

Model-based Fish Distributions and Habitat Descriptions for Arctic Cod (*Boreogadus saida*), Saffron Cod (*Eleginus gracilis*) and Snow Crab (*Chionoecetes opilio*) in the Alaskan Arctic

Model-based Fish Distributions and Habitat Descriptions for Arctic Cod (*Boreogadus saida*), Saffron Cod (*Eleginus gracilis*) and Snow Crab (*Chionoecetes opilio*) in the Alaskan Arctic

June 2021

Authors:

J. M. Marsh

F. J. Mueter

J. Pirtle

Prepared under BOEM Contract M19AC00009

By

College of Fisheries and Ocean Sciences

University of Alaska Fairbanks

17101 Point Lena Loop Road

Juneau, AK 99801

**U.S. Department of the Interior
Bureau of Ocean Energy Management
Sterling, VA**



DISCLAIMER

Study collaboration and funding were provided by the U.S. Department of the Interior, Bureau of Ocean Energy Management (BOEM), Environmental Studies Program, Washington, DC, under Agreement Number M19AC00009. This report has been technically reviewed by BOEM, and it has been approved for publication. The views and conclusions contained in this document are those of the authors and should not be interpreted as representing the opinions or policies of BOEM, nor does mention of trade names or commercial products constitute endorsement or recommendation for use.

REPORT AVAILABILITY

To download a PDF file of this report, go to the U.S. Department of the Interior, Bureau of Ocean Energy Management Data and Information Systems webpage (<http://www.boem.gov/Environmental-Studies-EnvData/>), click on the link for the Environmental Studies Program Information System (ESPIS), and search on 2021-056. The report is also available at the National Technical Reports Library at <https://ntrl.ntis.gov/NTRL/>.

CITATION

Marsh JM , Mueter FJ, Pirtle JL. 2021. Model-based Fish Distributions and Habitat Descriptions for Arctic Cod (*Boreogadus saida*), Saffron Cod (*Eleginus gracilis*) and Snow Crab (*Chionoecetes opilio*) in the Alaskan Arctic. Anchorage (AK): U.S. Department of the Interior, Bureau of Ocean Energy Management. 58 p. Report No.: OCS Study BOEM 2021-056. Contract No.: M19AC00009.

ACKNOWLEDGMENTS

This work was supported by the U.S. Department of Interior, Bureau of Ocean Energy Management (BOEM). A precursor to this project was funded by Alaska Sea Grant and National Oceanographic and Atmospheric Administration (NOAA) Habitat Conservation Division (HCD). NOAA HCD also provided office space and logistical support during the current project.

This study relied heavily on data collected and provided by others. This study would not have been possible without the following individuals that graciously shared biological survey data: Katrin Iken (UAF), Bodil Bluhm (UiT), Rebecca Haehn (NOAA), Robert Lauth (NOAA), Brenda Norcross (UAF), Brenda Holladay (UAF), Caitlyn Forster (UAF), Kimberly Rand (NOAA), Sean Burrell (BOEM), Lauren Divine (Aleut Community of St. Paul Island), Johanna Vollenweider (NOAA), Janet Duffy-Anderson (NOAA EcoFOCI), Libby Logerwell (NOAA EcoFOCI), Allison Dreary (NOAA EcoFOCI), Darcy Neff (AKMAP - NOAA Auke Bay Laboratories Nearshore Fish Atlas of Alaska), Vanessa von Biela (USGS) and Ashley Stanek (USGS).

We thank Steven Lewis (NOAA), Seth Danielson (UAF), Kathryn Hedstrom (UAF), Jacqueline Grebmeier (UMCES CBL), and Chris Jenkins (University of Colorado – DBSeabed) for providing environmental data.

We also would like to show our appreciation for the scientists and crews who aided in the following surveys: Arctic Marine Biodiversity Network (AMBON), Russian-American Long-term Census of the Arctic (RUSALCA), Chukchi Sea Offshore Monitoring in Drilling Area (COMIDA), Chukchi Sea Environmental Studies Program (CSESP), Arctic Ecosystem Integrated Survey (Eis), Arctic (IES) II, Beaufort Pilot Study, BeauFish, Transboundary, Arctic Nearshore Impact Monitoring in Development Area (ANIMIDA), NOAA Auke Bay Laboratories Nearshore Fish Atlas of Alaska (ABL_WCS, ABL_Arctic, AFF, USACE12, ACES, AKCH/AKMAP, Synthesis), ODO, Oshoro-Maru (OSM), Shelf Habitat and Ecology of Fish and Zooplankton (SHELFZ), and USGS Nearshore Fish Surveys in the Beaufort Sea.

Finally, we thank Ned Laman (NOAA), Jeremy Harris (NOAA), Chris Rooper (DFO) and James Thorson (NOAA) for their feedback on statistical analyses and sharing R code.

Contents

List of Figures.....	v
List of Tables.....	vi
List of Abbreviations and Acronyms.....	vii
1 Introduction	1
2 Methods.....	3
2.1 Study Area	3
2.2 Survey Data.....	4
2.3 Habitat Covariates	7
2.4 Species Distribution Models.....	12
2.4.1 Model Optimization	12
2.5 Distribution Mapping.....	13
2.6 Habitat Related Vital Rates.....	13
2.7 Warm Versus Cold Conditions	13
3 Results	15
3.1 Arctic Cod Distribution and Habitat Associations.....	15
3.1.1 Larval Arctic Cod	17
3.1.2 Age-0 Arctic Cod	20
3.1.3 Juvenile Arctic Cod.....	21
3.1.4 Mature Arctic Cod.....	23
3.1.5 Key Habitat Areas	24
3.2 Saffron Cod Distribution and Habitat Associations	25
3.2.1 Larval Saffron Cod.....	26
3.2.2 Age-0 Saffron Cod	27
3.2.3 Juvenile Saffron Cod	29
3.2.4 Mature Saffron Cod	30
3.2.5 Key Habitat Areas	32
3.3 Snow Crab Distribution and Habitat Associations	33
3.3.1 Immature Snow Crab	34
3.3.2 Adolescent Female Snow Crab	36
3.3.3 Adolescent Male Snow Crab	37
3.3.4 Mature Female Snow Crab	39
3.3.5 Mature Male Snow Crab.....	41
3.3.6 Key Habitat Areas	43
3.4 Habitat Related Vital Rates.....	44
3.5 Temporal Shifts Under Warm and Cold Conditions.....	48
3.5.1 Arctic Cod.....	49
3.5.2 Saffron Cod	50
3.5.3 Snow Crab	51
4 Conclusions	53

5 **References** 54

List of Figures

Figure 1.1. US Arctic Management Area (AMA)	3
Figure 2.1. Survey Locations within Arctic Management Area (AMA)	5
Figure 2.2. Near Surface Habitat Covariate Rasters (Explanatory Variables)	9
Figure 2.3. Near Bottom Habitat Covariate Rasters (Explanatory Variables)	10
Figure 2.4. Warm and Cold Years Based on Annual Mean Summer Bottom Temperature.....	14
Figure 3.1. Presence Only Data of Arctic and Saffron Cods	16
Figure 3.2. Predicted Distribution of Probability of Suitable Habitat for Larval Arctic Cod.....	17
Figure 3.3. Response Curves for the Most Influential Habitat Covariates in the MaxEnt Model Predicting Probability of Suitable Habitat for Larval Arctic Cod	18
Figure 3.4. Predicted Distribution of Probability of Suitable Habitat for Age-0 Arctic Cod.....	20
Figure 3.5. Response Curves for the Most Influential Habitat Covariates in the MaxEnt Model Predicting Probability of Suitable Habitat for Age 0 Arctic Cod	21
Figure 3.6. Predicted Distribution of Probability of Suitable Habitat for Juvenile Arctic Cod	22
Figure 3.7. Response Curves for the Most Influential Habitat Covariates in the MaxEnt Model Predicting Probability of Suitable Habitat for Juvenile Arctic Cod	22
Figure 3.8. Response Curves for the Most Influential Habitat Covariates in the MaxEnt Model Predicting Probability of Suitable Habitat for Mature Arctic Cod.....	23
Figure 3.9. Response Curves for the Most Influential Habitat Covariates in the MaxEnt Model Predicting Probability of Suitable Habitat for Mature Arctic Cod.....	24
Figure 3.10. Key Habitat Areas for Larval, Age 0, Juvenile and Mature Arctic Cod	25
Figure 3.11. Predicted Distribution of Probability of Suitable Habitat for Larval Saffron Cod	26
Figure 3.12. Response Curves for the Most Influential Habitat Covariates in the MaxEnt Model Predicting Probability of Suitable Habitat for Larval Saffron Cod.....	27
Figure 3.13. Predicted Distribution of Probability of Suitable Habitat for Age 0 Saffron Cod	28
Figure 3.14. Response Curves for the Most Influential Habitat Covariates in the MaxEnt Model Predicting Probability of Suitable Habitat for Age 0 Saffron Cod	28
Figure 3.15. Predicted Distribution of Probability of Suitable Habitat for Juvenile Saffron Cod	29
Figure 3.16. Response Curves for the Most Influential Habitat Covariates in the MaxEnt Model Predicting Probability of Suitable Habitat for Juvenile Saffron Cod	30
Figure 3.17. Predicted Distribution of Probability of Suitable Habitat for Mature Saffron Cod	31
Figure 3.18. Response Curves for the Most Influential Habitat Covariates in the MaxEnt Model Predicting Probability of Suitable Habitat for Mature Saffron Cod	32
Figure 3.19. Key Habitat Areas for Larval, Age 0, Juvenile and Mature Saffron Cod	33
Figure 3.20. Snow Crab Presence Data by Life Stage (colored dots)	34

Figure 3.21. Predicted Distribution of Probability of Suitable Habitat for Immature Snow Crab	35
Figure 3.22. Response Curves for the Most Influential Habitat Covariates in the MaxEnt Model Predicting Probability of Suitable Habitat for Immature Snow Crab	35
Figure 3.23. Predicted Distribution of Probability of Suitable Habitat for Adolescent Female Snow Crab	36
Figure 3.24. Response Curves for the Most Influential Habitat Covariates in the MaxEnt Model Predicting Probability of Suitable Habitat for Adolescent Female Snow Crab	37
Figure 3.25. Predicted Distribution of Probability of Suitable Habitat for Adolescent Male Snow Crab	38
Figure 3.26. Response Curves for the Most Influential Habitat Covariates in the MaxEnt Model Predicting Probability of Suitable Habitat for Adolescent Male Snow Crab	39
Figure 3.27. Predicted Distribution of Probability of Suitable Habitat for Mature Female Snow Crab	40
Figure 3.28. Response Curves for the Most Influential Habitat Covariates in the MaxEnt Model Predicting Probability of Suitable Habitat for Mature Female Snow Crab	41
Figure 3.29. Predicted Distribution of Probability of Suitable Habitat for Mature Male Snow Crab	42
Figure 3.30. Response Curves for the Most Influential Habitat Covariates in the MaxEnt Model Predicting Probability of Suitable Habitat for Mature Male Snow Crab	43
Figure 3.31. Key Habitat Areas for Immature, Adolescent and Mature Snow Crab	44
Figure 3.32. Potential Growth Rates, Approximate Abundance and Areas of High Productivity for Juvenile Arctic Cod and Juvenile Saffron Cod	46
Figure 3.33. Potential Growth Rates for Age 0 Arctic Cod (Top), Juvenile Arctic Cod (Middle) and Juvenile Saffron Cod (Bottom) During Warm Periods (Left), Cold Periods (Center) and the Difference (Right)	47
Figure 3.34. Differences Between Warm and Cold Periods for Near Surface Habitat Covariates	48
Figure 3.35. Differences Between Warm and Cold Periods for Near Bottom Habitat Covariates	48
Figure 3.36. Arctic Cod Habitat Suitability During Warm and Cold Periods and the Difference.	49
Figure 3.37. Saffron Cod Habitat Suitability During Warm and Cold Period and the Difference	50
Figure 3.38. Snow Crab Habitat Suitability During Warm and Cold Periods and the Difference.....	52

List of Tables

Table 2.1. Survey Data	6
Table 2.2. Life Stage Delineations.....	7
Table 2.3. Habitat Covariates Used as Explanatory Variables in Species Distribution Models.....	11
Table 3.1. Optimized MaxEnt Model Parameters and Habitat Covariate Importance (%). FC is the best feature class combination (l=linear, h=hinge, q=quadratic and p=product).	19

List of Abbreviations and Acronyms

ACC	Alaska Coastal Current
ACW	Alaska Coastal Water
AMA	Arctic Management Area
AUC	Area Under the receiver operating Curve
AW	Anadyr Water
BOEM	Bureau of Ocean Energy Management
BSW	Bering Shelf Water
EBT	Eastern Bottom Trawl
EEZ	Exclusive Economic Zone
EFH	Essential Fish Habitat
FMP	Fisheries Management Plan
NEPA	National Environmental Policy Act
NOAA	National Oceanic and Atmospheric Administration
NPFMC	North Pacific Fisheries Management Council
OCS	Outer Continental Shelf
PSBT	Plumb-Staff Beam Trawl
PSBTA	Modified Plumb-Staff Beam Trawl

1 Introduction

In 2009, the North Pacific Fishery Management Council (NPFMC) developed the Arctic Fishery Management Plan (FMP) that identifies three species as potential targets for future commercial fisheries within the US Arctic Management Area (AMA, **Figure 1.1**): Arctic cod (*Boreogadus saida*), saffron cod (*Eleginus gracilis*) and snow crab (*Chionoecetes opilio*) (NPFMC 2009). These species are key components of the Arctic marine food web, and both Arctic cod and saffron cod are important subsistence resources for coastal communities. The FMP describes preliminary stock assessments for each species and concludes that their low abundances, small size and life history characteristics at that time could not support a fishery. Therefore, commercial fishing is prohibited in the Arctic Management Area until sufficient data are available that may support the authorization of a sustainable fishery, while also ensuring the sustainability of other ecosystem components (NPFMC 2009). As the habitats of these three ecologically important species may be subjected to non-fishing effects, such as oil and gas activity, a better understanding of their current habitat distributions is required for managing living marine resources in the region.

A required component of the Arctic FMP is the identification of Essential Fish Habitat (EFH) that describes the distribution of key life stages of each potential target species to identify areas where a species may be impacted by anthropogenic activity. Current EFH definitions for Arctic species within the AMA are qualitative and are based on limited occurrence data available at the time. The description of EFH for each species in the Arctic FMP consists of polygons drawn around maps of survey distributions irrespective of life-stage. To improve upon these EFH descriptions, preliminary maximum entropy (MaxEnt) models (Phillips et al. 2006) were developed by the lead author with support from Alaska Sea Grant and NOAA's Habitat Conservation Division. These models were applied to combined juvenile and adult life stages to produce maps of potentially suitable habitat for each species.

The current project was funded to help further refine EFH for Arctic cod, saffron cod and snow crab in the Beaufort and Chukchi Seas using the most recent and best available science. In particular, the project incorporated new survey data from the Beaufort Sea, Barrow Canyon, and several nearshore surveys, and survey catch data were partitioned by life stage to develop life stage-specific models of habitat suitability. The resulting habitat maps and species distribution descriptions by life stage will strengthen the ability of natural resource managers to minimize potential impacts from development activities in the Alaskan Arctic nearshore and Outer Continental Shelf (OCS) regions. In addition, this project provides data needed to strengthen the impact assessment process during EFH consultations and National Environmental Policy Act (NEPA) analyses. With these models, we can identify core habitat characteristics most important to the distribution and habitat suitability of larval (where data are available), juvenile and adult Arctic cod, saffron cod and snow crab.

This project further extends the use of static habitat descriptions by including a temporal component that recognizes and accounts for dynamic changes in suitable habitat linked to environmental variability and climate change. As the climate continues to warm and the open water season is extended, increased vessel traffic, oil exploration and extraction, and the development of infrastructure to support these activities may have adverse effects on the three target species in Alaskan Arctic waters. Therefore, it is crucial to have an understanding of their current habitat use and how suitable habitat may expand and contract with

changes in climate and human activity. Rapid warming in the Arctic challenges the very concept of static EFH descriptions. As a result of these challenges, NOAA Division of Habitat Conservation and Alaska Fisheries Science Center Fisheries Biologists have recently recommended changes to the EFH description process to account for climate change. Therefore, we added a temporal component to habitat-linked species distribution models by dividing the biological survey and environmental data into shorter warm and cold time periods to examine potential shifts in the distribution of Arctic cod, saffron cod and snow crab over time by life stage.

A final extension and enhancement of EFH descriptions was explored here by linking vital rates (growth potential and body condition) to habitat characteristics (specifically temperature) for juvenile Arctic cod using recent laboratory studies on temperature-dependent growth (Laurel et al. 2016; 2017). Combining maps of vital rates with species distribution maps over warm and cold periods will increase our understanding of how species respond to climate shifts, consistent with the idea of developing dynamic EFH descriptions where possible. This approach will benefit BOEM by identifying key and vulnerable habitat areas for these species in the Outer Continental shelf regions of the Arctic under changing conditions.

To support the development of life-stage specific habitat models, dynamic models of habitat suitability, and habitat descriptions that account for the temperature dependence of fish growth and condition, our specific objective were to:

1. Identify core habitat characteristics most important to the distribution and habitat suitability of larval (where data are available), juvenile and adult Arctic cod, saffron cod and snow crab.
2. Refine text descriptions of what constitutes EFH for all life stages (larval, juvenile, and adult) of Arctic cod, saffron cod and snow crab in the Beaufort and Chukchi Seas.
3. Refine maps depicting spatial habitat distributions, by life stage (larval, juvenile, and adult), for Arctic cod, saffron cod, and snow crab in the Beaufort and Chukchi Seas.
4. Develop separate maps of distribution and habitat linkages for life stages of saffron cod, Arctic cod and snow crabs during warm and cold periods.
5. Develop maps indicating distribution shifts between warm and cold periods.
6. Develop maps of growth potential for juvenile Arctic cod overall, and separately for warm and cold periods.

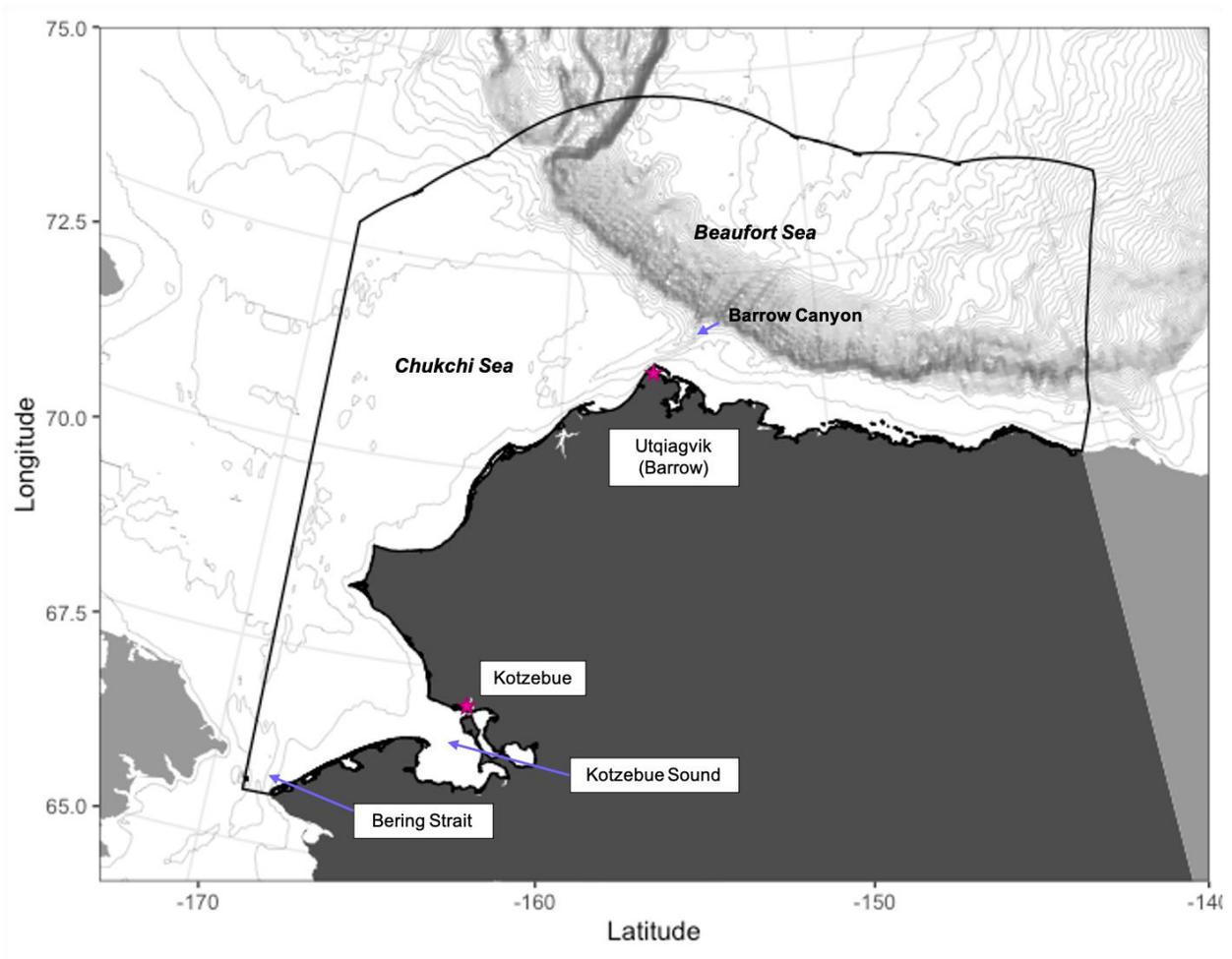


Figure 1.1. US Arctic Management Area (AMA)

Note: The AMA is outlined in black. Isobaths displaying depths of 25 m and from 50 m – 4000 m spaced every 50 m are in grey. Blue arrows are pointing to labeled bodies of water and labeled villages are marked with magenta stars.

2 Methods

2.1 Study Area

The portions of the Beaufort and Chukchi seas within the US Exclusive Economic Zone (EEZ, up to 200 miles offshore) comprise the Arctic Management Area (AMA; **Figure 2.1**). The Chukchi Sea has a broad, shallow shelf with an average depth of 52 m, while the Beaufort Sea has a relatively narrow shelf that extends 50 to 100 km offshore and an average depth of 1,004 m. We constrained the study area to encompass all waters from the coastline to depths less than 1250 m and latitudes less than 73.1° N, as biological survey data was not collected deeper than 1250 m or north of 73.1° N.

Ocean currents, wind, and the timing of ice melt largely influence the productivity within each region. Generally, during the open water season (summer months) currents flow northward through the Bering Strait and are comprised of three main water masses: Alaska Coastal Water (ACW), Bering Shelf Water

(BSW) and Anadyr Water (AW) (Weingartner 1997; Danielson et al. 2017). Along the coast, the relatively warmer and fresher Alaska Coastal Current (ACC) flows northeastward through Barrow Canyon (Weingartner et al. 2005). A large portion of the ACC empties into the Canada Basin (Gong and Pickart 2015), while some water continues eastward along the edge of the Beaufort Shelf where it becomes known as the Beaufort shelfbreak jet. In addition to water flowing in from the Chukchi, the Beaufort Sea receives input from the Mackenzie River (Carmack et al. 2015), Arctic and Atlantic Oceans. Farther offshore in the Beaufort Sea, areas of upwelling occur along the slope in the Beaufort Sea and Barrow Canyon leading to an increase in productivity in the water column (Hill and Cota 2005).

2.2 Survey Data

As there are no longstanding, systemic surveys in the AMA, we compiled biological survey data from numerous ecological research studies conducted between 2000 and 2018 (**Figure 2.1; Table 2.1**) in the US Chukchi and Beaufort Seas. Fish were collected nearshore and offshore, on the seafloor and throughout the water column using a variety of gear. The most common bottom trawl gear type was the plumb-staff beam trawl with a 4.1 m headrope, 5.1 m footrope and a 4 mm mesh cod-end liner in two configurations (PSBT and PSBTA). Regardless of configuration, the catchability remains similar (Norcross et al. 2018). In addition, a much larger 83-112 Eastern Bottom Trawl (EBT) was used during several surveys. The EBT has 25.3 m (83 ft) headropes, 34.1 m (112 ft) footropes and cod-ends with a stretched mesh size of 8.9 cm with and without 3.2 cm mesh liners. In addition to the larval occurrence data from the surveys listed in **Table 2.1**, data on larval saffron cod and Arctic cod caught in bongo nets were provided by the NOAA EcoFOCI group from the ECODAAT database.

Catch data were divided into life stages based on body length measurements for Arctic and saffron cods (Helser et al. 2017; Vestfals et al. 2020) and carapace width for snow crab (Conan et al. 1992; Divine et al. 2019; Table 2.2). Life stage divisions for Arctic and saffron cods included larvae, age-0, late juvenile (1-2 year olds) and mature (**Table 2.2**). Snow crab have sexually dimorphic growth after the immature stage (Conan et al. 1992), so older life stages were divided by sex. Snow crab data were divided into groups of immature individuals, adolescent males, adolescent females, mature males and mature females (Table 2.2). Occurrence data (presence/absence) by species and life stage was compiled at each survey location within the AMA.

For this report, we focused on the largest dataset with the best coverage, which includes presence and absence data from multiple gear types. Occurrence data were used because abundances are not comparable across all gear types. Prior to statistical modeling, we extracted presence location by life stage for each species and then eliminated duplicate data within each 1 km² grid cell. For warm and cold periods, we partitioned the raw data into warm and cold years and then eliminate duplicates by grid cell.

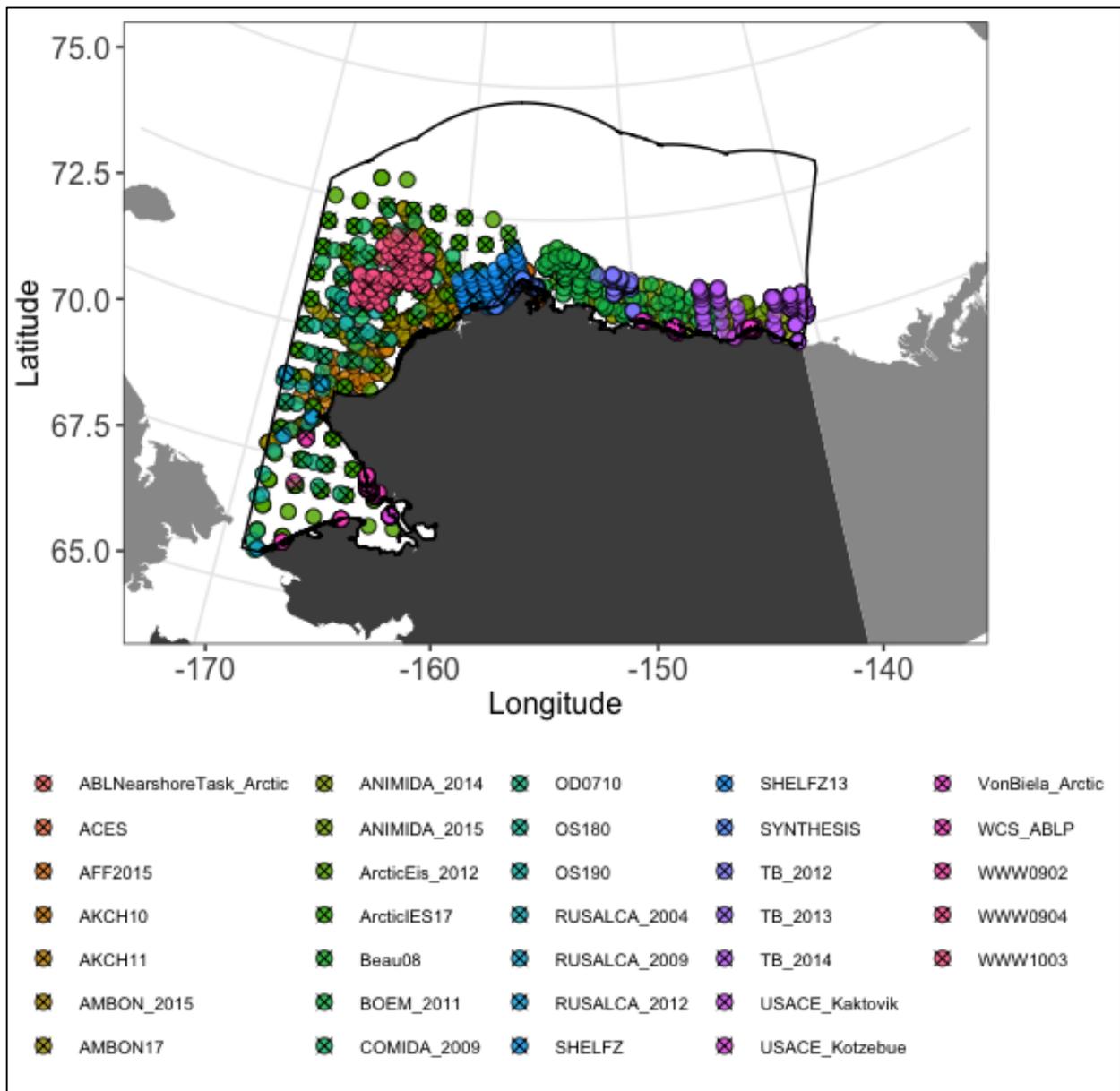


Figure 2.1. Survey Locations within Arctic Management Area (AMA)

Note: The AMA is outlined in black. Species distribution models were based on available occurrence data at these sites. Further survey information found in Table 2.1

Table 2.1. Survey Data

Years	Survey	Cruise Codes	Location	Gear	Hauls P/A	Months
2004, 2005, 2006, 2007, 2009	Synthesis	SYNTH04, SYNTH05, SYNTH06, SYNTH07, SYNTH09	Nearshore	Beach seine	46	Aug, Sept
2007, 2008, 2009	ABL_Arctic	ABL_Arctic07, ABL_Arctic08, ABL_Arctic09	Nearshore	OT	42	Aug, Sept
2012	USACE_Kaktovik	USACE12	Nearshore	Beach seine, OT	18	Aug
2013, 2014,	ACES	ACES13, ACES14	Nearshore	Beach seine, Ring Net, Tucker trawl, otter trawl	65	July, Aug
2015	AFF	AFF15	Nearshore	Beach seine, PSBT	83	July, Aug, Sept
2015, 2016, 2017, 2018	ABL_WCS	ABL_WCS15, ABL_WCS16, ABL_WCS17, ABL_WCS18	Nearshore	Fyke, Beach seine, gillnet, minnow trap, jig	380	Jun, Jul, Aug, Sept
2016	USACE_Kotzebue	USACE16	Nearshore	Beach seine, OT	11	Aug
2017, 2018	USGS	USGS17, USGS18	Nearshore	Fyke, PSBT, Beach seine	77	Jul, Aug
2004, 2009, 2012	RUSALCA	RUSALCA04, RUSALCA09, RUSALCA12	Chukchi	PSBT	13	Aug, Sept
2007	OD0710	OD07	Chukchi	PSBT	21	Sept
2007	OS180	OSM07	Chukchi	PSBT	9	Aug
2008	OS190	OSM08	Chukchi	PSBT	15	Jul
2008	Beaufort Pilot	Beau08	Beaufort	83-112	24	Aug
2009	COMIDA	COMIDA09	Chukchi	PSBT	30	Jul, Aug
2009, 2010	CSESP WWW	WWW809, WWW909, WWW10	Chukchi	PSBT, IKMT	91	Aug, Sept, Oct
2010, 2011	AKCH, AKMAP	AKCH10, AKCH11	Chukchi	PSBT	58	Aug, Sept
2011	BeauFish	BOEM_11	Beaufort	PSBT, IKMT, Bongo	81	Aug, Sept
2012	Transboundary	TB12	Beaufort	CBT, OT, PSBT-A	57	Sept
2012	Arctic Eis	ArcEIS12	Chukchi	PSBT, 83-112	111	Aug, Sept
2013	SHELFZ	SHELFZ13	Chukchi	Beach seine, Pelagic trawl, 83-112	63	Aug, Sept
2013	Transboundary	TB13	Beaufort	CBT, PSBT-A	63	Aug
2014	Transboundary	TB14	Beaufort	PSBT-A	68	Aug, Sept
2014, 2015	ANIMIDA	ANIMIDA14, ANIMIDA15	Beaufort	PSBT-A	47	July, Aug
2015, 2017	AMBON	AMBON15, AMBON17	Chukchi	PSBT-A	143	Aug, Sept
2017, 2019	Arctic IES II	ArcticIES17	Chukchi	PSBT-A	58	Aug

Table 2.2. Life Stage Delineations

Species	Larvae	Early Juvenile (Age-0; Immature)	Late Juvenile	Mature
Arctic cod (Length, mm)	< 30	31 – 70	71 – 120	> 120
Saffron cod (Length, mm)	< 27	28 – 70	71 – 190	> 190
Snow crab (Carapace width, mm)	--	< 34	Males: 35 – 61 Females: 35 – 46	Males: > 62 Females: > 46

2.3 Habitat Covariates

Several ecologically meaningful static and dynamic habitat covariates were considered for inclusion in the species distribution models. These potential explanatory variables were selected based on known ecological associations (Dawe and Colbourne 2002, Norcross et al. 2013, Marsh et al. 2019), past species distribution models for EFH (Laman et al. 2018) and availability.

The bulk of the dynamic habitat covariates were extracted from daily outputs (netcdf files) of the Pacific Arctic Regional Ocean Modeling System (PAROMS; Curchitser et al. 2013) run16 hindcast of Arctic4, provided by S. Danielson, UAF (pers. comm.). Specifically, each file contained a daily average of near surface and near bottom zonal and meridional current velocities, temperature and salinity for each 0.1° latitude and 0.2° longitude grid cell for the entire Arctic from 1980-2018. We extracted daily values from the summer months (July – September) during 2000-2018 by grid cell for each oceanographic variable (salinity, temperature and velocities from the surface or near bottom). We then computed the long-term average by grid cell as well as the minimum, maximum and variability (standard deviation). We chose only the summer months to align with the season when most surveys took place.

Sediment composition data for percent rock, gravel, sand, mud, and organic carbon and sediment size (ϕ = negative \log_2 -transform of grain size (mm)) was provided by C. Jenkins using dbSEABED protocols (Jenkins 1997). The larger the ϕ value the finer the grain size. Further, we downloaded ocean color data from the Moderate Resolution Imaging Spectroradiometer (MODIS) collected during July – September 2002-2018, which can be used as a proxy for primary productivity ($\text{gC}/\text{m}^2\text{-day}$) (Behrenfeld and Falkowski 1997). In addition, bathymetry data were provided by S. Lewis (Alaska Regional Office, Juneau, AK, pers. comm), slope and bathymetric position index (BPI) were derived using the benthic terrain modeler extension in ArcGIS version 10.7 (Wright et al. 2012).

Each habitat covariate was interpolated and converted to 1 km^2 raster grids in R (R core team 2020) using packages *gstat* (Pebesma 2004) and *raster* (Hijmans 2020). We used inverse distance interpolation with an inverse distance power set to 2.5 and the number of nearest observations set to 7 for the dynamic PAROMS covariates. Point data of bathymetric and associated terrain covariates were interpolated to a 100 m^2 grid to create a raster surface using natural neighbor interpolation (Sibson 1981) in ArcMap. Rasters of sediment related variables created with ordinary kriging with exponential variograms for the sediment related covariates (see methods in Jenkins 1997) and provided by Chris Jenkins. The longitude and latitude data for each tow (and all other geographical data for this study) were projected into the Alaska Albers Equal Area Conic projection (standard parallels = 55° and 65° N and center longitude =

154° W) and degrees of latitude and longitude were transformed into eastings and northings for modeling. We cropped the extent of each raster from the Alaskan coast to the outer edge of the AMA. The covariate rasters were further cropped to exclude areas in which we had no survey data (depths > 1250 m and latitudes > 73.1° N).

A pre-selection of covariates was done based on variance inflation factors (< 5) (Zuur et al. 2009) and Pearson's correlations with other variables (< 0.7). Several potential covariates were eliminated during the pre-selection procedure. The independent predictor variables used in the models are described in **Table 2.3**. These independent rasters were combined into two separate raster stacks for near surface (**Figure 2.2**) and near bottom (**Figure 2.3**) sets of explanatory variables.

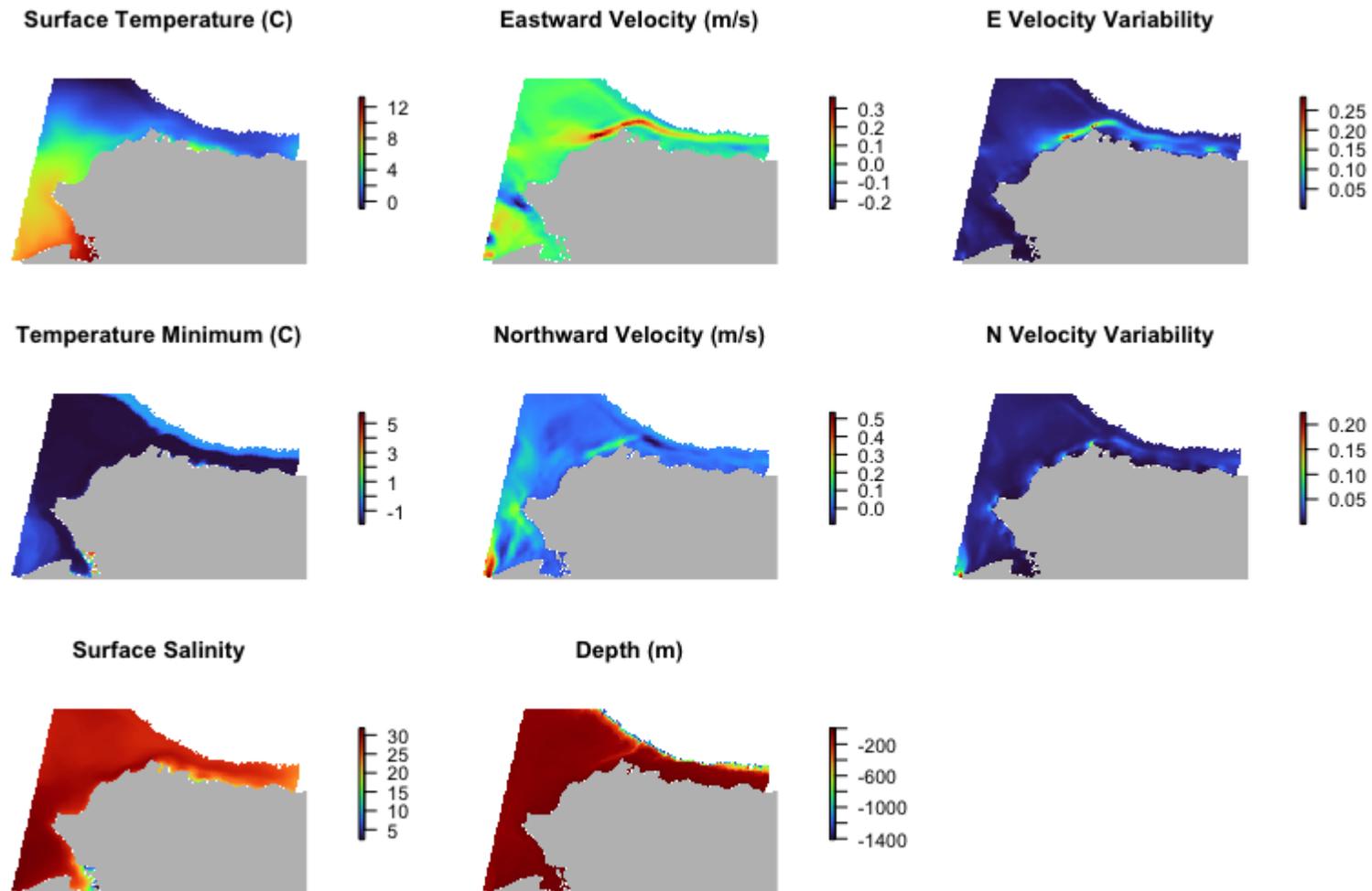


Figure 2.2. Near Surface Habitat Covariate Rasters (Explanatory Variables)

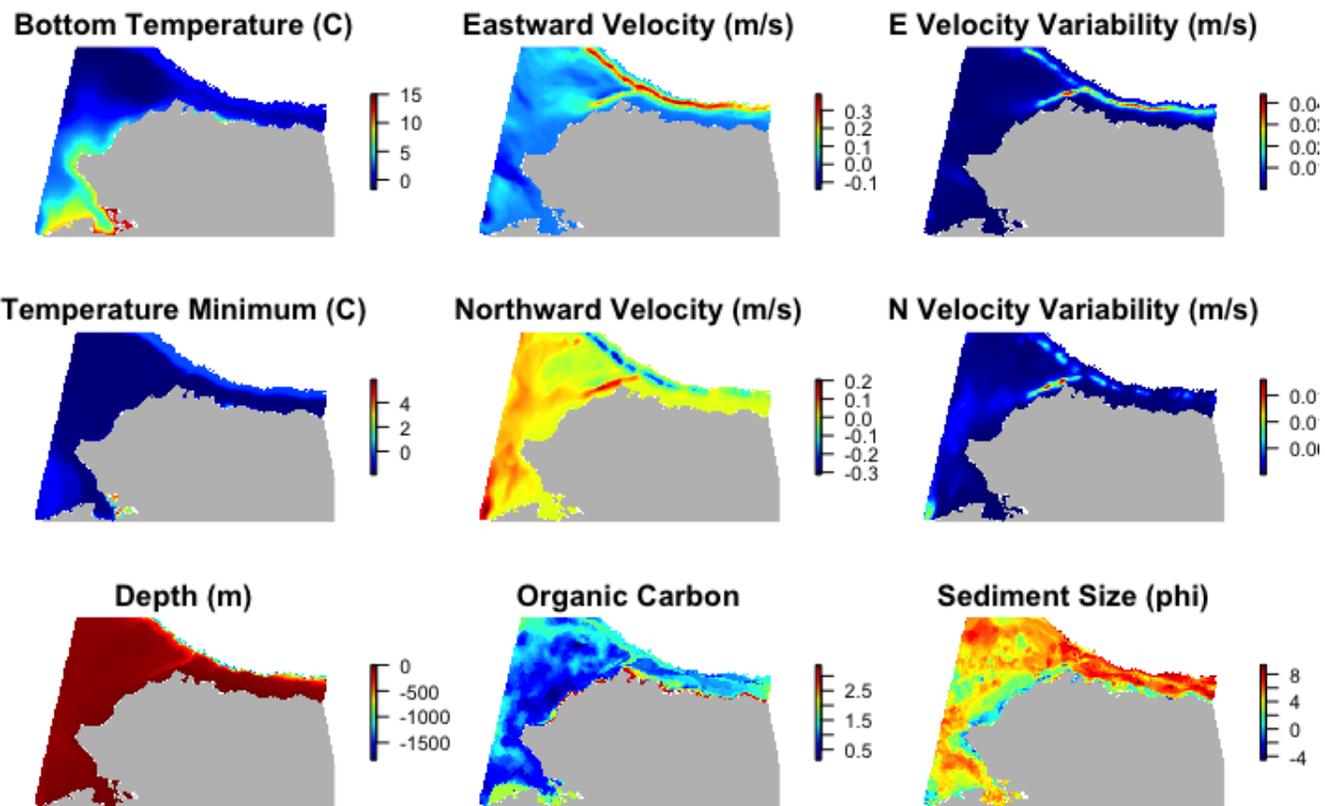


Figure 2.3. Near Bottom Habitat Covariate Rasters (Explanatory Variables)

Table 2.3. Habitat Covariates Used as Explanatory Variables in Species Distribution Models

Variable	Unit	Description of Prediction Raster	Interpolation method
Depth	meters (m)	Bathymetry of the seafloor based on acoustic seafloor mapping data and digitized, position corrected NOS charts (Lewis)	Natural neighbor
Bottom temperature	°C	Seafloor ocean temperature predicted from the Pacific Arctic ROMS (Danielson & Hedstrom) averaged for the bottom 5m across years (2000-2018) during summer months (Jul-Sep)	Inverse distance weighting
Minimum bottom temperature	°C	Seafloor ocean temperature predicted from the Pacific Arctic ROMS (Danielson & Hedstrom) averaged for the bottom 5m across summer months and years (2000-2018)	Inverse distance weighting
Bottom current Eastward velocity	m·sec ⁻¹	Seafloor ocean current components predicted from the Pacific Arctic ROMS (Danielson & Hedstrom) averaged for the bottom 5m across summer months and years (2000-2018)	Inverse distance weighting
Bottom current Northward velocity	m·sec ⁻¹	Seafloor ocean current components predicted from the Pacific Arctic ROMS (Danielson & Hedstrom) averaged for the bottom 5m across summer months and years (2000-2018)	Inverse distance weighting
Bottom current Eastward velocity variability	m·sec ⁻¹	Pooled standard deviation of seafloor ocean current velocities ROMS (Danielson & Hedstrom) from the bottom 5m across summer months and years (2000-2018)	Inverse distance weighting
Bottom current Northward velocity variability	m·sec ⁻¹	Pooled standard deviation of seafloor ocean current velocities ROMS (Danielson & Hedstrom) from the bottom 5m across summer months and years (2000-2018)	Inverse distance weighting
Sediment grain size	phi	Sediment grain size derived from sampling in the Alaskan Arctic and curated in the DBseabed database (Jenkins)	Ordinary kriging
Organic Carbon	--	Percent organic carbon from sampling sediment in the Alaskan Arctic and curated in the DBseabed database (Jenkins)	Ordinary kriging
Longitude*	m	Grid points spaced every 1 km ² within the Arctic Management Area in Alaska Albers Equal Area conic projection	--
Sea Surface temperature	°C	Seafloor ocean temperature predicted from the Pacific Arctic ROMS (Danielson & Hedstrom) averaged for the bottom 5m across years (2000-2018) during summer months (Jul-Sep)	Inverse distance weighting
Minimum bottom temperature	°C	Seafloor ocean temperature predicted from the Pacific Arctic ROMS (Danielson & Hedstrom) averaged for the bottom 5m across summer months and years (2000-2018)	Inverse distance weighting
Surface current Eastward velocity	m·sec ⁻¹	Seafloor ocean current components predicted from the Pacific Arctic ROMS (Danielson & Hedstrom) averaged for the bottom 5m across summer months and years (2000-2018)	Inverse distance weighting
Surface current Northward velocity	m·sec ⁻¹	Seafloor ocean current components predicted from the Pacific Arctic ROMS (Danielson & Hedstrom) averaged for the bottom 5m across summer months and years (2000-2018)	Inverse distance weighting
Surface current Eastward velocity variability	m·sec ⁻¹	Pooled standard deviation of seafloor ocean current velocities ROMS (Danielson & Hedstrom) from the bottom 5m across summer months and years (2000-2018)	Inverse distance weighting
Surface current Northward velocity variability	m·sec ⁻¹	Pooled standard deviation of seafloor ocean current velocities ROMS (Danielson & Hedstrom) from the bottom 5m across summer months and years (2000-2018)	Inverse distance weighting

2.4 Species Distribution Models

To link habitat covariates to species occurrence data, we explored the use of a number of state-of-the-art species distribution models. Due to the limited sampling with disparate gear types in the Alaskan Arctic and to maximize the use of available data, we focused on Maximum Entropy (MaxEnt) Models (Phillips et al. 2006, Elith et al. 2011) for this study. MaxEnt models estimate probability of suitable habitat based on species prevalence (point data) and the co-occurring habitat covariates (explanatory variables, as raster grids) relative to random background points. For each life stage/species combination we extracted predictor values from the habitat covariate raster stacks for each point presence data and for 10,000 random background points within the study area. These data sets were used to train the MaxEnt models and test model performance.

As larval Arctic cod and saffron cod primarily occur in the surface waters, we modeled their distribution using surface habitat variables (**Table 2.3; Figure 2.2**). Age 0 Arctic and saffron cods were modeled with both the bottom and surface covariates and we selected the model with the highest area under the receiver operating curve statistic (AUC, see below for details) for the remaining analysis. The models for the remaining species life stage combinations were run with the bottom covariate raster stack as the explanatory variables.

We modeled the probability of suitable habitat for all species and life stage combinations (**Table 2.2**) using presence only data from all gear types and the habitat covariates listed in Table 2.3 using *maxnet* v.0.1.2 package (Phillips et al. 2017) with a cloglog link run in R (R Core Team 2020). This newer version of the MaxEnt model implemented in *maxnet* reformulates the model as a non-homogenous Poisson process. This enables the user to estimate the relative abundance from the MaxEnt output by adding an additional parameter, the entropy, to the cloglog linear predictor and exponentiating the sum.

2.4.1 Model Optimization

We tuned the MaxEnt Models to optimize model parameters using K-fold cross validation. We randomly partitioned our presence data (from each species life combination) into 5 approximately equal subsets (K-folds). Each K-fold contained the full set of 10,000 background points. The models were trained on data from 4 K-folds, while model performance was tested on the K-fold that was left out. This process was repeated 4 more times, so each K-fold was used in turn as test data. The model performance as measured by two performance criteria (AUC and AICc, as described below) was then averaged over the 5 sets of test data. The parameters that we optimized were the regularization multiplier (beta), which influences model complexity (the lower beta, the more complex the model), and feature classes, which define the relationship between predictor variables. Model performance was evaluated for a range of beta values (0.5 – 3 in increments of 0.5) and feature class combinations (linear, hinge, quadratic and product) using the ENMeval package (Muscarella et al. 2014) in R. We selected the optimized parameter combinations from the model with the lowest Akaike's Information Criterion corrected for small sample sizes (AICc; Burnham and Anderson 2004, Warren and Seifert 2011). When the difference in AIC values was < 2, the more parsimonious model (fewer parameters) was selected (Burnham and Anderson 2002).

In addition to the AICc for the data set, average values for the AUC for the test data and training data were computed in ENMeval as a diagnostic measure. The AUC approximates the probability that a

randomly chosen presence observation would have a higher probability of presence than a randomly chosen absence observation: values > 0.5 are better than chance, > 0.7 are considered acceptable, > 0.8 are good and > 0.9 excellent (Hosmer and Lemeshow 2005). Using the optimized models and the raster habitat covariates we mapped the predicted probabilities of suitable habitat for each species and life stage and plotted the estimated effect of each covariate on habitat suitability.

2.5 Distribution Mapping

For each species and life stage, distribution maps were created based on the predicted probability of suitable habitat from the best model. A given species and life stage was considered absent in grid cells that had a probability of suitable habitat less than 5%. Habitat suitability maps show the smallest possible habitat area encompassing a given percentile of the cumulative habitat suitability over all grid cells. Cells where the probability of suitable habitat for a given species and life stage was greater than or equal to 5% were sorted in decreasing order and areas containing the upper 95%, 75%, 50%, and 25% of habitat suitability values were mapped. We consider areas representing the top 25% to be hotspots with the highest probability of suitable habitat and the top 50% to be the “core habitat”. The 95% level of areas where the species is present corresponds to the definition of EFH area in Alaska (Yoklavich et al. 2010, Sigler et al. 2012). We refer to these areas as key habitat areas rather than EFH areas as updated EFH maps have not yet been approved by the North Pacific Fisheries Management Council.

2.6 Habitat Related Vital Rates

In addition to mapping suitable habitat based on physical habitat characteristics, we created maps depicting estimated growth potential and potential productivity. Regions that are favorable to growth were identified and mapped by linking growth rates to habitat temperature for age 0 and juvenile Arctic cod and juvenile saffron cod. Potential growth rates were estimated and mapped based on laboratory studies of temperature-dependent growth (Laurel et al. 2016; 2017) by using temperature raster data as input to the temperature terms of the growth rate equations. To highlight areas of high potential productivity, we combined estimates of relative abundance with estimates of growth potential. Relative abundances for juvenile Arctic cod and juvenile saffron cod were estimated from the MaxEnt output by adding an additional parameter, the entropy, to the cloglog linear predictor and exponentiating the sum. We then took the product of the abundance and potential growth rate in each grid cell to map habitat-related growth potential and highlight physiologically important areas that may support higher Arctic cod and saffron cod biomass accumulation (higher productivity).

2.7 Warm Versus Cold Conditions

Warm and cold years (2000 – 2018) were determined by calculating the annual summer (July, August and September) mean of bottom temperatures within the Arctic Management Area where depths $< 1250\text{m}$. Years in which the mean summer bottom temperatures were higher than the overall summer mean from 2000 – 2018 were considered warm while those below the mean were considered cold (**Figure 2.4**). Separate habitat covariate sets were created for warm and cold years, respectively. For each species and life stage combination, species distribution was predicted on the warm and the cold covariate sets using the best-fit model for all the data combined. We looked for potential shifts in distribution between warm

and cold years by comparing the area occupied during each period and comparing differences between habitat suitability for each period.

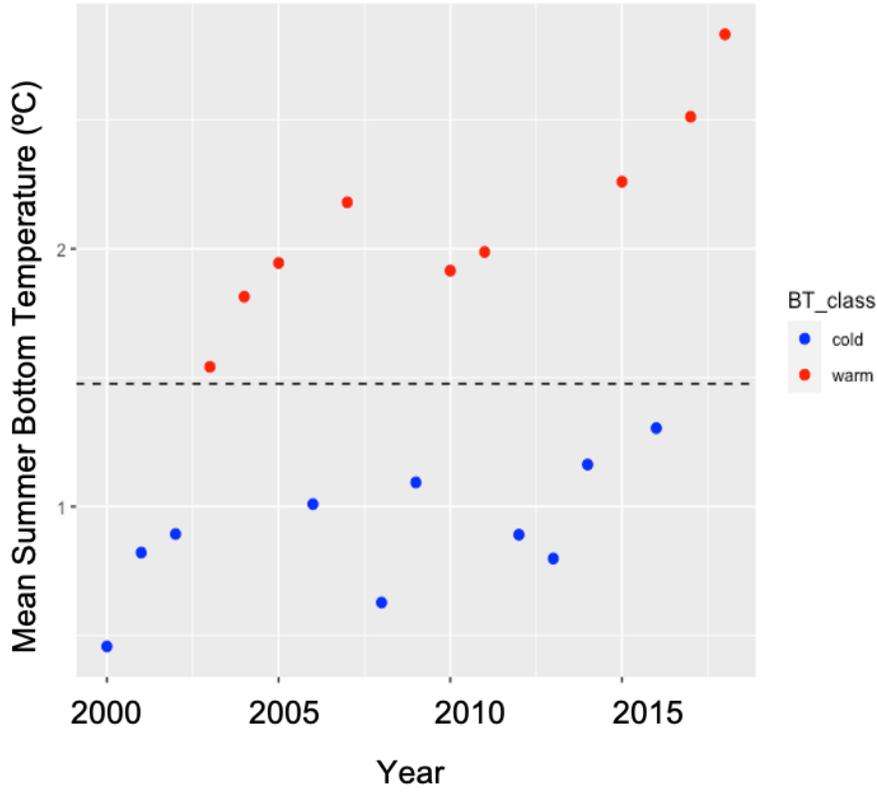


Figure 2.4. Warm and Cold Years Based on Annual Mean Summer Bottom Temperature

Note: The annual and overall (dashed line) mean summer bottoms temperatures were computed from the Pacific Arctic ROMs output within the Arctic Management Area.

3 Results

3.1 Arctic Cod Distribution and Habitat Associations

Arctic cod are the most abundant and widely distributed forage fish in the Alaskan Arctic (Lowry and Frost 1981; Barber et al. 1997; Logerwell et al. 2018) and provide an integral part of the Arctic food web (Welch et al. 1992; Loseto et al. 2009; Matley et al. 2012). They occurred throughout the sampling area in the Chukchi and Beaufort seas (**Figure 3.1**). They are adapted for polar conditions (low light and cold temperatures) with large eyes and the ability to synthesize antifreeze glycoproteins in order to withstand subzero temperatures. Past fisheries have found commercial uses for Arctic cod (Gjøsæter 1995), but due to their integral role in the ecosystem, there are concerns over commercial removals. Currently, commercial fishing is prohibited in the US Arctic due to insufficient data to assess the sustainability of a potential fishery (NPFMC 2009).

Arctic cod have slow growth rates, early maturation, and a short life-span, usually less than 7 years (Bradstreet 1986). They typically spawn under the ice in the middle of winter from December to March with peak spawn time occurring from January to February in Svalbard waters, Barents Sea and the US Arctic (Craig et al. 1982, Lowry and Frost 1983, Korshunova 2012, Vestfals et al. 2021) First maturity can occur as early as 1 year of age for males and 2 years of age for females in the coastal water of the Beaufort Sea (Craig et al. 1982). On average, females reach maturity at 3 (Barents Sea and Alaskan Arctic) years of age, while males tend to mature earlier at 2 years of age (Craig et al. 1982).

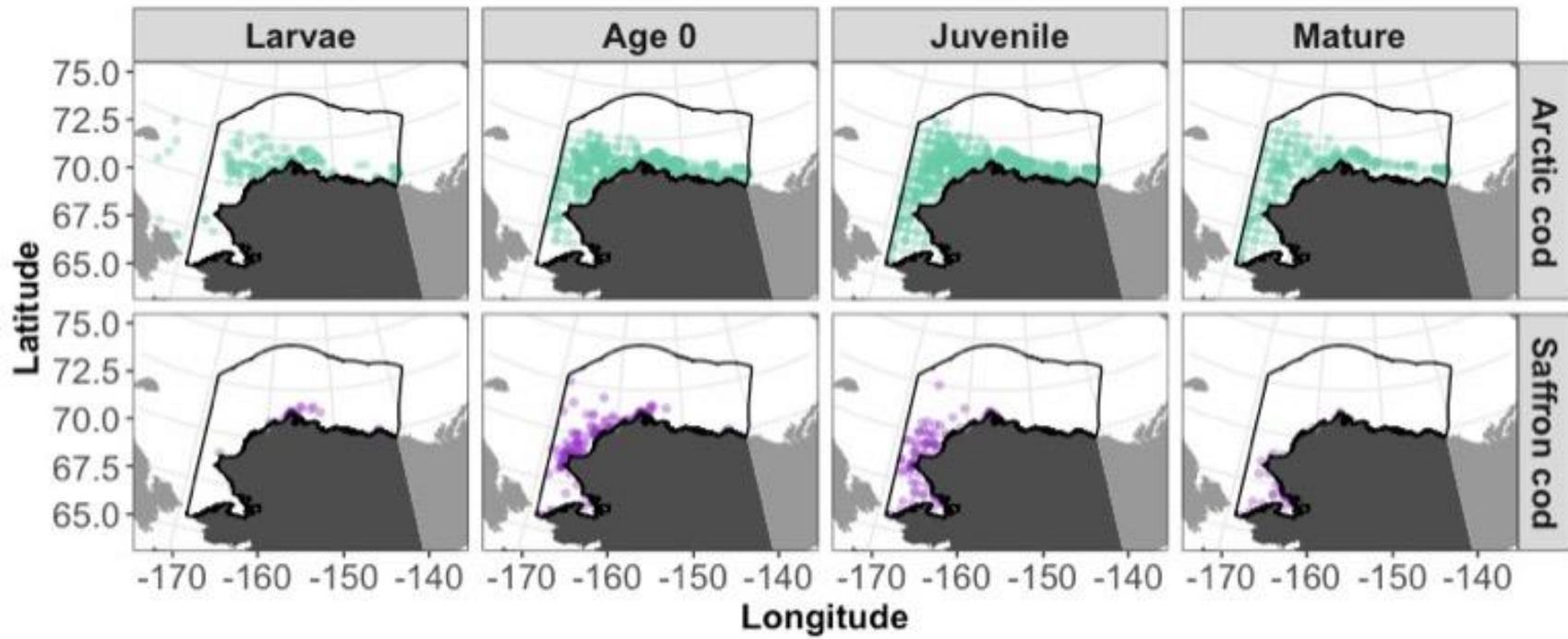


Figure 3.1. Presence Only Data of Arctic and Saffron Cods

3.1.1 Larval Arctic Cod

MaxEnt model predictions of suitable larval Arctic cod habitat was high in the northeast Chukchi Sea, especially along the coast, in coastal areas of the Beaufort Sea, and along the Beaufort shelf break (**Figure 3.2**). There is limited suitable habitat in the southern Chukchi Sea. Depth and surface temperature were the two most important habitat covariates determining the distribution of suitable larval Arctic cod habitat with a relative importance of just over 30% each (**Table 3.1**). The probability of suitable habitat was highest over a narrow range of temperatures, around 2 – 5 °C (**Figure 3.3**). Salinity and eastward velocity were the 3rd and 4th most important habitat variables, with relative importance of around 10% (**Table 3.1**). The probability of habitat suitability declined rapidly at salinities below 28. The model fits were considered good for the training data (AUC = 0.80) and acceptable for the testing data (avg. AUC = 0.76).

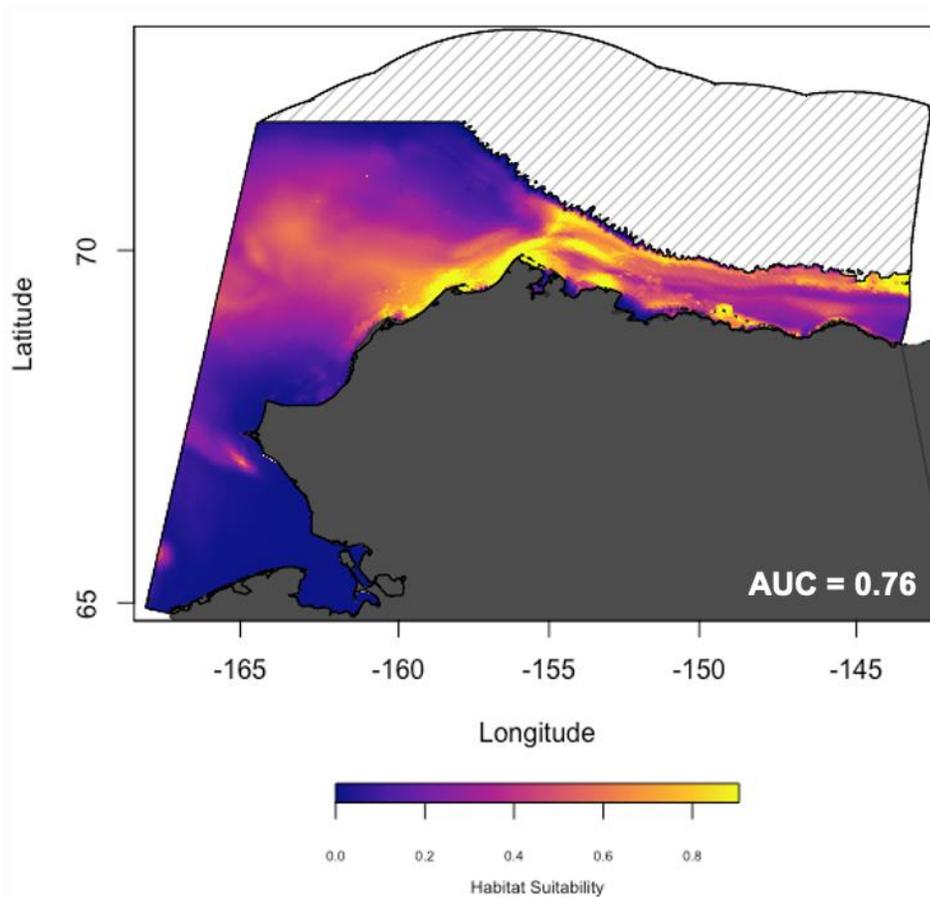


Figure 3.2. Predicted Distribution of Probability of Suitable Habitat for Larval Arctic Cod

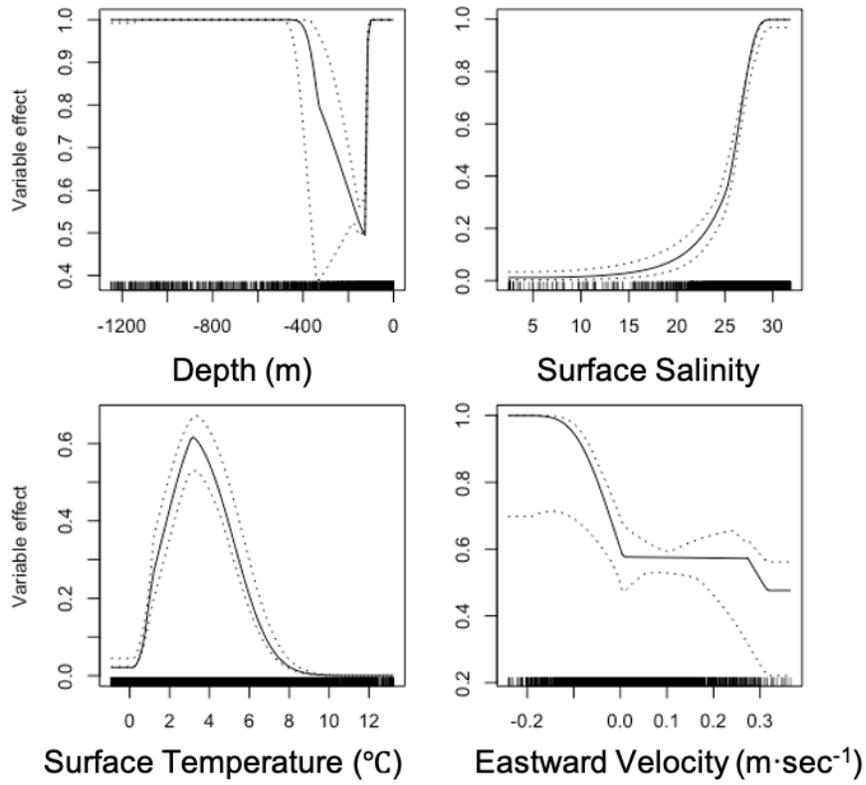


Figure 3.3. Response Curves for the Most Influential Habitat Covariates in the MaxEnt Model Predicting Probability of Suitable Habitat for Larval Arctic Cod

Table 3.1. Optimized MaxEnt Model Parameters and Habitat Covariate Importance (%). FC is the best feature class combination (l=linear, h=hinge, q=quadratic and p=product).

Species - Life stage	Presences	Beta	FC	AUC (SD)	Variable 1 (%)	Variable 2 (%)	Variable 3 (%)	Variable 4 (%)
Arctic cod - Larval	127	1	lpq	0.76 (0.02)	Depth (32)	Surface Temperature (31)	Salinity (11)	Eastward velocity (10)
Arctic cod - Age 0	427	1	lpqh	0.75 (0.02)	Surface Temperature (42)	Depth (27)	Eastward velocity variability (11)	Salinity (8)
Arctic cod - Juvenile	507	0.5	lpq	0.69 (0.03)	Depth (20)	Bottom Temperature (18)	Organic Carbon (16)	Northward Velocity (15)
Arctic cod - Mature	254	1.5	lpqh	0.69 (0.04)	Depth (27)	Organic Carbon (22)	Northward Velocity Variability (17)	Northward Velocity (13)
Saffron cod - Larval	22	2.5	lqh	0.8 (0.07)	Depth (68)	Northward Velocity (15)	SST (14)	--
Saffron cod - Age 0	128	2	lpqh	0.85 (0.02)	Bottom Temperature (32)	Sediment Size (20)	Northward Velocity Variability (17)	Organic Carbon (15)
Saffron cod - Juvenile	80	1.5	lpqh	0.82 (0.05)	Organic Carbon (37)	Bottom Temperature (35)	Min. Bottom Temperature (9)	Eastward Velocity Var. (6)
Saffron cod - Mature	26	2	l	0.86 (0.12)	Bottom temperature (37)	Organic Carbon (25)	Min. Bottom Temperature (21)	Sediment Size (6)
Snow crab - Immature	164	1.5	lp	0.75 (0.03)	Depth (16)	Bottom Temperature (16)	Longitude (12)	Eastward velocity Var (9)
Snow crab – Adolescent Female	142	2	l	0.71 (0.03)	Longitude (31)	Organic Carbon (17)	Bottom Temperature (14)	Northward Velocity Var. (14)
Snow crab – Adolescent Male	178	1.5	lqh	0.68 (0.05)	Longitude (15)	Eastward Velocity (15)	Organic Carbon (14)	Eastward velocity Var (12)
Snow crab – Mat. Female	90	1.5	lqh	0.70 (0.02)	Longitude (21)	Depth (19)	Northward Velocity (17)	Eastward Velocity (12)
Snow crab – Mature Male	122	1.5	lqh	0.71 (0.03)	Longitude (26)	Northward Velocity (15)	Bottom Temperature (12)	Eastward Velocity (9)

3.1.2 Age-0 Arctic Cod

MaxEnt model predictions of suitable age 0 Arctic cod habitat were high in the northeast Chukchi Sea, especially along the coast, around Barrow, and along the Beaufort shelf break (**Figure 3.4**). Similar to larval Arctic cod, there is limited suitable habitat in the southern Chukchi Sea. Surface temperature was the most important (42%) habitat covariate determining the distribution of suitable Age 0 cod habitat (**Table 3.1**). The probability of suitable habitat was highest at lower temperatures (1.5 – 4 °C,) though the overall range was wider than for larval Arctic cod (**Figure 3.5**). Depth, eastward velocity and salinity were the 2nd, 3rd and 4th most important habitat variables with relative importance of around 27%, 11% and 8%, respectively (**Table 3.1**). The probability of habitat suitability increased to a peak at salinities below 29 then declined rapidly (**Figure 3.5**). The model fits were considered acceptable for the training (AUC = 0.77) and testing (avg. AUC = 0.75) data. We reported predictions from the model fit to surface covariates as it resulted in a higher AUC.

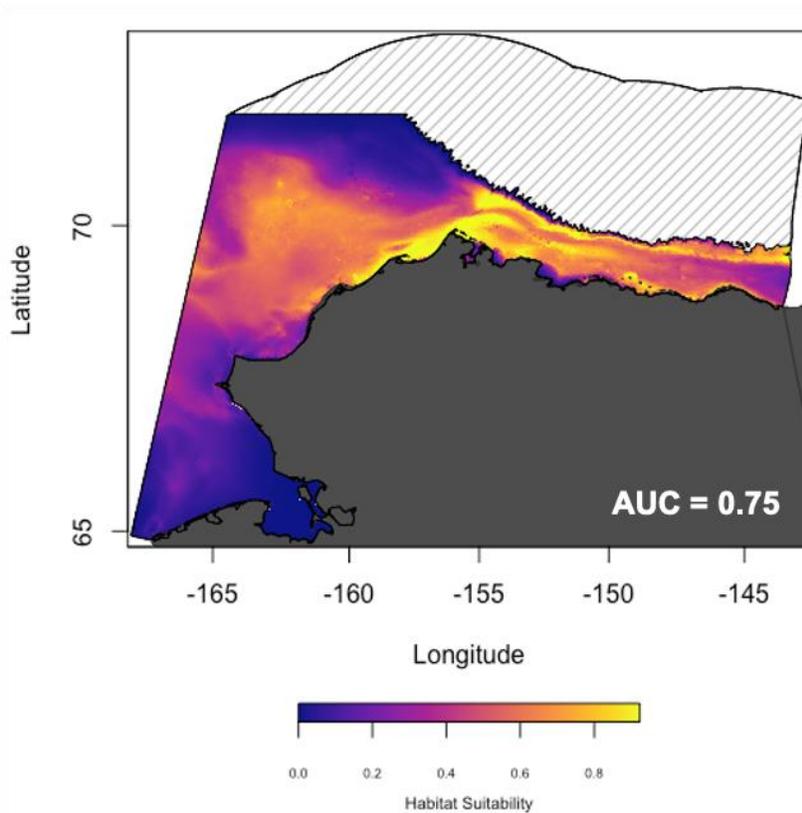


Figure 3.4. Predicted Distribution of Probability of Suitable Habitat for Age-0 Arctic Cod

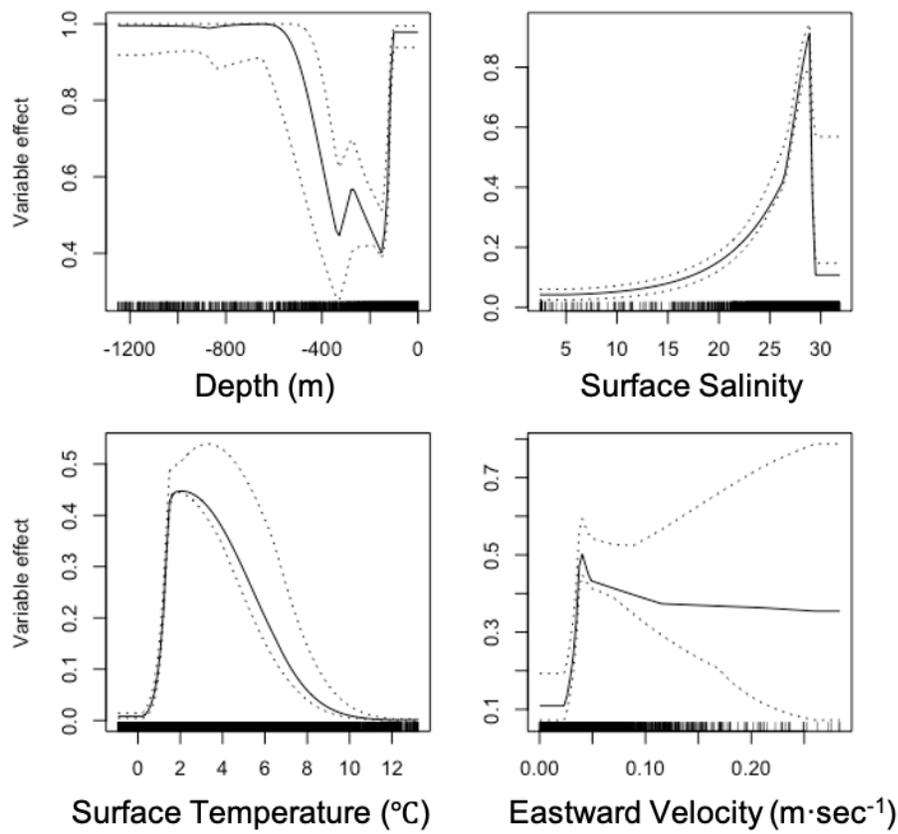


Figure 3.5. Response Curves for the Most Influential Habitat Covariates in the MaxEnt Model Predicting Probability of Suitable Habitat for Age 0 Arctic Cod

3.1.3 Juvenile Arctic Cod

MaxEnt model predictions of suitable juvenile Arctic cod habitat were high in the northeast Chukchi Sea, in Barrow Canyon, and along the Beaufort shelf break (**Figure 3.6**). The probability of suitable habitat is lower along the coast than for the earlier life stages. Depth and bottom temperature were the most important habitat covariates determining the distribution of suitable juvenile Arctic cod habitat (**Table 3.1**). Habitat suitability was high at intermediate depths. The probability of suitable habitat was higher over a larger range of temperatures when compared with earlier life stages (**Figure 3.7**). Percent organic Carbon and northward velocity were the 3rd and 4th most important habitat variables with relative importance of 16% and 15%, respectively (**Table 3.1**). The model fits were considered acceptable for the training data (AUC = 0.71) and better than chance for testing data (avg. AUC = 0.69).

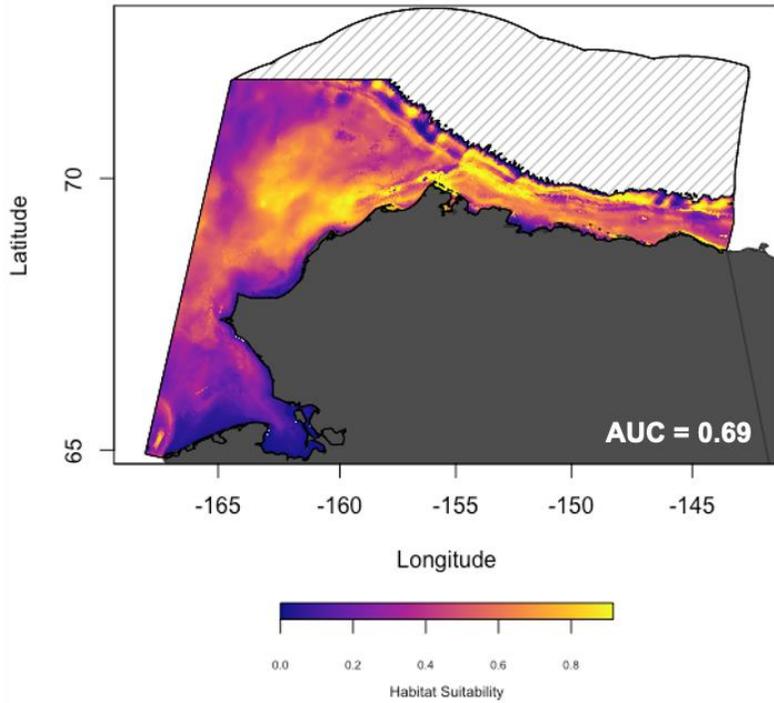


Figure 3.6. Predicted Distribution of Probability of Suitable Habitat for Juvenile Arctic Cod

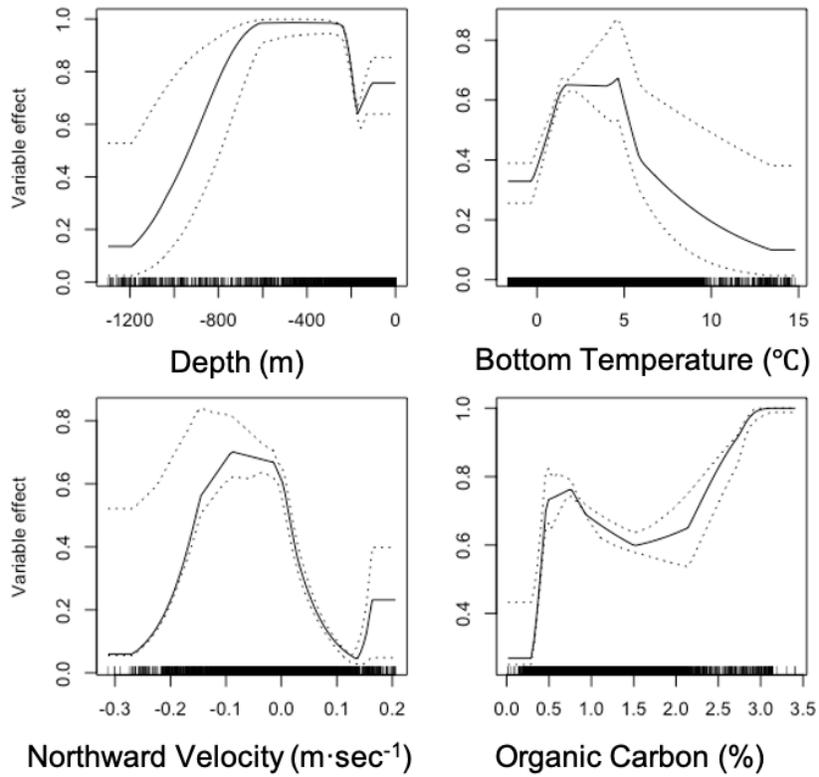


Figure 3.7. Response Curves for the Most Influential Habitat Covariates in the MaxEnt Model Predicting Probability of Suitable Habitat for Juvenile Arctic Cod

3.1.4 Mature Arctic Cod

MaxEnt model predictions of suitable mature Arctic cod habitat were relatively high over a broader area of the Chukchi Sea compared to those for other life stages with the highest habitat suitability in the Bering Strait, Barrow Canyon, and along the Beaufort shelf break (**Figure 3.8**). The probability of suitable habitat is lower along the coast than for the earlier life stages (including juvenile Arctic cod). Depth, organic carbon, northward velocity variability and northward velocity were the 4 most important habitat covariates determining the distribution of suitable mature Arctic cod habitat (**Table 3.1**). Habitat suitability was highest at intermediate depths from 200 – 500 m (**Figure 3.9**). Northward velocity variability and northward velocity were the 3rd and 4th most important habitat variables with relative importance of 17% and 13%, respectively (**Table 3.1**). Though not in the top 4, bottom temperature was the 5th most important habitat covariate with an importance of 9%. The probability of suitable habitat was higher over a larger range of temperatures when compared with earlier life stages (**Figure 3.9**). The model fits were considered acceptable for the training data (AUC = 0.73) and better than chance for testing data (avg. AUC = 0.69).

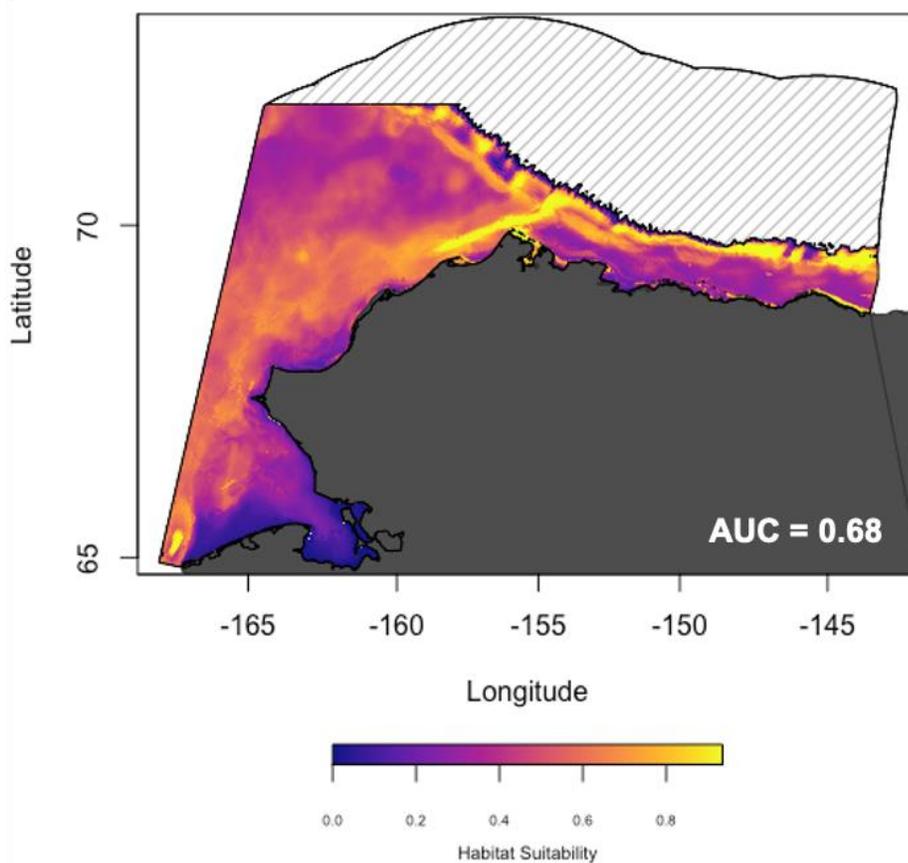


Figure 3.8. Response Curves for the Most Influential Habitat Covariates in the MaxEnt Model Predicting Probability of Suitable Habitat for Mature Arctic Cod

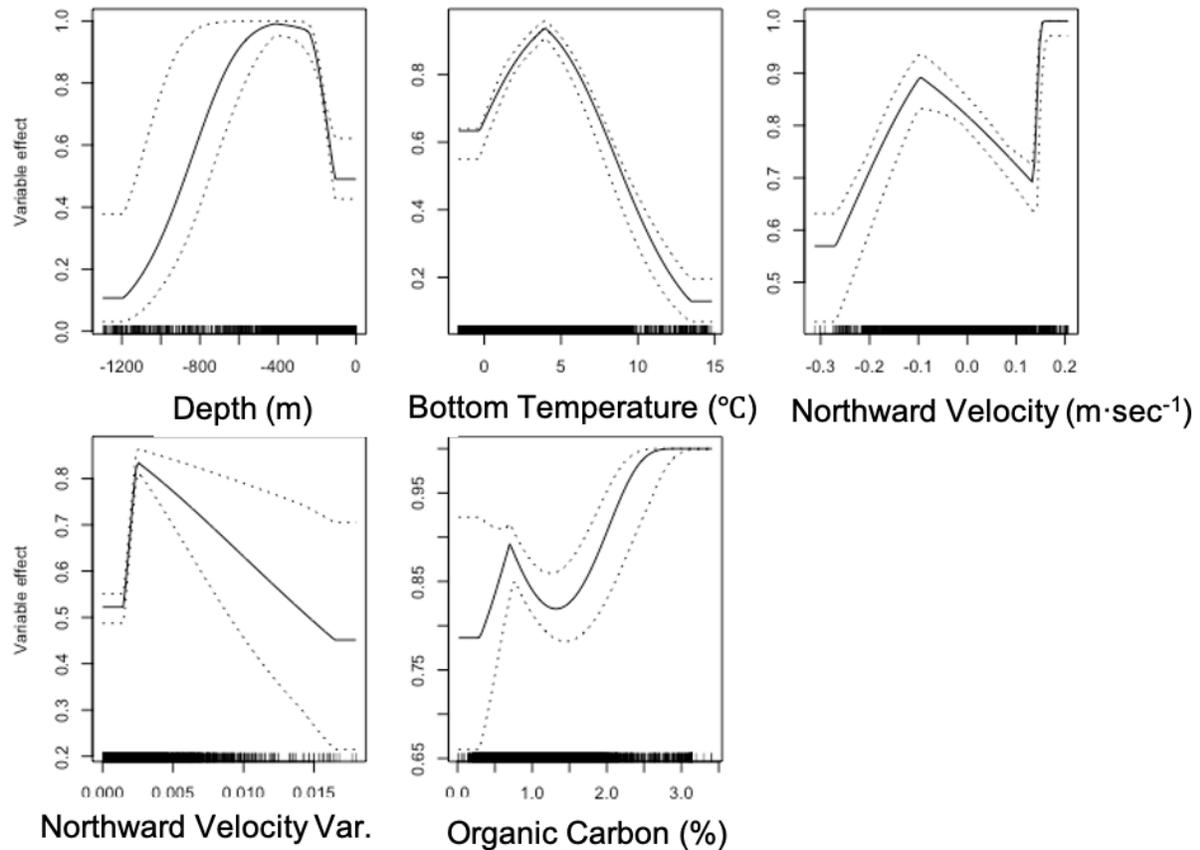


Figure 3.9. Response Curves for the Most Influential Habitat Covariates in the MaxEnt Model Predicting Probability of Suitable Habitat for Mature Arctic Cod

3.1.5 Key Habitat Areas

The area of suitable habitat increases with ontogeny for Arctic cod, as the probability of suitable habitat becomes less dependent on lower temperatures, particularly in the southern Chukchi Sea (**Figure 3.10**). The area upstream of Barrow Canyon, Barrow Canyon, and the Beaufort shelf break are hotspots for all life stages. It should be noted that the life stages are vertically stratified as larval and age 0 Arctic cod occur near the surface, while juvenile and mature Arctic cod tend to occur deeper in the water column or on the bottom. Larval and age 0 Arctic cod habitat hotspots are mainly concentrated in the northeast Chukchi Sea to the coast and in the western Beaufort Sea from the shelf break to the coast (**Figure 3.10**). Arctic cod seem to move offshore with maturity in the Beaufort Sea.

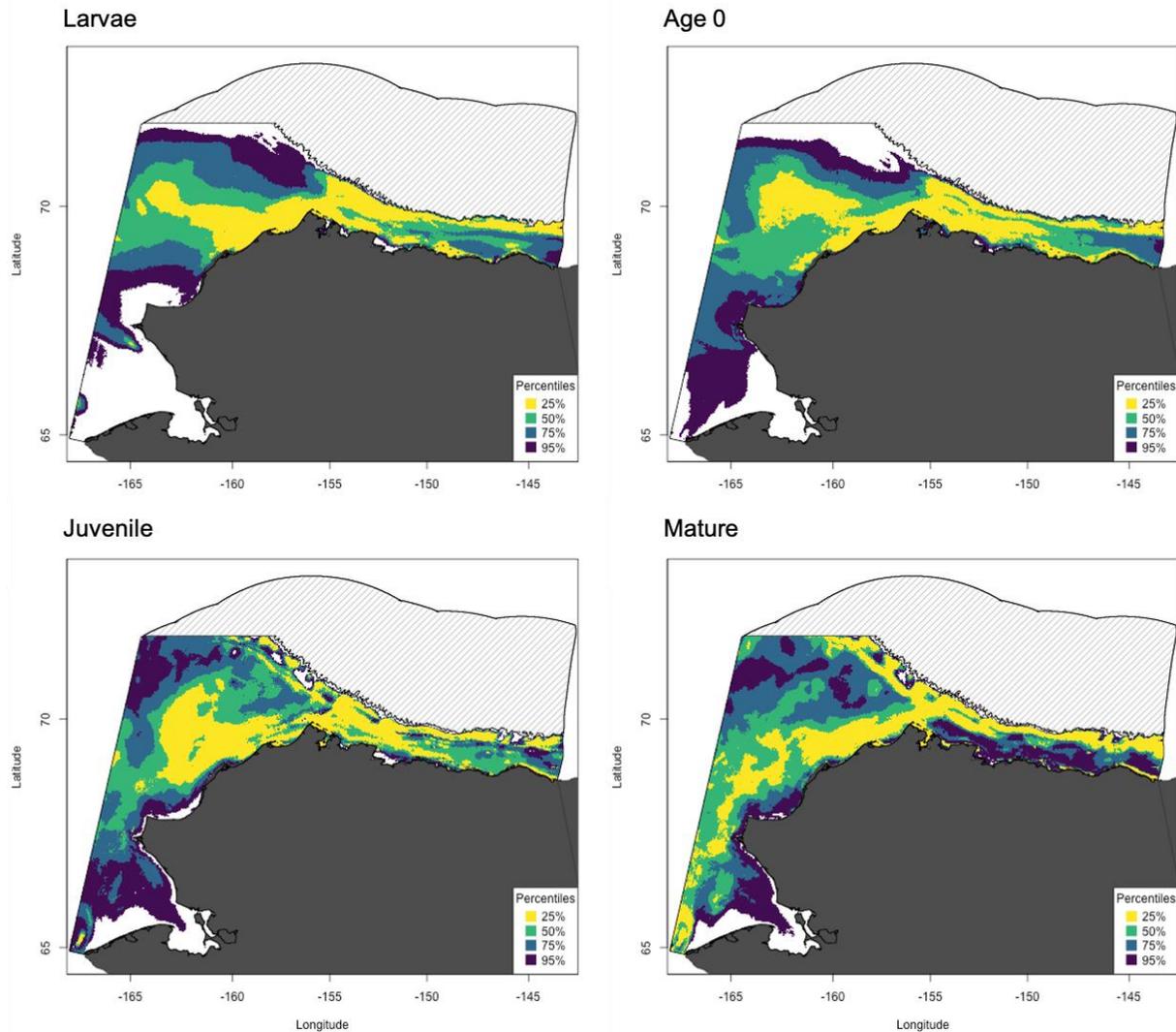


Figure 3.10. Key Habitat Areas for Larval, Age 0, Juvenile and Mature Arctic Cod

3.2 Saffron Cod Distribution and Habitat Associations

Saffron cod are abundant in coastal waters of the North Pacific Ocean and into the Arctic, typically occurring at depths from 0 – 50 m (Allen and Smith 1988) with a maximum depth of 300 m (Cohen et al. 1990). This is consistent with the survey prevalence data (**Figure 3.1**). The growth rate of juvenile saffron cod exceeds that of Arctic cod at temperatures above about 10 °C and their growth continues to increase at higher temperature (Laurel et al. 2016). Similarly, saffron cod adults have a faster growth rate and larger maximum length compared to Arctic cod (Helser et al. 2017). They have a maximum length of 60 cm, and typically mature at 2 - 3 years. Like Arctic cod, saffron cod have the ability to synthesize antifreeze glycoproteins and can withstand subzero temperatures as low as -1.8 C (Hargens 1972). Although less energy-dense than Arctic cod, they are an important component of the food web and are often found in the diets of ringed seals (*Phoca hispida*) in the Chukchi Sea (Lowry et al. 1980).

3.2.1 Larval Saffron Cod

MaxEnt model predictions of suitable larval saffron cod habitat were highest along the coast in the northeast Chukchi Sea and into the Beaufort Sea (**Figure 3.11**). There is limited suitable habitat offshore. Depth was by far the most important habitat covariate determining the distribution of suitable larval saffron cod habitat with a relative importance of 68% (**Table 3.1**). The probability of suitable habitat was highest at the shallowest depths and decreased rapidly below about 100 m (**Figure 3.11**). Northward velocity and surface temperature were the 2nd and 3rd most important habitat variables, with relative importance of around 15% and 14%, respectively (**Table 3.1**). The probability of habitat suitability was highest in waters with a strong northward component, probably reflecting a high prevalence in the coastal current over Barrow Canyon, and decreased with increasing surface temperatures above around 2 °C (**Figure 3.11**). The model fits were considered good for the training (AUC = 0.85) and testing (avg. AUC = 0.8) data.

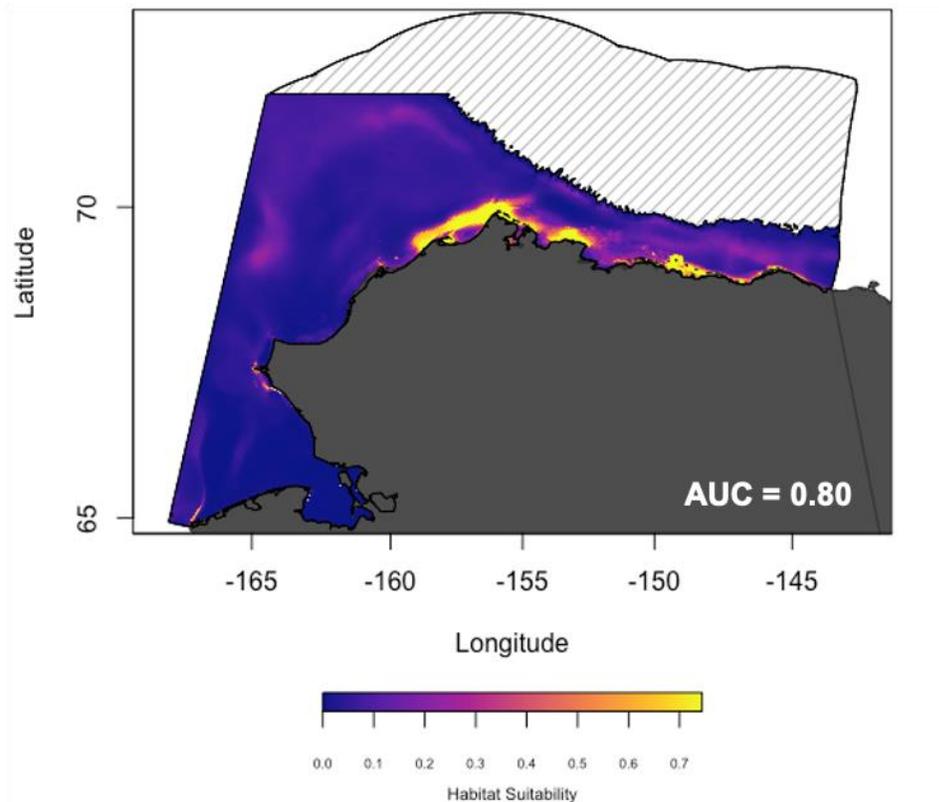


Figure 3.11. Predicted Distribution of Probability of Suitable Habitat for Larval Saffron Cod

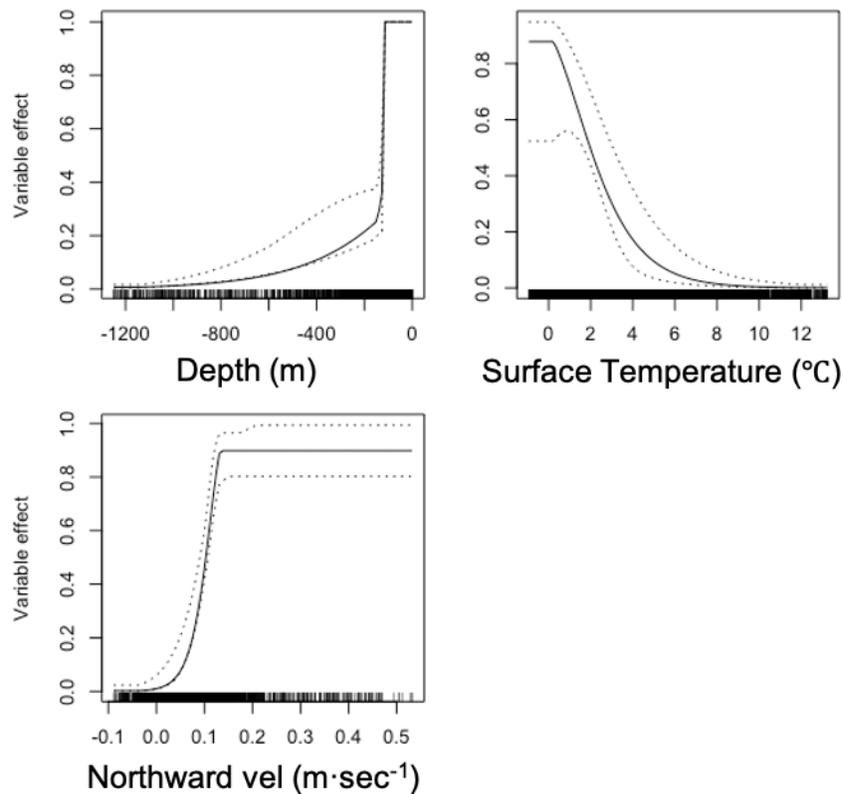


Figure 3.12. Response Curves for the Most Influential Habitat Covariates in the MaxEnt Model Predicting Probability of Suitable Habitat for Larval Saffron Cod

3.2.2 Age-0 Saffron Cod

MaxEnt model predictions of suitable age 0 saffron cod habitat was highest along the Chukchi Sea coast (excluding Kotzebue Sound) to Barrow (**Figure 3.13**). A high probability of suitable habitat extended offshore in the Chukchi Sea and in Bering Strait. Bottom temperature was the most important (32%) habitat covariate determining the distribution of suitable Age 0 saffron cod habitat (**Table 3.1**). The probability of suitable habitat increased with increasing temperatures and was highest above 8 °C (**Figure 3.14**). Sediment size, northward velocity variability and organic carbon were the 2nd, 3rd and 4th most important habitat variables with relative importance of around 20%, 17% and 15%, respectively (**Table 3.1**). The probability of habitat suitability decreased with finer sediment size (larger phi), increased with the sediment organic carbon content, and was higher at moderate levels of northward current variability (**Figure 3.14**). The model fits were considered good for the training (AUC = 0.88) and testing (avg. AUC = 0.85) data. We reported predictions from the model fit to the bottom covariates, as it resulted in a higher AUC.

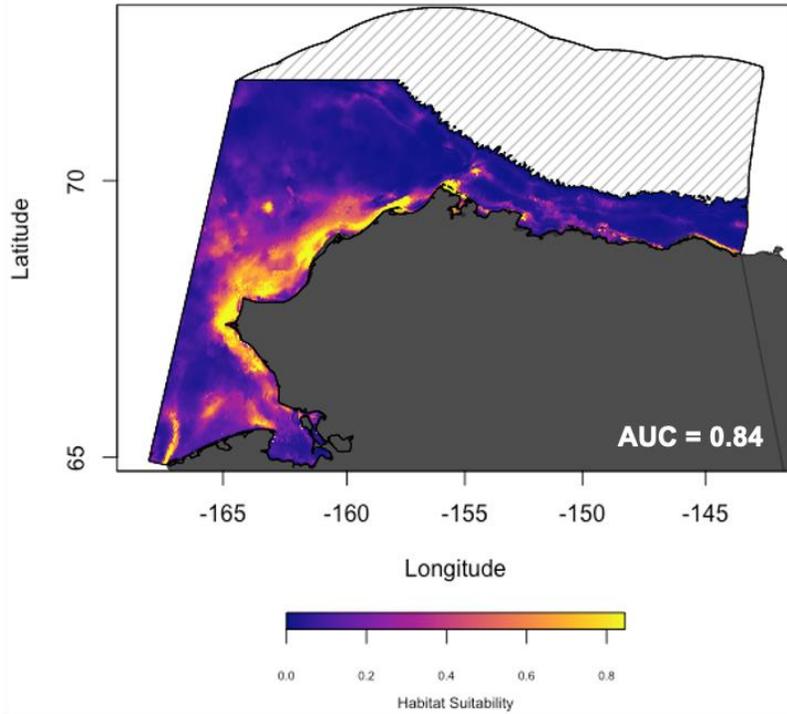


Figure 3.13. Predicted Distribution of Probability of Suitable Habitat for Age 0 Saffron Cod

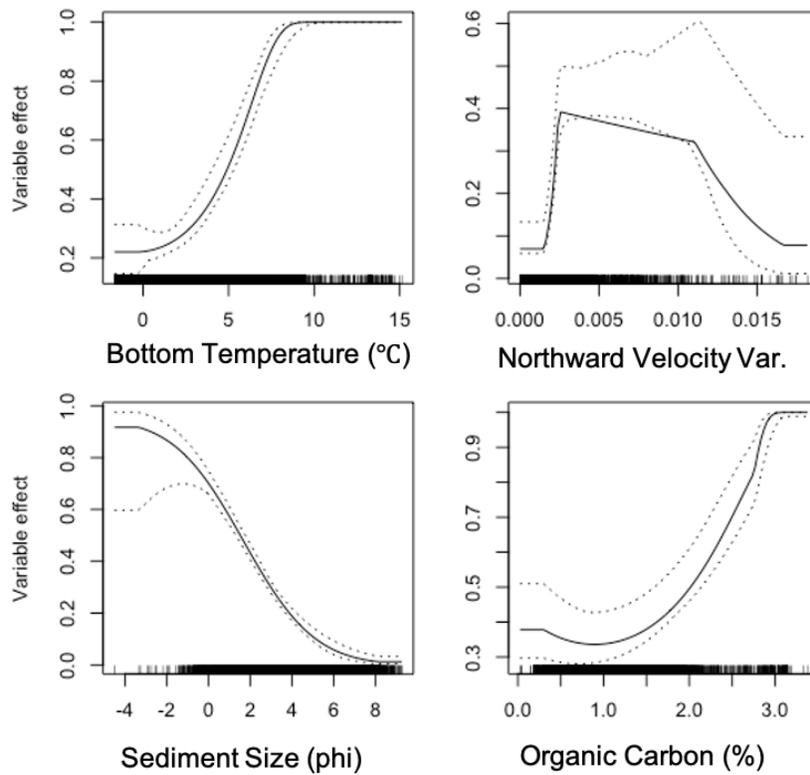


Figure 3.14. Response Curves for the Most Influential Habitat Covariates in the MaxEnt Model Predicting Probability of Suitable Habitat for Age 0 Saffron Cod

3.2.3 Juvenile Saffron Cod

MaxEnt model predictions of suitable age 0 saffron cod habitat was highest along the Chukchi Sea coast (excluding Kotzebue Sound) to Barrow (**Figure 3.15**). A high probability of suitable habitat extended offshore in the central Chukchi Sea and from the Bering Strait north. Organic Carbon and bottom temperature were the most important (37% and 35%, respectively) habitat covariates determining the distribution of suitable juvenile saffron cod habitat (**Table 3.1**). Similar to age 0 saffron cod, the probability of suitable habitat increased with increasing temperatures and was highest above 8 °C (**Figure 3.16**). The model fits were considered good for the training (AUC = 0.86) and testing (avg. AUC = 0.83) data.

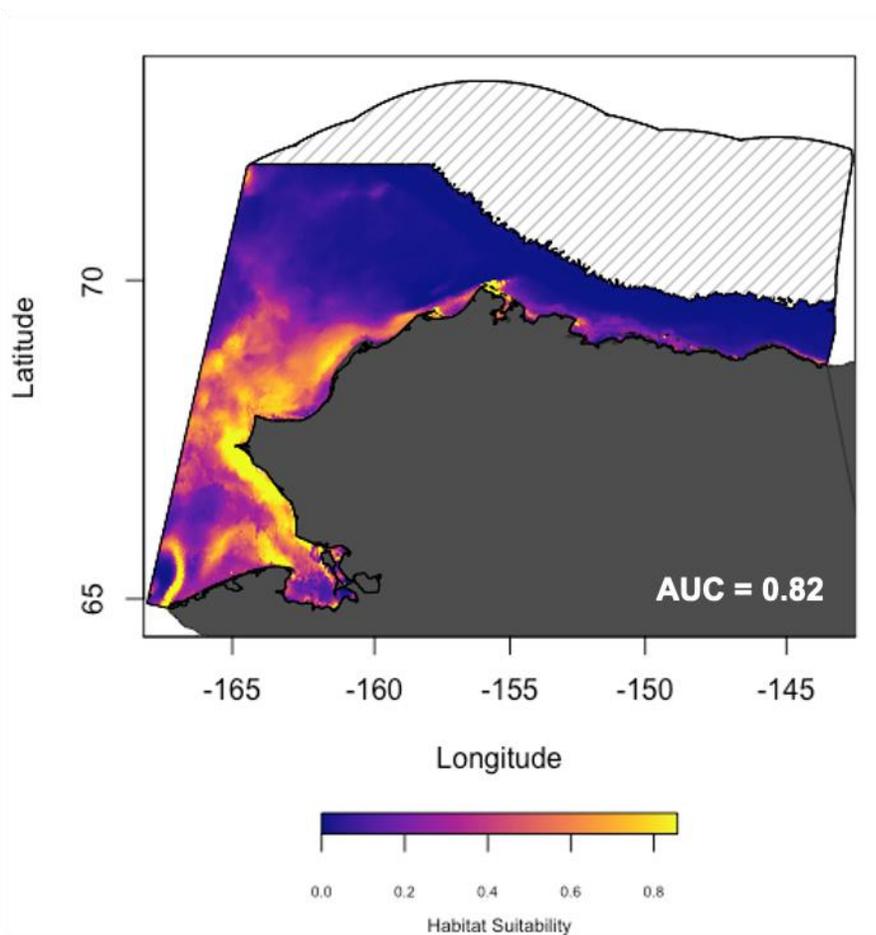


Figure 3.15. Predicted Distribution of Probability of Suitable Habitat for Juvenile Saffron Cod

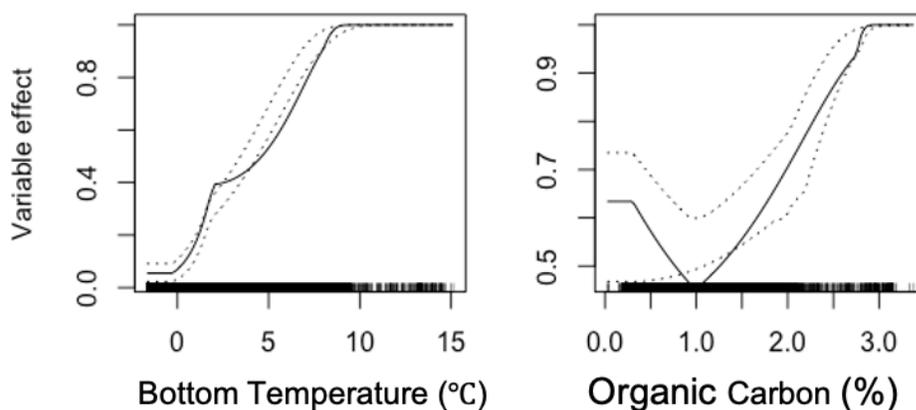


Figure 3.16. Response Curves for the Most Influential Habitat Covariates in the MaxEnt Model Predicting Probability of Suitable Habitat for Juvenile Saffron Cod

3.2.4 Mature Saffron Cod

MaxEnt model predictions of suitable mature saffron cod habitat was highest along the Chukchi Sea coast (including Kotzebue Sound) to the central Beaufort Sea (**Figure 3.17**). Bottom temperature was the most important (37%) habitat covariate determining the distribution of suitable mature saffron cod habitat (**Table 3.1**). Similar to age 0 and juvenile life stages, the probability of suitable habitat increased with increasing temperatures and was highest above 8 °C (**Figure 3.18**). Organic carbon, minimum bottom temperature and sediment grain size were the 2nd, 3rd and 4th most important habitat variables with relative importance of 25%, 21% and 6%, respectively (**Table 3.1**). Although probability of habitat suitability increased with temperature, it was highest when minimum bottom temperatures were relatively low (< 2 °C). Habitat suitability peaked at intermediate sediment grain sizes ($\phi=0$ to $\phi=1$) and decreased with finer sediment size (larger ϕ). The model fits were considered excellent for the training data (AUC = 0.91) and good for the testing data (avg. AUC = 0.86).

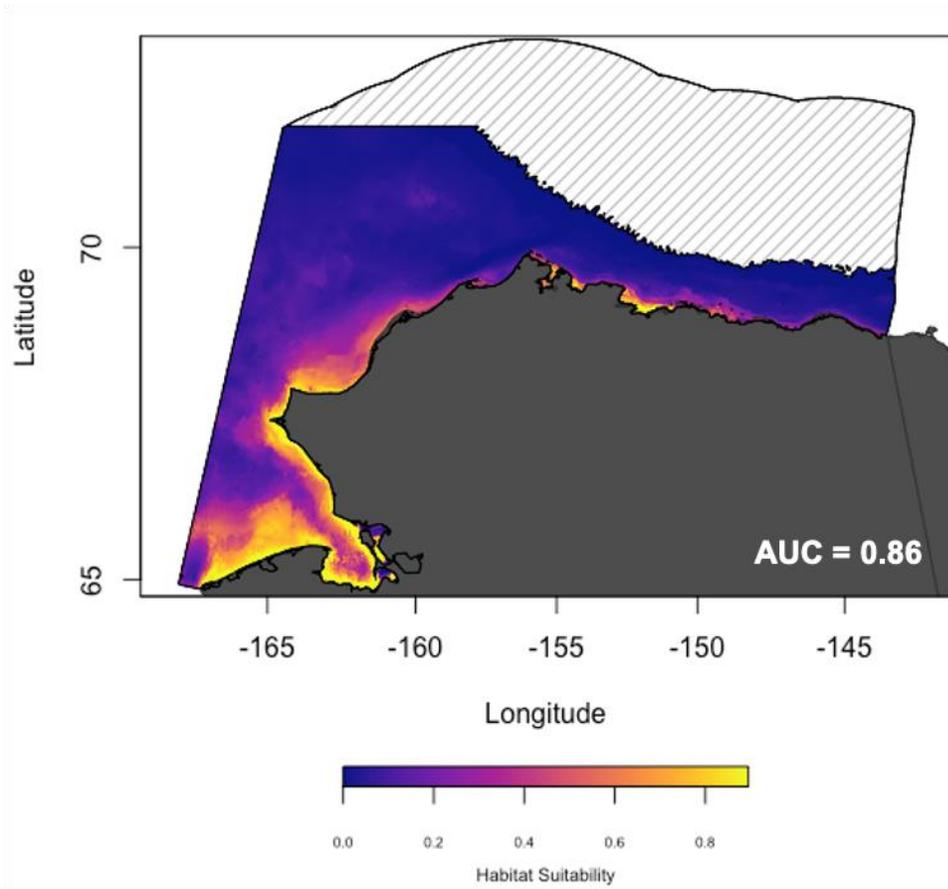


Figure 3.17. Predicted Distribution of Probability of Suitable Habitat for Mature Saffron Cod

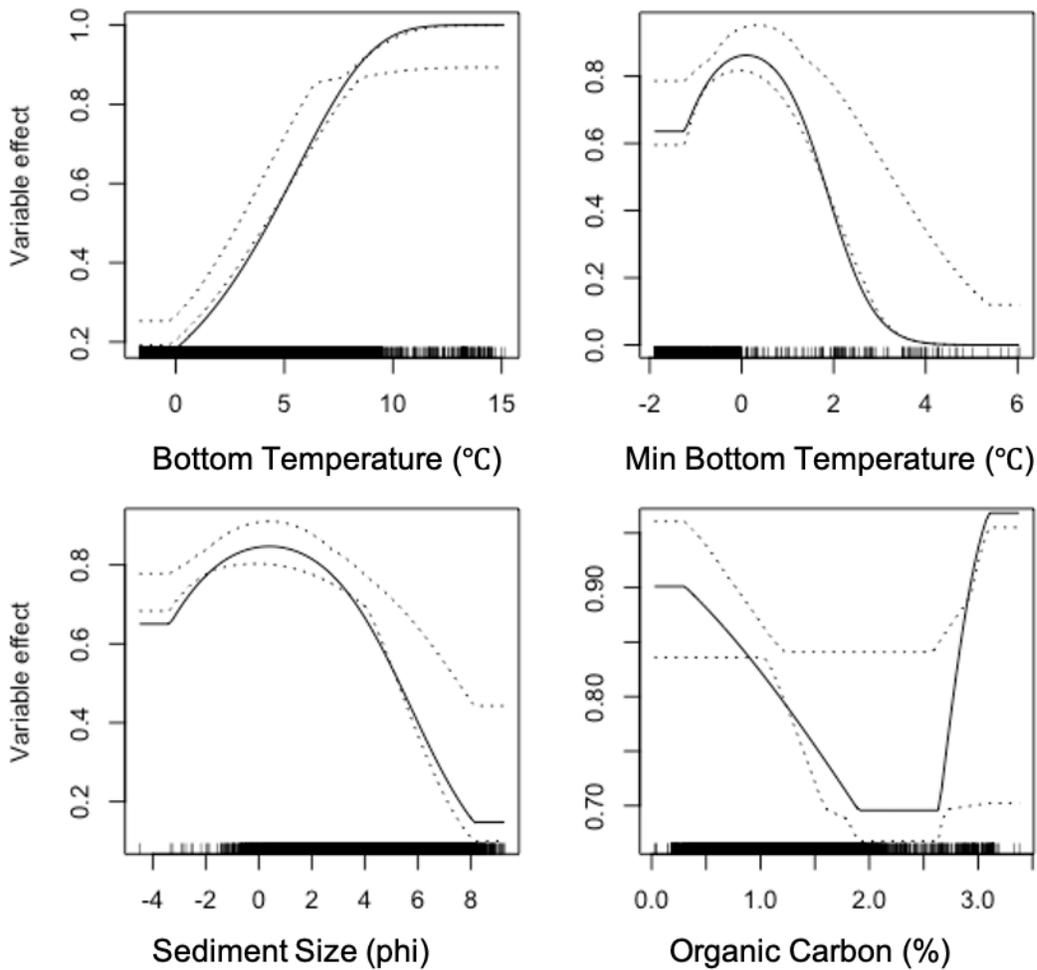


Figure 3.18. Response Curves for the Most Influential Habitat Covariates in the MaxEnt Model Predicting Probability of Suitable Habitat for Mature Saffron Cod

3.2.5 Key Habitat Areas

With the exception of larval saffron cod, whose suitable habitat occurred mostly in the Beaufort Sea and northern Chukchi Sea, habitat hotspots for older life stages occurred along the Chukchi Sea coast extending to various distances offshore and along the Beaufort Sea coast in nearshore waters (**Figure 3.19**). Kotzebue Sound was a habitat hotspot for mature saffron cod. Bottom temperature was likely an important factor driving the distribution of saffron cod, as age 0, juvenile and mature saffron cod have habitat hotspots in the warmer waters along the coast. Saffron cod seem to be moving southward and coastward with ontogeny. In contrast to Arctic cod suitable habitat remains similar with ontogeny, with the exception of larval saffron cod (**Figures 3.10 and 3.19**).

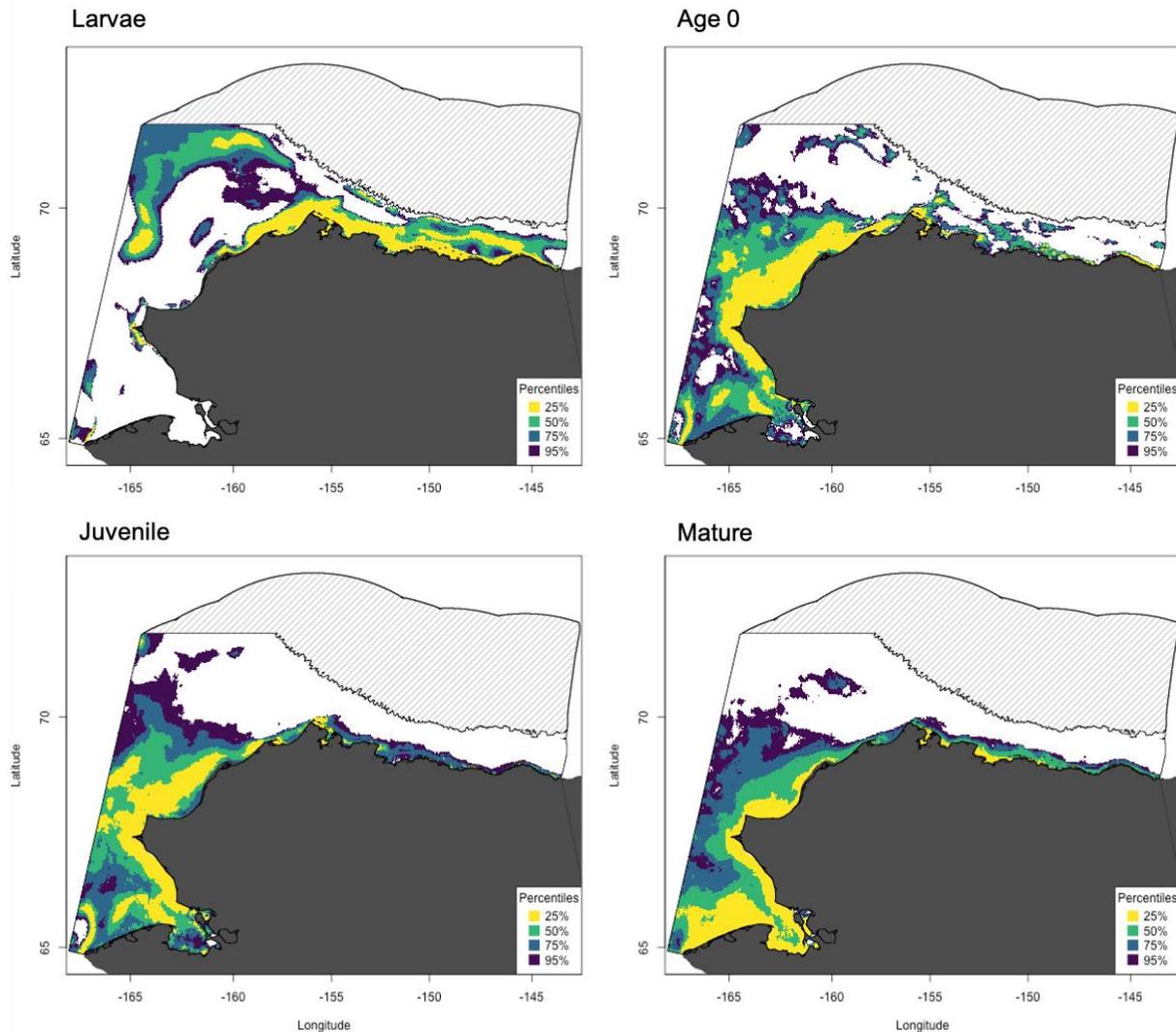


Figure 3.19. Key Habitat Areas for Larval, Age 0, Juvenile and Mature Saffron Cod

3.3 Snow Crab Distribution and Habitat Associations

Snow crab of various sizes occurred throughout the Chukchi Sea (**Figure 3.20**). Some snow crab occurred at intermediate depths in the western Beaufort Sea. Few snow crab were sampled in the eastern US Beaufort Sea, hence we included a longitude raster as a covariate in our MaxEnt models to account for the east-west gradient.

Snow crab have sexually dimorphic growth after the immature stages. Males grow faster and larger compared to females (Divine et al. 2019). Mature male snow crab are commercially harvested in the Bering Sea. A few males of harvestable size (carapace width >100 mm) were caught in the Beaufort Sea, but none in the Chukchi Sea (**Figure 3.20**)

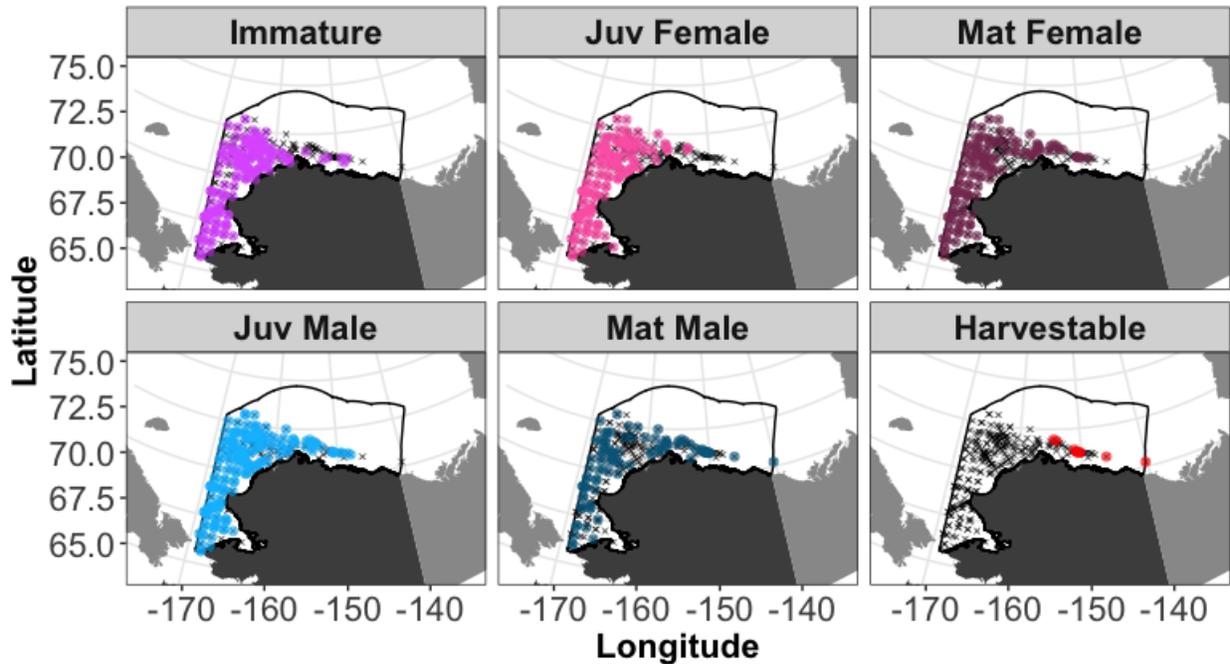


Figure 3.20. Snow Crab Presence Data by Life Stage (colored dots)

3.3.1 Immature Snow Crab

MaxEnt model predictions of immature snow crab habitat were highest at intermediate depths in the Chukchi Sea and western Beaufort Sea (Figure 3.21). Depth and bottom temperature were the most important habitat covariates determining the distribution of suitable immature snow crab habitat with a relative importance of 16% (Table 3.1). The probability of suitable habitat decreased with increasing bottom temperature and was highest over a narrow depth range peaking at approximately 100 m (Figure 3.22). Longitude and eastward velocity variability were the 3rd and 4th most important habitat variables with relative importance of 12% and 9%, respectively (Table 3.1). The probability of habitat suitability decreased with increasing longitude to the east (Figure 3.22). The model fits were considered acceptable for the training (AUC = 0.77) and testing (avg. AUC = 0.75) data.

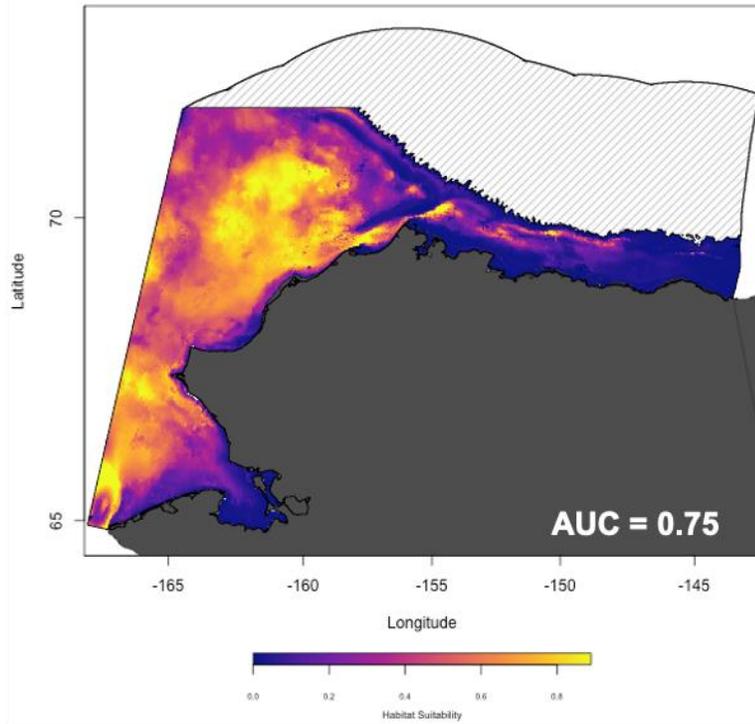


Figure 3.21. Predicted Distribution of Probability of Suitable Habitat for Immature Snow Crab

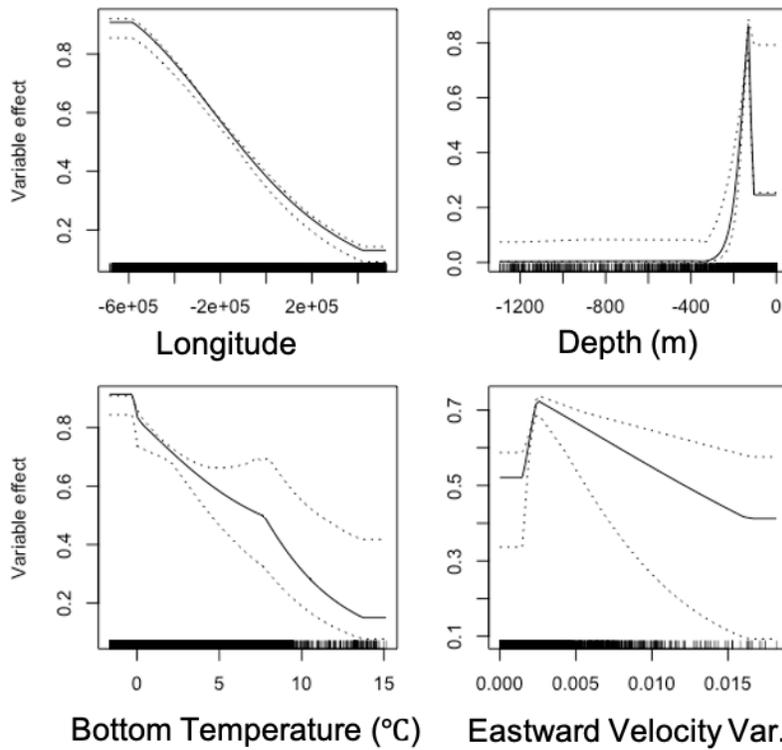


Figure 3.22. Response Curves for the Most Influential Habitat Covariates in the MaxEnt Model Predicting Probability of Suitable Habitat for Immature Snow Crab

3.3.2 Adolescent Female Snow Crab

MaxEnt model predictions of adolescent female snow crab habitat were highest at intermediate depths in the Chukchi Sea (**Figure 3.23**). Longitude was the most important habitat covariate (31%) determining the distribution of suitable adolescent female snow crab (**Table 3.1**). The probability of suitable habitat decreased with increasing longitude (**Figure 3.24**). Organic carbon, bottom temperature, northward velocity variability, and depth were the 2nd, 3rd, 4th and 5th most important habitat variables with relative importance of 17%, 14%, 14% and 11%, respectively (**Table 3.1**). Habitat suitability decreased with increasing organic carbon content and was consistently high at bottom temperatures below 8 °C before decreasing at higher temperatures (**Figure 3.24**). The model fits were considered acceptable for the training (AUC = 0.72) and testing (avg. AUC = 0.71) data.

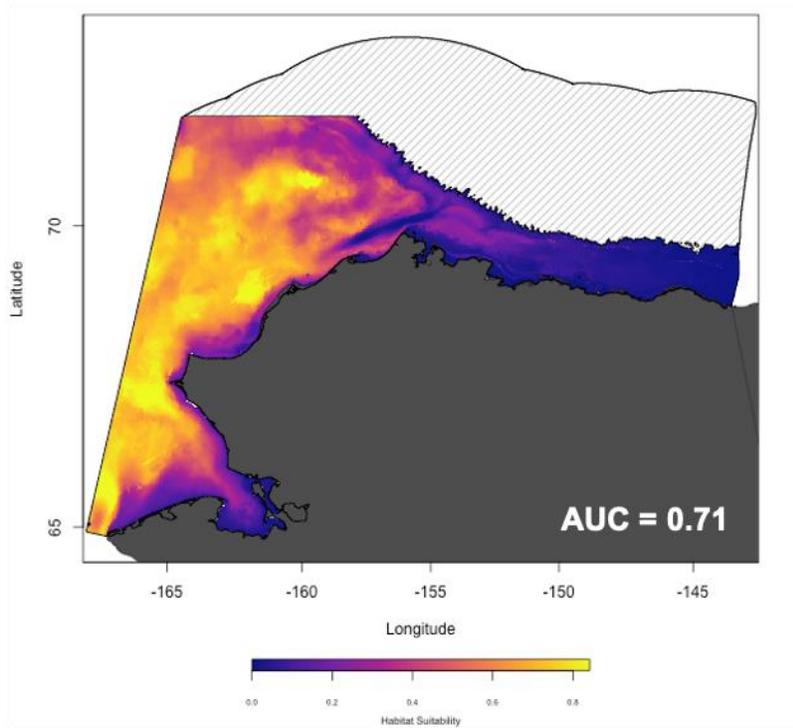


Figure 3.23. Predicted Distribution of Probability of Suitable Habitat for Adolescent Female Snow Crab

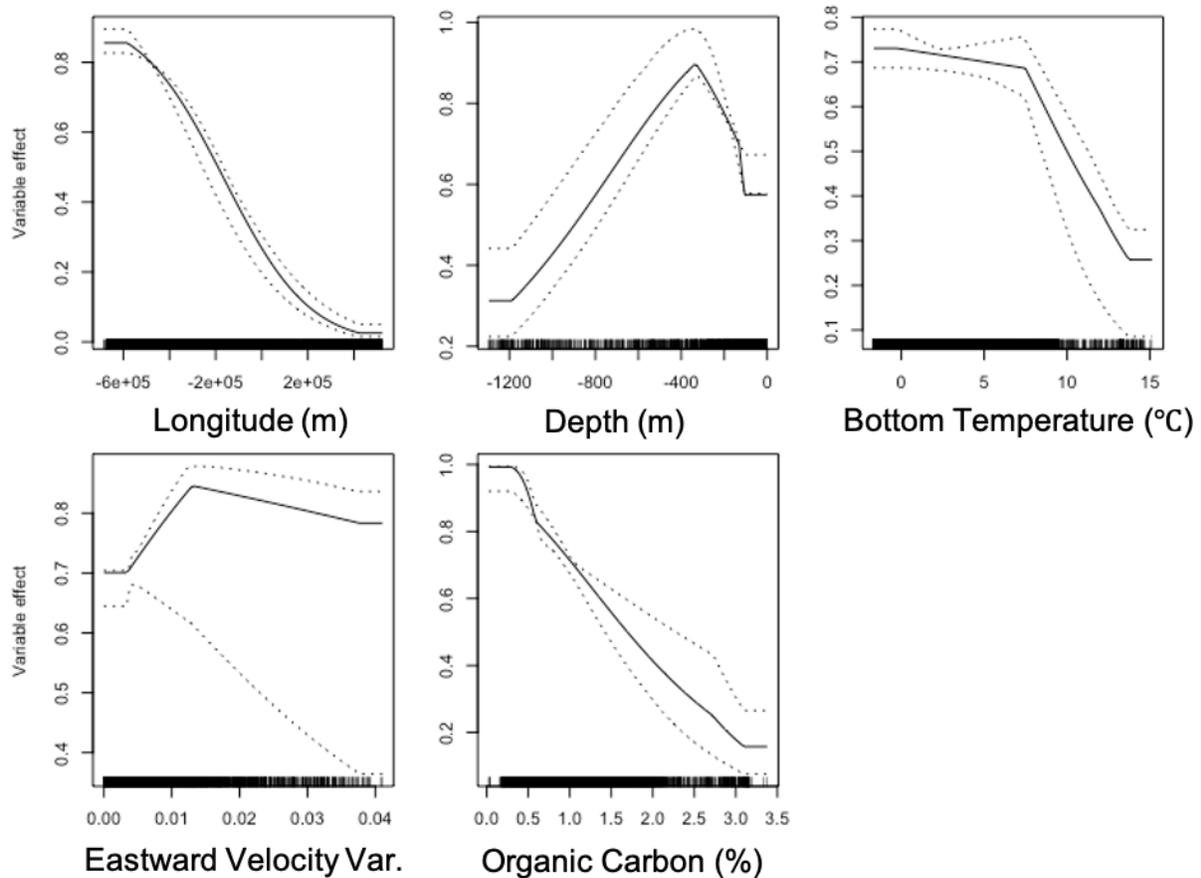


Figure 3.24. Response Curves for the Most Influential Habitat Covariates in the MaxEnt Model Predicting Probability of Suitable Habitat for Adolescent Female Snow Crab

3.3.3 Adolescent Male Snow Crab

MaxEnt model predictions of adolescent male snow crab habitat was highest offshore in the Chukchi Sea and along the slope in the Beaufort Sea (**Figure 3.25**). Predicted probability of suitable habitat was low in Barrow Canyon and at similar depths along the slope (**Figure 3.25**), although this is not evident in the depth response curve (**Figure 3.26**). Longitude and eastward velocity were the most important habitat covariates (15% each) determining the distribution of suitable adolescent male snow crab (**Table 3.1**). The probability of suitable habitat decreased to the east with increasing longitude and remained intermediate until increasing at the highest eastward velocity values (**Figure 3.26**), as evident in high habitat suitability along the Beaufort slope current. Organic carbon, eastward velocity variability, bottom temperature, and depth were the 3rd, 4th, 5th and 6th most important habitat variables with relative importance of 14%, 12%, 12% and 9%, respectively (**Table 3.1**). The probability of habitat suitability decreased with increasing organic carbon content and was high at temperatures below 8 °C before decreasing at higher temperatures (**Figure 3.26**) similar to the relationships for adolescent female snow crab. The model fits were considered acceptable for the training data (AUC = 0.72) and better than chance for the testing data (avg. AUC = 0.68).

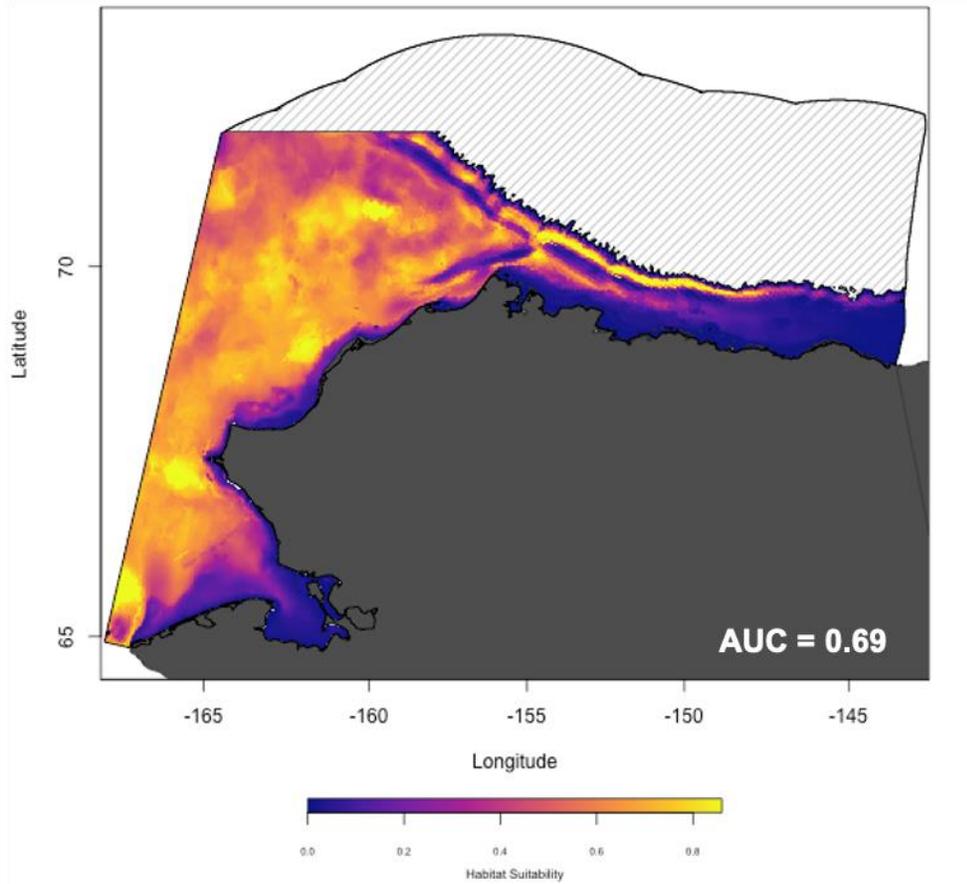


Figure 3.25. Predicted Distribution of Probability of Suitable Habitat for Adolescent Male Snow Crab

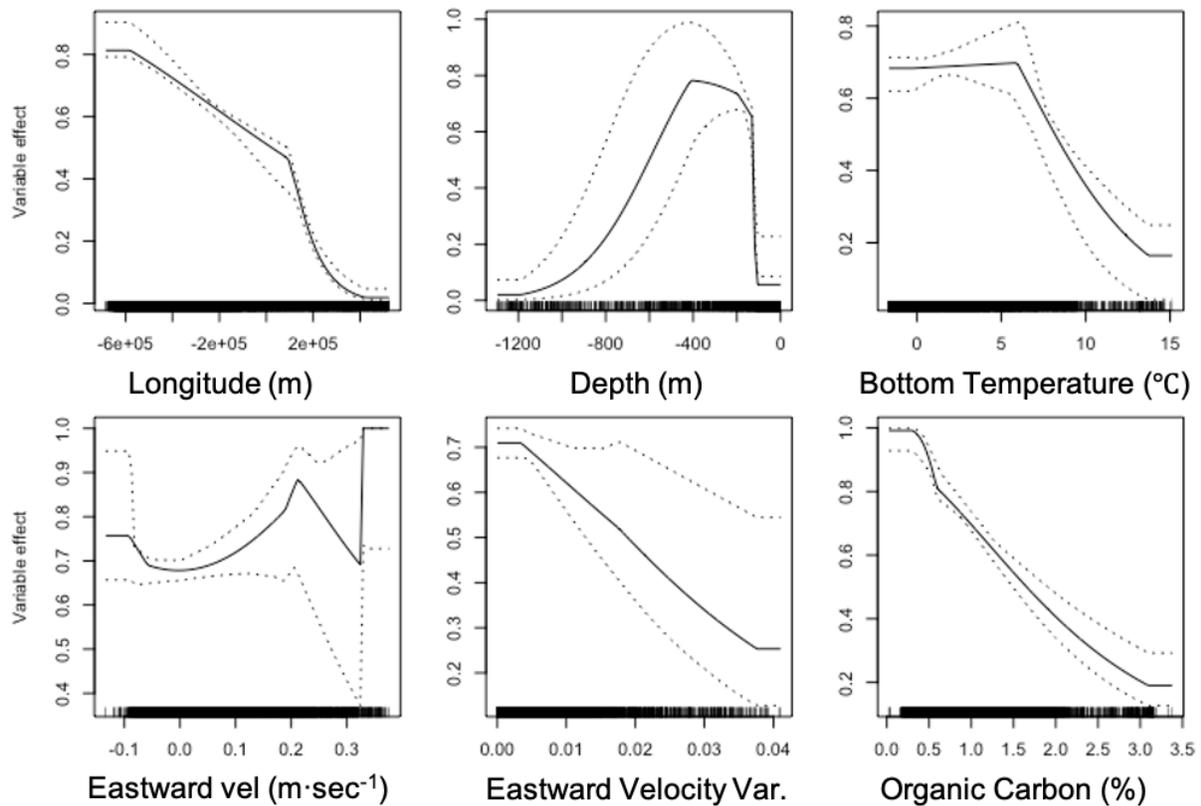


Figure 3.26. Response Curves for the Most Influential Habitat Covariates in the MaxEnt Model Predicting Probability of Suitable Habitat for Adolescent Male Snow Crab

3.3.4 Mature Female Snow Crab

MaxEnt model predictions of mature female snow crab habitat were highest offshore in the southern and central Chukchi Sea, near Barrow Canyon and along the slope in the Beaufort Sea (**Figure 3.27**). Longitude and depth were the most important habitat covariates (21% and 19%, respectively) determining the distribution of suitable mature female snow crab (**Table 3.1**). The probability of suitable habitat decreased to the east with increasing longitude and was highest at depths from 150 – 800 m (**Figure 3.28**). Northward velocity, eastward velocity, and bottom temperature were the 3rd, 4th, and 5th most important habitat variables with relative importance of around 17%, 12%, and 10%, respectively (**Table 3.1**). The probability of habitat suitability decreased with increasing eastward velocity and had a dome-shaped relationship with bottom temperature, peaking at 5.5 °C (**Figure 3.28**). The model fits were considered acceptable for the training data (AUC = 0.76) and better than chance for the testing data (avg. AUC = 0.70).

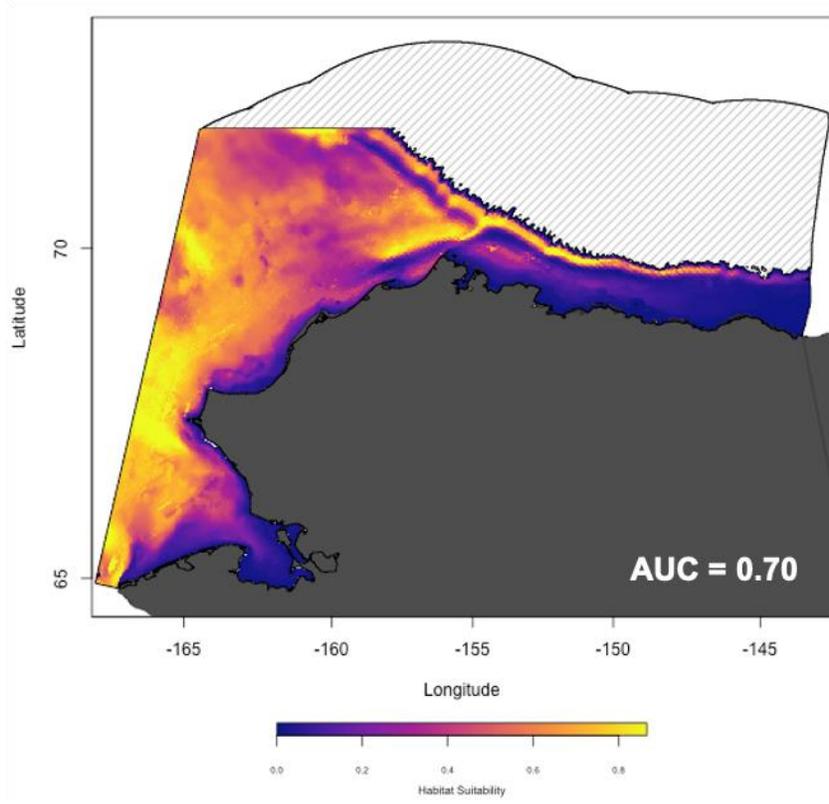


Figure 3.27. Predicted Distribution of Probability of Suitable Habitat for Mature Female Snow Crab

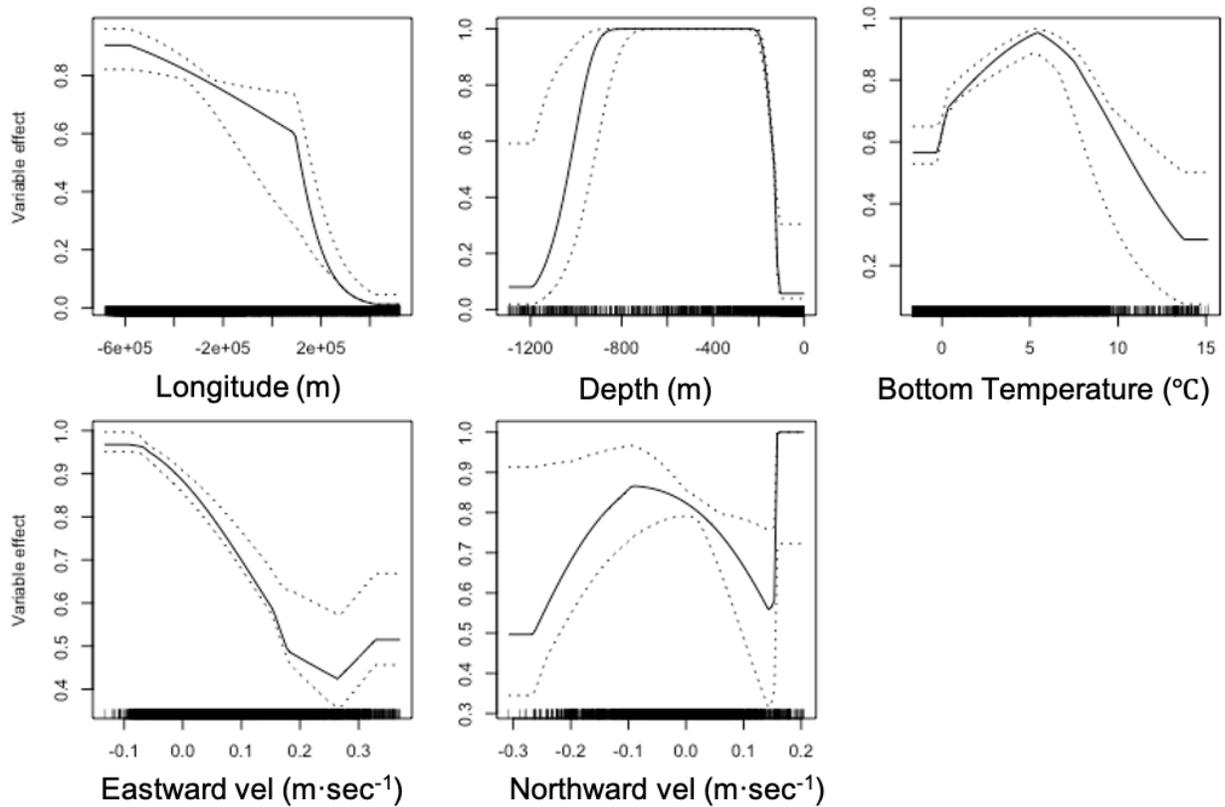


Figure 3.28. Response Curves for the Most Influential Habitat Covariates in the MaxEnt Model Predicting Probability of Suitable Habitat for Mature Female Snow Crab

3.3.5 Mature Male Snow Crab

MaxEnt model predictions of mature male snow crab habitat suitability was highest offshore in the southern, central and northwestern Chukchi Sea, in Barrow Canyon and along the slope in the Beaufort Sea (**Figure 3.29**). Longitude was the most important habitat covariate (26%) determining the distribution of suitable mature male snow crab (**Table 3.1**). The probability of suitable habitat was high at lower and intermediate longitudes and then rapidly decreased to the east (**Figure 3.30**). Northward velocity, bottom temperature, eastward velocity, and depth were the 2nd, 3rd, 4th, and 5th most important habitat variables with relative importance of 15%, 12%, 9%, and 9%, respectively (**Table 3.1**). The probability of habitat suitability increased with northward velocity, decreased with increasing eastward velocity, was highest at bottom temperatures from 0 to 4 °C and highest at depths of 250 – 600 m (**Figure 3.30**). The model fits were considered acceptable for the training (AUC = 0.78) and testing (avg. AUC = 0.71) data.

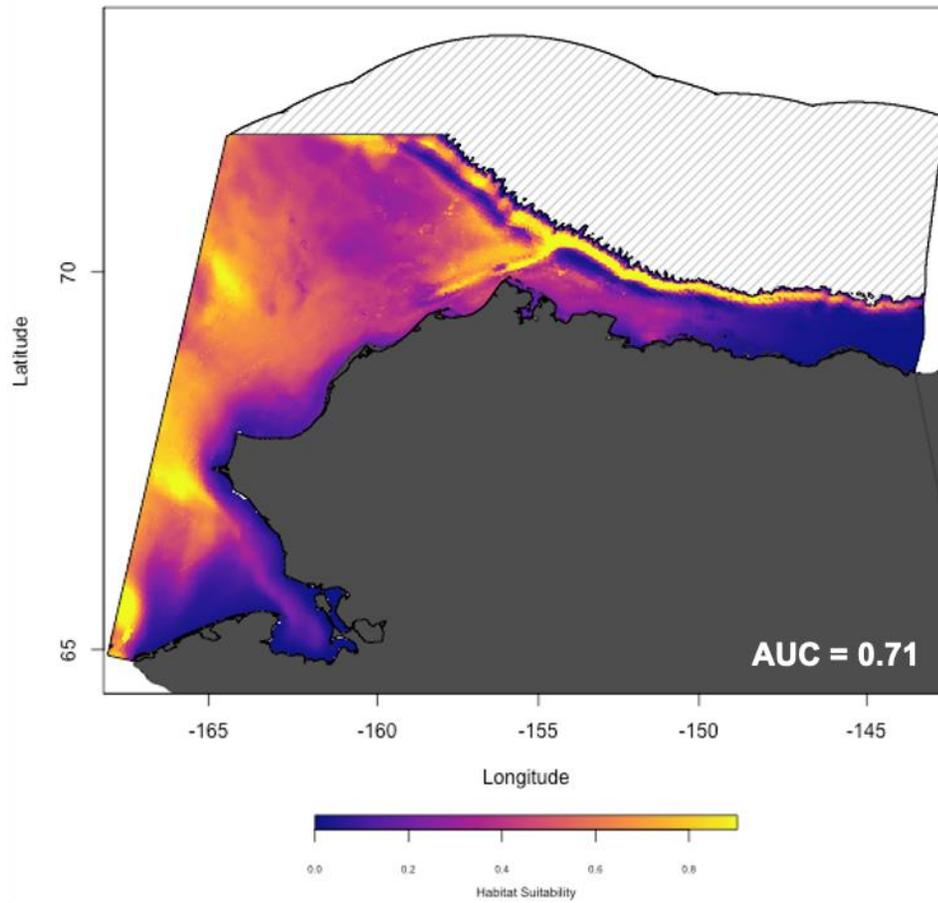


Figure 3.29. Predicted Distribution of Probability of Suitable Habitat for Mature Male Snow Crab

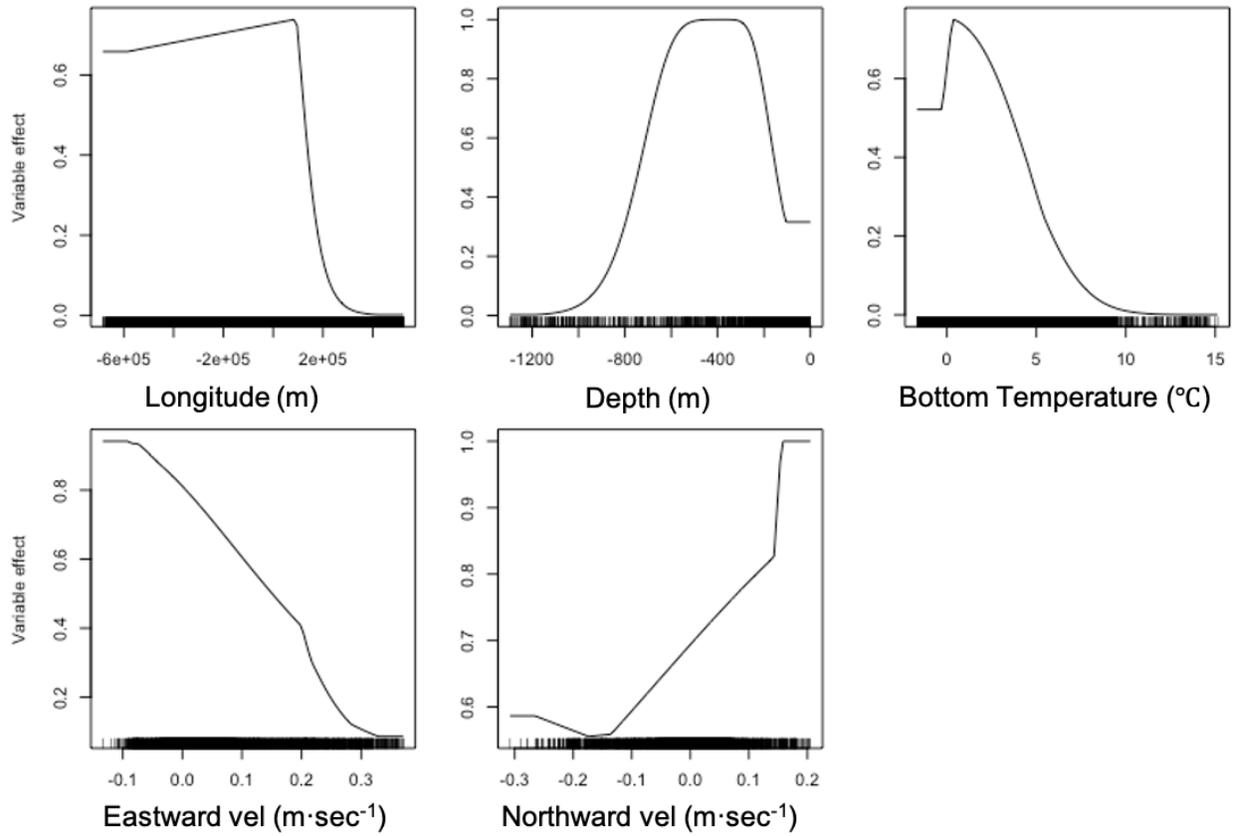


Figure 3.30. Response Curves for the Most Influential Habitat Covariates in the MaxEnt Model Predicting Probability of Suitable Habitat for Mature Male Snow Crab

3.3.6 Key Habitat Areas

For all life stages of snow crab, habitat hotspots occur offshore throughout the Chukchi Sea (**Figure 3.31**). For adolescent males, mature females and mature males, additional hotspots occur along the Beaufort slope (**Figure 3.31**). Barrow Canyon is a habitat hotspot for mature male and female snow crab. Snow crab tend to move to deeper water with ontogeny.

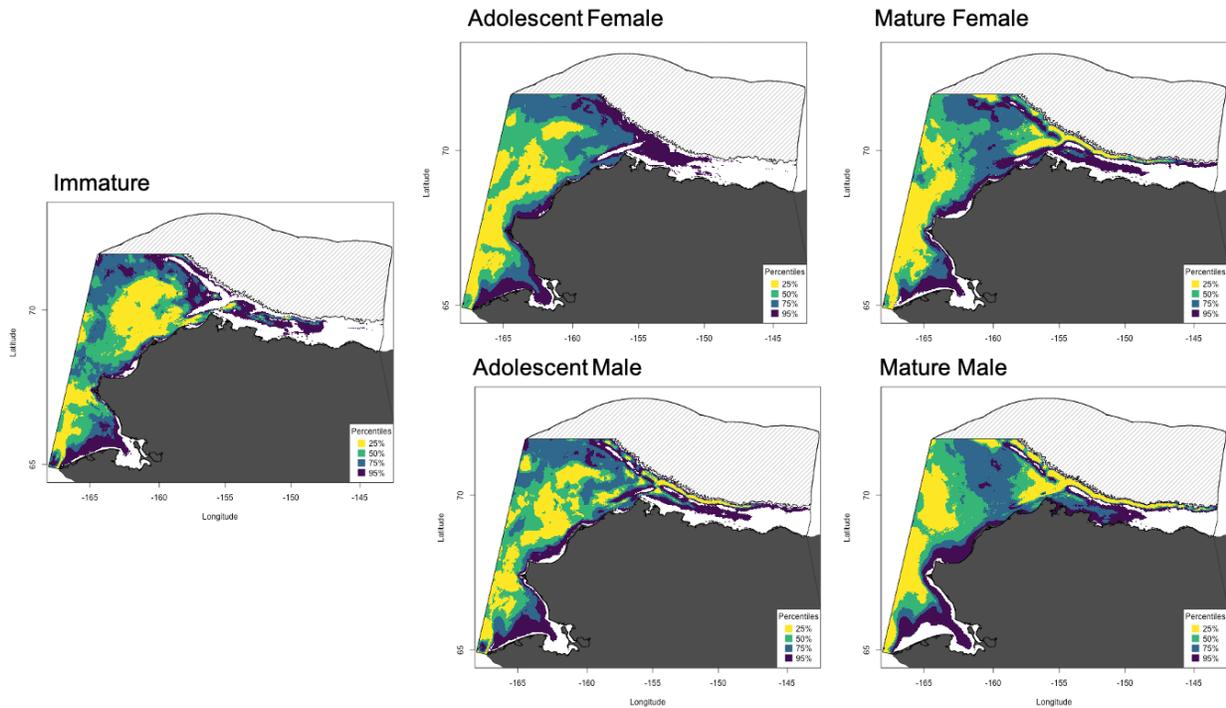


Figure 3.31. Key Habitat Areas for Immature, Adolescent and Mature Snow Crab

3.4 Habitat Related Vital Rates

We used temperature dependent growth rate equations obtained from Laurel et al. (2016; 2017) to convert temperature rasters (all years, warm years and cold years) to potential growth rate maps for age 0 and juvenile Arctic cod and for juvenile saffron cod (**Figure 3.32** column 1, **Figure 3.33** columns 1 and 2). For juvenile saffron cod, potential growth rate was highest in the southern Chukchi Sea, primarily along the coast, where the water was warmest. Potential growth rates were low in the northern Chukchi Sea and Beaufort Sea (**Figure 3.32**). Juvenile Arctic cod had higher potential growth rates than saffron cod over much of the Chukchi Sea and Beaufort Sea with the highest rates in the southern Chukchi Sea and in coastal waters. We converted the estimated probability of suitable habitat (**Figures 3.6** and **3.15**) to relative abundance (**Figure 3.32** column 2) and multiplied it by the potential growth rate in each grid cell to highlight potential areas of high production (**Figure 3.32** column 3). High productivity primarily reflects high estimated abundances for Arctic cod as the areas with high growth potential in the southern Chukchi Sea have very low abundances. In contrast, areas of high growth potential for saffron cod coincide with areas of high abundance, resulting in a similar pattern of high productivity along the coast of the southern Chukchi Sea.

We compared potential growth rates during warm and cold conditions and mapped the difference between warm and cold years for age 0 Arctic cod, juvenile Arctic cod and juvenile saffron cod (**Figure 3.33**). Warm years were associated with higher potential growth rates of age 0 and juvenile Arctic cod on the northern Chukchi Shelf and over much of the Beaufort Sea, particularly for age 0 Arctic cod (**Figure 3.33** rows 1 and 2). Only some nearshore areas in Kotzebue Sound were associated with a higher growth

potential for Arctic cod in cold years. The growth potential of juvenile saffron cod was higher in warm years over much of the Chukchi Sea, particularly in nearshore areas, but remained unchanged in the northern Chukchi Sea and Beaufort Sea (**Figure 3.33** row 3). There were no areas of higher growth for juvenile saffron cod in cold years.

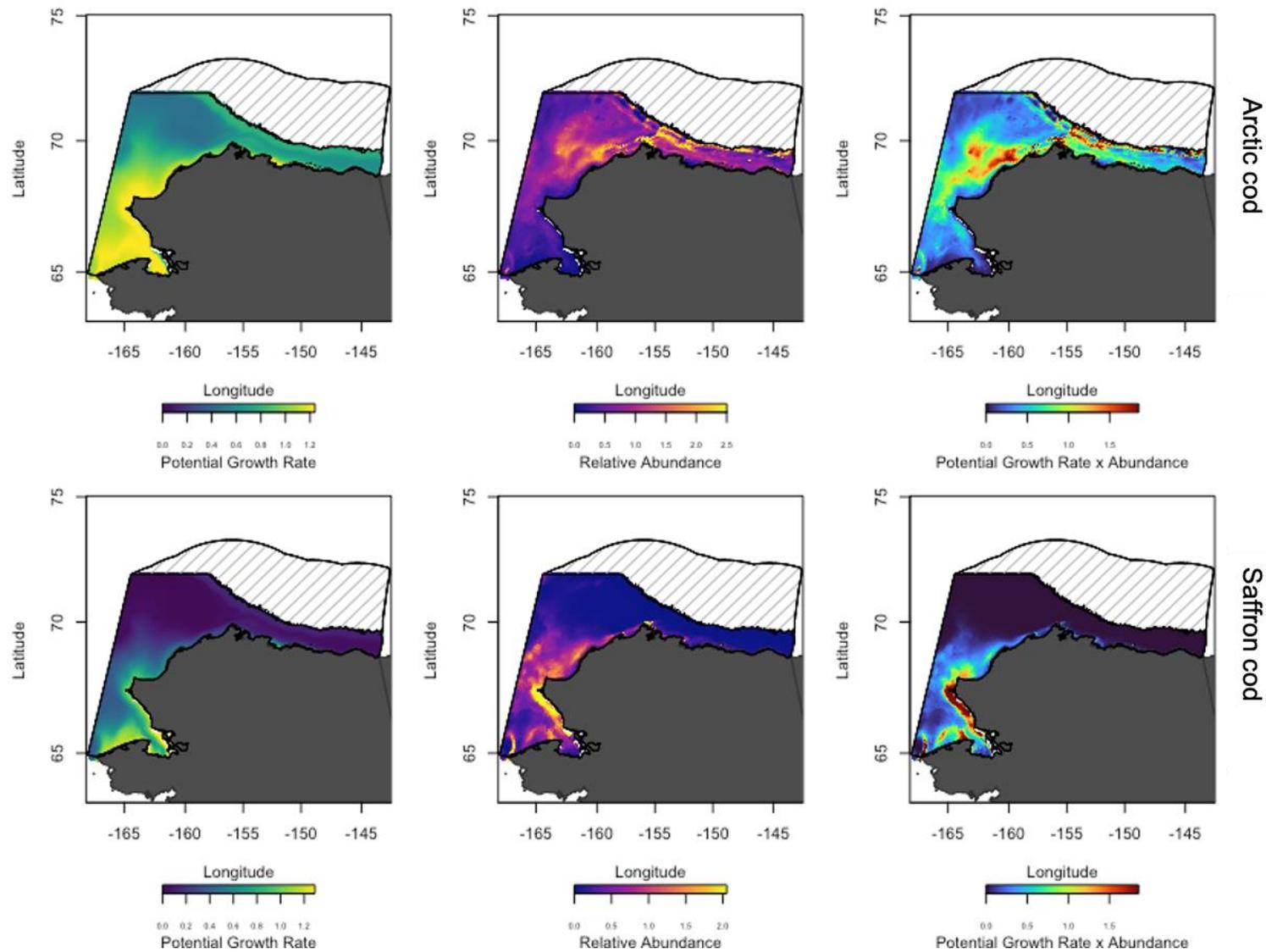


Figure 3.32. Potential Growth Rates, Approximate Abundance and Areas of High Productivity for Juvenile Arctic Cod and Juvenile Saffron Cod

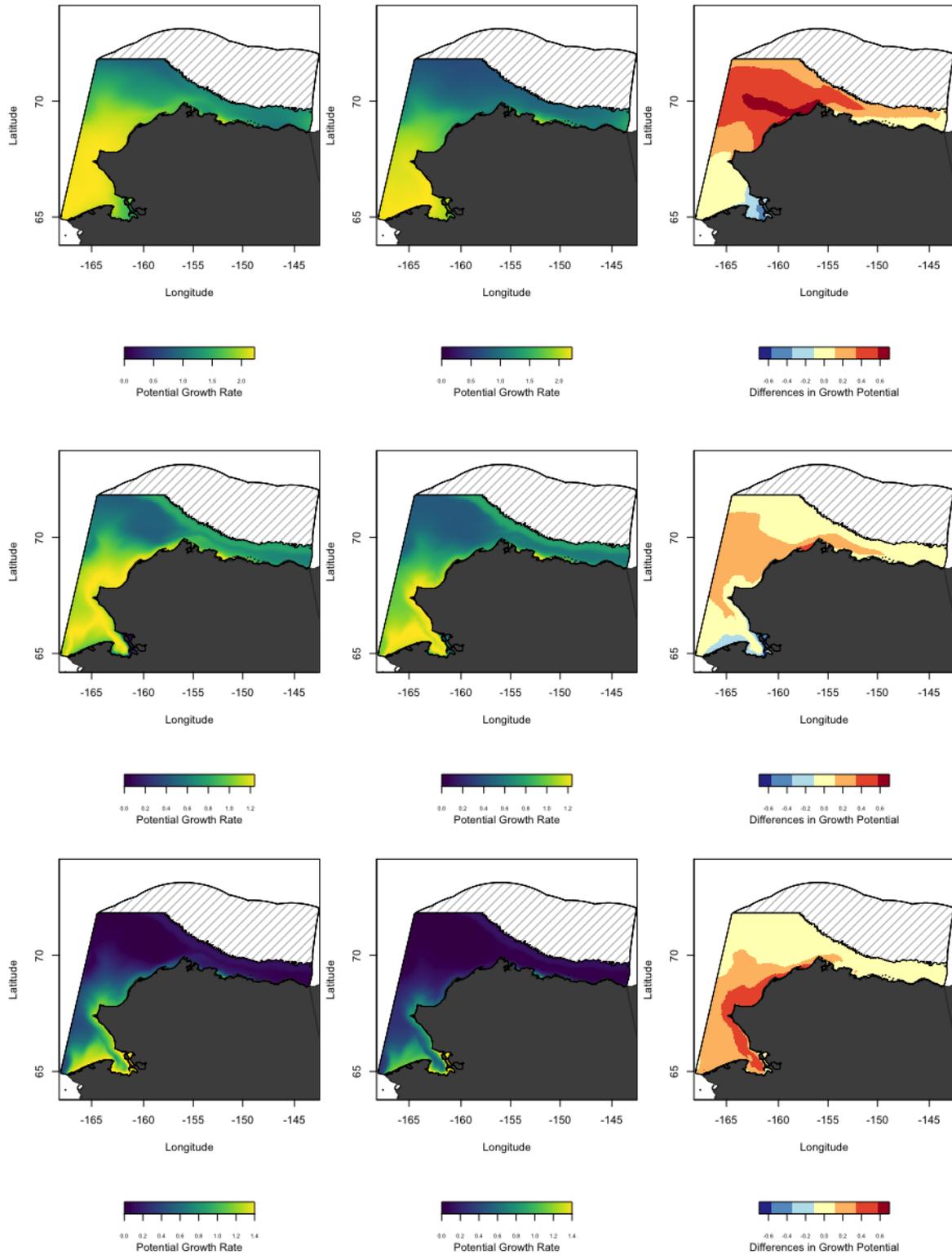


Figure 3.33. Potential Growth Rates for Age 0 Arctic Cod (Top), Juvenile Arctic Cod (Middle) and Juvenile Saffron Cod (Bottom) During Warm Periods (Left), Cold Periods (Center) and the Difference (Right)

3.5 Temporal Shifts Under Warm and Cold Conditions

In warm years, surface and bottom temperatures along the coast and surface temperatures over much of the northern Chukchi Shelf 2 – 3 °C warmer than in cold years due to atmospheric warming and advection of warmer water from the Pacific (**Figures 3.34** and **3.35**). This also resulted in higher minimum temperatures north of Bering Strait. Warmer years were associated with stronger northward and eastward velocities of surface waters over much of the Chukchi Sea shelf and through Barrow Canyon (**Figure 3.34**), as well as stronger eastward and northward flow at the bottom throughout the region (**Figure 3.35**), suggesting a higher inflow of Pacific waters into the Arctic. One exception was the enhanced southward and westward flow of bottom waters in Barrow Canyon during warm years, suggesting enhanced upwelling of Arctic waters through Barrow Canyon.

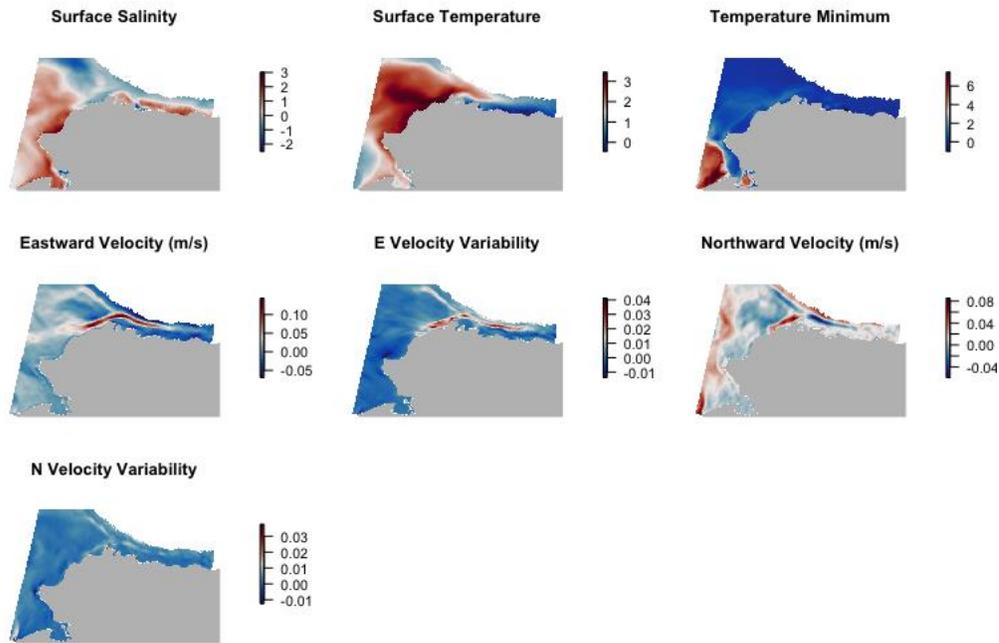


Figure 3.34. Differences Between Warm and Cold Periods for Near Surface Habitat Covariates

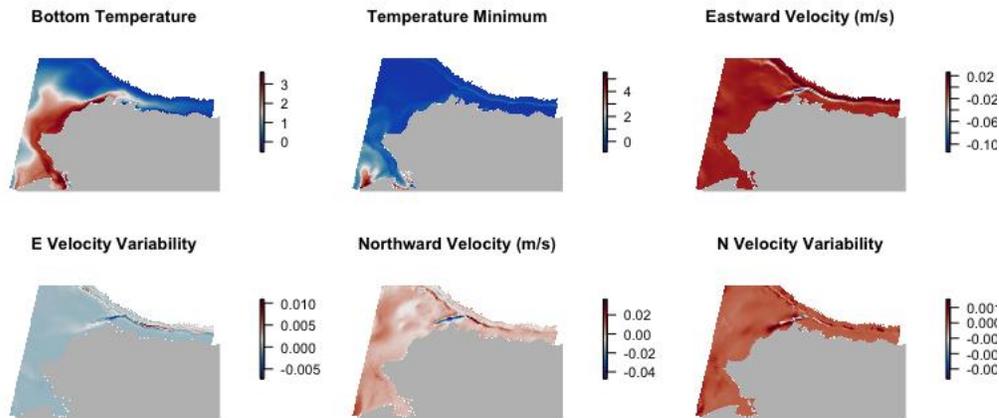


Figure 3.35. Differences Between Warm and Cold Periods for Near Bottom Habitat Covariates

3.5.1 Arctic Cod

In warm years Arctic cod appear to be pushed offshore, particularly in the northeast Chukchi Sea, possibly because nearshore waters are too warm (**Figure 3.36**). Habitat suitability of larval and age 0 stages increases in warm years on the northern portion of the Chukchi Shelf and along the outer Beaufort Shelf, consistent with enhanced transport of early life stages from the south in warm years. Early life stages of Arctic cod are more sensitive to temperature changes and had larger fluctuations in the area of suitable habitat between warm and cold years. There was a minimal difference in the probability of suitable habitat for mature Arctic cod between warm and cold years (**Figure 3.36**).

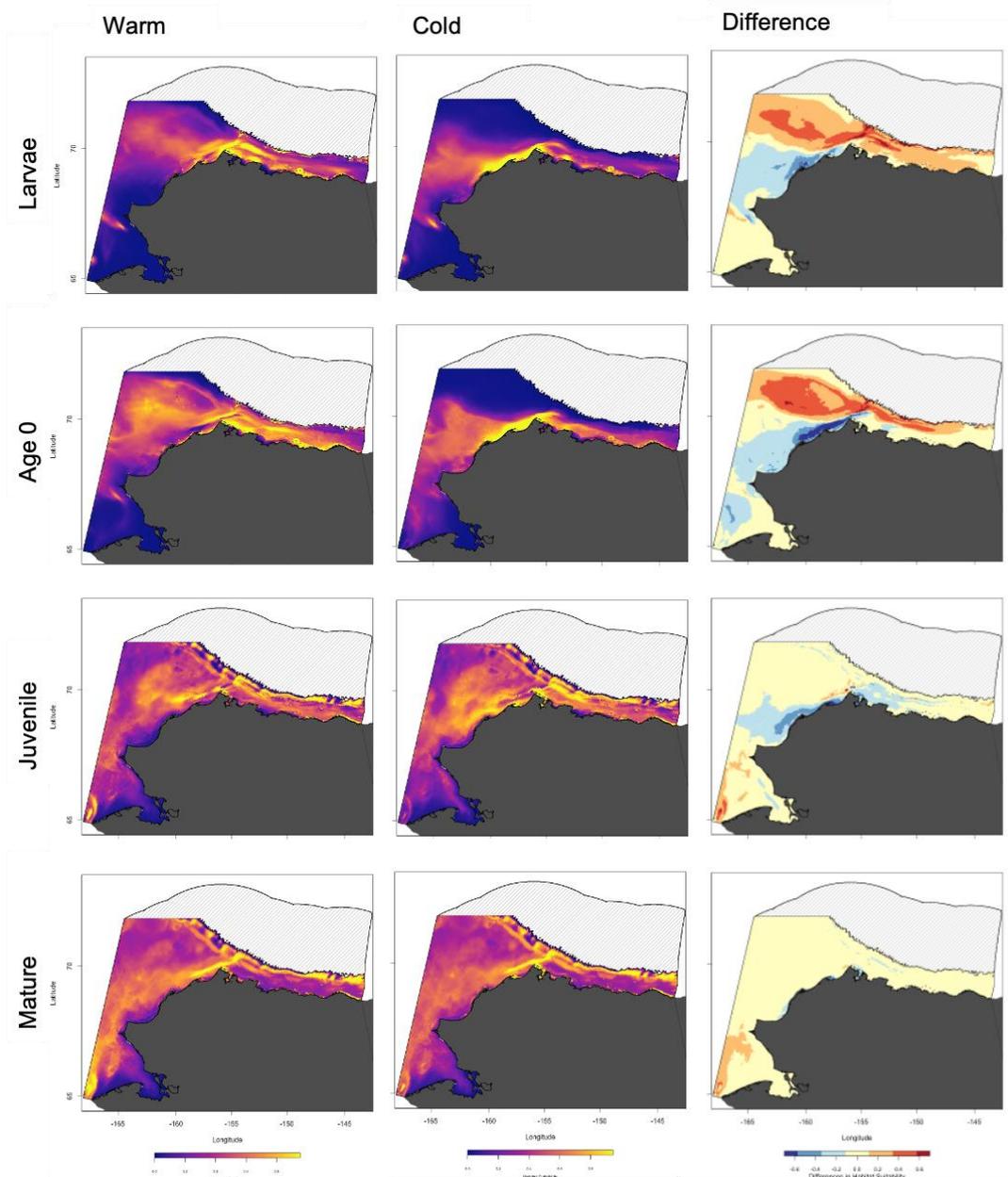


Figure 3.36. Arctic Cod Habitat Suitability During Warm and Cold Periods and the Difference.

Note: In right panel, red (blue) denotes higher probability of suitable habitat in warm (cold) years.

3.5.2 Saffron Cod

In warm years, older life stages of saffron cod spread out further from the coast in the southern and central Chukchi Sea and the area of suitable habitat increases (**Figure 3.37**). In cold years, there was an increase in habitat for larval and age 0 saffron cod along northern Chukchi coast (**Figure 3.37**). In contrast to Arctic cod, later life stages appear to be more sensitive to differences in temperature.

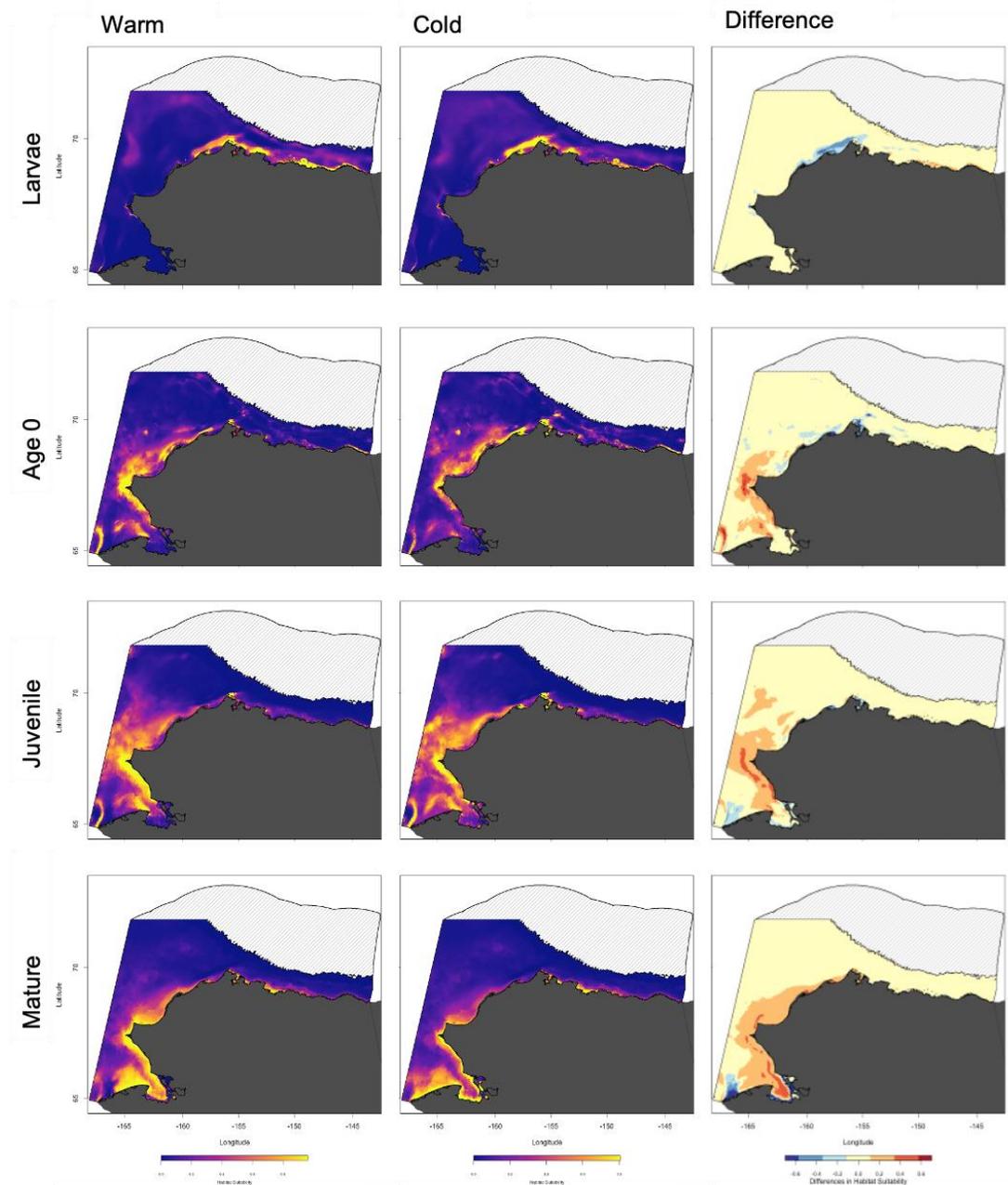


Figure 3.37. Saffron Cod Habitat Suitability During Warm and Cold Period and the Difference

Note: In right panel, red (blue) denotes higher probability of suitable habitat in warm (cold) years.

3.5.3 Snow Crab

Differences in habitat suitability for snow crab between warm and cold years were moderate compared to the two cod species. For immature and adolescent snow crab there was an increase in suitable habitat in cold years along the Chukchi Coast (**Figure 3.38**). Habitat suitability of immature crab increased during warm conditions from Bering Strait north to Point Hope. For mature male snow crab, temperature was an influential predictor of habitat suitability and the highest suitability occurred over a narrow range of cooler temperatures (**Figure 3.30**). As a consequence, they showed the largest changes in the probability of suitable habitat, which increased on the northern shelf during warm years and increased along the central Chukchi Sea coast during cold years (**Figure 3.38**).

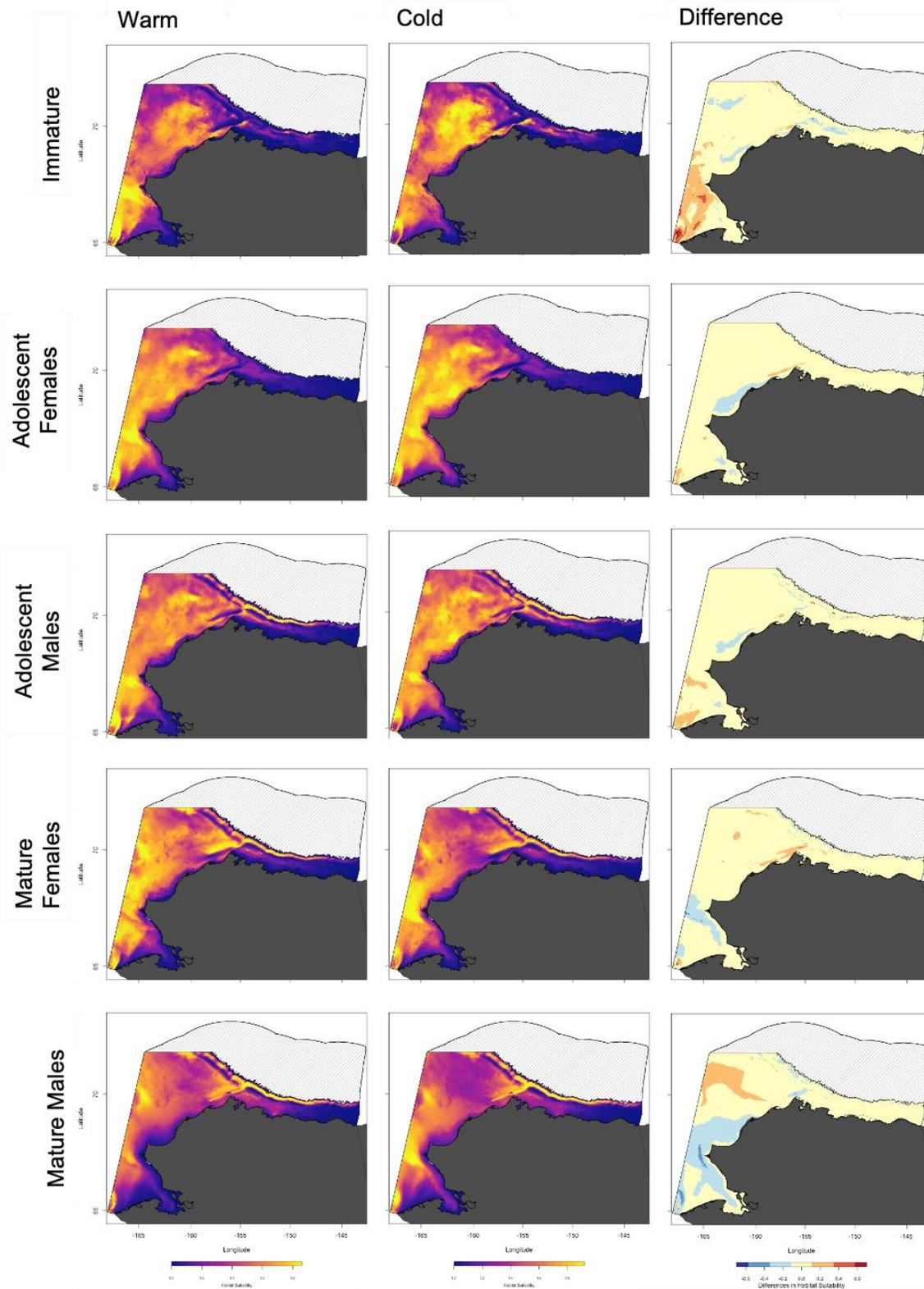


Figure 3.38. Snow Crab Habitat Suitability During Warm and Cold Periods and the Difference

Note: In right panel, red (blue) denotes higher probability of suitable habitat in warm (cold) years.

4 Conclusions

Increases in data availability from numerous surveys conducted since 2009 and advances in species distribution modeling allowed us to update and substantially refine habitat descriptions for three species by life stage in the Alaskan Chukchi Sea and Beaufort Sea. Model performance was acceptable or good in most cases, suggesting that our models provide an adequate basis for updated EFH descriptions for the target species. Moreover, the available data support the development of separate habitat models for warm and cold conditions as an essential step towards dynamic EFH descriptions. Finally, we showed that estimates of growth potential based on temperature-dependent growth rates from laboratory studies, where available, can be combined with abundance estimates to further improve habitat descriptions by estimating the potential productivity.

Temperature was an important habitat covariate for predicting the probability of suitable habitat for many of the life-stage species combinations. Early life stages of Arctic cod were more sensitive to temperature changes and had larger fluctuations in suitable habitat between warm and cold years. The area of suitable habitat decreased for Arctic cod in warm years and increased in cold years indicating climate warming may limit their distribution in the Chukchi Sea. Like early life stages of Arctic cod, larval saffron cod were limited to cooler temperatures. For all older life stages of saffron cod, habitat suitability increased with temperature and were consistent with laboratory growth studies from Laurel et al. (2016). Suitable habitat was greatest during warm periods for age-0 saffron cod, but was similar for older life stages. For adolescent snow crab, temperature fluctuations had limited influence on changes in habitat suitability. Mature males snow crabs were the most sensitive to changes in temperatures. Overall, these results support the idea that saffron cod may have a competitive advantage over Arctic cod in the Chukchi Sea in warmer years. Arctic cod may shift their distribution northward as well as mature snow crab. These results support the importance of adding a temporal component to EFH definitions, especially in a region experiencing rapid climate change.

As more surveys are conducted and more data becomes available, statistical modeling techniques in the Alaskan Arctic can advance and current models can improve. Future studies could include prey, predator or competitor species occurrence as potential explanatory variables. Predation pressure, prey availability and competition likely impact the distribution of these three ecologically important species (e.g., Marsh and Mueter 2019), especially if boreal gadids continue to shift northward (Hollowed et al. 2013, Fossheim et al. 2015, Thorsen et al. 2019). Pacific cod (*Gadus macrocephalus*) and walleye pollock (*G. chalcogrammus*) have been moving into the Alaskan Arctic (Stevenson and Lauth 2019, Marsh et al. 2020). The ecosystem including the habitat in the Alaskan Arctic is changing, therefore future species distribution models for EFH should take into account dynamic covariates as we demonstrate.

5 References

- Allen MJ, Smith GB. 1988. Atlas and zoogeography of common fishes in the Bering Sea and northeastern Pacific.
- Barber WE, Smith RL, Vallarino M, Meyer RM. 1997. Demersal fish assemblages of the northeastern Chukchi Sea, Alaska. *Fish Bull* 95:195–209.
- Behrenfeld MJ, Falkowski, PG. 1997. Photosynthetic rates derived from satellite-based chlorophyll concentration. *Limnology and Oceanography*. 42:1-20.
- Bradstreet MS. 1986. Aspects of the biology of Arctic cod (*Boreogadus saida*) and its importance in Arctic marine food chains. Department of Fisheries and Oceans, Central and Arctic Region.
- Burnham KP, Anderson DR. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer-Verlag, New York
- Burnham KP, Anderson DR. 2004. Multimodel inference: understanding AIC and BIC in model selection. *Sociological methods & research*. 33:261-304.
- Carmack E, Winsor P, Williams W. 2015. The contiguous panarctic Riverine Coastal Domain: a unifying concept. *Prog Oceanogr* 139:13–23.
- Craig PC, Griffiths WB, Haldorson L, McElderry H. 1982. Ecological studies of Arctic cod (*Boreogadus saida*) in Beaufort Sea coastal waters, Alaska. *Canadian Journal of Fisheries and Aquatic Sciences*. 39:395-406.
- Cohen DM, Inada T, Iwamoto T, Scialabba N. 1990. FAO species catalogue, vol 10. Gadiform fishes of the world. FAO Fish Synopsis No. 125, Rome. ISBN 92-5-102890-7
- Conan GY, Comeau M, Robichaud G. 1992. Life history and fishery management of majid crabs: the case study of the Bonne Bay (Newfoundland) *Chionoecetes opilio* population. *ICES CM* 21-24.
- Curchitser EN, Hedstrom K, Danielson S, Weingartner T. 2013. Adaptation of an Arctic Circulation Model. U.S. Department of the Interior, Bureau of Ocean Energy Management, Environmental Studies Program, Headquarters, Herndon, VA. OCS Study BOEM 2013-202. 82 p.
- Danielson SL, Eisner L, Ladd C, Mordy C, Sousa L, Weingartner TJ. 2017. A comparison between late summer 2012 and 2013 water masses, macronutrients, and phytoplankton standing crops in the northern Bering and Chukchi Seas. *Deep Sea Res Part II* 135:7–26.
- Dawe EG, Colbourne EB. 2002. Distribution and demography of snow crab (*Chionoecetes opilio*) males on the Newfoundland and Labrador Shelf. In: Paul AJ, et al. (eds) *Crabs in cold water regions: biology, management, and economics*. Alaska Sea Grant Coll Program, AK-SG-02-01, Fairbanks, AK, p 577–594.

- Divine LM, Mueter FJ, Kruse GH, Bluhm BA, Jewett SC, Iken K. 2019. New estimates of weight-at-size, maturity-at-size, fecundity, and biomass of snow crab, *Chionoecetes opilio*, in the Arctic Ocean off Alaska. *Fisheries Research*, 218:246–258. <https://doi.org/10.1016/j.fishres.2019.05.002>
- Elith J, Phillips SJ, Hastie T, Dudík M, Chee YE, Yates, CJ. 2011. A statistical explanation of MaxEnt for ecologists. *Diversity and distributions*. 17: 43-57.
- Fossheim M, Primicerio R, Johannessen E, Ingvaldsen RB, Aschan MM, Dolgov AV. 2015. Recent warming leads to a rapid borealization of fish communities in the Arctic. *Nature Climate Change*. 5:673–677.
- Frost KJ, Lowry LF. 1983. Demersal fishes and invertebrates trawled in the northeastern Chukchi and western Beaufort Seas, 1976-77.
- Gjørøseter H. 1995. Pelagic fish and the ecological impact of the modern fishing industry in the Barents Sea. *Arctic*. 48:267–278.
- Gong D, Pickart RS. 2015. Summertime circulation in the Eastern Chukchi Sea, *Deep Sea Res Part II*. 105:53–73.
- Hargens AR. 1972. Freezing resistance in polar fishes. *Science*. 176 :184-186.
- Helser TE, Colman JR, Anderl DM, Kestelle CR. 2017. Growth dynamics of saffron cod (*Eleginus gracilis*) and Arctic cod (*Boreogadus saida*) in the Northern Bering and Chukchi Seas. *Deep Sea Research Part II: Topical Studies in Oceanography*. 135:66-77.
- Hijmans, RJ. 2020. raster: Geographic Data Analysis and Modeling. R package version 3.4-5. <https://CRAN.R-project.org/package=raster>
- Hill V, Cota G. 2005. Spatial patterns of primary production on the shelf, slope and basin of the Western Arctic in 2002. *Deep Sea Research Part II: Topical Studies in Oceanography*. 52:3344-3354.
- Hollowed AB, Barange M, Beamish RJ, et al. 2013. Projected impacts of climate change on marine fish and fisheries. *ICES Journal of Marine Science*. 70:1023–1037.
- Hosmer DW, Lemenshow S. 2005. *Multiple Logistic Regression*. John Wiley and Sons, Inc.
- Jenkins CJ. 1997. Building Offshore Soils Databases. *Sea Technol*. 38:25-28.
- Korshunova E, 2012. Reproduction and winter biology of polar cod *Boreogadus saida* from Svalbard waters (Master's thesis, Universitetet i Tromsø).
- Laurel BJ, Spencer M, Iseri P, Copeman LA. 2016. Temperature-dependent growth and behavior of juvenile Arctic cod (*Boreogadus saida*) and co-occurring North Pacific gadids. *Polar Biol*. 39:1127-1135.

- Laurel BJ, Copeman LA, Spencer M, Iseri P. 2017. Temperature-dependent growth as a function of size and age in juvenile Arctic cod (*Boreogadus saida*). ICES Journal of Marine Science. 74:1614–1621. <https://doi.org/10.1093/icesjms/fsx028>
- Laman EA, Rooper CN, Turner K, Rooney S, Cooper DW, Zimmermann M. 2018. Using species distribution models to describe essential fish habitat in Alaska. Canadian Journal of Fisheries and Aquatic Sciences. 75:1230-1255.
- Logerwell E, Rand K, Danielson S, Sousa L. 2018. Environmental drivers of benthic fish distribution in and around Barrow Canyon in the northeastern Chukchi Sea and western Beaufort Sea. Deep Sea Research Part II: Topical Studies in Oceanography, 152:170-181.
- Lowry LF, Frost KJ. 1981. Distribution, Growth, and Foods of Arctic Cod (*Boreogadus saida*) in the Bering, Chukchi, and Beaufort Seas. Canadian field-naturalist. Ottawa, ON 95:186–191.
- Lowry LF, Frost KJ, Burns JJ. 1980. Feeding of bearded seals in the Bering and Chukchi Seas and trophic interaction with Pacific walruses. Arctic June 1:330-342.
- Loseto LL, Stern GA, Connelly TL, Deibel D, Gemmill B, Prokopowicz A, Fortier L, Ferguson SH. 2009. Summer diet of beluga whales inferred by fatty acid analysis of the eastern Beaufort Sea food web. J Exp Mar Biol Ecol 374:12–18.
- Marsh JM, Mueter FJ, Thorson JT, Britt L, Zador S. 2020. Sidebar 5.1: Shifting Fish Distributions in the Bering Sea. Richter-Menge, J. and M. L. Druckenmiller, Eds., 2020: The Arctic [in “State of the Climate in 2019”]. Bull. Amer. Meteor. Soc., 101: S239–S285, <https://doi.org/10.1175/BAMS-D-20-0086.1>.
- Marsh JM, Mueter FJ. 2019. Influences of temperature, predators, and competitors on polar cod (*Boreogadus saida*) at the southern margin of their distribution. Polar Biol. 43:995–1014.
- Marsh JM, Mueter FJ, Quinn, TJ II. 2019. Environmental and biological influences on the distribution and population dynamics of Arctic cod (*Boreogadus saida*) in the US Chukchi Sea. Polar Biol. 43:1055–1072.
- Matley JK, Crawford RE, Dick TA. 2012. Summer foraging behaviour of shallow-diving seabirds and distribution of their prey, Arctic cod (*Boreogadus saida*), in the Canadian Arctic. Polar Res. 31: 15894.
- Muscarella R, Galante PJ, Soley- Guardia M, Boria RA, Kass JM, Uriarte M, Anderson RP. 2014. ENM eval: An R package for conducting spatially independent evaluations and estimating optimal model complexity for Maxent ecological niche models. Methods in ecology and evolution, 5: 1198-1205.
- Norcross BL, Holladay BA, Mecklenburg CW. 2013. Recent and Historical Distribution and Ecology of Demersal Fishes in the Chukchi Sea Planning Area. Final Report to the Bureau of Ocean Energy Management, Alaska OCS Region, Anchorage, Alaska, 200 p.

- Norcross BL, Holladay BA, Apsens SJ, Edenfield LE, Gray BP, Walker KL. 2018. Central Beaufort Sea marine fish monitoring. Fairbanks AK: US Department of the Interior, Bureau of Ocean Energy Management, Final Report for OCS Study BOEM 2017-33
- [NPFMC] North Pacific Fisheries Management Council. 2009. Fishery management plan for fish resources of the Arctic management area. <http://www.npfmc.org/wpcontent/PDFdocuments/fmp/Arctic/ArcticFMP.pdf>
- Pebesma EJ. 2004. Multivariable geostatistics in S: the gstat package. *Computers & Geosciences*, 30: 683-691.
- Phillips SJ, Anderson RP, Schapire RE. 2006. Maximum entropy modeling of species geographic distributions. *Ecol Model* 190:231-259.
- Phillips SJ, Anderson RP, Dudík M, Schapire RE, Blair ME. 2017. Opening the black box: An open-source release of Maxent. *Ecography*, 40: 887-893.
- R Core Team. 2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Sibson R. 1981. A brief description of natural neighbour interpolation. *Interpreting multivariate data*.
- Sigler MF, Cameron MF, Eagleton MP, Faunce CH, Heifetz J, Helser TE, Laurel BJ, Lindeberg MR, McConnaughey RA, Ryer CH, Wilderbuer TK. 2012. Alaska Essential Fish Habitat Research Plan: a research plan for the National Marine Fisheries Service's Alaska Fisheries Science Center and Alaska Regional Office. AFSC Processed Rep. 2012-06
- Stevenson DE, Lauth RR. 2019. Bottom trawl surveys in the northern Bering Sea indicate recent shifts in the distribution of marine species. *Polar Biology*. 42:407-421.
- Thorson JT, Fossheim M, Mueter F, et al, 2019. Comparison of near-bottom fish densities show rapid community and population shifts in Bering and Barents Seas. Arctic Report Card 2019. Richter-Menge J, Druckenmiller ML, Jeffries M, Eds., <http://www.arctic.noaa.gov/Report-Card>
- Vestfals CD, Mueter FJ, Duffy-Anderson JT, Busby MS, De Robertis A. 2019. Spatio-temporal distribution of polar cod (*Boreogadus saida*) and saffron cod (*Eleginus gracilis*) early life stages in the Pacific Arctic. *Polar Biology*. 42:969-990.
- Vestfals CD, Mueter FJ, Hedstrom KS, Laurel BJ, Petrik CM, Duffy-Anderson JT, Danielson SL. 2021. Modeling the dispersal of polar cod (*Boreogadus saida*) and saffron cod (*Eleginus gracilis*) early life stages in the Pacific Arctic using a biophysical transport model. *Progress in Oceanography*, 196, p.102571.
- Warren DL, Seifert SN. 2011. Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. *Ecological Applications*. 21: 335-342.

- Weingartner TJ. 1997. A review of the physical oceanography of the northeastern Chukchi Sea. In Fish ecology in Arctic North America. American Fisheries Society Symposium (Vol. 19, pp. 40-59). Bethesda.
- Weingartner T, Aagaard K, Woodgate R, Danielson S, Sasaki Y, Cavalieri D. 2005. Circulation on the north central Chukchi Sea shelf, Deep Sea Res Part II. 52:3150–3174.
- Welch HE, Bergmann MA, Siferd TD, Martin KA, Curtis MF, Crawford RE, Conover RJ, Hop H. 1992. Energy flow through the marine ecosystem of Lancaster Sound region, Arctic Canada. Arctic. 45:343–357.
- Wright DJ, Pendleton M, Boulware J, Walbridge S, Gerlt B, Eslinger D, Sampson D, et al. 2012. ArcGIS Benthic Terrain Modeler (BTM), v. 3.0, Environmental Systems Research Institute, NOAA Coastal Services Center, Massachusetts Office of Coastal Zone Management. Available at: (<http://esriurl.com/5754>).
- Yoklavich M, Blackhart K, Brown SK, Greene C, Minello T, et al. 2010. Marine fisheries habitat assessment improvement plan. Report of the National Marine Fisheries Service Habitat Assessment Improvement Plan Team. US Dep. Commer., NOAA Tech. Memo. 129 p. NMFS-F/SPO-108.
- Zuur A, Ieno EN, Walker N, Saveliev AA, Smith GM. 2009. Mixed effects models and extensions in ecology with R. Springer Science & Business Media.



U.S. Department of the Interior (DOI)

DOI protects and manages the Nation's natural resources and cultural heritage; provides scientific and other information about those resources; and honors the Nation's trust responsibilities or special commitments to American Indians, Alaska Natives, and affiliated island communities.



Bureau of Ocean Energy Management (BOEM)

BOEM's mission is to manage development of U.S. Outer Continental Shelf energy and mineral resources in an environmentally and economically responsible way.

BOEM Environmental Studies Program

The mission of the Environmental Studies Program is to provide the information needed to predict, assess, and manage impacts from offshore energy and marine mineral exploration, development, and production activities on human, marine, and coastal environments. The proposal, selection, research, review, collaboration, production, and dissemination of each of BOEM's Environmental Studies follows the DOI Code of Scientific and Scholarly Conduct, in support of a culture of scientific and professional integrity, as set out in the DOI Departmental Manual (305 DM 3).