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Linkages between Alaskan sockeye salmon abundance, growth at sea, and climate, 1955–2002

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Abstract

We tested the hypothesis that increased growth of salmon during early marine life contributed to greater survival and abundance of salmon following the 1976/1977 climate regime shift and that this, in turn, led to density-dependent reductions in growth during late marine stages. Annual measurements of Bristol Bay (Bering Sea) and Chignik (Gulf of Alaska) sockeye salmon scale growth from 1955 to 2002 were used as indices of body growth. During the first and second years at sea, growth of both stocks tended to be higher after the 1976–1977 climate shift, whereas growth during the third year and homeward migration was often below average. Multiple regression models indicated that return per spawner of Bristol Bay sockeye salmon and adult abundance of western and central Alaska sockeye salmon were positively correlated with growth during the first 2 years at sea and negatively correlated with growth during later life stages. After accounting for competition between Bristol Bay sockeye and Asian pink salmon, age-specific adult length of Bristol Bay salmon increased after the 1976–1977 regime shift, then decreased after the 1989 climate shift. Late marine growth and age-specific adult length of Bristol Bay salmon was exceptionally low after 1989, possibly reducing their reproductive potential. These findings support the hypothesis that greater marine growth during the first 2 years at sea contributed to greater salmon survival and abundance, which in turn led to density-dependent growth during later life stages when size-related mortality was likely lower. Our findings provide new evidence supporting the importance of bottom-up control in marine ecosystems and highlight the complex dynamics of species interactions that continually change as salmon grow and mature in the ocean.

Keywords: Salmon; Growth; Survival; Competition; Climate change; North Pacific Ocean

1. Introduction

Many species in the Bering Sea and North Pacific Ocean underwent significant changes in abundance following the 1976–1977 climate shift (Beamish and Bouillon, 1993; Mantua et al., 1997). This shift was associated with a pronounced increase in the size and intensity of winter storms, which, in turn, resulted in an increase in winter sea-surface temperature (SST) in some northern regions. Following the transition, the abundance of some species assemblages increased (zooplankton, Pacific salmon, and groundfish) whereas others decreased

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(crustaceans, forages fishes, piscivorous birds, and pinnipeds) (Rogers, 1984; Alverson, 1992; Francis et al., 1998; Anderson and Piatt, 1999). During winter 1988–1989, another regime shift occurred in some components of the eastern North Pacific ecosystem (Hare and Mantua, 2000). In 1997, unusually warm SSTs and calm winds during summer had a profound impact on Bering Sea biota (Kruse, 1998; Napp and Hunt, 2001). Some evidence suggests that another regime shift occurred in 1998, but its effects on biota were greatest in southern regions (King, 2005). During 2001–2003, summer temperatures in the southeastern Bering Sea were exceptionally warm and, if they continue, could result in a shift from Arctic to sub-Arctic species (Overland and Stabeno, 2004). While climate shifts affect large geographical areas, regional differences in species responses to the shifts can be significant (King, 2005; Pyper et al., 2005).

Various hypotheses have been developed to explain the complex responses of species to shifts in oceanographic conditions in the North Pacific Ocean and Bering Sea (Gargett, 1997; Francis et al., 1998; Anderson and Piatt, 1999; Hollowed et al., 2001; Ware and Thomson, 2005). Building upon these hypotheses, Hunt et al. (2002) proposed the oscillating control hypothesis (OCH), which predicted that the pelagic ecosystem in the southeastern Bering Sea alternates between primarily bottom-up control in cold regimes and primarily top-down control in warm regimes. The OCH predicts that salmon abundance in the southeastern Bering Sea may increase during warm regimes in response to greater prey abundance.

Total abundance of Pacific salmon (*Oncorhynchus* spp.) in the North Pacific Ocean increased sharply from approximately 300 to 700 million adult salmon per year following the 1976–1977 climate shift, largely as a result of increases in northern regions (Rogers, 1987, 2001). Mechanisms leading to this increase in salmon abundance are largely unknown, but researchers have assumed that greater prey biomass in the ocean was a key factor (Francis et al., 1998; Beamish et al., 1999). Brodeur and Ware (1992) reported significantly greater biomass of zooplankton in the Gulf of Alaska after the mid-1970s, but no zooplankton biomass increase was detected in the southeastern Bering Sea where numbers of Bristol Bay sockeye salmon (*Oncorhynchus nerka*) significantly increased (Napp et al., 2002). However, based on cohort analysis, age-0 pollock (*Theragra chalcogramma*) were exceptionally abundant (Hunt et al., 2002), and young pollock may have contributed to the diet of sockeye salmon (Farley et al., 2005). Increases in salmon prey abundance in response to climate change are not well documented because Pacific salmon opportunistically consume a variety of prey that changes with their size, and because annual growth at sea of immature salmon is rarely measured. Prey species include squid, small fishes and euphausiids that are difficult to quantify, both in terms of abundance in the ocean and in the diet of salmon, which are distributed across broad oceanic regions (Pearcy et al., 1988; Cooney and Brodeur, 1998; Kaeriyama et al., 2004).

Although it is plausible that greater prey biomass caused greater salmon abundance after the 1976/1977 climate shift, the influence of prey biomass is complicated because size at age of adult salmon declined throughout most of the Pacific Rim during the past 30 years, suggesting that food availability limited rather than enhanced salmon growth (Peterman, 1984; Bigler et al., 1996; Cox and Hinch, 1997; Kaeriyama, 1998; Pyper and Peterman, 1999). Adult salmon abundance and mean size were inversely correlated with indices of zooplankton abundance in the Gulf of Alaska (Cooney and Brodeur, 1998), suggesting that salmon may reduce zooplankton abundance. Welch et al. (1995) hypothesized that warming SSTs in the North Pacific Ocean may cause salmon distribution to shift northward, resulting in a smaller foraging area and greater density dependence. Declining salmon size at age has raised concern regarding the capacity of the ocean to support wild salmon populations while hatcheries release approximately 5 billion juvenile salmon per year into the North Pacific Ocean (Cooney and Brodeur, 1998; Mahnken et al., 1998).

Alternative hypotheses on mechanisms leading to greater salmon abundance have been proposed. These include a shift in the diets of predators away from salmon in response to increasing abundance of alternative prey (Pearcy, 1997), or a change in the distribution of salmon relative to their predators (Rogers, 1984). Uncertainty regarding the mechanism(s) leading to greater salmon abundance also stems from the absence of data on numbers of salmon smolts leaving freshwater habitats prior to the mid-1970s (Bradford, 1995). Furthermore, the potential for increased salmon production from freshwater habitats in response to climate change is largely unknown (Hilborn et al., 2003).