Primary Productivity

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Primary productivity is the rate at which carbon dioxide is converted into organic material by autotrophs, or primary producers. Autotrophs collectively produce food that supports the food chain, hence they are referred to as primary producers. This conversion from the sun 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 SW, primary production is mostly generated from single-celled 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” prokaryotes), coccolithophorids (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-α 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, Duggins et al. 1989, Muller-Karger et al. 2005).

Sea-Ice Habitat

Primary productivity is highly seasonal in the Arctic and subarctic region due to the seasonal nature of light availability and presence of appropriate nutrients (Luo 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 at winter (Barber et al. 2008, 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. 2016). 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 (Schindlermeier and Alexander 1981, Olson and Strom 2002).

Ice does not have to be completely absent in order for photosynthesis to occur; ice algae have 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 disappearance of snow-covered, multi-year ice (Frey et al. 2011, Arriag et al. 2012, Arrigo 2014, Arriag 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 (Homer 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. 2002). In the northern Bering and Chukchi Seas, chlorophyll-α and NPP are tightly coupled with benthic biomass (Grebmeier et al. 1988, Spring and Milly 1992, Dunton et al. 2000, Grebmeier et al. 2004, Grebmeier et al. 2006b). Chlorophyll-α and NPP in the Beaufort Sea are less closely linked, except around Barter Island where both, tively high biomass and chlorophyll-α 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 disappear 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 light 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 2002). Decline in sea ice extent and warming seawater exacerbate environmental change in this already vulnerable ecosystem (Grebmeier 2002). 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. 2016b). Understanding the relationship between ice cover and productivity is essential in understanding Arctic marine ecology under reduced ice thickness and extent (Stowckell 2008).

The Arctic Ocean has experienced substantial warming in all seasons (Bulyevsv et al. 2010) with huge increases to its annual mean open-water area and surface air temperature (Arigo and van Dijken 2011). In the Bering Sea, however, warming has been mainly limited to summer, with little 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 air are from the nearby Arctic. The influence of the ice on the Bering Sea, so continued warming in the Arctic will likely lead to diminished ice coverage in the Bering Sea (Brown and Arriaga 2012, 2013).

MAPPING METHODS (MAP 3.1)

Map 3.1 shows maximum measured integrated chlorophyll content (mg/m2) 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 (Homer 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 (Arkhan et al. 2003, Grebmeier and Cooper 2004) by Grebmeier in the Earth Observing Laboratory online database as part of the Pacific Marine Arctic Regional Synthesis (PacMARIS) project.

To produce the primary productivity map, we interpolated the chlorophyll sample data in Esri’s Geostatistical Analyst extension using empirical Bayesian kriging with four sctors. 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 points.

The sea ice data shown on this map approximates median monthly sea-ice extent. The monthly sea-ice lines are based on 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 Method section for details.

Data quality

Integrated water column chlorophyll data are likely the best proxy available for the project area. However, much of the data used in this project reflects, as they were gathered long ago at 1959 (Arkhan 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, 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. 2001, Hill and Kota 2005, Arrigo et al. 2012, Frey et al. 2012, Boeius et al. 2015). 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 Arkhan (2013) and Grebmeier and Cooper (2004)

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. Coccolithophores blooms of this size and duration are becoming more common and may be a result of changing climate conditions.
Primary Productivity

The primary productivity map shows maximum measured integrated chlorophyll content (mg/m²) for the top 100 feet (30 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 make up the majority of water-column and sea-ice productivity in the Arctic. Throughout the winter, primary productivity in the Arctic is limited by available sunlight and sea ice coverage. As spring arrives, warming temperatures and longer days reduce ice coverage and allow sunlight to penetrate the water column to 650 feet (200 m), supplying photosynthetic organisms with the energy they need to turn carbon dioxide into organic material. This organic material forms the basis of the marine food web.

This region has recently experienced a much longer open-water period, with sea-ice retreat happening earlier and melting faster, resulting in substantial changes in primary productivity. When ice retreat is later, phytoplankton is under-utilized by water column grazers, and nutrients fall to the bottom of the sea, fertilizing benthic organisms. When the ice retreat is early, there is not enough sunlight to create a large ice-edge bloom. In that case, the bloom happens later and is utilized by zooplankton and fish, leaving little for the benthos. In this way, sea ice timing determines primary productivity patterns, timing, and abundance, driving the dynamics of a pelagic- versus benthic-dominated system.
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 phyyla. Two zooplankton groups of particular importance are crustacea: krill, also known as “ohausiids,” and copepods (Hopcroft et al. 2008). Many species of copepods and krill store lamps 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. 2015).

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, Ghashi 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, Ghashi 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 size-fish by phototaxis 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 benefitted from diets with energy-rich zooplankton (Stabian 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, 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, Alaska mackerel (Pleurogrammus monopterygius), and several rockfish species (Armstrong et al. 2005, Yang et al. 2006, Coyle et al. 2008, Boldt and Riopel 2009). When the pteropods are exposed to acidified waters, their shells dissolve (Ori 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**

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 Morissey and O’Brien (2015). Sample points for average annual zooplankton total carbon mass were extracted from the database and mapped. A 40x60 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.

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 (Fettner 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 oceanic 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 ON PAGES 50-51**

**MAP DATA SOURCES**


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

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 (euphausiids), and other small crustaceans such as copepods and bottom-dwelling amphipods. The entire North Pacific Ocean is home to a dynamic zooplankton landscape with species composition diversity, seasonal distributions, and a range of densities in different regions. Overall, major zooplankton species in 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*).
Benthic biomass 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 (EFH) (see Ecological Atlas).

## 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 Arctic contains the most diverse and dense aggregations of sponges (Lehner and Stone 2014) and support the most abundant deep-water corals of any high-latitude ecosystem (Helfman et al. 2005, Stone 2004), with high numbers of species (Stone 2014). Of the 88 species or subspecies of corals reported from the Aleutian Islands (Stone and Carrns 2017), more than 50 may be endemic to the region (Stone and Rooper 2017).

### DISTRIBUTION

The benthic community is dominated by several species of sponges, echinoderms (mainly sea urchins and sea stars), gastropods (mainly Nephropus spp., or true whelks), and bivalve mollusks (mainly Macoma caliginosa) (Felder et al. 2005, Sterkee and Gagea 2007, Buhl et al. 2009, Logan et al. 2010, Smith et al. 2011, Goddard et al. 2014, Godzimek 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 (Hoplometapobates trigenericus) (Goddard et al. 2013). Common Beaufort Sea species include brittle star (Ophiura sp.), mussels (Mytilus sp.), and the peanut worm (Glyptonotus margaretae) (Logerwell et al. 2010). In the EBS, purple-orange sea star, basket star (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.

### ECOLOGICAL ROLE

Benthic organisms provide and create habitat essential to fish and crabs. They rely on high production from the water column and are less affected by seasonal and annual variability than pelagic species (Buhl et al. 2008). Areas of very high primary productivity, such as Anadyr waters north of the Bering Strait, produce far more biomass than is consumed by zooplankton (Springer et al. 1989). This excess biomass feeds to the seafloor, providing food for the benthos (Sibert et al. 1988).

Habitat-forming invertebrates provide EFH for many commercially important species (Stone 2014). These include but are not limited to Anaspides maculosus (mussel), Lampsis albolineata (sea snail), Mesolimopsis cumingi (clam), and Stelodoryx oxeata (sea whip). Purple-orange sea star tends to be more common than consumed by zooplankton (Springer et al. 1989). This excess biomass feeds to the seafloor, providing food for the benthos (Sibert et al. 1988).

### 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-Fukasawa et al. 2014). The economic role of sea crab, Tanner crab, and red king crab is summarized later in this chapter.

### CONSERVATION ISSUES

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 chapter). One study showed that benthic communities were more abundant in colder years compared to average years, suggesting that as temperatures increase and are anomalously high, benthic biomass may decrease (Logerwell et al. 2010, Goddard et al. 2014, National Oceanic and Atmospheric Administration 2016a). This may threaten marine mammals such as whales, sea otters, sea lions, and walruses (Klima and Oliver 1989, Brown et al. 2017). The animals rely on these substrate invertebrates for them for 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 crustaceans) are preyed upon by grey whales (Eschrichtius robustus) and bearded seals (Erignathus barbatus) (Kim and Oliver 1989, Brower et al. 2017).

### OCEAN ACIDIFICATION

Ocean Acidiﬁcation could negatively affect many of the benthic organisms that require calcium carbonate to make their shells or tests. 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 crustaceans) are preyed upon by grey whales (Eschrichtius robustus) and bearded seals (Erignathus barbatus) (Kim and Oliver 1989, Brower et al. 2017).
Commercial fishing gears, particularly bottom trawls, can have long-term impacts on benthic habitat (Helsztynski et al. 2002, Withnell and Coon 2002, Rooper et al. 2016, Stone et al. 2017). It is important to consider the time for slower-growing, long-lived corals and sponges to rebuild or replace damaged structures when assessing habitat degradation and subsequent recovery (McConnaugha and Smith 2000, Andrews et al. 2002, Rooper et al. 2017). 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 (Faby et al. 2009), so as ocean temperatures rise, the effect from fishing will be exacerbated and increase recovery time.

**Mapping methods (3AJP 3.3)**

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 approximates median monthly sea-ice extent. The monthly sea-ice lines are based on an Audubon Alaska (2016a) 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.

**Travel Survey Data (National Oceanic and Atmospheric Administration 2016a)**

A benthic 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 Lauch 2016, Hoff 2016), Aleutian Islands (Raring et al. 2016), Gulf of Alaska (von Stовал and Raring 2016), and Beaufort Sea (Coast Guard 2016; Stone 2014). The 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 travel surveys. Catches included 1,356 benthic species or species groups recorded from the travel survey samples. Those included crabs, echinoderms (sea stars, sea cucumbers), tunicates, sponges, corals, invertebrates, amphipods, polychaetes, amphipods, and squids. Those are all relevant to benthic invertebrates. Of the observations made (species or species groups caught, identified, and weighed), there were:

- 216,158 in the EBS
- 79,674 in the Gulf of Alaska
- 60,831 in the Aleutian Islands
- 9,749 in the northern Bering Sea
- 1,269 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 *Ophiogomphus pacificus* (n = 10,566), Tanner crabs *Chionoecetes bairdii* (n = 10,566), snow crabs *Chionoecetes opilio* (n = 9,840), purple-orange sea stars *Asterias amurensis* (n = 8,185), and Oregon tritons *Flabellina oregonensis* (n = 7,865).

**PacMARS Benthic Infaunal Parameters (Grebmeier and Cooper 2014a)**

This dataset contained 2,015 unique sample points with summary measurements of average benthic macrofaunal 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-Wiener diversity and evenness indices, and number of grapsids collected per station were recorded for each sample. For the purposes of combining this dataset with travel survey sample data, this dataset was mapped based on wet weight biomass (gww/m²).

To obtain a continuous coverage estimate of the relative benthic biomass for our entire study area, we combined the macrofaunal benthic survey data from Grebmeier and Cooper (2014a) and a compilation of benthic invertebrate samples from the National Marine Fisheries Service travel survey data (discussed above). Both datasets contained 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.

**Analysis**

To obtain a continuous coverage estimate of the relative benthic biomass for our entire study area, we combined the macrofaunal benthic survey data from Grebmeier and Cooper (2014a) and a compilation of benthic invertebrate samples from the National Marine Fisheries Service travel survey data (discussed above). Both datasets contained 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 hectare
- For the travel survey data, average kilograms per hectare (kg/ha)
- Calculate the standard deviation per grid cell for each dataset separately
- To calculate the standard deviation per grid cell for each dataset, the following formula was used:
  \[ \sigma_{ij} = \frac{X_{ij} - \mu}{n} \]
  where \((X_{ij})\) is the standard deviation of grid cell \(i,j\) for the \(n^{th}\) dataset, \((\mu)\) is the average value for grid cell \(i,j\) for the \(n^{th}\) dataset, and \((n)\) are the overall mean and overall standard deviation of all the calculated grid cell average values for the \(n^{th}\) dataset.

Converting grid cell values to standard deviations 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 deviation close to zero means the value is well above average. Similarly, a negative standard deviation indicates the value is below average (Oceana and Kawerak 2014).

**Evaluating grid cells**

To evaluate grid cells to see those areas which are above average, or those areas with the highest benthic productivity, there were:

- Power = 2
- Search radius = variable
- Maximum search radius = 12 points

Converting grid cell values to standard deviations 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 deviation close to zero means the value is well above average. Similarly, a negative standard deviation indicates the value is below average. Converting grid cell values to standard deviations 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 deviation close to zero means the value is well above average. Similarly, a negative standard deviation indicates the value is below average.
Benthic invertebrates live on, in, or just above the seafloor. Some form structures that become habitats (epifauna), others live in the substrate (infrafauna), 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, crabs, and bivalves. 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.

Map Authors: Brianne Mecum, Marilyn Zaleski, and Jon Warrenchuk

Cartographer: Daniel P. Huffman

Snow crab, Chionoecetes opilio, is one of the most commercially valuable crab species. It prefers seafloor areas of sand and mud so it can quickly burrow.
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, 1-1°C) but females snow crabs, which occupy colder waters in the EBS compared to Tanner crabs, will brood for 2 years in water at 34 °F (1°C) (Morinou and Lanteigne 1998).

After hatching, the free-swimming larvae have two zonal 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).

Tanner crabs can be infected by a parasitic dinoflagellate, Hematochirium 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 crabs. Postlarval stages of snow crabs are more sensitive to increased atmospheric CO2 (Long et al. 2013). For many animals, the larval stage of development is their most vulnerable life history stage and loss of protection could mean lower survival, which would subsequently reduce recruitment to adulthood and the fishery (Punt et al. 2016).

**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). The distribution of snow crab is based, in part, on the temperature at which they live (Orensanz et al. 2007, Ernst et al. 2012). They therefore generally live closer to the coastal areas. For example, off the coast of Alaska and the Russian Federation, snow crabs are generally found at shallower depths than in the Bering Sea. The level of commercial fishing for snow crabs has increased over the past decade, with catches peaking 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 (Zeng 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).

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 for the EBS, smaller commercial harvest, and limited range, only Tanner crab EFH is mapped (Figure 3.4.1).

**CONSERVATION ISSUES**

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 (Jewett et al. 1996).

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

One 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 loss of protection could mean lower survival, which would subsequently reduce recruitment to adulthood and the fishery (Punt et al. 2016).
Snow Crab, also known as opilio crab, is the most commercially important crab species in North Pacific and North Atlantic waters. In Alaska, snow crabs are predominately found in the eastern Bering Sea, although their range extends north into the Chukchi and Beaufort Seas. Other populations of snow crab occur off of Russia, Japan, and Greenland, and in the Canadian North Atlantic. Throughout their range, snow crabs prefer seafloor areas of sand and mud. 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 cold water near the seafloor less than 35 °F [2 °C]), also shrinks and is limited to the northern Bering Sea. Juvenile snow crabs thrive in the cold pool and model predictions identify several locations for possible larval settlement in that area. However, the northward contraction of the cold pool has subsequently led to a northward shift in snow crab distribution. Snow crab habitat in the Arctic is defined as inner to middle shelf waters (0–330 feet [0–100 m] depth) with muddy substrates in high-latitude, continental-shelf regions.
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 are experiencing highs and lows (North Pacific Fishery Management Council 2018), 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), red 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 their behavior they are from in 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 snow crabs (Lithodes aequispinus) but differ in their range, physical appearance, and physiologic attributes. Aside from their numeric dominance, red king crabs off of Kodiak were still in the soft-shell phase. Red king crabs off of Kodiak were observed molting at night (Dew 1990) and female molting happens rather may offer safety in numbers while resting between daily foraging activities (36,500 ha) (Dew 2010). Unlike other crabs, these pods occur year-round and as the juveniles get larger, their growth increments increase 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 (1 mm) in 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 infrequently, with 1,000–40,000 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 molts. 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 egglaying

**DISTRIBUTION**

Red king crabs are generally distributed throughout the North Pacific from deep shelf waters (>200 feet or 250 m) to shallow, nearshore, intertidal environments (Stone et al. 1982, 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 Leon 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 (Bittray 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 (Hoppe and Kirenin 1972). Depending on their size, mature females produce eggs but off the coasts of Norway and Russia (Bittray et al. 2010). Once red king crabs become reproductively active, they begin seasonal molts. 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 egglaying. As juveniles, red king crabs forage on algae and the habitat-forming invertebrates they are important nursery habitat for the first year and a half of a red king crab’s life, after which the crab begins molting behavior on the seafloor (Dew 1990).

Paddling 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 et al. 2010). Red king crab populations 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 year-round and as the juveniles get larger, their growth increments increase.

Red king crabs molt to grow, molting numerous times (8-12) in their first year (Stoner 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 (1 mm) in their first year and as the juveniles get larger, their growth increments increase (Westphal et al. 2014).

Red king crab eggs hatch, the swimming larva go through four zoeal stages, then settle to the bottom as postlarval crab, and finally molt into the first juvenile crab stage to begin their lives on the seafloor (Seavers and Kittaka 1998). The juveniles hide among algae and habitat-forming invertebrates such as sponges, bryozoans, and hydrocorals (Gunther and Caussens 1977; Stevens and Kittaka 1999; Ptirte and Stoner 2010). These benthic invertebrates offer an important nursery habitat for the first year and a half of a red king crab’s life, after which the crab begins molting behavior on the seafloor (Dew 1990).

**ECOLOGICAL ROLE**

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

Red king crabs are vulnerable to predation by other crabs and fishes sharing their nursery habitat, including Pacific halibut (Hippoglossus stenolepis), northern rock sole (Laportesolepectra polynotus), and kelp greenlings (Hexagrammos decagrammus) (Dean et al. 2000, Stommer 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 1999) and so may pose little threat to juvenile red king crabs (Stoner 2009). Daly’s analysis and trophic modeling of the invasive red king crab in the Barents Sea showed that the threat to large sea stars may be increasing, introducing resource competition into the ecosystem, but that they are unlikely to compete for prey with most fish species (Fuhmann et al. 2017).

**ECONOMIC IMPACT**

Red king crabs are currently harvested commercially in Bristol Bay and Norton Sound (North Pacific Fishery Management Council 2014). 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 (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 much larger, with over 20 million crabs caught in the 1980s (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 activity, and the crab is used both locally and in sharing or trading for other resources with Kutchake residents, and similar communities away from king crab habitats (Georgette and Leon 1993, AmNach 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 red king crab stock is in decline with survey results of both males and females below the 10-year average, and an estimated 2% 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 Crabs (145° W to 160° W) in the Bristol Bay management area (North Pacific) and during the fall (October 15–November 30) in Area 306, spatial management areas in Bristol Bay (see Map 3.5). Both areas were established to reduce bycatch 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 ecosystems.
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 216 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 Quality
Travel 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 travel survey data estimates the distribution of red king crab during the summer months and may not represent the year-round distribution.

FIGURE 3.5-1  Red king crab and blue king crab Essential Fish 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 (2016a, b).

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Red King Crab (Paralithodes camtschatica)

Red king crabs are the largest-sized crab species in Alaska. Red king crabs are generally distributed throughout the North Pacific from deep shelf waters (<820 ft or 250 m) to shallows, 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 216. Another protected area is the Pribilof Islands Habitat Conservation Zone, which was established to protect the overfished blue king crab (P. platypus).

Red King Crab

OCEANA

Audubon ALASKA

Colored areas represent management areas for the red king crab. These areas are designed to protect the red king crab and its habitat. On the map, the management areas are represented by a red background. These areas were designated by the North Pacific Fishery Management Council (2015a). Map Authors: Brianne Mecum, Marilyn Zaleski, and Jon Wamenchuk. Cartographer: Daniel P. Huffman.
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BIOLOGICAL SETTING

ECONOMIC ATLAS OF THE BERING, CHUKCHI, AND BEAUFORT SEAS

References


