3 Beyond the Continental Margin

> *"The discovery is reported to have been taken as a result of the investigations of Professor David Starr Jordan and his assistants that the refuge of the salmon between the time of spawning in the Fraser and the return to the river fully matured is ten miles off the Vancouver Island."*
> British Colonist, August 18, 1909

Professor Jordan was President of Stanford University and a leading ichthyologist of his generation. His ideas about salmon migration and distribution at sea (Jordan, 1888), however, reflect how imagination (or bias) can entertain such fanciful stories when adequate data are not available to challenge them.

This section focuses on what is known about Fraser River sockeye salmon biology during the period after their postsmolt year and before the calendar year when they mature. For most Fraser River sockeye salmon, this is a 12-month period of finding food, growing, and avoiding predation and disease in the Northeast Pacific. For some life history types, typically those with slower growth rates, this can be a two-, or rarely, a three-year period.

3.1 Distribution and Migration

The distribution and movement of immature Fraser River sockeye salmon at sea is the least understood of all life history phases. Sockeye salmon that were tagged at sea were rarely recovered in fisheries the following calendar year, despite a significant effort directed at catching and releasing tagged salmon (Fig. 16). In 1962, for example, four Canadian chartered salmon fishing vessels were deployed from April to July, each making about seven trips of 10 to 15 days each during spring and summer throughout the Gulf of Alaska north of 45°N and west to 160°W (Anon., 1963). Each vessel was a ~24 m purse seiner that had been re-configured to catch salmon alive with baited floating longlines. Because it was not possible to determine, at the time of tagging, whether a fish was immature or maturing, it was not possible to know if the longline catches were representative of immature sockeye salmon populations. Only when the tag was recovered did the developmental state of the fish become known. The vast majority were maturing sockeye salmon.

Fishing gears tended to be selective for maturing sockeye salmon but the winter period, when the Gulf of Alaska is almost dominated by immature individuals, is poorly sampled. The first trans-Pacific winter survey for Pacific salmon was conducted by the Fisheries Agency of Japan only as recently as 1996 (Myers *et al.*, 1996). The *Kaiyo maru,* a large research stern trawler caught only 51 sockeye salmon from 22 stations in 1996 and half of these were taken in one set in the central Gulf of Alaska. Similar results with no catch were obtained from DFO surface trawl sampling the Gulf of Alaska in four years of sampling in the 1990s (Welch *et al.*, 2002b,c).

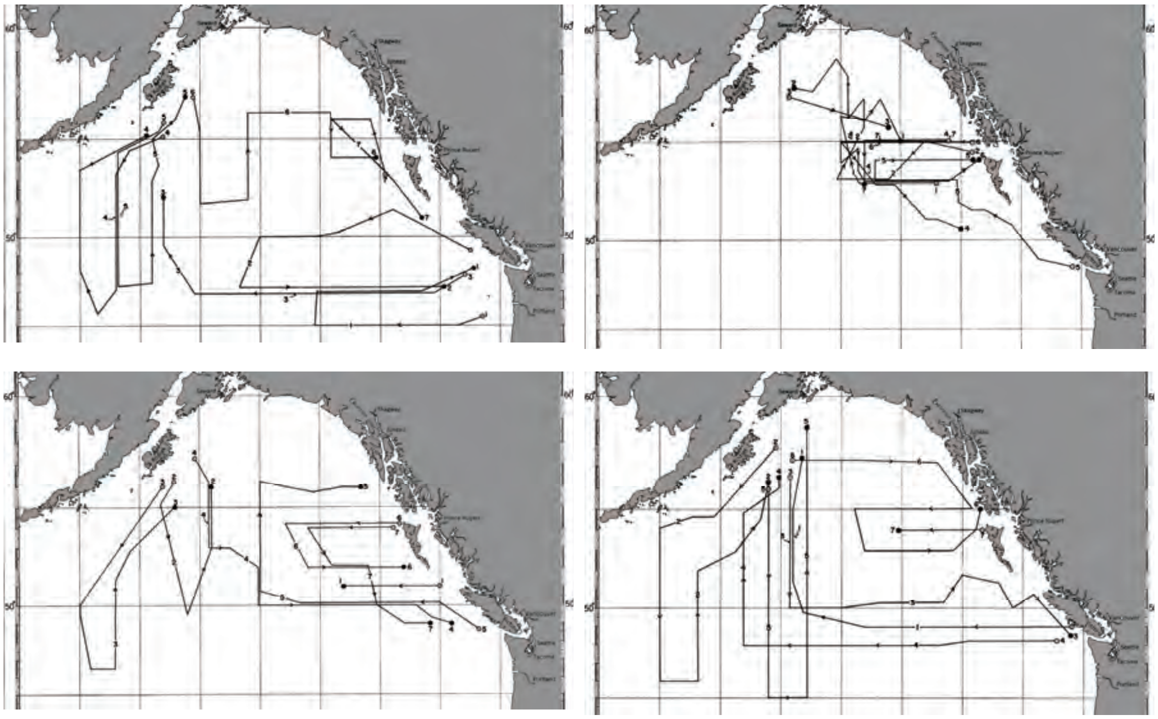

Fig. 16 Cruise tracks of four vessels conducting Fisheries Research Board of Canada salmon research with floating longline gear in the Gulf of Alaska in the spring and summer of 1962.

The distribution of immature Fraser River sockeye salmon on the high seas, determined from very few tags, differs somewhat from that of maturing fish (Fig. 17). Immature Fraser River sockeye salmon generally have a more southerly distribution (French *et al.*, 1976) than maturing fish and two immature Fraser River sockeye salmon were tagged considerably farther west than any maturing fish. Some of the difference between the two groups is a result of bias introduced by tagging maturing sockeye salmon during their homeward migration when they are expected to be closer to the Fraser River compared to fish that are not on a spawning migration.

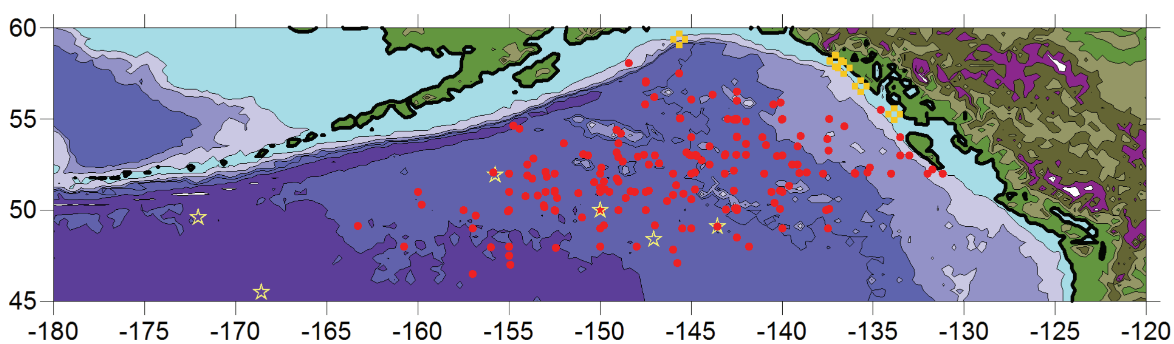

Fig. 17 Locations of sockeye salmon caught on floating longline gear, tagged and released on the high seas and subsequently recovered in Fraser River salmon fisheries. Life history stages are indicated by different symbols; red dots = maturing fish, beige stars = immature, mustard crosses = postsmolts. Database currently maintained by North Pacific Anadromous Fish Commission, Vancouver, B.C.

The feeding migrations of immature sockeye salmon are not well known because there are few direct observations (Royce *et al.*, 1968). Winter observations are rare so the period between postsmolt and immature is one of the least well known. Models of migration that involve loops around the Gulf of Alaska are among the more common because they follow the geostrophic currents (Fig. 18, Brett, 1983; Hinch *et al.*, 1995), but other models such as simple undirected swimming during the immature phase also gave satisfactory results when compared to the available data (Walter *et al.*, 1997).

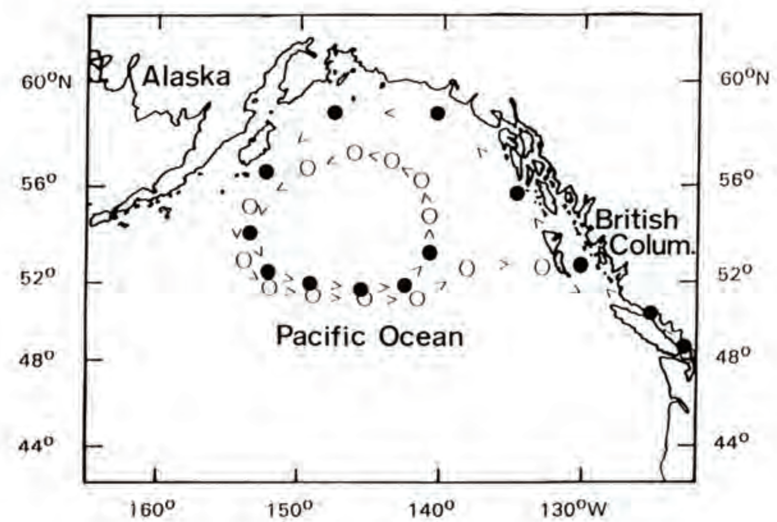

Fig. 18 Hypothetical migration of early Stuart sockeye. Closed and open circles represent the first and second year of ocean residency, respectively. From Brett (1983) in Hinch *et al.* (1995).

The general migratory routes of immature sockeye salmon at sea were not determined from tagging data alone (French *et al.*, 1976). Catches were taken by other gears for other purposes and these contributed significantly to the general understanding of the routes. However, they suffered from a lack of stock specificity. Sex and maturity were determined by visual inspection of the gonads. It is clear, however, from an examination of the length frequency data that immature sockeye salmon are under-represented in high seas catches, even when non-selective fishing gears (multi-mesh gillnets or seines) were used (Fig. 19). On average, immature fish must be more abundant than maturing fish because the latter have experienced at least an additional year of mortality that the former have not, yet the younger/smaller fish are rarely found as the most abundant size-class in the catch. Even in 1957, when the immature phase of a very large return of Late-run sockeye salmon to the Fraser River (in 1958) was at sea, the length frequency distribution resembled that of Figure 19. Either the gear favoured maturing salmon, or the immature salmon were elsewhere. As a consequence, it appears that some aspects of this life history stage are not as well known as for maturing fish.

French *et al.* (1976) described how immature sockeye salmon were found in winter (February) in parts of the ocean with sea surface temperatures (SSTs) in the range 5.6–6.7°C, whereas maturing sockeye salmon were found where SSTs in February were 2.2–4.4°C. In more contemporary sampling by Japanese research vessels to 2002, Nagasawa and Azumaya (2009) found that most age-x.1 sockeye caught in the North Pacific in June were immature and were found where the long-term average SSTs were in the range 5–8°C. The Gulf of Alaska was not sampled well during these surveys in June and long-term average temperatures there were higher. In July, immature sockeye salmon were found mainly along the Aleutian archipelago (probably Alaskan sockeye) and in the Gulf of Alaska (mixture of origins) at SSTs <12°C. The Gulf of Alaska was not sampled in August in Japanese research vessel surveys from 1972. The extent to which these temperature and abundance patterns applies to Fraser River sockeye salmon cannot be determined from these data.

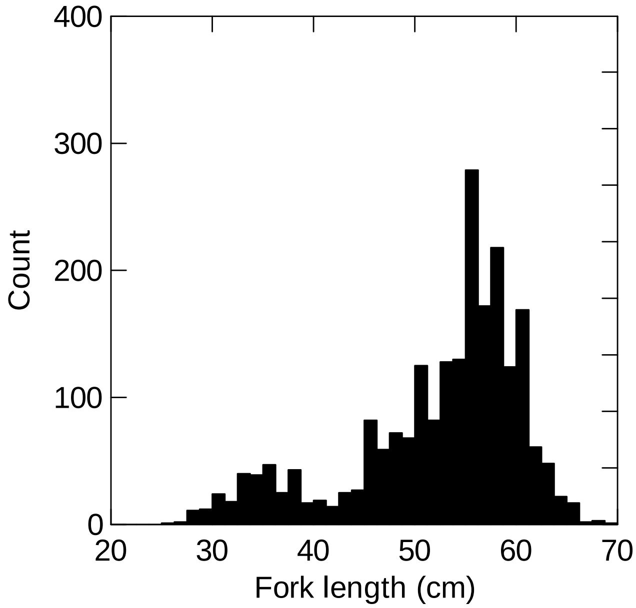

Fig. 19 Fork length distribution obtained from sockeye salmon caught multi-mesh gillnet sets in the Gulf of Alaska from 1956 to 1958. Data from Neave and Manzer (1957) and Manzer and Neave (1958, 1959).

While the general model of the distribution of sockeye salmon places them mostly offshore in their first year as immatures (Fig. 20), one cruise in late April to early May of 1998 (Fig. 21) found small (20–30 cm) immature sockeye salmon aggregated within 6 nmi of shore in the southeastern Bering Sea (Carlson *et al.*, 1998). This was the first such observation for the southeastern Bering Sea. The origins of these fish are unknown.

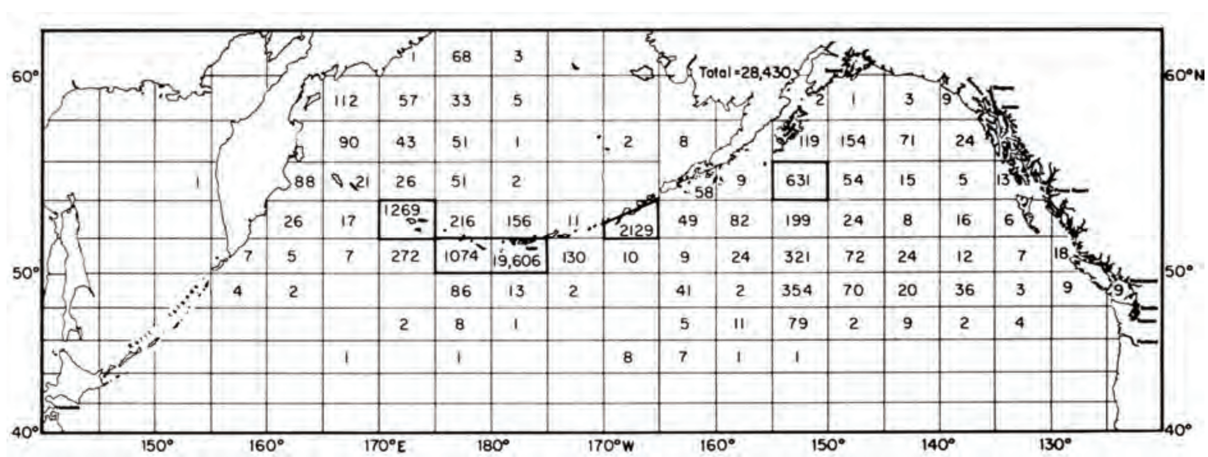

Fig. 20 Distribution of tagged age-x.1 sockeye salmon (nearly all immature) from 1956 to 1970. Areas with >500 fish tagged are outlined in bold. Reproduced from French *et al.* (1976).

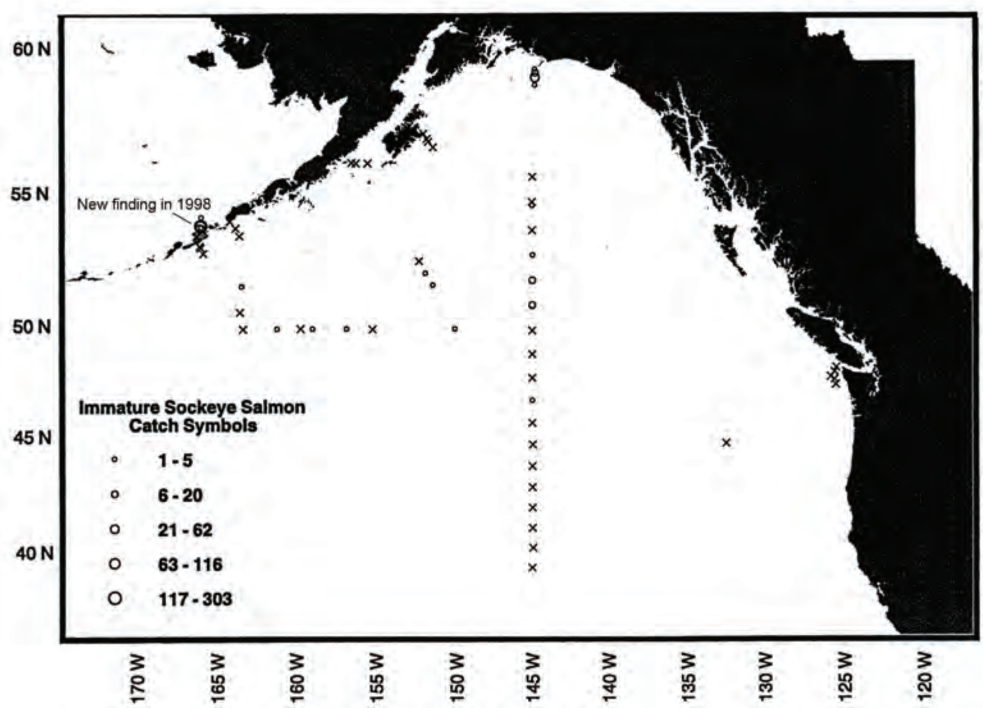

Fig. 21 Distribution of fishing stations (x) and catches of immature sockeye salmon in the Gulf of Alaska in spring 1998. Figure from Carlson *et al.* (1998).

Summary – From 1956 to 1970, 28,430 tags were applied to age-x.1 sockeye salmon and a Pacific-wide total of 150 of these tags was recovered (0.5%). The distribution of immature Fraser River sockeye salmon at sea is poorly known because so few tags have been recovered from these fish. A combination of factors is probably responsible for poor recoveries of immature sockeye: tagging mortality, high seas fisheries during that era, and natural mortality before maturing. Certainly, some postsmolts are known to follow the continental shelf. If all of them have this behaviour, it would place greater numbers of immature salmon in the western Gulf of Alaska by the end of the postsmolt migration. Indeed, the greatest number of tags applied to immature sockeye salmon of all origins in the Gulf of Alaska occurred south of Kodiak. As Alaskan sockeye salmon are known from this region, a significant fraction may have that origin. The fraction of westward migrating Fraser River sockeye salmon that leaves the shelf before reaching the western Gulf of Alaska is unknown. Neither gillnets nor longlines capture immature sockeye salmon in relation to their abundance. On average, it must be greater than the abundance of maturing fish because of the mortality that occurs in the year(s) between immaturity and maturity. However, most length frequency plots of sockeye salmon taken on the high seas feature a greater abundance of older fish (Fig. 19), so it is not unreasonable to assume that certain aspects of the distribution of this life history stage in the sea are known rather poorly.

3.2 Behaviour

Knowledge of the behaviour of immature sockeye salmon on the high seas has, for the most part, been obtained by catching salmon and inferring behaviour from the observed patterns in the catches. A potential explanation for the under-sampling of immature sockeye salmon in high seas catches (Fig. 19) is that they behave differently from maturing individuals, and as a result, are not equally vulnerable to the fishing gear.

Gillnet and floating longline are passive devices that require fish movement past the gear (directed in the case of gillnet) or feeding behaviour. The floating longline may also be selective for certain sizes of fish because of hook and/or bait size (Ralston, 1990). The purse seine, on the other hand, could potentially capture all size-classes if the immature and maturing fish occupy the same space.

Direct comparisons of the fishing characteristics of each gear at the same time and location in offshore waters are few. On May 26, 1964, a comparison of only longline and purse seine was conducted in INPFC area W5048 (between 48–50°N and 150–145°W). Immature sockeye salmon (~33 cm average) were fewer than larger individuals in both gears and the largest mode was represented in the longline but not the purse seine (Fig. 22). Potentially, immature fish are routinely under-represented in the seine gear in this region but this cannot be determined from one day of fishing. That the purse seine did not catch fish in the largest mode was attributed to their having set the net in only three of four compass directions during the experiment (Hartt, 1975). The inference is that they would have caught the larger mode if the 4th compass direction was sampled.

> *"a difference in behavior of a particular component of the stock that affected its availability to the gear could cause a serious bias in the composition of the catch."*
>
> Hartt, 1975

The same logic, turned around, may indicate that bias in the catch composition suggests that different components of the stock behave differently. How differently has yet to be fully examined.

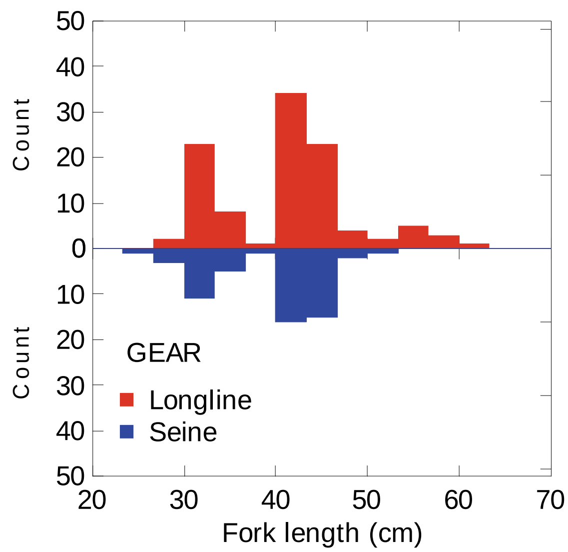

Fig. 22 Fork lengths of 167 sockeye salmon caught offshore in the Gulf of Alaska on May 26, 1964 during an experiment to compare the characteristics of seine (three sets combined) and longline gear (one morning set of 20 skates). Data from Hartt (1975).

Summary – The best evidence that immature sockeye salmon behave differently from maturing sockeye salmon it that they are not caught in adequate abundance in the gears typically deployed to catch them (purse seine, gillnet, longline). Multi-sized mesh gillnet and purse seine were thought to be non-selective. Immature salmon may lack the property of rapid and directed migrations that maturing salmon appear to exhibit. They have lower growth rates (Ishida *et al.*, 1998) than maturing fish and therefore, less energetic requirements. Immature sockeye salmon potentially have no need to maintain a near-surface distribution for orientation during migration so they may not be exposed equally to the floating longline bait. The nature of the behaviour difference is mostly a matter of speculation.

3.3 Feeding

> *"Nothing is known of their feeding-grounds in salt water as they [sockeye] are never found in the bays and inlets which distinguish the coast and where the spring and coho are so common. It is thought that their feeding-ground must be in the open sea."*
>
> Anonymous, 1911

Salmon on the high seas forage opportunistically with stomach contents often related to oceanic domains and availability of certain prey types (Pearcy *et al.*, 1988; Kaeriyama *et al.*, 2004). The first samples of sockeye salmon stomach contents from the Gulf of Alaska were collected by the Fisheries Research Board of Canada during a gillnet survey in the summer of 1958 (LeBrasseur, 1966). Immature fish were identified by visual inspection of the gonads. The most noteworthy characteristic of the stomach contents of immature sockeye salmon was the small amount of material found in the stomachs. Amphipods, euphausiids and squid contributed the most. LeBrasseur (1966) commented that there was a much greater difference in stomach contents among oceanographic domains than among species. Stomachs collected from salmon in the Alaskan Stream were dominated by fishes while those taken in the Subarctic Gyre were mostly squid.

A more complete analysis of the stomach content data that were collected from 1956 to 1964 (Table 2) considered the effects of SST, body weight, latitude, longitude, year, day of year, and time but they were able to describe only small amounts of variation in feeding probability (13%) and stomach fullness (16%) (Rand, 2002). The lengths and weights of these fishes reflect the multiple age-classes and their seasonal changes in the samples (Figs. 23 and 24). In this analysis, all individuals >500 g were pooled as "sub-adults" regardless of whether they would or would not mature in the upcoming summer, and there was no accounting for differences that might exist among stocks. LeBrasseur's comments, above, suggest that immature and maturing sockeye salmon have different feeding behaviours. Despite these shortcomings in the analysis, in the pooled results Rand (2002) found that the feeding and growth indices he developed were variable in space and time in the Gulf of Alaska. There was a negative association between increasing SST and feeding probability (determined from presence/absence of contents in stomachs) but stomach fullness increased in warmer SST. Feeding probabilities of larger sockeye salmon were higher in winter and spring and lower in summer. The lower feeding probability in larger sockeye salmon was interpreted as evidence of anorexia prior to the spawning migration (Rand, 2002) but the timing of the onset of anorexia is not well documented. He determined that there was a tendency for larger sockeye salmon to be caught farther north than smaller sockeye salmon in the winters of 1963 and 1964 (combined). There was a tendency for larger sockeye salmon to be caught further north in the spring of 1962. He also found that in both the springs of 1962 and 1963 there was a sharp reduction in his growth index along the southern Gulf of Alaska.

Table 2 Total numbers of immature sockeye salmon stomachs examined by the Fisheries Research Board of Canada from 1956 to 1964 by year and month.

Month	**1956**	**1957**	**1958**	**1959**	**1960**	**1962**	**1963**	**1964**	**Total**
1	0	0	0	0	0	0	37	35	72
2	0	0	0	0	0	0	1	11	12
4	0	0	0	0	0	11	69	0	80
5	9	3	70	29	0	14	93	0	218
6	1	132	39	177	2	78	0	0	429
7	49	113	0	19	7	18	0	0	206
8	0	17	4	0	0	0	0	0	21
11	0	0	0	0	0	0	3	0	3
Total	59	265	113	225	9	121	203	46	1041

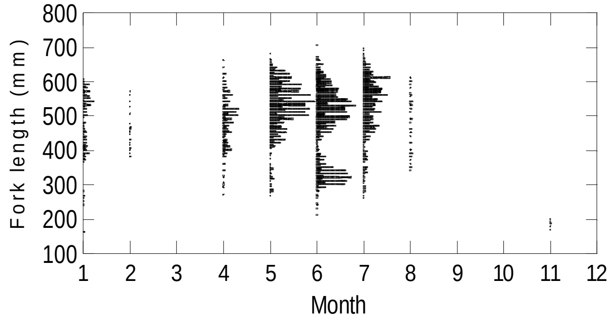

Fig. 23 Fork lengths (mm) of sockeye salmon taken by multi-mesh gillnets and floating longline gear in the Gulf of Alaska from 1956 to1964 that were examined for stomach contents. Samples in November were collected by mid-water trawl net in Hecate Strait.

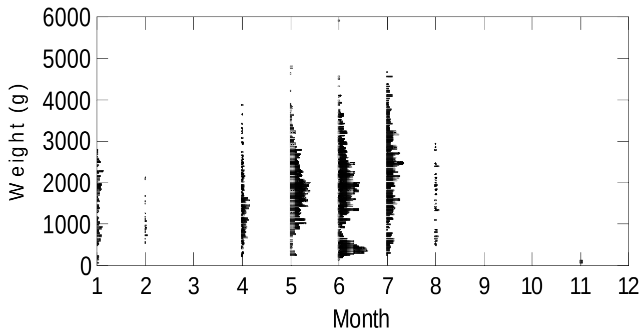

Fig. 24 Body weight (g) of sockeye salmon taken by multi-mesh gillnets and floating longline gear in the Gulf of Alaska from 1956 to 1964 that were examined for stomach contents. Samples in November were collected by mid-water trawl net in Hecate Strait.

In 1981, a joint Hokkaido University–Oregon State University study of diel feeding patterns was conducted during a 24-h period from July 13–14 on board the T/V *Oshoro maru* in the Subarctic Gyre between latitudes 54° 51.5′ and 54° 57.9′N, and longitudes 144° 55.1′ and 145° 11.3′W (Pearcy *et al.*, 1984). Two gillnets, each 800 m long and 6 m deep, with 300 m of 115-mm, 250 m of 121-mm, and 250 m of 130-mm (stretch) mesh, were alternately fished throughout the period. The total catch of sockeye salmon was the largest in night sets, as was the fraction of the catch taken in the uppermost part of the net. Prey composition for sockeye salmon had a diel pattern with euphausiids (predominantly *Euphausia pacifica* and *Thysanoessa longipes*) dominating at night (Pearcy *et al.*, 1984). Other common prey of sockeye salmon during this study were amphipods and fishes. Squids were more common in the afternoon/evening. Copepods formed <1% of the diet.

Kaeriyama *et al.* (2004) conducted an evaluation of salmon diets from 1994 to 2000 but did not distinguish between immature and maturing individuals. The stomach contents of sockeye, pink and chum salmon tended to be zooplankton during this period while the other species of salmon fed on squid and fishes.

Summary – Samples of stomach contents of sockeye salmon in the Gulf of Alaska were collected from 1956 to 1964. The results of a single year of sampling (1958) were published in 1966 (LeBrasseur, 1966). As there was a large return of Adams River fish in that year, it might be reasonable to assume that some of these fish were of Fraser River origin. Data from samples collected in the Gulf of Alaska in 1962 and 1963 were reported in 2002 (Rand, 2002) but this study did not distinguish between immature and maturing salmon although it did consider the effect of size (fork length) which can be a correlate of maturity at some sizes. Lebrasseur (1966) drew attention to how little material was found in the stomachs of immature sockeye salmon compared to maturing fish.

3.4 Growth

Stage-specific growth of individual immature Fraser River sockeye salmon can be measured from the amount of growth that occurred between the first and second marine annulus on fish scales (Fukuwaka and Kaeriyama, 1997), but this measurement was not made routinely, except during a brief period in the 1960s by the Stock Assessment Authority of the Fisheries Research Board of Canada. The growth of immature sockeye salmon can be measured on individual fish that were tagged as postsmolts and recovered at sea the following year (or more for fish older than age-1.2). Generally, fork length measurements will have been made on the latter, but they are so few that a representative estimate of the growth of immature sockeye salmon will not be possible. Furthermore, the stock of origin of these tagged fish will not be known.

3.4.1 Density-dependent growth (intra-specific)

Intra-specific density-dependent growth of Fraser River sockeye salmon during their immature year in the Gulf of Alaska has not been studied. However, it is known from other British Columbia sockeye populations that the largest correlations in mean fork length among different stocks are found in fish maturing in the same year. The mean size of returning adults in a cohort of sockeye salmon with a common ocean-entry year, but different return years, is uncorrelated (Godfrey, 1958; McKinnell, 1995). Examining immature Fraser River sockeye salmon for the property of density-dependent growth, in relation to salmon abundance (various species), will require annual measurements of mean growth from scales but this is not done routinely. One study examined annual growth variation in the Early Stuart stock (Fig. 25) and found that variations in the amount of growth in any year by a given fish is uncorrelated with the amount of growth observed at other ages for the same fish (Welch, 1997). The implication is that there is no persistence of faster or slower growth within individuals of a given stock. It was also found that the factors affecting growth in different years were correlated, suggesting that the oceanic factors affecting growth are stochastic rather than autocorrelated on an annual basis (Welch, 1997).

Long-term trends in growth of the Early Stuart stock were largely confined to postsmolts or maturing sockeye salmon (Welch, 1997). This was interpreted to mean that the coastal zone is food limited, *i.e.*, the increased salmon abundance that was observed at the time may have resulted in increased trophic competition in coastal waters. Long-term trends in growth were largely absent among immature stages in offshore regions for M2 in age-1.2 and -2.2. individuals, and M2 and M3 growth for age 1.3 individuals (see Figure 25 for definitions of M1 to M4).

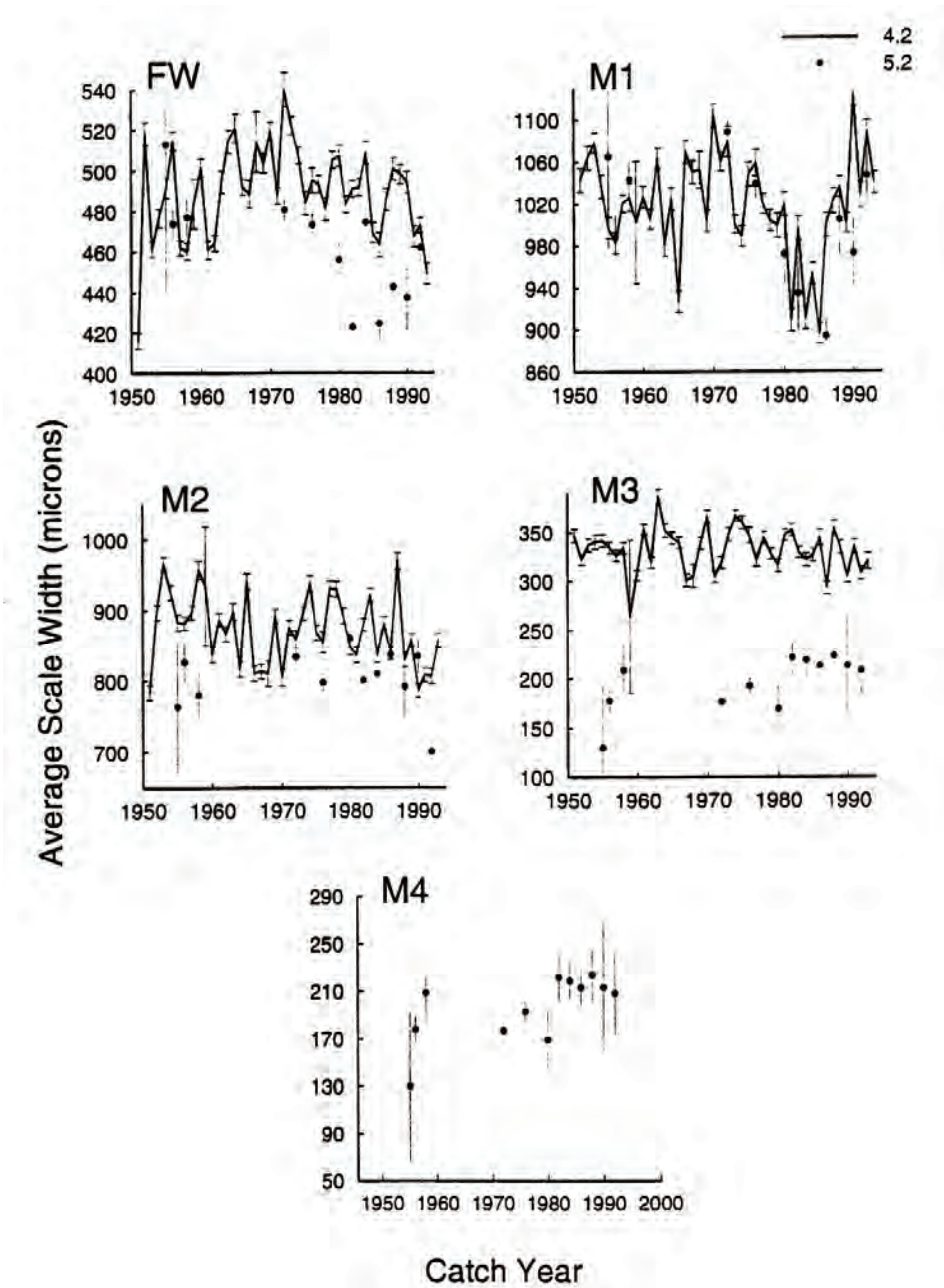

Fig. 25 Stage-specific variation in marine growth by year for the Early Stuart stock of Fraser River sockeye salmon. M1 to M4 indicates the years at sea. FW = freshwater, M1 = postsmolt, M2 = immature (mature for jacks), M3 = maturing year (age-1.2) or immature year (age-1.3) and M4 = maturing year (age-1.4). The pattern of variation at different ages is uncorrelated. Solid circles indicate fish that matured as age-1.3 and solid lines indicate fish that matured at age-1.2. Figure from Welch (1997).

Summary – Generally, the increase in fork length or mass of immature sockeye salmon is less than that of maturing sockeye salmon (Ishida *et al.*, 1998) because the immature fish do not have the joint energetic demands of a spawning migration and maturation. Maturing fish of the same length as immature fish tend to weigh more. Some measurements of annual growth of Fraser River sockeye salmon, determined from scale growth, exist but they are relatively rare.

3.5 Thermal Limits to Oceanic Distribution

In the 1990s, when the spectre of global warming began to feature more prominently in scientific discussion, a *thermal limit* hypothesis for Pacific salmon distribution attracted some attention (Welch *et al.*, 1995). The hypothesis followed from a report that the southern limit of Pacific salmon in the North Pacific Ocean is determined by the temperature of the surface waters. It argued that there are abrupt thermal limits to their horizontal distribution. The thermal limits in spring in the northeastern North Pacific were 8.9°C for sockeye salmon, 9.4°C for coho salmon, and 10.4°C for pink and chum salmon, although “spring” was not defined. This conclusion was followed by a more speculative paper (Welch *et al.*, 1998) showing how increasing concentrations of greenhouse gases in the atmosphere would lead to global warming which would raise near-surface ocean temperatures in the North Pacific, restricting the spatial distribution of Pacific salmon in July to a region of the northern Bering Sea, about 1300 km more northerly than latitudes they currently occupy (Fig. 26). The following material examines the thermal limit hypothesis using Intergovernmental Panel on Climate Change 4th Assessment Report (IPCC AR4; 2007) projections of SST in the North Pacific and salmon distribution data that were not available when the hypothesis was developed.

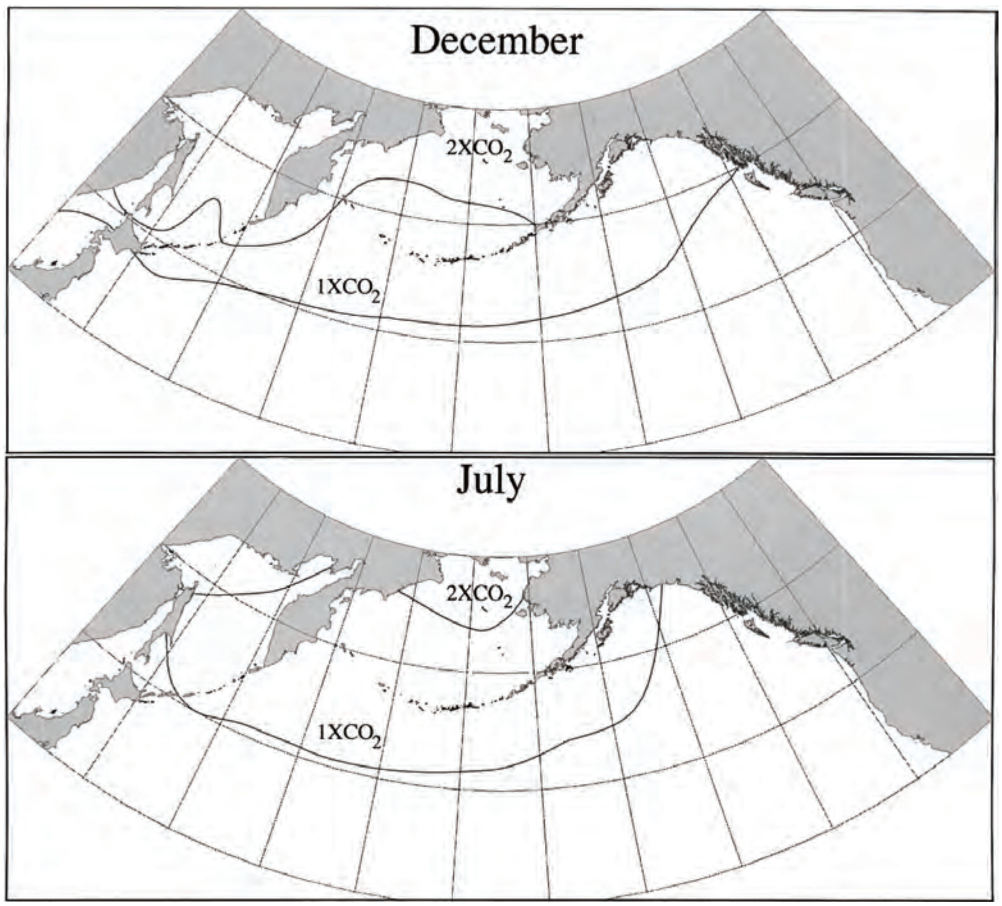

Fig. 26 Comparison of the predicted winter (7°C) and summer (12°C) positions of the sockeye salmon distribution under current and future climates. With a doubling of atmospheric CO_2, the area of acceptable thermal habitat in the North Pacific is predicted to decrease to zero in summer and decline sharply in winter. Figure from Welch *et al.* (1998).

3.5.1 Sockeye salmon in waters exceeding thermal limits

A survey to test the thermal limit hypothesis was conducted in March–April of 1995 (Welch *et al.*, 2002a). The 10.2°C isotherm was the hypothetical upper limit to salmon distribution. During the survey, 22 sockeye salmon were caught in two of a total of 44 tows that were distributed around the eastern Gulf of Alaska. No salmon of any species were caught at 75% of the stations. The survey was repeated in October–November of 1995 with essentially the same result: no salmon were caught in the Gulf of Alaska beyond 250 km from shore (Welch *et al.*, 2002b) although many (3,582) were caught on the shelf and 97% of these at bottom depths <200 m. After four years of catching no salmon in the deeper waters of the Gulf of Alaska, these offshore surveys were discontinued around 1998 (Welch *et al.*, 2002c). A number of explanations, some more plausible than others, come to mind for the lack of salmon: (1) the surveys were not conducted at locations where Pacific salmon occur, (2) the salmon were at depth beyond the reach of the surface trawl, or (3) the abundance of salmon was too low to be taken in the sampling conducted.

Welch *et al.* (1998) established the 12°C isotherm in July as a thermal limit to Pacific salmon distribution. The movement of this isotherm northward with global warming was hypothesized to restrict their distribution northward, eventually into the northern Bering Sea (Fig. 26). The ten warmest years (area-weighted average of gridded data within the bounds <160°W, >50°N) in July in the Gulf of Alaska were, in descending order: 1997, 2005, 2004, 1888, 1936, 1958, 1957, 1941, 1885, 1993). In some of these years, the T/V *Oshoro maru* made regular cruises to the Northeast Pacific. Until 2002, scientific activities in the region included the deployment of surface gillnets of varying mesh sizes during the night. The warmest years when the *Oshoro maru* was operating in the Gulf of Alaska were 1997, 1993, and 1983 but the ship cruise tracks in the Gulf of Alaska differed significantly among years. The only cruise with a north–south transect that spanned the hypothetical limit of 12°C was in 1997 (the warmest year). Sockeye salmon catches in July 1997 were more abundant at temperatures greater than the thermal limit (Fig. 27).

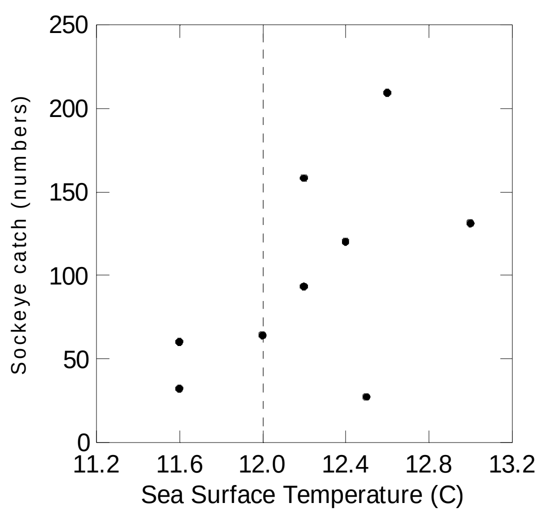

Fig. 27 Numbers of sockeye salmon caught in nightly gillnet sets by the T/V *Oshoro maru* at different stations along 145°W from July 3 to 12, 1997 *versus* SST measured at the stations. Vertical dashed line indicates the temperature of the Welch *et al.* (1998) thermal limit in July beyond which sockeye salmon should not be found.

During the latter half of the 1950s and in the 1960s, the Fisheries Research Board of Canada's North Pacific Survey conducted high seas fishing with gillnets and longlines throughout the Gulf of Alaska. Primary fishing stations were 50°N 155°W, 55°N 155°W, 50°N 145°W, 55°N 145°W, 58°N 145°W, 50°N 135°W, and 55°N 135°W. In 1957, for example, a total 997 sockeye salmon of unknown origin were caught in 71 nights of fishing. As the period of fishing extended from May until August of that year, it is possible to examine the relationship between the hypothesized thermal limit and sockeye salmon catches in the Gulf of Alaska. A two-sample Kolmogorov-Smirnoff test can be used to identify differences between catches above and below the hypothesized thermal limit. It indicated that there was no significant difference ($P > 0.97$) in the frequencies of sockeye salmon catches above and below the hypothesized thermal limit (Fig. 28).

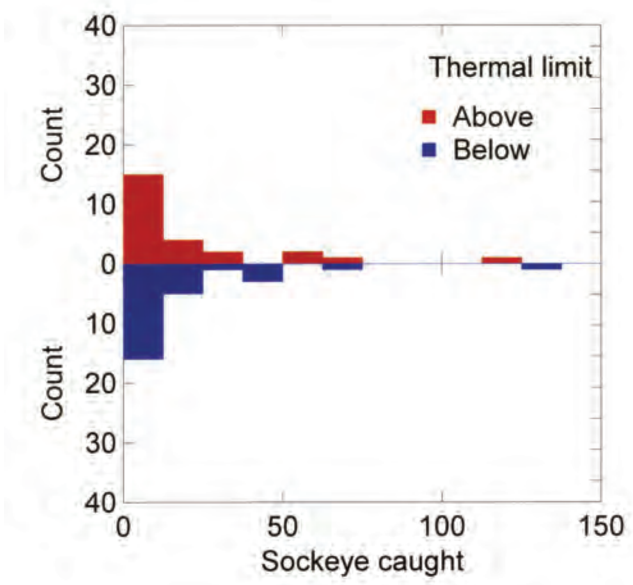

Fig. 28 Sockeye salmon caught above and below 12°C during exploratory fishing for salmon throughout the Gulf of Alaska, May to August 1957.

If the 12°C SST isotherm represents a physiological barrier to sockeye salmon distribution, they could not have reached the eastern Gulf of Alaska and its major southern sockeye salmon rivers (Skeena, Fraser, Columbia) in most years. From 1982 to 2009, surface waters >12°C in July occupy much, and in some years, all of the eastern Gulf of Alaska. In warmer years like 1997, 2004, and 2005, the northward (and westward) intrusion of the 12°C isotherm along the coast can extend past Kodiak Island (Fig. 29). In cold years, the 12°C isotherm extends in July only as far north as Haida Gwaii. Why 12°C should form a southern limit but not an eastern or northern limit is not explained by the hypothesis.

An alternative thermal response behaviour, where salmon might restrict their vertical migration to a few metres lower in the water column where water temperatures cool rapidly, was considered by the authors to be a novel behaviour that would not likely be adopted, even though this behaviour is used routinely by sockeye salmon fry in lakes (Levy, 1987; Clark and Levy, 1988; Schuerell and Schindler, 2003). Rand (2002) argued that the reduced abundance of sockeye salmon along the southern periphery of the Gulf of Alaska was equally likely to be explained by a sharp reduction in growth potential rather than a behavioural response to SST proposed by Welch *et al.* (1995). He described a sharp decline in both feeding and growth of sockeye salmon in 1962 and 1963 in a region south of 52°N. The part of the Gulf of Alaska from 55°N to 58°N was most favourable for sockeye salmon growth in these years. The growth potential dropped by one order of magnitude with a change in SST from 6 to 7°C.

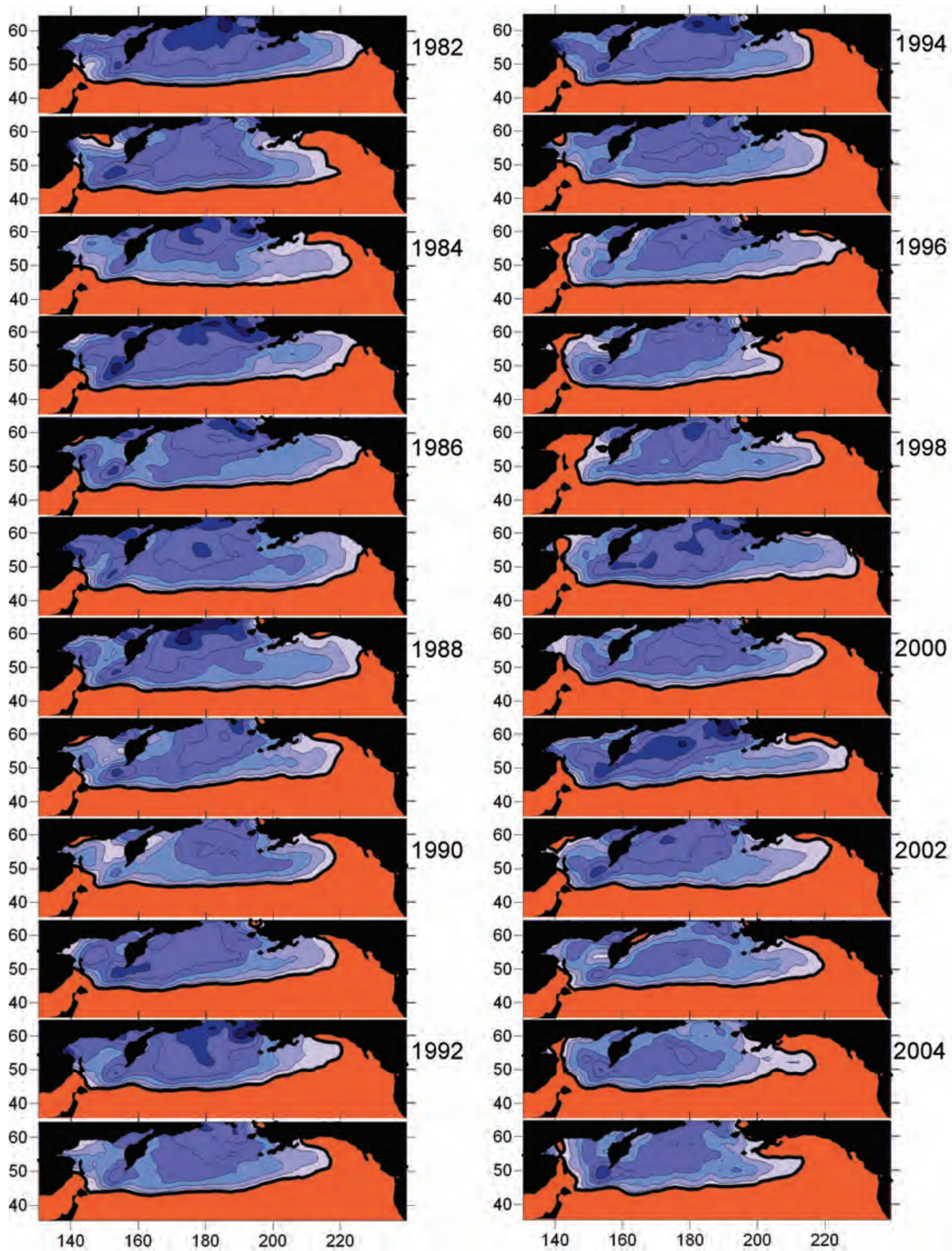

Fig. 29 Sea surface temperature contours for the month of July from 1982 to 2004 in the Gulf of Alaska. The thick contour indicates the 12°C isotherm and all regions warmer than that are coloured in red. Data are from the U.S. NOAA OIv2SST monthly gridded data.

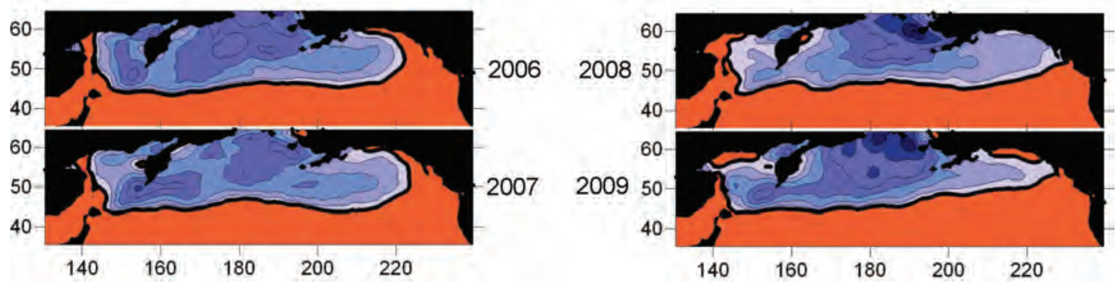

Fig. 29 Continued, 2006 to 2009.

3.5.2 Global climate model projections

IPCC AR4 (2007) model expectations for the future state of average July SST in the North Pacific are different from what was published over a decade ago, and was used to consider the future state of sockeye salmon distribution (Fig. 26). The IPCC A2 scenario (Fig. 30) anticipated a doubling of atmospheric CO_2, from late 20th century concentrations, by the mid-2080s. Four models (hadcm3, cccmat47, gfdl2.1, and mirocM) were selected for examination because they have a better representation of North Pacific SST variability (Wang *et al.*, 2010). For each model, the 10-year average July SST in the 2080s was computed from the average of 10 years of SSTs during the 2080s. Smoothing of the average SSTs was done by the kriging algorithm using the contouring package SURFER™.

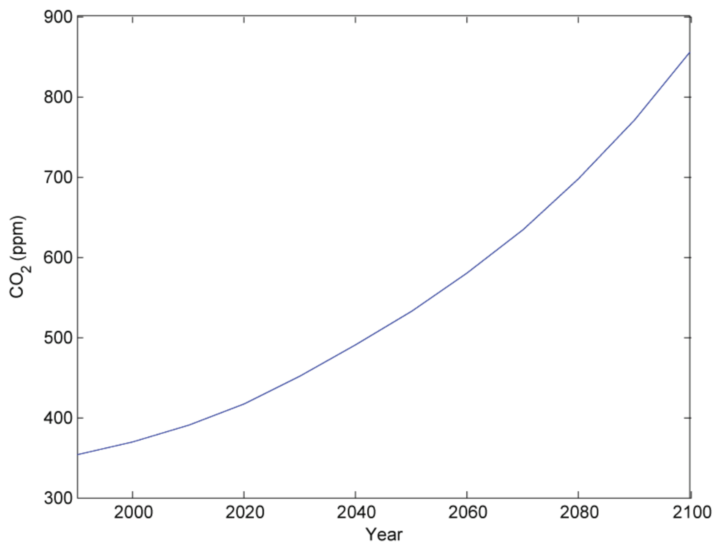

Fig. 30 Projections of atmospheric CO_2 concentrations under the A2 scenario (business as usual scenario).

With the exception of mirocM, these models suggest that, on average, SSTs <12°C will not be a significant part of the Gulf of Alaska at twice the late 20th century CO_2 concentrations (Fig. 31). However, none of these models yields a northward shift of the 12°C SST isotherm as extreme as was reported by Welch *et al.* (1998; see Figure 26). Each of these IPCC models has a region of the North Pacific, south of the Aleutian archipelago, with waters <12°C. It is worth remembering that these models are computed on a relatively coarse grid compared to the small- to meso-scale physical processes that can affect SSTs, especially on the continental shelves where these models are not expected to perform well.

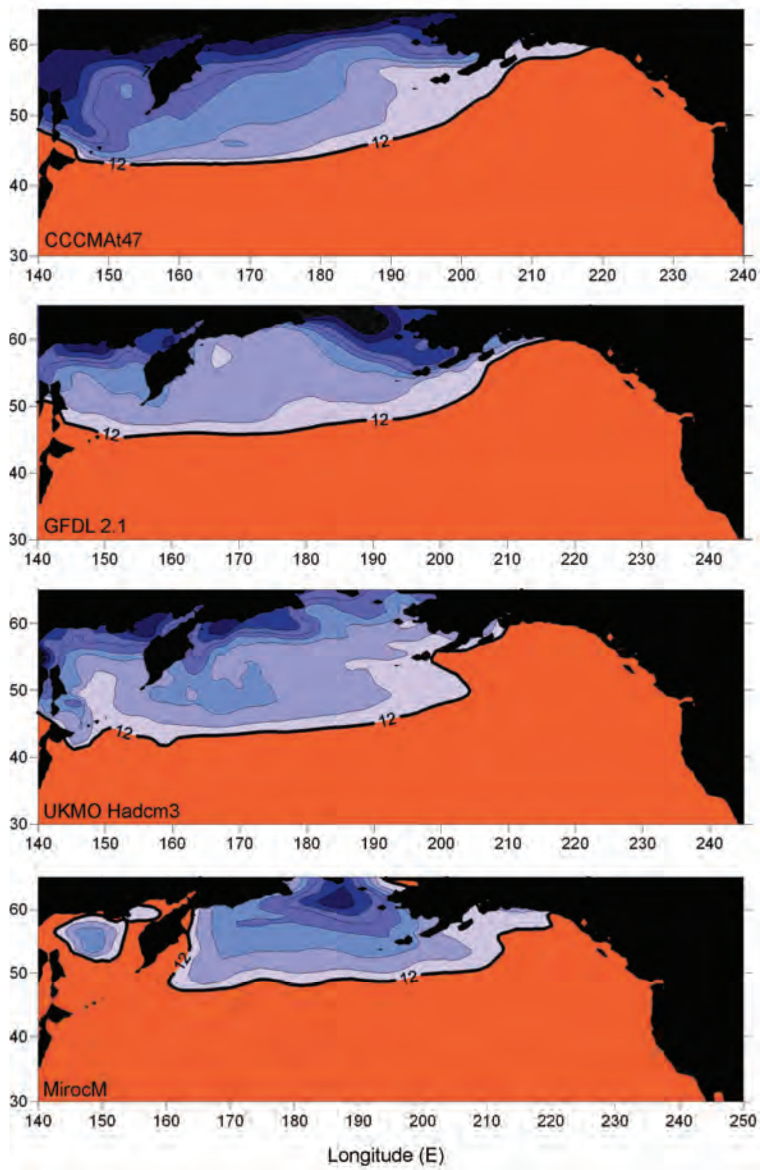

Fig. 31 Average location of the 12°C surface isotherm in the North Pacific Ocean in the 2080s based on output from four IPCC models (named in lower left of each panel). Red coloured regions exceed 12°C and contour intervals less than 12°C are spaced at 1°C.

What are currently considered July SST extremes at the beginning of the 21st century will become approximately the average state of nature with a doubling of CO_2 concentrations, according to these four models. The Julys of 1997 and 2005 (Fig. 29) were relatively extreme years of widespread strong, positive SST anomalies and they bear a qualitative resemblance to the projected average SSTs in the late 21st century, under scenario A2. Both of these years coincided with relatively strong biological anomalies in Fraser River sockeye salmon. The most noteworthy were later-than-average run timing in both years (Mcdonald, 2000; PSC, 2010), although much more extreme in 2005, and high in-river mortality in 1997 (Mcdonald, 2000). The total return of 7.1 million sockeye salmon to the Fraser River in 2005 was slightly higher than forecast but that total was a result of much lower than expected abundance of the Summer run and a much higher than expected abundance of the Late run (PSC, 2010). Peak run timing to Area 20 (western end of Juan de Fuca Strait) in 2005 exceeded previous extremes by six days (Early Stuart), seven days (Summer). The average timing for

Early Summers was exceeded by 29 days. The greater issue for the Fraser River sockeye salmon return in 1997 was the high in-river mortality and migratory anomalies (McDonald, 2000). However, both of these years of extreme SST had significantly greater returns than have occurred generally in the early 21st century.

The IPCC AR4 included an analysis of many numerical dynamical models to understand the future of Earth's climate in the 21st century (IPCC, 2007). Several of the models that are known to have a better representation of the North Pacific Ocean revealed that the location of the 12°C isotherm in July under a doubling of CO_2 (by the 2180s under the A2 scenario) is significantly farther south than was anticipated in the climate model used by Welch *et al.* (1998). The modelled future state of the surface ocean in the 2180s bears a qualitative resemblance to contemporary years that were considered relatively extreme (*e.g.*, 1957, 1983, 1997, 2005). In some of these years, salmon research was ongoing in July in the Gulf of Alaska so it is possible to examine their distribution relative to the thermal limit. For the years when comparisons are possible, salmon were equally abundant above and below the proposed thermal limit. Nevertheless, very warm years tend to affect some aspects of Fraser River sockeye salmon biology, such as the extremely late return timing in 2005 (Blackbourn, 1987; PSC, 2009).

Summary – The thermal limit hypothesis (Welch *et al.*, 1995) anticipates that SST, rather than other oceanographic properties, regulates the range of Pacific salmon in the North Pacific Ocean. It proposes that global warming will move the 12°C isotherm in July to the northern part of the Bering Sea and this will restrict the geographic range of sockeye salmon in the North Pacific Ocean to a region around Bering Strait by the year when atmospheric CO_2 concentration reaches double that observed in the late 20th century (Welch *et al.*, 1998). The hypothesis is controversial because it considers that horizontal movement in space is the only option available to the salmon to avoid warmer surface temperatures. Achieving a cooler temperature by vertical movement requires only a few metres of movement whereas achieving the same degree of temperature change requires a horizontal shift of hundreds of kilometres. Sockeye salmon are known to make vertical movements in the ocean (Pearcy *et al.*, 1984) and in lakes as juveniles to avoid warm surface temperatures.