



REVIEW

Impacts of marine heatwaves may be mediated by seabird life history strategies

Eric J. Woehler^{1,*}, Alistair J. Hobday²

¹Australasian Seabird Group, Hobart, Tasmania, Australia 7001

²CSIRO Environment, Hobart, Tasmania, Australia 7000

ABSTRACT: Marine heatwaves (MHWs) are periods of anomalously warm water associated with changes in ocean structure, based on the horizontal advection of water masses and atmospheric exchange of heat. The longest MHWs persist for many months, and dramatic effects on marine life have been reported from around the world. As top-order predators, seabirds are particularly sensitive to MHWs, with high levels of mortality associated with some events, but not with others. Thus, prediction of impacts is not straightforward, as mortality is not linearly related to simple measures of MHW intensity, persistence, and areal coverage. We describe biological responses expected for seabirds, based on demographic parameters and the geographic proximity and phenological timing of MHWs with respect to seabirds. The expected interactions between seabirds and MHWs will be complex (with some responses likely to be unpredictable) and will extend over broad spatial and temporal scales. The spatial proximity of anomalous marine conditions to breeding colonies, their overlap with foraging areas, and the degree to which MHWs coincide with pre-breeding and breeding seasons presently generate the greatest pressures on seabird populations. We posit that area-restricted seabird species, in terms of movement and breeding strategies, are at greater risk from MHWs, but that non-linear effects complicate prediction. The impacts of MHWs on seabirds may be mediated by their life history strategies.

KEY WORDS: Prediction · Marine heatwaves · Life history strategy · Seabirds

1. INTRODUCTION

Seabirds are long-lived, top-order marine predators, with individuals capable of living in excess of 60 yr in the absence of anthropogenic threats (Wooller et al. 1992, Schreiber & Burger 2001). As central-place foragers during their breeding season (Ashmole 1963), seabirds provide signals on the marine environment over time periods ranging between a day (e.g. foraging trip duration), to months or season (breeding success), or years to decades (population trends). Similarly, seabirds provide signals over spatial scales from local (colony extent), to regional (extent of foraging areas), to ocean basin (post-

breeding dispersion). Given their high visibility and wide-ranging oceanic habits, seabirds are unique in being able to concurrently provide signals from marine ecosystems at these spatial and temporal hierarchies (Woehler 2012).

The responses by seabirds to environmental stressors include mass die-offs (known as wrecks; e.g. Baduini et al. 2001a, Piatt et al. 2020, Romano et al. 2020, Glencross et al. 2021a), breeding failures (Gaston et al. 2009, Piatt et al. 2020), and decreasing populations and range contraction (Veit et al. 1996, 1997, Peron et al. 2010, Montevecchi et al. 2021). These signals can often be readily observed, so seabird time series have been widely used as indicators of general

*Corresponding author: eric.woehler@gmail.com

[§]Advance View was available July 20, 2023

environmental productivity (e.g. Reid et al. 2005, Gaston et al. 2009), impacts of overfishing (Cohen et al. 2014), impacts of pollution (Wilcox et al. 2015), and as climate canaries (Jenouvrier et al. 2005, Goyert et al. 2018).

While long-term climate warming has attracted much attention, extreme climate events (ECEs) are also increasing as part of a general climate change pattern (IPCC 2019). In the ocean, marine heatwaves (MHWs) have become a focus in recent years (Holbrook et al. 2020, Smith et al. 2023), with a documented increase in their frequency, intensity, and duration during the 20th century (Oliver et al. 2018a,b, 2021). MHWs modify the marine environment through changes in the horizontal advection of water masses, heat exchange with the atmosphere, and the vertical movement of heat in the water column (Holbrook et al. 2020).

MHWs adversely affect all trophic levels in the marine environment (Jackson et al. 2018, Arimitsu et al. 2021, Suryan et al. 2021) through a combination of top-down and bottom-up forcing from phytoplankton (Sanford et al. 2019, Hayashida et al. 2020, Montie et al. 2020, Jacobs et al. 2021), to zooplankton (Woodworth-Jefcoats et al. 2017, Evans et al. 2020, 2021, Ershova et al. 2021), large crustaceans (Pershing et al. 2018), fish (Cheung & Frölicher 2020, Arimitsu et al. 2021), and to top-order predators such as seabirds (Bond & Lavers 2014, Jones et al. 2018, Krüger et al. 2018, Osborne et al. 2020, Piatt et al. 2020, Montevecchi et al. 2021) and dolphins (Sprogis et al. 2018, Wild et al. 2019). It is already clear that MHWs can result in the decrease or loss of global marine biodiversity and the concomitant loss of ecosystem function (Smale et al. 2019, Ainsworth et al. 2020), and that repeat events can further limit

the recovery of natural systems (e.g. Goyert et al. 2018, Hughes et al. 2018).

With 70% of the Earth's surface comprised of marine ecosystems, and most ocean areas predicted to experience MHWs as near-permanent conditions by 2050 (Oliver et al. 2019), the importance of predicting ecosystem impacts is critical to developing adaptation options and building the case for rapid climate mitigation (Pittman et al. 2021). MHWs act as precursors to the longer-term normal—the greater the MHW, the farther into the future the MHW provides insights into likely conditions in marine environments (Fig. 1).

Given their demonstrated utility as ecological indicators (e.g. Frederiksen et al. 2007, Piatt et al. 2007, Gill et al. 2011, CCAMLR 2013, Hazen et al. 2019), and with high level of community interest, seabird studies can provide valuable insights (Sydemann et al. 2021), particularly when long periods of study allow the context of new stressors such as MHWs to be evaluated. However, until recently, relatively few studies had examined the responses by seabirds to MHWs. The most detailed responses have been described for 2 large MHWs: the 2014–2016 north-east Pacific and Gulf of Alaska event (Jones et al. 2018, Osborne et al. 2020, Piatt et al. 2020, Arimitsu et al. 2021, Suryan et al. 2021) and the 2011 Western Australia event (Pearce & Feng 2013, Oliver et al. 2017, Cannell et al. 2019, Evans et al. 2020, Woodworth et al. 2021).

Accordingly, in this study, we investigated the potential impacts (positive and negative) between seabirds and MHWs, with foci on seabird behavioural, phenological, and morphological responses to MHW events at different temporal and spatial scales. In Section 2, we review the expected impacts, supported by published observations in the peer-reviewed literature, followed by specific examples of how seabirds respond to MHWs through behavioural, phenological, physiological, and morphological changes. Based on this information, Section 3 explores how MHW impacts on seabirds may be predicted based on their life history strategies (LHSs), and that the impacts of MHWs on seabirds may be mediated by their LHSs—a hypothesis that can be tested as more data are collected. Section 4 concludes by considering how a future with more intense and longer MHWs may influence seabirds, and the importance of developing management responses to aid seabird persistence in a warming world.

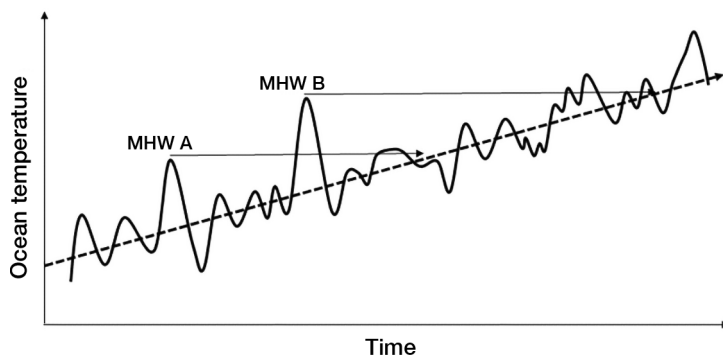


Fig. 1. Marine heatwaves (MHWs) are precursors to the longer-term normal. MHW 'A' provides insight into the average conditions likely some years into the future, while the stronger MHW 'B' provides insight even more years ahead. Solid line: actual temperature, dotted line: long-term warming trend

Table 1. Effect of marine heatwaves (MHWs) on prey availability, accessibility, and quality. A MHW that is the result of advection can lead to changes in water masses in a region and hence availability of prey for breeding seabirds. Changes in stratification due to heat input can concentrate or limit the accessibility of prey for diving seabirds. Changes in ocean productivity due to warming can change the quality of prey, affecting the energy that seabirds obtain from each prey item

MHW effect	Prey effect	Outcome	Examples
Advection of warmer water mass into area	Availability to seabirds increases	Preferred prey arrives in the area	Bancroft et al. (2004), Dunlop (2009), Gall et al. (2017), Jenkins & Davoren (2020)
	Availability to seabirds decreases	Preferred prey leaves the area	Velarde et al. (2015), Gall et al. (2017), Duffy-Anderson et al. (2019), Scopel et al. (2019), Kuletz et al. (2020), Arimitsu et al. (2021), Osborne et al. (2020), d'Entremont et al. (2022)
Stratification of local water mass due to atmospheric heat input	Accessibility to seabirds increases	Preferred prey concentrates closer to the surface	Ramírez et al. (2016)
	Accessibility to seabirds decreases	Preferred prey are not accessible to diving birds	Sydeman et al. (2015), Suryan et al. (2021)
Productivity of water mass changes	Quality of prey for seabirds increases	Diet quality and hence body condition increases	No evidence, but may occur when a more productive water mass appears in a species' foraging range
	Quality of prey for seabirds decreases	Diet quality and hence body condition decreases	Jenouvrier et al. (2015), Velarde et al. (2015), Fayet et al. (2017, 2021), Lotze et al. (2019), Piatt et al. (2020), Chaudhary et al. (2021)

2. MARINE HEATWAVES — OCEAN CHANGES THAT AFFECT SEABIRD ENVIRONMENTS

Warm-water events are widely classified as MHWs if they exceed the 90th percentile of the expected local water temperature for a period of at least 5 d (Hobday et al. 2016). They may last for hundreds of days and cover hundreds of kilometres (e.g. Hobday et al. 2018, Sen Gupta et al. 2020, and maps therein). MHWs change the physical, chemical, and biological properties of water masses at a range of temporal and spatial extents, depending on how they were formed (Holbrook et al. 2020) (Table 1). In general, MHWs are the result of heat retention in a region, primarily from heat advected from elsewhere (warm waters moving poleward: Benthuisen et al. 2014) or

heat absorbed from the atmosphere (surface heating: Benthuisen et al. 2018). Vertical mixing can then move heat deeper into the ocean (e.g. Schaeffer & Roughan 2017), where it can also be retained, priming subsequent MHW events (Scannell et al. 2020). Anomalously warm waters associated with heatwaves have been detected as deep as 400 m, but for most events, warming is restricted to the upper 50 m (Oliver et al. 2018b, Su et al. 2021).

A MHW that is the result of advection will see a local water mass replaced by another (Fig. 2). This warming will displace seabird prey species (zooplankton, fish, and cephalopods; e.g. Brodeur et al. 2005), altering the prey availability by moving the prey farther from seabird colonies. Such prey shifts due to both MHW and non-MHW causes have been

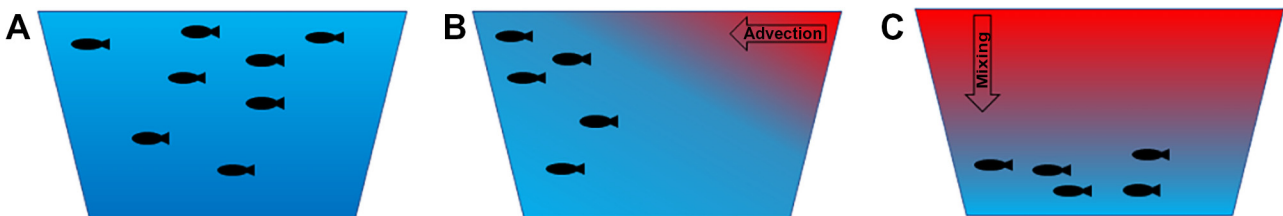


Fig. 2. Conceptual illustration of prey availability to seabirds. (A) Prey occur throughout the water column, and are accessible to both shallow- and deep-diving birds. (B) A marine heatwave (MHW) resulting from advection can reduce local prey availability close to a colony as the prey avoid the warm water. (C) A MHW with a deep, warm mixed layer may see cold-water prey move deeper, such that prey accessibility is reduced. References that illustrate these cases are provided in Table 1

shown to result in changed foraging behaviour for several species (e.g. Cohen et al. 2014, Scopel et al. 2019, Osborne et al. 2020) (Fig. 2B). Wide-ranging seabirds will be less affected than locally foraging seabirds, although all species may require greater energy use during foraging trips (e.g. Evans et al. 2021).

Local mixing of advected surface warming or atmospheric heat can drive prey deeper and reduce its accessibility to seabirds (Fig. 2C). In this case, the MHW will reduce prey capture for, and lessen energy flow to, those seabird species that capture cold-water prey taxa, as deeper diving requires more energy and may not be possible for all seabird species. Changes in winter stratification in the California Current over a 25 yr period resulted in parallel trends at multiple trophic levels, including seabird prey taxa and seabird population trends; the population trends were associated with weak changes in stratification and upwelling strengths (Sydeman et al. 2015). In the UK, higher breeding success of black-legged kittiwakes *Rissa tridactyla* was associated with weaker stratification before the breeding season (Carroll et al. 2015).

The converse can also occur: warmer surface waters can concentrate warm-water prey, facilitate greater prey capture, and enhance energy flow to seabirds, or force cooler-water prey species to deeper waters (Sydeman et al. 2021; Table 1). Prey suppression to deeper waters due to a MHW will differentially affect different species of seabirds, with shallower-diving species, such as cormorants, more likely to experience prey depletion. In contrast, generalist foragers such as storm-petrels that glean food from the ocean surface may be less affected, as they do not rely solely on prey concentrations. In addition to direct prey displacement horizontally or vertically, MHWs may reduce productivity due to changes in nutrient availability. Prey density may thus be reduced by bottom-up changes in food web productivity.

The MHW in the north-east Pacific Ocean and Gulf of Alaska in 2014–2016 resulted in broad-scale ecosystem impacts including reduced zooplankton abundance (Jones et al. 2018, Arimitsu et al. 2021); reduced forage fish abundance, availability, and nutritional quality (Arimitsu et al. 2021); and decreases in seabird breeding success (Osborne et al. 2020, Piatt et al. 2020, Suryan et al. 2021). Piatt et al. (2020) hypothesised that an 'ectothermic vice', incorporating metabolic responses by forage fish, increased competition with predatory fish, and reduced quality of prey taxa for seabirds, resulted in the extreme

mortality and reproductive failure of common murre *Uria aalge* between Alaska and California. Their model proposed that both the quality of prey taxa (forage fish) and their abundance decreased, resulting in starvation, die-off, and breeding failure of murre. General reductions in regional productivity have a wide spatial impact, as prey are not available elsewhere or they are deeper, thus increasing the energy demands on foraging seabirds.

2.1. Spatial and temporal overlaps between MHWs and seabirds

Seabirds can range widely over their lifetimes and annual life cycles—or be relatively restricted—and this movement capacity can influence the impact of a single MHW event. For simplicity, here we consider the annual life cycle of a seabird to comprise a breeding period with central-place foraging, and a non-breeding and spatially unrestricted period (cf. Wingfield et al. 2017, Fig. 3A). For some species, the foraging period may cover several years before breeding age is reached, and we include that life stage in the non-breeding period. Seabirds typically disperse following breeding or migrate between breeding and non-breeding locations (e.g. Loring et al. 2017, Campioni et al. 2020, Price et al. 2020).

During breeding, seabirds obtain their prey from the marine environments surrounding their nesting colonies, i.e. the 'central place' (sensu Ashmole 1963). The spatial and temporal overlaps or congruence between the seabirds' breeding seasons and their foraging range(s) and those of a MHW will determine the type and degree of impacts on the seabirds (Fig. 3). The greater the congruence between the spatial and temporal extents of the seabirds' breeding season and associated foraging trips with those of the MHW, the greater the potential impacts to seabirds will be.

The impacts of MHWs on seabirds are predicted to be greatest during breeding seasons (Ramírez et al. 2016), reflecting the elevated energy demands (i.e. prey consumption) associated with raising one or more chicks in addition to maintaining adult body condition, and the requirement to remain closer to the breeding site. Rapid warming post-2005 in the Gulf of Maine resulted in changes in the forage fish community used by breeding seabirds. Seabirds that previously relied on high energy-density fish experienced lower breeding success when chicks were fed on low energy-density prey species (Scopel et al. 2019).

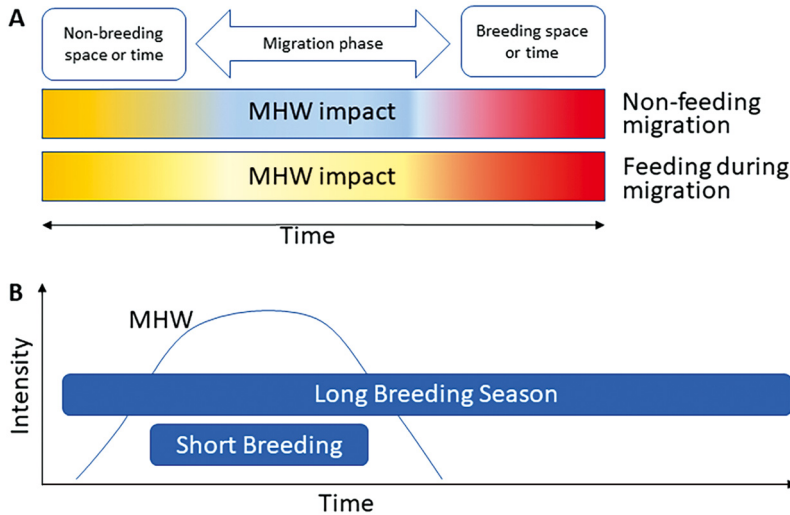


Fig. 3. Temporal variation in relative impact of marine heatwaves (MHWs) on seabird demography. (A) Impacts (red) are potentially greatest during breeding, as seabirds are central-place foragers; intermediate during the non-breeding period (greater flexibility in use of space); and least (blue) during any post-breeding dispersion/migration phase (particularly if feeding does not occur). (B) A MHW that temporally overlaps with a short breeding period will likely lead to greater impact than for a species with a breeding period longer than the duration of the MHW

If the MHW is relatively brief and/or spatially constrained, then the potential impacts may be expected to be less severe than if the MHW extends for longer and/or is less spatially constrained (Fig. 3B). Species that forage farther from their breeding sites (e.g. albatrosses and shearwaters) may be able to seek prey in waters away from the MHW more readily than near-shore foraging species such as penguins, cormorants, many alcid, and terns. Seabirds that undertake post-breeding dispersion or migration, such as penguins and shearwaters, respectively, are predicted to be decreasingly affected by a local MHW as the spatial and temporal congruences will be progressively poorer. Short-tailed shearwaters *Ardenna tenuirostris* undertake trans-hemispheric migrations from non-breeding areas in the North

Pacific Ocean to their breeding colonies in south-east Australia (Baduini et al. 2001b, Springer et al. 2018, Price et al. 2020). They do not stage while on migration (C. Price unpubl. data), and thus a MHW located along their migration routes would be unlikely to adversely affect actively migrating birds (Fig. 3A).

2.2. Observed seabird responses to MHWs

Seabirds can respond to the formation and/or presence of a MHW by behavioural, phenological, physiological, and morphological changes (Fig. 4). Changes in prey accessibility and availability forced by the MHW will see behavioural changes (manifested as changes in foraging areas and/or foraging trip dura-

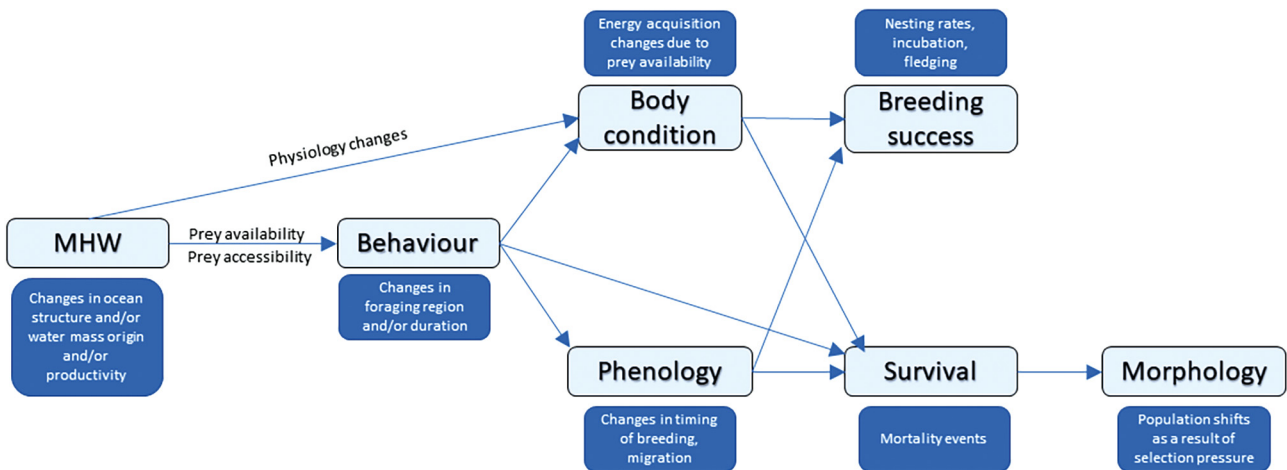


Fig. 4. Marine heatwaves (MHWs) change the environmental quality for seabirds via prey availability, accessibility, or quality. This can result in behavioural change(s), which in turn can influence body condition, phenology, breeding success, survival, and ultimately, morphology of the population. Changes can be positive or negative, depending on the nature of the environmental change

tions) and physiological changes, often seen as changes in body condition. If prey taxa availability and accessibility are increased, the body condition of seabirds will increase, due to improved prey and shorter and/or more frequent foraging trips for chick provisioning. Conversely, *sensu* Piatt et al. (2020), if prey availability and accessibility decrease, seabird foraging trips are longer, and body condition decreases (e.g. Osborne et al. 2020). Given the relatively sparse literature on seabird responses to MHWs, information about seabird responses to historical environmental forcing can be used to illustrate their potential responses to future MHWs. These direct and indirect responses serve as analogies for understanding the potential impacts of future MHWs on seabirds.

Seabird responses to environmental stress can be manifested through behavioural change (Fig. 4). Fayet et al. (2021) identified the distant foraging trips by Atlantic puffins *Fratercula arctica* in Norway to be driving the poor productivity of the colony, resulting in a decreasing population; they speculated that low prey availability near the colony may be exacerbated by intraspecific competition. Kitaysky & Hunt (2018) reviewed a series of studies in the Bering Sea where seabird foraging areas shifted in response to changes in surface water temperatures (e.g. Romano et al. 2020). Some species shifted to mid-continental shelf foraging areas in 'warm' years from inner shelf areas in 'cold' years, while other seabird species reversed their response. Changes in the near-surface distributions of prey species were correlated with these behavioural responses by the seabirds. Kowalczyk et al. (2015) detailed changes in the foraging areas used by little penguins *Eudyptula minor* during drought and heavy rain periods during 3 breeding seasons in south-east Australia, reflecting changes in prey diversity. In years of heavy rainfall, the penguins foraged farther and there was a concomitant increase in dietary diversity and breeding success. Jenouvrier et al. (2015) identified strong relationships between sea-ice extent and foraging trip duration and extent and breeding productivity in southern fulmars *Fulmarus glacialisoides*. Breeding black-legged kittiwakes changed their foraging behaviour (extended trip durations and farther locations) during the 2014 MHW in the North Pacific Ocean (Osborne et al. 2020).

If behavioural changes do not occur or cannot fully compensate for the changed environmental conditions, body condition can be affected (Fig. 4). Poor adult body condition typically leads to lower breeding success (Phillips et al. 2017). Winter body mass of little penguins correlated with egg laying and breed-

ing success (Salton et al. 2015), indicative of a carry-over effect of prey availability extending up to 6 mo. Hovinen et al. (2019) showed that prey species composition during the non-breeding season in 4 species of High Arctic seabirds contributed to changes in breeding success. Negative carry-over effects, manifested as poor body condition resulting in near-complete breeding failure, has also been shown in brown skuas *Stercorarius lonnbergi* in the Subantarctic (Grilli et al. 2018). Late-winter sea surface temperature (SST) changes impacted survival of juvenile black-browed albatross *Thalassarche melanophrys* (Jenouvrier et al. 2018), which may have been through reduced body condition.

Starvation is typically the primary cause of death in mass seabird die-offs, known as wrecks (e.g. Baduini et al. 2001a, Morley et al. 2016, Piatt et al. 2020, Tavares et al. 2020, Glencross et al. 2021a). Short-tailed shearwaters spend their non-breeding season in the North Pacific Ocean before returning to their breeding colonies in south-east Australia. An increase in the frequency and magnitude of episodic mass-mortality events in short-tailed shearwaters has been linked to the proposed competition with pink salmon *Oncorhynchus gorbuscha* in the North Pacific (Springer et al. 2018). Changes to prey during winter months, when prey resources are at their lowest, can exacerbate existing stressors or strongly influence demographic parameters. Winter foraging activities ended earlier and the timing of colony return was extended by elevated winter SSTs for adult black-browed albatrosses (Desprez et al. 2018). Fayet et al. (2017) showed that local winter prey availability was a key driver in Atlantic puffin migration routes, wintering areas, and colony productivity; long-term decreases in winter sea-ice extent have resulted in spatial shifts in their winter distributions (Patterson et al. 2021). Productive cold-water upwellings are critical winter- and migratory foraging areas for European roseate terns *Sterna dougallii* (Redfern et al. 2021). Severe winter storms reduced individual survival of European shags *Phalacrocorax aristotelis*, and were associated with very strong seasonal survival selection against resident (cf. migratory) individuals (Acker et al. 2021).

Changes in behaviour can also manifest as phenological changes (Fig. 4). Seabirds are typically long-lived with few offspring from any breeding season — the loss of one breeding season's efforts in years of poor prey availability (or accessibility) may be offset by future breeding efforts (Baduini & Hyrenbach 2003, Golet et al. 2004, Hipfner 2008, Champagnon et al. 2018). Tropical seabirds breeding on Pacific

Ocean islands will avoid or abandon breeding during El Niño–Southern Oscillation (ENSO) events (e.g. Schreiber & Schreiber 1984, Anderson 1989, Duffy 1990) as a trade-off between adult survival and committing scarce resources to offspring (Cubaynes et al. 2011). Poor prey availability and accessibility can delay the onset of breeding, or provide opportunities for first-time breeders to enter the breeding population, as pre-breeders may benefit from lowered competition with experienced breeders who may skip breeding (Moe et al. 2009, Cubaynes et al. 2011).

Seabirds may exhibit both immediate and lagged phenological responses to environmental stressors. Multi-decadal data sets for sooty terns *Onychoprion fuscatus*, bridled terns *O. anaethetus*, brown noddies *Anous stolidus*, and lesser noddies *A. tenuirostris* in Western Australia have revealed later laying of first eggs and later mean laying dates during ENSO events (Surman & Nicholson 2009, Surman et al. 2012). Longer time series for Antarctic-breeding petrels have identified later onset of post-migration arrival at colonies due to rising SSTs (Barbraud & Weimerskirch 2006, Barbraud et al. 2012, Chambers et al. 2014).

The breeding phenology of European storm-petrels *Hydrobates pelagicus* in the Western Mediterranean was related to the onset of stratification in late winter/early spring that resulted in elevated prey availability (Ramírez et al. 2016); delays in reproduction led to hatching and breeding failures. Poor breeding productivity and delayed migration following decreased prey availability are lagged responses to environmental stressor (Springer et al. 2018, Price et al. 2020, Glencross et al. 2021b) and represent a strategy to improve long-term survival.

The cumulative impacts of changes in environmental quality and body condition can influence breeding success (Fig. 4). An increased frequency of warm SST anomalies was predicted to reduce population growth in Heermann's gull *Larus heermanni* (Velarde & Ezcurra 2018). Likewise, studies on little penguins have shown decreased breeding success under MHW conditions in the warmer part of their range in Western Australia (Cannell et al. 2012) but increased success in south-eastern Australia (Cullen et al. 2009, Chambers et al. 2014). This disparity can be explained by the relative position of the MHW relative to the preferred environment of the species in question (Smale et al. 2019). MHWs that occur in the warmest part of the range may lead to poorer outcomes, while MHWs in the cool portion of the range may lead to improved performance. In extreme

cases, complete breeding failure can occur, as was documented for common murres throughout the north-east Pacific Ocean following the 2014–2016 MHW (Piatt et al. 2020). Atlantic puffin breeding success since 1880 has decreased as SSTs have increased around Iceland (Hansen et al. 2021).

Changes in adult and chick survival can arise from multiple circumstances. Under extreme circumstances such as strong ENSO events, changes in foraging behaviours, including diving, are insufficient or unable to offset the decreased availability and/or accessibility of prey taxa. Initial responses may involve the abandonment of breeding efforts, irrespective of the stage reached (eggs or chicks) but can extend to elevated levels of adult mortality, such as those seen during wreck events (Piatt et al. 2020). Wrecks can occur at any time or location during a seabird's lifetime (Glencross et al. 2021a).

Ultimately, differential survival among phenotypes can lead to natural selection and changes in morphology (Fig. 4). A number of studies on non-seabird species have suggested mechanisms by which extreme climate events could contribute to microevolution of species. Grant et al. (2017) suggested that extreme environmental perturbations such as heatwaves were small-scale analogies of the evolutionary changes observed in the fossil records. While no examples of such responses have yet been documented for seabirds, there is no reason to believe that the underlying mechanisms present in other bird families are absent in seabirds (van de Pol et al. 2017). Sauve et al. (2023) discussed the role of environmental drivers of phenotypic traits, including in seabirds. Inter-annual variability in environmental drivers related to climate change was predicted to see shifts in environmental determinants of traits.

Responses by seabirds to environmental drivers or pressures can be complex, unpredictable, and substantial. Several species of seabirds have expanded their range southward in Western Australia despite the increased frequency of ENSO events that decreased foraging opportunities in areas previously used (Bancroft et al. 2004); the expansions were potentially offset by the similar southward expansion of prey taxa, decreased intra-specific competition or the emergence of novel foraging areas (Dunlop 2009). Elegant terns *Thalasseus elegans* responded to a combination of oceanographic temperature anomalies (SST >1.0°C) and concurrent fishing pressures on prey species by shifting their nesting and foraging areas by 600 km (Velarde et al. 2015); the resultant population increase in the new area could only be explained by immigration. Gentoo penguins *Pygo-*

scelis papua and chinstrap penguins *P. antarctica* have increased their breeding distributions southward as sea ice extent decreases southward along the Antarctic Peninsula (Barbraud et al. 2012); this decrease in sea-ice extent has seen conspecific Adélie penguins *P. adeliae* populations (more closely associated with sea ice) decrease rapidly concurrently in the same area.

3. PREDICTING SEABIRD VULNERABILITY TO MHWs

Based on known seabird responses to environmental anomalies as described in the previous section, the expected interactions between seabirds and MHWs will be complex (with some responses likely to be unpredictable), and extend over broad spatial and temporal scales ranging from 10s to 1000s km, and from days to years. The responses by seabirds and the marine environment to the multiple stressors from MHWs may be additive or synergistic (sensu Halpern et al. 2008) and may be direct and/or indirect, i.e. lagged in time and/or space. Evidence suggests that the spatial proximity of anomalous marine conditions to breeding colonies, their overlap with foraging areas, and the degree to which MHWs coincide with pre-breeding and breeding seasons generate the greatest pressures on seabird populations and can be used to predict vulnerability (Fig. 5).

Depression of breeding productivity or complete breeding failure will be manifested in short- to long-term population decreases reflecting the temporal and spatial extents of poor breeding. The expected increase in the frequency and intensity of MHWs will compound existing pressures on all trophic levels of marine ecosystems (primary production: Lotze et al. 2019, Jacobs et al. 2021; zooplankton and commercial fish: Woodworth-Jefcoats et al. 2017; and *in toto*: Ainsworth et al. 2020, O'Hara et al. 2021). Seabirds typically have low annual productivity (generally 1–3 chicks yr^{-1}) offset by extended life expectancies (up to 60+ yr). Thus their breeding efforts involve a trade-off between an energy investment into egg production and offspring rearing, and the energy required for self-maintenance by the adults; this trade-off comes to the fore during times of poor prey availability, and in extreme cases, leads to complete abandonment of the breeding attempt (Schreiber & Schreiber 1984, Chambers et al. 2011, Cubaynes et al. 2011, Ponchon et al. 2014), allowing adults to breed in the future when conditions improve (Golet et al. 2004).

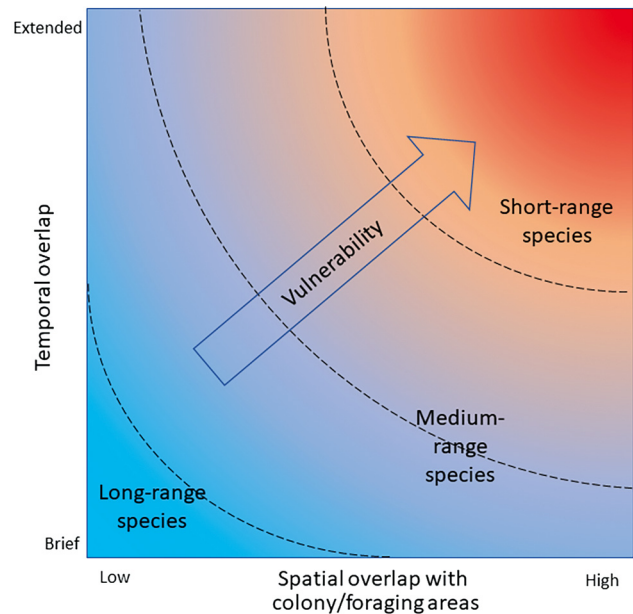


Fig. 5. Vulnerability of seabirds to marine heatwaves (MHWs) is related to the spatial overlap/proximity of the event to breeding and foraging areas, and to the duration of the temporal overlap. Vulnerability is indicated by warmer colours, and the dashed lines are representative of equivalent vulnerability. For example, an extended MHW with low spatial overlap will have a similar impact to a brief MHW that has high overlap

While instances exist of increased availability and accessibility of prey taxa to seabirds arising from MHWs, there are many more examples of decreased availability and accessibility of prey taxa to seabirds (Table 1). At present, there are no known instances where decreases in the productivity of a water mass leads to an increase in the quality of prey for seabirds that could be expected to result in a consequent increase in diet quality and body condition. In the Arctic, where MHWs may extend the length of production, some short-term benefits might be expected, such as extended periods of productivity or greater biomass. Breeding success of king penguins *Aptenodytes patagonicus* on the subantarctic Iles Kerguelen increased in warmer years when prey availability was higher (Brisson-Curadeau et al. 2023). Overall, our review did not identify widespread benefits to seabirds; additional pressures from MHWs will act to compound the existing threats to seabirds. How well seabird LHSs will respond to the predicted increase in frequencies and intensities of MHWs will determine their survival.

Based on semi-quantitative scoring of life history characteristics (Table 2), the seabird families predicted to be most susceptible to MHWs are penguins and cormorants. Penguins and cormorants are non-

Table 2. Selected life history characteristics for seabird families scored 1/2/3 relative to potential marine heatwave (MHW) impacts, and then summed as an overall susceptibility estimate (where higher scores indicate families that are more susceptible to MHW impacts). Scoring used for life history characteristics were: Foraging range: 1–distant/off-shore, 2–moderate, 3–near-shore; diving ability: 1–deep (>100 m), 2–moderate (10–100 m), 3–shallow/nil (<10 m); breeding season (incubation + brooding periods only) duration: 1–short (<100 d), 2–moderate (101–200 d), 3–long (>201 d); and mean age of first breeding (i.e. recruitment into breeding population): 1–(1–5 yr), 2– (6+ yr). Based on Appendix 2 in Schreiber & Burger (2001) and references therein

Family	Foraging range breeding	Foraging range non-breeding	Diving ability	Breeding season duration	Mean age of first breeding	Susceptibility
Skuas and jaegers (Stercorariidae)	3	1	3	1	1	9
Gulls, terns, and noddies (Laridae)	3	2	3	1	1	10
Tropicbirds (Phaethontidae)	2	2	3	2	1	10
Penguins (Spheniscidae)	3	2	1	3	2	11
Storm-petrels (Hydrobatidae)	2	1	3	2	2	10
Albatrosses (Diomedidae)	1	1	3	3	2	10
Petrels and shearwaters (Procellariidae)	1	1	2	2	2	8
Diving-petrels (Genus <i>Pelecyanoides</i> , Procellariidae)	3	1	2	2	1	9
Frigatebirds (Fregatidae)	1	2	3	3	1	10
Gannets and boobies (Sulids)	1	2	2	2	1	8
Cormorants (Phalacrocoracidae)	3	3	2	1	2	11
Murres, puffins, auklets, guillemots, and murrelets (Alcidae)	3	3	2	1	1	10

and relatively weak fliers, respectively, and both families have limited capacities to ‘escape’ proximate MHWs during their breeding seasons. Other seabirds that ranked highly susceptible included gulls, terns, noddies, tropicbirds, storm-petrels, albatrosses, frigatebirds, and murres and puffins (Alcidae). This disparate group shows few underlying commonalities beyond that many are tropical taxa (some terns and noddies [Family Laridae], tropicbirds, and frigatebirds — species likely under pressure from the decreasing marine species diversity in equatorial waters; Chaudhary et al. 2021). In addition, all 4 tropical groups are typically associated with opportunistic foraging in associations with tuna and dolphins (Gilman 2011).

The families ranked lowest for susceptibility to MHWs were petrels, shearwaters, gannets, and boobies (Table 2). Species in these families can forage far from colonies (hundreds of km or farther) and are capable of diving to as deep as 60–70 m. The ability to travel long distances and dive deep can provide some capacity for avoiding MHWs during their breeding seasons. Diving-petrels, skuas, and jaegers were ranked with intermediate susceptibilities, with distant foraging during the non-breeding seasons reducing their vulnerability to MHWs (Table 2). Overall, the scoring showed limited differences among seabird families (susceptibility scores were between 8 and 11, compared to the possible range of 5–15), emphasising that seabirds have relatively high vulnerability

to MHWs. In the future, this type of approach could be expanded and refined to resolve within-family differences by working through the ca. 300 seabird species, depending on future research foci.

The spatial and temporal overlap, and simple susceptibility scoring (Table 2), establish some grounds for predicting impacts of MHWs on seabirds. However, it is quite likely that some responses by seabirds to the synergistic effects of multiple stressors associated with MHWs will be unexpected and unpredictable based on our current state of knowledge, and almost certainly will be non-linear (Halpern et al. 2008). Some insights into such unpredicted and unanticipated responses may be obtained from current observations of seabird behaviours in response to contemporary extreme events. We have initially identified 3 broad categories of unexpected responses by seabirds (however, it is likely that other unexpected responses exist):

(1) Destructive synergies. For example, starving short-tailed shearwaters ingested pumice from an underwater eruption on their southward migration to their breeding colonies after spending their non-breeding season in the North Pacific Ocean (Roman et al. 2021). A possible explanation is that birds began their southward migration in poor body condition, resulting in widespread ingestion of the pumice encountered on migration, and their subsequent death from starvation (Roman et al. 2021).

(2) Opportunistic synergies. Seabirds foraging in oligotrophic and species-depauperate tropical waters will feed opportunistically on concentrations of pelagic fish formed by dolphins or tuna (Wells et al. 2016, Miller et al. 2018). Decreased species diversity in equatorial waters since the 1970s, including fish (Chaudhary et al. 2021), may result in this symbiotic, mixed-species feeding assemblage relationship collapsing as some deep-diving birds that help drive prey to the surface may be absent. This effect may also occur as a result of MHWs, and be widespread and apparently unrelated to simple estimates of susceptibility (Table 2).

(3) Ecological and evolutionary traps. Despite perceptions of high mate fidelity, seabirds will take on new breeding partners while their former partner is alive in an effort to improve their long-term breeding productivity (e.g. Bried & Jouventin 1999). The change in partners is typically associated with lower than average breeding success as the birds learn to coordinate their breeding behaviours; however, over time, their productivity increases (Bried et al. 2003). A change in breeding partner in response to poor prey conditions and resultant breeding failure would represent an unnecessary response by breeding adults to an episodic environmental stressor, with potential population-level consequences. Repeat MHWs in a region may lead to greater than expected decreases in breeding success as more birds re-partner in response to the previous breeding failure, i.e. an ecological trap (Schlaepfer et al. 2002, Robertson & Hutto 2006).

Researchers assessing the impact of MHWs on seabirds should be vigilant for unexpected individual and population responses, and in particular, for responses that may result in ecological or evolutionary traps (Schlaepfer et al. 2002, Grémillet & Boulinier 2009, Reynolds et al. 2015), as these will generate additional synergistic pressures on seabird populations (O'Hara et al. 2021). The semi-quantitative estimates of susceptibility (Table 2) serve as a first pass assessment of potential impacts but are unlikely to be sufficient, and additional case studies are clearly required.

4. THE FUTURE FOR SEABIRDS UNDER ENVIRONMENTAL STRESS — A SYNTHESIS

Seabirds have evolved LHSs in response to past and contemporary environmental variabilities in the marine environment (*sensu* Stommel 1963, Haury et al. 1978). With just ca. 3% of the world's 10 000 bird species considered to be seabirds, the 70% of the world's surface that is marine clearly presents many evolutionary challenges to birds. These strategies

include anatomical, physiological, and behavioural adaptations to facilitate seabird survival in their environment (e.g. van de Pol et al. 2017, Wingfield et al. 2017).

Blondin et al. (2022) suggested that while specialisation in diet and foraging behaviours, site fidelity, and parental investment strategies were beneficial in stable environments, they were likely to be disadvantageous in predicted increased environmental variability, and during periods of anomalous environmental conditions. The temporal and spatial scales of MHWs and ECEs are orders of magnitude more rapid than past processes that have shaped LHSs, and consequently have introduced new and additional pressures on seabirds. As seabirds are unable to rapidly alter their anatomy and physiology (but see Chevin & Hoffmann 2017, Grant et al. 2017 for non-seabird examples), there is limited capacity to adapt and respond to MHWs and ECEs beyond behavioural plasticity – such as extended foraging trips and phenological changes in migration and breeding (Table 1). However, these responses typically result in lower breeding success and reduced adult body conditions, subsequently manifested in decreasing populations.

MHWs are extreme events that impact the physical structure of the marine environment and the associated biological communities and ecological food webs. MHWs also represent a window into future environmental changes associated with global warming (Fig. 1). These anomalous high-temperature events occurring as part of a long-term warming trend are spikes that foreshadow projected conditions at some time in the future. The higher the spike, the greater the MHW anomaly and the farther into the future the MHW allows us to predict how seabirds may respond to projected environmental conditions (Fig. 1).

MHWs allow us to predict behavioural responses (and potentially to a lesser extent, anatomical and physiological responses) by seabirds to projected rises in ocean temperature and concomitant changes in marine biodiversity, trophic relationships and fluxes, and ecosystem services such as nutrient cycling (Smale et al. 2019). The various studies cited herein show mechanistic linkages between physical and biological oceanography, phytoplankton, zooplankton, fish, and seabirds – trophic relationships and numerical responses to changes at wide ranges of temporal and spatial scales that are most clearly signalled by seabird populations (Woehler 2012).

Extreme climatic events (*sensu* Marrot et al. 2017, van de Pol et al. 2017) are recent and contemporary manifestations of climate change, and are known

to be increasing in frequency (Ummerhofer & Meehl 2017). Marine heatwaves are extreme events in the marine environment that have increased in their spatial and temporal extents, with predicted increases in their frequencies (Oliver et al. 2018b). Prediction of marine heatwaves is now possible, with lead times of up to 5 mo (see <https://research.csiro.au/cor/research-domains/climate-impacts-adaptation/marine-heatwaves/>).

Given sufficient lead time for the prediction of heatwaves, and the susceptibility of seabirds as illustrated here, interventions for conservation can be considered (e.g. Alderman & Hobday 2017, Sydeman et al. 2021). Interventions for species such as shearwaters, e.g. reduced indigenous and recreational harvest levels (Fletcher et al. 2021), fisheries bycatch reduction for albatross from fisheries closures, and supplemental feeding for boobies can be implemented to enhance resilience to environmental stressors. Marine Protected Areas provide opportunities for seabird conservation at regional to ocean-basin scales (e.g. Connors et al. 2022, Kim et al. 2023). Given the trajectory of environmental stressors that impact seabirds, investigation and testing of interventions is urgent (Mason et al. 2021). Marine heatwaves provide contemporary insights into potential future scenarios for seabirds. These scenarios are also an opportunity to predict the impacts of MHWs and, finally, to investigate potential management responses that will further the conservation of seabirds.

Acknowledgements. We thank G. Tuck for his comments on an earlier draft, and the extensive comments from Sarah Ann Thompson and 2 anonymous reviewers that further improved this manuscript.

LITERATURE CITED

- folio disrupts energy flow to top pelagic predators. *Glob Change Biol* 27:1859–1878
- ✦ Ashmole NP (1963) The regulation of numbers of tropical oceanic birds. *Ibis* 103b:458–473
- Baduini CL, Hyrenbach KD (2003) Biogeography of procellariiform foraging strategies: Does ocean productivity influence provisioning? *Mar Ornithol* 31:101–112
- ✦ Baduini CL, Hyrenbach KD, Coyle KO, Pinchuk A, Mendenhall V, Hunt GL (2001a) Mass mortality of short-tailed shearwaters in the south-eastern Bering Sea during summer 1997. *Fish Oceanogr* 10:117–130
- ✦ Baduini CL, Lovvorn JR, Hunt GL Jr (2001b) Determining the body condition of short-tailed shearwaters: implications for migratory flight ranges and starvation events. *Mar Ecol Prog Ser* 222:265–277
- ✦ Bancroft WJ, Garkaklis MJ, Roberts JD (2004) Continued expansion of the wedge-tailed shearwater, *Puffinus pacificus*, nesting colonies on Rottneest Island, Western Australia. *Emu* 104:79–82
- ✦ Barbraud C, Weimerskirch H (2006) Antarctic birds breed later in response to climate change. *Proc Natl Acad Sci USA* 103:6248–6251
- ✦ Barbraud C, Rolland V, Jenouvrier S, Nevoux M, Delord K, Weimerskirch H (2012) Effects of climate change and fisheries bycatch on Southern Ocean seabirds: a review. *Mar Ecol Prog Ser* 454:285–307
- ✦ Benthuyzen J, Feng M, Zhong L (2014) Spatial patterns of warming off Western Australia during the 2011 Ningaloo Niño: quantifying impacts of remote and local forcing. *Cont Shelf Res* 91:232–246
- ✦ Benthuyzen JA, Oliver ECJ, Feng M, Marshall AG (2018) Extreme marine warming across tropical Australia during austral summer 2015–2016. *J Geophys Res Oceans* 123:1301–1326
- ✦ Blondin HE, Armstrong KC, Hazen EL, Oestreich WK and others (2022) Land-dependent marine species face climate-driven impacts on land and at sea. *Mar Ecol Prog Ser* 699:181–198
- ✦ Bond AL, Laviers JL (2014) Climate change alters the trophic niche of a declining apex marine predator. *Glob Change Biol* 20:2100–2107
- ✦ Bried J, Jouventin P (1999) Influence of breeding success on fidelity in long-lived birds: an experimental study. *J Avian Biol* 30:392–398
- ✦ Bried J, Pontier D, Jouventin P (2003) Mate fidelity in monogamous birds: a re-examination of the Procellariiformes. *Anim Behav* 65:235–246
- ✦ Brisson-Curadeau É, Elliott K, Bost CA (2023) Contrasting bottom-up effects of warming ocean on two king penguin populations. *Glob Change Biol* 29:998–1008
- ✦ Brodeur RD, Fisher JP, Emmett RL, Morgan CA, Casillas E (2005) Species composition and community structure of pelagic nekton off Oregon and Washington under variable oceanographic conditions. *Mar Ecol Prog Ser* 298: 41–57
- ✦ Campioni L, Dias MP, Granadeiro JP, Catry P (2020) An ontogenetic perspective on migratory strategy of a long-lived pelagic seabird: timings and destinations change progressively during maturation. *J Anim Ecol* 89:29–43
- ✦ Cannell BL, Chambers LE, Wooller RD, Bradley JS (2012) Poorer breeding by little penguins near Perth, Western Australia is correlated with above average sea surface temperatures and a stronger Leeuwin Current. *Mar Freshw Res* 63:914–925
- ✦ Acker P, Daunt F, Wanless S, Burthe SJ and others (2021) Strong survival selection on seasonal migration versus residence induced by extreme climatic events. *J Anim Ecol* 90:796–808
- ✦ Ainsworth TD, Hurd CL, Gates RD, Boyd PW (2020) How do we overcome abrupt degradation of marine ecosystems and meet the challenge of heat waves and climate extremes? *Glob Change Biol* 26:343–354
- ✦ Alderman R, Hobday AJ (2017) Developing a climate adaptation strategy for vulnerable seabirds based on prioritisation of intervention options. *Deep Sea Res II* 140: 290–297
- ✦ Anderson DJ (1989) Differential responses of boobies and other seabirds in the Galápagos to the 1986–87 El Niño–Southern Oscillation event. *Mar Ecol Prog Ser* 52: 209–216
- ✦ Arimitsu ML, Piatt JF, Hatch S, Suryan RM and others (2021)

- Cannell B, Thomson P, Schoepf V, Pattiaratchi C, Fraser M (2019) Impacts of marine heatwaves. In: Techera E, Winter G (eds) *Marine extremes: ocean safety, marine health and the blue economy*. Routledge, Abingdon, pp 123–140
- Carroll MJ, Butler A, Owen E, Ewing SR and others (2015) Effects of sea temperature and stratification changes on seabird breeding success. *Clim Res* 66:75–89
- CCAMLR (Commission for the Conservation of Antarctic Marine living Resources) (2013) CCAMLR Ecosystem Monitoring Program (CEMP). <https://www.ccamlr.org/en/science/ccamlr-ecosystem-monitoring-program-cemp>
- Chambers LE, Devney CA, Congdon BC, Dunlop N, Woehler EJ, Dann P (2011) Observed and predicted effects of climate on Australian seabirds. *Emu* 111:235–251
- Chambers LE, Dann P, Cannell B, Woehler EJ (2014) Climate as a driver of phenological change in southern seabirds. *Int J Biometeorol* 58:603–612
- Champagnon J, Lebreton JD, Drummond H, Anderson DJ (2018) Pacific Decadal and El Niño oscillations shape survival of a seabird. *Ecology* 99:1063–1072
- Chaudhary C, Richardson AJ, Schoeman DS, Costello MJ (2021) Global warming is causing a more pronounced dip in marine species richness around the equator. *Proc Natl Acad Sci USA* 118:e2015094118
- Cheung WWL, Frölicher TL (2020) Marine heatwaves exacerbate climate change impacts for fisheries in the northeast Pacific. *Sci Rep* 10:6678
- Chevin LM, Hoffmann AA (2017) Evolution of phenotypic plasticity in extreme environments. *Philos Trans R Soc B* 372:20160138
- Cohen LA, Pichegru L, Grémillet D, Coetzee J, Upfold L, Ryan PG (2014) Changes in prey availability impact the foraging behaviour and fitness of Cape gannets over a decade. *Mar Ecol Prog Ser* 505:281–293
- Conners MG, Sisson NB, Agamboue PD, Atkinson PW and others (2022) Mismatches in scale between highly mobile marine megafauna and marine protected areas. *Front Mar Sci* 9:897104
- Cubaynes S, Doherty PF Jr, Schreiber EA, Gimenez O (2011) To breed or not to breed: a seabird's response to extreme climatic events. *Biol Lett* 7:303–306
- Cullen JM, Chambers LE, Coutin PC, Dann P (2009) Predicting onset and success of breeding in little penguins *Eudyptula minor* from ocean temperatures. *Mar Ecol Prog Ser* 378:269–278
- d'Entremont KJN, Davoren GK, Walsh CJ, Wilhelm SI, Montevicchi WA (2022) Intra- and inter-annual shifts in foraging tactics by parental northern gannets *Morus bassanus* indicate changing prey fields. *Mar Ecol Prog Ser* 698:155–170
- Desprez M, Jenouvrier S, Barbraud C, Delord K, Weimerskirch H (2018) Linking oceanographic conditions, migratory schedules and foraging behaviour during the non-breeding season to reproductive performance in a long-lived seabird. *Funct Ecol* 32:2040–2053
- Duffy DC (1990) Seabirds and the 1982–1984 El Niño–Southern Oscillation. *Elsevier Oceanogr Ser* 52:395–415
- Duffy-Anderson JT, Stabeno P, Andrews AG III, Ciciel K and others (2019) Responses of the northern Bering Sea and southeastern Bering Sea pelagic ecosystems following record-breaking low winter sea ice. *Geophys Res Lett* 46:9833–9842
- Dunlop JN (2009) The population dynamics of tropical seabirds establishing frontier colonies on islands off southwestern Australia. *Mar Ornithol* 37:99–105
- Ershova EA, Kosobokova KN, Banas NS, Ellingsen I, Niehoff B, Hildebrandt N, Hirche HJ (2021) Sea ice decline drives biogeographical shifts of key *Calanus* species in the central Arctic Ocean. *Glob Change Biol* 27:2128–2143
- Evans R, Lea MA, Hindell MA, Swadling KM (2020) Significant shifts in coastal zooplankton populations through the 2015/16 Tasman Sea marine heatwave. *Estuar Coast Shelf Sci* 235:106538
- Evans R, Lea MA, Hindell MA (2021) Predicting the distribution of foraging seabirds during a period of heightened environmental variability. *Ecol Appl* 31:e02343
- Fayet AL, Freeman R, Anker-Nilssen T, Diamond A and others (2017) Ocean-wide drivers of migration strategies and their influence on population breeding performance in a declining seabird. *Curr Biol* 27:3871–3878.e3
- Fayet AL, Clucas GV, Anker-Nilssen T, Syposz M, Hansen ES (2021) Local prey shortages drive foraging costs and breeding success in a declining seabird, the Atlantic puffin. *J Anim Ecol* 90:1152–1164
- Fletcher D, Newman J, McKechnie S, Bragg C and others (2021) Projected impacts of climate change, bycatch, harvesting, and predation on the Aotearoa New Zealand tītī *Ardenna grisea* population. *Mar Ecol Prog Ser* 670: 223–238
- Frederiksen M, Mavor RA, Wanless S (2007) Seabirds as environmental indicators: the advantages of combining data sets. *Mar Ecol Prog Ser* 352:205–211
- Gall AE, Morgan TC, Day RH, Kuletz KJ (2017) Ecological shift from piscivorous to planktivorous seabirds in the Chukchi Sea, 1975–2012. *Polar Biol* 40:61–78
- Gaston AJ, Bertram DF, Boyne AW, Chardine JW and others (2009) Changes in Canadian seabird populations and ecology since 1970 in relation to changes in oceanography and food webs. *Environ Rev* 17:267–286
- Gill MJ, Crane K, Hindrum R, Arneberg P and others (2011) Arctic Marine Biodiversity Monitoring Plan (CBMP-Marine Plan), CAFF Monitoring Series Report No. 3, April 2011. CAFF International Secretariat, Akureyri. <https://www.caff.is/marine/marine-monitoring-publications/3-arctic-marine-biodiversity-monitoring-plan>
- Gilman EL (2011) Bycatch governance and best practice mitigation technology in global tuna fisheries. *Mar Policy* 35:590–609
- Glencross JS, Lavers JL, Woehler EJ (2021a) A proposed framework for reporting mass mortality (wreck) events of seabirds. *ICES J Mar Sci* 78:1935–1942
- Glencross JS, Lavers JL, Woehler EJ (2021b) Breeding success of short-tailed shearwaters following extreme environmental conditions. *Mar Ecol Prog Ser* 672:193–203
- Golet GH, Schmutz JA, Irons DB, Estes JA (2004) Determinants of reproductive costs in the long-lived black-legged kittiwake: a multiyear experiment. *Ecol Monogr* 74:353–372
- Goyert HF, Garton EO, Poe AJ (2018) Effects of climate change and environmental variability on the carrying capacity of Alaskan seabird populations. *Auk* 135:975–991
- Grant PR, Grant BR, Huey RB, Johnson MT, Knoll AH, Schmitt J (2017) Evolution caused by extreme events. *Philos Trans R Soc B* 372:20160146
- Grémillet D, Boulinier T (2009) Spatial ecology and conservation of seabirds facing global climate change: a review. *Mar Ecol Prog Ser* 391:121–137
- Grilli MG, Pari M, Ibañez A (2018) Poor body conditions during the breeding period in a seabird population with low breeding success. *Mar Biol* 165:142

- Halpern BS, McLeod KL, Rosenberg AA, Crowder LB (2008) Managing for cumulative impacts in ecosystem-based management through ocean zoning. *Ocean Coast Manag* 51:203–211
- Hansen ES, Sandvik H, Erikstad KE, Yoccoz NG and others (2021) Centennial relationships between ocean temperature and Atlantic puffin production reveal shifting decennial trends. *Glob Change Biol* 27:3753–3764
- Haury LR, McGowan JA, Wiebe PH (1978) Patterns and processes in the time–space scales of plankton distributions. In: Steele JH (ed) *Spatial patterns in plankton communities*. NATO Conference Series IV, Marine Science. Plenum Press, New York, NY, p 277–327
- Hayashida H, Matear RJ, Strutton PG (2020) Background nutrient concentration determines phytoplankton bloom response to marine heatwaves. *Glob Change Biol* 26: 4800–4811
- Hazen EL, Abrahms B, Brodie S, Carroll G and others (2019) Marine top predators as climate and ecosystem sentinels. *Front Ecol Environ* 17:565–574
- Hipfner JM (2008) Matches and mismatches: ocean climate, prey phenology and breeding success in a zooplanktivorous seabird. *Mar Ecol Prog Ser* 368:295–304
- Hobday AJ, Alexander LV, Perkins SE, Smale DA and others (2016) A hierarchical approach to defining marine heatwaves. *Prog Oceanogr* 141:227–238
- Hobday AJ, Oliver ECJ, Sen Gupta A, Benthuyssen JA and others (2018) Categorizing and naming marine heatwaves. *Oceanography* 31:162–173
- Holbrook NJ, Sen Gupta A, Oliver ECJ, Hobday AJ and others (2020) Keeping pace with marine heatwaves. *Nat Rev Earth Environ* 1:482–493
- Hovinen JEH, Tarroux A, Ramírez F, Forero M, Descamps S (2019) Relationships between isotopic ratios, body condition and breeding success in a High Arctic seabird community. *Mar Ecol Prog Ser* 613:183–195
- Hughes TP, Kerry JT, Baird AH, Connolly SR and others (2018) Global warming transforms coral reef assemblages. *Nature* 556:492–496
- IPCC (2019) Special report on the ocean and cryosphere in a changing climate. <https://www.ipcc.ch/srocc/>
- Jackson JM, Johnson GC, Dosser HV, Ross T (2018) Warming from recent marine heatwave lingers in deep British Columbia fjord. *Geophys Res Lett* 45:9757–9764
- Jacobs ZL, Yool A, Jebri F, Srokosz M and others (2021) Key climate change stressors of marine ecosystems along the path of the East African coastal current. *Ocean Coast Manag* 208:105627
- Jenkins EJ, Davoren GK (2021) Seabird species- and assemblage-level isotopic niche shifts associated with changing prey availability during breeding in coastal Newfoundland. *Ibis* 163:183–196
- Jenouvrier S, Weimerskirch H, Barbraud C, Park YH, Cazelles B (2005) Evidence of a shift in the cyclicity of Antarctic seabird dynamics linked to climate. *Proc R Soc B* 272:887–895
- Jenouvrier S, Péron C, Weimerskirch H (2015) Extreme climate events and individual heterogeneity shape life-history traits and population dynamics. *Ecol Monogr* 85: 605–624
- Jenouvrier S, Desprez M, Fay R, Barbraud C, Weimerskirch H, Delord K, Caswell H (2018) Climate change and functional traits affect population dynamics of a long-lived seabird. *J Anim Ecol* 87:906–920
- Jones T, Parrish JK, Peterson WT, Bjorkstedt EP and others (2018) Massive mortality of a planktivorous seabird in response to a marine heatwave. *Geophys Res Lett* 45: 3193–3202
- Kim MA, Harrison CS, Tasker ML (2023) Legal and cooperative mechanisms for conserving marine birds. In: Young L, VanderWerf E (eds) *Conservation of marine birds*. Academic Press, London, p 297–319
- Kitaysky AS, Hunt GL Jr (2018) Seabird responses to a changing Bering Sea. *Mar Ecol Prog Ser* 593:189–194
- Kowalczyk ND, Reina RD, Preston TJ, Chiaradia A (2015) Environmental variability drives shifts in the foraging behaviour and reproductive success of an inshore seabird. *Oecologia* 178:967–979
- Krüger L, Ramos JA, Xavier JC, Grémillet D and others (2018) Projected distributions of Southern Ocean albatrosses, petrels and fisheries as a consequence of climatic change. *Ecography* 41:195–208
- Kuletz K, Cushing D, Labunski E (2020) Distributional shifts among seabird communities of the Northern Bering and Chukchi seas in response to ocean warming during 2017–2019. *Deep Sea Res II* 181-182:104913
- Loring PH, Ronconi RA, Welch LJ, Taylor PD, Mallory ML (2017) Postbreeding dispersal and staging of common and arctic terns throughout the western North Atlantic. *Avian Conserv Ecol* 12:20
- Lotze HK, Tittensor DP, Bryndum-Buchholz A, Eddy TD and others (2019) Global ensemble projections reveal trophic amplification of ocean biomass declines with climate change. *Proc Natl Acad Sci USA* 116:12907–12912
- Marrot P, Garant D, Charmantier A (2017) Multiple extreme climatic events strengthen selection for earlier breeding in a wild passerine. *Philos Trans R Soc B* 372:20160372
- Mason C, Hobday AJ, Alderman R, Lea MA (2021) Climate adaptation interventions for iconic species. *Conserv Sci Pract* 3:e34
- Miller MGR, Carlile N, Phillips JS, McDuie F, Congdon BC (2018) Importance of tropical tuna for seabird foraging over a marine productivity gradient. *Mar Ecol Prog Ser* 586:233–249
- Moe B, Stempniewicz L, Jakubas D, Angelier F and others (2009) Climate change and phenological responses of two seabird species breeding in the high-Arctic. *Mar Ecol Prog Ser* 393:235–246
- 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
- Montie S, Thomsen MS, Rack W, Broady PA (2020) Extreme summer marine heatwaves increase chlorophyll a in the Southern Ocean. *Antarct Sci* 32:508–509
- Morley TI, Fayet al. Jessop H, Veron P, Veron M, Clark J, Wood MJ (2016) The seabird wreck in the Bay of Biscay and South-Western Approaches in 2014: a review of reported mortality. *Seabird* 29:22–38
- O'Hara CC, Frazier M, Halpern BS (2021) At-risk marine biodiversity faces extensive, expanding, and intensifying human impacts. *Science* 372:84–87
- Oliver ECJ, Benthuyssen JA, Bindoff NL, Hobday AJ, Holbrook NJ, Mundy CN, Perkins-Kirkpatrick SE (2017) The unprecedented 2015/16 Tasman Sea marine heatwave. *Nat Commun* 8:16101
- Oliver ECJ, Donat MG, Burrows MT, Moore PJ and others (2018a) Longer and more frequent marine heatwaves over the past century. *Nat Commun* 9:1324
- Oliver ECJ, Lago V, Hobday AJ, Holbrook NJ, Ling SD, Mundy CN (2018b) Marine heatwaves off eastern Tas-

- mania: trends, interannual variability, and predictability. *Prog Oceanogr* 161:116–130
- ✦ Oliver ECJ, Burrows MT, Donat MG, Sen Gupta A and others (2019) Projected marine heatwaves in the 21st century and the potential for ecological impact. *Front Mar Sci* 6:734
- ✦ Oliver ECJ, Benthuisen JA, Darmaraki S, Donat MG and others (2021) Marine heatwaves. *Annu Rev Mar Sci* 13: 313–342
- ✦ 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
- ✦ Patterson A, Gilchrist HG, Gaston A, Elliott KH (2021) Northwest range shifts and shorter wintering period of an Arctic seabird in response to four decades of changing ocean climate. *Mar Ecol Prog Ser* 679:163–179
- ✦ Pearce AF, Feng M (2013) The rise and fall of the 'marine heat wave' off Western Australia during the summer of 2010/2011. *J Mar Syst* 111–112:139–156
- ✦ Peron C, Authier M, Barbraud C, Delord K, Besson D, Weimerskirch H (2010) Interdecadal changes in at-sea distribution and abundance of subantarctic seabirds along a latitudinal gradient in the Southern Indian Ocean. *Glob Change Biol* 16:1895–1909
- ✦ Pershing AJ, Mills KE, Dayton AM, Franklin BS, Kennedy BT (2018) Evidence for adaptation from the 2016 marine heatwave in the Northwest Atlantic Ocean. *Oceanography* 31:152–161
- ✦ Phillips RA, Lewis S, González-Solís J, Daunt F (2017) Causes and consequences of individual variability and specialization in foraging and migration strategies of seabirds. *Mar Ecol Prog Ser* 578:117–150
- ✦ Piatt JF, Sydeman WJ, Wiese F (2007) Introduction: a modern role for seabirds as indicators. *Mar Ecol Prog Ser* 352: 199–204
- ✦ 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
- ✦ Pittman SJ, Yates KL, Bouchet PJ, Alvarez-Berastegui D and others (2021) Seascape ecology: identifying research priorities for an emerging ocean sustainability science. *Mar Ecol Prog Ser* 663:1–29
- ✦ Ponchon A, Grémillet D, Christensen-Dalsgaard S, Erikstad KE and others (2014) When things go wrong: intra-season dynamics of breeding failure in a seabird. *Ecosphere* 5:4
- ✦ Price CA, Hartmann K, Emery TJ, Woehler EJ, McMahon CR, Hindell MA (2020) Climate variability and breeding parameters of a transhemispheric migratory seabird over seven decades. *Mar Ecol Prog Ser* 642:191–205
- ✦ Ramírez F, Afán I, Tavecchia G, Catalán IA, Oro D, Sanz-Aguilar A (2016) Oceanographic drivers and mistiming processes shape breeding success in a seabird. *Proc R Soc B* 283:20152287
- ✦ Redfern CP, Kinchin-Smith D, Newton S, Morrison P, Bolton M, Piec D (2021) Upwelling systems in the migration ecology of roseate terns (*Sterna dougallii*) breeding in northwest Europe. *Ibis* 163:549–565
- ✦ Reid K, Croxall JP, Briggs DR, Murphy EJ (2005) Antarctic ecosystem monitoring: quantifying the response of ecosystem indicators to variability in Antarctic krill. *ICES J Mar Sci* 62:366–373
- ✦ Reynolds MH, Courtot KN, Berkowitz P, Storlazzi CD, Moore J, Flint E (2015) Will the effects of sea-level rise create ecological traps for Pacific island seabirds? *PLOS ONE* 10:e0136773
- ✦ Robertson BA, Hutto RL (2006) A framework for understanding ecological traps and an evaluation of existing evidence. *Ecology* 87:1075–1085
- ✦ Roman L, Bryan S, Bool N, Gustafson L, Townsend K (2021) Desperate times call for desperate measures: non-food ingestion by starving seabirds. *Mar Ecol Prog Ser* 662: 157–168
- ✦ Romano MD, Renner HM, Kuletz KJ, Parrish JK and others (2020) Die-offs, reproductive failure, and changing at-sea abundance of murres in the Bering and Chukchi Seas in 2018. *Deep Sea Res II* 181–182:104877
- ✦ Salton M, Saraux C, Dann P, Chiaradia A (2015) Carry-over body mass effect from winter to breeding in a resident seabird, the little penguin. *R Soc Open Sci* 2:140390
- ✦ Sanford E, Sones JL, García-Reyes M, Goddard JHR, Largier JL (2019) Widespread shifts in the coastal biota of northern California during the 2014–2016 marine heatwaves. *Sci Rep* 9:4216
- ✦ Sauve D, Friesen VL, Hatch SA, Elliott KH, Charmantier A (2023) Shifting environmental predictors of phenotypes under climate change: a case study of growth in high latitude seabirds. *J Avian Biol* 2023:e03062
- ✦ Scannell HA, Johnson GC, Thompson L, Lyman JM, Riser SC (2020) Subsurface evolution and persistence of marine heatwaves in the Northeast Pacific. *Geophys Res Lett* 47:e2020GL090548
- ✦ Schaeffer A, Roughan M (2017) Sub-surface intensification of marine heatwaves off southeastern Australia: the role of stratification and local winds. *Geophys Res Lett* 44: 5025–5033
- ✦ Schlaepfer MA, Runge MC, Sherman PW (2002) Ecological and evolutionary traps. *Trends Ecol Evol* 17:474–480
- ✦ Schreiber EA, Burger J (2001) *Biology of marine birds*. CRC Press, Boca Raton, FL
- ✦ Schreiber RW, Schreiber EA (1984) Central Pacific seabirds and the El Niño southern oscillation: 1982 to 1983 perspectives. *Science* 225:713–716
- ✦ Scopel L, Diamond A, Kress S, Shannon P (2019) Varied breeding responses of seabirds to a regime shift in prey base in the Gulf of Maine. *Mar Ecol Prog Ser* 626: 177–196
- ✦ Sen Gupta A, Thomsen M, Benthuisen JA, Hobday AJ and others (2020) Extreme marine heatwaves—the most intense, largest and longest events. *Sci Rep* 10:19359
- ✦ Smale DA, Wernberg T, Oliver ECJ, Thomsen M and others (2019) Marine heatwaves threaten global biodiversity and the provision of ecosystem services. *Nat Clim Change* 9:306–312
- ✦ Smith KE, Burrows MT, Hobday AJ, King NG and others (2023) Biological impacts of marine heatwaves. *Annu Rev Mar Sci* 15:119–145
- ✦ Springer AM, van Vliet GB, Bool N, Crowley M and others (2018) Transhemispheric ecosystem disservices of pink salmon in the Pacific Ocean macrosystem. *Proc Natl Acad Sci USA* 115:E5038–E5045
- ✦ Sprogis KR, Christiansen F, Wandres M, Bejder L (2018) El Niño Southern Oscillation influences the abundance and movements of a marine top predator in coastal waters. *Glob Change Biol* 24:1085–1096
- ✦ Stommel H (1963) Varieties of oceanographic experience. *Science* 139:572–576
- ✦ Su Z, Pilo GS, Corney S, Holbrook NJ, Mori M, Ziegler P

- (2021) Characterizing marine heatwaves in the Kerguelen Plateau region. *Front Mar Sci* 7:531297
- Surman CA, Nicholson LW (2009) The good, the bad and the ugly: ENSO-driven oceanographic variability and its influence on seabird diet and reproductive performance at the Houtman Abrolhos, Eastern Indian Ocean. *Mar Ornithol* 37:129–138
- ✦ Surman CA, Nicholson LW, Santora JA (2012) Effects of climate variability on breeding phenology and performance of tropical seabirds in the eastern Indian Ocean. *Mar Ecol Prog Ser* 454:147–157
- ✦ 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, Thompson SA, Santora JA, Koslow JA, Goericke R, Ohman MD (2015) Climate–ecosystem change off southern California: time-dependent seabird predator–prey numerical responses. *Deep Sea Res II* 112:158–170
- ✦ Sydeman WJ, Schoeman DS, Thompson SA, Hoover BA and others (2021) Hemispheric asymmetry in ocean change and the productivity of ecosystem sentinels. *Science* 372: 980–983
- ✦ Tavares DC, Moura JF, Merico A, Siciliano S (2020) Mortality of seabirds migrating across the tropical Atlantic in relation to oceanographic processes. *Anim Conserv* 23: 307–319
- ✦ Ummenhofer CC, Meehl GA (2017) Extreme weather and climate events with ecological relevance: a review. *Philos Trans R Soc B* 372:20160135
- ✦ van de Pol M, Jenouvrier S, Cornelissen JH, Visser ME (2017) Behavioural, ecological and evolutionary responses to extreme climatic events: challenges and directions. *Philos Trans R Soc B* 372:20160134
- ✦ Veit RR, Pyle P, McGowan JA (1996) Ocean warming and long-term change in pelagic bird abundance within the California current system. *Mar Ecol Prog Ser* 139: 11–18
- ✦ Veit R, McGowan J, Ainley D, Wahl T, Pyle P (1997) Apex marine predator declines ninety percent in association with changing oceanic climate. *Glob Change Biol* 3: 23–28
- ✦ Velarde E, Ezcurra E (2018) Are seabirds' life history traits maladaptive under present oceanographic variability? The case of Heermann's gull (*Larus heermanni*). *Condor* 120:388–401
- ✦ Velarde E, Ezcurra E, Horn MH, Patton RT (2015) Warm oceanographic anomalies and fishing pressure drive seabird nesting north. *Sci Adv* 1:e1400210
- ✦ Wells MR, Angel LP, Arnould JPY (2016) Habitat-specific foraging strategies in Australasian gannets. *Biol Open* 5: 921–927
- ✦ Wilcox C, Van Sebille E, Hardesty BD (2015) Threat of plastic pollution to seabirds is global, pervasive, and increasing. *Proc Natl Acad Sci USA* 112:11899–11904
- ✦ Wild S, Krützen M, Rankin RW, Hoppitt WJ, Gerber L, Allen SJ (2019) Long-term decline in survival and reproduction of dolphins following a marine heatwave. *Curr Biol* 29: R239–R240
- ✦ Wingfield JC, Pérez JH, Krause JS, Word KR, González-Gómez PL, Lisovski S, Chmura HE (2017) How birds cope physiologically and behaviourally with extreme climatic events. *Philos Trans R Soc B* 372:20160140
- Woehler EJ (2012) What do signals from seabirds tell us about the marine environments? In: Huettmann F (ed) *Protection of the three poles*. Springer, Tokyo, p 218–225
- ✦ Woodworth BK, Fuller RA, Hemson G, McDougall A, Congdon BC, Low M (2021) Trends in seabird breeding populations across the Great Barrier Reef. *Conserv Biol* 35: 846–858
- ✦ Woodworth-Jefcoats PA, Polovina JJ, Drazen JC (2017) Climate change is projected to reduce carrying capacity and redistribute species richness in North Pacific pelagic marine ecosystems. *Glob Change Biol* 23: 1000–1008
- ✦ Wooller RD, Bradley JS, Croxall JP (1992) Long-term population studies of seabirds. *Trends Ecol Evol* 7:111–114

*Editorial responsibility: Kyle Elliott,
Sainte-Anne-de-Bellevue, Québec, Canada
Reviewed by: S. Thompson and 2 anonymous referees*

*Submitted: January 18, 2023
Accepted: May 19, 2023
Proofs received from author(s): July 16, 2023*