REX WORKSHOP ON TRENDS IN HERRING POPULATIONS AND TROPHODYNAMICS

Co-convenors: Douglas E. Hay, Tokimasa Kobayashi, William T. Peterson and Vladimir I. Radchenko

A 2-day REX Workshop on "Trends in herring populations and trophodynamics" was convened prior to the Ninth Annual Meeting in Hakodate, Japan (October 20-21, 2000). Papers were presented by 8 speakers from among 25-30 participants. At the workshop, we learned that there are long time series (80+ years) of data for herring populations related to catch, size-at-age, length and weight, spawning time, distribution and age composition. Shorter time series are available for biomass estimates, age-structured abundances, survival index, production and instantaneous growth rates. Process studies have examined food habits and energetics, vertical distribution, timing of migration, age-specific habitat requirements, larval survival and distribution, juvenile abundance and distribution, genetic structure of populations, densities of herring aggregations, gonad weight and fecundity and key competitors and predators.

As a result of the workshop discussions, the following generalizations, observations and hypotheses were generated:

- 1. Herring populations are broadly distributed but geographically discrete.
- 2. The effects of fish community dynamics on herring size at age merit further study.
- 3. There are striking patterns in size-at-age including a pronounced decline since the 1970's for recruited herring adults.
- 4. There is some coherence in year-class strength among regions necessitating further analysis.
- 5. The frequency of year-class strength varies along a latitudinal cline.
- 6. There are recognizable types of herring. Lagoon herring are confined to Japan, Sakhalin Island and southeast Kamchatka. Coastal herring are small-sized and shortdistance migrators found ubiquitously but especially along the eastern Pacific Ocean. Oceanic herring are large, fast growing and

long distance migrating fish confined to Hokkaido-Sakhalin, Okhotsk, Kamchatsky and the Bering Sea.

- 7. Herring is an indicator species to investigate bottom-up response to climatic variability at various time scales.
- 8. Where data exist, there are strong links between zooplankton biomass and herring dynamics.
- 9. Numerical modeling suggests that environmental impacts on herring and zooplankton dynamics exceed those imposed by herring predation.

Those interested in more information and/or references to any of the above statements should contact William Peterson (bill.peterson@noaa.gov).

Another topic of discussion was the need for REX herring scientists to work with the MODEL Task Team on incorporating "fish" into the NEMURO model. At the present time, the NEMURO model is NPZ primarily an (Nutrients-Phytoplankton-Zooplankton) model. Both REX and MODEL scientists felt strongly that the time is right for MODEL to explore the ways and means of adding F (fish) to the NPZ formulations, and that herring would be an excellent model organism. We felt that herring would be a great choice because much is known about herring ecology, herring growth and feeding rates as well as trophodynamics in general. To facilitate this interaction, interested members of REX will work together to summarize herring population dynamics and trophodynamics parameters that are needed to model herring growth. Thus, as an inter-session topic, REX members will work (using e-mail) to complete a matrix of life history parameters, growth parameters in relation to environmental variables (seasonal cvcles of temperature. nutrients. and biomass of phytoplankton and zooplankton) for one or two herring stocks. Since such data will likely be variable among years and may be showing long-term trends, we may find it instructive to produce matrices for various decades (1970s, 1980s etc.).

A final discussion topic concerned the nature of future REX sessions. For PICES X we decided to focus on size-at-age for fish species other than herring within the PICES study region. We will look for patterns in size-at-age among genera and relate these to climate variables where possible. We will discuss environmental factors that may affect size-at-age and consider densitydependence and zooplankton biomass where possible. Fish species for which we expect to find considerable amounts of data include salmonids, whiting, halibut, mackerels, sardines and anchovies. A proposal was also received to consider a topic session on "Phytoplankton, zooplankton and nekton synchrony in the use of the spring bloom event in the North Pacific". The idea stems from an observation of several PICES scientists that there have been shifts in the timing of the seasonal peaks in zooplankton biomass. If a workshop focused on this topic, we would produce a review of the timing of spawning of herring stocks around the Pacific Rim in relation to the timing of the spring bloom and timing in peaks in zooplankton biomass. The first steps would be to make an inventory of herring spawning times, phytoplantkon biomass and copepod biomass.

Abundance, biology, and historical trends of Pacific herring, *Clupea pallasi*, in Alaskan waters

Fritz Funk

Alaska Department of Fish and Game, Division of Commercial Fisheries, P.O. Box 25526, Juneau, AK 99802-5526, U.S.A. E-mail: fritz_funk@fishgame.state.ak.us

Introduction

Alaska occupies the northeast corner of the range of Pacific herring, Clupea pallasi. Within this range the growth and recruitment patterns of Pacific herring are quite plastic, yet spatial and temporal patterns on differing scales link the biology of Pacific herring to the underlying physical oceanography and the biological elements of the ecosystem. The spatial and temporal patterns in growth and recruitment within Alaska provide linkages to herring biology at adjoining corners of the North Pacific. Much of what we have learned about herring biology has been motivated by the long history of commercial exploitation of herring. This paper describes the biology of herring in Alaska, the history of Alaskan herring fisheries, a sampling of the rich amount of information that can be mined from commercial catch records, and notes some new remote sensing technologies that may further increase our understanding of herring biology.

Biology of Pacific herring in Alaska

Pacific herring spawn at discrete locations from Dixon Entrance in Southeast Alaska to Norton

Sound (Fig. 1). Spawning occurs on intertidal and subtidal vegetation in late spring. The exact timing of spawning is closely related to temperature, and progresses around the Alaska coast from March in Southeast Alaska, to June in Norton Sound. In warmer years, herring spawning occurs coherently earlier throughout Alaska. However, there are some patterns in the time series of herring spawning that do not appear to be explained just by temperature variability. For example, at Sitka Sound, herring spawning has occurred three weeks earlier than in recorded history since 1993. The changes in spawn timing can be biologically significant, affecting seabirds, shorebirds, marine mammals, and piscivores that are focused on herring spawning in the spring.

The life history strategy of Pacific herring is distinctly different in the Gulf of Alaska compared to the Bering Sea. Bering Sea herring attain large body size (to 500 g), whereas Gulf of Alaska herring are approximately half that size. The eastern Bering Sea herring are long-distance migrators. The largest population spawns along the north shore of Bristol Bay, near the village of Togiak. Following spawning, these herring migrate in a clockwise direction down along the Alaska Peninsula, reaching the Unimak Pass area in early July (Funk 1990).



Fig. 1 Location of Alaska herring spawning populations, and timing of fisheries that targeted spawning herring in 1999, illustrating the south to north gradient in run timing, and the clockwise migration of Togiak-spawning herring around the eastern Bering Sea.

They feed along the continental shelf edge, slowly moving northward to overwinter near the Pribilof The Bering Sea herring life history Islands. strategy appears to be an adaptation to take advantage of the distant rich feeding grounds and benign overwintering areas on the continental shelf edge, while utilizing the protected inshore bays for summer larval nurseries. In contrast, Gulf of Alaska herring are smaller, have shorter lifespans, more frequent recruitment events and do not undergo long-distance migrations. In the Gulf of Alaska, recruitment events tend to occur synchronously over fairly broad areas which contain otherwise discrete spawning aggregations. Gulf of Alaska herring have some genetic distinction from Bering Sea herring (Grant and Utter 1984).

In addition to the spatial plasticity in body size, Fig. 2, top), successive age classes of herring undergo very large and biologically significant (up to 30%) changes in body size. These anomalies in growth are strongly autocorrelated, and appear almost cyclic in size-at-age time series that date back to the reduction fisheries of the early 1920s (Fig. 2, bottom). The cause of these apparent cycles in body size is not known, but the anomalies have been correlated to a time series of zooplankton abundance measured at Prince William Sound salmon hatcheries, and also to the Pacific Decadal Oscillation (Evelyn Brown, University of Alaska Fairbanks, pers. comm.). There is only a mild effect of density dependence seen in adult herring at studied locations in Alaska, such as Prince William Sound (Fig. 3). However, density dependence could be an important mechanism affecting larval and juvenile herring growth, for which little time series data exists.

Recruitment also shows signs of periodic autocorrelated anomalies. In the Gulf of Alaska recruitment time series, a four-year cycle of strong



Fig. 2 Spatial plasticity in size at age in Alaska herring (top) and temporal plasticity in body size in Sitka Sound herring, 1929-1999 (bottom), illustrating apparent decadal-scale cycles in growth anomalies. 1925-66 data are from Reid (1971).

year classes is apparent, although that pattern has changed recently (Fig. 4). Recruitment events occur more frequently in the Gulf of Alaska (typically averaging every fourth year), whereas in the Bering Sea, strong recruitment events occur much less frequently, typically averaging every tenth year. Most areas experienced a positive response in recruitment associated with the 1977 regime shift.

These recruitment indices were derived from routine agency stock assessments in support of fishery management. Year class abundance is quantified at a recruiting age of three in the Gulf of Alaska, and age four in the Bering Sea. Adult survival rate is usually treated as constant for stock assessment purposes. When this holds, the recruitment time series provide an excellent measure of abundance for comparison to longterm climate indices, particularly because herring



Fig. 3 Relationship of biomass to growth increment in grams for Prince William Sound herring, illustrating the occasional very weak density dependent effect.



Fig. 4 Year class size (millions) for Alaska herring stocks, illustrating the regional coherence and higher frequency of strong recruitment events among Gulf of Alaska stocks (Sitka to Kodiak), compared to the Bering Sea (Togiak).

early life history is fine-tuned to ocean processes with low tolerance for changing conditions. However, occasional adult herring epizootics have been observed in Prince William Sound, which can drastically alter adult survival rates. When adult survival rate changes substantially, the recruitment time series will not provide a good measure of adult abundance. Thus far, substantial changes in adult survival appear to be relatively rare, so that the recruitment indices typically provide a reliable index of abundance for both juveniles and adults.

Based on patterns in size-at-age and recruitment, Williams (1999) grouped Alaska herring into three categories: Bering Sea, Outer Gulf of Alaska, and Inner Gulf of Alaska. The spatial scale of these reflect groupings the spatial scale of oceanographic processes underlying herring productivity, as well as the different Bering Sea and Gulf of Alaska life history strategies. Fishery managers need to understand finer spatial scales of herring stock structure than these large groupings based on coherence in growth and recruitment anomalies. Because herring milt can be readily observed from aircraft and precisely defines spawning locations, fishery managers use maps of herring milt locations to define discrete groups of herring appropriately sized for management units.

Trends in herring abundance and historical catch in Alaska

Pacific herring have been commercially harvested in Alaska for over a century, beginning with fisheries for salt-cured and reduction products in Southeast Alaska. During the last two decades herring have been taken primarily for sac roe, with lesser amounts taken for bait. Harvest policies have become more conservative, resulting in more stable stock levels and overall catches. Herring fisheries provide an important contribution to the income of many Alaskan fishermen, with most of the harvest concentrated during the brief spring herring-spawning period.

Fishery history

Herring have supported some of Alaska's oldest commercial fisheries, and subsistence fisheries for herring in Alaska predate recorded history. The spring harvest of herring eggs on kelp has always been an important subsistence resource in coastal communities throughout Alaska. Traditional dried herring remains a major staple of the diet in Bering Sea villages near Nelson Island (Pete 1990), where salmon are not readily available.

Alaska's commercial herring industry began in 1878, when 30,000 pounds of salt-cured product were prepared for human consumption. By 1882, a reduction plant at Killisnoo in Chatham Strait was producing 30,000 gallons of herring oil The herring reduction industry annually. expanded slowly through the early 20th century reaching a peak harvest of 142,000 mt in 1934 (Fig. 5). Exploitation rates were quite high during the reduction fishery era, with large fluctuations in stock levels and annual harvests. As Peruvian anchovetta reduction fisheries developed, Alaska herring reduction fisheries declined, so that by 1967, herring were no longer harvested for reduction products in Alaska.

A Japanese and Russian trawl fishery for herring began in the central and eastern Bering Sea in the late 1950s, reaching a peak harvest of 146,000 mt in 1970. Much of the herring taken in these fisheries were from western Alaska coastal spawning stocks. These high harvests were likely not sustainable and the foreign fishery declined until it was eventually phased out with the passage of the Magnuson Fishery Conservation and Management Act in 1976.



Fig. 5 Harvests of Pacific herring in Alaska.

Contemporary fisheries

Substantial catches of herring for sac roe began in the 1970s as market demand increased in Japan, where herring harvests had declined dramatically. Presently, herring are harvested primarily for sac roe, still destined for Japanese markets. Statewide herring harvests have averaged approximately 45,000 mt in recent years, with a value of approximately \$30 million. In addition, about 400 mt of eggs on kelp, worth approximately 3 million, are harvested annually by commercial fisheries.

Approximately 25 distinct fisheries for Pacific herring occur in Alaskan waters (Table 1). Almost all of these herring fisheries are closely linked to a specific spawning population of herring. There are three general types of herring fisheries in Alaska, identified by season, product, gear and BOF regulations.

Most of the herring harvest currently occurs during sac roe fisheries, which targets herring just before their spring spawning period. Both males and females are harvested, although the sac roe fisheries target the much higher-valued roebearing females. Alaska statutes require that the males also be retained and processed and not discarded as bycatch. Herring fisheries usually incorporate spotter aircraft and are extremely efficient. On occasion the entire allowable harvest has been taken in less than one hour. However, most sac roe fisheries occur during a series of short openings of a few hours each, spanning approximately one week. Fishing is not allowed between these short openings to allow processors time to process the catch, and for managers to locate additional herring of marketable quality.

Spawn-on-kelp fisheries harvest intertidal and subtidal macroalgae with freshly deposited herring eggs. Both of these fisheries produce products for consumption primarily in Japanese domestic markets. Smaller amounts of herring are harvested from late July through February in herring food/bait fisheries, largely to provide bait in Alaskan longline and pot fisheries for groundfish and shellfish. Smaller amounts are used for bait in salmon troll fisheries, with occasional utilization for human or zoo food. Harvest policies used for herring in Alaska set the maximum exploitation rate at 20% of the exploitable or mature biomass, consistent with other herring fisheries on the west coast of North America. The 20% exploitation rate is lower than commonly used biological reference points (Funk 1991) for species with similar life history characteristics (Fig. 6). In some areas, such as Southeast Alaska, a formal policy exists for reducing the exploitation rate as the biomass drops to low levels. In other areas, managers similarly reduce the exploitation rate as abundance drops, without the more formal exploitation rate framework. In addition to exploitation rate constraints, minimum threshold biomass levels are set for most Alaskan herring fisheries. If the spawning biomass is estimated to be below the threshold level, no commercial fishing is allowed. Threshold levels are generally set at 25% of the long-term average of unfished biomass (Funk and Rowell 1995).



Fig. 6 Generalized exploitation rate/threshold harvest policy for herring fisheries in Alaska, illustrating the reduction in exploitation rate when abundance is near threshold, and showing biological reference points for exploitation rates.

Stock assessment technology

Spawn deposition surveys, acoustic surveys, and aerial school surface-area observations have

							Harv	vest Poli	cy	1999 Fi	shery
			Assessment	Biomass ³	Stock S	Status	Exploitation	n Rate J	Threshold		Catch
Fishery Area	Season	Gear ¹	Method ²	(mt)	Level	Trend	Framework	1999	(mt)	Duration	(mt)
Southeastern											
Kah Shakes/Cat I.	Sac Roe	Gn	ASA	7,370	Moderate	Stable	0-20%	0%0	5,443	I	0
Sitka Sound	Sac Roe	PS	ASA	39,553	High	Stable	0-20%	19%	18,144	1.3 hrs	7,711
Seymour Canal	Sac Roe	Gn	ASA	4,706	Moderate	Stable	0-20%	11%	2,722	11 hrs.	649
Hobart/Houghton	Food/Bait	PS,Gn	ASA	3,417	Moderate	Stable	0-20%	12%	1,814	2 hrs.	499
Craig, Tenakee	Food/Bait, Pd	PS, Pd	ASA	8,165	Moderate	Stable	0-20%	10%	7,257	5 days	1,238
Hoonah Sound	Spawn on Kelp	Pd	ASA	2,722	Moderate	Stable	0-20%	10%	1,814	20 days	115
Prince William Sound		PS,Gn,Pd,Hp	ASA	35,886	Low	Increasing	0-20%	15%	19,958	ı	0
Cook Inlet (Kamishak)	Sac Roe	PS	ASA	5,443-11,79.	Low	Stable	0-20%	0%0	7,257	ı	0
Kodiak	Sac Roe/Fd. Bait	PS,Gn,Tr	Catch, age comp.	Uncertain	Moderate	Stable	0-20%			30 days	1,488
Alaska Peninsula	Food/Bait	PS	(Harvest policy sp	ecified as 7%	allocation o	f Bristol Bay	v allowable c	catch)		13 hrs.	2,175
Bristol Bay (Togiak)	Sac Roe	PS,Gn,Hp	ASA	81,647	Moderate	Declining	20% max.	20%	31,752	32 hrs.	17,190
Kuskokwim Area											
Security Cove	Sac Roe	Gn	Annual Survey	2,776	Moderate	Declining	20% max.	20%	1,089	9 hrs.	973
Goodnews Bay	Sac Roe	Gn	Annual Survey	2,730	Moderate	Declining	20% max.	20%	1,089	49 hrs.	1,239
Cape Avinof	Sac Roe	Gn	Annual Survey	3,225	High	Stable	15% max.	15%	454	51 hrs.	484
Nelson Island	Sac Roe	Gn	Annual Survey	5,285	High	Declining	20% max.	17%	2,722	22 hrs.	1,239
Nunivak Island	Sac Roe	Gn	Annual Survey	3,011	Moderate	Declining	20% max.	20%	1,361	ı	0
Cape Romanzof	Sac Roe	Gn	Annual Survey	Uncertain	Moderate	Declining	20% max.	20%	1,361	13.5 hrs.	485
Norton Sound	Sac Roe	Gn, BS, Pd	Annual Survey	37,348	High	Stable	20% max.	20%	6,350	101 hrs.	2,357

Table 1Status of Alaska herring fisheries in 1999.

¹ Gears: Gillnet (Gn), purse seine (PS), pound spawn-on-kelp (Pd), hand-picked spawn-on-kelp (Hp), beach seine (BS), trawl (Tr). ² Assessment methods: Age-structured assessment models (ASA), synthesize several sources of abundance information.

³ Run biomass is defined as the proportion of the population which will return to spawn.

provided the primary stock assessment observations since the beginning of the sac roe fisheries in the 1970s. In most areas of Alaska, these observations are integrated with a time series of age composition and catch in stock assessment models for estimating abundance. In recent years we have been exploring remote sensing tools to augment the existing programs and to provide more synoptic coverage of herring stocks and fisheries.

A compact airborne spectrographic imager (CASI) has been successfully used to assess herring school surface areas when herring are in shallow coastal waters prior to spawning (Funk et al. 1995). Herring are color-adapted for a pelagic existence, so that they are readily discriminated from background water by multispectral methods using the green band of the reflected light spectrum. LIDAR, a scanning laser sensor, has also been successfully used to assess pelagic fish species (Churnside et al. 1997, Lo et al. 2000), including herring in Alaska. LIDAR provided acoustic-like information down to 50 m in the Gulf of Alaska during the summer of 2000 Oscillation (Evelyn Brown, University of Alaska Fairbanks, personal communication). LIDAR provides information about other light-reflecting targets in the water column in addition to fish, and may be particularly informative about the distribution of deeper scattering zooplankton layers near the limits of its attenuation. LIDAR information is acquired from aircraft that can synoptically survey large areas of the continental shelf, thus capturing "snapshots" of processes that are too dynamic to sample using conventional tools. Although the resolution of satellite multispectral sensors is getting sufficiently fine to discriminate herring schools, the frequent cloud cover over Alaskan coastal areas during the herring spring spawning period severely limits their application. Synthetic aperture radar (SAR) has been successfully used to describe the distribution of fishing fleets in Alaska, including Bering Sea crab and herring fisheries (Clemente-Colon et al. 1998). SAR uses microwave radiation and is not affected by cloud cover. In addition, SAR can discriminate ocean surface structures such as fronts and eddies, which provide meaningful augmentation to the distribution of fishing effort for determining the distribution of fishery target species.

Conclusions

Commercial fisheries provided motivation for collecting and archiving several long time series of basic biological information. "Data mining" from these time series may help elucidate important basin-wide ocean productivity mechanisms and may be helpful for understanding climate change. In particular, Pacific herring in Alaska display patterns of biologically significant, autocorrelated anomalies in body size, recruitment, and time of spawning. Examining these dramatic spatial and temporal patterns over broader geographical areas can help to generate hypotheses about productivity mechanisms to efficiently guide future research.

References

- Clemente-Colon, P., Montgomery, D., Pichel, W., and Friedman, K. 1998. The use of synthetic aperture radar observations as indicators of fishing activity in the Bering Sea. Journal of Advanced Marine Science and Technology Society, 4: 249-258.
- Churnside, J.H., Wilson, J.J., and Tatarskii, V.V. 1997. Lidar profiles of fish schools. Applied Optics 36: 6011-6020.
- Funk, F. 1990. Migration of Pacific herring in the eastern Bering Sea as inferred from 1983-88 joint venture and foreign observer information. Division of Commercial Fisheries, Alaska Department of Fish and Game, Regional Information Report 5J90-04, Juneau.
- Funk, F. 1991. Harvest policy implications of yield per recruit models for Pacific herring in Alaska. *In* Proceedings of the International Herring Symposium, Alaska Sea Grant Report AK-SG-91-01, Fairbanks, Alaska. pp. 453-462.
- Funk, F.C., Borstad, G.A., and Akenhead, S.A. 1995. Imaging spectrometer detects and measures the surface area of Pacific herring schools in the Bering Sea. Pages II-833-844. *In* Proceedings of the Third Thematic Conference on Remote Sensing for Marine and Coastal Environments, Seattle, Washington, 18-20 September, 1995.
- Funk, F. and Rowell, K. A. 1995. Population model suggests new threshold for managing Alaska's Togiak fishery for Pacific herring in

Bristol Bay. Alaska Fishery Research Bulletin 2:125-136.

- Grant, W.S., and Utter, F.M. 1984. Biochemical population genetics of Pacific herring (*Clupea pallasi*). Canadian Journal of Fisheries and Aquatic Sciences 41: 856-864.
- Lo, N.C.H., Hunter, J.R., and Churnside, J.H. 2000. Modeling statistical performance of an airborne lidar system for anchovy. Fish. Bull. 98: 264-282.
- Pete, M.C. 1990. Subsistence herring fishing in the Nelson Island and Nunivak Island districts, 1990. Technical Paper No. 196, Division of

Subsistence, Alaska Department of Fish and Game, Juneau.

- Reid, G.M. 1971. Age composition, weight, length, and sex of herring, *Clupea pallasii*, used for reduction in Alaska, 1929-66. NOAA Technical Report NMFS SSRF 634.
- Williams, E.H. 1999. Interrelationships of Pacific herring, *Clupea pallasi*, populations and their relation to large-scale environmental and oceanographic variables. Ph.D. Dissertation, School of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Juneau.

Historical trends of herring in Russian waters of the North Pacific

Nikolai I. Naumenko

Kamchatka Research Institute of Fisheries & Oceanography, 18 Naberezhnaya St., Petropavlovsk-Kamchatsky, 683600, Russia. E-mail: NNaumenko@kamniro.kamchatka.ru]

Three ecological forms of Pacific herring (Clupea pallasii) are found in the Far-Eastern Seas: marine, coastal, and lake-lagoon. Marine herring spend their entire life in salt-water or the ocean and it undertakes extensive migrations. When foraging, its natural habitat includes both shelf and bathypelagic waters. Lake-lagoon herring spend most of their life cycle in freshwater reservoirs and move to the neighboring waters to forage. Coastal herring inhabits the shelf zone of separate gulfs or big bays exclusively and does not migrate considerably. Russian waters of the Northwest Pacific are inhabited by 6 populations of sea herring and 20 populations of coastal and lakelagoon forms (Fig. 7). This ecological variety allows the species to obtain food resources of this area of water, and is responsible for its high abundance and wide distribution.

Marine herring are characterized by a pulsing natural habitat. During the growth of biomass it increases in abundance, but it also happens at the expense of bathypelagic waters and the populations in neighboring territories. Reduced abundance is usually associated with warm water masses, and is accompanied by a gradual cessation of reproduction in the southern parts of the range and a shifting of reproduction centers to the north.



Fig. 7 Distribution of marine herring in the Far Eastern Seas.

A remarkable peculiarity of the Pacific herring is considerable change in abundance and biomass of populations in different years. Fluctuations of the stock-size are conditioned by different productivity of generations. For the years of observation in large Far-Eastern populations of marine herring, generations have differed in number by one hundred times, and adjacent generations by 8 to 60 times. Often, year-class strength fluctuates with a definite periodicity, but in some intervals of time this cyclic pattern is broken.

Distinctions in abundance are evident in both yearclasses and populations in the northern and the southern herring groups. Southern populations (Peter the Great Bay, Sakhalin-Hokkaido and Dekastri) have no stable high frequency cycles of strong and poor year-classes. The difference in productivity between adjacent year-classes is relatively small. A five-year cycle of abundance is usual in the northern group of populations (Okhotsk, Gizhiginsk-Kamchatka, Korf-Karaginsk, Anadyrsk) and the distinction in productivity rate between year-classes is the highest. The abundant offspring in the northern populations occurs more often than once in 5 years, whereas in the southern populations it may be from 3-6 years, one after another. For a long time, strong year-classes have coincided in two populations: Okhotsk and Eastern-Bering Sea (Fig. 8) while Gizhiginsk-Kamchatka has experienced a long depression. During the last years a number of the species in the Japan Sea have approached historical minima and are in need of various protection measures.

The dynamics of the northern populations stocksize was different. The highest number of herring in the northern part of the Okhotsk Sea and the western part of Bering Sea was achieved in the 1950s and early 1960s, i.e. at the epoch of the maximum solar activity of the last secular cycle (Fig. 9).

The second half of the 1970s and the 1980s were characterized by a shift in the climate of the Northwest Pacific that badly influenced herring reproduction. During this period, all the northern populations were at a low level and universally, fishery activities were limited to a sparing mode. In the 1990s, spawning stocks of the Okhotsk, Gizhigisk-Kamchatka and Korf-Karaginsk herring experienced a series of average and relatively strong year-classes and the number of spawners greatly increased. These populations have now passed the crisis. The sparing mode of fisheries has ended and renewed intensive exploitation of the species occurs in the northern part of the Okhotsk Sea and western part of the Bering Sea.

Russian herring catches in the Far-Eastern Seas have experienced considerable fluctuations in different years. The catch peak occurred in the late 1920s to early 1930s (Fig. 10).



Fig. 8 Abundance of age 3 herring in the Eastern Bering Sea and Okhotsk populations.



Fig. 9 Historical trends of solar activity and the abundance of the northern herring group.



Fig. 10 Russian catches in different herring populations.

At that time the Sakhalin-Hokkaido population was intensively fished, providing an annual catch of 300,000-450,000 t. At the same time maximum catches of two Japan Sea populations were achieved – Peter the Great Bay (about 28,000 t in 1928) and Dekatstri (25,000 t in 1926). By the end of the 1930s the abundance of these two populations, and also the Sakhalin-Hokkaido population by the mid-1940s, were considerably depleted and the catches appreciably reduced. Exploration of the previously discovered stocks of herring being in the northern half of Okhotsk Sea and the western half of Bering Sea.

The Gizhiginsk-Kamchatka and Korf-Karaginsk herring have been the object of intensive fisheries since the late 1930s, and the Okhotsk herring since the mid-1940s. By the late 1950s to early 1960s, the catches of the first two populations had reached a historical maximum: 120,000-160,000 t and 100,000-260,000 t, respectively. Starting in the 1960s, the Okhotsk population held a leading position in herring catch. During some years (1963-1975) the whole volume of catch by the Soviet fishing companies exceeded 200,000 t. At the end of the 1960s, a regular peak of catches of the Pacific herring was noticed – somewhat more than 500,000 t – which was achieved mainly by an intensive catch of the Okhotsk foraging herring.

Since the mid-1970s, i.e. during last two decades, the herring catch in the Far East underwent a deep crisis. The abundance of all large marine herring populations was depleted. For each population they went to extremes in regulating the fishery – it was completely prohibited. At the West Bering Sea (the Korf-Karaginsk herring) and the North-East Okhotsk Sea (the Gizhiginsk-Kamchatka herring) the prohibition persisted for more than 10 years, 1970-1986 and 1974-1990 respectively. Nevertheless, in spite of the extreme management actions undertaken, the abundance of these populations increased only slowly during the early 1990s, and only during the last several years has a considerable increase in abundance been observed. In 1997-1999, Russian fishermen alone caught more than 300,000 t (in 1998 – over 400,000 t) of herring. In the near future they expect the species resources to be satisfactory.

The total catch of Pacific herring in Russia (USSR) since 1904 is 18,600,000 t, an average annual catch of 192,000 t. By population, the catch is distributed as follows: the Sakhalin-Hokkaido population -7,372,000 t, the Okhotsk population -6,987,000 t, the Korf-Karaginsk population -1,865,000 t, the Gizhiginsk-Kamchatka population -1,014,000 t, other (Peter the Great Bay, Dekastri, all coastal and lake-lagoon population) -1,407,000 t.

Trends in Pacific herring populations of British Columbia

Jake Schweigert

Fisheries & Oceans Canada, Pacific Biological Station, Nanaimo, B.C., Canada. V9R 5K6 E-mail: schweigertj@pac.dfo-mpo.gc.ca

Introduction

Herring have been one of the most important components of the British Columbia commercial fishery over the past century with catch records dating from 1877. The fishery has evolved from a dry salted product in the early 1900s, to a reduction fishery in the 1930s that collapsed in the late 1960s. After a four-year closure the current roe fishery began in 1972. Roe fisheries occur just prior to spawning when the fish are highly aggregated and very vulnerable to exploitation. Since 1983, herring roe fisheries have been managed with a fixed quota system. Under this system harvest levels are determined prior to the season based on a fixed percentage (20%) of forecast stock size. In addition, threshold biomass or cutoff levels were introduced in 1985 to restrict harvest during periods of reduced abundance.

In this report, long-term trends in several biological characteristics of British Columbia herring stocks are presented based on stock assessments from two analytical models. An escapement model reconstructs population abundance from surveys of the spawning beds and egg deposition. In addition, a catch-age or agestructured model is used to reconstruct stock abundance for the period 1951-2000. Trends in recruitment, harvest rate, total production, population growth rate, survival rate, size at age, and condition factor are also presented for each of the five major herring populations found within British Columbia.

Methods

Pacific herring abundance in most of North America is assessed annually through some form of spawn assessment survey since the eggs are adhesive to algae and remain attached intertidally Within British Columbia five until hatching. major migratory herring populations are recognized and assessed annually (Queen Charlotte Islands, Prince Rupert District, Central Coast, Georgia Strait, west coast of Vancouver Island). Annual estimates to total stock abundance and other biological characteristics for each herring stock were determined from the egg assessment surveys using the escapement model (Schweigert and Stocker 1988). Annual harvest rate for each stock was determined as the proportion of the estimated mature or spawning population removed by the fishery. Abundance of the year-classes in each stock was determined from the catch-age model and is the estimate of the number of 3 year old herring which recruit to the fishery.

Population production was determined as the growth in total biomass from year to year summed across ages following (Chapman 1968):

$$P_{at} = g_{at} \bullet \overline{B}_{at}$$

where

- P_{at} = Production of new biomass from age a to a+1 in year t to t+1;
- g_{at} = instantaneous growth rate in weight from age a to a+1 in year t to t+1;
- $\overline{B}_{at} = \frac{B_{at} + B_{a+1,t+1}}{2} = \text{average biomass at age a to}$ a+1 in year t to t+1.

The estimated average biomass also includes a component due to the annual production and loss of gonadal products. Weight of the gonad production was determined from the weight of individual fish at each age in each population using relationships developed by Ware (1985) for

females. Gonad production of males was assumed to follow the relationship for females.

An annual survival index was also estimated for each stock based on the return of the spawning run in year t+1 relative to the escapement the previous season:

$$SI_{at} = \frac{E_{a+1,t+1} + C_{a+1,t+1}}{E_{at}}$$

where

- SI_{at} = survival index of fish age a to a+1 in year t to t+1;
- E_{at} = estimated number of spawning fish at age a in year t;
- $C_{a+1,t+1}$ = estimated number of age a+1 fish caught in year t+1.

To investigate any long-term trends in population fitness that may be linked to food supply and ocean productivity, the average size at age was determined for each stock in each year. Unfortunately, no herring were aged during the period of the population crash from 1965-1970, so no information is available during this period. In addition, the average condition factor was calculated for each stock, each year, as:

$$CF_t = \frac{Weight_{at}}{Length_{at}^3}.$$

Results and discussion

Pacific herring were fished extensively for reduction from the early 1930s through the late 1960s when the stocks collapsed. During this period harvest rates frequently reached 70-80 % of the total available stock in each area. Much more conservative harvest rates occurred during the roe fishery of the past 30 years. Nevertheless. population abundance has fluctuated dramatically throughout both periods (Fig. 11) due to the recruitment of good or poor year-classes in each area (Fig. 12). Population production has also fluctuated markedly throughout this period. Production had generally been high in the 1950s and early 1960s reaching a minimum in the late 1960s as the stocks collapsed (Fig. 13). In all areas production increased rapidly in the early 1970s as stocks rebuilt, particularly in the south. In the 1980s and 1990s, stock production in the



Fig. 11 Trends in abundance of Pacific herring in B.C. from 1951-2000.

QCI, PRD, and WCVI has remained low whereas in the other two areas production has approached the levels of the 1950s. Total production has varied markedly between stocks averaging 5000 t in QCI, 5-10,000 t in PRD, 10-15,000 t in CC, 25-30,000 t in GS, and 15-20,000 t in WCVI. Population production of herring appears to be related largely to recruitment rather than changing growth patterns. Estimates of instantaneous population growth or the P/B ratio indicates higher levels of population turnover in the 1950s and 60s, when harvest rates were very high and the biomass was concentrated in the younger faster growing age classes. Since the early 1970s, population growth has been stable in all areas but population production as a whole has continued to fluctuate.

The survival index was variable particularly during the early part of the time series which may be due to poorer data quality. There is no indication that survival was better or worse during



Fig. 12 Recruitment trends in Pacific herring stocks of B.C. since 1951.



Fig. 13 Estimated population production for B.C. herring stocks from 1951-2000.



Fig. 14 Trends in estimated size-at-ages 3-6 for B.C. herring stocks since 1951.

periods of good recruitment. This suggests that factors affecting adult survival differ from those leading to enhanced survival and recruitment at juvenile stages. Further support for this hypothesis comes from an examination of the long-term trend in both size-at-age and condition factor.

The population characteristics investigated here do not indicate any long-term trends that might be associated with environmental effects on herring production. There appears to be some support for density dependent changes in growth rate. Size at age increased from the early 1960s through the mid-1970s, when coastwide herring abundance was greatly diminished (Fig. 14). Subsequently, size at age has declined in all areas although there is some evidence of a recent increase in some areas. Interestingly there is no evidence of any coincident changes in condition factor for these stocks (Fig. 15). The data suggest a slight increase in condition through the 1970s, but it has been stable over the past two decades.



Fig. 15 Trends in condition factor for B.C. herring stocks since 1951.

The most important component of the total annual production of herring stocks is the recruitment of young fish into the adult population. A better understanding of the effects of environmental conditions on the survival of juvenile herring is necessary to establish the links between herring production and the ocean environment.

References

- Chapman, D.W. 1988. Production. *In* Methods of assessment of fish production in fresh waters. *Edited by* W.E. Ricker. IBP Handbook No. 3. Blackwell Scientific Publications, Oxford pp. 182-196
- Schweigert, J.F., and Stocker, M. 1988. Escapement model for estimating Pacific herring stock size from spawn survey data and its management implications. N. Am. J. Fish. Management 8: 63-84.
- Ware, D.M. 1985. Life history characteristics, reproductive value, and resilience of Pacific herring (*Clupea harengus pallasi*). Can. J. Fish. Aquat. Sci. 42: 127-137.

Diet and feeding of juvenile Pacific herring

R. J. Foy¹ and Brenda L. Norcross²

- ¹ Fishery Industrial Technology Center, University of Alaska Fairbanks, 118 Trident Way, Kodiak, AK 99615-7401, U.S.A. E-mail: foy@sfos.alaska.edu
- ² Institute of Marine Science, University of Alaska Fairbanks, P.O. Box 757220, Fairbanks, AK 99775-7220, U.S.A. E-mail: norcross@ims.alaska.edu

Introduction

Herring are zooplanktivorous fish and depend on seasonal availability of prey for growth and energy storage (Blaxter and Holliday 1963). Herring are vertical migrators, so diel differences in spatial overlap with prey items are important for feeding (Blaxter and Holliday 1963). The diets of juvenile herring in Prince William Sound (PWS) vary on multiple spatial and temporal scales (Foy and Norcross 1999a). Feeding intensity is highest in May and June, when zooplankton biomass and energy density peaks (Foy and Norcross 1999a, b). Feeding in winter is below levels required for general maintenance (Foy and Paul 1999). Nearshore zooplankton abundance, diversity, and species composition in PWS have been linked to seasonal and annual trends in temperature and salinity (Foy 2000). Environmental variables influence fish condition directly by affecting growth rates and indirectly by altering the community structure of the prey. Juvenile herring growth rates in PWS were significantly correlated to average water temperatures in 1996 and 1997 (Stokesbury et al. 1999). Zooplankton species composition and abundance were significantly correlated to temperature and salinity in the same time period (Foy 2000). The objective of this study was to examine the response of juvenile herring feeding behavior to zooplankton availability and environmental conditions in PWS. To accomplish this, we establish trends in the herring diet composition and prey preference.

Methods

PWS is a large, fjord-type estuarine system consisting of numerous shallow bays, fjords, and tidewater glaciers located on the southern coast of Alaska (Niebauer *et al.* 1994; Fig. 16). We sampled fifteen times between March 1996 and

Prince William Sound



Fig. 16 Location of study sites in Prince William Sound, Alaska. Simpson, Eaglek, Whale and Zaikof Bays were sampled from 1996 until 1998.

March 1998, in two fjords with depths >250 m (Eaglek and Whale Bays), and two estuaries with depths <100 m (Simpson and Zaikof Bays). Within 7 days, each bay was sampled during the day: 0800-1559h, evening: 1600-2359h, morning: 0000-0759h. Data from the four bays were pooled for this study due to consistent interannual trends among bays.

Multiple samples were collected and processed from each sample site. Temperature loggers were deployed at a central location in each of the four bays at a depth of 5 m. Vertical zooplankton tows were made with a 0.5 m 300 μ m mesh ring net from multiple sites within the four bays.

Juvenile herring (<250 mm) schools (n=194) caught using a purse seine vessel with a 250 m x 34 m or 250 m x 20 m, 150 mm stretch mesh anchovy net or a trawl vessel with a 40 m x 28 m, 150 mm mesh mid-water wing trawl net. Depth of the tow was dependent on fish depth, determined by hydroacoustics. Fish were blotted dry, weighed to the nearest 0.01 g, and standard length (SL)

measured to the nearest 1.0 mm. Stomach content was reported as % body weight (%BW) by dividing the stomach content weight by total fish weight. Taxa from each stomach were enumerated and identified to the lowest possible taxonomic Post-processing analyses level. included determining taxa richness (number of taxa) and prev selectivity using Chesson's selectivity (a) index (Chesson 1978; 1983) (see Foy and Norcross 1999a and Foy 2000). For selection information of particular prey species see Foy (2000). Life history stages of prey were identified when possible and were limited mostly to egg, nauplius, larva, juvenile and adult male/female.

Results

Temperature in the nearshore surface waters ranged from 4.3 to 13.3° C in 1996, 3.5 to 14.8° C in 1997, and was 5.0° C in March 1998 (Fig. 17). Temperatures at 5 m were significantly different among months (F=155.4, df=14, P<0.01). Temperatures were coolest in March in 1997 and 1998, and warmest in August in 1996 and 1997. The fall of 1997 and the spring of 1998 were significantly warmer than those of the previous year.

The zooplankton density in the upper 30 meters seasonally and interannually variable. was Zooplankton density was highest in June 1996 at 3166 zooplankters per m^3 (Fig. 18, top). Zooplankton abundance decreased in the winter of 1996-1997 to less than 90 zooplankters per m³. Zooplankton densities were significantly higher in May 1997 than May 1996 (F=27.2, df=94, P<0.01). Zooplankton densities in July, August, and October 1997 were all significantly lower than in the same months in 1996 (P < 0.01). No sampling occurred in June 1997 to compare to The zooplankton species richness was 1996. highest in May of both 1996 (41 taxa) and 1997 (34 taxa) and lowest in October 1996 (28 taxa) and 1997 (23 taxa) (Fig. 19). There was an overall decreasing trend in the number of zooplankton taxa between May of 1996 and October 1997.

The number and diversity of prey taxa in the herring diets per fish varied among months and between 1996 and 1997. The number of prey per herring stomach in 1996 increased from 91 in

March to a peak of 1209 in July, and then declined to 3 in December (Fig. 18, bottom). Zooplankton density significantly accounted for variation in the density of prey in juvenile herring diets (F = 22.39, P = 0.0003, df = 15, $R^2 = 0.62$; Fig. 20). Species composition consisted mostly of small calanoid copepods and Cirripedia from March to June, while Cladocera and Larvacea became important between June and October. In 1997 the



Fig. 17 Average 5 m temperature from fixed temperature loggers and CTD casts in four Prince William Sound bays.



Fig. 18 Average (with standard errors) zooplankton density (count/m³) for each month (top), and average (with standard error) prey density (count/fish) in juvenile herring diets (bottom) from March 1996 to March 1998, in four Prince William Sound bays. Blank spaces represent months that were not sampled.



Fig. 19 The number of zooplankton taxa collected each month from March 1996 to March 1998, in four Prince William Sound bays. Blank spaces represent months that were not sampled.



Fig. 20 The density of prey in the herring stomachs regressed as a function of zooplankton density in the water column. Each point represents an average of data for a month.



Fig. 21 The number of prey taxa from juvenile herring diets collected from March 1996 to March 1998, in four Prince William Sound bays. Blank spaces represent months that were not sampled.

average number of prey was larger in May (398 prey per fish) than July (278 prey per fish). The dominant species in the diets varied between small copepods, large copepods, Cirripedia, Euphausiacea and Larvacea in 1997.

Juvenile herring had significantly more prey per fish in May 1997 than in 1996, corresponding to the increased availability of prey in May 1997 (F=12.3, df=354, P<0.01). The number of prev per fish for every other month in 1997 was significantly lower than in 1996 (P<0.01). The number of taxa in the diets of the herring was highest in July 1996 (9 taxa) and May 1997 (7 taxa) (Fig. 21). The lowest number of taxa in the diets occurred in December 1996 (2 taxa) and October 1997 (1 taxon). All 1997 months except May had fewer taxa in the diets than in 1996. The number of empty stomachs was highest in winter (November to March) and lowest from June to August (Fig. 22, bottom). The percentage of empty stomachs in October 1997 was three times greater than in October 1996.

Juvenile herring were more selective during the winter months when prey was scarce than in the summer months when prey was abundant (F=4.79, df=13, P<0.01; Fig. 22, top). Selectivity index values ranged from 0.17 to 0.65 in 1996 (monthly neutral value range = 0.06 to 0.14) and from 0.22 to 0.77 in 1997 (monthly neutral value range was from 0.04 to 0.22). Juvenile herring were significantly more selective in October 1997 than in October 1996 (P<0.01).

Diet taxa richness, evenness, composition and prey selectivity differed with time of day. The number of taxa in the diets was significantly higher from 1600 to 2359h than 0000 to 0759h or 0800 to 1559h. Evenness of prey taxa in herring diets was significantly higher from 0800 to 1559h (confidence interval: 0.64 ± 0.3), when diversity was low, than from 0000 to 0759h (confidence interval: 0.60 ± 0.3) or 1600 to 2359h (confidence interval: 0.60 ± 0.3). The diel difference in diet composition was due to the presence of large calanoid copepods from 0000 to 0759h. From 0800 to 1559h, invertebrate eggs, Oikopleura sp., and small calanoids dominated the diets. In the evening category (1600h to 2359h) small calanoid copepods and Cladocera were the most abundant in herring diets. Juvenile herring were significantly more selective from 0000 to 0759h than from 0800 to 1559h or from 1600 to 2300h.

Though similar times were sampled each year to avoid bias due to light levels, depth distribution of herring changed over the study. The monthly average fish depth in 1996 decreased from 32 m in March to 10 m in August, and then increased from 32 m to 38 m in the winter (Fig. 23). The monthly average fish depths in 1997 were deeper than in the summer of 1996, increasing from an average of 48 m in March to 28 m in August. Evenness of prey taxa in diets was higher for fish caught deeper in the water column than shallower suggesting that herring may be less selective in deeper water where light levels are lower.

Discussion

Zooplankton availability varies seasonally and annually among and within bays in PWS (Foy 2000). Zooplankton species composition and abundance are dependent on multiple biological and environmental factors. The seasonal variability in zooplankton density encountered in this project was typical given the strong seasonal production cycles in PWS. The decline in zooplankton density and number of taxa between 1996 and the fall of 1997 was, however, not expected. There was also a shift in species composition in the zooplankton community occurring particularly in the fall between 1996 and 1997 (Foy 2000).

The decline in zooplankton abundance observed in the summer of 1997 coincides with increased temperatures that occurred at the same time (Foy 2000). Temperatures were 2°C warmer in the fall and winter of 1997, and may have been instrumental in indirectly reducing zooplankton density and composition due top predation and species succession. Temperature has been found to affect the availability of zooplankton prey for Bering Sea larval herring (Maksimenkov 1982). Although higher temperatures may enhance zooplankton production, we speculate that the higher temperatures may have increased the herring demand on its prey population due to increased growth. These events combined with factors affecting stratification in the water column

such as increased temperatures and freshwater runoff, may have limited nutrient input to the euphotic zone in the fall, inhibiting productivity that could support secondary production. Our zooplankton sampling did not continue into the winter of 1997-1998 to study the effects of a warmer than normal winter in PWS.

Diel variability in the amount of feeding was encountered at multiple scales. Increased feeding from 1600 to 2359h is consistent with other studies of juvenile herring (Raid 1985; Arrhenius and Hansson 1994). Herring are visual feeders and they feed more in low light hours as they are vertically migrating to the surface (Blaxter *et al.* 1982). The increase in feeding on large calanoid copepods from 0000 to 0759h when there is most likely a large overlap of predator and prey distributions is suggestive of selective feeding due to the size of prey (Sandstrom 1980; Flinkman *et al.* 1991).

Seasonal species composition of prey in the diets was closely related to the species composition of zooplankton found in the nearshore PWS in 1996 and 1997 (Foy 2000) and in this region of the Northeast Pacific (Vogel and McMurray 1982; Cooney 1988). More feeding during the summer months was expected as a response to increased



Fig. 22 Average (with standard error) selectivity index (alpha) of prey in juvenile herring diets (top), and the percentage of juvenile herring stomachs empty (bottom) from March 1996 to March 1998, in four Prince William Sound bays. Blank spaces represent months that were not sampled.



Fig. 23 Average depth of capture of juvenile herring used in the diet analyses from March 1996 through March 1998.

zooplankton availability (Foy and Norcross 1999b, Foy 2000) following increased primary production during the spring in PWS (Goering et al. 1973). The species succession of prey in 1996 juvenile herring diets from spring (small Calanoida and invertebrate eggs) through summer (small Calanoida and Cladocera) was similar to the Baltic Sea herring diets (Mehner 1993, Arrhenius 1996), suggesting that the zooplankton species composition is similar at upper taxonomic levels in the nearshore areas of these two systems. In May 1997, species composition of prey found in the diets was similar to May 1996, but large changes in species abundance and composition occurred in July 1997 and subsequent months. Regression analyses suggest that increased temperature decreased the availability of prey and caused the fish to remain deeper in the fall, all of which may have influenced this change in diet composition. Similar trends in species composition were noted in the zooplankton community and speculated to be due to the increased temperatures (Foy 2000). The change in the depth of the fish (Fig. 23) may be due to either a direct response by the juvenile herring to the warmer temperatures or to the lack of available prey in the upper water column during the summer and fall of 1997.

The reduced incidence of feeding and fewer prey taxa ingested by juvenile herring in 1997 may be a response to the lower zooplankton availability. Food composition changed from being dominated

by Larvaceans and small calanoid copepods in the fall of 1996 to only small calanoids in 1997. If the densities of prey had been higher in 1997, having only small copepods (with higher energy density) to eat may have been positive for the condition of herring prior to overwintering. Studies estimating the assimilation rates given in situ prey compositions found that the smallest juvenile herring are liable to fall below basal metabolic demands in a year with temperatures similar to 1996 (Foy and Norcross 1999a). Warmer temperatures in the fall of 1997 increased growth rates of juvenile herring (Stokesbury et al. 1999). Consequently, herring predation pressure on the zooplankton community increased and led to lower prey concentrations in the fall. Lower feeding occurrence in the fall caused the herring to have a lower fall weight at length than in previous years (Stokesbury et al. 1999). Despite this, herring were in better energetic condition in the fall of 1997 than in 1996 (Paul and Paul 1998), and consequently, a larger number of smaller fish survived through the winter of 1997-1998 than in 1996-1997. The average length and weight of the fish that survived the 1997-1998 winter were smaller and lower than in previous years (Stokesbury pers. comm.), providing evidence that the smallest fish did not die from starvation during the winter as has been speculated in previous years (Paul et al. 1998; Foy and Paul 1999).

In conclusion, important mechanisms in the trophic relationship between herring and zooplankton and the environment exist in PWS. On seasonal scales, juvenile herring relied heavily on prey availability, with greater feeding, diet diversity, and opportunistic feeding in the spring when zooplankton were abundant. Seasonal and spatial fluctuations in temperature and its influence on zooplankton were important at this time. On diel scales, juvenile herring relied on vertical migration for greater prev overlap and higher diet diversity from 1600 to 2359h when the light levels were decreased. Juvenile herring switched to selective feeding from 0000 to 0759h when large calanoid copepods were present in the water column. Furthermore, we suggest that lower prey availability affects the feeding dynamics of juvenile herring. Evidence suggests that environmental conditions may have affected the prev resource base for herring in 1997.

Consequently, herring growth rates increased and the energy density of herring was high by fall 1997. However, we hypothesize that a combination of lower feeding in the fall and warm winter temperatures meant that the average condition of surviving fish in the spring was lower than previous years.

Acknowledgements

This project was funded by the Exxon Valdez Oil Spill Trustee Council through the Sound Ecosystem Assessment project. The findings presented are the authors' and not necessarily the Trustee Council's position. This paper is based on three papers by the authors:

- Foy, R.J., and Norcross, B.L. Temperature effects on zooplankton assemblages and juvenile herring feeding in Prince William Sound, Alaska. Proc. Herring 2000, Alaska Sea Grant (in press).
- Foy R.J., and Norcross, B.L. Seasonal zooplankton composition and abundance in Prince William Sound, Alaska. J. Planktology (in review).
- Foy R.J., and Norcross, B.L. Feeding characteristics of juvenile Pacific herring: Trends in prey availability and environmental conditions in the nearshore subarctic. Can. J. Fish. Aquat. Sci.(in review).

References

- Arrhenius, F. 1996. Diet composition and food selectivity of 0-group herring (*Clupea* harengus L.) and sprat (*Sprattus sprattus* (L.)) in the northern Baltic Sea. ICES J. Mar. Sci. 53: 701-712.
- Arrhenius, F., and Hansson, S. 1994. In situ food consumption by young-of-the-year Baltic Sea herring *Clupea harengus*: a test of predictions from a bioenergetics model. Mar. Ecol. Prog. Ser. 110: 145-149.
- Blaxter, J.H.S., and Holliday, F.G. 1963. The behaviour and physiology of herring and other clupeids. Adv. Mar. Biol. 1: 261-393.
- Blaxter, J.H.S., Russell, S.F.S., and Yonge, S.M. 1982. The biology of clupeoid fishes. Adv. Mar. Biol. 20: 1-223.
- Chesson, J. 1978. Measuring preference in selective predation. Ecology. 59: 211-215.

- Chesson, J. 1983. The estimation and analysis of preference and its relationship to foraging models. Ecology. 64: 1297-1304.
- Cooney R.T. 1988. Distribution and ecology of zooplankton in the Gulf of Alaska: a synopsis. Bulletin of the Ocean Research Institute, University of Tokyo, pp. 27-41.
- Flinkman J., Vuorinen, I., and Aro, E. 1991. Planktivorous Baltic herring (*Clupea harengus*) prey selectivity on reproducing copepods and cladocerans. Can J Fish Aquat. Sci 48: 73-77.
- Foy, R.J. 2000. Juvenile Pacific herring (*Clupea pallasi*) feeding ecology in Prince William Sound, Alaska. Ph.D. thesis, University of Alaska Fairbanks, Fairbanks, Alaska.
- Foy, R.J., and Norcross, B.L. 1999a. Spatial and temporal differences in the diet of juvenile Pacific herring (*Clupea pallasi*) in Prince William Sound, Alaska. Can. J. Zool. 77: 697-706.
- Foy, R.J., and Norcross, B.L. 1999b. Feeding behavior of herring (*Clupea pallasi*) associated with zooplankton availability in Prince William Sound, Alaska. Proceedings of Ecosystem Considerations in Fisheries Management. 16th Lowell Wakefield Fisheries Symposium. Anchorage, Alaska. September 30 – October 3, 1999. University of Alaska Sea Grant College Program Report No. 99-01. pp. 129-135.
- Foy, R.J., and Paul, A.J. 1999. Winter feeding and changes in somatic energy content for age 0 Pacific herring in Prince William Sound, Alaska. Trans. Am. Fish. Soc. 128: 1193-1200.
- Goering, J.J., Shiels, W.E., and Patton, C.J. 1973. Primary production. *In* Environmental studies of Port Valdez. *Edited by* D.W. Hood, W.E. Shiels and E.J. Kelley. Institute of Marine Science, Fairbanks.
- Maksimenkov, V.V. 1982. Correlation of abundance of food (for herring larvae) zooplankton and water temperature in the Korf-Karaginsk region of Bering Sea. Sov. J. Mar. Biol. 8: 132-136.
- Mehner, T. 1993. Distribution and diet composition of 0+ herring (*Clupea harengus* L.) and perch (*Perca fluviatilis* L.) in a shallow estuary of the Southern Baltic. Arch. Hydrobiol. 128: 309-316.

- Niebauer, H.J., Royer, T.C., and Weingartner, T.J. 1994. Circulation of Prince William Sound. J. Geophys. Res. 99: 14,113-14,126.
- Paul, A.J., and Paul, J.M. 1998. Spring and summer whole-body energy content of Alaskan juvenile Pacific herring. Alaska Fish. Res. Bull. 5: 131-136.
- Paul, A.J., Paul, J.M., and Brown, E.D. 1998. Fall and spring somatic energy content for Alaskan Pacific herring (*Clupea pallasi*) relative to age, size and sex. J. Exp. Mar. Biol. Ecol. 223: 133-142.
- Raid, T. 1985. The reproduction areas and ecology of Baltic herring in the early stages of development found in the Soviet zone of the

Gulf of Finland. Finnish Fisheries Research 6: 20-34.

- Sandstrom, O. 1980. Selective feeding by Baltic herring. Hydrobiologia 69: 199-207.
- Stokesbury, K.D.E., Foy, R.J., and Norcross, B.L. 1999. Spatial and temporal variability in juvenile Pacific herring, *Clupea pallasi*, growth in Prince William Sound, Alaska. Environ. Biol. Fish. 56: 409-418.
- Vogel, A.H., and McMurray, G. 1982. Seasonal population density distribution of copepods, euphausiids, amphipods and other holoplankton on the Kodiak shelf. National Ocean Service, Wilsonville, Oregon.

Dynamics of Sakhalin-Hokkaido herring growth rate and zooplankton biomass (Sea of Japan)

Elsa R. Ivshina

Sakhalin Research Institute of Fisheries and Oceanography (SakhNIRO), Yuzhno-Sakhalinsk, Russia. E-mail: elsa@tinro.sakhalin.ru

The Sakhalin-Hokkaido herring population has been in low abundance for several decades (Fig. 24). Fish growth rates, including herring, are closely connected with the state of population. A negative relationship between fish size and population abundance has been observed for Sakhalin-Hokkaido herring (Kitahama 1955; Motoda and Hirano, 1963).

On the whole, relatively low growth rates of Sakhalin-Hokkaido herring were recorded from 1955-1970 and 1990-1998, and much higher growth rates from 1970-1990. A comparison of the parameters of regression equations for linear growth of feeding herring during 1955-1959 and 1991 did not show certain differences (at P=0.05). Such regularity was marked both for immature and adult fish. The increase in growth rate during the 1970-1980s seemed to be due to a great decrease in abundance, but in the 1990s, a decrease in mean length and a further reduction of herring abundance and their main food competitors (walleye pollock, sardine) were recorded.

Fish growth is dependent on many factors including zooplankton abundance. The mean length fluctuations for Sakhalin-Hokkaido herring during 1955-1998, appeared to correspond to fluctuations of total zooplankton biomass in the area of feeding along southwestern Sakhalin coast. Herring growth rate did not vary much with year-class strength, but seemed to follow in parallel with fluctuations of total zooplankton biomass (Figs. 25 and 26). A supply with food organisms is perhaps one of the factors limiting herring growth in periods of low abundance.



Fig. 24 Catch of Sakhalin-Hokkaido herring.



Fig. 25 Total zooplankton biomass and mean length of ages 3-7 herring. Smoothed lines indicate 5 year running averages.



Fig. 26 Linear regression of total zooplankton biomass versus mean length by age.

Euphausiids as indicators of changing ocean conditions in the Oregon upwelling zone

William T. Peterson, Leah R. Feinberg and Julie E. Keister

National Marine Fisheries Service and Cooperative Institute for Marine Resource Studies, Hatfield Marine Science Center, 2030 S. Marine Science Drive, Newport, OR 97365, U.S.A. E-mail: bill.peterson@noaa.gov

We have been sampling off Newport Oregon on a biweekly basis since 1996, at stations located 1 and 5, 10 and 15 miles from shore. At each station, a CTD profile is taken, surface seawater

samples are collected with a bucket for later analysis of chlorophyll and nutrients, and a vertical plankton tow is taken with a 1/2 m diameter 202 mesh nets. From these samples, we have counted all zooplankton including euphausiid larval stages. In this brief paper, we discuss the data on euphausiid furcilia larvae from the station five miles (9 km) from shore. This station is designated as NH05 on the figures shown below.

Two species dominate the euphausiid assemblage off Oregon, Euphausia pacifica and Thysanoessa spinifera. Under "normal" ocean conditions, E. pacifica dominates offshore waters and T. spinifera shelf waters. We have found that this pattern of dominance varies depending upon physical conditions -T. spinifera dominates nearshore waters only during years of strong upwelling; during summers of weak upwelling, E. pacifica moves into shelf waters in significant numbers. Figure 27 illustrates this pattern for the May-September growth season. Weak upwelling years were 1996, 1997 and 1998; strong upwelling years were 1999 and 2000. During 1996, though T. spinifera dominated, there were significant numbers of E. pacifica furcilia present in shelf waters. During 1997, abundances of furcilia larvae of T. spinifera and E. pacifica were equal but in 1998, during the El Niño, E. pacifica was the dominant species.



Fig. 27 Time series of euphausiid furcilia densities at a NH05 (a station 5 miles off Newport, Oregon). Note that *Euphausia pacifica*, an oceanic species, were abundant from 1996-1998, and were the dominant species during the 1997-98 El Niño period. From spring 1999 until present, the coastal species, *Thysanoessa spinifera*, is the dominant form.

Also apparent in the data in Figure 27 is the longterm trend in declining abundances of *T. spinifera* from 1996-1998, followed by a trend toward increasing numbers in 1999 and 2000. *E. pacifica* showed the opposite pattern of increasing numbers from 1996-1998, then a decline to very low levels in 1999 and 2000. The same data are shown as a time series in Figure 28.



Fig. 28 Mean densities of euphausiid furcilia during the May-September upwelling season. Dominance shifts to *Euphausia pacifica* during the El Niño period, and returns to *Thysanoessa spinifera* in 1999.



Fig. 29 Changes in spawning season of euphausids at a station five miles off Newport, Oregon. In 1996-1998, spawning occurred only in late summer. Spawning times in 1999 and 2000 were greatly expanded and included major spawning in the spring and early summer months as well.

Another feature of euphausiid ecology that has shown significant change in the past five years is the length of the spawning season. We have found that the spawning season at NH05 in 1996-1998 was very short, lasting only a few weeks in July and August (Fig. 29). Beginning in 1999, the spawning season was extended from April through September. Euphausiid egg densities averaged over the summer also increased greatly and by 2000, numbers greater than 300 per cubic meter on average were seen. This compared to 1996-1998, when average abundances were approximately 20, 40 and 2 per cubic meter respectively. We do not know which species of which euphausiid produced these eggs because we have only recently been able to identify the eggs to species. We do know that the eggs in 2000 were *T. spinifera* but we will have to re-count the other samples to determine the relative abundances of *T. spinifera* and *E. pacifica* eggs. Given the inter-annual variability in dominance, we expect to find a dominance of *T. spinifera* eggs in 1996 and 1999, and *E. pacifica* eggs in 1997 and 1998.

Modeling environmental and predation-induced variability in euphausiid recruitment: Its dependence and impact on herring trophodynamics

Scott M. Rumsey

Oregon State University, U.S. Geological Survey, 3200 SW Jefferson Way, Corvallis, OR 97330, U.S.A. E-mail: Scott Rumsey@usgs.gov

and The interaction between predation zooplankton recruitment processes in determining the availability of euphausiid prey for adult Pacific herring. Clupea pallasi, was investigated. Variability in euphausiid recruitment is influenced by the magnitude of spawning input, environmentally induced variability in larval survivorship and development, as well as by predation on early life-history stages. Previous life-history modelling of euphausiid larval development has underscored how heterogeneity in the developmental environment can have more pronounced effects during particular stages of the euphausiid larval ontogeny and disproportionately influence subsequent recruitment (Rumsey and Franks 1999).

In this modelling work, however, I focus on the role of herring predation in determining variability in euphausiid abundances. Herring predation can impact euphausiid demography directly through consumption. Additionally, predation effects on euphausiids can be delayed, or indirect, by affecting adult abundance through predation on developing larvae, and by impacting larval euphausiids through predation on adults and subsequently diminishing the magnitude of spawning. Furthermore, I investigate the potential feedback on juvenile and adult herring of changes in their zooplankton prey preferences. Although copepods often dominate the diets of juvenile Pacific herring in the Eastern Pacific (Ivashina and Bragina 1999; Radchenko and Dulepova 1999), juvenile and larval euphausiids are often represented in stomach contents, and thus juvenile prey could potentially impact adult herring food availability.

A simple ecosystem model was developed to evaluate the impact of herring prey preferences on zooplankton dynamics, as well as that of juvenile (0+ age class) and adult (>3+ age class) herring. Juvenile herring prev consisted of varying proportions of copepod larvae, copepod adults, and euphausiid larvae. Adult herring prey were comprised of adult copepods and/or euphausiids (Fig. 30). The effect of predation was investigated by manipulating juvenile and adult herring preypreference values, and monitoring the impact on the model state variables (e.g. the abundances of copepod, euphausiid and herring adults and larvae/juveniles). Additionally, the impact on state variables of variations in the initial values of model parameters was determined, and compared with the manipulations of herring prey preference. This comparison provides insights into how predation mediated changes in state variables compare with environmentally forced changes. The results of these analyses are reported as

elasticities, or proportional effect on a given state variable for a given proportional manipulation of a model parameter. Elasticity values facilitate the comparison of parameters that differ in their units of measure and/or magnitude. Additionally, elasticities provide a robust statistic for the analysis of model results in spite of poorly constrained parameter values.

The response zooplankton and herring of abundances most pronounced for was manipulations of the initial values of model parameters (e.g. Bollens 1988). This observation impact of suggests а greater varving environmental conditions (especially primary productivity) on herring-zooplankton population dynamics than that of herring predation and prey preferences (Fig. 31).

Although not as pronounced as the initial value elasticities, elasticity values for varying herring prey preference produced as much as a 30% variation in the output of modeled zooplankton



Fig. 30 General model structure herringeupahausiid-copepod trophodynamic model.

populations. The influence of herring predation on modeled adult euphausiid abundance was primarily the result of direct predation by adult herring. The abundance of larval euphausiids, however, was controlled indirectly through predation on adult euphausiids and subsequent impacts on reproductive output (Fig. 32). Similar to the results for adult euphausiids, modelled copepod abundance was influenced directly by herring predation (Fig. 33).



Fig. 31 Elasticity of the state variable response to the manipulation of the initial values of model parameters.



Fig. 32 Elasticity of the euphausiid response to the manipulation of prey-preference parameters.



Fig. 33 Elasticity of the copepod response to the manipulation of prey-preference parameters.



Fig. 34 Elasticity of the herring response to the manipulation of prey-preference parameters.

Increased prey preference for copepod prey resulted in diminished adult herring abundance, indicating a cost associated with broader diet choice (Fig. 34, left). No such cost, however, was associated with changing prey preferences for juvenile herring (Fig. 34, right). Although juvenile herring benefited by increased predation on euphausiid larvae, there appears to be little indirect impact on adult herring through the reduction of their adult euphausiid prey (e.g. McGurk *et al.* 1993).

References

- Bollens, S. M. 1988. A model of the predatory impact of larval marine fish on the population dynamics of their zooplankton prey. J. Plank. Res. 10: 887-906.
- Ivashina, E.R., and Bragina, I.Y. 1999. On relationship between crustacean zooplankton (Euphausiidae and Copepods) and Sakhalin-Hokkaido herring (Tatar Strait, Sea of Japan). Rep. 1999 REX Task Team Workshop.
- McGurk, M.D., Paul, A.J., Coyle, K.O., Ziemann, D.A., and Haldorson, L.J. 1993.
 Relationships between prey concentration and growth, condition, and mortality of Pacific herring, *Clupea pallasi*, larvae in an Alaskan subarctic embayment. Can. J. Fish Aquat. Sci. 50: 163-180.
- Radchenko, V.L., and Dulepova, E.P. 1999. Shall we expect the Korf-Karaginsky herring migrations into the offshore western Bering Sea? PICES Sci. Rep. 15: 115-123.
- Rumsey, S., and Franks, P. 1999. Influence of variability in larval development on recruitment success in the euphausiid *Euphausia pacifica*: elasticity and sensitivity analyses. Mar. Biol. 133: 283-291.

Recent state of Japanese herring populations

Tokimasa Kobayashi and Keizo Yabuki

Hokkaido National Fisheries Research Institute, 116 Katsurakoi, Kushiro, Hokkaido, Japan. 085-0802 E-mail: tokikoba@hnf.affrc.go.jp

Judging from the fluctuation of the catch data, the stock condition of herring populations around Japan are in different phases. Hokkaido-Sakhalin population spawn in high salinity shallow waters, the life span is longer than 15 years, and migration range is wide within these populations. Annual catch had been maintained at more than three hundred thousand tons from the 1880s to the mid-1930s, with a historical peak of about one million tons in 1897. However the catch declined since the mid-1940s, and has been still at quite a low level since 1955, except the appearance of the 1983 year-class which was caught totally about one hundred thousand tons. The Mangoku-Ura population spawn in high salinity waters but migration range is smaller and life span is shorter than the Hokkaido-Sakhalin population. Its annual catch increased gradually from 1977, and reached about six hundred tons in 1984. But it decreased since 1987 due to the small recruitment relating to the rise of water temperature in the spawning season. For the Lake-Furen population which spawn in brackish lake, the annual catch had fluctuated below ten tons before 1984. Since 1985, it gradually increased and reached about seven hundred tons in 1997, but it decreased below fifty tons in 1999 and 2000, due to the weak year-classes of 1997 and 1998. Different phases of stock condition observed among each population may be deeply related to the inherent ecological and physiological abilities of adaptation to the number of oceanic condition factors.

Oil, disease and fishing as factors in the multiple collapses of the Prince William Sound herring population

Gary L. Thomas and Richard E. Thorne

Prince William Sound Science Center, P.O. Box 705, Cordova, AK 99574, U.S.A. E-mail: loon@pwssc.gen.ak.us

In 1993, the largest biomass of Pacific herring in history was predicted to return to Prince William Sound to spawn. Instead, there was a record low return. In the fall of 1993, we conducted an echointegration-purse seine assessment of the stock that confirmed the stock collapse to 20,000 metric tons (MT). After a fall 1993 fishery, acoustic surveys showed that the population further collapsed to 13,000 MT. With a moratorium on fishing, the population rebuilt to 23,000 MT and 38,000 MT in the falls of 1995 and 1996, respectively. However, the acoustic surveys in the springs of 1998 and 1999, after reopening the commercial fishery, showed the population to have collapsed again to about 17,000 MT. After test fishing in the spring of 1999, management cancelled the fishery. The spring survey 2000 showed the population to have fallen to a new, alltime low of 9,000 MT. Co-occurring with the collapses of the herring population in 1993 and 1997, were outbreaks of viral hemorrhagic septicemia. This suggests that the herring have a low immunity to disease after handling by fishing Researchers have suggested the operations. possibility of immune-system damage due to oil exposure in 1989. We present infrared observations of herring surfacing at night to replace air in their gas bladder as a plausible mechanism for oil exposure.

Temporal comparisons of juvenile and adult growth: Implications for changes in trophic conditions in shelf versus nearshore waters

Douglas E. Hay

Pacific Biological Station, Nanaimo, B.C., Canada. V9R 5K6 E-mail: hayd@pac.dfo-mpo.gc.ca

Many herring populations in the North Pacific had relatively high levels of abundance in the 1990s, but many populations also experienced a decline in growth rates (length-at-age) since the 1980s. This statement is based on data presented at the 1999 PICES REX Workshop in Vladivostok, and the 2000 Alaska Herring Symposium in Anchorage. Size-at-age has decreased in BC herring populations since 1980. As an example, Figure 35 shows the length-at-age of samples taken by purse seine, between February and April, in the same location in the Strait of Georgia, BC (near Denman Island). The mean lengths for each age and year are estimated from measurements of over 146,000 fish with about 6000 measurements used each year. Note that age 2 fish do not follow the declining trend. This pattern is seen in other herring populations, in the Pacific and Atlantic. Close inspection of many data presentations, such as the one shown here for the Strait of Georgia, indicates that the temporal decline in size-at-age is seen mainly in the older age groups - and it may not occur, or is much less pronounced and in the recruits or juveniles.

In 1977, there was a strong cohort of herring (and some other species) in much of Alaska and all northern BC populations (Fig. 36). In 1980, when the 1977 year class was age 3, the size-at-age was normal or slightly above average in most populations. In later years, at ages 5 and older, the size-at-age of this cohort decreased. Figure 37 shows the mean length-at-age of the 1977 cohort class (dark circle with lateral line) relative to those of other year classes from 1980 to 1996 from the Prince Rupert Region of northern BC.

A project requiring detailed analyses of scale growth started in 1999. A major objective was to examine and compare growth rates of the juvenile stages and the adult stages: between years, and areas. (In part, this project started as an outcome of a special PICES WG 3 meeting in 1995, in La Jolla, that recommended examination and comparison of early growth rates among North Pacific pelagic species.) In this project, the length of lateral scales, from the focus to the edge in a strait line, parallel to the midline of the fish (i.e. from nose to tail), was measured to the nearest 0.01 mm using a digital camera on a microscope (Fig. 38). Measurements on digital images were made using Sigmascan© software.

The scale-length - body-length relationship in herring is approximately linear (Fig. 39), and it is very consistent, both within and between various populations that have different growth rates. Therefore the length of annual growth increments on scales provides an index of past growth rates.

Temporal patterns of scale size-at-age, based on scale measurements between the focus and annuli, show temporal changes with time (Fig. 40), similar to those seen in Figure 1, except the scale measurements show growth patterns from ages 1-5 herring, (and not ages 2-8 as shown in Figure 35).



Fig. 35 Mean length of herring by age (\leq age 8). For ages 4 through age 8, mean length has decreased with age since 1972. The mean size of age 2 and 3 herring varied, and had a slight increasing trend in the 1980's, followed by a decrease in the 1990's.



Fig. 36 Distribution of herring populations with strong 1977 cohorts.



Fig. 37 Changes in relative length of the 1977 year-class.



Fig. 38 Herring scale, showing the position of the focus, annuli (a, b, c), and the relationship of scale growth to the length of a herring.



Fig. 39 The relationship between scale length (focus to outer edge) and fish length (standard length, from nose to end of the hypural plate).

Note that the long-term decrease in (scale) size-atage is seen for measurements from annuli 4-5, similar to that in Figure 35.

Temporal differences in juvenile growth are seen most clearly by a comparison of the inter-annuli distances on scales, with the first measurement as the distance between the focus and first annulus (Fig. 41). The top line in Figure 41 is the distance (mm) between the focus and first annulus, and represents the first year growth. First year growth increased in the 1980s (see arrow A in Figure 41) followed by a decrease in the 1990s (arrow B). Trends in second year growth were nearly the opposite, with a decrease in the 1980s (arrow C) and increase in the 1990s (arrow D). Adult growth also deceased in the 1990s (arrow E).



Fig. 40 Comparison of scale growth by time; data taken from Strait of Georgia.



Fig. 41 Inter-annulus comparison of growth, by age and year, from samples taken from the Strait of Georgia. Each bar represents a 95% CI about the mean. The arrows and letters depict periods of growth change (see text).

Biological implications

Juvenile herring surveys in the Strait of Georgia (SOG), conducted since 1990, indicate that age 0+ juveniles (< 12 months) spend the first year in SOG. In September, or about the end of their second summer, most age 1+ juveniles have left SOG, and few herring remain resident in SOG after their second year, except for some resident populations, which are usually found in specific locations. Consequently, age 0+ and age 1+ herring occupy different habitats, and may be subject to different trophic limitations and opportunities, that may affect their growth rates differently.

The causes of the recent (post 1980) declines in size-at-age of adult herring (mainly age 3 and older as depicted in Figure 35) could have several explanations. The size-at-age of adult herring represents the cumulative increments of growth from previous years. It is interesting to note that the relative contributions of growth from the first and second years of life may vary. In particular, the increasing rate of age 0+ growth in the 1980s

was not accompanied by increases in later years, and in general, size at age of older age classes declined at this time (Fig. 35). This may indicate that feeding conditions for age 0+ herring, in the inside waters of SOG, were good, but that feeding conditions for age 1+ juveniles and older age classes, which feed mainly on shelf waters, was poorer in the 1980s than during other decades. If so, these results are consistent with the observation that the strong 1977 year class had normal or good size-at-age for juveniles and young fish recruiting at age 3, followed by slower growth and reduced size-at-age for older age classes.

In summary, the detailed reconstruction of past growth rates of Strait of Georgia herring may have implications for other populations. Specifically we observed that first year growth rates varied with time, but appeared to increase in the 1980's, when growth rates of older age groups were in decline. This difference indicates that the processes that limited growth of adult fish in shelf waters may have been separate, and different than those which controlled the growth of age 0+ juveniles in inshore waters.