A MODELING INVESTIGATION OF MIGRATORY BEHAVIOR IN FISHES
A CASE STUDY WITH SOCKEYE SALMON

by

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Abstract

This thesis is composed of two separate spatially-explicit state-space dynamic models developed with the general objective of contributing to the understanding of migratory behavior in fish. The first model focuses on the behavior of mature adults during their reproductive migration, while the second focuses on the migratory tactics of fish during their migration cycle. Both models were applied to the marine migration of sockeye salmon (*Oncorhynchus nerka*) from the Fraser River.

The first model is based on the hypothesis that the migratory behavior of returning individuals arises as an adaptive response to minimize a measure of the total costs of migration, given an expectation of the state of the environment during the migration (defined in terms of currents, temperature, and risk of predation). The model predicts that the higher swimming speed observed when sockeye salmon reaches the coast, and the use of the Juan de Fuca as the primary route to reach the Fraser River, are likely a response to a higher risk of mortality in the coast. The model also indicates that given the short arrival time of individuals from the same race, they either start their migration from a short longitudinal range, or are distributed across a wider range and start their migration at different times, with individuals further away from the Fraser River starting earlier. Predicted swimming speed and orientation resulted very sensitive to the spatial distribution and value of predation risk. This model could not predict the oceanic migration route and the latitude of landfall of Fraser River sockeye. I concluded that the spatial distribution of mortality was not properly represented, or that the tradeoff used to define the model was not adequate.

The second model is based on the hypothesis that juvenile fish have a tradeoff between foraging activity and migration activity. The model was able to predict the following characteristics for sockeye salmon from the Fraser River: 1) Juveniles migrate along the coast and then move into the Alaska Gyre where they stay the rest of their oceanic residence. Model predictions do not support the commonly held hypothesis of an annual circuit around the Alaska Gyre. 2) The juvenile migration arises as a response to high zooplankton density in the coast at the time of the migration, although the high risk of mortality there creates a bottleneck in their life cycle. 3) The model predicts a seasonal growth pattern as a response to the seasonality of zooplankton density. 4) Juvenile fish display higher swimming migration activity than adults. 5) Individuals behaving optimally distribute below the observed thermal limits, however their distribution follows that of prey density. 6) The size-dependency of mortality observed during the smolt-to-adult phase likely arises from smaller individuals taking longer to swim through the coast.

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CHAPTER 1
MIGRATION IN FISH POPULATIONS

1.1 General Introduction

Movement patterns in animals occur across a wide range of spatial and temporal scales, ranging from the dashes of sculpins across a tide pool to continuous trans-oceanic movement of tuna (Quinn and Brodeur, 1991). Quinn and Brodeur classified patterns of movement into three arbitrary categories: 1) migration: movements of individuals coordinated in space and time; 2) dispersal/nomadism: undirected movement beyond the natal area or home range (nomadism differs from dispersal in that nomadic individuals wander continuously whereas dispersants eventually establish a home range); and 3) home range: staying within a well defined area for most of the routine activities during the life of the individual.

Migratory movements also occur across a broad spectrum of scales (reviewed in Quinn and Dittman, 1992). These movements range from the short daily feeding migrations of hammerhead sharks (*Sphyrna lewini*), juvenile sockeye salmon (*Oncorhynchus nerka*), and juvenile plaice (*Pleuronectes platessa*) to the long once-in-a-lifetime spawning migration of sockeye salmon (*O. nerka*) and Atlantic eel (*Anguilla anguilla*) (Burgner, 1991; Burrows, 1994; Clark and Levy, 1988; Harden-Jones, 1968; Klimley et al., 1988). My research interest here is on ontogenic migratory patterns which display the following four basic characteristics (Baker, 1978; Dingle, 1980; McDowall, 1997; Quinn and Leggett, 1987):

1) Closed loop cycle. The migratory cycle includes a return movement to the area of origin.

2) Synchronized migratory behavior. The initiation and cessation of the migratory movement is synchronized across the fraction of the population engaged in migration, and the migrants show a narrow range of variation in the direction of the movement.

3) Spatial and temporal predictability. Migratory individuals arrive to predictable locations at predictable times of the year.

4) Associated to ontogeny. The movement occurs at specific stages of development.

Typical examples of this type of migration are the pacific hake population (*Merluccius productus*) (Bailey et al., 1982), the Atlanto-scandian herring (*Clupea harengus*), Arcto-norwegian cod (*Gadus morua*), and Alaska pollock (*Theragra chalcogramma*) (in Harden-Jones, 1981), American shad (*Alosa sapidissima*) (Dadswell et al., 1987), North Sea plaice (*Pleuronectes platessa*) (Arnold, 1981), Gulf of California sardine (*Sardinops sagax*) (Sokolov, 1974), and several species of Pacific salmon (genus *Oncorhynchus*) (Groot and Margolis, 1991).

The evolution of migratory behavior in fishes is considered to be primarily driven by selection for more efficient feeding and growth or improved survival resulting from accessing seasonal changes in resources in other areas (Dingle, 1980; Gross, 1987; Gross et al., 1988; Harden-Jones, 1968; McDowall, 1997). Some evidence for this view came from the latitudinal distribution of diadromous species found by McDowall (1987) and its link to the differential availability of food between freshwater and saltwater (Gross et al., 1988). Anadromous species (fishes that migrate to freshwater to spawn) are more frequently found at higher latitudes (both north and south) where productivity is higher in the marine environment that in freshwater. Catadromous species (those that migrate to saltwater to spawn) are more common at lower latitudes where productivity is higher in freshwater than in saltwater.

Migratory behavior also has a strong relationship to primary life history traits like growth pattern, size and age at first maturity, and number and size of offspring (Dingle, 1980). Individuals from migratory species are typically larger that those who do not migrate, have delayed maturation, mature at larger sizes, grow faster, and (as a result of the larger body sizes) have higher fecundity (Roff, 1988). All these differences and the ability of migrants to access resources in other areas have resulted in quite successful populations. Migratory populations are notably abundant and have sustained some of the most productive fisheries in the world. The population of pacific hake (*Merluccius productus*) migrating along the US

west coast is the most abundant fish species caught in the area since 1966 (Methot and Dorn, 1995). The nine top species of fish in the world catch in 1977 were migratory species (Harden-Jones, 1981), and nearly 80% of the landings in the Atlantic and Gulf coast of USA consist of species that spawn in the ocean and have an estuarine phase during the early stages of development (Miller et al., 1985).

However, the movement of migrants through a sequence of distinct areas makes them susceptible to disturbances in each of those areas. Furthermore, migratory behavior often results in dense aggregation points along the migration route, which renders migrants highly vulnerable to exploitation and to any change in those environments. For instance, sockeye salmon (*O. nerka*) populations from the Fraser River become extremely vulnerable to fishing as they approach the river. Furthermore, a rockslide in Hell's Gate in 1913, a narrow reach 140 miles upstream from the mouth of the river, combined with the effects of fishing resulted in a near collapse of the races that spawn upriver from that point. It took several decades for these populations to recover (Foerster, 1968; Ricker, 1987).

In some instances the migration route occurs across more than one management jurisdiction, which often turns the management of the fishery into a political issue rather than into a conservation issue (Brower and Malcom, 1991). In the last decade the province of British Columbia had a major conflict with the states of Alaska and Washington about the fishing rights on British Columbia salmon stocks migrating along US shores. This problem is not confined to fish species; it has been documented for a wide range of animals, from butterflies in North America to large ungulates in Africa (Brower and Malcom, 1991). Overexploitation, habitat modification, and the crossing of political boundaries make the future of migratory species uncertain as a result of the very strategy that made them successful in the first place. Furthermore, as the effects of global warming become more apparent, the need for sound mitigation measures beyond mere harvest management will only increase.

A critical part of the solution to management and conservation of migratory species will have to come from a better understanding of the phenomenon of migration. However, the large spatial and temporal scales at which ontogenic migrations occur has resulted in

descriptive and fragmented research (Dingle and Gauthreaux, 1991), that has been unable to provide a framework with prediction capabilities to test hypotheses about the mechanisms that may be driving migratory behavior (e.g. Groot and Margolis, 1991). The optimality perspective of the theory of evolution may provide an objective framework for predicting migratory behavior, by viewing it as a life history strategy to maximize the reproductive fitness of an individual (Baker, 1978). This fitness-based perspective suggests that individuals should be expected to move to another area when the fitness value obtained there is larger than that of staying (Baker, 1978; Lomnicki, 1980).

The optimality perspective poses the challenges of measuring fitness and of quantifying the costs and benefits of migrating and the effects that environmental conditions along the migration route may have on fitness through the explicit representation of the tradeoffs among the components of fitness that are inherent to migratory behavior. For instance, the swimming activity required for migration likely comes at the expense of higher encounter rates with predators (Abrams, 1990; Abrams, 1991; Werner and Anholt, 1993), which has been shown to generate a strong risk averse behavior on the prey after the occurrence of an encounter (Abrahams, 1986; Abrahams and Dill, 1989). Such risk may have driven selection for the co-occurrence of schooling behavior along with migratory behavior in marine fishes (Roff, 1988). Schooling behavior is thought to reduce the risk of predation, although it increases competition for prey items (Pitcher and Parrish, 1993). Furthermore, the time allocated to migration likely reduces the time available for foraging, thus creating another tradeoff for migratory behavior.

Another common tradeoff for migratory fish is the high cost of the swimming activity during migration that could otherwise be allocated to growth and fecundity. This tradeoff has led to the prediction that migratory fish should swim with a high degree of orientation in a bioenergetically efficient manner. Optimal swimming speeds and highly orientated swimming activity in the appropriate direction should maximize the allocation of energy into reproduction rather than into movement, and reduce the risk of death by exhaustion during migration (Bernatchez and Dodson, 1987; Roff, 1991; Weihs, 1973; Weihs, 1987; Weihs and Webb, 1983). Furthermore, it has also been proposed that migratory fish should use

predictable advection patterns (currents) to reduce the cost of swimming, and as a mean to transport early life stages toward nursery areas (Arnold, 1981; Fortier and Leggett, 1982; Harden-Jones, 1981; Harden-Jones et al., 1978; Kasai et al., 1992; Miller et al., 1985; Parrish et al., 1981; Trump and Leggett, 1980).

One of the few methods capable of representing the factors that determine the reproductive fitness of an individual within a framework where it is possible explicitly to define relevant trade-offs among those factors and to make specific predictions about behavioral patterns that should result from selection to maximize fitness, is state space dynamic programming (see Tyler and Rose (1994) and Giske et al. (1998) for a review of spatially-explicit modeling of fish dynamics). This methodology provides a straightforward way to represent the link between individual growth, mortality, and fecundity through a single measurement of fitness (Mangel and Clark, 1986; Mangel and Clark, 1988), provides a framework to quantify the long-term consequences of short-term behaviors (e.g. foraging behavior, predator avoidance, swimming behavior), and yield testable predictions about specific behavior and life history phenomena (Clark, 1992; Clark, 1993). State space dynamic programming has been used to gain insight about a wide variety of evolutionary problems, ranging from the factors determining the vertical migration of juvenile sockeye salmon (Clark and Levy, 1988) and juvenile plaice (Burrows, 1994) to the potential impact of climate change on the life history of salmonids (Mangel, 1994).

1.2 Objectives

My research focused on two questions: 1) how should a mature/maturing individual move from the feeding grounds to the spawning grounds to maximize reproductive output, given a defined environmental configuration and a time-fixed environmental window for reproduction? 2) what migratory route and behavior would maximize the fitness of time-constrained juvenile individuals during their lifetime prior to spawning migration, given a set of environmental conditions?

Both questions are framed within the general principle of evolution stating that the primary drive of individuals is to survive and reproduce and that natural selection favors those traits that increase the fitness of individuals (Houston et al., 1988; Mangel and Clark, 1988). Migratory behavior is thus considered as a fitness maximizing behavior evolved as a response by time-constrained individuals to take advantage of predictable changes in the temporal and spatial distribution of environmental conditions, resources, and risks. Both questions were considered as state-dependent optimization problems, and as such the state space dynamic programming modeling method was used as described in Mangel and Clark (1988).

I selected sockeye salmon from the Fraser River (*Oncorhynchus nerka*) as the subject of this study, since sockeye salmon is a classical example of a migratory fish with an extremely long migratory circuit spanning several thousand kilometers. I also had the perception that there was a fair amount of information about the life history of this species and its environment, which would make this exercise simpler by removing problems associated with knowledge gaps. However, this proved not to be the case.

This thesis is structured as five chapters and an appendix. Chapter 2 provides a description of the life cycle of sockeye salmon, in as much detail as published data allow. In Chapter 3 I present a model for the estimation of optimal return routes for reproductive migrations constrained by environmental conditions, and its application to the sockeye salmon return migration. Chapter 4 presents a model for the estimation of optimal juvenile behavior of a migratory species, and its application to sockeye salmon. Chapter 5 contains the general conclusions of the results from Ch. 3 and 4, and some thoughts about possible ways to improve the predictive capabilities of both models. Finally, Appendix A contains an application of the 'Wisconsin model' to the bioenergetics of sockeye salmon; the structure of this model provides a direct and straightforward link between environment, behavior, growth, and reproductive output in fishes, and is a central building block for the models presented in Chapters 3 and 4.

CHAPTER 2

THE LIFE HISTORY OF SOCKEYE SALMON

2.1 Introduction

This chapter provides a description of the life history of sockeye salmon. The biology described is only that related to the models in Chapter 3 and 4 of this document. No attempt was done to document information on kokanee, a type of sockeye that do not migrate to the ocean. Whenever possible the information is for the sockeye salmon of the Fraser River.

Sockeye salmon (*Oncorhynchus nerka*) is distributed on both sides of the North Pacific Ocean. The main sockeye-bearing watersheds in the Canadian and American Northwest are the Fraser River drainage and the Bristol Bay region, generating more than 50% of the sockeye salmon production in North America (Burgner, 1991). Several other watersheds like the Nass-Skeena River, Somass River, and Rivers Inlet are or historically were also important for sockeye production.

Sockeye salmon is a semelparous species that uses up to five distinct habitats (natal stream, lake, river, coast, open ocean) during its life cycle. Adults return from the feeding grounds in the Northeast Pacific to spawn in their natal stream. Newly emerged fry migrate into nearby nursery lakes where they stay one or more years before smolting and initiating their migration to the ocean.

The freshwater and marine residence time of individuals varies considerably between populations and within some populations. Freshwater residence can vary from a few weeks to three years, while residence time in the ocean can vary from one to four years (Burgner, 1991). In the Fraser River, the dominant age group in females is 1.2 (1 year of lake residence and 2 years of marine residence), and contributes with an average of 88% of the age structure

(Healey, 1987). The second age group in importance is the 1.3 age group, with a contribution of 9% (average) to the age structure.

2.2　The Ocean Phase of the Reproductive Migration

Sockeye salmon start their spawning migration from feeding grounds in the Alaska Gyre (Fig. 2.1). Mature fish migrate towards the shore during the spring and summer months (French et al., 1976) and reach the natal river during the summer and fall (see Table 2.1) (Burgner, 1991).

The open ocean leg of the migration of maturing salmon is perceived as a rapid, well directed, and well-timed event (Burgner, 1991; French et al., 1976; Groot and Quinn, 1987; Royce et al., 1968). Early tagging studies showed that the swimming speed of the fish increases as the season progresses (Hartt, 1966). Tagged fish recovered while still on the high seas swam at an average rate of ~39 km per day, while those in their last 20 – 50 days at sea averaged 44 – 55 km/day for distances between 700 and 1,800 km (Hartt, 1966). Ultrasonic tagging studies off the British Columbia coast by Madison et al. (1972) and Quinn et al. (1989) confirmed these speeds, with an average of 46 km/d and 57 km/d respectively (nearly 1 body length per second in both cases), although they also observed that sockeye has a broad range of swimming speeds, from 8 to 140 km per day. Quinn (1988) also found a bipolar orientation in the swimming direction along the main axis of the coastline, and Madison et al. (1972) measured higher swimming speed during the day than those at night, and a change in the mean swimming speed from 0.83 body lengths per second during 1969 to 1.11 during 1970.

Race-specific migration routes are not known, however Groot and Quinn (1987) proposed a metapopulation migration pattern for the British Columbia and Washington races from tagging data pooled from 1958 to 1983 (Figure 2.1). This pattern shows that maturing individuals move northeastward in May and June, then southeastward along the Alaska panhandle and the Charlotte Islands towards Vancouver Island in July and August. Sockeye usually reach the coast at some point along the coast of the Queen Charlotte Islands and the northern tip of Vancouver Island, depending on environmental conditions prior to or during

the oceanic phase of the migration (Blackbourn, 1987; Groot and Quinn, 1987; Healey and Groot, 1987; Thomson et al., 1992). Sockeye salmon arrive to the mouth of the Fraser River and make river entry from early July to early October (Burgner, 1991).

Sockeye are known to reduce their swimming speed once they make landfall, and swim into deeper waters, with sudden dives and ascents, as they approach the mouth of the river (Quinn et al., 1989). There is no established explanation for this behavior; it may well be a response to an increasing allocation of time for orientation and navigation in the complex coastline, a response to predation risk, or a way to adjust physiology for the freshwater environment. The physiological changes required to enter the river may imply a cost in terms of time, metabolic energy, and survival. However to my knowledge the nature of this change and its costs are not known but presumed very low since tolerance increases with size and the returning migrants are large individuals. Furthermore, the genus *Oncorhynchus* is considered the most tolerant to changes in salinity of the subfamily salmoninae (Houston, 1961; McCormick and Saunders, 1987).
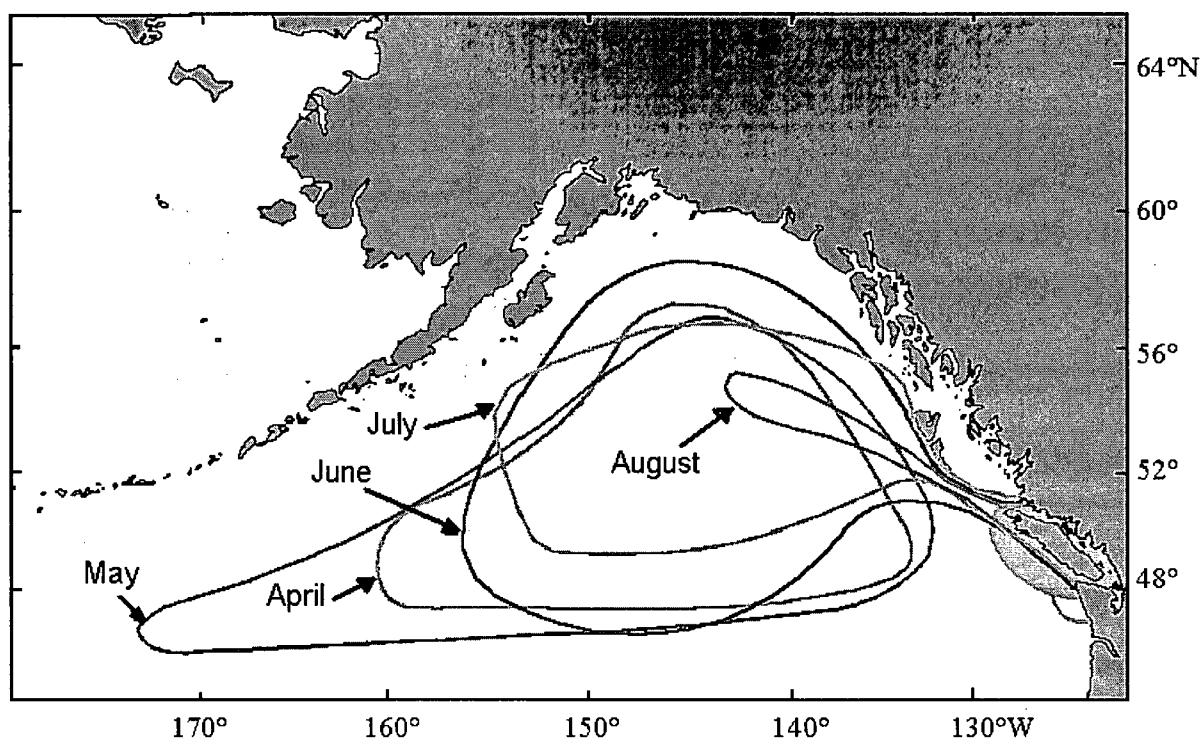
Figure 2.1. Monthly distribution of mature sockeye salmon returning to spawn in the Southern part of British Columbia and Northern part of Washington (marked in light grey).

Each race had a characteristic mean arrival date at the river mouth and spawning grounds prior to the 1990s (see Table 2.1), although apparent timing anomalies of earlier arrival times (in the order of weeks) have been observed in the last decade (C. J. Walters, UBC, Fisheries Centre, pers. comm.). The races from the Fraser River showed less than 1 week of interannual variation for the peak day of arrival (Blackbourn, 1987) while those from Bristol Bay showed two weeks (Burgner, 1991). Individuals from the same race arrive to the spawning grounds in a very short period, usually within 12 days (Gilhousen, 1960). There is no direct evidence on the mechanism(s) or cue(s) that trigger the onset of the return migration and create such precise synchronization in the arrival date. However, photoperiod is often argued to be the cue, because of its inherent precision and invariance to environmental conditions (Gilhousen, 1960).

Table 2.1. Upriver migration characteristics for 15 stocks of the Fraser River (from Gilhousen, 1980; Gilhousen, 1990; Idler and Clemens, 1959). Values in italic are average elevation values from the B. C. watershed database.

Race	River entry	Distance (km)	Elevation (m)	Spawning date
Early Stuart	July 8	1,152	687	August 5
Gates	July 23	600	*361*	August 30
Bowron	July 24	1,064	945	August 27
Pitt	July 27	97	near sea level	September 15
Seymour	August 3	483	347	August 30
Raft	August 3	820	*1,071*	September 1
Late Stuart	August 3	1,152	678	September 17
Horsefly	August 4	805	762	September 1
Chilko	August 6	596	1,172	September 25
Stellako	August 8	965	640	September 27
Birkenhead	August 18	425	*1,146*	September 25
Weaver	September	120	20	October 20
Adams	September	483	366	October 20
Harrison Rapids	October 1	129	10	November 15
Cultus	October 1	88	41	November 24

Several authors have hypothesized that the tight arrival pattern within a stock reflects the existence of a narrow optimal environmental "window" for the survival of the offspring in

the natal stream and nursery lake during early ontogenic stages (Burgner, 1991; Gilhousen, 1960; Quinn and Adams, 1996; Royal, 1953). Variation in spawning time among stocks results from an adaptation of each stock to the specific temperature regime and food production found in the natal stream and rearing lake. Miller and Brannon (1982) and Brannon (1987) suggested that this adaptation compensates for the effect of temperature on the developmental time of the embryo, and allows the fry to emerge during the spring production peak in the nursery lake.

Although interannual variation in arrival date for the races of salmon is small, there are evident management advantages in the accurate prediction of such dates. Uncertainty of even one week about peak arrival date can severely affect planning for fishery openings, and degrade the performance of in-season stock size assessments based on methods such as correlating run size with peak-week catches (Henderson et al., 1987; Woodey, 1987). Temperature has been the preferred explanatory variable to account for interannual variation, because of its effects on the physiology of fish. Gilhousen (1960) suggested that such variation may come from the effects of temperature on gonad development, or on the swimming speed of the fish. The effect that currents may have on the movement of the fish, by deflection of trajectory or increasing/decreasing ground speed, has also been proposed as a mechanism to explain interannual changes in the arrival date (Hamilton and Mysak, 1986; Thomson et al., 1992).

Blackbourn (1987) developed a simple hypothesis to explain variability in the arrival date of sockeye salmon in the Northeast Pacific. Sockeye salmon are thought to have upper thermal limits in their oceanic distribution (French et al., 1976; Welch et al., 1995; Welch et al., 1998). Blackbourn assumed that each stock of sockeye salmon has an optimal, not necessarily exclusive, area of distribution in the Northeast pacific where individuals stay within a narrow and stock-specific range of temperature within that area. Such areas presumably shift North or South with interannual variation in sea surface temperature. This shift would change the distance from the feeding grounds during the spring (prior to migration) to the river of origin, and with it the arrival date. During cold years salmon would be distributed South of their usual ranges, and would arrive earlier because of a decreased distance for the Fraser River salmon (but later for Alaska salmon). In warm years salmon

would distribute farther North and arrive later in the season for Fraser salmon and earlier for Alaska salmon. There is no direct evidence to substantiate this hypothesis, however Blackbourn (1987) and Quinn (1990) reported a correlation between temperature and arrival date consistent with this hypothesis for the Chilko River race (in the Fraser watershed) and the Naknek-Kvichak Rivers races in Alaska. This correlation broke down with data gathered since 1987 (M. Healey, UBC Fisheries Centre, Pers. Comm.)

Returning individuals seem to forage during the migration, although this is a contentious issue. Ricker (1962) found that sockeye caught in inside waters often have full stomachs, and Gilbert (1913) (in Gilhousen, 1980) indicates that Fraser river sockeye captured by the fishing fleet around Vancouver Island have food items in their stomach. On the other hand, high seas tagging studies have shown returning sockeye salmon traveling at 40-60 km/day for several weeks (Hartt, 1966). Those results led Quinn and Groot (1984) to propose that returning adults must swim continuously at nearly 1 body length per second with a high degree of directionality to achieve those distances, leaving nearly no time for the search and handling of prey associated with foraging. However by the time they enter the river, feeding ceases and the energy costs associated with gonad development, upriver migration, and spawning related activity are covered with stored energy reserves.

Fraser sockeye caught by the commercial fishery (mainly age 1.2) have a weight ranging from 2.1 to 2.8 kg (Gilhousen, 1980; Idler and Clemens, 1959), an average body length of 60 cm from tip of snout to fork of tail (Killick and Clemens, 1963), and energy density of 7.56 kJ/g wet weight (see Appendix A, and Brett, 1980). At Albion (64 km upriver from the mouth of the Fraser River) the body composition of a 2,531 g sockeye from the Stuart race was found to be 13% fat and 19 % protein; by the time they reached places like Forfar Creek (1,152 km upriver from the Fraser River mouth) to spawn, weight decreased to 1,976 g and body composition was 1% fat and 10% protein (gonads excluded Gilhousen, 1980). Rand and Hinch (1998) estimated that of the total energy used during the upriver migration, 84% is used for activity, 8.4 % is allocated to gonad development, and the remaining 7% to basal metabolism.

2.3 The Upriver Migration

Energy expenditures during upriver migration vary depending on the conditions of the reach of the river the fish is swimming, and the race to which the individual belongs. Races for which the upriver migration is short tend to spend more energy per kilometer traveled, while those races that have longer upriver migration (e.g. Stuart runs) have more oriented swimming behavior which increases efficiency (Bernatchez and Dodson, 1987; Gilhousen, 1980). An average metabolic cost value for Early Stuart, Chilko, and Adams stocks is 7.322 Joules/g/km (Gilhousen, 1980). This value can drastically change depending on temperature, flow, river slope and topography the migrant has to negotiate on different reaches of the river (Gilhousen, 1980; Hinch and Bratty, 2000; Hinch et al., 1996). Power consumption has been found to vary nearly three orders of magnitude during the migration, with observed values ranging from less than 1 J/s during periods of reduced activity up to 1,700 J/s during bursts for sockeye navigating through the Fraser river canyon (Rand and Hinch, 1998).

2.4 Gonad Development, Fecundity, and Spawning

Gonad development begins while salmon are still in the open ocean, and fish ripen during the upriver migration (Gilhousen, 1980; Idler and Clemens, 1959). The total fecundity of a female changes during the upriver migration (Burgner, 1991), presumably to compensate for variable bioenergetics costs. Ballantine et al. (1996) measured the largest increase in Early Stuart female gonad size after passing Hells Gate, a difficult point of passage in the river (Hinch and Bratty, 2000; Hinch et al., 1996). Once an average female reaches the spawning grounds, it releases 2,000 to 5,000 eggs (equivalent to 95% to 99% of all her eggs) in several batches of 550-950 eggs each, depending on its size and race (Foerster, 1968). Males fertilize those eggs with an efficiency ranging from 97.48% to 99.37% (average 98.45%) although this number may vary depending on the sex ratio and the prior reproductive activity of the male (data for natural redds only, from Mathisen (1955) in Foerster (1968), Table 18).

For any race and brood year, fecundity varies with body length in a linear fashion (Burgner, 1991; Foerster, 1968). See Healey (1987) for a power function fitted to the Iskut River commercial catch). Here I describe this relationship with data from the Adams, Chilko,

Horsefly, Late Nadine, Stellako, and Cultus stocks of Fraser River (data for the first five stocks was provided by the staff of the Pacific Salmon Commission, data for Cultus Lake are from Foerster, 1968). Each point represents the average fecundity for the average size of a female for a brood year (Figure 2.2). This relationship implies that migrating sockeye females must attain a body size larger than 21 cm to have a fecundity larger than 0. I am aware that fecundity-size relationships tend to be population specific, however the use of this relationship in this research requires to define it for a wide range of terminal body lengths.
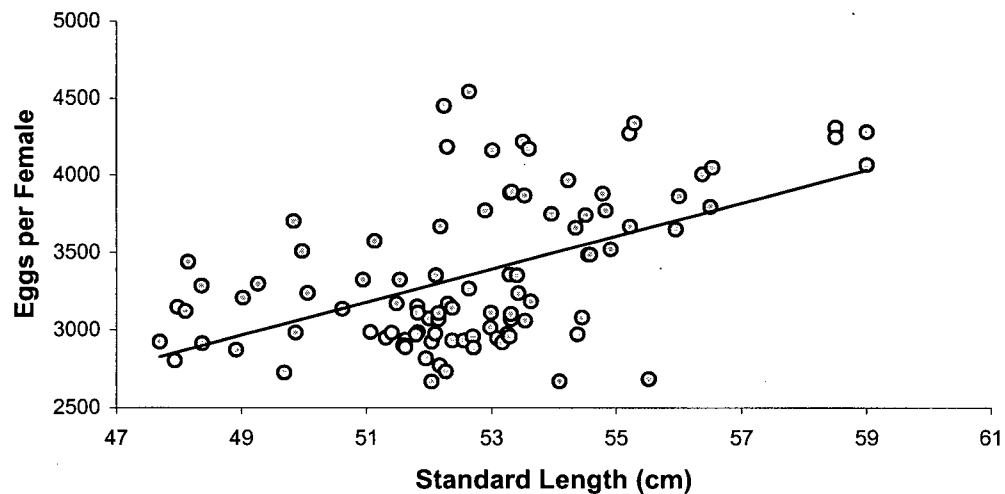
Figure 2.2. Fecundity - size relationship for female sockeye salmon from the Fraser River. Data are from the Adams, Chilko, Horsefly, Late Nadina, Stellako, and Cultus Lake stocks. Trend line is -2268.9 + 106.8 L (r = 0.523, n = 96).

Sockeye salmon females exhibit a trade-off between fecundity and egg size. Mathisen (1962 in Burgner, 1991) found that within a population, mean egg size increases with body length and the number of eggs per female is inversely related to egg size. Larger eggs hatch into bigger fry (Brannon, 1987) and have better survival rates (West and Larkin, 1987). However larger eggs have longer developmental times (Brannon, 1987) that result in late hatching and make the fry prone to emerge in a more competitive environment. Smaller eggs have some advantages over larger eggs; Healey (1987) suggest that smaller eggs may survive better in poor quality gravels (as is the case for coho salmon (Holtby and Healey, 1986), which would reduce competition for spawning grounds and egg mortality from nest digging activities by other females.

The egg size of sockeye salmon is small when compared with other species of salmon. Egg diameter ranges from 5.23 to 6.6 mm (average 5.67 mm) with dry weight ranging from 33.07 to 65.08 mg (average 45.73 mg) for stocks from the Fraser, Skeena, and Bristol Bay watersheds (Burgner, 1991). The energy content of an average egg has been estimated at 1,422.5 Joules (Dueñas 1980, in Brett, 1980). The efficiency at which gonads convert energy reserves into gametes is not known (Gilhousen, 1980).

2.5 Egg Development and Emergence

Egg development occurs in temperatures between 1 °C and 14.2 °C (Brannon, 1987) and the rate of development varies with the temperature regime (Burgner, 1991). Experimental data on the effects of temperature (held constant) on development time for 10 stocks from the Fraser River in Brannon (1987), Murray and McPhail (1988), and Beacham and Murray (1988) indicate that the time to yolk absorption decreases exponentially as temperature (in degree days) increases (Figure 2.3).

Brannon (1987) also noted that eggs compensate for the effect of low temperatures in development time. His data and those from Murray and McPhail (1988) and Beacham and Murray (1988) fit well to a logarithmic trend as shown in Figure (2.4). The model shows that most of the temperature compensation occurs below 5 °C. This compensation seems to decrease the impact of low temperatures on development time and to improve the odds that embryos will not miss the production peak in the nursery lake even in years with cold winter (Brannon, 1987).
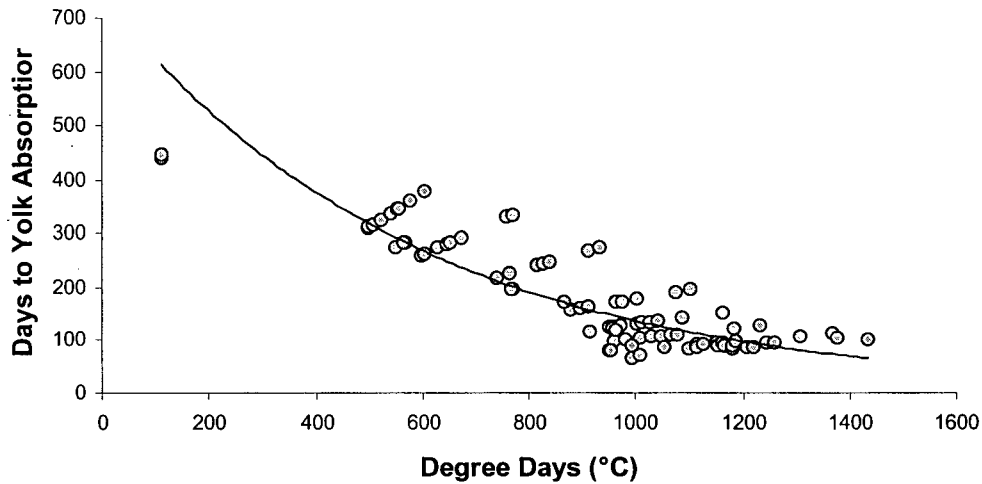
Figure 2.3. Egg development time as a function of accumulated temperature for sockeye salmon of the Fraser River (data from Beacham and Murray, 1988; Brannon, 1987; Murray and McPhail, 1988). Trend line is 740.64 $e^{-0.0017\,t}$ (linear r = 0.84, n = 93).
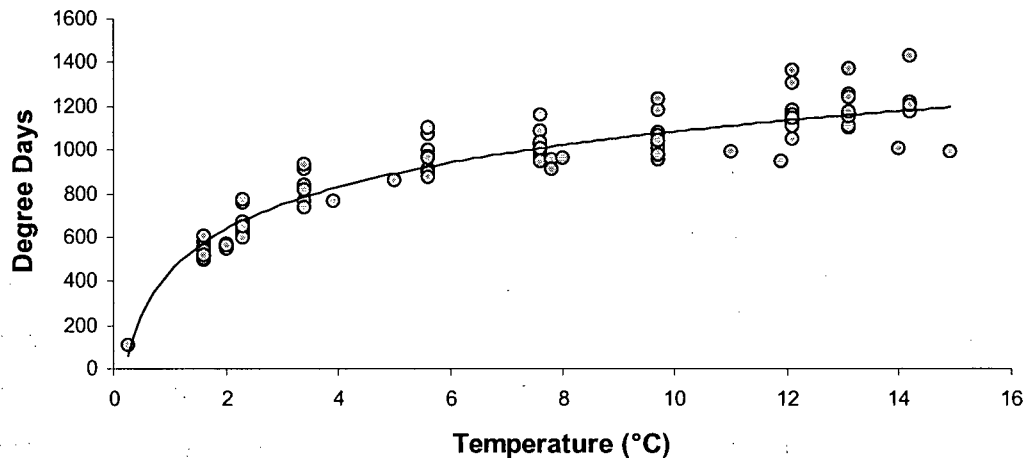
Figure 2.4. Temperature compensation on egg development expressed as degree days to yolk absorption for sockeye salmon (data from Beacham and Murray, 1988; Brannon, 1987; Murray and McPhail, 1988). Trend line is 443.41 + 278.43 Ln(t) (linear r = 0.937, n = 93).

Incubation temperature also affects the weight and size of alevin and fry (Beacham and Murray, 1988). Low incubation temperatures (4 to 8 °C) yield larger and heavier alevins and fry than higher temperatures, while extremely cold incubation temperatures (below 4 °C) produce lighter alevins. Beacham and Murray (1988) also detected race specific tolerances for extreme incubation temperatures. Embryos from races inhabiting coastal lakes survive better

at higher temperatures than those from interior lakes, while embryos from interior lakes survive better at low temperatures than their coastal counterparts.

Alevins begin emerging from the gravel at night during early to mid April. Emergence peaks in early May and ends in late May to early June (Burgner, 1991). When they enter the nursery lake as fry, their body size ranges from 25 to 31 mm, and weight between 0.1 and 0.2 g (McDonald and Hume, 1984). The emergence pattern observed across the distribution range of the species coincide with the seasonal abundance peak of zooplankton of the appropriate size in the rearing lake (Burgner, 1991).

2.6 Lake Residency

For the majority of the stocks, fry immediately migrate to the nursery lake after emerging from the gravel. In the Fraser River, under-yearlings from the Harrison Rapids race do not have lake residence; they migrate downriver to the estuary of the Fraser River and use it as a rearing area for at least 6 months Birtwell et al. (1987). Races that migrate into rearing lakes stay in the lake for at least 10 to 11 months and may stay there for as long as 4 years before smolting and initiating the seaward migration, or not migrate to the sea at all (Thorpe, 1987). Most races from the Fraser River (with the exception of the Harrison Rapids race) have a typical residence time of one year (Burgner, 1991).

Once in the lake, fry stay in the littoral area for a short period and then move into the limnetic zone, although direct migration into the limnetic area is also common (Burgner, 1991). While in the lake, the diet of the fry depends on the habitat they use and the food available. Foerster (1968) found that newly arrived juveniles feed mainly on larval stages of insects (chironomids, dipterans, stoneflies, caddis fly) before moving into the pelagic zone of the lake where they shift to larger pelagic zooplankton, particularly *Daphnia*, *Bosmina*, *Cyclops*, and *Epischura*. The typical feeding behavior of juveniles is to forage actively at dusk and dawn and to move into deep waters during the day. This behavior, and the formation of schools during light hours, are considered adaptations to cope with the risk posed by visual predators in the lake (Clark and Levy, 1988; Eggers, 1978; Levy, 1987).

The growth pattern of the fry in the lake has a consistent seasonal shape composed of three distinct phases. There is a period of exponential growth from the time of entry to the lake until mid-autumn, followed by a period of low or no growth from late fall and winter, and another period of fast growth in the spring before smolting and leaving the lake (Burgner, 1987; Eggers, 1978). Final weight and size of smolts varies among populations (see Figure 2.5) and is determined by the production capacity of the rearing lake, water temperature and thermal stratification, photoperiod and length of the growing season, turbidity and light attenuation, predator density, and density of sockeye fry and competitors (Burgner, 1987; Eggers, 1978; Foerster, 1968; Koenings and Burkett, 1987). Common competitors of sockeye fry in Fraser River lakes are the threespine stickebacks (*Gasterosteus aculeatus*), ninespine stickebacks (*Pungitius pungitius*), pond smelt (*Hypomesus olidus*), pygmy whitefish (*Prosopium coulteri*), and lake whitefish (*Coregonus clupeaformis*) (Burgner, 1987).
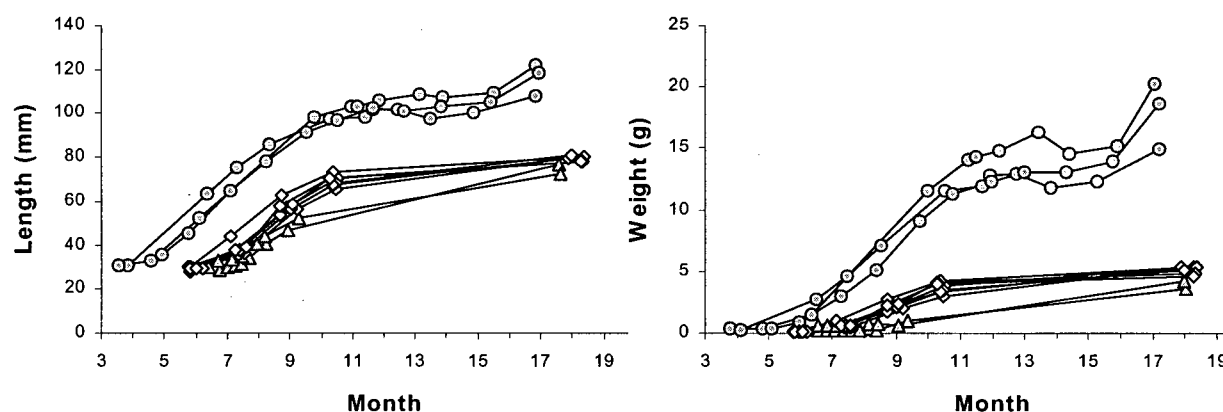
Figure 2.5. Seasonal growth pattern of juvenile sockeye salmon in Lake Washington (cohorts 1967-69 grey circles), Lake Aleknagik (cohorts 1964-65 grey triangles), and Babine Lake (cohorts 1965-67, 1970-72, 1976 empty diamonds) (data from Burgner, 1987; McDonald and Hume, 1984).

The density of sockeye fry and its competitors in the rearing lake are considered the most important factors in the determination of smolt size (Goodlad et al., 1974; Hyatt and Stockner, 1985). Hyatt and Stockner (1985) found a strong relationship between the wet weight of smolts after one year of lake residency and zooplankton biomass per fish (measured during July-September) for 14 coastal lakes in British Columbia (Fig. 2.6).
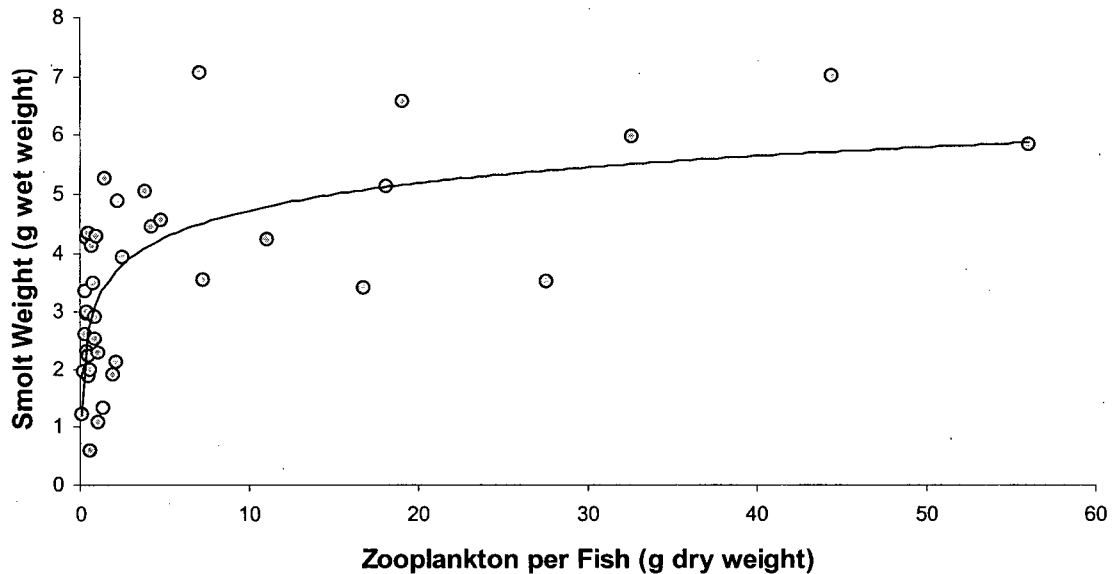
Figure 2.6. Relation between zooplankton biomass per fish and smolt weight in 14 coastal lakes of British Columbia (data from Hyatt and Stockner, 1985). Trend line $W_S = 3.1875 + 0.666$ Ln [Zoop] (linear r = 0.68, n = 39).

The biotic and abiotic characteristics of sockeye rearing lakes create a highly variable size at smolting within and between populations. Smolt body size ranges from 60 to 143 mm (Figure 2.7), and weight varies from 2 g to 27.3 g (Figure 2.8) for individuals that smolt after 1 year of lake residence (Burgner, 1991). Smolt size data from Hyatt and Stockner (1985) (Fig. 2.6) show that races from British Columbia coastal lakes reach smaller smolt sizes, ranging from 0.7 to 7 g. I estimated a mean weight of 5.8 g for Fraser River smolts from the values for Cultus, Chilko, Fraser, and Shuswap Lakes in Burgner (1991).
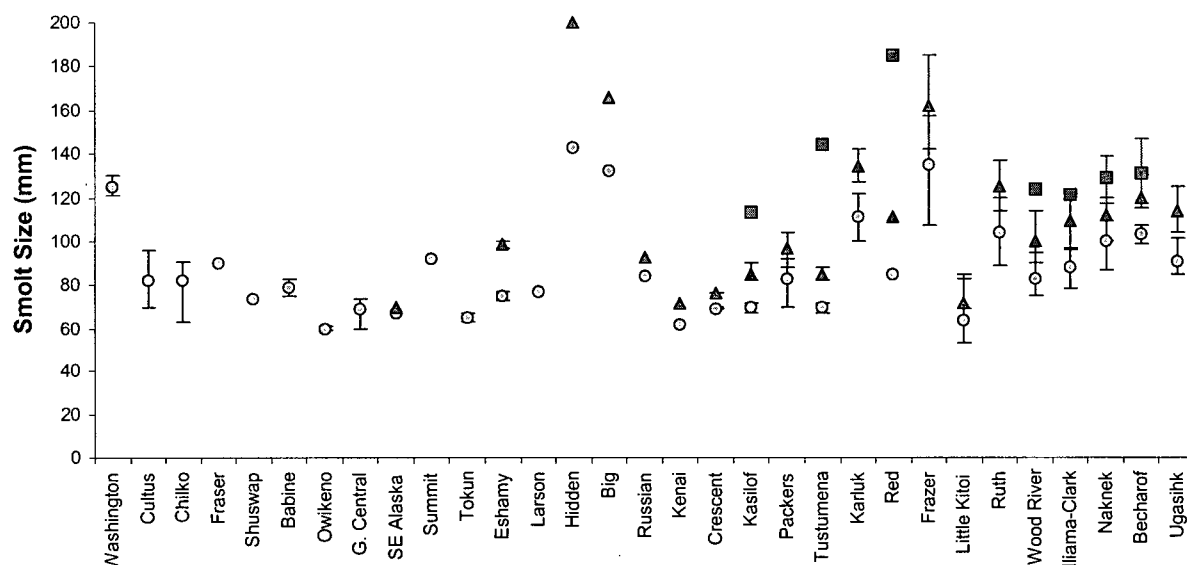
Figure 2.7. Average smolt size of sockeye salmon from 31 lakes in the West Coast of North America. Circles indicate the size of 1 year old smolts, triangles 2 years old, and squares 3 years old. Data from Table 8 in Burgner (1991). Error marks show minimum and maximum (when available).
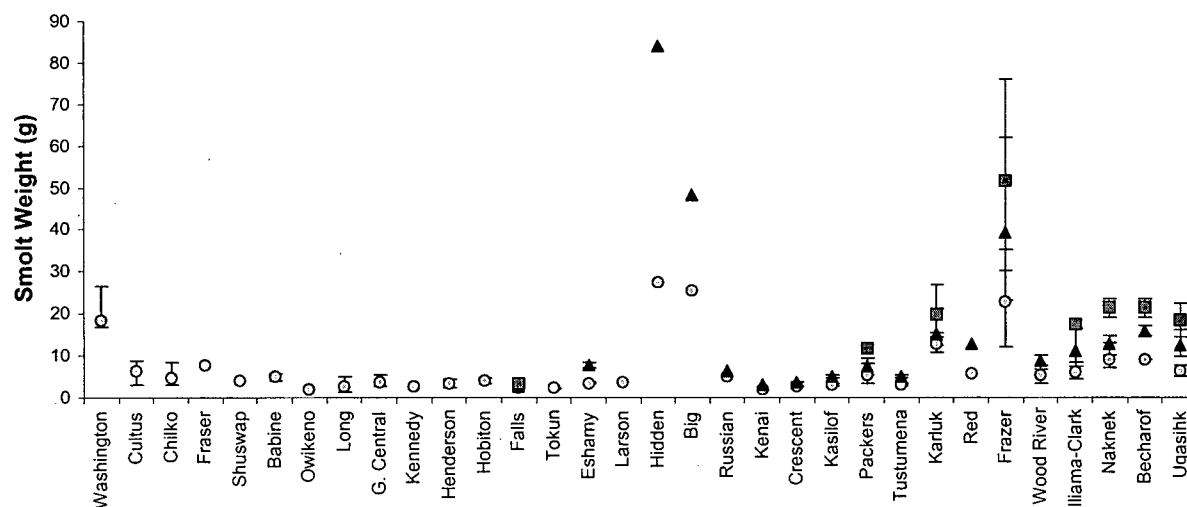
Figure 2.8. Average smolt weight of sockeye salmon from 32 lakes in the West Coast of North America. Circles indicate the weight of 1 year old smolts, triangles 2 years old, and squares 3 years old. Data from Table 8 in Burgner (1991). Error marks show minimum and maximum (when available).

2.7 Smolting and the Downriver Migration of Juveniles

Smolt transformation is a complex process involving physiological, anatomical, and behavioral changes that prepare salmon for life in the marine environment (Groot, 1982; Hoar, 1976; Schreck, 1982). The smolting juveniles become slimmer, more streamlined, acquire a silvery color, and become more tolerant to saltwater (Burgner, 1991). Physiological changes associated with smolting include increased metabolic rate, decrease in body fat, and accelerated growth rate (Hoar, 1976; McCormick and Saunders, 1987). Although there are no direct observations on the metabolic demands of smolting for sockeye salmon, respiration measures taken on Atlantic salmon (*Salmo salar*) show values 25% higher in smolts than in non-migrating juveniles (McCormick and Saunders, 1987). Woo et al. (1978) indicates that coho salmon smolts (*Oncorhynchus kisutch*) have lower values of protein (10.8 %), glucose (29.4%), and fat (37.9%) in serum, and 80% less fat in the muscle tissue. The increases in metabolic rate appear to be partly catabolic, possibly because of the energy requirements for smolting (McCormick and Saunders, 1987). However, it is not clear how much of this increased metabolism is due to the smolting process or to the growth experienced (Hoar, 1976). Woo et al. (1978) speculated that most of those expenses are likely due to the smolting process.

The onset of smolting is size-dependent in salmonids. There is an increasing ability to tolerate salinity at larger body size, presumably because larger fish have a regulatory system that is either more functional to a given salt gradient or capable of faster physiological adjustments to changes in salinity (Hoar, 1976).

Adjusting to salinity changes may affect the survival of salmonid smolts in the marine environment (McCormick and Saunders, 1987). However, when compared to other genera of the subfamily salmoninae, the genus *Oncorhynchus* have the smallest body size at smolting (Houston, 1961; McCormick and Saunders, 1987). The Harrison Rapids and East Alsek River races of sockeye salmon migrate to the estuary as fry, spending only a few weeks after emergence in freshwater (Birtwell et al., 1987; Burgner, 1991). This high salinity tolerance of the genus *Oncorhynchus* suggests that the mortality and metabolic costs of smolting are very small for sockeye smolts.

Smolting starts during the last months of the winter season prior to migration (Groot, 1982). Smolts initiate the migration soon after the ice cover breaks in the rearing lake during spring or early summer; varying from late April for smolts in Cultus Lake to late June or early July for those from Tazlina Lake in the Wood River (Burgner, 1991). The smolts migrate downriver from dusk to dawn in groups, peaking at around midnight, with individuals actively swimming downstream at average ground speeds of 40 km/d (Burgner, 1991; Foerster, 1968). While migrating downriver the smolts feed on crustacea (mainly cladocerans and copepods) and insects (chironomid larvae) (Birtwell et al., 1987).

2.8 Coastal Residence and Migration

Races from southern latitudes arrive earlier at the estuary that those from the north, and their arrival coincides with those of chum and pink salmon (Hartt, 1980). Smolts from Fraser River races arrive at the estuary from April to June (Hartt, 1980). At this time zooplankton abundance peaks, reaching in excess of 4,000 mg wet weight/m^3 in the Strait of Georgia (Parsons et al., 1970).

During their residence in the coastal zone, juvenile sockeye form shoals (Hartt and Dell, 1986) and forage on euphausids, fish larvae, copepods, amphipods, larval stages of ascideans, and insects (Foerster, 1968; Healey, 1980; Healey, 1991; Landingham et al., 1998). Juveniles show a very high apparent growth; Hartt (1980) measured growth rates from 0.11 to 0.16 cm/d for Fraser River sockeye, 0.1 to 0.18 for Skeena River sockeye, and from 0.05 to 0.1 cm/d for Bristol Bay sockeye. While in the Strait of Georgia, juvenile sockeye from the Fraser River grow from 106 to 185 mm (12.8 to 81.1 g) (see Figure 2.9) from May to October (Healey, 1980). Sampling in Hecate Strait during July and August of 1986 and 1987 also shown fish growing from an average of 17 g to 36 g (Healey, 1991), although the feeding rates found at that time were too low to explain the apparent growth rate of the juveniles.
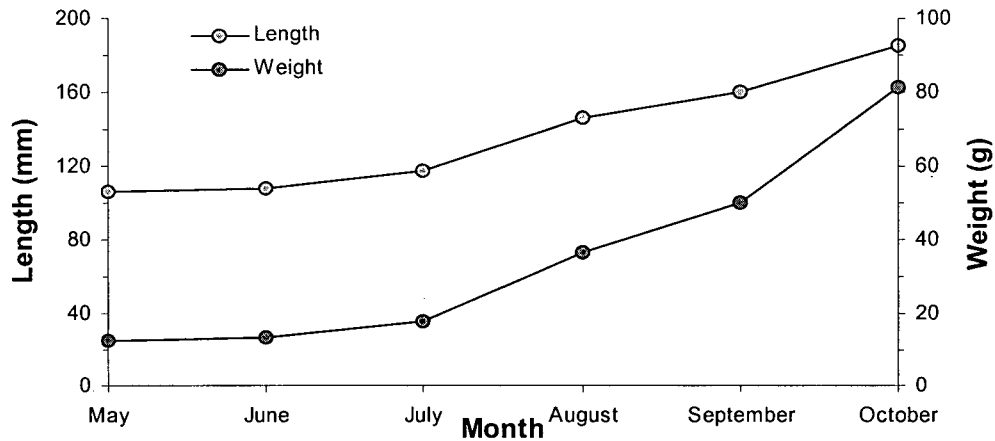
Figure 2.9. Mean growth of juvenile sockeye salmon in the Strait of Georgia (data from Healey, 1980).

Upon entrance to saltwater, smolts distribute in the top 10 m of the water column (Groot and Cooke, 1987), and move in a dominant northwestward direction (Hartt, 1980). Fraser River smolts navigate the complex geometry of the Georgia Strait and Johnstone Strait (Fig. 2.10A) at sustained speeds of 23 to 30 cm/s. Groot and Cooke (1987) indicate that the smolts take about one month to travel from the Fraser mouth to the northern part of the Strait of Georgia. Hartt (1980) and Groot and Cooke (1987) indicate that the smolt actively migrate while in the Strait of Georgia. They report that most of their samples taken between Vancouver Island, B. C. and Yakutat, AL. were obtained when the seine net was opened Southeast, and the few catches obtained from sets open Northwest may have resulted from the effect of tides. However some modeling evidence has pointed out that the magnitude and variability of the surface currents in the strait of Georgia, particularly wind driven currents that have been observed to reach over 50 cm/s, may be controlling the migration path of the smolts (Peterman et al., 1994). They found that the range of winds smolts encounter during April and May in the Strait of Georgia can explain the two routes reported by Groot and Cooke (1987). Furthermore, strong south-eastward wind events, occurring 18% of the time during April and May, are likely responsible for driving the juveniles along the east coast of Vancouver Island. They also found that smolts swimming at half a body length per second provide a mean residence time close to one month, which is the observed time of residence during the out-migration (Groot and Cooke, 1987).

By July, juveniles from NE Pacific races are moving Northwestward in the Gulf of Alaska at speeds of 14 to 26 km/d within 40 km from the coast, along a band of 1,800 km from Cape Flattery to Yakutat (Groot and Cooke, 1987; Hartt, 1980; Hartt and Dell, 1986). By August they also appear along the coast of central and Southwestern Alaska. Hartt and Dell estimate that juveniles swim at an average speed of 18.5 km/d during this period, and indicated that they seem to follow a definite migratory route. Tagging data show that by August some Fraser River sockeye can reach as far as the southern part of the Alaska Peninsula (Fig. 2.10B). Hartt and Dell (1986) report of one juvenile sockeye salmon tagged SW of Kodiak Island on August 30, 1958 was recaptured two years latter as a mature adult in the Strait of Georgia. At the location of tagging, the juvenile would have traveled 1,500 nautical miles from the Fraser estuary.

By early October juveniles are no longer found near the coast, and it has been assumed that by that time they moved into the open waters of the NE Pacific (Hartt and Dell, 1986; Healey, 1980). Hartt and Dell (1986) summarized the juvenile migration pattern of sockeye salmon as in Figure (2.11).
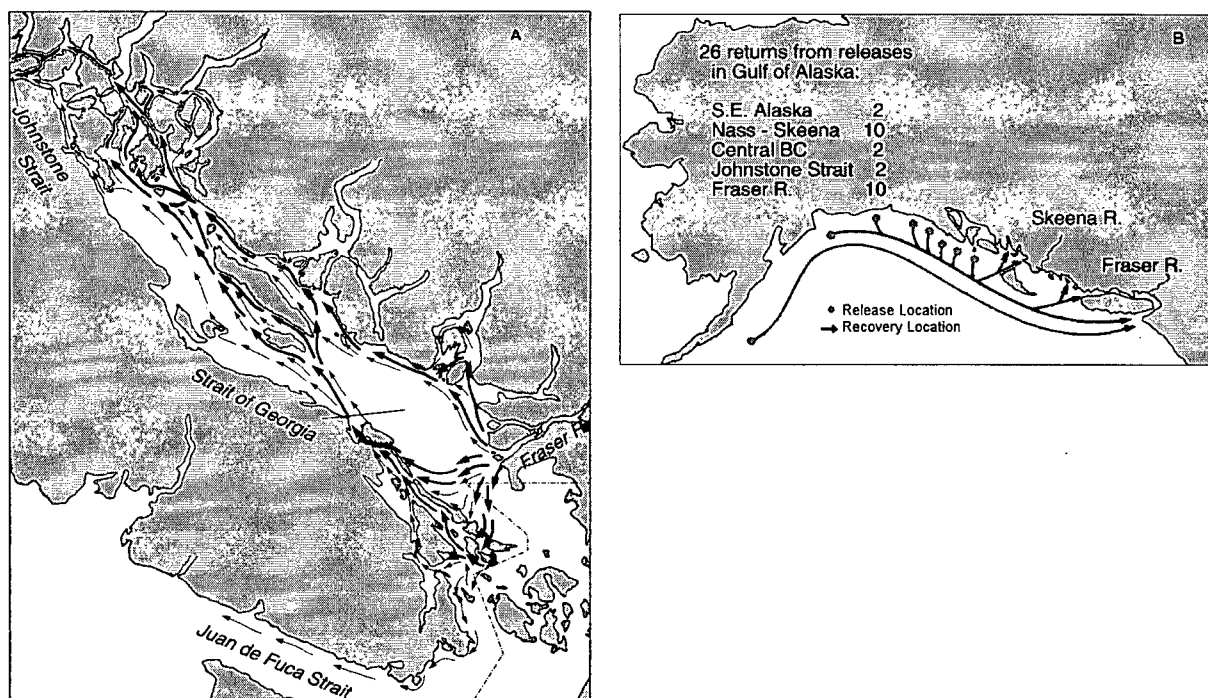
Figure 2.10. Juvenile coastal migration of sockeye salmon. Figure A shows the migratory route of Fraser River smolts (from Groot and Cooke, 1987). Figure B shows the tagging location of juvenile and their recovery points as adults of individuals from SE Alaska and British Columbia stocks (from Hartt and Dell, 1986).
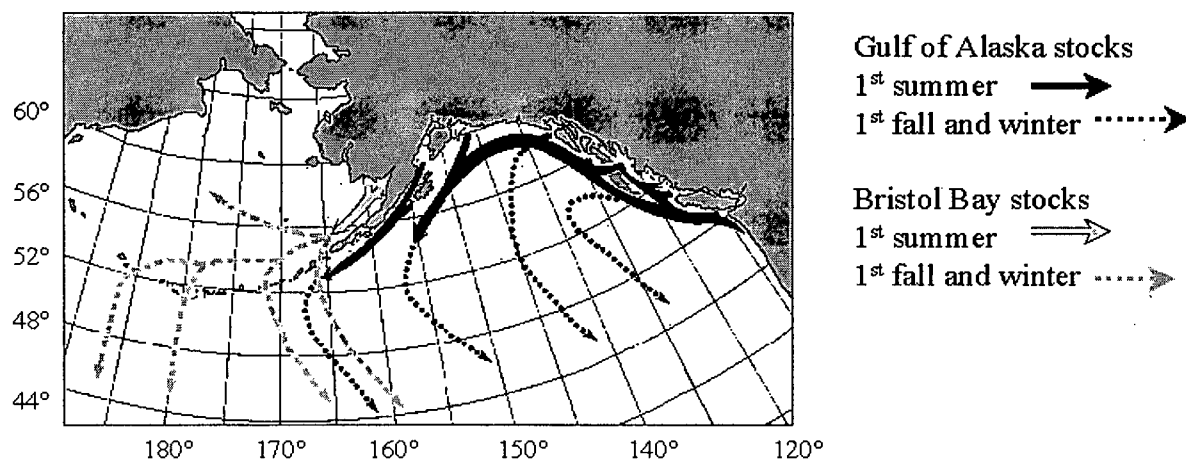
Figure 2.11. Migration pattern of juvenile north american sockeye salmon (from Hartt and Dell, 1986).

2.9 The Oceanic Phase

Once in the open ocean, sockeye salmon no longer form shoals, and instead are distributed at low densities in near surface waters (French et al., 1976). Tagging data indicate that sockeye salmon from Alaska, British Columbia and Washington are in the area ranging from 40° N to the Bering Sea (Burgner, 1991; French et al., 1976) and from 130° W to 170° E. The distribution of tags released in the open ocean and captured in the Fraser River or the Columbia River indicate that races from those rivers have a more restricted distribution (shown in Figure 2.12) within the Alaska Gyre.

									60°N
				1	5	8	1		
				4	16	38	9	1	
			1	14	38	38	24	13	
			3	26	42	15	11	1	75
Fraser R. 724 Columbia R. 12		2	4	5	10	7	8	2	64 / 230
Total 736			7	6	2		1		1

170° W   160°   150°   140   130°
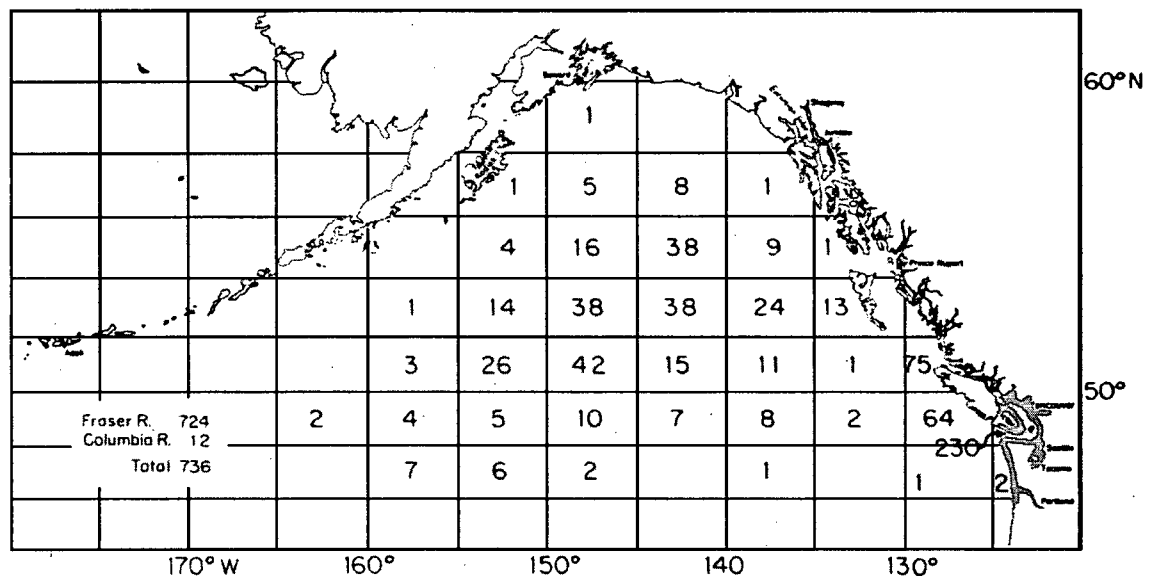
Figure 2.12. Distribution of tag releases of sockeye salmon recovered in the Fraser and the Columbia River (in thick grey lines) (from French et al., 1976).

Seasonal movements are complex, and have been correlated with seasonal changes in temperature, maturity stage, age and size, availability of prey organisms, and stock of origin (Burgner, 1991; Foerster, 1968; French et al., 1976; Welch et al., 1995; Welch et al., 1998).

Sockeye salmon distributions in the Gulf of Alaska show seasonally varying thermal boundaries (French et al., 1976; Welch et al., 1995; Welch et al., 1998). Mature individuals are found in cooler, and more northern, waters than immature individuals. During winter, immature individuals are present in waters of 2-7 °C and maturing individuals within 2-6 °C. In spring immature individuals distribute between 4-10 °C while maturing individuals are

between 1-10°C. In summer, immature sockeye are between 5.6-7.8 °C while mature individuals are found at 3.3-6.7 °C, although by this time mature individuals are returning to the natal streams to spawn.

Data from tagging, and from abundance and direction of migration based on purse seine catches, led French et al. (1976) to propose an open ocean migratory cycle (Figure 2.13) in which individuals from North American stocks complete a circuit around the Alaska gyre once for every year they stay in the ocean. This is the current perception of the migratory behavior of sockeye salmon (e.g. Brett, 1980; Hinch et al., 1995a; Hinch et al., 1995b), although an individual-based model, using time dependent swimming behavior and monthly surface currents fields, could only generate one loop around the Alaska Gyre for age 1.2 sockeye salmon (Walter et al., 1997).
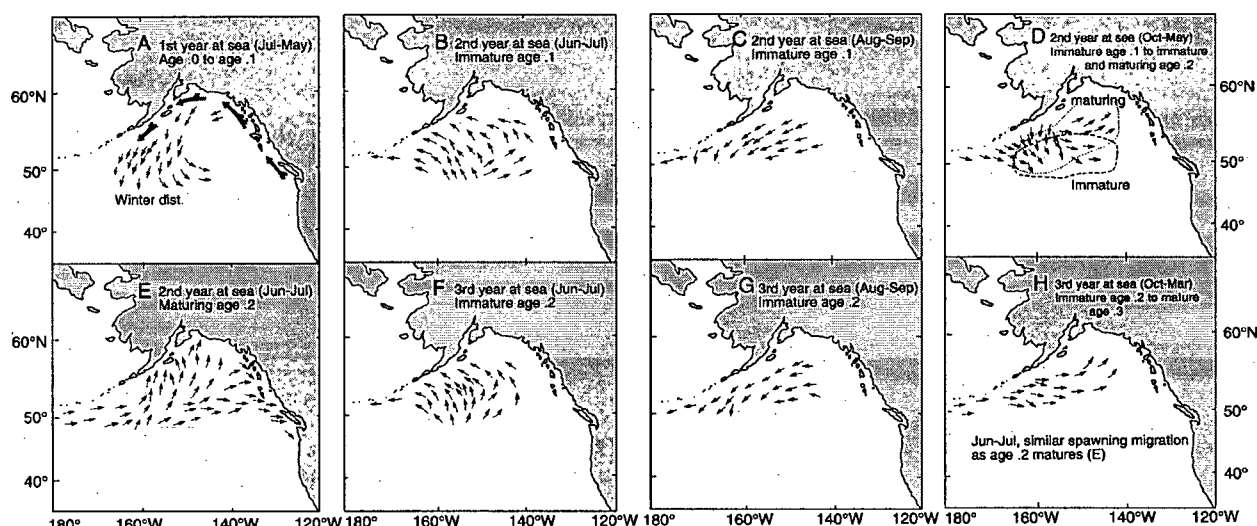
Figure 2.13. Schematic migration pattern of Northeast Pacific sockeye salmon (from French et al., 1976), Figure 94).

The diet of sockeye salmon in the open ocean varies depending on the geographic area (Burgner, 1991). In the central North Pacific the most important food items are copepods, euphausids, fish (myctophidae and juvenile cod), and squids, while in the central Northwest Pacific the most important items are euphausids and hyperid amphipods (Foerster, 1968; French et al., 1976). The foraging pattern also varies with the developmental stage of the fish.

LeBrasseur (1966) and LeBrasseur and Doidge (1966) found that immature fish have less food in their stomach than mature fish; amphipods were an important prey item in the diet of immature individuals and fish for maturing individuals. However French et al. (1976) argued that changes in diet between mature and immature individuals probably reflects the local availability of prey items encountered by fish as they move in their area of distribution.

Prey composition and stomach fullness of sockeye salmon show a diel pattern. Pearcy et al. (1984) found that sockeye feed primarily on squids, fishes, and amphipods during the day, and switch to euphausiids at night. They also found that stomach fullness at any given time of the day varies from 0 to 4% of body weight, with higher values occurring at night.

Cultus Lake fish grow to an average weight of 354 g between entrance to the sea and their first winter, then grow to 1,315 g over the next 12 months, and to 2,146 g during the first 5 months of the last year of residence in the ocean (from tables I and II in Ricker, 1962). Maturing fish are larger that immature fish at any given age (Figure 2.14). Growth in length is greatest during the first year while growth in weight is greatest during the second year (Burgner, 1991). Evidence from scale analysis suggests that the growth process slows or stops during the annulus formation period from November to January, however this evidence has been dismissed because of the lack of information about the frequency of ring formation in scales (Burgner, 1991). Furthermore most of the published work (French et al., 1976; Ricker, 1962; Ricker, 1976) refers to growth as a continuous process during the marine phase.

The final body size that sockeye achieve depends on the number of years spent in the ocean (Burgner, 1991; Foerster, 1968), with males reaching slightly larger sizes than females on average (Gilhousen, 1980; Idler and Clemens, 1959). Sockeye from Babine Lake reach a final weight of 774 g after 1 year of oceanic residence, Skeena river sockeye reaches 2,285 after 2 years and 2,919 after 3 years of residence (Brett, 1985), while the weight of ocean-2 female sockeye from Early Stuart, Adams, and Chilko races range between 2,100 and 2,800 g (Gilhousen, 1980; Idler and Clemens, 1959).
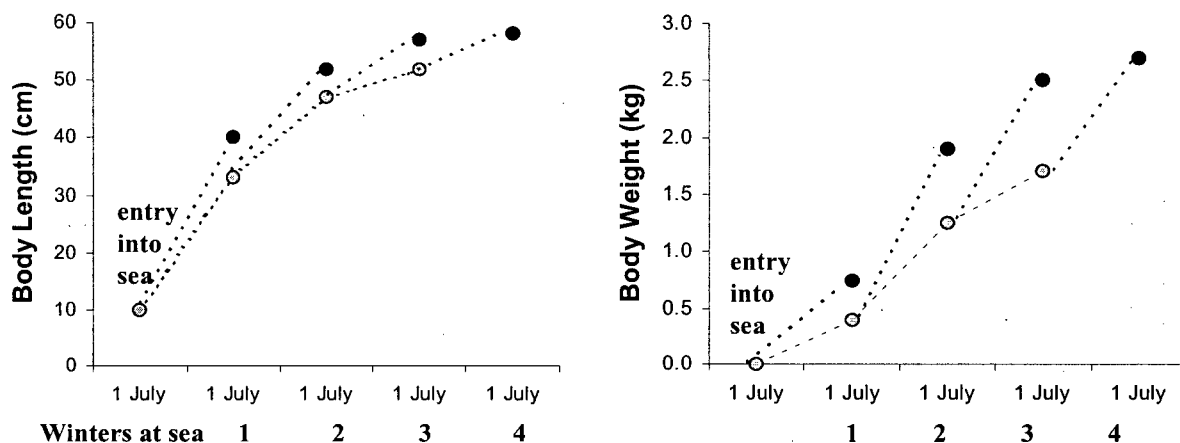
Figure 2.14. Sockeye salmon oceanic growth (from Lander et al (1966) in French et al. (1976), Fig. 36). Broken lines connect sequential stages and do not represent a growth pattern. Grey dots represent immature individuals, black dots mature individuals.

Density dependence has been detected in the growth rate and final body weight of several stocks from British Columbia and Alaska. This density-dependent effect arises during early ocean life and seems to be related to competition for food. It can cause 10-22% decrease in the final body weight of British Columbia sockeye during years of high abundance in the ocean (Peterman, 1984). Surface temperature also seems to affect the final weight and size of salmon. Hinch et al. (1995a), Ricker (1981) and Cox and Hinch (1997) found a trend towards smaller final weight with higher temperatures. Cox and Hinch (1997) speculated that this effect may come from increasing metabolic costs at higher temperature and/or by changes in the oceanic environment affecting the foraging ability of the fish.

2.10 Mortality

The mortality schedule of sockeye salmon is as complex as its life history. Each phase of its life has a specific mortality structure that can have any combination of density-dependent, density-independent, and/or size-dependent effects, and varies with race and brood year. Because of the information requirements of the models in Chapter 3 and 4, I divided the life cycle into two broad stages, the freshwater stage and the marine stage.

2.10.1 Mortality during the Freshwater Phase

Losses during this stage can be categorized into those occurring prior to the entrance to the lake, during lake residency, and during the downriver migration. Losses occurring prior to entrance to the nursery lake include those occurring during the spawning season, incubation, and from alevin emergence up to the moment of reaching the lake. Losses occurring after entrance to the nursery lake include those during lake residency. Given the resolution of available data on mortality, losses occurring during the downriver migration as smolts and during the upriver migration as mature adults were grouped in the marine stage.

2.10.2 Losses Prior to Lake Entrance

During the egg deposition period, a major cause of mortality is predation from exposure due to redd digging activity by other spawners. This factor is density dependent and can reach values up to 75% of total eggs deposited (Foerster, 1968; West and Mason, 1987). After the spawning season and during the incubation period, mortality is likely to occur from physical and chemical factors like freezing, desiccation, siltation, and reduced water flow (Burgner, 1991). Incubation temperature also has an effect on the survival from egg to alevin emergence. Beacham and Murray (1988) and Murray and McPhail (1988) indicate that survival is highest at an incubation temperature of 8 °C and decreases towards both extremes, although alevin survival is comparatively better at lower temperatures than at higher temperatures.

After emergence from the redd, fry mortality comes from predation by larger piscivore fish and varies considerably depending on the type and location of the spawning area, type and abundance of predators, and physical characteristics of the spawning stream (Burgner, 1991). Main predators during this stage are coho yearlings (*Oncorhynchus kisutch*), cutthroat trout (*O. clarki*), char (*Salvelinus maima*), and sculpins (*Cotus asper*) (Foerster, 1968). In British Columbia lakes, rainbow trout (*Oncorhynchus mykiss*) is considered a very important predator of fry migrating to the nursery lake (Foerster, 1968; Ginetz and Larkin, 1976).

Predation losses during fry migration decrease with increasing density (Foerster, 1968; West and Mason, 1987), presumably because of predator saturation. The only available

estimates of mortality for migrating fry are in Foerster (1968). He estimated 63% to 84% (average 74.5%) losses for migrating fry from Scully Creek (Lake Lakelse) from 1950 to 1953, and 66% in Six Mile Creek (Lake Babine). Foerster suggested that the average losses from fry emergence to nursery lake entry are between 50% to 75% in British Columbia lakes.

There are several mortality estimates for the stage from egg to nursery lake entry, condensing all the losses during development, emergence, and migration to the nursery lake. West and Mason (1987) estimated 80.8% egg-to-fry mortality in the Lower and Upper Pinkut Creek and 81.1% in Fulton River (Babine Lake) from 1964 to 1985. Bradford (1995) pooled the survival data from 9 lakes and estimated the egg-to-fry mortality at 93% (87.5% for British Columbia lakes). This is the most up-to-date estimate of mortality for the egg-to-fry stage.

2.10.3 Losses During Lake Residency

Mortality losses during lake residency result mainly from predation by piscivore fish and nematode parasitic infections (Burgner, 1991). Fish predators of sockeye fry include Dolly Varden (*Salvelinus malma*), pike-minow (*Ptychocheilus oregonensis*), char, cutthroat trout, rainbow trout, lake trout (*S. namaycush*), juvenile coho salmon, and northern pike (Burgner, 1991; Foerster, 1968; Ricker, 1941).

Annual mortality rates during lake residency vary from lake to lake. Foerster (1968) estimated rates from 94.15% to 97.19% (average 95.84%) for Cultus Lake, 8.4 % - 56.4% (average 36%) for Port John Lake, and 43.4% - 54.6% (average 47.4%) for Chilko Lake. West and Larkin (1987) and McDonald and Hume (1984) estimated values from 59.8% to 83.6% (average 71.92%) for Babine Lake sockeye. Bradford (1995) estimated a value of 70.77% for Babine, Chilko, and Lakelse races. This value is the most up-to-date estimate of mortality for the fry-to-smolt stage and I used it as a representative value for the races from the Fraser River.

Mortality seems to be density independent during lake residency in British Columbia races. In Babine Lake, West and Mason (1987) found 55% to 60% fry-to-smolt mortality rates

across a wide range of fry inputs from 1961 to 1982, and Ricker (1941) indicates that consumption of sockeye fry by fish predators in Cultus Lake was proportional to fry abundance across a wide range of fry abundance. The only evidence for density dependence in lake mortality is from Koenings and Burkett (1987). They found that fry survival decreases linearly with density (S = 58.62 - 0.0023 Density; r^2 = 0.98) in several oligotrophic lakes in Alaska.

There is some evidence of size-dependency in mortality. Babine Lake fry with fork length smaller than the mean fork length at emergence (29.55 mm in 1965 and 30.4 mm in 1978) had a fry-to-smolt mortality rate of 72.8 %, while fry with size above the mean had 56.6% (West and Larkin, 1987). However, those results may arise from events occurring during the fry migration to the rearing lake. In Cultus Lake, Foerster (1968) also found that tagged fry released at increasingly larger body size during several months had better monthly survival rates. Unfortunately, the release pattern does not permit a direct size-dependent interpretation of those results.

2.10.4 Mortality in the Marine Phase

Mortality processes occurring once the smolts migrate out of the nursery lake are not well understood. Although at each marine stage (juvenile coastal migration, oceanic residence, and return migration) mortality may have a habitat-specific structure, the available estimates are for the total marine mortality covering the smolt-to-adult stages, and the differentiation of mortality for each stage remains unsolved. Foerster (1968) indicates that the average mortality estimates for the smolt-to-adult stages range from 55.7 to 98.2% for six Pacific Northeast lakes and one Russian lake, and Ricker (1976) calculated between 57% and 68% for Karluk sockeye. The most up-to-date smolt-to-adult mortality estimate for Pacific Northwest stocks is 92% (Bradford, 1995).

Density-dependence and size-dependence of marine mortality have been explored (Brett, 1985). In regard to density dependence Hume et al. (1996) found no evidence for the period from fry to spawning adult for stock specific runs from Shuswap, Chilko, and Quesnel lakes in British Columbia, and Peterman (1978) and Peterman (1981) found inconclusive

evidence of density-dependent mortality between the number of migrating smolts and the number of returning adults for 9 Pacific Northwest and 1 Japanese stocks. However Peterman (1982) did find evidence of density-dependent mortality for the smolt-to-adult phase of Babine Lake sockeye salmon after correcting for measurement errors in the data, although his analysis could not resolve if it occurs during downriver migration or during marine residency. In regard to size-dependency of mortality, Henderson and Cass (1991), Koenings and Burkett (1987), Parker (1971), Ricker (1962), and McGurk (1996) did find evidence of it in the smolt-to-adult mortality of sockeye salmon. McGurk (1996) found that 33% of the variance in mean log-survival was explained by initial and final body weight for 32 North American nursery lakes. McGurk found that smolt-to-adult instantaneous mortality of pacific salmon scales well as a power of body weight ($Z \propto W^{-0.37}$) and that an average short term marine mortality value can be estimated from the relationship $Z = 0.528G$ if an independent estimate of the instantaneous growth rate (G) for the same short period is available.

To define the relationship between smolt size and smolt-to-adult mortality I used data in Ricker (1976) and Henderson and Cass (1991). Their data shows an exponential decrease in instantaneous mortality as smolt size increases (Fig. 2.15). Koenings and Burkett (1987) found that for smolt sizes larger than 140 mm ocean survival no longer increases and may actually decrease. However given the low average smolt size of Fraser River salmon (7 to 9 cm according to Burgner (1991)), Koenings and Burkett's relationship does not necessarily apply.

Smolt-to-adult survival pools all mortality processes occurring from the moment that smolts leave the nursery lake to the time when mature adults spawn in the natal stream. This long period contains 5 stages (downriver migration, coastal phase, open ocean phase, coastal phase of the return migration, and upriver migration) for which the structure of the mortality process may be particularly important in the definition of some traits in the life history of sockeye salmon (e.g. optimal foraging behavior, and optimal residence time in each habitat). For each phase there is a distinct set of predators and environmental conditions that may create a stage-specific mortality structure. This condition combined with the allometry of mortality prevents a direct allocation of a fraction of the smolt-to-adult mortality proportional to the time spent into each stage or area.
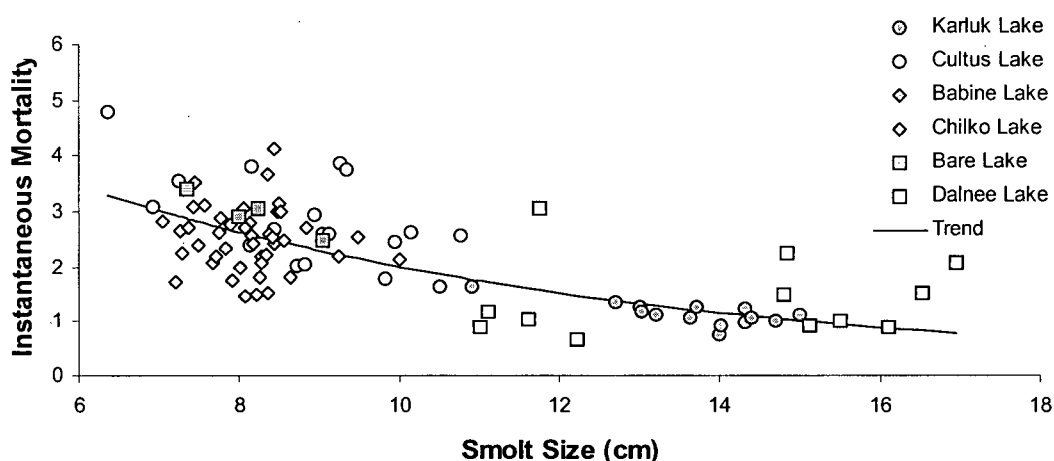
Figure 2.15. Smolt-to-adult instantaneous mortality rates (Z) for sockeye salmon in relation to smolt size (fork length) (data from Ricker (1962) and Henderson and Cass (1991)). Trend line was $Z = 7.82 \ e^{-0.13603 \ L}$ (linear r = 0.79, n = 80). Lake Dalnee data include fishing mortality and were not used in fitting the trend line.

2.10.5 Downriver Migration

During this phase, most of the mortality is due to predation from piscivore fish (rainbow trout, lake trout, char, dolly varden) and birds (Bonaparte and glaucous-winged gulls *Larus philadelphia* and *L. glaucescens*, great blue herons *Ardea herodias*, bald eagles *Haliaeetus leucocephalus*, belted kingfishers *Megaceryle alcyon*, and common merganser *Mergus merganser*) that congregate to forage on migrating smolts (Burgner, 1991; Ginetz and Larkin, 1976; Sawada, 1993; Wood, 1987). These predators can inflict heavy losses to migrating smolts; Crittenden (1994) indicates that predation mortality can be up to 85% during low abundance years. Wood (1987) estimated that the common merganser (*Mergus merganser*) actively preying on migrating juvenile pacific salmon (chum (*Oncorhynchus keta*), chinook (*O. tshawytscha*), coho (*O. kisutch*), and steelhead (*O. mykiss*)) from Vancouver Island can cause up to 8% mortality in smolt runs. Ruggerone and Rogers (1984) estimated that arctic char can cause losses of 8% during high density runs and up to 30% (ranging from 0% to 100%) during low smolt runs in the Little Togiak River, Alaska. Ruggerone and Rogers (1984) also found that survival during this stage is size-dependent. Those results show higher mortality for larger and smaller than average individuals. This size-

dependent mortality pattern was also found during the downstream migration of a coho salmon stock from Vancouver Island (Sawada, 1993).

Smolts have several behavioral mechanisms to reduce predation risk during the downriver migration: migration synchronization, schooling behavior, active downriver swimming, and preference for nocturnal movement (Burgner, 1991). This set of behaviors creates a depensatory effect in mortality, presumably because of predator satiation, limited predator population (Burgner, 1991; Ruggerone and Rogers, 1984) and perhaps limited time exposure to predation pressure.

2.10.6 Losses During the Coastal Stage

Once smolts reach the estuary, the main causes of mortality are apparently diseases and predation. Disease-related mortality seems to occur as a result of wounds from predator and parasite attacks (e.g. lamprey attacks) and has never been quantified (Hartt, 1980). Predation-related mortality while in the estuary is considered the main component of mortality. Species known to predate on juvenile salmonids in the coastal environment are the Beluga whales (*Delphinapterus leucas*) in Bristol Bay, Alaska, and harbor seal (*Phoca vitulina*) in the Columbia River (Fiscus, 1980), lampreys (*Lampetra tridentatus*) and sea lions (Hartt, 1980). Some of those predators seem to take a limited range of sizes of juvenile salmon; Ricker (1976) indicates that at about 250 g, juvenile salmon are no longer vulnerable to predation by birds. However this range implies that juvenile sockeye are exposed to those predators during the entire time they stay in the coast, since the size they reach at the time they leave the coast is about 80 g (see Figure 2.9).

Although smolt-to-adult survival decreases at larger smolt sizes (Figure 2.15) no inference can be made about where such dependency occurs. Size-dependent mortality does occur during the downriver migration (Ruggerone and Rogers, 1984). However the abundance and type of predators in the river is quite limited when compared with the coastal environment, and it is in the coastal environment where strong size-dependent predator-prey interactions should be expected to occur. The presence of large quantities of juvenile salmonids for 3 months every year no doubt creates the conditions for a complex

configuration of trophic interactions between juvenile sockeye and the coastal community of piscivore fishes. Hargreaves (1994) reported that there is a substantial interannual and seasonal variation in the distribution and abundance of predators in Barkley Sound (an inlet on the west coast of British Columbia) apparently from large scale changes in oceanic conditions. However, there are no estimates of the effects that they exert on growth and mortality of migrating juvenile salmonids.

Although the coastal environment provides better growth potential for juvenile fishes than the open ocean, the coast is also inhabited by a wide variety of potential predators. Predation theory indicates that survival rate depends on both size of the individual and its activity rate (Peterson and Wroblewski, 1984; Werner and Anholt, 1993). Encounter rate increases in relation to the activity level of both predator and prey (MacKenzie and Leggett, 1991; Werner and Anholt, 1993) and once an encounter happens, the probability of survival for the prey will depend on the predator-prey size ratio (e.g. Miller et al., 1988). Thus, for a given abundance of predators, those individuals with high growth rate resulting from longer foraging times should experience higher mortality than those with shorter foraging times; however the larger the individual, the more likely it will escape from a predator attack. I would expect salmon to have a comparatively higher mortality rate in the coast than in the open ocean, reflecting the fact that coastal predator density is higher than in the open ocean (see for instance Ch. 8 in Longhurst and Pauly, 1987).

2.10.7 High Seas Mortality

Consistent predators in the open ocean environment are salmon sharks (*Lamna ditropis*) and fur seals (*Callorhinus ursinus*) (Fiscus, 1980; Nagasawa, 1998; Ricker, 1976). Nagasawa estimated in 12.6 to 25.2% the losses of the total annual run of Pacific salmon from spring to autumn 1989 from salmon shark predation in the North Pacific Ocean. Salmon sharks and furs seals are large opportunistic predators that rely on random encounters with their prey to feed. Considering the comparatively large size of the predators, the probability of salmon surviving an attack should be very similar across a wide range of salmon body sizes. This suggests that the mortality rate should depend more on activity levels than in body size. If this is the case, it may lead sockeye to behave in a risk-averse manner, with shorter foraging

times during the early part of ocean residence, and postpone risky behavior (*sensu* Clark, 1992) as long as possible. This may explain the low food consumption levels and low growth rate of immature sockeye observed during the early period of residence in the open ocean, and increase in feeding during the sexual maturation period in the last year of ocean residence reported by LeBrasseur (1966), LeBrasseur and Doidge (1966), Ricker (1962), and Ricker (1976).

2.10.8 The Reproductive Migration

Once large and mature individuals reach the coast, the main predators they encounter there are blue shark (*Prionace glauca*), dogfish (*Squalus suckeyi*), halibut, killer whales (*Orcinus orca*), harbor porpoise (*Phocoena phocoena*), Dall's porpoise (*Phocoenoides dalli*), harbour seal (*Phoca vitulina*), northern sea lion (*Eumetopias jubatus*), and California sea lion (*Zalophus californianus*) (Fiscus, 1980; Ricker, 1976). Total mortality during this stage seems to be limited to about 5% according to Foerster (1968) because of the low abundance of those predators, the short residence time of migrating adults in the coastal environment, and predator saturation (Ricker, 1976). However this predation risk can increase when environmental conditions delay the upriver migration of mature sockeye (Fiscus, 1980).

2.10.9 Upriver Migration Mortality

Losses during the upriver migration fall into three categories: a) predation mortality; b) death from parasite attacks; and c) death by exhaustion. Predation mortality during this stage is higher in males because of their bright red color and larger body size, although most predators (bears, sea gulls, eagles, harbour seals) seem to prey on spent or dead sockeye and their total effect on the spawning stock is considered low (Burgner, 1991; Foerster, 1968).

Mortality associated with parasitic infections varies considerably and has been observed to reach up to 90% in the Chilko River stock during 1963 and 62% in the Horsefly River run during 1961 (Burgner, 1991). The most common pathogen associated with such mortality is the 'columnaris' disease that affects the gills and is caused by the bacteria *Flexibacter columnaris* (Gilhousen, 1990). Although exposure to this pathogen is common for

Fraser River sockeye, mortality from a columnaris infection seldom occurs at temperatures below 13 °C (Gilhousen, 1990). Other reported diseases are the bacterial kidney disease caused by *Corynebacterium* sp. which is lethal across a wide range of temperatures, *Aeromonas salmonicida* and *A. hydrophila*, infectious haematopoietic necrosis (IHN), the parasitic protozoan *Ichthyiophthirius multifiliis*, and a myxosporean (Burgner, 1991; Sanders et al., 1978). The overall mortality effect of disease and its dependency on temperature are not known but suspected to be high.

Mortality from exhaustion does not seem to play a regular role during the upriver migration, although electromyogram telemetry has shown that fish swimming throughout areas of difficult passage in the river incur high metabolic costs and increase their risk of death by exhaustion (Ballantine et al., 1996; Hinch and Bratty, 2000; Hinch et al., 1996). Furthermore, special circumstances like passage obstruction, too low or too high flow level, and high water temperature can increase the likelihood of exhaustion, particularly for those stocks that endure long upriver migrations (Gilhousen, 1990). The energy costs of the upriver migration are quite formidable; successful migrants from Chilko, Stuart, and Adams stocks use 75 - 95% of body fat and 40 - 60% of body protein (Gilhousen, 1980). Measurements of fat and protein content of dead individuals by Idler and Clemens (1959) and Gilhousen (1980) indicate that on average, male carcasses retain 43.6% of the total energy contained in the body at the beginning of the upriver migration, while female carcasses retain 34.7%. This fraction can be considered as an estimate of the limits of energy loss that individuals can take before death. There is no estimate of the extent of mortality attributable to death by exhaustion during the upriver migration.

The overall upriver mortality is very variable, ranging from near zero to about 90% (Gilhousen, 1990). Foerster (1968) assumed that on average the mortality during the upriver migration is about 5%. There is a concern that high mortality may now be occurring more frequently for Fraser River stocks, in conjunction with habitat and climate changes that may be causing higher summer temperatures.

Prespawning mortality, defined as that which occur after the individuals arrive at the spawning ground but before they complete spawning, is density independent and seems to

depend on environmental conditions like water temperature, river flow, and suspended solids Gilhousen (1990). Those factors are associated with increased metabolic costs and/or reduction in oxygen intake capacity, and predispose fish to death by infectious diseases. Barring unusual environmental conditions (like landslides, that can lead to very high mortality rates), Gilhousen indicates that this mortality is usually below 10% (5% on average).

2.11 Recruits per Female Production

Once mature females reach the spawning gravels their expected productivity (in terms of resulting mature recruits per female) is high but quite variable and depends on race, year, and stock density. DFO stock - recruitment data from 1948 to 1997 for 27 British Columbia races show values ranging from 0.00017 up to 1999 effective adult recruits per spawning female. The frequency distribution of these data (Figure 2.16) has a mode at 6 recruits/female and a mean of 9.9 recruits/female. The mean was estimated as $e^{(\Sigma \ln R/F)/n}$ to reduce the effect of extreme values.
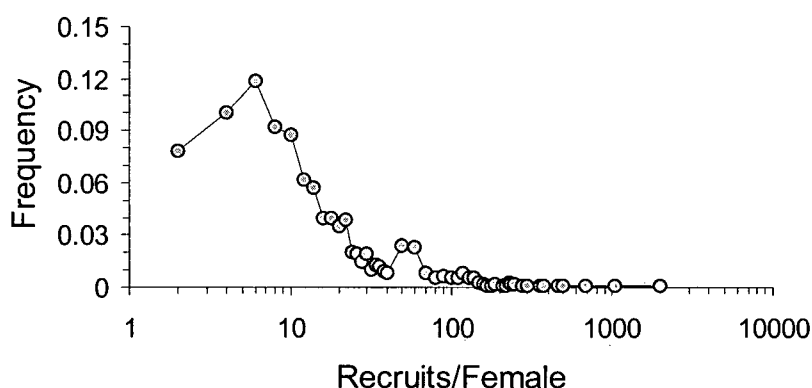
Figure 2.16. Frequency distribution of recruits per female for sockeye salmon Fraser River races (based on DFO recruitment data for 27 stocks from British Columbia).

Figure (2.16) shows that only 8% of the stock-recruitment data correspond to populations at unfished equilibrium (those with adult recruits/female = 2) and the rest of the distribution is dominated by highly productive stocks. This may be a result of the high level of exploitation which those populations have been exposed.

2.12 A Synthesis of the Life History Pattern of Fraser River Sockeye salmon

The life history cycle of Fraser River sockeye salmon that emerges from the above description is of races of individuals that return from shared feeding grounds in the Alaska Gyre to spawn in their natal streams during summer. Hatchlings emerge from the gravel the following spring (mid April to early June) and migrate to a nearby nursery lake where they stay for one year. At the moment of lake entrance they weight between 0.1 and 0.2 g and have experienced 87.5% mortality from the fertilized egg to the fry stage. During the year of lake residency juvenile experience a mortality rate average of 70.77%, and smolt at an average weight of 5.8 g. During early spring smolts begin the downriver migration and reach the estuary of the Fraser River by early May. When the smolts reach the estuary their body weight is about 12 g.

Once in the marine environment, they actively migrate northward in groups along a narrow band near the coast (see Fig. 2.10). By October-November the juvenile fish leave the coast and enter the Alaska Gyre. During their residence in the Strait of Georgia juvenile sockeye have a high apparent growth rate, reaching a weight of 80 g. After leaving the coastal environment juvenile disperse at low density into the Gulf of Alaska where they seem to prefer the central area (see Fig. 2.12).

The residence time in the open ocean is 20 to 23 months. While there, juvenile fish no longer swim in groups and move northward during the summer months and southward during winter. During the last 2-3 months maturing individuals initiate the return migration and reach the Fraser River mouth from early July up to early October. At the moment of entering the river, sockeye salmon weight 2.2 to 2.8 kg and have ceased feeding. Upon reaching the spawning grounds an average Fraser River female has an egg spawning potential of 2,000 to 5,000 eggs, from which an average of 9.9 will reach the next spawning stage as adult recruits.

During the marine stage sockeye salmon have a size-dependent mortality risk, with larger individuals having a decreasing risk. On average, a Fraser River sockeye salmon has a 94% risk of mortality from the smolt to adult period.

CHAPTER 3
SPAWNING MIGRATION IN FISH POPULATIONS: A CASE STUDY WITH SOCKEYE SALMON

3.1 Introduction

Harden-Jones (1968) described the migratory cycle in fishes as a sequence of movements between an adult feeding area, a spawning area, and a juvenile feeding area. Mature individuals move from their feeding grounds toward the spawning grounds to reproduce. The new cohort of individuals then moves to a juvenile nursery area and eventually to the adult feeding grounds where they reach maturity and repeat the cycle.

Reproductive migrations occur across a wide range of temporal and spatial scales, from daily events up to once-in-a-lifetime of the individuals (Quinn and Dittman, 1992). Daily migrations occur mainly in tropical areas and the migration distance is usually short. For instance, in the Red Sea a surgeonfish (*Acanthurus nigrofuscus*) migrates up to 2 km each evening along the shoreline to specific sites to mate and then offshore where they spawn (Myrberg et al., 1988). Annual and once-in-a-lifetime migrations are characteristic of temperate and boreal species. Migrants that undertake them must swim long distances to reach the spawning grounds (Quinn and Dittman, 1992). Examples of temperate species with an annual migration cycle are shad (*Alosa sapidissima*), pacific herring (*Clupea pallasi*), pacific hake (*Merluccius productus*), and North Sea plaice (*Pleuronectes platessa*) (Arnold, 1981; Bailey et al., 1982; Hourston, 1982; Quinn and Adams, 1996). Examples of species that migrate and reproduce once in their lifetime are Pacific salmon (*Oncorhynchus* spp) (Groot and Margolis, 1991), and American and European eels (*Anguilla rostrata* and *A. anguilla*) (Harden-Jones, 1968).

The theory of natural selection predicts that the objective of such migrations is to deliver the sexual products at a time and a location that would maximize the chances that early life stages will reach maturity and reproduce, subject to constraints imposed by the genotype and the phenotype of the migrant. However, the process of delivering gametes to the spawning grounds has costs. Adults incur a metabolic cost from the swimming activity

required to move from the feeding grounds to the spawning grounds, and a cost from an increased risk of mortality by exposure to a wide variety and abundance of predators (Bernatchez and Dodson, 1987; Millinski and Parker, 1991). Those costs generate a strong selection for anatomical, physiological, and behavioral traits that reduce energy expenditure and improve survival while traveling (Bernatchez and Dodson, 1987). Pelagic migratory species have streamlined bodies and high metabolic efficiency during swimming (Ware, 1975; Ware, 1978; Weihs, 1973; Weihs, 1987). Migratory behavior in marine fishes is also coupled with shoaling behavior (Roff, 1988), and shoaling is a well recognized behavior for predator avoidance (Pitcher and Parrish, 1993).

Migratory fish are also known for having good orientation and navigation abilities, allowing them to reach the spawning grounds from the feeding grounds (Bernatchez and Dodson, 1987; Quinn and Dittman, 1992; Roff, 1991). This is an essential ability for migratory species (Roff, 1991) as it provides individuals with the capability of returning to the spawning area and reduces travel time. Species like sockeye salmon often cover 1,000-2,000 km in 4-10 weeks to reach the natal river (Quinn, 1990; Quinn and Dittman, 1990; Quinn and Groot, 1984), and Pacific herring (*Clupea harengus pallasi*) converge to the macrophyte beds where they spawned before (Hourston, 1982). Fish have been shown to orient with sun position, polarized light patterns, chemical cues, and electric and magnetic fields (reviewed in Leggett (1977)). However most such studies have been done in controlled conditions and there is no evidence of the use of any of those clues by an individual while migrating in the field (Quinn and Dittman, 1992).

Reproductive migrations are also characterized by occurring within a short time span at a well determined time of the year, with a high synchronization of the initiation and cessation of the migration (Baker, 1978; Dingle, 1980; Harden-Jones, 1968; Quinn and Leggett, 1987; Sinclair and Tremblay, 1984). Those features are considered a parental adaptive response to synchronize spawning with the phase of the seasonal cycle in the spawning grounds that maximizes growth and survival during the early life stages of development (Gauthreaux, 1980). For instance, Brannon (1987) found that races of sockeye salmon from the Fraser River that spawn in sites with higher incubation temperature arrive later to the spawning grounds than those with cooler temperature. Brannon interpreted this

behavioral compensation for incubation temperature as a mechanism to synchronize fry emergence with the spring bloom in the nursery lake. Selection for reproductive timing is also at the core of the mechanisms used to explain recruitment success in clupeoid fishes (e.g. the match-mismatch theory of Cushing (1978), and the optimal environmental window of Cury and Roy, 1989). Cushing (1978) based his match-mismatch theory on the consideration of spawning time as a mechanism to synchronize the co-occurrence of larval stages of Atlantic herring (*Clupea pallasi*) with the appropriate phase of the annual plankton production cycle. Cury and Roy (1989) proposed the optimal environmental window concept from the consideration of spawning timing arising from a compromise between high productivity and strong turbulence.

It has also been postulated that adult migrants should swim with a high degree of orientation in a bioenergetically efficient manner to maximize energy allocation into reproduction rather than into movement (Roff, 1991; Weihs, 1973; Weihs, 1987; Weihs and Webb, 1983). There is the perception that some environmental factors, notably temperature and advection by currents, have an important effect on the costs of migration: temperature because of its effects in the metabolism of the fish, and advection because of its effects on orientation and swimming speed (Arnold, 1981; Harden-Jones, 1981; Harden-Jones et al., 1978; Hewitt, 1981; Hunter and Sharp, 1983; Leggett, 1977; Sinclair and Iles, 1989; Trump and Leggett, 1980; Weihs, 1987).

My aim in this chapter is to model the migratory behavioral tactics that would maximize reproductive output of a mature adult. Hopefully, such a model will allow prediction of how return migration patterns arise for species like sockeye salmon and how they may change should there be persistent changes in marine environmental conditions. Most of the features of reproductive migrations seem geared toward the reduction of travel time, total metabolic costs, and predation risk. Thus I hypothesize that the migratory behavior of mature adults returning to spawn minimizes an expectation of the total cost of migration, defined by metabolic costs of movement and the risk of predation, so as to maximize reproductive output on the spawning grounds. Their migratory behavior (swimming speed and orientation) in space and time is presumed to be an optimal response to the spatial and temporal distribution of risk of mortality, and to environmental variables known to influence

metabolic costs, like temperature and currents. If the geographic location of the spawning grounds is fixed, then there may be an optimal set of migratory behaviors that would maximize reproductive output at the spawning grounds given the location of the migrant at the time when it begins oriented swimming activity, the time to reproduction, and the environmental conditions along the route.

The objectives of this chapter are: 1) Develop a spatially-explicit state-dependent dynamic model for the estimation of optimal migratory behavior for the reproductive migration of a female fish based on the migration cost – reproductive output tradeoff. 2) Apply the model to the spawning migration of sockeye salmon from the Fraser River and estimate the optimal set of tactics for their return migration across the NE Pacific Ocean. 3) Estimate time and energy costs during the migration of sockeye salmon.

3.2 The Model

Individuals undergoing a reproductive migration have accumulated a large potential reproductive asset during the time prior to migration and face the problem of delivering it to the spawning area in the most efficient way. Their central problem is then how to select the best possible route to reach the spawning grounds from the current position, in the face of the conditions prevailing along the route. During this process a portion of the assets will be used to cover the metabolic costs of traveling, thus reducing the realized reproductive fitness at the spawning grounds, and some energy assets may be gained by foraging along the migration.

The state of the fish during the migration is defined in terms of its geographic location and total energy content (E). Energy content is further partitioned into structural energy and energy reserves. Structural energy is locked into body structures required for life support and reproduction and cannot be used for any other purpose. Energy reserves are completely flexible and can be used for any purpose including the creation of additional body structure.

Structural energy (E_s) is acquired during ontogeny and is closely related to growth in size. Early in life most of the surplus energy is used for structural growth (see Reiss (1989) and Tyler and Calow (1985) for reviews on the subject), and it is only later in life when the

growth rate decreases, that a larger fraction of surplus energy is allocated into reserves that can be used for reproduction (Calow, 1985).

Energy reserves can be further partitioned into those required for current reproduction purposes (E_r) (gamete production, territory defense, nest construction, etc.) and the remaining (E_o) to other purposes not related to the current reproductive effort. Under this partition, semelparous fishes would have all the available energy reserves allocated to current reproduction, while iteroparous fishes would have to tradeoff current reproductive output with future reproductive potential and allocate a large enough fraction of their energy reserves to ensure survival for the next reproductive cycle (Calow, 1985).

Total energy can then be represented as follows:

$$E = E_s + E_r + E_o \qquad \qquad \dots (3.1)$$

Once a migrant arrives to the spawning grounds, total energy and structural energy are fixed and reproduction can only occur if $E_r > 0$. At this point structural energy E_s and energy reserves E_o can be represented as fractions aE, and bE, of the total energy, while the energy allocated to reproduction can be represented as follows:

$$E_r = (\alpha + G) N \qquad \qquad \dots (3.2)$$

> Where
>
> > G = Energy density of one gamete
> >
> > N = Number of gametes produced
> >
> > α = Costs associated with the production and delivery of one gamete

Parameter α includes the metabolic cost of producing the gametes and all the associated activities needed for their delivery once the parent is in the spawning area (nest building, territory defense, mate selection, parental care, etc.). This simple formulation represents the cost of an average nest and contains two classical tradeoffs, parental care (controlled by α) versus total fecundity (N), and egg size (controlled by G) versus total number of eggs (N) for a female (see for instance Einum and Fleming, 2000). Equation (3.2)

does not consider that the associated costs of reproduction may change with the numbers of eggs deposited per nest (i.e. the cost per egg decreases as clutch size increases because the costs of nest building and protection remains the same regardless of the number of eggs laid in it). This consideration may have a significant effect on the number of eggs that a female may allocate per clutch once it reaches the spawning grounds. However the model developed in this chapter focus on the selection of optimal return trajectories relevant during the migration from the feeding grounds to the spawning grounds, and for that reason the clutch size tradeoffs at spawning are not represented here.

Given a total energy amount, the number of gametes (production potential) for an adult is defined in terms of the above parameters by:

$$N(E) = E \, (1 - a - b) / (\alpha + G) \qquad \qquad \dots (3.3)$$

Reproduction in migratory species is constrained in time and space and can only occur at the spawning site (with coordinates x_s, y_s) during the spawning time (T). Therefore, the expected reproductive output (F) of a female at time T can be represented as an energy and location dependent function as follows:

$$F(E, X, Y, T) = \begin{cases} N(E) & \text{if} \quad (X, Y) = (x_s, y_s); E_r > 0 \\ 0 & \text{otherwise} \end{cases} \qquad \dots (3.4)$$

Although Eq. (3.4) defines a positive fitness value for one point in space at time T, it can also represent an area and a season by assigning site and time specific habitat quality or survivorship on a grid. Habitat quality and survivorship can be defined in terms of development time, food availability, predator density at each site, advection, temperature, and any other variable of interest. For any other point in time and location, the fitness expectation of an individual at the spawning grounds during the spawning season is conditional on the current state of the individual, its geographic location, and the remaining time to the spawning event:

$$F(e, x, y, t) = \text{Max } E\{N(E(T)), X(T), Y(T) \mid E(T) = e, X(T) = x, Y(T) = y\} \quad \dots (3.5)$$

The decision about where to go is taken on the basis of the mortality risk of the target area (μ), the metabolic cost (m) required to reach the area, and the growth (g) achieved while in transit from location (x,y) to (x+δx, y+δy). δx, δy are displacements in the x and y directions given by the grid used to discretize the space where the optimization is carried out. Thus for any time t < T and location other than that defined in Eq. (3.4), individuals can maximize their fitness by optimizing their migration trajectory (swimming speed and orientation) as follows:

$$F(e, x, y, t) = \underset{\delta x, \delta y, v}{\text{Max}} \left[(1 - \mu_{x+\delta x, y+\delta y, t+\delta t}) F(e + g_{x+\delta x, y+\delta y, t+\delta t} - m_{x+\delta x, y+\delta y, t+\delta t}, x+\delta x, y+\delta y, t+\delta t) \right]$$

$$\ldots (3.6)$$

Where δt is the time required to move to the new position, v is the swimming speed of the migrant, and $\mu_{x+\delta x, y+\delta y, t+\delta t}$ is the mortality risk for moving over (δx, δy) in time δt. Notice that this equation is solved across space, and time is only being carried along in the calculations (time δt to move (δx, δy) implied by v and currents). Eq. (3.6) provides a simple way to deal with complex trajectory shapes by assuming linearity of the (δx, δy) trajectory at very short spatial scales. Furthermore, Eq. (3.6) works on complex coastal geometries as long as the δx, δy values are small and allow the explicit representation of those features.

Equation (3.6) provides a direct method for quantifying the effects of distance, environment, and mortality on the reproductive output of a migratory organism. It also contains an explicit accounting of the long term effects on fitness of short term decisions leading to energy gains (g - m) and expected mortality losses (μ) that a migrant may experience by moving to a particular area at any given point in time.

Notice that Eq. (3.6) defines a myopic (in space) model that searches the environment within a restricted region ($\pm$$\delta$x, $\pm$$\delta$y) around the current position to make a decision to where to move next. This implies that migrants can either assess the state of the environment within the region ($\pm$$\delta$x, $\pm$$\delta$y) or have an expectation of its state in order to make the decision. One could think that this assumption can be relaxed by reducing the region of interest ($\pm$$\delta$x, $\pm$$\delta$y) into a small area (say to a radius of 10 to 20 body lengths) where it would be reasonable to

presume that an individual can assess the environment. However, environmental conditions near the end of the route do have a bearing in the definition of the optimal migratory behavior throughout the whole process, as I found in this exercise. Thus the assumption of knowledge in a region beyond the sensorial range of migrants does not disappears by reducing the spatial scale at which the optimization is done. However, if we assume that individuals can determine their position we could relax the condition of omniscience by considering that the observed migratory behavior is a result of a blind process that rewards with a higher fitness value to those individuals that take the right decision at the right location, time, and physiological state. The omniscience condition can also be relaxed if the environment is structured in such a way that the state of the environment in the surrounding location can be used as a predictor of conditions further away. In both cases, this model can be used to ask the question of whether the principles defining the state dynamics of migrants as given in the model and the environmental conditions given are sufficient to explain the migratory behavior observed. This is quite convenient since it implies that the only restriction to define values for ($\pm\delta x$, $\pm\delta y$) is the level of spatial resolution available to describe the environment and/or the distance at which the correlation breaks down. In regard of the migrants ability to determine their location, it has been shown under controlled conditions that migratory fishes have a number of orientation and navigation abilities (see Leggett (1977) for a review on the subject). However there is no information on how a migrant actually navigates in the field (Quinn and Dittman, 1992) or if they actually can determine their location. Here I take the view of Healey and Groot (1987) and assume that long-range migrants, particularly sockeye salmon, are capable of a range of orientation and navigation abilities like compass orientation and bi-coordinate navigation.

3.2.1 Swimming orientation, Advection by Currents, and Travel Time

The calculation of the swimming orientation needed to reach a target destination along a linear trajectory is straightforward in the absence of advection by current. However in the presence of currents, the migrating fish has to adjust its swimming orientation to offset advection along the trajectory leading to the target location. Thus the swimming orientation and the travel time required to reach destination are dependent on the velocity of the current and swimming velocity of the fish, and one of them has to be known to determine the other. A

simple method to estimate traveling time (t_t) first and then swimming orientation in a bi-dimensional space was derived from the following considerations.

Assume that the migrating fish is in location h_i (with coordinates [x_i, y_i]) and chooses to move to h_j (with coordinates [x_j, y_j]) at a swimming speed of known magnitude S in the presence of a water velocity vector **U** with components (u_x, u_y). We can translate location h_i to the origin by calculating $m_x = (x_j - x_i)$ and $m_y = (y_j - y_i)$; coordinates (m_x, m_y) give the position of h_j under the translation. We also know from Pythagoras theorem that $S = (s_x^2 + s_y^2)^{1/2}$. Notice that at this point the (s_x, s_y) components of **S** are not known. However, if there is a swimming orientation that allows the fish to reach h_j from h_i, then the ground velocity of the fish is the addition of the velocity field of the fish (speed and orientation) and the current. With such ground velocity the point (m_x, m_y) will be reached in t_t time units, and the components of the solution are as follows:

$$(s_x + u_x)\, t_t = m_x\, ; \quad (s_y + u_y)\, t_t = m_y \qquad \qquad ...(3.7)$$

rearranging terms, substituting s_x and s_y in $S^2 = s_x^2 + s_y^2$, and setting it to 0:

$$0 = (m_x / t_t - u_x)^2 + (m_y / t_t - u_y)^2 - S^2 \qquad \qquad ...(3.8)$$

solving the square terms and multiplying by t_t^2;

$$0 = (u_x^2 + u_y^2 - S^2)\, t_t^2 - 2\, (m_x\, u_x + m_y\, u_y)\, t_t + (m_x^2 + m_y^2) \qquad \qquad ...(3.9)$$

All the components in Eq. (3.9) are known with the exception of t_t; however Eq. (3.9) is of a second order on t_t, with two solutions that can be determined using the well known solution for a quadratic equation:

$$t_t = \frac{-b \pm \sqrt{b^2 - 4ac}}{2a} \qquad \qquad ...(3.10)$$

Where:

$$a = u_x^2 + u_y^2 - S^2$$

$$b = -2 \, (m_x \, u_x + m_y \, u_y)$$

$$c = m_x{}^2 + m_y{}^2$$

Valid solutions are those for which $t_t > 0$, and $(b^2 - 4 \, a \, c) \geq 0$. Once t_t is known, the swimming orientation of the fish can be calculated from Eq. (3.7).

3.3 An application to the reproductive migration of sockeye salmon of the Fraser River

The reproductive migration of sockeye salmon occurs in two broad phases: the marine phase and the upriver phase. The marine phase covers the migration from the feeding grounds in the Alaska Gyre to the river mouth, while the freshwater phase goes from the mouth of the Fraser River up to the natal grounds where spawning takes place.

My interest here is in the optimal migratory route and behavior during the marine phase of the reproductive migration of a female sockeye salmon. At the large spatial scale at which the optimization is going to be performed, the cross-sectional variability in the river can not be represented. Thus the only valid direction for a spawner is upriver until it reaches the spawning grounds. Furthermore for each race the upriver distance is constant and so are the costs. Uncertainty in environmental conditions may result in changes in year-to-year upriver migration costs. However if the probability distribution of environmental events does not change, then the expectation of the total upriver migration costs does not change either. Adding a constant term to Eq. (3.4) does not change the optimal policy values for optimal speed and direction during the marine phase, thus the upriver migration need not be considered here.

The swimming behavior during the upriver migration may affect the amount of energy available for reproduction. Bernatchez and Dodson (1987) and Gilhousen (1980) found that races with longer upriver migration are more energy efficient than races with shorter upriver migration. Bernatchez and Dodson (1987) attribute this efficiency to a reduction in the wandering of fish across the width of the river and concluded that long upriver migrations

may impose a strong selection against wandering behavior. Those costs may set a lower limit for the total amount of energy available at the beginning of the migration or place an upper limit to fecundity or both. However within the same race those costs are considered constant and have no effect on the optimal policy for migration during the marine phase.

3.3.1 The marine phase of the reproductive migration

Races of sockeye salmon from the Fraser River start their reproductive migration from their feeding grounds in the Alaska Gyre during the spring and summer months (French et al., 1976). Prior to the onset of migration sockeye salmon races from the Fraser and the Columbia Rivers inhabit the Alaska gyre in a broad region north of 45°N and east of 165°W (French et al., 1976).

While in the ocean, returning sockeye salmon swim at a sustained speed of about 1 body length per second, covering 45 to 60 km/day and traveling distances up to 3,600 km to reach the mouth of the Fraser River (Groot and Quinn, 1987; Hartt and Dell, 1986; Madison et al., 1972; Quinn, 1988; Quinn et al., 1989). Once there they still face a trip upriver that can go for several hundred kilometers before reaching the natal stream (see Table 2.1).

Specific return routes for individual races are not known, although Groot and Quinn (1987) proposed a meta-population return migration pattern based on tagging data from 1958 to 1983 (Fig. 2.1). According to this pattern, mature individuals begin their return migration during the spring and summer months, moving northeastward at the early stages of the return migration and then southeastward later on. Migrants make landfall in a broad area off the west coast of the Queen Charlotte Islands, and follow the dominating angle of the coastline until they reach the northern tip of Vancouver Island. At this location, an annually varying fraction of the total run swims through Johnstone strait to reach the Fraser River (the northern route), and the rest of the fish move through the Strait of Juan de Fuca (the southern route). The fraction returning via the northern route is known as the Northern Diversion Rate (NDR) (Hamilton, 1985).

The NDR has bioenergetic consequences for the migrants and management implications for the fishery. The route through Juan de Fuca is longer than through Johnstone strait, and those migrants swimming through the Juan de Fuca Strait are exposed to more American fisheries (although some of the fishes migrating along the north route are also caught around Point Roberts near the Fraser River mouth).

Prior to 1977 and through most of the recorded history the NDR fraction has been in the order of 10% to 20% (Kolody, 1998). Deviations from this pattern were rare and when they occurred, warmer sea surface temperature on the west coast of Vancouver Island were also present (McKinnell et al., 1999). McKinnell et al. also indicate that the historically low values of the NDR index has led to the perception that migration through the northern route is an anomaly. Since 1978 the occurrence of large NDR values has become more frequent, and from 1992 to 1997 the NDR reached values above 50%, with the sole exception of 1996 which had a value of 35% (Kolody, 1998).

Several statistical models have been developed to predict the NDR for management purposes using sea surface temperature (SST) in one or more points along the B. C. coast and Fraser River discharge as predictors (e.g. Groot and Quinn, 1987; Hamilton, 1985; Hsieh et al., 1991; Xie and Hsieh, 1989). In a recent assessment of the models used to predict the NDR McKinnell et al. (1999) confirmed that SST at Kains Island from April to June give the highest correlates with NDR. They also found that during May SST at Kains correlates quite well with sea surface temperature across the NE region of the Gulf of Alaska, with peak correlation near the northwest tip of Vancouver Island. This pattern is no longer present for the month of July. They concluded that the NDR is determined by temperature conditions in the open ocean, for which the Kains Island index only works as a good forecast from April to June. They did not propose any hypothetical mechanism by which SST could control the route that sockeye salmon may follow as they reach Vancouver Island.

3.3.2 Environment Structure

The oceanic region between 45° - 60° N and 120° - 165° W where the reproductive migration occurs was digitized using a centered grid of 30 x 30 nautical miles. The grid was

laid on an Albers equal-area map projection (Snyder, 1983) and rendered from the mouth of the Fraser River (Fig. 3.1). Individual grid points in this region were categorized in one of two zones according to their average depth. The coastal zone (circles in Fig. 3.1) contains grid points with depths up to 1,500 m, and the marine zone (crosses in Fig. 3.1) contains grid point with depths higher than 1,500 m. I choose the partition at 1,500 m because this value defined coastal stations that were reasonably close to the coastline.
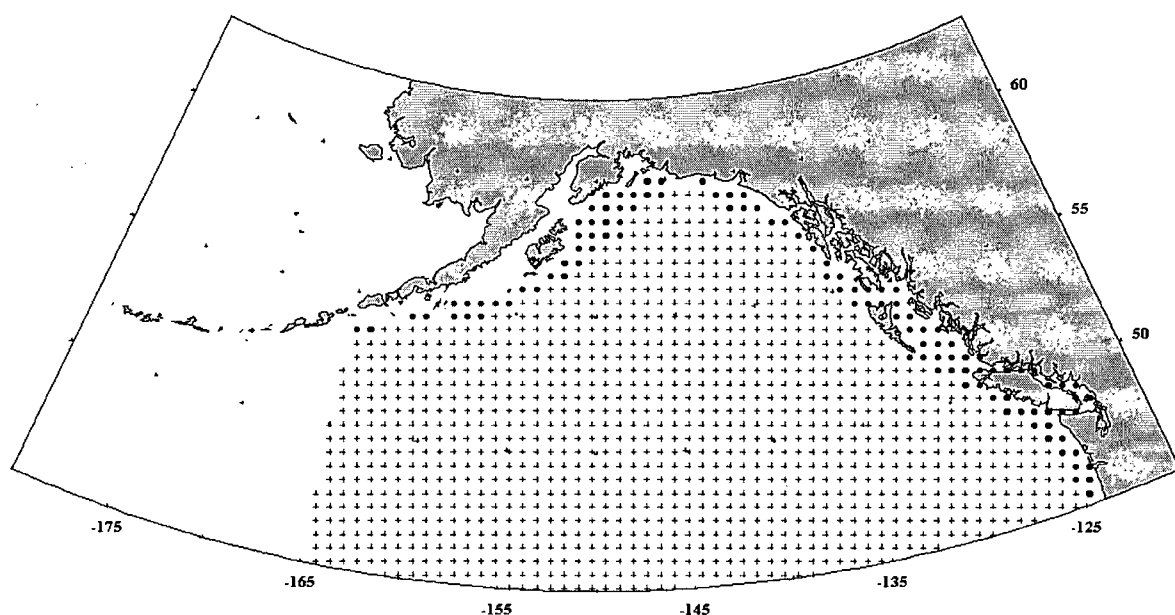
Figure 3.1 Gridded representation of the NE Pacific Ocean. Coastal gridpoints are represented as circles and oceanic gridpoints as crosses.

Sea surface temperature and surface currents were used to define the environmental attributes of the oceanic habitat. Sea surface temperature (SST) was extracted from the Comprehensive Ocean-Atmosphere Data Set (COADS). SST data are given as monthly averages from January 1950 to December 1992 on a 2° x 2° grid. Daily surface currents were calculated from barometric pressure data using the OSCURS numerical model by J. Ingraham (National Marine Fisheries Service, Seattle, USA) from January 1st, 1950 to December 31, 1993. The OSCURS model does not model small scale processes (like eddies) in the open ocean nor phenomena, like tides and estuarine circulation, that define coastal dynamics. See

Ingraham and Miyahara (1988) for a description of this model and Ingraham and Miyahara (1989) for the tuning of the model to the northeast Pacific conditions.

Each data set was averaged to create mean daily environmental condition fields to represent an average year. The COADS data set gives SST as monthly values, thus daily values were obtained from the mean monthly values with a cubic spline interpolation algorithm from Press et al. (1992). Both data series were also interpolated to the grid of interest (Fig. 3.1) with a bilinear interpolation algorithm from Press et al. (1992).

SST fields (Figure 3.2) show a gradual increase in temperature across the NE Pacific, propagating north and west from the coastal area towards the oceanic domain as the season advances. This appearance of smooth change is largely due to the broad spatial and temporal scale averaging of the COADS data, and the interpolation process applied to the data.
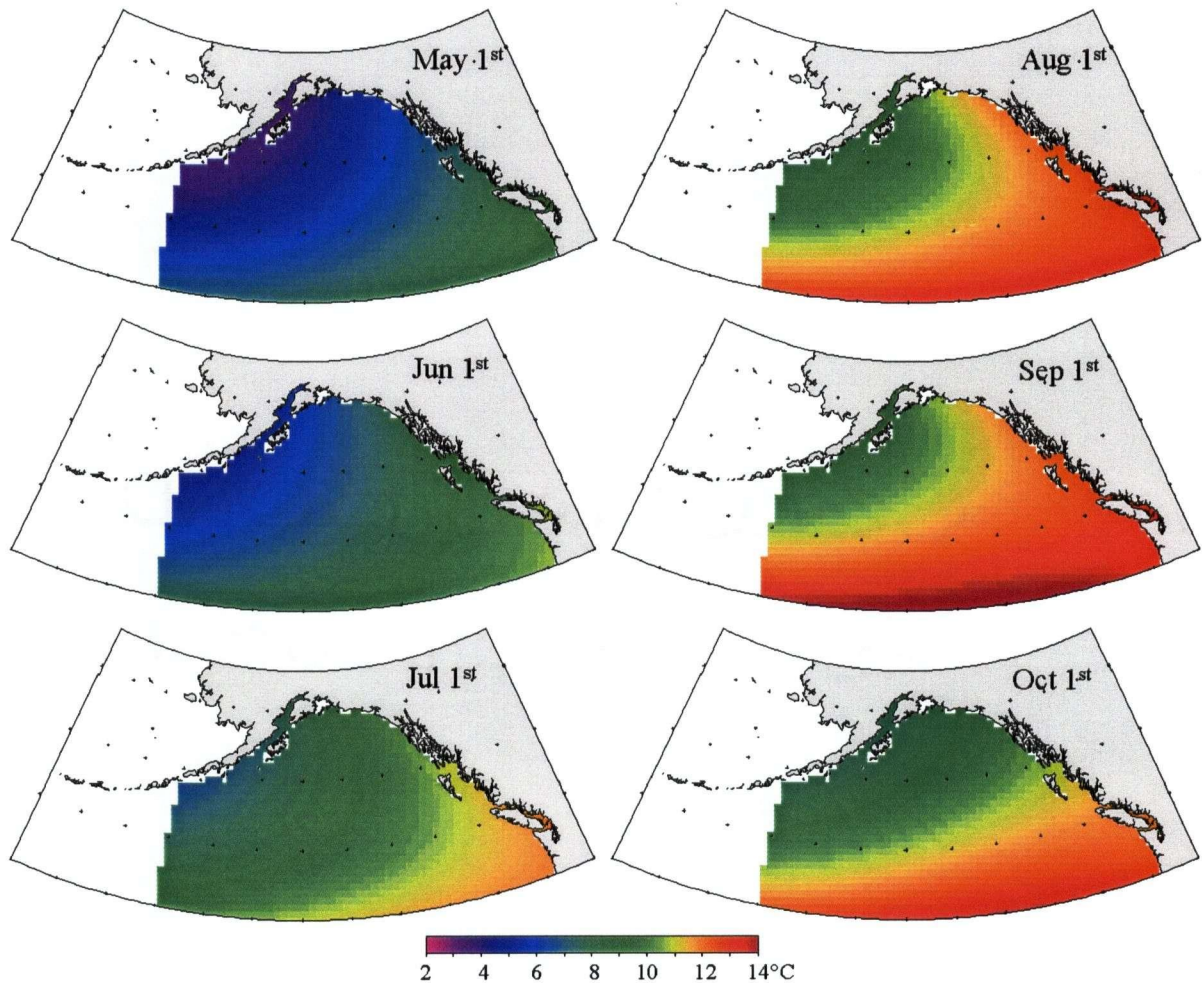
Figure 3.2. Mean daily sea surface temperature in the NE Pacific Ocean (1950-1992). SST plots are only for the first day of the months represented here.

Surface current fields (Figure 3.3) from OSCURS show the West Wind Drift Current (flowing west to east near the center of the grid) splitting into the California current and the Alaska current off the Queen Charlotte Islands as shown by Tabata (1982). The fields also show a contraction of the Alaskan Gyre as the season progresses, leaving the offshore area of Vancouver Island with weaker currents. Note that near-shore currents in the area of the Queen Charlotte Islands and northward are not being deflected to flow along the coast. This is a weakness of the OSCURS model, which is intended for the simulation of oceanic currents only. Near-shore currents were set to zero to reflect the net effect of tidal currents (see Bourque (1999) for an individual-based model that considers them).

0   44 cm/s
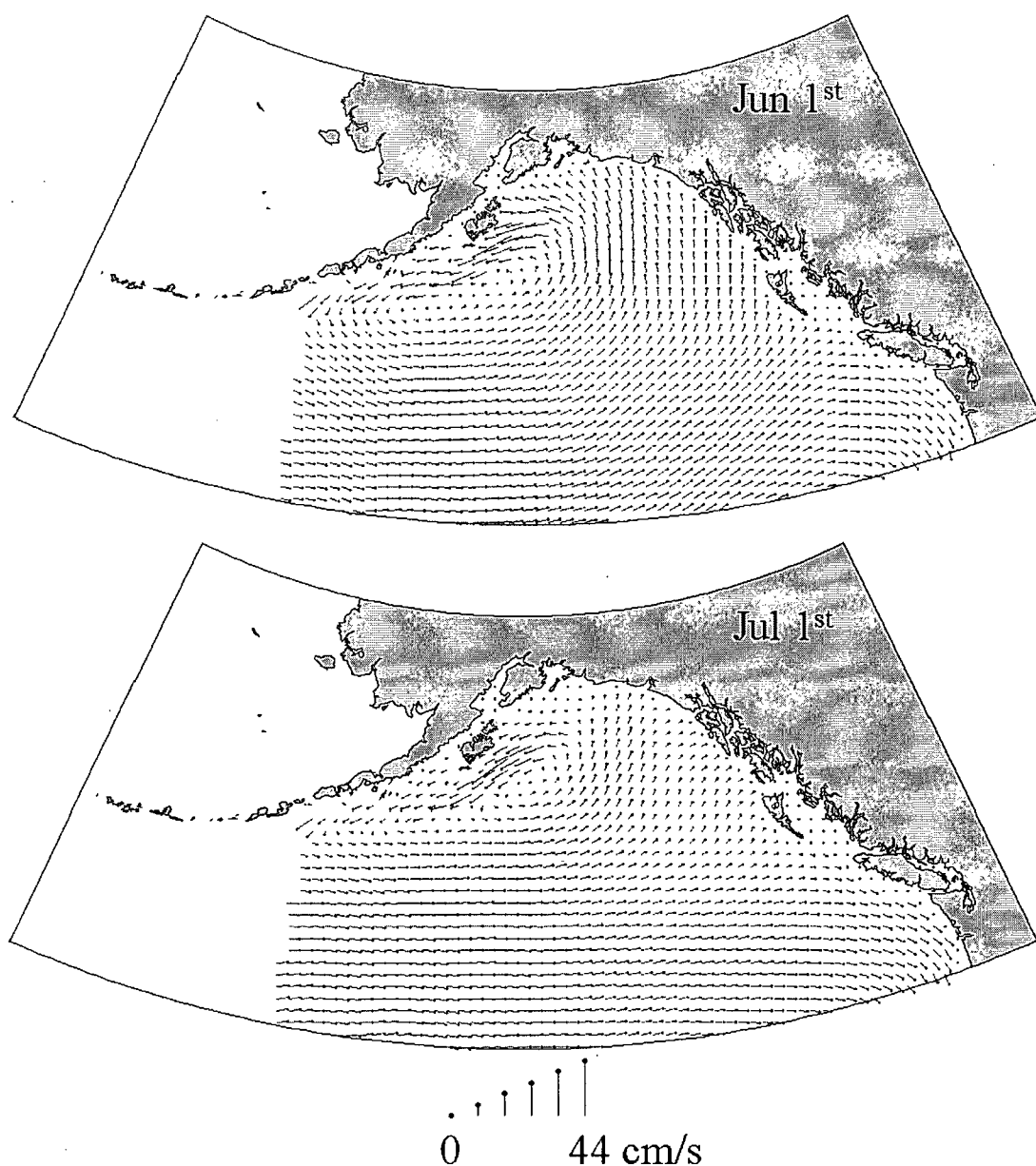
Figure 3.3. Mean daily surface currents in the NE Pacific Ocean (1950-1993). Surface currents are for the first day of each month only.

3.3.3 Mortality

During the marine phase of the migration, mature individuals move through two habitats: the open ocean (defined here as areas deeper than 1,500 m), and the coast (marine areas with depths up to 1,500 m). There are no reliable estimates of such risk for each of these areas or for the entire return migration phase. However, predation losses are considered low

because of a reduced residence period at any giving place, the low numbers of predators that can effectively forage on large sockeye, and predator saturation (Ricker, 1976). Fishing mortality was ignored here since it is unlikely this source of mortality has any bearing on the determination of the migration pattern observed.

Likely there is a differential risk of mortality between the coast and the open ocean, and it may play an important role in the selection of optimal migratory routes. For this reason I configured these two areas with different values for risk of mortality, with a higher value in the coast than that in the open ocean and explored what would be the optimal routes arising from such distribution of risk and environmental conditions.

Ricker (1962) estimated a monthly instantaneous mortality value between 0.0683 and 0.158 for Cultus Lake sockeye during the last two years in the marine environment. Likely, those values overestimate the losses during this period since they were based in smolt-to-adult survival data, which does not allow separation of mortality risk at any part of the marine life stage or area. Ricker (1976) also estimated mortality using an inverse weight method, which yielded 0.008 for a 1,510 g Karluk sockeye. Furnell and Brett (1986) used a similar method for Babine Lake sockeye and estimated a value of 0.004 for a 2,300 g fish (equivalent to a daily instantaneous mortality rate (z) of 0.000133 or a daily survival rate of 0.999867). That value was used here to define risk of mortality (μ) in the open ocean because of the similarity between the weight of Babine Lake sockeye and Fraser River sockeye.

Once sockeye salmon reach the coast, the mortality rate likely becomes density-dependent and time dependent (Fiscus, 1980; Ricker, 1976). During this period, the high densities of salmon rapidly saturate predators and overall losses are small. Foerster (1968) considered the losses for the whole coastal period to likely be around 5%. At a swimming speed of about 1 body length per second (Madison et al., 1972; Quinn, 1988; Quinn et al., 1989) the coastal residence period varies between 10 to 22 days depending on the latitude at landfall. Here it is assumed that the 5% loss corresponds to an average coastal residence time of 16 days, which results in a z value of 0.00321 (0.9968 survival rate). Coastal losses can increase dramatically when sockeye salmon delay river entrance and remain in the coast (Fiscus, 1980). Such losses are not represented here.

3.3.4 Female Condition and Reproductive Potential at River Entry

I configured the model to the characteristics of an Early Stuart female making river entry on July 8th (see Table 2.1). An average female of this race measures 53 cm in length and weights 2,455 g at Albion, 64 km above Fraser River mouth (Gilhousen, 1980). At this location, Gilhousen found that 12.6% of the weight is fat and 19.3% is protein. By the time this female spawns and dies at Forfar Creek (1,152 km above the Fraser River mouth), body weight has changed to 1,836 g of which 0.9% is fat and 11.65% is protein (Gilhousen, 1980). The energy content of this female changes from 20,264.11 kJ at Albion to 4,382.55 kJ retained in the carcass of spent fish at the spawning grounds (using 38.91 kJ per gram of fat and 17.51 kJ per gram of protein from Idler and Clemens, 1959). At the moment of death the carcass retains 21.6% of the initial energy content at Albion.

The length-fecundity relationship in Fig. (2.2) predicts that the average 53 cm female has an egg potential of 3,391 eggs at the spawning grounds. The energy content of an average egg (G) has been estimated at 1,422.5 Joules (Dueñas 1980, in Brett, 1980), representing a net energy investment of 4,824.4 kJ. Gonad production efficiency is not known (Gilhousen (1980), but see Wooton (1985) for a review of the subject). In this model, I assumed that the cost (α) of producing one gamete is 10% of the energy density of such gamete.

Thus at the moment of making river entry (on July 8th), a 53 cm sockeye salmon female has an egg production potential defined by Eq. (3.3) as follows:

$$N(E) = E (1 - a) / (\alpha + G_d) = 20,264.11 * 0.784 / (0.142 + 1.4225) = 10,153 \text{ eggs} \quad \ldots (3.11)$$

This fecundity value is two to five times higher than the 2,000 to 5,000 eggs at the spawning grounds reported by Foerster (1968), and (barring the imprecision associated to α) is a reflection of the cost of the upriver migration. Notice that b was set to zero because sockeye is a semelparous species, and all available energy is used in the current spawning event. The terminal function defined in Eq. (3.4) is then stated as:

$$F(E, x, y, T) = \begin{cases} N(E) & if \quad x, y = FraserRiver \\ 0 & otherwise \end{cases} \qquad \dots (3.12)$$

Notice that the factor $(\alpha + G_d)$ is constant and only scales Eq. (3.11). Furthermore, this factor becomes important once the female reaches the spawning grounds but not before. Since this model explores behavioral choices for migration routes in the marine environment, the factor $(\alpha + G_d)$ was removed from Eq. (3.4). This removal is convenient because there is no information on the value of α, and also changes the units of Eq. (3.4) from egg production potential to units of energy. The use of energy units simplifies the bioenergetics calculations and allows simple algebraic calculation of the realized fecundity for any upriver distance if desired.

3.3.5 Weight Dynamics and Foraging

The dynamics of body weight during migration are at best sketchy. Most of the Fraser sockeye return as age 1.2 individuals with a small percentage returning as ages 1.1 and 1.3 (Killick and Clemens, 1963). During their 26 months of marine residency individuals of age 1.2 grow to 56 cm in lenght and 2.1 to 2.8 kg in weight at the moment they reach the coast (Gilhousen, 1980; Idler and Clemens, 1959; Killick and Clemens, 1963). There is no information to determine at what point during migration growth ceases in sockeye salmon. Ricker (1962) assumed that growth continues up to the time the fish reaches freshwater because sockeye captured by the fishing fleet around Vancouver Island still have food items in their stomach.

Foraging during migration is an activity that could be in direct conflict with the purpose of the reproductive migration. Foraging requires the investment of time and direction of orientation in the search and handling of prey that could otherwise be allocated to migration. Sockeye salmon behavior in this sense offers conflicting views. Fishes caught near the coast often contain food items in their stomach (Ricker, 1962; Gilbert (1913) in Gilhousen, 1980). However, tracking of individuals fitted with ultrasonic tags also shows that individuals in the coast have strong swimming orientation, swim at near optimal swimming speed, and deviation from the main swimming direction seems to be a response to changes in

tidal currents or the presence of land (Healey and Groot, 1987; Quinn and Groot, 1984; Quinn et al., 1989; Stasko et al., 1976). This suggests that the search process required for foraging does not occur and that prey were consumed without the search process associated with foraging. Therefore, I assumed that sockeye does not allocate time to foraging during their return migration and that the content found in their stomach comes from food particles encountered by chance along their migration route. If this assumption is unfounded, the predictions of the model will reflect it.

Since foraging is not being considered, Eq. (3.6) can be rewritten as follows:

$$F(e, x, y, t) = \underset{\delta x, \delta y, v}{Max} (1- \mu_{x+\delta x, y+\delta y}) \; F(e - m_{x+\delta x, y+\delta y}, x + \delta x, y + \delta y, t + \delta t) \qquad \ldots (3.13)$$

Eq. (3.13) maximizes the fitness value defined in Eq. (3.12) by choosing the swimming speed and orientation that minimize metabolic costs and mortality, given the constraints imposed by surface currents, temperature, predation risk, and the geographic configuration of the area.

3.3.6 Bioenergetics

The relevant bioenergetics component for this model is respiration. Respiration accounts for the basal and active metabolism and is a function of body size (W), temperature (τ), and swimming speed (v). A fitted function for sockeye salmon is in Eq. (A.8). This equation estimates metabolic costs in grams per gram of body weight per day and was rearranged to provide respiration values in Joules per fish per day as follows:

$$m = 77.2863 \; W^{0.6486} \; e^{(0.0306\tau + 0.027861v)} \qquad \ldots (3.14)$$

Swimming speed is an important factor in the determination of the overall costs of migration since swimming activity is metabolically expensive (Boisclair and Leggett, 1989). Migrants in particular are believed to swim at metabolically efficient swimming speeds that minimize total metabolic costs during migration (Weihs, 1973; Weihs and Webb, 1983). As defined in Eq. (A.13), optimal swimming speed is affected by weight and temperature. The

temperature range in the NE Pacific Ocean from July to October where the reproductive migration occurs varies from 2 to 14 °C (Figure 3.2). Within this range the effect of temperature on optimal swimming speed is linear (Figure A.9) and follows the relationship $K_s(\tau) = 0.4 + 0.04\ \tau$. Therefore the optimal swimming speed here is calculated from the following equation:

$$v_{opt} = 34.2\ W^{0.1642}\ (0.4 + 0.04\ \tau) \qquad\qquad \dots (3.15)$$

In the context of this chapter, I find it reasonable to assume that the selection of a particular swimming speed may vary from one area to the next depending on the environmental conditions within the limits imposed by aerobic metabolism. Therefore, Eq. (3.15) is used to define an upper limit for swimming speed in the optimization process.

3.3.7 Optimization parameters

The optimization is done on the uniform grid given in figure (3.1). The optimization uses one value per environmental attribute when individuals migrate from point A to a neighbouring point B. This value was calculated as the arithmetic mean of the values of the two locations. This procedure was also applied to the risk of mortality. However, risk was further corrected by the number of days spent traveling for each A-B choice, since mortality risk was expressed on a daily basis.

Optimal swimming speed at each location was explored using sub-multiples of the physiological swimming speed v_{opt} in Eq. (3.11). The values ranged from 0.2 to 1.0 v_{opt} in increments of 0.05. The optimization process estimated the swimming speed and swimming orientation angles that minimize total losses during the migration. The model also estimated the migration time and energy required to reach the Fraser River from each grid point in figure (3.1).

3.3.8 A simple test of the model

The model was tested on a mesh of 30x30 cells, with 56.7 km cell size. Currents were set to zero, temperature was constant at 10° C, risk of mortality was set to 0, and the swimming speed was fixed at 1 body length/sec. The terminal payoff function used was defined as 15,887 kJ at the center of the mesh (X = 15, Y = 15) and zero everywhere else. Under this condition, the optimal trajectories are those that minimize distance and should generate a radial pattern where trajectories converge toward the goal.

The resulting pattern using δx, δy values of –1, 0, and 1 (figure 3.4a) shows linear trajectories at angles that are multiple of 45°. However, trajectories that fall in between show a stair-like pattern or cutouts that result in higher migration costs because of larger distances to swim. This discretization error arises from the search process being limited to the closest neighbor coordinate points implemented on the uniform grid. A two-cell look ahead search (δx, δy = –2, -1, 0, 1, 2) notably reduces this problem (figure 3.4b) and shows a closer approximation to the expected radial pattern. Thus, I used this search pattern to obtain the results below.

a   b
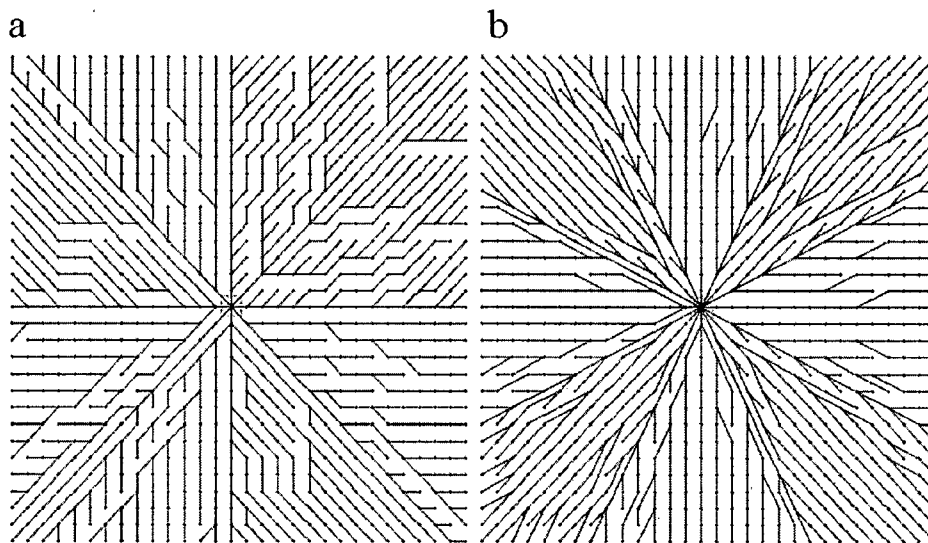
Figure 3.4. Optimal trajectories predicted for test conditions. Figure a is for a one-cell look-ahead search, and figure b is for a two-cell look-ahead search.

3.4 Results and Discussion

The optimal trajectories and the expected costs of the migration predicted by the model, with the mean temperature and current fields presented in Figs. (3.2 - 3.3), are shown in figures (3.5) through (3.7). Optimal trajectories show where migrants should go (Fig. 3.5a) and the swimming orientation required to achieve those trajectories (Fig. 3.5b). These results indicate that sockeye salmon can overcome even the strongest oceanic currents in the Alaska Gyre and reach the Fraser River in 110 days or less (Fig. 3.7a). The maximum expected loss in fecundity from metabolic costs and risk of mortality is nearly 3,000 eggs (Fig. 3.7b) for individuals starting their migration at the western edge of the grid. This value is close to the observed fecundity of small females (Fig 2.2).

The predicted optimal return trajectories (Fig. 3.5a) show three distinct features. 1) The majority of the trajectories in the open ocean are single straight lines (Fig. 3.5a). This suggests that the trajectories simply minimize distance to swim. This is a direct effect of the no-foraging constraint imposed in the model and the high metabolic cost of swimming activity. The only area where it is apparently optimal to take advantage of advection is at the north side of the West Wind Drift Current in the central and western part of the grid. Trajectories in that area go into the West Wind Drift Current, flowing towards the Pacific East coast. 2) The Johnstone Strait route is "closed" to migrants approaching the Fraser from the open ocean, i.e. the route is only optimal to use for those individuals located within a short and narrow band north of Vancouver Island. Migrants coming from the open ocean reach the Fraser River through the Strait of Juan de Fuca, which has a short coastal distance to the estuary of the Fraser River. 3) Optimal routes elsewhere in the coast lead to the open ocean.
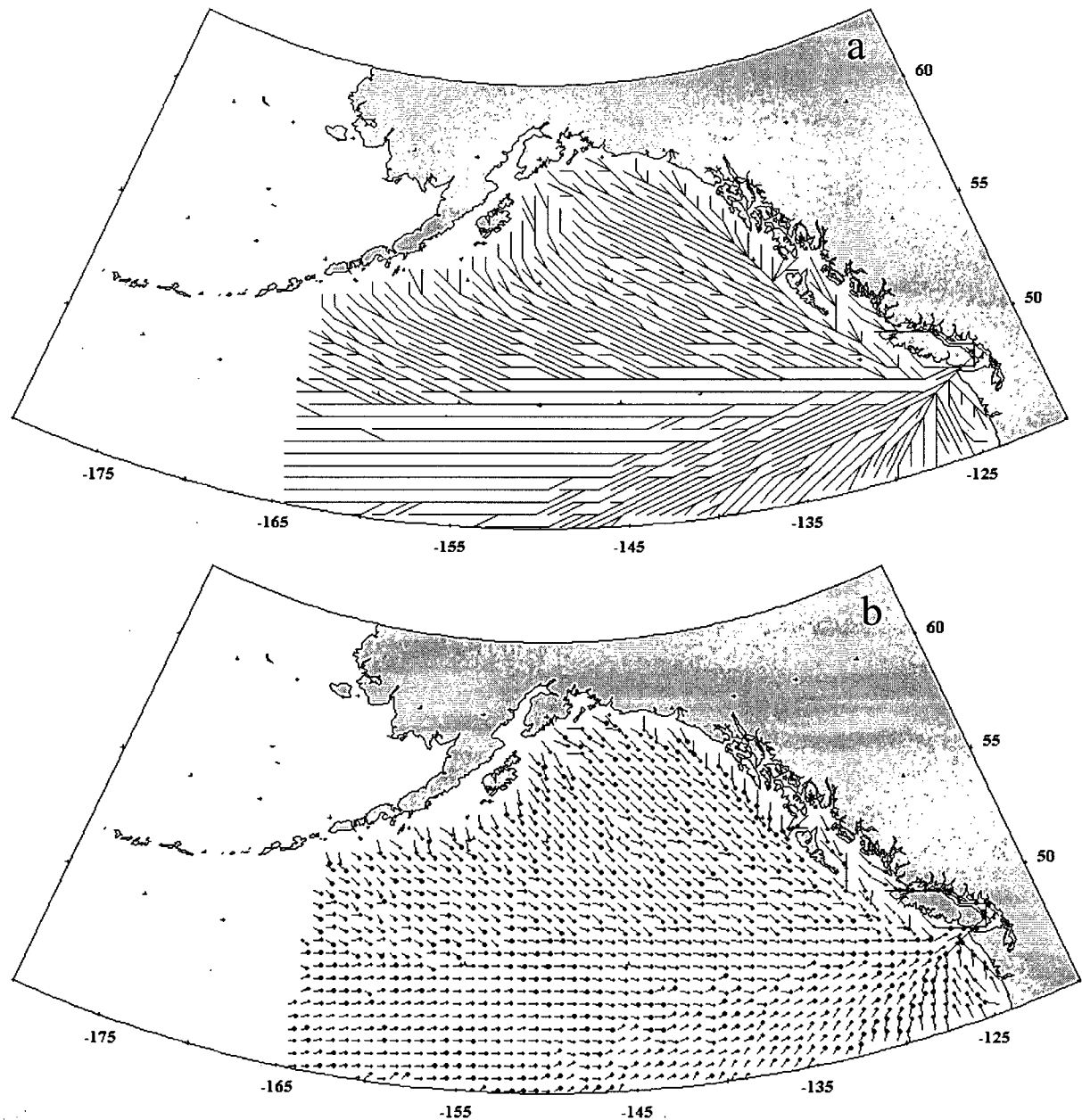
Figure 3.5. Optimal swimming trajectories (a) and swimming orientation (b) for the return migration of sockeye salmon under the assumption of 5% total coastal mortality.

The optimal swimming speed (Fig. 3.6a) and the metabolic costs per km (Fig. 3.6b) distributions show three features of interest. 1) The coastal zone between Washington and Kodiak Island has the highest swimming speeds (above 51 cm/s), and moderate metabolic costs (1,800 to 2,000 Joules/km). The prediction of higher swimming speed in the coast has been observed in the migratory behavior of returning sockeye salmon (Hartt, 1966; Madison

et al., 1972; Quinn, 1988), and the model associates it with the high risk of mortality in the coastal environment. High swimming speeds in the coast yield shorter passage times and a reduction in the time exposed to a high predation risk at the expense of higher metabolic costs. 2) There is a wide area in the southwestern edge of the NE Pacific characterized by low swimming speed (19 – 31 cm/s) and low metabolic cost (800 - 1,200 J/km). In this area, the West Wind Drift current flows toward Vancouver Island, advecting migrants towards the coast (Fig. 3.3), resulting in low optimal speeds and low metabolic costs. 3) There is a small region off the coast of Washington with the highest metabolic costs (2,150 to 2,300 J/km) and moderate swimming speeds of 43 to 47 cm/s. This area is where the California Current branches off the West Wind Drift Current and begins flowing south. Surface currents in the area are not particularly high, but migrants in it will have to swim against the current to reach the Fraser River, resulting in higher metabolic costs.

The distribution of swimming time required to reach the Fraser River from anywhere in the grid (Fig. 3.7b) shows a nearly concentric pattern radiating from the Fraser River. This distribution suggests that the optimal swimming speed at each location in the grid compensates for the effects of advection, keeping travel time dependent on distance to the Fraser River.

This distribution also shows that arrival time is position-dependent. Considering that individuals from the same population arrive to the spawning grounds within a short time span (usually 12 days according to Gilhousen, 1960), then the area of distribution at the onset of migration has to be longitudinally narrow or the onset of migration is position dependent, which implies that sockeye can determine their geographic location with accuracy. Individuals could also swim faster when the starting point is further away, however swimming activity is energetically expensive (Boisclair and Leggett, 1989) and the model indicates that such individuals would reduce travel costs by initiating the migration earlier.
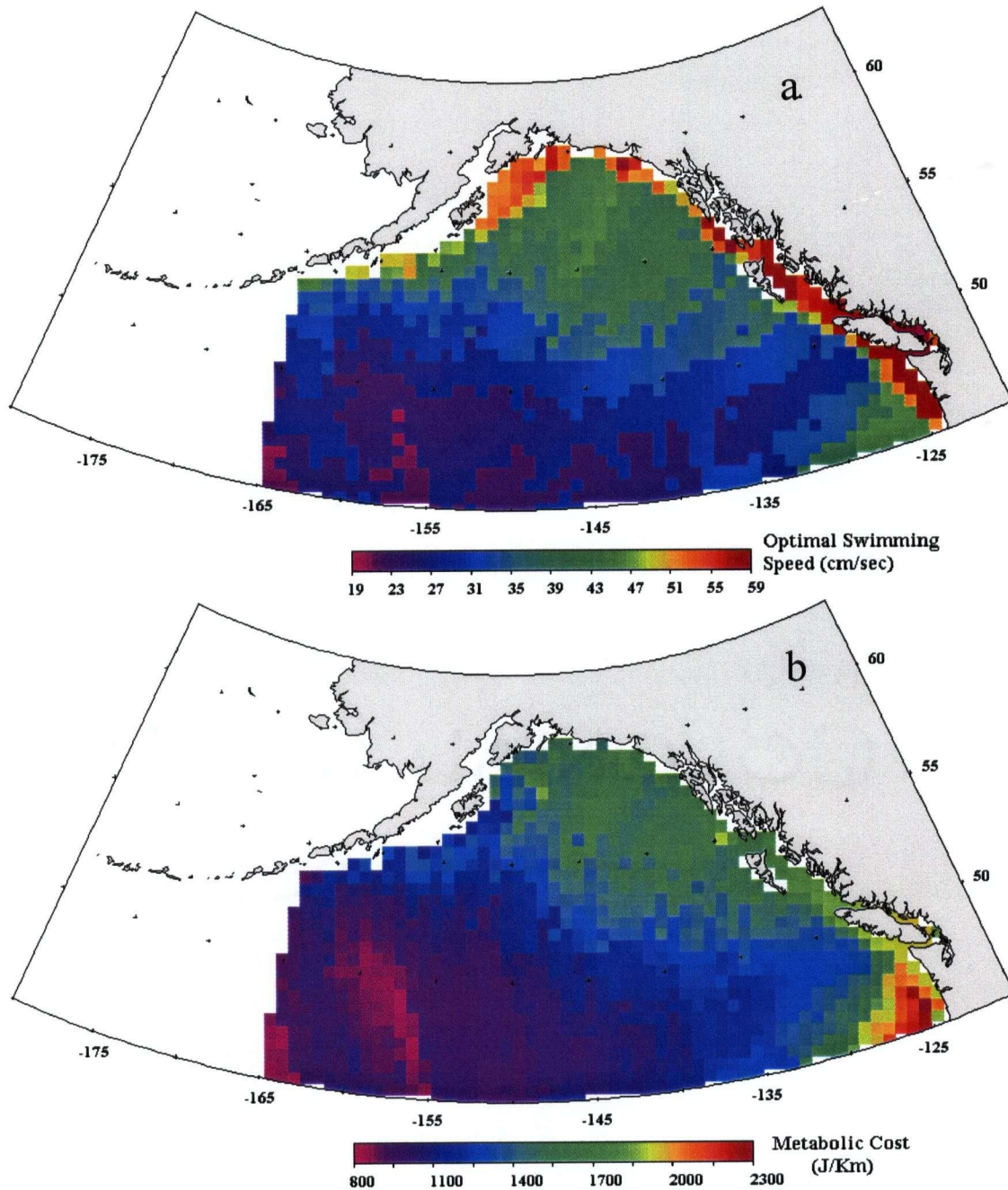
Figure 3.6. Optimal swimming speed (a) and metabolic cost of migration (b) of sockeye salmon in the NE Pacific Ocean under a 5% total coastal mortality.

The distribution of total expected costs (in egg-equivalent units. Fig. 3.7a) shows a small westward shift where the West Wind Drift current flows eastward and the optimum swimming speed is the lowest. Individuals that migrate along that current have a higher

fecundity expectation once they arrive to the Fraser River, although they will not necessarily arrive earlier because of their reduced optimal swimming speeds.
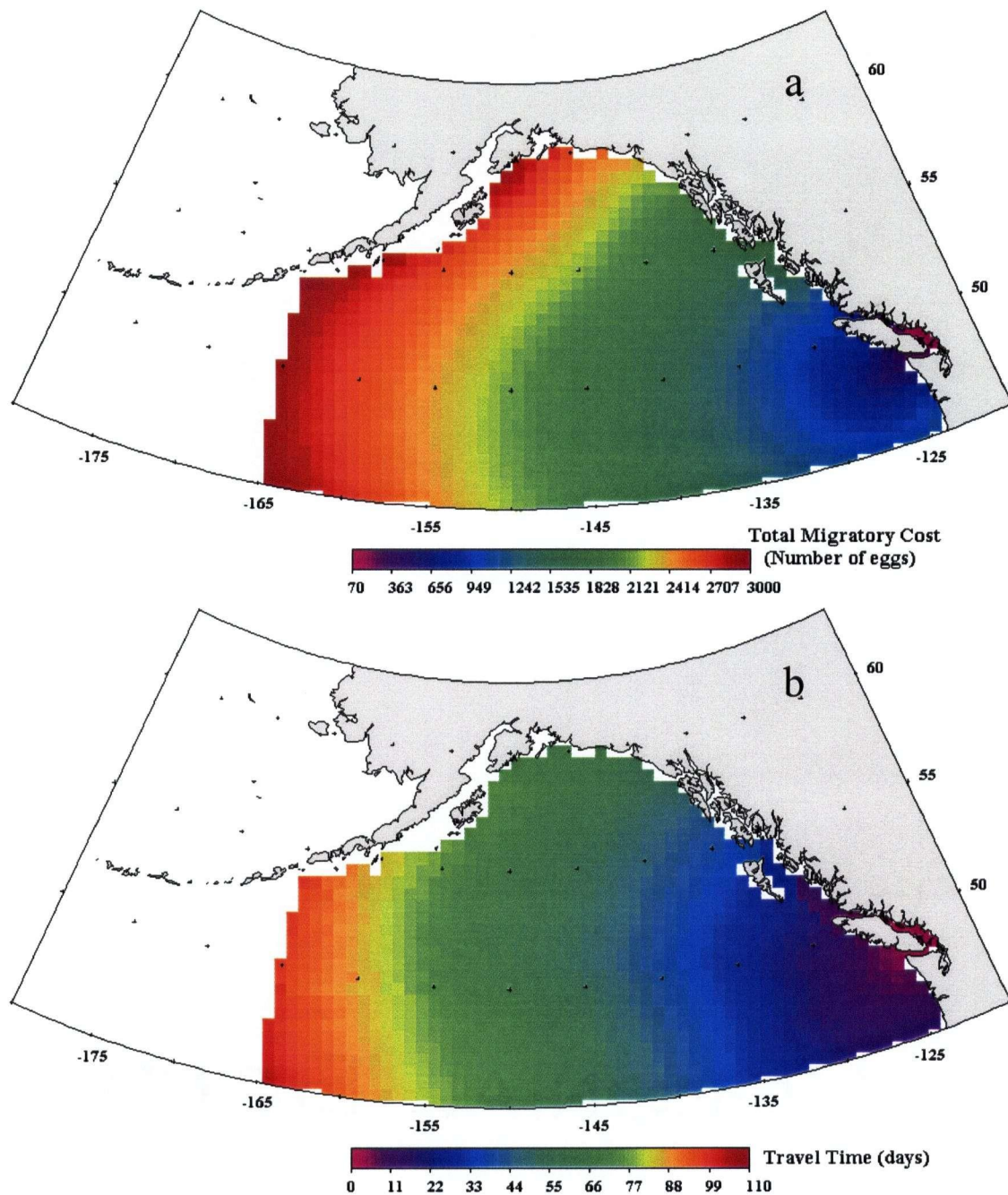
Figure 3.7. Total expected costs of migration in egg-equivalent units (a) and migration time required to reach the Fraser River mouth under a 5% total coastal mortality.

Overall, the main predictions of the model assuming a 5% total coastal mortality are as follows:

1) The West Wind Drift current flowing east towards the coast is the only large-scale oceanographic feature in the NE Pacific Ocean that provides a reduction in travel costs for sockeye. However, migrating sockeye salmon are capable of reaching the Fraser River from anywhere in the NE Pacific Ocean.

2) The highest optimal swimming speeds occur near the coast and arise as a behavioral response to a high risk of mortality there.

3) Optimal coastal routes lead to the oceanic environment north of the Johnstone route envelope, i.e. individuals there should not approach the coast.

4) The optimal location for the landfall of migrants coming from their feeding grounds is at the entrance of the San Juan de Fuca Strait, from which they proceed to the Fraser River mouth. The Johnstone Strait is a suboptimal route, and should not be used as a migration route for a total-cost minimizing sockeye salmon returning to the Fraser River to spawn.

Predictions 2) to 4) are optimal behavioral responses to the 5% total mortality rate used here to characterize the coastal environment. A risky environment should be avoided if possible, or swam through as fast as possible to reduce exposure time regardless of the metabolic costs incurred. Thus, coastal trajectories north of the Johnstone route envelope lead directly to the open ocean. Furthermore, any migrant in the coastal environment should swim nearly at the maximum speed defined by Eq. (3.15).

The model predicts that the Juan de Fuca Strait is the optimal route for reaching the river, as is believed to be the case (McKinnell et al., 1999). However the predicted latitude of landfall is just in front of the Juan de Fuca Strait and it should be off the west coast of the Charlotte Islands. One reason for the model to incorrectly predict the latitude of landfall is that it may be that coastal currents are not represented in the output of the OSCURS model and they may play an important role in the definition of this attribute. Detailed modeling of coastal currents and near-shore salmon migration (on scale of minutes) for the Queen Charlotte Sound area (Queen Charlotte to Vancouver Islands) by Bourque (1999) indicate that some wind/tide regimes may favor movement into the Johnstone Strait by fish approaching

the coast north of Vancouver Island. However, such mechanism would only be operational if migrating fish make landfall somewhere north of Vancouver Island, and the prediction of my model is that optimal landfall latitude is at the entrance of the Juan de Fuca Strait.

The Juan de Fuca Strait route provides the shortest coastal migration distance to reach the Fraser River for an individual coming from the open ocean, and it is also the route that minimizes exposure to the high risk of mortality in the coast. Thus, a reduction in the total mortality rate in the coast may provide the conditions for the model to shift north the predicted latitude of landfall. I found that a reduction of the total coastal mortality rate from 5% to 1% ($z = 0.0006281$) for the 16 days of coastal residency resulted in the extension of the Johnstone route. This extension creates a northern and a southern migration 'envelopes' with a boundary at the center of the Alaska Gyre (Fig. 3.8a). The northern envelope encompasses all the trajectories in the north (thick line Fig. 3.8a) and leads to the Fraser River through Johnstone Strait. The southern "envelope" encompasses those trajectories in the south and central part of the grid (thin line in Fig. 3.8a) and reaches the Fraser River throughout the Juan de Fuca Strait. The swimming orientation required to achieve the optimal trajectories in Fig. (3.8a) are given in Fig. (3.8b).
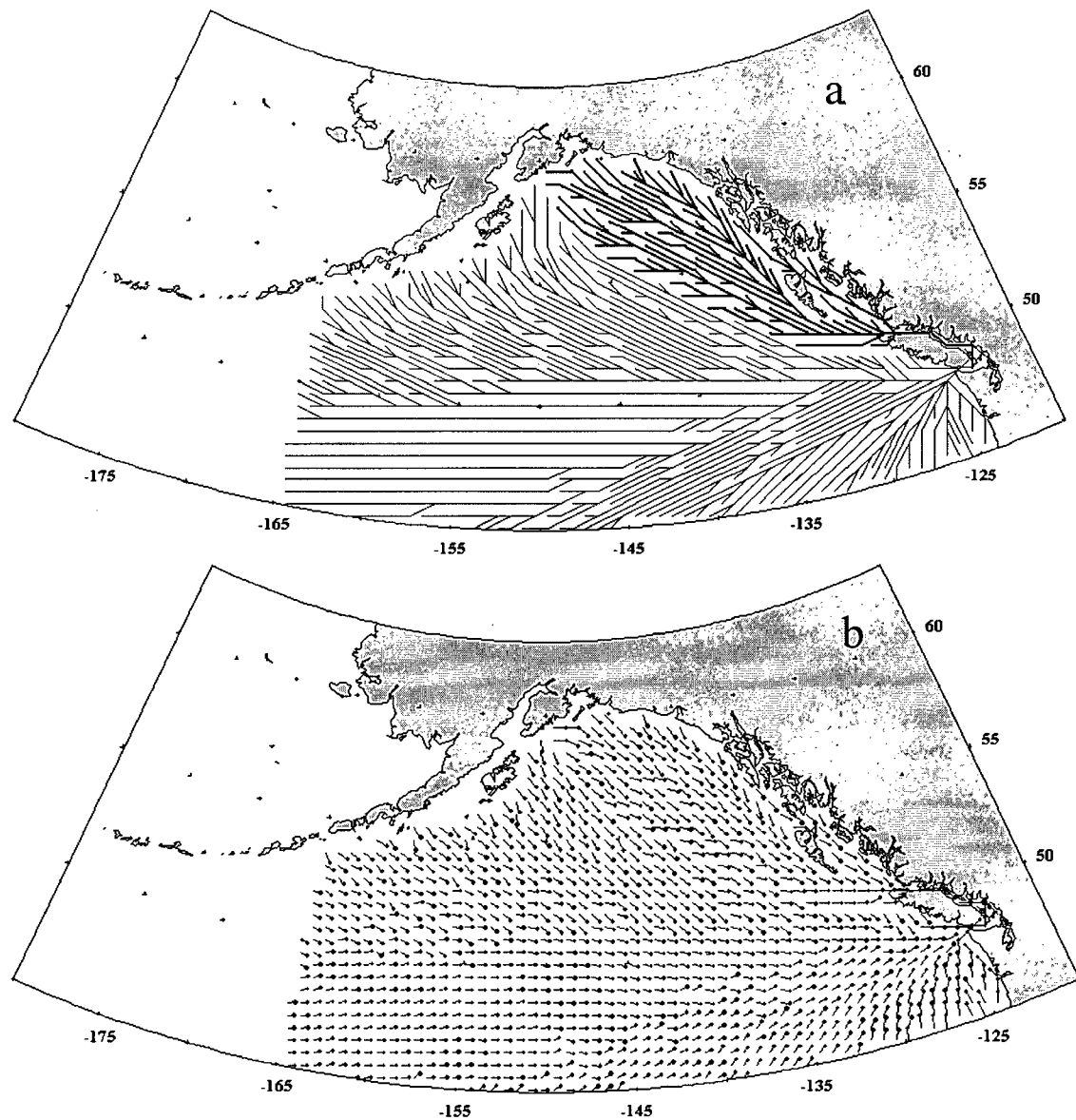
Figure 3.8. Optimal swimming trajectories (a) and swimming orientation (b) for the return migration of sockeye salmon, under the assumption of 1% total coastal mortality.

The spatial structure of migration time and swimming speed at 1% total coastal risk of mortality (Fig. 3.9) did not change in general. However, the decrease in mortality risk in the coast resulted in reduced optimal swimming speeds (figure 3.9a) and metabolic cost per kilometer traveled in the coast (figure 3.9b).
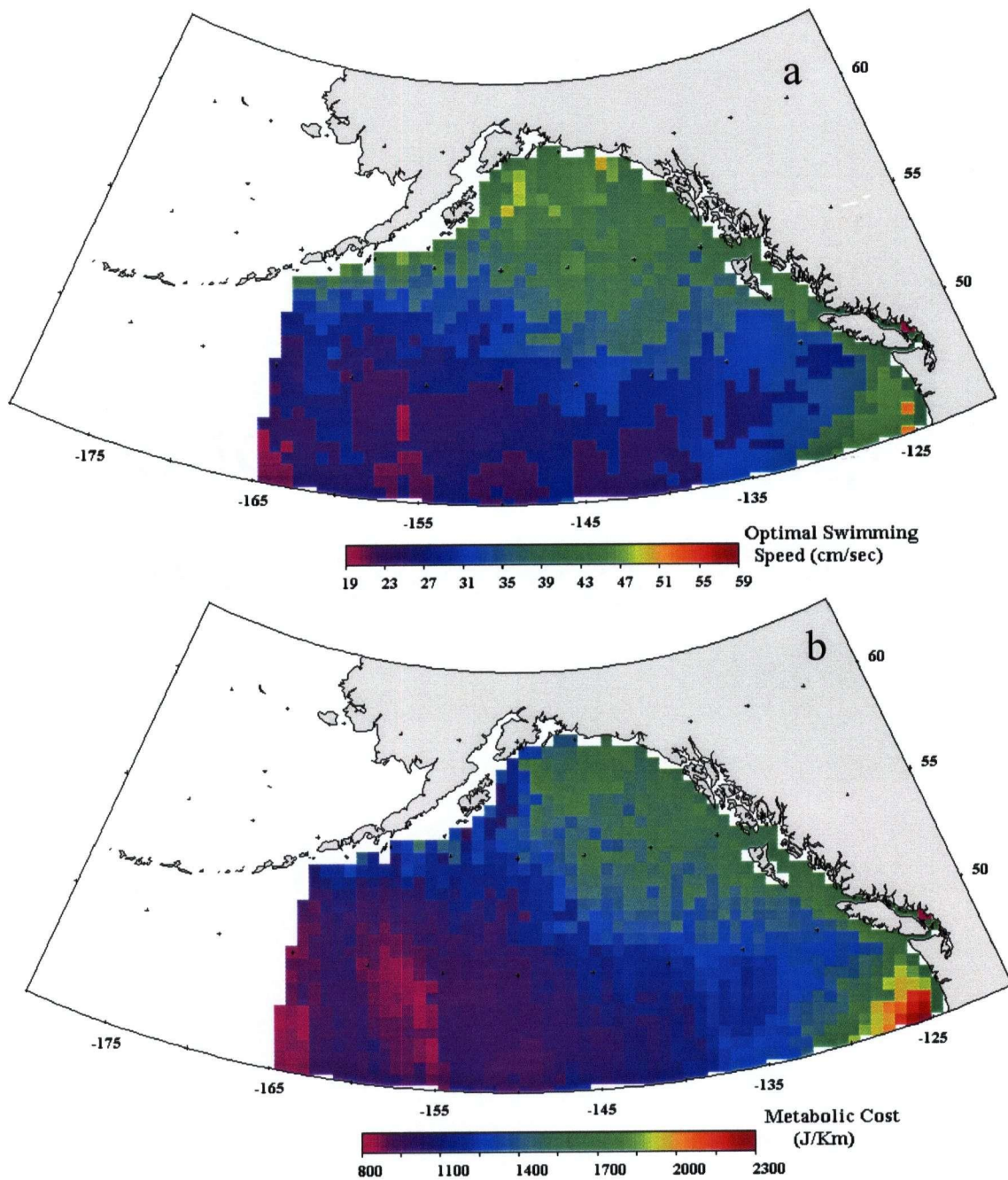
Figure 3.9. Optimal swimming speed (a) and metabolic cost of migration (b) of sockeye salmon in the NE Pacific Ocean under a 1% total coastal mortality.

The overall maximum traveling time did not change noticeably and a simulated migrant at the western edge of the grid still reaches the river in nearly 110 days (Fig. 3.10a). This insensitivity of traveling time is related to the fact that the change in mortality is restricted to the coastal zone, which makes for a small fraction of the total distance to travel.

However, the maximum expected cost of migration (Fig. 3.10b) was reduced (from 3,000 to 2,700 egg-equivalent units), and the spatial distribution of the total cost of migration (Fig. 3.10b) is shifted westward from that at 5% coastal mortality (Fig. 3.7a).
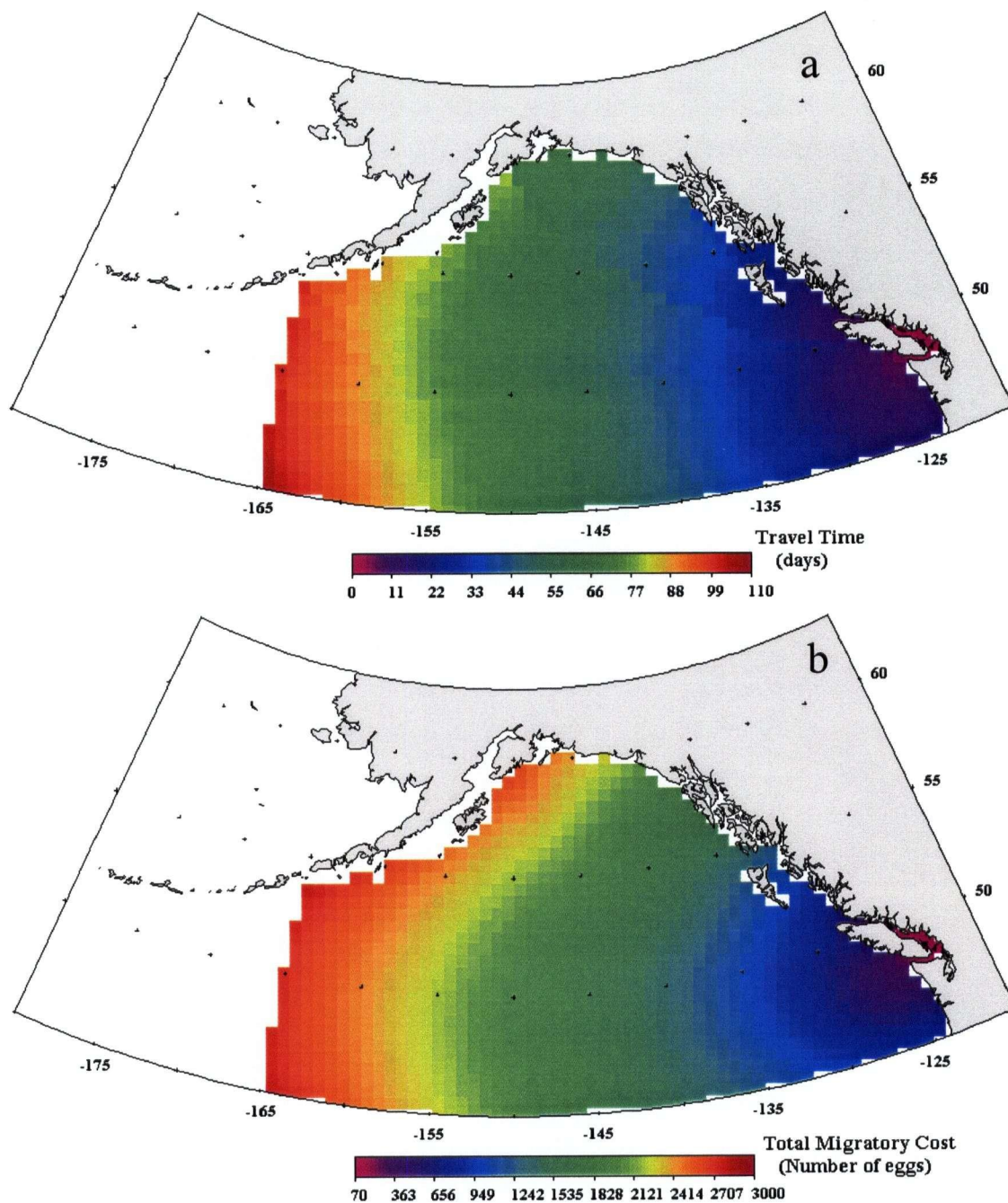
Figure 3.10. Migration time (a) and total expected costs of migration in egg-equivalent units (b) required to reach the Fraser River mouth under a 1% total coastal mortality.

The reduction in the risk of mortality in the coast did result in the expansion of the Johnstone Strait route to migrants coming from the open ocean, and reduced the total expected losses from migration. However, the model still predicts that individuals coming from the central part of the Gulf of Alaska, where they are believed to be at the onset of migration (Figure 2.1), make landfall at the southern tip of Vancouver Island and reach the Fraser River through the San Juan de Fuca Strait (Fig. 3.11).
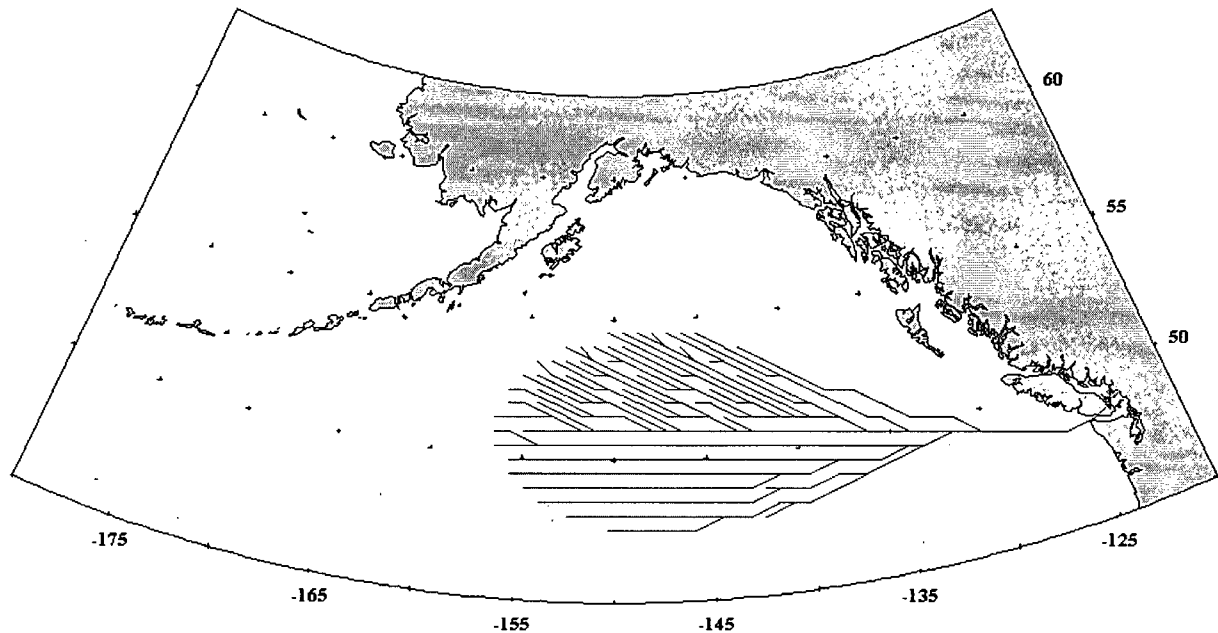
Figure 3.11. Optimal migration trajectory for a sockeye salmon stock from the Fraser assuming 1% total coastal mortality. Stock distribution prior to migration as in Groot and Quinn (1987).

Although the reduction in the coastal mortality rate opened the Johnstone migration route, the model does not predict the oceanic migration route nor the latitude of landfall as illustrated by Groot and Quinn (1987) (Fig. 2.1). Such discrepancies indicate a misrepresentation of the underlying dynamics of the migration process as stated here, and may arise from one of the following alternatives:

1) Sockeye salmon are not as good navigators as they are assumed to be in the model calculations. The navigation process used during their reproductive migration does not permit advection compensation and renders them unable to maintain an optimal route that minimizes

metabolic costs and risk of mortality. Thus, the migration pattern of Groot and Quinn (1987) is a result of advection processes occurring in the open ocean.

2) The spatial distribution of the risk of mortality in the oceanic environment is not homogeneous as stated here. There is higher risk of mortality in the southeastern NE Pacific or there is a high risk band along the West Wind Drift Current, and migrants have adapted their migration route to avoid that area. Thus, the migration pattern of Groot and Quinn (1987) is an adaptive response to the spatial distribution of risk of mortality.

3) The migration cost - reproductive output tradeoff as expressed in Eq. (3.13) does not adequately represents the events that shape the reproductive migration of sockeye salmon. Other factors, like foraging, also play an important role in the definition of the return route. Thus, the migration pattern of Groot and Quinn (1987) is a complex time-constrained optimal response to the spatial distribution of foraging opportunity, risk of mortality, and metabolic expenditures.

I feel that alternative (1) is the least likely. High seas tagging studies have shown sockeye swimming at 40-56 km/day ground speed (measured as a linear track from tagging point to recapture point) for several weeks at a time from the high seas to the coast (Hartt, 1966). According to Quinn and Groot (1984), a high degree of directionality is required to cover such distances given the limitation in swimming speed imposed by the aerobic capacity of the fish (a maximum of 1.6 body lengths per second for a 56 cm fish. See *Maximum Swimming Speed* in Appendix A). Furthermore, sockeye salmon seem capable of converging to the Fraser River from a wide area in the NE Pacific, which would not be possible without reasonable good navigation abilities (Quinn and Dittman, 1992).

Alternative (2) and (3) cannot be dismissed in the light of the results obtained here. Mortality is recognized as an important process shaping the life history of individuals and their behavior (Lima and Dill, 1990; Magnhagen, 1991; Milinski, 1993; Williamson, 1993). The current estimate for total mortality for the entire marine phase of sockeye salmon is 92% (Bradford, 1995), however there is no information on where and how it occurs.

Foraging is an important factor since it is directly related to growth and reproductive output capacity (Calow, 1985). The consideration of foraging as a relevant factor in the

definition of migration routes implies a trade-off based on a time budget conflict rather that one based on migration costs – reproductive output as in the model presented in this chapter. Migrants that forage during their reproductive migration face a time allocation conflict between the amount of time devoted to foraging and that to migration, assuming that effective foraging requires swimming direction choice behaviors to take advantage of spatial patchiness in food (i.e. devoting time to staying in food patches when encountered). Most migratory species have a limited window of opportunity to reach the spawning grounds and reproduce. Under those conditions it is reasonable to expect that as the time to the reproduction window gets closer, the time allocated to any activity in conflict with migration will be reduced or not performed depending on the distance to travel. Mature sockeye are commonly found with stomach content in and around Vancouver Island (Ricker, 1962, Gilbert (1913) in Gilhousen, 1980). However, there is no direct information about whether sockeye salmon actively search for prey during their reproductive migration, or if prey are simply encountered without a search process during migration. Considering the large distances covered in short time spans by tagged individuals (Hartt, 1966; Madison et al., 1972; Quinn and Groot, 1984), it is reasonable to consider that if foraging is important during the return migration, then the return route would occur along prey-rich areas where the foraging time-migration time tradeoff is minimal and does not interfere substantially with the process of migration.

3.5 Conclusion

The general results of the model predict that sockeye salmon can reach the Fraser River from anywhere in the NE Pacific Ocean. The maximum travel time predicted was 110 days for those individuals located at the western edge of the grid, and their total migration costs are nearly 3,000 egg-equivalent units of energy. The travel time required to reach the Fraser River is location dependent. Thus individuals from the same race either start their return migration from a relatively small longitudinal range at the same date, or start their migration at different dates according to their geographic position across a broader longitudinal range, or swim at higher speeds when starting from more distant points. The last two alternatives imply that migrants can assess their geographic location with some accuracy.

Predicted routes for the reproductive migration of sockeye salmon are sensitive to the distribution of the risk of mortality. The model predicts that over a 5% risk of mortality in the coast, the Johnstone Strait route is for all purposes closed to migration. Migrants approaching the coast from the open ocean reach the Fraser River through the Strait of Juan de Fuca. This route reduces exposure to risk of mortality by minimizing total coastal distance to travel. Furthermore, the high risk in the coast also results in optimal swimming speeds near the upper limit of the aerobic metabolism, and coastal migration trajectories that lead to the open ocean for nearly all the coastal zone. High swimming speed in the coast further decreases total mortality by reducing residence time in the coast.

The model also predicted that a reduction in the coastal mortality from 5% to 1% would result in lower optimum swimming speeds in the coast and an overall reduction in total migratory costs. Such a reduction in mortality also opened the Johnstone Strait route for individuals located along a wide corridor north of Vancouver Island. However the Johnstone Strait route remains closed for individuals approaching the coast from the central part of the Gulf of Alaska, where migrants are located prior to migration.

The migration costs – reproductive output tradeoff along with the environmental conditions and mortality risk as defined here, were not sufficient to predict the oceanic migration route as proposed by Groot and Quinn (1987) and the latitude of landfall. Likely such features of the reproductive migration of sockeye salmon are associated with a more complex spatial distribution of the risk of mortality, or with foraging during migration, or both. If foraging is an issue in the definition of such features, then a foraging time –migration time tradeoff may provide a better way to define the characteristics of the return migration of sockeye salmon.

CHAPTER 4

A SPATIALLY EXPLICIT STATE DEPENDENT DYNAMIC MODEL FOR MIGRATORY BEHAVIOR IN FISHES

4.1 Introduction

Most studies on fish migration have been concerned primarily with the mechanisms of migration and its links to regional production cycles and hydrographic circulation. Migration was considered a synchronized movement of individuals between a spawning area and a growth area, and the timing of the migration and the route of migration defined by seasonal changes in the environment, particularly productivity, currents, and temperature (Harden-Jones, 1968; Harden-Jones, 1981; Leggett, 1977). Although this view provided a wealth of information about who, where, and when, it did not give any insight into the functional or evolutionary characteristics of migration (Dingle and Gauthreaux, 1991).

Once migration was put in the context of evolutionary ecology and viewed as a fitness maximizing life history trait (Baker, 1978), some of its consequences for the life history of migrants have become apparent. Fish that migrate reach comparatively larger adult sizes, have delayed age at maturity, and increased fecundity (Roff, 1988; Roff, 1991). Migratory behavior also seems to dampen the stochasticity of the predator/prey fields and reduce the probability of predation and starvation during early life stages (Leggett, 1985). Furthermore, the wide range of environments available to migratory individuals have also resulted in complex and varied life history cycles, as is the case for salmonids (Healey, 1987; Thorpe, 1998). However, the increased level of activity required for migration also results in higher metabolic costs and an increased risk of encountering predators while migrating (Roff, 1988; Schaffer and Elson, 1975; Werner and Anholt, 1993), thus creating a trade-off between activity patterns and reproductive output.

In this Chapter I propose that the activity pattern - reproductive output tradeoff in migratory fishes arises from a time budget conflict between the time required for searching

during foraging and that required for the oriented movement required for migration. Migratory behavior results not only in high total metabolic costs from swimming and an increased risk of mortality, but also in lost foraging opportunities that otherwise would result in higher fecundity. On the other hand, migration also allows individuals to access resources elsewhere, either in the form of high prey density or reduced mortality or a combination of both, which should result in larger body size and higher fecundity.

The activity pattern - reproductive output tradeoff suggests that there may be an optimal set of tactics for migration that would allow migrants to maximize reproductive success. Such tactics should be closely related to the spatial structure of characteristics like foraging opportunities, risk of mortality, and environmental features affecting the cost of swimming like geographic configuration, currents, and temperature.

Fiksen et al. (1995) proposed a model to predict the horizontal migratory pattern of a fish, the Barents Sea capelin (*Mallotus villosus*) based on the same optimality principle as the one I develop here. Their model failed to predict the migration of the capelin and they suggested the following reasons for the failure: 1) The bioenergetics of capelin is not determined as yet; 2) the currents in the area of distribution reach similar or higher speeds than capelin and were not considered in the model; 3) the shoaling behavior of capelin was not considered and it affects the risk of mortality and the consumption rate; and 4) the depletion of prey by capelin was not considered. Here I develop a model that considers currents, which results in a very different representation of state dynamics. Furthermore the model in this chapter is based on a foraging time – migration time trade-off that, in my opinion, is at the core of migratory behavior. The model in Fiksen *et al.* is not based on that or any other explicit trade-off, and as a consequence foraging activity does not have any effect on migration activity and the metabolic cost associated to foraging was not considered.

The objectives of this chapter are to: 1) Develop a spatially-explicit state-dependent dynamics model for the estimation of optimal migratory tactics based on the foraging time – migration time tradeoff, 2) Determine if this tradeoff is capable of predicting the migratory cycle of sockeye salmon from the Fraser River given the geography and the environmental

features of the NE Pacific Ocean, and 3) Estimate the optimal set of migration tactics for animals subject to such a trade-off.

4.2 An Optimality Model for Fish Migration

4.2.1 Basic assumptions

The model focuses on the estimation of the effect of migratory behavior on the reproductive output of a female fish from a population that undergoes migration. This model is based on the premise that individuals are fitness optimizers and that migratory behavior is a hereditary trait subject to the process of natural selection. It is further assumed that the oriented swimming behavior required during active migration interferes with the search process required during foraging, and leads to a trade-off between migration time and foraging time. Within the daily activity schedule of an individual migrant this trade-off can be represented as:

$$24 = T_f + T_m + T_r \qquad \qquad ...(4.1)$$

Where

T_f = Daily hours allocated to forage

T_m = Daily hours allocated to migrate

T_r = Resting time

Any particular distribution of time between activities will depend on the current state of the individual, and the costs and opportunities for fitness enhancement locally and elsewhere within its range. Resting time here is used as a proxy for any sort of activity other than foraging or migration carried out during the day.

The state of the individual at any given time t is represented by its weight w_t and its geographic location h_i (referred as patch h_i afterwards). Migrants may reach a particular patch by active swimming or through drifting with the currents if possible.

Weight dynamics can be expressed in terms of the amount of food assimilated (G_t) and total metabolic costs (M_t) from time t to t+1. Total metabolic cost includes both basal and active metabolism. The weight of the individual at the beginning of time t+1 is then defined as:

$$W_{t+1} = W_t + G_t - M_t \qquad \qquad \dots (4.2)$$

G_t and M_t are variable and their values depend on the weight at time t, the patch occupied at time t, the activity level of the organism, and the time of the year if the biotic and abiotic attributes of the patches are seasonal in nature. If an individual moves from patch h_i to h_j then M_t is affected by the costs of moving. G_t is restricted to values equal or larger than 0, and has an upper limit defined by the gut capacity of the organism, which is a function of body size. At any given time, G_t depends on the density of food present in the patch and the time allocated to foraging, which in turn limits the maximum value that w_t can reach at time t+1 (see *The Dynamics of growth: foraging and metabolism* below for a more detailed description).

4.2.2 Dynamic Programming structure

Migratory species have time-and-space-constrained reproduction, they spawn at specific geographic locations during a specific time of the year. Some species have strong site fidelity and reproduce in the same place where they were born (like salmonids Burgner, 1991), while others reproduce in a wider region that have a particular condition during part of the year (like clupeoids in upwelling areas Blaxter and Hunter, 1982). Thus to reproduce, individual migrants have to survive to the spawning season (t_r) and invest some fraction of their stored energy to reach the spawning habitat (H_S) at that time.

The fitness value (F) during the last reproductive season of the lifetime of an individual (occurring at final time T), can be represented as a function of body weight and geographic location. F has a positive value if the final weight achieved is higher that a critical value (w_{crit}) below which reproduction is not feasible:

$$F(w,h,T) = \begin{cases} \varphi(w) & \text{if} \quad w \geq w_{Crit}; h = H_S \\ 0 & \text{otherwise} \end{cases} \qquad \ldots(4.3)$$

At any other point in time t, the expectation of reproductive output for those individuals that survive to spawn at time T is conditional on the state of the individual at that time t and its location (h):

$$F(w, h, t) = E\{F(W(T), H(T), T) \mid W(t) = w; H(t) = h\} \qquad \ldots (4.4)$$

The fitness representation in equation (4.3) is reasonable for individuals from semelparous species with fixed age at maturity. However, iteroparous fishes have reproduction windows that open every year after maturity at a specific time of the year (t_r). Thus each year at time t_r, mature individuals have to "decide" whether or not to initiate the migration to reproduce and the fitness expectation has to include a residual fitness resulting from future reproduction. If an individual decides to spawns, it will have a weight w'(w) and location h'(h), and if it does not spawn then the weight will be w"(w) and location h"(h). This can be represented as follows:

$$F(w,h,t) = \begin{cases} \varphi(w) + F(w'(w), h'(h), t+1) & \text{if} \quad t = t_r; h = H_S; w \geq W_{Crit} \\ F(w''(w), h''(h), t+1) & \text{otherwise} \end{cases} \qquad \ldots(4.5)$$

Notice that Eq. (4.5) is just a generalization of Eq. (4.3) and can easily account for semelparous species with variable age at maturity by setting residual fitness F(w, h, t+1) to 0. Equations (4.3) and (4.5) provide a straightforward method for quantifying the long-term consequences of short-term behavior on a measure of reproductive fitness (Clark, 1992; Clark, 1993; Mangel and Clark, 1988).

Transient dynamics are defined by the behavioral choices available to the individual at any given time and position. Individuals have to decide whether to stay in the current location (which may require active swimming to offset advection from currents), drift passively with the currents, or leave to any other location within range by actively swimming in a specific direction. Furthermore, individuals also have to decide how to allocate available time into the

activities at hand and how to go about them (i.e. optimal swimming speed for foraging or migration).

The patches can be defined in terms of any relevant characteristic as long as these characteristics can be related to the fitness equation. Typical optimality-based life history models define habitat characteristics in terms of predation risk and food concentration. For fish populations, temperature (affecting the developmental time during early life stages and the bioenergetics costs of respiration throughout their lifetime) and currents (because the advection they create) also have a strong bearing in the definition of the life history pattern of the organism. The swimming behavior of migratory juvenile and adult fishes has to account for the advection from currents, and in some instances juvenile or adult distribution patterns may depend on an expectation of advective displacement from/to the nursery areas during early ontogenic stages of the organism. Although staying in an area may be viewed as non-migratory behavior, it is in fact migration when considering that in a continuously moving environment, staying in an area requires oriented swimming to offset advection. I included staying as a distinct option in this model since it adds clarity to the model and simplifies the optimization calculation (see *Mechanics of movement* below).

An optimal sequence of migration decisions to maximize fitness can be estimated from the following dynamic programming equation:

$$F(w_t, h_i, t) = Max[F_{Drift}, F_{Stay}, F_{Migrate}] \qquad \ldots (4.6)$$

Where:

$$F_{Drift} = \underset{T_f, \upsilon}{Max}[\gamma_K F(w_t + (G - M)_{K,t}, h_k, t + 1)] \qquad \ldots (4.7)$$

$$F_{Stay} = \underset{T_f, T_m, \upsilon, v}{Max}[\gamma_i F(w_t + (G - M)_{i,t}, h_i, t + 1)] \qquad \ldots (4.8)$$

$$F_{Migrate} = \underset{L, T_f, T_m, \upsilon, v}{Max}[\gamma_L F(w_t + (G - M)_{L,t}, h_l, t + 1] \qquad \ldots (4.9)$$

K = Drift trajectory vector that starts in patch h_i and ends in h_k

L = Migration trajectory vector that starts in patch h_i and ends in h_l

$\gamma_K = e^{-(t_i m_i + \ldots + t_k m_k)}$ = Survival rate along drift trajectory vector K

$\gamma_i = e^{-t_i m_i}$ = Survival rate in patch i

$\gamma_{\mathbf{L}} = e^{-\left(t_i m_i + \dots + t_l m_l\right)}$ = Survival rate along migration trajectory vector $\mathbf{L}$

m_i, m_k, m_l = Instantaneous mortality rate in patches i, k, l

t_i, t_k, t_l = Residence time in patches i, k, l

$(G - M)_{i,t}$ = Growth in patch i during time t

$(G - M)_{\mathbf{K},t}$ = Growth along trajectory vector $\mathbf{K}$ during time t

$(G - M)_{\mathbf{L},t}$ = Growth along trajectory vector $\mathbf{L}$ during time t

v = Swimming speed during migration

υ = Swimming speed during foraging

Notice that the decisions to drift, stay, or migrate in Eq. (4.6) are taken every t time units (one month in the application to sockeye salmon below). However state dynamics for each of these options (Eq. 4.7 to 4.9) are calculated on a daily basis with a daily time partition for three possible behaviors (forage, rest, migrate) as expressed in Eq. (4.1). For instance, during the estimation of state dynamics for drifting, the daily time allocate to migration (i.e. oriented swimming) is always zero from time interval t to t+1 (see Eq. 4.7).

The structure of this model is quite general. It can be extended to represent any kind of life history pattern, included those of individuals where migration seems to occur as a response to gradients (e.g. clupeoids (see for example McCall, 1990)). This model can be used to ask questions about the optimal sequence of decisions that maximize fitness, or to test the validity of our beliefs about the conditions the individuals face in their natural surroundings, the effect that changes in the environment may have on the state and behavior of the individual, or whether a stated set of condition are sufficient to explain the life history pattern observed in the individuals of a population.

Individuals from some species migrate considerable distances during the early life stages by controlling their depth and taking advantage of the advection that currents can provide. Those species require at least a two-layer model to appropriately represent their life cycle. Although the structure of this model can consider such cases, the optimization problem rapidly becomes numerically intractable because of high dimensionality problems (see Mangel and Clark (1988) on the subject and possible ways around this problem).

As stated in Eq. (4.6) the model estimates the sequence of migratory behavior and the migratory trajectory that maximizes a measure of fitness as indicated in Eq. (4.5) subject to the constraints imposed by environmental conditions. Furthermore, the optimization process also estimates the growth pattern that would result from following the optimal migratory behavior and trajectory, and a profile describing the changes in fitness through time.

Notice that Eq. (4.6) does not have any explicit rule that would force individuals to migrate beyond those stated in the terminal condition equation (Eq. 4.3 and 4.5, individuals have to be in the spawning grounds during the spawning time to achieve reproductive fitness). If fitness maximization is contingent upon a migratory circuit, then the model implicitly assumes that the individuals have sufficient orientation and navigation abilities to move out of the natal site and return later in life. This assumption restricts the application of this model to those species that are capable of orientation and navigation.

4.2.3 The mechanics of movement

The dynamic programming equation defined in Eq. (4.6) requires the partition of the total inhabitable area into patches. The simplest way to accomplish this is by representing each patch as a cell in a grid array. Eq. (4.6) can then be evaluated for each option of migratory behavior explored, starting at each gridpoint at the beginning of time t.

4.2.3.1 Drifting

Drifting individuals are those that do not display any oriented swimming activity. The trajectory for those individuals depends only on the speed and direction of the currents starting from patch h_i during time t (defined as trajectory vector $\mathbf{K}$ in Eq. 4.7). Fitness for drifters is estimated at the patch reached at the end of time t (patch h_k in Eq. 4.7) from the growth and the mortality risk accumulated along the trajectory $\mathbf{K}$. In most cases fitness for the location reached at the end of time t does not coincide with fitness already calculated at the node of a patch, and must be interpolated.

4.2.3.2 Staying

For those individuals that stay in patch h_i (Eq. 4.8) the optimization problem is reduced to finding the swimming time and speed required to offset the effects of advection and the combination of foraging time and speed that maximizes fitness. Thus for each migration time explored, one must calculate the swimming speed that will offset the advection from the current and allow the individual to remain in patch h_i during each day from time t to t+1. This calculation can be done by solving the following equation:

$$v\, T_m = V \qquad\qquad\qquad ...(4.10)$$

where:

V = Speed of the current (in km/day)

v = Migratory swimming speed (in km/h)

T_m = Migration time (hours/day)

There is a constraint that swimming speed has to be within the scope of aerobic metabolism to be sustainable for the extended periods of time required for migration (Weihs, 1973; Weihs and Webb, 1983). This constraint actually simplifies the search for the optimal value since it creates an upper boundary on the maximum sustained speed that an individual of a given size can reach.

4.2.3.3 Migration

The behavioral option for migration (Eq. 4.9) is the most complex of all. The migrating individual has behavioral choices for swimming time and speed during foraging, and swimming orientation, speed, and time during migration. Those choices determine the feasibility of a trajectory and the total distance that the individual can travel during the duration of time t (defined as trajectory **L** in Eq. (4.9)) within the inhabitable area considered. Migrants also have to consider how to reach h_l starting from h_i (trajectory shape) and the moment within time interval t to leave the current patch (h_i) for those instances when the travel time required to reach target patch (h_l) is shorter than the length of the time interval (dt).

To reduce computer time I explored only linear trajectories starting at the beginning of time t. Any remaining time after reaching the target patch within time interval t is accounted for by applying the growth – mortality dynamics described for staying in current patch. The algorithm used for the calculation of the swimming orientation needed to reach a target patch in the presence of currents was that described in Chapter 3 (Eq. 3.7 to 3.10).

4.2.4 *The dynamics of growth: foraging and metabolism.*

The process of growth in fish species has been successfully represented with the bioenergetics model of Hewett and Johnson (1987) and Hewett and Johnson (1989) (Eq. 4.11). This model is based on the mass conservation principle where the food consumed (G) is partitioned into non-digestible matter (Egestion F), metabolic waste (Excretion E), Respiration (M), and the metabolic costs of digesting and assimilating the food (Heat Increment H). Any difference (either positive or negative) is allocated into growth as follows:

$$dw/dt = a\,(G - F - E - H) - M \qquad \qquad ...(4.11)$$

Where:

a = Prey-to-predator energy density ratio.

The representation of total metabolic costs in the bioenergetics model of Hewett and Johnson (1989) (Eq. 4.12) is very convenient. The model explicitly considers the effect of body weight allometry, temperature (τ), and swimming speed (v) in the total metabolic costs of the fish.

$$M = aw^b\,e^{c\tau}\,e^{dv} \qquad \qquad ...(4.12)$$

Equation (4.12) provides a direct method to quantify the metabolic cost of alternative behaviors. However, this equation provides respiration estimates on a daily basis, and to relate it to the time budget described in Eq. (4.1) the activity component (e^{dv}) has to be split into migration, foraging, and resting. Each activity is then weighted according to the number of hours on which it is carried out as follows:

$$M = aW^b \, e^{c\tau} \, (T_m e^{dv} + T_f e^{d\upsilon} + T_r e^{d\eta}) / 24 \qquad \ldots(4.13)$$

where:

ν = Migration speed (cm/s)

υ = Foraging speed (cm/s)

η = Resting speed (cm/s)

τ = Temperature (°C)

Food consumption (G) is a critical component in (4.11) and depends on prey density and the activity level of the forager (Abrams (1982); Aksnes and Giske (1993); Ware (1978); see also Holbrook and Schmitt (1988); Lima and Dill (1990); Milinski (1993) for reviews on the effects of predation risk on foraging behavior). There are several models available that link most if not all of the above mentioned components of foraging behavior for pelagic fishes (e.g. Aksnes and Giske, 1993; Gerritsen and Strickler, 1977; Giguère et al., 1982). A combination of any of those with the bioenergetics model described above can account for the behavior and physiology of most fish species. Here I used a simple area swept model that accounts for satiation as follows:

$$G = MIN \begin{cases} \beta F_C(V_f T_f + V_m T_m) \\ C_{Max} \end{cases} \qquad \ldots(4.14)$$

Where:

β = Foraging efficiency

F_C = Food concentration (in g/m^3)

$V_f = \pi \, r_f^2 \, v_f \quad$ (in m^3/h)

$V_m = \pi \, r_m^2 \, v_m \qquad$ (in m^3/h)

r_f = Reactive distance while foraging $\qquad$ (in m)

r_m = Reactive distance while migrating

v_m = Migration swimming speed $\qquad$ (in m/h)

v_f = Foraging swimming speed

C_{Max} = Maximum consumption

Equation (4.14) has a satiation limit (C_{Max}) defined by the gut capacity of the fish. It also considers the possibility of opportunistic foraging while the fish is actively migrating by defining a reactive distance parameter while migrating (r_m). The ration attained while migrating should be less that attained while foraging only, thus r_m should be smaller than r_f. Values of r_m closer to those for r_f would indicate that migratory fishes are not subject to the time trade-off expressed in Eq. (4.1) and imply that migratory behavior does not have any foraging penalty. As defined in Eq. (4.1) the trade-off assumes a r_m value of zero, i.e. individuals do not react at all toward prey while engaged in migratory behavior.

4.3 Application to a semelparous species: the marine migration of Fraser River sockeye salmon.

A species ideally suited for an application of this model is the sockeye salmon from the Fraser River. This species is perhaps one of the best examples of a fish species with an extremely long migration circuit and a complex life history pattern. Sockeye salmon sequentially use up to five habitats (natal stream-lake-river-coast-ocean) during their life cycle, and undergo a migratory circuit of thousands of kilometers in length.

This model focuses on optimal migratory routes and behaviors that maximize fitness. The life stages occurring in the freshwater environment (natal stream, lake, and river) do not offer route choices at the temporal and spatial scales used here, except as two-way paths that pose the problem of optimal age at departure (see Ludwig and Rowe (1990) and Rowe and Ludwig (1991) for state-space modeling of ontogenic habitat shifts in time constrained individuals). I am aware that juveniles entering the nursery lake may inhabit the littoral waters before moving into the limnetic environment (Burgner, 1991), however the spatial scale used here does not allow for the representation of these two habitats. Thus, the freshwater stages are not explicitly considered here. The mortality losses occurring in freshwater are accounted for in *Fecundity and Fitness*. I explicitly considered those losses in the model to directly compare observed terminal weight and mature recruits per female with predicted reproductive potential and terminal weight as performance indexes for the model. The growth achieved in freshwater is considered as an initial condition for the model.

4.3.1 Migratory circuit and growth

The description of the migratory circuit of sockeye salmon was given in chapter 2. However, the migratory pattern depicted there does not correspond to a particular race, rather it depicts the pattern of movement of all the NE Pacific populations of sockeye salmon. However, there is enough information to depict a reasonable migration pattern for the Fraser River races of sockeye salmon as follows:

1) Smolts reach the estuary of the Fraser River from April to June at a weight of 12 g.

2) Upon entrance to the marine environment, individuals actively migrate northwestward in a band within 40 km from the coast, some of them reaching as far as the Alaska Peninsula.

3) By October individuals disperse into the Gulf of Alaska. A large proportion of them remains there for 18 months, moving northward during the summer and southward during winter. Sockeye salmon reach 354 g in their first winter, 1,315 g in their second winter, and 2,400 g at the end of their marine residency period.

4) Mature adults return to spawn and make river entrance from early July to early October.

4.3.2 Habitat Attributes

NE Pacific sockeye races distribute North of 40°N in the Alaska Gyre (French et al., 1976). On this area I defined a centered square grid pattern with 189 km of horizontal distance between gridpoints (Figure 4.1). The grid was rendered from the mouth of the Fraser River on an Albers equal area map projection (Snyder, 1983). Note that at this resolution Vancouver Island and the Queen Charlotte Islands could not be represented in the grid.
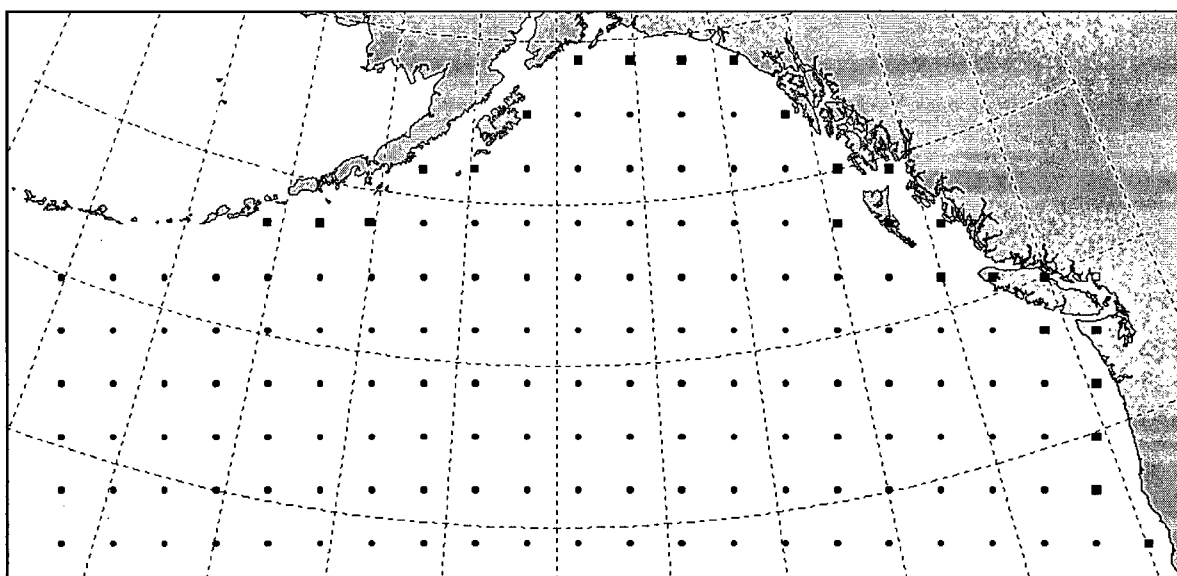
Figure 4.1. Gridded representation of the NE Pacific Ocean. Black squares represent coastal gridpoints, black circles oceanic gridpoints. The Fraser River mouth is marked with an empty square.

Each cell was characterized by monthly varying values of surface temperature, surface current, and zooplankton density. Risk of mortality was also used to characterize each cell. However mortality values were defined for two areas only, the coastal area and the oceanic area (filled squares and filled circles respectively in Fig. 4.1), and were set constant throughout the year (see *Mortality* below).

Monthly surface temperature values were calculated from the COADS surface temperature data set for the Northeast Pacific Ocean. COADS data are given as monthly values for quadrants of 2°x2° from 1950 to 1993. From those values, average fields were calculated for each month and then interpolated to the grid of interest (Figure 4.2). Average monthly values for currents were calculated from daily values generated with the OSCURS model and interpolated to the grid of interest (Figure 4.2). OSCURS data are courtesy of Dr. James Ingraham (see Ingraham and Miyahara (1988); Ingraham and Miyahara (1989) for a description of the OSCURS model and its tuning to the NE surface currents).
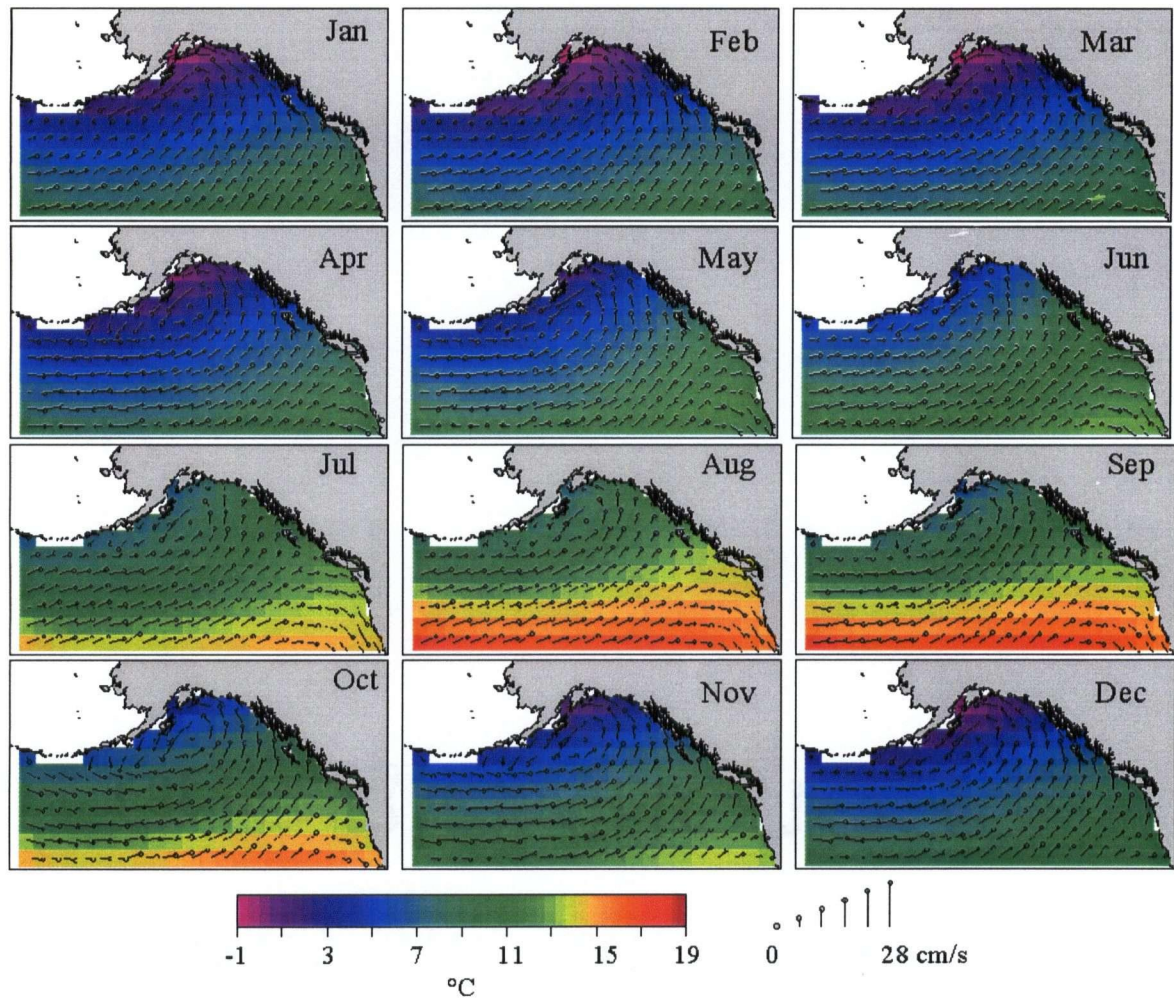
Figure 4.2. Monthly surface current and temperature fields in the NE Pacific.

Sockeye diet during coastal residence is composed of euphausids, fish larvae, copepods, amphipods, larval stages of ascideans, and insects (Foerster, 1968; Healey, 1980; Healey, 1991; Landingham et al., 1998). In the open ocean sockeye forage on squids, fishes, amphipods, and euphausiids, although the main prey items vary depending on their geographic location (Burgner, 1987; Foerster, 1968; French et al., 1976; Pearcy et al., 1984).

To represent the prey field I used zooplankton density data from several sources. Zooplankton biomass in the coast comes from data in Gardner (1976), Fulton et al. (1982), St. John (1989), Clifford et al. (1991), Yin (1994), Mackas (1992), and Parsons et al. (1970). The data in Gardner (1976) are for the combined biomass of *Calanus plumchrus*, *C. marshallae*, and *C. Pacificus*, which dominate the zooplankton community in the Strait of Georgia during

spring and summer (Harrison et al., 1983). Zooplankton data for the Northeast Pacific were those from Wadell and McKinell (1995), LeBrasseur (1965), Wen (1995), and some CalCOFI zooplankton survey data within the area of interest (courtesy of Dr. Paul Smith, NMFS, la Jolla Ca.).

Some of the data were reported in units of ind/m^3, ind/m^2 or g/m^2. Those values were converted to (mg wet weight)/m^3 either from the description of the sampling gear and sampling procedure provided in the reference or with the transformation procedure in Smith and Richardson (1977). Units of ind/m^3 were transformed to dry weight values using species-specific values from Mackas (1992) and a wet-to-dry conversion factor of 12.5% for zooplankton from Hewett and Johnson (1992). The CalCOFI survey data were given in ml of displaced volume/1000 m^3. They were converted to mg/m^3 using a conversion equivalence of 1 ml of displaced volume to 12.7 mg dry weight (from Table 101 in Sverdrup et al., 1942), and to wet weight as indicated before.

The raw zooplankton data (Figure 4.3) were grouped by months and by cell according to the grid pattern in Figure 4.1. The uneven temporal and spatial coverage of the data resulted in a rather sparse matrix. Gridpoint gaps with values for the previous and the following month were filled with the mean of those two values. Data were particularly scarce in the open ocean from September through December. The only point consistently represented was that of Station "P"; which shows an exponential-type decay in biomass values from May-June (with the highest value) to January (with the lowest biomass value). Based on this behavior, any missing data from September to December were interpolated with a power function (of the form Biomass = a $Month^b$) fitted to any available value from June to January for each node in the grid. Once completed, the zooplankton biomass fields were smoothed with the filter in Eq. (4.15).

$$Biomass_{i,j,t} = \left(\frac{1}{\sum s_{t,d}}\right)\sum_{k=i-1}^{i+1}\sum_{l=j-1}^{j+1}\sum_{m=t-1}^{t+1} s_{t,d} Biomass_{k,l,m} \qquad ...(4.15)$$

Where:

$s_{t,d} = s_t\ s_d$

s_t = Time weight; 1 for m = t and 0.5 for m ≠ t

$$s_d = 10 \,/\, [\text{distance between nodes } (i, j) \text{ and } (k, l)]$$

This filter is a weighted time-space moving average that smoothes the field locally and preserves high local values. The remaining empty values were interpolated by krigging (using Surfer from Golden Graphics ^{TM}). The resulting monthly mean zooplankton density fields (Figure 4.4) were considered as the zooplankton standing crop in the area.
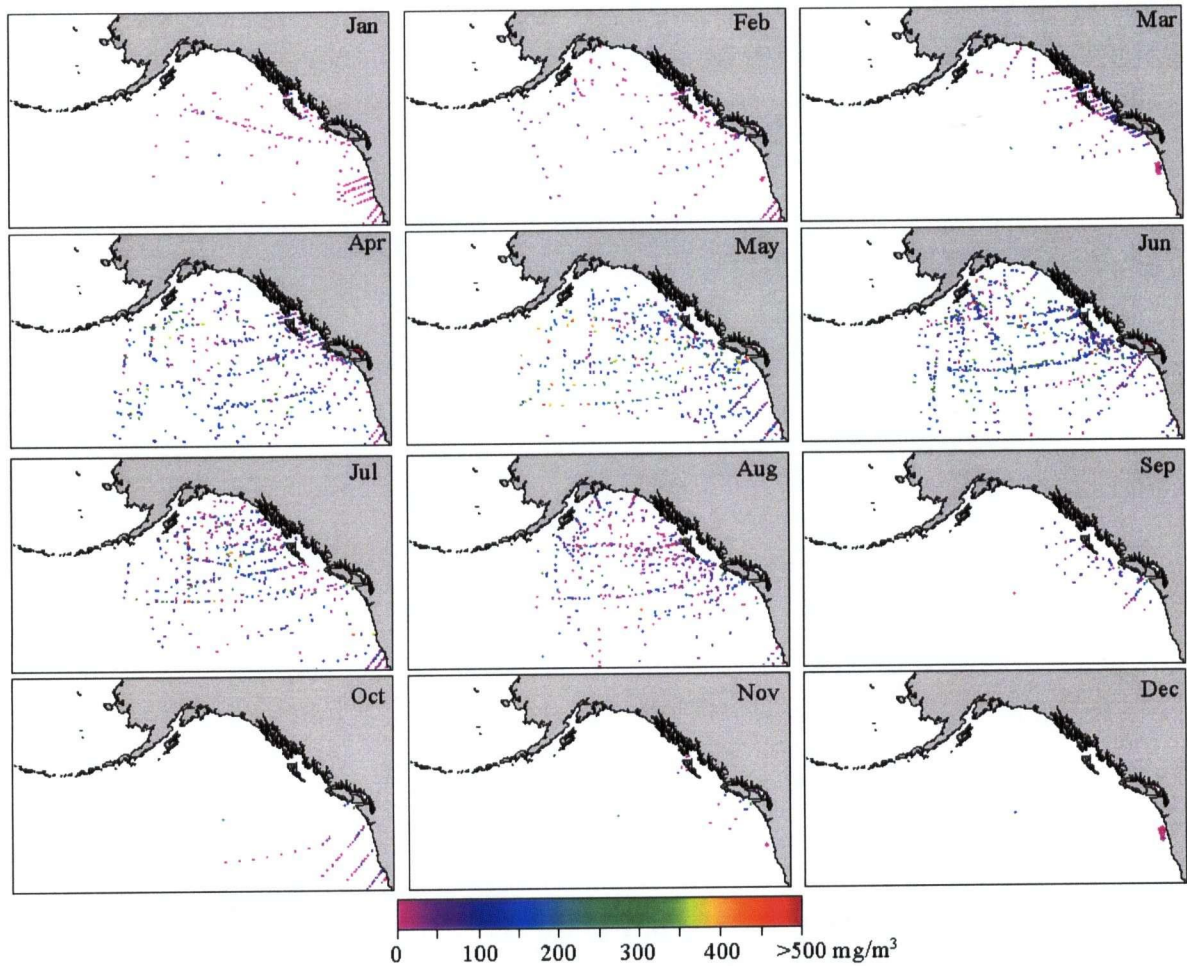
Figure 4.3. Spatial distribution of zooplankton density data across the NE Pacific grouped by month.

The interpolated zooplankton standing crop in Fig. (4.4) shows three main features: 1) There is an area in the south-central part of the Gulf of Alaska with high zooplankton density values from September to November. This feature is a result of the smoothing process (Eq. 4.15) to Station "P" data, which is the only point sampled in the region during these months.

2) This area and the coastal zone have the highest standing crop values and differ in the month at peak density (see Figure 4.5). Coastal production peaks in June while the open ocean peaks in September. 3) The density of zooplankton in the estuary of the Fraser River is remarkably high and reaches up to 30 g/m^3 in early spring.
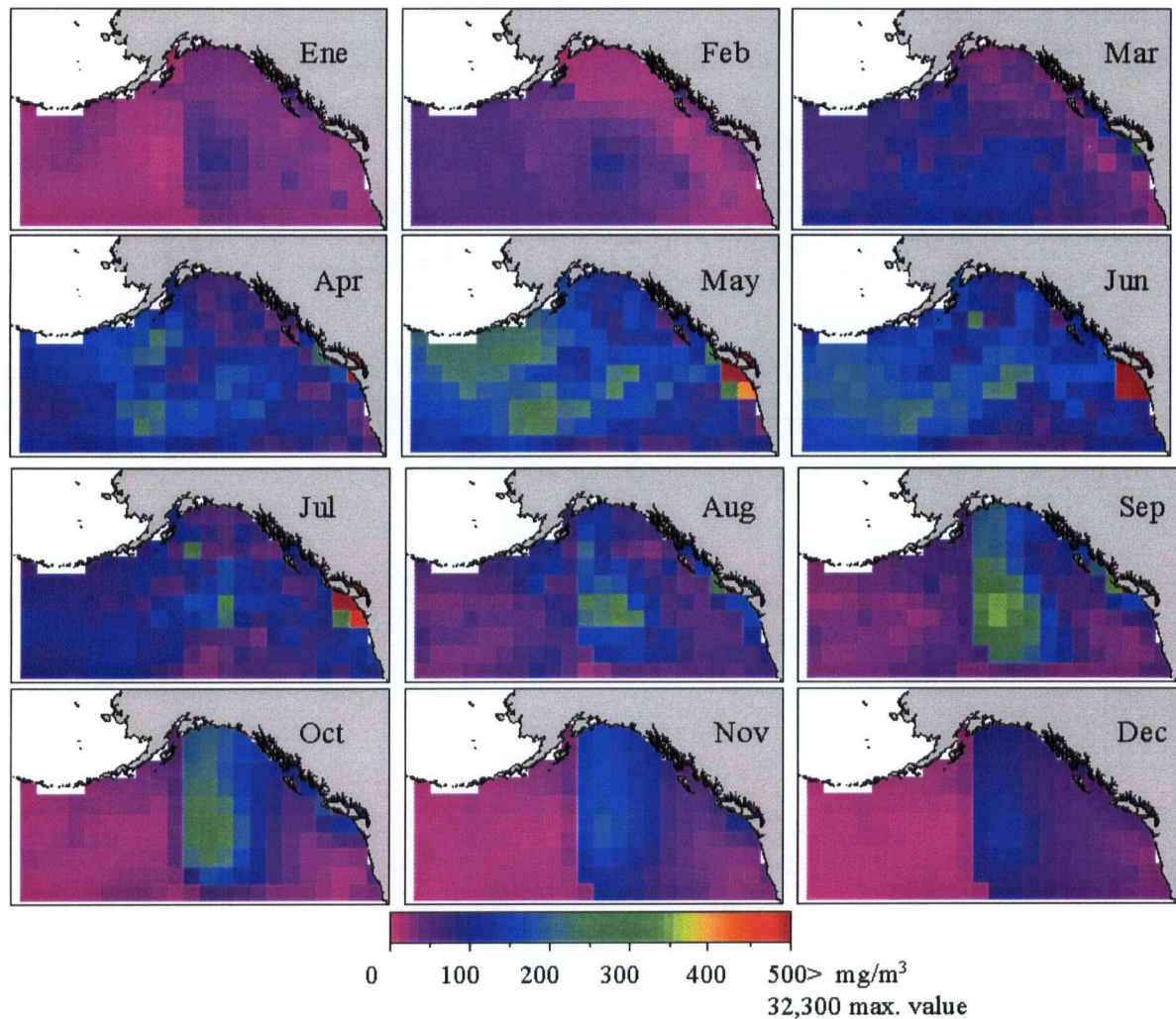
Figure 4.4. Monthly zooplankton standing crop density fields in the NE Pacific. See text for details.

The dynamics of temperature, surface currents, and zooplankton biomass are not of direct interest here; I consider them only as an input for the model and as such they will not be described any further or justified in any other way. See Brodeur and Ware (1992), Ware and

McFarlane (1989), and Ware and Thomson (1991) for a general description of zooplankton dynamics, composition, and interannual variability in the NE Pacific Ocean and Mackas (1992) and Parsons et al. (1970) for the British Columbia coast.
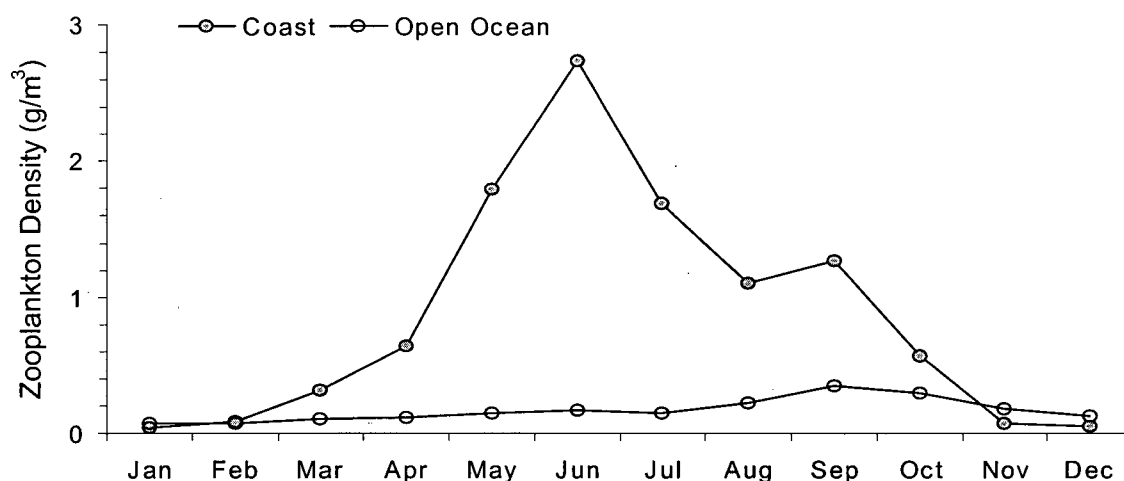
Figure 4.5. Seasonal changes in zooplankton standing crop for the coast and the open ocean. The coastal point mapped is in the Johnstone Strait. The open ocean point is located near Station P.

4.3.3 Marine Mortality

Losses experienced during the life cycle of sockeye salmon were divided into those occurring during the freshwater phase and those occurring during the marine phase. The losses during freshwater are accounted for in the *Fecundity and Fitness* section below. As in chapter 3, fishing mortality is not being considered a relevant force in the shaping of the observed migratory pattern of sockeye salmon.

Mortality processes after smolts migrate are not well understood. Smolts still have to complete downriver migration, coastal stage, marine stage, and reproductive migration before completing their life cycle, and in each phase mortality may have a habitat-specific structure. However, available information is for the total marine phase covering the smolt-to-adult stage, which shows size-dependency (Figure 2.15). The trend line in Fig. (2.15) predicts a 2.56 instantaneous mortality (8% survival rate for the 26 months of marine residency) for an

average smolt from the Fraser River (8.2 cm or 5.65 g Burgner, 1991), which is similar to the most up-to-date estimate from Bradford (1995).

The spatially explicit optimality model in Eq. (4.6) requires a mortality structure or value for each patch. Unfortunately, there is no information available on how to objectively allocate a mortality risk value to each grid point covering the area of distribution of sockeye salmon. Thus, I defined two broad zones in the grid, the coastal zone and oceanic environments (Figure 4.1). On those two zones the smolt-to-adult mortality was partitioned into the fraction occurring in the coast (referred as Z_C afterwards) and that occurring while in the oceanic environment (Z_O). Since there is no information available to determine the fraction of the total marine mortality that occurs in each environment, I explored the consequences of six hypotheses about partitioning of smolt-to-adult marine mortality relative to growth, reproductive output, and migration trajectory. Furthermore, the smolt-to-adult mortality shows size-dependency, therefore I also explored three hypothetical mortality structures that could generate the size dependency observed in the smolt-to-adult relationship:

1) Residence Time Mortality. Predation risk is constant for all body sizes. The size dependent relationship in Fig 2.15 arises from larger fish swimming faster that small fish, thus taking less time to leave riskier areas and reducing exposure time to such risk.

2) Size Dependent Mortality. Predation risk is not equal for individuals of different size. Smaller individuals are at higher risk than larger individuals.

3) Size and Activity Dependent Mortality. Increased activity levels result in increased encounter rates with predators, and the outcome of a predator-prey encounter is size dependent.

4.3.3.1 Residence Time Mortality

I partitioned the smolt-to-adult mortality into a fraction occurring during the 6 months of residence (184 days) in the coast and the remaining during the 20 months (607 days) of residence in the open ocean. The six fractions used and the equivalent daily mortality values are given in Table 4.1. Those particular values where selected on the perception that the coastal environment is riskier than the open ocean because of higher predator densities.

Table 4.1. Partition of smolt-to-adult instantaneous mortality between the coastal and oceanic environments.

% Smolt-to-adult mortality occurring in the coast	50 %	60%	70%	80%	90%	95%
Total coastal residence mortality	1.28157	1.53789	1.79420	2.05052	2.30683	2.43499
Daily mortality rate	0.00696	0.00835	0.00975	0.01114	0.01253	0.01323
Daily survival rate	0.99305	0.99167	0.99029	0.98891	0.98754	0.98685
% Smolt-to-Adult mortality occurring in the open ocean	50%	40%	30%	20%	10%	5%
Total oceanic residence mortality	1.28157	1.02526	0.76894	0.51263	0.25631	0.12815
Daily mortality rate	0.00211	0.00168	0.00126	0.00084	0.00042	0.00021
Daily survival rate	0.99789	0.99831	0.99873	0.99915	0.99957	0.99978

4.3.3.2 Size Dependent Mortality

The equation used to represent size-dependent instantaneous mortality was $Z = aW^b$ reported by Peterson and Wroblewski (1984) to occur across a wide range of species. The value used here for parameter $b = -0.37$ was estimated by McGurk (1996) for sockeye salmon. The value of the intercept a was estimated by iteration of equation (4.16) for each environment:

$$Z_h = a \sum_{t=0}^{T_r} W_{h,t}^{-0.37} \qquad \qquad \dots (4.16)$$

Where:

Z_h = Fraction of the smolt-to-adult instantaneous mortality occurring during residence in area h (i.e. coastal or oceanic area).

$W_{h,t}$ = Body weight in area h at day t.

T_r = Residence time in area h (184 days in the coast, 607 days in the open ocean).

Equation (4.16) distributes the smolt-to-adult mortality across a growth pattern on a daily basis. This method is similar to the inverse weight method in Ricker (1976), but differs in that Ricker assumed mortality to be inversely proportional to body weight (i.e. parameter b = -1.0). Notice that once the value of a is known, removing the summation in the right side of Eq. (4.16) results in an equation that estimates mortality risk on a daily basis.

Daily values for body weight in the open ocean were calculated from the instantaneous growth rate estimate of 0.003627 from the first to the second winter for 1.2 age type sockeye from Cultus Lake (Ricker, 1962). This age group is the dominant in all the races of the Fraser River and usually accounts for 88% of all the mature adults returning to spawn (Healey, 1987). The daily instantaneous growth rate in the coast was estimated at 0.0209 from mean smolt weight (5.8 g which includes the downriver migration period) and the weight (336 g) at first ocean annulus formation in the otholits (Ricker, 1962). Individuals leave the coast in September-October, and ring formation occurs between November and January (French et al., 1976). Thus an ocean growth equivalent of two months was removed from the 336 g by applying backward in time the open ocean instantaneous growth rate, resulting in a weight of 265 g at the moment of leaving the coast. Growth equations for this mortality reconstruction were:

$$W_t = 5.8 \ e^{0.0209 \ t} \qquad \text{For the coast} \qquad \qquad \text{...(4.17)}$$

$$W_t = 265 \ e^{0.003627 \ t} \qquad \text{For the open ocean} \qquad \qquad \text{...(4.18)}$$

Values for parameter (a) resulting from Eq. (4.16) for the partitions of total instantaneous mortality values occurring in the coast and in the open ocean (Table 4.1) are summarized in Table 4.2.

The mortality values used here were derived from a specific growth pattern (given in Eq. 4.17 and 4.18) defined for the sizes expected to occur in each habitat. This creates a bias towards high mortality rates for individuals larger that 265 g in the coast since mortality was estimated for sizes ranging from 5.8 to 265 g. Conversely, there is a bias towards lower mortality rates for individuals smaller than 265 g in the open ocean because it was derived

from a growth pattern for individuals larger than 265 g. However, such biases are not serious here given the wide range of coast - open ocean mortality values being explored.

Table 4.2. Size-dependent mortality coefficient (a) for coast-open ocean partitioning of smolt-to-adult mortality rates.

% Smolt-to-adult mortality occurring in the coast	50 %	60%	70%	80%	90%	95%
Total coastal residence mortality	1.2815	1.5378	1.7942	2.0505	2.3068	2.4349
Value of a in Eq. (4.17)	0.0249	0.0299	0.0348	0.0398	0.0448	0.0473
% Smolt-to-Adult mortality occurring in the open ocean	50%	40%	30%	20%	10%	5%
Total oceanic residence mortality	1.2815	1.0252	0.7689	0.5126	0.2563	0.1281
Value of a in Eq. (4.18)	0.0235	0.0188	0.0141	0.0094	0.0047	0.0023

4.3.3.3 Size and activity dependent mortality

The rationale for assuming an effect of activity on mortality comes from the presumption that the encounter rate between prey and predator increases as the combined area swept by predator and prey increases. This area swept is a function of time spent swimming during foraging and migration. The lower stomach content of immature individuals when compared with maturing individuals (LeBrasseur, 1966; LeBrasseur and Doidge, 1966) suggests that foraging activity is indeed restricted due to a mortality cost. Thus, the effect of activity on mortality was considered along with the effect of size.

The size dependency of mortality hypothesis was represented with the same structure as above, and the activity dependency was represented as a linear function of the daily pattern of hours spent foraging and migrating (T_m + T_f). Daily instantaneous mortality rate was assumed to vary as:

$$Z_{h,t} = a\, W_{h,t}^{-0.37} \left[\, a + b\, (T_m + T_f)\right] \qquad \dots (4.19)$$

Values for parameter a are given in Table 4.2. Values for a and b were arbitrarily chosen since there was no information available to define them. I assumed that in the absence

of sockeye activity, the daily instantaneous mortality would be reduced by half ($a = 0.5$). The slope was set at $b = 0.1$ so as to increase the daily instantaneous mortality by a factor of 2.9 when the full day is used for activity.

4.3.4 Fecundity and Fitness

Optimality models require the definition of a terminal fitness function to maximize over the life span of the individual. Here I used the fecundity function given in Fig. (2.2) to represent total reproductive output of an individual female. This function is usually defined in terms of body weight, however in sockeye salmon this function is defined in terms of body length since proper measurements of fecundity must be done when gonads are ripe. By that time a fair amount of body mass has been depleted and partially substituted with water (Gilhousen, 1980), which renders weight unreliable as a predictor variable.

State dynamics in the model are defined in terms of body weight, while the fecundity function (Eq. 4.20) is defined in units of length. Thus to associate fecundity to weight and define state dynamics in terms of weight only I converted length to weight with the length-weight equation $W = 0.00924364 \, L^{3.066}$. Parameter values for this equation were obtained by a least squares fit to log transformed W-L data in Brett (1964), Brett (1965), and Brett and Glass (1973) ($n = 80$, $r^2 = 0.94$). The range of body sizes in this data set was from 8 to 80 cm.

The fecundity function in Eq. (4.20) was adjusted for losses that occur during the freshwater phase, as described in Chapter 2: 5% upriver migration mortality, 3% female egg retention, 98.45% fertilization efficiency, 12.43% egg-to-fry survival, and 70.77% lake mortality. All those factors combined indicate that 3.3% of the eggs from a female entering the Fraser River will survive to leave the rearing lake as smolts. Only 0.26% of the fertilized eggs return as mature adults to spawn, equivalent to 10.6 recruits for a 59 cm (2.48 kg) female. This value is very close to the average adult recruits per female spawner value given in Chapter 2. Using these data the terminal fitness function is expressed as:

$$F(w(L), h, T) = \begin{cases} 0.033(-2268.9 + 106.8L) & L > 21; h = H_s \\ 0 & \textit{otherwise} \end{cases} \quad \dots (4.20)$$

Where

L = Body length (cm)

w(L) = Length – weight conversion function

h = Geographic location

H_S = Fraser River Estuary

T = Spawning time

Equation (4.20) indicates that only those females larger that 21 cm arriving at patch H_S at terminal time T have a positive reproductive value. Here patch H_S is defined at the mouth of the Fraser River (blue point in Fig. 4.1). Also notice that, being constant, the losses occurring while in freshwater have no real bearing on the decisions required to optimize F(w, h, T) during the marine phase since they only scale down the payoff function in Eq. (4.20). However, I explicitly considered those losses to compare model predictions with available recruits/female information.

4.3.5 Activity Schedule, Foraging and Bioenergetics

Energy gains and losses from foraging and metabolism were represented with the bioenergetics model in Eq. (4.11). This model is described in detail and fitted to sockeye salmon metabolism in Appendix A *Bioenergetics of sockeye salmon*. This model provides a detailed description of the energy budget of an individual on a daily basis, and explicitly describes the metabolic changes associated to body weight allometry, and the costs of activity and water temperature on respiration.

Migration time, foraging time and swimming orientation were defined as decision variables to be estimated by the optimization model in Eq. (4.6). Thus the daily activity pattern was partitioned into three components; time allocated to forage, time allocated to migration, and "resting" time as in Eq. (4.1). Migration time varied from 0 to 24 hours in increments of 3 h, and foraging time from 0 to 5 h in increments of 1 h, resulting in 41 behavioral choices that satisfied the condition $T_m + T_f \leq 24$. Resting time was calculated as $T_r = 24 - T_m - T_f$.

The bioenergetics model estimates respiration costs on a daily basis, and the two behavioral choices of activity (forage and migration) can be carried out both within a day. Thus, each activity component was scaled to the fraction of the day that it occupied as defined in Eq. (4.13).

To avoid additional computational burden associated with the choice of optimum swimming speed, the swimming speed during migration (v_m) was fixed to 1 body length per second (L/s) and foraging speed (v_f) to 0.75 L/s in Eq. (4.6 to 4.9). I assumed that during resting time any activity carried out by fish was non-directed and equivalent to the cost of swimming at 0.1 L/s.

During foraging an individual could not exceed its maximum consumption level according to its weight and the water temperature as defined in Eq. (A.2 to A.5) of Appendix A. Realized consumption (G) was calculated from the area swept model described in Eq. (4.14). Foraging reactive distance (r_f) was set at 48% L and correspond to the distance where coho salmon (*O. kisutch*) has $\cong$90% chance of initiating an attack on a prey item (Dunbrack and Dill, 1984). Foraging reactive distance while migrating (r_m) was set to zero.

The zooplankton data (see *Habitat Attributes* for a description of the data) did not allow for consideration of the effect of small scale food patchiness on growth. Furthermore, it was necessary to account for failing attacks on prey, the handling time cost incurred by the biting behavior of sockeye while foraging, and that not all of the zooplankton biomass reported are actual preys. All those factors reduce the effective prey density field as seen by the fish, and their combined effects were pooled into the scale parameter β (foraging efficiency) in Eq. (4.14). Since there is no information available to define a value for β I considered as plausible those values that predicted terminal weight and productivity close to the observed range (2.2 to 2.8 kg and 6 to 9.9 recruits per female).

4.3.6 State Space boundaries

The weight range used here (4 to 3,930 g) was discretized into 20 weight intervals defined by Eq (4.21). This discretization solves the problem of overrepresentation of weight

classes at one extreme of the weight range and under-representation at the other extreme resulting from the allometry of weight.

$$w_i = 4\,i^{2.3} \qquad\qquad\qquad\qquad .... (4.21)$$

Where

w_i = Weight value of interval i

Individuals of increasingly larger body lengths can cover increasingly larger distances within a month. Thus it was necessary to define a maximum search distance for each body size to limit the region where the optimization is going to be carried out. This maximum search distance (D_{max}) was define as follows:

$$D_{max} = q\,\upsilon(w)\,DM \qquad\qquad\qquad ....(4.22)$$

Where

$\upsilon(w)$ = Weight dependent swimming speed during migration in km/d.

DM = Number of days of month currently being processed

q = Scaling factor (1.1 used here)

The value of scaling factor q was chosen to ensure that the farthest cells searched during the optimization process fall just outside of the achievable range, thus forcing the process to consider all reachable gridcells.

During the optimization process, most decision choices in the dynamic programming equation (4.6) yielded weight values between those defined by Eq. (4.21). In those cases, the corresponding fitness value was linearly interpolated from the two closest points. The fitness value for any weight above 3,930 g was estimated as the corresponding value for a 3,930 g individual (i.e. the model assumes no gain in fitness for exceeding a terminal weight of 3.93 kg).

The behavioral option for drifting posed two problems. Some choices result in individuals reaching a boundary of the grid at the end of a time interval. Those choices were considered 'lost' and given a survival value of 0 resulting in a fitness value of 0 as the locally optimal solution in Eq. (4.7). It was also common for drifting to predict a location between

grid points at the end of a time interval. In those cases fitness was interpolated with a simple weighted average using the inverse of the distance to the four neighbor patches as weights.

The solution of Eq. (4.9) for migration required the use of one value per habitat attribute (food density, predation risk, temperature, and surface currents) for adjacent patches along the migration trajectory. This value was defined as the arithmetic mean between patch origin and patch destination for adjacent patches. Trajectories spanning more than two patches were split into a sequence of adjacent two-patch sub-trajectories and their habitat characteristics were averaged as before.

The optimization was carried out assuming that smolts reach the estuary of the Fraser River on May 1st and return as mature adults to the estuary 26 months later on July 1st to initiate the upriver migration. July 1st corresponds to the date when mature adults from the Early Stuart race reach the river (see Table 2.2), while May 1st is the month were most of the Fraser River smolts reach the estuary (Burgner, 1991).

4.4 Results and Discussion

The six coast-to-open ocean mortality allocation values (Z_C), for each one of three mortality structures, combined with four foraging efficiency values (β), resulted in 72 different cases explored. Each case is composed of a series of arrays containing the optimal migratory behavior for each month of marine life everywhere over the grid. The variables in each array were optimal migration time, optimal foraging time, optimal geographic location to go, achieved weight at the end of each month, fitness expectation at the beginning of each month, and average ration during each month.

Those arrays contain the optimal migratory behavior for any possible combination of date, weight, and geographic location. Thus, it was necessary to create a forward simulator to extract specific optimal policy trajectories from the optimal policy estimate given a combination of initial body weight, position, and date of entrance to the marine environment.

The simulator follows the state of an individual forward in time, as predicted by the optimal policy, that begins marine life at a given weight, month, and location. This model also tracks the value taken by the decision variables foraging time, migration time, and location to go and the auxiliary variable ration. Fitness and growth values for body weights other that those used in the optimization are linearly interpolated. Foraging time, migration time, and realized ration were not interpolated because they are dependent on the migration trajectory, which cannot be interpolated. Values for those variables correspond to those from the nearest weight class from which the optimal trajectory was extracted.

The relevance of the foraging efficiency and mortality scenarios reviewed here were first screened using terminal weight and the expected fitness in smolts per female smolt as qualitative performance indices. Values for those two variables were estimated for a 12 g individual leaving the Fraser River estuary on May 1st. Predicted values for those variables assuming residence time mortality are given in Table 4.3, for size dependent mortality the results are in Table 4.4, and for size and activity dependent mortality in Table 4.5. Plots of the optimal migration trajectories and profiles of the decision and auxiliary variables for each case reported in Tables 4.3 to 4.5 are in the Addendum at the end of this chapter.

In general, Tables 4.3 to 4.5 show that for a given value of Z_C, the terminal weight and expected fitness increase as the foraging efficiency value increases (β). This is a result of individuals being able to see an increasingly larger fraction of the zooplankton fields as prey, and achieving larger rations. Conversely, for a fixed foraging efficiency value, as the percentage of total mortality occurring in the coast (Z_C) increases, terminal weight decreases and the fitness expectation increases. This is a result of individuals leaving the prey rich coastal environment earlier which translates into lower growth, and moving into a increasingly safer environment which translates into higher smolts per female smolt values.

4.4.1 Residence Time Mortality

This mortality structure most closely predicted the observed terminal growth and fitness value of a 1.2 sockeye salmon from the Fraser River, at values $\beta = 0.18$ and $Z_C \geq 80\%$ (Table 4.3). However, all of the β and Z_C parameter combinations resulted in optimal migratory trajectories that go westward directly into the center of the Gulf of Alaska after 5

months of coastal residency and return to the Fraser River through the Juan de Fuca Strait. None of those parameter combinations along with the habitat configuration specified were sufficient to explain the northwestward migration of juvenile salmon along the coast (see Figures 4.19 to 4.22 in Addendum).

Table 4.3. Terminal weight (in g) and expected fitness (recruits/female) predicted values for the residence time mortality case. Values are for a 12 g smolt that begins the marine phase at the Fraser River estuary on May 1st. The values in italic are the closest match to the observed terminal weight and expected reproductive output.

Z_C	$\beta = 0.15$		$\beta = 0.18$		$\beta = 0.20$		$\beta = 0.25$	
	W_T	F_T	W_T	F_T	W_T	F_T	W_T	F_T
50%	1147	4.54	2509	6.15	3737	7.19	4040	9.07
60%	1147	4.58	2527	6.51	3084	7.84	4058	10.00
70%	841	4.84	2130	7.11	3112	8.75	3807	11.46
80%	763	5.27	*2207*	*7.97*	2899	9.93	3807	13.32
90%	764	5.87	*2207*	*9.07*	3089	11.42	3807	15.69
95%	696	6.22	*2207*	*9.72*	2943	12.29	3427	17.06

Values of β less than 0.18 predicted terminal weights below 1,150 g and female productivity below 6.3 while values of β greater than 0.18 resulted in terminal weights above 2,800 g and female productivity above 7.19 smolts/female. Those results are well outside the observed range for a 1.2 female from the Fraser River, and for this reason were not considered realistic.

At a foraging efficiency value of $\beta = 0.18$ and for all the six values of Z_C, the model yielded the closest match to the observed life history pattern of an age 1.2 sockeye salmon. The predicted terminal weight and expected fitness for a 12 g female smolt were well within the observed range of values for an age 1.2 individual (see Table 4.3). There was a parameter combination of $\beta = 0.2$ and $Z_C = 80\%$ which predicts a 2,899 g terminal weight and 9.93 smolts per female smolt. However, the terminal weight predicted by that combination is near the upper limit of the observed range, and the value of expected fitness is too low for such weight.

At a foraging efficiency (β) of 0.18 and for values of $Z_C \geq 80\%$ the model predicts very similar optimal migration trajectories and behaviors, with the only exception being the

fitness profiles which increase with Z_C. The optimal migration trajectory for those three parameter combinations is identical and is given in Figure (4.6). The optimal policy predicts 5 months of residence in Johnstone Strait, from which there is one month when is optimal to leave the coastal environment (month 5) only to come back the following month. Individuals leave the coast through the Queen Charlotte Strait, moving westward directly into the South center of the Gulf of Alaska rather than northwestward along the coast, then return to the Fraser River through the Juan de Fuca Strait. This policy predicts the use of the South Central region of the Gulf of Alaska as the oceanic residence of Fraser River sockeye. However, the policy does not predict the observed juvenile coastal migration where individuals actively move northwestward along the coast.
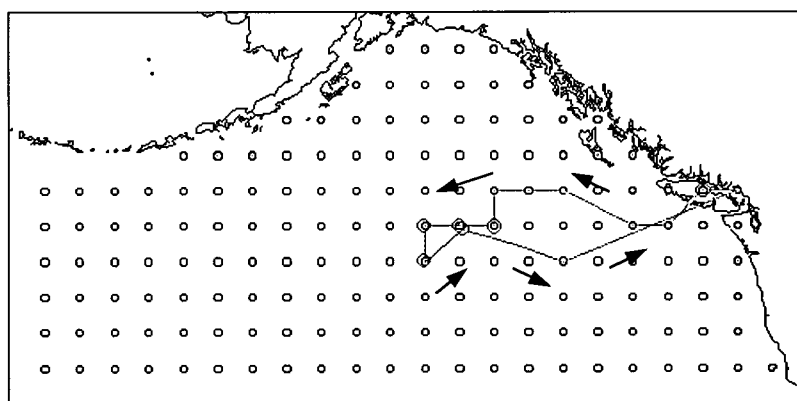
Figure 4.6. Optimal migratory trajectory for sockeye salmon with $\beta = 0.18$ under residence time mortality. Red lines indicate active swimming, green circles staying, and the blue line drifting. The trajectory is the same for values of ZC $\geq$ 70%. Arrows indicate the direction of the movement.

The optimal activity patterns for those six combinations of Z_C (Figure 4.7) are very similar although optimal policies for Z_C of 50% and 60% differ from the rest during the first two months and last three months of marine life. The activity patterns also show that once in the open ocean, migration activity is continuously reduced and reaches 0 during month 22, but then increases quite a bit during the last three months of marine residency. The drifting behavior for month 22 may be an artifact due to uncoupling between the zooplankton field and surface currents (i.e. there is no advection for zooplankton in this model).
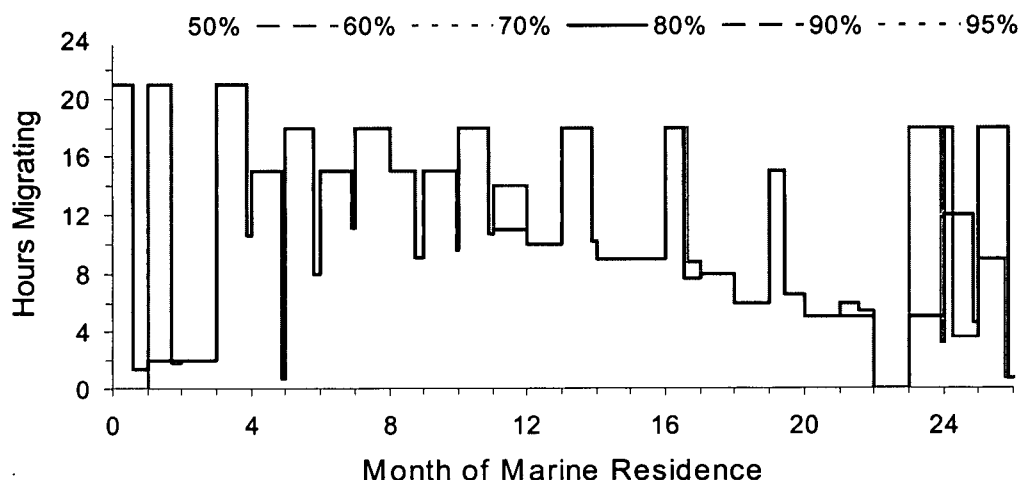
Figure 4.7. Optimal swimming activity schedule for sockeye salmon with β = 0.18 under residence time mortality. Month 0 corresponds to May.

The predicted optimal foraging time pattern was stable for a wide range of coast - ocean mortality conditions (Figure 4.8). The model predicts low foraging hours during early marine life (while individuals are still near the coast), however once in the open ocean foraging time is constant and maximum. This behavior is consistent with the higher zooplankton density in the coast than in the oceanic environment, and it is reasonable to expect a shorter time to satiation in the coast than in the open ocean. High prey abundance during early marine life may actually be a critical factor in the migration of salmonids considering that the smolting process in the nursery lake is characterized by higher respiration costs, fast growth in length, and a reduction in body fat (McCormick and Saunders, 1987; Woo et al., 1978). The smolting process in juvenile salmonids may result in individuals with low tolerance to starvation that require high food density upon arrival to the estuary and adjacent areas in order to minimize the probability of starvation.
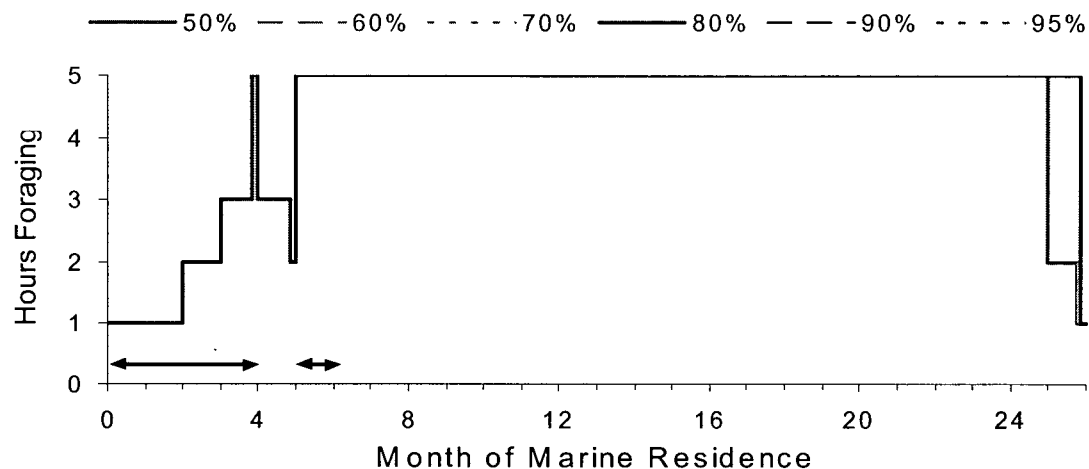
Figure 4.8. Optimal foraging activity schedule for sockeye salmon with $\beta = 0.18$ for 6 values of Z_C Residence Time Mortality. Month 0 corresponds to May. The arrows above the time axis indicate the months spent in the coast.

The realized ration profiles resulting from the optimal foraging pattern are also quite similar under all Z_C values explored (Figure 4.9). However, ration has a strong seasonal component reflecting changes in zooplankton abundance. Note that early in marine life the amount of time spent foraging has some of the lowest values, yet the ration attained is near the maximum ration for small individuals (~ 10% body weight). This is a direct result of the high prey concentration in and around the estuary of the Fraser River during late spring.
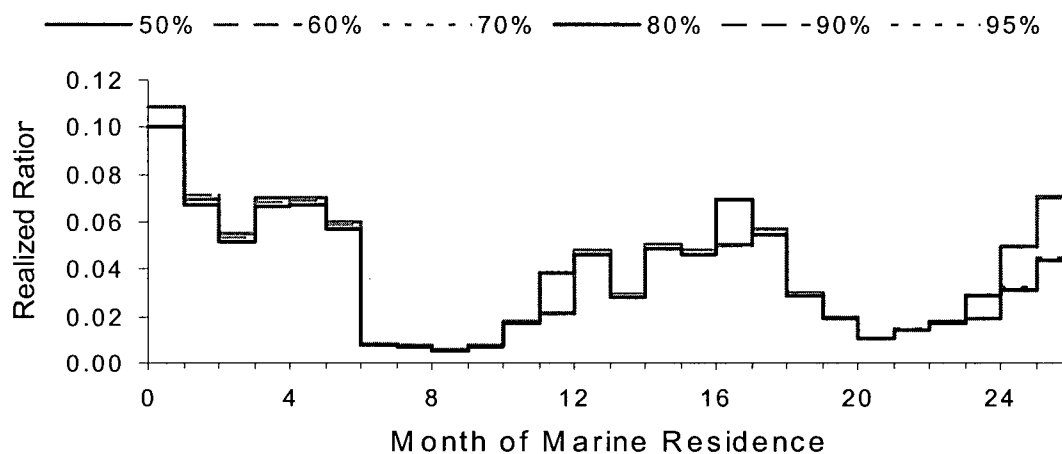
Figure 4.9. Realized ration for sockeye salmon with β = 0.18 for 6 values of Z_C Residence Time Mortality. Realized ration is expressed as a fraction of body weight. Month 0 corresponds to May.

The growth profiles predicted by this mortality structure for the six values of Z_C were seasonal and nearly identical during the first 23 months, with small differences during the last three months of marine life (Figure 4.10). The optimal policies for Z_C values of 50% and 60% predict that individuals would reach slightly larger terminal weights than those from 70% to 95%. All growth patterns show low or no growth from January to April and fast growth from May to December, which agrees well with the seasonal changes in zooplankton density. Most of the absolute growth occurs during the last five months of marine residence although the growth rate during those months is not as high as in previous seasons.
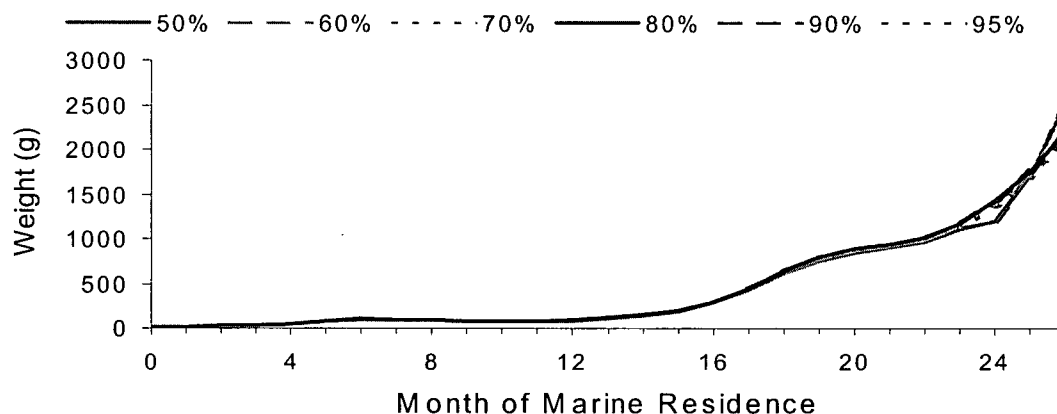
Figure 4.10. Growth pattern of sockeye salmon with a foraging efficiency of 0.18 for 6 values of Z_C Residence Time Mortality. Month 0 corresponds to May.

There is no direct evidence to support the seasonality of the predicted growth pattern. Burgner (1991) indicate that although sockeye scales show wide circuli in summer and narrow circuli in winter, these changes cannot be directly interpreted as a change in growth rate because the rate at which the circuli appear is not known. Brett (1980) and Furnell and Brett (1986) modeled seasonal growth pattern for sockeye salmon based on the assumption that temperature has a strong effect on growth. The prediction of my model is that seasonality of growth in the marine environment is a reasonable expectation, however it is directly related to seasonal changes in food abundance rather than temperature.

The fitness patterns predicted by the resident time mortality structure (Fig. 4.11) show several features of interest. All fitness patterns always increase through time. This comes from the semelparity of the species that implies only one payoff time, thus as individuals manage to survive and grow to the next time unit their fitness expectation increases. Notice that a considerable gain in fitness occurs during the first six months of marine life. Such increase comes from the higher risk of mortality in the coast, turning the survival of one more month into a large fitness gain.
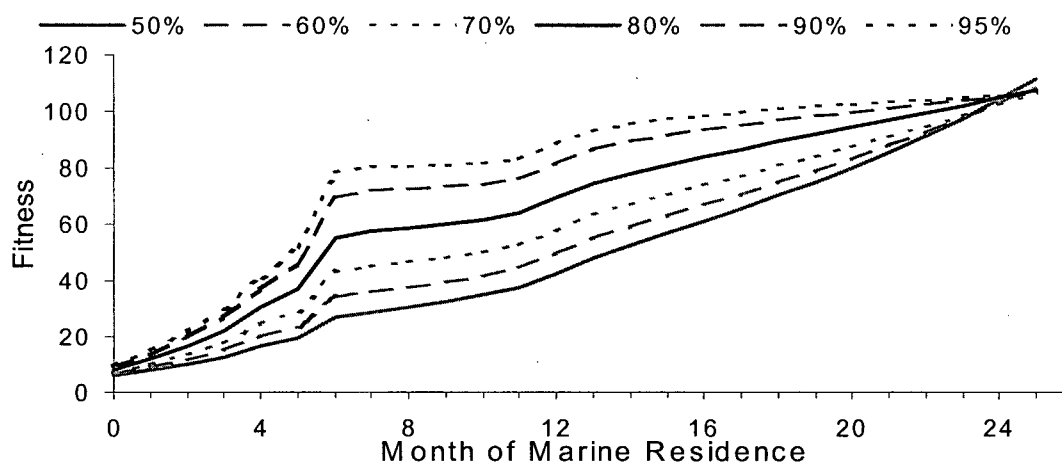
Figure 4.11. Fitness expectation of sockeye salmon with $\beta = 0.18$ for 6 values of Residence Time Mortality (Z_C). The fitness value is the expected payoff in smolts per female at the moment of river entry. Month 0 corresponds to May.

The fitness patterns for low values of Z_C fall below those for higher values of Z_C. This is a reflection of the smolt-to-adult mortality split between the coast and the open ocean. Lower values of Z_C have the implication of higher risk of mortality in the oceanic environment where sockeye spends 20 months of its marine life.

Finally, the shape of the fitness patterns changes with Z_C, shifting from nearly linear at 50% to a line at 95% that grows exponentially during the first 6 months and has two nearly flat phases after that. Notice that the reduction in fitness gains occurs during the no growth season, so it seems that the flattening of the fitness pattern is related to low growth. The slope is still positive but only because individuals have survived one month more.

4.4.2 Size Dependent Risk of Mortality

The predictions of the model based on size-dependent mortality show that nearly all combinations of Z_C and β tried overestimate terminal weight, and all the cases underestimate fitness (Table 4.4). The size dependency of mortality as stated here results in a strategy characterized by low growth while in the coast followed by high growth rates once in the open ocean, particularly during the last 6 months of marine life (see figures 4.23 to 4.26 in Addendum). This mortality structure creates a very unforgiving environment during early

marine life, and most gains in expected fitness occur after leaving the riskier coastal environment.

Table 4.4. Terminal weight (in g) and expected fitness (in recruits/female) predicted values for the size dependent mortality case. Values are for a 12 g smolt that begins the marine phase at the Fraser River estuary on May 1st.

	$\beta = 0.09$		$\beta = 0.11$		$\beta = 0.13$		$\beta = 0.15$	
Z_C	W_T	F_T	W_T	F_T	W_T	F_T	W_T	F_T
50%	4847	6.03	5715	6.75	6707	7.22	7322	7.46
60%	3593	4.41	4238	5.13	4467	5.69	4455	6.05
70%	3526	3.63	3895	4.41	3979	5.19	4139	5.76
80%	3260	3.12	3874	4.02	3739	5.11	4025	6.02
90%	2297	2.78	2314	3.86	2891	5.33	1469	6.71
95%	2196	2.66	1978	3.89	2822	5.61	1478	8.27

Size-dependent mortality often resulted in overshooting the state space limit for weight and the model predicted terminal weight values well above the 3,930 g limit in spite of the fitness cutoff imposed in the model (see *State Space Boundaries*). This behavior is a direct result of the power equation used to represent the size-dependency of mortality. The power equation has the strong implication that individuals are always at risk regardless of the behavioral pattern displayed, and the only way to reduce the risk is by growing. Furthermore, a weight gain has a double positive effect on expected fitness since larger weights reduce predation risk and increase fecundity.

Size dependent mortality also had an unexpected effect on the migratory behavior and migration trajectories. Since size-dependent mortality implies a higher risk of mortality for small individuals, then individuals allocate energy into growth that otherwise would be allocated into activity, resulting in the inhibition of migratory behavior. This diversion of energy results in very short migratory trajectories where individuals move to the nearest area defined as oceanic habitat to benefit from the comparatively low predation risk there. This mechanism made it possible to generate high terminal weights for foraging efficiency values as low as 9%. The size dependency of mortality as defined here is unlikely to be a valid representation of the mortality process encountered by sockeye salmon at sea.

4.4.3 Size and Activity Dependent Risk of Mortality

Just as with size dependent mortality, this structure results in overestimates of terminal weight and underestimates of fitness, although terminal weights are not as high as those predicted by size dependent mortality alone (Table 4.5). This mortality structure explicitly creates a mortality risk through movement, and not surprisingly resulted in optimal behaviors where migration activity and foraging were inhibited (see Figures 4.27 to 4.30 in Addendum at the end of this chapter).

There were several cases were the optimal policy predicts a migration into the center of the Gulf of Alaska. Those cases are characterized by a medium to high risk of mortality in the coast and high foraging efficiencies ($\beta \geq 0.15$) although most of those optimal trajectories do not predict the juvenile coastal migration. However at a foraging efficiency value of 0.30 (the highest value considered) and for $Z_C \geq 80\%$ the model made the best predictions of the juvenile coastal migration. Optimal migration trajectories during the juvenile stage run parallel to the coast as far as Kodiak Island before moving into the center of the Gulf of Alaska.

Table 4.5. Terminal weight (in g) and expected fitness (in recruits/female) predicted values for the activity dependent mortality case. Values are for a 12 g smolt that begins the marine phase at the Fraser River estuary on May 1st.

Z_C	$\beta = 0.12$		$\beta = 0.15$		$\beta = 0.20$		$\beta = 0.30$	
	W_T	F_T	W_T	F_T	W_T	F_T	W_T	F_T
50%	4457	8.89	4681	9.71	5460	10.83	3912	12.40
60%	4358	6.03	4644	6.63	5478	7.44	3923	8.59
70%	4009	4.30	4315	4.76	4082	5.45	4029	6.62
80%	4018	3.36	4300	4.08	3982	5.53	4182	7.32
90%	3767	3.53	1406	5.01	3890	7.17	4096	10.24
95%	3234	4.01	1268	5.90	3924	9.03	4256	13.16

This was the only mortality structure that predicted reduced or no foraging activity during winter months when zooplankton density is at its lowest, along with reduced foraging when zooplankton abundance peaks. As a result of the foraging strategy, individuals have an accelerated growth from March to October that ends abruptly and declines during the rest of

the year. The abrupt transition and the reduction in weight is not apparent at larger values of Z_C because of the benefits from lower mortality rates in the open ocean.

4.4.4 Environmental Factors and the Prediction of the Juvenile Coastal Migration

The residence time dependent mortality hypothesis explored here made the closest prediction of the characteristics observed in the migration of Fraser River sockeye salmon races, however it was unable to account for the juvenile coastal migration. This problem may arise from an incomplete representation of the biological processes occurring at the juvenile stage, from events occurring at time-space scales not considered in the model, or from an inadequate representation of habitat characteristics. Although I cannot dismiss the first two possibilities, most likely the problem comes from a less than adequate characterization of the zooplankton field, particularly in the area between mainland and the Queen Charlotte Islands in the Canadian coast. The zooplankton data used here provides nearly no samples from May to December (see Figure 4.3).

As a guide to provide a better spatial description of the zooplankton field in the coast, I used the monthly chlorophyll distribution in the NE Pacific (Figure 4.12) from the SeaWIFS color scanner as a reference (GIF images taken from www.marine.rutgers.edu/opp/swf/ Production/gif_files/). Those images show the development of high production areas from April to October off Oregon, Washington, British Columbia, and most of the Pacific coast of Alaska, and a semi-permanent band in the southern edge of the Alaska Gyre. A similar density distribution is reported for zooplankton biomass in the area by Ware and McFarlane (1989). Ware and McFarlane (1989) described the presence of large concentrations of zooplankton biomass (primarily composed of *Neocalanus plumchrus* and *N. christatus*) at the south and southeast edges of the Alaska gyre, presumably as a result of advection within the gyre. They indicate that *N. plumchrus* and *N. christatus* account for up to 75% of the zooplankton density in the central subartic domain and that abundances closely follow the primary production cycle.

Following the spatial structure of chlorophyll in the coast, I standardized the monthly zooplankton density values in the coast by replacing them with those from Johnstone Strait

(first cell west of the Fraser estuary in Figure 4.1). I choose the Johstone Strait area to represent the seasonal variation of zooplankton in the coast for the reason that it was well represented in the samples through the year and does not reach the extreme high values observed in the Fraser estuary.
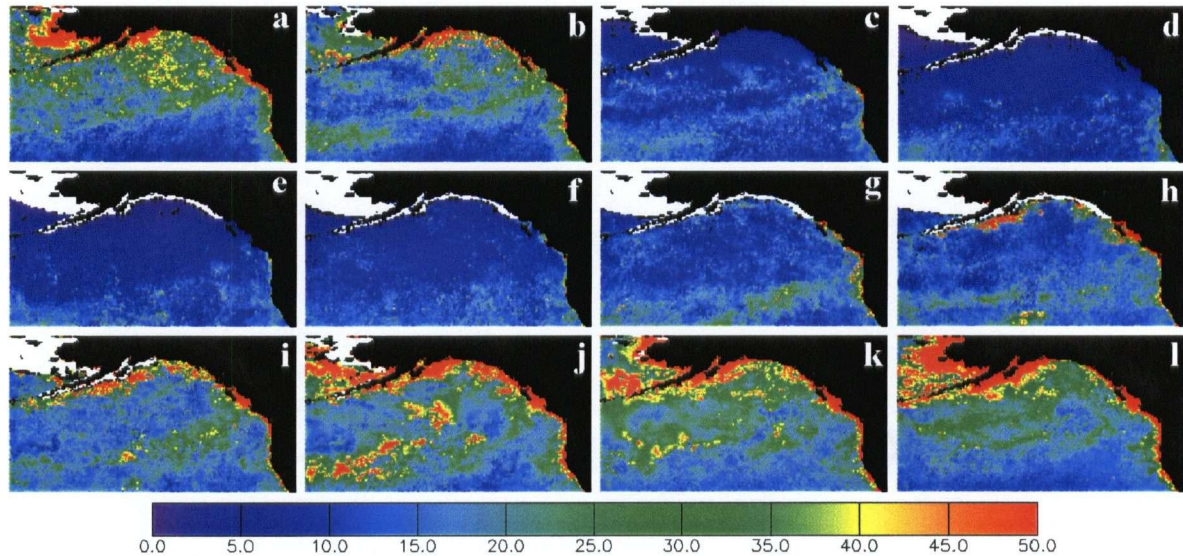
Figure 4.12. NE Pacific surface Chlorophyll (in g C/m2) as reported by the SeaWIFS color scanner. Images a to l are monthly mean values from September 1997 to August 1998.

With the coastal environment standardized this way, the model predicted the juvenile coastal migration under all combinations of Z_C tested (Figure 4.31 in Addendum). Furthermore, the fitness expectations were within the 6 to 10 smolts/female range estimated in chapter 2 (Table 4.6). However terminal weights were within the observed range only for values of $Z_C \geq 60\%$ and stable predicted values and migratory trajectories occurred for $Z_C \geq 80\%$ (Table 4.6, Figure 4.31).

Although the predicted terminal weight for $Z_C = 50\%$ was quite high (3,848 g), this policy predicts the closest match to the perceived migration route of juvenile sockeye salmon (Figure 4.13a) in which juveniles migrate Northeastward along the coast (see Figure 2.10). For values of $Z_C > 50\%$ the juveniles still migrate Northeastward although they leave the coast after reaching the Queen Charlotte Islands (see Figure 4.13b). The low values in zooplankton density used in earlier runs inhibited the use of this area for juvenile migration,

and had a strong effect on the trajectory. Considering that the migration trajectories for non-standardized coastal conditions (in Figure 4.6) go directly into the open ocean, it seems that the optimum migration trajectory is more sensitive to prey abundance than to the advection forces in that area.

Table 4.6. Terminal weight and fitness expectation predicted under the assumption of residence time mortality, a foraging efficiency value of 0.17, and standardized coastal zooplankton density.

Z_C	50%	60%	70%	80%	90%	95%
Terminal Weight (g)	3,848	2,583	2,526	2,363	2,359	2,357
Fitness (smolts/fem.)	6.71	7.06	7.66	8.48	9.50	10.08
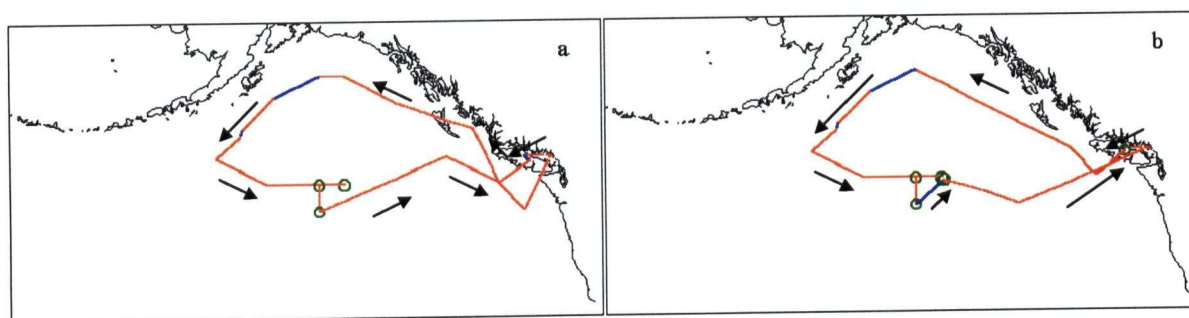
Figure 4.13. Optimal migratory trajectories predicted from residence time dependent mortality, a foraging efficiency of 0.17, and standardized coastal zooplankton density. Figure (a) is for $Z_C = 50\%$ and Figure (b) for $Z_C = 80\%$. Red lines depict active migration, blue lines drift, and green circles holding position in the center of the circle. Arrows depict direction of movement.

Notice that the optimal policy predicts a migratory trajectory that takes the juveniles off Vancouver Island (Fig. 4.13). In this location individuals can take advantage of the advection and reduced predation risk (this is the closest open ocean gridpoint to the release point in the Fraser River estuary). Such displacement has not been observed and likely is a result of the coarse grid used here that prevented the representation of Vancouver Island in the grid and the assumption of linear trajectories. One may think that the use of a non-uniform grid to improve the description of the topographic features of the region while keeping the number of gridpoints small would solve this problem. This is not the entirely case since this problem arises not only from the use of a coarse grid, but also from the assumption of linearity in migratory trajectories. Likely, the solution of this problem requires both, an

improved representation of the topography of the region (either by using a non-uniform grid or a uniform one at a higher resolution), and a reduction of the time increments from a month to a week or maybe less to reduce trajectory linearity to short distances (as in chapter 3).

On the basis of the two criteria that I used to discriminate between cases (terminal weight and expected fitness), $Z_C = 80\%$ was the one that provided the best match. The optimal policy for this case predicts terminal weight and expected fitness within the observed range and an optimal migratory route that closely follows the general migration pattern outlined by French et al. (1976), Groot and Cooke (1987), and Hartt and Dell (1986), although it predicts only one loop around the Gulf of Alaska. For this reason I examined it in more detail below. The predictions of the remaining five cases can be found in Figure 4.31 at the end of this chapter.

The environmental profiles encountered along the optimal migratory trajectory for $Z_C = 80\%$ (Fig. 4.13b) are shown in Figure 4.14. The temperature profile (Figure 4.14a) is several degrees below the sharp thermal limits reported for the distribution of sockeye salmon in the NE Pacific (thick line in Fig. 4.14a) (French et al., 1976; Welch et al., 1995; Welch et al., 1998). The zooplankton profile (in Figure 4.14b) shows that after 10 months of marine residency, the optimal migratory trajectory closely tracks the areas with the highest zooplankton density in the NE Pacific (thick line in Figure 4.14b). Since this model maximizes reproductive output, it follows that tracking the richest areas in the open ocean is a behavior that maximizes reproductive output. The thermal limits detected for sockeye salmon very likely arise from oceanographic features within the Alaska Gyre that correlate with zooplankton production and temperature. Such features can be seen in the seasonal phytoplankton distribution in Figure 4.12, where an area of high production in the open ocean flows northeast along the West Wind Drift Current. South of that band primary production is low, and if secondary production there is also low as Ware and McFarlane (1989) suggest, then this band may define the NE Pacific distribution limits for sockeye salmon. Notice that this association depends on an environment with a stable spatial structure, like the Alaska Gyre. Areas like the Northwestern Pacific, where the meanderings and eddies of the Oyashio and Kuroshio Currents create a complex spatial structure for production (see for instance Chapter 9 in Longhurst, 1998), would reduce the temperature – prey density association and

the sharpness in the thermal boundaries. Welch et al. (1995) did find that sockeye in the NW Pacific do not have such sharp temperature boundaries.

The advection flow encountered along the optimal migratory trajectory in Fig. 4.13b are depicted in Figure 4.14c, and the swimming velocity of the fish is shown in Figure 4.14d. The graphs show that while in the coast most of the time the advection experienced by migrants has a northward component, and once in the open ocean the currents encountered flow northeastward. In contrast the swimming behavior has a dominant southward component and once sockeye are in the open ocean, the predominant swimming direction is southwestward.

The optimal migration profile for Z_C = 80% has three periods of reduced or no migration activity lasting one to three months each (Figure 4.15). The first period occurs during the first four months of marine life while individuals are still in the British Columbia coast; the policy predicts a residence time of three months in the area. The second period occurs off Kodiak Island where the migration trajectory goes along the strong southwest branch of the Alaska current, and the third occurs in the center of the Gulf of Alaska. These last two periods occur at a time when zooplankton density is near its seasonal minimum values (see Figure 4.14b), and the optimal policy compensates for low food density by a reduction in migration activity.
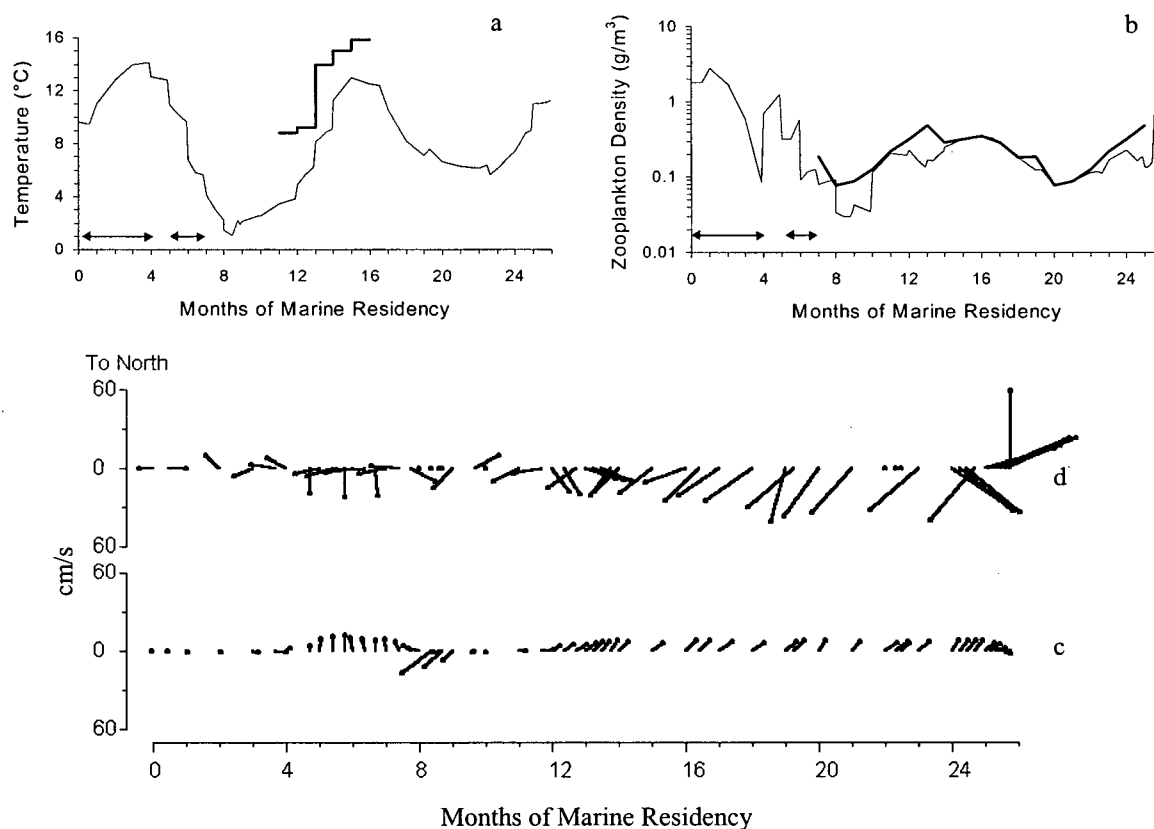
Figure 4.14. Temperature (a), zooplankton density (b), surface currents (c), and swimming velocity (d) profiles along the optimal migratory trajectory for $Z_C = 80\%$. Thick line in (a) represents the thermal limits found by Welch et al (1995). Thick line in (b) represents the maximum zooplankton density in the oceanic environment. Arrows indicate the months of coastal residence.

Literature on migration traditionally depicts adults as the active stage of the migratory cycle, and early life stages as the passive stage (Fortier and Leggett, 1982; Harden-Jones, 1981; Miller et al., 1985). My results show quite a different picture. The optimal migration trajectory requires a larger amount of time allocated to oriented swimming during the juvenile stage (after the first three months spent in the inside passages of Vancouver Island) than for mature adults returning to reproduce. The reproductive migration phase for adult fish begins two months prior to river entrance, and full allocation of time to migration activity is not required. The average amount of time committed to migration during the last two months of marine life was 13.5 hours per day, while juvenile use 18 hours per day for five months during their coastal migration. This is a reflection of the increasing swimming power of individuals as they grow, as can be seen in Fig 4.14d. In my opinion, the migration of juvenile

salmon is no small feat and perhaps even more remarkable than that of the adults given the large distance they must swim to reach the feeding grounds in the central NE Pacific. I suspect that the view of early life stages as passive should be limited to very first stages at best. Even pelagic larvae (e.g. clupeoids larvae, Blaxter and Hunter, 1982) are know to display vertical migration, and one year old juveniles of pacific hake (*Merluccius productus*) off the west coast of Baja California engage in the same migratory pattern as their adult counterpart, reaching progressively more northern areas each year.

The optimum daily foraging schedule in figure 4.15 (thick line) shows limited (albeit increasing) foraging activity during the first five months of marine residency then constant (and maximum) daily foraging hours afterwards. During those first five months of marine residency juvenile fishes encounter high zooplankton densities in the environment and are not required to invest larger amounts of time foraging to secure a large ration (in Figure 4.16). As zooplankton abundance decreases the optimal policy predicts increasingly longer foraging times and reaches the upper limit of 5 hours set in the model after 5 months, which is then maintained for the duration of the oceanic residency period.
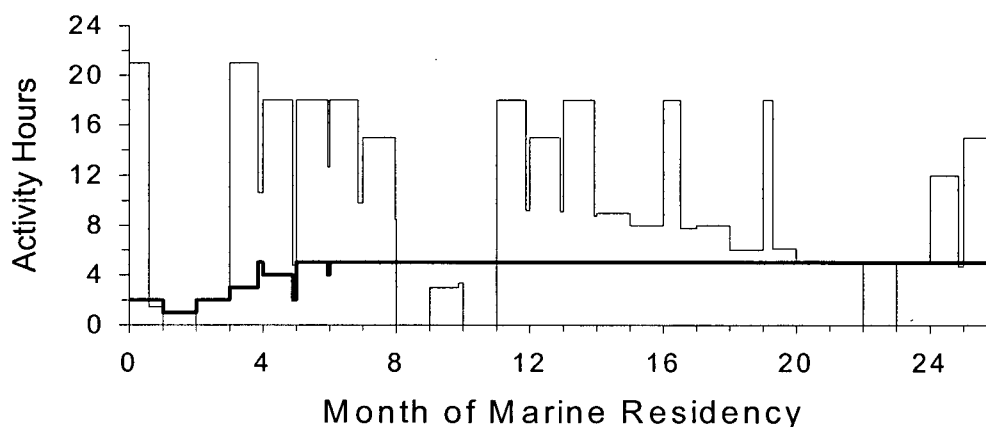
Figure 4.15. Optimal migration profile for $Z_C = 80\%$ under residence time dependent mortality, a foraging efficiency of 0.17, and standardized coastal zooplankton density. The thin line represents hours of oriented swimming and the thick line hours of foraging time per day.

The ration obtained from the foraging pattern described above shows a strong seasonal pattern (Figure 4.16) that follows that of zooplankton abundance (in Figure 4.14b). Individuals get the highest rations while they are in the coast (5% to 10%), and 0.5% to 5.4% depending on the season once they reach the open ocean. The summer ration in the open ocean ranges between 2.9% and 5.4%, which are reasonable close to the average 4% observed (Pearcy et al., 1984). Notice that the realized ration from month 10 to 19 is higher than that during the last six months of marine residency. This prediction does not agree with the available information which indicates that immature individuals consistently have lower stomach content than maturing individuals during the last months of marine life (LeBrasseur, 1966; LeBrasseur and Doidge, 1966). This suggests that foraging activity has a mortality cost as has been suggested by Abrams (1990), Abrams (1991), and Werner and Anholt (1993). Such risk was not represented under the assumption of Residence time mortality.
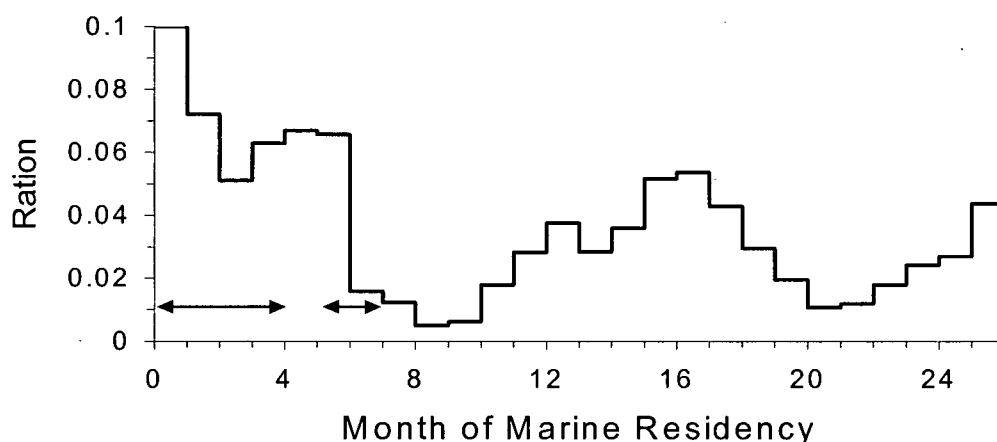
Figure 4.16. Predicted daily realized ration during marine residency. Ration values are expressed as a fraction of body weight, and the arrows indicate periods of coastal residency.

The optimal policy seasonal growth pattern (in Figure 4.17) follows that of the ration attained. The growth seasons have a peak from June to August while the juvenile are in the coast and from August to November once in the open ocean. Growth is minimum from December to March in both areas. Most gains in absolute weight occur during the last 10 months of marine residence.
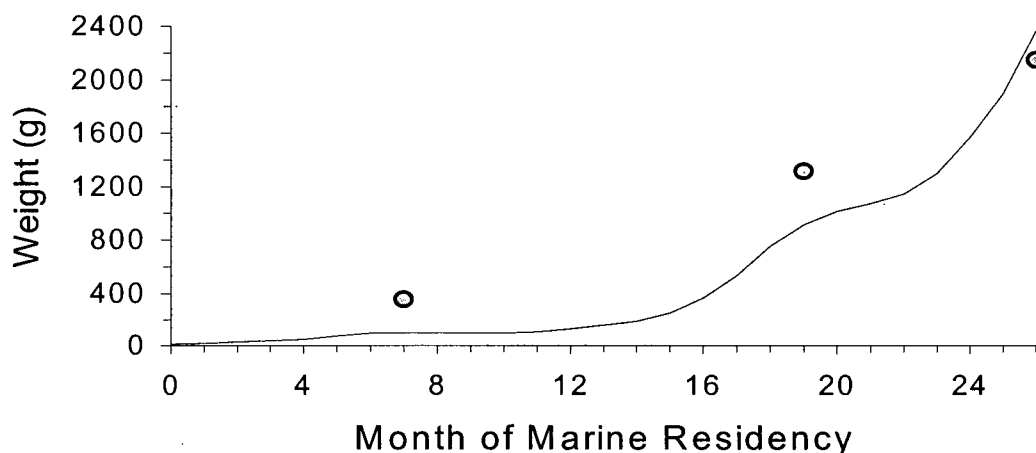
Figure 4.17. Predicted growth pattern with a foraging efficiency of 0.17 under residence time mortality and $Z_C = 80\%$. Filled circles are weight values for a 1.2 Cultus Lake sockeye salmon (from Ricker, 1962).

Comparing the predicted growth pattern with the weight reported by Ricker (1962) for age 1.2 Cultus Lake sockeye salmon (Fig. 4.17) shows that although the model makes a good prediction of terminal weight, it consistently underestimates weight during the marine residency phase. Those differences are evident after the first seven months of marine life just after juvenile leave the coast, which suggest that some relevant events occurring in the coast were not considered in the model. This discrepancy may be a consequence of the mortality process, which would shift the size distribution of juveniles towards larger body sizes and result in an overestimation of growth; that is, higher average weight may be a consequence of the trimming of small individuals, rather than growth. This model estimates the fate of individuals not distributions, and the state variable weight directly responds to changes in the foraging and activity patterns rather than to mortality.

Plankton patchiness is also a potential explanation of this discrepancy in weight. Patchiness implies a complex spatial structure in the distribution of zooplankton, with rich areas surrounded by nearly empty areas. In such an environment, there is a probability of not finding food in any given day. However once a patch is found the costs of movement are greatly reduced, and the chances of feeding to satiation in a short period of time are high. When the smolts arrive in springtime, the coast of British Columbia reaches its peak zooplankton density and individuals would have a high probability of finding large patches of

high zooplankton density. It is unfortunate that actual data on patchiness could not be incorporated in the model. All the sources consulted here to define the prey field reported the zooplankton data in the form of mean density, and none provided insight into the patch structure. However I find this explanation unlikely since the model predicts full ration even with a reduced amount of time allocated to foraging. Juvenile fish are definitely taking advantage of the high prey concentration in the coast.

The predicted fitness profile (in Figure 4.18) has two distinct intervals where there are gains in fitness expectation 1) during the first six months of marine life while individuals are in the coast and 2) during the remaining oceanic life. While in the coast the average rate of change in fitness is 8 smolts/female/month and the average growth rate is 14 g per month. In contrast, the fitness gain in the open ocean is only 3 smolts/female/month and the mean growth rate is 113 g per month.
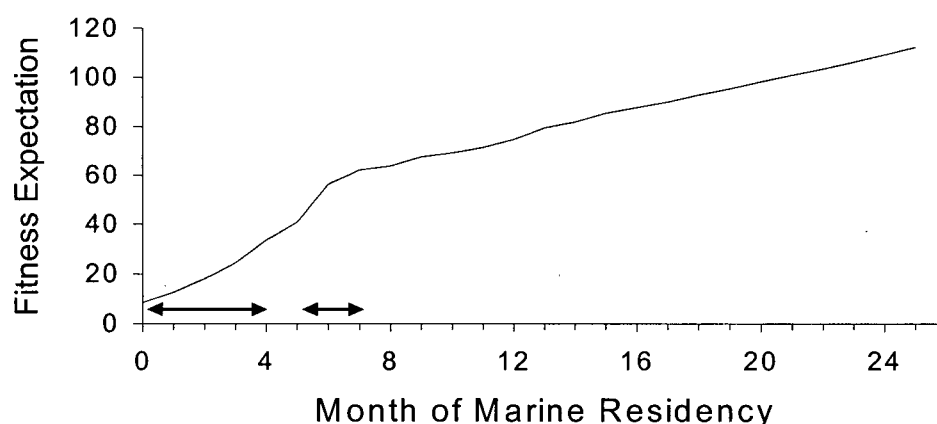
Figure 4.18. Fitness expectation (in smolts/female) for sockeye salmon with a foraging efficiency of 0.17 under residence time mortality, Z_C = 80%, and standardized coastal zooplankton density. The arrows mark the months spent in the coast.

Fitness gains in semelparous species are determined by weight gains and survivorship to spawning time. Surviving one month in a risky environment has a strong effect on fitness expectation even at low or no growth, because there is one less month of high mortality exposure to endure before spawning time. This is the case for the coastal environment where the low growth rate indicates that the main fitness gains come from survival. In the open

ocean the average growth rate is substantially larger, and the fitness gain only one third of that in the coast, thus fitness gains there are mainly determined by growth. This profile is a direct result of the high mortality risk defined to occur in the coast ($Z_C = 80\%$), which creates an important bottleneck in the migration cycle of sockeye salmon. This bottleneck may become critical if changing oceanographic conditions in the coast result in an increased risk of predation for smolts via changes in the distribution, species composition, or size of predators (Hargreaves, 1994). Such bottleneck may put depleted stocks at risk of local extinction, as was nearly the case for steelhead trout recently (Ward, 2000).

The values of fitness expectation and terminal weight in Table 4.6 indicate that the coastal juvenile migration can yield higher fitness values if juvenile fish could reduce the high risk of predation in the coast. In principle, juvenile fish capable of reducing mortality while in the coast may benefit from a higher growth rate and higher fecundity at maturity. A trait that may allow sockeye juvenile to accomplish just that is schooling behavior, and juvenile sockeye do form schools while migrating along the coast (Hartt and Dell, 1986). This trait comes with a downside in the form of increased competition for food (Pitcher and Parrish, 1993). Those two features could result in lower terminal weights and higher fitness expectations driving both values closer to the observed range. If schooling behavior has such an effect during the juvenile coastal migration, then I would expect the model to predict an optimal migration trajectory similar to that for $Z_C = 50\%$ (in Figure 4.12a). However, the optimal behavior during migration and the values for expected fitness and terminal weight would be closer to those predicted for a Z_C of 80%.

Predation risk patterns no doubt have a major bearing on the evolution of migratory tactics. Roff (1988) found that schooling behavior appears to be coupled with migratory behavior and suggested that migratory behavior may in fact be a consequence of the costs-benefits of schooling behavior. Roff argued that the evolution of schooling behavior in a population would reduce predation risk and result in an increase in abundance, which in turn would lead to the depletion of local resources and to an increased incentive to move elsewhere.

4.5 Conclusions

Predicted optimal migratory trajectory, terminal weight, and expected reproductive output of sockeye salmon are very sensitive to the structure of the mortality process during marine life. A size-dependent mortality hypothesis predicted individuals with very high terminal weight and low expected reproductive output. Hypothesizing size-and-activity dependent mortality predicted high terminal weight (but not as high as with size-dependent mortality) and low expected reproductive output, and inhibited migratory behavior because of the mortality cost of activity. A hypothesis that risk of mortality is proportional to the time of residence gave the best predictor of the terminal weight and expected reproductive fitness of sockeye salmon from the Fraser River.

Although the residence time mortality hypothesis was the best predictor of the terminal weight and expected reproductive output (at $\beta = 0.18$ and $Z_C \geq 80\%$), it did not correctly predict migration of juvenile salmon along the coast. This feature of the migration circuit appears to be linked to the high zooplankton density that develops along the coast of British Columbia and the southern coast of Alaska during spring and summer. As originally stated, estimated zooplankton density values north of Vancouver Island are low compared to those inside and around Vancouver Island. Such low values North of Vancouver Island resulted in optimal migration trajectories that go from Vancouver Island directly into the center of the Alaska Gyre. The coastal juvenile migration became part of the optimal migratory trajectory after setting all zooplankton values in the coast equal to those of the Inside Passage between Vancouver Island and the mainland. Those results suggest that the coastal migration observed in sockeye salmon has evolved as a behavioral response to the high zooplankton density in the coast.

Setting high zooplankton density along the coast resulted in a very stable migratory circuit across a wide range of Z_C values ($\beta = 0.17$ and $Z_C \geq 70\%$). The foraging efficiency parameter β acted only as a scaling factor for terminal weight and expected reproductive output.

The best combination of parameters found here ($\beta = 0.17$ and $Z_C = 80\%$) predicted a seasonal growth pattern that follows the seasonal changes in zooplankton density, with growth occurring from May to December. There is no direct evidence of seasonal growth, although scale analysis has shown wider circuli during summer than in winter. The model also underestimated weight as reported for age 1.2 Cultus Lake sockeye salmon. I believe this is a product of the confounding effects of growth and higher mortality for smaller individuals in the samples from which it was estimated.

The model also predicts a mortality-related bottleneck during the juvenile stage in the coast that has a strong effect on expected reproductive output. This condition may be exacerbated during warmer-than-average years when very active pelagic predators like mackerel become abundant in the coast of British Columbia.

Migration activity was predicted to be higher for small individuals than for large ones, even when compared to maturing adults returning to spawn. Calculated time allocated to migration activity decreases with time, perhaps as a reflection of the ability of larger individuals to reach target destinations faster.

High zooplankton density in the coast results in juvenile individuals reaching full ration with a reduced foraging activity. However, once juvenile reach the open ocean the time allocated to foraging reaches the highest value explored in the model (5 hours per day) and remains constant during the rest of the marine residence period.

The predicted ration achieved during the first year of open ocean residence was larger than that achieved during the last six months of residence. This result is not substantiated by the available data, which indicate that maturing individuals during those last months achieve comparatively larger rations than during their first year as immature. This discrepancy may come from the consideration that the time allocated to foraging does not carry a mortality cost for sockeye salmon. This is unlikely to be the case, as the main know predators in the open ocean (salmon sharks and fur seals) are active predators that likely rely on random encounters with their prey. Thus any increase in sockeye swimming activity for prey searching while foraging will also result in an increased probability of encountering one of these predators.

There is no evidence of an annual circuit around the Gulf of Alaska. The profile of environmental conditions along the optimal migratory trajectory shows that migrants seek and stay in areas with the highest zooplankton density values in the NE Pacific, and that the temperature in those areas is below the reported upper thermal boundaries for sockeye salmon in the open ocean. This behavior suggests an obvious proposition: sockeye salmon migrate to the open ocean as a strategy to minimize mortality and maximize growth, not to seek physiological temperature optima.

Finally, the model detected a strong dependency of the optimal migratory tactics on the constraints imposed by the spatial distribution of prey density and predation risk. If this is indeed the case for other migratory species, it provides a compelling argument to explain the poor performance of predictions for migration-related events based on statistical relationships with environmental variables so common in the fisheries oceanography literature.

4.6 ADDENDUM TO CHAPTER 4

OPTIMAL MIGRATORY TRAJECTORY AND BEHAVIOR PREDICTIONS FOR THE

MARINE PHASE OF SOCKEYE SALMON

This addendum contains graphical outputs for optimal migratory trajectories and behaviors predicted for all the mortality structures and foraging efficiencies explored there. The results are for the dominant age 1.2 life cycle pattern of the sockeye salmon from the Fraser River. Smolts were assumed to reach the Fraser River estuary on May 1st with a body weight of 12 g. The marine life stage was 26 months and mature adults reach the river estuary on July 1st.

The optimal policy for each case explored is presented as an optimal migratory trajectory plot for the conditions above described. The trajectory plot contains the tactics used to achieve it; active migration is represented in red, drifting in blue, and staying as a green circle centered where the fish holds position. Time plots for state, decision and auxiliary variables along the trajectory are also given. Swimming time and foraging time (in hour per day allocated to each activity) represent the optimal activity budget of the individual during each month of marine residency. Daily mean realized ration is given as a percent of wet weight. The fitness expectation represents the expected reproductive payoff in number of smolts per female at the end of the marine phase, given her current body weight, geographic location, and month, assuming that she behaves optimally for the remaining time of the marine phase.

Figure 4.19. Optimal migration trajectory, foraging and migration time budget, ration attained, fitness expectation, and growth pattern under the assumption of residence time mortality and a foraging efficiency $\beta = 0.15$. Cases a) to f) are for Z_C values of 50%, 60%, 70%, 80%, 90%, and 95% respectively.

Figure 4.20. Optimal migration trajectory, foraging and migration time budget, ration attained, fitness expectation, and growth pattern under the assumption of residence time mortality and a foraging efficiency β = 0.18. Cases a) to f) are for Z_C values of 50%, 60%, 70%, 80%, 90%, and 95% respectively.

Figure 4.21. Optimal migration trajectory, foraging and migration time budget, ration attained, fitness expectation, and growth pattern under the assumption of residence time mortality and a foraging efficiency β = 0.20. Cases a) to f) are for Z_C values of 50%, 60%, 70%, 80%, 90%, and 95% respectively.
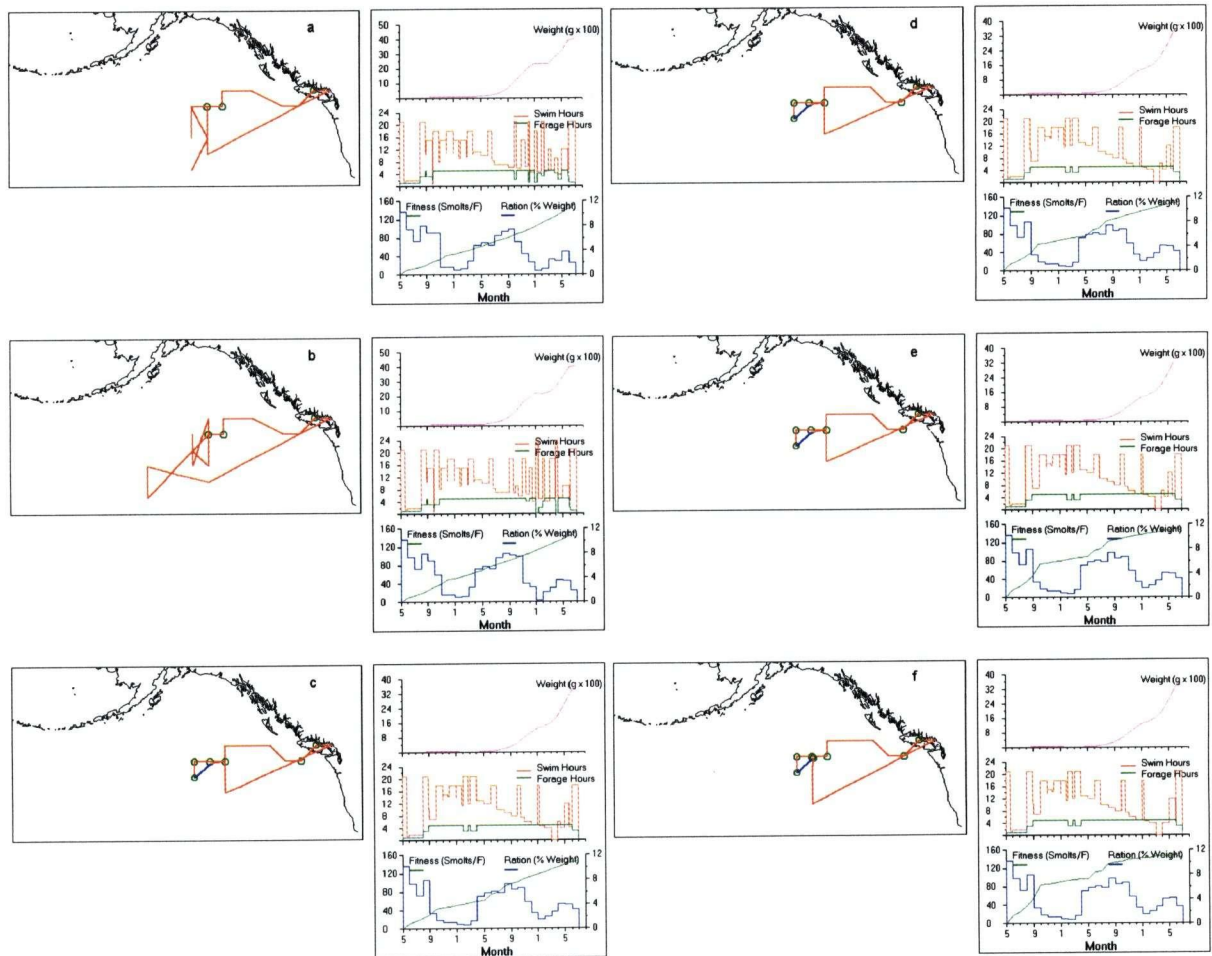
Figure 4.22. Optimal migration trajectory, foraging and migration time budget, ration attained, fitness expectation, and growth pattern under the assumption of residence time mortality and a foraging efficiency $\beta = 0.25$. Cases a) to f) are for Z_C values of 50%, 60%, 70%, 80%, 90%, and 95% respectively.
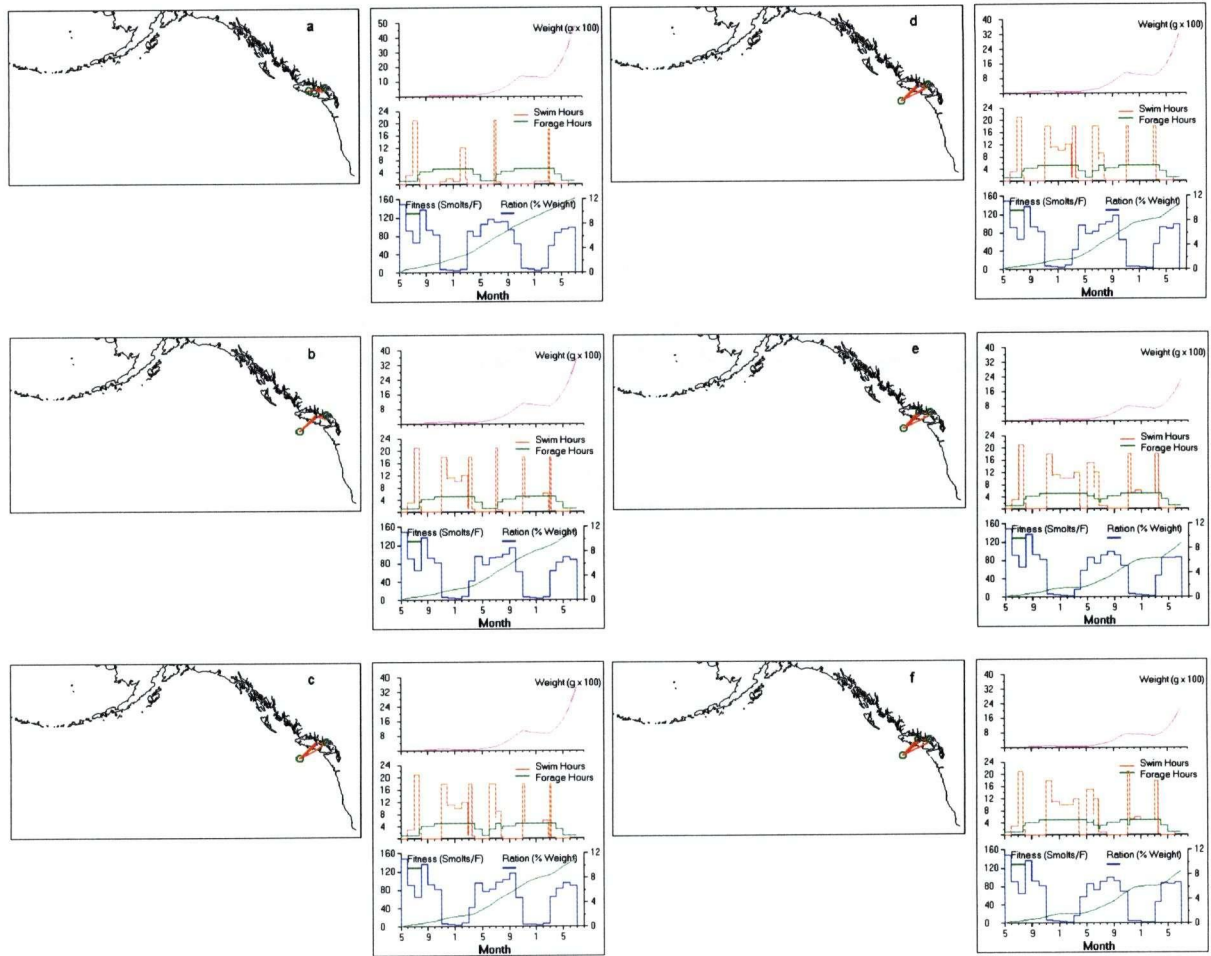
Figure 4.23. Optimal migration trajectory, foraging and migration time budget, ration attained, fitness expectation, and growth pattern under the assumption of size dependent mortality and a foraging efficiency $\beta = 0.09$. Cases a) to f) are for Z_C values of 50%, 60%, 70%, 80%, 90%, and 95% respectively.
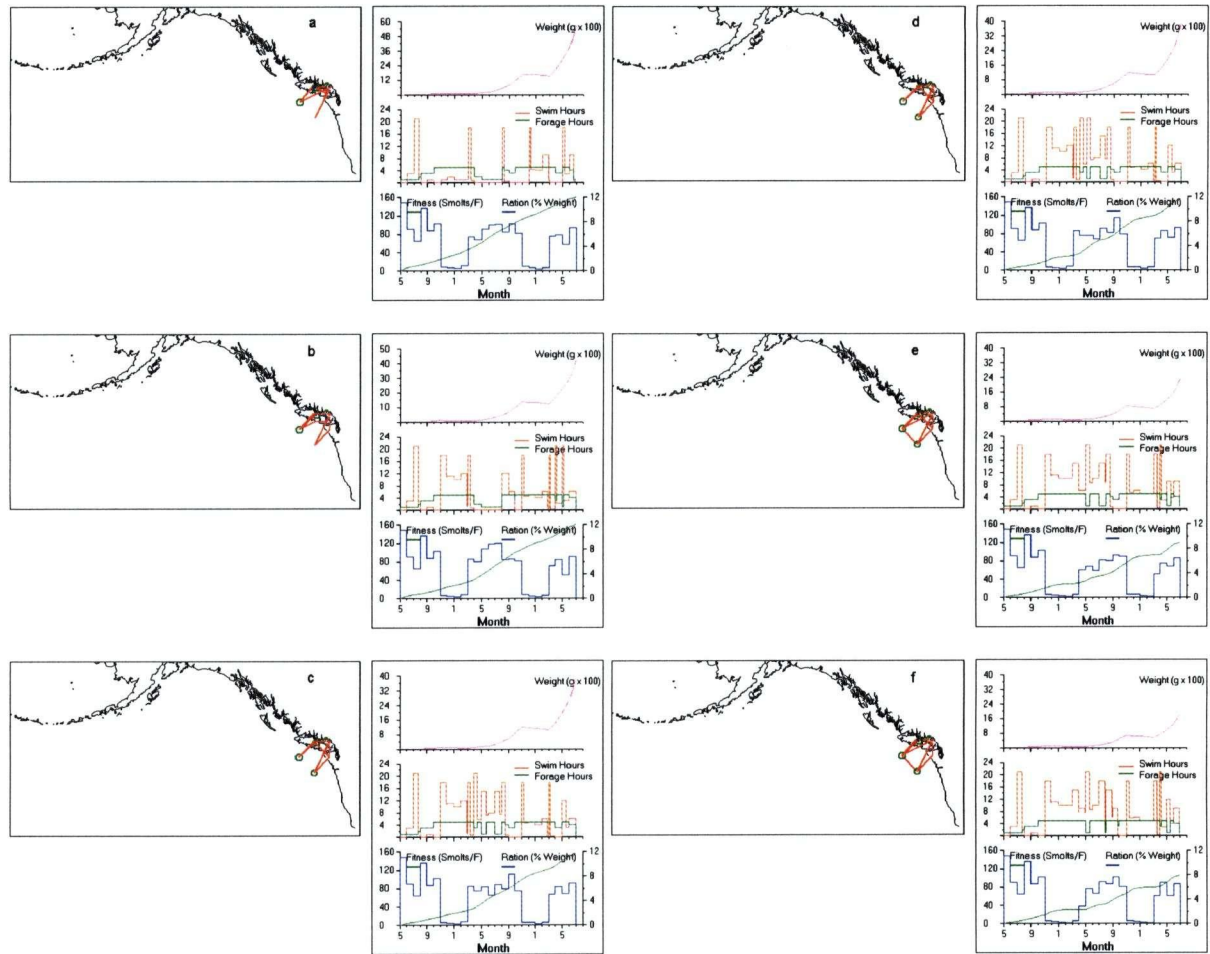
Figure 4.24. Optimal migration trajectory, foraging and migration time budget, ration attained, fitness expectation, and growth pattern under the assumption of size dependent mortality and a foraging efficiency $\beta = 0.11$. Cases a) to f) are for Z_C values of 50%, 60%, 70%, 80%, 90%, and 95% respectively.
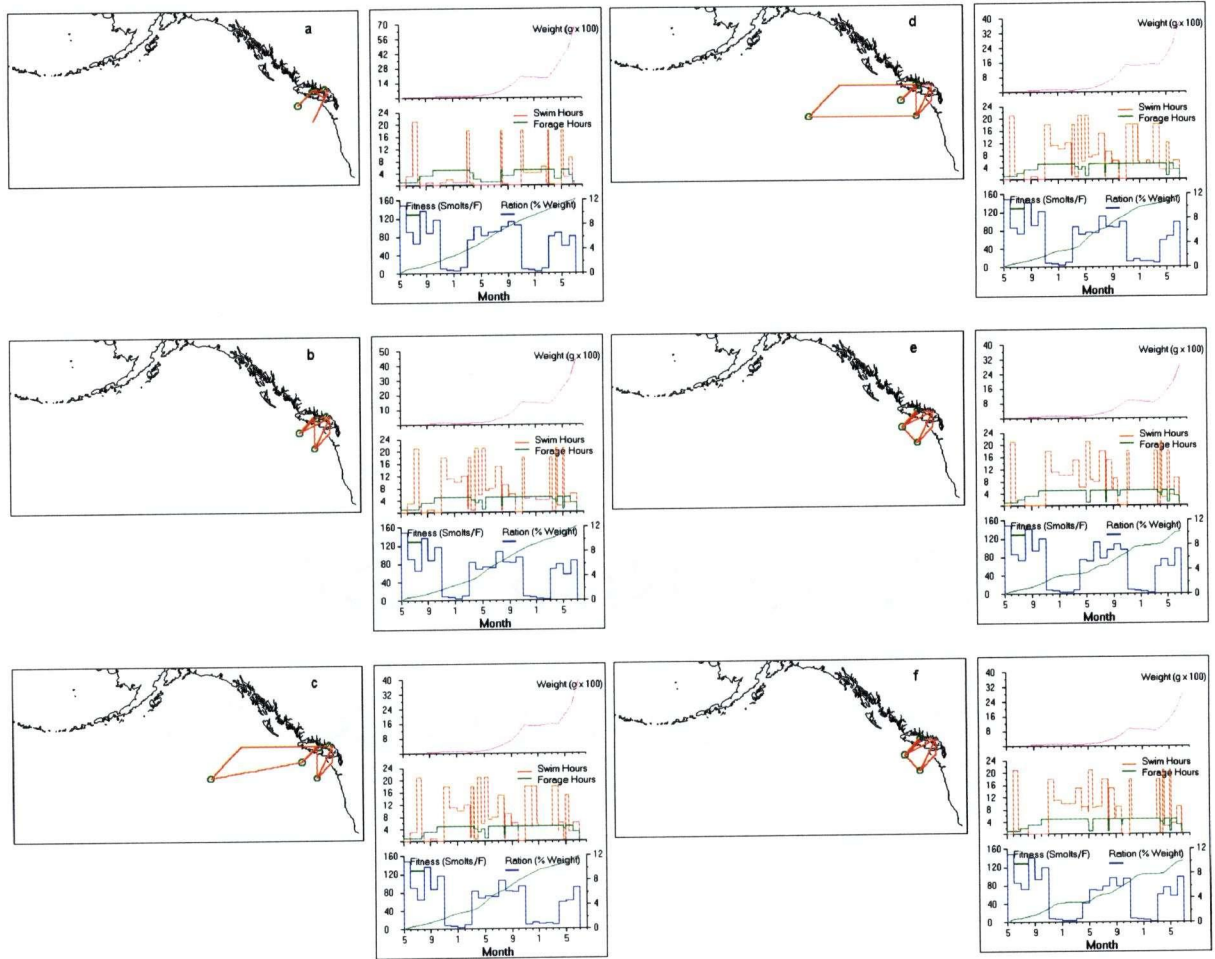
Figure 4.25. Optimal migration trajectory, foraging and migration time budget, ration attained, fitness expectation, and growth pattern under the assumption of size dependent mortality and a foraging efficiency $\beta = 0.13$. Cases a) to f) are for Z_C values of 50%, 60%, 70%, 80%, 90%, and 95% respectively.
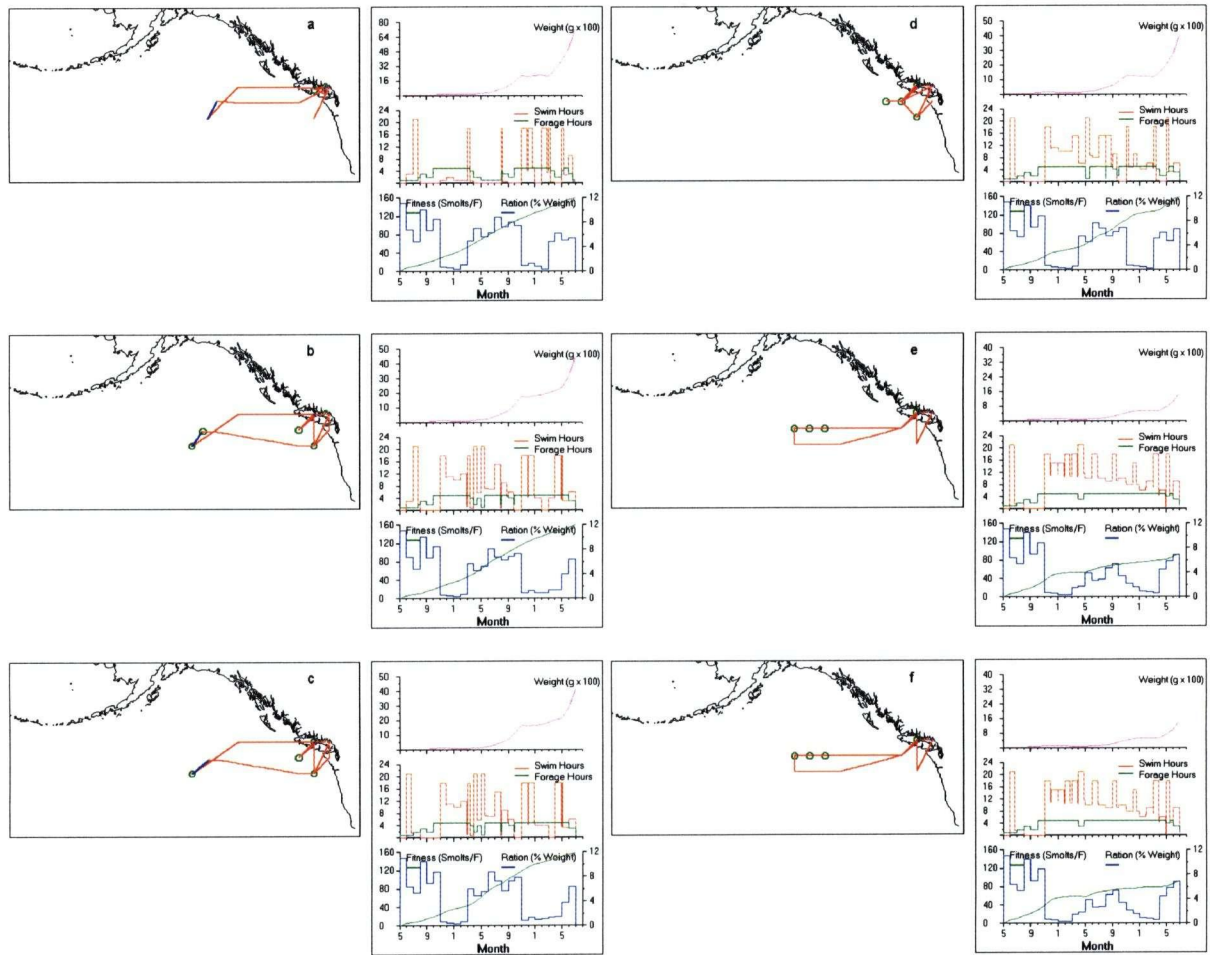
Figure 4.26. Optimal migration trajectory, foraging and migration time budget, ration attained, fitness expectation, and growth pattern under the assumption of size dependent mortality and a foraging efficiency $\beta = 0.15$. Cases a) to f) are for Z_C values of 50%, 60%, 70%, 80%, 90%, and 95% respectively.
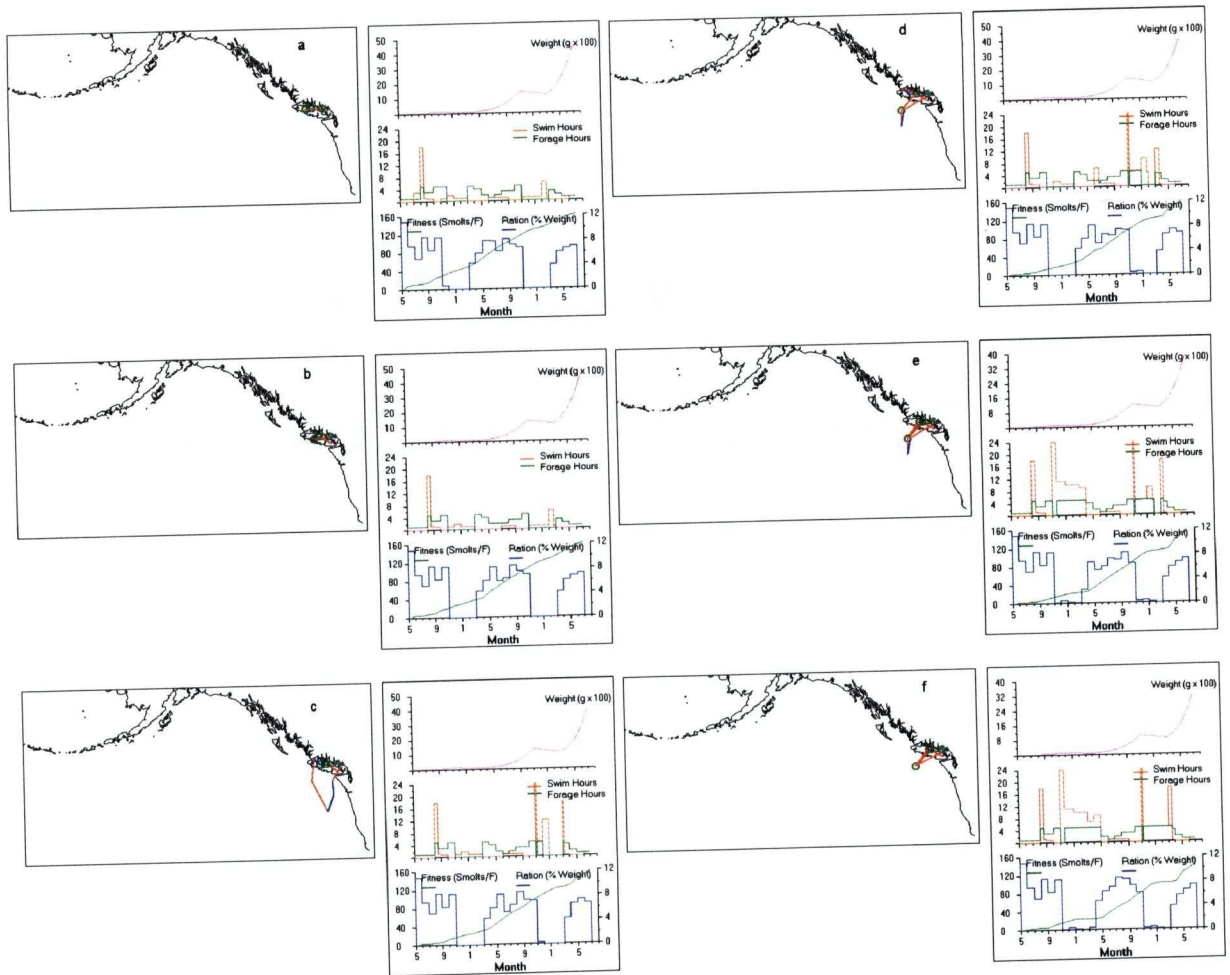
Figure 4.27. Optimal migration trajectory, foraging and migration time budget, ration attained, fitness expectation, and growth pattern under the assumption of size and activity dependent mortality and a foraging efficiency $\beta = 0.12$. Cases a) to f) are for Z_C values of 50%, 60%, 70%, 80%, 90%, and 95% respectively.
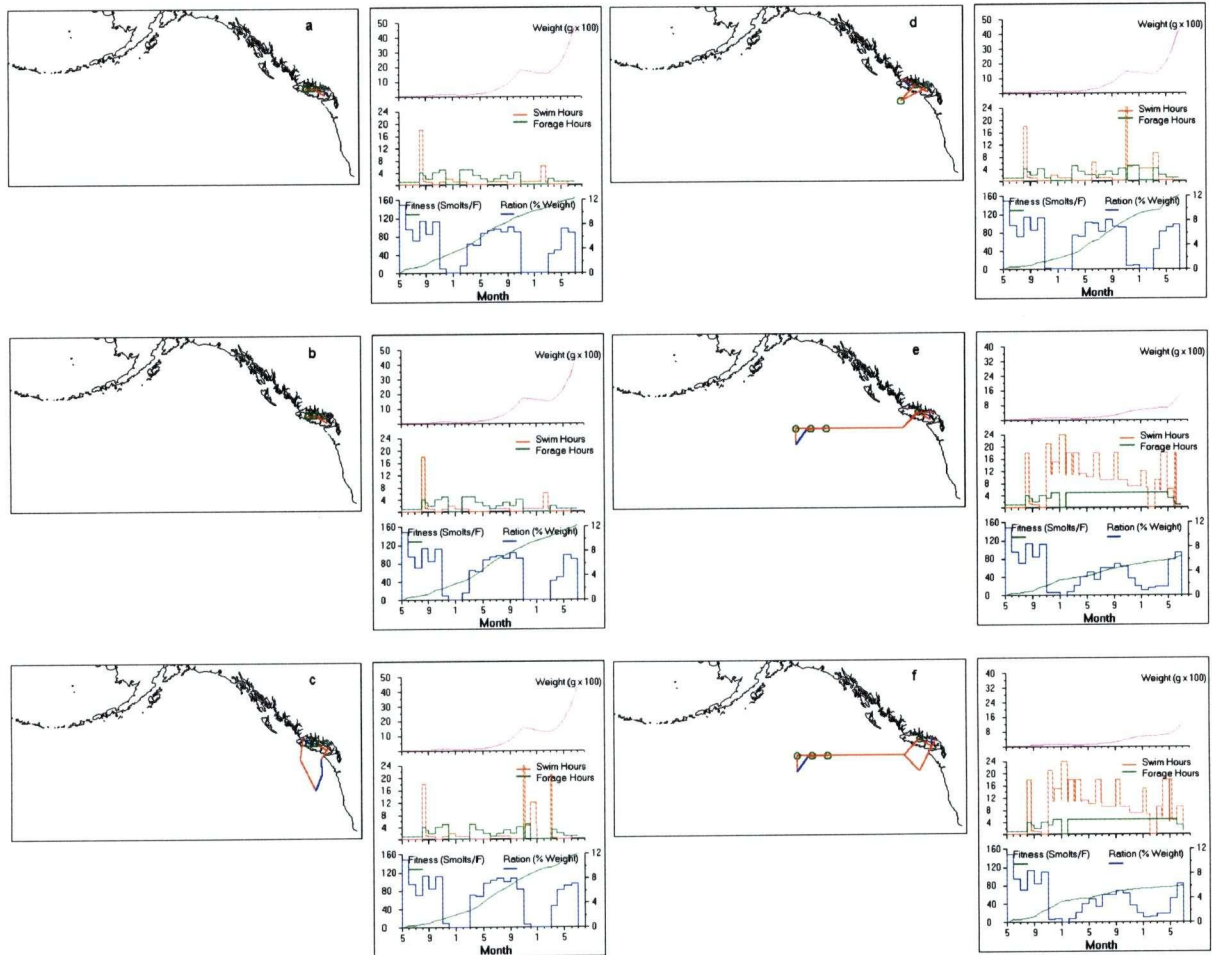
Figure 4.28. Optimal migration trajectory, foraging and migration time budget, ration attained, fitness expectation, and growth pattern under the assumption of size and activity dependent mortality and a foraging efficiency $\beta = 0.15$. Cases a) to f) are for Z_C values of 50%, 60%, 70%, 80%, 90%, and 95% respectively.
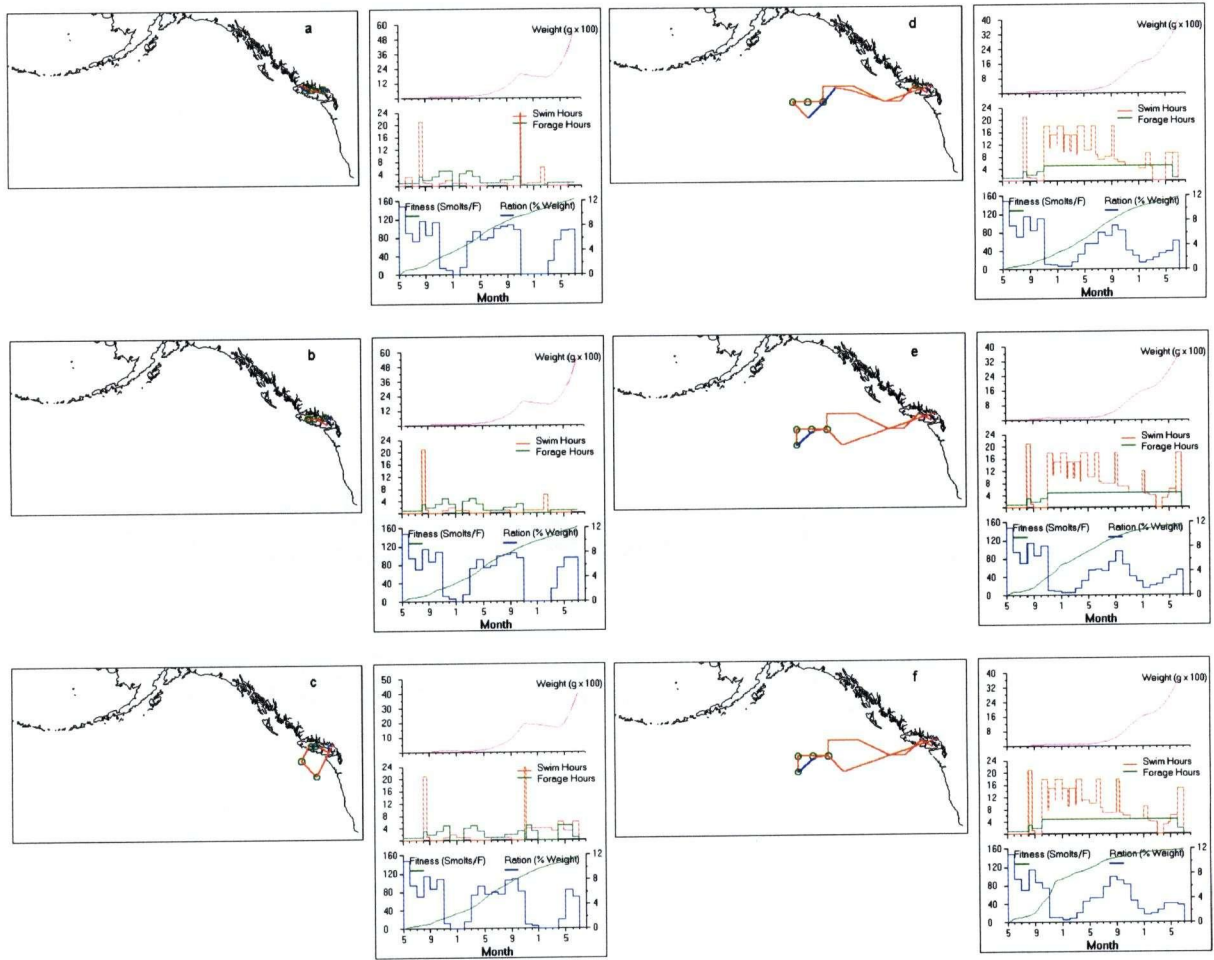
Figure 4.29. Optimal migration trajectory, foraging and migration time budget, ration attained, fitness expectation, and growth pattern under the assumption of size and activity dependent mortality and a foraging efficiency $\beta = 0.20$. Cases a) to f) are for Z_C values of 50%, 60%, 70%, 80%, 90%, and 95% respectively.
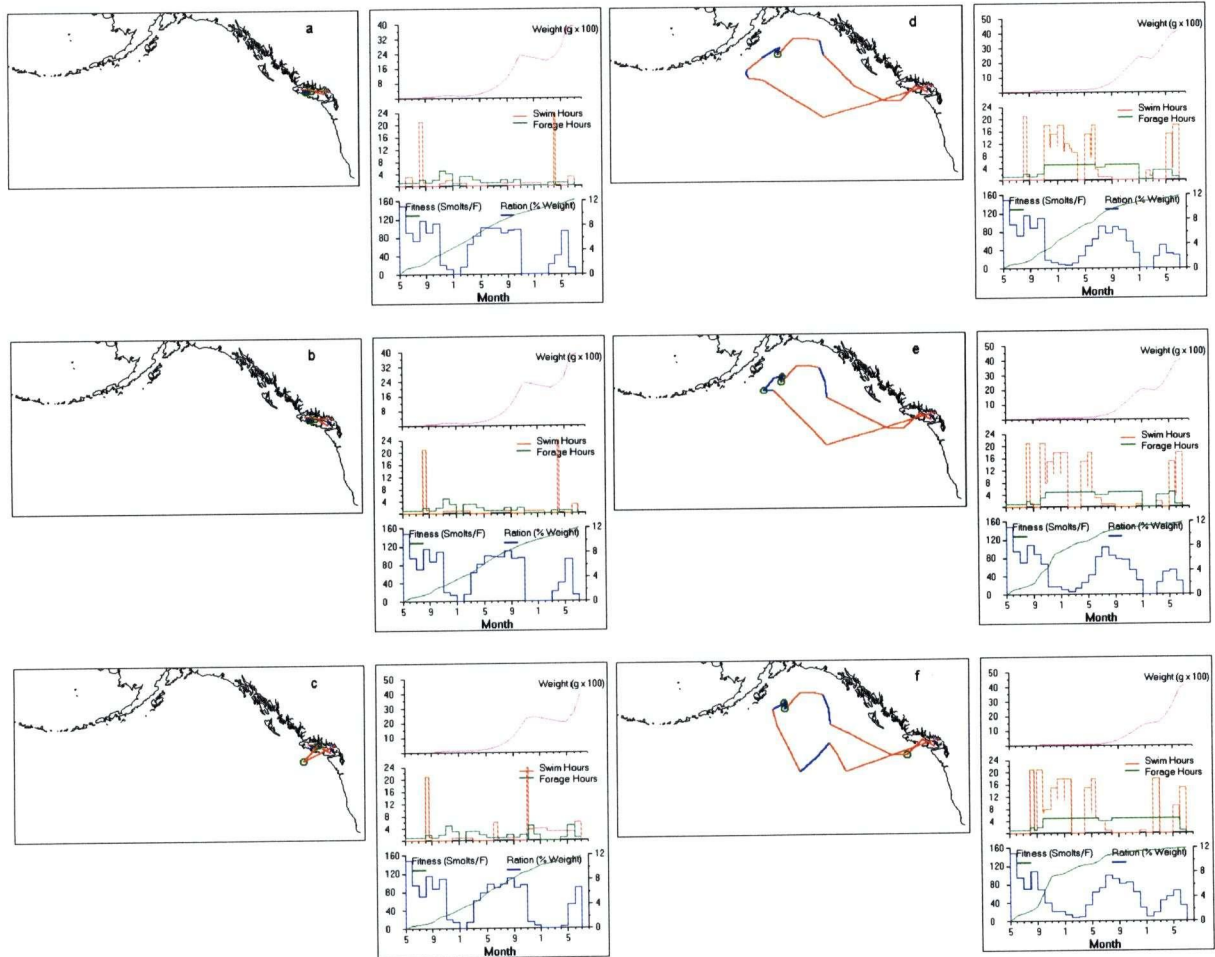
Figure 4.30. Optimal migration trajectory, foraging and migration time budget, ration attained, fitness expectation, and growth pattern under the assumption of size and activity dependent mortality and a foraging efficiency $\beta = 0.30$. Cases a) to f) are for Z_C values of 50%, 60%, 70%, 80%, 90%, and 95% respectively.
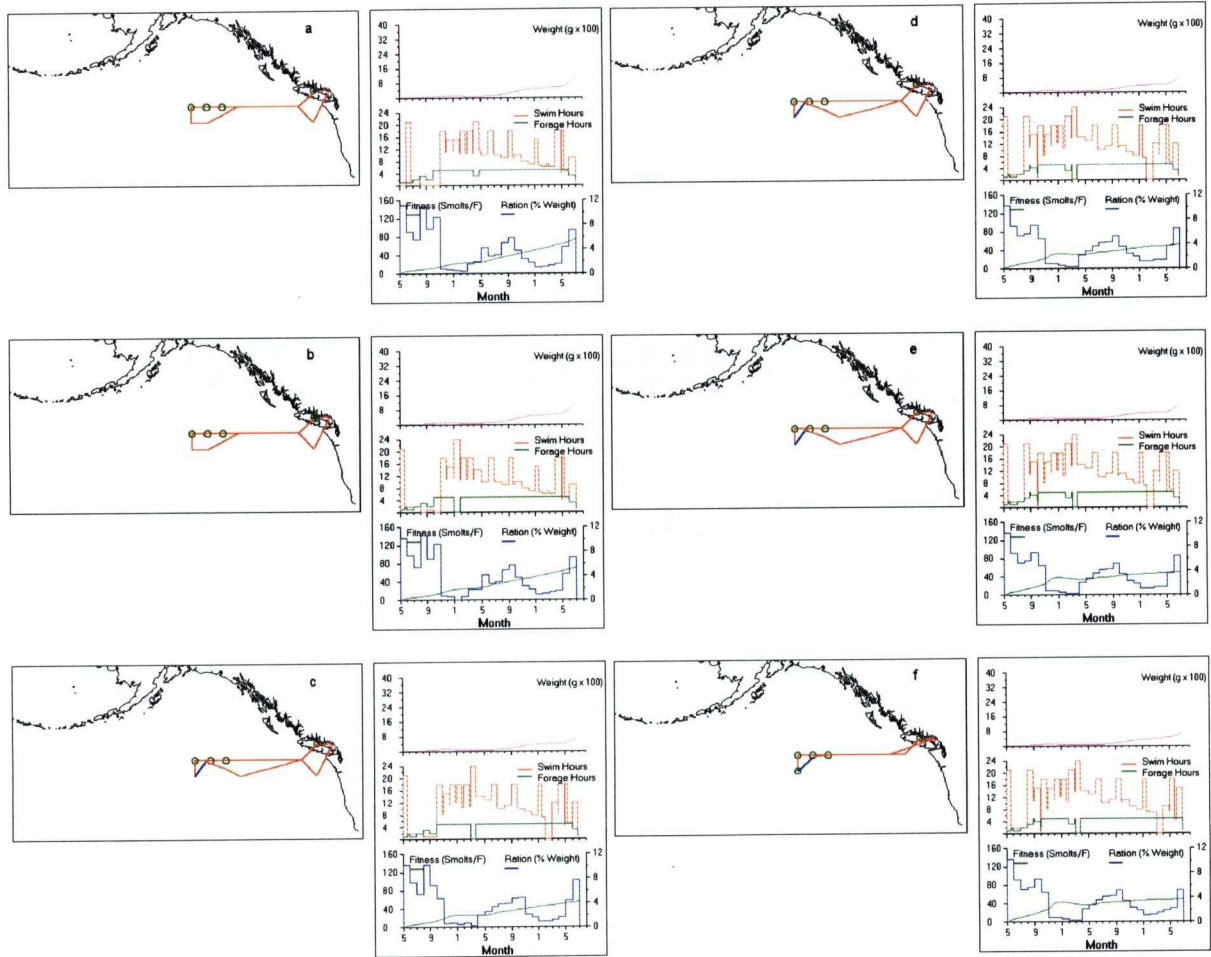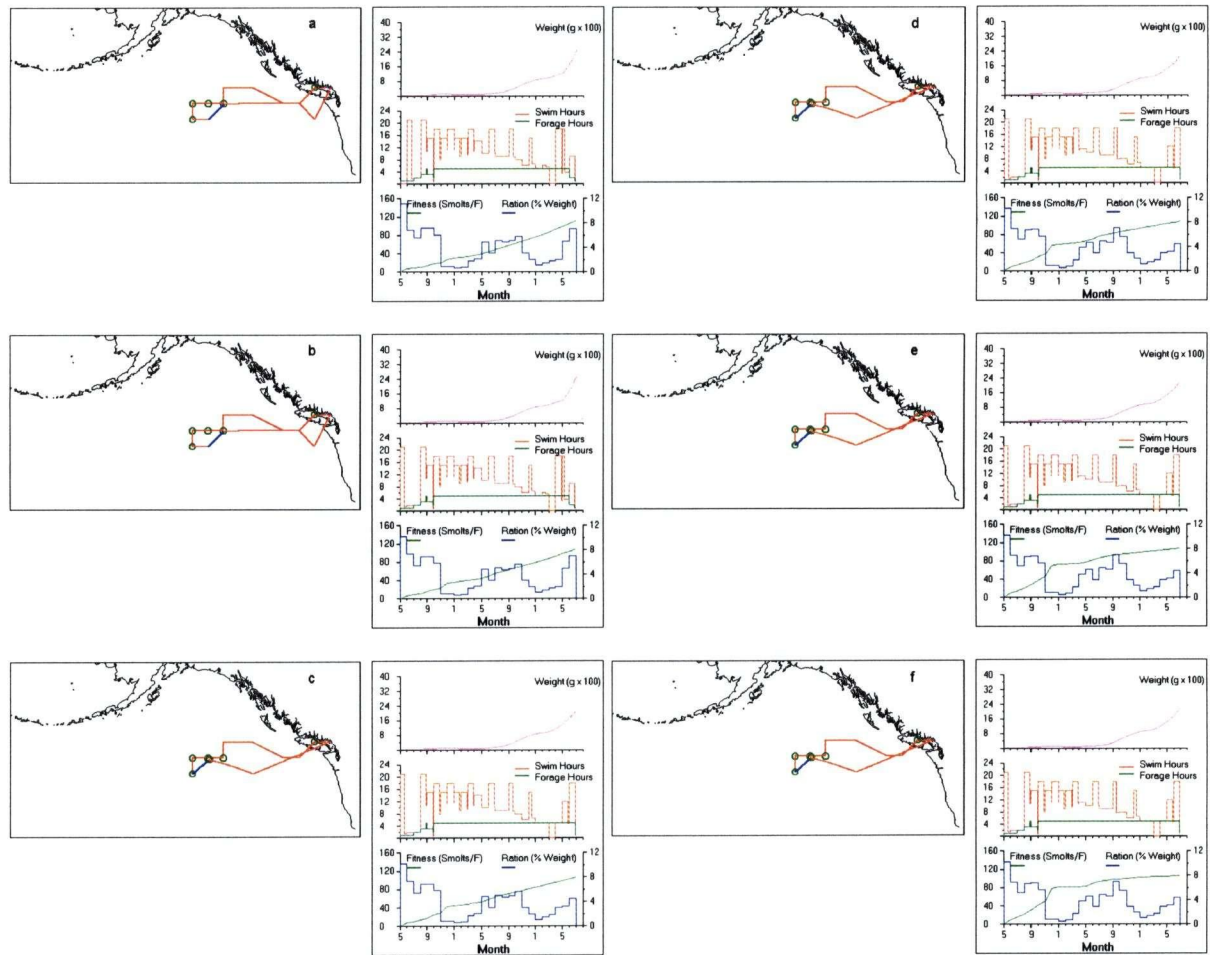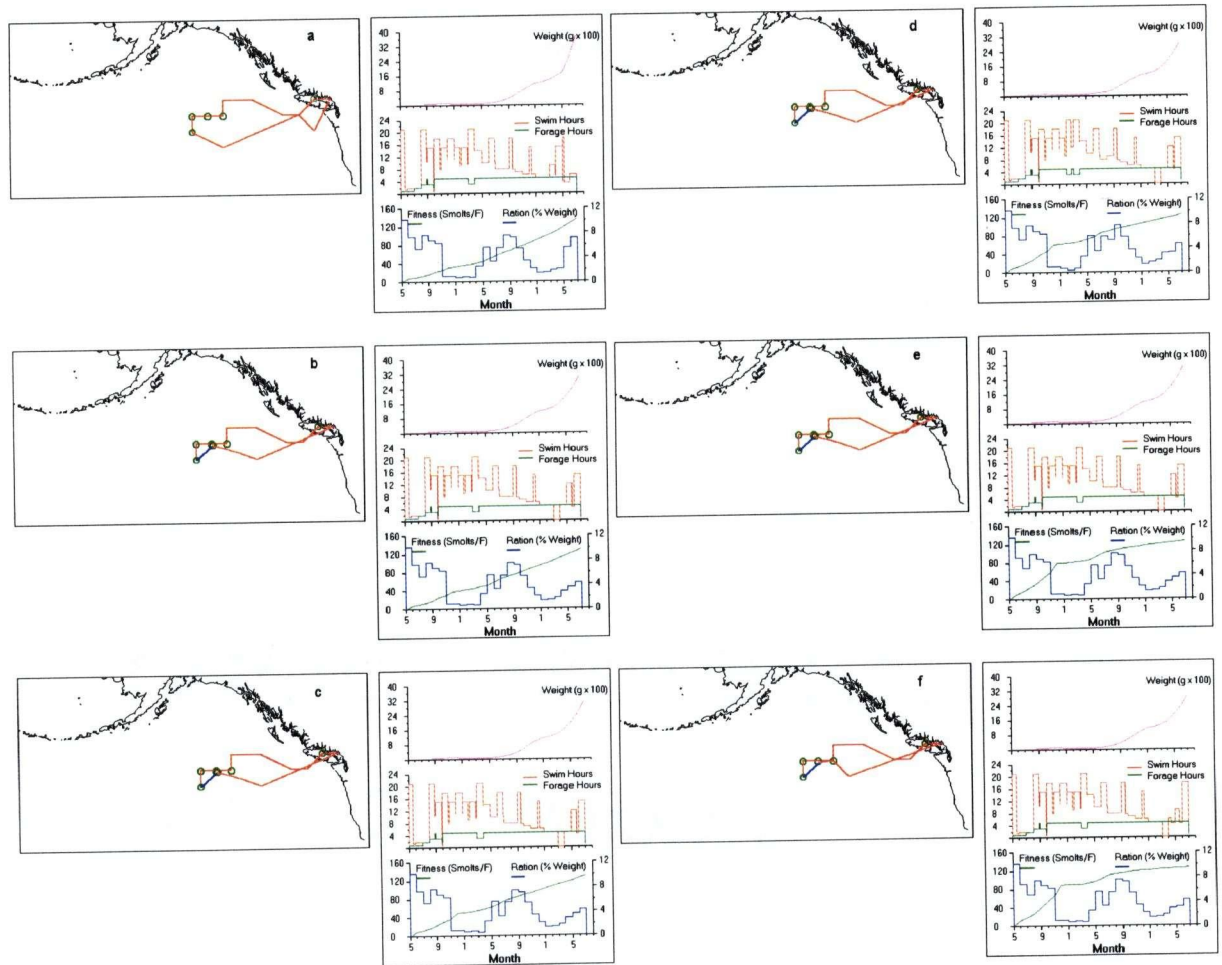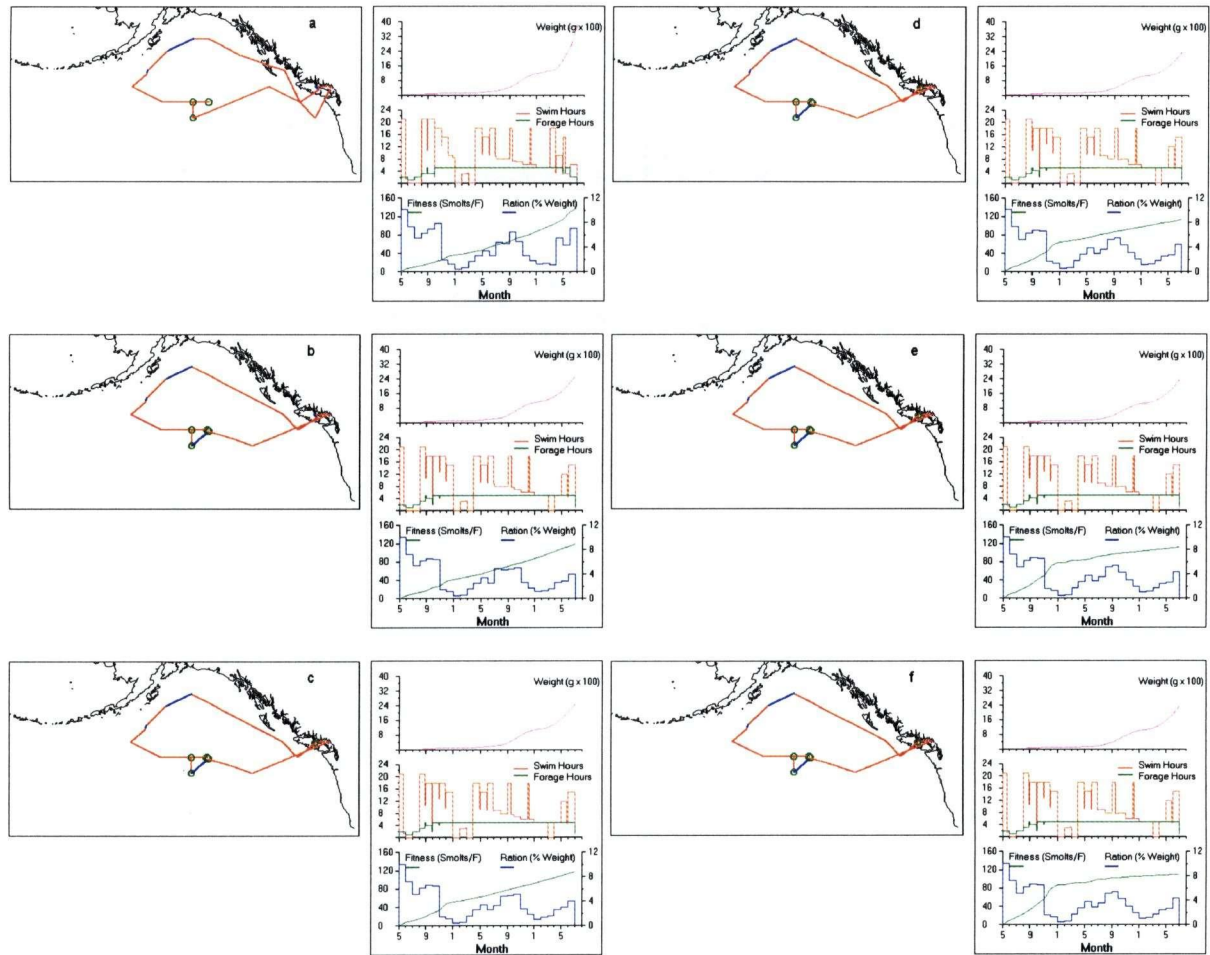
Figure 4.31. Optimal migration trajectory, foraging and migration time budget, ration attained, fitness expectation, and growth pattern under the assumption of residence time mortality and a foraging efficiency β = 0.17. Cases a) to f) are for Z_C values of 50%, 60%, 70%, 80%, 90%, and 95% respectively. Monthly zooplankton density in the coast has been set as that of Johstone Strait.

CHAPTER 5

CONCLUSIONS

The two fitness-based models presented in this thesis were developed as heuristic tools to further our understanding about migratory behavior of fishes in general and sockeye salmon in particular. These models focus on some aspects of the migratory behavior of sockeye salmon during the marine phase of its life cycle, and are based on the consideration of migratory behavior as a life history strategy that maximizes the reproductive fitness of individuals in a seasonal and heterogeneous environment. Each model was developed from a hypothetical tradeoff that I perceived as an important constraint in the migratory behavior of fishes.

The first model is based on the hypothesis that mature individuals returning to spawn are loss-minimizers, and their migratory behavior has been tuned by natural selection to minimize the risk of mortality and the metabolic costs from swimming activity during the reproductive migration. If so, the swimming speed and orientation of fish during migration are an optimal response to the spatial distribution of environmental conditions that determine the risk of mortality and metabolic costs. The second model examines the question of the migratory behavior and route that maximizes the reproductive fitness of migrants during their life cycle. This model is based on the hypothesis that migrants have a foraging time - migration time tradeoff in their daily activity schedule. Thus, the sequence and timing of movements that characterize the migratory circuit of migratory individuals arise as an optimal response to an expectation about the state of the environment, the current state of the individual, and the time remaining to reproduction.

Both models indicate that the most important factors controlling the shape of the migratory pattern observed are the spatial distribution of prey biomass, the spatial distribution of predation risk, and the structure of the predation process (e.g. size-dependent, activity-

dependent, residence time-dependent). These results were not unexpected; both models are based on the principle that future reproductive fitness accrues from survival and growth. The models emphasized the strong effect of the spatial distribution of mortality on migratory behavior. Areas of high risk resulted in higher swimming speeds and swimming orientation towards areas of lesser risk, or migratory behavior that avoids such areas altogether. The nature of the mortality process also has a strong effect on the pattern of growth and fitness payoff, and can even lead to the inhibition of migration. Those results are very much in line with the view of Lima and Dill (1990) about mortality risk as a strong selection force, which they succinctly stated as "few failures [...] are as unforgiving as the failure to avoid a predator: being killed greatly decreases future fitness".

The two models proposed here are process-based. Behavioral rules decide were individuals should go given the state of the environment and their own state. Those models are proving to be very powerful tools in addressing questions about the consequences of events not previously observed (e.g. Mangel (1994) on potential effects of global warming on salmon). However, to provide meaningful answers they do require a reasonable description of the environmental factors in the area within the reach of migrants, particularly the variability that those factors may have. The consideration of interannual environmental variability, particularly for those variables that are known to have a strong effect in the spatial distribution and density of fish, will provide a more realistic representation of the environment and improve the prediction capability of the models.

Undoubtedly a better knowledge about the process of mortality would lead to a better understanding of the migration process itself. Some advances have been made in mapping the spatial distribution of biomass using hydroacoustics methods (e.g. Brandt and Kirsh, 1993; Brandt et al., 1992) and in the measurement of the inter-annual variability in predator-prey interactions (e.g. Hargreaves, 1994). However, the large spatial and temporal scales at which ontogenic fish migrations occur make it unreasonable to expect a fine scale determination of the spatial distribution of predation risk anytime soon. I did find that even with the coarse definition (coast - open ocean) used to represent risk of mortality in the NE Pacific ocean in both models, the predictions were reasonably good and provided useful insight into the dynamics of sockeye salmon migration. Best of all, the models provided a powerful research

framework capable of linking the myriad of disconnected facts about the marine migration of sockeye salmon. Even with the limited amount of information available, those models were able to predict a range of behaviors observed during the migration of sockeye salmon, and to provide an explanation for them.

I consider that those models provide a reasonably good starting point to develop more comprehensive models for migratory behavior in fishes. The model for reproductive migration of sockeye salmon in Chapter 3 could be expanded to include foraging. This expansion would provide a better description of weight dynamics and force individuals to trade-off migration time with foraging time. Such trade-off would likely result in changes of the optimal return route during the early stage of the reproductive migration because of the growth that could be achieved by allocating time to forage during the migration and its effect in the fitness of the migrants. Foraging behavior during migration may also have the effect of increasing the swimming speed at which migrant move and on the starting time of the migration, although these two features can compensate each other. The application to sockeye salmon of the Fraser River could also be expanded to include the upriver migration. Such expansion could provide answers to questions about minimum viable starting body weight and the effect of changes on river flow and temperature on fecundity for races inhabiting coastal and high altitude lakes. I believe these questions are going to become quite relevant to the survival of sockeye salmon as the effects of global warming become more apparent in the future.

The state-dependent dynamic model for fish migration in Chapter 4 is also a very flexible framework for the study of fish migration. The model does not contain any explicit rule for movement and can be applied to a wide variety of spatial configurations and biological features. The use of the Wisconsin model for the modeling of the bioenergetics of fish was a really valuable aid within the dynamic programming structure. This model provided a direct and straightforward way to quantify the effect of any kind of activity on growth and also a direct association to the total reproductive output of an individual.

Besides of the estimation of the optimal migratory circuit given a configuration of the habitat, the model in Chapter 4 also provides an estimate of the fitness profile of a migrant,

which depicts how fitness changes through time. This profile can provide an objective way to identify bottlenecks in the life cycle of a migrant, and could be used to redirect research efforts accordingly. For example, the fitness profile for the marine phase of sockeye salmon shows a strong response to mortality during the coastal stage and a moderate one to prey density in the open ocean. Thus, research efforts should focus in gaining understanding on the dynamics of sockeye salmon predators in the coast and foraging dynamics of sockeye salmon in the open ocean.

The model in Chapter 4 is perhaps the best framework to develop a full life history model encompassing the five habitats used by sockeye salmon during their life cycle (natal stream, nursery lake, river, coast, and open ocean). Such a model could provide a reasonably good estimation of the relative importance of each one of those habitats in the fitness that individuals achieve during their life cycle. It could also provide a powerful and flexible tool for the exploration of the consequences of environmental changes in each habitat on the total reproductive output of salmon and the efficacy of any remediation measurement as well.

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APPENDIX A
BIOENERGETICS OF SOCKEYE SALMON

A.1 Introduction

Bioenergetics models are based on the energy conservation principle expressed as a balance equation to represent energy budgets. This principle implies that consumption (C) must equal respiration (R), egestion (F), excretion (E), heat increment (HI), and somatic and gonadic growth (ΔB) (Hewett, 1989; Kitchell et al., 1974; Stewart et al., 1983). These components form the basic bioenergetics equation:

$$C = R + HI + F + E + \Delta B \qquad \qquad ...(A.1)$$

The equations used here to represent each component of the bioenergetics equation follow the Wisconsin model published by Hewett (1989) and Hewett and Johnson (1992). This model has been successfully applied to a variety of tropical and temperate fishes (Hewett and Johnson, 1992) and provides a flexible and convenient modeling framework to link patterns of growth with specific behavioral decision for foraging and predator avoidance displayed by fish (Jobling (1994)). The Wisconsin model has been used to study problems associated with structural quality of the habitat in terms of growth (Brandt and Kirsh, 1993; Brandt et al., 1992; Goyke and Brandt, 1993), optimal foraging and life history (e.g Tyler and Calow, 1985), and to gain insight into the dynamics of aquatic ecosystems (e.g. Kitchell, 1992). I selected this model because it allows for the explicit quantification of the costs of alternative migratory behaviors at any body weight in a time-varying environment.

This appendix deals with the fitting of each component of the bioenergetics equation to experimental data on sockeye salmon physiology published mainly by Brett. The basic bioenergetics model (Eq. A.1) is given in an additive form, and for this reason each one of these components is expressed in the same currency, grams per gram of wet body weight per day (g/g/d). For convenience, the estimated parameter values for each component of the bioenergetics model are summarized in Table A.2 at the end of this Appendix.

There is an early publication on the bionergetics of sockeye salmon by Beauchamp et al. (1989). I choose not to use their model because in my opinion respiration and maximum consumption, arguably two of the most important components of the model, were not fitted properly. Parameters for the maximum consumption model, which varies with weight and temperature, were estimated on the basis of two data points, and the slope had to be readjusted because older organisms would have to consume food beyond their maximum consumption limit to achieve the growth observed in the marine environment. The parameters for respiration, which varies with weight, temperature, and activity, were estimated independently for each one of those variables. This resulted in a poor fit that the authors had to correct by comparing their estimates with those for rainbow trout (*O. mykiss*) and adjusting them by eye until the model gave close enough results. Beauchamp et al (1989) also fitted a model to estimate optimal swimming speed since there is the perception that individuals from migratory populations should move at optimal swimming speeds during migration (Ware, 1978; Weihs, 1973). Their model is a modification of a model based on hydrodynamic principles published by Ware (1978). Here I fitted a model for the estimation of optimal swimming speeds based on direct measurements for respiration.

A.2   Maximum Consumption Rate

The maximum consumption rate (C_{max}) measures the daily food intake capacity of an individual fish when fed to satiation. This rate sets an upper limit to foraging capacity, and has been found to vary with body size and ambient temperature (Elliot and Davison, 1975; Kitchell et al., 1977; Stewart et al., 1983). This rate can be represented as the product of two functions; a power function to account for the allometric effect of body weight, and a temperature dependent rate multiplier:

$$C_{max} = a \, W^b \, K(t) \qquad \qquad \dots (A.2)$$

Where

a = Scaling factor for the allometric function

W = Body weight (g)

b = Slope of the allometric function

K(t) = Temperature rate multiplier

The temperature rate multiplier K(t) acts as a shape function in this model, and for fishes inhabiting cool and cold waters Hewett and Johnson (1992) suggest to use the Thornton-Lessem function (Thornton and Lessem, 1978). This function is based on the premise that the biological process has a maximum at some optimum temperature. The function is formed as the product of two logistic equations. The first one describes the process from its lower temperature threshold up to the optimal temperature, and the second one describes the process from the optimal temperature to the maximum temperature threshold:

$$K(t) = \left[\frac{K_1 e^{\gamma_1 (t - T_1)}}{1 + K_1 (e^{\gamma_1 (t - T_1)} - 1)} \right] \left[\frac{K_4 e^{\gamma_2 (T_4 - t)}}{1 + K_4 (e^{\gamma_2 (T_4 - t)} - 1)} \right] \qquad \ldots (A.3)$$

$$\gamma_1 = \frac{1}{T_2 - T_1} Ln \frac{.98(1 - K_1)}{0.02 K_1} \qquad \ldots (A.4)$$

$$\gamma_2 = \frac{1}{T_4 - T_3} Ln \frac{.98(1 - K_4)}{0.02 K_4} \qquad \ldots (A.5)$$

Where

K(t) = Thornton-Lessem temperature rate multiplier (%)

t = Environmental temperature (°C)

K_1 = Rate multiplier near lower threshold temperature

K_4 = Rate multiplier near upper threshold temperature

T_1 = Lower threshold temperature (°C)

T_2 = Temperature at maximum reaction rate (°C)

T_3 = Temperature at maximum reaction rate (°C)

T_4 = Upper threshold temperature (°C)

The shape of this function is defined by the temperature and the rate value near the lower and upper temperature thresholds, and the temperature value from the maximum rate. Those values were taken from an experiment with sockeye fingerlings averaging 6 grams done by Brett et al. (1969) and from Brett and Higgs (1970) data for 30-40 g juvenile sockeye.

Note that to parametrize this function it is necessary to scale the consumption values to a range between 0 and 1. The values obtained for this function were $K_1 = 0.37$; $K_4 = 0.7$; $\gamma_1 = 0.2457$; $\gamma_2 = 3.0445$; $T_1 = 1 \, °C$; $T_2 = 19 \, °C$; $T_3 = 22 \, °C$; and $T_4 = 23 \, °C$. The data and the fitted model are shown in figure A.1.
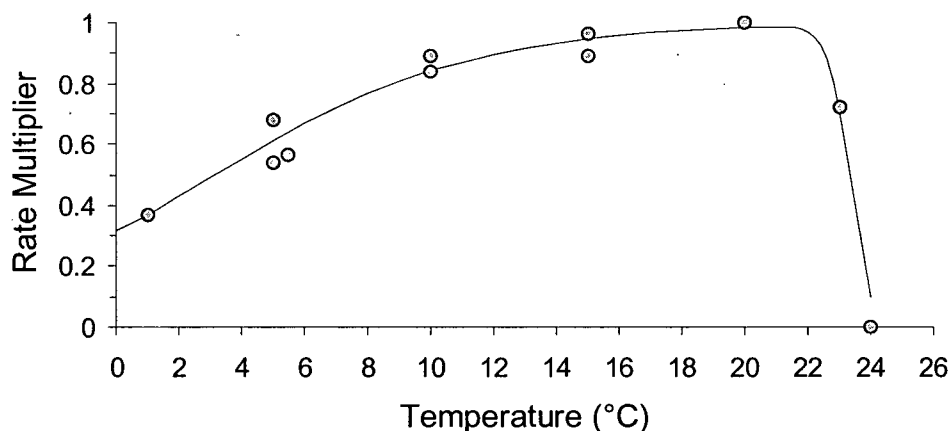
Figure A.1. Thornton and Lessem temperature rate multiplier for sockeye salmon fingerlings. Data taken from Brett et al (1969) and Brett and Higgs (1970).

The allometric part of equation (A.2) was fitted to maximum food intake measurements conducted on sockeye salmon ranging from 2 to 350 grams of weight and kept at 15°C by Brett (1971) (empty circles in Fig. A.2). Some data points at small body size fell outside of a 2-standard deviation interval and were removed (marked as triangles in Fig. A.2). Brett reports that those are probably errors resulting from handling the minute stomach content of small fish. The remaining data were corrected for temperature with the Thornton-Lessem factor and log-transformed before fitting to Eq. (A.2). The resulting parameter values ($a = 0.2335$; $b = -0.4052$; $n = 44$; $r^2 = 0.77$) indicate that a 1,500 g sockeye has a C_{max} of 0.012 g/g/d which is below the observed consumption levels (0.018-0.02 g/g/d for immature females and 0.021-0.023 g/g/d for males) of sockeye salmon in the NE Pacific (Brodeur, 1990). Brett (1971) did notice that ration size varies with the size of the previous ration and the time lapse between meals, and also that fishes routinely fed take smaller rations which leads to low C_{max} measurements during the experiments.

To correct this problem I used stomach content data for sockeye salmon in the NE Pacific published by LeBrasseur and Doidge (1966a), LeBrasseur and Doidge (1966b),

LeBrasseur and Doidge (1966c), and LeBrasseur and Doidge (1966d). Data points with stomach content larger than 30% the weight of the fish were considered outliers and removed from the data set (23 points from 3,833). The data were grouped into a matrix of frequency distributions of stomach content (discretized in 0.01/g/g intervals) per body weight (discretized in 10 g intervals). From this matrix, I estimated C_{max} as the average of the stomach content intervals with 20% of the highest values. The resulting values (not shown) were high (ranging in the order of 0.2 g/g for a 5 g fish to 0.12 g/g for a 465 g individual) when compared to the laboratory data obtained by Brett (1971) although they are not expressed in units of g/g/day. To adjust the data to g/g/d I used digestion time data from Brett and Higgs (1970) to estimate the time to 90% digestion, and transformed the stomach content data onto a daily basis. With the sole exception of the first three data points, the adjusted data (dark circles in Fig. A.2) do not show body weight allometry, which seems to be restricted to small body weights. Unfortunately the lack of stomach content data for low body weights prevented me from using them to define the shape of C_{max}. As a compromise I used the power model obtained from the lab experiments ($C_{max} = 0.2335 \ W^{-0.4052}$) for weights up to 21 g, and the mean of the corrected stomach content data (0.068 g/g/d before correcting for temperature) for bigger individuals (solid line in Figure A.2).
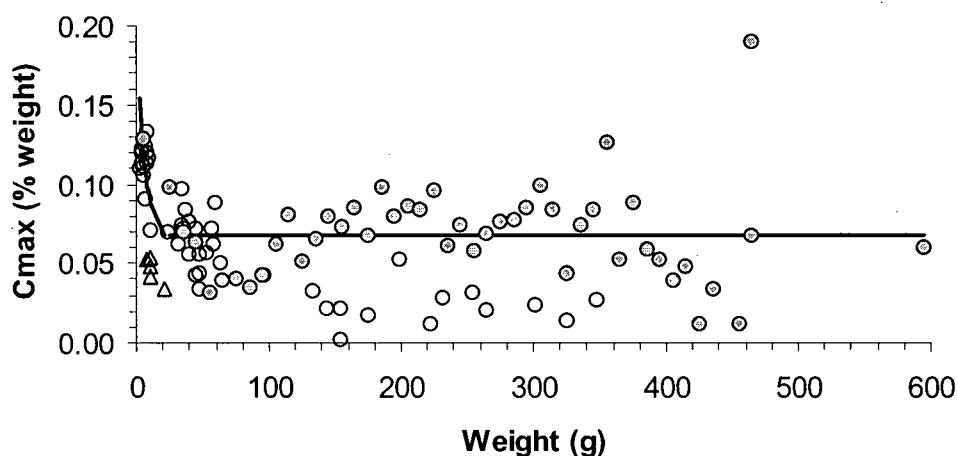
Figure A.2. Allometric component for Daily Maximum Consumption Rate (Cmax) of sockeye salmon. See text for an explanation of the figure.

The resulting 3-dimensional representation of Eq. A.2 (Fig. A.3) shows a strong effect of temperature on consumption capacity for sockeye, and weight allometry is restricted only to small body sizes.
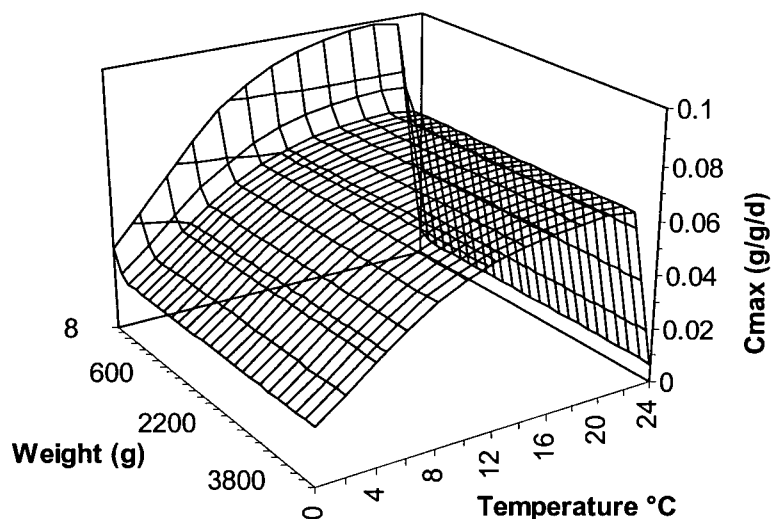
Figure A.3. Fitted maximum consumption rate model for sockeye salmon.

As stated before, C_{max} sets an upper limit to the foraging capacity of the fish. However, under field conditions the realized consumption (C_r) of an individual fish may vary accordingly with its current state (ontogenic, metabolic, and physical state), and the quality of the surrounding habitat (F(o,m,p)). The simplest representation used in bioenergetics to model realized consumption is as a fraction (p) of C_{max}. This representation is used when the bioenergetics model is used to calculate the food intake requirements to match a given growth pattern (Kitchell et al., 1977; Stewart et al., 1983). A more detailed representation of C_r can be achieved by using functional responses (e.g. Walters, 1986) which link prey abundance and the searching behavior of the predator with consumption, or with encounter rate models (e.g. Aksnes and Giske, 1993; Gerritsen and Strickler, 1977; Giguère et al., 1982) that can account for detailed state-dependent foraging behavior of the predator and for prey abundance. Those models may require the use of a trimming function of the form $C_r = MIN \{C_{max}, F(o,m,p,)\}$ to limit consumption to the handling capacity of the fish.

A.3 Energy Density of sockeye salmon

Energy density accounts for the caloric content in the body of the fish, which changes as the individual grows (Stewart et al., 1983). Modeling changes in energy content of body mass across all the life stages of an individual simplifies the conversion from food consumed into fish biomass, and improves the calculation of growth efficiency at any point during the life cycle (Kitchell, 1983).

Modeling energy density is entirely empirical, and the only requisite for a model to be considered appropriate is to properly describe the behavior of energy density content through the ontogeny of the fish. Stewart et al. (1983) and Hewett and Johnson (1992) suggest to model energy density either as a table schedule that can be interpolated to accommodate any time step involved in the computations, or by using two straight lines, switching from the first to the second where the lines intersect. For sockeye salmon data I found that a logarithmic model gave a good fit to the data.

Monthly ontogenic changes in sockeye salmon energy density estimates were published by Brett (1980) for Babine Lake sockeye salmon. His data show that energy density decreases after hatching but increases asymptotically later in life as (dry) body weight increases. There is also a small but noticeable seasonal oscillation in the energy density sockeye during the marine life stage, which peaks around November. Likely this variation comes from seasonal changes in quantity and quality of prey consumed by sockeye and is not intrinsic to their development pattern. Data in Brett (1980) were transformed from kcal per gram of wet weight to Joules per gram of wet weight using the equivalence of 1 kcal = 4,184 J (Libes, 1992). The data do not include energy density values for eggs (estimated at 370 cal by Dueñas (1980, cited in Brett, 1980) and spawned adult. These stages were ignored because they are not relevant for this research. The model and the data are shown in figure A.4. The fitted equation had a $r^2 = 0.9747$ (n = 32) and was as follows.

$$E_d = 4825.6 + 346.76 \, Ln \, (W) \qquad \qquad ...(A.6)$$

Where

E_d = Energy density (in Joules/gram of wet weight)
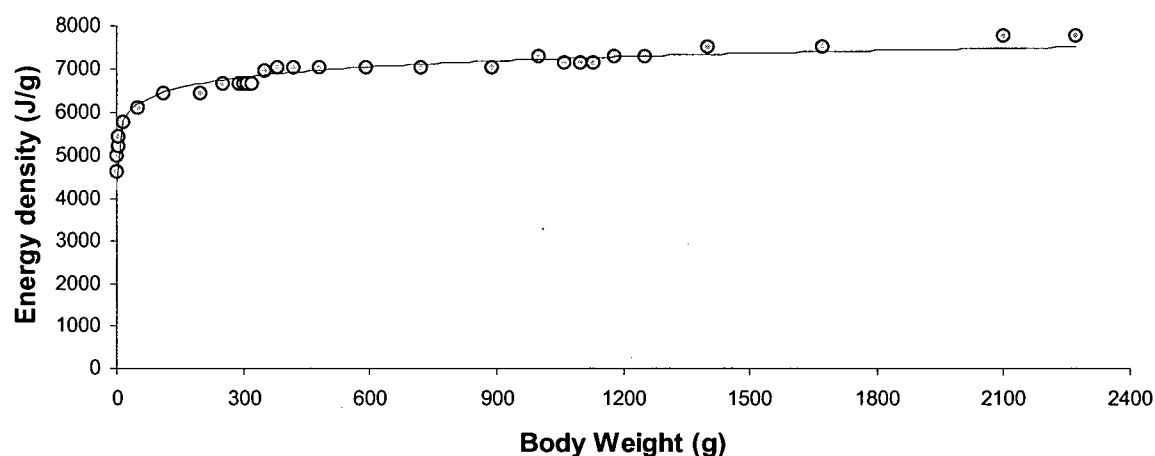
Figure A.4. Ontogenic changes in energy density of Sockeye salmon. Weight is expressed in grams of wet weight.

A.4 Total Metabolism

Total metabolic energy expenditure can be separated into two components: Respiration, and Heat Increment (or Specific Dynamic Action) (Elliot, 1976a; Stewart et al., 1983).

A.4.1 Respiration

Respiration costs arise from two components: standard metabolism that represents the metabolic costs incurred by the fish at rest, and the active metabolism representing the added costs associated with any behavioral activity (foraging, predator avoidance, migration, etc.) (Hewett and Johnson, 1992). At any level of activity and body weight, temperature has a significant effect in the metabolic costs. Standard metabolism is modeled as an allometric function of weight. Standard metabolism increases exponentially with temperature and swimming speed (representing active metabolism). The model for respiration (Eq. A.7) is expressed as a standard metabolic rate affected by two rate multipliers; one for temperature and another for activity.

$$R = \alpha W^{\beta} e^{\rho T} e^{\upsilon N} \qquad \qquad \qquad ...(A.7)$$

Where:

α = Scaling factor for the combined effect of standard metabolism, temperature, and activity (g/g/d)

β = Weight dependent coefficient for standard metabolism

ρ = Temperature dependent coefficient

υ = Activity dependent coefficient

W = Body weight (g)

T = temperature (°C)

v = Swimming speed (cm/sec)

Data for this model came from respiration measurements done by Brett (1964) and Brett (1965) on sockeye salmon. These measurements were taken for sockeye ranging from 3 to 1,400 g. of body weight, at temperatures from 5° to 24° C, and activity levels from 1 to 4 body lengths per second. In his reports, Brett indicated that respiration measurements may incur problems due to restless behavior at low swimming speed levels, non-conditioned fish (increased oxygen consumption), or high activity levels that may put the organism into anaerobic metabolism during the experiment. To avoid those problems, respiration values for restless behavior, critical speed, and non-conditioned fish as reported in the above references were removed from the data used to fit the model.

Fitting was done by linearizing the model using logarithms to homogenize variance across body weight. Best fit gave the following parameter values: α = 237.4825 mg O_2/Kg/h; β = -0.351; ρ = 0.0306; υ = 0.02786 (r^2 = 0.897, n = 41). A comparison between observed and predicted values shows a slight underestimation of respiration rates at values higher than 700 mg O_2/Kg/h (see Fig. A.5). In all likelihood this comes from the fact that most of the observations are below the 700 mg O_2/Kg/h level, and dominate the sum of squares in the regression.
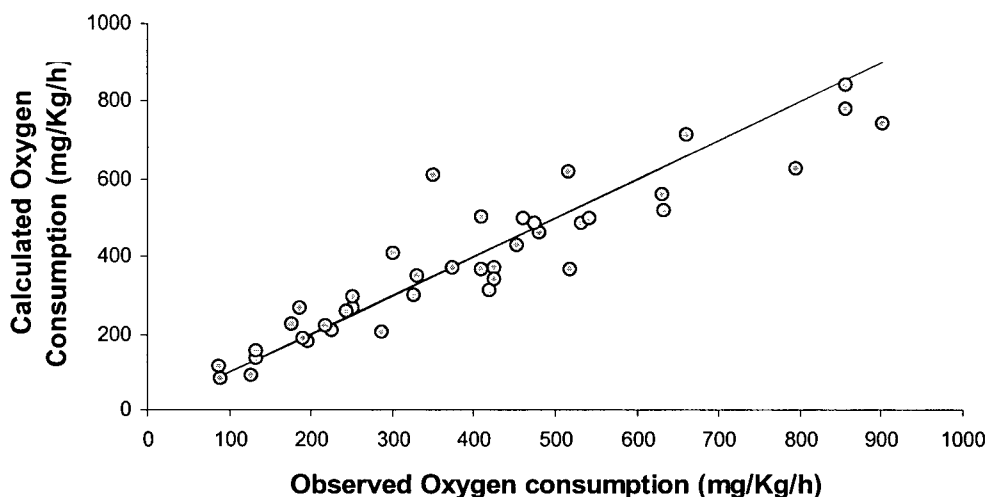
Figure A.5. Goodness-of-fit relationship between observed and predicted sockeye salmon respiration values around a 1:1 line.

The units of the intercept α were scaled to 0.0057 g O_2/g/d, and further converted to 77.2863 Joules spent per gram of wet weight per day with the use of an oxycaloric value of 13,560 J/g O_2 respired suggested by Elliot and Davison (1975) for a generalized salmonid. To transform those units into grams of body weight respired per gram of body weight per day we require the energy density of the fish, which can be obtained from equation (A.6) given above. The final model for the total metabolic rate is in equation (A.8). The fitted model (Fig. A.6) shows that the metabolic rate decreases as body size increases, and that activity has a stronger effect than temperature in the total metabolic rate.
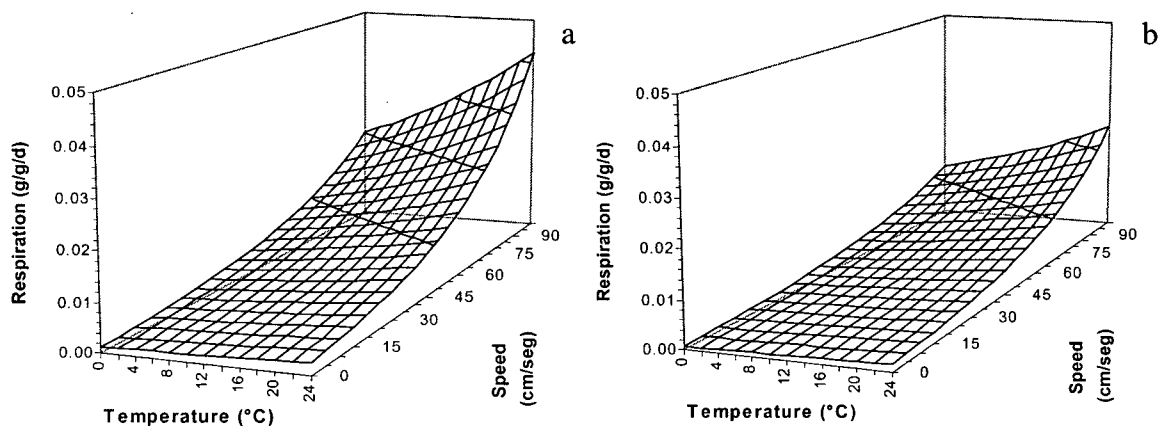
Figure A.6. Temperature and activity effects on metabolic rates for a 500 g (a) and a 2,000 g (b) sockeye salmon.

$$R = \frac{77.2863}{E_d} W^{-0.35143} e^{0.0306T} e^{0.027861v}$$

...(A.8)

A.4.2 Heat Increment (HI)

Heat Increment (or Specific Dynamic Action) is defined as the amount of energy released following the ingestion of a meal (Beamish, 1974). This release is generally assumed to be the result of the de-amination of amino acids in the liver (Brett and Groves, 1979). Dietary components seems to have a strong effect in HI values (Beamish and Trippel, 1990). Diets with high protein content have been positively correlated with HI, with little effect from carbohydrate and fat content (LeGrow and Beamish, 1986). This characteristic of HI may create a problem in the estimation of HI for fish fed with commercial food, and not their natural diet, during the experiments.

Although the definition of HI is straightforward, it has been hard to experimentally separate HI expenses from those arising from the mechanical aspects of feeding. Beamish and Trippel (1990) pooled both values together and referred to this value as Apparent Heat Increment (AHI). The AHI is used in this model.

AHI losses are modeled as a fraction of the digestible energy (consumed food - egested waste) (Beamish, 1974; Hewett and Johnson, 1992; Kitchell et al., 1977). This fraction has been found to range from 5 to 24% of the digestible energy depending on the species and the diet composition (Beamish and Trippel, 1990; Kitchell, 1983; Tyler and Calow, 1985). Since there is no available estimate of AHI for sockeye salmon, Beauchamp et al. (1989) suggested a value of 17.2% calculated by Beamish (1974) for largemouth bass fed on a diet of emerald shiners. Piscivorous fish have high AHI values probably because of the high protein content in fish (LeGrow and Beamish, 1986). However, the main items in the diet of sockeye are zooplankton during the freshwater phase (Doble and Eggers, 1978), and squid, zooplankton, and fish in the marine phase (LeBrasseur, 1966). When compared with fish, zooplankton have lower protein content (Jobling, 1994) which reduce the AHI value. Since the main component of the diet is zooplankton (see Table A.1), a value of 14% will be

used in this model. The presence of squid in the diet may also alter the AHI value, however their high water content may minimize their overall effect on AHI. The proposed model for AHI is then as follows:

$$AHI = 0.14 \, (C - F) \qquad\qquad ...(A.9)$$

A.5 Waste losses

A.5.1 Excretion

Waste losses account for the excretion of metabolic by-products and the egestion of indigestible matter as feces (Kitchell, 1983). For most teleost fishes the main excretion products are ammonia and urea (Brett and Groves, 1979). Kitchell et al. (1974) suggested to represent excretion losses as a constant proportion of consumption, however Elliot (1976b) found that in brown trout (*Salmo trutta*), excretion is also affected by temperature, body size, and realized consumption. Elliot also found that body size and realized consumption could both be accommodated in a single factor by representing realized consumption as a proportion of the maximum consumption for that body size ($p = C \, / \, C_{max}$). Since egested energy cannot be excreted, Stewart et al. (1983) modified the model to make it independent of the amount of non-digestible material present in the diet by removing this fraction from the ingested food. This modified version is perhaps the most complete model for excretion to date (Hewett and Johnson, 1992) and is the one used in this work. There are no experimental data available on excretion for sockeye salmon fed on a natural diet, thus the modified model for brown trout is used instead:

$$E \, / \, (C - F) = 0.0314 \, T^{0.58} \, e^{-0.299p} \qquad\qquad ...(A.10)$$

Where

$E \, / \, (C - F)$ = Proportion of the digestible ration excreted as waste

T = Temperature (°C)

p = Fraction of C_{max} consumed as ration

The parameter values indicate that the fraction of consumption being excreted increases with temperature and decreases with ration size. The model (figure A.7) also shows that temperature, rather than ration, has the strongest effect on the fraction of food excreted.
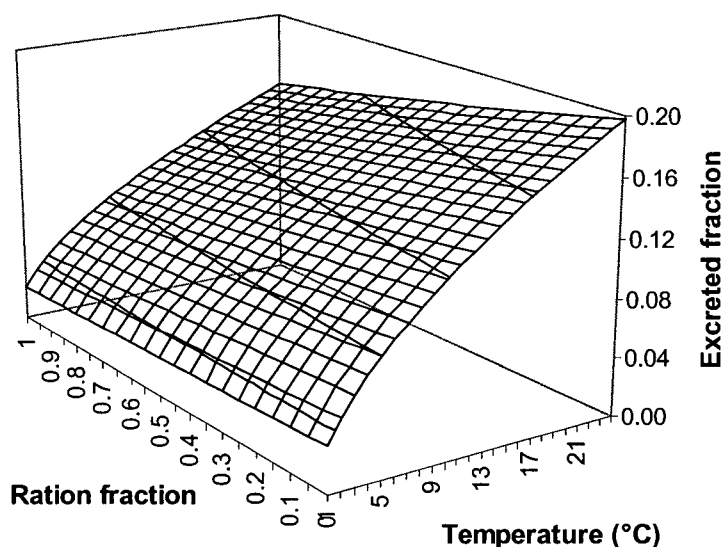
Figure A.7. Effect of temperature and ration size in the excretion losses for brown trout. Base model taken from Elliot (1976) and modified by Stewart et al (1983).

A.5.2 Egestion

Egestion refers to the expulsion of non-digestible components of the prey. Those components usually are chitin, cellulose, lignins, and keratin depending on the diet of the fish, as well as materials shed from the fish, like intestinal epithelial cells, mucus, and digestive enzymes (Brett and Groves, 1979). Egestion has been shown to change depending on diet quality, temperature, frequency of feeding, and ration (Brett and Groves, 1979, Elliot, 1976b). Of these factors, diet quality, temperature, and ration are perhaps the most important elements determining the amount of feces expelled by the fish (Elliot, 1976b). There are no measures of egestion available for sockeye salmon feeding on a natural diet. However, it is reasonable to assume that brown trout, a close relative of sockeye salmon, feeding on an amphipod species have similar egestion losses. For this species Elliot (1976b) found the following relationship:

$$F / C = 0.212 \ T^{-0.222} \ e^{0.631 \ p} \qquad \qquad \ldots (A.11)$$

Where

F / C = Proportion of daily intake lost as feces

T = Temperature (°C)

p = Proportion of the maximum ration consumed (C/C$_{max}$)

The model (shown in Fig. A.8) indicates that the fraction of the ration egested decreases with temperature and increases with ration size. It also shows that the chief factor determining the amount of waste egested is the size of the ration obtained.
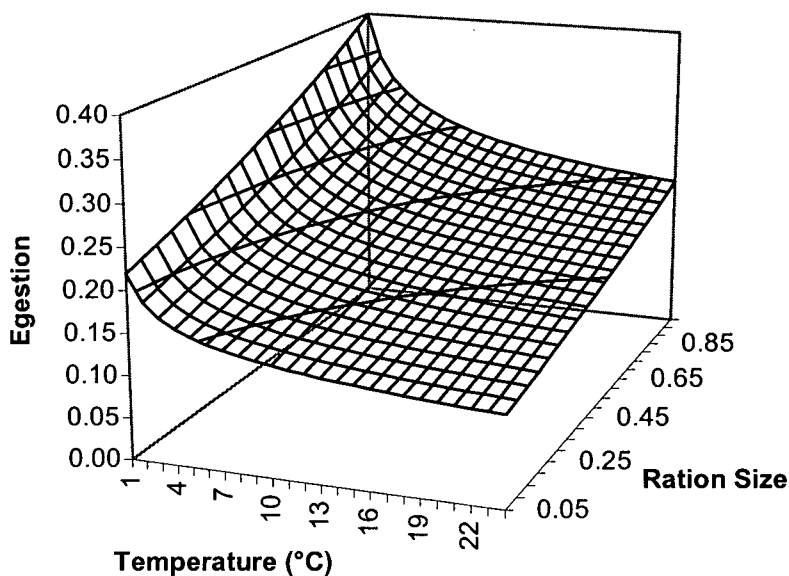
Figure A.8. Effect of ration size (as a proportion of C$_{max}$) and temperature in the proportion of the ration egested as feces (from Elliot (1976)).

Perhaps the only drawback in the application of Elliot's model to sockeye salmon egestion is the change in their diet as they move from the lake to the coastal domain and into the open ocean. To account for this kind of change, Stewart et al. (1983) adapted the model for a fish foraging in zooplankton at early age that becomes piscivorous latter on life. The correction accounts for unequal values of non-digestible matter between the two prey types. Hewett and Johnson (1992) further generalized it to a diet with multiple prey types. The generalized model is as follows:

$$F/C = [(0.212\ T^{-0.222}\ e^{0.631\ p} - 0.1)\ (1 - \Sigma\ IP_i\ D_i)/\ 0.9] + \Sigma\ IP_i\ D_i \qquad ...(A.12)$$

Where

IP$_i$ = Indigestible proportion of the ith prey

$$D_i = \text{Proportion of the i}^{th} \text{ prey in diet}$$

There is enough information on the feeding habits of sockeye salmon over all habitats used in their life history to calculate the proportion of prey in the diet of sockeye. During the freshwater stage sockeye fingerling feed mainly on macrozooplankton. The diet is composed of cladocerans, copepods, and insect larvae (Doble and Eggers, 1978; Goodlad et al., 1974; Hume et al., 1996; Ricker, 1937). Smolts migrating in Hecate Strait feed mainly on larval stages of ascideans, euphausids, copepods, amphipods, and fish larvae (Foerster, 1968; Healey, 1980; Healey, 1991; Landingham et al., 1998). The diet in the open ocean is mainly composed of euphausids, squid, and fish for maturing sockeye, while immature sockeye feed mainly on amphipods, euphausids, and squid (Brodeur, 1990; Hartt and Dell, 1986; LeBrasseur, 1966; LeBrasseur and Doidge, 1966a; LeBrasseur and Doidge, 1966b; LeBrasseur and Doidge, 1966c; LeBrasseur and Doidge, 1966d; Pearcy et al., 1984). To calculate the proportions needed in equation (A.12), prey items were categorized as zooplankton, amphipods, euphausids, squid, or fish, and are given in Table A.1. The indigestible fraction per prey type was calculated as an average from values for individual preys reported by Brett and Groves (1979). A value for the indigestible fraction of fish larvae was not available from Brett and Groves (1979), it is assumed to be larger than squid but smaller that adult fish; 0.05 was chosen to represent it.

Table A.1. Indigestibility values, energy content, and proportion in diet of prey categories for sockeye salmon. Proportion in diet is percentage by volume.

Habitat	Diet Composition	Proportion in diet	Indigestible fraction	Energy density (in kJ/g wet weight)
Lake	Zooplankton	1.0	0.1	3.34
Coast	Zooplankton	0.98	0.1	3.03
	Fish larvae	0.02	.05	4.18
Open Ocean	Squid	0.09	0.04	4.167
	Fish	0.14	0.078	6.868
	Euphausids	0.53	0.1	3.6
	Amphipods	0.18	0.1	5.49

The energy content of prey items is required to properly estimate the growth of sockeye from food consumption. The values used for each type of prey are given in Table A.1. Values were transformed to Joules by using a conversion factor of 4.184 J per calorie when required (Libes, 1992), and averaged in those cases where values for several species or

sampling seasons were available. Mean energy content for lake zooplankton was estimated at 3.34 kJ/g wet weight from data on *Diaptomus* and *Cyclops* (Schindler et al., 1971) and a dry-to-wet weight factor of 12.5% taken from Hewett and Johnson (1992) for copepods. Energy density of marine zooplankton in the coast was estimated at 3.03 kJ/g of wet weight from data on *Calanus plumchrus* and *C. marshallae* sampled in the Strait of Georgia, British Columbia by Gardner (1976). Values from both species were averaged and transformed to wet weight with a 12% dry-to-wet weight conversion rate. Squid energy content was estimated at 4.167 kJ per gram of wet weight from data on *Loligo brevis* (Thayer et al., 1973) and *Loligo pealei* (Steimle and Terranova, 1985). *L. pealei* data were transformed to wet weight applying a 18% dry/live weight factor from *L. brevis*. Energy density of fish was estimated at 6.868 kJ/g from the model of Hartman and Brandt (1995) by using an average dry/wet weight ratio of 28% from Hewett and Johnson (1992). Fish larvae energy density was estimated at 4.18 kJ/g from data in Thayer et al. (1973). Energy values for amphipods and euphausids were calculated at 5.49 kJ/g and 3.6 kJ/g respectively with the model of Platt et al. (1969) and carbon and ash content data in Parsons et al. (1984).

A.6 Optimal swimming speed

Kitchell (1983) suggested that energy allocation in fish occur in a hierarchical fashion; total metabolic costs being met first, HI and excretion acting as taxes on consumed energy, and the remaining surplus energy allocated into somatic and gonadic growth. Swimming activity is perhaps the most important factor in the determination of surplus energy. Swimming activity controls the efficiency of the energy intake process in pelagic fishes (Ware, 1975; Ware, 1978). Swimming is also an important fraction of the total metabolic costs, reaching up to 10 times the basal metabolic rate for a sockeye salmon moving at maximum sustained swimming speed (Brett, 1980). The high metabolic cost of movement has led to the idea that patterns of movement in fish like burst and glide, reduction of activity and migration to cooler waters during non-feeding periods, maintenance of feeding territories, and speed regulation are behavioral mechanisms that reduce those costs (Ware, 1983; Weihs, 1973; Weihs and Webb, 1983).

In migratory species like sockeye salmon, migration occurs on a spatial scale of thousands of kilometers and can represent a massive investment of energy that could otherwise be allocated into growth or reproduction (Roff, 1991; Ware, 1983). Efficient use of available energy during the migration is therefore essential, and can only be achieved by swimming at an optimal speed within the scope of the aerobic metabolism (Weihs, 1973).

Two approaches have been used to calculate optimal swimming speed in fish. Ware (1978) used hydrodynamic theory to estimate optimal swimming speed of a generalized salmonid as a function of size and temperature. Ware defined optimal cruising speed as the speed at which the total amount of energy expended per unit of distance traveled is minimal. His model represented total metabolism as the sum of basal and active metabolism. Basal metabolism was defined as a power function of body size while active metabolism was calculated as the power needed to overcome the drag of the body at any given speed. However, basal and activity metabolism have been found to be affected by temperature (Stewart et al., 1983), and for this reason his model is valid only within a narrow temperature range.

A more physiological approach was follow by Brett (1965), Brett (1967), Brett (1973), Brett and Glass (1973), and Brett et al. (1958). The focus of their research was to measure respiration levels of sockeye salmon across a wide range of swimming speed and temperature, and to determine the speed at which anaerobic metabolism occurs, which they defined as the critical speed. Their results indicate that salmon have an optimal swimming speed that varies with temperature and body weight. Their data show that, regardless of weight, sockeye salmon reach the highest maximum sustained swimming speed value at 15 °C, and that the value of such speed varies in an allometric fashion with body weight. Given those characteristics, optimal swimming speed (S_{opt}) was modeled with the same algebraic form used for C_{max}.

$$S_{opt} = a \ W^b \ K_s(t) \qquad\qquad ...(A.13)$$

The data for this model came from the experiments done by Brett (1965), Brett (1967), Brett (1973), Brett and Glass (1973), and Brett et al. (1958). Some of the data were given as

critical swimming speed, and for those cases, optimal swimming speed was calculated as 0.75 of critical speed. Since the data show that optimal swimming speed increases with temperature up to 15 °C and then decreases, the Thornton-Lessem function was used to model temperature dependency ($K_s(t)$ in Eq. A.13). To parametrize this function, the average optimal speed was calculated for three weight categories (2.6 g, 44.1 g, and 1,576 g). Only those data points with the same temperature and similar in body weight were used in the calculation of each average. The data points were further transformed into a 0-to-1 range across temperature by scaling them with the highest speed for each weight category and temperature. The parameter values obtained for this function are as follows: K_{s1} = 0.47; K_{s2} = 0.7; Y_1 = 0.1943; Y_2 = 0.2445; T_{s1} = 2 °C; T_{s2} = 22.65 °C; T_{s3} = 11.55 °C; and T_{s4} = 24 °C. The resulting model and the data are shown in figure A.9.
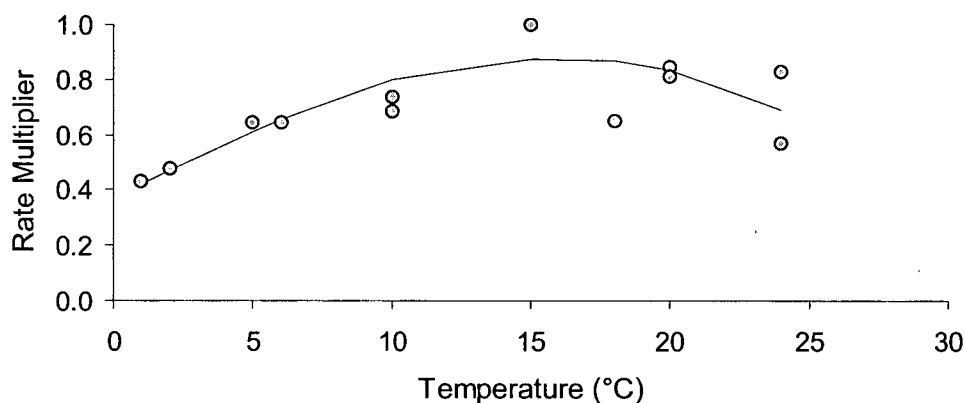
Figure A.9. Temperature rate multiplier for optimal swimming speed of sockeye salmon.

The body weight dependency was fitted to the complete data set after correcting them for temperature with their corresponding Thornton-Lessem value. The model was linearized using logarithms and fitted using least squares. The values for the parameters were a = 34.2 and b = 0.1642 (n = 54, r^2 = 0.88). A comparison between the observed and the calculated values for optimal swimming speed is shown in figure A.10, and the fitted model is shown in figure A.11.
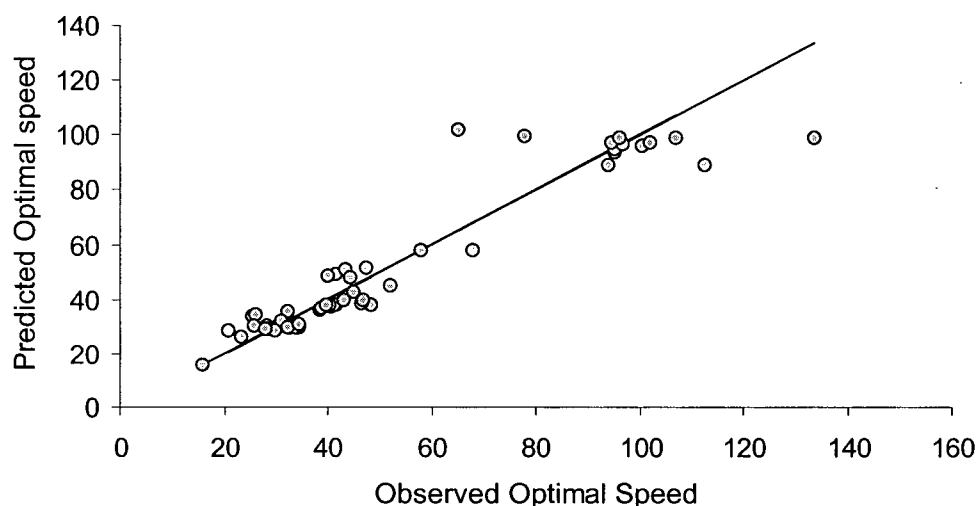
Figure A.10. Observed vs. predicted optimal swimming speed (cm/s) of sockeye salmon along a 1:1 line.

The model predicts that a 2.4 kg (56 cm body length) returning salmon has an optimum swimming speed of 91 cm/s or 1.6 body length/s. Such speed is well within the range of values observed in the field, but is higher than the observed average. Tagging data indicates that returning salmon can reach sustained swimming speeds of up to 2 body length/s although the average swimming speed is of 1 body length/s (Groot and Quinn, 1987; Madison et al., 1972; Quinn, 1988; Quinn et al., 1989).

Weihs (1973) suggested that the discrepancy between the physiological determination of optimal swimming speed and field measurements results from the inability of the fish to swim at a preferred swimming speed while being confined in the swimming chamber. However, it is not clear how such impediment would affect the estimation of the physiologically optimal swimming speed. I find it more reasonable to consider the shortcomings of field measurements of swimming speed. Traveling speed is always calculated by assuming the shortest path and there is no account of the effect that currents may have in the ground speed of the fish. Also, there is no consideration of the effects that constant attention to potential predators may have on swimming speed or the attention demands exerted by the guidance system while navigating across the spatial complexity of the coastline. Those two factors would result in lower swimming speeds. Laboratory experiments do not provide the fish with such stimulae, nor require the fish to use any sort of navigation

system. Lab experiments only provide estimates of the maximum aerobic activity scope of the fish and as such it will be used here.
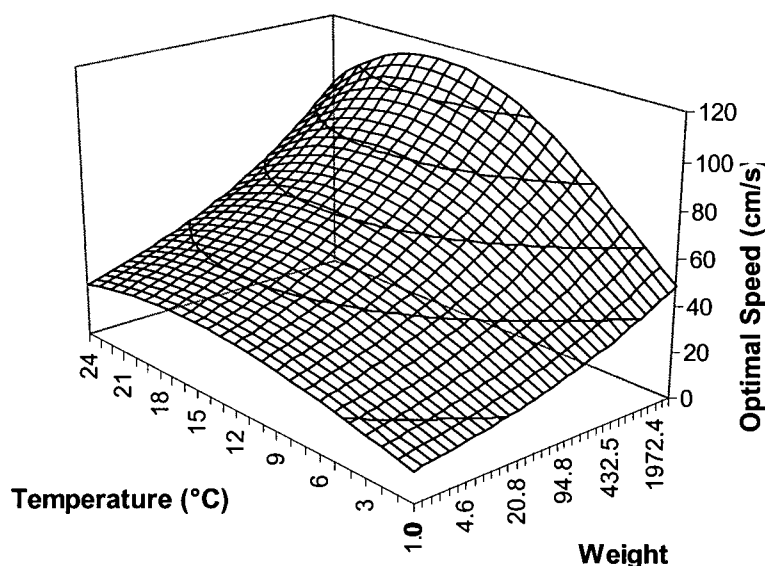
Figure A.11. Optimal swimming speed model for sockeye salmon.

A.7   Sensitivity Analysis

Sensitivity analysis was conducted to determine those parameters that have the strongest effect in the model, and for which errors in estimation may be critical. This analysis follows the suggestion of Kitchell et al. (1977). They indicate that sensitivity analysis for bioenergetics models should be done by determining the effects that a fixed percent change in each parameter of the model may have on annual growth in reference to the growth from a run done with the nominal parameter values. Optimal swimming speed was not included in this analysis.

The simulations were done for a 12 g individual that starts its marine life during early May. The seasonal temperature pattern used here was that of the center of the Gulf of Alaska (50° N and 140° W), and was extracted from the COADS surface temperature database. This location has a minimum temperature value at 6.1 °C during March, and peaks at 13.7 °C during August and September. It was further assumed throughout the simulations that the fish spends 24 hours a day moving at one body length per second, obtains a constant 64% of its

maximum ration, and the diet is entirely composed of zooplankton. For this reason equation (A.11) was used in the calculation of egestion. The average prey consumed contains 3,030 Joules per gram of wet weight (see Table A.1) and has no seasonal variation in its energy content. The simulation starts May 1st and proceeds for 26 months, which is the marine residency period for most of the sockeye salmon from the Fraser River.

The sensitivity of the model to each parameter was calculated by comparing a baseline terminal weight value estimated from parameter values in Table (A.2) and those resulting from a ±10% change applied to each parameter. Sensitivity was calculated as the percent of difference between those weights and the baseline value. During the calculations a numerical error occurred when $T_3 > T_4$ in Eq. (A.5). For this reason, the value γ_2 (Eq. A.5) and its counterpart γ_1 (Eq. A.4) were changed rather than the values of T_2 and T_3.

Under the conditions above stated and the parameter values in Table (A.2), the model predicts a terminal weight of 2.44 kg after 26 months of marine residency. The results of the sensitivity analysis (Figure A.12) indicates that terminal weight is most sensitive to errors in the parameters describing weight allometry and swimming activity in Respiration, the intercept of the Energy Density function, and weight allometry in Maximum Consumption. Respiration and maximum consumption are quite important components in the bioenergetics model, particularly the portion that describes the allometry of body weight in each one of those processes. The relevance of the intercept of the energy density model in body weight, second only to respiration, comes from its role as a conversion function from prey consumed to sockeye mass. Energy density during sockeye ontogeny varies from 4,500 J/g to 7,800 j/g, and at a value of 4,825 J/g the intercept should be the dominant parameter in the relationship.

I was expecting Maximum Consumption to have a larger effect on terminal weight, since an underestimation of it would require individuals to achieve full ration and forage full time to be able to reach the observed terminal weight. I suspect that the comparatively low sensitivity obtained here results from the model providing a consistently large daily ration.

Fortunately the models for Respiration, Energy Density, and Maximum Consumption agree well with the data (Figs A.1, A.2, A.4, and A.5) and errors in parameter values are

unlikely. Perhaps a cause for real concern is the limited coverage of weight values in Respiration (3 to 1,400 g) and Maximum Consumption (up to 460 g). Unfortunately, data availability at larger body weights is quite limited.
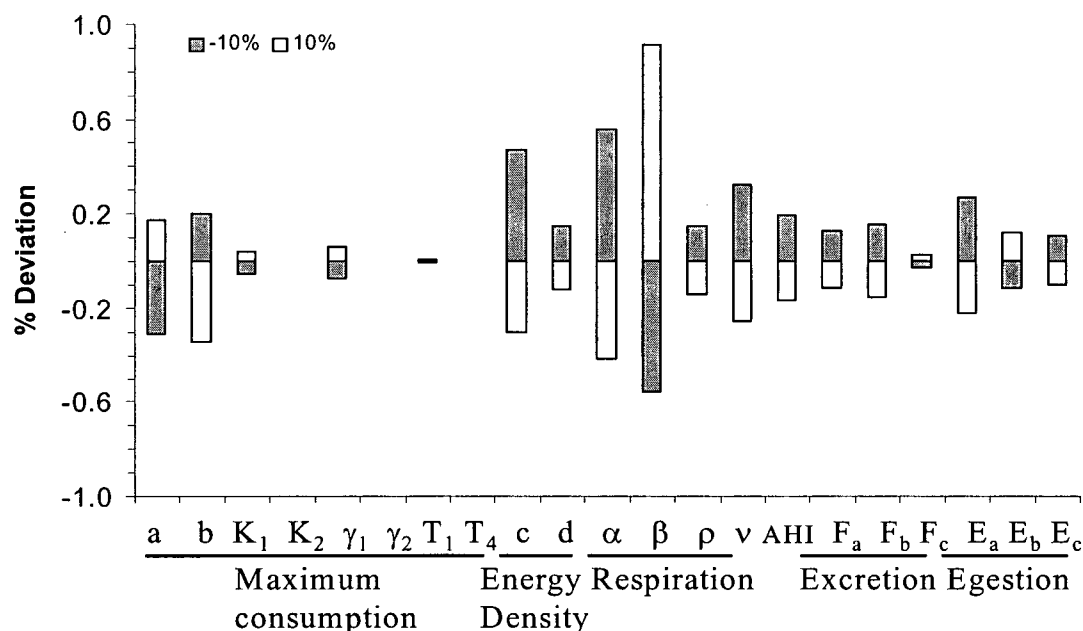
Figure A.12. Model sensitivity to a ±10% change in parameter values.

AHI and the excretion parameters show a small effect on growth. This comes with a relief since the data for these models are for brown trout. AHI has no relationship with the most expensive metabolic activities, and only acts as a fixed tax on consumption. The same can be argued for excretion. However, the intercept for egestion (E_a) has a stronger effect on growth. This parameter determines the amount of digestible food available for growth. This is unfortunate since there is no data available for sockeye salmon, and the values used here are those published by Elliot (1976b) for brown trout.

Overall, the main processes controlling growth are respiration, maximum consumption, and sockeye salmon energy density. Maximum consumption had a fair amount of experimental data available for small fishes and enough field measurements of stomach content for larger fish to describe the parameter properly. In the case of the respiration process, the model shows a good fit to the available data (see Fig. A.5), and errors in the estimation of the allometric effect of weight should be minimal.

Table A.2. Parameter values for the sockeye salmon bioenergetics model.

Description	Value	n	r^2	Reference
Maximum Consumption				
Intercept	0.2335	44	0.77	Brett (1971)
Weight exponent	-0.4052			
Constant for w > 21	0.068			
Thornton-Lessem function				
K_1		11		Brett et al (1969), Brett and
K_4	0.37			Higgs (1970)
γ_1	0.7			
γ_2	0.2457			
T_1	3.0445			
T_2	1.0 °C			
T_3	19.0 °C			
T_4	22.0 °C			
	23.0 °C			
Energy Density		32	0.9747	Brett (1980)
Intercept	4825.6			
Slope	346.76			
Respiration		41	0.8971	Brett (1964; 1965)
Intercept	77.2863			
Weight exponent	-0.3514			
Temperature coefficient	0.0306			
Activity coefficient	0.027861			
Apparent Heat Increment	0.14			
Excretion				Elliot (1976), Stewart et al
Intercept	0.0314	80	0.988	(1983)
Temperature Exponent	0.58			
Ration Coefficient	-0.299			
Egestion				Elliot (1976)
Intercept	0.212	76	0.9604	
Temperature exponent	-0.222			
Ration Coefficient	0.631			
Optimal Swimming Speed				Brett (1965; 1967; 1973),
Intercept	34.2	54	0.88	Brett and Glass (1973), Brett
Weight exponent	0.1642			et al (1958)
Thornton-Lessem function				
K_{s1}	0.47	14		
K_{s4}	0.7			
Y_1	0.1943			
Y_2	0.2445			
T_{s1}	2.0 °C			
T_{s2}	22.65 °C			
T_{s3}	11.55 °C			
T_{s4}	24.0 °C			

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