Vol. 620: 15–32, 2019
https://doi.org/10.3354/meps12978

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published June 18

Tracking jellyfish and leatherback sea turtle seasonality through citizen science observers

Bethany Nordstrom[1,*], Michael C. James[2], Kathleen Martin[3], Boris Worm[1]

[1]Biology Department, Dalhousie University, Halifax, Nova Scotia B3H 4R2, Canada
[2]Population Ecology Division, Fisheries and Oceans Canada, Dartmouth, Nova Scotia B2Y 4A2, Canada
[3]Canadian Sea Turtle Network, Halifax, Nova Scotia B3L 1A3, Canada

ABSTRACT: Every summer, endangered leatherback sea turtles *Dermochelys coriacea* migrate to temperate Atlantic Canadian waters to feed on gelatinous zooplankton ('jellyfish'). Jellyfish distributions often seem episodic, making them difficult to survey over broad scales. We use a citizen science approach to track spatio-temporal patterns and environmental drivers of jellyfish occurrence, and ask how this dynamic prey field shapes leatherback sea turtle distribution in Atlantic Canadian waters. A total of 104 citizen scientists completed weekly beach surveys over 6 years, observing >23 600 stranded jellyfish. We used these observations to describe jellyfish phenology. *Cyanea capillata* was the most commonly detected species (75.5% of all species-specific sightings), with peak temporal occurrence in July and peak spatial occurrence in the Gulf of St. Lawrence. Generalized linear modelling indicated that sea surface temperature and observer effort were significant positive predictors of *C. capillata* shoreline strandings. Leatherback presence was assessed by opportunistic observer sightings and cross-referenced with satellite telemetry data. Leatherback seasonality generally tracked jellyfish occurrence in Atlantic Canadian waters. On the Scotian Shelf, turtle distributions derived from historical and concurrent leatherback satellite telemetry and opportunistic sightings data lagged peak jellyfish occurrence by 2 wk; however, the pattern of relative timing was less clear during extensive turtle residency in the Gulf of St. Lawrence. These findings suggest that observations by the general public represent an important contribution to tracking the spatio-temporal distributions of jellyfish and that this information is useful in predicting dynamic habitat use for the endangered leatherback turtles that prey on them.

KEY WORDS: Gelatinous zooplankton · Jellyfish · Citizen science · *Cyanea capillata* · *Dermochelys coriacea* · Predator–prey relationship

1. INTRODUCTION

Predator-prey interactions play an integral role in shaping and maintaining ecological communities (Berger et al. 2001, Hawlena & Schmitz 2010). Determining relationships between predators and their prey is an important challenge in ecology (Bedford et al. 2015), and additionally so when considering threatened and endangered species (Williams et al. 2011, Canale & Bernardo 2015). The success of the predator species is impacted by prey quality and prey abundance (Boyd 2002). Furthermore, the movement and distribution of a predator can be influenced by spatio-temporal fluctuations of, or changes in, prey resource availability (Beauchamp et al. 2007, Heaslip et al. 2012). Future success of highly migratory threatened and endangered species depends on appropriate conservation in breeding and foraging areas. An enhanced understanding of how prey resource availability and the seasonality of foraging habitat affects predator distributions is a key, and often overlooked, part of identifying critical habitat for species conservation. In addition, understanding the seasonal characteristics of foraging habitat can play

*Corresponding author: bethany.nordstrom@dal.ca

an important role in developing conservation and management measures for threatened species, such as time-area closures of critical habitat designations (Graham et al. 2010, Heaslip et al. 2012).

In this study, we attempted to better understand the seasonal habitat use for leatherback sea turtles *Dermochelys coriacea* and their preferred jellyfish prey (Bleakney 1965, James & Herman 2001, COSEWIC 2012). Leatherback sea turtles are highly migratory, and undertake seasonal migrations from tropical nesting beaches to temperate foraging grounds. These migrations are believed to be driven by prey availability (James et al. 2006, Houghton et al. 2007). One of the largest seasonal aggregations of leatherbacks in the Atlantic Ocean occurs annually in the temperate waters of Atlantic Canada (James et al. 2006), where the species is recognized as endangered (COSEWIC 2012). Leatherbacks generally arrive in spring or summer, and initiate southward migration in the fall (James et al. 2005b). It has been estimated that during a single foraging season in Canadian waters, leatherbacks acquire between 29 and 59% of their annual energy budget (Wallace et al. 2018).

Leatherbacks in eastern Canada weigh 33% more than turtles with the same carapace length found on nesting beaches (James et al. 2005a), illustrating the importance of summer foraging grounds for building energy reserves (Wallace et al. 2018). While several studies suggest that leatherback seasonality is driven by the dynamics of their prey field (James et al. 2006, Heaslip et al. 2012, Gregr et al. 2015, Wallace et al. 2018), comparison of potential predator-prey overlap in this foraging area has not been previously explored.

There is also limited understanding of the extent to which oceanographic processes shape the spatio-temporal distribution of jellyfish in this area (James et al. 2005b, Doyle et al. 2007, Houghton et al. 2007). This knowledge could expand understanding of important habitat in Canadian waters, a priority of recovery plans for endangered species legislation (DFO 2011, Gregr et al. 2015). We attempted to answer the following research questions: What are the seasonal distributions and associated environmental correlates of large jellyfish occurring in Atlantic Canada? And how does this dynamic prey field shape seasonal leatherback sea turtle distribution in Atlantic Canada?

Surveying and quantifying regional spatio-temporal patterns of jellyfish via traditional plankton sampling methods has proven problematic (Graham et al. 2010). For example, 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). Aerial observations have been suggested as an alternative, but they are expensive, can only detect jellyfish visible in the top few metres of the water column, and do not allow for accurate species identification (Houghton et al. 2006, Benson et al. 2007, Magome et al. 2007). This is particularly relevant in areas such as Atlantic Canadian waters, because jellyfish are not always visible at the surface, even in areas where leatherbacks are observed handling prey (James & Mrosovsky 2004, James et al. 2005b, Hamelin et al. 2014).

Given these challenges, we took an alternative approach, building on a citizen science model originally initiated by the Canadian Sea Turtle Network (CSTN), an NGO in Halifax, Nova Scotia, focused on marine turtle conservation, research, and education. Citizen science, which 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), is increasingly seen as a viable research tool that can complement other approaches (Bonney et al. 2014). One of the most appealing aspects of citizen science is its ability to expand the range (both spatially and temporally) of a study at low cost (Freitag & Pfeffer 2013). Citizen science is also beneficial to researchers as it provides an opportunity to engage the general public in scientific inquiry (Dickinson et al. 2012). 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), we present the first attempt to link jellyfish observations gained from citizen science observers with sea turtle observations.

2. MATERIALS AND METHODS

2.1. Study region

Atlantic Canadian waters, found in the Northwest Atlantic Ocean, are known to be important seasonal foraging areas for leatherback sea turtles (James et al. 2006). Atlantic Canadian waters include the Bay of Fundy, Scotian Shelf, and Gulf of St. Lawrence (Fig. 1A). These productive waters are also home to several varieties of gelatinous zooplankton, including ctenophores, salps, and scyphozoan species such as lion's mane jellyfish *Cyanea capillata* and moon jellyfish *Aurelia aurita* (Sipos & Ackman 1968, James & Herman 2001, Heaslip et al. 2012).

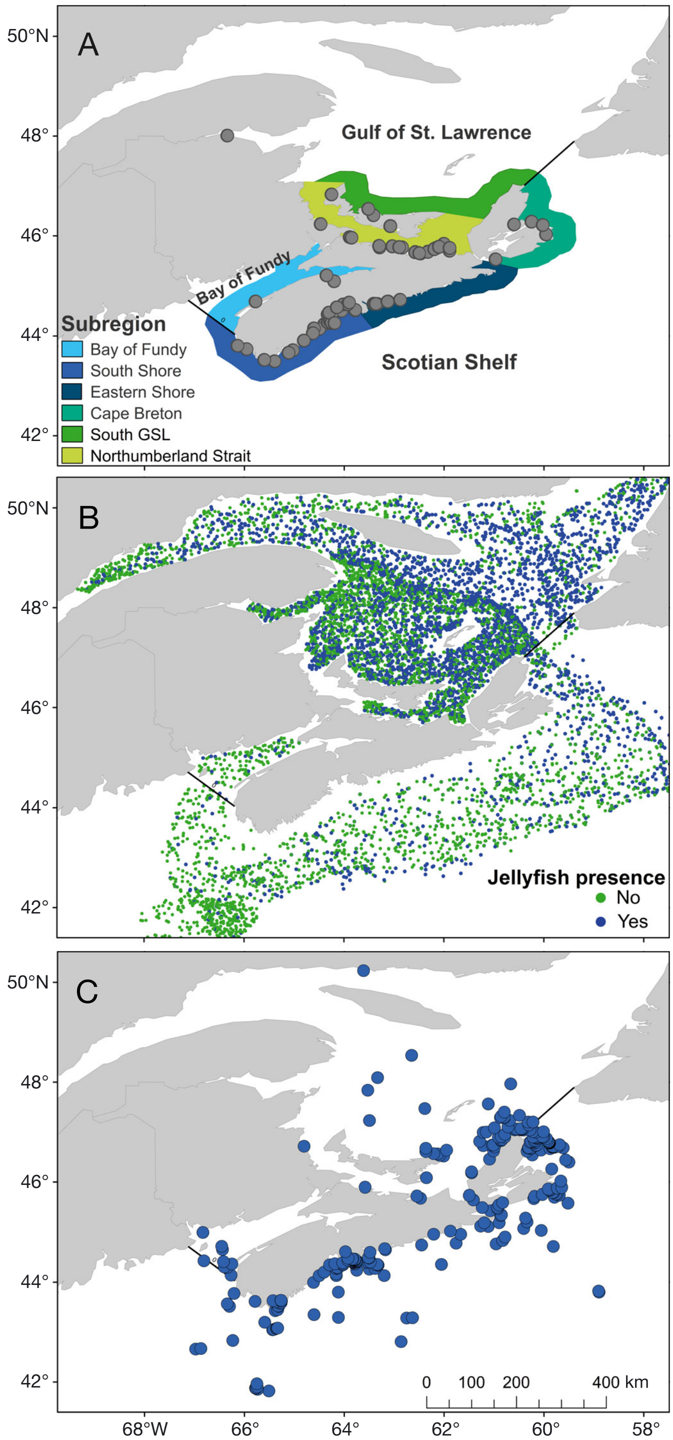

Fig. 1. Study area: (A) biogeographical regions (Bay of Fundy, Scotian Shelf, and Gulf of St. Lawrence – separated by black lines) and 6 subregions within, used to address seasonal jellyfish patterns from citizen science data; grey circles: locations of citizen scientists (2007–2017); (B) Fisheries and Oceans Canada (DFO) trawl survey jellyfish presence observations (2006–2017); and (C) blue circles: locations of citizen scientist observations of leatherback sea turtles (2007–2017). GSL: Gulf of St. Lawrence

2.2. Jellyfish data

The major data sources used for the study of jellyfish phenology were citizen observations augmented by scientific trawl survey data. A study of jellyfish strandings observed by citizen scientists (24 individual participants, 7 of whom took part for multiple years) was conducted by the CSTN from 2007 to 2010, and a similar but more extensive survey was implemented by Dalhousie University (Halifax, Canada) (51 individual participants, 14 of whom took part both years) in 2016 and 2017 to help determine jellyfish seasonality in Atlantic Canada through regular beach surveys. The primary difference between the 2 programmes were scale (number of citizen scientists involved and corresponding increase in geographic scale surveyed) and survey season length (CSTN: June–October, Dalhousie: April–October). CSTN citizen scientists were engaged by appealing to both established CSTN volunteers as well as through presentations and appeals to 2 field-naturalist organizations. In addition to working with local field-naturalist organizations, Dalhousie citizen scientists were engaged by using both traditional media (radio, web, TV) and the social media outlet Facebook.

In both cases, participants had access to the same stretch of beach for the entirety of the survey season, surveyed weekly. Beaches were distributed throughout the Canadian Maritime provinces (Nova Scotia, New Brunswick, and Prince Edward Island), with the majority of participants based in Nova Scotia, the home province for both CSTN and Dalhousie University. A sample of both rocky and sandy beaches were surveyed that border 3 oceanographically distinct regions: the Bay of Fundy, the Scotian Shelf, and the Gulf of St. Lawrence (Fig. 1). Participants were asked to conduct surveys at low tide, to record any sightings of stranded jellyfish by species, as well as to measure the bell diameter (cm) of stranded jellyfish. During mass stranding events, only the first 50 specimens encountered during a weekly survey were measured. Bell diameters were measured by placing a measuring tape on the outer edge of the bell and extending it to the other side (excluding tentacles). Each member of the citizen science network was mailed a survey kit which was comprised of: data sheets, survey guidelines, a jellyfish identification key, a tape measure, gloves, and an envelope with return postage. The jellyfish identification key included photographs, physical characteristics, and size range of common Atlantic Canadian jellyfish species (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m620p015_supp.pdf). The purpose of the key was to assist citizen scientists in differentiating between species of jellyfish. Citizen scientists also had direct contact via email with the project lead, where they could send in photographs or descriptions of jellyfish they were not confident identifying. At the end of the survey season, citizen scientists mailed the survey sheets back. After the completion of each jellyfish season, citizen scientists received both a thank-you letter and a report that detailed and contextualized the jellyfish data from that year.

Jellyfish catch per unit of observer effort (CPUE) was calculated per citizen scientist over each of the 6 years. Jellyfish diameter from the Dalhousie citizen science data was also plotted against time (2016 and 2017) to look for patterns in seasonal size distribution which might indicate reproductive cohorts of jellyfish. A loess curve was fit to the diameter data separately for *C. capillata* and *A. aurita*, first across all diameter measurements and then again by geographic region. Pearson's correlation coefficient was calculated to determine the strength of association between the date of jellyfish observation and its diameter.

In addition, opportunistic jellyfish observations (positive presence counts) were reported to a dedicated email contact (jellyfish@dal.ca). Citizen scientists submitting observations were asked to include the following information: species identification (if known; if not, a description including colour, shape, and distinguishing factors), number of jellyfish, location (latitude and longitude), date, and pictures if possible.

Observations of jellyfish presence or absence during scientific trawl surveys conducted between 2006 and 2017 were accessed from Fisheries and Oceans Canada (hereinafter DFO). Although the primary objective of the trawl surveys is to provide information on trends in biomass and abundance for groundfish species in the DFO Maritimes region (DFO 2016a,b), observers also record trawl bycatch, including jellyfish. Data was collected for the following Maritimes Regions, Northwest Atlantic Fisheries Organization (NAFO) Divisions: Scotian Shelf/Bay of Fundy (4VWX and a small portion of 5Y, occurring in July); Southern Gulf of St. Lawrence (4T, occurring in August and September); and Northern Gulf of St. Lawrence (4R, 4S, and northern part of 4T, occurring in August). Data from 2006 onwards for each region was collected from DFO with the intent of analysing jellyfish bycatch. Wet weight (kg) of jellyfish was reported for each trawl. Presence and absence of jellyfish bycatch in each trawl was also determined.

2.3. Leatherback data

The seasonal dynamics of leatherback turtles visiting the study area was assessed via data from 11 satellite-tagged leatherbacks that visited the region on 19 occasions between 2004 and 2017. Each turtle was satellite-tagged the previous year (n = 5 while foraging in Atlantic Canadian waters; n = 6 while nesting on a beach in Trinidad), and had returned to Atlantic Canada again to forage for jellyfish. Using tracks of returning leatherbacks was essential to capturing the complete foraging season (entering and exiting the regions in question) as opposed to just a portion of it, as well as to avoiding the introduction of tagging location bias. Leatherback residency time was determined for 3 oceanographically distinct Atlantic Canadian regions: Bay of Fundy, Scotian Shelf, and the Gulf of St. Lawrence, between 2004 and 2017. Residency time in days was calculated from entry and exit dates provided for leatherbacks in each region.

We also considered opportunistic sightings of leatherback turtles from citizen scientists (commercial fishers as well as members of the general public) submitted to the CSTN between 2007 and 2017 (n = 338). All sightings were of free-swimming turtles, and included associated latitude and longitude, and date observed.

2.4. Environmental data

We hypothesized that seasonal occurrence of jellyfish may be related to the seasonal dynamics of sea surface temperature (SST) and chlorophyll, both of which would affect jellyfish individual and population growth rates (Gröndahl 1988, Brewer & Feingold 1991, Decker et al. 2007, Holst 2012, Lucas et al. 2012). SST and chlorophyll *a* (chl *a*) data for 2016 and 2017 were provided by DFO (Advanced Very High Resolution Radiometer [AVHRR] SST Dataset, Remote Sensing Group, Bedford Institute of Oceanography [BIO]; Visible and Infrared Imaging Radiometer Suite [VIIRS] for chl *a*, version R2014: data courtesy of 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 2 wk intervals at 1.5 km resolution and converted for each of the 6 regions (completed in QGIS version 2.18.10). Intervals of 2 wk were chosen as a compromise between fine temporal resolution and data availability for jellyfish observations.

The mean value was extracted for each region over each time period for both SST and chl *a*.

2.5. Data analysis

2.5.1. Modelling environmental drivers of jellyfish

To test for a possible relationship between jellyfish sighting occurrence and environmental conditions, *C. capillata* data from 2016 and 2017 citizen science seasons was modelled against SST and chl *a* data from those same years. The Dalhousie citizen science data (2016 and 2017) was chosen because these years had the largest number of participants and, therefore, geographically dispersed data. *C. capillata* was chosen for this analysis, as it represented the majority of jellyfish sightings reported over the 2 year survey period (>90%). Citizen scientist locations (latitude and longitude) were binned into 1 of 6 geographically distinct subregions: South Shore, Eastern Shore, Cape Breton (each of these is part of the Scotian Shelf region); the Northumberland Strait and the Southern Gulf of St. Lawrence (each of these is part of the Gulf of St. Lawrence region); and the Bay of Fundy (Fig. 1A). These regions represent coastal waters stretching from the coastline to 25 km offshore.

All statistical modelling was done in R (version 3.4.2; R Core Team 2017). To evaluate a potential relationship between environmental parameters (see next paragraph) and presence/absence of *C. capillata*, 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, using the R package brglm (Kosmidis 2017).

Presence (or absence) of *C. capillata* was the dependent variable in the binomial GLM. Independent variables included: SST, chl *a*, effort (number of citizen scientists), effort (total number of survey weeks in 2 wk period), date (2 wk intervals), region, and year. Collinearity between model variables was tested using Pearson's correlation coefficients (r). Date (measured in 2 wk intervals) and 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, Aleksa et al. 2018), date was dropped from the model and not included in the analysis.

Model selection was done by comparing all possible subsets of the full model using Akaike's information criterion (AIC). Differences in AIC of <2 indicate there is not a substantial difference between the models (Burnham & Anderson 2002).

2.5.2. Modelling jellyfish–turtle seasonal overlay

We tested the hypothesis that leatherback residency was linked in a predictable way to jellyfish seasonal occurrence in Atlantic Canada. The area was broken into the 3 large oceanographically distinct regions: the Bay of Fundy, the Scotian Shelf, and the Gulf of St. Lawrence (Fig. 1A). Jellyfish data sources included: CSTN citizen science network, Dalhousie citizen science network, Dalhousie opportunistic sightings, and DFO trawl survey bycatch data. Leatherback data sources included turtle residency derived from satellite telemetry (DFO/CSTN) and opportunistic sightings from the CSTN.

Each of the 6 data sources (2 for leatherback and 4 for jellyfish) were normalized to range between 0 and 1, and binned into weekly intervals for the 2 main regions of interest: the Scotian Shelf and the Gulf of St. Lawrence (the Bay of Fundy was not included as there were no satellite-tagged turtles in that region, and also 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).

The peak of jellyfish occurrence for each jellyfish data source was then compared against both leatherback data sources in each region (Scotian Shelf and Gulf of St. Lawrence). A Wilcoxon rank sum test was used to test whether the timing of peak jellyfish occurrence was significantly different between the Scotian Shelf and the Gulf of St. Lawrence.

The 6 data sources were also analysed as 6 separate time series. Cross-correlation was used to test whether there were significant correlations at a variety of time lags between each leatherback and jellyfish source in each region (2 leatherback time series, 4 jellyfish time series, 2 regions — resulting in 16 different cross-correlations). All cross-correlation analysis was completed in R 3.4.2 (cross-correlation function, ccf). Missing values were excluded from the analysis. Cross-correlation analysis returns the correlation associated with each lag interval (in this case, for each week).

3. RESULTS

3.1. Jellyfish data

A detailed summary of the 6 years of citizen science results is given in Table 1. A total of 104 citizen scientists observed n = 23 611 stranded jellyfish. Observer effort varied year to year, with lowest effort of 5 citizen scientists (77 survey weeks) in 2010, and highest effort of 37 participants (515 survey weeks) in 2017. See Fig. 1A for citizen science spatial coverage (see Fig. S2 in the Supplement for citizen science locations broken into each year). As jellyfish in temperate waters are thought to consist of a single cohort that grows and matures synchronously through the summer months (Gröndahl 1988, Brewer 1989, Lucas 2001, Lucas et al. 2012), the citizen science surveys started in spring, as early as April 12 (2016), and ran as late as November 3 (2008) (Table 1). *Cyanea capillata* was the most dominant species of jellyfish identified over the 6 survey seasons (75.5 % of total observations); ctenophores made up 20.4 % of total observations; *Aurelia aurita* made up 3.7 %; and 0.3 % were 'other' jellyfish species (i.e. 'unknown' or unidentified jellyfish). There were variable numbers of jellyfish reported each year, and this was closely linked with observer effort. In 2008, the fewest jellyfish were observed (n = 1218, and 11 citizen scientists), while in 2017, citizen scientists reported the most jellyfish (n = 8545, and 37 citizen scientists) (Table 1). *C. capillata* was the dominant species observed in 2007, 2009, 2016, and 2017, comprising >70 % of observations in each of those years (Table 1). In 2008 and 2010, higher observations of ctenophores were reported than any other species (Table 1). Photographs submitted by citizen scientists in 2016 and 2017 helped confirm species identification, and demonstrated diversity of jellyfish observations (Fig. 2). Jellyfish observations were also broken up into the 6 subregions (Fig. 3), revealing highest survey effort on the South Shore, and Northumberland Strait (Fig. 3A). The amount of effort in each subregion also closely reflected the number of jellyfish strandings; however, South Gulf of St. Lawrence had low survey effort and high jellyfish abundance (Fig. 3B).

Opportunistic sightings of jellyfish were also collected in 2016 and 2017, resulting in 628 submissions from the general public. Again, *C. capillata* was the most dominant species of jellyfish identified over the 2 years (80.1 % of total observations), *A. aurita* made

Table 1. Citizen science jellyfish data. For peak seasonality, jellyfish observations (*Cyanea capillata* and *Aurelia aurita*) were binned into the first half of the month, and the second half of the month (using the numerical month number followed by '.1' or '.2' respectively, e.g. first half of July = 7.1; second half of July = 7.2). Percentages should be read vertically (e.g. as a % of total jellyfish for that year; or as a % of peak *C. capillata* seasonality values for that year). Dash: not applicable

	2007	2008	2009	2010	2016	2017	Total
No. of citizen scientists	10	11	12	5	29	37	104
No. of survey weeks	77	92	105	70	494	527	1365
Distance (m) per citizen scientist	1667	1809	1292	1924	798	968	–
Survey duration	May 4–Oct 3	Jun 7–Nov 3	May 25–Oct 5	Apr 22–Oct 4	Apr 12–Oct 6	May 4–Oct 19	–
Total jellyfish (n)	1241	1218	6283	2567	3757	8545	23611
C. capillata (n)	1065 (86 %)	328 (27 %)	4414 (70 %)	579 (23 %)	3359 (89 %)	8092 (95 %)	17837
A. aurita (n)	67 (5 %)	303 (25 %)	183 (3 %)	25 (1 %)	168 (4 %)	131 (2 %)	877
Ctenophore (n)	87 (7 %)	587 (48 %)	1686 (37 %)	1963 (76 %)	183 (5 %)	309 (4 %)	4815
Unknown (n)	22 (2 %)	0	0	0	47 (1 %)	13 (0.2 %)	82
First *C. capillata*	Jul 14	Jun 8	Jun 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*	Sep 10	Aug 22	Sep 7	Aug 18	Sep 1	Sep 28	–
Size range of *C. capillata* (cm)	3–34	2–60	3–30	4–61	3–34	2–44	–
First *A. aurita*	Jul 27	Jul 16	Jun 19	Jun 10	Jun 11	Jun 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	Sep 14	Sep 14	Aug 17	Aug 20	–
Size range of *A. aurita* (cm)	4–24	3–25	3–54	5–10	5–32	4–30	–
Jellyfish (n) per citizen scientist	124.1	110.7	523.6	513.4	129.6	230.9	–
C. capillata (n) per citizen scientist	106.5	29.8	367.8	115.8	115.8	218.7	–

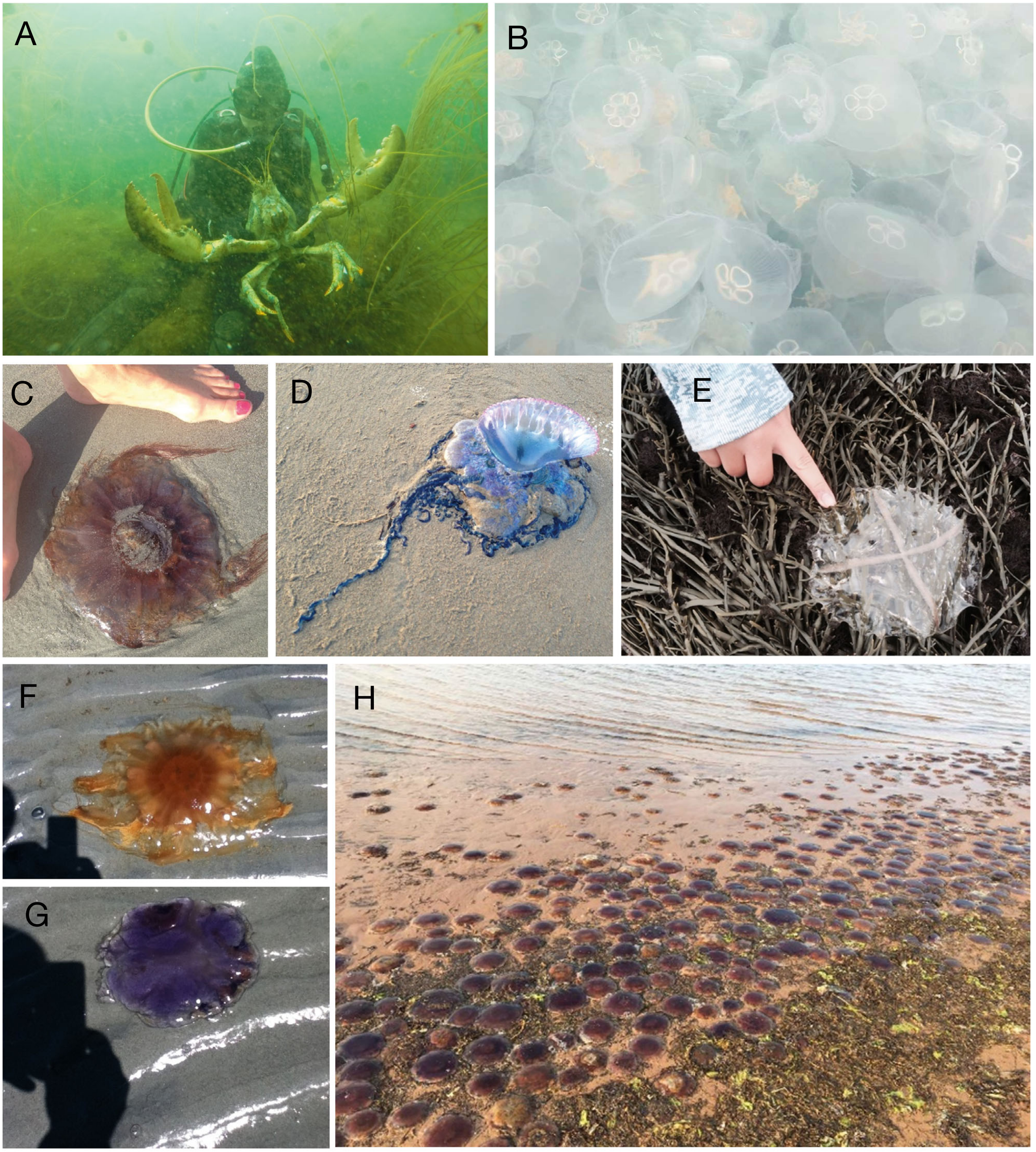

Fig. 2. Jellyfish sightings by citizen scientists, from a selection of >500 photos submitted by citizen scientists that demonstrate the range of species diversity and density: (A) a SCUBA diver holding an American lobster among *Cyanea capillata* mass occurrence (photo: J. Richard, Magdalen Islands, Quebec, August 2015); (B) a bloom of *Aurelia aurita* (photo: E. Burkes, Bras D'Or Lakes, Nova Scotia, July 2017); (C) a beached *C. capillata* (photo: K. Goudey, White Point Beach, Nova Scotia, July 2016); (D) a beached Portuguese man-o-war *Physalia physalis* (uncommon in Atlantic Canadian waters) (photo: S. Vaidya, Conrad's Beach, Nova Scotia, August 2017); (E) white-cross jellyfish *Staurophora mertensii* (photo: G. Turner, Point Prim, Nova Scotia, June 2015); (F) stranded *C. capillata* and (G) *C. capillata*, both showing colour variation (both photos: J. Bower, Shelburne, Nova Scotia, July 2016); and (H) mass stranding of *C. capillata* (photo: A. Howatt, Tracadie Bay, Prince Edward Island, July 2017)

up 9.6%, and ctenophores made up 3.8% of the observations. Interestingly, opportunistic sightings detected species that were not detected in the weekly citizen science beach surveys, including Portuguese man-o-war *Physalia physalis* (3.8% of observations), and white-cross jellyfish *Staurophora mertensii* (1.0% of observations) (Fig. 2D,E).

CPUE, or jellyfish per citizen scientist, varied throughout the 6 survey years, with lowest values in 2007 (124.1 jellyfish per citizen scientist) and highest in 2009 (523.6 jellyfish per citizen scientist) and 2010 (513.4 jellyfish per citizen scientist) (Table 1).

As *C. capillata* made up >75% of total jellyfish detections by citizen scientists, and as they are important prey for leatherback sea turtles in the Northwest Atlantic (James & Herman 2001, Wallace et al. 2015), we examined their seasonality in more detail. The highest abundance of *C. capillata* was in the month of July for all 6 survey seasons: 77% of *C. capillata* were reported in July, with 63% of all *C. capillata* reports coming in the second half of the month (Fig. 3D). *A. aurita* have been identified as preferred leatherback prey in other parts of the species' range (James & Herman 2001); however, they only made up 3.7% of total observations in our study region. Peak seasonality was more variable for *A. aurita*, ranging between the first half of July (2017) and the first half of September (2010) (although it should be noted that in the 2010 survey season, only 25 *A. aurita* were observed in total) (Table 1). A total of 81% of all jellyfish were detected in the months of July and August.

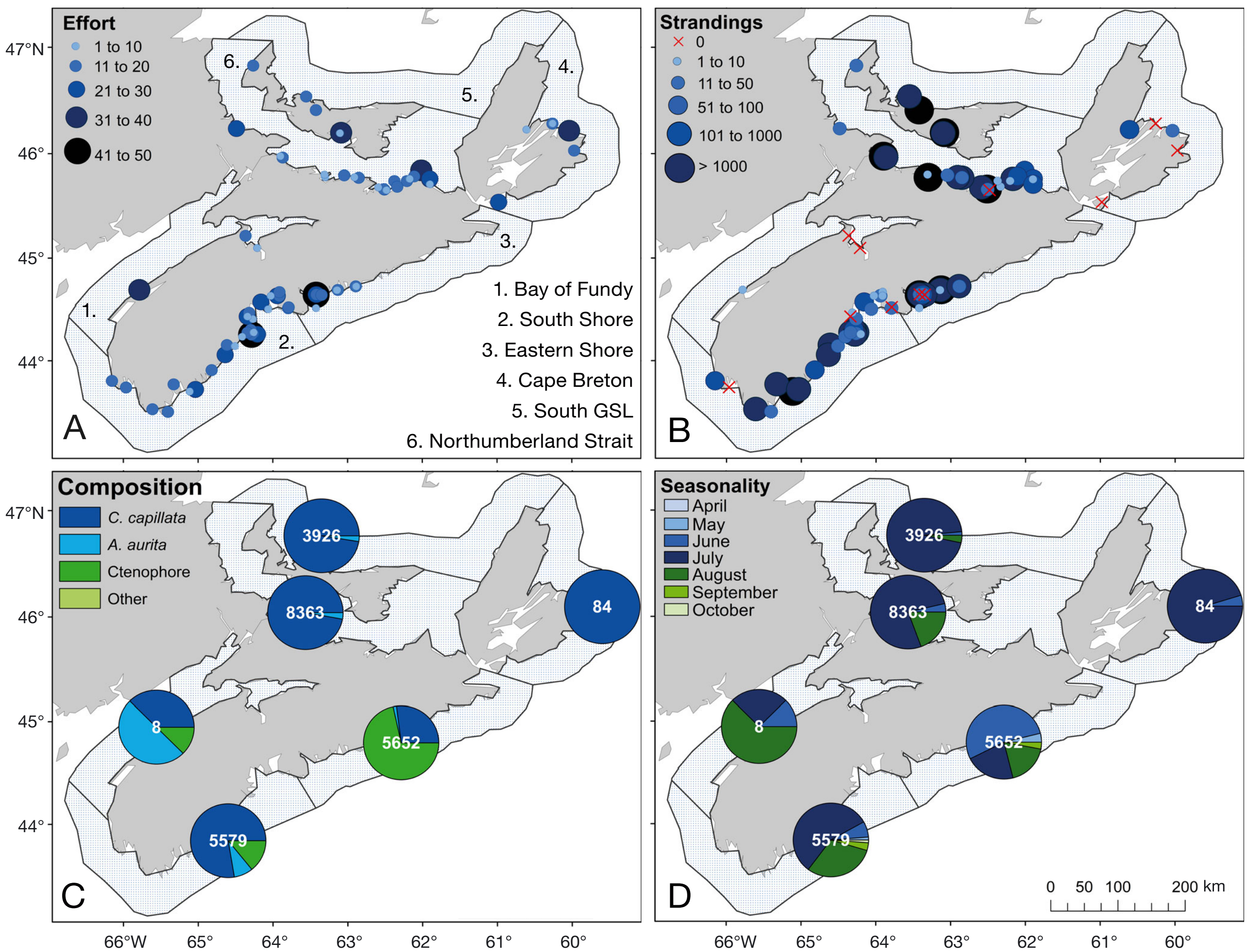

Fig. 3. Citizen science data 2006–2017: (A) survey effort: number of times each location was surveyed over the 6 years (each location is binned into its respective subregion); (B) total number of jellyfish strandings observed by citizen scientists at each location; (C) species composition within each subregion; and (D) seasonality (by month) of all jellyfish species in each subregion. Numbers inside circles in (C,D) are total number of jellyfish strandings observed in each subregion. *A. aurita*: *Aurelia aurita*; *C. capillata*: *Cyanea capillata*; GSL: Gulf of St. Lawrence

Spatially, *C. capillata* was the most observed species in 4 of the 6 subregions (South Gulf of St. Lawrence, Northumberland Strait, Cape Breton, and South Shore) (Fig. 3C). The Eastern Shore subregion had a high detection rate of ctenophores, and the Bay of Fundy subregion had very few jellyfish detections overall (8 jellyfish strandings over the 6 years of citizen science surveys) (Fig. 3C). Timing of the jellyfish strandings in the 6 subregions showed a similar pattern to spatial species composition. The vast majority of jellyfish sightings occurred in July (South Gulf of St. Lawrence, Northumberland Strait, Cape Breton, and South Shore). The Eastern Shore had the highest detection rate in June, and the Bay of Fundy had the highest stranding detection rate in August (Fig. 3D).

Bell diameter data for *C. capillata* and *A. aurita* were plotted against the day of the year. Loess curves fit to size data for 2016 and 2017 revealed that there was no obvious linear relationship between diameter and day of year for either *C. capillata* or *A. aurita*. Pearson's correlation did not reveal strong associations between *C. capillata* and day of year in either 2016 ($r = -0.0919$, $n = 640$, $p = 0.0201$) or 2017 ($r = 0.1405$, $n = 1649$, $p < 0.0001$); a weak correlation was seen, however, for *A. aurita* and day of the year in both 2016 ($r = 0.4965$, $n = 65$, $p < 0.0001$) and 2017 ($r = 0.4047$, $n = 121$, $p < 0.0001$) (see Figs. S3 & S4 in the Supplement).

3.2. Leatherback data

In total, there were 19 individual entry/exit records for 11 satellite-tagged leatherback sea turtles between 2004 and 2017: zero in the Bay of Fundy, 14 on the Scotian Shelf, and 5 in the Gulf of St. Lawrence. The mean time spent on the Scotian Shelf was 24 d (±27 d), and the mean time spent in the Gulf of St. Lawrence was 48 d (±11 d).

Opportunistic leatherback turtle observations collected by the CSTN ($n = 338$) were analysed separately for 3 oceanographically distinct regions: the Bay of Fundy, Scotian Shelf, and the Gulf of St. Lawrence (which include the 6 subregions; Fig. 1A). There were 10 leatherback turtle observations in the Bay of Fundy; all were close to the shared boundary with the Scotian Shelf (Fig. 1C). There were no turtle observations further inside the Bay of Fundy. There were 256 leatherbacks observed on the Scotian Shelf and 72 in the Gulf of St. Lawrence. Leatherbacks were observed most frequently along the Scotian Shelf in July (46% of observations) and August (46% of observations). Spatially, most of the leatherback observations in August were close to the Scotian Shelf/Gulf of St. Lawrence boundary. Observations in the Gulf of St. Lawrence were most frequent in August (41.7% of observations) and September (27.8% of observations).

3.3. Data analysis

3.3.1. Modelling environmental drivers of jellyfish

Among 6 candidate models (see Table S1 in the Supplement) testing for possible linkages between jellyfish present and environmental parameters, model polyS2 was chosen. The best model (polyS2) was selected based on AIC. It included the variables SST (3rd-order polynomial), chl *a*, region, and effort (survey weeks) (Table 2). Although one model had a slightly lower AIC, as well as an AIC value that differed by <2, we selected model polyS2 because it included an effect for subregion, which was of particular interest for this modelling exercise.

Observer effort emerged as the strongest predictor of jellyfish detection (Table 2, Fig. 4A), showing a positive correlation until about 20 survey weeks, where the relationship saturates. SST was also a significant predictor of jellyfish presence; however, it was slightly weaker than effort (Table 2, Fig. 4B). SST shows a positive correlation between 5 and 11°C, a negative trend from 11 to 18°C, and back to a positive trend from 18°C onward (Fig. 4B). Note: the

Table 2. Analysis of jellyfish occurrence and environmental drivers. Model output for the binomial generalized linear model (polyS2). Significant variables ($p < 0.05$) in **bold**. SST: sea surface temperature; (SST)2: second order polynomial term; (SST)3: third order polynomial term

Variable	Coefficient	SE	*z*-value	p
Intercept	−21.95	8.64	−2.54	0.011
SST	**5.277**	**2.15**	**2.46**	**0.014**
(SST)2	**−0.400**	**0.17**	**−2.36**	**0.018**
(SST)3	**0.009**	**0.004**	**2.23**	**0.026**
Chl *a*	−0.497	0.29	−1.74	0.082
Subregion2: South Shore	−1.561	1.55	−1.01	0.315
Subregion3: Eastern Shore	−0.491	1.19	−0.41	0.679
Subregion4: Cape Breton	−0.634	1.15	−0.55	0.582
Subregion5: South Gulf of St. Lawrence	0.636	0.99	0.64	0.519
Subregion6: Northumberland Strait	1.689	0.98	1.73	0.084
Effort (survey weeks)	**0.184**	**0.06**	**3.05**	**0.002**

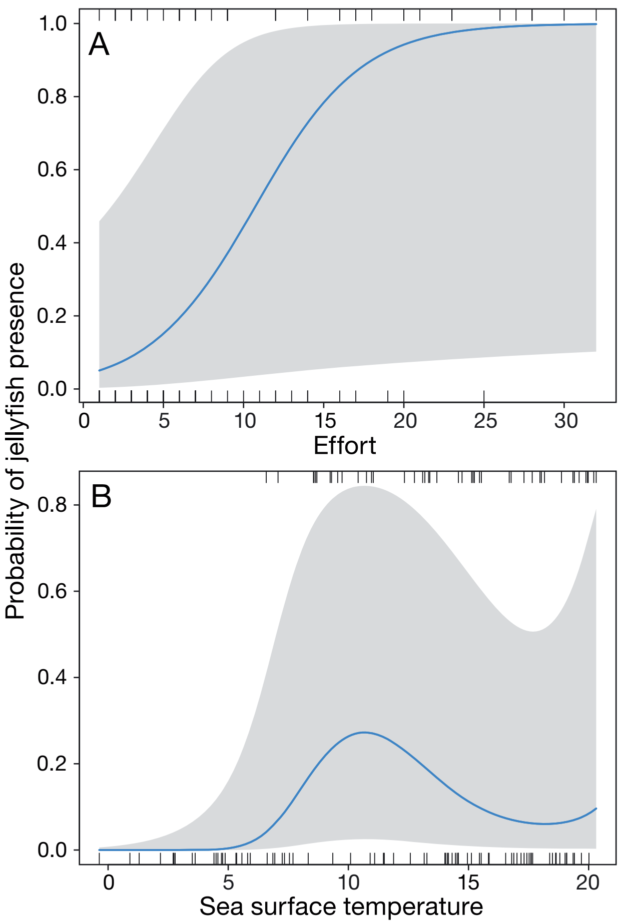

Fig. 4. Significant predictors of jellyfish occurrence: (A) effort (number of survey weeks) on jellyfish presence (probability scale) (from polyS2, the binomial generalized linear model); and (B) sea surface temperature (°C) on jellyfish presence (probability scale). Grey area: 95% CIs. Tick marks on *x*-axis represent each data point, whether or not *Cyanea capillata* were observed at that level of effort

large confidence bands in Fig. 4A,B are most likely a result of the sparseness of the data. Abundance of *C. capillata* in each of the 6 subregions increases with temperature up to approximately 20°C (Fig. 5).

3.3.2. Modelling jellyfish–turtle seasonal overlay

Peak proportions of observations in weekly intervals were compared among all data sources and all years (Fig. 6). Leatherback seasonality generally tracked jellyfish occurrence in Atlantic Canadian waters. More specifically, peak timing of residency among satellite-tagged leatherbacks occurs earlier on the Scotian Shelf than on the Gulf of St. Lawrence (Fig. 6A). This pattern is repeated for opportunistic sightings of leatherback turtles (Fig. 6B), jellyfish as bycatch in the DFO groundfish surveys (Fig. 6C), and the CSTN citizen science jellyfish observations (Fig. 6D). Note, however, that this pattern is reversed for the Dalhousie citizen science jellyfish observations (Fig. 6E) and the opportunistic jellyfish sightings (Fig. 6F); in these cases, observations peaked in the Gulf of St. Lawrence before they peaked on the Scotian Shelf. Overall, the timing of peak jellyfish occurrence was not significantly different between the 2 regions ($p = 0.6573$).

Cross-correlation analysis revealed an average lag of just over 2 wk of peak leatherback turtle presence behind jellyfish on the Scotian Shelf between the 2 leatherback data sources and 4 jellyfish sources. Leatherback residency had significant correlations from week −6 to 0, with highest correlations occurring with DFO jellyfish bycatch at week −2 (autocorrelation function [ACF] = 0.859), and opportunistic jellyfish sightings at week −4 (ACF = 0.724). Leatherback observations submitted to CSTN had significant correlations from week −4 to 1, with the highest correlations occurring with CSTN citizen science jellyfish observations at week 0 (ACF = 0.897) and Dalhousie citizen science observations at week −3 (ACF = 0.781). In contrast, there was no clear pattern of cross-correlation in the Gulf of St. Lawrence (see Figs. S5–S8 in the Supplement).

4. DISCUSSION

The principal objectives of this study were to better understand the seasonal distribution, species composition, and environmental drivers of common jellyfish occurring in Atlantic Canada, and to predict how a dynamic prey field may shape leatherback turtle distribution in this important foraging area. The results provide insights on both the phenology of jellyfish and on the previously undocumented seasonality of leatherback–jellyfish interactions in Atlantic Canadian waters. We hope that this information can contribute to the understanding of critical feeding habitat for this endangered turtle species in Canada. The results also highlight the utility of citizen science as an ecological research tool in data-poor situations.

Citizen science beach survey data provided a description of jellyfish seasonality, species composition, and regional distribution patterns (Fig. 3). Across all 6 years of citizen science jellyfish monitoring, the 2 most common scyphozoan species were *Cyanea capillata* (75% of total observations) and *Aurelia aurita* (3.7% of total observations). These species are consistently mentioned in previous studies on leath-

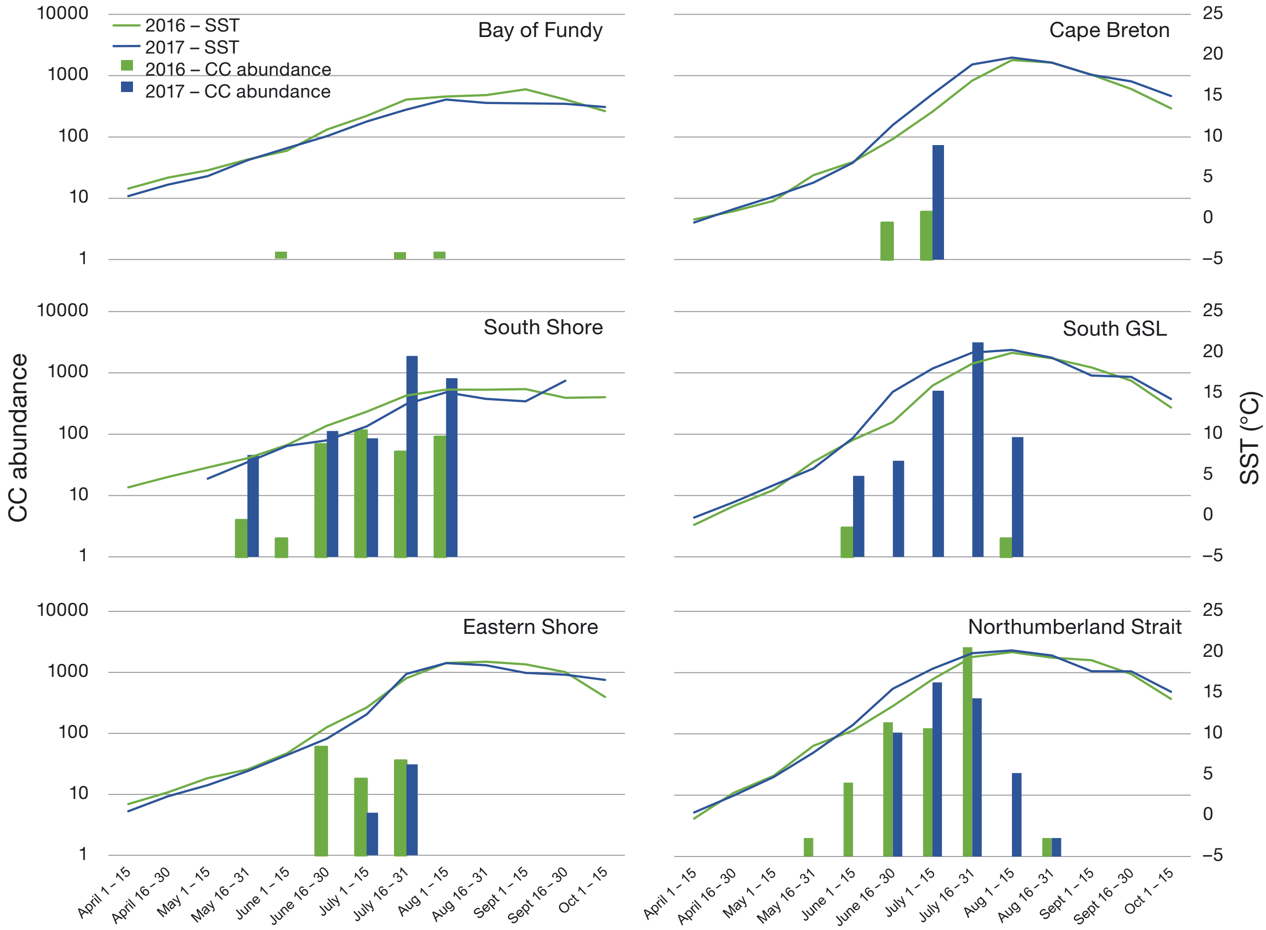

Fig. 5. Seasonality of *Cyanea capillata* (CC) abundance (from the Dalhousie citizen science network) and sea surface temperature (SST) (from the AVHRR SST Dataset, Remote Sensing Group, Bedford Institute of Oceanography) over time depicted in 2 wk intervals for each of the 6 regions. GSL: Gulf of St. Lawrence

erback sea turtle foraging ecology in Atlantic Canada (James & Herman 2001, James et al. 2006, Wallace et al. 2018). While ctenophores have not been identified as a primary food source for leatherbacks in this region, they were also prominent in the citizen science observations (20% of total jellyfish observations). Leatherback prey in Atlantic Canadian waters is typically described as large species of jellyfish (James & Herman 2001, James et al. 2005b, Heaslip et al. 2012); however, there have been documented cases of leatherback turtles elsewhere consuming small jellyfish *Linuche unguiculata* in high-density aggregations (Fossette et al. 2012). Ctenophores in Atlantic Canada are of similar size to *L. unguiculata*, and could offer potential feeding opportunities to foraging leatherbacks.

The most prominent jellyfish species observed by citizen science volunteers was *C. capillata*, with peak shoreline strandings in 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 strandings in Europe. Doyle et al. (2007) found maximum abundance of *C. capillata* to occur in late July in the Celtic and Irish Seas, and Pikesley et al. (2014) described the majority of *C. capillata* strandings occurring in the month of July in coastal UK waters. Stranding surveys conducted on the Isle of Anglesey found *C. capillata* most abundantly in July (Ionescu et al. 2016). This suggests that citizen science beach surveys can provide useful baseline information on jellyfish seasonality.

Generalized linear modelling suggested that observer effort and SST were statistically significant predictors of *C. capillata* strandings according to the citizen science data, but chl *a* and subregion were not. The significance of effort is important, and is widely understood to be a caveat to citizen science projects generally, as increased survey effort can increase the probability of detecting the target organisms (Houghton et al. 2007, Kéry et al. 2010).

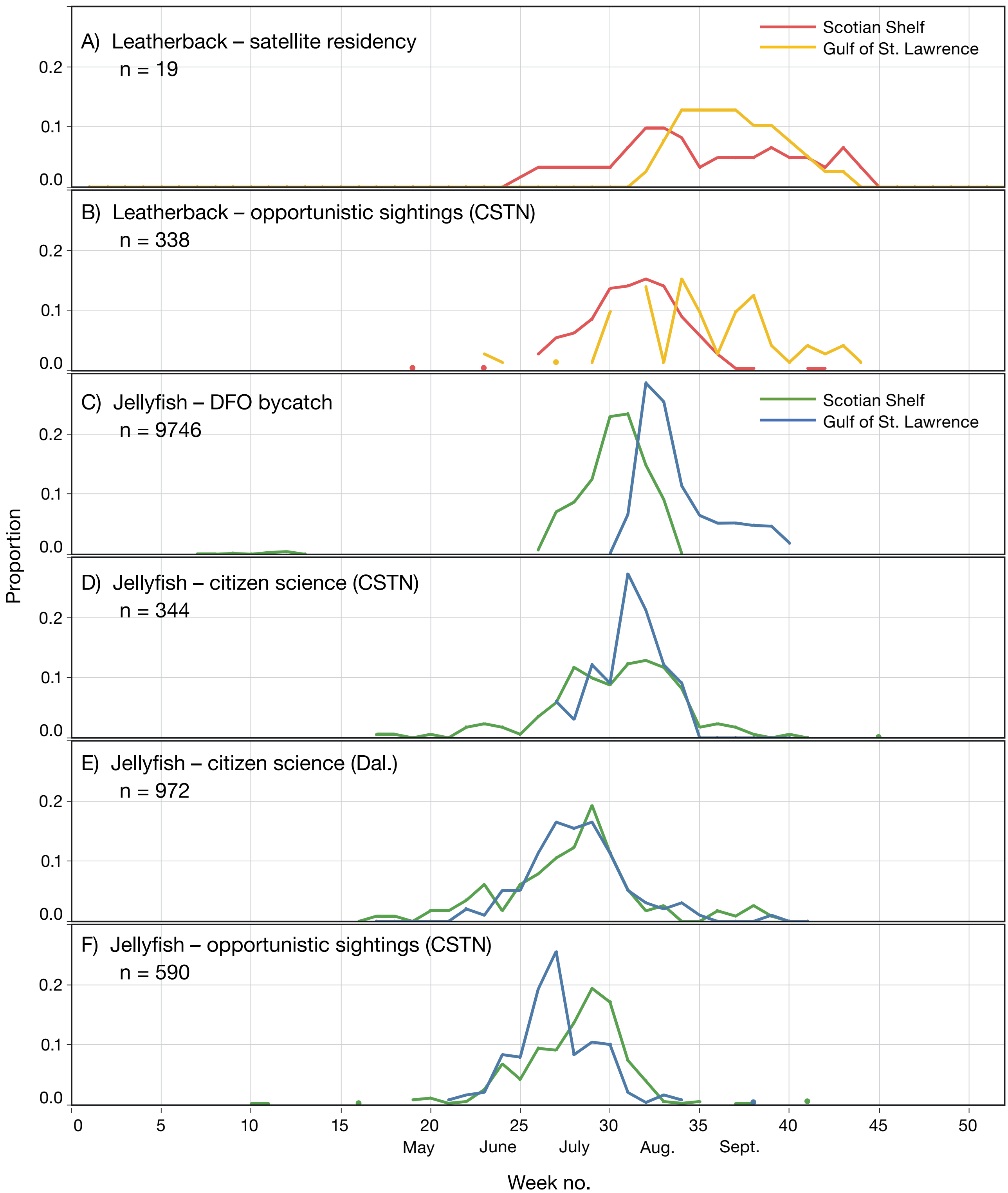

Fig. 6. Leatherback turtle and jellyfish seasonal overlap on the Scotian Shelf or Gulf of St. Lawrence; proportions of observations in weekly intervals (see Section 2.5.2); effort (n) includes zeros. (A) Residency of satellite-tagged leatherbacks, 2004–2017; (B) leatherback sightings reported to Canadian Sea Turtle Network (CSTN), 2007–2017; (C) jellyfish occurrence reported in Fisheries and Oceans Canada (DFO) groundfish surveys, 2006–2017; (D) jellyfish presence/absence reported in CSTN weekly beach monitoring programme, 2007–2010; (E) jellyfish presence/absence reported in Dalhousie University's weekly beach monitoring programme, 2016–2017; and (F) opportunistic jellyfish sightings reported by general public, 2016–2017

For this reason, detecting seasonal signals may be obscured by either too little or too much effort. Interestingly, the model fits (Fig. 4) suggested that detection probability increased at first with effort but was constant above 20 wk of survey effort, indicating a non-linear relationship. It is important to interpret this result in context, as other factors such as consistency of survey effort and environmental factors may also come into play. In our case, for example, there was lower survey effort in the fall (September and October), which may have led to low probability of jellyfish detection in that season.

SST was also a significant predictor of *C. capillata* strandings, which may relate to the influence of temperature in their life cycle and population growth rate. Many jellyfish species (including *C. capillata*) have a biphasic life cycle (Brotz et al. 2012, Holstein & Laudet 2014). Planula larva settle and develop into asexually reproducing sessile benthic polyps, which later release free-swimming ephyrae that mature into pelagic medusae, which reproduce sexually (Arai 1997, Holstein & Laudet 2014). The medusa stage is often what is popularly described as a 'jellyfish.'

For many jellyfish species, including *C. capillata*, ephyrae release occurs within a specific thermal range (Gröndahl 1988, Brewer & Feingold 1991, Holst 2012, Lucas et al. 2012). As *C. capillata* is described as a cold-water species that thrives in temperate and boreal waters (Holst 2012, Goldstein et al. 2017), the potential influence of SST on *C. capillata* presence observed for this species (our Figs. 4 & 5) may relate to its thermal biology. There is a positive correlation for jellyfish presence between 5° and 11°C, followed by a negative trend, and then a positive trend from 18°C onwards (Fig. 4). While the increase at lower temperatures may relate to increased production of ephyrae and medusae within an optimal thermal range, the increase at high temperature might indicate senescence, which may also lead to increased detection in beach strandings. Consistent with this hypothesis, the upper thermal limit where senescence of *C. capillata* medusae occurs was reported at 19.1°C (±2.3°C) in Connecticut waters (Brewer 1989). SST reaches values between 15° and 20°C in August in the Gulf of St. Lawrence, and can reach higher in the Northumberland Strait (Galbraith et al. 2016), likely leading to widespread senescence of medusae.

The modelling presented here only considered *C. capillata* stranded on coastlines. It is unknown to what degree jellyfish occurrence on beaches reflects occurrence in adjacent waters (Fleming et al. 2013). This is important to consider with species such as *C. capillata*, as they have been observed in the water column at depths associated with the thermocline, and therefore, temperatures differing from surface temperature (Bailey et al. 2012, Wallace et al. 2014). Many of the *C. capillata* reported in the citizen science data were most likely dead when they were washed ashore, indicated by the lack of oral arms and tentacles (e.g. Fig. 2G,H). Development of blastulae on oral arms has been attributed to the degeneration of *C. capillata*; 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* into late September and persisting into October (James et al. 2005b, 2006). This may suggest that although jellyfish strandings were not being observed by citizen scientists, there were still *C. capillata* available in adjacent waters.

While the present modelling results suggest SST is a primary driver of jellyfish presence, there may be other important variables missing. 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 (but not specifically *C. capillata*) occurrence (Decker et al. 2007, Aleksa et al. 2018). 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 & Jarms 2007, Holst 2012). Including salinity in future modelling could provide insight into the effects of salinity on the medusa stage of *C. capillata*.

Jellyfish populations in temperate waters are thought to typically produce a single cohort per year that grows and matures at the same time (Gröndahl 1988, Brewer 1989, Lucas 2001, Lucas et al. 2012); however, in our case there was no obvious single reproductive event visible in the bell diameter data. Assuming growth rate was relatively constant, a single cohort would have produced a visible relationship between day of the year and diameter of the jellyfish observed. These findings could indicate protracted ephyrae release, as the bell diameter range remained broad throughout the survey period (Fig. S3); this is also consistent with a study conducted in the Irish and Celtic Seas, where 3 species of jellyfish (including *C. capillata*) were all found to have broad size and weight ranges through the survey period (Houghton et al. 2007). Likewise, Ceh et al. (2015) found various-sized *Chrysaora plocamia* medusae throughout the growing season and attributed this to multiple cohorts of ephyrae. Yet, seasonal life cycles of temperate jellyfish are not completely understood and may vary. While our study was able to offer some insights into jellyfish phenology, locating polyp beds was not one of the original objectives of this research. Future study should consider observing polyp beds as an important part of the life cycle, from which strobilation periods and reproductive cohorts can be defined (Lucas et al. 2012, Goldstein et al. 2017).

The Bay of Fundy was not included in the comparison of peak leatherback and jellyfish occurrence. There were no leatherback turtles from the satellite telemetry data that entered the Bay of Fundy, and turtle sightings that were reported to the CSTN were observed in close proximity to the Scotian Shelf/Bay of Fundy boundary (Fig. 1C). These findings are consistent with studies of 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 & 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 movements of satellite-tagged leatherbacks in Atlantic Canadian waters (DFO 2011). Coincidentally, our citizen science programmes have revealed very few jellyfish observations in the Bay of Fundy, suggesting that a lack of prey may contribute to the scarcity of turtles here.

Consistent with known migration patterns, leatherback peak occurrence was earlier on the Scotian Shelf than the Gulf of St. Lawrence (Fig. 6). Leatherback turtles usually appear on the Scotian Shelf in early summer, and typically spend several weeks there 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 late September–October, when they begin migration southward (James et al. 2005b). As expected in a predator–prey relationship (Cushing 1990, Visser et al. 2011), there was significant temporal overlap between leatherbacks and jellyfish (our Fig. 6) on the Scotian Shelf, despite the earlier timing of peak leatherback occurrence in the 2 Dalhousie citizen science datasets.

The jellyfish data sources show seasonal differences in peak jellyfish occurrence between the Scotian Shelf and the Gulf of St. Lawrence. Two of the 4 data sources (DFO groundfish surveys and CSTN citizen science) indicated peak jellyfish occurrence on the Scotian Shelf before the Gulf of St. Lawrence (Fig. 6). The DFO groundfish surveys take place on the Scotian Shelf in July, and then in the Gulf of St. Lawrence in August and September. As the groundfish surveys only last about 1 mo in each region, temporal patterns of jellyfish are not represented completely, and therefore, it is important to consider other jellyfish data sources as well.

The 2 jellyfish sources from the Dalhousie citizen science programme showed peak occurrence of jellyfish in the Gulf of St. Lawrence slightly before the Scotian Shelf (Fig. 6). There was higher citizen science coverage in the Gulf of St. Lawrence region with this programme (Fig. S2), and therefore, the timing patterns in the Gulf of St. Lawrence may be better represented with these 2 data sources than the other 2 jellyfish data sources. If *C. capillata* polyp beds are located within the Gulf of St. Lawrence, one could expect earlier peak occurrence there, with a slight delay of Scotian Shelf jellyfish peak occurrence.

There were differences between lags and their correlation depending on the region. The Scotian Shelf cross-correlation indicated that jellyfish presence leads leatherback presence, independent of the data source used, by an average of 2 wk. 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). In contrast, there were no overall clear patterns of lag time observed for the Gulf of St. Lawrence region between leatherback and jellyfish occurrence. Time spent on the Scotian Shelf most likely depends on prey encounters and prey density, influencing leatherback arrival in the Gulf of St. Lawrence. Citizen science data revealed peak occurrence of *C. capillata* in July; however, there are documented cases of leatherbacks feeding on scyphomedusae in September in the Gulf region (James & Herman 2001, Wallace et al. 2015). This indicates there is a relatively wide temporal window for jellyfish in the Gulf of St. Lawrence. Satellite-tag data indicates that in recent years, tagged turtles spend over twice as long in the Gulf of St. Lawrence than they do on the Scotian Shelf, possibly taking advantage of persisting prey aggregations.

This study expands scientific knowledge on jellyfish phenology in the temperate North Atlantic, and provides insight into probable links between the endangered leatherback turtle, an obligate jellyfish predator, and their jellyfish prey field in Canadian waters. While there is an established amount of work on seasonal leatherback movements and migrations in Atlantic Canada (James et al. 2005a,b, 2006, 2007, Sherrill-Mix et al. 2007), there has been a lack of knowledge of the prey field. Using prey field data, the present findings corroborate both the definition of specific areas previously designated as important to leatherbacks in Canada and the energetic value of these areas to the species (Wallace et al. 2018). Enhanced understanding of how prey resource availability affects predator distributions is a key, and often missing part, of critical habitat identification. This is especially important when considering the stability of the Northwest Atlantic subpopulation of leatherback sea turtles. The global population trend of leatherback sea turtles is decreasing (Wallace et al. 2013), and a recent assessment of the Northwest Atlantic subpopulation suggests a decline based on leatherback nesting data (Northwest Atlantic Leatherback Working Group 2018). Future recovery of this subpopulation depends on appropriate conservation efforts in breeding and foraging areas (Tiwari et al. 2013). Atlantic Canadian waters provide leatherbacks 29–59% of their annual energy requirements (Wallace et al. 2018). Leatherbacks show fidelity to foraging grounds, returning annually to build energy reserves. Leatherback foraging grounds, such as those 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, contributing to the relative resilience and higher fecundity of the Northwest Atlantic versus Pacific populations (Wallace et al. 2018). Understanding the temporal aspects of the prey field can help managers predict the timing and residency of leatherbacks in the Atlantic Canadian Maritimes region, which may be helpful when trying to minimize the likelihood of negative human–turtle interactions.

While shedding light on predator–prey interactions, this case study highlights the utility of citizen science as an ecological research tool. The sightings data of leatherbacks and jellyfish between 3 different citizen science initiatives reveal matching seasonality between predator and prey in Atlantic Canadian waters, an observation that is corroborated by independently collected satellite tag and trawl survey data. Remarkably, the general conclusions that could be drawn from these very different data sources were quite similar (Fig. 6). Citizen science has been previously acknowledged as being highly effective at locating rare, elusive, and episodic organisms (Dickinson et al. 2010). Opportunistic sightings of jellyfish strandings have been collected by the general public to determine spatial and temporal patterns of jellyfish in other regions (Boero et al. 2009, Pikesley et al. 2014, Gatt et al. 2018, Record et al. 2018), and citizen science has been suggested as a valid tool in monitoring jellyfish distributions in space and time (Boero et al. 2009, Gatt et al. 2018). This is especially promising, as species groups like jellyfish that have episodic/ephemeral qualities are noted as notoriously difficult to survey and monitor at both local and broad scales (Brierley et al. 2005, Colombo et al. 2009, Graham et al. 2010). Having citizen scientists complete systematic shoreline surveys allowed for broader spatial and temporal coverage in this study, while maintaining a structured survey protocol. There are many ecological processes which occur at scales outside of the observational capabilities of individual researchers or instruments (Dickinson et al. 2010). In these situations, citizen science is a practical tool that can be utilized to investigate broad and regional-scale population trends, phenology, species interactions, and more (Dickinson et al. 2010), while improving ocean literacy and environmental awareness more generally (Bonney et al. 2009, Jordan et al. 2011).

5. CONCLUSION

The results of this study inform both our understanding of jellyfish phenology in Atlantic Canada and how the spatio-temporal patterns of common jellyfish species affect the seasonal migratory 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 species composition, seasonality, spatial distribution, and environmental drivers. Lion's mane jellyfish *Cyanea capillata* was the most commonly detected species (75.5% of all species-specific sightings), with peak temporal occurrence in July, and peak spatial occurrence in the Gulf of St. Lawrence. Generalized linear modelling indicated that SST and observer effort were significant positive predictors of *C. capillata* shoreline strandings. Leatherback seasonality generally tracked jellyfish occurrence in Atlantic Canadian waters. This project has shown that studying jellyfish at a regional scale is possible without costly 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 coastal habitat use of a migratory oceanic predator.

Acknowledgements. We gratefully acknowledge all of our citizen scientists for their collaboration and all who assisted with corresponding leatherback turtle biotelemetry and concurrent prey field research. This study is in part based on a MSc thesis by B.N. at Dalhousie University, Canada. For their various and important contributions to this paper, we also thank: L. Bennett, Blomidon Field Naturalists, E. Bond, E. Cantoni, C. Caverhill, Z. Chaisson, T. Clarke, T. Doyle, J. Emberley, Bert Fricker, Blair Fricker, J. Fricker, Halifax Field Naturalists, K. Hamelin, J. Mills Fleming, B. Mitchell, M. Nicholson, S. Plourde, J. Spry, J. Vavra, S. Whoriskey, S. Wilson, and J. Wolford. This work was supported with funding from Canadian Wildlife Federation, Conservation International, Environment and Climate Change Canada, Fisheries and Oceans Canada, Habitat Stewardship Program for Species at Risk, National Fish and Wildlife Foundation, National Marine Fisheries Service, Natural Sciences and Engineering Research Council of Canada, the Nova Scotia Graduate Scholarship, the Ocean Frontier Institute, and World Wildlife Fund Canada.

LITERATURE CITED

Aleksa K, Nero R, Wiggert J, Graham W (2018) Descriptive density models of scyphozoan jellyfish in the northern Gulf of Mexico. Mar Ecol Prog Ser 591:71–85

Arai MN (1997) A functional biology of Scyphozoa. Chapman & Hall, London

Bailey H, Benson SR, Shillinger GL, Bograd SJ and others (2012) Identification of distinct movement patterns in Pacific leatherback turtle populations influenced by ocean conditions. Ecol Appl 22:735–747

Beauchamp DA, Wahl D, Johnson BM (2007) Predator-prey interactions. In: Guy CS, Brown MJ (eds) Analysis and interpretation of inland fisheries data. American Fisheries Society, Bethesda, MD, p 765–842

Bedford M, Melbourne-Thomas J, Corney S, Jarvis T, Kelly N, Constable A (2015) Prey-field use by a Southern Ocean top predator: enhanced understanding using integrated datasets. Mar Ecol Prog Ser 526:169–181

Benson SR, Forney KA, Harvey JT, Carretta JV, Dutton PH (2007) Abundance, distribution, and habitat of leatherback turtles (*Dermochelys coriacea*) off California, 1990–2003. Fish Bull 105:337–347

Berger J, Stacey PB, Bellis L, Johnson MP (2001) A mammalian predator-prey imbalance: grizzly bear and wolf extinction affect avian neotropical migrants. Ecol Appl 11:947–960

Bleakney JS (1965) Reports of marine turtles from New England and Eastern Canada. Can Field Nat 79:120–128

Boero F, Putti M, Trainito E, Prontera E, Piraino S, Shiganova TA (2009) First records of *Mnemiopis leidyi* (Ctenophora) from the Ligurian, Thyrrhenian and Ionian Seas (Western Mediterranean) and first record of *Phyllorhiza punctata* (Cnidaria) from the Western Mediterranean. Aquat Invasions 4:675–680

Bonney R, Cooper CB, Dickinson J, Kelling S, Phillips T, Rosenberg KV, Shirk J (2009) Citizen science: a developing tool for expanding science knowledge and scientific literacy. Bioscience 59:977–984

Bonney R, Shirk JL, Phillips TB, Wiggins A and others (2014) Next steps for citizen science. Science 343:1436–1437

Boyd IL (2002) Integrated environment–prey–predator interactions off South Georgia: implications for management of fisheries. Aquat Conserv: Mar Freshw Ecosyst 12:119–126

Brewer RH (1989) The annual pattern of feeding, growth, and sexual reproduction in *Cyanea* (Cnidaria: Scyphozoa) in the Niantic River Estuary, Connecticut. Biol Bull 176:272–281

Brewer RH, Feingold JS (1991) The effect of temperature on the benthic stages of *Cyanea* (Cnidaria: Scyphozoa), and their seasonal distribution in the Niantic River estuary, Connecticut. J Exp Mar Biol Ecol 152:49–60

Brierley AS, Boyer DC, Axelson BE, Lynam CP, Sparks CA, Boyer H, Gibbons MJ (2005) Towards the acoustic estimation of jellyfish abundance. Mar Ecol Prog Ser 295:105–111

Brotz L, Cheung WWL, Kleisner K, Pakhomov E, Pauly D (2012) Increasing jellyfish populations: trends in Large Marine Ecosystems. Hydrobiologia 690:3–20

Brown MW, Tobin D (1999) Vessel and aerial surveys for North Atlantic Right Whales in Canadian waters, 1998. Final Rep: Contract F5245-8-0064. Bedford Institute of Oceanography, Halifax

Brown MW, Tobin D (2000) Surveillance of North Atlantic Right Whales in Canadian waters: 1999. Final Rep: Contracts F5245-9-0035, F5245-9-0193. Bedford Institute of Oceanography, Halifax

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer-Verlag, New York, NY

Canale GR, Bernardo CSS (2015) Predator-prey interaction between two threatened species in a Brazilian hotspot. Biota Neotrop 16:e0059

Ceh J, Gonzalez J, Pacheco AS, Riascos JM (2015) The elusive life cycle of scyphozoan jellyfish – metagenesis revisited. Sci Rep 5:12037

Colombo AG, Benovi A, Malej A, Lu i D and others (2009) Acoustic survey of a jellyfish-dominated ecosystem (Mljet Island, Croatia). Hydrobiologia 616:99–111

COSEWIC (Committee on the Status of Endangered Wildlife in Canada) (2012) COSEWIC assessment and status report on the Leatherback Sea Turtle *Dermochelys coriacea* in Canada. COSEWIC, Ottawa

Cushing DH (1990) Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. Adv Mar Biol 26:249–293

Decker MB, Brown CW, Hood RR, Purcell JE and others (2007) Predicting the distribution of the scyphomedusa *Chrysaora quinquecirrha* in Chesapeake Bay. Mar Ecol Prog Ser 329:99–113

DFO (Fisheries and Oceans Canada) (2011) Using satellite tracking data to define important habitat for leatherback turtles in Atlantic Canada. DFO Can Sci Advis Sec Sci Response 2012/036

DFO (2016a) 2015 Maritimes research vessel survey trends on the Scotian Shelf and Bay of Fundy. DFO Can Sci Advis Sec Sci Response 2016/011

DFO (2016b) Updated indices of abundance to 2015 for stocks of six groundfish species assessed by DFO Gulf Region. DFO Can Sci Advis Sec Sci Response 2016/016

Dickinson JL, Zuckerberg B, Bonter DN (2010) Citizen science as an ecological research tool: challenges and benefits. Annu Rev Ecol Evol Syst 41:149–172

Dickinson JL, Shirk J, Bonter D, Bonney R and others (2012) The current state of citizen science as a tool for ecological research and public engagement. Front Ecol Environ 10: 291–297

Doyle TK, Houghton JDR, Buckley SM, Hays GC, Davenport J (2007) The broad-scale distribution of five jellyfish species across a temperate coastal environment. Hydrobiologia 579:29–39

Fleming N, Harrod C, Houghton J (2013) Identifying potentially harmful jellyfish blooms using shoreline surveys. Aquacult Environ Interact 4:263–272

Fossette S, Gleiss AC, Casey JP, Lewis AR, Hays GC (2012) Does prey size matter? Novel observations of feeding in the leatherback turtle (*Dermochelys coriacea*) allow a test of predator-prey size relationships. Biol Lett 8:351–354

Freitag A, Pfeffer MJ (2013) Process, not product: investigating recommendations for improving citizen science 'success'. PLOS ONE 8:e64079

Galbraith PS, Chassé J, Caverhill C, Nicot P and others (2016) Physical oceanographic conditions in the Gulf of St. Lawrence in 2015. DFO Can Sci Advis Sec Res Doc 2016/056

Gatt MP, Deidun A, Galea A, Gauci A (2018) Is citizen science a valid tool to monitor the occurrence of jellyfish? The Spot the Jellyfish case in the Maltese Islands. In: Shim JS, Chun I, Lim HS (eds) Proc Int Coast Symp (ICS) 2018. J Coast Res Spec Issue 85:316–320

Goldstein J, Augustin CB, Bleich S, Holst S (2017) A matter of tolerance: distribution potential of scyphozoan polyps in a changing environment. Mar Ecol 38:e12457

Graham TR, Harvey JT, Benson SR, Renfree JS, Demer DA (2010) The acoustic identification and enumeration of scyphozoan jellyfish, prey for leatherback sea turtles (*Dermochelys coriacea*), off central California. ICES J Mar Sci 67:1739–1748

Gregr EJ, Gryba R, James MC, Brotz L, Thornton SJ (2015) Information relevant to the identification of critical habitat for Leatherback Sea Turtles (*Dermochelys coriacea*) in Canadian Pacific waters. DFO Can Sci Advis Sec Sci Res Doc 2015/079

Gröndahl F (1988) A comparative ecological study on the scyphozoans *Aurelia aurita*, *Cyanea capillata* and *C. lamarckii* in the Gullmar Fjord, western Sweden, 1982 to 1986. Mar Biol 97:541–550

Hamelin KM, Kelley DE, Taggart CT, James MC (2014) Water mass characteristics and solar illumination influence leatherback turtle dive patterns at high latitudes. Ecosphere 5:1–20

Hawlena D, Schmitz OJ (2010) Physiological stress as a fundamental mechanism linking predation to ecosystem functioning. Am Nat 176:537–556

Hay SJ, Hislop JRG, Shanks AM (1990) North Sea scyphomedusae — summer distribution, estimated biomass and significance particularly for 0-group gadoid fish. Neth J Sea Res 25:113–130

Heaslip SG, Iverson SJ, Bowen WD, James MC (2012) Jellyfish support high energy intake of Leatherback Sea Turtles (*Dermochelys coriacea*): video evidence from animal-borne cameras. PLOS ONE 7:e33259

Holst S (2012) Effects of climate warming on strobilation and ephyra production of North Sea scyphozoan jellyfish. Hydrobiologia 690:127–140

Holst S, Jarms G (2007) Substrate choice and settlement preferences of planula larvae of five Scyphozoa (Cnidaria) from German Bight, North Sea. Mar Biol 151: 863–871

Holstein TW, Laudet V (2014) Life-history evolution: at the origins of metamorphosis. Curr Biol 24:R159–R161

Hosia A, Augustin CB, Dinasquet J, Granhag L and others (2015) Autumnal bottom-up and top-down impacts of *Cyanea capillata*: a mesocosm study. J Plankton Res 37: 1042–1055

Houghton JD, Doyle TK, Wilson MW, Davenport J, Hays GC (2006) Jellyfish aggregations and leatherback turtle foraging patterns in a temperate coastal environment. Ecology 87:1967–1972

Houghton JDR, Doyle TK, Davenport J, Lilley MKS, Wilson RP, Hays GC (2007) Stranding events provide indirect insights into the seasonality and persistence of jellyfish medusae (Cnidaria: Scyphozoa). Hydrobiologia 589:1–13

Ionescu MS, Wilson SE, Evans EJ (2016) Jellyfish stranding observations around the Isle of Anglesey in the summer of 2014. Geo-Eco-Mar 22:109–118

James MC, Herman TB (2001) Feeding of *Dermochelys coriacea* on medusae in the Northwest Atlantic. Chelonian Conserv Biol 4:202–205

James MC, Mrosovsky N (2004) Body temperatures of leatherback turtles (*Dermochelys coriacea*) in temperate waters off Nova Scotia, Canada. Can J Zool 82:1302–1306

James MC, Ottensmeyer AC, Myers RA (2005a) Identification of high-use habitat and threats to leatherback sea turtles in northern waters: new directions for conservation: leatherback movements and conservation. Ecol Lett 8:195–201

James MC, Myers RA, Ottensmeyer CA (2005b) Behaviour of leatherback sea turtles, *Dermochelys coriacea*, during the migratory cycle. Proc R Soc B 272:1547–1555

James MC, Sherrill-Mix SA, Martin K, Myers RA (2006) Canadian waters provide critical foraging habitat for leatherback sea turtles. Biol Conserv 133:347–357

James MC, Sherrill-Mix SA, Myers RA (2007) Population characteristics and seasonal migrations of leatherback sea turtles at high latitudes. Mar Ecol Prog Ser 337: 245–254

Jordan RC, Gray SA, Howe DV, Brooks WR, Ehrenfeld JG (2011) Knowledge gain and behavioral change in citizen-science programs: citizen-scientist knowledge gain. Conserv Biol 25:1148–1154

Jordan R, Crall A, Gray S, Phillips T, Mellor D (2015) Citizen science as a distinct field of inquiry. Bioscience 65: 208–211

Kéry M, Royle JA, Schmid H, Schaub M, Volet B, Häfliger G, Zbinden N (2010) Site-occupancy distribution modeling to correct population-trend estimates derived from opportunistic observations. Conserv Biol 24:1388–1397

Kosmidis I (2017) Package 'brglm'. R package version 0.6.1. https://cran.r-project.org/web/packages/brglm/brglm.pdf

Lucas CH (2001) Reproduction and life history strategies of the common jellyfish, *Aurelia aurita*, in relation to its ambient environment. Hydrobiologia 451:229–246

Lucas CH, Graham WM, Widmer C (2012) Jellyfish life histories: role of polyps in forming and maintaining scyphomedusa populations. Adv Mar Biol 63:133–196

Lucas CH, Jones DOB, Hollyhead CJ, Condon RH and others (2014) Gelatinous zooplankton biomass in the global oceans: geographic variation and environmental drivers. Glob Ecol Biogeogr 23:701–714

Magome S, Yamashita T, Kohama T, Kaneda A, Hayami Y, Takahashi S, Takeoka H (2007) Jellyfish patch formation investigated by aerial photography and drifter experiment. J Oceanogr 63:761–773

Northwest Atlantic Leatherback Working Group (2018) Northwest Atlantic leatherback turtle (*Dermochelys coriacea*) status assessment (Wallace B, Eckert K, eds). Tech Rep No. 16. Conservation Science Partners and the Wider Caribbean Sea Turtle Conservation Network (WIDECAST), Godfrey, IL

Pikesley SK, Godley BJ, Ranger S, Richardson PB, Witt MJ (2014) Cnidaria in UK coastal waters: description of spatio-temporal patterns and inter-annual variability. J Mar Biol Assoc UK 94:1401–1408

Purcell JE (2012) Jellyfish and ctenophore blooms coincide with human proliferations and environmental perturbations. Annu Rev Mar Sci 4:209–235

R Core Team (2017) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. www.r-project.org

Record NR, Tupper B, Pershing AJ (2018) The jelly report: forecasting jellyfish using email and social media. Anthropocene Coasts 1:34–43

Sherrill-Mix SA, James MC, Myers RA (2007) Migration cues and timing in leatherback sea turtles. Behav Ecol 19:231–236

Silvertown J (2009) A new dawn for citizen science. Trends Ecol Evol 24:467–471

Sipos JC, Ackman RG (1968) Jellyfish (*Cyanea capillata*) lipids: fatty acid composition. J Fish Res Board Can 25: 1561–1569

Tiwari M, Wallace BP, Girondot M (2013) *Dermochelys coriacea* (Northwest Atlantic Ocean subpopulation). IUCN Red List of Threatened Species 2013: e.T46967827A46967830

Visser F, Hartman K, Pierce G, Valavanis V, Huisman J (2011) Timing of migratory baleen whales at the Azores in relation to the North Atlantic spring bloom. Mar Ecol Prog Ser 440:267–279

Wallace BP, Tiwari M, Girondot M (2013) *Dermochelys coriacea*. IUCN Red List of Threatened Species 2013: e.T6494A43526147

Wallace BP, Schumacher J, Seminoff JA, James MC (2014) Biological and environmental influences on the trophic ecology of leatherback turtles in the Northwest Atlantic Ocean. Mar Biol 161:1711–1724

Wallace BP, Zolkewitz M, James MC (2015) Fine-scale foraging ecology of leatherback turtles. Front Ecol Environ 3:1–15

Wallace BP, Zolkewitz M, James MC (2018) Discrete, high-latitude foraging areas are important to energy budgets and population dynamics of migratory leatherback turtles. Sci Rep 8:11017

Williams R, Krkošek M, Ashe E, Branch TA and others (2011) Competing conservation objectives for predators and prey: estimating killer whale prey requirements for Chinook salmon. PLOS ONE 6:e26738

Editorial responsibility: Graeme Hays, Burwood, Victoria, Australia

Submitted: December 17, 2018; Accepted: April 25, 2019
Proofs received from author(s): June 11, 2019