

Space Use Patterns and Population Trends of Southern Resident Killer Whales
(*Orcinus orca*) in Relation to Distribution and Abundance of Pacific Salmon
(*Oncorhynchus* spp.) in the Inland Marine Waters of Washington State and
British Columbia

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DEDICATION

I would like to dedicate this work to my Grandfathers: William H. McCluskey and Robert P. Hamilton. May we be forever united by Celtic currents.

CHAPTER 1: GENERAL INTRODUCTION

Overview

Killer whales (*Orcinus orca*) are long-lived top predators occurring in relatively low densities throughout their range (Dahlheim and Matkin 1994). As such, they have been viewed as indicators of ecosystem health and have become the focus of intensive study (Heimlich-Boran 1986). A population of killer whales in the Northeast Pacific, known as the southern resident community (SRC), has drawn considerable interest due to its proximity to urban areas, a long-term survey program on the population, and a recent decline in numbers that has led to the listing of the SRC as an Endangered Species under the US Endangered Species Act of 1973 as amended (ESA), the Canadian Species at Risk Act (SARA), and Washington State law (Baird 2001; Wiles 2004; NMFS 2005). A number of factors have been identified as possible causes in the recent decline of the SRC, including anthropogenic disturbance, high concentrations of contaminants, and a reduction in quality or quantity of preferred prey (Baird 2001; Krahn et al. 2002; Wiles 2004). This study investigates the relationship between the SRC and Pacific salmon (*Oncorhynchus* spp.) to better understand prey associations and to provide useful information for management actions.

Background information on killer whales will be presented in a general introduction. Much of the background information will be repeated in the introduction sections of the individual chapters, because chapters will be submitted separately for publication. The general introduction will give an overview of killer whale life history, emphasizing the global distribution and wide variety of foraging habits on the species level, contrasting with small populations that exhibit very

specific behaviors and distribution patterns unique to their habitats. This regional specialization of a dynamic top predator adds a unique challenge when formulating predictions or drawing conclusions pertinent to long or short term behavioral patterns. The focus of discussion will then shift more specifically to the SRC. Population status will be discussed, along with a brief review of the potential threats to the population. The potential threats of declining quality and quantity of prey will lead in to an overview of the status of salmon populations in the Pacific Northwest region of North America.

Killer Whale Biology

Killer whales inhabit all oceans of the world, but are most abundant in colder, more biologically productive regions (Heimlich-Boran 1988; Dahlheim and Heyning 1999; Baird 2001; Hoelzel et al. 2002). Killer whales are highly social cetaceans, traveling in matrilineal family groups known as pods which can range from two to 100 individuals. Groups of associating pods are known as a community (Hoelzel et al. 2002). While killer whales are not known to participate in lengthy seasonal migrations as most mysticete whales do, some individuals have been documented to have a range of as much as 140,000 km² (Baird 2001).

Male killer whales can live as long as 50-60 years and females have been observed to live into their 90s (Olesiuk et al. 1990; Ford et al. 2000). Reproductive maturity is reached between the ages of 12 and 16 in both sexes (Matkin et al. 1994). Sexual dimorphism is displayed in body length, and pectoral fin, fluke and dorsal fin shape and size (Baird 2001). Females typically bear their first calf at the age of 15 (Ford et al. 2000) after a gestation period of roughly 17 months, and will produce a calf approximately every 3-12 years (average interval of 5 years) until reproductive

senescence around the age of 40 (Olesiuk et al. 1990; Bain and Balcomb 1999; Baird 2001).

Ecotypes

Killer whales around the world have been divided into “eco-types” (Berzin and Vladimirov 1983; Ford et al. 2000; Pitman and Ensor 2003). In the eastern North Pacific different “eco-types” are based on genetic, acoustic, morphological, trophic and behavioral differences (Ford 1991; Baird and Dill 1996; Ylitalo et al. 2001; Morton and Symonds 2002). Resident type whales, also known as “fish-eaters”, prey on fish and cephalopods, live in larger multi-generational family pods, have unique complex vocal dialects, and generally remain in smaller home ranges (Deecke et al. 2002). Residents spend a greater proportion of time in deep water above high relief bathymetry while transients frequent shallow bays and coastlines (Nichol and Shackleton 1996; Baird 2001; Scheel et al. 2001). Transient killer whales, also known as “mammal-eaters”, forage on marine mammals, occasionally birds and terrestrial mammals, travel in smaller, more fluid matrilineal units, do not vocalize as frequently as residents, and do not typically have predictable seasonal ranges (Saulitis et al. 2000; Scheel et al. 2001). Resident and transient type pods overlap in geographic range, but do not socially interact (Symonds 2002) and individuals from one form have never been documented to emigrate to the other (Matkin 1994). Mitochondrial DNA (mtDNA) data suggest that resident and transient whales in the eastern North Pacific have not interbred for at least 10,000 years (Hoelzel et al. 2002). Different resident groups, such as the Northern Resident Community (NRC) and the Southern Resident Community (SRC), which share adjacent home ranges (Figure 1), are also genetically distinct from one another, indicating that the two communities do not interbreed (Bain and Balcomb

1999). Pods from the NRC have never been observed to interact with pods from the SRC (Osborne 1986).

Another type of killer whale in the NE Pacific has only recently been identified. This type has been termed “offshore”. Offshores live in large family pods, feed on fish and squid, and are very vocal, much like resident type whales. They are genetically and acoustically distinct from both transient and resident groups, but little else is known of these whales (Felleman et al. 1991; Ford et al. 2000; Baird 2001).

Foraging

Killer whales are thought to be opportunistic hunters, able to adapt their foraging strategy and diet to the particular region within which they live (Table 1.1).

However, as previously mentioned, killer whales have formed more specialized groups that may coincide in distribution but differ in dietary preferences (Felleman et al. 1991; Nichol and Shackleton 1996).

Table 1.1. List of known killer whale prey species.

	PREY SPECIES		REFERENCE(S)
FIN FISH			
Cods	Arctic cod	<i>Arctogadus glacialis</i>	Perez 1990
	Atlantic Cod	<i>Gadus morhua</i>	Christensen 1982; Dahlheim 1988; Simila and Ugarte 1993; Dahlheim and Heyning 1999
	Atlantic pollock/Saithe	<i>Pollachius virens</i>	Simila 1996
	Pacific cod	<i>Gadus macrocephalus</i>	Gaskin 1982; Perez 1990
	Saffron cod	<i>Eleginus gracilis</i>	Perez 1990
	Sanddab	<i>Citharichthys spp.</i>	Ford et al. 1998
Flatfish	Arrowtooth flounder*	<i>Atheresthes stomias</i>	Visser 2000

Table 1.1 Continued

	Atlantic halibut*	<i>Hippoglossus hippoglossus</i>	Gaskin 1982; Block and Lockyer 1988; Visser 2000
	Curlfin sole	<i>Pleuronichthys decurrens</i>	Ford et al. 1998
	Dover sole	<i>Microstomus pacificus</i>	Ford et al. 1998
	English sole	<i>Parophrys vetulus</i>	Ford et al. 1998
	Greenland halibut*	<i>Reinhardtius hippoglossoides</i>	Block and Lockyer 1988; Visser 2000
	Other flatfish	<i>Pleuronectiformes</i>	Dahlheim 1988; Perez 1990; Dahlheim and Heyning 1999
	Pacific halibut*	<i>Hippocampus stenolepis</i>	Dahlheim 1988; Perez 1990; Ford et al. 1998; Visser 2000; Ford and Ellis 2005
	Rex sole	<i>Glyptocephalus zachirus</i>	Ford et al. 1998
	Rock sole	<i>Lepidopsetta bilineata</i>	Ford et al. 1998
	Starry flounder	<i>Platichthys stellatus</i>	Ford et al. 1998
Herrings	Atlantic herring*	<i>Clupea harengus harengus</i>	Christensen 1982; Perez 1990; Simila and Ugarte 1993; Simila et al. 1996
	Pacific herring	<i>Clupea pallasii</i>	Ford et al. 1998; Ford and Ellis 2005
	Sardine	<i>Sardinella spp.</i>	Dahlheim 1988
Lampreys	Pacific lamprey	<i>Lampetra tridentatus</i>	Ford et al. 1998
Mackerels, Tunas, Bonitos	Atka mackerel	<i>Pleurogrammus monopterygius</i>	Dahlheim 1988; Perez 1990
	Big-eye tuna*	<i>Thunnus obesus</i>	Visser 2000; Visser and Bonoccorso 2003
	Bonito	<i>Sarda spp.</i>	Dahlheim 1988
	Mackerel*	<i>Scomber spp.</i>	Block and Lockyer 1988; Dahlheim 1988; Simila 1996
	Northern Bluefin tuna	<i>Thunnus thynnus</i>	Secchi and Vaske 1998; de Stephanis 2004
	Tuna*	<i>Thunnus spp.</i>	Dahlheim 1988; Secchi and Vaske 1998; Dahlheim and Heyning 1999; Visser 2000
	Yellow-fin tuna*	<i>Thunnus albacares</i>	Visser 2000; Visser and Bonoccorso 2003
	Indian tuna*	No Latin name given	Visser 2000
Molas, Ocean Sunfishes	Ocean sunfish	<i>Mola mola</i>	Visser and Bonoccorso 2003

Table 1.1 Continued

Perch-likes	Searcher*	<i>Bathymaster signatus</i>	Visser 2000
	Pacific moonfish	<i>Selene peruviana</i>	Dahlheim 1988
	Antarctic butterfish*	<i>Hyperoglyphe antarctica</i>	Visser 2000
	Trevalla*	<i>Hyperoglyphe porosa</i>	Dahlheim 1988; Visser 2000
	Bluenose grouper*	<i>Hyperoglyphe antarctica</i>	Visser 2000
	Snoek*	<i>Thyrsites atun</i>	Ryce and Saayman 1987
	Indo-Pacific sailfish	<i>Istiophorus platypterus</i>	Visser and Bonaccorso 2003
	Patagonia toothfish*	<i>Dissostichus eleginoides</i>	Visser 2000
	Weakfish	<i>Cynoscion guatucupa</i>	Ott and Danilewicz 1998
	Swordfish*	<i>Xiphias gladius</i>	Secchi and Vaske 1998; Visser 2000
Salmonids	Chinook salmon	<i>Oncorhynchus tshawytscha</i>	Ford et al. 1998; Ford and Ellis 2005
	Chum salmon	<i>Oncorhynchus keta</i>	Ford et al. 1998; Ford and Ellis 2005
	Coho salmon	<i>Oncorhynchus kisutch</i>	Ford et al. 1998; Ford and Ellis 2005
	Pacific Salmon*	<i>Oncorhynchus spp.</i>	Dahlheim 1988; Perez 1990; Frost et al. 1992
	Pink salmon	<i>Oncorhynchus gorbuscha</i>	Ford et al. 1998; Ford and Ellis 2005
	Sockeye salmon	<i>Oncorhynchus nerka</i>	Ford et al. 1998; Ford and Ellis 2005
	Steelhead salmon	<i>Oncorhynchus mykiss</i>	Ford et al. 1998; Ford and Ellis 2005
Scorpionfishes and Flatheads	Sablefish/blackcod*	<i>Anoplopoma fimbria</i>	Dahlheim 1988; Ford et al. 1998
	Great sculpin	<i>Myoxocephalus polyacanthocephalus</i>	Ford et al. 1998
	Pacific staghorn sculpin	<i>Leptocottus armatus</i>	Ford et al. 1998
	Greenling	<i>Hexagrammos spp.</i>	Dahlheim 1988; Ford et al. 1998
	Lingcod	<i>Ophiodon elongatus</i>	Dahlheim 1988; Ford et al. 1998
	Yelloweye rockfish	<i>Sebastes ruberrimus</i>	Ford et al. 1998
	Quillback rockfish	<i>Sebastes maliger</i>	Ford and Ellis 2005
Smelts	Capelin	<i>Mallotus villosus</i>	Perez 1990
	Smelts	<i>Osmeridae</i>	Perez 1990
ELASMOBRANCHS			
Sharks and Rays	Blue shark	<i>Prionace glauca</i>	Fertl et al. 1996
	Carcharhinid shark	<i>Carcharhinus spp.</i>	Dahlheim 1988; Fertl et al. 1996

Table 1.1 Continued

	Galapagos shark	<i>Carcharhinus galapagensis</i>	Fertl et al. 1996
	Grey reef shark	<i>Carcharhinus amblyrhynchos</i>	Visser and Bonoccorso 2003
	Reef shark	<i>Carcharhinus spp.</i>	Fertl et al. 1996
	Basking shark	<i>Cetorhinus maximus</i>	Fertl et al. 1996
	Blue spotted ray	<i>Dasyatis kuhii</i>	Visser and Bonoccorso 2003
	Long-tailed sting ray	<i>Dasyatis thetidis</i>	Fertl et al. 1996
	Short-tailed sting ray	<i>Dasyatis brevicaudata</i>	Fertl et al. 1996
	Eagle ray	<i>Myliobatis brevicaudatus</i>	Gaskin 1982; Fertl et al. 1996; Ott and Danilewicz 1998
	Giant manta ray	<i>Manta hamiltoni</i>	Fertl et al. 1996
	Manta ray	<i>Manta sp.</i>	Fertl et al. 1996
	Manta ray	<i>Manta birostris</i>	Visser and Bonoccorso 2003
	Rays	<i>Myliobatis spp.</i>	Ott and Danilewicz 1998
	Skates	<i>Rajidae</i>	Perez 1990
	Whale shark	<i>Rhincodon typus</i>	Fertl et al. 1996
	Hammerhead shark	<i>Sphyrna spp.</i>	Fertl et al. 1996
	Scalloped hammerhead shark	<i>Sphyrna lewini</i>	Visser and Bonoccorso 2003
	Sharks	<i>Squalidae</i>	Perez 1990
	Pacific electric ray	<i>Torpedo californica</i>	Dahlheim 1988; Fertl et al. 1996
	School shark*	<i>Galeorhinus galeus</i>	Visser 2000
CEPHALOPODS			
	Octopus	<i>Octopoteuthis spp.</i>	Dahlheim 1988; Ott and Danilewicz 1998
	Tuberculate pelagic octopus	<i>Ocythoe tuberculata</i>	Ott and Danilewicz 1998
	Arrow squid	<i>Loligo plei</i>	Ott and Danilewicz 1998
	Atlantic bird squid	<i>Ornithoteuthis antillarum</i>	Ott and Danilewicz 1998
	Eight-armed squid	<i>Gonatopsis borealis</i>	Ford et al. 1998
	Giant squid	<i>Architeuthis spp.</i>	Ott and Danilewicz 1998
	Red flying squid	<i>Ommastrephes bartrami</i>	Ott and Danilewicz 1998
	Rugose hooked squid	<i>Moroteuthis robsoni</i>	Ott and Danilewicz 1998
	Squid	<i>Histioteuthis spp.</i>	Ott and Danilewicz 1998

Table 1.1 Continued

	Squid	<i>Unidentified</i>	Christensen 1982; Dahlheim 1988; Simila and Ugarte 1993; Ford et al. 1998; Dahlheim and Heyning 1999
BIRDS			
Anseriformes	Black brant goose	<i>Branta nigricans</i>	Williams et al. 1990
	Common eider duck	<i>Somateria molissima</i>	Block and Lockyer 1988; Simila and Ugarte 1993; Simila 1996
	Common merganser	<i>Mergus merganser</i>	Williams et al. 1990
	Surf Scoter	<i>Melanitta perspicillata</i>	Ford et al. 1998
	White-winged scoter	<i>Melanitta fusca</i>	Williams et al. 1990; Ford et al. 1998
Charadriiformes	Atlantic puffin	<i>Fratercula arctica</i>	Williams et al. 1990
	Common Murre	<i>Uria aalge</i>	Block and Lockyer 1988; Williams et al. 1990
	Little auk	<i>Alle alle</i>	Simila and Ugarte 1993; Simila 1996
	Marbled Murrelet	<i>Brachyramphus marmoratus</i>	Ford et al. 1998
	Rhinoceros Auklet	<i>Cerorhinca monocerata</i>	Ford et al. 1998
	Black-legged kittiwake	<i>Rissa tridactyla</i>	Block and Lockyer 1988; Williams et al. 1990
Pelecaniformes	Cormorant	<i>Phalacrocorax spp.</i>	Ryce and Saayman 1987; Jefferson et al. 1991; Ford et al. 1998
	Cape gannet	<i>Morus capensis</i>	Williams et al. 1990
Sphenisciformes	Emperor penguin	<i>Aptenodytes forsteri</i>	Williams et al. 1990
	Jackass penguin	<i>Spheniscus demersus</i>	Ryce and Saayman 1987; Williams et al. 1990
	King penguin	<i>Aptenodytes patagonicus</i>	Ryce and Saayman 1987; Williams et al. 1990; Guinet 1992
	Macaroni penguin	<i>Eudyptes chrysolophus</i>	Williams et al. 1990
	Penguins	<i>Eudyptes spp.</i>	Guinet 1992
	Rockhopper penguin	<i>Eudyptes chrysocome</i>	Williams et al. 1990
	Rockhopper penguin	<i>Eudyptes cristatus</i>	Ryce and Saayman 1987
Procellariiformes	Northern fulmar	<i>Fulmarus glacialis</i>	Simila and Ugarte 1993; Simila 1996
	White-chinned petrel	<i>Procellaria aequinoctialis</i>	Williams et al. 1990

Table 1.1 Continued

MAMMALS			
Artiodactyla	Deer	<i>Odocoileus spp.</i>	Dahlheim 1988; Jefferson et al. 1991
	Moose	<i>Alces alces</i>	Dahlheim and Heyning 1999
	Pig	<i>Sus spp.</i>	Jefferson et al. 1991
Carnivora	River otter	<i>Lontra canadensis</i>	Ford et al. 1998; Jefferson et al. 1991
	Sea otter	<i>Enhydra lutris</i>	Perez 1990; Jefferson et al. 1991; Estes et al. 1998
	Walrus	<i>Odobenus rosmarus</i>	Lowry 1987; Dahlheim 1988; Jefferson et al. 1991; Frost et al. 1992; Melnikov and Zagrebina 2005
Cetacea	Bowhead whale	<i>Balaena mysticetus</i>	Campbell et al. 1988; Dahlheim 1988; Perez 1990; Jefferson et al. 1991; Melnikov and Zagrebina 2005
	Northern Right whale	<i>Eubalaena glacialis</i>	Gaskin 1982; Jefferson et al. 1991
	Southern Right whale	<i>Eubalaena australis</i>	Jefferson et al. 1991
	Blue whale	<i>Balaenoptera musculus</i>	Gaskin 1982; Block and Lockyer 1988; Dahlheim 1988; Wenzel and Sears 1988; Jefferson et al. 1991
	Bryde's whale	<i>Balaenoptera edeni</i>	Silber et al. 1990; Jefferson et al. 1991
	Fin whale	<i>Balaenoptera physalus</i>	Block and Lockyer 1988; Jefferson et al. 1991
	Humpback whale	<i>Megaptera novaeangliae</i>	Whitehead and Glass 1985; Wenzel and Sears 1988; Jefferson et al. 1991; Florez-Gonzalez et al. 1994
	Minke whale	<i>Balaenoptera acutorostrata</i>	Gaskin 1982; Lowry et al. 1987; Dahlheim 1988; Wenzel and Sears 1988; Jefferson et al. 1991; Ford et al. 1998
	Sei whale	<i>Balaenoptera borealis</i>	Gaskin 1982; Dahlheim 1988; Jefferson et al. 1991
	Bottlenose dolphin	<i>Tursiops truncatus</i>	García-Godos 2004

Table 1.1 Continued

	Common dolphin	<i>Delphinus delphis</i>	Dahlheim 1988; Jefferson et al. 1991
	Dolphins	<i>Delphinidae</i>	Ryce and Saayman 1987; Jefferson et al. 1991
	Dusky dolphin	<i>Lagenorhynchus obscurus</i>	Jefferson et al. 1991
	Franciscana dolphin	<i>Pontoporia blainvillei</i>	Ott and Danilewicz 1998; César de Olivira Santos and Netto 2005
	Killer whale#	<i>Orcinus orca</i>	Dahlheim and Heyning 1999
	Long-finned Pilot whale	<i>Globicephala melas</i>	Block and Lockyer 1988; Jefferson et al. 1991
	Pacific white-sided dolphin	<i>Lagenorhynchus obliquidens</i>	Ford et al. 1998
	Short-finned Pilot whale	<i>Globicephala macrorhynchus</i>	Dahlheim 1988; García-Godos 2004
	Spinner dolphin	<i>Stenella longirostris</i>	Visser and Bonaccorso 2003
	Striped dolphin	<i>Stenella coeruleoalba</i>	Gaskin 1982; Dahlheim 1988
	Gray whale	<i>Eschrichtius robustus</i>	Lowry et al. 1987; Dahlheim 1988; Wenzel and Sears 1988; Jefferson et al. 1991; Ford et al. 1998; Melnikov and Zagrebin 2005
	Pygmy Sperm whale	<i>Kogia breviceps</i>	Jefferson et al. 1991
	Beluga whale	<i>Devinapterus leucas</i>	Lowry et al. 1987; Dahlheim 1988; Wenzel and Sears 1988; Jefferson et al. 1991; Frost et al. 1992; Melnikov and Zagrebin 2005
	Narwhal	<i>Monodon monoceros</i>	Campbell et al. 1988; Wenzel and Sears 1988; Jefferson et al. 1991
	Burmeister's porpoise	<i>Phocoena spinipinnis</i>	Ott and Danilewicz 1998
	Dall's porpoise	<i>Phocoenoides dalli</i>	Gaskin 1982; Dahlheim 1988; Wenzel and Sears 1988; Perez 1990; Jefferson et al. 1991; Ford et al. 1998
	Finless Porpoise	<i>Neophocaena phocaenoides</i>	Dahlheim 1988

Table 1.1 Continued

	Harbor porpoise	<i>Phocoena phocoena</i>	Block and Lockyer 1988; Dahlheim 1988; Perez 1990; Jefferson et al. 1991; Ford et al. 1998
	Sperm whale	<i>Physeter macrocephalus</i>	Ambom et al. 1987; Jefferson et al. 1991; Pitman and Chivers 1999; Visser and Bonaccorso 2003; García-Godos 2004
	Baird's Beaked whale	<i>Berardius bairdii</i>	Dahlheim 1988; Perez 1990
	Cuvier's Beaked whale	<i>Ziphius cavirostris</i>	Dahlheim 1988; Jefferson et al. 1991
	Northern Bottlenose whale	<i>Hyperoodon ampullatus</i>	Jefferson et al. 1991; Simila and Urgarte 1993
Pinnipedia	California sea lion	<i>Zalophus californianus</i>	Gaskin 1982; Dahlheim 1988; Jefferson et al. 1991; Ford et al. 1998
	Cape fur seal	<i>Arctocephalus pusillus</i>	Williams et al. 1990
	South American Fur Seal	<i>Arctocephalus australis</i>	García-Godos 2004
	South American sea lion	<i>Otaria flavescens</i>	Lopez and Lopez 1985; Jefferson et al. 1991
	Steller sea lion	<i>Eumetopias jubatus</i>	Gaskin 1982; Dahlheim 1988; Perez 1990; Jefferson et al. 1991; Frost et al. 1992; Ford et al. 1998; Melnikov and Zagrebin 2005
	Bearded seal	<i>Erignathus barbatus</i>	Lowry et al. 1987; Dahlheim 1988; Perez 1990; Jefferson et al. 1991
	Crabeater seal	<i>Lobodon carcinophaga</i>	Jefferson et al. 1991
	Gray seal	<i>Halichoerus grypus</i>	Gaskin 1982; Block and Lockyer 1988; Jefferson et al. 1991
	Harbor seal	<i>Phoca vitulina</i>	Dahlheim 1988; Jefferson et al. 1991; Frost et al. 1992; Ford et al. 1998
	Harp seal	<i>Phoca groenlandica</i>	Jefferson et al. 1991
	Hooded seal	<i>Cystophora cristata</i>	Jefferson et al. 1991
	Leopard seal	<i>Hydrurga leptonyx</i>	Jefferson et al. 1991
	Northern Elephant seal	<i>Mirounga angustirostris</i>	Gaskin 1982; Dahlheim 1988; Jefferson et al. 1991; Ford et al. 1998

Table 1.1 Continued

	Northern fur seal	<i>Callorhinus ursinus</i>	Dahlheim 1988; Perez 1990; Jefferson et al. 1991
	Ribbon seal	<i>Phoca fasciata</i>	Lowry et al. 1987
	Ringed seal	<i>Phoca hispida</i>	Lowry et al. 1987; Dahlheim 1988; Perez 1990; Jefferson et al. 1991; Melnikov and Zagrebin 2005
	Seals	<i>Phocidae</i>	Lowry et al. 1987; Ryce and Saayman 1987
	Southern Elephant seal	<i>Mirounga leonina</i>	Lopez and Lopez 1985; Jefferson et al. 1991; Guinet 1992
	Spotted seal	<i>Phoca largha</i>	Lowry 1987
	Weddell seal	<i>Leptonychotes weddellii</i>	Jefferson et al. 1991
Sirenia	Dugong	<i>Dugong dugon</i>	Jefferson et al. 1991
OTHER			
	Salps#	<i>Iasis zonaria</i>	Ott and Danilewicz 1998
	Sea turtles	<i>Cheloniidae</i>	Secchi and Vaske 1998; Jefferson et al. 1991
	Leatherback sea turtle#	<i>Dermochelys coriacea</i>	Caldwell and Caldwell 1969
	Jellyfish		Simila 1996

#From stomach sample/ could be secondary prey

*species depredated from fishing activities

The foraging behavior of killer whales is highly dependent on prey preference and geographic location (Felleman et al. 1991). Unique foraging behaviors have been documented off Norway, the Crozet Islands in the Southern Indian Ocean, New Zealand, Antarctica, Patagonia, and the NE Pacific (Lopez and Lopez 1985; Similä and Ugarte 1993; Guinet and Bouvier 1995; Dahlheim and Heyning 1999; Saulitis et al. 2000; Nottestad et al. 2002). In the inland marine waters of Washington State and British Columbia, fish eating pods of killer whales appear to use high relief bathymetry to aid in the concentration and capture of salmon and possibly other species (Heimlick-Boran 1988; Felleman et al. 1991). The whales search for food cooperatively by foraging in spread-out subgroups, which serves to increase their search area or “school window”. Prey capture however, is carried out individually

(Heimlick-Boran 1988). Percussive behavior, which is slapping the surface of the water with pectoral or dorsal fin(s), flukes, or the entire body, has been suggested to be a form of cooperative herding and has been observed to be characteristic of subgroups that contain calves (Osborne 1986).

Prey Associations

Every predator must invariably be closely tied to its prey resources. In some cases predators preferentially hunt preferred prey regardless of the abundance of that prey resource or the abundance of other prey in the same geographic space and time (Hayes and Harestad 2000; van Baalen et al. 2001). More commonly observed are foraging strategies that exploit whatever prey is available for the highest possible energy gained in exchange for the lowest possible energy cost of search, capture, handling, and consumption. This entails either switching from species to species as prey populations fluctuate, or preying on multiple species in an opportunistic fashion (O'Donoghue et al. 1998; Salamolard et al. 2000; van Baalen et al. 2001).

There have been many studies documenting spatial correlations between predator and prey, most of which have focused on terrestrial animals. If prey preference has a direct link to most efficient energy gain, then it must also have a direct relationship to the abundance and distribution of available prey. A predator's spatial and temporal distribution, therefore, must overlap with the spatial and temporal distribution of adequate prey. This spatial and temporal correlation is also referred to as the aggregative response. Aggregative responses are influenced by the tendencies of predators to congregate in areas of high prey densities, the tendencies of prey to avoid areas with high risk of predation, and the proportion of predators foraging on a specific prey species (Fauchald and Erikstad. 2002).

Patterns of spatial distribution of social carnivores are driven by the availability of limited resources, in particular food. These food-driven patterns thus impact density and population dynamics of predator populations (Valenzuela and Macdonald 2002). Specifically, switching among habitat types may occur in response to changes in the relative density of prey, which determines the relative profitability of foraging in different habitats (O'Donoghue et al. 1998). At large scales, it would be expected that predators occupy the same general areas as their prey, forming positive associations. At smaller scales, the association would be expected to be determined by the predator's search efficiency relative to the escape abilities of the prey (Fauchald and Erikstad 2002).

The dynamics of prey availability have been seen to affect predators in a variety of ways, such as distribution patterns and social hierarchies. Most importantly, predator abundances are directly related to prey abundances. This is seen in a study by Patterson and Messier (2001) who tested predictions that reproductive success, incidence of delayed dispersal, and coyote and wolf densities are correlated positively with prey density. Inversely, they tested whether the incidence of extraterritorial excursions are correlated negatively with prey density. They found that the density of wolves and the abundance of coyotes were closely linked to prey abundance, generally supporting their prediction that differences in prey availability would exert an influence on the social ecology of a behaviorally plastic carnivore. In a different study in the Yukon, coyote abundance increased 600% in only 3 years in response to increasing hare numbers, but the subsequent coyote decline after a crash in hare numbers was equally rapid and severe. Others have also concluded that the distribution and abundance of prey represent the most important factors influencing spatial dynamics and social structure for most medium to large sized carnivores (Valenzuela and Macdonald 2002). Carroll et al.

(2003) found that prey density explains up to 72% of the variation in wolf density in areas where human caused mortality of wolves is low.

Predator-prey relationships are not as well documented in the marine environment, but examples do exist that demonstrate associations between predators and their prey. For instance, fluctuations and abundance of preferred prey has been seen to affect seabird abundance, demography, activity and foraging strategies (Fauchald and Erikstad 2002). Inter-annual prevalence of rockfish in murre (*Uria aalge*) diet correlated closely with their availability in National Marine Fishery Service (NMFS) trawls (Ainley et al. 1996). Likewise, high concentrations of sea lions in the northern Gulf of California have related to high abundances of pelagic prey species such as Pacific sardine (*Sardinops caeruleus*), Pacific mackerel (*Scomber japonicus*), Pacific thread herring (*Opisthonema libertate*), and anchoveta (*Cetengraulis mysticetus*). The availability and abundance of the prey species was found to influence sea lion diet (García-Rodríguez and Aurióles-Gamboa 2004). In Alaska, Steller sea lions (*Eumetopias jubatus*) are most abundant near the mouth of the Copper River during the late spring and early summer when sockeye salmon (*Oncorhynchus nerka*) are present in high numbers. Later in the season, when coho salmon (*O. kisutch*) are the most abundant prey species, Steller sea lions have largely left the area in search of other prey and are replaced by a higher presence of harbor seals (*Phoca vitulina*) (Hobson et al. 1997). Off the northeastern coast of Scotland, harbor seals showed an aggregative response to freshwater and estuarine areas through which migrating Atlantic salmon (*Salmo salar*) pass, with a peak in both sightings of seals and presence of salmon in July (Middlemas et al. 2006).

The resource dispersion hypothesis predicts that where resources are patchily dispersed, home-range size is positively correlated with distance between patches (Valenzuela and Macdonald 2002), which again links space use to prey availability.

Sea otters (*Enhydra lutris*) in California have the opportunity to emigrate when prey abundances decrease, but in past decades Aleutian Island sea otters have done so only rarely due to large expanses of deep water between islands and competition with other otters at destination islands associated with populations near carrying capacity. Therefore, Alaskan otters may be less selective and more opportunistic in their choice of prey (Ostfeld 1982). For most species, particularly marine, it is not well known what factors, such as interactions with con-specifics, influence the ability to expand foraging areas. This study will investigate whether the SRC appear to expand areas of use during periods of apparently lower prey abundance.

Spatial Associations of Killer Whales and their Known Prey

Killer whales around the globe have displayed temporal and spatial correlations with their preferred prey species. In the South Indian Ocean, killer whale occurrence can be correlated with that of southern elephant seals (*Mirounga leonina*) (Pistorius et al. 2002) and penguins (*Eudyptes* spp.) (Ryce and Saayman 1987; Williams et al. 1990; Guinet 1992; Ballard and Ainley 2005). Killer whales have also been spatially correlated with northern elephant seals (*Mirounga angustirostris*) at San Benitos Island, California, and herring (*Clupea harengus*) in the Northeast Atlantic (Heimlich-Boran 1988). Another study found that 17 whales in northern Argentina had a strong association with the distribution (breeding cycle) of South American sea lions (*Otaria flavescens*) and southern elephant seals (Iñíguez 2001). The occurrence of transient whales in southern British Columbia coincides with the time when harbor seal pups are weaned, and the presence of

residents in the same area appears to be closely tied with peak abundance of various species of salmon (Heimlich-Boran 1988; Baird 2001).

In a study of the NRC, Nichol and Shackleton (1996) used sighting and acoustic data to calculate the average number of whales present in the Johnstone Strait study area each month between 1985 and 1989. They compared this information with estimates of sockeye, pink (*O. gorbuscha*), and chum salmon (*O. keta*) abundance calculated from commercial catch and spawning escapement data obtained from the Department of Fisheries and Oceans Canada (DFO). Abundance estimates of chinook (*O. tshawytscha*) and coho salmon were not available and were not included in the analysis. The study found that individual pods associated with different runs of salmon. Pods A1, A5, and C1 were positively correlated with sockeye and pink salmon; pods A4, D1, and H1 were associated with sockeye only; and pod G1 associated with chum only. Despite the relatively high abundance of salmon in the Johnstone Strait area between July and October, only half of the NRC pods appeared to be present during the period of highest salmon abundance (Nichol and Shackleton 1996).

The presence of prey does not necessarily equate to a predator foraging on that prey (Ryce and Saayman 1987). Scale samples have been taken near foraging killer whales in Prince William Sound to investigate prey preferences. Of 63 scale samples collected over a five year period (1991-1992, 1994-1996), 94% were from coho salmon, with the remaining 6% consisting of chinook and chum. Thirty-eight predation events were also observed during the study period. Thirty-six of these involved the capture of salmon, one of herring, and one of halibut (*Hippoglossus stenolepis*). Despite the presence of large runs of pink and sockeye salmon in

Prince William Sound, no predation on either species was documented (Saulitis et al. 2000).

Ford et al. (1998) collected scale and other tissue samples near foraging NRC and SRC whales over a twenty year period. Ninety-six percent of the scales sampled were from salmonids, the majority of which were chinook. Observed kills and harassments were also dominated by salmonid prey, most of which were chinook. These observations were strengthened by more recent analysis that determined a correlation between trends in survival patterns of SRC and chinook salmon abundance in British Columbia (Ford et al. 2005).

Heimlich-Boran (1986) compared the distribution and frequency of SRC sightings with sports fishery catch data recorded by the Washington Department of Fish and Wildlife (WDFW) from 1976-1978. It was concluded that when there was an increase in the number of salmon, there was also an increase in the frequency of killer whale sightings. The correlations were particularly significant for sightings of SRC whales in the southern portion of Puget Sound.

The Southern Resident Community

SRC of killer whales reside mainly in the waters off of British Columbia, Canada and Washington State, US ranging as far north as the Queen Charlotte Islands and as far south as Monterey Bay, California (Ford et al. 2005) (Figure 1.1). The summer range of the SRC centers around the San Juan and Gulf Island Archipelagos, while the winter range is uncertain (Osborne 1999). The SRC consists of three associated family pods named “J”, “K”, and “L”. J pod is the most frequently observed of the resident pods, being encountered at least once in every month since the inception of the population survey in 1974. K pod is observed less

frequently than J pod, but has still been encountered in all months of the year. L pod is the largest of the three pods and is often divided into smaller subgroups, which are kinship units. L pod is seen roughly as often as K pod (Heimlich-Boran 1986).

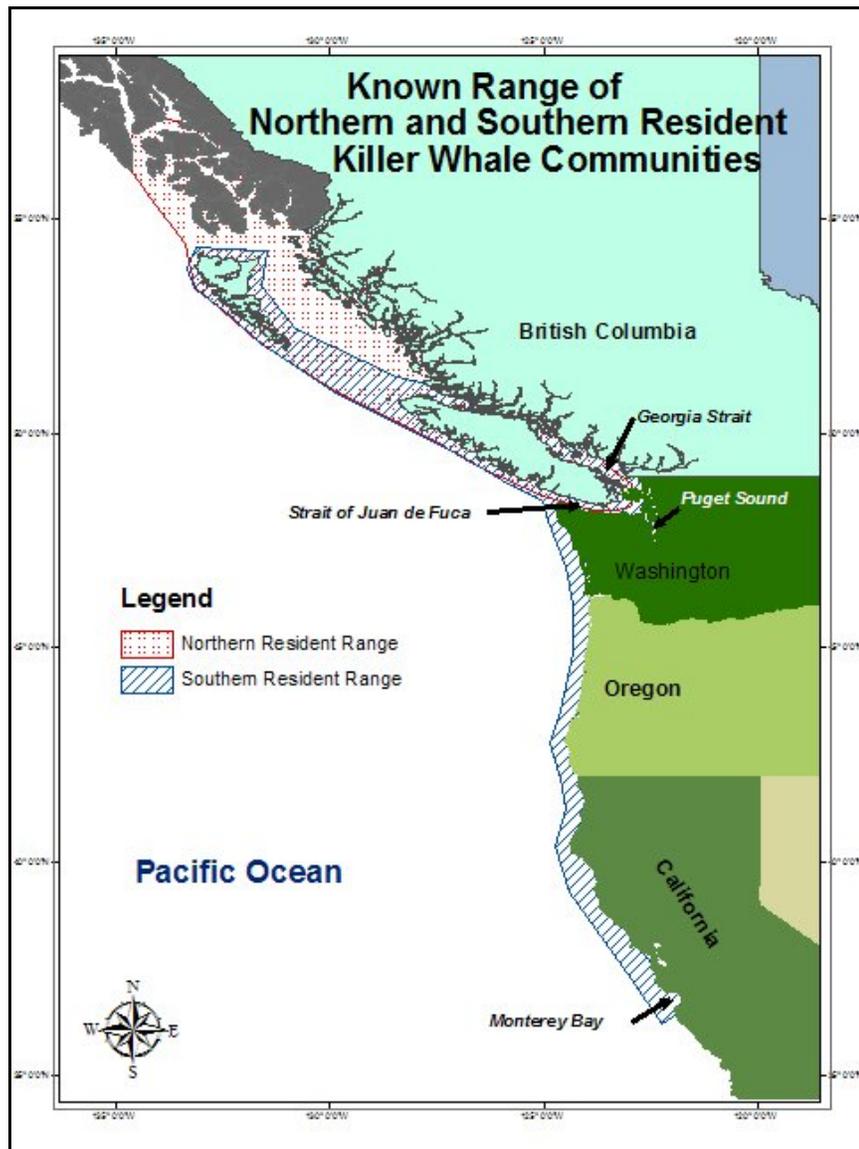


Figure 1.1. Known range of northern and southern resident killer whale communities. Note: offshore distribution is unknown.

Because they occupy relatively protected inland waters in the vicinities of major metropolitan centers, and are individually recognizable through scars, nicks, scratches and pigmentation patterns on their bodies, SRC whales are perhaps the most closely monitored and best known cetacean population in the world (Osborne 1986; Ford et al. 2000; Baird 2001).

The population of the SRC has fluctuated over the 30 plus years of observation (Figure 1.2). The SRC consisted of 70 whales in 1974 when an annual census began (Bain and Balcomb 1999). By the mid 1990s the population had increased to 98 whales. By 2001 the population decreased to 80 individuals, representing a nearly 20% decline (Grant and Ross 2002). The population decline in the late 1990s invoked concern for the future of this genetically and acoustically distinct community and led the Canadian government to list the SRC as “endangered” by the Committee on the Status of Endangered Wildlife in Canada and for the United States government to list the SRC as “depleted” under the Marine Mammal Protection Act (Baird 2001; Krahn et al. 2002) and “Endangered” under the ESA in December 2005 (NMFS 2005). From 2001 to 2005 the population increased to 89 individuals. This recent increase is likely attributed to more favorable ocean conditions and higher survival of salmonid populations in recent years off the coasts of Washington and British Columbia (PSARC 2003). However, the fluctuations in population could potentially be attributed to natural variation. Whatever the reason, the SRC remains an extremely small and isolated population and is therefore vulnerable to extinction.

Potential Threats to the SRC

There are several potential factors driving SRC population dynamics. Prior removal of individuals, contaminants, disease, anthropogenic disturbance, climate change,

and declining quality and quantity of salmon prey are repeatedly cited as the most likely threats (Bain and Balcomb 1999; Ross et al. 2000; Baird 2001; Erbe 2002; Williams et al. 2002). These factors will briefly be outlined, as there is overlap and interaction between all possible threats to the SRC.

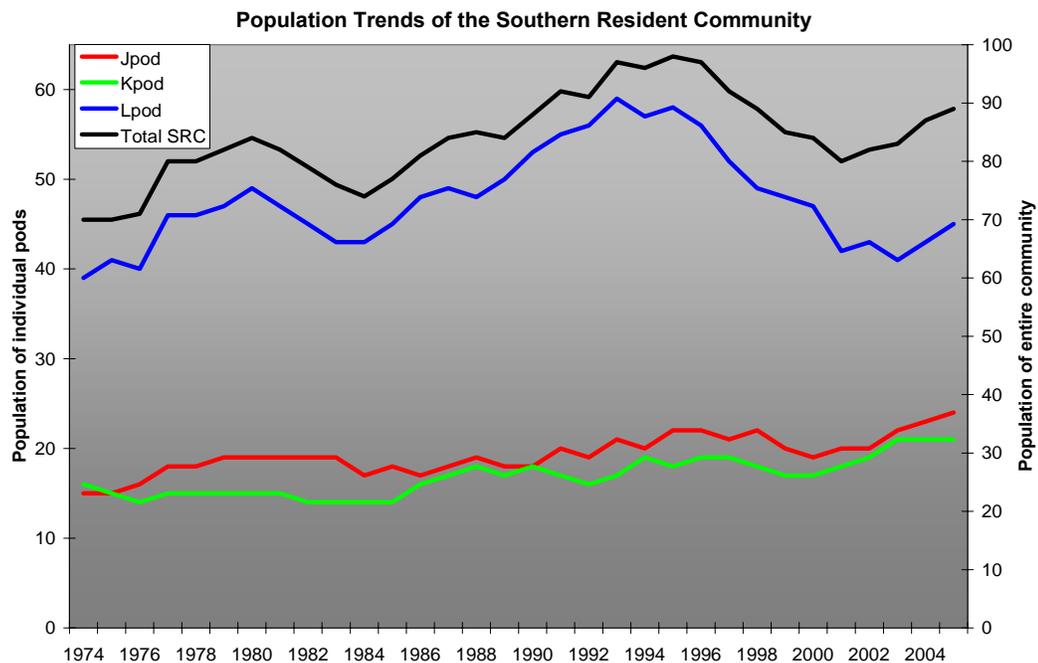


Figure 1.2. Total SRC population trend (right vertical scale) plotted with population trends of individual pods (left vertical scale). Data courtesy of the Center for Whale Research, Friday Harbor, WA.

Live-Harvest

Prior to the Marine Mammal Protection Act of 1972, SRC whales were harvested in the live-capture fishery of the 1960s and 1970s for the aquarium trade. The removal of 48 whales during this era likely had a detrimental affect on the reproductive and mortality rates of the population in subsequent years (Matkin et al. 1994; Baird 2001). More specifically, the change in population age structure caused by the removal of a large proportion of calves negatively affected

reproductive rates in the following decades. By the early 1980s females born prior to the capture era were nearing the end of their reproductive years, and females born after the capture era were just reaching reproductive age (Bain and Balcomb 1999). This lack of females at the height of their reproductive potential likely influenced the 11% population decline experienced in the early 1980s. However, by the mid 1990s the age structure of the SRC was more balanced and it is unlikely that lasting consequences of whale removals significantly contributed to the decline experienced in the latter 1990s.

Contaminants

SRC whales are exposed to both global and local sources of contaminants. This population of whales spends a significant amount of time in industrialized near-shore areas, where they are exposed to toxic effluent (Baird 2001; Ross 2006). The long-range air transport of polychlorinated biphenyls (PCBs), dichlorodiphenyl-trichloroethane (DDT), and other contaminants serve as a more global source of toxic exposure for the whales (Hayteas and Duffield 2000; Ross et al. 2000; Ylitalo et al. 2001). The contaminants bio-accumulate up the food-chain, becoming concentrated in high trophic level species (Baird 2001; Grant and Ross 2002; Rayne et al. 2004). Killer whales are particularly vulnerable to accumulating persistent organic pollutants (POPs) such as PCBs and DDT because of their high trophic level, long life span, extensive lipid reserves and relative inability to eliminate many of the compounds (Gaskin 1982; Grant and Ross 2002). PCB concentrations in the tissues of SRC whales are among the highest of any marine mammal on the planet (Ross et al. 2000; Gaydos et al. 2004). While the manufacture of PCBs and DDT has been banned in North America, new compounds have been developed comparable in toxicity whose production has increased in recent years. One such class of compounds is polybrominated diphenyl

ethers (PBDEs) which are used as a flame retardant. Increasing concentrations of PBDEs have been detected in the tissues of SRC whales, and may pose a threat comparable to other POPs (Rayne et al. 2004; Ross 2006). In other marine mammals, POPs and PBDEs have been seen to cause reproductive impairment, reduced plasma retinol and thyroid hormone levels, impaired immune function, skeletal abnormalities, physiological and organ disorders, cancer and endocrine disruption, as well as a disruption of vitamin A metabolism (Hayteas and Duffield 2000; Ross et al. 2000; Ylitalo et al. 2001; Grant and Ross 2002; Borrell et al. 2004; Wolkers et al. 2004; Ross 2006).

Disease

Contaminant concentrations in the tissues of marine mammals have been suggested to have a direct association with mortality from disease and may play a role in the decline or lack of recovery of threatened and endangered wildlife populations (Gayado et al. 2004). A mass mortality event of Baltic seals caused by morbillivirus infections has been suspected of being linked with high concentrations of immuno-suppressing pollutants (Ciesielski et al. 2004). Other marine mammal epizootics have also been linked with high concentrations of PCBs and other contaminants (Borrell et al. 2004). An example is a morbillivirus induced mass mortality event of 1987-1988 involving bottlenose dolphins along the US Atlantic coast. The animals had high levels of POPs, and as a result had compromised immune systems, which is hypothesized to have been an important contributing factor in the mortality event (Hansen et al. 2004). High levels of POPs in the SRC increase host susceptibility to infectious diseases, and pathogens that are not documented to cause severe health problems in other odontocete species may be causing problems for this population. However, due to limited knowledge

of infectious disease in wild killer whales, it is difficult to predict what role disease might have in contributing to a decline or suppression of recovery of the SRC. Because of their small population size and gregarious social nature, the introduction of a highly virulent and transmissible pathogen has the “potential to catastrophically affect the long-term viability of the population” (Gayado et al. 2004).

Vessel Noise/ Disturbance

Vessel activity and noise from commercial shipping, fishing, whale watching, and recreational boating have been increasing in the area around the San Juan and Gulf Island Archipelagos, the core summer habitat of the SRC (Baird 2001). The average number of boats traveling with SRC whales increased roughly five-fold from 1990-2000, the same period as the latest declining trend in whale population (Foote et al. 2004). The global commercial whale watching industry is worth a minimum of US\$1 billion annually and is not likely to decrease in the foreseeable future (Constantine et al. 2004). Killer whales have the most sensitive hearing reported of any odontocete (Morton and Symonds 2002). The effects of vessel traffic and noise are thought to include avoidance behavior, habitat displacement, masking of navigational and communication clicks and calls, and short and long-term hearing impairment or loss (Bain and Dahlheim 1994; Erbe 2002; Morton and Symonds 2002). Because killer whales rely heavily on their acoustic ability to navigate, forage, and communicate, noise capable of masking calls or damage hearing may have long-term detrimental effects on a whales’ ability to reproduce and survive (Erbe 2002; Williams et al. 2002).

Climate Change

Warming water temperatures and decreased productivity have direct effects on salmon survival which in turn have been linked to survival rates of the SRC (Ford et al. 2005). Biological responses to climate change include fluctuating phytoplankton abundance, changing zooplankton production, and shifting migration patterns and biomass of marine species (Hirons et al. 2001). The fluctuations in fish abundance as a result of large-scale climate changes have been observed to be both large-scale and regional (McFarlane et al. 2000). Beginning in the early 1990s marine survival of coho salmon declined by 40-60% in the Puget Sound-Georgia Strait Basin and off the coasts of Washington, Oregon, and California. This decline in survival coincided with dramatic changes in April flows from the Fraser River and the Aleutian Low Pressure Index, both indicators of climate change (Beamish et al. 2000). This trend has been seen with other salmon species as well. Climate indices indicate a major regime shift occurred in 1977, after which salmon catches in British Columbia increased from the low levels sustained from the mid 1950s to the mid 1970s to historically high levels through the early 1990s. Another climate regime shift in the late 1980's resulted in decreased marine survival of several commercially important fish species, including salmon. By the mid-1990s salmon catches hit record low levels (McFarlane et al. 2000). Salmon survival, and therefore abundance, appears to be directly affected by recent patterns of ocean climate. Therefore, changes in climate are also likely to affect prey availability for the SRC.

Declining Quantity and Quality of Wild Salmon

Despite, or partially due to, large hatchery additions, stocks of wild salmon, particularly coho and chinook, continue to decline (Beamish et al. 1997). Since the early 1900s, developments such as hydropower, fishing, logging, mining, agriculture, hatchery production, urban growth (Nehlsen et al. 1991), and climate

change have caused extensive losses in salmon and steelhead populations and their habitats (Noakes et al. 2000). The Columbia River is just one example of a region-wide phenomenon. While about 75% of Columbia River fish are of hatchery origin, natural production in the Columbia Basin fell to 4-7% of pre-development levels by the early 1990s (Nehlsen et al. 1991). Not only have wild salmon stocks experienced declines in abundance, but the size and age class structure of both wild and hatchery fish have undergone relatively rapid change in recent decades.

Salmon are generally smaller in size today than they were 50 years ago (Ricker 1981; Cox and Hinch 1997). Forty-five of the 47 populations of Pacific salmon are decreasing in average body size (Bigler et al. 1996). From 1951-1975 the average weight of adult pink, coho, and chinook caught in British Columbia decreased by 5-25%. Similar declines have been observed for chum in Alaska and Asian waters, and for sockeye in the Fraser River (Cox and Hinch 1997). The decreasing size can be explained by density dependent growth and selection of larger, older fish by selective fisheries, leaving the younger, smaller fish to breed (Bigler et al. 1996).

As mean sizes of Pacific salmon have decreased, so too have mean ages at maturity. The troll fishery (targeting chinook and coho) in some areas takes both maturing fish and those that will not mature in the current year. Older ocean-type chinook salmon are exposed to harvest for a longer period of time than faster growing, younger fish because of relatively near-shore, local distributions in relation to their natal rivers (Healey 1991; Brodeur et al. 2004). As fishing effort increases, fewer fish survive to be caught at older ages. The age of maturity is negatively correlated with rate of growth (Ricker 1981). As hatcheries have selected for faster growth, they have also selected for lower age at maturity, which in turn has fostered the production of smaller, younger returning spawners (Larson

et al. 2004). Commercial troll and ocean sport fisheries select for earlier age at maturity in chinook, which has caused a decline of the mean age of spawners of at least 0.7 years since the first part of the 20th century in the Klamath and Sacramento Rivers (Reisenbichler 1997). The mean age of Kuskokwim River chinook has decreased, while that of Yukon River chinook has remained unchanged. In British Columbia the average age of chinook has decreased (Bigler et al. 1996). Genetically based changes become more rapid with decreased mean generation time, which has been exemplified by stocks of chinook up and down the west coast of North America (Ricker 1981).

Environmental conditions of hatchery rearing have also been implicated in above normal occurrence of precocious male parr (11-80% compared to 1% in wild stocks) (Larsen et al. 2004). A balanced range of ages of maturity increases the stability and greater total production of salmon over several decades, particularly for populations subject to very high mortality. Therefore the decreased existence of older fish will likely have a detrimental effect on populations of Pacific salmon into the future (Reisenbichler and McIntyre 1977). This in turn could have a detrimental effect on the SRC, due to the decreased availability of salmon, particularly if a higher proportion of the stocks remain in freshwater, maturing as precocious parr, and are therefore unavailable to foraging whales.

This Study

Sufficient quality and quantity of available prey is a basic survival need for any population. Populations of Steller sea lions, northern fur seals, and harbor seals have declined for more than two decades, particularly in the western Gulf of Alaska and the Bering Sea. The declines are speculated to be driven in part by food limitation, possibly due to the decline in clupeid fishes and increase in gadid fishes.

The large-scale declines seen in the Bering Sea and Gulf of Alaska pinnipeds are particularly alarming because they seem to have occurred over a relatively short period of time. During the same period, some populations of the same species have remained stable or have even increased in other parts of the North Pacific (Hirons et al. 2001). The decline of the SRC from 1996 to 2001 was more severe than declines in other killer whale populations, such as the NRC. This would infer that the SRC was exposed for a time to conditions that were more acutely unfavorable than those affecting the geographically adjacent NRC (Ford et al. 2005). As proper nutrition is a primary need of any species, understanding SRC prey associations is a crucial first step toward developing population models suitable for application to conservation and management issues.

This thesis represents a pioneering effort to link the spatially explicit movement behavior of the SRC with spatially distributed estimates of salmon abundance. The thesis addresses issues of representation, characterization, and modeling of individual pod movement (J, K, and L) by statistical week from 1991 through 2001, and reports the results of a series of spatial pattern analytical approaches used to investigate variations in shape and size of pod movement behavior between and within salmon management areas. The movement behavior of each pod of the SRC is modeled as “space use polygons” by statistical week. The shape of “space used” is then spatially intersected with salmon management areas which contained attributes of weighted fish catch for each statistical week. In this way, quantitative pattern metrics are derived for use areas as a function of an external parameter, in this case, fish density.

Four researchable questions and their associated testable hypotheses related to shape metrics of pod space use and the distribution of salmon abundance estimates are:

- 1) During periods of population decline are the movement behaviors of the pods different from those behaviors observed during periods of population increase? It was hypothesized that the mean total area of each space use polygon and the complexity of that shape (measured by shape index) are higher in the latter 1990s (when the population was decreasing) than in the early 1990s (when the population was increasing).

As a corollary, I hypothesized that:

L pod overall uses significantly more space and has higher movement shape complexities than either J or K pods because the decline of L pod during the latter 1990s was greater than the decline observed in the other pods.

- 2) Are the movement behaviors of the pods different during periods of relatively lower and higher salmon abundance? It was hypothesized that years of relatively high salmon abundance, measured as low, medium, and high total run-size, would correspond to years of lower space use and lower movement complexity on the part of the whales. This was expected to be particularly evident during years of high chinook abundance.
- 3) Do weekly space use polygons have higher complexity, or are they larger in size during the late spring and early summer season than those at the end of

the summer and fall? It was hypothesized that space use areas would be larger in size and have higher complexity values early in a year because salmon are present in the region in higher numbers during the late summer and early fall than in other seasons of the year. Therefore it was expected that the pods would exhibit more searching behavior in the first half of the year, exploring the region for potential food patches. It was also expected that during periods of higher salmon abundance, the pods would limit their movement patterns to exploit more concentrated prey.

- 4) Are whales distributed in relation to salmon abundance, measured as catch density and catch per unit effort? It was hypothesized that whales are distributed within the salmon management areas of highest salmon catch density more often than would be expected by chance. It was also hypothesized that the whales spend a higher proportion of time in management areas of high catch per unit effort than low catch per unit effort.

This study also tested the relationship between the SRC at the population and pod levels to different species of salmon at various spatial scales and temporal lag periods. Four questions and their researchable hypotheses related to population trends are as follows:

- 1) Are the population trends of the SRC more frequently correlated with population trends of certain species of salmon more than others? It was hypothesized that the strongest correlations between the SRC and salmon using escapement and total run size estimates would be with chinook and

chum based on previous prey studies of North Pacific resident type killer whales.

- 2) Do the population trends of the different SRC pods exhibit different correlation patterns with population trends of salmon? It was predicted that L pod would exhibit correlation patterns that are different from J & K pods.
- 3) Are there differences in correlation frequency among the spawning regions? The third hypothesis predicted that positive correlation between the whales and salmon would not occur with the same frequency across all spawning regions analyzed.
- 4) Is there a time lag duration that produces the highest number of significantly positive correlations between the whale and salmon population trends? It was hypothesized that a time lag period of one year would produce the most frequent correlations between whale and salmon population trends due to a predicted lag in either mortality or birth rate.

Chapter 2 will discuss the methods used to represent the observational whale data in a spatial model to produce space use shapes. The amalgamation of various data sources, data gaps, and caveats will be described. The analysis of the spatial data as well as the metrics used to quantify the space use shapes will be explained. Results of the analysis of movement shape area and complexity over time will be presented. Movement area and shape in relation to seasonal scale will be discussed as well as results of whale presence in management areas of highest salmon abundance.

Chapter 3 will describe the methods used to test correlations between whale population trends and salmon population trends. Results from the statistical analysis will be presented and discussed in relation to the hypotheses previously given regarding population trend relationships.

CHAPTER 2: SPATIALLY EXPLICIT DESCRIPTION OF THE TEMPORAL BEHAVIOR OF WHALE MOVEMENT IN RELATION TO PREY AVAILABILITY

INTRODUCTION

The spatial distribution and characterization of the spatial structure of animal population interactions to changes in their environment has become increasingly important in marine ecosystem research (Monestiez et al. 2006). Insight into behavioral choices in the use of space is vital to the study of populations and individuals at many levels and for many disciplines, including population biology, conservation biology, and behavioral ecology (Whitehead 2001). A critical issue in these types of studies is the consideration of spatial and temporal patterns of both predator and prey when characterizing trophic relationships. The spatial dynamics and social structure of most medium to large-sized carnivores is most significantly influenced by the distribution and abundance of preferred prey (Patterson and Messier 2001). Predators can influence encounter rates with preferred prey species by modifying their own searching behavior in response to the distribution and abundance of prey. However, the spatial distributions of fish are particularly poorly known at small temporal and spatial scales, creating a unique challenge in spatial modeling to support investigations of piscivorous marine predator movements in relation to prey densities (Bailey and Thompson 2006). This study describes a spatially explicit characterization of whale movement behavior as a necessary step in the investigation of spatial association between whales and their known prey.

The Southern Resident Community (SRC) of killer whales has been studied in the inland marine waters of Washington State (WA) and British Columbia (BC) since the mid-1970's (Balcomb and Bigg 1986). The SRC is comprised of three

matrilineal pods designated “J”, “K”, and “L” (Ford et al. 2000) totaling 89 whales in 2005 (Balcomb et al. unpublished data). The population has fluctuated since the inception of the annual census, but a declining trend of approximately 20% from 1996 to 2001 raised concerns for the small, genetically and behaviorally isolated population and led to determination of an “endangered” status under Canadian federal law, Washington State law, and US federal law (Heimlich-Boran 1988; Ford 1991; Baird 2001; Hoelzel et al. 2002; Krahn et al. 2002; Wiles 2004; NMFS 2005). Several factors have been cited as potentially contributing to this decline, insufficient quantity or quality of prey being one (Baird 2001; Krahn et al. 2002; Wiles 2004). The SRC appears to specialize on salmonid prey, preferentially selecting for chinook salmon (*Onhorhynchus tshawytscha*) (Ford et al. 1998; Ford and Ellis 2005). Many stocks of salmon in the Puget Sound region have declined in both abundance and body size in recent decades (Bledsoe et al. 1989; Nehlsen et al. 1991; Bigler et al. 1996), potentially creating a food limitation for the southern resident whale population.

The goal of this study was to introduce a method of modeling the space use of the SRC over a range of temporal scales, and to use quantitative metrics to describe the shape and location of these use areas to characterize the relationship between whale movement and trends in prey availability. Whale sighting data obtained from The Whale Museum (TWM, Friday Harbor, Washington USA) are used in conjunction with commercial salmon catch data from 1991 to 2001, a time period which includes both increasing and decreasing population size in SRC. This modeling environment is used to address three primary questions related to the SRC movement behavior: (1) What are the observable differences in behavior during a period of population increase and a period of decrease? (2) What are the observable differences in behavior during time periods of high and low availability of prey?

and (3) What are the observable differences in whale behavior as the location of higher prey availability changes?

Background

Every individual in the SRC is recognizable through pigmentation patterns of the saddle patch, and dorsal fin shape and size, offering a unique opportunity to not only census the population, but to visually track individual pods over long time periods and large areas (Bain and Balcomb 1999; Ford et al. 2000). The charisma and relatively easy identification of members of the SRC has led to the accumulation of sighting data from researchers, members of the public, whale watch companies, fishermen, ferry workers, and dedicated volunteers in all months of the year from a wide variety of vantage points and platforms throughout the inland marine waters of WA and southern BC. Effort has varied across years and seasons and sightings are extremely rare off the outer coast, where it is assumed that all three pods spend at least some part of the winter and spring months (Osborne 1999).

Previous studies of association patterns between the northern and southern resident communities and their salmon prey have found spatial overlap on very coarse geographical scales for the limited time periods investigated. In a study of the northern resident community (NRC), Nichol and Shackleton (1996) used sighting and acoustic data to calculate the average number of whales present in the Johnstone Strait study area each month between 1985 and 1989. They compared this information with estimates of sockeye (*Oncorhynchus nerka*), pink (*O. gorbuscha*), and chum salmon (*O. keta*) abundance calculated from commercial catch and spawning escapement data obtained from the Department of Fisheries

and Oceans Canada (DFO). Abundance estimates of chinook and coho salmon (*O. kisutch*) were not available and were not included in the analysis. The study found that individual pods associated with different runs of salmon. Pods A1, A5, and C1 were positively correlated with sockeye and pink salmon; pods A4, D1, and H1 were associated with sockeye only; and pod G1 associated with chum only. Despite the relatively high abundance of salmon in the Johnstone Strait area between July and October, only half of the NRC pods were found to be positively correlated with salmon runs (Nichol and Shackleton 1996).

In a study of SRC prey associations, Heimlich-Boran (1986) compared the distribution and frequency of SRC sightings with sports fishery catch data recorded by the Washington Department of Fish and Wildlife (WDFW) from 1976-1978. It was concluded that when there was an increase in the number of recreationally caught salmon, there was also an increase in the frequency of killer whale sightings. The correlations were particularly significant for sightings of SRC whales in the southern portion of Puget Sound. The four year study of northern residents and the three year study of southern residents represent important initiations of the study of spatial relationships between killer whales and their primary prey. However, the short duration of time studied both in number of years and coverage across seasons, as well as the limited salmon data used, gives cause for further investigation.

Quantifying movement behavior is an important technique to aid in our understanding of foraging strategies in the marine environment (Bailey and Thompson 2006). Other studies have shown that predator space use reflects foraging strategy and prey availability (Anderson et al. 2005; Bailey and Thompson 2006; Righton and Mills 2006). For example, when comparing territory size and

shape of coral-feeding fish, Righton and Mills (2006) found that the generalist forager, who was feeding on a relatively evenly distributed food resource, had small territories with clear boundaries. In contrast, the specialist forager, who was feeding on patchily distributed food resources, showed considerable variation in range size with less clear borders. Applying spatial statistical techniques to animal movement behavior can help elucidate patterns unobservable by other means (Mitchell 2005).

Research Questions

Four general questions and their associated hypotheses were tested.

Question 1: Are the movement behaviors of the pods different during periods of population increase and decline?

Hypothesis 1: Whale movement behavior would show evidence of increased searching, quantified by higher space use and more convoluted movement shape, for less abundant or more patchily distributed prey resources during periods of whale population decline. In particular, L pod movement patterns were expected to be larger and more complex than either J or K pod's movement patterns.

Metrics: In this context whale movement is summarized by two terms; first, as the mean of the area of all use polygons for all pods and, second, as the mean of the landscape shape index of those use polygons. These were compared between years when the whale population was increasing (early 1990s) and decreasing (latter 1990s).

Discussion: Population decline is an indication of stress and it is likely that the stress experienced by the SRC during the latter half of the 1990s was due, at least in part, to insufficient prey availability. This hypothesis investigated the assumption that predators can adapt their distribution patterns and foraging strategies to changes in prey abundance or patchiness (Bailey and Thompson 2006). L pod was expected to show the highest space use and most convoluted movement patterns of the two pods because the decline of L pod during the latter 1990s was greater than the decline observed in the other pods.

Question 2: Are the movement behaviors of the pods different during periods of relatively lower and higher salmon abundance?

Hypothesis 2: Years of relatively high salmon abundance, particularly years of relatively high chinook abundance, would correspond to years of lower space use and lower movement complexity on the part of the whales.

Metrics: Total run-size data were used as a proxy to describe relative salmon abundance and was binned into low, medium, and high categories for each year between 1991 and 2001.

Discussion: Prey availability has been seen to influence the distribution and movement behavior of predators in a variety of environments (Barros and Wells 1998; García-Rodríguez and Aurióles-Gamboa 2004; Austin et al. 2006; Bailey and Thompson 2006) and was expected to drive the distribution patterns of the SRC.

Question 3: Are the movement behaviors of the pods different between the late spring/ early summer and the late summer/ fall periods?

Hypothesis 3: The pods would exhibit more searching behavior in the first half of the year, exploring the region for potential food patches. This would be expressed in smaller and less complex space use areas in the late summer/ fall compared to the late spring/ early summer period.

Metrics: In this context whale movement is summarized by two terms; first, as the mean of the area of all use polygons for all pods and, second, as the mean of the landscape shape index of those use polygons. These were compared between weeks 1-29 and weeks 30-52 within each year (1991-2001).

Discussion: Salmon are present in the region in higher numbers during the late summer and early fall than in other seasons of the year. It was therefore expected that during periods of higher salmon abundance, the pods would limit their space use to exploit more concentrated prey.

Question 4: Is there a relationship between the distribution of whale observations and salmon catch?

Hypothesis 4: The whales spend the highest proportion of weeks in the management areas of highest salmon catch per unit effort (CPUE). This would be most evident during the latter 1990s when the whale population was decreasing and prey availability was thought to have been lower. In particular, the whales would spend the highest proportion of time in management areas of high chinook CPUE.

Metrics: In this context, the proportion of weeks whales were observed in a given year were categorized into bins of relatively high, medium, and low salmon CPUE.

Discussion: Salmon are considered the preferred prey of the SRC (Ford et al. 1998; Ford and Ellis 2005). Prey occurring in relatively higher concentrations are generally more efficiently captured (Gende and Quinn 2004; Fraser et al. 2006; Zhao et al. 2006). It was therefore expected for the pods to preferentially seek out those areas where salmon were occurring at the highest concentrations, regardless of species. If there is a significant relationship between salmon catch density and whale presence, it was expected that whales would occur in the management areas of highest salmon catch density more often than by random chance. Because chinook salmon do not tend to be caught in as great of numbers relative to other species, and are expected to occur in less concentrated aggregations, the whales are expected to spend the highest proportion of time in management areas of high chinook CPUE.

METHODS

All available whale sightings recorded between 1991 and 2001 within southern Georgia Strait, the Strait of Juan de Fuca, and Puget Sound were obtained from TWM. Daily whale observations were converted to weekly space use areas by pod and spatially intersected with fish catch data by salmon management areas. Because the salmon management areas differ substantially in size, fish catch was standardized by calculating numbers of fish caught per unit area for each salmon management polygon.

Whale Data

Whale sightings consist of a compilation of data from TWM's Soundwatch Program, TWM's archives, researcher Robert Otis of Ripon College (Ripon, Wisconsin USA), the Center for Whale Research (CWR, Friday Harbor, Washington USA), the commercial Whale Watcher's Spotting Network

(Sidney, BC Canada), and OrcaNetwork (Greenbank, Washington USA).

Data were organized, pods separated into different tables, and daily sightings grouped into statistical weeks. Statistical weeks are defined as the time period from Monday to the following Sunday. Because the first statistical week in January may consist of as little as one day, statistical weeks are numbered up to 53 instead of the actual 52 7-day weeks that comprise a year.

Sightings represent the location of a pod or pods of whales on a specific day and often at a specific time. Sightings are made from shore, from vessels, and occasionally from the air. Sightings are made by researchers, trained volunteers, and by the general public. Pod identity is determined by recognizing one or more individuals in the group by unique dorsal fin size and shape, scarring and nick patterns, and coloration pattern of the saddle patch. Sightings have been compiled from the mid-1970s to the present. However, effort in sightings varies across years, seasons, weather conditions, and daytime vs. nighttime hours. Only sightings that included date, pod identity, and geographic coordinates were included in the analysis. Although L pod has been observed traveling as separate sub-pods, there is inconsistency in the sighting records identifying whether a sub-pod or all of L pod was sighted. Therefore only sightings generically identified as L pod were used. The geographic coordinates represent the centroid of a pre-defined grid that has been used by TWM. Each grid cell is approximately 25 km². This scale is sufficiently fine to represent an entire pod's location due to the constant movement of the pod and distance between individuals, even when occupying a relatively small space.

Data were sorted into two categories for every statistical week, pod, and year. Weekly point files consist of days in which there is either one sighting, or multiple sightings of a pod at the exact same coordinates. Weekly line files consist of days in which there are at least two sightings at different coordinates. These files were then used to generate line and point coverage files within ArcGIS 9.0 (ESRI, Redlands, CA USA). The line and point coverages were combined by statistical week. Each weekly coverage therefore contained daily movement paths nested within a weekly coverage.

An Arc Macro Language (AML) model was written and run that executed several steps in the process of converting observational point data to movement shape polygons. The line and point coverages were cleaned (digitizing errors which may cause topological errors were removed), then buffered by 2500 meters to create use areas. Sighting locations are approximate and because a group of whales occupies an area, as opposed to a fixed point, a use area extrapolated around the recorded whale locations creates a more accurate representation of movement space. Topography was built for the movement polygons and land was erased. In some cases sightings were made on either side of an island, but not at points around either end. While it is apparent that the whales swam around the island in order to get to the other side, it is not known which direction they went or how direct their line of travel was. These movement paths were not assumed to follow a set protocol, and therefore the movement polygons represent a minimum space use by the whales by modeling the minimum distance between known locations. These weekly space use areas were then intersected onto a coverage layer of combined US and Canadian salmon management areas (see Figure 2.2). All coverage files were then converted into a raster grid format in order to utilize the software program Fragstats (version 3). Grid size was 100 m^2 . Each grid had attributes of the

salmon management area that it overlaid and thus whale movement polygons were linked to salmon catch data. All data coverages were projected in universal transverse mercator (UTM) coordinates. Some of the whale sighting records were in latitude and longitude coordinates and therefore needed to be defined and reprojected into UTM. A land coverage was created using WA and BC shoreline coverages. Coverages of US and Canadian salmon management areas were combined to create an international coverage of management areas. A US regional management area coverage was created by dissolving border lines between salmon management areas (Figure 2.1).

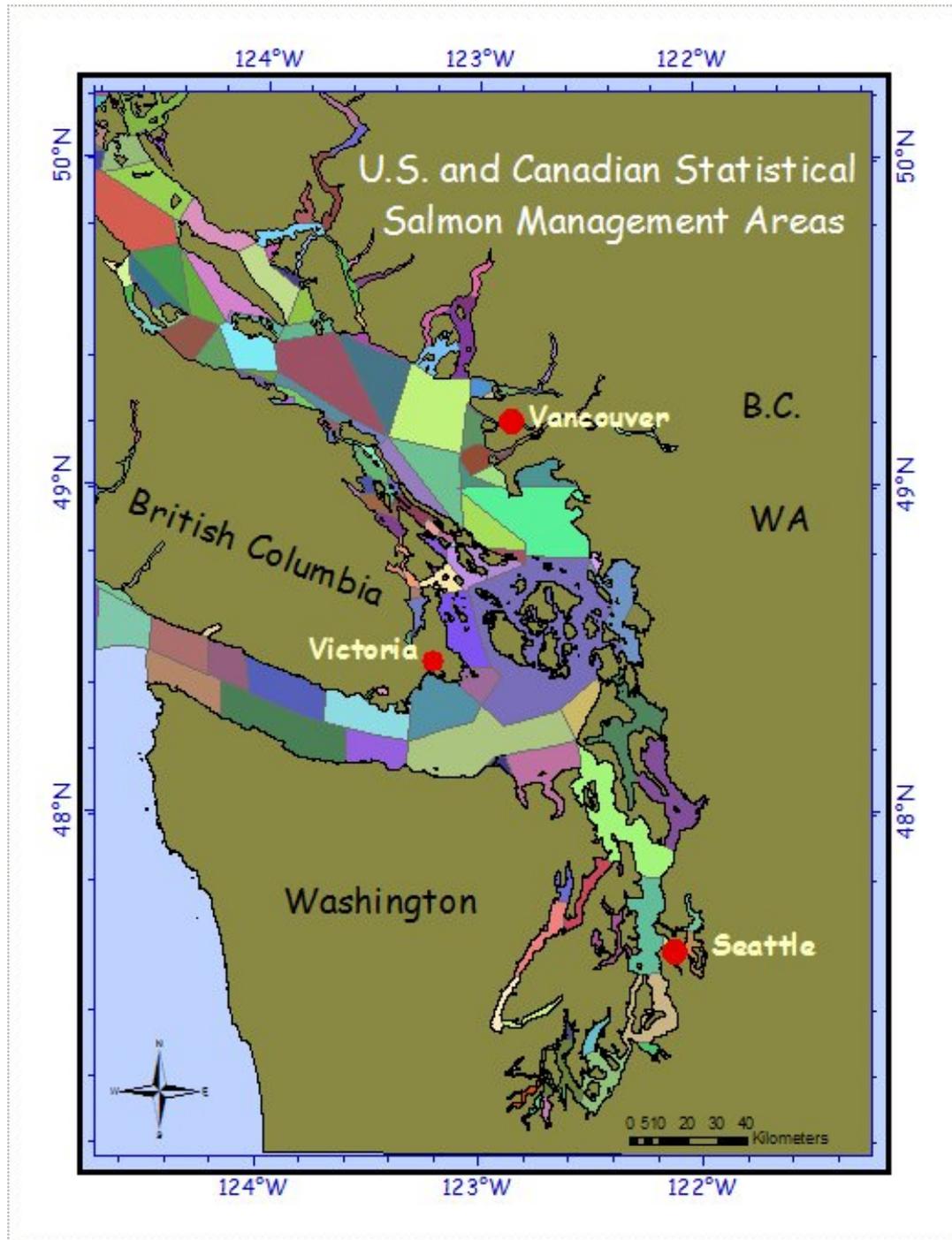


Figure 2.1. Salmon management areas in Washington State and British Columbia inland marine waters.

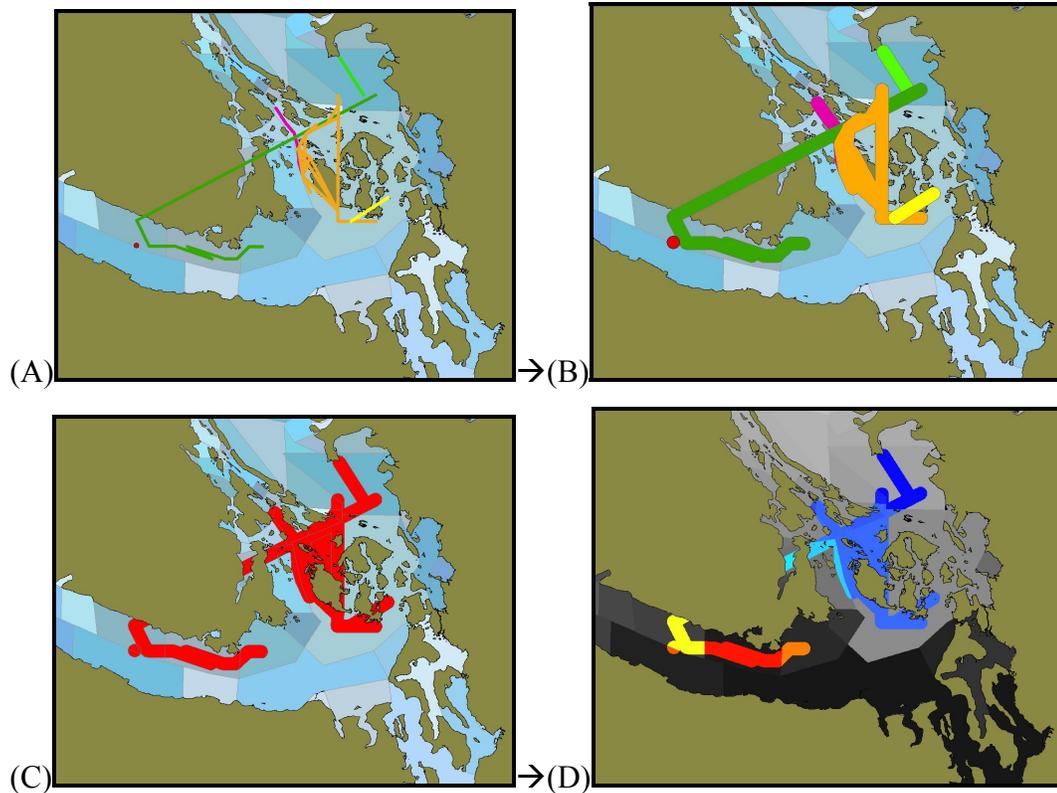


Figure 2.2. An example of one week of sighting data taken from one pod in one year. The observational point data are converted to daily movement lines and points, which have been grouped by week (A). The lines and points are buffered to create space use polygons (B). The polygons are joined where there is overlap and land is erased (C). Polygons are then converted from vector to raster format and intersected with the management area grid (D).

Salmon Catch Data

Commercial salmon ticket catch data were obtained from the WDFW and the DFO, and were summarized by year, week, and species. They were then grouped by numbered statistical fish management areas throughout WA and BC waters.

Management areas range in shape and size depending on the exact location. Salmon caught anywhere within a management area are recorded for that area. The whale sighting data are specific enough (commonly exact latitude and longitude) that encounters can be assigned to a specific salmon management area (Nichol and Shackleton 1996; Heimlich-Boran 1988). The management areas were assigned a

new numerical identification, as the conventional identification consisted of both numbers and letters which can not be properly read by Arc software.

Salmon catch data from BC were recorded in gross pounds caught per statistical week (the statistical weeks differed between the US statistical week by one day, but this discrepancy was assumed to not alter the data in a meaningful way). In order to match the BC data with the US data, average weights were obtained for each species of salmon in each management area for each year investigated. These average weights were converted from kilograms to pounds, and then used to estimate number of fish caught.

Hypothesis Testing

By quantifying whale movement and space use, it was possible to test differences in movement behaviors of the pods between time periods. With salmon abundance categorized by space and time it was possible to test for relationships between whale movements and metrics of salmon catch. Following are the four previously stated hypotheses and the methodology for testing each one. Interpretation of possible results is also described.

Testing Whale Movement Behavior Across Time—Grouped Years

It was hypothesized that in the early 1990s whales would show smaller space use and less complex movement shapes than during the late 1990s. In particular, L pod movement patterns were expected to be larger and more complex than either J or K pod's movement patterns.

Two pattern metrics were calculated to address questions of whale movement: 1) Total area (TA) which quantified space used by a pod in a given week (measured in

hectares (ha)); and 2) Landscape Shape Index (LSI, equation 1), which is a measure of shape complexity. LSI is interpreted such that a LSI value of 1 represents a perfect circle, the simplest possible shape, and the minimum possible LSI value. The higher the value, the more convoluted the shape pattern.

$$\text{LSI} = \text{perimeter} / (2 * \sqrt{(\pi * \text{area})}) \quad (1)$$

To test for significant difference between the annual means of TA and LSI from the early 1990s and the latter 1990s, t-tests were performed using the software program SPSS 13.0 (Chicago, IL USA). First, serial autocorrelation between the two time periods were tested for each pod as well as all whales and found to be insignificant. For all tests performed, alpha values of .05 and .01 were considered significant.

Interpretation of Grouped Years Results

A relationship of higher space use and movement complexity and a decreasing population trend could suggest that movement behaviors can be used as an indicator of population stress. If higher TA used or higher complexity of whale movement patterns was correlated to years of lower salmon abundance, and therefore presumed lower availability, it was likely that whales spent more time searching for food, potentially expending more energy per unit of energy gained, when salmon were less available. Likewise, if less TA was used or lower complexity of whale movement patterns were correlated with higher salmon abundance, it would be concluded that whale movement patterns were driven, at least in part, by salmon abundance. If no correlations were found, it would be concluded that factors other than salmon abundance were driving whale shape area patterns at the time steps analyzed, and that research efforts should be focused on addressing those other factors.

Testing Whale Movement Behavior in Relation to Annual Salmon Abundance

It was also hypothesized that years of relatively high salmon abundance, particularly years of relatively high chinook abundance, would correspond to years of lower space use and lower movement complexity on the part of the whales.

This hypothesis was examined by visually comparing annual whale movement behavior with relative salmon abundance. Total run sizes of chinook, chum, and all salmon species combined were graphed. Total run-sizes for each year between 1991 and 2001 were binned as Low, Medium, or High. To bin the total run-size data, the highest number of each species, or combined species, was divided by three to give the parameters for the range of values between each category of Low, Medium, or High.

Interpretation of Salmon Abundance Results

If it appears that smaller space use and less convoluted movement patterns corresponded to years of relatively high salmon abundance, while higher space use and more convoluted movement patterns were associated with years of lower salmon abundance, it would be inferred that prey availability had some measurable affect on whale spatial characteristics.

Testing Whale Movement Behavior Across Time—Within Years

Movement patterns were also expected to show distinguishable differences on an intra-annual scale. It was hypothesized that the pods would exhibit larger and more complex space use areas in the late spring/ early summer period compared to the late summer/ fall.

T-tests were used to ascertain statistical differences between pattern metrics measured in weeks during the spring and early summer against pattern metrics measured in weeks during the late summer and fall. Weeks up to 30 (approximately the third week of July) were grouped as ‘early’ and weeks from 31 to the end of the year were grouped as ‘late’.

Interpretation of Intra-annual Results

Interpretations of these results were similar to the grouped years comparison. Investigating movement shapes within years tested whether a relationship existed between whale movement pattern and seasonal changes in the whale’s environment. It was assumed in this analysis that salmon presence is what drives a relationship of whale movement pattern across a year. However, if no seasonal change of whale movement was detected then it would be concluded that factors other than salmon presence noticeably influenced whale movement behavior on temporal scales among seasons within years.

Testing Whale Presence in Relation to Salmon Abundance

The fourth hypothesis stated there would be a significant relationship between whale distribution and salmon catch. Specifically, it was expected that whales would be observed in the management area of highest salmon catch density for each week more often than expected by random chance. On the annual scale, it was hypothesized that the whales spend the highest proportion of weeks in the management areas of highest salmon catch per unit effort (CPUE), particularly areas of highest chinook CPUE.

In this analysis commercial salmon catch was used as a proxy for salmon presence and relative abundance at the weekly and annual scale. Two different approaches

were used to look at whale distribution in relation to relative salmon abundance. The first involved using the density of salmon catch data on a weekly scale and the second approach used CPUE data on an annual scale.

Density

Salmon catch data from WA and southern BC were combined and sorted so that tables were created that listed the management area that recorded the highest density of catch for each week of each year, regardless of species. Density of catch was calculated by dividing the catch per week per species in each year by the total area of the salmon management polygon in which the catch was made as a means to standardize the data (illustrated in Figure 2.3). A probability of whether a pod of whales occurred in that catch area by random chance was calculated by dividing the area of each management polygon with the combined areas of all the management polygons. Observed pod presence or absence within the management area of highest recorded salmon catch density was tallied for each week of each year. A chi squared test was performed for each pod and each year of the study to determine if pod presence in areas of highest salmon catch density was greater than that expected by random chance.

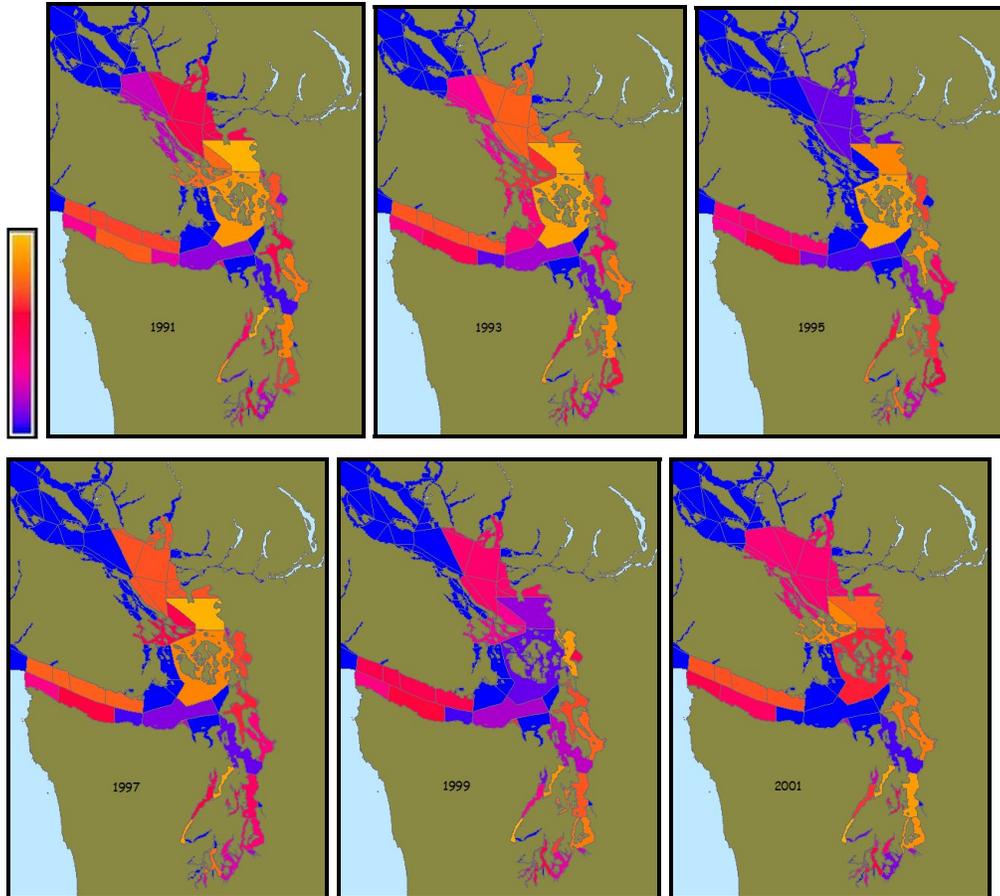


Figure 2.3. A visual representation of catch density for odd years between 1991 and 2001. Yellow coloration depicts management areas reporting the highest total salmon catch density for that year. Blue coloration depicts management areas reporting the lowest salmon catch density for that year. Catch density within management areas changes year to year, but appears relatively comparable between BC and WA waters.

CPUE

To test the proportion of weeks the whales were sighted in management areas of High, Medium, and Low CPUE for a given year, CPUE data were sorted and summarized to obtain an average annual CPUE value for each species of salmon from 1991-2001. Because CPUE data were not available for BC waters, only US data were used. The highest CPUE value for a given year was divided by three to determine the range in values that defined each category. This method in dividing

the values was chosen as the best approach because it most accurately represented the data, meaning the data were not artificially divided into three equal bins. Each management area was assigned to a High, Medium, or Low category for relative CPUE for chinook, chum, and all salmon species combined, for each year. The number of weeks each pod spent in those management areas was then tallied for each year. Graphs were created which depicted the proportion of time each pod spent in the management areas of relatively High, Medium, and Low CPUE from 1991-2001. Commercial catch effort was accounted for by incorporating CPUE into the analysis of this study.

Interpretation of Whale Distribution Results

If whales were sighted in the management areas of highest salmon catch density more often than by chance, it would be concluded that the distribution of the whales was influenced by the highest concentration of salmon. The hypothesis of non-random distribution would be rejected if the whales did not occur in the salmon management areas of highest salmon catch density for each week more often than by chance alone. This would indicate that the whales were not preferentially occupying areas of higher salmon density and their movement patterns were not deliberately associated to presence of the highest density of salmon catch.

If whales appeared to be spending a greater proportion of the weeks that they were sighted per year in areas of high CPUE, it would be concluded that they were selectively distributed based on prey concentrations similar to those attracting commercial fishermen. If however, the whales did not appear to be spending the greatest proportion of the weeks sighted in areas of high or medium CPUE, it would be concluded that either the whales were more proficient at finding salmon

than fishermen were, or they were spending time in certain areas for reasons other than prey availability. For this analysis it was assumed that commercial catch data can be used as a proxy for salmon presence and relative abundance among management areas. It was also assumed in the case of comparing CPUE and whale distribution that the US catch data are representative of overall CPUE for the region and that the whales spend a significant portion of their time in US waters.

Time Frame

Salmon data are more numerous prior to the early 1990s due to more intense harvesting in more areas across more of the calendar year compared to present practices. Earlier whale sighting data however, while available, are largely incomparable in recorded effort to data collected in more recent years. Therefore the years 1991-2001 were chosen as the best time series in which the two datasets can most accurately be associated. This time frame also includes years of SRC population increase (1991-1995) and years of population decline (1996-2001). A hierarchical model of daily sightings nested into statistical weeks was created for J, K, and L pods based on the finest resolution of salmon catch, which is weekly. The scales of analysis include weeks, seasons, years, and multi-year time frames.

Caveats

Weekly whale space utilization polygons did include small land masses (less than 0.5 km²). These small islands were not removed from the space use polygons because they were assumed to be small enough to not elicit a behavioral response from the whales, such as changing movement behavior, on a scale that would have influenced the weekly space use polygon. Since the entire space use model is a conceptualization of weekly distribution, meant to represent an area probably occupied by the whales, inclusion of small land masses was not expected to alter

the use area. Scale can always be finer, but it is not clear at what point refinement of scale becomes completely inconsequential to the question at hand. Small land masses as well as shallow land masses potentially could have caused small scale movement pattern differences, however it is not believed that leaving such physical features in the movement patterns significantly altered the shape metrics.

Numbers of whale sightings per month and year were plotted from 1991-2001 to explore possible changes in whale observational effort across time (Figure 2.4). A t-test was performed to determine whether the frequency of sightings in the early 1990s was significantly different than the frequency of sightings in the latter 1990s. Results indicate that there is a significant difference between mean number of sightings per year from 1990 to 1995 compared to mean number of sightings per year from 1996 to 2003. This is likely due to the initiation of the Whale Watchers Spotting Network in 1996, an organization dedicated to locating the whales and broadcasting their position to whale watch companies via pager.

The Spotting Network runs during the summer months, when J, K, and L pods are frequently sighted in the waters of the San Juan and Gulf Island Archipelagos. It would therefore be expected that the observed increase in frequency of sightings in the years 1996-2004 would be most notable in the summer months. When number of sightings recorded from January through April of each year were compared between the earlier and later 1990s no significant difference was found. However, when the number of sightings recorded from May through August, and September through December were tested for differences between the early and latter 1990s, significant differences were found (Figure 2.5). These differences could be largely attributed to the contribution of the Spotting Network. The proportion of each year's sightings recorded from January through April, May through August, and

September through December were also calculated. These ratios were then tested for significant difference between 1990-1995 and 1996-2003. There were significant differences found in the proportion of sightings made in the January through April period across the years tested. However, no difference was found in the proportion of sightings in the May through August and September through December periods between 1990-1995 and 1996-2003.

Because there are significant differences in the number of sighting records between the two time periods analyzed, any increase in pod space use could at least partially be attributed to a higher number of recorded locations. However, the higher number of sighting records were not necessarily all unique, meaning that multiple observations for the same time and location may have been recorded. The number of unique sighting locations per day in the early and late 1990s were not tested for differences. So the possibility that the increase in recorded whale observations does not reflect an increase in number of unique sighting locations per day remains unknown. The higher number of sightings in 1990 compared to 1991 through 1995 would indicate that the overall lower number of sightings recorded for the next five years are low because of whale behavior and not entirely for lack of sighting effort.

The differences in number of sightings between the two time periods tested suggest that caution be taken when inferring any definitive conclusions. However, given the lack of differences between the proportion of summer and fall seasonal sightings between the early and latter 1990s and the possibility that the higher number of sightings recorded since 1996 do not represent a higher number of unique whale locations, it was assumed that the sighting data was suitable to model differences in whale movement behavior across time.

Sightings Per Year

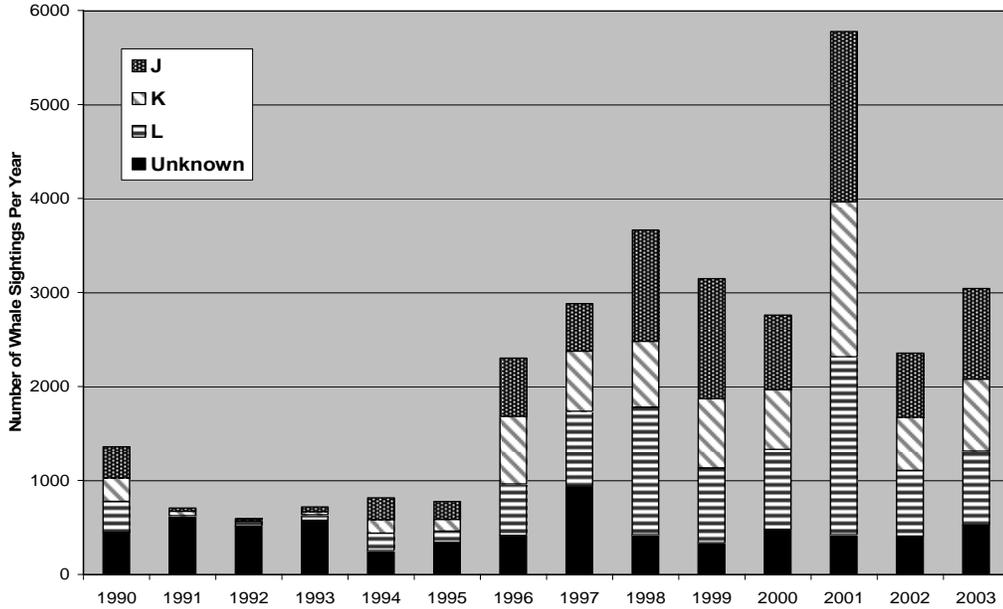


Figure 2.4. Number of SRC sightings per year from 1990-2003: broken out by identified pod and unknown orcas.

Seasonal Sightings

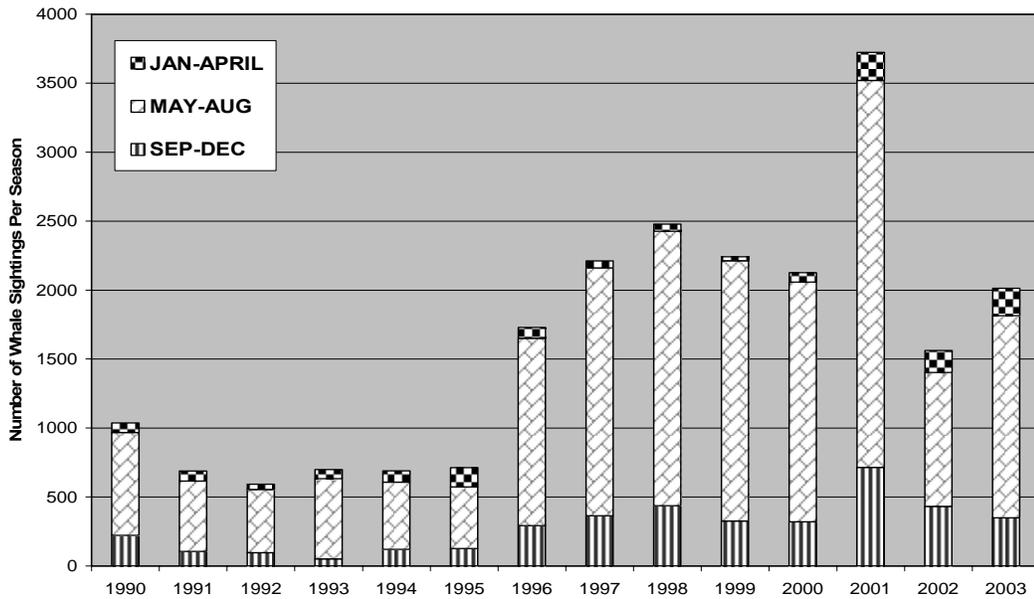


Figure 2.5. Number of SRC sightings per year from 1990-2003, broken out by grouped months: January through April; May through August; and September through December.

RESULTS OF SHAPE PATTERN METRIC ANALYSES

Shape Metrics Across Years

Results of t-test analysis indicate that mean TA values of the total SRC for years 1991 through 1995 are significantly different from mean TA values for years 1996 through 2001 ($p \leq .0001$). Mean LSI values of the total SRC from the early 1990s are also significantly different than the mean LSI values from the latter 1990s ($p \leq .002$). When the analysis was performed on individual pods the same results were found (Figures 2.6 and 2.7). J pod showed significantly different mean TA and LSI values from 1991 to 1995 compared to the period 1996 to 2001 ($p \leq .003$ and $p \leq .003$ respectively). Likewise, K pod was found to have significantly different mean values of TA and LSI between the two time periods ($p \leq .001$ and $p \leq .012$ respectively). When the mean TA and LSI values of the two time periods were tested for L pod, the differences were significant with p values of $p \leq .003$ and $p \leq .012$, respectively (mean values for TA and LSI are displayed on tables 2.1 and 2.2).

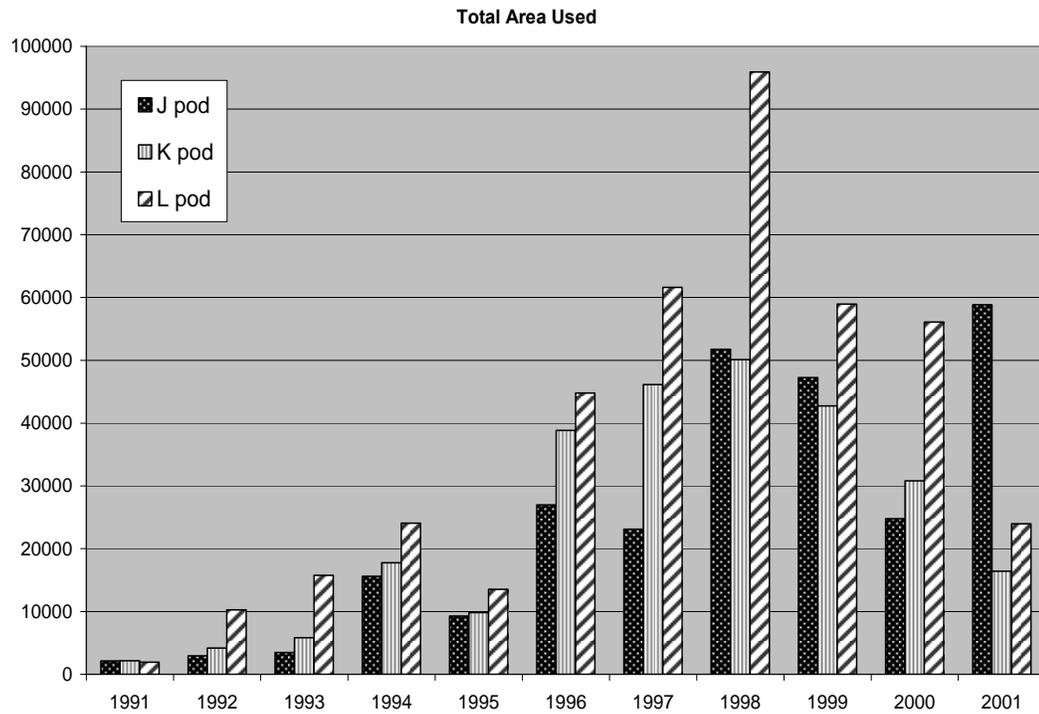
Table 2.1. Mean annual TA values (ha) for each pod and the entire SRC.

Averaged Annual TA

	J	K	L	SRC
1991	2138	2184	1915	2079
1992	2955	4197	10266	5806
1993	3466	5819	15765	8350
1994	15605	17771	24072	19150
1995	9286	9839	13526	10884
1996	26997	38842	44788	36876
1997	23120	46132	61627	43626
1998	51747	50110	95893	65916
1999	47249	42768	58939	49652
2000	24796	30802	56087	37228
2001	58873	16400	23980	33084

Table 2.2. Mean annual LSI values (see equation 1) for each pod and the entire SRC.**Averaged Annual LSI**

	J	K	L	SRC
1991	1.53139	1.60362	1.47830	1.53777
1992	1.80361	2.01460	2.44267	2.08696
1993	1.85263	1.94094	3.09042	2.29466
1994	3.26025	3.53893	3.52498	3.44139
1995	2.77575	2.93149	2.83836	2.84853
1996	3.34665	3.98081	4.23715	3.85487
1997	3.45890	4.66297	5.02050	4.38079
1998	4.73834	4.68404	5.24450	4.88896
1999	4.54586	4.60561	4.23589	4.46245
2000	3.40734	3.47547	3.94492	3.60924
2001	5.16514	2.51535	2.79269	3.49106

**Figure 2.6.** Total annual space use (ha) by pod from 1991-2001.

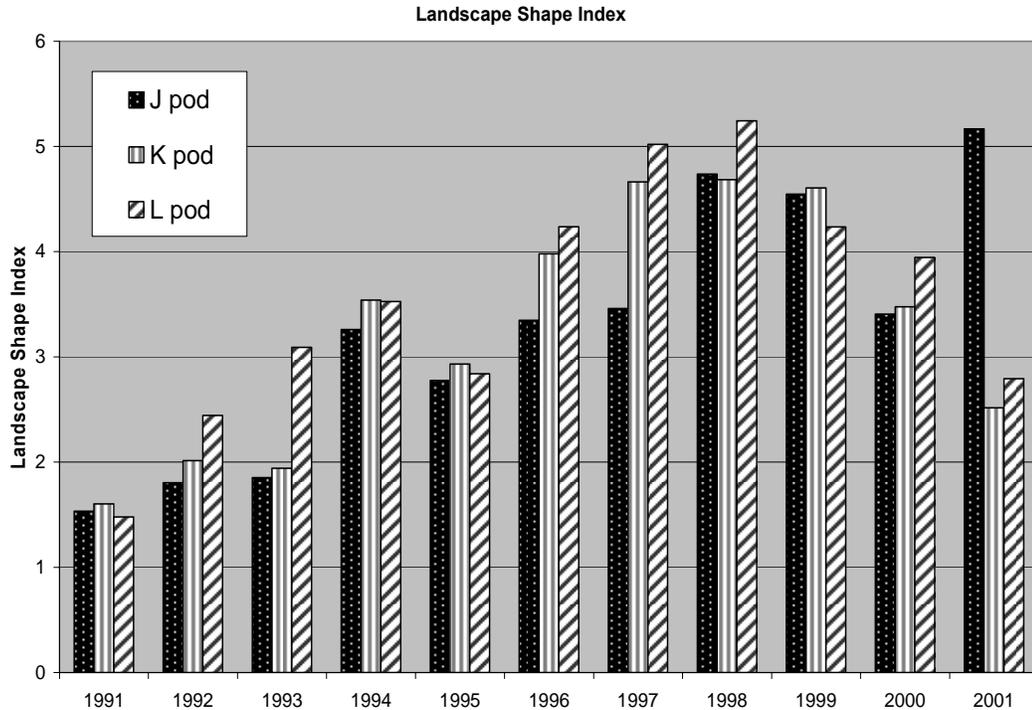


Figure 2.7. Average annual landscape shape metric (see equation 1) by pod from 1991-2001.

Whale Movement Behaviors in Relation to Annual Salmon Abundance

When relative abundance of chinook, chum, and all salmon species combined for each year were compared to trends in the TA and LSI across time, no immediate pattern emerged (Figure 2.8). 2001 was the only year in which chinook, chum, and all species had relatively high abundance based on total run-size. Both K & L pods showed similar TA use in 2001 as they did in 1994, when chum salmon abundance was high, chinook abundance was low, and all species combined was medium. The average LSI of K & L pods in 2001 was similar to LSI values observed in 1994 and 1995 when the whale population was still increasing. J pod showed their highest TA and LSI values for all the years analyzed in 2001, in sharp contrast to both K & L pods. J pod's behaviors are particularly puzzling in light of the relatively low TA and lower LSI observed in 2000, the only year when chinook, chum, and all species

of salmon had relatively low abundances. The TA and LSI values of all three pods showed a peak in 1998. This corresponded to low relative abundance of chinook and all species combined, and relatively high abundance of chum. This same pattern of high chum and low chinook and all species was also observed in 1992 when both TA and LSI values of the pods were generally low.

Relative Abundance of Chinook, Chum, and All Species of Salmon

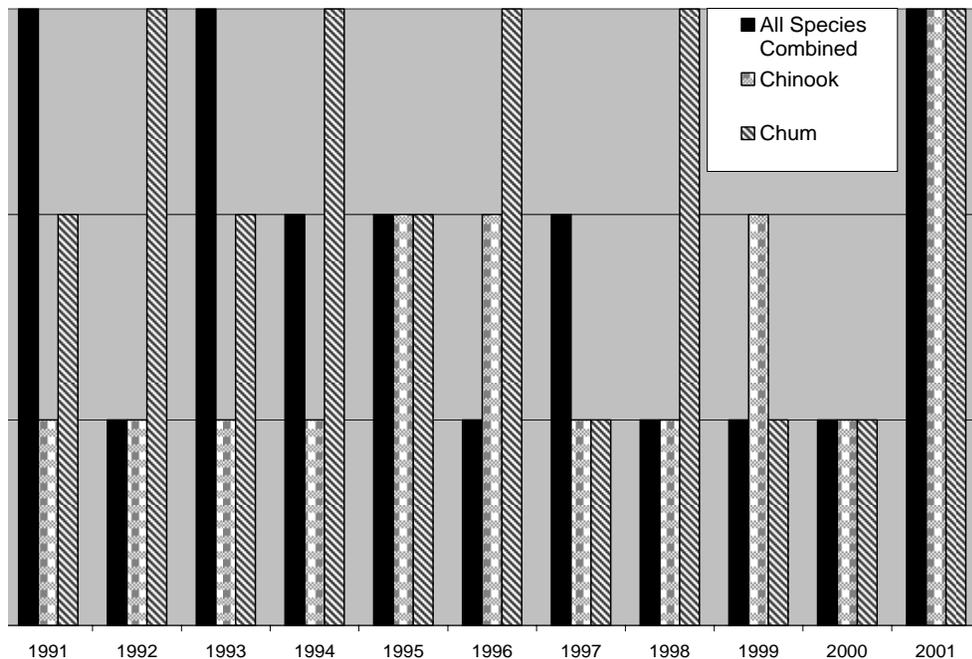


Figure 2.8. Total run-size of chinook, chum, and all salmon species combined categorized into relatively Low, Medium, or High values for years 1991-2001. Run-size data includes the inland marine waters of Washington State as well as Fraser River pink and sockeye abundance.

Shape Metrics Within Years

When differences in TA and LSI were tested on an intra-annual scale, results were generally insignificant (Figures 2.9-2.12). The mean TA used by J pod up to week 30 was statistically not different from the mean TA used in week 30 to the end of the year, with the exception of the years 1996 ($p \leq .001$) and 2001 ($p \leq .008$). K pod showed significant intra-annual differences in TA in years 2000 and 2001 ($p \leq .024$).

and $p \leq .036$ respectively). Similar to J pod, L pod showed significant differences in TA values between the first and second part of the year in 1996 ($p \leq .018$) and 2001 ($p \leq .011$).

Only two years showed significant differences between the mean LSI up to week 30 and the mean LSI from week 30 to the end of the year for J pod. Mean LSI values from 1995 and 1996 showed significant difference between the two time periods ($p \leq .017$ and $p \leq .011$, respectively). Results showed that the mean LSI values for K pod were statistically different between the spring- early summer and late summer- early fall in years 2000 ($p \leq .040$) and 2001 ($p \leq .040$). The years 1996 and 2001 had statistically different LSI values in the weeks prior to week 30 compared to after week 30 for L pod ($p \leq .022$ and $p \leq .008$). The relative abundance of salmon was not the same among the years in which the pods showed significant intra-annual differences in space use.

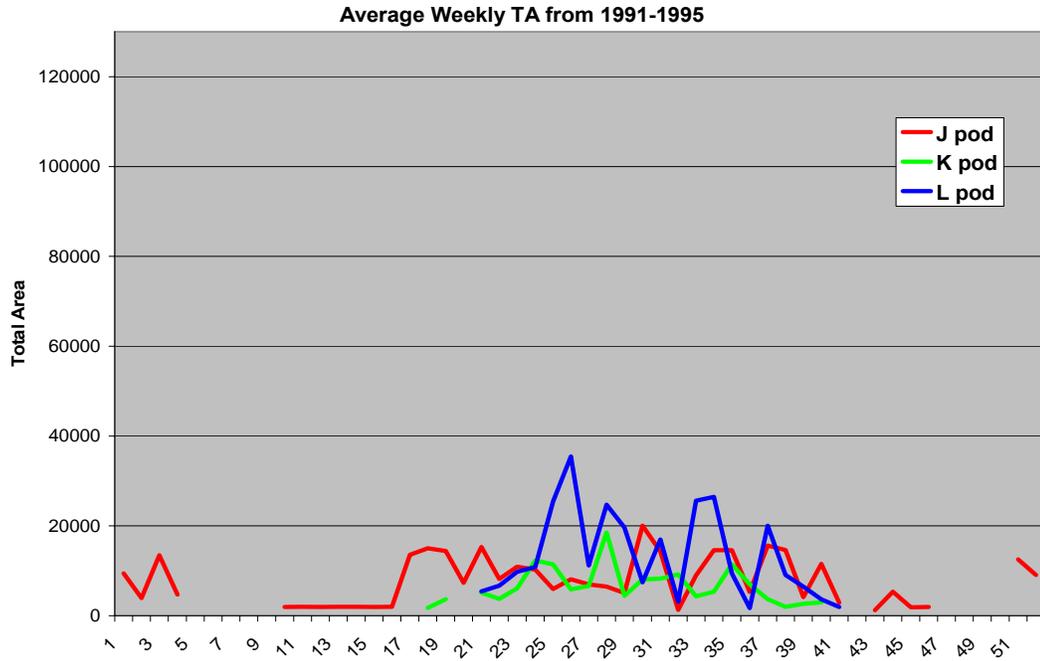


Figure 2.9. Averaged total area (ha) of weekly space use polygons for J, K, and L pods from 1991-1995.

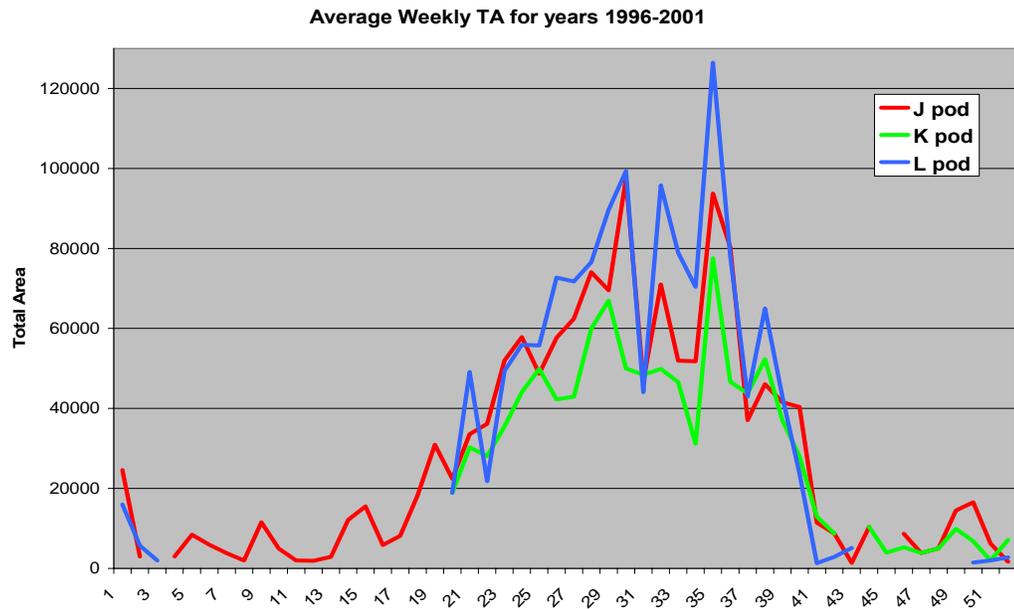


Figure 2.10. Averaged total area (ha) of weekly space use polygons for J, K, and L pods from 1996-2001.

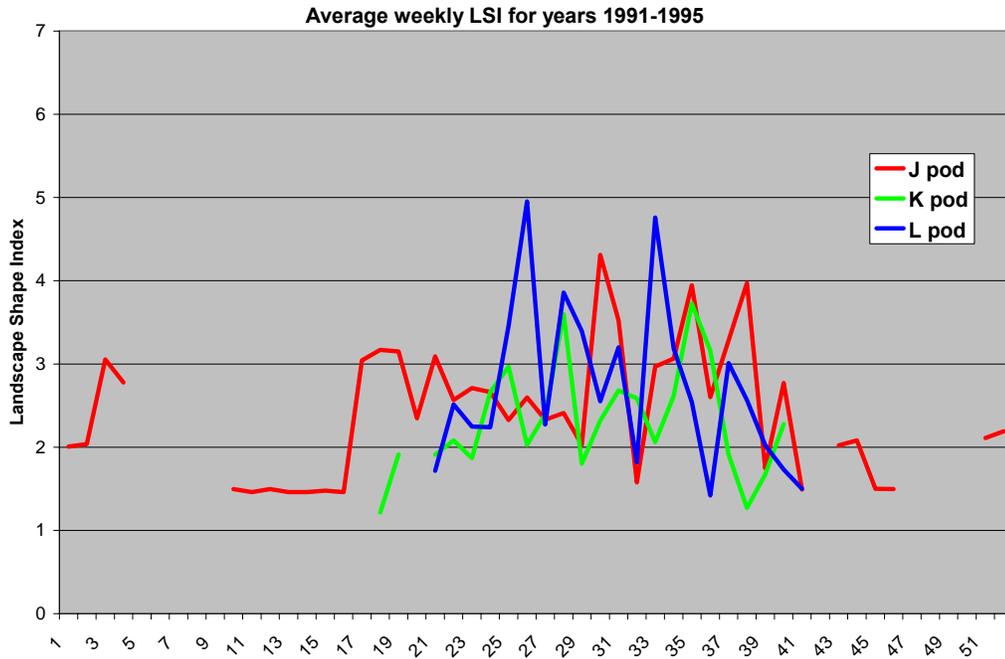


Figure 2.11. Averaged weekly landscape shape index values (see equation 1) for J, K, and L pods from 1991- 1995.

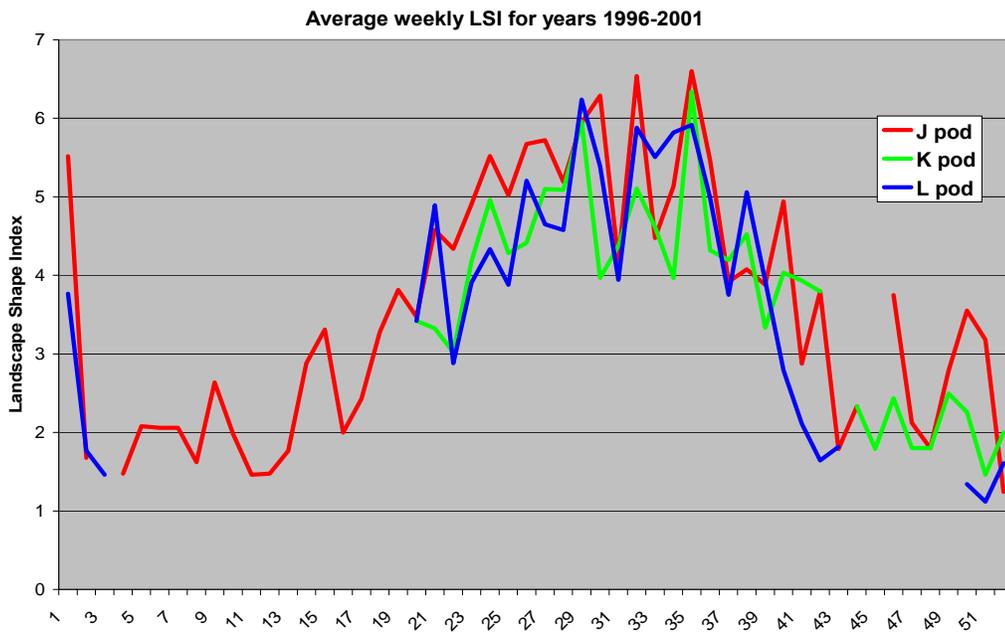


Figure 2.12. Averaged weekly landscape shape index values (see equation 1) for J, K, and L pods from 1996- 2001.

RESULTS OF WHALE DISTRIBUTION ANALYSIS RELATIVE TO SALMON CATCH

Whale Distribution in Relation to the Highest Density of Salmon Catch

Chi square tests were performed to analyze whale distribution in relation to the salmon management area of highest salmon catch density per week over each year analyzed (Table 2.3). Results show that there is no overall pattern of whale preference for the management area of highest reported salmon catch density. 1994 and 2000 were the only years to show significantly non-random distribution, indicating that either factors other than reported density of commercial salmon catch are driving SRC distribution patterns, or that higher relative densities of specific species influence distribution rather than the highest density regardless of species.

Table 2.3. Results of χ^2 test of random distribution of whales in salmon management areas of highest reported density of salmon catch per week.

YEAR	chi2obs	df	sig (α)
1991	1.977	52	No
1992	1.658	53	No
1993	62.527	53	No
1994	149.053	51	p<0.001
1995	38.170	51	No
1996	0.106	52	No
1997	10.776	48	No
1998	1.569	42	No
1999	0.192	48	No
2000	373.570	43	p<0.001
2001	1.170	48	No

Whale Distribution in Relation to CPUE of Salmon Catch

When the proportion of weeks whales were sighted in management areas of relatively High, Medium, or Low CPUE data were compared across years and pods some interesting patterns emerged (Figures 2.13-2.15). Contrary to the predicted outcome that whales would spend the greatest proportion of their time in areas of

high CPUE, it appears that a higher proportion of weeks were spent in areas of medium or low CPUE. There appears to be substantial variation in the results among years. When all species of salmon were combined, the whales seemed to generally spend the highest proportion of weeks in areas of either medium or low CPUE in the early 1990s, and either high or low CPUE areas in the latter 1990s. In 2001, the pattern returned to that of the early 1990s. This seems reasonable in light of the relatively high abundance of salmon in 2001, especially compared to the latter 1990s (Figure 2.8). 1997 was the only year in which all three pods spent the majority of the weeks they were sighted in areas of high CPUE. Generally, there were no obvious differences among the pods for any of the years analyzed. This was true for all salmon species as well as chinook and chum specifically.

Perhaps the most surprising results were those comparing the proportion of weeks whales were sighted in areas of High, Medium, and Low chinook CPUE. It was hypothesized that the whales would spend the greatest proportion of their time in areas of high chinook CPUE. However, the results indicate that all three pods spent the majority of their time in areas of low chinook CPUE. L pod in particular, spent 100% of the weeks they were sighted in areas of low chinook CPUE.

When chum salmon CPUE data were compared to proportion of weeks whales were sighted in the management areas, the results indicate that with the exception of 1992 and 1999, the whales spent the majority of the weeks they were sighted in areas of low chum CPUE. In 1992 all three pods spent 100% of the time they were sighted in areas of medium chum CPUE. In 1999 the whales spent the majority of the time they were sighted in areas of high chum CPUE. J & K pods were spotted in areas of high chum CPUE in approximately 85% of the weeks they were observed, and in areas of medium chum CPUE in approximately 15% of the weeks

they were spotted. In 1999, L pod was sighted in areas of high chum CPUE every week that it was observed.

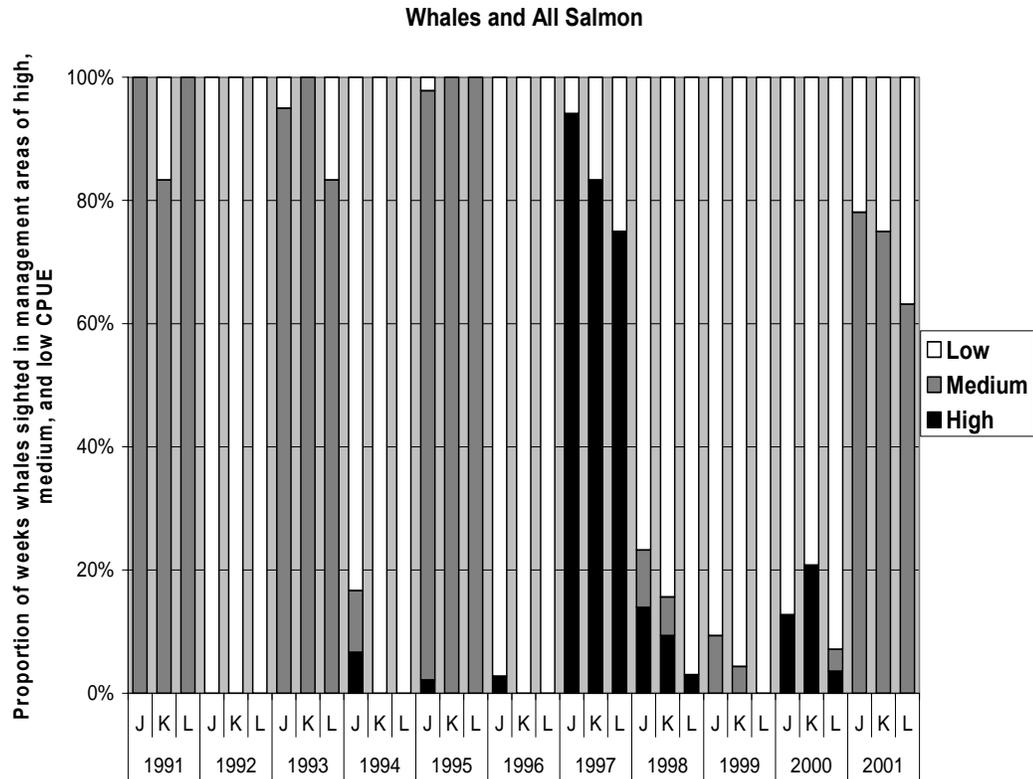


Figure 2.13. Relative proportion of weeks whales of J, K, and L pods were sighted in management areas of high, medium, and low CPUE of all salmon species combined from 1991-2001. Management areas are in US waters only.

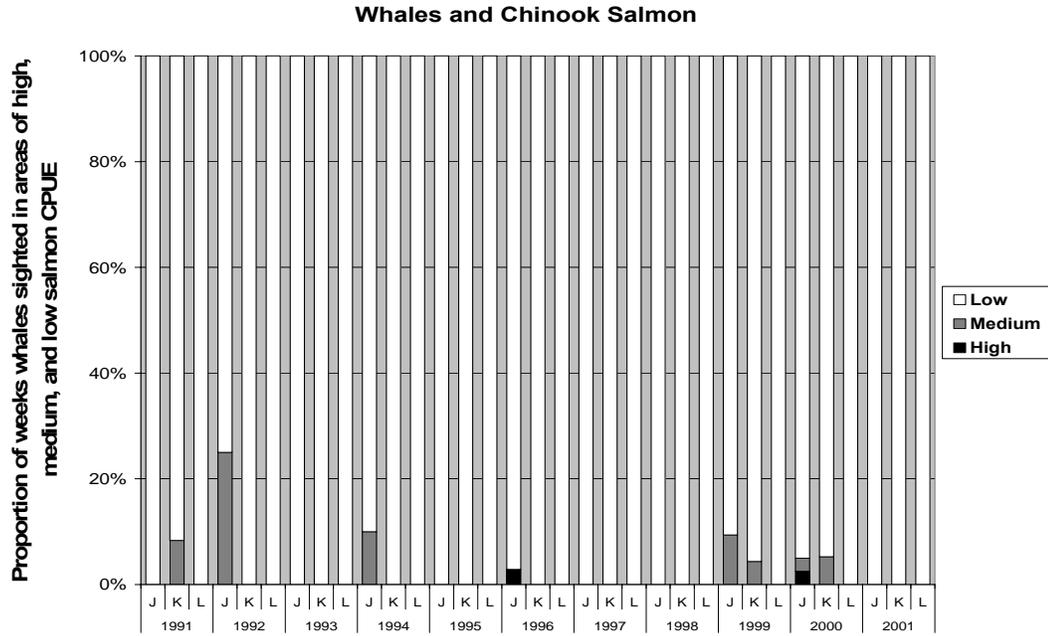


Figure 2.14. Relative proportion of weeks whales of J, K, and L pods were sighted in management areas of high, medium, and low CPUE of chinook salmon from 1991-2001. Management areas are in US waters only.

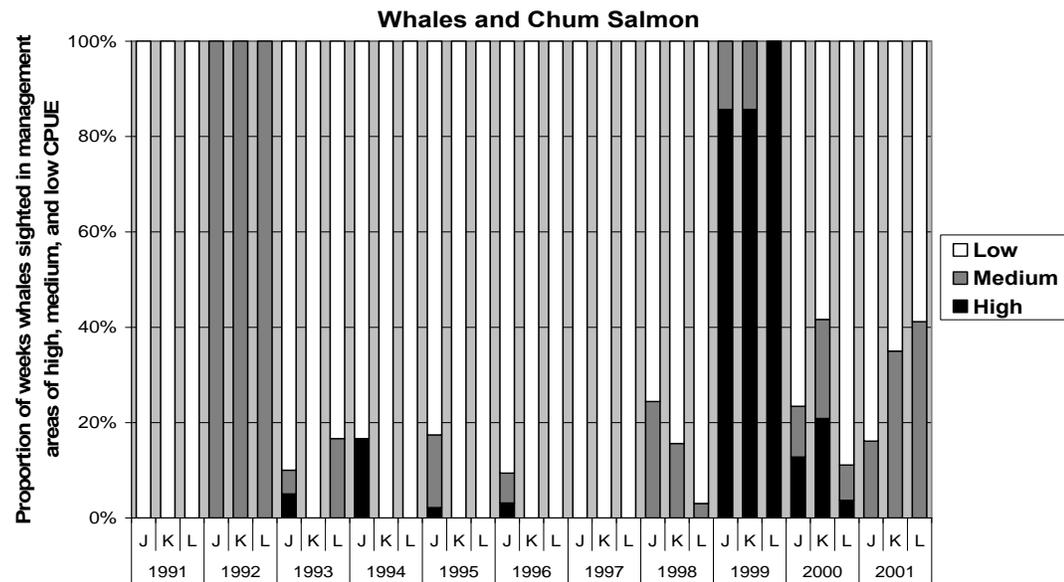


Figure 2.15. Relative proportion of weeks whales of J, K, and L pods were sighted in management areas of high, medium, and low CPUE of chum salmon from 1991-2001. Management areas are in US waters only.

DISCUSSION

Differences in movement patterns of the SRC were found between the early and latter 1990s, which coincides with differences in general salmon abundance and whale population trend during the same time periods. When whale movement patterns were analyzed for differences at an intra-annual scale, the results were inconclusive. Generally, whales were not found to distribute themselves preferentially in areas of highest salmon catch, however these analyses may reflect inappropriateness of temporal or species scale more than true randomness of distribution on the part of the whales.

Early 1990s vs. Late 1990s

The first hypothesis stated that movement behaviors of the pods are different during periods of population decline compared to periods of population increase. Both TA and LSI values for all three pods were significantly different between the early 1990s when the population was increasing and the latter 1990s when the population was decreasing. The relationship between whale movement behavior and population trend indicates that movement shape parameters could be an indication of population stress. Specifically, higher TA and LSI values could be a sign of higher energetic cost. The TA and LSI values were lower in the first half of the 1990s, when overall abundance of chum and all salmon species combined was higher than in the second half of the 1990s. This result was consistent with the prediction that years of higher salmon abundance would correspond with years of lower search effort, quantified as lower TA and LSI values. However, overall chinook abundance did not have a clear distinction between the early and latter 1990s and, therefore, there was no clear association with movement behavior as hypothesized. L pod was predicted to exhibit the highest area use and movement complexity of the three pods based on the higher mortality rates observed for L pod

whales. Generally, L pod did show higher TA and LSI values than either J or K pod, with the exception of 2001 when J pod showed the highest area use and movement shape complexity, which is discussed later.

The abundance of North Pacific salmon nearly doubled during 1975-1993 (Bigler et al. 1996). This period was then followed by a declining trend through the latter 1990s, reaching the lowest abundance in the 1997-1999 time period due to decreased oceanic productivity. Abundances of all species of salmon in southern BC were lower during this period compared to salmon runs in northern BC and southeastern Alaska. Size and condition of fish were also lower. In 1999, ocean conditions began to improve for juvenile salmon survival, exemplified by record high returns of pink to the Fraser River and sockeye to Barkley Sound in 2001 (DFO 2000; 2002). This supports the hypothesis that the SRC had adequate prey available during the early 1990s when their population was increasing, and therefore would have movement shapes that covered less area and were less complex than in the latter 1990s when the population was declining.

The differences in mean values of both TA and LSI between the early 1990s (1991-1995) and the latter 1990s (1996-2001) for the entire SRC as well as each individual pod were significant. However, it is difficult to separate these results from the significantly different sighting effort between the two time periods. Both TA and LSI values peaked in 1998, after which TA and LSI values began an overall decline. SRC whales were qualitatively observed to be nutritionally stressed more in 1998 than in any other year the SRC has been studied. Whales were considered nutritionally stressed if they exhibited “peanut head”, a narrowing of girth directly behind the head, or when shoulder blades could be discerned through the blubber (C. Emmons, pers. comm.). This peak in TA used by the whales and

LSI complexity mirrors low numbers of returning adult salmon and below normal juvenile survival, particularly for coho and chinook in the Strait of Georgia region (DFO 2000).

The distribution patterns of juvenile salmon also changed during the latter 1990s. Beginning in the mid 1990s nearly all of the juvenile coho left the Strait of Georgia and did not return until their spawning migration. In 2000 and 2001 there was a dramatic increase in the abundance of juvenile chinook, coho, and chum salmon in the Strait of Georgia. The presence or absence of juveniles in the inland waters is attributed to changes in climate and oceanography (DFO 2002). It is not known whether juvenile salmon make up a significant proportion of the SRC diet. It is known that if juveniles are not present in the region, the whales do not have the opportunity to supplement their diet with juveniles, as was the case in the latter 1990s.

J pod showed their highest TA and LSI values for all the years analyzed in 2001, in sharp contrast to both K & L pods. This would indicate that the movement patterns of J pod were driven by influences other than the driving influences of K or L pods. In this case, it is thought that while K & L pods responded to more favorable prey availability in 2001 by lowering the energetic cost of searching, quantified by lower TA and LSI values, J pod did not respond to increased prey abundance in a predicted manner. J pod's behaviors are particularly puzzling in light of the relatively low TA and lower LSI observed in 2000, the only year when chinook, chum, and all species of salmon had relatively low abundances.

The TA and LSI values of all three pods showed a peak in 1998. This corresponded to low relative abundance of chinook and all species combined, and relatively high

abundance of chum. This same pattern of high chum and low chinook and all species combined was also observed in 1992 when both TA and LSI values of the pods were generally low. This could either indicate that variables other than prey availability were driving movement patterns in at least one of those years, or the difference in the number of sightings between 1992 and 1998 were responsible for creating very different pictures of space use behavior by pod.

It would be particularly interesting to investigate whether the declining trend in TA and LSI values after 1998 continue to the present time since the SRC population began increasing in 2002. Since sighting effort has remained relatively consistent from the inception of the whale watchers spotting network in 1996, the comparison of late 1990s and early 2000s would be more informative than the comparison between the early and latter 1990s and is recommended for future study. Whale observations from 2002 to the present were not included in this study because they were not available at the inception of this project, and because availability of salmon data lags behind the present by 2 or more years.

Other top predators have displayed changes in spatial behavior related to prey availability. Patterson and Messier (2001) found that coyote densities and incidence of delayed dispersal were positively correlated with prey density. In other words, the coyotes generally stayed in the same area for a longer period of time during times of more favorable prey conditions. Conversely, coyotes were found to move around more in a searching pattern during periods of lower prey density (Patterson and Messier 2001). Similar examples are known for consumers at lower trophic levels. Eurasian red squirrels (*Sciurus vulgaris*) alter their home range size in response to food availability. Squirrels expanded their space use in years of low

food abundance and decreased their space use in years of relatively high food abundance (Wauters et al. 2005).

The findings that the SRC displays more convoluted movement patterns and uses more space during periods of decreased prey availability also seems logical in view of studies of the other killer whale populations. For example, in areas where salmon densities were lower, NRC whales were observed to travel greater distances, therefore expending more energy to obtain fewer calories (Nichol and Shackleton 1996). Hall (1986) observed that whales in Prince William Sound appeared to be more “relaxed” during peak salmon runs, meaning that the whales spent more time investigating the survey vessel, and more “aloof”, meaning that the whales were not very approachable or interested in the survey vessel during the winter months when salmon were not as abundant. This is consistent with the conclusion that a significant portion of a whales’ time must be spent hunting when the biomass of prey organisms is reduced whereas relatively little time is necessary to seek prey when large runs of salmon are present (Hall 1986).

Killer whales are not continually foraging, and are also utilizing space for resting, traveling, and socializing. However, foraging occupies more of the whales’ time than any other activity. Nichol and Shackleton (1996) concluded that A1 pod of the NRC spent 38% of the day foraging. SRC whales were observed to forage 42% of the day in one study and 47% of the day in a study a couple of years later (Heimlich-Boran 1986, 1988; Felleman et al. 1991). Space use has commonly been referred to as home range: the area in which an individual or population forages, mates, cares for young, and defends territory (South 1999). Unlike most terrestrial mammals, killer whales are not tied to a den, nest, burrow, or other central place when raising young. They are also not restricted in time or place for breeding and

do not appear to defend a territory against conspecifics. Their movement behaviors, therefore, can be assumed to be driven primarily by the search for adequate prey patches.

Spring- Early Summer vs. Late Summer-Fall

It was predicted that TA and LSI values would be higher in the late spring and early summer compared to the TA and LSI values observed in the late summer and fall. This prediction was based on the relatively high abundance of salmon migrating through the study region in the late summer and fall time period compared to other seasons. It was found that the differences in TA and LSI values between the two intra-annual time periods tested were generally insignificant. This result is most likely due to the scarcity of sightings in the spring rather than a true reflection of whale movement behavior. While J pod has been sighted in all months of the year, K & L pods are typically not seen in the waters around the San Juan and Gulf Islands, where the whales are most often sighted, before May or June in most years, and in some years not before July (Osborne 1999).

Landscape indices should be analyzed at different scales to adequately investigate pattern (Li and Wu 2004). TA and LSI were therefore analyzed from multi-annual to seasonal scales. The hypothesis of higher complexity of movement and more space use in the spring-early summer period compared to the late summer-fall period was based on the idea that whales do not have to search as much for prey or cover as large an area seeking prey in the latter half of the year. The late summer-fall period is when salmon are moving through the region in high concentrations and are presumed to be more available to the whales. If sockeye and pink salmon dictated whale behavior, changes in whale movement and space use should be particularly evident. However, if the southern residents are foraging selectively on

chinook salmon, there may not be a detectable change in whale movement behavior as chinook are migrating towards river mouths in the spring and early summer as well as late summer and fall. The Fraser River supports the largest number of chinook runs in Western North America (Dempson et al. 1998). It is therefore likely that chinook are migrating towards or in the vicinity of the Fraser for much of the year which is in contrast to the intense peaks of abundance of sockeye, coho, and pink runs occurring in the late summer through fall.

By averaging the quantified values of whale movement behavior over a week period, it was possible to decipher a more general pattern to the whale's movements by smoothing out outliers that may be driven by other behaviors. During a week period, the areas most important to foraging would be expected to be those that are occupied most frequently. It was also possible to then compare the commercial fish catch data with the whale movement data on the same scale. Salmon are not likely present in one area for a day only, but for weeks or months in various concentrations. Peak pulses of salmon runs generally last from a week to several weeks (Candy and Quinn 1999). A weekly scale was expected to be coarse enough to show patterns of movements in areas representative of the availability of prey, while still being fine enough to demonstrate more subtle differences that might reflect different species or runs of salmon. In order to compare time scales and movement patterns, annual LSI averages were calculated as well and compared to the salmon data. This comparison allowed examination of differences in time and space when salmon were available in relatively high concentrations and when they may not be available at all as prey.

The hypothesis that whales do not travel over as much area or in as erratic a pattern when fish are more available than when they are less available assumes that the

prey resource is somewhat static and does not quickly learn and adopt evasive anti-predator behavior. If a patch of salmon were to become more adept at evading predation by whales within a short period of time (less than a week) of being exposed to predation pressure, then it would be more profitable for the whales to continually search for naïve prey patches rather than remaining in one area. However, while salmon are available in a given management area for weeks, or even months at a time, individual fish are continuously moving through in their migrations towards their natal watersheds (Candy and Quinn 1999). It is therefore theoretically possible for the whales to remain in a relatively small area while “naïve” fish continuously move through. As these are adult fish nearing the end of their life, it is reasonable to assume that they have encountered many predators throughout their migrations, including other groups of killer whales, and it would therefore be inaccurate to assume that they are naïve.

For tests of differences in whale movement within years, results have less to do with variations in sighting effort across years and more to do with true differences in shape patterns. When sighting effort was broken out into seasonal effort, there were no obvious discrepancies between proportion of sightings reported by season from year to year (Figure 2.5). Yet the consistent scarcity of whale observations up to week 30 may be the cause of the lack of significant differences seen in LSI and TA values between the two time periods. It is likely that if more observational data were available for the whales in the late winter and spring months that their movement patterns would be more complex and the space used larger than what is observed in the late summer through fall seasons. The one year all three pods did exhibit significant intra-annual differences in shape metrics was 2001. 2001 was also the year with substantially more whale sightings than any other year analyzed, and more whale sightings in each season. This made 2001 a better representation of

whale movement behavior across the year. Overall, however, the available data may not be sufficiently complete to adequately compare movement behavior across seasons within years.

Whale Presence in Management Areas Reporting Highest Salmon Catch Density

Based on evidence that indicates salmonids are the preferred prey of the southern residents, it was hypothesized that there would be a significant relationship between whale distribution and salmon catch. Yet the whales generally did not appear to be present in the management area with the highest density of salmon catch for a given week more often than would be expected by chance. These results indicate that the whales are not preferentially occupying areas of higher salmon density, and may be distributing themselves based on other factors, such as alternative prey species, or areas with physical features that concentrate fish prey. It is also possible that the whales are more proficient at finding salmon than the commercial fishermen, and the commercial data is not an accurate representation of the distribution and abundance of salmon.

Evaluation of whale presence in management areas of highest salmon catch density was the first step in examining whale presence in association with known salmon presence at the weekly temporal scale. The results indicated that in only two years out of the eleven analyzed was whale presence considered non-randomly distributed. Overall this would indicate that either whales were not preferentially occurring in management areas that reported the highest density of fish catch, or the whales were in those areas and not observed. The majority of management areas reporting the highest density of fish catch during the late winter and spring were located in the Strait of Juan de Fuca. It is likely that if whales were present in the Strait in the spring months when inclement weather can greatly interfere with

visual observations, and where there are fewer people watching for whales, frequency of observation would be biased low. The majority of management areas reporting the highest density of salmon catches in the summer and fall months were located in the area around the San Juan Islands and throughout Puget Sound. If the whales were in either of these regions they are more likely to be reported due to higher concentrations of people on the look-out for whales and more vantage points from land from which to spot whales.

It is possible that the SRC occurs in areas of the highest density of particular species rather than in areas of the highest density of any species. A follow-up analysis might examine whale presence in the management areas reporting the highest chinook or chum catch. It might be found that whales do occur preferentially in those areas.

For weeks when at least one pod occurred in the management area of highest density of salmon catch, the catch was of sockeye for 12 weeks, chinook for 2 weeks, and coho for 1 week. Sockeye is one of the most abundant of the salmon species in the Puget Sound-Georgia Basin region and while they are available for a relatively short period of time as fish are migrating through the region toward the Fraser River and the Lake Washington watershed (Burgner 1991; Hodgson and Quinn 2002), these results would indicate that the whales are positioning themselves where the highest concentrations of fish are observed. If this is true, then results of species specific analysis might not be significantly different from these results.

It is also possible that whales are creatures of habit and occupy areas of predictable aggregations of prey rather than areas of the highest prey density. Despite the

ability to travel large distances per day, the whales distribute themselves with incomplete knowledge of prey distributions throughout their range (Bailey and Thompson 2006) and perhaps must therefore chose foraging grounds based on physical features or previous experience.

The weekly scale may in fact be too fine to adequately evaluate whale presence in relation to density of salmon catch. Salmon catch is contingent on regulations while whale foraging behavior is not. By stepping back to a two, three, or four week scale, a different picture might emerge. The week of highest density of catch may not properly reflect the week of highest fish concentration in the area. The whales themselves may in fact be better indicators of fish abundance and an analysis of the frequency of sightings per area throughout a 2 week or month long period may show higher association with the fish catch data. Another approach might be to look at whether the whales were present in the area of highest density of fish catch in the week prior to or the week following the reported high catch.

The scale of individual management areas may be too fine as well. By comparing regions of fish catch density and whale presence, it is likely that higher correlation would be found. Yet caution should be used with a larger scale. Correlation is certain to be found if the area in question is broad enough, yet biological meaning at too large a spatial scale can become unclear. If the areas evaluated are so large as to encompass most or all of the whales' average distribution, it would be impossible to decipher selection of one area over another based on differences in habitat parameters.

Whale Presence in Areas of Highest CPUE

Generally, the whales did not appear to spend the highest proportion of time that they were observed in management areas reporting the highest CPUE. This seemed particularly true for CPUE of chinook, the whales preferred prey species. It is possible that whales competed with fishermen for chinook or scared chinook away from fishing vessels, thus lowering the CPUE reported in those management areas where whales were.

Fishing activity may also deter whales from an area of concentrated salmon. While this is always a possibility, the occurrence of killer whales actively depredating fish from fishing gear in many parts of the world (Dahlheim 1988; Ott and Danilewicz. 1998; Secchi and T. Vaske 1998; de Stephanis 2004; Kock et al. 2006) along with personal observations of the SRC among purse seine operations indicates that this type of interaction is unlikely for this group of whales.

It is also possible that fishery regulations limit the picture of relative salmon abundance and distribution to the point of being an inaccurate proxy for prey availability. While density of salmon catch per management area appeared comparable between BC and WA waters (Figure 2.3), CPUE may not be equal. If this is the case, and CPUE is generally higher in BC waters, then it is likely that the whales are not spending the highest proportion of time in areas of high CPUE on the US side of the border because they are in areas of even higher salmon CPUE in BC.

Changes in regulations, season timing, and gear types are recognized as potentially influencing the results. Because of this, results are interpreted as representing minimal associations and relative presence. When fish are caught in a particular area at a particular time, it is assumed that that specific species of salmon is

present, and its relative abundance is proportional to catches in other areas at the same time period. However, it is not assumed that fish are absent in areas reporting no catch. Recreational and commercial catch data from Georgia Strait were considered to be representative of total abundance through the early 1990s (Sweeting et al. 2003). Catch can be regarded as the lower bound to run size with reasonable certainty (Bledsoe et al. 1989). In other studies, catch data have been used as an index of relative abundance of returning adult salmon (Middlemas et al. 2006). Because of biases and inconsistencies with all salmon data, assumptions are unavoidable. The analyses in this study represent a reasonable interpretation of the data at hand.

Differences Among Pods?

Any differences in movement behavior or space use seen among the pods may help elucidate the differences in survival rates among the pods, specifically between L pod and J & K pods. Because L pod experienced the most intense mortality rates during the last period of population decline (Figure 1.2), it was expected that L pod would display the most complex distribution patterns and have the highest space use of any of the SRC pods. L pod did in fact display overall higher TA used than the other two pods, particularly in 1998, the year of lowest salmon abundance in the study region.

As the largest pod, it is possible that L pod exhausts prey patches more quickly than either J or K pods and must therefore spend more time traveling between prey patches. The difference between L pod and J & K pods was not as pronounced when comparing annual LSI values. Generally, L pod's movement complexity was higher than the other two pods. K pod appeared to have the second highest TA and LSI values, followed by J pod. The exceptional year to this pattern was 2001, when

J pod had both TA and LSI values far exceeding those of either L or K pods. Both K & L pods had TA and LSI values in 2001 comparable to those observed in the early 1990s, which fits with the increase in salmon abundance in 2001 (Figure 2.8). The high TA and LSI values observed for J pod during that year does not fit with the expected pattern. This discrepancy could not be attributed to an increase in sightings of J pod in 2001, as the number of sightings recorded were similar to those recorded for K & L pods. If the number of sightings in a year determined TA and LSI values, then all pods would show roughly the same space use and movement shape complexity.

By treating all L pod sightings as one pod, it is possible that the space use of L whales was over-represented. L pod has been seen to travel in separate sub-pods, creating the opportunity for two different groups of whales in two separate locations to be identified as L pod. This would consequently exaggerate the space use of the sub-pods. This is an important distinction if the questions asked concern the movement behaviors of individual matriline. If, however, a coarser comparison between pods is being made, then perhaps combining the distribution patterns of the sub-pods does not exaggerate pod movements. It can be argued that the movement behavior of the pod is a combination of the movement behaviors of the individual matriline put together. The fact that matriline within L pod occasionally travel independently of each other, while matriline within J & K pods tend not to separate, is an informative difference between the pods. Therefore, representing the space use of all of the sub-groups does not over-represent the movement behavior of the pod as a whole.

While the trends in the TA and LSI are similar among the three pods, with the exception of 2001, there are observable pod differences. Space use differences

among the pods may be attributed to differing demographics and cultural differences between the extended family groups. Whatever the ultimate cause, differences in movement patterns are seen and L pod did in fact exhibit the highest space use and movement complexity, suggesting that L pod whales expended the most energy traveling during the study period.

Significance

The SRC consists of fewer than 90 individuals (Balcomb, unpublished data). Their extremely small population size along with their genetic and behavioral isolation from other killer whale communities has fueled concern over the future viability of the population. This study has been an important step in modeling the space use of the SRC and linking that movement behavior to variables such as population trends and relative prey availability. A simple conceptual model of whale space use was used, making as few assumptions as possible, as a first approach to representing the observational whale data in a meaningful way. The landscape metrics chosen for analysis were favored over other measured metrics because they were considered to have biological meaning. Energy expenditure and search behavior are closely tied to foraging effort (Hoelzel 1991; South 1999). Many studies have selected landscape metrics by the convenience of software programs rather than the ecological relevance to the system (Li and Wu 2004). Li and Wu (2004) also warned that the “indiscriminate use of landscape indices hinders efforts to establish relationships between spatial pattern and process, especially in correlation analysis.” This study aimed to avoid such a pitfall.

CHAPTER 3: POPULATION TRENDS OF WHALES AND SALMON

INTRODUCTION

There are three known eco-types of killer whales (*Orcinus orca*) in the northeast Pacific Ocean. “Transient” type whales live singly or in small pods, predate on marine mammals, are generally quiet, and do not have predictable seasonal ranges (Baird and Dill 1996). “Offshore” killer whales were first documented in the mid-1990s and little is known of their life history. They appear to travel in large pods, are highly vocal, and forage on fish (Baird 2001). “Resident” killer whales live in large family pods, forage on fish, are highly vocal, and can have predictable summer home ranges (Felleman et al. 1991). The southern resident community of killer whales (SRC) has been studied since the mid-1970s in the inland marine waters of southern British Columbia (BC) and Washington State (WA). The SRC is made up of three matrilineal pods, “J”, “K”, and “L”, and together they are acoustically, genetically, socially, and morphologically distinct from any other community of killer whales (Balcomb and Bigg 1986; Dahlheim and Heyning 1999; Hoelzel et al. 2002; Krahn et al. 2002).

The SRC has fluctuated in numbers over the past three decades of study (Bain and Balcomb 1999). A precipitous decline from 98 to 80 whales in the latter 1990s prompted research into the possible causes of the decline (Baird 2001; Krahn et al. 2002). One of the potential factors contributing to the waning population is food limitation. Predator-prey relationships are complex and a critical component of any species life history. Better understanding of a predator’s dependence upon its primary prey is crucial for informed management decisions.

Small populations are prone to loss of genetic diversity and productivity from genetic drift and inbreeding depression. They are prone to extinction due to random fluctuations in survival or reproductive rates, variation in environmental conditions such as a reduction in food supply, or dispensatory effects. Even populations with over 500 individuals may be at risk of extinction depending on the circumstances involved (Reisenbichler 1997). As the SRC population is below 100 individuals, it is at greater risk of extinction, warranting an increased need for research that better directs management decisions affecting the SRC. It is critical to develop a better understanding of the pod and species-specific associations between the SRCs and their presumed prey if effective management of both the SRC population and the salmon stocks on which they depend is to be implemented.

Killer Whale Diet

As a global species killer whales (*Orcinus orca*) are generalist predators, consuming a wide variety of prey (Table 1.1) and employing a wide range of foraging tactics to capture that prey (Dahlheim 1981; Similä et al. 1996; Dahlheim and Heyning 1999). However, at the population level killer whales appear to specialize in what and how they hunt (Christensen 1982; Hoelzel 1993; Baird and Dill 1996; Visser 1999). Available evidence suggests that the SRC of killer whales feeds preferentially on salmonids, specifically selecting chinook salmon (*Oncorhynchus tshawytscha*) (Felleman et al. 1991; Ford et al. 1998; Ford and Ellis 2005; Ford et al. 2005). When the SRC population declined from 98 whales in 1995 to 80 whales in 2001, food limitation was speculated to be a factor in the decline (Krahn et al. 2002; Wiles 2004). Population trends of wild salmon runs in the Pacific Northwest of North America have generally declined in both body size and weight over the past several decades (Ricker 1981; Bledsoe et al. 1989; Bigler et al. 1996; Beamish et al. 1997; Cox and Hinch 1997; Noakes et al. 2000). In some

instances hatchery fish have supplemented or even replaced wild runs. While there are numerous direct and indirect detrimental effects of hatchery fish on wild populations (Nehlsen et al. 1991; Beamish et al. 1997; Reisenbichler 1997; Morishima and Henry 2000; Sweeting et al. 2003), it is assumed that killer whales make no distinction between fish of different origin.

Predator-Prey Relationships

Predators selectively forage for preferred prey species. Their diets do not necessarily reflect population densities of available prey (Matsuda et al. 1987). Specialization is expected to occur when the quality of preferred prey species becomes marginally profitable due to competition and ultimately depletion of available prey. Specialization is also likely when prey types vary widely in quality, and require differing levels of effort and experience to capture and consume (Lyons 1991).

Salmon are both large bodied fish and relatively high in caloric value. They are generally distributed within 100 meters of the surface, and tend to aggregate above seamounts and at river mouths, making them easier to capture than deep dwelling or sparsely distributed fish species (Candy and Quinn 1999). It is therefore understandable if SRC show preference for salmon above other species of fish in the region. This has been seen in tissue sampling studies of foraging northern resident community killer whales (NRC). During July through August of 2004 90% of the test fishery catches off northeastern Vancouver Island were comprised of sockeye (*Oncorhynchus nerka*) and pink (*O. gorbuscha*) salmon which were migrating through the area. Scales and other tissues collected near foraging whales however, consisted of 95% chinook (*O. tshawytscha*) and 5% coho (*O. kisutch*), indicating intense selectivity on the part of the whales that was independent of prey

abundance (Ford and Ellis 2005). Age-selectivity was also observed by Ford and Ellis (2005). The mean age of chinook captured by whales was 4.20 years, while the mean age of chinook in the region is 3.52 years. The whales appear not only to be species selective, but to feed preferentially on larger individuals within that species. Studies of the NRC have also found spatial overlap of pods and specific species of salmon, suggesting that there may be pod-specific prey preferences (Nichol and Shackleton 1996). Observations of whales in central and southern Puget Sound appear to overlap with the timing of chum salmon (*O. keta*) runs (Heimlich-Boran 1986). It is likely that southern residents exhibit similar selectivity to the NRC in their foraging habits.

Salmon production varies from region to region, potentially making certain locations more profitable foraging grounds than others. Tides, currents, bathymetry, and other physical and biological factors influence the productivity of different areas, making some locations more successful salmon rearing or aggregating habitat. It is therefore expected that whales have a higher number of significant correlations with salmon destined for spawning regions that are more productive than others.

Because killer whales are long-lived animals, it can be expected that there is a lag period between changes in prey availability and whale population size changes, whether through mortality or birth rate. The approximately 17 month gestation period, 1.5 year lactation period (Baird 2001), and the necessary relative fitness of an adult female prior to conception also suggests that a population reaction to food supply in the form of birth rate would not be immediate. Increased mortality due to an insufficient food supply may be recorded within the same year of the onset of nutritional stress, or 1, 2, perhaps even 3 years from the time of lowered prey

availability. Studies of other killer whale populations have found that population dynamics are driven more by changes in survival than changes in reproductive output (Olesiuk et al. 1990; Olesiuk et al. 2005). The results of Ford et al. (2005) indicate that a one year lag between chinook abundance index and deviation from expected whale mortality proved the most significant in their analysis. However, they found that 0 to 2 year lag periods were also statistically significant in their analysis.

Objectives

Given predator responses in other systems to variations in prey abundance or availability, and the SRC preference for salmonid prey, testing correlations between salmon and whale population trends is a significant step towards understanding killer whale foraging ecology and population dynamics. Correlations between specific pods, species, or regions would be particularly beneficial in aiding management plans aimed at bolstering the SRC or particular salmon run populations. Likewise, if strong relationships are not found between the SRC and salmon populations, more research effort should be focused on potentially available alternative prey species, or other factors viewed as possibly significant in the long-term survival of the SRC.

Four hypotheses were tested regarding relationships between the population trends of whales and salmon: (1) correlations between whales and salmon are species specific (2) correlations between whales and salmon are pod specific (3) correlations between whales and salmon are region specific (4) a one year time lag between salmon abundance and whale abundance will produce the highest number of significant positive correlation.

The first hypothesis states that correlations between the SRC and salmon are species specific. It is predicted that J, K, and L pods exhibit stronger correlations with chinook and chum salmon than with any other species. If correlations are found between salmon numbers and the whale population size, it can be concluded that relationships with different salmon species, or associated covariates, influence SRC population dynamics.

The second hypothesis states that correlations between whales and salmon are pod specific. It is predicted that L pod would exhibit correlation patterns that are different from J & K pods. This is predicted because L pod has experienced the most extreme fluctuations in population of the three pods (Figure 1.2), and it is presumed that prey availability has been a factor in pod survival rates. Therefore, L pod is expected to show different prey associations. If correlations are found to be pod specific, with particular differences evident between L pod and the rest of the population, it can be concluded that relationships with different salmon species may influence population dynamics.

The third hypothesis states that correlations between the whales and salmon are region specific. It is hypothesized that the whales will have higher correlation to chum salmon destined for central (CPS) and southern Puget Sound (SPS) than other regions because chum salmon is the dominant species in southern Puget Sound. It is also hypothesized that the whales will be more highly correlated to chinook salmon migrating to south Puget Sound, as stocks from that region have had the highest run sizes of all the analyzed chinook populations throughout the 1990s. If whales are positively correlated with coho salmon, it is expected that the region of most correlations would be northern Puget Sound (NPS), based on run-size data. The San Juan Island region (SJI) (as defined below) is expected to have

the highest correlations of pink and sockeye salmon due to the high output of these species from the Fraser River watershed.

The fourth hypothesis states that time lags of particular durations will produce more significant correlations between whales and salmon than others. Specifically, it is hypothesized that a one year lag period between salmon abundance and whale abundance will produce more significant correlations between salmon and whales than lag periods of any other duration. If correlations at the one year lag period are found more frequently than correlations at any other lag period then it can be concluded that the one year lag period best predicts population reaction of whales to salmon abundance. If no single time lag duration appears more frequently than any other it can be concluded that reaction of whales to salmon abundance is not limited to a specific time lag. Time lags may be specific to each salmon species' life-history, previous physical condition, and other factors such as fecundity and mean age of the whales.

METHODS

Population Data

Annual census data of the SRC were obtained from the Center for Whale Research (CWR). Each individual in the SRC is identifiable by natural variation in saddle patch coloration and dorsal fin size and shape (Balcomb and Bigg 1986). Births, deaths, and associations have been recorded from 1974 to present (Bain and Balcomb 1999). This dataset is an exact annual record of population size and is not an estimate, which is very unusual in animal population studies. Every year of

available data were used in this analysis (1974-2005). These data represent total annual abundance of the SRC, as well as annual abundance for each pod.

Two sets of salmon data were used to test for correlations with whale numbers, (1) total run-size and (2) escapement data (figures 3.2-3.5). All species of eastern Pacific salmon were used in these analyses, where available: chinook, early chum (or summer chum), normal chum (or fall chum), late chum (or winter chum), coho, pink, and sockeye. Total run size data were used as a proxy for salmon population sizes. Total run size refers to the combination of catch and spawning population (escapement) and is calculated annually (Scott and Geiger 2000; PFMC 2006). Run size data were obtained from the Washington Department of Fish and Wildlife (WDFW) and the Pacific Fishery Management Council (PFMC) and were summed into management area and regional totals for each species (Figures 3.1, 3.6 and 3.7). The availability of data varied in space and time for each species of salmon. Available run-size data by year for each species spawning in each region analyzed are summarized in table 3.1. The average annual run-size numbers for each species and region are displayed in Appendix table A1.

Table 3.1. Summary of available total run-size data by region, species, and year. SJdF= the Strait of Juan de Fuca; SJI= San Juan Islands and Fraser River; NPS= Northern Puget Sound; CPS= Central Puget Sound; SPS= Southern Puget Sound; and HC= Hood Canal.

Total Run-Size

SPECIES	SJdF	SJI	NPS	CPS	SPS	HC	Total PS
Chinook	1981-2004	1981-2004	1981-2004	N/A	1981-2004	1981-2004	1981-2004
Early Chum	1974-2004	N/A	N/A	N/A	1968-2004	1974-2004	1974-2004
Normal Chum	1968-2002	N/A	1968-2002	N/A	1968-2002	1968-2002	1968-2004
Late Chum	N/A	N/A	N/A	N/A	N/A	N/A	1968-2002
Coho	1981-2004	1981-2004	1981-2004	N/A	1981-2004	1981-2004	1981-2004
Pink	1981-2003	1969-2005	1981-2003	N/A	1981-2003	1981-2003	1981-2003
Sockeye	N/A	1968-2004	N/A	N/A	N/A	N/A	N/A

Salmon escapement data were also tested against whale population data because there is a longer time series of escapement data available than for total run size. Escapement data were also tested to explore any differences in the results of escapement versus total run size. Escapement refers to the number of reproductively mature fish entering freshwater to spawn (Knudsen 2000). It is therefore an estimate of the number of fish which were not harvested, and are presumed to make up the spawning population of that year. Freshwater mortality is generally not reflected in escapement numbers, unless the estimates are based on counts made near the actual spawning grounds. Escapement estimates are generally based on counts taken at fish ladders, weirs, traps, or by aerial or foot survey (Zhenming et al. 2001). Both commercial and recreational catch regulations are based on escapement goals for a particular stock each year. The estimated number of fish beyond the minimum number needed to sustain the population is allocated to the respective fisheries. Therefore escapement is managed to remain relatively constant year to year (Scott and Geiger 2000). However, predicting run size is very

difficult and there is wide fluctuation observed year to year. Because escapement numbers are managed, they are not a reliable indicator of salmon abundance. However, escapement can be used as a measure of the minimum number of salmon potentially available to the SRC in a given year.

Total annual salmon escapement data obtained from WDFW, PFMC, the Canadian Department of Fisheries and Oceans (DFO), and the Muckleshoot Indian Tribe were summed into management area and regional totals for each species (Figures 3.1, 3.6 and 3.7). Total escapement refers to returning adults of both wild and hatchery origin. Management area and region totals include escapement estimates of salmon runs returning to spawn in rivers draining into those management areas. Years of escapement data varied by species, but all years available were used in the analysis. The years of available escapement data for each species spawning in each region analyzed are summarized in table 3.2. The average annual escapement numbers for each species and region are displayed in Appendix table A2.

The most recent chum salmon data (1998-2004) were not available by river, and therefore could not be divided by region in the same manner that previous data were. The data were grouped by regions that matched those used in this study with the exception of southern Puget Sound. Where this study differentiated between southern and central Puget Sound, the most recent years of chum data lumped the escapement data in a region designated “South Puget Sound”. Data grouped like this only went back as far as 1981, so altering the regions in this study to lump south and central Puget Sound together would have resulted in a loss of more than a decade of salmon data. To combat this issue, the recent years of escapement in “South Puget Sound” were divided into the regions central and southern Puget Sound. The proportion that “South Puget Sound” escapement made up of the

summed escapement for central and southern Puget Sound was calculated for each year and then averaged. This average proportion was then used to calculate the percentage of the “South Puget Sound” data assigned to SPS and the percentage assigned to CPS. These calculations provide a reasonable estimate of the proportion of fish bound for rivers in the two regions. The estimates are not exact, but the escapement estimates are not precise either. As long as trends in the data are preserved, the exact number of fish in either region is not critical.

Table 3.2. Summary of available escapement data by region, species, and year. SJdF= the Strait of Juan de Fuca; SJI= San Juan Islands and Fraser River; NPS= Northern Puget Sound; CPS= Central Puget Sound; SPS= Southern Puget Sound; and HC= Hood Canal.

Escapement

SPECIES	SJdF	SJI	NPS	CPS	SPS	HC	Total PS
Chinook	1968-2004	1968-2004	1968-2005	1968-2005	1968-2005	1968-2004	1968-2004
Early Chum	1968-2004	N/A	N/A	N/A	1968-2004	1968-2004	1968-2004
Normal Chum	1968-2002	1968-2002	1968-2002	1968-2002	1968-2002	1968-2002	1968-2002
Late Chum	N/A	N/A	N/A	N/A	1968-2004	N/A	N/A
Coho	1968-2004	1968-2004	1968-2004	1968-2004	1968-2004	1968-2004	1968-2004
Pink	1969-2003	1969-2003	1969-2003	1969-2003	1969-2003	1969-2003	1969-2003
Sockeye	N/A	1968-2004	N/A	1972-2004	N/A	N/A	1972-2004

As with all population estimates, there are caveats with regard to use of these data. For escapement data, caveats include variation among rivers surveyed, time spent surveying, and methodology used to calculate numbers of returning fish (Bledsoe et al. 1989; Zhenming et al. 2001). However the data represent the best available estimates of numbers of salmon potentially available as prey to the SRC on an annual scale.

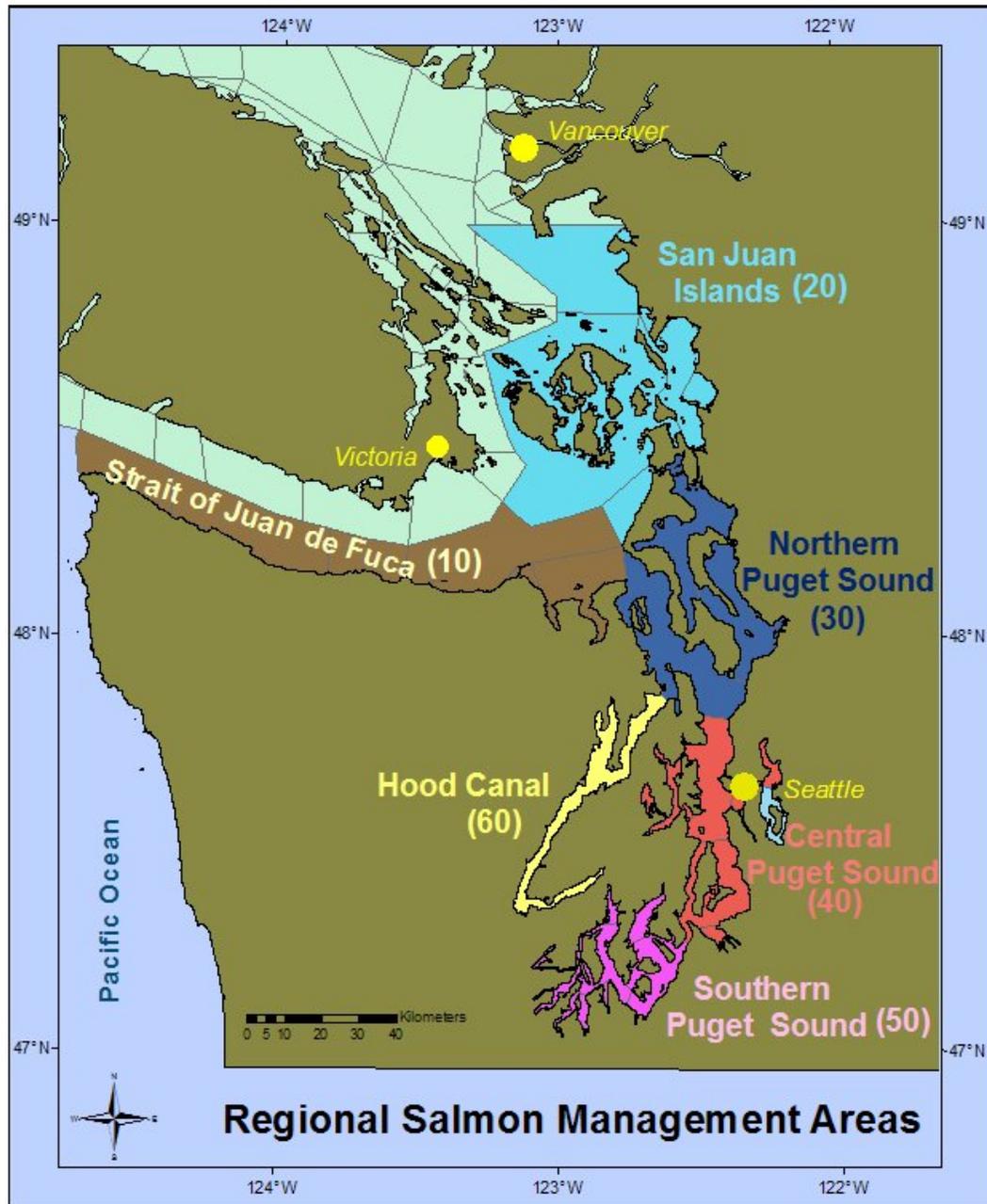


Figure 3.1. Regions of escapement grouping. Strait of Juan de Fuca (SJdF), San Juan Islands (SJI), Northern Puget Sound (NPS), Central Puget Sound (CPS), Southern Puget Sound (SPS), and Hood Canal (HC). Note: sockeye escapement and total run size of pink and sockeye returning to the Fraser River is grouped in SJI.

Total Run-Size of Puget Sound Salmon

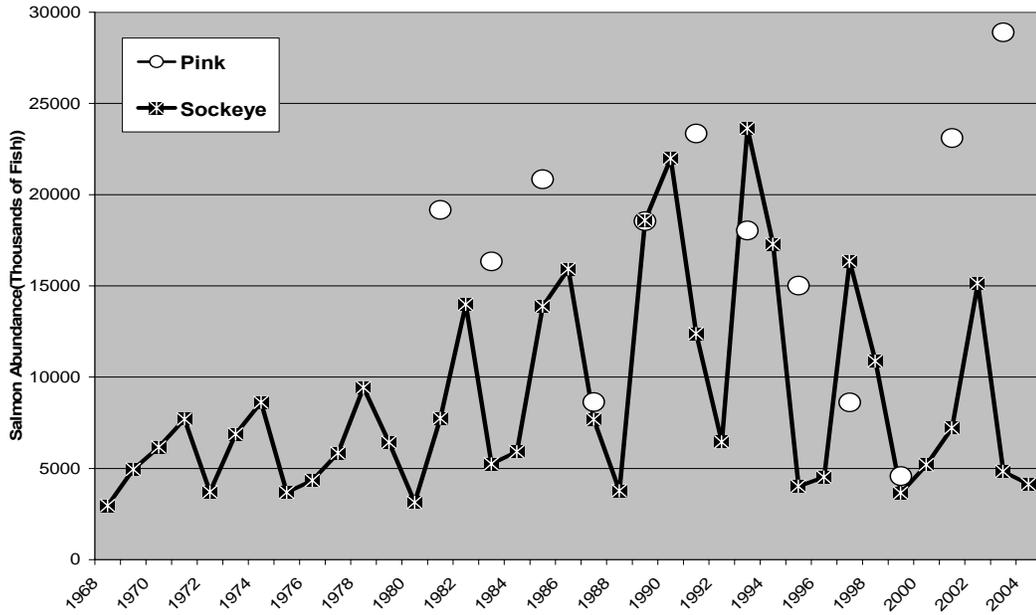


Figure 3.2. Total run-size data of Puget Sound pink and sockeye salmon, totaled by species and year from 1968-2004.

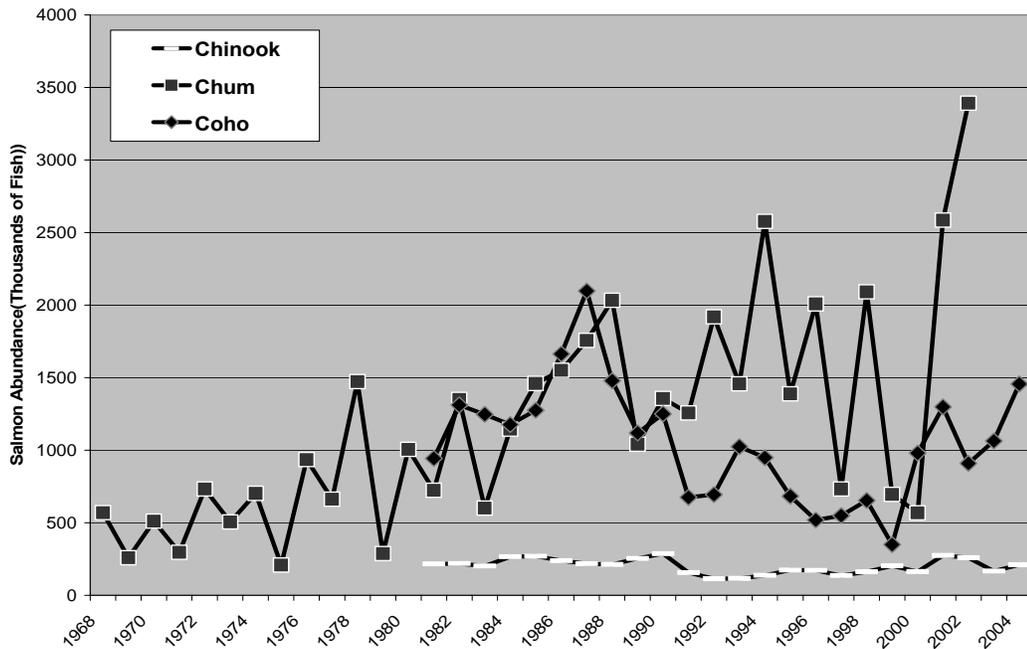


Figure 3.3. Total run-size data of Puget Sound chinook, chum, and coho salmon, totaled by species and year from 1968-2004.

Escapement of Puget Sound Salmon

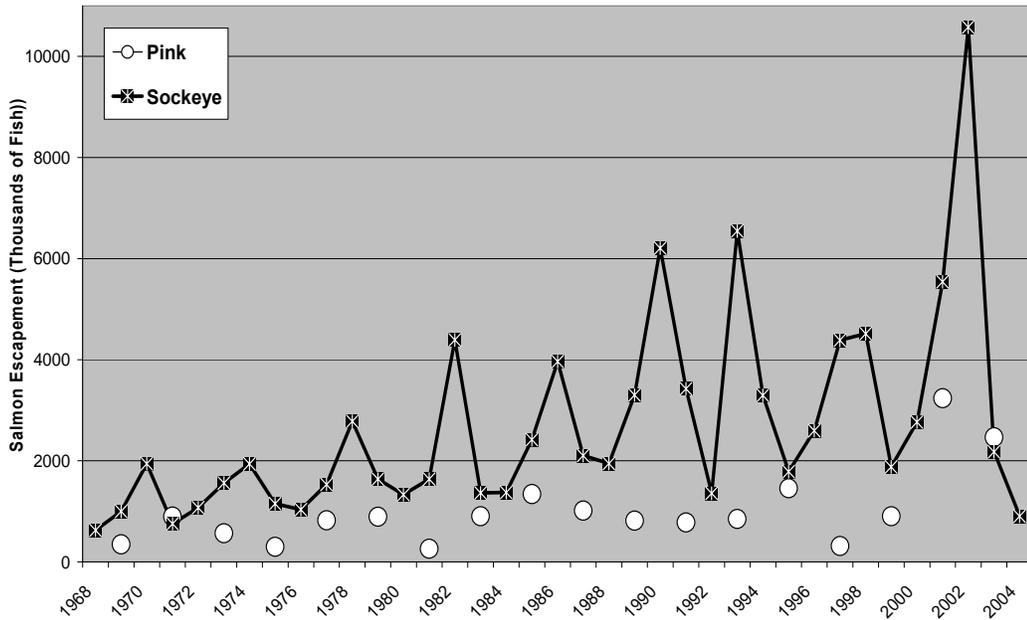


Figure 3.4. Escapement data of Puget Sound pink and sockeye salmon, totaled by species from 1968-2004.

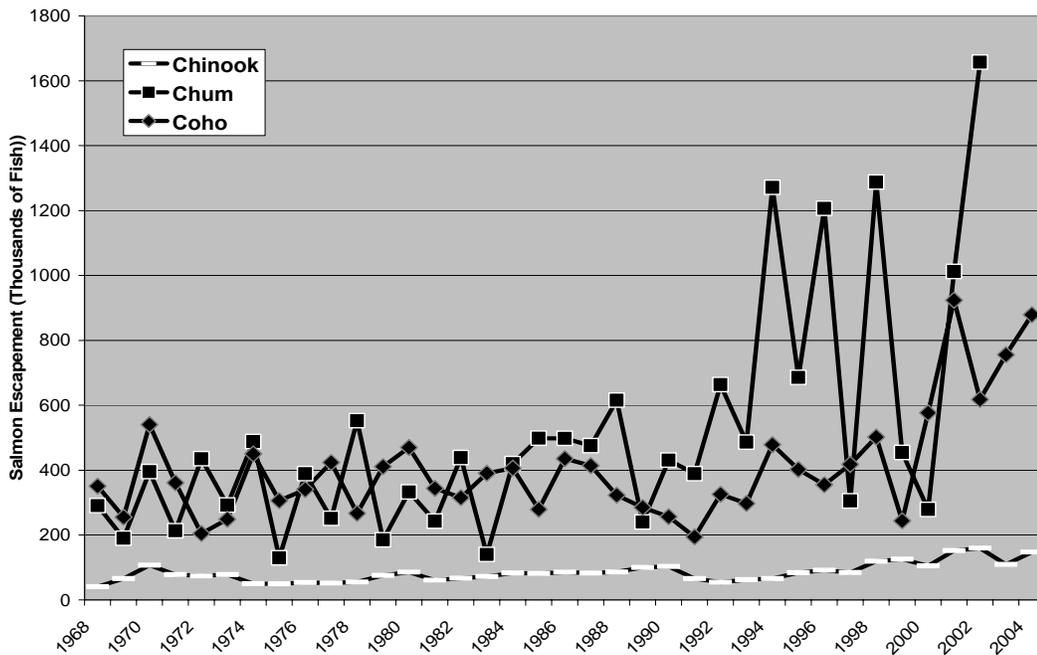


Figure 3.5. Escapement data of Puget Sound chinook, chum, and coho salmon, totaled by species from 1968-2004.

Average Salmon Abundance By Region

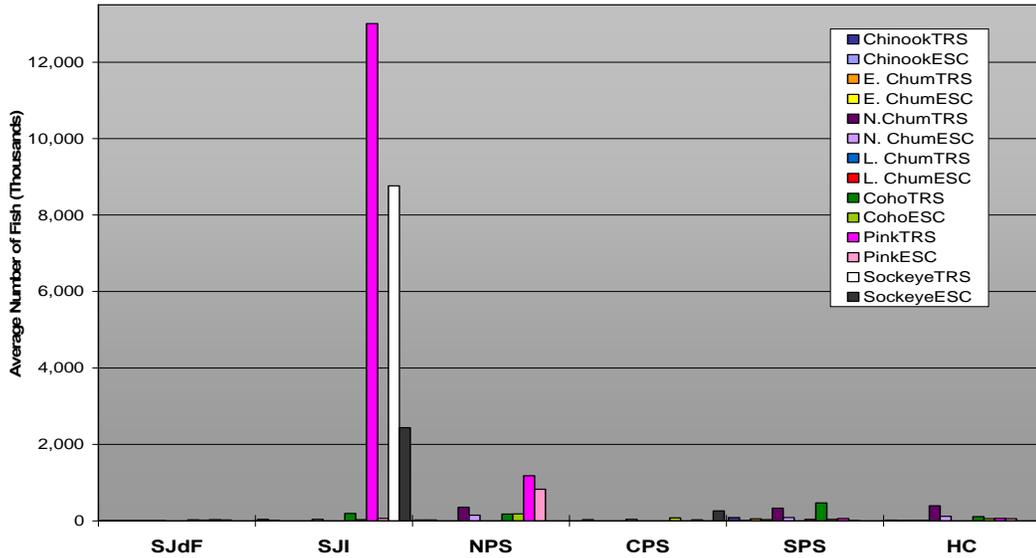


Figure 3.6. Salmon total run-size and escapement data for all species averaged across years of available data for each study region.

Average Salmon Abundance By Region: Minus Pink and Sockeye

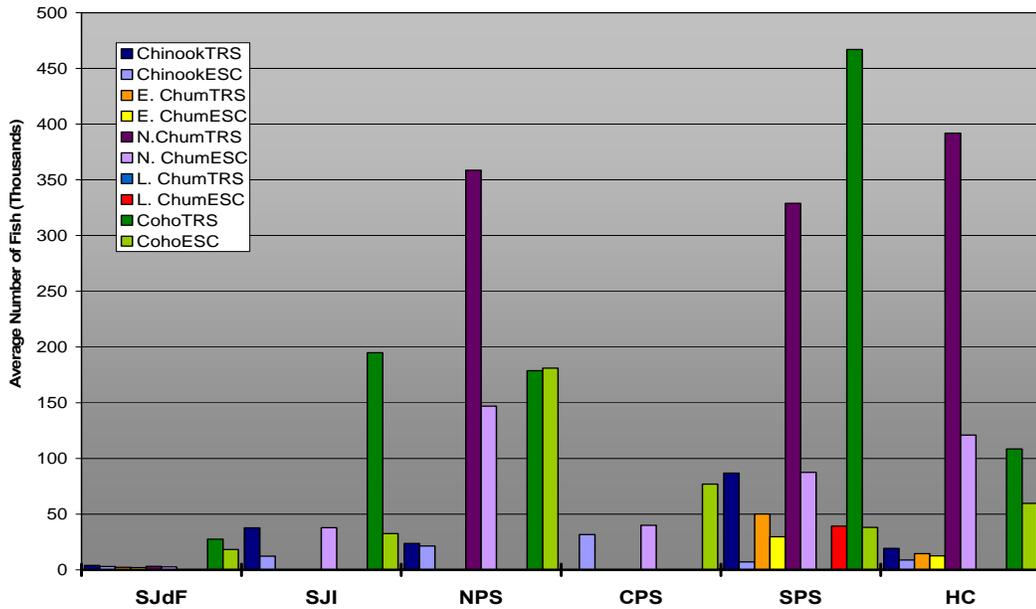


Figure 3.7. Salmon total run-size and escapement data for all species except for sockeye and pink, averaged across years of available data for each study region.

Annual Population Trend Analysis

Annual whale abundance data and salmon total run-size and escapement data were plotted to visually explore patterns between salmon population trends and trends in total whale population. The wide scattering and non-normality of the data (Figures 3.2-3.5) led to the conclusion that the Spearman's rank correlation test would be most appropriate to investigate correlations between salmon abundance and SRC population trends (Equation 2). Spearman's rank correlation test evaluates the significance of correlations between two monotonically increasing or decreasing data series and is not affected by changes in scale (for example, pink escapement numbers and whale population numbers are on scales that are orders of magnitude different from one another) (Zar 1999).

Autocorrelation tests were performed and the results were insignificant. All statistical analyses were performed using the statistical software package SPSS (version 13.0, Chicago, Illinois USA). Alpha values of both 0.05 and 0.01 were used in the synopses of these results. Whales and salmon were considered correlated when the correlation coefficient was significant for two or more time lag periods. Significant correlations for only one time lag duration were considered chance results. Significant correlations across all lag periods tested were considered to have the strongest relationship. Spearman's Rank Correlation Coefficient is calculated as follows:

$$r_s = \frac{\sum(R_{i1} - \bar{R}_1)(R_{i2} - \bar{R}_2)}{[\sum(R_{i1} - \bar{R}_1)^2 \sum(R_{i2} - \bar{R}_2)^2]^{1/2}} \quad (2)$$

Where: r_s = Spearman rank correlation coefficient

\bar{R}_1 = the mean of the ranks R_{i1}

\bar{R}_2 = the mean of the ranks R_{i2}

The ranks R_{i1} and R_{i2} are the integers $1, \dots, n$, therefore, $\bar{R}_1 = \bar{R}_2 = (n+1)/2$.

Time lag periods of 0-5 years were used to test correlations between fluctuating salmon availability and demographic trends of SRC whales. It is not known which time lag duration represents the most realistic offset when comparing salmon and SRC population trends, therefore a range was tested.

Salmon data from all regions were totaled and tested against total SRC population as well as for each pod. Individual pod data were also tested against each species of salmon for each spawning region where data were available.

RESULTS

SRC and Total Salmon by Species

When total run size data for the different species of salmon were tested against SRC population trend data, results indicated strong relationships between the whales and some salmon species, and no significant relationships with others. There was significant positive correlation between the whales and early chum, normal chum, and chinook, and negative correlations with coho. There were no significant correlations between the whales and late chum (Table 3.3).

Table 3.3. Correlation strengths between SRC and totaled salmon by species using run-size data. Negative correlations are indicated by the negative sign (-) following the species name.

All Whales and Toted Species (Total Run-Size)

Toted Species	Significant at α 0.05	Significant at α 0.01
0 Year Lag	Early Chum	Coho (-)
1 Year Lag	Normal Chum	Coho (-), Early Chum
2 Year Lag	Normal Chum	Coho (-), Early Chum, Normal Chum
3 Year Lag	Chinook	Coho (-), Early Chum, Normal Chum
4 Year Lag	Early Chum, Pink	Chinook, Normal Chum
5 Year Lag		Chinook, Normal Chum

When escapement data were used to test total salmon by species against the total SRC population, three species, normal chum, early chum, and sockeye, showed strong correlation (Table 3.4). Contrary to observational and scale sampling evidence of chinook predation, and correlation results using total run size data, no significant correlations between total chinook and total SRC whales were found. The other differences found between run size and escapement data correlations with SRC were the negative correlations found with coho when using run size data, which were not found when escapement data were used.

Table 3.4. Correlation strengths between SRC and totaled salmon by species using escapement data.

All Whales and Toted Species (Escapement data)

Toted Species	Significant at α 0.05	Significant at α 0.01
0 Year Lag	Early Chum, Normal Chum	
1 Year Lag	Early Chum, Sockeye	Normal Chum
2 Year Lag		Normal Chum, Sockeye
3 Year Lag		Normal Chum, Sockeye
4 Year Lag	Normal Chum	Sockeye
5 Year Lag	Normal Chum	Sockeye

Whales and Total Salmon by Region

Results indicate region-specific differences in correlation patterns between the SRC and total run size of salmon (Table 3.5). Chinook and normal chum salmon were positively correlated with the whales in the SJdF region. Coho and early chum

salmon showed significant negative correlations with the whales in that region. Sockeye salmon was the only species to show positive association with the SRC in the SJI region (meaning Fraser River sockeye), while chinook and coho both had negative correlations with the whales. Like in the SJI region, both chinook and coho showed negative correlation with the whales in NPS. Similar to results from the SJdF region, normal chum was positively correlated with the whales in NPS. In SPS normal and early chum were positively correlated with the whales and no species exhibited negative correlation. Normal chum and pink salmon were positively correlated with the SRC in the HC region. As in the SJdF, early chum from HC showed negative correlation with the whales.

Table 3.5. Significant correlations between SRC and totaled salmon by species and region using run-size data.

All Whales by Region (Total Run-Size)

The SJdF region	Significant at α 0.05	Significant at α 0.01
0 Year Lag	Early Chum (-)	Coho (-)
1 Year Lag		Coho (-)
2 Year Lag	Early Chum (-)	Coho (-)
3 Year Lag	Chinook	Coho (-)
4 Year Lag	Normal Chum	Chinook
5 Year Lag		Chinook, Normal Chum

SJI	Significant at α 0.05	Significant at α 0.01
0 Year Lag		Chinook (-), Coho (-)
1 Year Lag	Coho (-)	Chinook (-)
2 Year Lag	Sockeye	Chinook (-)
3 Year Lag	Sockeye	
4 Year Lag		
5 Year Lag		

Table 3.5 Continued

NPS	Significant at α 0.05	Significant at α 0.01
0 Year Lag		Chinook (-), Coho (-)
1 Year Lag	Coho (-), Normal Chum	Chinook (-)
2 Year Lag	Chinook (-), Coho (-), Normal Chum	
3 Year Lag	Coho (-)	Chinook (-), Normal Chum
4 Year Lag		Chinook (-), Normal Chum
5 Year Lag		Chinook (-), Normal Chum

SPS	Significant at α 0.05	Significant at α 0.01
0 Year Lag	Normal Chum	
1 Year Lag		Early Chum, Normal Chum
2 Year Lag		Early Chum, Normal Chum
3 Year Lag		Early Chum, Normal Chum
4 Year Lag		Early Chum, Normal Chum
5 Year Lag	Pink	Early Chum, Normal Chum

HC	Significant at α 0.05	Significant at α 0.01
0 Year Lag	Chinook (-)	Normal Chum
1 Year Lag		Normal Chum
2 Year Lag	Early Chum (-)	Normal Chum
3 Year Lag	Pink	Early Chum (-), Normal Chum
4 Year Lag		Early Chum (-), Normal Chum, Pink
5 Year Lag	Chinook	Early Chum (-), Normal Chum, Pink

Generally similar patterns of correlation were observed when salmon escapement data were tested with SRC population data by region (table 3.6). A few differences however did emerge. In the SJdF region, chinook and normal chum were positively correlated with the whales, while early chum and coho showed inverse correlation. These were the same correlations observed when total run-size data were used. In the SJI region, normal chum, chinook, and sockeye all showed positive correlations with the whales (in this case all sockeye are bound for the Fraser River watershed). This differed from the results using total run-size data which indicated statistically negative correlations between whales and chinook salmon in the SJI region, and no significant relationship with normal chum. In NPS, the only significant correlation between whales and salmon was with chinook. This differed from the total run-size

results for NPS which showed negative correlations with chinook and coho and positive correlations with normal chum. Chinook and normal chum both had significantly positive correlations with the whales in CPS. Sockeye (in this case bound for the Lake Washington watershed) showed a negative relationship in CPS. No comparison with total run-size data for CPS was possible as there were no total run-size data from rivers draining into that region. Correlations between salmon and whales in SPS were similar between the two datasets. Both indicated strong positive correlations with early and normal chum. One difference was the strongly positive correlation of chinook with whales when using the escapement data, but not when the total run-size data were used. Analysis using both total run-size and escapement data resulted in negative correlations between whales and early chum and positive correlations between whales and normal chum in HC. The difference between the results of the two datasets were positive correlations with pink salmon when using the total run size data that did not exist when the escapement data were used, as well as negative correlations with coho when the escapement data were tested that did not occur when total run-size data were used.

Table 3.6. Significant correlations between SRC and totaled salmon by species and region using escapement data.

All Whales by Region (Escapement)

SJdF	Significant at α 0.05	Significant at α 0.01
0 Year Lag	Early Chum(-)	Chinook
1 Year Lag		Chinook
2 Year Lag	Early Chum(-)	Chinook
3 Year Lag	Early Chum(-), Normal Chum	Chinook, Chum, Coho(-)
4 Year Lag	Early Chum(-), Normal Chum	Chinook, Chum, Coho(-)
5 Year Lag	Pink(-)	Chinook, Early Chum(-), Coho(-), Normal Chum

Table 3.6 continued

SJI	Significant at α 0.05	Significant at α 0.01
0 Year Lag	Normal Chum, Sockeye	
1 Year Lag	Normal Chum, Sockeye	
2 Year Lag		Sockeye
3 Year Lag		Sockeye
4 Year Lag	Chinook	Sockeye
5 Year Lag	Chinook	Sockeye

NPS	Significant at α 0.05	Significant at α 0.01
0 Year Lag		
1 Year Lag		
2 Year Lag		
3 Year Lag	Chinook	
4 Year Lag		Chinook
5 Year Lag	Chinook	

CPS	Significant at α 0.05	Significant at α 0.01
0 Year Lag	Chinook, Sockeye(-)	Normal Chum
1 Year Lag	Chinook, Sockeye(-)	Normal Chum
2 Year Lag		Normal Chum
3 Year Lag		Normal Chum
4 Year Lag	Normal Chum	
5 Year Lag		

SPS	Significant at α 0.05	Significant at α 0.01
0 Year Lag		Chinook, Early Chum, Normal Chum
1 Year Lag		Chinook, Early Chum, Normal Chum
2 Year Lag		Chinook, Early Chum, Normal Chum
3 Year Lag		Chinook, Early Chum, Normal Chum
4 Year Lag	Chinook	Early Chum, Normal Chum
5 Year Lag	Chinook	Early Chum, Normal Chum

HC	Significant at α 0.05	Significant at α 0.01
0 Year Lag		Normal Chum
1 Year Lag		Normal Chum
2 Year Lag	Early Chum(-), Pink	Normal Chum
3 Year Lag		Early Chum(-), Normal Chum
4 Year Lag	Coho(-), Normal Chum	Early Chum(-)
5 Year Lag	Coho(-)	Early Chum(-)

Pod and Totaled Salmon by Species

When the scale of analysis was decreased to pod, species, and area specificity, different correlation patterns emerged. Pods were tested against totaled salmon species and then tested against the different salmon species in each of the regions using both total run-size and escapement data (Tables 3.7-3.14). J pod appeared to be positively correlated to early and normal chum when both total run-size and when escapement data were used. Differences between the results of the two datasets included negative correlations between J pod and chinook and coho when using total run-size compared to positive correlations between chinook and coho when escapement data were used. Positive correlations between sockeye salmon and J pod were evident when escapement data were tested, but not when total run-size data were tested.

Like J pod, K pod also showed positive correlations with early and normal chum when using both total run-size and escapement datasets. Differences between the results of the two datasets include positive correlations with chinook and sockeye when escapement data were used which were not evident when using total run-size data. K pod was the only pod to show significant correlations with totaled pink salmon, which occurred when using both sets of salmon data.

When using total run-size data, L pod showed a unique pattern of negative correlations with both chinook and coho salmon at early time lag periods, and positive correlations at later time lag periods. Like J & K pods, L pod showed positive correlation with normal chum, but unlike J and K, lacked correlation with early chum. L pod was the only pod to show positive association with sockeye when total run-size data were used (Table 3.7). Interestingly, L pod showed no significant correlations with escapement data of totaled species (Table 3.8).

Table 3.7. Correlation strengths between the pods and totaled salmon by species using run-size data.**Pods and Totaled Species (Total Run-Size)**

J pod and Totaled Species	Significant at α 0.05	Significant at α 0.01
0 Year Lag		Chinook (-), Coho (-)
1 Year Lag	Chinook (-)	Early Chum
2 Year Lag	Early Chum, Coho (-)	
3 Year Lag	Normal Chum	Early Chum
4 Year Lag	Early Chum	
5 Year Lag		Early Chum, Normal Chum

K pod and Totaled Species	Significant at α 0.05	Significant at α 0.01
0 Year Lag	Normal Chum	Early Chum
1 Year Lag	Normal Chum, Pink	Early Chum
2 Year Lag	Pink	Early Chum, Normal Chum
3 Year Lag	Early Chum, Normal Chum	
4 Year Lag	Normal Chum	
5 Year Lag		Coho (-)

L pod and Totaled Species	Significant at α 0.05	Significant at α 0.01
0 Year Lag	Coho (-)	Chinook (-)
1 Year Lag	Chinook (-)	
2 Year Lag	Sockeye	
3 Year Lag	Normal Chum, Sockeye	
4 Year Lag	Coho, Normal Chum, Sockeye	
5 Year Lag	Chinook, Normal Chum, Late Chum	Coho, Pink

Table 3.8. Correlation strengths between the pods and totaled salmon by species using escapement data.

Pods and Totaled Species (Escapement)

J pod and Totaled Species	Significant at α 0.05	Significant at α 0.01
0 Year Lag	Normal Chum, Coho	Chinook, Early Chum
1 Year Lag		Chinook, Early Chum, Normal Chum, Coho
2 Year Lag	Chinook, Early Chum, Normal Chum, Coho	Sockeye
3 Year Lag	Chinook, Early Chum	Normal Chum, Sockeye
4 Year Lag	Normal Chum	Sockeye
5 Year Lag	Early Chum	Normal Chum, Sockeye

K pod and Totaled Species	Significant at α 0.05	Significant at α 0.01
0 Year Lag	Coho, Sockeye	Chinook, Early Chum, Normal Chum
1 Year Lag		Chinook, Early Chum, Normal Chum
2 Year Lag	Sockeye	Chinook, Early Chum, Normal Chum, Pink
3 Year Lag	Early Chum, Pink	Chinook, Normal Chum, Sockeye
4 Year Lag		Chinook, Normal Chum, Sockeye
5 Year Lag	Normal Chum	Chinook, Sockeye

L pod and Totaled Species	Significant at α 0.05	Significant at α 0.01
0 Year Lag		
1 Year Lag		
2 Year Lag	None	
3 Year Lag		
4 Year Lag		
5 Year Lag		

Pod and Salmon Species by Region

Correlations between the SRC and the different species of salmon appear to vary between the various regions tested. Generally, the results were similar when total

run-size and escapement data were used. Below is a summary of the results by region. For these results, significance level is not shown. All significant correlations had a p value of .05 or lower. For correlation coefficient and p-value results see Appendix tables A2-A14.

The SJdF region

Chinook salmon was the only species that was consistently significantly positively correlated with the SRC pods in the SJdF region. L pod showed positive correlations with normal chum as well as chinook. All three pods were significantly negatively correlated with early chum. J and L pods were also negatively correlated with coho salmon (Table 3.9).

Table 3.9. Significant ($p < 0.05$) positive and negative correlations between salmon and J, K and L pods in the SJdF region using both salmon total run-size and escapement data.

The SJdF region

J Pod (Total Run-Size)

The SJdF region	Year Time Lags					
	0	1	2	3	4	5
Chinook						
E. Chum					-	
N. Chum						
Coho	-	-	-			

Table 3.9 continued
J Pod (Escapement)

The SJdF region	Year Time Lags					
	0	1	2	3	4	5
Chinook	+	+	+	+	+	+
E. Chum					-	-
N. Chum						
L. Chum						
Coho						
Pink						

K Pod (Total Run-Size)

The SJdF region	Year Time Lags					
	0	1	2	3	4	5
Chinook						
E. Chum					-	-
N. Chum						
Coho						

K Pod (Escapement)

SJdF	Year Time Lags					
	0	1	2	3	4	5
Chinook	+	+	+	+	+	+
E. Chum					-	-
N. Chum						+
L. Chum						
Coho						
Pink						-

Table 3.9 continued

L Pod (Total Run-Size)

SJdF	Year Time Lags					
	0	1	2	3	4	5
Chinook				+	+	+
E. Chum	-	-	-			
N. Chum				+	+	+
Coho	-	-	-	-	-	

L Pod (Escapement)

SJdF	Year Time Lags					
	0	1	2	3	4	5
Chinook		+	+	+	+	+
E. Chum	-	-	-	-		
N. Chum				+	+	+
L. Chum						
Coho	-	-	-	-	-	-
Pink						

The SJI Region

Overall in SJI, J & K pods showed very similar correlation patterns. They were both positively correlated with normal chum, coho, and sockeye, and were mostly negatively correlated with chinook. L pod did not appear to be strongly correlated with any species other than sockeye. The negative correlations with chinook are surprising given the positive correlations observed in adjacent the SJdF region (Table 3.10).

Table 3.10. Significant ($p < 0.05$) positive and negative correlations between salmon and J, K and L pods in the SJI region using both salmon total run-size and escapement data.

SJI

J Pod (Total Run-Size)

	Year Time Lags					
SJI	0	1	2	3	4	5
Chinook	-	-	-	-	-	-
Coho						
Pink			+			
Sockeye						

J Pod (Escapement)

	Year Time Lags					
SJI	0	1	2	3	4	5
Chinook						
N. Chum	+	+	+	+		
L. Chum						
Coho	+	+	+	+	+	
Pink						
Sockeye		+	+	+	+	+

K Pod (Total Run-Size)

	Year Time Lags					
SJI	0	1	2	3	4	5
Chinook	-	-	-	-	-	
Coho						-
Pink						
Sockeye						

Table 3.10 continued
K Pod (Escapement)

SJI	Year Time Lags					
	0	1	2	3	4	5
Chinook						+
N. Chum			+	+		+
L. Chum						
Coho	+	+	+	+	+	+
Pink						
Sockeye	+	+	+	+	+	+

L Pod (Total Run-Size)

SJI	Year Time Lags					
	0	1	2	3	4	5
Chinook	-					+
Coho						+
Pink						+
Sockeye			+	+	+	

L Pod (Escapement)

SJI	Year Time Lags					
	0	1	2	3	4	5
Chinook					+	+
N. Chum						
L. Chum						
Coho						
Pink						
Sockeye						

The NPS Region

J pod showed very few significant correlations with any salmon in NPS. All three pods did show positive association with normal chum. K & L pods also showed negative correlations with chinook. Overall, all three pods had more similar correlation patterns in NPS than in any of the other regions tested. (Table 3.11).

Table 3.11. Significant ($p < 0.05$) positive and negative correlations between salmon and J, K and L pods in the NPS region using both salmon total run-size and escapement data.

NPS**J Pod (Total Run-Size)**

NPS	Year Time Lags					
	0	1	2	3	4	5
Chinook						
N. Chum				+		+
Coho						
Pink						

J Pod (Escapement)

NPS	Year Time Lags					
	0	1	2	3	4	5
Chinook					-	
N. Chum						
L. Chum						
Coho						
Pink						

Table 3.11 continued

K Pod (Total Run-Size)

NPS	Year Time Lags					
	0	1	2	3	4	5
Chinook			-	-	-	
N. Chum	+	+	+	+	+	
Coho						
Pink						

K Pod (Escapement)

NPS	Year Time Lags					
	0	1	2	3	4	5
Chinook						-
N. Chum						
L. Chum						
Coho						
Pink				+		

L Pod (Total Run-Size)

NPS	Year Time Lags					
	0	1	2	3	4	5
Chinook	-	-	-			
N. Chum				+	+	+
Coho	-					
Pink						

Table 3.11 continued
L Pod (Escapement)

NPS	Year Time Lags					
	0	1	2	3	4	5
Chinook		-	-	-	-	-
N. Chum						
L. Chum						
Coho	-					
Pink						

The CPS Region

Total run-size data were not available for CPS, therefore only escapement data were tested. J & K pods had the same correlations patterns in CPS. Both pods were positively correlated with chinook and normal chum. L pod had only one significant correlation in this region, which was a negative correlation with sockeye at the one year time lag (Table 3.12).

Table 3.12. Significant ($p < 0.05$) positive and negative correlations between salmon and J, K and L pods in the CPS region using salmon escapement data. Total run-size data were not available for this region.

CPS

J Pod (Escapement)

CPS	Year Time Lags					
	0	1	2	3	4	5
Chinook	+	+	+	+	+	
N. Chum	+	+	+	+	+	+
L. Chum						
Coho						
Pink						
Sockeye					-	

Table 3.12 continued
K Pod (Escapement)

CPS	Year Time Lags					
	0	1	2	3	4	5
Chinook	+	+	+	+	+	+
N. Chum	+	+	+	+	+	
L. Chum						
Coho						
Pink						
Sockeye						

L Pod (Escapement)

CPS	Year Time Lags					
	0	1	2	3	4	5
Chinook						
N. Chum						
L. Chum						
Coho						
Pink						
Sockeye		-				

The SPS Region

The results of both total run-size and escapement analysis were very similar in the SPS region. J & K pods displayed positive correlations with chinook, early chum, and normal chum across several of the year time lags. J & K pods also showed significant negative correlations with coho salmon. The correlations between L pod and the different species of salmon were not so distinct. There were both negative and positive correlations between L pod and coho. There were a few positive correlations between L pod and early chum (at one lag time period), normal chum (at one lag time period), and pink (at two lag time periods) (Table 3.13).

Table 3.13. Significant ($p < 0.05$) positive and negative correlations between salmon and J, K and L pods in the SPS region using both salmon total run-size and escapement data.

SPS

J Pod (Total Run-Size)

SPS	Year Time Lags					
	0	1	2	3	4	5
Chinook						
E. Chum	+	+		+	+	+
N. Chum	+	+	+	+	+	+
Coho	-	-	-	-	-	-
Pink						

J Pod (Escapement)

SPS	Year Time Lags					
	0	1	2	3	4	5
Chinook	+	+	+	+	+	+
E. Chum	+	+	+	+	+	+
N. Chum	+	+	+	+	+	+
L. Chum						
Coho						
Pink						

K Pod (Total Run-Size)

SPS	Year Time Lags					
	0	1	2	3	4	5
Chinook	+	+				
E. Chum	+	+	+	+	+	+
N. Chum	+	+	+	+	+	+
Coho	-	-		-	-	-
Pink					-	

Table 3.13 continued
K Pod (Escapement)

SPS	Year Time Lags					
	0	1	2	3	4	5
Chinook	+	+	+	+	+	+
E. Chum	+	+	+	+	+	+
N. Chum	+	+	+	+	+	+
L. Chum						
Coho						
Pink						-

L Pod (Total Run-Size)

SPS	Year Time Lags					
	0	1	2	3	4	5
Chinook						
E. Chum		+				
N. Chum					+	
Coho					+	+
Pink					+	+

L Pod (Escapement)

SPS	Year Time Lags					
	0	1	2	3	4	5
Chinook						
E. Chum						
N. Chum	+	+				
L. Chum						
Coho	-	-				
Pink						

The HC Region

J & K pods were positively correlated with normal chum across all lag time periods using both total run-size and escapement data sets, indicating very strong relationships between J's and K's and chum salmon. L pod also showed strong association with normal chum in HC. Generally, the relationship patterns between the pods and coho were unclear, showing both positive and negative correlations in the same region. Overall, there was a pattern of negative correlation between all three pods and early chum. HC showed the most pod-specific correlation patterns of any of the regions (Table 3.14).

Table 3.14. Significant ($p < 0.05$) positive and negative correlations between salmon and J, K and L pods in the HC region using both salmon total run-size and escapement data.

HC**J Pod (Total Run-Size)**

	Year Time Lags					
HC	0	1	2	3	4	5
Chinook						
E. Chum						
N. Chum	+	+	+	+	+	+
Coho						-
Pink						

J Pod (Escapement)

	Year Time Lags					
HC	0	1	2	3	4	5
Chinook	+					
E. Chum					-	-
N. Chum	+	+	+	+	+	+
L. Chum						
Coho	+	+	+			
Pink						

Table 3.14 continued

K Pod (Total Run-Size)**Year Time Lags**

HC	0	1	2	3	4	5
Chinook						
E. Chum				-	-	-
N. Chum	+	+	+	+	+	+
Coho						
Pink						

K Pod (Escapement)**Year Time Lags**

HC	0	1	2	3	4	5
Chinook	+	+	+	+		
E. Chum					-	-
N. Chum	+	+	+	+	+	+
L. Chum						
Coho	+					
Pink		+	+			

L Pod (Total Run-Size)**Year Time Lags**

HC	0	1	2	3	4	5
Chinook	-	-	-			
E. Chum	-	-	-	-	-	-
N. Chum	+	+	+	+	+	+
Coho	-	-	-	-		
Pink						+

Table 3.14 continued
L Pod (Escapement)

HC	Year Time Lags					
	0	1	2	3	4	5
Chinook						
E. Chum	-	-	-	-	-	-
N. Chum		+	+			
L. Chum						
Coho				-	-	-
Pink						

Salmon to Salmon Correlations

Due to the observed significantly inverse correlations between the pods and certain salmon species in particular regions, correlations among salmon species were tested using Spearman's Rank Correlation. Totaled salmon species and species by region were tested against each other to investigate possible salmon to salmon associations. It was speculated that in cases where whales were inversely correlated with salmon, the inverse correlation was due to a negative interaction between that species of salmon and a species with which the whales were positively correlated.

Several positive correlations between totaled salmon species were observed (Table 3.15). However, there were no significant inverse correlations between totaled salmon when using either total run-size or escapement data. A few negative correlations did exist between different species of salmon at the regional scale (Tables 3.16 and 3.17). These results are relatively consistent with correlations observed between these spawning regions and the pods. Results of these tests using total run-size data found significant negative correlations between chinook in SJI and normal chum from HC as well as early chum from SPS. J & K pods showed

negative correlations with chinook from SJI and positive correlations with normal chum from HC and early chum from SPS. For total run-size data results, L pod showed positive correlations to both chinook from SJI and normal chum from HC. L pod had no significant correlations with early chum from SPS. Chinook in NPS showed significant inverse correlations with pink from HC. All three pods showed negative correlations with chinook from NPS, but only L pod showed a significant relationship with pink from HC, which was positive. When escapement data were used, results indicate significant negative correlations between chinook in the SJdF region and early chum in HC. This correlation is plausible in light of the significant positive relationships found between all three pods of whales and chinook and the significant negative relationships found between the pods and early chum salmon in the SJdF and HC regions. It is reasonable to believe that early chum originating from Hood Canal could interact with chinook originating from the Strait of Juan de Fuca since Hood Canal drains directly into the Strait.

Table 3.15. Significant correlations between totaled salmon species in Puget Sound using run-size data (upper right of matrix) and escapement data (lower left of matrix). Correlations were considered significant at both the .05 and the .01 alpha levels. There were no significant negative correlations between species.

Correlations Between Totaled Salmon Species

-Escapement-

	Chinook	E. Chum	N. Chum	L.Chum	Coho	Pink	Sockeye
Chinook			+		+	+	+
E. Chum			+		+		
N. Chum		+		+		+	+
L. Chum	+		+		+		
Coho	+			+			
Pink		+	+	+	+		
Sockeye							

-Total Run-Size-

Table 3.16. Significant inverse correlations between salmon species by region using run-size data.**Negative Correlations Between Salmon Species By Region**

Species and Region	Significant at α 0.05	Significant at α 0.01
	Chinook (SJI) and Normal Chum (HC)	Chinook (SJI) and Early Chum (SPS) Chinook (NPS) and Pink (HC)

Table 3.17. Significant inverse correlations between salmon species by region using escapement data.**Negative Correlations Between Salmon Species By Region**

Species and Region	Significant at α 0.05	Significant at α 0.01
	Chinook (SjDf) and Early Chum (HC)	None

Lag Periods

There were no significant differences observed among the numbers of correlations found at each time lag period tested (Table 3.18).

Table 3.18. Number of positively significant correlations at each time lag period for all correlation tests between whales and salmon (results of total run size and escapement data are combined).

	0	1	2	3	4	5
TOTAL TRS	14	20	22	29	31	35
TOTAL ESC	43	45	47	45	39	37
TOTAL	57	65	69	74	70	72

Results in Relation to Length of Data Time Series

No pattern was seen between the number of years data were available for a particular species and the number of significant correlation results with that species (tables 3.1 and 3.2).

DISCUSSION

Specialist predators often show a stronger numerical response, in either density or breeding parameters, to variations in prey abundance than do generalist predators (Salamolard et al. 2000). As specialist predators, it was predicted that the southern residents exhibit a numerical response to fluctuations in salmon abundance. The results of this study indicate that the SRC do show numerical responses to population fluctuations of salmon (Tables 3.3 and 3.4). In addition, correlations between whales and salmon appear to be pod, species, and region specific.

Results varied somewhat depending on the salmon dataset being tested. As predicted, chinook, chum, and sockeye were positively correlated with the whales at the total population level. Chum continued to be positively correlated with nearly all three pods in all six regions when the population trends of the pods were tested against the population trends of geographically specific spawning stocks. However, no single time lag period appeared to produce more positively significant correlation results than any other. Possible explanations for this are discussed later.

This study compared trends in killer whale abundance to total abundance and escapement of Pacific salmon at different temporal and spatial scales. Analysis of this kind has not been carried out in such detail and over such a long time frame. The results suggest that chinook and chum salmon are generally the most closely associated species with SRC population fluctuations. These results confirm the importance of these species to the overall survival of the southern resident population. The region specific correlations found between the whales and species of salmon offer the most important information for future management decisions regarding the SRC and the various salmon stocks.

Correlations at the Species Level

The much larger size of coho, pink, and sockeye runs, compared to chinook salmon, would suggest strong correlations may be found between those species and the SRC. However, the whales appear to be most strongly correlated to chinook and chum salmon, as was hypothesized. Chinook salmon are the largest of the salmon species and possess the highest average lipid content, making them a favorable prey item (Healey 1991; Brett 1995; Bigler et al. 1996). Historically, chinook were potentially available in near-shore waters all year round, in concentrations far exceeding recent abundance estimates (Noakes et al. 2000). The SRC may have developed specialized foraging tactics to capture chinook, which are not as efficient at capturing smaller bodied species that tend to be found in higher aggregations like pink and sockeye (Ford and Ellis 2005). Killer whales around the globe have developed specific strategies for pursuing and capturing their preferred prey (Ford and Ellis 2005). SRC whales have likely evolved specialized foraging behaviors to exploit 'reliable' chinook runs. While sockeye, pink, and coho runs can be relatively large, their availability to the whales as they migrate from off-shore waters to the river mouths of their natal watersheds is ephemeral (Burgner 1991; Heard 1991; Sandercock 1991). Perhaps representing an important food source while those species are available to the whales, it is possible that sockeye, pink, and coho are simply not available for a long enough period to significantly drive SRC population dynamics (Figure 3.8). The scarcity of positive correlations found between the SRC and pink, coho, and Lake Washington sockeye salmon, along with the infrequent tissue evidence of these species found near foraging whales (Ford and Ellis 2005), supports this theory.

Fraser River sockeye appear to be an exception to this conclusion. All three pods showed positive correlation to Fraser River sockeye, yet sockeye tissue samples were rare during collections carried out in the studies by Ford and Ellis (2005) and

Ford et al. (1998). No study has been able to follow the whales on a constant basis. It is possible that the SRC consumes sockeye during times and in areas where tissue samples have not been collected, for example during nighttime hours, inclement weather, or at a depth that is not conducive to collecting prey fragments at the surface. Personal observation of whales taking sockeye salmon is consistent with linkages between sockeye and the SRC.

Chum are the second largest of the Pacific salmon species and have the broadest geographical distribution (Salo 1991). Movement patterns of the SRC as well as scale sampling evidence suggests association between the whales and chum runs, particularly with J & K pods (Heimlich-Boran 1986; Nichol and Shackleton 1996; Ford et al. 1998; McCluskey unpublished data). However, Ford et al. (2005) found that survival patterns of northern and southern resident whales were strongly correlated with fluctuations in abundance of chinook salmon, but not with chum. Ford et al.'s results differ from the results presented here. The SRC was positively correlated with chum at the community and pod specific scales. Chum are the most abundant salmon species in the late fall and early winter months, making them potentially available as prey long after coho, pink, and sockeye have entered freshwater. Escapement of chum into Puget Sound rivers is comparably much higher than escapement to spawning areas in the Strait of Juan de Fuca and San Juan Island regions. The narrow channels and strong currents of Puget Sound may aid in the capture of chum migrating into that region, adding to the importance of chum as a prey species for the whales.

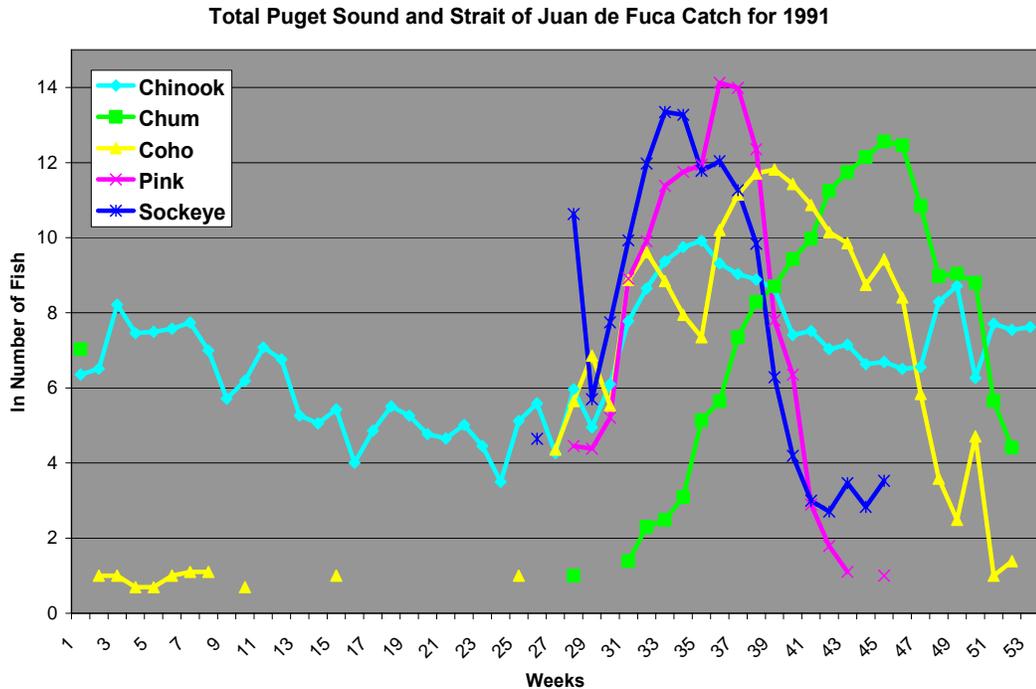


Figure 3.8. Natural log of total catch of all species of salmon within US waters of Puget Sound and the Strait of Juan de Fuca in 1991. Chinook salmon were caught in all weeks of the year while larger runs of coho, pink and sockeye were caught during a roughly 20 week period from mid-summer through mid- autumn. Note that the catch of chum salmon peaks after the catch of coho, pink, and sockeye have diminished.

Region Specific Correlations

When correlations between salmon and whales were tested at the regional scale, it was apparent that the spawning area of each salmon species influenced the strength of relationship with the whales as a whole, as well as individual pods. There were a few differences in correlation pattern when total run-size and escapement data were tested, but overall both datasets told the same story. Discrepancies usually involved either coho or chinook, with one case involving early chum. In these discrepancies, one dataset produced significant positive correlations between whales and salmon, while the other dataset produced significant negative correlations. This happened in seven instances, three of which were in the SJI region, and the other four cases

were scattered among the SJdF, NPS, SPS, and HC regions. The region specific correlations that did occur are generally shared across pods, indicating repeated pattern and adding credence to the conclusion that correlations are not random.

Results generally support the region specific hypotheses stated earlier. Chum salmon appear to be most highly correlated with the SRC as well as each individual pod in southern Puget Sound, as hypothesized. However, chum are also positively correlated with the whales to some degree in every region, indicating strong association with chum stocks regardless of run size.

Totaled whales and J & K pods were all positively correlated with chinook in southern Puget Sound, as predicted. However, L pod appeared to have the strongest positive association (i.e., meaning significant correlation results from both total run-size and escapement data) with chinook from the SJdF region. These stocks have had the lowest total run-size of any of the analyzed chinook stocks since at least 1981. Reasons for association between L pod and the SJdF region chinook must be other than number of fish spawning in that area.

Nearly all significant correlations with coho salmon were negative. In regions where there were positive associations using one dataset, the other dataset produced significantly negative correlations. The contradictory correlations between coho and the SRC lead to the conclusion that there is lack of functional connection between the two species at any scale.

Fraser River sockeye (SJI) had the highest positive correlations with the whales, as hypothesized. CPS was the only other region where sockeye spawn in any great number, and the significant correlations found there were all negative. The Fraser

River watershed is one of the largest salmon producing watersheds in the world, comprising more than 30 separate stocks of sockeye returning each year to spawn (Roos 1991). The volume of fish returning to this river within a few months time would provide both numbers and concentrations of prey attractive to foraging whales.

There were very few positive correlations between the whales and pink salmon, and no region showed consistent correlations with every pod. Contrary to the hypothesis that SJI would produce the most positive correlations between whales and pink salmon, it was HC that showed positive associations between totaled whales and K & L pods. The SJI region did have the second highest number of significant correlations: both J and L pods showed positive associations with pink salmon in the SJI region. There were no positive associations between whales and pink salmon in the Strait of Juan de Fuca or in central or southern Puget Sound. This makes sense in light of the low number of pink runs that spawn in those regions.

The significant positive correlations between the whales and salmon at the regional scale did not appear to reflect abundances of potentially available species (see table A1). While normal chum were correlated with the whales in every region analyzed, other species were correlated in some regions and not in others. For example, both coho total run-size and escapement data produced positive correlations with the SRC in the SJI region, yet no significant correlations existed with coho in the neighboring NPS region which also supports high numbers of coho salmon. In fact, normal chum was the only species in NPS to show positive association with the whales and that was only when total run-size data were used. The results of these analyses indicate that certain spawning regions produce more significant

correlations with the whales, indicating that there are specific variables associated with those spawning stocks that are not reflected simply in their population size that makes them favorable prey. For example, the same species destined for different spawning regions is likely to have different run timing. There is also variation in body size and condition of different stocks of the same species, which can be related to the physical characteristics of the watersheds in which the salmon spawn (Burgner 1991). These variables likely contribute to the profitability of the whales foraging on certain species from some spawning regions and not others.

Lag Periods

There were no significant differences in the number of correlations observed at each of the lag periods tested. The hypothesis that a one year lag period would produce the highest number of significant correlations is therefore rejected. It is concluded that the population reaction of whales to salmon abundance is not limited to a one year time lag. Time lags may be specific to each salmon species' life-history, previous physical condition, and other factors such as fecundity and mean age of the whales.

Is L Pod Doing Anything Different from J & K pods?

Overall L pod appears to have different correlation patterns with salmon than J & K pods, as hypothesized. When testing total run-size data of totaled salmon by species against each pod, L pod showed significant positive correlation with sockeye while neither J nor K pods did. L pod lacked significant positive correlations with early chum, with which both J & K pods were correlated. When the escapement data were used L pod did not show any highly significant relationships with totaled salmon species when both J & K pods did. L pod showed significantly higher

correlation to pink salmon than either J or K pods. L pod's region specific correlations with early chum differed from either J or K pods.

L pod's relationship with normal chum appears to be different as well in that L pod did not show as many significant correlations with normal chum. These correlations coincide with movement data showing that L pod does not utilize Puget Sound as frequently or consistently as either J or K pods (see previous chapter). J & K pods seem to utilize Puget Sound the most in the autumn months, coinciding with the timing of chum runs (Heimlich-Boran 1986). If L pod is not selectively foraging on chum in the inland waters in the autumn and early winter months, it is likely that they are preying upon non salmonid species, or a less abundant species, as no other species of salmon is aggregating at comparable densities to chum during those months. From observational evidence of body condition of some returning whales in the late spring, winter appears to be the most nutritionally stressful period of the year for the SRC (K. Balcomb pers. comm.). If L pod is not exploiting chum salmon to the extent that J & K pods are, it is likely that they are not substituting energetically comparable prey and consequently are suffering higher mortality rates than the other pods.

It can be concluded that L pod's relationship to salmon as a whole is not as strong as the other southern resident pods, and therefore L whales are most likely foraging on alternative prey species. Increased foraging effort has been seen to result in decreased body mass and nutritional stress in other marine mammals (Le Boeuf and Crocker 2005). Lower nutritional value or higher energetic cost of capturing alternative prey are possible reasons that L pod suffered a higher mortality rate in the latter 1990s than either J or K pods.

A possible explanation for the higher mortality rates experienced by L pod in the latter half of the 1990s could be the presence of a higher proportion of calves and juveniles than either J or K pods. Ford and Ellis (2005) found that resident killer whales share captured prey, particularly adult females with their offspring. If L pod adults had to help provision juveniles and calves more often than the other pods, individual caloric intake might be lowered and overall nutritional stress would be higher. In studies of other marine mammals, maternal physical condition reflected prey availability and foraging success, which directly affected their ability to provision their offspring (Le Boeuf and Crocker 2005). However, the proportions of juveniles and calves in L pod were no different than the other pods in either the early or the latter 1990s. It is therefore more likely that a difference in prey choice, foraging locations, or other behavioral differences resulted in the higher mortality rates experienced by L pod.

Escapement vs. Total Run-Size

Both escapement and total run-size data were used to analyze relationships of whale and salmon population trends from two related, but distinct perspectives. Escapement data are directly related to the number of spawners and therefore the juvenile recruitment of the following year. Escapement data were used in this context to represent the minimal number of fish potentially available as prey to the whales. In some cases fishing pressure is heavy and total run-size may not be reflective of what is actually available to the whales. Total run-size was used as well because it is a better indicator of stock variation and is the closest index of overall salmon abundance.

Because it is not known which dataset best represents numbers of fish potentially available to the whales in a given year, and therefore would represent the

correlations with the most substantial biological meaning, significant correlations resulting from the use of both datasets for each species and region can be regarded as bearing the most ecologically significant weight. In some cases, the average abundance of species using total run-size or escapement data was not substantially different. For example, the difference between average run-size and escapement of chinook spawning in the SJdF region was less than 1000 fish. However, the difference in average run-size and escapement of chinook in SPS was approximately 80,000 fish (table A1). Yet the whales showed positive correlations with chinook from these two regions when both datasets were tested. In such cases, it is reasonable to assume that these correlations are not spurious and that there is biological merit to the results indicating population correlation between the SRC and chinook from the SJdF and SPS.

Lack of Correlations with Late Chum and Pink

Lack of correlations between late chum and the SRC pods might be attributed to a shorter time series of data. Late chum runs are not as large as normal chum (WDFW catch data) and could therefore not have as significant an impact on whale population trends. Late chum could simply not be as available to foraging whales as other species or runs. K & L pods are generally not sighted in the inland waters from late fall to late spring and sightings of J pod become very irregular and infrequent in the winter months (Osborne 1999). Late chum are therefore running through the Puget Sound region at a time when the whales are less likely to be present.

There were no instances of positive correlations observed between whales and pink salmon when both total run-size and escapement data were used, contrary to occurrences with most other species. Infrequency of significant correlations

between the pods and pink salmon could be attributed to the small body size and limited time pink salmon spend in the Georgia Strait-Puget Sound Basin. Because pink salmon have are only available every other year, the whales are not as likely to have adapted feeding strategies that relied on pink salmon runs. If the whales were to show positive correlation with pink, it would be expected that these correlations would be with pink returning to spawn in the Fraser River, or rivers draining into northern Puget Sound, which support the largest pink runs in the trans-boundary region (Heard 1991; Ruggerone and Goetz 2004). None of the pods did show positive correlations with pink in either of these areas, strengthening the idea that the SRC is not reliant on pink salmon.

Inverse Correlations

Salmon species that showed positive or negative correlations with either totaled whales or individual pods also showed positive correlation with each other, with one exception. Totalled whales and totaled coho had a significantly inverse relationship when total run-size data were used. Yet coho also showed a positive relationship with chinook salmon, one of the species with which the whales had positive correlation.

While the only negative correlations found between the whales and salmon totaled by species involved coho, a number of negative correlations were found between whales and salmon on the region specific scale. The inverse correlations found between the whales and certain salmon species from certain regions could be attributed to a number of variables. It is possible that correlations were found simply by chance, given the number of tests performed. It is also possible that there are relationships between salmon species themselves that have direct impacts on whale population trends. For instance in years when one species of salmon

produces a large cohort of juveniles, juveniles from another species could suffer higher mortality rates. A negative correlation results with the species that drives the preferred species to lower abundance in years of higher productivity for that negatively correlated species. Interactions of this sort have been observed between pink and a number of other salmon species. In years of abundant juvenile pink salmon, juvenile chum exhibit lower growth and feeding rates (Salo 1991). Density dependent competition with pink salmon has also been seen to affect sockeye, coho, and chinook salmon growth (Ruggerone and Goetz 2004). Competition between adjacent year classes within the same species may also influence ocean growth and survival (Salo 1991).

When salmon population trends were tested for significant relationships using both the total run-size and the escapement data, chinook from the Strait of Juan de Fuca, San Juan Islands, and northern Puget Sound regions showed significant inverse correlations with early chum, normal chum, and pink from the southern Puget Sound and Hood Canal regions. Rearing conditions in southern Puget Sound and Hood Canal are similar in terms of vegetative eco-regions, climate, and topography, while rearing conditions in northern Puget Sound and the Strait of Juan de Fuca area are similar in biological and physical environment (Bailey et al. 1994; Weitkamp et al. 1995). It is likely that years of favorable conditions in either the northern or the southern areas produced cohorts of juveniles that dominated those from the dissimilar areas. It is therefore not surprising that the most significant negative correlations between salmon were between species born in different regions and habitats.

Every significant inverse correlation involved chinook and another species of salmon. This would indicate that either chinook have a particularly strong effect on other species or vice versa.

Significance of Results

Considering the number of correlation tests run in these analyses, it is expected that some significant correlations are derived by chance. A total of 1,560 correlation tests were run between whales and salmon, including each time lag period tested. The number of correlations expected by chance at the 0.05 significance level would be approximately 78. The number of correlations expected by chance at the 0.01 significance level would be approximately 15.6. Overall, for an average significance level of 0.03, 46.8 correlations would be expected to result in significant correlations by chance alone. The number of observed significant correlations was 571. 218 of these were significant at the 0.05 alpha level and 353 were significant at the 0.01 alpha level. Keeping the possibility of random correlations appearing significant when they are not in mind, there were a substantial number of correlations observed in this analysis. In fact, the likely number of chance correlations is extremely small compared to the number of significant correlations actually observed (8.1%). It can therefore be concluded that the correlation patterns observed in this study are not due to the number of significant correlations expected by chance when performing such a large number of statistical tests.

Statistically significant correlations do not necessarily describe cause and affect. They do describe relationships, and in this case, the relationship between salmon and whale population trends. There appears to be significant relationships between whales and salmon at very specific regional, pod, and species scales. This would

imply that salmon population trends or availability does affect whales, but not in general terms. Specific runs of salmon are tied to whale population dynamics, implying that there are unique characteristics of those runs, possibly including abundance, caloric value, or tendencies to aggregate in dense patches in habitats easily exploited by the whales. Pod specific differences in correlation patterns imply that much of the relationship between salmon and whales is determined by the behavior of the whales themselves. There may be social drivers that dictate where pods concentrate their foraging efforts based on learned behavior passed across matrilineal generations over time. There may also be a partitioning of habitat or resources among the pods to avoid or minimize direct competition for prey. J & K pods combined roughly equal the number of whales in L pod. It is possible that J & K pods occupy the same or similar foraging niches, while L pod occupies one substantially different.

The pod, species, and region specific results of these analyses are particularly important for management directed at the conservation of both salmon and the SRC. While evidence of species preference existed, there has not previously been knowledge of the specific spawning regions producing the runs of salmon most closely associated with whale population trends. These results show correlation patterns between whales and salmon on an annual scale and therefore are not dependent on the same restraints affecting prey tissue sampling or stomach content analysis studies. Results from these types of studies are restricted to the time and place where the sampling occurred, which up to this point has not been carried out through much of the winter and spring months, and in only a limited portion of the SRC range. These results provide guidelines for prioritizing the species of salmon spawning in specific geographic regions on which to focus conservation efforts. Due to the more extreme fluctuations in population in L pod, it may also be

desirable to focus conservation efforts on spawning regions of salmon most closely correlated with L pod.

Future Analysis

Future research on SRC spatial and temporal prey associations could broaden the time frame analyzed in an effort to discern longer term patterns. However, as previously stated, the data quality and consistency in both more recent years and years further back in time would make conclusions drawn from such comparisons more tenuous than from years of more equal robustness, such as the period analyzed in this work.

Future studies could also incorporate more Canadian data than was incorporated here, specifically salmon escapement numbers for more rivers in BC. Instead of using numbers of fish for analysis of catch density and escapement correlations to whales, biomass could be used. This would eliminate the bias of changing sizes of salmon across time. However, it would not reflect the potential added effort on behalf of a whale to obtain a higher number of individual fish representing a constant biomass.

Using different parameters of whale population would also be recommended for future analysis. For example, mortality, birth, or growth rates of each whale pod could be compared to salmon population numbers across time. Since mortality rates of killer whales have been found to be a better indicator of population trend in other populations (Olesiuk et al. 2005), testing mortality rates against salmon abundance is suggested as a priority.

Optimal foraging theory predicts that diet composition should depend on density and relative value of preferred prey, independently of the abundance of alternative prey. It also predicts that diet breadth should increase when abundance of preferred prey decreases (Salamolard et al. 2000). Future analysis should break down the population trends of both whales and salmon to test if correlation strengths significantly differ between time periods. Space use patterns of the SRC differed between the early 1990s (population increasing) and the late 1990s (population decreasing; see Chapter 2). If correlation strengths are significant in the early 1990s and non-existent in the latter 1990s it could be concluded that the whales likely broadened their diet or switched prey species entirely.

Another proposed cut-off to test whether correlation between predator and prey populations have changed between time periods is based on differences in salmon marine survival rates. Studies have shown that marine survival rates of many Puget Sound salmon stocks have decreased since the 1980s due to warmer sea surface temperatures caused by more frequent El Niño/Southern Oscillation events and general climactic warming (Beamish et al. 2000; McFarlane et al. 2000; Ruggerone and Goetz 2004). It would be interesting to divide the salmon population trend data into pre-and post 1985 and test against southern resident population data to see if there are any changes in correlation pattern. It is possible that the whales have switched preferred prey species as the profitability of predating on certain stocks has changed.

Predators will switch to lower quality prey only when more profitable prey has been reduced to low levels (van Baalen et al. 2001). The alternative prey

hypothesis predicts that a predator with a strong preference for a main prey category that fluctuates in numbers between years will switch to alternative prey when the main prey is scarce (Ainley et al. 1996; Patterson et al. 1998). However, prey switching appears to be an extreme adaptation to declining abundance of preferred prey and has rarely been documented in top predators (Table 3.19), and therefore may not be likely to occur in a specialist forager like the SRC. Prey switching is not expected when predators have strong preferences for specific prey, and when there is little variation among individuals in their preferred prey species (O'Donoghue et al. 1998). Some predators have shown a very low rate of switching behavior, regardless of the density of their preferred prey species. One such predator is the wolf, which continues to prefer to hunt moose, despite decreasing densities of moose and the presence of more abundant caribou (Hayes and Harestad 2000).

Population associations of the SRC and salmon would therefore not be expected to diminish with time, but the investigation would be no less interesting. Predicting when switching might occur and how long a switch in target prey species might last would be difficult to do with any confidence. Any switching behavior to alternative prey species has been observed to be temporary, with a single exception (Table 3.19). While the predation pressure is targeted at the alternative prey, the original preferred prey is theoretically able to increase in numbers, thus preventing unbounded oscillations in population density. As there are energetic benefits of the preferred prey, predators switch back once the more profitable prey species has recovered (van Baalen et al. 2001). There is no evidence for predation pressure to continue on alternative prey species when populations of the alternative prey are decreasing while preferred prey becomes more abundant in the same

region. In the exceptional case, preferred prey of Dall's porpoises in the Western North Pacific were no longer available due to severe over-fishing of the prey resource, with no known recovery of the stock (Ohizumi et al. 2000).

Table 3.19. Summary of studies specifically observing the occurrence of prey switching.

SOURCE	LENGTH OF STUDY	PREDATOR(S) STUDIED	PREY SWITCHING OBS?	SWITCH BACK?
Kjellander and Nordström 2003	28 years	Red Fox	Yes	Yes
Patterson et al. 1998	6 years	Coyote	No	N/A
O'Donoghue et al. 1997	9 years	Coyote and Lynx	Coyote-No; Lynx showed "some evidence of switching"	Yes
Leckie et al. 1998	5 years	Red Fox	Yes	Yes
Ohizumi et al. 2000	sampled stomachs in 1988 and 1996	Dall's Porpoise	Yes	No- original prey no longer available
Sidorovich et al. 2003	11 years	Wolves	Yes	Yes
Ostfeld 1982	2 years	Sea Otter	Yes	unknown
Hayes and Harestad 2000	7 years	Wolves	No	N/A
Ainley et al. 1996	4 years	Murres	Yes	Yes

Testing for significant relationships in population trend between the SRC and other potential prey species is recommended. Tissues of Pacific halibut, rockfish, and herring have been collected near foraging whales, and found in stomachs of southern resident whales (Felleman et al. 1991; Ford et al. 1998; Ford and Ellis

2005), and therefore represent potential prey populations to analyze. Any positive correlations found may elucidate what the whales feed on in the winter and spring months, or results may support the mounting evidence that the SRC are salmonid specialists.

CONCLUSIONS

Overall, the SRC appears to have a stronger relationship with chinook and chum than to the generally more abundant species of salmon. The whales showed significant positive correlation to normal chum salmon in every spawning region analyzed. The second most frequently correlated species was chinook, which showed positive correlation with the whales when both total run-size and escapement data were used in three of the six regions tested. Chinook are larger than any other species of salmon, with a higher lipid content (Brett 1995). Most importantly, they are present in near-shore areas year-round (Healey 1991) and therefore potentially available as prey. Although pink, coho, and sockeye salmon runs are relatively large in comparison to chinook runs, their availability is ephemeral as they migrate through the inland waters, and therefore does not seem to significantly impact population dynamics of the SRC (Burgner 1991; Heard 1991; Sandercock 1991; Ford et al. 2005).

Natural variability is magnified in small populations and the reasons for births and deaths are complex. This analysis is not meant to elucidate the finest details of correlations between whale and salmon population trends. In reality, relationships between whale pods and different salmon species, as well as between the salmon species themselves, are intricate and uncertain. Rather, this study represents an effort to determine more general patterns, if they exist, at multiple scales. There is a need for a fuller picture of SRC prey preferences, particularly during non-summer

months and when the whales are distributed off the outer coast, so that resources most crucial to the survival of the population can be protected. Any relationships that can be shown, even on a coarse scale, to be significant could have important implications in the management of both the SRC and the salmon runs on which they appear to depend. In this vein, the results of this study indicate that chinook from the SJdF, CPS, and SPS, chum from every region analyzed, and Fraser River sockeye are the most significantly associated with the SRC. As such, these populations of salmon can be considered of the highest priority to protect for the future survival of the SRC.

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APPENDIX: Salmon Abundance and Correlation Tables**Table A1.** Total salmon run-size and escapement data average over the years of available data for each species and region.**Average Abundance**

Species	Data							
		SJdF	SJI	NPS	CPS	SPS	HC	Total PS
Chinook	TRS	3,977	37,689	23,679	N/A	86,780	19,294	201,238
	ESC	3,046	12,240	21,475	31,701	7,047	8,825	84,334
E. Chum	TRS	2,247	N/A	N/A	N/A	50,199	14,497	68,508
	ESC	1,976	N/A	N/A	N/A	29,636	12,565	44,177
N. Chum	TRS	3,176	N/A	358,572	N/A	328,911	391,815	1,165,149
	ESC	2,696	37,847	146,946	39,924	87,455	120,821	435,688
L. Chum	TRS	N/A	N/A	N/A	N/A	N/A	N/A	62,746
	ESC	N/A	N/A	N/A	N/A	39,198	N/A	N/A
Coho	TRS	27,468	194,961	178,721	N/A	467,006	108,411	1,057,141
	ESC	18,300	32,550	181,117	76,986	38,110	59,604	406,667
Pink	TRS	31,078	13,010,359	1,181,346	N/A	63,917	65,158	17,094,021
	ESC	22,276	66,836	829,683	27,840	5,613	57,927	1,010,176
Sockeye	TRS	N/A	8762022	N/A	N/A	N/A	N/A	N/A
	ESC	N/A	2,440,084	N/A	261,301	N/A	N/A	2,673,136

Table A2. Correlations between J, K, and L pods and chinook salmon by region and lag period using total run-size data. Yellow highlight indicates a correlation significant at $\alpha=0.05$. Pink highlight indicates a correlation significant at $\alpha=0.01$. No highlight indicates no significant relationship was found.

J POD (Total Run-Size)

Chin SJdF	Jpod	Jlag1	Jlag2	Jlag3	Jlag4	Jlag5
Correlation Coefficient	-0.06326	0.067231	0.000501	0.095573	0.212613	0.367596
Sig. (2-tailed)	0.769035	0.754938	0.998191	0.672236	0.354812	0.110824
Chin SJI						
Correlation Coefficient	-0.78986	-0.7731	-0.6487	-0.59959	-0.58194	-0.47468
Sig. (2-tailed)	4.43E-06	9.47E-06	0.000813	0.003184	0.005648	0.034446
Chin NPS						
Correlation Coefficient	-0.13533	-0.18159	-0.44048	-0.51377	-0.81525	-0.55634
Sig. (2-tailed)	0.528375	0.395753	0.035415	0.014451	6.73E-06	0.010851
Chin SPS						
Correlation Coefficient	0.099528	0.153199	0.182743	0.383723	0.345455	0.220252
Sig. (2-tailed)	0.643575	0.474802	0.403946	0.077906	0.125078	0.350766
Chin HC						
Correlation Coefficient	-0.05174	-0.08242	0.038542	0.033184	0.091608	0.109131
Sig. (2-tailed)	0.81024	0.701805	0.861397	0.883448	0.692896	0.646956

K POD (Total Run-Size)

Chin SJdF	Kpod	Klag1	Klag2	Klag3	Klag4	Klag5
Correlation Coefficient	0.301679	0.244339	0.14173	-0.00807	0.060834	0.170397
Sig. (2-tailed)	0.151957	0.249873	0.518876	0.971565	0.793363	0.472604
Chin SJI						
Correlation Coefficient	-0.66249	-0.61957	-0.60655	-0.46048	-0.30174	-0.33835
Sig. (2-tailed)	0.00042	0.001243	0.002152	0.031036	0.183741	0.144524
Chin NPS						
Correlation Coefficient	-0.14638	-0.23455	-0.42987	-0.58209	-0.5224	-0.39242
Sig. (2-tailed)	0.494897	0.269943	0.040633	0.004482	0.015122	0.087008
Chin SPS						
Correlation Coefficient	0.459817	0.410773	0.249728	0.266048	0.165215	0.096983
Sig. (2-tailed)	0.023778	0.046158	0.25048	0.231402	0.474183	0.684187
Chin HC						
Correlation Coefficient	0.218029	0.291196	0.283391	0.255311	0.04586	-0.00154
Sig. (2-tailed)	0.306082	0.167419	0.190074	0.251487	0.843523	0.994842

Table A2 continued

L POD (Total Run-Size)

Chin SJDf	Lpod	Llag1	Llag2	Llag3	Llag4	Llag5
Correlation Coefficient	0.015935	0.144138	0.276925	0.427197	0.485185	0.515461
Sig. (2-tailed)	0.941086	0.501613	0.20082	0.047368	0.025785	0.020012
Chin SJI						
Correlation Coefficient	-0.41554	-0.32795	-0.26941	-0.03568	0.176433	0.480967
Sig. (2-tailed)	0.043443	0.117704	0.21381	0.87473	0.444247	0.031807
Chin NPS						
Correlation Coefficient	-0.49848	-0.44586	-0.41677	-0.32342	-0.14909	-0.0392
Sig. (2-tailed)	0.013166	0.028988	0.047885	0.14204	0.518929	0.869663
Chin SPS						
Correlation Coefficient	-0.12617	-0.12405	-0.11414	-0.04561	0.004884	0.107089
Sig. (2-tailed)	0.556879	0.563606	0.604045	0.840274	0.983236	0.65316
Chin HC						
Correlation Coefficient	-0.66827	-0.57249	-0.46143	-0.25998	0.032552	0.383718
Sig. (2-tailed)	0.000358	0.003461	0.026671	0.242612	0.888601	0.094882

Table A3. Correlations between J, K, and L pods and chinook salmon by region and lag period using escapement data. Yellow highlight indicates a correlation significant at $\alpha= 0.05$. Pink highlight indicates a correlation significant at $\alpha= 0.01$. No highlight indicates no significant relationship was found.

J POD (Escapement)

Chin SJDf	Jpod	Jlag1	Jlag2	Jlag3	Jlag4	Jlag5
Correlation Coefficient	0.35819	0.42399	0.42487	0.50451	0.58101	0.69248
Sig. (2-tailed)	0.04787	0.01559	0.01535	0.00323	0.00049	0.00001
Chin SJI						
Correlation Coefficient	-0.05447	-0.03811	0.10652	0.01227	-0.03011	0.09592
Sig. (2-tailed)	0.77103	0.83596	0.56176	0.94686	0.87004	0.60151
Chin NPS						
Correlation Coefficient	-0.08440	0.08031	-0.18236	-0.10298	-0.50061	-0.29966
Sig. (2-tailed)	0.64606	0.66218	0.31782	0.57488	0.00352	0.09567
Chin CPS						
Correlation Coefficient	0.64096	0.60322	0.59560	0.42737	0.36862	0.25746
Sig. (2-tailed)	0.00008	0.00026	0.00032	0.01470	0.03789	0.15486
Chin SPS						
Correlation Coefficient	0.65731	0.61084	0.58649	0.64058	0.52868	0.50507
Sig. (2-tailed)	0.00004	0.00020	0.00042	0.00008	0.00187	0.00320
Chin HC						
Correlation Coefficient	0.42102	0.19853	0.09834	0.15039	0.05075	-0.01097
Sig. (2-tailed)	0.01834	0.27603	0.59234	0.41133	0.78268	0.95249

Table A3 continued

K POD (Escapement)

Chin SJdF	Kpod	Klag1	Klag2	Klag3	Klag4	Klag5
Correlation Coefficient	0.56355	0.59206	0.58812	0.56190	0.65385	0.67470
Sig. (2-tailed)	0.00096	0.00036	0.00040	0.00082	0.00005	0.00002
Chin SJI						
Correlation Coefficient	-0.19460	-0.05546	-0.00204	0.12835	0.31883	0.36853
Sig. (2-tailed)	0.29415	0.76306	0.99116	0.48389	0.07531	0.03794
Chin NPS						
Correlation Coefficient	0.03913	0.12686	-0.01113	-0.15988	-0.29806	-0.44143
Sig. (2-tailed)	0.83160	0.48900	0.95180	0.38208	0.09754	0.01143
Chin CPS						
Correlation Coefficient	0.71537	0.65008	0.55345	0.43215	0.41082	0.36538
Sig. (2-tailed)	0.00000	0.00006	0.00102	0.01351	0.01951	0.03974
Chin SPS						
Correlation Coefficient	0.81144	0.78288	0.74115	0.73930	0.71222	0.68310
Sig. (2-tailed)	0.00000	0.00000	0.00000	0.00000	0.00000	0.00002
Chin HC						
Correlation Coefficient	0.48702	0.53119	0.49688	0.44143	0.31234	0.24204
Sig. (2-tailed)	0.00546	0.00176	0.00382	0.01143	0.08179	0.18198

Table A3 continued

L POD (Escapement)

Chin SJdF	Lpod	Llag1	Llag2	Llag3	Llag4	Llag5
Correlation Coefficient	0.30759	0.36897	0.45176	0.53466	0.53733	0.49746
Sig. (2-tailed)	0.09231	0.0377	0.00944	0.00162	0.00152	0.00377
Chin SJI						
Correlation Coefficient	0.02224	0.1257	0.17697	0.27934	0.4122	0.44547
Sig. (2-tailed)	0.90549	0.49302	0.33256	0.12155	0.01906	0.01062
Chin NPS						
Correlation Coefficient	-0.29404	-0.40393	-0.44142	-0.58091	-0.4927	-0.35266
Sig. (2-tailed)	0.10237	0.02186	0.01143	0.00049	0.00417	0.04774
Chin CPS						
Correlation Coefficient	0.08711	0.00864	-0.09501	-0.16393	-0.2933	-0.25048
Sig. (2-tailed)	0.63546	0.96258	0.60498	0.36999	0.10327	0.16675
Chin SPS						
Correlation Coefficient	0.21612	0.19645	0.12497	0.13581	0.03804	0.04925
Sig. (2-tailed)	0.23483	0.28119	0.49558	0.45862	0.83624	0.78894
Chin HC						
Correlation Coefficient	-0.00303	-0.14169	-0.2141	-0.34402	-0.29257	-0.27695
Sig. (2-tailed)	0.98708	0.4392	0.23934	0.05386	0.10417	0.1249

Table A4. Correlations between J, K, and L pods and early chum salmon by region and lag period using total run-size data. Yellow highlight indicates a correlation significant at $\alpha=0.05$. Pink highlight indicates a correlation significant at $\alpha=0.01$. No highlight indicates no significant relationship was found.

J POD (Total Run-Size)

Echum SJdF	Jpod	Jlag1	Jlag2	Jlag3	Jlag4	Jlag5
Correlation Coefficient	-0.03359	0.033583	-0.20641	-0.18452	-0.39778	-0.37595
Sig. (2-tailed)	0.857649	0.857664	0.273797	0.337948	0.036056	0.053284
Echum SPS						
Correlation Coefficient	0.396649	0.466218	0.280139	0.491685	0.440564	0.571618
Sig. (2-tailed)	0.02716	0.007156	0.120437	0.004263	0.011615	0.000632
Echum HC						
Correlation Coefficient	0.006758	0.059993	0.015615	-0.10869	-0.32661	-0.37511
Sig. (2-tailed)	0.97122	0.748522	0.934729	0.574636	0.089825	0.053859

Table A4 continued

K POD (Total Run-Size)

Echum SJdF	Kpod	Klag1	Klag2	Klag3	Klag4	Klag5
Correlation Coefficient	0.036147	0.015419	-0.08605	-0.29283	-0.40837	-0.55502
Sig. (2-tailed)	0.846918	0.934388	0.651168	0.123178	0.030971	0.002657
Echum SPS						
Correlation Coefficient	0.60301	0.63135	0.574039	0.444022	0.391348	0.423435
Sig. (2-tailed)	0.00033	0.000107	0.000592	0.010903	0.026767	0.015742
Echum HC						
Correlation Coefficient	0.07678	0.085357	-0.07793	-0.39155	-0.54978	-0.54674
Sig. (2-tailed)	0.681415	0.647994	0.682285	0.035683	0.00244	0.003168

L POD (Total Run-Size)

Echum SJdF	Lpod	Llag1	Llag2	Llag3	Llag4	Llag5
Correlation Coefficient	-0.5884	-0.60192	-0.47807	-0.32678	-0.1967	-0.07112
Sig. (2-tailed)	0.000499	0.000341	0.007539	0.083586	0.315739	0.724446
Echum SPS						
Correlation Coefficient	0.291087	0.353029	0.236333	0.2367	0.347332	0.344943
Sig. (2-tailed)	0.112123	0.047489	0.192831	0.19212	0.051444	0.053178
Echum HC						
Correlation Coefficient	-0.57732	-0.55465	-0.55189	-0.5304	-0.51806	-0.53886
Sig. (2-tailed)	0.000673	0.001203	0.001569	0.003078	0.004744	0.003731

Table A5. Correlations between J, K, and L pods and early chum salmon by region and lag period using escapement data using escapement data. Yellow highlight indicates a correlation significant at $\alpha=0.05$. Pink highlight indicates a correlation significant at $\alpha=0.01$. No highlight indicates no significant relationship was found.

J POD (Escapement)

Echum SJdF	Jpod	Jlag1	Jlag2	Jlag3	Jlag4	Jlag5
Correlation Coefficient	0.00512	0.0251	-0.23069	-0.22939	-0.448	-0.42406
Sig. (2-tailed)	0.97819	0.89156	0.20398	0.20662	0.01013	0.01557
Echum SPS						
Correlation Coefficient	0.61781	0.66029	0.50154	0.64319	0.54336	0.64914
Sig. (2-tailed)	0.00021	0.00004	0.00345	0.00007	0.00131	0.00006
Echum HC						
Correlation Coefficient	0.19945	0.15169	-0.03978	-0.17474	-0.36026	-0.38387
Sig. (2-tailed)	0.28205	0.40725	0.82886	0.3388	0.04282	0.03009

K POD (Escapement)

Echum SJdF	Kpod	Klag1	Klag2	Klag3	Klag4	Klag5
Correlation Coefficient	0.06698	0.02968	-0.10461	-0.28563	-0.43419	-0.59607
Sig. (2-tailed)	0.72035	0.87191	0.56883	0.11304	0.01303	0.00032
Echum SPS						
Correlation Coefficient	0.76208	0.78807	0.73447	0.63821	0.52359	0.50412
Sig. (2-tailed)	0.00000	0.00000	0.00000	0.00008	0.00210	0.00326
Echum HC						
Correlation Coefficient	0.24198	0.16878	0.01706	-0.28860	-0.45812	-0.54177
Sig. (2-tailed)	0.18968	0.35578	0.92615	0.10918	0.00837	0.00136

Table A5 continued

L POD (Escapement)

Echum SJDf	Lpod	Llag1	Llag2	Llag3	Llag4	Llag5
Correlation Coefficient	-0.58359	-0.58513	-0.4859	-0.35946	-0.3012	-0.22248
Sig. (2-tailed)	0.00057	0.00044	0.00481	0.04332	0.09389	0.221
Echum SPS						
Correlation Coefficient	0.20275	0.23266	0.10016	0.12754	0.18414	0.20564
Sig. (2-tailed)	0.27401	0.20005	0.58548	0.48667	0.31303	0.25884
Echum HC						
Correlation Coefficient	-0.50132	-0.52412	-0.59616	-0.6592	-0.68456	-0.7226
Sig. (2-tailed)	0.00407	0.00208	0.00032	0.00004	0.00002	0

Table A6. Correlations between J, K, and L pods and normal chum salmon by region and lag period using total run size data. Yellow highlight indicates a correlation significant at $\alpha=0.05$. Pink highlight indicates a correlation significant at $\alpha=0.01$. No highlight indicates no significant relationship was found.

J POD (Total Run-Size)

Nchum SJDf	Jpod	Jlag1	Jlag2	Jlag3	Jlag4	Jlag5
Correlation Coefficient	-0.02057	0.00543	-0.03154	0.03327	0.03978	0.12418
Sig. (2-tailed)	0.91565	0.97727	0.86626	0.85653	0.82886	0.49833
Nchum NPS						
Correlation Coefficient	0.19316	0.32931	0.20498	0.43647	0.17678	0.37959
Sig. (2-tailed)	0.31541	0.07557	0.26865	0.01251	0.33309	0.03213
Nchum SPS						
Correlation Coefficient	0.48290	0.57963	0.45788	0.65471	0.42848	0.48629
Sig. (2-tailed)	0.00797	0.00079	0.00959	0.00005	0.01442	0.00477
Nchum HC						
Correlation Coefficient	0.45029	0.61177	0.60388	0.62664	0.53481	0.52886
Sig. (2-tailed)	0.01424	0.00033	0.00032	0.00012	0.00161	0.00186

Table A6 continued

K POD (Total Run-Size)

Nchum SJdF	Kpod	Klag1	Klag2	Klag3	Klag4	Klag5
Correlation Coefficient	-0.14209	-0.01557	0.03859	0.08736	0.08402	0.22924
Sig. (2-tailed)	0.46219	0.93493	0.83669	0.63449	0.64754	0.20691
Nchum NPS						
Correlation Coefficient	0.37148	0.36909	0.46150	0.44680	0.38912	0.31104
Sig. (2-tailed)	0.04724	0.04473	0.00897	0.01036	0.02772	0.08314
Nchum SPS						
Correlation Coefficient	0.48680	0.57416	0.60505	0.56996	0.42418	0.36891
Sig. (2-tailed)	0.00741	0.00091	0.00031	0.00066	0.01554	0.03773
Nchum HC						
Correlation Coefficient	0.57636	0.65853	0.65263	0.60409	0.46554	0.41509
Sig. (2-tailed)	0.00107	0.00008	0.00007	0.00025	0.00725	0.01816

L POD (Total Run-Size)

Nchum SJdF	Lpod	Llag1	Llag2	Llag3	Llag4	Llag5
Correlation Coefficient	0.07407	0.20401	0.32100	0.40081	0.51659	0.58422
Sig. (2-tailed)	0.70258	0.27953	0.07828	0.02300	0.00247	0.00045
Nchum NPS						
Correlation Coefficient	0.17232	0.30747	0.29250	0.35285	0.43205	0.44528
Sig. (2-tailed)	0.37138	0.09836	0.11031	0.04761	0.01353	0.01065
Nchum SPS						
Correlation Coefficient	0.34119	0.36098	0.34162	0.27805	0.36681	0.32068
Sig. (2-tailed)	0.07009	0.05002	0.05998	0.12335	0.03892	0.07354
Nchum HC						
Correlation Coefficient	0.46710	0.53333	0.58662	0.53882	0.52155	0.40191
Sig. (2-tailed)	0.01063	0.00241	0.00052	0.00146	0.00220	0.02259

Table A7. Correlations between J, K, and L pods and normal chum salmon by region and lag period using escapement data. Yellow highlight indicates a correlation significant at $\alpha= 0.05$. Pink highlight indicates a correlation significant at $\alpha= 0.01$. No highlight indicates no significant relationship was found.

J POD (Escapement)

Nchum SJDf	Jpod	Jlag1	Jlag2	Jlag3	Jlag4	Jlag5
Correlation Coefficient	0.16973	0.14430	0.09892	0.12670	0.13711	0.16769
Sig. (2-tailed)	0.37875	0.44679	0.59652	0.48958	0.45429	0.35895
Nchum SJI						
Correlation Coefficient	0.60833	0.53776	0.39378	0.45153	0.20857	0.07677
Sig. (2-tailed)	0.00046	0.00218	0.02839	0.00948	0.25197	0.67621
Nchum NPS						
Correlation Coefficient	0.07375	0.21750	0.00000	0.25653	-0.10224	0.16061
Sig. (2-tailed)	0.70379	0.24826	1.00000	0.15640	0.57766	0.37988
Nchum NPS						
Correlation Coefficient	0.56041	0.55451	0.51399	0.62348	0.43945	0.50061
Sig. (2-tailed)	0.00157	0.00147	0.00310	0.00014	0.01185	0.00352
Nchum SPS						
Correlation Coefficient	0.55791	0.64074	0.61207	0.71290	0.62255	0.69356
Sig. (2-tailed)	0.00166	0.00014	0.00025	0.00000	0.00014	0.00001
Nchum HC						
Correlation Coefficient	0.55740	0.59819	0.64975	0.69710	0.56177	0.51734
Sig. (2-tailed)	0.00168	0.00048	0.00008	0.00001	0.00082	0.00243

Table A7 continued

K POD (Escapement)

Nchum SJdF	Kpod	Klag1	Klag2	Klag3	Klag4	Klag5
Correlation Coefficient	0.00225	0.10526	0.18104	0.22834	0.23390	0.35466
Sig. (2-tailed)	0.99075	0.57988	0.32972	0.20876	0.19758	0.04640
Nchum SJI						
Correlation Coefficient	0.36698	0.26847	0.40085	0.36612	0.34665	0.37020
Sig. (2-tailed)	0.05020	0.15144	0.02543	0.03931	0.05194	0.03701
Nchum NPS						
Correlation Coefficient	0.30194	0.23576	0.31243	0.22591	0.12761	0.03654
Sig. (2-tailed)	0.11141	0.20978	0.08705	0.21379	0.48644	0.84263
Nchum NPS						
Correlation Coefficient	0.61588	0.61702	0.64650	0.62263	0.44643	0.34387
Sig. (2-tailed)	0.00038	0.00028	0.00009	0.00014	0.01043	0.05397
Nchum SPS						
Correlation Coefficient	0.73621	0.81849	0.76453	0.78066	0.68940	0.59518
Sig. (2-tailed)	0.00001	0.00000	0.00000	0.00000	0.00001	0.00033
Nchum HC						
Correlation Coefficient	0.60813	0.67049	0.70266	0.63840	0.44847	0.37262
Sig. (2-tailed)	0.00047	0.00005	0.00001	0.00008	0.01004	0.03570

Table A7 continued

L POD (Escapement)

Nchum SJDf	Lpod	Llag1	Llag2	Llag3	Llag4	Llag5
Correlation Coefficient	0.21926	0.28810	0.35429	0.38982	0.44946	0.52206
Sig. (2-tailed)	0.25313	0.12261	0.05052	0.02742	0.00986	0.00218
Nchum SJI						
Correlation Coefficient	0.26812	0.25440	0.13847	0.10163	0.10236	0.11504
Sig. (2-tailed)	0.15965	0.17489	0.45756	0.57995	0.57720	0.53068
Nchum NPS						
Correlation Coefficient	-0.00790	0.07090	0.00930	0.04576	0.06689	0.06873
Sig. (2-tailed)	0.96756	0.70965	0.96040	0.80360	0.71604	0.70857
Nchum NPS						
Correlation Coefficient	0.36317	0.31505	0.22680	0.14831	0.09630	0.08803
Sig. (2-tailed)	0.05282	0.08993	0.21983	0.41791	0.60008	0.63188
Nchum SPS						
Correlation Coefficient	0.46365	0.37570	0.26117	0.24295	0.25655	0.21520
Sig. (2-tailed)	0.01130	0.04076	0.15586	0.18030	0.15638	0.23687
Nchum HC						
Correlation Coefficient	0.36613	0.46912	0.39054	0.27731	0.19076	0.04025
Sig. (2-tailed)	0.05078	0.00892	0.02984	0.12438	0.29566	0.82688

Table A8. Correlations between J, K, and L pods and late chum salmon by region and lag period using escapement data. Yellow highlight indicates a correlation significant at $\alpha = 0.05$. Pink highlight indicates a correlation significant at $\alpha = 0.01$. No highlight indicates no significant relationship was found.

J POD (Escapement)

Lchum SPS	Jpod	Jlag1	Jlag2	Jlag3	Jlag4	Jlag5
Correlation Coefficient	0.26785	0.20987	0.03160	0.06525	-0.09350	-0.20021
Sig. (2-tailed)	0.14517	0.24896	0.86368	0.72274	0.61074	0.27192

K POD (Escapement)

Lchum SPS	Kpod	Klag1	Klag2	Klag3	Klag4	Klag5
Correlation Coefficient	0.31468	0.24019	0.10720	0.06454	-0.15598	-0.22535
Sig. (2-tailed)	0.08468	0.18546	0.55922	0.72562	0.39394	0.21495

Table A8 continued

L POD (Escapement)

Lchum SPS	Lpod	Llag1	Llag2	Llag3	Llag4	Llag5
Correlation Coefficient	-0.18921	-0.16962	-0.15345	-0.08270	-0.01819	0.14610
Sig. (2-tailed)	0.30801	0.35335	0.40175	0.65273	0.92127	0.42494

Table A9. Correlations between J, K, and L pods and coho salmon by region and lag period using total run-size data. Yellow highlight indicates a correlation significant at $\alpha=0.05$. Pink highlight indicates a correlation significant at $\alpha=0.01$. No highlight indicates no significant relationship was found.

J POD (Total Run-Size)

Coho SJdF	Jpod	Jlag1	Jlag2	Jlag3	Jlag4	Jlag5
Correlation Coefficient	0.073413	0.060825	-0.0896	-0.18251	-0.24912	-0.32968
Sig. (2-tailed)	0.733171	0.777686	0.684339	0.416252	0.276156	0.155754
Coho SJ						
Correlation Coefficient	-0.63418	-0.59944	-0.49904	-0.32669	-0.4185	-0.31518
Sig. (2-tailed)	0.000875	0.001963	0.015345	0.137829	0.059015	0.175871
Coho NPS						
Correlation Coefficient	-0.14638	0.125618	0.003504	0.105272	0.096221	0.011447
Sig. (2-tailed)	0.494897	0.558634	0.987341	0.641038	0.67821	0.961797
Coho SPS						
Correlation Coefficient	-0.75624	-0.58357	-0.66522	-0.51149	-0.50945	-0.46552
Sig. (2-tailed)	1.91E-05	0.002758	0.000533	0.01497	0.018327	0.038594
Coho HC						
Correlation Coefficient	0.098179	0.226112	-0.05156	-0.33813	-0.3058	-0.53573
Sig. (2-tailed)	0.648098	0.288045	0.81528	0.123771	0.177626	0.014909

Table A9 continued

K POD (Total Run-Size)

Coho SJdF	Kpod	Klag1	Klag2	Klag3	Klag4	Klag5
Correlation Coefficient	-0.03096	0.107982	0.052853	-0.04092	-0.05915	-0.01004
Sig. (2-tailed)	0.885818	0.615504	0.810715	0.856525	0.79896	0.966483
Coho SJI						
Correlation Coefficient	-0.55679	-0.25712	-0.26628	-0.22246	-0.24458	-0.51138
Sig. (2-tailed)	0.004713	0.225167	0.2194	0.319703	0.285281	0.021189
Coho NPS						
Correlation Coefficient	0.302056	0.319519	0.287418	0.199984	0.135585	-0.21012
Sig. (2-tailed)	0.151421	0.128016	0.183583	0.372223	0.557876	0.373925
Coho SPS						
Correlation Coefficient	-0.44269	-0.45051	-0.39967	-0.44204	-0.52705	-0.62803
Sig. (2-tailed)	0.030287	0.027157	0.05883	0.039416	0.014088	0.003026
Coho HC						
Correlation Coefficient	0.210953	0.233665	0.009564	-0.09048	-0.12362	-0.39628
Sig. (2-tailed)	0.32243	0.271807	0.965455	0.688824	0.593431	0.083673

L POD (Total Run-Size)

Coho SJdF	Lpod	Llag1	Llag2	Llag3	Llag4	Llag5
Correlation Coefficient	-0.77216	-0.8904	-0.87274	-0.77825	-0.53711	-0.34904
Sig. (2-tailed)	9.86E-06	0.000001	0.000001	2E-05	0.012048	0.131465
Coho SJI						
Correlation Coefficient	-0.27848	-0.17817	-0.02282	0.201644	0.358074	0.551076
Sig. (2-tailed)	0.187604	0.404879	0.917673	0.368185	0.110982	0.01179
Coho NPS						
Correlation Coefficient	-0.50197	-0.38079	-0.21484	-0.05211	0.209636	0.398041
Sig. (2-tailed)	0.012441	0.066393	0.324908	0.817853	0.361747	0.082187
Coho SPS						
Correlation Coefficient	-0.23614	-0.06507	0.141902	0.332485	0.541017	0.722958
Sig. (2-tailed)	0.266609	0.762605	0.518366	0.130571	0.011323	0.000317
Coho HC						
Correlation Coefficient	-0.57181	-0.55634	-0.50658	-0.4384	-0.31576	-0.1764
Sig. (2-tailed)	0.003509	0.004755	0.013635	0.041259	0.163212	0.456893

Table A10. Correlations between J, K, and L pods and coho salmon by region and lag period using escapement data. Yellow highlight indicates a correlation significant at $\alpha= 0.05$. Pink highlight indicates a correlation significant at $\alpha= 0.01$. No highlight indicates no significant relationship was found.

J POD (Escapement)

Coho SJDf	Jpod	Jlag1	Jlag2	Jlag3	Jlag4	Jlag5
Correlation Coefficient	0.23767	0.23722	0.19595	0.00837	-0.1861	-0.2361
Sig. (2-tailed)	0.19795	0.19112	0.28246	0.96375	0.30784	0.19327
Coho SJI						
Correlation Coefficient	0.57317	0.57403	0.54355	0.46454	0.36825	0.29074
Sig. (2-tailed)	0.00075	0.00059	0.0013	0.00739	0.0381	0.10646
Coho NPS						
Correlation Coefficient	0.10894	0.26341	0.22196	0.24185	0.17864	0.11135
Sig. (2-tailed)	0.55965	0.14521	0.22212	0.18235	0.32795	0.54404
Coho CPS						
Correlation Coefficient	0.1972	0.29668	0.33033	0.18961	-0.05744	-0.20374
Sig. (2-tailed)	0.28764	0.09917	0.06482	0.29862	0.75484	0.26338
Coho SPS						
Correlation Coefficient	-0.00143	0.10745	-0.00186	0.11172	-0.14964	-0.15588
Sig. (2-tailed)	0.99389	0.55833	0.99194	0.54269	0.41367	0.39424
Coho HC						
Correlation Coefficient	0.50846	0.55643	0.39264	0.15756	-0.06135	-0.16286
Sig. (2-tailed)	0.00349	0.00094	0.02622	0.38912	0.73872	0.37316

Table A10 continued

K POD (Escapement)

Coho SJdF	Kpod	Klag1	Klag2	Klag3	Klag4	Klag5
Correlation Coefficient	0.12141	0.10573	0.02745	-0.07735	-0.10591	-0.18670
Sig. (2-tailed)	0.51529	0.56467	0.88144	0.67392	0.56398	0.30625
Coho SJI						
Correlation Coefficient	0.45762	0.58554	0.60075	0.60965	0.53305	0.53806
Sig. (2-tailed)	0.00964	0.00043	0.00028	0.00021	0.00168	0.00149
Coho NPS						
Correlation Coefficient	0.32509	0.31215	0.30343	0.26690	0.22776	-0.04062
Sig. (2-tailed)	0.07435	0.08198	0.09136	0.13977	0.20995	0.82531
Coho CPS						
Correlation Coefficient	0.20747	0.34869	0.24130	0.15728	-0.00334	-0.22108
Sig. (2-tailed)	0.26275	0.05048	0.18337	0.38996	0.98553	0.22399
Coho SPS						
Correlation Coefficient	0.00368	0.07178	0.02504	-0.00241	-0.06751	-0.15665
Sig. (2-tailed)	0.98434	0.69625	0.89180	0.98955	0.71352	0.39190
Coho HC						
Correlation Coefficient	0.44639	0.40817	0.26006	0.06557	0.01261	-0.13003
Sig. (2-tailed)	0.01183	0.02039	0.15059	0.72143	0.94538	0.47813

Table A10 continued

L POD (Escapement)

Coho SJdF	Lpod	Llag1	Llag2	Llag3	Llag4	Llag5
Correlation Coefficient	-0.51562	-0.64235	-0.61561	-0.70888	-0.68774	-0.56019
Sig. (2-tailed)	0.00299	0.00007	0.00018	0.00001	0.00001	0.00086
Coho SJI						
Correlation Coefficient	0.02365	-0.02977	-0.07645	-0.07810	-0.07792	0.01268
Sig. (2-tailed)	0.89950	0.87150	0.67751	0.67091	0.67165	0.94509
Coho NPS						
Correlation Coefficient	-0.35982	-0.27860	-0.16080	-0.05587	-0.04411	0.03179
Sig. (2-tailed)	0.04679	0.12258	0.37930	0.76136	0.81057	0.86286
Coho CPS						
Correlation Coefficient	-0.18011	-0.21593	-0.12644	-0.01856	-0.12588	-0.29146
Sig. (2-tailed)	0.33227	0.23524	0.49048	0.91969	0.49239	0.10555
Coho SPS						
Correlation Coefficient	-0.44957	-0.41257	-0.21024	0.00092	-0.00882	0.08013
Sig. (2-tailed)	0.01117	0.01894	0.24812	0.99602	0.96178	0.66286
Coho HC						
Correlation Coefficient	-0.13200	-0.21568	-0.34093	-0.42014	-0.55587	-0.51746
Sig. (2-tailed)	0.47904	0.23581	0.05620	0.01666	0.00096	0.00242

Table A11. Correlations between J, K, and L pods and sockeye salmon by region and lag period using total run-size data. Yellow highlight indicates a correlation significant at $\alpha=0.05$. Pink highlight indicates a correlation significant at $\alpha=0.01$. No highlight indicates no significant relationship was found.

J POD (Total Run-Size)

Sock SJI	Jpod	Jlag1	Jlag2	Jlag3	Jlag4	Jlag5
Correlation Coefficient	-0.06266	0.087369	0.208199	0.14481	0.179572	0.206154
Sig. (2-tailed)	0.73772	0.634443	0.252839	0.429085	0.3254	0.257635

K POD (Total Run-Size)

Sock SJI	Kpod	Klag1	Klag2	Klag3	Klag4	Klag5
Correlation Coefficient	0.091483	0.128347	0.097188	0.229801	0.296942	0.283032
Sig. (2-tailed)	0.624522	0.48389	0.596695	0.205783	0.098862	0.116494

Table A11 continued

L POD (Total Run-Size)

Sock SJI	Lpod	Llag1	Llag2	Llag3	Llag4	Llag5
Correlation Coefficient	0.300183	0.304513	0.389416	0.351375	0.373244	0.32289
Sig. (2-tailed)	0.100848	0.090159	0.027594	0.048611	0.03537	0.071467

Table A12. Correlations between J, K, and L pods and sockeye salmon by region and lag period using escapement data. Yellow highlight indicates a correlation significant at $\alpha=0.05$. Pink highlight indicates a correlation significant at $\alpha=0.01$. No highlight indicates no significant relationship was found.

J POD (Escapement)

Sock SJI	Jpod	Jlag1	Jlag2	Jlag3	Jlag4	Jlag5
Correlation Coefficient	0.27092	0.36658	0.54448	0.56641	0.48462	0.56046
Sig. (2-tailed)	0.14044	0.03905	0.00127	0.00073	0.00494	0.00085
Sock CPS						
Correlation Coefficient	-0.15358	-0.20839	-0.25319	-0.17425	-0.43631	-0.36021
Sig. (2-tailed)	0.40944	0.25241	0.16207	0.34851	0.01593	0.05493

K POD (Escapement)

Sock SJI	Kpod	Klag1	Klag2	Klag3	Klag4	Klag5
Correlation Coefficient	0.41596	0.44198	0.46480	0.54807	0.60260	0.57200
Sig. (2-tailed)	0.01994	0.01132	0.00736	0.00117	0.00026	0.00063
Sock CPS						
Correlation Coefficient	-0.22626	-0.15543	-0.13243	-0.25484	-0.29124	-0.31150
Sig. (2-tailed)	0.22098	0.39565	0.46998	0.16649	0.11841	0.09999

L POD (Escapement)

Sock SJI	Lpod	Llag1	Llag2	Llag3	Llag4	Llag5
Correlation Coefficient	0.33718	0.25379	0.25692	0.24699	0.23082	0.22200
Sig. (2-tailed)	0.06361	0.16103	0.15576	0.17294	0.20373	0.22203
Sock CPS						
Correlation Coefficient	-0.34971	-0.36773	-0.25306	-0.17976	-0.04753	-0.03534
Sig. (2-tailed)	0.05380	0.03839	0.16229	0.33322	0.80303	0.85557

Table A13. Correlations between J, K, and L pods and sockeye salmon by region and lag period using total run-size data. Yellow highlight indicates a correlation significant at $\alpha=0.05$. Pink highlight indicates a correlation significant at $\alpha=0.01$. No highlight indicates no significant relationship was found.

J POD (Total Run-Size)

Pink SJI	Jpod	Jlag1	Jlag2	Jlag3	Jlag4	Jlag5
Correlation Coefficient	0.222413	0.354848	0.538866	0.35335	0.161212	0.080851
Sig. (2-tailed)	0.40771	0.177454	0.031256	0.179419	0.550866	0.765964
Pink NPS						
Correlation Coefficient	0.053486	0.1181	0.217116	0.272553	-0.05583	-0.24078
Sig. (2-tailed)	0.868875	0.714701	0.49788	0.417451	0.87049	0.502778
Pink SPS						
Correlation Coefficient	-0.43859	-0.29704	-0.11746	-0.40652	-0.19075	-0.31487
Sig. (2-tailed)	0.153791	0.348455	0.716199	0.214712	0.57424	0.375545
Pink HC						
Correlation Coefficient	-0.17829	-0.00358	0.284743	0.457335	0.521071	0.154347
Sig. (2-tailed)	0.579317	0.991193	0.369701	0.157273	0.100256	0.670294

K POD (Total Run-Size)

Pink SJI	Kpod	Klag1	Klag2	Klag3	Klag4	Klag5
Correlation Coefficient	0.054275	0.274035	0.292479	0.3068	0.179407	0.221909
Sig. (2-tailed)	0.841767	0.304393	0.271647	0.247764	0.50615	0.4088
Pink NPS						
Correlation Coefficient	0.20016	0.562367	0.525051	0.120676	-0.21561	-0.28672
Sig. (2-tailed)	0.532801	0.057	0.079629	0.723763	0.524307	0.421873
Pink SPS						
Correlation Coefficient	-0.14921	-0.03559	-0.16408	-0.32026	-0.61329	-0.26179
Sig. (2-tailed)	0.643487	0.912556	0.610361	0.336983	0.044793	0.465002
Pink HC						
Correlation Coefficient	0.243832	0.359488	0.342742	0.473421	0.225193	0.099728
Sig. (2-tailed)	0.445039	0.251095	0.275441	0.141333	0.505565	0.784002

Table A13 continued

L POD (Total Run-Size)

Pink SJI	Lpod	Llag1	Llag2	Llag3	Llag4	Llag5
Correlation Coefficient	-0.10464	0.192168	0.200443	0.329642	0.400885	0.54694
Sig. (2-tailed)	0.699734	0.475841	0.456672	0.212462	0.123841	0.028342
Pink NPS						
Correlation Coefficient	-0.22378	-0.04241	0.150613	0.304177	0.41458	0.373104
Sig. (2-tailed)	0.484452	0.895893	0.640335	0.363127	0.204877	0.288275
Pink SPS						
Correlation Coefficient	-0.24476	-0.07774	0.325745	0.534613	0.80638	0.91747
Sig. (2-tailed)	0.443262	0.810213	0.301483	0.090202	0.002715	0.000184
Pink HC						
Correlation Coefficient	-0.02098	0.155486	0.350263	0.479308	0.583145	0.789024
Sig. (2-tailed)	0.948402	0.629428	0.264344	0.135765	0.059696	0.00666

Table A14. Correlations between J, K, and L pods and sockeye salmon by region and lag period using escapement data. Yellow highlight indicates a correlation significant at $\alpha=0.05$. Pink highlight indicates a correlation significant at $\alpha=0.01$. No highlight indicates no significant relationship was found.

J POD (Escapement)

Pink SjdF	Jpod	Jlag1	Jlag2	Jlag3	Jlag4	Jlag5
Correlation						
Coefficient	-0.09092	-0.16619	-0.41710	-0.03444	-0.36257	-0.39677
Sig. (2-tailed)	0.74725	0.53845	0.10799	0.89925	0.16755	0.12811
Pink SJI						
Correlation						
Coefficient	0.34915	0.27699	-0.24318	0.26052	-0.13707	0.19764
Sig. (2-tailed)	0.20212	0.29900	0.36411	0.32980	0.61272	0.46313
Pink NPS						
Correlation						
Coefficient	0.35460	0.38928	-0.03685	0.48361	0.15770	0.19913
Sig. (2-tailed)	0.19468	0.13613	0.89224	0.05771	0.55969	0.45968
Pink CPS						
Correlation						
Coefficient	-0.24913	0.03444	0.26382	-0.16470	0.31540	-0.43720
Sig. (2-tailed)	0.37057	0.89925	0.32349	0.54217	0.23407	0.09038
Pink SPS						
Correlation						
Coefficient	-0.36188	-0.23207	-0.24466	-0.42073	0.02948	-0.32341
Sig. (2-tailed)	0.18503	0.38710	0.36112	0.10464	0.91371	0.22176
Pink HC						
Correlation						
Coefficient	0.06728	0.18865	0.35667	0.26501	0.33456	0.01198
Sig. (2-tailed)	0.81169	0.48410	0.17508	0.32122	0.20531	0.96488

Table A14 continued

K POD (Escapement)

Pink SJdF	Kpod	Klag1	Klag2	Klag3	Klag4	Klag5
Correlation Coefficient	0.10115	-0.06851	0.00302	-0.27552	-0.26685	-0.58233
Sig. (2-tailed)	0.71984	0.80096	0.99116	0.30167	0.31775	0.01794
Pink SJI						
Correlation Coefficient	0.37516	0.47360	0.47942	0.26510	0.30454	0.18617
Sig. (2-tailed)	0.16823	0.06387	0.06023	0.32106	0.25144	0.48999
Pink NPS						
Correlation Coefficient	0.25379	0.56445	0.64376	0.61211	0.45983	0.18765
Sig. (2-tailed)	0.36140	0.02274	0.00712	0.01173	0.07313	0.48646
Pink CPS						
Correlation Coefficient	0.02575	0.21893	0.16885	-0.14595	-0.37992	-0.38276
Sig. (2-tailed)	0.92743	0.41528	0.53188	0.58964	0.14664	0.14340
Pink SPS						
Correlation Coefficient	0.12873	0.03872	-0.01206	-0.38722	-0.43721	-0.51084
Sig. (2-tailed)	0.64750	0.88678	0.96464	0.13840	0.09037	0.04316
Pink HC						
Correlation Coefficient	0.34022	0.54658	0.53822	0.48403	0.28796	-0.01936
Sig. (2-tailed)	0.21468	0.02847	0.03150	0.05746	0.27947	0.94326

Table A14 continued

L POD (Escapement)

Pink SJdF	Lpod	Llag1	Llag2	Llag3	Llag4	Llag5
Correlation						
Coefficient	-0.47943	-0.41834	-0.41710	-0.44199	-0.36257	-0.44790
Sig. (2-tailed)	0.07055	0.10684	0.10799	0.08651	0.16755	0.08189
Pink SJI						
Correlation						
Coefficient	-0.03936	-0.03991	-0.24318	-0.21730	-0.13707	0.01626
Sig. (2-tailed)	0.88925	0.88333	0.36411	0.41885	0.61272	0.95234
Pink NPS						
Correlation						
Coefficient	-0.21467	0.05026	-0.03685	0.15373	0.15770	0.19217
Sig. (2-tailed)	0.44231	0.85335	0.89224	0.56973	0.55969	0.47584
Pink CPS						
Correlation						
Coefficient	-0.20215	0.09313	0.26382	0.17295	0.31540	0.21138
Sig. (2-tailed)	0.46999	0.73157	0.32349	0.52182	0.23407	0.43193
Pink SPS						
Correlation						
Coefficient	-0.45438	-0.46120	-0.24466	-0.21434	0.02948	0.04139
Sig. (2-tailed)	0.08884	0.07216	0.36112	0.42536	0.91371	0.87903
Pink HC						
Correlation						
Coefficient	0.10912	0.25573	0.35667	0.24982	0.33456	0.31486
Sig. (2-tailed)	0.69866	0.33908	0.17508	0.35075	0.20531	0.23492