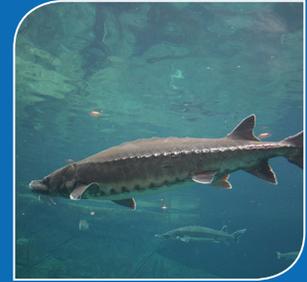
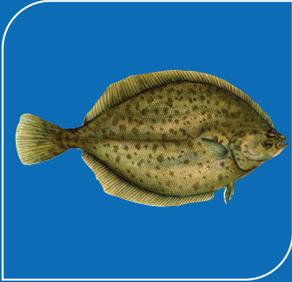




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Scientific publications by ICNAF and NAFO have been in existence since ICNAF began in 1949 with the ICNAF Special Publication series dealing with proceedings of scientific symposia. The ICNAF Research Bulletin was started in 1964 to provide a means of publishing results of scientific research relevant to ICNAF. The *ICNAF Research Bulletin* was terminated in September 1979 after the issue of Number 14. The first volume of the NAFO Journal of Northwest Atlantic Fishery Science was published in December 1980, after NAFO came into force replacing ICNAF in 1979.

The Northwest Atlantic fisheries have a rich history, and a great deal of research has been sponsored and encouraged by NAFO and its predecessor ICNAF. NAFO has been a leader amongst international organizations in the application of science to fishery management and in the regulation of fisheries in areas beyond national jurisdiction. In accordance with its mandate to disseminate information on fisheries research to the scientific community, the Scientific Council of NAFO publishes the *Journal of Northwest Atlantic Fishery Science*, which contains peer-reviewed primary papers, and NAFO Scientific Council Studies, which contains unrefereed papers of topical interest and importance to the Scientific Council. Lists of these and other NAFO publications are given on the back of this issue.

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Predictive Models of Yellowtail Flounder Bycatch in the U.S. Sea Scallop Fishery on Georges Bank

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Abstract

Many commercial fisheries face bycatch challenges. Avoiding non-target species while maximizing harvest of target species may require fishing differently across seasons and years, so the ability to predict bycatch occurrence is important for efficient and sustainable fishing operations. We demonstrate a potential application of bycatch predictions in the Atlantic sea scallop (*Placopecten magellanicus*) fishery. Catch data from a bycatch survey were used to develop models for yellowtail flounder (*Limanda ferruginea*) bycatch in the scallop fishery in response to environmental variables, and the models were validated using at-sea observer data. Results indicate that location (latitude, longitude, management area), temperature, zenith angle (a proxy for ambient light), and temporal effects (season, month, year) affect the presence and abundance of yellowtail flounder bycatch in the scallop fishery. Simple models with a subset of variables (latitude, longitude, and month) were fitted to help predict the magnitude and location of bycatch prior to fishery openings and in areas with no bycatch information. This study demonstrates how predictive models can be used to avoid bycatch species.

Keywords: Atlantic sea scallop, bycatch avoidance, generalized additive model, yellowtail flounder

Introduction

Bycatch is a common problem in commercial fisheries, and there are a variety of solutions to achieve bycatch reduction (O’Keefe *et al.*, 2013; Pérez Roda *et al.*, 2019). Gear modifications can prevent or reduce capture of unwanted species, fishing behaviour modifications can give non-target species an opportunity to escape fishing gear before being brought on board the vessel, and spatiotemporal measures can help fishing vessels avoid encounters with bycatch species. Avoiding bycatch species requires knowledge of where they co-occur with targeted species. This knowledge may be based on distribution maps from surveys or previous fishing, in-season communications, and predictive maps based on environmental models. We focus on predictive modelling as a potential resource for bycatch avoidance efforts.

Many advances have been made in species distribution modelling, with increasing aim towards ecological sensibility and interpretability (Guisan *et al.*, 2006;

Valavanis *et al.*, 2008). Predictive mapping and distribution modelling are often used to support sustainable resource use. Generalized additive models and maximum entropy modelling have been used to predict abundance of pink shrimp (Politou *et al.*, 2008), squid habitat (Sanchez *et al.*, 2008), probability of occurrence and abundance of hake (Tserpes *et al.*, 2008), habitat overlap of alewife, herring, and Atlantic mackerel (Turner *et al.*, 2016), abalone fishing grounds (Jalali *et al.*, 2015), and skate egg nursery habitat (Rooper *et al.*, 2019).

In the current study, we use generalized additive models to predict yellowtail flounder (*Limanda ferruginea*) bycatch in the Atlantic sea scallop (*Placopecten magellanicus*) fishery in the northeast US. The most productive fishing grounds for Atlantic sea scallop are on Georges Bank (Caddy, 1989; Fig. 1). Although the scallop resource on Georges Bank is healthy, the yellowtail flounder stock status is poor (TRAC, 2019), resulting in low bycatch quotas that constrain the scallop fishery.

The scallop fishery is managed by a rotational harvest strategy in which the Bank is divided into closed, access, and open areas (NEFMC, 2004). No harvesting is allowed in closed areas. “Access areas” are open to the scallop fleet for a limited number of trips in certain months and are closed in years when small scallops are abundant. Open areas are available year round to the scallop fishery. Prior to 2018, the fishery opened annually on March 1, and subsequently has opened on April 1. A majority of effort typically occurs in the spring and summer months, peaking in or around May. The scallop fishery management plan combines multiple regulatory techniques including quotas, days-at-sea limits in open areas, trip limits, and limited number of trips to and seasonal closures of access areas. The variety of regulations lends itself to some of the temporal effort patterns seen in the fishery over time, for example, there has traditionally been a surge in fishing activity in access areas when they first open.

In 2010, researchers at the University of Massachusetts Dartmouth School for Marine Science and Technology

(SMAST) implemented a voluntary yellowtail flounder bycatch avoidance system in the scallop fishery (O’Keefe and DeCelles, 2013). Scallopers collected and reported bycatch data daily. SMAST staff used the data to prepare advisory reports, which were distributed to participating captains (O’Keefe and DeCelles, 2013). One challenge in the bycatch avoidance system was an inability to provide accurate advice on bycatch hotspots before the start of the fishing season and in areas in which data were not available.

Yellowtail flounder catch rates and abundance are related to abiotic environmental factors such as temperature, depth, and substrate (DeLong and Collie, 2004; Simpson and Walsh, 2004; Methratta and Link, 2007) and with biotic factors such as density of co-occurring species (Hyun *et al.*, 2014). Seasonal (DeLong and Collie, 2004; Pereira *et al.*, 2012; Winton *et al.*, 2017) and diel variation is common in yellowtail flounder catches (*e.g.*, Casey and Meyers, 1998; Cadrin and Westwood, 2004; Walsh and Morgan, 2004; Truesdell, 2013). However, there is less information

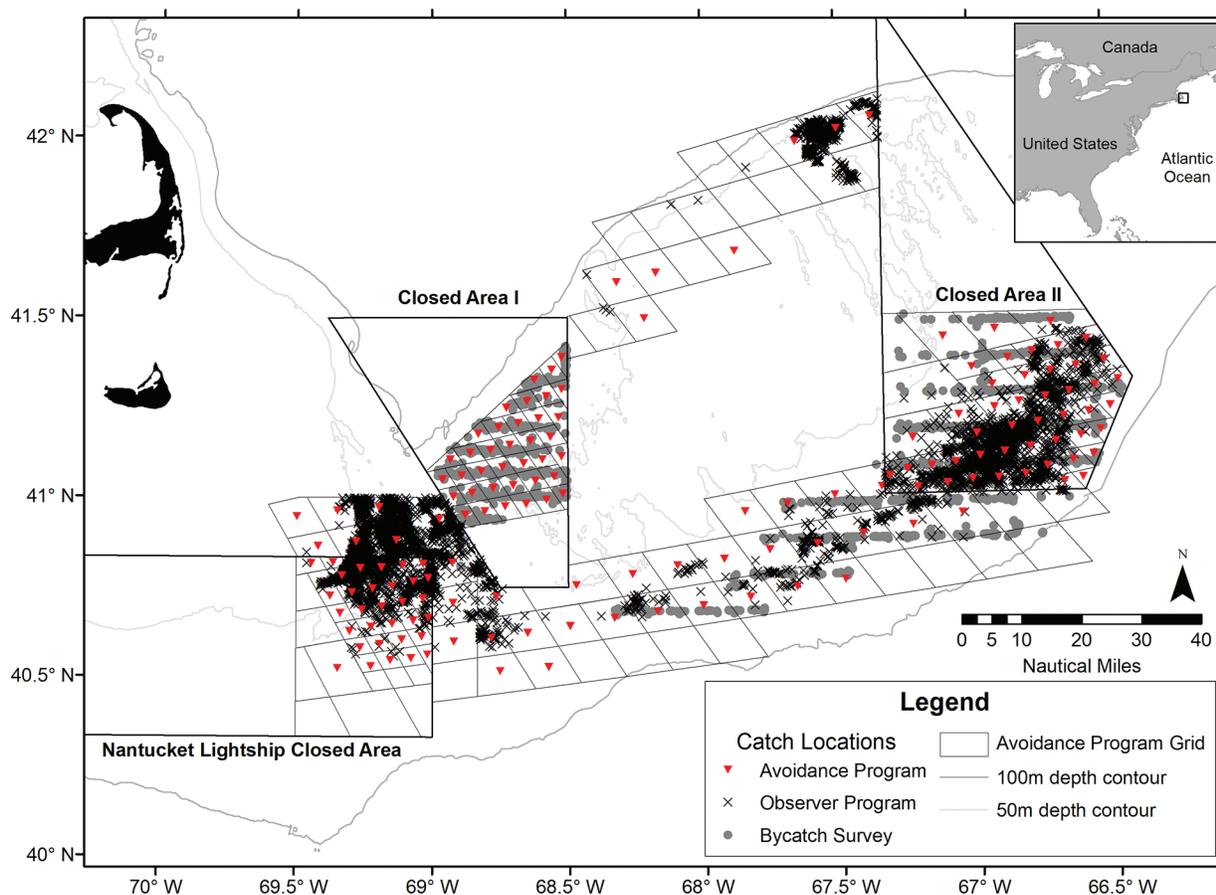


Fig. 1 The Georges Bank study area showing 50m and 100m depth contours and Nantucket Lightship Closed Area, Closed Area I, Closed Area II, and the distribution of catch data from the bycatch avoidance program (red triangles), Observer Program (black X), and bycatch survey (gray circle).

available on the relationships between bycatch of yellowtail flounder in the scallop fishery and environmental factors (Smolowitz *et al.*, 2012; NEFSC, 2013).

The New England Fishery Management Council (NEFMC, 2013) developed seasonal and area restrictions for the scallop fishery based on yellowtail flounder bycatch analyses by Smolowitz *et al.* (2012) and the Council's Scallop Plan Development Team. Smolowitz *et al.* (2012) found that the bycatch rate of yellowtail flounder was greatest from August to October and that yellowtail flounder were more abundant on eastern Georges Bank. Average annual yellowtail flounder bycatch in the scallop fishery was reduced after the time-area closures were implemented (NEFMC, 2018), but the measures have not been evaluated to determine if changes in environmental variables affecting yellowtail flounder could be used to refine the closures.

We developed two types of models for predicting the location and amount of yellowtail flounder taken in the sea scallop fishery. An exploratory set of models (hereafter the “complex” models) was based on survey catch data and a relatively wide range of environmental data, including data that was not available during preparation of advisory reports for the bycatch avoidance program, and may not be routinely available for programs based on fishery-dependent data. The “simple” model was based on additional catch data and a smaller set of variables that could be incorporated into the bycatch avoidance program to predict yellowtail flounder bycatch hotspots in near real time. We evaluated both model types by cross validation to determine and compare predictive power. Finally, the simple model was used to produce prediction maps of the type used in advisory reports. The maps were mailed to participants in the bycatch avoidance program before the beginning of the fishing season to identify bycatch hotspots where captains' reports were not available.

Materials and methods

Data

Our study focuses on the scallop fishery taking place on Georges Bank, an underwater plateau varying in depth from approximately 50–100 metres located approximately 100 kilometres off the coast of Massachusetts. Much of the bank is open to scallop fishing, with access areas (open on a restricted basis to scallop fishing for a limited number of trips) located within three closed areas (Fig. 1). We used data from three monitoring and research programs to build and validate bycatch models and prediction maps.

Data from a cooperative seasonal bycatch survey from 2011 to 2014 (Smolowitz *et al.*, 2012) were used in

building complex and simple models (Table 1). The bycatch survey was designed to provide spatio-temporal data on scallop meat yield and groundfish bycatch (Smolowitz *et al.*, 2012). It employed commercial scallop vessels to tow scallop survey dredges at systematic stations on Georges Bank. Weight of scallop meats and the number of yellowtail flounder were recorded for each tow along with start and end coordinates of tow, bottom water temperature, vessel speed, depth, and other factors (Smolowitz *et al.*, 2012; Goetting *et al.*, 2013; Huntsberger *et al.*, 2015). Weight of yellowtail flounder was calculated using the length weight relationship parameters provided by Wigley *et al.* (2003). A small number of tows that caught neither scallops nor yellowtail flounder (15 out of 2 158) were excluded. Substrate data are from SMAST Scallop Video Survey maps (Harris and Stokesbury, 2010). Raster values were extracted to tow locations in ArcGIS v10.2 (ESRI, 2013).

Scallop vessel catch data from the National Marine Fisheries Service (NMFS) Northeast Fisheries Observer Program (“Observer Program”) during years 2009 through 2011 on Georges Bank were used in cross validation to test the simple models and in creating prediction maps. Location, time and date, tow duration, scallop meat weight, yellowtail flounder weight, and a smaller set of environmental factors were recorded for each haul (Table 1). Only hauls when the observer was on-watch and all data fields were complete were used. In all data sets, entries were also excluded if gear issues were recorded that were likely to affect catch (*e.g.*, large holes).

The bycatch avoidance program data from 2010 through 2013 were included in the combined dataset used to create prediction maps based on the selected simple models. The central point of each grid cell was used as the catch location. Each data entry for the bycatch avoidance program consists of latitude and longitude of the reporting cell centroid, date, scallop meat weight, yellowtail flounder catch, and total number of tows.

Geographic coordinates (latitude and longitude) of the tow start point (or reporting cell centroid) were projected into the Universal Transverse Mercator (UTM) Zone 19 using the R package *rgdal* (Bivand *et al.*, 2014). The projected coordinates (northing and easting, in metres) were used in models and maps.

Statistical Methods

A large proportion of tows from each data set contained zero yellowtail flounder (30% of bycatch survey records, 48% of observer program records, and 42% of avoidance program records). To accommodate the high occurrence of

Table 1. Descriptive statistics for variables from each data source. Yellowtail kg per hour or per haul are for the full datasets; D:K ratio and yellowtail proportion are for the data subsets when hauls of zero yellowtail or zero scallops are excluded.

Catch Data Source	Variable	Minimum	Maximum	Mean	Median	Standard Deviation
Bycatch Survey	scallop catch (kg/hr)	0	1791.52	91.77	48.82	155.41
	yellowtail flounder catch (kg/hr)	0	250.07	7.59	2.61	14.50
	D:K ratio (kg scallops/kg yellowtail)	0.0006	44.84	0.46	0.12	2.09
	proportion yellowtail flounder	0.0006	0.98	0.17	0.10	0.19
	beginning latitude	40.67	41.50	41.12	41.08	0.18
	beginning longitude	-68.98	-66.45	-67.69	-67.30	0.87
	bottom temperature (°C)	4.45	17.67	9.64	9.34	2.82
	depth (m)	40.96	101.30	70.72	69.49	10.38
	zenith angle	17.64	149.59	66.31	65.6	24.74
SMAST Bycatch Avoidance Program	scallop catch (kg/haul)	0	636.16	89.84	68.04	73.32
	yellowtail flounder catch (kg/haul)	0	30.84	0.61	0.09	1.85
	D:K ratio (kg scallops/kg yellowtail)	0.0002	1.36	0.02	0.00	0.06
	proportion yellowtail flounder	0.0002	0.58	0.02	0.00	0.04
	beginning latitude	40.52	42.05	41.09	41.10	0.24
	beginning longitude	-69.5	-66.47	-68.08	-68.68	1.06
	depth (m)	28.21	108.25	69.00	69.47	12.28
Observer Program	scallop catch (kg/hr)	0	7984.00	510.30	289.50	720.77
	yellowtail flounder catch (kg/hr)	0	136.08	3.46	0.82	7.56
	D:K ratio (kg scallops/kg yellowtail)	0	7.00	0.03	0.00	0.16
	proportion yellowtail flounder	0	0.88	0.03	0.00	0.06
	beginning latitude	40.56	42.10	41.05	41.05	0.35
	beginning longitude	-69.46	-66.47	-68.20	-68.92	1.05
	depth (m)	23.77	91.44	64.85	67.67	10.22
	zenith angle	17.37	161.64	71.16	68.5	33.98

zero catches, we applied a hurdle model-based approach (*e.g.*, Stefánsson, 1996; Maunder and Punt, 2004; Truesdell, 2013) in which the response variable (total bycatch proportion = total yellowtail catch divided by total yellowtail plus scallop catch) is modelled in two parts: a binary response and a conditional positive value response. The first part of the model uses a binomial distribution and represents the probability of catching at least one yellowtail flounder (henceforth referred to as the “bycatch probability”). Separately, the non-zero values are modelled using a beta distribution and represent the magnitude of the bycatch relative to the scallop catch (bycatch proportion) given that some bycatch occurred (henceforth referred to as the “conditional bycatch proportion model”). This

two-step model gives an understanding of two parts of the bycatch process: probability of bycatch occurring (from the bycatch probability step) and the relative proportion of bycatch (from the conditional bycatch proportion step). Generalized additive models of the catch data were built using forward selection based on AIC (Akaike, 1974) and the percentage of deviance explained. K-fold cross validation scores were also used for final model selection.

Generalized additive models with the binomial family and logit link function were developed for the presence-absence component of the model. The logit function is the inverse of the logistic function, given by the following formula:

$$\text{logit}(p) = \ln\left(\frac{p}{1-p}\right)$$

where p is the proportion of interest. For the complex model, the response variable (probability of yellowtail flounder in the catch) for tow i was modelled as:

$$\begin{aligned} \text{logit}(y_i) = & \beta_0 + f_1(\text{easting}_i) + f_2(\text{temperature}_i) + \beta_1 * \text{year}_i + \beta_2 * \text{season}_i \\ & + f_3(\text{zenith}_i) + \beta_3 * \text{area}_i + \beta_4 * \text{season}_i * \text{area}_i \\ & + f_4(\text{temperature}_i, \text{depth}_i) + \beta_5 * \text{year}_i * \text{area}_i + f_5(\text{easting}_i, \text{season}_i) \\ & + f_6(\text{northing}_i, \text{season}_i) + f_7(\text{northing}_i, \text{temperature}_i) + f_8(\text{depth}_i, \text{area}_i) \\ & + \beta_6 * \text{year}_i * \text{season}_i + f_9(\text{zenith}_i, \text{season}_i) + \varepsilon_i \end{aligned}$$

where each f is a smooth function of the covariates associated with tow i , β_0 is the intercept and other β terms are coefficients specifying the effect of the corresponding covariates, easting and northing are projected longitude and latitude, and ε is a binomially distributed error term. For the simple model, the probability of yellowtail flounder for tow i was modelled as:

$$\begin{aligned} \text{logit}(y_i) = & \beta_0 + f_1(\text{easting}_i) + f_2(\text{northing}_i) + f_3(\text{month}_i) + f_4(\text{easting}_i, \text{month}_i) \\ & + f_5(\text{easting}_i, \text{northing}_i) + \varepsilon_i \end{aligned}$$

where all notation is as above.

Conditional bycatch proportion was modelled using the beta distribution with logit link. The beta distribution is a flexible distribution for modelling proportions bounded between zero and one. Records with a bycatch proportion of 1 (*i.e.* they caught at least one yellowtail flounder and no scallops) were recoded as the next highest

proportion observed. Nineteen records (0.9%) from the bycatch survey data and twenty-one records (0.5%) from the avoidance program data contained only yellowtail flounder. The next highest proportions observed in the data were 0.98 and 0.58 respectively. For the complex model, the response variable (proportion of yellowtail flounder in the catch) for tow i was modelled as:

$$\begin{aligned} \text{logit}(y_i) = & \beta_0 + \beta_1 * \text{area}_i + f_1(\text{easting}_i) + f_2(\text{northing}_i) + f_3(\text{temperature}_i) \\ & + f_4(\text{depth}_i) + f_5(\text{zenith}_i) + \beta_2 * \text{year}_i + \beta_3 * \text{season}_i \\ & + f_6(\text{temperature}_i, \text{area}_i) + f_7(\text{depth}_i, \text{season}_i) + f_8(\text{northing}_i, \text{easting}_i) \\ & + f_9(\text{northing}_i, \text{season}_i) + \beta_4 * \text{year}_i * \text{area}_i + f_{10}(\text{easting}_i, \text{season}_i) \\ & + f_{11}(\text{easting}_i, \text{temperature}_i) + \beta_5 * \text{season}_i * \text{area}_i + \varepsilon_i \end{aligned}$$

where notation is as above except that the error term (ε) is beta distributed. For the simple model, the proportion of yellowtail flounder in the catch for tow i was modelled as:

$$\begin{aligned} \text{logit}(y_i) = & \beta_0 + f_1(\text{easting}_i) + f_2(\text{northing}_i) + f_3(\text{easting}_i, \text{northing}_i) \\ & + f_4(\text{easting}_i, \text{month}_i) + f_5(\text{northing}_i, \text{month}_i) \\ & + f_6(\text{easting}_i, \text{northing}_i, \text{month}_i) + \varepsilon_i \end{aligned}$$

where notation is as above except that the error term (ε) is beta distributed. We used thin plate regression splines for all one-dimensional smooth terms and tensor product smooths for all two-dimensional smooth terms (comprised of cyclic cubic regression splines for month interactions and thin plate regression splines for all other variables) in all models.

The predicted total bycatch proportion would conventionally be calculated as the product of the two predicted values (probability of bycatch times predicted magnitude of conditional bycatch proportion). However, this approach to deriving predicted values provides similar values for a high probability of small bycatch and low probability of large bycatch, which is undesirable for issuing advisories. Therefore, we present the predictions from the two model steps separately, as a probability of encounter and conditional bycatch proportion without presenting the total bycatch proportion estimated by the product of the two.

Probability of yellowtail flounder bycatch and bycatch proportions (yellowtail flounder weight divided by the total weight of yellowtail flounder plus scallop meats) were the response variables in modelling. We explored relationships of yellowtail flounder bycatch with a variety of environmental factors: tow location (management area, latitude and longitude), year, season, month, time of day, zenith angle, bottom temperature, depth, and sediment coarseness for each tow were potential explanatory variables for complex models (Table 1). Relatively simple models were explored for potential use in the bycatch avoidance program using variables limited to those that were available in the program data (*i.e.*, latitude, longitude, month or season, and “area”: Nantucket Lightship Closed Area Access Area, Closed Area I Access Area, Closed Area II Access Area, open areas (Fig. 1)). Area was

considered in addition to tow coordinates to capture the effect of differing management and fishing behaviour across these broad locations.

Simple and complex models were selected in two steps. The first step was to identify a subset of potential models with lowest AIC and highest percentage deviance explained. The second step used 10-fold cross validation to determine the preferred model. The model that explained the most variation in extrinsic data (based on deviance explained and mean absolute prediction error, MAPE) was selected as the best model. The data were divided into 10 test groups, and the model was repeatedly fit to a portion of the data, each time leaving out one of the test groups. Then the percentage of deviance explained and the MAPE were compared across models. MAPE is the average of the absolute difference between predictions and observations in the test data:

$$MAPE = \frac{\sum_{i=1}^n abs(y_i - \hat{y}_i)}{n}$$

The larger the percentage deviance explained and the smaller the MAPE, the better the model explains the data. Due to differences in temporal coverage across datasets, the cross-validation step was completed for each model type (simple probability, simple proportion, complex probability, and complex proportion) fit to the survey data and to the Observer Program data separately (*i.e.* models

Table 2. Selected models. Dev is the deviance explained for the models fit to the whole dataset. The cross-validation column is the average deviance explained in a subset of data left out when fitting the models. Mean MAPE is the mean absolute prediction error averaged across ten subdivisions (see methods for further explanation). For consistency with programmatic advisories, MAPE is calculated based on D:K ratio, not proportion (the direct model output). East and north correspond to the longitude and latitude of the tow coordinates projected into the Universal Transverse Mercator coordinate system, zone 19.

Model	Model Terms	Dev (%)	Cross Validation Average Dev (%)	
Bycatch probability	f(east) + f(north) + f(temp) + year + f(depth) + season + f(zenith) + area + season*area + f(temp, depth) + year*area + f(east, season) + f(north, season) + f(north, temp) + f(depth, area) + year*season + f(zenith, area)	41%	29%	
Simplified bycatch probability	f(east) + f(north) + f(month) + f(east, month) + f(east, north)	24%	Survey subset: 26%	Observer data: 34%
Mean MAPE				
Bycatch proportion	area + f(east) + f(north) + f(temp) + f(depth) + f(zenith) + year + season + f(temp, area) + f(depth, season) + f(north, east) + f(north, season) + area*year + f(east, season) + f(east, temp) + area*season	48%	0.385	
Simplified bycatch proportion	f(east) + f(north) + f(month) + f(east, north) + f(east, month) + f(north, month) + f(east, north, month)	43%	Survey subset: 0.390	Observer data: 0.040

were fit to a data from a single source and cross-validated with a subset from the same source then the process was repeated with data from the next source).

Results

The selected bycatch probability model included the main effects of longitude, bottom temperature, year, season, zenith angle, area and several interaction terms (Tables 2 and 3). Probability of bycatch was significantly greater in 2014 relative to 2011. There was significantly higher bycatch probability in winter relative to fall, and in fall

relative to summer in Closed Area I. Probability of bycatch was greater in Closed Area II than in Closed Area I. In Closed Area II, bycatch probability was significantly lower in 2013, and significantly higher in 2014 relative to 2011. However, in the open area to the southwest, bycatch probability was significantly lower in 2012, 2013, and 2014 relative to 2011.

Bycatch probability decreased with increasing temperature (Fig. 2A–B) and increased as zenith angle increased from 20 to 60 degrees (Fig. 2C). In the summer, bycatch probability decreased at from west to east (Fig. 2D),

Table 3. Relative goodness-of-fit for candidate bycatch probability models, ranked from best to worst fit. All candidate models are binomial GAMs with logit link. AIC = Akaike information criterion, rounded to the nearest whole number; edf = estimated degrees of freedom in the model; Δ = AIC difference, rounded to the nearest whole number; Dev = percent deviance explained for the models fit to the whole dataset; Cross-Val. Ave. Dev. = average deviance explained in a subset of data left out when fitting the models. East and north correspond to the longitude and latitude of the tow coordinates projected into the Universal Transverse Mercator coordinate system, zone 19.

Model	AIC	edf	Δ	Dev	Cross-Val. Ave. Dev.
f(east) + f(north) + f(temp) + year + f(depth) + season + f(zenith) + area + season*area + f(temp, depth) + year*area + f(east, season) + f(north, season) + f(north, temp) + f(depth, area) + year*season + f(zenith, area)	1738	97.16	0	41.1%	29.1%
f(east) + f(north) + f(temp) + year + f(depth) + season + f(zenith) + area + season*area + f(temp, depth) + year*area + f(east, season) + f(north, season) + f(north, temp) + f(depth, area) + year*season	1748	85.75	10	39.8%	29.2%
f(east) + f(north) + f(temp) + year + f(depth) + season + f(zenith) + area + season*area + f(temp, depth) + year*area + f(east, season) + f(north, season) + f(north, temp) + f(depth, area)	1760	80.96	22	39.0%	29.1%
f(east) + f(north) + f(temp) + year + f(depth) + season + f(zenith) + area + season*area + f(temp, depth) + year*area + f(east, season) + f(north, season) + f(north, temp)	1773	78.58	35	38.3%	29.4%
f(east) + f(north) + f(temp) + year + f(depth) + season + f(zenith) + area + season*area + f(temp, depth) + year*area + f(east, season) + f(north, season)	1790	65.19	52	36.6%	29.4%
f(east) + f(north) + f(temp) + year + f(depth) + season + f(zenith) + area + season*area + f(temp, depth) + year*area + f(east, season)	1819	57.13	81	34.9%	28.3%
f(east) + f(north) + f(temp) + year + f(depth) + season + f(zenith) + area + season*area + f(temp, depth) + year*area	1839	47.01	101	33.3%	28.6%
f(east) + f(north) + f(temp) + year + f(depth) + season + f(zenith) + area + season*area + f(temp, depth)	1865	39.95	128	31.8%	27.7%
f(east) + f(north) + f(temp) + year + f(depth) + season + f(zenith) + area + season*area	1906	40.66	168	30.3%	26.1%
f(east) + f(north) + f(temp) + year + f(depth) + season + f(zenith) + area	1985	32.56	247	26.7%	23.1%
f(east) + f(north) + f(temp) + year + f(depth) + season + f(zenith)	1991	30.21	253	26.3%	22.8%
f(east) + f(north) + f(temp) + year + f(depth) + season	1999	25.32	261	25.6%	22.7%
f(east) + f(north) + f(temp) + year + f(depth)	2011	21.44	273	24.8%	22.2%
f(east) + f(north) + f(temp) + year	2025	21.86	288	24.3%	21.9%
f(east) + f(north) + f(temp)	2049	18.55	311	23.2%	21.3%
f(east) + f(north)	2103	13.87	365	20.8%	19.3%

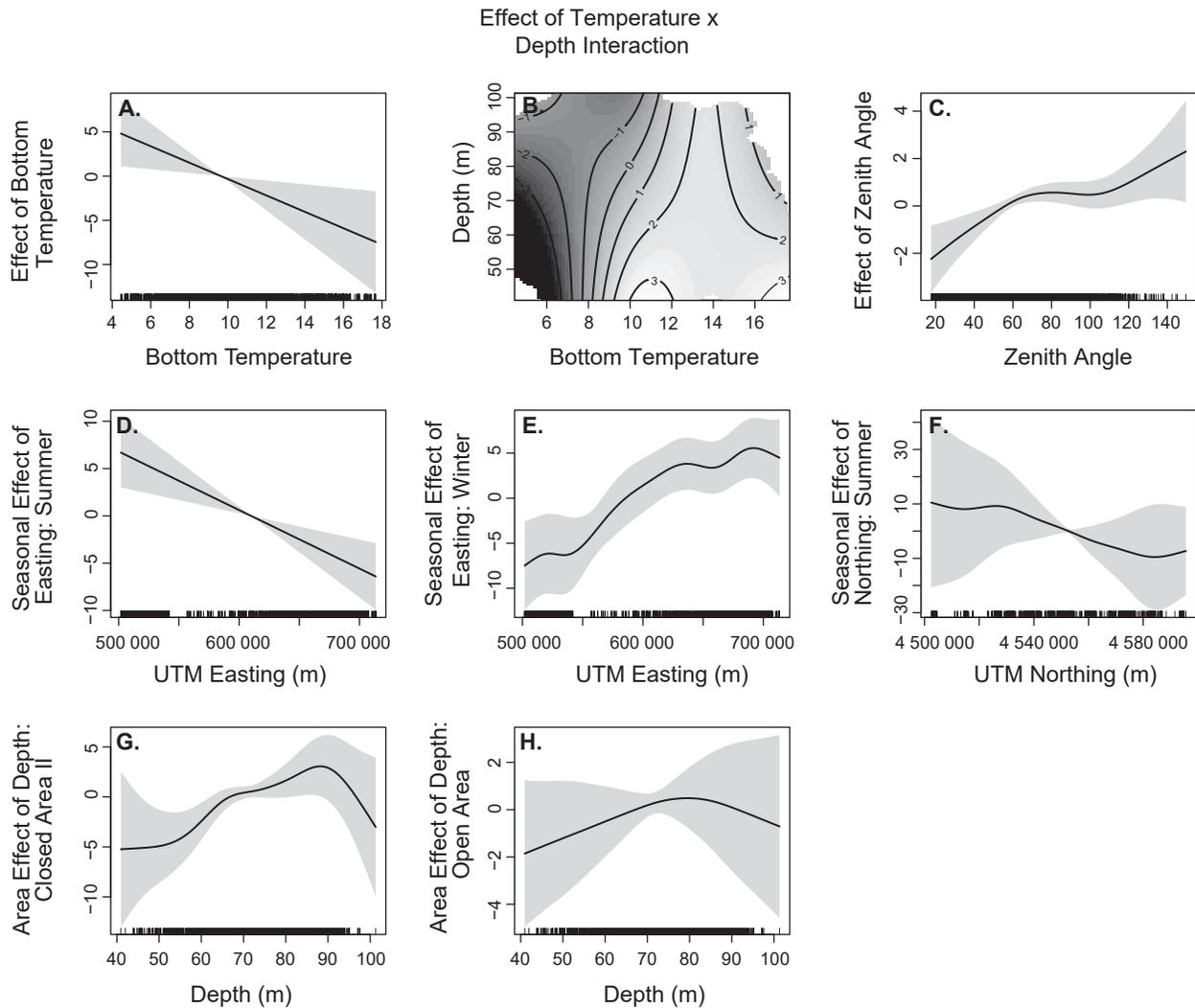


Fig. 2 Effects of the significant smooth functions in the complex bycatch probability model fitted to the survey data. The gray shading on one-dimensional smooths represents the 95% confidence bands. For the two-dimensional smooth the gradient indicates increasing effect from dark to light, with contours overlaid with specific values. UTM Easting and Northing are projected longitude and latitude, respectively, in the Universal Transverse Mercator Zone 19.

and the pattern is reversed in the winter with probability increasing from west to east (Fig. 2E). Bycatch probability decreased as latitude increased in the summer months (Fig. 2F). In Closed Area II as well as the open area to the southwest of Closed Area II, bycatch probability decreased at depths beyond approximately 90 m (Fig. 2G–H).

The selected model for conditional bycatch proportion included main effects of area, latitude, longitude, bottom temperature, depth, zenith angle, year, season, and some interaction terms (Table 2 and 4). Conditional bycatch proportion increased each year from 2011 to 2014, with 2012–2014 each being significantly greater than 2011. Conditional bycatch proportion was greater in winter

and lower in summer relative to the fall. Relative to Closed Area I in 2011, conditional bycatch proportion was significantly lower in most other areas in later years. Relative to Closed Area I in the fall, conditional bycatch proportion was lower in the winter in Closed Area II and the open area to the southwest. Bycatch proportion was generally greatest at the northernmost latitudes at mid-to-easternmost longitudes (Fig. 3A–C). Conditional bycatch proportion decreased slightly with increasing zenith angle (Fig. 3D). In fall, winter, and spring, conditional bycatch proportion increased with increasing latitude (Fig. 3E–G). In fall, bycatch proportion was minimized at intermediate longitude (Fig. 3H). Conditional bycatch

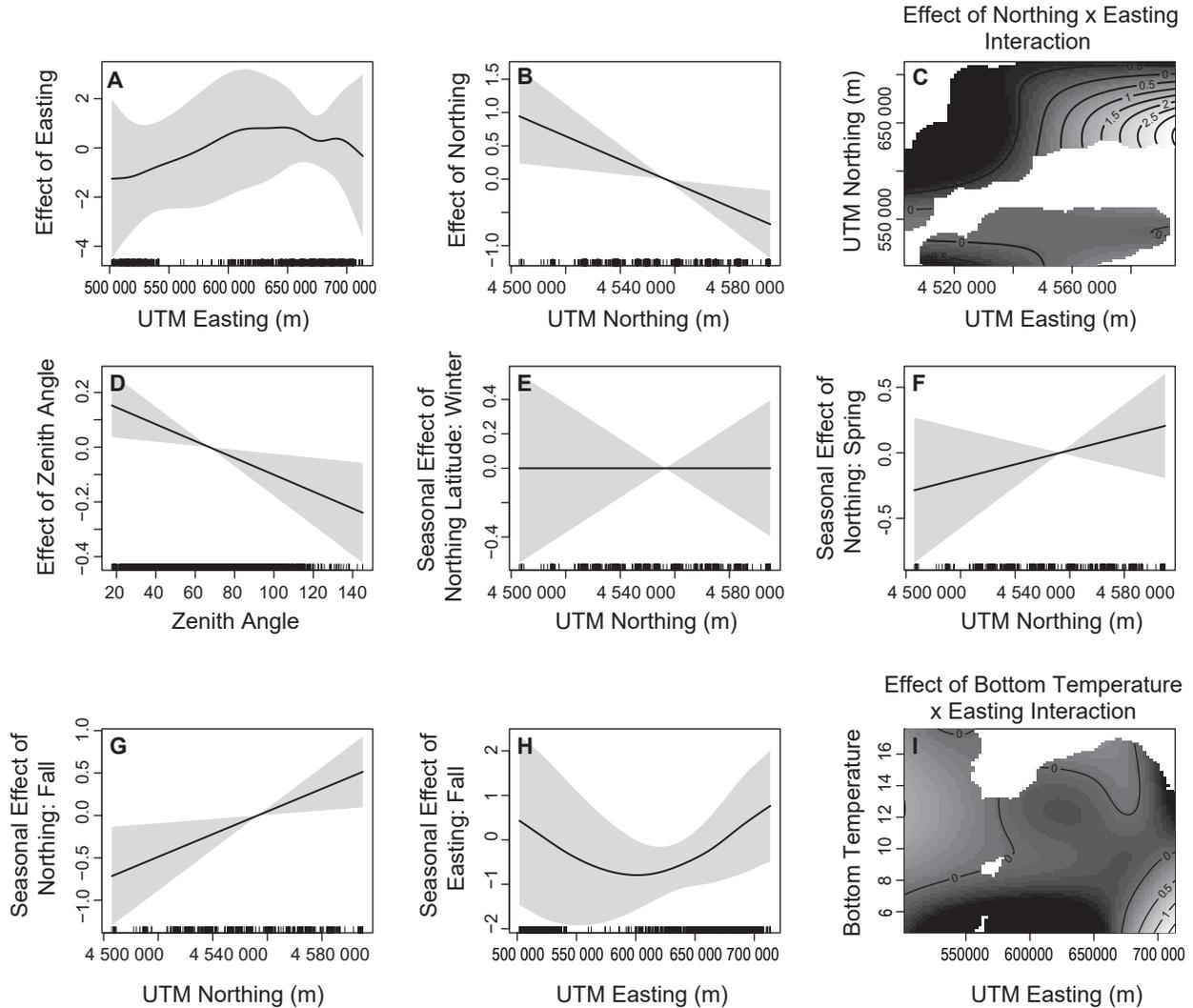


Fig. 3 Effects of the significant smooth functions in the complex bycatch proportion model fitted to the survey data. The gray shading on one-dimensional smooths represents the 95% confidence bands. For the two-dimensional smooth the gradient indicates increasing effect from dark to light, with contours overlaid with specific values. UTM Easting and Northing are projected longitude and latitude, respectively, in the Universal Transverse Mercator Zone 19.

proportion generally peaked around 12° C, with varying intensity of the peak across longitudes; highest conditional bycatch proportions were towards the east at moderate temperatures (Fig. 3I). The mean MAPE of the total bycatch proportion (translated to ratio of discarded fish to kept scallops for programmatic consistency) is 0.39 kg yellowtail flounder/kg scallops.

The selected simple bycatch probability model included the main effects of longitude, latitude, and month with interactions (Tables 2 and 5). Bycatch probability generally increased from west to east, but there were significant interactions between month and longitude

that indicated bycatch probability dipped mid-year at the eastern edge of the study area and peaked mid-year in the western region (Fig. 4A). Bycatch probability peaked along middle latitudes and towards east and west, with lower probability to the north and at central longitudes (Fig. 4B).

The selected simple model of conditional bycatch proportion includes longitude, latitude, month, and two- and three-way interactions and fit the data relatively well (Tables 2 and 6). Conditional bycatch proportion peaked at intermediate latitude, and the effects of latitude and longitude changed seasonally (Fig. 5).

The predicted probability of bycatch was high throughout the year in Closed Area II, generally lower in Closed Area I, and much more variable in Nantucket Lightship Closed Area (Fig. 6). In Closed Area I, bycatch probability was lowest in September and October, then increased through the winter and spring months. In Nantucket Lightship Closed Area, high bycatch probability was most widespread in August through October then contracted in

December through February with a more even mix of high and low probabilities the rest of the year. The northern open area generally had low probabilities throughout the year. However, there was less data from this area than any of the other areas (Fig. 1). Predicted conditional bycatch proportion in the southern open area was subtly variable over the course of the year with higher probabilities occurring near Closed Area II.

Predicted conditional bycatch proportions were greatest in the northwest corner of the Closed Area II access area (Fig. 7). Conditional bycatch proportion in the southern open area was greatest during the early part of the year and decreased around June through August and increased again through the end of the year.

In general, the simple models (both for probability and conditional bycatch proportion) performed similarly to the complex models for explaining deviance in bycatch data. Compared to the complex model, the simple bycatch probability model explained 17% less of the deviance when the model was fit to the full dataset, and cross validation average deviance explained was slightly lower for the simple model fit to survey data and slightly higher for the simple model fit to observer data compared to the complex model fit to all data (Table 2). The complex bycatch proportion model explained about 5% more deviance when the model was fit to all data than the simple model explained (Table 2). MAPE was similar for the complex model fit to all data and the simple model fit to the survey data, and the MAPE was much lower for the simple model fit to observer data than the complex model fit to all data (Table 2).

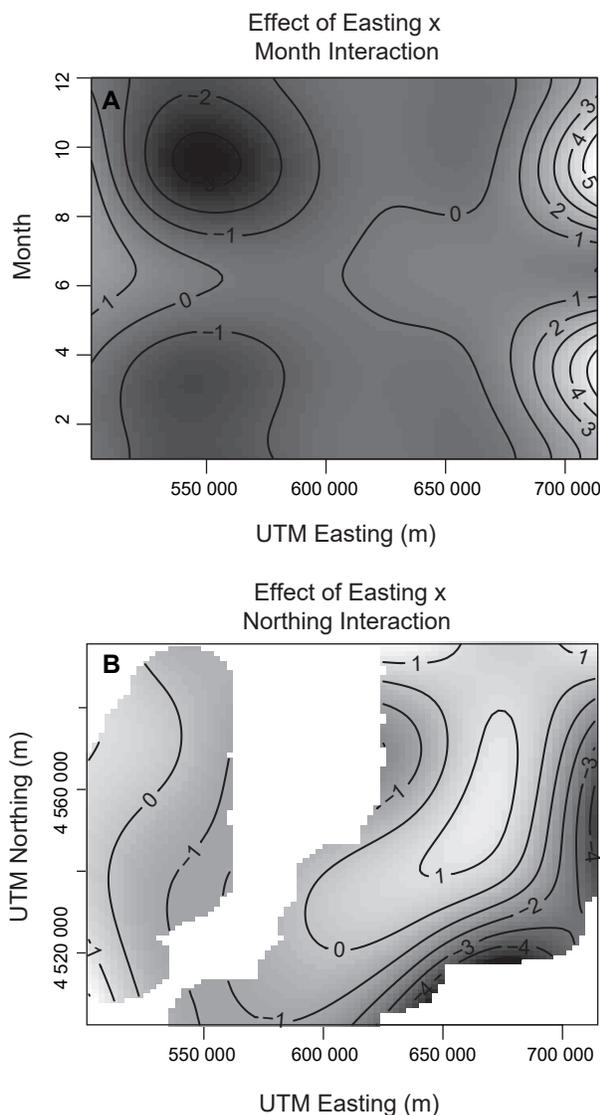


Fig. 4. Effects of the significant smooth functions in the simplified bycatch probability model fitted to the survey data. The gradient indicates increasing effect from dark to light, with contours overlaid with specific values. **A)** The effect of easting (*i.e.* projected longitude) varies over the course of the year. **B)** The interaction of northing and easting gives an overall location effect.

Discussion

Probability and magnitude of yellowtail flounder bycatch in the Georges Bank scallop fishery varied in space and time and with environmental variables. Similar to the findings of Helser and Brodziak (1996), DeLong and Collie (2004), and Hyun *et al.* (2014), the probability of catching yellowtail flounder decreased as bottom temperature increased. Depth was not a significant main effect, as it was in previous studies (*e.g.*, Helser and Brodziak, 1996; DeLong and Collie, 2004; Truesdell, 2013), but it had significant interactions with temperature and area. Sediment type was also not a significant factor in any of the models, contrary to the findings of DeLong and Collie (2004) and Truesdell (2013). DeLong and Collie (2004) found yellowtail flounder prefer sand, sand-shell hash, and rock-sandy sediments. The lack of depth and habitat effects in our models may result from the bycatch survey being limited to the distribution of the scallop

fishery and consequently including a narrower range of depth and substrate. The relative homogeneity of habitat in the scallop fishing grounds may explain why variables that would be expected to be significant predictors were not ultimately included in our selected models.

Similar to our results, Helser and Brodziak (1996), and Truesdell (2013) also found seasonal effects, whereas NEFMC (2013) and Smolowitz *et al.* (2012) considered month instead of season. Short seasonal migrations have been documented in tagging studies (Royce *et al.*,

Table 4. Relative goodness-of-fit for candidate bycatch proportion models of yellowtail flounder proportion of catch translated to D:K ratio, ranked from best to worst fit. All candidate models are beta GAMs with logit link. AIC = Akaike information criterion, rounded to the nearest whole number; edf = estimated degrees of freedom in the model; Δ = AIC difference, rounded to the nearest whole number; Dev = percent deviance explained for the models fit to the whole dataset; Mean MAPE = mean absolute prediction error averaged across ten subdivisions (see methods for further explanation). MAPE is calculated based on D:K ratio, not proportion (the direct model output). East and north correspond to the longitude and latitude of the tow coordinates projected into the Universal Transverse Mercator coordinate system, zone 19.

Model	AIC	edf	Δ	Dev.	Mean MAPE
area + f(east) + f(north) + f(temp) + f(depth) + f(zenith) + year + season + f(temp, area) + f(depth, season) + f(north, east) + f(north, season) + area*year + f(east, season) + f(east, temp) + area*season	-2890	64.88	0	48%	0.385
area + f(east) + f(north) + f(temp) + f(depth) + f(zenith) + year + season + f(temp, area) + f(depth, season) + f(north, east) + f(north, season) + area*year + f(east, season) + f(east, temp)	-2890	60.58	0	48%	0.386
area + f(east) + f(north) + f(temp) + f(depth) + f(zenith) + year + season + f(temp, area) + f(depth, season) + f(north, east) + f(north, season) + area*year + f(east, season)	-2857	50.52	32	45%	0.388
area + f(east) + f(north) + f(temp) + f(depth) + f(zenith) + year + season + f(temp, area) + f(depth, season) + f(north, east) + f(north, season) + area*year	-2862	50.02	28	45%	0.389
area + f(east) + f(north) + f(temp) + f(depth) + f(zenith) + year + season + f(temp, area) + f(depth, season) + f(north, east) + f(north, season)	-2771	43.54	118	40%	0.391
area + f(east) + f(north) + f(temp) + f(depth) + f(zenith) + year + season + f(temp, area) + f(depth, season) + f(north, east)	-2754	40.91	136	39%	0.395
area + f(east) + f(north) + f(temp) + f(depth) + f(zenith) + year + season + f(temp, area) + f(depth, season)	-2678	32.24	212	34%	0.399
area + f(east) + f(north) + f(temp) + f(depth) + f(zenith) + year + season + f(temp, area)	-2676	29.41	214	34%	0.400
area + f(east) + f(north) + f(temp) + f(depth) + f(zenith) + year + season	-2653	26.48	236	32%	0.403
area + f(east) + f(north) + f(temp) + f(depth) + f(zenith) + year	-2627	24.07	263	30%	0.403
area + f(east) + f(north) + f(temp) + f(depth) + f(zenith)	-2565	18.93	324	26%	0.406
area + f(east) + f(north) + f(temp) + f(depth)	-2564	17.88	326	26%	0.406
area + f(east) + f(north) + f(temp)	-2544	14.11	346	24%	0.408
area + f(east) + f(north)	-2483	9.97	406	20%	0.416
area + f(east)	-2412	8.53	478	15%	0.423
area	-2337	3.00	553	9%	0.430

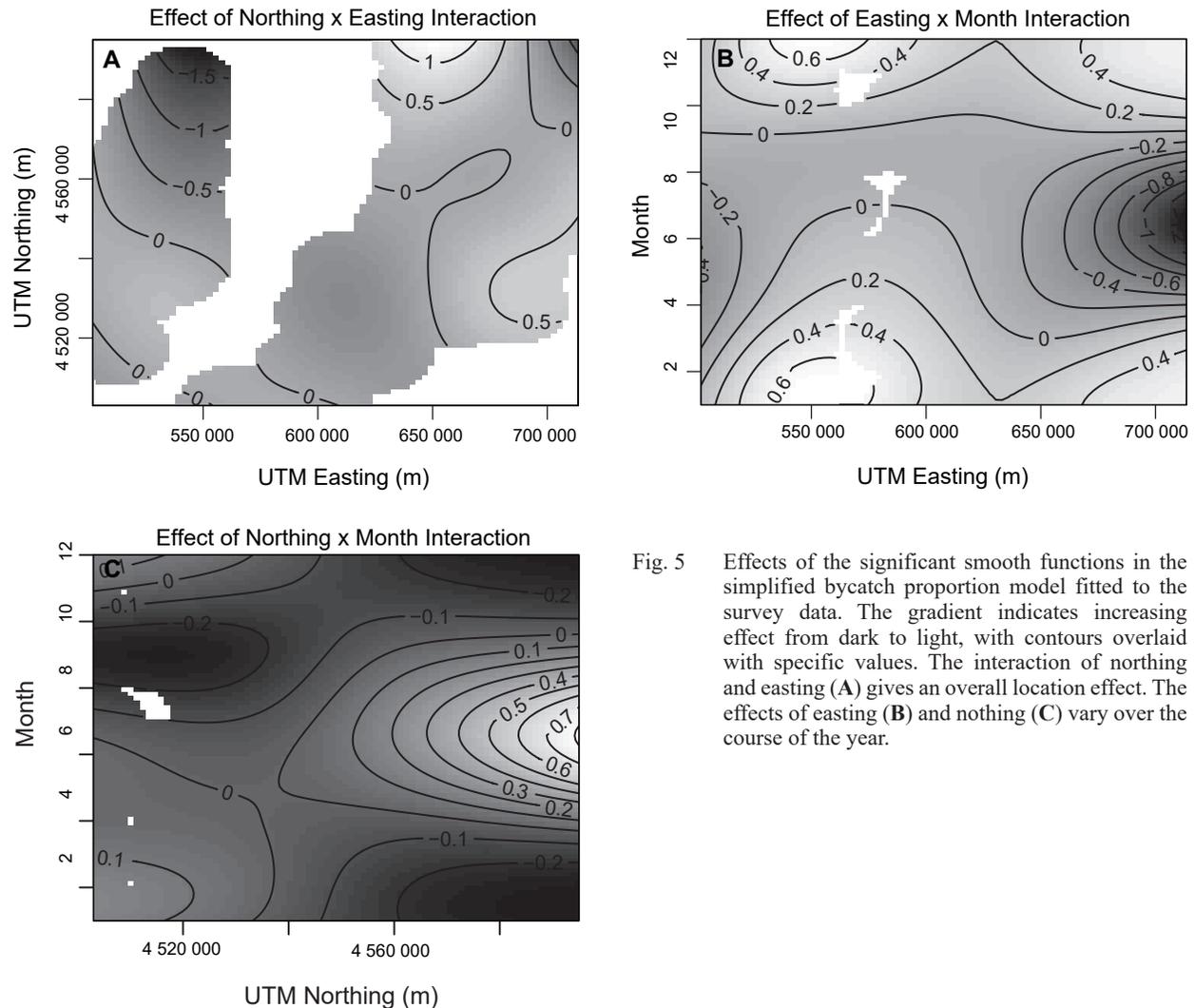


Fig. 5 Effects of the significant smooth functions in the simplified bycatch proportion model fitted to the survey data. The gradient indicates increasing effect from dark to light, with contours overlaid with specific values. The interaction of northing and easting (A) gives an overall location effect. The effects of easting (B) and nothing (C) vary over the course of the year.

Table 5. Relative goodness-of-fit for candidate simplified bycatch probability models, ranked from best to worst fit. All candidate models are binomial GAMs with logit link. AIC = Akaike information criterion, rounded to the nearest whole number; edf = estimated degrees of freedom in the model; Δ = AIC difference, rounded to the nearest whole number; Dev = percent deviance explained for the models fit to the whole dataset; Cross-Val. Ave. Dev. = average deviance explained in a subset of data left out when fitting the models (either 10% of the survey data or the observer data set). East and north correspond to the longitude and latitude of the tow coordinates projected into the Universal Transverse Mercator coordinate system, zone 19.

Model	AIC	edf	Δ	Dev.	Cross-Val. Ave. Dev. (survey subset)	Cross-Val. Ave. Dev. (observer)
$f(\text{east}) + f(\text{north}) + f(\text{month}) + f(\text{east, month}) + f(\text{east, north})$	12 693	56.26	0	24%	26.4%	34.2%
$f(\text{east}) + f(\text{north}) + f(\text{month}) + f(\text{east, month})$	13 204	35.68	511	20%	24.7%	31.3%
$f(\text{east}) + f(\text{north}) + f(\text{month})$	13 479	25.63	786	19%	21.3%	29.4%
$f(\text{east}) + f(\text{north})$	13 521	18.55	828	18%	19.8%	28.0%
$f(\text{north})$	15 457	9.96	2764	6%	4.8%	20.2%
$f(\text{east})$	13 981	9.90	1287	15%	14.7%	23.3%

1959; Lux, 1963; Cadrin and Westwood, 2004; Wood and Cadrin, 2013). Similar to NEFMC (2013) and Smolowitz *et al.* (2012), we found that Closed Area II had significantly greater bycatch probability than Closed Area I, and there was a significant interaction between area and year. DeLong and Collie (2004), Simpson and Walsh (2004), and NEFMC (2013) report effects of latitude and longitude. Similarly, we found that longitude had a significant positive effect, and although latitude did not have a significant main effect, there were significant interactions of latitude with temperature and season.

Zenith angle had a significant positive effect, but there were relatively few observations at night, (corresponding to zenith angles between 90 and 180 degrees—zenith angle is approximately 90° at sunrise and sunset). Despite the

limited range of observations, our results are consistent with Truesdell’s (2013) findings of a nearly linear positive effect of zenith angle, meaning yellowtail flounder are caught more at night. These results are also consistent with other studies that found flounders were caught more at night than during the day (Sissenwine and Bowman, 1978; Shepherd and Forrester, 1987; Walsh, 1988, 1991; Casey and Myers, 1998). A potential mechanism for this daily variability in catch is more frequent off-bottom movements at night (Cadrin and Westwood, 2004; Walsh and Morgan, 2004) and diel differences in diet of yellowtail flounder (Pitt, 1976; Langton, 1983; Collie, 1987).

NEFMC (2013) suggest different effects by month. In Closed Area II, peak catches were in October with smallest catches occurring May through July, and bycatch was

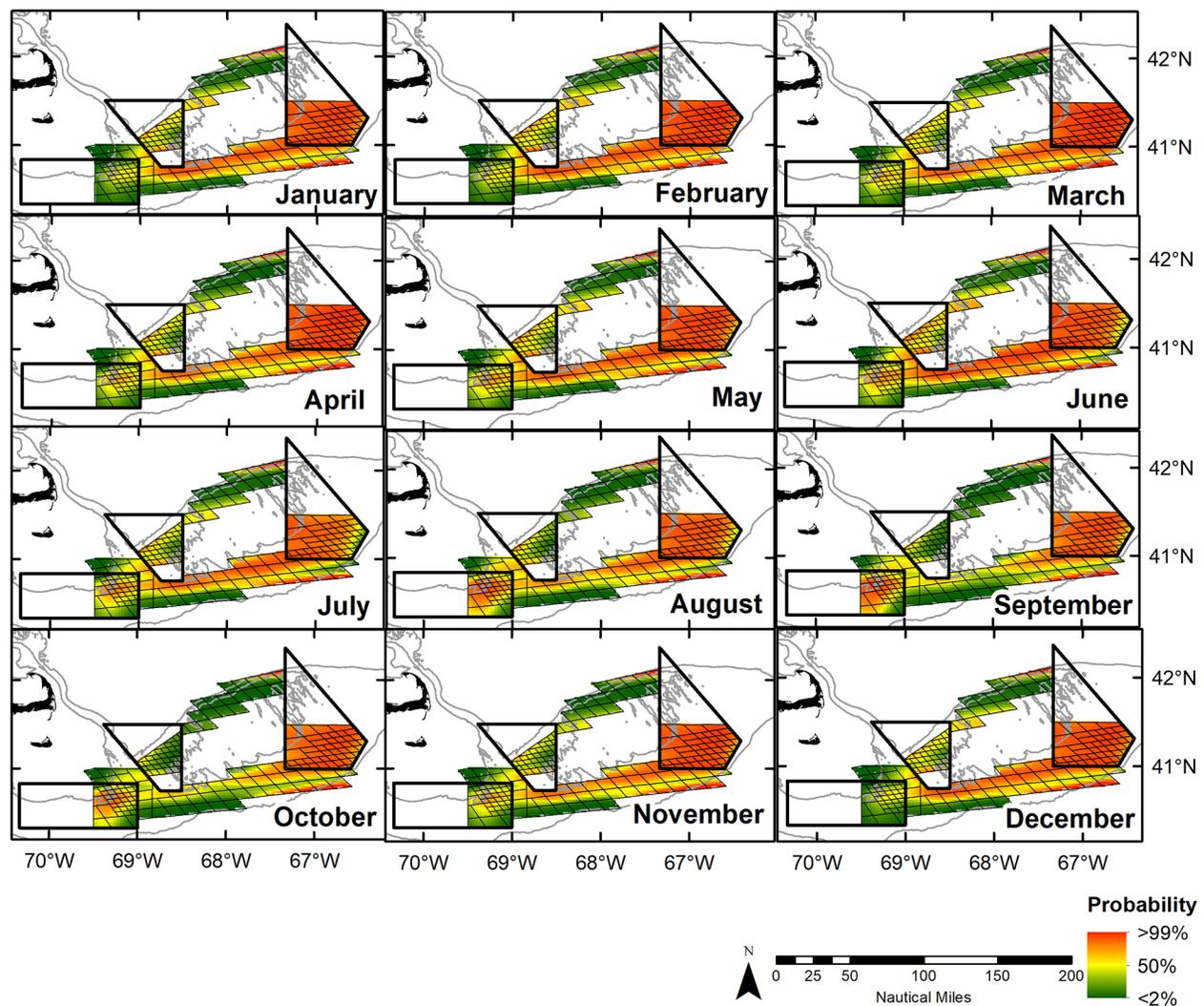


Fig. 6 Prediction for each month based on the simplified bycatch probability model fitted to all data. Low probability of catch is represented in green with increasing probability transitioning to yellow then to red.

relatively constant across months in Closed Area I and Nantucket Lightship. Smolowitz *et al.* (2012) found the greatest bycatch in August through October in Closed Area II. However, the response variable in these two studies was bycatch rate in numbers, rather than the proportion of yellowtail flounder in the total catch (weight) as in our model. The location effects in our models are consistent with DeLong and Collie's (2004) model of essential fish habitat for Georges Bank yellowtail flounder, which indicated highest abundances to the east and along the southern edge of the Bank. Unlike the findings of other studies, bottom temperature and depth (*e.g.*, Helser and Brodziak, 1996; DeLong and Collie, 2004; Simpson and Walsh, 2004; Truesdell 2013), substrate (Simpson and Walsh, 2004; Truesdell, 2013), and zenith angle (Truesdell, 2013) were not significant in the conditional bycatch proportion model, but interactions between these and other variables were significant. For example, interaction of depth and season was significant, suggesting greater proportional catches at varying depths during different seasons.

Fishing behaviour and weather (*e.g.*, wind, wave height) were not included but may have significant impacts

on catch. Similarly, the abundance of predator or prey species was not examined, and biological factors could be significant determinants of yellowtail flounder abundance.

The purpose of developing simple models in addition to the complex models was to develop a useful tool for the bycatch avoidance program by using only data that is collected in the program. The ideal models combine simplicity of structure and data requirements with similar performance to the selected complex models. Each of the simple models includes only combinations of latitude, longitude, area, and month and their interactions. This is the simplest set of data requirements, and these factors may reflect underlying effects of other factors that were significant in the complex models. Statistically, relatively little is gained by including the additional environmental factors after the spatiotemporal component is accounted for, particularly in the conditional bycatch proportion models. Moreover, the numerous terms and especially interactions in the complex models make interpretation difficult.

Our approach to modelling the probability of yellowtail flounder bycatch (the bycatch probability step) and

Table 6. Relative goodness-of-fit for candidate simplified bycatch proportion models of yellowtail flounder proportion of catch translated to D:K ratio, ranked from best to worst fit. All candidate models are beta GAMs with logit link. Deviance explained is for the models fit to the whole dataset. AIC = Akaike information criterion, rounded to the nearest whole number; edf = estimated degrees of freedom in the model; Δ = AIC difference, rounded to the nearest whole number; Dev = percent deviance explained for the models fit to the whole dataset; Mean MAPE = mean absolute prediction error averaged across ten subdivisions of the survey and the observer datasets (see methods for further explanation). MAPE is calculated based on D:K ratio, not proportion (the direct model output). East and north correspond to the longitude and latitude of the tow coordinates projected into the Universal Transverse Mercator coordinate system, zone 19.

Model	AIC	edf	Δ	Dev.	Mean MAPE (survey)	Mean MAPE (observer)
f(east) + f(north) + f(month) + f(east, north) + f(east, month) + f(north, month) + f(east, north, month)	-27 754	64.86	0	43%	0.390	0.040
f(east) + f(north) + f(month) + f(east, north) + f(east, month) + f(north, month)	-27 639	50.47	116	41%	0.389	0.040
f(east) + f(north) + f(month) + f(east, north) + f(east, month)	-27 578	42.82	176	40%	0.395	0.041
f(east) + f(north) + f(month) + f(east, north)	-27 441	33.91	313	37%	0.399	0.042
f(east) + f(north) + f(month)	-27 093	25.03	662	32%	0.408	0.045
f(east) + f(north)	-26 621	17.01	1134	25%	0.417	0.048
f(north)	-25 964	9.45	1790	14%	0.431	0.049
f(east)	-26 290	9.50	1464	19%	0.425	0.049

relative density of yellowtail flounder in positive tows (the conditional bycatch proportion step) is a means for providing captains with information to avoid bycatch. The outputs of both models should be considered in advising the fleet. Combining the two steps of the model through multiplication to derive an average prediction is common statistical practice (*e.g.*, Truesdell, 2013; Jacobson *et al.*, 2015) and is informative for patterns of average catch, but the combined output is not well suited for developing advisories for the scallop fleet. For example, a patchy bycatch distribution might have a bycatch probability of $p = 0.10$ and expected value of 0.04 kg yellowtail/ 1kg scallop meat, so the expected composite value would be $0.10 \times 0.04 = 0.004$ kg yellowtail / 1 kg scallop meat. The combined expected value is low yellowtail flounder catch.

However, the more accurate and useful interpretation is that nine out of ten tows are likely to contain no yellowtail flounder, and one tow is expected to contain a large yellowtail flounder catch. Predicting the timing and location of such large bycatch events is difficult in fisheries (Bethoney *et al.*, 2013). Captains are concerned about high bycatch events occurring when a Fisheries Observer is on board the vessel because observed discarding levels are used to estimate total fishery discards. Captains worry that a small number of tows with unusually large yellowtail flounder discards will cause the fishery level discard estimate to be high. Observer samples of bycatch ratios are expanded to the entire fishery to determine if the bycatch quota has been exceeded and if additional bycatch reduction measures (*e.g.*, in-season closures,

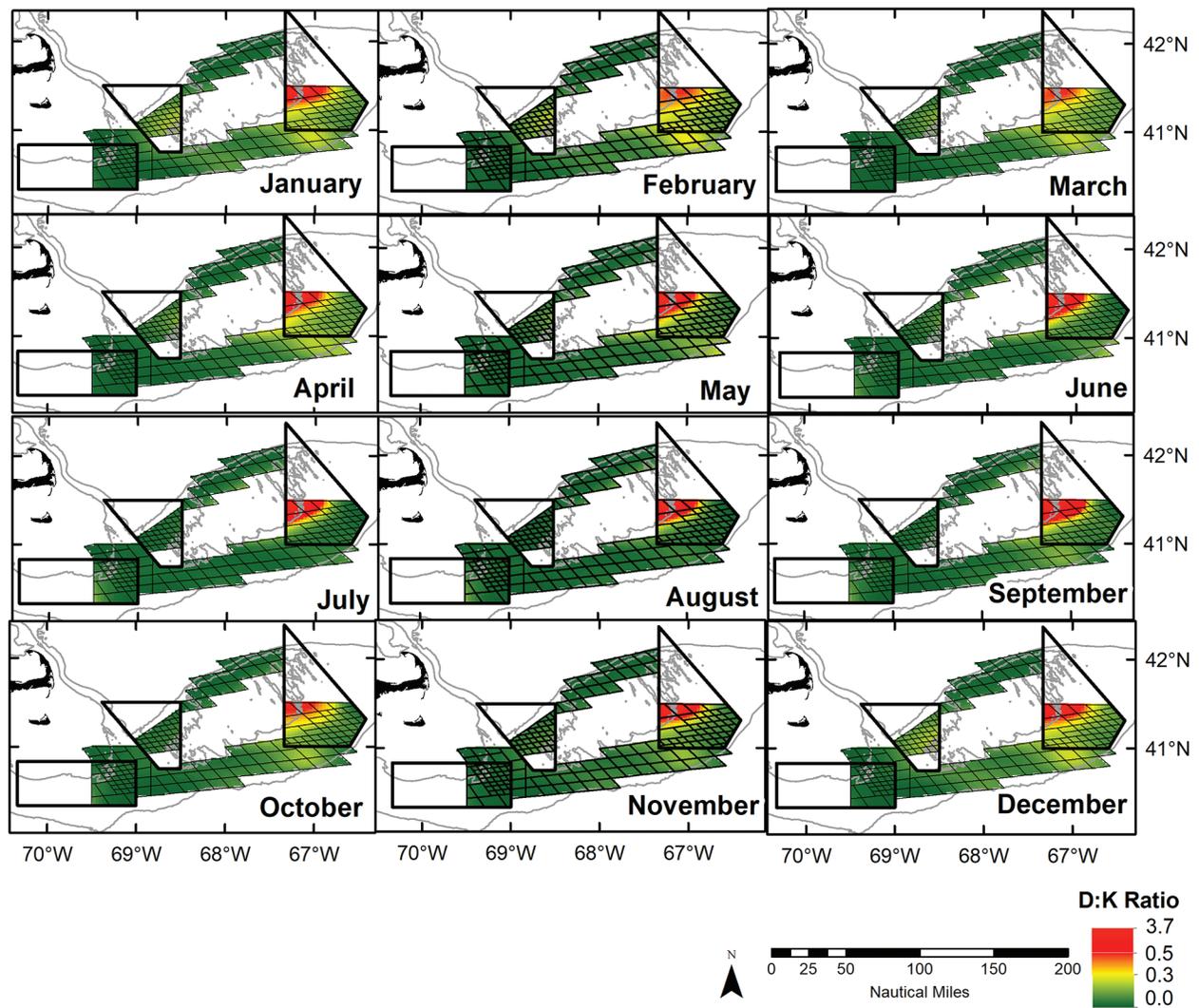


Fig. 7 Prediction for each month based on the simplified bycatch proportion model fitted to all data. The model output (a proportion) is converted to the discard: kept (D:K) ratio. Low D:K is represented in green and transitions to yellow to red as it increases.

closed areas, gear modifications) need to be applied. In this sense, these areas of highly variable bycatch are riskier than the combined average would imply. Thus, a location with a high probability of bycatch with a low conditional proportion would be indicated in an advisory as a low-risk area, whereas a low probability of bycatch with a high conditional proportion would be indicated as a medium-risk area.

The model-building methods and communication of spatial predictions through advisory maps is a useful framework for yellowtail flounder bycatch in the sea scallop fishery as well as other fisheries that face bycatch challenges. Forecasts and predictions in easy-access formats were developed for fishers to efficiently target bluefin tuna (Eveson *et al.*, 2015) and to avoid bycatch of loggerhead turtles (Howell *et al.*, 2008), alosines (Bethoney *et al.*, 2017), and several species in the Spanish Cantabrian Sea otter trawl fishery (Vilela and Bellido, 2015). The SMAST bycatch avoidance program functioned on a cooperative, voluntary basis. However, the models produced in this work could also be informative in the context of a formal management system. Such management considerations have been explored in other contexts (Lewison *et al.*, 2015), including habitat-based predictions of southern bluefin tuna catch (Hobday and Hartmann, 2006; Hobday *et al.*, 2011), blue marlin catch models (Walsh *et al.*, 2006), and theoretical move-on rules for the New England Multispecies fishery (Dunn *et al.*, 2014).

Predictive models are often used for supporting sustainable resource use. We demonstrate an application of such models as a component of a cooperative bycatch avoidance system. The ability to anticipate unfavourable fishing conditions (*e.g.*, interactions with unwanted species or low density of target species) will remain an important component of sustainable fishing.

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Scale growth rates and scale circulus deposition rates of marine-stage Atlantic salmon *Salmo salar* raised under semi-natural conditions

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Abstract

Scale circuli yield valuable information about the life history, age, and growth of a fish. However, because circuli formation is influenced by somatic growth, the rate at which circuli are formed and the factors influencing these rates must be taken into account for the given life stage of the study species. Scales were collected from Atlantic salmon raised in marine net pens off of the coast of Maine in order to characterize the formation of scale circuli and the growth of scales during the ocean phase, and to relate circulus deposition and scale growth rate to water temperature. Fish were sampled 13 times over a period of 25 months. Neither circulus deposition rate nor growth rate were constant through time and the same trend held when circulus deposition and growth were related to thermal experience. Both rates decreased over the course of the study, presumably related to the fish reaching sexual maturity. The results of this study indicate that the pattern of circulus deposition and scale growth of Atlantic salmon vary greatly during the early marine phase, and this dynamic should be taken into account when assessing growth, especially over short time periods.

Keywords: Atlantic salmon, Gulf of Maine, scale circuli, scale growth

Introduction

In 1910, Lea, who was studying herring at the time, showed that scale growth is proportional to body length (Lea, 1910). He found that the relative spacing of annuli was so consistent for single scales that this spacing could be used to back-calculate growth that took place in previous years of the fish's life. His detailed observations on scale structure and ages were not the first of their kind (Dahl, 1907), and nor were they the last. Havey (1959) reported that scales represent a reliable method for aging Atlantic salmon *Salmo salar*. Similar observations have been made for a range of species, juvenile steelhead

Oncorhynchus mykiss (Beakes *et al.*, 2014) and northern pike *Esox lucius* (Laine *et al.*, 1991) among them. Although other hard structures, such as otoliths, may be more reliable especially in older age classes of fish (Robillard *et al.*, 1996; Braaten *et al.*, 1999), many state and provincial agencies in the United States and Canada prefer to use scales over these other hard structures for aging common game species (Maceina *et al.*, 2007). Scales require relatively little time and expense to age (Beakes *et al.*, 2014) and, importantly, can be collected non-lethally. This is especially critical when researchers are working with threatened or endangered species.

Atlantic salmon have experienced marked declines across their range, particularly in southern North America, necessitating non-lethal methods of population assessment (Parrish *et al.*, 1998). A recent experimental study by Thomas *et al.* (2019) found that scale growth and circulus deposition in Atlantic salmon post-smolts was variable and increased with increasing temperatures when food was held constant. They concluded that, while there was a strong relationship between scale and somatic growth, circulus deposition rates must be interpreted in light of the fish's thermal history in order to be more accurately used as a proxy for growth (Thomas *et al.*, 2019).

The objective of the current study was to describe the scale growth rates and scale circulus deposition rates of marine-stage, net-pen raised Atlantic salmon. Growth and circulus deposition rates were tracked for two seawinters, and related to time and water temperature, as well as somatic growth. The scale samples used here were collected originally by Sheehan *et al.* (2005) as part of a larger study to assess phenotypic variation among stocks. We hypothesized that circulus deposition rates would not be constant through time but that they may be related to the thermal experience (water temperature) to which the fish were exposed.

Materials and methods

Field sampling

The field portion of this project was initiated in May 1998 when 6000 1+ Atlantic salmon smolts representing three rivers of origin were stocked into two marine net pen rearing facilities off the coast of Maine. Smolts originated from broodstock that were taken from the Dennys, East Machias, and Machias Rivers. The stocks from these rivers are all part of the Gulf of Maine Distinct Population Segment (GOM DPS), which was listed as Endangered under the Endangered Species Act (Endangered and Threatened Species, 2009) due to continued declines (National Research Council, 2004). The original broodstock were brought into captivity as parr, raised to maturity, and spawned at Craig Brook National Fish Hatchery in East Orland, ME during November 1996. Two thousand smolts from each stock were randomly chosen to be placed in net pens at either Site 1 or 2 (Cross Island or Deep Cove, see Sheehan *et al.* 2005 for more details [Fig. 1]) on 5 May 1998. The selected smolts were randomly divided between the two Sites, for a total of 3 000 smolts in each net pen (Sheehan *et al.*, 2005). While they were in the net pen the fish were fed to satiation, per industry standards (Sheehan *et al.*, 2005).

The salmon were sampled a total of 13 times between May 1998 and June 2000 (Table 1), with the first sampling event (hereafter "Event") taking place in freshwater rearing facilities prior to release into the net pens and Events 2–13 taking place in seawater. At every Event a seine was pulled through the net pen at each site. At least 30 fish from each stock at each site were measured (mass [grams] and total length [millimeters]) and a sample consisting of 1–16 scales was taken (Sheehan *et al.*, 2005). Fish were sampled only at a single Event and recaptured individuals were released back into the net pen without having a second scale sample taken to avoid collecting regenerated scales from standardized scale sampling areas below the dorsal fin. However, recaptured individuals were weighed and measured each time they were recaptured. Previously sampled fish were identified with a uniquely-coded colored Visual Implant Elastomer tag (VIE, Northwest Marine Technology, Inc.). The colors of these VIE tags were specific to each stock and therefore also useful for stock identification. Sheehan *et al.* (2005) also obtained hourly water temperatures across the duration of the study at each of the two rearing sites using remote temperature loggers. At the end of the initial study the adults at Site 1 were released into the wild. However, disease concerns at Site 2 necessitated that the fish be sacrificed rather than stocked. The disease in question, infectious salmon anemia (ISA), was detected in the same bay as these fish, and all fish used in the samples reported by this paper were asymptomatic. Because presence of the disease does not necessarily imply infection (McBeath *et al.*, 2009), and because all of the salmon used in this study were asymptomatic for ISA, it is unlikely that this disease influenced growth rates or scale circulus deposition patterns.

Laboratory methods

Scales were air-dried after collection, and cleaned by gently rubbing them between the fingertips in a dish of soapy water. Before and after mounting, the scales were placed in paper scale envelopes and stored in cardboard boxes that were kept indoors. Beginning in the fall of 2017, the slides were photographed under either 2.5x or 10x magnification on a ZEISS Axioplan 2 microscope (ZEISS International, Oberkochen, Germany) with a microscope-mounted digital camera (SPOT Insight 2 MP Color Mosaic; Diagnostic Instruments, Sterling Heights, Michigan). Previous to recording any data from the scales, a photograph of a stage micrometer at both 2.5x and 10x magnification was used to produce an appropriate calibration for the images. Each scale was uniquely coded based on the fish identifier coupled with a sequential numbering on each slide. All scales were photographed regardless of condition or regeneration status, but scales with

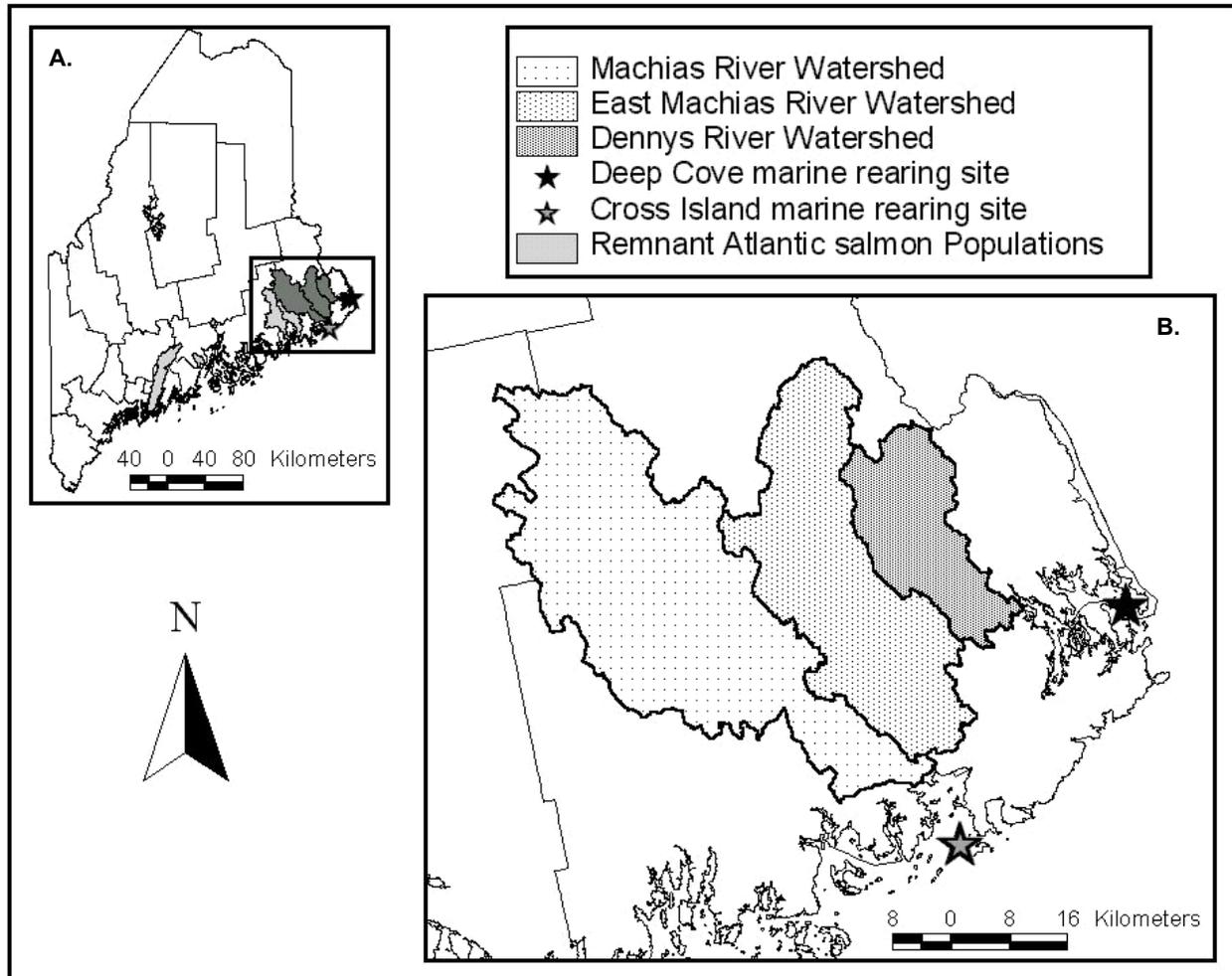


Fig. 1. Map from Sheehan *et al.* (2005) showing A) the locations of remnant salmon populations as well as the rivers of origin for the stocked smolts and the stocking sites and B) the relative locations of the rivers of origin and Site 1 (gray star) and Site 2 (black star).

regenerated centers or cracked edges were not processed further because they may not be useful for accurately determining age or growth (Blair, 1942; McNicol and MacLellan, 2010).

One reader processed each photograph of usable scales, which resulted in 1–11 replicates per fish. The number of replicates equaled the number of usable (whole, non-regenerated) scales available for each fish. We did not use the same number of replicates for each fish because this would have required using only one scale per fish, as some fish only had one usable scale available. Instead, we averaged the scale size and circulus number of all available scales for fish which had multiple usable scales. To obtain these measurements, the reader obtained circuli counts and spacing for each usable scale using ImagePro Premier software (Media Cybernetics, 2012), in which a

calibrated line, placed by the reader, was applied to the scale image that measured the total length from the center of the nucleus along the longest axis of the scale. ImagePro automatically placed markers on the line at the outside edge of every circulus based on the light/dark transition in the pixels. These markers could be examined and manually shifted or removed by the reader to make sure they had been placed on actual circuli. For each image, ImagePro also generated a data table that contained the number of markers (circuli) attributed to the scale and the distance from the nucleus to each circulus, as well as the total distance from the nucleus to the outside edge of the scale. The distances from the nucleus to each circulus were retained but are not reported here. The scale length and number of circuli on each scale were averaged among individual fish.

Table 1. Sampling dates for all Events that took place in the marine environment. Days in net pen is the total number of days between stocking fish in the net pen (5 May 1998) and the sampling Event. Accumulated thermal units (ATUs) are the averaged cumulative water temperatures for the two sites as of the day of the Event. Because the date of the first Event coincided with the day the fish were stocked into the net pens, those data have been omitted to include only marine growth. Weight records were incomplete for Events 4, 5, 7, 8, and 12.

Event	Sample date	Number of fish sampled	Median total length (mm) [standard dev.]	Median weight (g) [standard dev.]	Days in net pen	ATU (°C)
2	6/17/1998	167	235 [19.6]	109.1 [27.5]	43	285.5
3	7/14/1998	178	258 [17.7]	146.6 [31.4]	70	526.7
4	10/16/1998	52	379 [29.3]	NA	164	1488.6
5	11/13/1998	137	383 [39.0]	NA	192	1712.4
6	4/16/1999	162	438 [62.1]	790.0 [305.7]	346	2141.7
7	5/14/1999	143	450 [56.4]	NA	374	2296.4
8	6/14/1999	159	491 [65.4]	NA	405	2544.0
9	7/19/1999	132	521 [73.8]	1310.0 [585.5]	440	2902.6
10	8/17/1999	117	567 [72.5]	1770.0 [784.8]	469	3246.4
11	10/15/1999	68	539 [72.0]	1955.0 [737.0]	528	3994.1
12	11/19/1999	54	561 [79.8]	NA	563	4350.3
13	6/14/2000	156	695 [86.4]	3760.0 [1808.7]	771	5461.1

Data analysis

Reading multiple scales from the same individual can reduce sampling error, especially when sample sizes are low (Haraldstad *et al.*, 2016). We measured all of the usable scale available for each fish, which ranged from 1–11 scales with a median of 2 scales per fish. Circulus counts and scale radius measurements among scales collected from the same individual fish were averaged.

Scale radius and fish total length were compared using simple linear regression (SLR). Differences in scale growth rate and circulus deposition rate between net pen sites were compared using a Welch two-sample t-test (W-2s t-test) with $\alpha = 0.05$ because the variances in growth rates and circulus deposition rates were found to be unequal, and the W-2s t-test should be robust to non-normality. Rates were compared as both daily rates, and relative to water temperature. Accumulated thermal units (ATUs) were used to describe the thermal experience of the fish throughout the study. Accumulated thermal units were obtained by summing the mean daily water temperatures (°C) between Events. All water temperatures above 0°C were included in the calculation of ATU and negative temperatures were treated as 0°C (Boyd *et al.*,

2010; Chezick *et al.*, 2014). Scale growth rates and circulus deposition rates relative to time and ATUs were also compared among stocks of origin using ANOVA with $\alpha = 0.05$.

Scale growth rates and circulus deposition rates were averaged among sampling Events across the duration of the study and among stocks and sites to ascertain the presence of any relationships between these rates and either time or water temperature. Growth and circulus deposition were calculated between Events, so there are a total of 12 growth/ circulus deposition intervals among the 13 sampling Events. However, data from Event 1 were omitted because Event 1 took place in the freshwater rearing facilities, leaving a total of 11 growth/circulus deposition intervals for the analysis. Using these results we also calculated the number of days required for a single scale circulus to form.

Results

A total of 1 525 fish among all stocks and net pen sites was sampled over the duration of the project. The difference in mean water temperature between Site 1 and Site 2 was only 0.15°C (Site 1=7.45°C, Site 2=7.6°C). Therefore,

the temperatures from the two sites were averaged, and the resulting temperature time series was used for all further analyses (Fig. 2). Additionally, two large gaps in temperature data from Site 2 made it impossible to calculate reliable scale growth rates or circulus deposition rates on a pen-specific basis

Daily scale growth rate and daily scale circulus deposition rate were higher at Site 1 than at Site 2 (daily scale growth: W-2s t-test, $t=3.6$, $P<0.05$; daily circulus deposition: W-2s t-test, $t=2.8$, $P<0.05$). As expected, when scale growth and circulus deposition rate were related to ATUs both rates were higher at Site 1 than at Site 2 (daily scale growth: W-2s t-test, $t=3.5$, $P<0.05$; daily circulus deposition: W-2s t-test, $t=2.7$, $P<0.05$). There were no differences in scale growth rates or circulus deposition rates among stocks for either daily rates or rates compared to ATUs (daily scale growth: ANOVA $F_{2,1522}=0.42$, $P>0.05$; daily circulus deposition: ANOVA $F_{2,1522}=0.31$, $P>0.05$; scale growth per ATU: ANOVA $F_{2,1522}=0.31$, $P>0.05$; circulus deposition per ATU: ANOVA $F_{2,1522}=0.28$, $P>0.05$). Therefore, the data for scale growth rate and circulus deposition rate, respectively, were combined for all stocks within a site but the sites were treated separately for the remainder of the analysis.

Relationship of scale growth rate to days spent in net pen and water temperature

Scale radius and fish total length showed a strong relationship at both sites when the data were considered as a whole (Site 1: SLR, adjusted $R^2=0.95$, $P<0.001$; Site 2: SLR, adjusted $R^2=0.93$, $P<0.001$ [Fig. 3]). However, daily growth rates showed a non-linear, negative trend through time (Fig. 4a–b). Among Events, the daily scale growth rate was not consistent (Site 1: ANOVA, $F_{1,692}=1207$, $P<0.05$; Site 2: ANOVA, $F_{1,829}=1272$, $P<0.05$). The same trend was evident in the relationship between scale growth and water temperature through time (Site 1: ANOVA, $F_{1,692}=864.8$, $P<0.001$; Site 2: ANOVA, $F_{1,829}=1229$, $P<0.001$ [Fig. 4c–d]).

Relationship of circulus deposition rate to days spent in net pen and water temperature

Circulus deposition rate showed similar patterns to scale growth rate through time. Circulus deposition rate was not constant through time (Site 1: ANOVA, $F_{1,692}=1183$, $P<0.001$; Site 2: ANOVA, $F_{1,829}=1030$, $P<0.001$) and

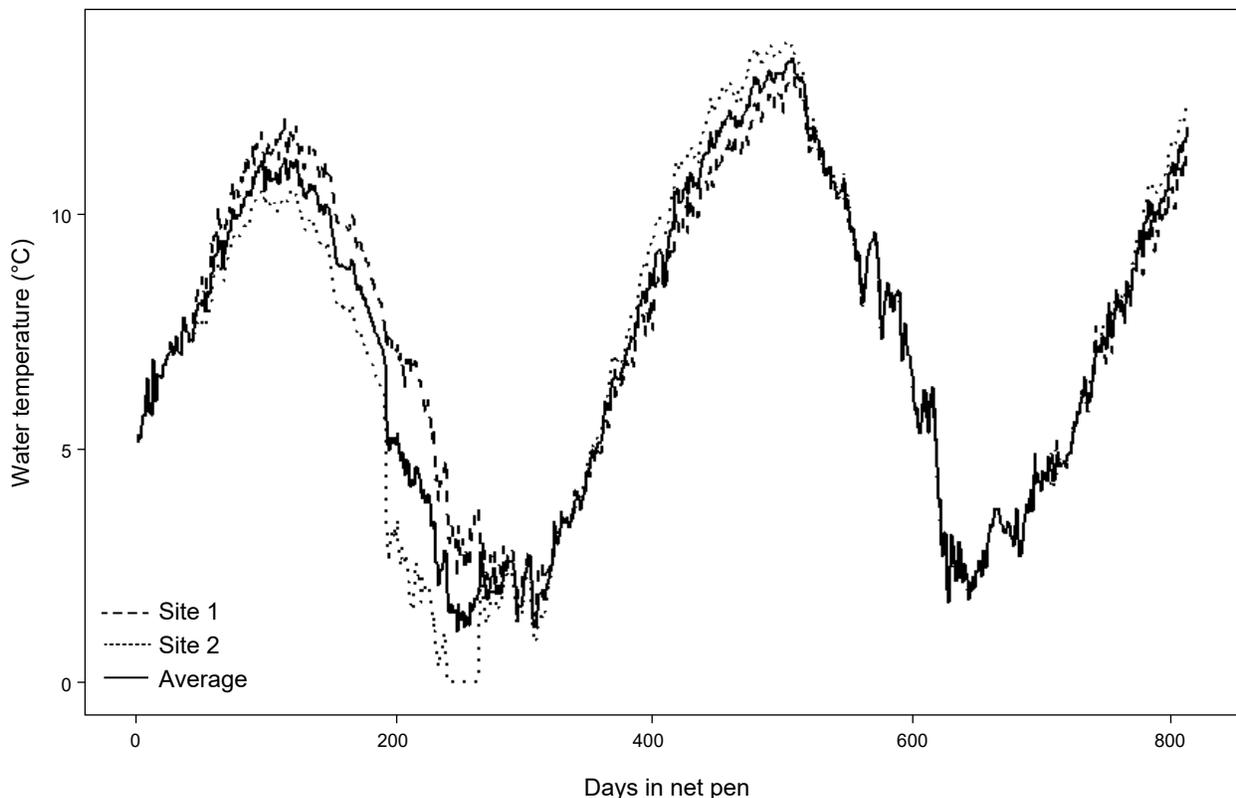


Fig. 2. Time series of water temperature of the two net pen sites throughout the study period, and their average. Site 1= dashed line; Site 2= dotted line; Average of Site 1 and Site 2= solid line.

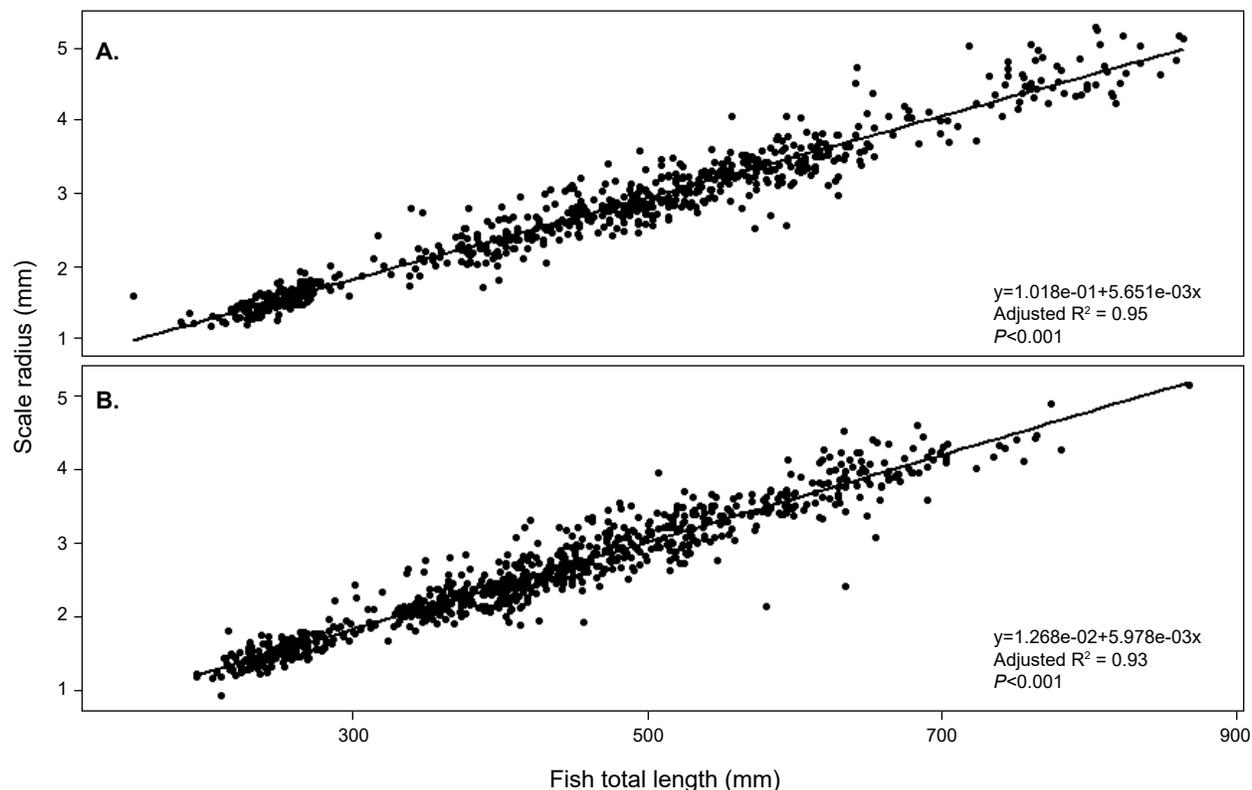


Fig. 3. Relationship of scale radius to fish total length at Site 1 (A) and Site 2 (B).

showed a sharp decrease throughout the first five sampling Events (192 days post-stocking, [Fig. 5a–b]). The relationship between circulus deposition rate and water temperature was also not constant among Events, with the steepest decrease in circulus deposition rates occurring among the first three sampling Events (Site 1: ANOVA, $F_{1,692}=898.9$, $P<0.001$; Site 2: ANOVA, $F_{1,829}=1036$, $P<0.001$ [Fig. 5c–d]).

When scale circulus deposition rate was measured on a daily interval, each circulus required an average of 2.7 days to form at Site 1, with a range of 0.79–10.4 days. At Site 2, a single circulus formed on average every 3 days, with a range of 0.79–12 days. When considered relative to water temperature, a single circulus was deposited when a fish had experienced 5–75.5 ATU, with a mean of 19 ATU per circulus at Site 1. The temperature experience required for a single circulus to form on fish at Site 2 was similar, with an average of 20.5 ATU and a range of 5.3–82 ATU. The highest circulus deposition rates relative to both time and ATUs occurred between entrance to the marine environment and Event 2, the first marine sampling Event, while the lowest rates occurred among the final Events of the study.

Discussion

Our study demonstrated that scale growth rates and circulus deposition rates in marine-stage Atlantic salmon are not constant through time. Daily growth and circulus deposition rates decreased over the course of our study, with the highest rates occurring during the first year of marine habitation and the lowest rates occurring when the study was terminated at the end of two and a half growing seasons. The same trends were seen when scale growth rate and circulus deposition rate were plotted relative to thermal experience.

Decreasing somatic growth as fish approach sexual maturity could explain the trends seen in scale growth and circulus deposition rate. At the end of the original study, the salmon were 3+ years old and had spent two winters (1998–1999, 1999–2000) in the sea. This is a typical age for US Atlantic salmon to make their first spawning migration (Gardner, 1976). However, the maturity status of the fish used in this study was not recorded, so it is not known how sexual maturity may have affected scale growth and circulus deposition rates for these particular fish.

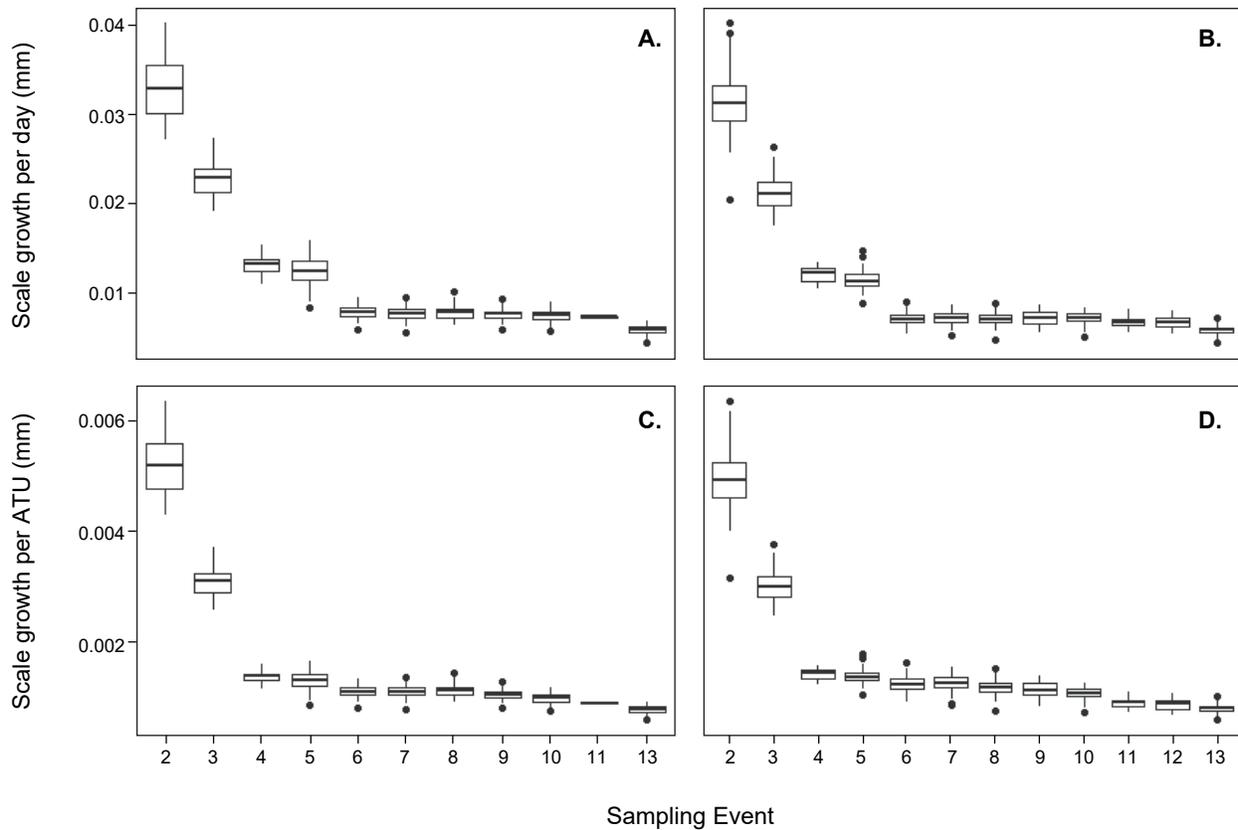


Fig. 4. Daily scale growth rate at Site 1 (A) and Site 2 (B), and the relationship between scale growth rate and accumulated thermal units (ATU) at Site 1 (C) and Site 2 (D) over the duration of the study.

Studies of Pacific salmonids have also found that marine growth, as evidenced by scale circulus spacing and circulus deposition rate, decreases through time, and may be at least partially attributable to a reduction in somatic growth as the fish ages. Barber and Walker (1988) found that scale circulus spacing decreased between the first and second year at sea in adult Sockeye salmon *O. nerka*. Fisher and Percy (2005) compared circulus deposition rates in juvenile and maturing Coho salmon *O. kisutch*. On average, juvenile coho salmon deposited a new scale circulus every 5.3 days, whereas maturing fish deposited a new circulus every 7.6 days. Thomas *et al.* (2019) reported a rate that ranged between 16.2 days per circulus for Atlantic salmon held at low water temperatures (6°C) to 5.1 days per circulus for fish held at higher temperatures (15°C). They found that circulus deposition rate was also affected by the consistency of food availability. These circulus deposition rates are similar to those seen in our study fish when the first five sampling Events, which cover the first year at sea, are compared with later sampling Events.

Barber and Walker (1988) also found strong correlations between increasing photoperiod and increasing fish growth. They attributed some of the patterns in circuli spacing that they saw to changes in food availability (Barber and Walker, 1988). Neither the photoperiod nor the food availability experienced by our fish represented natural conditions. Because Atlantic salmon in the wild are transient and spend a majority of their time at high latitudes, they experience a greater seasonal fluctuation in photoperiod than salmon that are confined to the Maine coast. In addition, our fish were fed to satiation, a condition which undoubtedly does not occur in the wild. However, net pen studies such as this one can be useful for conducting long term sampling of fish held under semi-natural conditions.

Fish in the current study were only sampled during a single sampling Event; any fish that were recaptured at subsequent Events were put back in the net pen and a new fish obtained in their place. Future studies aimed at gaining a detailed understanding of Atlantic salmon

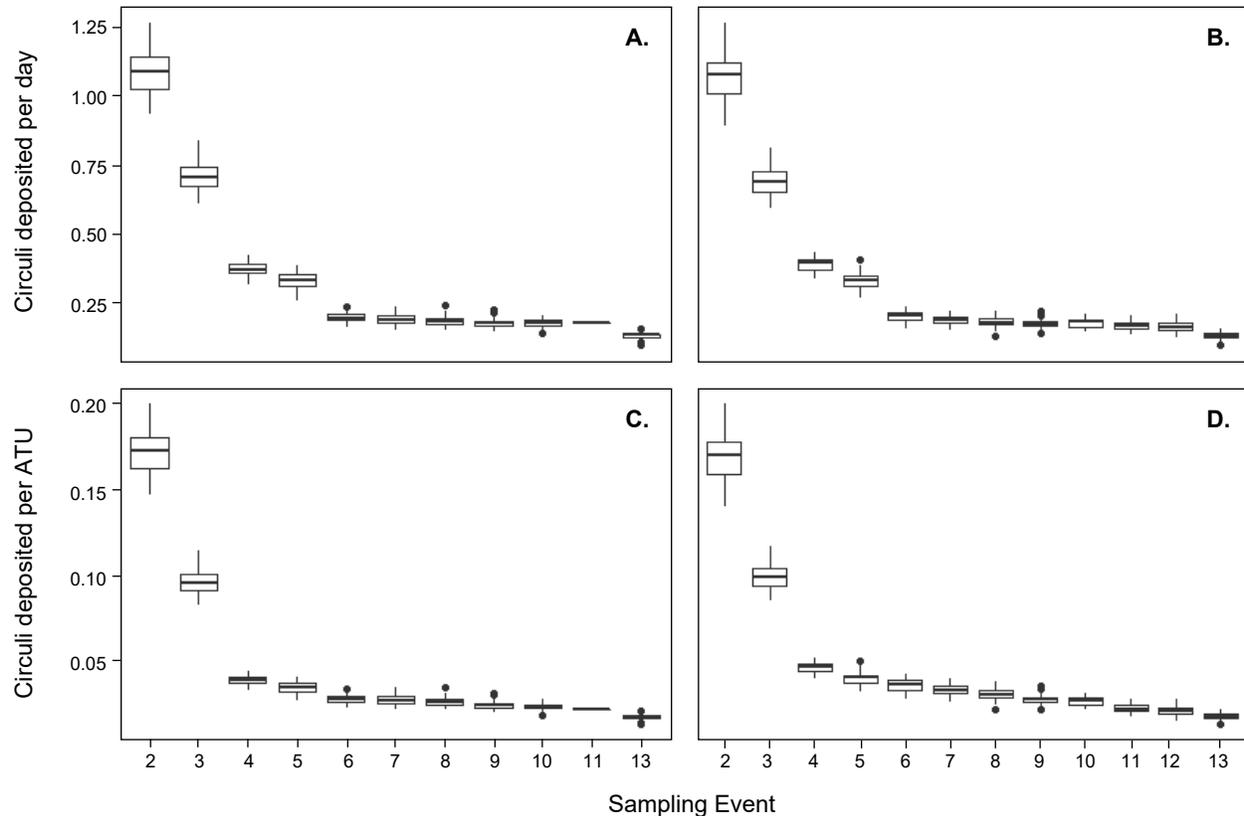


Fig. 5. Daily circulus deposition rate at Site 1 (A) and Site 2 (B), and the relationship between circulus deposition rate and accumulated thermal units (ATU) at Site 1 (C) and Site 2 (D) over the duration of the study.

post-smolt scale growth rates and circulus deposition rates would benefit from frequent, repeated sampling of known individuals. Sampling events outside of the growing season would also yield beneficial information about seasonal changes in growth and circulus deposition rates. Such a sampling scheme could retain important information about individual variability in growth and circulus deposition rates and also allow for a more detailed understanding of scale formation and growth relative to different aspects of the fish's life history.

The present study expands upon previous work on Atlantic salmon marine-stage growth (*i.e.*, Thomas *et al.*, 2019) by tracking growth and circulus deposition rates in the marine environment through two sea-winters, under a semi-natural temperature and photoperiod regime. Under these conditions, which more closely mimic those experienced by fish in the wild than previous laboratory studies, both scale growth and circulus deposition rates were non-constant and decreased through time. Acknowledgement of these fluctuating growth and circulus deposition rates in further studies of Atlantic salmon could help researchers obtain more detailed information about growth patterns in this species.

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Novel observations of capelin (*Mallotus villosus*) spawning directly on a brown algae species (*Desmarestia viridis*) in coastal Newfoundland, Canada

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Abstract

Capelin (*Mallotus villosus*) is a key forage fish species within its circumpolar range. This species' importance lies in its role in the typical marine 'wasp-waist' food web, where capelin acts as a conduit for energy flow from lower to higher trophic levels. Herein we describe a novel observation of capelin spawning subtidally on an annual brown algae species, *Desmarestia viridis*, during July–August 2019 in Placentia Bay, Newfoundland, Canada. Based on extensive video surveys of the seabed along with shoreline surveys and sediment sampling, we did not find other nearby sites with typical capelin subtidal and intertidal spawning habitat (*i.e.* medium sand to pebble gravel). Findings suggest that capelin spawned directly on this brown algae species, *D. viridis*. Eggs adhered to *D. viridis* developed normally and hatched successfully. As temperatures of intertidal areas are predicted to increase above temperatures suitable for capelin egg rearing (2–12°C) with climate change, *D. viridis* may become a high-quality subtidal spawning habitat for capelin and other fish species. In support, this algal species is adapted to colonize high disturbance areas, allowing protection from egg predators in a high flow environment while also being resistant to urchin grazing.

Keywords: Capelin; spawning habitat; *Mallotus villosus*; Northwest Atlantic; Newfoundland; *Desmarestia viridis*

Introduction

Capelin *Mallotus villosus* (Müller, 1776) is an important forage fish species both commercially and ecologically in many northern marine ecosystems, whereby it plays a key role in funnelling energy from lower to higher trophic levels (Lavigne, 1996; Carscadden and Vilhjalmsson, 2002). In the Northwest Atlantic, the capelin population on the Newfoundland shelf collapsed in 1991 (Buren *et al.*, 2014) and has yet to recover (Buren *et al.*, 2014, 2019). The lack of recovery is thought to be related to bottom up processes, whereby changing seasonal sea ice dynamics and timing of spawning limit recruitment due to mismatches between larval emergence and favourable environmental conditions (*i.e.* low predator and high prey densities) for larval survival (Buren *et al.*, 2014; Mullaney *et al.*, 2016; Murphy *et al.*, 2018; Lewis *et al.*, 2019). Although the

primary reproductive mode in coastal Newfoundland is thought to be intertidal ('beach') spawning (Nakashima and Wheeler, 2002), there are also historical reports of widespread and consistent subtidal spawning (Templeman 1948), which are further supported by more recent studies (Nakashima and Wheeler, 2002; Davoren *et al.*, 2006). As capelin eggs become sticky after fertilization (Davenport *et al.*, 1986), the spawning site becomes the egg-rearing site. Although larvae hatch in good condition from some subtidal sites (Penton and Davoren, 2008) but not others (Nakashima and Wheeler, 2002), incubation is often longer in subtidal habitat compared to beach habitat due to cooler water temperatures (Penton *et al.*, 2012), resulting in longer exposure to egg predators (Frank and Leggett, 1984), less growth/development time prior to winter, and potentially a higher probability of temporal mismatches with favorable environmental conditions. Overall, little

information exists regarding the contribution of subtidal habitat to capelin recruitment (Davoren *et al.*, 2007).

Similar to intertidal spawning habitat, studies have linked subtidal capelin spawning locations primarily with a sediment size range (0.5–25mm; Templeman, 1948; Nakashima and Wheeler, 2002; Davoren *et al.*, 2007; Penton and Davoren, 2012, 2013) and secondarily with a temperature range (2–12°C; Carscadden *et al.*, 1989; Davoren, 2013; Crook *et al.*, 2017), with highest hatching success between 4–7°C (Penton and Davoren, 2013). For subtidal spawning, bathymetric features such as depressions (*i.e.*, trenches or ‘holes’) are also important, as they retain suitable spawning sediment in specific areas (Penton and Davoren, 2012). This sediment size range is key for proper oxygenation and waste removal (Penton *et al.*, 2012) and temperature range is vital to reduce the rate of abnormal egg development (Shadrin *et al.*, 2020). As fertilized capelin eggs adhere to all nearby structures, eggs have been anecdotally observed and reported adhered to algae by local fishers, along with other structures (*e.g.*, traps, trawls, other fishing nets and anchors) from 5–45m depth (Templeman, 1948). Adherence to algae and these other structures, however, is thought to occur incidentally, whereby eggs drift from nearby sediment-based spawning sites.

Here we describe a novel observation of capelin spawning subtidally on brown algae, *Desmarestia viridis*, during July–August 2019 (Fig. 1) in Placentia Bay, Newfoundland, Canada. *D. viridis* is a canopy-forming, annual brown algal species that is usually found in nearshore intertidal and subtidal areas (<12m) at higher latitudes, most often in Arctic or sub-Arctic regions (van Oppen *et al.*, 1993). We investigated whether capelin spawned directly on *D. viridis* or whether the capelin eggs adhered to this algal species incidentally. These observations were made while investigating the spatial extent of subtidal spawning of capelin within this Newfoundland bay.

Materials and Methods

Underwater camera surveys were conducted during July–August, 2019 on the east coast of Placentia Bay, Newfoundland, Canada (Fig. 2A) within 12 areas highlighted as being potentially important for subtidal capelin spawning during fisher interviews adapted from Sjare *et al.* (2003). To determine camera survey sites, a 4.6km by 2.3km rectangle was drawn around the center of each of the 12 potential subtidal spawning areas identified by interviewees. Within each of these 12 rectangles, we used ArcMap 10.3.1 to generate 10 random sites at least 500m apart, which was based on the size of the chartered fishing

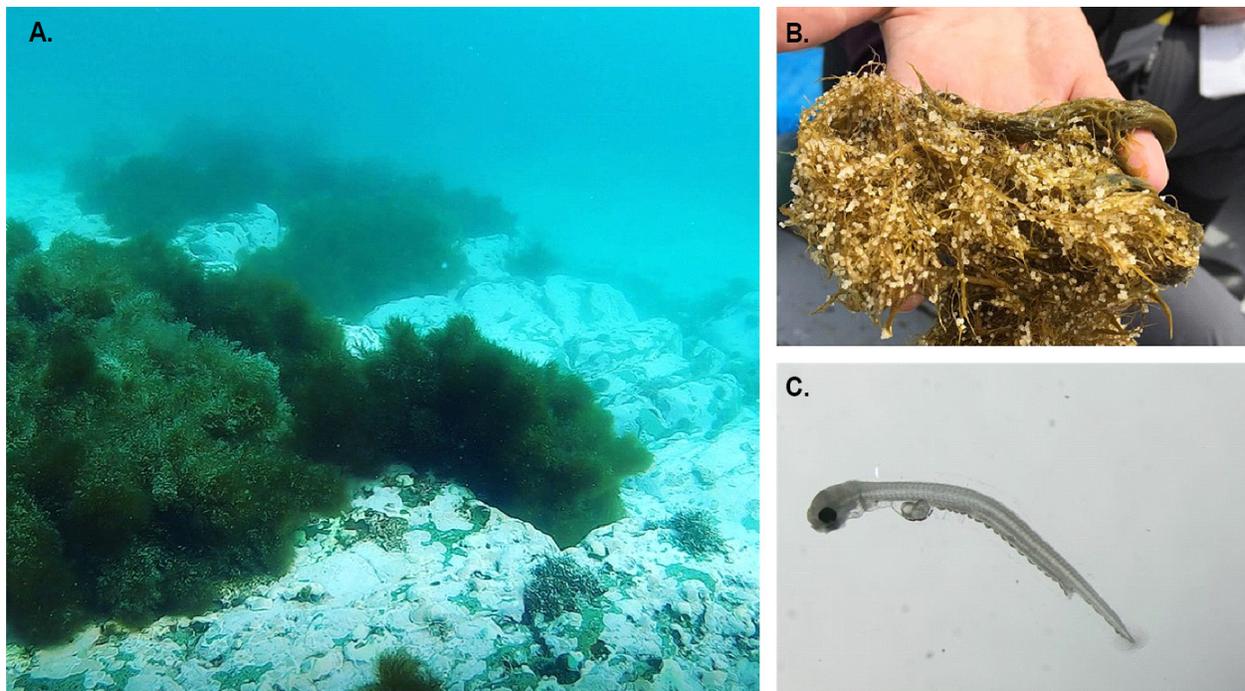


Fig. 1. Screenshot from camera surveys conducted on 20 July 2019 showing *Desmarestia viridis* covered in adherent capelin (*Malotus villosus*) eggs (A). Photograph of a sample of *D. viridis* covered in yellow capelin eggs collected on 20 July 2019 (B). A microscope (Olympus SZX7, 25X magnification) photograph of the capelin larvae that hatched from laboratory-raised eggs found on *D. viridis* (C).

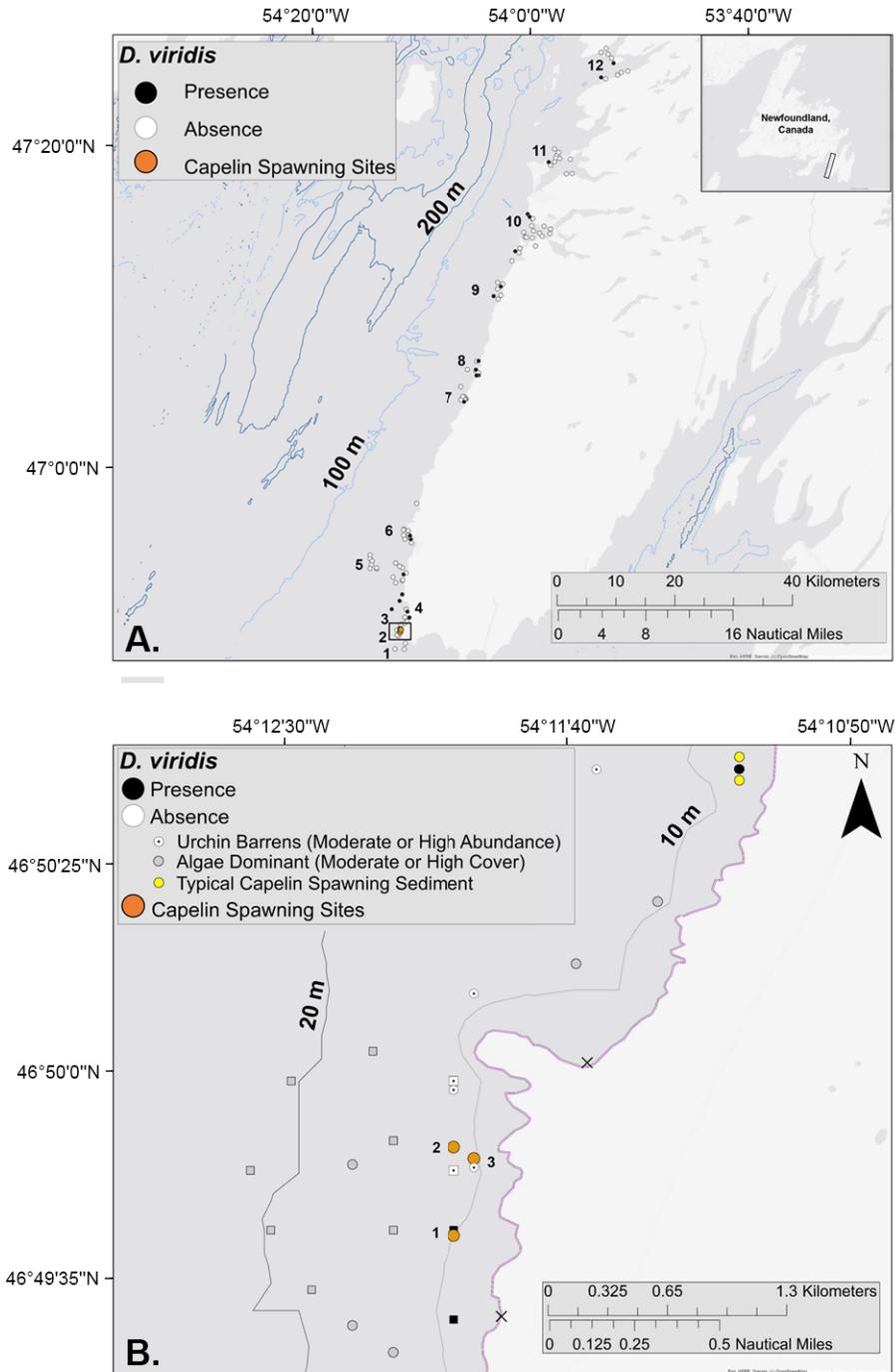


Fig. 2. The location of the east coast of Placentia Bay, Newfoundland, Canada (A, inset). (A) The distribution of *Desmarestia viridis* along the east coast of Placentia Bay based on the 136 sites surveyed during July–August, 2019 within the 12 areas highlighted as being potentially important for subtidal capelin (*Mallotus villosus*) spawning during fisher interviews. The sites where capelin eggs were adhered to *D. viridis* are indicated (capelin spawning sites) and the square indicates the region highlighted in B. (B) The fine-scale distribution of *D. viridis* with adherent capelin eggs (capelin spawning sites 1–3) and without capelin eggs, along with nearby sites that were both absent of *D. viridis* and one of the following: algal-dominated, urchin barrens, or typical capelin subtidal spawning sediment (medium sand to pebble gravel). Squares represent the 11 delineation sites, while circles represent the original randomly generated sites. The purple line along the coast indicates the area searched with binoculars for typical capelin intertidal spawning habitat and evidence of intertidal spawning, while the black Xs indicate beaches, which were comprised of large cobbles and boulders.

vessel (6m) and expected drift, to reduce the probability of covering the same area in separate surveys. In addition to these 120 random sites, other sites were added based on the previous fishing experience and knowledge of chartered fishers in the area, for a total of 136 sampling sites.

Prior to beginning camera surveys, we regularly contacted local fishers and monitored a citizen-science social media platform (www.ecapelin.ca) to ensure that boat-based surveys began after capelin had arrived in coastal regions and had begun spawning in the bay. We sequentially visited each site, during which we deployed a metal frame (meshless crab or lobster pot) with two underwater video cameras (GoPro Hero 7) attached along with a data logger (Star-Oddi DST) that measured temperature (°C) and salinity via conductivity (mS/cm) every 5 s. The metal frame was lowered to the seabed where it remained for 5 min to allow instrumentation to calibrate, and then was lifted ~ 1m off the seabed and allowed to drift for 4 min on average (± 6 s), or ~ 250–300m, to explore more of the seabed immediately adjacent to each site for the presence of capelin eggs.

After the camera surveys were completed at each site, mean depth, temperature and salinity were derived from the data logger. Videos for each survey site were analyzed to determine the dominant sediment type, occurrence of capelin eggs, along with a qualitative index (*i.e.*, high, moderate, low, and zero) of the percent cover of *D. viridis* and other algal species, and abundance of green urchins (*Strongylocentrotus droebachiensis*). For this paper, we focus on *D. viridis* because this was the only algal species on which adherent capelin eggs were found. We used the Wentworth Scale to qualitatively classify the dominant granulated sediment type on videos (Wentworth, 1922).

To determine if capelin eggs were present, sediment was sampled using a 15-cm² Ponar Grab system. Capelin eggs adhered to algae were also incidentally sampled when algae became tangled in our metal frame. Eggs were preserved in Stockard's (50 mL formaldehyde, 37% solution; 40mL glacial acetic acid; 60mL glycerin; 850mL sea water) and later examined under a dissecting microscope (Olympus SZX7) to determine species identity based on egg size and colour (Fridgeirsson, 1976), as well as comparison to reference capelin egg samples collected from active capelin spawning sites in other areas of Newfoundland. We also quantified the percentage of eggs in different developmental stages within at least one random sample of 50–100 eggs from each site. Following Frank and Leggett (1981), early developmental stages (Stages I–II) represented recent spawning, while later developmental stages (Stages III–VI) represented stages closer to hatching. Eggs adhered to algae were also lab-

reared within a controlled environmental chamber at ~8°C until hatch to confirm species identity using morphological characteristics (Fahay, 2007).

Ethical Statement

The care and use of experimental animals complied with Canadian Council of Animal Care animal welfare laws, guidelines and policies as approved by Canadian Council of Animal Care (Protocol: F16-017/1/2/3).

Results

During July–August 2019, we completed camera surveys at 136 unique sites within 12 potential subtidal capelin spawning areas in eastern Placentia Bay to determine the occurrence of capelin eggs (sampling dates: 16, 20, 21, 23, 25, 27 July and 6, 7, 9, 15 August). On 20 July 2019, we discovered eggs adhered to *D. viridis* during camera surveys at three sites within 128–483m of each other in one of the 12 potential areas (Fig. 2B). The seabed substrate was characterized as bedrock with no granulation at all three sites (Fig. 1A). While drifting away from each site, we did not find more typical capelin spawning sediment or capelin eggs adhered to any structures immediately adjacent to each site. We collected eggs from two of the three sites on the day of discovery (20 July), which were lab-raised to hatch and later identified as capelin larvae (Fig. 1B, 1C). Initial egg samples revealed 57% of capelin eggs at site 1 were in earlier stages of development (Stages I–II), while a lower percentage (17%) were in early stages at site 2 (Table 1). These three sites were revisited on August 1, 10 and 11, 2019. On 1 August, we only sampled eggs to monitor development (no camera surveys), but were unable to obtain a sample from sites 2 and 3 due to high tidal activity. Eggs sampled at site 1 on 1 August were all in later stages (III–VI), indicating no recent spawning. Note that abnormally developing, empty or dead eggs were not found in any sample. On 10 and/or 11 August, capelin eggs were no longer found adhered to algae at any of the three sites and the percent cover of *D. viridis* was lower relative to 20 July (Table 1). Temperature-based incubation duration was estimated for each site to be 16–21 d from 20 July, based on the equation in Frank and Leggett (1981), suggesting that the eggs had likely hatched by 10/11 August.

To determine if there was a nearby beach spawning site, we thoroughly surveyed the coastline from the boat (~ 500m offshore) using binoculars (purple line; Fig. 2B) within ~ 5km north and south of the three spawning sites during work at or nearby these sites (20–21, 23 July; 1, 10–11 August). The general topography of the coastline was 120m cliffs, with two 2m wide beach sites. However,

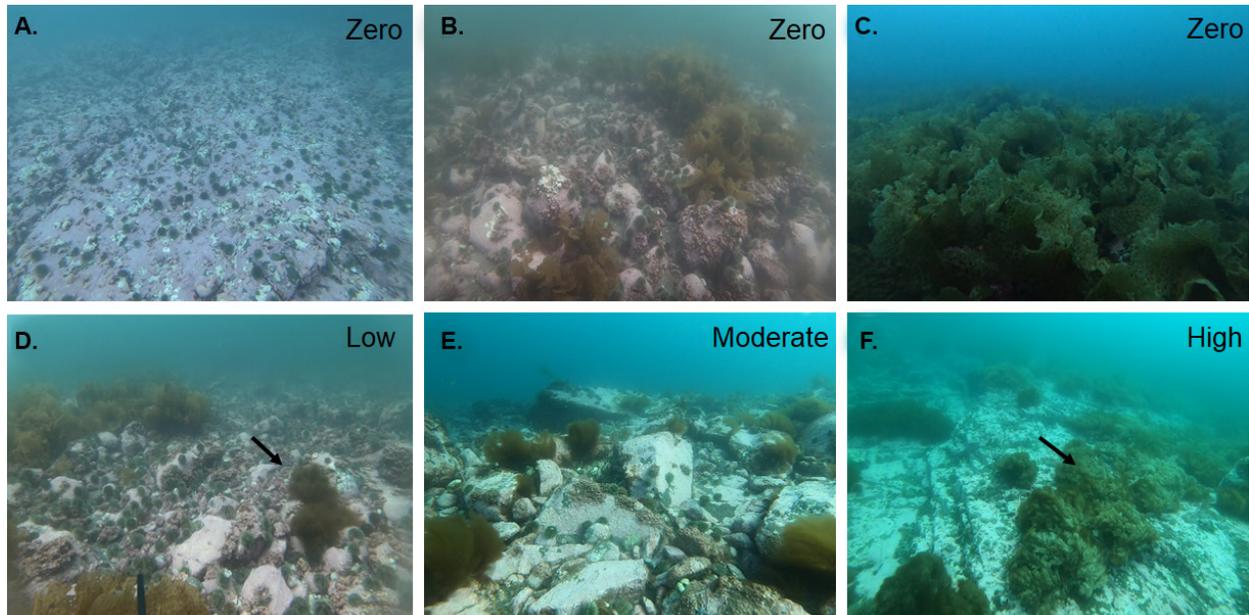


Fig. 3. Photographs from underwater video (GoPro Hero 7) during surveys for capelin (*Mallotus villosus*) subtidal spawning habitat in July–August, 2019 in Placentia Bay, Newfoundland, Canada. Examples of sites where *D. viridis* was absent (A–C) are shown, including low algal cover and a high density of green urchins *Strongylocentrotus droebachiensis* (A), moderate cover of *Agarum clathratum* (B), and high cover of *A. clathratum* (C). Examples of low, moderate, and high density of *D. viridis* (D–F) are also shown, including *A. clathratum* present with low *D. viridis* cover (D). Note the arrows indicate *D. viridis* (D) and yellow capelin eggs adhered to *D. viridis* (F).

these beaches were composed mostly of larger cobble and boulders fallen from the cliffside. The next nearest site with typical capelin spawning sediment (0.5–25mm) was 2.5km north of our sites (Fig. 2B, yellow circles), but eggs were not found adhered to the sediment when sampled on 21 and 23 July.

To determine if there was a subtidal spawning bed with more typical capelin spawning sediment size ranges from which fertilized eggs may have incidentally drifted to our three subtidal spawning sites, we conducted additional camera surveys on 10 August. To do this, we generated 11 more camera survey sites (‘delineation sites’) in a diamond-like shape around our three capelin spawning sites. Delineation sites were spaced ~500m apart to cover as much of the un-surveyed area near the three spawning sites while minimizing repeatedly covering the same areas (Fig. 2B, squares). Based on video analysis, all delineation sites were identified as bedrock with no granulation and *D. viridis* was only present at two of the shallowest sites (8–10m; Fig. 2B). The remaining nine delineation sites had either high densities of green urchins and very little to no algal species ($n = 2$ sites; Fig. 3A) or high percent cover of other algal species ($n = 7$ sites; Fig. 3B, 3c). Capelin eggs were not found adhered to *D. viridis*, other algal species or bedrock at or nearby any of the 11 delineation sites.

We revisited these sites during 2020 and 2021 to determine if *D. viridis* remained present and capelin eggs were consistently adhered. On 5 August 2020, we conducted camera surveys at all three spawning sites from 2019 and all 11 delineation sites. At the three sites where capelin eggs had been found adhered to *D. viridis*, capelin eggs were not present and *D. viridis* was absent at sites 1 and 2 (Table 1); however, *D. viridis* was present 100m inshore from the original location of site 1. Site 3 was the only site with *D. viridis* present but no capelin eggs were found. Of the 11 delineation sites, *D. viridis* was present again at the same two inshore sites (8–9m) from 2019, and the remaining nine sites continued to be characterized as bedrock with no granulation with either high densities of green urchins and little to no algal cover ($n = 2$ sites; Fig. 3A) or high percent cover of other algal species ($n = 7$ sites; Fig. 3B, 3c). During 2021, we revisited the three spawning sites from 2019 on 12–15 July and *D. viridis* was found with capelin eggs adhered on 15 July nearby site 1.

Discussion

During July 2019, we documented capelin spawning on the algal species *D. viridis*. After systemically surveying adjacent and nearby subtidal areas as well as intertidal areas along the coast (Fig. 2B), we were unable to find

Table 1. Depth, temperature, salinity and percent cover of *Desmarestia viridis* (i.e. high, moderate, low, zero) at each of the three sites at which capelin eggs were found adhered to *D. viridis* during July and August 2019, which were resurveyed during August 2020. Samples of capelin eggs were obtained on 20 July 2019 during underwater camera surveys and egg sampling was also attempted on 1 August 2019 without camera surveys. The percentage of eggs in early developmental stages (Stages I–II) and later stages (Stages III–VI) are indicated for each sample. All capelin eggs were absent by 10 and 11 August 2019 during camera surveys.

Sites with capelin eggs	Date	<i>D. viridis</i> cover	Depth (m)	Bottom Temperature (°C)	Salinity (mS/cm)	Eggs Present?	Stages I–II (%)	Stages III–VI (%)
Site 1 [46.828°N, 54.200°W]	20 Jul 2019	High	10	4.3	43.7	Yes	57	43
	1 Aug 2019	-	-	-	-	Yes	0	100
	10 Aug 2019	Low	10	7.6	46.4	No	-	-
	11 Aug 2019	Moderate	10	10.9	49.2	No	-	-
	5 Aug 2020	Zero	11	11.3	46.3	No	-	-
Site 2 [46.831°N, 54.199°W]	20 Jul 2019	Low	10	4.6	44.0	Yes	17	83
	1 Aug 2019	-	-	-	-	No	-	-
	10 Aug 2019	Zero	12	7.4	46.0	No	-	-
	5 Aug 2020	Zero	14	9.7	44.4	No	-	-
Site 3 [46.830°N, 54.199°W]	20 Jul 2019	Moderate	9	4.7	43.7	Yes	-	-
	11 Aug 2019	Zero	10	8.1	46.6	No	-	-
	5 Aug 2020	Low	11	8.2	43.7	No	-	-

subtidal or intertidal capelin spawning sites on typical sediment (i.e. medium sand to pebble gravel; Nakashima and Wheeler, 2002; Penton and Davoren, 2012). Although we cannot rule out that capelin spawned on small patches of undetected intertidal or subtidal sediment nearby our three algal capelin spawning sites, it is unlikely that eggs drifted from these sites and adhered only to *D. viridis* in the high densities observed despite the concurrent presence of other algal species. Overall, this evidence suggests that capelin spawned directly on *D. viridis*.

As the capelin eggs likely hatched successfully from *D. viridis* in the field, this algal species may represent a favourable capelin spawning habitat. Indeed, *D. viridis* may provide protection for developing eggs from predators, by providing a refuge for eggs away from benthic-feeding predators, such as flounder (Frank and Leggett, 1984), crabs (Mikkelsen and Pedersen, 2017), and amphipods (DeBlois and Leggett, 1993). Additionally, the sweeping motion of the algal branches deters urchin

predation, allowing *D. viridis* to form high-density algal beds in regions with high wave action (Konar, 2000; Gagnon *et al.*, 2006) and providing further protection from pelagic fish egg predators (Gagnon *et al.*, 2006; Blain, 2013). Therefore, depositing eggs on *D. viridis* in areas of high wave action may provide a fixed incubation habitat with low predation for capelin eggs. The sweeping motion also likely results in regular oxygen replenishment and waste removal from the water surrounding eggs. Although the high acidity (H₂SO₄) of *D. viridis* might be considered an unsuitable, or even detrimental, incubation habitat for capelin eggs, sulphuric acid is only released at senescence, which is initiated >12°C (Blain and Gagnon, 2013; Gagnon *et al.*, 2013). Indeed, although *D. viridis* can survive short periods of average ocean temperatures up to 23°C (Breeman, 1988), it undergoes a rapid die-off when average temperatures are >12°C for extended periods (e.g. ~ 1 month; Gagnon *et al.*, 2013) and reproduction is inhibited at 10°C (Breeman, 1988). The higher temperatures during 2020 (8.2–11.3°C; Table 1), therefore,

might explain the lower presence and density of *D. viridis* at the same inshore sites relative to 2019. Overall, if the conditions are favorable (*i.e.* high wave action and $\leq 12^{\circ}\text{C}$), *D. viridis* may be a high-quality incubation habitat for capelin eggs. In support, we found many sites with high algal cover in our study area, but never found capelin eggs attached to algal species other than *D. viridis*. Previous studies also reported that *D. viridis* is a preferred algal species for fish egg deposition in coastal Newfoundland relative to other algal species (*e.g.*, *Desmarestia aculeata*, *Agarum clathratum*; Blain, 2013).

As *D. viridis* is resistant to urchin predation in areas of high wave action, it is highly successful at colonizing these areas (Konar, 2000; Gagnon *et al.*, 2006). This might explain the high densities of *D. viridis* observed (Fig. 3D–F) in inshore, shallow areas (2019: $10 \pm 4\text{m}$; 2020: $13 \pm 4\text{m}$), which are known to be high disturbance areas due to wave action. Other nearby sites, however, also had high densities of green urchins (Fig. 3A), which matched the description of green urchin barrens, previously defined as areas where algae is absent with high sea urchin densities (Konar, 2000). Previous studies in coastal Newfoundland have identified *D. viridis* as a first successional stage in the recolonization of urchin barrens, allowing the colonization of other algal species, such as the perennial *Agarum cribrosum* (*e.g.*, Fig. 3B, 3C, and 3D) and *Alaria esculenta* (Gagnon *et al.*, 2003; Molis *et al.*, 2009). This might explain the deeper sites farther offshore being dominated by these other algal species (Fig. 3B–C) in our study area. As algal beds are important for a variety of ecosystem functions (*e.g.*, fixed carbon source/primary productivity, habitat/shelter), shifts from algal-dominated to urchin-dominated alternative stable states (Folke *et al.*, 2004; Stewart and Konar, 2012; Filbee-Dexter and Scheibling, 2014) can be considered a collapse of the algal bed ecosystem (Chapman, 1981; Chapman and Johnson, 1990; Filbee-Dexter and Scheibling, 2014; Graham, 2004). Indeed, the lack of algal beds results in the reduction in fixed carbon and shelter availability which cascades up the food web negatively affecting higher trophic levels (Gaines and Roughgarden, 1987; Duggins *et al.*, 1989).

Although capelin eggs were only found adhered to *D. viridis* at three of the 25 sites this algal species was observed during 2019, citizen science reports of capelin beach spawning (www.ecapelin.ca) suggested that capelin likely did not move further north of our three spawning sites into Placentia Bay during this year. Additionally, although capelin eggs were only found adhered to *D. viridis* at these three sites during two out of three years, citizen science reports (www.ecapelin.ca) suggested lower spawning capelin biomass during the year when capelin spawn

was not found adhered to this algal species (2020) relative to the two years when capelin eggs were found adhered (2019, 2021). These observations suggest that *D. viridis* may be used as an alternate subtidal spawning habitat when spawning capelin and this algal species co-occur and are both at least moderately abundant. The extent and consistency *D. viridis* is used as a spawning habitat by capelin is an important avenue for future research.

The high overlap between favourable habitat characteristics of incubating capelin eggs and *D. viridis* in coastal Newfoundland, including temperature ($2\text{--}12^{\circ}\text{C}$; Penton and Davoren, 2012; Davoren, 2013; Crook *et al.*, 2017) and depth ($< 40\text{m}$; Penton and Davoren, 2012), suggest that the distribution of subtidal capelin spawning sites and that of *D. viridis* are similar. Current climate change models for Newfoundland predict that by 2063 bottom temperature will increase up to $0.4\text{--}2.1^{\circ}\text{C}$ along the coast (Loder *et al.*, 2013). Although capelin may be more likely to shift their range in response to this predicted change in ocean climate over the long-term (Rose, 2005), short-term responses may be habitat shifts within their current range. With continued increases in temperature and temperature variability at intertidal capelin spawning sites, capelin may initially occupy cooler subtidal habitat more relative to warm, beach spawning habitat to ensure offspring survival (Nakashima and Wheeler, 2002; Davoren, 2013; Penton and Davoren, 2013; Crook *et al.*, 2017). If spawning habitat is limited, as suggested by ongoing beach spawning habitat restoration work, this shift may lead to lower availability of favourable spawning habitat resulting in a recruitment bottleneck. The widespread distribution of *D. viridis* in nearshore regions (25 out of 136 sites; Fig. 2A), however, may reduce the chances of a climate change-induced bottleneck if subtidal beds of *D. viridis* are commonly used as spawning habitat by capelin. Alternately, as *D. viridis* is an annual species and is sensitive to variation in temperature (Blain and Gagnon, 2013; Gagnon *et al.*, 2013), the occurrence of this algal species may also decrease within their current range in the future. Nonetheless, as *D. viridis* is resistant to urchin grazing in areas with high wave action, this species may be able to colonize newly or highly disturbed areas with suitable temperature, thereby dynamically establishing favourable annual subtidal spawning habitat for capelin.

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Contributions

L.M.B. was responsible for data generation, survey design, project design, data analysis, fieldwork, and manuscript preparation. Further, L.M.B. acquired additional funding from the University of Manitoba.

G.K.D. contributed to project design, acquired the majority of the funding from Fisheries and Oceans Canada through the Coastal Environmental Baseline Program, provided edits and feedback on the project as it developed and established the original idea for the project.

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A Preliminary Abundance Estimate of an Atlantic Sturgeon (*Acipenser oxyrinchus oxyrinchus*) Contingent Within an Open Riverine System

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Abstract

Abundance estimates are essential for fisheries management, but estimating the abundance of open populations with low recapture rates has historically been unreliable. However, by using mark-recapture data modulated with survivability parameters obtained from analysis of acoustic telemetry data, more accurate abundance estimates can be made for species that exhibit these characteristics. One such species is the Atlantic sturgeon, for which abundance estimates were designated a research priority following precipitous population declines throughout the 20th century. We addressed this research need in the Saco River Estuary (SRE), a system where the Atlantic sturgeon has been extensively studied using mark-recapture and acoustic telemetry methods since 2009. These data were analyzed using Bayesian analysis of a Lincoln-Peterson estimator, constrained with parameters from a Cormack-Jolly-Seber model, to provide an initial abundance estimate for the system. The resulting estimate indicated that approximately 3 299 (95% Credible Interval: 1 462–6 828) Atlantic sturgeon utilize the SRE yearly, suggesting that the SRE provides critical foraging habitat to a large contingent of the species within the Gulf of Maine. The present study demonstrated the method utilized herein was effective in generating a reasonable estimate of abundance in an open system where recapture events are rare, and therefore may provide a valuable technique for supplying initial estimates of fish abundance in additional systems that display similar characteristics.

Keywords: Atlantic sturgeon, Gulf of Maine, abundance, acoustic telemetry, mark-recapture

Introduction

Estimating fish abundance is a cornerstone of fisheries management, especially for those species that are listed under the Endangered Species Act. Abundance information is used for establishing management strategies, determining species status, and measuring population recovery (Couturier *et al.*, 2013). In the absence of abundance estimates, managers cannot effectively assess and implement stock management strategies, which may lead to further degradation of a stock. Despite the importance of quantifying abundance, this has not been accomplished for many fish stocks, particularly for those that exhibit open populations: The presence of both emigration and immi-

gration within open populations violates the assumptions of traditional mark-recapture estimation techniques, which require closed systems (Seber, 1986). When utilized, these traditional methods yield highly variable and imprecise predictions (Kendall, 1999). As a result, some past studies have estimated the abundance of open populations by analyzing aspects of the species life history where the population displays closed behavior. For example, salmon population studies have performed mark-recapture techniques on salmon parr, when the juvenile fish are unable to leave their natal estuaries (Rodgers *et al.*, 1992). Similarly, the Hudson River Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*) population was estimated using juveniles younger than two years of age, ensuring that

fish were confined to the river system (Peterson *et al.*, 2000). This approach is not always possible, and as such, additional methods for estimating open population abundance are needed.

In recent years, several new techniques have been established for estimating abundance with mark-recapture data within open systems, including various parameterizations of the Jolly-Seber model (JS). These models account for fish movements in and out of the system by estimating catchability parameters, such as apparent survival and return probability (Seber, 1986). However, mark-recapture sampling procedures often violate model assumptions, resulting in biases that cause these models to generate errant abundance estimates (Carothers, 1973). The Cormack-Jolly-Seber (CJS) model was formulated to accurately estimate catchability parameters through the inclusion of external covariates (Lebreton *et al.*, 1992), but this model lacks the ability to provide an abundance estimate. As a result, studies began utilizing acoustic encounter histories to better approximate these catchability parameters, which are then treated as fixed and incorporated into Jolly-Seber models, such as the POPAN formulation, and used to estimate abundance (Withers *et al.*, 2019). Furthermore, Bayesian estimation techniques have been employed to reduce model uncertainty by incorporating prior knowledge into abundance estimates (Dudgeon *et al.*, 2015; Ketz *et al.*, 2018). Despite these advances in modeling procedures, these techniques still suffer from significant shortcomings, primarily that they are computationally difficult and often suffer from inflation bias due to low recapture numbers (Carothers, 1973; Cowen and Schwarz, 2006; Haxton and Friday, 2019). As a result, abundance estimation for open populations with rare recapture events remains difficult. The Atlantic sturgeon is one species that exhibits these characteristics and currently lacks abundance estimates.

The Atlantic sturgeon is a large, long lived, mobile, anadromous fish species inhabiting coastal waters and estuaries along the eastern seaboard of North America (NOAA, 2019). Due to its size and accessibility, this species faced intense fishing pressure that resulted in precipitous population declines throughout the 20th century (Altenritter *et al.*, 2017). These population declines led to both a moratorium being placed on all harvest in 1998 (ASMFC, 2021) and the species being listed under the United States Endangered Species Act in 2012. Here, Atlantic sturgeon were separated into five distinct population segments (DPS), with the Gulf of Maine (GOM) DPS listed as Threatened, and all others as Endangered (NOAA, 2019). As such, abundance estimates are a research priority for the species (ASSRT, 2007); however, the aforementioned shortcomings in abundance estimation

methods have limited our understudying of this ecological parameter for Atlantic sturgeon (Hilton *et al.*, 2016), as the species exhibits open populations. Atlantic sturgeon sub-adult and adult individuals are highly migratory, traveling long distances between multiple river systems during summer months and wintering in coastal marine waters (Altenritter *et al.*, 2017). Despite these movement patterns, Atlantic sturgeon are known to exhibit fidelity to both foraging grounds and natal spawning rivers (Fernandes *et al.*, 2010). Since this species regularly returns to specific estuaries over time, their abundance will vary across river systems, and therefore the number of Atlantic sturgeon must be estimated for each respective river system (Wirgin *et al.*, 2018).

The Saco River Estuary (SRE) in the GOM is a unique system for Atlantic sturgeon. After extirpation in the 1960s, they were discovered to have returned to the river system in 2007 (Furey and Sulikowski, 2011). Since this re-emergence, the fish have been extensively studied using both mark-recapture and acoustic telemetry methods. These efforts have shown Atlantic sturgeon are unable to spawn in the SRE, and instead are using the system as a foraging ground (Novak *et al.*, 2017). The primary use of the SRE as a foraging habitat indicates that all individuals using the SRE are adults and sub-adults from other natal estuaries in the GOM DPS, resulting in an open and highly variable contingent comprised of multiple spawning populations (Wippelhauser *et al.*, 2017). The nature of this system and the extensive dataset available provides an opportunity to estimate how many Atlantic sturgeon use the SRE as a foraging ground. Given this opportunity, the goals of this study were (1) to develop an appropriate method for approximating fish abundance using a synthesis of mark-recapture, acoustic telemetry, and Bayesian estimation techniques, and (2) to apply this method to Atlantic sturgeon within the SRE in order to estimate the number of individuals utilizing the river system.

Methods

This study was a component of a larger investigation of Atlantic sturgeon within the SRE, which was comprised of long-term acoustic monitoring and mark-recapture sampling spanning 2009–2018. As a result, capture and tagging efforts varied over time, particularly during initial years of the study. As such, standardized efforts from 2014–2018 will be detailed here.

Fish Capture

Atlantic sturgeon were captured and sampled from mid-May through mid-November each year, with a target frequency of one sampling attempt per week. Given

seasonal variability, this did not always occur during the spring and late autumn, where the majority of sampling opportunities occurred during the summer months. Fish were captured using gillnets (91.4 m long, 2 m high), which were composed of either 15.24 or 30.48 cm bar mesh. These nets were placed between the jetties at the mouth of the Saco River, where they were deployed for a standard of 15 minutes, as longer net soaks yielded too many individuals. The nets were hand hauled, and all entangled sturgeon were extracted and brought onto the deck of the boat. Sturgeon were then transported back to the University of New England dock, where they were washed with estuarine water to oxygenate their gills during the five minute steam. At the dock, fish were placed into net pens ($2.1 \times 0.9 \times 0.9$ m) for a recovery period (~15 min) before undergoing research and handling protocols outlined by Kahn and Mohead (2010). The protocols constituted measuring fork length to the nearest mm, visually searching for external tags, and scanning (AVID PowerTracker VIII) for internal PIT tags. If no tags were detected, a 134.2-kHz PIT tag (model HPT12, Biomark) was inserted adjacent to the dorsal fin. As a secondary means of identification, we inserted a spaghetti T-bar tag on the opposing side of the dorsal fin. Following tagging procedures, fish were then released back into the river.

In addition to these traditional tagging efforts, a subsample of fish was also affixed with acoustic transmitters following the methods in Novak *et al.* (2017). These individuals were selected to reflect the size range of all captured individuals, but only those deemed to be in the best condition, or lacking physical injury, were selected to be acoustically tagged. We surgically implanted an acoustic transmitter (model V16; 69 KHz, 16 mm diameter, approximate 2 500-d battery life; VEMCO, Halifax, Nova Scotia) into the abdominal cavity of these fish. A 5-cm incision was made on the midline of the body on the ventral surface, where the transmitter was anteriorly inserted after being coated in antibiotic ointment. The incision was closed using one or two polydioxanone sutures (PDO II violet monofilament absorbable suture; Oasis, Mettawa, Illinois), which was then coated in additional antibiotic ointment. The surgical process lasted approximately 10 minutes, and fish were then returned to the net pen for a recovery period prior to release.

Acoustic Monitoring

Following the methods of Novak *et al.* (2017), we deployed an acoustic array within the SRE seasonally from 2009–2018. A total of seven acoustic receivers (model VR2W; VEMCO, Halifax, Nova Scotia) were distributed from the mouth of the Saco River to the Cataract dam

at river km 10 (Fig. 1), where their placement served to maximize the area where tagged fish would be detectable within the SRE. These receivers were deployed each year during the month of May and were removed from the river in late November or early December. During this deployment period, receivers were downloaded once per month; any required maintenance was performed during these data collection periods. Additionally, during the winter months, two receivers were placed at the river mouth. These receivers remained deployed from the removal of the acoustic array in early winter until its re-deployment in the spring. This ensured that throughout the entire year no acoustically tagged fish could enter or leave the river system without being detected by an acoustic receiver.

From the acoustic data, we created a binary annual encounter history for the presence-absence of acoustically tagged fish for each year the acoustic array was deployed. The acoustic data were also used to calculate Atlantic sturgeon residence time, T_{res} , within the SRE. For all acoustically tagged fish that were found to have returned in 2017, the year with the largest number of active acoustic transmitters, we tallied the number of days that each fish spent within the river system: The median number of days present across all individuals provided T_{res} . Finally, we created a distribution of the number of distinct acoustically tagged Atlantic sturgeon detected per month, ranging from May to November. Here, the total detections from 2017 were used, as this was the year with the largest number of transmitted fish returning ($n = 36$). These detections were filtered by month to contain only unique fish detections, which were then used to calculate the proportion of total yearly unique detections, and hence represent the proportion of the total population present each month.

Data Analysis

Catchability Parameters: The annual acoustic encounter history was analyzed using a Cormack-Jolly-Seber (CJS) model in program MARK through the RMark interface (RMark, 2013). This analysis estimates both the probability of apparent annual survival (Φ) and the probability of return (p) of an open population (Lebreton *et al.*, 1992). Given that acoustic tag batteries only lasted seven years, and that this study covers a 10-year time period, some tags were known to have expired during the study. As such, these tags were removed from the analysis following expiration. The candidate model set included all combinations, where the estimated Φ and p parameters were either constant (c) or time dependent (t) (Perlut and Strong, 2016), and the individual covariate of fork length (fl) was included in estimating Φ . Program MARK applies an information theoretic approach, where all models

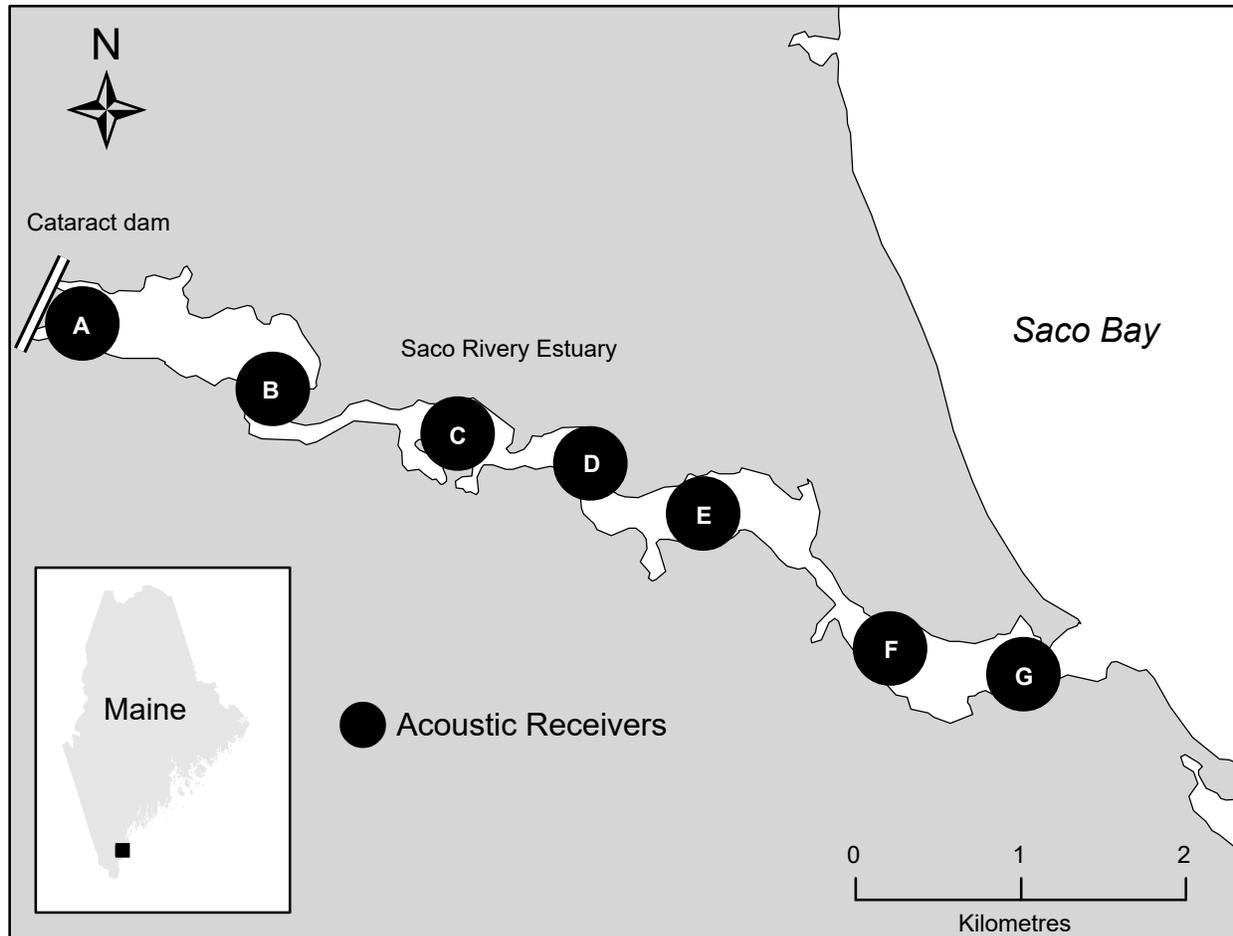


Fig. 1: Map of the Saco River Estuary, where each of the seven acoustic receivers' locations and approximate detection range is represented by black circles. Receivers were placed from the Cataract Dam (A) to the University of New England Marine Science Center beach (G).

with $\Delta\text{AIC} < 2.0$ are considered biologically relevant models in explaining variation in the dataset. Biologically significant covariates within these top ranking models were identified as those whose 95% confidence interval of the beta estimates did not include zero (Burnham and Anderson, 2002).

The estimates for the Φ and p parameters obtained from the acoustic encounter history were then treated as fixed parameters (Withers *et al.*, 2019) and used to determine the number of catchable tagged fish each year (C_y) via equation 1:

$$C_y = \sum_{t=2009}^{y-1} \left(m_t \times \prod_{j=t+1}^y (\Phi_j \times p_j) \right) \quad (1)$$

The number of fish tagged, or marked, in a study year (m_t) was multiplied by the product of the probability that those fish survived and returned each of the following study years ($\Phi_j \times p_j$), up to year y , yielding the number of

Atlantic sturgeon tagged in year t that return to the system in year y . Then, by summing across all Atlantic sturgeon tagged in study years prior to year y , we calculated the total number of catchable tagged fish in year y . Here, t ranged from 2009 to 2017 and y from 2010 to 2018.

Abundance Estimate: In order to estimate abundance for each year, we used the Lincoln-Peterson (Seber, 1986) mark-recapture model. This estimator states the ratio of captured marked to unmarked fish is equivalent to the ratio of all previously marked fish to total fish abundance; however, this model is traditionally used to estimate closed populations, requiring the model to be reworked in order to estimate the number of Atlantic sturgeon utilizing the SRE, an open system where fish are not always catchable. As a result, the model was modified to estimate abundance annually by using C_y . Annual abundance, N_y , can be represented as:

$$N_y = \frac{C_y}{r_y/m_y} \quad (2)$$

Here, annual abundance can be estimated by dividing the catchable tagged population in a given year by the ratio of marked (r_y) to unmarked (m_y) capture events in that same year. Uncertainty in this approach can be mitigated by incorporating prior knowledge (Madigan and York, 1995) and recasting the Lincoln-Peterson estimator in a Bayesian framework. We accomplished this by representing the ratio of marked to unmarked capture events as the probability that a captured fish is marked, or $p(t)_y$. Each year can then be considered an individual mark-recapture experiment, with unique yearly values of $p(t)_y$. This parameter was then estimated separately for each year y using the rjags package in R (Plummer, 2019). A binomial likelihood was used, where:

$$L(p(t)_y | r_y, m_y) = \binom{m_y}{r_y} \times p(t)_y^{r_y} (1 - p(t)_y)^{m_y - r_y} \quad (3)$$

Three separate beta priors were then utilized, with parameters (1, 1), (6, 54), and (9, 81). These three parameterizations represent a noninformative (uniform prior) and two informative priors with the probability that a given fish is tagged centered around 0.1. The informative priors represent prior estimates, with 95% confidence, that $p(t)_y$ is between (0.038, 0.187) and (0.047, 0.169), respectively. As the experts, these priors were selected to represent a plausible range of $p(t)_y$ values: This included the exclusion of extremely low $p(t)_y$ values, where low numbers of recapture events, and correspondingly low recapture probabilities, can lead to inflation bias in abundance estimation (Haxton and Friday, 2018). Informative prior selection

then served to prevent inflation bias by constraining the upper bound on the abundance estimate, therefore providing a more conservative estimate of the contingent size.

We ran Markov Chain Monte Carlo estimations for each of these priors, with an adaptive phase of 1 000 iterations, followed by 10 000 iterations of draws from the posterior distribution that were summarized to estimate the probability of a captured fish being tagged. Model performance was evaluated with both density and trace plots for each of the Markov chains. The annual mean and 95% credible set abundance estimates were then obtained using the yearly mean and 95% credible set estimates of $p(t)_y$. Following this, every draw for each $p(t)_y$ posterior distribution was used to calculate an annual abundance estimate, generating posterior distributions of abundance estimates in each year. These posterior distributions were then pooled together, with the final estimate of abundance and the 95% credible set being taken as the mean and 95% credible interval of the pooled distribution.

Results

Between 2009–18, a total of 762 Atlantic sturgeon were conventionally tagged in the SRE. These fish ranged in size from 65–199 cm in FL, with a mean \pm SD length of 127.5 ± 23.4 cm. Of these tagged fish, 30 were recaptured in subsequent years (Table 1). Additionally, 74 Atlantic sturgeon were implanted with acoustic transmitters, ranging from 77–190 cm in FL with a mean \pm SD 137.1 ± 23.7 cm. In 2016–18, where sampling efforts were standardized, the catch per unit effort (CPUE) was 0.47 fish per minute in a 91.4 m net.

Table 1. Summary of all model parameters utilized in calculating N_y , with $p(t)_y$ representing the parameter estimates for the beta(1,1), beta(6,54), and beta(9,81) priors, respectively.

YEAR	Φ	P	M_T	M_Y	R_Y	C_Y	$P(T)_Y$
2009	0.959	1	33	33	NA	NA	NA
2010	0.959	1	54	55	NA	NA	NA
2011	0.959	0.898	96	96	NA	NA	NA
2012	0.959	0.903	60	64	4	155	(0.072, 0.079, 0.083)
2013	0.959	1	100	103	3	186	(0.038, 0.055, 0.062)
2014	0.959	0.774	132	136	4	274	(0.036, 0.050, 0.057)
2015	0.959	0.64	60	64	4	300	(0.076, 0.081, 0.085)
2016	0.959	0.82	80	82	2	222	(0.035, 0.056, 0.064)
2017	0.959	0.619	58	64	6	237	(0.107, 0.096, 0.098)
2018	NA	NA	98	104	6	175	(0.066, 0.073, 0.077)

During the 2017 season, where the acoustic array was deployed for 180 days, the median residency time (T_{res}) was 15.5 days. The monthly distribution of the percent of the population available for capture indicated sturgeon abundance peaked from July to September, with roughly 20% of the contingent present during each of these three months (Fig. 2).

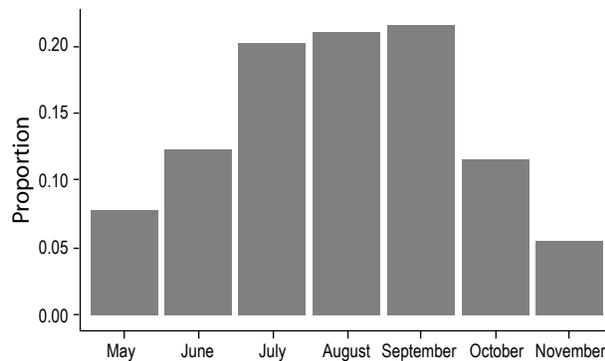


Fig. 2: The proportion of the SRE Atlantic Sturgeon contingent present by month. While sturgeon are present for a total of six months each year, abundance peaks from July to September.

The top ranked CJS survival model was $\Phi_c p_t$, which explained ~85% of the variation in the detection data. The probability of apparent survival Φ was constant, while the probability of return p was time dependent: Fork length was not included in the final model. The resulting apparent survival estimate was 0.959, and the annual detection probability estimate varied from 0.619 to 1 throughout the study. These parameter estimates were then used to calculate the catchable tagged population for each year from 2012 to 2018. Abundance estimation was not conducted until 2012 due to the small number of individuals tagged in years prior (2009–2011). The annual $p(t)$, estimates from the Bayesian analysis with the noninformative and two informative priors ranged from 0.035 to 0.107, with trace and density plots indicating clear model convergence across study years and priors. Values for $p(t)$, and all other abundance estimation parameters are summarized in Table 1.

The constrained Lincoln-Peterson model, for each of the three priors, yielded overall abundance estimates of 5 492 (95% Credible Interval: 1 374–17 989), 3 693 (95% Credible Interval: 1 476–8 436), and 3 299 (95% Credible Interval: 1 462–6 828) sturgeon that utilize the SRE over the course of the year. Estimates of abundance for each year across the three priors are described in Table 2.

Discussion

While many current abundance estimation methods struggle to generate reasonable estimates of abundance for open populations, where recapture events are rare, the present study established an alternate approach that effectively approximated the number of Atlantic sturgeon utilizing the SRE. Using the most informative prior (Beta (9, 54), the initial application of this method suggested that the SRE provides foraging habitat (Novak *et al.*, 2017) to approximately 3 299 Atlantic sturgeon each year. The mean estimates from all three priors were remarkably similar, indicating that results were primarily driven by the data likelihood; however, the incorporation of prior knowledge using the informative priors constrained the 95% credibility interval by significantly lowering the upper-bound, providing a more conservative credible set for the contingent abundance estimate. Furthermore, the lower bound on the population estimate was robust, as for all priors used, the data strongly suggested that the SRE is utilized by approximately 1 400 Atlantic sturgeon each year.

In addition to the abundance estimate, the CJS analysis also performed well, where the top ranked model explained 85% of acoustic data variability and provided reasonable estimates of both apparent survival and return probability. The present study found a remarkably high rate of annual apparent survival, 95.9%, which is consistent with estimates from previous acoustic telemetry studies of sturgeon populations. For example, Withers *et al.*, (2019) found survival rates of 94.6% for lake sturgeon (*Acipenser fulvescens*) in Lake Erie, while Hightower *et al.*, (2016) found a survival rate of 86.0% for Atlantic sturgeon in the Carolina DPS. Additionally, while all sturgeon emigrated from the SRE each winter, the CJS return rates suggested that 62–100% of surviving sturgeon would return to the estuary in the following year. This finding indicates high site fidelity and long-term usage of the SRE within the Atlantic sturgeon GOM population, as well as confirms findings of past studies, which found return rates of 69% (Wippelhauser *et al.*, 2017). Further, these annual return rates are similar to those of Atlantic sturgeon from the Penobscot River (up to 95%), a nearby system deemed an important estuary for the GOM Atlantic sturgeon DPS (Altenritter *et al.*, 2017). As a result of this designation and the abundance estimate herein, the present study suggests the SRE is also a river system critical to the Atlantic sturgeon GOM DPS.

The SRE is a relatively small estuarine system, and so the estimated abundance may appear disproportionately high, but our abundance estimate is supported by other data. For

Table 2. Yearly sturgeon abundance estimates (Ny), and 95% credible intervals, using each of the three priors.

YEAR	BETA(1,1)		BETA(6, 54)		BETA(9, 81)	
2012	2 152	(1 078-6 660)	1 973	(1 111-4 008)	1 876	(1 172-3 456)
2013	4 902	(2 250-17 929)	3 367	(1 971-7 280)	2 997	(1 864-5 641)
2014	7 585	(3 750-23 170)	5 461	(3 271-11 084)	4 817	(3 030-8 764)
2015	3 968	(2 029-11 719)	3 718	(2 206-7 593)	3 531	(2 221-6 517)
2016	6 266	(2 664-29 934)	3 983	(2 260-8 993)	3 476	(2 112-6 873)
2017	2 224	(1 239-5 363)	2 460	(1 555-4 590)	2 442	(1 613-4 277)
2018	2 654	(1 374-6 479)	2 396	(1 480-4 654)	2 276	(1 492-3 921)

example, the standardized CPUE from 2016–2018 was 0.31 Atlantic sturgeon per hour per metre of net soaked. A similar study on the Penobscot River had an average annual CPUE of only 0.016 sturgeon per hour per metre of net (Altenritter *et al.*, 2017), and while this is a much larger system, both density and catch rate of Atlantic sturgeon in the SRE are higher. Further, not all the fish are utilizing the river system concurrently. A median residency time of 15.5 days suggests high turnover rates within the system, and the proportion of the contingent present within a given month never exceeds 22%. With acoustic data and sampling indicating sturgeon are prevalent within the river from mid-May through mid-November (Novak *et al.*, 2017), the aforementioned data suggests approximately 330 Atlantic sturgeon are within the river during the months of July, August, and September, when abundance is highest. Conversely, in the late spring and autumn months, closer to 165 fish are within the river system at any given time. In all, the abundance estimates from this study indicate that the SRE is supporting a large, but highly variable, contingent of Atlantic sturgeon each year.

Despite the ability to derive both reasonable population estimates and catchability parameters within the SRE, there are caveats to this approach. The current study used existing software in a two-step approach, providing a mathematically simplistic and user-friendly model; however, this required CJS parameter estimates from the first step to be treated as fixed parameters when estimating abundance (Dudgeon *et al.*, 2015), and therefore uncertainty in these parameters was not incorporated into the final estimate of abundance. In addition, we assumed that contingent size was constant across years, and as such, the final estimate of abundance was taken as the mean from a pooled distribution across years. Violation of this assumption would require independent abundance estimates for each study year, but abnormally low numbers of recapture events across years may lead to high levels of uncertainty

and inflated abundance estimates (Withers *et al.*, 2019). Bayesian estimation can mitigate this uncertainty by using informative priors to constrain the credible set (Madigan and York, 1995), but increased recapture rates are needed to provide more precise abundance estimates. It is therefore recommended that the population estimates produced by the methods herein are used as approximate estimates for the magnitude of abundance, and that these estimates are only generated when studies have many years of mark-recapture data.

Given the assumptions of our approach, additional efforts are needed to improve and refine this method of abundance estimation. An integrated Bayesian modeling approach would better quantify model uncertainty, but this requires the CJS model to be coded into the rjags package (Dudgeon *et al.*, 2015). Additionally, shortcomings in data collection must be addressed in order to improve model performance: Low recapture rates continue to restrict mark-recapture abundance estimation effectiveness, with large amounts of long-term data being required for estimates to be reliable (Haxton and Friday, 2018; Withers *et al.*, 2019). Until further model development occurs, our approach provides a useful method for generating preliminary estimates of fish abundance in numerous systems where this has historically been unfeasible.

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- Ávila de Melo, A. M., Power, D. , and Alpoim, R. MS 2005. An assessment of the status of the redfish in NAFO Division 3LN, *NAFO SCR Doc.*, No. 52, Serial No. N5138, 19 p.

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