SYMPOSIUM

Predicting the Distribution and Ecological Niche of Unexploited Snow Crab (*Chionoecetes opilio*) Populations in Alaskan Waters: A First Open-Access Ensemble Model

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Synopsis Populations of the snow crab (*Chionoecetes opilio*) are widely distributed on high-latitude continental shelves of the North Pacific and North Atlantic, and represent a valuable resource in both the United States and Canada. In US waters, snow crabs are found throughout the Arctic and sub-Arctic seas surrounding Alaska, north of the Aleutian Islands, yet commercial harvest currently focuses on the more southerly population in the Bering Sea. Population dynamics are well-monitored in exploited areas, but few data exist for populations further north where climate trends in the Arctic appear to be affecting species' distributions and community structure on multiple trophic levels. Moreover, increased shipping traffic, as well as fisheries and petroleum resource development, may add additional pressures in northern portions of the range as seasonal ice cover continues to decline. In the face of these pressures, we examined the ecological niche and population distribution of snow crabs in Alaskan waters using a GIS-based spatial modeling approach. We present the first quantitative open-access model predictions of snow-crab distribution, abundance, and biomass in the Chukchi and Beaufort Seas. Multi-variate analysis of environmental drivers of species' distribution and community structure commonly rely on multiple linear regression methods. The spatial modeling approach employed here improves upon linear regression methods in allowing for exploration of nonlinear relationships and interactions between variables. Three machine-learning algorithms were used to evaluate relationships between snow-crab distribution and environmental parameters, including TreeNet, Random Forests, and MARS. An ensemble model was then generated by combining output from these three models to generate consensus predictions for presence–absence, abundance, and biomass of snow crabs. Each algorithm identified a suite of variables most important in predicting snow-crab distribution, including nutrient and chlorophyll-*a* concentrations in overlying waters, temperature, salinity, and annual sea-ice cover; this information may be used to develop and test hypotheses regarding the ecology of this species. This is the first such quantitative model for snow crabs, and all GIS-data layers compiled for this project are freely available from the authors, upon request, for public use and improvement.

Introduction

Changing climate in the Arctic is manifesting itself in many ways including rising temperatures and changing sea-ice conditions. These conditions appear to be causing changes in marine communities (Grebmeier et al. 2006), including northward contractions of the ranges of Arctic species and invasion of North Pacific species onto the Arctic shelf

(Orensanz et al. 2004; Sirenko and Gagaev 2007; Mueter et al. 2009). Range extension and colonization of new habitat may appear to benefit the invading species, but these shifts may also alter competitive and predatory interactions within existing communities, many of which are poorly understood. Moreover, increasingly ice-free northern waters are expected to lead to increased human

activity in Arctic seas (Johnsen et al. 2010). The effects of human activity and climatic change on Arctic and sub-Arctic marine ecosystems cannot be accurately predicted in space and time without improved knowledge of species' current ranges and scales of movement or dispersal, yet such data are relatively scarce at high northern latitudes (Piepenburg et al. 2011). In addition, quantitative descriptions of habitat requirements for Arctic species are urgently needed to address issues in international conservation and management now facing this pristine ecosystem (Johnsen et al. 2010).

Fish and shellfish populations are still unexploited in Alaskan waters north of the Bering Strait. In 2009, the North Pacific Fisheries Management Council recommended a moratorium on Arctic fishing that was approved by the US Secretary of Commerce. Nonetheless, the current trend toward reduced annual cover of sea ice has opened the door for future fisheries development in this region. While the Bering Sea and Gulf of Alaska are home to several commercially harvested crab species, including Tanner (*C. bairdi*), red king (*Paralithodes camtschaticus*), and Dungeness (*Cancer magister*), only the snow crab (*Chionoecetes opilio*) is abundant in more northerly Alaskan waters (Paul et al. 1997; Feder et al. 2005; Bluhm et al. 2009; Rand and Logerwell 2011). However, while population dynamics and distribution of commercial species are monitored by state and federal management agencies in fisheries areas, many basic parameters for a successful management strategy are poorly characterized in northern populations.

Commercial crab species in Alaska have undergone great fluctuations in population size in recent decades (Woodby et al. 2005; Zheng and Kruse 2006). For snow crabs, efforts to understand these trends could greatly benefit from improved, quantitative mapping, and characterization of fundamental niche requirements throughout their current range. Here we apply, for the first time, a spatial modeling approach using machine-learning and ensemble-modeling methods for predicting spatial distribution of snow crabs in under-surveyed portions of their Alaskan range. In addition, we identify key environmental determinants of this distribution that may represent important niche descriptors and/or metrics of ecosystem change in the region.

Study area and the distribution of snow crabs

Snow crabs are widely distributed in the Bering, Chukchi and Beaufort Seas and in the northwestern Atlantic, and an introduced population has recently been discovered in the Barents Sea (Jadamec et al. 1999; Alvsvåg et al. 2009). Here we focus on Alaskan snow-crab stocks throughout the latitudinal extent of their known range, extending from the Bering Sea north to the Arctic Ocean. This region comprises a system of seasonally ice-covered waters with predominant hydrographic flow from south to north through the Bering Strait. The Chukchi Sea extends ~800 km north from the Bering Strait, averaging ~50 m in depth. Flow across the Chukchi shelf is predominantly northward toward the shelf break, where it either becomes entrained into an eastward flowing current, or spills over into the Arctic Ocean and travels clockwise in the Beaufort Gyre (Weingartner et al. 2005). The continental shelf narrows in the adjacent Beaufort Sea and descends into the Canada Basin. Snow-crab habitat appears to be limited mainly to the shallower shelf and slopes (<300 m; 520 m maximum recorded depth) (Yosho and Hayashi 1994; Lovrich et al. 1995; Comeau et al. 1998; Ernst et al. 2005); however, sampling at deeper depths in Arctic waters has been limited.

Seasonal ice typically covers the Eastern Bering Sea (EBS) from November to June (Stabeno et al. 2001). This winter sea ice contributes to the formation of a large body of cold bottom-water over the central shelf, which is trapped by a relatively warm and fresh layer of sea-ice melt as the ice retreats (Stabeno et al. 2001). This "cold pool" can be 40–50 m thick and generally persists throughout the summer with temperatures <2°C over much of the area (Wyllie-Echeverria and Wooster 1998; Stabeno et al. 2001). Inter-annual variability in the location and extent of this cold pool influences snow-crab distribution (Orensanz et al. 2004; Ernst et al. 2005).

Snow-crab fisheries and management

Historically the EBS snow-crab fishery has been the largest and most valuable crab fishery in the US (e.g., see NPFMC 2010), and constitutes one of the most commercially valuable Canadian and Greenlandic fisheries in the northwestern Atlantic as well (FRCC 2005). EBS harvests increased during the 1980s as catches of the warmer-water relative, Tanner crab (*C. bairdi*), began to decline and fisheries were closed. Since that time, EBS snow crabs have undergone large fluctuations in population size, and were declared overfished in 1999 (e.g., NPFMC 2009).

The EBS snow-crab fishery is managed as one continuous population extending into Russian waters (NPFMC 2010). Recent genetic data for snow crabs in Alaskan waters support this strategy,

indicating a high degree of gene flow across most of the region (Albrecht 2011). Snow crabs produce two planktonic zoeal stages and a third settling stage (megalopa) that last ~3–5 months in total (Somerton 1981; Jadamec et al. 1999; Orensanz et al. 2004; Kogane et al. 2005; Webb et al. 2006). This relatively long planktonic phase may facilitate long-distance dispersal between widely-distributed populations. Little attention has been paid to *C. opilio* stocks in the Chukchi and Beaufort Seas (but see Paul et al. 1997; Feder et al. 2005; Bluhm et al. 2009; Rand and Logerwell 2011). However, despite their distance from the Bering Sea, these northern populations may be partially sustained by propagules advected north from more intensively-fished areas further south. Water masses passing through the Bering Strait can travel as far as Point Barrow on the northwestern coast of Alaska in as little as 6 months (Winsor and Chapman 2004), providing a potential mechanism for long-distance larval transport and connectivity across the latitudinal extent of the range. Thus, assessment of habitat characteristics at this broader regional scale may provide further insight into snow-crab biology and ecology throughout its range.

The limited studies of northern populations suggest some ecological differences in snow crabs on either side of the Bering Strait (e.g., smaller-sized adults in the north). Other potentially important environmental features such as sea-ice dynamics—a major environmental driver in the north—have not been examined. The strong temperature-dependence of adult body size (Orensanz et al. 2007; Burmeister and Sainte-Marie 2010) also suggests this species is likely to be affected by changing climate in the Arctic. Indeed, evidence to this effect has already been reported (Orensanz et al. 2004). This species is particularly well-suited to spatial modeling given the wealth of distribution data available in fishery regions. Model predictions presented here represent informed hypotheses that can be further tested as new data become available; thus, all data layers incorporated into this model are available from the authors in an open-source format for such additional work. We assess the quality and accuracy of these predictions and identify data needs for improving the accuracy of the models.

Materials and methods

Response variables: snow-crab distribution

We compiled published and unpublished snow-crab data from trawl surveys conducted in the Bering, Chukchi and Beaufort Seas (summarized in Table 1). Overall, this compilation of data constitutes a unique, digital, geo-referenced open-access database for Alaskan snow crabs. Data from the Bering Sea were obtained from the National Oceanic and Atmospheric Administration-National Marine Fisheries Service (NOAA-NMFS) Eastern Bering Sea trawl survey (Chilton et al. 2009). The purpose of this annual survey is to collect data on abundance and biomass of commercial crab and groundfish species, and it has been conducted each summer since 1975. Here we use data from the 2009 survey, which constitutes the most recent dataset available at the time we began our analysis. All station locations and sampling procedures are reported in detail by Chilton et al. (2009). Briefly, these surveys used a standard Eastern otter trawl with 3.5 inch mesh and 1¼ inch cod-end liner, and a 17.2-m horizontal opening towed at ~3 knots for 1.5 nmi (30 min duration), according to standard NOAA protocols (Stauffer 2004). The sampling area consists of a continuous grid composed of Alaska Department of Fish and Game (ADF&G) commercial crab fishery management units, which are each subdivided into contiguous 20 x 20 nm cells. A trawl is conducted in each

Table 1 Sources of data on snow crab and the units for crab abundance and biomass reported in each study

Projects	References	Region	Abundance units reported	Biomass units reported
RUSALCA[a] 2004	Bluhm et al. (2009)	Chukchi Sea	# Ind/1000 m^2	g/1000 m^2
NOAA BASIS 2007	Bluhm et al. (2009)	Chukchi Sea	# Ind/1000 m^2	g/1000 m^2
Japanese R/V *Oshoro Maru* expedition 2008	Bluhm et al. (2009)	Chukchi Sea	# Ind/1000 m^2	g/1000 m^2
Chukchi Bight/Kotzebue Sound 1976	Feder et al. (2005)	SE Chukchi Sea	# Ind/1000 m^2	kg/km^2
RUSALCA[a] 2009	B. Bluhm et al. (unpublished data)	Chukchi Sea	# Ind/1000 m^2	g/1000 m^2
NOAA-MMS Beaufort Sea Survey 2008	Rand and Logerwell (2011)	Beaufort Sea	# Ind/1000 m^2	kg/km^2
NOAA-NMFS Eastern Bering Sea trawl survey 2009	Chilton et al. (2009)	Bering Sea	# Ind/km^2	kg/km^2

[a]RUSALCA (Russian–American Long-term Census of the Arctic) funded by NOAA-CIFAR (Cooperative Institute for Arctic Research). All units were standardized before incorporation into the models.

cell, and the geo-referencing point for that sample is reported as the cell's midpoint. In some high-sampling-density areas (locations known to have high biomass of crabs), additional samples are taken at the corners of the grid squares.

Many of the data from the Chukchi Sea were collected on a series of expeditions in 2004, 2007, 2008, and 2009. Details of sampling and stations for 2004, 2007, and 2008 collections were reported by Bluhm et al. (2009). Data from 2009 are unpublished, and were obtained directly from the project leader (B. Bluhm et al., unpublished data). All samples from these expeditions were collected according to the same protocol, using a plumb-staff beam trawl with a 2.26-m effective opening and a net mesh of 7 mm with a 4-mm cod-end liner, towed at 1.5 knots. The duration of each tow ranged from 1 to 6 min, yielding a swept area between 107 and 1257 m^2. The ship's GPS was used to record a start and end position for each trawl, and the geo-reference point for each sample is reported as the midpoint of the trawled line. An additional data set from the Southeastern Chukchi Sea (Feder et al. 2005) was also included in our analysis. Samples were collected aboard a NOAA vessel in 1976, using an Eastern otter trawl with a 17-m horizontal opening. Data are publicly available through the Arctic Ocean Diversity (ArcOD) database (www.arcodiv .org/Database/Data_overview.html).

Data from the Beaufort Sea were obtained from a 2008 survey conducted by NOAA-NMFS and Minerals Management Service. Details of stations and sampling were reported by Rand and Logerwell (2011), and data on snow-crab abundance and biomass from each station were obtained directly from the authors. Samples were collected using an Eastern otter trawl configured and deployed with the same protocol used by NOAA-NMFS surveys in the Bering Sea (Stauffer 2004). Geo-referenced sampling locations were reported as the starting point for each trawl, as recorded by the ship's GPS.

Predictor variables

In order to characterize key habitat characteristics for snow crabs in a multivariate fashion, remotely-sensed and/or point-sampled data for environmental and biological predictor variables were compiled from various publicly-available sources (summarized in Table 2) and imported into ArcGIS using c. 10-km pixel size (WGS84 Mercator projection in meters). The study area encompasses the region of biological interest for snow crabs in Arctic and sub-Arctic Alaska, and is bounded by a box with the coordinates for each corner as follows: NW, 170°E 77°N; SW, 170° 57°N; NE, 144°W, 77°N; SE, 144°W, 57°N.

We present the first digital compilation of over 20 potential habitat predictors for snow crabs in Arctic and sub-Arctic Alaska. While this selection of potential predictors may not be exhaustive, those variables we have included serve as proxies for many additional, related habitat characteristics (c.f., Drew et al. 2011). Salinity, temperature, nutrient, chloropigment, and oxygen layers are available from the World Ocean Atlas (WOA). We used layers comprised of "statistical temporal means," which represent the average of interpolated values at each standard depth for each variable in every 1° latitude × longitude square containing at least one measurement. We have selected monthly layers from January, April, and August for our analysis; these months represent the winter ice-covered period, annual ice retreat/spring bloom conditions, and late summer ice-free conditions in our study area. Remotely-sensed measurements of the extent of sea-ice in August, January, and April (low ice → high ice) were obtained from the National Ice Center's archive (www.natice.noaa.gov; 2005). For each month, an index of percent-coverage (0–100%) of each grid cell in our data projection was calculated by averaging across data from all years.

Three datasets (MACROBEN, SCOC, and TOC) for benthic parameters that cannot be remotely sensed were compiled by Grebmeier et al. (2006). Similarly, sediment grain-size data (SEDIGRAIN) were obtained from the National Geophysical Data Center (www.ngdc.noaa.gov). These measurements require laboratory analysis and thus consisted of a series of geo-referenced data points distributed throughout the region, in contrast to the higher-resolution remotely-sensed data. We used the raw data from these sources to create predictive GIS-data layers for our analysis in the same manner as described for the data on crabs (see below), thereby providing complete coverage of the study area for these variables.

Data mining and modeling

Each snow-crab sampling location was overlain with data layers for all 20 environmental predictor variables using the publicly-available application Hawth's tools (www.spatialecology.com/htools/tooldesc.php) implemented in ArcGIS 9.3. This procedure produces a data cube consisting of the crab response-data (dependent variables) and their underlying

Table 2 List of 20 environmental predictors (independent variables) incorporated in predictive models of snow-crab presence–absence, abundance, and biomass

Variable names	Time period(s) used	Abbreviation	Units	Data source
Apparent O_2 utilization	Jan, April, Aug	AOU	mol O_2/m^3	World Ocean Atlas 2005[a]
Surface (Chl-a)	Jan, April, Aug	CHLA	mg/l	World Ocean Atlas 2005
(Chl-a) standard deviation	Jan, April, Aug	CHLASTD	mg/l	World Ocean Atlas 2005
Depth	N/A	BATH1	M	www.ngdc.noaa.gov/mgg/bathymetry/relief.html
Proximity to nearest coastline	N/A	DIST1	Index of proximity (m)	Esri proximity tools based on www.ngdc.noaa.gov/mgg/shorelines/shorelines.htm
Dissolved O_2	Jan, April, Aug	DO2	mol O_2/m^3	World Ocean Atlas 2005
Maximum sea-ice cover	Jan, April, Aug	ICEM	% coverage	www.natice.noaa.gov/products
Salinity	Jan, April, Aug	SAL	Ppm	World Ocean Atlas 2005
Mixed-layer depth	Jan, April, Aug	MLD	M	World Ocean Atlas 2005
Nitrate concentration	Jan, April, Aug	NIT	mmol/m^3	World Ocean Atlas 2005
Phosphate concentration	Jan, April, Aug	PHO	mmol/m^3	World Ocean Atlas 2005
Silicate concentration	Jan, April, Aug	SIL	mmol/m^3	World Ocean Atlas 2005
Solar radiation dose	Jan, April, Aug	SRD	watts/m^3	Valina and Simó (2007), as in Humphries (2010)
Sea surface Temperature	Jan, April, Aug	SST	°C	World Ocean Atlas
SST standard deviation	Jan, April, Aug	SSTSD	°C	World Ocean Atlas 2005
Human footprint	Cumulative (1960–2007)	HUM1	Index of Human Impact	Halpern et al. (2008)
Sediment grain size (modeled)	N/A	SEDIGRAIN	Mean size, phi scale	www.ngdc.noaa.gov/mgg/geology/size.html
Infaunal biomass (>1 mm) (modeled)	N/A	MACROBEN	gC/m^2	Grebmeier et al. (2006) and references therein
Sediment community O_2 consumption	N/A	SCOC	mmol/m^2/d	Grebmeier et al. (2006) and references therein
Total organic carbon, surface sediments (modeled)	N/A	TOC	% C	Grebmeier et al. (2006) and references therein

[a]The World Ocean Atlas is an open-source data archive available through the NOAA National Oceanographic Data Center (www.nodc.noaa.gov/OC5/WOA05/pr_woa05.html). Full documentation and details of all data collection and analysis are available through the web portal. GIS-formatted data layers were compiled from earlier projects (Rutzen 2008; Humphries 2010; Oppel and Huettmann 2010). All layers are available from the authors upon request.

environmental predictors (independent variables). The predictor variables were then used to estimate a relative index of occurrence (presence or absence of snow crabs) and relative indices of abundance and biomass in all un-sampled locations to generate a predictive surface layer for the entire study area. Such layers indicate general trends, e.g., hot- and cold-spots, and their underlying predictive drivers (e.g., Cushman and Huettmann 2010; Drew et al. 2011). By examining the relative importance of each predictor variable included in the models, we then constructed a quantitative description of the

ecological niche for this species. Response curves for the top predictor variables were evaluated to determine the strength and nature of the relationship between the dependent variable and each relevant independent variable.

Three different machine-learning modeling algorithms were applied to this data set: Random Forests (bagging; for classification) (Breiman 2001), TreeNet (boosting) (Elith et al. 2008), and MARS (Multiple Adaptive Regression Splines) (Elith et al. 2005). The default (or closely related) model settings that were used are well-known to perform best for

most applications (Salford Systems Ltd; D. Steinberg, personal communication). All of these algorithms are well-described for many disciplines, and widely used in similar applications (e.g., Meißner and Darr 2009; Oppel and Huettmann 2010; Wei et al. 2010; Huettmann et al. 2011). All methods were implemented using the latest Salford Systems Predictive Modeling Suite (Salford Systems Ltd, www.salford-systems.com). In order to further optimize model predictions, output from each algorithm was combined in an "ensemble" model (c.f., Araujo and New 2006) that provides a consensus output for all three scenarios. Here, we apply the most robust approach to ensemble forecasting by reporting an averaged index across all three models. The model predictions were internally assessed for error, and represent quantitative hypotheses to be further tested in the field. All input data and prediction layers are available, upon request, in an open-access format (Esri grids), with the specific goal of refining model predictions through incorporation of additional data over time. Metadata are available through the National Biological Information Infrastructure (NBII) database (http://metadata.nbii.gov/ clearinghouse).

We first constructed a binary (i.e., presence–absence) type model following standard procedures (e.g., Hegel et al. 2010; Drew et al. 2011). All "presence" data were compiled from the data sources described above and compared with "confirmed-absence" locations (i.e., sites physically sampled at which no crabs were found). However, instances of confirmed absence were relatively rare and thus presented a bias due to undersampling in some areas (e.g., Chukchi Sea) relative to other well-sampled areas (e.g., Bering Sea) where collections were specifically designed to target high abundance of crabs. Since confirmed-absence data is difficult to obtain (researchers seldom report what they did not find), we apply a standard pseudo-absence procedure (cf., Engler et al. 2004; Hegel et al. 2010) in which 412 "pseudo-absence" data points were generated using Hawth's tools. These points are randomly distributed, and occur in higher densities in areas where real sampling locations are sparse (Fig. 1). This method allows for the entire study area to be "sampled" in a random fashion. Although this approach can be less desirable than one using confirmed-absence data, the method is widely used in cases such as ours in which sampling design was not optimized for a spatial modeling approach (e.g., Ohse et al. 2009; Hegel et al. 2010; Drew et al. 2011).

We built upon the binary presence–absence model to develop predictions of the continuous response variables: abundance and biomass of snow crabs. These models also lack confirmed-absence data but include some locations with low or zero biomass. Models were fit to explain gradients in biomass and abundance throughout the region. The model output consists of gradients in the relative index of crab biomass or abundance; true zero-abundance and biomass are not predicted by this method.

The accuracy of each model was assessed internally, using one of two robust and standard metrics: receiver operating characteristic (ROC) curve (for categorical variables, i.e., presence–absence type data) or area under the curve (AUC) from gains curves (for continuous response variables, i.e., abundance and biomass) (c.f., Pearce and Ferrier 2000). Both metrics are derived from internal bootstrapping-like procedures performed in the Salford Software Suite. They estimate the ratio of true-positive to false-positive model predictions, and can range from 50% to 100%. Values greater than 80% are typically considered "good" to "excellent."

Results

Accuracy statistics for the model and importance rankings for the top five predictor variables identified by each modeling algorithm for each of the three dependent variables (snow-crab presence–absence, abundance, and biomass) are summarized in Tables 3–5. Random Forests (RFs) does not provide estimates of accuracy or rankings of importance for continuous variables when implemented in the Salford Software Suite used here, so RF results are only shown for the presence–absence analysis. ROC or AUC values for all models except one are >80%, suggesting robust predictions that are further strengthened through ensemble averaging. However, ROC and AUC curves are intended for use with true presence and absence data, and thus may be somewhat inflated by the use of pseudo-absence data (c.f., Hegel et al. 2010). All model results are scale-sensitive and only apply to the pixel sizes used (c.f., Huettmann and Diamond 2006; Cushman and Huettmann 2010; Drew et al. 2011).

Presence–absence models

The presence/pseudo-absence models show good ROC curves of over 85% (see Fig. 2 for example), with the best ROC value produced by RF (91%) (Table 3). However, an independent dataset was not available with which to test model accuracy, so these tests are based on internal, spatial cross-validation tests in the Salford Software Suite. Nonetheless, the spatial predictions of the model for presence–absence match known distributions in this region
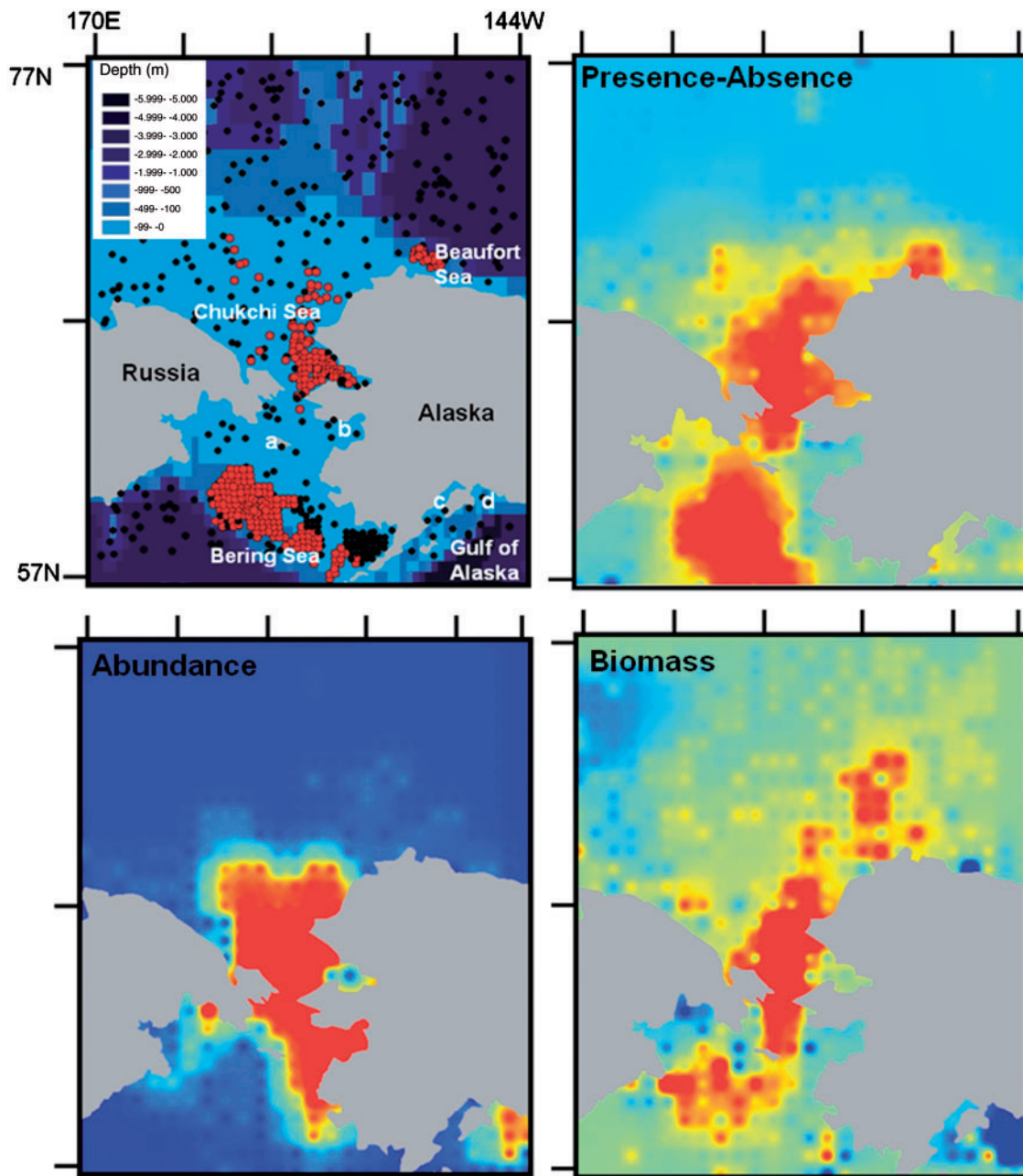
Fig. 1 (Top left panel) Map of study area showing actual sampled locations from which snow-crab data were obtained ("confirmed presence–absence;" red circles) as well as "pseudo-absence" data points (black circles). Map projection is in WGS 84 Mercator (m). Geographic landmarks are labeled as follows: (**a**) St. Lawrence Island, (**b**) Norton Sound, (**c**) Cook Inlet, and (**d**) Prince William Sound. Ensemble model predictions for snow-crab presence–absence (Top right), abundance (Bottom left), and biomass (Bottom right). For all ensemble prediction figures, red areas indicate high index and blue areas indicate low index.

relatively well (Fig. 1), with the exception of the relatively high index of presence in Cook Inlet where no known stocks currently exist. This region is, however, inhabited by closely-related tanner crabs (*C. bairdi*) which overlap in range with snow crabs and likely share many habitat characteristics. This observation thus highlights that the models may describe the wider potential for occurrence, and not necessarily the realized, ecological niche.

The most robust model predictions (RF) place all three temperature variables in the top five most important predictors of presence–absence (Table 3). Salinity and nutrient concentrations also fell among the top five predictors in all three models. The response curves for each of the top predictors from MARS and TreeNet are shown in Fig. 3 (no such graphics are produced by RF as implemented by the Salford Software Suite). The index of crab

Table 3 Accuracy of model predictions (ROC) and importance rankings for the top five most important variables for snow-crab presence/pseudo-absence identified by each of the three modeling algorithms

	MARS c. 85%		TreeNet 89%		Random Forests 91%	
ROC						
Rank	Predictor	Importance (%)	Predictor	Importance (%)	Predictor	Importance (%)
1	Nitrogen concentration (April)	100.00	Infaunal biomass	100.00	Standard deviation sea surface temperature (April)	100.00
2	Standard deviation sea surface temperature (January)	95.24	Chlorophyll-*a* concentration(August)	81.32	Standard deviation sea surface temperature (January)	98.01
3	Chlorophyll-*a* concentration (August)	76.83	Nitrogen concentration (January)	73.86	Sea surface temperature (August)	94.68
4	Sea-ice cover (August)	67.90	Salinity (April)	71.70	Salinity (April)	93.88
5	Phosphate concentration (April)	56.70	Sediment grain size	56.74	Nitrogen concentration (January)	88.53

Table 4 Accuracy of model predictions (AUC) and rankings of importance for the top five most important variables for snow-crab abundance identified by each modeling algorithm

	MARS c. 90%		TreeNet c. 85%	
AUC (gains)				
Rank	Predictor	Importance (%)	Predictor	Importance (%)
1	Phosphate concentration (January)	100.00	Standard deviation of sea surface temperature (August)	100.00
2	Dissolved oxygen (January)	68.02	Infaunal biomass	35.20
3	Total organic carbon in surface sediments	46.68	Total organic carbon in surface sediments	24.68
4	Salinity (April)	38.66	Chlorophyll-*a* concentration (August)	20.10
5	AOU April	18.39	Dissolved oxygen (August)	7.76

Note that the Random Forests does not allow analysis of continuous variables, and is not included here.

Table 5 Accuracy of model predictions (AUC) and rankings of importance for the top five most important variables for snow-crab biomass identified by each modeling algorithm

	MARS c. 75%		TreeNet c. 80%	
AUC (gains)				
Rank	Predictor	Importance (%)	Predictor	Importance (%)
1	Sea surface temperature (August)	100.00	Nitrogen concentration (January)	100.00
2	Phosphate concentration (January)	43.59	Infaunal biomass	82.50
3	Total organic carbon	38.31	Total organic carbon	74.53
4	Nitrogen concentration (January)	29.02	Salinity (April)	54.24
5	Human Footprint	13.58	Solar radiation dose (January)	50.52

Note that the Random Forests does not allow analysis of continuous variables, and is not included here.

presence shows a negative relationship with nitrate concentration (Fig. 3a, MARS). TreeNet identified infaunal biomass (MACROBEN) as the top predictor (Fig. 3b). However, the shape of the relationship suggests that there is a threshold value of infaunal biomass above which the index of crab presence does not change. This relationship may indicate that the presence of infaunal organisms is a proxy for some
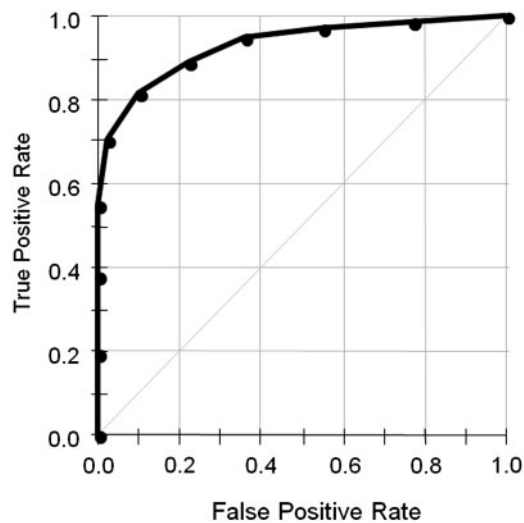
Fig. 2 ROC curve for the MARS model of snow-crab presence–absence. ROC = 85%.

lower limit of food availability, but that the amount of infaunal biomass *per se* does not affect the distribution of crabs. MARS also indicates that sea-ice coverage may influence distribution.

Abundance models

The abundance (and biomass) models are based on slightly fewer data points due to nonquantitative sampling of snow crabs at some sites. However, the performance of the abundance model is equally strong (>85%). MARS shows the highest accuracy (90%). However, the ensemble prediction (Fig. 1) gives a low index of abundance in the fishery region of the Bering Sea, and shows high abundance in the innermost portion of Norton Sound, where snow crabs are not typically abundant (e.g., Chilton et al. 2011). High abundance is also predicted for Prince William Sound, which is inhabited only by
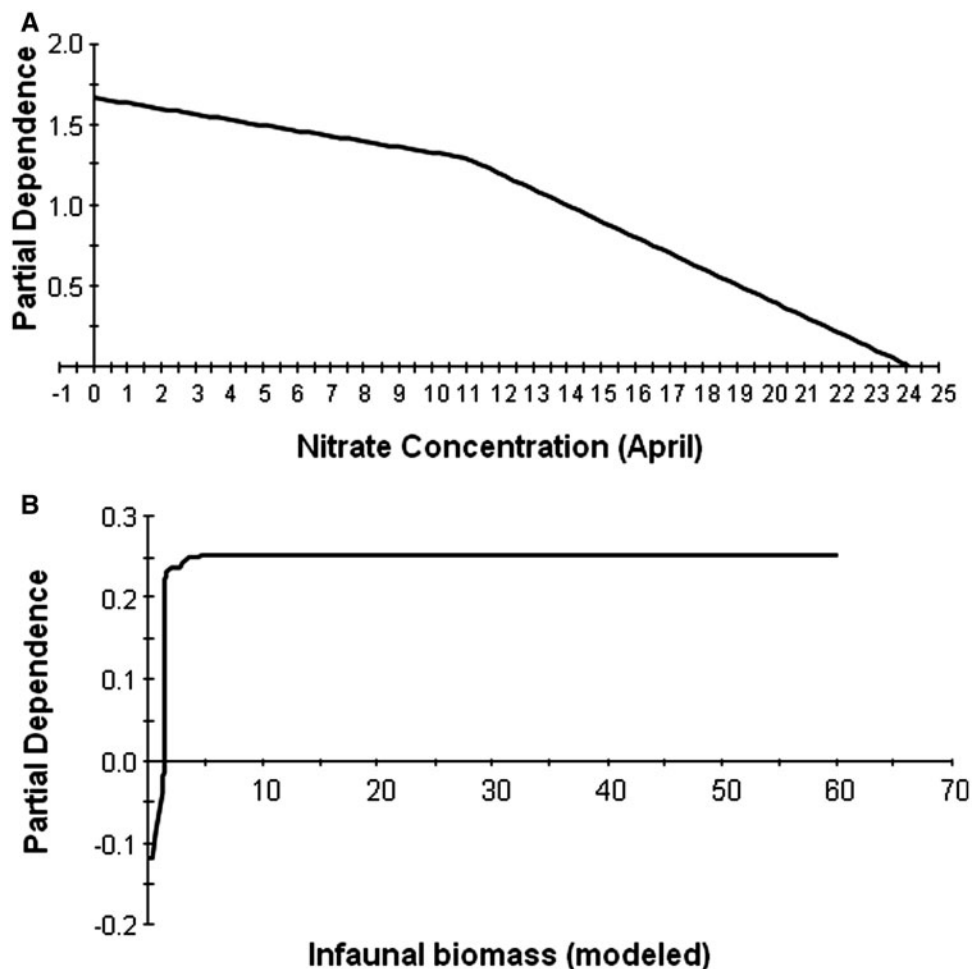
Fig. 3 Response curves for the top predictors for each of two model algorithms, (**A**) MARS, (**B**) TreeNet, for the ensemble average of snow-crab presence/absence. Values on the *x*-axis are taken from GIS-data layers and the *y*-axis represents a relative index of occurrence (RIO).
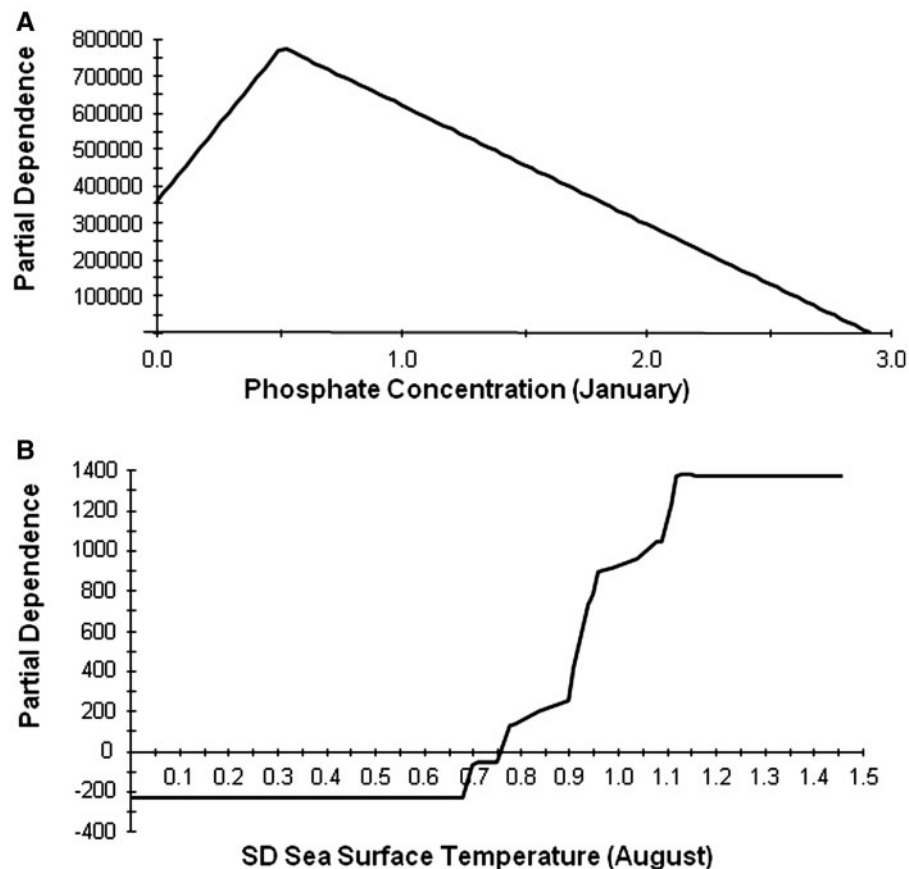
Fig. 4 Response curves for the top predictor for each of the two model algorithms, (**A**) MARS, (**B**) TreeNet, for the model of snow-crab abundance. Values on the x-axis are taken from GIS-data layers and the y-axis represents a relative index of occurrence (RIO).

the congeneric species, *C. bairdi* (Tanner crab). Again, models may reflect the potential rather than the realized niche. Nonetheless, while performance may be sub-optimal, the model predictions represent a gradient in predicted abundance, and thus highlight areas of relatively higher and lower abundances based on the input data. Thus, a low index of abundance does not mean snow crabs are absent, but rather that they are less abundant than in some other areas.

Each modeling algorithm identified a different suite of important predictor variables (Table 4). MARS identified winter nutrient and oxygen concentration as the top two predictors, whereas TreeNet identified variability in summer temperature as the most important variable. Various measures of productivity (Chl-*a*, organic carbon in sediments, and infaunal biomass) ranked second, third, and fourth, with similar importance. Response curves for the top predictor in each model are shown in Fig. 4. Both models did identify organic carbon content of the sediment as an important predictor, and the

response curves for both models indicate a threshold value of ∼1.1% (data not shown).

Biomass models

Although the biomass models yielded the least robust predictions of our three models, they still had gains-based accuracy estimates of c. 80% (TreeNet) and 75% (MARS) (Table 5). The biomass ensemble prediction (Fig. 1) matches known distribution better than the abundance model, picking up the population in the Bering Sea fishery area and showing a low index of biomass in Prince William Sound. However, deep-water areas in the Arctic basin yield a high index of biomass that may be an overestimate, although this region remains relatively unexplored and new data may support or refute this observation. The ensemble model predicts a biomass peak north of St. Lawrence Island, and up through the Bering Strait.

As in the abundance models, both MARS and TreeNet identified organic carbon in surface sediments (modeled) as the third most important
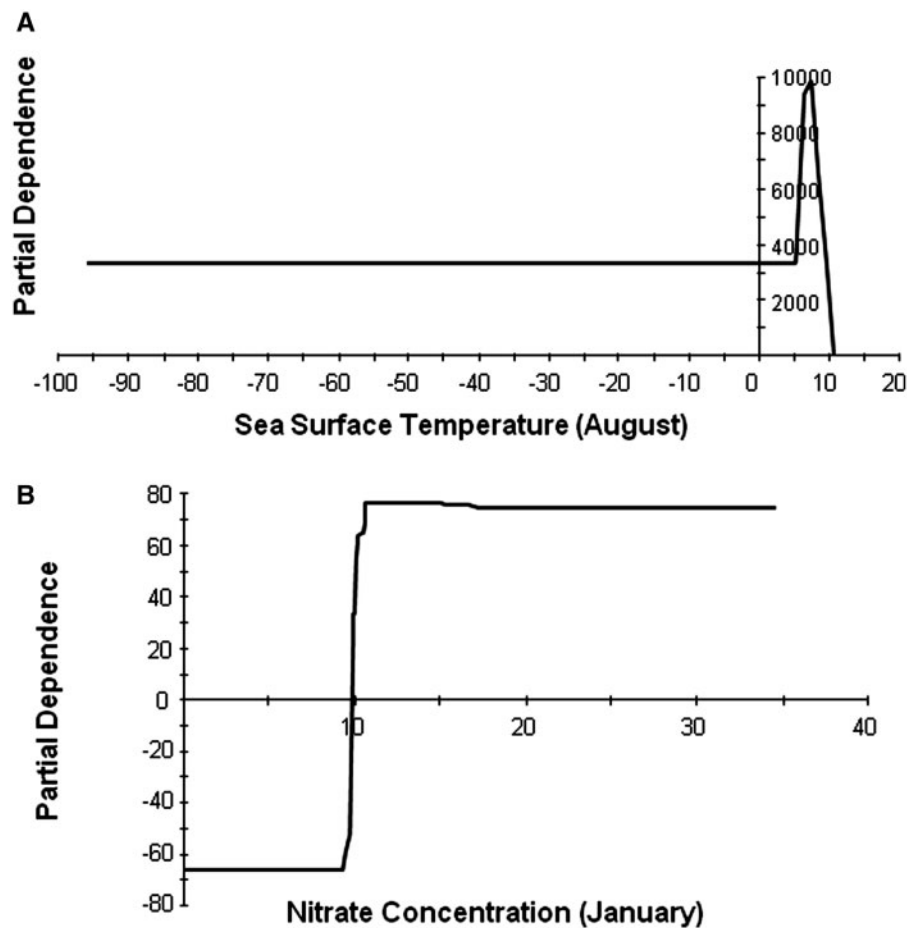
Fig. 5 Response curves for the top predictor in each of the two model algorithms, (**A**) MARS, (**B**) TreeNet, for the ensemble average for the model of snow-crab biomass. Values on the *x*-axis values are taken from GIS-data layers and the *y*-axis represents a relative index of occurrence (RIO).

predictor variable, and the response curves again show a similar threshold value of ~1.1%. The top predictors were also the same as in the abundance models, with MARS ranking sea surface temperature in summer at the top, and TreeNet ranking nutrients (nitrate) in winter at the top. Response curves for these two top predictors are shown in Fig. 5. TreeNet also predicted infaunal biomass (modeled) as the second most important predictor in both the biomass and abundance models. The MARS biomass model was the only one to identify human footprint index as an important predictor variable.

Discussion

Although population dynamics models and individual-based models of larval dispersal are making important contributions to fisheries management, particularly south of the Bering Strait (e.g., Ernst et al. 2005; Parada et al. 2010), we present the first application of a GIS-based open-access ensemble

modeling approach to predicting the distribution of snow crabs, and the first to include populations north of the Bering Strait. All input data, metadata, and predictions are available for public use to serve as informed hypotheses for further improvement and testing. While improvements are needed, these first results are already encouraging and provide a new digital research platform with which to develop additional hypotheses. Two out of three ensemble models (presence–absence, biomass) perform very well internally, as assessed with ROC and AUC/gains criteria that indicate "good" to "very good" accuracy. The presence–absence model also reproduces the known distribution of snow crabs in this region well. The third model (abundance) performs well internally, but lacks some accuracy of spatial prediction, and awaits improvement through addition of new data. At a minimum, the model may help to identify priority information needs. All three models identify a comparable suite of quantitative environmental predictors that constitute a

multi-dimensional niche description for this species. Although this initial description may not be contain every specific niche requirement, our meta-analysis reveals that temperature, nutrient concentrations, and indicators of food availability (infaunal biomass, Chl-a concentration) were among the top predictor variables in all cases.

Observed versus predicted distribution, abundance, and biomass

The presence–absence model (Fig. 1) appears relatively consistent with published accounts of snow-crab occurrence. However, the abundance model (Fig. 1) does not predict large Bering Sea populations, and the biomass model (Fig. 1) is more consistent with actual observations in the Bering Sea (e.g., Lovvorn 2010; Chilton et al. 2011). Taken together, these predictions may support observations of high densities of smaller-sized crabs in the southern Chukchi Sea (Bluhm et al. 2009), and larger crabs in the Bering Sea (Somerton 1981; Paul et al. 1997; Bluhm et al. 2009; Chilton et al. 2009). Adult size is highly variable, but is on average much lower in the Chukchi Sea (~65 mm CW; Paul et al. 1997; Bluhm et al. 2009) than in the EBS (>100 mm CW; Somerton 1981). A recent survey in the Beaufort Sea—the first in several decades—found that females were of comparable size to those in the neighboring Chukchi population, whereas males at some locations reached near-legal size (as large as 119 mm CW) (Rand and Logerwell 2011) and may thus be of interest for commercial exploitation. Interestingly, recent work also suggests increasing biomass of snow crabs in the Chukchi Sea over the past few decades (Feder et al. 2005; Bluhm et al. 2009), and this trend may be reflected in our modeling results. Alternatively, the discrepancies in abundance and biomass models may reflect differences in sampling gear on either side of the Bering Strait; larger otter trawls used in the EBS surveys may be less effective in capturing smaller individuals than are the beam trawls used in the Chukchi Sea. Nonetheless, the data-mining techniques employed here are very robust to noise, and are well-suited to identifying prominent signals even in "messy" data (e.g., Craig and Huettmann 2009).

High biomass in the Beaufort Sea sampling region (Rand and Logerwell 2011) is picked up in the ensemble model (Fig. 1), whereas the abundance model shows a lower index (Fig. 1). High biomass was also predicted for the deeper waters of the high Arctic. Few records exist for this region, but this trend could conceivably be real. Depth at which suitable habitat is found ranges from 4 to 520 m in the Pacific, but large males are found at depths up to 1400 m in the northwestern Atlantic (e.g., Yosho and Hayashi 1994; Lovrich et al. 1995). Recent observations of large males at deeper stations (~500 m) in the Beaufort Sea could reflect a deeper-dwelling population. Snow crabs were not reported in deep waters of the nearby Canada Basin (MacDonald et al. 2010), but the congener Chionoecetes tanneri has been recorded on seamounts in the Gulf of Alaska at depths of ~700 m (Hughes 1981; Raymore 1982).

Characteristics of the ecological niche

The nonlinear multivariate predictors of snow-crab distribution largely included climate-related parameters (temperature), as well as nutrients and indicators of food availability (e.g., phosphate and nitrate concentration, infaunal biomass, organic carbon). Particularly striking was the inclusion of all three temperature variables in the top five of the most important predictors of snow-crab presence/pseudo-absence in the most robust of all the models (RF; Table 3). Growth and reproduction of snow crabs are highly temperature-dependent, and increasing temperatures in the Pacific–Arctic region are thought to be driving a northward contraction of the range of this species (Orensanz et al. 2004). Temperature-dependence in size-at-maturity is thought to be responsible for a latitudinal cline in adult body sizes observed in the Pacific and Atlantic (Somerton 1981; Orensanz et al. 2007; Burmeister and Sainte-Marie 2010). Juveniles are particularly stenothermic, and field and laboratory studies with Atlantic C. opilio suggest they prefer temperatures <1.5°C (Dionne et al. 2003). In the EBS, juvenile recruitment is the strongest over the central shelf, where temperatures are typically <2°C due to the presence of the cold pool (Ernst et al. 2005).

Total organic carbon (TOC; modeled) in surface sediments was among the top predictors in all models for both abundance and biomass, and in all cases response curves indicated a threshold index of ~1.1% organic carbon, above which indices of occurrence did not improve. TreeNet also identified infaunal biomass among the top predictors for all three response variables, showing a similar threshold index response at ~2 gC/m^2 (Fig. 3b). These two variables may be useful in identifying the lower-limits of food availability below which snow crabs are not found. Chionoecetes crabs are generalist feeders known to feed on algae, mollusks, crustaceans, polychaetes, echinoderms, and fishes (e.g., Jewett and Feder 1983; Wieczorek and Hooper 1995;

Lovvorn 2010). Thus, presence of crabs is not likely to be dependent on the distribution of particular prey species, while carbon measures such as those used here may be useful indicators.

Insights into snow-crab ecology may also be obtained from variables that were not consistently among the top five predictors (e.g., depth of the mixed-layer; sediment grain-size). For example, sediment grain-size is considered an important habitat characteristic for many benthic communities (e.g., Feder et al. 1994; Meißner and Darr 2009), particularly infauna, yet this and other studies (e.g., Bluhm et al. 2009) suggest it may be less important for larger epibenthic organisms at the scale examined here.

Directions for future research

Despite ''good'' to ''very good'' accuracies (achieved by machine learning and ensemble modeling), our models still highlight some key needs for additional data. For example, the pooling of response data generated by different methods (e.g., otter trawls versus beam trawls) is a common problem in integrating datasets to assess regional or global patterns (e.g., Gray 2002; Neal et al. 2011). For spatial modeling purposes, confirmed-absence data obtained using appropriate sampling design are also highly desirable, yet are often not included in biological surveys. In addition, while physical characteristics of the ecological niche may be relatively well-represented by our approach, community interactions and ontogenetic movement patterns are not incorporated. In particular, predation by fishes has been suggested as an important mechanism governing snow-crab recruitment (e.g., Zheng and Kruse 2006). Future iterations of this approach may be greatly improved by the incorporation of high-quality data for abundance and biomass of predators. Independent, alternative data for use in assessing models are also urgently needed to improve model accuracy. Our estimates of accuracy based on internal, nonspatial assessments of predictions may not be ideal, but are improved by the use of ensemble model averaging (c.f., Araujo and New 2006). Moreover, increased availability of data in public databases will greatly enhance continued efforts in modeling (see Piepenburg et al. 2011 for an example).

The models presented here provide evidence of the utility of such an approach for developing predictions, as well as for designing field surveys and experiments. They also highlight gaps in information and the need for increased public archiving of field data (e.g., Bluhm et al. 2010). Improved model predictions of snow-crab distribution may be extremely useful in identifying key habitat characteristics that serve as proxy variables for monitoring and assessment of the health of ecosystems or populations, particularly if such variables can be quantified using remote sensing or other methods less costly and labor-intensive than trawling surveys in remote regions. Predictive spatial models are also useful in back-casting applications when there is an interest in constructing historical distributions of species for the purposes of identifying shifts in ranges over ecological and evolutionary time scales (e.g., Drew et al. 2010).

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