Oceanography and Marine Biology

An Annual Review, Volume 63

Editors in Chief: P. A. Todd and B. D. Russell
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First published 2025

ISBN: 9781032964768 (hbk)
ISBN: 9781041079927 (pbk)
ISBN: 9781003589600 (ebk)

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DOI: 10.1201/9781003589600-2

The funder for this chapter University of Victoria, Dept. of Biology, Canada

CRC Press
Taylor & Francis Group
Boca Raton London New York

CRC Press is an imprint of the
Taylor & Francis Group, an **informa** business

Oceanography and Marine Biology: An Annual Review, 2025, **63**, 42–96
© P. A. Todd, B. D. Russell, M. Byrne, L. B. Firth, D. A. Hemraj, A. J. Lemasson, E. M. Marzinelli,
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ECOLOGICAL RESPONSES TO EXTREME CLIMATIC EVENTS: A SYSTEMATIC REVIEW OF THE 2014–2016 NORTHEAST PACIFIC MARINE HEATWAVE

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Abstract Marine heatwaves, which are becoming more prolonged, frequent and intense under climate change, now pose a significant threat to ocean species and ecosystems. Long-term observational studies that encompass these events can offer critical insights into how continued climate change will alter marine life across scales, from physiological effects on individuals to altered species interactions to ecosystem-scale processes. Between 2014 and 2016, the Northeast Pacific experienced what, to this day, remains the longest recorded marine heatwave globally, triggering a wide range of ecological responses. We conducted a systematic review of observational studies from this heatwave and synthesised the documented ecological impacts. We identified 331 relevant English-language primary reports (from 2256 records recovered), including both peer-reviewed and grey literature. In total, 240 species were found outside of their typical geographical ranges during the heatwave, with many of them ($n = 101$) found further north than ever before. The prolonged heatwave also drove kelp forest declines, reorganised plankton communities, altered offshore oceanographic productivity and impacted seagrass meadows and intertidal habitats. Cascading indirect effects of the heatwave were also far-reaching, driving record seabird die-offs, unusual mortality events in humpback whales, reduced abundance and nutritional quality of forage fish, the near extinction of a key rocky shore predator, *Pycnopodia helianthoides*, and closures of multiple fisheries, driven by changes in species interactions, disease proliferation or habitat loss. This comprehensive analysis highlights the need to better understand and mitigate the impacts of marine heatwaves, emphasising the urgency to strengthen marine ecosystem resilience in a warming world.

Keywords: Climate Change; Marine Heatwave; Environmental Drivers; Range Shifts; Foundation Species; Species Interactions; El Niño; Ocean Currents

DOI: 10.1201/9781003589600-2

Introduction

Marine heatwaves (MHWs) are now among the primary driving forces of ecological change in the ocean (Smale et al. 2019, Oliver et al. 2021, Wernberg et al. 2024). MHWs are discrete anomalously warm water events and are often also associated with changes in current dynamics and ocean nutrient cycling (Peña et al. 2019, Smith et al. 2021, Kauppi & Villnäs 2022, Hauri et al. 2024). Although different criteria can be used to define MHWs (Hobday et al. 2016, Gruber et al. 2021, Oliver et al. 2021, Amaya et al. 2023, Sen Gupta 2023), they are often considered to be periods where water temperatures exceed the 90th percentile of historical average temperatures for a minimum of 5 days (Hobday et al. 2016). These extreme events are becoming longer, more intense and more frequent under climate change (Oliver et al. 2019, 2021), posing an ever growing threat to marine ecosystems (Arias et al. 2023, Wernberg et al. 2024). MHWs can trigger a multitude of ecological changes with potentially lasting impacts on the structure and functioning of affected ecosystems (Smale et al. 2019, Smith et al. 2023, Wernberg et al. 2024). These impacts stem from both the direct physiological effects of warming, which include population die-offs (Wernberg et al. 2016, Hughes et al. 2018, Smale et al. 2019, Coleman & Wernberg 2020) and species range shifts (Pinsky et al. 2013, Sanford et al. 2019, Pinsky et al. 2020, Harvey et al. 2022), as well as from subsequent indirect effects resulting from shifts in community dynamics (e.g. Vergés et al. 2019, Hamilton et al. 2021). MHWs offer important opportunities for 'natural experiments' that can test fundamental ecological hypotheses (Sagarin & Pauchard 2010) and have become the focus of a growing number of observational studies in recent years (Smith et al. 2023). As these extreme weather events become even more prevalent (Oliver et al. 2018, 2019), developing an integrative view of their impacts from such studies will be essential for predicting their consequences and effectively managing future ocean ecosystems (Smith et al. 2021, Hollarsmith et al. 2022, Starko et al. 2024b).

Between late 2013 and 2016, the Pacific coast of North America experienced a prolonged period of persistently warm temperatures, reaching 2°C–6°C above historical averages (Di Lorenzo & Mantua 2016, Oliver et al. 2018) (Figures 1 and S1). While in any particular locality, this was experienced as a series of shorter marine heatwaves (*sensu* Hobday et al. 2016) (Figure 1B), it is generally treated as a single continuous event (e.g. Cavole et al. 2016, Smith et al. 2021), with the exact location of peak temperature anomalies changing as the heatwave progressed (Figure 1C). Moreover, in some localities, the MHW lasted almost the entirety of any given year between 2014 and 2016 (Figure 1C), highlighting its extreme duration. The MHW began in October 2013, when sea surface temperature (SST) anomalies appeared offshore (Bond et al. 2015, Peterson et al. 2015, Di Lorenzo & Mantua 2016). This mass of warm water, termed 'the Blob' (Bond et al. 2015), moved eastwards and made landfall throughout the Northeast Pacific between spring and fall of 2014 (depending on location). The arrival of this warm water was sudden in many cases; in Newport, Oregon, coastal ocean temperatures increased by nearly 7°C in 1 hour (Peterson et al. 2015). Simultaneously, a second pool of warm upper ocean water formed in spring 2014 in southern California and Baja Mexico, and, by fall 2014, these two anomalies merged along the coast. By fall 2015, the region was met with a second period of rapid warming from the south, linked to El Niño conditions (Jacox et al. 2016). The heatwave persisted until summer 2016 in the California Current (Di Lorenzo & Mantua 2016, Jacox et al. 2016) and longer further north (Figures 1 and S1). The initial temperature anomalies were associated with a persistent high-pressure system known as the 'Ridiculously Resilient Ridge', which reduced the loss of thermal energy from the ocean to the atmosphere and reduced ocean mixing through unusually calm winter conditions (Bond et al. 2015, Di Lorenzo & Mantua 2016, Amaya et al. 2020, Gruber et al. 2021). Climate models indicate that this period of extreme temperatures was seven times more likely due to climate change (than it would have been before anthropogenic greenhouse gas emissions), and that return periods of similar events will be greatly reduced under future climate scenarios (Oliver et al. 2018). Thus, although this event was the longest and among the most extreme on record, similar events are expected to become more common in the future (Frölicher et al. 2018, Oliver et al. 2018, 2019). Given that this event only began at the end of 2013 and did not fully manifest until 2014, we herein refer to it as the 2014–2016 MHW.

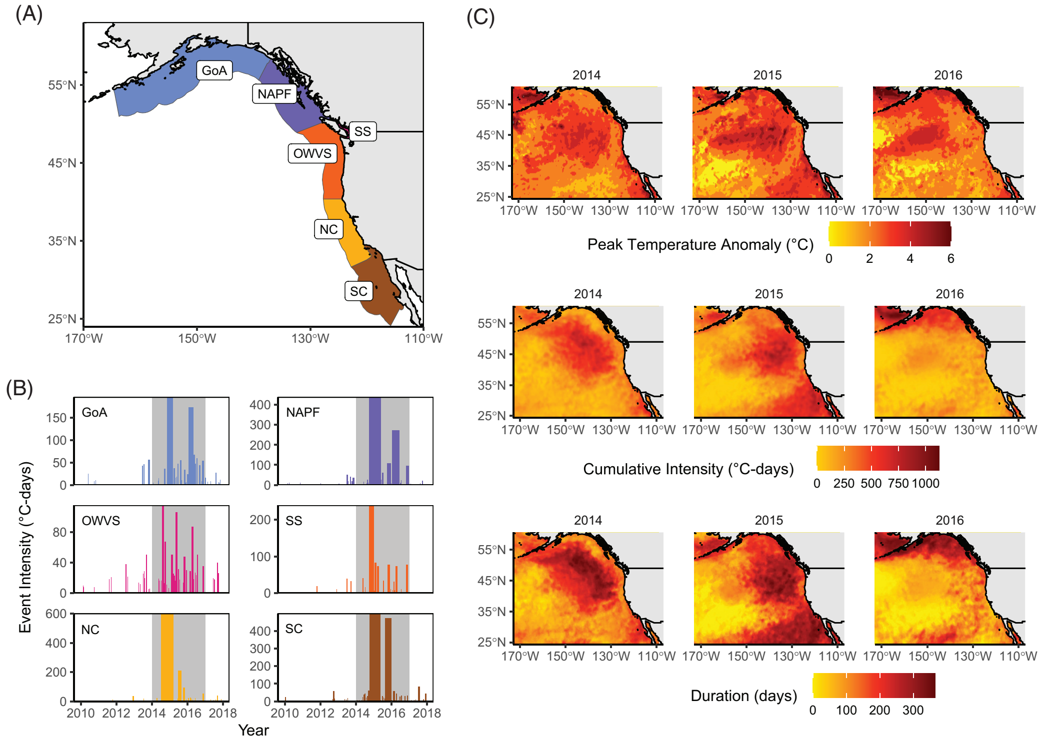

Figure 1 Spatial and temporal patterns of the 2014–2016 marine heatwave (MHW). (A) Map of the six Northeast Pacific ecoregions impacted by the heatwave (Gulf of Alaska (GoA), Northeast Pacific Fjordlands (NEPF), Salish Sea (SS), Oregon, Washington, Vancouver Coast and Shelf (OWVS), Northern California (NC) and Baja/Southern California Bight (SC)). (B) Temporal changes in the cumulative intensity (i.e. the integral ocean temperature anomaly over the duration of the event in °C × days) of MHW events from 2010 to 2020 for representative coastal areas within each of the six ecoregions, with the duration of each event in days shown by the bar width. (C) Spatial variation in the peak temperature anomaly (°C), cumulative intensity (°C-days) and duration (days) of the MHW for each year of the event. See Supplementary Materials (Extended Methods) for details.

The 2014–2016 MHW had a wide range of impacts on a diversity of species, altering coastal and offshore productivity and degrading marine habitats in both shallow coastal waters (Rogers-Bennett & Catton 2019, e.g. McPherson et al. 2021, Whalen et al. 2023) and the deep sea (Gasbarro et al. 2019). This event was also associated with severe economic costs, with commercial fisheries closures resulting from severe declines in fish stocks causing hundreds of millions of dollars (USD) in losses alone (Smith et al. 2021, Free et al. 2023). The impacts of this MHW, both transient and persistent, have been the focus of numerous observational studies, making it one of the best documented climatic events on record. For this reason, it offers an exceptional case study into how prolonged MHWs are likely to continue altering marine ecosystems in the future. Still, the narrow taxonomic and geographic scope of most studies has limited understanding of the overall scope and nature of this prolonged and widespread heatwave. Cavole et al. (2016) presented an initial review of the ecological impacts of the MHW throughout the Northeast Pacific, but it was published before the event had ended. Since then, over 200 additional studies examining various ecological impacts of the MHW have been published. More recently, multiple studies have aimed to synthesise ecological patterns (e.g. Thompson 2018, Beas-Luna et al. 2020, Suryan et al. 2021, Free et al. 2023), offering a foundation for understanding particular impacts. However, these have been region- or system-specific, precluding a comprehensive assessment of impacts along the broader west coast of North America. Consequently, there is a need to comprehensively synthesise the ecological observations of this prolonged event in order to better understand its overall impacts and how these fit into the broader context of other marine heatwaves.

Here, we present a systematic review of the observed ecological impacts of the 2014–2016 MHW on temperate marine ecosystems. We defined the geographical scope of our review as extending from the temperate Baja California (south to the Tropic of Cancer) to the Gulf of Alaska; we did not include the Bering Sea, the Aleutian Islands or the Gulf of California. We specifically aimed to provide an integrative account of ecological patterns and their drivers in each of the major marine ecosystems. Wherever possible, we also aimed to disentangle the direct effects (i.e. those caused by direct physiological responses to the MHW) and indirect effects (i.e. those caused indirectly through ecological interactions) of the MHW, highlighting cascading effects of species-level impacts on the broader ecosystem. We compiled all available information on range shifts and changes in species geographic distributions that occurred during the multiyear heatwave, highlighting its impacts on the distributional patterns of species on the west coast of North America. Finally, we created a summary, synthesis and discussion of the diversity of impacts observed in a wide range of coastal and offshore ecosystems.

Review methods

Literature review – search strategy

We conducted a systematic literature review with the aim of identifying the range of ecological responses by marine populations, species, communities and ecosystems to the 2014–2016 marine heatwave. Thus, our goal was not to answer a yes or no question, as is typical of systematic reviews, but instead to identify and synthesise the diversity of impacts (and their drivers) for ecosystems that experienced this MHW. In doing so, we hope to facilitate deeper understanding of the impacts of MHWs, which could help us better manage ecosystems in the face of extreme events and better respond to rapid environment change.

Our review was primarily led by two key questions:

1. Which different species or ecosystems were impacted by the MHW, and what were the spatial and temporal patterns in these impacts?
2. To what extent were impacts of the 2014–2016 MHW driven by direct effects of warm waters versus indirect effects caused by changes in species interactions?

Because our goal was to review and synthesise impacts across study systems and regions, a single search string was not sufficient to capture relevant information from such a breadth of fields and sources. Our scoping and search strategy therefore involved multiple databases and tools. We began with a structured search in Web of Science (accessed through the University of Victoria) using the following search string: ‘(blob OR heatwave OR El Niño OR “temperature anomaly”) AND (Alaska OR British Columbia OR Oregon OR Washington OR California OR Baja)’ and restricted to 2014 or later. This initial search was intentionally broad to return as many possibly relevant papers as possible. We also conducted an additional search in Web of Science using the search term ‘“sea star wasting” OR “seastar wasting”’ because the MHW was also associated with the sea star wasting disease (SSWD) epidemic, which caused mass mortality of sea stars (e.g. Harvell et al. 2019) with downstream consequences for shallow benthic ecosystems (e.g. Wilkes 2019, Traiger et al. 2022). Our Web of Science queries returned 2303 and 87 hits, respectively. These results were manually screened for relevance (see below) by at least one reviewer, yielding a total of 199 studies. The majority of these studies ($n = 125$) were checked by two reviewers with nearly identical conclusions on inclusion (97% consistency across reviewers).

To avoid biases associated with use of a single database, we next followed these initial searches up with similar searches on Google Scholar, using various, simplified combinations of the same search terms above (e.g. 'blob Alaska') as well as 'heatwave*', 'range shift*', 'North* Pacific', 'North* Pacific heatwave' (for full list of search terms, see Supplementary Materials). These searches often yielded large numbers of results that were impractical to comprehensively screen in full (e.g. North* Pacific heatwave yields >17,000 results since 2014). Thus, because our goal was to supplement our more comprehensive Web of Science search and identify key papers that we may have missed, we focused on papers that Google Scholar deemed most relevant. Sorting by 'relevance', we screened papers manually for inclusion in our review (see inclusion criteria below) and stopped each search once thirty results in a row were either irrelevant or already captured by our Web of Science search. All searching was done in English because Canada and the USA are majority English countries. However, we acknowledge that this may have caused us to miss Spanish language publications from northern Mexico. We only systematically reviewed papers published up to 31 March 2023. However, some studies published or released after this cut-off date that were considered highly relevant to this review (i.e. provided new patterns or observations requiring discussion in the text) were also included. These are papers that were identified by authors who were still monitoring the literature closely or were suggested by reviewers as highly relevant.

We also identified several additional papers ($n=16$ studies) through incidental citation tracking while performing the review and included some studies from our personal reference libraries or suggested by reviewers that were not captured in the original searches ($n=52$ studies). This was predominantly grey literature (e.g. government reports) that is not indexed by Web of Science, including reports from Fisheries and Oceans Canada's State of the Pacific annual volumes. Finally, we selectively used LitMaps software (Kaur et al. 2022) to identify studies that we may have missed on topics that were poorly represented by the structured search (e.g. impacts on eelgrass, deep sea) and to confirm that our structured searches had sufficiently captured the relevant literature. Although we uncovered a very limited number of new studies using this method ($n=6$), most papers were captured by our Web of Science or Google Scholar searches. To reduce duplication of the same patterns reported multiple times in technical volumes, reports published by Fisheries and Oceans Canada as an output from the State of the Pacific Ocean meeting were only included until 2018. A flow chart overviewing our study identification, screening and inclusion steps is provided in Figure S2.

Literature review – inclusion criteria and data synthesis

We chose to be as inclusive as possible with respect to source type. We therefore included peer-reviewed literature, government and/or technical reports and graduate theses. We focused our collation efforts only on primary sources that included observational data on biological consequences and thus we did not include experiments conducted to simulate the impacts of the event. We also only included review papers if they provided new data or a novel analytical approach. For a study to be included, it had to meet the above criteria and receive a 'yes' answer to the following questions:

1. Does this study contain observational biological data collected either during the 2014–2016 marine heatwave or spanning it (e.g. before and after, during and after)?
2. Does this study include information from our geographical study area (i.e. temperate Baja California to the Gulf of Alaska)?

After screening studies for these inclusion criteria, we identified 331 studies for our review. We conducted a narrative review on all studies and then used mixed methods (qualitative and quantitative) to synthesise key patterns observed across some ecosystems. We grouped reports based on which ecosystem type(s) they included and on which ecoregion(s) (based on the scheme by Spalding et al. (2007)) the study was focused, and we wrote short summaries of each paper to help with our narrative syntheses. We also conducted three separate analyses alongside our narrative review. These focused on (1) range shifts, (2) kelp forest impacts and (3) changes in iconic rocky shore species.

Our first quantitative analysis focused on range shifts documented during the MHW. During the initial annotation stage, we noted which studies contained information on changes in species geographical distributions. While the majority of studies used in this analysis came from the structured search described above, we also included additional searching on Google (generic search engine) for news articles reporting range shifts and screened news articles that were cited in past syntheses (e.g. Cavole et al. 2016). Although these news articles were not included in our bibliography list, we have provided a list of news articles that we screened for range shift data in the Supplementary Materials. To compile and synthesise data on range shifts, we conducted a quantitative analysis by extracting data on two different types of shifts: (1) range shifts and (2) unusual occurrences. Range shifts were defined as expansions or contractions of the latitudinal limits, longitudinal limits or habitat types where any individual of a species was found during the heatwave. Range 'expansion' was defined to mean that during the MHW at least one individual of a given species was recorded somewhere that species had never been recorded pre-MHW. Range 'contractions' referred to cases where, during the heatwave, a species was not present somewhere that species had previously been reliably recorded before the heatwave. 'Unusual occurrences' were defined as observations of a species that were within its established latitudinal, longitudinal or habitat range, but where individuals had not been present immediately before the MHW. In most cases, this represented instances where a species was occasionally or rarely (but not reliably) distributed near its absolute northern limit and was also found there during the heatwave. However, these also included cases where a particular life stage was seen post-MHW when only a different life stage had been present pre-MHW. Thus, unusual occurrences could be life-stage specific. Often unusual occurrences were sightings where a species is considered rare, or where it had only been seen during previous El Niño events. For both range shifts and unusual occurrences, strandings were excluded and considered to be outside of the range of a species both pre- and post-MHW. When multiple reports of the same species were identified, we collapsed these into a single datapoint (using the largest reported range shift distances) before presentation to minimise the impacts of reporting biases. We aimed to extract data on pre- and post- (or during) MHW distributions. From all relevant studies, we extracted both previous northern range limits (absolute limits for range shifts and typical limits for unusual occurrences) and the new (i.e. during or post-MHW) range limits. When the distance between the new and previous range limit was given in kilometres, we included that measure; otherwise, we estimated distance using degrees latitude (using the conversion: $1° = 111.1$ km). We also noted species name, general taxonomic group and, where possible, the cause of the range shift (e.g. immigration, emigration, die-off, introduction).

We also conducted additional analyses on kelp forests and two iconic rocky shore taxa (*Fucus* spp. and *Mytilis* spp.). To gain insight into spatial patterns of impacts on kelp forests at a finer scale than ecoregions, we grouped kelp studies spatially as follows: Baja, Southern California, Central and Northern California, Oregon, Washington, British Columbia and Gulf of Alaska. We also recorded the qualitative response to the event, as follows: (1) declines, (2) stable and (3) variable. This final category was used when conflicting results were observed across sites, and this was identified as a key pattern by the authors. We did this for all studies that included kelp forest abundance before and during the MHW. We did not consider recovery from negative impacts in this analysis. We also collated data on changes in the abundance of *Fucus* spp. and *Mytilis* spp. where available. For each site, we compared the abundance of each taxon before the MHW (an average of 2009–2013 where data were available) to that during and immediately following (average of 2014–2017) for studies showing abundance through time. We then calculated the proportional change in abundance of each taxon at the site level and mapped these values to look for spatial patterns.

A list of references included in our synthesis is provided in the Supplementary Materials. Data presented in the main text of this article were either provided directly by the authors, downloaded from public data repositories or extracted from publications using WebPlotDigitizer software (Pacifica, California, USA).

Breadth of impacts

The far-reaching impacts of the 2014–2016 Northeast Pacific marine heatwave – across a diversity of species from the bottom to the top of the food web (Figure 2) and in all marine ecosystems across the entire focal region – are evidenced by the 331 studies examining its ecological

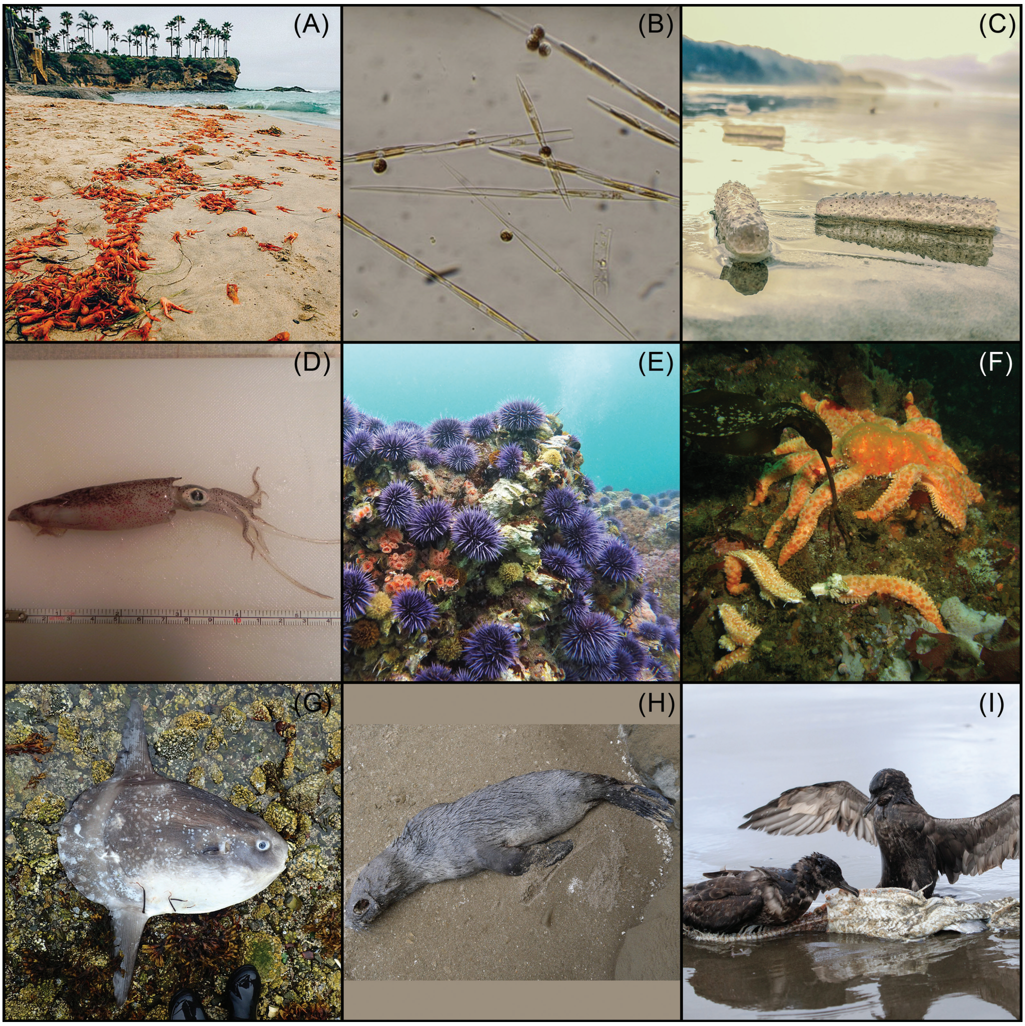

Figure 2 Examples of impacts during the 2014–2016 marine heatwave. (A) Pelagic red crabs (*Grimothea planipes*) washed up on a beach in California in June 2015 (Credit: Dirk Dallas); (B) harmful algal blooms caused by *Pseudo-nitzschia* spp. (Credit: Oregon State University); (C) pyrosomes (*Pyrosoma atlanticum*) washed up on a beach in Oregon in summer 2017 (Credit: Tiffany Boothe/Seaside Aquarium); (D) California market squid (*Doryteuthis opalescens*) found in stomach of Chinook Salmon in Sitka Sound, Alaska in 2017 (Credit: Karen Johnson); (E) urchin barrens (formed by *Strongylocentrotus purpuratus*) in Monterey, California became prevalent as the loss *of Pycnopodia helianthoides* by SSWD (F; photo from 2014) led to a release on the urchin populations, leading to overgrazing of kelp forests (Credit: Zachary Randell, Janna Nicols); (G) dead ocean sunfish (*Mola mola*) on the beach in Bamfield, British Columbia in August 2016 (Credit: Kristina Tietjen); (H) dead Guadalupe fur seal (*Arctocephalus townsendi*) in June 2016 (Credit: John Vonderlin); and (I) two short-tailed shearwaters (*Ardenna tenuirostris*) feeding on a salmon carcass at the mouth of Big Creek, Alaska Peninsula, Alaska in summer 2017 (Credit: Gerritt Vyn).

effects (Figure 3). We classified these studies based on geography – using the marine ecoregion framework (Spalding et al. 2007) – and ecosystem type. More studies examined impacts in the three southernmost ecoregions compared to the northern ecoregions, but there were at least 40 studies in each ecoregion. The Oregon, Washington and Vancouver Coast and Shelf (OWVCS) ecoregion, which spans the Canada-USA border, had the most studies (~30%; Figure 3A), likely reflecting its large size (e.g. linear extent of shoreline) and relatively high population density. In contrast, there was a much less even spread of studies across ecosystem types, with approximately 60% of papers focusing on the MHW's impacts on shallow pelagic ecosystems, almost 20% and 10% on rocky shore and kelp forests, respectively, and only a handful on seagrass meadows, the deep sea or sandy beaches (Figure 3B). Although the distribution of papers across ecosystem types might imply that shallow pelagic ecosystems were the most impacted, there are likely strong biases in research effort across these different ecosystem types. Studies on shallow pelagic ecosystems span multiple disciplines including biological oceanography, remote sensing, fisheries, ecology and more, meaning that there are likely more studies on these ecosystems than any other even in the absence of this extreme MHW. This ecosystem type is also the most expansive, covering the entire study region, likely contributing to this publication discrepancy compared to other ecosystem types.

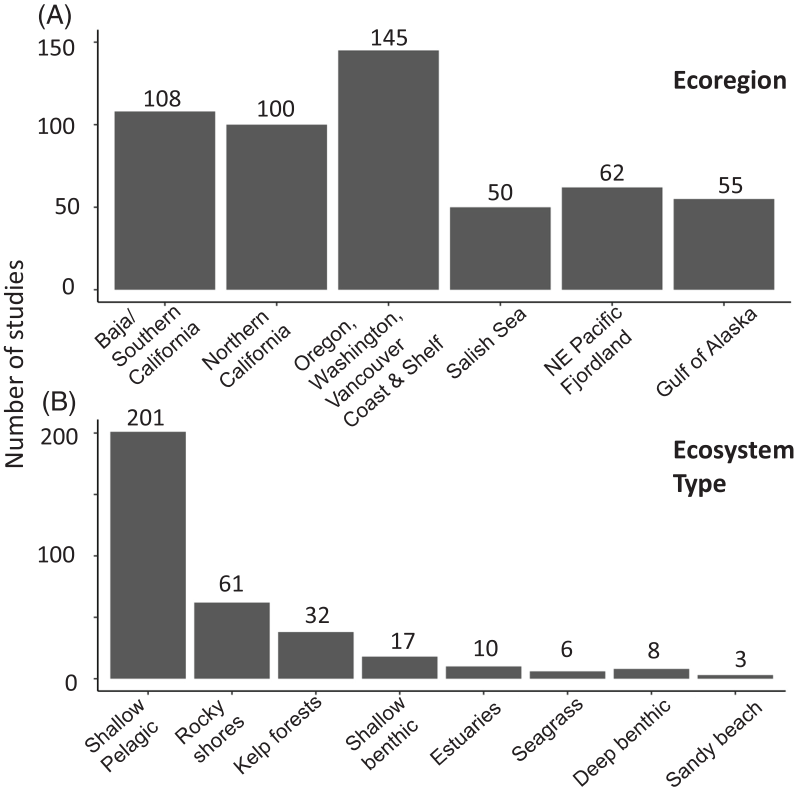

Figure 3 A summary of observational studies on the ecological impacts of the 2014–2016 marine heatwave organised by (A) ecoregion and (B) ecosystem type; those that include multiple ecoregions or ecosystems are included in multiple categories. Studies further offshore than the ecoregions in Figure 1 (i.e. part of the 'high seas' ecoregion) were included in the nearest coastal ecoregion. See Supplementary Information for Review Methods.

Species on the move: range shifts and unusual occurrences

The 2014–2016 marine heatwave precipitated distinct shifts in species distributions across a broad taxonomic spectrum, with numerous species documented at latitudes outside their historical ranges (e.g. Cavole et al. 2016, Goddard et al. 2016, Sanford et al. 2019). In total, we identified 101 range shifts (Figure 4A), which are defined broadly as the occurrence of a species outside of its previously documented range (including the arrival stage, as in Bates et al. 2014). While recognising that a true range shift can include the requirement of establishing a sustained population (Pinsky et al. 2020), our definition is consistent with most studies documenting species' distribution changes during MHWs (e.g. Goddard et al. 2016, Sanford et al. 2019). However, ~44% (44/101) of range shifting species were observed outside of their pre-MHW ranges for two or more years, suggesting that several species may have developed persistent populations during the event. Beyond range shifts, even more species (*n* = 139) were identified as having unusual occurrences during the heatwave (Figure 4B), in which they were found beyond their typical northernmost boundary, but not at a completely unprecedented latitude (i.e. not beyond their absolute range) (e.g. Sanford et al. 2019). For both range shifts and unusual occurrences, invertebrates made up the majority of observations, followed by fishes (Figure 4A and B). Both phenomena were also documented in birds and mammals, while unusual occurrences (but not range shifts) were also documented for reptiles (i.e. sea turtles) and eukaryotic phytoplankton (Figure 4B). In many cases, unusual occurrences included species that periodically shift further north in warm years, including past marine heatwaves like the 1997–1998 El Niño (e.g. Pearcy 2002). Although some of these distributional changes have persisted following the event (e.g. Yamada et al. 2021, Keener et al. 2023), many may represent transient responses to

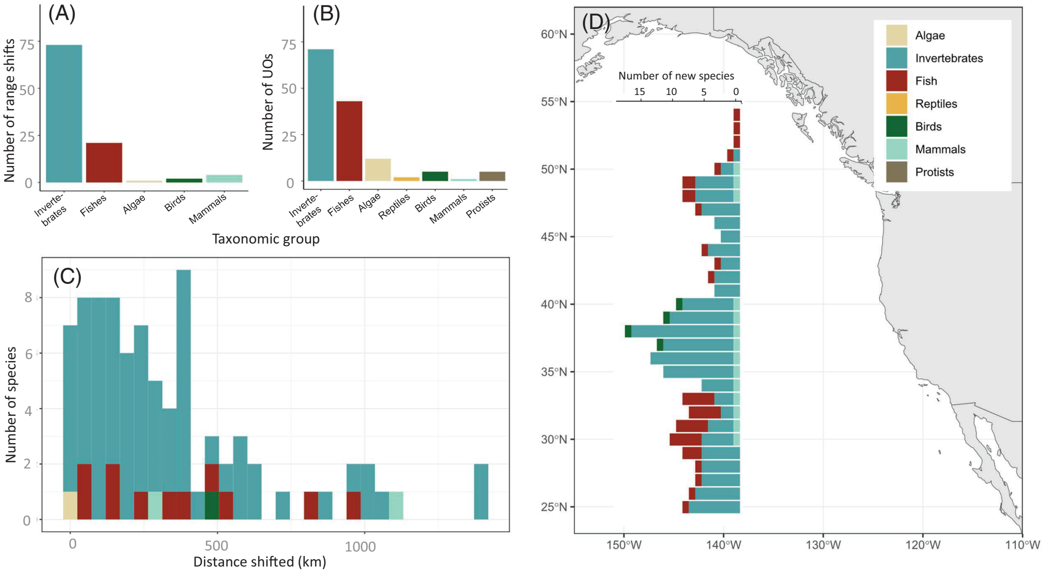

Figure 4 Overview of range shifts reported during or shortly after the 2014–2016 marine heatwave. Shown are the number of (A) latitudinal range shifts and (B) unusual occurrences (UOs), both separated by taxonomic group. (C) A histogram of the distance shifted (in kilometres) during each latitudinal range shift. (D) The number of new species introduced into each latitudinal increment because of a latitudinal range shift during the marine heatwave. Note that shifts of less than a degree that resulted in the same whole degree value are not shown in panel (D). Moreover, species whose exact previous or observed northern limit was unreported or could not be inferred are not shown.

elevated temperatures and associated modifications in ocean circulation dynamics. Unfortunately, the persistence of many range shifts remains unclear due to the paucity of follow-up studies.

Among the range shifts for which we could directly extract or calculate geographic distance, 80% of species ($n=66/83$) shifted by less than 500 km, with a mean shift of 343 km and median shift of 255 km (Figure 4C). However, several range shifts exceeded this distance with four species, including one marine mammal (Northern right whale dolphin*: Lissodelphis borealis*) and three invertebrates (Venus girdle: *Cestum veneris*; a pteropod: *Hyalocylis striata* and a sea slug: *Placida cremoniana*), shifting over 1000 km (Goddard et al. 2016, Becker et al. 2019, Sanford et al. 2019; Figure 4C). *Cestum veneris* and *P. cremoniana*, both of which have pelagic early life stages, shifted approximately 1400 km north from their previous range limit, the greatest change observed in any species. Most range shifts were documented in the southern parts of our study region in Baja California and California, and although this may reflect a true ecological pattern, it is heavily confounded by large differences in human population density (and therefore survey effort) across the coast. For example, one study alone in California documented 37 range shifts (Sanford et al. 2019), leveraging monitoring initiatives in the area to identify changes in species distributions. No comparable study exists for British Columbia or Alaska.

Invertebrate species made up the largest share of range shift ($n=72$) and unusual occurrence ($n=70$) observations during the MHW. Range shifting invertebrates included offshore species like *Pyrosoma atlanticum,* which became a dominant member of the pelagic zooplankton community as it shifted northwards (Brodeur et al. 2018, Schram et al. 2020), and coastal species such as the 26 nudibranch species that shifted to varying degrees along the coast of California (Goddard et al. 2018, Sanford et al. 2019). Of the remaining range shifting invertebrate species, 11 were holoplanktonic gastropods (including pteropods), six were crabs (five coastal and one pelagic) and the remainder were made up of a small number of representatives ($n=1$–3) from a diversity of invertebrate groups (e.g. copepods, brittle stars, ctenophores and cnidarians).

Numerous fishes also shifted northwards during the MHW. Twenty-two species underwent range shifts, including large pelagic fishes (e.g. swordfish: *Xiphias gladius*; wahoo: *Acanthocybium solandri* and Auxis: *Auxis* spp.) and coastal sharks (whitenose: *Nasolamia velox* and whitetip reef: *Triaenodon obesus*) (Feeney & Lea 2016, Becerril-Garcia et al. 2018, Halpin et al. 2018, Walker Jr et al. 2020, Thompson et al. 2022). Two subtropical blenny species shifted north to Southern California (*Labrisomus xanti* and *Ophioblennius steindachneri*) (Love et al. 2016, Walker Jr et al. 2020), as did two species of grouper (*Alphestes immaculatus* and *Mycteroperca rosacea*) (Lonhart et al. 2019, Walker Jr et al. 2020). Forty-two fish species also had unusual northern occurrences. This included the ocean sunfish (*Mola mola*) (Bond et al. 2015, Cavole et al. 2016) and the Pacific bonito (*Sarda chiliensis*) (Cavole et al. 2016, Sakuma et al. 2016) that were found in the Gulf of Alaska, which is considered unusual, but not completely unprecedented.

Only a small number of other taxa (algae, mammals, reptiles and birds) experienced range shifts or unusual occurrences (Figure 4A and B). Two species of birds, both petrels (wedge-rumped storm petrel: *Oceanodroma tethys* and band-rumped storm petrel: *Hydrobates castro*) experienced northward range shifts (McClatchie 2016, Sanford et al. 2019). However, six bird species experienced unusual occurrences including the Guadalupe murrelet (*Synthliboramphus hypoleucus*) in Washington, the kelp gull (*Larus dominicanus*) in the Farallon Islands near San Francisco (McClatchie 2016, Sanford et al. 2019) and the black-footed albatross (*Phoebastria nigripes*) off the coast of Vancouver Island, British Columbia (King et al. 2018). Northward range shifts were also documented for four cetacean species, including the Northern right whale dolphin (*Lissodelphis borealis*), bottlenose dolphin (*Tursiops truncatus*), short-beaked common dolphin (*Delphinus delphis*) and pygmy killer whale (*Feresa attenuata*) (Halpin et al. 2018, Becker et al. 2019, Sanford et al. 2019). Only one species of red algae (Rhodophyta) was considered to have experienced a northward range shift: *Dasya binghamiae* shifted ~7 km north during the MHW (Sanford et al. 2019). Interestingly, two species of macroalgae

(*Desmarestia dudresnayi* and *Odonthalia flocossa*) shifted further south than previously recorded (Williams et al. 2018), although the exact reasoning for this remains unclear. Although no sea turtles experienced true range shifts, two species of tropical sea turtle, the green turtle (*Chelonia mydas*) and the olive ridley turtle (*Lepidochelys olivacea*), were observed in unusual locations, off the coast of Washington – north of their typical range but not at unprecedented latitudes.

We also identified a dozen range shifts and thirteen additional unusual occurrences that were not latitudinal in nature but instead involved changes in longitude or habitat use. For example, two bird species, the fork-tailed storm petrel (*Oceanodroma furcata*) and the short-tailed shearwater (*Ardenna tenuirostris*), moved eastward onshore and were observed foraging on land for the first time during the MHW (Robinson et al. 2018a). Seven invertebrate species that were previously only found in offshore environments (at a particular latitude) moved inshore for the first time (Galbraith & Young 2016, Peterson et al. 2017, Becerril-Garcia et al. 2018, Schram et al. 2020, Yamada et al. 2021). This includes the invasive European green crab (*Carcinus maenus*), a tunicate (*P. atlanticum*) and two copepods (*Clausocalanus* spp.) among others. Similarly, six invertebrate species and four fish species that are typically offshore (but have been documented in coastal waters rarely) were found in coastal waters during the MHW (Sakuma et al. 2016, Auth et al. 2018, Lilly & Ohman 2018, Brodeur et al. 2019, Welch et al. 2019, Yamada et al. 2021). An example of a range shift involving a change of habitat use is the California sea hare (*Aplysia californica*), which was only observed in bays north of 42°N prior to the MHW but during the event was observed on the outer coast (Goddard et al. 2016). Similarly, the California bubble (*Bulla gouldiana*, Gastropoda) moved from purely sheltered habitats into more exposed ones (Goddard et al. 2018).

In addition to absolute range limits, there is evidence that some pelagic and/or motile species experienced shifts in population density across space. Numerous species of invertebrates, fish, mammals, reptiles and birds reportedly had higher than usual densities towards northern parts of their range. This includes planktonic species such as by-the-wind sailors (*Velella velella*), which became more abundant in Washington and British Columbia (Jones et al. 2021) than is typical, as well as benthic species such as nudibranchs and other sea slugs, which also became more abundant towards the northern edges of their continuous range (Goddard et al. 2018, Sanford et al. 2019). The northern elephant seal (*Mirounga angustirostris*) was found to be more abundant in its Gulf of Alaska foraging grounds than usual (Holser 2020), and the Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) was found in high abundances in the northern California Current system, likely indicative of movements of large numbers of individuals (Becker et al. 2019). The loggerhead turtle (*Caretta caretta*) was found in coastal waters at unusual abundances linked to compression of coastal upwelling off the California coast: normally between 1 and 4 turtles are spotted annually in this coastal region (with records dating to 1992), whereas during the MHW, in 2015, 265 loggerhead turtles were spotted near the coast – greatly increasing the risk of turtle bycatch in California's Drift Gillnet fishery (Welch et al. 2019). Similarly, humpback whale (*Megaptera novaeangliae*) densities were unusually high close to shore in California (Santora et al. 2020) and in the Gulf of Alaska (Arimitsu et al. 2021). Overall, there were dozens of examples of species experiencing changes in density, and many were not associated explicitly with northern range shifts or unusual occurrences.

Impacts on coastal benthic ecosystems

Marine disease

The 2014–2016 MHW was also associated with one of the worst invertebrate epidemics ever reported (Harvell et al. 2019). Although the epidemic began in 2013 shortly prior to the MHW, available evidence suggests that the high temperatures of the heatwave facilitated its spread and increased its severity (Kohl et al. 2016, Harvell et al. 2019). Sea Star Wasting Disease (SSWD) spread rapidly throughout rocky shore ecosystems of the entire coastal Northeast Pacific, affecting at least 20 asteroid species between Mexico and Alaska (Harvell et al. 2019). Losses were high, especially in the nearshore predator the sunflower sea star (*Pycnopodia helianthoides*), which became functionally extinct from Baja California to Cape Flattery, Washington (>99% loss) and experienced severe population declines (~89% losses) in British Columbia and Alaska (Hamilton et al. 2021). Similarly, populations of the ochre star (*Pisaster ochraceus*) declined by two-thirds in Washington and were decimated on the Oregon coast (Eisenlord et al. 2016, Cerny-Chipman et al. 2017). Initially, the disease outbreak was attributed to a densovirus that seemed capable of transmitting SSWD between individuals. However, because this pathogen had been present on sea stars in the Northeast Pacific for at least 60 years, researchers hypothesised that current population sizes and/or environmental conditions must be interacting with the densovirus to cause an outbreak (Hewson et al. 2014). After the densovirus failed to transmit SSWD between *P. ochraceus* and *Evasterias troschelii* individuals, however, the connection between densovirus and SSWD was suggested to be location and/or species-specific (Hewson et al. 2018).

Regardless of the pathogenic source of SSWD, multiple lines of evidence suggest there was a positive association between outbreaks of SSWD and elevated ocean temperatures, suggesting that increased physiological stress may decrease the immune response of infected sea stars (Harvell et al. 2019) (Figure 5). Previous wasting disease outbreaks in the NE Pacific occurred during the anomalously warm conditions of the 1982–1983 and 1997–1998 El Niño events (Bates et al. 2009, Menge et al. 2016), and several lab experiments have supported the hypothesis that there is a relationship between temperature and SSWD infection and/or mortality rates. For example, *P. ochraceus* exposed to SSWD survived twice as long when they were kept in seawater at 9°C than when they were kept at 12°C (Kohl et al. 2016). Disease onset was faster, and mortality was more likely for juvenile and adult *P. ochraceus* individuals kept at 19°C than those kept at 12°C (Eisenlord et al. 2016).

During the 2013–2015 outbreak, the decline of *P. helianthoides* populations in shallow water was associated with maximum SST anomalies both within and across regions (Harvell et al. 2019, Figure 6A). Outbreaks in California and Oregon began earlier than those further north in Washington and British Columbia (Hewson et al. 2014), and these outbreaks tended to be more intense (Hamilton et al. 2021). In Washington and British Columbia, the rate of infection among *P. ochraceus* was higher in regions with locally higher water temperatures (e.g. Puget Sound) than cooler outer coast waters (Eisenlord et al. 2016, Kohl et al. 2016). Spatial correlations between temperature and SSWD prevalence were further mirrored by seasonal patterns, with higher rates of *P. ochraceus* infection during the summer than the winter (Kohl et al. 2016).

The extent of this outbreak continues to have lasting effects on coastal ecosystems. *Pycnopodia helianthoides* is now considered Endangered under the IUCN Red List (Gravem et al. 2021) and has become functionally extinct across much of the Northeast Pacific. Estimates suggest that more than 99% of *P. helianthoide*s were lost between Baja California and Cape Flattery, Washington, while approximately 88% were lost from the Salish Sea (Canada and USA), British Columbia and Alaska (Hamilton et al. 2021). The loss of *P. helianthoides* and declines in other key predators such as *P. ochraceus* have driven cascading effects in subtidal and intertidal ecosystems (see sections below) and altered the competitive hierarchy among sea star species themselves. For example, in Burrard Inlet, British Columbia, the dominant sea star predator has shifted from *P. ochraceus* to *E. troschelii* (Kay et al. 2019; Figure 6B) due to inequality in the sensitivities of these species to SSWD.

Beyond SSWD, eelgrass wasting disease (EWD) also increased during the heatwave in some areas and was associated with eelgrass (*Zostera marina*) declines as an indirect impact of the MHW (Figure 5). Although the disease, which is caused by the protist *Labyrinthula zosterae*, was already common in the Northeast Pacific before the heatwave, anomalously warm temperatures

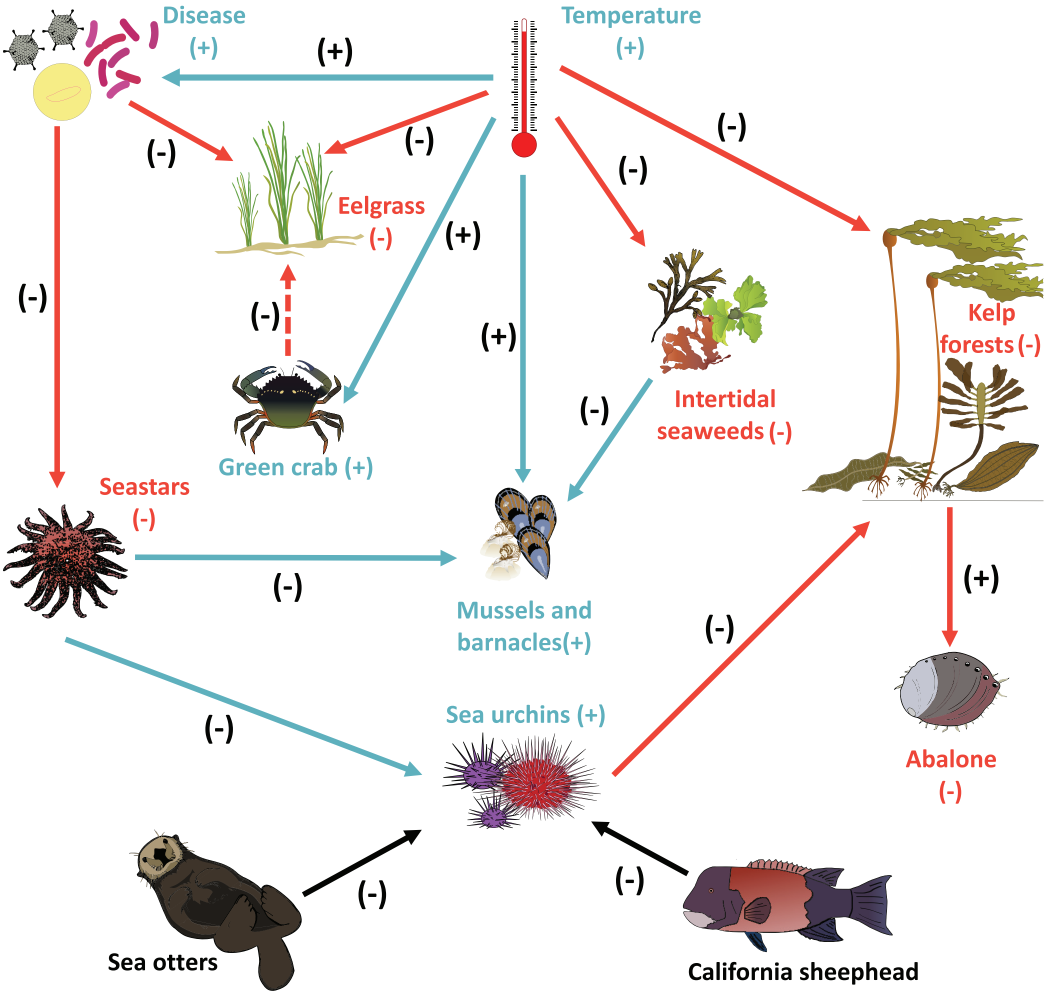

Figure 5 Network diagram describing the impacts of the 2014–2016 marine heatwave on coastal benthic ecosystems. Each entity (taxon or driver) is labelled with coloured text and a (+) or (–) sign indicating whether it increased (blue, +) or decreased (red, –) during the MHW. The black text reflects entities on which the MHW is thought to have had little to know direct effect. Each arrow is labelled with a positive (+) or negative (–) sign that indicates the directionality of the interaction under normal conditions, while the arrow colour indicates whether the entity at the head of each arrow was impacted positively (blue), negatively (red) or neutrally (black) by the interaction during the MHW. The dashed arrow indicates an interaction that is likely but was not directly demonstrated by observational studies during the heatwave. Note that sea otters and green crabs have patchy distributions across the study region and California sheephead are only found in southern portions of the study region.

during the event substantially increased its prevalence and severity at least in the San Juan Islands, Washington, where a 60%–90% infection rate was found in 2017 (Groner et al. 2021). More recent sampling suggests that outbreak conditions have remained high across a broad latitudinal range, from Washington to Alaska, with disease prevalence still exceeding 60% in the subtidal and 50% in the intertidal zone (Graham et al. 2023).

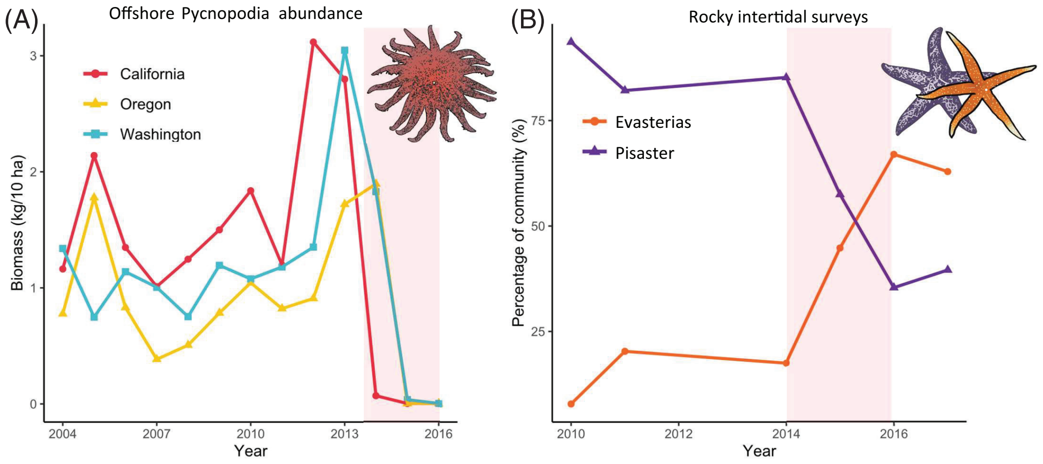

Figure 6 Example impacts of Sea Star Wasting Disease (SSWD). (A) Estimates of biomass for *Pycnopodia helianthoides* from offshore of the continental USA. (Data are from annual offshore trawl surveys and were extracted from Harvell et al. (2019).) (B) Relative abundances of *Evasterias troschelii* and *Pisaster ochraceus* from a site on Mayne Island, British Columbia. (Data were extracted from Kay et al. (2019).) In both panels, the timing of the MHW is shown in pink shading.

Rocky shore ecosystems

Rocky shores experienced a wide variety of effects during the 2014–2016 marine heatwave, including direct physiological effects on many inhabitants of these ecosystems as well as indirect effects, driven mostly by the cascading impacts of SSWD. Many rocky intertidal organisms, especially invertebrates with pelagic life stages such as mollusks and crustaceans, expanded northwards, potentially altering the species pool at locations along much of the coast (e.g. Sanford et al. 2019; see range shift section above). Moreover, several species experienced substantial changes in abundance during the MHW including habitat-forming foundation species like mussels and seaweeds (Suryan et al. 2021, Weitzman et al. 2021, Whalen et al. 2023), whose declines are expected to have cascading effects on the diversity and functioning of rocky shore ecosystems (Harley et al. 2006, Wernberg et al. 2024).

Across study sites in British Columbia and Alaska, cover of the intertidal specialist rockweed (genus *Fucus*) declined (Suryan et al. 2021, Weitzman et al. 2021, Whalen et al. 2023). Losses were extensive at some sites with >75% declines on Calvert Island (Central Coast of British Columbia) and >50% declines in parts of Alaska (Weitzman et al. 2021). Declines were also documented in California and the San Juan Islands of Washington, but *Fucus* abundance remained stable in Oregon and along the outer coast of Washington (Figure 7). Two other closely related fucoid algae, *Silvetia compressa* and *Pelvetiopsis limitata*, also declined considerably in some localities (Figure S3; Graham et al. 2018). For example, *S. compressa* declined at sites throughout the Southern California Bight and Channel Islands, including by as much as 50% at sites on San Clemente Island, California (Graham et al. 2018). Overall, these losses suggest that intertidal fucoid species may be particularly susceptible to marine heatwaves. We hypothesise that this reflects the fact that these intertidal species are found high on the shore and therefore may live close to their thermal limits (Harley 2011, Whalen et al. 2023).

Unlike rockweeds, some intertidal invertebrates, including mussels (*Mytilus* spp.), increased considerably in abundance along some parts of the coast (Figure 7). In both British Columbia and Alaska, mussels and barnacles increased substantially in abundance, presumably in response to

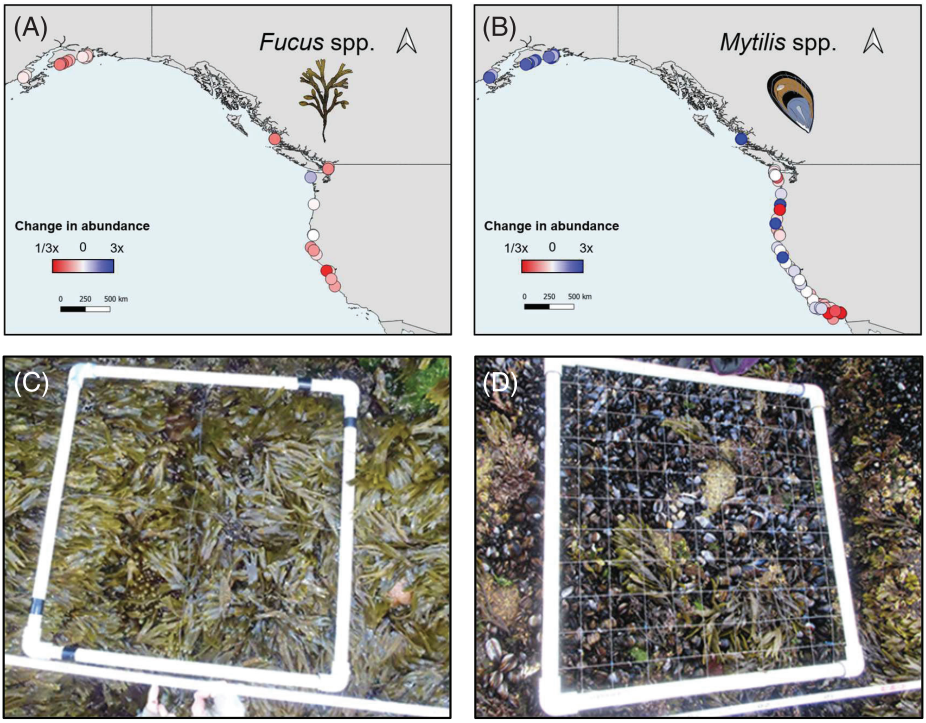

Figure 7 Changes in abundance of two iconic rocky intertidal species. Changes in percentage cover of (A) *Fucus* spp. (mostly *Fucus distichus*) and (B) *Mytilus* spp. (*Mytilus californianus* and *Mytilus trossulus*) expressed as log response ratios comparing pre-heatwave (depending on data availability; see Supplementary Materials) averages and averages during the MHW (2014–2016). (Data from Weitzman et al. (2021), Miner et al. (2021), Suryan et al. (2021), Traiger et al. (2022), Whalen et al. (2023) and Meunier et al. (2024).) (C) Quadrat photo taken on Calvert Island (British Columbia) from a long-term survey in 2012 showing dominance of *Fucus distichus*. (D) Photo of the same quadrat taken in 2019, showing dominance of *Mytilus*. (Photos in C and D are adapted from Whalen et al. 2023.)

decreased competition from seaweeds (Whalen et al. 2023) and changes in recruitment patterns. In contrast, mussel abundance remained stable along much of the coast of continental USA, despite evidence of increases in mussel growth and decreases in mussel recruitment in Oregon during and following the MHW (Traiger et al. 2022, Menge et al. 2023). The exception here was the Southern California Bight, where mussel abundance decreased (Figure 7). Given that these declines occurred towards the warm range-edge of *Mytilus* spp., this likely reflects direct effects of exceeding thermal tolerance thresholds during 2014–2016 MHW. In contrast to the increases in barnacles observed on the shore in British Columbia and Alaska, barnacle recruitment was reduced in Southern and Baja California (Pineda et al. 2018).

Surfgrass (*Phyllospadix* spp.), another important component of rocky shore ecosystems, appeared resistant to the MHW, at least in British Columbia and Oregon. On the Central Coast of British Columbia, surfgrass abundance remained largely unchanged during the heatwave with slight (but insignificant) increases, although it may have moved to lower tidal elevations (Whalen et al. 2023). Further south in British Columbia (Barkley Sound, Vancouver Island), surfgrass also showed little change in distribution or abundance when compared to data from the mid-1990s despite many other species in the area declining over the same period (Starko et al. 2019), implying limited impacts during the 2014–2016 event. Long-term monitoring data from sites in Oregon reveal slight increases in surfgrass abundance during and following the MHW (Meunier et al. 2024). However, surfgrass may have already been increasing in some of these places before the MHW (Meunier et al. 2024).

Beyond impacts on individual taxa, the MHW also altered general patterns of community composition and structure in some places. The MHW had homogenising effects on intertidal communities in the Gulf of Alaska, leading to greater similarity in community composition across sites after compared to before the MHW (Weitzman et al. 2021). In both British Columbia and Alaska, there were increases in bare substrate after the heatwave, suggesting that the overall community-level abundance (i.e. total percentage cover) had decreased during warm temperatures of the MHW. At rocky intertidal sites on the Central Coast of British Columbia, the MHW also altered patterns of zonation along the shore, with several seaweed and invertebrate species shifting down the shore to lower vertical elevations (Whalen et al. 2023). This likely reflects extreme stresses associated with the high intertidal zone during the MHW, which would have decimated some community members at their upper elevation limits. This pattern is somewhat analogous to vertical migration observed on mountain slopes, where species migrate to higher and cooler elevations when exposed to warming air temperatures (Urban 2018).

SSWD had a variety of secondary impacts on rocky shore ecosystems, acting as an ecological release for sessile invertebrates (Figure 5). Declines in *Pisaster ochraceus* led to decreased predation rates on mussels, which are known to dominate the rocky intertidal zone when predators are absent (Menge et al. 2016), likely contributing to some of the patterns described above. Moreover, in Central California following the onset of SSWD, the abundance of *P. ochraceus* was correlated with the diversity of tidepools, and infected stars were associated with reduced tidepool diversity, implying that infected stars are less able to serve as effective keystone predators (Wilkes 2019). Consequently, in addition to the impacts of the MHW itself, SSWD likely also contributed to community-level shifts that occurred during this period.

Seagrass meadows

Although only a handful of studies assessed the impacts of the 2014–2016 MHW on eelgrass meadows (*Zostera marina*) and their associated communities, unlike for surfgrass, all found evidence of direct negative impacts (Figure 5). Eelgrass meadows in the San Juan Islands, Washington, declined in shoot density by 60% during the event and had not recovered by 2017 (Groner et al. 2021). Eelgrass (and associated macroalgae) inhabiting the estuaries of the Washington and Oregon coast also declined in density and biomass compared to previous sampling, with little recovery as of 2019 (Magel et al. 2022, Marin Jarrin et al. 2022). Finally, there is some evidence that eelgrass meadows in southern California experienced reductions in leaf area and shoot density between 2013 and 2014 (Ha & Williams 2018), although given the lack of historic data, it is difficult to separate the effect of the marine heatwave from interannual variability.

The direct impacts of MHWs on eelgrass meadows seem to be mediated by a variety of environmental and physical factors. For example, eelgrass meadows in shallower estuaries were found to be more negatively impacted than those in deeper estuaries on the Washington and Oregon coast, presumably due to differences in exposure to elevated ocean temperatures (Magel et al. 2022). By contrast, *Z. marina* growing in deeper estuaries experienced neutral impacts and even some positive increases in eelgrass biomass in one estuary (Magel et al. 2022), highlighting potential refugia from future MHW events. Impacts also differed along estuarine gradients within Coos Bay, Oregon, with stronger *Z. marina* declines occurring further up-estuary and away from oceanic influences, where waters tend to be shallower and warmer for more extended periods of time, especially during 2014–2016 (Marin Jarrin et al. 2022).

The MHW not only impacted eelgrass habitats but also their associated communities. Epiphyte loads peaked and epifaunal invertebrates declined during the onset of the MHW in eelgrass meadows within Bodega Bay, California (Ha & Williams 2018). Invasive green crabs (*Carcinus maenas*), which are known to cause disturbance in eelgrass meadows (e.g. Matheson et al. 2016), were documented in the Salish Sea for the first time, establishing in the Strait of Juan de Fuca and the Strait of Georgia (Yamada et al. 2021) (Figure 5). Cool waters at the entrance to the Juan de Fuca Strait likely served as a thermal barrier to colonisation prior to the heatwave, which previously prevented larvae from entering the Salish Sea during winter storm events (Behrens Yamada et al. 2022). Fish use of eelgrass habitats also changed during the MHW. On the southwestern coast of Vancouver Island, fish assemblages in eelgrass meadows showed detectable differences in their relative abundances (i.e. catch per unit effort) in 2015 and 2016 compared to other years in a 17-year time series spanning 2005–2021 (Robinson et al. 2022). Out of 18 fish species commonly caught in eelgrass, seven (silverspotted sculpin: *Blepsias cirrhosis*; padded sculpin: *Artedius fenestralis*; threespine stickleback: *Gasterosteus aculeatus*; crescent gunnel: *Pholis laeta*; penpoint gunnel: *Apodichthys flavidus*; kelp clingfish: *Rimicola muscarum* and kelp greenling: *Hexagrammos decagrammus*) showed reduced abundance (measured as catch per unit effort: CPUE) during the MHW, while two young-of-the-year rockfish species (*Sebastes melanops* and *Sebastes caurinus*) increased in abundance. Despite these compositional changes, total eelgrass fish biomass was not significantly different during the MHW compared to other years (Robinson et al. 2022). While there were multiple processes that led to eelgrass declines (Figure 5), it remains unclear how widespread and persistent these changes were given the small number of focused studies on a small percentage of the coast.

Kelp forests

The MHW had spatially variable but substantial effects on kelp forests and seaweed communities throughout the Northeast Pacific (Figure 8). Losses of kelp forests (i.e. habitats formed by the Laminariales) occurred both as a direct consequence of increased temperature stress (Cavanaugh et al. 2019, Starko et al. 2022) and as an indirect consequence of urchin overgrazing stemming from the loss of the predatory sea star, *Pycnopodia helianthoides*, which triggered trophic cascades favouring sea urchins (Schultz et al. 2016, Burt et al. 2018, Rogers-Bennett & Catton 2019, Starko et al. 2022) (Figure 5). Examples of population booms and overgrazing have been documented for all three rocky shore sea urchin species (purple urchin: *Strongylocentrotus purpuratus*; red urchin: *Mesocentrotus fransciscanus* and green urchin: *Strongylocentrotus droebachiensis*) (Schultz et al. 2016, Rogers-Bennett & Catton 2019, Starko et al. 2022, Tolimieri et al. 2023). Direct and indirect MHW impacts may have compounded one another (Rogers-Bennett & Catton 2019), with decreased growth from heat stress making kelp even more sensitive to overgrazing, and potentially also had variable impacts on kelp forests at different depths (Starko et al. 2022). Depending on locality, these impacts were either temporary (e.g. Cavanaugh et al. 2019, Tolimieri et al. 2023) or persistent following the MHW (e.g. McPherson et al. 2021, Starko et al. 2022, 2024a).

While direct and indirect impacts have been documented across many kelp species, the two floating kelp species, giant kelp (*Macrocystis pyrifera/tenufolia;* see Lindstrom (2023) for taxonomic debate) and bull kelp (*Nereocystis luetkeana*), are best studied. Giant kelp forests experienced climate-driven declines near their southern range limit, in Baja California and Southern California (Arafeh-Dalmau et al. 2019, Cavanaugh et al. 2019), but showed relative stability further north in California, and largely recovered in the 2 years after the MHW while remaining diminished near their southern limits (Arafeh-Dalmau et al. 2019, Cavanaugh et al. 2019). In the Channel Islands, giant kelp forests were more resilient within marine protected areas (MPA) because California sheephead (*Semicossyphus pulcher*) fished in unprotected areas kept urchin populations under control and prevented the increase in urchin barrens observed in other areas (Eisaguirre et al. 2020), highlighting the role of trophic redundancy (Figure 5). Bull kelp forests also declined towards the southern edge of their distribution in Northern and Central California (Rogers-Bennett & Catton 2019, Hollarsmith

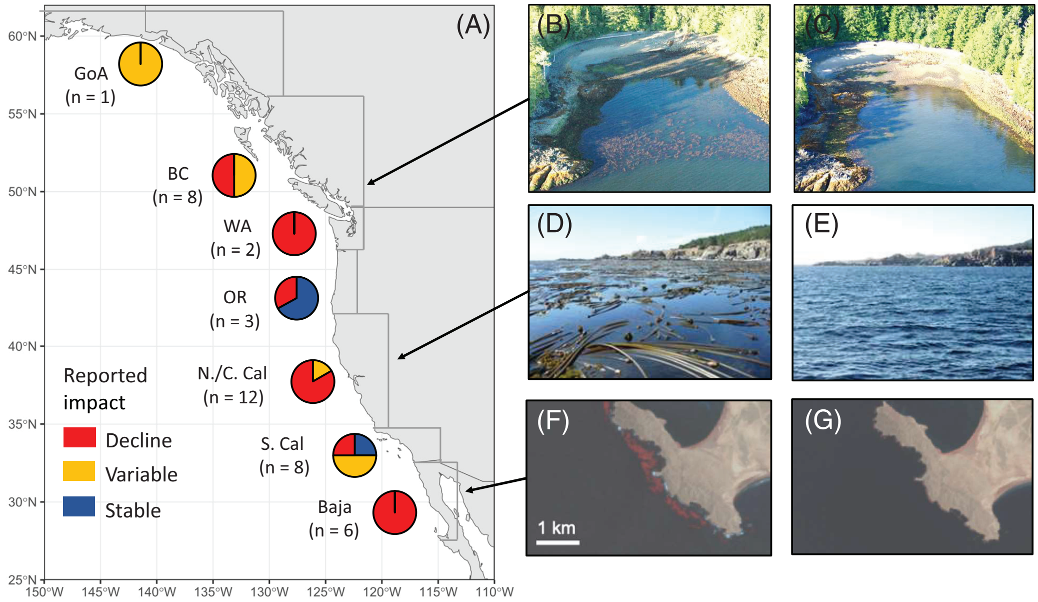

Figure 8 Variable impacts of the 2014–2016 marine heatwave on kelp forest ecosystems. (A) An overview of reported impact from studies ($n = 31$) on kelp forest abundance within each region (Baja, Southern California, Northern and Central California, Oregon (OR), Washington (WA), British Columbia (BC) and Gulf of Alaska (GoA)). Studies were deemed to report variable impacts if there were clear spatial patterns with areas of stability and areas of clear decline. (B, C) The loss of a fringing giant forest in Barkley Sound, British Columbia (Credit: ShoreZone Initiative (B) and Samuel Starko (C)). (D, E) The loss of a bull kelp forest in Northern California (adapted from Rogers-Bennett & Catton 2019; Credit: Cynthia Catton). (F, G) Satellite images showing canopy kelp aerial coverage (in red) at a site in Bahia Tortugas before (June 2009) and after (June 2016) the marine heatwave (adapted from Bell et al. 2023). Declines include both temporary reductions in kelp during the MHW and longer-term declines that persisted in years following the event.

et al. 2020, Finger et al. 2021, McPherson et al. 2021), but were stable further north off the coast of Oregon (Hamilton et al. 2019) and only experienced one unusually low abundance year along the outer coast of Washington (Berry et al. 2019). In Northern and Central California, urchin overgrazing played an important role in driving these losses, and, unlike Southern Californian giant kelp forests, which largely showed the ability to recover following the heatwave, bull kelp forests in Central California remained devastated several years after the event, having largely transitioned to urchin barren ecosystems (McPherson et al. 2021). This persistent loss of bull kelp forests has had cascading effects on the broader nearshore community, including drastic impacts on the commercially important red abalone (*Haliotis rufescens*) population and reduced body condition in years following the MHW (Rogers-Bennett et al. 2021, Rogers-Bennett & Catton 2022).

Perhaps unexpectedly, floating kelp forests in the inner waters of Washington and British Columbia, at the range centre of both canopy-forming species, also experienced climate-driven kelp forest losses or declines with direct links to the 2014–2016 MHW (Figure 8; Starko et al. 2019, Berry et al. 2021). Kelp in these regions may be more sensitive than outer coast populations due to differences in the environmental conditions they experience (Starko et al. 2019, Berry et al. 2021) and/or genetic differentiation of populations with different environmental tolerances (Hollarsmith et al. 2020). For example, floating kelp forests in Barkley Sound (British Columbia), the Strait of Georgia (British Columbia) and Puget Sound (WA) all experienced declines during the MHW (Berry et al. 2019, Starko et al. 2022, 2024a; Figure 8). These inshore areas experience high seawater residence times that produce local and/or regional temperature gradients, causing them to reach temperatures that exceed known thresholds for kelp during warm summers (Starko et al. 2022, 2024a). During the MHW, these warm areas experienced substantial losses of floating kelp (even in the absence of urchins; Starko et al. 2022), similar to those observed near the southern range limits of both species (Berry et al. 2019, Starko et al. 2022, 2024a). Importantly, cooler areas nearby, such as the outer coast of Washington or Vancouver Island or regions of local mixing (e.g. channels with currents), tended to remain more stable during and following the MHW (Starko et al. 2022, 2024a, Tolimieri et al. 2023).

Declines in floating and understory kelp were also observed on the Central Coast of British Columbia but likely in response to urchin overgrazing without a clear link to temperature (Burt et al. 2018, Starko et al. 2024a). Similar to southern regions with California sheephead, there is some evidence that parts of the coast with sea otters (*Enhydra lutris*) appeared to maintain larger kelp forests, likely through trophic redundancy (Burt et al. 2018, Starko et al. 2024a) (Figure 5). Kelp forest change in the Gulf of Alaska (based on a dataset of multiple kelp species) was also highly variable with some sites experiencing declines and others experiencing increases or no change (Beas-Luna et al. 2020). Overall, mid-range impacts on canopy-forming kelp forests were highly variable with local areas of sensitivity and tolerance to the 2014–2016 MHW. Moreover, in cases where kelp forests were impacted, recovery was highly variable from immediate, full recovery (e.g. Tolimieri et al. 2023, Starko et al. 2024a) to virtually no recovery at all (e.g. McPherson et al. 2021, Starko et al. 2022).

Intertidal and understory kelp species also experienced impacts throughout the Northeast Pacific linked to both warming and cascading effects of SSWD (Schultz et al. 2016, Burt et al. 2018). Urchin abundances increased across the coast of British Columbia following the loss of *Pycnopodia*, driving declines in understory subtidal kelp species in the Strait of Georgia and on the Central Coast of British Columbia (Schultz et al. 2016, Burt et al. 2018). Moreover, negative impacts on intertidal kelp abundance and growth rates were observed during the MHW along the coast of Oregon (Spiecker & Menge 2022, Meunier et al. 2024), and warming caused declines in intertidal kelp cover in Barkley Sound, British Columbia and on the Central Coast of British Columbia (Starko et al. 2019, 2022, Whalen et al. 2023). However, along the outer coast of Vancouver Island, populations of *Postelsia palmaeformis* (a high intertidal, high wave exposure kelp species) remained stable between 2007 and 2021, suggesting minimal impacts of the MHW on this species (Csordas et al. 2023). Thus, the spatial extent and species-specific variation in these impacts remain poorly understood.

Impacts on offshore pelagic and benthic ecosystems

Microalgae production and composition

The MHW caused large anomalies in oceanographic conditions across the Northeast Pacific. High temperatures strengthened stratification in coastal, shelf and oceanic zones (McClatchie 2016, Peña et al. 2019, Delgadillo-Hinojosa et al. 2020, Long et al. 2021). This thermal stratification significantly reduced upwelling and vertical mixing, reducing the supply of nutrients to surface waters (Leising et al. 2014, McClatchie 2016, Peña et al. 2019, Delgadillo-Hinojosa et al. 2020) (Figure 9A). For example, within a transect spanning from the southern British Columbia shelf to the central Northeast Pacific Ocean, when compared to the last three decades, February 2015 surface nutrients were the lowest observed (on average less than 50% of normal values), and summer nitrate depletion extended further offshore than previously recorded (Peña et al. 2019). Further south, along the California Current System, upwelling seasons between 2014 and 2015 were between 50%–72% shorter and 36%–46% less intensive when compared to 1967–2007, with nutrient supply to the euphotic zone declining by 50% from 2013 to 2014–2015 (Closset et al. 2021); and in parts of Baja

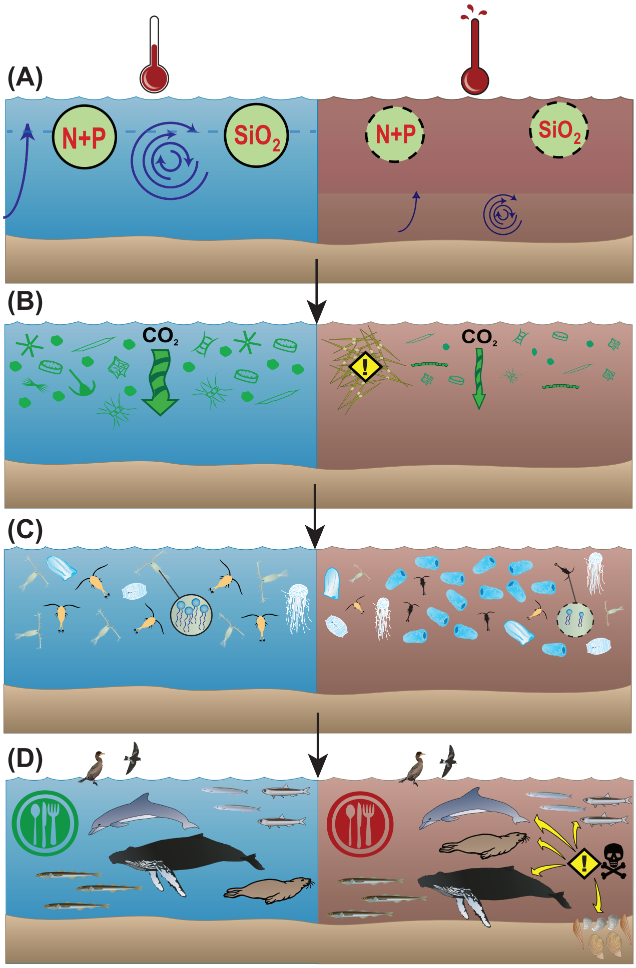

Figure 9 Cascading effects of the marine heatwave through pelagic ecosystems. High temperatures (right) compared to normal conditions (left). Panels depict the marine heatwave causing (A) strong and deepening stratification, reduced upwelling and mixing and reduced nutrients in surface waters. This led to (B) reduced primary production (indicated by the CO_2 and reduced size of green down arrow symbols) and chlorophyll-a concentrations, phytoplankton populations dominated by those with smaller particle sizes and toxic algal blooms (toxin indicated by yellow diamond and exclamation point). These changes caused zooplankton assemblages (C) to become dominated by gelatinous taxa (with large blooms of pyrosomes) and shift towards smaller lipid-poor copepod species. Overall, this led to (D) poor feeding conditions for a range of vertebrate species, and harmful effects of the toxic blooms on many large vertebrates and commercial fish and shellfish.

California, nitrate concentrations in 2014–2015 were between 40% and 81% lower when compared to the 2008–2015 mean (Delgadillo-Hinojosa et al. 2020).

Where these oceanographic changes occurred, phytoplankton productivity and community composition were substantially altered. Significant reductions in primary production, chlorophyll-a concentration and phytoplankton biomass were recorded across coastal zones of the California Current System (CCS) and Baja California (Peterson et al. 2017, Kahru et al. 2018, Delgadillo-Hinojosa et al. 2020) and also in shelf and oceanic zones of the CCS and British Columbia (Whitney 2015, Morrow et al. 2018, Yang et al. 2018; Figure 9B). This included record negative chlorophyll-a anomalies in the CCS, with values in 2014–2016 lower than the whole period of satellite observations between 1997 and 2013 (Peterson et al. 2017, Kahru et al. 2018). Moreover, phytoplankton biomass and primary production values in 2016 were the lowest captured across 13 years of data in the CCS (Gómez-Ocampo et al. 2018), with chlorophyll-specific growth rates around 2–3 times lower in 2014 and 2016 when compared to cooler El Niño-neutral years (2006–2008), even under similar light conditions (Morrow et al. 2018). Further offshore, in the North Pacific Transition Zone of British Columbia (i.e. where the subtropical and subarctic gyres meet), chlorophyll levels in 2014 hit their lowest levels since satellite measurements began in 1997 (Whitney 2015). Across the study area, phytoplankton communities also generally shifted towards dominance of smaller and warm tolerant species, such as single celled diatoms, flagellates and cyanobacteria, often accompanied by a net reduction in diatom abundance and/or biomass (Peterson et al. 2017, Yang et al. 2018, Peña et al. 2019, Delgadillo-Hinojosa et al. 2020, Kenitz et al. 2020, Arteaga & Rousseaux 2023, Strom 2023).

Despite widespread oceanographic changes driven by the MHW, the effects were far from spatially or temporally uniform. In the Gulf of Alaska, although both large positive temperature and negative nitrate anomalies were recorded during 2014–2015 (Arteaga & Rousseaux 2023), chlorophyll anomalies were generally positive, reaching their highest levels of around 30% above long-term (2002–2021) climatological means (Wyatt et al. 2022, Arteaga & Rousseaux 2023). This pattern was attributed to the predominance of generally iron-limited and large-sized phytoplankton species in this region being less affected by the nutrient-limiting MHW conditions, and to small phytoplankton (particularly dinoflagellates) greatly increasing in density (Batten et al. 2022, Arteaga & Rousseaux 2023). Further, chlorophyll concentrations around coastal and shelf regions of Vancouver Island, British Columbia, were generally within the range of observed values from previous years, potentially due to sustained land-based nutrient supplies (Johannessen et al. 2019). Moreover, further offshore in high-nutrient-low-chlorophyll (HNLC) oceanic zones where iron and light limit productivity, phytoplankton productivity increased during the heatwave (Peña et al. 2019, Long et al. 2021, Arteaga & Rousseaux 2023). Large spatial variation was also recorded across the CCS. In transitional and southern zones, significant negative sustained chlorophyll anomalies were recorded; however, within central and northern zones, where upwelling remained relatively strong, there were fewer impacts and, in some cases, increases in phytoplankton biomass and production (McClatchie 2016, De la Cruz-Orozco et al. 2017, Gómez-Ocampo et al. 2018). There were also temporal fluctuations in the heatwave effects on phytoplankton communities. Seasonal fluctuations were observed in the CCS with both positive and negative chlorophyll anomalies at different times over the 3 years (McClatchie 2016, Peterson et al. 2017, Gómez-Ocampo et al. 2018). Within the Canadian Pacific, the effects were largely constrained to 2014 and 2015, with nutrient conditions and phytoplankton largely returning to expected distributions by late 2015 and into 2016 (Yang et al. 2018, Peña et al. 2019).

Harmful algal blooms

In spring 2015, an unprecedented toxic bloom of the diatom *Pseudo-nitzschia* spp. (predominantly *Pseudo-nitzschia australis*) occurred across much of the coast of the study area (McCabe et al. 2016, Ryan et al. 2017, Trainer et al. 2020; Figure 9B). Although blooms of this species have occurred regularly over recent decades in different parts of the region (see references within McCabe et al. 2016) – for example, in coastal waters of Oregon, blooms occurred every year from ~2000 to 2016 (Peterson et al. 2017) – they do not always cause toxic events. The toxic bloom in 2015 was notable in its extent, ranging from Santa Barbara, California in the south, across the western USA coast, to British Columbia (McCabe et al. 2016, Trainer et al. 2020) and into parts of the Gulf of Alaska (Leising et al. 2015, McClatchie 2016). The bloom was also significant due to its duration – in some cases lasting over 6 months (Leising et al. 2015, Du et al. 2016), its abundance – comprising up to 90% of all diatoms off the Oregon coast (Du et al. 2016) and its toxicity – for example, in Monterey Bay, toxigenic cell densities were up to $2.53 \times 10^6 \mathrm{L}^{-1}$ and domoic acid (DA) concentrations as high as 31,700 ng L^{-1}, an order of magnitude higher than average conditions over the previous 8 years (Figure 10; Ryan et al. 2017).

Pseudo-nitzschia australis is known to be resistant to high temperatures, it is also particularly efficient at nutrient acquisition under deplete conditions. This is because it can utilise a variety of nitrogen sources and complex trace metals, and has very high maximal rates of nitrate uptake when compared to other commonly found phytoplankton in the region (Du et al. 2016, McCabe et al. 2016, Trainer et al. 2020). The initiating conditions for the bloom were thought to occur in the fall of 2014 (McClatchie 2016), where the warm, highly stratified, nutrient deplete oceanographic conditions (described above) enabled *P. australis* to outcompete other diatom species and survive further north than its typical range (Free et al. 2023). When these conditions were proceeded by the onset of the spring seasonal upwelling starting in February 2015, and several late spring storms, the new injection of nutrients allowed the bloom to quickly develop and to be maintained through the spring and into the summer of 2015, while the storms facilitated transport of the bloom from offshore waters to the coast (Du et al. 2016, McCabe et al. 2016, McClatchie 2016, Ryan et al. 2017). The extreme toxicity of the bloom was attributed to widespread silicate/silicic acid limitation stress (i.e. anomalously low silicate:nitrate ratios) stemming from the MHW (Du et al. 2016, Ryan et al. 2017, Trainer et al. 2020). In some regions, this was driven by the presence of silicate-deplete upwelling waters (Ryan et al. 2017, Trainer et al. 2020), while in other regions, it was thought that the sustained high temperatures through the upwelling season during the heatwave led to accelerated growth rates of the bloom and resulted in silicic acid limitation (Du et al. 2016, Trainer et al. 2020).

The harmful effects of the bloom were widespread, and it represented the largest geographic extent of detection of the biotoxin DA in marine mammals ever recorded globally (McCabe et al. 2016). High levels of DA were recorded in stranded whales, dolphins, porpoises, seals and sea lions across the U.S. coast from southern California to northern Washington between March and

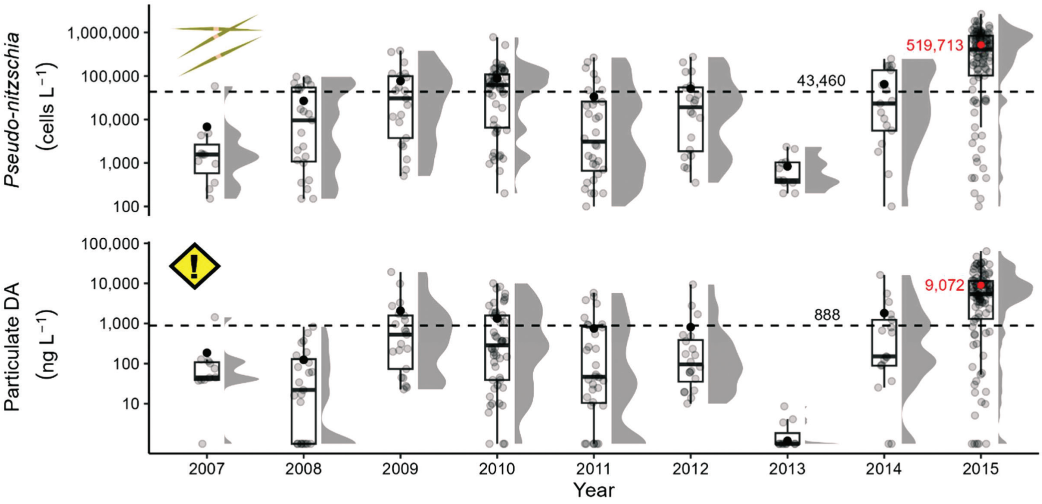

Figure 10 Density of *Pseudo-nitzschia* cells (top panel) and concentration of particulate domoic acid (DA) (bottom panel) from repeated surveys of the water column within Monterey Bay, California in 2007–2015. Grey points show all replicates across the year (shown jittered at the x-axis within each year), with the mean value shown in black (except 2015 which is shown in red). The distribution of values within each year is indicated by a box plot (overlayed) and adjacent density plot. Dashed lines with accompanying values in black indicate the mean across 2007–2014. The mean value from 2015 is shown in red. Note the logarithmic scale of the y-axis in both panels. (Data provided by Dr. John Ryan. For more information on sampling design and methodology, see Ryan et al. (2017).)

November 2015 (Figure 9D); this includes 229 documented cases of stranded sealions with suspected DA toxicosis in Central California alone (McCabe et al. 2016). In a survey of planktivorous fish from Northern British Columbia to Baja California in June–September 2015, all individuals analysed contained measurable DA with the highest concentration measured in Northern anchovy (*Engraulis mordax*) viscera from Baja California at 3239 ppm (Trainer et al. 2020) more than 150× the safe concentrations for human consumption (<20 ppm) (Kumar et al. 2009). The toxic event also had significant socioeconomic consequences, as it led to widespread closures of bivalve, crustacean and anchovy fisheries across coastal waters of the western USA and Vancouver Island, British Columbia for up to a year (McCabe et al. 2016). In 2015, the related closure of the California Dungeness crab fishery, which represents over a quarter of the state's annual fisheries revenue, led to a loss of >US$25 million and fishers shifting to alternate fisheries to try to offset socioeconomic losses (Fisher et al. 2021). Recreational fisheries were also affected, including the razor clam (*Siliqua patula*) fishery in Oregon and Washington (Ekstrom et al. 2020, Free et al. 2023). Overall, it is estimated that closures associated with recreational fisheries caused an estimated loss of US $22 million in tourism.

Toxic algal blooms were not restricted to that of *P. australis*. Blooms of dinoflagellates from the genus *Alexandrium* (often dominated by Alexandrium catenella) can produce significant concentrations of paralytic shellfish saxitoxins (Vandersea et al. 2018). In the Gulf of Alaska, toxic blooms occur seasonally within bays and fjords. Monitoring data from 2012 to 2017 in Cook Inlet found that bloom development was positively correlated with water temperature, while temperature anomalies greater than 1–2°C were correlated with increased risk of paralytic shellfish poisoning across the Gulf from 1998 to 2017 (Vandersea et al. 2018). During the heatwave, saxitoxin was also commonly recorded within seabirds (within both die-off and healthy individuals), forage fish and invertebrates, however its contribution towards mortality events was uncertain (Van Hemert et al. 2020).

Zooplankton composition

While the effect of the MHW on total zooplankton biomass, abundance and displacement volume was spatially and temporally highly heterogeneous (McClatchie 2016, Suryan et al. 2021, La Rosa-Izquierdo et al. 2022, Winans et al. 2023), changes to zooplankton community structure were widespread, with prolonged shifts documented across phyla and in almost every region of the Northeast Pacific (Figure 9C). Copepod assemblages shifted significantly, from communities dominated by cold-temperate species to ones dominated by subtropical-tropical species. Across most of the coast, copepod assemblages changed from larger lipid-rich northern species to small lipid-poor southern species, with the effects remaining until at least 2017 (McClatchie 2016, Peterson et al. 2017, Ashlock et al. 2021, Suryan et al. 2021) (Figure 11A), and returning to normal conditions by 2022 (Ostle & Batten 2023). Within the CCS, this included the lowest biomass of northern lipid-rich cold-water copepods observed over a 20+ year time series (Wells et al. 2017) (Figure 11A), and the arrival of at least 17 subtropical/tropical species that were never previously recorded or rarely observed, thus leading to the highest observed copepod species richness recorded over these two decades (Leising et al. 2015, McClatchie 2016, Peterson et al. 2017). Across British Columbia and the Gulf of Alaska, there was a significant reduction and, in some cases, near absence of the normally dominant boreal to subarctic copepod species, including *Neocalanus plumchrus*, *Pseudocalanus* spp., *Acartia longiremis* and *Calanus marshallae,* with replacement by warm water species including *Calanus pacificus*, *Oithona* spp. and *Pleuromamma* spp. (Galbraith & Young 2016, Ashlock et al. 2021), leading to an increase in community thermal index (CTI) (Batten et al. 2022). In the subtropical Baja California region, there were also clear signs of copepod community tropicalisation with 87% of species recorded during 2014 considered tropical and 95% in 2015 (Beltrán-Castro et al. 2020), with tropical and equatorial species dominating total copepod abundance (La Rosa-Izquierdo et al. 2022). While these changes were widespread, they were not

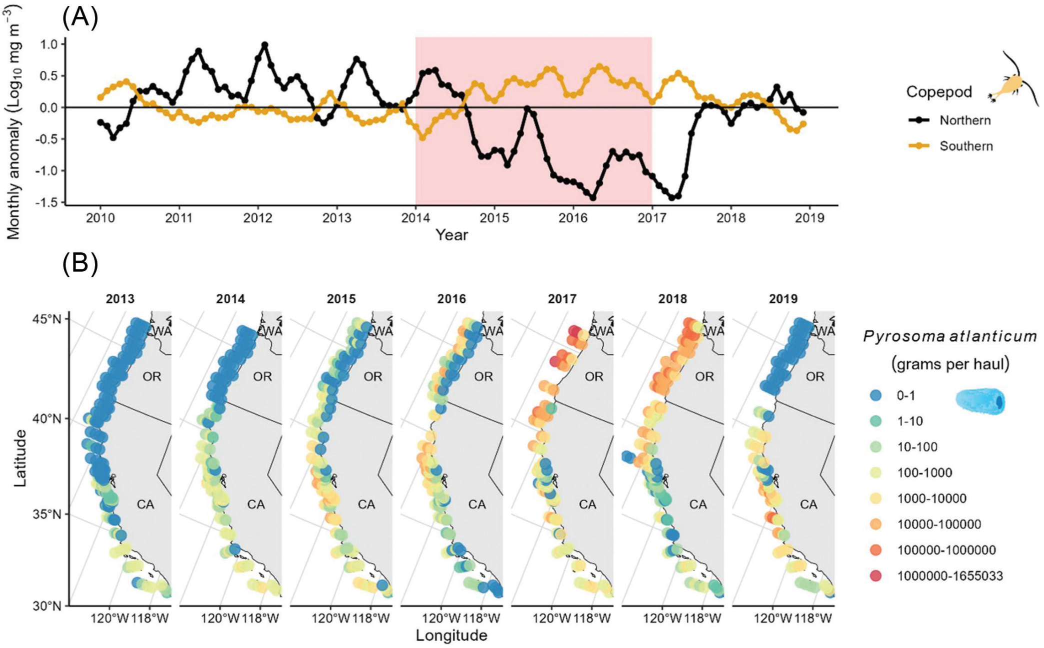

Figure 11 Notable changes in the zooplankton community of the California Current System (CCS) during the MHW. (A) Monthly anomalies in copepod biomass of Northern (lipid-rich) and Southern (lipid-poor) populations from the Newport Hydrographic Line, Oregon, from 2010 to 2019. The main period of the MHW is highlighted in pink. Data extracted from Figure 16 in Thompson (2019). For more information on sampling design and methodology, see original publication. (B) Biomass of *Pyrosoma atlanticum* during May–June from repeated midwater trawl surveys in 2013–2019 across the CCS. The colours indicate the grams per haul on a log scale ranging from low biomass (in blue), to high biomass (in red). Some stations contain replicate trawls within a single year; where this occurred, the mean value across trawls is shown. (Data provided by Dr. Rebecca Miller. For more information on sampling design and methodology, see Miller et al. (2019).)

uniform, with lesser effects recorded at the local level in some more isolated sounds and inlets, potentially due to less influence from oceanic advection (Batten et al. 2022, McKinstry et al. 2022, Winans et al. 2023).

One impact of the MHW, which occurred across almost the entire study area, was a significant increase, and often dominance, of gelatinous zooplankton, including pelagic tunicates (e.g. salps, doliolids, pyrosomes and larvaceans), ctenophores, Medusozoa (i.e. Hydrozoa and Scyphozoa) and gymnosomes, which lasted from late 2014 to as late as 2019 in some regions (Galbraith et al. 2016, McClatchie 2016, Peterson et al. 2017, Thompson 2018; Figures 9C and 11A). The most notable change was the dramatic increase in the biomass of the normally offshore and southern pyrosome (*Pyrosoma atlanticum*) across the Gulf of Alaska, British Columbia and the CCS (Figure 11B); with its presence a new record for the northern Gulf of Alaska (Brodeur et al. 2018, 2019, Galbraith & Young 2017, Miller et al. 2019, Sutherland et al. 2018). Highest abundances and biomass were recorded in 2017 with up to 3 colonies per m^3 and over 200,000 kg km^{-3} in some areas (Brodeur et al. 2018). There were also notable increases in doliolids, particularly in northern regions spanning from the northern CCS to the Gulf of Alaska (Galbraith & Young 2016, Peterson et al. 2017, Pinchuk et al. 2021, Venello et al. 2021; Figure 9C), with densities up to 3847 individuals per m^3 recorded in August 2016 in the Gulf of Alaska (Pinchuk et al. 2021). Other pelagic tunicates with anomalously high biomass during the heatwave included the salps *Thetys vagina* and *Thalia democratica*, which were previously rarely recorded in northern regions, with comparative decreases in normal resident species (Galbraith & Young 2017, Lüskow et al. 2022, Miller et al. 2019). These northern areas also experienced increases in southern Medusozoa species and concomitant decreases in those with northern affinities (Brodeur et al. 2019, Galbraith & Young 2017, Jones et al. 2021, Morgan et al. 2019). One of the only areas where these changes did not occur was Baja California where a low abundance of gelatinous zooplankton was recorded (McClatchie 2016, Wells et al. 2017).

Conversely, the MHW negatively impacted euphausiids (krill). Total euphausiid abundance, biomass and individual size were significantly reduced in Baja California and across the CCS, although this effect was largely restricted to these southern regions (Lavaniegos et al. 2019, McClatchie 2016, Peterson et al. 2017, Sakuma et al. 2016). Euphausiid biomass in parts of the Northern CCS was the lowest recorded in 20+ years (McClatchie 2016, Peterson et al. 2017, Wells et al. 2017) and the two dominant krill species in Baja California were reduced by ~95% relative to 1999–2010 levels (Lavaniegos et al. 2019). Species with substantial declines again had more cold-temperate affinities, including *Thysanoessa spinifera*, *Euphausia pacifica* and *Nematoscelis difficilis*, with concomitant increases, and often dominance, of subtropical species including *Nyctiphanes simplex*, *Euphausia recurve* and *Euphausia eximia* (McClatchie 2016, Peterson et al. 2017, Lilly & Ohman 2018, Cimino et al. 2020). In parts of the northern CCS (e.g. Oregon), there were periods during the MHW where adults of the cold-temperate species were largely absent (Peterson et al. 2017), although there were reports of exceptionally high abundances and/or biomass of juvenile furcilia stages in coastal waters of Washington and northern Oregon (Morgan et al. 2019), likely indicating poor survivorship, migration or shifts in phenology. Significant declines in krill biomass were also recorded during the heatwave in the Gulf of Alaska (Arimitsu et al. 2021), including an abrupt community shift, with the loss of previously dominant cold-water species T. inermis and T. longipes by 2015 and an increase in warmer water species *T. spinifera* and *E. pacifica* (Arimitsu et al. 2021). In contrast, euphausiid biomass and abundance in British Columbia increased somewhat during the MHW, including for cold-temperate species (Evans et al. 2023, Galbraith et al. 2015, 2016, Phillips et al. 2022, Winans et al. 2023).

Other zooplanktonic assemblages that underwent increases in abundance or even range shifted into new ecosystems included foraminifera in the northern CCS (Lane et al. 2023), heteropods in Baja California (Aceves-Medina et al. 2020, Moreno-Alcántara et al. 2020) and thecosomatous pteropods in British Columbia (Galbraith et al. 2015, 2016, Galbraith & Young 2017). There was also a clear shift in the micronekton community across the CCS with juvenile fish and squid that are normally associated with southern regions showing anomalously high abundance across the CCS, and the arrival of subtropical and tropical juvenile fish species in the south (Leising et al. 2014, 2015, Sakuma et al. 2016, Wells et al. 2017, Brodeur et al. 2019).

Other offshore invertebrates

The marine heatwave also had noteworthy impacts on cephalopods and crustaceans. Warm waters led to a northward movement of the California market squid (*Doryteuthis opalescens*), which have long been an important fishery in both Mexico and California (Van Noord & Dorval 2017, Chasco et al. 2022, Free et al. 2023). Because of the northward shift in *D. opalescens*, a booming novel recreational fishery has developed in Oregon since the start of the MHW and persisted until at least 2020 (Free et al. 2023). Several crustaceans also experienced range shifts, unusual occurrences or changes in density associated with the MHW (Sanford et al. 2019). For example, pelagic red crab (*Grimothea planipes*), which is usually restricted to Baja, also shifted north and became abundant along the coasts of California and Oregon (Cimino et al. 2021; Figure 2), becoming a major part of the diet of bluefin tuna in this region (Free et al. 2023). In the northern CCS around Washington and Oregon, the highest biomass of zoea of the Pacific sand crab (*Emerita analoga*) was recorded from a 20-year time series (Morgan et al. 2019); while even further north, in the southern Salish Sea, several crustacea including amphipods, crab larvae, shrimp and mysids showed positive biomass anomalies (Winans et al. 2023).

According to Free et al. (2023), shrimp and prawns were the only fishery to experience near-universal increases in value during the MHW. While increases in global market prices of shrimp likely contribute to this, gross landing data from California, Washington, British Columbia and Alaska also were higher during and following the MHW than they were before (Figure 12A). Although the mechanistic link between marine heatwave dynamics and shrimp abundance remains unclear, Free et al. (2023) suggest that this must reflect an unusually high recruitment cohort in 2013. We further speculate that changes in environmental conditions or food web dynamics likely also facilitated higher growth and/or survival in this cohort, driving overall increases in population size of shrimp and prawns.

Demersal fishes

Due to spatial heterogeneity in effects of the heatwave on bottom water temperatures, as well as links between pelagic and benthic processes, the impact on groundfish populations was highly variable (Workman et al. 2017, Chalifour et al. 2019, Li et al. 2019, Rogers et al. 2021). This is clear in an Atlantic-Pacific-wide meta-analysis of marine heatwave impacts on demersal fishes covering 25 years of surveys (Fredston et al. 2023). Although they found notable impacts of the 2014–2016 heatwave on demersal fishes, tropicalisation of communities was not consistent across the region, and mean changes in biomass were within the bounds of natural variability (Fredston et al. 2023). One notable impact of the MHW was on Pacific cod (*Gadus macrocephalus*) populations in the Gulf of Alaska (Suryan et al. 2021, Free et al. 2023), where groundfish surveys revealed a 71% decline in abundance (Barbeaux et al. 2020) coincident with some of the worst spawning conditions estimated over a 26-year time period (1994–2019); the probability of a successful hatch in 2015, 2016 and 2019 being 57%–59% that of average non-heatwave years (Laurel & Rogers 2020). This was largely attributed to the higher energetic demands associated with living in warm water, coupled with limitations in food availability during the MHW (Barbeaux et al. 2020, Blaisdell et al. 2021, Laurel et al. 2021). These negative impacts were reflected in the gross landings in both British Columbia and Gulf of Alaska, but the worst impacts were not seen until the years following the event (Figure 12B). Similarly, walleye pollock (*Gadus chalcogrammus*) were also significantly impacted in the Gulf of Alaska with the lowest levels of larvae caught in 2015 when compared to

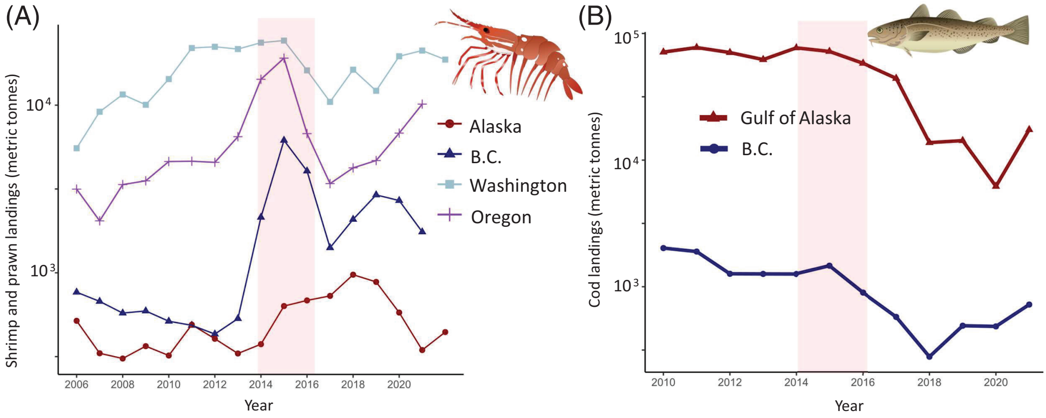

Figure 12 Gross landings of shrimp and prawns (A) and Pacific cod (B) in Canada and the USA, illustrating reductions in cod and increases in shrimp production during the MHW. (Data for the USA are adopted from Hulson et al. 2022 or NOAA landings database (https://www.fisheries.noaa.gov/), while data from British Columbia are from Fisheries and Oceans Canada (https://www.dfo-mpo.gc.ca/stats/commercial/sea-maritimes-eng.htm).) Pink rectangles indicate the timing of the marine heatwave.

a 30-year time series and low survivorship throughout that summer (Rogers et al. 2021). In contrast, Pacific hake (*Merluccius productus*) populations in the CCS and British Columbia responded positively to the MHW, with high larval and juvenile densities (Auth et al. 2018, Brodeur et al. 2019, Morgan et al. 2019), as well as the highest total biomass in 2015 (2.16 million metric tonnes) when compared to all previous years in the 17-year survey. However, the distribution of Pacific hake was somewhat limited with lower densities around Northern British Columbia (Gauthier et al. 2016). Rockfish species also increased in some coastal and offshore areas of the CCS and British Columbia, with high surveyed catches of larvae, juveniles and adults (Sakuma et al. 2016, Daly et al. 2017, Wells et al. 2017, Free et al. 2023). For example, following high recruitment during the MHW, adult shortbelly rockfish (*Sebastes jordani*) populations became hyperabundant near the shelf break in Oregon and Washington in 2018–2019. This caused significant bycatch, nearly exceeding allowable limits that would trigger a closure of the hake fishery (Thompson et al. 2019a, Free et al. 2023). Lastly, within the Gulf of Alaska, sablefish (*Anoplopoma fimbria*) steadily increased in abundance and biomass from 2015, with above-average recruitment from 2014 (Goethel et al. 2023), leading to notable increases within seabird diets during the MHW (Arimitsu & Hatch 2023).

Pelagic fishes

The effects of the heatwave were positive for many offshore pelagic fish species and negative for others. Among forage fishes, the heatwave caused record abundances and biomasses of northern anchovy (*Engraulis mordax*) larvae and juveniles across the study region (Leising et al. 2015, Auth et al. 2018, Thompson et al. 2019a, 2022, Free et al. 2023). This resulted in significant increases in adult abundance at the northern end of their range in British Columbia from 2015 (Perry et al. 2017, Chalifour et al. 2019, Duguid et al. 2019), and although adult abundance and biomass remained low across the CCS during the heatwave (Leising et al. 2015, Wells et al. 2017), strong cohorts during the heatwave led to increased adult anchovy abundance to record high levels from 2017/2018 into 2019 (Wells et al. 2017, Thompson et al. 2019a, 2022). Pacific pompano (*Peprilus simillimus*), which are normally limited to the southern CCS, were also found in high abundance from 2015 to 2017 in the northern CCS near Oregon, reaching their highest abundance since 1998 (Wells et al. 2017, Auth et al. 2018, Morgan et al. 2019). Similarly, chub mackerel (*Scomber japonicus*) and jack mackerel (*Trachurus symmetricus*) were found in particularly high abundance from 2015 to 2017 in the northern CCS (Wells et al. 2017, Morgan et al. 2019). Within the southern CCS, Mexican lampfish (*Triphoturus mexicanus*) are at the northern limits of their distribution, but during the heatwave, both the larvae and adults underwent significant increases in abundance (Koslow et al. 2019, Nielsen et al. 2021, Thompson et al. 2022), with the highest adult abundance observed since 1951 (Wells et al. 2017).

However, some forage fish species declined during the marine MHW, including Pacific capelin (*Mallotus catervarius*) in the Gulf of Alaska (McGowan et al. 2020, Arimitsu et al. 2021, Suryan et al. 2021). In shelf regions, capelin abundance plummeted by at least 98% between 2013 and 2015, reaching the lowest observed numbers in almost two decades (Arimitsu et al. 2021), also reducing in mean length and body condition (Thompson et al. 2019b). Pacific sand lance (*Ammodytes personatus*) were also impacted due to poor feeding conditions (Figure 9D) and were reported to have significantly lower growth, body condition, nutritional value and body-length in parts of British Columbia and the Gulf of Alaska, although these effects were not ubiquitous and the impact on overall abundance was unclear (Biela et al. 2019, Chalifour et al. 2019, Thompson et al. 2019b, Arimitsu et al. 2021, Suryan et al. 2021, Robinson et al. 2023b). There was also some evidence of reduced body condition, spawn and larvae densities for Pacific herring (*Clupea pallasii*) across the study region (Leising et al. 2015, Gorman et al. 2018, Brodeur et al. 2019, Suryan et al. 2021), although patterns were highly spatially variable, including for changes in overall abundance and distribution (Flostrand et al. 2015, Boldt et al. 2017, Cleary et al. 2017, Arimitsu et al. 2021). Pacific sardine (*Sardinops sagax*) had spatially heterogeneous changes in larvae abundance with both increases and decreases recorded during the heatwave (Leising et al. 2015, Auth et al. 2018, Nielsen et al. 2021, Thompson et al. 2022). Within the adults, however, there was a marked shift in distribution northwards (Muhling et al. 2020) and continued declines in population sizes, although this trend had been noted prior to the heatwave (Leising et al. 2015, Petatán-Ramírez et al. 2019, Thompson et al. 2019a, Free et al. 2023).

Large piscivores which increased in abundance during the heatwave included albacore tuna (*Thunnus alalunga*) in British Columbia (Holmes 2016) and bluefin tuna (*Thunnus thynnus*) across the USA and Mexico (Free et al. 2023). There were also many new appearances and rare occurrences of large predatory piscivorous and benthivorous teleost fish and elasmobranchs across the region, particularly of tropical species moving into California (Walker Jr et al. 2020), but also first recordings of swordfish (*Xiphias gladius*) (Halpin et al. 2018) and louvar (*Luvarus imperialis*) (Brooks et al. 2016) in coastal British Columbia and whitetip reef sharks in Baja California (Becerril-Garcia et al. 2018). After invertebrates, fish were the group with the largest number of species that were observed further north than ever before (see range shift section above).

Pacific salmon

Due to a wide range of abiotic and biotic factors influencing population status for anadromous Pacific salmon (*Oncorhynchus* spp.), changes from the heatwave were highly variable between species, locations and years of the heatwave, including for juvenile condition, distribution and abundance, and for adult returns and spawning (Trudel et al. 2015, Hyatt et al. 2016, King & Baillie 2017, McKinnell 2017, Wells et al. 2017, Grant et al. 2019). Generally, the warm water conditions experienced during the heatwave are thought to have had negative impacts throughout the salmon life cycle, with some mixed effects due to trophic interactions during the marine stage and rare positive effects in the case of range expansion (Crozier & Siegel 2023). In the Columbia River (Washington and Oregon), for example, juvenile steelhead (*Oncorhynchus mykiss*) exhibited particularly poor body conditions and returns were among the lowest in the previous 30 years (Thalmann et al. 2020). However, in Washington, juvenile survival significantly increased in Puget Sound during the heatwave, which was posited to be a trophic effect linked to high anchovy abundance (Moore et al. 2021). The broad-scale changes in zooplankton composition (detailed above), particularly the shift in copepods from larger lipid-rich northern species to small lipid-poor southern species, decreased food quality for migrating juvenile salmon during the heatwave. These cascading effects of diminished food availability for zooplanktivorous fish persisted for 8 years after the heatwave, finally appearing to return to normal in 2022 (Ostle & Batten 2023). In the northern CCS, particularly around Oregon, juvenile Chinook salmon (*Oncorhynchus tshawytscha*) were recorded to have poor body condition, high percentages of empty stomachs (Figure 9D) and high early mortality, leading to significantly reduced adult returns primarily in 2016–2019 (Daly et al. 2017, Wells et al. 2017, Free et al. 2023). In British Columbia, however, Chinook populations continued their long-term decline, with no clear attribution of effects from the heatwave (Grant et al. 2019, 2021a). Sockeye salmon (*Oncorhynchus nerka*) populations seemed to be particularly impacted by the heatwave. In many parts of the Gulf of Alaska and British Columbia, sockeye had high juvenile mortality and low abundance (Hyatt et al. 2016, 2017, King & Tucker 2018); they also significantly shifted their migration routes to northern passages (Lapointe et al. 2015), had extremely low adult returns with high en route mortality (Hyatt et al. 2016, 2017, Patterson et al. 2016, Grant et al. 2021b, Lindley et al. 2021) and exhibited higher egg retention rates (Carey et al. 2021). Impacts on pink (*Oncorhynchus gorbuscha*), coho (*Oncorhynchus kisutch*) and chum salmon (*Oncorhynchus keta*) were variable across the coast with shifts in the return timing of certain stocks of each species (McKinnell 2017). Of particular note are pink salmon populations from Alaska; in 2016, the harvest of pink salmon was the lowest in 20 years in Prince William Sound and parts of Southeast Alaska (McKinnell 2017).

Seabirds and marine mammals

Seabirds incurred significant indirect impacts from the heatwave as a result of altered oceanographic conditions, which led to changes in zooplankton communities as well as forage fish abundance and quality as prey (Jones et al. 2018, Robinson et al. 2018a, Piatt et al. 2020, Arimitsu et al. 2021). These cascading effects led to changes in seabird foraging behaviour, at-sea distribution, and caused unprecedented die-offs along the coast (Jones et al. 2018, Robinson et al. 2018a, Piatt et al. 2020). During the winter of 2014/2015, record numbers of dead Cassin's auklets (*Ptychoramphus aleuticus*) were observed on beaches in Washington, Oregon and Central California (Jones et al. 2018), with encounter rates of dead auklets exceeding baseline numbers 100-fold (Figure 13). This unprecedented increase in mortality, coupled with likely shoreward shifts in at-sea distribution, was linked to regional shifts and declines in zooplankton productivity due to the MHW (Jones et al. 2018, 2023). Then, between summer 2015 and spring 2016, around 62,000 common murres (*Uria aalge*) washed up on beaches from Alaska to California, with approximately one million total murres dying during this period (Piatt et al. 2020). In the Gulf of Alaska, encounter rates of dead murres were more than 10,000 times greater between December 2015 and January 2016 than they were on

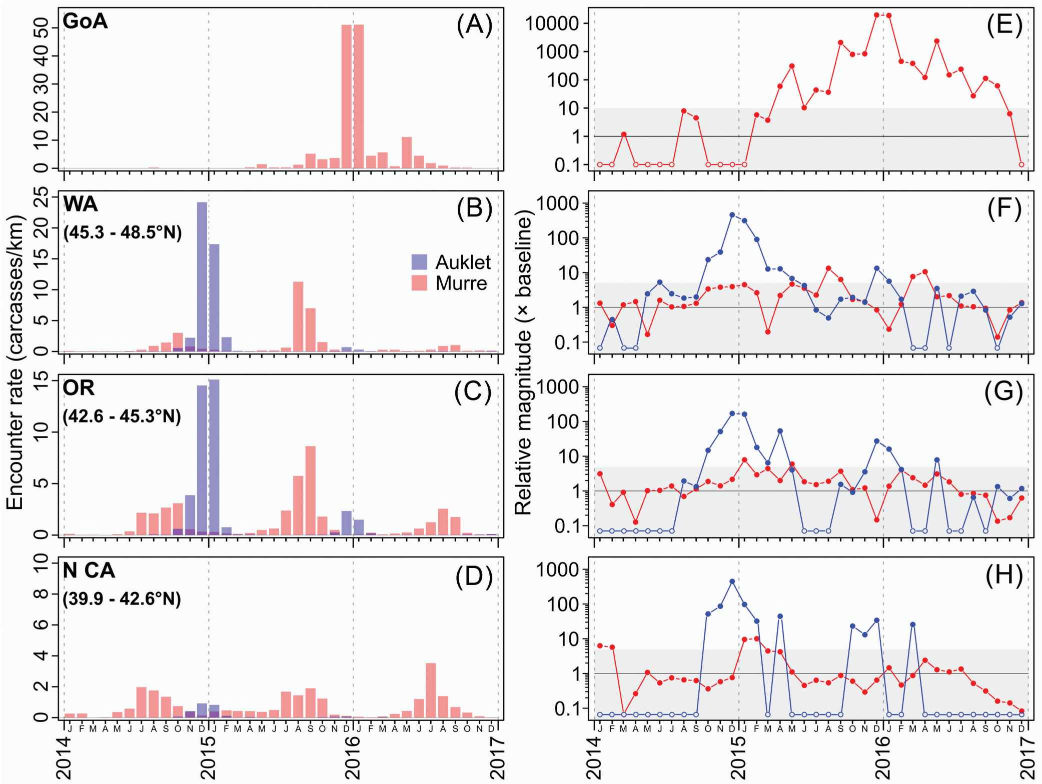

Figure 13 Observations of dead seabirds (auklets and murres) through time across four regions. GoA, Gulf of Alaska; WA, Washington; OR, Oregon; N CA, Northern California. (A–D) Encounter rate (carcasses per km) of auklets (Cassin's auklets and unknown small alcids) and murres (common murres, thick billed murres [only in Alaska] and unknown murres) in each region during the 2014–2016 marine heatwave. (E–H) Relative magnitude of month-averaged encounter rates compared to long-term baseline average (× baseline). Baselines were calculated based on monthly means from the following year ranges, excluding 2014–2016: GoA: 2006–2023; WA: 2000–2023; OR: 2000–2023; N CA: 2006–2023. (Figure produced by T. Jones with data provided by COASST: http://COASST.org.)

average since 2016 (Figure 13), once again due to a combination of increased mortality and changes in at-sea distribution. Systematic necropsies showed that virtually all murres were emaciated, linking mortalities to the low abundance and quality of forage fishes (Arimitsu et al. 2021), although it is possible that exposure to the HAB neurotoxins saxitoxin (STX) and DA was a secondary contributor to mortality in some cases (Van Hemert et al. 2020, Gibble et al. 2021). In 2016 and 2017, fork-tailed storm-petrels (*Oceanodroma furcata*) and short-tailed shearwaters (*Ardenna tenuirostris*) were recorded consuming beach-cast salmon for the first time ever (Figure 2), suggesting a continued lack of forage fish offshore (Robinson et al. 2018a).

Seabirds in the Bering Sea, many of which would seasonally inhabit other parts of the coast (e.g. Orben et al. 2015), also experienced significant impacts. Follow-on heating in the Bering Sea, resulting in record-low sea-ice extent in the winter of 2017–2018 (Stabeno & Bell 2019), was also associated with mortality events and depressed breeding success of local breeding birds (murres, fulmars and puffins; Romano et al. 2020, Van Hemert et al. 2021, Jones et al. 2023). Moreover, some trans-hemispheric migrants that over-winter in the Bering Sea were also negatively affected (e.g. short-tailed shearwaters; Glencross et al. 2021, Jones et al. 2023).

The unprecedented coast-wide impacts of the MHW on adult seabirds also led to systematic reproductive failures during breeding seasons. In the Gulf of Alaska, reproductive productivity of the black legged kittiwake declined during the MHW due to low abundances of capelin near nesting sites (Osborne et al. 2020). Similarly, in both Oregon and Alaska, 22 common murre nesting sites had complete reproductive failure between 2015 and 2017 (Piatt et al. 2020). For both species, changes to foraging patterns during breeding season were observed in response to unfavourable oceanic conditions, with kittiwake travelling further distances while foraging in search of prey and murres spending more time foraging in estuaries that acted as refugia against warming waters (Loredo et al. 2019, Osborne et al. 2020). Impacts on reproduction continued after the heatwave ended for both species, suggesting that unfavourable foraging conditions persisted for years after the MHW (Osborne et al. 2020, Piatt et al. 2020, Schoen et al. 2022). However, some seabirds showed resilience to the effects of the MHW (e.g. Hipfner 2017, Robinson et al. 2023a). Breeding success of the largest Cassin's auklet breeding colony, which is located on Triangle Island, British Columbia, remained near the long-term average during the MHW (Hipfner 2017). The auklet's reproductive success has been attributed to them shifting their foraging location to the refugia of nearby productive upwelling waters (Hipfner 2017, Domalik et al. 2018).

Like seabirds, marine mammals were primarily impacted indirectly by the heatwave; within the pinnipeds, the most intense impacts were generally seen at southern latitudes. Increased water temperatures and reduced prey availability for pregnant and lactating Guadalupe fur seal (*Arctocephalus townsendi*) and California sea lion (*Zalophus californianus*) females led to decreased birth rates as well as higher mortality in neonates once born (DeLong et al. 2017, Laake et al. 2018). On the Baja California peninsula during the heatwave, neonates in Guadalupe fur seal colonies had reduced birth weights and growth rates, and ultimately, increased mortality, attributed to emaciation, which was 3× higher than before the heatwave (Gálvez et al. 2020, 2023). Adult fur seals foraged further northwards and into open water during the heatwave, and scat analyses suggest that their dietary niche expanded, suggesting a lack of preferred prey availability (Amador-Capitanachi et al. 2020). Similarly, California sea lions within the CCS travelled longer distances to forage for less energy-rich prey during the MHW (Robinson et al. 2018b), and as a result, their pups suffered higher levels of mortality due to starvation (Banuet-Martínez et al. 2017, Laake et al. 2018). Surviving California sea lion pups were often emaciated (Lowry et al. 2022), resulting in reduced immune system capacity (Banuet-Martínez et al. 2017) and physiological irregularities related to increased atypical erythrocyte morphologies, which are expected to reduce the pups' foraging abilities as they grow (Flores-Morán et al. 2017). On Santa Margarita Island, the most southern California sea lion breeding colony, surveys in 2013–2015 recorded the lowest population abundances since surveys began in 1979 (Pelayo-González et al. 2021).

Conversely, elephant seal (*Mirounga angustirostris*) breeding colonies in the CCS were resilient to the MHW. Unlike California sea lions and Guadalupe fur seals, elephant seals practise capital breeding, meaning they feed their pups with milk produced from fat reserves accumulated before the breeding season. As such, elephant seal reproductive success is linked to prey availability much farther north, in the Gulf of Alaska, where despite geographic shifts to the western side of the Alaskan gyre, their prey quality remained stable during the MHW (Holser 2020). This east-west disparity of foraging quality in the Gulf of Alaska was also noted for the Steller sea lions (*Eumetopias jubatus*), where reduced survival of adult females occurred in the eastern but not western Gulf during the MHW (Hastings et al. 2023).

Cetaceans were also subject to several impacts during the MHW. The northernmost occurrence for common bottlenose dolphins in the Northeast Pacific was recorded in July 2017, with a group of approximately 200 common bottlenose dolphins (*Tursiops truncatus*) observed 180 km off the west coast of northern Vancouver Island, British Columbia. Approximately 70 false killer whales (*Pseudorca crassidens*) were also sighted with these bottlenose dolphins, marking the first record of false killer whales in offshore waters of British Columbia (Halpin et al. 2018). In Glacier Bay National Park, Alaska, humpback whale (*Megaptera novaeangliae*) calf survival dropped 10-fold in 2013, and midsummer calf losses jumped from 1.9% in pre-MHW years (1986–2013) to 19% during and after the MHW (2014–2018) (Gabriele et al. 2022). Between 2015 and 2019, calf production remained far below historic levels (from 0.27 calves per adult female before MHW to 0.041 during/ after MHW). Similar patterns of reduced calf survival were observed in Prince William Sound, Alaska (Arimitsu et al. 2021). Low forage fish and zooplankton prey availability during and after the MHWs were suspected as the main drivers of reduced humpback whale survival and reproductive success (Gabriele et al. 2022). In California, socio-ecological factors led to record numbers of whale entanglements in the central CCS crab fishery. Habitat compression of coastal upwelling and changes in availability of forage species (krill and anchovy) led to a shoreward distribution shift of foraging humpback whales in 2016. During this time, domoic acid contamination prompted an unprecedented delay in the opening of California's Dungeness crab fishery, inadvertently causing high temporal overlap between the whale's distribution and the crab fishery, leading to record entanglements (Santora et al. 2020).

Impacts on deep benthic and demersal ecosystems and species

Impacts of the marine heatwave extended as far as benthic deep-sea and mesophotic ecosystems, with expanding areas of hypoxia apparently driving some of the effects. In Saanich Inlet, British Columbia, the abundant habitat-forming pennatulacean octocoral (*Halipteris willemoesi*) decreased in abundance by 92.3% between 2013 and 2016, and three species of pandalid shrimp (*Pandalus platyceros*, *Pandalus jordani* and *Pandalus hypsinotus*) disappeared from benthic community surveys (at depths of 40–140 m) entirely in 2016 (Gasbarro et al. 2019). This shift in benthic community composition was driven by large increases in the seafloor area that were bathed in anoxic and hypoxic waters, resulting in a 58% decline in the total abundance of 46 species compared to before the heatwave. Hypoxia-tolerant species experienced milder losses. Two species, the burrowing white sea cucumber (*Pentamera calcigera*) and the striped nudibranch (*Armina californica*), which feeds on the octocoral, appeared for the first time in the community in 2016 (Gasbarro et al. 2019).

Elsewhere in British Columbia, in Barkley Canyon (985 m depth), there was an increase in the abundance of tanner crabs (*Chionoecetes opilio*) and increased variability in the abundance of other macrofauna (sablefish: *Anoplopoma fimbria*, mycids: *Eucopia* spp.) in early 2014 (Chauvet et al. 2018). Chauvet et al. (2018) hypothesised that this may have been the result of changes in surface productivity or mixed layer depth, but the exact mechanism remains unclear. At ~400 m depth off Vancouver Island, British Columbia pink sea urchins (*Strongylocentrotus fragilis*) also experienced shifts in abundance and steady movement into shallower waters, at a mean rate of 3.5 m per year, between 2013 and 2020. These urchins graze, in part, on detrital seaweeds, and it was hypothesised that they may have moved to shallower waters as food sources and oxygen levels declined at depth (Command et al. 2023).

In contrast to changes in deep-sea benthic megafaunal communities observed in British Columbia, monitoring on the Monterey Fan (Station M – depth: ~ 4000 m) revealed only very limited effects of the 2014–2016 marine heatwave (Kuhnz et al. 2020). For example, while declines in total echinoderm numbers were observed between 2014 and 2018, numbers did not fall below background levels in the time series, dating back to 1989, and did not correlate with clear changes in benthic environmental parameters (Kuhnz et al. 2020). In general, we know very little about how marine heatwaves occurring mostly in surface waters impact deep-sea ecosystems.

Discussion

Direct versus indirect effects of the heatwave

The 2014–2016 MHW imposed a multitude of direct ecological impacts associated with elevated temperature, including significant shifts in species distributions and abundances. Key examples of direct habitat impacts include the die-back of canopy-forming kelp species directly associated with warm water (Cavanaugh et al. 2019, Starko et al. 2022), the decline in eelgrass beds in Oregon's estuaries (Magel et al. 2022) and elevation shifts in intertidal species along rocky shores (Whalen et al. 2023; Table 1). Moreover, both phytoplankton and zooplankton communities were reorganised with changes in the timing and intensity of seasonal productivity and the increased prevalence of distinct species associated with warm water (e.g. Peterson et al. 2017, Kahru et al. 2018, Delgadillo-Hinojosa et al. 2020). In both coastal and offshore systems, the heatwave also drove changes in the geographical distribution of numerous species, with over 100 range shifts and over 130 unusual occurrences documented. Most range shifts occurred in invertebrates, likely due to the high prevalence of pelagic larval stages for dispersal, but species were impacted from across the tree of life, from algae to marine mammals. Many of these spatial changes likely represent direct responses in increased temperature, although some, such as those of marine mammals, occurred in response to shifting food availability. The extent to which these changes will have long-lasting ecosystem impacts, through enduring range shifts with established populations in new locations and reorganised ecological communities, remains to be seen.

Although warm temperatures had direct impacts on a wide range of organisms, the indirect impacts of the marine heatwave were often equally or more important in driving the responses of species and ecosystems to the event (Table 1). Indirect effects (*sensu* Wootton 1993) arose through ecological interactions, primarily changes in trophic or pathogenic interactions resulting from warm water temperatures. For example, many seabird and marine mammal species were deeply affected by reduced food availability, leading to record seabird die-offs (e.g. Piatt et al. 2020), unusual mortality events of humpback whales (Cheeseman et al. 2024) and high neonate mortality in California sea lions and Guadalupe fur seals (DeLong et al. 2017, Laake et al. 2018, Amador-Capitanachi et al. 2020, Gálvez et al. 2020). As many marine mammals adjusted their foraging patterns in an attempt to compensate for altered food availability, this also led to record whale entanglements in California (e.g. Santora et al. 2020). SSWD, which drove declines in sea stars, altered the dynamics of rocky shore and kelp forest ecosystems: declines in the sea star *Pisaster ochraceus* led to increased mussel cover in some places (Traiger et al. 2022) but not others (Figure 7), and created an ecological opportunity for its competitor, *Evasterias troschelii*, flipping the dominance between the two species in Burrard Inlet, B.C. (Kay et al. 2019). We also consider reduced nutrients from thermal stratification, which strongly influenced the observed changes in phytoplankton assemblages, to be an indirect effect since the nutrients are generally depleted by microbial activity (and is therefore an ecological rather than physical process). For example, the toxic *Pseudo-nitzschia* spp. bloom that closed several key fisheries in 2015 is

Table 1 Examples of Direct and Indirect Effects for a Range of Ecosystem Types and/or Taxonomic Groups

Ecosystem	Direct Effect	Indirect Effect
Rocky shores	Warm temperatures cause intertidal species to shift down in elevation (Whalen et al. 2023)	Sea star wasting impacts *Pisaster* which then alters the abundance of mussels (Traiger et al. 2022)
Kelp forests	Warm temperatures cause mortality and die-back in canopy-forming kelp species across the NE Pacific coast (e.g. Cavanaugh et al. 2019, Starko et al. 2022)	SSWD impacts *Pycnopodia* which causes the proliferation of urchins, decimating forests in California and British Columbia (Schultz et al. 2016, e.g. Burt et al. 2018, Rogers-Bennett & Catton 2019)
Eelgrass meadows	Warmer temperatures were associated with declines in eelgrass abundance in estuaries in Oregon (Magel et al. 2022).	Warm temperatures make eelgrass more susceptible to eelgrass wasting disease (Groner et al. 2021).
Phytoplankton	Warmer temperatures likely contributed to large number of range shifts observed across various phytoplankton taxa (e.g. Peterson et al. 2017).	Thermal stratification led to reduced nutrients, which facilitated the largest toxic algae bloom in history by the diatom, *Pseudo-nitzschia* (e.g. McClatchie 2016).
Zooplankton	Warmer temperatures likely contributed to increase in southern copepods in British Columbia and Alaska (Batten 2015, Batten et al. 2022, McKinstry et al. 2022)	Doliolids were abundant on the coastal shelf of Northern California in 2015, likely reflecting a microbial loop more typical of offshore than coastal (Peterson et al. 2017)
Fishes	Changes in environmental conditions contributed to recruitment failure of Pacific cod due to narrow thermal tolerance (Barbeaux et al. 2020)	Reduced food availability for some fish species led to poor body condition and/or reduced populations (e.g. Biela et al. 2019, Thalmann et al. 2020)
Seabirds	Multiple birds found further north than usual, including two latitudinal range shifts (e.g. Merlo et al. 2018, Sanford et al. 2019).	Reduced abundance and quality of forage fish causes large die-offs in multiple seabird species (e.g. Jones et al. 2018, 2023, Piatt et al. 2020).
Cetaceans	Bottlenose dolphins shift north, including persistent population in Salish Sea (Halpin et al. 2018, Keener et al. 2023)	Humpback whales in California concentrated in coastal waters due to low offshore food availability, increasing fishing entanglements (Santora et al. 2020). Humpback whale population declined by ~7000 due to limited prey resources (Cheeseman et al. 2024)
Pinnipeds	No clear direct effect of temperature	Reduced food led to physiological stress, emaciation, poor reproduction and/or reduced pup survival in populations of Guadalupe seal and California sealion (DeLong et al. 2017, Gálvez et al. 2020)
Sea turtles	Loggerheads found close to shore and two other species found north of previous range limit	No clear indirect effect
Deep sea	No clear direct effect of temperature	Anoxia causes substantial damage to deep-sea gorgonian ecosystem (Gasbarro et al. 2019)

believed to be largely linked to reduced nutrients and stratified waters (Du et al. 2016, McCabe et al. 2016). Many of the largest socioeconomic impacts also were driven by indirect effects of the heatwave, including changes in food web dynamics (e.g. Cavole et al. 2016, Rogers-Bennett & Catton 2019, Arimitsu et al. 2021) and impacts of the most extensive harmful algal bloom recorded, which closed multiple fisheries for record periods of time (Free et al. 2023).

The importance of indirect heatwave effects is often overlooked when considering how longer, more frequent and more intense marine heatwaves will impact the ocean environment (Vergés et al. 2016). Although some observed phenomena, such as range shifts into traditionally cooler waters or die-offs towards species' warm range-edges, are clear expectations of marine heatwaves

(Pinsky et al. 2013, Vergés et al. 2014, Wernberg et al. 2016), a wide range of unexpected impacts materialised because of indirect effects (Table 1). This underscores a major challenge associated with understanding MHWs and predicting their outcomes in the future. If some of the greatest impacts result from indirect effects linked to changes in habitat or the biomass and composition of lower trophic levels, then these effects are likely to be completely missed by our current methods to predict climate change impacts, which rely on modelling the likely impacts of warming or heatwaves on individual species. A great deal of experimental work has highlighted how warm temperatures not only alter individual species but also the structure of communities (and therefore ecosystems). For example, species range shifts can lead to novel species interactions, with potentially lasting effects on ecosystem structure and function (Zarzyczny et al. 2023). Our synthesis of the 2014–2016 MHW strongly supports that this should be a major expectation for future ecosystems as they continue to experience intensifying MHWs.

Ramifications of a multiyear heatwave

The multiyear nature of the 2014–2016 marine heatwave appears to have been critical in driving the range of responses observed. The MHW lasted 3 years, in some locations lasting >300 days in a year, making it unprecedented in length (Figure 1C). Moreover, in Alaska, British Columbia and Baja California, warm conditions persisted in the years following with continued impacts into 2017 or later (Figure S1). Because the heatwave lasted so long, the region was warmer than usual through all seasons and for multiple generations of some short-lived species. This likely explains the scale of change that was observed, including hundreds of distributional shifts (including a handful over 1000 km), the collapse of the Pacific cod fishery and a record bloom of toxic *Pseudo-nitzschia* spp. and some of the largest kelp forest losses reported globally (Filbee-Dexter et al. 2022; Wernberg et al. 2024). Some heatwave impacts also took up to a year or more to manifest, such as the *Pyrosoma atlanticum* bloom; while this species started showing up in greater abundance than usual in 2014, it didn't reach peak biomass until 2015–2017, and the impacts persisted through to 2019 depending on the region (Miller et al. 2019, Schram et al. 2020).

With prolonged, multiyear marine heatwaves expected to become more common as climate change continues (Oliver et al. 2019), resource managers, industry and policymakers need to become better 'prepared for the unexpected', with adaptive strategies to respond (Fisher et al. 2021, Boyce et al. 2024, Starko et al. 2024b). These might include fisheries closures and diversification of fisheries harvest portfolios to buffer against individual closures (Fisher et al. 2021). Concurrently, enhancing the climate resilience of marine protected areas is urgently needed; a recent review highlighted the need for improved climate adaptation strategies in MPA management plans (Bryce & Hunter 2024). Multiple government agencies already publish regular ocean ecosystem status reports summarising the current state of knowledge (e.g. NOAA's Ecosystem Status Reports, Fisheries and Oceans Canada's State of the Pacific reports), but given the potentially enormous socioeconomic impacts of marine heatwaves (e.g. Cheung et al. 2021, Smith et al. 2021, Free et al. 2023), more systematic incorporation of climate change and the potential ramifications of MHWs into fisheries stock assessments, ecosystem-based fisheries management and management harvesting decisions is urgently needed (Boyce et al. 2021). This includes better anticipatory science, such as incorporating forecasted marine heatwaves into allowable catches for commercial harvests, precautionary catch limits to enhance long-term resilience in the face of increasing MHWs and other adaptive management strategies.

Aftermath of the event

While only some studies that we reviewed had followed up on the ecosystem impacts of the MHW, those that have revealed high variation in the trajectories of taxa following the event. While some taxa and some systems experienced a rapid reversion to pre-MHW conditions, other systems had sustained or continued effects. For example, kelp forests along the outer coast of Washington, which were negatively impacted in 2014–2015, recovered completely within only a year (Tolimieri et al. 2023). In contrast, kelp forests in Northern California (Rogers-Bennett & Catton 2019, McPherson et al. 2021) and some parts of British Columbia (Starko et al. 2022, 2024a) did not rebound following their initial decline. Continued warm conditions in British Columbia and Alaska since the MHW have likely also exacerbated the impacts of the discrete MHW, leading to persistent impacts in some systems (Suryan et al. 2021, Starko et al. 2022, 2024a). In fact, many significant impacts in British Columbia and Alaska were observed in 2017, after the MHW had already dissipated further south (e.g. *Pyrosoma atlantica* bloom; Miller et al. 2019, Schram et al. 2020).

Several of the largest impacts of the marine heatwave have persisted following the event, leaving a long-lasting legacy throughout the Northeast Pacific. For example, recovery from SSWD has been variable, with some species rebounding quickly and others failing to do so. Of particular note is that the sunflower star, *Pycnopodia helianthoides*, remains functionally absent from most of the continental USA and about 90% lower than pre-SSWD levels in British Columbia and Alaska (Hamilton et al. 2021). This continues to have indirect impacts on coastal ecosystems (Suryan et al. 2021, Whalen et al. 2023, Starko et al. 2024a). Many fishery species remain impacted in the years following the MHW. For example, the Pacific cod population in the Gulf of Alaska has shown little-to-no recovery at least to the end of 2022 (Hulson et al. 2022) and Northern anchovy remained at high abundance in the CCS into 2023 (Harvey et al. 2023). Moreover, some key changes in offshore plankton composition have persisted for several years following the event, only just beginning to return to normal over the past couple of years. As research effort continues into population and ecosystem dynamics of the Northeast Pacific, it will become increasingly clear how long-lasting the various impacts of this MHW have been.

Comparisons to other MHWs

The 2014–2016 marine heatwave in the Northeast Pacific, despite its exceptional duration and geographic scope, shares many ecological impacts with other MHWs observed worldwide. These recurrent patterns, including changes in primary productivity, shifts in species distributions and community composition, disease outbreaks, mass mortalities and fisheries disruptions, emphasise the urgent need for enhanced monitoring and adaptive management strategies (Smith et al. 2021, 2023). By understanding the similarities and differences between MHWs, we can better predict and mitigate the future consequences of these extreme events on marine ecosystems and the human communities that rely on them.

Changes in marine species distribution are a common feature of MHWs. For example, the 2011 Western Australia MHW drove significant poleward expansions of tropical and subtropical species and contractions of cool water species (Wernberg et al. 2012, 2016, Lenanton et al. 2017). Moreover, zooplankton and several fish species shifted distributions during the 2015/2016 Tasman MHW tracking temperature such that warm water species were seen out of range (Oliver et al. 2017, Evans et al. 2020). However, the prevalence of distributional shifts ($n=101$ range shifts and 139 unusual occurrences) associated with the 2014–2016 MHW appears far higher than other events of this nature. These biogeographical changes can disrupt existing ecological interactions and create new ones, potentially leading to long-term community restructuring (Vergés et al. 2014, Zarzyczny et al. 2023).

Coastal foundation species (e.g. corals, seaweeds and seagrasses) have repeatedly suffered from thermal stress during MHWs (Wernberg et al. 2016, 2024, Smale 2020). The 2014–2016 MHW drove substantial declines in kelp forests and seagrass meadows along some parts of the coast similar to the 2011 Western Australian MHW (Wernberg et al. 2016, Arias-Ortiz et al. 2018), the 2015/2016 Tasman Sea MHW (Thomsen et al. 2019, Tait et al. 2021), multiple MHWs in Northern Europe (Filbee-Dexter et al. 2020, 2022) and many others (Smale 2020, Wernberg et al. 2024). The 2014–2016 Northeast Pacific MHW also occurred concurrently with a large tropical MHW driven by the associated El Niño, which caused the 3rd global bleaching event, devastating coral reefs across the Pacific and Indo-Pacific (Hughes et al. 2018, Eakin et al. 2019). Substantial losses in foundation species are a growing outcome of MHWs and can profoundly alter the structure and function of coastal ecosystems (Wernberg et al. 2024). Indeed, a subsequent MHW has now triggered the 4th global coral bleaching event (NOAA 2024). Thus, further efforts to mitigate the impacts of MHWs on coastal habitats or to restore them following these events are paramount.

Another prevalent pattern across MHWs is the alteration in primary productivity and shifts in phytoplankton species composition (e.g. Hayashida et al. 2020, Chauhan et al. 2023). Several other MHWs, including the 2003 MHW in Europe (e.g. Gómez & Souissi 2008) and the 2015/2016 Tasman Sea MHW (e.g. Chiswell & Sutton 2020) led to substantial changes in phytoplankton dynamics, mirroring the pronounced shifts observed during the 2014–2016 event. Harmful algal blooms (HABs) have also been a common consequence of MHWs, as exemplified by the unprecedented 2015 blooms discussed herein (McCabe et al. 2016, Ryan et al. 2017, Trainer et al. 2020, Figure 9B) and the extensive toxic algae proliferation documented during MHWs in South Australia (Roberts et al. 2019) and the Southwest Atlantic (Trainer et al. 2020). These shifts in primary productivity and phytoplankton communities can have cascading effects on entire marine food webs (e.g. Piatt et al. 2020, Santora et al. 2020) as we have discussed above.

Disease outbreaks and mass mortality events have also been more prevalent during MHWs, affecting a wide range of marine organisms. Disease prevalence in corals has long been tied to elevated sea temperatures during tropical MHWs (Heron et al. 2010, Brodnicke et al. 2019, Burke et al. 2023). Moreover, the 2014/2015 Tasman Sea MHW saw die-offs of multiple invertebrates, including the blacklip abalone (*Haliotis rubra*), and recurrent MHWs in the Mediterranean have driven repeated die-offs of several species (Garrabou et al. 2022). As we have outlined above, the 2014–2016 event coincided with a massive die-off of sea stars along the Pacific coast of North America due to a disease outbreak (Eisenlord et al. 2016, Harvell et al. 2019, Hamilton et al. 2021) and led to mass mortality of seabirds, like the common murres, due to reduced prey availability (e.g. Piatt et al. 2020, Jones et al. 2023), offering another set of similarities between the 2014 and 2016 MHW and other events.

The impacts of MHWs extend beyond ecological consequences, affecting socioeconomic systems such as fisheries (Smith et al. 2021, Free et al. 2023); the 2014–2016 MHW was no exception. This event led to substantial fisheries impacts (Smith et al. 2021, Free et al. 2023), including temporary closure of major fisheries like the Dungeness crab fishery (Fisher et al. 2021) and the collapse and prolonged closure of others such as the Pacific cod fishery (Hulson et al. 2022). MHWs in other systems have similarly driven fisheries closures or decreases in fishery yields (Caputi et al. 2016, Smith et al. 2021). Both the 2014–2016 MHW and other MHWs have also driven opportunistic, short-lived fisheries. For example, squid featured as opportunistic fisheries further north of their typical ranges both during the 2014–2016 MHW and the 2012 MHW in the Northwest Atlantic (Mills et al. 2013). These fisheries impacts underscore the far-reaching implications of MHWs on human communities and economies that depend on marine resources.

Research needs

Our synthesis highlights the critical importance of long-term monitoring initiatives in capturing and contextualising the impacts of extreme events. While some observations during the MHW were made opportunistically (e.g. news reports of range shifts), much of our understanding of the impacts of this event is based on the analysis of long-term monitoring datasets. Continuing and enhancing ecological monitoring and observation will be essential for efforts to quantify and understand the ecological changes that are occurring in the face of climate change (Likens & Lambert 1998, Sagarin & Pauchard 2010, Elmendorf et al. 2015). This will be critical for identifying the factors that confer resilience to these communities, thereby guiding efforts to bolster ecosystem recovery in the aftermath of heatwaves. There is a clear bias in monitoring efforts towards areas that are densely populated (e.g. see Figure 7), which is expected given the inaccessibility of remote coastlines for regular fieldwork. Much of British Columbia and parts of Alaska remain poorly monitored, for instance. Utilising remote sensing tools (Cavanaugh et al. 2021) or planning periodical monitoring of these poorly understood regions would enable scientists and managers to better track changes in these ecosystems or even establish baselines from previously collected data.

Investigations into the recovery of marine ecosystems following this MHW will also be vital for informing conservation strategies, and we expect they will continue over coming years. For example, we documented that kelp forests throughout the Northeast Pacific were impacted by this MHW (Figure 8). While recovery trajectories since this event have been characterised in some places, there remain many regions with no published follow-up data. We suspect that many interesting datasets characterising recovery trajectories across a diversity of ecosystems already exist but have yet to be published due to the time lag between data collection and publication. Future synthesis may be helpful to compare and contrast across different systems once more is known and published on recovery following the event.

Our comprehensive review of this unprecedented marine heatwave also highlights some key ecosystems whose responses to the MHW were captured in only a limited number of places, underscoring an urgent need for targeted research effort. There were very limited studies on the impacts of this prolonged MHW on seagrass meadows or on the deep sea. Seagrass meadows are widespread ecosystems throughout the study region, yet we only identified six studies that documented impacts of the MHW. Given that these studies revealed impacts that were locally variable depending on conditions directly surrounding a given meadow (Magel et al. 2022, Marin Jarrin et al. 2022), there is a clear need for further work exploring status and trends in seagrass abundance and health in the context of recent warming, starting with this event. Similarly, we found very few studies that described impacts of the MHW on the deep sea. While this is perhaps not surprising given that warm temperatures were mostly isolated to the surface waters initially, warmer waters entered deep-sea ecosystems in years following the event (Jackson et al. 2018). Moreover, surface warming impacted the oxygenation of deep waters with documented impacts on Vancouver Island (Gasbarro et al. 2019, Command et al. 2023), but it remains unclear whether these impacts were widespread. Future work should aim to better characterise the impacts of MHWs on deep-sea ecosystems.

Research into indirect effects and trophic interactions altered by MHWs more generally will also be essential for unravelling the complex web of ecological relationships affected by these events, which is critical for forecasting the cascading impacts of warming on biodiversity and ecosystem functioning (Vergés et al. 2016, Harvell et al. 2019). Our synthesis clearly captured widespread ecosystem-scale impacts that resulted from indirect rather than direct impacts of warming during the MHW. Further developing theory and understanding of how these indirect effects unfold in the face of marine heatwaves will be an important area of continued research.

Finally, our synthesis highlights the critical challenge posed by climate change and the need to continue research effort into both climate change mitigation and ecosystem adaptation. Efforts should focus on climate change mitigation, such as reducing greenhouse gas emissions, and adaptation strategies, including habitat protection and restoration (Coleman & Goold 2019, Coleman et al. 2020, Eger et al. 2023, Wood et al. 2024). to enhance the resilience of marine ecosystems to climate variability. Collaborative efforts among scientists, policymakers and stakeholders are essential for implementing effective conservation and management strategies in response to the ongoing challenges presented by climate change. The 2014–2016 MHW serves as a potent reminder of the fragility of marine ecosystems to extreme climate events, emphasising the need for a concerted research effort aimed at understanding, predicting and mitigating the impacts of such phenomena on our oceans.

Conclusions

The 2014–2016 marine heatwave remains the longest event of its kind on record. Its wide range of impacts on a diversity of taxa and ecosystems highlights the potential for heatwaves to now profoundly alter the ocean. Our review underscores that heatwave impacts manifest not only through direct physiological stress, but also through significant indirect ecological impacts. Changes in habitat and food availability, even if short-lived, had cascading effects across trophic levels. Many of these observed impacts would not have been anticipated by single species models, highlighting the importance of ecosystem-based modelling approaches for improving predictions of marine heatwave impacts. While much remains to be learned about how marine heatwaves are altering our oceans, by synthesising the tremendous amount of work focused on this record-breaking event, we provide insights into how marine environments will look under future heatwaves. Moving forward, enhanced understanding of the extent to which the impacts of marine heatwaves on species and ecosystems are enduring or transient will be critical, especially as heatwave frequencies increase, limiting the time for recovery between successive events. With marine heatwaves now one of the predominant signatures of climate change, understanding the nature, breadth and duration of their impacts, as well as how these events interact with underlying gradual ocean climate change, is critical if we are to effectively manage our current and future oceans.

Acknowledgements

We thank the hundreds of authors who have dedicated their research efforts to studying the ecological impacts that we reviewed here, and the photographers and researchers for providing data and photographs, including Dr. John Ryan and Dr. Rebecca Miller. We thank the Coastal Observation and Seabird Survey Team (https://COASST.org) for providing the seabird mortality data presented in Figure 13 and are grateful to T. Jones for producing this figure. Data in Figure 7 include those from several long-term monitoring efforts worth particular acknowledgement, including the Alaska Ocean Observing System, Gulfwatch Alaska, Herring Research and Monitoring and the Multi-Agency Rocky Intertidal Network (MARINe). We acknowledge that the University of Victoria is located on the unceded land of the WSANEC, Esquimalt and the Songhees First Nations in British Columbia and that the University of Western Australia is on the traditional territory of the Whadjuk Noongar People in Western Australia. We pay our respects to these groups who remain the traditional custodians of these lands that we are grateful to share and enjoy. SS, LC, RH, DM, JM, MC, BT and JKB acknowledge funding from the Natural Sciences and Engineering Research Council of Canada, SS, GE, KB, SD, KLT, MC and JKB acknowledge funding from Mitacs, GE and JM acknowledge funding from Oceans North, JM acknowledges funding from Fisheries and Oceans Canada. SS acknowledges funding from the Forrest Research Foundation as recipient of an FRF Fellowship. Some of the images were made available by the IAN Network. The authors declare no competing interests.

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Supplementary Materials are provided online at: https://www.routledge.com/9781032964768