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Biological Impacts of the 2013–2015 Warm-Water Anomaly in the Northeast Pacific

Winners, Losers, and the Future

Photo credit: Kaitlyn B. Lowder

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ABSTRACT. A large patch of anomalously warm water (nicknamed “the Blob”) appeared off the coast of Alaska in the winter of 2013–2014 and subsequently stretched south to Baja California. This northeastern Pacific warm-water anomaly persisted through the end of 2015. Scientists and the public alike noted widespread changes in the biological structure and composition of both open-ocean and coastal ecosystems. Changes included geographical shifts of species such as tropical copepods, pelagic red crabs, and tuna; closures of commercially important fisheries; and mass strandings of marine mammals and seabirds. The ecological responses to these physical changes have been sparsely quantified and are largely unknown. Here, we provide a bottom-up summary of some of the biological changes observed in and around the areas affected by the Blob.

INTRODUCTION

Starting in the winter of 2013–2014, a large patch of anomalously warm water (dubbed “the Blob”) formed in the north-eastern Pacific. By the end of 2015, this warm-water anomaly (WWA) stretched from Alaska to Baja California. With the warm water came numerous strange occurrences. An unprecedented harmful

algal bloom stretched from the Aleutian Islands down to southern California. Mass strandings of marine mammals and seabirds occurred along the west coast of the United States and Canada. Warm-water species such as thresher sharks, hammerhead sharks, and mahi mahi (aka dolphinfish) were sighted farther north than ever before. Tuna crabs covered

beaches along the central and southern coast of California. Bluefin tuna appeared in record numbers in California waters. Such shifts in migration of this scale had not been previously observed for nektonic species (Table 1). The consequences of the WWA were far-reaching, and may presage future ecological shifts as global temperatures rise.

TABLE 1. Unusual sightings of species associated with the 2013–2015 warm-water anomaly in the northeastern Pacific. B = Bird. M = Marine mammal. F = Fish. I = Invertebrate. R = Reptile. NC = No change. NA = Not applicable.

Sightings	Common Name	Scientific Name	Sightings Site	Typical Northernmost Distribution	Range Extension (km)
Mass Strandings	Brown Booby (B)	<i>Sula leucogaster</i>	37.72°N ¹	27.84°N ²⁰	1,360
	Tristram's Storm-Petrel (B)	<i>Oceanodroma tristrami</i>	37.72°N ¹	21.00°N ²¹	3,670
	Guadalupe Fur Seal (M)	<i>Arctocephalus townsendi</i>	37.00°N ²	NC	NA
Shift in Distribution	Blue Marlin (F)	<i>Makaira nigricans</i>	59.80°N ³	34.00°N ²²	3,400
	Largemouth Blenny (F)	<i>Labrisomus xanti</i>	32.84°N ⁴	28.18°N ²³	540
	Louvar (F)	<i>Luvarus imperialis</i>	53.64°N ⁵	47.40°N ²²	1,000
	Mahi Mahi (F)	<i>Coryphaena hippurus</i>	59.80°N ³	47.40°N ²²	1,700
	Scalloped Hammerhead (F)	<i>Sphyrna lewini</i>	59.80°N ³	34.43°N ²²	3,300
	Slender Snipefish (F)	<i>Macroramphosus gracilis</i>	47.40°N ⁶	34.01°N ²²	1,700
	Smooth Hammerhead (F)	<i>Sphyrna zygaena</i>	59.80°N ³	37.00°N ²²	2,800
	Thresher Shark (F)	<i>Alopias vulpinus</i>	59.80°N ⁷	53.64°N ²²	1,030
	Wahoo (F)	<i>Acanthocybium solandri</i>	59.80°N ³	32.55°N ²²	3,500
	Whitetail Damsel (F)	<i>Stegastes leucurus</i>	33.38°N ⁸	29.03°N ²²	460
	Yellowtail (F)	<i>Seriola lalandi</i>	59.79°N ⁹	53.64°N ²²	1,030
	Yellowfin Tuna (F)	<i>Thunnus albacares</i>	59.80°N ¹⁰	49.30°N ²²	1,570
	Greater Argonaut (I)	<i>Argonauta argo</i>	36.80°N ¹¹	34.00°N ²²	640
	Painted Sea Urchin (I)	<i>Lytechinus pictus</i>	36.80°N ¹²	34.45°N ²²	290
	Spiny Black Urchin (I)	<i>Arbacia stellata</i>	37.00°N ¹²	27.84°N ²⁴	1,200
	Tuna Crab (I)	<i>Pleuroncodes planipes</i>	36.80°N ¹³	27.84°N ²⁵	1,200
	Green Sea Turtle (R)	<i>Chelonia mydas</i>	33.53°N ¹⁴	32.71°N ²⁶	120
Shift in Abundance	Alaskan Pollock (F)	<i>Gadus chalcogrammus</i>	59.80°N ¹⁵	NC	NA
	Albacore (F)	<i>Thunnus alalunga</i>	59.79°N ⁹	59.79°N ²²	NA
	Bluefin Tuna (F)	<i>Thunnus orientalis</i>	59.80°N ¹¹	59.79°N ²²	NA
	Krill (I)	<i>Euphausia pacifica</i>	37.00°N ¹⁶	NC	NA
Repeating Unusual Record	Bullseye Puffer (F)	<i>Sphoeroides annulatus</i>	34.05°N ¹⁷	33.86°N ²²	NA
	Ocean Sunfish (F)	<i>Mola mola</i>	59.80°N ¹⁰	59.79°N ²²	NA
	Pacific Bonito (F)	<i>Sarda chiliensis</i>	59.79°N ⁹	59.79°N ²²	NA
	Skipjack Tuna (F)	<i>Katsuwonus pelamis</i>	59.80°N ¹⁰	59.60°N ²²	NA
	Tope Shark (F)	<i>Galeorhinus galeus</i>	53.64°N ⁵	53.64°N ²²	NA
	Whale Shark (F)	<i>Rhincodon typus</i>	36.97°N ¹⁷	36.97°N ²²	NA
	Humboldt Squid (I)	<i>Dosidicus gigas</i>	59.80°N ¹⁰	34.45°N ²⁷	NA
	Pilot Whale (M)	<i>Globicephala</i> sp	59.80°N ¹⁸	59.80°N ²⁵	NA
	Pygmy Killer Whale (M)	<i>Feresa attenuata</i>	36.80°N ¹⁸	23.15°N ²⁸	1,770
	Yellow-Bellied Sea Snake (R)	<i>Pelamis platura</i>	34.19°N ¹⁹	30.00°N ²⁹	260

¹ Welch, 2015; ² Branson-Potts, 2016; ³ Thomas, 2015a; ⁴ Dobuzinskis, 2015; ⁵ Miller, 2015a; ⁶ NOAA NWFSC, 2015c; ⁷ Simons, 2015; ⁸ Bushing, 2015; ⁹ CWPA, 2015; ¹⁰ Medred, 2014; ¹¹ Werner, 2015; ¹² West, 2016; ¹³ Izadi, 2015; ¹⁴ Dowd, 2015; ¹⁵ Rosen, 2015b; ¹⁶ NOAA NWFSC, 2015a; ¹⁷ Hicks, 2015; ¹⁸ Agha, 2014; ¹⁹ Workman, 2016; ²⁰ BirdLife International, 2015a; ²¹ BirdLife International, 2015b; ²² Love et al., 2005; ²³ Ramirez-Valdez et al., 2015; ²⁴ Kroh and Mooi, 2015; ²⁵ Putnam-Abbott and Haderlie, 1980; ²⁶ Seminoff, 2004; ²⁷ Zeidberg and Robinson, 2007; ²⁸ Taylor et al., 2008; ²⁹ Bartlett and Bartlett, 2009

PHYSICAL ENVIRONMENT

The WWA initially developed near Alaska in the winter of 2013–2014, stretching to Baja California by the end of 2015. The WWA was attributed to strong positive anomalies in sea level pressure across the Pacific Northwest (nicknamed the “ridiculously resilient ridge”; Swain, 2013), which suppressed heat loss from the ocean to the atmosphere (Bond et al., 2015; Swain, 2015). Sea surface temperatures (SST) were 1°C–4°C higher than average along the west coast of North America (Figure 1). The WWA progressed in several distinct phases: it began as a single patch (and became known as the Blob) in the Gulf of Alaska in 2013, spanning at least 1,600 km horizontally and 90 m in depth (Bond et al., 2015). A second patch of anomalously warm water began to appear farther south in the spring of 2014, ultimately spanning from Oregon to Baja California. Both the magnitude and geographical extent of the WWA varied seasonally and annually.

The presence of the WWA led to shifts in several physical properties and

processes. The reduction of heat flux from the ocean weakened typical winter storm and wind patterns; this increased ocean stratification and altered processes such as wind-driven Ekman transport and pumping, which in turn affected the timing and location of upwelling and downwelling along the coast (Dewey, 2016). In the Southern California Bight, increased thermal stratification led to a reduction in the vertical mixing of colder deep waters with surface waters, effectively reducing the nutrient fluxes up to the euphotic zone and deepening the nutricline (Zaba and Rudnick, 2016). Additionally, a weakening in the horizontal advective transport of colder waters from north to south in the California Current System (CCS) coincided with the North Pacific Transition Zone (a highly productive front where cold Arctic water meets warmer subtropical water) moving farther north than usual (Peterson et al., 2015b; Whitney, 2015; Dewey, 2016). These physical and chemical anomalies led to a cascade of effects that propagated throughout the oceanic food web.

PHYTOPLANKTON

Time series of chlorophyll-*a* (Chl-*a*) anomalies calculated using Moderate Resolution Imaging Spectroradiometer (MODIS) Aqua satellite data reveal latitudinal trends in phytoplankton biomass changes (Figure 2). South of 34.5°N, Chl-*a* anomalies were persistently negative throughout the two-year WWA. Farther north, Chl-*a* anomalies tended to be negative in winter/spring and positive in late summer/fall. The decreased Chl-*a* concentrations in southern waters are consistent with the deep nutricline and euphotic zone observed in the region by Zaba and Rudnick (2016). It is likely that the enhanced vertical stratification caused by anomalous surface warming, combined with the deep nutricline in this region, led to decreased nutrient fluxes to the euphotic zone, with a consequent decrease in total phytoplankton biomass.

Published measurements of changes in phytoplankton community composition during the WWAs are scant. However, comparable warming events in this region, such as El Niño, may serve as

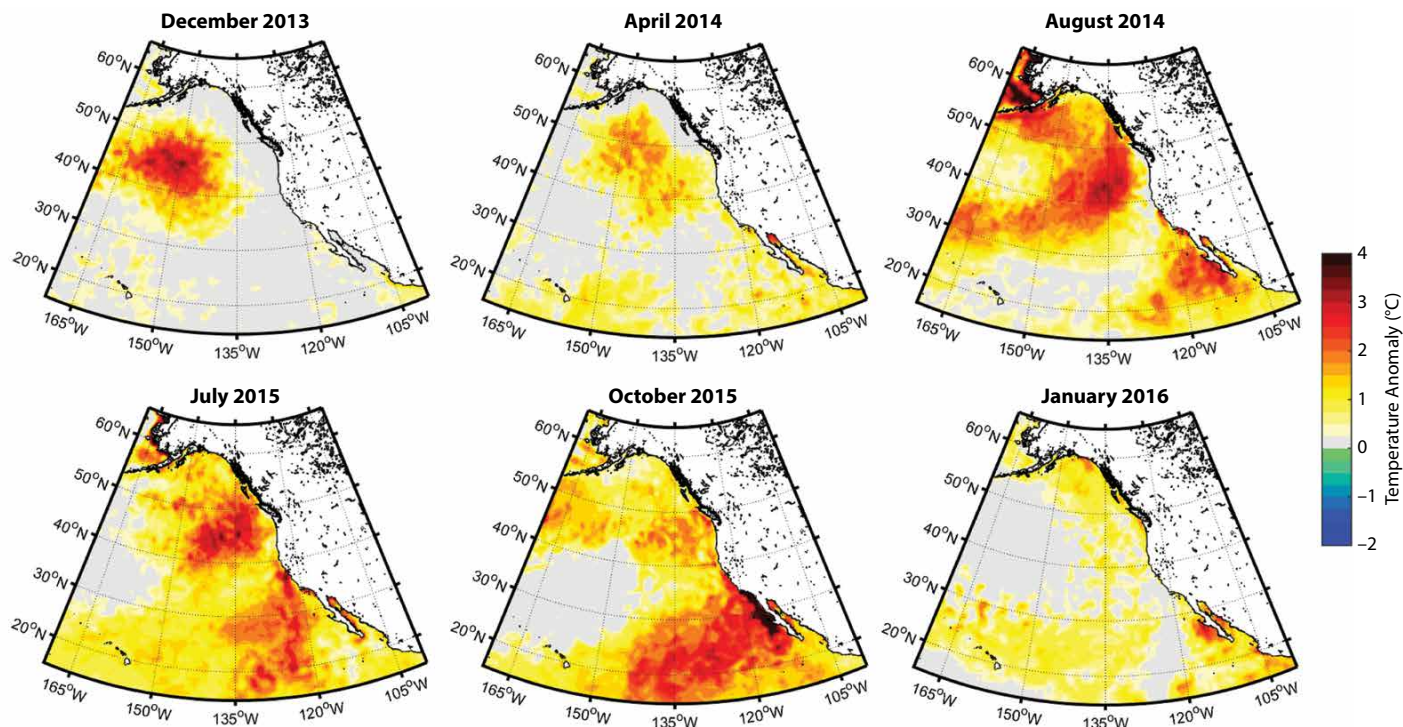


FIGURE 1. Sea surface temperature (SST) anomalies showing the progression of the warm water anomaly (WWA) from December 2013 through January 2016 in the northeastern Pacific Ocean. Temperature data were obtained from the National Oceanic and Atmospheric Administration (NOAA, 2016b).

analogues for the changes that occurred. During El Niño, the phytoplankton community composition typically shifts from larger species toward communities dominated by nano- and pico-phytoplankton (Iriarte and Gonzalez, 2004; Kosro et al., 2006; Kudela et al., 2006). Smaller phytoplankton tend to support food webs dominated by smaller (protist) zooplankton, with less energy from primary production available to larger organisms. These changes to the phytoplankton community will thus propagate throughout the food web, driving profound changes in the biomass and species composition of the zooplankton and their predators during the WWA of 2013–2015.

HARMFUL ALGAL BLOOM

A record-breaking harmful algal bloom (HAB) coincided with the WWA along the west coast of North America in 2015. The HAB was dominated by the diatom genus *Pseudo-nitzschia*, which produces the potent neurotoxin domoic acid (DA). DA bioaccumulates in the aquatic food web and causes death and disability in seabirds and marine mammals, as well as amnesic shellfish poisoning in humans. The 2015 HAB began in May and subsequently grew into one of the largest and most severe HABs ever recorded, stretching from southern California to the

Aleutian Islands (NOAA Climate, 2015; NOAA NWFSC, 2015b; NOAA Ocean Service, 2015; Doughton, 2016).

HABs are not uncommon in the northeastern Pacific. Blooms occur most frequently in the late summer and fall and typically last a few weeks (Bates et al., 1998; KQED Science, 2015; Doughton, 2016). In contrast, this bloom persisted from May to October (Stephens, 2015). The HAB also produced extremely high concentrations of DA, making it the most toxic and longest-lasting bloom of at least the past 15 years (Hickey and Ma, 2015; NOAA Ocean Service, 2015; Doughton, 2016). In May 2015, NOAA measured the highest local concentrations of DA ever recorded both off the central Oregon coast and in Monterey Bay, California (Hickey and Ma, 2015; NOAA NWFSC, 2015b). During a typical *Pseudo-nitzschia* bloom, DA concentrations of 1,000 ng L⁻¹ are considered high; by mid-May, concentrations in Monterey Bay had reached 10 to 30 times this level (NOAA Climate, 2015).

In addition to its geographic extent, timing, duration, and toxicity, the bloom was unusual because it consisted of several species of harmful algae producing multiple toxins at the same time (KQED Science, 2015; Doughton, 2016). Toxins from dinoflagellates that cause paralytic

shellfish poisoning and diarrhetic shellfish poisoning were found along with DA in shellfish in Puget Sound and along the Washington coast (NOAA Ocean Service, 2015; NOAA NWFSC, 2015b; Doughton, 2016). Combined with the record-breaking concentration of DA, these algal toxins resulted in the closure of several economically important fisheries and were implicated in the mortality of many top predators.

ZOOPLANKTON AND INVERTEBRATES

Reduction in phytoplankton availability and elevated sea surface temperatures caused significant changes in zooplankton and marine invertebrate populations along the North American west coast. Populations experienced fluctuations in abundance, and communities showed changes in species composition. Many species appeared to shift their distributions northward as a response to forcings from the WWA.

In North Pacific waters, copepod biodiversity and biomass have long been used as indicators of local water masses. In winter, northern CCS waters are typically dominated by a high-diversity, low-biomass community of subtropical copepods, indicative of a water source from the south. In the spring, colder water from the north advects with it a lower-diversity but higher-biomass community of subarctic copepods. This annual cycling is known to change with shifts in the Pacific Decadal Oscillation: the positive, warm phase leads to conditions favoring warm-water species, regardless of season (Peterson and Schwing, 2003). Subarctic copepods, which grow in cold, high-productivity waters, contain large quantities of fatty acids and wax esters (NOAA Fisheries, 2015b). In contrast, subtropical copepod species found in the relatively barren waters of the subtropics tend to be much smaller and less nutritious than their cold-water counterparts (Kintisch, 2015; Leising et al., 2015).

In 2015, there was no shift in the spring copepod community from warm- to

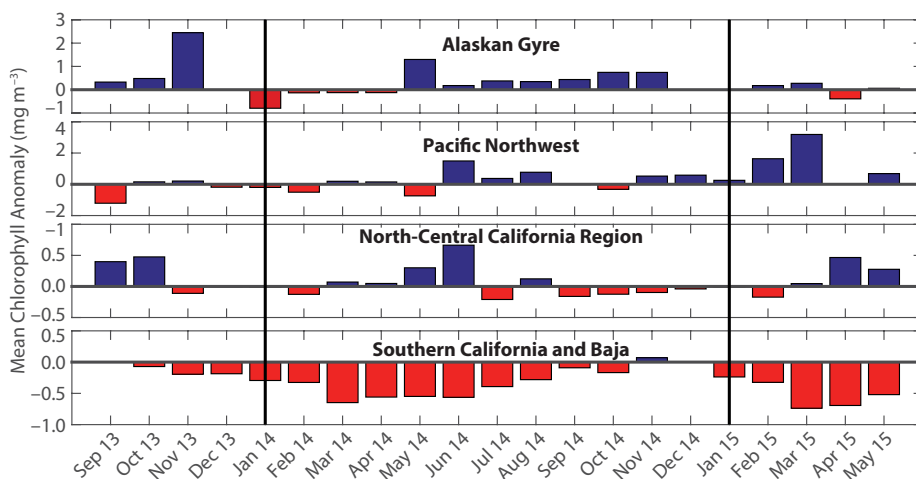


FIGURE 2. Monthly chlorophyll-*a* anomalies from September 2013 through May 2015 in the Alaskan Gyre, Pacific Northwest, North-Central California, and Southern California and Baja coastal regions. Anomalies were calculated for regions between the coast and 200 km offshore using data from the National Aeronautics and Space Administration MODIS Aqua website (NASA, 2016). Red boxes indicate negative anomalies, while blue boxes are positive anomalies.

cold-water species. Observations along the coast of Oregon revealed that subarctic copepods were rare, while an assortment of 17 different warm-water species proliferated (Kintisch, 2015; Leising et al., 2015; Figure 3). Because copepods are a major dietary component for many ocean inhabitants, this difference in nutritional quality likely had significant impacts that propagated throughout the marine ecosystem. This phenomenon extended beyond the northern CCS; subtropical species of zooplankton were observed from Baja California to Oregon (NOAA NWFS, 2015a).

Krill populations were also affected by the strange oceanic conditions of the WWA. These zooplankton are a vital component of the oceanic food web, providing nutrition for organisms ranging from fish to whales (Everson, 2000). A dominant euphausiid in the CCS is *Euphausia pacifica*, which ranges from San Diego, California, to Canada (Brinton, 1976; Siegel, 2011). The highest densities of *E. pacifica* occur during years of strong upwelling, correlated with high abundances of phytoplankton (Brinton, 1976; Siegel, 2011). During the WWA, decreased upwelling along the southern CCS led to decreased phytoplankton biomass, which led to declines in *E. pacifica* populations (Leising et al., 2015). After multiple years of unusually high, stable krill abundances, 2015 was among the lowest in 18 years of monitoring; large adult *E. pacifica* in particular were noticeably absent (Peterson et al., 2015a).

The market squid is an important member of the food web along the eastern Pacific Ocean, and represents one of the most important fisheries in the United States. Market squid are usually found in highest abundance in the southern CCS. Typically, only about 20% of the annual Californian squid catch comes from central and northern California, with the remainder coming from southern Californian waters. In 2014, more than 50% of the state's catch came from central and northern Californian waters, with the majority of the catch coming

from Monterey Bay (Urton, 2014). As of February 2016, the market squid catch was only 35% of the limit (CAFW, 2015), a strong contrast to the previous season when 97% of the catch limit was reached three months before the season closed in March. Multiple reports of market squid in Alaska in early 2016 (Columbia Basin Bulletin, 2015; Miller, 2015b; Milstein, 2015) support the hypothesis that the market squid population along the eastern Pacific migrated north—to the northern limit of their range—in response to the WWA (CAFW, 2015). Indeed, market squid were observed reproducing in Alaskan waters in 2015—the first time this was ever recorded (Miller, 2015b). During strong El Niño seasons, Humboldt squid have also been observed migrating far north into cooler waters with a preferable food supply, further suggesting that squid will shift their distribution to more

hospitable areas during unusual warming (Keyl et al., 2008). Whether squid populations can successfully persist at these higher latitudes is not known.

One species that was found in spectacularly high abundances in the CCS as a result of the WWA was the pelagic red crab. Typically found in large numbers off the coast of Baja California, massive aggregations of the crabs were observed at sea, and began washing onto the beaches of southern California in mid-May of 2015. This continued through June, and again farther north in October on the beaches of Monterey Bay (Izadi, 2015; McDermott, 2015). Mass strandings of these crabs in California are rare, usually coinciding with El Niño (Lluch-Belda et al., 2005). The appearance of pelagic red crabs in California preceded the El Niño signal by several months, supporting a correlation with

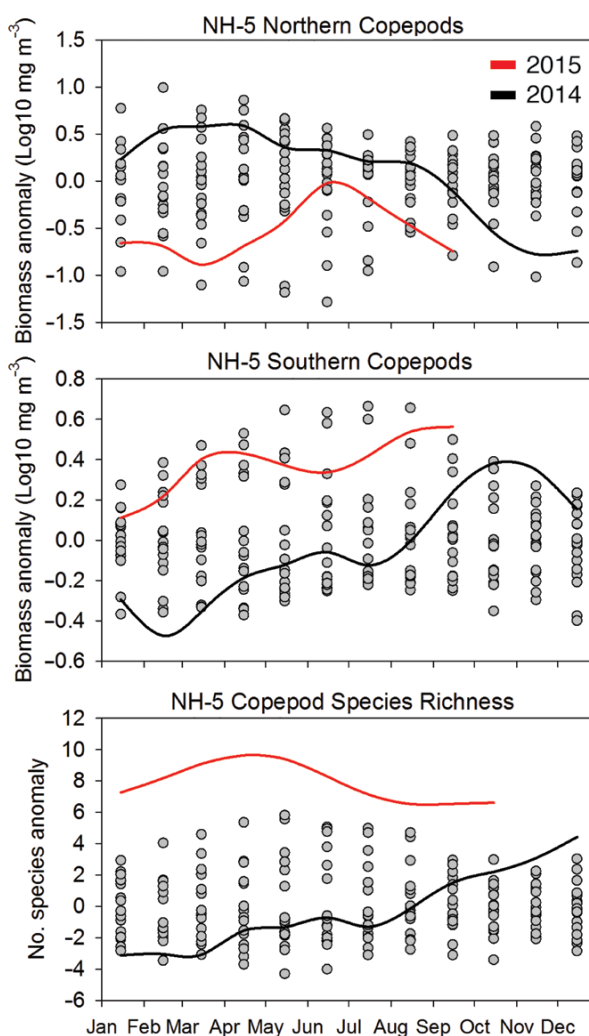


FIGURE 3. Time series anomalies from 1997 to 2015 at station NH-5 (44.6517°N, 124.1770°W) along the Newport Hydrographic Line. Copepod biomass and species richness anomalies are integrated over the upper 60 m. Red lines = 2015, black lines = 2014, and dots = previous years. All data were smoothed with a three-month running mean to remove high-frequency variability. Figure modified from Leising et al. (2015)

the WWA rather than with El Niño. Red crabs are also known as “tuna crabs” due to their frequent consumption by Pacific tuna species (Conrad, 2015). During the summer of 2015, many local species, including fishes, birds, and sea lions, were observed feasting on these crustaceans as they washed ashore (Samenow, 2015).

MARINE FISH

Many pelagic marine fish responded to the WWA by expanding or compressing their geographical ranges, shifting their regional population structures, and/or incorporating alternative prey into their diets. Lea and Rosenblatt (2000) observed a northern latitudinal shift in 29 families of tropical fishes during the El Niño phenomenon of 1997–1998. Similarly, the WWA allowed tropical species to venture as far north as Alaska and subarctic species to be displaced thousands of miles from their natal distribution ranges (Table 1; Bond et al., 2015; Brooks et al., 2016). Anomalous advection patterns in the upper ocean, coupled with poleward transport of larvae and juvenile fishes, may explain the abnormal occurrence of several species (Lea and Rosenblatt, 2000): the reef cornetfish (*Fistularia commersonii*) in the waters of Laguna Beach, California (Love, 2016); largemouth blenny (*Labrisomus xanti*) off La Jolla, California (Hicks, 2015; Mack, 2015); and the slender snipefish (*Macroramphosus gracilis*) in northern California waters (Milstein, 2015). Research surveys during the summer of 2015 reported unusual sightings in the Gulf of Alaska of southern marine species such as the ocean sunfish (*Mola mola*), the blue shark (*Prionace glauca*), and the thresher shark (*Alopias vulpinus*). These species are known to migrate seasonally in response to changing temperature across long latitudinal ranges (Smith et al., 2008; Cartamil et al., 2010; Potter and Howell, 2010; Brooks et al., 2016).

California fishermen reported an unusual abundance of pelagic migratory species such as Pacific bluefin tuna (*Thunnus orientalis*), louvar (*Luvarus*

imperialis), skipjack tuna (*Katsuwonus pelamis*), finescale triggerfish (*Balistes polylepis*), albacore tuna (*Thunnus alalunga*), Pacific pompano (*Peprilus simillimus*), yellowfin tuna (*Thunnus albacares*), yellowtail (*Seriola lalandi*), dorado (*Coryphaena hippurus*), wahoo (*Acanthocybium solandri*), blue marlin (*Makaira nigricans*), and hammerhead sharks (*Sphyrna* spp.) venturing farther north than their known seasonal geographic distributions (Lea and Rosenblatt, 2000; Domeier et al., 2005; Milstein 2015; NOAA SWFSC, 2015b; Brooks et al., 2016). These pelagic species were also caught closer inshore (Milstein, 2015); tuna, for example, were caught only 12–80 km offshore instead of the more typical 96–160 km offshore, creating one of the most profitable sport fishing seasons in Southern California (Hendricks, 2015).

Conditions were more challenging for pollock and salmon fisheries in Alaska and the Pacific Northwest. Coho salmon and Alaskan pollock are highly reliant on lipid-rich, cold-water copepod species to sustain their growth, particularly during their early life stages. The progressive decline in cold-water copepod abundance during the WWA decreased recruitment and increased mortality rates in both fish species. Chinook salmon prefer a diet of fish and lipid-rich krill. Data from 1981–1985 and 1998–2011 revealed that during warm-water regimes, Chinook salmon substituted juvenile rockfish and crab larvae for krill in their diet (Daly and Brodeur, 2015). Although they consumed 30% more food during warm-water conditions, the Chinook were smaller and thinner due to the decrease in available prey quality. This shift in diet away from krill was likewise observed in Chinook salmon during the WWA. Populations responded to the WWA by extending northward to the Gulf of Alaska (Floyd, 2015), perhaps searching for appropriate conditions and prey (Welch et al., 1998; Cheung et al., 2015). The National Oceanic and Atmospheric Administration (NOAA) reported that

in the summer of 2015, the number of salmon across all species migrating back to the Columbia River basin was the lowest in at least 25 years (Peterson et al., 2015a). However, spring and fall returns of Chinook salmon in the Columbia River were high (WDFW, 2015). Until the current cohort of juveniles return as adults to spawn, it is impossible to determine the full impact of the WWA on salmon populations.

Forage fish—including sardine, anchovy, and mackerel—dominate intermediate trophic levels and sustain the upper echelons of marine food webs (Allen et al., 2006; Atkinson et al., 2014). Sardine and anchovy populations in the CCS historically fluctuate with changes in ocean temperature: anchovy abundance is typically high during a cool-water regime while sardine abundance tends to be high under a warm-water regime (Chavez et al., 2003; MacCall et al., 2012). Despite the seemingly favorable conditions of the WWA, the current population of eastern Pacific sardines is estimated to be approximately 10% (97,000 to 133,000 metric tons) of the 2007 population (Leising et al., 2015). During CalCOFI (California Cooperative Oceanic Fisheries Investigations) CUFES (Continuous, Underway Fish Egg Sampler) sampling in the winter and spring of 2015, sardines spawned 90–110 km offshore of the California–Oregon border (41°N–43°N)—between 445 km and 556 km farther north than anticipated. This spawning occurred in water temperatures of 12°C–13°C, at the lower end of the sardines’ thermal spawning tolerance of 13°C–25°C (Lluch-Belda et al., 1991; NOAA SWFSC, 2015a). Factors other than temperature, such as flow patterns, upwelling, and biotic conditions, may have been behind the northward movement (e.g., Lluch-Belda et al., 1991; Lindegren et al., 2013). Egg densities in 2015 were dramatically lower than in spring collections from 2000 to 2013 (Peterson et al., 2015a). Though the exact cause of the unusually low sardine abundance is unknown, Sugimoto et al.

(2001) suggested that poor feeding conditions for sardine juveniles may have been responsible for successive recruitment failures during past warm-water periods. Poor recruitment in successive cohorts coupled with fishing rates set by more favorable oceanographic conditions may result in the eventual collapse of the fish stock (Zwolinski and Demer, 2012).

Sardines were not the only forage fish to move northward; anchovy also migrated farther north, and tropical mackerel expanded their range to Vancouver Island, British Columbia (Pearcy, 1992; Stouder et al., 1997; Weber and McClatchie, 2011). Predation by mackerel in northern waters was an additional source of mortality for juvenile salmon (Stouder et al., 1997). The reduction and shift in communities of forage fish have had huge effects on regional marine food webs.

As prey species migrate in response to oceanic conditions, so do predators. The movement of tuna crabs into southern California may have attracted Pacific tunas and subsequently other top predators, such as sharks, into more northern territory. Carnivorous fish follow their planktivorous prey, and as a result, many fish distributions are linked to distributions of phytoplankton (Dini and Carpenter, 1992). If anomalies like the WWA occur more frequently in the future, fish community composition and dynamics in the eastern Pacific have the potential to cause cascading effects in marine systems (Lea and Rosenblatt, 2000; Bond et al., 2015; Cheung et al., 2015).

MARINE MAMMALS AND SEABIRDS

The changing distribution and abundance of zooplankton and forage fish reverberated through the food web. Many mass strandings of marine mammals and mass die-offs of marine seabirds occurred in the eastern Pacific during the WWA (Drake, 2015; NOAA Fisheries, 2015a; Welch, 2015). These events are indicative of imbalances in the ecosystem that leave many species vulnerable. While

some predators such as sharks are able to migrate in search of food, many seabirds and sea lions are tied to breeding grounds and thus limited in their capability to respond to changing prey distributions.

Forage fish depletion in WWA waters has exacerbated the food shortages plaguing California sea lions. In 2013, the animals, primarily juveniles, began stranding in record numbers (NOAA Fisheries, 2015a). Strandings reached their peak during the WWA in early 2015, with over 3,300 individuals stranded between January and May, a value 10 times higher than normal (NOAA Fisheries West Coast, 2015). Adult sea lions are known to be opportunistic predators, with diets typically dominated by sardines, anchovies, and squid (McClatchie et al., 2016). Adult males do not contribute to parental care, allowing them to easily venture north to seek out preferred prey (Bartholomew, 1967; Ono et al., 1987). Adult females, on the other hand, must remain at rookeries to support their pups, limiting the range that they can travel to acquire food. In the case of nursing sea lion mothers, a diet rich in sardine and anchovy is optimal; low availability of these forage fish correlates with decreased pup weight (McClatchie et al., 2016). Analyses suggest that the food available—mainly pelagic red crab, rockfish, and squid—lacks the nutritional quality and quantity necessary to sustain both mothers and pups (NOAA Fisheries, 2015a; McClatchie et al., 2016). Thus, the driver of the strandings appears to be food shortages, worsened by changes in prey abundance and distribution associated with the unusual WWA (NOAA Fisheries West Coast, 2015).

An unprecedented number of dead juvenile Cassin's auklets washed ashore in the western United States, beginning in the fall of 2014 (Welch, 2015). The strandings increased over the winter, with as many as 50,000 to 100,000 dead birds found on the Pacific coast (Welch, 2015). Necropsies determined that the cause of death was starvation (Welch, 2015). The 2014 summer breeding season was

particularly strong, and therefore some increase in the mortality rate of juvenile auklets was expected as the birds began foraging on their own. However, the actual death toll far surpassed what could plausibly be attributed to the greater number of juveniles (Welch, 2015). In the central CCS, auklets forage primarily on krill, whereas in the northern CCS they consume mostly large, cold-water copepods (Bertram et al., 2001). The abundance and breeding season success of Cassin's auklets depends on the availability of these krill and copepods (Sydeman et al., 2006; Manugian et al., 2015). In 2015, these primary food sources were absent, and warm-water copepods were a primary source of food (Kintisch, 2015). It is likely that the shift in zooplankton caused by the WWA led to a decrease in the quality of food available to the auklets, which led to the mass die-off seen in the winter of 2015.

Cassin's auklets and California sea lions weren't the only top predators suffering from a lack of food. Guadalupe fur seals and the common murre both stranded in record numbers. Like the auklets and the sea lions, starvation was likely a driver (NOAA Fisheries, 2015c; Newbern, 2016). Common murrens began washing up on the shores of Alaska in March 2015, with strandings of the emaciated seabirds reaching record numbers by the winter of 2015–2016 (Joling, 2015; Newbern, 2016). A large winter storm compounded the lack of quality food, and without adequate nutrition, many murrens may have lacked the energetic resources to survive the storm (Newbern, 2016). Previous research has implicated increases in SST as a factor in murre abundance declines (Irons et al., 2008). In the United States, 80 Guadalupe fur seals stranded, over eight times the typical number (NOAA Fisheries, 2015c; Branson-Potts, 2016). Like the California sea lions, the stranding fur seals were young and emaciated (NOAA Fisheries, 2015c). The pinniped also appeared to be expanding its range. Normally confined to Baja California, the fur seals appeared

as far north as Vancouver Island, presumably following the northward range shifts of the squid and fish they forage during the WWA (Pauly et al., 1998; Bailey, 2016; Branson-Potts, 2016).

The lack of quality food for these top predators was compounded by DA bioaccumulation from the record breaking *Pseudo-nitzschia* HAB. Testing by the Wildlife Algal-toxin Research and Response Network found the toxin in 36 stranded marine mammals and three seabirds ranging from Washington to Southern California (Milstein, 2015). California sea lions faced a one-two punch: already suffering from the reduction in forage fish availability, what sardines and anchovies they did find were contaminated with DA (NOAA Climate, 2015). Tests conducted on several dead sea lions revealed the animals had lethal concentrations of the toxin in their systems, and in September 2015, the Marine Mammal Center in Sausalito, California, announced that 75% of the sea lions in their care were suffering from DA poisoning (The Marine Mammal Center, 2015; Milstein, 2015). Mothers exposed to sublethal doses of DA may have impaired hunting skills due to neurologic damage, further decreasing the nutrition available for juvenile sea lions (Cook et al., 2015). The combination of changing prey dynamics and the toxic *Pseudo-nitzschia* bloom has struck a blow to this species, and similar scenarios may have occurred with other species as well. The HAB may be a cause of marine mammal deaths as far north as Alaska where 44 baleen whales stranded—more than three times the average—including nine fin whales that died together at Kodiak Island (NOAA Climate, 2015; Hopcroft, 2016). Trophic transfer of toxins from the unprecedented HAB is a primary suspect given the timeframe and location of these deaths, but other causes may yet be found (NOAA Climate, 2015).

While changing prey distributions and DA have harmed some marine mammals, not every species has been negatively affected. The increase in Chinook

salmon in the Gulf of Alaska and the Columbia River basin has been a boon for fish-eating killer whales. Killer whales in Alaska have stayed in the area longer than normal, feasting on the increased salmon stock (Hopcroft, 2016). Endangered southern resident killer whales have had a baby boom, with eight calves born since December 2014, a birth rate not seen for decades (Le, 2015). A large fall return of Chinook salmon in the Columbia River basin may have supported the increase in births (Ford et al., 2010; WDFW, 2015). However, given the decrease in the krill that sustains the juvenile Chinook, it is unknown whether Chinook salmon abundance will be high enough in next few years to support this growing population. Clearly, the success of top predators is largely dependent on how the lower trophic levels respond to changes in the physical oceanographic environment.

ECONOMIC IMPACTS

Both commercial and recreational fisheries were closed due to the unprecedented HAB that coincided with the WWA, resulting in economic losses of millions of dollars. The Dungeness crab fishery from Washington to California was particularly hard hit: closures and delays in the 2015–2016 season due to unsafe DA concentrations affected shellfish sales as well as industry job security, with losses through February of 2016 estimated at \$48 million (Cestone, 2016). The California commercial Dungeness crab fishery remained closed as of March 2016 (Cestone, 2016). In the Pacific Northwest, recreational harvesting of the Pacific razor clam was prohibited, leading to economic losses of \$22 million, including decreased tourism to coastal clamming areas (Wekell et al., 1994; Mapes, 2015). Additional fisheries, including northern rock crab, various bivalves, and anchovies, were closed in 2015 due to the toxin (California Department of Public Health, 2015; Duggan, 2015; CDFW News, 2016).

The WWA caused economic losses due to the reduction in the abundance of prey available for commercially valuable

species. The Alaskan pollock fishery is the largest in the United States, averaging 1.4 billion kilograms annually and accounting for almost one-third of all US seafood landings by weight (Alaska Department of Fish and Game, 2014; NOAA AFSC, 2016). The WWA led to poor pollock recruitment in the Bering Sea due to the paucity of its preferred prey, lipid-rich, cold-water copepods. The lack of a suitably nutritious diet resulted in relatively thin pollock that had difficulty surviving the winter and that exhibited an increased rate of cannibalism (Colton, 2015). The low recruitment in 2015 may result in decreased catches in 2017 and 2018; as of early 2016, it is unclear whether or not the quota for 2016 will be affected. Given the size of the pollock fishery, the reduction in the pollock population due to the WWA may have an outsized economic impact.

The commercial salmon fishery in the Pacific Northwest (comprised of Chinook, chum, coho, pink, and sockeye salmon) is one of the largest in the United States, estimated at more than \$600 million in 2014 (NOAA AFSC, 2016). Various stages of the salmon life cycle can be stressed by increased surface temperatures, and such temperature increases combined with reductions in nutritious krill and cold-water copepods drive increased mortality of juvenile salmon, decreased adult size, and poor recruitment. As of early 2016, estimates of these losses have yet to be determined.

Not all economic effects of the WWA were negative. Pacific bluefin tuna, an overexploited species, expanded in geographic extent due the massive increase of its prey, the pelagic red crab, and favorable water conditions off the West Coast (Craig Heberer, NOAA, *pers. comm.*, 2015). Increased local catches reduced the price per kilogram of the fish at market. In October of 2015, whole tuna were sold at a fresh fish market in San Diego, California, for \$1.35 per kilogram—quite a reduction from the (admittedly unusual) \$7,928 per kilogram price commanded by a single tuna in Japan in 2013

(Leschin-Hoar, 2015).

The United States has the largest whale watching industry in the world, with millions of whale watchers and revenues of approximately \$1 billion each year (O'Connor et al., 2009). The WWA brought unusual species of whales to many locations on the West Coast, boosting the industry. A record number of whale sightings occurred in San Diego, California, in 2015, with a wider array of species represented than normal (Brennan, 2015). Even the rare Bryde's whale was observed off Orange County, California; this species is rarely encountered north of Mexico (Thomas, 2015b). One possible explanation is that they shifted their migration patterns due to the WWA (Toby Garfield, NOAA, *pers. comm.*, 2015).

THE WWA VS. EL NIÑO

The first signs of the 2015–2016 El Niño were seen in August 2015; measurements indicated that this El Niño would be one of the strongest on record (NOAA NWFSC, 2015c). At the time, it was unclear how the southern El Niño would interact with the WWA in the north: would the warm waters persist or would they dissipate in response to changes in atmospheric forcing from the high pressure ridge of the northern WWA region to the low pressure system associated with El Niño (Rasmusson and Wallace, 1983; NOAA ESRL, 2016)? However, the WWA was composed of two patches that were not both expected to respond in the same way to El Niño conditions. While the northern WWA region dissipated, the second, southern patch, off Baja California was expected to persist throughout the El Niño (Yulsman, 2015). Recent SST anomaly measurements seem to support this “decoupling” of the two WWA patches, with lower temperatures observed in the north and a persistent patch of warm water near Baja California (Figure 1). It is uncertain whether this southern warm patch was part of the WWA or of the El Niño, as similar warm patches off Mexico have been observed in

previous El Niño events. That being said, the main distinction between the two phenomena is that El Niño warms the surface waters from below, while the WWA was caused by reduced heat loss from surface waters to the atmosphere (Zaba and Rudnick, 2016). This mechanistic difference in the origin of the warm water could potentially lead to a distinctive signal in affected physical and biological processes and may be used to distinguish between the two phenomena. A comparison of monthly averages of SST clearly shows that the WWA greatly decreased from fall 2015 to January 2016, particularly in the North Pacific (Figure 1).

FUTURE OUTLOOKS

To some, the WWA represents a harbinger of things to come: SSTs are predicted to rise with increasing global temperatures. To see if this scenario might be true, we compared predicted SST anomalies in the North Pacific from 2050 to 2099 to the averages of 1956 to 2005 (Figure 4; Riahi et al., 2011; NOAA, 2016a). In our model, the anomalies ranged from about 1.5°C–4°C above the

historical temperature values. These temperature anomalies are comparable to those observed throughout the WWA, which ranged between 1°C and 4°C, supporting the contention that the observed WWA is a good predictor of future ocean conditions.

The main difference between the WWA and the future outlook is that in the future, the entire water column is expected to warm more evenly. This will enhance ocean vertical stratification, a process already observed in the subarctic Pacific (Larsen et al., 2007) and in the Okhotsk Sea (Nakanowatari et al., 2007)—both critical sites for the formation of the dense water that carries oxygen to the northeastern Pacific. Increased ocean stratification reduces ventilation of interior waters, inducing potentially hypoxic conditions. This situation will affect demersal and benthic fish communities, as already observed for mesopelagic fish in the California Current (Koslow et al., 2011).

While the 2013–2015 WWA is an imperfect predictor of what the future may hold, many of the biological and physical

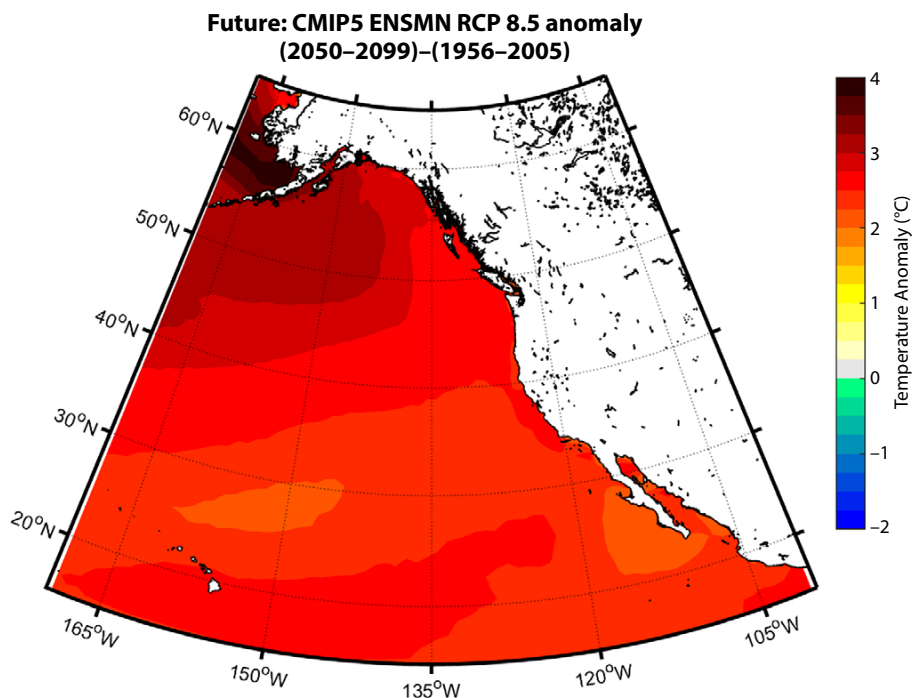


FIGURE 4. Temperature anomalies predicted for 2050–2099 using the RCP8.5 climate 368 model, calculated relative to temperature records from 1956–2005. Data were obtained from the NOAA climate change Web portal (NOAA, 2016a).

shifts observed during this long-lasting event could happen more frequently as global temperatures continue to rise. For instance, increased temperatures are expected to result in more numerous and longer-lasting HABs, which would have severe ecological and economic consequences such as those observed during the WWA (Harvell et al., 1999; Sekula-Wood et al., 2011). Furthermore, increased temperatures could change the geographic range of many species, which, as we have shown, can have profound ramifications throughout the oceanic food web.

To better predict the changes that may occur with increasing ocean temperatures requires better monitoring of phytoplankton, nutrients, and upwelling along the entire coastline to develop a

more cohesive understanding of how they change over time and to build a baseline of the region that can be used as a comparison for any future anomalies.

CONCLUSIONS

The WWA of 2013–2015 resulted in many changes in northeastern Pacific ecosystems (Figure 5). Increased vertical stratification due to the WWA along with decreased nutrient flux to the surface appeared to be responsible for the observed reduction in total phytoplankton biomass. This decrease in phytoplankton availability, along with elevated sea surface temperatures, caused significant changes in zooplankton and marine invertebrate populations, with many species shifting their distributions toward

cooler, more northern waters. Sightings suggest that tropical invertebrates such as tuna crabs were followed northward by their predators, tuna, which were in turn followed by their predators, sharks. Increased proportions of less-nutritious warm-water copepod species and decreased abundance of krill were observed in the WWA regions. This loss of high-quality food caused population declines of many fish and seabird species and contributed to record marine mammal strandings. Concomitantly, the record-breaking concentration of DA during the persistent HAB was implicated in mass mortalities of several species and resulted in the closure of many fisheries. Economically, the effects of geographical shifts and the HAB have led to millions of dollars in losses among fishing industries. This is worrisome because the WWA may be a harbinger of things to come. As SSTs continue to rise with increasing global temperatures, many of the same scenarios observed during the WWA may be repeated, with dramatic ecological and economic consequences. ☐

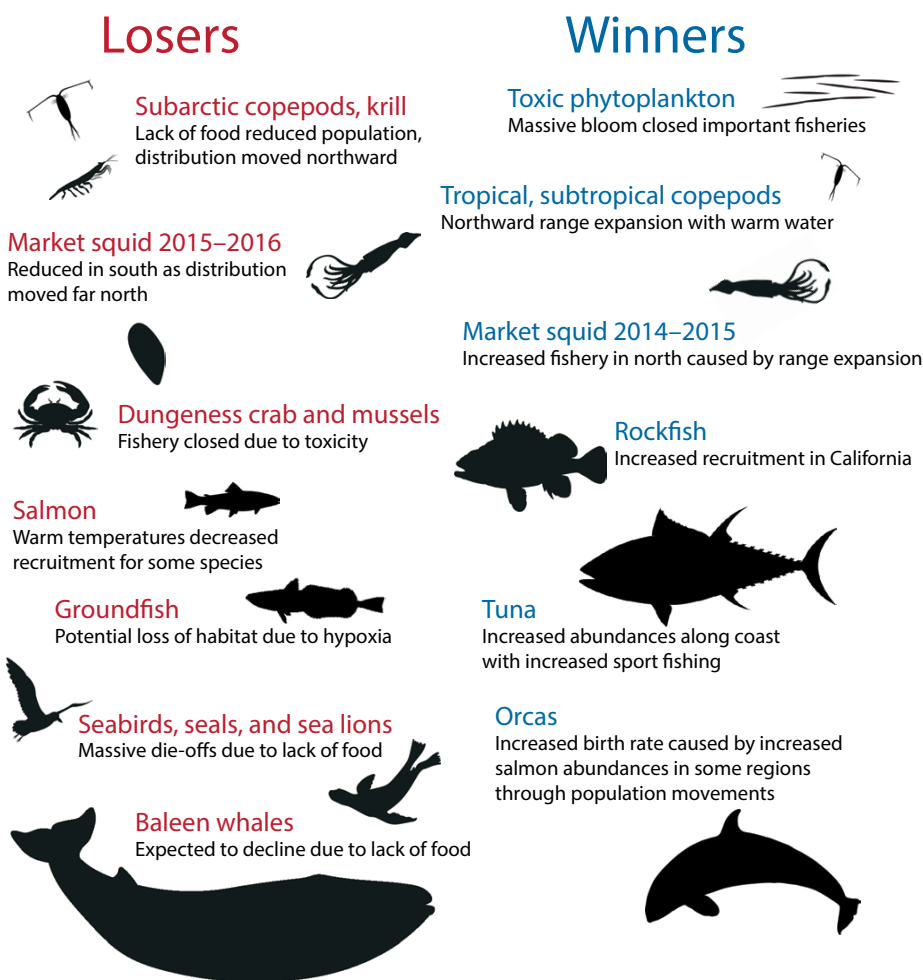


FIGURE 5. Organisms observed to be positively and negatively impacted by the WWA. Negatively affected organisms are labeled as “Losers” (left column), while organisms positively affected are labeled as “Winners” (right column). Organisms are presented in both columns from lower (top of the column) to higher (bottom of the column) trophic levels.

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