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Original Article

Planktonic to sessile: drivers of spatial and temporal variability across barnacle life stages and indirect effects of the Pacific Marine Heatwave

Sarah B. Traiger[1,*], James L. Bodkin[1], Robert W. Campbell[2], Heather A. Coletti[3], Daniel Esler[1], Kris Holderied[4], Katrin Iken[5], Brenda Konar[5], Caitlin A. E. McKinstry[6], Daniel H. Monson[1], Jessica L. Pretty[2], Martin Renner[4], Brian Robinson[1], Robert M. Suryan[7] and Benjamin P. Weitzman[8]

[1]Alaska Science Center, U.S. Geological Survey, 4210 University Drive, Anchorage, AK, 99508, USA
[2]Prince William Sound Science Center, 1000 Orca Inlet Road, Cordova, AK, 99574, USA
[3]Southwest Alaska Inventory & Monitoring Program, National Park Service, 240 West 5th Avenue, Anchorage, AK, 99501, USA
[4]NOAA National Centers for Coastal Ocean Science, 95 Sterling Highway, Homer, AK, 99603, USA
[5]University of Alaska Fairbanks, 2150 N Koyukuk Dr, Fairbanks, AK, 99775, USA
[6]Native Village of Eyak, 110 Nicholoff Way, Cordova, AK, 99574, USA
[7]Auke Bay Laboratories, NOAA Alaska Fisheries Science Center, 17109 Point Lena Loop Rd, Juneau, AK, 99801, USA
[8]Marine Mammals Management, U.S. Fish & Wildlife Service, 1011 E Tudor Rd, Anchorage, AK, 99503, USA

[*]Corresponding author: straiger@usgs.gov

Corresponding editor: John Dolan

ABSTRACT

Barnacles are a foundation species in intertidal habitats. During the Pacific Marine Heatwave (PMH), intertidal barnacle cover increased in the northern Gulf of Alaska (GoA); however, the role of pelagic larval supply in this increase was unknown. Using long-term monitoring data on intertidal benthic (percent cover) and pelagic larval populations (nauplii and cyprid concentrations), we examined potential environmental drivers (temperature, chlorophyll-a, mixed layer depth) of larval concentration and whether including larval concentration at regional and annual scales improved intertidal barnacle percent cover models in two study regions in the GoA. In both regions, larval concentrations were slightly higher following the PMH. Percent cover models were improved by including cyprid concentrations (but not nauplii), and the effect strength varied by site and tidal elevation. This indicates that larval concentration contributes as a bottom–up driver of benthic barnacle abundance. There is little evidence of a direct effect of the PMH on either life stage. Instead, our results may illustrate the positive feedback between life stages, where higher adult benthic abundance increased larval concentrations, which then supplied more new recruits to the benthos. As heatwaves continue to occur, integrating various data types can provide insights into factors influencing both benthic and pelagic communities.

KEYWORDS: intertidal; barnacle; larvae; chlorophyll-a; temperature; heatwave

INTRODUCTION

Barnacles are an important component of coastal ecosystems, both in their benthic forms and as part of the plankton community in their larval forms. Once reproductive, sessile adult barnacles release larval planktonic nauplii, followed by a non-feeding planktonic cyprid stage, which then settle on a hard substrate in nearshore habitats and become sessile suspension-feeding juvenile and adult barnacles (Hentschel and Emlet, 2023). Settlement is the process of larvae attaching to a substrate (Holmes *et al.*, 2005), while recruitment is defined as the number of new individuals quantified at a given life stage. In the context of intertidal barnacle cover, recruitment is often defined as some time period post-settlement, typically more than 24 hours or once barnacle spat becomes visible (Raimondi, 1990; Pineda *et al.*, 2009). In the intertidal, barnacles can facilitate colonization by other species (Menge *et al.*, 2011); compete with macroalgae for space (Dayton, 1971); and are prey for nearshore taxa such as sea stars, whelks, and birds (O'Clair and O'Clair, 1998). In the water column, barnacle nauplii can occur at high concentrations in some seasons at high latitudes (McKinstry *et al.*, 2022) and can be important prey for larval fish (Turner, 1984) and hoplonemertean larvae (von Dassow *et al.*, 2022). Describing spatial and temporal variability of planktonic barnacle larvae is important for understanding their role in the pelagic ecosystem and determining mechanisms of variability in abundance of the benthic sessile form, which is usually studied without knowledge of larval supply.

Drivers of barnacle larval concentration are likely to be factors that affect larval food supply (Starr *et al.*, 1991), their physiological rates (Desai and Anil, 2000), predation (Thorson, 1950), and their ability to maintain their position in the water column (Hagerty *et al.*, 2018). Barnacle larvae in temperate regions have

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distinct seasonal cycles because adult barnacles time the release of nauplii to coincide with phytoplankton blooms (Starr *et al.*, 1991), and temperature also provides a cue for larval release and correlates with peak abundance of the larval pool (Fernandes *et al.*, 2012). However, barnacle larvae can be abundant throughout the year if multiple species with different seasonal patterns are present (Lang and Ackenhusen-Johns, 1981). As barnacle nauplii are omnivores, preferring diatoms and small flagellates (Turner *et al.*, 2001), phytoplankton concentrations can affect their survival and abundance. Thermal stratification can help larvae remain in the upper water column where food is more abundant, and barnacle larval concentrations have been found to be positively correlated with thermal stratification within 1 km of shore (Hagerty *et al.*, 2018; Yamhure *et al.*, 2021). Many of these environmental conditions are affected by marine heatwaves, such as the 2014–2016 Pacific Marine Heatwave (PMH) in the Gulf of Alaska (Suryan *et al.*, 2021).

Gulf of Alaska marine ecosystems were significantly affected by the PMH, with major declines in pelagic birds, marine mammals, and forage fish (Suryan *et al.*, 2021). However, increases in some zooplankton populations were observed (Suryan *et al.*, 2021; Batten *et al.*, 2022) and overall phenology and zooplankton community structure in the Gulf of Alaska also were affected by the PMH (McKinstry and Campbell, 2018; McKinstry *et al.*, 2022). In rocky intertidal habitats, barnacle cover increased during the PMH, while macroalgal cover declined, leading to a functional shift in the available habitat (Weitzman *et al.*, 2021). However, the effects of the PMH on barnacle larval concentrations and the role of larval supply in the increase in barnacle cover are unknown. Studies in other regions indicate that marine heatwaves can affect zooplankton communities. In Tasmania, some meroplankton were positively affected by increased temperatures (Evans *et al.*, 2020). In Oregon and Washington, densities of crustacean zooplankton decreased, and gelatinous zooplankton increased during a heatwave (Brodeur *et al.*, 2019). In the Salish Sea, high temperatures during the PMH may have contributed to higher growth and biomass of zooplankton during and after the heatwave (Winans *et al.*, 2023). Understanding drivers of barnacle larval variability from long-term time series of larval and benthic abundance can help to determine the effects of large-scale events, like marine heatwaves, on barnacles throughout their life cycle.

Barnacle recruitment in the intertidal is dependent in part on larval supply, and knowledge of the abundance and variability of the larval pool could help uncover the mechanisms behind the temporal and spatial variability of sessile populations (Pineda *et al.*, 2009). Effects of larval supply on intertidal invertebrate abundance have mainly been studied in barnacles at small spatial scales (i.e. sites separated by <10 km) (Gaines and Roughgarden, 1985; Minchinton and Scheibling, 1991) with fine temporal resolution (larval supply or barnacle recruitment monitored daily to weekly) (Shanks, 1986; Gaines and Roughgarden, 1987; Farrell *et al.*, 1991; Bertness *et al.*, 1996). At small spatial scales, site-specific features such as the presence of kelp forests and wind direction influence barnacle larval retention and supply to the intertidal (Gaines and Roughgarden, 1987; Bertness *et al.*, 1996). Studies with fine temporal resolution have demonstrated the effects of coastal upwelling, tides, and internal waves on the timing and magnitude of cyprid settlement and barnacle recruitment in California (Shanks, 1986; Farrell *et al.*, 1991) and Oregon (Dudas *et al.*, 2009). Over annual time scales, differences in barnacle settlement and population structure among years have been shown to depend on the strength of upwelling (Barshis *et al.*, 2011). Relationships between barnacle larval supply and recruitment may be different in non-upwelling systems and protected bays and fjords along the Gulf of Alaska, which has not been studied previously. In Nova Scotia, barnacle recruitment in May is strongly related to sea surface temperatures in April, presumably due to higher survival and growth of the larval stages (Scrosati and Ellrich, 2024). Long-term trends in sessile barnacle abundance may be related to temperature effects on reproduction and larval supply, so determining the drivers of larval abundance can help explain sessile barnacle trends (Little *et al.*, 2021).

Given the high spatial and temporal variability of intertidal barnacle abundance (Raimondi, 1990; Little *et al.*, 2021) and their importance to nearshore ecosystems, information about the role of any potential drivers of variability in barnacle abundance is valuable. Monitoring programs for invertebrate benthic stages and larval planktonic stages are rarely coordinated and, thus, typically cover different spatial scales and have different temporal resolution. Here, we consider two regions of Alaska with varying oceanographic conditions, Prince William Sound, an inland sea, and Kachemak Bay, a fjord connected to lower Cook Inlet, both with long-term coastal monitoring programs, to examine the relationships among environmental drivers, planktonic barnacle larval concentrations, and intertidal benthic barnacle percent cover. Our research objectives were to (i) describe temporal and spatial variation in barnacle larval concentration to investigate potential environmental drivers and the influence of the PMH on planktonic larval concentrations and (ii) explore whether models of intertidal barnacle percent cover are improved by the inclusion of regional-scale estimates of larval concentrations.

MATERIALS AND METHODS

Study metrics and regions

Planktonic barnacle larvae and water-column environment (temperature, chlorophyll-a concentration, water-column stability (Campbell, 2017; Holderied *et al.*, 2023) along with intertidal barnacle percent cover, water, and air temperatures (Dean and Bodkin, 2011, U.S. Geological Survey & National Park Service Southwest Alaska Inventory and Monitoring Network, 2016; U.S. Geological Survey & National Park Service Southwest Alaska Inventory and Monitoring Network, 2022) were monitored in Prince William Sound and Kachemak Bay. Prince William Sound (PWS) is an inland sea characterized by an estuarine-fjord system with multiple sub-basins (Fig. 1). Ocean water generally enters PWS through Hinchinbrook Entrance to the east and exits through Montague Strait to the west (Niebauer *et al.*, 1994). PWS receives freshwater from the Copper River via the Alaska Coastal Current, as well as from streams, rivers, and icefields within the sound. PWS is divided into four hydrological areas: northwest, east, central sound, and Gulf of Alaska (Musgrave *et al.*, 2013). The northwest and east areas both have large freshwater influence from rivers, but the northwest has greater freshwater influence from glacial melt (Musgrave *et al.*, 2013). The central Sound and Gulf of Alaska areas are more influenced by exchange with the Gulf of Alaska (Musgrave *et al.*, 2013). Barnacle larval concentration, water column temperature, and chlorophyll-a concentration were monitored at 12 stations throughout PWS (see Barnacle Larvae and Water-column Environment below, Fig. 1). Intertidal sessile barnacle percent cover and both water and air temperatures were monitored at five rocky intertidal sites, all located within the northwestern hydrographic area (see Intertidal Barnacle Percent Cover and Temperature below, Fig. 1). The five intertidal sites were randomly selected from all identified sheltered rocky shoreline in western PWS (Dean *et al.*, 2014).

Kachemak Bay is a fjord connected to lower Cook Inlet (Fig. 1). Hereafter, we use KBAY to refer to the general region of Kachemak Bay and lower Cook Inlet, to distinguish it from PWS, and we use "Kachemak Bay" when we specifically reference the bay separate from lower Cook Inlet. Ocean water enters the lower Cook Inlet through Kennedy Entrance (Johnson, 2021). Currents flow into Kachemak Bay along the southern side of the bay. Freshwater inputs from rivers at the head and southern side of the bay, including glacial inputs, produce currents that flow north across the bay and then to the west along the northern side of Kachemak Bay. Kachemak Bay is split into an outer bay and an inner bay by the Homer Spit, with generally more oceanic influences in the outer bay and more freshwater influences in the surface waters of the inner bay. Eddies in outer Kachemak Bay can divert some of the surface water from the Gulf and Inlet from entering the bay past the Homer Spit (Gatto, 1982). Outside of Kachemak Bay, currents flow northward along the eastern side of Cook Inlet and southward along the west side of Cook Inlet. Barnacle larval concentration, water column temperature, and chlorophyll-a concentration were monitored at 17 stations in lower Cook Inlet and Kachemak Bay (see Barnacle Larvae and Water-Column Environment below, Fig. 1). These 17 stations are part of six transects. Three transects cross lower Cook Inlet, two transects cross outer Kachemak Bay, and one transect spans the along-bay oceanographic gradients along the axis of Kachemak Bay. Intertidal barnacle percent cover and both water and air temperatures were monitored at six rocky intertidal sites, with two sites on the northern side of outer Kachemak Bay and four sites on the southern side of outer Kachemak Bay (see Intertidal Barnacle Percent Cover and Temperature below, Fig. 1). The six intertidal sites selected were similar in slope, substrate, and exposure (Konar *et al.*, 2007).

Our analysis for our second research objective, to explore whether models of intertidal barnacle percent cover are improved by the inclusion of regional-scale estimates of larval concentrations, relies on two assumptions. First, we assume that barnacle larval tow samples are composed, at least in part, of the species we sampled in the intertidal. The taxonomic resolution of the intertidal barnacle percent cover and barnacle larvae data sets match, with both at family Cirripedia level. Our second assumption is that barnacle larval concentration averaged across stations within each region reflects the larval supply to our sites to some degree at an annual timescale. In each region, the barnacle larval stations and intertidal sites are connected by surface currents.

Barnacle larvae and water-column environment

In PWS, pelagic stations were sampled six to nine times per year from 2010 to 2021. In KBAY, pelagic stations were sampled quarterly, bimonthly, or monthly (Fig. 1, Table S1). In KBAY and lower Cook Inlet, the western and middle stations on transects 6, 7, and 3 were sampled from 2012 to 2017. The eastern stations on transects 6, 7, and 3 and all the stations on transects 4 and 9 were sampled from 2012 to 2021. The stations on the along-bay (AB) transect were sampled from 2017 to 2020.

Barnacle larvae were collected and processed following McKinstry and Campbell (2018) and McKinstry *et al.* (2022). Briefly, we sampled barnacle larvae using a 0.6 m diameter bongo net (PWS 202 μm mesh size, KBAY 333 μm mesh size) towed vertically from 50 m or just above the bottom, with one tow per station. Barnacle nauplii are 0.59 and 0.53 mm long in PWS and KBAY, respectively, and cyprids are 1 and 0.94 mm long in PWS and KBAY, respectively, and are therefore likely to be caught in the nets used in this study. Barnacle larvae were preserved in 5% formalin and identified in subsamples containing at least 400 zooplankton individuals, with ~200 of the most abundant taxa (not limited to barnacles) (Lund *et al.*, 1958), and barnacle larvae were identified at the class level (Cirripedia) to stage (nauplii and cyprids).

Temperature, chlorophyll-a concentration, and salinity were monitored using conductivity–temperature vs depth profiler (CTD) casts at each station (Campbell, 2018; McKinstry *et al.*, 2022). In PWS, casts were conducted at each station on the same day as barnacle larvae sampling. In KBAY, most casts were conducted at the same time and location as the barnacle larvae sampling, but, occasionally, casts were not conducted on the same day. For stations where a cast was not conducted on the same day, CTD data collected at the same station or a nearby station within 1 day of the barnacle larval sampling were used in analyses (see Table S2 for details).

Intertidal barnacle percent cover and temperature

The barnacle percent cover and intertidal temperature data came from two separate monitoring programs that were merged into the Gulf Watch Alaska program (Konar *et al.*, 2007; Dean *et al.*, 2014). Intertidal barnacle and bare space percent cover were estimated once annually between May and July at 0.5 and 1.5 m above mean lower low water (MLLW). In PWS, percent cover was estimated by the proportion of points (grid of 25 points) occupied by barnacles within 12 0.25 m^2 quadrats at each tidal elevation approximately annually since 2010 (Table S1). In KBAY, barnacle and bare space percent cover were estimated visually within 10 1 m^2 quadrats annually since 2012. A detailed comparison of the two percent cover sampling methods was conducted by Konar *et al.* (2016), revealing generally similar physical characteristics, and common intertidal elevations were being monitored, allowing for robust interpretation of drivers and causes of change in the intertidal system (Coletti *et al.*, 2016; Weitzman *et al.*, 2021). The barnacles present in the intertidal in these regions include *Balanus glandula*, *Chthamalus dalli*, *Semibalanus balanoides*, and *S. cariosus*. All barnacle species

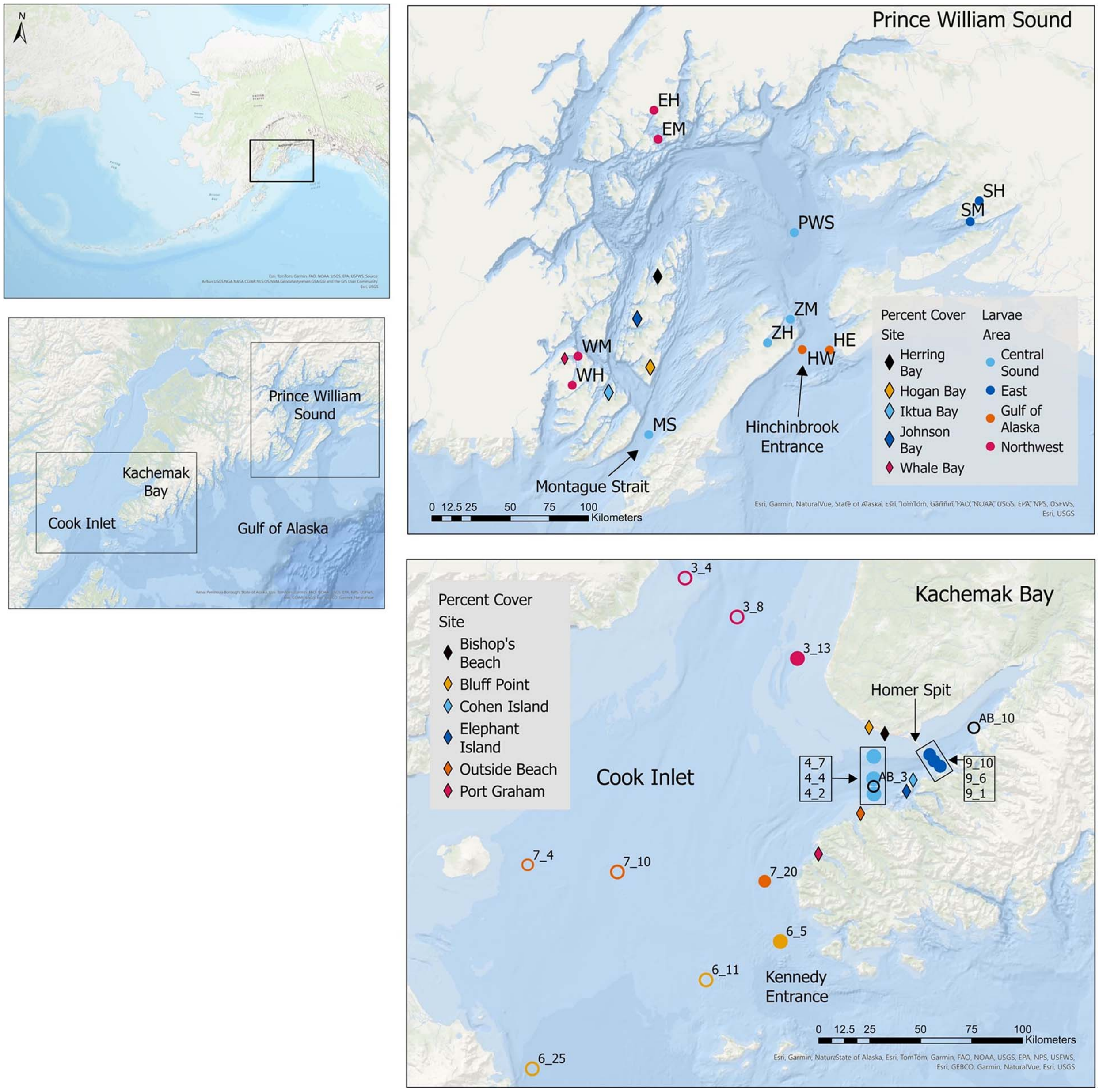

Fig. 1. Map of study areas with inset maps for PWS and KBay. Diamond symbols are barnacle percent cover sampling sites, and circles are barnacle larvae sampling stations. In the Kachemak Bay map, the open circles indicate stations that were not included in the linear mixed-effect models of barnacle percent cover.

and sizes were lumped into a single category of "Barnacle" when percent cover was surveyed in the field. Bare space was defined as the area of rock not covered by any sessile invertebrate or algae.

Intertidal air and water temperatures were monitored using Honest Observer by Onset (HOBO) V2 temperature loggers (Onset Computer Corporation, Bourne, MA, USA) with an accuracy of ±0.2°C placed at 0.5 m MLLW at each intertidal site. Loggers recorded temperature every 20, 30, or 60 minutes. Data were separated into water and air temperatures based on water level predictions from the nearest tide station and standardized such that there was a temperature reading every 30 minutes. When the temperature was recorded other than every 30 minutes, we used a loess smoothing function (PROC LOESS, SAS Institute Inc., Cary, NC, USA) to interpolate a temperature for every 10-minute interval and then used only the 30-minute interval values. We never used an interpolated value if there was a recorded temperature value, and HOBOs have been programmed consistently to record at 30-minute intervals since 2018. For water temperatures, seasonal values were derived by averaging the mean daily temperature within each season, and, for air temperature, we averaged the daily minimum (winter) or daily maximum air temperature (summer). Spring was defined as March through May, summer as June through August, autumn as September through November, and winter as December through February.

Data analysis—barnacle larvae spatial and temporal variation and drivers

To describe spatial and temporal variation in barnacle larvae and investigate potential drivers, barnacle nauplii and cyprid concentrations (individuals m^{-3}) were $\log_{10}$(individuals $+1$) transformed to stabilize variance and analyzed using generalized additive models (GAMs) with the *mgcv* package (v. 1.8-42) in R (Wood, 2004; RCoreTeam, 2020). Separate analyses were conducted for PWS and KBAY. Sine- and cosine-transformed ordinal days were included in the candidate models to describe the seasonality of larval concentrations. This enabled us to examine the linear effects of season across a continuous summer-winter axis [sine(day)] and a continuous spring–autumn axis [cosine(day)]. Year was included as a smoothed parameter using a cubic regression spline.

To investigate spatial variability in larval concentrations, parameters representing position in space were included in the models depending on the region. Distance from land was included in the GAMs (Table S3). As larvae are released from adult barnacles in the nearshore, we expect stations closer to land to have higher concentrations as larvae diffuse through the water. At small spatial scales, barnacle nauplii have been found at higher concentrations farther from shore (up to 1.1 km, Tapia and Pineda, 2007); however, at the larger distances from shore included in this study (maximum of 18.87 and 31.87 km in PWS and KBAY, respectively), we expect lower nauplii concentrations with increasing distance from shore. In PWS, distance from the station in the center of the region ("PWS" station, Fig. 1) was included as a proxy for position within the region. Distance from the PWS station was used rather than latitude or longitude because latitude and longitude are oblique to the coastlines in PWS. In KBAY, the stations are well separated by latitude (in particular, the three transects in lower Cook Inlet) and longitude, so these variables were included as smooth parameters.

Temperature anomalies were included in the GAMs to investigate the effects of temperature separate from seasonal effects. For nauplii, temperature anomalies were calculated based on mean temperature from 0 to 5 m depth because barnacle nauplii are more abundant near the surface (Hagerty *et al.*, 2018; Bonicelli *et al.*, 2023). For cyprids, temperature anomalies were calculated based on mean temperature from 15 to 30 m depth because barnacle cyprids are more abundant deeper in the water column (Hagerty *et al.*, 2018; Bonicelli *et al.*, 2023). To create the baseline temperature for each region separately, data from all years were used to create a smoothed series of temperatures across all ordinal days using the *smooth* function in Matlab (MathWorks Inc., version 9.14.0 R2023a, Natick, MA) with a 30-day window. The mean temperature for each depth bin (0–5 or 15–30 m) for a particular day was then subtracted from the smoothed value for that day for the corresponding depth bin. Thus, the temperature anomaly represents how much higher or lower the observed temperature was on a particular day compared to the value from that day of the year from the smoothed temperature created using all years of data. In PWS, the temperature anomalies for each station were calculated using baseline smoothed temperature from the same stations. In KBAY, the temperature anomalies for each station were calculated using baseline smoothed temperature data from the mid-bay Station 6 of Transect 9, as this station had the most complete temporal coverage.

Chlorophyll-a concentration was included in GAMs for nauplii but not cyprids because cyprids are a nonfeeding stage. Chlorophyll-a concentration was integrated across depth using the *trapz* function in Matlab.

The depth of maximum buoyancy frequency was included in the GAMs as an ecologically relevant proxy for mixed-layer depth (Carvalho *et al.*, 2017). Brunt–Väisälä buoyancy frequency (N^2) was calculated using the *gsw-Nsquared* function from the Gibbs Seawater Oceanographic Toolbox (version 3.0) in Matlab (McDougall and Barker, 2011). Inputs to the function included absolute salinity, conservative temperature, and absolute pressure.

Data analysis—barnacle percent cover models

To investigate whether the addition of regional-scale nauplii or cyprid concentration improved models of barnacle percent cover, we used linear mixed-effects models with the *lmer* function from the *lme4* (v. 1.1-34) package in R (Bates *et al.*, 2015; RCoreTeam, 2020). Adjusted R^2 values were obtained using the *rsq.lmm* function from the *rsq* (v. 2.6) package (Zhang, 2023). We first used AICc (corrected Akaike information criterion) to find the best-supported model only including predictor variables specific to each intertidal site: percent cover of the bare substrate at a 1-year lag, and seasonal water and air temperatures. A one-year lag was used for the percent cover of bare substrate because we assume that bare space previously available is a more relevant predictor of the density of juvenile barnacles in any given year than bare space in the current year; barnacle percent cover and bare space at a single time point would be inversely autocorrelated. Temperature metrics included: mean daily mean water temperature in spring, summer, autumn, and winter; mean daily minimum air temperature in winter; and mean daily maximum air temperature in summer. An interaction between site and elevation was included as a fixed effect, and year was included as a random effect in all models.

We next added barnacle nauplii and cyprid concentration to the best-supported model to see if including larval concentrations improved the model. We included barnacle nauplii and cyprid concentration averaged across all stations for 12 months prior to benthic sampling in the analysis. For the KBAY analysis, we only included barnacle nauplii and cyprids from stations that were sampled in all years, which included all stations from transects 4 and 9 and the eastern stations from transects 6, 7, and 3 (Table S1). Because the barnacle percent cover included a range of individual sizes (and thus ages), nauplii and cyprid concentrations were also included with lags. Although barnacles can settle in high numbers, transforming from planktonic cyprids to the benthic life stage, their percent cover may be relatively low due to their small initial size. However, their percent cover may be greater in following years as individuals grow larger (e.g. *S. cariosus* can reach 55–60 mm diameter (Newman and Abbott, 1980), and uncrowded *B. glandula* can reach 20 mm diameter (O'Clair and O'Clair, 1998). For this reason, an increase in barnacle percent cover may be related to higher larval concentrations years earlier. *B. glandula* reach mature size in 2 years (O'Clair and O'Clair, 1998), while *S. cariosus* mature in 1 year (Noda, 2004).

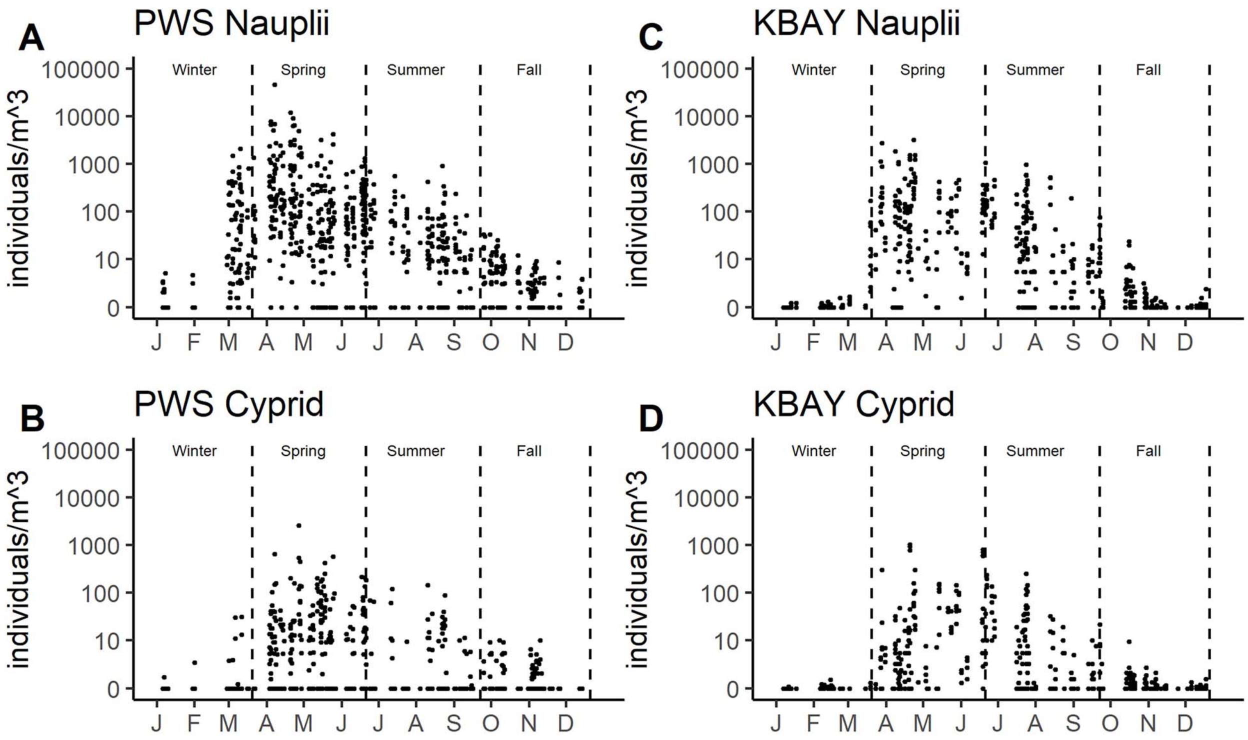

Fig. 2. Barnacle larval concentration by day of the year in PWS (**A**, **B**) and KBAY (**C**, **D**). Letters on the horizontal axis indicate months. Vertical dashed lines indicate seasons.

Table I: *GAMs of barnacle nauplii and cyprid concentrations in PWS and KBAY*

	Model formula	**ΔAIC**
PWS Nauplii	sine(Day) + cosine(Day) + s(Year) + Distance from land + Distance from PWS station + chlorophyll a + max N_2 depth	−1.129
PWS Cyprids	sine(Day) + cosine(Day) + s(Year)	−3.940
KBAY Nauplii	sine(Day) + cosine(Day) + s(Year) + s(Latitude)	−3.825
KBAY Cyprids	sine(Day) + cosine(Day) + s(Year) + s(Longitude)	−5.723

Mature individuals of these species may have settled 1–2 years prior, so nauplii or cyprid concentrations at a 1- or 2-year lag might contribute to variability in barnacle percent cover. In PWS, barnacle larval concentrations at 1- and 2-year lags were included in the analyses, while only 1-year lags were included for KBAY because of the shorter timeseries (and, therefore, lower sample size) in that dataset.

RESULTS

Barnacle larval spatial and temporal variation and drivers—PWS

Nauplii and cyprids in PWS followed a clear seasonal trend of rapidly increasing in the late winter and spring and then declining through the summer and autumn (Fig. 2). This is also demonstrated by the positive effect of the sine-transformed ordinal day (indicating that there were more nauplii and cyprids in spring than autumn) and a negative effect of the cosine-transformed ordinal day (indicating more nauplii and cyprids in summer than winter) (Table I, Table S4, Fig. S1).

In PWS, nauplii concentration varied among years with lower concentrations in 2013 and higher concentrations during and after the PMH, in 2015–2017, followed by a downward trend (Table II, Fig. 3A). Cyprid concentration had a slightly different trend, with low concentrations from 2010 to 2015 and then higher concentrations from starting at the end of the PMH, 2016–2018 (Fig. 3B). Temperature anomalies at 0–5 and 15–30 m were high during the PMH, but the highest anomaly observed during the time series was at 0–5 m in 2019 (Fig. 3C).

The predictor variables related to location within PWS, distance from land and distance from the station in the middle of the sound (PWS station), were included in the best-supported GAM for nauplii but not cyprids (Table I, Table S4). There was a negative effect of increasing distance from land on nauplii concentration, with the lowest nauplii concentration at the station farthest from land, the PWS station (Fig. 4A). There was a small negative effect of distance from the central sound PWS station on nauplii concentration (Fig. 4B). Nauplii concentration was higher at the head of bays compared to the mouth of bays (Figs 1 and 4B).

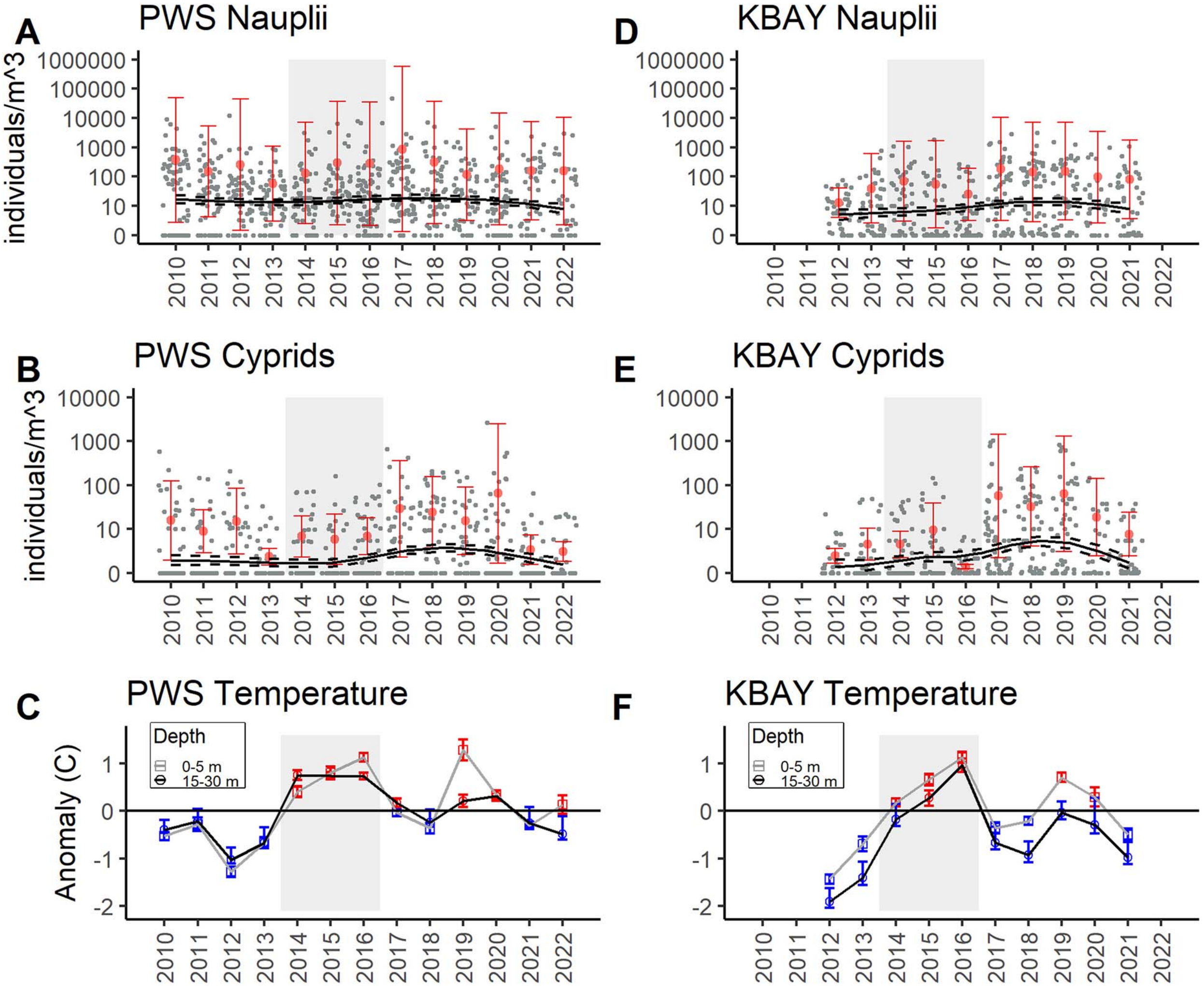

Fig. 3. Trends in barnacle nauplii and cyprid concentration among years and temperature anomalies in PWS and KBAY. In (**A**, **B**, **D**, **E**), large solid circles are the calendar year mean ± se. The solid line is the smoothed Year parameter from the GAM, and the dashed lines show the 95% confidence intervals. The shaded area indicates the years of the Pacific Marine Heatwave (2014–2016).

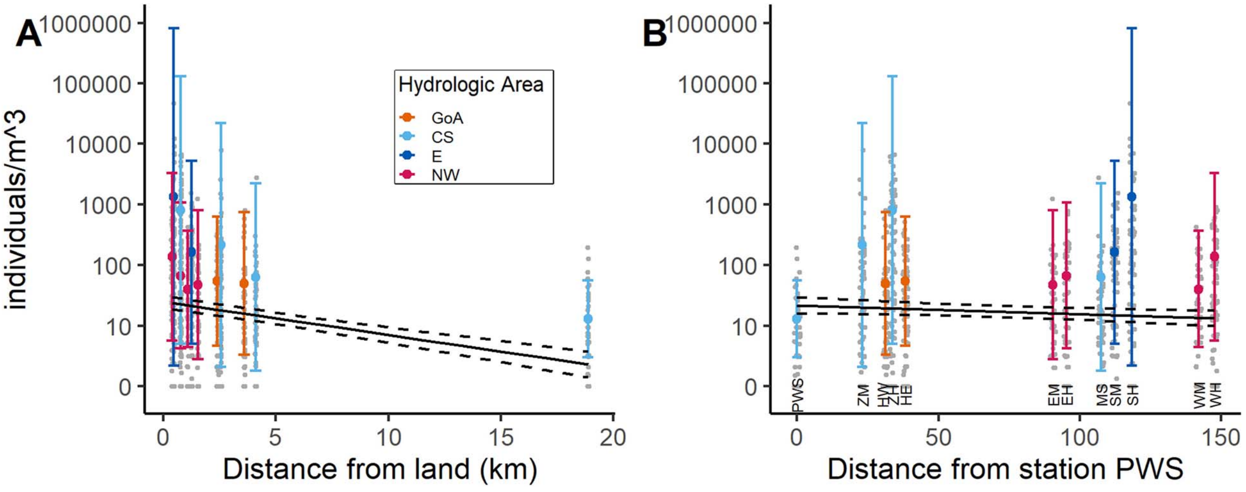

Fig. 4. Effect of (**A**) distance from land and (**B**) distance from the PWS station on barnacle nauplii in Prince William Sound. Points color-coded by hydrologic area (see Fig. 1) are station means ± se. The solid line is the effect from the GAM, and the dashed lines show 95% confidence intervals.

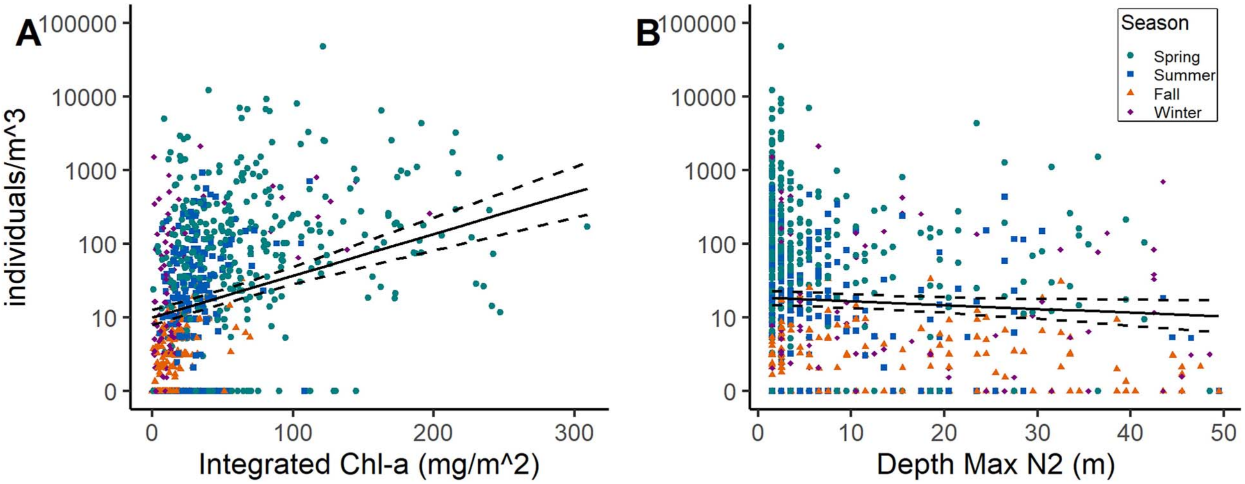

Fig. 5. (**A**) Effect of chlorophyll-a concentration on nauplii concentration in PWS, and (**B**) the effect of depth of maximum buoyancy frequency (N^2) on nauplii concentration in PWS. The black line is the effect from the GAM, and the dashed lines show 95% confidence intervals.

Depth-integrated chlorophyll-a concentration and depth of maximum buoyancy frequency were included in the best-supported GAM model for nauplii in PWS (Table I, Table S4). Chlorophyll-a concentration had a positive effect on nauplii concentration (Fig. 5A). Chlorophyll-a concentration varied among years from 26.534 (± 2.873) mg/m^2 [mean ± standard error (se)] in 2020 to 52.977 (± 6.049) mg/m^2 in 2015 (Fig. S2A). Chlorophyll-a concentration was most variable among stations in spring and was highest at stations in the Central Sound hydrologic area and the WH station in the Northwest hydrologic area (Fig. 1, Fig. S2B). The depth of maximum buoyancy frequency had a negative effect on nauplii concentration (Fig. 5B). The depth of maximum buoyancy frequency was generally deeper in autumn and winter and was deeper at the stations in the Gulf of Alaska and Central Sound hydrologic areas (Fig. S3).

Barnacle larval spatial and temporal variation and drivers—Kachemak Bay and lower Cook Inlet

Nauplii and cyprids in KBAY followed the same seasonal trend as in PWS, appearing in high concentrations in spring and declining through the summer and autumn (Fig. 2). For both nauplii and cyprids, the sine-transformed ordinal day had a positive effect on concentration, and the cosine-transformed ordinal day had a negative effect on concentration (Table I, Table S4, Fig. S1).

Nauplii and cyprids in KBAY had somewhat similar trends across years (Fig. 3). Nauplii and cyprid concentrations were lower in the first year of sampling in 2012 with an increasing trend through 2019 and then declining concentrations in 2020 and 2021. Nauplii and cyprid concentrations were unusually low in 2016. Nauplii concentration was slightly higher for several years after the PMH, from 2017 to 2019, while the increase in cyprids during that time was more apparent. Temperature anomalies were generally higher during the PMH, although the temperature anomaly at 15–30 m was still negative in 2014 (Fig. 3F). Temperature anomalies at 0–5 m were also positive during a heat spike in 2019 and 2020 but lower than during the peak anomalies during the PMH.

Nauplii concentration in KBAY increased with latitude, with higher concentrations at the stations within Kachemak Bay and at transect 3, the transect north of Kachemak Bay (Table I, Fig. 6). Cyprid concentration increased with decreasing longitude, with higher concentrations at stations closer to the head of Kachemak Bay compared to the outer bay and lower Cook Inlet (Fig. 6).

Integrated chlorophyll-a concentration and depth of maximum buoyancy frequency were not included in the best-supported models of barnacle larval concentration in KBAY (Table I). Integrated chlorophyll-a concentration was generally higher in KBAY than in PWS, with annual means above 50 mg/m^2 and spring and summer mean concentrations above 100 mg/m^2 at many of the stations within Kachemak Bay (Fig. S4). The depth of maximum buoyancy frequency was also generally deeper in KBAY than PWS, with a seasonal mean depth >20 m at many stations (Fig. S5).

Barnacle percent cover models—PWS

For barnacle percent cover in PWS, the best-supported model with only local predictor variables included an interaction between site and elevation and mean water temperature in spring (Table II). Adding an interaction between cyprid concentration and elevation improved the model, decreasing AICc by 2.73, and adjusted R^2 increased slightly from 0.82 to 0.83 (Table II). Barnacle percent cover was higher at 1.5 m than at 0.5 m at all sites (Fig. S6). Barnacle percent cover at both elevations followed similar trends over time, with generally lower cover in early years, peaking in 2017, 1 year after the end of the PMH, and declining cover in 2018–2022 (Fig. 7A). Mean water temperature in spring increased during the PMH in 2015 and 2016 and remained higher in the years after the heatwave than the three years prior to the heatwave (Fig. 7B). Although temperature differed among sites, all sites followed the same general trend (Fig. S7). Mean water temperature in spring had a positive effect on barnacle percent cover (0.089 ± 0.026, effect ± se, Table S5). Cyprid concentration in PWS followed a similar temporal pattern to barnacle percent cover, with lower concentrations in

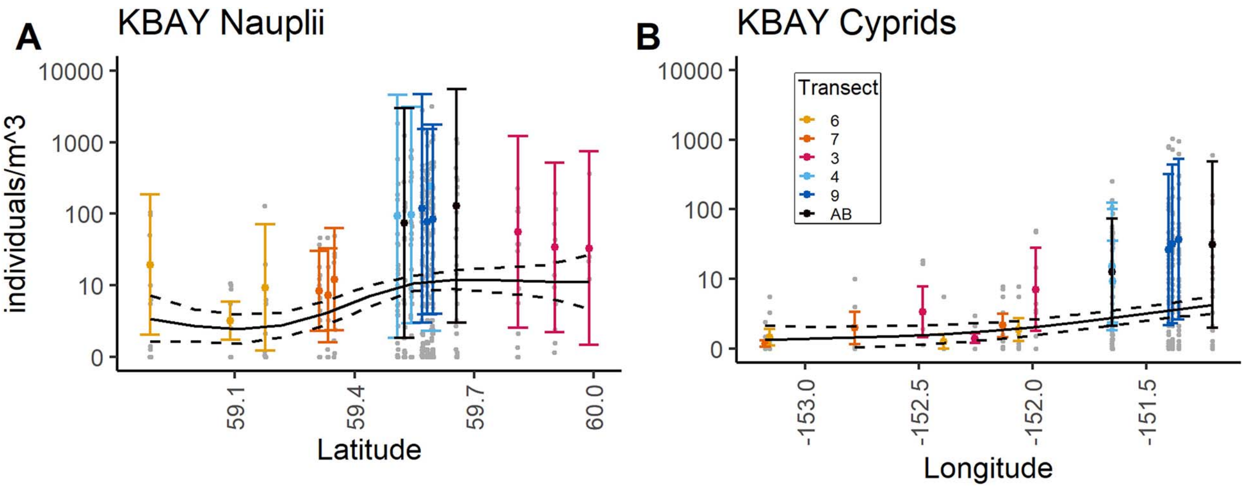

Fig. 6. Effects of latitude and longitude on nauplii and cyprid concentration in KBAY. Points color-coded by transect are station means ± se. The black line is the effect from the GAM, and the dashed lines show 95% confidence intervals.

Table II: *Best-supported linear mixed-effects models of barnacle percent cover*

Prince William Sound	**Model**	**ΔAICc**	**adj. R^2**
Best local model + Larvae	Site∗Elevation + Spring water temperature +Cyprid∗Elevation	0	0.83
Best local model	Site∗Elevation + Spring water temperature	2.73	0.82
Kachemak Bay	Model	ΔAICc	adj. R^2
Best local model + Larvae	Site∗Elevation + Summer max air temperature + Autumn water temperature + Cyprid lag1∗Site∗Elevation	0	0.77
Best local model	Site∗Elevation + Summer max air temperature + Autumn water temperature	14.89	0.72

2013–2016 and higher concentrations after the PMH in 2017–2019 (Fig. 7C). Although there was a large increase in cyprid concentration in 2020, there were no barnacle percent cover data for that year. Cyprid concentration had a positive effect on barnacle percent cover at both elevations, with a stronger effect at 0.5 m MLLW than at 1.5 m (Fig. 7D).

Barnacle percent cover models—Kachemak Bay and lower Cook Inlet

For barnacle percent cover in KBAY, the best-supported model with only local predictor variables included an interaction between site and elevation, mean daily mean water temperature in autumn, and mean daily maximum air temperature in summer (Table II). Adding an interaction between cyprid concentration at a 1-year lag, site, and elevation improved the model, lowering AICc by 14.89 and increasing the adjusted R^2 from 0.72 to 0.77 (Table II). Barnacle percent cover was similar between elevations at most sites, but, at two sites, Outside Beach and Port Graham, barnacle cover was higher at 0.5 m than 1.5 m (Fig. S6). Barnacle percent cover increased at both elevations during and after the PMH, from 2014 to 2018 (Fig. 8A). Barnacle cover at 0.5 m declined from 2018 to 2019, then was similar for 3 years. Barnacle cover at 1.5 m varied slightly from year to year from 2017 to 2021 but was generally higher than in 2014 to 2016. While there is only 1 year of pre-PMH intertidal temperature data to compare to, intertidal summer air and autumn water temperatures were mostly similar during and after the PMH (Fig. 8B). Summer maximum air temperatures were dissimilar among sites during the PMH, with higher temperatures at Port Graham and lower temperatures Bishop's Beach compared to the other four sites (Fig. S7). Autumn water temperature was also especially low at Bishop's Beach and Bluff Point compared to the other sites (Fig. S7). Mean water temperature in autumn and maximum air temperature in summer both had positive effects on barnacle percent cover (0.293 ± 0.078 and 0.066 ± 0.048 (effect ± se), respectively, Table S6). Cyprid concentration was higher after the PMH, from 2017 to 2021, than during and before the PMH (Fig. 8). Cyprid concentration with a 1-year lag generally had a positive effect on barnacle percent cover (Fig. 8C). There was a negative effect of cyprid concentration with a 1-year lag at 1.5 m at Bluff Point (Fig. 8C).

DISCUSSION

In this study, we gained insight into the indirect effects of the PMH on benthic and pelagic life stages of barnacles by synthesizing across disparate disciplines in a long-term monitoring program. While post-settlement mechanisms, rather than larval supply, likely explained the increase in barnacle percent cover during the PMH (Weitzman *et al.*, 2021), the continued increase in percent cover and a slight increase in larval concentration following the PMH may illustrate positive feedback between life stages, where higher adult benthic abundance increased larval

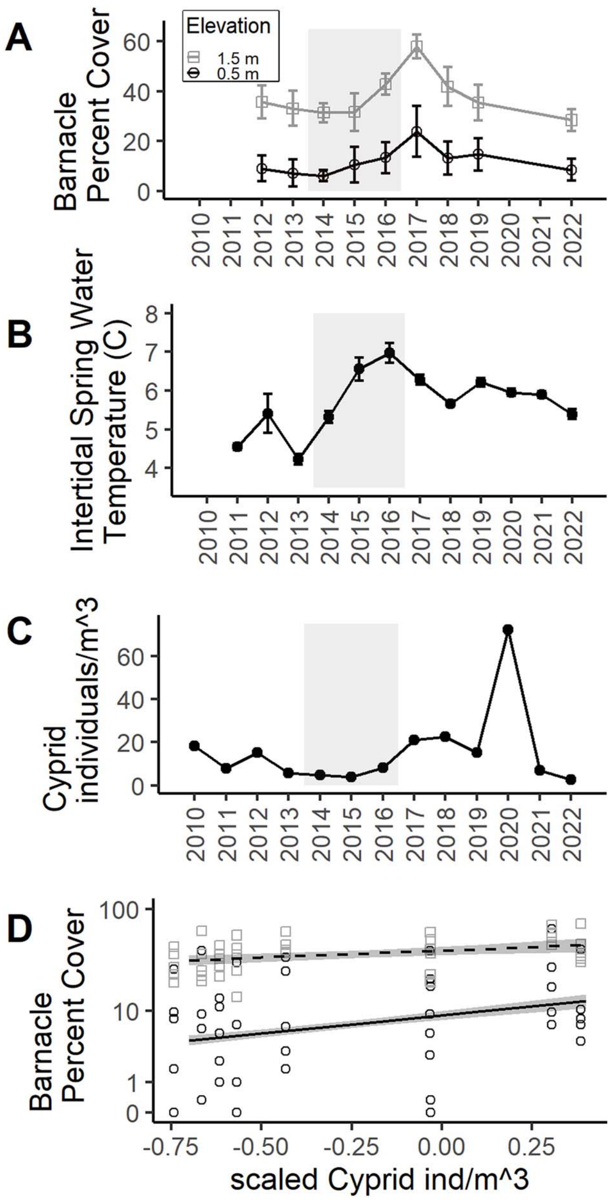

Fig. 7. Barnacle percent cover, intertidal temperature, and cyprid concentration at PWS. (**A**) Timeseries of barnacle percent cover at 0.5 and 1.5 m mean lower low water, (**B**) timeseries of intertidal spring water temperature, (**C**) timeseries of mean cyprid concentration 12 months prior to intertidal sampling, and (**D**) model estimated effect of cyprid concentration on barnacle percent cover at each elevation. The shaded area in (A–C) indicates the years of the Pacific Marine Heatwave (2014–2016). In (C), cyprid concentration for each year is the mean of all samples from 1 June from the previous year to 31 May of the current year.

concentrations, which then supplied more new recruits to the benthos. There was no evidence of a direct effect of the PMH on barnacle larvae, as temperature was not included in the best-supported GAMs and there were no increases in concentrations during the PMH; however, the effect of the PMH on barnacle larvae may have been indirect, for example, through increases in the reproductive benthic stage. There was considerable variability in the concentration of barnacle nauplii and cyprids among seasons, years, and locations, which could have important effects on the marine ecosystem. Barnacle nauplii, in particular, are an important prey item in the pelagic ecosystem (Turner, 1984) and can exert top–down pressure on phytoplankton communities (Fernandes *et al.*, 2012). Spatial and temporal variability in barnacle nauplii abundance results in variability in their effects on the pelagic ecosystem. Many ecological studies have focused on post-settlement drivers of nearshore communities (Connell, 1974; Kunze *et al.*, 2021); however, knowledge of the effects of large-scale events like heatwaves on larval stages and estimates of larval supply is lacking. In this study, we found that including larval concentration in models helped explain some variability in benthic populations of intertidal barnacles. Processes affecting the larval stages can have discernable impacts on the benthic populations, so incorporating larval concentration data where they are available may help explain benthic population dynamics. Despite differences in spatial and temporal scale, there is value in synthesizing across monitoring programs.

Due to the ephemeral nature of meroplankton, high seasonal variability in barnacle larval concentration is to be expected (Highfield *et al.*, 2010; Fernandes *et al.*, 2012). We observed a clear seasonal pattern in barnacle nauplii and cyprid concentration across both regions, which was consistent with observations of barnacle larvae in other locations [e.g. Irish Sea (Salman, 1982), Spain (Macho *et al.*, 2010)]. As phytoplankton blooms provide a cue for the release of barnacle nauplii (Starr *et al.*, 1991), it was not surprising that chlorophyll-a concentration was correlated to nauplii concentration in PWS; however, it was surprising that this was not the case in KBAY. Chlorophyll-a concentration was generally lower in PWS than KBAY, so phytoplankton may have been a more limiting resource, and thus cue for larval release, in PWS than KBAY. Barnacle nauplii were correlated to seasonal changes in chlorophyll-a concentration, rather than interannual variability in chlorophyll-a, as chlorophyll-a concentration was highly variable among years and trends did not correspond to those of nauplii. Similarly, in a 15-year timeseries of meroplankton abundance (dominated by Mytilidae and Cirripedia) and chlorophyll-a in the subtropical southwestern Atlantic, the timing of the phytoplankton bloom determined the timing of the annual peak of meroplankton abundance, although annual variation in meroplankton abundance was not fully explained by chlorophyll-a (Fernandes *et al.*, 2012). Seasonal variability in barnacle nauplii concentration was also correlated to the depth of maximum buoyancy frequency in PWS, as the depth of maximum buoyancy frequency had a negative effect on nauplii concentration, and the depth of maximum buoyancy frequency was generally deeper in the autumn and winter when nauplii were less abundant.

Barnacle larval concentration did not appear to be strongly affected by the PMH directly, as concentrations during the PMH years (2014–2016) were mostly similar to the years prior, and temperature anomalies were not included in the best-supported models of larval concentration. However, there was a notable increase in cyprid concentration in the years following the PMH in both regions. We might have expected cyprid concentrations to increase during the PMH because changes in temperature and food availability can affect rates of development and the amount of time meroplankton spend in the plankton

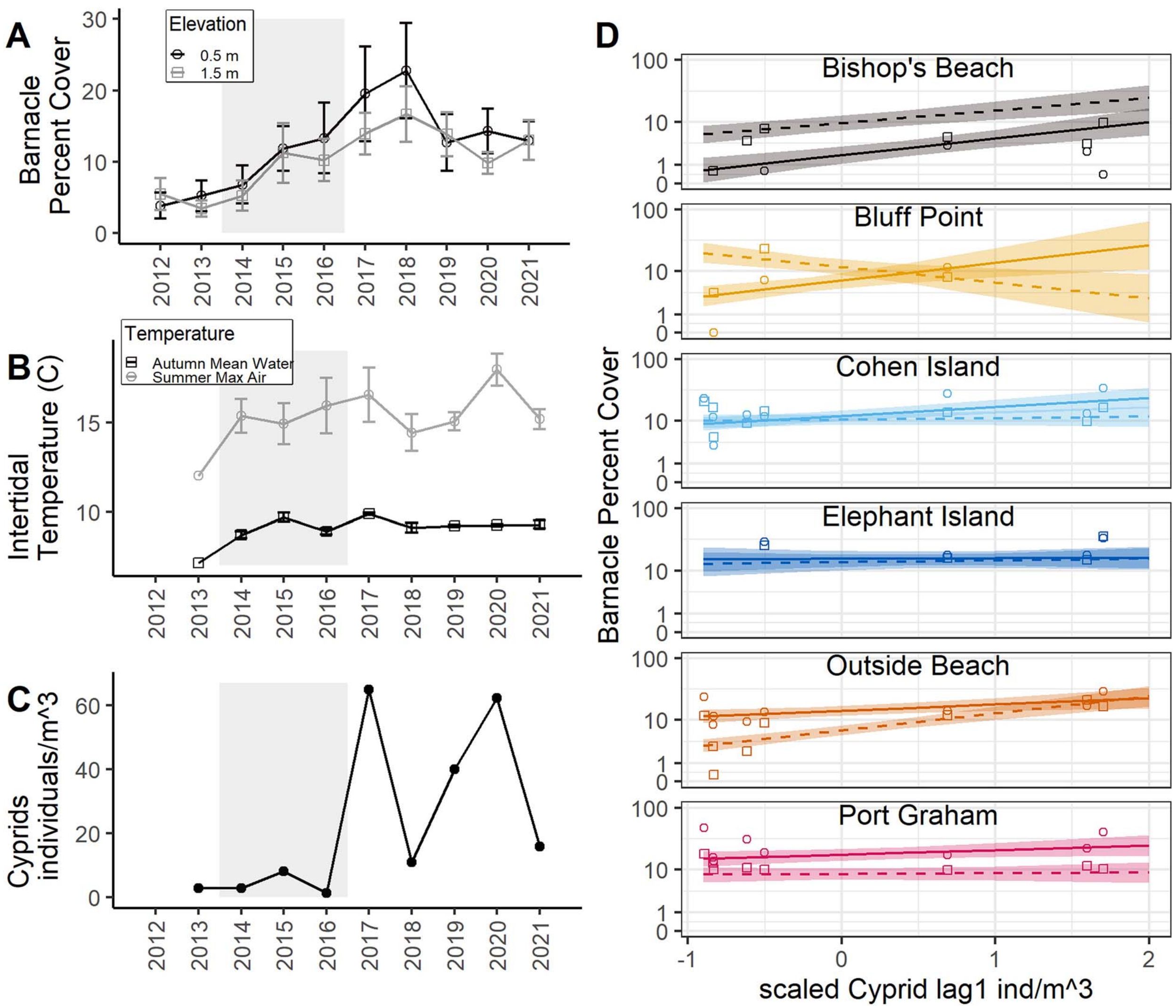

Fig. 8. Barnacle percent cover, intertidal temperature, and cyprid concentration in Kachemak Bay. (**A**) Timeseries of barnacle percent cover at 0.5 and 1.5 m mean lower low water, (**B**) timeseries of summer maximum air temperature and autumn water temperature, (**C**) timeseries of cyprid concentration 12 months prior to intertidal sampling, and (**D**) effects of barnacle cyprid concentration at a 1-year lag on barnacle percent cover by site and elevation. Site colors in (D) correspond to the map in Fig. 1. Note that only data from 2014 onward were included in the linear mixed-effect models. The shaded area in (A, B) indicates the years of the Pacific Marine Heatwave (2014–2016). In (C), cyprid concentration for each year is the mean of all samples from 1 June from the previous year to 31 May of the current year.

(O'Connor *et al.*, 2007; Hentschel and Emlet, 2023), so barnacle nauplii may have progressed to the cyprid stage faster during the PMH. However, other factors such as predation may have masked any effect of increased temperature on barnacle larval development. The higher larval concentrations in the years following the PMH may be explained by the reproductive output of the sessile stage, as barnacles increased in benthic cover during the PMH. Interannual variation in meroplankton may be observed where environmental changes impact the reproductive output of adult stages, through effects on fecundity or abundance. For example, in the North Sea, elevated water temperature increased the reproductive output of the sea urchin *Echinocardium cordatum* in the benthos, which contributed to increased larval abundance (Kirby *et al.*, 2007). A stock–recruitment relationship was also observed across the Great Barrier Reef (~1800 km), where variation in coral recruitment was best explained by adult fecundity (Hughes *et al.*, 2000). The PMH led to increased intertidal barnacle and mussel cover in the Gulf of Alaska (including the sites in this study) (Weitzman *et al.*, 2021). Because larval concentrations were not elevated during the PMH, the increase in barnacle percent cover may not have been related to increased settlement. Instead, the mechanism behind the increase in barnacle percent cover during the PMH may have been reduced competition for space with macroalgae, which declined during the PMH (Weitzman *et al.*, 2021). Increased abundance of barnacles in the intertidal could have contributed to increased larval abundance in the years following the PMH reported in this study. However, the mechanistic relationship of which came first, the benthic barnacle or the planktonic larvae, remains unclear for the Gulf of Alaska.

Meroplankton abundance can be very patchy through space. Concentrated patches of meroplankton can form where water flows converge or in areas with vertical currents (Shanks *et al.*, 2003). Within each region, we observed hotspots with higher barnacle larval concentrations. In PWS, barnacle nauplii appeared to be more concentrated at the head of bays than at the mouth of bays. In KBAY, there were higher barnacle larval concentrations within Kachemak Bay than in lower Cook Inlet. This could be a result of the greater extent of barnacles in the rocky intertidal within Kachemak Bay compared to lower Cook Inlet, or to hydrodynamic forces concentrating larvae within Kachemak Bay, where known eddies and patterns of circulation influence the passive transport of particles (Johnson, 2021). This would be in line with a study of brachyuran crab larvae in KBAY that found that larvae released within or near KBAY were retained within KBAY, possibly due to larval behavior or the formation of a hydrographic front (Murphy and Iken, 2014). Barnacle nauplii in PWS increased with decreasing distance from shore, which may be related to their dispersal through the ocean after being released from sessile populations. Cyprid larvae must return to the nearshore to settle on a hard substrate. In southern California, late-stage barnacle nauplii were found farthest from shore (1.1 km), while barnacle cyprids were found closest to shore (0.3 km) (Tapia and Pineda, 2007). Contrary to our expectations, distance from shore was not included in the best-supported models of cyprid concentration in PWS or KBAY. This may be because cyprids were highly variable through time, and other factors such as year and day of the year better explained variability. Or it may be that distance from shore is not important at larger spatial scales (i.e. > 1.1 km from shore). Circulation from wind and tidal currents are particularly important factors for PWS and KBAY, creating non-linear pathways for particles to be passively transported throughout the system; it is probable that patterns of circulation and local eddies, as evidenced in KBAY (Johnson, 2021), shape patterns of meroplankton distribution and abundance more so than simple linear distances to shore or a station.

The addition of cyprid concentration significantly improved linear mixed-effect models of intertidal barnacle percent cover in both regions. As sessile barnacle populations are dependent on the larval pool for settlement and recruitment of new individuals, it was not unexpected that there were overall positive effects of cyprid concentration on barnacle percent cover. What is somewhat surprising is that we were able to detect this effect on barnacle populations of mixed sizes (not only including recent settlers) and that we were able to detect this effect using regional scale mean cyprid concentration rather than site-specific estimates of larval supply.

Barnacle percent cover varied considerably between regions and the way cyprid concentration was included in models also differed between regions. In PWS, the best-supported model included an interaction between cyprids and elevation, while, in KBAY, it included an interaction between cyprids at a 1-year lag, elevation, and site. The interaction with the site in KBAY likely reflects the effects of site-specific hydrodynamic features on larval supply to sites. Differences in hydrodynamic features among sites can lead to accumulated differences in larval supply and retention over time, leading to variation in settled population abundances (Bertness *et al.*, 1996). Larval abundance can vary greatly at small spatial scales, such as sampling locations being offshore versus inshore of kelp forests (Gaines and Roughgarden, 1987). The coastline within Kachemak Bay is highly variable with many islands, small bays, and kelp forests, creating a complex hydrodynamic environment. The difference between regions in whether cyprids with no lag or with a 1-year lag best explained that variation in barnacle percent cover may be related to differences in post-settlement mortality within 1 year of settlement in each region. Barnacle percent cover was generally lower in KBAY than in PWS. One possible explanation for these trends is that barnacle percent cover in PWS may be higher because early post-settlement mortality may be lower, leading to high cover of young individuals. In contrast, barnacle percent cover at KBAY may be composed of fewer large individuals that have survived longer, leading to a stronger effect of cyprid concentration at a 1-year lag. Further differences in benthic barnacle cover may be explained by local differences in intertidal habitats, which, while mostly identical and monitored at consistent tidal elevations (0.5 and 1.5 m MLLW), do differ somewhat across regions where KBAY boasts a wider intertidal zone than PWS due to the shoreline, slope, exposure, and currents (Konar *et al.*, 2016). The influence of cyprid concentration on barnacle percent cover is context-dependent, as is the relationship between barnacle recruits and adult abundance (Menge, 2000).

CONCLUSIONS

Determining spatial and temporal variability in larval stages of nearshore taxa is informative, as they play a significant role in the pelagic ecosystem before settling to the seafloor to influence the benthic ecosystem. Meroplankton may become more dominant than holoplankton in response to climate-driven changes (Kirby *et al.*, 2007), so they may play an even larger role in the future. The effects of marine heatwaves on meroplankton may be direct, with increases in abundance during the heatwave (Evans *et al.*, 2020), or the effects may be indirect, mediated through complex competitive interactions in the benthic population, leading to increased adult abundance (Weitzman *et al.*, 2021), and reproductive output, leading to higher larval concentrations in years following, as may have occurred in our study areas. As climate events such as heatwaves continue to occur, we expect changes to be observed in nearshore monitoring programs, with each event providing an opportunity to test for ecological relationships between environmental drivers and connections across planktonic and benthic life stages. Where information about larval supply to specific sites at small time scales is lacking, data from existing monitoring programs targeting larval stages could provide useful information on the variability and abundance of the larval pool. Continued monitoring and synthesis of seemingly disparate data may yield important insight into the drivers of change across the benthic and pelagic habitats. By integrating sampling programs covering the life stages of barnacles, we identified mechanisms affecting recruitment and population variability through a major climate event. Continued efforts to monitor ecosystem responses to multiple climate events will enable a greater understanding of recruitment relationships and population dynamics in a changing climate.

SUPPLEMENTARY DATA

Supplementary data can be found at *Journal of Plankton Research* online.

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DATA AVAILABILITY

The data used in this study are openly available through the Gulf Watch Alaska data portal at gulfwatchalaska.org, the U.S. Geological Survey (2016, 2022), and at DataONE at: https://search.dataone.org/view/10.24431/rw1k21g (Kachemak Bay and Cook Inlet larval concentrations and CTD data) and https://search.dataone.org/view/10.24431/rw1k19 (Prince William Sound larval concentrations and CTD data).

REFERENCES

Barshis, D. J., Sotka, E. E., Kelly, R. P., Sivasundar, A., Menge, B. A., Barth, J. A. and Palumbi, S. R. (2011) Castal upwelling is linked to temporal genetic variability in the acorn barnacle Balanus glandula. *Mar. Ecol. Prog. Ser.*, **439**, 139–150. https://doi.org/10.3354/meps09339.

Bates, D., Maechler, M., Bolker, B. and Walker, S. (2015) Fitting linear mixed-effects models using lme4. *J. Stat. Softw.*, **67**, 1–48.

Batten, S. D., Ostle, C., Hélaouët, P. and Walne, A. W. (2022) Responses of gulf of Alaska plankton communities to a marine heat wave. *Deep. Res. Part II Top. Stud. Oceanogr.*, **195**, 1–9. https://doi.org/10.1016/j.dsr2.2021.105002.

Bertness, M. D., Gaines, S. D. and Wahle, R. A. (1996) Wind-driven settlement patterns in the acorn barnacle Semibalanus balanoides. *Mar. Ecol. Prog. Ser.*, **137**, 103–110. https://doi.org/10.3354/meps137103.

Bonicelli, J., Jeneral, M. J., Bularz, B., Weidberg, N., Plummer, K. A., Calderón, R., Cifuentes, U., Alarcón, D. *et al.* (2023) Diel variability in the vertical distribution of coastal barnacle larvae in the bay of Cartagena, Chile. *Rev. Chil. Hist. Nat.*, **96**, 1–17. https://doi.org/10.1186/s40693-023-00116-2.

Brodeur, R. D., Auth, T. D. and Phillips, A. J. (2019) Major shifts in pelagic micronekton and macrozooplankton community structure in an upwelling ecosystem related to an unprecedented marine heatwave. *Front. Mar. Sci.*, **6**, 1–15.

Campbell, R. (2017) Oceanographic conditions in Prince William sound, CTD, chlorophyll-a, and zooplankton data: 2013-2016, gulf watch Alaska environmental drivers component. *Res. Work*.

Campbell, R. W. (2018) Hydrographic trends in Prince William sound, Alaska, 1960–2016. *Deep. Res. Part II Top. Stud. Oceanogr.*, **147**, 43–57. https://doi.org/10.1016/j.dsr2.2017.08.014.

Carvalho, F., Kohut, J., Oliver, M. J. and Schofield, O. (2017) Defining the ecologically relevant mixed-layer depth for Antarctica's coastal seas. *Geophys. Res. Lett.*, **44**, 338–345. https://doi.org/10.1002/2016GL071205.

Coletti, H. A., Bodkin, J. L., Monson, D. H., Ballachey, B. E. and Dean, T. A. (2016) Detecting and inferring cause of change in an Alaska nearshore marine ecosystem. *Ecosphere*, **7**, 1–20. https://doi.org/10.1002/ecs2.1489.

Connell, J. H. (1974) Field experiments in marine ecology. In Mariscal, R. (ed), *Experimental Marine Biology*. Academic Press, New York, pp. 21–54, https://doi.org/10.1016/B978-0-12-472450-1.50007-5.

Dayton, P. K. (1971) Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecol. Monogr.*, **41**, 351–389. https://doi.org/10.2307/1948498.

Dean, T. A. and Bodkin, J. L. (2011) SOP for sampling of intertidal invertebrates and algae on sheltered rocky shores - version 4.6: Southwest Alaska inventory and monitoring network. Natural resource report NPS/SWAN/NRR—2011/397. Fort Collins.

Dean, T. A., Bodkin, J. L. and Coletti, H. A. (2014) *Protocol Narrative for Nearshore Marine Ecosystem Monitoring in the Gulf of Alaska: Version 1.1 Natural Resource Report NPS/SWAN/NRR – 2014/756*, National Park Service, Fort Collins, Colorado.

Desai, D. V. and Anil, A. C. (2000) Influence of temperature on the starvation threshold of nauplii of barnacle *Balanus amphitrite* (Cirripdeia: Thoracica). *Indian J. Mar. Sci.*, **29**, 69–72.

Dudas, S. E., Grantham, B. A., Kirincich, A. R., Menge, B. A., Lubchenco, J. and Barth, J. A. (2009) Current reversals as determinants of intertidal recruitment on the Central Oregon coast. *ICES J. Mar. Sci.*, **66**, 396–407. https://doi.org/10.1093/icesjms/fsn179.

Evans, R., Lea, M. A., Hindell, M. A. and Swadling, K. M. (2020) Significant shifts in coastal zooplankton populations through the 2015/16 Tasman Sea marine heatwave. *Estuar. Coast. Shelf Sci.*, **235**, 1–11, 106538. https://doi.org/10.1016/j.ecss.2019.106538.

Farrell, T. M., Bracher, D. and Roughgarden, J. (1991) Cross-shelf transport causes recruitment to intertidal populations in Central California. *Limnol. Oceanogr.*, **36**, 279–288. https://doi.org/10.4319/lo.1991.36.2.0279.

Fernandes, L. D. D. A., Quintanilha, J., Monteiro-Ribas, W., Gonzalez-Rodriguez, E. and Coutinho, R. (2012) Seasonal and interannual coupling between sea surface temperature, phytoplankton and meroplankton in the subtropical south-western Atlantic Ocean. *J. Plankton Res.*, **34**, 236–244. https://doi.org/10.1093/plankt/fbr106.

Gaines, S. and Roughgarden, J. (1985) Larval settlement rate: a leading determinant of structure in an ecological community of the marine intertidal zone. *Proc. Natl. Acad. Sci.*, **82**, 3707–3711. https://doi.org/10.1073/pnas.82.11.3707.

Gaines, S. D. and Roughgarden, J. (1987) Fish in offshore kelp forests affect recruitment to intertidal barnacle populations. *Science (80-.)*, **235**, 479–481. https://doi.org/10.1126/science.235.4787.479.

Gatto, L. W. (1982) Ice distribution and winter surface circulation patterns, Kachemak Bay. *Alaska. Remote Sens. Environ.*, **12**, 421–435. https://doi.org/10.1016/0034-4257(82)90017-7.

Hagerty, M. L., Reyns, N. and Pineda, J. (2018) Constrained nearshore larval distributions and thermal stratification. *Mar. Ecol. Prog. Ser.*, **595**, 105–122. https://doi.org/10.3354/meps12561.

Hentschel, B. T. and Emlet, R. B. (2023) Metamorphosis of barnacle Nauplii: effects of food variability and a comparison with amphibian models. *Ecology*, **81**, 3495–3508. https://doi.org/10.1890/0012-9658(2000)081[3495:MOBNEO]2.0.CO;2.

Highfield, J. M., Eloire, D., Conway, D. V. P., Lindeque, P. K., Attrill, M. J. and Somerfield, P. J. (2010) Seasonal dynamics of meroplankton assemblages at station L4. *J. Plankton Res.*, **32**, 681–691. https://doi.org/10.1093/plankt/fbp139.

Holderied, K., Mckinstry, C. and Schloemer, J. (2023) Oceanographic monitoring in cook inlet and Kachemak Bay, zooplankton data, 2012-2019, gulf watch Alaska environmental drivers component. *Res. Work.*. https://doi.org/https://search.dataone.org/view/10.24431/rw1k21g.

Holmes, S. P., Walker, G. and Van Der Meer, J. (2005) Barnacles, limpets and periwinkles: the effects of direct and indirect interactions on cyprid settlement and success. *J. Sea Res.*, **53**, 181–204. https://doi.org/10.1016/j.seares.2004.05.004.

Hughes, T. P., Baird, A. H., Dinsdale, E. A., Moltschaniwskyj, N. A., Pratchett, M. S., Tanner, J. E. and Willis, B. L. (2000) Supply-side ecology works both ways: the link between benthic adults, fecundity, and larval recruits. *Ecology*, **81**, 2241–2249. https://doi.org/10.1890/0012-9658(2000)081[2241:SSEWBW]2.0.CO;2.

Johnson, M. A. (2021) Subtidal surface circulation in lower cook inlet and Kachemak Bay, Alaska. *Reg. Stud. Mar. Sci.*, **41**, 101609. https://doi.org/10.1016/j.rsma.2021.101609.

Kirby, R. R., Beaugrand, G., Lindley, J. A., Richardson, A. J., Edwards, M. and Reid, P. C. (2007) Climate effects and benthic – pelagic coupling in the North Sea. *Mar. Ecol. Prog. Ser.*, **330**, 31–38. https://doi.org/10.3354/meps330031.

Konar, B., Iken, K., Coletti, H., Monson, D. and Weitzman, B. (2016) Influence of static habitat attributes on local and regional rocky intertidal community structure. *Estuar. Coasts*, **39**, 1735–1745. https://doi.org/10.1007/s12237-016-0114-0.

Konar, B., Iken, K., Pohle, G., Miloslavich, P., Cruz-Motta, J. J., Benedetti-Cecchi, L., Kimani, E., Knowlton, A. *et al.* (2007) Surveying Nearshore Biodiversity. In Rigby, P. R., Iken, K. and Shirayama, Y. (eds.), *Sampling Biodiversity in Coastal Communities: NaGISA Protocols for Seagrass and Macroalgal Habitats*, NUS Press, Kent Ridge, pp. 25–41.

Kunze, C., Wölfelschneider, M. and Rölfer, L. (2021) Multiple driver impacts on rocky intertidal systems: the need for an integrated approach. *Front. Mar. Sci.*, **8**, 1–13.

Lang, W. H. and Ackenhusen-Johns, A. (1981) Seasonal species composition of barnacle larvae (Cirripedia: Thoracica) in Rhode Island waters, 1977-1978. *J. Plankton Res.*, **3**, 567–575. https://doi.org/10.1093/plankt/3.4.567.

Little, C., Trowbridge, C. D., Williams, G. A., Hui, T. Y., Pilling, G. M., Morritt, D. and Stirling, P. (2021) Response of intertidal barnacles to air temperature: long-term monitoring and in-situ measurements. *Estuar. Coast. Shelf Sci.*, **256**, 1–13, 107367. https://doi.org/10.1016/j.ecss.2021.107367.

Lund, J. W. G., Kipling, C. and Le Cren, E. D. (1958) The inverted microscope method of estimating algal numbers and the statistical basis of estimations by counting. *Hydrobiologia*, **11**, 143–170. https://doi.org/10.1007/BF00007865.

Macho, G., Vázquez, E., Giráldez, R. and Molares, J. (2010) Spatial and temporal distribution of barnacle larvae in the partially mixed estuary of the Ría de Arousa (Spain). *J. Exp. Mar. Bio. Ecol.*, **392**, 129–139. https://doi.org/10.1016/j.jembe.2010.04.017.

McDougall, T. J. and Barker, P. M. (2011) *Getting Started with TEOS-10 and the Gibbs Seawater (GWS) Oceanographic Toolbox*, SCOR/IAPSO WG127.

McKinstry, C. A. E. and Campbell, R. W. (2018) Seasonal variation of zooplankton abundance and community structure in Prince William sound, Alaska, 2009–2016. *Deep. Res. Part II Top. Stud. Oceanogr.*, **147**, 69–78. https://doi.org/10.1016/j.dsr2.2017.08.016.

McKinstry, C. A. E., Campbell, R. W. and Holderied, K. (2022) Deep-Sea research part II influence of the 2014 – 2016 marine heatwave on seasonal zooplankton community structure and abundance in the lower cook inlet, Alaska. *Deep. Res. Part II Top. Stud. Oceanogr.*, **195**, 105012. https://doi.org/10.1016/j.dsr2.2021.105012.

Menge, B. A. (2000) Recruitment vs. Postrecruitment processes As determinants of barnacle population abundance. *Ecol. Monogr.*, **70**, 265–288. https://doi.org/10.1890/0012-9615(2000)070[0265:RVPPAD]2.0.CO;2.

Menge, B. A., Hacker, S. D., Freidenburg, T., Lubchenco, J., Craig, R., Rilov, G., Noble, M. and Richmond, E. (2011) Potential impact of climate-related changes is buffered by differential responses to recruitment and interactions. *Ecol. Monogr.*, **81**, 493–509. https://doi.org/10.1890/10-1508.1.

Minchinton, T. E. and Scheibling, R. E. (1991) The influence of larval supply and settlement on the population structure of barnacles. *Ecology*, **72**, 1867–1879. https://doi.org/10.2307/1940984.

Murphy, M. and Iken, K. (2014) Larval brachyuran crab timing and distribution in relation to water properties and flow in a high-latitude estuary. *Estuar. Coasts*, **37**, 177–190. https://doi.org/10.1007/s12237-013-9668-2.

Musgrave, D. L., Halverson, M. J. and Pegau, W. S. (2013) Seasonal surface circulation, temperature, and salinity in Prince William sound. *Alaska. Cont. Shelf Res.*, **53**, 20–29. https://doi.org/10.1016/j.csr.2012.12.001.

Newman, W. A. and Abbott, D. P. (1980) Cirripedia: the barnacles. In Morris, R. H., Abbot, D. P., and Haderlie, E. C. (eds.), *Intertidal Invertebrates of California*. Stanford University Press, Stanford, pp. 504–535.

Niebauer, H. J., Royer, T. C. and Weingartner, T. J. (1994) Circulation of Prince William sound. *Alaska. J. Geophys. Res.*, **99**, 113–126.

Noda, T. (2004) Large-scale variability in recruitment of the barnacle Semibalanus cariosus: its cause and effects on the population density and predator. *Mar. Ecol. Prog. Ser.*, **278**, 241–252. https://doi.org/10.3354/meps278241.

O'Clair, R. M. and O'Clair, C. E. (1998) *Southeast Alaska's Rocky Shores: Animals*, Plant Press, Auke Bay, AK.

O'Connor, M. I. O., Bruno, J. F., Gaines, S. D., Halpern, B. S., Lester, S. E., Kinlan, B. P. and Weiss, J. M. (2007) Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. *Proc. Natl. Acad. Sci.*, **104**, 1266–1271. https://doi.org/10.1073/pnas.0603422104.

Pineda, J., Reyns, N. B. and Starczak, V. R. (2009) Complexity and simplification in understanding recruitment in benthic populations. *Popul. Ecol.*, **51**, 17–32. https://doi.org/10.1007/s10144-008-0118-0.

Raimondi, P. T. (1990) Patterns, mechanisms, consequences of variability in settlement and recruitment of an intertidal barnacle. *Ecol. Monogr.*, **60**, 283–309. https://doi.org/10.2307/1943059.

RCoreTeam (2020) *R: A Language and Environment for Statistical Computing*.

Salman, S. D. (1982) Seasonal and short-term variations in abundance of barnacle larvae near the south-west of the Isle of Man. *Estuar. Coast. Shelf Sci.*, **15**, 241–253. https://doi.org/10.1016/0272-7714(82)90061-0.

Scrosati, R. A. and Ellrich, J. A. (2024) Massive barnacle recruitment on the Gulf of St. Lawrence coast of Nova Scotia (Canada) in 2024 linked to increased sea surface temperature. *Peer J*, **12**, e18208. https://doi.org/10.7717/peerj.18208.

Shanks, A. L. (1986) Tidal periodicity in the daily settlement of intertidal barnacle larvae and an hypothesized mechanism for the cross-shelf transport of cyprids. *Biol. Bull.*, **170**, 429–440. https://doi.org/10.2307/1541852.

Shanks, A. L., Largier, J. and Brubaker, J. (2003) Observations on the distribution of meroplankton during an upwelling event. *J. Plankton Res.*, **25**, 645–667. https://doi.org/10.1093/plankt/25.6.645.

Starr, M., Himmelman, J. H. and Therriault, J. C. (1991) Coupling of nauplii release in barnacles with phytoplankton blooms: a parallel strategy to that of spawning in urchins and mussels. *J. Plankton Res.*, **13**, 561–571. https://doi.org/10.1093/plankt/13.3.561.

Suryan, R. M., Arimitsu, M. L., Coletti, H. A., Hopcroft, R. R., Lindeberg, M. R., Barbeaux, S. J., Batten, S. D., Burt, W. J. *et al.* (2021) Ecosystem response persists after a prolonged marine heatwave. *Sci. Rep.*, **11**, 1–17.

Tapia, F. J. and Pineda, J. (2007) Stage-specific distribution of barnacle larvae in nearshore waters: potential for limited dispersal and high mortality rates. *Mar. Ecol. Prog. Ser.*, **342**, 177–190. https://doi.org/10.3354/meps342177.

Thorson, G. (1950) Reproductive and larval ecology of marine bottom invertebrates. *Biol. Rev.*, **25**, 1–45. https://doi.org/10.1111/j.1469-185X.1950.tb00585.x.

Turner, J. T. (1984) The feeding ecology of some zooplankters that are important prey items of larval fish. *NOAA Technical Report NMFS*, **7**, 1–28. https://repository.library.noaa.gov/view/noaa/5581/noaa_5581_DS1.pdf.

Turner, J. T., Levinsen, H., Nielsen, T. G. and Hansen, B. W. (2001) Zooplankton feeding ecology: grazing on phytoplankton and predation on protozoans by copepod and barnacle nauplii in Disko Bay, West Greenland. *Mar. Ecol. Prog. Ser.*, **221**, 209–219. https://doi.org/10.3354/meps221209.

U. S. Geological Survey – Alaska Science Center and National Park Service – Southwest Alaska Inventory and Monitoring Network (2022) *Rocky Intertidal Data from Prince William Sound, Katmai National Park and Preserve, and Kenai Fjords National Park: U.S. Geological Survey Data Release (ver 2.0, October 2023): U. S. Geological Survey Data Release*, https://doi.org/10.5066/F7513WCB

U. S. Geological Survey – Alaska Science Center, National Park Service – Southwest Alaska Inventory and Monitoring Network, and University of Alaska Fairbanks – College of Fisheries and Ocean Sciences (2016) *Intertidal Temperature Data from Kachemak Bay, Prince William Sound, Katmai National Park and Preserve, and Kenai Fjords National Park (ver 4.0, September 2023): U. S. Geological Survey Data Release*, https://doi.org/10.5066/F7WH2N3T

von Dassow, G., Mendes, C. B., Robbins, K., Andrade, S. C. S. and Maslakova, S. A. (2022) Hoplonemertean larvae are planktonic predators that capture and devour active animal prey. *Invertebr. Biol.*, **141**, 1–24.

Weitzman, B., Konar, B., Iken, K., Coletti, H., Monson, D., Suryan, R., Dean, T., Hondolero, D. *et al.* (2021) Changes in rocky intertidal community structure during a marine heatwave in the northern gulf of Alaska. *Front. Mar. Sci.*, **8**, 556820. https://doi.org/10.3389/fmars.2021.556820.

Winans, A. K., Herrmann, B. E. L. and Keister, J. E. (2023) Spatiotemporal variation in zooplankton community composition in the southern Salish Sea: changes during the 2015–2016 Pacific marine heatwave. *Prog. Oceanogr.*, **214**, 103022. https://doi.org/10.1016/j.pocean.2023.103022.

Wood, S. N. (2004) Stable and efficient multiple smoothing parameter estimation for generalized additive models. *J. Am. Stat. Assoc.*, **99**, 673–686. https://doi.org/10.1198/016214504000000980.

Yamhure, G. M., Reyns, N. and Pineda, J. (2021) High larval concentrations and onshore transport of barnacle Cyprids associated with thermal stratification. *Front. Mar. Sci.*, **8**, 748389. https://doi.org/10.3389/fmars.2021.748389.

Zhang, D. (2023) Rsq: R-squared and related measures R package version 2.6.