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Contribution to the Theme Section 'How do marine heatwaves impact seabirds?'

Lack of strong responses to the Pacific marine heatwave by benthivorous marine birds indicates importance of trophic drivers

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ABSTRACT: The Pacific marine heatwave (PMH) of 2014–2016 was an intense, long-lasting environmental disturbance expressed throughout the north Pacific. While dramatic consequences of the PMH on pelagic food webs have been well documented, effects on nearshore food webs, i.e. those based on macroalgal primary productivity, benthic invertebrate intermediate consumers, and specialized benthivorous top predators including some marine birds, are not well understood. We conducted summer and winter coastline marine bird surveys in 2 National Parks in the northern Gulf of Alaska from 2006 to 2022. We evaluated changes in abundance of benthivorous marine birds in relation to the PMH, after accounting for effects of season and region. We also evaluated changes in abundance of nearshore benthic invertebrate prey to allow specific consideration of a prey-based mechanism for effects of the PMH across food webs. We found that benthivorous marine birds, consisting of sea ducks and shorebirds, did not show a strong response to the PMH, unlike significant effects demonstrated by piscivorous birds in pelagic biomes. In contrast to extreme reductions in quantity and quality of forage fish documented elsewhere, we found that common benthic invertebrate prey abundance remained relatively stable. Our results support the hypothesis that, across food webs, top predator responses to the PMH were driven primarily by how and whether the PMH affected their prey availability. These findings show how a large-scale environmental perturbation affects biological communities differently through various trophic pathways, which provides insight into ecosystem resiliency and can inform management strategies in the face of persistent climate change.

KEY WORDS: Nearshore marine ecosystem · Benthivore · Marine bird · Population trends · Trophic interactions · Food web effects · Benthic prey

1. INTRODUCTION

Marine heatwaves have increased in frequency and intensity across the globe (Hobday et al. 2018, Oliver et al. 2018), and those trends are projected to continue (Frölicher et al. 2018). Because variation in ocean temperature is widely understood to have important effects on marine biological communities (Ainley et al. 1995, Francis et al. 1998, Anderson & Piatt 1999, Abookire & Piatt 2005, Beuchel et al. 2006), understanding drivers and consequences of marine heatwaves on ecosystem structure and function is critical (Sen Gupta et al. 2020). The Pacific marine heatwave (PMH) of 2014–2016 was a well-documented, intense, and long-lasting event (Di Lorenzo & Mantua 2016, Amaya et al. 2020), with abnormally high temperatures measured in both offshore and nearshore habitats (Danielson et al. 2022). The resulting anomalously high ocean temperatures affected many marine organisms (Suryan et al. 2021). Effects

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were particularly evident within pelagic food webs that originate with phytoplankton primary producers and have forage fish and zooplankton as intermediary consumers, with piscivorous and planktivorous seabirds and marine mammals as top predators (von Biela et al. 2019, Arimitsu et al. 2021). Dramatic effects (such as mass mortality and widespread reproductive failures) of the PMH on top-level predators in pelagic food webs included marine birds (Piatt et al. 2020, Corcoran 2021, Schoen et al. 2024 [this Theme Section]) and whales (Gabriele et al. 2022).

The north Pacific coastline also supports a robust and productive nearshore community that is distinct from pelagic food webs. Specifically, the nearshore food web originates with macroalgae, seagrasses, and phytoplankton as primary producers (Duggins et al. 1989, von Biela et al. 2016), has a diverse set of intermediary benthic invertebrate consumers (Menge 1992), and has specialized top-level predators including sea stars, sea otters, and benthivorous marine birds (Paine 1974, Estes et al. 1978, Coletti et al. 2016). Lower trophic levels within nearshore food webs in rocky intertidal habitats were shown to respond to the PMH through decreases in some macroalgal species and increases in some species of intermediary benthic consumers (Weitzman et al. 2021). However, effects were muted relative to those observed in pelagic systems with dramatic declines in forage fish quality and abundance (Arimitsu et al. 2021) and their predators (Schoen et al. 2024). The relatively minor effects observed in nearshore rocky intertidal communities (Weitzman et al. 2021) were not a result of less extreme temperature change, as PMH-related temperature anomalies were as pronounced in intertidal habitats as in open ocean environments (Danielson et al. 2022). Understanding differential resilience of food webs across nearshore and pelagic environments to marine heatwaves provides important perspective on how these events will continue to shape future marine ecosystems.

To date, effects of the PMH on benthivorous marine bird communities have not been evaluated. To do so, we used systematic nearshore marine bird surveys conducted before, during, and after the PMH in 2 coastal National Parks in Alaska (USA) to quantify changes in abundance of marine invertebrate-consuming avian species. We also analyzed benthic invertebrate abundance in these same parks over the same time period, to evaluate changes in prey base for benthivores as a result of the PMH. This allows specific consideration of a food-based hypothesis for effects of the PMH, i.e. if trends in prey abundance during the PMH are mirrored by trends in abundance of their predators, we can conclude that food has a strong mediating effect of the PMH on upper trophic levels.

These data and analyses allow for a contrast between pelagic food webs for which effects are well-documented and nearshore food webs that have been less studied. Our study supports conclusions about which components of marine systems are more strongly affected by marine heatwaves. These conclusions may improve predictive power and inform management strategies in the face of persistent climate change and projected increases in frequency and intensity of marine heatwaves in the future.

2. MATERIALS AND METHODS

2.1. Bird surveys

We conducted small boat-based surveys to quantify abundance and estimate density of nearshore marine birds along the coastlines of Katmai National Park and Preserve and Kenai Fjords National Park (hereafter referred to as Katmai and Kenai Fjords, respectively) in the northern Gulf of Alaska from 2006 to 2022, as part of the Gulf Watch Alaska monitoring program (http://gulfwatchalaska.org). In each of these 2 regions, surveys were conducted nearly annually in the summer (late June to early July), and approximately biennially in the winter (March, occasionally early April). Summer surveys began in 2006 in Katmai and 2007 in Kenai Fjords, and winter surveys began in 2009 and 2007, respectively. We systematically selected survey transects to cover approximately 20% of all shoreline habitat, including islands, within each park (Fig. 1). Transects were generally up to 5 km long by 200 m wide, and centered 100 m away from the shoreline, with 30 transects in Katmai and 43 in Kenai Fjords. We counted all birds within a 100 m radius of the survey vessel, including up to 100 m above the surface of the water, and operated under the assumption that all birds within the transect were detected. We attempted to sample each transect during each survey, but occasionally were unable to do so. Two observers identified and counted all birds on land, water, or air within the sampling boundary while a third person recorded the observations on a field laptop. For details on survey protocol and sampling design, see Bodkin (2011). To evaluate the response of benthivorous invertebrate-consuming marine birds to the PMH, we limited our analysis to those of invertebrate-consuming birds that are most closely associ-

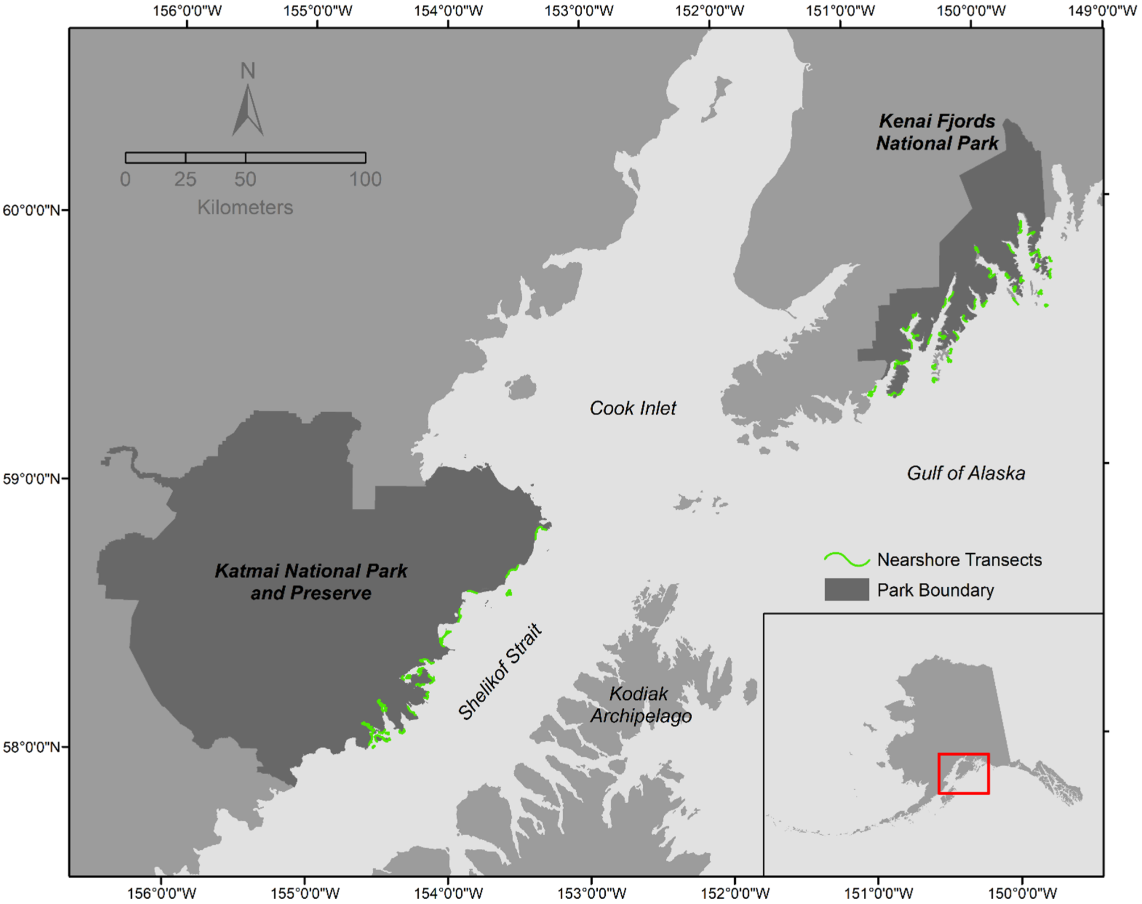

Fig. 1. Nearshore marine bird survey transects (green) in Katmai National Park and Preserve and Kenai Fjords National Park, Alaska, USA

ated with nearshore marine food webs (DeGange & Sanger 1986) and have not previously been studied with respect to PMH effects (Table 1).

2.2. Prey sampling

We sampled intertidal benthic invertebrates that are commonly consumed by nearshore marine birds. Prey taxa that we sampled consisted of clams (Infraclass: Heteroconchia), limpets *Lottia persona*, and Pacific blue mussels *Mytilus trossulus*. Prey were sampled in June or July at 5 sites each in Katmai and Kenai Fjords. Clams were sampled biennially, and limpets and mussels were sampled nearly yearly. Rocky intertidal sites, where limpets were sampled, were selected using generalized random tessellation stratified sampling from maps of sheltered rocky shoreline (Dean et al. 2014). Mussel sampling sites were selected by finding the closest mussel bed (defined as 100 m of contiguous mussels) to each rocky intertidal site, and clam sampling sites were selected by finding the nearest site with 100 m of contiguous soft-sediment habitat. Additional information on these sites is available elsewhere (Bodkin et al. 2016, Konar et al. 2016, Weitzman et al. 2017).

At each site, prey abundance was quantified within quadrats equally spaced along a sampling transect, with the location of the first quadrat placed at a randomly chosen starting point. The number of replicate quadrats varied among prey taxa, with 12 quadrats for clam sampling, 6 for limpets, and 10 for mussels. Given the potentially high number of young mussel recruits, we only counted mussels greater than 20 mm in shell length because mussels smaller than 20 mm are less likely to be consumed by birds (Bodkin et al. 2016). For example, the mean ± SD shell length of mussels consumed by black oystercatchers is 31.25 ± 0.14 mm (Coletti et al. 2017). Due to the size of openings in sieves used to sample clams, we only detected clams larger than, or equal to, 14 mm in length. For limpet sampling, all sizes were counted.

Table 1. Abundance and relative abundance of benthivorous marine bird species observed on coastline surveys from 2006 to 2022 in Katmai and Kenai Fjords National Parks, Alaska, USA. Season (winter, summer) and region (Katmai, Kenai Fjords) of primary occurrence is noted. Abundance is calculated as the sum of all individuals of a given species, and relative abundance is the abundance of a given species divided by the sum of all individuals of all species

Order	Common name	Scientific name	Season	Region	Abundance	Relative abundance
Anseriformes	Harlequin duck	*Histrionicus histrionicus*	Both	Both	29367	0.44
Anseriformes	Barrow's goldeneye	*Bucephala islandica*	Winter	Both	10062	0.15
Anseriformes	Surf scoter	*Melanitta perspicillata*	Both	Both	8124	0.12
Anseriformes	Black scoter	*Melanitta americana*	Winter	Katmai	5181	0.08
Anseriformes	White-winged scoter	*Melanitta deglandi*	Both	Katmai	4115	0.06
Anseriformes	Long-tailed duck	*Clangula hyemalis*	Winter	Katmai	2159	0.03
Anseriformes	Bufflehead	*Bucephala albeola*	Winter	Both	2102	0.03
Anseriformes	Emperor goose	*Anser canagicus*	Winter	Katmai	1137	0.02
Anseriformes	Greater scaup	*Aythya marila*	Infrequent	Infrequent	576	0.01
Anseriformes	Common goldeneye	*Bucephala clangula*	Infrequent	Infrequent	231	<0.01
Anseriformes	Steller's eider	*Polysticta stelleri*	Infrequent	Infrequent	140	<0.01
Anseriformes	Common eider	*Somateria mollissima*	Infrequent	Infrequent	19	<0.01
Charadriiformes	Black oystercatcher	*Haematopus bachmani*	Summer	Both	1767	0.03
Charadriiformes	Rock sandpiper	*Calidris ptilocnemis*	Winter	Both	1284	0.02
Charadriiformes	Black turnstone	*Arenaria melanocephala*	Infrequent	Infrequent	268	<0.01
Charadriiformes	Surfbird	*Calidris virgata*	Infrequent	Infrequent	166	<0.01
Charadriiformes	Ruddy turnstone	*Arenaria interpres*	Infrequent	Infrequent	28	<0.01
Charadriiformes	Whimbrel	*Numenius phaeopus*	Infrequent	Infrequent	15	<0.01
Charadriiformes	Semipalmated plover	*Charadrius semipalmatus*	Infrequent	Infrequent	10	<0.01
Charadriiformes	Spotted sandpiper	*Actitis macularius*	Infrequent	Infrequent	3	<0.01
Charadriiformes	Solitary sandpiper	*Tringa solitaria*	Infrequent	Infrequent	1	<0.01
Charadriiformes	Wandering tattler	*Tringa incana*	Infrequent	Infrequent	1	<0.01

2.3. Data analysis

To test for differences in benthivorous marine bird and benthic prey abundance before and after the onset of the PMH, we used generalized linear mixed-effects models in R (R Core Team 2022) using the 'glmmADMB package' (Bolker et al. 2012). To account for overdispersion, we used a negative binomial error distribution with log-link function and evaluated final model fit from residual plots. Given the varying size of survey transects and prey sampling area, we included transect area (km^2) and prey sampling area (m^2) as offset terms in our models. Because survey transects were repeated each year, we included transect as a random effect (73 levels). Abundance at each survey transect was calculated for benthivores overall by summing the number of all birds whose diets are dominated by benthic invertebrates (Table 1). Fixed factors considered in our overall abundance model included PMH (2 levels: before the onset of the PMH, from 2006 to 2013; and after the onset, from 2014 to 2022), season (2 levels: summer, winter), and region (2 levels: Katmai and Kenai Fjords). Although the PMH began in 2014 and remained through 2016, anomalously warm periods continued in later years as well (Danielson et al. 2022) and this 2-factor-level approach of before and after the onset of the PMH allows for detection of a PMH effect whether it be immediate, prolonged, or lagged. In addition to main effects of all variables, we also included an interaction between PMH and season, recognizing that the effect of the PMH could vary seasonally. We also included an interaction between season and region, allowing seasonal differences in abundance to vary by region. Our candidate set of models included all combinations of main effects and interactions, with any model including interactions also including main effects, and a null model. Akaike's information criterion (AIC) was used to rank support for models in the candidate set. Although we modeled abundance (with sampling area included as an offset), we chose to graphically display trends in the data using density, rather than abundance, to account for differences in sampling area.

We also modeled variation in abundance trends within species. In this analysis, we focused on the most common benthivorous marine birds during the seasons and within the regions in which they regularly occur (Table 1). Species were modeled individually, with PMH, season, and region as fixed factors, and an interaction between PMH and season. For species exhibiting strong seasonality (which we defined as being present in all years for either summer or winter and absent in over half the years in the other season), season was excluded as a factor and only data from the season in which they were common were modeled. Similarly, there were some species that commonly occurred in only one of the regions; in those cases, only that region was used in species-specific analyses.

For benthic prey abundance models, each taxon was analyzed in separate candidate model sets with fixed factors of PMH and region included as main effects. Season was not included as a factor because we only sampled in the summer, and these generally sessile prey are not expected to vary seasonally. Quadrat sampling replicates (12 levels for clams, 6 levels for limpets, and 10 levels for mussels) nested within site (5 levels) were included as random effects. For all analyses, the threshold was set at 0.05 when interpreting significance of effect sizes of parameter estimates.

Table 2. Ranking of generalized linear mixed-effects models of overall benthivorous marine bird foraging guild abundance in the Gulf of Alaska. All models include an offset term for sampling area and a random effect of transect. ΔAIC: difference in Akaike's information criterion (AIC) between the best model and the one being compared; ω: Akaike weight; df: degrees of freedom in the model; PMH: Pacific marine heatwave

Model	ΔAIC	ω	df
Abundance ~ Season × Region + PMH	0.0	0.46	8
Abundance ~ Season × Region	0.9	0.29	7
Abundance ~ Season × Region + PMH × Season	1.3	0.24	9
Abundance ~ PMH + Season + Region	13.3	<0.01	7
Abundance ~ PMH × Season + Region	14.4	<0.01	8
Abundance ~ Season + Region	14.9	<0.01	6
Abundance ~ Season	44.6	<0.01	5
Abundance ~ Region	571.0	<0.01	5
Abundance ~ 1	603.0	<0.01	4
Abundance ~ PMH	604.0	<0.01	5

3. RESULTS

3.1. Benthivore overall abundance

The best supported models of benthivore abundance included a 2-way interaction between season and region, indicating that season and region were important drivers of abundance (Table 2). In contrast, there was little support for an effect of the PMH on overall benthivore abundance (Fig. 2). The inclusion of PMH, or the interaction between PMH and season, to models did not substantially increase model support, demonstrating that season and region were much stronger drivers of abundance than

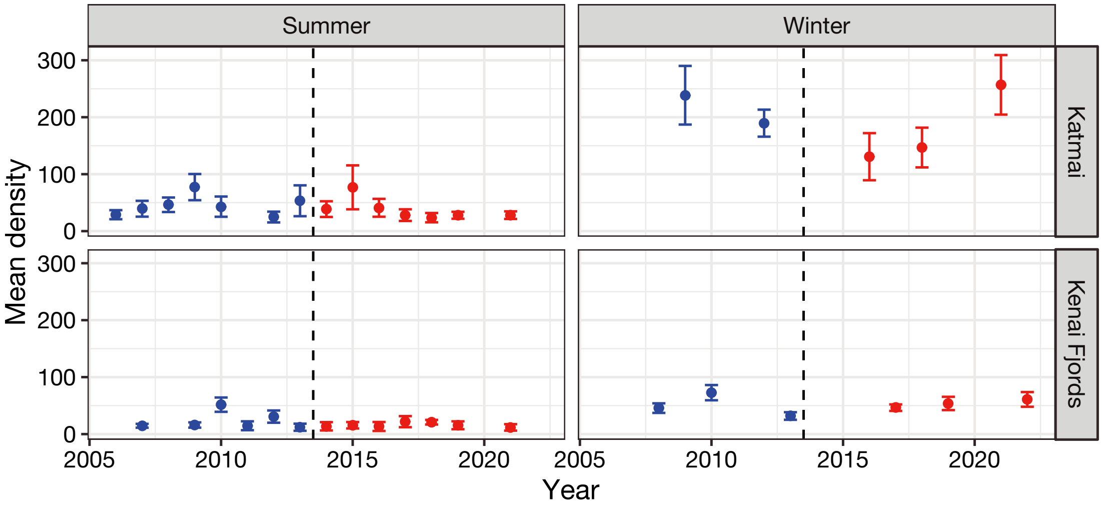

Fig. 2. Mean density (n km^{-2}) and SE estimates of benthivorous marine birds (i.e. sea ducks and shorebirds) before (2006–2013; blue) and after (2014–2022; red) the onset of the heatwave (dashed line) from summer and winter coastline surveys in Katmai and Kenai Fjords National Parks, Alaska

Table 3. Mean ± SE densities of the avian benthivore guild (n km^{-2}), benthivorous marine birds species (n km^{-2}), benthic marine prey (n m^{-2}), and percent change after the onset of the Pacific marine heatwave (PMH). PMH effect and direction of change are based on AIC model selection and parameter estimates. Densities and percent change are only shown for the season of primary occurrence, or in the case of prey, the season when they were sampled. **Bold** font denotes taxa that were significantly correlated with the PMH

Group	PMH effect	Direction of change	Summer density			Winter density		
			Before onset of PMH	After onset of PMH	Percent change	Before onset of PMH	After onset of PMH	Percent change
Benthivores	No		33.30 ± 3.84	25.20 ± 2.66	−24	103.00 ± 9.24	107.00 ± 9.30	4
Barrow's goldeneye	**Yes**	**Positive**				**23.90 ± 45.70**	**28.10 ± 46.10**	**18**
Black oystercatcher	**Yes**	**Positive**	**1.45 ± 0.23**	**1.62 ± 3.37**	**12**			
Black scoter	No					10.60 ± 24.50	13.30 ± 39.20	25
Bufflehead	No					3.91 ± 12.60	6.24 ± 18.40	60
Emperor goose	No					1.22 ± 6.86	4.60 ± 32.10	277
Harlequin duck	No		22.00 ± 3.04	18.50 ± 44.80	−16	30.30 ± 30.00	27.90 ± 30.30	−8
Long-tailed duck	**Yes**	**Negative**				**7.00 ± 15.70**	**4.52 ± 10.80**	**−35**
Rock sandpiper	No					3.11 ± 14.70	2.72 ± 15.10	−13
Surf scoter	No		4.02 ± 1.07	3.02 ± 21.80	−25	8.93 ± 16.40	11.00 ± 21.40	23
White-winged scoter	No		3.10 ± 0.85	0.63 ± 6.33	−80	4.92 ± 11.00	4.53 ± 12.00	−8
Clam	**Yes**	**Negative**	**67.70 ± 4.66**	**74.80 ± 4.55**	**10**			
Limpet	**Yes**	**Positive**	**17.30 ± 1.50**	**21.90 ± 1.98**	**27**			
Mussel	**Yes**	**Positive**	**1801 ± 131**	**2621 ± 237**	**46**			

the PMH. Furthermore, the effect size of PMH in the top model was weak (estimate ± SE: −0.13 ± 0.08) and not significant ($p = 0.09$). This is consistent with small differences in overall benthivore density before and after the PMH (Table 3); densities trended slightly lower after the PMH in summer and slightly higher after the PMH in winter.

3.2. Species abundance

Similar to benthivore overall abundance, most benthivorous species were not strongly affected by the PMH (Fig. 3, Table 3). The inclusion of PMH, or the interaction between PMH and season, to models did not substantially increase model support for most species (Table S1 in the Supplement at www.int-res.com/articles/suppl/m737p215_supp.pdf). However, for Barrow's goldeneye and black oystercatcher abundance, the best supported models included correlations with the effect of the PMH. The best supported model of Barrow's goldeneye winter abundance indicated a moderate positive increase in abundance after the onset of the PMH (estimate ± SE: 0.32 ± 0.16, $p = 0.04$). Likewise, the best supported model of black oystercatcher summer abundance also indicated a moderate positive relationship with the effect of PMH (estimate ± SE: 0.33 ± 0.11, $p < 0.01$). For both of these species, the percent change in density after the onset of the PMH was also positive (Fig. 3, Table 3). In contrast, long-tailed duck winter abundance declined after the PMH (Fig. 3, Table S1). The best supported model of long-tailed duck abundance indicated a negative relationship with PMH (estimate ± SE: −0.75 ± 0.18, $p < 0.01$).

3.3. Prey abundance

To identify potential mechanisms driving relationships of marine birds with the PMH, we tested for an effect of PMH on the abundance of clams, limpets, and mussels, which are important benthic invertebrate prey for avian benthivores. The best supported models of abundance for all 3 prey types included a fixed effect of PMH (Table 4), although the direction of change differed among them (Fig. 4, Table 3). For clams, the best supported model indicated a negative relationship with PMH (estimate ± SE: −0.27 ± 0.08, $p < 0.01$). However, this decrease in clam abundance after the onset of the PMH only occurred in Kenai Fjords and not Katmai (Fig. 4). Overall, when averaged across regions, clam density was actually higher after the onset of PMH (Table 3). In contrast, both limpets and mussels increased in abundance after the onset of the PMH (Table 4). The best supported models of limpet and mussel abundance indicated a positive correlation with PMH (estimate ± SE: 0.21 ± 0.09, $p < 0.01$, and 0.54 ± 0.10, $p < 0.01$, respectively).

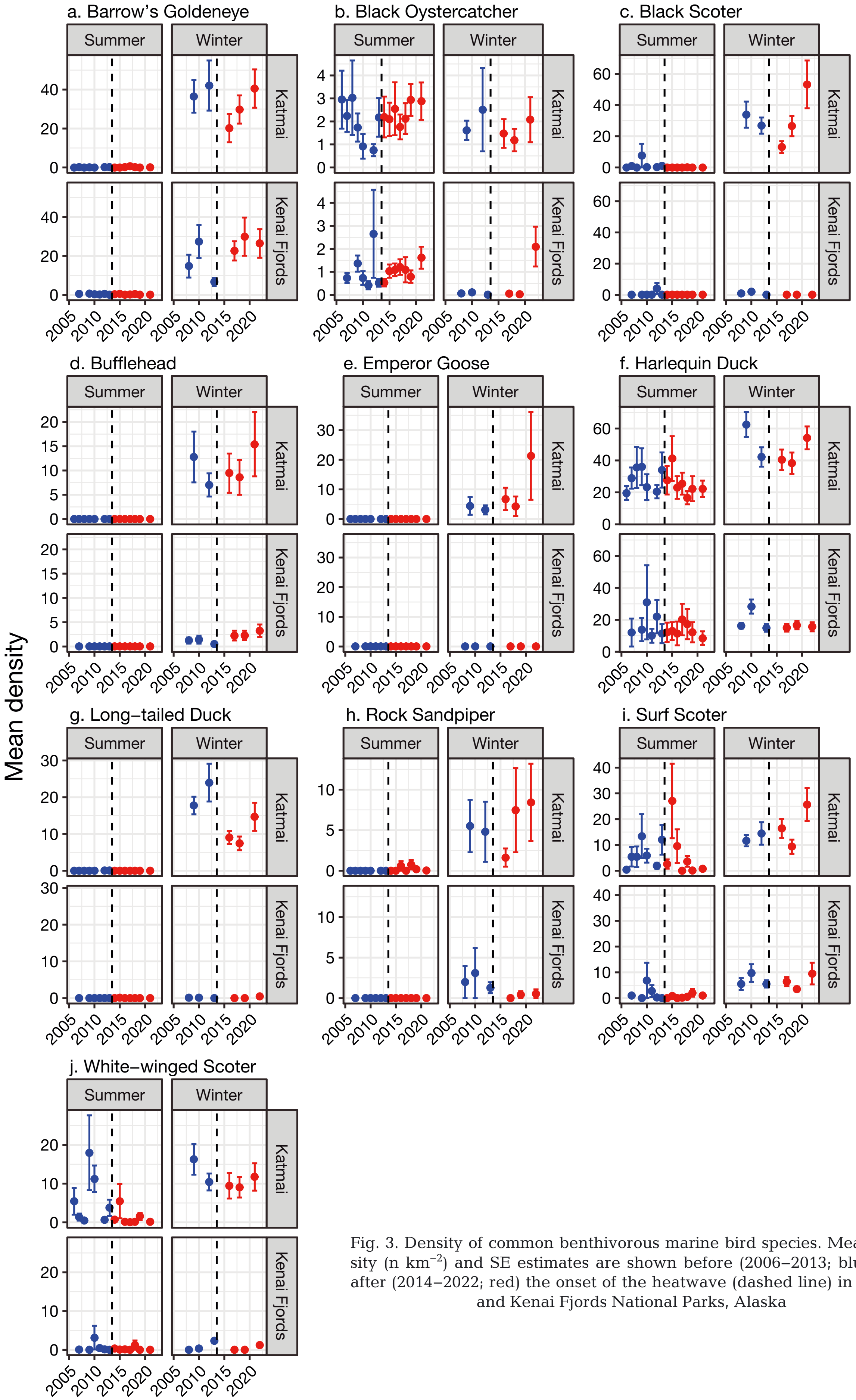

Fig. 3. Density of common benthivorous marine bird species. Mean density (n km^{-2}) and SE estimates are shown before (2006–2013; blue) and after (2014–2022; red) the onset of the heatwave (dashed line) in Katmai and Kenai Fjords National Parks, Alaska

Table 4. Ranking of generalized linear mixed-effects models of benthic marine prey abundance in the Gulf of Alaska. Prey types (clam, limpet, and mussel) were analyzed in separate candidate model sets. All models include an offset term for sampling area and a random effect of replicate nested within site. ΔAIC: Akaike information criterion (AIC) between the best model and the one being compared; ω: Akaike weight; df: degrees of freedom in the model; PMH: Pacific marine heatwave

Prey type	Model	ΔAIC	ω	df
Clam	PMH	0.0	0.65	5
	PMH + Region	1.3	0.34	6
	Null	8.2	0.01	4
	Region	9.6	0.01	5
Limpet	PMH	0.0	0.58	5
	PMH + Region	1.8	0.24	6
	Region	3.0	0.13	4
	Null	4.8	0.05	5
Mussel	PMH	0.0	0.68	5
	PMH + Region	1.5	0.32	6
	Null	28.1	0.00	4
	Region	29.9	0.00	5

4. DISCUSSION

Our findings are the first to document the relationship between avian marine benthivores and the PMH. In contrast to dramatic effects of the PMH on pelagic food webs shown in this Theme Section and elsewhere (Piatt et al. 2020, Schoen et al. 2024), our results demonstrate that top-level predators specializing on benthic invertebrate prey exhibited little response to the PMH, presumably as a consequence of the lack of strong effects of the PMH on nearshore prey abundance. Unlike extreme reductions in quantity and quality of forage fish (von Biela et al. 2019, Arimitsu et al. 2021), common invertebrate prey species abundance remained relatively stable in association with the PMH, with only slight declines observed for clams in one region and slight increases for limpets and mussels in both regions. Following suit, most marine birds specializing in benthic invertebrate prey did not show significant changes in abundance either. Our results, in conjunction with published work on pelagic food web responses to the PMH, demonstrate that variation in prey abundance was mirrored by variation in predator abundance, which supports the hypothesis that food has a strong mediating effect of the PMH on upper trophic levels across food webs and suggests that direct physiological effects of varying temperature on birds were less significant.

In the absence of strong effects of the PMH, inherent seasonal and regional sources of variation were the primary drivers that influenced abundance of benthivorous marine birds. Seasonal variation is expected due to the life history of many nearshore marine bird species, particularly sea ducks, which winter in nearshore habitats before moving inland to nest during summer (Derksen et al. 2015). Regional differences in abundance between Katmai and Kenai Fjords are also expected as these two regions are geomorphologically dissimilar. The shallow, mixed sediment expanses in Katmai support high densities of clams, whereas the steep and deep fjord landscape

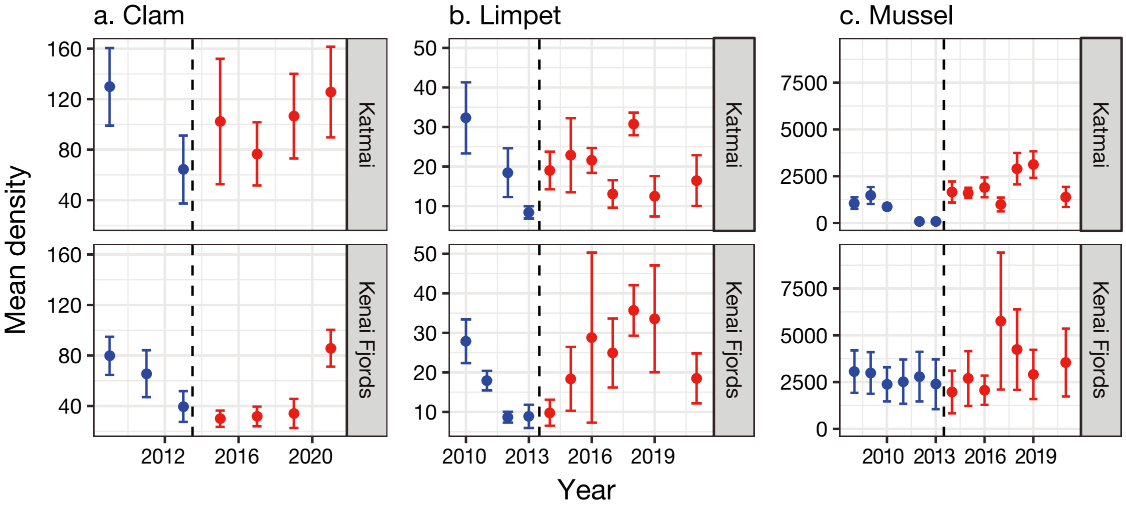

Fig. 4. Nearshore benthic marine prey density before and after the onset of the Pacific marine heatwave. Mean density (n m^{-2}) and SE estimates of (a) clam (all species observed), (b) limpets *Lottia persona*, and (c) mussels *Mytilus trossulus* are shown before (2008–2013; blue) and after (2014–2022; red) the onset of the Pacific marine heatwave (dashed line) in Katmai and Kenai Fjords National Parks, Alaska

of Kenai Fjords is dominated by narrow, rocky intertidal habitat, favoring mussels and limpets.

For some individual species, we did detect differences in abundance after the onset of the PMH. Barrow's goldeneye and black oystercatchers, both species for which mussels constitute a high proportion of their diets (Esler et al. 2000, Robinson et al. 2018), had slightly higher abundance following the PMH. Mussels also increased during and after the PMH (Weitzman et al. 2021, Traiger et al. 2022), which suggests the possibility that increased prey availability could be related to their increased abundance. Long-tailed ducks, which have a highly variable diet that occasionally includes forage fish, declined in abundance after the onset of the PMH. However, long-tailed ducks also are known to have low site fidelity and high propensity for movement within seasons (Robertson & Savard 2020), making it more difficult to attribute abundance trends to local conditions.

Although our findings, and the results from the literature for piscivorous birds, suggest that marine birds were affected indirectly by the PMH via trophic pathways rather than directly via physiological mechanisms, we cannot rule out the possibility that individual birds may incur physiological effects. Given that sea surface temperature in the Gulf of Alaska is positively correlated with air temperature (Danielson et al. 2022), unusually warm air temperatures that occurred in conjunction with the PMH could potentially have delayed physiological effects on developing young. For example, heat exposure has been found to decrease telomere length in nestlings which can reduce life span and fitness (Eastwood et al. 2019). Mechanisms that link heat exposure to reduced telomere length may include oxidative damage, glucocorticoid stress, dehydration, higher metabolic rate, nutrition reduction, and elevated heat shock protein levels (Maeda et al. 2014, Reichert & Stier 2017, Angelier et al. 2018). In these high-latitude study areas, air temperature at benthivore nest sites was likely not high enough to have direct lasting physiological consequences.

The differential responses of intermediary prey within nearshore versus pelagic food webs to the PMH is striking and suggests that different mechanisms of change were operating in each respective food web. The collapse of forage fish populations, which sustain the majority of predators within pelagic food webs, is believed to be driven by a reduction in phytoplankton biomass and a restructuring of zooplankton communities that favored low-energy species (Piatt et al. 2020). Simultaneously, warmer ocean temperatures increased the metabolic demands of both ectothermic forage fish and predatory groundfish. Under these conditions, forage fish had to meet their higher energetic demands with lower quality and less abundant prey while under higher predation pressure from groundfish. As a result, forage fish populations decreased dramatically in quality and quantity (von Biela et al. 2019, Arimitsu et al. 2021). This ectothermic vise hypothesis, as it has been coined, offers a plausible explanation of the mechanisms underlying the dramatic decline of forage fish in pelagic systems (Piatt et al. 2020).

In nearshore food webs, intermediary prey did not substantially decline with respect to the PMH, with evidence of only slight changes in abundance across all sampled taxa in some species. In contrast to pelagic systems, where phytoplankton dominate the base of the food web, primary producers in nearshore systems consist of macroalgae, sea grasses, and phytoplankton (Duggins et al. 1989, von Biela et al. 2016). This diversity of primary producers in the nearshore food web combined with planktonic subsidies from the pelagic realm (Zuercher & Galloway 2019) may allow for consumers there to be buffered against environmental changes compared to food webs largely supported by a single source (Huxel et al. 2002). Although benthic invertebrates are ectothermic like forage fish, they are well adapted to highly dynamic intertidal environments where they are exposed to a wide range of physical conditions such as extreme heat, freezing temperatures, fluctuating salinity, and wave forcing (Carroll & Highsmith 1996). The diverse sources of primary production in nearshore food webs may also be related to why benthic prey taxa were not negatively affected by the PMH.

Of the benthic prey we examined, mussels increased in abundance with respect to the PMH, consistent with analyses of Weitzman et al. (2021) and Traiger et al. (2022). This increase may be a result of a reduction in predation and competition for space. Rockweed *Fucus distichus*, a macroalga that is an intertidal foundational species and important habitat former, declined throughout the Gulf of Alaska concurrent with the onset of the PMH (Weitzman et al. 2021). After undergoing a major recruitment event, mussels occupied the empty space left in the absence of *F. distichus*. At the same time, sea stars (*Evasterias troschelii*, *Pisaster ochraceus*, and *Pycnopodia helianthoides*), important predators of intertidal invertebrates, were impacted by a major outbreak of sea star wasting disease (Konar et al.

2019). This reduction in predation pressure and increase in available space allowed mussels to increase in density and persist (Traiger et al. 2022).

Despite the release from predation pressure by sea stars, clams slightly declined in abundance. Although clams are a food source for *P. helianthoides*, which declined after the PMH (Traiger et al. 2022), sea otters were still present and are a major clam predator (Kvitek et al. 1992). Clam declines were modest, e.g. relative to those observed in forage fish, and were evident in only one of our study regions (Kenai Fjords), which suggests that a broad-scale phenomenon like the PMH was not driving local-scale variation.

Limpets showed evidence of a slight increase in abundance after the onset of the PMH. The limpet species in this study occurs in the high intertidal zone and is unlikely to be strongly affected by sea stars, which favor mid- to low intertidal zones (O'Clair & O'Clair 1998) but may have benefitted from increases in available space with the decline in macroalgal species such as *F. distichus* (Weitzman et al. 2021).

Although benthic marine invertebrates are susceptible to extreme climatic events, they did not exhibit strong region-wide declines with respect to the PMH, likely due to lack of high daytime temperature coinciding with extreme low tides. In contrast, the 2021 heatwave in British Columbia, Canada, coincided with low tides, resulting in mass mortality of intertidal invertebrates including mussels and clams (White et al. 2023). Overall, these factors worked in concert to buffer benthic prey taxa from the negative effects of the PMH in the Gulf of Alaska.

Through ecosystem-wide monitoring, we have been able to assess variable responses to a large-scale, cross-ecosystem perturbation. Our findings show how an extreme environmental perturbation affects biological communities through trophic pathways. As ecosystems continue to shift in response to climate-change-driven stressors, such as marine heatwaves, it is imperative to collect and interpret data not just species by species, but to examine communities as a whole. Contrasting community responses provides important insight into ecosystem resiliency, improves predictive power, and can inform management strategies in the face of persistent climate change.

Data availability. The data used in this study are openly available. They can be accessed via the following links: https://doi.org/10.5066/F7416V6H, https://doi.org/10.5066/F71834N0, https://doi.org/10.5066/F7513WCB, and https://doi.org/10.5066/F7FN1498.

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