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Spatial distribution of benthic flora and fauna of coastal placentia bay, an ecologically and biologically significant area of the island of newfoundland, atlantic Canada

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Coastal habitats have the potential to be biodiversity hotspots that provide important ecosystem services, but also hotspots for human development and exploitation. Continued use of coastal ecosystem services requires establishing baselines that capture the present state of the benthos. This study employs habitat mapping to establish a baseline describing the spatial distribution of benthic organisms along the western coast of Placentia Bay, an Ecologically and Biologically Significant Area (EBSA) in Newfoundland, Canada. The influence of seafloor characteristics on the distribution of four dominant epifaunal assemblages and two macrophyte species were modelled using two machine learning techniques: the well-established Random Forest and the newer Light Gradient Boosting Machine. When investigating model performance, the inclusion of fine-scale (<1 m) substrate information from the benthic videos was found to consistently improve model accuracy. Predictive maps developed here suggest that the majority of the surveyed areas consisted of a species-rich epifaunal assemblage dominated by ophiuroids, porifera, and hydrozoans, as well as prominent coverage by *Agarum clathratum* and non-geniculate crustose coralline algae. These maps establish a baseline that enables future monitoring of Placentia Bay's coastal ecosystem, helping to conserve the biodiversity and ecosystem services this area provides.

KEYWORDS

marine habitat mapping, machine learning, multiscale, benthic epifauna, benthic algae

Introduction

Human reliance on coastal ecosystem services places stress on benthic habitats, which may impact future availability of those services (Costanza et al., 1997; Barbier et al., 2011) and also biodiversity (Lotze et al., 2006), warranting management actions that balance coastal ecosystem function and human use. Considering the modern trend of increased utilization of ocean resources (Bennett et al., 2019), it is imperative to understand the current distribution of biota and non-living resources (i.e. oil, mined goods), against which change can be monitored over time (Shumchenia and King, 2010; Siwabessy et al., 2018). Conserving ecosystem function and services requires effective ecosystem-based management, which aims to preserve biodiversity and functionality by recognizing complex ecological linkages at varying scales, instead of relying on policies managing individual species (O'Higgins et al., 2020). The resultant holistic management therefore works to balance stakeholder involvement with sustainable practice (Long et al., 2015).

The benthos plays an important role in providing physical structure to the marine environment, supporting the ecological niches of other biota and serving as an indicator of ecosystem health which may be monitored to inform conservation priorities (Brey, 2012; Oug et al., 2012, Alexandridis et al., 2017). Benthic epifaunal invertebrates form the trophic basis for marine food webs (Iken et al., 2010), influencing both benthic and pelagic zones *via* cycling of energy, nutrients, and organic matter (Sandnes et al., 2000; Hajializadeh et al., 2020; Lam-Gordillo et al., 2021), and acting as ecosystem engineers (Reise, 1985; Meadows et al., 2012). The majority of benthic species are relatively immobile, if not completely sessile (Bilyard, 1987), and are long-lived, resulting in prolonged exposure to stressors and disturbances (Wei et al., 2019; Meng et al., 2021). Therefore, long-term monitoring of ecosystem function and health may benefit from the inclusion of epibenthic invertebrates as bioindicators.

Brown kelp, primarily of the order *Laminariales*, are one particular taxon known to enhance local biodiversity (Steneck et al., 2002; Krumhansl et al., 2016). They act as both primary and secondary producers, sequester carbon, provide shelter from predators, act as nursery grounds (Gagnon et al., 2003), and provide the physical framework to increase habitat complexity (Steneck et al., 2002). Kelp beds in temperate and sub-polar coastal regions of the northwest Atlantic are subject to periodic decimation by the herbivorous green sea urchin (*Strongylocentrotus droebachiensis*), resulting in coastal barrens that are less productive, which may extend 1000s of km (Filbee-Dexter and Scheibling, 2014). In the Northeast Atlantic, some of the few remaining floral species not consumed by urchins may include the kelp *Agarum clathratum* and non-geniculate crustose coralline algae (CCA). *A. clathratum* presumably deters urchins *via* phenolic compounds that render them unpalatable (Vadas, 1968; Vadas, 1977). For urchins, CCA are a poor nutritional substitute compared to kelps (Agatsuma, 2000; Kelly et al., 2008). Both *A. clathratum* and CCA are associated with a unique suite of invertebrates [Ojeda and Dearborn, 1989; Freiwald, 1993; Bégin et al., 2004; Swanson et al., 2006; Chenelot et al., 2011; Blain and Gagnon, 2014; Tebben et al., 2015; Jørgensbye and Halfar, 2017], potentially boosting subtidal biodiversity.
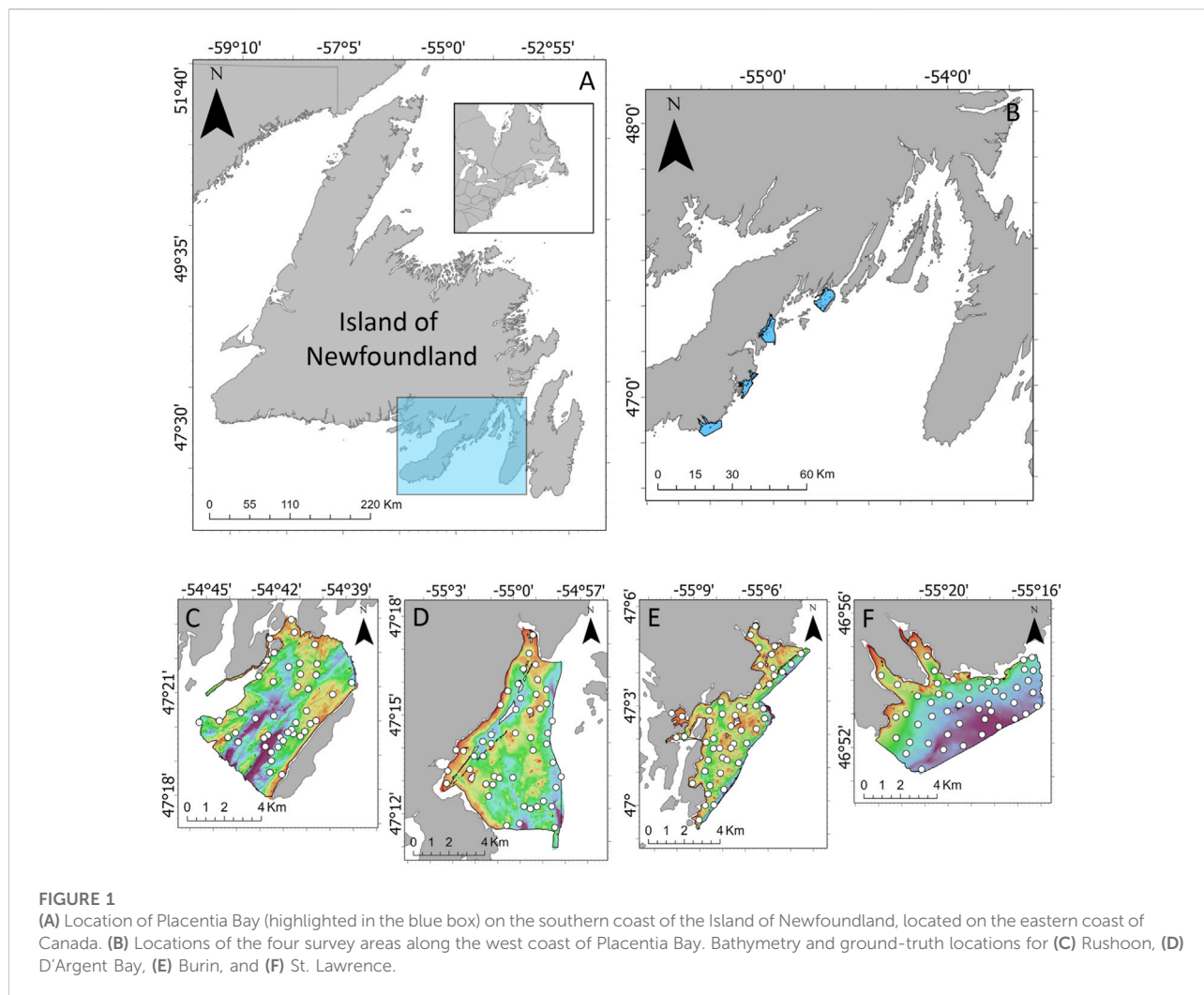
Benthic fauna and flora associate strongly with the physical structure of the seafloor (Auster and Langton, 1998; Kostylev et al., 2001), and geospatial models based on remotely sensed data may be used to support our understanding of spatial ecological patterns and the physical factors that drive them. The defined species-environmental relationships can be used to develop a baseline grounded in the function of an ecosystem that qualifies the composition and distribution of the benthos in a target area. These resultant habitat maps have been utilized for fisheries management (Brown et al., 2012), to inform effective Marine Protected Areas (MPAs) (Lacharite and Brown, 2019), for observing the impacts following ecological disturbance (e.g. oil spills (Botello et al., 2015)), and the first step in the establishment of long-term monitoring programs of coastal biodiversity (Obst et al., 2018). The effectiveness of a baseline relies on accurate and robust modelling techniques employed during its development, and these techniques are being improved continuously as there is an urgent need for such spatial data products.

This study aims to establish a baseline describing the benthic epifaunal assemblages and two marine algae species (*A. clathratum* and CCA) found in the subtidal zone of an Ecologically and Biologically Significant Area (EBSA) in Newfoundland, Canada (Templeman, 2007; DFO, 2016). An EBSA is an area notable for its distinct ecosystem characteristics, role in species' life stages (i.e. feeding/spawning grounds), resilience, and socio-economic utilization (DFO, 2004). The Placentia Bay EBSA has exhibited growth in vessel traffic and coastline activities that will likely shift the state of the benthos (DFO, 2007; LGL, 2018). The baseline established here will enable documenting changes to the dominant epifauna and marine algae using spatially explicit predictions of their current distribution based on the relationships with the physical structure of the seafloor. While modeling the relationship between seafloor features and biota, the performance of a new machine-learning algorithm, Light Gradient Boosting Machine (LightGBM), is tested against a well-established algorithm, Random Forest (RF). The predictive models and habitat maps developed in this study may be applied for future monitoring of changes in ecosystem structure and health within the Placentia Bay EBSA.

Methods

Study area

Placentia Bay is a deep-water embayment located on the southern side of the Island of Newfoundland, in the province of

FIGURE 1
(A) Location of Placentia Bay (highlighted in the blue box) on the southern coast of the Island of Newfoundland, located on the eastern coast of Canada. (B) Locations of the four survey areas along the west coast of Placentia Bay. Bathymetry and ground-truth locations for (C) Rushoon, (D) D'Argent Bay, (E) Burin, and (F) St. Lawrence.

Newfoundland and Labrador (Atlantic Canada). Following an overview of its ecosystem status, present fish distribution and spawning locations, and a species inventory, Placentia Bay was designated by the Government of Canada Department of Fisheries and Oceans as an EBSA (Templeman, 2007; DFO, 2016). Any severe disturbance (i.e. oil spill) would be of greater ecological consequence within the EBSA boundary than if the same perturbation occurred beyond its extent (DFO, 2004). Placentia Bay hosts important capelin spawning beaches, seagrass meadows, seabird colonies, and herring aggregations (Sjare et al., 2003). It is also a location where charismatic megafauna such as whales (DFO, 2018) and leatherback turtles (DFO, 2012b) may be observed. Paired with its ecological relevance, Placentia Bay has local socio-economic importance, including traditional and commercial fisheries of groundfish and shellfish (Robichaud and Rose, 2006; DFO, 2012a; DFO, 2019), a growing finfish aquaculture industry (LGL, 2018), and frequent marine traffic, including oil tankers. Placentia Bay is considered to be amongst marine areas at greatest risk of oil spill across Canada (DFO, 2007).

Four survey areas along the west coast of Placentia Bay were selected for this study: Rushoon, D'Argent Bay, Burin and St-Lawrence (Figure 1). These sites are notable for their local ecological importance. Rushoon was the northernmost site surveyed, and is likely one of the more pristine of the four due to its remoteness. This may be subject to change, as development of salmon aquaculture progresses in the area, which may impact the local environment (LGL, 2018). Further southwest, D'Argent Bay was selected for its capelin spawning sites, herring aggregations, and high occurrence of whales (Sjare et al., 2003). Burin is near a relatively large cluster of towns, including the towns of Burin and Marystown. Finally, closest to the mouth of Placentia Bay, St. Lawrence was selected for its capelin spawning sites, as well as its role as an important seabird habitat (White, 2018).

TABLE 1 Acquisition information for multibeam echosounder (MBES) and ground-truth (GT) surveys.

Site	Survey period—MBES	MBES survey area (km^2)	Survey period—gt	Number of sites	Camera system
Rushoon	June—July 2019	39	August 2019	44	FDR-X300
D'Argent Bay	December, February 2018 and April 2019	43	July—August 2019	48	
Burin	May 2019	24	July 2020	50	Deep Trekker DTPod
St. Lawrence	July—August 2020	37	August 2020	50	

Environmental survey

Multibeam echosounder (MBES) surveying was carried out between winter 2018 and summer 2020 (Table 1) on board the 27' Fisheries and Marine Institute research vessel *D. Cartwright*. MBES uses sound waves that travel from the sensor to the seafloor and back again, forming a swath of depth soundings across the path of the vessel. As sound waves echo back from the seafloor, the strength of their return is also measured, and this acoustic backscatter can be indicative of substrate types. Harder substrates like bedrock or boulders return a higher backscatter signal, while softer sediments like mud or sand will produce a weaker signal (Lamarche et al., 2011; Lurton and Lamarche, 2015; Calvert et al., 2015). Bathymetry and backscatter were collected using a Kongsberg EM 2040P, operating at 400 kHz. Positioning data were obtained using a Fugro 3,610 differential GPS with a Seastar subscription that provided spatial accuracy of up to 8 cm. Sound Velocity Profiles (SVP) between the transducer and seafloor were obtained using an AML BaseX sound velocity profiler, while sound velocity measurements at the MBES transducer head were obtained by an AML Micro SV sound speed sensor.

Raw sonar files for each survey area were imported into the Quality Positioning Services (QPS) Qimera v2.0.3 software. Bathymetric data were adjusted for Rushoon and D'Argent Bay using observations from the Argentia tide station (Station #835, https://www.tides.gc.ca/en/stations/835) and for Burin and St. Lawrence using the St. Lawrence tide station (Station #755, https://www.tides.gc.ca/en/stations/00755).). SVPs were imported into each respective Qimera project: 25 for D'Argent Bay, 19 for Rushoon, 19 for Burin, and 17 for St. Lawrence. Spline filters were employed to automatically remove outliers, and once processing was completed, a bathymetric surface was exported as a Floating Point GeoTIFF Grid at 5 × 5 m spatial resolution for each area. Processed files were additionally exported to. GSF format, and were imported into QPS Fledermaus Geocoder Toolbox (FMGT) v.7.8.4. For backscatter processing. Backscatter mosaics were exported at 5 × 5 m spatial resolution. All environmental rasters were projected to UTM Zone 21.

Bathymetric surfaces were used to derive terrain features that have been found to influence benthic biota distribution. These features can act as surrogates for variables that are difficult to measure directly (e.g. slope can act as a proxy for finer-scale currents). Six terrain features identified by Lecours et al., 2016a that capture a large amount of topographic information were calculated in ESRI ArcGIS using the Terrain Attribute Selection for Spatial Ecology toolbox (TASSE) (Lecours, 2015). These included slope (change in elevation), eastness and northness (orientation, calculated as the sine and cosine of slope), relative difference to the mean value (RDMV; relative position), and standard deviation (SD) of bathymetry (a measure of rugosity). Additionally, bathymetric position index (BPI) and vector ruggedness measure (VRM) were also selected to potentially provide information on seafloor structure. BPI is an adaptation of the topographic position index (Weiss, 2001) that measures the relative position of an area to the surrounding seabed (Lecours et al., 2016b). Positive and negative values represent peaks and troughs, respectively. VRM incorporates both slope and aspect in a single measure of surface roughness that is independent of slope (Hobson, 1972; Sappingtom et al., 2007; Martín-García et al., 2013), unlike SD. BPI, and VRM were derived from the bathymetric surfaces using the Benthic Terrain Modeller (BTM) Version 3.0 (Wright et al., 2012). Additionally, a layer measuring the distance from the coast was calculated within each survey area using the 'Euclidean Distance' tool in ESRI ArcGIS, which has previously been used to inform on benthic assemblage distributions (Degraer et al., 2008; Richmond and Stevens, 2014; Vassallo et al., 2018).

Features were derived from backscatter mosaics based on the spatial distribution of the varying shades of grey denoting backscatter intensity (Haralick et al., 1973). Three features were calculated using a grey-level co-occurrence matrix *via* the R package 'GLCM' (Zvoleff, 2020): contrast (local variation), homogeneity (closeness of distribution), and entropy (randomness) (Haralick et al., 1973). These features were selected for their common application in previous studies of similar systems (Blondel and Sichi, 2009; Samsudin and Hasan, 2017; Shang et al., 2021).

Terrain features were calculated across a range of spatial scales (i.e. using moving-windows of varying sizes), as no single scale can account for all ecological processes of a benthic ecosystem (Dolan, 2012; Lecours et al., 2015). All features (except for BPI) were derived using a 3x3-cell window, with

TABLE 2 Multiscale environmental features calculated at each site.

Feature	Scale (m)	Unit	Software	Software source
Bathymetry (m)	-	meters	-	-
Slope	15, 45, 175	degrees	TASSE	Lecours, (2015)
Eastness	15, 45, 175	unitless	TASSE	Lecours, (2015)
Northness	15, 45, 175	unitless	TASSE	Lecours, (2015)
RDMV	15, 45, 175	unitless	TASSE	Lecours, (2015)
SD	15, 45, 175	meters	TASSE	Lecours, (2015)
Fine BPI	15, 45, 175	meters	BTM	Wright et al. (2012)
Broad BPI	15, 45, 175	meters	BTM	Wright et al. (2012)
VRM	15, 45, 175	unitless	BTM	Wright et al. (2012)
Backscatter	-	Value (dB)	-	
Contrast	15, 45, 175	unitless	GLCM	Zvoleff (2020)
Entropy	15, 45, 175	unitless	GLCM	Zvoleff (2020)
Homogeneity	15, 45, 175	unitless	GLCM	Zvoleff (2020)
Distance to Coast (km)	5	meters	'Euclidean Distance'	
Bedrock (%)		%	ImageJ	
Boulder (%)		%	ImageJ	
Gravel (%)		%	ImageJ	
Fine sediment (%)		%	ImageJ	
Red Algae (%)		%	ImageJ	
Agarum clathratum (%)		%	ImageJ	
Saccharina latissima (%)		%	ImageJ	

additional scales obtained using the "calculate-average" approach (Dolan and Lucieer, 2014; Misiuk et al., 2021), by focal averaging using increasing window sizes (13 × 13-and 35 × 35-cell windows; Table 2). BPI layers were calculated by setting the outer and inner radii (in cells) of an annulus (ring-shape) and calculating the mean elevation value of all cells within the analysis neighborhood (Walbridge et al., 2018). BPI was calculated using the Benthic Terrain Modeler Toolbox, with outer and inner radii of 60 and 3, 150 and 45, 260 and 13, 630 and 195, 700 and 35, and 1750 and 525 cells.

Benthic biota

Ground-truthing sites (*n* = 192) across all four survey areas were selected using a Generalized Random Tessellation Stratified (GRTS) survey design (Supplementary Table S1) (Stevens and Olsen, 2004), stratified by bathymetry and backscatter. For the St. Lawrence sites, MBES data were unavailable prior to ground-truthing, and bathymetry was interpolated from depth soundings on a nautical chart (e.g. Great St. Lawrence Harbour, Marine Chart CA4642_2). Ground-truthing consisted of underwater

video with two systems: a Sony FDR-X3,000 Action Cam (1920 × 1,080 pixels, 60 frames/sec), contained in a Deep Blue Abysso waterproof housing, paired with two 3,500 lumen neutral white light Cree LED bulbs and two green lasers spaced 10 cm apart; and a Deep Trekker DTPod (1920 × 1,080 pixels, 30 frames/sec) with an integrated light and two red lasers spaced 2.5 cm apart. For both systems, a live video feed was used to adjust the height of camera above the seabed. Boat positioning at the start and end of each transect was obtained using the onboard Garmin GPS 16x; the midpoint of each transect was used to extract point-wise data from terrain features.

Two-minutes of continuous video were annotated using the Monterey Bay Aquarium Research Institute's (MBARI) Video Annotation and Reference System (VARS) (Schlining and Stout, 2006). The presence or absence of *Agarum clathratum* and non-geniculate coralline algae (CCA) were recorded. Because of varying coverage across different ground-truthing sites, CCA were divided into three classes: full coverage, partial coverage, and absent. The full-coverage class was assigned when most of the seafloor was covered by CCA. Partial coverage was given when at least half of the substrate was covered. If little to no CCA was present, the site was marked as absent. Because abundance of

S. droebachiensis may influence macroalgae distributions, counts at each site were included as a possible predictor variable.

All epifauna larger than 2 cm were counted and identified to the lowest possible taxonomic level, using expert knowledge and published species guides (Gosner, 1979; Harvey-Clark, 1997; Martinez and Martinez, 2003; Fox et al., 2014; Salvo et al., 2018). When species identification was not feasible, a morphotype approach was employed (Howell et al., 2019). The total number of individual species/morphotypes per transect was calculated and converted to densities by estimating the total area recorded for each transect. Using the Blender v.2.8.2, 12 frames at 10 s intervals were extracted and the distance between lasers was measured and used to calculate transect width with ImageJ. This was averaged and multiplied by the total length of the transect. Species/morphotypes that had an abundance of <5 individuals across all ground-truthing sites were removed to reduce the influence of low-abundance species. The dominant assemblages for ground-truthing sites with <5 faunal counts could not be characterized (De la Torriente et al., 2018); these sites were removed prior to analysis.

The species matrix was Hellinger transformed to reduce the importance of larger epifaunal abundances (Legendre and Gallagher, 2001; Borcard et al., 2011). Faunal assemblages were clustered using the average hierarchical clustering method 'Unweighted Pair-Group Method using arithmetic Averages' (UPGMA) (Sokal and Michener, 1958), with hierarchical relationships plotted as a dendrogram. The UPGMA approach is fast, simple, and may even outperform other clustering algorithms (Kreft and Jetz, 2010). Dissimilarity values between two branches of the derived dendrogram (i.e., "fusion levels") were plotted to determine the optimal number of faunal assemblages. Silhouette widths were additionally calculated and plotted for each fusion level, providing a metric for distinguishing assemblages. Silhouette widths range from -1 to 1, with one representing assemblages that are clearly distinguished (Borcard et al., 2011). Once faunal assemblages were identified, the characteristic species or morphotypes of each assemblage were identified using an IndVal procedure (Legendre, 2013). A species accumulation curve was developed for each assemblage to identify if species richness was effectively captured (Ugland et al., 2003; Bevilacqua et al., 2018).

Model development

For both the assemblages and for each marine algae taxa model, a Boruta Feature Selection (Kurse and Rudnicki, 2010) algorithm was run separately to include terrain features grouped by scale (window of analysis: 3 × 3, 13 × 13, 35 × 35 cells) in order to reduce the number of candidate terrain features and promote model parsimony and support performance (Nemani et al., 2021). Important variables are

identified by the Boruta wrapper as it compares the importance of a variable with a randomly shuffled version containing the same distribution of values (i.e., "shadow features"). A variable is deemed important if it consistently contributes more to the model than its shadow variable. Degenhardt et al., 2019 found that the Boruta algorithm generally outperformed other selection methods, and previous successful applications can be found in Li et al., 2016, Diesing and Thorsnes, (2017) and Nemani et al., 2021. Variables identified as "important" or "tentative" were selected for model training here. Variables were further dropped that had absolute correlation values exceeding 0.7, as determined using the R function 'corrplot' (Wei, 2013). In these cases, the variable with the lower impact on model accuracy was dropped.

Separate multiclass classification Random Forest (RF) and Light Gradient Boosting Machine (LightGBM) models were developed for the epifaunal dataset, the *A. clathratum* dataset, and the CCA dataset. Each model was trained with 2/3 of the samples, which included a proportional representation of classes (i.e. presence and absence of *A. clathratum* or epifaunal assemblage). The remaining 1/3 was reserved to test model performance. Model accuracy was assessed using the test data by computing a confusion matrix of predicted and observed classes (Congalton, 1991), from which overall accuracy and Cohen's kappa were derived. Overall accuracy is the number of accurately predicted classifications divided by the total number of observations. The kappa statistic incorporates the chance of random agreement between observed and predicted classes based on their prevalence (Cohen, 1960; Allouche et al., 2006). Both the RF and LightGBM models were run with and without fine-scale (<1 m) substrate % coverage to understand the importance of fine-scale features in explaining spatial patterns. Using both the RF and LightGBM models and the environmental data layers, full-coverage predictive maps were developed for the distribution of epifaunal assemblages, presence/absence of *A. clathratum*, and for the absence/partial/full coverage of CCA. Since substrate % coverage features were not spatially continuous, full-coverage predictions were based on the terrain feature-only models.

RF is a well-established ensemble machine-learning algorithm that builds a 'forest' of classification trees from which predictions are obtained through majority voting. It employs 'bagging', where the data are repeatedly bootstrapped to train different classification trees (Quinlan, 1986), which are uncorrelated. Additionally, each tree split uses a random subset of variables, instead of the entire set. RF models were trained using the R package 'randomForest' (Liaw and Weiner, 2002), with the default number of variables included in each split ('mtry') retained for each model. Random Forest has been used successfully for predictive models with limited sample sizes similar to the number of observations in this study (Stephens and Diesing, 2014; Robert et al., 2015; McLaren

TABLE 3 Parameters selected for LightGBM model tuning.

| Parameter	Description	Range tested
'objective'	Sets the model as regression or classification	'multi_class' *
'metric'	How the model performance is evaluated	'multi_error' *
'num_class'	Number of classes predicted	number of faunal assemblages*
'is_unbalance'	Algorithm automatically balances weights of classes	TRUE, FALSE
'force_col_wise'	Manages model instability when there is a large number of columns (features)	TRUE, FALSE
'max_depth'	Controls the maximum distance between a tree's root node and each leaf node	10, 20, 40, 80
'num_leaves'	Maximum number of leaves for each learner; manages complexity; adjust with 'max_depth'	(2^{max_depth})
'learning_rate'	Boosting learning rate	0.05, 0.1, 0.25, 0.5
'num_iterations'	Number of trees to build; with larger values, adjust with smaller 'learning_rate'	100, 200, 300, 400
'feature_fraction'	Sets % of features selected as a subset for each iteration (tree)	0.8, 0.9, 0.95
'lambda_l1'	L1 regularization	0.2, 0.4
'lambda_l2'	L2 regularization	0.2, 0.4
'min_gain_to_split'	Sets the minimum improvement value when evaluating gains at a split	0.2, 0.4
'early_stopping_rounds'	Stops training when validation metric does not improve; adjust with 'num_iterations'	10% of 'num_iterations'

* Core features that do not change during any model iteration.

TABLE 4 Indicator species by IndVal analysis of faunal assemblages.

Name	*n* sites	Indicator morphotype/species	Species present	Unique to this cluster	Images*
OPH	*64*	Ophiuroidea spp. Porifera sp.5 Hydrozoa sp.1	51	8	
SDR	*21*	*Strongylocentrotus droebachiensis* Stauromedusae sp.2	20	none	
MIX	*26*	Hormathia sp.1 Cerianthidae sp.3 Cnidaria sp.1 Sagittidae sp.1	42	1	
EPA	*8*	*Echinarachnius parma* *Pseudopleuronectes americanus*	15	1	

n indicates the number of ground-truthing sites identified as containing each assemblage.
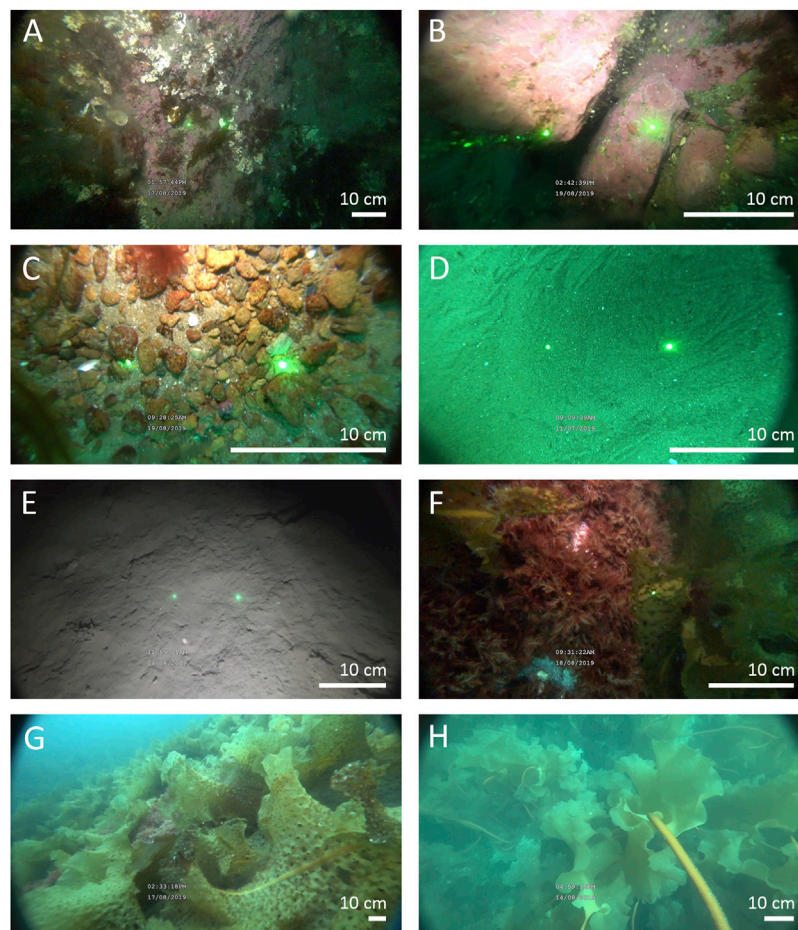
FIGURE 2
Images of the substrate classes identified during video annotation: **(A)** bedrock, **(B)** boulder, **(C)** gravel mix, **(D)** fine-sediment (sand), **(E)** fine-sediment (mud), **(F)** filamentous red algae (excluding coralline algae), **(G)** *Agarum clathratum*, and **(H)** sugar kelp (*Saccharina latissima*). Distance between lasers was 10 cm for the Sony FDR-X300 camera and 2.5 cm for the Deep Trekker DTPod.

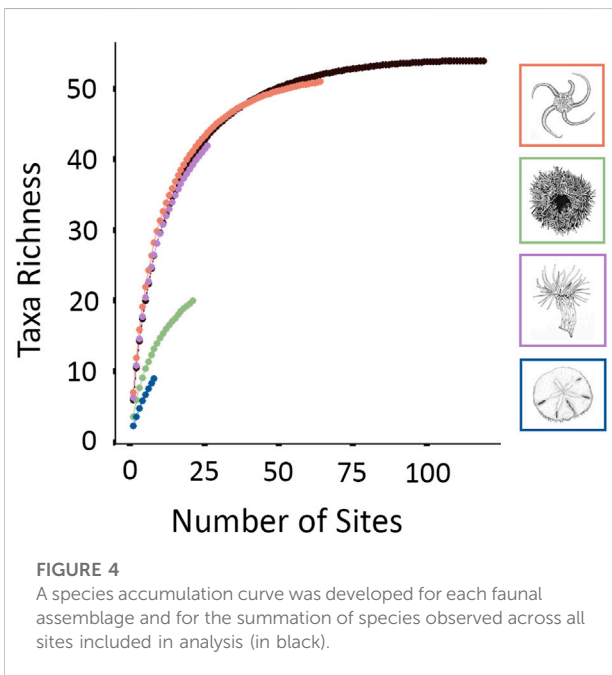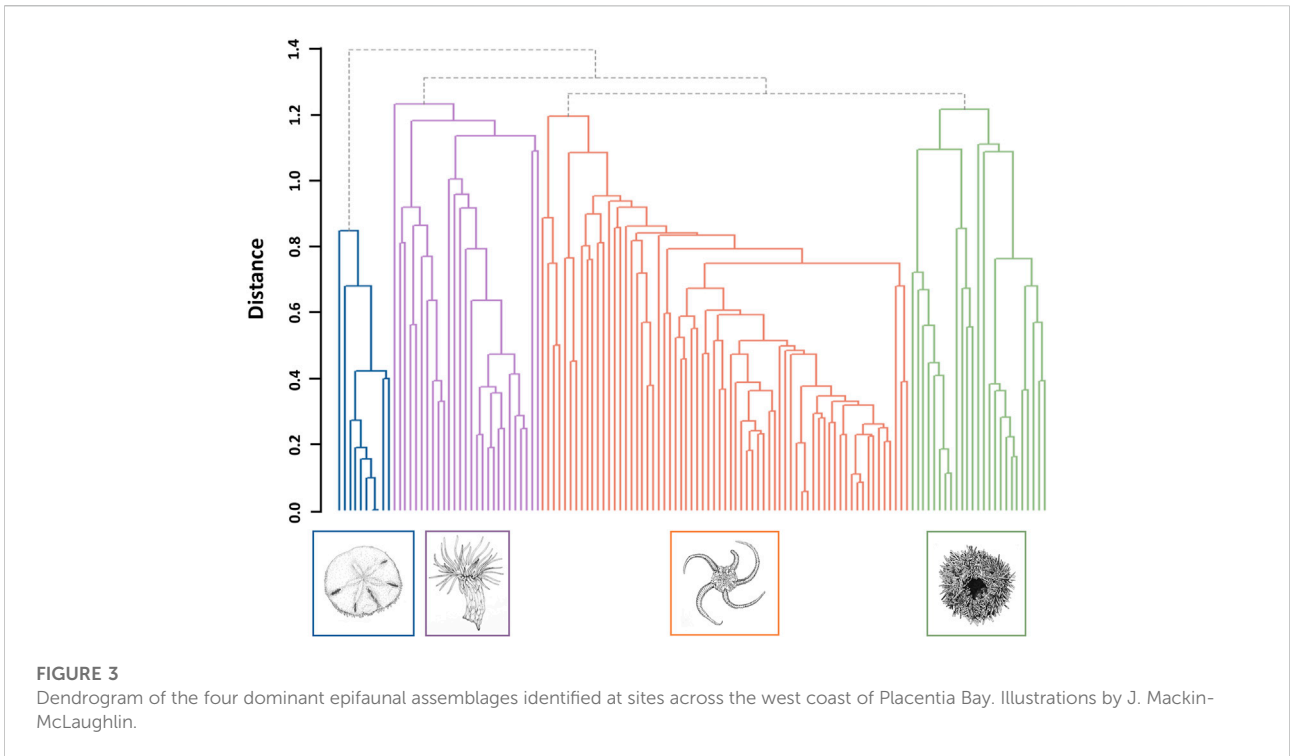et al., 2019; Misiuk et al., 2019; Ilich et al., 2021; Janowski et al., 2021).

LightGBM is a relatively recent Gradient Boosting Decision Tree algorithm (Ke et al., 2017). Unlike RF, LightGBM uses 'boosting' rather than 'bagging' to enhance performance. Boosting is another ensemble method in which classification trees are grown on the residuals from previous trees (Vaghela et al., 2009; Schapire and Freund, 2013). Tree growth and learning rate are controlled by a suite of tunable parameters (Table 3). The parameters recommended in the LightGBM release 3.2.1.99 guide (Zhang et al., 2012) were chosen to tune the model.

A variable importance plot was derived for each model, ranking variables based on their predictive importance. The RF model used Gini Importance, which measures the total decrease in node impurity by calculating the sum over the number of splits including a variables, across all trees

(Friedman et al., 2001). LightGBM implements a gain-based method that is similar to the Gini Importance used by RF (Lundberg et al., 2020), but excludes unimportant features. Univariate partial dependence plots were derived from the best-performing model to visualize the relationship between an individual variable and a faunal assemblage or marine algae (Marini et al., 2015; Vassallo et al., 2018).

By comparing model accuracy and ranked variable importance, preliminary modelling using the derived terrain features suggested that important variables may be missing. Substrate heterogeneity information extracted from videos of the seafloor was tested to improve model performance. Substrate observations were obtained from the underwater video collected for biological analysis (described below). An image was extracted every 10 s from each video using Blender v.2.8.2 and images were imported to ImageJ (Image processing and analysis in Java). A 50-square grid was superimposed on each image and each square

FIGURE 3
Dendrogram of the four dominant epifaunal assemblages identified at sites across the west coast of Placentia Bay. Illustrations by J. Mackin-McLaughlin.

FIGURE 4
A species accumulation curve was developed for each faunal assemblage and for the summation of species observed across all sites included in analysis (in black).
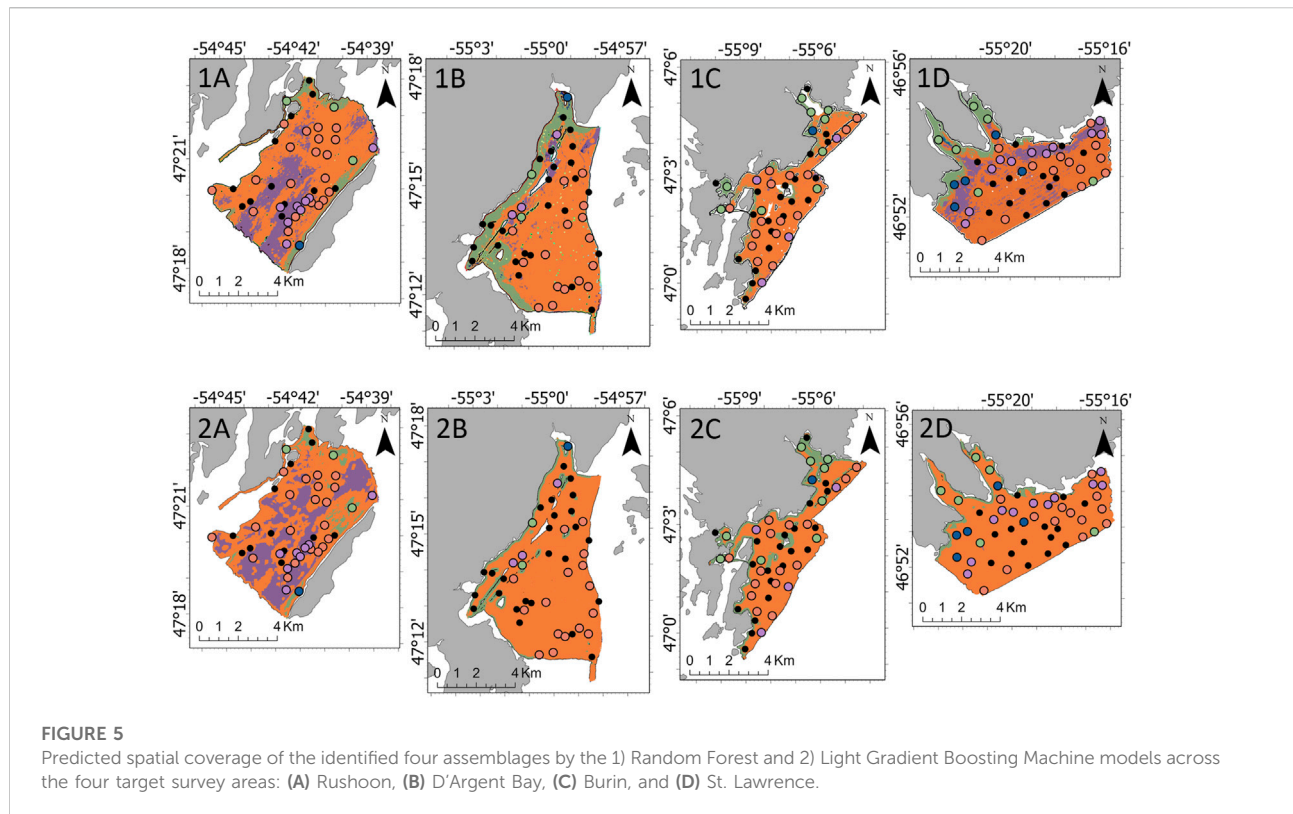
was labelled as one of seven classes: bedrock, boulder, gravel-mix, fine sediment (including both mud and sand), red algae (excluding coralligenous algae), *Agarum clathratum*, and *Saccharina latissima* (Figure 2). Following Connell et al., 2014,

red algae can be qualitatively categorized as turfs (i.e. loosely to densely aggregated filamentous algae <15 cm tall and covering an area greater than 1 m²). Biogenic substrates were included because observing the sediment underneath was often not possible and algae presence is likely to influence the presence of other epifauna. The number of occurrences of each class was divided by the total number of grids for a ground-truth site, yielding fine-scale (<1 m) percent cover for each substrate class.

Results

Epifaunal assemblages

Of the 192 ground-truthing sites collected, 117 fulfilled the criteria for assemblage identification. One site (Rushoon-53) exhibited two distinct epifaunal assemblages and substrate types, and was split into two, producing 118 total samples. From these, a total of 12,096 individuals were counted and 55 taxa were identified (Supplementary Table S2), 14 of which (25.5%) were identified to species level. The brittle star morphotype 'Ophiuroidea spp.' had the highest overall abundance (6,693 individuals; 55.5% of all counts), followed by 'Hormathia sp.1' (1,631 individuals; 13.5%), *Strongylocentrotus droebachiensis* (766 individuals; 6.3%), and *Echinarachnius parma* (627 individuals; 5.2%). Porifera had the highest taxa diversity with 14 morphotypes. Echinodermata was

FIGURE 5
Predicted spatial coverage of the identified four assemblages by the 1) Random Forest and 2) Light Gradient Boosting Machine models across the four target survey areas: **(A)** Rushoon, **(B)** D'Argent Bay, **(C)** Burin, and **(D)** St. Lawrence.
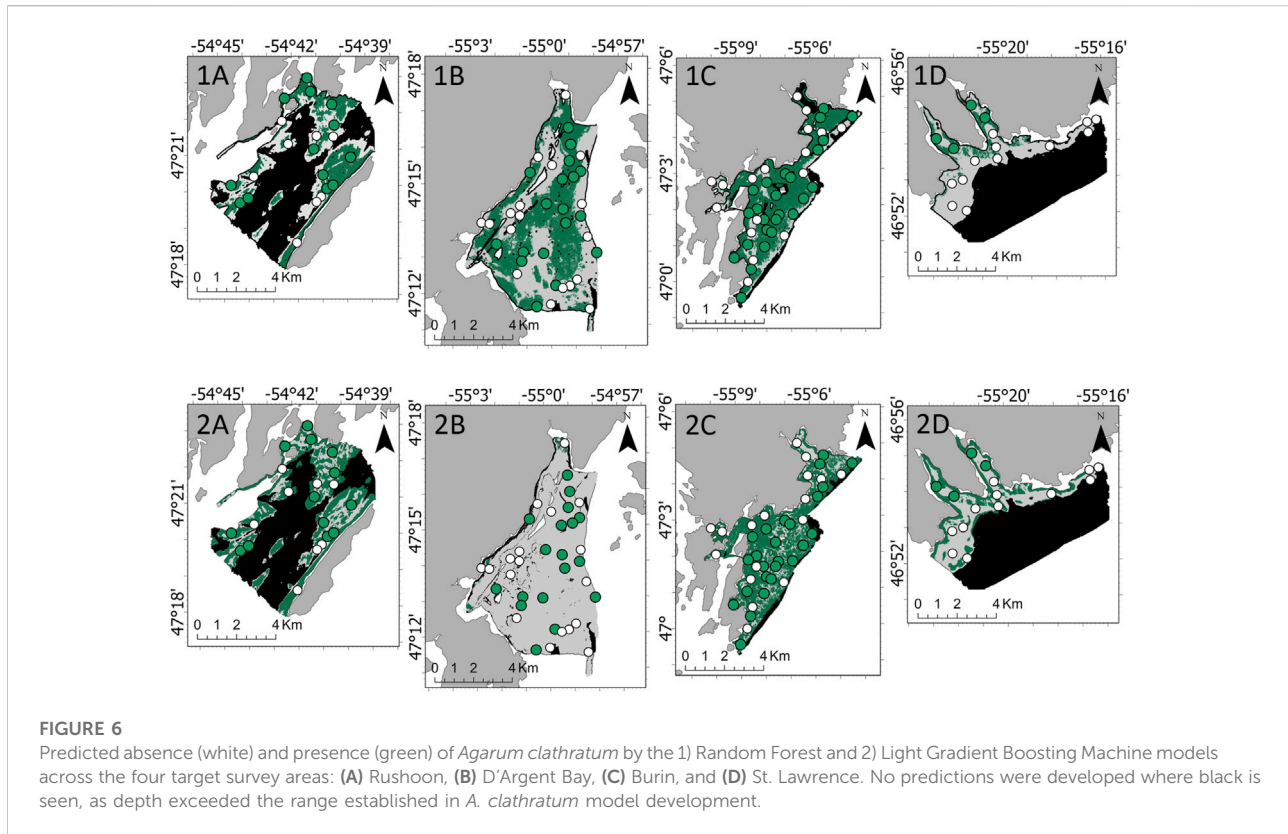
second in taxa diversity (7 morphotypes; six species), followed by Cnidaria (8 morphotypes; two species).

Four epifaunal assemblages were identified (Figure 3; Table 4). Sixty-four of 119 sites (53.8%) were identified as OPH, typified by 'Ophiuroidea spp.', 'Porifera sp.5', and 'Hydrozoa sp.1'. OPH contained the highest taxa richness (51 taxa: 39 morphotypes, 12 species), as well as the most taxa unique to a single assemblage (8 taxa). SDR represented 21 sites (17.6%) and contained 13 morphotypes and seven species, with *S. droebachiensis* and 'Stauromedusae sp.2' as the typifying taxa. MIX was found at 26 sites (21.8%) and had the second highest taxa richness, with 30 morphotypes and 12 species. It was typified by 'Hormathia' sp.1', 'Cerianthidae sp.3', 'Cnidaria sp.1', and 'Sagittidae sp.1'. EPA was the rarest assemblage, with only eight representative sites (6.7%). EPA had the lowest taxa richness, with only eight morphotypes and seven species, and was typified by *E. parma* and *Pseudopleuronectes americanus*, with the former unique to this assemblage. While OPH exhibited the highest taxa richness, species accumulation curves indicate that the species/morphotypes richness of SDR, MIX, and EPA are underrepresented (Figure 4). Greater surveying effort could reveal additional species/morphotypes for each assemblage. However, this lack of plateau may also be the result of removing species with <5 occurrences across all ground-truthing sites.

Model performance and predicted distribution

Following the Boruta algorithm and assessment of collinearity, 18 variables were included in the epifaunal models, 18 in the *A. clathratum* models, and 24 in the CCA models. Without fine-scale substrate % features, the RF model accuracy was 61.0% (kappa = 0.31) and the LightGBM model accuracy was 68.3% (kappa = 0.47). With the addition of fine-scale substrate features, the epifaunal RF test accuracy increased to 78.1% (kappa = 0.62), and the LightGBM model accuracy increased to of 78.1% (kappa = 0.62). Both the RF and LightGBM models overestimated the occurrence of OPH, and as a result, a large number of SDR and MIX observations were incorrectly classified as OPH. This is evidenced in the RF and LightGBM predictive maps, where OPH was predicted to cover the majority of each survey area, excluding Rushoon (Figure 5). RF, however, included a greater coverage of SDR along the coastal side of D'Argent Bay and of MIX along the interior of St. Lawrence. LightGBM underestimated the coverage of both SDR and MIX in D'Argent Bay and St. Lawrence, respectively, even though ground-truthing sites assigned as those assemblages were observed. RF correctly identified all EPA observations while LightGBM was unable to correctly predict any of the EPA sites.

Only ground-truthing sites within the observed depth range for each marine algae were included. For *A. clathratum* model

FIGURE 6
Predicted absence (white) and presence (green) of *Agarum clathratum* by the 1) Random Forest and 2) Light Gradient Boosting Machine models across the four target survey areas: **(A)** Rushoon, **(B)** D'Argent Bay, **(C)** Burin, and **(D)** St. Lawrence. No predictions were developed where black is seen, as depth exceeded the range established in *A. clathratum* model development.

development, 115 sites at a depth range of 15–66 m were included. *A. clathratum* was present at 60 of 115 ground-truth sites, the majority of which occurred in Burin (25 of 60 sites; 41.7%). *A. clathratum* was present at over 50% of sites in all survey areas except for St. Lawrence. Model performance without fine-scale substrate % features was 82.1% (kappa = 0.64) for the RF model and 87.2% (kappa = 0.74) for the LightGBM model. Maps derived from these models predicted a majority coverage of *A. clathratum* across Burin, though a patchwork of absences is predicted by LightGBM in the interior of Burin's extent. Differences in predicted *A. clathratum* extent is apparent in Rushoon and St. Lawrence. The greatest discrepancies were observed in D'Argent Bay though, with very little coverage predicted by LightGBM compared to RF (Figure 6).

132 sites were included in the CCA model at a depth range of 15–78 m. For CCA, 42 sites had full coverage (31.8%) and 31 sites had partial coverage (23.5%). Rushoon had the highest number of ground-truthing sites with full coverage off CCA (15 of 27). Aside from one instance of full coverage, the northeastern coast of St. Lawrence was characterized by partial coverage of CCA. Few absences of CCA were observed in D'Argent Bay (7 out of 36 sites) and Burin (11 out of 45 sites). When models were developed without fine-scale substrate % coverage, the CCA RF model had an accuracy of 68.9% (kappa = 0.49) and the LightGBM model had an accuracy of 68.9% (kappa = 0.51).

Predictive maps derived from these differed in the concentration of absences, with LightGBM predicting an underestimation across all four survey areas of both partial and full coverage (Figure 7).

The accuracy of all marine algae models was increased with the introduction of fine-scale substrate % coverage features. The *A. clathratum* RF and LightGBM model accuracies increased to 89.7% (kappa = 0.80) and 92.3% (kappa = 0.85), respectively and both the CCA RF and LightGBM accuracies increased to 82.2% (kappa = 0.72).

Species-Environment relationships

Depth was the most important variable for explaining the distribution of epifaunal assemblages, according to the RF model (Figure 8). OPH and MIX were associated with deeper portions of the surveyed areas, while SDR and EPA were generally observed at depths shallower than 50 m. Relationships between EPA and the five most important variables appeared opposite to those observed for the other assemblages (according to the best-preforming RF model) (Figure 9). EPA was the only assemblage that was more prevalent with increased coverage of fine sediment and flat terrain. Assemblages SDR, MIX, and OPH appeared more
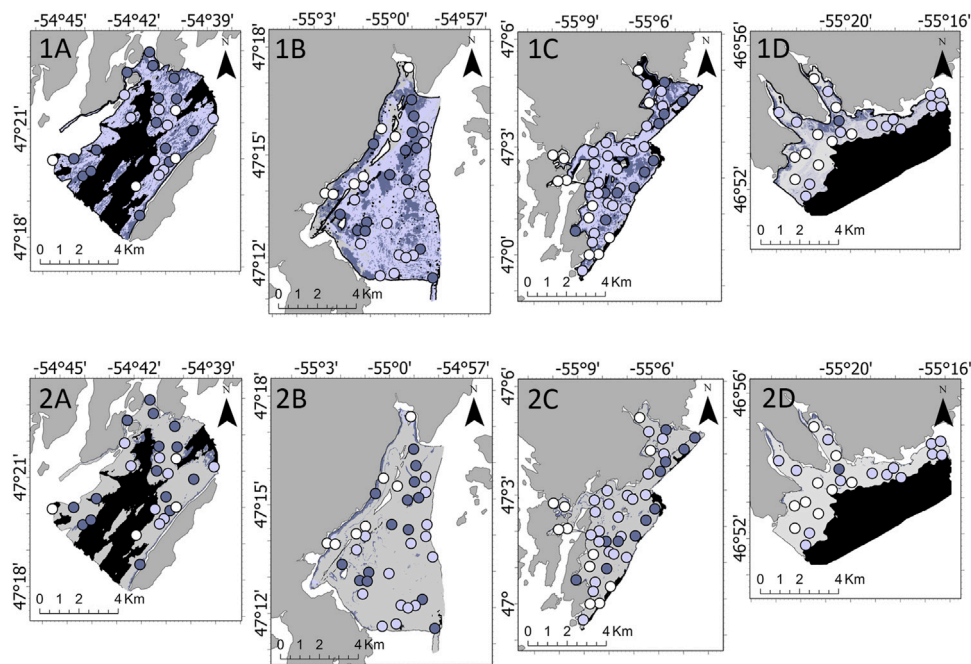
FIGURE 7
Predicted absence (white), partial coverage (light purple), and full coverage (dark purple) of non-geniculate crustose coralline algae (CCA) by the
1) Random Forest and 2) Light Gradient Boosting Machine models across the four target survey areas: **(A)** Rushoon, **(B)** D'Argent Bay, **(C)** Burin, and **(D)**
St. Lawrence. No predictions were developed where black is seen, as depth exceeded the range established in CCA model development.

prevalent at areas of rugged and boulder terrain, according to models. EPA was most prevalent within 2 km of the coast, with decreasing occurrence with greater distance. Unlike SDR and MIX, OPH was most prominent at sites closer to shore, but also occurred at the furthest offshore sites that were sampled.

Fine-scale substrate % coverage was identified as being even more important than depth to explain the spatial patterns of both *A. clathratum* and CCA models (Figure 8). Specifically, the presence of even low % coverage of fine sediment influences the presence of both *A. clathratum* and CCA. The predicted presence of either marine algae was higher with increasing coverage of harder substrates, including both boulder (%) and gravel (%) coverage (Figure 10).

According to both RF and LightGBM models, bathymetry was the second most important variable influencing the distribution of *A. clathratum*, with the majority of occurrences constrained to depths of 15–48 m. Bathymetry appeared less important for predicting CCA distribution in the RF model, and was not included at all in the CCA LightGBM model. The model suggested that softer sediments were more influential than harder substrate in determining the presence of *A. clathratum* (Figure 10). For CCA models, partial and full coverage were associated with higher backscatter values, while sites with absences were characterized by lower backscatter (Figure 11).

Discussion

The west coast of Placentia Bay hosts a diverse and heterogeneous collection of benthic invertebrates, with prominent populations of *A. clathratum* and substantial CCA coverage. Fine-scale (<1 m) substrate features appear highly important for explaining observed spatial patterns. Performance improved in all cases when substrate features were included in the models, yet ultimately, these variables could not be used for continuous spatial prediction due to their discontinuous coverage. This highlights the importance of fine-scale substrate as a benthic habitat driver. Nonetheless, the models developed in this study provide valuable insight into the species-environment relationships driving the distribution of the heterogeneous benthic biota found in Placentia Bay–a necessary step in establishing a baseline for monitoring changes over time.

Depth has often been identified as an important variable in explaining benthic biota distribution (Bekkby et al., 2009; Gorman et al., 2013; Neves et al., 2014; Schückel et al., 2015; Bekkby et al., 2019). However, depth is likely acting as a proxy for other co-varying and harder to characterize variables, such as light availability, temperature, salinity, wave action, or ice scouring (Elith and Leathwick, 2009; Sandman et al., 2013). For example, in the case of the spatial distribution
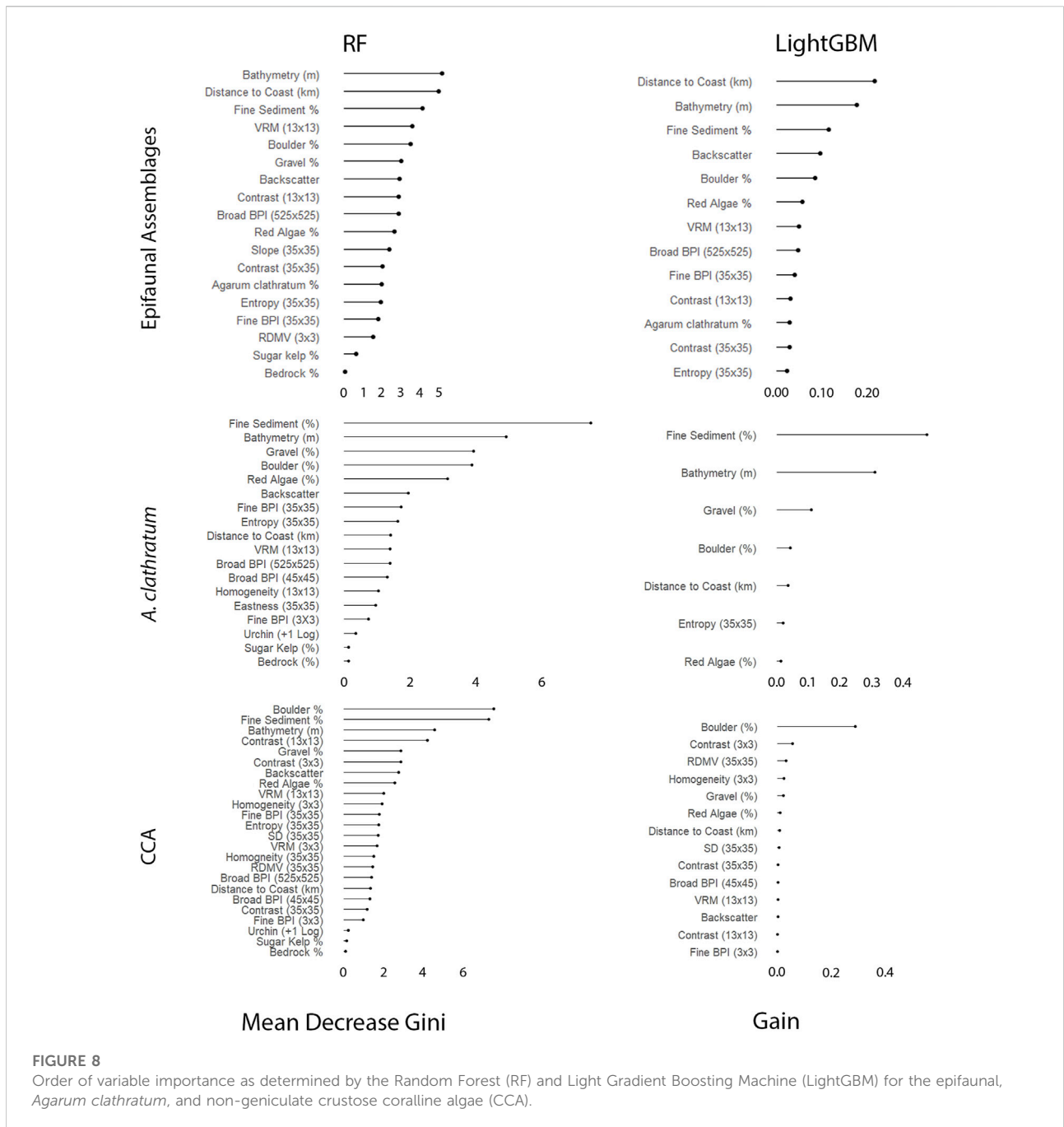
FIGURE 8
Order of variable importance as determined by the Random Forest (RF) and Light Gradient Boosting Machine (LightGBM) for the epifaunal, *Agarum clathratum*, and non-geniculate crustose coralline algae (CCA).

of *A. clathratum* and CCA within Placentia Bay, depth likely acts as a proxy for light attenuation. *A. clathratum* extends to greater depths than most kelp species due to its shade-tolerance (Krause-Jensen et al., 2019), with an observed depth limit in this study of up to 66 m, consistent with findings along coastal Greenland (Krause-Jensen et al., 2019). CCA are even more tolerant of low-light conditions due to their low photosynthetic capacity (Littler et al., 1985; Roberts et al., 2002; Nelson, 2009). CCA are found within

most coastal habitats (Littler et al., 1985), including Antarctica (Zaneveld and Sanford, 1965; Schwarz et al., 2005; Castellan et al., 2021), and are observed at depths greater than any other local marine algae species (McConnaughey and Whelan, 1997). This may explain the exclusion of bathymetry from the CCA LightGBM model. Dean et al., 2015 observed a similar pattern with coralline algae along the Great Barrier Reef, where depth had little effect on their distribution compared to physical features.
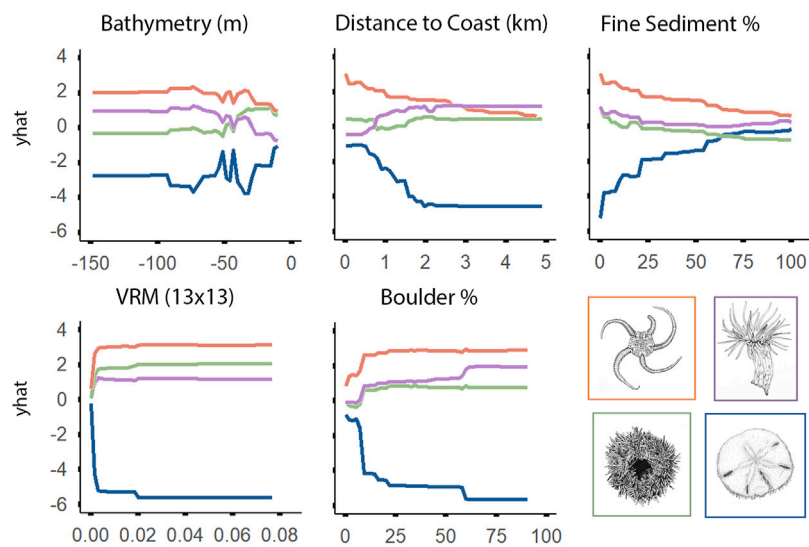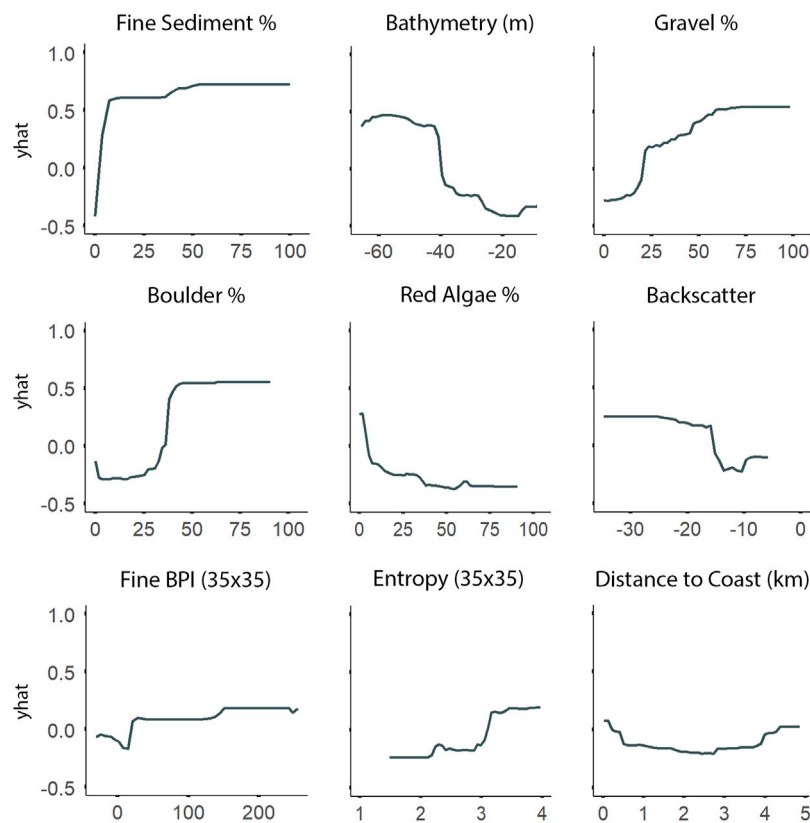
FIGURE 9
Univariate partial dependence plots derived from the Random Forest classification model for the top five most important explanatory environmental features explaining the distribution of individual epifaunal assemblages. The 'yhat' axis refers to the value of partial dependence function. The partial response of the epifaunal assemblages to all features is provided in Supplementary Figure S1.

In the case of EPA, shallower depths may be associated with a greater abundance of food for the typifying species *E. parma*, such as benthic diatoms, which are known to migrate to shallowed depths as they grow older and larger (Cabanac and Himmelman, 1996; Cabanac and Himmelman, 1998). In contrast, OPH and MIX were found across most of the depth range surveyed. The dominant epifauna of these assemblages included porifera and cnidarians, with dense ophiuroid beds in OPH and abundant *Hormathia* sp.1 aggregations in MIX. As these epifauna rely on filter- and suspension-feeding techniques, their survival may depend on food transport from the euphotic zone (Maldonado et al., 2017). Food transport may be constrained by both hydrography and depth in coastal environments (Grebmeier and Barry, 1991; Graf, 1992; Piepenburg, 2005; Sswat et al., 2015).

Mean current circulation in Placentia Bay is counterclockwise, with currents entering on the eastern coast and exiting on the west (Ma et al., 2012). The west coast is therefore subject to upwelling currents that may be beneficial to filter- and suspension feeders (Ma et al., 2012), such as the porifera and cnidarians (i.e. *Hormathia* sp.1) observed within the OPH and MIX assemblages. Sponge aggregations (Hogg et al., 2010) and *Hormathia digitata* (Dunlop et al., 2020) are known to associate with strong, nutrient-enriched currents delivering a constant food supply–though the current strength in these small embayments is strongly influenced by the complex bathymetry and shoreline (Largier, 2020). *A. clathratum* and CCA were found on westward-facing substrate in line with Placentia Bay's south westerly currents [Supplementary Figures S2,3].

Kelp beds are well-adapted to environments of moderate wave exposure (Gorman et al., 2013; Bekkby et al., 2019), as wave action boosts nutrient supply and uptake, ensures continuous light exposure (Hurd et al., 1996; Hepburn et al., 2007; Bekkby et al., 2019), and reduce survivability of epiphytes (Strand and Weisner, 1996). However, at exposed areas such as St. Lawrence, which may experience excessive wave action, growth may be inhibited due to abrasions or transport (Marrack, 1999; Sañé et al., 2016).

With the exception of EPA, hard substrates were associated with suitable habitat for all epifaunal assemblages, *A. clathratum,* and CCA. Fine sediments and sedimentation may reduce habitat suitability for these sessile organisms by inhibiting feeding strategies. Large kelps such as *A. clathratum* additionally require a stable foundation for holdfast attachment to endure currents and storm surge (Morrison et al., 2009; Watanabe et al., 2014; Masteller et al., 2015). In contrast, *E. parma* would preferentially inhabit coarse sand areas (Stanley and James, 1971; Sisson et al., 2002), enabling filtering where coarse sand traps particulate matter for consumption without excess fouling (Bland et al., 2019), and burying to avoid predation (Manderson et al., 1999; Pappal et al., 2012) and damaging storm surge (O'Neill, 1978). Distance from the coast may act as a surrogate for sedimentation rate (Stephens and Diesing, 2015; Misiuk et al., 2018). In the case of CCA, growth occurs only on hard substrate (Connell, 2005; Gagnon et al., 2012, Jørgensbye and Halfar, 2017), with fine sediment additionally reducing light availability for photosynthesis (Konar and Iken, 2005; Jørgensbye and Halfar, 2017).
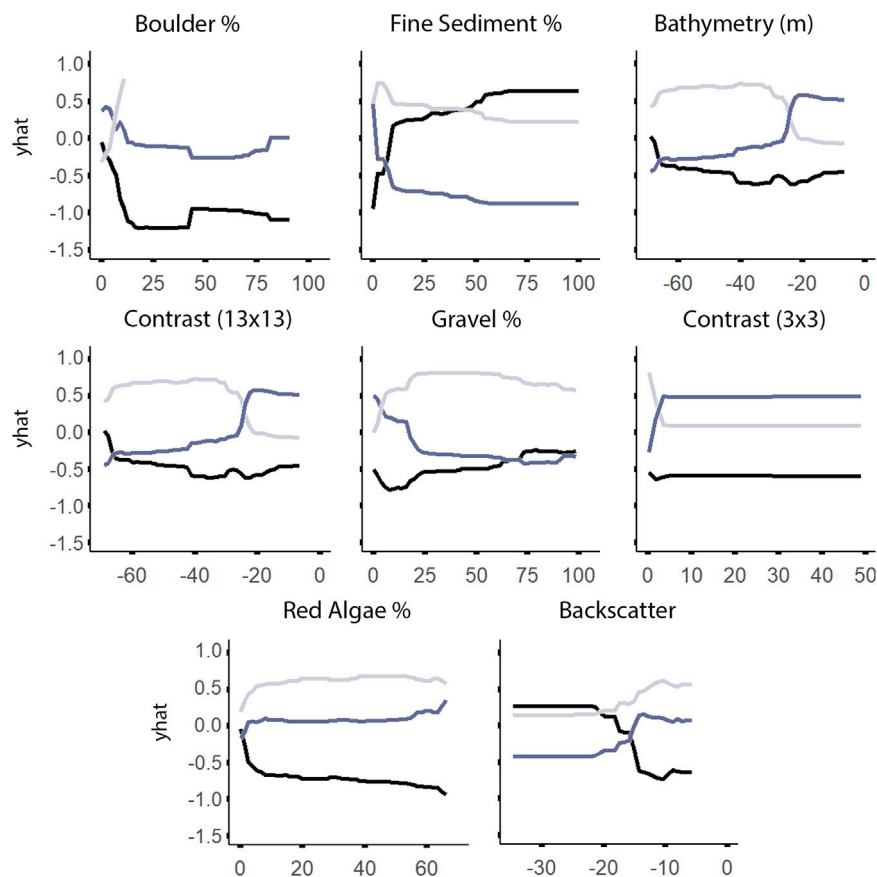
FIGURE 10
Partial dependence plots derived from the Random Forest classification model for the most important explanatory environmental features describing the distribution of *Agarum clathratum*. The 'yhat' axis refers to the value of partial dependence function. The partial response of *A. clathratum* to all features is provided in Supplementary Figure S2.

Smaller grain sizes, like gravel, are more likely to be reworked in a dynamic environment, limiting consistent light exposure and increasing physical damage and making it more difficult for CCA to establish growth due to abrasion (Foster, 2001; Hetzinger et al., 2006).

Removal of fine-scale substrate features from the RF models produced a substantial drop in predictive accuracy (~25%). Owing to the highly heterogeneous nature of the seafloor in Placentia Bay, the ability to capture increased structural complexity can allow for the identification of potential 'keystone structures', (i.e. structures that directly bolster species richness) (Tews et al., 2004). For example, 'Hormathia sp.1' was often seen attached to the sporadic boulders scattered across the silt-covered seafloor in the deep channels within Rushoon. Drop stones resulting from glacial retreat (Shaw et al., 2011) have been shown to increase diversity of more homogeneous sediment dominated areas (Meyer et al., 2016). This fine-scale feature cannot currently be captured by acoustic surveying techniques such as MBES, but new methods such as synthetic apertures sonar may provide this capability (Gini et al., 2021).

Increased physical habitat complexity has previously been linked to increases in abundance and diversity (Barry and Dayton, 1991; Bracewell et al., 2018). In coastal environments, rocky shores play a critical role in structuring coastal benthic communities (Menge, 1982; Underwood and Denley, 1984). Within Placentia Bay, boulder and gravel fields occur along the offshore extent of D'Argent Bay and Burin and along the shoreline of Rushoon and St. Lawrence. These fields may provide a level of stability and topographical diversity that could increase structural availability for sessile invertebrates (MacArthur and Wilson, 1967; Liversage and Chapman, 2018; Franz et al., 2021), such as the sponges and anemones observed in Rushoon and St. Lawrence. These areas were found to be associated with a higher presence of arcto-boreal species, such as the different morphotypes of porifera and anthozoan as well as species of echinoderms and crustaceans. 1,064 individuals from 25 morphotypes of the Phylum Porifera were recorded in these areas, further increasing habitat complexity by acting as biogenic substrate for associated fauna (Buhl-Mortensen et al., 2017; Hogg et al., 2010, Maldonado et al., 2017). Those areas may represent rocky reefs–an ecologically important habitat

FIGURE 11
Univariate partial dependence plots derived from the Random Forest classification model for the most important explanatory environmental features describing the distribution of non-geniculate crustose coralline algae (CCA). The 'yhat' axis refers to the value of partial dependence function. The partial response of absence, partial coverage, and full coverage of CCA to all features is provided in Supplementary Figure S3.

characterized as a subtidal natural hard substrate, which has been linked to increased biodiversity (Taylor, 1998; Kostylev et al., 2005; Wahl, 2009).

Rocky reefs from temperate to Arctic environments are often covered with canopy-forming kelp species. Likely, the dense coverage of *A. clathratum* observed in the subtidal would also contribute to increased epifaunal richness (Blain and Gagnon, 2014; Teagle et al., 2017). Fewer species were observed than expected in the SDR assemblage, but this may have resulted from limited visibility of the seafloor due to obstruction by *A. clathratum* blades.

Few other brown kelp species were observed during ground-truthing an exception being two sites in Rushoon fully covered by the sugar kelp *S. latissima*. *A. clathratum* was often found to co-exist with red algae though. The potential for increased coverage by red algae is an example of an observable change made possible by comparing to the baseline established in this study. As compared to kelp beds, low-lying red algae turfs are a fast-growing and stress-tolerant opportunistic group (Airoldi, 1998;

Filbee-Dexter and Wernberg, 2018), and high turnover rates allow them to succeed kelp forests that have been weakened by thermal stress (Scheibling and Gagnon, 2006; Filbee-Dexter et al., 2016; Wernberg et al., 2019). Kelp is more susceptible to stress due to ocean warming and increased storm activity, concurrent with cyclical herbivorous pressure by *S. droebachiensis* (Filbee-Dexter and Wernberg, 2018). Once it supersedes kelp, red algae turfs cover the substrate, preventing kelp from resettling and inducing phase shifts to environments with reduced oxygen and increased sediment accumulation (Gorgula and Connell, 2004), further negatively impacting settlement of kelp spores (Norton and Fetter, 1981; Gorman and Connell, 2009; Connell and Russell, 2010). Kelp is susceptible to stress due to ocean warming and increased storm activity, concurrent with cyclical herbivorous pressure by *S. droebachiensis*. No observations of turf-dominated areas show shifting back to kelp (Filbee-Dexter and Wernberg, 2018).

The performances of the RF algorithm, which is well-established in the field of benthic habitat mapping, and the newer LightGBM

were comparable considering only model accuracy and variable importance estimates. However, disagreements occurred over the predictions of the rarer assemblages, especially when both model types were used to develop predictive maps. LightGBM is a powerful modelling technique, but it was developed to manage large datasets (e.g., 1,00,000 s of observations) (Ke et al., 2017). Sample sizes of this magnitude are uncommon in marine ecology [Benkendorf and Hawkins, 2020; Luan et al., 2020]. The small sample size in this study likely resulted in overfitting of the LightGBM models, apparent, for example, in the prediction of CCA absences. Ground-truthing samples indicated extensive full and partial coverage of CCA in D'Argent Bay and Burin; however, LightGBM predicted very sparse CCA coverage for most of the areas.

LightGBM advertises faster training speed, low memory usage (Ke et al., 2017; McCarty et al., 2020), and in-depth control over boosting and model learning *via* tunable parameters. The latter point, though, requires the user to be confident in their understanding of each parameter. In contrast, RF has only two parameters that generally require manipulation, and even appears quite robust to these in practice, making it a more user-friendly algorithm (Brieman, 2001; Liaw and Weiner, 2002). RF has demonstrated repeated success in benthic habitat mapping studies comparing techniques (Lucieer et al., 2013; Robert et al., 2015; Rooper et al., 2017; Misiuk et al., 2019; Pillay et al., 2020; Shang et al., 2021). However, RF may be biased towards computational efficiency in favor of accuracy (Fernandez-Delgado et al., 2011; Wainberg et al., 2016). The comparison carried out here supports the continued use of RF as a modelling technique that can perform well with the limited amount of data that is common in marine studies. It will be of great interest to determine whether the newer LightGBM algorithm shows better performance with larger datasets.

The subtidal zone of western Placentia Bay is host to a diverse and heterogeneous benthic environment that supports multiple ecosystem services. The baseline information provided by this study provides information necessary to monitor potential changes in biodiversity and ecosystem function within the Placentia Bay EBSA. The communities of OPH and MIX are notable for their epifaunal diversity, comprising structure-forming sessile invertebrates. Biogenic structural heterogeneity is often linked to increased biodiversity (Buhl-Mortensen et al., 2010; Thomsen et al., 2010; Lefcheck et al., 2017; Kazanidis et al., 2021), which may support ecosystem health. Coastal townships of Placentia Bay also rely on the health of this benthic ecosystem, which support local livelihoods, but which may be threatened under increased anthropogenic activity (e.g. aquaculture, oil shipping) and shifts in ocean temperature and pH (Doney et al., 2009). Proactive management action may mitigate potential detrimental changes brought on by these stressors.

Conclusion

The predictive maps developed in this study indicate a heterogenous benthic ecosystem in the western part of the Placentia Bay EBSA, composed of habitat-forming biotasuch as marine algae and sessile invertebrates including porifera and anemones. This contributes substantiallyto baseline understanding of marine epifaunal distributions and richness in a subtidal area of recognized ecological and socio-economic importance. Concurrent with predictive geospatial modelling, investigation of fine-scale (<1 m) substrate characteristics highlight their importance as benthic habitat drivers. All models tested here performed better with the addition of discrete fine-scale substrate observations compared to the use of spatially continuous acoustic backscatter proxies. The LightGBM models had higher accuracies, but often demonstrated signs of overfitting as compared with the predictive maps derived from the RF models. The fundamental knowledge derived from these models provide information that is critically needed for monitoring the health of the Placentia Bay EBSA over time.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: https://slgo.ca/en/coastal-environment-baseline-program/.

Author contributions

JM-M collected ground-truthing data for Burin and St. Lawrence, with Rushoon and D'Argent Bay collected by SN. Acoustic surveying of all study areas was conducted on the R/V Cartwright by AT and Kirk Regular (latter not included). Data processing, analysis, and model development and interpretation was conducted by JM-M with assistance from SN and BM. JM-M and SN collaborated in creating a species guide for the identification of all observed benthic flora and fauna (>2 cm) to the lowest taxonomic level possible. BM assisted with processing multibeam echosounder data from the survey areas. Project initiation with the Fisheries and Oceans Canada and the organization of fieldwork was led by KR. All writing was inititally done by JM-M with editorial input from SN, AT, BM, KR, EE, and PG.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fenvs.2022.999483/full#supplementary-material

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