Vol. 737: 1–8, 2024
https://doi.org/10.3354/meps14625

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published June 6

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

INTRODUCTION

Mechanisms by which marine heatwaves affect seabirds

J. F. Piatt[1,*], M. L. Arimitsu[2], S. A. Thompson[3], R. Suryan[4], R. P. Wilson[5], K. H. Elliott[6], W. J. Sydeman[3]

[1]US Geological Survey, Alaska Science Center, Anchorage, AK 99508, USA
[2]US Geological Survey, Alaska Science Center, Juneau, AK 99801, USA
[3]Farallon Institute, Petaluma, CA 94952, USA
[4]NOAA, Alaska Fisheries Science Center, Auke Bay Laboratories, Juneau, AK 99801, USA
[5]School of Biological Sciences, Swansea University, Singleton Park Campus, Swansea SA2 8PP, UK
[6]McGill University, Ste. Anne de Bellevue, QC H9X 3V9, Canada

ABSTRACT: Marine heatwaves (MHWs) are characterized by periods of extreme warming of local to basin-scale marine habitat. Effects of MHWs on some seabirds (e.g. mass die-offs) are well documented, but mechanisms by which seabirds respond to MHWs remain poorly understood. Following from a symposium at the 3rd World Seabird Conference, this Theme Section presents recent research to address this knowledge gap. Studies included here spanned one or more MHW event, at spatial scales from individual seabird colonies to large marine ecosystems in subtropical, temperate, and polar oceans, and over timespans from months to decades. The findings summarized herein indicate that MHWs can affect seabirds directly by creating physiological heat stress that affects behavior or survival, or indirectly by disrupting seabird food webs, largely by altering metabolic rates in ectothermic prey species, leading to effects on their associated predators and prey. Four main mechanisms by which MHWs affect seabirds are (1) habitat modification, (2) physiological forcing, (3) behavioral responses, and (4) ecological processes or species interactions. Most seabird species have experienced limited effects from MHWs to date, owing to ecological and behavioral adaptations that buffer MHW effects. However, the intensity and frequency of MHWs is increasing due to global warming, and more seabird species may have difficulty coping with future heatwave events. Also, MHW impacts can persist for years after a MHW ends, so consequences of recent or future MHWs could continue to unfold over time for many long-lived seabird species.

KEY WORDS: Marine heatwaves · Seabirds · Forage fish · Die-off · Reproductive failure · Heat stress · Metabolic scaling

1. MARINE HEATWAVES AND THEIR SEABIRD-RELEVANT CHARACTERISTICS

Marine heatwaves (MHWs) are defined by periods of anomalously high ocean temperatures, caused by a mix of drivers that often includes seasonality and persistence of atmospheric high-pressure systems, weakened surface winds, reduced vertical mixing of the water column, horizontal advection of warm water, and reduced ocean heat flux to the atmosphere (Hobday et al. 2018, Sen Gupta et al. 2020). MHWs have been increasing in frequency and intensity over the past few decades (Oliver et al. 2018), sometimes with severe consequences for seabirds and their marine

*Corresponding author: jpiatt@usgs.gov

Publisher: Inter-Research · www.int-res.com

habitats (Piatt et al. 2020). Generally, MHWs appear to be the result of local-scale processes acting on the mixed layer, which can be modulated by the remote influence of major climate modes (Di Lorenzo & Mantua 2016, Holbrook et al. 2019). Other modes of warming include quasi-annual variability (e.g. El Niño Southern Oscillation, ENSO), multi-decadal oscillations (e.g. Pacific Decadal Oscillation, PDO), and global warming. Slow, upward-trending global warming fuels an increasing intensity in the cyclical/periodic modes that may be additive in producing particularly strong MHW events (Sen Gupta et al. 2020).

Sen Gupta et al. (2020) recently identified 62 of the 'most extreme' MHWs of the past 4 decades based on maximum areal intensity, severity, and duration. The median duration of these extreme MHW events was ~70 d (10th–90th decile was between 40 and 160 d). The median areal extent of severe MHWs was ~1.6 million km^2 (range 0.3–12 million km^2). Maximum durations could be much longer (>700 d, Hobday et al. 2018). Furthermore, very strong ENSO events (e.g. in 1997/1998, 2015/2016) can enhance the intensity, duration, and spatial extent of some MHWs through atmospheric teleconnections (Di Lorenzo & Mantua 2016). For example, the Pacific MHW in 2014–2016 (the 'Blob') was the longest known MHW event, triggered in 2014 by a persistent high-pressure system over the United States (US) Pacific Northwest (Bond et al. 2015). As MHW waters of the Blob moved eastward, they merged with the 2015/2016 ENSO signature and intensified warm sea surface temperature (SST) anomalies along the US Pacific west coast and Gulf of Alaska into the spring of 2016 (Sen Gupta et al. 2020).

MHW characteristics that are pertinent to evaluating effects on seabirds include: (1) Location and spatial extent — MHWs may be produced by a mix of drivers that can promote local to regional warming almost anywhere on the globe, but particularly in temperate and subtropical waters that host the majority of global seabird populations (Paleczny et al. 2015). Many MHWs have moderate to large areal dimensions, which are large enough to affect entire seabird colony nesting and foraging areas, migration routes, or overwintering areas. (2) Duration — the more extreme MHWs typically persist for 1–6 mo, and only a few have persisted for a year or more. These longer duration MHWs may affect seabirds at multiple stages of their life cycle (breeding, spring or fall migration, molt, overwintering periods), thereby potentially influencing key population parameters, such as adult and juvenile survival, which often drive population change. (3) Seasonality — MHW intensity has a distinct seasonality and tends to peak during summer, when many seabird populations are constrained to attend their breeding colonies. (4) Intensity — MHW intensity (cumulative heat retention) develops more quickly and reaches greater extremes than typically observed during ENSO and PDO events (Holbrook et al. 2019), creating greater potential for impacts to seabirds and their prey despite their shorter duration.

2. STUDIES OF MHW EFFECTS ON SEABIRDS

Until recently, relatively few papers have examined responses of seabirds to heatwaves or attempted to elucidate mechanisms that result in minor effects or significant impacts on seabird biology (Woehler & Hobday 2024 in this Theme Section). To help fill these gaps in our understanding, a symposium on 'Mechanisms by which heatwaves impact seabirds' was organized for the 3rd World Seabird Conference (WSC3) in Tasmania, Australia, in October 2021. Seven WSC3 contributions and 6 subsequent papers submitted to this Theme Section are presented here and contain recent advances in our understanding of how heatwaves affect seabirds. In Section 3, we place these latest findings in context (see Table 1) with 7 other recent papers that were presented at WSC3 but published independently. Together, these 20 publications helped us to identify specific mechanisms that transform ocean heatwaves into effects on seabirds, the types of mechanisms that are most common, and the associated effects or consequences (impacts) for each type of mechanism.

Effects of MHWs on seabirds are documented in the contributions to this Theme Section (including reviews by Oswald & Arnold 2024 and Woehler & Hobday 2024; all articles cited in this paragraph are in this Theme Section). They include shifts in distribution at sea (Cushing et al. 2024, Kuletz et al. 2024), reduced food quality and foraging success (C. Robinson et al. 2024, Wagner et al. 2024), reduced body condition (Schoen et al. 2024), heat stress (Mason et al. 2024, Olin et al. 2024), reproductive failures at colonies (Olin et al. 2024, Schoen et al. 2024), mass die-offs at sea (Jones et al. 2024), lower chick and/or adult survival (De la Cruz-Pino et al. 2024, Mason et al. 2024), and declines in abundance (Cannell et al. 2024, Schoen et al. 2024). However, the mechanisms by which MHWs facilitate these outcomes are not always clear, such as why MHWs affect certain species (Cannell et al. 2024) yet leave others unaffected (e.g. benthic-feeding marine birds, B. Robinson et al. 2024).

3. MECHANISMS OF MHW EFFECTS

We identified 4 types of mechanisms by which heatwaves can generate effects on seabirds via changes in marine habitats and/or animal physiology, behavior, or ecology (Table 1). Mechanisms may operate directly or indirectly. Indirect effects are far more common and complex than direct effects, as suggested for climate change effects on marine vertebrates in general (Sydeman et al. 2015). Despite many examples of MHW effects on some seabird species, MHWs have actually had limited effects on most marine bird species (e.g. B. Robinson et al. 2024, Woehler & Hobday 2024). Where effects do occur, there may be lingering consequences for seabirds for a considerable time after the MHW has ended (Cannell et al. 2024, Jones et al. 2024, Schoen et al. 2024). The main types of mechanisms that translate heatwave forcing into effects on seabirds operate through four factors: habitat modification, physiological forcing, behavioral responses, and ecological processes or interactions (Table 1).

Two-thirds of all direct or indirect mechanisms are physiologically driven, often in association with other mechanisms (Table 1). For endothermic seabirds, direct mechanisms revolve around physiological efforts to maintain a constant temperature, with some behavioral help to cool the body, and some consequential biological processes (e.g. breeding failure, predation) if they cannot (Table 1). Metabolic scaling — the relationship between temperature, metabolism, and organism size — is the primary constraint that scales up the food web to influence biological, ecological, and evolutionary processes (Bruno et al. 2015), and it creates an indirect pathway for most mechanisms by which MHWs impact marine food webs and seabirds. For ectothermic members of marine food webs, external temperature controls rates of chemical and enzyme reactions, metabolism, and higher functions such as assimilation efficiency, growth, and fecundity (Brett 1971). Most marine ectotherms are fine-tuned to work optimally over a relatively narrow and species-specific range of temperatures (Bruno et al. 2015, Pauly & Lam 2023). In response to temperature, physiological factors help determine where and when prey are likely to be concentrated, as well as the quality, quantity, and diversity of prey that are likely to be available to seabird predators (Grémillet et al. 2008). In turn, seabirds respond with behavioral mechanisms in the search for adequate prey, which might mean foraging farther or deeper, abandoning old foraging areas for new, migrating to more productive wintering grounds, switching prey types when preferred prey are unavailable, and abandoning egg-laying or chicks when prey are scarce (Cairns 1988, Piatt et al. 2007, Elliot et al. 2008). These behavioral mechanisms may then lead to ecological mechanisms of change, such as reduction of clutch size, predation of unattended eggs or chicks, reproductive failure, reduced adult survival, match-mismatch to food supplies, and competition with other upper trophic level predators for limited prey (Piatt et al. 2020, d'Entremont et al. 2023, De la Cruz-Pino et al. 2024, Marsteller et al. 2024, Schoen et al. 2024).

Direct effects of extreme heat can overwhelm thermoregulatory systems of seabirds and any behavioral means of cooling, which may cause heat stress or death. Seabirds on terrestrial breeding colonies can be stressed directly by extreme air temperatures associated with MHWs, but we are unaware of similar effects reported yet for MHWs and birds at sea, as in most cases water temperature is below the upper critical temperature of birds (e.g. Choy et al. 2021). Additionally, heat stress at colonies during marine or terrestrial heatwaves may occur more often than has previously been reported (Mason et al. 2024, Olin et al. 2024, Oswald & Arnold 2024). The physiological response by seabirds to heat stress can be mitigated by adaptive behaviors (with some fitness costs); however, effects of these behavior modifications can be magnified by ecological interactions such as predation and competition (Table 1).

Indirect effects are almost entirely mediated by the effect of heating on marine habitat and food webs, followed by behavioral or biological consequences for seabirds. Therefore, indirect effects can be quite complex, in part because individual mechanisms may be additive and/or amplified biologically over time. For example, the most common effect of a heatwave (by definition) is to heat surface layers of water (Holbrook et al. 2019). When warm water habitat is mixed, stratified, deepened, or advected, and/or these conditions persist over periods of months to years, then habitat modification becomes an important physical mechanism that promotes more complex biological responses in the ecosystem. For example, ectothermic forage fish have narrow optimal temperature ranges, they will usually retreat (horizontally or vertically) from warmer-than-usual water if they are distressed, and so become unavailable to colony-based breeding seabirds. Even during a relatively brief heatwave, this mechanism can result in a temporary abandonment of nest sites and chicks (for ca. 5–20 d; Montevecchi et al. 2021). Similar effects on seabirds may also occur due to a temporal 'match-mismatch' between seabirds and their prey (d'Entremont et al. 2023, Woehler & Hobday 2024), when intense MHWs extending over seasons and years may affect phenology, species

Table 1. Mechanisms by which marine heatwaves impact seabirds in colonies and at sea, as identified in papers stemming from the WSC3 symposium on the same topic (see Section 2). Direct effects: direct response by birds, eggs, or chicks to warm temperatures. Indirect effects: seabirds respond to changes in prey quality, distribution, or abundance that result from warm temperatures influencing seabird habitat. Limited effects: selected seabirds may be strongly impacted, but coexisting seabirds just partially impacted, if at all. Mechanism types relevant to seabirds — H: habitat modification; P: physiological responses; Be: behavioral responses; Ec: ecological processes or biological interactions

Effect	Type	Mechanism description	Potential consequence or response	Reference
Direct	P	Heat stress, heat exceeds thermoregulation capacity	Egg/chick/adult hyperthermia, mortality, breeding failure, colony abandonment	10,11,13
	P Be	Heat stress, adult behavior modification, self-cooling	Adjusted time-energy budgets, reduced fitness	11,13
	P Be Ec	Heat stress, adult behavior modification, reduced nest attendance by adult	Egg/chick exposure to predators, weakening of pair bond	11,13
Indirect	H P	Stratification and variable oceanic mixed-layer depth may restrict forage taxa to thermally tolerable depths	Changes in foraging effort, adult body condition, chick feeding, survival	1,6,20
	H Ec	Warm winter/spring temperatures alter phytoplankton, zooplankton and forage fish phenology	'Match-mismatch' owing to seasonality of resource availability during constrained breeding season	5,8,14,18,20
	H Be Ec	Advection of warm water current in spring/summer; new/old prey taxa carried in/out of colony range	Colony foraging success disrupted, may affect condition, reproduction or survival	2,3,6,9,18,20
	H Be Ec	Warm water on migration/overwintering ground affects prey abundance/distribution/quality	Shifts in timing/site of post-breeding migrations and molt, body condition, survival, future reproduction	2,7,8,9,16,20
	P	Increased metabolic rate/food needs of ectothermic prey can limit growth, size, and fat storage of prey	Poor quality of prey, limiting biomass/energy intake by seabirds	1,14,16,18,19
	P Be Ec	Reduced bottom-up production, food quality, body condition, recruitment, survival of forage fish	Increased foraging effort/cost, reduces body condition, chick feeding, fledging success	1,4,6,8,12,14,16,17,18,20
	Ec	Ecosystem-wide bottom-up effects synchronously reduce most prey, a 'portfolio effect'	Synchronous loss of multiple forage taxa may cause major die-off events due to starvation	1,14
	P Ec	Increased metabolic rate/food intake of groundfish, which then consume more forage fish biomass	Increased top-down competition for prey, reduces food available to seabirds leading to starvation	1,14,18
	P Ec	Synergistic interaction of bottom-up and top-down metabolic effects on fish, an 'ectothermic vise'	Poor quality and low abundance prey, reduces seabird reproduction/survival	1,8,14,17
Limited	Be Ec	Species with generalist diet or those feeding on less heat-impacted food webs can buffer against variability in 1 or more prey species	Responds to loss of important prey by low-fitness-cost switch to other prey species	3,8,15,18,19
	Be Ec	Species able to exploit more marine habitats (e.g. can fly further, dive deeper)	More flexibility when warm waters are near colony or restricted to upper layer	3,8,12,15,17,20
	P Ec	Species have flexible life history traits adaptive for buffering against extreme thermal regimes	Flexible clutch size, flexible chick meal-load capacity, flexible breeding season duration	4,17,19,20

[1]Arimitsu et al. (2021), [2]Cannell et al. (2024), [3]Cushing et al. (2024), [4]De la Cruz-Pino et al. (2024), [5]d'Entremont et al. (2023), [6]Evans et al. (2021), [7]Glencross et al. (2021), [8]Jones et al. (2024), [9]Kuletz et al. (2024), [10]Mason et al. (2024), [11]Olin et al. (2024), [12]Osborne et al. (2020), [13]Oswald & Arnold (2024), [14]Piatt et al. (2020), [15]B. Robinson et al. (2024), [16]C. Robinson et al. (2024), [17]Schoen et al. (2024), [18]Suryan et al. (2021), [19]Wagner et al. (2024), [20]Woehler & Hobday (2024)

composition, and magnitude of phytoplankton and zooplankton blooms and associated forage fish predators (Batten et al. 2022).

During longer-than-average MHWs (i.e. >70 d), multiple indirect mechanisms have the potential to synergistically disrupt food webs and amplify effects on seabirds over parts or all of their annual life history cycle, leading to seabird breeding failures, overwinter mortality, and/or population declines (Glencross et al. 2021, Cannell et al. 2024, Jones et al. 2024, Schoen et al. 2024). Played out over weeks and months, warm waters will also increase metabolic rates and therefore food demands of all ectotherms, as metabolic scaling with temperature is highly conserved across taxa and environments (Bruno et al. 2015). This ordinary physiological response can result in extraordinary biological consequences (Table 1) for every ectothermic organism from plankton to large groundfish (Arimitsu et al. 2021, Gomes et al. 2024, Reum et al. 2024). Over months and seasons, just 2 phenomena — ectothermic metabolism and thermal optima — will begin to transform communities, as taxa with tolerance for higher temperatures begin to replace cold-water adapted taxa, ecosystem structure is disrupted by changes in biomass demand and energy flux up food chains (Gomes et al. 2024, Reum et al. 2024), and new or altered communities may be redistributed within or among ecosystems by advection of warm currents (Daly et al. 2017, Kuletz et al. 2024, Woehler & Hobday 2024). Shifts in primary and secondary food production can produce advected communities dominated by smaller and/or lower-quality individuals (Suryan et al. 2021, Batten et al. 2022).

The change to smaller-sized species within lower trophic level communities combined with higher metabolic rates and food requirements driven by increased temperatures can lead to reduced growth rates and poor body condition in forage taxa (Daly & Brodeur 2015, von Biela et al. 2019, Arimitsu et al. 2021, C. Robinson et al. 2024). Depending on the seasonality of these combined mechanisms, effects can vary drastically. Over the summer seabird breeding seasons, colony-based foraging success may be disrupted, leading to decreased fledging success or adult survival (Piatt et al. 2020, Cannell et al. 2024, Kuletz et al. 2024). Over the winter non-breeding periods, they may disrupt migration behavior, molt, survival, and future reproduction in seabirds (Glencross et al. 2021, Jones et al. 2024). Over all the seasons (1+ year), this chronic effect can inhibit growth, lipid storage, survival, and recruitment of multiple forage species leading to synchronous collapse of the forage fish community (i.e. a 'portfolio effect', Arimitsu et al. 2021).

Depletion of prey abundance can be further accelerated by a large increase in food intake required by large ectothermic groundfish stocks after significant ocean warming (Holsman & Aydin 2015). Because groundfish usually consume 1–2 orders of magnitude more forage fish than seabirds in most northern shelf ecosystems (Gaichas et al. 2009), the ordinary physiological response of groundfish to increased water temperature can add 'competition from groundfish' to the list of mechanisms that lead to significant biological impacts on seabirds. The co-occurrence of bottom-up and top-down forces may create an 'ectothermic vise' on forage fish (or 'metabolic mis-match'; Reum et al. 2024), a mechanism identified as a likely contributor to the extreme mass die-offs of seabirds, cod, and whales in the North Pacific after the Pacific MHW of 2014–2016 (Barbeaux et al. 2020, Piatt et al. 2020, Cheeseman et al. 2024).

Whereas the above direct and indirect effects have been observed for 20 or more species, MHWs have so far had limited effects on most other seabirds in the areas covered by investigations listed in Table 1. Not all MHWs diminish bottom-up productivity or fish growth, recruitment, or survival (Amaya et al. 2020, Gomes et al. 2024, Woehler & Hobday 2024). In part, this is because effects depend on the thermal plasticity and temperature optima of species/communities involved, and whether these communities occur at the center or edge of their thermal optimum ranges (Bennett et al. 2021).

Seabirds mitigate direct and indirect negative MHW impacts by employing useful adaptations and flexible life history traits. For the direct mechanism (heat stress), all seabirds have some capacity for cooling themselves or their chicks, e.g. evaporative cooling, shading, swimming, drinking water, wing spread, and gular fluttering (Olin et al. 2024, Oswald & Arnold 2024). All indirect mechanisms affect or involve some aspect of food acquisition, including prey distribution, abundance, phenology, diversity, size, and energy content. Any seabird species that has more flexibility for dealing with interruptions in prey availability or quality seem to have an advantage over those that have little flexibility.

For example, during the Pacific MHW of 2014–2016, common murres *Uria aalge* in the Gulf of Alaska experienced a population crash in their pelagic forage fish prey, whereas congeneric thick-billed murres *U. lomvia* were virtually untouched (Piatt et al. 2020), because they have a more diverse diet that includes benthic fish and pelagic invertebrates (Will et al. 2020). During this same heatwave, rhinoceros auklets *Cerorhinca monocerata* in the California Current System

and black-legged kittiwakes *Rissa tridactyla* in the Gulf of Alaska were likely able to compensate for small size and low quality of prey in chick meal loads by increasing load size (multiple prey) for delivery to chicks, thereby reducing negative effects on breeding success (Schoen et al. 2024, Wagner et al. 2024). Species with lower foraging costs (e.g. less wing loading) may be able to travel longer distances to find prey patches (Osborne et al. 2020). Those with more flexible clutch size and fledgling periods can buffer during warm years and still manage to produce chicks or maintain the same lifetime production of offspring as more conservative egg layers (De la Cruz-Pino et al. 2024, Schoen et al. 2024). Species that forage on more diverse prey (i.e. generalist predator strategies), or on less affected food webs, e.g. benthic–coastal versus pelagic–shelf prey communities, may almost entirely escape the impact of even the most severe heatwaves, if their foraging habitats are less affected (Cushing et al. 2024, B. Robinson et al. 2024).

4. MHWS CAN HAVE LINGERING EFFECTS ON SOME SEABIRDS

The most extreme (acute) effects of MHWs were generally observed during and after peak temperature anomalies (Table 1). As temperatures returned to pre-heatwave levels, most of the extreme consequences ceased, but some effects continued for months and seemed to carry over even into the following year(s). For example, the largest die-off of common murres ever recorded occurred in the Gulf of Alaska during a few winter months (Nov 2015–Feb 2016) after peak temperature anomalies in summer 2015, when murres had failed to produce any chicks at 3 colonies — a highly unusual event (Piatt et al. 2020). Die-offs had stopped by summer of 2016, but 12 murre colonies in the Gulf of Alaska and Bering Sea still failed to produce chicks that year. During 2017, 8 colonies continued to fail. At 2 peripheral colonies, murres failed again in 2018. By 2019, although productivity recovered to about half that observed in the past, colony attendance had declined by 50% (Schoen et al. 2024). The Gulf of Alaska marine ecosystem revealed similar patterns. Some forage fish, other seabirds, marine mammals, groundfish, and salmon showed marked declines in body condition, reproductive success, or population size between the time assessments were made prior to 2014 and those made in 2015–2017, leveling off or increasing only slightly by 2018 (Suryan et al. 2021). Community analyses revealed that over half of 187 biological time series showed significant multi-year responses to the heatwave, with little recovery by 2018, suggesting that the Gulf of Alaska post-heatwave marine ecosystem was distinct from the pre-heatwave state (Suryan et al. 2021).

Lingering effects of MHWs were observed in 10 of the 20 papers cited in Table 1, including MHWs in the northeast Pacific in 1997/1998, 2014–2016, and 2019 (e.g. Jones et al. 2024, Schoen et al. 2024); off Western Australia in 2011/2012 (e.g. Cannell et al. 2024); and in the Northern Bering/Chukchi Seas in 2019/2020 (e.g. Jones et al. 2024, Kuletz et al. 2024). In addition to the lagged population recoveries noted in the previous paragraph, black-legged kittiwakes in Cook Inlet (Gulf of Alaska) also had breeding failures and lower than normal colony counts during and after the Pacific MHW of 2014–2016 (Schoen et al. 2024). GPS tracking of kittiwakes foraging from Middleton Island in the Gulf of Alaska before (2012/2013), during (2015/2016) and after (2017/2018) the MHW revealed dramatic changes in foraging behavior that included increased distances and different locations during and after the heatwave, suggesting the system had not recovered for 2 yr following the MHW (Osborne et al. 2020). Some forage fish species in the Gulf of Alaska that diminished in age at maturity, size, energy value, or abundance during 2015/2016, also lagged for at least 1–2 yr in their recovery to pre-MHW conditions (Arimitsu et al. 2021). In the Salish Sea (Washington, USA), rhinoceros auklet bill-load energy values were low in 2016 and 2017, and burrow occupancy rates declined by 20% in 2017, suggesting carry-over effects from the Pacific MHW of 2014–2016 may have extended a year for those auklets and their prey (C. Robinson et al. 2024, Wagner et al. 2024). In Western Australia, little penguins *Eudyptula minor* reduced breeding success owing to a loss of preferred forage fish in diets during the 2011 MHW, and breeding failures, diet shift, and starvation mortalities carried over into the 2012 breeding season as well (Cannell et al. 2024). A prolonged post-heatwave depression in forage species biomass or nutritional quality (e.g. von Biela et al. 2019, Arimitsu et al. 2021) would also play some role in lingering effects on seabird predators, as prey stocks must also undergo recovery after the primary heatwave event.

Evidence for carry-over effects also comes from the analysis by Jones et al. (2024) of beached bird recoveries on beaches following heatwaves off the California coast in 1997/1998, 2015/2016, and 2019/2020. After normalizing seabird carcass encounter rate data and plotting mortalities downstream from MHWs, a clear pattern emerged: Anomalously high seabird mortality rates peaked during the height of MHW temperature

anomalies, but after these events, seabird mortality rate anomalies dropped below average for about the same length of time the preceding heat anomalies had persisted (e.g. 1–2 yr). This period of reduced mortality after die-offs contrasts with evidence (previous paragraph) for lingering reductions in food availability. However, it might reflect an adjustment period as substantially reduced seabird populations grow back to a new, reduced carrying capacity (Jones et al. 2024).

In conclusion, for the studies considered here, exceptionally warm ocean temperatures had direct and indirect effects on some seabirds, particularly species that specialized on diminished pelagic prey resources. However, seabirds capable of mitigating heat stress or shifting prey resources experienced more limited effects. Identifying mechanisms for carry-over effects or recovery from MHWs would be fertile ground for more research. As global warming increases the frequency, magnitude, and duration of MHWs, understanding thresholds of thermal tolerance will inform management decisions and conservation of seabirds in the future.

Acknowledgements. We are grateful to all the participants of the 'Mechanisms of heatwave impact on seabirds' symposium held at the 3rd World Seabird Conference hosted by the World Seabird Union, and conference organizers in Australia. Discussions and correspondence before, during, and after this symposium, as well as the papers submitted by attendees to the MEPS Theme Section and elsewhere helped to shape our thinking about this topic. We thank Christine Paetzold, Dan Esler and John Pearce for helpful comments on the paper. Funding for this work was provided by the US Geological Survey Alaska Science Center. Funding for W.J.S. and S.A.T.'s participation was provided by National Science Foundation award no. 2142918 and North Pacific Research Board project number 2105. Any use of trade, firm, or product names is for descriptive purposes and does not imply endorsement by the US Government.

LITERATURE CITED

Amaya DJ, Miller AJ, Xie SP, Kosaka Y (2020) Physical drivers of the summer 2019 North Pacific marine heatwave. Nat Commun 11:1903

Arimitsu ML, Piatt JF, Hatch S, Suryan RM and others (2021) Heatwave-induced synchrony within forage fish portfolio disrupts energy flow to top pelagic predators. Glob Chang Biol 27:1859–1878

Barbeaux SJ, Holsman K, Zador S (2020) Marine heatwave stress test of ecosystem-based fisheries management in the Gulf of Alaska Pacific cod fishery. Front Mar Sci 7:1–21

Batten SD, Ostle C, Hélaouët P, Walne AW (2022) Responses of Gulf of Alaska plankton communities to a marine heat wave. Deep-Sea Res II 195:105002

Bennett JM, Sunday J, Calosi P, Villalobos F and others (2021) The evolution of critical thermal limits of life on Earth. Nat Commun 12:1198

Bond NA, Cronin MF, Freeland H, Mantua N (2015) Causes and impacts of the 2014 warm anomaly in the NE Pacific. Geophys Res Lett 42:3414–3420

Brett JR (1971) Energetic responses of salmon to temperature. A study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). Am Zool 11:99–113

Bruno JF, Carr LA, O'Connor MI (2015) Exploring the role of temperature in the ocean through metabolic scaling. Ecology 96:3126–3140

Cairns DK (1988) Seabirds as indicators of marine food supplies. Biol Oceanogr 5:261–271

Cannell BL, Kendall WL, Tyne JA, Bunce M, Hetzel Y, Murray D, Radford B (2024) Marine heatwaves affect breeding, diet and population size but not body condition of a range-edge little penguin colony. Mar Ecol Prog Ser 737: 193–213

Cheeseman T, Barlow J, Acebes JM, Audley K and others (2024) Bellwethers of change: population modelling of North Pacific humpback whales from 2002 through 2021 reveals shift from recovery to climate response. R Soc Open Sci 11:231462

Choy ES, O'Connor RS, Gilchrist HG, Hargreaves AL, Love OP, Vézina F, Elliott KH (2021) Limited heat tolerance in a cold-adapted seabird: implications of a warming Arctic. J Exp Biol 224:jeb242168

Cushing DA, Kuletz KJ, Sousa L, Day RH, Danielson SL, Labunski EA, Hopcroft RR (2024) Differential response of seabird species to warm- and cold-water events in a heterogeneous cross-shelf environment in the Gulf of Alaska. Mar Ecol Prog Ser 737:31–58

Daly EA, Brodeur RD (2015) Warming ocean conditions relate to increased trophic requirements of threatened and endangered salmon. PLOS ONE 10:e014406

Daly EA, Brodeur RD, Auth TD (2017) Anomalous ocean conditions in 2015: impacts on spring Chinook salmon and their prey field. Mar Ecol Prog Ser 566:169–182

De la Cruz-Pino G, Velarde E, Marín-Hernández M, Inzunza ER, Ezcurra E (2024) Survival vs. reproduction: dimorphic life history strategy in Heermann's gulls during warm ocean temperature anomalies. Mar Ecol Prog Ser 737:183–191

d'Entremont KJN, Pratte I, Gjerdrum C, Wong SNP, Montevecchi WA (2023) Quantifying inter-annual variability on the space-use of parental northern gannets (*Morus bassanus*) in pursuit of different prey types. PLOS ONE 18: e0288650

Di Lorenzo E, Mantua N (2016) Multi-year persistence of the 2014/15 North Pacific marine heatwave. Nat Clim Chang 6:1042–1046

Elliott KH, Woo K, Gaston AJ, Benvenuti S, Dall'Antonia L, Davoren GK (2008) Seabird foraging behaviour indicates prey type. Mar Ecol Prog Ser 354:289–303

Evans R, Lea MA, Hindell MA (2021) Predicting the distribution of foraging seabirds during a period of heightened environmental variability. Ecol Appl 31:e02343

Gaichas S, Skaret G, Falk-Petersen J, Link JS and others (2009) A comparison of community and trophic structure in five marine ecosystems based on energy budgets and system metrics. Prog Oceanogr 81:47–62

Glencross JS, Lavers JL, Woehler EJ (2021) Breeding success of short-tailed shearwaters following extreme environmental conditions. Mar Ecol Prog Ser 672:193–203

Gomes DGE, Ruzicka JJ, Crozier LG, Huff DD, Brodeur RD, Stewart JD (2024) Marine heatwaves disrupt ecosystem

structure and function via altered food webs and energy flux. Nat Commun 15:1988

Grémillet D, Lewis S, Drapeau L, Van Der Lingen CD and others (2008) Spatial match-mismatch in the Benguela upwelling zone: should we expect chlorophyll and sea-surface temperature to predict marine predator distributions? J Appl Ecol 45:610–621

Hobday AJ, Oliver ECJ, Sen Gupta A, Benthuysen JA and others (2018) Categorizing and naming marine heatwaves. Oceanography (Wash DC) 31:162–173

Holbrook NJ, Scannell HA, Sen Gupta A, Benthuysen JA and others (2019) A global assessment of marine heatwaves and their drivers. Nat Commun 10:2624

Holsman KK, Aydin K (2015) Comparative methods for evaluating climate change impacts on the foraging ecology of Alaskan groundfish. Mar Ecol Prog Ser 521:217–235

Jones T, Parrish JK, Lindsey J, Wright C and others (2024) Marine bird mass mortality events as an indicator of the impacts of ocean warming. Mar Ecol Prog Ser 737:161–181

Kuletz KJ, Gall AE, Morgan TC, Prichard AK and others (2024) Seabird responses to ecosystem changes driven by marine heatwaves in a warming Arctic. Mar Ecol Prog Ser 737:59–88

Marsteller CE, Arimitsu ML, Schoen SK, Stark SB, Piatt JF (2024) Predator disturbance contributed to common murre *Uria aalge* breeding failures in Cook Inlet, Alaska, following the 2014–2016 Pacific marine heatwave. Mar Ornithol 52:129–139

Mason C, Hobday AJ, Alderman R, Lea MA (2024) Shy albatross *Thalassarche cauta* chick mortality and heat stress in a temperate climate. Mar Ecol Prog Ser 737:137–145

Montevecchi WA, Regular PM, Rail JF, Power K and others (2021) Ocean heat wave induces breeding failure at the southern breeding limit of the northern gannet *Morus bassanus.* Mar Ornithol 49:71–78

Olin AB, Dück L, Berglund PA, Karlsson E, Bohm M, Olsson O, Hentati-Sundberg J (2024) Breeding failures and reduced nest attendance in response to heat stress in a high-latitude seabird. Mar Ecol Prog Ser 737:147–160

Oliver ECJ, Donat MG, Burrows MT, Moore PJ and others (2018) Longer and more frequent marine heatwaves over the past century. Nat Comm 9:1324

Osborne OE, O'Hara PD, Whelan S, Zandbergen P, Hatch SA, Elliott KH (2020) Breeding seabirds increase foraging range in response to an extreme marine heatwave. Mar Ecol Prog Ser 646:161–173

Oswald SA, Arnold JM (2024) Challenges of quantifying direct heat stress effects of climate change on seabirds. Mar Ecol Prog Ser 737:25–29

Paleczny M, Hammill E, Karpouzi V, Pauly D (2015) Population trend of the world's monitored seabirds, 1950–2010. PLOS ONE 10(6):e0129342

Pauly D, Lam ME (2023) Too hot or too cold: the biochemical basis of temperature–size rules for fish and other ectotherms. Environ Biol Fishes 106:1519–1527

Piatt JF, Harding AMA, Shultz M, Speckman SG, van Pelt TI, Drew GS, Kettle AB (2007) Seabirds as indicators of marine food supplies: Cairns revisited. Mar Ecol Prog Ser 352:221–234

Piatt JF, Parrish JK, Renner HM, Schoen SK and others (2020) Extreme mortality and reproductive failure of common murres resulting from the northeast Pacific marine heatwave of 2014–2016. PLOS ONE 15:e0226087

Reum JCP, Woodworth-Jefcoats P, Novaglio C, Forestier R and others (2024) Temperature-dependence assumptions drive projected responses of diverse size-based food webs to warming. Earths Futur 12:e2023EF003852

Robinson B, Coletti HA, Ballachey B, Bodkin JL, Kloecker K, Traiger SB, Esler D (2024) Lack of strong responses to the Pacific marine heatwave by benthivorous marine birds indicates importance of trophic drivers. Mar Ecol Prog Ser 737:215–226

Robinson CLK, Bertram DF, Shannon H, von Biela VR, Greentree W, Duguid W, Arimitsu ML (2024) Reduction in overwinter body condition and size of Pacific sand lance has implications for piscivorous predators during marine heatwaves. Mar Ecol Prog Ser 737:89–99

Schoen SK, Arimitsu ML, Marsteller CE, Piatt JF (2024) Lingering impacts of the 2014–2016 northeast Pacific marine heatwave on seabird demography in Cook Inlet, Alaska (USA). Mar Ecol Prog Ser 737:121–136

Sen Gupta A, Thomsen M, Benthuysen JA, Hobday AJ and others (2020) Drivers and impacts of the most extreme marine heatwave events. Sci Rep 10:19359

Suryan RM, Arimitsu ML, Coletti HA, Hopcroft RR and others (2021) Ecosystem response persists after a prolonged marine heatwave. Sci Rep 11:6235

Sydeman WJ, Poloczanska E, Reed TE, Thompson SA (2015) Climate change and marine vertebrates. Science 350: 772–777

von Biela VR, Arimitsu ML, Piatt JF, Heflin B, Schoen SK, Trowbridge JL, Clawson CM (2019) Extreme reduction in nutritional value of a key forage fish during the Pacific marine heatwave of 2014–2016. Mar Ecol Prog Ser 613: 171–182

Wagner EL, Pearson SF, Good TP, Hodum PJ, Buhle ER, Schrimpf MB (2024) Resilience to a severe marine heatwave at two Pacific seabird colonies. Mar Ecol Prog Ser 737:101–120

Will A, Thiebot JB, Ip HS, Shoogukwruk P and others (2020) Investigation of the 2018 thick-billed murre (*Uria lomvia*) die-off on St. Lawrence Island rules out food shortage as the cause. Deep Sea Res II 181–182:104879

Woehler EJ, Hobday AJ (2024) Impacts of marine heatwaves may be mediated by seabird life history strategies. Mar Ecol Prog Ser 737:9–23