PART IV

Oceans Present – Animal Movements

Chapter 14

Tracking Fish Movements and Survival on the Northeast Pacific Shelf

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14.1 Introduction

The Pacific Ocean Shelf Tracking Project (POST) is one of the 14 field projects of the Census of Marine Life. POST began in 2001 (see Box 14.1) as an ambitious experiment to study the movements and survival of salmon in the ocean using a large seabed network of acoustic receivers to track individual acoustically tagged fish. The successful proof-of-concept, and the fact that compatible receivers and tags were in use by other researchers on the West Coast, helped POST mature and diversify into a complex infrastructure that is now regarded as an indispensable tool for understanding the behavior of many marine species that move along the continental shelves. Operationally, POST is a non-profit program run by an independent board, and hosted by the Vancouver Aquarium. POST's mission is to facilitate the development of a large-scale acoustic telemetry network along the entire length of the West Coast of North America, working through contractors and partners who deploy the array, and through collaborative relationships with independent principle investigators who conduct their own research projects using the array. POST maintains a public database where currently over 6.2 million detections of over 12,000 tags and 18 species are securely stored, and may be searched and shared by anyone.

POST is distinguished by three attributes:

1) A reliance on acoustic tags and a large network of strategically located receivers (Fig. 14.1).

Life in the World's Oceans, edited by Alasdair D. McIntyre

Box 14.1

POST Technology and History

Acoustic tags have been in use for 50 years (Johnson 1960), but in 2001 a fisheries biologist, David Welch, and his colleagues proposed to the Alfred P. Sloan and Gordon and Betty Moore Foundations to design and build a very large network of listening lines to track salmon in the ocean. They reasoned that satellite tags were too big to use on salmon, archival tags were too unlikely to be recovered (and their light-based geo-location estimates were too inaccurate at the time), and radio tags, although useful for tracking salmon in rivers, were useless in the ocean because of rapid attenuation of electromagnetic signals in seawater.

POST was built around acoustic tags and receivers manufactured by a Canadian company, Vemco (www.vemco.com). Vemco's tags could be implanted in small fish, detected at relatively long distances, programmed to have relatively long tag lifespans and, most importantly, the system generated few false-positive signals. Several studies have assessed the effects of the tags on the survival and behavior of fish that carry them (Lacroix *et al.* 2004; Zale *et al.* 2005; Welch *et al.* 2007; Chittenden *et al.* 2009a; Rechisky & Welch 2009), and helped to define fish size limits for tagging. Early on, the number of available unique tag identification numbers was small so they were re-used, which quickly became very confusing on the large scale of the POST array. POST helped to motivate the development of a system with many identification numbers that are unique worldwide.

Early Vemco receivers had short battery lives and could not be used in deep water, but by the time POST was scaling up, several thousand second-generation VR-2 receivers had been sold on the West Coast. These receivers were tough, reliable, had batteries that lasted one year, and, with a maximum depth of about 500 m, could be deployed almost anywhere along the continental shelf. Most importantly, all of the tags and receivers were compatible. However, the early receivers had to be physically retrieved to download the data. Most of the original POST network has now been replaced with a newer generation of VR-3 receivers equipped with long-lived batteries (four to seven years) and acoustic modems by which a boat can download data from the surface without physically recovering the receiver. This has generated significant cost savings over the life of the array and made it easier to keep receivers in position full-time, year-round.

Welch's research and development company, Kintama Research Corporation, tackled the problems of deploying large-scale arrays and developed the architecture and tag programming for the original demonstration array forming the core of POST. They designed specialized protective flotation collars and anchors (Fig. 14.3), improved moorings to reduce losses to trawling and storms, and built portable surgery stations and data-recording systems for large-scale tagging. They are currently modeling optimal array geometries for specific research projects, which depend on a host of factors including the research objectives, noise level in the area of the line, behavior of the tagged animal, tag parameters (loudness and programming), and position of the receiver relative to features such as the surface, the bottom, thermoclines, and haloclines. Where measurable, POST lines have obtained high enough detection efficiencies to produce useful survival estimates for juvenile salmon (Melnychuk 2009).

With support from US and Canadian government agencies and foundations, the POST array is maturing into a network of highly engineered, long listening lines that now spans 3,000 km from California to Alaska and is maintained year-round for use by any researcher. POST shares data with independent researchers who maintain their own, smaller receiver networks (some in grids or other geometries). We have begun the process of integrating POST data into large-scale ocean-observing systems including OBIS (see Chapter 17), the Ocean Tracking Network, and the Global Ocean Observing System (GOOS) system.

2) A focus on studying the behaviors of marine species, including long-distance migrations.
3) A focus on estimating survival by deploying acoustic receivers in long, relatively straight lines that stretch from the coastline to the edge of the continental shelf, or across straits between land bodies (Figs. 14.1 and 14.2). The lines are designed to have a high probability of detecting animals that cross them, and the effect is to compartmentalize large areas so that survival can be estimated within each area.

Although not an exclusive focus, POST fills a technological gap as a method to study the movements of small-bodied marine animals (10 cm – 1 m in length, including the juveniles of larger species), which are abundant, important in oceanic food chains, and generally difficult to study.

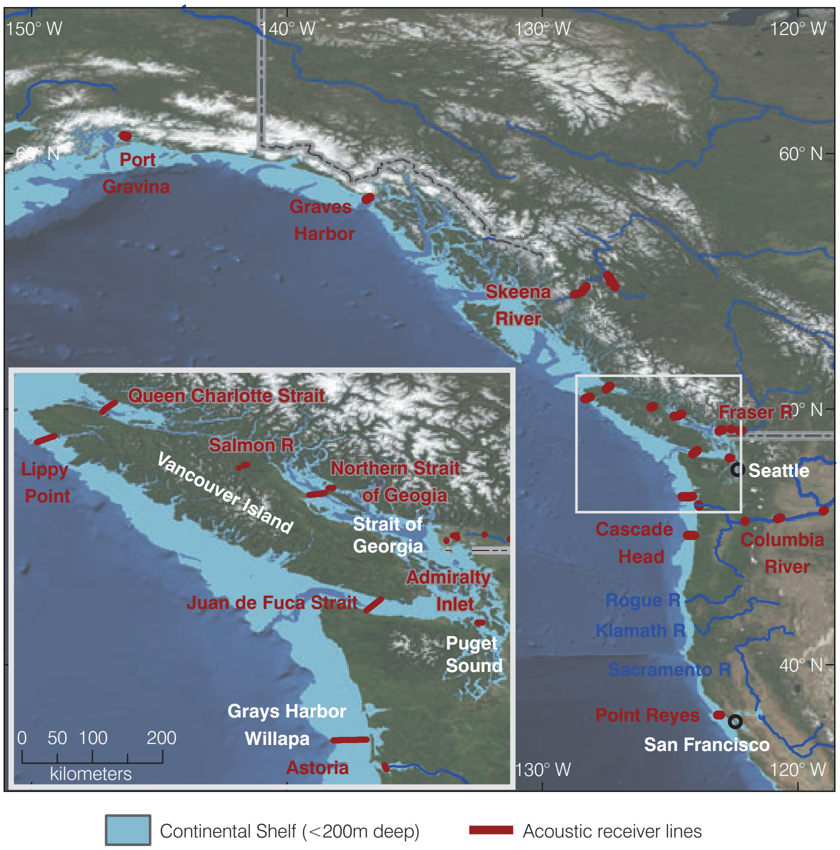

Fig. 14.1
The POST array as of 2009. Lines of acoustic receivers are shown in red. Permission of POST 2009.

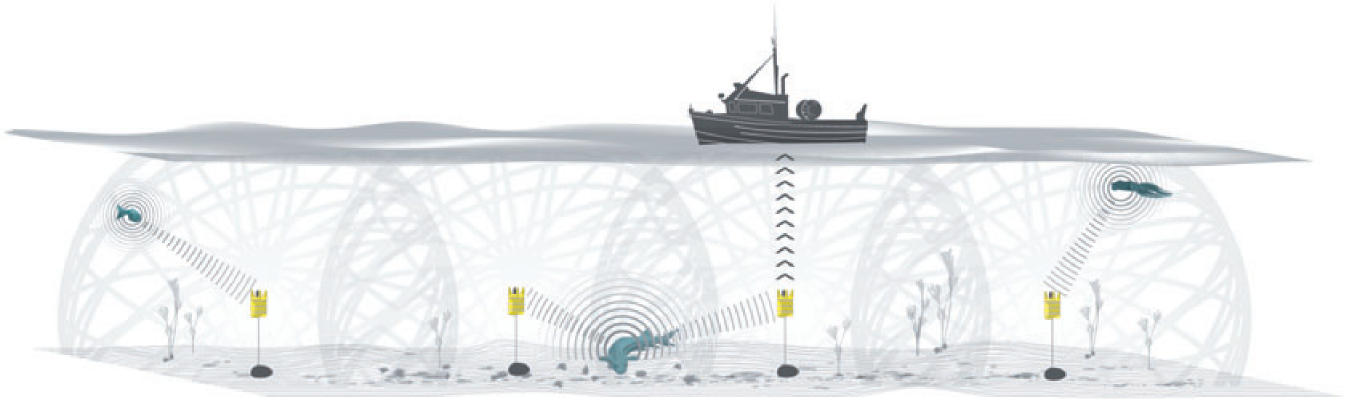

Fig. 14.2
A conceptual diagram of a POST receiver line. The spheres show hypothetical detection limits for the receivers. The tagged animals are being detected by different receivers (yellow objects tethered to the sea floor), and the ship is downloading information from a receiver, via an acoustic modem. Permission of POST 2009.

14.1.1 The questions that motivated POST

POST was originally designed to answer two questions about salmon. Salmon are among the most culturally and economically important species on the Pacific Northwest coast of North America, and have sustained human populations there since prehistoric times. The freshwater portion of salmon life cycles may be observed with relative ease, yet in the early 1990s, the renowned salmon biologist William Pearcy noted that the ocean life-history of Pacific salmon was a “black box”, constrained by the enormous difficulty of studying salmon on the high seas (Pearcy 1992).

The first of the questions was, "When and where do juvenile salmon die in the ocean?" It was known that very few of the juvenile salmon that left a river mouth would return as adults, and there were many theories about what happened to those fish. One theory was that the out-migrating cohorts suffered high mortality immediately upon entry to the ocean, and that the magnitude of that mortality would determine how many adult salmon returned from each cohort. Receiver lines were also designed to help clarify the details of movement patterns, which were known in a general way from recaptures of passive tags.

The second question was, "Are salmon as specific in their use of the ocean as they are in their use of rivers?" This was nicknamed the "two zip code" theory, the idea being that salmon could have one address in freshwater and a second address in the ocean. Even in mid-ocean, the marine environment is much less homogeneous than it appears to the human eye. At different scales, natural change encompasses variation such as decadal oscillations that affect sea surface temperatures and upwelling over vast areas, seasonally fluctuating currents that bring warm water into cold seas and spin off rings of warmer water which persist for months, and short-term turbulence from surface winds and currents that can mix thermally stratified water layers or concentrate surface debris, creating feeding grounds for marine animals. The POST idea was that some of the puzzling variation in survival that we observe in neighboring salmon populations might be due to their occupation of different parts of the ocean, or the timing of those uses, as some earlier studies suggested (Mckinnell *et al.* 1997). This question was distinguished from the first by the need to track juvenile salmon longer and farther and the need to understand how they used deeper water beyond the edge of the continental shelf.

POST's founders knew the network might prove useful for other species as well. The continental shelves are the most productive oceanic regions, and many commercially important species spend much of their life cycles on the shelf (Pauly & Christensen 1995). Seasonal upwelling of cold, nutrient-rich water supports high species diversity, commercially important fisheries, and large populations of marine mammals, seabirds, and fish in the Pacific Northwest (Keiper *et al.* 2005). The shelves also suffer the heaviest anthropogenic impacts from fishing, shipping, oil exploration, marine aquaculture, and land-based activities that export sediment, fertilizers, and pollutants.

14.1.2 How successful has POST been?

The signature of the early POST results is just how surprising they have been. The effort to study salmon survival in the ocean, while still in its early stages, has led to an explosion of applications to other species and a great expansion of the questions being asked: in a sense, POST has highlighted how little we know about the behavior of marine animals (Table 14.1). POST has now been used to study 18 species including salmon, salmon sharks, two species of squid, rockfish, ling, white sturgeon, and English sole.

However, there is still a long way to go toward answering the original questions. Measuring the survival of salmonids along the continental shelf with high accuracy and precision is still a goal that will require further methodological refinement and testing, as well as an expansion beyond the large, hatchery-raised fish that have been the focus of many salmon studies, to smaller wild fish and a larger range of life histories. Making sense of survival estimates in the context of natural and anthropogenic variation in ocean conditions will require long-term studies for which POST has begun to lay a baseline. Results from salmonid studies so far have highlighted enormous diversity among populations. Some appear to suffer high mortality in-river, others in inland marine waters and still others in deeper water beyond the reach of the current array. Although some populations appear to have experienced high mortality immediately upon ocean entry in some years, enough populations have shown alternative mortality patterns that it is safe to conclude there is no single answer to where and when salmon die in the ocean. From the perspective of conservation and management, this means that it may be difficult to identify the causes of weak or strong returns of adult salmonids without detailed, population-specific data.

The question of whether salmon have "two zip codes" was technologically the more difficult of the two original questions that motivated POST. Evidence from shelf waters suggests that there is inter-annual variation in migration patterns, for example in the proportion of Georgia Strait fish that migrate north rather than south in a given year. POST has been unable to test the "two-zip code" theory in deeper waters, but it is a goal that seems closer than ever to being answerable. In the chapter summary we discuss some new directions in technology that will help to move tracking off the continental shelf.

14.1.3 The value of movement and survival data

Nearly every marine species moves in order to take advantage of the ocean's physical and biological diversity. There are large differences in temperature, pressure, salinity, oxygen levels, and other parameters from the surface to the depths, from the equator to the poles, and from the shoreline to the mid-ocean. Productivity varies over many orders of magnitude from rich coastal upwelling zones to the barren mid-ocean waters. Where an animal goes determines what it experiences. We attempt to understand where animals go, the conditions they experience, and the internal

Table 14.1

Examples of technological and research questions currently being addressed by projects that use the POST array, with a brief summary of results to date.

Technological question	Application	Results so far
Can receiver lines be engineered so that it is possible to estimate the survival rates of migrating fish?	Juvenile salmonids in rivers Juvenile and adult salmonids on the marine continental shelf	Yes. Detection efficiency can vary with conditions such as flow rates Yes, but work remains to calibrate estimates, esp. on outer coast. High detection efficiency (85–95%) appears routinely achievable.
Do acoustic tags (which are larger than some other tag types) cause little enough additional mortality to be useful for survival studies of small animals?	Salmon smolts as small as 130 mm length, herring, small squid, other forage fish	Positive evidence so far; more studies are underway. Tag-to-body-size ratios do influence survival, and smaller tags will enable a wider variety of species, life stages, and stocks to be tagged.
Research goal/question	**Example**	**Results so far**
Describe residency, coast-wide movements, and interchange between major river basins of anadromous species	Green sturgeon and white sturgeon (California to British Columbia)	For green sturgeon, unusual northwards winter migration was discovered, plus complex, previously unknown marine behavior including substantial interchange between rivers.
Characterize movements of an apex predator at nested scales	Sixgill sharks in Puget Sound	Sharks are relatively sedentary on short time scales, move much more on longer scales. Puget Sound may be a nursery.
Characterize speed of migration	Salmonids	Speed is more variable in freshwater than in the marine environment, and migration of some species is faster and more directed than others. Juveniles of some species (for example, steelhead) cover long distances very fast.
Partition mortality between life-history phases (downriver migration, estuary, and early ocean)	Steelhead (British Columbia and Puget Sound)	The baseline of survival rates thus far suggests a diversity of patterns for different stocks, and finds differences between hatchery and wild fish.
Locate areas of high mortality for endangered stocks	Coho salmon (Strait of Georgia)	High-mortality areas seem to be stock-specific. Evidence for fall migration out of the strait; possible mortality in summer.
Investigate the impact of freshwater mitigation efforts on anadromous species	Chinook salmon (Columbia and Fraser Rivers)	Surprising and still controversial preliminary results find no evidence that passage through dams causes delayed mortality, and find similar survival rates in a dammed and an undammed river.
Search for physiological explanations of a major mortality event	Later-run adult sockeye salmon (Fraser River) that do not delay river entry and die in-river	High water temperatures probably exceed salmon physiological limits; hormonal changes while fish are at sea may cause them to enter the river early.

mechanisms that drive their behaviors, because for marine species, being in the right place at the right time may mean surviving instead of dying, being able to grow instead of going hungry, or reproducing instead of having no offspring. Even not moving has consequences, because the ocean is dynamic and change can visit a sedentary animal.

Movement and survival data are useful in many aspects of fisheries management. These data can help us to understand immigration and emigration from fish populations and to parse out some of the complexity observed in natural mortality rates; both are among the factors that limit the accuracy of stock size predictions. Some species are vulnerable during a brief window when they congregate at some life-history stage, or are sedentary, and movement data are useful for describing how species use habitat. Spatially resolved survival data are critical for restoration efforts, which benefit from a detailed understanding of a species' full life cycle to identify survival bottlenecks. Marine protected areas are an understudied new management tool, and there are many questions about how – and even whether – they work. Dispersal patterns may determine when a protected area will be a source of juveniles that can recolonize nearby exploited areas and boost depleted populations, or when will it be too small or unconnected to do so (Botsford *et al.* 2009). Finally, there is growing acknowledgement in fisheries management that it is important to preserve natural genetic and life-history biodiversity, and movement data suggest that there may be variation we are not aware of in the life histories of many species.

Indirect human impacts on the ocean – including climate change, acidification, and a host of effects that are produced by a growing population (increased shipping, increased light and noise, increased mineral exploitation, and others) – now threaten to exceed, perhaps greatly, our direct impact through fisheries. The accumulation of carbon dioxide in the Earth's atmosphere is changing global atmospheric temperatures, oceanic currents, ocean chemistry, and weather (IPCC 2007; Fabry *et al.* 2008). If we are to have any ability to respond to coming changes, we must understand a great deal more about the extent to which movement behavior is evolutionarily flexible, and how it may be changed by intense natural selection.

14.1.4 Acoustic tracking in the context of other technologies

Tagging can be used to understand where an animal goes, the conditions it experiences and, to a limited degree, its internal state. The smaller an animal is, the more difficult it is to track and the less sophisticated the tag can be. Tags can be categorized by how much information they provide about the time between capture and recovery, and by how data are retrieved. It is relatively easy to attach a sophisticated tag to a marine animal. The challenge is to retrieve the data, and there are only two solutions: to recover the tag physically, or to transmit the data to a receiver (which may be on land, in space, or underwater on a variety of platforms including fixed moorings, gliders, or other animals).

14.1.4.1 Chemical, biological, and genetic tracking

Many animals have natural markings that can be useful in movement studies (Payne *et al.* 1983). In addition, our environment leaves "natural tags" in our bodies that can be deciphered for information about where we have been, including ratios of stable isotopes, chemical signatures in otoliths (Barnett-Johnson *et al.* 2008), and even parasites (Timia 2007). Genetics are widely used for information about origins and mixing of stocks (Habicht *et al.* 2007; Seeb *et al.* 2004), and fatty acid ratios in the tissues of predators can help to identify the prey species and proportions eaten (Iverson *et al.* 2004). These methods are very useful because (1) the marking is already done for us by nature, and (2) even the smallest larvae retain readable signatures. However, calibration of the methods is complex and none yields detailed movement information. In addition, some require lethal sampling. The only way to study the movements of tiny larvae has been to take regular samples at grid points (see www.calcofi.org) but only very limited inferences about movement can be made from such data.

14.1.4.2 Non-electronic tags

The simplest tags are passive physical devices or marks such as freeze brands, fin clips, and spaghetti tags used to identify individual fish. Since 1968, US and Canadian institutions have released over 600 million salmon batch-marked with coded-wire tags in the largest tagging program on Earth. The main drawback to non-transmitting tags is that the vast majority are never seen again. Therefore, large sample sizes are needed, the species of interest must be the target of a substantial fishery, and any tagging data must be interpreted cautiously because the results are influenced by the movements, techniques, gear, and reporting behavior of the fishermen themselves. Information gathered from a physical tag usually can be summarized as two data points (release and recapture locations), plus associated dates and measurements. These studies leave many questions open. What route did the animal take? How did it respond to the conditions it encountered? What happened to most of the animals that were not seen again? Is the behavior observed representative of the population?

14.1.4.3 Electronic tags

A passive integrated transponder (PIT) tag is a semi-passive radio-frequency device that transmits a unique identification number when excited by a signal from a scanner. The scanner must be close to the tag (usually 45 cm or less). PIT tags have been used to tag 1 million to 2 million salmon per year since the 1980s, and fish are recorded as they pass through dams where expensive infrastructure has been used to channel and separate tagged juveniles and adults from other fish. In these situations, PIT tags are powerful tools, although the information each tag provides is limited.

14.1.4.4 Archival tags

Archival tags store data from one or more sensors on a computer memory chip. Sensors may record internal or external conditions, such as light levels and temperature that can be analyzed to provide rough estimates of latitude and longitude. Non-transmitting archival tags must be physically retrieved. Larger archival tags transmit data by radio signals to satellite or cell phone networks, and this capability to obtain fisheries-independent, detailed tracks is unmatched. With archival tags, it is possible to begin to understand the complex questions of why animals go where they go, how they navigate, and to observe detailed behavior in the wild. Unfortunately, most species are too small to carry satellite tags, and archival tags are not particularly useful for measuring survival, except in studies of hooking mortality.

14.1.4.5 Acoustic tags

The POST system is based on tags that transmit data to a network of submerged receivers. Each tag transmits an

Fig. 14.3
Acoustic receiver deployed in a tank at the Vancouver Aquarium. The receiver (soda-bottle-sized black object) is protected by the yellow flotation collar, which suspends it off the bottom and protects it from trawl nets and other disturbances, without compromising its ability to listen for tags. In an ocean deployment, the anchor would be much larger. Photograph: John Healy, Vancouver Aquarium.

individual identification code as a train of acoustic pulses at 69 kHz, approximately once a minute for 4–12 months, depending on battery and programming. The smallest tags (7 mm diameter × 18 mm length) can be surgically implanted in fish as small as 130 mm in length, and a new generation of higher-frequency tags may be used in fish as small as 95 mm. The two tag models most commonly used in POST have an approximate functional range of 200–400 m, depending on a host of conditions including ambient noise. Receivers record tag identification numbers plus associated detection times. Vemco's acoustic communications (see Box 14.1) are engineered to have a low rate of false-positive signals. The receivers wait for echoes to die down between pulses received from the tag, so the amount of information that can be transmitted is small (Grothues 2009). However, acoustic tags cost less than one-tenth as much as satellite tags, and may be manufactured with very long battery lives (more than 10 years), so in addition to being the method of choice for small species, they are also useful for long deployments on larger species.

14.2 Contributions from the POST Array to Marine Science

This section reviews species-specific accounts of some of the most important results so far from research that has taken advantage of the POST array.

14.2.1 A brief introduction to salmon

The fact that POST began in the North American Pacific Northwest made it almost inevitable that it would focus on anadromous species like salmon which use both fresh and saltwater. Salmon (*Oncorhynchus* spp.) spawn in freshwater rivers and streams, their eggs develop and hatch, and after a few days to two years in freshwater the juveniles swim to the ocean. In the ocean, they mature and grow to full size and sexual maturity before returning to spawn in their natal stream. Anadromous species come into more intimate contact with humans than purely marine species. In the prosperous Northwest, the human population now affects every part of the salmon freshwater life-stage. Many Northwest salmon populations declined dramatically during the twentieth century, and contributing factors include habitat destruction by agriculture, logging, and development, pollution, overfishing, negative impacts of large hatchery programs, hydropower and water storage dams, and changing climate patterns.

Luckily, salmon are extremely adaptable. The evolutionary history of salmon is one of repeated recolonization of rivers as the Northwest was covered and uncovered by glaciers (Waples *et al.* 2008), and Pacific salmon fisheries are still economically, socially, and environmentally important. Even today, many insects, birds, and mammals living as far inland as 1,500 km from the ocean owe much of their growth to ocean-derived nutrients carried in the bodies of salmon, although the total weight of Pacific salmon runs in this southern portion of their range may now be less than 10% of historical levels (Gresh *et al.* 2000).

Salmon management in the Pacific Northwest is a complex pastiche of efforts to regulate and mitigate human impacts. Some of the more complicated controversies involve efforts to reduce mortality of juveniles and adults at hydropower dams, to supplement natural populations with hatchery-raised fish, and to farm non-native Atlantic salmon along the Pacific coast.

14.2.2 Studies of survival

The next three sections on steelhead, coho salmon, and chinook salmon highlight the original purpose of the POST array, which was to study when and where salmon die in the ocean. Conservation strategies rely on knowledge of when and how much mortality occurs in the population of interest, and why. Most marine species are observed only when they are caught, usually as adults. An estimate of ocean survival for a salmon cohort may be a single number that integrates a 15,000 kilometer voyage from Oregon to Japan via Alaska and back over as long as five years, but it has been impossible to partition such survival estimates by location and time period. Despite sometimes being able to measure freshwater survival fairly accurately, we observe large, unexplained year-to-year variation in overall survival rates, as well as surprisingly large differences between closely neighboring stocks, both of which indicate the importance of ocean survival.

Technically, it is more difficult to study survival than movement, because when an animal is not detected, we must determine what happened. As long as the animal cannot swim around the end of a line, there are only four possibilities: (1) the animal died, (2) it slipped through the line undetected, (3) its tag stopped functioning or was lost, and (4) the animal took up residence between lines. The problem of tag loss can be solved by double-tagging studies (Wetherall 1982), and the residence problem can be addressed by adding additional lines or by using active tracking to locate missing tags. The most difficult problem is estimating the probability of detecting an animal that passes through a line (Fig. 14.4), and it is traditionally solved by jointly estimating detection probabilities and survival with mark-recapture models (Amstrup 2005). Producing survival estimates with narrow confidence intervals requires lines that are highly likely to detect passing fish. One of the real triumphs of POST has been to demonstrate that it is possible to maintain high-efficiency marine receiver lines and to produce survival estimates for migrating juvenile salmon in rivers and on the continental shelf. However, the system works best when animals are migrating in one direction and pass through lines that completely cross rivers or inland waterways, and work remains to understand better methodological issues such as tag effects, and to expand the range of salmonid stocks, sizes, and life histories tagged to a more representative sample of the natural range.

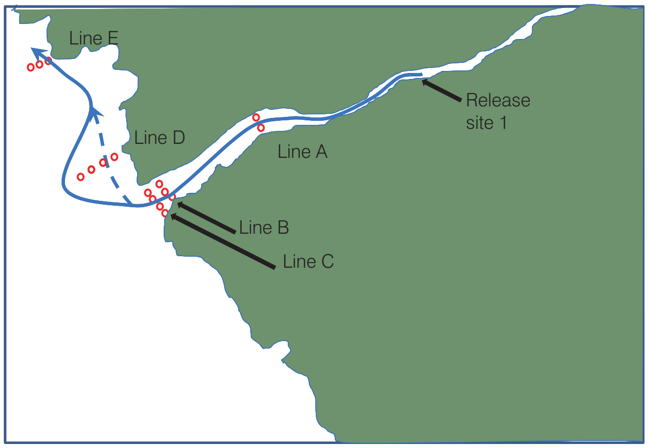

Fig. 14.4
The probability of detecting a fish that swims through a line of receivers can be estimated when a group of tagged fish is observed again after passing through the line, and the number detected can only unambiguously be related to detection probability if they *must* have passed through it. In the figure, if fish are migrating in the direction indicated by the blue arrow, detection efficiency can be measured for the array lines A, B, and C. However, detection efficiency cannot be estimated at line E (the terminal line, given the direction of the fish movement) without additional assumptions. Because fish may go around the end of the line at D, the probability that a fish passes undetected through line D (dashed line) is confounded with the probability that it swims around the end of the line.

14.2.2.1 Steelhead

Background

Steelhead are renowned for their long-distance migrations in the North Pacific. They are the anadromous form of rainbow trout (*Oncorhynchus mykiss*), but are often managed alongside the five species of Pacific salmon based on their behavior. Steelhead juveniles rear in swift streams and creeks, then migrate as smolts to the ocean for their adult life. Unlike other Pacific salmonids, steelhead are iteroparous, meaning adults can spawn in freshwater, return to the ocean for one or more years, and then spawn again. Widely distributed from California to Alaska, steelhead are highly sought after by anglers in recreational fisheries, but most southern populations are currently much smaller than they were historically.

Much like coho salmon, the downstream and early marine migration period is thought to be critical in determining recruitment of steelhead (Pearcy 1992). Smolt-to-adult survival rates generally declined throughout much of their southern range beginning in the 1990s, mirroring the declines in abundance. Low smolt-to-adult survival rates (less than 5%) have generally persisted to the present. There is regional variation in smolt-to-adult survival even at relatively small scales, however; populations from Washington State's inshore Puget Sound typically have had lower survival than those from the outer west coast, and similarly, populations from British Columbia's east coast of Vancouver Island bordering on the Strait of Georgia have typically had lower survival than those from the west (outer) coast of Vancouver Island despite geographic proximity. Variation in survival rates among years and watersheds raises a number of questions. Where and when do mortality periods predominantly occur? Does variation in migration rate or behavior contribute to variation in mortality?

Findings

Several steelhead populations were studied under POST to quantify their mortality rates during this critical period, and

Table 14.2

Survival rates of steelhead, from studies that tagged a total of 21 experimental groups of wild and hatchery fish.

	Survival (%) to marine entry		Survival (%) to exit from inshore waters	
Watershed	**Wild**	**Hatchery**	**Wild**	**Hatchery**
Cheakamus River (British Columbia)[a]	64–84	33–43	18–39	3
Hood Canal (Washington)[b]	78–96	88	22–40	15
Puget Sound rivers (Washington)[c]	74–87	74–76		
Keogh River (British Columbia)[d]			55	17–47

[a] Estimates from Melnychuk *et al.* (2009), four wild and three hatchery groups.
[b] Estimates from Moore *et al.* (2010), four wild and one hatchery groups.
[c] Estimates from Goetz *et al.* (2010), four wild (Skagit, Green, Puyallup, Nisqually Rivers) and two hatchery (Green, Puyallup) groups.
[d] Estimates from Welch *et al.* (2004), one wild and two hatchery groups.

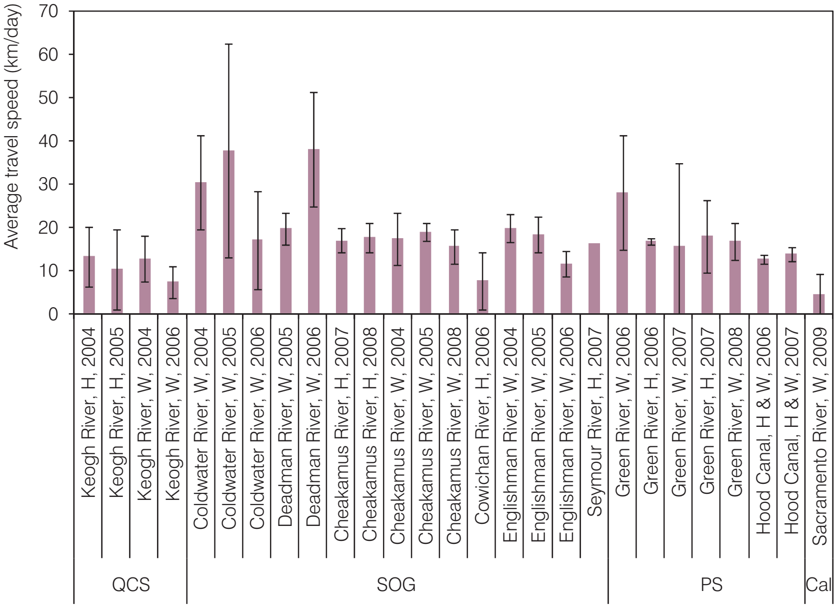

Fig. 14.5
Average travel speeds of steelhead smolt populations during the early ocean migration. Travel rates are calculated as shortest in-water migration distances from river mouth receiver stations to stations at exit points from inshore waters, divided by the average travel time to complete this distance. Error bars show ±1 standard deviation. Populations are grouped by area: Queen Charlotte Strait (QCS), British Columbia; Strait of Georgia (SOG), British Columbia; Puget Sound (PS), Washington State; and California (Cal). Wild (W) and hatchery-reared (H) populations are distinguished. Travel speeds are calculated from POST data (QCS, SOG, PS-Green River) or provided by Moore *et al.* (2010) and B. McFarlane (personal communication).

to compare survival among wild and hatchery-reared populations (Table 14.2). Survival from release to the river mouth and from release to exit from inshore areas was assessed for populations from British Columbia and Washington State. Populations differed in the distances they migrated, but within each watershed, survival of wild populations was generally greater than that of their hatchery-reared counterparts during the smolt migration. The high mortality incurred during the downstream and early ocean migrations is surprising, considering how little time steelhead spend in these areas. Steelhead smolts generally exhibited rapid movements downstream, through estuaries, and out of the inshore areas of the Strait of Georgia or Puget Sound within a few weeks of being released. Travel speeds downstream varied widely, depending mostly on river flow. Those from Fraser River populations varied from 53 to 81 km per day on average, whereas those from smaller rivers varied from 0.2 to 17 km per day. After ocean entry, however, average travel speeds were remarkably similar among populations, varying little with mean body length (which ranged from 161 to 203 mm; travel speeds were estimated over distances ranging from less than 20 to more than 400 km (Fig. 14.5).

It appears that mortality rates (on a per-day or per-kilometer basis) are considerably higher during the downstream migration than during the early ocean migration, but the agents of this freshwater mortality are not well known. Much mortality occurs soon after release, especially in hatchery fish that generally have little exposure to predators or natural selection pressures before release. Considerable mortality also occurs beyond the areas of study of the current POST system over the remaining year(s) of ocean life, as smolt-to-adult survival of many populations is typically less than 5%.

One exception to the fast, directed migrations of steelhead smolts is that typically around 5–10% of fish within a cohort will residualize, or fail to migrate downstream (Melnychuk *et al.* 2009). Residual steelhead may either delay their migration for a year or take up permanent freshwater residence. This sort of flexibility in life-history strategies is yet another example of the variability that makes it challenging to estimate survival of salmonids. There is still much to be learned about steelhead ecology and life history from tagging studies, and additional technologies will likely be required to extend investigations further along the ocean life-history trajectory of steelhead.

14.2.2.2 Coho salmon

Background

Coho salmon (coho; *Oncorhynchus kisutch*) in the Strait of Georgia have exhibited unusual behavior and survival patterns during recent decades. Once the target of a major year-round fishery, the Strait of Georgia coho all but disappeared during the mid-1990s (Beamish *et al.* 1999). Their marine survival had dropped from 10% (during the 1980s) to 2% (Beamish *et al.* 2000), and marked coho that would normally have spent their entire lives within the strait were being observed off the outer coast of Vancouver Island (Weitkamp *et al.* 1995). The general opinion at the time was that overfishing was to blame, but when the fishery was closed in 1998, no noticeable effect on coho marine survival followed (Bradford & Irvine 2000).

Some investigators hypothesized that climate was playing a key role (Beamish *et al.* 1999). Correlations were found between the sudden changes in coho survival and climate regime shifts (Hare *et al.* 1999). As average sea surface temperatures in the Pacific increased, northern coho populations grew, whereas many southern stocks faced extinction (Coronado & Hilborn 1998). The advancing onset of spring plankton blooms was identified as a possible negative influence on the later-migrating species such as coho (Beamish *et al.* 2008). Further potential causes emerged, including the long-term effects of hatchery production, increasing predator populations, pollutant levels, and other side effects of human development (Araki *et al.* 2007; Bradford & Irvine 2000).

Research on the marine portion of the coho life cycle has been limited by technology. Trawl surveys were initiated in 1997 to examine the distribution and growth of juvenile coho in the Strait of Georgia (Beamish *et al.* 2008). Catch surveys and mark–recapture methods have been used to examine the distribution and growth of juvenile coho in the ocean (Beamish *et al.* 2008). However, these methods are less effective as population sizes and catch rates decline. The POST array has provided researchers with another opportunity to investigate the behavior and potentially the survival patterns of these coho stocks.

Findings

The migratory behavior and survival of coho smolts from various river systems were examined to identify key freshwater and marine mortality areas. The Thompson River (a tributary of the Fraser River) coho population is extremely endangered and concern has been raised about poor habitat quality in the watershed and a lack of research being done (Irvine & Bradford 2000). For these reasons, 190 hatchery-reared coho smolts were implanted with acoustic tags over three consecutive years and tracked using the POST array. Survival to the mouth of the Fraser River was found to be extremely low during 2004 and 2005 (0–6% and 7%, respectively). The freshwater survival of other Thompson River salmon species was higher (Welch *et al.* 2008, Chittenden *et al.* 2010), as were the survival rates of coho during 2006 and in other river systems (Chittenden *et al.* 2008). The low freshwater survival of Thompson River coho may be a key reason for the endangered status of this stock. Further work needs to pinpoint high mortality areas in the Thompson/Fraser watershed and possible causes for the low survival.

Marine survival was evaluated by tracking 173 tagged juvenile coho in the Strait of Georgia during 2006 and 2007. The fish left the Strait of Georgia through the Juan de Fuca Strait primarily from October to December, and the remaining coho either died or took up residence in the strait (Fig. 14.6) (Chittenden *et al.* 2009b). The proportion of fish surviving and migrating from the strait was smaller in a group of fish tagged in July (19%) than in a group tagged in September (52%), suggesting that coho may have suffered high mortality during the summer (Chittenden *et al.* 2009b). A small proportion of the acoustically tagged

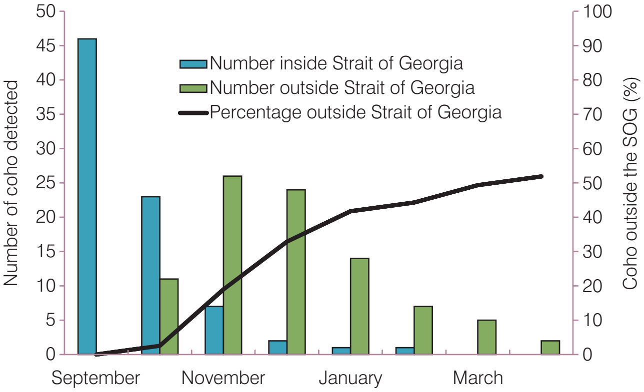

Fig. 14.6
Evidence of unexpected autumn migration timing for juvenile coho from protected waters to the open ocean: the location of tagged juvenile coho salmon by month, from September 2006 to April 2007, expressed as the number of fish detected within or outside of the Strait of Georgia.

Strait of Georgia coho (4%) was also detected on the outer coast POST array as far south as Oregon (750 km from the release site) (Chittenden *et al.* 2009b). These studies demonstrate that coho survival is stock-specific and probably dependent on ecosystem dynamics in both fresh and saltwater.

The long-term effects of hatchery releases on wild coho populations may be part of the reason for lower survival rates. A study comparing hatchery and wild smolts in Campbell River, British Columbia, found differences in physiology, travel time, survival, and migratory behavior, with wild fish spending less time in the river and estuary, arriving at POST arrays sooner than hatchery fish (Chittenden *et al.* 2008). Scientists are working to understand what effects these differences may have on ecosystem dynamics in the Strait of Georgia as well as the relative roles that genetics and rearing environment play on the phenotypic expression of coho young.

The story of the disappearance of coho salmon from the Strait of Georgia is complex. Some stocks have been found to suffer high mortality before they leave freshwater, whereas others have high mortality in the early marine phase. Long-term telemetry studies will help to understand the effects of climate, and other ecosystem dynamics, on the inter-annual variability of coho distributions, behavior, and survival.

14.2.2.3 Chinook salmon

Background

Within the Columbia River basin in the Northwestern United States, the completion of the Snake River dams in the late 1970s coincided with a "regime shift" to warmer ocean conditions that was generally considered to be deleterious to salmon survival in the southern portions of their range (Hare *et al.*1999). The subsequent rapid decline of spring-type chinook (*Oncorhynchus tshawytscha*) in the Snake River (an upper tributary of the Columbia) resulted in this population being classified as threatened under the US Endangered Species Act. The listing had major economic consequences for the fishing industry and for the operators of the dams, who have spilled water to accommodate salmon migration, resulting in lost potential revenue ever since. Over the past several decades, improvements in fish passage at the dams and the implementation of a fish transportation program to bypass the impounded section of the river basin have improved the survival of seaward migrating juveniles (smolts) (Muir *et al.* 2001), but adult return rates have not substantially improved (Williams 2008; Schaller *et al.* 2007).

Because high in-river smolt survival has not improved adult returns from the ocean, it has been hypothesized that dam passage or transportation around the dams may reduce the fitness of Snake River smolts by impairing their survival after they migrate from the hydrosystem (the impounded section of the river basin) into the coastal ocean. This is referred to as the "delayed mortality" hypothesis. POST brings a new dimension to our ability to test the hypothesis. Survival estimates were previously available only for the entire life-history period from smolt out-migration until adult return to the river, some two to three years later, resulting in a significant knowledge gap about ocean survival and especially whether the very poor adult survival still observed was caused by the operation of the hydro dams (see, for example, Schaller *et al.* 1999; Budy *et al.* 2002; Budy and Schaller 2007).

Findings

From 2006 to 2009, 4,000 hatchery-reared juvenile stream-type chinook salmon (130–200 mm fork length) originating from the Columbia River basin were tagged and tracked down the river and along the Pacific shelf as they swam north, in order to address several significant management issues. Five of the smolts were detected in Alaska, 2,500 km from their release point. A summary of the findings includes the following.

- A comparison of acoustic tags with much smaller PIT tags demonstrated that in-river survival estimates from the two tag types were statistically indistinguishable (Fig. 14.7), which suggests that there was not enough additional mortality caused by the larger acoustic tags greatly to bias the survival estimates relative to estimates made with PIT tags.

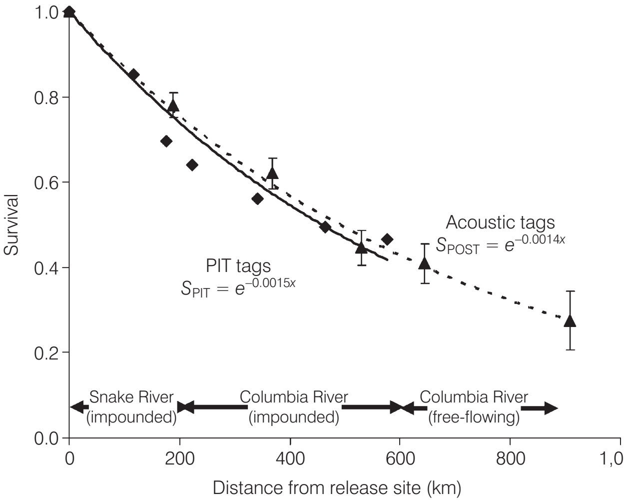

Fig. 14.7
Survivorship of spring chinook smolts released in the Snake River basin in 2006 (first published in Welch *et al.* (2008)). Diamonds represent NOAA PIT tag survival estimates within impounded sections of the river. Triangles represent POST survival estimates within the river and onto the continental shelf of Washington State, USA. Error bars show one standard error.

- A large-scale experimental comparison of survival in two tributaries of the Columbia, the Snake and Yakima Rivers (which join the Columbia mainstream at approximately the same location), to test the delayed mortality hypothesis also found similar survival rates. Juvenile salmon from the Snake River must pass through eight dams on their way to the sea, whereas juveniles from the Yakima River pass through only the four lowest dams. As survival of Yakima fish to adulthood is four times greater than the survival of the Snake River fish, these contrasting adult survival rates contributed to the development of the delayed mortality hypothesis.

  Initial results from the 2006 (Rechisky *et al.* 2009) and 2008 (Porter *et al.* 2009) studies indicated that lower-river survival (from below the final dam to the first ocean detection line, a distance of 274 km) was similar for the Snake and Yakima River populations. Survivorship from release to the first ocean detection site (911 km for the Snake populations, 655 km for the Yakima populations) was also similar, indicating that the fourfold greater survival observed in adult return rates in favor of the Yakima population may develop later in the marine life-history phase and could possibly be attributed to different ocean life-history strategies (perhaps owing to migration to different ocean regions). Because of the current rather coarse spacing of the marine sub-arrays, finer-scale arrays are needed to better assess the behavior and survival of the two populations.
- A costly mitigation effort was evaluated: many out-migrating Snake River juvenile salmon have been transported via barge around the entire dam system for several decades in hopes that eliminating dam-caused mortality would improve adult return rates (Williams 2008) as over half the in-river migrants die before reaching the final hydropower dam. However, despite near-perfect survival of the barged fish during transport, transported smolts do not return at twice the rate of the smolts that migrated downstream through the dams before reaching the ocean (Schaller *et al.* 2007; Muir *et al.* 2001).

  The POST system was used to compare survival of transported and in-river fish as they swam through the estuary and onto the continental shelf. Smolts migrating the entire length of the river and smolts first transported by barge were observed to have similar survival through the estuary to the first ocean detection site in both 2006 and 2008. Overall, the number of transported hatchery fish surviving to the first ocean sub-array was greater than that of the in-river migrants, as expected based on the initial survival benefits from transportation. However, the data also indicate that survival rates in the ocean and river are very similar. The solution to the transportation paradox may therefore have a very simple explanation: survival per unit time may be quite similar in the ocean and the river. If true, transporting smolts around the dams may provide little benefit simply because the smolts are transported between two environments that currently have approximately equal survival prospects; because the total lifespan is unchanged, smolts that would otherwise die in-river during migration may simply die in the ocean – at about the same rate – if they are transported.
- A large-scale acoustic telemetry comparison was made of the dammed Columbia and the un-dammed Fraser Rivers (Welch *et al.* 2008), which found that in-river survival rates of steelhead and chinook hatchery smolts were similar in both rivers. The reasons for the similarity are not yet clear.

The ability to estimate survival over thousands of kilometers is now in the near future. The POST array will contribute to testing numerous hypotheses about the effect of dam passage on ocean survival, migration timing, and survival by size, as well as how ocean climate change will affect the future sustainability of salmon populations, all of which is essential knowledge for improving decision-making regarding the sustainability of Pacific salmon.

14.2.3 Studies of movements, life history, and habitat use

The biggest surprise of the POST project occurred when green and white sturgeon were detected by chance far beyond areas they were thought to use. The very large scale of the POST array and its integrated data management system will make such serendipitous discoveries ever more likely as the number of tagged species increases. Such discoveries emphasize how little we know about the movements of marine animals. In this section, we report on three studies of sharks and sturgeon, which all show how the POST array can be combined with smaller, local receiver networks to study movements. Although lines of receivers are not strictly necessary for studying movement, they have proven useful.

14.2.3.1 Green sturgeon

Background

Green sturgeon (*Acipenser medirostris*) are a rare and poorly understood species. They are anadromous, and known to use just three rivers for spawning. Aggregations of green sturgeon have been noted in summer months in various Pacific coast estuaries, especially Willapa Bay and Grays Harbor, Washington, the lower Columbia River in Washington and Oregon, and several smaller estuaries on the Oregon coast (Adams *et al.* 2007). Much of the lifetime of green sturgeon is spent in marine waters, and although they have been observed in coastal waters between Baja

California (Mexico) and the Bering Sea (Moyle 2002), nothing is known of their migratory behavior.

In 2007, the US listed the southern distinct population segment of green sturgeon as a threatened species under the US Endangered Species Act (Adams *et al.* 2007). Several critical questions were unresolved in the status review that led to this listing, however, including the following:

- Where do green sturgeon in summer aggregations originate?
- What proportion of the population occurs in these aggregations?
- Do green sturgeon migrate frequently among different areas and habitat types or do they reside in more restricted areas?

The deployment of the POST array provided a backbone of receiver arrays in the coastal ocean throughout the purported range of green sturgeon from southeast Alaska to Washington starting in 2003, which provided an opportunity to address these critical questions. The POST array was augmented by receivers in the coastal ocean off central Oregon and in Monterey Bay, California, in estuaries and bays in Washington, Oregon, and California, and in known (Rogue River, Klamath-Trinity River, Sacramento River) or suspected (Umpqua River, Oregon, and Eel River, California) spawning rivers for green sturgeon. Green sturgeon were captured and tagged in spawning rivers and in estuaries where summer aggregations occur.

Findings

The augmented POST array showed that green sturgeon made surprisingly long and rapid seasonal migrations along the west coast of North America (Lindley *et al.* 2008). Many tagged green sturgeon moved northward past the northern end of Vancouver Island in the late fall, overwintering somewhere north of Vancouver Island, and then made rapid southward migrations in the spring to return to spawning rivers or summering grounds in various estuaries in Washington, Oregon, and California. This sort of poleward migration in winter is highly unusual in the animal kingdom. Many green sturgeon were observed making these migrations annually, while a subset appeared to overwinter off Oregon without making extensive migrations (Fig. 14.8).

Closer examination of the migratory behavior of individual green sturgeon showed that there is substantial diversity among fish that is not explained simply by the location of capture and release. Most notably, many green sturgeon tagged in the Rogue River, but also some from the Sacramento and Klamath Rivers, spend summers almost exclusively in the Umpqua River estuary, whereas other groups of fish exhibited characteristic patterns of use of the

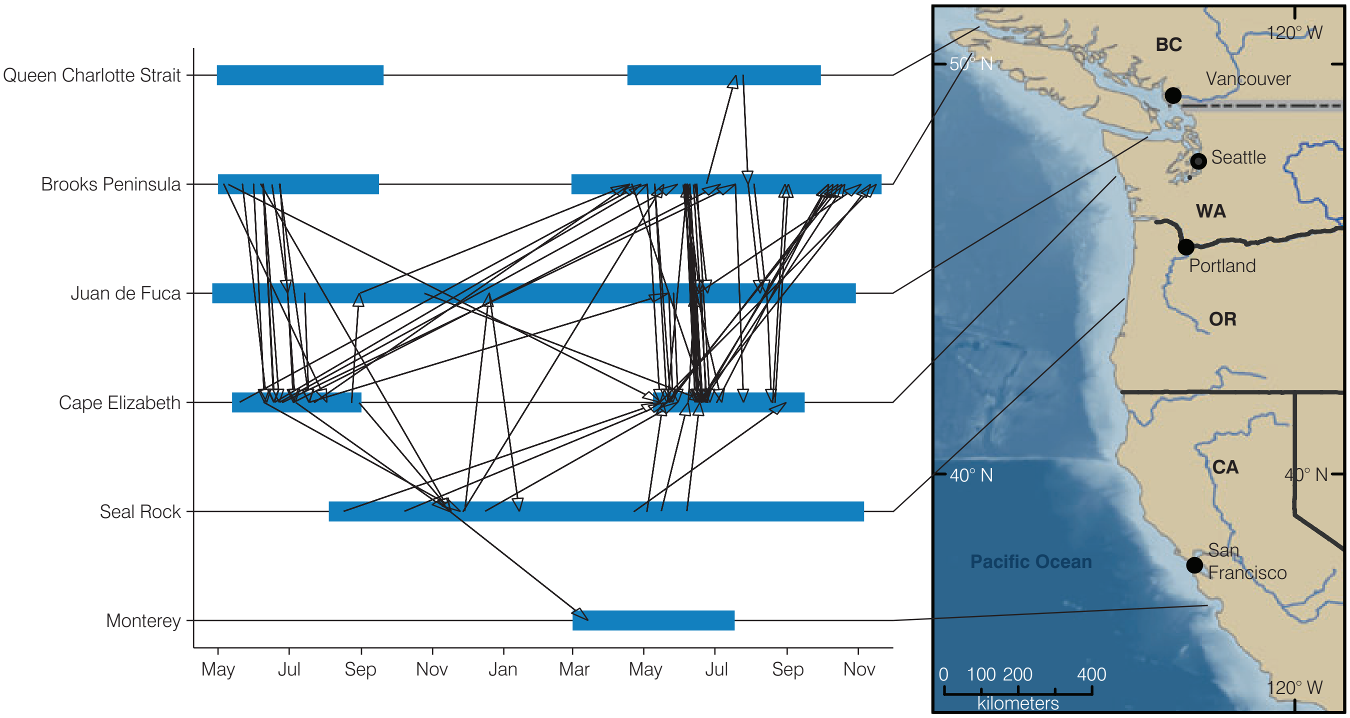

Fig. 14.8
Sturgeon movements along the Pacific coast, by date (modified from Lindley *et al.* 2008). The blue bars show periods during which receivers were deployed, and the arrows between them link detections of individual sturgeon. The map shows the locations of the receivers.

lower Columbia River, Grays Harbor, Willapa Bay, and San Francisco Bay.

Although the appearance of green sturgeon as bycatch in specific coastal fisheries had provided some indication of the species' marine distribution, the telemetry results have greatly expanded our insight into the extent and diversity of their marine movements. The data have opened and sharpened several questions. How stable are these behavior patterns and aggregations over years, and to what extent do they represent behaviors and habitat use peculiar to discrete sub-populations? What mechanism(s) underlies the surprising northward migration in the fall and winter? More generally, an important but difficult question is the basis for behavioral diversity in green sturgeon: is migratory behavior determined genetically or is it learned (Culum & Kevin 2003)?

Acoustic telemetry has spurred a quantum advance in our understanding of the migratory behavior of adult green sturgeon and has generated valuable demographic information (Erickson & Webb 2007). It would be extremely fruitful to apply the same methods to sub-adult green sturgeon, whose behavior is completely unknown, as well as to other migratory acipenserids, including the Atlantic sturgeon (*A. oxyrinchus*) and the shortnose sturgeon (*A. brevirostrum*).

14.2.3.2 White sturgeon

Background

White sturgeon are the largest (by length and weight) freshwater fish in North America, and one of the longest freshwater fishes in the world. In the Fraser River of British Columbia, white sturgeon can attain confirmed lengths to 6.1 m and weights to 629 kg (Scott & Crossman 1973). They are also late to mature (15–20 years for males, 20–30 years for females) and long lived (150+ years). They are truly living fossils, exhibiting little change in morphology from fossil records dating back 65 million years. Current research suggests that green sturgeon and white sturgeon use different sets of watersheds for spawning (Lindley *et al.* 2008). Distribution of white sturgeon is limited to western North America, with strong evidence that spawning occurs in only three major watersheds: the Sacramento River (California), the Columbia River (Oregon/Washington/British Columbia), and the Fraser River (British Columbia). Overfishing and habitat loss has decreased the populations of white sturgeon significantly, and in Canada all of the Fraser River stocks have been classified as "endangered" by the Committee on the Status of Endangered Wildlife in Canada and most have been listed for protection under the Species at Risk Act.

Findings

Current stock monitoring and assessment of lower Fraser River white sturgeon by the Fraser River Sturgeon Conservation Society suggests that this population is declining, and has suffered a 27% loss in total abundance since 2003 (Nelson *et al.* 2008). Interestingly, the greatest decline in this population has occurred in the lower age groups (fish younger than 10 years old), which suggests that there is either a recruitment issue or perhaps young sturgeon are leaving the lower Fraser River (that is, migrating to marine environments). To address the question of residency and migration of lower Fraser River white sturgeon, 110 specimens of various sizes and ages were captured and acoustically tagged in the lower Fraser River over three seasons (summer and fall 2008, spring 2009). Twelve acoustic receiver stations have been established at strategic locations in the lower Fraser River and estuary to augment existing POST receiver stations in the same area. All acoustic tags have been detected since release, and the majority of tagged sturgeon have moved considerable distances within the lower Fraser River study area. This three-year project, conducted in partnership with POST and local Aboriginal communities, is providing novel and useful information regarding inter- and intra-annual movements and habitat preferences of endangered lower Fraser River white sturgeon.

14.2.3.3 Sixgill sharks

Background

The sixgill shark, *Hexanchus griseus*, is one of the largest predatory sharks and is found in nearly all temperate and tropical seas of the world, preying on a wide variety of resources. Their basic life history (slow growth, late maturity, low fecundity) suggests they would be susceptible to exploitation and other environmental perturbations. Understanding how large predators use habitat through time and space is critical to successful management. The spatial distributions of populations are created by movement behavior (Turchin 1991); the impact of predators on local prey populations is relative to how much time they spend moving through different habitats (Fortin *et al.* 2005); and the susceptibility of populations to exploitation or environmental perturbations is dependent on their movement patterns (Kritzer & Sale 2006).

Findings

The project reported here took advantage of an array of acoustic receivers at more than 200 sites throughout Puget Sound established by a consortium of researchers, in addition to active acoustic tracking methods. From September 2004 to October 2008, Vemco acoustic transmitters were implanted into 59 sub-adult sixgill sharks ranging in size from 109 cm to 293 cm total length (6–173 kg). Movements of individuals were monitored for up to four years.

The spatial patterns of movement for sixgill sharks differ greatly depending on the temporal scale measured. Daily, individuals moved very little, averaging 0.2–3.1 km per day, with smaller individuals moving four times as far as larger

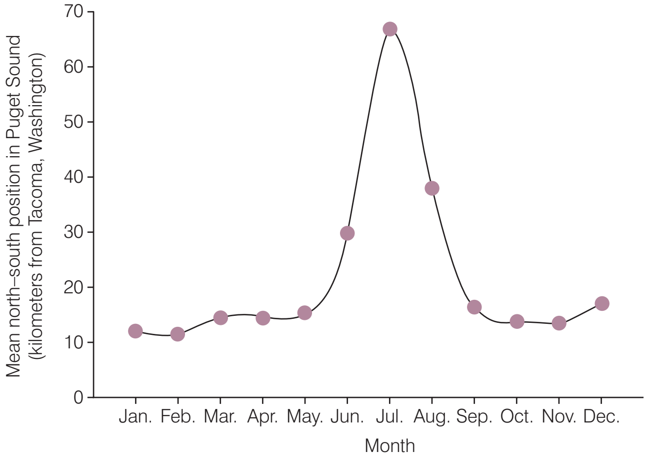

Fig. 14.9
An example of seasonal movements, which occur on a scale midway between smaller daily movements, and larger dispersal over the scale of years. Mean location of sixgill sharks in Puget Sound in 2006 as measured along a latitudinal gradient from the southern main basin (Tacoma, Washington) northward.

individuals (Andrews *et al.* 2007). Moreover, passive receivers detected sharks at the same location as the day before 76% of the time. Seasonally, tagged sixgill sharks occupied a narrow region (8 km latitudinal range) in the southern main basin of Puget Sound during the autumn and winter and then dispersed northward during the late spring and summer to all parts of the main basin (120 km latitudinal range) (Fig. 14.9). At the yearly scale, most tagged sixgill sharks were exclusive residents of Puget Sound from 2004 to 2007. In 2006, 10% of tagged individuals left Puget Sound, whereas in the summer of 2008, 46% of tagged individuals had left Puget Sound. The sharks that left were detected most frequently in the Strait of Georgia (approximately 350 km) or Strait of Juan de Fuca (200 km), with the farthest detected individual at Point Reyes, CA (approximately 1400 km). Four individuals that have left and come back to Puget Sound were absent from 1 month to 1.5 years.

Sixgill sharks show consistent patterns of movement, both vertically (Andrews *et al.* 2009) and horizontally, across multiple temporal scales, with most sub-adults residing in Puget Sound yearlong. The most plausible hypothesis for these stable patterns is that sharks are following prey populations at various temporal scales until they reach a certain size or age, when they make large movements out of Puget Sound. It is possible that the sub-adults that left Puget Sound in 2008 were members of a large recruiting cohort that is now leaving its rearing area. Pregnant and other large individuals (longer than 3 meters) have been seen in Puget Sound, but most adults are seen on the outer coast as bycatch from longline fisheries.

14.2.3.4 Other species

The POST array has also been used to study habitat use by ling cod in Prince William Sound, Alaska, and rockfish in the Strait of Georgia, and the movements of bull trout, market squid, and English sole in Puget Sound. The study of English sole was particularly interesting because it showed that sole, which are used as indicators of sediment contamination, spend less time at contaminated sites than had been presumed. This suggests that contaminated sediments may have larger impacts on fish health than has been previously calculated (Johnson *et al.* 2002; Moser *et al.* 2010).

14.3 Interdisciplinary Studies as a Model for Future Research: Sockeye Salmon

This section reviews several linked studies that have taken a multi-disciplinary approach to investigating why a valuable population of salmon has suffered very high mortality. Some of the studies were done in laboratories or outside the POST array. The array was used to identify the travel rates, migration timing, and fates of individual fish in a series of manipulative field experiments. Acoustic tracking thus acted as a bridge between laboratory studies of physiological limits and field studies of actual performance of migrating fish, and helped to integrate those results with physiological measures of fish condition and genetic stock identification. The section demonstrates how experimental approaches can be combined with observation and auxiliary data to derive the maximum value from acoustic telemetry. As such, it is a model for future studies.

14.3.1 Background

Recent advances in physiological telemetry are now making possible the study of marine species at spatiotemporal scales that encompass the complete ocean life history of the individual animal, thus enabling investigators to explore questions about “why” and “how” animals behave or survive the way they do. The behavioral physiology of Pacific salmon spawning migrations has been most thoroughly studied in sockeye salmon (*O. nerka*) hailing from the Fraser River in British Columbia (reviewed in Hinch *et al.* 2006). The Fraser River is Canada’s most productive salmon system, and sockeye are the most abundant species after pink salmon (*O. gorbuscha*). Like all Pacific salmon, sockeye exhibit a high degree of genetic and phenotypic diversity, and in the Fraser River there are upwards of 150 distinct stocks (that is collections of distinct populations) which spawn throughout the watershed. Some of these travel as little as 100 km upriver to reach natal spawning areas whereas others travel over 1,200 km. At the start of the freshwater spawning migration, sockeye stocks can differ greatly in characteristics like morphology, fecundity, and energetics, which provides ample opportunity to explore the intraspecific bases of diversity.

One of the most distinctive behavioral traits in Fraser River sockeye is the highly predictable within-stock timing of their spawning migrations. The migrations of sockeye into the Fraser River are classified into four broad run-timing groups, each composed of several distinct stocks and populations. Fraser sockeye begin departing the high seas of the North Pacific Ocean in early June, with the early Stuart stock complex entering the river in early July, the early summer stocks in mid-July, the summer-run stocks in early August, and the late-run stocks in September and October. Understanding the mechanisms that control this variation in migration timing is interesting from an evolutionary point of view, but this understanding is critical for those tasked with the management of Fraser River sockeye salmon fisheries, particularly when so much depends on pre- and in-season predictions of coastal and river migration timing of these stocks.

14.3.2 Conservation crisis and research approach

Late-run sockeye will characteristically delay their migration from the ocean to the river for four to six weeks by "holding" in the Strait of Georgia within the Fraser River Estuary (Fig. 14.1) (Cooke *et al.* 2004). This scale of holding behavior is unique among sockeye anywhere, and has likely evolved to avoid peak summertime water temperatures in the Fraser River and prolonged exposure to various pathogens (Hinch 2009). Since 1995, segments of all late-run stocks have entered the river with little or no delay in the Strait of Georgia, and these early timed migrants suffer extraordinarily high mortality during the migration (Fig. 14.10). Depending on the year, 50–95% of late-run sockeye have perished during the river migration (Cooke *et al.* 2004) representing more than 4,000,000 individuals over that time period. The problem of early migration is a clear and ongoing economic and conservation crisis, and the long-term sustainability of key sockeye stocks in the Fraser is in jeopardy (Cooke *et al.* 2004; Crossin *et al.* 2008).

A team of investigators determined that potential causes for this seemingly maladaptive change in migration behavior involved changes in how maturing salmon use endogenous or exogenous cues to time their migration into freshwater (Cooke *et al.* 2004). However, it was clear that uncovering the specific factors responsible would be challenging as there was surprisingly little basic information known about how Pacific salmon, or most fish for that matter, control the timing of their migrations, or how large changes in migration timing leads to extraordinarily poor survival. To fill these gaps in our general knowledge, and to get to the core of this specific problem, field studies began in 2003. Key to these studies was the use both of large-scale observational studies and field experiments that involved the integration of individual-based physiological biopsy of plasma and tissue with positional acoustic and radio telemetry tracking of individually tagged adults (reviewed in Cooke *et al.* 2008). Research in 2003 used a pilot version of the POST acoustic telemetry array and an expanded version in 2006. A companion radio telemetry array was also used in both years (Robichaud & English 2007).

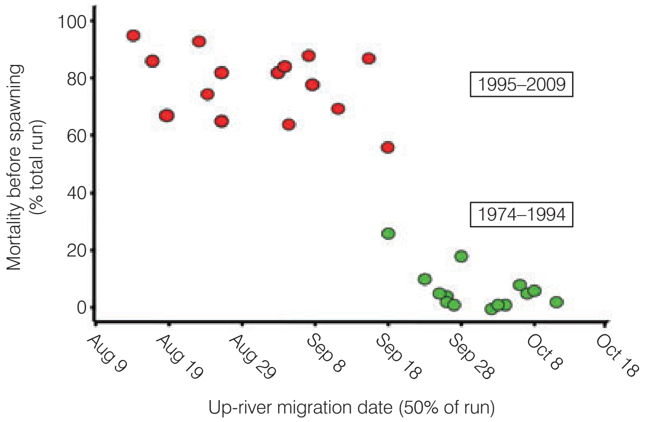

Fig. 14.10
Since 1995, certain populations of sockeye salmon homing to the Fraser River have migrated into freshwater three to six weeks earlier than the historical norm, probably dying as a result.

14.3.3 Observational studies: physiological correlates of migration rates and survival

Over those two study years, more than 1,000 adult sockeye were tagged, biopsied, and then tracked from locales 200 or 800 km from the mouth of the Fraser River, using the POST array. Reproductive preparedness was repeatedly identified as a key physiological system driving ocean migration behavior. For example, 200 km from the river, early timed late-run migrants had elevated plasma concentrations of reproductive hormones, including testosterone, 11-ketotestosterone, and estradiol, suggesting that advanced reproductive preparedness may be triggering early migrations (Cooke *et al.* 2006). In a separate study involving both late-run and summer-run sockeye, Crossin *et al.* (2009a) confirmed that plasma testosterone concentrations strongly correlated with migration rates at locales 200 and 800 km distant from the river. The data also suggested that the physiological mechanisms responsible for causing early timed migrations may be triggered in the open ocean (Hinch *et al.* 2006; Crossin *et al.* 2009b).

Marine mortality of tagged fish also showed strong relations to their physiology at time of tagging. Fraser sockeye from several stock groups that perished in the Strait of Georgia before reaching the Fraser mouth were more physiologically stressed, based on plasma ion, glucose, and lactate measures, than those that survived to enter the river (Cooke *et al.* 2006). Late-runs that perished in the ocean were also less physiologically prepared for freshwater entry (that is, higher plasma chloride and total osmolality) than those that survived (Crossin *et al.* 2009a). Reproductive and osmoregulatory preparedness play interacting roles both in river entry timing and subsequent ability to reach spawning areas. Specifically, sockeye that delayed river entry in the Strait of Georgia and subsequently reached spawning areas had initially high somatic energy, low testosterone levels, and low gill Na^+,K^+-ATPase activity. In contrast, salmon that entered the river directly without delay in the Strait of Georgia and subsequently failed to reach spawning areas had initially lower energy, higher testosterone, and higher gill Na^+,K^+-ATPase activity (Crossin *et al.* 2009a). The implication is that a successful strategy to reach spawning areas is to spend time in the Strait of Georgia becoming more reproductively mature while restructuring gill physiological systems to enable freshwater entry. Fish that were reproductively mature and entered the river before changing their gill structure were likely to perish during the freshwater migration. Taken together, these results indicate that early migrations and high mortality are related to advanced reproductive schedules and poorly prepared osmoregulatory systems for the transition from salt to freshwater.

14.3.4 Interventional studies: field experiments to test observational hypotheses

14.3.4.1 Maturation enhancement experiment

That advanced reproductive development may cause sockeye to migrate faster was tested by injecting gonadotropin-releasing hormone (GnRH) and/or testosterone, as a means of altering maturation rates, into acoustic tagged Fraser sockeye 800 km from the mouth of the Fraser River (Crossin *et al.* 2009b). No differences in travel rates were detected between hormone injected ($n = 6$) and non-injected ($n = 6$) sockeye to the "first" POST acoustic lines situated at northern Vancouver Island (approximately 460 km from release) (Fig. 14.1). However, pre-injection levels of testosterone did correlate with travel rates, a finding consistent with the original hypothesis (Crossin *et al.* 2009b). These results suggest that maturation rates are set in the open ocean and that coastal hormone interventions may be too late to affect behavioral change. Small sample sizes may also have limited this investigation.

14.3.4.2 Osmoregulation experiment

That ill-prepared osmoregulatory systems may cause sockeye to migrate faster and earlier out of the Strait of Georgia into the Fraser River was tested by capturing late-run sockeye in the ocean near the mouth of the Fraser River, transporting them to a nearby marine laboratory for experimental exposure for about one week under three different salinity conditions (freshwater, 0‰; iso-osmotic, 13‰; saltwater, 28‰) and then acoustic tagging and releasing them to continue their migration. The three salinity treatments produced post-treatment sockeye with different gill Na^+,K^+-ATPase concentrations (freshwater < iso-osmotic < saltwater) and freshwater-treated sockeye ($n = 7$) entered the Fraser River approximately two days faster than iso-osmotic ($n = 12$) or saltwater ($n = 5$) post-release sockeye. This two-day "estuarine holding" expressed by the saline treatments was a strong effect as it reflected the average Strait of Georgia holding period for late-run sockeye that year (Hinch 2009).

So far, research suggests that the phenomenon of early migration of late-run sockeye may have its roots in the high seas, based on the reproductive hormone findings and recent functional genomics disease assessments (Miller *et al.* 2007), though is likely also driven by coastal environmental variables such as salinity and fish abundance (reviewed in Hinch 2009). Continued experiments using POST arrays are needed to establish how oceanographic conditions trigger or control physiological, and hence behavioral, changes in individual migrating and maturing salmon, and how other environmental factors, both endogenous such as disease states and exogenous such as local abundance, mediate these behavioral changes.

14.4 Summary and New Directions

Even at this early stage, POST has been a surprisingly successful experiment. The varied research applications of the acoustic receiver array have proven that it is possible to monitor both localized and long-distance movements of marine animals on the continental shelf. The high efficiency of marine receiver lines has made it possible to measure survival of juvenile salmon in the ocean, although methodological refinement and testing is needed to improve the accuracy and precision of the measurements. Researchers have discovered very interesting behaviors with implications for conservation and management, and the technology has served as an important component in an extensive, cooperative research effort. Our technical knowledge of large-scale arrays has advanced dramatically since the inception of POST.

Our knowledge of where animals go has increased substantially for green sturgeon, sixgill sharks, and several other species we knew little about. Results have helped to confirm movement patterns of salmonids and have enhanced our understanding of their rates of travel. We are beginning to assemble a valuable library of behaviors that helps us to assess how much variation exists between individuals, populations, and species, and helps account for life-history transitions such as maturation or use of different habitats. The study of sixgill sharks highlights the fact that movement behaviors can seem very different, depending on the temporal and spatial scales on which they are observed, and is a reminder of the importance of year-round monitoring, long-duration studies and large receiver arrays.

One of the consequences of where animals go is whether they survive. Finer-scale estimates of survival in the ocean and the identification of mortality hot spots should help to calibrate life-cycle models and illuminate the practical question of what limits population growth. POST studies have begun to create a baseline understanding of how juvenile salmonid mortality is apportioned between freshwater, residence in estuaries and the transition to saltwater, and the first weeks and months at sea when young salmon typically remain over the continental shelf, and to document inter-annual and inter-population variation in those rates. Researchers are just beginning to estimate survival rates of longer-lived species such as sturgeon using detections of long-lived tags (Lindley *et al.* 2008). As data accumulate, the fitness consequences of various life-history strategies or events may be estimated, and the results can be synthesized into bioenergetic and ecosystem models.

We are beginning to understand the environmental conditions animals experience on their journeys, and we expect rapid progress in this area. Environmental conditions can be assessed by archival tags or by overlaying oceanographic data with animal tracks. In combination with laboratory studies, such information can guide us in understanding the preferences and physiological limits of marine species, which will ultimately help us to quantify and predict the effects of changing ocean conditions on growth and survival.

14.4.1 Unknowns

There are still many unknowns. Many of the results raised new questions. For example, we have observed that stream-type chinook have similar survival rates in the dammed Columbia and the un-dammed Fraser, but we do not know why, or whether those relative rates will hold over time. We know that many juvenile coho and chinook are never detected on the marine lines after they leave river mouths in the Strait of Georgia, but we are not certain whether they die or take up residence in the Strait. We see that neighboring steelhead stocks on Vancouver Island have different survival rates, and our data suggest that migration routes may play a role. We do not understand why Puget Sound steelhead disappear once they leave Puget Sound, nor why juvenile steelhead are not detected on POST's Southeast Alaska line.

We have not tackled one of the original POST questions: where do salmon go in the deep ocean, beyond the shelf? Are they as discriminating about their use of specific areas or features in the deep ocean as they are about their use of freshwater habitats? The inter-annual variability in migration routes that we see on the shelf suggests that salmon are seeking out particular conditions, rather than particular locations. Archival tags may soon begin to yield answers to some of these puzzles.

Interesting new questions include the following. Why are there marked differences among members of the West Coast green sturgeon population in their use of estuaries? What are green sturgeon doing in their "playground" off the northwest end of Vancouver Island, and what attracted an enormous ball of thousands of white sturgeon to the Bonneville dam in 2008? Are sixgill sharks using Puget Sound as a breeding ground? Why did 10 million fewer sockeye than predicted return to the Fraser River in 2009, at the same time that the Columbia River had record sockeye runs?

In most cases, we still are far from understanding the internal mechanisms that drive behavior. These reactions are the key to how species will respond to cyclical annual and decadal changes in ocean conditions (El Niño, Pacific Decadal Oscillation), as well as to long-term directional climate change like ocean acidification, warming, and changes in currents.

Finally, we are barely beginning to use movement data to tell us about species interactions. Understanding species interactions is a lofty goal, but as more species are tagged and tag technology advances, we will be able to ask questions about when and where predators and prey co-occur, an important step to understanding how they impact each other.

14.4.2 Technological developments that could change the game

14.4.2.1 Extending the scope: larger arrays, smaller tags, deeper water

The simplest approach to improving the tracking potential of the POST system is to expand the array. Expansion by in-filling between existing lines will answer questions such as whether chinook and coho that disappear in the Strait of Georgia have died or taken up residence there. Expansion by adding new lines will make new studies possible. A line planned for one of the major straits between the Gulf of Alaska and the Bering Sea will enable study of species interchange between the two seas.

Acoustic tags are getting smaller, and with every decrement in size we can tag earlier life stages and new species. Vemco's newest generation of smaller acoustic tags (V5) will make it possible to tag juveniles of some of the most important salmon stocks, as well as some of the mid-trophic level "forage fish" species that are currently too small to tag. However, smaller tags come with a cost; in this case, a higher-frequency (180 kHz) signal that requires new generation of receivers, and a lower range that requires much closer spacing between receivers. Satellite and archival tags are also getting smaller, and analytical techniques for deriving latitude and longitude from light and temperature data have advanced greatly.

Tests of receiver deployments in deeper water are underway in Alaska to determine the usefulness of acoustic arrays for monitoring valuable groundfish stocks such as halibut and sablefish. The extent of lifelong migratory behavior and seasonal movements by halibut and the question of interchange between seemingly separate stocks of sablefish remain pressing fishery management questions. Deeper receivers may also be useful in the future for linking to data cables from oceanographic arrays.

14.4.2.2 Large-scale monitoring

One of POST's founding Board members founded a worldwide extension of POST, the Ocean Tracking Network (OTN; www.oceantrackingnetwork.org). Collaborators will deploy and maintain their own receiver networks, and OTN will coordinate data management so that a detection of a tagged animal in any country will be discoverable by the researcher who tagged the fish. Many countries are currently working toward implementation of ocean observing systems as part of the Global Ocean Observing System (GOOS). As POST contributes biological observations to regional GOOS organizations such as the Northwest Association of Networked Ocean Observing Systems (NANOOS), opportunities arise to marry acoustic receivers with other sensors on platforms such as oceanographic buoys and sea gliders, and to integrate oceanographic data with tracking data. A richer understanding of biological oceanography will help with efforts to model the movements of very small animals such as larvae (Gawarkiewicz *et al*. 2007), which will remain too small to track for the foreseeable future, and it will sharpen our knowledge of how changes in ocean conditions affect the movement patterns of many species.

14.4.2.3 Using big animals to track smaller animals: business-card tags

An exciting recent technological development has been the manufacture of the "business-card tag", a miniaturized receiver joined with a standard transmitter. The tag not only transmits but also listens. A business-card tag can be put on a large animal such as a seal, sea lion, or shark (Stokesbury 2010). If the animal can be recaptured, the business-card tag will contain a record of every other acoustic tag that swam within the detection radius (approximately 0.2–1 km, depending on the tag). This technology transforms the large animal into a roving reporter. If the animal is double-tagged with a global positioning system (GPS) satellite tag, positioning data can be combined with the receiver log to show exactly where the animal went and what other tagged animals it heard.

14.4.2.4 Integrating archival and acoustic tags: getting to the critical "why" questions

The primary technological goal of the Ocean Tracking Network is the development of joint acoustic/archival tags. These "fully integrated" tags will archive data from sensors that monitor variables such as water temperature and light levels, internal body temperature, stomach pH or heart rate, and will include a miniaturized receiver that listens for other tagged fish. Fully integrated tags will communicate by spread-spectrum acoustic signals to achieve high data rates, so that an animal can download information about where it has been, what it experienced, and what other tags it heard, as it swims past a receiver line. This will require a new generation of receivers that will probably be more expensive and consume much more power. The payoff, however, will be an enormously rich data stream that finally solves the problem of obtaining information about what an animal experienced between the points where it was detected, and it will use large animals to track smaller animals.

14.4.2.5 Synergies from large-scale infrastructure and opportunities for collaborative studies

As arrays grow, the number of species that can be profitably studied increases, the cost per unit of data declines, and opportunities for collaboration increase. The professional data-sharing network that grows with a large array is one of its most valuable products. The study of Fraser River sockeye demonstrates that many tagging studies could be improved by integrating laboratory experiments with manipulative field experiments, observations, other types of tagging, and non-lethal assays, and that telemetry has a powerful role to play in validating and confirming indirect methods of studying movement.

Finally, the POST approach opens doors to the study of forage fish like herring, anchovies, sardines, and eulachon: these are critically important mid-trophic level fish that feed nearly all of the ocean's larger fish, seabirds, and marine mammals, including most of the species that humans exploit. The ability to measure how forage fish react to environmental changes is a key requirement for predicting the impact of climate change on ocean ecosystems.

14.5 Summary

The value of the POST experience has been to show clearly that large-scale acoustic arrays are practical and enormously useful for illuminating the life histories of the host of species that spend most of their lives on the continental shelves. A defining characteristic of results from the POST array so far is that they have been surprising and unpredicted. That realization should be a warning that we may not know enough yet to generalize to new species and situations, and we have barely begun to deal with a key complication, which is that species interact. New technologies like POST bring opportunities to answer old questions, ask new ones, and enrich existing studies with new collaborations. We are confident that the POST infrastructure will continue to be a rich source of new discoveries for many years to come.

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