ISSN 1429-2335

Bulletin
of the Sea Fisheries Institute

3(151) 2000

CONTENTS

Scientific papers

LEONARD EJSYMONT and KENNETH SHERMAN
Poland and United States' Cooperation
in Fisheries Ecology: A Multidecadal Retrospective 3

MORGAN S. BUSBY, ANN C. MATARESE, DEBORAH M. BLOOD and MAŁGORZATA KONIECZNA
Advancements in Ichthyoplankton Taxonomy in the Northeastern Pacific Ocean
and Bering Sea: Research Conducted by the Alaska Fisheries Science Center 1965-1999 11

ARTHUR W. KENDALL, JR.
Status of Recruitment Studies of Northeast Pacific Fishes 21

ALLYN B. POWELL, DONALD E. HOSS, MAŁGORZATA KONIECZNA and LEONARD EJSYMONT
Summary of Ichthyoplankton Research by the NOAA Beafort Laboratory in Florida Bay,
Everglades National Park, Florida, USA 43

JOANNE LYCZKOWSKI-SHULTZ, MAŁGORZATA KONIECZNA and WILLIAM J. RICHARDS
Occurrence of the Larvae of Beryciform Fishes in the Gulf of Mexico 55

JACK W. JOSSI and JOSEPH KANE
An Atlas of Seasonal Mean Abundances of the Common Zooplankton
of the United States Northeast Continental Shelf Ecosystem 67

KENNETH SHERMAN
Marine Ecosystem Management of the Baltic and Other Regions 89

BENJAMIN H. SHERMAN
Marine Disease, Morbidity and Mortality,Toward a Baltic Sea Ecological Disturbance
Information System 101

PIOTR MARGOŃSKI
Impact of Hydrological and Meteorological Conditions on the Spatial Distribution
of Larval and Juvenile Smelt (*Osmerus eperlanus*) in the Vistula Lagoon (Southern Baltic Sea) 119

INSTRUCTIONS FOR AUTHORS

GENERAL INFORMATION

The Bulletin of the Sea Fisheries Institute is a scientific journal which accepts papers from all over the world. Foreign authors are requested to submit their papers in English, the research staff of the SFI in Polish and authors not associated with the SFI in Polish and English.

Papers submitted to the Bulletin are classified according to the following three categories: 1) scientific papers, 2) short communications, 3) varia.

The Editorial Staff will accept a paper and assign it to one the above categories. Papers accepted for publication in the *Bulletin* may not be published elsewhere. Publication in the *Bulletin* is free of charge.

TYPESCRIPT FORM

Papers should be submitted in two copies of single-sided, double-spaced typescript on A4 paper and a diskette containing all the material in the article must be included. Words to be set in italic type, i.e. Latin names of species and genera, as well as symbols for the values of variables, should be underlined with a wavy line (~~~~~). No other underlineation should be used.

In the papers from categories 1 and 2, the following order is required:

1. **Title**: brief (up to 100 characters).
2. **First and last name of the author** and **the name of the affiliated institution**.
3. An **abstract** must precede every scientific paper, research report and other paper; length – one typewritten page at the most.
4. **Key words**: a few terms which enable a given paper to be found among computer files.
5. **Text.** The length of the typescript of papers from category 1 should not exceed 40 pages, and papers from category 2 – 15 pages. In papers from categories 1 and 2, the traditional division is used: 1) introduction, 2) materials and methods, 3) results, 4) discussion, 5) references. The results of measurements should be given in metric system units and their abbreviations should comply with the International System of Unit (SI).
6. **Acknowledgments** should be limited to the necessary minimum (the initials and the last name of the person they are addressed to, without listing scientific titles or names of institutions).
7. **References** should be put in alphabetical order, with the year of publication directly after the author's name and should list solely the papers referred to in the text. (e.g. Smith 1990). Titles of journals – in full form. Titles of papers – in the original language. The exception is titles in Russian which are in a non-Latin alphabet, such as Cyrilic, which should be translated into either English or Polish.
8. **Footnotes** should be marked with Arabic numerals in superscript (...[1]), and numbered in succession throughout the text, except for tables; footnote content should be on separate sheets of paper.
9. **Tables** should supplement, not duplicate, data contained in the text or figures. Tables should be numbered and each one should be on a separate sheet of paper. All tables must have titles; all references to them should be placed within the text. Each column in a table is supplied with a heading, explaining the content of the column. Footnotes in tables should be marked with letters in italics, in superscript (e. g. Years[a]), and their explanation should be placed under the table.
10. **Figures**. Successive numeration with a reference to each number in the text should be used. Captions must be on a separate sheet of paper. Abbreviations, terms and symbols used in figures must correspond to those used in the text. After scaling, each figure, placed on a separate sheet of paper and marked with a successive number and the author's name, must fit into a column of the *Bulletin*; this should be taken into account by using the appropriate thickness of lines and size of legends in the figures. Only computer generated figures are acceptable. Both a printout and a diskette are required. Papers can be illustrated with photographs in black and white or color. The total content of drawings and photographs must not exceed 30% of the paper.

SAVING TEXT ONTO DISKETTE

Files should be saved on diskette in a format which can be opened by our editorial office. The preferred format is Word for Windows. Please save computer generated figures on diskette in the format which they were created.

REVIEWS

Upon receiving a review, the authors is obliged to revise the paper and to explain in writing which of the reviewer's suggestions he or she has taken into account, and what he or she disagrees with and why.

PROOF-READING

A ten day limit is given for proofreading. At this stage no changes in text content are allowed and only technical corrections will be accepted.

PRESENTATION COPIES

Each author published in categories 1, 2 and 3 receives one copy of the *Bulletin*; the authors of the papers form category 1 additionally receive ten offprints of their paper, and from category 2 – five.

Editorial Office Address:
Center for Scientific Information and Publishing
Sea Fisheries Institute
Kołłątaja 1, 81-332 Gdynia, Poland

WSKAZÓWKI DLA AUTORÓW

INFORMACJE OGÓLNE

The Bulletin of the Sea Fisheries Institute jest czasopismem naukowym, przyjmującym prace z całego świata. Autorzy obcojęzyczni proszeni są o składanie prac w języku angielskim, pracownicy MIR – języku polskim, a pozostali autorzy – w języku polskim i angielskim.

Prace złożone klasyfikowane są według trzech kategorii: 1) artykuły naukowe, 2) noty, 3) varia.

O przyjęciu pracy i zakwalifikowaniu jej do określonej kategorii decyduje Zespół Redakcyjny. Prace przyjęte do druku nie mogą być publikowane w innym czasopiśmie. Publikacja jest bezpłatna.

FORMA MASZYNOPISU

Prace należy składać w 2 egzemplarzach maszynopisu pisanego jednostronnie, formatu A4, z podwójnym odstepem (konieczna jest dyskietka z całością materiału). Słowa, które powinny być złożone drukiem pochyłym (kursywą), tzn. łacińskie nazwy gatunków i rodzajów oraz symbole wielkości zmiennych należy podkreślić wężykiem (~~~~~). Innych podkreśleń nie należy stosować.

W pracach kategorii 1 i 2 obowiązuje następująca kolejność:

1. Tytuł: krótki (do 100 znaków).

2. Imię i nazwisko autora oraz **nazwa i adres instytucji macierzystej.**

3. Abstrakt musi poprzedzać każdy artykuł naukowy i notę; objętość – najwyżej 1 strona maszynopisu.

4. Słowa kluczowe: kilka pojęć pozwalających na odszukanie danej pracy w systemach komputerowych.

5. Tekst. Objętość maszynopisu prac kategorii 1 nie powinna przekraczać 40 stron, a kategorii 2 – 15 stron. W pracach kategorii 1 i 2 stosuje się tradycyjny podział: 1) wstęp, 2) materiał i metoda badań, 3) wyniki badań, 4) dyskusja, 5) bibliografia. Wyniki pomiarów należy podawać w jednostkach miar przyjętych w systemie metrycznym, a ich skróty – zgodnie z Międzynarodowym Układem Jednostek Miar (SI).

6. Podziękowania należy ograniczyć do niezbędnego minimum (inicjały imienia i nazwisko osoby, do której są adresowane, bez wymieniania tytułów naukowych i nazw instytucji).

7. Bibliografię należy zestawiać w porządku alfabetycznym, podając bezpośrednio po nazwiskach autorów rok wydania i wymieniając tylko prace cytowane w tekście (np. Kowalski 1990). Tytuły czasopism – w pełnym brzmieniu. Tytuły prac – w językach oryginału (z wyjątkiem tytułów w języku rosyjskim wydrukowanych alfabetem niełacińskim, np. cyrylicą, które należy przetłumaczyć na język polski lub angielski).

8. Przypisy oznacza się cyfrą arabską we frakcji górnej (...[1]) i numeruje kolejno w całym tekście, z wyjątkiem tabel; treść przypisów – na osobnych stronach.

9. Tabele są dodatkowym źródłem informacji; nie należy powtarzać w nich danych występujących w tekście lub na rysunkach. Tabele numerowane, każda na osobnej stronie, muszą mieć tytuł; powołanie na nie należy umieścić w tekście. Każdą kolumnę w tabeli opatruje się tzw. „główką" wyjaśniającą zawartość kolumny. Przypisy w tabelach należy oznaczyć literami, kursywą, we frakcji górnej (np. Lata[a]), a ich objaśnienie umieścić pod tabelą.

10. Ilustracje. Obowiązuje kolejna numeracja z przywołaniem każdego numeru w tekście. Podpisy pod ilustracjami – na osobnej kartce. Stosowane na rysunkach skróty, terminy i symbole muszą odpowiadać użytym w tekście. Każdy rysunek, umieszczony na osobnej kartce oraz opisany kolejnym numerem i nazwiskiem autora, po wyskalowaniu musi zmieścić sie w kolumnie; trzeba to uwzględnić stosując odpowiednią grubość linii i wielkość opisów na rysunkach. Redakcja przyjmuje wyłącznie rysunki wykonane techniką komputerową (konieczny wydruk i dyskietka). Prace można ilustrować fotografiami (mogą być kolorowe). Łączna objętość rysunków i zdjęć nie może przekraczać 30% objętości pracy.

ZAPIS TEKSTU NA DYSKIETCE

Plik powinien być zachowany na dyskietce w takim formacie, aby umożliwić odczytanie go w programach przez nas stosowanych. Preferowanym formatem jest Word for Windows. Rysunki wykonane techniką komputerową prosimy zapisywać na dyskietce w formacie wykonania.

RECENZJE

Po otrzymaniu recenzji autor jest zobowiązany do poprawienia pracy i wyjaśnienia na piśmie, co uwzględnił z sugestii recenzenta, a z czym się nie zgadza i dlaczego.

KOREKTA AUTORSKA

Na wykonanie i odesłanie korekty autorskiej przewiduje się termin 10-dniowy. Na tym etapie nie należy dokonywać zmian autorskich w tekście, a jedynie poprawić usterki techniczne.

EGZEMPLARZE AUTORSKIE

Każdy autor opublikowanego artykułu otrzymuje 1 egzemplarz czasopisma, autorzy prac kategorii 1 otrzymują ponadto 10 nadbitek swej pracy; kategorii 2 – 5 nadbitek.

Adres Redakcji:
Ośrodek Informacji Naukowej i Wydawnictw
Morski Instytut Rybacki
ul. Kołłątaja 1, 81-332 Gdynia,
tel.: 058 620 17 28 (centrala).

BULLETIN OF THE SEA FISHERIES INSTITUTE
3 (151) 2000

Status of Recruitment Studies of Northeast Pacific Fishes

Arthur W. Kendall, Jr.
Alaska Fisheries Science Center, Seattle, WA 98115, USA

Abstract. Recruitment research is vital to fisheries management, since year-class strength is the most significant biological variable affecting abundance of high latitude fish populations. Year-class strength is usually not well correlated with spawning stock size or environmental variables. Variable survival of early life stages (eggs and larvae) is critical in determining year-class size. The recruitment problem has a long history in fisheries research and its study continues today. The history of such studies in the temperate and subarctic northeast Pacific are traced back to work on Pacific halibut by W. F. Thompson and others. With the discovery in 1980 of a concentrated spawning aggregation of walleye pollock in Shelikof Strait, Gulf of Alaska, recruitment research found a focus that led to expanded studies there and in the Bering Sea. This research has led to annual forecasts of relative year-class strength that help guide management of pollock harvests. In the future, more emphasis needs to be placed on time-scales other than interannual and ecosystem responses such as system productivity, changes in species dominance, and system maturity. This emphasis will require complex long-term and multi-trophic level studies.

Keywords: walleye pollock, Bering Sea, Gulf of Alaska, year-class strength, climate change, FOCI, Johan Hjort

INTRODUCTION

One of the most pervasive characteristics of marine fish populations is that they vary tremendously in abundance over time. At least ten-fold variations in abundance over a few years are common. This creates major problems for the fishing industry and fisheries managers alike: what are the sources of these variations (how much is due to fishing and how much is due to natural variations?), and how can we manage fisheries in the face of them? It has long been realized that natural fluctuations in abundance are largely due to variations in the size of year classes caused by events that modify mortality of young stages from eggs through early juveniles (Smith 1994). Stock sizes are largely determined by the abundance of their component year classes. Although the goal of considerable research has been to understand the causes of fluctuations in year-class strength, this goal remains elusive, and variations in recruitment are still the major source of biological variability facing fisheries managers (Sissenwine 1984; Rothschild 1986). Since mortality of early, mainly planktonic stages is implicated, recruitment

studies involve the interaction of fish and their environment: physical and chemical, as well as biological. However, simple correlations of year-class strength with spawning potential of the population or environmental variables believed to be important to the survival of young stages are almost always ineffective predictors.

Although several hypotheses have been developed to explain the recruitment process (e.g. variations in food production for first-feeding larvae, drift of later larvae in relation to nursery areas (Hjort 1926), timing of the spring bloom in relation to the hatching period of larvae (Cushing 1975), and turbulence and stratification and their effect on larval food (Lasker 1975), none alone has proven sufficient. In at least some cases, interannual differences in survival of juveniles may also be important (Sissenwine 1984). Density-dependent effects also must be important, but they have rarely been convincingly demonstrated (see Myers and Cadigan 1993). We are left with the conclusion that the recruitment process must involve the cumulative effects of many factors acting at different times during the early life histories of fishes. The most critical factors may vary with species, and even for one species, may not be the same every year.

As a result of our difficulties in understanding the recruitment process, fisheries must be managed conservatively, assuming the majority of year classes will be weak. When recruitment is stronger, this results in setting harvest levels that are lower than necessary to maintain a population. If recruitment could be accurately predicted, fisheries harvest strategies could take better advantage of the occasional strong year class. Understanding longer term environmental changes (e.g. climate) and their impact on ecosystems including fished stocks could lead to significant changes in management strategies (Steele 1996).

This paper sets the stage for and describes recruitment studies that have been conducted on marine fishes in the temperate and subarctic northeast Pacific Ocean and eastern Bering Sea. After examining the progress and status of our understanding of recruitment processes of fishes in this area, the potential future direction of such studies is outlined.

HISTORICAL BACKGROUND OF RECRUITMENT RESEARCH

Johan Hjort can be thought of as the father of recruitment studies in fisheries (Kendall and Duker 1998). Although initially a proponent of the widely accepted migration hypothesis to explain fluctuations in fish abundance, through studies of age structure of fish populations and the work of G.O. Sars (Sars 1877), Hjort realized that these fluctuations were mainly caused by variations in year-class strength: “The rich year classes appear to make their influence felt when still quite young; in other words, the numerical value of a year class is apparently determined at a very early stage, and continues in approximately the same relation to that of other year classes throughout the life of the individuals” (Hjort 1914). As mechanisms for establishing year-class strength, he suggested the importance of food for newly hatched larvae and drift to nursery areas: “As factors, or rather events which might be expected to determine the numerical value of a new year-class, I drew attention to the following two possibilities:

(1) That those individuals which at the very moment of their being hatched did not succeed in finding the very special food they wanted would die from hunger. That in other words the origin of a rich year-class would require the contemporary hatching of the eggs and the

development of the special sort of plants or nauplii which the newly hatched larva needed for its nourishment.

(2) That the young larvae might be carried far away out over the great depths of the Norwegian Sea, where they would not be able to return and reach the bottom on the continental shelf before the plankton in the waters died out during the autumn months of their first year of life" (Hjort 1926).

Through his publications and work with ICES (from its beginning in 1902 until his death in 1948, at which time he was its president), Hjort's insight into the causes of fluctuations in the abundance of fishes has stimulated fisheries scientists through the twentieth century. As a result of Hjort's first hypothesis, the period when larvae are changing from getting nourishment from their yolk to when they must feed exogenously became known as the "critical period", and it continues to be a central theme of recruitment research (see May 1974).

In 1914, Hjort undertook a comprehensive investigation of Atlantic waters off the outer coast of Nova Scotia (Hjort 1919; Coker 1962). At the beginning of his survey of fisheries resources, he found himself without needed instruments, so he traveled to Harvard University to borrow them from Henry Bryant Bigelow, who was studying the oceanography, plankton and fish of the Gulf of Maine (Hubbard 1993). During this visit, it is apparent that fluctuations in fish abundance were discussed (see Hubbard 1993). Certainly Hjort's ideas are reflected in the research of two of Bigelow's later students, Lionel Albert Walford and Oscar Elton Sette.

Sette's first published paper dealt with the Pacific sardine fishery. It mentioned interannual fluctuations in abundance, a theme that would pervade the rest of his career (Sette 1920). Two years after graduating from Stanford University in 1922, Sette began his career as a Federal fisheries biologist in Washington, D.C. He was soon puzzling over variations in Atlantic mackerel landings which led him to his doctoral work and a classic publication on the effect of the environment on larval survival, and ultimately year-class strength of Atlantic mackerel (Sette 1943a). Sette concluded, by measuring interannual changes in drift and mortality of cohorts of larvae, that increased mortality during the transition from yolk to exogenous food sources was not a major contributor to variations in mortality, but that variations in drift caused by winds seemed to be correlated with year-class strength. Thus, Sette rejected Hjort's first hypothesis (the critical period) but concurred with his second hypothesis (drift). This was a pioneering study in that population estimates of larval growth and mortality rates were calculated.

Sette conducted these studies in a laboratory on the Harvard University campus. During this period, from 1928-1937, Walford was studying recruitment of haddock at Harvard. Walford was a California native and, like Sette, a Stanford graduate. Hjort's influence on Walford's work is clearly seen in the introduction to the paper on haddock recruitment that resulted from his thesis research, although he did not cite Hjort's studies (Walford 1938).

In 1937, Sette and Walford returned to California to lead Federal investigations into fluctuations in the sardine population and became organizers of what would become the California Cooperative Oceanic Fisheries Investigations (CalCOFI). Sette maintained that to manage fisheries properly, the causes of fluctuations must be understood. Man's impact through fishing could only be evaluated in the context of environmentally induced changes in abundance and distribution. He developed an exhaustive plan for studies that emphasized understanding causes of mortality of young stages (Sette 1943b). CalCOFI has been the largest and most long-lasting of the fisheries oceanography studies in the United States (Scheiber 1990). From the beginning, the program had a broad emphasis: to study the sardine, its environment, and the effects of fishing on the species: "Ultimately we hope to be able to predict what the effect of the environment is on spawning success" (Lasker 1965). The impacts of large-scale

circulation variations on the California Current became appreciated, starting with the 1957-58 El Niño. However, understanding the causes of fluctuations in abundance of sardines, including the role of man, continued to be an elusive goal (Marr 1960; Radovich 1960; Murphy 1961).

Pacific coast fisheries matters were under the dominating influence of William F. Thompson when Sette and Walford returned to California to investigate the causes of the declines in sardine catches. Thompson advocated studying fisheries themselves rather than fish ecology to develop means for managing them. He felt that the abundance of fish stocks would be correlated with catch rates. Sette's study plan for sardine research, which included ecological studies on all life history stages, as well as studies on the impact of the fisheries, was in stark contrast to the more narrowly focused research that would have been advocated by Thompson.

Besides undertaking extensive studies of catch records and age composition, as well as conducting tagging studies, Thompson conducted pioneering studies of Pacific halibut early life history (Thompson and Van Cleve 1934). He thoroughly and accurately illustrated and described their eggs and larvae, and related their distribution to ocean currents and temperature. He conducted these studies at a time when Pacific halibut populations were beginning to rebound from severe overfishing. The International Fisheries Commission had established regulations for the fishery in order to reduce the catch, which Thompson believed had reached levels where egg output was insufficient to replenish the stocks. He considered the impact of environmental factors on survival of eggs and larvae to be less important in determining year-class success than the number of eggs produced at the existent low population levels. He suggested annual monitoring of eggs in the plankton as a means of measuring population size as it increased due to fishing restrictions. There is evidence that Thompson and his colleagues knew of the broadly and ecologically based approach to fisheries issues seen in Sette's plan, but that he felt with limited resources available, studying the fisheries themselves would be sufficient (Scheiber 1994). The continued successful fishery for Pacific halibut is raised as evidence of the value of Thompson's management strategy of controlling fishing effort in response to variations in catch rates, and during his career accorded him considerable political clout and approval from the industry. However, his thesis that variations in abundance were the result of fishing pressure rather than environmental factors led to one of the most contentious debates in the history of fisheries science (the Thompson-Burkenroad Debate: see Skud 1975).

As concerns over fluctuating and heavily fished stocks mounted around the country, discussions were held in La Jolla, California in 1968 among several Federal scientists involved in early life history studies to investigate expanding the type of work CalCOFI was doing. These discussions resulted in a nationwide program: MARMAP (Marine Resources Monitoring, Assessment, and Prediction). Among its goals, this program intended to standardize collection of fish egg and larval data as well as environmental data and to determine seasonal and annual variability in biological and environmental components of the shelf ecosystem that influence the size of recruiting fish populations (Sibunka and Silverman 1984). Several factors conspired to limit participation of scientists from the northeast Pacific in MARMAP: the lingering effects of the Thompson model for fisheries research, an emphasis on Pacific salmon research, and minimally exploited marine fish populations.

NORTHEAST PACIFIC RECRUITMENT STUDIES

The Fish Fauna

When compared with life histories of fishes in other areas, several life history features of northeast Pacific fishes stand out which impact their potential as subjects for recruitment studies. Few northeast Pacific fishes spawn pelagic eggs (Fig. 1), whereas in other areas this is the dominant pattern. This is partially because an inordinate portion of northeast Pacific fishes are scorpaeniforms (Table 1) and most of them produce demersal eggs (e.g. cottids, hexagrammids). Also, within the scorpaeniforms, another group – the speciose and abundant rockfishes (*Sebastes*) – are live-bearers, releasing late yolk-sac larvae. The absence of pelagic eggs constrains the recruitment research that can be done since sampling demersal eggs cannot be done with plankton nets, making their distribution and mortality difficult to assess. Furthermore, larvae from demersal eggs are usually larger and initially better developed than those from pelagic eggs, so starvation is not as much of a factor, and thus larval mortality rates are reduced. In the northeast Pacific, walleye pollock (*Theragra chalcogramma*) and the flatfishes are the most important harvested marine fishes with pelagic eggs. To date, marine recruitment research in the northeast Pacific has focused almost exclusively on the large, ecologically and economically important pollock populations.

Early Studies

Besides considerable descriptive work on early life histories of fishes, and the work of Thompson on halibut, relatively little work was done on recruitment of marine fish of the northeast Pacific until the 1980s. An exception was work on Pacific hake, initiated out of Seattle; however, hake were found to spawn mainly off California (Bailey 1981), so this early life history work was discontinued. Also, Canadian researchers examined the early life history characteristics (egg development and survival in relation to temperature and salinity) of selected species and related them to survival and recruitment (see Alderdice 1985). Until the early 1980s, most fisheries in the northeast Pacific, except those for salmon, crab, and halibut, were rather undeveloped, and conducted mainly by foreign fleets, so there was little impetus for extensive recruitment research.

Gulf of Alaska Research

The increase in the domestic groundfish industry following the discovery of a large spawning aggregation of walleye pollock in Shelikof Strait, Gulf of Alaska, in 1980 opened the way for an extensive recruitment study entitled FOCI (Fisheries-Oceanography Coordinated Investigations). The program goal of FOCI is to understand the relationship between variations in the physical and biological environment and year-class strength of economically important fish and shellfish in Alaska waters using field, laboratory, and modeling studies. In response to several adjacent strong year classes in the late 1970s, pollock in Shelikof Strait reached peak abundance in 1981, and a large fishery developed there on the prespawning fish (Megrey 1989; 1990). This population seemed to be marked by large variations in year-class strength, which made it attractive for FOCI recruitment studies. FOCI studies on this population have been funded since 1985 and primarily involve a collaboration of National Oceanic and Atmospheric Administration (NOAA) physical scientists from the Pacific Marine Environmental Laboratory

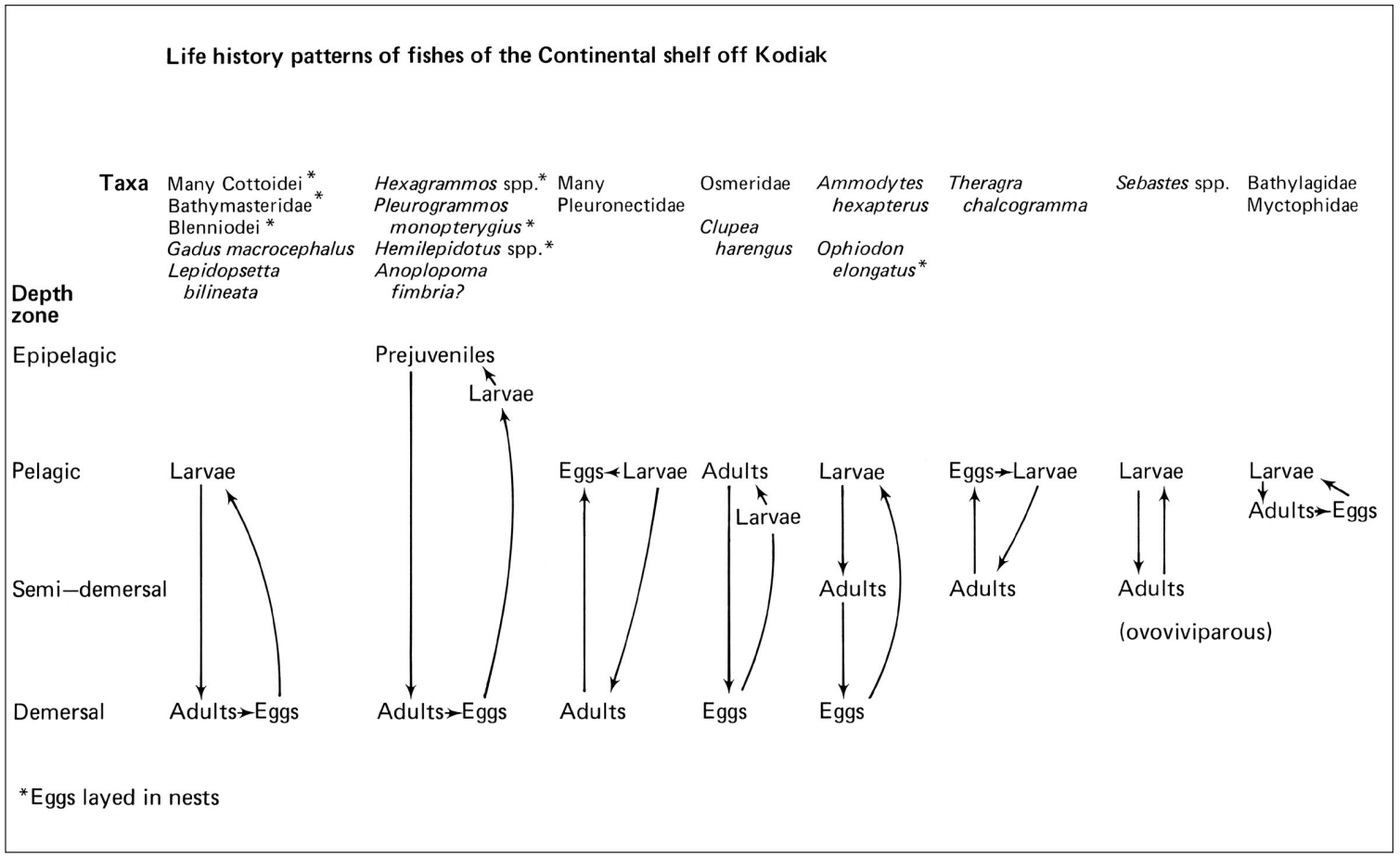


Fig. 1. Representative early life history modes of northeast Pacific subarctic fishes. From Kendall 1981.

Table 1. Taxonomic distribution of fishes worldwide and in the northeast Pacific[1]

Order	Site of egg Development[2]	Families		Numbers of species			Percent of marine species by order		% marine species in NE Pacific
				Worldwide		NE Pacific			
		World	NE Pacific	Marine	Freshwater	Marine	Worldwide	NE Pacific	
Albuliformes	P	3	1	29		2	0.1	0.3	6.9
Anguilliformes	P	15	8	738	6	10	3.2	1.6	1.4
Clupeiformes	P/D	5	2	357	72	5	1.5	0.8	1.4
Osmeriformes	P/D	13	6	236	42	33	1.0	5.2	14.0
Salmoniformes	P/D	1	1	66	45	17	0.3	2.7	25.8
Stomiiformes	P	4	3	321		23	1.4	3.7	7.2
Aulopiformes	P	13	6	219		10	0.9	1.6	4.6
Myctophiformes	P	2	2	241		22	1.0	3.5	9.1
Lampridiformes	P	7	2	19		2	0.1	0.3	10.5
Ophiiformes	P/D	5	3	355	5	10	1.5	1.6	2.8
Gadiformes	P/D/V	12	5	482	1	19	2.1	3.0	3.9
Batrachoidiformes	D	1	1	69	5	1	0.3	0.2	1.4
Lophiiformes	P	16	2	297		7	1.3	1.1	2.4
Atheriniformes	P/D/V	8	1	285	146	2	1.2	0.3	0.7
Beloniformes	P/D	5	1	191	51	1	0.8	0.2	0.5
Stephanoberyciformes	P	9	4	86		10	0.4	1.6	11.6
Beryciformes	P	7	1	123		1	0.5	0.2	0.8
Zeiformes	P/D	6	1	39		1	0.2	0.2	2.6
Gasterosteiformes	P/D	11	3	257	19	4	1.1	0.6	1.6
Scorpaeniformes	P/D/V	25	10	1271	52	273	5.4	43.4	21.5
Perciformes	P/D/V	148	27	9293	1922	143	39.7	22.7	1.5
Pleuronectiformes	P/D	11	3	570	4	32	2.4	5.1	5.6
Tetraodontiformes	P/D	9	1	339	12	1	1.4	0.2	0.3
Totals among orders in the NE Pacific		336	94	15883	2382	629			
Totals worldwide		422		23420	9621				

[1] The numbers of families and species worldwide are from Nelson (1994), those which may occur in marine waters of the northeast Pacific are from Matarese *et al.* (1989). Of the worldwide total of 38 orders of teleosts, 23 occur in the northeast Pacific.

[2] P = pelagic eggs, D = demersal eggs, V = viviparity, Data largely from Breder and Rosen (1966) and Matarese *et al*. (1989).

(PMEL) and biologists from the Alaska Fisheries Science Center (AFSC). The initial paradigm was that recruitment is largely set during the egg and larval stages of pollock by their response to a variety of physical (e.g. advection, turbulence) and biological (e.g. nutrition, predation) processes that determine survival to the juvenile stage. It is thought that surviving larvae pass through a sequence of events during development and that processes which occur during each stage determine the numbers of fish entering the succeeding stage. The hypothesis being tested is that for successful recruitment, transport during the egg and larval stages must be such that most early juveniles reach nursery areas along the Alaska Peninsula. Processes occurring during this transport to juvenile nursery areas are also thought to be important.

Each year adult pollock return to the same deep area (>250 m) of Shelikof Strait (Fig. 2) in a remarkably consistent migratory cycle to spawn (Kim and Nunnallee 1990). Although pollock eggs are found throughout the Gulf of Alaska, most adults migrate to Shelikof Strait for spawning, and subsequent development of eggs and larvae occurs there and in downstream waters (Dunn and Matarese 1987; Kim 1989; Kendall and Picquelle 1990). Spawning is concentrated in late March-early April. Because of the large size of the spawning population, the localized nature of the spawning area, the short duration of the spawning season, and the lack of strong currents at depth, a large "patch" of eggs is produced that can be recognized through plankton surveys of the region. The eggs quickly rise from their deep hatching depth (150-250 m) to the upper 50 m of the water column (Kendall *et al*. 1994), where they usually drift to the southwest in the prevailing currents through late April and May. It appears that the larvae usually take one of two routes as they exit Shelikof Strait: along the Alaska Peninsula in the relatively slowly moving coastal waters or over the sea valley in the more rapidly moving Alaska Coastal Current (ACC) (Kim and Kendall 1989). Variations in prey production and distribution may affect pollock larval growth and survival (Incze *et al*. 1990; Incze and Ainaire 1994; Bailey *et al*. 1995; Theilacker *et al*. 1996). Pollock in Shelikof Strait seem to be vulnerable to starvation-induced mortality for the first 2 weeks following the yolk-sac stage, which

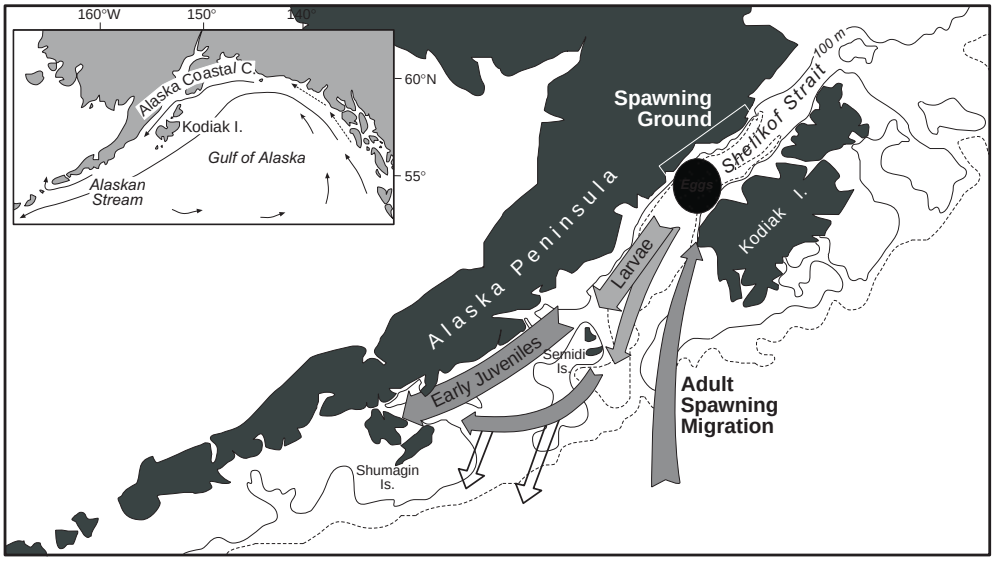


Fig. 2. Features of the early life history of walleye pollock in the Shelikof Strait region, Gulf of Alaska. From Kendall *et al*. 1996.

occurs between the end of April and early May for most larvae. FOCI research has elucidated the dominant current and mesoscale features in the Shelikof Strait region: the ACC, eddies generated by baroclinic instability, and an estuarine-like flow of slope waters into the sea valley, and has provided a better understanding of the influence of atmospheric processes on regional oceanography.

Pollock larvae are often associated with eddies that are frequently created in lower Shelikof Strait (Schumacher *et al*. 1993). Apparently larvae are incorporated into eddies as they rise from their hatching depths to surface waters. Since larvae are frequently found in large patches, and the patches have been associated with eddies on several occasions, the question arises as to what advantage this presents to the larvae. In early May 1989, both naupliar concentration (the primary larval food source) and RNA/DNA ratio of larvae were higher in a patch (Fig. 3) indicating that larvae had been feeding more successfully there than larvae outside the patch which could have contributed to decreased growth rates or increased mortality outside the patch (Canino *et al*. 1991). Current meter records showed the passage of several eddies through the area during spring and summer, and that the currents at the time of the larval study were consistent with the presence of an eddy (Bograd *et al*. 1994). Later in the year, naupliar abundance was greater both in and out of the patch. In addition to providing a good feeding environment, larvae in eddies may be retained in Shelikof Strait longer than those outside eddies, and thus their probability of transport to nursery areas may be improved.

Field data indicate that wind and mixing may also affect larval survival. Bailey and Macklin (1994) suggested several reasons for this relationship, including increased larval prey production in stratified conditions early in the season facilitated by reduced wind-generated turbulence. Laboratory studies (Davis and Olla, in press) and limited field information (Kendall *et al*. 1994) indicate that pollock larvae avoid turbulence above threshold levels, which inhibits swimming and feeding. The presence of relatively warm water initially and the presence of eddies may provide additional favorable conditions for enhanced stratification and larval survival. In some years (e.g. 1989) conditions seemed favorable for early larval survival, but recruitment was weak, suggesting that events later in the early life history of the year class had a negative effect on survival. Larval survival was found to be a necessary, but not sufficient, condition for

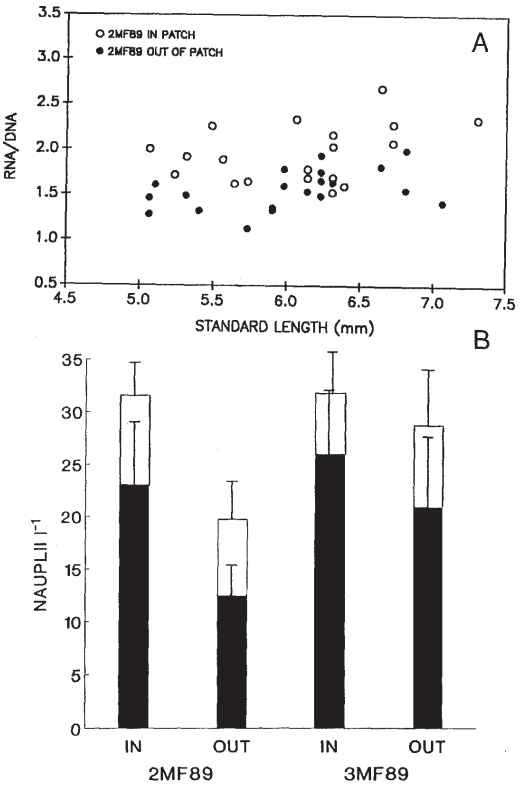


Fig. 3. Comparison of in and out of patch conditions. A. RNA/DNA ratios of walleye pollock larvae. Higher ratios indicate larvae in better condition. B. Naupliar concentration (0-40 m). Black bars = mean integrated, and open bars = maximum concentrations. Error bars represent one standard deviation of the mean. From Canino *et al.* 1991.

good recruitment: in some years, events during the age-0 juvenile stage further influence the size of the year class (Bailey *et al*. 1996).

FOCI developed a coupled biophysical model of the dynamics of the early life stages of pollock in Shelikof Strait. It consists of a semispectral primitive equation model (SPEM) of the regional circulation (Hermann and Stabeno 1996) dynamically coupled with an individual-based model (IBM) that follows young fish through the egg, larval and juvenile stages (Hinckley *et al*. 1997). The trajectories of individual fish through space are computed by treating them as floats, and by using flow fields from the SPEM model. Within the IBM itself, the egg, yolk-sac larval, feeding larval, and juvenile stages are modeled with processes appropriate to each life stage. Prey concentrations are simulated by a Nutrient--Phytoplankton-Zooplankton (NPZ) submodel which dynamically produces food of the appropriate size and type for larvae in a spatially explicit manner. The IBM-SPEM model is a valuable tool to explore the influence of various biological and physical mechanisms on the distribution and survival of young pollock in Shelikof Strait. For example, several times and places for spawning were entered into the model to evaluate drift of eggs and larvae (Hinckley *et al*. in press). Modeled spawning in Shelikof Strait in April resulted in the largest proportion of late larvae reaching the Shumagin Island nursery area.

FOCI found several environmental factors that contribute to interannual variation in survival of eggs and larvae, and found that recruitment is largely set during these stages in most years. This work led to development of a conceptual model of the recruitment process of pollock spawned in Shelikof Strait (Fig. 4). To evaluate the conceptual model, studies are needed to resolve the mechanisms involved, and also to continue the correlative modeling investigations.

FOCI is now providing estimates of relative year-class strength that are considered in management of the Gulf of Alaska pollock fishery. Year-class strength is forecast as weak, average or strong two and three years before the year class recruits to the fishery based on scoring of the biological and physical factors deemed important in the conceptual model (Table 2).

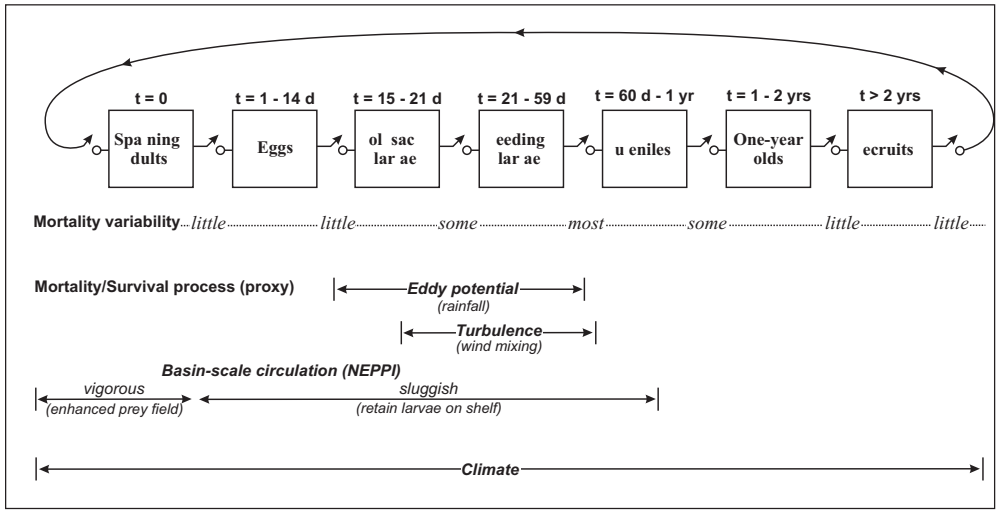


Fig. 4. Conceptual model of the recruitment process of walleye pollock in the Shelikof Strait region, Gulf of Alaska. From Megrey *et al*. 1996.

Table 2. Forecasts of Shelikof Strait walleye pollock recruitment based on FOCI research (from http://www.pmel.noaa.gov/foci/forecast/quant.html).

Year		Element								Total	Initial forecast	Revised forecast	Observed[1]
		Time series model	Time sequence	Hydro length	Rain[2]	Mixing[2]	Advection	Larval abundance	Puffin diet				
1999	Weight	0.00	0.23	0.00	0.23	0.23	0.16	0.15	0.00	1.00			
	Rank		s		a	a-s	a	w-a					
	Score	0.00	2.70	0.00	1.85	2.26	2.00	1.70	0.00		1.98	2.14	
	Total	0.00	0.62	0.00	0.43	0.52	0.32	0.26	0.00	2.14	a	a	
1998	Weight	0.00	0.00	0.00	0.25	0.25	0.25	0.25	0.00	1.00			
	Rank				s	a	a	w					
	Score	0.00	0.00	0.00	2.73	2.18	1.67	1.00	0.00		1.90		
	Total	0.00	0.00	0.00	0.68	0.55	0.42	0.25	0.00	1.90	a		
1997	Weight	0.00	0.21	0.00	0.27	0.15	0.27	0.10	0.00	1.00			
	Rank		a		a-s	a	a-s	a					
	Score	0.00	2.00	0.00	2.44	2.00	2.40	2.00	0.00		2.23		
	Total	0.00	0.42	0.00	0.66	0.30	0.65	0.20	0.00	2.23	a-s		a
1996	Weight	0.00	0.00	0.00	0.25	0.25	0.25	0.25	0.00	1.00			
	Rank				w-a	w-a	a-s	a-s					
	Score	0.00	0.00	0.00	1.72	1.67	2.50	2.50	0.00		2.10		
	Total	0.00	0.00	0.00	0.43	0.42	0.63	0.63	0.00	2.10	a		w
1995	Weight	0.30	0.20	0.00	0.13	0.13	0.13		0.00	1.00			
	Rank	a	s		a-s	a	a	s					
	Score	1.67	3.00	0.00	2.34	1.67	1.67	3.00	0.00			2.00	
	Total	0.50	0.60	0.00	0.29	0.21	0.21	0.38	0.00	2.19	a-s	a	a
1994	Weight	0.50	0.00	0.00	0.13	0.13	0.13	0.13	0.00	1.00			
	Rank	a			s	s	s	a					
	Score	1.67	0.00	0.00	2.34	2.34	2.34	2.00	0.00			2.51	
	Total	0.84	0.00	0.00	0.29	0.29	0.29	0.25	0.00	1.96	a	a-s	a-s
1993	Weight	0.80	0.00	0.00	0.00	0.00	0.00	0.20	0.00	1.00			
	Rank	a						a					
	Score	2.00	0.00	0.00	0.00	0.00	0.00	2.00	0.00			2.14	
	Total	1.60	0.00	0.00	0.00	0.00	0.00	0.40	0.00	2.00	a	a	w-a
1992	Weight	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00			
	Rank		s										
	Score	0.00	3.00	0.00	0.00	0.00	0.00	0.00	0.00			1.75	
	Total	0.00	3.00	0.00	0.00	0.00	0.00	0.00	0.00	3.00	s	w-a	w

[1] Observed recruitment is based on 20, 40, 60, 80 percentiles of estimated recruitment time series as of September 1999.

[2] 1995 and previous forecasts use qualitative estimates of mixing and rain.

Data element score assignments: weak = 1.0, weak-average=1.5, average=2.0, average-strong=2.5, strong=3.0

Recruitment forecast score continuum: 1.0<=weak<1.4<=weak-average<1.8<=average<2.2<=average-strong<2.6<=strong<3.0

Bering Sea Research

Pollock dominate the ecosystem of the Bering Sea, providing most of the food for the extensive marine mammal and bird populations found there (e.g. Lowry *et al*. 1996; Sinclair *et al*. 1996; Springer and Byrd 1989). In the eastern Bering Sea, there are large interannual variations in recruitment of pollock (more than one order of magnitude), and these drive the population size and thus fishery quotas and harvest levels, and probably have a major impact on other components of the ecosystem as well. To develop an understanding of stock structure and recruitment variation in Bering Sea pollock, the Coastal Ocean Program (COP) of NOAA funded an interdisciplinary seven-year (1991-1997) study, the Bering Sea Fisheries Oceanography Coordinated Investigations (BS FOCI; Schumacher and Kendall 1995). The program goals were to: 1) determine pollock stock structure in the Bering Sea and its potential relationship to physical oceanography, and 2) examine pollock recruitment processes in the eastern Bering Sea. Two of the program's hypotheses were: 1) interannual variability of larval survival is due, in part, to variability in food resources, and 2) prey densities in the Oceanic Region are generally less than those encountered in the Shelf Region. A major assumption was that springtime production of most larval prey was initiated by the phytoplankton bloom.

Pollock in the Bering Sea do not form one homogeneous population, but the actual stock structure is not well known. Within the eastern Bering Sea, there are several spawning areas, and these may also be discrete stocks (Hinckley 1987; Bailey *et al*. 1999). These spawnings result in a broad geographic distribution of pollock eggs (Fig. 5). Pollock spawn mainly in two distinct regions in the southeast Bering Sea: the Oceanic Region and the Shelf Region. Spring phytoplankton bloom dynamics vary between the two regions as a result of dissimilarities in their physical characteristics. This leads to differences in conditions that affect the survival of larvae emerging in the two regions (Napp *et al*. 2000).

In the Oceanic Region, advection is strong, but variable, and mesoscale features (eddies) are common. Conditions outside mesoscale features show low interannual variability. Variability in observed plankton standing stocks may be largely due to advective rather than local processes. Larval prey concentrations in the Oceanic Region are generally low and are dominated by less preferable prey for pollock larvae. This may necessitate the larvae supplementing their diet with protists. Mesoscale features may contain much higher prey densities with a larger proportion of the prey types preferred by first-feeding larvae. In some years the Bering Slope Current is eddy-rich, and pollock larvae are found in association with these eddies (Schumacher and Stabeno 1994). To the extent that phytoplankton biomass is a proxy for larval prey concentrations, larvae that find themselves in these dynamic features may have a lower probability of starvation than those outside such features.

In the Shelf Region, advection is generally low, but there is considerable interannual variability from a complex set of forcing functions: sea ice, wind mixing, temperature, and insolation result in phytoplankton blooms with different timing, magnitude, and transfer efficiencies to the zooplankton and nekton (or benthos). Sea ice affects the stability and temperature of the water column, the developmental rate of larvae, and the timing of the phytoplankton bloom (and potentially the match/mismatch of larvae and prey). Ice cover and the cold pool also influence distributions of higher trophic level biota (Ohtani and Azumaya 1995; Wyllie-Echeverria 1995). In the Shelf Region, preferred prey have been found to be a larger fraction of the available prey than in the Oceanic Region, but copepod nauplii were still at minimal levels for growth and survival (Napp *et al*. 2000).

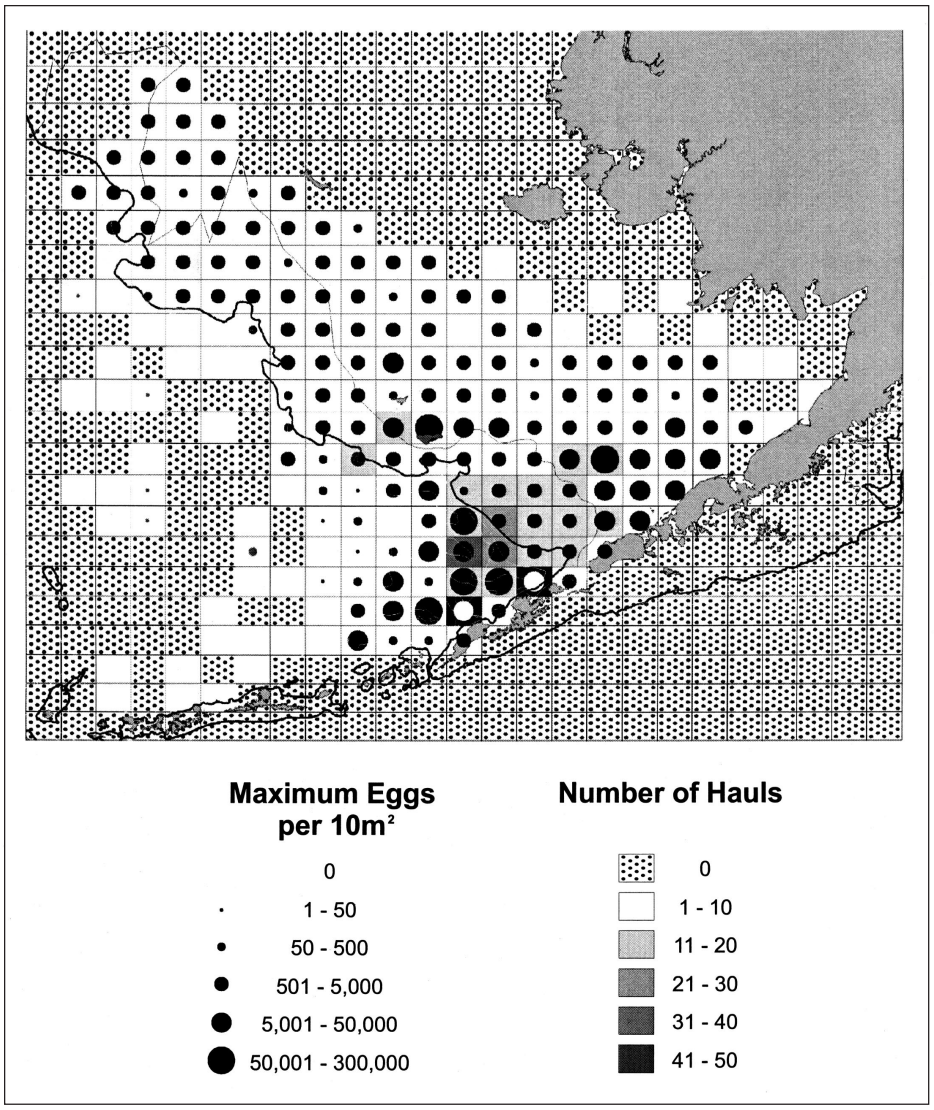


Fig. 5. Historical distribution of maximum densities of walleye pollock eggs in the southeastern Bering Sea (Dell Arciprete, pers. comm.). Data are from 15 cruises, February to May, 1971-1993. Sampling quadrants are the dark squares and the black dots are where eggs were found. From Napp *et al*. 2000.

Formation of sea ice in the eastern Bering Sea generally begins in November with maximum ice extent occurring in late March. A bloom of phytoplankton associated with the sea ice (Stabeno *et al*. 1998) accounts for 10 - 65 % of the total annual primary production (Niebauer *et al*. 1990). Previously unreported under-ice spring phytoplankton bloom dynamics were observed using moored biophysical instruments (Fig. 6). In 1995, a heavy ice year, the under-ice bloom persisted despite an unstable water column: Lagrangian drifters with optical sensors did not detect a subsequent main bloom. Spring winds that year were not strong enough to

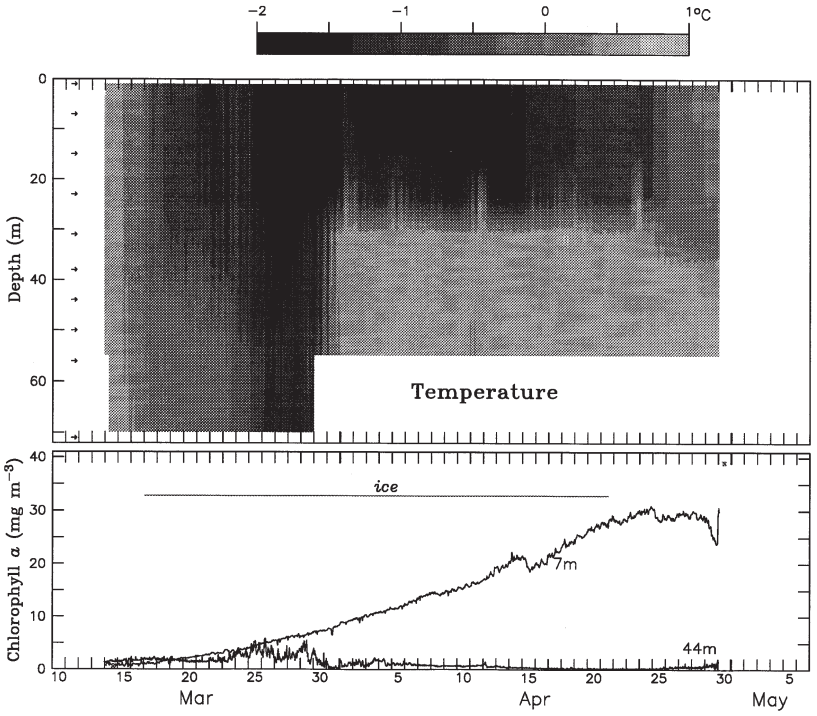


Fig. 6. Time course of a spring phytoplankton bloom under sea ice on the southeastern Bering Sea shelf during a heavy ice year (1995). Upper panel shows temperature with depth, lower panel shows period of ice cover and chlorophyll concentration (mg · m^3) at 7 and 44 m. Modified from Stabeno *et al*. 1998.

erode the pycnocline and replenish surface nutrients. In 1996, a year with minimal ice, the spring bloom was not detected until the first week of May. Thus, the presence or absence of sea ice and springtime winds has an influence on the timing, location, and number of spring blooms. Variability between these two physical factors (ice and wind) may have a strong impact on larval pollock survival in the spring.

Thus, it is believed that the key to interannual variation in food for first feeding pollock larvae in the Oceanic Region is advection, while in the Shelf Region it is the coupled dynamics of the atmosphere-ice-ocean system. While the BS FOCI was unable to relate feeding success of early larvae directly to year-class success of Bering Sea pollock, a conceptual model of this portion of the life history was developed (Fig. 7), which has provided guidance for future studies.

Partially as a follow up to the BS FOCI, NOAA's COP has funded a further multi-year (1996-2000) study, the Southeast Bering Sea Carrying Capacity (SEBSCC) program looking more broadly at the role of pollock in the Bering Sea ecosystem. Emphasis is on the juvenile stage of pollock; at this time they are preyed upon by a variety of predators including adult pollock, groundfish, marine mammals and seabirds. They are abundant enough to compete for food (zooplankton) with other components of the pelagic ecosystem. There is evidence that cannibalism may be a major source of mortality of juvenile pollock, and interannual differences in the overlap of juveniles and adults may influence year-class success (Bailey 1989). SEBSCC is examining oceanographic and biological factors that may influence the productiv-

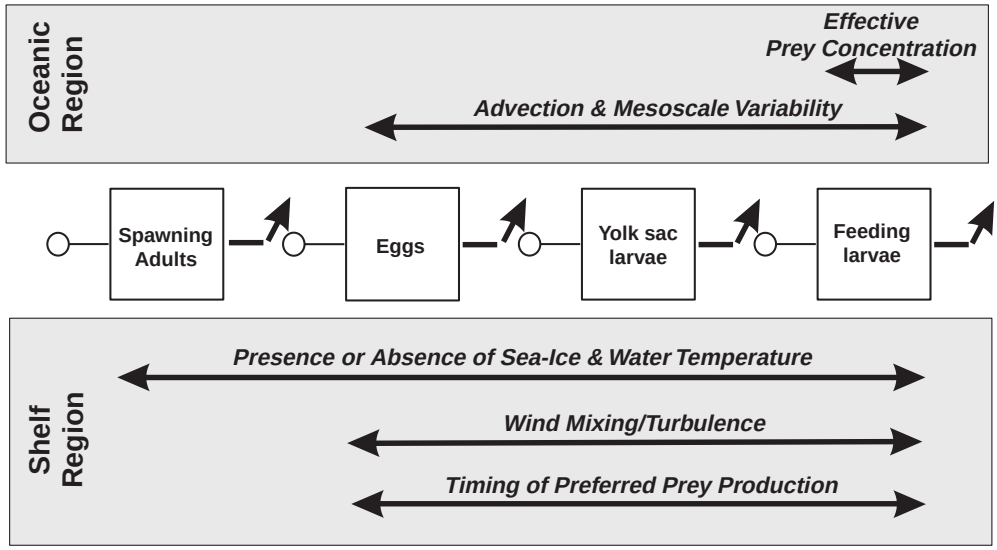


Fig. 7. Conceptual switch model of walleye pollock early larval dynamics for the Oceanic and Shelf Regions of the southeastern Bering Sea. From Napp *et al*. 2000.

ity of the area and the distribution and abundance of juvenile pollock. It appears that SEBSCC field studies are observing major ecosystem changes in the Bering Sea (Macklin 1999). Unusually warm surface water occurred in the summers of 1997 and 1998 and large blooms of coccolithophorids were seen for the first time in the Bering Sea (Vance *et al*. 1998). The causes and impacts of these blooms are not yet fully understood, but there were concomitant major seabird die-offs and lower-than-expected salmon runs (Kruse 1998). The influence of these unusual conditions on pollock recruitment is the subject of ongoing research (Napp and Hunt, accepted).

FUTURE DIRECTIONS

Time scales of variability and biological responses

While most recruitment research to date has focused on interannual variations in year-class strength of individual species or stocks, it is becoming increasingly apparent that inter-species and inter-year patterns of recruitment exist. For examples consider: sardine and anchovy recruitment varies over a cycle of about 60 years in eastern boundary currents around the world (Baumgartner *et al*. 1992; Klyashotorin and Smirnov 1995), the gadoid outburst in the North Sea (Cushing 1980), shifts in dominance between herring and mackerel in the northwest Atlantic (Skud 1982), a correlation between recruitment of cod and pollock in the eastern Bering Sea, and the inverse relationship between production of several Pacific salmon stocks in Alaska waters and those off the west coast of the United States (Mantua *et al*. 1997). Besides interannual

variability and local conditions, recruitment is likely affected by environmental processes that vary on large spatial and low frequency temporal scales. Future recruitment studies should not ignore these environmental processes and how they affect recruitment.

Significant advances have been made in the last decade in understanding climate variation and its impact on the ocean. The atmosphere varies on several time scales from diel, to event (storm), to seasonal, to interannual, to decadal, and longer (global climate change). The importance of decadal variability on marine communities and productivity is just now being recognized (Francis *et al*. 1998). Decadal variability is due to a number of processes that can act together or oppose each other to produce conditions observed at any one time. Extreme conditions occur when all of these processes push the climate in the same direction. In the north Pacific, the El Niño-Southern Oscillation is the best understood large-scale process that affects the climate and ocean. El Niños are now being forecast and their influence on the weather and physical ocean conditions are predicted (Chen *et al*. 1995). They impact ocean productivity through disturbance of coastal upwelling. Distributions of marine organisms are changed due to warming of the water. El Niños seldom last more than a few months and occur once or twice a decade. Although El Niños originate in the tropics, the effects of some of them on the ocean can be measured at high latitudes. These effects reach high latitudes both through direct transfer of energy and through teleconnections between atmospheric conditions in the tropics and at higher latitudes.

The next longer scale of climatic variation in the north Pacific is characterized by the Pacific Decadal Oscillation (PDO)(Mantua *et al*. 1997). The phase of the PDO changes at frequencies of about 20-30 years. Negative PDO values are associated with relatively warm sea surface temperatures in the northeast Pacific. PDO was negative through most of the 1960s and 1970s and has been mainly positive since 1977. The abrupt change in magnitude and sign of the PDO between 1976 and 1977 (Miller *et al*. 1994) coincided with dramatic changes in population levels of numerous species in the northeast Pacific and has been termed a Regime Shift (Beamish *et al*. 1999). The entire ecosystem of the region may have shifted from one steady state condition to another at this time. Enhanced primary productivity caused by higher temperatures and shallow mixed layer depths following the 1977 regime shift may have worked its way up the food chain through increased zooplankton abundance (Brodeur and Ware 1992) to produce the high abundances of Alaska salmon that have been present since then.

At an even longer time scale, current increasing temperatures may signal global climate change. Schumacher *et al*. (submitted) have reported recent increases in temperature and decreases in sea ice in the Bering Sea, and Wiles *et al*. (1998) have reported recent warming in the Gulf of Alaska. Several groups of north Pacific and Bering Sea marine animals are showing long-term monotonic changes in abundance (e.g. Roemmich and McGowan 1995; Hill and Demaster 1988; Brodeur *et al*. 1999). Whether these are responses to conditions associated with gradual large-scale increases in temperature, and whether these changes are partially or wholly man-induced are subjects of considerable ongoing research.

A new paradigm for recruitment research

Given that lower frequency (longer than interannual) variations in recruitment are commonplace, and may be the most important mode in determining abundances of many stocks, and that recruitment patterns of co-occurring species are often inter-related, how should we study

recruitment? Statistical procedures examining patterns of recruitment in relation to environmental variables may point to areas of importance, but they are unlikely to produce an understanding of biological responses to the environment. They will be no more effective for understanding or predicting recruitment than stock/recruitment based studies have been in the past. An understanding will involve examining mortality/survival of eggs, larvae and juveniles: what are the age-specific rates, how do they vary, and what are the causes of variation? We should try to pry open the black box of recruitment since this holds the key to longer term trends (Steele 1996).

Thinking that one factor acting on one life stage is responsible for recruitment variation will continue to be unsuccessful. Even for one species, the factors and stages that are critical may vary with time. Therefore, I propose that to understand recruitment well enough to produce forecasts that managers need, research must consider year-class variation in light of longer time scales and ecosystem processes.

Time scales: Single season or short-term projects will not provide the answers. Recruitment in many species is autocorrelated: year-class strength varies on time scales longer than interannual. Studies of even five years duration may only observe one general level of recruitment, or at best the transition from one level to another. While there are interannual variations in the environment, these occur in the context of longer scales of variability. Climatic events such as regime shifts may create perturbed ecosystems that take several years to regain a state of maturity, where biological processes are more important than physical processes in determining population levels. There are variable lags between changes in abundance of long-lived predators and their prey in their response to low frequency environmental conditions. Recruitment studies must take into account the climatic state of each year under investigation. Clearly, long time scales (20-40 years) must be considered. Retrospective, laboratory and modeling studies can partially augment field studies to extend the time horizon.

Multiple trophic levels: The importance of both bottom-up (food) and top-down (predation) processes probably varies among species and stages within a species, and may change under different environmental conditions. The basic productivity (carrying capacity) of ocean systems seems to change under different climatic regimes (e.g. Roemmich and McGowan 1995; Polovina *et al*. 1994). Interannual and longer time scale temperature differences may impact the timing of the spring bloom and rate of reproduction and development of copepods which provide food for larvae and cause a mis-match between food availability and occurrence of larvae. The abundance and distribution of larval and juvenile predators may likewise be impacted by large-scale atmospheric and oceanic conditions, and thus influence survival. Also, the effects of parasites and diseases cannot be ruled out as sources of mortality. Therefore, recruitment studies must examine factors affecting production and distribution of trophic levels both above and below the early stages of fishes.

Multi-species focus: Since recruitment of several species in an area often seems to be related either positively or negatively, more understanding should be gained by studying them together. In fact, the recruitment process of one such species may never be understood without taking into consideration co-occurring species. In some cases, different temperature regimes seem to favor one species over another, but what is the actual causal mechanism? For example, is it development rate of the eggs and larvae, or does temperature affect the production of larval food: timing and preferred species? Once a species becomes dominant, can it prevent another species from assuming that role through predation or competition?

CONCLUSIONS

Recruitment variation was a major focus of fisheries research through most of the twentieth century, but year-class strength continued to be as unpredictable as it was in Hjort's time at the beginning of the century. With the beginning of a new century, and its promise of better tools to apply to the problem, should we expect to increase our understanding? I think the answer is yes, but only if we look at the problem from a much broader perspective than we have in the past. Will we have a chance to do so? Only our funding agencies can answer that. "I continued to work intermittently on the Stock Recruitment Relationship. We now know that the only way in which the problem will be solved is in the examination of the dynamics of life in the larval stages. The research is needed and, without it, management will remain self-defeating. Paymasters will learn this, if slowly, so slowly" (Cushing 1996).

REFERENCES

Alderdice, D.F. 1985. A pragmatic view of early life history studies of fishes. Trans. Amer. Fish. Soc. 114: 445-451.

Bailey, K.M. 1981. Larval transport and recruitment of Pacific hake *Merluccius productus*. Mar. Ecol. Prog. Ser. 6:1-9.

Bailey, K.M. 1989. Interaction between the vertical distribution of juvenile walleye pollock *Theragra chalcogramma* in the eastern Bering Sea, and cannibalism. Mar. Ecol. Prog. Ser. 53: 205-213.

Bailey, K.M., M.F. Canino, J.M. Napp, S.M. Spring, and A.L Brown. 1995. Contrasting years of prey levels, feeding conditions and mortality of larval walleye pollock *Theragra chalcogramma* in the western Gulf of Alaska. Mar. Ecol. Prog. Ser. 119:11-23.

Bailey, K.M., R.D. Brodeur, and A.B. Hollowed. 1996. Cohort survival patterns of walleye pollock, *Theragra chalcogramma*, in Shelikof Strait, Alaska: a critical factor analysis. Fish. Oceanogr. 5 (Suppl. 1): 179-188.

Bailey, K.M. and S.A. Macklin. 1994. Analysis of patterns in larval walleye pollock *Theragra chalcogramma* survival and wind mixing events in Shelikof Strait, Gulf of Alaska. Mar. Ecol. Prog. Ser. 113:1-12.

Bailey, K.M., T.J. Quinn, P. Bentzen, and W.S. Grant. 1999. Population structure and dynamics of walleye pollock, *Theragra chalcogramma.* Adv. Mar. Biol. 35:177-253.

Baumgartner, T.R., A. Soutar, and V. Ferreira-Bartrina. 1992. Reconstruction of the history of Pacific sardine and northern anchovy populations over the past two millennia from sediments of the Santa Barbara Basin. CalCOFI Rep. 33:24-40.

Beamish, R.J., D.J. Noakes, G.A. McFarlane, L. Klyashtorin, V.V. Ivanov, and V. Kurashov. 1999. The regime concept and natural trends in the production of Pacific salmon. Can. J. Fish. Aquat. Sci. 56:516-526.

Bograd, S.J., P.J. Stabeno, and J.D. Schumacher. 1994. A census of mesoscale eddies in Shelikof Strait, Alaska, during 1989. J. Geophys. Res. 99:18243-18254.

Brodeur, R.D., C.E. Mills, J.E. Overland, G.E. Walters, and J.D Schumacher. 1999. Evidence for a substantial increase in gelatinous zooplankton in the Bering Sea, with possible links to climate change. Fish. Oceanogr. 8: 296-306.

Brodeur, R.D. and D.M. Ware. 1992. Interannual and interdecadal changes in zooplankton biomass in the subarctic Pacific Ocean. Fish. Oceanogr. 1:32-38.

Canino, M.F., K.M. Bailey, and L.S. Incze. 1991. Temporal and geographic differences in feeding and nutritional condition of walleye pollock larvae *Theragra chalcogramma* in Shelikof Strait, Gulf of Alaska. Mar. Ecol. Prog. Ser. 79:27-35.

Chen, D., S.E. Zebiak, A.J. Busalacchi, and M.A. Cane. 1995. An improved procedure for El Niño forcasting: implications for predictability. Science 269:1699-1702.

Coker, R. E. 1962. This great and wide sea. Harper Torchbooks, Harper & Row, New York. 235 p.
Cushing, D. H. 1975. Marine ecology and fisheries. Cambridge University Press. 278 p.
Cushing, D. H. 1980. The decline of the herring stocks and the gadoid outburst. J. Cons. Explor. Mer. 39: 70-81.
Cushing, D.H. 1996. Towards a science of recruitment in fish populations. Ecology Institute, Germany. 175 p.
Davis, M.W. and B.L. Olla. In review. Behavioral responses of walleye pollock, *Theragra chalcogramma,* larvae to experimental gradients of seawater flow: implications for vertical distribution, feeding and growth. Environ. Biol. Fish.
Dunn, J.R. and A.C. Matarese. 1987. A review of the early life history of Northeast Pacific gadoid fishes. Fish. Res. 5: 63-184.
Francis, R.C., S.R. Hare, A.B. Hollowed, and W.S Wooster. 1998. Effects of interdecadal climate variability on the oceanic ecosystems of the NE Pacific. Fish. Oceanogr. 7: 1-21.
Hermann, A.J. and P.J. Stabeno. 1996. An eddy resolving model of wind- and buoyancy-forced circulation in the western Gulf of Alaska. I. Model development and sensitivity analyses. J. Geophys. Res. 101: 1129-1149.
Hill, P.S. and D.P. Demaster. 1998. Alaska marine mammal stock assessments, 1998. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-97, 166 p.
Hinckley, S. 1987. The reproductive biology of walleye pollock, *Theragra chalcogramma, i*n the Bering Sea, with reference to spawning stock structure. Fish. Bull., U.S. 85: 481-498.
Hinckley, S., A. Hermann, and B.A. Megrey. 1997. Development of a spatially explicit, individual-based model of marine fish early life history. Mar. Ecol. Prog. Ser. 139: 47-68.
Hinckley, S., A.J. Hermann, K.L. Meir, and B.A. Megrey. In press. The importance of spawning location and timing to successful transport to nursery areas: a simulation modeling study of Gulf of Alaska walleye pollock. ICES J. Mar. Sci.
Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp. P.-v. Reun. Cons. Int. Explor. Mer. 20: 1-228.
Hjort, J. 1919. Canadian fisheries expedition, 1914-1915. Dep. Nav. Serv., Ottawa. 495 p.
Hjort, J. 1926. Fluctuations in the year classes of important food fishes. J. Cons. Int. Explor. Mer. 1: 5-38.
Hubbard, J. M. 1993. An independent progress: The development of marine biology on the Atlantic coast of Canada 1898-1939. Ph.D. Dissert. Univ. Toronto. 446 p.
Incze, L. S. and T. Ainaire. 1994. Distribution and abundance of copepod nauplii and other small (40-300 μm) zooplankton during spring in Shelikof Strait, Alaska. Fish. Bull., U.S. 92: 67-78.
Incze, L. S., P. B. Ortner, and J. D. Schumacher. 1990. Microzooplankton, vertical mixing and advection in a larval fish patch. J. Plank. Res.12:365-379.
Kendall, A.W., Jr. 1981. Early life history of eastern North Pacific fishes in relation to fisheries investigations. Washington Sea Grant Tech. Rep., Univ. Washington, Seattle. 81-3. 7 p.
Kendall, A.W., Jr. and G.J. Duker. 1998. The development of recruitment fisheries oceanography in the United States. Fish. Oceanogr. 7:69-88.
Kendall, A.W., Jr., L. S. Incze, P.B. Ortner, S.R. Cummings, and P.K. Brown. 1994. The vertical distribution of eggs and larvae of walleye pollock, *Theragra chalcogramma,* in Shelikof Strait, Gulf of Alaska. Fish. Bull., U.S. 92:540-554.
Kendall, A.W., Jr., J. D. Schumacher, and S. Kim. 1996. Walleye pollock recruitment in Shelikof Strait: applied fisheries oceanography. Fish. Oceanogr. 5 (Suppl. 1): 4-18.
Kendall, A.W., Jr. and S. J. Picquelle. 1990. Egg and larval distributions of walleye pollock, *Theragra chalcogramma*, in Shelikof Strait, Gulf of Alaska. Fish Bull., U.S. 88:133-154.
Kim, S. 1989. Early life history of walleye pollock, *Theragra chalcogramma*, in the Gulf of Alaska. In: Proceedings of the international symposium on the biology and management of walleye pollock, November 14-16, 1988, Fairbanks, AK, p. 117-139. Alaska Sea Grant Rep. 89-1, Univ. Alaska, Fairbanks, 789 p.

Kim, S. and A. W. Kendall, Jr. 1989. Distribution and transport of larval walleye pollock (*Theragra chalcogramma*) in Shelikof Strait, Gulf of Alaska, in relation to water movement. Rapp. P.-v. Réun. Cons. int. Explor. Mer. 191: 127-136.

Kim, S. and E. P. Nunnallee. 1990. Distribution of walleye pollock, *Theragra chalcogramma,* spawning in Shelikof Strait, Gulf of Alaska, based on acoustic and ichthyoplankton surveys 1981, 1984, and 1985. Bull. Korean Fish. Soc. 23: 425-438.

Kruse, G. H. 1998. Salmon run failures in 1997-1998: A link to anomalous ocean conditions? Alaska Fish. Res. Bull. 5: 55-63.

Klyashtorin, L. and B. Smirnov. 1995. Climate-dependent salmon and sardine stock fluctuations in the North Pacific. Can. J. Fish Aquat. Sci., Special Pub. 121: 687-689.

Lasker, R. 1965. Symposium on larval fish biology. Preface. CalCOFI Rep. 10:12.

Lasker, R. 1975. Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. Fish. Bull., U.S. 73: 453-462.

Lowry, L. F., V. N. Burkanov, and K.J. Frost. 1996. Importance of walleye pollock, *Theragra chalcogramma*, in the diet of phocid seals in the Bering Sea and northwestern Pacific Ocean. In: Ecology of Juvenile Walleye Pollock, *Theragra chalcogramma,* R. D. Brodeur, P. A. Livingston, T. R. Loughlin, and A. B. Hollowed (eds.), U. S. Dep. Commer., NOAA Tech. Rep. NMFS 126, p.141-152.

Macklin, S. A. (Ed.) 1999. Report on the FOCI international workshop on recent conditions in the Bering Sea. U. S. Dep. Commer., NOAA ERL Spec. Rep., Jan. 1999. 47 p.

Mantua, N. J., S. R. Hare, Y. Zhang, J. M. Wallace, and R. C. Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. Bull Am. Meteorol. Soc. 78: 1069-1079.

Matarese, A. C., A.W. Kendall, Jr., D. M. Blood, and B. M. Vinter. 1989. Laboratory guide to early life history stages of Northeast Pacific fishes. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 80. 652 p.

Marr, J. C. 1960. The causes of major variations in the catch of the Pacific sardine, *Sardinops caerulea*, (Girard). In: Proceedings of the world scientific meeting on the biology of sardines and related species. H. Rosa, Jr. and G. Murphy Eds. 3. FAO. p. 667-791.

May, R .C. 1974. Larval mortality in marine fishes and the critical period concept. In: The early life history of fish. J.H.S. Blaxter, ed. Springer-Verlag, New York. p. 3-19.

Megrey, B. A., A.B. Hollowed, S.R. Hare, S.A. Macklin, and P.J. Stabeno. 1996. Contributions of FOCI research to forecasts of year-class strength of walleye pollock in Shelikof Strait, Alaska. Fish. Oceanogr. 5 (Suppl. 1): 189-203.

Megrey, B. A. 1989. Population dynamics of walleye pollock (*Theragra chalcogramma*) in the Gulf of Alaska. Ph.D. Dissertation, University of Washington, Seattle, WA, 385 p.

Megrey, B. A. 1990. Population dynamics and management of walleye pollock stocks in the Gulf of Alaska, 1976-1986. Fish. Res. 11: 321-354.

Miller, A. J., D. R. Cayan, T. P. Barnett, N. E. Graham, J. M. Oberhuber. 1994. The 1976-77 climate shift in the Pacific Ocean. Oceanography 7: 21-26.

Murphy, G. I. 1961. Oceanography and variations in the Pacific sardine population. CalCOFI Rep. 8: 55-64.

Myers, R. A. and N. G. Cadigan. 1993. Density-dependent juvenile mortality in marine demersal fish. Can. J. Fish. Aquat. Sci. 50: 1576-1590.

Napp, J. M., A. W. Kendall, Jr., and J. D. Schumacher 2000. A synthesis of biological and physical processes affecting the feeding environment of larval walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea. Fish. Oceanogr. 9: 147-162.

Napp, J. M. and G. L. Hunt, Jr. Anomalous conditions in the Southeastern Bering Sea, 1997: Linkages between climate, weather, and biology. Fish. Oceanogr. accepted.

Nelson, J. S. 1994. Fishes of the world. 3rd Ed. John Wiley & Sons, New York.

Niebauer, H. J., V. A. Alexander, and S. Henrichs. 1990. Physical and biological oceanographic interaction in the spring bloom at the Bering Sea marginal ice edge zone. J. Geophys. Res. 95: 22,229-22,242.

Ohtani, K. and T. Azumaya. 1995. Interannual change of the sea conditions on the continental shelf and its influence on abundance of walleye pollock in the eastern Bering Sea. Can. J. Fish Aquat. Sci., Spec. Pub. 121: 87-95.

Polovina, J.J., G.T. Mitchum, N.E. Graham, M.P. Craig, E.E. Demartini, and E.N. Flint. 1994. Physical and biological consequences of a climate event in the central North Pacific. Fish. Oceanogr. 3: 15-21.

Radovich, J. 1960. Some causes of fluctuations in catches of the Pacific sardine *Sardinops caerulea* (Girard). In: Proceedings of the world scientific meeting on the biology of sardines and related species. H. Rosa, Jr. and G. Murphy Eds. 3. FAO. p. 1081-1093.

Roemmich, D. and J. McGowan. 1995. Climatic warming and the decline of zooplankton in the California Current. Science 267: 1324-1326.

Rothschild, B. J. 1986. Dynamic of marine fish populations. Harvard Univ. Press, 277 p.

Sars, G. O. 1877. Report of practical and scientific investigations of the cod fisheries near Lofoten Islands, made during the years 1861-1869. Translat. by H. Jacobsen. In Rep. U.S. Comm. Fish. 5: 565-661.

Scheiber, H. N. 1990. California marine research and the founding of modern fisheries oceanography: CalCOFI's early years, 1947-1964. CalCOFI Rep. 31: 63-83.

Scheiber, H.N. 1994. Modern U.S. Pacific oceanography and the legacy of British and Northern European science. In: Man and the maritime environment. S. Fisher (ed.). Exeter Maritime Studies Number 9. University of Exeter Press. p. 36-75.

Schumacher, J. D. and A.W. Kendall, Jr. 1995. An example of fisheries oceanography: walleye pollock in Alaskan waters. Rev. Geophys. Suppl. 33: 1153-1163.

Schumacher, J. D. and P.J. Stabeno. 1994. Ubiquitous eddies of the eastern Bering Sea and their coincidence with concentrations of larval pollock. Fish. Oceanogr. 3: 182-190.

Schumacher, J. D., P.J. Stabeno, and S. J. Bograd. 1993. Characteristics of an eddy over a continental shelf: Shelikof Strait, Alaska. J. Geophys. Res. 98: 8395-8404.

Schumacher, J. D., N.A. Bond, R.D. Brodeur, P.A. Livingston, J.M. Napp, and P.J. Stabeno. Changes in the physical environment of the Eastern Bering Sea and some potential consequences for biota. In: Large Marine Ecosystems of the World--Trends in Exploitation, Protection, and Research. Hempel, G. and K. Sherman (Eds.). submitted.

Sette, O. E. 1920. The sardine problem in the Monterey Bay district. Calif. Fish Game. 6: 181-182.

Sette, O. E. 1943a. Biology of the Atlantic mackerel (*Scomber scombrus*) of North America. Pt. 1: Early life history, including growth, drift, and mortality of the egg and larval populations. U.S. Fish Wildl. Serv., Fish. Bull. 50: 149-237.

Sette, O. E. 1943b. Studies on the Pacific pilchard or sardine, (*Sardinops caerulea*). 1. – Structure of a research program to determine how fishing affects the resource. U. S. Fish Wildl. Serv., Spec. Sci. Rep. 19, 27 p.

Sibunka, J. D. and M .J. Silverman. 1984. MARMAP surveys of the continental shelf from Cape Hatteras, North Carolina, to Cape Sable, Nova Scotia (1977-1983). Atlas No. 1. Summary of operations. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-F/NEC-33, 306 p.

Sinclair, E. H., G. A. Antonelis, B.W. Robson, R. R. Ream, and T. H. Loughlin. 1996. Northern fur seal, *Callorrhinus ursinus*, predation on juvenile walleye pollock, *Theragra chalcogramma*. In: Ecology of Juvenile Walleye Pollock, *Theragra chalcogramma,* R.D. Brodeur, P. A. Livingston, T. R. Loughlin, and A.B. Hollowed (eds.). U.S. Dep. Commer., NOAA Tech. Rep. NMFS 126, p. 167-178.

Sissenwine, M.P. 1984. Why do fish populations vary? In: R.M. May, ed. Exploration of marine communities. Springer-Verlag, Berlin. p. 59-94.

Skud, B.E. 1975. Revised estimates of halibut abundance and the Thompson-Burkenroad debate. Int. Pac. Halibut Comm. Sci. Rep. 56, p 1-36.

Skud, B.E. 1882. Dominance in fishes: the relation between environment and abundance. Science. 216: 144-149.

Smith, T. D. 1994. Scaling fisheries. The science of measuring the effects of fishing, 1855-1955. Cambridge Univ. Press.

Springer, A. M. and G. V. Byrd 1989. Seabird dependence on walleye pollock in the southeastern Bering Sea. Pages 667-679 In: Proceedings of the International Symposium on the Biology and Management of Walleye Pollock. Alaska Sea Grant, AK-SG-89-01.

Stabeno, P. J., J. D. Schumacher, R. F. Davis, and J. M. Napp. 1998. Under-ice observations of water column temperature, salinity and spring phytoplankton dynamics: Eastern Bering Sea shelf, 1995. J. Mar. Res. 56: 239-255.

Steele, J. H. 1996. Regime shifts in fisheries management. Fish. Res. 25: 19-23.

Theilacker, G. H., K. M. Bailey, M. F. Canino, and S. M. Porter. 1996. Variations in larval walleye pollock feeding and condition: a synthesis. Fish. Oceanogr. 5 (Suppl. 1): 112-123.

Thompson, W.F. and R. Van Cleve. 1934. The life history of the Pacific halibut. 2. Distribution and early life history. Rep. Int. Fish. Comm. 9. 184 p.

Vance, T. C., C. T. Baier, R. D. Brodeur, K.O. Coyle, M. B. Becker, G. L. Hunt, Jr., J. M. Napp, J. D. Schumacher, P. J. Stabeno, D. Stockwell, C. T. Tynan, T. E. Whitledge, T. Wyllie-Echeverria, and S. Zeeman. 1998. Aquamarine waters recorded for the first time in eastern Bering Sea. Eos. Trans. Amer. Geophys. Union. 79: 121,126.

Walford, L.A. 1938. Effect of currents on distribution and survival of the eggs and larvae of the haddock (*Melanogrammus aeglefinus*) on Georges Bank. Bull. U. S. Bur. Fish. 49: 1-73.

Wiles, G. C., R. D. D'Arrigo, and G. C. Jacoby. 1998. Gulf of Alaska atmosphere-ocean variability over recent centuries inferred from coastal tree-ring records. Climate Change 38: 289-306.

Wyllie-Echeverria, T. 1995. Sea-ice conditions and the distribution of walleye pollock (*Theragra chalcogramma*) on the Bering and Chukchi Sea Shelf. Can. Spec. Pub. Fish. Aquat. Sci. 121: 131-136.

The Bulletin of the Sea Fisheries Institute *was first issued in 1970.*
Since 1992, three issues of the Bulletin have been published annually.
Papers concerned with fishery-related sciences, i. e., fishery biology,
ichthyology, physical and biological oceanography, sea-food technology and processing,
fishing gear technology and marine environment conservation issues
will be considered for publication in the Bulletin.
Prior to publication, articles are reviewed by recognized authorities in the field.

The Bulletin of the Sea Fisheries Institute *is indexed and abstracted in ASFA and FSTA.*

EDITORIAL STAFF

Editor in Chief – Tomasz B. Linkowski (Director)
Guest Editor – Kenneth Sherman
(Northeast Fisheries Science Center, Narragansett, RI, USA)
Senior Publication Officer – Elżbieta Stawska
Translators and Proof-readers – Jennifer & Tymon Zielińscy
Technical Editor – Lucyna Jachimowska

SCIENTIFIC ADVISERS

E. Aro – Finnish Game and Fisheries Research Institute, Helsinki, FINLAND
P. Gasjukov – AtlantNIRO, Kaliningrad, RUSSIA
L. Hernroth – Institute of Marine Research, Lysekil, SWEDEN
E. Ojaveer – Estonian Marine Institute, Tallinn, ESTONIA
A. I. L. Payne – CEFAS, Lowestoft Laboratory, Lowestoft, UK
T. Penczak – University of Łódź, Łódź, POLAND
J. Piechura – Institute of Oceanology PAN, Sopot, POLAND
M. Protasowicki – Agricultural Academy of Szczecin, Szczecin, POLAND
K. Sherman – Northeast Fisheries Science Center, Narragansett Laboratory, Narragansett, RI, USA
J. Świniarski – Agricultural Academy of Szczecin, Szczecin, POLAND
W. Załachowski – Agricultural Academy of Szczecin, Szczecin, POLAND

EDITORIAL OFFICE ADDRESS

Sea Fisheries Institute. Scientific Information and Publishing Center
Kołłątaja 1, 81-332 Gdynia, POLAND
http: //www.mir.gdynia.pl
e-mail: bulletin@mir.gdynia.pl

THIS JOURNAL IS SUPPORTED FINANCIALLY
by
THE STATE COMMITTEE FOR SCIENTIFIC RESEARCH, POLAND