Bulletin of the National Salmon
Resources Center, No. 3: 29-38
December 2000

さけ・ます資源管理センター
研究報告 第 3 号 29-38頁
2000年12月

REVIEW

Japanese Salmon Research in the Ocean: A Review and Future Issues

Shigehiko Urawa*[1], Yukimasa Ishida*[2], and Masa-aki Fukuwaka*[2]

*[1]*Research Division, National Salmon Resources Center, Fisheries Agency of Japan, 2-2 Nakanoshima, Toyohira-ku, Sapporo 062-0922, Japan (urawa@salmon.affrc.go.jp)*
*[2]*Hokkaido National Fisheries Research Institute, Fisheries Agency of Japan, 116 Katsurakoi, Kushiro, Hokkaido 085-0802, Japan*

Abstract.— This paper provided a review on the results of Japanese salmon research conducted in 1993-2000 under the Science Plan decided by the North Pacific Anadromous Fish Commission (NPAFC). Recent developments of stock identification techniques and high-seas salmon population surveys provided new information for the ocean distribution of chum salmon: Japanese chum salmon inhabit the Okhotsk Sea in the early ocean life, pass the first winter in the western North Pacific Ocean, and then migrate to the Bering Sea by the next summer. Coastal surveys suggested that major salmon mortalities occur in the early ocean life, but the causes of juvenile mortalities have not been well understood. Scale pattern analysis suggested that Japanese chum salmon suffer from growth reduction in the Bering Sea, resulting in increase of age at maturity. A long term biological monitoring in the subarctic North Pacific Ocean found a negative relationship between macro-zooplankton and pink salmon biomass. A similar biological monitoring should be necessary in the Bering Sea. The extremely low lipid contents in the muscle of overwintering salmon indicated a great difficulty for them to survive in winter. Future research issues are (1) juvenile salmon studies in the Okhotsk Sea, (2) winter salmon studies in the North Pacific Ocean, (3) salmon ecology studies in the Bering Sea, and (4) monitoring of major salmon stocks. These issues are indispensable for the sustainable stock management of Pacific salmon.

Key words: Pacific salmon, life history, population dynamics, distribution, ocean ecosystem, review

Introduction

The North Pacific Anadromous Fish Commission (NPAFC) was established under the Convention for the Conservation of Anadromous Stocks in the North Pacific Ocean, signed on February 11, 1992 and entered into force on February 16, 1993 by Canada, Japan, the Russian Federation and the United States. The primary objective of NPAFC is to promote the conservation of anadromous stocks in the North Pacific Ocean and adjacent waters.

At the 1993 NPAFC annual meeting, the Committee on Scientific Research and Statistics (CSRS) identified two critical issues for research by the parties: (1) factors affecting current trends in ocean productivity, and (2) factors affecting changes in biological characteristics such as growth, size and age at maturity, oceanic distribution, survival, and abundance of Pacific salmon. The CSRS developed the NPAFC Science Plan to address these two critical issues by three components: (1) life history of salmonids, (2) salmonid population dynamics, and (3) salmonid habitat and ecosystem. Each component has several items that identify questions relating to the two critical issues (Appendix 1). Under the NPAFC Science Plan, the Parties make each research plan, cooperating in the scientific research.

Abstracts of the recent results by Japanese salmon research were compiled by Fisheries Agency of Japan (1997) and Urawa and Ishida (1998, 1999). The purposes of this paper are to review the results of Japanese salmon research related with the present NPAFC Science Plan in 1993-2000, and to propose future research

Contribution A No. 20 from the National Salmon Resources Center.

for the appropriate conservation and utilization of Pacific salmon.

Life History of Salmonids

Spatial distribution

Intensive high-seas tag releases showed approximate ocean distribution of Japanese chum salmon (*Oncorhynchus keta*) (see Ogura 1994), but the ocean migration route was not been decided especially during the early ocean life period and winter season. Recent developments of stock identification techniques and salmon population surveys have provided new information for the ocean distribution of chum salmon (see a review by Urawa 2000).

In coastal waters of northern Japan, juvenile chum salmon change their spatial distribution from inshore to offshore regions with their growth (Kaeriyama 1986; Fukuwaka and Suzuki 1998a). Juvenile chum salmon migrate from Japanese coasts to the Okhotsk Sea in the first summer, and reside there by late fall (Ueno 1998; Urawa et al. 1998b). When the sea surface temperature (SST) decreased less than 5°C in the Okhotsk Sea, juveniles migrated to the western North Pacific Ocean, where they overwintered with other Asian juvenile stocks (Urawa and Ueno 1997, 1999; Urawa et al. 1998b). In summer, Japanese immature and maturing chum salmon were abundant in the Bering Sea, but rarely in the North Pacific waters (Urawa et al. 1997; Urawa 2000). In the following winters, Japanese immature chum salmon were mainly distributed in the Gulf of Alaska (Urawa et al. 1997).

Seawater temperature should be an important factor to affect the ocean distribution of salmon, but favorite temperatures differ depending on fish species and season. In winter, most salmonids were captured in northern waters of the North Pacific Ocean at SST 4-8°C (Ueno et al. 1999). Planktophagous salmonids may have a survival strategy to stay in such cold waters in order to reduce their energetic consumption, because zooplankton as prey is not abundantly available in winter (Nagasawa 2000).

In the Bering Sea, CPUE of pink salmon (*O. gorbuscha*) was extremely higher in odd years than in even years, while chum salmon showed opposite CPUE trends. Chum salmon shifted their distribution to southeastward in odd years. These results suggest that the spathial distribution of chum salmon may be affected by abundance of pink salmon (Azumaya et al. 1999).

Maturing salmon with depth-sensing ultrasonic transmitters moved in particular directions and maintained their ground speeds and directions during day and night (Ogura and Ishida 1995; Ogura 1999). Archival tags showed that maturing chum salmon dived into mid-waters (about 50 m in depth) and rose to surface waters very frequently at daytime, which might be related to location and orientation for their homing migration (Wada and Ueno 1999). In the Pacific coasts of northern Honshu where SST was over 20°C in fall, adult chum salmon frequently dived to depths exceeding 100-400 m before returning to the native river (Ono 2000; Tanaka et al. 2000). Duration of deep dives tended to be prolonged as the thermal difference between sea surface and bottom water increased, indicating that salmon sought the coolest thermal refuge that they could exploit by vertical movement. Thermal refuge could be a way for salmon to minimize metabolic energy cost (Tanaka et al. 2000).

It is still unclear why Japanese chum salmon concentrate in the Okhotsk Sea at juvenile stage and in the Bering Sea at immature and maturing stages. Further studies are necessary to clarify relations between oceanographic conditions, productivity of food organisms, and salmonid distribution.

Growth and maturity

Density dependence is one of possible causes for the recent increase of age and decrease of size at maturity for chum salmon in the North Pacific Ocean (Ishida et al. 1993; Kaeriyama 1996a). Limited prey resources in the ocean may lead to density-dependent growth of Pacific salmon during rapidly growing season (Ishida et al. 1998). A scale pattern analysis showed that Japanese chum salmon suffered from growth reduction after the second year of ocean life (Kaeriyama 1998). Urawa (2000) estimated that these growth reduction may occur in the Bering Sea, where chum salmon density increases in summer. A growth reduction of chum salmon in the third year of ocean life may be partly due to a requirement of immature age 0.2 fish to consume a large amount of prey (Ishida and Davis 1999).

Techniques to estimate somatic growth or age of chum and sockeye salmon (*O. nerka*) have been improved using otolith or scale patterns (Fukuwaka 1996; Fukuwaka and Kaeriyama 1997; Endo et al. 1998), while biochemical approach is also useful to assess somatic growth. Contents of nucleic acids or lipids suggested that strategies of resource allocation for somatic growth is different among Pacific salmon, and growth characteristics depend on life stages (Azuma et al. 1998). The total lipid content and lipid classes in the muscle and liver of pink and chum salmon were examined for estimating their trophic condition in the ocean (Nomura et al. 1999, 2000). The extremely low lipid contents in winter suggest that chum and pink salmon are confronted with a great difficulty to live during this season. Further studies of seasonal and spatial variation in lipid content among North Pacific salmonids may better estimate changes in trophic conditions experienced by salmon during their high seas residency.

Endocrinological studies found that homing migration relates closely to gonadal maturation of Pacific salmon (Fukaya et al. 1998; Kitahashi et al. 1998a, 1998b; Ueda 1998). The fecundity of mature female chum and sockeye salmon was positively correlated with their fork length, but the egg size did not show any correlations with the body size (Ishida et al. 1995; Kaeriyama et al. 1995). However, it is not known how growth variations affect maturation and reproduction.

Feeding ecology

In coastal waters, juvenile chum salmon fed more on large zooplankton such as copepods or polychaetes, when such organisms were abundant or when stomach fullness of fish was high (Suzuki and Fukuwaka 1998). In inshore waters (5-15 m in depth) where juvenile chum salmon were distributed, prey zooplankton was less than at deeper layer (30 m) in offshore waters (Seki and Shimizu 1998).

In the central North Pacific and the Bering Sea, age 0.1 chum salmon fed a relatively high proportion of amphipods as compared to the other age groups, while prey composition was similar among older chum salmon (age 0.2 to 0.5) (Ishida and Davis 1999). In the same regions, chum salmon changed their dominant diet from gelatinous zooplankton (such as pteropods, appendicularians, or jellyfishes) in 1991, when pink salmon were abundant, to a diet of crustaceans (such as euphausiids, copepods, or amphipods) in 1992, when pink salmon were less abundant (Tadokoro et al. 1996). Local crustacean biomass had significant negative correlation with the CPUE of pink salmon in 1991 and that of chum salmon in 1992.

Salmonid Population Dynamics

Abundance, monitoring, and forecasting

The synchronous decreasing body size and increasing age at maturity of Hokkaido chum salmon occurred in face of rising marine survival rates and ocean conditions favorable for growth, suggesting that reduced growth and increasing age at maturity was due to density dependent intraspecific competition and high abundance of chum salmon in the North Pacific Ocean (Kaeriyama 1996a, 1996b, 1998).

Every summer, salmon stock assessment researches were conducted in the North Pacific Ocean and Bering Sea. Abundance of salmon in offshore areas based on CPUE of research gillnet operations may be used to develop pre-season forecasts of Japanese chum salmon and Bristol Bay sockeye returns (Ishida and Ito 1998).

Mortality

Fukuwaka and Suzuki (1998b) calculated that in the Sea of Japan the early ocean mortality of chum salmon accounted for 97.4% of their total ocean mortality. However, few studies clarified the causes of ocean mortalities in juvenile salmon.

Field and experimental studies showed that the ectoparasitic flagellate *Ichthyobodo necator* cause high mortalities among juvenile chum salmon soon after migrating into the coastal seawater (Urawa 1993, 1996a, 1996b). Further studies should be conducted to evaluate other pathological organisms as the cause of natural mortalities of salmon.

Although over 90 fish species have been reported to occur with chum salmon juveniles, there is no evidence that fish predation has much impact on the number of returning adult chum salmon in Japan (Nagasawa and Kaeriyama 1995; Nagasawa and Mayama 1997; Nagasawa 1998b). On the other hand, rhinoceros auklets (*Cerorhinca monocerata*) and black-tailed gulls (*Larus crassirostris*) have been recorded as predators of juvenile chum salmon. These seabirds abundantly breed in northern Japan, and the impact of their predation on chum salmon populations may be significant (Nagasawa 1998b). More field and experimental works are necessary to assess the mortality of juvenile chum salmon caused by fish and seabird predation.

Relatively high positive correlation coefficients were found between the survival rate of Russian pink salmon and SST in the Okhotsk Sea and the waters off the East Kamchatka during fry emigration period in August (Azumaya et al. 1998). The survival rate of Alaskan pink salmon was also positively related to SSTs in the waters along the west coast of North America in August. These results suggest that the survivals of pink salmon are affected by SST changes.

Salmon shark (*Lamna ditropis*) occupy the highest trophic level in the food web of subarctic waters, where salmonids are their major prey item. Nagasawa (1998a) estimated that salmon sharks consumed 73-146 $\times 10^6$ salmonids from spring to autumn in 1989, which corresponded to 12.6-25.2% of the total annual run of Pacific salmon for that year. Salmon shark may highly cause the ocean mortality of immature and maturing salmon.

Stock interaction

Kawamura et al. (1998) showed potential feeding interactions between chum salmon and fat greenling (*Hexagrammos otakii*) juveniles along the northern coast of Hokkaido. In the Okhotsk Sea, prey species (diet niche) overlap was highest between pink and chum salmon, but inter-specific competition might be lesser importance in their diets (Tamura et al. 1999).

Hiyama et al. (1999) suggested that there were density-dependent effects on the body size and spawning success of pink salmon in the Japan Sea. It is suggested that an interaction between pink and chum salmon changes the spatial distribution of chum salmon in the offshore waters (Azumaya et al. 1999).

Stock identification

Scale characters of chum salmon collected in Japanese and Russian local stocks were compared to establish a stock identification technique and baseline data on scale characters (Niita and Ueno 1999). These results demonstrated that scale characters used in this study were effective for stock identification of age 4 maturing fish and not sufficient for of age 3 maturing fish. Other new characters are necessary to identify the stock origin of chum salmon.

A genetic stock identification technique using allozyme variations has been well developed, and this technique is frequently applied for the stock identification of high-seas chum salmon (Urawa and Ueno 1997, 1999; Urawa et al. 1997, 1998b, 2000a).

The continental origins of chinook salmon (*O. tshawytscha*) in the North Pacific Ocean and Bering Sea were successfully estimated by using two freshwater parasites (*Myxobolus arcticus* and *M. kisutchi*) as biological tags (Urawa et al. 1998a). However, parasite species useful as biological tags are limited.

Recently thermal otolith marking has been applied to hatchery-released juvenile salmon for their identification in the western coasts of North America. Many thermally marked chum and pink salmon were recaptured in the Gulf of Alaska (Kawana et al. 1999; Urawa et al. 2000a). Japan also started thermal mark releases in the spring of 1999. An initial aim of the thermal mark program is to provide information for the ocean migration and survival of each regional salmon stock in Japan. The number of thermal mark releases from hatcheries in Japan are planned to increase year by year (Urawa et al. 2000b).

Salmon Habitat and Ecosystem

Physical-biological interaction and productivity

Year-to-year variations in biomass of phytoplankton and macrozooplankton, and abundance of pink salmon were examined in summers from 1985 to 1994 in the subarctic North Pacific Ocean. After 1989, phytoplankton biomass and pink salmon abundance showed corresponding yearly patterns, whereas the pattern shown by macrozooplankton biomass was always the inverse of that shown by phytoplankton and salmon. These patterns suggest that macrozooplankton biomass remained low when pink salmon were abundant due to the intense feeding impact of pink salmon, which in turn allowed phytoplankton biomass to remain high as a result of the lesser grazing effect of macrozooplankton (Shiomoto et al. 1997). Similar relationships among phytoplankton, macrozooplankton, and salmonid biomass were observed along the north-south transect in the North Pacific Ocean and Bering Sea in the summers of 1992 and 1993 (Nagasawa et al. 1999).

East-west distributions of total and size-fractionated chlorophyll a concentration and primary productivity were determined at the surface in the subarctic North Pacific during November and December 1992. This survey suggested that more turbulent water column conditions induced by high wind velocity was an advantageous factor for survival of large phytoplankton in the surface layer, and hence the high total chlorophyll a concentration and primary productivity were achieved in the western and central subarctic North Pacific (Shiomoto et al. 1999).

Climate change effects

During the period from the mid-1970s to the late 1980s, the Aleutian Low Pressure Index (ALPI) was high, but both sea surface temperature and zooplankton biomass in the Oyashio region remained low. Although the annual catch of pink salmon along the east coast of Sakhalin gradually increased from the 1960s to 1977, it declined from 1978 to 1984 despite decreasing catches by the Japanese high-seas salmon fishery. The coastal catch trend was similar to long-term changes in zooplankton biomass in the Oyashio region, suggesting that east Sakhalin pink salmon production was affected by climate and zooplankton production in this region (Nagasawa 1998c; Nagasawa et al. 1999). Pink salmon catch on the east coast of Sakhalin declined from mid-1970s to the late 1980s but sharply increased in 1989. Catch of pink salmon on the Hokkaido coast showed a similar trend and dramatically increased 1991. Pink salmon from these regions stay as juveniles in the Okhotsk Sea. The low catch for the mid-1970s through the 1980s was closely related to increased sea-ice cover in the southern Okhotsk Sea in response to intensifying of the ALPI. The 1989-1991 sharp increase in catch was in accordance with decreased sea-ice cover in the southern Okhotsk Sea corresponding to weakening of the ALPI (Nagasawa et al. 2000). Return rates of Japanese chum salmon did not indicate a significant relation with the ALPI. However, carrying capacity estimated for odd-year pink salmon in the North Pacific Ocean indicated a significant relation with the ALPI (Kaeriyama 1997). Because the impact of the ALPI differs between regions in North America and Asia, and also among salmon species, research on climate change and ocean production is needed on both regional and whole North Pacific scales (Nagasawa 1998c).

Future Salmon Research

Several questions identified in the NPAFC Science Plan have been resolved in cooperation with scientists of Canada, Russia and the United States, while others are not yet settled (Appendix 1). The major purpose of Japanese salmon research is to accomplish sustainable fisheries, balancing the conservation and use of salmon stocks in the North Pacific ecosystem. Recent studies are showing the main ocean distribution of Japanese chum salmon. They inhabit in the Okhotsk Sea in the first summer and fall, overwinter in the western North Pacific Ocean, and migrate to the Bering Sea by the next summer. Immature chum salmon migrate to the Gulf of Alaska for overwinter after intensive feeding in the Bering Sea. In accordance with these seasonal migration, we should concentrate future salmon studies to population dynamics and ocean ecosystems in specific waters. These research are (1) juvenile salmon studies in the Okhotsk Sea, (2) winter salmon studies in the North Pacific Ocean, (3) salmon ecology studies in the Bering Sea, and (4) monitoring of major salmon stocks. The former three issues have been adopted into the new NPAFC Science Plan (North Pacific Anadromous Fish Commission 2000).

Juvenile salmon studies in the Okhotsk Sea

The previous studies indicated that Asian salmon stocks inhabit in the Okhotsk Sea during summer and fall in the first year of ocean life. The early ocean life in Pacific salmon may be the most critical period. In order to develop the demography of juvenile salmon, we should concentrate the following research items:

Seasonal distribution and migration of juvenile salmon
Population size and survival estimates of juvenile salmon
Feeding competition and growth change of juvenile salmon
Primary production and food animals

Winter salmon studies in the North Pacific Ocean

Recent winter salmon studies indicate that Japanese chum salmon stay in the western North Pacific Ocean during the first winter, while in the Gulf of Alaska during the following winters. Biochemical analysis suggests that winter is one of the critical periods for salmon population. To elucidate impacts of winter ocean environments on salmon survivals, future research issues are:

Winter distribution and habitat environment of salmon
Population size and survival estimates of overwintering salmon
Survival strategies of salmon in winter

Salmon ecology studies in the Bering Sea

Recently, the depression of ocean growth was observed in salmon stocks originating both the Asian and American coasts. Current studies suggest that salmon growth reduction may occur in the Bering Sea, when many salmon migrate in the waters for their feeding and growth in summer. To clarify relations between the growth and mortality of salmon and the carrying capacity in the Bering Sea, we should focus the following research items:

Climate change and primary production
Production of food animals
Population size and distribution of major salmon stocks
Feeding competition and growth change of salmon

Monitoring of major salmon stocks

A monitoring program should be continued to assess the status of major salmon stocks in Japan for their proper management.

Annual changes in the number of adult returns
Annual changes in body size and age at maturity, and fecundity
Genetic monitoring for stock conservation

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海洋における日本のサケ属魚類に関する研究：総説と将来の課題

浦和茂彦・石田行正・福若雅章

NPAFC科学計画のもとに1993-2000年に行われたサケ・マス資源に関する日本の研究成果を要約すると共に，サケ・マス類の持続的資源管理に必要な将来の研究課題を提案した．近年発達した系群識別技術と海洋での資源調査により日本系サケの海洋分布に関する新たな情報が得られ，日本系サケは海洋生活初期にオホーツク海に生息し，北西太平洋で最初の越冬をした後，次の夏までにベーリング海へ回遊することがわかった．海洋生活初期の死亡が高いことが沿岸調査により示唆されたが，死亡要因は十分解明されていない．ベーリング海で日本系サケの成長速度が減少し，結果的に成熟年齢が高くなったことが鱗相分析により推定された．北太平洋亜寒帯での長期モニタリング調査によると大型動物プランクトンとカラフトマスのバイオマスには負の関係がみれれた．同様の調査がベーリング海でも必要であろう．越冬期のサケ・マス類の筋肉中における脂肪含量が極端に低いことから，サケ・マス類にとって冬期に生残することは非常に困難であることが示唆された．将来の研究課題として，（1）オホーツク海におけるサケ・マス幼魚調査，（2）北太平洋における冬期サケ・マス調査，（3）ベーリング海におけるサケ・マス類生態調査，（4）主要なサケ・マス類系群のモニタリングが上げられる．

Appendix 1. A contribution of Japanese salmon research to clarify questions identified in the NPAFC Science Plan.

Questions	References
1. Life History of Salmonids	
1.1 Spatial Distribution	
When and where do salmon concentrate in highest density?	Azumaya et al. 1999; Urawa 2000
Does sea surface temperature regulate salmon distribution?	Ueno 1998
Does interaction between different species and different stocks affect the distribution?	Azumaya et al. 1999
Are juvenile salmon distributed in oceanographically protected waters?	Ueno 1998
Is salmon distribution related to distribution of predators or competitors?	Azumaya et al. 1999
Do oceanographic conditions and productivity of food organisms affect salmonid distribution, and is there a trend in this influence at various periods during their life history?	
1.2 Growth and Maturity	
When and where does growth variation of salmon occur?	Ishida et al. 1993, 1998; Kaeriyama 1998
Which life history stages is the most important for determining growth variation (juvenile, immature, maturing, or returning adult)?	Kaeriyama 1998
What factors (salmon density, sea temperature, food resources, competitors, predators) affect growth variation?	Kaeriyama 1998
How does growth variation affect maturation and reproduction?	
1.3 Feeding Ecology (Diet)	
Is salmon diet species-specific?	Ishida and Davis 1999
Is the composition of food specific to salmon species?	
Does salmon diet change by salmon density?	Tadokoro et al. 1996
Does salmon diet reflect the abundance of food items?	Suzuki and Fukuwaka 1998
Does salmon diet affect salmon growth, and survival?	
Does salmon diet relate to salmon distribution and population numbers?	
Does salmon abundance regulate food supply or does food supply regulate salmon abundance?	Shiomoto et al. 1999
2. Population Dynamics	
2.1 Abundance, Monitoring, and Forecasting	
Does salmon abundance on the high seas provide a good estimate of adult returns? Where and When?	Ishida and Ito 1998
What are the most important and effective monitoring items?	
How can carrying capacity be estimated?	
What determines changes in carrying capacity of salmon?	
How can a strategy of forecasting be determined for the commercial returns in various populations?	
What factors are related to changes in carrying capacity?	Ishida et al. 1995
Do changes in carrying capacity alter salmon abundance and production?	
What are the environmental variables that control carrying capacity?	
Does carrying capacity change with changing climate? If so, by what mechanism?	
Can the Ricker model be used to estimate the carrying capacity of salmon?	
2.2 Mortality	
What factors are related to salmon survival (return rate)?	Azumaya et al. 1998
Do predators and/or competitors affect salmon survival?	Nagasawa 1998a, 1998b
What is the relationship among starvation, disease, temperature, and mortality?	Urawa 1996a, 1996b; Nomura et al. 1999
Does over-wintering affect mortality?	Nomura et al. 1999; Nagasawa 2000
Which period is critical for determining the abundance of the various species, populations, and age-groups?	Fukuwaka and Suzuki 1998b
2.3 Stock Interaction	
Does stock interaction affect growth, distribution, diet, and reproduction?	Kawamura et al. 1998; Tamura et al. 1999

Appendix 1. (continued)

Questions	References
2.4 Stock Identification	
Are baseline data (genetic, parasite, etc.) stable?	Urawa et al. 1998a
What salmon stocks are identifiable with each of the various techniques?	Urawa et al. 2000a
How accurate and precise are the stock identification estimates?	Niita and Ueno 1999; Urawa et al. 2000a
3. Salmon Habitat and Ecosystem	
3.1 Physical-biological Interaction and Productivity	
Does the Aleutian Low affect production?	Kaeriyama 1997
Does salmon abundance affect productivity?	Shiomoto et al. 1997
Is productivity in the western, central, and eastern North Pacific different?	Shiomoto et al. 1999; Nagasawa 2000
3.2 Climate Change Effects	
Does sea ice affect salmon production?	Nagasawa et al. 2000
What are the effects on southern distribution limits of salmon?	Ueno et al. 1999
What are the effects on food supply and predators of salmon?	Nagasawa 1998c
In what way do meteorological changes affect productivity? Is there a trend?	
3.3 Regime Effects (Temporal and Spatial)	
How can regime shifts be detected?	
Are ancient salmon otoliths and scales available for retrospective analyses?	
Are regime shifts reflected in hard parts (scales, otoliths, etc.)?	
Are there other indicators (parameters) that permit tracking the changes?	