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The Forgotten Coast: A Synthesis of Current Knowledge of Southern Chukchi Sea Lagoon Ecosystems

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ABSTRACT. In the Southern Chukchi Sea Region (SCSR) of the Alaskan Arctic, approximately 40% of the coastline consists of freshwater-brackish lagoons and the gravel spits that separate them from the ocean. These lagoons are important rearing, feeding, and spawning habitats for diverse fish and invertebrate assemblages composed of freshwater, diadromous, and marine taxa. Many of these species are prey for a suite of marine mammals and avian predators in addition to being important to the food security of subsistence users from the surrounding region. Despite recognition of the ecological and cultural importance of these habitats from as far back as the 1950s, the body of knowledge surrounding lagoons of the SCSR contains many knowledge gaps and fails to comprehensively capture the dynamic nature of both biotic and abiotic factors that define the functional ecology of these habitats. This report synthesizes the available knowledge of SCSR lagoons, including geomorphology, hydrology, food web structure, and local knowledge. We also recommend avenues of future study, such as characterizing the basal trophic levels of lagoon food webs. Only by constructing a more detailed and comprehensive knowledge base of SCSR lagoon ecology will management and conservation efforts in the region be able to address and mitigate potential threats resulting from expanding infrastructure and global climate change, while simultaneously supporting the diverse portfolio of lagoon habitats that have a vital role in regional subsistence practices and food security.

Key words: coastal lagoons; Arctic Ocean; Chukchi Sea; ecology; fish assemblages; ecosystem resilience; climate change; human impacts; subsistence harvest; conservation

RÉSUMÉ. Dans la région sud de la mer des Tchouktches (SCSR) de l'Arctique alaskien, environ 40 % du littoral est composé de lagunes d'eau douce et d'eau saumâtre ainsi que de flèches littorales en gravier les séparant de l'océan. Ces lagunes sont d'importants habitats d'alevinage, d'alimentation et de frai pour divers assemblages de poissons et d'invertébrés composés de taxons d'eau douce, de taxons diadromes et de taxons marins. Grand nombre de ces espèces servent de proies à un ensemble de mammifères marins et de prédateurs aviaires en plus de jouer un rôle important en matière de sécurité alimentaire chez les utilisateurs de subsistance de la région environnante. Même si la reconnaissance de l'importance écologique et culturelle de ces habitats remonte aux années 1950, l'ensemble de connaissances entourant les lagunes de la SCSR comporte de nombreux écarts et ne saisit pas entièrement la nature dynamique des facteurs biotiques et abiotiques qui définissent l'écologie fonctionnelle de ces habitats. Ce rapport synthétise les connaissances actuelles au sujet des lagunes de la SCSR, y compris la géomorphologie, l'hydrologie, la structure du réseau alimentaire et les connaissances locales. Nous recommandons aussi des possibilités d'études futures, comme la caractérisation des niveaux trophiques de base des réseaux alimentaires des lagunes. Seule l'élaboration d'une base de connaissances plus exhaustive et détaillée de l'écologie des lagunes de la SCSR permettra aux efforts de gestion et de conservation déployés dans la région de gérer et d'atténuer les menaces découlant de l'expansion des infrastructures et du changement climatique mondial tout en soutenant simultanément la gamme diverse d'habitats de lagunes qui jouent un rôle vital dans les pratiques de subsistance et la sécurité alimentaire de la région.

Mots clés : lagunes côtières; océan Arctique; mer des Tchouktches; écologie; assemblages de poissons; résilience de l'écosystème; changement climatique; impacts humains; récolte de subsistance; conservation

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BACKGROUND

Globally, coastal lagoons are important ecotones where freshwater and marine ecosystems interface. Lagoon systems occur in tropical (Lin et al., 2001), temperate (McGlathery et al., 2001), and Arctic (Klemsdal, 1986; Dunton et al., 2012; Krylenko, 2017) regions. Lagoons are frequently associated with ecological processes that support elevated levels of seasonal productivity and biodiversity. These seasonally freshwater-brackish environments can be vital habitats for fishes, invertebrates, birds, and marine mammals, and often act as migration corridors for diadromous biota (Tibbles, 2018). In the Arctic, the margins of the southern Chukchi Sea Region (SCSR), which border the Bering Strait, are characterized by a prominent array of lagoons. We calculate that approximately 40% of the 950 km Alaskan coastline from the Bering Strait to the Canadian border comprises the frequently narrow and wave-washed berms associated with these lagoons. The northerly group of these habitats along the Beaufort Sea coast in both Alaska and Canada is generally characterized by larger lagoons (e.g., Elson and Simpson; Harris et al., 2017). However, lagoons along the coastline of the SCSR are more variable in size. On the adjacent Russian coast of the SCSR, Krylenko (2017) reports similar lagoon systems along 49% of the coastline. Thus, lagoons are widely present across the Arctic and play an important role within the broader coastal landscape.

In the SCSR, lagoon habitats and associated biota act as essential support for adjacent human communities. Indigenous residence on coastal lands of the Alaskan Arctic has been traced back over 4000 years, underlining the longevity and strength of ties between coastal ecosystems and contemporary Alaska Native Peoples (Anderson and Freeburg, 2013). Drawn by the productivity, biodiversity, and accessibility of the lagoons, the subsistence use of these habitats is commonplace among coastal communities in the region. Indigenous knowledge holders and researchers alike acknowledge the SCSR lagoons specifically as hosts to thriving fish communities and places of import for subsistence fish harvest (Uhl, 2004; Georgette and Shiedt, 2005; Raymond-Yakoubian, 2013; Logerwell et al., 2015). Further, these lagoons are known as important stopover or staging areas for migrating shorebirds and seabirds (Springer et al., 1984; Haynes et al., 2017b), which are valued for their eggs, and as habitat for breeding waterfowl (Schmidt et al., 2014), which are harvested for meat. SCSR lagoons are also associated with feeding marine mammals such as beluga (*Delphinapterus leucas*), gray whale (*Eschrichtius robustus*), bearded seal (*Erignathus barbatus*), and ringed seal (*Pusa hispida*; Frost et al., 1993). These species are harvested for meat and blubber as well as other products, such as hide and baleen, which are used for traditional clothing and crafts. For centuries, the broad range of biota supported by coastal lagoons has played a central role in the robust tradition of subsistence use and continues to do so for the coastal communities of the SCSR.

Yet while ecologically and culturally significant, lagoons of the SCSR, which are potentially sensitive to a myriad of threats, are still understudied. As early as 1961, oceanographer Martin Johnson, while surveying SCSR lagoons in preparation for the U.S. Atomic Energy Commission's Project Chariot, invoked a 1958 report by R.H. Fleming that recognized the scientific importance of understanding the physical and biological processes that define lagoon environments (Johnson, 1966:679):

> The geological and oceanographic processes that have led to development and life history of these features are of major scientific interest. Because each of them may represent a variable but unique micro-environment, the biology of these lagoons is also of unusual interest because [the lagoons] represent a transitional series of marine to fresh-water environments. At one extreme these lagoons are, in effect, the complex estuaries of rivers that flow only during the summer. At the other extreme the older lagoons, now permanently isolated from the sea and clogged with sediment and vegetation, are only distinguishable from aerial photographs. Between these two extremes are bodies of water, varying greatly in size, that must from time to time be flooded with sea water and then are closed off again and slowly diluted by the accumulation of precipitation and runoff.

Almost six decades later, coastal habitats in the SCSR, including lagoons, are experiencing the impacts of a rapidly changing climate as well as increased infrastructure development, including heightened transportation activity (particularly shipping) and construction of coastal structures such as causeways for village relocation efforts (Alaska DOT&PF, 2018). The predicted vulnerabilities of coastal habitats to such threats are well articulated in numerous scientific and policy-related publications (e.g., Arctic Council, 2009; Huntington et al., 2015; Alaska DOT&PF, 2018). Indeed, the Bering Strait in particular is frequently identified as an area of critical concern for potential oil spills because of a combination of increasing vessel traffic, high biological productivity (Springer et al., 1996), concentration of marine wildlife, and widespread subsistence use critical to the food security of coastal Indigenous villages in the surrounding area (Aurand and Essex, 2012; Moerlein and Carothers, 2012; ICC-A, 2015). Despite concerns over the vulnerability of these habitats and associated implications for local food security and ecosystem function, there is still a profound dearth of available information on the driving mechanisms and ecological dynamics of SCSR lagoon systems. Such information is vital for managers seeking to mitigate the impacts of coastal development and the expansion of the transportation sector, while simultaneously attempting to anticipate shifts in local ecologies and village infrastructure needs stemming from global climate change. Therefore, measures must be taken to address these gaps and should

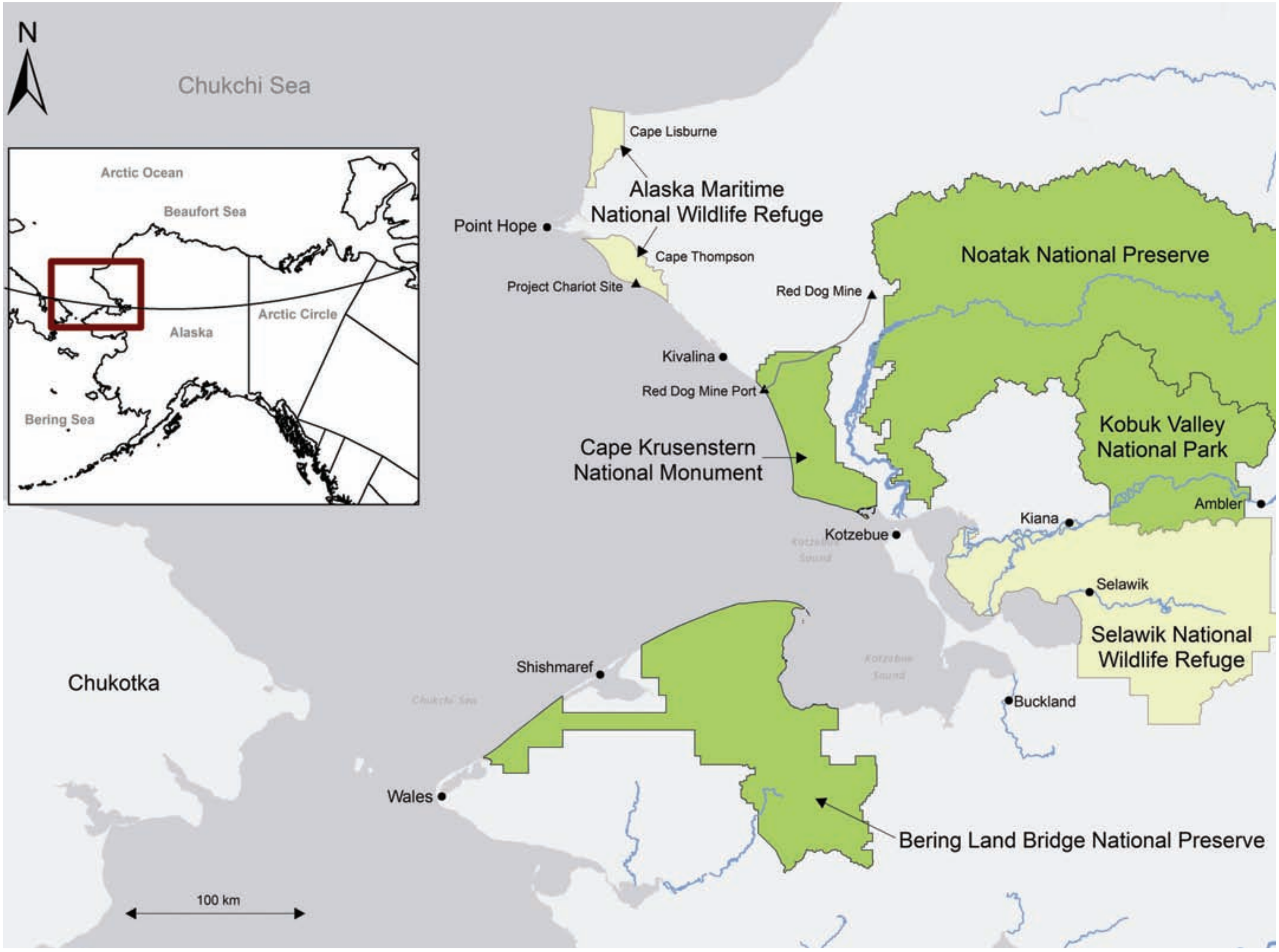

FIG. 1. Alaska coastline of the southern Chukchi Sea between Point Hope in the north and Wales in the south. Villages are denoted by circles, other points of interest are denoted by triangles, National Park lands are shown in green, and National Wildlife Refuge lands are shown in yellow. The Delong Mountain Transportation System (Red Dog Mine access road) is shown as a gray line. The village of Ambler is also shown, near the terminus of the proposed Ambler Road, which is to be extended from Alaska's Dalton Highway.

include an expansion of current efforts to produce a typology and framework for studying SCSR lagoons (e.g., Lawler et al., 2009; Krylenko, 2017; Jones et al., 2018) in the effort to provide further baseline information on the ecological dynamics of lagoon habitats.

This report synthesizes current knowledge about SCSR lagoon ecosystems, focusing on the lagoons located on the Alaska side of the Bering Strait, from the village of Wales in the south to Point Hope in the north (Fig. 1). This study encompasses seasonally brackish-freshwater lagoons as well as the freshwater drainages that feed them and extends out along the marine shelf to include the narrow estuarine band of the Chukchi Sea through which fishes and other aquatic organisms transit between lagoons. We focus specifically on the relatively common classification type of intermittently open and closed lagoons (Tibbles et al., 2018). Finally, we discuss lagoon ecosystems in the context of environmental and anthropogenic-induced changes occurring in the region, with conclusions, implications, and recommendations for future direction.

PREVIOUS STUDIES

Despite continued significant knowledge gaps in the area of SCSR lagoons, there have been calls for more focused research on the ecology of these habitats since the mid-twentieth century. Until recently, the most significant scientific investigations of the lagoons in the SCSR were associated with two large environmental assessments. The first began in the late 1950s in association with the U.S. Atomic Energy Commission's plans to detonate nuclear explosives in the effort to showcase civilian application of nuclear technology at Cape Thompson under the title of Project Chariot (O'Neill, 1994). The preliminary efforts for this project included over 40 broad-ranging baseline ecological studies that covered the abiotic and biotic aspects of the region, and lagoon exploration focused exclusively on those surrounding Cape Thompson (Fig. 1; Tash, 1964; Wilimovsky and Wolfe, 1966; Vandegraft, 1993). The second major scientific effort occurred in the late 1970s and early 1980s during the planning of the port facility for

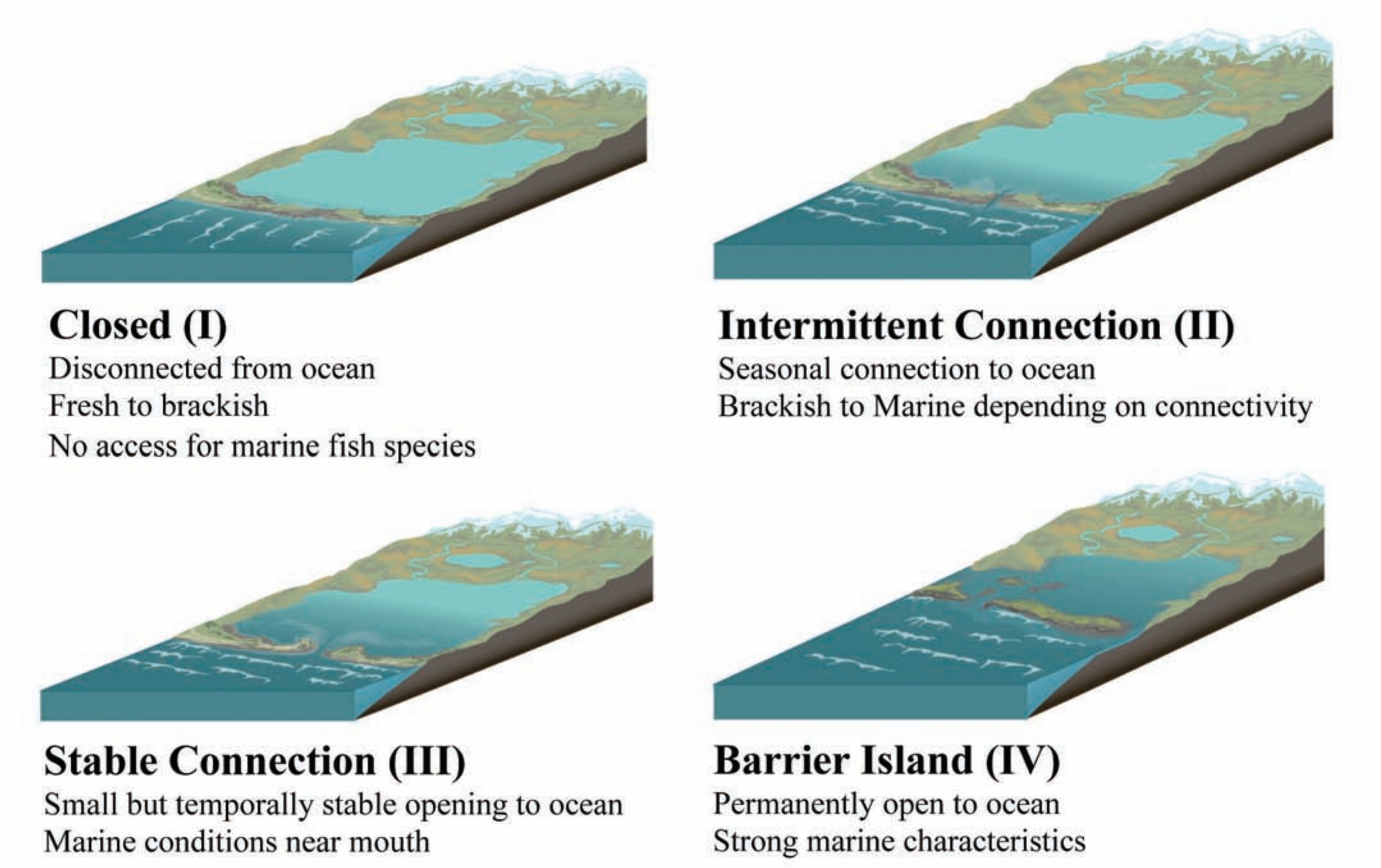

FIG. 2. Classification of southern Chukchi Sea lagoons based on physical dynamics associated with connectivity to the marine environment. Roman numerals in parentheses correspond to lagoon typology as listed in text and Table 1. Artwork by Megan Perra (Feral Five Creative Co.)

the now-operational Red Dog Mine just south of Kivalina (Blaylock and Houghton, 1983). The environmental studies associated with this development assessed invertebrate and fish ecology. In addition to these two biological assessments, a survey of coastal characteristics and processes was undertaken by the U.S. Geological Survey in the context of archeological sites, focusing primarily on abiotic processes such as beach deposition and the physical layout of the coast (Hopkins, 1977).

More recent studies include a series of publications and reports featuring SCSR coastal lagoons, with particular focus on fish ecology (Reynolds, 2012; Haynes et al., 2017a, b; Tibbles and Robards, 2018; Tibbles et al., 2018). Many of these publications were spawned from multiyear monitoring and research investigations associated with long-term monitoring efforts by the Wildlife Conservation Society (WCS) and National Park Service (NPS) at Cape Krusenstern National Monument and Bering Land Bridge National Preserve (Fig. 1) under the auspices of the broader NPS Vital Signs Program (Lawler et al., 2009).

Indigenous knowledge and anthropological information in the region have been well documented, with particular focus on subsistence food gathering (Georgette and Shiedt, 2005; Anderson and Freeburg, 2013; Raymond-Yakoubian, 2013). Research in this area has incorporated long-term observation of subsistence and cultural practices in surrounding communities, following residents such as Bob Uhl, who lived and travelled year-round within Cape Krusenstern National Monument (Uhl, 2004).

PHYSICAL ENVIRONMENT

Geomorphology

Consistent among research has been the recognition of the profound seasonal and interannual dynamics within individual SCSR lagoons, as well as the physical dissimilarities that exist between them (e.g., Johnson, 1961; Pinchuk et al., 2020). While there is some debate about the differentiation between lagoons and estuaries (Kennish and Paerl, 2011; Pérez-Ruzafa et al., 2019), with several different methods for classification (e.g., Krylenko, 2017; Tibbles, 2018), for the purposes of this article, we define lagoons as bodies of water typically located parallel to the marine coastline, separated from the ocean by a gravel berm or spit of land, exhibiting some degree of connectivity to the marine environment (and intrusion of saltwater), but not completely open to the ocean (excludes bays or sounds). SCSR lagoons can range in connectivity to the ocean and the physical characteristics of these connections generally delineate a typology of four distinct types (Fig. 2): I) closed,

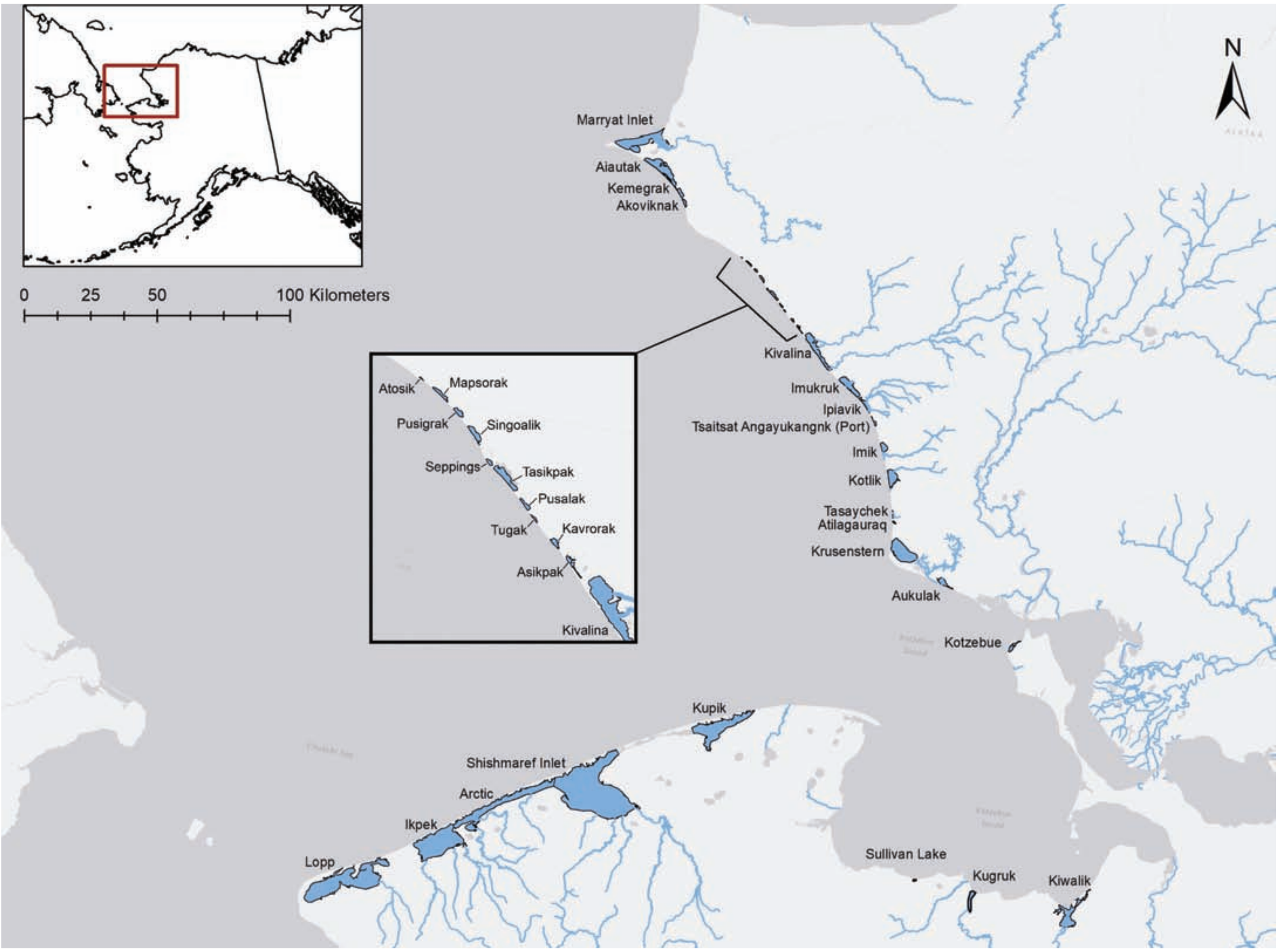

FIG. 3. Lagoons along the Alaska coast of the southern Chukchi Sea. See Table 1 for lagoon type and physical information (if available).

II) intermittent, III) stable-channel, and IV) open with barrier island (Horrell, 1992; Lin et al., 2001; McGlathery et al., 2001; Reynolds, 2012; Schallenberg and Saulnier-Talbot, 2016; Tibbles, 2018). Closed lagoons do not exhibit a connection to the ocean because of accumulated beach sediment deposition or loss of freshwater input over time, yet may still have two-way hyporheic flow through the gravel spit separating the lagoon from saltwater, depending on the amount of freshwater influx to the lagoon or the hydraulic pressure exerted upon the gravel spit by the ocean (Kjerfve, 1986).

In contrast, intermittent lagoons are fully connected to the ocean periodically via a channel formed by a breach in the gravel spit. Breaching events occur when the lagoon becomes overly full from freshwater input or if marine wave or tidal action causes a breach from the seaward side (e.g., Kotlik Lagoon; Fig. 3; Tibbles, 2018). Connection channels commonly occur just before the open water season and remain through mid-summer, although breaching events may not occur consistently every year (K. Fraley, pers. obser.; Tibbles, 2018). Many intermittent lagoons display multiple connected periods per year driven by spring freshwater runoff and high precipitation or storm events (Lee Harris, pers. comm. 2016); annual variability in the number of connected periods as well as the duration of connectivity to the ocean is high (Fraley et al., 2021a). The channel connection to the ocean generally occurs at the same location in intermittent lagoons, although it has been known to vary within and across seasons. Additionally, the length of the channel ranges between lagoons, some having direct connection to the ocean via a breach in the gravel spit directly on the marine edge, and others achieving connectivity to the ocean many kilometers away via river channels (e.g., Krusenstern Lagoon; Fig. 3).

Stable channel lagoons maintain an open-channel connection to the ocean during the entirety of the open-water season (e.g., Kivalina Lagoon; Alaska DOT&PF, 2018). While stable open-channel connectivity can be influenced by coastal geology and relief, this phenomenon generally occurs in lagoons with major freshwater river inputs, where the volume of freshwater influx maintains the lagoon channel outflow to the sea. Typically, the channel (or channels) to the sea remains in the same location within and across years. Finally, open lagoons are perennially connected to the ocean and have multiple broad openings and barrier islands that may change in configuration over years (e.g., Shishmaref Inlet and Ikpek Lagoon; Fig. 3; M. Robards, pers. obser.). Open lagoons are deeper, perpendicular to the coast, and exhibit daily, rapid influx and outflow of water following tidal changes, whereas estuaries or embayments are completely open to the ocean with little-to-no barrier island protection (Kennish and Paerl, 2011; Tibbles, 2018; Pérez-Ruzafa et al., 2019). We have focused on named lagoons along the coastline of the SCSR, although this list may not be comprehensive. Notable waterbodies in the SCSR we have excluded based on our definition of what constitutes a lagoon include Selawik Lake (nearly completely freshwater; Brown, 2013), Eischoltz Bay, and Sisualik and Espenberg Lagoons, which exhibit patchy barrier islands and are almost completely open to the ocean.

The bottom substrate of SCSR lagoons is typically a fine mud, with areas of coarser substrate at channels with increased water flow (e.g., Blaylock and Houghton, 1983). These lagoons are generally shallow (< 2 m; Table 1) compared to lagoons farther north in the Chukchi or Beaufort Seas (Reynolds, 2012). Due to a combination of shallow depths, fine-grain substrate, and changeable winds and tidal influence, the bottom topography of SCSR lagoons frequently changes throughout an open-water season, with areas of sediment buildup shifting in distribution throughout the main body of the lagoon (K. Fraley, pers. obser.). However, seasonal trends in these changes have yet to be quantified, with little past research examining the timing of and specific changes to lagoon bathymetry.

Hydrology and Water Chemistry

SCSR lagoon hydrology characteristics vary by location (Fig. 3; Table 1), depending on freshwater flows into the lagoon as well as oceanic connectivity (Blaylock and Houghton, 1983; Fraley et al., 2021a). The region is subject to small semidiurnal tides (diurnal range of ~ 0.2 m), with storm-driven shelf waves propagating through the southern Chukchi Sea into the body of lagoons (Danielson et al., 2020; Hennon et al., 2020). Wind is the primary driver of water-column mixing within the central body of these shallow habitats, especially for larger or closed channel lagoons, such as Krusenstern Lagoon, in which marine tidal action plays a limited role in lagoon-wide mixing. Winds that drive water movement within lagoons can also affect the flow of marine water into and out of the main body through the mouth of the lagoon, impacting both salinity and temperature and exerting a greater influence on water levels in the SCSR lagoons than the relatively minor lunar tides (Mojfeld, 1986). However, in calm conditions, small tidal amplitudes contribute to increased water flow velocities through lagoon mouths exceeding 2 m/s, with volumes reaching discharge rates of 473 m^3/s (Jones and Burger, 2014) due to the restricted cross-sectional area of the mouths.

Water-chemistry parameters at SCSR lagoons fluctuate in response to myriad factors. Season-long monitoring of water chemistry at Aukulak Lagoon during 2016 revealed several noticeable trends in temperature (seasonal decrease), salinity (seasonal decrease), and turbidity (reduction in overall variability) during the open-water season (Supplementary Appendix: Fig. S1). However, these trends range widely between locations and seasons. Salinities in the region's lagoons vary across and within years (Table 1; Supplementary Appendix: Fig. S1; Smith et al., 2019), even at daily intervals, presumably caused by the dual influences of connection to the ocean (increases salinity) and freshwater influx (decreases salinity). For example, three lagoons studied in the open-water seasons of 2015 – 17 in Cape Krusenstern National Monument (Krusentstern, Aukulak, and Kotlik lagoons) ranged in salinity from 0.2‰ to 26.9‰, depending on the lagoon, month sampled, and year (Smith et al., 2019). During the same study period, temperatures ranged from 2.69°C to 18.35°C and were also variable between and among locations, years, and months. While there was not a clear monthly pattern of salinity within years, temperature typically followed a discernable seasonal trend, peaking in July at values between 11°C and 18°C then decreasing from August into September reaching values as low as ~2°C – 5°C early in September. Temperature data collection did not extend past mid-September, which is typically the beginning of lagoon freeze-up. Johnson (1966) reported little or no thermal or haline stratification of lagoons near Cape Thompson, supporting the aforementioned wind-driven mixing that occurs within these lagoons throughout the open-water season. During the summer months (from June to September 2015 – 17), pH ranged from 7.4 to 10.6, dissolved oxygen from 94% to 129%, turbidity from 0.7 to 9.7 NTU, and conductivity from 3505 to 46,167 mS/cm in the Cape Krusenstern lagoons (Smith et al., 2019).

SCSR lagoons are ice covered from early October to early May and are thought to be disconnected to the ocean during much of this time because of low water levels, *kaimoo* (a flat rampart of alternating layers of beach sediment and ice; Moore, 1966), and bedfast ice around the channels to the ocean (Wilimovsky and Wolfe, 1966). For lagoons less than about 2 m in depth, ice becomes bedfast within the central body in mid- to late winter (Tibbles et al., 2018). For deeper lagoons, liquid water remains below the ice, but can be subfreezing (as low as −3.4°C), hypersaline (as high as 52.7‰), and hypoxic (as low as ~20% DO; Tibbles et al., 2018), which would not support life for most biota. Additionally, freshwater sources that feed the lagoons may also freeze to the bottom, and although liquid water usually remains in larger rivers or in proximity to groundwater springs throughout the winter, these areas may be limited and disconnected (Chuck Schaeffer, pers. comm. 2016). Thus, the areas of exploitable winter habitat for aquatic biota drastically decrease.

TABLE 1. Named lagoons along the Alaska coast of the southern Chukchi Sea ordered from north to south. Lagoon type is listed if known. Mean physical data are included for lagoons with data available. Asterisk in Alaska's Anadromous Waters Catalog (AWC) column indicates a designated anadromous water flows into the lagoon in question. Other lagoons exist in the SCSR, but are not included here unless named or studied. Sisualik and Espenberg, while lagoons in name, did not fit the definition of lagoons as stated in this review and thus are not included.

Lagoon	Type[1]	Mean depth (m)	Mean salinity (ppt)	Study	Conservation unit/ land management	AWC*	Closest community (distance km)	Field work conducted[2]
Marryat Inlet	III	–	–	Tibbles et al., 2020	Alaska Native (Tigara Corp)	Y*	0	FCA, WC
Aiautak	U	< 2.5	0.53	Wilimovsky & Wolfe, 1966	Alaska Native (Tigara Corp)	N	11	WC
Kemegrak	I	1.3–3	1.2	Pinchuk et al., 2020	Alaska Native (Tigara Corp)	N	28	FCA, Z, PP, WC, AV
Akoviknak	I	1.3–3	1.9	Pinchuk et al., 2020	Alaska Native (Tigara Corp)	N	32	FCA, Z, PP, WC, FSI, FC, AV
Atosik	I	1.3–3	1.6	Pinchuk et al., 2020	FWS (AMNWR)	N	51	FCA, Z, PP, WC, AV
Mapsorak	II	1.3–3	0.7	Pinchuk et al., 2020	FWS (AMNWR)	N	47	FCA, Z, PP, WC, AV
Pusigrak	U	1.3–3	1	Blaylock & Houghton, 1983	FWS (AMNWR)	N	44	FCA, SC, WC
Singoalik	II	1.3–3	9.3	Pinchuk et al., 2020	State/BLM	N	40	FCA, Z, PP, WC, AV
Seppings	U	1.3–3	0.8	Johnson, 1966	State	N	35	Z, WC
Tasikpak	U	1.3–3	0.7	Johnson, 1966	State/BLM	N	30	Z, WC
Pusalak	I	1.3–3	3.6	Johnson, 1966	BLM	N	27	Z, WC
Tugak	II	–	–	–	BLM	N	24	–
Kavrorak	U	–	–	–	Alaska Native (NANA)	N	20	–
Asikpak	II	–	–	–	Alaska Native (Kivalina Sinuakmuet)	N	15	–
Kivalina	III	–	–	–	Alaska Native (Kivalina Sinuakmuet)	Y*	0	–
Imukruk	U	–	1.1	Blaylock & Houghton, 1983	Alaska Native (Kivalina Sinuakmuet)/BLM	Y*	6	FCA, SC, WC
Ipiavik	II	–	6.2	Blaylock & Houghton, 1983	NANA/NPS (Cape Krusenstern)	Y*	16	FCA, SC, WC
Tsaitsat Angayukangnk (Port)	II	–	1.4	Blaylock & Houghton, 1983	NANA/Private	N	26	FCA, SC, WC
Imik	II	0.9	2.5	Reynolds, 2012	NPS (Cape Krusenstern)	Y	35	FCA, WC, Z
Kotlik	II	2.1	15.1	Smith et al., 2019	NPS (Cape Krusenstern)	Y*	46	FCA, FC, FSI, FD, PP, Z, SC, ST, Z
Tasaychek	II	–	7.5	Smith et al., 2019	NPS (Cape Krusenstern)	Y*	61	FCA, FSI, WC
Atilagauraq	II	–	20	Smith et al., 2019	NPS (Cape Krusenstern)	N	64	FCA, WC
Krusenstern	II	2.4	3	Smith et al., 2019	NPS (Cape Krusenstern)	Y*	48	FCA, FC, FSI, FD, PP, Z, SC, ST, Z
Aukulak	II	1.4	15.7	Smith et al., 2019	NPS (Cape Krusenstern)	Y	32	FCA, FC, FSI, FD, PP, Z, SC, ST, Z
Kotzebue	III	–	–	–	State	N	0	–
Kiwalik	IV	–	–	–	State	N*	29	–
Kugruk	III	–	–	–	State	Y*	6	–
Sullivan Lake	U	–	–	–	State	N	18	–
Kupik	IV	–	20.5	Smith et al., 2019	NANA/NPS (Bering Land Bridge)	N	40	FCA, WC
Shishmaref Inlet	IV	–	–	–	NANA/NPS (Bering Land Bridge)	N*	0	–
Arctic	IV	–	–	–	NANA/NPS (Bering Land Bridge)	N*	10	–
Ikpek	IV	–	23	Smith et al., 2019	NANA/NPS (Bering Land Bridge)	N*	48	FCA, WC
Lopp	IV	–	–	–	NANA/NPS (Bering Land Bridge)	N*	3	–

[1] Lagoon types: I = closed, II = intermittent, III = stable-channel, and IV = open with barrier island; U = unknown.

[2] FCA = fish community and abundance, FC = fish contaminants, FSI = fish stable isotopes, FD = fish diet, PP = primary productivity, WC = water chemistry, AV = avian surveys, SC = secondary consumers, ST = seasonal trends, Z = zooplankton.

GENERAL ECOLOGY

Basal Resources

Arctic coastal lagoons can be highly productive on a seasonal basis. The foundation of lagoon food webs, at least for the neighboring Beaufort Sea lagoons, arises predominantly from allochthonous deposits (e.g., carbon, nitrogen, and organic debris) from terrestrial and freshwater inputs with some supplementary autotrophic growth (Dunton et al., 2012), although the sources remain relatively understudied in lagoons of the SCSR. Little benthic aquatic plant growth is present, with only occasional and patchy occurrence of seagrasses (M. Robards, pers. obser.), however blue-green algal blooms are common in the lagoons of Cape Krusenstern National Monument and Cape Thompson (Thessen et al., 2012; Smith et al., 2019) and are typically modulated by habitat factors such as water temperature, salinity, turbidity, and water mixing (Hughes et al., 2011).

Zooplankton assemblages of lagoons within Cape Krusenstern National Monument and Cape Thompson vary widely across locations, although they can be stable within lagoons across years (Johnson, 1961, 1966; Tash, 1964; Tash and Armitage, 1967; Pinchuk et al., 2020). Zooplankton assemblages consist of a mixture of marine, brackish, and freshwater taxa including cyclopoids, copepods, and harpacticoids (Schizas and Shirley, 1994) and are significantly different from those of nearshore marine waters of the Chukchi Sea (Pinchuk and Eisner, 2017). Biomass ranged widely among Cape Krusenstern and Cape Thompson individual lagoons, years, and even months (17.5 – 2196 mg m^{-3}), indicating the dynamic nature of this important basal food web component. However, the relative abundance of euryhaline- and stenohaline-dominant taxa is associated with both the mean and variation in lagoon salinity (O'Brien et al., 2004; Pinchuk et al., 2020). Unlike lagoons of Capes Krusenstern and Thompson, there is little information outlining baseline zooplankton assemblages farther south at the lagoons along the Seward Peninsula.

The primary consumers in these lagoon food webs are benthic invertebrates of marine, terrestrial, and freshwater origin that feed upon zooplankton, algae, bacteria, or detritus (Blaylock and Houghton, 1983; Feder et al., 2005, 2007; Tibbles and Robards, 2018). These include Diptera larvae (e.g., Chironomidae spp.), Mysidae, Bivalvia, and Amphipoda. The distribution and abundance of these benthic invertebrates within lagoons are likely driven by salinity and temperature, in association with their respective life histories, but their ecology has not been examined closely in the region despite the aforementioned invertebrate taxa being found in the diets of all seven fish species examined by Tibbles and Robards (2018).

Fishes

Biodiversity and relative abundance of fishes can range widely from year to year, by lagoon, and within season. Assemblage composition within a given lagoon depends largely upon time of open or closure to the marine environment as well as number and size of freshwater inputs into the lagoon. For example, WCS sampling efforts at Aukulak Lagoon, which in some years exhibits one of the more diverse fish assemblages of any lagoon in Cape Krusenstern National Monument (Smith et al., 2019), have produced no fish for the duration of an open-water season after the lagoon failed to open up to the marine environment during breakup (Smith et al., 2019). Additionally, during that same season, the freshwater inlet at Aukulak had noticeably lower discharge than previously observed (B. Smith, pers. obser.). Similarly, some of the smaller lagoons at Cape Thompson (Atosik and Kemegrak), which sometimes remain closed to the marine environment for years at a time, have produced fewer or no fish and lower overall biodiversity during sampling efforts (Smith et al., 2019). Despite inconsistencies in fish community composition, many lagoons possess a diversity of species that reflects a complex and dynamic food web.

The trophic level above primary consumers is represented by small-bodied marine and freshwater microbenthivore and planktivore prey fishes that are commonly found in lagoons throughout the SCSR study area (Table 2). These can include ninespine stickleback (*Pungitius pungitius*), slimy sculpin (*Cottus cognatus*), pond smelt (*Hypomesus olidus*), Alaska blackfish (*Dallia pectoralis*), tubenose poacher (*Pallasina barbata*), and Pacific herring (*Clupea pallasii*; Blaylock and Houghton, 1983). The ecology of these small-bodied forage species is not comprehensively described, despite their importance as primary prey items for larger piscivorous fish species and birds of subsistence-harvest importance (Tibbles and Robards, 2018). For instance, diet information from Tibbles and Robards (2018) shows that ninespine stickleback and Pacific herring predominantly consume Chironomidae, Mysidae, and Copepoda, but diet composition can be variable between lagoons, presumably due to variability in relative prey availability. Furthermore, stable isotope analyses ($\delta^{15}N$ and $\delta_{13}C$) at Cape Krusenstern lagoons indicate that Pacific herring trophic ecology is not particularly dependent on lagoon connectivity to the sea or freshwater input but is associated with the distance of a lagoon from the sea (Fraley et al., 2021a), with variety in trophic feeding positions potentially increasing with lagoon distance from the sea. It is likely that Pacific herring (as well as other marine taxa) only rear and feed in lagoons and do not successfully overwinter (Tibbles et al., 2018). In fact, this species has been observed spawning in relatively low-salinity lagoon habitats; given the short incubation time of their eggs (~ 2 weeks; Funk, 2007), it is possible that these efforts are successful, however, this dynamic has not been investigated in depth. Pacific herring are just one example of a secondary consumer species bearing an intricate relationship with lagoon habitats and, while baseline knowledge of the community composition of this trophic level within SCSR lagoons exists, further research is needed to develop a better understanding of the ecology of many of these species.

The next trophic tier consists of larger-bodied invertivorous whitefishes including Bering cisco (*Coregonus laurettae*), least cisco (*C. sardinella*), humpback whitefish (*C. pidschian*), and other Coregoninae species (Table 2). These fishes typically rear and feed in lagoon habitats and may overwinter and spawn in the associated freshwater inlets (Craig et al., 1985; Tallman et al., 2002), although most are thought to originate from large source river systems such as the Noatak or Kobuk Rivers. Species within this grouping swim along the coastline in the nearshore marine environment during the open-water season and will transit between lagoons (Craig et al., 1985; Tallman et al., 2002; Georgette and Shiedt, 2005; Padilla et al., 2016). Possibly as a result of migratory behaviors, these middle-tiered species are commonly found in lagoons throughout the study area (Table 2), sometimes in high relative abundance compared to piscivorous fishes (Smith et al., 2019). The diet of these species is generally limited to items such as Chironomidae, Mysidae, and Bivalvia and does not often include smaller forage fishes consumed by larger predator species, particularly those of marine origin (Tibbles and Robards, 2018). Furthermore, stable isotope analyses indicate that humpback whitefish trophic ecology is influenced by the duration of lagoon connectivity to the sea (Fraley et al., 2021a), with longer duration of connectivity exhibiting higher mean $\delta^{13}C$ values (indicating uptake of more marine-derived nutrients), but shorter trophic length (less variability in positioning in the food chain or smaller realized niche due to competition from marine taxa). However, a broader understanding of the intricacies surrounding whitefish ecology with regards to SCSR lagoons is important for a comprehensive view of lagoon trophic dynamics and should include further study of migratory behaviors, shifts in range extent, and trends in year-to-year distribution and abundance.

Additionally, several species of Pacific salmon, including pink (*Oncorhynchus gorbuscha*), chum (*O. keta*), and coho (*O. kisutch*), occur in lagoons of the SCSR, most frequently present in those of Cape Krusenstern National Monument (Table 2). Both juveniles and adults have been observed using these lagoons (and are recorded in Alaska's Anadromous Waters Catalog), with juveniles feeding in the relatively sheltered habitat and adults transiting through these areas enroute to freshwater spawning grounds (Smith et al., 2019). Juvenile salmon likely fit somewhere between lower trophic levels and invertivorous whitefishes, while adult salmon fit between invertivorous whitefish and generalist predators. As juveniles and adults, salmon only remain in lagoons for a short period of time before migrating to the ocean or to spawning rivers (Logerwell et al., 2015). Significant pink and chum salmon runs occur in larger rivers in the region (e.g., Kobuk and Noatak Rivers), accounting for the presence of these species in the adjacent lagoons. Although sockeye (*O. nerka*), Chinook (*O. tshawytscha*), and coho salmon runs occur in the region, they are relatively small and patchy compared to other regions of Alaska, and run sizes of salmon of all species diminish with increasing latitude (Wilimovsky and Wolfe, 1966; Moss et al., 2009). Recently, however, certain salmon species have become more prevalent in the Arctic because of milder freshwater overwintering conditions as a result of climate warming (Nielsen et al., 2013). Given the typical pelagic feeding behavior of juvenile salmon within coastal lagoons (Moss et al., 2009), it is likely that these fishes, based on size classes most commonly encountered throughout sampling efforts, are feeding upon zooplankton and suspended invertebrates, although diet and ecology studies of salmon species of the SCSR lagoons have not yet been conducted (Logerwell et al., 2015). With an extensive body of knowledge on Pacific salmon from other regions and past SCSR research investigating the diet of whitefishes in lagoons, there is a solid foundation of information on the ecology of species in these groups.

Finally, the apex of the aquatic food web in SCSR lagoons comprises the larger-bodied generalist fishes that feed upon a mixture of macroinvertebrates and smaller fishes, depending on the body size and age of the predator fish (Tibbles and Robards, 2018). These generalist fish include marine species such as starry flounder (*Platichthys stellatus*), saffron cod (*Eleginus gracilis*), diadromous inconnu (*Stenodus nelma*), and Dolly Varden charr (*Salvelinus malma*), and occasionally freshwater Arctic grayling (*Thymallus arcticus*) (Blaylock and Houghton, 1983; Johnson et al., 2007). The variety of prey items targeted by species of this category appears to be somewhat opportunistic, reflecting a certain degree of foraging plasticity. Similar to Pacific herring, stable isotope analyses of starry flounder (which is widely distributed throughout lagoons of the SCSR) in Cape Krusenstern lagoons indicate that distance of the lagoon from the sea was an important driver of mean $\delta^{15}N$. Starry flounder from lagoons farther from the ocean exhibited lower mean values of $\delta^{15}N$, which suggests that predator species feed either on items lower in the food chain or less-enriched by marine-derived nutrients (i.e., freshwater prey) when occupying lagoons farther from the ocean. These findings together with those of Tibbles and Robards (2018) suggest that these species are well suited to transitioning between freshwater habitat, brackish lagoon ecosystems, and the ocean, however, additional study would be useful to develop a better understanding of these movements and associated shifts to targeted prey.

These larger-bodied predator fishes are routinely caught by sampling efforts in lagoons of Cape Krusenstern (Smith et al., 2019) and have been encountered at sample sites in Bering Land Bridge and Cape Thompson lagoons, yet seem to be less widely dispersed throughout these areas as compared to invertivorous whitefish species (Table 2). These larger predator fish are known to migrate through lagoons, spending time in the marine habitat before returning to freshwater areas. Both inconnu and Dolly Varden migrate great distances through freshwater and marine environments (e.g., hundreds of kilometers up the Kobuk River or across the Bering Strait to Russia) during feeding movements and spawning migrations (Alt, 1977; Courtney et al., 2016). Inconnu commonly migrate along the SCSR coastline and enter lagoons temporarily for rearing and feeding before presumably moving back to large rivers (e.g., Selawik River) to spawn and to large sounds or bays to overwinter (e.g., Hotham Inlet; Smith et al., 2015). The prevalence of inconnu farther from known summer and overwinter areas (i.e., Hotham Inlet) is increasing according to reports from local fishermen (Cyrus Harris and Johnson Stalker, pers. comm. 2016; Jones, 2006), suggesting significant alteration to movement patterns and potential impacts to regional abundance of lower trophic level fish. As movement patterns continue to shift for inconnu as well as other species of this trophic classification, it will be important to expand research efforts to assess the progression of migratory behavior as well as potential ecological repercussions both within and apart from SCSR lagoon ecosystems.

Other Biota

Use of the lagoon habitats by terrestrial and avian biota has been informally documented during field data collection efforts (e.g., Smith et al., 2019) as well as formally studied (e.g., Haynes et al., 2017b; Table 1). Other visitors to SCSR lagoons include marine mammals such as bearded seals (*Erignathus barbatus*), gray whales (*Eschrichtius robustus*), and beluga (*Delphinapterus leucas*; Frost et al., 1993). These species typically remain near the mouth of lagoons, where they forage for fish and invertebrates, avoiding the shallow and potentially hazardous confines of the lagoon. Additionally, seabirds, shorebirds, and waterfowl utilize SCSR lagoons for feeding, breeding, and refugia during the open-water season (Springer et al., 1984; Schmidt et al., 2014; Haynes et al., 2017b). Species such as the Yellow-billed Loon (*Gavia adamsii*), Common Merganser (*Mergus merganser*), and several within the Laridae family (for example, the Bonaparte's Gull [*Chroicocephalus philadelphia*] and Caspian Tern [*Hydroprogne caspia*]) are piscivorous and routinely observed foraging at the mouth and in the central body of the lagoon (Haynes et al., 2015, 2017b). Additionally, several species of the Charadriidae family are commonly seen foraging in silt deposits at the lagoon edge and will nest in adjacent protected grassy areas (Cunningham et al., 2016; B. Smith, pers. obser.) Terrestrial and semi-aquatic mammalian predators are also present and prey upon fish and invertebrates in SCSR lagoons (Marcot et al., 2015; Chuck Schaeffer, Cyrus Harris, and Johnson Stalker, pers. comm. 2016). These predators include brown bear (*Ursus arctos*), red fox (*Vulpes vulpes*), Arctic fox (*Vulpes lagopus*), American mink (*Neovison vison*), and river otter (*Lontra canadensis*). With a variety of terrestrial and avian species utilizing SCSR lagoon habitats, several of which are of subsistence importance, continued characterization and monitoring of these communities will be necessary to understand the potential scope of ecological perturbations.

Seasonal Patterns

During the open-water months, SCSR lagoon ecosystems are productive, with prolonged photoperiods boosting autotrophic growth as well as an abundance of seasonal visitors offering a variety of both freshwater and marine-sourced ecosystem subsidies (e.g., enriched nutrients from senescent spawning salmon and bird feces; Rinella et al., 2013; Zmudczyńska-Skarbek and Balazy, 2017). However, given the length and harshness of lagoon winter conditions (i.e., polar night; Krylenko, 2017) and the absence of seasonally migratory species at this time, many of these lagoons reset each year with any overwintering aquatic biota moving into lacustrine systems (some of which in this region have year-round springs), into the ocean, or perishing if they become trapped (Tibbles et al., 2018; Chuck Schaeffer, pers. comm. 2016). The overwintering success of marine taxa trapped in lagoons and their associated freshwater systems is unknown, and it is likely that complete or very high mortality occurs (Blaylock and Houghton, 1983; Chuck Schaeffer, pers. comm. 2016). As previously mentioned, circumstances surrounding the apparent lack of fishes in Aukulak Lagoon during the summer of 2017 (Smith et al., 2019) suggest that this low relative abundance was a by-product of the absence of connectivity to the ocean and the inability for fishes to overwinter in lagoon habitat. While sampling efforts at Aukulak Lagoon the previous summer had produced fish (Smith et al., 2019), results from the 2017 field season indicate that fishes observed in 2016 became trapped in the lagoon after autumn close-up and perished during the winter. Further, even resilient freshwater-oriented species can be negatively affected by overwintering conditions; for example, Blaylock and Houghton (1983) recorded a ninespine stickleback mass overwintering mortality event in Port Lagoon. Thus, SCSR coastal lagoons exhibit extremes of low and high productivity on a seasonal cycle, with a stark contrast between high relative biotic abundance and diversity during the open-water summer season and potentially uninhabitable conditions during the winter.

ANTHROPOGENIC INTERACTIONS

Subsistence Use

SCSR lagoons are visited by subsistence users of the adjacent Indigenous communities (Table 1) primarily for fishing. Subsistence fishing occurs throughout the open-water season, but especially in the autumn when whitefish contain eggs and are in the best body condition (Georgette and Shiedt, 2012; Chuck Schaeffer, pers. comm. 2016). Subsistence users also visit the lagoons during the winter and spring seasons, sometimes harvesting fish from under the ice in lagoons and associated river channels (Cyrus Harris and Johnson Stalker, pers. comm. 2016). Fishermen typically spend days to weeks either camping at or traveling back and forth to harvest sites (fish camps) where they

FIG. 4. A channel and pot fish trap used to capture fish for subsistence harvest deployed at the Krusenstern Lagoon/Tukrok River outflow to the Chukchi Sea, Anigaaq, Cape Krusenstern National Monument, Alaska. Photo inset shows humpback whitefish caught using this method. Photo courtesy of Susan Georgette.

catch, process, and preserve the fish (Uhl, 2004; Raymond-Yakoubian, 2013). Motor vessels and snowmobiles are typically used to access fishing sites, which can be more than 40 km away from the homes of fishermen. Methods of capture include setting gillnets (3- to 6-inch square mesh openings) in the lagoons and at the mouths, angling, or using a traditional channel and pot technique where a flowing channel is dug through the gravel spit on the lagoon side for fish to swim into and become trapped as they attempt to exit lagoons (Fig. 4; Magdanz et al., 2010; Cyrus Harris and Johnson Stalker, pers. comm. 2016).

Fish are eaten fresh (particularly the eggs, if available), dried, smoked, or in the case of whitefish, caught in autumn, fermented, frozen, and subsequently eaten with seal oil (Cyrus Harris and Johnson Stalker, pers. comm. 2016). Some harvested fish are also used as sled dog food. Fishermen often share their catch with other community members, and Elders are especially fond of receiving the frozen fermented whitefish, a common food of their youth. These practices are an important cultural tradition for Indigenous residents who rely on the ecological health of local resources to maintain subsistence into the future (John and Pearl Goodwin, pers. comm. 2016). Local residents occasionally dig channels from closed lagoons to the ocean to facilitate fish movement into and out of lagoons in an effort to ensure fish survival and propagation for future catches (Bob Schaeffer, pers. comm. 2016).

Target subsistence species include several Coregoninae (humpback whitefish, broad whitefish [*Coregonus nasus*], and least cisco) and some larger-bodied omnivorous fishes including, Dolly Varden, inconnu, saffron cod, Pacific herring, and Pacific salmon species (pink and chum) (Georgette and Shiedt, 2005; Magdanz et al., 2010; Whiting et al., 2011; John and Pearl Goodwin, pers. comm. 2016). Coregoninae in coastal lagoons have been found to contain particularly high energy density (averaging up to 11.8 kJ/g wet weight) and represent a nourishing food source (Fraley et al., 2021b). While salmon are an important food resource for subsistence fishermen in the greater Alaska Arctic region and are captured in coastal and freshwater habitats (Whiting, 2006; Magdanz et al., 2010), they are not commonly the top harvested fish species from the SCSR (Wilimovsky and Wolfe, 1966; Magdanz et al., 2010). Dolly Varden and saffron cod typically comprise the largest amount of catch by weight (Magdanz et al., 2010). For example, fishermen in Kivalina in 2007 harvested only an estimated 613 individual salmon of various species totaling 1563 kg compared to over 20,000 Dolly Varden (>30,000 kg) and over 25,000 saffron cod (>2200 kg) (Magdanz et al., 2010). Because of the subsistence importance of some of the Coregoninae species, changes in movement patterns of large predatory fish (adult salmon, inconnu, etc.) are of particular interest to local fishermen due to their potential to alter the abundance of lower trophic level species and propagate a trophic cascade that may affect stocks of more commonly caught fishes such as humpback whitefish. Continued investigation into the ecology of lagoon habitats and associated fish species, particularly shifts in range extent and abundance, is therefore critical to the health of subsistence practices of the surrounding communities of SCSR lagoons (see Table 1 for the distance of each lagoon to the closest community).

Infrastructure Development

Anthropogenic development along the coastline of the SCSR is limited, yet several undertakings, including infrastructure development, mineral extraction, shipping, and oil and gas exploration, pose potential direct and indirect threats to lagoon ecosystem health. Direct threats to lagoons occur primarily as a result of coastal infrastructure development. Construction of roads, port facilities, causeways, and marinas have the potential to impact lagoon habitats by altering their geomorphology, hydrology, and geochemistry, with further implications for biotic assemblages (Supplementary Appendix: Fig. S2; Schallenburg and Saulnier-Talbot, 2016). Past and current infrastructure construction projects in the region include the Kotzebue lagoon airstrip (Alaska DOT&PF, 2015), the Kivalina Evacuation and School Site Access Road (Alaska DOT&PF, 2018), and the port facility at Red Dog Mine (Blaylock and Houghton, 1983). While many lagoons along the SCSR are not close to villages and would not be directly impacted (Table 1), present and future infrastructure development projects pose potential risk for several SCSR lagoons (e.g., Marryat Inlet, Kivalina Lagoon, Port Lagoon, and Shishmaref Inlet).

Indirect impacts to lagoons can occur as a by-product of increased shipping activity, resource extraction, and infrastructure development. Marine shipping in the region is expected to continue increasing as Arctic seas become more navigable and resource extraction opportunities more widely accessible (Smith and Stephenson, 2013). This increase causes a rise in noise and contaminant pollution in the Chukchi Sea (Huntington et al., 2015) with the potential for introduction of non-native biota via ballast water (Jing et al., 2012), which may have broader implications for lagoon ecosystems (Supplementary Appendix: Fig. S2; Gollasch et al., 2015). Some of the primary indirect threats of resource extraction and associated infrastructure development to SCSR lagoons include an increase in contaminants entering lagoons or their associated freshwater environments through pollutant discharge and emissions, increased turbidity as a result of erosion, and increased risk of catastrophic chemical spills that could enter lagoons through freshwater tributaries or the marine openings (Chapman et al., 2000; Truett and Johnson, 2000; Hasselbach et al., 2005; Lin et al., 2020). Resource extraction occurring in the headwaters of the drainages that feed the SCSR lagoons is of particular concern due to the potential for downstream impacts to the lagoon ecosystem (Truett and Johnson, 2000). For example, the most prominent resource extraction project in the region is the Red Dog Mine (1989), a large open pit mine in the headwaters of the Wulik River, which is a tributary of Kivalina Lagoon, as well as the associated Delong Mountain Transportation System and the port facility that abuts Port Lagoon (Quakenbush and Citta, 2009; Brumbaugh et al., 2010). Pollutants and toxicants in the mine runoff, emissions, and fugitive ore dust have caused issues in the past and remain a concern for the Wulik River drainage and adjacent habitats and have the potential to impact downstream lagoons (Chapman et al., 2000; Kelley and Hudson, 2007; Brumbaugh et al., 2010; Pemberton, 2010). Elevated contaminants have been noted in marine mammals in the region as well as in terrestrial plants and animals (Quakenbush and Citta, 2009; Brumbaugh et al., 2010), and atmospheric deposition and accumulation of contaminants in subsistence-harvested species are of particular concern in local communities (Cyr et al., 2019; Fraley et al., 2020; Lin et al., 2020), with a legacy stretching back to the Project Chariot Proposal at Cape Thompson in the early 1960s (O'Neill, 1994).

Additionally, infrastructure development associated with resource extraction projects, such as the proposed Ambler Mining District Industrial Access Project (Ambler Road; BLM, 2020), which would be constructed through the upper Kobuk River drainage, has larger implications for region-wide Coregonidae spawning populations as well as pollution and drainage dynamics (Yu et al., 2021), with potential for degraded fish populations, contaminated wild foods, and increased erosion impacting turbidity levels of downstream ecosystems, including SCSR lagoons (Supplementary Appendix: Fig. S2). With a wide variety of associated environmental impacts as well as uncertainty surrounding the stability and longevity of resource extraction operations (e.g., recent catastrophic tailing dam failures at Mount Polley Dam; Oboni and Oboni, 2020), it is critical to develop a better understanding of how these operations and associated infrastructure developments might affect lagoon habitats. While there is ongoing research into contaminant levels among various fish species of SCSR lagoons as well as water-chemistry monitoring including turbidity measurements (Smith et al., 2019), it is still unclear how many of these direct and indirect threats might impact lagoon ecology. Currently, there is a dearth of available evidence outlining specific outcomes of resource extraction and infrastructure development to adjacent and downstream lagoon habitats, with little information showing how lagoon communities respond to these external stressors. While evidence exists to suggest a broad scope of detrimental ecological outcomes from these human activities (Truett and Johnson, 2000; Hasselbach et al., 2005; Lin et al., 2020), there is little formal scientific study exploring specific vulnerabilities of and changes to SCSR lagoons. Only when more comprehensive research of these impacts has been completed, starting with more in-depth study of pristine lagoon conditions, can management efforts effectively implement conservation measures to protect SCSR lagoon habitats, particularly as the Arctic begins to open up to further resource extraction opportunities that will require increased shipping activity and infrastructure development (Decker et al., 1989; Raynolds et al., 2020).

CLIMATE CHANGE

In addition to the potential for expansion of anthropogenic development in the region, climate change in the Arctic is occurring at an increasingly rapid rate, faster than anywhere else on the globe (IPCC, 2007; Thoman and Walsh, 2019) and is therefore of great concern in the context of SCSR lagoons. Most notably, in Northwest Alaska, air temperatures have increased by 2.4°C since 1969 (Thoman and Walsh, 2019), with potential direct and indirect impacts to Alaskan Arctic ecosystems. Habitat alteration from rising temperatures can occur as a result of permafrost thawing and subsequent alteration of nutrient flux (Walvoord and Striegel, 2007; Harris et al., 2018) and shoreline erosion (Jones et al., 2009; Mason et al., 2012), all of which can occur along tributaries feeding into SCSR lagoons as well as in the central body of the lagoon itself. Temperature anomalies associated with climate change have also altered seasonal periodicity, resulting in changes to the timing and duration of ice-free seasons in marine, freshwater, and brackish habitats (Arp et al., 2018; Farquharson et al., 2018), potentially disrupting the natural seasonal cues that fish and other biota utilize for spawning and migration timing. Furthermore, a widely documented outcome of rising temperatures across the Arctic has been the northward range expansion of subarctic biota (Nielsen et al., 2013; Natsuike et al., 2017), which has the potential to alter biotic assemblages of SCSR lagoons, having larger implications for trophic dynamics, species distribution and abundance, and even subsistence use (Supplementary Appendix: Fig. S2). For example, Pacific salmon species are becoming more prevalent in Arctic waters as overwintering success becomes increasingly possible (Moss et al., 2009; Nielson et al., 2013), with juvenile coho salmon observed in SCSR lagoons in 2018 for the first time since recent sampling efforts began (Smith et al., 2019). It is suggested that shifts in the distribution and abundance of certain fishes in marine areas around lagoons have the potential to increase the likelihood of commercial fishery exploitation of the SCSR in the future (Datsky, 2015), which could result in cascading effects to food webs of lagoon habitats. Finally, increased water temperatures generally require higher metabolic rates for fish and other ectotherms, resulting in a need for greater food intake to compensate (Laurel et al., 2016) and having potential indirect impacts to trophic dynamics in lagoon systems.

Other direct and indirect effects of climate change in the region are wide ranging, from altered freshwater runoff volume and timing (Nummelin et al., 2016; Stuefer et al., 2017) to increased incidence of wildfires (Melvin et al., 2017) and wildlife diseases (Sformo et al., 2017). Indeed, fish diseases not previously seen in Arctic rivers (e.g., saprolegniasis) have been identified in similar habitats farther to the north (Sformo et al., 2017), suggesting the potential for parallel expansion into SCSR lagoon-associated rivers. While the impacts of climate change to Arctic ecosystems, both direct and indirect, are well studied (e.g., IPCC, 2007; Mason et al., 2012; Moerlein and Carothers, 2012; Holbech and Pederson, 2018), there is little information regarding how SCSR lagoon ecosystems are shifting in response to these pressures. To understand SCSR lagoons in the context of climate change, and indeed lagoon systems throughout the Arctic, it is important to expand the preexisting knowledge base outlined above to address gaps we have highlighted here. Although it is difficult to imagine a situation in which global climate change will not have significant impact on Arctic lagoon ecology, a more comprehensive body of knowledge extending to all facets of this ecosystem will enable research efforts to more accurately identify long-term shifts occurring within these dynamic habitats as a result of climate change.

CONCLUSIONS AND RECOMMENDATIONS

Exhibiting high levels of seasonal productivity and biodiversity, the lagoons of the SCSR act as vital habitat for a wide variety of species, serving as feeding areas, migration corridors, and stopover sites for various fishes, birds, and marine mammals of subsistence value to adjacent communities. However, despite research initiatives beginning as early as the 1950s (e.g., Tash, 1964; Wilimovsky and Wolfe, 1966; Vandegraft, 1993) as well as existing documentation outlining predicted vulnerabilities of the region to threats such as infrastructure development and climate change (e.g., Arctic Council, 2009; Huntington et al., 2015; Alaska DOT&PF, 2018), many knowledge gaps remain in our understanding of the ecology of SCSR lagoon habitats. Of primary concern is the ecology of lagoon basal food web taxa such as Mysidae, Diptera, and Bivalvia; knowledge gaps in this area translate to cascading uncertainties surrounding lagoon food web dynamics. While research investigating diet composition of larger fishes has highlighted the ecological importance of these taxa as primary prey items (Tibbles and Robards, 2018), little documentation exists on their movement and ecology in the SCSR lagoons. By addressing this knowledge gap, we would gain a more accurate understanding of lagoon trophic dynamics and how changes in habitat conditions may affect the base of the food chain. To complete a more in-depth view of lagoon basal resources, the magnitude of cross-ecosystem subsidies such as salmon- and seabird-derived marine nutrients (Rinella et al., 2013; Zmudczyńska-Skarbek and Balazy, 2017) and terrestrial allochthonous inputs would also be important to quantify to understand factors that may influence lagoon productivity. Additionally, the highly variable and changeable geomorphology and hydrology of these lagoons, driving alteration to water chemistry with further implications to biotic assemblages and primary productivity, has yet to be comprehensively documented on a seasonal and yearly basis and requires further long-term monitoring efforts. Lagoon classification also might be extended to several other coastal water bodies in the region, however further investigation is required to determine qualification for this designation.

Additional research into distribution and abundance trends among smaller forage fish species is vital to understanding the dynamics of lagoon trophic systems. Assessing movements of higher trophic level fish species into and out of the lagoons is also important to understanding potential trophic reverberations of fluctuating predation levels as these species migrate. Building upon Tibbles et al. (2018), further investigation into under-ice movements, behavior, and survival during the winter months of marine and freshwater fish (and invertebrate) taxa occupying SCSR lagoons is needed to identify the importance of lagoon connectivity to the sea for marine fishes. This investigation would also shed valuable light upon the seasonal ecological reset that appears to occur throughout many lagoons as a result of overwintering mortality, and might help researchers understand how the various fish species respond to this phenomenon. Finally, additional investigation into contaminants such as mercury and per- and polyfluoroalkyl substances (PFAS; known to be prevalent in Arctic biota) in fish species of subsistence importance (Lin et al., 2020) would provide better insight into how these contaminants are taken up and move through the food chain and the potential effects on people who consume subsistence fishes.

Currently, the research needs outlined above are a primary limitation in providing effective management and conservation of lagoon habitats in the face of threats stemming from anthropogenic activity. For example, a more comprehensive understanding of SCSR habitats would enable prioritization of resource allocation such as oil and chemical spill response in the region. With a finite scope, oil spill response is prioritized for habitats identified as ecologically productive, particularly those important to subsistence use, such as lagoons. As the Arctic opens to new resource extraction opportunities, the need for rapid response is critical in any contamination scenario and, in the case of SCSR lagoons, would be further catalyzed by the shallow nature of these habitats, which expedites mixing and spread of any contaminant. A better understanding of lagoon ecology and the ability to prioritize these habitats applies to inland mineral extraction operations as well, with expedited response vital to protecting the watersheds that feed coastal lagoons, such as the Wulik River, from spills and contamination events such as tailing dam failures.

Additionally, a broader and more detailed record of SCSR lagoon ecology is critical to monitoring the long-term impacts of global climate change, particularly in identifying potential ecosystem perturbations at an early stage. If such perturbations can be identified (e.g., permafrost thaw slumps causing high turbidity or decreasing freshwater input resulting in unreliable lagoon-ocean connectivity), it may be possible to protect lagoon habitats and the population health of important subsistence fishes associated with them through measures such as terrestrial and marine erosion control (Mason et al., 2012) or mechanical facilitation of lagoon-ocean connectivity for fish passage and regulation of habitat conditions (Horrell, 1992; Jellyman et al., 1996). However, gaps in the current body of knowledge on these lagoons prevent management efforts from identifying and implementing metrics for assessing these perturbations, making efficient and effective response measures unrealistic.

Currently, primary management efforts in the region that apply to lagoons include land-use protections associated with federal ownership designations (e.g., Cape Krusenstern National Monument; Table 1; Fig. 1), harvest management regulations enforced by the Alaska Department of Fish and Game, and federal regulations requiring environmental impact statements and approvals for extensive development projects. There are also extensive tracts of tribal lands and privately managed lands in the region for which management strategies have been developed in some cases. Additionally, many tributaries feeding SCSR lagoons are designated by the State of Alaska as "Anadromous Waters." This designation provides habitat protections such as preventing streambed disturbance and prohibiting construction of structures disrupting fish passage in these waterbodies (Table 1). In order to address and mitigate the impacts of infrastructure expansion and global climate change on the lagoons of the SCSR, research efforts must seek to fill the knowledge gaps while accounting for a broad array of management regimes and land ownership. The diverse portfolio of lagoon habitats represented in the SCSR facilitate ecological robustness and play a vital role in regional subsistence practices. A wider body of knowledge surrounding these habitats is vital to protecting and managing them to promote long-lasting ecological and community resilience within the greater Alaskan Arctic region.

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