence on the Scotian Shelf by 2 weeks, on average.

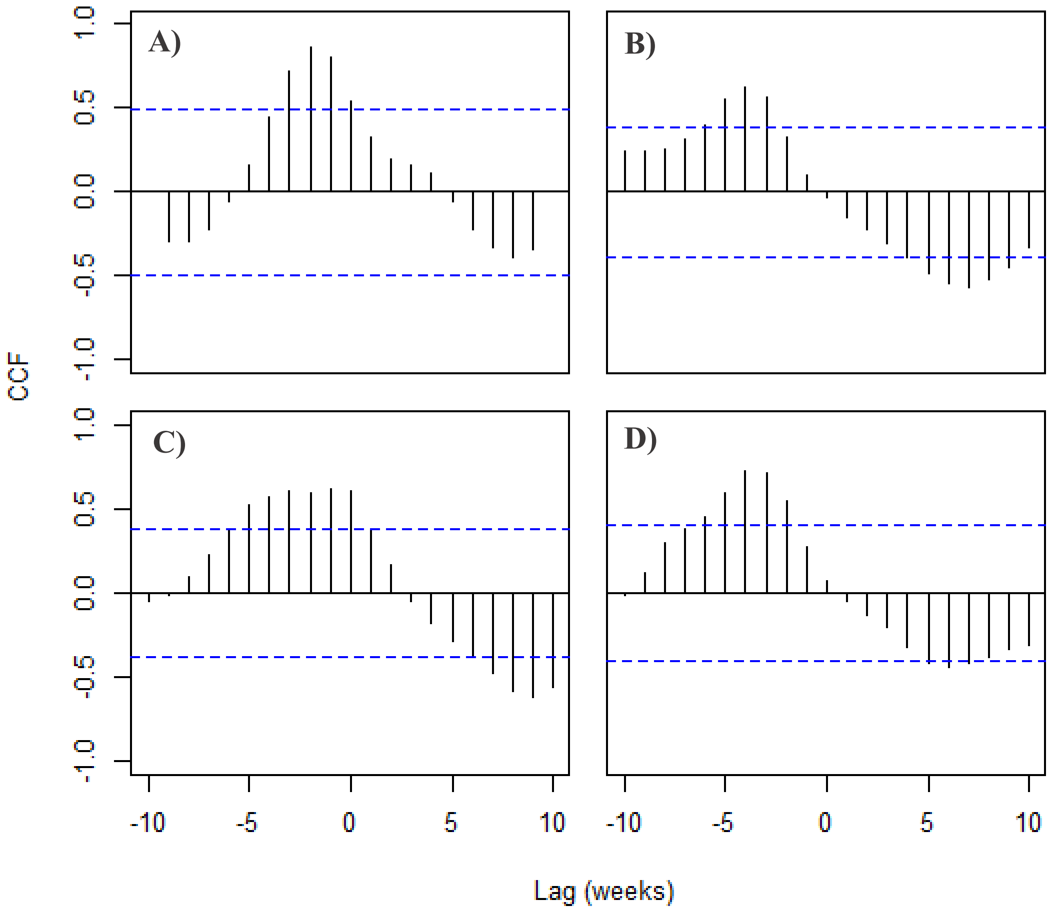

Figure 3.4 - Cross correlation function for leatherback residency and Scotian Shelf jellyfish sources for all years. A) DFO gfs jellyfish bycatch; B) Dalhousie citizen science jellyfish network; C) CSTN citizen science jellyfish network; D) opportunistic email jellyfish sightings.

In contrast to the cross correlation results of leatherback residency with the jellyfish sources on the Scotian Shelf, the Gulf of St. Lawrence showed no clear pattern of cross correlation, with lags ranging from -10 to 3 (see Figure 3.5).

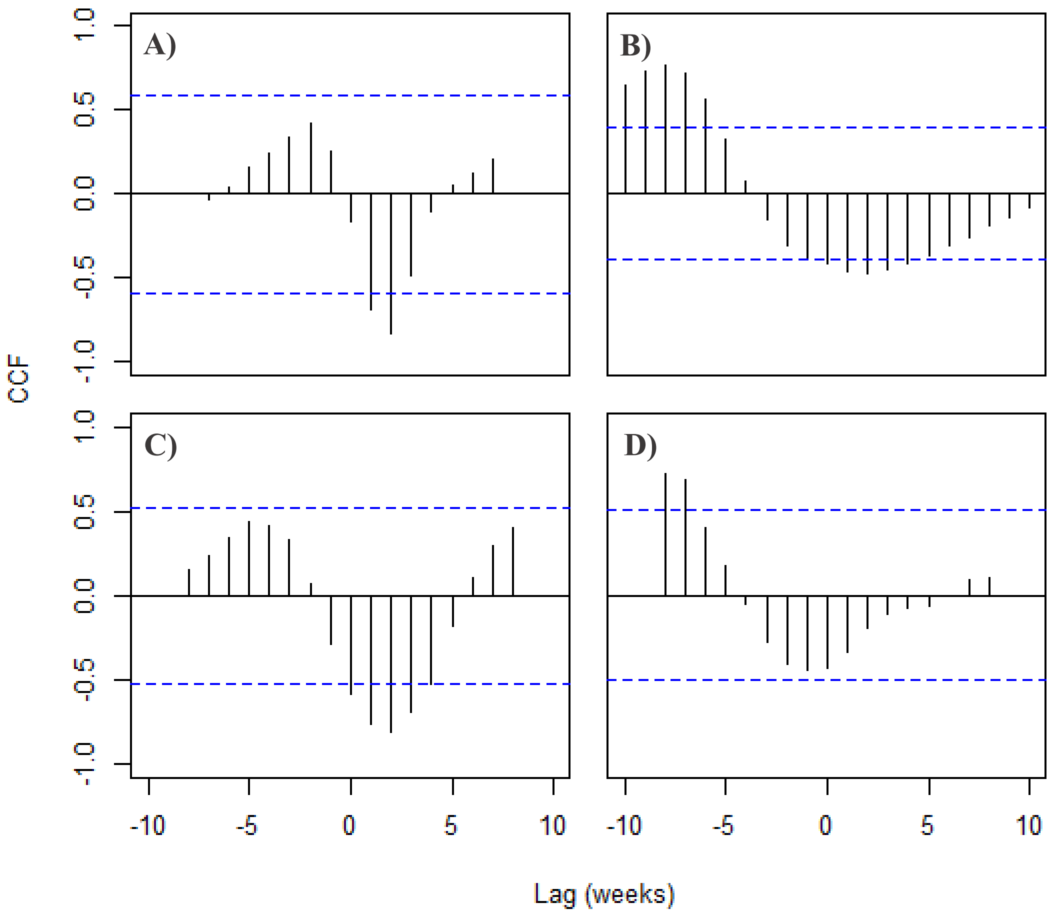

Figure 3.5 - Cross correlation function for leatherback residency and Gulf of St. Lawrence jellyfish sources for all years. A) DFO gfs jellyfish bycatch; B) Dalhousie citizen science jellyfish network; C) CSTN citizen science jellyfish network; D) opportunistic email jellyfish sightings.

Figure 3.6 illustrates the cross correlations of CSTN leatherback observations with each of the four jellyfish sources on the Scotian Shelf. Leatherback observations and DFO jellyfish bycatch had significant correlations from week -1 to 0; with the highest correlation at week 0 (ACF = 0.715), indicating no lag between the two (Figure 3.6A). Leatherback observations and the Dalhousie citizen science jellyfish observations had significant correlations from week -4 to -1; with the highest correlation at -3 weeks (ACF = 0.781), indicating a lag of leatherback observations behind the Dalhousie citizen science jellyfish observations (Figure 3.6B). Leatherback observations and CSTN citizen science jellyfish observations had significant correlations from week -2 to 1; with the greatest correlation at week 0 (ACF =0.897), indicating no lag between the two (Figure 3.6C). And finally, leatherback residency and opportunistic jellyfish email reports had significant correlations from week -4 to -1; with the greatest correlation at -3 weeks (ACF = 0.768), indicating a lag of leatherback behind the jellyfish email reports (Figure 3.6D). The average lag of leatherback presence behind jellyfish is -1.5 weeks, indicating peak leatherback turtle presence may lag behind jellyfish presence on the Scotian Shelf by 1.5 weeks.

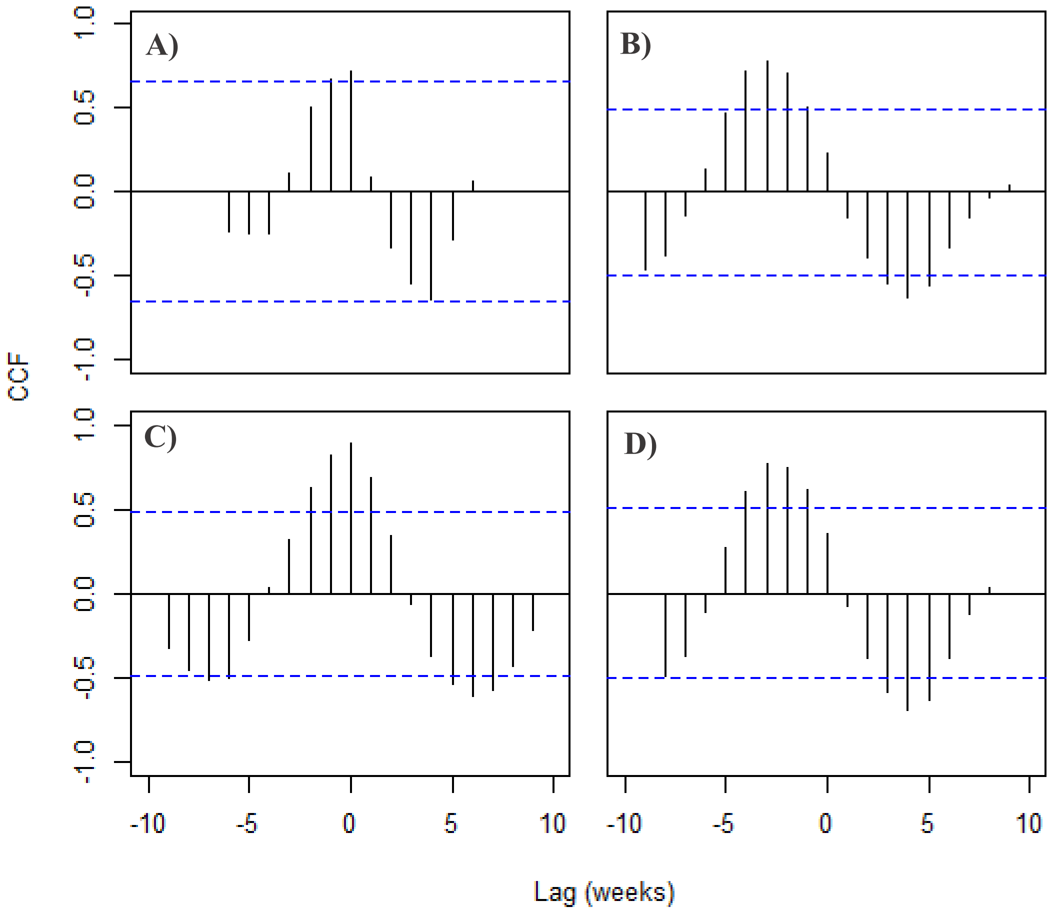

Figure 3.6 - Cross correlation function for CSTN leatherback sightings and Scotian Shelf jellyfish sources for all years. A) DFO gfs jellyfish bycatch; B) Dalhousie citizen science jellyfish network; C) CSTN citizen science jellyfish network; D) opportunistic email jellyfish sightings.

Cross correlations of CSTN leatherback observations with each of the four jellyfish sources in the Gulf of St. Lawrence is illustrated in Figure 3.7. Similarly to the cross correlation of leatherback residency with the jellyfish sources on the Gulf of St. Lawrence, the CSTN leatherback observations and jellyfish sources showed no clear pattern of cross correlation, and no statistically significant correlations (Figure 3.7).

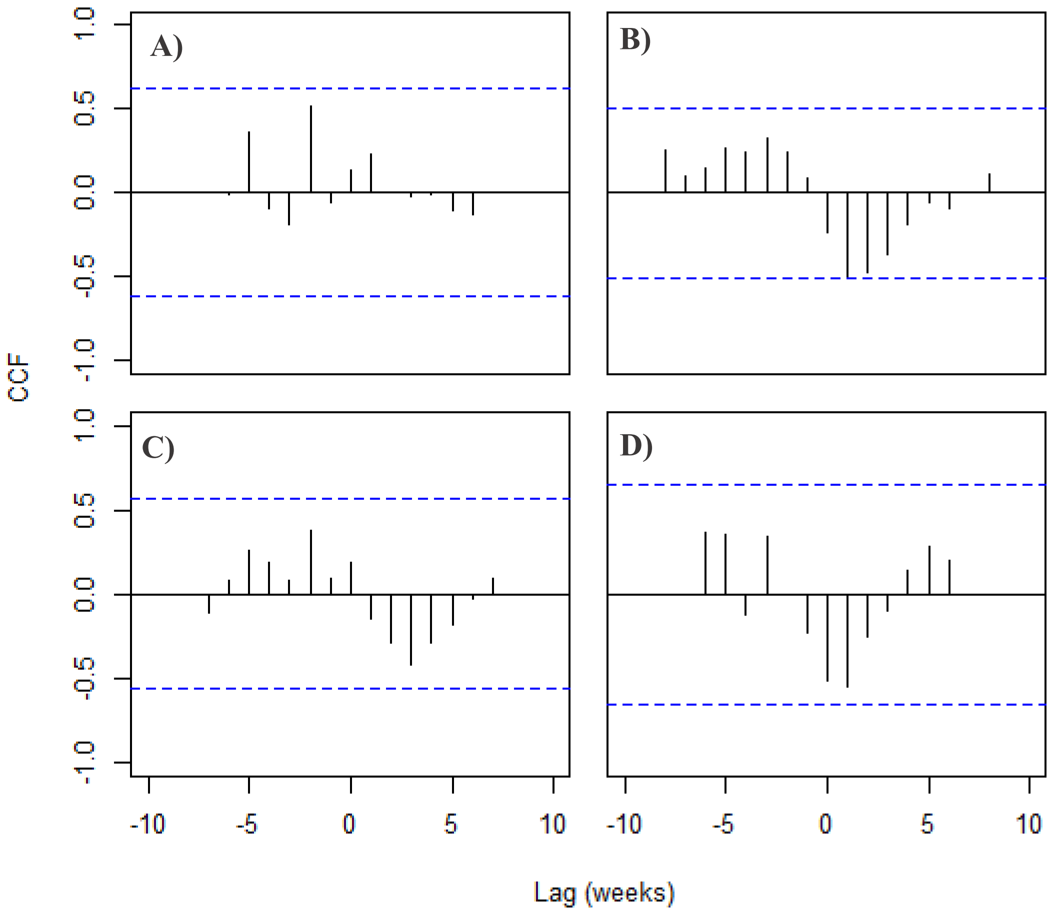

Figure 3.7 - Cross correlation function for CSTN leatherback sightings and Gulf of St. Lawrence jellyfish sources for all years. A) DFO gfs jellyfish bycatch; B) Dalhousie citizen science jellyfish network; C) CSTN citizen science jellyfish network; D) opportunistic email jellyfish sightings.

3.4 Discussion

The primary objective of this chapter was to determine to which degree to jellyfish seasonality and leatherback seasonality overlap. This was assessed by comparing seasonal peak abundances of jellyfish and leatherback data sources, and cross-correlating these data sources to determine whether jellyfish sightings can predict leatherback turtle presence at various time lags.

Leatherback presence peaked on the Scotian Shelf before the Gulf of St. Lawrence. Jellyfish data sources had conflicting temporal patterns. The DFO groundfish survey bycatch data and CSTN citizen science network peaked on the Scotian Shelf before the Gulf of St. Lawrence, however, both of the Dalhousie citizen science data sources (weekly beach surveys and opportunistic sightings) peaked on the Gulf of St. Lawrence slightly before the Scotian Shelf.

Cross-correlations revealed clear patterns on the Scotian Shelf, with leatherback turtle presence lagging jellyfish presence by approximately two weeks. There were no clear patterns of lag time observed for the Gulf of St. Lawrence region.

3.4.1 Overlay analysis

The Bay of Fundy was not included in the comparison of peak leatherback and jellyfish occurrence. There were no leatherback turtles from the satellite residency data that entered the Bay of Fundy, and those that were reported to the Canadian Sea Turtle Network were observed in close proximity to the Scotian Shelf/Bay of Fundy boundary (Figure 3.1). These findings are consistent with studies on leatherback presence in Atlantic Canadian waters, which note few volunteer sightings (James et al. 2006), no leatherback sightings during aerial surveys conducted for right whales (Brown and Tobin

1999, 2000), and no satellite tagged leatherbacks entering the Bay of Fundy (James et al. 2006). The Bay of Fundy was also not highlighted as important habitat for leatherback turtles based on relative probability of satellite tagged leatherbacks in Atlantic Canadian waters (DFO 2011). Likewise, citizen science programs revealed few jellyfish observations, and DFO groundfish survey bycatch highlighted the Bay of Fundy region as a statistically significant cold spot of jellyfish occurrence (see Chapter 2). It is probable that the Bay of Fundy is less suitable habitat for jellyfish, and therefore may not be considered important habitat for leatherback sea turtles in Atlantic Canada.

For both leatherback data sources, peak occurrence was earlier on the Scotian Shelf than the Gulf of St. Lawrence (Figure 3.2). This is consistent with what is known about leatherback migration to northwestern Atlantic waters. Leatherback turtles appear on the Scotian Shelf early summer, where they may spend several weeks before proceeding north towards Cape Breton, the Cabot Strait, Newfoundland, and the Gulf of St. Lawrence (James et al. 2006; Hamelin et al. 2014). When they reach the northern extent of their migration, leatherbacks persist typically until October, where they then begin migration southward (James et al. 2005b).

The jellyfish data sources revealed inconsistencies in peak occurrence between the Scotian Shelf and the Gulf of St. Lawrence. Two of the four data sources (DFO groundfish surveys, and CSTN citizen science) indicated peak jellyfish occurrence on the Scotian Shelf before the Gulf of St. Lawrence (Figure 3.2). The DFO groundfish surveys take place on the Scotian Shelf in July, in the Gulf of St. Lawrence in August and September. As the groundfish surveys only last approximately one month in each region, temporal patterns of jellyfish are not represented completely, and therefore other jellyfish data sources should be considered when discussing peak occurrence on the Scotian Shelf and Gulf of St. Lawrence. The CSTN citizen science network had greater coverage and survey effort along the Scotian Shelf coast than the Gulf of St. Lawrence (Chapter 2- Figure 2.3). In 2010 there were no citizen scientists surveying in the Gulf of St. Lawrence region; in 2007 and 2008 there was one citizen scientist located along the Northumberland Strait; and in 2009 there were five citizen scientists surveying along the Northumberland Strait. This mismatch in effort between the two regions could affect conclusions, indicating the Scotian Shelf has more and earlier jellyfish reports. The CTSN has experienced low participation of the general public in the Gulf of St. Lawrence region in tracking and sighting projects of leatherback turtles previously (Hamelin et al. 2017). It is unsure what contributed to these regional differences, but lower survey effort may not have accurately captured jellyfish timing in the Gulf of St. Lawrence.

The two jellyfish sources from the Dalhousie citizen science program showed peak occurrence of jellyfish on the Gulf of St. Lawrence slightly before the Scotian Shelf (Figure 3.2, Table 3.3). There was higher citizen science coverage in the Gulf of St. Lawrence region with this program, and therefore the timing patterns in the Gulf of St. Lawrence may be better represented with these two data sources than the other two jellyfish data sources. If *C. capillata* polyp beds are located within the Gulf of St. Lawrence (see Chapter 2 discussion), one could expect earlier peak occurrence there, with a slight delay of Scotian Shelf jellyfish peak occurrence.

3.4.2 Cross-correlation function (lag)

There were differences between lags and their correlation depending on the region. The Scotian Shelf cross-correlation indicated that jellyfish presence leads leatherback presence (or that there is a slight lag time of predator associated with prey). Seasonal migratory predators have been shown to occur during the peak abundance of their prey items, maximizing seasonal prey availability (Cushing 1990; Visser et al. 2011). The jellyfish sources lead the leatherback sources on the Scotian Shelf by an average of two weeks. According to these data sources, jellyfish are present earlier in the season than leatherback turtles.

It is important to note that leatherback turtles are also found beyond the Scotian Shelf slope, and outside the regional extent of this thesis (James et al. 2006; Jonsen et al. 2007), where they exhibit different foraging tactics than those observed in more coastal waters. There are cases of return-tracked leatherbacks that have migrated north from tropical waters and spent extended time in offshore waters during the spring and early summer before moving onto the Scotian Shelf (James et al. 2005b). Leatherbacks tend to dive deeper and longer in offshore waters (James et al. 2005b), indicating that jellyfish prey may occur deeper compared with coastal or shelf waters. While the pelagic medusae stage of scyphozoan jellyfish typically only survives one year in temperate waters (Lucas et al. 2012; Gregr et al. 2015), there are recorded circumstances of medusae overwintering (Ceh et al. 2015). For example, large medusae of *C. capillata* have been documented in offshore waters of the North Sea in winter months, when they would otherwise have been expected to senesce (Hay et al. 1990). While there are no documented cases of large overwintering *C. capillata* in offshore waters in the northwest

Atlantic, opportunities for sampling jellyfish off the shelf are rare, thus the size distribution and relative abundance or presence and absence of *C. capillata* in these areas is not understood. It is also possible that other jellyfish species are present in these deeper offshore waters that were not accounted for in this thesis.

Spending time in high latitude offshore waters before moving onto the Scotian Shelf may be attributed to optimal foraging theory, which predicts that large predators will consume large prey to maximize net gain of energy intake (Stephens and Krebs 1986). In marine ecosystems prey size often increases with predator size (Costa 2009), however size relationships between predator-prey can vary depending on prey dynamics and prey density (Fossette et al. 2012). Leatherback prey in Atlantic Canadian waters is often described as large species of jellyfish (James and Herman 2001; James et al. 2005b; Heaslip et al. 2012), however there have been documented cases of leatherback turtles elsewhere consuming small jellyfish (4g) in high-density aggregations (Fossette et al. 2012). Prey abundance and prey size are likely both critical aspects of optimal foraging for leatherback turtles. In fact, prey size has been found to influence leatherback energy consumption more than number of prey captured (Wallace et al. 2018). The citizen science data revealed that the *C. capillata* and *A. aurita* observed earliest in the season in coastal waters are quite small (refer to Chapter 2: Figure 2.13 and 2.14). If smaller, early season jellyfish are present in fewer numbers on the Scotian Shelf, they may not be exploited profitably by foraging turtles, resulting in a lag of leatherback presence following jellyfish presence on the Scotian Shelf.

There were no overall clear patterns of lag time observed for the Gulf of St. Lawrence region between leatherback and jellyfish occurrence. Leatherback turtles generally arrive in the Gulf of St. Lawrence after passing through the Scotian Shelf (James et al. 2006). Time spent on the Scotian Shelf most likely depends on prey encounters and prey density, influencing the arrival to the Gulf of St. Lawrence. Citizen science data revealed peak occurrence of *C. capillata* in July, while the DFO groundfish surveys revealed jellyfish are present in the water column of the Gulf of St. Lawrence through August and into September. This indicates is a relatively wide temporal window for jellyfish in the Gulf of St. Lawrence. Residency time of the satellite tagged turtles indicates they spend over twice as long in the Gulf of St. Lawrence then they do on the Scotian Shelf (Table 3.1), possibly taking advantage of persisting prey aggregations.

Spatial patterns of *C. capillata* from the citizen science data reveal higher abundance and catch per unit effort in the Gulf of St. Lawrence than on the Scotian Shelf. The optimized hot spot analysis highlighted hot spots within the Gulf of St. Lawrence, and in particular, the areas east and north of the Magdalen Islands as hotspots of jellyfish bycatch in the DFO ground fish surveys. These findings are consistent with one of the three areas of important habitat defined by DFO (DFO 2011): the southeastern Gulf of St. Lawrence, portions of the Magdalen Shallows and waters off Cape Breton Island including the Cabot Strait and Sydney Bight. Perhaps leatherbacks are using the Scotian Shelf as a movement corridor, foraging when they can, before moving into the Gulf of St. Lawrence to build up large fat reserves feeding on predictable prey aggregations.

3.5 Conclusion

This chapter was a first attempt to quantify how leatherback turtles in Atlantic Canada use and respond to the distribution and timing of their prey. While patterns were evident when visually examining peak occurrences of leatherback sources to jellyfish data sources in both the Gulf of St. Lawrence and on the Scotian Shelf, cross-correlation indicated that the Scotian Shelf had a more discernible pattern between timing of seasonal jellyfish occurrence and leatherback occurrence. On the Scotian Shelf, the difference between jellyfish occurrence and leatherback occurrence averaged two weeks. These timings are important to understand, as leatherback presence in Atlantic Canadian waters is attributed to jellyfish seasonality (James et al. 2005b; Houghton et al. 2007) – however it had not previously been addressed. This chapter corroborates the results from Chapter 2 that identify the Eastern Gulf of St. Lawrence as important jellyfish habitat, and also suggest that due to longer leatherback residency time in the Gulf of St. Lawrence, leatherbacks may use Scotian Shelf as a foraging corridor to move through to foraging grounds in or near the Gulf of St. Lawrence.

Chapter 4 - Conclusion

The main objective of this thesis was to better understand the spatio-temporal distribution, species composition, and environmental drivers of large jellyfish occurring in Atlantic Canada, and to predict how a dynamic prey field may shape leatherback turtle distribution in this important foraging area. To do this, several approaches were taken, including: collection and analysis of citizen science, groundfish survey bycatch and satellite tagging data, using generalized linear modelling, geostatistical tools, and time-series analysis. This information is deemed important to further clarify critical habitat for this endangered species in Atlantic Canadian waters.

Chapter 2 explored the phenology of jellyfish in Atlantic Canada, by combining several data sources, including: citizen science jellyfish beach surveys, opportunistic sightings of jellyfish, and Fisheries and Oceans Canada (DFO) groundfish survey by-catch data. Citizen science data provided a description of jellyfish seasonality, species composition and regional distribution patterns. The most prominent species in the citizen science program was *C. capillata,* with peak strandings in July. This is consistent with other jellyfish stranding studies that included *C. capillata* (Doyle et al. 2007; Houghton et al. 2007; Pikesley et al. 2014). Across all six years of the citizen science jellyfish monitoring project, the two most common scyphozoan species were *C. capillata* and *A. aurita*. This is consistent with the limited previous literature describing these as the primary identifiable species in studies of leatherback sea turtle foraging ecology in the Maritimes Region (James and Herman 2001; James et al. 2006). If they are the most common species on the Atlantic Canadian coast, they are likely critical to an obligate jellyfish predator. Spatial patterns from the citizen science data broadly corroborated jellyfish occurrence ‘hotspots’ from the DFO bycatch records. The Gulf of St. Lawrence region had the highest jellyfish abundance and observations per unit effort, and areas within the Gulf of St. Lawrence (the areas east and north of the Magdalen Islands) were delineated as hotspots of jellyfish occurrence from the DFO data. Sea surface temperature and survey effort were found to be significant predictors of *C. capillata* detections.

Chapter 3 considered how jellyfish distribution patterns from Chapter 2 may affect foraging leatherback sea turtles in Atlantic Canada. Jellyfish seasonality was compared to leatherback residency in Atlantic Canadian waters, and lag-correlation analysis was used to estimate the temporal correlation between high jellyfish and leatherback presence. Jellyfish occurrence on the Scotian Shelf peaked on average two weeks before leatherback turtle occurrence, while the Gulf of St. Lawrence showed no distinct cross-correlation pattern. A high match of temporal overlap of the predator and its prey if often expected (Cushing 1990; Visser et al. 2011). The lack of clear pattern on the Gulf of St. Lawrence might be attributed to the wide temporal range of jellyfish occurring there (peak seasonality in July and persisting into September). These temporal patterns, along with spatial jellyfish patterns determined in Chapter 2, support the idea that areas within the Gulf of St. Lawrence representing important habitat for leatherback turtles (DFO 2011).

The results of this thesis inform both our understanding of jellyfish phenology in Atlantic Canada, and how the spatio-temporal patterns of common jellyfish species affect the movement and distribution of leatherback turtles. These results are relevant to the discussion of critical habitat. For the first time, we have been able to determine basic aspects of jellyfish phenology in Atlantic Canada, such as approximate seasonality, spatial distribution, and environmental drivers. This project has shown that studying jellyfish at a regional scale is possible without expensive aerial surveys, or complex acoustic or camera systems. Citizen science is a promising avenue for projects such as this, with a large temporal and spatial study period (Silvertown 2009; Pikesley et al. 2014). Results from this work have provided a baseline of understanding of jellyfish in Atlantic Canada, and how they influence habitat use of a migratory predator.

4.1 Limitations

While the CSTN pilot citizen science project operated for four seasons, and the Dalhousie citizen science project operated for two seasons, they had different levels of effort, making spatial and temporal comparisons difficult. The Dalhousie citizen science project had more extensive coverage across the Maritimes region, and allowed us to determine spatio-temporal patterns of jellyfish occurrence for those years. However, not having a long time series already established, it was not possible to determine whether spatial and temporal trends are shifting and changing. The Northwest Atlantic has been warming since 1980, and is projected to keep warming faster than other ocean basins (Barnett et al. 2001; Lee et al. 2011; Saba et al. 2016). It is uncertain how this will impact jellyfish species in the Maritimes region. Generally, jellyfish populations are expected to increase with increasing ocean temperatures (Purcell 2005; Holst 2012). However, the cold water *C. capillata* is predicted to suffer from warming temperatures (Holst 2012), thought to perhaps experience northward distribution shifts. Another limitation of the citizen science network is geographic biases in sampling effort. This project did not have any coverage on Newfoundland, where there have been reports of foraging leatherbacks previously (James et al. 2006; DFO 2011), and where DFO trawl survey data indicated seasonal hotspots of jellyfish occurrence from 2014 to 2017.

A missing component to this thesis was the connection between jellyfish strandings and jellyfish in the water column. Using jellyfish strandings on beaches as an index of what is happening at sea may not be an accurate representation (Fleming et al. 2013). This thesis addressed coastal waters in Atlantic Canada, however it is important to realize that both jellyfish and leatherback turtles occur off the Scotian Shelf (James et al. 2006). Offshore leatherback foraging is likely an essential aspect of the predator-prey relationship, but was outside the scope of the present work.

There were some limitations associated with the DFO groundfish surveys. The surveys took place in different months. The Scotian Shelf surveys (including the Bay of Fundy) occurred in July, and the Gulf of St. Lawrence surveys occurred in August and September. While all surveys have similar objectives and regional protocols, constraints such as different timing need to be considered when conducting analysis of combined regional data-set (Chadwick et al. 2007). This limited how the data could be used – for example, spatial distributions of jellyfish were examined using the bycatch data, but it would not make sense to compare the regions temporally. However, this data represents one of the only available datasets with information on jellyfish in Atlantic Canada.

4.2 Management applications

This thesis not only aimed to improve the scientific knowledge on jellyfish phenology, but also wished to provide information useful for discussion of critical habitat designation for the endangered leatherback sea turtle in Atlantic Canada. As jellyfish provide important foraging opportunities for leatherback turtles, understanding their spatio-temporal patterns can improve our understanding of how leatherback turtles use Atlantic Canadian waters. While there is an established amount of work on seasonal leatherback movements and migrations in Atlantic Canada (James et al. 2005a,b; James et al. 2006; James et al. 2007; Sherill-Mix et al. 2007), there has been a lack of knowledge on the prey field.

Resource managers will be better equipped to designate critical habitat of leatherback turtles using aspects of this thesis that characterize prey resource availability. This is especially important when considering the stability and growth of the Northwest Atlantic subpopulation of leatherback sea turtles. Atlantic Canadian waters provide leatherbacks with over 50% of their annual energy requirements (Wallace et al. 2018). Leatherbacks show fidelity to foraging grounds, returning annually to build energy reserves. Foraging grounds, such as the ones found in Atlantic Canada should be high conservation priority, as they offer reliable resources to meet necessary energy demands in a relatively short time period. In fact, resource availability has been compared between the East Pacific and Northwest Atlantic subpopulations, where lower resource availability coupled with continuous anthropogenic threats (poaching, entanglement in fishing gear, etc.) has been linked to lower resilience and lower fecundity in the East Pacific subpopulation – where there has been a 90% decline in leatherback abundance (Wallace et al. 2018). This illustrates why maintaining the quality of and understanding the jellyfish prey field is critical to the management and recovery of leatherback turtles in Atlantic Canadian waters.

Critical habitat requires functional components of the habitat used by species at risk to be understood and protected (DFO 2011). In the case of leatherback sea turtles, one of those components is the quality of seasonal foraging habitat. Results from this thesis can inform on the status of foraging habitat. Characteristics of spatial and temporal distribution were determined: spatially, *C. capillata* was found more abundantly throughout the Gulf of St. Lawrence, and hotspots of jellyfish occurrence were identified within the Gulf of St. Lawrence region. Temporally, jellyfish are reported as early as June, peak in July, and persist into September. Leatherback turtles on the Scotian Shelf appear to lag peak jellyfish occurrence by an average of two weeks. While this was the first attempt, and results may be subject to data biases, this information can still provide helpful clues regarding seasonal predator-prey timing. Understanding the temporal aspects of the prey field can help managers to predict the timing and residency of leatherbacks in the Maritimes region, which may be helpful when trying to minimize the likelihood of negative human-turtle interactions.

Jellyfish populations may not be static in space and time (Heaslip et al. 2012). While the results of this thesis indicate that *C. capillata* seasonality was consistent, it revealed a possible spatial shift in jellyfish distributions over time. Although habitat trends for both leatherbacks and their jellyfish prey are not available in long time series in Atlantic Canada, it is predicted that climate change may affect their distributions and perhaps abundance (Lynam et al 2010; COSEWIC 2012; Wallace et al. 2018). The Northwest Atlantic is warming faster than other ocean basins (Barnett et al. 2001; Lee et al. 2011; Saba et al. 2016), and in fact the Maritimes region has seen warmer than usual temperatures in 2014, 2015 and 2016 (Galbraith et al. 2016; Hebert et al. 2016; Hebert et al. 2018). This thesis showed a northward shift of jellyfish hotspots in the DFO groundfish surveys in 12 years of data. While this analysis did not include sea surface temperature records over these 12 years, it is possible that this shift could be attributed to the recent warming water temperatures. Management should be able to account for distribution shifts at a meso-scale. Perhaps delineation of critical habitat for the leatherback turtle should be approached using a dynamic management method, rather than the traditional static delineations (Wallace et al. 2018). Dynamic management is designed so it can respond rapidly to changes in the marine environment, through the use of near real-time data (biological, oceanographic, and economic data) (Maxwell et al. 2015). If shifts in prey distributions can be monitored and determined, shifts in leatherback turtle distribution can be properly planned for. Dynamic management may be an ideal way to approach a system such as leatherback-jellyfish predator-prey dynamics.

This thesis has also illustrated how data already collected by Fisheries and Oceans Canada can be utilized to continue understanding jellyfish distributions in Atlantic Canadian waters. Jellyfish as bycatch in the groundfish surveys can be used for long-term monitoring throughout the Bay of Fundy, Scotian Shelf and Gulf of St. Lawrence. While it may be difficult to get accurate estimates of abundance/weight of jellyfish using this data, understanding spatial patterns based on presence and absence is still useful. Future surveys could place more emphasis on trying to identify individual jellyfish species wherever possible.

4.3 Future research

The results of this thesis prompt several future research avenues and questions. This research was able to offer insights into several aspects of jellyfish (in particular *C. capillata*) phenology, but was only able to hypothesize on an important aspect of scyphozoan life cycle. Locating polyp beds was not one of the original objectives of this thesis, however it is a critical component to fully understanding spatio-temporal patterns of jellyfish (Lucas et al. 2012; Goldstein et al. 2017). As discussed in this thesis, there are specific environmental ranges these species of jellyfish need to successfully establish polyps, although these conditions do vary regionally (Gröndahl 1988; Brewer and Feingold 1991; Holst 2012; Lucas et al. 2012). Future research should work towards identifying specific polyp beds of *C. capillata* and *A. aurita*.

There is a need for more extensive fine-scale study of the jellyfish in known foraging grounds in Atlantic Canada. This thesis attempted two seasons of field work using underwater camera systems, and acoustics. According to surface observations, leatherbacks are found feeding on *C. capillata* off the coast of Cape Breton Island until late September (James et al. 2005b). Field work off the coast of Nova Scotia has revealed that jellyfish are not always found at the surface, even when a leatherback is observed handling prey at the surface (James and Mrosovsky 2004; James et al. 2005b; Hamelin et al. 2014). Footage from animal-borne cameras found that leatherbacks generally exploit prey at depths close to 30 m (Wallace et al. 2015). Recent research has suggested that *C. capillata* is often associated with the thermocline (Bailey et al. 2012; Wallace et al. 2014; Hamelin et al. 2014). This highlights a need for more extensive in-situ jellyfish sampling, and predator-prey interactions at depth.

There should also be an effort to continue spatio-temporal sampling of jellyfish in Atlantic Canada. Access to longer time series of jellyfish patterns can yield enhanced understanding of jellyfish. These sampling efforts could continue through citizen science, or dedicated sampling through government. Establishing longer time series, it may be possible to determine whether spatial and temporal trends of jellyfish are shifting and changing. Research on the role of other biotic and abiotic factors in explaining jellyfish occurrence and aggregations is also needed. Spatio-temporal patterns of jellyfish could be modelling in accordance with not included in this thesis, such as salinity, currents, wind direction, light, etc. Dedicated jellyfish sampling could include at sea sampling and shore based sampling to get a better understanding of coastal jellyfish versus at sea jellyfish occurrence.

A final suggestion of future research would be to continue building on the citizen science network established in this thesis. While still collecting jellyfish observations, an expanded citizen science network would also record other marine species of interest. It could answer a range of questions, including shifting species distributions and how ecosystems are changing with a changing climate. The Northwest Atlantic is warming faster than other ocean basins (Barnett et al. 2001; Lee et al. 2011; Pershing et al. 2015; Saba et al. 2016). Climate change can impact the geographical distribution of a species, where distribution limits are expanded or contracted in response changing conditions (Burrows et al. 2014). Redmap, based out of Australia (Pecl et al. 2014), is a citizen science project designed to capture early signals of what species may be changing their distributions in coastal marine environments (Pecl et al. 2014). A citizen science program similar to Redmap, could help identify species range-shifts in Atlantic Canadian waters under changing climates. Additional research effort or management focus can be applied to these range-shifts, helping enhance the understanding of climate change impacts on coastal marine ecosystems in Atlantic Canadian waters.

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Appendices

Appendix A: Field work attempts

A.1: In-situ camera tows

Many aspects of leatherback foraging behavior and jellyfish characteristics have been inferred indirectly, for example, using diet analysis, oceanographic conditions and leatherback dive patterns (Heaslip et al. 2012). The only studies to directly observe foraging at depth were performed using animal-borne cameras off the coast of Nova Scotia (Heaslip et al. 2012; Wallace et al. 2015). While these studies are providing invaluable information regarding foraging success, handling time, encounter rate, etc., there is a need for more extensive in-situ study of the leatherback prey field. Without a complete understanding of prey behavior, predator-prey dynamics are open to misinterpretation (James and Herman 2001).

According to visual observations, leatherbacks are found feeding on *C. capillata* off the coast of Cape Breton Island until late September (James et al. 2005b). Field work off the coast of Nova Scotia has revealed that jellyfish are not always found at the surface, even when a leatherback is observed handling prey at the surface (James and Mrosovsky 2004; James et al. 2005b; Hamelin et al. 2014). Footage from animal-borne cameras found that leatherbacks generally exploit prey at depths close to 30 m (Wallace et al. 2015). Recent research has suggested that *C. capillata* is often associated with the thermocline (Bailey et al. 2012; Wallace et al. 2014; Hamelin et al. 2014). This highlights a need for more extensive in-situ jellyfish sampling, and predator-prey interactions at depth.

Field work was proposed that would be able to address research gaps in jellyfish abundance/distributions at depth. The objective of this field work was to estimate the density and describe patches of jellyfish (specifically *C. capillata* and *A. aurita*) in a high-use leatherback foraging area off the coast of Nova Scotia. The field had three main objectives, to 1) determine areas of high jellyfish abundance at a fine-scale; 2) help create a better understanding of prey patchiness; and 3) determine water column characteristics and its relation to jellyfish presence by depth.

To attempt to answer these questions, a GoPro camera (GoProHERO4) was be towed along transects while visually surveying for leatherback sea turtles off the coast Neil's Harbour, Cape Breton in August 2016 (Aug. 11th to Aug. 19th). An underwater camera (SplashCam SideWinder 360) was dropped at each location when a turtle was being processed. This area has been studied since 1999 (Archibald and James 2016), and is considered a high-use foraging habitat based on previous leatherback telemetry and archival tagging research (James et al. 2005a; James et al. 2006; Wallace et al. 2015). The months of August and September represent peak leatherback occurrence in this area, based on patterns from previous reports (James et al. 2006; James et al. 2007). To piggyback on the existing research platform; this field work was opportunistic, and following haphazard unmarked non-linear transect survey (HUNTs) (Archibald and James 2016).

Previous studies have indicated that *C. capillata* is associated with the thermocline (Heaslip et al. 2012; Hamelin et al. 2014; Wallace et al. 2014), therefore that depth was the main focus for the camera tows. Camera drops were also completed, with the objective of establishing vertical density patterns. The SplashCam also recorded temperature and depth, and had a live-feed cable that was viewed in real time on the boat. Research in the area suggested the thermocline at an average depth of 37 m (Hamelin et al. 2014), and successful prey captures were shown from the animal-borne turtle cameras to be around 30 m (Wallace et al. 2015). This fairly narrow depth range was the targeted depth for the horizontal GoPro camera tows. The depth at which the camera was towed was controlled by the speed of the boat and the amount of cable let out. A CTD (conductivity, temperature, depth) was also cast at opportune times, such as when the SplashCam was dropped to do a vertical water column survey. The CTD recorded a data point every 0.5 seconds, and recorded temperature, depth, salinity, conductivity, and density

Leatherback turtles were observed and processed on the boat, which provided opportunities for horizontal GoPro camera trawl surveys, vertical SplashCam water column surveys, and CTD drops. Observed leatherback turtles were observed handling jellyfish at the surface, indicating prey were present in the general vicinity. However, the camera work was not successful.

There was no external lighting on the GoPro camera system, and the footage from these horizontal tows was dark below 25 metres with limited visibility. No jellyfish were identified from eight horizontal camera tows, or eight vertical SplashCam drops. Depth restrictions on the GoPro were 60m, however the cable was let out while the boat was not moving, and then it would slowly raise in the water column until the boat reached 3 to 3.5 knots. Calculations on how much cable to let out were determined before field work occurred with test camera tows in the Halifax area. According to these calculations, it was difficult to get the GoPro system below 30 meters.

C. capillata do not usually form dense surface aggregations typical of many other medusa species, making them more difficult to study (Purcell 2003; Bastain et al. 2011; Doyle et al. 2017). *C. capillata* can actively swim to some extent, both horizontally and vertically, meaning their movement is not completely dictated by tides and currents (Costello et al. 1998; Moriarty et al. 2012). It is unsure how this impacts the spatial dynamics of *C. capillata.* Density of *C. capillata* is often less than other species, such as *A. aurita* (Barz and Hirche 2007; Doyle et al. 2017), making it harder to study their patch dynamics.

A.2: In-situ acoustic sampling

Acoustic methods are frequently used to determine the distribution and abundance of both fish and zooplankton (Brierley et al. 2001, 2005). Acoustic methods can cover large areas efficiently, provide enhanced vertical and horizontal resolution, and even taxonomic information (Warren and Smith 2007; Graham et al. 2010). Acoustic target strength (TS) of the species of interest is required to convert raw acoustic data into abundance estimates. At a specific frequency, the TS enumerates the proportion of sound energy backscattered from an object (Brierley et al. 2005). While originally thought to be weak sound scatters due to the high fluid body composition (Stanton et al. 1996; Warren and Smith 2007; Colombo et al. 2009), recent studies have shown that jellyfish do produce sufficient amounts of sound scattering, and they have been successfully surveyed using acoustic echosounders (Brierley et al. 2001, 2005; Colombo et al. 2009; Purcell 2009; Crawford 2016).

Acoustic surveys were proposed for the 2017 field season. The proposed work was meant to help estimate the density and describe patches of jellyfish (*C. capillata*) in a high-use leatherback foraging area off the coast of Nova Scotia. Specifically, acoustic surveys were going to be used to try and: 1) determine areas of high jellyfish abundance at a fine-scale; 2) help create a better understanding of prey patchiness; and 3) determine water column characteristics and its relation to jellyfish presence at depth.

Acoustic gear was tested in the tower tank of the Aquatron at Dalhousie University (Halifax, Nova Scotia). The tower tank is 10 meters deep and 3.6 meters wide. Individual signals of *C. capillata* were picked up and visible in this controlled environment (Figure A.1). Acoustic surveys were conducted while visually surveying for leatherback sea turtles off the coast of Cape Breton from August 20th – 29th, 2017. This area has been studied since 1999 (Archibald and James 2016), and is considered a high-use foraging habitat based on previous leatherback telemetry and archival tagging research (James et al. 2005a; James et al. 2006; Wallace et al. 2015). The months of August and September represent peak leatherback occurrence in this area, based on patterns from previous reports (James et al. 2006; James et al. 2007; Wallace et al. 2015). To piggyback on the existing research platform; this field work was opportunistic, and therefore follow the haphazard unmarked non-linear transect survey (HUNTs) (Archibald and James 2016).

The acoustic surveys were carried out on a 12 m lobster fishing vessel. Acoustic surveys were planned to be run continuously (both when leatherbacks are present feeding, and absent). While acoustic studies on *C. capillata* are limited, the target strength (required to convert echo intensity to animal numerical density) for this species of jellyfish has been described in the range of -75 to -58dB (Crawford 2016). A hydroacoustic dual beam system was used (BioSonics equipped with 38, 120 and 200 kHz), with a minimum detection threshold of -75 dB. Evaluation of echograms was to be done using software including: Visual Acquisition and Visual Analyzers (BioSonics), and Echoview (Myriax Software) – which would allow for estimations of the abundance and density of *C. capillata* in a high-use leatherback foraging area. A CTD was also to be cast when a leatherback sea turtle is foraging. The CTD records a data point every 0.5 seconds, and records temperature, depth, salinity, conductivity, and density.

The largest obstacle for this acoustic work was interference with the BioSonics system. Being unable to test the equipment before field season – it was uncertain whether interference would occur. Diagonal striated bands of constant acoustic intensity were observed throughout the survey period. It was not clear if the interference was coming from the boat hull, vibrations from the engine, or vibrations from the acoustic securing structure. To try and combat this interference, range settings (including ping interval) were adjusted, a stay was fastened to secure the acoustic bracket to the boat, the engine was turned off, and equipment was re-adjusted – however none of these solutions worked. It is possible the interference was due to issues with the equipment, or due to modal interference, which sometimes occurs in acoustic signals that are spread over distances (Yang et al. 2017). The result of modal interference is striated bands of acoustic activity visualized on the signal receiver (Yang et al. 2017).

Another obstacle in the field, was that there were no leatherback turtles observed (except for one, on the last day out, that was on the move and not feeding). One of the objectives of the acoustic sampling was to survey areas where leatherbacks were observed foraging, and areas where leatherbacks were not foraging.

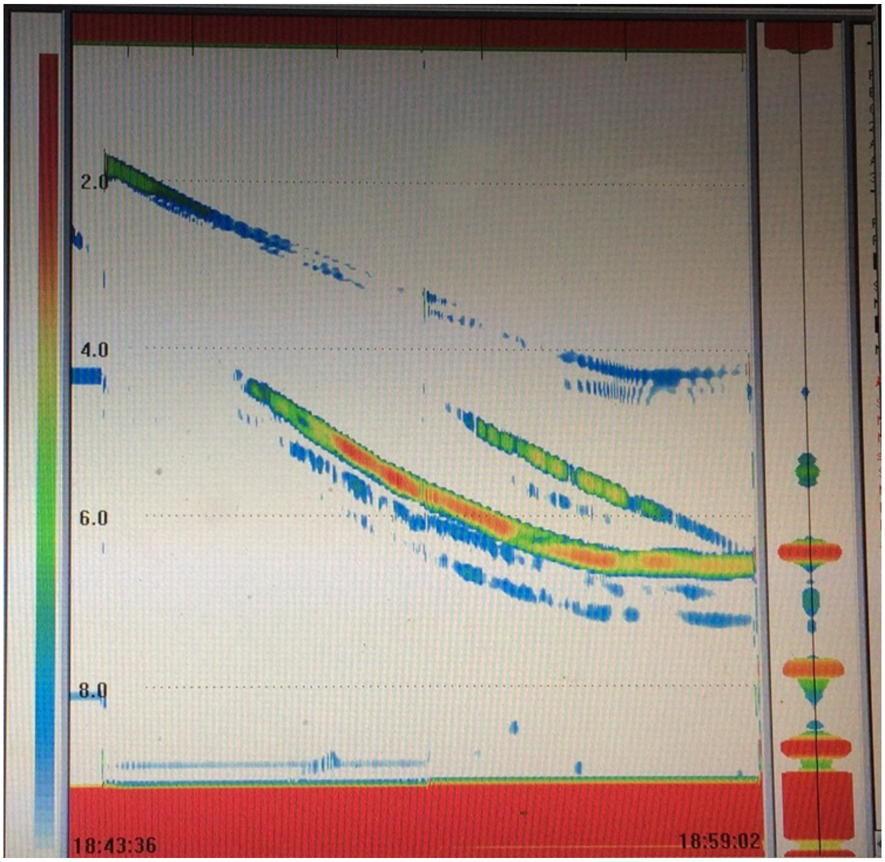
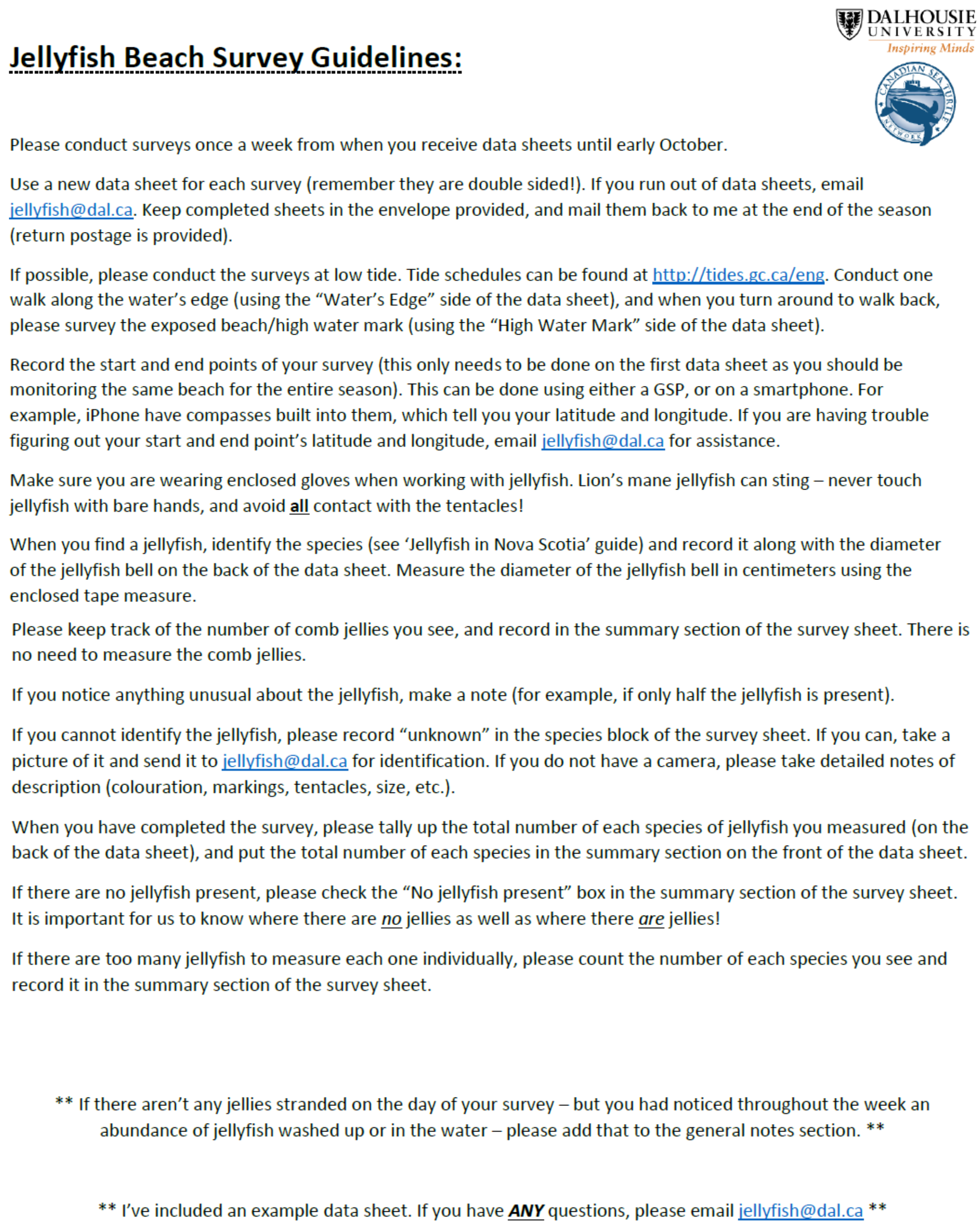


Figure A.1 - Signal of three C. capillata descending in the tower tank, at Dalhousie University. Y-axis is depth (m), and x-axis is time.

Appendix B: Citizen Science Survey Sheets.



Jellyfish Beach Survey Guidelines:

Please conduct surveys once a week from when you receive data sheets until early October.

Use a new data sheet for each survey (remember they are double sided!). If you run out of data sheets, email jellyfish@dal.ca. Keep completed sheets in the envelope provided, and mail them back to me at the end of the season (return postage is provided).

If possible, please conduct the surveys at low tide. Tide schedules can be found at http://tides.gc.ca/eng. Conduct one walk along the water's edge (using the "Water's Edge" side of the data sheet), and when you turn around to walk back, please survey the exposed beach/high water mark (using the "High Water Mark" side of the data sheet).

Record the start and end points of your survey (this only needs to be done on the first data sheet as you should be monitoring the same beach for the entire season). This can be done using either a GSP, or on a smartphone. For example, iPhone have compasses built into them, which tell you your latitude and longitude. If you are having trouble figuring out your start and end point's latitude and longitude, email jellyfish@dal.ca for assistance.

Make sure you are wearing enclosed gloves when working with jellyfish. Lion's mane jellyfish can sting – never touch jellyfish with bare hands, and avoid **all** contact with the tentacles!

When you find a jellyfish, identify the species (see 'Jellyfish in Nova Scotia' guide) and record it along with the diameter of the jellyfish bell on the back of the data sheet. Measure the diameter of the jellyfish bell in centimeters using the enclosed tape measure.

Please keep track of the number of comb jellies you see, and record in the summary section of the survey sheet. There is no need to measure the comb jellies.

If you notice anything unusual about the jellyfish, make a note (for example, if only half the jellyfish is present).

If you cannot identify the jellyfish, please record "unknown" in the species block of the survey sheet. If you can, take a picture of it and send it to jellyfish@dal.ca for identification. If you do not have a camera, please take detailed notes of description (colouration, markings, tentacles, size, etc.).

When you have completed the survey, please tally up the total number of each species of jellyfish you measured (on the back of the data sheet), and put the total number of each species in the summary section on the front of the data sheet.

If there are no jellyfish present, please check the "No jellyfish present" box in the summary section of the survey sheet. It is important for us to know where there are ***no*** jellies as well as where there ***are*** jellies!

If there are too many jellyfish to measure each one individually, please count the number of each species you see and record it in the summary section of the survey sheet.

** If there aren't any jellies stranded on the day of your survey – but you had noticed throughout the week an abundance of jellyfish washed up or in the water – please add that to the general notes section. **

** I've included an example data sheet. If you have ***ANY*** questions, please email jellyfish@dal.ca **

Jellyfish Beach Survey Sheet

Name: ____

Location ……… **Town/City:** ______________________ **Beach:** ______________________

Starting Point (decimal degrees): ________________ **N** ________________ **W**

Ending Point (decimal degrees): ________________ **N** ________________ **W**

Total Distance Surveyed (m): ________________

Date: ______________ **Start Time:** ______________ **End Time:** ______________

Tide: ☐ Low ** ☐ High ☐ Transitioning – low to high ☐ Transitioning – high to low

** Please survey at low tide if possible

Prevailing weather condition: ☐ Foggy ☐ Overcast ☐ Raining ☐ Sunny ☐ Windy

Was there a storm within the last 24 hours? ☐ Yes** ☐ No

** If yes, please briefly describe in general notes

Survey Summary (Tally up recorded jellyfish of each species from the back of the data sheet)

Species:	**Number:**
Lion's mane jellyfish	
Moon jellyfish	
Comb jellyfish	
Other	

OR: **No jellyfish present** ☐

General Notes: ____

____

____

____

____

____

*** Please turn over and complete survey …**

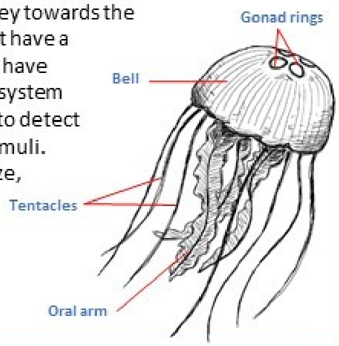
Water’s edge walk		
Species (lion, moon, unknown)	Diameter (cm)	Notes (anything unusual)

High water mark walk		
Species (lion, moon, unknown)	Diameter (cm)	Notes (anything unusual)

Jellyfish in Nova Scotia:

WHAT IS A JELLYFISH?

Jellyfish are gelatinous, free-swimming organisms, with an umbrella shaped bell, and trailing tentacles. The tentacles are used to catch prey, and the oral arms move the prey towards the mouth. They don't have a brain, but instead have a simple nervous system that allows them to detect light and other stimuli. Jellyfish vary in size, shape, colour, tentacle length and density.



LION'S MANE (*Cyanea capillata*)

Characteristics: Large jellyfish, varying in colour (deep red, orange, purple and brown) depending on size and location. Has 8 clusters of long tentacles.

Size: Up to 60 cm (can grow up to 2 m diameter, but not likely in our waters)

Can it sting? ***Yes***, always wear gloves, and ***do not*** touch tentacles

COMB JELLY (Ctenophore)

Characteristics: Not a true jellyfish, ctenophores are in a category (phylum) of their own. Transparent and spherical, with 8 rows of comb-like cilia (which help them move through the water).

Size: Less than 3 cm

Can it sting? No

MOON JELLY (*Aurelia aurita*)

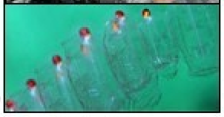
Characteristics: Moon jellies have a transparent bell, with 4 petal (or moon) shaped gonads visible through the top of the bell.

Size: Up to 25 cm bell diameter

Can it sting? Yes, however very mild. Wear gloves as precaution.

Less common species:

WHITE CROSS
(*Staurophora mertensii*)



SALP – individual or aggregated

How to measure bell diameter:

1. Wear gloves

2. Extend the tape measure so that it reaches from one edge of the bell to the other (don't include tentacles in measurement)

3. Record (cm's) on data sheet

Photograph references:

1. https://s-media-cache-ak0.pinimg.com/236x/9d/b5/06/9db5063f001a5297fede0683c9eb1a6f.jpg
2. Chris Harvey –Clark
3. http://img07.deviantart.net/8bbd/i/2009/215/9/2/lion__s_mane_jellyfish_by_rukyspooky.jpg
4. http://1.bp.blogspot.com/-DXWyQ0hI30A/TmhD7oWFIrI/AAAAAAAAAuo/YuXDdKt452Q/s1600/Lion%2527s+Mane+Jellyfish2.jpg
5. http://3.bp.blogspot.com/-gCeZmc87LbA/UoSUHT8Y0TI/AAAAAAAAAOFc/tVE8qI5Sp6Q/s1600/jellyfish.jpg
6. http://images.fineartamerica.com/images/artworkimages/mediumlarge/1/moon-jellyfish-aurelia-aurita-in-sea-peter-lilja.jpg
7. http://farm7.static.flickr.com/6074/6053245479_18fc5c4116_m.jpg
8. http://www.gettyimages.ca/detail/photo/salps-washed-up-on-beach-amphipod-inside-royalty-free-image/549804485
9. http://community.lovenature.com/2015/09/14/the-natural-word-salps/

Appendix C: Regional diameter measurements against day of year

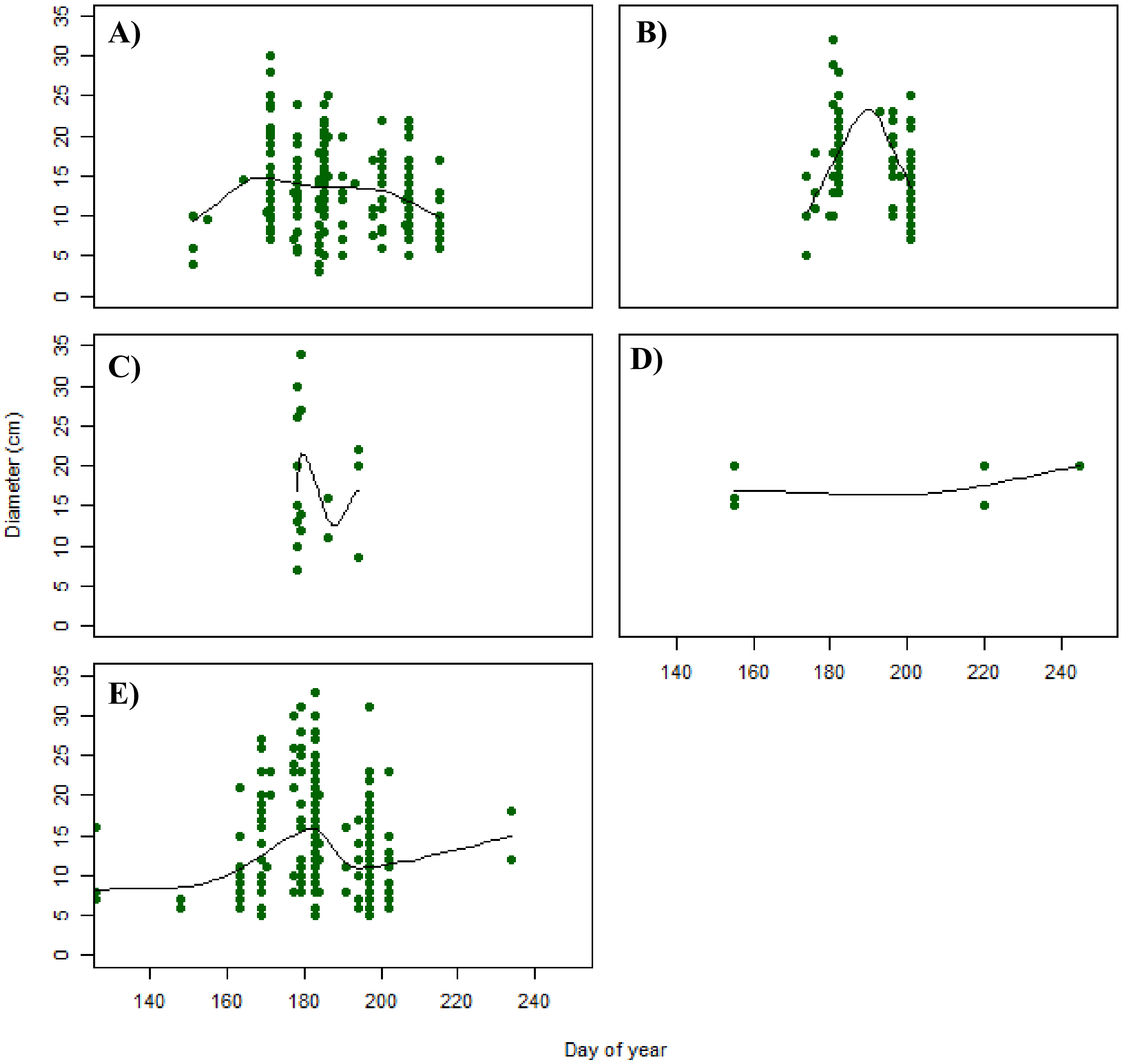


Figure C.1 - *C. capillata* diameter measurements (cm) against the day of year in each region in 2016. A) South Shore; B) Eastern Shore; C) Cape Breton; D) Gulf of St. Lawrence; E) Northumberland Strait. Bay of Fundy was excluded as there were no C. capillata observed there in 2016.

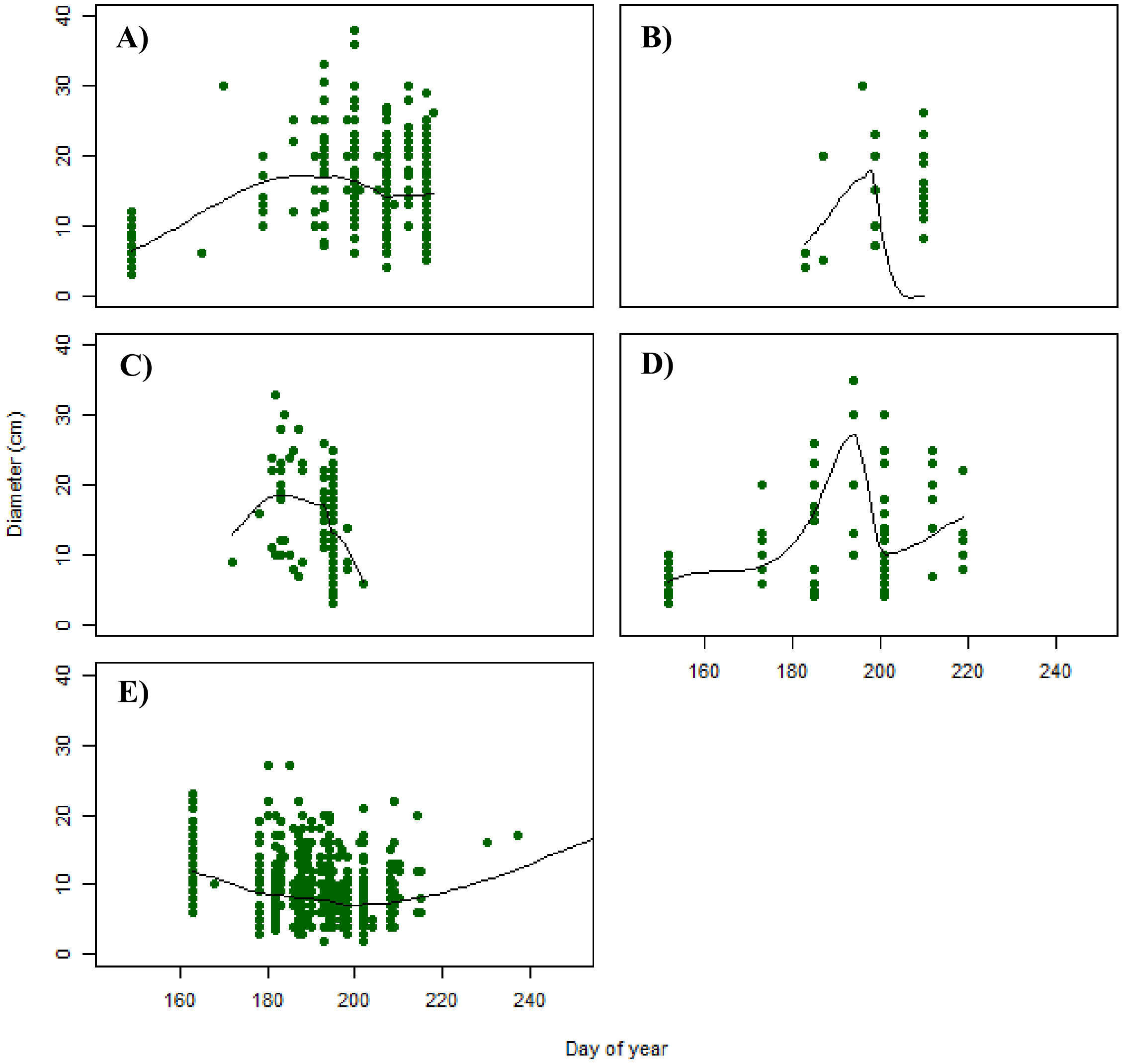


Figure C.2 - *C. capillata* diameter measurements (cm) against the day of year in each region in 2017. A) South Shore; B) Eastern Shore; C) Cape Breton; D) Gulf of St. Lawrence; E) Northumberland Strait. Bay of Fundy was excluded as there were very few C. capillata observed there in 2017 (n = 3).