DIRECTIONAL SELECTION BY FISHERIES AND THE TIMING OF SOCKEYE SALMON (ONCORHYNCHUS NERKA) MIGRATIONS

THOMAS P. QUINN,1 SAYRE HODGSON,2 LUCY FLYNN, RAY HILBORN, AND DONALD E. ROGERS

Fisheries Research Institute, School of Aquatic and Fishery Sciences, Box 355020, University of Washington, Seattle, Washington 98195 USA

Abstract. The timing of migration from feeding to breeding areas is a critical link between the growth and survival of adult animals, their reproduction, and the fitness of their progeny. Commercial fisheries often catch a large fraction of the migrants (e.g., salmon), and exploitation rates can vary systematically over the fishing season. We examined daily records of sockeye salmon (Oncorhynchus nerka) in the Egegik and Ugashik management districts in Bristol Bay, Alaska (USA), for evidence of such temporally selective fishing. In recent years, the early migrants have experienced lower fishing rates than later migrants, especially in the Egegik district, and the median migration date of the fish escaping the fisheries has been getting progressively earlier in both districts. Moreover, the overall runs (catch and escapement) in the Egegik district and, to a lesser extent the Ugashik district, have been getting earlier, as predicted in response to the selection on timing. The trends in timing were not correlated with sea surface temperature in the region of the North Pacific Ocean where the salmon tend to concentrate, but the trends in the two districts were correlated with each other, indicating that there may be some common environmental influence in addition to the effect of selection. Despite the selection, both groups of salmon have remained productive. We hypothesize that this resilience may result from representation of all component populations among the early and late migrants, so that the fisheries have not eliminated entire populations, and from density-dependent processes that may have helped maintain the productivity of these salmon populations.

Key words: evolution; fisheries; migration; salmon; selection.

INTRODUCTION

The exploitation of living resources for human use (e.g., logging, hunting, fishing) inevitably alters such attributes of the species as density and age composition. In addition, long-term exposure of selective exploitation can have evolutionary effects. These selective effects have been studied with increasing intensity in the case of fisheries, though changes (e.g., reduced age at maturity) can also be affected by concurrent climate variation and changes in competition. Here we point out that fisheries can also be selective with respect to migratory timing, a highly heritable trait in salmonid fishes. As with age at maturity and growth, the detection of evolutionary change caused by temporally selective fishing is difficult to disentangle from environmental change. However, this potentially very important process merits further investigation.

The timing of breeding migrations is a critical life history event in the lives of animals. Adults store energy, leave feeding areas, and arrive at distant locations in time to acquire desirable breeding sites, compete for mates, reproduce, and, in many cases, care for offspring. The timing of breeding affects progeny fitness as well, so adult migration timing is a pivotal link between generations (Dingle 1996). The subject has been extensively studied in birds, where there is abundant evidence that the timing of arrival on breeding grounds affects reproductive success (Smith and Moore 2005). This apparently directional selection for earlier breeding is countered by other forms of selection such as weather patterns affecting adult survival (Brown and Brown 2000).

These issues are exemplified in anadromous salmon; these fishes migrate from feeding areas in the ocean to breeding sites that may be thousands of km away in an entirely different habitat. Conditions at sea are at most weakly correlated with those on the spawning grounds (in terms of density, predation, temperature, river flow, and so forth), so salmon migration timing is largely under genetic control. This is illustrated by the very regular, predictable sequence of migration and spawning by populations returning to discrete breeding areas (Killick 1955, Ricker 1972, Hodgson and Quinn 2002). The breeding date varies systematically among populations, consistent with the temperature regime that the embryos will experience during incubation (Brannon 1987, Webb and McLay 1996), so juveniles emerge to feed when local conditions are favorable. Controlled
experiments have demonstrated that the timing of migration and breeding are highly heritable in various species including rainbow trout, Oncorhynchus mykiss (Siitonen and Gall 1989), pink salmon, O. gorbuscha (Smoker et al. 1998), chinook salmon, O. tshawytscha (Quinn et al. 2000), and chum salmon, O. keta (Sato et al. 2000). There is some interannual variation in the timing of salmon arrival in coastal areas that is explained, in a statistical sense, by sea surface temperatures (Blackbourn 1987, Hodgson et al. 2006) and ocean currents (Thomson et al. 1994), and migration in rivers is affected by temperature and flow (Major and Mighell 1967, Gilhousen 1990, Quinn and Adams 1996, Hodgson et al. 2006). However, the timing of maturation and migration are under much less environmental control in salmon than in most teleost fishes (Quinn and Adams 1996).

Given the high heritability, it is not surprising that the timing of migration and reproduction in salmon responds quickly to selection. Spawning operations in hatcheries can deliberately (Crawford 1979) or inadvertently (Quinn et al. 2002) favor early returning salmon and shift the modal spawning date by weeks or months. This phenomenon is well known but the possible effects of selective fishing on migratory timing have been largely ignored. Salmon fisheries commonly take more than half the surviving adults before they spawn (Chapman 1986, Labelle et al. 1997, Hilborn et al. 2003), when natural mortality is otherwise generally low. If exploitation rates vary with date, fishing mortality could be a powerful form of selection, and might shift the population’s timing away from the period that evolved through natural selection.

There is great interest in the evolutionary effects of fishing, and this is a significant issue for conservation and sustainability of fish populations. Most research has examined the effects of selective fisheries on life history traits such as age and size at maturity (Handford et al. 1977, Ricker 1981, Policansky 1993, Conover and Munch 2002, Conover et al. 2005, Hutchings 2005), rather than migration timing. However, growth and age at maturity of fishes are strongly influenced by environmental factors such as temperature and prey availability. Indeed, fishing reduces competition and faster growth can result (Lorenzen and Enberg 2002). In salmon, the genetic influence on timing of migration and spawning is particularly strong, thus timing should be susceptible to the selective effects of fishing.

The sockeye salmon of Bristol Bay, Alaska were chosen for studying the potential effect of fisheries on run timing because (1) high-quality, long-term data were available, (2) the fishing is conducted only with one type of gear (gillnets) in spatially defined areas, (3) the populations are all wild, and so the effects of selective breeding in hatcheries (Quinn et al. 2002) do not complicate analyses, and (4) preliminary analysis indicated that fishing was selective with respect to return date. The fisheries are organized into five districts (Fig. 1). The managers try to ensure that the number of salmon needed to reach the system’s carrying capacity (i.e., the “escapement goal”) is achieved (Minard and Meacham 1987). The managers have pre-season forecasts of the expected abundance of salmon but the safest way to meet the escapement goal is to restrict fishing at the beginning of the migration period until it is clear that the goal will be met, at which time the fishing effort can increase to take advantage of the “surplus” salmon.

The Bristol Bay sockeye salmon fisheries are generally considered to be a model of sustainable management, and the overall productivity of the complex of populations depends on the persistence of the many distinct populations within each system (Hilborn et al. 2003). The purpose of this study was to quantitatively determine whether temporal selection has taken place, and whether the timing of migration has changed over time. We examined daily records from two of the five districts, Egegik and Ugashik, over a 35-yr period. The fisheries in each of these districts target salmon migrating to a single lake (Becharof and Ugashik lakes, respectively), and we assumed that detection of evolutionary change would be easier in these systems compared to ones with more complex geography and population structure (Fig. 1).

**Methods**

We first compiled data, provided by the Alaska Department of Fish and Game (ADFG), on the timing of catches in the commercial districts for each day that the fisheries were open, and the daily counts of salmon migrating upriver. These data allowed us to determine whether or not the fish escaping to spawn are migrating earlier than in the past years. We then sought to determine if the overall runs, including the catch, have been coming earlier. However, the salmon require several days to migrate from the locations where fishing takes place to the towers where they are counted (based on tagging studies and observations of modal arrival patterns). Therefore, one cannot simply combine the dates of capture in fisheries and the dates of passage upriver. Reconstruction of the true run timing requires estimation of the appropriate lag times, which may vary among years, as well as the proportions of the run that contribute to the catch and escapement in each year.

We omit a detailed description of the run reconstruction model (Flynn et al. 2006) for the sake of brevity but it was based on the following assumptions. (1) Fish arrive in the commercial fishing districts according to a normal distribution, modified by daily process error parameters (see Flynn et al. 2006: Eq. 1). (2) Residence time in the commercial fishing district is normally distributed, with outmigration probabilities calculated from a truncated normal distribution (see Flynn et al. 2006: Eq. 5). The mean of this distribution decreases linearly as the run progresses and the parameters of this linear function are estimated individually for each year (see Flynn et al. 2006: Eq. 4), and (3) in-river migration...
time is also normally distributed. Probabilities of passing the counting tower are calculated from a truncated normal distribution (see Flynn et al. 2006: Eq. 8), the mean of which is fixed according to estimates compiled by ADFG and is constant both between and within seasons. The standard deviation is also constant and fixed at 0.5 in both cases.

For graphical purposes, we divided the 35-year period (1969–2003) into five sets of seven years, and plotted both the average arrival to the fishery by date and the un-weighted average proportion of fish arriving on that date which were estimated by run reconstruction to have been caught (on that date or after time spent pooling) by the commercial fishery (Fig. 2). However, all analyses were conducted on the annual records. When the raw escapement and catch data were examined, we used the annual median dates rather than means because the openings and closures of the fisheries resulted in non-normal distributions of the data.

Warmer sea surface temperatures (SST) have been associated with earlier timing of sockeye salmon to Bristol Bay (Burgner 1980) and elsewhere (Blackbourn 1987), and recent SST have tended to be warmer than those in the past (Hodgson et al. 2006). Temperature might affect run timing by various mechanisms, including effects on the feeding distribution prior to homeward migration (Blackbourn 1987), through connections to the onset of maturation, and by altering swimming speed, hence the rate of travel from feeding areas (see discussion in Flynn and Hilborn 2004). To account for possible correlation between ocean temperatures and sockeye salmon timing, we obtained monthly mean SST from 1969 to 2002 (2003 data were not available) by combining data from two sources. Empirical orthogonal functions of monthly SST (Smith et al. 1996), based on the Comprehensive Ocean-Atmospheric Data Set (Slutz et al. 1985), were used for the 1969–1981 period. For the subsequent period, data consisting of optimally interpolated SST data from ships, buoys, and satellites were used (Reynolds and Smith 1994). Steven Hare (International Pacific Halibut Commission, Seattle, Washington, USA) provided these data, averaged over a 2° latitude by 2° longitude grid to match the grid used by (Smith et al. (1996), and updated through 2002. Anomalies from the 1969–2002 mean SST were calculated for each grid area and each month.

During the winter at sea, Bristol Bay sockeye separate into immature and maturing groups. The maturing fish migrate towards to Bristol Bay in the spring, and most enter the Bering Sea through passes in the Aleutian

![Map of Bristol Bay, Alaska, USA, showing the five commercial fishing districts (in black) and the major rivers mentioned in the text: (1) Togiak, (2) Wood, (3) Nushagak, (4) Kvichak, (5) Naknek, (6) Egegik, and (7) Ugashik. Stars indicate the locations where the salmon migrating into to the Egegik and Ugashik systems are counted. The map was produced with the aid of software developed by Wessel and Smith (1991).](attachment://map.png)
Island chain (French and Bakkala 1974). Records of sockeye salmon tagged at sea in June (Myers et al. 1996) indicated that 67% of the salmon that returned to Bristol Bay had been tagged in the ocean area 52°–56° N and 152°–176° W. We therefore averaged SST anomalies from this area to create an index of SST for comparison to run timing. SST data from June were used rather than other months because the migration occurs in late June and early July, and June data showed the highest correlations to Bristol Bay run timing.

RESULTS AND DISCUSSION

The observed median dates of upstream migration by salmon that escaped the fisheries became earlier from 1969 to 2003 in both the Ugashik ($r^2 = 0.115, P < 0.05$) and Egegik districts ($r^2 = 0.362, P < 0.001$; Fig. 3). These trends could have resulted from a change in the overall migration pattern or merely a greater tendency in recent years to catch fish at the end of the run. Analysis of the reconstructed total runs (catch and escapement) revealed
that (1) the fishing rates have varied over the course of
the migration period, (2) the patterns of selection
differed between the two districts, and (3) the patterns
changed over the decades (Fig. 2). Over the 35-year
period (about six or seven generations), sockeye salmon
in the Egegik district experienced selection that tended
to be stabilizing in the early years (higher mortality on
both early and late fish than those with intermediate
timing) but it became progressively more directional
since then. In the most recent period, the probability of
being caught for a fish reaching the fishery on each day
increased dramatically during the season (Fig. 2).
Sockeye salmon in the Ugashik district also experienced
stabilizing selection in the early period, followed by less
regular patterns, and a tri-modal pattern in the most
recent years, with heaviest fishing at the beginning,
middle, and end of the run, with less intensive fishing
during the two intermediate parts (Fig. 2). These
complex patterns of selection may explain, in part, the
low regression coefficients for simple linear models.

To estimate the changes in selection more quantita-
tively, we compared the median of the reconstructed
overall run timing with the median escapement date for
each year in each district. There was a significant slope
over the years for the Egegik district ($r^2 = 0.23$, $P =
0.003$), indicating that the escapement has been coming
from a progressively earlier part of the run over time.
However, there was no significant slope in the Ugashik
data ($r^2 = 0.001$), though there was considerable
variation among years. Further analysis of the strength
of selection in the two districts was conducted by
dividing the runs into three periods of equal length (in
days) and comparing the average daily harvest rate in

![Fig. 2. Continued.](image)

![Fig. 3. Temporal trends in median date of escapement by sockeye salmon in the Egegik and Ugashik districts of Bristol Bay, Alaska, from 1969 to 2003. Day 1 of the year is 1 January.](image)
the first one-third of the run (Egegik, 10–26 June; Ugashik, 10–27 June) to that in the final one-third of the run in each year (Egegik, 15–31 July; Ugashik, 17 July–3 August). In the Egegik district, there was a significant increase in the harvest rate at the end, relative to that in the beginning ($r^2 = 0.25$, $P = 0.002$; Fig. 4) whereas, in the Ugashik district, there was no trend over the 35 years in the average harvest rate in the late period compared to the early period in each year ($r^2 = 0.02$).

Not only have the median escapement dates become earlier in both districts over the years (by about 10 days since the late 1960s in Egegik) but the runs as a whole have gotten earlier (Fig. 5). This change has more pronounced in the Egegik district ($r^2 = 0.176$, $P = 0.012$) than the Ugashik district ($r^2 = 0.104$, $P = 0.058$). These trends are consistent with a genetic change induced by temporally selective fisheries but other possible explanations must be considered. There was no significant correlation between run timing and surface water temperatures in the region of the ocean occupied by these salmon, so the trend towards earlier timing was not simply caused by changing thermal regimes at sea (Egegik, $r^2 = 0.04$, $P = 0.23$; Ugashik, $r^2 = 0.04$, $P = 0.28$). Multiple regression analyses using year and SST as factors confirmed the results of simple regression. For Egegik, the combined model was significant ($P = 0.033$) but year was responsible for the relationship ($P = 0.021$) rather than SST ($P = 0.639$). The combined model for Ugashik was not significant but, as with Egegik, the association was stronger for year than SST.

The absence of relationship between SST and run timing contrasts with an earlier report that early runs to Bristol Bay were associated with warm spring temperatures (Burgner 1980). However, his analyses were based on a shorter period of record than ours and the results were influenced by a few extreme values. A subsequent report relating SST to run timing for other sockeye salmon populations (Blackbourn 1987) did not select ocean regions and months a priori based on the known distribution of salmon but rather selected periods of time and regions that generated the highest correlations. This approach, and the absence of correction for multiple comparisons, tended to inflate the strength of the relationships between timing and SST.

There may be some relationship between SST and adult salmon migratory timing but it did not appear to cause the patterns observed here. However, the apparent absence of correlation between run timing and SST does not mean that there is no environmental influence on timing, and there are many possible correlates (currents, salinity, prey, and so forth). Rather than regress run timing against other variables, we elected to simply see if the reconstructed run timing patterns in the two districts were correlated, and they were ($R = 0.59$, $P < 0.01$). This correlation might merely result from the fact that the
runs were getting earlier in both districts over the same time period rather than from a true connection between the two runs. We therefore removed the effect of year by taking the difference between the median date in one year and the next for each district, and examining the two series of differences for a correlation (Quinn et al. 2006). Despite the absence of a year effect, the two series were still significantly correlated \( R = 0.61, P < 0.01 \). This is consistent with other evidence of correlated timing of sockeye salmon runs even in the absence of significant correlations with SST (Hodgson et al. 2006).

The indication that some environmental factor influences the two runs, however, does not mean that there cannot also be an effect of the fishery. Without a better understanding of the environmental factor(s) involved it is not possible to disentangle the underlying effects of selection and the environment.

Finally, we note that the salmon experienced some fishing pressure outside the districts where they were recorded, both from other districts within Bristol Bay and along their migration route prior to entering the bay, and trends in those interceptions could create or mask trends in timing. Significant interception outside of Bristol Bay only occurs south of the Alaska Peninsula and these catches are capped at a maximum of 8% of the Bristol Bay run, so there is little likelihood that those fisheries biased our estimates of run timing. The sockeye salmon populations are initially mixed as they approach and enter Bristol Bay but become increasingly segregated as they reach the fishing districts (Straty 1975, Flynn et al. 2003). Tagging studies showed that homeward migrating fish move among districts (Straty 1975) so some interceptions undoubtedly occur. For them to cause the trend towards earlier run timing, the interceptions would need to have been both important numerically and shifting in timing. The lack of quantitative data on interceptions makes it impossible to discount this possibility but the most striking trend towards earlier timing in Egegik does not have an obvious basis in interceptions (e.g., increased catches of early fish bound for other districts, reduced interception of later fish from other districts, greater interception of late Egegik fish elsewhere, and so on).

The absolute change in run timing, about four days, was slight but these runs are so compressed and otherwise vary so little in timing from year to year that this change in significant. Moreover, because the selection on timing at Egegik (Fig. 4) has been strongest in recent years, we would not expect a linear trend in run timing, and inspection of the data (Fig. 5) indicates that most of the change has happened recently. Finally, the salmon are four to six years old at maturity so the effects of strong selection in the most recent years have not yet been seen in the return timing of their progeny.

The implications of temporally selective fishing for the sustainability of the populations depend on interactions between the timing of migration and breeding. Bristol Bay sockeye salmon populations show very compressed migratory timing, compared to Pacific salmon in general and sockeye salmon elsewhere. About 80% of the salmon pass the fisheries or are caught in about two weeks (e.g., Fig. 2), but breeding takes place from late July into September, depending on the hydrology and thermal regimes at the breeding sites (Hilborn et al. 2003). If each district includes populations with discrete timing of migration and spawning, as is the case for sockeye salmon population complexes elsewhere such as the Fraser River, British Columbia (Killick 1955), Karluk Lake, Alaska (Gard et al. 1987), and Bear Lake, Alaska (Boatright et al. 2004), then late migrating populations might be fished at excessive levels. The result could be a trend towards earlier migration as a whole because the early populations would become numerically dominant. This scenario is plausible, though studies of other Bristol Bay population complexes suggest that all populations enter fresh water with similar timing, regardless of their spawning location and date (Smith 1964, Rowe 1985, Jensen and Mathisen 1987). It is not clear why the entry patterns are synchronous rather than sequential in some systems but the consequence is that heavy exploitation of late-migrating fish would probably not eliminate or greatly reduce late-spawning populations.

Alternatively, it is possible that within each population, early arriving individuals tend to spawn earlier, and so the fisheries might be selecting for early spawning within rather than between populations. This fishery selection would be resisted by natural selection. Early arriving salmon would experience high levels of competition on the breeding grounds, decreasing their fitness relative to that of salmon returning later. Moreover, fish breeding too early would produce progeny emerging before the increase in food availability and mild temperatures the next spring (Schindler et al. 2005), and this would opposes the directional selection within populations.

The total runs of sockeye salmon have been much higher recently than in the past (Egegik, average = 4.488 million from 1980–2005 vs. 0.994 million from 1955–1979; Ugashik, 1.925 million from 1980–2005 vs. 0.388 million from 1955–1979). These increases in abundance have come despite very high fishing rates in the recent years (average = 67% in the Ugashik and 82% in the Egegik districts [Hilborn et al. 2003]; updated with ADFG data). Thus, there is presently no evidence that the fishing has reduced the fitness of the population complexes. Nevertheless, migration is a key element in the life history of salmon populations, and the unusually compressed, apparently synchronous timing of Bristol Bay populations has been taken for granted but never explained. If changing environmental conditions and selective fisheries destabilize this behavior pattern, unexpected consequences might result.

In conclusion, we believe that examination will reveal many fisheries for anadromous salmonids with strong temporal biases, so the effects of selection may be
widespread. Indeed, this is likely to be the case for fisheries in general. Many fisheries exploit migratory species, both because these species tend to be abundant and because the essential features of migration (coordination of movements in space and time) greatly increase capture efficiency. Temporal closures are a traditional form of fisheries management (Rounsefell 1975), and the examples range from lingcod, Ophiodon elongatus: closed in Washington State waters from October 15 to March 16 (Washington Department of Fish and Wildlife, general marine regulations, 2006) to striped bass, Lutjanus carponotatus: proposed closures on the Great Barrier Reef during the nine day periods around the new moon in October, November and December (Kritzer 2004). In other cases (e.g., blue sharks, Prionace glauca), differences in migration pattern and timing can cause differences in exploitation rate as a function of sex and maturity state (Campana et al. 2006). Thus depending on the nature of the fishery and the management approach, some degree of selection with respect to timing of migration or breeding is likely to occur in many instances. The balance between genetic and environmental control of migration and breeding timing may vary among fishes, and instances of shifting migration timing such as Atlantic cod, Gadus morhua, (Comeau et al. 2002) may have an entirely environmental basis. Nevertheless, selective fishing can exert strong pressure on the population if the trait has a genetic basis, and this possibility merits consideration.

ACKNOWLEDGMENTS

We thank the Alaska Department of Fish and Game for access to their data; the Pacific Seafood Processors Association, the Washington Sea Grant Industrial Fellowship Program, the National Science Foundation’s Long Term Research in Environmental Biology and BioComplexity programs, and the Gordon and Betty Moore Foundation for financial support; and Robert Francis for assistance with the analyses.

LITERATURE CITED

Blackbourn, D. J. 1987. Sea surface temperature and pre-season prediction of return timing in Fraser River sockeye salmon (Oncorhynchus nerka). Canadian Special Publication of Fisheries and Aquatic Sciences 96:296–306.


