A critical review of Pacific salmon marine research relating to climate

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Several studies in the North Pacific Ocean have documented the consequences of rising sea surface temperatures and the advancement of the spring freshet on ocean productivity. The altering of ocean productivity has also been correlated with changes in the marine survival and geographic occurrence of some Pacific salmon populations. Knowledge of the marine survival and position of salmon in the Pacific Ocean are derived typically from mark-recapture studies. As a result, the migratory behaviour and associated survival estimates of salmon in real time are not known. Major information gaps also exist in terms of stock-specific marine behaviour and survival—especially as they relate to recent changes in climate. Acoustic telemetry and other modern tools enable researchers to answer specific questions about environmental, physiological, and genetic effects on individual salmon survival and behaviour, which had not been possible previously. As climate trends increasingly exceed those found in historical records, there is an urgent need for information that will improve fishery management and conservation decisions. International, multidisciplinary research teams using modern technologies could accomplish this.

Keywords: acoustic telemetry, ecosystem dynamics, environment, hatcheries, marine survival, migratory behaviour.

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Introduction

Pacific salmon (*Oncorhynchus* spp.) have existed in the North Pacific Ocean for more than five million years (Neave, 1958; Shedlock *et al.*, 1992; McPhail, 1997). Natural climatic changes have caused fluctuations in salmon abundance over several thousand years (Finney *et al.*, 2000), but an impressive adaptive ability (Hendry *et al.*, 2000) has been one of the main factors enabling salmonid survival to this day. However, recent changes in climate are unprecedented (Emanuel, 2005; Jouzel *et al.*, 2007). Scientists have declared that the major trends in climate observed in the past 50 years have been caused by human activity, and warn that if present emission levels continue, global climate systems could be damaged irreversibly (IPCC, 2007).

The great diversity of Pacific salmon has been attributed to the major changes in topography, climate, and glaciations taking place on the west coast of North America during the past five million years (Montgomery, 2005). Each species of Pacific salmon has a unique migratory strategy, timing of life stages, rates, and routes of travel, habitat use, and responses to environmental factors such as flow rates, temperature, and salinity (French *et al.*, 1976; Groot and Margolis, 1991; Waples *et al.*, 2001; Mueter *et al.*, 2002). For example, pink salmon (*Oncorhynchus gorbuscha*) have a 2-year life cycle, migrating to the ocean quickly, and returning after 18 months to spawn and die (Heard, 1991), whereas sockeye salmon (*Oncorhynchus nerka*) spend the first few years of their life in freshwater before travelling great distances in the ocean and returning up to four years later (Burgner, 1991). Although some pink and coho salmon (*Oncorhynchus kisutch*) spend their entire marine life in coastal waters, juvenile steelhead trout (*Oncorhynchus mykiss*) prefer offshore areas (Pearcy and Masuda, 1982; Argue *et al.*, 1983; Hartt and Dell, 1986; Fisher and Pearcy, 1988). Within each species, there are thousands of spawning populations, and variation exists among stocks co-inhabiting the same river system (Groot and Margolis, 1991). For example, in the Fraser River watershed of British Columbia (Figure 1), the timing of sockeye-salmon outmigration tends to depend on the lake system in which the stock originates (Burgner, 1991). Therefore, with the high degree of variability that exists between species, stocks, and brood years, the task of understanding ecosystem effects on Pacific salmonid migratory behaviour has been a challenge even without taking climatic effects into account.

Interactions between short-term climate patterns, decadal regimes, and long-term climate-change trends are complex. Fishery scientists face the challenging task of distinguishing between the influences of 6–18 month weather patterns (e.g. *El Niño*), 20–30-year regimes (e.g. the Pacific Decadal Oscillation), and longer term climate change on salmon populations (Philander, 1983, 1990; Rasmussen and Wallace, 1983; Kerr, 1995; Mantua *et al.*, 1997). The Pacific Decadal Oscillation, a large-scale climate pattern in the North Pacific, has had direct impacts on salmon populations (Mantua *et al.*, 1997;

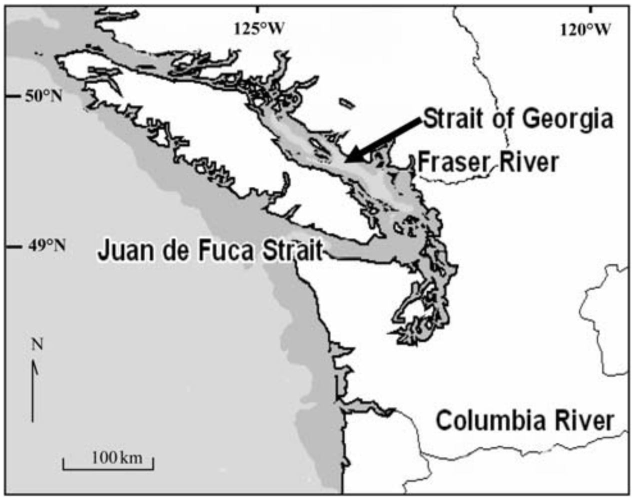

Figure 1. The Columbia and Fraser Rivers, the Strait of Georgia, and the Juan de Fuca Strait, off the west coast of North America.

Beamish *et al.*, 1999a; Hare and Mantua, 2000), and regime shifts have been correlated with significant changes in migratory patterns, abundance, and marine-survival rates (Beamish *et al.*, 1997a, 2004; Welch *et al.*, 2000; Hobday and Boehlert, 2001). However, these relationships may change during *El Niño* years. Similarly, long-term climate-change trends may counteract decadal regime effects over time, which could alter the marine environment in unforeseeable ways (IPCC, 2007).

If the consumption rate of Pacific salmon is to continue at present levels, improvements in the precision of fisheries data and climate-prediction capabilities are essential (Bardach and Santerre, 1981; Cole, 2000). Whereas the freshwater part of the salmonid life cycle has been the primary focus of research to date, scientific information about estuarine and early marine survival for Pacific salmon stocks is lacking (Pearcy and Masuda, 1982; Perry *et al.*, 1998; Brodeur *et al.*, 2000; Weitkamp and Neely, 2002; Beamish *et al.*, 2003). The need for marine-ecosystem assessments of anadromous salmon has been demonstrated globally (Beamish and Mahnken, 1999; DFO, 2000; CEC, 2002; NOAA, 2002). Moreover, ecosystem-based fishery management that incorporates both biotic and abiotic data from an ecosystem rather than from solely a target-species perspective is essential to maintaining fisheries as sustainable, particularly with the changing marine environment (Beamish and Mahnken, 1999). The use of new technologies, combined with the outputs of environmental monitoring systems, could improve our limited understanding of how climatic changes affect the marine survival and migratory behaviour of Pacific salmon. This review outlines current literature pertaining to climate effects on Pacific salmon and describes where knowledge gaps could be filled by the employment of electronic devices and other advancing technologies.

Pacific climate

Ecological research aimed at the long-term conservation of natural resources is a priority as changes in the environment become more extreme (Mote *et al.*, 2003; Stern, 2007). Ice cores in Antarctica provide evidence that atmospheric levels of carbon dioxide (CO_2) are higher now than they have been in the past 800 000 years and are increasing at a rate never before recorded (Petit *et al.*, 1999; Jouzel *et al.*, 2007). If current trends continue, the average surface air temperature of the northern hemisphere is estimated to rise by more than 3°C by 2050 (Mann *et al.*, 1999). Elevated levels of CO_2 in the atmosphere also increase the acidity of the oceans, which could have major effects on the future of marine ecosystems (Caldeira and Wickett, 2003). The earth's rising surface temperature has resulted in disturbing changes in the cryosphere, the frozen areas of the earth's surface. Ice breakup in spring is happening earlier than it did 50 years ago, the area and thickness of ice sheets are decreasing, and precipitation patterns are changing (Magnuson *et al.*, 2000; Livingstone, 2001; Robertson *et al.*, 2001). The cryosphere is an integral part of the global ecosystem, controlling the water supply to many areas, and influencing ocean currents (Magnuson, 2002). Rising sea levels attributable to the thermal expansion of the oceans and the increased melting of ice are altering coastal habitat (Morris *et al.*, 2002). The disappearance of the polar ice cap and other important ice sheets will transform the marine environment in ways that can only be speculated upon (Alley, 2002). Global temperature increases are positively correlated with zonal wind strength (Kalnay *et al.*, 1996; Emanuel, 2005; IPCC, 2007), which is a major driver of oceanic currents (Munk, 1950; McGowan *et al.*, 1998; Walther *et al.*, 2002).

Oceanic currents are the circulation system of marine ecosystems (McPhaden and Zhang, 2002). Cold, nutrient-rich waters from the deep are drawn up to the surface, allowing for the growth of phytoplankton, which form the base of the ocean food chain (Pickett and Schwing, 2006). Phytoplankton are extremely sensitive to temperature, nutrient concentrations, and sunlight levels, making them good indicators of climate-pattern changes and environmental conditions (Roemmich and McGowan, 1995). If the currents change, the depth and concentration of nutrient layers change, and ocean productivity is affected (McGowan *et al.*, 1998). These effects are manifested in Pacific salmon size, abundance, marine survival, and migratory behaviour (Bardach and Santerre, 1981; Johnson, 1988; Beamish, 1993; Beamish *et al.*, 1999a, b, 2000, 2008; McFarlane *et al.*, 2000; Hobday and Boehlert, 2001; Mote *et al.*, 2003; Tolimieri and Levin, 2004).

Correlations between population size and climatic indices have been recorded in many species, including Pacific salmon (Beamish and Bouillon, 1993; Williams, 1998; Cole, 2000). From the subtropic to the Arctic zones of the Atlantic and Pacific Oceans, the productivity of the main commercial fish stocks is closely related to the atmospheric-circulation index (a measure of the dominant direction of air-mass transport) and the earth-rotation velocity index (a measure of Earth's rotational velocity, which affects the length of day; Klyashtorin, 1998). The Aleutian low-pressure index, a measure of the area of the North Pacific covered by the Aleutian low-pressure system $<$100.5 kPa, also correlates with the catch of Pacific salmon (Beamish and Bouillon, 1993). Downtown and Miller (1998) reported that the catch of sockeye, pink, and chum salmon (*O. keta*) in Alaska was affected by the temperature at the time and location of the return migration, as well as environmental conditions during the smolt run. An assessment of sockeye salmon along the eastern Bering Sea shelf found that the diet, condition, and distribution varied with ocean temperature (Farley *et al.*, 2007). Not all salmon stocks appear to be affected equally during climate shifts, however. Although salmon populations off Oregon and Washington approached all-time lows in 1972, abundances in Alaska increased significantly

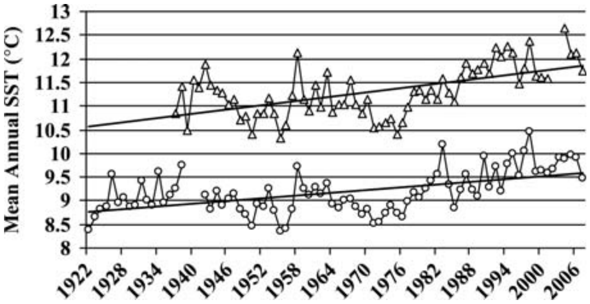

Figure 2. Mean annual SST in the Strait of Georgia from 1922 to 2007. Data from the Race Rocks Lighthouse (48°18′N 123°32′W) in the Strait of Juan de Fuca are shown as open circles, and data from the Entrance Island Lighthouse (49°13′N 123°48′W) in the Strait of Georgia as open triangles (after Environment Canada, 2008).

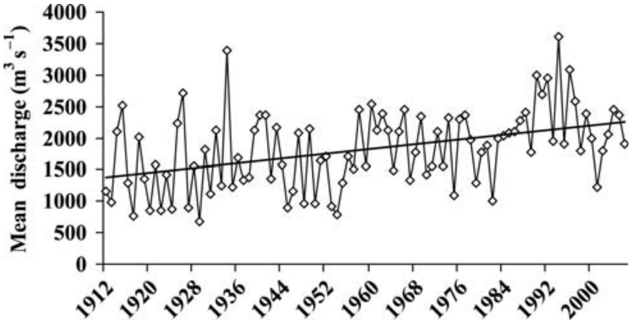

Figure 3. The April mean daily discharge of the Fraser River at Hope, British Columbia, from 1912 to 2006 (after Environment Canada, 2008).

(Coronado and Hilborn, 1998; Bradford, 1999; Hare *et al*., 1999; Welch *et al*., 2000; Hobday and Boehlert, 2001). Ocean productivity is the main determining factor of overall marine survival for salmon, and northern waters are increasing in productivity whereas the biomass in southern waters declines (Nickelson, 1986; Fisher and Pearcy, 1988; Beamish and Bouillon, 1993; Hare and Francis, 1995; Mantua *et al*., 1997; Beamish *et al*., 2000).

Climate affects salmonids at all life stages. The early marine-survival rate of Pacific salmon is influenced by individual body size (Holtby *et al*., 1990; Beamish *et al*., 1997b). The number of juveniles to reach a critical size by a particular time has been associated with brood-year survival and abundance (Beamish and Mahnken, 2001; Ruggerone *et al*., 2007). If prey availability is low, juvenile salmon may not reach their critical body size before winter, and suffer high mortality as a result (Beamish and Mahnken, 2001). As adults, shifting currents and higher water temperatures may affect the ability of salmon to return to natal streams to spawn (Richter and Kolmes, 2008). Researchers in Canada, Japan, Russia, and the United States have found correlations between changes in climate and the migratory behaviour of Pacific salmon populations (Welch *et al*., 1998; Beamish *et al*., 1999b). Transpacific surveys conducted by the Japanese and Canadian Governments during the 1990s, in addition to historical data collected since the 1950s, found strong sea surface temperature (SST) limits for sockeye salmon that affected their migratory behaviour and could restrict the species to the Bering Sea within 50 years (Welch *et al*., 1998). Sockeye salmon in the Columbia River, WA (Figure 1), have been migrating upriver more than a week earlier on average than they did 50 years ago (Quinn *et al*., 1997). In the Straits of Georgia and Juan de Fuca (Figure 1), the average annual SSTs have increased by 1°C over the past century (Environment Canada, 2008; Figure 2), and adult Fraser River sockeye have been returning to rivers on the west coast of Vancouver Island to spawn (McKinnell *et al*., 1999). Migratory routes of coho salmon in the Strait of Georgia have altered since 1995, when most resident juvenile coho salmon left the Strait during late autumn (Beamish *et al*., 1999b). Moreover, the final ocean weight of Fraser River sockeye decreased with increasing SST, potentially affecting their reproductive success (Hinch *et al*., 1995; Pyper and Peterman, 1999). Temperature barriers exist not only because of lethal temperature limits, but also as a result of tight energy budgets faced by salmon during winter (Richter and Kolmes, 2008). When prey availability is low, salmon need to keep their basal metabolism at a minimum, because metabolism increases exponentially with temperature (Brett *et al*., 1969). Therefore, the migratory behaviour, feeding behaviour, and trophic dynamics of Pacific salmon can be affected when the fish are faced with climate-induced changes in water temperature and prey resources (Kaeriyama *et al*., 2004).

Other effects of climate, such as an earlier onset of spring, can further affect salmon stocks (Beamish *et al*., 1999a). The mean daily discharge of the Fraser River in April has been increasing (Environment Canada, 2008; Figure 3), indicative of an advancing spring freshet, and an earlier marine productivity bloom (Beamish and Mahnken, 2001). This trend favours smolts that migrate out earlier in spring (Beamish *et al*., 1999a; Beamish and Mahnken, 2001). Therefore, earlier migrating species such as pink and chum salmon may have an advantage over later migrating coho and Chinook (*Oncorhynchus tshawytscha*) salmon (Beamish *et al*., 2000). Additionally, as wild smolts migrate downstream earlier, hatchery fish generally have a static release time, which may contribute to their reduced marine survival (Beamish *et al*., 2008).

Electronic devices as tools to study climatic effects

Marine research on salmon has typically made use of catch data from fishing vessels to estimate population sizes and migration patterns (Beamish *et al*., 2003). Coded-wire tags (CWTs) enabled researchers to tag large numbers of young salmon, with each stock given a unique identifier. CWTs and other mechanical tags have provided a vast amount of stock-migratory data, but the technology requires the recapture of tagged fish. Little detailed and accurate information can be gained about a fish's habitat use, swimming speed, small-scale movements, exact timing of migration, or residence times from such mechanical tags, so the influences of a rapidly changing environment on fish movement, survival, and growth are limited to speculation. For a thorough review of the CWT programme and biases in catch-data models, see Hankin *et al*. (2005).

Modern stock-identification methods, such as microsatellite, DNA-based, genetic stock-identification technology, and single-nucleotide polymorphisms (SNPs), could allow any fish caught in the ocean to be traced back to a specific stock and brood year (Nielsen *et al*., 1997; Bravington and Ward, 2004; Liu and Cordes, 2004). Although these methods may provide a wealth of distribution data for individual stocks in time, they still require the capture of fish in the ocean and do not allow for the monitoring of a live fish within its natural environment. The lack of information regarding the spatial and temporal migratory patterns and survival of individual stocks and how they react to changing environmental conditions is the primary reason that fisheries models provide unreliable estimates of predicted returns and, as a result, are limited in their usefulness to management plans and conservation strategies. Moreover, as some salmon stocks become more threatened, catch data are in some cases non-existent, and the removal of large numbers of endangered fish from the sea for research is controversial. The primary knowledge gaps in Pacific salmon biology as it relates to climate include stock-specific marine survival and marine migratory behaviour, and ecosystem dynamics. Each of these will now be examined in turn in relation to the use of new electronic devices.

Marine survival of Pacific salmon

Advances in hydroacoustic telemetry during the past 30 years allow for marine-survival data to be obtained independent of fish harvest. Fish as small as 11 cm can be tagged without adverse effects on growth or survival (Chittenden *et al*., 2009), making field studies of Pacific salmon species with smaller smolts possible (Chittenden *et al*., 2008). Reviews of early acoustic-telemetry work are provided by Ireland and Kanwisher (1978), Mitson (1978), and Stasko and Pincock (1977). Later studies are summarized in Baras (1991), Arnold and Dewar (2001), and Jepsen *et al*. (2002). Coded acoustic transmitters have also been developed that contain an electromyograph (EMG) to record heart rate, feeding activity, breathing activity, swimming speed, and acceleration and movement patterns of individual fish as they pass through different environments (e.g. Armstrong *et al*., 1989; Whitney *et al*., 2007). A comprehensive review of the applications of EMG tags is given by Cooke *et al*. (2004a). Additionally, archival and coded tags that monitor temperature, depth, oxygen, pH, and light levels experienced by the fish are available (e.g. from VEMCO Ltd, Halifax, NS, USA, or Thelma AS, Trondheim, Norway).

Earlier work correlating climatic indices to the catch and return rates of Pacific salmon stocks provide little detail in terms of the mechanisms of environmental effects on salmon populations, the location of high marine-mortality areas, or how individual fish respond to environmental changes. Acoustic telemetry has been used to study the early marine survival of steelhead trout (Welch *et al*., 2004; Melnychuk *et al*., 2007) and sockeye salmon (Cooke *et al*., 2005a), using listening lines of hydrophone receivers moored on the seabed (the Pacific Ocean Shelf Tracking project, POST; Welch *et al*., 2003). These studies are good examples of how acoustic telemetry can be employed to fill the knowledge gaps in stock-specific, marine-survival rates, but they do not incorporate climate data. Only one published report could be found regarding climate effects on the marine survival of Pacific salmon using acoustic telemetry. Crossin *et al*. (2008) examined the relationship between exposure to high temperature during spawning migration and the survival, behaviour, and physiology of adult sockeye salmon. They found that fish exposed to higher temperatures during their homing migration had significantly less survival to the spawning site and higher infection levels of *Parvicapsula minibicornis*. EMG tags monitoring heart beat, feeding rate, depth, or swimming speed can indicate metabolic rates, or whether a fish has died (Cooke *et al*., 2004a), if detected by a manual-tracking device or autonomous underwater vehicle/glider (Webb Research Company, Falmouth, MA, USA). Telemetry data can be analysed in conjunction with environmental data (e.g. water temperature, pH, salinity, current, dissolved oxygen, pollutants) recorded by archival tags or sensors located near the detected fish. Correlations and detailed behaviour patterns can then be discovered.

The long-term monitoring of every Pacific salmon stock, including yearly baseline health assessments, would be ideal. However, there are many limitations to this type of work and, in particular, the cost and time involved. Transmitters and receivers are expensive; perhaps with time the cost of this equipment will decrease, but as with most new technologies not yet widely used, considerable funding is required for acoustic- and satellite-telemetry studies. Deploying receiver equipment, manual tracking, and analysing telemetry data are time-consuming and require expertise, although permanent listening arrays, gliders, and databases that automatically edit and animate telemetry data may help cut down on time costs. There is also a possibility that the tags affect the fish. Although tag-effect studies have been done on Atlantic salmon *Salmo salar* (Greenstreet and Morgan, 1989; Moore *et al*., 1990; Lacroix *et al*., 2004), Chinook salmon (Anglea *et al*., 2004), coho salmon (Moser *et al*., 1990; Chittenden *et al*., 2009), sockeye salmon (Steig *et al*., 2005), and steelhead trout (Brown *et al*., 1999; Welch *et al*., 2007), every stock is unique and it is advisable to conduct a tag-effect trial with each project. Some fish are too small to tag; pink and chum salmon, for example, have smolts that cannot be implanted with the available sizes of acoustic transmitters. Therefore, those species would need to be caught at sea (e.g. with a purse-seine) once they have grown to a more adequate size, for studies of early marine survival. Finally, causal relationships are difficult to determine in these types of open-field experiment. Laboratory studies investigating individual and multiple environmental stressors on the physiology and health of tagged stocks are proposed as a complement to fieldwork.

Marine migratory behaviour of Pacific salmon

Coded acoustic transmitters and archival tags have been developed that can be used to study the marine migratory behaviour of individual fish over several years (Moore and Potter, 1994; Johnstone *et al*., 1995; Voegeli *et al*., 1998; Thorstad *et al*., 2004; Finstad *et al*., 2005). In addition to the marine-survival studies mentioned previously, these technologies have been used to track the marine migratory behaviour of coho (Moser *et al*., 1991; Ogura and Ishida, 1992; Miller and Sadro, 2003; Chittenden *et al*., 2008), sockeye (Crossin *et al*., 2007), Chinook (Candy *et al*., 1996), and chum salmon (Yano *et al*., 1997). Acoustic telemetry can take a multidisciplinary approach, integrating physiological, environmental, and behavioural parameters in hypothesis-driven field experiments (Cooke *et al*., 2008). Temperature and light levels experienced by pink, coho, and chum salmon and steelhead trout in the North Pacific were analysed by Walker *et al*. (2000), who found that the offshore distribution of salmon may be more linked to prey distribution than SST. Teo *et al*. (2004) used light-level and SST data recorded by electronic tags to validate geolocation estimates. There is also ongoing monitoring of returning Fraser River sockeye salmon to test the hypothesis that as river temperatures increase annually, disease and parasite levels are rising, and the timing of the return migration and the reproductive success of this species are being affected (Cooke *et al*., 2004b; Crossin *et al*., 2008).

With the number and variability of Pacific salmon stocks in existence, the gap in stock-specific, marine-migratory-behaviour research, especially as it relates to climate, is significant. The generalized home ranges of the Pacific salmonids have been described (Groot and Margolis, 1991). However, as the marine climate changes, the migratory behaviours of some populations are changing (McKinnell *et al.*, 1999; Beamish *et al.*, 2008), and stock-specific migratory ranges remain a mystery. Climate-induced changes in the migratory behaviour of coho and Chinook salmon in the Strait of Georgia (Figure 1) were investigated by Chittenden *et al.* (in press), in collaboration with the POST project. That study required the use of acoustic tags to answer specific questions about migration timing and marine-mortality rates, possible size effects on migratory behaviour and survival, and differences between early- and late-summer groups. Manual tracking, though time-consuming, can provide a continuous stream of information about the migratory behaviour of an individual fish within its environment. For example, the migratory behaviour of Atlantic salmon post-smolts tagged and manually tracked with acoustic-depth-sensing transmitters was enhanced with information about light intensity (Davidsen *et al.*, 2008) and temperature (N. Plantalech Manel-la, unpublished data) recorded from the tracking vessel. A relevant but non-salmonid study in South Africa examined environmental factors (turbidity, salinity, temperature, tidal phase) that may influence the movement of spotted grunters (*Pomadasys commersonnii*) in an estuary (Childs *et al.*, 2008). Using coded EMG transmitters (e.g. monitoring feeding, swimming, or heart rates) and environment-sensing transmitters (e.g. depth, temperature, salinity) in manual-tracking studies expands the possibilities of analysing the physical responses of fish to environmental cues. Mooring arrays of fixed hydrophone receivers with attached environment-monitoring devices to track tagged fish, though not as data-rich as manual tracking, are likely to be less time-consuming and could provide a larger and more representative sample of fish populations. Moored listening stations can relay telemetry and environmental data to satellites, which in turn can send the real-time data directly to the offices of fishery managers. Therefore, as temperatures and current patterns change in areas of prime Pacific salmon habitat, fishery managers can observe how tagged fish are reacting, and adjust their management decisions accordingly. This could be especially effective for restricting fishing when the adults of an endangered salmon stock are migrating through an area. The topic of combining telemetry with other new technologies will be further discussed below. Satellite tags (recording depth and temperature, for example) attached externally to migrating species can be programmed to pop-off and transmit when the fish has remained at one depth for an extended period (e.g. from Microwave Telemetry Inc., Columbia, MD, USA). This technology is being used by researchers studying the marine migratory behaviour of Atlantic salmon (A. H. Rikardsen *et al.*, unpublished data), European eels (*Anguilla anguilla*; K. Aarestrup *et al.*, unpublished data), and many other species [e.g. the Tagging of Pacific Predators (TOPP) project; Weng *et al.*, 2005; Shillinger *et al.*, 2008]. As yet, no results of studies using satellite tags to follow the open-ocean migratory behaviour of adult Pacific salmon have been published. This new tool is a key to an uncharted area of Pacific salmon behaviour.

Ecosystem dynamics

New molecular and genomic techniques are revolutionizing marine microbiology by permitting the study of marine ecosystems from the microbe up, in efforts to understand the complex interactions between organisms within their changing environment (Doney *et al.*, 2004). This new interdisciplinary science will include information gained from marine fisheries research and will help to improve the understanding of Pacific salmon marine biology. Telemetry and other observational tools can contribute in a multitude of ways. The ecosystem effects of the annual release of billions of hatchery-reared salmon into the Pacific Ocean by the United States, Canada, Russia, and Japan are relatively unknown (Beamish *et al.*, 1997b), but differences in performance, survival, behaviour, and physical condition between wild and hatchery-reared salmon have been found (Fleming and Gross, 1993; Shrimpton *et al.*, 1994; Berejikian *et al.*, 1996; Nielsen *et al.*, 1997; Weber and Fausch, 2003; Hill *et al.*, 2006; Araki *et al.*, 2007; Chittenden *et al.*, 2008). If hatchery programmes continue to be used as a mitigative strategy, their ecological effects must be understood and best-practice strategies should be created. In addition to the use of electronic devices, the possibility of using otoliths and scales to distinguish between salmon of wild and hatchery origin would allow any fish captured in the ocean to be a source of data and could further the study of hatchery fish in the Pacific ecosystem (Hartt and Dell, 1986; Schwartzberg and Fryer, 1993; Zhang and Beamish, 2000).

Interspecific studies using electronic devices are not yet common. Telemetry was used in the study of an Oregon estuary that found harbour seals (*Phoca vitulina*) to be preying heavily on returning adult salmon (Wright *et al.*, 2007). In Norway, the interaction between Atlantic salmon smolts, Atlantic cod (*Gadus morhua*), and saithe (*Pollachius virens*) is being studied in an estuary and fjord system (E. B. Thorstad *et al.*, unpublished data). Acoustic technologies were also used to monitor fish aggregations in Marine Protected Areas (e.g. O'Dor *et al.*, 2001; Cooke *et al.*, 2005b; Meyer *et al.*, 2007), at aquaculture sites (e.g. Begout Anras and Lagardere, 2004; Cubitt *et al.*, 2005; Conti *et al.*, 2006), and around fish-aggregating devices (e.g. Ohta *et al.*, 2001; Dagorn *et al.*, 2007). Most of these studies dealt with one or two species, however, and did not examine environmental influences on behaviour.

When advanced technologies are combined, the benefits are great. Sonar and light detection and ranging (lidar) technologies allow for the study of salmon-aggregation behaviour in the ocean (Gauldie *et al.*, 1996; Misund, 1997; Tollefsen and Zedel, 2003; Churnside and Wilson, 2004). Monitoring stations could be positioned on the bottom of the ocean scanning upwards, or on the surface scanning downwards, at important migratory passageways to observe groups of fish passing (Doksæter *et al.*, 2009; Johansen *et al.*, 2009). Environmental sensors could be attached to the stations to monitor climate conditions in the area (e.g. including the levels of marine productivity). These observatory nodes could also be fixed to ocean platforms or to the bottom of slow-moving vessels. Combining acoustic telemetry with these other imaging technologies would effectively enable researchers to study individual fish of known stock, size, and physical condition within aggregations, as well as their inter- and intraspecific behaviours.

Sea-floor sensor arrays allow the observation of oceanic conditions and ecosystem productivity in real time. Examples of large-scale, sea-floor arrays include the American National Science Foundation's Ocean Observatories Initiative (OOI), Japan's Dense Ocean Floor Networking system for Earthquakes and Tsunamis (DONET), and the European Multidisciplinary Seafloor Observatories research infrastructure (EMSO). Data from these underwater-monitoring systems as well as other governmental environmental recording stations could be used by fisheries scientists in conjunction with marine survival and migratory data from acoustic technologies.

International telemetry projects aimed at studying marine ecosystems have governments and scientists working in collaboration. The TOPP and POST projects, as parts of the Census of Marine Life, have extended the boundaries of marine science in the Pacific (Welch *et al*., 2003; Shillinger *et al*., 2008). Marine animals from squid to salmon smolts have been tracked across the Pacific with satellite tags and acoustic arrays, including some mammals that have collected vast amounts of environmental data along their journeys (Weng *et al*., 2005). These projects allow for the study of inter- and intraspecific interactions within ecosystems. New technologies that enhance the observation of ecosystem dynamics are being developed: a "chat" tag, for example, designed to upload and download information from nearby chat tags so that interactions are recorded and can be passed onto a receiver later (VEMCO Ltd). Moreover, there are plans for receivers attached to vessels, floats, marine mammals, or gliders that can record data from any other tagged animal in their vicinity, as well as environmental data, before relaying the information to satellites from the surface. Dalhousie University's Ocean Tracking Network (OTN) is developing a global infrastructure to integrate projects collecting data on marine animals in relation to the changing ocean environment. International collaborations such as the examples described here contribute vital information about marine life to the United Nations Intergovernmental Oceanographic Commission's Global Ocean Observing System (GOOS). Although progressive and necessary to deal with existing knowledge gaps, however, these initiatives have limitations that include the challenge of dealing with the vast quantities of data produced and gaining enough buy-in from researchers, governments, and funders to support the infrastructure required for long-term studies.

Conclusion

Salmon have adapted to changes in climate over millions of years, but literature on the mechanisms of environmental effects on salmon productivity in the Pacific is limited. Although most Pacific salmon research has focused on freshwater survival (Pearcy and Masuda, 1982; Beamish *et al*., 2003), recent declines in the marine-survival rates of many stocks add urgency to the need for information about their ocean phase (Beamish *et al*., 2008). Very little is known about current stock-specific marine survival and migratory behaviour. Therefore, the mechanisms of short- and long-term changes in survival and behaviour attributable to environmental factors and ecosystem dynamics remain a mystery. Such knowledge gaps are a serious challenge to fishery managers trying to predict accurately how salmonid populations will be affected by harvesting and a changing climate. Coordinated international research efforts using advanced electronic technologies to investigate the consequences of short- and long-term climate trends on ecosystem dynamics and individual salmon populations are vital to the predictive ability of fishery managers and the conservation of Pacific salmon.

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