

NGA Phase II Proposal:

LTER: NGA Phase-II: Resilience and Connectivity Across Transitions in the Northern Gulf of Alaska Ecosystem

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Submission Date: 3-2-23

Award Period:
10-1-23 to 9-30-28

OVERVIEW

The Northern Gulf of Alaska (NGA) is a highly productive subarctic marine ecosystem sustaining one of the world's largest fisheries, iconic high latitude species, ecotourism, cultural continuity, and food security for coastal communities. The NGA LTER overarching conceptual framework is that intense environmental variability – both temporally and spatially – has yielded a highly resilient ecosystem through species adaptation and community organization. Building off 25 years of multidisciplinary observations along the Seward Line in LTER's five core areas, NGA Phase-II seeks improved mechanistic understanding of this biome's key communities, ecological processes, and responses to climate change. The NGA biome comprises a mosaic of habitats postulated to underlie the high productivity and resilience of the ecosystem. Phase-II studies and associated broader impacts will focus on growing and interpreting long-term data sets; studying functional redundancy in the context of disturbance and long-term change, as well as relationships between redundancy and resilience; and investigating oceanographic fronts, associated ecotones, and their combined role in supporting key ecosystem properties that generate resilience. We propose to tackle each element with a combination of observational methodologies, process studies, and modeling.

INTELLECTUAL MERIT

Building on long-term data sets for the region and findings from Phase-I, NGA Phase-II research has three primary goals. First, continue collection and analysis of long-term ecosystem data (abiotic and biotic) to better understand species abundance and connectivity, and their relationships to event-scale and long-term change. Second, explore functional redundancy as an underpinning of resilience. Despite a relatively modest species richness, the NGA hosts numerous instances of trophically comparable taxa throughout the foodweb; we posit that these taxa, with differing nutritional strategies, life histories, and phenological expression, comprise functional redundancy. This redundancy stabilizes variability at higher trophic levels, thereby conferring resilience (i.e., maintenance or recovery of key emergent ecosystem properties in response to disturbance). The degree to which redundancy stabilizes communities has not been well explored in pelagic marine ecosystems. Third, investigate the role of fronts and associated ecotones in the NGA. New technologies acquired during Phase-I can overcome historical limitations to the observation of fronts and their constituent communities at biologically relevant spatial and temporal scales. We hypothesize that fronts exert a disproportionate influence on key ecosystem properties (e.g., production, export, biological diversity) and are thus related to whole-ecosystem resilience. Further, fronts are likely to be influenced by event-scale and long-term environmental change. Our observations and experimentation under each of these three themes will be coupled to modeling activities that will parameterize the relevant physical and biological relationships, and will then use these biome-specific formulations to explore current and future climate scenarios predicted for the NGA. We will further explore ecological theory through collaboration with other LTER sites.

BROADER IMPACTS

In the mid-1970s the NGA underwent an ecological regime shift into a new stable state that has persisted for over four decades. Such shifts have major relevance to national fisheries as well as local communities dependent on NGA ecosystem services. Understanding the resilience of the NGA to both short- and long-term change is of great relevance to all stakeholders in the region; accordingly, NGA science will continue to inform regional fisheries management through several of data products. The NGA is increasingly networked with schools locally and statewide, including programs for Alaska Native students. NGA is also building connections to local communities and Tribal governments, while striving to broaden participation at all levels within the site. The NGA Schoolyard program, proposed collaborations with other programs targeting under-represented groups, and our leveraged Teacher-at-Sea program provide an array of outreach opportunities with a strong diversity, equity and inclusion focus. University-level impact occurs through our interdisciplinary REU program, graduate student and early career scientist training. The importance of the NGA is reflected by the numerous agencies and organizations that contribute to, and in turn leverage, the NGA infrastructure.

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I. OVERVIEW

I.A. INTRODUCTION. The Northern Gulf of Alaska (NGA) is a highly productive subarctic marine biome that supports a rich, diverse ecosystem and sustains one of the world's largest commercial fisheries (Mundy et al. 2010), as well as iconic species of seabirds and marine mammals. Ecotourism dependent on all of these elements is a prominent component of the Alaskan economy. The NGA also provides cultural continuity and subsistence-based food security for Indigenous and rural communities along its boundaries (Richardson & Erikson 2005). Although LTER-funded field work initiated only in 2018, NGA builds upon 25 years of multidisciplinary observations along the Seward Line and more than a half century of hydrographic observations at coastal station GAK1 (Fig. 1). These time series illuminate pronounced seasonal and inter-annual variability, a defining characteristic of this biome. Nutritional and life history strategies of dominant NGA species have evolved in response to this variability; we hypothesize these adaptations confer resilience to this ecosystem's functioning. Nonetheless, the 1976 phase change of the Pacific Decadal Oscillation (PDO) triggered an ecological regime shift by driving components of the system past a tipping point and into a new stable state that has mostly persisted more than four decades. The regime shift resulted in a transition from a shrimp-dominated benthic trawl fishery to one dominated by gadids and flatfish (Anderson & Piatt 1999) and triggered basin-wide shifts in the productivity of salmon species across the North Pacific (Mantua et al. 1997). The NGA LTER Program seeks to understand the capacity of the NGA ecosystem to buffer climate variability and long-term change, and to better understand the elements that confer resilience or sensitivity to that variability and change.

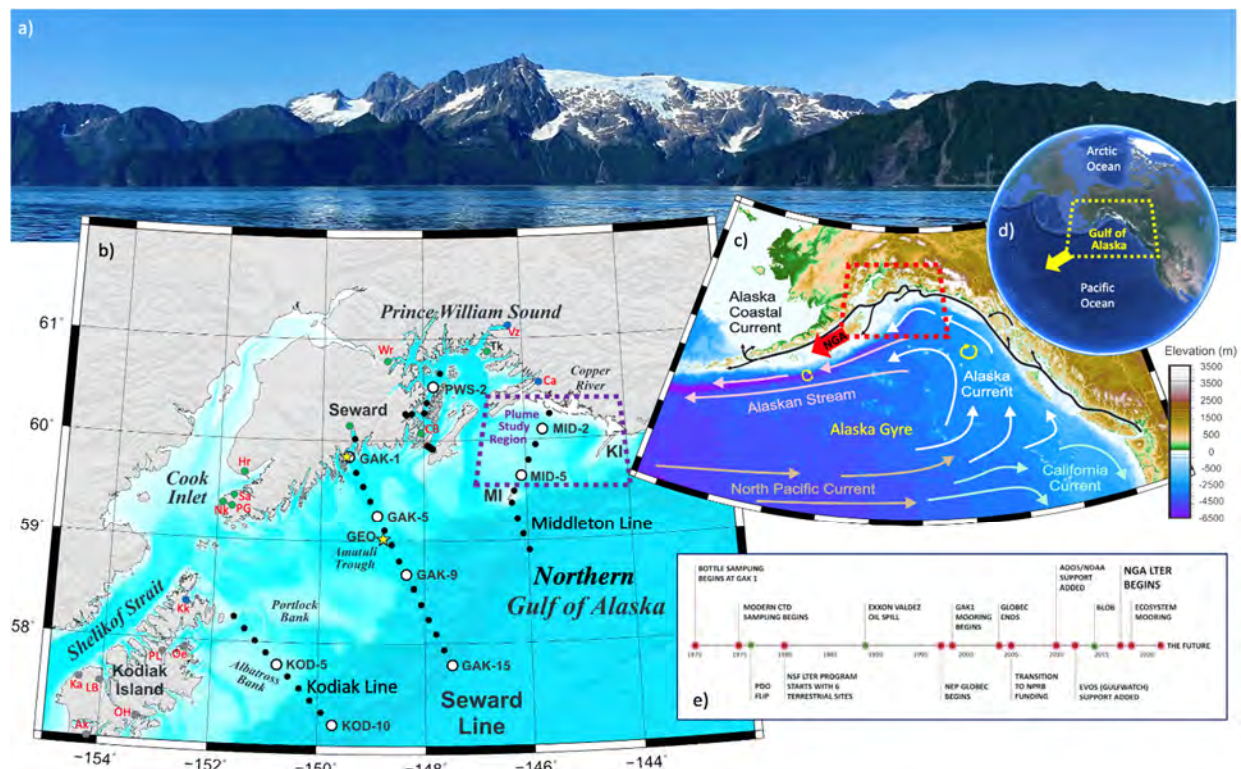


Fig. 1. Northern Gulf of Alaska coastal viewscape; study area; main circulation pathways/bathymetry; timeline of important events. Observations from station GAK1 (1970) and the Seward Line (1997) are the longest in the time series; the Middleton (MID), Kodiak (KOD), and Prince William Sound (PWS) stations are also regularly sampled for our standard (black circles) or more intensive (white circles) measurements. Stars: GAK1 and GEO mooring locations; Purple dotted line: Phase-I Copper River plume study. Coastal communities we collaborate with: Phase-I and -II (green circles); Phase-II (blue circles); future (gray circles). Community abbreviations (in red) include: Ak-Akhiok; Ca-Cordova; Hr-Homer; CB-Chenega Bay; Ka-Karluk; Kk-Kodiak; LB-Larsen Bay; Nk-Nanwalek; Oe-Ouzinkie; OH-Old Harbor; PG-Port Graham; PL-Port Lions; Sa-Seldovia; Tk-Tatitlek. Vz-Valdez; Wr-Whittier.

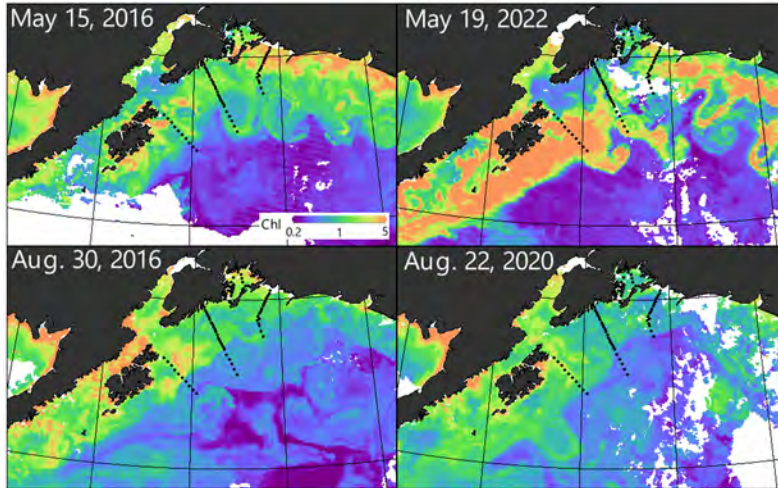


Fig. 2. Sea surface chlorophyll-a (mg m^{-3}) in contrasting springs and summers in the NGA study region. Note contrast between heatwave spring (2016) and more typical phytoplankton bloom (2020). Mesoscale eddies and sharp cross-shelf gradients (frontal zones) are also evident.

The NGA comprises a dazzlingly complex mosaic of features, processes and ecosystem dynamics (Fig. 2). The deep (200-300 m) continental shelf is bounded by coastal mountain ranges inshore and a trench offshore, cross-cut by deep canyons that are interspersed with shallower banks, and bordered by sounds, fjords, and island archipelagos. The physical regime is highly energetic with large (2-8 m) tidal ranges, frequent strong winds that are often intensified by topographic steering, and large oceanic transports by along-shelf currents, including the wind- and freshwater-driven Alaska Coastal Current (ACC) (Weingartner et al. 2005; Stabeno et al 2016) and the

subpolar Alaska Gyre (Fig. 1) (Hristova et al. 2019). While nearshore waters can become nitrate-deplete and Fe-replete in summer, the oceanic Gulf is a high nitrate-low chlorophyll (HNLC) ecosystem that is chronically iron-limited (Wu et al. 2009). This cross-shelf gradient in nutrients along with large freshwater inputs at the coast leads to strong along-shelf and cross-shelf zonation in planktonic communities (Coyle & Pinchuk 2005, Strom et al. 2006). Mesoscale eddy propagation along the shelf break (Okkonen et al. 2003) and wind-driven transport lead to episodic and biologically important cross-shelf exchanges (Cooney 1986, Mackas & Coyle 2005).

Oceanographically and biologically the NGA is highly seasonal, with winter storms driving persistent coastal downwelling that relaxes during summer months. Coastal freshwater input increases through the summer and fall as a result of rain plus snow and glacier melt (Royer 1982, Beamer et al. 2016). Seasonal sunlight and vertical mixing gradients are strong but spatially variable, resulting in an interannually variable spring bloom of diatoms that can support a rich community of zooplankton including protists, copepods, and euphausiids. The summer water column tends to be strongly and shallowly stratified with lower primary production levels, while fall mixing can yield a second annual bloom whose strength and composition contrasts strongly with that of the spring. Throughout the summer, tidally driven mixing near banks and vertical transport associated with fronts likely sustains high levels of primary productivity in some locations (Fig. 2; Coyle et al. 2012, 2019). Owing to this spatial and temporal complexity, primary production in the NGA can be variously and synergistically limited by light, nitrogen, iron, and grazing. At higher trophic levels, nutritional and life history strategies of ecologically and economically important taxa are clearly adapted to this quasi-predictable, seasonal boom-and-bust production cycle.

I.B. ECOLOGICAL FRAMEWORK AND HYPOTHESES. Our overarching conceptual framework posits that the NGA is a highly resilient ecosystem because of biological adaptations to the intense levels of environmental variability. We define resilience as the recovery of key emergent ecological properties (e.g., a diatom-dominated spring bloom; hot spots of high summer production; high biomass of large, lipid-rich copepods; high rates of particle export to depth; efficient transfer of production to upper trophic levels) following disturbance. As a complex adaptive system (Gell-Mann 1994), these emergent properties arise from the interplay of physical and chemical drivers with the genetic repertoire of the ecosystem's lower trophic level communities that in turn are key to maintenance of high productivity at upper trophic levels, including commercially harvested groundfish (e.g., sablefish, pollock, rockfish),

seabirds, and marine mammals. Our approach to evaluating resilience is through a combination of long-term observations, targeted process studies, and modeling, including:

- Examining the recovery (or lack thereof) of emergent properties following disturbance;
- Distinguishing food web pathways that exhibit varying sensitivity to disturbance;
- Tying observations of lower trophic level responses to their consequences for higher trophic levels under different (in time and space) conditions;
- Examining the occurrence and consequences of biological community strategies thought to promote resilience, such as nutritional plasticity and species redundancy;
- Assessing the importance of various iron and macronutrient sources and transfer rates;
- Relating environmental conditions and processes to the ecological state of the NGA.

This resilience framework informed our LTER Phase-I hypotheses, which centered on the interplay between the hydrologic cycle and ecosystem emergent properties. Our Phase-II proposal builds upon the foundational framework from Phase-I: evaluating ecosystem resilience through a combination of long-term observations, modeling, and targeted field ‘process’ studies. Ecologists are rallying behind the need to understand resilience in the context of climate change and climate variability (e.g., Gladstone-Gallagher et al. 2019, MeerBeek et al. 2020, Capdevila et al. 2021, Cowles et al. 2021) and the need to establish comparative and quantitative metrics across ecosystem and disturbance types (Ingrisch & Bahn 2018). Functional redundancy (e.g., Biggs et al. 2020, De Battisti 2021), spatial connectivity (e.g., Van Looy et al. 2018), and niche partitioning (e.g., Fox & Bellwood 2013) are proposed mechanisms that confer resilience, with work during (and prior to) Phase-I revealing complex associations between environmental drivers and ecological communities. In Phase-II we propose to further inspect these relationships within and across steep, natural gradients: oceanographic fronts.

Fronts are commonly associated with enhanced productivity and biomass across trophic levels (Acha et al. 2015, Prants 2022) through both stimulation of production and aggregation of biomass. This understanding has grown out of foundational marine literature focused on spatial heterogeneity (“patchiness”; e.g., Steel 1974, Steel 1976) that suggested populations cannot survive on “average” concentrations; thus, mechanisms leading to concentrated patches - and the detection of patches by predators - are crucial to ecosystem function. Ecologically, the study of fronts remains an active area of research for phytoplankton (e.g., Li et al. 2012, Hernández-Carrasco et al. 2018, Kahru et al. 2018), zooplankton (e.g., Alabaina & Irigoien 2004, Greer et al. 2015), fish (e.g., Prants et al. 2022), seabirds plus mammals (e.g., Bost et al. 2009, Scales et al. 2014, Cox et al. 2018), and entire ecosystems (e.g., Karati et al. 2018). The physical, chemical and biological interactions at such features have also been the subject of biophysical modeling studies (e.g., Woodson & Litvin 2015, Levy et al. 2015, Mahadevan et al. 2016). In addition to the standard definition of fronts that describes lateral (i.e., horizontal) gradients, a similarly important boundary occurs vertically at oceanic density gradients (pycnoclines) that create water column stratification (Acha et al. 2015), with the intensity and depth of those pycnoclines evolving interannually, seasonally and at time scales as short as minutes. In marine systems, front-associated ecotones (i.e., transitional communities) may or may not harbor increased diversity (e.g., Mousing et al. 2016, Morales et al. 2018, Ramond et al. 2021), and there are likely to be contrasting responses at the species level (Mangolte et al. 2022). If upper ocean fronts are of fundamental importance to productivity and resilience in pelagic marine ecosystems, then it is concerning that ocean warming may lead to a reduction in their frequency (Kahru et al. 2018). Despite this global-scale interest, there have been no studies focused on the ecological role of fronts in the NGA.

Since GLOBEC, we have been aware of broad discontinuities in community composition across the Seward Line (Coyle & Pinchuk 2005), and LTER Phase-I has confirmed that contrasting habitats exist in cross-shelf transects that span two or more water mass endmembers. Yet the precise location and function of these transition zones remain poorly constrained. We propose that NGA frontal features lead to productive ecotones that significantly increase diversity, the magnitude and duration of productivity, and carbon export. We have recently acquired new sampling tools that allow detailed *in situ* mapping of these

features to identify their footprints across multiple trophic levels: gliders and the new Deep-focus Plankton Imager (DPI – see Facilities & Equipment supplement). Such systems have been shown to highly resolve frontal features and thin layers (Greer et al. 2015, Ohman et al. 2019, Greer et al. 2020), including those in the NGA (Fig. 3).

Our Phase-II effort is also maturing through entrainment of scientific collaborators who bring new expertise, scientific questions, and investigative tools to the program. As part of our PI succession plan, new Phase-II PI Gwenn Hennon (UAF) will be taking on the phytoplankton (chlorophyll-a, primary productivity) measurements from Phase-I PI Strom, while also adding a molecular component that will bolster the program’s ability to test new process-based hypotheses targeting microbial function and interactions. Phase-II collaborators Lenz (UHawaii) and Questel (UAF) formalize use of molecular approaches within zooplankton studies. New Phase-II collaborator Kate Stafford (Oregon State University; OSU) brings marine mammal and underwater acoustics expertise to the program.

For Phase-II, we will continue to explore aspects of hypotheses proposed during Phase-I and propose the following new hypotheses for Phase-II directed studies:

1. *Functional redundancy occurs at multiple trophic levels in the NGA, conferring resilience to disturbance and long-term change.*
2. *Ecotones created by frontal systems support increased productivity, trophic transfer and carbon export, contain unique communities, and enhance NGA ecosystem resilience.*
3. *Frontal systems exert a disproportionate role in the NGA that varies seasonally, interannually, and over longer periods of climate change. Increases in frontal complexity, persistence, and frequency favor highly connected planktonic species that stabilize populations at higher trophic levels.*

Our NGA conceptual model links these key oceanographic and ecological features of the NGA with their response to temporal variability, including long-term change (Fig. 4). The box model component allows for depiction of hypotheses and relationships specific to various research foci (see below for versions addressing functional redundancy and frontal boundaries).

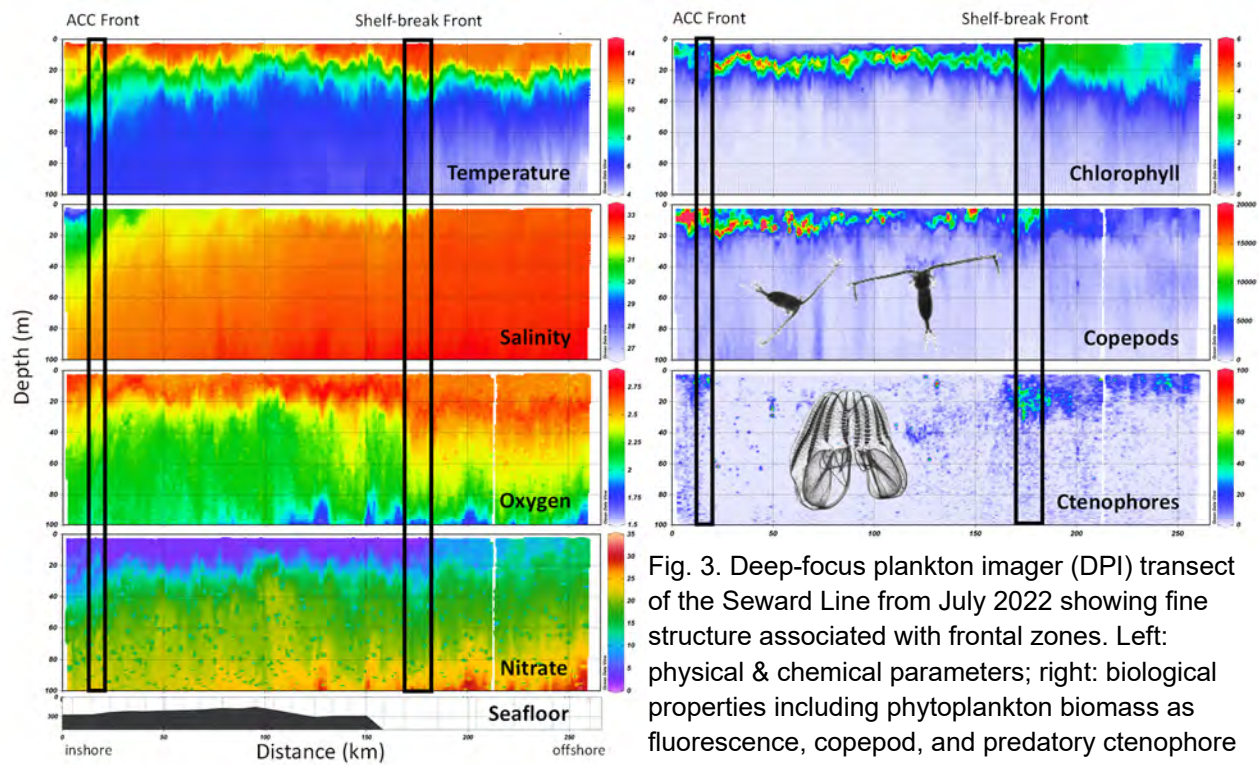


Fig. 3. Deep-focus plankton imager (DPI) transect of the Seward Line from July 2022 showing fine structure associated with frontal zones. Left: physical & chemical parameters; right: biological properties including phytoplankton biomass as fluorescence, copepod, and predatory ctenophore abundance. Images are shadowgraphs from DPI.

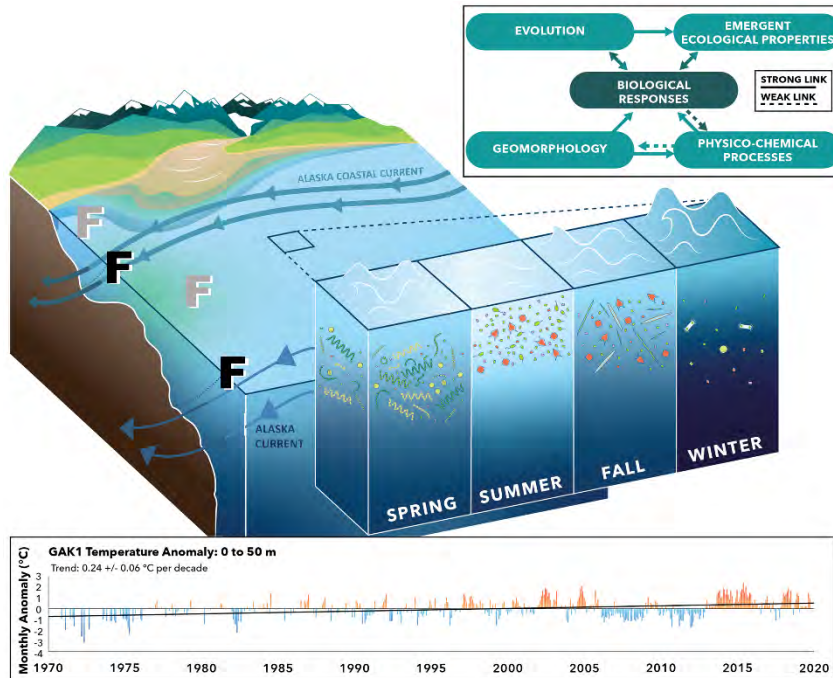


Fig. 4. NGA conceptual model showing 3-D representation of subarctic biome, including seasonal cycle of sea state, water column irradiance, and corresponding phytoplankton community structure; 5-decade time series of upper water temperature anomalies at station GAK1; and box model of interacting components. Note long-term warming and recent heatwave events (2014-16 and 2019) in temperature time series. F = frontal zone; fronts labeled in black (associated with ACC and shelfbreak) are one focus of proposed Phase-II research. The front associated with the Copper River plume (in gray, near shore) was studied during Phase-I.

I.C. SITE HISTORY. Beginning with physical oceanography studies in the 1970s, sampling in the NGA has focused on a 250 km transect that originates near Seward, Alaska (i.e., the Seward Line) at hydrographic station Alaska-1 (GAK1) and extends across the continental shelf into oceanic waters at station GAK15, plus stations in western Prince William Sound (PWS). In 1997, the Global Ocean Ecosystem Dynamics (GLOBEC) program (jointly funded by NOAA and NSF) ushered in a modern era of multidisciplinary Seward Line sampling, with regular measurements of ocean physics, macronutrients, phytoplankton biomass (e.g., chlorophyll), several size classes of zooplankton, and observations of seabirds and marine mammals. From 1997-2004 cruises occurred 6-7 times per year to describe the seasonality of this ecosystem (Weingartner et al. 2002, Coyle & Pinchuk 2003, 2005, Childers et al. 2005, Strom et al. 2006, 2007), and determine rates of production, growth (Strom et al. 2006, 2010, Liu & Hopcroft 2006a,b, 2007, 2008, Pinchuk et al. 2006, 2007, Napp et al. 2005) and feeding (Strom et al. 2007, Liu et al. 2005, 2008) by key elements of the pelagic community. When GLOBEC ended, a consortium of funders worked together to maintain Core Measurements of physics, macronutrients, chlorophyll-a, and zooplankton each May and September, with contributions that grew over time from the Alaska Ocean Observing System (AOOS), the North Pacific Research Board (NPRB), and the Exxon Valdez Oil Spill Trustee Council (EVOSTC). Microzooplankton, primary production and seabird observations were added back as funding grew over time. About half of the funding went to the 18 days of annual ship charter. The LTER funding brought with it access to R/V *Sikuliaq* on one, and then (beginning in 2020) two cruises each year, and funding to support additional scientists, graduate students, broader spatial and temporal coverage, a wider spectrum of measurements, process studies, modeling, and expanded E&O activities.

II. RESULTS OF PRIOR SUPPORT

II.A. PHASE-I HYPOTHESES. Environmental disturbance is a regular feature of the NGA ecosystem, creating a mosaic of habitats and setting the stage for the evolution of species strategies that are sufficiently diverse to succeed in this milieu. Our program employs multiple simultaneous approaches, including long term monitoring, process studies, and modeling experiments. Below, we summarize our approach and findings related to our Phase-I hypotheses. We then describe three emergent Phase-I

research themes with accompanying results, indicating how these lead to our proposed Phase-II focus areas. Our ‘top ten’ Phase-I publications are indicated in **bold** throughout this section.

NGA Phase-I hypotheses centered on the interplay between the hydrologic cycle and ecosystem emergent properties whose maintenance or recovery we define as resilience and which appeared key to the high and strongly seasonal NGA production regime:

1. *Changes in the hydrologic cycle affect spring bloom production through changes in cloud cover, the stratification/mixing balance, macro- and micronutrient supplies, and lateral transport pathways.*

We undertook ship-based surveys each spring and conducted primary production experiments daily across this domain. Combined with satellite imagery, we made advances in understanding including: i) the distribution and fate of plume waters under the influence of the shelf wind field; ii) the potential for dissolved iron availability to regulate spring production; iii) biases in spring interannual nutrient availability that derive from time of sampling; iv) interconnections between reduced light availability and decreased spring production during warm years; v) the existence of predictive relationships between phytoplankton community size composition and overall spring bloom magnitude; vi) interannual variation in timing and dominance of large copepod (*Neocalanus*) sister species.

2. *Hot spots of high summer primary and secondary production result from interactions between the fresher ACC and more saline offshore waters as promoted by shelf geomorphology and regional winds; hot spot timing and magnitude will be influenced by changes in the hydrologic cycle.*

Summer process cruises surveyed the Copper River plume using a combination of towed and shipboard mapping technologies combined with remote sensing data. Shipboard experiments looked at coupling between phytoplankton growth and grazing loss rates, as well as the influence of Fe-rich plume waters on offshore HNLC communities. Coupling 3D circulation with food web models let us examine consequences of decadal-scale climate change (past and projected future) on freshwater-dependent ecosystem processes. Findings are summarized below.

3. *Nutritional and life history patterns of NGA consumers minimize trophic mismatch, buffering spatial and temporal variability in lower trophic level production and leading to resilience in the face of long-term climate change in the NGA.*

The NGA LTER framework combined with leveraged funds allowed us to explore mixotrophy by planktonic protists, a significant but hitherto unrecognized aspect of NGA food webs. Applying molecular and morphometric techniques to the NGA’s major spring zooplankton group, we gained insights into *Neocalanus* life history strategies and physiological responses to food availability. Seabird responses to the NGA habitat mosaic as well as to heatwave disturbance events were also put into life history and functional group frameworks. Along with new expertise in our Phase-II project (microbial diversity and network analysis: Hennon; marine mammal behavior and habitat use: Stafford), these findings position us to investigate the relationships among functional redundancy, habitat use, diversity, and ecosystem resilience in Phase-II.

II.B. THEME 1: FRESHWATER INPUT AND IMPACT. Massive freshwater discharges from the NGA’s mountainous rim affect the oceanography and ecology of the ecosystem and are highly sensitive to climate warming and precipitation changes (Beamer et al. 2017). The best recent modeling efforts (Hill et al. 2015, Beamer et al. 2016) put average annual discharge at $850 \pm 120 \text{ km}^3 \text{ yr}^{-1}$, approximately 1.6x that of the Mississippi River. The strongly seasonal freshwater inputs (mainly from summer and fall snow and ice melt) have major ecological implications. These include transport of organisms in buoyancy-driven currents such as the ACC (Royer 1982; Weingartner et al. 2005) and regulation of summer primary and secondary production over the entire shelf by vertical density stratification. In addition, the interplay between iron-rich low-salinity waters and iron-limited but macronutrient-rich offshore waters is a key determinant of summer production in the extensive transition zone between these regions. The many unknowns surrounding the magnitude, distribution, future trajectory, and ecological effects of freshwater inputs into the NGA led us to choose this phenomenon as the focus of our Phase-I process studies. Data

on freshwater distributions and their effects were obtained on all cruises, as well as through modeling efforts. In addition, three 5-day process studies focused on the Copper River plume region (Figs. 1, 5) during summers 2019, 2020, and 2022. These efforts directly address our first two Phase-I hypotheses, and indirectly inform the third.

Freshwater dispersal from nearshore plumes to the larger shelf follows distinct pathways indicative of time variant and persistent steering mechanisms, including wind and bathymetry, respectively. Using Self-Organizing Mapping techniques (Kohonen, 1998) with remote sensing data, we showed that the Copper River plume has 4 primary spatial modes (i.e. east-west and onshore-offshore extent) related to season and winds (Reister, in prep.). Linked hydrological and 3-D ocean circulation models show enhanced freshwater transport along the shelf break associated with the offshore deflection of the ACC as it flows past Kayak Island (Danielson et al. 2020). Ecological effects of these distribution patterns are numerous. A coupled circulation-biogeochemistry model showed that summer and fall coastal inorganic carbon chemistry is highly sensitive to freshwater inputs (Hauri et al. 2020 and references therein), influencing the aragonite saturation state that regulates calcification in shelled plankton such as pteropods. These planktonic gastropods can be important mediators of export from surface to deep waters in the NGA (see below). In contrast to other dissolved lithogenic trace elements (e.g., Mn and Al) in low salinity waters, which decrease in concentration by several orders of magnitude as the fresh waters mix and advect away from the source, concentrations of dissolved Fe remain relatively constant (Fig. 5C;

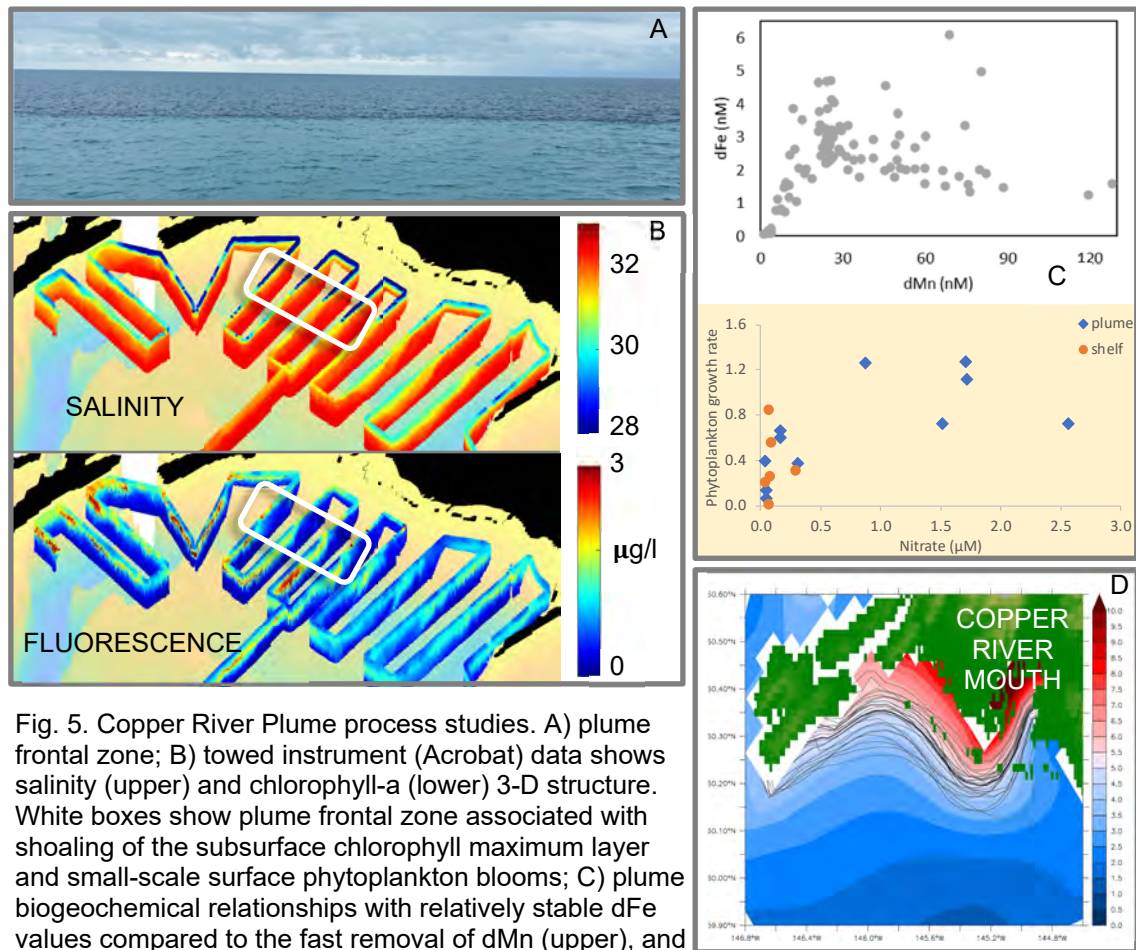


Fig. 5. Copper River Plume process studies. A) plume frontal zone; B) towed instrument (Acrobat) data shows salinity (upper) and chlorophyll-a (lower) 3-D structure. White boxes show plume frontal zone associated with shoaling of the subsurface chlorophyll maximum layer and small-scale surface phytoplankton blooms; C) plume biogeochemical relationships with relatively stable dFe values compared to the fast removal of dMn (upper), and elevated surface nitrate near plume edges associated with higher phytoplankton intrinsic growth rates (1/d) relative to non-plume shelf waters; D) model surface dFe in the plume study region during summer (Jul-Aug) showing interannual (1994-2020) variability in the 5nM dFe isoline.

Kandel & Aguilar-Islas 2021, Ortega & Aguilar-Islas, in prep.), as dFe is stabilized by Fe-binding organic ligands (e.g., Aguilar-Islas et al. 2016). This allows plume transport to potentially bring iron-rich nearshore waters into close proximity with nitrogen-rich but iron-limited offshore waters. A manipulation experiment showed that plume water supplied iron and stimulated net production and photosynthetic efficiency of offshore, HNLC communities. However, the composition of the resulting community was dramatically different from that resulting from ‘artificial’ fertilization with FeCl₃ (Mazur 2020). This supports observations that natural Fe sources stimulate different phytoplankton responses (e.g., Browning et al. 2014) relative to FeCl₃ additions, and invites reinterpretation of the many previous iron enrichment studies that used inorganic iron additions as proxies for natural enrichment processes.

Fine-scale mapping of the river plume and associated features (Fig. 5B) reveals that elevated phytoplankton biomass (as chlorophyll-*a*) does not map directly onto lower salinity waters. Though these fresher waters contain abundant silicic acid and dissolved iron (Fig. 5D), they have high suspended sediment loads that can contribute to phosphate removal, and are naturally low in nitrate. Patches of higher chlorophyll-*a* and elevated phytoplankton growth rates were sporadically associated with the plume edge frontal zone, likely due to entrainment of nutrients from deeper waters (Fig. 5C). However, light limitation due to suspended sediments and grazing by an active microzooplankton community can reduce primary production in the plume. Fresher waters provide a refuge from crustacean zooplankton; but once salinities exceed ~20, abundant small copepods can also readily crop larger phytoplankton. Ballasting of particulate organic matter by river-borne sediments can greatly enhance vertical exports. Thus, development of blooms in the plume region depends on “windows of opportunity” in which light availability, iron, macronutrients, and reduced grazing and sinking losses all coincide. Our frontal zone focus in Phase-II evolved in part from these observations, and will include fronts with greater spatial and temporal predictability, such as the shelf break front (Okkonen et al. 2005, Shotwell et al. 2014) (Fig. 4).

Building upon the fine-scale environmental and plankton community measurements collected near the Copper River plume, we are conducting a series of numerical experiments with the NGA model to explore the sensitivity of lower trophic ecosystem response to variations in the seasonality and magnitude of freshwater discharge. These experiments are based on running the same 28 years (1993-2020) with different freshwater seasonal cycles corresponding to historical and projected end-of-the-century conditions under moderate and strong anthropogenic warming scenarios. These simulations will allow us to determine not only how particular ecosystem components and trophic relationships respond to a change in the seasonality and magnitude of freshwater inputs in the NGA, but also how other important high and low frequency disturbances (e.g., eddies, marine heatwaves, subpolar gyre intensity) map onto (and modulate) the nearshore environmental gradients and planktonic community dynamics currently associated with winter precipitation patterns and summer river discharge.

II.C. THEME 2: ECOLOGICAL RESPONSES TO EXTREME EVENTS. The most ecologically significant disturbance events in the NGA in recent years have been marine heatwaves. A record-setting heatwave in terms of both intensity and duration (Hobday et al. 2018) affected our site between fall 2014 and spring 2016, before the inception of our LTER field effort in 2018 (Fig. 6). A shorter but similarly intense heatwave affected the area in 2019 (Danielson et al. 2022). Findings from our pre-LTER time-series provide context for the interpretation of the 2019 event and point to ecosystem structural and functional attributes that confer resilience.

The intense and long-lasting 2014-16 heatwave (Jackson et al. 2018) led to a substantial reconfiguration of lower trophic levels in the NGA, with some surprising ‘winners’ and ‘losers’ (Strom et al. 2023). September communities, which normally experience some of the highest NGA seasonal temperatures along with variability in the timing of the summer-fall transition, were relatively robust to the heatwave, supporting our contention that exposure to high levels of natural variability predisposes the NGA to resilience. However, southern zooplankton species characteristic of temperate biomes did increase, likely due to unusually high survival during normal northward transport (Strom et al., in prep). In contrast to

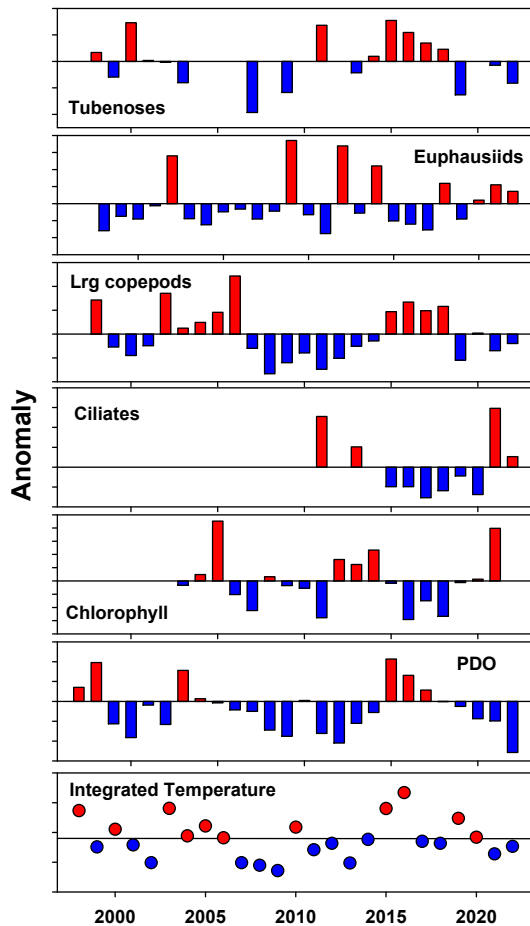


Fig. 6. NGA spring responses to recent marine heatwaves, as anomalies relative to long-term means. Tubenoses (seabirds including fulmars, petrels, shearwaters) are abundance anomalies, plankton are biomass anomalies. Spring chlorophyll-a is cumulative anomaly (from remote sensing) for spring bloom period April - June. PDO is calculated for preceding October to March.

analysis of Litzow et al. (2020) found high resilience in comparison with previous ‘regime shift’ periods such as the late 1970s. These contrasting conclusions highlight the sensitivity of resilience findings to time span and ecosystem component (i.e. proportion of lower versus higher trophic levels) considered by the analyses.

The 2019 heatwave provided an opportunity to bring LTER resources and conceptual frameworks to the study of such disturbance events. Several Phase-I findings suggest mechanisms by which the NGA achieves resilience; all of these will be further investigated in Phase-II.

A. Species ‘redundancy’. The large-bodied copepods that dominate spring NGA zooplankton communities have radiated into a species complex (*Neocalanus cristatus*, *N. plumchrus*, *N. flemingeri*) that are key biomass and energy conduits to higher trophic levels (Yamamura et al. 2002, Buckley et al. 2016). Despite environmental variability, they collectively show limited interannual response in

fall, the spring bloom was strongly affected by the heatwave with reduced chlorophyll-a biomass and a near absence of large diatoms (Fig. 6). Underlying mechanisms are under investigation but likely involve multiple interacting conditions, including reduced total nutrient availability and persistent cloud cover. Low light conditions increase the phytoplankton iron requirement (Raven 1999), and relative to available nitrate, iron tends to be scarce in spring before seasonal runoff ramps up (Aguilar-Islas et al. 2016). Surprisingly, this reorganization of the primary producer trophic level had little effect on the abundance of large copepods (Fig. 6 and Batten et al., 2018), although their lipid stores were substantially reduced. Much more strongly affected were euphausiids (krill) and forage fish such as sand lance, capelin, and juvenile pollock (Arimitsu et al. 2021; Suryan et al. 2021), likely due to a combination of limited dietary breadth and temperature-related metabolic increases in these species and in their ectothermic predators (Barbeaux et al. 2020, Holsman & Aydin 2015).

Krill and forage fish are key intermediaries in the food web leading to seabirds and commercially harvested groundfish, many of which fared poorly during the heatwave. Piscivorous seabirds such as common murrelets suffered extreme mortalities (Piatt et al. 2020, Arimitsu et al. 2021) and recruitment of groundfish including walleye pollock and Pacific cod reached historically low levels (Laurel et al. 2020; Rogers et al., 2021), leading to the closure of the directed Pacific cod federal fishery in the GOA. Large marine mammals (e.g., humpback whales) showed similar declines (Gabriele et al. 2022). Suryan et al. (2021) showed that some ecosystem effects persisted years after the 2014-2016 marine heat wave, suggesting a degree of system vulnerability (low resilience) to large, prolonged disturbance events. In contrast, the longer-duration and more fisheries-focused

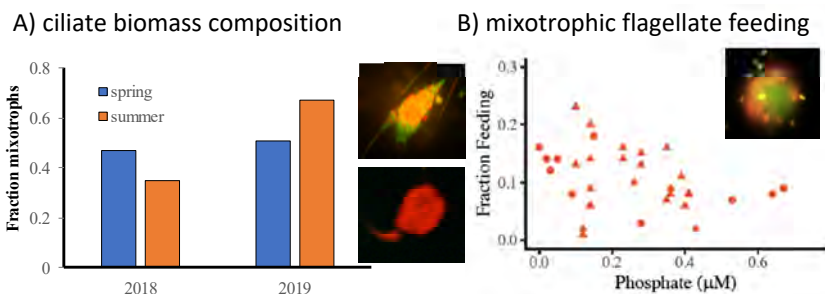


Fig. 7. Protist mixotrophy in the NGA. A) contribution of mixotrophic ciliates to total ciliate biomass in the spring and summer. Center epifluorescence micrographs show ciliates with retained chloroplasts fluorescing orange and red. B) Incidence of feeding by mixotrophic flagellates was negatively correlated with phosphate concentration in summer and fall 2019. Micrograph shows photosynthetic dinoflagellate with ingested (yellow) cyanobacterium.

even during metabolically stressful conditions, e.g., low prey availability (Roncalli et al. 2022). Thus, niche partitioning and physiological plasticity appear to buffer the genus's sensitivity to interannual variability in the timing and magnitude of the spring bloom.

B. High incidence of mixotrophy among photosynthetic protists. Several projects leveraging NGA platforms and resources have revealed that nutritional plasticity is widespread among groups historically considered either “phytoplankton” or “microzooplankton”. A significant proportion of NGA photosynthetic flagellates (i.e., most of the phytoplankton biomass outside of blooms) are mixotrophs (Busse 2021, O’Hara 2023). Feeding by photosynthetic protists provides an alternate means of accessing nutrients when dissolved organic and inorganic forms are limiting, and is known to stabilize food webs (e.g., Jost et al. 2004). Similarly, the NGA ciliate community, which comprises the majority of the larger micrograzers in the ecosystem, contains a high proportion of species that retain phytoplankton chloroplasts and are thus both consumers and primary producers (Strom et al. submitted; Fig. 7). This strategy is thought to enhance survival when prey is episodically scarce, and again buffers the food web against large excursions in primary producer biomass (Stoecker et al. 2017).

C. High export fluxes when least expected. During the heatwave summer of 2019 we saw unexpectedly high carbon export fluxes relative to primary production (O’Daly et al. submitted; Fig. 8). The long-standing oceanographic paradigm is that vertical exports are highest when primary production is dominated by large cells such as chain diatoms. Our summer 2019 phytoplankton community, in contrast,

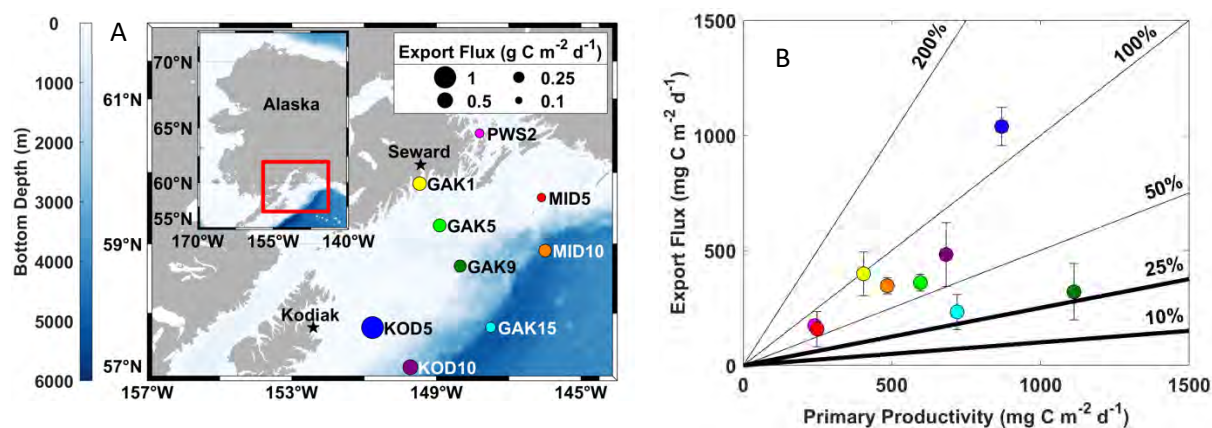


Fig. 8. Vertical exports of carbon from the upper water column during summer 2019. A) Measured flux rates. B) Flux rates as a function of primary production in the overlying water, with contours of export efficiency. Global export efficiencies are about 10% for open ocean and 25% for continental shelves.

abundance (Fig. 6). While their ecological distinctions are still under investigation, advances in species Phase-I funding have revealed differences in life history timing (i.e., emergence from diapause - Roncalli et al. 2018, 2020; lipid storage, entry into diapause - Coleman 2022). Transcriptomic studies supported by leveraged funding show extensive physiological acclimatization by *N. flemingeri*, allowing continued protein synthesis

comprised mainly picocyanobacteria and small (<10 μm) phytoflagellates (Cohen 2022). A recent review (Richardson 2019) indicates that small cell-dominated communities can be efficiently exported by aggregation, mineral ballasting, and incorporation into zooplankton wastes, especially those produced by mucous net feeders such as pteropods, larvaceans, and salps. All of these are potentially significant in the NGA and potentially lead to resilience through maintenance of a key emergent property (i.e., high vertical exports and primary productivity) even in the face of ecosystem changes (increasing dominance of very small phytoplankton) expected as the ecosystem warms (Dutkiewicz et al. 2013; Moran et al. 2010).

II.D. THEME 3: MANIFESTATION OF LONG-TERM CHANGE. The NGA ecosystem is experiencing long-term warming (Danielson et al. 2022), comparable to or exceeding that at other coastal marine LTER sites (Fig. 4; Ducklow et al. 2022). Along with this, as discussed above, freshwater inputs are increasing as melting of glaciers and snowfields accelerates, bringing along additional suspended sediment into the system. While surface NGA waters are freshening, deep waters are becoming increasingly saline (Kelley 2015). Thus, not only are temperature and salinity conditions changing per se, but the density gradients that resist vertical mixing are becoming more pronounced and shallower, with potential consequences for the subsurface supply of nutrients into the euphotic zone. Fronts are one of the quasi-persistent features of the stratified NGA that can overcome such barriers to vertical transport (Chapman and Lentz 1994), potentially conferring resilience through strengthened subsurface nutrient supplies. In Phase-II our focus on frontal zones is intended to elucidate the mechanisms, present significance, and potential long-term trajectory of these features.

Using field observations to inform model development enhances our ability to generate long-term historical simulations and regional climate projections while simultaneously providing context for spatial patterns and temporal variability measured in situ. Significant time was spent during Phase-I to incorporate information from field measurements, laboratory experiments, and expert knowledge into the NGA modeling framework. Notable milestones include: (1) improving coastal freshwater fluxes in the model (Danielson et al. 2020), (2) reformulating the lower trophic ecosystem model to include key functional groups (i.e., differentiating between small vs. large microzooplankton and between non-diapausing vs. diapausing large copepods), (3) parameterizing phytoplankton growth and zooplankton grazing rates with field data wherever possible, and (4) refining our formulation for iron-limitation by adding a particulate iron component and parameterizing leaching and scavenging rates based on existing NGA observations. These improvements resulted in a 28-year historical simulation (1993-2020) that closely reproduces vertical profiles and seasonal patterns of nutrients concentrations, chlorophyll, and key zooplankton taxa. While not all aspects of interannual variability have been evaluated (e.g., response to extreme heat events), we have been able to use the historical simulation to characterize changes in trophic relationships and energy transfers during periods of increased vs. decreased nitrate availability (Fig. 9), which is one of the dominant modes of variability in the NGA associated with fluctuations in subpolar gyre intensity and winter atmospheric forcing (Fiechter & Moore 2009, Hauri et al. 2021). Progress made during Phase-I sets the stage for more in-depth analyses of how ecosystem resilience is promoted by functional redundancy, such as differences in life cycle timing between large diapausing copepods or the ability of large microzooplankton to perform mixotrophy.

NGA long-term data sets, compiled during Phase-I and drawing in part on pre-LTER NGA data, reveal environmental responses - and striking response contrasts - in several key ecosystem components (Fig. 6). Biological responses fall into one of three groups: *i*) anomalies that correspond to long-term abiotic change (e.g. two-decade declines in tufted puffins; Cushing et al. 2023); *ii*) anomalies that correspond with shorter-term marine heatwave events or phases of the PDO (e.g. calanoid copepods; most seabird taxa; ciliates; spring chlorophyll); *iii*) anomalies independent of either long-term change or heatwave events (e.g., fall chlorophyll; Ducklow et al. 2022 their Fig. 7). Future NGA research will apply new identification and analysis techniques to historic and currently collected samples, to better understand the co-occurrence of species or guilds and their relationships to environmental variables.

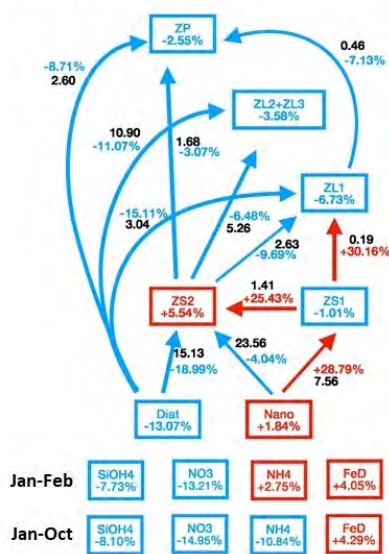
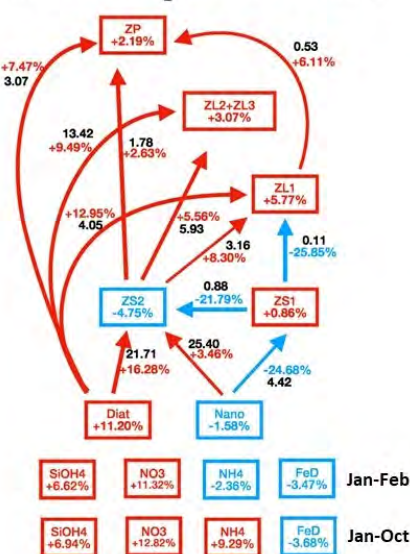
Decreased Nitrate Availability**Increased Nitrate Availability**

Fig. 9. Schematic summarizing simulated changes in phyto- and zooplankton biomasses and trophic transfers for years of decreased (left) and increased (right) nitrate availability. Biomass and flux differences are expressed in percent change relative to their mean over years (1994-2020). For trophic transfers, annual fluxes are listed to contrast relative importance of trophic pathways. Red (blue) boxes and arrows indicate value above (below) normal. Key findings are: (1) diatom biomass increases and decreases proportionally to nitrate availability, (2) increased nitrate availability favors direct trophic transfer from diatoms to copepods (ZL1-3) and krill (ZP), (3) despite increased grazing on diatoms, large microzooplankton (ZS2) decreases during periods of enhanced nitrate availability due to increased top down control from copepods and krill, and (4) nanophytoplankton and small microzooplankton (ZS1) are relatively unaffected by nitrate availability

II.E. DATA AVAILABILITY

Data are publicly available within 2 years of collection at DataONE, accessible through that portal and the NGA website. A table of these published data sets through to the end of 2020 (32 published, 12 in review) can be found in the Dataset supplemental section. Although most LTER data are served through EDI, that was not a strict requirement when our Phase-I proposal was submitted. All data will become discoverable through EDI during Phase II (see Data Management Plan). An inventory of samples collected and archived by NGA scientists can be found on our website (“Physical Sample Archive” under “Data” tab), with long-term plans to archive these at UAF’s Museum of the North - a nationally recognized repository.

II.F. EDUCATION & OUTREACH PROGRAM

A. Schoolyard Ecology. We created a suite of interactive and immersive activities to help students and educators discover the NGA LTER, learn about science practices, and make comparisons between their home ecosystems and the NGA. Our new Food Webs of the Northern Gulf of Alaska virtual field trip was created for use by 5th-9th grade classes and homeschool groups and aligns with Next Generation Science Standards as well as Alaska Cultural, Reading, and Writing Standards. It includes a video game, food web video, species profile cards, a student webpage with guiding questions for independent learners, and lesson plans with 6 activities for teachers (Fig. 10). These activities explore the topics of food webs, environmental variability, and marine ecology. The virtual field trip webpage and video game were each accessed over 600 times in 2022, with an average engagement time of 3 minutes and 41 seconds for the video game. Viewers are also typically spending over 3 minutes viewing the species profile cards, with over 230 unique page views in 2022. Overall visits to the Education & Outreach tab on NGA website have more than doubled over the last three years as the virtual field trip was published. The materials have been successfully utilized by the NGA education team with students from Chugach School District (61, K-12), Seward (25, 4th-5th grade), and the Alaska Native Science and Engineering Program (437, middle school). We have also developed additional curricular materials and interactive presentations for the Chugach School District, loaning oceanography equipment for student environmental monitoring projects (2020-2022), leading virtual and in-person plankton laboratories (2021-2022), and helping students to create their own hydrophone (2023).

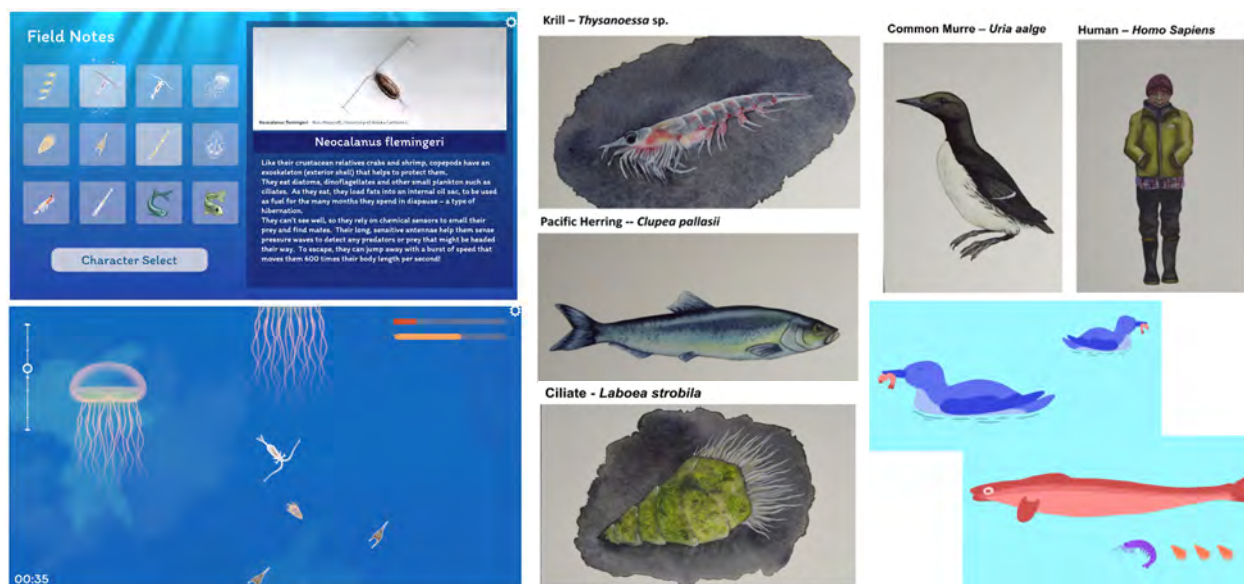


Fig. 10. Images from “Food Webs of the Northern Gulf of Alaska” virtual field trip. L: screenshots of video game as it is played; Center and upper R: images and text from species profile cards; Lower R: animation stills from food web video.

B. Research Experiences for Educators. We hosted 8 educators aboard NGA research cruises: 4 formal K-12 educators (AK-2, NY, HI), 2 informal science educators (AK-2), 1 community college instructor (IL), and 1 science communicator (AK). These educators created lesson plans, videos, community presentations, and journalism pieces for Alaskan radio and print media, reaching a range of ages and audiences from around the country. This effort was supported in 2019 and 2020 by NOAA Teacher At Sea, with a pause in recent years due to COVID. In 2022 we focused on offering at-sea opportunities to local educators and science communicators with 2 participants.

C. Research Experiences for Undergraduates (REU). 12 REU students participated in Phase-I NGA research with over half being members of groups underrepresented in science; another 5 REU students will join us in summer 2023. We host students in alternating years so that they can work within a larger cohort. During 2019, students were able to go to sea on the summer research cruise. Students in 2021 participated in a virtual REU program, with opportunities for science communication, coding literacy, career exploration, and community building alongside one-on-one mentored research projects.

D. Graduate Students. At present there are 5 PhD and 7 MS students working on projects associated with NGA LTER. An additional 8 MS students have already graduated. All students have participated in our research cruises working in a multidisciplinary environment. The large number of students has been possible through TA/RAships, a tuition match program provided by the UAF Provost, and leveraging of other funding by PIs in addition to support from the Phase-I LTER award.

II.G. DIVERSITY, EQUITY AND INCLUSION (DEI). The effort to create a more diverse, equitable, inclusive and welcoming NGA community was a major focus during Phase-I. Since 2019 an NGA scientist has served on the network-wide DEI committee; in that same year we formed the NGA DEI committee with representation from students, postdocs, staff, partners, and PIs. Our Executive Committee also has representation from each of these groups. Guided by the NGA DEI committee, we have developed a living document to describe our vision and outline short-term and mid-term steps towards achieving this vision. (This document and other resources described in this section can be found on our website.) We also developed an NGA Code of Conduct, which specifies expectations during remote and in-person interactions, gives information about reporting pathway options, and provides resources from the institutions that make up our community. This document is provided to new participants, to meeting participants, and to field participants. All relevant documents are made easily available onboard during

cruises. To further improve the field work experience, we have focused on participant preparations and expectations, and providing mechanisms for feedback. A student-developed video was created to show new participants what to expect from a research cruise in the NGA (available in the Field Resources page of our website). We collaborated with the BLE LTER to offer a voluntary Bystander Intervention training for all NGA participants in 2022, facilitated by AdvanceGEO. We developed a post-cruise survey to allow field participants to voice concerns and suggestions. This anonymous survey provides the Executive Committee with general information about each field effort and gives participants an additional opportunity to provide information about field-related issues and successes. There is a mechanism that allows participants to further discuss concerns with a trusted member of the NGA community. Time is also devoted to discussion of DEI topics during annual All-Hands and weekly Executive Committee meetings. In response to concerns introduced through these discussions, we created a monthly newsletter and improved pre-cruise planning protocols.

Additional NGA DEI initiatives focus on Schoolyard Ecology (see above) and undergraduate participation. Our REU selection rubric gives preference to students who have not had extensive prior research opportunities. In addition, we were able to re-allocate funds to support an REU with Alaska Native heritage in 2021 and are doing so again in 2023; this REU position allows for a flexible schedule and academic background to better meet the needs and interests of Alaska Native students.

II.H. SUPPLEMENTAL SUPPORT. Due to COVID-associated delays in the NGA's mid-term review, funding was extended into a 6th year via a Supplemental award. NSF also provided equipment supplements to all the marine LTER sites, with NGA funds (\$135K) used to acquire mooring releases, a new in situ particle analyzer (deep-LISST), and trace-metal sampling bottles that entered service during 2022. Results from these supplements are integrated into prior sections.

III. RESPONSE TO MIDTERM REVIEW

Our mid-term site review was very positive overall, with praise from reviewers for our collaborative science, inclusivity, and response to pandemic challenges. There were six recommendations from the review panel: three relate to Information Management and are addressed in that supplementary document, while the other three are addressed below.

A. Clearly define the core measurements of the NGA LTER given this would inform any triage strategies if there are substantive changes in partner programs. NGA science is supported by several federal and Alaska State agencies in addition to NSF (detailed in the Collaborations section, below). Collective funding by non-NSF partners represents about one-third of the overall budget supporting shipboard, mooring, and other field activities. Should support from partner programs decrease, Core Measurements to be maintained would be *i*) hydrographic, chemical, lower trophic level (plankton) measurements and seabird observations for the Seward Line in spring and fall and *ii*) process studies as described below. This would maintain our longest-running time series that are key to understanding ecosystem responses to disturbance (as well as collecting data in all 5 LTER core areas) and allow us to further our mechanistic understanding of ecosystem processes leading to resilience, as outlined in our hypotheses.

B. More solidly establish cross-LTER site interactions; highlight the strong relationships with partners and collaborators. Since the mid-term review our cross-site collaborations have grown considerably. The NGA contributed to two recent synthesis publications (Ducklow et al. 2022, Harms et al. 2021) and is part of three recently funded synthesis proposals. Our Education and Outreach coordinator (Gavenus) also works with the Beaufort Lagoon Ecosystems (BLE) site, and the E&O plan outlined below contains an explicit partnership with the Bonanza Creek (BNZ) boreal forest site to involve students in their Climate Scholars program in NGA marine science. Collaborations with regional partners outside of LTER have also grown. These are described in detail in sections below but involve new funding and research partners (e.g., Murdock Foundation, National Park Service) and growing connections to coastal communities and Tribes. We also continue to partner with NOAA Alaska fisheries programs.

C. Develop postdoctoral and student mentoring standards or plans. While our proposal does not request funding for a postdoc, we plan to build on NGA’s collaborative, multi-disciplinary foundation to offer a more expansive opportunity for these early-career scientists during Phase-II. Overall goals are to provide leadership training and to invite all participants to experience the variety of NGA science disciplines, modes of investigation, and outreach opportunities. With respect to field work, we will consistently offer pre-cruise orientations and planning meetings as implemented during the past several years. Post-docs and other early career scientists will be given opportunities for cruise planning and execution leadership, particularly during the summer process cruises. While at sea, students, post-docs, and educators will have the option of participating in the spectrum of sampling and data collection activities from physics to seabirds. Outside of field work, we plan to regularly offer a weekly thematic Journal Club during the academic year and to continue offering data management/analysis and DEI training. These NGA-wide opportunities bring together students, staff, and faculty from across institutions and disciplines.

IV. NGA PHASE-II RESEARCH PLAN

IV.A. HYPOTHESES AND THEMES. NGA Phase-II continues much of the framework from Phase-I: evaluating resilience through a combination of long-term observations and targeted studies within the mosaic of features that characterize the region. Many aspects of resilience – the recovery after disturbance – can only be evaluated through long-term observations and models, while the mechanisms that may favor resilience can be studied with shorter-term observational or experimental approaches that inform model development. In Phase-II we will specifically focus on i) the study of functional redundancy in the context of disturbance and long-term change, as well as relationships between redundancy and resilience (Fig. 11) and ii) frontal features, associated ecotones, and their combined role in key ecosystem properties that generate resilience within the NGA (Fig. 12). We propose to tackle each with a combination of observational methodologies, process studies, and modeling approaches.

Our specific Phase-II Hypotheses are:

1. *Functional redundancy occurs at multiple trophic levels in the NGA, conferring resilience to disturbance and long-term change.*
2. *Ecotones created by frontal systems support increased productivity, trophic transfer and carbon export, contain unique communities, and enhance NGA ecosystem resilience.*
3. *Frontal systems exert a disproportionate role in the NGA that varies seasonally, interannually, and over longer periods of climate change. Increases in frontal complexity, persistence, and frequency favor highly connected planktonic species that stabilize populations at higher trophic levels.*

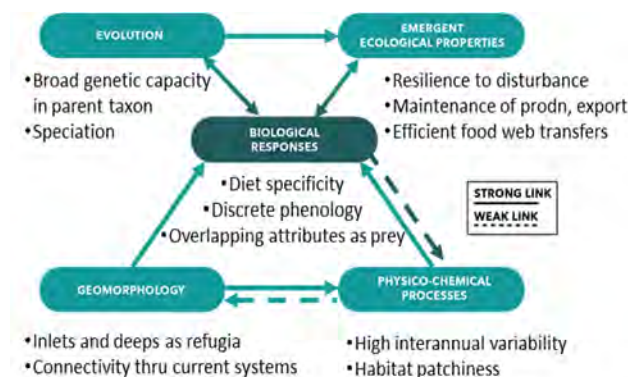


Fig. 11. Conceptual model diagram for functional redundancy theme of NGA Phase-II research.

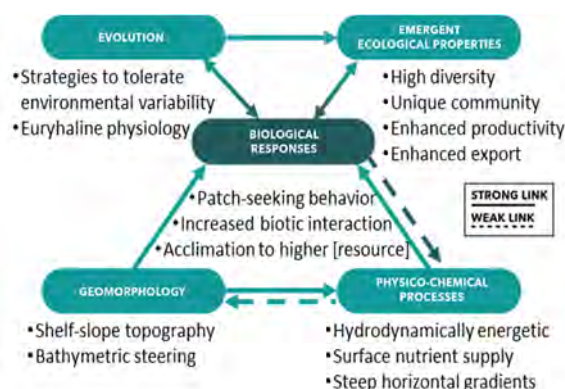


Fig. 12. Conceptual model diagram for front and ecotone theme of NGA Phase-II research.

A. Functional redundancy. Functional redundancy (e.g., Biggs et al. 2020, De Battisti 2021) has been proposed as an important mechanism conferring ecosystem resilience. While even closely related species may co-exist due to niche partitioning (e.g., Fox and Bellwood 2013, Cleary et al. 2016, Cabrol et al. 2019), minor differences in the environment (biotic or abiotic) may favor one species over another, or even alter the redundancy between species (Fetzer et al. 2015). When redundancy is high, predators may be little affected by a shift in prey availability if losses in one species are offset by gains in another. However, it is unclear how redundancy and associated species diversity are affected by climate change (Thakur et al. 2017). In the NGA we see examples of functional redundancy at multiple trophic levels despite the relatively low diversity of prominent species in this biome.

Phase-I research highlighted the importance of mixotrophic (chloroplast-retaining) ciliates to the NGA planktonic food web (Fig. 7). Retrospective analysis of ‘microzooplankton’ samples showed periods of alternating dominance by *Mesodinium* spp. (probably *rubrum* plus *major*) and *Strombidium* spp. (Fig. 13). While the two have strongly contrasting chloroplast-hosting strategies in terms of source specificity and longevity (e.g. Hansen et al. 2013, Stoecker et al. 1988/89), they are similar in size and may represent redundancy in the important predator-prey link with mesozooplankton (Calbet & Saiz 2005). Phase-I model results highlighted the sensitivity of the “large microzooplankton” trophic linkage to environmental shifts and consequent fluxes through the food web (Box ZS2 in Fig. 9). During Phase-II modeling we will incorporate an explicit parameterization for mixotrophic ciliates (e.g., photosynthetic potential and cost of mixotrophy) based on field and laboratory measurements from Phase-I and elsewhere (Stoecker et al. 2017). These model simulations will provide insight into factors promoting the success of mixotrophs in the highly dynamic NGA environment, including how their presence confers resilience to food web structure and higher trophic level productivity. We will also use co-occurrence analysis on 16S and 18S rRNA amplicon sequence variants to infer key microbial interactions in the NGA (Fig. 14). These analyses have already uncovered evidence for strong correlations between *Mesodinium* spp. and cryptophyte prey *Teleaulax* spp. in the NGA, suggesting that network analyses such as these can reveal ecologically meaningful interactions and trophic relationships (e.g., Needham et al. 2018).

In the copepods, we see an example of functional redundancy in the three species of *Neocalanus* that dominate the spring bloom, as well as the three species of *Pseudocalanus* that become increasingly prominent as the season progresses (e.g., Coyle & Pinchuk 2003, 2005). *Neocalanus* species partition the habitat somewhat through timing of their spawning (Miller & Clemons 1988, Mackas & Tsuda 1999), spatial (vertical) segregation (Mackas et al. 1993, Coyle & Pinchuk 2005; Tsuda et al. 2014), differences in first feeding stage (Saito & Tsuda 2000), differences in diapause timing/stage (Miller & Clemons 1988, Mackas & Tsuda 1999), differences in body-size at stage (Coleman 2022), and likely in difference of their optimal prey size (as suggested by intersetal distances in their mouthparts). Nonetheless, there is also

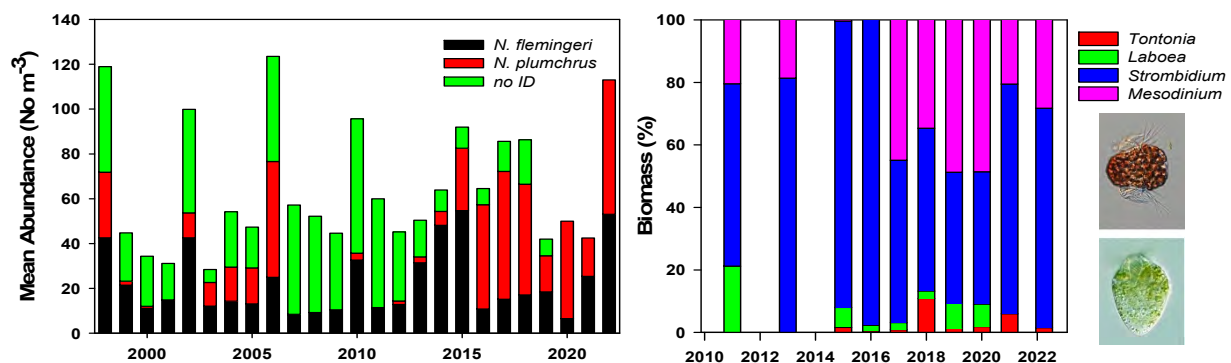
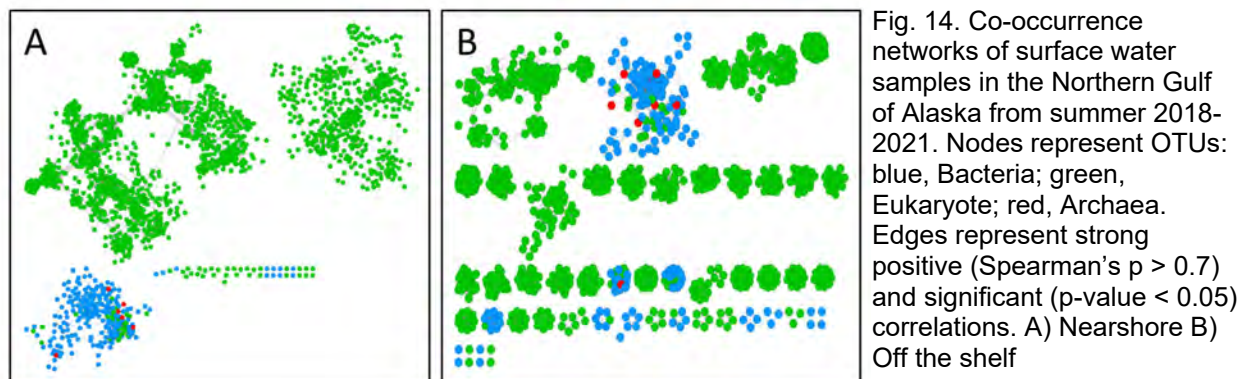


Fig. 13. Functional redundancy in spring NGA planktonic food web, including A) alternation between *Neocalanus flemingeri* and *N. plumchrus* as dominant large-bodied zooplankton species; B) alternation between *Mesodinium* and *Strombidium* as dominant mixotrophic ciliate genera.



considerable overlap in all of these characteristics. We have long noted shifts in life-stage prominence associated with warm and cold years (Liu & Hopcroft 2006b), but recent improvements in species identification at earlier life stages are revealing significant shifts in the relative abundance of each species, both amongst the cross-shelf domains as well as between years, although their combined abundance appears to be relatively stable (Fig. 13A). Using our long-term data, we propose a deeper analysis of the environmental factors associated with these shifts. We will also use the NGA model framework to explore the importance of functional redundancy in *Neocalanus* through sensitivity experiments informed by Phase-I observations. The resulting simulations will help assess the resilience of food web structure and higher trophic level productivity to (i) imposing small variations in the parameterization of the large diapausing copepod functional group (e.g., diapause timing), and (ii) introducing redundancy by splitting the large diapausing copepod functional group into three “sibling” species parameterized to reflect differences in their observed biology, including life history.

By summer and fall, *Pseudocalanus* is the biomass dominant copepod in the ecosystem, and is represented by three species (Napp et al. 2005, Questel et al. 2016). Unlike *Neocalanus*, only the adult females of *Pseudocalanus* can be reliably separated using morphological characteristics. Adults do show habitat partitioning and different environmental preferences (Yamaguchi et al. 1997, 1998, Napp et al. 2005, Hopcroft & Kosobokova 2010). As an alternative to morphology, all life stages can be separated using species-specific PCR (e.g., Bucklin et al. 1998, Bailey et al. 2016, Ershova et al. 2017). Using this approach reveals that habitat partitioning occurs at all life stages and that the spatial distribution of younger stages may differ significantly from adults if the habitat no longer favors recruitment (Ershova et al. 2017). Using this species-specific PCR approach, we propose to examine both redundancy and niche partitioning across time using samples collected from both Phase-I and Phase-II.

B. Fronts and ecotones. Frontal structures, and the ecotones created at these environmental transitions, are commonly associated with enhanced productivity and biomass across a wide spectrum of trophic levels (e.g., Olson et al. 1994, Ribalet et al. 2010, Acha et al. 2015, Prants 2022) through both stimulation of productivity and aggregative mechanisms. The high productivity found at frontal regions has long been exploited by fisheries (e.g., Druon et al. 2021) and therefore should be better incorporated into models (e.g., Woodson & Litvin 2015). Given their ecological importance, there is growing consensus that frontal regions should be prioritized for conservation efforts (e.g., Scales et al. 2014, Miller & Christodoulou 2014).

Frontal features have been studied elsewhere in Alaskan waters, particularly in relation to upper trophic levels (e.g., Iverson et al. 1979, Decker et al. 1996, Gende & Sigler 2006). Although several studies have assessed their physical structure and functioning in the NGA (Weingartner et al. 2005, Williams et al. 2007), their ecological importance has seldom been considered for this system (e.g., Shotwell et al. 2014). If fronts are a key to ecosystem productivity and resilience, then as their relative footprint increases, we might expect productivity to increase, thereby increasing the capacity of the system to sustain ecosystem services. There is already evidence that ocean warming can lead to a reduction in the frequency of fronts

in some ecosystems (Kahru et al. 2018). If this occurs in the NGA, then warming (as continuous long-term change or episodic events) could lead to reductions in production and resilience.

The challenge in studying fronts and their ecotones is the scale and intensity of effort required to identify and sample them. From a physical perspective, front complexity can be described in a dynamical framework by quantifying characteristics of the thermohaline structure along a vertical section that bisects the front, by assessing time evolution and length scales via analysis of remote sensing data and numerical model output, or by directly measuring scales of variability associated with frontal density overturns and turbulent velocity microstructure. While assessments of front character and functioning is somewhat tractable for physics and phytoplankton biomass (as in situ fluorescence), both logistics and cost can become intractable for high-resolution biological and biogeochemical sampling and rate measurement. The DPI provides a tool for high resolution study and mapping of fronts (Greer et al. 2015, Greer et al. 2020), including: physical and chemical features defining the frontal structures, particle size spectra for estimating aggregation and flux, spectral and fluorescent signatures for assessing phytoplankton, imaging for quantifying zooplankton, and acoustics for assessing micronekton and fish biomass and distributions. Supplemented with shipboard underway sensors plus seabird and mammal observations (Cushing et al. 2023), we can simultaneously examine frontal impacts across trophic levels. The existing historical simulation and planned Phase-II downscaled climate projections will provide important context for interpreting field measurements across spatiotemporal scales and trophic levels. Additionally, the model will shed light on how frontal processes currently shaping the NGA ecosystem mosaic will respond to long-term change, and whether present-day disturbances are indicative of more permanent future ecosystem states.

IV.B. APPROACH

A Overview. Phase-II proposed efforts continue our core time series, address our new hypotheses, and encompass the 5 LTER core areas. Although we greatly expanded our sampling intensity during Phase-I to understand the mosaic nature of the NGA, this level of effort is not sustainable going forward. For Phase-II (Table 1), we propose to maintain Phase-I's three cross-shelf transects during spring cruises when the timing of the bloom is not spatially synchronous and processes set up that influence ecosystem state for the remainder of the year. Early May and mid-September represent our core 25-year time series, and the latter can be adequately monitored by the Seward Line and PWS stations alone. In addition to these annual 'survey' cruises, two longer summer 'process' cruises during Phase-II will focus on frontal features and associated processes, with transect sampling restricted to the Seward Line to provide ecosystem state context.

Table 1. Field sampling plan. Note that all cruises sample in PWS, as funded by partner programs.

Season	Frequency	Duration	Lines	Other
Spring (early May)	annual	17 days	GAK, KOD, MID, PWS	DPI, mooring
Summer (July)	2025, 2027	25 days	GAK, PWS	DPI, process work
Fall (mid Sept)	annual	9 days	GAK, PWS	

B. LTER Core Areas in the NGA

1. Patterns and controls of primary production: Primary production rates will be measured directly on all cruises, yielding estimates for spring, summer, and fall. Primary production will also be estimated from satellite ocean color and can be extrapolated from chlorophyll data in surface waters (e.g., Strom et al. 2016). Controls on primary production (e.g., light, micro- and macronutrients, grazing, sinking) will be assessed through field measurements, relationships to environmental conditions, and modeling studies (see below) that examine the influence of frontal dynamics on the along- and cross-shelf distribution of limiting nutrients (i.e., nitrate and iron) and phytoplankton community structure and production.

2. *Spatial and temporal population dynamics and food web interactions*: Sampling is explicitly designed to capture the spatial and temporal dynamics of key populations in the NGA, including phytoplankton, zooplankton of various sizes and trophic levels, fishes (acoustically), and seabirds. Food web interactions will be assessed directly through experiments on process cruises and indirectly through comparison of species abundance variations. Model simulations will be used to characterize biomass production, trophic transfer, and food web controls (e.g., bottom-up vs. top-down) at the spatial and temporal scales associated with frontal processes shaping planktonic habitats and community structure in the NGA.

3. *Patterns and controls of organic matter accumulation and decomposition*: Concentrations of DOC and POC are measured on all cruises. Short-term measurements of particulate export (from drifting sediment trap arrays), productivity, and associated environmental variables will allow us to examine seasonal cycles of organic matter accumulation and removal from the upper water column and relate these to seasonal and interannual changes. A 30-year historical simulation and 21st century downscaled climate projections will provide a baseline for identifying the current and future dominant physical and biogeochemical processes that control vertical and lateral export of organic matter on seasonal to interannual time scales.

4. *Patterns of inorganic inputs and movements of nutrients*: Dissolved inorganic macronutrient concentrations are measured on all cruises, with deep-water spring concentrations providing estimates of nutrients supplied to the ecosystem via late winter deep mixing. Iron size classes, chemical speciation and particle reactivity are measured in surface waters and, in spring and summer, with vertical resolution. The modeling component will explore how micro- and macro-nutrient supply and exchange across the NGA mosaic is controlled now and in the future by the interplay between changing freshwater discharge and coastal frontal dynamics.

5. *Patterns and frequency of disturbances*: We will use a combination of observational and hindcast modeling methods to characterize disturbance in the NGA across a range of time and space scales. Meteorological observations provide data on cloud cover, irradiance and wind speeds. The mid-shelf mooring provides a high-frequency and multi-disciplinary view of the marine ecosystem from a single location, while PAR and ocean color data from remote sensing provide a basin-scale view of irradiance and phytoplankton variability. Runoff timing and intensity will be assessed from individual USGS gauging stations and Hill's terrestrial discharge modeling. Size, location, intensity and frequency of mesoscale eddies and Alaska Current (AC) flow field variations will all be obtained from satellite altimetry products. Unusual warm and cold events will be evident from our shipboard and mooring observational program in conjunction with partner and agency-collected observations. Larger-scale disturbances will be tracked through the use of readily available indices (PDO, NPGO, NGAO, ENSO, PNA, NPI, and Bakun upwelling) and reanalysis products (ECMWF ERA5). The existing historical simulation and planned downscaled climate projections will be used to determine how decadal variability (e.g., that associated with the PDO and NPGO) and extreme events (e.g., those associated with ENSO and large marine heatwaves) modulate and reshape frontal dynamics, nutrient exchange, and planktonic habitats expected to occur seasonally in the NGA.

C Long-term Observations: Core Measurements

1. *Shipboard studies*: Our longest ship-based time series consists of the Seward Line (15 stations) and western PWS (7 stations) sampled during May and early September for the past 25 years (Fig. 1). The LTER Phase-I expansion added the upstream Middleton and downstream Kodiak lines encompassing known productivity hot-spots, and summer cruises that included process studies. The first-order driver of production variability is the intense seasonality of the system (Brickley & Thomas 2004, Waite & Meuter 2013). The early May at-sea period captures the peak productivity associated with the spring bloom and allows us to examine interannual variation in nutrient delivery and phenological shifts (i.e., Mackas et al. 2012) in the large *Neocalanus* copepods that dominate the spring zooplankton community. September cruises capture the end of the low-productivity oceanographic summer, when nitrate is depleted and smaller phyto- and zooplankton dominate, and can encounter the transition to the stormy fall mixing and

nutrient replenishment period. Changes in the microzooplankton community and lower trophic level transfer efficiencies appear to accompany this seasonal transition (Strom et al. 2019), while changes in iron speciation (Aguilar-Islas et al. 2016) indicate seasonal differences in iron sources. The summer (July) cruises implemented with the LTER provide important context to the seasonal cycle and opportunities to conduct process-oriented studies at a time of year when stratification and cross-shelf frontal zones are well established.

Overall core oceanographic sampling methodology has remained stable since sampling began in the fall of 1997 (Weingartner et al. 2002). All hydrographic and bottle-based work is conducted during the day (e.g., 911plus CTD, dissolved inorganic carbon (DIC), macronutrients, chlorophyll a, phyto- and microzooplankton composition/biomass), as well as collection of the smaller zooplankton species (150 μ m Calvet net) that do not migrate vertically nor avoid collection. Since 2014, optical measurements of the particle size distribution (2.5 μ m – 2.5 cm) have been conducted in conjunction with CTD rosette casts using an integrated Underwater Vision Profiler (UVP5, recently upgraded to UVP6) and Laser In Situ Scattering and Transmissometer (LISST) to explore particle dynamics (Guidi et al. 2008, Picheral et al. 2010). The LTER greatly expanded the breadth of daily measurements that deepen our understanding of ecosystem processes, including micronutrient sampling (Aguilar-Islas et al. 2016), primary production via ^{13}C uptake, dissolved organic carbon (DOC), and particulate organic carbon (POC). Seabird and mammal observations are made during daytime transits between stations. At night, sampling is conducted for the larger and more mobile zooplankton (500 μ m Multinet), many of which can only be sampled efficiently during their daily migration toward the surface, under the cover of darkness.

2. *Moorings*: A mooring measuring temperature and salinity hourly at six depths has been annually deployed at Seward Line station GAK1 (Fig. 15h) since 2000 (Janout et al. 2010) and we deployed a more highly instrumented mooring on the mid/outer shelf (see locations in Fig. 1A) beginning in 2019. This moored Gulf of Alaska Ecosystem Observatory (GEO) installation is one of a small network of

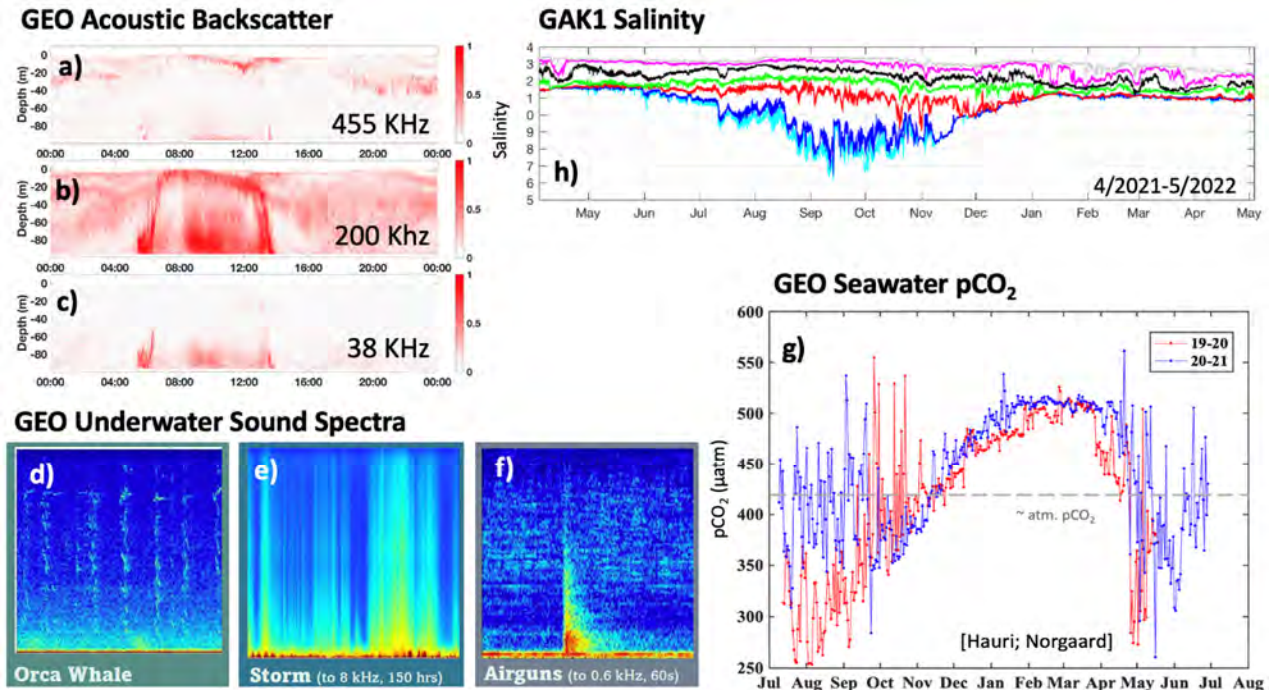


Fig. 15. Examples of temporally high-resolution *in situ* data collected year-round by autonomous moored samplers. From the GEO mooring: 24 hours of (a) high-, (b) mid- and (c) low-frequency acoustic backscatter; underwater sound spectra showing (d) orca whale calls, (e) wind/wave noise from a storm event and (f) a seismic air gun blast; (g) two years of pCO₂ data. From the GAK-1 mooring: (h) one year of salinity measured at seven depth levels every 15 minutes.

similarly instrumented moorings in each of Alaska's three large marine ecosystems (Arctic, Bering & NGA) and comprises part of AOOS's ecosystem monitoring build-out plan (McCammon 2013). Similar to the Chukchi Ecosystem Observatory (CEO; Danielson et al. 2017), the GEO collects water velocity, wave height, pressure, temperature, conductivity/salinity, photosynthetically available radiation, colored dissolved organic matter, optical backscatter, nitrate, pH, pCO₂, chlorophyll *a* fluorescence, passive acoustic recordings, and active acoustic volume backscatter at 38, 125, 200, and 255 KHz. The GEO and CEO moorings each have a 24-bottle sediment trap (see Particulate Matter section) and a 47-place bag sampler that collects whole water samples for macronutrient and eDNA analyses (Fig. 15).

D. Process Studies (Summer Only)

1. Rationale: Investigations across the Copper River plume during NGA Phase-I revealed the importance of this plume's frontal system in mediating the fate of Copper River freshwater and in setting a gradient of habitat types between the mouth of the Copper River and offshore waters (Fig. 5). Our Phase-II summer process cruises will target frontal systems beyond the Copper River (Fig. 4) that likely exert disproportionate influences on the NGA's biodiversity, functioning, and resilience (Fig. 12). The ecological mosaic that comprises the NGA marine system derives structure from the environmental factors that regulate physical and chemical stratification and front locations: underlying bathymetry, terrestrial freshwater runoff, ocean-atmosphere heat fluxes, tides, and wind. Together, these factors set the strength and location of the ACC and AC flows and associated fronts. The ACC front is associated with the seaward edge of that coast-hugging current, while the shelfbreak front is associated with the Alaska Current and the corresponding sharp depth discontinuity at the outer edge of the shelf (Figs. 1,4). Lateral and residual vertical circulations associated with such fronts can be the source of new nutrients and productivity, support elevated biomass at numerous trophic levels, and potentially host species assemblages that contrast with coastal and mid-shelf communities. We will explore how these fronts alter trophic structures and microbial interactions with network analysis of 16S and 18S samples collected across the NGA; preliminary data indicate that microbial networks have fewer interacting partners in offshore communities, suggesting more specialized interactions (Fig. 14). Using summary statistics such as degree centrality and betweenness we plan to quantify which microbes are the key nodes in the NGA and how that corresponds with their distributions over fronts.

In addition to seasonal monitoring activities, we propose to conduct process cruises targeting these two key front systems (i.e., ACC and shelfbreak) that significantly contribute to the NGA's ecological and oceanographic structure. Experimental and high-resolution observational studies conducted within and across these features will constitute an important aspect of our investigation of ecosystem resilience, as we focus on the nature and response of emergent properties to natural and experimentally generated gradients and perturbations. These features can also represent space-for-time substitutions that may provide insight into probable ecosystem structure and function in response to projected climate variability. We anticipate shifting our focus to other significant features (e.g., production 'hot spots' associated with shallow banks or mesoscale eddies) during future funding cycles. Experimental and/or modeling work will include: (1) investigations of controls of nutrient delivery to the euphotic zone; (2) studies that target advective lateral convergence/divergence and vertical suction/pumping processes; (3) observations of phytoplankton community responses; (4) estimation of lower trophic level connectivity; and (5) quantification of biodiversity. High resolution assessment of species' distributions will be coupled to rate measurements (e.g., nutrient supply, primary production, nutrient uptake, grazing, secondary production) to investigate how the community is shaped by, and shapes, the environment.

2. Field Plan: Summer cruise *process study* work will commence following a survey occupation of the Seward Line (see Core Measurements), including a DPI transect (see below for details) across the entire line. These measurements will establish the cross-shelf context and front locations (Fig. 16). A subsequent series of DPI transects will provide a quasi-synoptic snapshot of a targeted frontal zone, including waters within and adjacent to the front. DPI data will provide requisite information regarding

frontal structure and ecotone. Based on the DPI transect results, a series of 5-7 GPS-tracked marker buoys (drogued to 15 m) will be deployed across the front in order to establish a Lagrangian reference frame and permit repeated sampling of specific water masses over time. At each particular front, a series of three to five 24-h process stations will be occupied, with at least one on either side of the front and one or more (for repeat occupation) within the front. The study will conclude with DPI surveys to assess hydrographic changes. This *process study* schedule will be repeated 2-3 times per summer cruise as time allows.

During the front occupation a broad suite of measurements and experiments conducted both within and on either side of the front will focus on rate measurements and repeated inventory of abundance and/or biomass to establish change over time. The Lagrangian reference frame will allow monitoring of the planktonic ecosystem and environment independent of changes due to lateral advection. In addition to Core Measurements, specialized operations will provide improved study of ecosystem processes (Fig. 16): **1:** (Hypothesis 2) Measurements of *in situ* microstructure will assess turbulent mixing and enable estimates vertical fluxes of macro- and micro-nutrients. **2:** (Hypothesis 2) *In situ* pump deployments will obtain size fractionated particle composition information, including elemental ratios and genomic context. These data will be spatially extended with *in situ* optical data (UVP6 and LISST DEEP) and observations of sinking particle flux (drifting sediment traps) to assess relationships among particle composition, size distribution, export flux, and functional types with physical and biological processes. **3:** Iron physicochemical speciation (important to its bioavailability) data will inform about size (particulate to soluble), particle reactivity (e.g., acid leachable), and organic complexation of dissolved iron. **4:** (Hypothesis 1-2) Relative roles of macronutrient limitation, microzooplankton grazing, and copepod grazing in regulating phytoplankton growth rates, community composition, and biomass accumulation will be measured using a modified dilution technique (Strom et al. 2007, Strom & Fredrickson 2008, Nejstgaard et al. 2001). **5:** (Hypothesis 3): Copepod egg production experiments (EPR; Hopcroft et al. 2005, Napp et al. 2005) will connect lower trophic level productivity to the higher trophic levels based on taxa-specific fecundity.

E. General Methodology

1. Hydrography (Danielson): High-resolution vertical profiling of temperature, salinity, chlorophyll fluorescence, PAR, O₂, and beam transmission to within 4 m of the bottom will be collected at stations. Underway data will be collected continuously from shipboard sensors including Doppler current profilers and a broad suite of atmospheric and sea-chest sensors that *Sikuliaq* carries (e.g., pCO₂, NO₃, surface radiative fluxes, PAR). Discrete oxygen and salinity samples will be collected from rosette bottles for calibration of high-resolution sensors. The physical and chemical data will be used to quantify the seasonal and interannual distributions of water masses in cross- and along-shelf gradients. Data sources providing broader spatial and temporal context include remote sensing products, ARGO buoy data, the Gulf Watch Alaska (GWA)-supported continuous measurements at GAK1, and climate indices including the PDO and the NPGO and atmospheric reanalysis products (e.g., ECMWF-ERA5 wind fields). The NGA LTER cruises will also provide a platform for the recovery of Slocum gliders operated by Danielson's lab. The gliders will expand our seasonal coverage of the NGA hydrography, provide near-

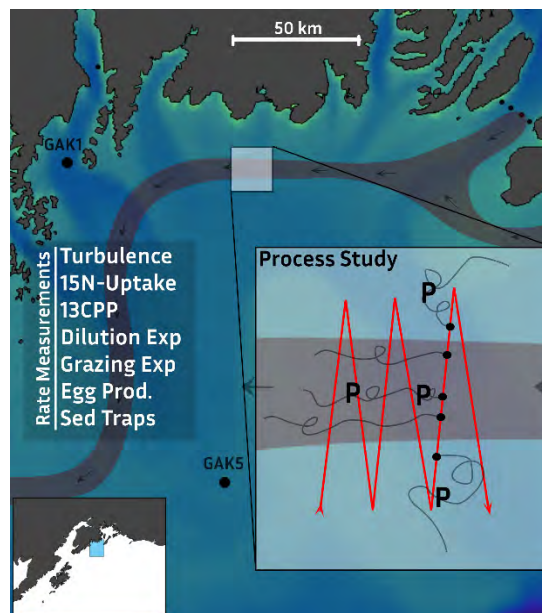


Fig. 16. Conceptual diagram of proposed frontal zone process study along ACC front. Included are DPI transects (red), drifter buoys (black) and track lines, and location of process studies (P). Additional CTD cast locations and shelfbreak front are not shown.

real time data from the winter into the spring bloom, and collect ancillary acoustics, optics and microstructure data.

2. *Towed Vehicle (Hopcroft)*: The DPI (see Facilities & Equipment supplemental for detailed description) is a 500m-rated undulating towed vehicle communicating to *Sikuliaq* via fiber-optics. The package includes numerous sensors for real-time high-resolution imaging of ecosystem physical, chemical, and biological properties. A smaller towed vehicle (Sea Sciences Acrobat) is available as a backup to the DPI that was used in the Phase-I plume mapping study and is outfitted with physical, chemical, and optical phytoplankton pigment sensors.

3. *Macronutrients and Iron (Aguilar-Islas)*: Vertical nutrient profiles and process study samples will be obtained from the regular CTD rosette packages (macronutrients only), and from a dedicated trace metal clean CTD rosette package (Aguilar-Islas et al. 2013) (iron and macronutrients) deployed using an Amsteel-Blue synthetic line and a dedicated winch and block. Underway surface sampling will be done with a towed trace-metal-clean surface sampler (Aguilar-Islas et al. 2016) outfitted with salinity sensor. Trace metal clean techniques utilized in the sampling, processing and analysis of all Fe samples will follow those approved standards (GEOTRACES, 2019). Filtered (0.2 μm and 0.02 μm) and unfiltered samples will be collected at stations to complete vertical profiles. Determination of all iron fractions by ICP-MS and assessment of organic iron binding ligands by CLE-CSV follows published protocols (Aguilar-Islas et al. 2013, 2016) as does macronutrient analysis (GO-SHIP Repeat Hydrography Nutrient Manual; Becker et al. 2020).

4. *Carbonate Chemistry (Hauri)*: Using EVOSTC leveraged funding, samples will be collected according to the best practices (Dickson et al. 2007) and analyzed for dissolved inorganic carbon (DIC), total alkalinity (TA) and pH (Aßmann et al. 2011, Seelmann et al. 2019). A CO₂ Seaglider (measures pCO₂, O₂, CTD, Chl-a, backscatter, and CDOM) will additionally complement the carbonate chemistry component at a high resolution as funding from outside sources allows.

5. *Organic Matter (Kelly)*: Water column samples for POC, PIC and DOC will be collected and analyzed using established protocols (Nakatsuka et al. 2004). Spatial distributions of particulate matter will be optically determined from the CTD-rosette mounted UVP6, LISST-DEEP, transmissometer, and fluorometer. The LISST DEEP targets small (2.5-500 μm) particles while the UVP6 images larger particles and plankton between 100 μm to 5 cm. These optically-derived particle distributions will be used to quantify lateral and vertical fluxes using regional circulation products, suspended particulate concentrations, and empirical parameterizations using size-specific settling velocities and carbon contents (e.g. Fender et al. 2019, Guidi et al. 2008) optimized over the course of this study.

Year-round time series of sinking particle fluxes will be assessed with a moored 24-bottle sediment trap (100 m depth) at the GEO mooring, while short-term deployments (~24 hours) of drifting sediment traps (Knauer et al., 1979) will provide contemporaneous measurements of export production at depths ranging from 40-200 m (Kelly et al. 2018, 2021). All trap cups will be poisoned with formalin brine, and samples will be filtered and analyzed for pigments, organic and inorganic C, N, P, and Si. Large volume *in situ* pumps (3 x McLane LVP) will be deployed on process studies to collect particles from larger volumes (hundreds of liters) than typically available and are suitable for elemental ratios (e.g., Stukel & Kelly 2019), including trace metals and omic analyses.

6. *Chlorophyll and primary production (Hennon & Kelly)*: Profiles of Chlorophyll-*a* (Chl-*a*) will be measured (acidification method; Parsons et al. 1984) at all stations, with size-fractionated Chl-*a* (20 μm pore-size PC filters) measured at select stations. Remote sensing of Chl-*a* (e.g., NASA's MODIS Aqua) will provide regional-scale context (Waite & Mueter 2013) and will be validated using continuous underway optical absorption and attenuation collected on each cruise (Burt et al. 2018; Lowin et al. in prep). Depth-integrated primary production will be measured during 24-h deckboard incubations using ¹³C-bicarbonate uptake (Hama et al. 1983, Imai 2002).

7. *Phytoplankton/Microzooplankton abundance, biomass and community composition (Hennon & Strom):*

Community composition samples will be collected primarily at intensive stations (Fig. 1) and during process studies. Microscopy and flow cytometry: formalin-fixed samples will be collected for inverted light microscopy (diatom and dinoflagellate identification); and glutaraldehyde-fixed samples for epifluorescence microscopy (nano- and picophytoplankton identification and enumeration; Strom et al. 2006) and analysis with a Guava 5ST flow cytometer. For morphological identification of microzooplankton, acid Lugol's fixation and inverted light microscopy will be used to identify, count and size all microzooplankton $\geq 15 \mu\text{m}$ using a semi-automated digitizing system (Strom et al. 2007, 2019) to yield abundance, biomass and composition. DNA analysis: genomic DNA and rRNA sequences from filtered seawater will be amplified using 18S V9 primers (Amaral-Zettler et al. 2009) to assay eukaryotic diversity and 16S V4 primers (806R: Apprill et al. 2015, 515F: Parada et al. 2015) to assay prokaryotic diversity. Co-occurrence network analysis (Fig. 13) will be performed on amplicon sequence variants using statistically significant Spearman rank correlations (> 0.7 , Bonferroni corrected p-value < 0.05) to assess potential microbial interactions in the system and how they differ over spatial temporal gradients.

8. *Meso/Macrozooplankton (Hopcroft, Lenz, Questel):* During daytime, zooplankton samples will be collected with a metered Quad net (25 cm). One pair (150 μm mesh) samples small, primarily early copepodid stages of calanoids (e.g., Coyle & Pinchuk 2003, 2005), while the second pair (0.05 mm mesh) samples nauplii, the smallest copepod stages, and larvaceans. Along the Seward Line, station work during night will use a 0.25- m^2 Hydrobios Multinet system with 500- μm mesh nets to assess large zooplankton and micronekton, such as euphausiids (important components in the diet of many fish, sea-birds and marine mammals). A 5 m^2 Methot net is run near-surface for 20 minutes to census large jellies during summer & fall (Cotea Islas & Hopcroft, in revision). For expediency, MID and KOD stations (now occupied only in spring) will be sampled at night with 60 cm diameter 0.5 mm mesh Bongo net. Zooplankton samples will be preserved (10% formalin), and analyzed to the lowest taxonomic category possible, including developmental stage. At process stations along the Seward Line, an additional Quadnet and multinet are taken for preservation in 95% ethanol for molecular studies and/or live sorting. Taxonomic processing builds off established methods (Coyle & Pinchuk 2005) adding measures of animal length, and prediction of weight from length to the protocol as done in Phase-I.

To examine functional redundancy, we will examine how species phenology and population size vary across stations and years using morphological and molecular species-specific PCR (Bucklin et al. 1998) for *Neocalanus* and *Pseudocalanus*, respectively. We have already developed species-specific primers for the four *Pseudocalanus* species in our region (Ershova et al. 2017), allowing us to separate species by simple gel electrophoresis, and will retrospectively examine samples spanning recent heatwave events.

9. *Fisheries (Cushing):* *Sikuliaq* has routinely collected and archived calibrated multi-frequency fisheries acoustics data (EK80) during Phase-I and an EK60 system is now installed for our annual fall cruise on the *Tigllax*. Beginning in Phase-II, in collaboration with researchers with Gulf Watch Alaska, a Ph.D. student will process a subset of these data (using Echoview) from the ship and the DPI, characterizing patterns of acoustical backscatter attributed to small pelagic fish and zooplankton. These patterns, and other zooplankton data (samples and DPI) will be related to foraging activities and distribution of seabirds (see next section). The student will compare acoustically measured prey-field characteristics to distributions of focal seabird species with differing diets and foraging modalities.

While this proposal cannot accommodate a traditional fisheries component, we anticipate continued collaboration with both NOAA and Alaska State fisheries scientists. NOAA Eco-FOCI fisheries surveys with associated oceanographic measurements are on-going from Kodiak westward to the Shumagin Islands since 1984. Eco-FOCI has biannual spring cruises (May/June) to assess larval fish distribution. During summer and/or fall NOAA also conducts assessment surveys for both demersal and pelagic species either annually or biannually throughout the coastal Gulf. Several biophysical moorings are maintained within our study area in support of those programs. Additional information on salmon returns and other upper trophic level populations is available annually via the Alaska Department of Fish and

Game (ADF&G). We routinely provide our Multinet drogue samples and one side of our Bongo net collections to NOAA for larval fish analysis from spring surveys.

10. Seabirds & Marine Mammals (Cushing & Stafford): Seabird observations (25-year time series with gaps in the mid-2000s) are conducted by USFWS with additional support from NGOs. The NGA sampling design provides an opportunity to examine seabird responses to seasonal and interannual variability and cross-shelf gradients of physical and biological parameters (Sousa 2011, Cushing et al. 2023). Spring cruises occur during the pre-breeding period, while summer cruises occur when breeding birds are provisioning their young. Fall cruises take place during a time when birds must prepare for harsh winter conditions or long migrations. Observations are made following a modified line-transect protocol (USFWS 2008) to estimate densities (birds km⁻²) of seabirds, while marine mammal observations are semiquantitative (occurrence data). Processed data are submitted to the North Pacific Pelagic Database.

Passive acoustic monitoring is an increasingly important tool for understanding habitat usage by marine mammals (Van Parijs et al. 2021) with underwater sound (Fig. 15d-f) recently designated as an Essential Ocean Variable. To better understand how vocalizing mammal species use NGA habitats and other aspects of the NGA soundscape, a hydrophone recording package has been deployed on the GEO mooring since 2019; a PhD student is already engaged in analysis of these recordings.

F. Modeling (Fiechter & Hill)

Modeling activities for Phase-II build on Phase-I efforts which focused on (1) implementing a biogeochemical model of intermediate complexity representing key NGA organisms and informed by field measurements, and (2) investigating the impact of river discharge on planktonic community structure. The modeling effort during Phase-II will complement and enhance field activities by providing long-term spatiotemporal context for the historical and future variability of the frontal processes that shape the NGA ecosystem mosaic, and by conducting sensitivity experiments to examine how planktonic species attributes and trophic redundancy may lead to ecosystem resilience in the highly dynamic frontal regions and habitats of the NGA.

1. Model Framework: The ocean circulation model is an implementation of the Regional Ocean Modeling System (ROMS), and the biogeochemical model coupled to it is a derivative of the North Pacific Ecosystem Model for Understanding Regional Oceanography (NEMURO) model reconfigured to account for the key planktonic organisms in the NGA region (called “NEMUGA”). ROMS is a hydrostatic, primitive equation model that employs terrain-following coordinates in the vertical, and orthogonal curvilinear coordinates in the horizontal. ROMS is specifically designed for regional applications and its advanced numerical algorithms and grid-structure make it well suited for modeling coastal regions characterized by complex bathymetry and coastlines (Shchepetkin & McWilliams 2005, Haidvogel et al. 2008). During Phase-I, we implemented ROMS for the NGA region with a horizontal resolution of 4.5 km and 50 vertical levels with stretching to increase resolution near the surface. The geographical extent was chosen to be sufficiently wide to resolve eddy activity along the shelfbreak and in the basin, yet sufficiently small to perform multi-decadal simulations at the relatively high-resolution needed to capture coastal dynamics associated with river discharge. Danielson et al. (2020) describe the linking of the Hill river runoff and the ROMS circulation model, thereby allowing our best high-resolution terrestrial discharge estimates to drive the coastal wall boundary condition of the ocean model. The original NEMURO was specifically developed to represent lower trophic level ecosystem processes in the Pacific and has been successfully implemented in the California Current (Chenillat et al. 2013, Fiechter et al. 2018), Gulf of Alaska (Fiechter & Moore 2009) and other regions of the North Pacific (Kishi et al. 2011). During Phase-I, we reconfigured NEMURO with NGA-specific functional groups and field-derived rates as described in Results of Prior Support (above).

2. Historical Simulation: The current configuration of the coupled ROMS-NEMUGA model was run in hindcast mode during Phase-I to produce a 28-year historical simulation at 4.5km horizontal resolution for 1993-2020 including (1) open ocean boundary forcing from the GLORYS global reanalysis for

physical variables and GLORYS-BGC hindcast for biogeochemical variables, (2) surface atmospheric forcing from the global ERA5 reanalysis, and (3) freshwater forcing at the coast from the hydrological model of Hill et al. (2015). Physical variability in the historical simulation was evaluated against satellite observations for sea surface height and temperature and against long-term in situ temperature and salinity measurements at GAK 1. Biogeochemical variability was evaluated against in situ and satellite observations for chlorophyll and existing measurements (including those collected during Phase-I) of nutrients, size-fractionated chlorophyll, microzooplankton, copepods, and euphausiids along the Seward Line. The model-data comparisons for biogeochemical variables were primarily focused on evaluating and improving the ability of the model to reproduce vertical and seasonal dynamics, although significant effort also went into understanding the mechanisms associated with planktonic biomass variability and trophic transfers on an interannual basis and contrasting anomalous years (i.e., low vs. high nitrate and cool vs. warm conditions, including the 2014-16 large marine heatwave) (Conte et al., in prep and Fig. 9).

3. Downscaled Climate Projections: During Phase-II, we will use the coupled ROMS-NEMUGA model to generate high-resolution (4.5 km) dynamically downscaled climate projections (2000-2100) for the NGA region. The effort will leverage on-going work to generate downscaled physical projections at ~10km resolution for the entire Northeast Pacific as part of a recently NSF-funded project (“Collaborative Research: Tradeoffs between phenology and geography constraints in response to climate change across species life cycles,” lead PI Cianelli; co-PI Fiechter). We will use NE Pacific downscaled projections to specify open ocean boundary conditions, river discharge and atmospheric forcing for the high-resolution NGA projections, and will augment the projections with NEMUGA’s biogeochemical fields. Downscaled climate projections will consist of a mini-ensemble of four earth system models (ESMs) from the Coupled Model Intercomparison Project Phase 6 (CMIP6) under the “middle-of-the-road” shared socioeconomic pathway (SSP2-4.5), a scenario with intermediate challenges to mitigation and adaptation (O’Neill et al., 2017). We focus on the SSP2-4.5 scenario because it reaches approximately 4.5 W m^{-2} radiative forcing by 2100, corresponding to ~2-3°C global warming, ranges that were recently suggested as most plausible future scenarios (Burgess et al. 2022). We plan to use four ESMs that best capture the range of uncertainties under SSP2.4-5 scenario, namely the Geophysical Fluid Dynamics Laboratory (GFDL) ES4M (Dunne et al., 2020), the Institut Pierre Simon Laplace (IPSL) CM6A-LR (Boucher, 2020), the Community Earth System Model Version 2 (CESM2) WACCM (Danabasoglu et al. 2020), and the U.K. Earth System Model (UKESM1) 0-LL (Sellar et al. 2020).

4. Modeling Tasks for Phase-II: The overarching objective for the numerical experiments in Phase-II is to explore frontal processes in the NGA region and their impact on nutrient exchange and habitat structuring for the planktonic community. Due to their highly dynamic nature, fronts are notoriously difficult to characterize based solely on in situ observations; therefore, the model will provide important spatiotemporal context to interpret field measurements. By implementing and analyzing high-resolution downscaled climate projections, we will also be able to determine how frontal processes will respond to future changes in river discharge and long-term warming. This information will be useful to understand whether observed responses during strongly anomalous conditions associated with changes in the strength or position of the ACC and Alaskan Stream are informative about future ecosystem states. Conversely, in situ physical and ecological measurement made across fronts during Phase-II will help refine model formulation (e.g., assess the need to increase horizontal resolution) to improve the ability of the model to reproduce small scale variations in planktonic responses across sharp environmental gradients. Specific modeling activities planned for Phase-II that contribute to our overarching objective are outlined below:

Year 1: (i) Generate high-resolution downscaled physical projections for the NGA, and (ii) Generate high-resolution downscaled biogeochemical projections for the NGA.

Years 2-3: (i) Examine processes controlling historical and future frontal dynamics in the NGA, (ii) Examine nutrient and plankton responses to frontal dynamics in the NGA, and (iii) Examine impacts of low frequency basin-scale variability on frontal dynamics in the NGA.

Years 4-5: (i) Examine how planktonic attributes (e.g., diapause, thermal responses, and mixotrophy) can lead to resilience in the NGA highly dynamic frontal environment, (ii) Examine how frontal dynamics in the NGA coincide with planktonic habitats controlled by bottom-up and top-down processes, and (iii) Examine how trophic redundancy and diversity may create ecosystem resilience in regions and habitats of the NGA.

The core NGA LTER modeling activities will also synergize with other modeling efforts currently ongoing in the Gulf of Alaska. These include parallel studies aimed at (i) understanding the historical and future drivers of oxygen and inorganic carbon chemistry (C. Hauri, pers. comm.), (ii) investigating the effect of the North Pacific heatwave on groundfish productivity and exploring future fisheries management strategies (A. Rovellini, pers. comm.), and (iii) determining how the occurrence and duration of abnormal events affect small pelagic fishes and marine food web processes (B. Diaz, pers. comm.).

V. BROADER IMPACTS

V.A. EDUCATION AND OUTREACH ACTIVITIES. As we move into the next stage of the NGA Education program, we strive to build respectful and reciprocal relationships, especially locally. We know that science in the Gulf of Alaska should serve and be in open communication with the residents of coastal communities, and especially with the Native villages and Tribes of the region. We will focus on fostering connection to place and making links between the NGA science and learners' own knowledge, culture, and experiences. The Report of the Working Group on Culturally Responsive Science Outreach and Engagement (2019) requests more student-centered, culturally responsive learning opportunities where students can engage meaningfully in science learning and practices. The long-term nature and ecological focus of LTER is especially well-suited for cultivating and sustaining these sorts of relationships and learning experiences. Therefore, our next steps for NGA Schoolyard Ecology will focus primarily on serving youth living along the coast of the NGA, with an emphasis on rural and remote schools (Fig. 17); we will distribute materials created for local participants more broadly through our website, social media, the LTER Network education resources, and various marine education listservs. We will deepen local partnerships and increase statewide impact while continuing to reach more audiences beyond the state.



Fig. 17. Students and teachers in the village of Tatitlek collect a plankton sample during a school visit from the NGA education team.

A. *Schoolyard Ecology.* Phase-II programs will build on our existing collaboration with the Chugach School District (CSD), providing multi-day visits and curricular support to K-12 schools in the villages of Tatitlek and Chenega Bay and the town of Whitter (Figs. 1, 17). We will continue to develop participatory, place-based, culturally responsive activities for students, with guidance from the CSD, Chugach Regional Resources Commission (CRRC), and Chugachmiut Heritage Preservation (CHP) as to what topics and approaches are most relevant to their learners. We will offer similar activities to other schools in the region, leveraging existing funding through two grants associated with NGA (PhytoCLAS and Zooplankton), as well as the CORaL Network. These efforts will be led by the Center for Alaskan Coastal Studies (CACS).

The Alaska Native Science and Engineering Program (ANSEP) serves as a bridge for connecting Alaskan students with NGA. This makes NGA a perfect case for ANSEP students from around the state to learn about oceanography, marine ecology, and careers in these fields. We initiated engagement activities with ANSEP in 2021 and will continue to facilitate activities for ANSEP middle school academy students at the Anchorage campus, developing additional curricula and materials that take better advantage of seasonal phenomena as anchor points for learning about NGA science and science practices. Half-day programs will reach up to 550 students per year, with opportunities for NGA graduate students to assist and build their education skills. All materials will be made available more broadly through our website for use by other educators.

In addition to the direct activities above, CACS facilitates multi-day field trips and boat-based field trips for 1,000+ students each year. Participating classes come from around the state, and grades 4-12 are most frequently served. These field trips focus on Alaska coastal ecology and oceanography, including plankton collection and labs. NGA will provide specific training to CACS educators on the science ideas, practices, and equipment used in NGA as well as knowledge that is emerging from both the long-term time series and process studies.

B. *Teachers and Informal Educators.* NGA will continue our partnership with the NOAA Teacher at Sea (TAS) program to host 2-3 educators per year on NGA research cruises. TAS recruits and selects the teachers, with input from NGA, and provides structure and support for the teacher throughout their research experiences. NGA will make 1-2 additional berths available per year for Teachers at Sea and/or science communicators, artists, or knowledge bearers from the local region in an ‘at-sea residence’. Participants are expected to create a lesson plan, presentation, work of art, or media product that helps tell the story of NGA, with guidance provided by Gavenus and teacher products made available through the TAS website. All participants receive pre-cruise training as well as follow-up support as they return to their classroom and/or community.

C. *Undergraduate education.* The NGA REU program will continue as described in Results of Prior, with cohorts every other year including at least 1 student with Alaska Native heritage or ties to the region. These cohorts will align with the summer cruises with available berthing to ensure field participation. NGA has developed a structured REU program that includes weekly activities, time for independent research projects, and formal presentation of results. Feedback will be solicited from students mid-program, just prior to and several months after completion. UAF PIs also leverage NGA data and infrastructure to engage their undergraduates in research through partnerships with URSA (Undergraduate Research and Scholarly Activity), which provides funds and mentoring support.

We will also partner with the Bonanza Creek (BNZ) LTER summer Climate Research Intensive (see letter of support). This program for first-generation college students includes 7-8 Climate Scholars each from the University of Alaska Fairbanks and Santa Clara Community College. Twice during Phase-II, participants in the BNZ LTER research intensive will travel from Fairbanks to Homer and Kachemak Bay for a marine field study experience. They will stay at either the NOAA/UAF Kasitsna Bay Laboratory or the Peterson Bay Field Station operated by CACS. During their 5-6 days on the coast, students will learn

from NGA researchers and educators and develop their own marine science research projects, culminating in a community presentation in Homer or Seldovia.

D. Graduate Education. We request funds to support three MS and one PhD student during Phase-II, and will include additional students with internal UAF support. As well, UAF is offering a tuition match for each LTER-supported graduate student, and we anticipate additional involvement from UCSC and UHawaii students, in part through leveraged projects. In addition to the above, cruises will continue to host graduate volunteers, plus students conducting their own research.

E. Tribal Governments. CRRC is the environment and subsistence regional organization for the seven Tribes of the Chugach region (Prince William Sound and coastal Kenai Peninsula). NGA researchers and educators will attend quarterly or annual meetings of the CRRC, when invited and appropriate. This has been identified with CRRC as a good step. Sometimes participation in these meetings will simply be to listen, and other times researchers may have the opportunity to present about the overall NGA or provide updates. In addition, we expect that new opportunities will emerge for community meetings and dialogues through the CORaL Network (see Collaborations, below), with whom we will work to identify the best format and approach for these events.

F. General Public. The PIs regularly give presentations in communities throughout Alaska regarding their research, including findings from the Seward Line program. The Alaska Marine Science symposium is regularly attended by the public as well as by agency and university members. NGA researchers often attend and participate with community members in the Kodiak Science Conference, Kachemak Bay Science Conference, and Prince William Sound Natural History Symposium. The datasets generated under NGA will be accessible through intuitive visualizations on NGA and AOOS websites (see Data Management Plan).

Public radio is a crucial and well-enjoyed staple of coastal Alaska. The NGA is utilizing an existing “Kachemak Currents” radio series produced by the CACS and airing on local public radio in the Seward, Homer, and Kachemak Bay areas. These radio segments are four minutes long and focus on natural history in the area and seasonal phenomena. We will continue to create approximately monthly segments with an NGA focus. NGA graduate students and other personnel will be encouraged to write these pieces, with guidance from CACS educators.

Leveraging funding from an NSF Careers Award (#1654663), we are working with the Alaska Sea Life Center (ASLC) to design an exhibit that shares NGA science. Our mutual goal is to create something that is immersive and interactive, with a component that allows members of the public to meaningfully contribute to science, helping to democratize who gets to be a scientist. Annual visitation to the ASLC is anticipated to be approximately 150,000 as visitor numbers recover from the impacts of the pandemic.

V.B. APPLICATIONS OF RESEARCH TO MANAGEMENT

The NGA contributes to management for a variety of state and federal agencies. Our most prominent contributions are to the NOAA Ecosystem Status reports published annually in conjunction with the North Pacific Fisheries Management Council (Ferriss & Zador 2020, 2021, 2022). The NGA contributes to four sections of these reports that inform setting fisheries quotas for the Gulf of Alaska annually. NGA participates in quarterly meetings leading up to the final Report. The NGA also collects zooplankton samples and provides associated abiotic and biotic data each spring used by NOAA’s ECOFOCI larval fish assessment. These are critical data for the years between their biannual surveys in the NGA. Passive acoustic work funded by the National Parks Service is being used to assess both habitat usage by marine mammals, and to monitor anthropogenic noise in the NGA. Our seabird component provides the largest single source of data on the NGA shelf available to the Fish and Wildlife Service for assessing the state of this trophic component, notably including the status of several “species of concern” (Fig. 18). In leveraged research, post-doc Dias contributes to food web modeling focused on the non-recovery of PWS herring following their 1990s fishery collapse, while partnering with complementary food-web models at NOAA. Finally, local communities have great interest in the results of Hennon’s phytoplankton research

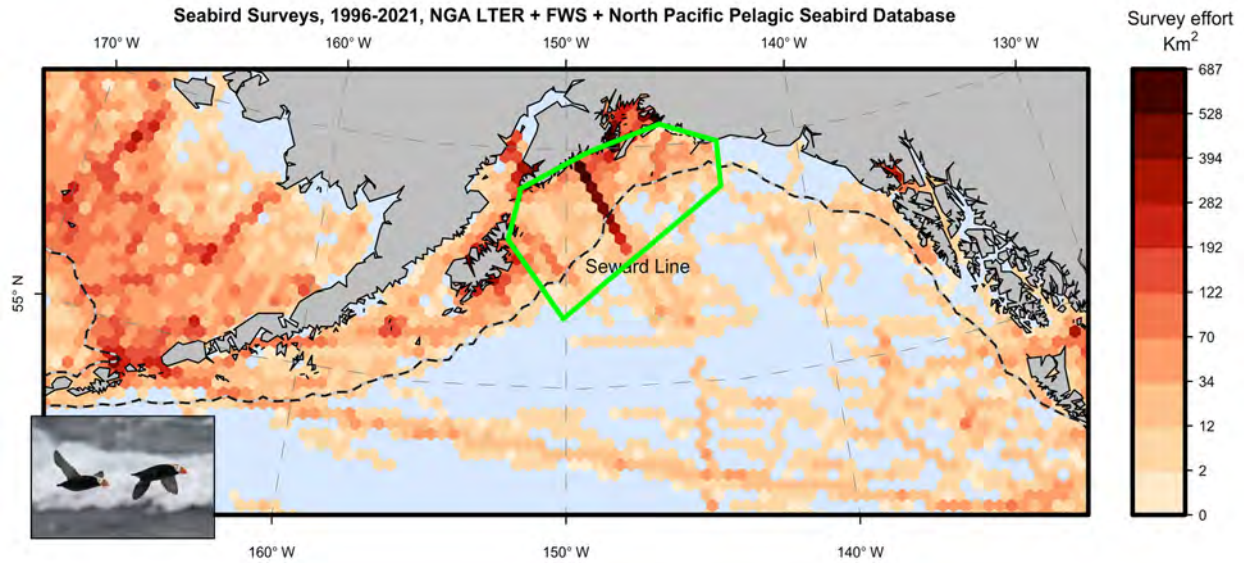


Fig. 18. The NGA-LTER provides one of the largest sources of at-sea data that is available to manage seabirds in the NGA region. Over 85% of the observation inside our study domain (green box) come from Seward Line / LTER surveys and they are the only significant source of ongoing contemporary observations for the wider NGA shelf region.

because it helps detect Harmful Algal Blooms that have become of increasing concern in NGA waters. Similar local interest occurs regarding Hauri's contributions to the Alaska Ocean Acidification Network.

VI. COLLABORATIONS AND RELATED RESEARCH

VI.A. LTER PROGRAM INTEGRATION. NGA personnel are involved several recently funded LNO synthesis proposals, including one on Pelagic Community Structure with the three other pelagic marine sites (CCE, PAL, NES), one on Marine Consumer Nutrient Dynamics, and a SPARC project spanning the marine-coastal-terrestrial spectrum (Producers, Consumers, and Disturbance). More broadly, NGA maintains active involvement with other LTERs as witnessed by two recent collaborative publications (Harms et al. 2021; Ducklow et al. 2022). NGA actively participated in both 2018 and 2022 All-Scientists Meetings in Pacific Grove with numerous investigators, staff, post-docs and students attending. NGA scientist Kelly was a CCE graduate student and maintains active collaborations with CCE through inter-operable carbon export and bio-optic measurements, while Strom collaborates with NES scientists on molecular characterization of protist communities. In 2022, a Beaufort Lagoon Ecosystems (BLE) graduate student participated in the NGA fall cruise and the two sites will partner in Phase-II to build upon this successful test of concept. We have invited the Arctic (ARC) and Bonanza (BNZ) LTERs to participate as well, striving to provide networking opportunities and diverse field experiences for students across Alaska LTERs. The NGA LTER is one of the sites included in the recently submitted NSF proposal "RaMP: Long Term Networked Ecological Research for the Future (LT-NERF)". The proposal targets post-baccalaureate environmental biologists who have had few or no undergraduate research opportunities. If successful, fellows will promote further synthesis with other sites, enhance our education activities, and provide another opportunity to increase diversity. Finally, E&O opportunities are coordinated between the Beaufort Lagoons (BLE) through our shared E&O PI, Gavenus, who is also participating in an E&O coordination effort across all 4 Alaska LTER sites.

VI.B. ALASKA REGIONAL EFFORTS. Regional partners provide leveraged support to maintain long term environmental monitoring programs (e.g., GAK1 & GEO mooring, Seward Line – see below). Tight integration of NGA with regional partners directly benefits i) science objectives through additional resource allocations; ii) student opportunities through networking and ancillary dataset access; and iii)

public discourse through alignment and coordination of outreach efforts. Hopcroft, Danielson, Strom and Kuletz have contributed variously to four recent synthetic manuscripts on the NGA region (Litzow et al., Suryan et al., Arimitsu et al., Danielson et al.) looking at long-term change and the impact of the recent North Pacific marine heatwave.

NGA scientists also provide regional leadership. Hopcroft serves on the science advisory committee of Gulf Watch Alaska. Aguilar-Islas serves on the scientific advisory committee of the Prince William Sound Regional Citizens' Advisory Council. Danielson serves on the ASLC's Scientific Advisory Committee, and works closely with the National Park Service (NPS) in coastal waters from Glacier Bay (Southeast Alaska) to Cook Inlet. The NPS awarded Danielson funding to mentor a PhD student whose work will bridge NGA sampling near the Copper River and NPS sampling near the tidewater glacier in Disenchantment Bay (just upstream of the NGA shelf).

NGA is actively engaged with regional Tribal and community partners. Tribal communities on the shores of the NGA comprise a mosaic of linguistic and cultural diversity, with a variety of governance structures and entities. Therefore, our engagement strategy must be flexible and responsive. Efforts to work collaboratively with local communities will be bolstered by the newly established CORaL (Community-Organized Restoration and Learning) Network where Gavenus has a key role. Funded by EVOSTC, the CORaL Network (Fig. 19) is designed to leverage and build the capacity of existing resources within the *Exxon Valdez* Oil Spill-impacted region to ensure that current scientific information, skills, and activities are publicly accessible and serve ongoing needs as identified by local communities. Core partners in the CORaL Network include the ASLC, Alaska Sea Grant, Alutiiq Museum and Archaeological Repository (AMAR), CACS, CRRC, and PWS Science Center. CHP also has a growing role in the network. CRRC and CHP are regional Tribal entities, serving and representing the seven Tribes of the Chugach region (coastal Kenai Peninsula and Prince William Sound). AMAR was created and is governed by the Tribes of the Kodiak Archipelago. These three entities function as important bridges to Alaska Native communities and especially the smaller, extremely remote villages. NGA researchers and educators will be invited by the CORaL Network to attend trainings on cultural protocols, local governance and history, and cultural humility; to participate in community and regional meetings and other opportunities to share science and learn together; to facilitate opportunities for young adults to participate in research activities; and to facilitate place-based marine science learning opportunities through local schools and informal settings. Additionally, NGA is a committed partner with the UAF Tamamta ("All Of Us") program, whose goal is to support Alaska Native people and communities in place-based co-production of environmental knowledge (Aguilar-Islas, Hennon, Danielson, and Hauri are Tamamta Faculty).

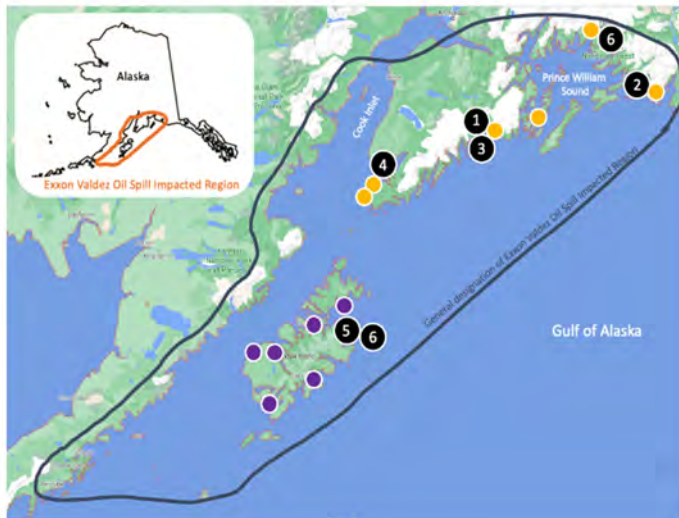


Fig. 19. Locations of key organizations leading the CORaL Network: 1) ASLC (Seward), 2) PWS Science Center (Cordova), 3) CRRC (Seward), 4) CACS (Homer), 5) AMAR (Kodiak), and 6) Alaska Sea Grant (Kodiak and Valdez). Yellow dots indicate communities served and represented by Chugach Regional Resources Commission: Eyak Tribe (Cordova), Tatitlek, Valdez Tribe, Chenega, Qutekcak Tribe (Seward), Port Graham, and Nanwalek. Purple dots indicate communities for which the Alutiiq Museum and Archaeological Repository will serve as a liaison: Akhiok, Chiniak, Karluk, Larsen Bay, Old Harbor, Ouzinkie, and Port Lions.

VI.C. RELATED RESEARCH. Other research awards during Phase-I, totaling >\$7M, contribute to the breadth and depth of observations within this biome. Strom's study of mixotrophy has provided evidence on how nutritional plasticity helps confer resilience to the lower trophic levels. Kelly is adding important dimensions to our broadscale understanding of primary production through a combination of in situ optics and satellite-based observations and was awarded an NSF OCE Postdoctoral Research Fellowship to add silica-cycling measurements to the NGA. Hennon is focused on understanding the role of specific phytoplankton groups and microbial interactions within the NGA. Hopcroft has quantified the unexpected biomass of large jellies in NGA surface waters using a Methot Trawl net. Work on zooplankton transcriptomics (Lenz & Hopcroft) is providing insights into the physiological ecology of the spring-dominant *Neocalanus* copepods, including responses to food limitation and diapause. Work on zooplankton genetics (Questel) is elucidating the biodiversity present in the Gulf and paving the way for more extensive use of metabarcoding for quantifying zooplankton community composition. Funding for deep-water exploration by NOAA OER (Hopcroft & Questel) has provided insights into the composition of deep-water. Finally, additional modeling and sampling activities (Hauri et al.) are investigating trajectories in ocean acidification, thereby helping to reveal whether a broader suite of parameters may be valuable to the current NGA observational and modeling frameworks.

VII. SUPPLEMENTAL SUPPORT

NGA LTER measurements are built upon historical support by a consortium of funders as described in Site History (above). The consortium still contributes ~\$500K annually but activities and personnel have increased significantly through LTER support. EVOSTC also continues to support the GAK1 mooring (~\$150K annually). A long-term commitment has been expressed by AOOS & NPRB, while EVOSTC funding is uncertain after early 2027 (NGA priority setting was described in our "Response to Mid-Term Review" section, above). During Phase-I, several investigators leveraged NGA infrastructure to acquire new assets. With matching support from partners, the Murdock Foundation funded the GEO mooring (~\$700K) and DPI (~\$750K) undulating platform (See Facilities & Equipment Supplement); these are greatly enriching our suite of observations and have reshaped how we frame and address research questions including those in the present proposal. Similarly, support of autonomous glider technology from AOOS and NOAA (~\$2.5M) and glider technological development for pCO₂ studies (~\$1.2M) is providing broad-scale observation for periods outside those sampled by oceanographic cruises.

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Author & title in bold: Top Ten publication

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