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Migratory patterns of pelagic fishes and possible linkages between open ocean and coastal ecosystems off the Pacific coast of North America

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Abstract

We review studies relevant to the migration of pelagic fishes between the coastal and open-ocean ecosystems off the subarctic coast of North America. We review the life history strategies of these migratory fish and to compare to the life history strategies of major coastal migrants. The oceanography in this region is dominated by north and south currents that provide a boundary between the offshore and coastal waters. Commercial fisheries off the west coast of North America are virtually all inshore of this oceanographic separation. Migrations for some species in these major fisheries are also north and south rather than east and west. However, exceptions occur for Pacific salmon, species associated with seamounts, and for transitional pelagic species such as tuna, squid and sharks.

Three species of Pacific salmon, sockeye, pink and chum salmon, migrate along the coast in their first marine year and move off shore in the fall and winter in their first marine year. Three other species, coho salmon, chinook salmon, and steelhead trout, also migrate offshore, although they are less abundant and some stocks remain within the coastal regions. Pacific salmon species are a dominant daytime biomass in the surface waters in the offshore areas.

It is known that albacore tuna and some sharks migrate between the offshore and coastal areas, but more research is needed to assess the relative importance of these migrations. Although the biomass of species on seamounts is small relative to coastal areas, the similarity in fauna is evidence that there is recruitment from coastal ecosystems.

1. Introduction

The purpose of this symposium was to collate biological and physical data on coastal and open-ocean waters in the north Pacific in an attempt to describe potential transfers of energy between the two ecosystems. The coastal ecosystems off the west coast of North America are readily separated from offshore ecosystems by the Alaska and California Current systems, which flow north and south respectively off the west coast of North America. Despite this natural boundary, some

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pelagic fishes migrate between the open ocean and coastal systems. Pacific salmon are the group of fishes that clearly dominate migrations between the coastal and open-ocean ecosystems. Major offshore migrations occur for sockeye salmon (*Oncorhynchus nerka*), pink salmon (*O. gorbuscha*), chum salmon (*O. keta*), and steelhead trout (*O. mykiss*) (Groot and Margolis, 1991). Less extensive migrations occur for coho (*O. kisutch*) and chinook salmon (*O. tshawytscha*). By international agreement through the North Pacific Anadromous Fish Commission, there is no fishing for Pacific salmon on the high seas. It is during their return to the coastal marine waters as adults that they are fished. The individuals that escape the fishery migrate into fresh water, spawn, and die. The anadromous behaviour of Pacific salmon benefits the salmon by providing a relatively safe refuge in fresh water for the individual fish to spawn and for the young to rear. The migrations into the vast feeding areas of the subarctic Pacific allow Pacific salmon to grow larger and be more abundant than would result from a life history that confined them to fresh water. Associated with the anadromous behaviour is a transport of energy/nutrients (as accumulated body mass) from the open ocean into fresh water. Energy is produced in coastal and freshwater ecosystems through photosynthesis. Additionally, the products of primary production can be transported into these ecosystems through the decay of fish that accumulated body mass in the open ocean. The release of nutrients in fresh water can be incorporated into the trophodynamics of fresh water as well as being washed into estuaries and nearshore marine areas.

Other fishes such as albacore tuna (*Thunnus alalunga*) and selected elasmobranches move between the open ocean and coastal waters. The relationship between fish fauna on seamounts and coastal ecosystems is poorly understood. Given the increasing interest in seamounts as potential marine protected reserves, we briefly review their potential linkages within coastal ecosystems. Seamounts also offer insights into the behaviour of populations of coastal marine fishes. It is believed that the colonization of seamounts is through accident or some random event. However, it is also possible that the dispersion of coastal fishes to seamounts and to other coastal habitats is through processes that have resulted in species adaptations at the larval and juvenile stages. According to this idea, the abundance on seamounts is regulated more by available habitat than by the randomness of currents. In addition, we describe some major north–south migrations within the coastal ecosystem, since these movements redistribute energy obtained from the open ocean with coastal ecosystems. This symposium was a focus for fish movement between coastal and offshore areas. However, in order to appreciate the relevance of such movements to major fish species, we believe that it is important for a reader not familiar with fish and fisheries to have some information about major coastal migrations. Furthermore, there are unsolved mysteries relating to the reasons some of our major species migrate. Dismissing coastal migrations as having little relevance to offshore–inshore migrations at best is premature.

2. Domains of the Northeast Pacific Ocean

The open-ocean and coastal areas have sufficiently distinct bio-physical characteristics that allow boundaries to be identified (Ware and McFarlane, 1989): the Coastal Upwelling, the Coastal Downwelling and the Central Subarctic Domains (Fig. 1). The Coastal Upwelling Domain lies adjacent to the coast from Baja California to the northern tip of Vancouver Island and is characterized by an equatorward flowing shelf-break current, and the equatorward flowing branch of the Subarctic Current called the California Current. The Coastal Downwelling Domain (Fig. 1) extends from Queen Charlotte Sound in British Columbia, northward along the coast of southeast Alaska to Prince William Sound, and then westward along the Aleutian islands. The dominant features are the Alaska Current and Alaska Coastal Current. The Alaska Current flows adjacent to the coast of North America and sweeps poleward, seaward of the continental margin. The Central Subarctic Domain (open ocean, Fig. 1) is bounded by the Subarctic Current to the south, the Alaska Current to the east, and the Alaska Stream to the north.

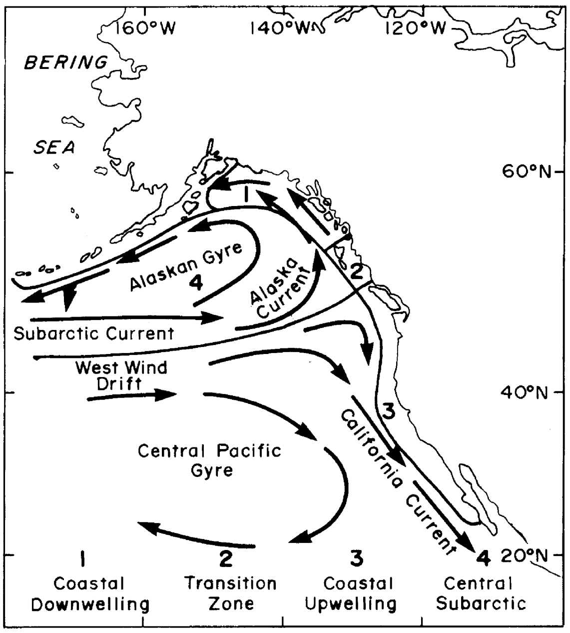

Fig. 1. Approximate areas of oceanic domains and prevailing current directions in the northeast Pacific Ocean (Ware and McFarlane, 1989).

The Alaska gyre is the dominant feature within this zone.

3. Pacific salmon as the dominant group migrating between open ocean and coastal systems

Pacific salmon are generally believed to be one of the dominant species in the surface waters of the open ocean in the subarctic Pacific. This belief is well-founded, but the documentation is seldom presented. One reason that the abundances of Pacific salmon are difficult to compare to other species is that non-selective fishing methods have only recently been used. In addition, day and night-time fishing is necessary. These data are now being collected and reported mainly as specific cruise reports or seasonal research summaries. We are not aware of any comprehensive summary of the recent studies by all nations. Data that can be used to document the dominance of Pacific salmon are available from the scientific publications presented to the Committee for Statistics and Scientific Research of the North Pacific Anadromous Fish Commission. We used the results of trawl studies in the winter in the Gulf of Alaska (Nagasawa et al., 1995; Ueno et al., 1996; Ishida et al., 1998) to show that Pacific salmon are a dominant biomass of the subarctic Pacific. In these studies, a trawl net that had a 50-m vertical opening and a width of 70 m was towed at the surface for 1 h at a speed of about 5 knots in the Gulf of Alaska. The codend mesh ranged from 11 to 13 mm. All surveys were conducted from November to March on the Japanese research vessel, *Kaiyo Maru*. There were 70 sets in total for the three cruises. The catches in Table 1 identify a total catch of 4538 Pacific salmon with the largest catches for pink and chum salmon, which are also the most abundant of the Pacific salmon. Catches of other species included myctophids (Myctophidae), unidentified squid, and northern anchovy (*Engraulis mordax mordax*). Pacific salmon (Table 1) are a significant biomass in the open ocean and the dominant biomass of species that migrates from the open ocean to coastal systems.

Table 1
Catches in surface trawls from three Japanese research cruises in the Gulf of Alaska from November to March 1992, 1996 and 1998 (Nagasawa et al., 1995; Ueno et al., 1996; Ishida et al., 1998)

Species	Catch (numbers)
Chum salmon	2671
Pink salmon	1380
Sockeye salmon	265
Coho salmon	153
Chinook salmon	69
Total Pacific salmon	4538
Myctophids	15,107
Anchovy	19,874
Squid	23,160
Tuna	13
Other	530

4. Pacific salmon distribution and biology

In order to appreciate the magnitude of influence that Pacific salmon have on coastal systems via their migration and transfer of energy from open ocean, it is important to review their widespread distribution and unique biology. A summary of the distribution of Pacific salmon of North American origin has recently been published by Russian scientists (Gritsenko, 2002). This atlas of the marine distribution of various stocks of Pacific salmonids during the spring-summer feeding period and prespawning migration is based on tagging data collected from 1956 to 2000 (updated from Myers et al., 1996). The tagging studies were on the high seas and the recoveries were in the coastal areas or the spawning rivers. Earlier summaries have been published (Neave et al., 1976; Ogura, 1994; Myers et al., 1996), but the Russian study includes more recent information. From 1956 to 2000 there were 20,500 fish of all salmon species that were tagged and recaptured. In our report, we reproduce the figures from Gritsenko (2002) with tagging locations shown in black (Figs. 2–7). The extreme boundary for all tags represents the outermost distribution for the group of stocks over the tagging study. Obviously, the distribution will be affected by a variety of conditions including temperature and the presence of prey. However, these distribution charts clearly indicate the general feeding areas of Pacific salmon of North American origin. The life histories of the

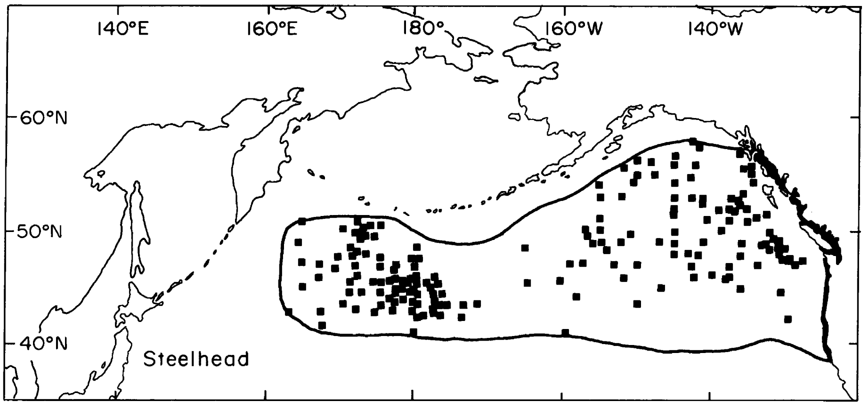

Fig. 2. Distribution of steelhead trout of North American origin in the North Pacific. Solid squares represent the release locations of tagged salmon that were subsequently recaptured in coastal spawning locations.

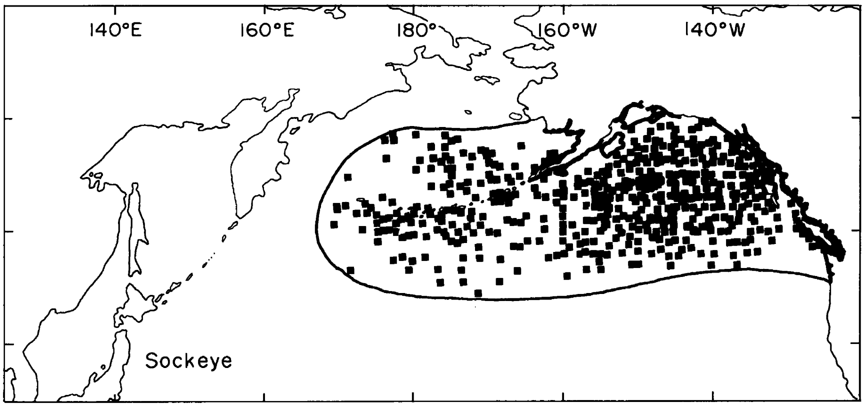

Fig. 3. Distribution of sockeye salmon of North American origin in the North Pacific. Solid squares represent the release locations of tagged salmon that were subsequently recaptured in coastal spawning locations.

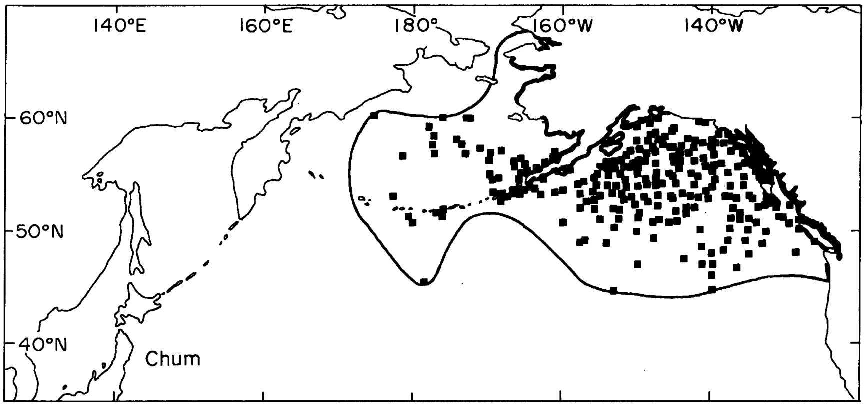

Fig. 4. Distribution of chum salmon of North American origin in the North Pacific. Solid squares represent the release locations of tagged salmon that were subsequently recaptured in coastal spawning locations.

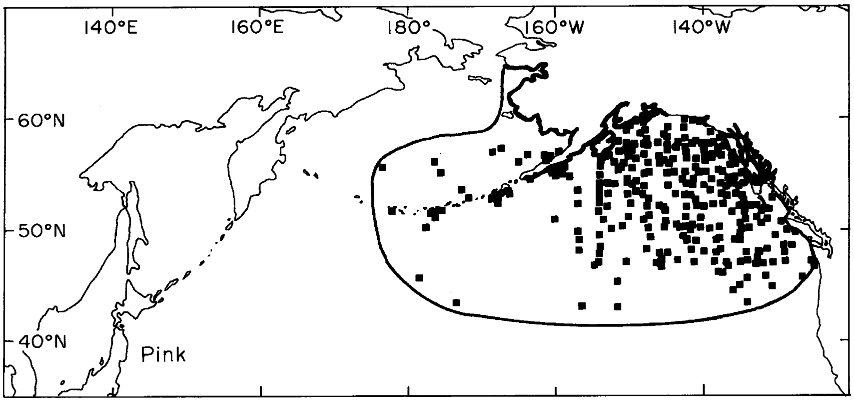

Fig. 5. Distribution of pink salmon of North American origin in the North Pacific. Solid squares represent the release locations of tagged salmon that were subsequently recaptured in coastal spawning locations.

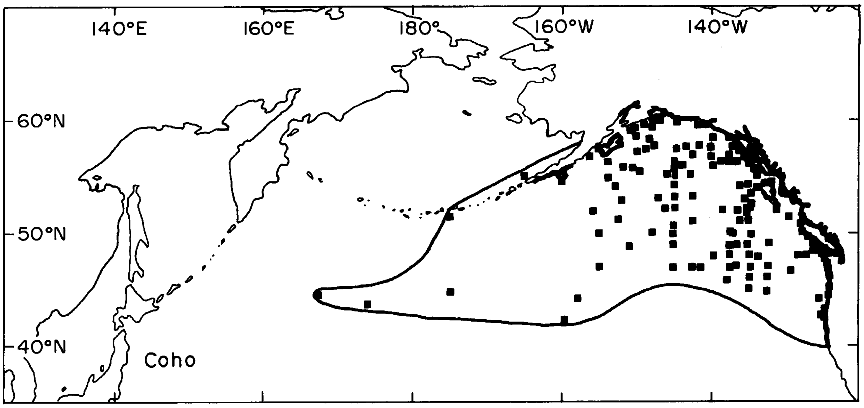

Fig. 6. Distribution of coho salmon of North American origin in the North Pacific. Solid squares represent the release locations of tagged salmon that were subsequently recaptured in coastal spawning locations.

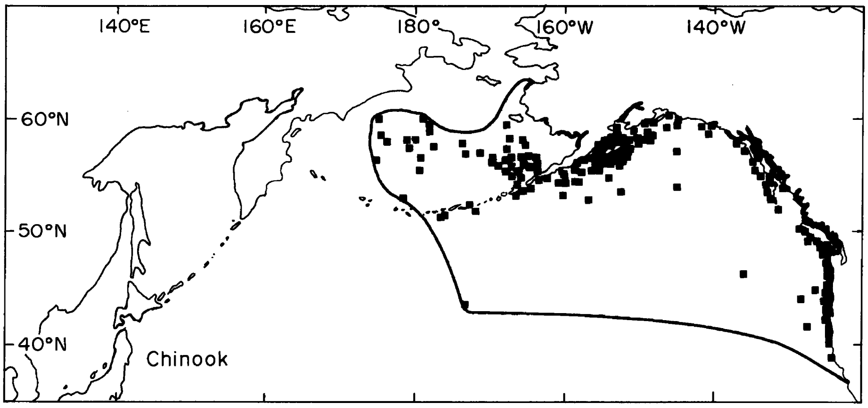

Fig. 7. Distribution of chinook salmon of North American origin in the North Pacific. Solid squares represent the release locations of tagged salmon that were subsequently recaptured in coastal spawning locations.

following species, including their proposed migration patterns, have been summarized in Groot and Margolis (1991). In addition, new ideas about the early migration have been proposed by Welch et al. (2002). The reader is referred to these reports for a more detailed description of the seasonal and age specific migrations. Here we show the extent of the migrations to document the area of the open ocean that is habitat for juvenile Pacific salmon.

4.1. Steelhead

Steelhead is the common name used for the anadromous type of rainbow trout. Steelhead is much less abundant than its Pacific salmon relatives, but it has an impressive offshore migration behaviour. Steelhead may move immediately out to open-ocean waters, rather than migrating north through coastal waters (Fig. 2). Steelhead have a more western and southern distribution than the other Pacific salmon. Some steelhead remain in the open ocean for one winter.

4.2. Sockeye salmon

Sockeye salmon, also inhabit areas in the western North Pacific open ocean waters, but are concentrated in the Gulf of Alaska and the Bering Sea (Fig. 3, Burgner, 1991). Sockeye salmon migrate northward along the coast in their first marine summer and move into the open ocean in the fall or early in the next year (Burgner, 1991). Most sockeye remain in the open ocean for two winters. Sockeye salmon at the southern end of their ocean distribution appear to have a greater range in the timing of their return to fresh water.

Alaskan stocks that inhabit both the Bering Sea and the Gulf of Alaska have considerable overlap in their distribution with sockeye stocks from the south (British Columbia). Peterman (1984a,b) proposed that there is a trophic interaction of British Columbia and Alaskan sockeye stocks in the Gulf of Alaska. Royce et al. (1968) estimated that sockeye salmon are almost continual travellers, with annual migrations that exceed 3700 km. Even more noteworthy is the speed, precision, and the accuracy of the migration back into the coastal zone, and then to the exact area where the salmon were hatched (Burgner, 1991).

4.3. Chum salmon

Chum salmon are distributed similar to sockeye salmon, except juveniles may remain in the coastal areas longer in their first year and more individuals may spend more than two winters in the high seas. Chum salmon from North America are not commonly reported from the western Pacific (Fig. 7, Salo, 1991). The farthest westward that North American chum have been reported was 178° 30′E for chum salmon from the Yukon River; however, there is overlap of stocks of Asian and

North American origin (Salo, 1991). Most chum salmon of North American origin spend three winters in the ocean, but a smaller percentage spend four winters and less than 5% spend five winters. Stocks are mixed in the Gulf of Alaska. For example, chum salmon returning to Alaska have been tagged from off British Columbia through to the Central Aleutian Islands (Salo, 1991). Chum salmon increase their weight between 60% and 92% in their final marine year (Ricker, 1964). This would mean that chum salmon feed extensively immediately before they return to coastal areas. Recent research by Beamish and Mahnken (2001) and Beamish et al. (2004) showed that juvenile coho salmon, in their first ocean year, had better survival over the first ocean winter if they grew to a critical size by early summer. It is possible that the amount of growth achieved in the final marine years is related to the overall spawning success. This is an hypotheses, but it may be an important issue as global warming increases surface temperatures increasing the maintenance energy levels of Pacific salmon on the high seas.

4.4. *Pink salmon*

Pink salmon are the most abundant of the Pacific salmon, both in biomass and in numbers. They are the least dependent of fresh water. They are the smallest of Pacific salmon but have the largest rate of growth. Pink salmon in some rivers, such as the Fraser River, may spawn only every other year. Pink salmon are common near the mouths of shorter streams and rivers. Migration into the open ocean is believed to occur in mid-summer (Healey, 1980), although recent studies have found large abundances of pink salmon inshore as late as September (Richard Beamish, unpublished data). They remain at sea for one winter and return to spawn in the following summer and fall. Pink salmon are common in the Gulf of Alaska but relatively few are found west of 160° west longitude (Fig. 5, Heard, 1991). Pink salmon, perhaps more than other Pacific salmon, are known to produce large abundances of adults very quickly from small biomasses as well as the opposite (Heard, 1991). This is important as pink salmon may be one of the best biological indicators of ecosystem change (Beamish and Mahnken, 2001).

4.5. *Coho salmon*

Some coho have been observed in the Gulf of Alaska and even in the western Pacific (Fig. 6, Sandercock, 1991). However, coho are mainly a coastal species, not moving too far offshore. Coho spend one winter in the ocean, thus the extent of their migrations is limited. However, most coho appear to migrate north in the fall within the coastal area and return along the coast to spawn in the late summer and fall of the next year (Hartt and Dell, 1986; Sandercock, 1991). Coho are not abundant relative to most other salmon species, but they are widespread. They also have a diversity of life history types that results in a wide range of spawning migration times.

4.6. *Chinook salmon*

Chinook salmon are virtually a coastal migrant, with very few fish found outside of the 200-mile limits of Canada and the United States (Fig. 7, Healey, 1991). Chinook may live as long or longer in the ocean than chum or sockeye salmon and can grow to the largest sizes of all Pacific salmon (Healey, 1991). The factors that affect the migratory patterns of chinook are complex as there are a variety of patterns for stocks that spawn close to each other in fresh water (Healey, 1991). Chinook salmon have two life history types. The ocean type enter the ocean in their first year in fresh water and migrate less in the ocean. The stream type spend one winter in fresh water, enter the ocean in their second freshwater year, and tend to migrate farther. Relative to other species, few chinook have been captured in the open ocean (Fig. 7, Healey, 1991). The few that have been captured came from widely distributed spawning areas.

5. Pacific salmon energy input to freshwater and coastal systems

Pacific salmon are the major group of fishes that migrate between open-ocean and coastal systems.

Pacific salmon have a great impact on the energy input to coastal and freshwater systems. Recently it has been shown that in fresh water, decaying salmon carcasses provided important nutrients to freshwater ecosystems (Stockner and Ashley, 2003). Larkin and Slaney (1997) reported that the average proportion of nitrogen and phosphorus in a Pacific salmon was 3.04% nitrogen and 0.36% phosphorus by body weight. Gresh et al. (2000) used these percentages to estimate that prior to the major commercial fisheries, spawning salmon in the northeast Pacific ecosystem produced 6,850,000 kg of nitrogen and 810,000 kg of phosphorus. They argue that the high exploitation rates in the 1900s resulted in a nutrient deficit in the rearing areas of Pacific salmon that may even have caused ecosystem failure, greatly reducing the abundance of some stocks. The literature is clear that marine nutrients that are derived from the decaying carcasses of salmon are important to the productivity of some lakes and streams (Stockner and Ashley, 2003), including the production of aquatic plants and organisms as well as riparian production (Cedarholm et al., 2000a,b). Using the statistical records of the International North Pacific Fisheries Commission and the North Pacific Anadromous Fish Commission, we estimated that the average annual catch of all Pacific salmon by all countries from 1990 to 1999 was 852,000 tonnes. Using an average exploitation rate of 60%, this would indicate that the total average annual biomass of the adults was 1,420,000. If all of these fish returned to spawn, using the Larkin and Slaney (1997) estimates of an average contribution of nitrogen and phosphorus, the average production of all adults in the absence of fishing in the 1990s, would produce about 43,170 tonnes of nitrogen and 5110 tonnes of phosphorus.

While it is possible to estimate the amount of nitrogen and phosphorus that might be added to freshwater ecosystems in the absence of fishing, it is more difficult to quantify the importance of the reduced nutrients. Stockner and Ashley (2003) estimate that marine derived total phosphorus currently accounts for 15–40% of the annual load for sockeye producing lakes (Stockner, 1987). Sockeye salmon from the Fraser River were fished at an almost constant rate of 70–80% in recent years (Beamish et al., 1998). This means that, in the absence of fishing, most of the phosphorus load could come from the sockeye carcasses. Perhaps an even better example of the importance of lost nutrients was the estimate of a loss of between 225 and 275 tonnes of phosphorus due to Pacific salmon fishing by Canada over the past century (Stockner and Ashley, 2003). Apparently this loss would be sufficient to produce more than 100,000 tonnes of living autotrophic plant biomass. When one recognizes that, in the absence of fishing, additions of approximately 5100 tonnes of phosphorus could be made to coastal ecosystems throughout the range of Pacific salmon, it becomes clear that marine derived nutrients from decaying Pacific salmon carcasses represent an important transfer of energy from open-ocean ecosystems.

6. Other species migrating between open-ocean and coastal systems

There are examples of other species moving from open-ocean systems to coastal systems off the northeast Pacific ocean. Albacore tuna are not only important commercially, but are highly migratory between the open ocean and coastal areas, particularly in the Coastal Upwelling Domain. Elasmobranchs are apex predators, some of which make extensive migrations between open oceans and coastal systems.

6.1. *Albacore tuna*

Albacore tuna dominate tuna catches in the northeast Pacific Ocean. Landings of albacore tuna in the northeast Pacific averaged 15,000 tonnes in the 1970s, and have been variable since 1980 ranging from 1297 to 11,823 tonnes. In some years, albacore tuna represent a large proportion of the biomass in the Central Pacific Gyre. Albacore tuna reside in the open ocean, but some migrate inshore and northward along the west coast of North America (Coastal Upwelling Domain) during the summer months. In particular, during warmer years, albacore tuna migrate closer to shore and farther north, supporting moderately sized commercial fisheries in coastal waters. Both Canadian and United States commercial and recreational fishermen catch albacore tuna in the coastal areas from July through to November, depending on the surface water temperatures. Most catches occur at sea-surface temperatures from 16 to 18 °C. In recent years the international fishery for albacore tuna started in early April in areas northwest of Midway Island (Childers, 2002). By July and August, the fishery expanded to the east and to the west along the coast of North America (Shaw and Stocker, 2002) from off the west coast of Vancouver Island to California (Fig. 8). The movement of albacore tuna into the coastal zone is temperature related, but it is also associated with feeding. Thus, some of the production in the coastal regions in the summer contributes to the total production of the albacore tuna population in the open ocean.

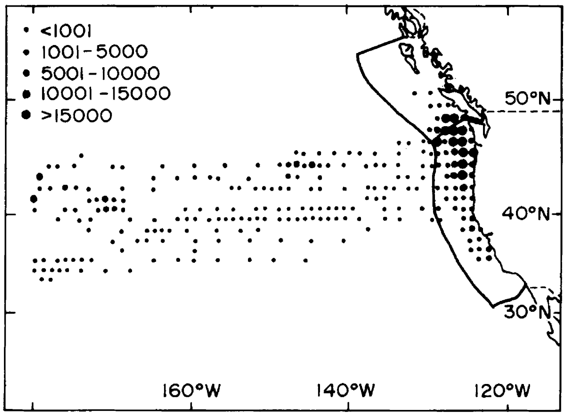

Fig. 8. Canadian North Pacific albacore tuna catch in 2000 (Shaw and Stocker, 2002).

6.2. Elasmobranchs

McKinnell and Seki (1998) examined the distribution and relative abundance of sharks captured in the Japanese high-seas squid driftnet fishery in the North Pacific Ocean from 1990 to 1991 and an experimental driftnet fishery in coastal waters off British Columbia from 1985 to 1987. They reported that elasmobranchs accounted for 1.07% of the total Japanese driftnet catch (Fig. 9) monitored by onboard observers. Blue sharks (*Prionace glauca*) accounted for 93.7% ($n = 188,200$) and salmon sharks (*Lamna ditropis*) 5.23% ($n = 10,496$) of this catch. In the Canadian experimental fishery, both blue and salmon shark catches were an order of magnitude higher in the coastal waters than in the high-seas driftnet fishery and the average size of blue sharks was larger than those captured in the high seas fishery. This phenomenon also was reported by Caillet and Bedford (1983), who reported catching larger blue sharks in coastal waters off California than on the high seas. The data presented by McKinnell and Seki (1998) were in agreement with a generalized blue shark migration model developed by Nakano (1994). He identified the nursery area and location of subadults (females north and males south) as central North Pacific. Adults were found throughout the whole nursery and rearing area as well as closer to the coast. McKinnell and Seki (1998)

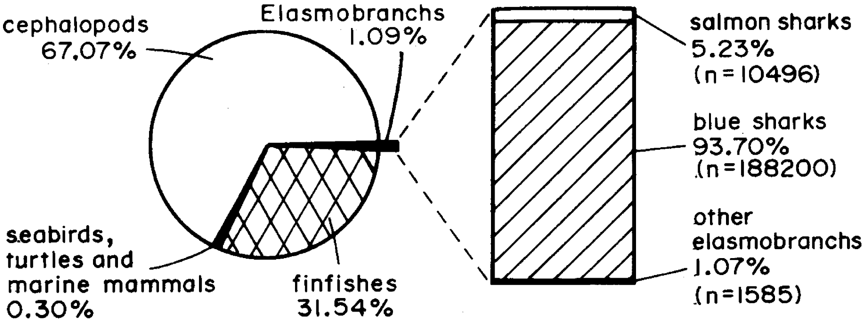

Fig. 9. Catch composition (% of numbers caught) of elasmobranchs incidentally taken in the Japanese North Pacific high-seas driftnet fishery (1990–1991) reported by onboard observers (McKinnell and Seki, 1998).

concluded that both blue and salmon shark abundance was greater near the western coast of Canada (North America) and that feeding adult blue shark were more coastal, therefore contributing to a transfer of nutrients to the open ocean during spawning.

Nagasawa (1998) presented monthly catches of salmon sharks that clearly indicate northward movement into the western and central north Pacific Ocean in spring and a southward migration in autumn. Catches in the eastern Pacific (eastern gyre and coastline of the Gulf of Alaska) were highest in summer (July). In the eastern Pacific Ocean, greatest densities were found between 50 to 60°N, from coastal to offshore waters. There is an annual north and south movement, but salmon sharks are found in the Gulf of Alaska during all months of the year. Recently, the Alaska shark assessment program deployed satellite linked tags on salmon sharks in Prince William Sound, Alaska (Hulbert et al., in press). Position data from these tags indicated sharks moved out of the Sound, through the open Gulf or along the coast with some releasing off Oregon and northern California. Fig. 10 shows the tracks of 10 salmon sharks released in July 2000 and 2001 that were deployed from between 22 and 203 days. It is clear that these sharks move throughout the open ocean and coastal areas of the northern North Pacific Ocean.

Other sharks that are less abundant contributed to transfer of energy between open-ocean and coastal systems. We did not include these sharks, but it was difficult to exclude one of these species. It is impressive that spiny dogfish (*Squalus acanthias*) tagged off the west coast of Canada are recaptured off Japan (Fig. 11, McFarlane and King, 2003). Although the migration from one coast to another appears to be rare relative to the abundances of spiny dogfish (about 71,000 dogfish were tagged and released in the Canadian zone and 41 have been recaptured off Japan), the migration

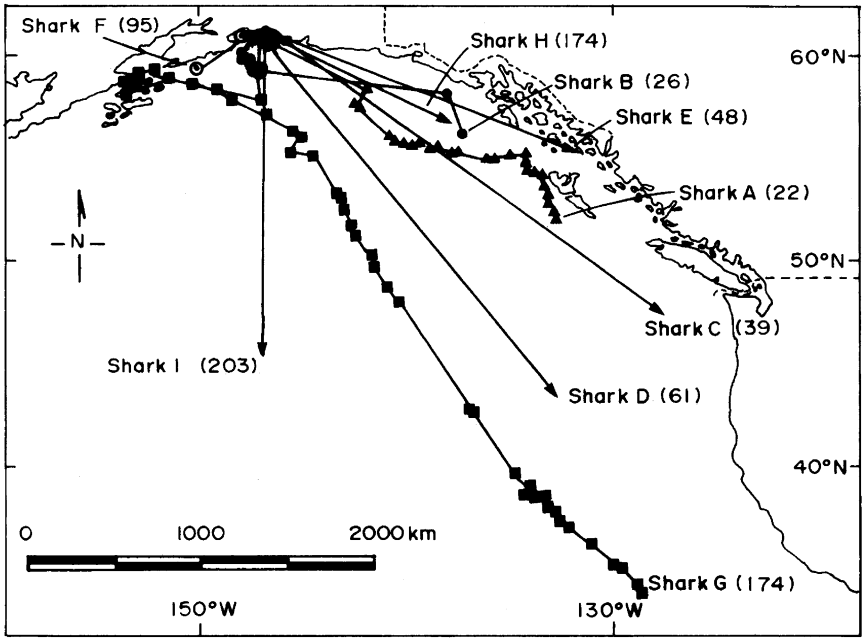

Fig. 10. Track positions of 10 salmon sharks tagged in Prince William Sound during July 1999–2001. Location coordinates are from Argos Satellite-derived end-point positions (sharks A–D; sharks F–I) and from Global Positioning System at time of release, recapture location (shark E). Multiple intermediate locations from SPOT2 tags are indicated for sharks A, B and G. Numbers in parentheses indicate days at large. Lines with arrows indicate net direction of movement (Hulbert et al., in press).

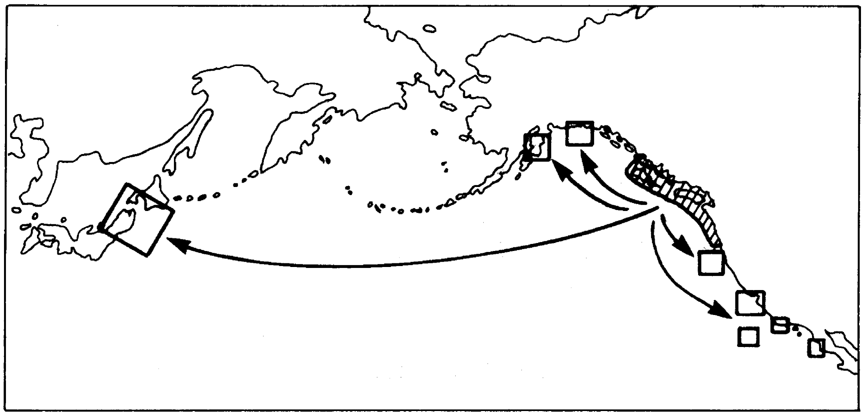

Fig. 11. Release (hatched area) and recovery positions of tagged spiny dogfish. Recaptures from Canadian releases were made from Mexico to Alaska through to Japan (McFarlane and King, 2003).

from the coastal zone of one continent to the coastal zone of another is difficult to ignore.

7. North–south coastal migrations

Virtually all of the commercial fisheries occur in coastal waters. Three major fisheries are for species that undergo extensive migrations within the coastal ecosystem either as juveniles or as adults. Pacific halibut, Pacific hake, and Pacific sardine are three of the most abundance species in the Coastal Upwelling and Coastal Downwelling Domains. While the north–south migration of these species is limited to coastal waters only, they may be important mechanisms for the redistribution of energy between the Coasal Upwelling and Coastal Downwelling Domains.

7.1. Pacific halibut

Pacific halibut (*Hippoglossus stenolepis*) occur from California to the Bering Sea. It is believed that the major spawning areas are north of Canadian waters and that juveniles rear in these areas. Some juveniles migrate back into the feeding areas off Canada and off the area from Washington State to California (Skud, 1977), although the details of the recruitment of these juveniles are poorly understood. There also is a lack of understanding of the migrations of mature halibut at the southern range of their distribution. Once halibut mature, it is generally believed that extensive north and south migrations are restricted (Skud, 1977; Thompson and Van Cleve, 1936). However, the International Pacific Halibut Commission continues to conduct tagging studies and we should be prepared for surprises. The major spawning areas are identified in Fig. 12.

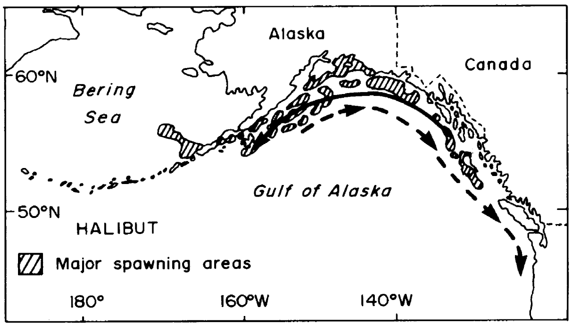

Fig. 12. Major spawning areas of Pacific halibut (hatched areas). Solid arrows represent proposed movement of eggs and larvae, and broken arrows represent proposed migration of some juveniles.

7.2. Pacific hake

The major population of Pacific hake (*Merluccius productus*) is found off the west coast of North

America. There are smaller, distinct stocks such as in the Strait of Georgia, Puget Sound, and a variety of inlets (Beamish and McFarlane, 1985). The offshore population spawns off southern California (Fig. 13) and the juveniles and adults rear from California to off Vancouver Island (Dorn and Saunders, 1997). The coastal population has a seasonal feeding migration in which the larger and older fish usually move north as far as Vancouver Island. The movement north is related to temperature (Ware and McFarlane, 1995) as indicated by the almost doubling of the biomass off Canada in the warm years of the 1990s (McFarlane et al., 2000). In fact, in 1998, the feeding migration was as far as southeast Alaska, with a small number of individuals remaining to spawn off Vancouver Island (McFarlane et al., 2000). In the late summer and fall, Pacific hake generally return to the spawning areas off California.

7.3. Pacific sardine

The coastal migratory behaviour of Pacific sardine (*Sardinops sagax*) is still poorly understood despite a prolonged period of extensive research designed to explain the spectacular decline in abundance in the late 1940s. The fishery for Pacific sardines off the west coast of North America was the largest in the early 1900s and one of the most valuable. The fishery off Canada was believed by some to be part of a genetically distinct population that spawned at the northern limit of the spawning distribution (Felin, 1954; Radovich, 1982, Fig. 14). Others believed that it was one population in which the older fish migrated successively farther north as they aged (Schweigert, 1988). The fishery for Pacific sardines quickly became the largest fishery in the 1920s through to the late 1940s, when it collapsed. Initially the collapse was blamed on over fishing, but recently it

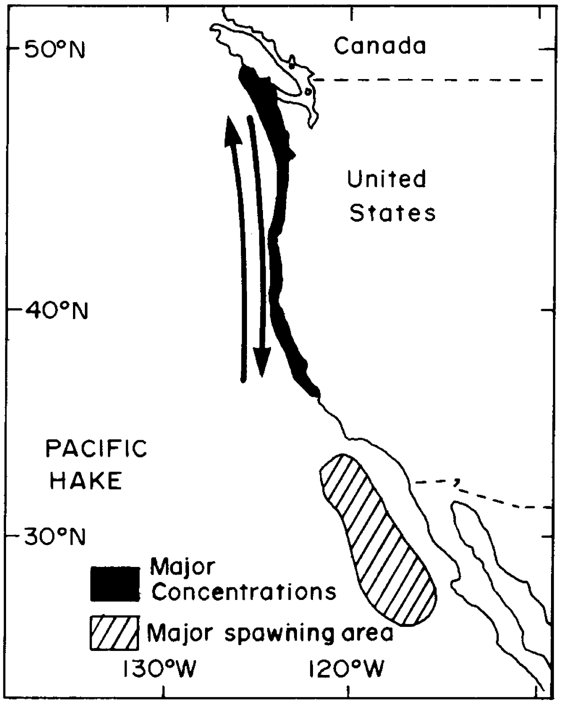

Fig. 13. Major summer concentrations and winter spawning areas of Pacific hake. Arrows indicate spring and fall migration route.

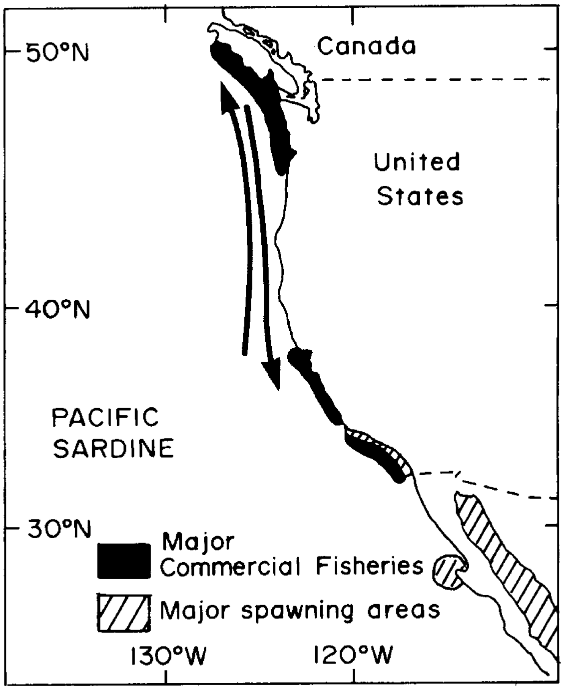

Fig. 14. Major summer concentrations and winter spawning areas of Pacific sardines. Arrows indicate spring and fall migration route.

is accepted that it was a combination of over fishing at a time of exceptionally poor marine survival (MacCall, 1979; Ware and Thomson, 1991). Virtually no Pacific sardines were reported in the Canadian zone until the early 1990s (Hargreaves et al., 1994). Pacific sardines are now migrating into the Canadian zone, and it appears that a small number may even be resident (McFarlane and Beamish, 1999; McFarlane et al., 2000).

8. Seamounts

There are approximately 46 seamounts off the west coast of North America that are less than 1000 m below the surface (Fig. 15, courtesy of John Dower, University of Victoria, Victoria, British Columbia, Personal Communication). The combined surface area of seamounts that could support fish is small relative to the coastal areas. However, the species on these seamounts provide evidence of dispersion from the coastal area to the open ocean. A number of seamounts have been sampled for resident fishes (Table 2); however, here we only consider the species found on Bowie Seamount, 180 km west of the Queen Charlotte Islands (Fig. 15) (Beamish and Neville, 2003; Canessa et al., 2003). We use this as representative of other seamounts because this seamount has reported fisheries for over 20 years, resulting in a better understanding of the fish fauna than other seamounts. The species composition on Bowie Seamount (Table 3) is comprised of species typically found in coastal areas. But how do these coastal species arrive on the seamount? The dominant species tend to be top predators (Beamish and Neville, 2003) such as sablefish, Pacific halibut, and rockfish, especially rougheye rockfish (*Sebastes aleutianus*). There is tagging evidence that shows that sablefish tagged along the coast migrate out to Bowie Seamount and sablefish tagged at the seamount are captured along the coast (Beamish and Neville, 2003; Whitaker and McFarlane, 1997). There are DNA analyses that show that the yelloweye rockfish (*Sebastes ruberrimus*) on the seamount cannot be distinguished from those along the coast (Yamanaka et al., 2001). Whether the dispersion of coastal fishes to seamounts is direct (e.g., juvenile fish actively migrating) or indirect (e.g., juvenile fish randomly dispersed via currents), there clearly is an association between the fish fauna on Bowie Seamount and probably on other seamounts with the coastal fish fauna.

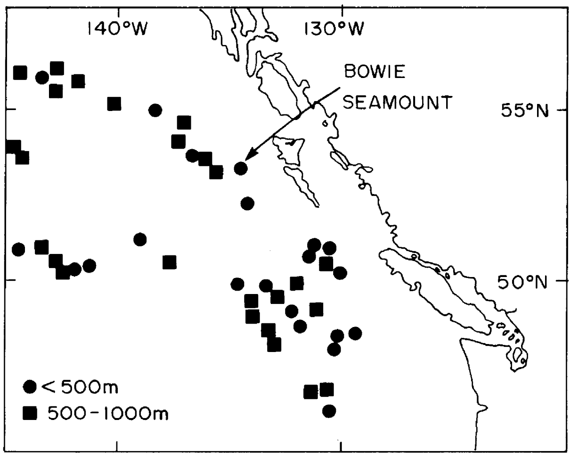

Fig. 15. Location of shallow seamounts off the west coast of North America. Solid circles indicate seamounts where the surface is less than 500 m and solid squares indicate seamounts where the surface is between 500 and 1000 m. (Figure was provided by J. Dower.)

Table 2
Major seamounts that have been biologically sampled in the northeast Pacific

Seamount	Latitude	Longitude
Pratt	56.17	142.50
Bowie	53.30	135.63
Cobb	46.77	130.82
Guide	37.02	123.33
Davidson	35.72	122.72
Erben Tablemount	32.87	132.53
Fieberling Tablemount	32.37	127.83
Seamount 9 mi. NW of Los Islotes	24.70	110.53
Seamount 350	23.00	124.83
Hurricane Bank	16.87	117.50
Dowd Guyot	13.47	120.00
Volcano 7	13.33	102.50

Latitudes and longitudes are in decimal degrees (http://seamounts.sdsc.edu/ accessed December 11, 2003).

Table 3
Fish species identified at Bowie Seamount

Common name	Scientific name
Elasmobranchs	
Basking shark	*Cetorhinus maximus*
Blue shark	*Prionace glauca*
Brown cat shark	*Apristurus brunneus*
Pacific sleeper shark	*Somniosus pacificus*
Spiny dogfish	*Squalus acanthias*
Longnose skate	*Raja rhina*
Snipe eels	
Unidentified	*Nemichthyidae*
Dragonfishes	
Highfin dragonfish	*Bathophilus flemingi*
Longfin dragonfish	*Tactostoma macropus*
Viperfishes	
Pacific viperfish	*Chauliodus macouni*
Myctophids	
Broadfin lampfish	*Lampanyctus ritteri*
Moras	
Pacific flatnose	*Antimora microlepis*
Gadids	
Pacific cod	*Gadus macrocephalus*
Walleye pollock	*Theragra chalcogramma*
Eelpouts	
Longsnout eelpout	*Bothrocara remigerum*
Twoline eelpout	*Bothrocara brunneum*
Rattails	
Pectoral rattail	*Coryphaenoides pectoralis*
Roughscale rattail	*Coryphaenoides acrolepis*
Pomfret	
Pacific pomfret	*Brama japonica*
Wolffishes	
Wolf eel	*Anarrhichthys ocellatus*
Prowfishes	
Prowfish	*Zaprora silenus*
Ragfishes	
Ragfish	*Icosteus aenigmaticus*
Rockfishes	
Rougheye rockfish	*Sebastes aleutianus*
Pacific ocean perch	*Sebastes alutus*
Aurora rockfish	*Sebastes aurora*
Redbanded rockfish	*Sebastes babcocki*
Shortraker rockfish	*Sebastes borealis*
Silvergray rockfish	*Sebastes brevispinis*
Darkblotched rockfish	*Sebastes crameri*
Splitnose rockfish	*Sebastes diaploproa*
Widow rockfish	*Sebastes entomelas*
Yellowtail rockfish	*Sebastes flavidus*
Rosethorn rockfish	*Sebastes helvomaculatus*
Quillback rockfish	*Sebastes maliger*
Vermillion rockfish	*Sebastes miniatus*
China rockfish	*Sebastes nebulosus*
Tiger rockfish	*Sebastes nigrocinctus*
Bocaccio rockfish	*Sebastes paucispinis*
Canary rockfish	*Sebastes pinniger*
Redstripe rockfish	*Sebastes proriger*
Yellowmouth rockfish	*Sebastes reedi*
Yelloweye rockfish	*Sebastes ruberrimus*
Harlequin rockfish	*Sebastes variegatus*
Shortspine thornyhead	*Sebastolobus alascanus*
Longspine thornyhead	*Sebastolobus altivelis*
Sablefishes	
Sablefish	*Anoplopoma fimbria*
Flatfish	
Pacific halibut	*Hippoglossus stenolepis*
Deepsea sole	*Embassichthys bathybius*
Dover sole	*Microstomus pacificus*
Petrale sole	*Eopsetta jordani*
Rock sole	*Glyptocephalus zachirus*
Arrowtooth flounder	*Atheresthes stomias*
Sculpins	
Red Irish lord	*Hemilepidotus hemilepidotus*
Unidentified	*Cottidae*
Snailfishes	
Blacktail snailfish	*Careploctus melanurus*
Sunfishes	
Ocean sunfish	*Mola mola*

9. Conclusions

The purpose of the PICES symposium was to examine the linkages involving the transfer of energy between open ocean and coastal ecosystems. One of these linkages is through the migration of fishes between the two systems. In this study we identified the important pelagic fish migrations that could serve as mechanisms for the transfer of energy. Pacific salmon clearly are the major group of species that migrate between coastal and open oceans. Their anadromous behaviour allows them to have safe refuge for reproduction in fresh water, and a vast feeding area for growth and survival in the ocean. Upon returning to coastal systems they spawn and die. Energy in the form of nitrogen and phosphorus, obtained as body mass in the open ocean, is transferred to freshwater system through the decay of adult salmon carcasses. It is probable that these marine derived nutrients also available to coastal marine ecosystems by predation upon returning adults, through the flow of fresh water into the ocean and by the eventual emergence of Pacific salmon smolts into the marine habitat.

Other species are known to move between the coastal and open-ocean ecosystems. Albacore tuna and elasmobranchs probably contribute to transfers of energy through migration. Although coastal migrations were not a key component of this review, we note that transfers of biomass occur among coastal ecosystems as well, which redistribute energy that was produced in the surface waters of the open ocean in phytoplankton and transferred up the food chain to fishes. The energy exchange between coastal areas and seamount are relatively minor and poorly studied; however, the similarities in fish fauna suggest continuous exchange between these areas and it is important to recognize that the exchanges occur. Overall, our study shows that there are connections between freshwater, coastal and open-ocean waters that link the production in these ecosystems. The most important connection is for Pacific salmon that utilize the production in the open ocean to support large abundance and grow to sizes that enable Pacific salmon to migrate back into fresh water, migrate through the currents and hazards in fresh water, mature sexually, and spawn successfully—all with very little feeding once the migration begins in the open ocean.

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