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Climate Change and Ocean Ecology of Northwest Steelhead

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Climate plays a key role in steelhead habitat. This is true for steelhead in freshwater, estuaries, and even in the North Pacific Ocean. Most steelhead research has focused on freshwater ecology, for in streams and rivers steelhead are much more accessible than they are at sea. It is probably not a surprise then, that climate impacts on steelhead in their freshwater habitats have received a fair bit of attention from scientists. One of us (NM) co-authored an article in the January 2005 issue of *The Osprey* focused on global warming, steelhead freshwater ecology, and steelhead fishing (Available at: http://www.ospreysteelhead.org/archives/TheOspreyIssue50.pdf). In the eight years since, we and others have focused new attention on the ocean ecology of steelhead, and how global warming might impact steelhead at sea.

> *That steelhead have been successful for 6 million years gives us hope they will be able to adapt.*

Knowledge of the entire life history of steelhead is fundamental to understanding the potential effects of climate change on this species. Steelhead exhibit a wide range of variation in freshwater and ocean life-history patterns. For example, degree of anadromy (some mature in freshwater without migrating to the ocean), adfluvial (within-river) migration, freshwater residency of pre-smolts (1-7 years; smoltification is the physiological transition stage between freshwater and ocean habits, when juveniles become silvery and streamlined), ocean entry timing of smolts (early spring to mid summer), pre-spawning ocean age structure (typically, 1-3 years), maturity type (ocean-maturing or stream-maturing), seasonal races and run-timing of adults (winter, spring, summer, fall), fecundity (number of eggs, 2,500-10,000), and iteroparity (repeat spawning, 0-6 times, sometimes skipping a year between spawning events). This tremendous variation reflects the wide range of genetic adaptation and plastic response (ability of an individual fish to modify its physical characteristics) to environmental conditions.

These multiple life-history strategies enable steelhead to adjust rapidly to new environmental conditions, provid-

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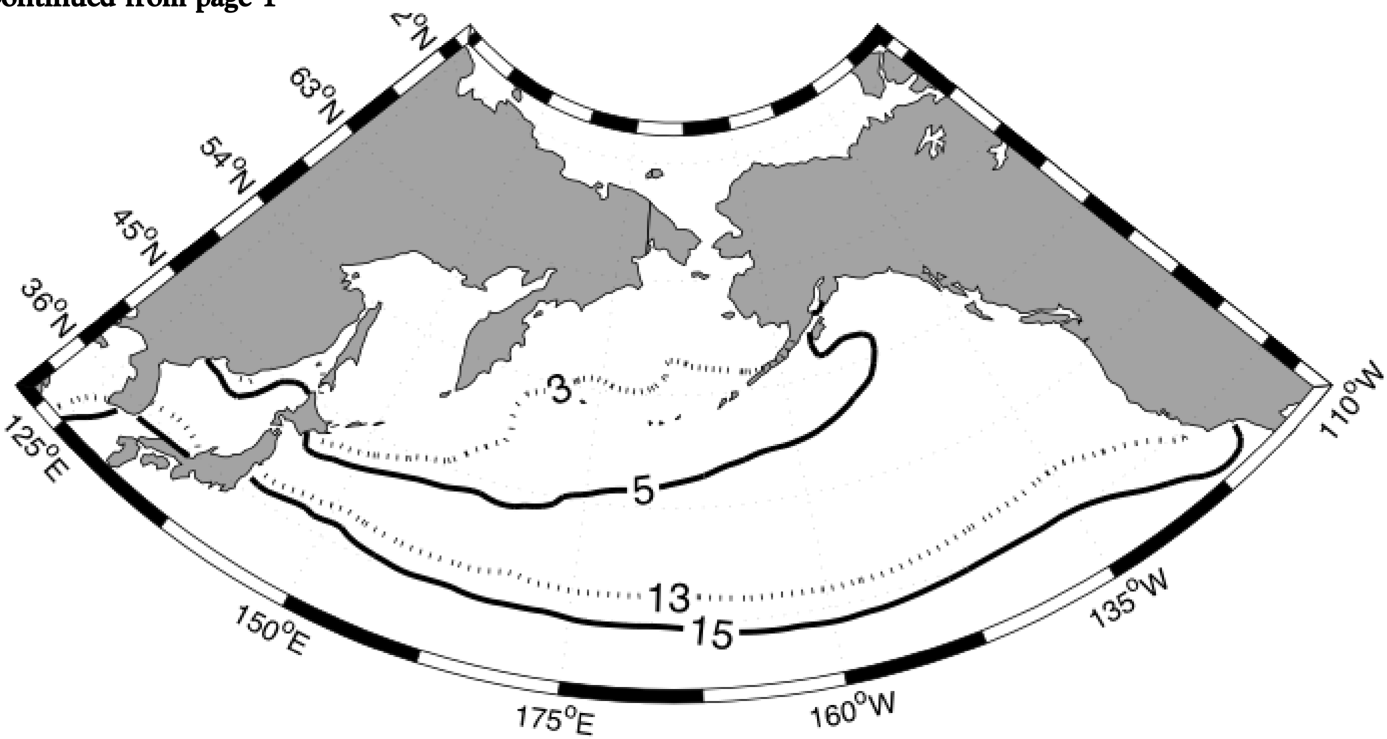

Figure 1. Average sea surface temperature in April-May-June for 1971-2000, with solid contours indicating steelhead high seas habitat between the 5 and 15°C isotherms. Actual temperatures vary between months, seasons, years and decades. Dashed contours for the 3 and 13°C isotherms indicate one scenario for steelhead high seas habitat in spring after a 2°C warming of the North Pacific Ocean, which is expected to happen sometime in the 2nd half of this century.

ing a survival advantage over other less adaptable species. The successful adaptation to artificial habitats (hatcheries, rearing pens, holding ponds, reservoirs), as well as its ability to establish anadromous runs in non-native oceans (southwestern Atlantic ocean off Patagonia) and in the Great Lakes, bears testimony to the ability of this ancient (~6 million years old) species to adapt to diverse and often unfavorable environmental conditions. In fact, unfavorable environmental conditions in freshwater and ocean habitats drive anadromy in this species.

While fly fishers are usually well versed in the freshwater life history of their favorite fish, the all-important ocean phase that produces the large adult fish of a steelheader's dreams is more of a mystery. There is still much to discover and learn, but nearly 60 years of marine research focused primarily on abundant species important to commercial fisheries (sockeye, pink, chum, coho, and Chinook salmon) have provided a basic scientific understanding of steelhead ocean ecology, that is, the relationship between steelhead and their ocean environment.

In their natural habitat in the North Pacific Ocean, steelhead migrate and feed in the near-surface (epipelagic) and surface (neustonic) ocean layers. Limited data from electronic tags that record ambient temperature and swimming depths indicate maximum dives to depths of about 50 meters (164 ft) and most time spent in the top few meters. Upper ocean temperature is the primary physical factor influencing the distribution of steelhead in the open ocean. Thus, lines on a map connecting points with the same sea surface temperature, called isotherms, can be used to roughly approximate distribution. In general, steelhead distribution in the open ocean is located between the 15°C (59°F) isotherm (southern boundary) and 5°C (41°F) isotherm (northern boundary) (Figure 1). These boundaries shift between months, seasons, years, and decades. During all seasons, the main body of feeding-migrating steelhead is located north of the Subarctic Ocean Boundary, defined by the vertical 34.0 (salinity) isohaline, and south of the Aleutian Island chain (Figure 2). However, steelhead do venture outside of these bounds seeking productive feeding grounds— southwards into the transition zone between subarctic and subtropical waters in spring and northwards into the Bering Sea in summer. The known northwestward extent of North American steelhead distribution, which extends into the Russian Exclusive economic (200-mile) zone in the western North Pacific, is in late summer-early fall. In winter, the distribution of both North American and Russian steelhead shifts eastward, and by the following spring the main body of feeding-migrating steelhead is at the southernmost extent of its open-ocean range in productive waters of the eastward flowing Subarctic Current and the transition domain (located just north of the Subarctic Boundary) in the central and eastern subarctic North Pacific. As first noted

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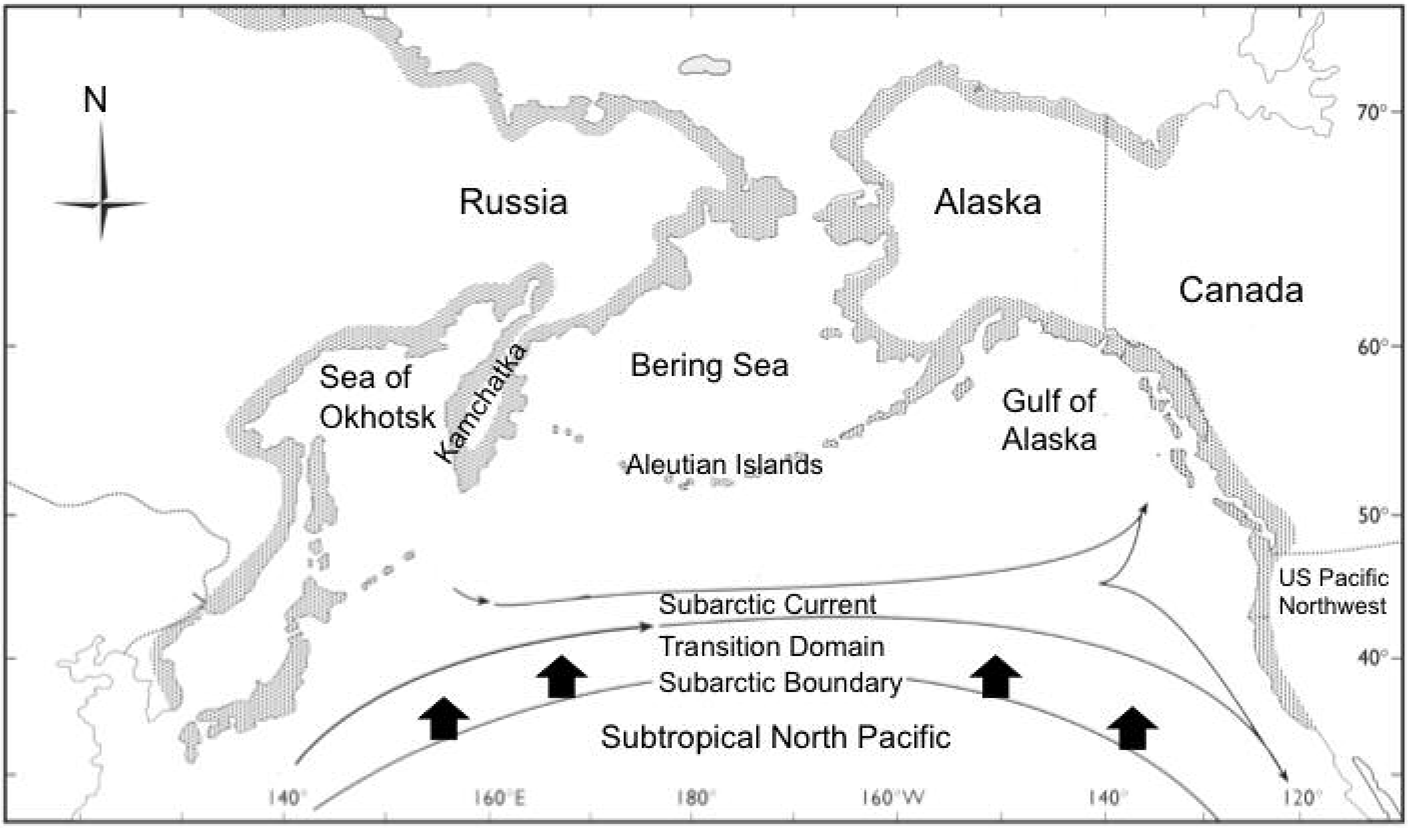

Figure 2. Map of the North Pacific Ocean showing the relative positions of oceanographic features that define steelhead habitat. The actual spatial locations of these features shift on decadal, annual, seasonal, and monthly scales. The main body of feeding-migrating steelhead is located north of the Subarctic Ocean Boundary (indicated by upward facing black arrows) and south of the Aleutian Islands chain. Source: Modified from base map in Quinn (2005); shading indicates the coastal range of all species of Pacific salmon and steelhead (Oncorhynchus spp.).

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by a Canadian scientist, Dr. David Welch, the open-ocean latitudinal ranges of upper and lower sea surface temperature limits in spring and freshwater spawning distribution of North American steelhead are roughly matched, suggesting that thermal requirements of steelhead at ocean entry might drive freshwater distribution.

Within the broad range of thermal habitats, currents, and oceanic domains occupied by steelhead, the most important factor regulating steelhead distribution is the location of their preferred prey. At ocean entrance, juvenile steelhead feed primarily on small fish and zooplankton in inland and coastal marine habitats. In North America, juveniles migrate rapidly to open-ocean habitats beyond the continental shelf in the Gulf of Alaska, where they feed on larval and juvenile fish and small squid. Older age groups of steelhead are capable of consuming a large variety of prey species in marine habitats. But food habits data indicate that steelhead prefer to feed on relatively few species of highly visible and abundant fish and squid. The single most important prey of steelhead in the open ocean is the minimal armhook squid *Berryteuthis anonychus* (Figure 3). While in pelagic habitats near or over the continental shelf, steelhead diets are often dominated by fish.

Analyses of two long time series of open-ocean steelhead food habits data by our graduate student Margaret "Megan" Atcheson showed significant year-to-year variation in primary prey, as well as stomach fullness, average prey energy density, and percentage of steelhead with empty stomachs, and higher year-to-year variation in far offshore regions. Variability in steelhead diets probably reflects changes in the availability of preferred prey. As opportunistic predators, steelhead can readily switch their prey. When prey abundance is low, steelhead may feed non-selectively on prey of various sizes and species, while at high prey densities selection of a single species of large prey and high diet overlap with other species may occur.

Research led by a Japanese scientist, Dr. Masahide Kaeriyama, and expanded by Megan Atcheson's recent work, demonstrates that climate-driven changes in ocean conditions can affect diets, growth, and ecological interactions of steelhead migrating in the North Pacific Ocean. For example, strong climate changes related to El Niño and La Niña during 1997-1999 coincided with a large decrease in squid in the summer diets of steelhead in the Gulf of Alaska. The decrease in dietary squid was even larger in the central Subarctic North Pacific, where steelhead compete for food with pink

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salmon, particularly during odd-numbered years when the abundance of Asian pink salmon is extremely high. In 1997 steelhead diets in the central Subarctic North Pacific contained the highest proportion of marine debris, including potentially toxic plastic, observed over the 19-year time series of data. Recent decades have brought record high levels of pink salmon abundance throughout most of the North Pacific region, supporting the idea that late 20th century warming of the North Pacific Ocean and salmon rivers of the Pacific Rim was good for pink salmon.

Global warming and changes in the high seas distribution of steelhead

Pioneering research by Dr. David Welch predicted a substantial reduction in open ocean thermal habitats of steelhead by middle of the 21st century under a climate change scenario with doubled atmospheric $CO2$ concentrations. New analyses by our Post-Doctoral student, Dr. Omar Abdul-Aziz, modeled reductions in potential open-ocean thermal habit of steelhead in summer under 3 different scenarios representing relatively low, medium, and higher rates of climate warming. Each warming scenario results in a northward shift and east–west contraction in the southern (warmest) thermal boundary, particularly in the Subarctic North Pacific, Okhotsk Sea, and Gulf of Alaska by the 2040s and substantial reductions in these regions by the 2080s. In the 1980s, estimated potential thermal habitat of steelhead during winter covered an east–west band, including most of the Gulf of Alaska and Subarctic North Pacific; however, the Okhotsk Sea, Bering Sea, and Arctic Ocean did not provide any potential thermal habitat suitable for steelhead during winter. Modeled changes in potential winter thermal habitat by the 2040s and 2080s showed a northward shift of the northern (coldest) boundary in most of the Bering Sea and Okhotsk Sea; however, these habitat gains were almost completely offset by almost equal losses due to the northward shift of the southern (warmest) boundary. Thus, the total area of potential winter habitat in future periods was similar to the past or reduced only slightly (1%–2%), which was less than typical year to year variations in 1980s potential habitat caused by short term climate changes. In Figure 1 we show the 3° and 13°C isotherms to illustrate how a 2°C warming in the North Pacific, which is expected to happen in the mid to late 21st century, could shift springtime open ocean thermal habitat for steelhead to the north. In summary, a warming climate may result in a northward shift in steelhead distribution. As temperatures warm in the Bering Sea, conditions may be more favorable for steelhead in eastern Kamchatka and western Alaska streams, regions that currently host only resident rainbow trout.

Due to bioenergetic constraints, warming ocean temperatures may have a greater impact on older age groups of steelhead. For example, bioenergetic model simulations by Megan Atcheson used to estimate tradeoffs between metabolic demands and growth potential indicate that optimal temperatures for growth in the open ocean are 14°C (57.2°F) for juvenile (ocean age-0) steelhead and 12°C

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As the worldwide climate warms, so do the world's oceans. For now, we can only speculate on what the long-term impacts might be for steelhead, salmon and other ocean life. Photo by Jim Yuskavitch.

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(53.6°F) for older (ocean age-1) steelhead. However, observed distribution of juvenile steelhead in the Gulf of Alaska at less than optimal temperatures for growth suggests that when temperatures are within the range of thermal tolerance, other factors may play an important role in open-ocean distribution of steelhead.

The stomach of this high seas hatchery-origin steelheaded included a minimal armhook squid and juvenile rockfish. Photo by R.V. Walker

In the 1990s and 2000s, summer sea surface temperatures (SSTs) did not reach optimal temperatures for open-ocean steelhead growth except during the El Niño summer of 1997. Modeled growth potential of steelhead under future SST scenarios showed reduced growth as temperatures warm beyond the optimum growth temperature for a given feeding rate and body mass of steelhead. The combined reduction in physiological maximum feeding rate and increasing metabolic costs prevent any potential increases in steelhead feeding rate or energetic prey quality from sustaining historical growth rates. The resulting growth decline might become a strong selective force in shifting the geographic distribution of steelhead in the ocean and perhaps in freshwater.

Ocean acidification, sometimes called global warming's evil twin, is a related threat that may cause dramatic changes in steelhead habitat at sea. Ocean acidification is likely to have a large impact on open ocean food webs, particularly in regions where epipelagic squid are the preferred prey of steelhead. Squid are very sensitive to acidic (low pH) conditions, which interfere with oxygen binding at the gills, reducing oxygen consumption and scope for activity. This is an extremely important area for future open-ocean research on steelhead, squid, and ocean food webs more generally.

On one hand, the fact that steelhead have been a successful species for 6 million years should give us hope that they will be able to adapt to the many environmental changes related to global warming predicted for the near and distant future. On the other hand, recent CO2 measurements have documented atmospheric concentrations exceeding 400 parts per million, something that is estimated to have not happened for at least 3 million years. Even more disturbing is the fact that the ongoing rise in atmospheric and oceanic CO2 has been compressed into a blink of geologic time, with no signs of slowing down. The bottom line is that the North Pacific Ocean is crucial habitat for steelhead, and climate change and acidification threats to habitat in the ocean may become as great as those in our most imperiled streams.

Source material and additional reading:

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