

Critical Research Needs for Forage Fish within Inner Shelf Marine Ecosystems

James W. Rivers  | Department of Forest Engineering, Resources, & Management, Oregon State University, 216 Peavy Forest Science Complex, Corvallis, OR 97331-5704. Email: jim.rivers@oregonstate.edu

Jennifer Bailey Guerrero | Department of Forest Engineering, Resources, & Management, Oregon State University, Corvallis, OR

Richard D. Brodeur | National Oceanic and Atmospheric Administration, Northwest Fisheries Science Center, Newport, OR

Gregory K. Krutzikowsky | Oregon Department of Fish and Wildlife, Newport, OR

Lindsay J. Adrean | Department of Forest Engineering, Resources, & Management, Oregon State University, Corvallis, OR

Scott A. Heppell | Department of Fisheries, Wildlife, and Conservation Sciences, Oregon State University, Corvallis, OR

Kym C. Jacobson | National Oceanic and Atmospheric Administration, Northwest Fisheries Science Center, Newport, OR

Kristen Milligan | Marine Studies Initiative, Oregon State University, Corvallis, OR

S. Kim Nelson | Department of Fisheries, Wildlife, and Conservation Sciences, Oregon State University, Corvallis, OR

Daniel D. Roby | Department of Fisheries, Wildlife, and Conservation Sciences, Oregon State University, Corvallis, OR

William J. Sydeman | Farallon Institute, Petaluma, CA

Leigh G. Torres | Marine Mammal Institute, Department of Fisheries, Wildlife, and Conservation Sciences, Oregon State University, Corvallis, OR

John A. Barth | Marine Studies Initiative, Oregon State University, Corvallis, OR

Forage fish are a critical component of marine ecosystems because they integrate energy across trophic levels within marine food webs. Many studies have highlighted the importance of this group, and past research efforts have focused largely on studying forage fish within offshore and estuarine areas. In contrast, limited information is available for forage fish on the inner continental shelf (<50 m water depth), where they encounter a range of anthropogenic stressors and support critical apex predator populations, including species of conservation concern. We highlight the importance of forage fish within inner shelf marine ecosystems using examples from the Northern California Current and describe outstanding research needs for forage fish within this topical area. Addressing these research needs is a critical step for maintaining productive forage fish populations within inner shelf ecosystems considering the social-, management-, and climate-driven changes that are expected to impact coastal regions in the coming decades.

INTRODUCTION

Forage fish, defined here as a broad range of small pelagic schooling fishes from several families (e.g., Clupeidae, Engraulidae, Osmeridae, Ammodytidae), are a critical component of ocean ecosystems because of the role they play within marine food webs (Alder et al. 2008; Pikitch et al. 2014). Forage fish are the nexus between lower and upper trophic levels because they serve as an energy transfer portal from plankton to apex predators that live both above and below the surface of the water (Figure 1). Indeed, their role in nutrient conversion is so important that forage fish can serve as a bottleneck for energy transfer across trophic levels, which, in turn, can lead to pronounced changes within marine communities. Forage fish can also exert “wasp-waist control” in marine ecosystems, where they exhibit top-down control on zooplankton and bottom-up control of upper trophic predators (Cury et al. 2000). In addition, the rapid and large population fluctuations that forage fish exhibit in response to environmental change (Pikitch et al. 2014) can serve as especially strong

demographic drivers of upper trophic levels during forage fish population downturns, such as occurred during the 2014–2016 marine heatwave in the northeastern Pacific when unproductive ocean conditions led to the death of 530,000 to 1.2 million common murre *Uria aalge* (Piatt et al. 2020).

In addition to their ecological importance, forage fish also play a vital role in food security and economic development worldwide, accounting for 25–30% of global fish landings annually (Alder et al. 2008; Alheit et al. 2019). For example, the Anchoveta *Engraulis ringens* is currently ranked first in marine capture fisheries production, comprising 10% of the world total and representing twice as much as the second-ranked species (<https://bit.ly/33704Zd>). Forage fish landings are used as bait and for human consumption, although they more typically support broader reduction industries that produce fishmeal and fish oil. In addition, forage fish provide indirect economic benefits by supporting upper trophic predator populations (Santora et al. 2020). As a prey source for larger finfish, forage fish

also support commercial fisheries for many other species, as well as a range of related industries that include recreational angling, tourism, and wildlife watching (Alheit et al. 2019). Thus, despite their small stature, forage fish have an outsized impact through their contributions to the structure and functioning of marine food webs (Hazen et al. 2019) and via the economic benefits they provide to coastal communities (Alder et al. 2008).

Due to their economic and ecological importance, forage fish have been a priority for researchers throughout the world (Alheit et al. 2019). Yet, even though they inhabit a range of habitats—from the open ocean to continental and insular shelf areas, and into bays and estuaries—our understanding of marine forage fish is almost entirely based on studies conducted on the outer shelf and in oceanic and estuarine areas. In contrast, very little information is available regarding forage fish over the inner continental shelf (i.e., areas within 5 km of the coast with water depths <50 m; Kirincich et al. 2005). For example, a Web of Science search conducted in September 2020 located 22,837 entries using the search term “forage fish,” yet only 1.4% of these entries also included the key words “inner shelf” or “nearshore.” Although a recent volume (Alheit et al. 2019) indicates that more attention is being paid to forage fish in some coastal areas, our understanding of forage fish remains biased strongly towards offshore and estuarine waters. Thus, an improved knowledge of forage fish dynamics in inner shelf areas is needed for proper management and conservation of coastal ecosystems, for several reasons. First, the inner shelf includes locations often targeted for conservation measures, such as marine reserves and protected areas, yet these areas are also at risk from a multitude of anthropogenic pressures. Coastal areas immediately adjacent to the inner shelf support a large and increasing human population with easy access to the ocean that puts pressure on marine habitats through recreational activities, commercial fisheries, a growing aquaculture industry, runoff of pollutants and wastewater, vessel fuel spills, and nearshore infrastructure development for navigation and renewable energy. Second, inner shelf areas provide critical connectivity for fishes that move between shallow water areas and deepwater areas between life stages, and for central-place foragers, such as seabirds and marine mammals that breed in coastal areas. Third, the influence of anthropogenic climate change is pronounced in inner shelf ecosystems and can lead to a range of impacts, such as increases in low oxygen events, ocean acidification, rising sea levels, and ocean warming (Harley et al. 2006). Finally, factors affecting primary productivity and the distribution of consumers and predators are highly dynamic, localized, and linked to natural and anthropogenic features (Santora et al. 2020). Taken together, this indicates that our understanding of forage fish in offshore waters is unlikely to translate directly to forage fish inhabiting inner shelf systems and ultimately handicaps our ability to model the impacts of different management policies and a changing climate on upper-trophic level predators and the ecosystem as a whole.

In October 2019, approximately 50 representatives from state and federal agencies, policymakers, nongovernmental organizations, private companies, and academia gathered in Newport, Oregon to discuss the impacts of existing knowledge gaps related to forage fish research. The day-long event began with presentations to provide background knowledge

regarding the inner shelf zone, forage fish ecology, and links between forage fish and their predators. It was then followed by small and large group discussions to identify major informational needs pertaining to forage fish and articulate steps that could be taken to advance our understanding of this group. In this article, we distill the knowledge gaps initially identified by participants at the 2019 workshop into a priority list of key research needs that we view as being the most important for advancing our knowledge base and, ultimately, implementing science-informed, ecosystem-based management. Although all coastal ecosystems have forage fish that support fisheries and apex predator populations, we frame our discussion on forage fish research needs by highlighting examples from the Northern California Current (NCC), because this system has many aspects to it that are well studied, including work by members of our research group that encompasses oceanographic processes, forage fish, and apex predators. We begin by providing a brief overview of the NCC upwelling ecosystem for context before highlighting four critical research needs that are needed to improve our understanding of forage fish ecology and enhance the conservation of the inner shelf ecosystems in which they are found (Alder et al. 2008; Pikitch et al. 2014; Alheit et al. 2019).

FORAGE FISH RESEARCH WITHIN THE NORTHERN CALIFORNIA CURRENT

The NCC spans from Vancouver Island, British Columbia, Canada to Cape Mendocino, California and supports a diverse suite of marine life. Productivity in this system is driven by seasonal, wind-driven coastal upwelling (Checkley and Barth 2009) that stem from winds generated by atmospheric pressure systems (i.e., North Pacific High) that blow southward along the coast from approximately March to October each year. This results in a deficit of water near the coast that initiates upwelling of cold, nutrient-rich waters from below. As this nutrient-rich water moves into the photic zone in the coastal ocean, it fuels phytoplankton blooms that serve as the basis of a rich food web from zooplankton to large, upper trophic predators. As in other regions, feeding habits of forage fish in the NCC vary seasonally and between years depending on environmental conditions, with diets consisting primarily of phytoplankton, copepods, and euphausiids during cool upwelling periods (Peck et al. 2021).

Efforts to gain an ecosystem-scale understanding of forage fish stock dynamics across the entire California Current ecosystem were initiated nearly 100 years ago and have been driven largely by the needs of fisheries management (Peck et al. 2021). Much of our understanding of forage fish abundance and distribution patterns in the NCC comes from regional surveys in coastal waters (Emmett et al. 2006). These surveys primarily used surface trawls and have taken place from late spring to early fall, although recent studies have progressed to using vessel-mounted acoustics that are supplemented with trawling to ground-truth acoustic signals (Phillips et al. 2017; Peck et al. 2021). Moored acoustic systems have been used to examine diel and seasonal variations in forage fish in a few locations (Kaltenberg et al. 2010). Shipboard acoustic and aerial surveys combined with net sampling have been used to characterize forage fish biomass in the California Current ecosystem for stock assessments (<https://bit.ly/3G8CEBm>) used to manage fisheries by the Pacific Fishery Management Council and the National Marine Fisheries Service. Nevertheless, the great

majority of surveys in the NCC and other eastern boundary upwelling ecosystems have been conducted in the mid to outer shelf areas, neglecting forage fish found in the inner shelf waters where they may be exposed to environmental drivers and processes on different scales, and where management may include individual state and/or regional policies.

RESEARCH NEEDS FOR FORAGE FISH WITHIN THE NCC INNER SHELF MARINE ECOSYSTEM

Research Need #1: Expanding Surveys of Forage Fish Abundance and Distribution

Effective continual monitoring is needed to track interannual variability in the abundance and distribution of all forage fishes (i.e., fished and unfished species), along with funding for such work. Most forage fish surveys have focused on fished species in mid-shelf and offshore waters, and only recently have inner shelf waters been surveyed using unmanned surface vehicle technologies and industry vessels (<https://bit.ly/3pZx-HVL>). Furthermore, relatively few NCC forage fish species undergo formal biomass assessments or even regular monitoring of their population status (Table 1). For example, the Northern Anchovy *E. mordax* uses the inner shelf from spring to fall and is a key prey type for numerous upper trophic-level predators (Brodeur et al. 2014; Szoboszlai et al. 2015; Litz et al. 2019); this species also supports a significant commercial baitfish market in the NCC. The central stock of Northern Anchovy, centered in California, is currently undergoing a stock assessment, the last of which was conducted in the 1990s (Jacobson et al. 1995). In contrast, there is no formal assessment for the northern stock of this species, which has shown signs of increasing population size in recent years (Auth et al. 2018). Abundance and distribution surveys for nonfished forage fish species that are found in inner shelf areas, such as the Pacific Sand Lance *Ammodytes personatus* are not undertaken in the coastal waters off the state of Washington, Oregon, or northern California, despite it being found in the diets of >100 species of fish, seabirds, and marine mammals (Szoboszlai et al. 2015). However, there has been some research conducted on Pacific Sand Lance in the inland waters from Alaska to Puget Sound (Baker et al. 2019 and references therein). Similarly, there are no efforts underway to survey the abundance and distribution of smelts (Osmeridae) in the marine waters of the NCC, even though they too are an important diet item for many predators. Given the key role that forage fish play in marine ecosystems and the lack of monitoring programs and survey work for forage fish within the inner shelf for use in stock assessments, there is great need for baseline survey work to provide a scientific basis for management. Moreover, establishment of regular abundance and distribution surveys will also facilitate hypothesis testing related to the ecological drivers of forage fish abundance and their influence on the population dynamics of their predators (see below).

Research Need #2: Understanding Bottom-Up Control of Forage Fish Populations

Although characterizing interannual population variability of forage fish populations is important, quantifying the drivers of that variability is the only means by which to develop predictive, mechanistic scenarios for future conditions. This includes understanding both abiotic and biotic drivers of bottom-up control of forage fish populations (Peck et al. 2021), including those that lead to large-amplitude population fluctuations of forage fish. In the NCC, interannual variation in the

lipid and fatty acid content of forage fish has been observed under different ocean conditions (Litz et al. 2010), and seasonal variation in these measures for both phytoplankton and copepod communities highlight the strong role oceanographic conditions can play in influencing predator-prey interactions at lower trophic levels (Miller et al. 2017). For example, fatty acid profiles differed and total lipid was lower in zooplankton collected in the winter of 2014–2015 during a marine heatwave compared to those collected during the cooler 2012–2013 winter (J. Fisher, Oregon State University, personal communication). Trophic position can vary as well for many forage fish species, with a more direct link to bottom-up processes during years with stronger, more productive upwelling (Brodeur and Pearcy 1992; Miller et al. 2010). However, to identify mechanisms and predict outcomes requires data on how nearshore oceanographic processes affect the lower trophic levels upon which forage fish feed, as well as data on forage fish abundance, growth, body condition, reproduction, and survival.

More research is also needed to determine the relative contributions of bottom-up and top-down processes in driving changes in forage fish stock abundance and prey quality (Boldt et al. 2019), as well as evaluating the role that competition among forage fish species play in influencing their population dynamics in inner shelf waters. Recent empirical work (Miller et al. 2010) in the California Coastal Current has questioned the validity of the wasp-waist paradigm in some years, and some modeling work suggests that trophic interactions may be more species-specific than ecosystemwide (Kaplan et al. 2019). Nevertheless, a well-informed predictive model based on a more mechanistic understanding of the interactions of bottom-up and top-down forcing on forage fish populations that includes the ecological specifics of the inner shelf, including its functional role as a significant spawning and nursery area for some forage fishes, would be of great benefit.

Research Need #3: Evaluating Links Between Forage Fish and Upper Trophic Predators

Information on predators of forage fish on inner shelf areas is limited, yet such information is critical for constructing dynamic food web models that can assess the mechanism(s) that drive complex trophic relationships. A wide variety of marine predators depend on forage fish as their primary prey, including elasmobranchs, teleosts (e.g., demersal fishes, salmon, tuna), seabirds, cetaceans, and pinnipeds (Brodeur et al. 2014; Pikitch et al. 2014; Szoboszlai et al. 2015; Hazen et al. 2019), many of which are of conservation concern. For example, Pacific salmon *Oncorhynchus* spp. comprise a number of species and stocks in the NCC that are classified as either threatened or endangered under the U.S. Endangered Species Act, and these species often consume forage fish (Brodeur et al. 2014). Similarly, the marbled murrelet *Brachyramphus marmoratus*, which is also listed as globally endangered (<https://www.iucnredlist.org/>), feeds primarily on forage fish in inner shelf waters of the NCC during the breeding season and is unable to nest successfully without an abundant supply of forage fish prey (Betts et al. 2020). Indeed, recent work using high-throughput genetic sequencing found more than a dozen forage fish species were used by murrelets during the breeding season, including commercially important species (Fountain et al., unpublished data). Many seabirds and pinnipeds are restricted to nearshore areas during the production of young, because they implement a central place foraging strategy that constrains foraging activities to areas that are in close proximity

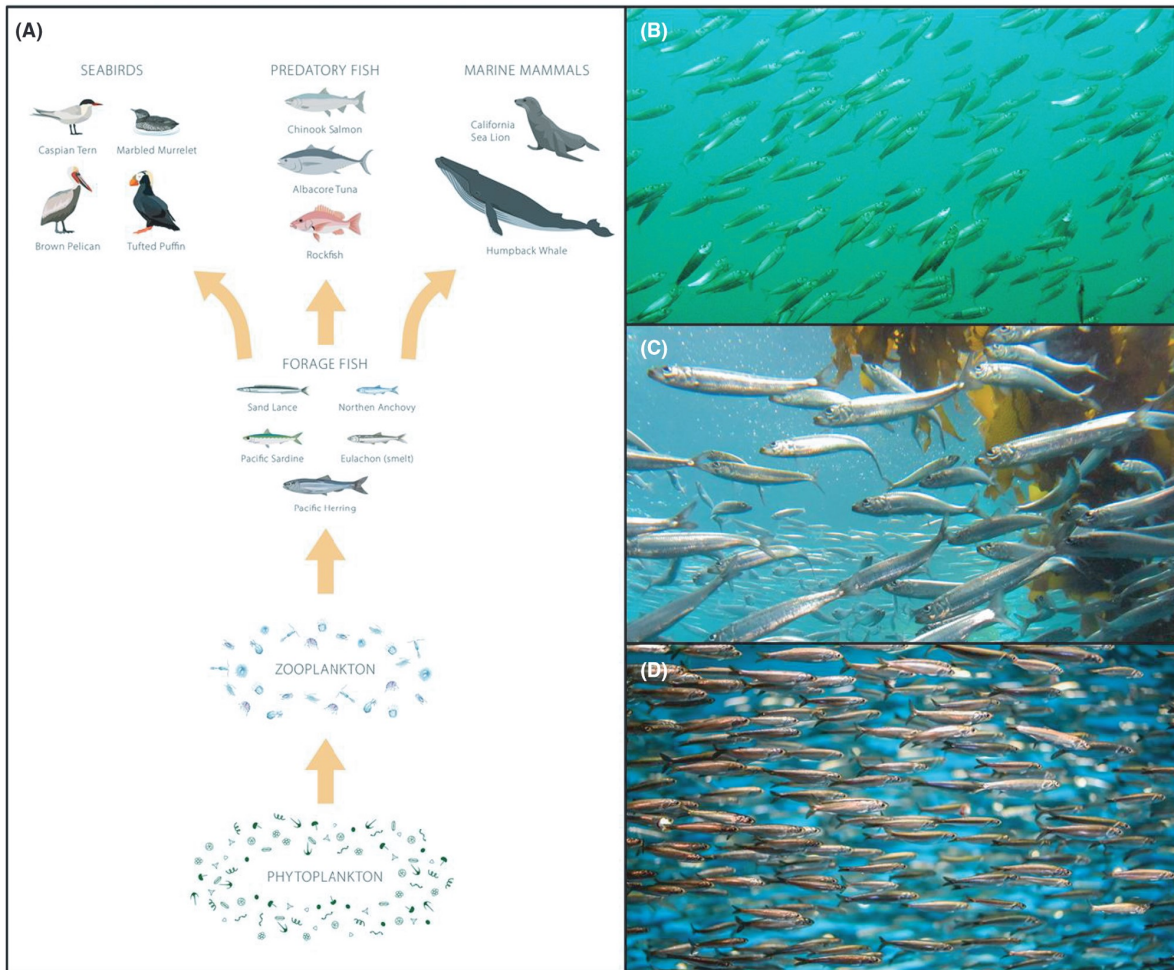


Figure 1. (A) Forage fish are a critical nexus within marine food webs because they transfer energy (arrows) from lower trophic levels to upper trophic levels comprised of predatory fish, marine mammals, and seabirds. Forage fish represent a wide range of species, with the (B) Pacific Herring *Clupea pallasii*, (C) Pacific Sardine *Sardinops sagax*, and (D) Northern Anchovy *Engraulis mordax* being especially important in coastal ecosystems along the western coast of North America. Photo/illustration credits: (A) Moni Kovacs and Kathleen Cantner, (B) Janna Nichols, (C) Geoff Shester, and (D) National Marine Fisheries Service.

to nesting colonies, rookeries, and haulout sites. Finally, it is possible that large releases of hatchery salmon into the NCC ecosystem creates both predation and competition challenges for forage fishes (Thayer et al. 2014; Litz et al. 2019). Although this is likely a transient event as smolts migrate offshore and prespawning adults migrate back inshore, the magnitude of such impact is currently unknown and should be the focus of future work.

Given that changes in the forage fish community can have a strong effect on the productivity and survival of many predators (Cury et al. 2011; McClatchie et al. 2016; Piatt et al. 2020), better assessment of the dietary preferences of different predator species, and how their preferences shift in space and time are also needed. For example, Gladics et al. (2014) used a combination of methods to examine nearshore interactions between the piscivorous common murre, three piscivorous fishes, and forage fish across contrasting ocean conditions, and could serve as a model for future work. Such data will help to prioritize conservation actions for key prey species in inner shelf food webs, and for those species that

might shift into that role with projected climate change. A promising first step in this direction would be the undertaking a comprehensive review of previous work on nearshore apex predator diets; such an effort should fill species- and guild-specific data gaps, as well as generate a preliminary list of forage fishes that are especially important for supporting predator populations. In addition to understanding the trophic relationships between forage fish and their predators, it is also critical to locate and protect inner shelf foraging hotspots of upper trophic predators given that the ocean is spatially heterogeneous with respect to forage fish distribution (e.g., Phillips et al. 2017). This is a key consideration for conservation and management of central place foragers such as seabirds and pinnipeds, because their reproductive success depends on the proximity of forage fish to terrestrial breeding areas. If those hotspots are consistent both spatially and temporally, they may warrant consideration for protection from human activities.

Decreased primary productivity and warm sea surface anomalies have led to extreme variability in marine food webs,

with cascading negative impacts on survival, productivity, and physiological condition of apex predators (Figures 2A, 2B; McClatchie et al. 2016; Piatt et al. 2020; Soledad Lemos et al. 2020). Examining the effects of extreme shifts in ocean conditions on forage fish availability will help to reveal mechanisms underpinning this relationship. It is also important to identify spatially explicit differences in population trends of key forage fishes to evaluate spatial variation in bottom-up and top-down forces linked to forage fish abundance. Detailed diet studies of upper trophic predators are a requisite by which spatial and temporal changes in forage fish availability and relationships to ocean climate can be evaluated. However, such research needs to go beyond documenting prey use alone and must include a focus on temporal and spatial variation in the energetic profitability of consuming different forage fishes (Litz et al. 2019). Energy content is a product of both body size and energy density and varies as a function of ocean conditions (von Biela et al. 2019); therefore, studies evaluating how forage fish availability affects populations of apex predators should include assessments of the taxonomic composition of forage fish found in predator diets, as well as their size and energy density.

Research Need #4: Predicting the Effects of Future Climate Change

Although it is impossible to accurately predict the long-term effects of anthropogenic climate change on marine communities, recent anomalies may provide a preview of future changes that are expected in NCC nearshore areas. From

2014–2016, the NCC experienced one of the most extensive warming events of the past 2 decades when a reduction in winter storms in the Gulf of Alaska created a warm water lens that shifted south and prevented sustained upwelling in the NCC (Bond et al. 2015); it was then followed by one of the warmest El Niño events on record in the North Pacific (Jacox et al. 2016). The fallout of this extended warming period propagated throughout the northeastern Pacific and the impacts on forage fish populations are thought to have been extensive (Arimitsu et al. 2021). In the absence of their normal crustacean prey, many forage fish diets shifted to gelatinous and lipid-poor, warmwater zooplankton species during warm years, such as occurred during the North Pacific marine heatwave of 2015–2016 (Brodeur et al. 2019; von Biela et al. 2019). These alternative prey taxa are thought to be less energetically profitable and led to lower fish body condition (Brodeur et al. 2019), which likely drove down forage fish productivity and energy content. This, in turn, negatively impacted food resources for higher trophic level predators during anomalously warm ocean years (McClatchie et al. 2016; Piatt et al. 2020; Soledad Lemos et al. 2020). Warming ocean temperatures are also likely to increase metabolic demand of forage fish species and alter the foraging behavior and profitability of their predators (Piatt et al. 2020).

The large sea surface temperature anomalies of the 2014–2016 marine heatwave (Bond et al. 2015) also resulted in an unprecedented expansion of toxic algal blooms that closed commercial fisheries, and the toxins likely propagated up the food web to stranded marine mammals via

Table 1. Forage fish species found in inner shelf waters of the Northern California Current (NCC). Included are fish species that are part of the forage base throughout their entire lives, as well as species where only the juvenile stage fills that role (e.g., salmon, rockfish). Information on stock assessments or at least some form of population biomass estimates for the species and whether they are listed under the Endangered Species Act (ESA) is provided. Predators that feed on these species are listed by group: birds (B), marine mammals (M), and fish (F). Fisheries that do or have targeted these species are also noted. Portions of a species' life cycle spent in nearshore waters is either partial (P) or full (F). Occupation of the NCC is either resident (R) or transient (T). Fisheries that target each species include commercial (C), sport (S), tribal (T), or none (N). Invertebrate species that are part of the forage base, such as squid, krill, and mysids, are not included.

Species	Assessed?	ESA Listed?	Predators	Full/partial life cycle	Resident/Transient	Target fishery
Pacific Herring <i>Clupea pallasii</i>	Some	No	B, M, F	P	R	C, S, T
Pacific Sardine <i>Sardinops sagax</i>	Yes	No	B, M, F	P	T	C
Northern Anchovy <i>Engraulis mordax</i>	Yes ¹	No	B, M, F	P	R	C
Whitebait Smelt <i>Allosmerus elongatus</i>	No	No	B, M, F	P	R	S
Surf Smelt <i>Hypomesus pretiosus</i>	No	No	B, M, F	F	R	S, T
Night Smelt <i>Spirinchus starksi</i>	No	No	B, M, F	P	R	C, S
Longfin Smelt <i>S. thaleichthys</i>	No	No	B, M, F	P	R	S
Eulachon <i>Thaleichthys pacificus</i>	No	Yes	B, M, F	P	R	S, T
Pacific Sand Lance <i>Ammodytes personatus</i>	No	No	B, F	F	R	N
Top Smelt <i>Atherinops affinis</i>	No	No	B, M, F	P	R	S
Pacific Mackerel <i>Scomber japonicus</i>	Yes	No	M	P	T	C
Chinook Salmon <i>Oncorhynchus tshawytscha</i>	Yes	Some	B, M, F	P	R	C, S, T
Chum Salmon <i>O. keta</i>	No	No	B, M, F	P	R	C, S, T
Coho Salmon <i>O. kisutch</i>	Yes	Some	B, M, F	P	R	C, S, T
Pink Salmon <i>O. gorbuscha</i>	No	No	B, M, F	P	R	C, S, T
Sockeye Salmon <i>O. nerka</i>	No	Some	B, M, F	P	R	C, S, T
Juvenile rockfish <i>Sebastes</i> spp.	Adults only	No	B, M, F	P	R	N

¹Stock assessment undertaken only for the central subpopulation

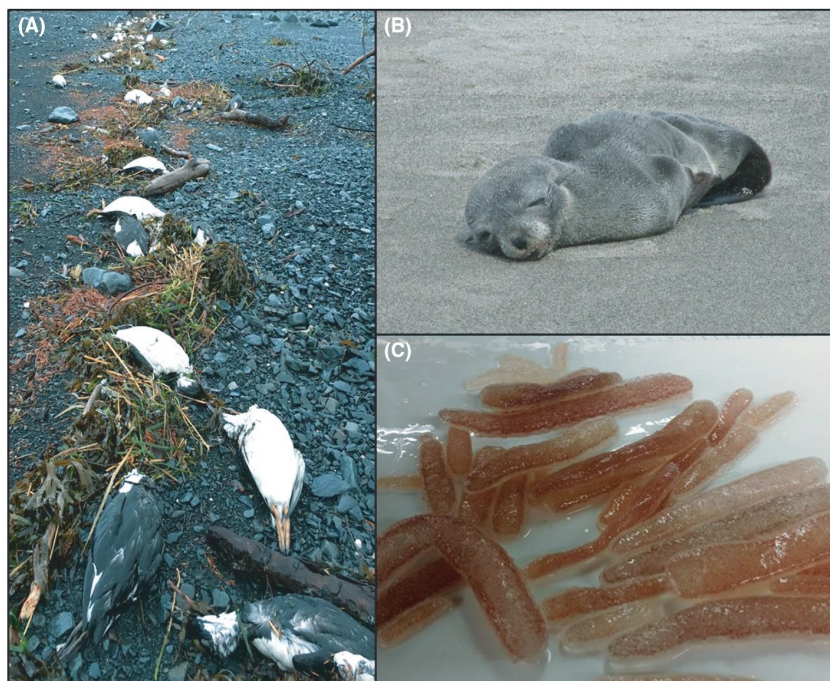


Figure 2. Recent changes in the coastal marine ecosystems have led to (A) large-scale seabird die-offs, as shown by this common murre *Uria aalge* mortality event, and (B) reduced body condition of marine mammals, such as this Guadalupe fur seal *Arctocephalus townsendi*. Mortality and reduced health can occur in apex predators due to reductions in the availability of the forage fish upon which they depend. In addition, changes in ocean conditions are also leading to an influx of new species into coastal ecosystems, such as (C) the pyrosome *Pyrosoma atlanticum*, which has been found to be abundant and widespread in coastal waters of the Northern California Current during recent warming events; the impact of pyrosomes on forage fish prey availability is currently unknown. Photo credits: (A) David Irons, (B) Jane Holbrook, Oregon Marine Mammal Stranding Network, (C) Richard Brodeur.

forage fish that consumed plankton (McCabe et al. 2016). Copepod assemblages failed to undergo the typical transition from warmwater, lipid-poor species to coolwater, lipid-rich species during summer months (Fisher et al. 2020), and colonial gelatinous pyrosomes moved north (Figure 2C), substantially reducing phytoplankton biomass (O'Loughlin et al. 2020). The timing and spawning of pelagic fishes were also altered, with Northern Anchovy and Pacific Sardine *Sardinops sagax* larvae present year-round, indicating nearly continuous nearshore spawning in species that normally spawn offshore during the summer months (Auth et al. 2018). Although the full extent of how these especially warm conditions impacted marine food webs is still being realized, it appears likely that this type of anomalous event will increase with projected climate change in the NCC ecosystem.

Given that climate-driven changes are creating conditions outside the range of recent historical variation, it is perhaps not surprising that current forage fish distribution and production models have experienced reduced predictive ability (Muhling et al. 2020). Findings such as these emphasize the importance of research to better understand forage fish distribution and abundance, their underlying population drivers and population variability, and their interaction with apex predators; projected climate change scenarios lend urgency and add heightened importance to this work. Recent anomalous events also demonstrate the need for

studies aimed at understanding fundamental responses to climate warming, such as full lifecycle physiological tolerances (Muhling et al. 2020). Although we view all of the research needs we have outlined as important, the anomalous events recorded in recent years may only hint at the full scope of how anthropogenic climate change may alter inner shelf marine ecosystems globally, including forage fish. Thus, undertaking research to improve our understanding of forage fish in inner shelf systems at present provides the best opportunity to gain the knowledge needed to conserve and manage this key group as our oceans continue to be impacted by a changing climate.

CURRENT CHALLENGES AND FUTURE OPPORTUNITIES FOR UNDERSTANDING FORAGE FISH IN THE NCC

Forage fish are well recognized for both their economic value and their ecological importance, and this recognition has been better acknowledged recently by federal-, state-, tribal-, and local-level policy processes. For example, federal legislation in the United States has included fishery management plan amendments designed to protect unfished forage species and adopt a broader and more comprehensive view of ecosystem-based fishery management (<https://bit.ly/3JOL5UD>). Although not specifically aimed at addressing inner shelf areas, this represents a promising step towards broader recognition of the economic and ecological values that forage fish provide, and the importance of their

Table 2. Examples of approaches to advance recommendations of (1) expanding surveys of forage fish abundance and distribution, (2) understanding bottom-up control of forage fish populations, (3) evaluating links between forage fish and upper trophic predators, and (4) predicting the effects of future climate change in inner shelf marine ecosystems.

Challenge	Operational Needs	Examples of Solutions
Nascent public policy recognition of inner shelf forage fish research needs	Ecosystem-based public policy for understanding forage fish and associated trophic structures	<ul style="list-style-type: none"> Ecosystem-based amendments to United States fishery management plans including highly migratory species (https://bit.ly/3JOL5UD) Financial support structures connected to public policy directives
Primarily short-term, small spatial scale research	Identify and augment existing long-term platforms and programs for inner shelf forage fish and predator monitoring and process studies; create new platforms	<ul style="list-style-type: none"> Newport Hydrographic Line (Auth et al. 2018) National Oceanic and Atmospheric Administration Cooperative Institutes Marine Biodiversity Observation Networks (Duffy et al. 2013) Partnership for Interdisciplinary Studies Coastal Oceans (Menge et al. 2019) International Long-Term Ecological Research Network (Muelbert et al. 2019)
	Intentional opportunities for knowledge networking	<ul style="list-style-type: none"> Symposia co-convened by professional societies representing the different disciplines Researcher field exchanges
	Unite oceanography, climate science, fisheries, upper trophic level research	<ul style="list-style-type: none"> Cooperative research agreements
	Identify and fill gaps in data access and sharing; repository crosswalks	<ul style="list-style-type: none"> DataOne (www.dataone.org)
Hazards of work in nearshore	Invest in and operationalize new technologies using mobile and/or long-distance sampling	<ul style="list-style-type: none"> Autonomous underwater vehicles Sail drones environmental DNA analysis Optical and acoustic data Drone imagery
	Use vessels suitable for surveying and sampling in the inner shelf	<ul style="list-style-type: none"> Collaborations with industry

conservation for both ecosystem functions and human populations (Anstead et al. 2021).

In our view, we predict that several obstacles that have historically constrained research on forage fish within inner shelf systems may be overcome using diverse approaches that have been implemented in other settings (Duffy et al. 2013; Kuebbing et al. 2018; Menge et al. 2019; Muelbert et al. 2019; Table 2). As is common for other interdisciplinary and long-term ecosystem research, a combination of limited budgets and the short-term nature of funding cycles for research and monitoring ultimately restricts the scope of projects to short time periods and prevents capturing longer-term fluctuations in forage fish populations. The shallow nearshore environment also imposes a unique set of logistical challenges that can impede forage fish research. These areas contain hazards to both navigation and working conditions that are particularly pronounced in rough weather, and larger research vessels designed to work in deeper open waters are ill equipped to handle such conditions. Additionally, the patchy nature of forage fish necessitates surveying large areas of the ocean, requiring extremely mobile and/or long-endurance sampling platforms. Translating correlative observations into causal mechanism for predictive modeling remains difficult because of these pronounced limitations and obstacles.

The development and funding of a long-term monitoring and research programs designed to address the research needs described herein provides the best opportunity to advance our knowledge base for inner shelf forage fish (Table 2). Annual assessments of forage fish are critical for documenting population fluctuations related to local conditions and basin-scale

anomalies, in addition to determining harvest levels for targeted forage fish fisheries that also provide an adequate prey base for upper trophic predators. Such a nearshore program could benefit existing observation platforms and monitoring programs by augmenting offshore surveys that specifically target mapping and sampling of forage fish, such as the long-term ichthyoplankton data being collected along the Newport Hydrographic Line in the NCC (Auth et al. 2018). Additional data can be obtained by combined observational approaches, through traditional sampling methods that are tailored for use by recreational anglers and citizen scientists, as well as new technological approaches that include autonomous underwater vehicles, sail drones, environmental DNA analysis, optical and acoustic data, and imaging from aerial drones, among others. These emerging technologies provide new horizons for research in the undersampled nearshore zone, enabling us to overcome many historical challenges due to logistical hazards. With respect to funding, a multidisciplinary, multiagency cooperative approach that implements the sharing of financial responsibility and resources would lead to the procurement of comprehensive data sets that would fulfill the needs of researchers, managers, and policymakers alike. Although establishing and funding new cross-agency forage fish research programs will be challenging, we are optimistic that impediments to such programs will be outweighed by the value of the new information they produce, and that steps can be taken now to move towards this larger goal. This is especially true given that research on forage fishes on the inner shelf must be undertaken soon if we are to address the social-, management-, and climate-driven changes that are expected in coastal

regions and their associated marine ecosystems in the coming decades.

ACKNOWLEDGMENTS

Funding for this work was provided by the Marine Studies Initiative at Oregon State University, the College of Forestry at Oregon State University, and the USDA National Institute of Food and Agriculture, McIntire Stennis project 1014995. We thank the attendees of the 2019 Forage Fish Workshop for thoughtful discussion regarding forage fish research needs within inner shelf marine ecosystems. There is no conflict of interest declared in this article.

ORCID

James W. Rivers  <https://orcid.org/0000-0001-5041-6002>

REFERENCES

- Alder, J., B. Campbell, V. Karpouzi, K. Kaschner, and D. Pauly. 2008. Forage fish: from ecosystems to markets. *Annual Review of Environment and Resources* 33:153–166.
- Alheit, J., A. Bertrand, R. D. Brodeur, S. Garrido, M. A. Peck, M. Quaas, D. Reid, D. Robert, S. Somarakis, A. Takasuka, O. Thébaud, and V. Trenkel, editors. 2019. Drivers of dynamics of small pelagic fish resources: biology, management and human factors. *Marine Ecology Progress Series* 617–618:1–376.
- Anstead, K. A., K. Drew, D. Chagaris, A. M. Schueller, J. E. McNamee, A. Buchheister, G. Nesslage, J. H. Uphoff Jr., M. J. Wilberg, A. Sharov, M. J. Dean, J. Brust, M. Celestino, S. Madsen, S. Murray, M. Appelman, J. C. Ballenger, J. Brito, E. Cosby, C. Craig, C. Flora, K. Gottschall, R. J. Latour, E. Leonard, R. Mroch, J. Newhard, D. Orner, C. Swanson, J. Tinsman, E. D. Houde, T. J. Miller, and H. Townsend. 2021. The path to an ecosystem approach for forage fish management: a case study of Atlantic Menhaden. *Frontiers in Marine Science* 8:607657.
- Arimitsu, M. L., J. F. Piatt, S. Hatch, R. M. Suryan, S. Batten, M. A. Bishop, R. W. Campbell, H. Coletti, D. Cushing, K. Gorman, R. R. Hopcroft, K. J. Kuletz, C. Marsteller, C. McKinstry, D. McGowan, J. Moran, S. Pegau, A. Schaefer, S. Schoen, J. Straley, and V. R. von Biela. 2021. Heatwave-induced synchrony within forage fish portfolio disrupts energy flow to top pelagic predators. *Global Change Biology* 27:1859.
- Auth, T. D., E. A. Daly, R. D. Brodeur, and J. L. Fisher. 2018. Phenological and distributional shifts in ichthyoplankton associated with recent warming in the northeast Pacific Ocean. *Global Change Biology* 24:259–272.
- Baker, M. R., M. E. Matta, M. Beaulieu, N. Paris, S. Huber, O. J. Graham, T. Pham, N. B. Sisson, C. P. Heller, A. Witt, and M. R. O'Neill. 2019. Intra-seasonal and inter-annual patterns in the demographics of sand lance in response to environmental drivers in the North Pacific. *Marine Ecology Progress Series* 617–618:221–244.
- Betts, M. G., J. M. Northrup, J. A. Bailey Guerrero, L. J. Adrean, S. K. Nelson, J. L. Fisher, B. D. Gerber, M.-S. Garcia-Heras, Z. Yang, D. D. Roby, and J. W. Rivers. 2020. Squeezed by a habitat split: warm ocean conditions and old-forest loss interact to reduce long-term occupancy of a threatened seabird. *Conservation Letters* 13:e12745.
- Boldt, J. L., M. Thompson, C. N. Rooper, D. E. Hay, J. F. Schweiger, T. J. II Quinn, J. S. Cleary, and C. M. Neville. 2019. Bottom-up and top-down control of small pelagic forage fish: factors affecting age-0 herring in the Strait of Georgia, British Columbia. *Marine Ecology Progress Series* 617–618:53–66.
- Bond, N. A., M. F. Cronin, H. Freeland, and N. Mantua. 2015. Causes and impacts of the 2014 warm anomaly in the NE Pacific. *Geophysical Research Letters* 42:3414–3420.
- Brodeur, R. D., J. C. Buchanan, and R. L. Emmett. 2014. Pelagic and demersal fish predators on juvenile and adult forage fishes in the Northern California Current: spatial and temporal variations. *California Cooperative Oceanic Fisheries Investigation Reports* 55:96–116.
- Brodeur, R. D., M. E. Hunsicker, A. Hann, and T. W. Miller. 2019. Effects of warming ocean conditions on feeding ecology of small pelagic fishes in a coastal upwelling ecosystem: a shift to gelatinous food sources. *Marine Ecology Progress Series* 617–618:149–163.
- Brodeur, R. D., and W. G. Pearcy. 1992. Effects of environmental variability on trophic interactions and food web structure in a pelagic upwelling ecosystem. *Marine Ecology Progress Series* 84:101–119.
- Checkley, D. M., and J. A. Barth. 2009. Patterns and processes in the California Current system. *Progress in Oceanography* 83:49–64.
- Cury, P., A. Bakun, R. J. M. Crawford, A. Jarre, R. A. Quinones, L. J. Shannon, and H. M. Verheye. 2000. Small pelagics in upwelling systems: patterns of interaction and structural changes in “wasp-waist” ecosystems. *ICES Journal of Marine Sciences* 57:603–618.
- Cury, P. M., I. L. Boyd, S. Bonhommeau, T. Anker-Nilssen, R. J. M. Crawford, R. W. Furness, J. A. Mills, E. J. Murphy, H. Osterblom, M. Paleczny, J. F. Piatt, J.-P. Roux, L. Shannon, and W. J. Sydeman. 2011. Global seabird response to forage fish depletion: one-third for the birds. *Science* 334:1703–1706.
- Duffy, J. E., L. A. Amaral-Zettler, D. G. Fautin, G. Paulay, T. A. Ryneanson, H. M. Sosik, and J. J. Stachowicz. 2013. Envisioning a marine biodiversity observation network. *BioScience* 63:350–361.
- Emmett, R. L., G. K. Krutzikowsky, and P. J. Bentley. 2006. Abundance and distribution of pelagic piscivorous fishes in the Columbia River plume during spring/early summer 1998–2003: relationship to oceanographic conditions, forage fishes, and juvenile salmonids. *Progress in Oceanography* 68:1–26.
- Fisher, J., D. Kimmel, T. Ross, S. Batten, E. Bjorkstedt, M. Galbraith, K. Jacobson, J. E. Keister, A. Sastri, K. Suchy, and S. Zeman. 2020. Copepod responses to, and recovery from, the recent marine heatwave in the northeast Pacific. *PICES Press* 28:65–71.
- Gladics, A. J., R. M. Suryan, R. D. Brodeur, L. M. Segui, and L. Z. Filliger. 2014. Constancy and change in marine predator diets across a shift in oceanographic conditions in the Northern California Current. *Marine Biology* 161:837–851.
- Harley, C. D. G., A. R. Hughes, K. M. Hultgren, B. G. Miner, C. J. B. Sorte, C. S. Thornber, L. F. Rodriguez, L. Tomanek, and S. L. Williams. 2006. The impacts of climate change in coastal marine systems. *Ecology Letters* 9:228–241.
- Hazen, E. L., B. Abrams, S. Brodie, G. Carrol, M. G. Jacox, M. S. Savoca, K. L. Scales, W. J. Sydeman, and S. J. Bograd. 2019. Marine top predators as climate and ecosystem sentinels. *Frontiers in Ecology and the Environment* 17:565–574.
- Jacobson, L. D., N. C. H. Lo, S. F. Jr Herrick, and T. Bishop. 1995. Spawning biomass of the Northern Anchovy in 1995 and status of the coastal pelagic fishery during 1994. National Marine Fisheries Service, Southwest Fisheries Science Center, Administrative Report LJ-95-11. La Jolla, California.
- Jacox, M. G., E. L. Hazen, K. D. Zaba, D. L. Rudnick, C. A. Edwards, A. M. Moore, and S. J. Bogard. 2016. Impacts of the 2015–2016 El Niño on the California Current system: early assessment and comparison to past events. *Geophysical Research Letters* 43:7072–7080.
- Kaltenberg, A. M., R. L. Emmett, and K. J. Benoit-Bird. 2010. Timing of forage fish and seasonal appearances in the Columbia River plume and link to oceanographic conditions. *Marine Ecology Progress Series* 419:171–184.
- Kaplan, I. C., T. B. Francis, A. E. Punt, L. E. Koehn, E. Curchister, F. Hurtado-Ferro, K. F. Johnson, S. E. Lluch-Cota, W. J. Sydeman, T. E. Essington, N. Taylor, K. Holsman, A. D. MacCall, and P. S. Levin. 2019. A multi-model approach to understanding the role of Pacific Sardine in the California Current food web. *Marine Ecology Progress Series* 617–618:307–321.
- Kirincich, A. R., J. A. Barth, B. A. Grantham, B. A. Menge, and J. Lubchenco. 2005. Wind-driven inner shelf circulation off central Oregon during summer. *Journal of Geophysical Research* 110:C10S03 Available: <https://bit.ly/331gke5> (January 2022).
- Kuebbing, S. E., A. P. Reimer, S. A. Rosenthal, G. Feinberg, A. Leiserowitz, J. A. Lau, and M. A. Bradford. 2018. Long-term research in ecology and evolution: a survey of challenges and opportunities. *Ecological Monographs* 88:245–258.
- Litz, M. C., R. D. Brodeur, R. L. Emmett, S. S. Heppell, R. S. Rasmussen, L. O'Higgins, and M. S. Morris. 2010. The effects of variable oceanographic conditions on forage fish lipid content and fatty acid composition in the Northern California Current. *Marine Ecology Progress Series* 405:71–85.
- Litz, M. N. C., J. A. Miller, R. D. Brodeur, E. A. Daly, L. A. Weitkamp, A. G. Hansen, and A. M. Claiborne. 2019. Energy dynamics of subyearling Chinook Salmon reveal the importance of piscivory to short term growth during early marine residence. *Fisheries Oceanography* 28:273–290.
- McCabe, R. M., B. M. Hickey, R. M. Kudela, K. A. Lefebvre, N. G. Adams, B. D. Bill, F. M. D. Gulland, R. E. Thomson, W. P. Cochlan, and V. L. Trainer. 2016. An unprecedented coastwide toxic algal bloom linked to anomalous ocean conditions. *Geophysical Research Letters* 43:10366–10376.

- McClatchie, S., J. Field, A. R. Thompson, T. Gerrodette, M. Lowry, P. C. Fiedler, W. Watson, K. M. Nieto, and R. D. Vetter. 2016. Food limitation of sea lion pups and the decline of forage off central and southern California. *Royal Society Open Science* 3:150628.
- Menge, B. A., K. Milligan, J. E. Caselle, J. A. Barth, C. A. Blanchette, M. H. Carr, F. Chan, R. K. Cowen, M. Denny, S. D. Gaines, G. E. Hofmann, K. J. Kroeker, J. Lubchenco, M. A. McManus, M. Novak, S. R. Palumbi, P. T. Raimondi, G. N. Somero, R. R. Warner, L. Washburn, and J. W. White. 2019. PISCO: advances made through the formation of a large-scale, long-term consortium for integrated understanding of coastal ecosystem dynamics. *Oceanography* 32:16–25.
- Miller, J. A., W. T. Peterson, L. A. Copeman, X. Du, C. A. Morgan, and M. N. C. Litz. 2017. Temporal variation in the biochemical ecology of lower trophic levels in the Northern California Current. *Progress in Oceanography* 155:1–12.
- Miller, T. W., R. D. Brodeur, G. Rau, and K. Omori. 2010. Prey dominance shapes trophic structure of the Northern California Current pelagic food web: evidence from stable isotopes and diet analysis. *Marine Ecology Progress Series* 420:15–26.
- Muelbert, J. H., N. J. Nidzieko, A. T. R. Acosta, S. E. Beaulieu, A. F. Bernardino, E. Boikova, T. G. Bornman, B. Cataletto, K. Deneudt, E. Eliason, A. Kraberg, M. Nakaoka, A. Pugnetti, O. Ragueneau, M. Scharfe, T. Soltwedel, H. M. Sosik, A. Stanisci, K. Stefanova, P. Stephan, A. Stier, J. Wikner, and A. Zingone. 2019.ILTER - The International Long-Term Ecological Research Network as a platform for global coastal and ocean observation. *Frontiers in Marine Science* 6:527.
- Muhling, B., S. Brodie, J. Smith, D. Tommasi, C. Gaitan, E. Hazen, M. Jacox, T. Auth, and R. D. Brodeur. 2020. Predictability of species distributions deteriorates under novel environmental conditions in the California Current System. *Frontiers in Marine Science* 7:589.
- O'Loughlin, J. H., K. S. Bernard, E. A. Daly, S. Zeman, J. L. Fisher, R. D. Brodeur, and T. P. Hurst. 2020. Implications of *Pyrosoma atlanticum* range expansion on phytoplankton standing stocks in the Northern California Current. *Progress in Oceanography* 188:102424.
- Peck, M. A., J. Alheit, A. Bertrand, I. A. Catalan, S. Garrido, M. Moyano, R. Rykaczewski, A. Takasuka, and C. D. van der Lingen. 2021. Small pelagic fish in the new millennium: a bottom-up view of global research effort. *Progress in Oceanography* 191:102494.
- Phillips, E. M., J. K. Horne, and J. E. Zamon. 2017. Predator-prey interactions influenced by a dynamic river plume. *Canadian Journal of Fisheries and Aquatic Sciences* 74:1375–1390.
- Platt, J. F., J. K. Parrish, H. M. Renner, S. K. Schoen, T. T. Jones, M. L. Arimitsu, K. J. Kuletz, B. Bodenstein, M. Garcia-Reyes, R. S. Duerr, R. M. Corcoran, R. S. A. Kaler, G. J. McChesney, R. T. Golightly, H. A. Coletti, R. M. Suryan, H. K. Burgess, J. Lindsey, K. Lindquist, P. M. Warzybok, J. Jahncke, J. Roletto, and W. J. Sydeman. 2020. Extreme mortality and reproductive failure of common murrelets resulting from the northeast Pacific marine heatwave of 2014–2016. *PLOS One* 15:e0226087.
- Pikitch, E. K., K. J. Rountos, T. E. Essington, C. Santora, D. Pauly, R. Watson, U. R. Sumaila, P. D. Boersma, I. L. Boyd, D. O. Conover, P. Cury, S. S. Heppell, E. D. Houde, M. Mangel, E. Plaganyi, K. Sainsbury, R. S. Steneck, T. M. Geers, N. Gownaris, and S. B. Munch. 2014. The global contribution of forage fish to marine fisheries and ecosystems. *Fish and Fisheries* 15:43–64.
- Santora, J. A., N. J. Mantua, I. D. Schroeder, J. C. Field, E. L. Hazen, S. J. Bograd, W. J. Sydeman, B. K. Wells, J. Calambokidis, L. Saez, D. Lawson, and K. A. Forney. 2020. Habitat compression and ecosystem shifts as potential links between marine heatwave and record whale entanglements. *Nature Communications* 11:article 536.
- Soledad Lemos, L., J. D. Burnett, T. E. Chandler, J. L. Sumich, and L. G. Torres. 2020. Intra- and inter-annual variation in gray whale body condition on a foraging ground. *Ecosphere* 11:e03094.
- Szoboszlai, A. I., J. A. Thayer, S. A. Wood, W. J. Sydeman, and L. E. Koehn. 2015. Forage species in predator diets: synthesis of data from the California Current. *Ecological Informatics* 29:45–56.
- Thayer, J. A., J. C. Field, and W. J. Sydeman. 2014. Changes in California Chinook Salmon diet over the past 50 years: relevance to the recent population crash. *Marine Ecology Progress Series* 498:249–261.
- von Biela, V. R., M. L. Arimitsu, J. F. Platt, B. Heflin, S. K. Schoen, J. L. Trowbridge, and C. M. Clawson. 2019. Extreme reduction in nutritional value of a key forage fish during the Pacific marine heatwave of 2014–2016. *Marine Ecology Progress Series* 613:171–182. **AFS**