BIOLOGICAL SETTING





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Primary Productivity

Melanie Smith, Max Goldman, Jon Warrenchuk, and Erika Knight

Primary productivity is the rate at which carbon dioxide is converted into organic material by autotrophs, or primary producers. Autotrophs collectively produce ecosystem food that supports the food chain, hence they are referred to as primary producers. This conversion from the simple into the complex happens via two key processes: photosynthesis and chemosynthesis. Primary production via photosynthesis forms the base of the entire food web, both on land and in the oceans.

DISTRIBUTION

In the ocean, photosynthesis only happens in the top 650 feet (200 m) of the water column, as adequate sunlight cannot penetrate any deeper. Below the 200 meter isobath, primary producers rely on the process of chemosynthesis for energy production, through which inorganic compounds such as hydrogen sulfide, sulfur, iron, hydrogen, or ammonia are used in place of sunlight as a catalyst for energy production. Chemosynthesis is rare, and is only common among extremophilic and deep-sea organisms.

In the Arctic, primary production is mostly generated from singlecelled microscopic algae in ice and sea water, collectively known as phytoplankton (Frey et al. 2012, Frey et al. 2015). This marine phytoplankton community is a diverse group that includes species of diatoms (symmetrical, silica-based, single-celled algae), dinoflagellates ("tailed" protists), coccolithophrids (calcium carbonate-based algae), and others. Seaweeds and photosynthetic bacteria are also substantial contributors to primary productivity (Duggins et al. 1989, Frey et al. 2015). Measurements of the algal pigment chlorophyll (chlorophyll-a) serve as a proxy for the amount of algal biomass present, as well as overall plant health.

ECOLOGICAL ROLE

Phytoplankton are the basic building block of the marine food web. Some of the energy produced via photosynthesis is consumed during the process; however, most of this energy contributes to the organism's growth, which later becomes available energy to water column grazers that eat phytoplankton. Net primary productivity (NPP) refers to the productivity available to support consumers and the benthos in the sea. Phytoplankton are responsible for nearly all of the primary production in marine ecosystems and almost half of the total photosynthesis on the planet, with 10–15% of global production occurring on the continental shelves alone (Falkowski et al. 1998, Morel and Antoine 2002, Muller-Karger et al. 2005).

Sea-Ice Habitat

Primary production is highly seasonal in the Arctic and subarctic region due to the seasonal nature of light availability and presence of appropriate nutrients (Loeng et al. 2005). Each spring, sea-ice margins begin to retreat and daylight hours lengthen, exposing the water column to the sunlight that was not available all winter (Barber et al. 2015, Leu et al. 2015). In the eastern Bering Sea, the timing of the sea-ice retreat influences the timing of a spring phytoplankton bloom (Sigler et al. 2014). A second phytoplankton bloom occurs in the fall (possibly triggered by re-suspension of nutrients from storms) and the magnitude of the fall bloom is related to the strength of the spring bloom (Sigler et al. 2014). The timing of the sea ice retreat also influences the species composition of the phytoplankton community (Schandelmeier and Alexander 1981, Olson and Strom 2002).

Ice does not have to be completely absent in order for photosynthesis to occur; ice algae has proven to be an integral component of Arctic ecosystem functions. Similarly, under-ice algal blooms are becoming more prevalent, as evidenced by recent observations of massive under-ice blooms, which are likely resulting from diminished ice conditions and the near disappearance of snow-covered, multi-year ice (Frey et al. 2011, Arrigo et al. 2012, Arrigo 2014, Arrigo and van Dijken 2015). A study in the nearshore Beaufort Sea suggests that ice algae provides about two-thirds and phytoplankton provides about one-third of spring NPP (Horner and Schrader 1982). A second Arctic-wide study found that ice algae makes up on average 57% of the water column and sea ice productivity (Gosselin et al. 1997).

Variation in ice cover is the dominant factor in the spatial pattern of primary production from phytoplankton (Wang et al. 2005, Stabeno et al. 2012). In the northern Bering and Chukchi Seas, chlorophyll-a and NPP are tightly coupled with benthic biomass (Grebmeier et al. 1988, Springer and McRoy 1993, Dunton et al. 2005, Grebmeier et al. 2006a, Grebmeier et al. 2006b). Chlorophyll-a and NPP in the Beaufort Sea are less closely linked, except around Barter Island where both relatively high biomass and chlorophyll-a are found (Dunton et al. 2005, Grebmeier and Harvey 2005).

Under cool conditions, sea ice melts later in the spring. The nutrients released by the ice disperse over a larger spatial extent as the sea ice slowly retreats, at a time when there is ample daylight to fuel an ice-edge or under-ice phytoplankton bloom. Under these conditions, the spatial and temporal extent of the spring bloom favor the production of large, lipid-rich copepods and euphausiids, and this provides a food source that increases the survival of juvenile pollock (Hunt et al. 2011, Sigler et al. 2016).

CONSERVATION ISSUES

Grebmeier et al. (2006b) show that the northern Bering and Chukchi Seas are shifting away from tight coupling of pelagic-benthic productivity, coinciding with lower benthic prey populations, higher pelagic fish populations, reduced sea ice, and increased air and ocean temperatures (Grebmeier 2012). Decline in sea-ice extent and warming seawater exacerbate environmental change in this already vulnerable ecosystem (Grebmeier 2012). Climate change may potentially break this short link between primary productivity and the benthos, converting the area to a pelagic- rather than benthic-oriented system (Grebmeier 2012, Grebmeier et al. 2014, Grebmeier et al. 2015b). Understanding the relationship between ice cover and productivity is essential in understanding Arctic marine ecology under reduced ice thickness and extent (Stockwell 2008).

The Arctic Ocean has experienced substantial warming in all seasons (Bekryaev et al. 2010) with huge increases to its annual mean openwater area and surface air temperature (Arrigo and van Dijken 2011). In the Bering Sea, however, warming has been mainly limited to summer, with little to no change to its open-water area (Brown et al. 2011). Ice coverage in the Bering Sea is more closely tied to atmospheric circulation and bathymetry than elsewhere, though the cold water and surface air from the nearby Arctic influence the formation of ice in the Bering Sea, so continued warming in the Arctic will likely lead to diminished ice coverage in the Bering Sea (Brown and Arrigo 2012, 2013).

MAPPING METHODS (MAP 3.1)

Map 3.1 shows maximum measured integrated chlorophyll content (mg/m^2) for the top 330 feet (100 m) of water-column depth during the open-water season. Chlorophyll is used as a proxy for primary productivity because it is found in phytoplankton and algae, which are estimated to make up approximately 57–67% of water-column and sea-ice productivity in the Arctic (Horner and Schrader 1982, Gosselin et al. 1997).

Our map is based on data from water-column samples collected and analyzed for chlorophyll content across the Beaufort and Chukchi Seas, and the eastern portion of the Bering Sea. These samples were collected over several decades (1959–2012) and compiled into two datasets (Ashjian 2013, Grebmeier and Cooper 2014b) in the Earth Observing Laboratory online database as part of the Pacific Marine Arctic Regional Synthesis (PacMARS) project.

points.

The sea-ice data shown on this map approximate median monthly sea-ice extent. The monthly sea-ice lines are based on an Audubon Alaska (2016) analysis of 2006–2015 monthly sea-ice extent data from the National Snow and Ice Data Center (Fetterer et al. 2016). See Sea Ice Mapping Methods section for details.

Data Quality

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3.1

To produce the primary productivity map, we interpolated the chlorophyll sample data in Esri's Geostatistical Analyst extension using empirical Bayesian kriging with four sectors. In instances where there were multiple sample values in one location, we used only the maximum value at that location for the interpolation. The resulting raster was clipped to a 62-mile (100-km) buffer around the sample

Integrated water column chlorophyll data are likely the best proxy available for the project area. However, much of the data used in this interpolation are old, as they were gathered as long ago as 1959 (Ashjian 2013). The open-water season is an important time for production, as sea-ice cover does not limit light penetration into the water column. While algal growth at the ice edge, in polynyas, in and under the ice, and in melt ponds may also contribute significantly to primary productivity, accurate measurements are not available for the project

area (Krembs et al. 2000, Hill and Cota 2005, Arrigo et al. 2012, Frey et al. 2012, Boetius et al. 2013). Kelp forests may also significantly increase primary production in nearshore environments, especially along the Aleutian Islands (Duggins et al. 1989). However, we were unable to find spatial information regarding kelp forests in our project area.

While there are satellite data available for the region, these data may not reflect biomass accurately because of subsurface plumes of phytoplankton and, in coastal waters, the turbidity and dissolved organic matter content of river inputs (Chaves et al. 2015, Tremblay et al. 2015).

Reviewer

Michael Sigler

MAP DATA SOURCES

Integrated Chlorophyll Sample Data (mg/m²) for 0-100 m **Depth:** Audubon Alaska and Oceana (2017) based on Ashjian (2013) and Grebmeier and Cooper (2014b)

Sea Ice: Audubon Alaska (2016) based on Fetterer et al. (2016)



The aquamarine color is a coccolithophorid phytoplankton bloom that occurred around the Pribilof Islands in the eastern Bering Sea in 2014. Coccolithophore blooms of this size and duration are becoming more common and may be a result of changing climate conditions.

Primary Productivity

Map Authors: Erika Knight, Brianne Mecum, and Melanie Smith Cartographer: Daniel P. Huffman



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3.1

OCEANA

Audubon Alaska

Zooplankton

Marilyn Zaleski and Brianne Mecum

Zooplankton are tiny animals living and swimming in the water column that link primary producers to most other animals in the marine ecosystem. Zooplankton include a diverse assemblage of larval fishes (called ichthyoplankton), larval crabs, pelagic snails (pteropods), arrow worms, krill, and other small crustaceans such as bottom-dwelling amphipods. Zooplankton are abundant, widely distributed, and encompass thousands of species across multiple phyla. Two zooplankton groups of particular importance are crustaceans: krill, also known as "euphausiids," and copepods (Hopcroft et al. 2008). Many species of copepods and krill store lipids and therefore supply their predators with an energy-rich food source (Davis et al. 1998).

DISTRIBUTION

The entire North Pacific Ocean is home to a dynamic zooplankton community that differs in abundance and species composition over time and space. Major zooplankton species in the shelf region of the North Pacific include copepods (Calanus marshallae and C. glacialis, Neocalanus cristatus, and Pseudocalanus spp.), krill (Thysanoessa spp.), amphipods (Themisto spp.), and larval walleye pollock (Gadus chalcogrammus) (Hopcroft et al. 2005, Coyle et al. 2008, Eisner et al. 2014, Sigler et al. 2016). Different species of zooplankton are found in waters farther offshore; these include the copepods Neocalanus spp., Eucalanus bungii, and Metridia pacifica, and krill Thysanoessa raschii (Eisner et al. 2014). In contrast, smaller zooplankton, like bivalve larvae, keep to inshore waters (Eisner et al. 2013).

Zooplankton distribution changes over time and is strongly influenced by ocean conditions, ice coverage, and phytoplankton blooms (Hunt et al. 2002, Coyle et al. 2008, Ohashi et al. 2013, Sigler et al. 2016). Late sea-ice retreats, caused by a colder winter/spring, lead to early spring phytoplankton blooms; whereas early ice retreats, caused by a warmer winter/spring, lead to later open-water blooms (Hunt et al. 2002, Sigler et al. 2016). Warmer waters and earlier sea-ice retreats favor the production of jellyfish and small copepods like *Pseudocalanus* spp.; colder waters favor larger zooplankton such as copepods (C. marshallae and C. glacialis), and krill (Coyle et al. 2008, Ohashi et al. 2013, Eisner et al. 2014).

ECOLOGICAL ROLE

Zooplankton bridge the trophic gap between primary producers and larger predators, and represent nearly every taxonomic group of fish and invertebrates during part, if not all, of their lifecycle (Sigler et al. 2016). They repackage the energy fixed by photoplankton and provide a prey base that is diverse in size and nutritional quality to larger predators (Hunt et al. 2002). For example, walleye pollock, as a predator, benefits from diets with energy-rich zooplankton (Siddon et al. 2014, Moss et al. 2016). Major prey items for walleye pollock, a commercially important groundfish, are C. marshallae copepods, krill, Sagitta elegans arrow worms, the pteropod Limacina helicina, amphipods, and larval decapod crustaceans (Coyle et al. 2008, Moss et al. 2016).

CONSERVATION ISSUES

Changes to zooplankton communities can lead to changes at higher trophic levels that ultimately affect commercial fisheries and subsistence harvests (Hopcroft et al. 2008, Eisner et al. 2014). As the climate changes, the ocean absorbs more heat and CO₂ from the atmosphere, which affects the productivity and physiology of all marine life including zooplankton (see also the summary and maps of Climate in the Physical Settings Chapter). Ocean acidification is of particular concern to animals with calcium-carbonate shells, such as pteropods (Fabry et al. 2009). These planktonic snails are important prey items for juvenile fishes including pink salmon (Oncorhynchus gorbuscha), Pacific cod (Gadus macrocephalus), walleye pollock, Atka mackerel (*Pleurogrammus monopterygius*), and several rockfish species





This pteropod is showing some effects of ocean acidification on its calcareous shell including ragged, dissolving shell ridges, severe abrasions, and weak spots of the surface.

(Armstrong et al. 2005, Yang et al. 2006, Coyle et al. 2008, Boldt and Rooper 2009). When the pteropods are exposed to acidified waters, their shells dissolve (Orr et al. 2005), hindering their health and protection from predators.

Crustacean zooplankton species will also be vulnerable to the effect of ocean acidification. Larval Antarctic krill (*Euphausia superba*) experienced shell dissolution and growth irregularities under acidified conditions (Kawaguchi et al. 2010). Juvenile red king crabs (Paralithodes camtschaticus) and Tanner crabs (Chionoecetes bairdi) grew slower and ultimately had decreased survival rates when exposed to projected future levels of ocean acidification (Long et al. 2013). These impacts to important prey items for the marine ecosystem and important harvest species for Alaskan communities need to be considered for future management plans.

MAPPING METHODS (MAP 3.2)

All zooplankton data for the study region were obtained from COPEPOD: The Global Plankton Database (National Oceanic and Atmospheric Administration 2012). This database is a synthesis of zooplankton data collected from various studies. Details on how zooplankton data were combined and calculated can be found in Moriarty and O'Brien (2013). Sample points for average annual zooplankton total carbon mass were extracted from the database and mapped. A 60x60 km grid was then overlaid on data points within the extent of the study area. The average carbon mass (measured in mg carbon per m³) per grid cell was then calculated. Those grid cells with associated average values were then converted to points based on the centroid of each grid cell. To create a continuous coverage over the entire study area, those points were interpolated using the Inverse Distance Weighted tool in ArcMap version 10.5 using a power of 2 and a search radius of 12 points.



3.2

The sea-ice data shown on this map approximate median monthly sea-ice extent. The monthly sea-ice lines are based on an Audubon Alaska (2016) analysis of 2006–2015 monthly sea-ice extent data from the National Snow and Ice Data Center (Fetterer et al. 2016). See Sea Ice Mapping Methods section for details.

Data Quality

Because this dataset was created with the express purpose of creating a continuous global coverage for zooplankton biomass, this dataset generally has excellent spatial coverage. Some of the more remote, offshore areas may be represented by only a few data points, which may be the case in the far western Bering Sea. In this case, small hotspots may likely be represented by single measurements at historical sampling locations. There were no sample points for the waters of the Beaufort Sea and the western Chukchi Sea. We suspect that weather, ice conditions, and remoteness play the largest role in this lack of data and that this is not an indication of low zooplankton productivity. As climate change continues to impact ice conditions in the Arctic it is possible that future researchers will have increased sampling opportunities to measure zooplankton abundance in this region.

Reviewer

• David Kimmel

MAP DATA SOURCES

Zooplankton: Oceana (2017b) based on Moriarty and O'Brien (2013) and National Oceanic and Atmospheric Administration (2012)

Sea Ice: Audubon Alaska (2016) based on Fetterer et al. (2016)



A zooplankton sample with bright orange krill amongst ctenophores (otherwise known as comb jellies). These planktonic species were caught off of Maine, but krill and ctenophores are ubiquitous in the Arctic and occur worldwide.

Zooplankton

Map Authors: Brianne Mecum, Marilyn Zaleski, and Jon Warrenchuk Cartographer: Daniel P. Huffman



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Benthic Biomass

Marilyn Zaleski and Brianne Mecum

Benthic invertebrates live on or in the seafloor. Some benthic invertebrates form structures that become habitats, others live in the substrate, and some are mobile and travel on the surface of the seafloor. Benthic invertebrates comprise a large proportion of the total marine biomass and species diversity in the eastern Bering Sea (EBS), Chukchi Sea, and Beaufort Sea. Their aggregate role in the ecosystem is an important transfer of energy from lower to upper trophic levels (Coyle et al. 2007). They also form Essential Fish Habitat (EFHs) (see Ecological Role).

Corals, anemones, sponges, and tunicates are components of the benthic landscape. These sessile invertebrates offer refuge from ocean currents and protection from predators, and, in doing so, offer nursery habitats for other invertebrates and for several fish species. Habitat-forming benthic invertebrates are highly diverse (Table 3.3-1). The Aleutians contain the most diverse and dense aggregations of sponges (Lehnert and Stone 2014) and support the most abundant deep-water corals of any high latitude ecosystem (Heifetz et al. 2005, Stone 2014), with higher coral diversity than some tropical reefs (Stone 2014). Of the 88 species or subspecies of corals reported from the Aleutian Islands (Stone and Cairns 2017), more than 50 may be endemic to the region (Stone and Rooper 2017). Tunicates belong in the phylum Urochordata, closely related to the phylum Chordata which includes all vertebrates.

The benthic community is dominated by several species of crustaceans, echinoderms (mainly urchins and sea stars), gastropods (mainly Neptunea spp. or true whelks), and bivalve mollusks (mainly Macoma calcarea) (Feder et al. 2005, Sirenko and Gagaev 2007, Bluhm et al. 2009, Logerwell et al. 2010, Smith et al. 2011, Goddard et al. 2014, Grebmeier et al. 2015a, National Oceanic and Atmospheric Administration 2016a). Common epifaunal species in the Chukchi Sea include the green sea urchin (Strongylocentrotus droebachiensis), purple-orange sea star (Asterias amurensis), and fuzzy hermit crab (Pagurus trigonocheirus) (Goddard et al. 2014). Common Beaufort Sea species include brittle stars (class Ophiuroidea), mussels (Musculus spp.), and the peanut worm (Golfingia margaritacea) (Logerwell et al. 2010). In the EBS, purple-orange sea stars, basket stars (*Gorgonocephalus* eucnemis), and sponges make up the majority of surveyed benthic organisms (National Oceanic and Atmospheric Administration 2016a). Snow crab (*Chionoecetes opilio*) and Tanner crab (*C. bairdi*), along with red king crab (*Paralithodes camtschaticus*), are also important benthic invertebrates and are summarized separately in this Atlas.

DISTRIBUTION

The shelf environment of the EBS, north through the Bering Strait, in Norton Sound, and alongshore of the Chukchi Sea supports relatively high benthic biomass comprised of, but not limited to, the animals listed in Table 3.3-1 (Logerwell et al. 2010, Goddard et al. 2014, National



Sea stars, barnacles, green sea urchins, limpets, and mussel shells are all part of the benthic community and found here in an Aleutian tidepool.

Cora

Sea ras Gersemia I

Deep-sea Fanellia co Bubblegu

> Paragorgi Alaska s

Halipteris v Red tree Primnoa

Orange Ptilosarcu

Red mushr Anthoma

Articulated b Isidella

Pink orange m Alcyoniu Alaska c

Caryophyllia

Oceanic and Atmospheric Administration 2016a). The species composition differs depending upon sediment type and depth, with the 165-foot (50-m) isobath generally dividing a benthic community of sea stars from a deeper benthic community of crabs and gastropods (Yeung and McConnaughey 2006).

While survey data are more limited in the Arctic compared to the EBS, sediment size and composition, along with zooplankton populations, water temperature and salinity, and ice gouging, are major factors regulating benthic community structure and diversity (Grebmeier et al. 1989, Barber et al. 1994, Bluhm et al. 2008, Pisareva et al. 2015).

Corals are widespread throughout the Aleutian Islands, Bering Sea, and Chukchi Sea. Coral gardens, composed of a variety of coral and sponge assemblages differentiated by species diversity and densities, are found in shallow and deep-sea rocky substrates of the Aleutian Islands (Stone 2014). In the mud/sand/gravel substrates of the Bering Sea, sea whips dominate the middle domain, and soft corals such as sea raspberries populate the relatively shallow inner and middle domains (Logerwell et al. 2010, Goddard et al. 2014, National Oceanic and Atmospheric Administration 2016a). Tunicates have a distribution similar to the soft corals, while anemones are more consistently found along the middle and outer domain of the EBS (Logerwell et al. 2010, Goddard et al. 2014, National Oceanic and Atmospheric Administration 2016a). The Aleutian al. 2011).

Although water temperatures are rising, evidence is inconclusive about how benthic biomass will be affected (see also the discussion and climate projection map for benthic infauna under Climate in the previous Islands benthic environment is heavily structured with sponges (Stone et chapter). One study showed that benthic organisms were more abundant in colder years compared to average years, suggesting that as temperatures increase and are anomalously high, benthic biomass may decrease ECOLOGICAL ROLE (Coyle et al. 2007). However, in northern latitudes, changing species Benthic organisms provide and create habitat essential to fish and composition and range expansions northward may increase benthic biomass. Historical epibenthic sampling between the 1970s and 1990s crabs. They rely on high primary production from the water column and are less affected by seasonal and annual variability than pelagic species revealed increased abundance and biomass for the northeastern Bering (Bluhm et al. 2008). Areas of very high primary productivity, such as and Chukchi Seas (Feder et al. 2005), and warmer-water species were Anadyr waters north of the Bering Strait, produce far more biomass found in the northern Bering and Chukchi Seas, a potential outcome of a than is consumed by zooplankton (Springer et al. 1989). This excess warming climate (Sirenko and Gagaev 2007). Climate change may also biomass falls to the seafloor, providing food for the benthos (Grebmeier affect the trophic linkages between benthic invertebrates and primary et al. 1988). production (Grebmeier et al. 2006b).

Habitat-forming invertebrates provide EFH for many commercially important species (Stone 2014). These include but are not limited to Atka mackerel (Pleurogrammus monopterygius) (Malecha et al. 2005, Stone 2006), red king crab (Pirtle and Stoner 2010), and several rockfishes (Stone et al. 2017). Corals, in particular, are long-lived and grow

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TABLE 3.3-1. Habitat-forming invertebrates species diversity, showing species commonly identified in the National Marine Fisheries Service Trawl Surveys (National Oceanic and Atmospheric Administration 2016a).

als	Anemones	Sponges	Tunicates
pberry	White-plumed anemone	Clay pipe sponge	Sea potato
rubiformis	Metridium farcimen	Aphrocallistes vastus	<i>Styela rustica</i>
fan coral	Tentacle-shedding anemone	Barrel sponge	Sea onion
ompressa	Liponema brevicornis	Halichondria panacea	Boltenia ovifera
um coral	Reticulate anemone	Tree sponge	Sea peach
a arborea	Actinauge verrilli	Suberites montalbidus	Halocynthia aurantium
ea whip	Swimming anemone	Scapula sponge	Sea grape
willemoesi	Stomphia coccinea	Stelodoryx oxeata	Molgula griffithsii
e coral	Christmas anemone	Cloud sponge	Hairy tunicate
a willeyi	Urticina crassicornis	Rhabdocalyptus spp.	Halocynthia hispidus
sea pen	Rough purple anemone	Stone sponge	Glassy tunicate
Is gurneyi	Paractinostola faeculenta	<i>Stelletta</i> spp.	Ascidia paratropa
oom coral	Chevron-tentacled anemone	Spud sponge	Sea pork
<i>stus</i> spp.	Cribrinopsis fernaldi	Histodermella kagigunensis	Aplidium californicum
amboo coral	Frilled anemone	Club sponge	Broad-base tunicate
a spp.	<i>Metridium senile</i>	Tedania kagalaskai	Cnemidocarpa finmarkiensis
ushroom coral	Hot dog anemone	Calcareous finger sponge	Sea glob
<i>um</i> spp.	Bathyphelia australis	Geodinella robusta	<i>Aplidium</i> spp.
up coral	Cowardly anemone	Lacy basket sponge	Sea blob
a alaskensis	Stomphia didemon	Regadrella okinoseana	<i>Synoicum</i> spp.

slowly (Andrews et al. 2002), so it takes years before a colony effectively becomes fish habitat (Stone et al. 2017). The animals that rely on these structural invertebrates use them for both shelter and food.

Some benthic invertebrates are preyed upon by marine mammals: Macoma bivalves are important food for walruses (Odobenus rosmarus divergens) (Fukuyama and Oliver 1985) while amphipods (small infaunal crustaceans) are preyed upon by gray whales (*Eschrichtius* robustus) and bearded seals (Erignathus barbatus) (Kim and Oliver 1989, Brower et al. 2017).

ECONOMIC IMPACT

In addition to the economic value of commercially important species that rely on benthic invertebrates, there is subsistence harvest for human use. Alaska Native communities harvest invertebrates like the orange tunicates known as sea peaches that are pushed up to the shore by sea ice and storms (Raymond-Yakoubian et al. 2014). The economic role of snow crab, Tanner crab, and red king crab are summarized later in this chapter.

CONSERVATION ISSUES

Ocean acidification could negatively affect many of the benthic organisms that require calcium carbonate to make their tests or shells. The Arctic is affected by ocean acidification more so than other areas with longer periods where the water is so acidic it can dissolve calcium carbonate (Bates et al. 2009, Fabry et al. 2009).

Commercial fishing gears, particularly bottom trawls, can have long-term impacts on benthic habitat (Heifetz 2002, Witherell and Coon 2002, Rooper et al. 2016, Stone et al. 2017). It is important to consider the time necessary for slow-growing, long-lived corals and sponges to rebuild or replace damaged structures when assessing habitat degradation and subsequent recovery (McConnaughey and Smith 2000, Andrews et al. 2002, Rooper et al. 2011). When corals are damaged by fishing gear, they can take decades to recover, and repeated fishing disturbances in an area can slow growth rates further (Stone et al. 2017). Additionally, some coral growth is negatively affected by warmer waters (Stone et al. 2017) and ocean acidification (Fabry et al. 2009), so as ocean temperatures rise, the effect from fishing will be exacerbated and increase recovery time.

MAPPING METHODS (MAP 3.3)

BIOLOGICAL SETTING

Benthic biomass was estimated by combining two datasets: one with robust spatial coverage in the Chukchi, Beaufort, and northern Bering Seas and another with robust spatial coverage from the northern Bering Sea to the Aleutian Islands. Combining these two datasets provided us with survey data for benthic invertebrates throughout the majority of our study area. Those two studies, as well as the methods used to combine them, are outlined below.

Also shown on Map 3.3 are the locations of documented coral and sponge gardens in the Aleutian Islands. Those locations are from Stone (2014) and National Oceanic and Atmospheric Administration (2016a).

The sea-ice data shown on Map 3.3 approximate median monthly sea-ice extent. The monthly sea-ice lines are based on an Audubon Alaska (2016) analysis of 2006–2015 monthly sea-ice extent data from the National Snow and Ice Data Center (Fetterer et al. 2016). See Sea Ice Mapping Methods section for details.

Trawl Survey Data (National Oceanic and Atmospheric Administration 2016a)

A trawl survey database was created by combining multiple bottom trawl surveys which employed consistent methodologies and sampled waters within the US exclusive economic zone (EEZ) of the Bering Sea (Conner and Lauth 2016, Hoff 2016), Aleutian Islands (Raring et al. 2016), Gulf of Alaska (von Szalay and Raring 2016), Chukchi Sea (Goddard et al. 2014), and Beaufort Sea (Logerwell et al. 2010). This database contained 29,296 sample points and has excellent spatial and temporal coverage for much of our study area, though less so in the Arctic.

From that database, the catches of all benthic invertebrates were summed for each haul of the trawl surveys. Catches included 1,356 benthic species or species groups recorded from the trawl survey samples. These included crabs, echinoderms (sea stars, sea urchins, sea cucumbers), bivalves, sponges, corals, tunicates, anemones, worms, snails, and octopus. Not included were jellyfish and ctenophores, salps, and squids since these are pelagic rather than benthic organisms.

Of the observations made (species or species groups caught, identified, and weighed), there were:

- 216,138 in the EBS
- 79.674 in the Gulf of Alaska
- 60,301 in the Aleutian Islands
- 9,749 in the northern Bering Sea
- 3,269 in the Bering Sea slope
- 2,705 in the Chukchi Sea
- 387 in the Beaufort Sea

The most common species of benthic invertebrates were basketstars *Gorgonocephalus eucnemis* (n = 11,549), Tanner crabs *Chionoecetes bairdi* (n = 10,566), snow crabs *Chionoecetes opilio* (n = 9,840), purple-orange sea stars Asterias amurensis (n = 8,185), and Oregon tritons Fusitriton oregonensis (n = 7,865).



Brittle stars are predominant in the Beaufort Sea as well as the outer domain of the eastern Bering Sea. Here one is climbing on a dead octocoral

PacMARS Benthic Infaunal Parameters (Grebmeier and Cooper 2014a)

This dataset contained 2,015 unique sample points with summary measurements of average benthic macroinfaunal taxa to the family level collected using a van Veen grab (0.1 m² sediment grab). Three to five samples were taken at each station and parameters of station, abundance, wet weight biomass, carbon dry weight biomass, number of taxa, Shannon-Weaner diversity and evenness indices, and number of grabs collected per station were recorded for each sample. For the purposes of combining this dataset with trawl survey sample data, this dataset was mapped based on wet weight biomass (gww/m^2) .

Analysis

To obtain a continuous coverage estimate of the relative benthic biomass for our entire study area, we combined the macroinfaunal benthic survey data from Grebmeier and Cooper (2014a) and a compilation of benthic invertebrate samples from the National Marine Fisheries Service trawl survey data (discussed above). Both datasets measured benthic biomass; however, because their survey methods and measurements differ, simply combining the datasets would be inappropriate. Instead, the Oceana Important Ecological Area approach was used (Oceana and Kawerak 2014). This method provides a framework for combining multiple types of data regardless of their sample design, measurements, units, or whether they are quantitative or qualitative in nature. Using this method allows us to see those areas which are above average, or those areas with the highest benthic productivity.

The steps for the Important Ecological Area approach were:

- Overlay 60x60 km grid on top of entire extent of all survey points
- Calculate the average value of all sample points within each grid cell for each dataset separately
 - For the PacMARS data, average biomass of macrofauna in grams wet weight per meter squared (gww/m²)
 - For the trawl survey data, average kilograms per hectare (kg/ha)
- Calculate the standard deviate per grid cell for each dataset separately

$$Z_{ij} = \frac{X_{ij} - \sigma_{ij}}{\sigma_{ij}}$$

dataset.

- grid cell of the two datasets

- in ArcMap version 10.5:
 - Power = 2



Where (Z_{ij}) is the standard deviate of grid cell j for the i^{th} dataset, (X_{i}) is the average value for grid cell j for the ith dataset, and (X) and (σ) are the overall mean and overall standard deviation of all the calculated grid cell average values for the *i*th

Join the two datasets together using the grid cell unique identifier to ensure both datasets align properly, and then calculate the weighted average standard deviate, weighted by sample size, per

Join the weighted average standard deviate values back to the 60x60 km grid to view spatial distribution

Convert grid cells to points based on the center of each cell

To obtain continuous coverage, interpolate those points using the Inverse Distance Weighted tool with the following parameters

Search radius = variable Maximum search radius = 12 points

Converting grid cell values to standard deviates allows us to see how far above or below average each value is from the mean relative to the dispersion of the data. A standard deviate close to zero means the value is close to average, while a large standard deviate means the value is well above average. Similarly, a negative standard deviate indicates the value is below average (Oceana and Kawerak 2014).

Data Quality

The NOAA trawl database contained 29,296 sample points and had excellent spatial and temporal coverage for much of our study area, though less so in the Arctic. Bottom trawl surveys in the Aleutian Islands were conducted every 3 years from 1983 to 2000 and on even years from 2002 to 2016. Surveys on the Bering Sea slope were conducted on even years from 2002 to 2016, except for 2006 and 2014. Surveys on the EBS shelf were conducted from 1982 to 2016. Surveys in the northern Bering Sea occurred from 1982 to 2010. Gulf of Alaska surveys were conducted in 1984 and 1987, every 3 years from 1990 to 1999, and on odd years between 2001 and 2015.

The PacMARS infaunal biomass dataset contained 2.015 unique sample points with summary measurements of average benthic macroinfaunal taxa to the family level. This dataset had excellent spatial coverage from 1970 to 2012 in the northern Bering Sea and Chukchi Sea, including both US and Russian waters. Sample data also included some coverage in the nearshore Beaufort Sea, in both US and Canadian waters. This dataset, however, lacked sample data in the southern Bering Sea and Aleutian Islands.

These two datasets were combined to utilize the best of both, as described above.

Reviewers

- Robert Stone
- Cynthia Yeung
- Jacqueline Grebmeier

MAP DATA SOURCES

Benthic Biomass: Oceana (2017a) based on Conner and Lauth (2016), Goddard et al. (2014), Grebmeier and Cooper (2014a), Hoff (2016), Logerwell et al. (2010), Oceana and Kawerak (2014), Raring et al. (2016), and von Szalay and Raring (2016)

Coral and Sponge Gardens in the Aleutian Islands: National Oceanic and Atmospheric Administration (2016a); Stone (2014)

Sea Ice: Audubon Alaska (2016) based on Fetterer et al. (2016)

BENTHIC BIOMASS

55

Benthic Biomass

Map Authors: Brianne Mecum, Marilyn Zaleski, and Jon Warrenchuk Cartographer: Daniel P. Huffman



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Victoria I.

OCEANA Audubon Alaska

become habitats (epifauna), others live in the substrate (infauna), while mobile benthic invertebrates travel on the surface of the seafloor. Benthic invertebrates comprise a large proportion of the biomass and species diversity in the eastern Bering Sea (EBS), Chukchi Sea, and Beaufort Sea, and include crustaceans, sea stars, bivalves, snails, corals, and sponges. Here, the combined biomass of benthic invertebrates is displayed from two survey datasets as a relative biomass index using standard deviates: a value near zero represents an area with approximate average biomass, a negative value represents an area with relatively low benthic biomass, and a positive value represents an area with relatively high benthic biomass. The higher the relative biomass index, the greater the relative benthic biomass. Hot spots of benthic biomass in the shelf environment of the EBS middle domain, the Bering Strait, and alongshore of the Chukchi Sea are comprised of, but not limited to, sea stars, corals, sponges, tunicates, snails, bivalves, and crabs. Coral gardens are found in shallow and deep-sea environments; hard corals and sponges are found along the Aleutians and at depth along the Bering Sea shelf break, and soft corals populate the EBS inner and middle domains.

Chionoecetes Crabs

Marilyn Zaleski and Brianne Mecum

Snow Crab

Chionoecetes opilio

Snow crab (*Chionoecetes opilio*), also known as opilio crab, is the

et al. 2014). They are well known by American consumers as the

most valuable commercial crab species in North Pacific (North Pacific Fishery Management Council 2015) and North Atlantic waters (Hébert

animal behind "all-you-can-eat" crab legs at popular seafood restau-

is a lesser-known, albeit slightly larger crab found in both the eastern Bering Sea (EBS) and the Gulf of Alaska. While Tanner crabs are

discussed in this summary and their distribution is mapped in Figure

These crabs are brachyurans, or true crabs, with a body covered in a hard exoskeleton that they must shed, or molt, in order to grow larger

(Moriyasu and Mallet 1986). Molting is instrumental in crab survival as

it also enables them to repair any damaged or lost limbs. In contrast to

other crabs, snow and Tanner crabs experience a terminal, or final molt

after which they live out their lives without molting for seven to ten

more years (Kon et al. 2010). Due to the lack of further molting, these

crabs are unable to replace any loss or damage to the carapace, claws,

or legs (Conan and Comeau 1986). The terminal molt also essentially marks the beginning of their adulthood (see Life Cycle section).

Snow and Tanner crabs differ from each other visually by their eye color, shape, and size. Snow crabs have green eyes while Tanner crabs have red eyes. Snow crab bodies are approximately equal in width

3.4-1, they are not mapped on a large scale in this atlas.

rants and as "opies" on the reality TV series *Deadliest Catch*. Their congener (same genus, different species) the Tanner crab (*C. bairdi*),

Chukch Crab EFH

Tanner Crab C. bairdi

FIGURE 3.4-1. Snow crab and Tanner crab Essential Fish Habitats, showing overlapping distributions which offer opportunities for hybridization. Figure adapted from National Oceanic and Atmospheric Administration (2016b).

TABLE 3.4-1. Comparative body measurements and clutch sizes
 between snow and Tanner crabs.

	Snow Crab (Chionoecetes opilio)	Tanner Crab (C. bairdi)
Average size (mature males)	3.8 inches (96 mm) carapace width ¹	3.6 inches (91 mm) carapace width ¹
Average size (mature females)	1.9 inches (48 mm) carapace width ¹	2.7 inches (68 mm) carapace width ¹
Clutch size (number of eggs)	88,500-116,000 ²	89,000-424,000 ¹

Sources: ¹ North Pacific Fishery Management Council (2016); ² Conan et al. (1989) and Comeau et al. (1999)

Tanner crabs range across the EBS in a similar, although more southerly, distribution to snow crabs, and they are also found in the Gulf of Alaska. Snow crab habitat in the Arctic is defined as inner to middle shelf waters (0-326 ft; 0-100 m depth) with muddy substrates in high-latitude, continental-shelf regions (North Pacific Fishery Management Council 2009). Throughout their range, snow and Tanner crabs prefer seafloor areas of sand and mud so they can quickly burrow to escape from predators (Stevens et al. 1994, Conan et al. 1996). Snow and Tanner crabs produce hybrid offspring in the area of their distributional overlap (Merkouris et al. 1998, Urban et al. 2002) (Figure 3.4-1).

LIFE CYCLE

A male will mate with a female for the first time after her terminal molt, which happens in the winter (Ernst et al. 2005). Males fight for the opportunity to mate by grasping a female prior to her molting and protecting her through the molt. Both snow and Tanner crab females can store sperm in excess of what is needed for fertilization of a given clutch; during subsequent mating seasons females can either mate again as a hard-shelled adult or fertilize a clutch with the stored sperm (Paul 1984, Sainte-Marie and Carriére 1995). Each fertilized clutch, whether from fresh or stored sperm, can produce tens to hundreds of thousands of embryos, a number that increases with female size and is greater in the larger Tanner crabs than smaller snow crabs (Webb and Bednarski 2010, Webb et al. 2016).



160

140

120 -

100

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40

20 -

tons)

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Council (2016).



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62-63 PAGES NO

> and length, while Tanner crab bodies are wider than they are long (Jadamec et al. 1999). Tanner crabs were targeted for commercial fishing in the Bering Sea before snow crab, with a shift to snow crab as Tanner crab abundance decreased (Figure 3.4-2) (North Pacific Adult male snow and Tanner crabs are larger than females of the same species (Table 3.4-1), a pattern known as sexual dimorphism. This size difference allows for males to grasp and protect smaller females during

DISTRIBUTION

the mating process.

Fishery Management Council 2015).

In Alaska, snow crabs are predominately found in the EBS, although their range extends north into the Chukchi and Beaufort Seas (Bluhm et al. 2009, Hardy et al. 2011, Rand and Logerwell 2011, Ravelo et al. 2015). Other populations of snow crab occur off of Russia, Japan, and Greenland, and in the Canadian North Atlantic. A small population, likely introduced, has also been discovered in the Barents Sea, north of Russia (Alvsvåg et al. 2009, Agnalt et al. 2011). Although snow crabs are not directly associated with sea ice, they are affected by how changes in sea ice impact bottom temperatures. With sea-ice coverage contracting, the Bering Sea cold pool (a mass of water less than 35° F [2° C]), also shrinks and is limited to the northern Bering Sea (Orensanz et al. 2004). This northward contraction of the cold water preferred by juvenile snow crabs (Dionne et al. 2003) has subsequently led to a northward shift in their distribution (Orensanz et al. 2004, Zheng and Kruse 2006, Burgos et al. 2013).

There are an estimated 897,000 metric tons, or roughly 17.4 billion individual snow crab in the EBS as of 2015 (North Pacific Fishery Management Council 2015). Snow crab biomass is estimated at 30,000 metric tons in the Beaufort Sea (North Pacific Fishery Management Council 2009) and 161,000 metric tons, which is roughly 4.5 billion crabs, in the Alaska Chukchi Sea (Goddard et al. 2014).



FIGURE 3.4-2. Historical total retained catch of eastern Bering Sea snow and Tanner crabs. Adapted from North Pacific Fishery Management





Pictured is a pair of mating snow crabs in Bonne Bay, Newfoundland, Canada. Snow crab males grasp and guard their smaller female mates. Note the tiny anemone that is living on the back of the female.

Brooding female snow and Tanner crabs will often mound together prior to releasing their hatched babies (Stevens et al. 1994, Sainte-Marie et al. 2008). Females of both species will incubate clutches for one year in normal conditions (30–34 °F; -1 to 1 °C) but female snow crabs, who occupy colder waters in the EBS compared to Tanner crabs, will brood for 2 years in water < 34 °F (1 °C) (Moriyasu and Lanteigne 1998). After hatching, the free-swimming larvae have two zoeal larval stages, in which they stay in the upper mixed layer of the water column, and one megalopae larval stage, when they begin to seek out suitable nursery habitat before settling to the bottom as benthic juveniles (Kruse et al. 2007). The larvae molt from one stage to the next as they grow, just as juveniles and adults molt to grow. For larval crabs, it takes two to six months to go from the first zoeal stage to the first benthic juvenile stage (Kruse et al. 2007, Yamamoto et al. 2014). Once they have settled, juvenile crabs look just like mini versions of the adults.

Snow and Tanner crabs are reproductively mature after they molt for the last time (Otto 1998), but this terminal molt is not dependent on size. The terminal molt may be triggered by age, but growth is temperature-dependent so there is variability in the size at maturity for the crabs based, in part, on the temperature at which they live (Orensanz et al. 2007, Ernst et al. 2012). They therefore generally mature smaller at higher latitudes (Burmeister and Sainte-Marie 2010), so average Chukchi and Beaufort snow crabs are smaller than their Bering Sea counterparts (Hardy et al. 2011). While the average life span of snow and Tanner crabs is uncertain, aging crabs is a current research topic (Fonseca et al. 2008, Allain et al. 2011, Kilada et al. 2017) and researchers estimate that both crab species may live up to 20 years (Turnock and Rugolo 2011).

ECOLOGICAL ROLE

Tanner crabs are benthic forage feeders. They primarily eat polychaete worms and bivalves, but also brittle stars, snails, and other crustaceans (Squires and Dawe 2003, Divine et al. 2017). Among the "other crustaceans" they eat, snow crabs have been recorded cannibalizing other snow crabs (Lovrich and Sainte-Marie 1997). Another prominent predator of snow and Tanner crabs is the Pacific cod (Gadus macrocephalus). Their stomach contents have contained up to 22% juvenile snow crabs and up to 10% juvenile Tanner crabs (Livingston 1989). In fact, predation by Pacific cod on snow crab in the EBS has been hypothesized to influence the strength of recruitment to the fishery (Burgos et al. 2013). Marine mammals, including walrus (*Odobenus* rosmarus divergens) and bearded seals (Erignathus barbatus), feed on Arctic snow crabs; in fact, snow crabs make up close to 20% of bearded seal diets in the Chukchi Sea (Whitehouse 2013).

ECONOMIC IMPACT

The commercial fishery for snow crabs occurs in the EBS and represents the largest and most valuable crab fishery in the US (North Pacific Fishery Management Council 2010). During the 2014–2015 season, 34,300 metric tons of male snow crabs were caught and retained (North Pacific Fishery Management Council 2015). After a peak in catches in the early-to-late 1990s, the snow crab population started to decline and the fishery collapsed by 1999 and went through a rebuilding period (Zheng et al. 2002). The population was declared rebuilt in 2011 (North Pacific Fishery Management Council 2011). Currently, there is no commercial fishing for any species in the Arctic, and for snow crabs a fishery is unlikely due to the small size of the crabs (most are smaller than the commercially desired 4-inch [10-cm] width) (North Pacific Fishery Management Council 2009).





Just like the snow crab, Tanner crabs have experienced high and low stock abundance. The EBS stock has a single overfishing limit, but separate total allowable catches are set for crabs east and west of 166° W longitude, and both fisheries have been intermittently opened and closed for the past two decades. Currently, the female population is below the threshold needed for a commercially viable total allowable catch, so a multi-vear closure of the EBS fishery until 2019 is being discussed (North Pacific Fishery Management Council 2016).

CONSERVATION ISSUES

(Jewett et al. 1996).

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A Tanner crab on deck showing its wide carapace and red-tinted eyes.

A primary management concern for snow and Tanner crabs is proper management of current and future fisheries. Oil spills are another potential human-caused impact on snow crabs in the Arctic as oil and gas exploration and extraction activity increase in the region. Not only is there a probability for immediate effects from an oil spill, but lingering oil can affect the benthic environment beyond the initial event

Tanner crabs can be infected by a parasitic dinoflagellate, Hematodinium sp., which causes bitter crab syndrome (Meyers et al. 1996). The infection leads to a high mortality rate and, while the tissue is not harmful to humans, it causes the crabs to taste bitter and therefore lose their market value (Meyers and Burton 2009). As seen elsewhere, rising ocean temperatures have increased harmful algal blooms (Patterson 2015), so managers must watch for a rise in dinoflagellate production and cases of bitter crab syndrome.

A final concern is how ocean acidification will affect snow and Tanner crab productivity. Ocean acidification affects any animal with calcium carbonate shells by dissolving their exoskeletons; this dissolution can affect larval snow and Tanner crabs by slowing their growth and reducing their calcium content (Long et al. 2013). For many animals, the larval

stage of development is their most vulnerable life history stage and less protection could mean lower survival, which would subsequently reduce recruitment to adulthood and the fishery (Punt et al. 2016).

MAPPING METHODS (MAP 3.4)

The relative abundance of snow crab was estimated by interpolating datasets from bottom trawl surveys which employed similar and consistent methodologies and sampled waters within the US exclusive economic zone (EEZ) of the Bering Sea (Conner and Lauth 2016, Hoff 2016), Aleutian Islands (Raring et al. 2016), Gulf of Alaska (von Szalay and Raring 2016), Chukchi Sea (Goddard et al. 2014), and Beaufort Sea (Logerwell et al. 2010). Data points for snow crab presence and absence were extracted and mapped based on catch per unit effort (CPUE) in kilograms per hectare. To obtain continuous coverage across the study area, data points were interpolated using the Inverse Distance Weighted tool in ArcGIS version 10.5 based on CPUE values. A radius of the 12 nearest points was set as the search distance and interpolation was limited to the study area boundaries of the trawl surveys.

Possible nursery sites for snow crab were digitized directly from Figure 9 in Parada et al. (2010) which depicts the centroids of areas of potential larval settlements based on a model of individual-based larval transport from 1978 to 2002. The south and southwesterly migration arrows were digitized from Figure 7 in the same study which summarizes the general migration patterns of female snow crab.

The general distribution of snow crab is based on adult and juvenile snow crab Essential Fish Habitat (EFH) areas which were obtained directly from National Oceanic and Atmospheric Administration (2016b). Snow crab EFH is described as habitats along the inner (0-165 feet [0-50 m]), middle (165-330 feet [50-100 m]), and outer shelf (330-660 feet [100-200 m]) throughout the Bering Sea and Aleutian Islands wherever there are substrates consisting mainly of mud. Due to their smaller overall population, limited distribution in the EBS, smaller commercial harvest, and limited range, only Tanner crab EFH is mapped (Figure 3.4-1).

Data Quality

Trawl survey data sampling was conducted within the US EEZ, therefore there is little to no coverage on the Russian side of the Bering Sea. The interpolation of the trawl survey data estimates the distribution of snow crab during the summer months and may not represent the yearround distribution.

Bottom trawl surveys in the Aleutian Islands were conducted every three years from 1983 to 2000 and on even years from 2002 to 2016. Surveys on the Bering Sea slope were conducted on even years from 2002 to 2016 except for 2006 and 2014. Surveys on the EBS shelf were conducted from 1982 to 2016. Surveys for the northern Bering Sea occurred from 1982 to 2010. Gulf of Alaska surveys were conducted in 1984 and 1987, every 3 years from 1990 to 1999, and on odd years from 2001 to 2015. Bottom trawl surveys in the Beaufort and Chukchi Seas occurred in 2008 and 2012, respectively. Data for the Beaufort and Chukchi Seas do not represent multi-year surveys or long-term trends like data for the Bering Sea.

Reviewer

Joel Webb

MAP DATA SOURCES

Trawl Density: Oceana (2017d) based on Conner and Lauth (2016), Goddard et al. (2014), Hoff (2016), Logerwell et al. (2010), Raring et al. (2016), and von Szalay and Raring (2016)

Possible Nursery Sites: Parada et al. (2010)

Essential Fish Habitat: National Oceanic and Atmospheric Administration (2016b)

Management Areas: National Oceanic and Atmospheric Administration (2016a)

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Snow Crab

Map Authors: Brianne Mecum, Marilyn Zaleski, and Jon Warrenchuk Cartographer: Daniel P. Huffman



3.4

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Paralithodes camtschaticus Brianne Mecum and Marilyn Zaleski

Red king crabs (Paralithodes camtschaticus) are the largest crab species in Alaska waters and have historically dominated Bristol Bay (North Pacific Fishery Management Council 2016). They are commercially valuable, although their stocks throughout Alaska have experienced highs and lows (North Pacific Fishery Management Council 2016), and their harvest affects the benthic community food web.

Red king crabs have a hard exoskeleton made out of chitin and grow by molting. Unlike snow and Tanner crabs (*Chionoecetes opilio* and *C*. bairdi, respectively), which have a terminal molt to maturity (see Snow and Tanner Crabs Summary), king crabs continue molting throughout their lifecycle after maturing (McCaughran and Powell 1977). This is one reason red king crabs are relatively large in size compared to other crab species in the shared marine ecosystem. Another difference between king crabs and snow crabs is the number of legs they have, signifying the infraorder they are in from Order Decapoda; king crabs are Anomurans and have six walking legs, while snow crabs are Brachyurans and have eight walking legs.

Red king crabs are closely related to blue king crabs (*Paralithodes* platypus) and golden king crabs (Lithodes aequispinus) but differ in their range, physical appearance, and physiologic attributes. Aside from the differences in coloration, there are also differences in number and morphology of spines on their carapaces, shape to their rostrum (central forward-pointing spine above the eyes), and overall different average sizes which direct their legal harvest size limits (see Table 3.5-1).

DISTRIBUTION

Red king crabs are generally distributed throughout the North Pacific from deep shelf waters (<820 feet or 250 m) to shallow, nearshore, intertidal environments (Stone et al. 1992, Zheng and Kruse 2006). They range from Southeast Alaska, along the Aleutian Islands, throughout Bristol Bay and the eastern Bering Sea (EBS), north to Kotzebue Sound, and westward toward Japan and Russia. Red king crabs are harvested in Kotzebue Sound (Georgette and Loon 1993) at the northern range limit of the species in Alaska. Globally, the northernmost red king crab stock is an introduced population in the Barents Sea off the coasts of Norway and Russia (Britayev et al. 2010). Bristol Bay is home to the most abundant, actively fished population of red king crab in the world (Daly et al. 2016). The majority of large males targeted by the fishery are found in the central and southern areas of Bristol Bay near the Alaska Peninsula (Daly et al. 2016).

LIFE CYCLE

Females mature between five to nine years old (Powell 1967, Loher et al. 2001) and are then reproductively active for up to ten more years (Hoopes and Karinen 1972). Depending on their size, mature females produce 7,000–490,000 eggs in a single clutch, with larger females producing more offspring (Swiney et al. 2012). Once red king crabs become reproductively active, they begin seasonal migrations. They spend their winters in nearshore Bristol Bay along the north shore of the Alaska Peninsula in order to molt and mate, then move into deeper offshore waters in the spring after mating and egg extrusion



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A red king crab showing its abdominal flap and stretching its long legs while standing atop a pile of sea stars.

golden king crabs.

Red and golden king crab: NOA Alaska Fisheries Science Cente Blue king crab: Celeste Lero



Center (2010b); ⁴Donaldson and Byersdorfer (2005).

et al. 2014).

After red king crab eggs hatch, the swimming larvae go through four zoeal stages, then settle to the bottom as postlarval glaucothoe, and finally molt into the first juvenile crab stage to begin their lives on the seafloor (Stevens and Kittaka 1998). The juveniles hide amongst algae and habitat-forming invertebrates such as sponges, bryozoans, and hydroids (Sundberg and Clausen 1977, Stevens and Kittaka 1998, Stoner 2009, Pirtle and Stoner 2010). These benthic invertebrates offer important nursery habitat for the first year and a half of a red king crab's life, after which the crab begins podding behavior on the seafloor (Dew 1990).

Podding behavior is unique to red king crabs and involves hundreds to thousands of crabs clustering together in dense aggregations grouped by maturity (juvenile vs. adult) and sex (Dew 1990, Dew 2010). Red king crab pods can cover vast areas of the seafloor, with one such aggregation in southern Bristol Bay estimated around 90,000 acres (36,500 ha) (Dew 2010). Unlike other crabs, these pods occur yearround and are not specifically tied to mating or molting behaviors, but rather may offer safety in numbers while resting between daily foraging excursions (Dew 1990, Dew 2010).

Red king crabs molt to grow, molting numerous times (8–11) in their first year (Westphal et al. 2014). They continue to molt several times per year in the following two to three years post-settlement, after which they molt annually in the spring (Dew 1990). Growth is temperature-dependent, and they grow faster at higher temperatures, attaining larger sizes at similar ages (Stoner et al. 2010). On average, they can grow up to 0.5 inch (11 mm) during their first year, and as the juveniles get larger, their growth increments increase (Westphal et al. 2014).

The molting process makes crabs vulnerable to predators while they are still in the soft-shell phase. Red king crabs off of Kodiak were observed molting at night (Dew 1990) and female molting happens relatively synchronously, which likely offers some protection from visual predators. Male attendance during the female molting and mating period may also reduce predation during this vulnerable period.

ECOLOGICAL ROLE

As juveniles, red king crabs forage on algae and the habitat-forming invertebrates they use for their nursery environment (Pirtle and Stoner 2010). Once they grow larger and shift into podding behavior and seasonal migrations, they eat benthic invertebrates, including bivalves, snails, polychaete worms, sea stars, and anemones, as well as smaller red king crabs (Dew 1990, Stoner 2009, Britayev et al. 2010). If the red king crabs are in a pod, they will disperse in order to forage at night then cluster back together during the day (Dew 1990).

TABLE 3.5-1. Morphological differences in harvestable red, blue, and

ANCE		*
Red King Crab Paralithodes camtschaticus	Blue King Crab P. platypus	Golden King Crab Lithodes aequispinus
6.5 inches (165 mm) ¹	5.5 inches (140 mm) ²	5.7 inches (145 mm) ³
3 pairs ⁴	2 pairs ⁴	5-9 ⁴
Single sharp spine ⁴	Biramous spine, 2 prongs ⁴	Down-curved with paired tip ⁴

Sources: ¹Alaska Fisheries Science Center (2010c); ²Alaska Fisheries Science Center (2010a); ³Alaska Fisheries Science

(Stone et al. 1992, Zheng and Kruse 2006, Chilton et al. 2010). For mature females, mating occurs in the spring in shallow water within hours of molting. Large hard-shell males will grasp females during the pre-molt period, assist with molting, mate with the female, and guard the females after mating for hours or days (Powell et al. 1974, Webb

Red king crabs are vulnerable to predation by other crabs and fishes sharing their nursery habitat, including Pacific halibut (*Hippoglossus* stenolepis), northern rock sole (Lepidopsetta polyxystra), and kelp greenlings (Hexagrammos decagrammus) (Dean et al. 2000, Stoner 2009, Daly et al. 2012). Although Pacific cod (*Gadus macrocephalus*) are important predators of snow crabs in the Bering Sea (Burgos et al. 2013), they were found to eat less than 4% of the female red king crab stock during a 1980s study (Livingston 1989) and so may pose little threat to juvenile red king crabs (Stoner 2009). Diet analysis and trophic modeling of the invasive red king crab in the Barents Sea showed that they eat similar prey items to large sea stars and snails, introducing resource competition into the ecosystem, but that they are unlikely to compete for prey with most fish species (Fuhrmann et al. 2017).

ECONOMIC IMPACT

Red king crabs are currently harvested commercially in Bristol Bay and Norton Sound (North Pacific Fishery Management Council 2016). Fisheries in the Pribilof Islands and Western Aleutian Islands were active historically but closed in 1999 and 2004, respectively (North Pacific Fishery Management Council 2016). Norton Sound supports summer and winter commercial fisheries as well as a winter subsistence fishery (Ahmasuk et al. 2008, North Pacific Fishery Management Council 2016). Bristol Bay is the largest fishery with harvests around 1.5 million crabs, although historically the peak catch was larger, with over 20 million crabs caught in the 1980 season (North Pacific Fishery Management Council 2016). The Bristol Bay fishery is worth \$50–100 million in gross revenue and provides \$10–15 million in fishing crew and processing wages (North Pacific Fishery Management Council 2015).

Subsistence catch of king crab from Nome and the Seward Peninsula is a historically important community harvest, and the crab are used both locally and in sharing or trading for other resources with Kotzebue residents, and similar communities away from king crab habitats (Georgette and Loon 1993, Ahmasuk et al. 2008).

CONSERVATION ISSUES

Many crab populations in Alaska have declined in part due to fishing harvests that were too high in the past. Efforts to rebuild crab populations have met with varying degrees of success in Alaska, and currently only two out of eight historical red king crab fisheries are still open (North Pacific Fishery Management Council 2016). The Bristol Bay stock is in decline with survey results of both males and females below the 10-year average, and an estimated 21% decrease in mature male biomass between 2015 and 2016 (North Pacific Fishery Management Council 2016).

Red king crabs are protected from trawling year-round in the Red King Crab Savings Area and seasonally (March 15–June 15) in Area 516, spatial management areas in Bristol Bay (see Map 3.5). Both areas were established to reduce by catch and protect migration of red king crab from shallow to deeper waters after molting and mating (North Pacific Fishery Management Council 2016). Despite these protections, the Bristol Bay red king crab stock is in decline and the fishery, as well as other EBS crab fisheries, are being more conservatively managed (North Pacific Fishery Management Council 2016).

Another protected area is the Pribilof Islands Habitat Conservation Zone, which was established to protect the overfished blue king crab population (Figure 3.5-1). The directed fishery for blue king crab off of the Pribilof Islands has been closed since 1999 and does not show signs of rebuilding (Daly et al. 2016). Blue king crab bycatch is therefore a limiting factor in the ability to catch red king crab in areas where their populations overlap.

A final conservation issue for red king crabs, and all crustaceans, is the effect of ocean acidification on their exoskeletons.

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RED

ECOLOGICAL ATLAS OF THE BERING, CHUKCHI, AND BEAUFORT SEAS



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Habitat, showing overlap including around the Pribilof Islands. Interactions with blue king crabs precipitated the establishment of the Pribilof Islands Habitat Conservation Zone. Figure adapted from National Oceanic and Atmospheric Administration (2016b).

MAPPING METHODS (MAP 3.5)

The relative abundance of red king crab was estimated by interpolating datasets from bottom trawl surveys which employed similar and consistent methodologies and sampled waters within the US EEZ of the Bering Sea (Conner and Lauth 2016, Hoff 2016), Aleutian Islands (Raring et al. 2016), Gulf of Alaska (von Szalay and Raring 2016), Chukchi Sea (Goddard et al. 2014), and Beaufort Sea (Logerwell et al. 2010). Data points for red king crab presence or absence were extracted and mapped based on catch per unit effort (CPUE) in kilograms per hectare. To obtain continuous coverage across the study area, data points were interpolated using the Inverse Distance Weighted (IDW) tool in ArcGIS version 10.5 based on CPUE values. A radius of the 12 nearest points was set as the search distance and interpolation was limited to the study area boundaries of the trawl surveys.

The red king crab generalized distribution polygon was digitized from North Pacific Fishery Management Council (2015) which broadly describes the range of red king crab in Alaskan waters.

Essential Fish Habitat (EFH) areas for red king crab were obtained directly from National Oceanic and Atmospheric Administration (2016b). These EFH areas are considered to be the general distribution for late juvenile and adult red king crab. These areas are described as being located in bottom habitats along the nearshore (spawning aggregations) and the inner (0-165 feet [0-50 m]), middle (165-330 feet [50-100 m]), and outer shelf (330-660 feet [100-200 m]) throughout the Bering Sea and Aleutian Islands wherever there are substrates consisting of sand, mud, cobble, and gravel.

Management area polygons were all obtained directly from National Oceanic and Atmospheric Administration (2016a). These areas were displayed because they are known important areas for red king crab spawning or migration. National Marine Fisheries Service Management Area 516 is closed to commercial bottom trawling from March 15 to June 15 to protect spawning stock of red king crab. The Red King Crab Savings Area is closed year-round to commercial bottom trawling to protect important red king crab habitat and migration area and to protect spawning stock biomass. Additionally, the Pribilof Islands Habitat Conservation Area is closed year-round to commercial bottom trawling to protect blue king crab from overexploitation as bycatch.

Data **Ouality**

Trawl survey data sampling was conducted within the US EEZ, therefore there is little to no coverage on the Russian side of the Bering Sea for red king crab. The interpolation of the trawl survey data estimates the distribution of red king crab during the summer months and may not represent the year-round distribution.

Bottom trawl surveys in the Aleutian Islands were conducted every 3 years from 1983 to 2000 and on even years from 2002 to 2016. Surveys on the Bering Sea slope were conducted on even years from 2002 to 2016 except for 2006 and 2014. Surveys on the EBS shelf were conducted from 1982 to 2016. Surveys for the northern Bering Sea occurred from 1982 to 2010. Gulf of Alaska surveys were conducted in 1984 and 1987, every 3 years from 1990–1999, and on odd years from 2001 to 2015. Bottom trawl surveys in the Beaufort and Chukchi Seas occurred in 2008 and 2012, respectively. Data for the Beaufort and Chukchi Seas do not represent multi-year surveys or long-term trends like data for the Bering Sea.

Reviewer Joel Webb

MAP DATA SOURCES

Trawl Density: Oceana (2017c) based on Conner and Lauth (2016), Goddard et al. (2014), Hoff (2016), Logerwell et al. (2010), Raring et al. (2016), and von Szalay and Raring (2016)

Distribution: North Pacific Fishery Management Council (2015)

Essential Fish Habitat: National Oceanic and Atmospheric Administration (2016b)

Management Areas: National Oceanic and Atmospheric Administration (2016a)

Red King Crab

Trawl [Density	(kg/ha)
0.1	10.0	55.6





C. T. I. C. - O. C. E. A. N.





Red King Crab (Paralithodes camtschaticus)

Red king crabs are the largest-sized crab species in Alaska waters. Red king crabs are generally distributed throughout the North Pacific from deep shelf waters (<820 ft or 250 m) to shallow, nearshore, intertidal environments. They range from Southeast Alaska, along the Aleutian Islands, throughout Bristol Bay and the eastern Bering Sea, north to Kotzebue Sound, and westward toward Japan and Russia. Bristol Bay is home to the most abundant actively fished population, though the stock is currently in decline and the fishery is being conservatively managed. The majority of large males targeted by the fishery are found in the central and southern areas of Bristol Bay near the Alaska Peninsula. Molting and mating red king crabs are protected from trawling year-round in the Red King Crab Savings Area and seasonally in Area 516. Another protected area is the Pribilof Islands Habitat Conservation Zone, which was established to protect the overfished blue king crab (*P. platypus*).

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- Agnalt, A.-L., V. Pavlov, K. E. Jørstad, E. Farestveit, and J. Sundet. 2011. The snow crab, Chionoecetes opilio (Decapoda, Majoidea, Oregoniidae) in the Barents Sea, In In the Wrong Place - Alien Marine Crustaceans: Distribution, Biology and Impacts, B. S. Galil, P. F. Clark, and J. T. Carlton eds., pp. 283-300, Springer, Dordrecht, Netherlands,
- Ahmasuk, A., E. Trigg, J. Magdanz, and B. Robbins. 2008. Bering Strait Region Local and Traditional Knowledge Pilot Project: A Comprehensive Subsistence Use Study of the Bering Strait Region. North Pacific Research Board Final Report #643. Kawerak, Inc., Nome, AK.
- Alaska Fisheries Science Center. 2010a. Blue King Crab. NOAA Fisheries Service Alaska Fisheries Science Center. National Oceanic and Atmospheric Administration, Seattle, WA.
- . 2010b. Golden King Crab. NOAA Fisheries Service Alaska Fisheries Science Center. National Oceanic and Atmospheric Administration, Seattle, WA.
- _. 2010c. Red King Crab. NOAA Fisheries Service Alaska Fisheries Science Center. National Oceanic and Atmospheric Administration, Seattle, WA.
- Allain, R. N., M. Moriyasu, B. D. Crawford, and S. C. Courtenay. 2011. Lipofuscin quantification as a potential tool for age estimation in snow crabs, (O. Fabricius, 1788) (Decapoda, Oregoniidae) Crustaceana 84:1441-1463.
- Alvsvåg, J., A.-L. Agnalt, and K. E. Jørstad. 2009. Evidence for a permanent establishment of the snow crab (Chionoecetes opilio) in the Barents Sea. Biological Invasions 11:587-595.
- Andrews, A. H., E. E. Cordes, M. M. Mahoney, K. Munk, K. H. Coale, G. M. Cailliet, and J. Heifetz. 2002. Age, growth and rediometric age validation of a deep-sea, habitat-forming gorgonian (Primnoa resedaeformis) from the Gulf of Alaska. Hydrobiologia 471:101-110.
- Armstrong, J. L., J. L. Boldt, A. D. Cross, J. H. Moss, N. D. Davis, K. W. Myers, R. V. Walker, D. A. Beauchamp, and L. J. Haldorson. 2005. Distribution, size, and interannual, seasonal and diel food habits of northern Gulf of Alaska juvenile pink salmon, Oncorhynchus gorbuscha. Deep Sea Research Part II: Topical Studies in Oceanography 52:247-265
- Arrigo, K. R. 2014. Sea ice ecosystems. Annual Review of Marine Science 6:439-467.
- Arrigo, K. R., D. K. Perovich, R. S. Pickart, Z. W. Brown, G. L. van Dijken, K. E. Lowry, M. M. Mills, M. A. Palmer, W. M. Balch, and F. Bahr. 2012. Massive phytoplankton blooms under Arctic sea ice. Science 336:1408-1408.
- Arrigo, K. R. and G. L. van Dijken. 2011. Secular trends in Arctic Ocean net primary production. Journal of Geophysical Research: Oceans 116:C09011.
- 2015. Continued increases in Arctic Ocean primary production. Progress in Oceanography 136.60-20
- Ashjian, C. J. 2013. Integrated Chlorophyll (0-100 m, mg/m²), All Data. Version 1.0. UCAR/NCAR Earth Observing Laboratory, Accessed online at https://doi.org/10.5065/D69C6VFZ.
- Audubon Alaska. 2016. Monthly Sea Ice Approximate 2006-2015 Medians GIS File. Audubon Alaska, Anchorage, AK.
- Audubon Alaska and Oceana. 2017. Interpolated Primary Productivity GIS File. Audubon Alaska, Anchorage, AK,
- Barber, D. G., H. Hop, C. J. Mundy, B. Else, I. A. Dmitrenko, J.-E. Tremblay, J. K. Ehn, P. Assmy, M. Daase, and L. M. Candlish, 2015. Selected physical, biological and biogeochemical implications of a rapidly changing Arctic Marginal Ice Zone. *Progress in Oceanography* 139:122-150.
- Barber, W. E., R. L. Smith, and T. J. Weingartner. 1994. Fisheries Oceanography of the Northeast Chukchi Sea - Final Report. OCS MMS 93-0051. Minerals Management Service, Alaska OCS Region, Anchorage, AK.
- Bates, N. R., J. T. Mathis, and L. W. Cooper. 2009. Ocean acidification and biologically induced seasonality of carbonate mineral saturation states in the western Arctic Ocean. Journal of Geophysical Research: Oceans 114
- Bekryaev, R. V., I. V. Polyakov, and V. A. Alexeev. 2010. Role of polar amplification in long-term surface air temperature variations and modern Arctic warming. *Journal of Climate* 23:3888-3906.
- Bluhm, B., K. Dunton, J. Grebmeier, and B. Sirenko. 2008. Benthos, In Arctic Ocean Synthesis: Analysis of Climate Change Impacts in the Chukchi and Beaufort Seas with Strategies for Future Research. R. Hopcroft, B. Bluhm, R. Gradinger, T. E. Whitledge, T. Weingartner, B. Norcross, and A. Springer eds., pp. 56-65. University of Alaska Fairbanks, Institute of Marine Science, Fairbanks, AK.
- Bluhm, B. A., K. Iken, S. Mincks Hardy, B. I. Sirenko, and B. A. Holladay. 2009. Community structure of epibenthic megafauna in the Chukchi Sea. Aquatic Biology 7:269-293.
- Boetius, A., S. Albrecht, K. Bakker, C. Bienhold, J. Felden, M. Fernández-Méndez, S. Hendricks, C. Katlein, C. Lalande, and T. Krumpen. 2013. Export of algal biomass from the melting Arctic sea ice. Science 339:1430-1432.
- Boldt, J. L. and C. N. Rooper. 2009. Abundance, condition, and diet of juvenile Pacific Ocean perch (Sebastes alutus) in the Aleutian Islands. Fishery Bulletin 107:278-285.
- Britayev, T. A., A. V. Rzhavsky, L. V. Pavlova, and A. G. Dvoretskij. 2010. Studies on impact of the alier red king crab (Paralithodes camtschaticus) on the shallow water benthic communities of the Barents Sea. Journal of Applied Ichthyology 26:66-73.
- Brower, A. A., M. C. Ferguson, S. V. Schonberg, S. C. Jewett, and J. T. Clarke. 2017. Gray whale distribution relative to benthic invertebrate biomass and abundance: Northeastern Chukchi Sea 2009–2012. Deep-Sea Research Part II: Topical Studies in Oceanography.
- Brown, Z. W. and K. R. Arrigo. 2012. Contrasting trends in sea ice and primary production in the Bering Sea and Arctic Ocean. ICES Journal of Marine Science 69:1180-1193.
- . 2013. Sea ice impacts on spring bloom dynamics and net primary production in the eastern Bering Sea. Journal of Geophysical Research: Oceans 118:43-62.
- Brown, Z. W., G. L. van Dijken, and K. R. Arrigo. 2011. A reassessment of primary production and environmental change in the Bering Sea. Journal of Geophysical Research: Oceans 116:C08014.
- Burgos, J., B. Ernst, D. Armstrong, and J. Orensanz. 2013. Fluctuations in range and abundance of snow crab (Chionoecetes opilio) from the eastern Bering Sea: What role for Pacific cod (Gadus macrocephalus) predation? Bulletin of Marine Science 89:57-81.

- Burmeister, A. and B. Sainte-Marie. 2010. Pattern and causes of a temperature-dependent gradient of size at terminal moult in snow crab (Chionoecetes opilio) along West Greenland. Polar Biology 33.775-788
- Chaves, J. E., P. J. Werdell, C. W. Proctor, A. R. Neeley, S. A. Freeman, C. S. Thomas, and S. B. Hooker. 2015. Assessment of ocean color data records from MODIS-Agua in the western Arctic Ocean. Deep Sea Research Part II: Topical Studies in Oceanography 118, Part A:32-43.
- Chilton, E. A., R. J. Foy, and C. E. Armistead, 2010. Temperature effects on assessment of red king crab in Bristol Bay, Alaska, In Biology and Management of Exploited Crab Populations under Climate Change. G. H. Kruse, G. L. Eckert, R. J. Foy, R. N. Lipcius, B. Sainte-Marie, D. L. Stram, and D. Woodby eds. Alaska Sea Grant AK-SG-10-01, University of Alaska Fairbanks, Fairbanks, AK
- Comeau, M., M. Starr, G. Y. Conan, G. Robichaud, and J.-C. Therriault. 1999. Fecundity and duration of egg incubation for multiparous female snow crabs (Chionoecetes opilio) in the fjord of Bonne Bay, Newfoundland. Canadian Journal of Fisheries and Aquatic Sciences 56:1088-1095.
- Conan, G. Y. and M. Comeau. 1986. Functional maturity and terminal molt of male snow crab, Chionoecetes opilio. Canadian Journal of Fisheries and Aquatic Sciences 43:1710-1719.
- Conan, G. Y., M. Moriyasu, D. R. Maynard, and Y. Chiasson. 1989. Factors influencing egg production in decapod Crustacea with two case studies: Chionoecetes opilio and Homarus americanus in the Gulf of St. Lawrence. ICES CM 1989/Mini 04.
- Conan, G. Y., M. Starr, M. Comeau, J. C. Therriault, G. Robichand, and F. X. M. Hernandez, 1996, Life history strategies, recruitment fluctuations, and management of the Bonne Bay Fjord Atlantic snow crab (Chionoecetes opilio), In Proceedings of the International Symposium on the Biology, Management and Economics of Crabs from High Latitude Habitats. October 1995, Anchorage, AK.
- Conner, J. and R. R. Lauth. 2016. Results of the 2013 Eastern Bering Sea Continental Shelf Bottor Trawl Survey of Groundfish and Invertebrate Resources. NOAA Technical Memorandum NMFS-AFSC-331, National Oceanic and Atmospheric Administration, Seattle, WA.
- Coyle, K. O., B. Konar, A. Blanchard, R. C. Highsmith, J. Carroll, M. Carroll, S. G. Denisenko, and B. I. Sirenko, 2007. Potential effects of temperature on the benthic infaunal community on the southeastern Bering Sea shelf: Possible impacts of climate change. Deep Sea Research Part II: Topical Studies in Oceanography 54:2885-2905.
- Coyle, K. O., A. I. Pinchuk, L. B. Eisner, and J. M. Napp. 2008. Zooplankton species composition, abundance and biomass on the eastern Bering Sea shelf during summer: The potential rol of water-column stability and nutrients in structuring the zooplankton community. Deep Sea Research Part II: Topical Studies in Oceanography 55:1775-1791.
- Daly, B., G. L. Eckert, and T. D. White. 2012. Predation of hatchery-cultured juvenile red king crabs (Paralithodes camtschaticus) in the wild, Canadian Journal of Fisheries and Aquatic Sciences 70:358-366.
- Daly, B. J., C. E. Armistead, and R. J. Foy. 2016. The 2016 Eastern Bering Sea Continental Shelf Bottom Trawl Survey: Results for Commercial Crab Species. NOAA Technical Memorandum NMFS-AFSC. National Oceanic and Atmospheric Administration, Kodiak, AK
- Davis, N. D., K. W. Myers, and Y. Ishida. 1998. Caloric value of high-seas salmon prey organisms and simulated salmon ocean growth and prey consumption. North Pacific Anadromous Fish Commission Bulletin No. 1.146-162
- Dean, T. A., L. Haldorson, D. R. Laur, S. C. Jewett, and A. Blanchard. 2000. The distribution of nearshore fishes in kelp and eelgrass communities in Prince William Sound, Alaska: Associations with vegetation and physical habitat characteristics. Environmental Biology of Fishes 57:271-287.
- Dew, C. B. 1990. Behavioral ecology of podding red king crab, Paralithodes camtschatica. Canadian Journal of Fisheries and Aquatic Sciences 47:1944-1958.
- . Podding behavior of adult king crab and its effect on abundance-estimate precision. In Biology and Management of Exploited Crab Populations Under Climate Change, G. H. Kruse, G. L. Eckert, R. J. Foy, R. N. Lipcius, B. Sainte-Marie, D. L. Stram, and D. Woodby eds. Alaska Sea Grant, University of Alaska Fairbanks, Fairbanks, AK
- Dionne, M., B. Sainte-Marie, E. Bourget, and D. Gilbert. 2003. Distribution and habitat selection of early nthic stages of snow crab Chionoecetes opilio. Marine Ecology Progress Series 259:117-128.
- Divine, L. M., B. A. Bluhm, F. J. Mueter, and K. Iken, 2017. Diet analysis of Alaska Arctic snow crabs (Chionoecetes opilio) using stomach contents and $\delta^{13}C$ and $\delta^{15}N$ stable isotopes. Deep Sea Research Part II: Topical Studies in Oceanography 135:124-136.
- Donaldson, W. E. and S. C. Byersdorfer. 2005. Biological Field Techniques for Lithodid Crabs. Alaska Sea Grant College Program AK-SG-05-03, University of Alaska Fairbanks, Fairbanks, AK,
- Duggins, D. O., C. A. Simenstad, and J. A. Estes. 1989. Magnification of secondary production by kelp detritus in coastal marine ecosystems. Science 245:170-173.
- Dunton, K. H., J. L. Goodall, S. V. Schonberg, J. M. Grebmeier, and D. R. Maidment. 2005. Multi-decadal synthesis of benthic-pelagic coupling in the western Arctic: Role of cross-shelf advective processes. Deep Sea Research Part II: Topical Studies in Oceanography 52:3462-3477.
- Eisner, L., N. Hillgruber, E. Martinson, and J. Maselko. 2013. Pelagic fish and zooplankton species assemblages in relation to water mass characteristics in the northern Bering and southeast Chukchi seas. Polar Biology 36:87-113.
- Eisner, L. B., J. M. Napp, K. L. Mier, A. I. Pinchuk, and A. G. Andrews III. 2014. Climate-mediated changes in zooplankton community structure for the eastern Bering Sea. Deep Sea Research Part II: Topical Studies in Oceanography 109:157-171.
- Ernst, B., D. A. Armstrong, J. Burgos, and J. M. Orensanz. 2012. Life history schedule and periodic recruitment of female snow crab (Chionoecetes opilio) in the eastern Bering Sea. Canadian Journal of Fisheries and Aquatic Sciences 69:532-550.
- Ernst, B., J. M. Orensanz, and D. A. Armstrong, 2005, Spatial dynamics of female snow crab (Chionoecetes opilio) in the eastern Bering Sea. Canadian Journal of Fisheries and Aquatic Sciences 62:250-268.
- Fabry, V. J., J. B. McClintock, J. T. Mathis, and J. M. Grebmeier. 2009. Ocean acidification at high latitudes: The bellweather. Oceanography 22:160-171.
- Falkowski, P. G., R. T. Barber, and V. Smetacek. 1998. Biogeochemical controls and feedbacks on ocean primary production. Science 281:200-206.

Feder, H. M., S. C. Jewett, and A. Blanchard, 2005, Southeastern Chukchi Sea (Alaska) epibenthos, Polar Biology 28:402-421.

Data Center, Boulder, CO.

Bering Sea. Alaska. Ophelia 24:17-36.

in Oceanography 44:1623-1644.

of Marine Science 4:63-78

Progress in Oceanography 136:92-114.

Oceanography 71:331-361.

Series 51:253-269

Progress Series 48:57-67

Sea. Science 311:1461-1464.

471:19-28.

52.3344-3354

Fishery Bulletin 70:225-226.

- Fetterer, F., K. Knowles, W. Meier, and M. Savoie, 2016. Sea Ice Index, Version 2, National Snow and Ice
- Fonseca, D. B., B. Sainte-Marie, and F. Hazel. 2008. Longevity and change in shell condition of adult male snow crab Chionoecetes opilio inferred from dactyl wear and mark-recapture data. Transactions of the American Fisheries Society 137:1029-1043.
- Frey, K. E., K. R. Arrigo, and W. J. Williams 2012. Primary Productivity and Nutrient Variability, In Arctic Report Card 2012. M. O. Jeffries, J. A. Richter-Menge, and J. E. Overland eds. Accessed online at http://www.arctic.noaa.gov/reportcard.
- Frey, K. E., J. C. Comiso, L. W. Cooper, R. R. Gradinger, J. M. Grebmeier, and J.-É. Tremblay. 2015. Arctic Ocean Primary Productivity, In Arctic Report Card 2015. M. O. Jeffries, J. A. Richter-Menge, and J. E. Overland eds. Accessed online at http://www.arctic.noaa.gov/Report-Card.
- Frey, K. E., D. K. Perovich, and B. Light. 2011. The spatial distribution of solar radiation under a melting Arctic sea ice cover. Geophysical Research Letters 38:L22501.
- Fuhrmann M M T Pedersen and F M Nilssen 2017 Trophic niche of the invasive red king crab Paralithodes camtschaticus in a benthic food web. Marine Ecology Progress Series 565:113-129.
- Fukuyama, A. K. and J. S. Oliver, 1985. Sea star and walrus predation on bivalves in Norton Sound.
- Georgette, S. and H. Loon, 1993, Subsistence Use of Fish and Wildlife in Kotzebue, a Northwest Alaska Regional Center. Technical Paper No. 167. Alaska Department of Fish and Game, Juneau, AK.
- Goddard, P., R. Lauth, and C. Armistead, 2014. Results of the 2012 Chukchi Sea Bottom Trawl Survey of Bottomfishes, Crabs, and Other Demersal Macrofauna. NOAA Technical Memorandum NMFS-AFSC-278. National Oceanic and Atmospheric Administration, Seattle, WA.
- Gosselin, M., M. Levasseur, P. Wheeler, R. Horner, and B. Booth, 1997. New measurements of phytoplankton and ice algal production in the Arctic Ocean. Deep-Sea Research Part II: Topical Studies
- Grebmeier, J. M. 2012. Shifting patterns of life in the Pacific Arctic and sub-Arctic Seas. Annual Review
- Grebmeier, J. M., B. A. Bluhm, L. W. Cooper, S. L. Danielson, K. R. Arrigo, A. L. Blanchard, J. T. Clarke, R. H. Dav. K. E. Frev. R. R. Gradinger, M. Kedra, B. Konar, K. J. Kuletz, S. H. Lee, J. R. Lovvorn, B. L. Norcross, and S. R. Okkonen, 2015a, Ecosystem characteristics and processes facilitating persistent macrobenthic biomass hotspots and associated benthivory in the Pacific Arctic.
- Grebmeier, J. M. and L. W. Cooper, 2014a, PacMARS Benthic Infaunal Parameters, Version 1.0, UCAR/ NCAR - Earth Observing Laboratory. Accessed online at https://doi.org/10.5065/D6H70CVR.
 - . 2014b. PacMARS Integrated Chlorophyll-a (1985-2012). Version 1.0. UCAR/NCAR Earth Observing Laboratory. Accessed online at https://doi.org/10.5065/D6F47M47.
- Grebmeier, J. M., L. W. Cooper, C. A. Ashjian, B. A. Bluhm, R. B. Campbell, K. E. Dunton, J. Moore, S. Okkonen, G. Sheffield, J. Trefry, and S. Y. Pasternak. 2015b. Pacific Marine Arctic Regional Synthesis (PacMARS) Final Report, North Pacific Research Board, Anchorage, AK,
- Grebmeier, J. M., L. W. Cooper, H. M. Feder, and B. I. Sirenko, 2006a, Ecosystem dynamics of the Pacific-influenced northern Bering and Chukchi Seas in the Amerasian Arctic. Progress in
 - . 2014. Ecosystem dynamics of the Pacific-influenced northern Bering and Chukchi Seas in the Amerasian Arctic (updated sampling dataset). Progress in Oceanography 71:331-361.
- Grebmeier, J. M., H. M. Feder, and C. P. McRov, 1989. Pelagic-benthic coupling on the shelf of the northern Bering and Chukchi Seas. II. Benthic community structure. Marine Ecology-Progress
- Grebmeier, J. M. and H. R. Harvey, 2005. The western Arctic Shelf-Basin Interactions (SBI) project: An overview. Deep-Sea Research Part II: Topical Studies in Oceanography 52:3109-3115
- Grebmeier, J. M., C. P. McRoy, and H. M. Feder. 1988. Pelagic-benthic coupling on the shelf of the northern Bering and Chukchi Seas. I. Food-supply source and benthic biomass. Marine Ecology-
- Grebmeier, J. M., J. E. Overland, S. E. Moore, E. V. Farley, E. C. Carmack, L. W. Cooper, K. E. Frey, J. H. Helle, F. A. McLaughlin, and S. L. McNutt. 2006b. A major ecosystem shift in the northern Bering
- Hardy, S. M., M. Lindgren, H. Konakanchi, and F. Huettmann, 2011, Predicting the distribution and ecological niche of unexploited snow crab (Chionoecetes opilio) populations in Alaskan waters: A first open-access ensemble model. Integrative and Comparative Biology 51:608-622.
- Hébert, M., E. Wade, P. DeGrâce, J.-F. Landry, and M. Moriyasu. 2014. The 2013 Assessment of the Snow Crab (Chionoecetes opilio) Stock in the Southern Gulf of St. Lawrence (Areas 12, 19, 12E and 12F). Research Document 2014/084. DFO Canadian Science Advisory Secretariat, Ottawa, Canada.
- Heifetz, J. 2002. Coral in Alaska: Distribution, abundance, and species associations. Hydrobiologia
- Heifetz, J., B. L. Wing, R. P. Stone, P. W. Malecha, and D. L. Courtney. 2005. Coral of the Aleutian Islands. Fisheries Oceanography 14:131-138.
- Hill, V. and G. Cota. 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
- Hoff, G. R. 2016. Results of the 2016 Eastern Bering Sea Upper Continental Slope Survey of Groundfish and Invertebrate Resources. NOAA Technical Memorandum NMFS-AFSC-339. National Oceanic and Atmospheric Administration, Seattle, WA.
- Hoopes, D. and J. Karinen. 1972. Longevity and growth of tagged king crabs in the eastern Bering Sea.
- Hopcroft, R., C. Ashjian, S. Smith, and K. Kosobokova. 2008. Zooplankton, In Arctic Ocean Synthesis: Analysis of Climate Change Impacts in the Chukchi and Beaufort Seas with Strategies for Future Research. R. Hopcroft, B. Bluhm, R. Gradinger, T. E. Whitledge, T. Weingartner, B. Norcross, and A. Springer eds. University of Alaska Fairbanks, Institute of Marine Science, Fairbanks, AK.
- Hopcroft, R. R., C. Clarke, R. J. Nelson, and K. A. Raskoff, 2005. Zooplankton communities of the Arctic's Canada Basin: The contribution by smaller taxa. Polar Biology 28:198-206.

- Horner, R. and G. C. Schrader. 1982. Relative contributions of ice algae, phytoplankton, and benthic microalgae to primary production in nearshore regions of the Beaufort Sea. Arctic 35:485-503.
- Hunt, G. L., Jr. P. Stabeno, G. Walters, E. Sinclair, R. D. Brodeur, J. M. Napp, and N. A. Bond, 2002. Climate change and control of the southeastern Bering Sea pelagic ecosystem. Deep Sea Research Part II: Topical Studies in Oceanography 49:5821-5853.
- Hunt, G. L., Jr, K. O. Coyle, L. B. Eisner, E. V. Farley, R. A. Heintz, F. Mueter, J. M. Napp, J. E. Overland, P. H. Ressler, S. Salo, and P. J. Stabeno. 2011. Climate impacts on eastern Bering Sea foodwebs: A synthesis of new data and an assessment of the Oscillating Control Hypothesis. ICES Journal of Marine Science 68:1230-1243.
- Jadamec, L. S., W. E. Donaldson, and P. Cullenberg. 1999. Biological Field Techniques for Chionoecetes crabs. University of Alaska Sea Grant AK-SG-99-02, Fairbanks, AK.
- Jewett, S. C., T. A. Dean, and D. R. Laur. 1996. Effect of the Exxon Valdez oil spill on the benthic invertebrates in an oxygen-deficient embayment in Prince William Sound, Alaska. In Proceedings of the Exxon Valdez Oil Spill Symposium. American Fisheries Society, Bethesda, MD.
- Kawaguchi, S., H. Kurihara, R. King, L. Hale, T. Berli, J. P. Robinson, A. Ishida, M. Wakita, P. Virtue, S. Nicol, and A. Ishimatsu. 2010. Will krill fare well under Southern Ocean acidification? Biology Letters 7:228-291.
- Kilada, R., J. B. Webb, K. W. McNeel, L. S. Slater, Q. Smith, and J. Ferguson. 2017. Preliminary assessment of a direct age-determination method for 3 commercially important crustaceans from Alaska. Fishery Bulletin 115:42-49.
- Kim, S. L. and J. S. Oliver, 1989. Swarming benthic crustaceans in the Bering and Chukchi Seas and their relation to geographic patterns in gray whale feeding. Canadian Journal of Zoology 67:1531-1542.
- Kon, T., M. Ono, and Y. Honma. 2010. Histological studies on the spent ovaries of aged snow crabs Chionoecetes opilio caught in the Sea of Japan. Fisheries Science 76:227-233.
- Krembs, C., R. Gradinger, and M. Spindler. 2000. Implications of brine channel geometry and surface area for the interaction of sympagic organisms in Arctic sea ice. Journal of Experimental Marine Biology and Ecology 243:55-80.
- Kruse, G. H., A. V. Tyler, B. Sainte-Marie, and D. Pengilly. 2007. A workshop on mechanisms affecting year-class strength formation in snow crabs (Chionoecetes opilio) in the eastern Bering Sea. Alaska Fishery Research Bulletin 12:277-290.
- Lehnert, H. and R. P. Stone. 2014. Two new species of sponges (Porifera, Demospongiae) from the Aleutian Islands, Alaska. Journal of the Marine Biological Association of the United Kingdom 96:673-680.
- Leu, E., C. Mundy, P. Assmy, K. Campbell, T. Gabrielsen, M. Gosselin, T. Juul-Pedersen, and R. Gradinger. 2015. Arctic spring awakening-steering principles behind the phenology of vernal ice algal blooms. Progress in Oceanography 139:151-170.
- Livingston, P. A. 1989. Interannual trends in Pacific cod, Gadus marcocephalus, predation on three ommercially important crab species in the eastern Bering Sea. Fisheries Bulletin 87:807-827.
- Loeng, H., K. Brander, E. Carmack, S. Denisenko, K. Drinkwater, B. Hansen, K. Kovacs, P. Livingston, F. McLaughlin, and E. Sakshaug. 2005. Marine systems, In Arctic Climate Impact Assessment. C. Symon, L. Arris, and B. Heal eds., pp. 453-538. Cambridge University Press, New York, NY.
- Logerwell, E., K. Rand, S. Parker-Stetter, J. Horne, T. Weingartner, and B. Bluhm. 2010. Beaufort Sea Marine Fish Monitoring 2008: Pilot Survey and Test of Hypotheses. BOEMRE 2010-048. Minerals Management Service, Anchorage, AK.
- Loher, T., D. A. Armstrong, and B. G. Stevens, 2001, Growth of juvenile red king crab (Paralithodes) camtschaticus) in Bristol Bay (Alaska) elucidated from field sampling and analysis of trawl survey data. Fishery Bulletin 99:572-587.
- Long, W. C., K. M. Swiney, C. Harris, H. N. Page, and R. J. Foy. 2013. Effects of ocean acidification on juvenile red king crab (Paralithodes camtschaticus) and tanner crab (Chionoecetes bairdi) growth, condition, calcification, and survival. PLoS ONE 8:e60959.
- Lovrich, G. A. and B. Sainte-Marie. 1997. Cannibalism in the snow crab, Chionoecetes opilio (O. Fabricius) (Brachyura: Majidae), and its potential importance to recruitment. Journal of Experimental Marine Biology and Ecology 211:225-245.
- Malecha, P. W., R. P. Stone, and J. Heifetz. 2005. Living substrate in Alaska: Distribution, abundance and species associations, In Benthic Habitats and the Effects of Fishing, P. W. Barnes and J. P. Thomas eds., pp. 289-299. American Fisheries Society Symposium 41, Bethesda, MD.
- McCaughran, D. A. and G. C. Powell. 1977. Growth model for Alaska king crab (Paralithodes camtschaticus). Journal of the Fisheries Research Board of Canada 34:989-995.
- McConnaughey, R. A. and K. R. Smith. 2000. Associations between flatfish abundance and surficial sediments in the eastern Bering Sea. Canadian Journal of Fisheries and Aquatic Sciences 57:2410-2419.
- Merkouris, S. E., L. W. Seeb, and M. C. Murphy. 1998. Low levels of genetic diversity in highly exploited populations of Alaskan Tanner crabs, Chionoecetes bairdi, and Alaskan and Atlantic snow crabs, C. opilio, Fishery Bulletin 96:525-537.
- Meyers, T. and T. Burton. 2009. Hematodinium sp. Bitter crab disease of Tanner crabs, In Diseases of Wild and Cultured Shellfish in Alaska, pp. 84-89. Alaska Department of Fish and Game. Commercial Fisheries Division, Anchorage, AK.
- Meyers, T., J. Morado, A. Sparks, G. Bishop, T. Pearson, D. Urban, and D. Jackson, 1996, Distribution of bitter crab syndrome in Tanner crabs (Chionoecetes bairdi, C. opilio) from the Gulf of Alaska and the Bering Sea. Diseases of Aquatic Organisms 26:221-227.
- Morel, A. and D. Antoine. 2002. Small critters-Big effects. Science 296:1980-1982.
- Moriarty, R. and T. D. O'Brien, 2013. Distribution of mesozooplankton biomass in the global ocean. Earth System Science Data 5:45-55.
- Morivasu, M. and C. Lanteigne, 1998, Embryo development and reproductive cycle in the snow crab. Chionoecetes opilio (Crustacea: Majidae), in the southern Gulf of St. Lawrence, Canada. Canadian Journal of Zoology 76:2040-2048.
- Moriyasu, M. and P. Mallet. 1986. Molt stages of the snow crab Chionoecetes opilio by observation of morphogenesis of setae on the maxilla. Journal of Crustacean Biology 6:709-718.
- Moss, J. H., M. F. Zaleski, and R. A. Heintz. 2016. Distribution, diet, and energetic condition of age-0 walleye pollock (Gadus chalcogrammus) and Pacific cod (Gadus macrocephalus) inhabiting the Gulf of Alaska, Deep Sea Research Part II: Topical Studies in Oceanography 132:146-153.

- Muller-Karger, F. E., R. Varela, R. Thunell, R. Luerssen, C. Hu, and J. J. Walsh. 2005. The importance of continental margins in the global carbon cycle. Geophysical Research Letters 32:L01602.
- National Oceanic and Atmospheric Administration. 2012. COPEPOD: The Global Plankton Database. Annual Carbon Mass [Excel file]. National Oceanic and Atmospheric Administration. Accessed online at http://www.st.nmfs.noaa.gov/copepod/biomass/biomass-fields.html.
- . 2016a. AFSC/RACE: Alaska Groundfish Survey 1982-2015 for web. Alaska Fisheries Science Center Groundfish Assessment Program, Seattle, WA. Accessed online at http://www.afsc.noaa. gov/RACE/groundfish/survey_data/
- . 2016b. Essential Fish Habitat (EFH) Mapper. GIS Shapefiles. National Oceanic and Atmospheric Administration, Seattle, WA. Accessed online at http://www.habitat.noaa.gov/protection/efh/ efhmapper/index.html
- North Pacific Fishery Management Council. 2009. Fishery Management Plan for Fish Resources of the Arctic Management Area. North Pacific Fishery Management Council, Anchorage, AK.
- 2010. Stock Assessment and Fishery Evaluation Report for the King and Tanner Crab Fisheries of the Bering Sea and Aleutian Islands Regions. North Pacific Fishery Management Council, Anchorage, AK
- 2011. Stock Assessment and Fishery Evaluation Report for the King and Tanner Crab Fisheries of the Bering Sea and Aleutian Islands Regions. North Pacific Fishery Management Council, Anchorage, AK,
- 2015. Stock Assessment and Fishery Evaluation Report for the King and Tanner Crab Fisheries of the Bering Sea and Aleutian Islands Regions. North Pacific Fishery Management Council, Anchorage, AK.
- . 2016. Stock Assessment and Fishery Evaluation Report for the King and Tanner Crab Fisheries of the Bering Sea and Aleutian Islands Regions. North Pacific Fishery Management Council, Anchorage, AK
- Oceana, 2017a, Interpolated Benthic Biomass GIS File, Oceana, Juneau, AK,
- . 2017b. Interpolated Zooplankton GIS File. Oceana, Juneau, AK
- . 2017c. Red King Crab GIS File, Oceana, Juneau, AK
- . 2017d. Snow Crab GIS File. Oceana, Juneau, AK
- Oceana and Kawerak. 2014. Appendix: Oceana's quantitative procedure for identifying important ecological areas at higher levels of ecological complexity, In Marine Life and Subsistence Use Data Synthesis. Oceana and Kawerak eds., pp. 317-325, Juneau, AK.
- Ohashi, R., A. Yamaguchi, K. Matsuno, R. Saito, N. Yamada, A. Iijima, N. Shiga, and I. Imai. 2013. Interannual changes in the zooplankton community structure on the southeastern Bering Sea shelf during summers of 1994-2009. Deep Sea Research Part II: Topical Studies in Oceanography 91.11-56
- Olson, M. B. and S. L. Strom. 2002. Phytoplankton growth, microzooplankton herbivory and community structure in the southeast Bering Sea: Insight into the formation and temporal persistence of an Emiliania huxleyi bloom. Deep Sea Research Part II: Topical Studies in Oceanography 49:5969-5990.
- Orensanz, J., B. Ernst, D. A. Armstrong, P. Stabeno, and P. Livingston. 2004. Contraction of the geographic range of distribution of snow crab (Chionoecetes opilio) in the eastern Bering Sea An environmental ratchet? California Cooperative Oceanic Fisheries Investigations 45:65-79.
- Orensanz, J. M., E. Billy, and D. A. Armstrong. 2007. Variation of female size and stage at maturity in snow crab (Chionoecetes opilio) (Brachyura: Majidae) from the eastern Bering Sea. Journal of Crustacean Biology 27:576-591.
- Orr, J. C., V. J. Fabry, O. Aumont, L. Bopp, S. C. Doney, R. A. Feely, A. Gnanadesikan, N. Gruber, A. Ishida, and F. Joos. 2005. Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. Nature 437:681-686.
- Otto, R. S. 1998. Assessment of the eastern Bering Sea snow crab, Chionoecetes opilio, stock under the terminal molting hypothesis. In Canadian Special Publication of Fisheries and Aquatic Sciences 125: Proceedings of the North Pacific Symposium on Invertebrate Stock Assessment and Management. G. S. Jamieson and A. Campbell eds., pp. 109-124. National Research Council of Canada, Ottawa, Canada.
- Parada, C., D. A. Armstrong, B. Ernst, S. Hinckley, and J. M. Orensanz. 2010. Spatial dynamics of snow crab (*Chionoecetes opilio*) in the eastern Bering Sea–Putting together the pieces of the puzzle. Bulletin of Marine Science 86:413-437.
- Patterson, B. 2015. Massive Toxic Algae Blooms May Prove a Sign of Climate Change to Come. Scientific American, August 11, Accessed online at https://www.scientificamerican.com/article/ massive-toxic-algae-blooms-may-prove-a-sign-of-climate-change-to-come/.
- Paul, A. J. 1984. Mating frequency and viability of stored sperm in the Tanner crab *Chionoecetes bairdi* (Decapoda, Majidae). Journal of Crustacean Biology 4:375-381.
- Pirtle, J. L. and A. W. Stoner. 2010. Red king crab (Paralithodes camtschaticus) early post-settlement habitat choice: Structure, food, and ontogeny. Journal of Experimental Marine Biology and Ecology 393:130-137.
- Pisareva, M. N., R. S. Pickart, K. Iken, E. A. Ershova, J. M. Grebmeier, L. W. Cooper, B. A. Bluhm, C. Nobre, R. R. Hopcroft, H. Hu, J. Wang, C. J. Ashjian, K. N. Kosobokova, and T. E. Whitledge. 2015. The relationship between patterns of benthic fauna and zooplankton in the Chukchi Sea and physical forcing. Oceanography 28:68-83.
- Powell, G. C. 1967. Growth of King Crabs in the Vicinity of Kodiak Island, Alaska. Alaska Department of Fish and Game, Juneau, AK.
- Powell. G. C., K. E. James, and C. L. Hurd. 1974. Ability of male king crab Paralithodes camtschatica, to mate repeatedly, Kodiak Alaska, 1973. Fishery Bulletin 72:17.
- Punt, A. E., R. J. Foy, M. G. Dalton, W. C. Long, and K. M. Swiney. 2016. Effects of long-term exposure to ocean acidification conditions on future southern Tanner crab (Chionoecetes bairdi) fisheries management. ICES Journal of Marine Science 73:849-864
- Rand, K. M. and E. A. Logerwell. 2011. The first demersal trawl survey of benthic fish and invertebrates in the Beaufort Sea since the late 1970s. Polar Biology 34:475-488.
- Raring, N. W., E. A. Laman, P. G. von Szalay, C. N. Rooper, and M. H. Martin. 2016. Data Report: 2012 Aleutian Islands Bottom Trawl Survey. NOAA Technical Memorandum NMFS-AFSC-332. National Oceanic and Atmospheric Administration, Seattle, WA.

- Ravelo, A. M., B. Konar, and B. A. Bluhm. 2015. Spatial variability of epibenthic communities on the Alaska Beaufort Shelf. Polar Biology 38:1783-1804.
- Raymond-Yakoubian, J., Y. Khokhlov, and A. Yarzutkina. 2014. Indigenous Knowledge and Use of Bering Strait Region Ocean Currents. Kawerak, Inc., Nome, Ak
- Rooper, C. N., P. J. Etnoyer, K. L. Stierhoff, and J. V. Olson. 2016. Chapter 4: Effects of fishing gear on deep-sea corals and sponges in US waters, In State of Deep-Sea Coral and Sponge Ecosystems of the United States. T. F. Hourigan, P. J. Etnoyer, and S. D. Cairns eds., pp. 4-1-4-19. National Oceanic and Atmospheric Administration, Silver Spring, MD.
- Rooper, C. N., M. E. Wilkins, C. S. Rose, and C. Coon. 2011. Modeling the impacts of bottom trawling and the subsequent recovery rates of sponges and corals in the Aleutian Islands, Alaska. Continental Shelf Research 31.1827-1834
- Sainte-Marie, B. and C. Carriére, 1995. Fertilization of the second clutch of eggs of snow crab. Chionoecetes opilio, from females mated once or twice after their molt to maturity. Fishery Bulletin 93:759-764
- Sainte-Marie, B., T. Gosselin, J. M. Sévigny, and N. Urbani. 2008. The snow crab mating system: Opportunity for natural and unnatural selection in a changing environment. Bulletin of Marine Science 83:131-161
- Schandelmeier, L. and V. Alexander. 1981. An analysis of the influence of ice on spring phytoplankton population structure in the southeast Bering Sea. Limnology and Oceanography 26:935-943.
- Siddon, E. C., T. Kristiansen, F. J. Mueter, K. K. Holsman, R. A. Heintz, and E. V. Farley. 2014. Spatial match-mismatch between juvenile fish and prey provides a mechanism for recruitment variability across contrasting climate conditions in the eastern Bering Sea. PLoS ONE 8:e84526.
- Sigler M F F J Mueter B A Blubm M S Busby F D Cokelet S J Danielson A De Robertis J B. Eisner, E. V. Farley, K. Iken, K. J. Kuletz, R. R. Lauth, E. A. Logerwell, and A. I. Pinchuk. 2016. Late Summer Open Water Zoogeography of the Northern Bering and Chukchi Seas. OCS Study BOEM 2011-AK-11-08 a/b. Bureau of Ocean Energy Management, Alaska OCS Region, Anchorage AK
- Sigler, M. F., P. J. Stabeno, L. B. Eisner, J. M. Napp, and F. J. Mueter. 2014. Spring and fall phytoplankton blooms in a productive subarctic ecosystem, the eastern Bering Sea, during 1995-2011. Deep Sea Research Part II: Topical Studies in Oceanography 109:71-83.
- Sirenko, B. Land S. Y. Gagaev. 2007. Unusual abundance of macrobenthos and Pacific species invasions into the Chukchi Sea. Russian Journal of Marine Biology 33:355-364.
- Smith, K. R., R. A. McConnaughev, and C. E. Armistead, 2011, Benthic Invertebrates of the Eastern Bering Sea: A Synopsis of the Life History and Ecology of Snails of the Genus Neptunea. National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Alaska Fisheries Science Center, Seattle, WA.
- Springer, A. M. and C. P. McRoy. 1993. The paradox of pelagic food webs in the northern Bering Sea-III: Patterns of primary production. Continental Shelf Research 13:575-599.
- Springer, A. M., C. P. McRoy, and K. R. Turco. 1989. The paradox of pelagic food webs in the northern Bering Sea-II: Zooplankton communities. Continental Shelf Research 9:359-386.
- Squires, H. J. and E. G. Dawe. 2003. Stomach contents of snow crab (Chionoecetes opilio, Decapoda, Brachyura) from the northeast Newfoundland shelf. Journal of the Northwest Atlantic Fishery Science 32:27-38.
- Stabeno, P. J., N. B. Kachel, S. E. Moore, J. M. Napp, M. Sigler, A. Yamaguchi, and A. N. Zerbini. 2012. Comparison of warm and cold years on the southeastern Bering Sea shelf and some implications for the ecosystem. Deep Sea Research Part II: Topical Studies in Oceanography 65:31-45.
- Stevens, B. G., J. A. Haaga, and W. E. Donaldson, 1994, Aggregative mating of tanner crabs. Chionoecetes bairdi. Canadian Journal of Fisheries and Aquatic Sciences 51:1273-1280
- Stevens, B. G. and J. Kittaka, 1998. Postlarval settling behavior, substrate preference, and time to metamorphosis for red king crab Paralithodes camtschaticus. Marine Ecology Progress Series 167.197-206
- Stockwell, D. 2008. Phytoplankton (Primary Production), In Arctic Ocean Synthesis: Analysis of Climate Change Impacts in the Chukchi and Beaufort Seas with Strategies for Future Research. R. Hopcroft, B. Bluhm, R. Gradinger, T. Whitledge, T. Weingartner, B. Norcross, and A. Springer eds. Institute of Marine Sciences, University of Alaska, Fairbanks, AK,
- Stone, R. P. 2006, Coral habitat in the Aleutian Islands of Alaska: Depth distribution, fine-scale species associations, and fisheries interactions. Coral Reefs 25:229-238.
- , 2014. The Ecology of Deep-Sea Coral and Sponge Habitats of the Central Aleutian Islands of Alaska. NOAA Prefessional Paper NMFS 16. National Oceanic and Atmospheric Administration, Seattle, WA.
- Stone, R. P. and S. D. Cairns. 2017. Deep-sea coral taxa in the Alaska region: Depth and geographical distribution, In The State of Deep-Sea Coral and Sponge Ecosystems of the United States: 2017. NOAA Technical Memorandum CRCP-3. T. F. Hourigan, P. J. Etnoyer, and S. D. Cairns eds. National Oceanic and Atmospheric Administration, Silver Spring, MD,
- Stone, R. P., H. Lehnert, and H. Resiwig. 2011. A Guide to the Deep-Water Sponges of the Aleutian Island Archipelago, NOAA Professional Paper NMFS 12, National Oceanic and Atmospheric Administration. Seattle, WA.
- Stone, R. P., P. W. Malecha, and M. M. Masuda, 2017. A five-year, in situ growth study on shallow-water populations of the gorgonian octocoral Calcigorgia spiculifera in the Gulf of Alaska. PLoS ONE 12:e0169470.
- Stone, R. P., C. E. O'Clair, and T. C. Shirley. 1992. Seasonal migration and distribution of female red king crabs in a Southeast Alaskan estuary. Journal of Crustacean Biology 12:546-560.
- Stone, R. P. and C. N. Rooper. 2017. State of deep-sea coral and sponge ecosystems in the Alaska region, In The State of Deep-Sea Coral and Sponge Ecosystems of the United States: 2017. NOAA Technical Memorandum CRCP-3. T. F. Hourigan, P. J. Etnoyer, and S. D. Cairns eds., pp. 3-1-3-34. National Oceanic and Atmospheric Administration, Silver Spring, MD.
- Stoner, A. W. 2009. Habitat-mediated survival of newly settled red king crab in the presence of a predatory fish: Role of habitat complexity and heterogeneity. Journal of Experimental Marine Biology and Ecology 382:54-60.
- Stoner, A. W., M. L. Ottmar, and L. A. Copeman. 2010. Temperature effects on the molting, growth, and lipid composition of newly-settled red king crab. Journal of Experimental Marine Biology and Ecology 393:138-147.

Sundberg, K. A. and D. Clausen. 1977. Post-larval king crab (Paralithodes camtschatica) in Kachemak Bay, Lower Cook Inlet, Alaska, 1976, In Environmental Studies of Kachemak Bay and Lower Cook Inlet. Vol 5: I-36. L. L. Traskey, L. B. Flagg, and D. C. Burbank eds. Alaska Department of Fish and Game, Anchorage, AK,

Shellfish Research 31:925-933.

Grant, AK-SG-02-01, Fairbanks, AK,

Seattle, WA.

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REFERENCES

- Swiney, K. M., W. C. Long, G. L. Eckert, and G. H. Kruse. 2012. Red king crab, Paralithodes camtschaticus, size-fecundity relationship, and interannual and seasonal variability in fecundity. Journal of
- Tremblay, J.-É., L. G. Anderson, P. Matrai, P. Coupel, S. Bélanger, C. Michel, and M. Reigstad. 2015. Global and regional drivers of nutrient supply, primary production and CO₂ drawdown in the changing Arctic Ocean. Progress in Oceanography 139:171-196.
- Turnock, B. and L. Rugolo. 2011. Stock Assessment of Eastern Bering Sea Snow Crab (Chionoecetes opilio). National Marine Fisheries Service, Anchorage, AK
- Urban, D., D. Penguilly, L. Jadamec, and S. C. Byersdorfer. 2002. Testing carapace morphology characteristics for field identification of Chionoecetes hybrids, In Crabs in Cold Water Regions Biology, Management, and Economics. A. J. Paul, E. G. Dawe, R. Elner, G. S. Jamieson, G. H. Kruse, R. S. Otto, B. Sainte-Marie, T. C. Shirley, and D. Woodby eds., pp. 97-113. University of Alaska Sea
- von Szalay, P. G. and N. W. Raring, 2016. Data Report: 2015 Gulf of Alaska Bottom Trawl Survey. NOAA Technical Memorandum NMFS-AFSC-325. National Oceanic and Atmospheric Administration,
- Wang, J., G. F. Cota, and J. C. Comiso. 2005. Phytoplankton in the Beaufort and Chukchi Seas: Distribution, dynamics, and environmental forcing. Deep Sea Research Part II: Topical Studies in
- Webb, J. B. and J. Bednarski. 2010. Variability in reproductive potential among exploited stocks of Tanner crab (Chionoecetes bairdi) in southeastern Alaska., In Management of Expoited Crab Population Under Climate Change, G. H. Kruse, G. L. Eckert, R. J. Foy, R. N. Lipcius, B. Sainte-Marie, D. L. Stram, and D. Woodby eds., pp. 295-317. Alaska Sea Grant College Program AK-SG-10-01, University of Alaska Fairbanks, Fairbanks, AK.

- Webb, J. B., L. M. Slater, G. L. Eckert, and G. H. Kruse. 2016. The contribution of fecundity and embryo guality to reproductive potential of eastern Bering Sea snow crab (Chionoecetes opilio). Canadian Journal of Fisheries and Aquatic Sciences 73:1800-1814.
- Webb, J. B., L. M. Stichert, Q. Smith, and K. McNeel. 2014. A Pilot Study Investigating the Applicability of a Novel Direct Aging Technique to Commercially Important Crustaceans in Alaska. Regional Operational Plan CE.5.J.2014.02, Alaska Department of Fish and Game, Juneau, AK.
- Westphal, M. J., G. L. Eckert, and S. L. Tamone. 2014. Comparison of first year growth among field, hatchery- and laboratory-raised juvenile red king crab, Paralithodes camtschaticus (Tilesius, 1815), in Alaska. Journal of Crustacean Biology 34:319-325.
- Whitehouse, G. A. 2013. Preliminary Mass-Balance Food Web Model of the Eastern Chukchi Sea. NOAA Technical Memorandum NMFS-AFSC-262. National Oceanic and Atmospheric Administration Seattle, WA.
- Witherell, D. and C. Coon. 2002. Protecting Gorgonian corals off Alaska from fishing impacts. In Proceedings of the First International Symposium on Deep Sea Corals. Ecology Action Center, Halifax Canada
- Yamamoto, T., T. Yamada, H. Fujimoto, and K. Hamasaki. 2014. Effects of temperature on snow crab (Chionoecetes opilio) larval survival and development under laboratory conditions. Journal of Shellfish Research 33:19-24.
- Yang, M.-S., K. Dodd, R. Hibpshman, and A. Whitehorse. 2006. Food Habits of Groundfishes in the Gulf of Alaska in 1999 and 2001. NOAA Technical Memorandum NMFS-AFSC-164. National Oceanic and Atmospheric Administration, Seattle, WA.
- Yeung, C. and R. A. McConnaughey. 2006. Community structure of eastern Bering Sea epibenthic invertebrates from summer bottom-trawl surveys 1982 to 2002. Marine Ecology Progress Series 318.47-63
- Zheng, J. and G. H. Kruse. 2006. Recruitment variation of eastern Bering Sea crabs: Climate-forcing or top-down effects? Progress in Oceanography 68:184-204.
- Zheng, J., S. Siddeek, D. Pengilly, and D. Woodby. 2002. Overview of Recommended Harvest Strategy for Snow Crabs in the Eastern Bering Sea. Regional Information Report No. 5J02-03. Alaska Department of Fish and Game, Juneau, AK,