Marine Pelagic Ecosystem Responses to Climate Variability and Change

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The marine coastal region makes up just 10% of the total area of the global ocean but contributes nearly 20% of its total primary production and over 80% of fisheries landings. Unicellular phytoplankton dominate primary production. Climate variability has had impacts on various marine ecosystems, but most sites are just approaching the age at which ecological responses to longer term, unidirectional climate trends might be distinguished. All five marine pelagic sites in the US Long Term Ecological Research (LTER) network are experiencing warming trends in surface air temperature. The marine physical system is responding at all sites with increasing mixed layer temperatures and decreasing depth and with declining sea ice cover at the two polar sites. Their ecological responses are more varied. Some sites show multiple population or ecosystem changes, whereas, at others, changes have not been detected, either because more time is needed or because they are not being measured.

Keywords: oceanography, coastal ecosystems, climate change, ecology, marine biology

The marine pelagic biome covers 70% of the Earth's surface and accounts for about half the global primary productivity (Field et al. 1998). Coastal and continental margin ocean ecosystems at the edge of the marine realm command a disproportionate share of the primary productivity relative to their share of total ocean area, owing to their shallow depth and a variety of mechanisms enhancing nutrient inputs and light availability (Liu et al. 2000). In pelagic ecosystems, primary production is carried out by unicellular phytoplankton that, despite rapid turnover times of just a few days, comprise less than 1% of the global photosynthetic biomass because of efficient coupling with herbivores. Ocean primary production is about half of the global total in spite of the small producer stock. This lower trophic level system, in turn, supports high secondary production and top predators, including fisheries harvests. Coastal fisheries comprise approximately 80% of the global total.

As we show below, marine coastal ecosystems respond to climate and environmental forcings over a wide range of scales, extending from seasonal and annual and interannual to subdecadal and multidecadal. The five marine pelagic sites of the US Long Term Ecological Research (LTER) Network considered here (https://lternet.edu/site and below) are all experiencing long-term climate warming (figure 1, supplemental figures S1–S3). Are the plankton-based ecosystems at the five sites responding similarly or differently to this common forcing? Sorting out this complex structure of ecosystem variability is simply not possible without an organized suite of long-term observations and experiments embedded in a network of individual local to regional sites (Likens 1988). Sustaining such observations is the main goal of the LTER program.

The present article is part of a special issue that marks the 40th anniversary of the US National Science Foundation's LTER program. The timing is appropriate as longer term variability and secular trends may become detectable in four or five decades. The companion papers in this special issue highlight how LTER addresses the climate responses of forest and fresh water, dry lands and marine land-margin ecosystem sites to climate change, highlighting LTER research.

The sites. There are eleven marine sites in the US LTER Network. Six are land-margin ecosystems, each with strong terrestrial influence and a dominant benthic or macrophytic primary producer (Reed et al. 2022, this issue). The phytoplankton-based water column ecosystems at the other five marine sites are the subject of this article. The Beaufort Lagoons site is exceptional in this context: It is a very shallow (approximately 3 meters [m] deep) system with a dominant benthic ecosystem underlying a water column plankton system influenced by sea ice, such as the Palmer Station LTER system.

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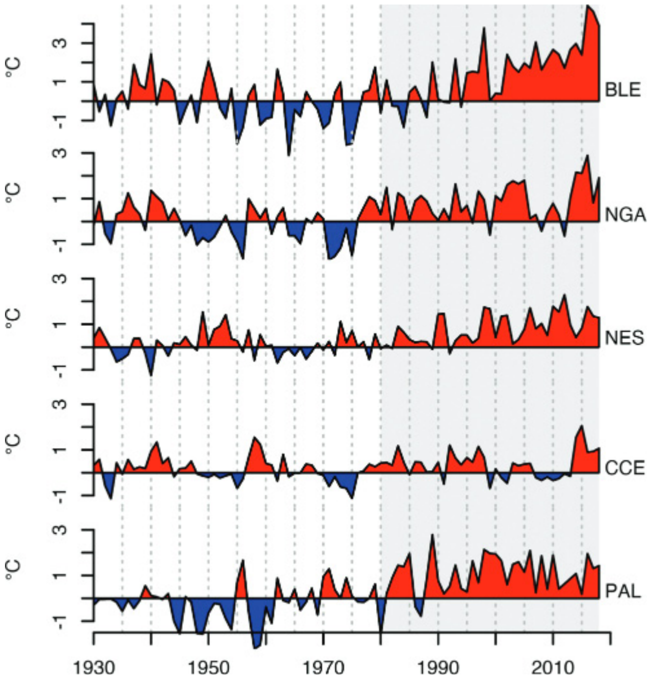

Figure 1. Annual surface air temperature anomalies (relative to 1951–1980) at the five coastal marine LTER sites, 1930–2019. These data are from the GISS Surface Temperature Analysis ver. 4 (GISTEMP v4). Monthly average temperature anomalies based on the 1951–1980 period were annually averaged for plotting. Note the near absence of negative anomalies after approximately 1980.

The five marine planktonic LTER sites joined the LTER Network, starting with Palmer Station in 1990 and the California Current Ecosystem in 2014 and continuing with the addition of Beaufort Lagoons, the Northeast US Shelf, and the Northern Gulf of Alaska in 2017 (https://lternet.edu/site; table 1). They all brought legacy data sets including important series of observations on climate change and ecosystem response (supplemental figures S4–S6). They are all continental margin ocean ecosystems, fundamentally affected by coastal circulation and mixing (figure 2). They all support productive fisheries (see the final section). Within this broad categorization, the sites range widely in their physical environment, geography, bathymetry, and terrestrial influences. The two polar sites (Palmer Station and Beaufort Lagoons) are dominated by seasonal sea ice cover but differ by thousands of meters in depth. In both sites, seasonal light availability limits primary production because of seasonal darkness, sea ice cover and deep mixing. The Northeast US Shelf and the Northern Gulf of Alaska are both continental shelf sites that extend into oceanic deep water. Both of these sites are influenced by river runoff and glacier melting. All five sites demonstrate complex interactions with coastal and open ocean processes. The California Current ecosystem is an eastern boundary current system with strong coastal upwelling. It is virtually an open ocean site, with a narrow shelf and minor terrestrial inputs. The four deepwater sites are predominantly pelagic ecosystems. The shallow Beaufort Lagoons site is dominated by a highly productive benthic community with avian predators. The continental shelves of Antarctica are very deep (approximately 500 m) compared with the global mean of approximately 100 m as a result of the great weight of the polar ice cap. The great depth plus iceberg scouring and coastal margin fast ice limit benthic influences.

Terrestrial freshwater inputs vary, including insignificant amounts in the California Current ecosystem, glacial meltwater with little associated organic matter in Alaska and Antarctica, and massive erosion-induced sediment and nutrient inputs from high latitude rivers and permafrost thaw in the Arctic (Beaufort Lagoons). The Northeast US Shelf site receives fresh water from Arctic sources (Karchner et al. 2005, Greene et al. 2013), as well as glacial meltwater originating from Greenland (Proshutinsky et al. 2015). At the Northern Gulf of Alaska site, the runoff of fresh water stems from a limited number of discrete point-source rivers (e.g., the Copper, Kenai, and Susitna rivers) and an extensive network of small flows that contribute about half of the total terrestrial discharge (Royer 1982). Together, these rivers represent one of the largest freshwater inputs to the world ocean (700–1000 cubic kilometers per year; Royer et al. 1983, Wang et al. 2004, Hill et al. 2015).

Approach. An important objective of the LTER marine pelagic sites is to gain a better understanding of how plankton ecosystems respond to climate variability and climate change, as part of a broader effort to analyze responses to climate change across all the LTER sites (Jones and Driscoll 2022, this issue). In the present article, we follow a conceptual model in which climate forcings are modulated through the geophysical environment to elicit ecosystem responses, including critical transitions or regime changes: from climate to ocean physical processes to ecosystems and ecosystem services (figure 2). This simple stimulus–response model has been useful in previous syntheses of climate variability and ecosystem response (Greenland et al. 2003). In the following sections, we address the physical and ecological responses at each site, with a summary and synthesis of the similarities and differences among them. The data supporting our findings are available in the LTER data portal of the Environmental Data Initiative (https://portal.edirepository.org/nis/home.jsp). Finally, we speculate on how their ecosystem services such as fisheries might be responding to a combination of climate-forced ecological change and overexploitation.

Physical and ecological responses to climate variability and climate change

Climate variability is manifested as irregular, interannual to decadal and longer period oscillations (climate modes; figure 3 and table 2) in atmospheric pressure and attendant variations in prevailing winds and associated meteorological conditions, such as the El Niño–Southern Oscillation

Table 1. Coastal marine LTER sites arranged by increasing latitude, south to north.

Site	Started	Ecosystem type	Latitude	Longitude	Fishery	Depth (in meters)	Air temperature (in degrees Celsius)	Water temperature (in degrees Celsius)
California Current Ecosystem	2004	Ocean pelagic	34.0 N	121 W	California market squid, California spiny lobster, northern anchovy, Pacific sardine	20–4500	10–25	13–23
Northeast US Shelf	2017	Continental shelf	40.7 N	70.9 W	Cod, flounder, scallop, lobster	50–3000	–3–26	4–22
Northern Gulf of Alaska	2017	Subpolar shelf and fjord	57.0 N	148.7 W	Pollack, rockfish, Halibut	20–4400	–15–25	3–17
Palmer	1992	Marginal ice zone	64.75 S	64.1 W	Krill	75–4000	–6.8–2.3	–1.8–4
Beaufort Lagoons	2017	Polar estuary including benthic	71.3 N	156.8 W	Seal, whales (indigenous fishers)	0–8	–28–8	–2–12

(ENSO) or the high-pressure zone over Antarctica (the Southern Annular Mode). The climate modes cause the ocean to warm and cool and increase or decrease mixing and stratification. The effects of these basin scale climate modes on physical drivers of ecosystem structure and function provide clues to how ecosystems will respond to longer term climate change. All five of the pelagic sites respond to interannual climate forcings at a range of scales (figure 3). The major climate modes likely affect all terrestrial and marine LTER sites (e.g., Hudson et al. 2022, this issue).

Coupled ocean–atmosphere models suggest that, with continued climate warming, increasing warming and freshening of the upper ocean will lead to stronger water column stratification, increased light availability averaged over the mixed layer, and declining mixing rates and nutrient supply, ultimately affecting primary productivity and food web dynamics (Bopp et al. 2001, Bahl et al. 2020, Elsworth et al. 2020, Kwiatkowski et al. 2020). In contrast, declining sea ice will decrease stratification, with simultaneous competing effects on light and nutrients.

Physical and ecosystem responses to climate forcings are superimposed on higher frequency variability, complicating trend detection and characterization. In many cases seasonal variability and interannual variations in ecosystem components may be well characterized but observations have not been carried out long enough to link the changes to longer-period climate variations. This point was elegantly illustrated in Magnuson (1990), which addressed the invisible present in ecology, which has been reinforced by a recent cross-LTER site synthesis (Rastetter et al. 2021). Model experiments suggest that it can take decades to more than 100 years to statistically confirm ecological trends (McKinley et al. 2016, Henson et al. 2018), depending on the variance of the response variables, although shorter-term changes have been reported (Litzow et al. 2020). To put these points in perspective, few ocean time series extend beyond 30 years (O'Brien et al. 2016), which is probably insufficient for detection of climate trends. Notably, the California Cooperative Oceanic Fisheries Investigations program (CalCOFI) underlying the California Current ecosystem (figure 4) and legacy observations in the Northeast US Shelf extend beyond 70 years (figure 5). Although observations on Adélie penguins near Palmer Station, in Antarctica, started in 1975, totaling nearly five decades (figure 6e), the expanded program of supporting hydrological and food web observations only started in 1992. The Northern Gulf of Alaska site has legacy physical observations going back 50 years, but the current biological time series is only 25 years long (figure 7). The Beaufort Lagoons site started in 2017 with approximately 40 years of legacy data on meteorology and sea ice loss (supplemental figure S6).

The impacts of short-term (seasonal) meteorological forcing of mixed layer dynamics, convection, and upwelling on ocean biology are relatively well characterized and have been represented in ocean models for many decades (Sverdrup 1953). Vertical mixing brings nutrients from deeper water into the illuminated euphotic zone but also mixes phytoplankton down into the dark subsurface waters. Other physical forcing mechanisms influencing the rates of production include oceanic fronts, fresh water, and sediment inputs, sea ice melting, alongshore coastal currents, shelf–slope exchange mechanisms, mesoscale eddies, coastal up- and downwelling, cross-shelf transport, turbulence, and stratification (Beardsley et al. 1977, Linder and Gawarkiewicz 1998, Robinson et al. 2004, Shearman and Lentz 2004, Fratantoni and Pickart 2007, Stukel et al. 2017). We are just beginning to understand how such physical perturbations influence

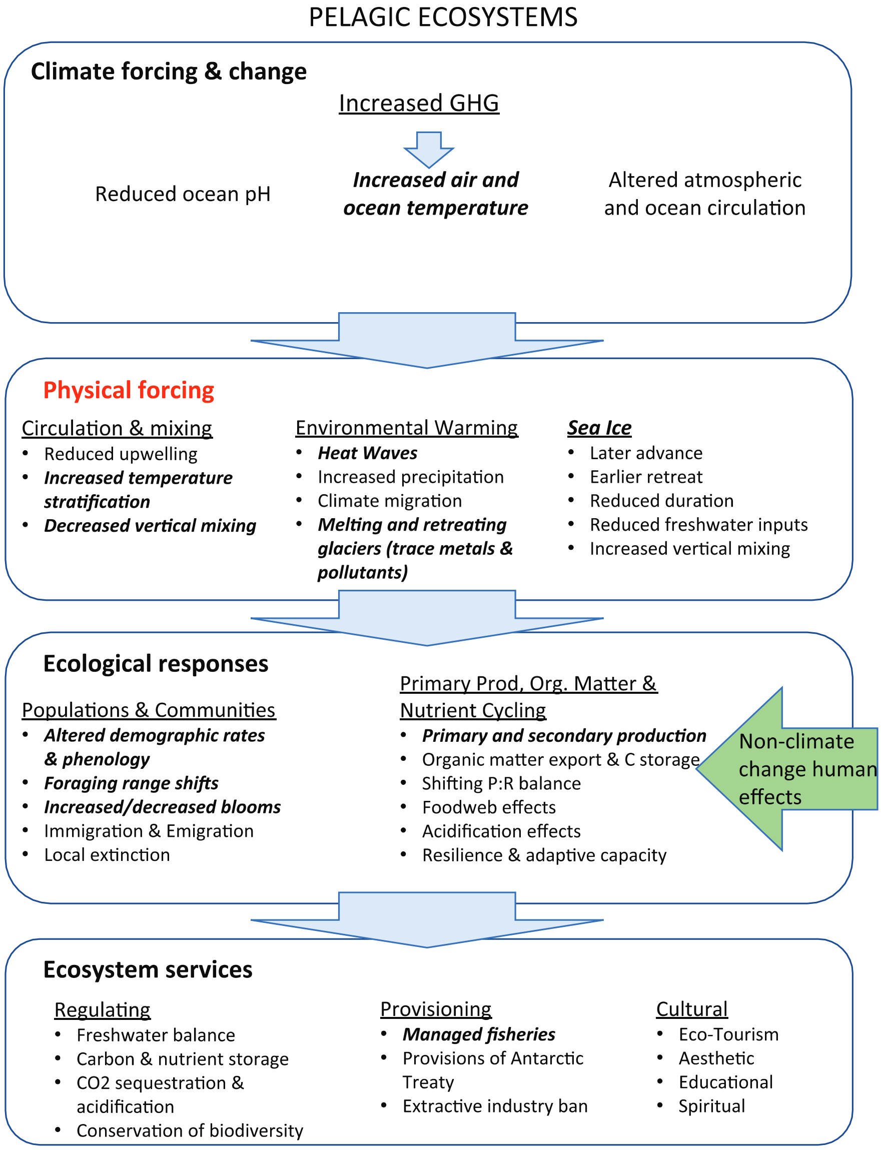

Figure 2. Conceptual diagram showing how marine physical processes respond to climate variability and change and how processes in marine ecosystems respond indirectly to climate forcings as modulated the physical system. Environmental forcings and ecological responses are the main focus of this article. Coastal fisheries are presented as an example of the ecosystem services that are affected by climate forcings. Major areas of focus in this article are in bold italics. Each of the four groups of LTER sites has a version of this diagram. Note that, in many cases, the signs of trends are established for climate and physical variables but not for ecological responses.

plankton trophodynamics and other ecosystem processes; the ecological responses to physical forcing can be highly nonlinear.

The impacts of climate variability on ocean ecosystems may be direct, because organisms physiology respond to increased temperatures, salinity, or other factors (figure 2; Reed et al. 2022, this issue). But in addition, climate variability drives physical changes in the environment that ultimately drive increases or decreases in primary production. Such changes at the base of food webs are linked to bottom-up responses by phytoplankton and small grazers and can be passed to upper trophic levels. In contrast, the responses to climate variability by top predators (marine mammals, fish, seabirds) can trigger top-down responses, such as trophic cascades, affecting intermediate trophic links such as macrozooplankton and, in turn, phytoplankton at the base of the food web. Top-down cascades in response to climate variability have not been conclusively identified at the LTER sites because of time-series duration, as well as other confounding effects (e.g., commercial harvests). Evidence for conditional top-down control has been found in the California Current ecosystem (Lindegren et al. 2017). Wasp-waist dynamics have been suggested to be particularly important in coastal upwelling ecosystems, where a very high biomass of intermediate trophic levels such as small pelagic fishes can simultaneously exercise top-down control on their prey and bottom-up control on their predators (Cury et al. 2000). Large-scale changes in the balance between pelagic and benthic systems have also occurred (Grebmeier et al. 2006 and see the Beaufort Lagoons section below).

In each section below, we move from physical to biological systems; from lower to higher trophic levels; and from smaller, short-lived organisms to larger, longer-lived species. Influences at all of these levels can cause responses to climate variability. Only a few fundamental variables are needed to characterize physical oceanographic systems (temperature, salinity, and velocity). In contrast, seemingly countless variables are required to characterize biological systems ranging from their evolutionary histories, genomic compositions, and cellular physiology to life histories, behavior, population dynamics, and ecology. Therefore, in moving from describing physical to describing ecological responses to climate variability, we move from areas of greater to lesser certainty in our synthesis. Similarly, uncertainty increases as our focus moves from lower to higher trophic levels. Marine food webs typically include smaller (microscopic) and larger organisms with generation times (life histories) ranging from hours to decades, respectively. The responses of different groups of organisms to environmental changes and climate forcing are likely related to the time scales of both the forcings and the life histories of the organisms (Hsieh and Ohman 2006, Bestelmeyer et al. 2012), but abrupt changes commonly occur across scales (Ratajczak et al. 2018).

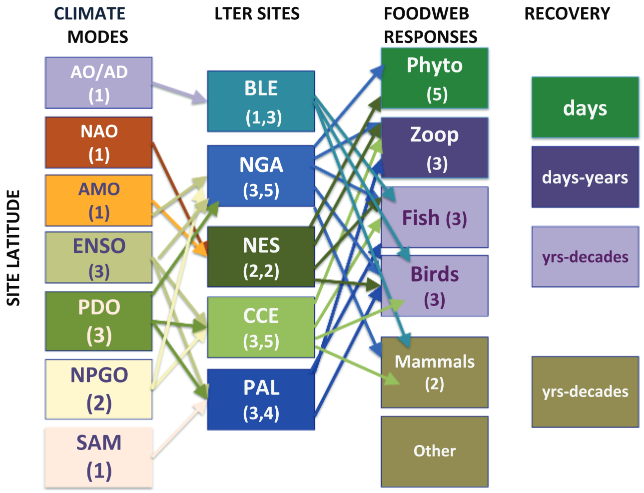

Figure 3. Network diagram showing hemispheric-scale climate influences on marine pelagic sites, an indication of sites experiencing longer-term climate impacts on pelagic food webs. See table 1 for the sites. The colors for climate and site boxes are arbitrary. The colors of the recovery column correspond the food web colors in the response column. The arrow colors reflect the origin of the flows to impacts. The numbers in the compartments are the numbers of (from and to) connections for each influence or impact. The phytoplankton show long-term impacts at all five sites. The phytoplankton arrows from California Current ecosystem and Palmer are not included for clarity.

California Current Ecosystem

The California Current system is a biologically productive oceanic region influenced by the configuration of the wind patterns along the coast that favors the existence of large-scale coastal upwelling and offshore Ekman pumping. The region has been sampled in its physics, chemistry, and ecology by the CalCOFI program for over seven decades (figure 4). Since 2014, the pelagic region west of the Southern California Bight has also been the site for the California Current Ecosystem LTER (Ohman et al. 2013), which has collected a wide variety of long time series of ecological observations from various platforms, both autonomous and shipboard, with measurements linked to experimental process cruises designed to better understand physical–biological interactions. The focus of much of this research involves understanding the physical and ecological processes that are involved in California Current system dynamics and how climate variations and change exert controls on these physioecological variations.

Physical responses. Occurring on interannual timescales, ENSO is a reversal of the prevailing easterly wind direction in the tropical Pacific, strongly affecting eastern boundary currents such as the California Current system in which the California Current Ecosystem site is situated. ENSO provides mechanisms affecting different oceanic LTER sites concurrently, through long-distance physical connections that can propagate through the atmosphere and ocean (Alexander et al. 2002). The main effect in the California Current is to reduce upwelling and in the Gulf of Alaska to drive downwelling, in addition to upper-ocean warming during peak winter El Niño conditions (Jacox et al. 2015). Atmospheric teleconnections associated with ENSO also extend across the North American continent during the winter season and into the South Pacific as far as Antarctica during austral summer.

A composite approach comparing the impacts of ENSO on the California Current Ecosystem site can be useful as a first-order estimate (Cordero-Quiros et al. 2019), but each ENSO event has different characteristics (Capotondi et al. 2015) that need to be identified and explained in the context of a generalized eastern boundary upwelling system response. Eastern Pacific and Central Pacific El Niños can have different consequences for zooplankton in the California Current region (Lilly et al. 2019, Lilly and Ohman 2021). Because ENSO is known to have predictable components, it logically becomes a primary target for improving our understanding of how it affects these sites (Capotondi et al. 2019) and whether we can exploit ENSO forecasts for applications to local forecasts of societally relevant variables such as fisheries (see the final section below).

On longer time scales, decadal changes in the strength and positioning of the subtropical atmospheric high pressure and the subarctic low pressure zones result in gyre-scale circulation changes that affect the intensity and water-mass characteristics of both the equatorward surface current and the poleward undercurrent in the California Current system (Miller et al. 2015). This is particularly important when considering the quality of upwelled waters, because nutrient and oxygen content are modulated during transit from remote regions to the US West Coast (Rykaczewski and Dunne 2010). These gyre-scale circulation changes are associated with basin-wide decadal variations that are, in turn, associated with the Pacific Decadal Oscillation and the North Pacific Gyre Oscillation for the Pacific Ocean LTER sites (Di Lorenzo and Ohman 2013). The Pacific Decadal Oscillation is primarily driven by the Aleutian low-pressure system, which drives a pattern of sea surface temperature anomalies that is coherent along the US West Coast and into the Gulf of Alaska (Newman et al. 2016). It also regulates ocean current anomalies that weaken the southward flowing California Current and strengthen the northward flowing Alaska Current during the warm Pacific Decadal Oscillation phase. Temperature and drought conditions in the Desert Southwest of the United States are also linked to Pacific Decadal Oscillation variability (Hudson et al. 2022, this issue). Similarly, the North Pacific Gyre Oscillation is primarily driven by the North Pacific Oscillation, which controls an open ocean pattern of sea surface temperature anomalies that is coherent from the central Gulf of Alaska southward to the subtropics (Ceballos et al. 2009). The decadal frequency of cold months is similar, but these two

Table 2. Regional to global scale climate modes representing analogs of climate change for understanding marine physical–biological responses to climate variability.

Climate mode	Index	Time scale	Region
El Niño–Southern Oscillation	SLP Tahiti-Darwin	2–7 years	Tropical Pacific to global
North Atlantic Oscillation(Arctic Oscillation)	SLP Azores-Iceland	Decadal?	North Atlantic
Northern Annular Mode	SLP, 35 and 65 North	Approximately decadal	North Atlantic, Pacific
Southern Annular Mode	Multivariate records at 40 and 65 South	Subdecadal	Southern Ocean
Pacific Decadal Oscillation	Subtropical Pacific SST	20–30 years	California Current, Northern Gulf of Alaska
Arctic dipole anomaly		Multidecadal	Arctic Ocean, North Atlantic
Atlantic Multidecadal Oscillation	North Atlantic SST	60–80 years	

Note: See table 1 for sites and the figures for ecosystem responses at the pelagic LTER sites. *Abbreviations:* SLP, sea level pressure; SST, sea surface temperature.

sites have different trends in frequency of hot months (supplemental figures S2 and S3).

The Scripps Pier, in California, exhibits a 105-year trend of rising sea surface temperature in the California Current (figure 4c) that is embedded in the climate noise of natural ocean variability on interannual to decadal timescales (Rasmussen et al. 2020). On this global-change timescale, the trapping of heat by greenhouse gases results in oceanic stratification changes, vertical mixing alterations, expansion, and intensification of the Hadley cell and its upwelling wind fields (Amaya et al. 2016), repositioning of the subtropical high pressure patterns by land–sea temperature contrast changes, and alteration of the pathways of source waters that affect the upwelling in the California Current system, as well as sea level rise affecting estuaries (Bakun et al. 2015).

Ecological responses. The California Current Ecosystem site is forced by processes on multiple time and space scales, including the seasonal onset of upwelling that leads to a spring bloom (Hickey 1988). Enhanced stratification and consequent reductions in vertical mixing and upward nutrient fluxes can inhibit primary production and possibly interfere with phenological timing between lower trophic level production and grazing (McGowan et al. 2003). This can also alter carbon export to storage in deep sediments (Stukel et al. 2018). Long-term changes in winds may ameliorate or exacerbate these effects, depending on their location and seasonal timing (Sydeman et al. 2014).

The long-term warming of the mixed layer in the California Current Ecosystem site (figure 4c) has been accompanied by a change in the euphausiid (krill) community, with a progressive increase in abundance of midlatitude euphausiid species ($p < .0001$, figure 4d). This euphausiid increase is probably related to increased food supply, as was indicated by the long-term decrease in water column transparency and increase in chlorophyll *a* (a proxy for phytoplankton biomass; Aksnes and Ohman 2009). The phytoplankton increase is likely related to a long-term increase in concentration of macronutrients in deep source waters to the California Current region (Bograd et al. 2015). Changes in California Current krill biomass have been related to changes in timing of arrival of blue whales on their feeding grounds (Szesciorka et al. 2020).

In addition to these long-term progressive changes as described above, there are important sources of natural multidecadal variability in the California Current region, including the Pacific Decadal Oscillation and the North Pacific Gyre Oscillation. Another assemblage of euphausiids, whose geographic centers tend to be in lower latitudes, shows no long-term temporal trend in abundance ($p < .40$, figure 4b) but clear low-frequency variability in association with the Pacific Decadal Oscillation ($r = .61$, $p < .00001$; figure 4a). This association appears to be mediated by changes in ocean circulation, with a time-lagged response of the euphausiids as explained by the double integration hypothesis (Di Lorenzo and Ohman 2013).

However, in addition to secular trends and decadal-scale variability, on interannual timescales in the California Current region, El Niño and La Niña events represent a source of strong forcing that also influences euphausiid abundances, especially for the low-latitude species (figure 4b; Lilly et al. 2019, Lilly and Ohman 2021). We highlight these multiple scales of ocean forcing and ecosystem response with euphausiids because the CalCOFI's or the California Current Ecosystem site's zooplankton time series extends to over 70 years; however, many other properties of the California Current's pelagic ecosystem also covary with these changes in the plankton (Lindegren et al. 2013).

Marine heat waves (when temperatures are in the outer 10% of their frequency distribution; www.ncdc.noaa.gov/climate-information/extreme-events) are becoming more frequent as the incidence of cold spells declines (supplemental figures S1–S3). All-time record high Scripps Pier temperatures (since 1916) were set four times in the span of 9 days in August 2018, associated with a regional warming in the Southern California Bight and along the coast of Baja California. A much larger-scale summer extreme anomaly occurred in 2019, in the central North Pacific (Amaya et al.

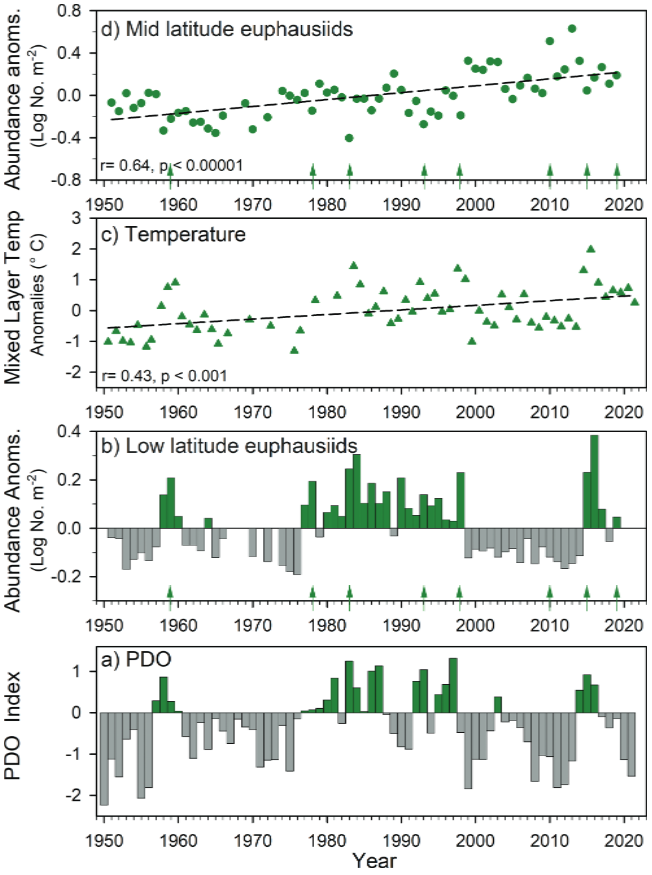

Figure 4. Secular change and low-frequency variability in the California Current ecosystem, as is exemplified by euphausiids (krill), a dominant form of zooplankton in this pelagic ecosystem. The results illustrate that midlatitude euphausiid species show (d) a long-term increase that parallels the (c) long-term increase in mixed layer temperature. In contrast, low-latitude euphausiid species show (b) no long-term trend ($p > .40$). Instead, they show multidecadal variability that parallels (a) the Pacific Decadal Oscillation, with which they are highly correlated ($r = .61$, $p < .00001$). In addition to the secular trends and multidecadal variability, both groups of euphausiids—especially the low-latitude species—show strong interannual variability that is related to El Niño, the arrows in panels (a) and (c). The California El Niño events were identified as they were described in Lilly and Ohman (2021). Euphausiid and mixed-layer temperature data from springtime CalCOFI cruises, Southern California region. The plots without significant secular trends are plotted as standardized anomalies to highlight interannual variability. The plots with significant trends are presented as scatter plots with regression lines.

2020), but not near the coast, where normal winds control upwelling. The ecological consequences of these major events are not yet clear.

The oxygen minimum zone has also experienced long-term changes in the California Current system. CalCOFI records indicate that, at depths relevant to demersal fish habitats, dissolved oxygen was low in the 1950s, rose to peak levels in the 1970s, and then steadily declined to low values again in recent years (McClatchie et al. 2010). The potential ecological impacts of these changes in environmental chemistry and related changes in partial pressure carbon dioxide and pH are under investigation.

Northeastern US shelf

The Northeast US Shelf is a highly productive large marine ecosystem (https://ioc.unesco.org/topics/large-marine-ecosystems). The wide temperate continental shelf system is bounded on the landward side by dense human population centers and on the seaward side by a dynamic shelf break frontal zone marking the separation between the cold shelf and the relatively warm and salty slope sea. The region's planktonic food web supports valuable commercial fisheries (table 1), as well as iconic and threatened marine mammals and birds. Long-term warming (figures 1, 5a) is coincident with multidecade declines in mixed layer depth and chlorophyll concentration (figure 5b, 5c). Interannual and interdecadal fluctuations in higher trophic levels are documented (figure 5d, 5e), with some links to physical habitat changes and range shifts. Direct food web connections are difficult to untangle in the face of high temporal and spatial variability, but linked fluctuations between key planktonic taxa and the forage fish assemblage are apparent with appropriate time lags and consideration of multispecies interactions (Suca et al. 2021b).

Physical responses. The Northeast US Shelf experiences interannual to decadal-scale variability in temperature and salinity in addition to warming trends (figures 1 and 5). Notably, the warming rate has increased in recent decades (Pershing et al. 2015, Thomas et al. 2017); as the Atlantic Multidecadal Oscillation index has remained in its warm phase. This is linked to large-scale forcing as the Atlantic Multidecadal Oscillation index corresponds to the leading mode of sea surface temperature variability for the whole North Atlantic from the equator to approximately 70 degrees (°) north (Deser et al. 2010). Furthermore, the Atlantic Multidecadal Oscillation index may be associated with the basin-scale Atlantic meridional overturning circulation (Knight et al. 2005). In addition, at the Northeast US Shelf site, circulation and water mass properties are further complicated by sources of variability at interannual scales. The North Atlantic Oscillation index, for example, has been linked to interannual variability in shelf–slope exchange (Mountain 2012).

Seasonal to interannual changes in atmospheric pressure, air temperature, and wind speed affect both transport from the north and precipitation and evaporation patterns that, in turn, affect local heating and cooling. In addition, the position of the Gulf Stream varies on interannual to decadal scales (Rossby and Gottlieb 1998, Andres 2016), accompanied by changes in the frequency and location of warm core

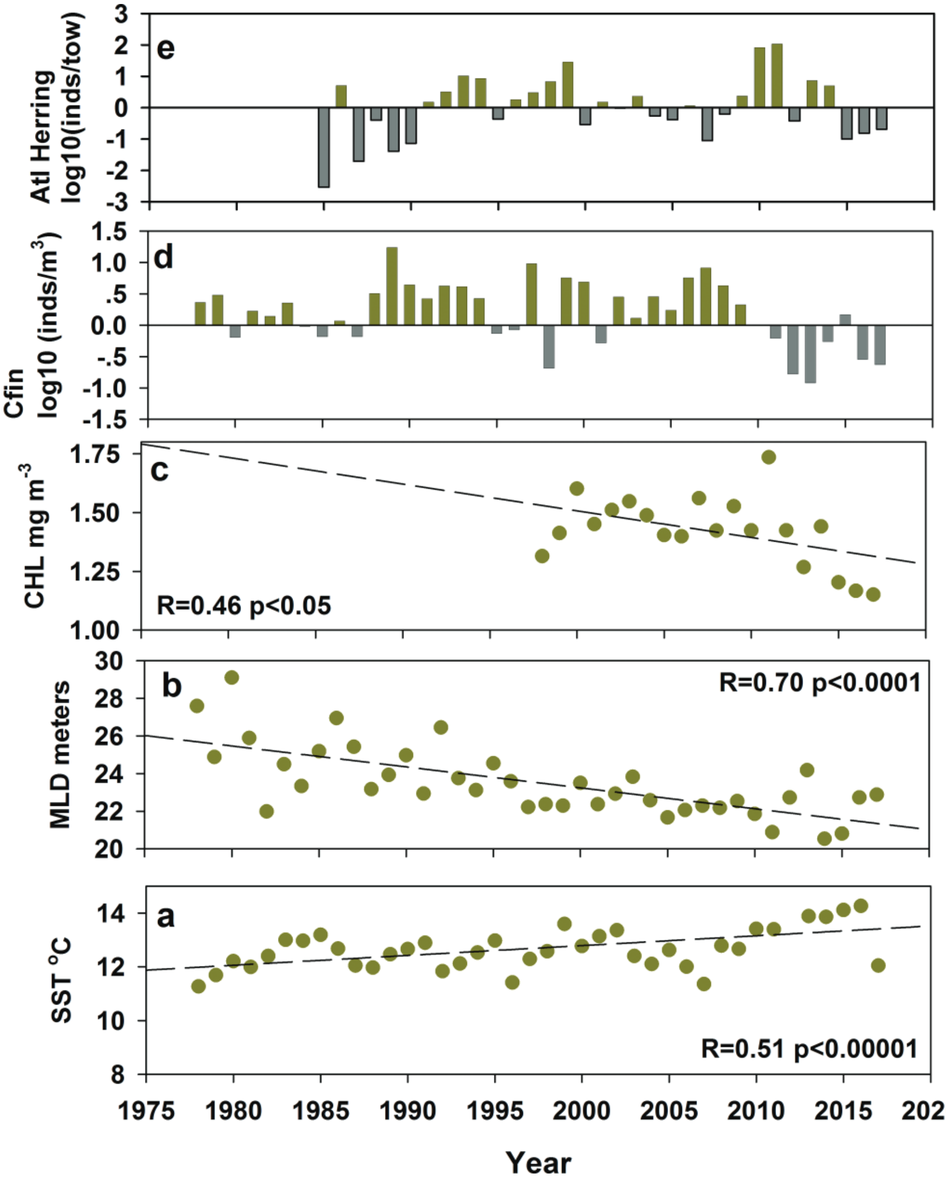

Figure 5. Northeast US shelf interannual variability and long-term trends. (a) Sea surface temperature. (b) Mixed-layer depth (MLD). c) Chlorophyll concentration (CHL). d) Calanus finmarchicus *abundance. (e) Atlantic herring (*Clupea harengus*) abundance averaged over the entire southern New England shelf. The sea surface temperature and MLD data are derived from data-assimilative hydrodynamic model output for years from 1978 to 2017 based on the Northeast Coastal Ocean Forecast System (http://fvcom.smast.umassd.edu/necofs). MLD was computed as the uppermost depth at which the water density was 0.03 kilograms per cubic meter higher than the surface water density. CHL was derived from a 4-kilometer resolution ocean color remote sensing product (GLOBCOLOUR, https://hermes.acri.fr). The* Calanus finmarchicus *abundance data were collected during the Marine Monitoring Assessment and Prediction (1977–1987) and the subsequent Ecosystem Monitoring (*EcoMon; 1988 *to the present) programs conducted by the US NOAA Northeast Fisheries Science Center. The* Calanus finmarchicus *time series is presented as abundance anomaly using an approach described in Kane (2007) to minimize the potential sampling bias caused by irregular sampling dates. The log area weighted stratified mean abundance of Atlantic herring was calculated from the Northeast Fisheries Science Center spring bottom trawl survey in each year for the strata within the Southern New England ecoregion. The strata were restricted to those that continued to be sampled after the change from the NOAA ship* Albatross IV *to the NOAA ship* Henry Bigelow. *Haul-specific catches of Atlantic herring for the* Henry Bigelow *collections were calibrated to match those of the* Albatross IV *according to the calibration factor and recommendations within Miller and colleagues (2010). The Atlantic herring time series data were provided by Justin Suca, using survey data and an early version of data processing code provided by David Richardson at NOAA Northeast Fisheries Science Center. More information about the trawl survey data can be found in Suca and colleagues (2021a).*

rings that can impinge on the shelf (Gangopadhyay et al. 2019). A notable manifestation of these interacting phenomena is that the general warming trend has been accompanied by significant changes in the seasonal cycle of warming and cooling in recent decades. As was indicated by sea surface temperature, summer is warmer and longer, with higher spring warming and later fall cooling rates supporting an increased sea surface temperature range over the annual cycle (Friedland and Hare 2007, Thomas et al. 2017).

Seawater temperatures have been rising throughout the Northeast US Shelf for decades, as is documented in the record of more than100 years in Woods Hole, Massachusetts (figure 5a; Nixon et al. 2004), data sets covering more than 150 years from ship-based observations, regional monitoring buoys, and satellite-derived sea surface temperature records, with some evidence that warming has been faster than other ocean regions and has accelerated in recent decades (Mills et al. 2013). Recent anomalously warm conditions have been linked to variability in the jet stream and possibly with northward diversions of the Gulf Stream (Chen et al. 2014) and have led to dramatic impacts on marine life across a wide range of trophic levels, including commercially important species. Projections suggest that faster than average warming will continue over the shelf region (Saba et al. 2016).

In the Northeast US Shelf region, freshwater inputs derive from two regional sources: the Gulf of Maine and the Mid-Atlantic Bight. In the Gulf of Maine, the total volume transport from river discharge is two orders of magnitude smaller than the along-shelf transport and cross-shore slope water intrusion (Smith et al. 2001). The St. Lawrence River enters the Gulf of St. Lawrence first and then enters the Gulf of Maine via the Scotian Shelf, while mixing with offshore waters along the way. The freshwater contribution of the St. Lawrence River is about half of total fresh water entering the Gulf of Maine (Houghton and Fairbanks 2001) and could significantly affect the surface salinity of the Gulf of Maine. Consequently, stratification patterns and phytoplankton bloom dynamics could be affected (Ji et al. 2007). In the Mid-Atlantic Bight, the contribution of water volume transport from river discharge is also at least two orders of magnitude smaller than the along-shelf inflow from the upstream Gulf of Maine. Nonetheless, river contribution to the Mid-Atlantic Bight does influence surface salinity variability (Whitney 2010), will likely affect stratification, and has some ecological consequences.

In contrast to the general warming trends for the entire Northeast US Shelf region over the last four decades, salinity has not shown a monotonic trend, instead varying regionally and temporally. There also have been significant trends in increased precipitation over the Northeast United States over the period of 1950–2020 (Campbell et al. 2022). There was a significant freshening event in the 1990s across the Northeast US Shelf, but salinity returned to prior levels and has been relatively stable over the last two decades. The 1990s freshening coincided with the large-scale great salinity anomaly that occurred over the entire North Atlantic (Belkin 2004) and may be linked to enhanced Arctic freshwater outflow (Karchner et al. 2005, Greene et al. 2013), with additional contributions from Greenland melting (Proshutinsky et al. 2015). Additional salinity variability at interannual time scales is associated with variability in alongshore salt transport, regulated by regional wind forcing (Li et al. 2014, Feng et al. 2016, Grodsky et al. 2017). The superposition of these local, regional, and basin-scale phenomena leads to changes in temperature and salinity that control seasonally varying stratification regimes on the Northeast US Shelf. Regionally, the Mid-Atlantic Bight region tends to be temperature dominated through a larger portion of the year (as is suggested by the opposite trend of sea surface temperature and mixed-layer depth in figure 5a, 5b), whereas the Gulf of Maine is more influenced by salinity and fresh water (Li et al. 2015). These regional differences in hydrography have different influences on nutrient and phytoplankton dynamics across the Northeast US Shelf (Zang et al. 2021).

Ecological responses. Primary producers can be influenced by both direct and indirect temperature effects on the Northeast US Shelf (Zang et al. 2021). The overall phytoplankton biomass (represented as chlorophyll-*a* concentration) declined on the southern New England Shelf over the last four decades (figure 5c), coinciding with the general warming trend in the region. The numerically dominant phytoplankton are picophytoplankton (less than 2 micrometers) of the genus *Synechococcus*, which exhibit concentration and division rate changes that are strongly seasonal and linked to temperature, both seasonally and interannually (Hunter-Cevera et al. 2016, Hunter-Cevera et al. 2019). Although they are less abundant, eukaryotic picophytoplankton exhibit similar seasonality and contribute disproportionately to primary production compared to *Synechococcus* (Fowler et al. 2020). Diatoms, important contributors to microphytoplankton biomass, have more complicated temperature and seasonal responses that likely reflect the combined effects of direct thermal impacts, stratification-mediated changes in light and nutrients, and temperature sensitive trophic impacts through grazing and parasitism (see below). These physiological and ecological impacts of temperature can lead to important impacts on annual cycles and interannual variability. For example, in nearshore waters of the northern Mid-Atlantic Bight, earlier spring blooms of *Synechoccous* occur in years with earlier spring warming (Hunter-Cevera et al. 2016) and larger blooms of an important diatom species occur in colder winters (Peacock et al. 2014). Across the Mid-Atlantic Bight, wind appears to be a key driver modulating thermal stratification and late fall and winter bloom dynamics (Xu et al. 2013), whereas, in the Gulf of Maine, earlier spring blooms occur when winter–spring stratification is stronger because of surface freshening (Ji et al. 2007, 2008, Song et al. 2010). Fall bloom timing in the Gulf of Maine seems to be negatively correlated with sea surface temperature and salinity, with higher temperatures and salinity resulting in earlier blooms (Song et al. 2010). Variability in bloom timing, magnitude, and extent are linked to zooplankton in complex ways that vary regionally across the Northeast US Shelf (Friedland et al. 2015).

Copepods, a major group of mesozooplankton in the Northeast US Shelf region, play an important role linking lower and higher trophic levels (Sherman et al. 1987, Durbin and Casas 2006). The diversity of copepods changes spatially and over seasonal and interannual time scales on the Northeast US Shelf (Johnson et al. 2011, Morse et al. 2017). Each copepod species exhibits a characteristic life cycle and seasonal or spatial pattern. For instance, in the Gulf of Maine, *Calanus finmarchicus*, *Pseudocalanus*, and *Metridia* are cold-water taxa that avoid the warm surface layer (more than 10–12 degrees Celsius [°C]) during summer and fall and produce large spring populations. *Centropages*, *Temora*, and *Paracalanus* are warm-water species and are most abundant during late summer and fall. *Oithona* is plentiful throughout the Georges Bank and Gulf of Maine region year-round. The spatiotemporal distribution patterns of different zooplankton species vary significantly even under the same physical environment, largely because of their unique life history strategies interacting with surrounding environment, including the temperature and food-dependent egg production and development and growth rates, temporally and spatially varying mortality rate caused by predation or starvation, and the interaction of physical transport and biological behaviors (Ji et al. 2009). From a bottom-up point of view, changes in water-column stability can lead to shifting bloom seasonality and, consequently, the variability of zooplankton abundance and productivity (Durbin et al. 2003, Pershing et al. 2005, Greene 2013). Meanwhile, the role of top-down control in zooplankton variability is also important (Frank et al. 2005, 2011, Ji et al. 2013, Ji et al. 2021).

Trophic interactions that appear sensitive to temperature, salinity, and stratification impacts are varied and complex to diagnose on the Northeast US Shelf. At the bottom of the food web, impacts include temperature regulation of parasite-mediated mortality for diatoms (Peacock et al. 2014). Decadal scale shifts zooplankton community structure (Kane 2007, Pershing et al. 2010, Morse et al. 2017) have potentially affected the recruitment of fish populations in the region (Pershing et al. 2005, Friedland et al. 2015). The large lipid-rich copepod species, *Calanus finmarchicus*, shows strong interannual variability and doesn't appear to respond linearly with the warming trend (figure 5d). The variability of *C. finmarchicus* has also been directly linked to changes in regional fisheries species (e.g., Suca et al. 2021b) and top predators (Record et al. 2019). On the Southern New England shelf, the abundance anomaly of *C. finmarchicus* has a significant correlation ($r = .45$ and $p < .01$) with Atlantic herring (*Clupea harengus*) with a time lag of 4 years even though this pattern is not readily visible in figure 5d, 5e. A 4-year lag makes biological sense, given that age 3 (parental condition) and age 4 (larval prey) fish are a large part of the survey catch of Atlantic herring and that the availability of *C. finmarchicus* could affect the parental condition and larval feeding and, therefore, the production and survival of herring larvae.

The rapid warming of the Northeast US Shelf region in recent decades has resulted in the expansion of warmer water habitats and a concomitant decline in cooler water habitats in the system (Friedland et al. 2013). Important patterns included a northward (or deeper) shift in the distributions of many planktonic and nektonic organisms (Nye et al. 2009, Fogarty et al. 2012). In addition to direct effects on thermal habitat, warming combines with salinity changes to affect the seasonal cycle of stratification. This, in turn, affects nutrient supply and light availability in near surface layers, which could lead to shifts in phenology across different trophic levels (Staudinger et al. 2019).

Palmer Station

The Palmer Station LTER region extends approximately 800 kilometers (km) from 64° to 70° south, along the western coast of the Antarctic Peninsula, and approximately 200 km from the immediate coastal area offshore to beyond the continental shelf into the southern boundary of the Antarctic Circumpolar Current. This region is sampled via research icebreaker cruises occupying 25–30 fixed station locations each Austral summer (January–February). Regular cruises started in January 1993, eventually building up the 30-year record from which this account stems. The region is experiencing rapid atmospheric and ocean warming leading to a decline in annual sea ice extent of about 50 days in the northern part of the study area since 1978. In contrast, in the south sea ice cover still persists through most of the summer, preventing easy access, such that sampling the entire grid is not always possible.

Physical responses. In the western Antarctic Peninsula region, ENSO is a dominant mode that interacts with the Southern Annular Mode (table 2) to provide different climate effects (Stammerjohn et al. 2008). Prevailing winds are driven by the north–south movement and position of the circumpolar westerly wind belt, or the Southern Annular Mode in its positive (warmer, less sea ice) and negative states (colder, more ice). These patterns are intensified by ENSO. Coincidence of the negative ENSO state (La Niña) with the Southern Annular Mode in its positive state strengthens the Southern Annular Mode in its positive state state, and ENSO in its positive state or the Southern Annular Mode in its negative state has the opposite effect. The region was dominated by the Southern Annular Mode in its negative state in the 2000s, contributing to the trends of increasing sea surface temperature and sea ice decline, but the Southern Annular Mode in its positive state conditions prevailed during the late 2000s to early 2010s with opposite effects as revealed in the record of sea ice cover (figure 6a). Establishing and explaining long-term trends is complicated by interannual shifts in sea ice duration and mixed layer depth (figure 6a, 6b; Brown et al.

2019). A pattern of interannual fluctuations in air temperature changed to all positive anomalies after 1980 (figure 1).

Surface air temperature has been increasing along the western Antarctic Peninsula at least over the instrumental record of the past approximately 70 years (Vaughan et al. 2003). The duration of sea ice cover in the region has declined by 50–75 days since 1978 (figure 6a; Stammerjohn et al. 2008). The sea ice's advance and retreat and, therefore, the duration of sea ice cover are sensitive to shifts in wind direction (northerly or southerly) that bring warmer or colder air into the region and blow sea ice toward or away from the coast. The duration of sea ice cover regulates light input for primary production, and ice melting stabilizes the upper water column, further affecting light availability. Therefore, interannual to decadal climate variability expressed by wind patterns influences ocean mixed layer dynamics through sea ice extent and duration (figure 6a, 6b) and, in turn, controls primary production and ensuing trophodynamic phenomena through changes in mixed layer depth and water column stratification (Brown et al. 2019).

Interannual variability in glacier inputs of fresh water has also been linked to the Southern Annular Mode and ENSO (Meredith et al. 2013, Meredith et al. 2017). Terrestrial freshwater input to the shelf along the western Antarctic Peninsula is thought to make negligible to minor contributions to the macronutrient (nitrogen, phosphorus) budget of the shelf, although it can be a critical source of micronutrients such as iron for coastal waters (Annett et al. 2015, Henley et al. 2017). In addition, these freshwater inputs are critical in modulating the surface mixed layer depth and upper-ocean stratification, both of which are key determinants of marine productivity on the shelf (Venables et al. 2013, Carvalho et al. 2017, Carvalho et al. 2020).

Ecological responses. Antarctic plankton ecosystems exhibit seasonal patterns (phenologies) dominated by spring blooms of large diatoms that are replaced by smaller-cell species in the summer because of changes in mixing, stratification, light, and nutrient availability. Phytoplankton cell size is a key determinant of grazer community composition, responses and phenology, and ultimately of upper-level predators and fisheries. Diatoms are the preferred food of Antarctic krill (*Euphausia superba*). Krill, in turn, are the major diet component for penguins, seals and whales. Diatoms and fecal pellets of krill are heavy and sink rapidly, enhancing vertical carbon exports. Diatoms are replaced in the seasonal phytoplankton succession by cryptophytes (Moline et al. 2004, Moline et al. 2008) that are too small to be grazed by krill, favoring other herbivores such as microzooplankton (Garzio and Steinberg 2013) and gelatinous grazers, principally salps. The cryptophytes are typically found in low-salinity waters such as nearshore regions affected by seasonal glacier melting but might be expanding their ranges in response to larger-scale changes in hydrology and mixed layer depth (Brown et al. 2021).

Chlorophyll-*a* concentrations demonstrate a long-term increase along the western Antarctic Peninsula (figure 6c; Brown et al. 2019). This increase was also observed in remote ocean color imagery comparing the periods 1978–1986 and 1998–2006 (Montes-Hugo et al. 2009) and covering the mid- to southern part of the peninsula coterminous with the Palmer sampling region. Montes-Hugo and colleagues (2009) also inferred from discrete diatom pigment (fucoxanthin) measurements that diatoms were increasing in the same region. In contrast, total chlorophyll and fucoxantin were declining over the area of the peninsula to the north of the Palmer sampling region. These changes were ascribed to increases in wind speed (and probably mixed layer depth) and cloud cover. The observations and conclusions of Montes-Hugo and colleagues (2009) were updated to 2012, with the same general results, except that the region of chlorophyll-*a* decline had migrated south by approximately 200 km, into the Palmer region. In addition, large-cell phytoplankton (diatoms) were increasing all along the continental shelf, whereas they were declining in favor of smaller species (cryptophytes) in the slope water and Antarctic Circumpolar Current region (Bahlai et al. 2021).

The macrozooplankton (larger than 1 millimeter) community along the western Antarctic Peninsula is typically dominated by krill, which have recruitment cycles of 4–6 years, as was shown by varying size classes of the dominant krill cohort. These recruitment cycles, intrinsic to long-lived krill species, are strengthened by the Southern Annular Mode or ENSO cycle cited earlier (Saba et al. 2014). High-ice years have more ice melt that stratifies the upper water column more strongly (figure 6b), promoting larger diatom blooms (figure 6c). Larger blooms favor krill recruitment, which, in turn, supports successful breeding in Adélie penguins (see below). Humpback whales require dense aggregations of krill and in recent years, favorable conditions have led to high pregnancy rates (Pallin et al. 2018).

Antarctic krill require sea ice for successful reproduction and juvenile survival. Weak-swimming juveniles use the underside of the ice pack as a refuge to evade predators and they graze on epontic diatoms. A long-term, large-scale circumpolar decline in krill related to declining sea ice, seen in northern Antarctic seas (Atkinson et al. 2009; the same region as the chlorophyll decline noted above) is not observed in the Antarctic Peninsula region (Steinberg et al. 2015), a region of chlorophyll-*a* increase.

Copepods dominate mesozooplankton (more than 0.2 millimeters) abundance (but not biomass) and sometimes equal krill in their herbivorous grazing impact (Bernard et al. 2012, Gleiber et al. 2015). In contrast to Antarctic Krill, there was an *increasing* trend in total copepods and several dominant copepod species from 1993 to 2013 along the western Antarctic Peninsula (figure 6d). Like the krill, copepods responded to interannual variations and trends in the Southern Annular Mode, sea ice duration and phytoplankton (Gleiber 2014). Copepods also serve as a major diet item

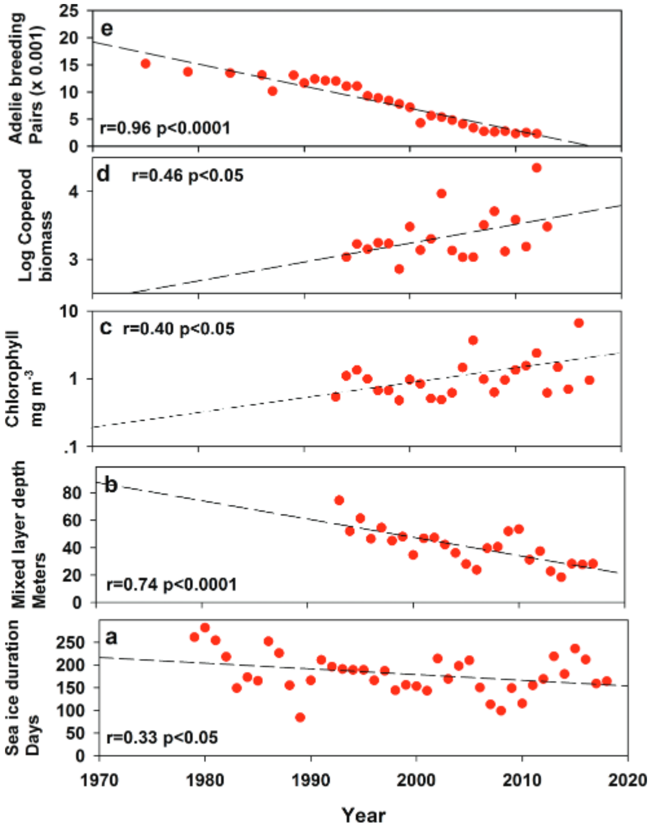

Figure 6. Secular trends on the western Antarctic Peninsula shelf. The data in plots (a)–(d) averaged over the summer (December to February) and over the Palmer Station LTER shelf–slope study region extending from 64 to 70 degrees south latitude. (a) Duration of sea ice of cover (http://pal.lternet.edu/data, Palmer data set 151, S. Stammerjohn, University of Colorado). (b) Mixed layer depth determined as the depth of maximum Brunt–Visala frequency, N^2 as described in Brown and colleagues (2019). (c) Chlorophyll-*a* concentration (http://pal.lternet.edu/data, Palmer data set 24, O. Schofield, Rutgers University). (d) Total copepod abundance (Gleiber et al. 2014, 2015). (e) Breeding pairs of Adélie penguins in the Palmer Station region, derived from annual census records (Fraser et al. 2013; from William R. Fraser, Polar Oceans Research Group, Sheridan Montana).

for krill. These changes may elicit responses by top predators over interannual to decadal time scales.

The Adèlie penguin population in the northern Antarctic Peninsula region has been in decline since at least 1975 (figure 6e; Fraser et al. 2020) with the tight coupling between the environmental variability and biophysical properties alluding to possible mechanisms. A pattern of anomalously high diatom blooms associated with the Southern Annular Mode in its negative state condition promotes krill recruitment and enhanced Adélie foraging and penguin chick survival, whereas the Southern Annular Mode in its positive state leads more precipitation causing higher thermoregulatory costs for chicks without waterproof feathers (Cimino et al. 2014, Saba et al. 2014). Adult Adélie penguin foraging trip durations are shorter during years when small krill are abundant, which has positive impacts on chick fledging mass and survival, because chicks are provisioned more frequently (Fraser and Hofmann 2003). A recent period of dominance by the Southern Annular Mode in its positive state and lower sea ice (figure 6a) in the region might culminate in failures in krill and penguin recruitment.

The hypothesis that the Adélie penguin decline is a bottom-up food web process with a marine origin is consistent with observations of krill decline in the northern Antarctic Peninsula region. But it is inconsistent with observations that gentoo and chinstrap penguins are *increasing* in the same area and also depend on krill (Trivelpiece et al. 2011). Furthermore, krill are not decreasing in the Palmer region and southward along the mid- to lower western Antarctic Peninsula (Steinberg et al. 2015). The near extirpation of baleen whales because of commercial whaling in the early to midtwentieth century may have led to an expansion of krill stocks (the krill surplus hypothesis), further complicating these dynamics (Laws 1977, Savoca et al. 2021). Increasing humpback whale populations and high pregnancy rates further suggest krill stocks are not limiting.

Stronger westerly winds, warmer and wetter conditions, and a trend toward increasing late spring snowfalls along the peninsula associated with long-term atmospheric warming can have consequences for terrestrial breeding polar seabird species with life histories unsuited to subpolar conditions. In addition to the other trends already noted suggesting the marine food web as cause for long-term (approximately 50 years) penguin declines, terrestrial effects also drive changes in Adélie penguin demography. Fraser and colleagues (2013) showed that penguin colonies on southwest-facing slopes experienced greater snow accumulation and more rapid rates of decline than penguins nesting on northeast-facing slopes. Adélie penguin breeding success and chick survival are also linked to nest site microclimate conditions, where snow can delay breeding phenology, drown eggs or small chicks, decrease breeding success and lower chick fledging mass, with the potential for snow effects being amplified by landscape aspect.

Northern Gulf of Alaska

The physical ocean environment in the Northern Gulf of Alaska also responds to climate variability over interannual scales with changes in mixed layer temperature and depth (figure 7a, 7b). In turn, the Northern Gulf of Alaska's planktonic ecosystem has also varied over interannual time scales for both phytoplankton and zooplankton (figure 7c, 7e), but the observed patterns do not suggest longer-term directional trends. Similarly, at higher taxonomic grouping tubenose seabirds show no systematic changes (figure 7f), although individual species can show a variety of patterns over the 25 years of observations. These patterns and the lack thereof are explored below.

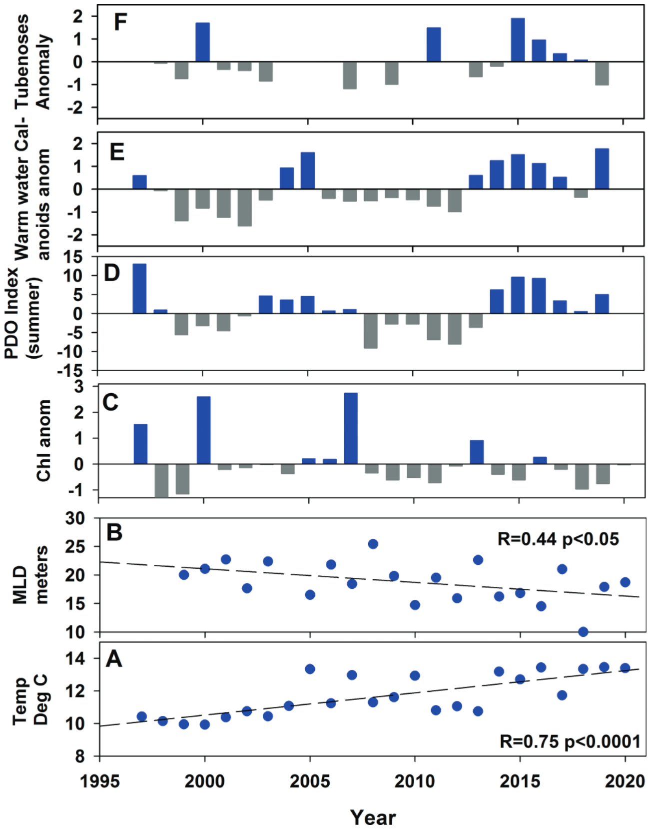

Figure 7. Example Northern Gulf of Alaska Seward Line time series: (a) Temperature in the mixed layer. (b) Mixed layer depth during September. (c) Chlorophyll anomalies (in grams of chlorophyll per square meter) during September. (d) Summer (April to September) Pacific Decadal Oscillation index. (e) Warm-water calanoid copepod anomaly (as the log of individuals per cubic meter). (f) Tubenose seabird anomaly (as the log of individuals per square kilometer).

Physical responses. As with the California Current ecosystem, gyre-scale circulation changes associated with the Pacific Decadal Oscillation and North Pacific Gyre Oscillation influence the Northern Gulf of Alaska (Di Lorenzo et al. 2015) driving patterns of sea surface temperature anomalies (Newman et al. 2016) and strengthening the Alaska Current during the warm Pacific Decadal Oscillation phase. Both ENSO (Royer 2005) and marine heat waves (Walsh et al. 2018) occur as secondary influences. Over the long-term, warming tends in surface waters and increased heat content are clear (Suryan et al. 2021), consistent with shifts in the frequency of hot and cold months over decades (supplemental figure 1). These trends are now apparent across the entire Northern Gulf of Alaska shelf (figure 7a) and accompany a reduction in the mixed depth layer (figure 7b), suggesting a long-term increase in the intensity of stratification.

Seasonal wind-driven mixing drives seasonal inputs of macronutrients to surface waters with resultant phytoplankton cycles (Childers et al. 2005) typical of mid- to high latitudes. The rocky nature of the Northern Gulf of Alaska coastline means that macronutrient runoff in these waters is low, but iron concentration is high. This contributes to the post–spring bloom period contrasts of high-iron low-nitrate coastal water to the low-iron high-nitrate offshore waters (Aguilar-Islas et al. 2016). The mechanisms mixing these water types appear critical in driving much of the productivity in this domain (Coyle et al. 2012, Coyle et al. 2019) and are an ongoing topic of study in the Northern Gulf of Alaska.

Ecological responses. The Northern Gulf of Alaska has a large array of mechanisms that appear to sustain high overall ecosystem productivity from spring through fall. Atmospheric drivers affect many of these physical processes and can both change the timing and amplitude of the spring bloom, as well as standing stocks and productivity during summer and autumn (figure 7c). In general, earlier, more protracted, and more intense stratification is thought to lead to reduced primary production and phytoplankton standing stock (Strom et al. 2016). Satellite observations show that some years even lack a significant spring bloom altogether, but no long-term trends have been established in other seasons. There is a pronounced contrast between the large-cell dominated spring bloom, and a small-cell dominated summer and fall phytoplankton community (Coyle et al. 2012, Aguilar-Islas et al. 2016, Strom et al. 2010). A variety of factors, but particularly warm springs, can lead to greatly reduced spring blooms with limited contribution by large cells (Ferriss and Zador 2022). Phytoplankton community structure, in turn, likely correlates with the degree of export flux.

Microzooplankton, primary consumers of phytoplankton in the Gulf of Alaska, are characterized by a seasonal shift from ciliates in spring to a flagellate-dominated community in autumn (Strom et al. 2007, Strom et al. 2019). Many of these species are mixotrophic so functionally comprise a substantial fraction of the phytoplankton. Similarly, there is a seasonal progression from large-body *Neocalanus* copepods (figure 7e) in spring to smaller species during midsummer through autumn (Coyle and Pinchuk 2003, 2005). Simultaneously, there is typically an increase in biomass and relative importance of euphausiids moving from spring to fall (Pinchuk et al. 2008). Gelatinous zooplankton also can be abundant during the fall and, at times, even during the spring (Doubleday and Hopdroft 2015).

In the late 1970s, a cool to warm transition in the Pacific Decadal Oscillation was associated with a lasting transformation of the Gulf of Alaska benthic community from shellfish to finfish (Anderson and Piatt 1999). Although planktonic communities were not adequately examined at that time, in the most recent decades temperature-driven shifts in phenology and species composition are apparent across multiple planktonic trophic levels (Pinchuk et al. 2008, Sousa et al. 2016, Strom et al. 2016). Some changes affect resident communities, whereas others pertain to increased abundance of southern species. Abundance of warm water species (figure 7e) during fall is highly correlated ($r^2 = .5$) to the

Pacific Decadal Oscillation during prior months (figure 7d), confirming prior conjecture that their prevalence arose from increased northward advection or survival during warm years (Batten et al. 2018, McKinstry and Campbell 2018).

In addition to vibrant commercial fisheries, the Northern Gulf of Alaska also supports many iconic species of seabirds that exploit both zooplankton and forage fish as prey. These populations appear to respond variably to climate fluctuations (figure 7f), in part driven by changes in their forage base (Goyert et al. 2018). Finally, the Northern Gulf of Alaska supports a range of marine mammals (Rone et al. 2017), for which some populations have undergone considerable fluctuations in recent decades (Trites et al. 2007).

Marine heat waves (when temperatures are in the outer 10% of their frequency distribution) are becoming more frequent as the incidence of cold spells declines (supplemental figures S1–S3). Most recently, changes associated with North Pacific marine heat wave or El Niño one-two punch from 2013–2016 (Bond et al. 2015, Amaya et al. 2016)—riding on a positive Pacific Decadal Oscillation—affected all trophic levels including fisheries, seabirds and marine mammals in the Northern Gulf of Alaska and California Current (Arimitsu et al. 2021, Suryan et al. 2021). During the heatwave, the contribution of smaller, less lipid-rich California Current species reached a peak level (figure 7e). These warm years then resulted in poor survival of forage fish (Zador and Yasumiishi 2017) and commercial species (Rogers et al. 2021) and consequently forced many seabirds inshore, where food was presumed to be more abundant but major mortality may still occur (Piatt et al. 2020).

Beaufort Lagoons Ecosystem

The Arctic Ocean environment, particularly the western Arctic region that includes the Alaskan Beaufort and Chukchi Seas, has demonstrated strong responses to atmospheric warming as documented by a 40% decrease in summer sea ice extent and a dramatic decrease in sea ice duration over the past two decades (supplemental figure S6). The changes in ice extent and extended open-water season have important implications for these very productive shallow (less than 3 m deep) lagoons located at the land–sea interface. These coastal systems demonstrate clear seasonality as they transition from 8 months of ice cover to open water, with significant increases in both benthic chlorophyll and faunal abundance at very low water column chlorophyll concentrations (figure 8c, 8d). The important links between physical drivers and ecological responses play a distinct role in the importance of these nearshore systems to the subsistence lifestyles of native Inupiat people who reside on the Arctic coast.

Physical responses. In the Arctic, the recent decade has seen the predominance of a large spatial scale atmospheric pattern known as the Arctic dipole anomaly in addition to the Arctic Oscillation to explain recent record lows in sea ice. The Arctic dipole anomaly recognizes the existence of low atmospheric sea level pressure on the Siberian side of the Arctic that is balanced by high sea level pressure on the North American side (Overland et al. 2018). The summer Beaufort high sea level pressure represents a major shift for the Alaskan Arctic that has produced an increase in easterly winds, driving sea ice offshore, and initiating the Arctic amplification, the dramatic and unprecedented atmospheric warming of the Arctic at double the global rate (Wendisch et al. 2017) as reflected by sea ice loss (supplemental figure S6). Radiative forcing, the positive feedbacks related to the surface albedo effect, is mainly responsible for the rapid pace of Arctic amplification, which is pronounced in the Beaufort because of the increased frequency of easterly winds (Frey et al. 2015). The acceleration of ice loss in the Pacific Arctic sector and throughout the Arctic is reflected in model projections that indicate an ice-free Beaufort Sea by 2050 (Notz and SIMIP Community 2020).

The Arctic amplification has resulted in an increase in mean annual air temperatures in the central Arctic of a least 2°C (Overland et al. 2018) coupled to a two-thirds decrease in ice volume, and increases in annual open-water durations for the Beaufort Sea, ranging from 17 to 54 days (Bonsell and Dunton 2018). The striking 40% decline in sea ice extent in the Arctic Ocean since the onset of satellite observations nearly four decades ago has occurred in parallel with unprecedented warming (supplemental figures S1–S3) that has thawed and degraded permafrost over northern Alaska, Russia, and Canada. The unabated rate of sea ice loss, approximately 13% loss in area per decade (Serreze and Stroeve 2015), unleashed a cascade of events that threaten the ecological stability of the region. Ice retreat from coastal areas has been greatest in the western Arctic. In the Alaskan Beaufort Sea, the ice-free season has increased by 41 days over 33 years (Frey et al. 2015), more than double that of the entire Arctic (Parkinson 2017).

The rate of ice loss in the Beaufort Sea is considerably higher than in the overall Arctic and decreasing at a rate of 17.3% per decade, and, on the basis of the rate of decline, the Beaufort Sea will likely experience entirely ice-free summers within the next two decades (Babb et al. 2019). In addition, the loss of over 70% of perennial sea ice has enhanced heat flux into the Arctic Ocean and increased the vulnerability of the sea ice to disruption by major storms, further accelerating ocean warming (Wendisch et al. 2017). Some model projections indicate that the tipping point for the new Arctic occurred as early as 2015 (Sea Ice Forum, http://tinyurl.com/y5hekyza). The profound changes have not escaped the attention of native Inupiat Eskimos who reside in three villages across the Beaufort Sea coast. The villagers complain of shortened hunting and fishing seasons, unstable and rotten ice, and changes in the distribution and abundance of important subsistence species (Huntington et al. 2017, 2020).

The high rate of ice loss in the Alaskan Beaufort Sea produces greater fetch, allowing waves to generate over increasingly larger expanses of open ocean. Thomson and Rogers (2014) predicted a higher wave climate for the Beaufort Sea,

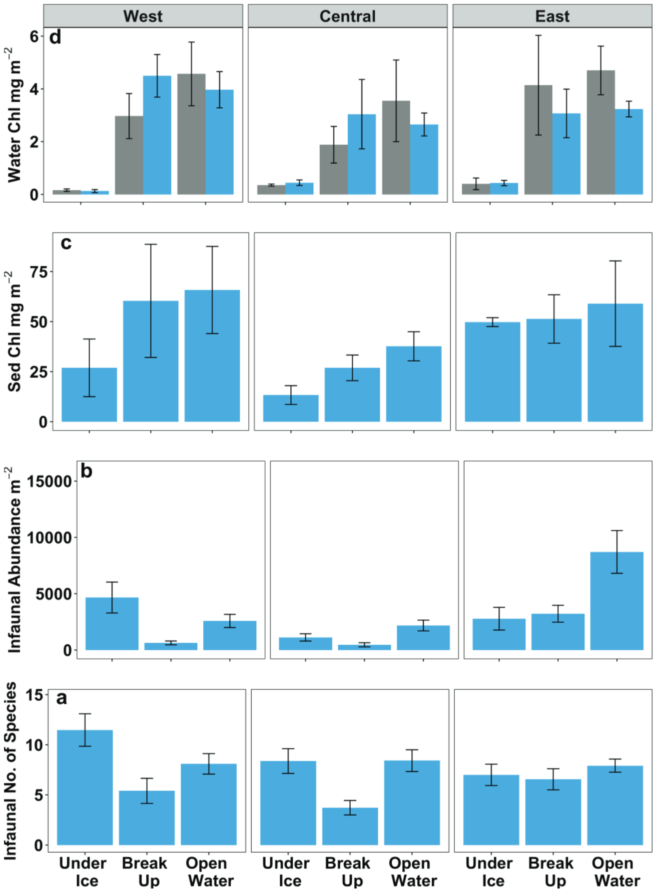

Figure 8. Seasonal variations in water column (d) and benthic chlorophyll a *(c) in relation to the abundance (b) and diversity (a) of infauna within replicate lagoon systems across 500 kilometers of Beaufort Sea coast from three nodes: the western (near Point Barrow), central (near Prudhoe Bay), and eastern (at Barter Island). Seasonal variations were captured by sampling during the period of total ice cover (April), sea ice breakup and the onset of river discharge (June), and the summer open-water period (August). Coincident trends in increasing benthic chlorophyll* a *and infaunal abundance are apparent with season. The period of total ice cover (1.5–1.8 meters of ice thickness) extends from early November to mid-June. Marine benthic fauna experience salinities that approach 0 for a week or more during the spring freshet. The water depth in the lagoons average about 3 meters. The bottom (less than 1.5 meters from the bed) and surface (less than 3 meters down) chlorophyll-*a *levels are depicted in gray and blue bars, respectively (d). Light levels are low during the ice-covered period, are highest following the spring freshet, but decrease again as ice retreats and winds resuspend sediments and decrease light availability in these shallow estuarine systems.*

especially as waves transition from wind-driven seas into large nearshore swells. Wave height is of particular concern in the Beaufort Sea, because more than half of the coastline encloses shallow lagoons, bays, and sounds that lie at the interface between marine and terrestrial systems. In addition to the changes in nearshore ice conditions (Mahoney et al. 2014), coastal erosion has risen dramatically, permafrost is thawing leading to increased annual river discharge and changes in the timing of freshet (event-scale springtime freshwater discharge; Peterson et al. 2006), thermokarst development has increased (Rawlins et al. 2019), and summer open-water underwater irradiance has decreased (Bonsell and Dunton 2018). Connectivity between lagoon and Beaufort Sea waters is also expected to change as rising sea levels and sea ice loss continue to produce waves that frequently override and erode barrier islands that protect the coastal lagoons, affecting the depth and width of passes between the coastal lagoons and open sea. These processes ultimately control coastal erosion and watershed export to the coastal ocean (Jones et al. 2009), with significant implications for water column characteristics and the exchange of carbon, water, and nutrients on the inner shelf.

The Arctic Ocean receives approximately 11% of global river discharge while accounting for only approximately 1% of global ocean volume (McClelland et al. 2012). In Canada, the Mackenzie River delivers substantial quantities of fresh water to the ocean, where it is largely trapped as a floating freshwater lake—Lake Herlinveaux—in spring. Much of this water is received during the spring freshets, extreme events that occur every May and June in the High Arctic coastal system, because the rivers are frozen for nearly 8 months annually. In these events, an enormous amount of riverine melt water, trapped for the previous 8 months, is released all at once. The result is a massive freshening of coastal waters in which salinities drop from well above 30 to nearly 0 in just days. Nutrient inputs from these rivers draining the Arctic tundra are also high—for example, with nitrate concentrations averaging 100–200 micromols per liter. In view of the dominance of river inputs, these coastal lagoon systems are termed *polar estuaries*.

Ecological responses. In the Beaufort Sea, the delivery of over 50% of annual freshwater discharge in 2 weeks from North Slope rivers (McClelland et al. 2014) and a profound seasonality related to an 8–9-month period of ice cover dictates the large extremes in temperature, salinity, oxygen, and pH of Arctic lagoon systems. The ranges in the physical complexity and connectivity of these lagoons play a major role in their overall primary productivity and response to changes in the delivery of fresh water, nutrients, and organic matter. In more open embayments that are aligned with prevailing winds, inputs of organic matter from erosion and sediment resuspension become major physical disturbances that attenuate light. The decrease in underwater irradiance results in a shoaling of the critical depth, limiting production to the short period following ice breakup (Bonsell and Dunton 2018) when light and nutrients are simultaneously available for use. However, with rapid ice retreat in early summer, primary production is restricted to ever shorter windows as wind-driven waves and swells resuspend bottom sediments and facilitate erosion that is increasingly compromised by permafrost degradation.

In contrast to open embayments, semienclosed lagoons are less affected by wind and wave fetch that cause erosional and resuspension processes. Primary production is likely to extend into the early open-water season until nutrients are depleted. In the future, lower nutrient inputs in lagoons with restricted openings to the coastal ocean may be supplemented by increased nutrient loading from rivers and streams as the proportion of subsurface runoff to total runoff increases with permafrost degradation (Rawlins et al. 2019).

Despite extreme seasonal variations in Beaufort Sea physical conditions, secondary production, as is reflected in the epibenthic (polychaete worms, bivalve mollusks and crustaceans) and pelagic (copepods, pteropods and arctic cod) biota of lagoon waters, is remarkably abundant and diverse (figure 8a, 8b; Dunton et al. 2012). These organisms are critical prey for thousands of shore birds representing over 60 species that breed and raise their young over the short summer period (Brown 2006). On the basis of isotopic data, a high percentage of carbon is derived from terrestrial sources (Dunton et al. 2012, Harris et al. 2018), but recent evidence suggests that there are strong seasonal shifts in dependence on marine versus terrestrial carbon. Such seasonal dependencies are aligned with the high availability of presumably terrestrial dissolved organic carbon during peak flow in spring and lower concentrations of dissolved organic carbon during the ice-covered period when exchanges are limited to the coastal ocean (Connolly et al. 2020) and benthic microalgae are prevalent. Finally, the resiliency of benthic fauna to extremes in temperature (–2°C to 12°C) and salinity (from nearly 0 during the spring freshet to over 90 during the period of ice cover) is of great ecological importance because many are key prey species in lagoon food webs.

Measurements of benthic infaunal abundance and diversity, along with in situ chlorophyll during the progression from 8 months of ice cover, to breakup, followed by open water illustrates the increased availability of autogenous carbon in concert with benthic production (figure 8). Seasonal increases in benthic chlorophyll are aligned with increases in infaunal abundance (especially polychaete worms) and, in some lagoon systems, with increased benthic diversity. The high concentration of sediment chlorophyll *a* (frequently over 75 milligrams [mg] per square meter [m^2]) dwarfs inputs of water column chlorophyll *a* (breakup and open water integrated concentrations average less than 5 mg per m^2) by over an order of magnitude (figure 8). Benthic infauna are important prey of many species of fish (e.g., Arctic char, Arctic cisco, least cisco), major components in the diets of native Inupiat people for their subsistence lifestyle. Decadal changes in body condition of these diadromous fish, as was noted by von Biela and colleagues (2011), may reflect the differential abundance of autogenous versus allochthonous sources of organic carbon. Indicators of ecosystem shifts are often reflected in changes in the relative abundance or overall body condition of high trophic level organisms (Moore et al. 2014), as was noted by the higher energy density in juvenile herring that have access to advected zooplankton (Gorman et al. 2018). Consequently, the response of these species to warming temperatures and decreasing ice extent are of considerable concern.

Synthesis of climate responses at marine pelagic LTER sites

All five pelagic LTER sites are sensitive to interannual climate variability over a range of scales (table 3). The physical system is responding to climate variability at all sites, principally by surface mixed layer warming and changes in mixed layer depth (figures 4c, 5a, 5b, 6b, 7a, 7b, and supplemental figure S4). Ecological responses are more variable (e.g., supplemental figure S5). In some cases, variability in ecosystem properties and populations or functional groups (e.g., zooplankton herbivores) corresponds to particular modes of climate variability such as the Pacific Decadal Oscillation (figures 4a, 4b, 7d, and 7e), whereas others do not (e.g., upper trophic levels at Northern Gulf of Alaska and Northeast US Shelf; figures 5e and 7e). Nonetheless, all these responses to climate variability suggest ocean systems are vulnerable to long-term warming. The surface ocean is warming at the four deepwater pelagic sites (more than 20 years). There are significant declines in sea ice cover at the two polar sites. Mixed layer depth has shoaled at the Palmer Station, Northern Gulf of Alaska, and Northeast US Shelf sites, as is predicted by climate models, although at varying rates (supplemental figure S4). Long-term ecological trends have been established at three of the four sites with at least two decades of observation (figures 4–7, supplemental figures S4 and S5).

Several of these responses are shared across sites. For example, Northern Gulf of Alaska, Palmer Station, and California Current ecosystem are influenced by ENSO and the Pacific Decadal Oscillation. Beaufort Lagoons and Palmer Station are experiencing significant loss of sea ice cover. Sites may share responses but some are opposite in sign, such as chlorophyll concentration at Palmer Station and Northeast US Shelf. The causes of these trends are still uncertain. For example, although the decline in Adélie penguins at Palmer Station LTER is highly significant (figure 6e), there is no consensus regarding the underlying mechanisms. Finally, we note that we can only examine trends for those variables that were selected for observation two or more decades ago. Other variables might be responding invisibly to climate change without our knowledge.

Ecosystem change and ecosystem services: Coastal fisheries

In the preceding sections, we presented examples of changes in marine pelagic systems, some of which qualify as abrupt changes in dominant state (e.g., figure 6e; Bestelmeyer et al. 2012). Such changes are widespread in coastal and open ocean regimes (Beaugrand et al. 2019). The examples we

Table 3. Major processes and responses among sites.

Site	Long-term atmospheric warming?	Mixed layer response to LTW or SIC	Phytoplankton response to LTW (bottom up)	Herbivore response to LTW	Upper trophic level LTW responses(top down)	SIC
California Current Ecosystem	Yes	Warming	No response detected	Krill increasing	No response detected	–
Northeast US Shelf	Yes	Warming	Decreasing	No response detected	No response detected	–
Northern Gulf of Alaska	Yes	Warming, shallowing	No response detected	No response detected	No response detected	–
Palmer Antarctica	Yes	Warming, shallowing	Increasing	Copepods increasing	Adélie penguins declining	Declining
Beaufort Lagoons	Yes	No	No	N/a	??	Declining

Note: See the text and figures 4–8. *Abbreviations:* LTW, long-term warming; SIC, sea ice cover. [a]There are also terrestrial factors contributing to Adélie declines; see Fraser and colleagues (2013).

have highlighted suggest changes of state that may occur in response to particular forcings, such as atmosphere and ocean warming and acidification. The ocean carbonate system, from which pH can be derived, is measured at all five sites, and a long term trend of declining pH has been established at the California Current Ecosystem site (Taylor Wirth, Scripps Institute of Oceanography, San Diego, California, United States, personal communication, April 23, 2022). In terrestrial ecosystems, the mechanisms causing long-term ecosystem responses to particular external forcings can be tested and verified by replicated experimental treatments (e.g., soil warming, carbon dioxide enhancement, controlled burning, grazer exclusion) at ecosystem scales (years to decades). Such ecosystem-scale perturbation experiments are rarely feasible in marine pelagic environments, because of the confounding effects of storms and lateral transport.

One exception is artificial, open ocean iron fertilization (Boyd et al. 2007), now banned out of concern for unknown and unintended consequences (Tollefson 2008). In lieu of deliberate experimental treatments, ocean ecologists have relied on long-term observations, natural or unintended experiments, and modeling studies. Fishing, human predation on the upper trophic levels of marine food webs, represents one such major unintended experiment at the global scale.

Global fisheries, the majority of which are in coastal and ocean margin regions, supply about 15% of human protein consumption. Overfishing is not a recent phenomenon. Over human history, most fish populations to which humans have had access (starting with inland and shallow coastal habitats) have been overexploited, starting around 90,000 BCE (Pauly et al. 2005). Since the Industrial Revolution, the application of agricultural, military, and industrial technology to fishing has extended overexploitation to the global scale. Overexploitation of top predators has caused fundamental shifts in marine food webs, creating anthropogenic ocean ecosystems. When overfishing results in collapse of target top predator species, fishing targets successively lower trophic level species (Pauly et al. 1998), potentially devastating food webs. In a global analysis of dynamic properties of fishery-supporting food webs, du Pontavice and colleagues (2019) showed that trophic transfer efficiency and biomass residence times have declined, and will continue to do so as the ocean warms under various Intergovernmental Panel on Climate Change scenarios of carbon dioxide emissions (Bindoff et al. 2019). Furthermore, they suggested that these changes were due to the combined effects of fisheries overexploitation and ocean warming. The impacts of multiple stressors (climate change, acidification, eutrophication, toxicants) imply that restoration of sustainable fishing practices alone will not lead to the recovery the of ecosystems supporting global fisheries. Finally, bycatch, the unintentional capture of nontarget species, further exacerbates the damage inflicted by fishing. Each of the marine sites considered in the present article supports major local or regional fisheries (table 1). These fishery-supporting ecosystems are subject to such combined stresses as we show briefly in closing.

The Northeast US Shelf is a multifaceted and diverse ecosystem that exhibits a range of sensitivities, threshold responses, adaptive capacities, resistance to disturbance, and patterns of recovery that vary with trophic level. Although plankton respond on short time scales, their taxonomic and functional diversity promote aspects of resilience to severe perturbations in biomass and productivity at the base of the food web. Nonetheless, changes in food web structure in the plankton are associated with shifts in timing and quality of food available for higher trophic levels. Combined with changes in habitat (e.g., temperature regime) and other direct pressures (e.g., harvesting), these food web shifts propagate to important changes in abundance, seasonality, and spatial distribution of higher trophic levels including commercially important species (figure 5e; Lucey and Nye 2010, Bell et al. 2015, Kleisner et al. 2017, Pershing et al. 2021). The region supports four main types of valuable fisheries: groundfish (e.g., cod), small pelagic fish (e.g., herring), shellfish (e.g., sea scallop), and crustacea (e.g., lobster). Examples of long-term responses to the combined pressures of climate and harvesting pressure across these fisheries include a general decline in groundfish since the 1960s, exemplified by cod but also for other species, such as haddock, silver hake, and yellowtail flounder. Some species have also exhibited distinct range shifts, such as highly fluctuating stocks of small pelagic fish, exemplified by herring and sand lance (Suca et al. 2021a, 2021b) and by mackerel and menhaden, a multidecade increase in sea scallops, and dramatic fluctuations and spatial shifts in lobster linked to warming trends (increasing in the Gulf of Maine but decreasing in the Southern New England region).

Amid several important commercial fisheries in the California Current Ecosystem region, the Pacific sardine fishery extending from Southern California to the Gulf of Alaska is illustrative of the interplay among the internal dynamics of the forage and recruiting populations, commercial exploitation, and possibly climate variability (Lindegren et al. 2013). The paleorecord (Soutar and Isaacs 1969) of preserved fish scales in sediment cores extending back approximately 1700 years (well before fishing) reveals natural population collapses and recoveries over 500-year time scales, as well as multidecadal cycles, suggesting long-term resilience (McClatchie et al. 2017). Climate fluctuations have been suggested as an external driver but with little corroborating evidence. Fishery-based stock data show a rapid major collapse between 2005 and 2011, with no recovery to date (Hill et al. 2019). The collapse has no clear relation to the recent warming events (Amaya et al. 2016) but continued regional warming in the California Current region may be suppressing recovery.

Given the importance of its fisheries, many Northern Gulf of Alaska stocks have been monitored for the past 40–50 years. It remains debated to what degree the collapse of the Pacific herring fisheries within the Prince William Sound ecosystem was driven by climate versus the Exxon *Valdez* oil spill (Pearson et al. 2011). The responses of species to climate variability and change vary considerably. Nonetheless, several species of forage fish clearly suffered during the recent marine heat wave. The biomass of several apex fish stocks after the heat wave were some of the lowest observed during the 30 years of surveys (Rogers et al. 2021).

By their very nature, lagoon ecosystems of the Beaufort Sea—which are subject to freezing; ice scour; and extremes in temperature, salinity, light, and dissolved oxygen—define resilience. Despite the extreme seasonality of these coastal lagoons, benthic epifauna either survive freezing or rapidly populate previously ice-bound shallow areas in time to serve as food resources for a variety of higher trophic level consumers that include several species of anadromous fish and migrating ducks. Native Alaskan Inupiat subsistence fishers and hunters depend heavily on these marine resources, which they begin harvesting in the spring along with marine mammals (seals and beluga whales) that feed in the lagoons or directly along the coastal margin of lagoon inlets and barrier islands. The cultural importance of these harvests extends over 500 km of coast, from the native village of Utqiaġvik at Point Barrow to Kaktovik, on Barter Island. The fishery resources exploited include salmon, Arctic char, Dolly Varden trout, broad whitefish, Arctic cisco, least cisco, and other species. These fish, along with Arctic cod, are key prey species for migrating beluga whales and ringed seal, which are also important food sources for native Inupiats. Consequently, there remains a heavy need for a cosharing of knowledge and cooperative research to address local concerns on the effect of changing temperatures and ice conditions on harvestable resources that are ultimately dependent on a sound ecological system.

Globally, and for the four deepwater pelagic LTER sites, krill play an important role in ecosystem function and serve as prey for seabirds, marine mammals, and commercially important species. Krill fishing is banned along the US West Coast (PFMC 2008), but small fisheries exist in the northern hemisphere off British Columbia and Japan, and the largest fishery occurs in the Southern Ocean (Nicol and Endo 1999, Nicol and Foster 2016), where Antarctic krill is mainly harvested to produce fish bait or aquaculture feed (Nicol et al. 2012). The central location for this international krill fishery is north–northeast of the Antarctic Peninsula (Reid 2019). Obtaining krill biomass estimates to set annual catch limits has been a challenge because of the enormous spatial distribution range that krill occupy (Atkinson et al. 2009, Cavan et al. 2019). Krill removals are considered to be at precautionary levels, but negative fishery impacts on food webs, predators, biogeochemical cycles, and other ecosystem processes are still possible (Pauly et al. 1998, Nicol et al. 2012, Plagányi and Butterworth 2012, Watters et al. 2020).

Conclusions

Marine plankton ecosystems absorb direct, intentional (fisheries, aquaculture, waste disposal), unintentional (pollution, eutrophication), and accidental (oil spills) impacts from at least 40% of the world's population living within 100 km of a coast. Overlying these directly imposed disturbances are indirect, global scale anthropogenic forcings including climate change and ocean acidification that pose an even greater threat to ecosystem integrity. In the present article, we catalog some of the mechanisms linking climate variability and change to ecosystem responses in marine pelagic plankton systems (figures 4–8). Long-term observations show that these ecosystems suffer abrupt, nonlinear changes of state affecting the goods and services they provide. It is critical to continue and expand our observational and theoretical capabilities if we are to understand how ecosystems respond to climate variability and trends.

All sites are experiencing surface atmosphere warming. There has been slightly more summer warming in the Northeast US Shelf and Northern Gulf of Alaska but more winter warming in the Beaufort Sea and Antarctic Peninsula and year-round warming in the California Current. All sites experience interannual to interdecadal climate variability, eliciting changes in the physical ocean system including winds, upwelling, surface warming and declining sea ice cover.

The physical ocean system is responding to multidecadal climate warming at all five sites. The surface ocean is warming at the four deepwater sites. The two polar sites have exhibited dramatic declines in sea ice cover, and mixed layer depth has shoaled (shallowed) at the Palmer Station, Northern Gulf of Alaska, and Northeastern US Shelf sites.

All sites (except the benthic-dominated Beaufort Lagoons site) demonstrate changes in the magnitude, seasonality, and composition of phytoplankton blooms in response to changes in nutrient delivery and mixed layer depth, although longer-term trends have not been confirmed at some sites. Changes in herbivore populations and upper trophic levels are evident at some (but not all) sites. In general, there is more uncertainty in detecting changes in populations with increasingly longer life spans and generation times. Many marine and terrestrial LTER sites are just approaching the age at which ecological responses to climate variability and climate change might be detected and verified.

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Supplemental material

Supplemental data are available at *BIOSCI* online.

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