

18TH LOWELL WAKEFIELD FISHERIES SYMPOSIUM



HERRING

EXPECTATIONS

FOR A NEW MILLENNIUM

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EDITORS**

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About the Symposium

Herring 2000: An International Symposium on Expectations for a New Millennium is the eighteenth Lowell Wakefield symposium. The program idea was suggested by Fritz Funk of the Alaska Department of Fish and Game as a follow-up to the 1980 Alaska Herring Symposium and the 1990 International Herring Symposium. The meeting was held February 23-26, 2000, in Anchorage, Alaska. Contributors gave 45 oral and 14 poster presentations.

The symposium was organized and coordinated by Brenda Baxter, University of Alaska Sea Grant College Program, with the assistance of the organizing committee. Organizing committee members are Fritz Funk, Alaska Department of Fish and Game; Doug Hay, Department of Fisheries and Oceans, Canada; A.J. Paul, University of Alaska Fairbanks, Institute of Marine Science; Connie Ryan, California Department of Fish and Game; Rob Stephenson, Department of Fisheries and Oceans, Canada; Reidar Toresen, Marine Research Institute, Norway; Dave Witherell, North Pacific Fishery Management Council; and Mei-Sun Yang, U.S. National Marine Fisheries Service, Alaska Fisheries Science Center.

Symposium sponsors are Alaska Department of Fish and Game; North Pacific Fishery Management Council; U.S. National Marine Fisheries Service, Alaska Fisheries Science Center; and Alaska Sea Grant College Program, University of Alaska Fairbanks.

The Lowell Wakefield Symposium Series

The University of Alaska Sea Grant College Program has been sponsoring and coordinating the Lowell Wakefield Fisheries Symposium series since 1982. These meetings are a forum for information exchange in biology, management, economics, and processing of various fish species and complexes as well as an opportunity for scientists from high latitude countries to meet informally and discuss their work.

Lowell Wakefield was the founder of the Alaska king crab industry. He recognized two major ingredients necessary for the king crab fishery to survive—ensuring that a quality product be made available to the consumer, and that a viable fishery can be maintained only through sound management practices based on the best scientific data available. Lowell Wakefield and Wakefield Seafoods played important roles in the development and implementation of quality control legislation, in the preparation of fishing regulations for Alaska waters, and in drafting international agreements for the high seas. Toward the end of his life, Lowell Wakefield joined the faculty of the University of Alaska as an adjunct professor of fisheries where he influenced the early directions of the university's Sea

Grant Program. This symposium series is named in honor of Lowell Wakefield and his many contributions to Alaska's fisheries. Three Wakefield symposia are planned for 2002-2004.

Proceedings Acknowledgments

This publication presents 49 symposium papers. Each full-length paper was reviewed by two peer reviewers, extended abstracts had one review each, and papers were revised according to recommendations by associate editors who generously donated their time and expertise: Fritz Funk, Jim Blackburn, Doug Hay, A.J. Paul, Rob Stephenson, Reidar Toresen, and Dave Witherell.

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Nomenclature Note

The specific epithet for Pacific herring is correctly spelled with a double i: *Clupea pallasii* Valenciennes, 1847. The name has appeared in literature with or without the second i, depending on prevailing opinion. The *International Code of Zoological Nomenclature*, fourth edition (1999), which took effect January 1, 2000, clarifies that the spelling of a species name given in the original description of the species is to be retained. Therefore, the spelling *pallasii* is retained herein.

The Role of Herring Investigations in Shaping Fisheries Science

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Abstract

Herring (Atlantic, Baltic, and Pacific) have contributed to major fisheries and have been important to coastal communities for centuries. As a result, herring has been the subject of considerable scientific study, and it is not surprising that herring fisheries and herring research have been at the core of several major developments in fisheries science and fisheries management. Early theories regarding migration, the development of the population/stock concept, and tracking and quantification of year classes were based largely on herring investigations. More recently herring research has been key to development of hydroacoustics methods, hypotheses on population regulation and abundance, the link between fisheries dynamics and hydrography, and a number of innovative approaches to fisheries regulation and management. These developments have shaped fisheries science and had an impact on science generally. In spite of severe depletion or collapse of several major stocks at some point in the last few decades, herring remain the subject of major fisheries and of research. Future research developments might be expected, as in the past, to reflect the major initiatives and general themes of fisheries science and management modified by specific issues concerning herring fisheries.

Introduction

Not only has the herring from earliest times been the commercial fish of northern waters (after stealing the crown from the cod, *Gadus morhua*, perhaps as early as the tenth century), but it was in northern Europe that taxonomy, fishery science and biology first took on a modern aspect . . . contributions to

ichthyology tended to come from countries . . . where herring was exploited and from time to time held the fate of empires. (Whitehead 1985, pp. 3, 4)

As a recruit to fisheries research in the early 1980s, I became intrigued by the evolution in fisheries science and management. I knew in working on herring assessment and research that I was working in support of a prominent fishery, and that this species seemed to have its fair share of literature. I was following in the footsteps of a number of revered scientists who had worked on various herring fisheries. I remember, for example the excitement of first reading A.G. Huntsman's papers on Bay of Fundy herring (Huntsman 1917, 1918), realizing that he had been in the same location and looking at the same fishery more than 70 years earlier. I then remember becoming somewhat dismayed to see how many of the obvious questions (1) had been thought of, (2) had been worked on by my predecessors, and (3) apparently could not be resolved by some of the most prominent fisheries scientists of the past. I became aware of the fact that some of what has been done and published has, sadly, been forgotten and ignored, and that much research in science is spent rediscovering and revisiting some basic biological questions. It was obvious, however, that there had certainly been some great breakthroughs in the past century—and that many of these had been the direct result of work on herring.

In this paper I attempt to evaluate how large an impact studies of herring and herring fisheries have had. I make the claim that work on herring, more than that on any other fish, has shaped the development of fisheries biology and fisheries management. Further, I contend that this trend should continue in the future. I suggest that some reflection on historical herring research reminds us of some basic characteristics of fisheries research—including the persistence of several major themes and recurrent interest in ideas, some of which were generated more than a century ago.

Over a little more than a century there have been huge developments in fisheries science and fisheries management. This period has been marked by industrialization of fisheries, with rapid development in fishing technology and expansion of fisheries. It has also been a period of profound development in concepts (including recognition of the concept of overfishing), the emergence of fisheries management (and in the last few decades the “modern fisheries management experiment” [Stephenson and Lane 1995]), and improved analytical capabilities.

Cushing (1988) in describing the historical development of fisheries and fisheries science claims that fisheries science has two roots. First, there was development of marine biology in the nineteenth century, resulting from a Victorian interest in the sea, and characterized by an increase in descriptive natural history, and the great expeditions of the 1800s. Second, the first period of industrialization, in which there was an increasing interest in exploitation (and eventually in overfishing), led to the development of quantitative fisheries science as shown, for example in the figure summarizing the development of assessment methods which appears in Caddy (1999, p. 7).

The period beginning about 1875 appears to have been especially significant, for it was about that time that there was a change from descriptive to quantitative scientific investigation, the development of major research programs on fisheries, and the beginnings of fisheries science as the entity we know today. The first paragraph in Tim Smith's book *Scaling Fisheries* (1994) sets the scene in this period:

In 1864 the Norwegian government asked George Ossian Sars, son of the pioneering Norwegian marine biologist Michael Sars, to determine why the cod catches from the Lofoten Islands in northern Norway fluctuated so greatly. . . . A few years later, after several visits to the coastal fisheries, Sars asked for and, to his surprise, was loaned a ship to extend his studies offshore. Within twenty years Norway had established a scientific agency to study the fluctuations in its fisheries, and had outfitted it with a ship, laboratories, and a fish hatchery. By the turn of the century many other countries had joined Norway in establishing agencies for the scientific study of their fisheries, many of which joined in an international research organisation in 1901. What was it about fisheries that justified the creation, and continues to justify the funding, of national and international research programs?

The problem that Sars began to address more than 100 years ago [why fish catches vary] was important then, and remains important today.

Herring Have Supported Important Fisheries for Centuries

Mitchell (1864) stated, "Until salt was used, it was probable that the commerce in herrings was inconsiderable," but cited a number of early written accounts of the use of herring dating to the eleventh century and some earlier. The importance of herring to the economics and culture of coastal communities of Europe for many centuries is well documented, and is reflected, for example in the persistence of the Baltic herring markets of Turku and Helsinki, Finland, which have taken place each autumn for more than 200 years.

Whitehead's introductory paper from the proceedings of the 1983 International Symposium on the Biological Characteristics of Herring and Their Implication for Management, summarized the prominent position of *Clupea harengus* or "king herring" (Whitehead 1985):

Lacepede . . . lavished upon it suitably flowery phrases (Lacepede 1803, p. 429): [translated] "Herring is one, the use of whose natural production has decided the destiny of empires. The bean of coffee, the leaves of tea, the spices of the tropics, the worms that make silk, are of smaller influence on the nations richness than the herring of the Atlantic Ocean. A luxury or whim comes first to mind; but the real place is claimed by herring."

Linnaeus (1758, p. 318) said it all in two words *copiosissimus* piscis [= the most prolific of fish]. *Copiosissimus* the fish, which by the twelfth century had become a staple in the European diet. . . . *Copiosissimus* too the literature, which reflects the number of studies, the sheer man-hours, the salaries, the equipment, the running costs of institutes and ships—the capital investment whose main-spring (if not ultimate goal) is the greater exploitation of *Clupea* as a resource.

The historical importance of herring in Europe is affirmed by Alan Davidson in the new *Oxford Companion to Food* (Davidson 1999), “Herring . . . of all fish probably the one which has most influence on the economic and political history of Europe.”

Themes in Herring Research

There is a rich and diverse literature concerning herring. As in other fields of science, there has been a continuous expansion in literature, particularly during the twentieth century. It seems convenient to divide herring research into the periods before and after 1875.

Prior to 1875 Herring Studies Were among the Earliest Marine Scientific Investigations

It was inevitable that the economic importance of herring led to a great deal of attention and interest. Prior to about 1875, the issue was almost exclusively explanation of the variability in catches which had so much impact on social and economic affairs of some nations. Since the beginning, herring fisheries had to cope with large variations in catches, caused by large variations in abundance, and this fueled concern, speculation, documentation, and eventually scientific study. Among the longest of any fisheries data series available are some Swedish (Bohuslan) and Norwegian herring fisheries for which records go back some 500 years (Csirke 1988).

During the eighteenth century, accounts of herring feature in early writings on marine fisheries such as astronomer Edmond Halley (of Halley’s Comet fame; 1728), *Atlas Maritimus et Commercialis*; Johann Anderson (1746), *Accounts of Iceland, Greenland and the Davis Strait*; James Anderson (1785), *Account of the Present State of the Hebrides and Western Coasts of Scotland*. It was the subject of at least one entire book, *Natural History of Herring*, by British naval physician Solas Dodd (1752).

Johann Anderson wrote in the preface to his book (1746) that he thought the most important part of the book was his herring migration theory. This is now referred to as the “polar migration theory,” and indeed this was one of the major fisheries science ideas generated from observations on herring.

Observations and accounts of this type continued through most of the nineteenth century. Explanation of the variability in catches remained the issue. There seems to have been little further development, but much observation, that provided the context for later developments.

After 1875 Herring Studies Contributed to the Development of Fisheries, Fisheries Science, and Fisheries Management

The progression of major themes in herring research is evident from an examination of the literature since 1875 (Table 1). For the period since

Table 1. Decadal chronology of major themes in published herring research.

Ancient times	Herring fisheries documented as early as 240 A.D.
1860s	The existence of winter and summer herring is noted. These are not considered different enough to be called different species. Food, feeding and behavior of Atlantic herring from Europe and eastern North America. Migration patterns observed. Examination of spawning beds and substrates. Attempts to incubate eggs.
1880s and 1890s	Heinke's theory of races in fish stocks.
1910s	Hjort's publications on stock fluctuations and dynamics and the existence of races of herring in northern Europe and eastern Canada.
1920s	Stock and population structure and dynamics—using races, vertebral counts and spawning season to distinguish races. Attempts to distinguish races using vertebral counts and spawning season. Use of scales for aging. Studies of food and feeding behavior of adults and larvae. Length and age at maturity. Assessment methodology—attempts to introduce a mathematical or statistical approach. Migration of shoals. Hypotheses about the cyclical nature of population fluctuations. Examination of the influence of quantity of spawning herring on the size of the stock of following year.
1930s	Tags used to study migration. Comparisons of the recovery rates of external tags and internal tags in the body cavity. Use of electromagnetic detectors to collect tags in fish processed for fish meal. Stock and population structure and dynamics—attempts to distinguish races (including spring vs. fall spawners) using morphological features, vertebral counts and growth increments from scales. Maturity in relation to age and length. Factors affecting year-class strength, including hydrography. Lunar influence on fishing.

Table 1. (Continued.) Decadal chronology of major themes in published herring research.

1930s (Contd.)	Spawning waves observed with the oldest fish spawning first and leaving earlier than the younger fish.
1940s	<p>Examination of geographic variations in vertebral counts: northern vs. southern.</p> <p>Use of vertebral variations to distinguish populations.</p> <p>Studies of age and length at maturity and the relationship between age and length and fecundity.</p> <p>Stomach content analysis in relation to the distribution of plankton populations.</p> <p>Tagging in the Pacific.</p> <p>Concern over overfishing in Alaska.</p>
1950s	<p>Double helix structure of DNA molecule published in 1953.</p> <p>Methods published for the isolation of DNA from herring roe and sperm.</p> <p>Sonic sounders used to locate pelagic fish and to study the behavior and size of herring schools.</p> <p>Lab studies on herring behavior, feeding, and shoaling and on fertilization and development of herring eggs.</p> <p>Behavior studied in response to hydrographic conditions and light.</p> <p>Continued interest in distinguishing populations based on vertebral counts and morphological variations.</p> <p>Studies of oogenesis and spermatogenesis.</p> <p>Comparisons of the effectiveness of different gear types.</p>
1960s	<p>Forecasting catches based on larval recruitment and age composition.</p> <p>Maturity scale for gonadal development recommended by Herring Committee to ICES in 1965.</p> <p>Continued interest in the use of tags, morphometrics, and meristics to determine homing, migration patterns for spawning, and feeding and population mixing on the offshore feeding areas.</p> <p>Fish pumps.</p> <p>Characterization and identification of spawning grounds and substrates.</p> <p>Use of acoustics to locate herring and to study the size of herring schools.</p> <p>Internal and external tags used in studies of migration and homing.</p>
1970s	<p>Larval surveys and larval abundance indices used for estimating stock size.</p> <p>Larval retention areas.</p>

Table 1. (Continued.) Decadal chronology of major themes in published herring research.

	<p>Concern over the mismanagement of herring stocks.</p> <p>Concern with toxicological issues—pollution, oil, PCBs, and heavy metals.</p> <p>Tagging using external tags, internal tags, and parasites as biological tags (<i>Anisakis</i> spp.).</p> <p>Distinguishing stocks and populations using otoliths, morphometrics, and meristics.</p> <p>Effect of hydrographic, oceanographic, and environmental factors on eggs and embryonic development.</p>
1980s	<p>Tagging using external tags, internal tags and parasites as biological tags.</p> <p>Multispecies and environmental models as well as single species models.</p> <p>Study of effects of hydrographic, oceanographic, and environmental factors on egg and larval development and on spawning.</p> <p>Continued refining of acoustic techniques for locating and measuring herring schools.</p> <p>Comanagement.</p> <p>Locating spawning grounds and categorizing spawning behavior, duration and intensity.</p> <p>Concern with toxicological issues particularly in the Baltic—pollution, oil, heavy metals, and radiation fallout from Chernobyl.</p> <p>Continued attempts to distinguish populations with tools such as genetics, otolith structure, tagging, biological tags, morphometrics, and meristics.</p> <p>The effect of climate and the environment—El Niño, Mount St. Helens, and the increase in atmospheric CO₂.</p>
1990-1999	<p>The arrival of the “precautionary approach.”</p> <p>Interactions between herring fisheries and the environment.</p> <p>Environmental approach and multispecies models.</p> <p>Acoustics—multi-beam and side-scan sonar.</p> <p>Genetics—microsatellite DNA.</p> <p>Fisheries management science and comanagement of resources with industry.</p> <p>Concern with toxicological issues, particularly in the Baltic and western North America—pollution, heavy metals, and oil (<i>Exxon Valdez</i>).</p> <p>Continued attempts to distinguish populations with some new tools (genetics, elemental analysis of otoliths) and some old (otoliths, vertebral counts).</p> <p>Consideration of role of herring as forage.</p>

1920, this is based on topics of papers on Pacific, Baltic, and Atlantic herring (with herring in the title), which were listed in *Biological Abstracts* (1920s to 1970s) or in *Aquatic Sciences and Fisheries Abstracts* (since 1975). For the earlier period it is based largely on historical summaries and existing syntheses of the development of fisheries science, including an examination of the herring research preceding and during the early years of the International Council for the Exploration of the Sea (Stephenson and Clark 2002).

The literature indicates that herring research seems to have been influenced by three general factors:

1. It has reflected and contributed to general developments in fisheries research and management, for example:
 - Migration patterns as the explanation of fluctuation in catch
 - Existence of separate populations/stocks
 - Aging, year classes, stock fluctuations
 - Concept of overfishing
 - Stock assessment methodologies
 - Acoustic methods
 - 1950s interest in genetics following Watson and Crick
 - Fisheries management
 - Feeding, trophic relationships, multispecies aspects
2. It has reflected issues or changes in the use and demand for herring, including:
 - Practical aspects of management of herring fisheries
 - Development of major fish meal markets
 - Use of herring in animal/livestock feed
 - Herring as feed in aquaculture
3. It has responded to unique or local issues and perturbations, such as:
 - *Exxon Valdez* oil spill in Alaska
 - Release of radioactivity at Chernobyl
 - Eruption of Mount St. Helens
 - El Niño events

Herring Studies Have Contributed to Several Major Developments in Fisheries Science and Management

Modern taxonomy, fishery science, and biology were born in Europe. This, together with the long-standing economic importance of the herring, has given *Clupea harengus* (and its close relative *C. pallasii*) a prestige and literature that quite outshadows those of any other. (Whitehead 1985)

There have been a number of major developments in fisheries science and management based largely on herring work. These include:

A. Polar Migration Theory

The earliest major development in fisheries science based primarily on herring appears to be the herring migration theory put forward by Johann Anderson (1746). According to Anderson's theory (Wegner 1993 and pers. comm.):

The north Polar Sea is the real home of the herring. Beneath the permanent ice cover the herring is safe from its "enemies," such as different fishes, whales (who cannot come up for air under ice), gulls, and fishermen of all nations. Below the ice the herring is undisturbed and grows rapidly reaching a maximum size due to plentiful food. However, because of the increasing population and diminishing food supply the main shoal of herring leave this safe area and migrate south early (January) each year.

As soon as the shoal reaches the open waters its "enemies" pounce on it and drive the fish permanently further south. Fishermen catch large amounts of herring in certain well-known areas according to the seasons. . . .

The remaining herring which have not been eaten by predators or caught by fishermen at various places along the way, join up with the juvenile herring from different spawning grounds toward the end of the year and return again to the "real north" to reproduce the stock beneath the ice.

Wegner points out that the polar migration theory was able to answer the most important questions concerning Atlantic herring at the time. Herring were different lengths and weights in different places because of the distance away from the plentiful food of the north, and the energy needed to escape predators. The absence of herring on a well-known fishing ground was due to predation. Changing migration patterns were a reflection of changing predator behavior. In addition to the main spawning beneath the polar sea there was spawning at different times and locations during the migration.

Toward the end of the nineteenth century, there was considerable speculation about the large variations in abundance of herring and views that challenged the polar migration theory. William Marshall, for example in the book *Die Deutschen Meere und ihre Bewohner* (1895) summarizes the theories related to why herring come to spawning grounds some times and not others (translated by C. Hammer):

Since man is very much involved in this matter, he has long been looking for an explanation for this awkward phenomenon. In older times there was talk about punishment from God for the fishermen and merchants who have become rich and "übermutig." From the Baltic the herring are reported to have vanished since cannons producing considerable noise were used in the sea battle. For this reason one claims to have noticed unusual migrations of the herring during the Swedish Russian war in 1789, and then again it is reported that the water is poisoned by the remains of culling of whales and seals and

the cooking of the oil. The trawl nets are accused for destroying the seabed and at the same time killing eggs and herring larvae. Then the steamships have been made responsible for creating too much water movement, as if turbulence in the water body has not been there before mankind has thought about steamships. The Dutch fishermen talk about a king of herring who leads the schools, apparently they assume several kinds of non-herring fish for this purpose [the German name of John Dory (*Zeus faber*) is Heringskonig, i.e. king of herring, who is coming into the North Sea in summer and forages on herring; remarks by Hammer]. If this fish is caught and not set free, his “folk” disintegrate into small bunches and get lost, not having the appropriate knowledge.

The polar migration theory was broadened to include other species, and developed to include the influence of oceanographic conditions (in addition to predation) on migration routes and remained popular until undermined by the work on herring by Heincke at end of the nineteenth century (Sinclair 1997). It was still a popular working hypothesis at the beginning of the twentieth century (Sinclair 1997) and the influence is seen, for example in Huntsman’s conclusions regarding migratory “processions” of herring around the Bay of Fundy (Huntsman 1918).

About the end of the twentieth century, there was a great increase in the documentation of fisheries, in scientific study, and literature. The field of fisheries science began to develop at a great rate. Herring was an important species, and remained the subject of several further developments.

B. Population Thinking

Sinclair and Solemdal (1988), and Sinclair (1988, 1997) chronicle the important development of “population thinking” which took place in fisheries biology between 1878 and 1930. During this period, research on the interannual variability in abundance and on intraspecific variability in body form led to a major change in thinking—from consideration of species as types (later known as the essentialist species concept) to consideration of the species made up of groups of populations (component populations).

This shift had a great deal to do with herring, through the work of Heincke. Sinclair (1997) discusses how Heincke (1878, 1882, 1898) undermined the polar migration theory:

He [Heincke] initiated his work in the early 1870s within the context of the herring overfishing debate in the Baltic. There were two schools of thought. Based on the work of the Swedish natural historian Nilsson, it was believed that there were many local forms of herring in the Baltic, each form having a limited distributional area with short seasonal migrations. Under this interpretation there was considerable scope for overfishing, even with the simple harvesting technology of the time. The second school of thought, championed by the Danish scientist Henrik Krøyer, favored the traditional interpretation based on Anderson’s “migration” theory, with local overfishing being impossible. The public debate was heated, but unresolved based on the methodologies used at the time to identify the putative local forms.

Heincke approached the issue by carrying out a detailed life history study of two herring spawning components off Kiel—the spring and autumn spawners.

He sampled spawning fish, the early larval stages, the postlarvae and the juveniles of the two components. . . . He concluded, using primitive multivariate statistics, that the two herring spawning groups were separate races of the same species, and that the racial differences of herring become expressed during the transition from the larval stage to the definitive (juvenile) stage. He hypothesized that the migrations of herring races were based on both reproductive and feeding instincts. The time and location of spawning was selected in relation to seasonal plankton dynamics and the transport of larvae.

The development of population thinking involved the shift from the species to the population as the appropriate unit of study. The work of Hjort (synthesized in the paper of 1914) generalized the findings of Heincke on herring to other commercial species, and clearly identified the significance of "population thinking" to fisheries management. This development, which began with Heincke's 1878 paper, represents the second major advance based largely on herring, and one which was of great significance:

The early debate concerning the existence of several self-sustaining populations within the distributional limits of marine species centered on Atlantic herring in the northeast Atlantic. Fr. Heincke convincingly resolved the controversy by extensive sampling of herring and sprat for the analysis of a large number of meristic and morphometric characters, and the development of new statistical methodology (including rudimentary multivariate statistics). (Sinclair and Solemdal 1988)

Reconstructing the lineage of historical ideas is difficult. It is clear, for example, that as early as the 1860s J.M. Mitchell (*The Herring: Its Natural History and National Importance*, 1864) disagreed with the prevailing migration theory, and anticipated the concept of populations that appeared about 1914. Mitchell proposed that herring live in the seas adjacent to the coasts or bays where they spawn, and after spawning they return to sea in the neighborhood where they feed until spawning again. The fry continue near the spawning ground until they are of sufficient size. He proposed 11 pieces of evidence to support this:

1. Every year, at a certain period of the year, a particular size of herring always resorts to the same place (i.e., herring caught off Stadland, Norway, is much larger than those on the west of Scotland). Because of this size differentiation, they can't all be from one large group.
2. Quality. The fish caught off Shetland were not as fat as those from Thurso. There are marked differences in appearance and quality between fish of different areas.
3. Time of appearance. For example, herring are caught in Loch Fyne before any are caught near Cape Wrath.
4. There was no well authenticated instance of herring being seen approaching south from a high north latitude.
5. No shoals of herring were known from Greenland seas or found in the stomachs of herring predators from those areas.

6. Whales that feed principally on herring frequent the shores of Britain and Norway year-round.
7. Bloch (no reference) had established that fish of similar size to herring could not make, from spring to autumn, the long voyage attributed to herring.
8. Herring may be found in some localities year-round.
9. No shoals of herring have ever been seen returning to the north from the south.
10. Why would the smallest herring from a large school go to the Baltic and larger ones to the North Sea?
11. Other fish have similar habits in spawning: salmon, sprat, shad, and pilchards.

This is one of several instances of ideas in the literature that seem to pre-date the sources normally cited.

C. Age Determination, Year-Class Strength, and Prediction

Studies of age structure in herring populations in the early 1900s represent the third major advancement in fisheries science based on herring. In 1907 J. Hjort proposed applying the approaches of vital statistics (human demography) to fish using rings in the scales of herring at a meeting of the International Council for the Exploration of the Sea (ICES) (Hjort 1908 cited by Smith 1988). Although the idea was not embraced totally by ICES, Hjort and colleagues continued their studies. They noted that the relative number at successive ages varied in both herring and cod, and in 1929 Hodgson (1957) was able to use this method to forecast the impact of the strong 1924 year class on the herring fishery.

Much of the discussion and synthesis of the work of Heincke and of Hjort took place in committees of the newly formed ICES (see review by Stephenson and Clark 2002). The combined impact of the last two advancements was a very large change in thinking—a replacement rather than a modification of ideas—and has been termed by Sinclair (1997) a true paradigm shift. The work originating largely from observation of herring certainly set the course for fisheries science and management which persists to this day. The concept of self sustaining stocks or populations forms the basis of assessment and management, and age-based assessment methods are prominent. Interestingly, the prominence of herring in the further evolution and application of the age-based assessment technique was replaced by groundfish species which seemed to offer better case studies. It is noteworthy that herring assessments of this type often suffer from poor abundance indices and lack of recruitment indices, and actually do not perform very well (Stephenson 1997).

D. Hydroacoustic Estimation of Fish Abundance

Undoubtedly, the development of hydroacoustic estimation of fish distribution and abundance is a major scientific development based on herring research. An interesting and important early study was that carried out with an echo sounder by Skipper Ronald Balls when fishing for herring in the North Sea during the 1930s (Thomasson 1981). Balls, a drifter skipper, undertook pioneering work using a Marconi 424 echo sounder during fishing operations on his own vessel *Violet and Rose*. He kept detailed records of his observations which he published, among other places, in the *ICES Journal du Conseil* (Balls 1948):

It was through a hint from Dr. Hodgson of the Fisheries Laboratory, Lowestoft, that I first became interested in the idea of using the echo sounder for spotting herring shoals, and in 1933 I fitted an instrument to my drifter *Violet and Rose* YH 757.

The seven years' experience with the Echometer in herring fishing, on which this account is based, was gained, not in a research vessel, but under ordinary commercial drifter conditions. My idea was to find out whether or not the machine could increase catching efficiency; therefore my working notes had to be absolutely unbiased, and whereas a properly organized experiment in this field would have had the advantage of more copious and detailed notes, this is perhaps balanced in my amateur attempt by keenness of observation and the length of time covered.

Balls reported that the Echometer worked with "steadily increasing efficiency" for locating herring on 400 nights on the summer fishing grounds but not well in the East Anglian autumn fishery, suggesting "that some change in local conditions on the two fishing grounds is the cause."

This account is of interest not only because it helped establish the validity of hydroacoustics, but also for the role of the fishing industry in the development. Balls addresses this issue in the paper, first talking about his crew, then about the role of the fishing industry in research:

Some of these men had sailed with me for ten years, and would handle a plankton indicator with the same professional discernment as they mended or shot a net. But they still maintained a chilly silence at most "scientific stuff" I mentioned. And it was with a source of secret amusement and some wonder to see one of them calmly watching the sounder as I steered.

For the scientist, there is a source of much material on herring behaviour in the fishermen's knowledge if it could be properly tapped.

This field has developed greatly, especially with technical developments of the past 35 years (including echo integration, improved scientific sounders, development of linearity principle, and studies of target strength), and acoustic surveys are used as the basis for several major herring assessments (e.g., Ona 2001). In a recent development industry (purse seine) vessels are making quantitative surveys using their own equipment (Stephenson et al. 1999, Melvin et al. 2001).

E. Hypotheses on Population Regulation and Abundance

Notwithstanding a rich literature on population regulation and its central role in mathematical population genetics and evolutionary theory, an understanding of the control of abundance has not materialized. (Sinclair 1988, p. 2)

Debate has continued throughout much of the past century both in fisheries and general ecology on a number of issues surrounding the question of population regulation. Sinclair (1988) identifies four components to this issue:

1. What determines the differences between species in population richness?
2. Why are the component populations of a particular species distributed in the observed geographical patterns?
3. What processes control the absolute abundance of the populations (or what controls their means)?
4. What processes control the temporal fluctuations in abundance of the individual populations (or what controls their variances)?

In fisheries, the factors contributing to recruitment variability have been (and still are) a popular topic of research. Herring studies have contributed to the notions of a critical period (Hjort 1914) and to the further development and elaboration of this in Cushing's "match/mismatch" hypothesis (Cushing 1969, 1995). But the major recent advancement in this field is linked explicitly to herring. In the "herring hypothesis" of Iles and Sinclair (1982) observations on herring distribution and abundance are linked to physical oceanographic conditions, as follows: "The number of herring stocks and the geographic location of their respective spawning sites are determined by the number, location and extent of geographically stable larval retention areas."

According to this hypothesis (commonly called the "larval retention hypothesis") the very existence of a population depends on the ability of larvae to remain aggregated. Iles and Sinclair attributed the persistence of herring populations to the presence of locations where the physical oceanography was such that larvae from a spawning group, with the use of specific behavior (such as appropriately timed vertical movement) could maintain an aggregated distribution. Further, Iles and Sinclair argued that population abundance is a function of the physical system underlying larval retention—pointing out that small stocks are associated with small hydrographic features and large stocks with large features. The herring hypothesis addressed both the geographical or spatial basis of herring populations and the control of mean abundance.

Sinclair (1988) extended and generalized the herring hypothesis in his "member/vagrant" hypothesis in an attempt to account for the four questions mentioned above in a wide range of sexually reproducing populations. The herring hypothesis has generated considerable discussion

and research, especially in the area of linkages between fish and hydrographic conditions.

Research in herring continues to contribute to the issue of the structure of fish populations. There has been continued discussion about stock complexity and the exact nature of herring populations, the metapopulation concept, and the relevance of the scale of the population to intraspecific biodiversity and to management (McQuinn 1997, Stephenson 1999, Stephenson et al. 2001, Smedbol and Stephenson 2001).

F. Linking Fisheries Dynamics with Hydrography

Hay et al. (2001) point out that the impact of ocean environment or long term climate change on herring abundance and distribution is a common theme among the world's herring fisheries. Although the mechanisms are not fully understood, the link between fisheries dynamics and hydrography has been clearly established in herring. Zebdi and Collie (1995) demonstrated large-scale coincidence in recruitment patterns of herring throughout the North Pacific in relation to climate forcing. Diagnoses of the major herring stock collapses have pointed not only to the obvious impact of high fishing mortality, but also to periods of low recruitment which are ultimately linked to environmental conditions (Stephenson 1997), and papers at this Herring 2000 symposium (Toresen and Ostvedt 2001, Ivshina 2001), documented the relationship between environmental change and large historical fluctuations in the abundance of the major Norwegian spring-spawning and Sakhalin-Hokkaido stock complexes.

Work on herring has led to major recent advancement in modeling the interaction of larval fish and hydrography (summarized by Heath 1992, Stephenson and Clark 2002), including the first published three-dimensional hydrodynamic model of the advection of fish larvae (Bartsch et al. 1989).

G. Advances in Fisheries Management

The historical importance of herring fisheries led to some of the earliest restrictions in fishing practices. In the northwest Atlantic herring fisheries, for example, there have been closed seasons and restrictions on use of torches to attract herring for well over a century (Scattergood and Tibbo 1959). While there was almost no management restriction of international fisheries involved in the major herring collapses of the late 1960s and early 1970s (Jakobsson 1985), since that time herring fisheries have featured in the development of several aspects of modern fisheries management including early quotas (in both the Pacific [Parsons 1993] and Atlantic [Iles 1993]), minimum landing size, seasonal and area closures, limited entry, and other effort restrictions. More recently, herring fisheries have also been the subject of innovative management schemes involving individual vessel quotas (Stephenson et al. 1993), comanagement and within season management regimes (Stocker 1993, Iles 1993, Stephenson et al. 1999).

The Potential Role of Herring Studies in Future

In spite of severe depletion or collapse of several major herring stocks at some point in the last few decades (see for example Jakobsson 1985, Stephenson 1997) most stocks have recovered and herring remain the subject of major fisheries and of research. Research developments might be expected, as in the past, to reflect the major initiatives and general developments in fisheries science and management modified by specific issues concerning the harvesting and use of herring and local events. Prediction of the future role of herring studies requires anticipation of the future direction of fisheries science and management generally.

Stephenson and Lane (1995) presented a critique of the current state of fisheries science and management. Fishery failures have continued in spite of recent management. There has been the realization that fisheries are complex, multidisciplinary systems requiring a more comprehensive approach to management than has been used to date. At the same time, there have been changing views on management structures and strategies, and evolving international standards. They proposed a more integrated approach involving fisheries science, fisheries management, and techniques from the field of management science in a new “fisheries management science.” According to this view future management should focus on integrated fisheries, rather than just fish populations. It requires a more holistic view, including a combination of biological, social, and economic consideration of the fishery system.

The recent paper by Caddy (1999) also expresses the growing concern at the “uncertain effectiveness of most fisheries assessment and management approaches” and calls for an examination and change in management. The paper points out that recent international agreements provide the basis for construction of appropriate management frameworks. It discusses, among other things, the need for broader, multidisciplinary approaches, consideration of the broader ecosystem, the complications of overlapping jurisdictions, and the consideration of non-exploitive benefits.

I would suggest that herring studies may help to advance scientific thinking at least in the following areas:

The ecology of herring:

- Population structure, especially the nature of complex populations
- Intraspecific biodiversity and sustainability
- Biological reference points for conservation
- Interaction between herring and hydrography

The role of herring in the broader ecosystem:

- Pelagic fishery system structure and function
- Herring as a food item for other species
- Responses of fish populations to toxins and anthropogenic effects

Management of herring fisheries:

- Innovative methods of pelagic fish survey and assessment
- Evaluation of herring fishery systems
- Methods of integrating biological with social and economic aspects
- Increased role of industry in science and management
- Management in accordance with increasing standards implied by recent concepts such as the “precautionary approach” and “convention on biological diversity”

I suggest that herring studies will continue to help define and resolve major concepts in fisheries science. At the moment, this seems to be happening in the area of the structure and regulation of populations. I further suggest that herring studies may help equate fisheries concepts with those of terrestrial ecology, for example in work on complex population structure and metapopulations.

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Temperature Effects on Zooplankton Assemblages and Juvenile Herring Feeding in Prince William Sound, Alaska

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Abstract

The Pacific herring (*Clupea pallasii*) population in Prince William Sound, Alaska, declined in 1993, prompting questions regarding feeding ecology of juveniles and their nursery areas. To study the feeding ecology of juvenile herring we investigated prey availability and herring diets within four nursery areas from May 1996 to March 1998. Quality of nurseries was evaluated with respect to zooplankton community structure and variables affecting that community. Zooplankton distribution was significantly influenced by seasonal and annual environmental factors among bays in Prince William Sound. The diets of juvenile herring were examined and related to prey availability. Prey densities, incidence of feeding, and prey taxa richness increased during the spring months and were minimal during the winter. Prey selection was highest during the winter months when prey availability was lowest. Lower zooplankton densities in the fall of 1997 than in 1996 were correlated to warmer water temperatures. Consequently, feeding by juvenile herring decreased in the fall and winter of 1997-1998. Increased temperatures may be responsible for higher growth rates and higher winter survival of juvenile herring observed that year in Prince William Sound.

Introduction

The importance of successful feeding in early stages of fish development is well documented (Hjort 1914; Lasker 1975, 1978; Houde 1987; Anderson 1988). Food limitation and/or quality can increase density-dependent mortality, thus affecting year-class strength (Walters and Juanes 1993). Fish growth rates affected by prey availability and temperature regulate recruitment by influencing mortality rates (Ware 1975, Shepherd and Cushing 1980, Anderson 1988). Atlantic herring (*Clupea harengus*) are prey-limited in the winter months and must reach a satisfactory level of condition prior to fasting during the winter (Blaxter and Holliday 1963). The juvenile development stage is especially critical for Pacific herring < 250 mm (*Clupea pallasii* Valenciennes 1847), which incur a substantial amount of mortality during their first winter (Paul et al. 1998; Foy and Paul 1999; V.E. Patrick, manuscript in review; K.D.E. Stokesbury, University of Massachusetts Dartmouth, manuscript in review).

We investigated juvenile herring feeding in Prince William Sound (PWS), Alaska, to find possible mechanisms for decreased adult biomass from 1993 to 1999. The cause of the population decline has been speculated to be the result of high incidence of disease in adults (Marty et al. 1998). Disease was likely a mechanism of mortality within the herring population that was directly linked to fish condition and nutritional status (Pearson et al. 1999).

In 1996 and 1997, feeding by juvenile herring and availability of prey varied seasonally among bays in PWS and were at their peak in May (Foy and Norcross 1999a). Prince William Sound zooplankton abundance and biomass were highest from May to July in herring nursery areas (Foy and Norcross 1999b, and manuscript in review). Shifts in prey species composition and decreased prey abundance prior to winter suggested that herring feeding would be minimal (Foy and Norcross, manuscript in review).

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 was significantly correlated to temperature and salinity in the same time period (Foy and Norcross, manuscript in review). The objective of this study was to examine the response of juvenile herring feeding behavior to zooplankton availability and environmental conditions in PWS.

Materials and Methods

Prince William Sound is a large, fjord-type estuarine system consisting of numerous shallow bays, fjords, and tidewater glaciers located on the southern coast of Alaska in the North Pacific Ocean (Niebauer et al. 1994; Fig. 1). We sampled 15 times between March 1996 and March 1998 in two deep

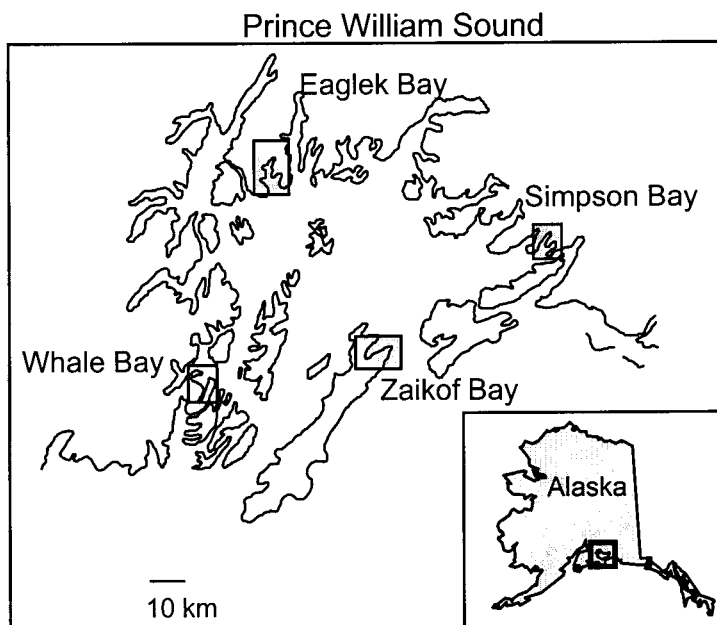


Figure 1. Location of study sites in Prince William Sound, Alaska. Simpson, Eaglek, Whale and Zaikof bays were sampled from 1996 until 1998.

fjords with depths > 250 m (Eaglek and Whale bays) and two estuaries with depths < 100 m (Simpson and Zaikof bays; Table 1). Data from the four bays were pooled for this study due to consistent interannual trends among bays.

Temperature loggers (Onset Computer Corporation) were deployed at a central location in each of the four bays at a depth of 5 m. Temperatures were sampled every 30 minutes from October 1996 until March 1998. Prior to October 1996, at the same sites temperature loggers were deployed, conductivity and temperature at depth (CTD) measurements were taken at 1 m intervals with a SeaBird SEACAT SBE 19 instrument. Tows occurred once per month and were from the surface to 1 m from the maximum depth. Only CTD data from a depth of 5 m were used in this study. An analysis of variance and a post hoc Tukey test were used to test for differences in the average temperature among months (Zar 1996).

Zooplankton were collected by vertical tows ($n = 535$) with a 0.5-m-diameter 300-mm-mesh ring net. Three to five stations located equidistant from the head to the mouth of each bay were sampled to determine small-scale heterogeneity in zooplankton community structure. A net was

Table 1. Numbers of zooplankton tows and juvenile herring stomachs sampled from March 1996 to March 1998 in Prince William Sound.

Month	Number of zooplankton tows	Number of stomachs
Mar 1996	0	335
May 1996	31	391
Jun 1996	34	371
Jul 1996	12	135
Aug 1996	33	257
Oct 1996	35	270
Nov 1996	10	144
Dec 1996	7	80
Feb 1997	12	80
Mar 1997	70	153
May 1997	65	294
Jul 1997	63	267
Aug 1997	62	298
Oct 1997	47	105
Mar 1998	49	102
Total	530	3,282

lowered to 30 m and then retrieved at a constant speed (0.5 m per second) to avoid bias associated with net avoidance. Volume filtered was determined by multiplying the area of the ring net mouth by the depth of the tow. Wire angle was noted in order to maintain consistency on depth sampled between tows and to calculate volume sampled. Samples were immediately preserved in a 10% buffered formaldehyde solution. All taxa from subsamples split with a Folsom splitter were identified to species and life stage when possible.

Juvenile herring schools ($n = 193$) were targeted acoustically and collected with a commercial purse-seine vessel with a 250-m \times 34-m or 250-m \times 20-m, 150-mm stretch-mesh anchovy seine net or a trawl vessel with a 40-m \times 28-m, 150-mm-mesh midwater wing trawl net. Herring < 250 mm were considered to be nonspawning juveniles less than 3 years old (Stokesbury et al. 2000). Between 15 and 20 fish were randomly chosen from each catch and preserved in a 10% buffered formaldehyde solution for at least 24 hours prior to being transferred to 50% isopropanol for diet

analysis. Post-processing analyses included determining taxa richness (number of taxa), prey energy density, and prey selectivity (see Foy and Norcross 1999a, submitted b).

Juvenile herring food preferences were estimated by Chesson's selectivity (a) index (Chesson 1978, 1983):

$$\alpha_i = \frac{r_i / n_i}{\sum_{j=1}^m r_j / n_j}$$

where r_i is the proportion of taxa i in the herring diet, n_i is the proportion of taxa i in the environment, m is the number of prey taxa, and j represents each taxa. Diet proportions, r_i , were calculated for the stomach contents of each fish sampled. Zooplankton proportions in the environment, n_i , were calculated from samples collected from multiple sites within the four bays during the same sampling periods that the fish were caught. The selectivity index ranges from 0 (avoidance) to 1 (selection) and a value of $1/m$ represents neutral selection. An analysis of variance and a post hoc Tukey test were used to test for differences in the average selectivity of all taxa among months (Zar 1996). For selection information of particular prey species see Foy and Norcross (submitted a).

Results

Temperatures 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. 2). Temperatures at 5 m were significantly different among months ($F = 155.4$, d.f. = 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 m was seasonally and interannually variable. Zooplankton density was highest in June 1996 at 3,166 zooplankters per m^3 (Fig. 3). Zooplankton abundance decreased in the winter of 1996-1997 to less than 90 zooplankters per m^3 . Zooplankton densities were significantly higher in May 1997 than May 1996 ($F = 27.2$, d.f. = 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 1996. The zooplankton species richness was highest in May of both 1996 (41 taxa) and 1997 (34 taxa) and lowest in October 1996 (28 taxa) and 1997 (23 taxa; Fig. 4). 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

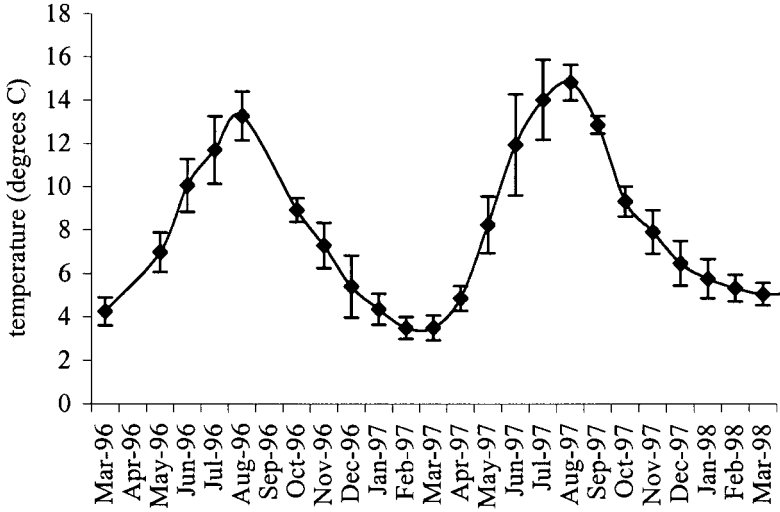


Figure 2. Average temperature at depth of 5 m from fixed temperature loggers and CTD casts in four Prince William Sound bays.

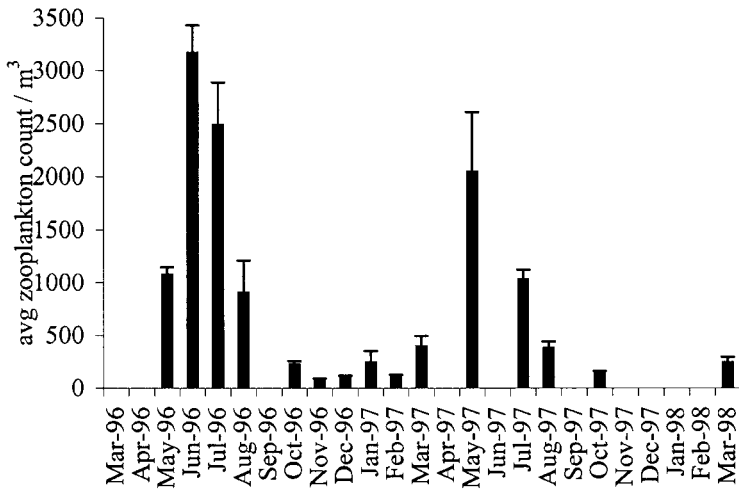


Figure 3. Average (standard error) zooplankton density (count per m^3) for each month from March 1996 to March 1998 in four Prince William Sound bays. Blank spaces represent months that were not sampled.

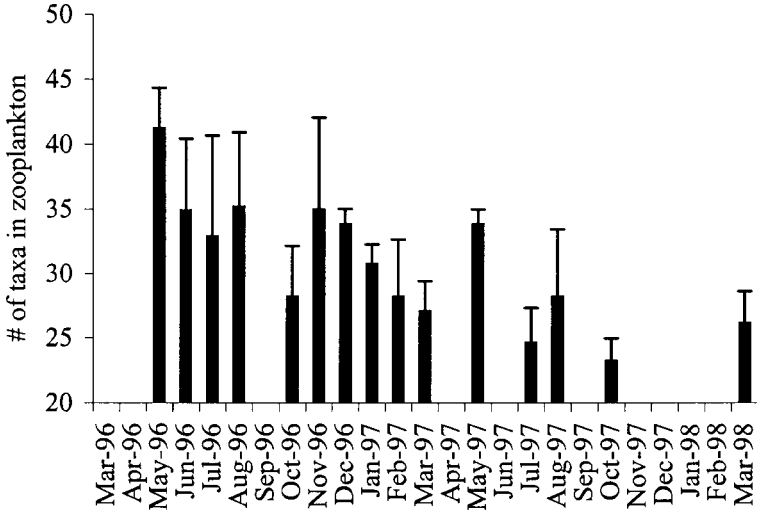


Figure 4. Number of zooplankton taxa collected each month from March 1996 to March 1998 in four Prince William Sound bays. Blank spaces represent months that were not sampled.

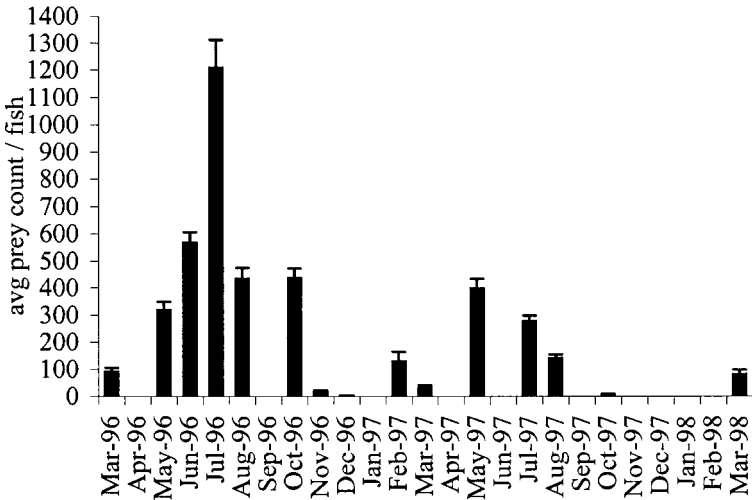


Figure 5. Average (standard error) prey density (count per fish) in juvenile herring diets from March 1996 to March 1998 in four Prince William Sound bays. Blank spaces represent months that were not sampled.

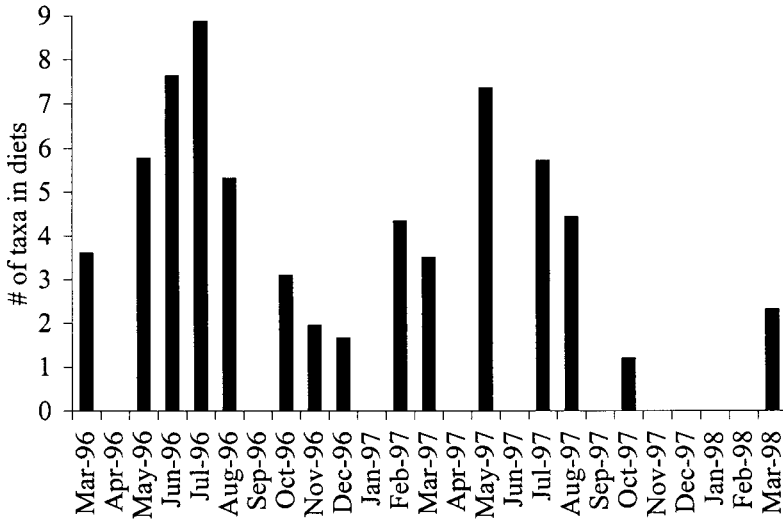


Figure 6. Number of prey taxa in juvenile herring diets from stomachs collected from March 1996 to March 1998 in four Prince William Sound bays. Blank spaces represent months that were not sampled.

1,209 in July and then declined to 3 in December (Fig. 5). Species composition consisted mostly of small calanoid copepods and Cirripedia from March to June whereas Cladocera and Larvacea became important between June and October (Table 2). In 1997 the 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 among 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 ($F = 12.3$, $d.f. = 354$, $P < 0.01$). The number of prey 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. 6). The lowest number of taxa in the diets occurred in December 1996 (2 taxa) and October 1997 (1 taxon). All months in 1997 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. 7). 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

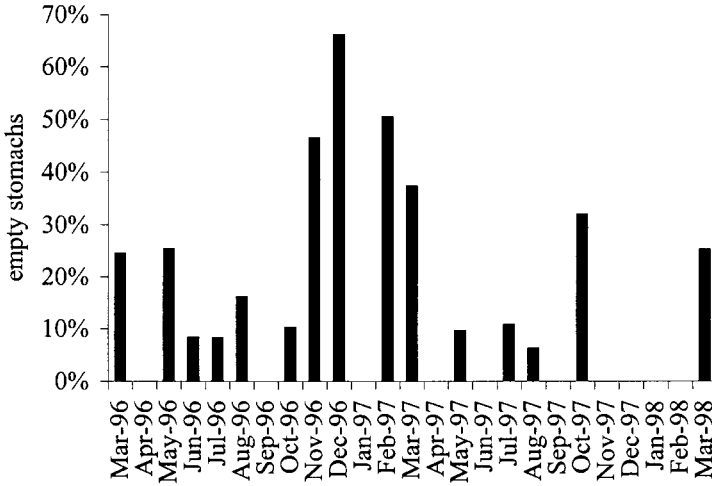


Figure 7. Percentage of juvenile herring stomachs that were empty from March 1996 to March 1998 in four Prince William Sound bays. Empty spaces represent months that were not sampled.

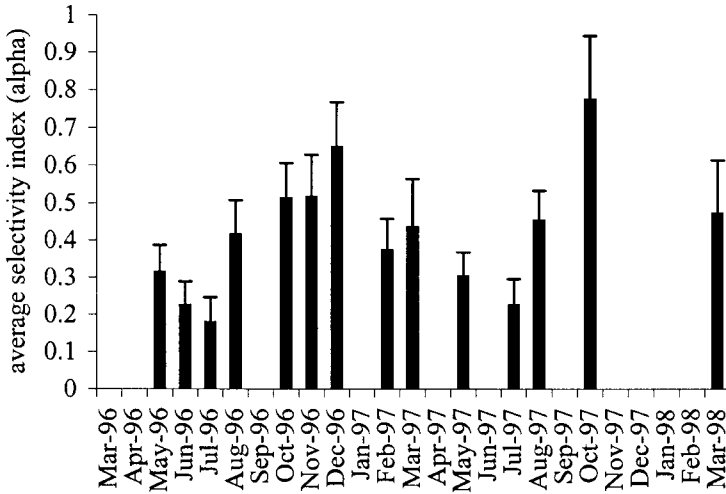


Figure 8. Average (standard error) selectivity index (alpha) of prey in juvenile herring diets from March 1996 to March 1998 in four Prince William Sound bays. Blank spaces represent months that were not sampled.

Table 2. Composition by taxon of stomach contents and number of prey per fish for each month sampled from March 1996 to March 1998. Only values greater than 0.5% of the total sum of taxa abundance from each month are reported.

Tax	1996												1997			1998		
	Mar	May	Jun	Jul	Aug	Oct	Nov	Dec	Feb	Mar	May	Jul	Aug	Oct	Mar			
Arthropoda, Copepoda, Calanoida	38	129	125	740	138	98	2	1	28	9	88	64	72	2	1			
<2.5 mm	4	53	45	9	71	3	1	87	13	103	5							
>2.5 mm					2													
Cyclopoida	1																	
Harpacticoida	29	83	52					1	2		184	11	1	1	61			
Cirripedia cyprid and nauplius																		
Malacostraca																		
Euphausiacea	12	12	4	7		3	1	1	1	3		41	3	3	1			
Mysidacea							1	1										
Amphipoda					29								8					
Branchiopoda																		
Cladocera		11	277	119	22					2		26	9		9			
Decapoda megalops and zoea												29	23					
Ostracoda	1	4	3							4								
Mollusca																		
Bivalvia larvae			23	55	3													
Gastropoda juveniles	0		7	12		3	0											
Amnelida																		
Polychaeta juveniles			4															
Urochordata																		
Larvacea				143	144	326	8		9	2		66	7		2			
Bryozoa																		
Cyphonautes larvae						2							13					
Chaetognatha													1					
Miscellaneous																		
Fish egg (1.0 mm)	3														5			
Fish larvae									1									
Invertebrate egg (<0.2 mm)	1	11	24	109	15	3						3		1	1			

($F = 4.79$, d.f. = 13, $P < 0.01$; Fig. 8). Selectivity index values ranged from 0.17 to 0.65 in 1996 (monthly neutral value range = 0.06-0.14) and from 0.22 to 0.77 in 1997 (monthly neutral value range = 0.04-0.22). Juvenile herring were significantly more selective in October 1997 than in October 1996 ($P < 0.01$).

Discussion

This study analyzed the response of herring feeding behaviors to the availability of zooplankton affected by environmental fluctuations over a short temporal scale. Changes in the interaction between predator and prey communities have been studied in relation to environmental conditions (Ware 1991, McGowan et al. 1998). Seasonal patterns of feeding responses were expected due to increased productivity in Prince William Sound in April (Goering et al. 1973). Feeding by herring during the winter is not well documented (Hay et al. 1988, Rudstam 1988) but is minimal in Prince William Sound (Foy and Paul 1999). Feeding during the summer and fall is then likely critical for energy storage prior to overwintering (Quast 1986, Paul et al. 1998, Paul and Paul 1998a, Foy and Paul 1999).

Zooplankton availability varies seasonally and annually among and within bays in PWS (Foy and Norcross, submitted a). 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 and Norcross, manuscript in review). We encountered large densities of *Paracalanus parvus* in all the bays sampled in the fall of 1997. This species is not usually encountered north of the Queen Charlotte Islands in British Columbia (Giesbrecht 1892 as cited in Cameron 1957, Ermakova 1994), suggesting that higher temperatures observed in 1997 were responsible for its presence in PWS.

The decline in zooplankton abundance observed in the summer of 1997 coincides with increased temperatures that occurred at the same time (Foy and Norcross, submitted a). Temperatures were 2° warmer in the fall and winter of 1997 and may have been instrumental in indirectly reducing zooplankton density and composition due to 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 demand by herring 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.

The reduced incidence of feeding and fewer prey taxa ingested observed in the 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 (Table 2). 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 1998b) 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 (K.D.E. Stokesbury, Center for Marine Science and Technology, University of Massachusetts Dartmouth, 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, we have speculated on how lower prey availability affects the feeding dynamics of juvenile herring. Evidence suggests that environmental conditions may have contributed by affecting the prey 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 in previous years. Although no direct correlations have been made, we can speculate that lowered spring condition factor in herring may have enabled diseases to proliferate in the herring population (Marty et al. 1998, Pearson et al. 1999), ultimately leading to another herring crash in 1999 (Alaska Department of Fish and Game, Commercial Fisheries Division, Cordova, pers. comm.).

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Is the Production of Coho Salmon in the Strait of Georgia Linked to the Production of Pacific Herring?

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Abstract

There was no relationship between the trends of adult coho salmon abundance and adult herring biomass from 1952 until the present. In particular, coho abundance trends increased during the period of extremely low herring biomass in the late 1960s and early 1970s. In contrast, coho abundance was low during the period of high herring biomass in the 1990s.

A change in the ocean environment in the 1990s increased coho marine mortality, possibly due to reduced growth rates of coho during their first marine summer. Juvenile herring and juvenile coho consume some similar prey. Thus, it is possible that when the ocean environment changed in the 1990s, the marine carrying capacity for coho was reduced, and herring affected coho survival by competing for similar prey.

Introduction

In recent years there has been a dramatic reduction in the abundance of coho salmon (*Oncorhynchus kisutch*) at the southern limit of its distribution (Beamish et al. 2000). In British Columbia, the abundance of some stocks is so low that restrictions were placed on all salmon fishing (DFO 1998) contributing to the lowest total commercial catches in history (Fig. 1). Maturing coho traditionally feed on Pacific herring (*Clupea pallasii*), a behavior that does not go unnoticed by recreational fishermen. This predator and prey association is believed by some to be related to the low abundance of coho in the late 1990s.

A recent hypothesis explaining the natural regulation of coho abundance identifies an early marine predation period and summer growth rates as the mechanisms that regulate the final abundance (Beamish and Mahnken 1999). Traditionally, marine survival of coho was seen to be a predation-related mechanism (Pearcy 1992). A diversity of predators spread

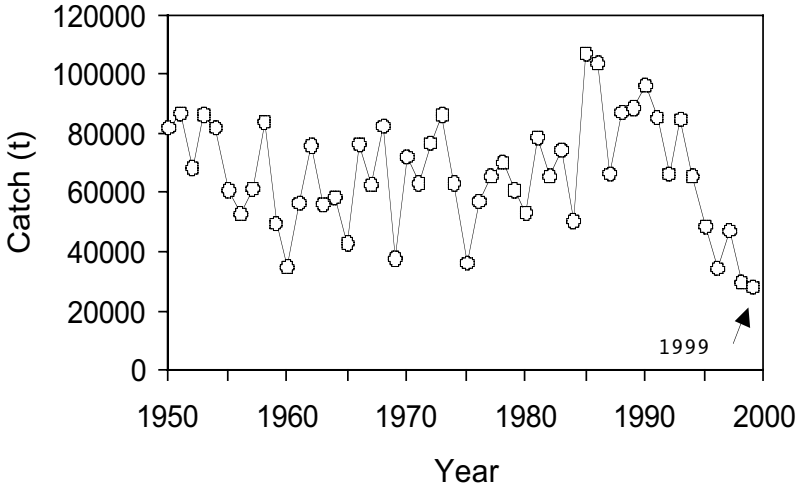


Figure 1. Total Canadian commercial catch of salmon (all species) from 1950 to 1999.

out over the range of coho salmon killed between 85% and 98% of the coho smolts shortly after they entered the ocean. According to a recent hypothesis (Beamish and Mahnken 1999), relatively large numbers of coho escape this early predation period. A second period of major mortality occurs in the fall and is related to the ability of an individual to grow to a critical size. Coho not reaching this critical size are unlikely to survive. This hypothesis links climate and carrying capacity and emphasizes the importance of the availability of preferred food for juvenile coho survival. If the critical size, critical period hypothesis is valid, interspecific competition for food could contribute to the late summer and winter mortalities.

In this study we examine the trends of herring biomass in relation to the total returns of coho to determine if trends in one species are related to trends in the other. There have been some extreme fluctuations in abundances that facilitate the comparison. We use information on the diets of juvenile coho salmon and herring to examine the possibility that Pacific herring in recent years may actually contribute to the decreased marine survival of coho through competition. Because competition may be more critical during some climate regimes than others (Beamish et al. 1999b), we also examine recent changes in abundance to recent climate.

Methods

Herring biomass was determined by constructing year-class strengths using age estimates of spawning fish and estimates of the density of eggs (Schweigert and Fort 1999). Adult coho abundance was reconstructed using a combination of estimates of catch, exploitation rates, marine survivals, and hatchery and wild percentages. From 1952 to 1974, year of entry into the sea (1950 to 1972 brood years), the total commercial catch in the Strait of Georgia was obtained from the Department of Fisheries and Oceans (DFO) catch database which was described by Kuhn (1988). Sport catch from 1953 to 1974 (1952 to 1973 year to sea) was from Argue et al. (1983). We used the 1953 sport catch to represent the 1952 catch. We used exploitation rates of 50% and 75% which approximate the range reported by Argue et al. (1983). Because only a portion of coho remain in the Strait of Georgia, we added the returns from coho that move out of the Strait of Georgia in their first marine year and are fished off the west coast of Vancouver Island (Beamish et al. 1999a) to estimate the total number of adults produced. We used an average percentage of 41.5% from Beamish et al. (1999a) that migrated offshore from 1973 to 1987 (year-to-sea) to estimate the average percentage that moved offshore from 1954 to 1974. The total returns, therefore, were the total catch multiplied by the inverse of the estimated average exploitation rates.

Estimates of total returns from 1975 to 1999 were reconstructed by estimating the total number of hatchery and wild smolts entering the Strait of Georgia and using estimates of their marine survival. Smolt releases from Canadian hatcheries into the Strait of Georgia were obtained from the DFO catch database (Kuhn 1988). Fry releases were not included because marine survival is believed to be very low. The percentage of hatchery and wild coho from 1975 to 1994 was from Kadowaki et al. (1994) and from R.M. Sweeting (manuscript in review) for the years 1996, 1997, and 1998. Marine survival rates for coho were from Beamish et al. (2000). Total returns were the total hatchery and wild smolt production multiplied by the marine survival.

Abundance trends of coho and herring were compared using least squares regression analysis (Zar 1984).

Diet contents of ocean-age juvenile coho and juvenile Pacific herring age 1+ and 2+ were analysed by Haegele (1997) from samples collected in the Strait of Georgia in June-July and August-September, 1990-1993. The results of this study were compared with the diet of juvenile coho collected from the Strait of Georgia in June-July and September of 1997 and 1998 in our study (King and Beamish 1999). The two studies identified prey categories differently. To compare the two studies, we combined the prosobranchs, pteropods, cladocerans, ostracods, barnacles, and larvaceans from Haegele (1997) into the "other" category and combined crab and

shrimp from Haegele (1997) into the “decapod” category. Haegele (1997) reported diet in numbers of prey items in stomachs. The diets from our 1997 and 1998 studies were reported as the percentage volume of each prey category. To compare the diets from the two studies we measured 100 individual widths and lengths of *Pseudocalanus minutus* and *Neocalanus plumchrus*, and 30 widths and lengths of *Euphausia pacifica* to estimate the relative volumes among the three species.

Environmental Indices

Vertical temperature profiles were taken 8-20 times each month in the deep water at the Nanoose Bay Naval Underwater Weapons Test Range approximately midway between the north and south boundaries of the Strait of Georgia. The temperature profiles were collected using several different continuous temperature and depth instruments (for a history of the Nanaimo site, see Beamish et al. 1995).

Fraser River flow data were obtained from the Water Resources Branch, Environment Canada, and are shown as average annual and average April flow in m³ per second (Beamish et al. 1995, 1999a). The annual period is expressed as an anomaly from the long-term mean for both data series. The annual period is from April 1 to March 31.

Results

Adult herring biomass estimates are shown beginning in 1951 (Fig. 2). The abundance prior to the mid-1960s was large, as were the removals from fishing (Fig. 2). Abundance declined in the mid-1960s and the fishery was closed from 1968 to 1971. The abundance of herring increased in the late 1970s and has remained high relative to the levels in 1950s although there were reductions in the mid-1980s. A small fishery started in 1972 and has remained at low levels relative to the 1950s and early 1960s.

The total returns of coho using a 50% exploitation rate resulted in approximately 50% higher total returns from 1952 to 1976 than the 75% exploitation rate, but the trend is identical to the 75% exploitation rate (in Fig. 3 we show only the reconstructed total returns using the 75% exploitation rate). Total returns of coho calculated using a 50% exploitation rate fluctuated from 1952 to 1992 around a mean of 1.6 million coho (S.D. \pm 580,000). Large abundances were indicated for 1969 and 1970, the years immediately following the lowest herring biomass in the time series. The abundance of coho increased in the 1970s and 1980s, prior to the decline in the mid-1990s (Fig. 3A). If we used a 75% exploitation rate prior to 1975, coho abundance increased substantially immediately after the collapse of the herring stocks. Beginning in 1993 there was a dramatic and unprecedented decline in the total coho returns. The decline was precipitous without any of the variation in the abundance trend common in the earlier part of the time series.

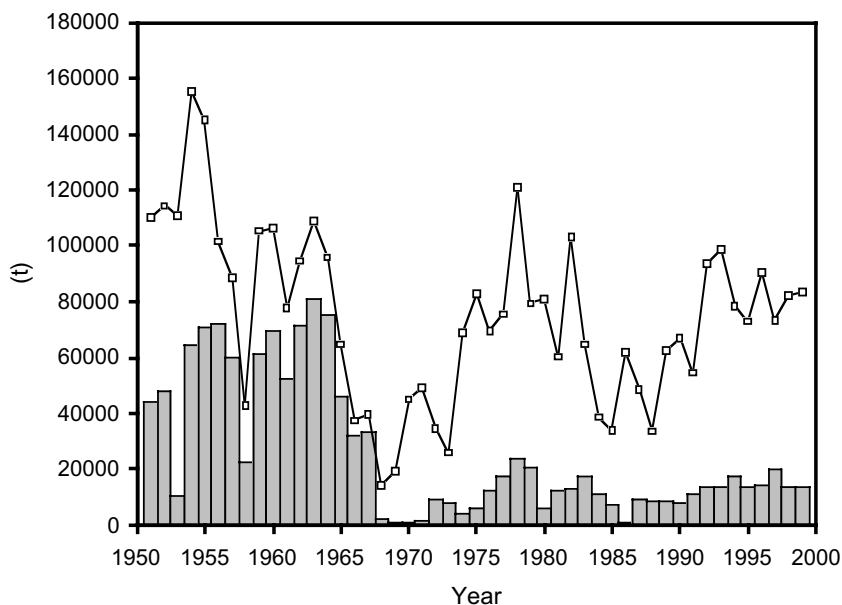


Figure 2. Pacific herring biomass (solid line) and catch (shaded bars) from 1950 to 1999.

There was no change in the releases of hatchery coho but the total number of hatchery and wild coho declined slightly to an average of 16.2 million after 1993 compared to the average up to 1993 of 19.3 million (Fig. 4). The total number of smolts entering the Strait of Georgia increased in the 1980s. Wild smolt abundance declined in the 1990s from an average of 13.6 million from 1975 to 1992 to 7.1 million from 1993 to 1999. Currently the percentage of wild smolts (offspring of naturally spawning parents) is the lowest in the data series.

There was no relationship between the trends in total coho returns and adult herring biomass (Fig. 3). The dramatic decline of herring in the mid-1960s was associated with large and consistent adult coho abundances. The high abundances of herring in the 1990s were associated with dramatic declines in numbers of adult coho. For both the 50% and 75% exploitation rates there was no significant relationship ($P > 0.40$, $r^2 < 0.01$). The use of the range in exploitation rates shows that in general coho abundance fluctuated around the changing trends of herring and not in association with the trends. We lagged the relationship of coho with herring by 1, 2, and 3 years to test the possibility that large herring abundances affected coho adult production through improved escapements and egg to smolt survival resulting in larger coho abundances 1-3 years later. For the 75% exploitation rate the r^2 was < 0.001 , 0.04, and 0.03 for all three

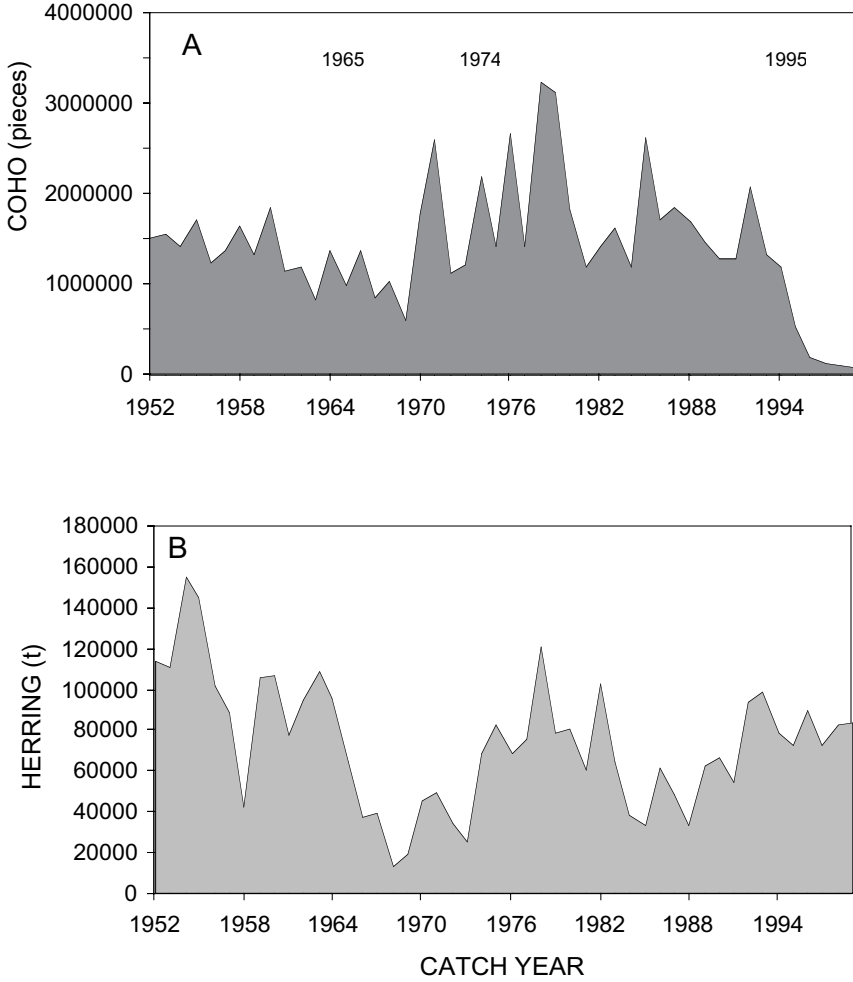


Figure 3. Abundance of adult coho (A) and herring (B) in the Strait of Georgia from 1952 to 1999. Coho abundance (A) was estimated using a 75% exploitation rate from 1952 to 1976.

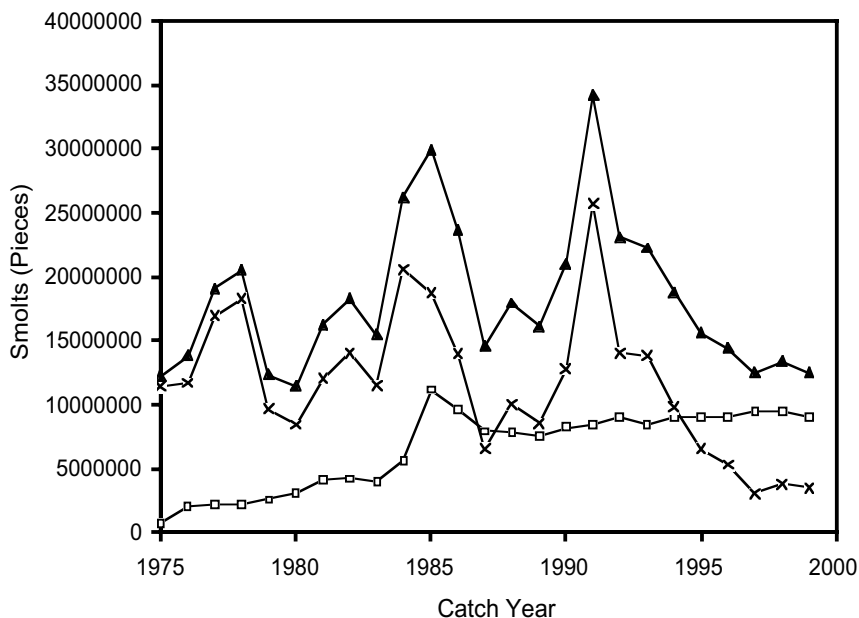


Figure 4. Hatchery (open square), wild (x), and total (triangle) coho salmon smolt abundances in the Strait of Georgia from 1975 to 1999. Wild coho estimates were based on hatchery numbers correlated from percentage of hatchery fish in the catch and known hatchery releases.

lags with P values of 0.99, 0.20 and 0.23, respectively. For the 50% exploitation rate, r^2 was 0.001, 0.025, and 0.011 with P values of 0.78, 0.29, and 0.48 for the three lags. There was an indication of lower coho abundances in the early to mid-1960s, but this was during a period of high herring abundance (Fig. 2) and not at the time of reduced herring abundances in the late 1960s and early 1970s.

The diets of ocean-age 0 coho and age 1+ and 2+ herring (Table 1) show the preference of herring for copepods and small eggs of invertebrates and the preference of coho for small fish as prey. However decapods, amphipods, and euphausiids are prey common to both diets. Based on measurements of length and width of copepods and euphausiids we estimated that 1 euphausiid equals approximately 20 *P. minutus* and 10 *N. plumchrus*. Haegele (1997) reported that invertebrate eggs and copepods constitute approximately 75% of the herring diet (by numbers). Our estimates of the relative volume between copepods and euphausiids indicate that in the summer samples the volume of euphausiids in the stomachs of herring would be approximately 2 times the volume of eggs and copepods combined. In the fall samples, euphausiids account for about half the vol-

Table 1. Diet of age 1+ and 2+ herring and ocean age-0 juvenile coho, 1990-1993 (Haegele 1997) and diet of ocean age juvenile coho, 1997 and 1998 (King and Beamish 1999).

	Herring		Coho		Coho		Coho		Coho		Coho	
	1990-93 Jun-Jul N	1990-93 Jun-Jul N	1997 Jun-Jul Volume (%)	1998 Jun-Jul Volume (%)	1990-93 Aug-Sept N	1990-93 Aug-Sept N	1997 Aug-Sept Volume (%)	1998 Aug-Sept Volume (%)	1990-93 Aug-Sept N	1990-93 Aug-Sept N	1997 Aug-Sept Volume (%)	1998 Aug-Sept Volume (%)
Invertebrate eggs	57,803	75	—	—	12,697	25	—	—	—	—	—	—
Copepods	79,213	428	0	0.34	92,969	248	0.05	0.25	—	0.05	0.25	0.25
Decapods	3,339	12,535	52.65	45.76	543	9,282	1.48	3.68	—	1.48	3.68	3.68
Amphipods	12,027	1,546	0.62	8.86	1,817	10,389	10.79	1.16	—	10.79	1.16	1.16
Euphausiids	26,519	85	1.03	6.39	5,629	2,520	51.72	60.20	—	51.72	60.20	60.20
Insects	22	16	0.1	0.06	232	91	0.5	10.72	—	0.5	10.72	10.72
Teleosts	119	858	45.56	38.45	4	10	35.28	14.05	—	35.28	14.05	14.05
Other	8,594	83	0	0.14	18,222	1,326	0.06	0.42	—	0.06	0.42	0.42
Unknown	—	—	—	—	—	—	0.05	—	—	0.05	—	—
Chaetognaths	—	—	—	—	—	—	—	0.13	—	—	—	—
Total prey (N)	187,636	15,626	—	—	132,113	23,891	—	—	—	—	—	—
Fish examined (N)	1,991	222	272	573	1,375	148	652	733.00	—	652	733.00	733.00
Fish with food (N)	1,235	163	257	545	818	93	548	564.00	—	548	564.00	564.00
Prey per fish (N)	152	96	—	—	162	257	—	—	—	—	—	—

A dash indicates no data.

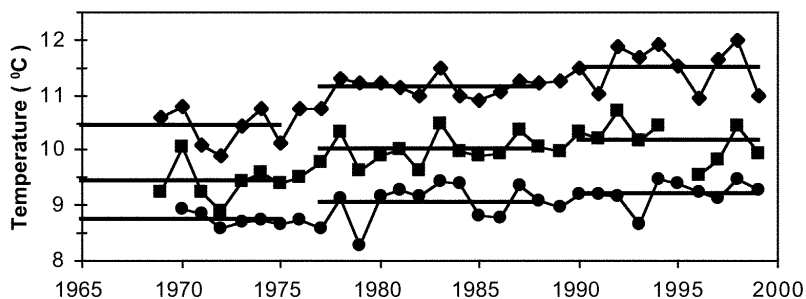


Figure 5. Central Strait of Georgia temperatures ($^{\circ}\text{C}$) from 1969 to 1999. Temperatures are shown for surface, 10 m, and bottom (395 m). Data from 1969 to 1989 from Fissel et al. (1991), and from 1990 to present courtesy of W. Funk (Nanoose Bay Naval Base).

ume of copepods and invertebrate eggs. As euphausiids, decapods, and amphipods are common items in the diets of herring and coho, a large portion of the diet of the two fishes is similar. The diet composition of coho in our study was quite similar to the diets observed by Haegele (1997, Table 1). In both studies, decapods, amphipods, euphausiids and fish (teleost) accounted for most of the diet, confirming that the data from the earlier study can be combined with our study to show that the two species overlap in their feeding habitats.

Climate Indicators

In this report we show three indicators of climate and climate change in the Strait of Georgia. There are other indicators of large-scale climate change events in the subarctic Pacific (Mantua et al. 1997, Beamish et al. 1999b, McFarlane et al. 2000a) which indicate trends in the climate and ocean environment changes in 1977 and 1989.

Temperature on the surface, at 10 m, and near the bottom has increased since the 1970s (Fig. 5). Surface temperatures averaged almost 1°C higher in the 1990s than in the early 1970s. The increases in temperatures are shown as step increases because in previous reports we showed that significant step-ups in surface temperature occurred (Beamish and Neville 1999). Increases in temperature occurred at other depths although the increases were smaller than at the surface.

Total discharge from the Fraser River increased from 1950 to 1976, decreased from 1977 until 1995, and in recent years has undergone extreme fluctuations (Fig. 6A). In the 1990s the spring freshet began earlier. April flows increased in recent years (Fig. 6B). We used the date at which the average March flow doubled as an indicator of the onset of the spring flows. In the 1980s, the average March flow was $1,012 \text{ m}^3$ per second. In April, during the 1980s this value doubled by April 19 (on average). From

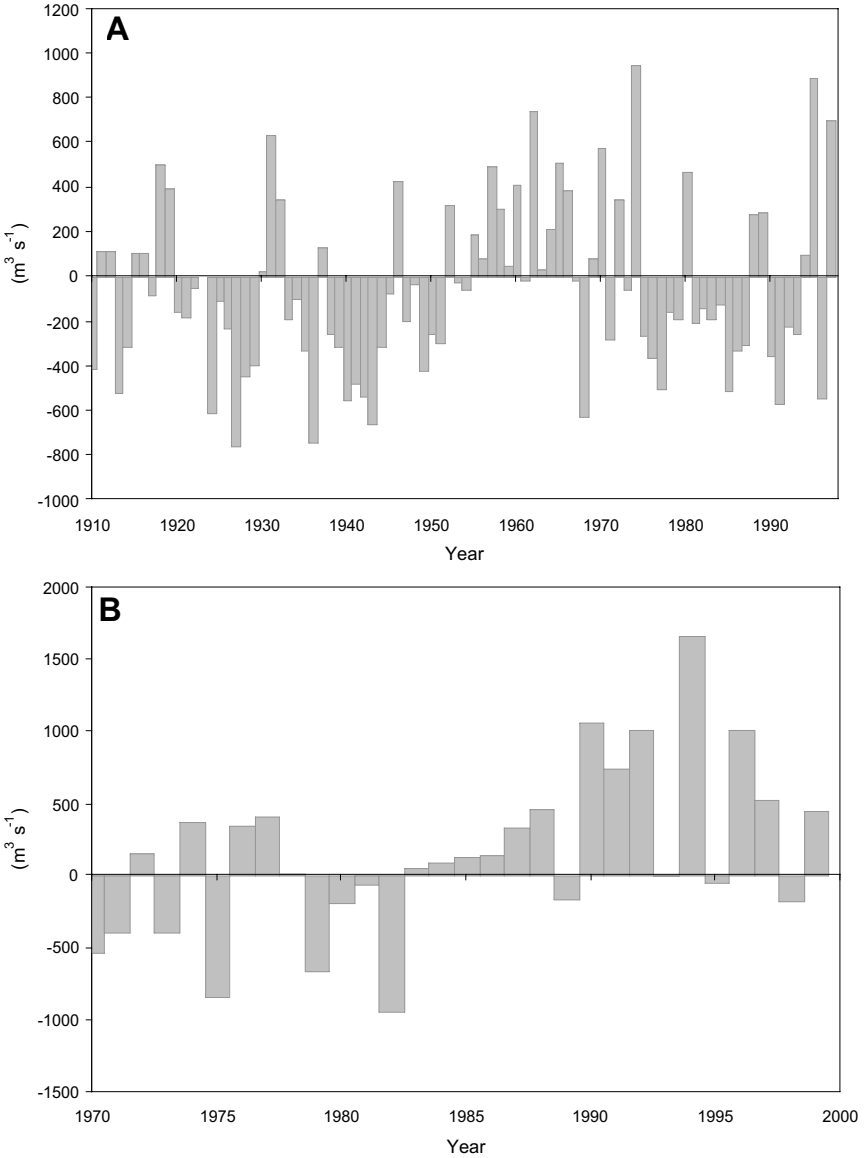


Figure 6. Flow rates from the Fraser River at Hope (Water Resources Branch, Environment Canada) shown as anomalies from a long-term mean. (A) Average annual (April-March) flow (m^3 per second) from 1910 to 1999. (B) Average April flow (m^3 per second) from 1970 to 1999.

1990 to 1997 the March average flow was 1,044 m³ per second. The doubling of this value was reached an average 10 days earlier (April 9). In 1998 the March value doubled on April 24, and in 1999 on April 19.

Discussion

Coho in their second marine year feed extensively on herring (Healey 1976). Because of this preference, there is concern that catching too many herring will affect coho survival. We show that in the Strait of Georgia there is no relationship between the 50-year trends in herring and adult coho abundance. From 1967 through to 1971 when the herring population collapsed there was no impact on coho abundance. These results are consistent with the findings of Healey (1976), who concluded that the collapse of the herring stocks in the 1960s did not affect the production of any of the salmon species. A reverse situation occurred in the 1990s when herring abundance was high and coho abundance declined dramatically. Despite the large herring abundance, a herring fishery, and a relatively large and constant supply of coho smolts, the abundance of coho declined to historical low levels.

The testing of the abundance trends showed no correlation, but it is important to note that our time series for coho is a reconstruction based on reported catches, estimated hatchery and wild percentages, and two average exploitation rates that represented the possible ranges at a period when catch data are missing or approximate. There are other reconstructions of total coho returns for the Strait of Georgia stocks. The total returns estimated by Argue et al. (1983) are lower than ours from 1952 to 1976. They identified a decrease in coho returns in the early 1960s, and a return to higher abundances in the late 1960s through to the mid-1970s. Despite being lower, the Argue et al. (1983) estimates corroborate our observations that coho abundance increased during the low biomass period for herring in the late 1960s and early 1970s. Another time series of total coho returns is from 1984 to 1999, by Holtby et al. (2000). Their estimated total returns for the late 1990s are about 3 times larger than ours. However, both time series show that total coho returns were extremely low, relative to total returns in the 1980s and early 1990s. Thus both reconstructions show a dramatic decline in coho production at a time when herring biomass was at very high levels.

The decline in coho abundance was associated with a decline in marine survival from approximately 15% or higher in the 1970s and 1980s to less than 2% in the late 1990s (Beamish et al. 2000). Over the period of decline, smolt releases from hatcheries remained constant but there was a decline in wild smolt production. The decline in coho survival was synchronous throughout the southern distribution of coho, indicating that the decline resulted from a common factor (Beamish et al. 2000). A logical factor would be climate. There was a shift in the climate and ocean state in 1989 (Beamish et al. 1999b, Watanabe and Nitta 1999, McFarlane et al. 2000) and we identify a change at about this time in our study. The de-

cline in coho in the 1990s appears to be associated with a less favorable marine habitat or a reduced capacity of the marine ecosystem resulting in reduced growth of coho in the summer of their first marine year (Beamish and Mahnken 1999). If this critical size, critical period hypothesis is valid, species competing for prey of coho could reduce their growth rate. The changes after 1989 were responsible for a new behavior in which virtually all coho left the Strait of Georgia (Beamish et al. 1999a). The response was related to an increase in sea level height and changes in surface winter salinities (Beamish et al. 1999a). This change is also associated with an earlier movement of copepods into the surface layers (Bornhold et al. 1998) and improved survival of larval hake and herring (Beamish and McFarlane 1999).

Invertebrates such as euphausiids, decapods, and amphipods common to herring diets were also an important part of the coho diet. Juvenile herring were an important part of the diet of juvenile coho. If the amount of growth over the first marine summer is related to brood year strength, and herring are an important prey, why is there no evidence of a relationship between herring abundance and coho abundance? Herring abundance was high during the 1990s and we know that relatively large numbers of coho juveniles survive until the fall of the first ocean year (Beamish et al. 2000). Perhaps coho direct their feeding during the first marine summer toward invertebrates such as euphausiids and feed opportunistically on juvenile herring. Juvenile herring would be both prey and competitor and the importance of this competition would be related to the favorability of the oceanic conditions.

The Strait of Georgia was warmer in the 1980s and 1990s, and the surface waters were fresher in the winters in the 1990s (Beamish et al. 1999a). There also were substantially more competitors such as herring and hake (McFarlane et al. 2001) and chum salmon (*O. keta*) (Beamish and Folkes 1998). The warmer ocean required that coho consume more food to maintain metabolic requirements (Jobling 1994). We speculate that it is the availability of preferred invertebrate prey that is important for coho growth rates during the first marine summer. Factors that reduce the availability of such prey contributed to the increased marine mortality of coho. While this is speculation, our point is that it is clear that looking at the dynamics of only a single species overlooks the ecosystem impacts that influence the abundance trends of the species. All species compete for habitat and natural processes provide the selection that limits the size of their populations. Human intervention into this natural process should be assessed more as an aggregate impact than a single species impact.

Acknowledgments

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Common Factors Have Opposite Impacts on Pacific Herring in Adjacent Ecosystems

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Abstract

The biomass of Pacific herring off the west coast of Vancouver Island was low in the 1990s as a result of Pacific hake predation. The biomass of Pacific herring in the Strait of Georgia was high in the 1990s despite large biomasses of Pacific hake. The Strait of Georgia is connected to the west coast of Vancouver Island by the Juan de Fuca Strait and herring move freely between the two areas. The opposite trends in the biomasses of herring in these two adjacent ecosystems were a consequence of different restructuring of the ecosystems in response to a common climate-related change.

Introduction

There is evidence that climate and climate change profoundly impact fish populations (Kawasaki and Omori 1988, Beamish and Bouillon 1993, Mantua et al. 1997, Beamish et al. 1999b, Clark et al. 1999, McFarlane et al. 2000). For example, Pacific halibut (*Hippoglossus stenolepis*) abundance follows trends related to climate and ocean conditions that persist on a decadal time scale (McCaughran 1999). There are other examples of synchronous changes in the dynamics of species that are linked to large-scale changes in climate ocean conditions (McFarlane et al. 2000). Evidence is accumulating to show that fish dynamics and environmental conditions can be stable on decadal scales (regimes), and shift abruptly from one steady state to another (Isaacs 1975, Beamish et al. 1999b). Regime shifts in 1925, 1947, 1977 (Francis and Hare 1994, Minobe 1997, Beamish et al. 1999b), and 1989 (Beamish et al. 1999b, McFarlane et al. 2000) have been identified. An important theoretical consideration in the regime concept is that the responses of fish populations can be specific to particular ecosystems (Beamish et al. 1999b) rather than specific to a surrogate such as temperature.

Regimes and regime shifts could be an important factor regulating the abundance of Pacific herring (*Clupea pallasii*). This contrasts with the view that the abundance of herring stocks is controlled primarily by fishing. In this study we compare the response of herring stocks in the Strait of Georgia and off the southwest coast of Vancouver Island (La Perouse Bank area) to climate-related changes that occurred in their ecosystems, particularly after 1989. Proving this relationship requires a better understanding of ecosystem dynamics as well as an awareness that past interpretations probably were an oversimplification of the population dynamics of herring. We can, however, show that an explanation used to explain low herring abundance in one area can be applied to an adjacent ecosystem to explain high herring abundance.

Materials and Methods

Study Area

The Strait of Georgia is located between Vancouver Island and the British Columbia mainland (Fig. 1). It is a semi-enclosed sea connected to the Pacific Ocean in the north by Johnstone Strait and in the south by Juan de Fuca Strait. For a detailed description see Thomson (1981) and Beamish and McFarlane (1999).

The La Perouse Bank region (Fig. 1) is located off the west coast of Vancouver Island, at the northern terminus of the coastal upwelling domain (McFarlane et al. 1997). This production system is characterized by a relatively narrow continental shelf, intense wind-induced upwelling in summer, and high phytoplankton and euphausiid biomass.

Key Species

In the Strait of Georgia echo-integration surveys were conducted on spawning concentrations of Pacific hake (*Merluccius productus*) during February–March 1981, 1988, 1993, and 1996. Echo-integration was conducted on predetermined parallel tracklines spaced 6 km apart. Calibrated acoustic systems were used on all surveys. Fishing was used to identify targets and echograms were examined to eliminate bottom interference, plankton concentrations, and nontarget fish. Standard target strength length relationships were used to convert acoustic backscatter to fish density. Geographic information system (GIS) procedures were used to convert fish density measurements to the biomass estimates reported in Kieser et al. (1999). Abundance in 1977 was estimated using biomass at age data (Saunders and McFarlane 1999) from 1981 to 1983 and removing the contribution of the strong 1977 and 1978 year classes.

Echo-integration surveys have been conducted along the U.S. and Canadian west coasts on a triennial basis since 1977 (Wilson and Guttormsen 1997). The procedures were similar to the Strait of Georgia procedures. The surveys are conducted during summer when hake distribution is at the northern limit. In addition, echo-integration surveys have been con-

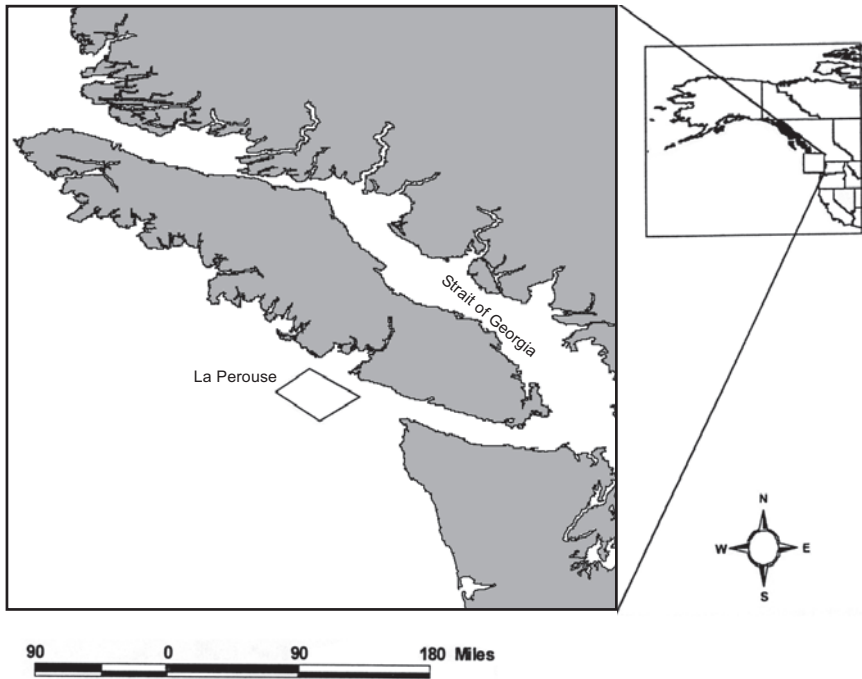


Figure 1. The location of the Strait of Georgia and the La Perouse area off the west coast of Vancouver Island.

ducted annually since 1990 off the west coast of Canada during August. Hake biomass in the La Perouse area was also estimated using midwater trawl surveys for 1970, 1974, and 1975 (Ware and McFarlane 1995).

Pacific herring stock biomass in the Strait of Georgia and off the west coast of Vancouver Island was obtained from Schweigert and Fort (1999) using two assessment models: an age-structured model and an escape-ment model.

Biological Data

Biological data were collected from hake and herring captured during commercial and research trawling operations in the Strait of Georgia and off the west coast of Vancouver Island. Fork length, sex, and maturity were recorded for all hake sampled and paired otoliths were collected for age determination from fish from selected trawl sets.

Stomach contents for all hake sampled were identified to lowest taxonomic group possible, and volume (cc) estimated for each prey item. All herring were counted and where possible, measured for length. In the

Strait of Georgia, stomach contents were analyzed for 3 years in the 1970s, 3 years in the 1980s, and 5 years in the 1990s. Off the west coast of Vancouver Island stomach contents were analysed in 1983 and 1985 to 1997.

Environmental Data

In this report we use water temperature and the Aleutian low pressure system as climate indicators. We chose the Aleutian low pattern because it is the dominant winter atmospheric feature, and is related to wind circulation patterns, ocean circulation patterns, and temperatures. For a detailed description of climate change in the subarctic Pacific see Beamish et al. (1999b), Mantua et al. (1997), and McFarlane et al. (2000).

In the Strait of Georgia vertical temperature profiles were taken 8-20 times each month in the deep water at the Nanoose Bay Naval Underwater Test Range approximately midway between the north and south ends of the Strait of Georgia. The temperature profiles were collected using several different continuous temperature and depth instruments (for a history of the Nanoose site, see Beamish et al. 1995). Sea surface temperature data from the west coast of Vancouver Island were accessed through the Institute of Ocean Sciences website (<http://www.ios.bc.ca/ios/osap/data>). Temperature data at depth were obtained from R.E. Thomson (Institute of Ocean Sciences, Sidney, B.C.).

We obtained the Aleutian Low Pressure Index (ALPI) from the Pacific Biological Station website (<http://www.pac.dfo-mpo.gc.ca/sci/sa-mfpd/english/clm-indxl.htm>) which has been updated from Beamish et al. (1997).

Data Analysis

We used intervention analysis, which accounts for unusual events in a time series that modify a Box-Jenkins ARIMA (Auto Regressive Integrated Moving Average) model (Box and Jenkins 1976, Noakes 1986), to test for significant regime-shift signals (1977 and 1989) in the sea surface temperature index (SST) in both areas and the ALPI. Interventions in the form of abrupt steps are introduced to the model and their significance tested as a change in mean in the time series at that point.

We used ANCOVA with stepwise regression analysis to test for the best description of the change in female hake size at age 4. We used 1993, 1994 and 1995 as years to describe a possible change in mean size. ANCOVA tested for a change in mean size (intercept) in 1993, 1994, or 1995 and for differences in the rate of change (slope) of size before and after those shift years.

Results

Strait of Georgia

From 1977 to 1980 the biomass of Pacific hake increased from approximately 60,000 t to 80,000 t (Fig. 2a). The estimates in 1988 and 1993

indicate a higher abundance than in 1977 with 1993 as the largest biomass. The 1981 and 1988 estimates were acoustic estimates. Swept volume estimates were similar (Shaw et al. 1990). There was a small fishery throughout the study period (average 3,200 t annually) with maximum removals of 11,859 t in 1995 (Saunders and McFarlane 1999).

There were large decreases in the size of age 4 hake during this period (Fig. 3a). From 1979 to 1981, the mean size of 4-year-old fish declined 7.0% in length and 16.3% in weight. The next shift in size trends occurred in the mid-1990s. ANCOVA identified a change in mean size in 1994 as the best descriptor for the change in hake size at age 4 ($T=6.84$, $r^2=0.72$, $P<0.0001$).

The new mean was 13.0% lower in length and 51.2% lower in weight. The sizes from 1995 to 1998 remained about constant (Fig. 3a). The change in size was apparent in the mean length of all age groups in the commercial fishery averaged for the mid-1980s and mid-1990s (Fig. 4a).

Annual catches of herring averaged 13,300 t from the mid-1970s to the mid-1980s, and 14,400 t in the 1990s (Fig. 5a). The abundance of herring increased abruptly from 1974 to 1978 to levels approaching those that supported the high catches of the mid-1950s to 1960s (Schweigert and Fort 1999). Despite an almost constant removal since the mid-1970s (Fig. 5a), abundance declined in the mid-1980s to low levels of 40,000 to 50,000 t and then increased to approach historical high levels (mean = 90,000 t) in the early 1990s (Fig. 6a). This high abundance was maintained throughout the 1990s by above-average survival of year classes in 1989, 1990, 1991, 1993, 1994, and 1995 (Schweigert and Fort 1999).

Herring was a common prey item in the diet of Pacific hake in the Strait of Georgia in the 1970s and 1980s, but disappeared completely from the diet in the 1990s (Table 1). D. Hay (Pacific Biological Station, Nanaimo, B.C., pers. comm.) found a similar percentage of herring (13%) in hake diets in a 1983 study. In another study (Shaw et al. 1985), it was shown that hake outside the main concentrations and closer to shore, had the highest percentage of herring in their diets. In March and April 1981, hake were estimated to consume 4,000-8,000 t of herring (McFarlane and Beamish 1985) at a time when the biomass of herring was estimated to be 60,000 t, and the fishery took 12,000 t (Schweigert and Fort 1999).

West Coast of Vancouver Island

Hake abundance in the La Perouse area has fluctuated around 210,000 t since 1977 (Fig. 2b). However, the total abundance of hake off the west coast of Canada increased dramatically in the 1990s associated with an increased migration north of the LaPerouse area beginning in the early 1990s (Fig. 2b). There was no trend in size at age during the 1980s or 1990s (Fig. 3b) and the mean length in the commercial fishery has not changed (t -test, $P>0.05$) (Fig. 4b).

Levels of catch of Pacific herring averaged 16,000 t in the late 1970s and about 5600 t since (Fig. 5b). Herring abundance in the early 1970s

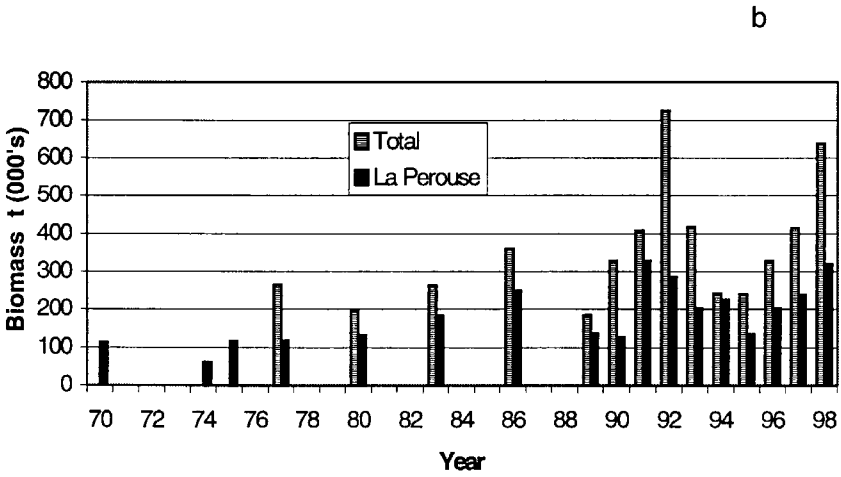
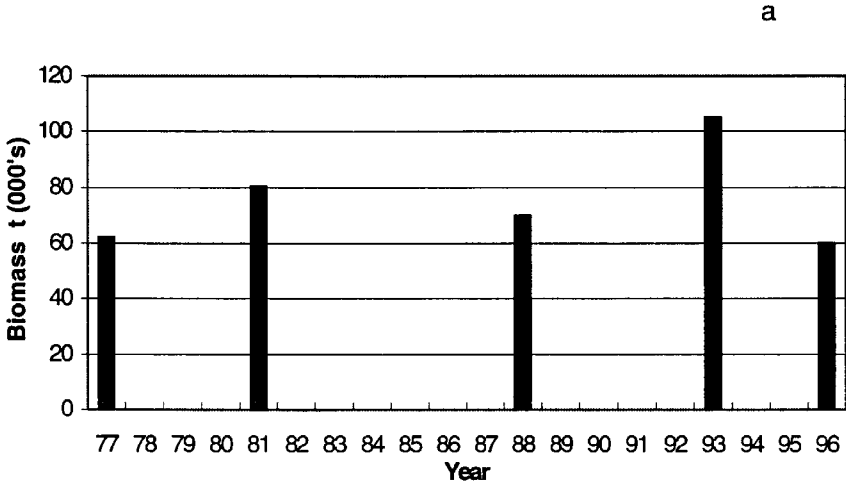


Figure 2. Biomass estimates (t) of Pacific hake in (a) the Strait of Georgia and (b) the La Perouse area.

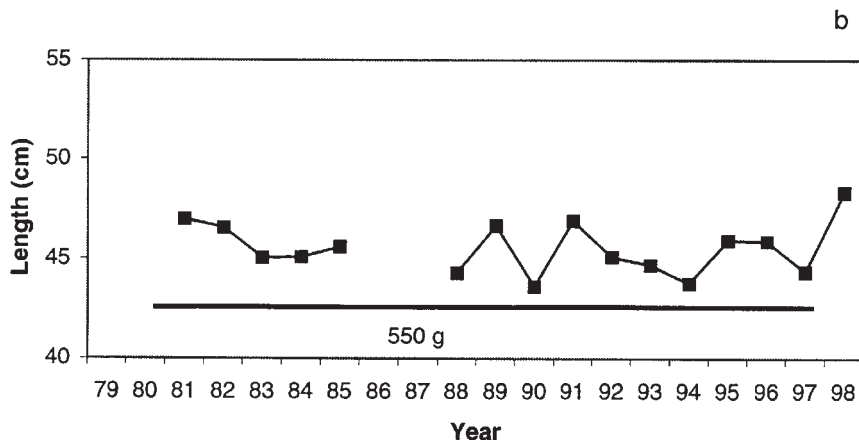
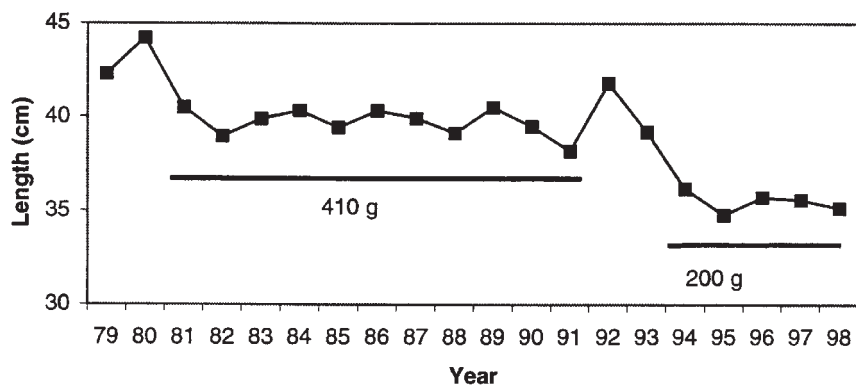


Figure 3. Trends in mean length and weight at age 4 for female Pacific hake from (a) the Strait of Georgia (1979-1998) and (b) the La Perouse area (1981-1998).

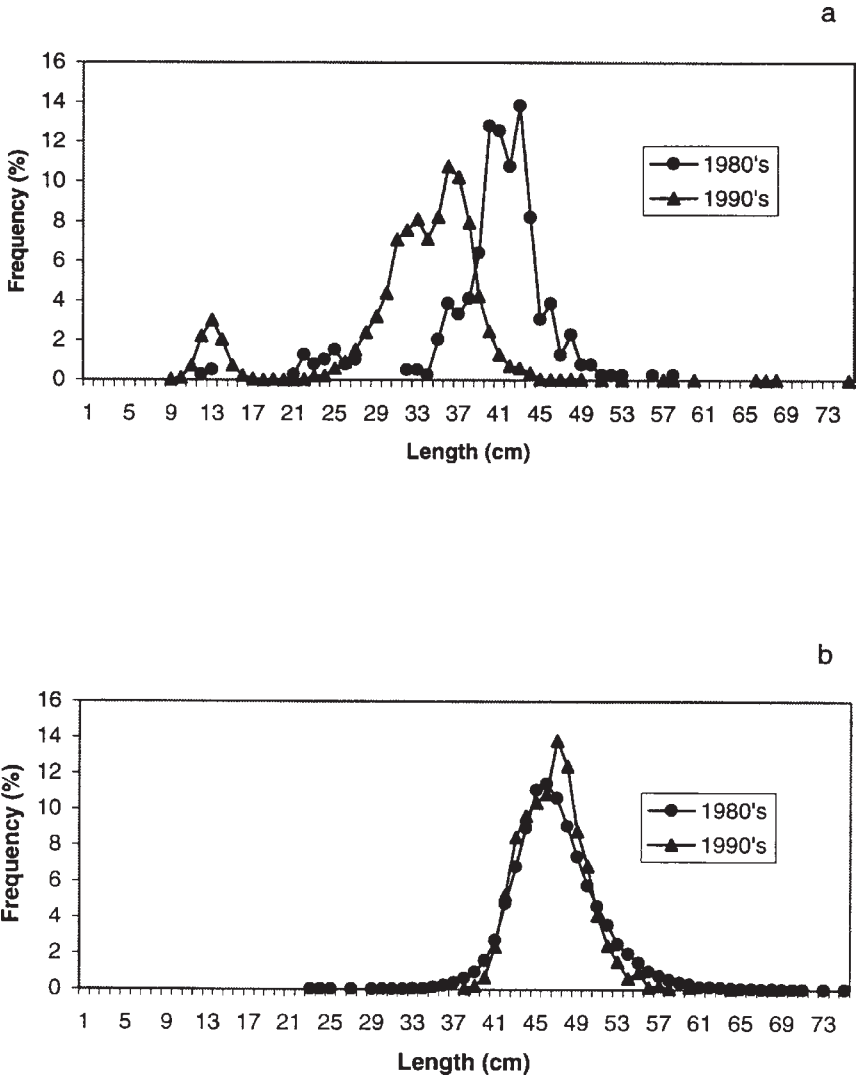


Figure 4. Mean size of Pacific hake in the commercial fishery during the 1980s and 1990s from (a) the Strait of Georgia and (b) the La Perouse area.

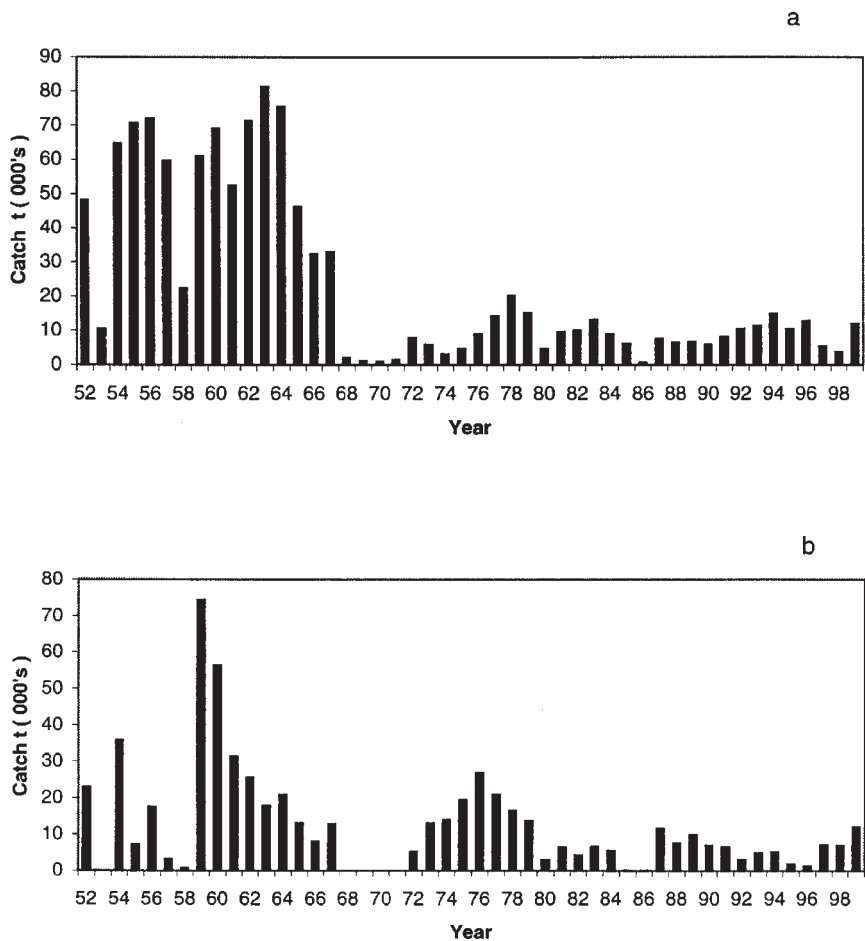


Figure 5. Annual catch (t) of Pacific herring (1952-1999) from (a) the Strait of Georgia and (b) the west coast of Vancouver Island.

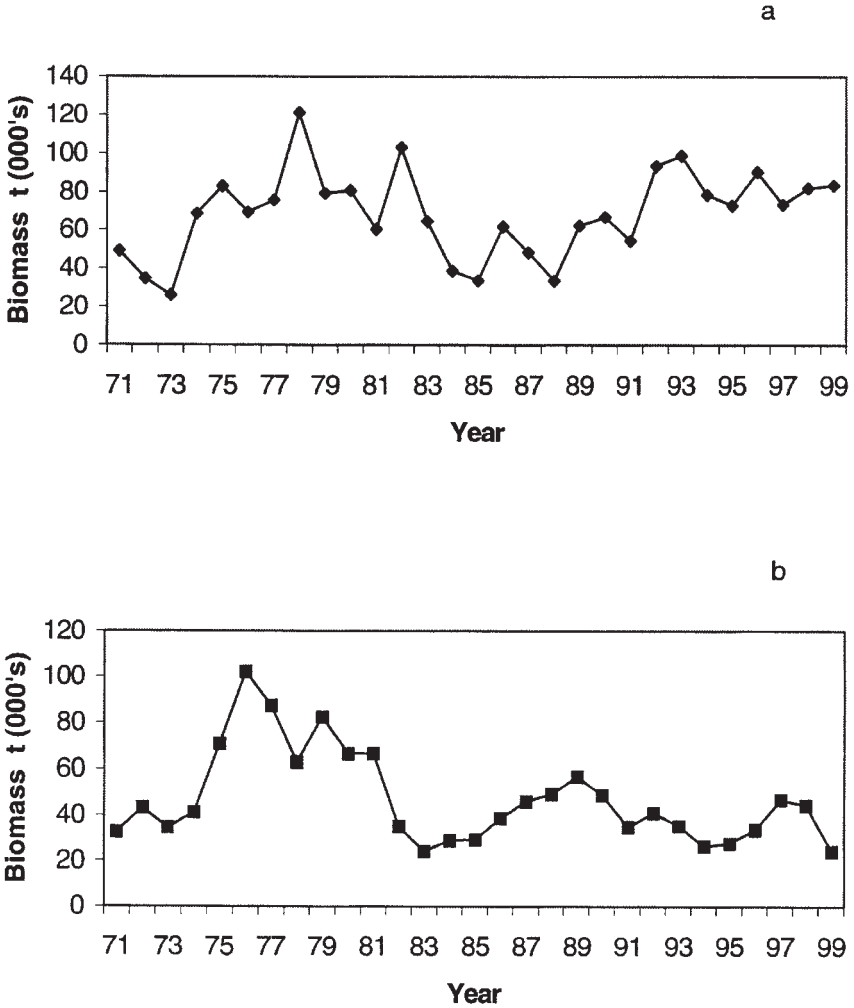


Figure 6. Biomass estimates (t) of Pacific herring in (a) the Strait of Georgia and (b) the west coast of Vancouver Island.

Table 1. Percentage of herring (volume) in the diet of hake in the Strait of Georgia.

Year	Month	Number sampled	% herring in diet
1974	Feb	601	10.0
1975	Jan-May	3,293	23.3
1976	Jan-May	2,552	9.9
1981	Feb-May	2,072	5.7
1983	Feb and Apr	2,597	30.3
1985	Mar	607	2.1
1995	Feb-Apr	572	0.0
1996	Feb-Mar; Oct-Nov	570	0.0
1997	Feb; Sep-Oct	447	0.0
1998	Feb-Mar; Sep	307	0.0

ranged from 42,963 t to 102,160 t (1972-1976) and declined to approximately 30,000 t in the mid-1980s and has fluctuated between 24,000 t and 57,000 t since. Since 1990 the mean annual biomass decreased to 35,000 t (Fig. 6b). The percentage of herring in the stomachs of hake ranged from 9.2% to 58.7% from 1983 to 1997 (Table 2).

Environment

Throughout the study period the surface, 10 m, and bottom temperatures in the Strait of Georgia increased (Fig. 7a). We showed the increases as step increases. Intervention analysis indicated these stepwise increases were significant (Beamish et al. 1999b). The average surface temperature changed from 10.45°C prior to 1977 to 11.3°C in the 1980s and 11.7°C in the 1990s (Fig. 7a). The sea surface temperature (Fig. 7b) in the La Perouse area showed a significant increase in mean trends after 1977 and another increase (not significant) after 1989 (Beamish et al. 2000).

The Aleutian low pressure index (ALPI) showed a significant upward shift ($P < 0.05$) after 1977 followed by a decline after 1989 (Fig. 8). Because the ALPI is a standardized anomaly and is a measure of the area of the winter low pressure (December to March), an upward shift in the index is an indication that the area of low pressure has increased. After 1989 the area of low pressure is about average for the time series. The Aleutian low is the dominant climatic feature in the North Pacific in winter. Its intensity and location determines atmospheric and ocean circulation patterns and temperatures (McFarlane et al. 2000). These basinwide changes have consequences for coastal areas like the west coast of Vancouver Island and the Strait of Georgia.

Table 2. Percentage of herring (volume) in the diet of hake off the west coast of Vancouver Island (La Perouse).

Year	Month	Number sampled	% herring in diet
1983	Jul-Aug	1,377	57.0
1985	Jul-Aug	820	40.0
1986	Jul-Aug	2,386	9.2
1987	Jul-Aug	1,824	28.0
1988	Jul-Aug	3,219	58.7
1989	Jul-Aug	1,148	11.8
1990	Jul-Aug	998	30.5
1991	Jul-Aug	1,105	25.8
1992	Jul-Aug	1,663	36.2
1993	Jul-Aug	953	58.5
1994	Jul-Aug	907	18.6
1995	Jul-Aug	916	39.2
1996	Jul-Aug	836	26.8
1997	Jul-Aug	462	17.3

Discussion

Pacific hake is the dominant resident species in the Strait of Georgia (Beamish and McFarlane 1999). Off the west coast of Vancouver Island, in the La Perouse Bank area, Pacific hake are part of a large migratory stock which, during the 1960s, 1970s, and 1980s spawned off Baja California in the winter and migrated north to summer feeding grounds (Francis 1983). Prior to 1990, approximately 25-30% of the mature biomass moved into Canadian waters. Since the early 1990s approximately 40% of the stock has been present in the Canadian zone (Wilson and Guttormsen 1997, Wilson et al. 2000).

The fishery for Pacific herring dominated catches in the Strait of Georgia and off the west coast of Vancouver Island from the early 1950s until the mid-1960s (Schweigert and Fort 1999). The fishery collapsed in the mid-1960s and was closed from 1967 to 1971. The fishery reopened in 1972 and has been less than 15% (Strait of Georgia) and 30% (west coast of Vancouver Island) of the previous fishing.

Herring are now at high levels of abundance in the Strait of Georgia and low levels of abundance off the west coast of Vancouver Island. Predation on herring by hake off the west coast of Vancouver Island increased in direct relation to the increased northward migration of Pacific hake (Ware and McFarlane 1995). The warmer surface water is associated with the increased hake abundance. Off the west coast the high percentage of

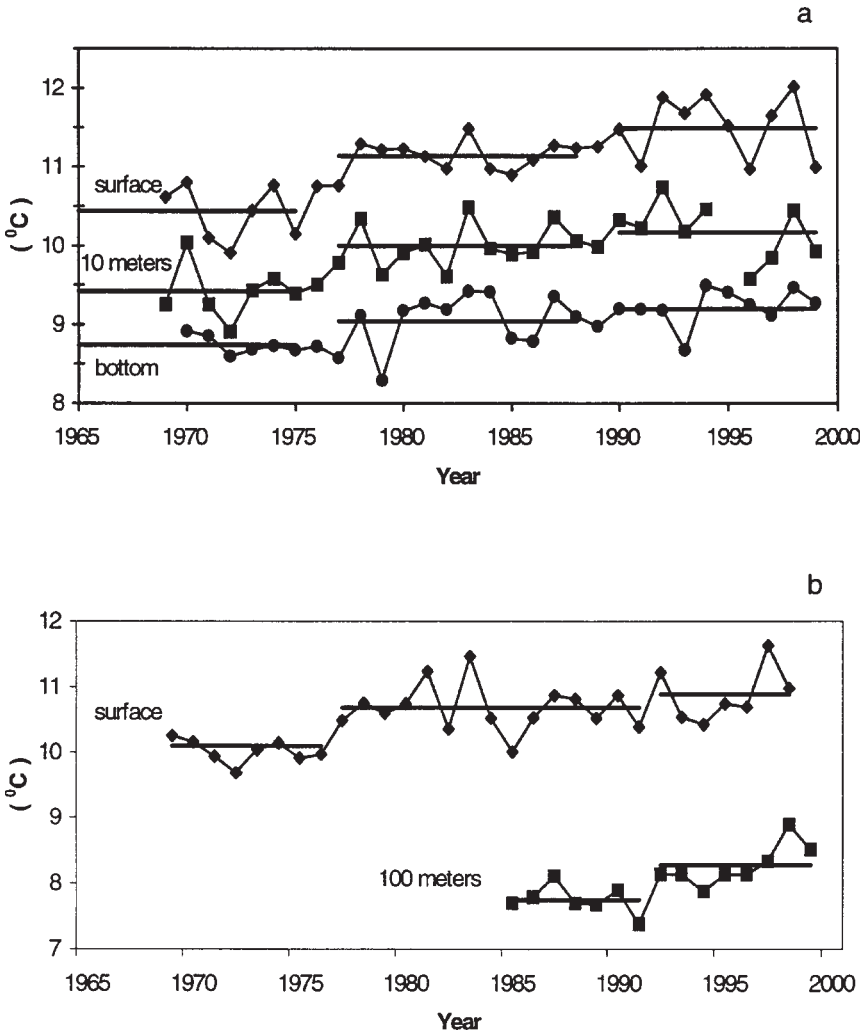


Figure 7. The average annual seawater temperature at (a) surface, 10 m, and bottom in the Strait of Georgia; and (b) surface and 100 m off the west coast of Vancouver Island. Solid horizontal lines indicate average temperature for regime.

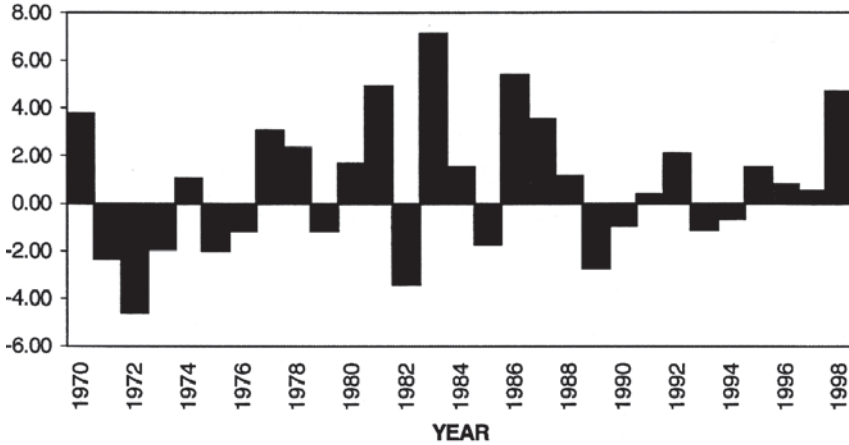


Figure 8. The Aleutian low pressure index (ALPI), 1970-1998. It is calculated as the mean area (km^2) with sea level pressure ≤ 100.5 kPa and is expressed as an anomaly from the 1950-1997 mean.

herring in the diet of hake (approximately 37% annually) is clear evidence of the preference of hake for herring as a prey. This preference for herring and the large biomass of hake has been shown to be the principal cause of the low abundance of herring in this area (Ware and McFarlane 1995). Hake in the Strait of Georgia reduced their predation on herring despite having a high biomass. After 1989, there was a shift to higher mean sea surface temperatures in both areas that was part of a large-scale shift in climate/ocean conditions as seen in the change in the pattern of the Aleutian low.

Herring in the Strait of Georgia have a high biomass even though the surface waters are also warmer. The increased temperature in the Strait of Georgia was not associated with a reduction in herring abundance as reported for the west coast of Vancouver Island. Instead it was associated with improved hake survival, reduced individual hake growth, and the elimination of predation on herring. Our observations of the elimination of herring in the diet of hake in the 1990s is consistent with observations of Tanasichuk et al. (1991), that hake less than 40 cm prey almost exclusively on euphausiids.

The factor common to both ecosystems was climate and climate change. The well-known climate shift of 1977 (Francis and Hare 1994, Minobe 1997, Beamish et al. 1999b) was associated with an increase in temperature in both ecosystems and an intensification of the Aleutian low pressure system in the subarctic Pacific. Our proposal of a 1989 regime shift (Beamish et al. 1999b, McFarlane et al. 2000) has now been identified

in other studies (Hare and Mantua 2000) and appears to be receiving cautious acceptance. In the Strait of Georgia, this change was associated with an increase in ocean temperatures. Other changes such as increases in sea level heights (Beamish et al. 1999a), an earlier spring freshet (Beamish and McFarlane 1999) in the Fraser River, and changes in dominant wind direction (Beamish et al. 1999a) have also been noted. Off the west coast of Vancouver Island, sea surface temperature increased and the Aleutian low pressure system was reduced in intensity. In other publications (Beamish et al. 1999a, McFarlane et al. 2000) we suggest that a common factor may trigger these hemispheric shifts in climate/ocean ecosystems.

It is the nature of the "reorganization" of the ecosystem after a regime shift that determines the impacts on a species. A measure of the change, such as temperature, is only one factor affecting the dynamics of populations. The climate changes in 1977 and 1989 elicited opposite responses from herring in two adjacent ecosystems. This was despite similar temperature trends in these two systems. This suggests that physical factors need to be related to ecosystem dynamics and not just to the observed effect on a single species. It also means that once we see indications that climate/ocean conditions are changing we need to identify the new "ecosystem organization" and adapt our management strategies to this new reality. While the relationships we propose in this report may be viewed as speculative, they identify the need to reevaluate past explanations. How speculative is this explanation relative to other interpretations? A conclusion that probably is commonly accepted is that herring management should consider herring as a component of ecosystem processes that are affected by the natural and fishing effects on herring.

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Trophic Position of Pacific Herring in Prince William Sound, Alaska, Based on Their Stable Isotope Abundance

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Abstract

Acting as a conveyor of energy between the plankton and piscivorous organisms, Pacific herring (*Clupea pallasii*) play an important ecological role in Prince William Sound and other coastal waters of the northeast Pacific Ocean. Because of a regional isotopic gradient and the fidelity of consumer isotopic composition with that of their diet, natural carbon and nitrogen stable isotope abundance was used as a tool to determine Prince William Sound herring trophic position. Nitrogen stable isotope abundance was used in this study to estimate and provide evidence for consistency in herring trophic level. Some seasonal variability during the 1994 to 1998 study period was noted. Assuming that energy available for the highest trophic levels is determined primarily by the number of trophic steps, trophic level consistency suggests that energy per unit of biomass is propagated in proportion to its variability at the food web base. Previously, herring carbon isotopic composition suggested the latter to vary on annual time scales. Forage levels for herring consumers may thus fluctuate in accordance with herring food chain length and variability in planktonic productivity patterns. Measurable trophic level shifts would be significant given the narrow-ranging well-defined herring trophic level found in this study.

Introduction

The failure of several Prince William Sound (PWS), Alaska, vertebrate species to recover from population crashes following the 1989 T/V *Exxon Valdez* oil spill has raised concerns that shifts in food web structure may have occurred. Of particular concern is recruitment of *Clupea pallasii* (Pa-

cific herring), presently at a historical low in abundance in PWS, a fjord-like inland sea that receives oceanic water from the Gulf of Alaska (GOA) via the Alaska coastal current (Niebauer et al. 1994). Furthermore, Pacific herring play a key role in the subarctic Pacific pelagic ecosystems by being in an intermediary trophic position between plankton and consumers of herring such as other fishes, birds, and mammals including humans. Recently, Kline (1999b) has shown through the use of natural stable carbon isotope abundance ($^{13}\text{C}/^{12}\text{C}$) that herring in PWS may be dependent upon carbon generated in the Gulf of Alaska and that the degree of this dependency fluctuates from year to year.

Stable isotope ratios effectively provide empirical evidence of trophic relationships in marine food webs because of their predictable relationship when comparing their abundance in consumers and diet. Nitrogen stable isotope ratios provide excellent definition of relative trophic level (Fry 1988). The heavy isotope of nitrogen, ^{15}N , is enriched by about 0.34% (or 3.4 per mil in conventional delta units, see Materials and Methods) with each trophic level (Minagawa and Wada 1984) and has been shown to accurately indicate the relative trophic status of species within an ecosystem (Cabana and Rasmussen 1994). Trophic level as used here refers to the average number of feeding steps between predators and their prey. For example, if the diet of predator A was 100% prey B, there would be 1.0 trophic levels between them. However, if A also consumed C, and C was also part of the diet of B, the trophic level difference between A and B would most likely \neq 1.0. The effective trophic level difference between A and B would then depend upon the relative contribution of B and C in the composition of A's diet as well as the relative trophic level differences between B and C.

Carbon stable isotope ratios ($^{13}\text{C}/^{12}\text{C}$) can effectively be used to trace multiple sources of carbon into food webs once it is established that an ecosystem has carbon sources with distinctive isotopic signatures (Fry and Sherr 1984). This latter point has been established since GOA and PWS carbon sources for PWS had distinctive carbon isotope signatures of about -23 and -19 (in $\delta^{13}\text{C}$ units), respectively (see Kline 1999b). Accordingly, stable carbon isotopes measured in herring and other biota suggested that in some years the GOA may supply the majority of carbon for the PWS pelagic ecosystem (Kline 1999b).

An Ecopath (Christensen and Pauly 1992) model and $^{15}\text{N}/^{14}\text{N}$ natural abundance data predicted corroborating trophic levels for pelagic biota including herring from PWS (Kline and Pauly 1998) but did not provide details relating patterns of variability of relative trophic level between herring and secondary pelagic producers and between herring and potential teleost consumers. Kline's (1999a) $^{15}\text{N}/^{14}\text{N}$ inventory for herring from 1994 and 1995 suggested only slight interannual and intersite variability while Kline and Pauly (1998) determined trophic levels of 3.3 and 3.33 (where herbivores are trophic level = 2) based on Ecopath and isotopic analyses of $N = 459$ herring, respectively. Since these publications, a more

extensive isotopic database has been generated for herring ($N > 2,000$) and other pelagic biota of PWS for the period 1994-1998 from which patterns of GOA carbon were found from $^{13}\text{C}/^{12}\text{C}$ data (Kline 2001). The purpose of this study was to use the extensive $^{15}\text{N}/^{14}\text{N}$ data to assess the trophic position of PWS herring during this period seeking potential ontogenetic, spatial, and temporal patterns.

Assessing the trophic position of PWS herring was accomplished through three tasks: (1) by assessing effects of $^{15}\text{N}/^{14}\text{N}$ variability of PWS herbivorous copepods used as the trophic baseline (Kline 1999b); (2) by assessing herring ontogenetic $^{15}\text{N}/^{14}\text{N}$ shifts and hence trophic level shifts based on fish size; and (3) by assessing PWS herring temporal and spatial $^{15}\text{N}/^{14}\text{N}$ variability from a four-bay time series.

Materials and Methods

Data Generation

The rationale for, and detailed description of methods used to generate the isotopic database for this study form a major portion of Kline (1999b) and so are only given briefly here. Copepods were picked in the field from plankton samples that were made with either ring nets or a MOCNESS system and in the case of the large-sized species, *Neocalanus cristatus*, analyzed as individuals. Other *Neocalanus* spp. were analyzed by pooling two individuals together. Fishes were collected with seines, traps, and trawls. Herring data for those up to a length of about 150 mm were largely a part of a collaborative effort with A.J. Paul who measured whole-body energetic content of the same individual fish (Kline 1999b). Herring and other fishes were analyzed in replicate and data averaged to provide one isotopic datum per fish for each element (N and C). Only stable isotopes of N are considered here. N stable isotope ratios, $^{15}\text{N}/^{14}\text{N}$ are expressed in delta (δ) units as the per mil deviation from the $^{15}\text{N}/^{14}\text{N}$ content of air N_2 .

Data Selection

The mean $\delta^{15}\text{N}$ values of terminal feeding stages of *Neocalanus cristatus* and *Neocalanus* spp. were pooled from PWS and GOA spring (1995) or May (1996-1997) oceanographic sampling stations (Kline 1999b). *Neocalanus* spp. included *N. cristatus*, *N. plumchrus*, and *N. flemingeri* (1996-1997) from the GOA or PWS. A portion of these data were extracted from published data (Kline 1999a,b) while others are reported here for the first time. Obtained similarly were the pooled $\delta^{15}\text{N}$ values of diapause stage *Neocalanus cristatus* and *Neocalanus* spp. from the appropriate deep habitat in PWS (Kline 1999b).

All herring sampled from April 1994 to March 1998 for which length data (standard length) were available were pooled and analyzed for trend using a scatterplot and regressed for best fit using R^2 and P values. Commencing in the fall of 1995, juvenile herring approximately < 15 cm in

length were sampled at four sites (see Norcross and Brown 2001, this volume) within PWS at approximately 1.5 month intervals between March 1996 and October 1997 (Kline 2000). This four-bay time series enabled assessing finer scale temporal variability in several parameters (whole-body and diet energetics, growth, diet composition) for age 0 and 1 PWS herring than had been previously examined (Norcross et al. 1996). Approximately $N = 25$ from each site-sampling which were isotopically analyzed are reported here with S.D. estimation. Age 0 and 1 herring were pooled for this analysis since it was not possible to split the data by age and also retain both the temporal and spatial coverage. Thus ontogenetic effects were examined using a separate data selection that also benefited by including data from additional PWS sites (Kline 1999b).

Comparing the trophic level of herring to other organisms from PWS was facilitated by pooling $\delta^{15}\text{N}$ data of herbivorous copepods and large teleosts to reflect herbivores (potential herring forage) and piscivores (potential herring predators), i.e., expected to have, respectively, lower and higher trophic levels. Diapausing *Neocalanus cristatus* were selected as a proxy for the PWS herbivore trophic level based upon their previous use and the observation that the fraction originating from the GOA matched the fraction of GOA carbon in PWS herring (Kline and Pauly 1998, Kline 1999b). Potential piscivores consisted of larger-sized (> 20 cm) taxa. Juvenile stages (< 20 cm) and taxa known to have similar trophic level as herring (Kline and Pauly 1998) were therefore excluded. The N for copepods and teleosts selected were approximately 700, sufficient for generation of histograms for comparison with herring $N \cong 2,000$.

Trophic level was determined by comparing $\delta^{15}\text{N}$ values to a reference value (Vander Zanden et al. 1997). The $\sigma^{15}\text{N}$ of higher trophic levels were calculated by adding the trophic enrichment factor, 3.4 (Minagawa and Wada 1984, Kline 1997), to the reference value. The herbivorous copepod *Neocalanus cristatus*, i.e., trophic level = 2, was used as the reference (Kline and Pauly 1998, Kline 1999b).

The following formula was used to calculate trophic level:

$$TL_i = (\delta^{15}N_i - \delta^{15}N_H / 3.4) + 2$$

where TL_i is the trophic level of organism i , $\delta^{15}N_i$ is the mean $\delta^{15}\text{N}$ value of organism i , and $\delta^{15}N_H$ is the mean herbivore $\delta^{15}\text{N}$ value.

Statistical analysis of the data was facilitated by using the Statview 4.5 (Abacus Concepts, Inc., Berkeley, CA) computer program while the Deltagraph 3.1 (Delta Point, Inc., Monterey, CA) computer program was used to generate the figures.

Table 1. Mean $\delta^{15}\text{N}$ and S.D. of terminal feeding and diapause stages of the large (length \cong 9 mm) herbivorous copepod *Neocalanus cristatus* (except as noted) from PWS and the GOA; data came from indicated sources.

Sample	$\delta^{15}\text{N}$	S.D.
Feeding		
Prince William Sound		
1995 ^a	8.6	1.1
1996 ^b	8.3	0.8
1997 ^c	8.9	1.2
1996 ^{c,d}	8.6	0.7
1997 ^{c,d}	8.9	0.9
Gulf of Alaska		
1995 ^a	7.3	0.7
1996 ^b	8.5	1.1
1997 ^c	7.8	1.3
1996 ^{b,c,d}	8.8	1.0
1997 ^{c,d}	7.6	1.0
Diapause		
Prince William Sound		
1994 ^a	8.7	1.6
1995 ^a	7.8	2.8
1996 ^b	8.6	1.5
1996 ^{b,c,d}	8.5	1.1
1994-1996 ^c	8.4	2.0

^aKline 1999b.

^bKline 1999a.

^cThis study.

^dAll *Neocalanus* spp., otherwise only *N. cristatus*.

Results

There were only slight variations in the mean $\delta^{15}\text{N}$ values for the species *Neocalanus cristatus* and for the three *Neocalanus* species. (Table 1). The lowest $\delta^{15}\text{N}$ value of 7.3 was found for 1995 feeding stage GOA *N. cristatus* while the highest $\delta^{15}\text{N}$ value of 8.9 was found for both feeding stage PWS *N. cristatus* and PWS *Neocalanus* spp. mean values in 1997. Diapausing copepods had a smaller range in values reflecting the integration of GOA and PWS copepod sources also suggested through their $\delta^{13}\text{C}$ values (Kline 1999b). Note, however, that the mean diapausing value for *N. cristatus* in

1995 and 1996, 7.8 and 8.6, respectively, more closely matched those from the GOA, 7.3 and 8.5, respectively, rather than those from PWS, 8.6 and 8.3, respectively, corroborating the significant contribution of GOA-generated production for PWS deduced from $\delta^{13}\text{C}$ (Kline 1999b). The mean $\delta^{15}\text{N}$ for all 1996 diapausing species, 8.5, was ^{15}N -depleted compared to both PWS and GOA but more closely matched PWS at 8.6 than the GOA at 8.8. The collective mean for *N. cristatus* sampled diapausing from the entire study, 8.4 ± 2.0 (S.D.), is discussed in greater detail below in relation to herring and potential piscivorous teleosts.

There was only a slight shift in $\delta^{15}\text{N}$ and hence trophic level (TL) as a function of size for PWS herring (Fig. 1). Only herring < 100 mm were TL < 3.0 while very few herring at any size were TL > 3.5. The slight $\delta^{15}\text{N}$ shift with size was reflected in the regressions which only explained 16% of the variability. There appears to be a trophic level break for herring < 70 mm as these were mostly TL < 3.0 whereas the majority of the larger herring were between TL = 3 and TL = 3.5.

Spatial and temporal variability of PWS herring $\delta^{15}\text{N}$ and hence trophic level was only slight (Fig. 2). The low trophic levels during the summer months can, in part, be explained by age-0 fish < 70 mm. Although some of the variability among sites might be explained by unequal representation of the two year classes (Norcross et al. 1996), age-1 herring at sites with lowest mean TL had lower TL than those from sites with higher mean TL.

There was slightly more than one trophic level difference between herring and herbivores while there was slightly less than one trophic level difference between herring and their potential predators (Fig. 3). Diapausing *Neocalanus cristatus* copepods ($N=669$) which were used as the trophic level = 2.0 (herbivore) baseline had a mean $\delta^{15}\text{N} = 8.39$ with a standard deviation of 2.01. They were slightly skewed to higher values (skewness = 0.79) and were leptokurtic (kurtosis = 3.46). Large teleosts (> 20 cm; $N=727$) had a mean $\delta^{15}\text{N} = 14.66$ (interpreted trophic level = 3.85) with a standard deviation of 1.22 (0.36 trophic levels) were similarly leptokurtic (kurtosis = 3.37) and positively skewed (skewness = 0.73). Herring ($N=2,084$), which had a mean $\delta^{15}\text{N} = 12.47$ (interpreted trophic level = 3.20) with a standard deviation = 0.60 (0.18 trophic levels), were more strongly leptokurtic (kurtosis = 4.72) and skewed to lower $\delta^{15}\text{N}$ (skewness = -1.02). The negative skewness was due to the lower trophic level of smaller herring while the high kurtosis and narrow standard deviation suggests a well-defined $\delta^{15}\text{N}$ -based trophic level for herring. The difference of 1.20 trophic levels between herring and herbivores is consistent with herring also consuming carnivorous zooplankters. The difference of 0.65 trophic levels between herring and large teleosts is consistent with prey-switching by larger fishes. For example, PWS walleye pollock (*Theragra chalcogramma*), a major constituent taxon, consume zooplankters (including *Neocalanus* spp.) as well as herring and other prey. However, note the positive skewness and sample distribution indicating that teleosts can feed as high as trophic level five.

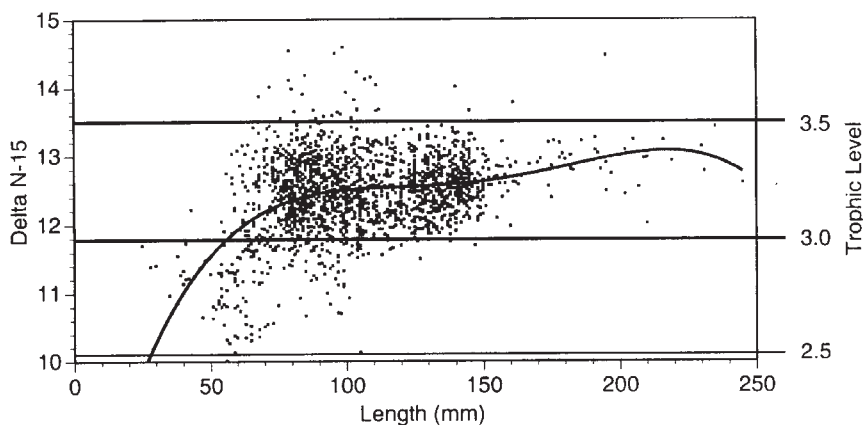


Figure 1. Scatterplot of $\delta^{15}\text{N}$ versus standard length for Prince William Sound, Alaska herring sampled between April 1994 and March 1998 with interpreted trophic levels. The fourth order polynomial shown provided a better fit to the data than a linear regression, explaining 16% of the variability compared to 10%, respectively (coefficient and regression $P < 0.0001$).

Discussion

Herring production levels is of concern for recruitment of herring, presently at a historical low in abundance in PWS. In particular, forage levels for herring consumers may fluctuate in accordance with herring food chain length and variability in planktonic productivity patterns if these factors are important to herring productivity. While carbon stable isotope ratios provided strong evidence for large interannual-scale shifts in source of production supporting PWS, measurable trophic level shifts would be significant given the narrow-ranging well-defined herring trophic level found in this study. The narrow $\delta^{15}\text{N}$ range of herring compared to herbivores conferred a well-defined trophic position during the period of this study.

Potential errors in estimating herring trophic level from $\delta^{15}\text{N}$ were likely to be less than about $\frac{1}{3}$ trophic levels based on the relatively small temporal and spatially dependent departures of mean herbivore $\delta^{15}\text{N}$ from a value of 8.4. The sources of $\delta^{15}\text{N}$ variation arise in the phytoplankton, varying among phytoplankton species because of size and species-dependent differences in isotopic fractionation and isotopic effects arising from their selective draw-down of ^{14}N in the dissolved inorganic nitrogen pool (see review by Owens 1987). Kline 1999b estimated that 40% of $\delta^{15}\text{N}$ variability of PWS zooplankton could be ascribed to nitrogen dynamics while spatial gradients accounted for 1 per mil differences, equivalent to the trophic fractionation of about $\frac{1}{3}$ trophic levels. However, the spatial gra-

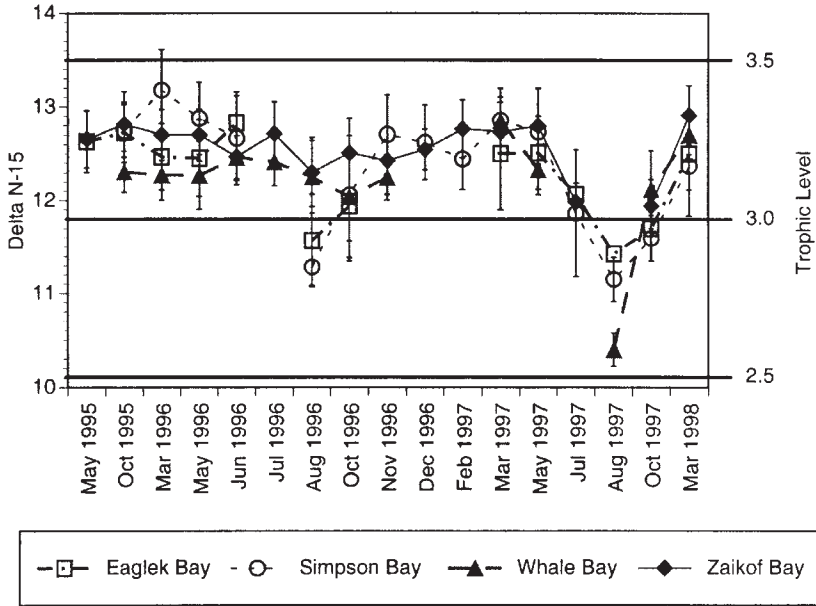


Figure 2. Temporal and spatial variability in $\delta^{15}\text{N}$ and interpreted trophic level for Prince William Sound herring. Error bars depict standard deviations. Lower trophic levels occurred during summer when new recruits were small. Trophic level variability was otherwise slight. Norcross and Brown (2001, this volume) show the locations and provide a description of the four-bay sampling program.

dent was weaker in later years of the study so $\delta^{15}\text{N}$ -based errors should be less than $\frac{1}{3}$ trophic level overall.

There were a few copepods with anomalous $\delta^{15}\text{N}$ values for a herbivore. One interpretation for copepods with very high $\delta^{15}\text{N}$ and hence a high trophic level is feeding on micro-heterotrophs dependent upon fish detritus, either spawned-out salmon carcasses or anthropogenic fish wastes such as from the numerous PWS processing plants. Since these were small in number they had only negligible effect for this study since the central value of a large sample size was used for the calibration point ($\delta^{15}\text{N} = 8.4$). Furthermore, carnivorous copepods and omnivorous euphausiids and amphipods had appropriate $\delta^{15}\text{N}$ values, consistently higher than 8.4 (Kline 1999b).

The relatively slight shifts of herbivore $\delta^{15}\text{N}$ cannot explain the pattern of herring seasonal shifts $\delta^{15}\text{N}$ up to near 3 per mil. Therefore, a seasonal shift to lower trophic level feeding interpretation is more valid. The pre-

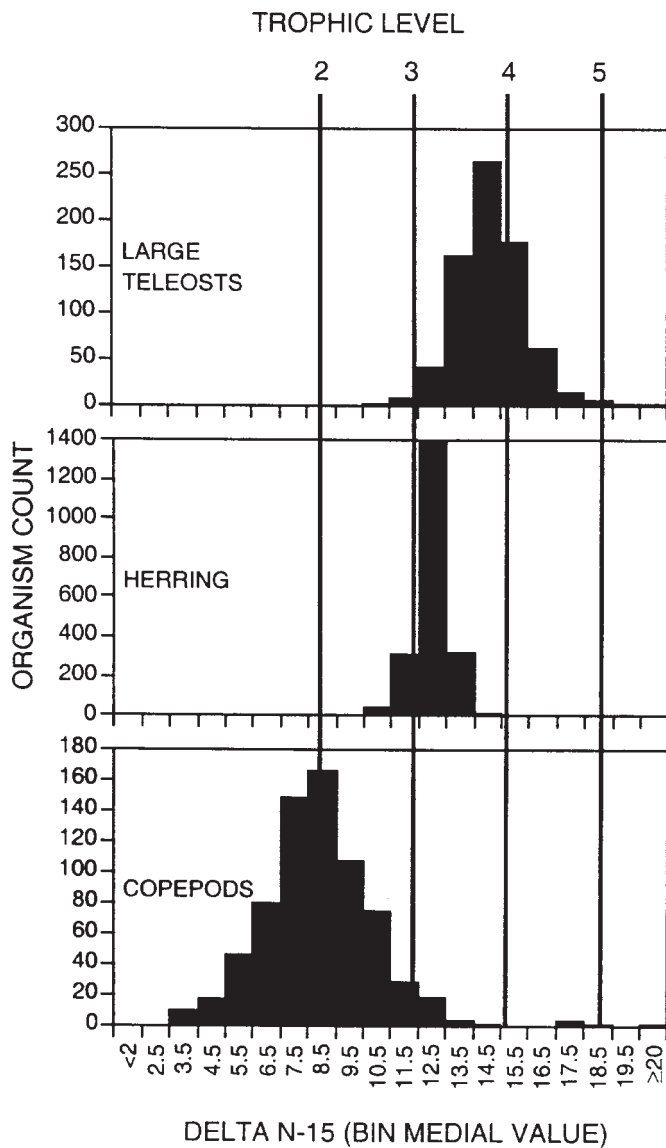


Figure 3. Comparison of $\delta^{15}N$ and interpreted trophic level variability through histograms of a large database.

ponderance of smaller newly recruited herring in summer and their suggested ontogenetic trophic level shift at ~ 7 cm length found in summer can only explain a part of this shift since both age classes apparently shifted to lower trophic levels during summer of 1997.

An Ecopath model for the same time period as these data conferred trophic levels of 3.10 and 3.03 for adult (fish > 18 cm) and juvenile herring, respectively (Okey and Pauly 1998: table 74), slightly lower than the over all trophic level estimate of 3.2 for all stages estimated here. These differences could be explained in part by seasonal shifts since Alaska field data (used for Ecopath input) tend to have a “summer-bias” which is when trophic levels are lower. The less than 0.1 trophic level difference between adult and juvenile herring found by Ecopath is closely reflected by the $\delta^{15}\text{N}$ -based trophic levels. However, the range in herring trophic level independent of fish length as well as variability in space-time was greater than the small differences found for the two herring Ecopath functional groups. Given that the number of functional groups that can be incorporated into an Ecopath model is limited to 50 (Okey and Pauly 1998), it would be prudent to pool herring into one. Given a standard deviation of 0.18 trophic levels for the $\delta^{15}\text{N}$ -based trophic level of PWS, the Okey and Pauly (1998), Ecopath-based trophic level was in good agreement, closely reflecting the previous Ecopath-isotope comparison of Kline and Pauly (1998). This assessment thus increases our confidence that we have made a good estimation of the trophic status of PWS herring.

Nitrogen stable isotope abundance thus provided a good estimate for herring trophic level. There was very little ontogenetic trophic change in herring larger than about 70 mm. Herring trophic level was generally constant over the 4-year time period of this study although some seasonal variability was noted. If trophic level shifted on longer time scales, e.g., decadal, these shifts should be considered significant given the narrow-ranging, well-defined herring trophic level found in this study.

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Pacific Herring in the Western Bering Sea Predatory Fish Diet

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Extended Abstract

Pacific herring, *Clupea pallasii*, inhabiting the western Bering Sea belong to the Korf-Karagin population distributed in Korf and Karagin bays and adjacent waters. In the past that population was one of most abundant in the North Pacific. During periods of high abundance, herring were distributed to Cape Navarin in the north and to southeastern Kamchatka in the south. The maximal annual harvest (268,000 metric tons) was recorded in 1961. As a result of climatic change and overexploitation the abundance of herring in the western Bering Sea sharply declined (Kachina 1986a). Now the herring stock is in a depressed condition and there is no herring fishery.

Investigations were conducted aboard the Japanese trawler *Kayomaru* No. 28 during May-July 1997 on the western Bering Sea continental slope from the eastern part of Olyutorsk Bay (168°E) to the border of the U.S. Exclusive Economic Zone (177°30'W) east of Cape Navarin. A total of 170 bottom trawl hauls (47 during the bottom trawl survey and 123 during bottom trawl commercial fishing operations) were made using bottom trawls with horizontal and vertical mouth openings of about 25-30 m and 5-7 m, respectively. Mesh size was 100 mm. During the investigations, data on spatial distribution, size composition, and stomach contents of the most abundant species were obtained. Stomach sampling and processing were conducted using standard methods (Yang 1993, 1996). Below we characterize some features of spatial distribution and size composition of Pacific herring in the western Bering Sea during summer 1997, and importance of herring in the diets of some fishes.

During summer 1997 Pacific herring were caught only in the central part of Olyutorsk Bay (Figs. 1 and 2), which is one of the usual feeding areas for herring in the western Bering Sea (Kachina and Prokhorov 1966). Maximum catches consisted of more than 1,500 specimens per hour of trawling. Herring size (Fig. 3) ranged in fork length from 24 to 33 cm, with

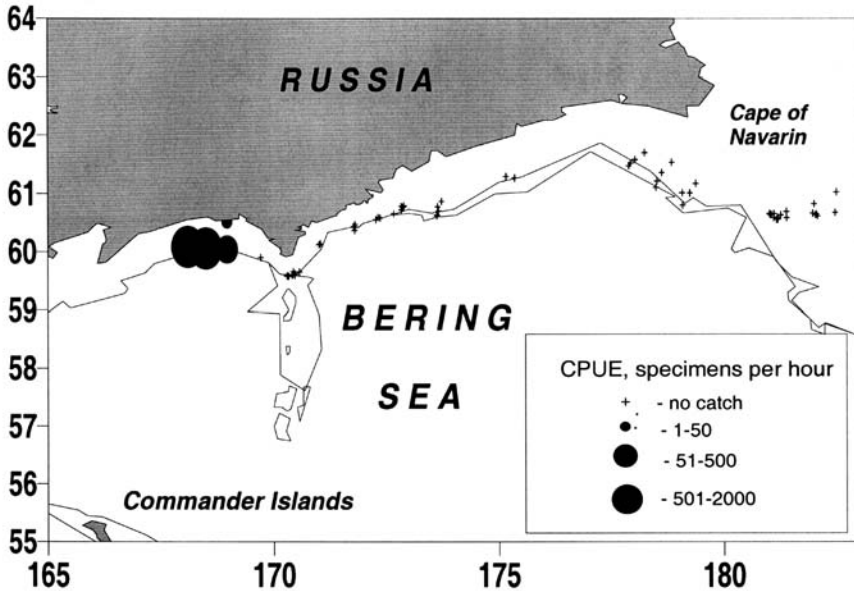


Figure 1. Distribution and relative abundance of Pacific herring categorized by CPUE (kg per hour trawling) in May-July 1997 in the western Bering Sea (thin lines are isobaths).

a mean and S.D. of 28.79 ± 0.12 , which is very similar to 1971 to 1975, when herring fork length was 24 to 33 cm and mean length was 28.4 cm (Kachina 1986b). In 1938-1943 herring in the western Bering Sea were larger, from 25 to 33 cm with a mean length of about 32.0 cm (Panin 1950). Herring body weight in 1997 ranged from 180 to 460 g with a mean and S.D. of 309.0 ± 10.86 g, which was considerably larger than in 1958-1968, when mean body weight did not exceed 286 g (Kachina 1970). During the period of our research, herring fed intensively and most of the fish (83.9% of the females and 54.2% of the males) were in postspawning condition.

Herring were found in fish stomachs from 21 bottom trawl hauls (mostly in the central part of Olyutorsk Bay), while herring were caught in only 8 hauls (Fig. 1). In addition, feeding on herring by fishes was noted in two catches located outside of Olyutorsk Bay (Fig. 2). This probably occurred because near-bottom herring schools generally cannot be caught by bottom trawls. However, predatory fishes (halibuts, shortraker rockfish, skates, large pollock, etc.) may forage some distance from the bottom (Orlov 1997, 1998). During our investigations herring were found in the stomachs of 10 fish species. According to percent by weight herring were very important (Table 1) in the diets of Alaska skate, *Bathyraja parmifera*

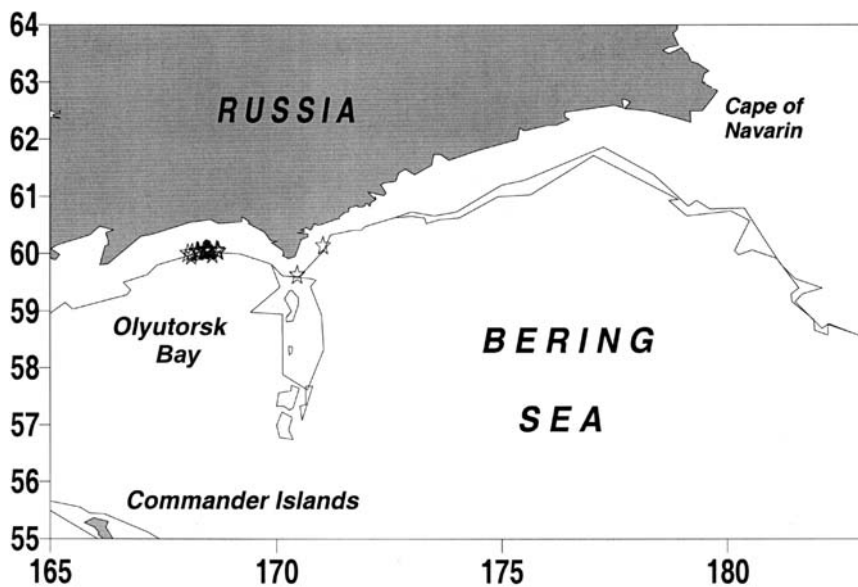


Figure 2. Map showing bottom trawl stations (stars) at which herring were found in predator stomachs (thin lines are isobaths).

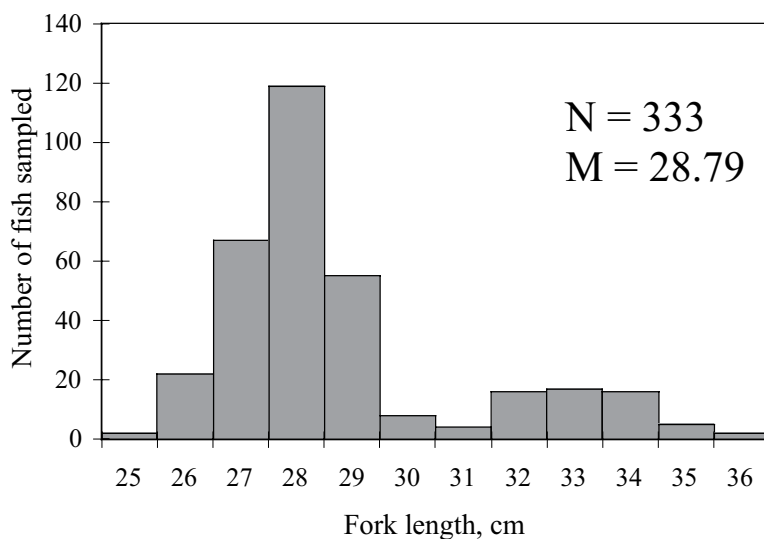


Figure 3. Length frequencies of Pacific herring in the western Bering Sea in May-July 1997 (n = number of fish measured; M = mean length, cm).

Table 1. Importance of Pacific herring and occurrence of fishes in stomachs of some predators that consumed Pacific herring in the western Bering Sea in 1997.

Prey category	1	2	3	4	5	6	7	8	9	10
Number of stomachs analyzed	151	113	68	139	93	2,113	301	262	446	590
Number of stomachs contained food	127	86	58	123	84	1,673	107	206	181	411
Predator's mean length (SL), cm	139.87±	80.00±	69.82±	75.38±	63.82±	51.72±	61.30±	73.92±	54.83±	69.30±
	2.74	1.74	0.56	2.98	1.09	0.15	0.64	0.76	0.37	0.043
Predator's mean weight, kg	26.035±	4.607±	1.936±	4.596±	1.557±	0.973±	4.323±	5.250±	1.828±	3.573±
	2.294	0.285	0.041	0.481	0.064	0.008	0.125	0.271	0.271	0.086
Total prey weight, g	46,057	9,089	2,048	8,050	2,515	na	2,880	31,715	10,794	80,316
Herring weight, g	100	3,055	235	475	30	na	648	3,665	1,116	7,123
Herring weight, % of stomach contents	0.22	33.61	11.47	5.90	1.19	na	22.50	11.56	10.34	8.87
Frequency of occurrence, %										
Pacific lamprey, <i>Entosphenus tridentatus</i>							0.9			
Pacific herring, <i>Clupea pallasii</i>	0.8	23.4	8.6	4.1	1.2	0.2	7.5	15.5	8.8	12.4
Pacific blacksmelt, <i>Bathylagus pacificus</i>					0.8					
Northern smoothtongue, <i>Leuroglossus schmidti</i>			1.7	0.8		7.0	3.7			0.2
Chum salmon, <i>Oncorhynchus keta</i>	1.6									
Salmon unidentified, <i>Oncorhynchus</i> spp.	1.6									
Northern lampfish, <i>Stenobrachius leucopsarus</i>	0.8	1.2					1.9		0.6	0.5
Garnet lampfish, <i>S. nannochir</i>		1.2	1.7	2.4	1.2	0.2	12.2			2.2

Table 1. (Continued)

Prey category	1	2	3	4	5	6	7	8	9	10
Lanternfish unidentified, Myctophidae			1.7	0.8		4.2	20.6			4.9
Giant grenadier, <i>Albatrossia pectoralis</i>	7.9							0.5		0.5
Popeye grenadier, <i>Coryphaenoides cinereus</i>	7.9							0.5		0.2
Walleye pollock, <i>Theragra chalcogramma</i>	3.9	10.5		8.1	2.4		0.9	18.5	13.8	19.0
Threespine stickleback, <i>Gasterosteus aculeatus</i>		1.2								
Shortraker rockfish, <i>Sebastes borealis</i>		1.2								
Atka mackerel, <i>Pleurogrammus monopterygius</i>			1.7							
Porehead sculpin, <i>Icelus canaliculatus</i>		1.2								
Armorhead sculpin, <i>Gymnocalanthus detrisus</i>				0.8						
Spinyhead sculpin, <i>Dasycottus setiger</i>										0.2
Darkfin sculpin, <i>Malacocottus zonurus</i>	0.8	1.2						1.5	1.1	
Blackfin poacher, <i>Bathagonus nigripinnis</i>								1.0		
Japanese dog poacher, <i>Percis japonica</i>				0.8						

na = not available

(1 = Pacific sleeper shark, *Somniosus pacificus*; 2 = Alaska skate, *Bathyraja parmifera*; 3 = whitebrow skate, *B. aleutica*; 4 = Aleutian skate, *B. aleutica*; 5 = Okhotsk skate, *B. violacea*; 6 = walleye pollock, *Theragra chalcogramma*; 7 = shortraker rockfish, *Sebastes borealis*; 8 = Pacific halibut, *Hippoglossus stenolepis*; 9 = Kamchatka flounder, *Atheresthes evermanni*; 10 = Greenland turbot, *Reinhardtius hippoglossoides*.)

Table 1. (Continued.) Importance of Pacific herring and occurrence of fishes in stomachs of some predators that consumed Pacific herring in the western Bering Sea in 1997.

Prey category	1	2	3	4	5	6	7	8	9	10
Forktail snailfish, <i>Careproctus furcellus</i>	2.4					0.1				0.2
Dimdisc snailfish, <i>Elasodiscus tremebundus</i>		1.6							1.0	
Snailfish unidentified, Liparidae					0.8					0.2
Longsnout prickleback, <i>Lumpenella longirostris</i>		2.3			4.9				1.1	
Ebony eelpout, <i>Lycodes concolor</i>	0.8						0.9	0.5	1.1	
Shortfin eelpout, <i>L. brevipes</i>		1.2						0.5	1.1	0.7
Black eelpout, <i>L. diapterus</i>								0.5		0.7
Kamchatka flounder, <i>Atheresthes evermanni</i>	2.4									
Flathead sole, <i>Hippoglossoides elassodon</i>								0.5		0.2
Unidentified fish	8.7	2.3	5.2	9.8	3.6	0.1	15.9	4.9	13.8	5.1
Fishery offal	10.2	19.8	20.7	12.2	9.5	8.7	3.7	29.6	40.9	43.3

na = not available

(**1** = Pacific sleeper shark, *Somniosus pacificus*; **2** = Alaska skate, *Bathyraja parmifera*; **3** = whitebrow skate, *B. minispinosa*; **4** = Aleutian skate, *B. aleutica*; **5** = Okhotsk skate, *B. violacea*; **6** = walleye pollock, *Theragra chalcogramma*; **7** = shorttraker rockfish, *Sebastes borealis*; **8** = Pacific halibut, *Hippoglossus stenolepis*; **9** = Kamchatka flounder, *Atheresthes evermanni*; **10** = Greenland turbot, *Reinhardtius hippoglossoides*.)

(33.61% by weight); whitebrow skate, *B. minispinosa* (11.47%); Pacific halibut, *Hippoglossus stenolepis* (11.56%); Greenland turbot, *Reinhardtius hippoglossoides* (8.87%); Kamchataka flounder, *Atheresthes evermanni* (10.34%); and shortraker rockfish, *Sebastes borealis* (22.50%). According to frequency of occurrence, which was estimated as the number of stomachs that contained that food item divided by the total number of stomachs examined, herring occupied the second place after walleye pollock, *Theragra chalcogramma*, in most predator diets. During the period of herring high abundance (1950s and 1960s) the frequency of occurrence in stomachs of Pacific halibut in the western Bering Sea according to Novikov (1964, 1974) was 3.1-4.0% (15.5% in our study), and its weight percentage according to Gordeeva (1954) was 2-3 % (11.56% in our study). Other fishes that consumed herring in the past according to Gordeeva (1954) and Novikov (1974) were shortraker rockfish (frequency of occurrence 10.7 and 7.5% in the 1950s to 1960s and 1997, respectively); sablefish, *Anoplopoma fimbria* (frequency of occurrence 0.6 and 0.0%, respectively); and Pacific cod, *Gadus macrocephalus* (0.8 and 0.0% by weight, respectively). Published information on diets of Pacific sleeper shark, skates, and walleye pollock in the western Bering Sea in the 1950s and 1960s is lacking.

Pacific herring also play an important role in the diets of many commercially important fishes of the eastern Bering Sea (Lang et al. 1991, Livingston et al. 1993), where its main consumers are large walleye pollock and Pacific cod. Herring composed (by weight) 0.6-1.8% of the diet of walleye pollock, and 1.0-6.4% of the Pacific cod diet (Lang et al. 1991, Livingston et al. 1993, Lang and Livingston 1996). Other predatory fishes consumed herring too. Herring (by weight) made up 3.2% of the diet for sablefish; 3.1-7.9% for arrowtooth flounder, *Atheresthes stomias*; 0.6-0.7% for Greenland turbot; and 0.6-4.8% for Pacific halibut (Brodeur and Livingston 1988, Yang and Livingston 1986, Lang et al. 1991, Livingston et al. 1993, Lang and Livingston 1996, Mito et al. 1999). Herring are also of considerable importance in the diet of Pacific halibut in British Columbia waters (Best and St.-Pierre 1986). Some predators consumed herring in the Aleutian Islands area, where its weight in stomach contents made up 0.52% for Pacific cod, 0.49% for arrowtooth flounder, and 1.72% for Pacific halibut (Yang 1996). In the Gulf of Alaska the percentage by weight of herring in predator stomachs was 0.20% for walleye pollock, 0.37% for Pacific cod, 9.15% for arrowtooth flounder, and 2.21% for sablefish (Yang 1993).

Results of our study showed that consumption of Pacific herring in the western Bering Sea by predators in the present period considerably increased in comparison with that of the 1950s and 1960s, when herring were more abundant. On the other hand, most western Bering Sea predators fed on herring more intensively than in areas of the northeastern Pacific although the present level of Korf-Karagin herring abundance is very similar to that of herring belonging to eastern Bering Sea and Gulf of Alaska populations (Naumenko 2000). It seems contradictory. However, we suggest that the reason for these oppositions were not related to the level of herring abun-

dance in the western Bering Sea and were associated with the fact that our study coincided with herring feeding, when they formed dense schools. The biological condition of herring and decline of predatory fish abundance within Olyutorsk Bay from May to July may confirm the above suggestion.

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Herring Abundance, Food Supply, and Distribution in the Barents Sea and Their Availability for Cod

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Abstract

The role of herring in the food base of Arcto-Norwegian cod in the 1980s and 1990s was examined by a review of historical data. The main factor influencing the availability of herring to cod is its distribution in the Barents Sea. When herring abundance is relatively low, its distribution is spatially restricted. The prey of herring also varies spatially: herring mainly feed on copepods in the west and on euphausiids in the central and eastern areas. Capelin is the main competitor for the food of herring. Fluctuations in the abundance of capelin affect the availability of food to herring, which affects their seasonal feeding rhythms, fat accumulation, and vertical distribution. Capelin abundance also affects the consumption of herring by cod.

Introduction

After a stock decline in the 1970s, Norwegian spring-spawning herring recovered and regained their previous place in the Barents Sea ecosystem in the 1980s and 1990s. During the period of decline the role of herring as prey for cod changed. In the 1970s, following the sudden decrease in abundance, herring were not available to cod. At that time cod fed mainly on capelin, which had increased in abundance (Ponomarenko and Yaragina 1985). In the period from 1984 to 1997, the issue of the role of herring as food for cod arose because of the relatively low abundance of herring and because of sharp fluctuations in capelin numbers (ACFM 1998). Also, during this period, temperatures increased and this also affected the distribution of fishes. Distribution also related to the availability of planktonic food organisms.

The most favorable periods for cod are those when wintering herring occupy bottom depths and are not very mobile. The duration of this period can vary from 2 to 4 months (between November and February). The duration depends on wintering conditions and the level of accumulated fat, which does not usually exceed 10-20% or an index of fatness of 2-3 in young herring (Rudakova 1966). Feeding intensity of herring is indicated by the level of fat reserves from January to March. At this time herring migrate to the middle and deeper depths where there are concentrations of overwintering small crustaceans. From February on they migrate vertically following the plankton (Tikhonov 1939, Boldovsky 1941). This behavior makes it possible for herring to be consumed by cod in the late winter and spring and also during the autumn feeding from August to October. The availability of herring is also influenced by their horizontal migrations within the Barents Sea, with seasonal movements to the west at the end of winter and to the east in summer. These variations can cause the migrations of cod and herring to be either coincident or independent.

The present paper considers the interaction of plankton condition, year-to-year changes in feeding intensity and fatness of herring, and the characteristics of the vertical and local distribution of herring which influenced their availability for cod in the 1980s-1990s.

Data Sources and Methods

Herring data were taken from catches of research vessels and bycatch of fishing vessels. Zooplankton data were obtained from annual assessment surveys in autumn-winter and spring. Data on plankton condition were obtained for 1985-1993, and data on the distribution, feeding, and fatness of herring, as well as data on cod feeding, was collected from 1985 to 1996. A field analysis of feeding (by the frequency of occurrence of particular food organisms) shown as a percentage of the total number of all fish with food, was made using the determination of index of stomach fullness and degree of fatness. Data on the consumption of food by cod was examined by quantitative analyses of weights of gut contents (about 90,000 specimens) and field observation based on incidence of prey species in guts (>55,000 specimens).

Year-to-Year and Seasonal Variations of Herring Distribution in the Barents Sea

In the 1950s-1960s herring distribution was related to their total abundance and to oceanographic factors. Marti (1956) and Shutova-Korzh (1960, 1962) concluded that the duration of the presence of herring in the Barents Sea depends on abundance and year-class strength. During periods with poor year classes, herring remain only for 2-3 years, whereas during periods of abundant year classes, herring may remain up to 7 years. Further,

Table 1. Absolute abundance of herring (billions) in the Barents Sea from 1984 to 1997 (ACFM 1998).

1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997
21.4	10.9	3.0	0.0	0.0	0.0	4.4	29.5	52.3	130.0	85.5	17.3	4.2	6.4

during warm years, herring are broadly distributed to the northwestern, eastern, and southeastern areas and to the entrance into the White Sea, but not in the western and central areas. In cold years, herring distribution was limited by the central and coastal branches of the North Cape Current. Table 1 shows the absolute abundance of herring (billions) in the Barents Sea from 1984 to 1997.

When the area of distribution of herring suddenly decreased in concert with the decrease in abundance, temperature may have played a smaller role in their distribution. This was more apparent in the western and central areas in 1986, 1987, 1990, and 1992 and especially in the eastern areas where herring were infrequent even in the very warm years. Herring were almost absent in the northeastern areas, where there was an increase in abundance and habitat of capelin, the main food competitor.

Herring distribution is strongly linked to its food base in the main habitats. In the western areas the spring phytoplankton bloom begins earlier. This area also supports a high density and the bloom has a long duration. Herring migrate here after wintering, and the concentrations of herring mainly depend on the biomass of copepods. Alternately, in the central and eastern areas, where the summer and autumn feeding occurs, herring depend on the density of euphausiid concentrations (Manteifel 1941).

The residence time of herring varies among different areas. In cold years in the western areas of the Barents Sea, they are limited to 1-2 seasons (often January-February and March-April or March-April only), when herring constitute 56-83% of the total fish biomass in the area. In warm years large herring concentrations are observed for a longer period (two to three seasons) in these areas. A large proportion of the herring remain to overwinter in this area. In cold years in the central sea, herring occur mainly in winter-spring and winter seasons, but in warm years this area became more important for feeding in the summer and autumn.

The seasonal distribution of herring was more clearly defined in the eastern areas where overwintering of herring also occurred in warm years. In this area there is a good correspondence between the depth distribution of herring, the level of plankton development, and the biological condition (fatness) of herring. The onset of migration and its duration in different areas vary and depend directly on conditions of herring feeding and level of their fatness.

Feeding of Herring: Food Composition, Dynamics of Feeding, and Fatness

In 1985, a year of moderate temperatures and in spite of the high fat index (>2) in 2-year-old herring, their feeding activity in the central area wintering grounds increased unusually early, in the middle of January, and at great depths. This was probably connected with the increased demand for food of these young herring. The low biomass of plankton in 1985, exacerbated by the increased early consumption by herring, led to a sharp decrease of herring fatness (~ 0) by mid-February. This promoted more feeding activity and a gradual movement of herring to shallower depths, as well as feeding on euphausiids (in addition to *Calanus*). Herring fed intensively on euphausiids until mid-March. In the majority of western and coastal areas, where herring were at different depths, their feeding and fatness in the spring-winter period was variable. Herring became fat in September-October because of intensive summer-autumn feeding. In spite of the average fatness level, some fish continued to consume food. From October to December, herring migrated to the central areas for wintering after feeding (but did not move to the greatest depths) and had a high index of fatness (1.57-2.44).

In 1986, a year with features peculiar to a cold year, the broad distribution and a low feeding activity promoted a slower expenditure of fat reserves in age-3 herring. These fish began feeding actively in the wintering grounds of the west and central areas when their fatness index ranged from 1.7 to 2.2. This occurred from mid- to late February at depths of 200-250 m. In spite of a relatively low level of plankton development in some areas (e.g., euphausiids in the western sea), the food supply of herring was high because of the sudden decrease of capelin abundance. Herring fed predominantly on euphausiids, and that promoted a high level of fatness between February and March-May. Later, these herring followed the euphausiids and *Calanus* up in the water column, staying at depths of 150-180 m from March to the middle of May, and at the 100-m depth at the end of May. In contrast, in the coastal waters of Murmansk, the main food of herring in the end of May was the deeper small crustaceans. Herring made daily vertical migrations to feed on these at depths of 210-265 m. Because of this intensive feeding, which lasted until October and which was mainly on a high biomass of euphausiids, the herring fat index was between 2.2 and 3.0 by September. Feeding also continued in October in the upper layers (20-30 m). Herring fatness at the end of the season fluctuated greatly (from 1 to 2.4) depending on the food supply in different areas. It was lowest in the extreme western areas, where the maturing herring were concentrated and spending their energy on gonad maturation. During this warm period herring feeding also was influenced by such factors as increased metabolism (an effect of high temperature) and the expansion of herring distribution as well as the behavior and abundance

of plankton organisms, and the plankton consumption by other fish species which also had increased in abundance.

In 1991, there was a sudden increase of capelin but their impact on plankton abundance was not as great. Herring feeding was good due to high biomass levels of *Calanus* and euphausiids. At this time, however, there were only limited data available on herring feeding so only the main seasonal stages of feeding are described. On the overwintering grounds, the feeding was early, beginning in February, and at shallow depths (100-150 m). The later summer-autumn feeding period in western areas ended in early October when herring had a high fatness index (2-3). In the central areas, at a large range of depths (140-240 m), small concentrations of herring with low fatness were found.

In 1992-1993, when the abundance of capelin and herring was high, the biomass of euphausiids was particularly low. The biomass of *Calanus*, however, was relatively high, and that determined their important role in the food of herring in that year. Herring distribution between years was similar to that of other years, although it varied seasonally. In the anomalous warm year of 1992, as with other warm years, the beginning of active feeding of herring in the western areas was in mid-February (at 140 m depth) when the fatness index of herring was high. Their food was diverse, with a slight preponderance of euphausiids and *Calanus*. The subsequent spring-summer feeding of herring was very poor, however, because of the rapid sinking of *Calanus* to the great depths. As a result, herring fatness in August-September was low and did not exceed 1.1-1.2. In October in some areas, herring did not eat. At the end of the feeding season, which lasted till November, herring sank to depths of 150-250 m, and herring fatness fluctuated between 1 and 1.7. In the extreme western areas fatness was higher.

In 1993, the main changes in herring feeding, fatness dynamics, and distribution were associated with *Calanus*, the biomass of which increased two-fold compared to 1992, probably because of the reduction in capelin abundance. Herring fatness did not exceed 1 in January-February because it was low prior to the overwintering period. In the majority of areas the feeding began early: late January in the central sea, and early February in the western areas. In central areas, a large number of fish with low fatness were in the upper 50-m layer from the end of the previous year. In most herring habitats they fed consistently on *Calanus* and a little on euphausiids at different depths (60-220 m) during the whole winter-spring period. Exceptional herring habitats were found in some western and, especially, coastal areas, where feeding on euphausiids was intensive (in the latter case it took place at 50-m depths).

Regular (though moderate) feeding on *Calanus* promoted high fatness of herring until the end of March. However, variable summer feeding (on *Calanus*, mainly) caused reduction and fluctuation of fatness in western and coastal areas. September was a turning point in the year for herring, since some fish then ceased feeding, which led to highly variable fatness

in the population. The most stable situation was observed in the extreme western part of the sea where herring with high fatness (2-3) continued feeding. In the other areas, local and moderate feeding on *Calanus* also continued at a fatness level of 1.1-2.15. At the end of September-October in most of the area, herring ceased eating almost completely. Their fatness fluctuated greatly in the coastal areas and not very much in the western and central areas (from 1.32 to 2.34 in total). In many cases, herring continued to stay in the upper layers. The fish migrated to greater depths only at the end of December where they overwintered at a fatness level of 1.55-2.43.

In subsequent years (1994-1996), capelin abundance was lower and herring feeding changed. In spite of the limited data for those years, it seems that the situation changed back to that seen in previous years, where normal herring seasonal feeding and fat accumulation were promoted by the increased abundance of plankton, especially euphausiids. Under such conditions the herring fat reserves were spent more slowly, and the herring stayed longer on the overwintering grounds.

The Availability of Herring and Their Consumption by Cod

Since the 1930s, it has been known that the importance of herring as food for cod was related to the abundance of herring (Zatsepin and Petrova 1939). In some years (1936, 1937) cod fed on herring during the whole year, but maximally in winter-spring and autumn-winter. Herring accounted for 50-70% of the food of cod, and capelin a much smaller amount. In those years, the occurrence of herring in the summer feeding of cod was also very high (to 30-40%).

In the 1950s-1960s herring were important in the diet of cod (Shutova-Korzh 1966). Cod ate herring more often in the western and central areas, where herring comprised between 28-58% and 37-66%, respectively, of stomach contents. There was no apparent relationship between the intensity of cod feeding on herring. In spite of large year-to-year fluctuations in capelin between the 1930s and 1960s, the incidence of capelin as food for cod was rather stable at 20-23%. After a sudden reduction of herring abundance, in the 1970s, this value began to rise to 40%, on average (Ponomarenko and Yaragina 1985). In the 1980s-1990s, capelin were more abundant than herring (ACFM 1998) and were also more dominant in the food of cod. Nevertheless, in some seasons and years there were conditions when herring were more available. This was especially true in the western areas, where the occurrence of herring in cod stomachs was 46-98%. The heightened consumption of herring occurred at times of both high and low herring abundance. This tendency was seen in the central and coastal areas as well. The characteristics of cod feeding on herring were influenced by several factors, including year-to-year fluctuations of the

feeding rhythm, fat accumulation, and feeding behavior of herring, the direction and dates of their feeding and wintering migrations, as well as the availability of capelin for cod.

The clearest link between cod and herring is seen in years of abundant year classes of herring, such as 1983 and 1991-1992. The unusual data for 1984 (Orlova et al. 1989) proved that cod consumed herring yearlings as early as May, but mainly later in the year (September-October) over a broad range within the central areas. In 1985-1986, in spite of an early increase of herring feeding activity and their migration to middle depths, good conditions for cod to feed on herring still existed. In 1986, herring were intensively consumed by cod as a result of the overlap of concentrations of cod and herring (in the western and central areas). The consumption of herring was intensive on the slopes of the Murmansk Bank and Central Plateau in February during the period that herring feed on euphausiids. A very important factor in that period was the presence of some cod, feeding on herring, at medium depths. These cod were found in catches taken by a pelagic trawl (Ajiad 1990). The percentage of herring in cod food in those catches was 26.6% by weight versus 4.8% in cod caught by a bottom trawl. In the areas of main cod concentrations (Finnmarken and Demidov banks and Murmansk Tongue) cod fed mainly on capelin during the period of their limited local spatial overlap. Capelin and herring were found in equal numbers in cod stomachs (1 specimen per stomach, on average) despite the larger size of the herring (up to 19 cm). In March, the area of cod feeding on herring extended to the west (Murmansk Tongue and Demidovskaya Bank) where the incidence of herring in cod stomachs was 13-14% (or 1 herring for every 2 feeding cod). This coincided with herring feeding on *Calanus* and euphausiids as they did in February. Also in 1986, a low level of cod feeding on herring was found in the coastal areas as well (in February-April and June-August). In autumn the level of cod feeding on herring was low because of their migration to the west. The total weight of herring consumed by cod fluctuated from 2% (1984) to 5.3% and 5% (1985 and 1986, respectively).

In 1992, the main consumption of herring by cod was at the end of the year when large concentrations of migrating cod overlapped those of wintering herring (in the western and central areas). The percentage of young herring in the diet of young cod ranged between 9% and 17% in the northern part of the Novaya Zemlya shallows and the Kanin Bank.

The diet of cod in 1993 was influenced by the prolonged duration of the main concentrations of capelin on the overwintering grounds. This led to an earlier start of cod feeding on herring. It began in February and was most intensive (up to 62% and 23%, respectively, on the Finnmarken and Malangen banks. In other areas, where cod fed on capelin in March-April, only single specimens of herring were found in cod. In May, the feeding of cod was diverse. Herring occurred in cod diets in the area from Nordkyn Bank to the northwestern slope of Murmansk Bank, and in large quantities (to 18-40%) in some areas. The weights of herring in cod diets in

1992-1993 were high, 9.6% in each. In more recent years (1994-1996) capelin abundance decreased, and the boundary of the feeding area of cod extended to the east. As a result, cod fed regularly on herring despite the drop in herring abundance. The feeding took place during different seasons: in 1994, in winter-spring, mainly; and 1995-1997, in spring and autumn-winter seasons, and sometimes in summer. However, the weight of herring in cod stomach contents sharply decreased over the period: from 6.8% and 7.3 % (in 1994 and 1995, respectively) to 1.4% and 0.1% (in 1996 and 1997, respectively).

The total annual consumption of herring by cod (in absolute values) was not large, especially when compared to the consumption of capelin. Even in the years of increased cod feeding on herring it did not exceed 190,000-235,000 t, and the maximum was 383,000 t in 1992. Thus, it is evident that the level of herring consumption in the 1980s-1990s was much lower than that in the 1930s-1950s compared to capelin consumption, and in some years was even smaller than that of other major food items such as shrimp, polar cod, and euphausiids.

Summary and Conclusions

The role of Barents Sea herring in the food of cod was assessed from the results of long-term investigations on the relationship of the horizontal and vertical distribution of herring, with herring feeding conditions in the Barents Sea, and on the general availability of food for cod. In the 1980s-1990s, when herring abundance was low, the main areas of their distribution and feeding were the western and central sea. In the western areas, the distribution of herring was mainly associated with *Calanus* biomass, whereas in the central and eastern areas the association was with euphausiid abundance.

Large fluctuations in abundance of capelin, the main food competitor of herring, impacted the availability of herring for cod. In some years, capelin abundance was enhanced by fluctuations in plankton abundance, and this varied between cold and warm periods. Herring in their 2nd and 3rd year (ages 1+ and 2+) were relatively abundant in the Barents Sea during moderately cold (1985-1986) and warm (1991-1993) periods. In those years, food conditions changed the traditional seasonal pattern of herring feeding, fattening, and vertical distribution.

The diversity of seasonal rhythms of feeding and fat accumulation in herring is associated with the variability of their food base, and this results in large differences in their behavior, including vertical migration. These migrations affect the availability of herring for cod, although the main factor affecting the consumption of herring is its relative abundance compared to capelin. This was especially seen in those years when a sudden change in the ratio of herring and capelin occurred in the Barents Sea. At the same time, independent of the level of consumption of capelin, the availability of herring to cod is more associated with the longer duration

of herring in the bottom and middle depths during the winter-spring and autumn-winter periods. At the present level of abundance, herring do not occupy a dominant position in the diet of cod. However, given the generally low abundance of fish prey for cod, herring do add some stability to the cod diet.

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