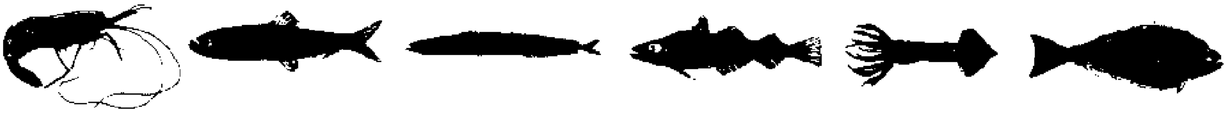
SPECIES SYNOPSES

Life Histories of Selected Fish and Shellfish of the Northeast Pacific and Bering Sea



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Norman J. Wilimovsky
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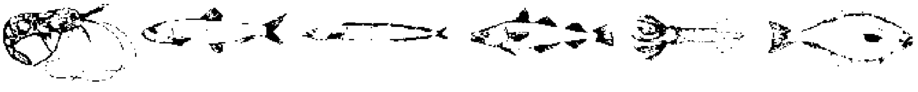

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CONTENTS

PREFACE

In May 1983, a workshop was held at Lake Wilderness, Washington, to review existing knowledge on ocean and fish variability and to develop a strategy for investigating the ocean-fish interactions. One element proposed in the strategy was the preparation of annotated survival tables, in the form of species "schemata" or syntheses. The rationale for such a presentation is given in the proceedings of the workshop (published by the Washington Sea Grant Program as *From Year to Year: Interannual Variability of the Environment and Fisheries of the Gulf of Alaska and the Eastern Bering Sea):*

> A logic is required for identifying information needs and for organizing information about a stock and its environment in a way that suggests testable hypotheses. Such a conceptual framework was developed within which information on life history, on the influence at any development stage of the survival factors of food, predation and physiology, and on the effects of abiotic phenomena on these survival factors could be compiled. . . . With such tabulations, hypotheses of interaction and control would be constructed and tested with available time series and with simulation and analytical models; filed observations would be planned to investigate clues revealed by the analysis. Laboratory and enclosure experiments would also be required to determine rates and fluxes; at each stage, the cost-effectiveness of obtaining the desired information would be evaluated.

Subsequently, preparation of such compilations was endorsed by IRIS (International Recruitment Investigations in the Subarctic), a collaborative effort among fourteen research institutions in the Pacific Northwest seeking understanding of ocean-fish interactions and their effect on variability in abundance and distribution of fish stocks. Editors were selected and it was agreed that syntheses would be prepared initially for a few stocks to gain experience with available data and to demonstrate the utility of such compilations for recruitment research. The stocks described in this publication were selected on the basis of author interest rather than of systematic coverage or representation.

All papers were refereed. Technical editing was done by Dora P. Henry and copy was prepared by Marcus Duke, both of the College of Ocean and Fishery Sciences, University of Washington. Additional support was provided by the Washington Sea Grant Program.

In an outline prepared in January 1985, the editors stated "It is expected that the primary readership will comprise oceanographers and modelers but the schemata also should serve other biologists and fishery managers as a review of current knowledge and an introduction to the literature of species presently or potentially of commercial value in the northern Pacific." If these syntheses are found to serve these purposes, it is hoped that additional ones can be prepared.

Warren S. Wooster
Seattle • February 1988

NORTHERN PINK SHRIMP, *Pandalus borealis*, IN THE GULF OF ALASKA AND EASTERN BERING SEA

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1 BACKGROUND

1.1 Literature Search

Since the late 1920s, many papers have been published on species ecology, reproductive biology, distribution and fisheries of shrimp, including *Pandalus borealis* (Kroyer). In addition, annotated bibliographies (Ippolito et al. 1980), reports (Armstrong et al. 1981; Walline and Sibley 1984) and the proceedings of an international symposium (Frady 1981) have provided summaries of the available literature. Many Russian shrimp papers have been translated (Fisheries Research Board of Canada Translation Series, cited in Ippolito et al. 1980); a substantial number of articles appear in the Japanese literature (e.g., Kurata 1957; Ito 1976). Several summaries of regional shrimp fisheries and management plans have been published by FAO (e.g., Ivanov 1969; Rasmussen 1969). Management policy was best summarized during the 1979 international pandalid shrimp symposium (Frady 1981) and nothing has been formulated since that date for the northeastern Pacific. Annual data on commercial landings of pandalid shrimp are provided by the Pacific Marine Fisheries Commission (PMFC Annual Report); limited or occasional data are provided by the U.S. Department of Commerce (Annual Report: Fisheries of the United States) or trade publications (e.g., Pacific Packers 1981 and Seafood Leader 1985 reports). Our review of the primary literature is current through 1985.

1.2 Unit Stocks and Their Relationships

Analysis of genetic and morphological differences between *P. borealis* stocks from Yakutat (139°W, 59°N), Kodiak Island (153°W, 57°N), the Alaska Peninsula (161°W, 56°N), and the southeastern Bering Sea led Gardner (1983) to conclude that these are separate unit stocks. In the Gulf of Alaska, hydrological conditions within embayments and their associated offshore canyons largely remain uncoupled from a predominant southwesterly flow offshore (Schumacher and Reed 1983). Since these areas serve as adult habitat and spawning grounds, opportunity for significant passive export or import of larvae and adults is thought to be small (Ingraham 1981). Observation of newly hatched larvae near bottom on spawning grounds and their later appearance inshore of spawning grounds (Berkeley 1930) have been suggested as evidence that larval behavior serves to discourage dispersal (Fox 1972). These observations support the hypothesis that populations of single embayments and offshore canyons constitute unit stocks. This hypothesis provides the conceptual basis for separate management of unit stocks (Alaska Department of Fish and Game [ADF&G] 1983).

1.3 The Fishery

1.3.1 Relative Size and Importance. *P. borealis* constitutes from 85% to 100% of the commercial shrimp landings from the Gulf of Alaska and the eastern Bering Sea (Orth et al. 1979; ADF&G 1983; PMFC 1985). From 1969 through 1980 these landings averaged 39,674 mt per year, with an average yearly wholesale value of about $25 million (ADF&G 1982). Landings from 1966 to 1976 averaged 36% of the annual world production of pandalid shrimp (computed from data of Orth et al. 1979). The 10 year annual (1974-1983) total landing for Alaska, including the southeastern Bering Sea, was 31,000 mt, equal to 59% of the total pandalid (*P. borealis* plus *P. jordani*) landings from California to Alaska (PMFC 1985).

1.3.2 Age at Recruitment. At present no minimum size restrictions apply to the harvest of *P. borealis* in the Gulf of Alaska and the eastern Bering Sea. Although *P. borealis* becomes vulnerable to conventional fishing gear by age 1, reluctance of processors to purchase small shrimp focuses fishing pressure on older age classes (ADF&G 1983).

1.3.3 Characteristics of Harvested Fish. The bulk of the commercial catch of *P. borealis* is comprised of ages 2 to 5, which range from 76.2 mm to 127 mm in total length and from 3.1 g to 7.5 g in total weight. Since pandalid shrimp are protandric hermaphrodites (see 2.1), most of the fishery targets on the older and larger females.

1.3.4 Types and Selectivity of Gear. Harvest of *P. borealis* is accomplished almost exclusively by use of bottom trawls, usually used in a fishing configuration of twin high-opening otter trawls of 18-20 m footrope length. Otter trawls fitted with tickler chains or roller gear are flown several feet off bottom , usually resulting in small incidental catches of benthic and demersal species, such as crab, flounder (Pleuronectidae) and halibut (*Hippoglossus stenolepis*). In an effort to reduce selectivity for pelagic and demersal fish species, large mesh trawl wings have been used, but they also were ineffectual as large incidental catches of cod (*Gadus macrocephalus*), pollock (*Theragra chalcogramma*) and other fish are common.

1.3.5 Distribution of Fishing Effort. Because of gear requirements, effort generally is restricted to areas where the bottom is soft or even. Diel migrations of the shrimp restrict effort to daylight hours when shrimp typically are concentrated near bottom. Although *P. borealis* has been taken at depths exceeding 1,000 m, the bulk of the commercial harvest is from depths between 36 and 185 m (Orth et al. 1979).

Historically, fishing effort targeting on *P. borealis* ranged from southeastern Alaska to the Pribilof Islands. In 1955, the *P. borealis* fishery in southeastern Alaska produced a harvest of 1,500 mt (North Pacific Fisheries Management Council [NPFMC] 1976). A Kodiak District shrimp fishery, initiated in 1959, produced 1,318 mt, then expanded rapidly in catch and effort until 1977 when a peak catch of 54,000 mt was obtained. Subsequently, stocks in the Kodiak District began to decline and effort shifted westward to the Chignik, South Peninsula and Aleutian districts. The percentage of the shrimp harvest attributable to the districts west of Kodiak was 2-13% before 1971, increased to 71% in 1977 and gradually decreased to 3.2% by 1983 (Jackson et al. 1983).

Within the Western Region of the Alaska State management plan, districts from Kodiak through the Bering Sea have been established (ADF&G 1983). Since the late 1970s, many districts have been closed for periods of 3 to 5 years and quotas often are set for individual bays that are opened or closed by emergency order. A quarterly quota system for each area was instituted in 1971 by the Alaska Board of Fisheries. By 1979 this system had evolved to a single harvest period, beginning in June and extending until quotas are filled (ADF&G 1983). Currently, harvest periods, where allowed, begin in June, and a second harvest period may be permitted following a fall survey of abundance.

Prior to the exclusion of Japanese and Soviet fishermen from the *P. borealis* fishery within the Fisheries Conservation Zone (FCZ) in 1977, trawlers of both countries targeted on *P. borealis*. From 1960 to 1969 a Japanese effort targeted shrimp stocks northwest of the Pribilof Islands. This fishery yielded a peak harvest of 30,000 mt in 1963 but was abandoned in 1969 following severe stock declines (Armstrong et al. 1981). In the Gulf of Alaska, Japanese and Soviet effort targeted shrimp stocks around Kodiak and the Shumagin Islands. Between 1964 and 1968, the Japanese fishery resulted in an annual harvest of 231 to 2,000 mt (Ronholt et al. 1978). A Soviet fishery was initiated in 1964, expanded rapidly and reached a peak harvest of 12,000 mt in 1966. Following a ban on foreign fishing within the 12-mile limit, Soviet catches declined dramatically to 2,000 mt in 1973 and 1,000 mt in 1974 (NPFMC 1976).

1.4 Distribution and Abundance of the Population

P. borealis is a discontinuous amphiboreal species and occurs in major oceans of high northern latitude (Rasmussen 1967; Ito 1976). It is the target of commercial fisheries in the northeastern and northwestern Pacific, as well as in the Gulf of Maine, North Atlantic and North Sea. Stocks in the northeastern Pacific Ocean range from the Pribilof Islands south to the Columbia River (see reviews in Frady 1981). The largest concentrations are along the continental shelf from Cook Inlet westward around Kodiak Island, along the Alaska Peninsula, then through Unimak Pass to the Bering Sea as far as the Pribilof Islands (NPFMC 1978; Ingraham 1981). *P. borealis* tolerates a salinity range of 25.9°/₀₀ to 35.7°/₀₀ (Fox 1972) and a temperature range of -1.67°-12.2°C (Butler 1964). Within its range, *P. borealis* is most concentrated in areas with strong horizontal temperature gradients where different water masses interact.

P. borealis is semi-benthic with a diel vertical migration from a near-bottom position during the day to a more homogeneous distribution in the water column at night (Barr 1970). In contrast to an eastern Bering Sea seasonal migration of 50-60 km, considered to be a possible response to extreme cold water temperatures (Ivanov 1969), stock migrations along the coast of the Gulf of Alaska are not considered to be significant (NPFMC 1976). Some evidence suggests a general shoreward spawning migration in the fall.

Significant variability in population density and estimated abundance of shrimp stocks occurs among similar bays. Along the mainland section of the Kodiak District (ADF&G 1983:315), assessment surveys in 1981 and 1982 indicated standing stocks of 500 to 1,000 mt in some bays compared to zero to 20 mt in bays of comparable size, separated by only 13 to 40 km. Catch per unit effort (CPUE) data (thousands of shrimp per distance towed) from a single bay in the same district showed a 3.5-fold difference in abundance of certain size classes (carapace length [CL] 12-14 mm) over the years 1979 through 1982 (ADF&G 1983).

1.5 Current Status of Stocks and of Management Measures

All exploited stocks of *P. borealis* in the Gulf of Alaska and eastern Bering Sea are currently in a state of decline, continuing a trend which has been evident since the mid-1970s. At the present time, there is no fishery in the southeastern Bering Sea (PMFC 1985). The 1982-83 seasonal harvest of pandalid shrimp from the entire Westward Region (ADF&G 1983:18) was 4,871 mt, the lowest since 1964 and only 50% of the 1981-82 seasonal harvest. Though management policies restricting fishing effort have contributed to low harvest levels, consistently low abundance of stocks in the restricted areas suggests that unrestricted fishing effort would not significantly increase harvest levels (Jackson et al. 1983).

The Alaska Department of Fish and Game, recognizing that "a genuine concern exists for the survival and recovery of this [shrimp] resource" (ADF&G 1983:310), has adopted two management policies for the Kodiak District. The first treats shrimp populations within individual bays as separate, manageable stocks and characterizes the status of each stock by two indices of abundance. The Representative Biomass Index (RBI) is derived as the historic mean of fall abundance indices from trawl surveys in the years after initial stock exploitation but prior to any significant period of decline (Jackson et al. 1983). A Minimum Acceptable Biomass Index (MABI), set at 40% of the RBI, is considered the point below which the potential for stock recovery is reduced significantly. Abundance indices determined by trawl surveys performed prior to each fishing season serve to classify each stock as: "healthy" (recent index at or above RBI), "recovering" or "severely depressed" by comparing the initial RBI and MABI for that stock. Severely depressed stocks are closed to all fishing until there are indications of recovery. Although an annual harvest rate is usually derived from RBI and MABI, CPUE data from a voluntary trawl logbook program, as well as age and species composition data from samples of commercial catches, may be used to modify harvest levels (Jackson et al. 1983).

A second management policy, the "Mainland Management Strategy," is a response to industry pressure and contention that shrimp schools constantly migrate and cannot be managed as discrete units (ADF&G 1983). This experimental program is being tested in a portion of the Kodiak District where there is a 9-month fishery that can be closed only for illegal practices, wasteage and catch of very small shrimp.

1.6 Recruitment Variability

Interannual variability in recruitment has been noted for populations in the Bering Sea and Gulf of Alaska. For example, the very strong 1971 year class in the Kodiak District was followed by weak year classes (Anderson 1981). Relative year-class strength is estimated by cohort analysis of the commercial catch and of trawl survey data. However, age-1 shrimp may not be adequately sampled due to their size (Anderson 1981; Jackson et al. 1983). Reported segregation of populations by size, sex or age (NPFMC 1976) may bias age distribution in both commercial and scientific samples. Abundant time-series data for shrimp numbers, size frequency and sex by area in the Kodiak District have been used to estimate growth and mortality rates for strong year classes (Anderson 1981). Long-term weak recruitment of shrimp in this district is circumstantially linked to fishing, but natural mortality caused by cod and pollock predation may be more important. Populations of these predators have increased significantly in the area since the late 1970s. Stomach analyses show they are nonselective predators with regard to size of shrimp; this could account for the simultaneous decline of all age/size groups (ADF&G 1983). Interannual variability in recruitment caused by temperature perturbations to larvae and first year juveniles may affect year-class strength (Ivanov 1969; Haynes and Wigley 1969). For some Bering Sea populations, severe winters, measured by the extent of ice cover during the first juvenile winter, apparently produce weak year classes (Ivanov 1969).

1.7 Age Determination and Validation

Age classification of *P. borealis* is based on modal lengths in size-frequency analyses of samples from scientific surveys and commercial catches. Since growth rates may vary between stocks and between years, age-length relationships may not be consistent between stocks or between years for a single stock. Bias in determinations of age composition may be introduced by reduced vulnerability of the youngest year classes (0+, 1+) to sampling gear and also by reduced or negligible growth of individuals near the upper limits of the age range (asymptotic length = 29.0 mm CL; Anderson 1981). Additional factors confounding the determination of population age structure are individual variability in growth rates and differential growth rates between age classes, which may cause overlap of length modes for adjacent age classes, especially during the period of sexual transition (Skuladottir 1981a). The maximum age of *P. borealis* in both the Gulf of Alaska and the Bering Sea is thought to be 6.5 years. Although no single age class is consistently dominant, strong year classes that result in temporary dominance of age classes within stocks have been documented. It is not yet known if the occurrence of dominant year classes is positively correlated with large reproductive effort or favorable environmental conditions for larval and juvenile survival (Ivanov 1969).

1.8 Age Composition of the Population

Some of the best information regarding age composition of *P. borealis* populations is provided in the Japanese literature, e.g., see review by Kurata (1981). Age composition varies tremendously depending on the strength of year classes. Strong year classes were noted in the early 1970s (1971 through 1973) along the west Kamchatka Peninsula, and both recruitment and stock size decreased in 1974 and 1975 (Kitano and Yorita 1978). Anderson (1981) used modal analyses of a 7-year time-series (shrimp surveys around Kodiak Island) to detect and follow growth and mortality of a very strong 1971 year class. Evidence of cyclic commercial catches along the Washington coast was used by Balsiger (1981) to underscore the importance of occasional, large year classes.

In the Sea of Japan as many as 7 to 8 year classes, including immature stages, males, transitional stages and females comprise the population. The percentage composition of large, mature females in the population often reflects variable fishing pressure on stocks since females comprise the bulk of landings. A long time-series of Iceland length-frequency data was analyzed by the deviation method (length-frequency distributions subtracted from means of several years) to identify strong year classes (Skuladottir 1981a). He also highlighted potential error in setting size-at-age relationships, as differential growth rates can result in more than one year class being the same size (mean or range).

2 SPAWNING ADULTS

2.1 General Description

P. borealis is a protandric hermaphrodite (Butler 1964; Rasmussen 1967). Sexually mature individuals generally function as males for one or two years prior to development of female characteristics. Occasionally the male stage is bypassed, but a more common deviation from strict protandry involves initial development of male characteristics followed by transition to the female mode prior to the first spawning (Balsiger 1981). Intense fishing pressure and a high resultant adult mortality rate may provoke a population response in *P. borealis* to mature directly as females, or sooner after attaining male maturity than would occur if mortality was lower (Charnov 1981). A high incidence of small females that bypassed the reproductively functional male stage has been correlated positively with weak year classes of large females. A high incidence of small females may also result from heavy selective removal of larger females by fishing (Charnov et al. 1978; Charnov 1981).

2.1.1 Size and Age Ranges. While size at sexual maturity appears to be relatively constant in geographically distinct populations, age at maturity is variable and may reflect growth differences due to water temperature (Rasmussen 1969). In general, individuals at higher latitudes mature at a later age. For Bering Sea populations, Ivanov (1969) found that by age 3 most individuals were mature males with an average carapace length (CL) of 22 mm; at age 5 and an average CL of 27 mm, most individuals had changed to females. Females may live for 6.5 years but many are sterile (Davis 1982). In populations along the western Alaska Peninsula males generally mature by age 2 and have an average CL of 19 mm; transition to females occurs at age 4 and an average CL of 25 mm. In the Sea of Japan, *P. borealis* mature as males at age 2; females mature at age 4 and survive to age 9 and reach a maximum CL of about 35 mm (Kurata 1981). In contrast, populations of *P. borealis* in Iceland reach a maximum CL of 29 mm and an age of 11 years (Skuladottir 1981b).

2.1.2 Type of Spawning Behavior. Spawning occurs once a year, generally during autumn. Following molt of the female into breeding dress (increased setae on pleopods), spermatophores are attached to the ventral abdomen by a male during copulation. Fertilization occurs as eggs are extruded from the gonopores over the sperm masses. Fertilized eggs are affixed to the forward four pairs of pleopods and abdominal segments of the female, and developing embryos are carried until they hatch as zoea larvae (Fox 1972). Egg hatching, accompanied by vigorous movement of the pleopods, usually occurs at night and takes up to 48 hours to complete (Fox 1972). Both timing of spawning and duration of embryonic development vary between geographically distinct populations. At higher latitudes, or in colder water, spawning occurs earlier, and eggs are carried for a longer period than at lower latitudes or in warmer water (Rasmussen 1969).

2.1.3 Fecundity. In all *P. borealis* population studies, fecundity is positively correlated with female size (e.g., Charnov 1981; Kurata 1981). A range of 300 to 3,400 eggs per clutch is reported for the species worldwide (Armstrong et al. 1981). No estimate of average clutch size is available for Bering Sea populations, but females from southeastern Alaska are reported to carry an average of 2,150 eggs (Hynes 1930). Laboratory studies of temperature effects on clutch and egg size in Gulf of Alaska *P. borealis* indicate that the lowest (3°C) of three experimental temperatures resulted in the largest clutch and egg sizes, while the highest temperature (9°C) resulted in the smallest (Nunes 1984). Observations of resorption of maturing oocytes by female *P. borealis* during warm water temperatures in the Gulf of Maine suggest that when temperature regimes place heavy metabolic burdens on females or are unfavorable for larval survival adult somatic growth and maintenance may be favored over reproductive effort in partitioning of physiological resources (Nunes 1984).

2.2 Distribution and Abundance

2.2.1 Duration of Spawning. Time of spawning varies among geographically distinct populations. Since water temperature greatly affects the rate of embryonic development, high latitude or cold water populations generally spawn prior to warm water conspecifics and have a longer incubation period (Rasmussen 1969; Kurata 1981). Shrimp in the Bering Sea spawn in early August and September and have an average ovigerous period of 8.5 months (Armstrong et al. 1981). Populations around Kodiak Island spawn from late August through September and eggs hatch in April or May, whereas a population in southeastern Alaska spawned in mid October through November (Ippolito 1981). Populations off British Columbia spawn in November (Butler 1980). Over the species range in northern European waters, time of spawning varies by 3 months, and duration of the ovigerous period is 5 months longer between northern and southern extremes of the European range (Rasmussen 1969).

2.2.2 Large-scale Patterns. Large-scale spawning migrations are unknown for *P. borealis* in the Gulf of Alaska and eastern Bering Sea, and spatial distribution is consistent over time. Extreme fluctuations in abundance have been reported for *P. borealis* worldwide, and some factors affecting abundance have been studied. For example, fishing mortality may be a significant cause of high interannual variability in stock abundance. Other biotic and abiotic factors that may affect interannual differences in mortality include large fluctuations in predator abundance and in water temperatures experienced by spawning adults or larval stages (Balsiger 1981). In the Gulf of Alaska and Bering Sea, the *P. borealis* fishery, based on very large year classes, had rapid expansion of fishing effort (ADF&G 1983). Increases in abundance within a population's range appear to be followed by severe declines.

2.2.3 Small-scale Patterns. No migrations for spawning or hatching activity have been observed for *P. borealis* populations in the Gulf of Alaska or Bering Sea. A winter shoreward migration of ovigerous females reported for Gulf of Maine stocks is hypothesized as an attempt to keep eggs at warmer temperatures (Balsiger 1981); however, not all ovigerous females migrate shoreward to hatch their eggs (Haynes and Wigley 1969).

2.2.4 Maximum and Mean Abundances. No estimates of density of *P. borealis* during spawning or hatching are available. Relative shrimp densities (lb caught/travel hr), based on commercial fisheries in the Kodiak District, show substantial variation between local bays but greater interannual variation (up to five-fold) within individuals bays (Jackson et al. 1983). Bottom photography and direct observations from submersibles have been used to estimate on-bottom density in the Bering Sea, North Atlantic and Barents Sea (see reviews in Ivanov 1981). Photographic observations of *P. borealis* in a commercial fishing area in the Bering Sea indicated a mean density and maximum of 1.1 m^{-2} and 4 m^{-2}, respectively (Ivanov 1981). Average density as determined by photographs of *P. borealis* on bottom in Greenland waters is less than 0.7 m^{-2} in offshore areas and up to a maximum of 6.7 m^{-2} within bays.

2.2.5 Vertical Distribution. Diel vertical migrations are well documented for mature adults worldwide (Horsted and Smidt 1956; Barr 1970; Pearcy 1970). Both spawning and hatching take place on or near bottom. In the Gulf of Alaska, *P. borealis* migrate vertically in the water column during hours of darkness to an off-bottom distance that is negatively correlated with size, e.g., large females comprise a substantial proportion of the shrimp found near-bottom (Barr 1970). Haynes and Wigley (1969) noted a complete absence of ovigerous females in Gulf of Maine midwater samples, where nearly all shrimp were mature males.

2.3 Feeding

2.3.1 Habitat. Feeding habitat is both benthic and pelagic, although utilization of the two food resources may vary geographically, seasonally, daily and with reproductive state (Butler 1971). Depth range of feeding activity includes the entire water column. Mature males probably use pelagic food resources to a greater degree than ovigerous females as they migrate vertically to a lesser extent, if at all.

2.3.2 Prey Species. The material found in the stomach of mature *P. borealis* includes: sediment, diatoms, foraminifera, other protozoa, euphausiids, mysids, copepods, crab, shrimp and barnacle larvae, small shrimp, echinoderms, annelids, bivalve molluscs and fish (Barr 1970; Butler 1971; Feder and Jewett 1981a,b). No systematic study of the relative importance of prey by stage of prey, time of day, year or between years exists for adult *P. borealis* populations.

2.3.3 Prey Density Requirements. Not applicable.

2.3.4 Factors Affecting Availability of Prey. No data are available.

2.3.5 Temporal Patterns of Energy Storage. Bioenergetic partitioning in *P. borealis* has not been determined. Since ovigerous females do not molt until eggs are hatched, energy for somatic growth and reproduction is acquired partially during the ovigerous period. Mature female *P. borealis* reproduce either annually or biennially depending on the area (Kurata 1981), suggesting that energy acquisition (as affected by factors such as temperature and food supply) may not always provide surplus energy for reproduction. Since spawning occurs in the fall, mobilization of energy for growth and reproduction of mature female *P. borealis* occurs during the summer when food production and supply are greatest.

2.3.6 Evidence of Food Limitation. No data are available.

2.4 Predation

2.4.1 Predator Species. Predators of *P. borealis* in the Gulf of Alaska and eastern Bering Sea include: cod, pollock, sculpins, sole, tomcod, arrowtooth flounder, dogfish, halibut, salmon and seals (Fox 1972; also see food webs, Feder and Jewett 1981b). *P. borealis* is identified as the dominant prey of Pacific cod in some parts of the Gulf of Alaska and the southeastern Bering Sea (Feder and Jewett 1981a,b). Mortality of *P. borealis* by predation is considered to be potentially high (Fox 1972). Recent increases in by-catches of Pacific cod and pollock during trawl operations for *P. borealis* in the Gulf of Alaska have led several investigators to hypothesize a significant role of predation in severe reductions of shrimp stocks in that region (Jackson et al. 1983).

2.4.2 Effect on Spawning Adults. The magnitude of adult mortality caused by predation on *P. borealis* is not quantified in the literature. Due to the large number of predator species, mortality by predation is considered to be potentially high (Fox 1972).

2.5 Other Factors Affecting Adults

2.5.1 Biotic. Incidence of diseases in *P. borealis* is not well documented. Parasites in the North Pacific include a rhizocephalan, *Sylon hippolytes*, and a bopyrid isopod, *Bopyroides hippolytes*. Females infected with *S. hippolytes* apparently are never ovigerous (Butler 1980). Parasitism of *P. borealis* in the North Atlantic by a second bopyrid isopod, *Hemiarthrus abdominalis*, causes a 50% reduction in female fecundity. An intramuscular microsporidian parasite has been found in several pandalid species, including *P. borealis*, in the North Pacific but the incidence is low, so it is not considered a significant source of mortality (Butler 1980). In *P. borealis* from the Gulf of Alaska and the Gulf of Maine, a "black spot disease" affecting adult gill lamellae has been noted (Fox 1972); also, an unidentified egg parasite with a taxonomic affinity to dinoflagellates is indicated as a source of egg mortality (Stickney 1978). Incidence of the latter disease is usually 2-5% but can reach 30%; development rate of the parasite is negatively correlated with water temperature (Stickney 1981).

2.5.2 Abiotic. Temperature effects on fecundity and duration of embryonic development have been noted (Nunes 1984). In laboratory studies, egg size and larval size at hatching were greatest and egg mortality and larval viability were highest at 3°C and lowest at 9°C. The demise of entire *P. borealis* stock in some Greenland fjords has been attributed to winter water temperatures below -1.6°C (Smidt 1981). In contrast, declines in Gulf of Maine *P. borealis* stocks appear to follow above-normal winter water temperatures, possibly due to early hatch of larvae prior to plankton blooms.

2.5.3 Total Mortality. Coefficients of total instantaneous mortality (Z) estimated for year classes in two geographically distinct populations of adult *P. borealis* are similar. Coefficients of 0.66 for a dominant year class in Pavlov Bay, Alaska, and a mean value of 0.64 for several year classes from the Gulf of St. Lawrence were calculated by Anderson (1981) and Frechette and LaBonte (1981), respectively. Due to uncertainty of age determination by modal analysis of length frequency data, age-specific estimates of Z in a dominant Pavlov Bay year class were calculated for overlapping pairs of age classes; no attempt was made to separate fishing (F) and natural mortality (M) nor to distinguish sources of natural mortality. In the northwestern Gulf of St. Lawrence study, Frechette and LaBonte (1981) separated estimates of F and M by age classes and calculated a range for F of .23 to .38 with little apparent interannual variability. The range for M was .24 to .80, suggesting that natural mortality is a more important determinant of interannual variability in Z. For west Greenland populations, a coefficient of 1.5 following first spawning for M and an estimated coefficient of .4 for F have been used for stock management (Ulltang 1981).

2.6 Laboratory Holding and Rearing

Detailed methodology for spawning adults of *P. borealis* under laboratory conditions are provided by Nunes (1984). Price and Chew (1972) designed a recirculating system that was successful in spawning several pandalid species.

3 EGGS

3.1 General Description

At spawning, eggs are green and ovoid; they range in length from 1.10 to 1.20 mm and in width from 0.88

to 0.90 mm; egg volume ranges from 0.40 to 0.48 mm^3 and increases by 8% to 30% prior to hatching (Nunes 1984). Eggs are carried on pleopods of the female until larvae hatch as zoea. Eggs are lecithotropic, cleavage is superficial and development is indirect (Berkeley 1930).

3.2 Distribution and Abundance

3.2.1 Duration of Egg Stage. Duration of embryogenesis corresponds to duration of the ovigerous period of mature females, which varies significantly at different temperature regimes (see 2.2.1). Eggs are carried for about 5 months at water temperatures typical of British Columbia and the Gulf of Maine, but up to 9 months at the latitude of Spitsbergen (Haynes and Wigley 1969).

3.2.2 Large-Scale Patterns. Egg patterns in time and space correspond to the distribution of ovigerous females (see 2.2.1). Duration of the ovigerous period is known to vary with ambient temperature, and interannual variability in egg abundance is tied to abundance and size of ovigerous females, as well as to interannual variability in fecundity and egg mortality due to biotic (2.5.1) and abiotic (2.5.2) factors.

3.2.3 Small-scale Patterns. These are the same as those for ovigerous females (2.2.3).

3.2.4 Maximum and Mean Abundances. Estimates of mean abundance of *P. borealis* eggs in the field apparently have not been reported. The value of this parameter is expected to be a function of fecundity and density and age of ovigerous females.

3.2.5 Vertical Distribution. (See 2.2.5.)

3.3 Feeding

Not applicable.

3.4 Predation

3.4.1 Predator Species. Predators of eggs are the same as predators of ovigerous females (2.4.1). Selective predation on ovigerous females and their eggs has only been documented as an indirect consequence of shrimp fisheries. The winter inshore fishery for *P. borealis* in the Gulf of Maine targets almost exclusively on stocks of ovigerous females concentrated during their winter egg hatching migration (Bliss 1982).

3.4.2 Effect on Eggs. No estimates of predation impact on egg survival have been reported.

3.5 Other Factors Affecting Eggs

3.5.1 Biotic. A peridean egg parasite that may kill up to 30% of a given brood of *P. borealis* eggs has been reported in the Gulf of Maine (Stickney 1978, 1981). Since infection and loss of eggs from the infected egg mass is an ongoing process, commonly observed infection rates of 2-5% may belie the magnitude of the cumulative mortality resulting from such infections. A similar egg parasite is thought to infect eggs of *P. borealis* stocks in the Gulf of Alaska (Stickney 1981).

3.5.2 Abiotic. Thermal history of spawning females may determine the quantitative or qualitative contribution to their eggs. Nunes (1984) noted that female *P. borealis* reared at 3°C prior to spawning had larger eggs and the resultant larvae were more viable than those reared at 6°C or 9°C. Also, egg losses were lowest at 3°-6°C. As the greatest abundance of ovigerous *P. borealis* is found in Gulf of Alaska waters ranging from 3.4°-5.5°C, this correlation with the laboratory finding suggests selective behavior by *P. borealis* may serve to maintain eggs within a temperature range consistent with that of lowest egg loss. During a winter of extreme cold temperatures in western Gulf of Alaska waters, up to 84% of female *P. borealis* lost all their eggs and 25% of females carrying eggs produced only partial clutches (Nunes 1984). Egg loss rates of 95% are reported for ovigerous females in West Greenland waters during winters of low water temperature. However, Stickney (1981) failed to detect any temperature effect on egg survival among captive *P. borealis* from the Gulf of Maine during incubation at various temperatures between 2° to 10°C but did find egg mortalities of 20% to 30% within a given temperature treatment.

3.5.3 Total Mortality. (See 3.5.2.)

3.6 Laboratory Holding and Rearing

Haynes (1976), Stickney (1981) and Nunes (1984) give methods for holding eggs through hatching.

4 LARVAE

4.1 General Description

Development of larvae from British Columbia, Hokkaido, Japan, and the Gulf of Alaska is described by Berkeley (1930), Kurata (1964) and Haynes (1979), respectively. Larvae possess few chromatophores and may be orange or transparent depending on the state of the chromatophores. Slight differences in number of larval stages, mean size of stages and in timing of morphological development exist between larvae of *P. borealis* from the Gulf of Alaska and those from British Columbia and Japan (Haynes 1979). Larval *P. borealis* from the Gulf of Alaska pass through six stages, five zoea and one megalops (mysis), prior to metamorphosis to the first juvenile stage (Haynes 1979). In the southeastern Bering Sea, larvae of *P. borealis*, which occur in the plankton from April to August, require about 12 to 20 days to complete each zoeal stage (Armstrong et al. 1981). Mean total length (anterior tip of rostrum to posterior tip of telson) of a related species, *P. hyposinotus*, increases from 6.7 mm for the first stage zoea to 18.5 mm for the megalops (Haynes 1976).

4.2 Distribution and Abundance

4.2.1 Duration of Larval Stages. In the southeastern Bering Sea, *P. borealis* larvae have an intermolt period of 2 to 3 weeks for each larval stage (Armstrong et al. 1981). Duration of the entire larval phase is estimated at 3 to 4 months (Nunes 1984). Based on laboratory rearing experiments of *P. borealis* larvae from the Gulf of Alaska, temperature variations in the range of 3° to 9°C may cause interannual variability in hatching time and duration of the larval phase (Nunes 1984).

4.2.2 Large-scale Patterns. Larvae of *P. borealis* are hatched at depths of 90 to 200 m or more (Berkeley 1930; Armstrong et al. 1981), and the first two larval stages remain near the origin of hatch. Subsequent stages apparently move or are transported to shallower, inshore waters where metamorphosis to the juvenile stage occurs and where juveniles spend the first summer (Berkeley 1930). In both the Gulf of Alaska and the eastern Bering Sea, larvae are found in the water column from April through September. In the southeastern Bering Sea during the years 1977 through 1981, all larval stages occurred in greatest abundance between the 100 to 200 m isobaths, although abundance over the shelf break was sometimes high (Armstrong et al. 1981). In June 1979 the estimate of *P. borealis* larvae per 100 m^{-2} was 2,000, whereas in June 1981 it was 200 (Armstrong et al. 1981).

4.2.3 Small-scale Patterns. Around Kodiak Island, larvae of *P. borealis* are most concentrated adjacent to or within coastal embayments in early spring; less dense offshore concentrations are found during the summer (Dunn et al. 1980). These data suggest the possibility of offshore larval transport with time and/or the existence of offshore populations that hatch larvae later than inshore populations.

4.2.4 Maximum and Mean Abundances. Densities of larvae recorded around Kodiak Island in 1978 range from 0-4,500/100 m^{-2}, with a mean density of 480/100 m^{-2} inshore and 44/100 m^{-2} offshore, at depths of 40-2,000 m (Dunn et al. 1981). Mean density of larvae over the depth interval 100 to 200 m in the southeastern Bering Sea ranges from 250/100 m^{-2} in April to over 1300/100 m^{-2} in June, and reported maximum densities of larvae are 6,000 to 7,000/100 m^{-2} (Armstrong et al. 1981).

4.2.5 Vertical Distribution. Around Kodiak Island, most larvae were found between 30 and 70 m. During day and night sampling, 85% and 70%, respectively, of all larvae were captured within this depth range (Dunn et al. 1980). In the southeastern Bering Sea, larvae were slightly more abundant in the upper 40 m (Armstrong et al. 1981). Berkeley (1930) noted the complete absence of pandalid larvae in the upper 7.8 m off British Columbia and also documented a tendency of *P. danae* larvae to occupy deeper waters as larval development proceeds. In addition, an ontogenetic migration into shallow water by *P. borealis* was hypothesized on the basis of the shallow-water distribution of early juvenile stages (Berkeley 1930).

4.3 Feeding

4.3.1 Habitat. No specific study of feeding ecology of *P. borealis* larvae has been undertaken. Vertical migrations are postulated to enhance feeding opportunities (Nunes 1984).

4.3.2 Prey Species. Laboratory studies by Stickney and Perkins (1981) indicate that *P. borealis* larvae from the Gulf of Maine efficiently capture and consume particles 0.1 to 1.0 mm in diameter but do not appear to be aggressive feeders and neither attack nor pursue prey. In gut analyses of captured larvae, diatoms, primarily *Coscinodiscus* spp., are the dominant recognizable prey, followed by remains of larval crustaceans, polychaetes and other invertebrates. Mineral grains also occur in larval guts, suggesting possible utilization of epiphyte-coated suspended particles as a food source of unknown importance. Laboratory-reared larvae are reported to require animal food by the second zoeal stage to complete development through metamorphosis (Nunes 1984).

4.3.3 Prey Density Requirements. In laboratory studies, stage one zoeae required a mixed copepod density of at least 80 l^{-1} for consistent feeding success (Paul et al. 1979). In other laboratory studies, consumption increased with prey concentration, but no maximum consumption was defined. Diatom density significantly affected larval molt frequency and survival at cell concentrations below 1 X 10^3 *Coscinodiscus* spp. l^{-1} and 1 X 10^7 *Skeletonema* spp. l^{-1} (Stickney and Perkins 1981). Densities for successful laboratory feeding exceed prey concentrations in the field, suggesting that feeding opportunities are sporadic and must rely upon encounters with patches, having higher densities of prey.

4.3.4 Factors Affecting Availability of Prey. Meteorological and hydrological events that concentrate or disperse prey organisms, as well as factors determining temporal coincidence of larvae with peaks of prey abundance, affect availability of prey. Timing of larval hatching relative to prey availability may determine year-class success. Such timing is in part determined by temperature conditions extant during oogenesis, spawning and incubation of eggs (Nunes 1984).

4.3.5 Temporal Patterns of Energy Storage. Not applicable.

4.3.6 Evidence of Food Limitation. Only during the first three zoeal stages are larvae of *P. borealis* particularly vulnerable to starvation, and starvation effects are reversible at all stages.

4.4 Predation

4.4.1 Predatory Species. Predators of *P. borealis* larvae are not documented but presumably include planktivorous fish, euphausiids and hydrozoan medusa. Cannibalism among larval *P. borealis* is common in laboratory cultures (Stickney and Perkins 1981).

4.4.2 Effect on Larvae. No data are available.

4.5 Other Factors Affecting Larvae

4.5.1 Biotic. Starvation of laboratory-reared *P. borealis* was found to extend the duration of the larval phase and to increase the total number of zoeal molts required to attain juvenile metamorphosis (Nunes 1984).

4.5.2 Abiotic. In laboratory experiments, metabolic requirements for first stage larvae of *P. borealis* at 6°C were 63% greater than those for the same stage larvae at 3°C, but both feeding rate and survival increased with rearing temperature (Paul and Nunes 1983; Nunes 1984). For example, under conditions of high temperature and low food availability, increased feeding activity may offset increased metabolic demand. Rearing temperature and food quality and availability affect length of larval stages and total number of molts required to reach the juvenile stage. These factors ultimately affect larval mortality by increasing exposure to predation and by exposing larvae to increased risk of molt-related mortality (Nunes 1984).

4.5.3 Total Mortality. (See 4.5.2.)

4.6 Laboratory Holding and Rearing

Larvae can be successfully reared through all stages under laboratory conditions (Stickney and Perkins 1981; Nunes 1984).

5 JUVENILES

5.1 General Description

Juvenile *P. borealis* resemble the adult form morphologically except for lacking secondary sexual characteristics (Berkeley 1930). The first juvenile stage of *P. borealis* from Kachemak Bay, Alaska, has a mean total length of 18.4 mm, with a range of 15.1 to 21.0 mm (Haynes 1979). Calculations from length frequency histograms for late stage juveniles from Bering Sea winter samples indicate a maximum and mean carapace length of 18 mm and 15 mm, respectively (Ivanov 1969). Similar calculations for Gulf of Alaska juveniles also indicate a mean carapace length of 15 mm, but a maximum length of 16 mm. Minimum age at this stage is 16 months for both populations.

5.2 Distribution and Abundance

5.2.1 Duration of Juvenile Stage. In the Gulf of Alaska and eastern Bering Sea the juvenile stage lasts about a year.

5.2.2 Large-scale Patterns. Metamorphosis to the juvenile stage is thought to occur inshore of spawning grounds where juveniles spend their first summer before rejoining the adult population during the first winter (Berkeley 1930). Around Kodiak Island, small juveniles have been taken in plankton tows from midsummer through fall (Dunn et al. 1980). In the following year, juveniles were reported in the Bering Sea from August to July and in the Gulf of Alaska from September to June (Ivanov 1969).

5.2.3 Small-scale Patterns. There is little information on juvenile distribution. In British Columbia, dense concentrations of juveniles are reported from areas somewhat shallower than those where adult density is high (Berkeley 1930).

5.2.4 Maximum and Mean Abundances. No estimates of juvenile density have been reported. Biomass estimates (wet weight) for total shrimp (juveniles plus adults) caught by trawl ranged from 0.0025 g to 0.235 g m^{-2} in Prince William Sound, Alaska (Feder and Hoberg 1981).

5.2.5 Vertical Distribution. No data are available.

5.3 Feeding

5.3.1 Habitat. No data are available.

5.3.2 Prey Species. No data are available.

5.3.3 Prey Density Requirements. No data are available.

5.3.4 Factors Affecting Availability of Prey. No data are available.

5.3.5 Temporal patterns of Energy Storage. No data are available.

5.3.6 Evidence of Food Limitation. No data are available.

5.4 Predation

5.4.1 Predator Species. These are similar to those cited for adults (2.4.1).

5.4.2 Effect on Juveniles. No data are available.

5.5 Other Factors Affecting Juveniles

5.5.1 Biotic. No data are available.

5.5.2 Abiotic. No data are available.

5.5.3 Total Mortality. No estimates of mortality are reported for this stage, primarily because shrimp do not recruit to survey gear until ages 2 to 3 years (Anderson 1981).

5.6 Laboratory Holding and Rearing

No data are available.

6 CURRENT HYPOTHESES ON FACTORS AFFECTING YEAR-CLASS ABUNDANCE

Current hypotheses about factors that affect year-class abundance include: (1) nonselective predation on juvenile and adult stages, (2) selective predation on ovigerous females, (3) temperature effects on fecundity, egg and larval mortality, (4) environmental effects on larval food availability.

(1) Non-selective predation: Large apparent increases in abundance of cod (*G. macrocephalus*) and pollock (*T. chalcogramma*) in the Gulf of Alaska and Bering Sea, coincident with severe declines in all age classes of *P. borealis* in these areas, suggest predation as a cause of declining shrimp stocks (Jackson et al. 1983).

(2) Selective predation on ovigerous females: Selective removal of ovigerous or mature females through targeting of fishing effort on larger shrimp may result in an imbalance in the stock sex ratio. Low abundance of large females within a population may promote early transition to the female mode by mature males. Fecundity of small females is less than that of large females (Charnov 1981).

(3) Temperature effects on fecundity, egg and larval mortality: Temperature has been shown to exert significant effects on several critical aspects of reproduction (Nunes 1984). Fecundity is reduced or eliminated by very high or low temperatures during oogenesis (Nunes 1984). Egg mortality is increased by low temperatures, due possibly to increased exposure of eggs to predators as a consequence of a lengthened developmental period (Stickney 1978, 1981; Nunes 1984). Larval mortality is increased at temperature extremes, e.g., at high temperatures by reduced viability during embryogenesis and at low temperatures by a prolonged larval phase (Nunes 1984).

(4) Environmental effects on larval food availability: Prey items sufficient for successful larval feeding are not homogeneously distributed in the water column, and larvae may actively regulate their position to coincide with dense aggregations of food items. Weather factors such as storms that promote mixing of the water column may disperse food items. Hydrological and meteorological factors that impede nutrient-rich oceanic upwelling may decrease levels of larval food. In addition to direct effects of starvation, limitation of food may increase the duration of the larval phase, necessitating additional molts to reach the juvenile phase, thereby exposing larvae longer to predators.

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PACIFIC SAND LANCE, *Ammodytes hexapterus*, WITH NOTES ON RELATED *Ammodytes* SPECIES

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1 BACKGROUND

1.1 Literature Search

An intensive literature search, except for Japanese and Soviet literature, which was not as thorough, was completed in December 1986. The emphasis of the search was on the sand lance of the northeastern Pacific, including the Bering Sea.

1.2 Unit Stocks and Their Relationships

The taxonomy of *Ammodytes* species is uncertain. The species are primarily distinguished on the basis of geographic distribution and meristic counts. However, meristic counts frequently exhibit wide variation and latitudinal clines (Richards et al. 1963; Reay 1970; Winters 1970; Scott 1972b; Richards 1982). In this report, the general classification scheme proposed by Reay (1970) will be followed. *Ammodytes hexapterus* (AH) is the only sand lance reported from the northeastern Pacific (Hart 1973). They are found in shallow nearshore waters from California to the Beaufort Sea (Trumble 1973; Craig 1984). As detailed taxonomic studies have not been carried out, the relationship of AH to sand lance from other areas has not been determined. Consequently, *Ammodytes* species from the northwestern Pacific/Japan and the northwestern and northeastern Atlantic also will be considered.

Two species of *Ammodytes*, AH and *A. personatus* (AP), have been reported from the northwestern Pacific; AH generally is restricted to north of 45°N latitude (Kitaguchi 1979). The two species are distinguished by meristic counts, with AH having the higher number of vertebrae and dorsal fin rays (Lindberg 1937; Kitaguchi 1979). Both species show a greater number of vertebrae with increasing latitude (Kitaguchi 1979). Andriyashev (1954) considered them to be conspecific, and Hashimoto (1984a) suggested that *Ammodytes* may be represented by three subspecies along the coast of Japan.

Two other species of *Ammodytes*, a northern offshore species, *A. dubius* (AD), and a southern inshore species, *A. americanus* (AA), have been reported from the northwestern Atlantic (Reay 1970). However, overlap in geographic range and clines (latitudinal and inshore-offshore) in meristic counts that may be correlated with environmental conditions suggests the possibility that only a single species occurs in this area (Richards et al. 1963; Winters 1970; Scott 1972b; Richards 1982). Two species, *A. tobianus* (AT) and *A. marinus* (AM), are found in the northeastern Atlantic, but only AM will be considered in this report, as AT does not resemble closely the species from other areas (Reay 1970).

1.3 The Fishery

1.3.1 Relative Size and Importance. Except for occasional small bait fisheries in Washington and British Columbia, no fishery currently exists in the northeastern Pacific, although there is some potential (Trumble 1973). In Japan the fishery takes about 100,000 ton per year (Kitaguchi 1977). No fishery for sand lance exists in the northwestern Atlantic, although feasibility studies indicate considerable potential (R. Smith, Univ. New Hampshire, pers. comm.). The European fishery landed 200,000 mt in 1968 (Reay 1970).

1.3.2 Age at Recruitment. In Japan, sand lance (AP) usually enter the fishery at age 1, but 0-age fish may enter late in the season, particularly if the year class is strong (Kitaguchi 1977). In the North Sea, recruitment to the AM fishery may begin at age 6 months but most enter at age 1 (Macer 1966; Reay 1970).

1.3.3 Characteristics of Harvested Fish. Length of AP/AH in the Japanese fishery ranges from 8 to 26 cm (Kitaguchi 1977). In the northeastern Atlantic fishery, AM range from 5-25 cm in length (Macer 1966).

1.3.4 Types and Selectivity of Gear. In Japan, a variety of seines, lift nets and bottom trawls are used for the sand lance fishery (Inoue et al. 1967). The European fishery primarily uses a high opening bottom trawl with a 6 mm cod-end mesh (Macer 1966; Macer and Burd 1970). The selection length for this gear was estimated to be approximately 8-9 cm (Reay 1970).

1.3.5 Distribution of Fishing Effort. The Japanese sand lance fishery takes place in depths of 80 m or less, in areas of sand and shell bottom (Kitaguchi 1977). In southern areas, the AP fishery runs from mid-March to late June (Inoue et al. 1967), but at higher latitudes the season is somewhat later, sometimes extending from April to December (Kitaguchi 1977).

The European AM fishery is conducted in depths of less than 40 m in sand-bottom areas, primarily on offshore banks (Macer 1966). The fishing season extends from April to September, with very low catches at other times of the year (Macer 1966; Reay 1970). Fishing takes place almost exclusively during daylight hours (Macer 1966).

1.4 Distribution and Abundance of the Population

Sand lance are abundant in shallow nearshore areas.

1.5 Current Status of Stocks and of Management Measures

No information is available on the status of stocks of AH in the northeastern Pacific, since no fishery currently exists and AH are not sampled by conventional research trawls.

1.6 Recruitment Variability

Evidence for AH recruitment variability is mainly circumstantial. For example, the presence or absence of sand lance in seabird stomachs has been noted during trophic studies (Vermeer 1979; Drury et al. 1981; Springer et al. 1984). In Japan, there is considerable variability in the percentage of 0-age fish in AH/AP catches (Hamada 1966a,b,c; Inoue et al. 1967; Kitaguchi 1977; Nagoshi and Sano 1979).

Larval surveys in the northwestern Atlantic indicate large interannual variation in sand lance (AA/AD) recruitment. Between 1974 and 1979, abundance of larval sand lance increased by a factor of 20 (Smith et al. 1978; Sherman et al. 1981), which reflects a 50-fold change in adult spawning biomass (Meyer et al. 1979; Morse 1982).

1.7 Age Determination and Validation

Age determination for sand lance species is based on surface readings of whole otoliths (Kitakata 1957; Macer 1966; Scott 1968,1973; Reay 1970, 1972; Kitaguchi 1977; Winters 1981). Validation of ages has been attempted by observing the annual pattern of ring formation (Kitakata 1957; Reay 1972; Kitaguchi 1977).

1.8 Age Composition of the Population

In sand lance fisheries, age composition is apparently subject to variation with time of year, area and gear in addition to interannual differences (Inoue et al. 1967). AH collected by beach seine from the vicinity of Kodiak Island, Alaska, ranged from age 0 to 5, with age 1 fish most abundant (Dick and Warner 1982). However, differences in age composition between AH collected by beach seine and those dug from gravel beaches indicate that beach seines were not effective in sampling older age classes (Dick and Warner 1982).

In northern areas of Japan where both AP and AH occur, most of the catch is composed of ages 1-3, and fish over age 4 are uncommon; there is some evidence of interannual variability (Kitaguchi 1977). In contrast, in the Seto Inland Sea fishery, 0-age fish comprise about 80% of the catch and age-2 fish less than 5% (Inoue et al. 1967), whereas in the Harima-Nada and Osaka Bay fishery, age-1 AP account for 20-77% of the catch (Hamada 1966a).

Macer (1966) reported that the percentage of older fish (AM) in the catch decreased during the last part of the season, and Winslade (1974c) suggested this was due to age related differences in timing of overwintering (see 2.2.5). The maximum age of AD in Newfoundland is age 10 or over (Winters 1983). Ages 3-5 predominate in the survey catches, but the relative abundance of AD older than age 6 has been increasing since the late 1970s (Winters 1983). In the northeastern Atlantic, the maximum age of AM is 9, but ages 1-3 account for the majority of the catch (Reay 1970).

2 ADULTS

2.1 General Description

2.1.1 Size and Age Ranges. Based on a small sample size (n=7) of mature fish, AH in the vicinity of Kodiak Island, Alaska, mature at ages 2-3; the smallest mature sand lance observed was 128 mm (Dick and Warner 1982). In the Soya Strait region of Japan, most sand lance (AH/AP) spawn at the end of their second year but some spawn at age 1 (Kitaguchi 1979). Most AP from Ise Bay to the south mature at ages 1-2 at lengths greater than 110 mm (Nagoshi and Sano 1979).

In the North Atlantic, AA usually are mature (102-114 m) at the end of their first year (Richards 1982). Scott (1968) reported that most AD mature at age 2 at lengths between 180 and 200 mm, whereas Winters (1983) found that 50% were mature at age 3 at 180 mm in length. Most AM are mature at age 2, but large (100 mm) individuals may mature at age 1 (Macer 1966).

2.1.2 Type of Spawning Behavior. Most species of sand lance spawn once a year (Reay 1970). Unimodal distributions of egg diameters in ovaries of mature AH (Pinto 1984), AD (Scott 1972a) and AM (Macer 1966) indicate a single spawning per year. AA that spawned in laboratory holding tanks had very few eggs remaining in their ovaries, indicating that all the eggs to be spawned in a year are released in a single batch (Smigielski et al. 1984).

2.1.3 Fecundity. Fecundity-length relationships (F = number of eggs, L = length in cm) have been determined as follows:

AA: $F = 0.328\ L = 3.857$ (Westin et al. 1979);
AM: $F = 2.046\ L = 3.055$ (Macer 1966).

Sand lance (probably AM) between 120 and 195 mm (standard length) off the Murman coast had between 3300 and 22,100 eggs (average 6800) per female (Andriyashev 1954).

2.2 Distribution and Abundance

2.2.1 Duration of Spawning. Most information for the time of spawning of sand lance is based on the occurrence of early larvae. In Puget Sound, Washington, yolk-sac AH larvae are most abundant in late January to early March (R. Trumble, Washington Dep. Fisheries, pers. comm.) and spawning occurred in outdoor holding tanks in mid-March (Pinto 1984). Off the west coast of Vancouver Island, larval AH began to occur in February (Mason et al. 1981a, b). Larval surveys in the Kodiak region indicated late winter (February-March) spawning (Rogers et al. 1979; Kendall et al. 1980). However, Dick and Warner (1982) reported intertidal spawning off Kodiak Island in October. Spawning of sand lance (AH/AP) in the Soya Strait region of Japan occurred between January and early May, and there was some evidence of interannual variation (Kitaguchi 1977).

2.2.2 Large-scale Patterns. In general, sand lance occur in shallow nearshore areas, usually in depths less than 100 m, with sand or sand-gravel substrates. They are abundant from spring to late summer and uncommon during the remainder of the year when they presumably are buried in the sand (Leim and Scott 1966; Reay 1970; Trumble 1973). While inshore-offshore movements have been reported by a number of authors, there is no evidence of large-scale migrations of any sand lance species (Reay 1970). AH juveniles and adults are commonly abundant in nearshore waters during spring-summer but are rarely sampled during late fall and winter (Barton 1978; Fresh 1979; Blackburn and Jackson 1980; Blackburn et al. 1980). According to Blackburn and Jackson (1980), AH are inactive during the winter and are often found buried in intertidal sand. In the Bering Sea, they have been reported from 0-100 m but are most common in depths less than 50 m (Shuntov, in Macy et al. 1978).

2.2.3 Small-scale Patterns. All species of sand lance exhibit schooling behavior, often forming large aggregations (Reay 1970; Trumble 1973). Meyer et al. (1979) observed schools of AA ranging in number from approximately a hundred to tens of thousands; the largest fish were in the center surrounded by smaller fish.

2.2.4 Maximum and Mean Abundances. No information on abundance of AH is available. An estimate of spawning biomass of sand lance (AA/AD) in the northwestern Atlantic from larval survey data indicated that biomass increased 50-fold between 1974 and 1978 (Morse 1982).

2.2.5 Vertical Distribution. Seasonal and diurnal variations in the catch of sand lance are thought to be, at least partially, the result of their habit of burrowing in the sand when not feeding. On the basis of underwater observations of AH, Hobson (1986) reported that some sand lance were buried in the sand at all times of the day, but most were feeding in the upper levels of the water column during the day and buried in the sand at night. Trawl catches of AH were much reduced at night (Macer 1966).

2.3 Feeding

2.3.1 Habitat. Sand lance (AH) feed primarily in the water column, although epibenthic invertebrates occasionally appear in their diet (Simenstad et al. 1979; Rogers et al. 1979).

2.3.2 Prey Species. Calanoid copepods are the major prey for AH adults and juveniles from the western Aleutians (Simenstad et al. 1978), Kodiak (Harris and Hartt 1977a, b; Rogers et al. 1979) and Washington (Simenstad et al. 1977,1979; Cross et al. 1978). Other prey are crustacean larvae, mysids, gammarid amphipods, harpacticoid copepods, chaetognaths, larvaceans and polychaetes. According to Rogers et al. (1979), epibenthic invertebrates, particularly mysids and gammarid amphipods, increased in relative importance for AH during autumn and winter; however, total stomach content weight was much lower. AA made a similar shift to benthic prey during early spring when zooplankton abundance was low (Richards 1982). The prey spectra of other species of sand lance are very similar to that of AH (see Inoue et al. 1967; Sekiguchi et al. 1974,1976; Kitaguchi 1977; and Hashimoto 1982 for AP; Richards 1965, 1982; and Meyer et al. 1979 for AA; Scott 1973 for AD and Macer 1966 for AM).

2.3.3 Prey Density Requirements. Not applicable.

2.3.4 Factors Affecting Availability of Prey. Since calanoid copepods are the primary prey of sand lance, any factors affecting their abundance and distribution presumably could affect sand lance feeding. Calanoid copepods also are preyed on to a great extent by juvenile Pacific herring that frequently co-occur with sand lance (Harris and Hartt 1977a, b; Simenstad et al. 1979).

2.3.5 Temporal Patterns of Energy Storage. Seasonal variation in fat content has been demonstrated for AP (Inoue et al. 1967; Sekiguchi et al. 1976) and AM (Kuhl and Luhman, in Winslade 1974c). Lowest values were recorded at the beginning of the feeding period and peak fat content is reached at the end of the feeding season just prior to a prolonged period of dormancy during which the sand lance remain buried in the sand. Fat supply is probably important for maintenance metabolism and gonad maturation (Winslade 1974c; Sekiguchi et al. 1976).

2.3.6 Evidence of Food Limitation. No data available.

2.4 Predation

2.4.1 Predator Species. A wide variety of marine fish, seabirds and mammals are major predators of AH over their entire range (Tables 1-3).

2.4.2 Effect on Spawning Adults. No estimates of the importance of predation have been made for AH, although apparently it is very high. Evidence for species from the northwestern Atlantic (Sherman et al. 1981; Winters 1983) and the North Sea (Andersen and Ursin 1978) suggests decreased levels of predation on sand lance have led to large increases in sand lance populations.

2.5 Other Factors Affecting Adults

2.5.1 Biotic. Mass mortalities of sand lance along the coast of England has been associated with blooms of *Gonyaulax* sp (Adams, in Reay 1970). (See 2.5.2 for laboratory experiments related to food availability.)

2.5.2 Abiotic. As a consequence of their habit of burrowing into sandy bottoms for extended periods, sand lance usually are found in association with sand and fine gravel bottoms (Reay 1970; Trumble 1973). Both particle size and circulation appear to be important factors, although specific habitat requirements are unknown. Laboratory experiments showed that AH avoided oiled sand (Pearson et al. 1984; Pinto et al. 1984). AH mortality was noted in connection with oil pollution and detergent cleanup in the Torrey Canyon oil spill (Smith, in Reay 1970).

Table 1. Marine fish predators of sand lance (AH).

SPECIES	AREA	STUDY
Pacific cod	Aleutians Kodiak British Columbia	Simenstad et al. 1977 Jewett 1978; Hunter 1979 Westrheim and Harling 1983
Halibut	S.E. Bering Sea W. Aleutians Kodiak Gulf of Alaska/ Bering Sea	Smith et al. 1978 Simenstad et al. 1977 Hunter 1979 Best and Hardman 1982
Hake	British Columbia	Outram and Haegele 1972
Rock sole	Kodiak British Columbia	Harris and Hartt 1977; Hunter 1979 Westrheim and Harling 1983
Yellowfin sole	Kodiak	Harris and Hartt 1977; Rogers et al. 1979
Sand sole	Kodiak	Hunter 1979
Petrale sole	British Columbia	Westrheim and Harling 1983
Lingcod	British Columbia	Hart 1973
Rockfish (black, yellowtail, dusky, widow)	Gulf of Alaska Rosenthal 1983	Rosenthal et al. 1981, 1982;
Salmon (chum sockeye)	W. Aleutians	Simenstad et al. 1977
Salmon (chinook, coho, sockeye, pink)	British Columbia	Beacham 1986
Great sculpin	Kodiak	Harris and Hart 1977

Table 2. Marine seabird predators of sand lance (AH).

SPECIES	AREA	STUDY
Black-legged kittiwake	Chukchi Sea	Swartz 1966; Springer and Roseneau 1979; Springer et al. 1984
	Norton Sound	Drury et al. 1981
	S. Bering Sea/Gulf of Alaska	Hatch et al. 1978
Common murre	Chukchi Sea	Swartz 1966; Springer et al. 1984
	Norton Sound	Drury et al. 1981
	E. Bering Sea	Ogi and Tsujita 1973
	Kodiak	Drury et al. 1981
Thick-billed murre	Chukchi Sea	Swartz 1966; Drury et al. 1981; Springer et al. 1984
Tufted puffin	Chukchi Sea	Swartz 1966
	W. Aleutians	Vermeer 1979
	Gulf of Alaska	
	British Columbia	
	Washington	Wilson 1977; Wilson et al. 1984
Horned puffin	Chukchi Sea	Swartz 1966
	Norton Sound	Drury et al. 1981
	Pribilof Islands	Hunt et al. 1981
	Gulf of Alaska	Manual and Boersma 1978
	N. Gulf/S. Bering	Hatch et al. 1978
Rhinoceros auklet	Gulf of Alaska	Leschner in Vermeer 1979
	British Columbia	Vermeer 1979
	Washington	Wilson 1977; Wilson and Manuwal 1986
Ancient murrelet	British Columbia	Sealy 1975
Sooty shearwater	British Columbia	Sealy 1975
Pelagic cormorant	Chukchi Sea	Swartz 1966
	British Columbia	Robertson 1974
Double-crested cormorant	British Columbia	Robertson 1974
Red-throated loon	British Columbia	Reimchen and Douglas 1984

Table 3. Marine mammal predators of sand lance (AH).

SPECIES	AREA	STUDY
Fur seal	E. Aleutians	Taylor et al., in Simenstad et al. 1979
	W. Gulf of Alaska	Wilke and Kenyon 1957; Kajimura 1984
	Kodiak	Macy et al. 1978
Harbor seal	Gulf of Alaska	Pitcher 1980
	Oregon	Brown and Mate 1983
Stellar sea lion	Gulf of Alaska	Wilke and Kenyon 1952; Pitcher 1981
Spotted seal	E. Bering Sea	Lowry and Frost 1981
Minke whale	N. Pacific	Nemoto 1959; Frost and Lowry 1981; Kajimura 1984
Sei whale	Bering Sea	Frost and Lowry 1981
Humpback whale	Alaska	Huey, in Simenstad et al. 1979

Temperature and light also appear to be important factors. When water temperatures reach 20°C, AP burrow in the sand and become dormant (Nagoshi and Sano 1979). For adult AD, however, increased temperature is associated with growth (Winters 1983). White Sea sand lance (AM) are reported to bury themselves in response to reduced light levels (<0.1 lux) and predators (Girsa and Danilov 1978).

In laboratory experiments, the activity of adult AM was directly related to food availability, light intensity, and temperature (Winslade (1974a,b,c). If food was present, activity was high during the day and low at night when they mostly remained buried in the sand (Winslade 1974a). When abundant food was available, swimming activity was maximum at light intensities of 100 and 1000 lux , much reduced at 10 lux and very low at 1 lux; the threshold level (light intensity at 50% maximum activity) was 20 lux (Winslade 1974b). Diurnal and seasonal variations in catch of sand lance on the fishing grounds correlated with estimated light intensity of about 100 lux at the bottom (Winslade 1974b). Activity during daylight was high at 10 and 15°C and much lower at 5°C (Winslade 1974c). The percentage of the annual catch in April (the first month of the fishery) showed a positive correlation with temperature in April, indicating that initial availability in the spring may be more related to temperature than to food availability (Winslade 1974c). Burying in the sand at the end of the summer may be related to fat content, as well as to decreasing levels of food availability, light intensity and temperature (Winslade 1974c). Older fish are reported to disappear from the catches earlier in the summer, possibly due to reduced requirements for growth and/or earlier accumulation of fat (Winslade 1974c).

2.5.3 Total Mortality. For a fished population of adult AM, total annual mortality was estimated at 65-75% (Z=1.2) (Macer 1966, cited in Reay 1970). Based on age composition data from other stocks, Reay (1970) suggested fished and unfished stocks have similar mortality rates. Winters (1983), who investigated AD mortality rates in Newfoundland between 1968 and 1979, reported a steady decrease in mortality rates from Z-values of over 1.0 to less than 0.5. Since there is no fishery for sand lance in Newfoundland, these rates are considered to be natural mortality. The increase in sand lance survival was correlated with a decline in cod stocks, known to be major predators on AD.

2.6 Laboratory Holding and Rearing

Spawning of adult sand lance in the laboratory has been reported for AH by Pinto (1984), for AA by Smigielski et al. (1984) and for AM by Winslade (1971; 1974a,b,c).

3 EGGS

3.1 General Description

The sand lance egg, which usually contains a single yellow oil globule, is nearly spherical, demersal and adhesive (Reay 1970; Trumble 1973). According to Pinto (1984), AH eggs from the northeastern Pacific range from 0.8-1.22 mm, with a mean diameter of 1.00 mm. Mean diameters of egg of other *Ammodytes* species are 0.66 mm for AP, 0.83 mm or 1.00 mm for AA, 1.00 mm for AD and 1.02 mm for AM (Williams et al. 1964; Inoue et al. 1967; Winslade 1971; Scott 1972a; and Smigielski et al. 1984).

3.2 Distribution and Abundance

3.2.1 Duration of Egg Stage. In the laboratory, incubation time for AH eggs was approximately 24 days at 9°C (Pinto 1984). Japanese sand lance (AP) eggs hatched in 33 days at 6.2°C and 13 days at 15.7°C (Inoue et al. 1967) and AP or AH eggs hatched in about 22 days at 6.9° to 10°C (Kitaguchi 1977). According to Yamashita and Aoyama (1985), median hatching time for AP eggs was 51 days at 6.5°C, 25 days at 10.5°C and 20 days at 15.5°C. Average hatching time for AA eggs was 62 days at 2°C and 30 days at 10°C (Smigielski et al. 1984). Experiments on AP eggs (Yamashita and Aoyama 1985), AA eggs (Smigielski et al. 1984) and AM eggs (Winslade 1971) showed that incubation times were long and variable and that temperature and oxygen were important factors.

3.2.2 Large-Scale Patterns. No information on egg distribution is available, but presumably eggs would be found in the same general areas as adults since spawning migrations are not known (Reay 1970).

3.2.3 Small-scale Patterns. No data available.

3.2.4 Maximum and Mean Abundances. No data available.

3.2.5 Vertical Distribution. Sand lance eggs are demersal and adhesive, although they are occasionally collected from the water column, probably as a result of currents bringing the eggs off the bottom (Williams et al 1964; Senta 1965).

3.3 Feeding

Not applicable.

3.4 Predation

3.4.1 Predator Species. Large numbers of late stage AD eggs were found in stomachs of the yellowtail flounder (*Limanda ferruginea*) in the northwestern Atlantic (Scott 1972a).

3.4.2 Effect on Eggs. No data available.

3.5 Other Factors Affecting Eggs

3.5.1 Biotic. No data available.

3.5.2 Abiotic. According to Inoue et al. (1967), AP had a low hatch rate at 15.7°C and a maximum hatch rate at 8.2°C. In a laboratory study on AA, incubation time and time to hatch completion increased with decreasing temperatures (10°-2°C) (Smigielski et al. 1984). The authors suggest that in the natural environment mechanical action may be a factor in reducing incubation times. Experiments on AM eggs indicated hatching time may be affected by factors other than temperature, e.g., incubation time and mortality increased with decreasing oxygen concentrations (9.5-4.0 ppm) (Winslade 1971). No eggs hatched at 2.1 ppm; however, early stage embryos were able to tolerate low oxygen concentrations for about a week and to complete development if subsequently shifted to higher concentrations. Winslade (1971) suggested that the ability to retard development and survive periods of low oxygen levels may be of particular adaptive value, since sand lance spawn on sandy bottoms and eggs could become temporarily buried in shifting sand.

3.5.3 Total Mortality. No data available.

3.6 Laboratory Holding and Rearing

Techniques for incubation of sand lance eggs are described by Winslade (1971), Pinto (1984) and Smigielski et al. (1984).

4 LARVAE

4.1 General Description

Larvae of the five species of *Ammodytes* considered herein have been described by the following: Pinto 1984 (AH); Kobayashi 1961 (AP); Richards 1965 (AA/AD); Smigielski et al. 1984 (AA); Scott 1972a (AD); Einarsson 1951, Macer 1966, Winslade 1971 (AM).

AH larvae hatched at 9°C were 5.3 mm in length, had pigmented eyes but did not have a complete gut or functional jaws (Pinto 1984). At the end of one week, the yolk sac was not completely absorbed and the intestines and jaws were still not completely developed.

AP larvae hatched at 6.5°C were 4.7 mm in length (Yamashita and Aoyama 1985). Some larvae began feeding within 2 days, and 50% of the larvae were feeding successfully within 5 days. Yolk-sac absorption was 95% complete by 6 days and 100% complete by 12 days after hatching. Larvae were able to survive without food for a long time after hatching: time to 50% mortality was approximately 11, 16 and 21 days after hatching at 15.5°, 10.5° and 6.5°C, respectively. No clear "point of no return" was noted. The period of recoverable starvation (from normal onset of feeding to irreversible starvation) was estimated as about 9 days.

AA larvae hatched at four different temperature regimes (2, 4, 7 and 10°C) and had a complete gut and functional mouth; some individuals in each of the four groups began to feed within hours of hatching (Smigielski et al. 1984). At 7°C, 50% of larvae 6.5 mm in length were feeding within 2 days. Yolk-sac absorption took 3 days and oil globule absorption 7 days. For AM larvae, yolk-sac and oil globule absorption took about 2 weeks at 7°C and slightly less time at 10°C (Winslade 1971). After 13 days, 16% of larvae at 7°C and 58% at 10°C had begun to feed. However, newly hatched larvae were able to survive for a considerable length of time without food: time to 50% mortality was 28 days at 7°C and 19 days at 10°C.

Yamashita and Aoyama (1985) determined growth rates of 0.12 mm in length and 4.2% dry weight per day for AP reared in the laboratory at 6.5°C. Growth rates for the two northwestern Atlantic sand lance have been estimated from length frequency distributions as follows: AA, 11.7 mm per month (Norcross et al. 1961) or 10.9 mm per month (Smith et al. 1978); AD, 5.9 mm per month (Scott 1972a). Smigielski et al. (1984) estimated growth rates for AA to range from 2.4-5.62% dry weight per day at 2°C and 10°C, respectively, corresponding to length increases of 2.7 mm and 11.3 mm per month for 155 days of growth. Buckley (1984) estimated minimum growth rates to prevent starvation in AA larvae to be 2.4%, 2.5% and 3.4% change in protein content per day at 2, 4 and 7°C, respectively.

4.2 Distribution and Abundance

4.2.1 Duration of Larval Stages. AA laboratory studies show that at 7°C yolk-sac absorption takes place in 3 days at about 6.5 mm in length, oil globule absorption in 7 days at 7.2 mm and 50% first feeding in 2 days at 6.5 mm (Smigielski et al. 1984). With increasing temperature, size at yolk-sac absorption decreased but no differences in size at oil globule absorption or at first feeding were observed. Metamorphosis to the juvenile stage occurred at 29 mm in length, which took 131 days at 4°C and 102 days at 7°C. Schooling behavior was observed at 25-30 mm (90 days at 7°C).

Laboratory-reared AM larvae completely absorbed yolk sacs and oil globules in 14-15 days at 7°C and in 12 days at 10°C (Winslade 1971). AM larvae completed metamorphosis at lengths between 30 mm and 40 mm (Macer 1966).

4.2.2 Large-scale Patterns. Sand lance larvae (AH) generally occur in shallow (less than 200 m) nearshore areas of the Bering Sea and northeastern Pacific Ocean (Trumble 1973; Macy et al. 1978; Rogers et al. 1980). AH larvae were most abundant in early April in the Bering Sea (Waldron and Vinter 1978) and March-April in the Kodiak area (Rogers et al. 1979; Kendall et al. 1980). In Washington, small larvae (less than 10 mm) were reported from late January to early May in Skagit Bay (Blackburn 1973) and from mid-January to late March in Puget Sound (R. Trumble, Washington Dep. Fisheries, unpublished data). Recently, hatched larvae (AA/AD) that were most abundant in shallow nearshore areas gradually dispersed offshore in the northwestern Atlantic (Richards and Kendall 1973).

No information is available on interannual variability in AH larval abundance. However, sand lance larvae (AA/AD) have shown very large interannual changes in abundance (approximately a 20-fold increase between 1974 and 1979) (Smith et al. 1978; Sherman et al. 1981; Morse 1982).

4.2.3 Small-scale Patterns. Altukhov (1978) reported that AM larvae in the White Sea were concentrated in areas of "eddying currents."

4.2.4 Maximum and Mean Abundances. In the eastern Bering Sea, sand lance (AH) larvae were the third most abundant species in bongo net samples (1908/10 m^2) despite their occurrence in less than 25% of the samples (Waldron and Vinter 1978). AH larvae were also abundant in ichthyoplankton samples from the vicinity of Kodiak Island (Dunn and Naplin 1974; Rogers et al. 1979; Kendall et al. 1980). Larval AP densities in Otsuchi Bay, Japan, averaged 105.6/100 m^3 in 1981-82 (Yamashita et al. 1984b).

In the Georges Bank region, concentrations of sand lance larvae (AA/AD) were over 100,000/10 m^2 (Smith et al. 1978). Mean abundance in this region ranged from 10 to 1018 per 10 m^2 between 1974 and 1979 and accounted for 55-98% of the larvae in winter samples (Sherman et al. 1981).

4.2.5 Vertical Distribution. In Kodiak Island samples, AH larvae were most abundant at 10 and 30 m depths during the day and were somewhat deeper at night (Rogers et al. 1979). Inoue et al. (1967) and Yamashita et al. (1985) reported similar results for AP larvae; they were 6-10 m below the surface during the day and deeper at night and also were more concentrated above thermoclines. Yamashita et al. (1985) reported vertical migration in larval AP as small as 5-6 mm, although larger larvae had a greater vertical range. AA larvae also were found to be near the surface during the day and deeper at night (Richards and Kendall 1973).

4.3 Feeding

4.3.1 Habitat. (See 4.2.5.)

4.3.2 Prey Species. In the Strait of Georgia (under the Fraser River plume), larval sand lance (AH) less than 20 mm in length fed on prey less than 500 μ in diameter, mainly copepod eggs and nauplii (LeBrasseur et al. 1969). Larger larvae (20-40 mm) fed on larger (0.5-1.5 mm) zooplankton, primarily species of *Microcalanus, Oithona* and *Pseudocalanus* and nauplii of larger copepods. AP larvae fed mostly on small copepods, copepod nauplii and cladocerans (Inoue et al. 1967; Sekiguchi et al. 1974).

According to Covill (1959), the primary prey items for larval AA between 3.2 and 23.1 mm in length were copepod nauplii and copepods. Phytoplankton, an important component of the diet for small larvae (less than 5 mm), decreased in importance with increasing size of larvae. Phytoplankton appeared to be more important in winter (Dec-Feb.) than in spring (March-April) for the same size class of larvae. Ryland (1964) noted that AM larvae fed only during daylight. Diatoms and dinoflagellates were important items in the diet of AM larvae less than 8 mm in length, and larger larvae fed mostly on copepod nauplii and appendicularians.

4.3.3 Prey Density Requirements. Laboratory studies of Winslade (1971), Buckley et al. (1984) and Yamashita and Aoyama (1986) showed that newly hatched AM, AA and AP larvae are capable of surviving up to 2 weeks without food (see also 4.1).

4.3.4 Factors Affecting Availability of Prey. No data available.

4.3.5 Temporal Patterns of Energy Storage. Not applicable.

4.3.6 Evidence of Food Limitation. LeBrasseur et al. (1969) reported that over 50% of AH larvae less than 40 mm in length in the Strait of Georgia had empty stomachs and suggested that concentrations of microzooplankton were limiting survival.

The smallest size group of AA larvae in Long Island Sound had the highest percentage (19%) of empty stomachs (Covill 1959). AA survival to metamorphosis at food concentrations of 200, 500 and 1000 rotifers/liter (corresponding to 0.16, 0.40 and 0.80 calorie/liter) was estimated to be 0.12%, 5.75% and 11.74%, respectively (Buckley et al. 1984). Since these estimates were based on a larval period of fixed length (102 days), slower growth at lower food concentrations would extend the larval period and increase mortality (Buckley et al. 1984). Although survival rates at the above food concentrations are comparable to those of other species, the caloric requirements appear to be lower, indicating possible adaptation to survival at low food concentrations (Buckley et al. 1984). Comparison of RNA-DNA ratios in larval sand lance (probably AA) collected from the northwestern Atlantic indicated that, in 1982, larvae were generally in poorer condition than larvae collected in 1981, and that some of the 1982 larvae were apparently losing weight (Buckley 1984).

4.4 Predation

4.4.1 Predator Species. Marine fish, particularly juveniles, are major predators of larval AH, e.g., in Bristol Bay, sockeye salmon juveniles (Straty 1974) and sockeye adults (Nishiyama 1974); in nearshore Kodiak, walleye pollock and juvenile pink salmon (Rogers et al. 1979); in Cook Inlet, sockeye and coho salmon juveniles and staghorn sculpins (Blackburn et al 1980); in Chatam Sound, juvenile coho salmon (Manzer 1969); in the Strait of Georgia and Saanich Inlet, juvenile salmonids, including coho, chum, sockeye and king salmon and steelhead trout, *Salmo gairdnerii*, (Barraclough 1967; Barraclough et al. 1968; Robinson et al. 1968); in the Strait of Juan de Fuca, juvenile coho and, to a lesser extent, juvenile chinook and herring (Cross et al. 1978). Arctic terns were a major predator of larval AH in Alaska (Bent, cited in Ainley and Sanger 1979). (See also Tables 1-3.)

Predation by the hyperiid amphipod *Parathemisto japonica* on larval AP (Yamashita et al. 1984a, b) was estimated to be an important source of mortality. In the laboratory, both newly hatched and post-yolk sac larvae (13-15 days old; 6.0-6.3 mm standard length) were vulnerable to amphipod predation.

4.4.2 Effect on Larvae. No data available.

4.5 Other Factors Affecting Larvae

4.5.1 Biotic. No data available.

4.5.2 Abiotic. Inoue et al. (1967) suggested that wind is an important factor in larval dispersal. At low temperatures, growth is slower and time to metamorphosis is longer for AA larvae (Smigielski et al. 1984). However, daily mortality rates of AA larvae in the laboratory are not affected by temperatures between 2° and 9°C (Buckley et al. 1984). AM larvae survive longer without food at lower temperatures (Winslade 1971).

4.5.3 Total Mortality. For larval sand lance (AA/AD) in the northwestern Atlantic, instantaneous mortality rates between 1974 and 1980 ranged from .207-.363, corresponding to a daily mortality of 6-10% for larvae of 5-27 mm (Morse 1982). In laboratory experiments, the daily instantaneous mortality rate for AA larvae between hatching and day 16 was 0.01 and was unaffected by feeding level or temperature (Buckley et al. 1984). Mortality rates for older larvae (30-43 days) ranged from 0.2-0.02 and decreased with increasing food level.

4.6 Laboratory Holding and Rearing

Winslade (1971) and Smigielski et al. (1984) describe techniques for rearing larvae of AM and AA, respectively.

5 JUVENILES

5.1 General Description

At 7°C, metamorphosis to the AA juvenile phase takes place at a length of about 29 mm, approximately 102 days after hatching (Smigielski et al. 1984). The juvenile stage may last from 1-3 years, depending on the area (see 2.1.1).

5.2 Distribution and Abundance

5.2.1 Duration of Juvenile Stage. (See 5.1.)

5.2.2 Large-scale Patterns. Juveniles commonly co-occur with adults, although they may also be present in inshore areas where adults are absent (Richards et al. 1963; Reay 1970). Reay (1970) suggested that this is due to the wide dispersal of juveniles rather than to separate nursery areas. AH juveniles are abundant along sandy beaches and in shallow nearshore areas of the Bering Sea (Macy et al. 1978), Norton Sound (Barton 1978), Kodiak Island (Blackburn and Jackson 1980) and Cook Inlet (Blackburn et al. 1980). Juveniles (0-age and age 1) exhibit an onshore migration during the summer in some areas, and there is some evidence that migration takes place earlier in the summer for age 1 fish (Barton 1978; Blackburn and Jackson 1980; Blackburn et al. 1980). Large interannual variations have been reported in the catch of 0-age AP in Japan (Hamada 1966a, b, c; Inoue et al 1967; Nagoshi and Sano 1979).

5.2.3 Small-scale Patterns. Juvenile AH have been observed schooling with similar-size juvenile herring (Hobson 1985). Richards (1976) reported similar observations for AA. AA schooling behavior begins at 25-30 mm, about the time of metamorphosis to the juvenile stage (Smigielski et al. 1984).

5.2.4 Maximum and Mean Abundances. No estimates of abundance are available.

5.2.5 Vertical Distribution. Juveniles may be more numerous than adults in surface waters at night, based on catches of AP (Senta 1965b) and AM (Macer 1966). In the laboratory, burrowing behavior in AA juveniles is first observed when they are between 35 and 40 mm in length (Smigielski et al 1984).

5.3 Feeding

5.3.1 Habitat. Juveniles feed almost exclusively in the water column, but no information is available on foraging depth range.

5.3.2 Prey Species. Studies of the food habits of juvenile AH from the Chukchi Sea (Springer et al. 1984), western Aleutians (Simenstad et al. 1978), Kodiak (Harris and Hartt 1977a, b; Rogers et al. 1979), Cook Inlet (Blackburn et al. 1980) and the Strait of Georgia (Barraclough 1967) agree in the predominance of copepods in the diet. Other prey items of some importance include other crustacean larvae, larvaceans, cladocerans, chaetognaths, fish larvae, mysids and gammarid amphipods. In the lower Cook Inlet area, Blackburn et al. (1980) reported that harpacticoid copepods were important in April, along with shrimp and fish larvae, while calanoid copepods were most abundant the remainder of summer.

5.3.3 Prey Density Requirements. No data available.

5.3.4 Factors Affecting Availability of Prey. No data available.

5.3.5 Temporal Patterns of Energy Storage. No data available.

5.3.6 Evidence of Food Limitation. A high negative correlation was found between the size of age 1 AP and the abundance of adult fish, indicating possible competition for food (Hamada 1967). Nagoshi and Sano (1979) reported a similar significant negative correlation between growth and abundance in 0-age AP. Sekiguchi et al. (1976) showed that 0-age AP do not begin to accumulate fat reserves until attaining 45-50 mm in length and that fat content increased with increasing length; consequently, reduced growth could affect survival by reducing energy reserves during the dormancy period.

5.4 Predation

5.4.1 Predator Species. (See Tables 1-3 and 4.4.1.)

5.4.2 Effect on Juveniles. No data available.

5.5 Other Factors Affecting Juveniles

5.5.1 Biotic. No data available.

5.5.2 Abiotic. Winters (1981) reported a significant positive relationship between water temperature and first year growth in AD.

5.5.3 Total Mortality. No data available.

5.6 Laboratory Holding and Rearing

(See 2.6.)

6 CURRENT HYPOTHESES ON FACTORS AFFECTING YEAR-CLASS ABUNDANCE

Environmental effects: Hamada (1966c) correlated increased catches of 0-age sand lance (AP) with low water temperatures during the spawning season and also with the number of days with westerly winds during the three weeks following peak spawning.

Density-dependent effects on recruitment: A strong negative correlation (r = -.87) between the percentage of age-1 AP in the catch and the catch of 0-age fish was observed by Hamada (1966a). In addition, Hamada (1967) reported a negative correlation ($r = -.81$) between the number of eggs spawned and the catch of 0-age AP.

Density-dependent effects on growth: Small size of age-1 AP was correlated with large catches of adult (2-3 years old) fish (Hamada 1967). Similarly, Nagoshi and Sano (1979) found a negative correlation ($r = -.86$) between growth of 0-age AP and an index of population density.

Food availability: The availability of adequate food has frequently been suggested as an important factor in larval mortality. Low food availability may lead to reduced growth and consequently a prolonged larval phase and increased vulnerability to predation (Buckley 1984). Laboratory studies on AA larvae provide estimates of minimum growth rates necessary to prevent starvation at a range of temperatures and a model predicting recent larval growth based on RNA-DNA ratios and temperature (Buckley 1984; Buckley et al 1984). Larvae (probably AA) collected during 1981 and 1982 indicate differences in larval condition (RNA-DNA ratio) that could be attributed to food availability (Buckley 1984). Although no direct evidence was presented to indicate differences in larval survival, based on RNA-DNA ratios, a higher percentage of larvae were in poor condition in 1982, and some had apparently been losing weight (Buckley 1984).

Replacement and predation: Andersen and Ursin (1978) presented the hypothesis that the reduction of herring and mackerel stocks have resulted in their replacement in the North Sea ecosystem by small, fast growing opportunistic species such as sand lance. However, the lack of prior data on the abundance of sand lance makes the hypothesis difficult to test unless herring and mackerel stocks return to former levels of abundance.

Sherman et al. (1981) presented a similar hypothesis for changes in the ecosystem structure of the northwestern Atlantic. Larval surveys indicated a substantial increase in the abundance of sand lance (AA/AD) larvae between 1974 and 1979 which apparently reflects a large increase in spawning stock biomass (Morse 1982). The authors suggest that this rapid increase in sand lance population size was directly related to the reduction of mid-size predators, such as cod, haddock, hake, mackerel and herring.

Both sand lance (AD) and capelin are important prey items for Atlantic cod off Newfoundland (Lilly 1982; Lilly and Fleming 1981; Winters 1983). Winters (1983) hypothesized that recent increases in sand lance (AD) abundance were attributable to decreases in cod biomass on the Newfoundland Grand Bank between 1968 and 1979. The presence of greater percentages of older age groups indicated reduced mortality, and a change in the dominant age group from age 4 to age 3 suggested increased recruitment. Using data from research trawl surveys, Winters (1983) found significant negative correlations of sand lance abundance and recruitment with cod biomass.

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PACIFIC HERRING, *Clupea harengus pallasi,* IN THE NORTHEAST PACIFIC AND BERING SEA

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1 BACKGROUND

1.1 Literature Search

Literature pertinent to the fisheries oceanography of Pacific herring in the northeastern Pacific Ocean was reviewed. Most of the papers pertain to British Columbia herring and the remainder to Gulf of Alaska, eastern Bering Sea, Washington, Oregon and California herring. Where appropriate, information is included on Atlantic herring (*Clupea harengus harengus*), which has a similar life-history.

1.2 Unit Stocks and Their Relationships

In the eastern Pacific, herring occur from Baja California, Mexico, to the Beaufort Sea (Hart 1973) and in the western Pacific from the Yellow Sea (Tang Qiseng 1980) to the east Siberian Sea (Svetovidov 1952). The structure and genetic relationships among stocks within this range is not clearly understood. Using electrophoretic analyses, Grant (1979) distinguished herring in the northwestern Pacific and the Bering Sea from herring in the northeastern Pacific to the south and east of Kodiak Island. This geographic variation may reflect isolation and divergence during glacial periods. Within the eastern Pacific range, many stocks have been identified, e.g., one or more stocks in California (Miller and Schmidtke 1956; Spratt 1976, 1981), one in Oregon (Steinfeld 1972) and three or more in Puget Sound (Gonyea and Trumble 1983). For British Columbia, nine "major" and 22 or possibly more "minor" stocks were identified (Taylor 1964). Rounsefell (1930) distinguished five or more stocks in southeastern Alaska, as well as populations in Yakutat Inlet, Prince William Sound, Cooke Inlet and around Kodiak Island. At least three stocks have been identified within the Bering Sea (Barton and Wespestad 1980), and there are indications that the stock composition is equally complex in the Asian and Soviet regions (Haegele and Schweigert 1985; Hay 1985).

The diversity of Pacific stocks may equal or even exceed that of Atlantic herring. To explain Atlantic herring diversity, Iles and Sinclair (1982) hypothesized that each stock represents an adaptation to unique hydrographic features, especially those that help in the retention of larvae during early development. Further, they suggested that the size of each stock is related to the size of each retention area. This model also may apply to Pacific herring as they spawn, with few exceptions, in coastal indentations or in inshore channels, bays or fjords, where the local circulation patterns may promote larval retention.

1.3 The Fishery

1.3.1 Relative Size and Importance. On the Pacific Coast of North America, indigenous peoples have harvested herring and herring spawn since 800 B.C. (Hourston and Haegele 1980; Fried and Wespestad 1985). In Japan, records of herring catches go back to 1477 (Morita 1985). Japanese herring catches, once reaching nearly one million mt per year, decreased gradually until negligible quantities were landed in the late 1950s (Motoda and Hirano 1963). Pacific herring were sold fresh in the San Francisco area in the gold rush era (Eldridge and Kaill 1973). Subsequently, export markets developed and dry-salted herring were sold to the Orient. In British Columbia and Alaska, herring were sold commercially for bait, mainly to halibut fleets (Bell 1981).

A recent review of Pacific herring fisheries and management in the eastern Pacific (Trumble and Humphreys 1985) is summarized below. In the mid-1950s, the spawning population in the San Francisco Bay and Tomales Bay area was estimated at about 16,000 ton (Miller and Schmidtke 1956). More recently, Spratt (1981) reported stock estimates varying between about 5000 ton in the early 1970s to 53,000 ton during the 1980 spawning season. Catches in Oregon have been very small, less than 100 ton (Steinfeld 1972). Estimates of Washington herring fisheries were less than 500 ton until 1957 (Ketchen et al. 1983). At present, there are three commercial herring fisheries in Puget Sound: one for sac-roe and two for bait. The sac-roe fishery, centered on spawning grounds in spring, is the largest in tonnage and revenue. The bait fisheries for commercial and sport fishing utilize juvenile herring. The fishery for sac-roe is seasonal, the others operate nearly year-round (Trumble 1983).

In British Columbia, the first commercial herring catch, 75 ton, was in 1877. From 1904 to 1934, between 30,000 and 85,000 ton were taken annually for a dry salted herring fishery developed for export. In 1935 a fishery for reduction began (Hourston and Haegele 1980) and by 1940 the entire coast was fished extensively. Annual fishing mortality rates estimated at 75-90% in the 1950s did not cause noticeable declines in the populations (Hourston 1980); in fact, during 1959-1962, good year classes produced abundant catches. However, fewer young-of-the-year herring were observed in the 1961 catches, and most stocks began to decline in 1963 (Taylor and Wickett 1967; Hourston 1980). The reduction fishery stopped in 1967 following a fishing closure that lasted 4 years. By the early 1970s, southern British Columbia stocks regained or surpassed previous levels, but northern stocks may not have fully recovered (Hourston 1980; Webb 1983). A new fishery, for roe, began in the early 1970s. In this fishery, which averages about 30,000 mt per year, mature herring are captured near or on spawning grounds. The roe is extracted, brined and exported, mainly to Japan. Also, there are two smaller fisheries, a bait fishery, supporting recreational salmon fisheries, and a "food fishery" in fall months.

Herring were first fished commercially in the Gulf of Alaska in the 1880s. A fishery for reduction to fish meal peaked at 70,000 ton in 1929, declined after the second World War and ended in the 1960s for economic reasons (Wespestad and Fried 1983). A sac-roe and spawn-on-kelp fishery, developed in the 1970s (Blankenbeckler 1980; Wespestad and Fried 1983), continues, as does the bait fishery. Average annual catch from the sac-roe fishery was 5500 ton in the 1970s (Wespestad and Fried 1983).

A salted herring fishery that operated in the eastern Bering Sea from 1928 through the 1940s caught about 3000 ton annually (Wespestad and Fried 1983). The Soviet Union began a trawl fishery there in 1959 and later was joined by Japan. The catch peaked in 1970 at 140,000 ton, then declined due to lower abundance and restrictions by the U.S. government. The United States began fishing in the Bering Sea in 1977. Catches in the late 1960s and early 1970s contained older, larger herring than in the late 1970s, and recruitment has increased since 1972 (Wespestad and Barton 1980). Present abundance measures cannot be compared directly to early numbers, however, because fishing intensity has increased. Therefore, it is difficult to assess catch and catch per unit effort (CPUE) data (Wespestad and Barton 1980). Further, CPUE data are not available for most Alaskan herring stocks. Using a model of the eastern Bering Sea ecosystem, Laevastu and Favorite (1978) estimated a minimum of 2.75 million mt of herring would be needed to maintain the ecosystem in equilibrium.

1.3.2 Age at Recruitment. Herring recruit into the sac-roe fishery when mature (see 2.1.1) and into bait and reduction fisheries when younger, usually at age 2.

1.3.3 Characteristics of Harvested Fish. Geographical and temporal variation among herring stocks is too great for precise summaries about size and age of catches. In general, smaller fish were captured during the reduction fishery era: new recruits made up the bulk of the harvest and the average age was 3 years and average total length 170 mm for the Washington fishery (Trumble and Humphreys 1985).

Length and weight for British Columbia seine-captured herring ,averaged for each age group for a 10-year period (1971-1980), are as follows: age 2, 158 mm, 52 g; age 3, 185 mm, 85 g; age 4, 203 mm, 116 g; age 5, 214 mm, 141 g; age 6, 223 mm, 161 g; age 7, 231 mm, 176 g; age 8, 235 mm, 190 g; age 9, 236 mm, 191 g; age 10+, 248 mm, 230 g (from Tables 14.2 and 15.2, Hourston 1981).

1.3.4 Types and Selectivity of Gear. The early commercial fisheries in the northeastern Pacific mainly used drag- or beach seines (Taylor 1964). From the 1930s to the 1960s, in British Columbia, as well as elsewhere on the coast, purse-seines became the most effective gear, accounting for most of the catch, but drift- or gillnets and midwater bottom trawls were also used. In contrast, the Japanese herring fishery used stationary traps or weirs (Morita 1985). Trawling for herring was prohibited in 1980 (Fried and Wespestad 1985). Since the roe fishery started in the early 1970s, monofilament gillnets have become one of the principal capture methods (Barton and Wespestad 1980; Spratt 1981). Selectivity of monofiltran monofilament gillnets was described by Hay et al. (1986).

1.3.5 Distribution of Fishing Effort. In general, fishing effort is proportional to abundance of accessible stocks but also is related to availability of markets. British Columbia and southeast Alaska had the largest meal and reduction fisheries, with most of the effort in the fall months. Since the initiation of the fishery for roe, fishing effort has increased, especially in the Bering Sea, but also in California and south central Alaska (e.g., Prince William Sound) (Randall 1986).

1.4 Distribution and Abundance of the Population

Following spawning, most herring move offshore in small, fast-moving schools to feed. In the fall, having aggregated into larger schools, the herring return inshore and by spring school densely near spawning grounds (Taylor 1964). (See also 1.3.1 and 1.5.)

1.5 Current Status of Stocks and of Management Measures

The Washington catch was estimated at 14,000 ton in 1973-1974 but declined to 9000 ton by 1979, about 7% of British Columbia's yield. An approximate 20% harvest is maintained (Trumble 1983), but no catches were allowed between 1983 and 1986 because of low abundance.

Since 1980, the total annual catch in British Columbia is estimated at 30,000 mt (Webb 1983) and abundance at about 200,000-300,000 mt (Haist et al. 1985). Because spawners are so vulnerable to overfishing and the fishing fleet is large, the roe fishery is strongly regulated. Present fishing practices allow a 20% harvest of specific adult stock biomass (Haist et al. 1985).

In southeastern Alaska, the catch from sac roe, bait and food fisheries that was 13,000 ton in 1979 (Blankenbeckler 1980) declined to 8000 ton by 1982 (Wespestad and Fried 1983). In the Bering Sea, about 27,000 ton of herring were caught in 1982 (Wespestad and Fried 1983).

1.6 Recruitment Variability

Recruitment biomass can vary among years by a factor of ten . Strong year-classes may dominate occasionally and three to four years of poor recruitment are not uncommon. In Washington a strong year-class contributes substantially to, and dominates, the fishery for about four years (Trumble 1983).

1.7 Age Determination and Validation

In Washington, British Columbia and Alaska, age routinely is estimated from scales and occasionally from otoliths; the latter method is used mainly in California (Spratt 1981).

1.8 Age Composition of the Population

The Washington sac-roe fishery, generally dominated by herring of ages 4 to 6, has taken, since 1980, a large number of age-2 herring. Subsequent observations (Buchanan 1983) show mean age, length and abundance decreasing, in part, due to loss of age 6 and older fish (Trumble 1983).

In the 1960s, southern British Columbia stocks generally were dominated (50-75%) by age-3 fish and northern populations by a combination of ages 3, 4 and sometimes older cohorts (Taylor and Wickett 1967). This pattern continued in the northern part, at least through the late 1970s, but the single cohort dominance in southern British Columbia gave way to additional, in some years older, year-class dominance (Hourston and Schweigert 1980). Recent data suggest a return to the age composition of the 1960s (Stocker et al. 1985). The age composition in seine catches, averaged from 1971-1980 for the entire British Columbia coast, is as follows: age 2: 2.9%; age 3: 31.5%; age 4: 28.8%; age 5: 18.9%; age 6: 11.5%; age 7: 5.0%; age 8: 1.4%; age 9: 3%; age 10+: 0.1% (from Table 13.2, Hourston 1981).

2 SPAWNING ADULTS

2.1 General Description

2.1.1 Size and Age Ranges. In the southern parts of their range (Baja California and the Yellow Sea), herring generally mature at age 2 (Tang Qisheng 1980; Spratt 1981). To the north, mature herring are usually older: age 3 in British Columbia (Taylor 1964; Hay 1985) and ages 3 to 5 in the Bering Sea (Barton and Wespestad 1980). Pacific herring can live for 15-16 years, although few live beyond age 9 (Reid 1972).

2.1.2 Type of Spawning Behavior. Oocytes of Pacific herring mature synchronously and spawning occurs once a year. Spawns may occur in "waves," separated by roughly two-week intervals (Haegele and Schweigert 1985; Hay 1985). In contrast to Atlantic herring, Pacific herring are exclusively spring spawners (Haegele et al. 1981). Pacific herring spawn intertidally or subtidally on eelgrass (*Zostera* sp.) in sheltered bays and on open sand beaches, and also on rockweed (*Fucus* sp.) on rocky shores; virtually no spawning occurs on exposed coasts (Taylor 1964). Earliest spawning fish are frequently larger and older, a trend observed throughout their range, e.g., California (Spratt 1981), British Columbia (Hay 1985), Japan (Motoda and Hirano 1963) and the Sea of Okhotsk (Svetovidov 1952). Detailed ethological analysis by Hourston et al. (1977) and Stacey and Hourston (1982) indicated that the texture of the substrate is a vital factor in determining the precise location of spawn deposition.

2.1.3 Fecundity. Within British Columbia populations, the number of eggs produced is nearly proportional to female body weight (Ware 1985). When compared over a broad geographic range, size-specific fecundity varies inversely with latitude (Paulson and Smith 1977; Rabin and Barnhart 1977; Hay 1985). This trend is offset, however, by the tendency of female size and age to increase with latitude. Some evidence suggests that egg weight may also increase with latitude (Hay 1985), but this has not been established with certainty. However, in southern British Columbia, large females do produce larger eggs than small females (Kingston 1982). Relative fecundity is approximately 200 eggs produced in one year per gram of female total weight (Hay 1985). If an even sex ratio is assumed, then relative fecundity corresponds to about 100 eggs per gram of spawning fish, equivalent to 10^8 eggs per mt.

2.2 Distribution and Abundance

2.2.1 Duration of Spawning. In general, Pacific herring spawn later at higher latitudes (Blaxter 1985; Hay 1985). In Washington, spawning generally occurs in March (Trumble 1980) and in British Columbia from mid-February to mid-June, usually peaking in March (Taylor 1964). However, time of spawning in adjacent areas has been reported to vary, e.g., by one month in Washington (Trumble 1980) and by two to three months in British Columbia (Haegele and Schweigert 1985; Hay 1985). Spawning may span several months because maturation cycles may not be controlled by one set of photoperiod or temperature conditions. It is also possible that races may respond differently to environmental conditions (Blaxter and Hunter 1982). Specific timing of spawning may have evolved in part to enhance egg and larval retention in nearshore areas (Stevenson 1962; Iles and Sinclair 1982). Consequently, production, timing and placement of larvae can be fairly precise (Cushing 1982; Blaxter and Hunter 1982).

Interannual variability in peak spawning times for individual populations have a one-week standard deviation around the long-term mean (Cushing 1969; Wespestad and Fried 1983). Spawning in San Francisco and Tomales bays peaked in February until the late 1960s. By the late 1970s, it occurred half a month earlier (Spratt 1983). Higher mean March temperatures result in earlier spawning in the Strait of Georgia (Hay 1985). Although the environmental variable(s) controlling spawning time have not been identified, Blaxter and Hunter (1982) suggest that spawners may control their ripeness and modify spawning time over several years.

2.2.2 Large-scale Patterns. During April and May, adult British Columbia herring move from spawning grounds to offshore feeding grounds, a 500-km expanse between the Strait of Juan de Fuca and Hecate Strait to the north, where they usually remain during the summer (Hourston and Haegele 1980). During October to December, adults stop feeding and move to overwintering locations (Taylor 1964; Carlson 1980;

Hay 1985), but few data exist on exact migration routes in British Columbia. Timing of migrations varies from year to year and among populations (Taylor 1964); for example, inshore migration of lower east coast stocks of Vancouver Island occurs in late October and November, but upper west coast stocks migrate inshore from December to February.

Herring distributions in southeast Alaska have similar patterns from year to year. After moving in search of food during summer, they migrate in fall to overwintering areas (Carlson 1980) close to spawning grounds (Kolloen and Smith 1953; Blankenbeckler 1977). Migration patterns in the Bering Sea are similar to, but longer than, those in British Columbia and southeastern Alaska because distances from wintering grounds near the shelf edge to coastal spawning grounds are longer. Based on growth and behavioral differences, stocks north of Norton Sound probably stay there year-round, overwintering under the ice in coastal lagoons and bays (Barton 1978).

2.2.3 Small-scale Patterns. Herring schools move back and forth with the tide along the shoreline of principal summer feeding areas. The longest axes of distribution lie in the direction of tidal currents (Bolster 1958). Tyurmin (1973) observed pre-spawning Sea of Okhotsk herring in ribbons, often tens of kilometers in length. Size, configuration and density of herring schools are highly variable. Changes occur on seasonal, daily and hourly scales. Schooling breaks apart at night (Welsby et al. 1964), apparently in response to change in light intensity. No single shape or density appears best suited for all purposes, suggesting that schooling variability may be an adaptation to changing conditions or even to the physiological state of individual fish (Blaxter and Hunter 1982).

2.2.4 Maximum and Mean Abundances. Ocean stock biomass may comprise hundreds of thousands to millions of ton, while inshore stock biomass may be hundreds to thousands of ton. The reason for this variability is uncertain, but small stocks seem as self-maintaining as larger ones, bringing into question some fundamental assumptions on minimum number necessary for successful recruitment (Ricker 1963; Blaxter and Hunter 1982).

Tibbo and Brawn (1960) estimated the density of a herring school in the Bay of Fundy, New Brunswick, using echo-sounding to determine the dimensions of the school followed by seining to estimate the number of individuals. A minimum density of 1 lb per cu ft (about 16 kg per cu m) was estimated but, as some of the fish escaped during seining, the actual density was probably higher.

2.2.5 Vertical Distribution. At the British Columbia feeding grounds, adult herring are found at 100-150 m (Hourston and Haegele 1980). In the Gulf of Alaska, vertical distribution is most likely controlled by temperature, especially in late summer (Carlson 1980). For example, in summer, most adults are at 5-37 m. When temperatures drop in November and December, schools remain close to the bottom during the day and rise and disperse at night and, by January and February, are at their deepest (50-80 m). Bering Sea herring also are deeper in winter than in summer (Wespestad and Fried 1983). Depth segregation with age may occur in some months. Depth preference is influenced by bottom depth, temperature profile, food, predators, turbidity and light (Blaxter and Hunter 1982). The role of light is complex. According to Blaxter and Hunter (1982), light intensity is the principal trigger of vertical migration.

2.3 Feeding

2.3.1 Habitat. In Barkley Sound, British Columbia, Hourston (1959) found newly metamorphosed herring aggregating in small schools and by mid-July there were 5000-20,000 herring in the schools. Subsequently, the school size increased as the herring concentrated in fewer locations closer to the open Pacific and, by September or October, offshore migrations began and school sizes swelled to above one million individuals.

2.3.2 Prey Species. Adults off Washington and British Columbia consume mainly euphausiids and decapod larvae. Prey size increases as herring get larger (Fresh 1983). Adult herring feed by picking at relatively large food organisms in the water column. Filter feeding has been observed in the laboratory (Blaxter 1985).

2.3.3 Prey Density Requirements. Not applicable.

2.3.4 Factors Affecting Availability of Prey. All life history stages of herring rise toward the surface to feed and feeding peaks at dawn and dusk. At night adult herring are inactive (Blaxter and Holliday 1963) and metabolism may be reduced (Blaxter and Hunter 1982).

2.3.5 Temporal Patterns of Energy Storage. Regional differences in growth rates of Pacific herring are attributed to available surplus energy for spawning adults (Ware 1985). Specific causes and consequences of these differences are not clear. Proximate analyses of British Columbia herring show that oil content is highest in summer (about 50% of dry weight) and decreases to a minimum (about 25%) near spawning time (Hart et al. 1940). Somatic growth is most rapid in summer; gonadal growth occurs mainly during winter (Hay 1985). Growth rates of Bering Sea herring decrease from south to north (Wespestad and Fried 1983). In the eastern Bering Sea, growth rate among herring stocks varies from year to year. Although adjacent stocks have most similarity, individual cohorts within each stock may show distinct growth patterns. Growth rate differences of herring spawned at different times of year usually are less than those of individual year classes at different locations (Rowell 1983).

2.3.6 Evidence of Food Limitation. At high herring abundances, food may be limited. Haist and Stocker (1985) reported that the growth rate of cohorts from 1970-1972 was higher than determined previously or subsequently. These cohorts were spawned when total stock abundances in British Columbia were at record low levels. In contrast to other fishes, herring may be less prone to food limitation, due to their feeding on zooplankton, which have much shorter generation times than larger organisms consumed by other species and, consequently, the effect of grazing may not last as long (Ware 1980).

2.4 Predation

2.4.1 Predator Species. Based on scat analysis, herring is the most important prey species of Steller and California sea lions (*Eumetopias jubatus* and *Zalophus californianus*) in the southern Strait of Georgia, and perhaps elsewhere (Bigg 1985). Herring, as they migrate closer to the southwestern coast of Vancouver Island, are also eaten by fur seals (*Callorhinus alascanus*) (Taylor 1971b). In the Bering Sea, sperm whales are a major predator of herring (Laevastu and Favorite 1978). Other marine mammals probably prey on herring, but there is little documentation.

Seabirds are major predators of herring in overwintering and spawning areas in southern Strait of Georgia (Furness 1982).

Throughout British Columbia, Pacific cod (*Gadus macrocephalus*) may be an important predator: an estimated 39-43% of all cod landed in British Columbia between 1950 and 1980 contained herring in their guts, although the incidence was seasonal and varied among locations (Westrheim and Harling 1983). According to Jones and Geen (1977), herring are a dominant prey organism of the dogfish (*Squalus acanthias*) and they have been found in guts of Pacific hake (*Merluccius productus*) (Outram and Haegele 1972). Other fish predators of herring in British Columbia waters are hake (Ware and MacFarlane 1986) and salmonids, particularly chinook (*Oncorhynchus tshawytscha*) and coho (*O. kisutch*) (Healey 1976). Pollock (*Theragra chalcogramma*), as well as sperm whales, are major predators of herring in the Bering Sea (Laevastu and Favorite 1978).

2.4.2 Effect on Spawning Adults. Variations in predation are hypothesized to cause changes in herring biomass in the eastern Bering Sea (Laevastu and Favorite 1978). During some years, predation by hake in southern British Columbia waters may be sufficient to cause major depressions in herring recruitment (Ware and McFarlane 1986). Herring account for more than 50% of the diet, by weight, of adult and subadult chinook in Puget Sound (Fresh 1983).

2.5 Other Factors Affecting Adults

2.5.1 Biotic. In the Bering Sea, herring generally occur off the shelf in summer (Wespestad and Barton 1980), possibly to avoid heavy phytoplankton blooms (1-3 g per m^3), associated with poor feeding and also thought to clog gills (Rumanstev and Darda 1970).

2.5.2 Abiotic. The summer distribution of herring in the eastern Bering Sea may be influenced by shelf temperature. Surveys in August show almost one order of magnitude more herring on warm than cold sides of 4° isotherms (Wespestad and Fried, unpub. data). During summer, adult herring prefer water warmer than 3°C, while juveniles are found usually in cooler water (Rumanstev and Darda 1970).

Fall migrations in southeast Alaska may be linked to water column destratification. In autumn, schools go deeper as air temperature, sea surface temperature and day length decrease and mean wind velocity and surface turbulence increase. The resultant upwelling and water column destratification (Bruce et al. 1977) create fairly uniform temperatures at all depths, and zooplankton decrease (Carlson 1980). When this occurs, herring migrate from open passages to sheltered wintering grounds (e.g., Auke Bay, Fritz Cove). Destratification over a few days is probably more important as a migrating cue than gradual environmental changes. In February and early March, herring move off wintering grounds and concentrate near the bottom (73-110 m) closer to spawning grounds (Lynn Canal), where they remain until late April-early May when sea surface temperatures rise to 5-6°C, plankton blooms and spawning commences (Carlson 1980).

According to Rabin (1977), Pacific herring prefer estuarine water for spawning. Salinity may affect autumn distributions in the Bering Sea. Adults occur between the 32 and 33°/oo isohalines and juveniles between 31 and 32°/oo, with slight overlap. In the Gulf of Alaska, however, distribution has little relation to salinity (Carlson 1980). Ice fishing surveys suggest some Bering Sea herring stocks may overwinter beneath the ice (Shaboneev 1965; Wespestad and Barton1980). This may reduce their vulnerability to some major predators, e.g., adult pollock, which are not found under ice. Interannual differences in air temperatures affect total ice cover and could change predation pressures.

2.5.3 Total Mortality. Annual natural mortality of British Columbia adult herring is estimated to be 30% (or an instantaneous rate of 0.36) and seems to increase with age (Schweigert and Hourston 1980). In the Queen Charlotte Islands, Tester (1955) estimated 32%, 47% and 60% annual natural mortality for ages 3-4, 4-5 and 5-9 herring, respectively. Annual total rates in Barkley Sound from 1910 to 1915, when fishing was negligible, was about 60% for ages 6-9 herring (Taylor 1964), probably due to predation (Hourston and Haegele 1980). (See also 2.4.2.)

Fishing accounted for about 60% of most British Columbia herring populations each year from 1953 until the mid 1960s (Taylor 1964). Natural mortality was an estimated 15-20%, resulting in 75-80% total mortality. However, it is difficult to separate short-term natural and fishing mortality because of the high interannual variability in recruitment. Variable age at recruitment, which extends the contribution to the fishery of one year class over several years, also masks the effects of fishing (Trumble 1983).

2.6 Laboratory Holding and Rearing

Adult herring can be maintained indefinitely in captivity when fed on trout pellets, fresh and dried zooplankton or flesh of clam and other marine organisms (Blaxter and Hunter 1982). Herring mature sexually in captivity but may not spawn. Viability of eggs and larvae of captured sexually mature females that did not spawn in captivity or were prevented from spawning decreases with time (Hay 1986).

3 EGGS

3.1 General Description

Eggs are demersal and adhesive, therefore, their spatial and temporal patterns of distribution are fixed when spawned. They are deposited mainly on bottom vegetation, especially eelgrass (*Zostera* sp.) and rockweed (*Fucus* sp.) (Haegele and Schweigert 1985). Ovulated but unfertilized eggs are about 0.9 mm in diameter. After fertilization, eggs hydrate and expand to 1.0 to 1.5 mm in diameter and have a mean weight of 2.3 mg (Hay and Miller 1982).

3.2 Distribution and Abundance

3.2.1 Duration of Egg Stage. Incubation time is roughly 2-3 weeks at ambient temperatures. Equations relating incubation time to temperature and salinity were developed by Alderdice and Velsen (1971).

3.2.2 Large-Scale Patterns. (See 2.1.2.)

3.2.3 Small-scale Patterns. (See 2.1.2.)

3.2.4 Maximum and Mean Abundances. The density of eggs per unit area is dependent on the surface area of the substrate and the substrate location within the intertidal or subtidal zone (Haegele et al. 1981; Haegele and Schweigert 1985). Extreme and exceptional densities are listed by Hay (1985), but normally the density varies between 10^5 and 10^6 eggs per m^3 (Haegele and Schweigert 1985). Hourston et al. (1984) reported that the viable hatch rate decreased at higher egg densities.

3.2.5 Vertical Distribution. (See 3.1.)

3.3 Feeding

Not applicable.

3.4 Predation

3.4.1 Predator Species. Marine birds, mollusks and amphipods are common predators of Pacific herring in Washington (Palsson 1984). In British Columbia, gulls and diving ducks, mostly scoters, are major egg predators (Taylor 1964).

3.4.2 Effect of Predation. Marine birds and invertebrate predation has been estimated to cause 95-99% egg mortality in Washington (Palsson 1984). Egg mortality due to bird predation is also high in British Columbia (Outram 1958). (See also 3.5.3.)

3.5 Other Factors Affecting Eggs

3.5.1 Biotic. Mortality from epizootics, such as fungi, is undocumented for Pacific herring eggs. Egg and female sizes (length and width) are positively correlated (Kingston 1922). Generally, larger older herring spawn earlier than smaller younger ones (Hay 1985), a trend also documented for other fishes (Horral 1981).

3.5.2 Abiotic. Herring spawning ground temperatures range from 3-20°C along the eastern Pacific coast and 4.4-12°C (usually 10-12°C) in British Columbia (Hart 1973; Trumble 1983; Haegele and Schweigert 1985). According to Alderdice and Velsen (1971), optimal temperatures for incubation of Pacific herring eggs is 5-9°C. Higher temperatures decrease incubation time, and larvae are smaller than those hatched at lower temperatures. Atlantic herring also have shorter incubation times at warmer temperatures and eggs spawned later in the season are smaller (Blaxter and Hunter 1982).

A neritic, reduced salinity environment is necessary for optimal incubation; in the laboratory optimal salinity is 16°/₀₀, but Pacific herring often spawn in salinities of 28°/₀₀ or greater (Alderdice et al. 1979). Low salinities result in larger eggs, shorter incubation time and longer standard length at hatching in the Barents Sea and the northwestern Pacific (Dushkina 1973).

Taylor (1971a) reported that hatching success declines with water depth: eggs at 18 m have only 10-12% the hatching success of eggs near the surface. The explanation for this is uncertain but, if not an artifact (his controls had abnormally low hatching success), may be related to circulation patterns in the intertidal zone. Exposure of eggs in the intertidal zone to air raises their temperature and reduces survival (Jones 1972). Dessication also reduces survival (Palsson 1984).

Depending on the substrate and local circulation, eggs more than four layers deep may smother (Alderdice and Hourston 1985). Survival is dependent on adequate supply of oxygen and removal of CO_2 and metabolic waste by water flow around the eggs. Transport, which is a function of osmotic pressure within eggs, natural convection, wave surge and possibly vertical angle on the substrate, is influenced by egg layering and density. Siltation retarded embryonic herring development but did not affect mortality, except at low oxygen levels (McQuinn et al. 1983).

3.5.3 Total Mortality. Egg mortality in British Columbia, which varies with location, has been documented as high as 56-99%. Bird predation is fairly constant at each location and may be as high as 40% in some intertidal zones (Outram 1958). Egg mortality in the Oregon intertidal zone has been estimated as 20% during cool, moist weather and 50% in warm, dry weather (Steinfeld 1972). (See also 3.4.2.)

3.6 Laboratory Holding and Rearing

Eggs can be incubated readily in the laboratory. See Blaxter and Hunter (1982) and references therein.

4 LARVAE

4.1 General Description

Herring larvae, which are 8.5-9.0 mm long when hatched (Alderdice and Velsen 1971), are transparent and have a large yolk sac. In the Strait of Georgia, they grow 0.48-0.52 mm per day (Alderdice and Hourston 1985).

4.2 Distribution and Abundance

4.2.1 Duration of Larval Stages. The yolk sac is absorbed by 5-6 days after hatching (Hourston 1980). Within two months, larvae reach a length of 2.5-4.0 cm; they continue to grow throughout the summer, reaching a length of about 80-90 mm by early fall (Hourston 1958).

4.2.2 Large-scale Patterns. Herring nursery areas are close to spawning grounds, often directly offshore, and larvae can be found in enclosed areas, where dispersal is slow, eight weeks after hatching (Trumble 1983). Stevenson (1962), who observed fewer larvae in the water column with time and distance from spawning grounds in British Columbia concluded that distribution of newly hatched herring larvae in Barkley Sound was determined by tidal flow and net offshore advection. The ebbing tide carried larvae away from spawning grounds, but few returned in the inflowing current. Although Stevenson could not demonstrate high mortality in larvae advected offshore (predation was evident but not high, no starving larvae were found and temperatures and salinities were within tolerable levels), only larvae that remained within the nursery area were inferred to comprise the eventual cohort. Larvae advected offshore apparently never rejoined those retained inshore and were presumed to have died.

A diffusion model depicted larval movement from spawning grounds in Bristol Bay (Checkley, in Wespestad and Fried 1983). Storms, or their deviation from usual tracking, can disrupt larval retention mechanisms, causing large advections from nursery grounds and resulting in poor year classes in the Bering Sea (Wespestad and Fried 1983).

Dispersal patterns also may be important in determining year-class strength of Atlantic herring (Hewitt 1981; Iles and Sinclair 1982). As suggested for Barkley Sound (Stevenson 1962), physical aspects of the environment, e.g., tidal currents, may structure herring stocks.

4.2.3 Small-scale Patterns. Recently hatched larvae are concentrated near spawning areas; as they grow older they gradually disperse (Stevenson 1962; Alderdice and Hourston 1985).

4.2.4 Maximum and Mean Abundances. Based on Alderdice and Hourston's (1985) analyses and on data published by Stevenson (1962), larval densities are estimated at 100-200/m^3 for recently hatched larvae near spawning grounds to less than 1/m^3 for older larvae further offshore.

4.2.5 Vertical Distribution. In British Columbia, newly hatched larvae are concentrated in the upper 2 m. They move deeper and are less aggregated after yolk-sac absorption (Stevenson 1962). At night, older larvae ascend and descend in the water column more than young larvae and are more often seen at the surface (Blaxter and Hunter 1982). Atlantic herring larvae can make diurnal migrations to 75-100 m; they become regular once feeding begins (Seliverstov, in Parrish et al. 1981). Norwegian herring larvae are most abundant at 20-40 m during the day and diffuse vertically above 20 m at night (Dragesund 1970).

Depth distribution also can influence offshore transport of larvae as a result of horizontal current velocity (dependent on depth and tidal stage) and buoyancy. Due to the mean landward tidal flow below and mean seaward flow nearer the surface, larvae tend to be retained in the spawning area during the yolk-sac stage. After the yolk sac is absorbed, larvae are more buoyant and subject to vertical ascent and horizontal drift into the estuary (Henri et al. 1985). Larval aggregations up to several kilometers from spawning grounds resulted from tidal action. An inverse correlation exists between tidal current velocity and larval abundance in the water column.

4.3 Feeding

4.3.1 Habitat. Gut fullness studies suggest that larval herring feed during the day (Bainbridge and Forsythe 1971). Significant numbers of herring, however, regurgitate when handled roughly in capture (Kjelson et al. 1975; Hay 1981) and in fixation (Rosenthal 1969), which may confound larval gut analyses (Blaxter and Hunter 1982). In laboratory studies, lower limits of visual acuity are 0.1-0.01 lux, equivalent to light levels at late dusk or early dawn. Visual acuity improves with growth (Blaxter and Hunter 1982), perhaps extending feeding periods into the night.

4.3.2 Prey Species. Copepod larvae are the main food item. Phytoplankton, tintinnids, ciliates, fish eggs, copepod eggs and mollusc larvae are also eaten (e.g., Wailes 1936; Bainbridge and Forsythe 1971). As larvae grow, they take larger prey, ranging from naupliar to adult copepods. For herring 10 and 30 mm in length, optimal prey size is 66% and 80% of mouth width, respectively (Beyer 1980).

4.3.4 Prey Density Requirements. Prey densities for successful feeding have been determined only in laboratory studies. Haegele and Outram (1978) observed about 35% survival of Pacific herring over the first five weeks of feeding. Atlantic herring reared with brine shrimp densities of 0.3 ml^{-1} and above showed greater growth and survival than at lower food densities (Werner and Blaxter 1980). At high prey densities, survival was above 40% over the first five weeks of feeding. In both studies, asymptotic growth and survival curves flattened out at high prey concentrations. Werner and Blaxter (1980) calculated a threshold prey density of 0.171 brine shrimp ml^{-1}, far greater than average zooplankton concentrations in nature, for Atlantic herring larvae to survive with 10% weekly mortality but suspected their value might be low. Most estimates of zooplankton standing stock, spatially averaged and probably underestimated, are lower than necessary to support herring larvae in the laboratory. Zooplankton concentrations in patches, however, have been observed to exceed 60,000 m^{-3} (0.06/ml), which approaches the minimum density required by herring larvae in laboratory studies (Werner and Blaxter 1980). Recent observations from field enclosures, however, suggest that laboratory estimates of required food densities may be an order magnitude too high (Oiestad and Moksness 1981); nevertheless, it seems likely that herring must encounter concentrated prey aggregations in order to survive.

4.3.4 Factors Affecting Availability of Prey. Herring larvae, for the most part, feed in the euphotic zone, above 20 m. Small copepods, such as *Pseudocalanus* spp., are the dominant zooplankton in surface waters of the Strait of Georgia during winter, especially nearshore, although absolute abundances are small. *Neocalanus* spp. dominate in spring but are not as abundant to the south, where shallow depths (<200 m) and greater mixing are a barrier to the deep-water adult stage. Large zooplankton remain in the upper 50 m above the pycnocline from early spring through summer. Ninety percent of zooplankton production in the Strait of Georgia takes place from March to May (Harrison et al. 1983).

4.3.5 Temporal Patterns of Energy Storage. Not applicable.

4.3.6 Evidence of Food Limitation. Herring larvae must begin feeding within a few days after yolk-sac absorption. According to McGurk (1984), Pacific herring larvae have 6 to 8.5 days after yolk-sac resorption to begin successful feeding before irreversible starvation occurs, the time varying directly with larval size and inversely with temperature. "Point of no return" for newly feeding larvae occurs after about 40% of time elapses from initial starvation to death (Blaxter and Ehrlich 1974).

Opinion is divided on whether starvation is a critical factor in clupeoid larval survival in nature. Abrupt larval mortality, undocumented to date, would suggest the occurrence of a critical period (Lasker 1985). Based on finding that 57-68% of British Columbia herring larvae had food in their guts, Alderdice and Hourston (1985) postulated that food probably is not a major influence on survival.

Food competition has not been documented. Several empirical correlations, however, suggest the possibility of competition. For example, the relationship of Gulf of Maine herring year-class abundance apparently is influenced by abundance of co-occurring mackerel larvae that may compete with larval Atlantic herring (Skud 1982).

4.4 Predation

4.4.1 Predator Species. Larval herring are subject to predation by filter feeders, e.g., pilchard, entrappers, e.g., gelatinous zooplankton (Stevenson 1962; Arai and Hay 1982; Möller 1984; Purcell 1986) and hyperiid amphipods (Westerhagen et al. 1979). The major predators of clupoid larvae in decreasing order in Barkley Sound, British Columbia, were ctenophores, jellyfishes and chaetognaths (Stevenson 1982).

4.4.2 Effect on Larvae. Although it has been known that predators have the potential to consume significant numbers of larval herring (Lasher 1985), only recently has there been direct evidence to implicate predation on larvae as a major cause of mortality (Purcell 1986; Purcell et al. 1987). Predation by a jellyfish, *Aequorea victoria*, on yolk-sac larvae may be devastating. In Kulkit Bay, British Columbia, in one episode, herring larvae density decreased from an average maximum of $264/m^3$ to $3.5/m^3$ in 3 days. Predation rate was estimated to be 3-50% per hour (Purcell 1986). Cannibalism by juveniles and adults occurs in laboratory studies, but is probably limited in nature (Hourston et al. 1981).

4.5 Other Factors Affecting Larvae

4.5.1 Biotic. Parasites are known to infect Atlantic herring larvae (Tibbo and Graham 1963) but have not been reported in Pacific herring. Schooling may be an important factor in larval survival. Large mortalities among offshore advected larvae may result from visual separation, which inhibits the ability to school and may be a stressor even if food is adequate and predation low (Shaw 1961; Stevenson 1962; Hunter 1981). However, Marliave (1980) found that isolation of herring from 43 days after hatching through metamorphosis did not result in mortality.

4.5.2 Abiotic. According to Alderdice and Hourston (1985), salinity probably has little direct effect on larval Pacific herring mortality in the Strait of Georgia. They determined a salinity range of 2-28°/oo and a lethal upper boundary salinity of 27.5-31.7°/oo. Pujita and Kokudo (1927) reported optimal survival of Japanese herring larvae at 25°/oo. Laboratory experiments indicate that salinity tolerance of herring may be influenced by incubation conditions (Alderdice and Hourston 1985).

Large size at hatching and fast growth at high temperatures reduce the period of high vulnerability to predation (Blaxter and Hunter 1982). Yolk-sac duration is influenced by metabolic rate, largely a function of temperature and size. At 8°C, larvae from large and small eggs survived 28 and 15 days, respectively, after hatching, when no food was provided (Blaxter and Hunter 1982).

4.5.3 Total Mortality. Neither the cause nor variability of mortality is understood, nor are the relative contributions of suspected factors known. In the Strait of Georgia, mortality rates are probably 45% and 9% per week in nearshore and offshore waters, respectively, during the first few weeks following hatching (Alderdice and Hourston 1985). As the season progressed, Stevenson (1962) found daily larval mortality rates in Barkley Sound decreased from 34% in April to 22% in May.

4.6 Laboratory Holding and Rearing

Maximum recommended rearing density usually is 5-10/l, but it is lower for older larvae. Larvae have been reared successfully in tanks, using the rotifer *Brachionus plicatilis, Artemia* nauplii and wild plankton for food. Under best feeding conditions, with up to 1000 prey organisms/l, 50% survive to metamorphosis (Blaxter and Hunter 1982).

5 JUVENILES

5.1 General Description

Newly metamorphosed juvenile herring resemble small adults. They increase in length and weight from about 35 mm and 5 g to 70-100 mm and about 40 g by the end of their first summer but grow little during the following winter (Hourston 1959a). By the end of their second summer, they are about 150 mm and 60 g in length and weight (Hourston and Haegele 1980). Some investigators recognize two stages: the juvenile, from metamorphosis through the latter part of the first year (July to March), and the pre-recruit, the second-year herring. Sexual maturity usually is reached at age 3, but small numbers of immature (ages 3-4) fish are found among juvenile schools in British Columbia (Taylor 1964).

Average age of Pacific herring at sexual maturity increases with latitude (see 2.1.1). The juvenile stage usually ends at the beginning of age 2 off San Francisco, of age 3 off British Columbia and in the Gulf of Alaska and of age 4 in the Bering Sea (Wespestad and Fried 1983).

5.2 Distribution and Abundance

5.2.1 Duration of Juvenile Stage. (See 5.1.)

5.2.2 Large-scale Patterns. The horizontal distribution of juvenile herring is determined by active swimming rather than by passive drift (Hourston 1959a). During their first summer, juveniles form large schools in southeastern Barkley Sound, British Columbia, away from spawning grounds. According to Hourston and Haegele (1980), schooling results from gradual dispersion and reconcentration rather than from simple migration. In British Columbia, juveniles form increasingly larger schools and remain in inshore feeding areas until fall, when most move deeper, but a few stay close to shore year-round (Hourston 1959a). Depths at the offshore feeding grounds, several to tens of kilometers from the outer coast, are 100-200 m at bank edges (Taylor 1964). Major British Columbia offshore grounds are off the mouth of the Strait of Juan de Fuca in the south and Hecate Strait in the north where juvenile schools consist of millions of individuals (Hourston and Haegele 1980). Unrecruited juveniles (ages 1, 2 and some 3) outnumber recruited adults (Taylor 1964). Interannual variability is not well documented.

Distribution of the eastern Bering Sea herring during their first 2-3 years is little known (Wespestad and Barton 1980). In both the eastern and western Bering Sea, 0-age and age-1 herring are found in areas of lower temperatures, inshore of adults (Prokhorov 1968; Wespestad and Fried 1983).

5.2.3 Small-scale Patterns. Juveniles are known to form dense schools in shallow, inshore water (Hourston 1959a, b). (See also 5.2.5.)

5.2.4 Maximum and Mean Abundances. No available data.

5.2.5 Vertical Distribution. Juveniles in British Columbia inshore nursery areas stay at 3-15 m during the day and 1-7 m at dawn and dusk. On offshore feeding grounds, age-1 juveniles remain at 150-200 m and age-2 juveniles at 100-150 m, where they usually mix with adults (Hourston1959b). In the Bering Sea, juvenile herring are generally found deeper in winter than in summer.

5.3 Feeding

5.3.1 Habitat. Juveniles are strong swimmers and move toward the surface at dawn and dusk to fed (Hourston 1959a).

5.3.2 Prey Species. In Puget Sound, juveniles consume copepods, decapod larvae and euphausiids (Fresh 1983). Newly metamorphosed British Columbia herring prey mostly on small zooplankton, such as copepods, barnacle and mollusc larvae, bryozoans, rotifers and larval fishes. Copepods are the predominant food organism throughout the juvenile stage in British Columbia (Wailes 1936; Barraclough 1967) and for juvenile Sea of Okhotsk herring (Guryeva 1973).

5.3.3 Prey Density Requirements. Average small zooplankton displacement volumes in Barkley Sound during Hourston's (1959a) study of juvenile herring were 0.29 cc/m^3.

5.3.4 Factors Affecting Availability of Prey. Productivity and distribution of zooplankton affect availability of prey for juvenile herring. Inshore areas with bottom vegetation, such as in the Fraser estuary, support higher standing stocks of zooplankton than areas with little vegetation (Levings 1983). Zooplankton are most concentrated and visible at dawn and dusk (Hourston 1959a). (See also 4.3.4.)

5.3.5 Temporal Patterns of Energy Storage. No data available.

5.3.6 Evidence of Food Limitation. There is no evidence of food limitation among juveniles; in fact, sufficient food probably exists at both inshore and offshore feeding grounds (Hourston and Haegele 1980). However, in years of very abundant herring larvae, food may be limited at the time of metamorphosis (Hourston 1959a). Maturation rate may be associated with food supply; it has been accelerated by increasing food supply in laboratory rearing (Hay 1985) but verification in nature is lacking.

Geographical separation (Wespestad and Fried 1983) may minimize competition for prey between juveniles and adults. Fresh (1983) believed herring could outcompete and possibly adversely affect juvenile coho salmon in Puget Sound because of the considerable diet overlap. Nonetheless, competition has never been documented for juveniles. Levings (1983) found length/weight differences in juveniles as strong within as between years in the Strait of Georgia. In contrast, Gulf of Maine juveniles showed little year-to-year length/weight difference, but wide seasonal variation from 1964 to 1968 (Chenoweth 1970).

5.4 Predation

5.4.1 Predator Species. Juvenile ling cod (*Ophiodon elongatus*) were major predators of juvenile herring at Grays Harbor, Washington (Grosse 1982) and the Strait of Georgia (Phillips and Barraclough 1978). (See also 3.4.1.)

5.4.2 Effect on Juveniles. Extent of juvenile predation, though not known is not believed to have major impact on subsequent adult abundance.

5.5 Other Factors Affecting Juveniles

5.5.1 Biotic. No available data.

5.5.2 Abiotic. Vertical water column stability and reduced turbulence, associated with areas sheltered from prevailing winds and currents, characterize juvenile rearing grounds. Nonconsistent trends in temperature, salinity or food resources were found among nursery grounds, though salinities in most areas were below 28% (Hourston 1959a). However, his data on food supply may be incomplete. Levings (1983) found that juvenile abundances in the Fraser River estuary may be influenced by salinity and food supply. Evidence of density-dependent growth was found among juvenile (age-2) herring on the west coast of Vancouver Island and much of the variation in growth rates and abundance was explained statistically by spring sea surface temperature (Haist and Stocker 1985). No correlations with other environmental factors were found.

Ambient temperatures and salinities probably do not affect survival of juvenile herring directly but may affect distribution . In the Bering Sea, juveniles are found in lower salinities than adults (Wespestad and Fried 1983) and usually in lower temperatures than adults (Rumyantsev and Darda 1970). Juveniles can survive salinities ranging from 5-6°/oo to 40-50°/oo (Blaxter and Halliday 1963).

5.5.3 Total Mortality. Little information is available on natural mortality rates of juvenile herring. Mortality rates are believed to be lower for juveniles than for larvae and probably are comparable to those of adults (Taylor 1964). Hourston and Haegele (1980) estimated 20% total annual mortality of first-year juveniles.

5.6 Laboratory Holding and Rearing.

(See 2.6.)

6 CURRENT HYPOTHESES ON FACTORS AFFECTING YEAR-CLASS ABUNDANCE

In a review of factors limiting clupeoid abundance, Lasker (1985) concluded that the fundamental questions remain unanswered: We still do not know, unequivocally, the life history stages during which year-class strength is established or even the important biotic or abiotic factors. It is clear, however, that clupeoids undergo substantial variations in natural abundance and are susceptible to overexploitation. Blaxter and Hunter (1982) speculate that in the absence of density-dependent responses, as appears to be the case, the ability of clupeoids to stabilize populations diminishes. Herring may be more sensitive to fishing mortality and environmental change than species with more stable populations.

Pacific herring year-class abundance may be established shortly after metamorphosis, while juveniles are still inshore (Hourston 1959a). This conclusion is based on correlations of juvenile and later adult abundances. For clupeoids in general, year-class strength appears to be set within the first six months (Smith 1985).

Population fluctuations from other causes sometimes mimic the effects of density dependence. For example, if herring populations were influenced by density dependent factors, we would expect an increase in individual growth rates when populations are less numerous. This ostensibly occurred in the North Sea in the early 1950s: when the number of older fish declined, younger herring grew faster and matured earlier, suggesting density dependence. The increased growth in the young fish, however, was probably caused by a two- to threefold increase in copepods (*Calanus*) that happened at the same time (Cushing and Burd 1957). Another North Sea stock sharing the same nursery area in the eastern North Sea also grew faster. Both populations changed recruitment patterns, probably altering their vulnerability to fishing. Copepods were not related directly to herring number but to faster growth rates of herring. Cushing (1982) speculated that the increase in copepods may have been due to an invasion of Atlantic oceanic water into the North Sea.

Within the Strait of Georgia, weak year classes frequently follow strong ones with a fourfold difference between highest and lowest (Stocker et al. 1985). There is little or no relationships between egg number deposited during spawning and resulting year-class strength: good year classes can result from poor spawnings and vice versa (Larkin and Ricker 1964; Taylor and Wickett 1967). There is some evidence, however, of a density-dependent relationship between spawning stock biomass and the number of recruits joining the spawning stock (Taylor 1964; Stocker et al. 1985).

Taylor and Wickett (1967) correlated year-class strength of British Columbia herring with onshore transport. They developed an index of water movement based on oceanographic factors off British Columbia. The average north-south component of onshore wind-driven surface water from December to March was their measure of amount and direction of onshore current. When net movement is northward, water is held against the coast (onshore transport) and year classes are more abundant than when water moves offshore (southward).

Long-term, large-scale events seem likely to affect herring in the northeastern Pacific, but data on interannual differences are insufficient to draw adequate conclusions. Though many large-scale correlations between environmental factors and herring abundance have been identified, mechanisms are incompletely studied; investigations have been few, brief and localized.

Wickett (1975) hypothesized that reduced offshore upwelling was responsible for decreases in British Columbia herring abundances in the late 1960s. Conditions reversed in the 1970s and upwelling increased. Wickett used salinities at Ocean Weather Station Papa (50°N, 145°W) and the Queen Charlotte Islands, lagged nine months, as an indicator of water column stability, which he considered appropriate because of similarity between offshore British Columbia and the Gulf of Alaska. Zooplankton biomass at Station P was greater in years of more upwelling (Fulton 1978). Eighty-five percent of the variance in annual mean year-class strength was explained by mean January-December salinity of that year and is attributed to yearly changes in availability of food resources for age-2 herring. Seasonal variations within a single year were not evaluated. Wickett (1975) hypothesized that recruitment of herring is determined at age 2 during the first offshore migration. If events in earlier life history stages were crucial, an inverse relation between recruitment and salinity would be expected, since more frequent and intense storms would cause greater runoff and advect larvae offshore. As a direct relationship was found, however, Wickett (1975) concluded that recruitment number is determined at later life stages. To be a legitimate counterargument, however, salinities during larval rather than juvenile stages should be used. Wickett also assumed a priori that decreased growth in fishes leads to smaller populations.

Ketchen et al. (1983) correlated weak year classes in British Columbia herring with high March sea surface temperatures ($R^2 = 0.3$); some strong year classes, however, occurred in cold years. They speculated that water temperatures or related factors at time of spawning influence egg to larval survival.

Year-class strength of Alaskan herring around Prince William Sound correlated with average mean March-June air temperatures ($r^2 = 0.73$), a period encompassing spawning and hatching (Rounsefell 1930). Air temperature was highly correlated with sea surface temperature. The period examined spanned four months; the effects could be associated with food supply or predators. Temperature probably did not exceed larval tolerances and may have been a proxy for offshore advection (Anthony and Fogarty 1985).

Pacific herring year-class abundance has been correlated both directly (e.g., southeastern Alaskan herring, Favorite and McLain 1973) and inversely (e.g., Hokkaido herring, Uda 1952) with winter and spring temperatures. Ware and McFarlane (1986) found a strong negative correlation between temperature and herring year-class strength in southern British Columbia and suggested that a northward extension of hake during warm years might increase predation on herring.

Year-class strength of herring in the eastern Bering Sea has been related to temperature and predation by pollock (Laevastu and Favorite 1978; Laevastu 1983). Herring-stock size, but not year-class strength, also has been related to available spawning area (Wespestad and Fried 1983). One Bering Sea ecosystem model (Laevastu 1983) indicated that temperature affects pollock directly and herring indirectly; warmer temperatures are thought to increase pollock biomass by accelerating growth, thereby inducing greater predation on herring. Anomalously low temperatures would have the reverse effect. This proposed mechanism presupposes no direct effect of temperature on growth or biomass of herring which, considering they too are poikilotherms (cold-blooded), seems unlikely. Wespestad and Fried (1983) believe that advection of larvae from nursery grounds may be the principal determinant of year-class strength in the eastern Bering Sea. The effects are probably large scale, for most major stocks in this region undergo similar interannual variations in abundance (Fried et al. 1982).

Pearcy (1983) suggested a correlation between El Niño-Southern Oscillation events and abundant herring year classes in the northeastern Pacific. The 1926, 1929, 1939-1940, 1951, 1953, 1957 and 1958 year classes in southeastern Alaska, and the latter two in the Bering Sea as well, were strong, and all were El Niño years. According to O'Brien (1978), however, 1929, 1939-1940, 1951 and 1953 were not major El Niño years. A 5-6 year cycle of 12-month running mean sea level from Astoria, Oregon, to Kodiak, Alaska, in phase with 5-6 year sea surface temperature maxima, usually peaks in El Niño years (Pearcy 1983). Mysak et al. (1982) supported this idea, arguing that baroclinic waves driven by cycles in the Southern Oscillation affect the entire northeastern Pacific and its biota. Widespread high sea levels and warmer sea surface temperatures associated with (6-year) Kelvin wave cycles correlate with high herring abundances in British Columbia.

Mysak et al. (1982), like Stevenson (1962), hypothesized that climate ultimately affects herring abundance. Yet the pathways have little in common: Stevenson's is driven by coastal climate from the preceding winter affecting onshore/offshore advection and is more localized, whereas Mysak et al. envisioned large-scale, longer-term atmospherically forced currents parallel to shore, creating good or bad environments. Nonetheless, high sea levels are associated with onshore convergence and reduced offshore transport (Pearcy 1983), which, according to both theories, are advantageous to herring.

If stocks in different locations have coherent population fluctuations, large-scale events are likely responsible (Pearcy 1983). Examples in addition to those cited above include: (1) the coherence among British Columbia stocks; (2) strong year classes in 1926 and 1931 in southeastern Alaska, Prince William Sound and around Kodiak (Dahlgren and Kolloen 1943); (3) weak year classes in the 1960s following strong ones in the late 1950s in northern British Columbia, southeastern Alaska and the Bering Sea (Pearcy 1983); and (4) similar fluctuations in Atlantic herring stocks in Nova Scotia waters, the western Gulf of Maine and on Georges Banks (Anthony and Fogarty 1985). Though tempting to attribute all coherences to large-scale environmental events, simultaneous utilization of new fishing techniques (Hourston 1980; Jakobsson 1985) or mixing among stocks (e.g., British Columbia) may be equally important.

With a sufficiently long time series of biological data (i.e., abundance) and a variety of physical environmental factors for comparisons, correlation with at least one variable is likely. Often the best possible r^2 values are sought, regardless of the possibility of a mechanism, and frequently with statistical problems inherent (McCaughran 1983). If correlations are more than spurious, they may suggest possible interactions, generate testable hypotheses and, to the benefit of fisheries management, provide some prediction of future abundances. The next logical step is to explain causal mechanism(s). Otherwise, we have no additional understanding of the system.

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WALLEYE POLLOCK, *Theragra chalcogramma*, IN THE EASTERN BERING SEA

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1 BACKGROUND

1.1 Literature Search

Although a formal literature search was not conducted, numerous papers and the references therein, e.g., Hamai et al. 1971; Nishiyama and Haryu 1981; Smith 1981; Francis and Bailey 1983; Nishiyama and Harano 1983; Paul 1983; Clarke 1984; Dagg et al. 1984; Nishimura and Yamada 1984 and Walline 1985, were scanned for relevant walleye pollock information. In addition, a great deal of "grey" literature was searched, e.g., "processed reports" of the National Marine Fisheries Service, Seattle, documents submitted to the International North Pacific Fisheries Commission and progress reports from the PROBES project (see McRoy et al. 1985). In keeping with the preliminary nature of most "processed reports" or progress reports, data generally are not repeated here. Instead, the findings are summarized and the interested reader is referred to the original investigator for details. Finally, in a few cases, manuscripts being prepared for publication were made available by the authors. The data from these manuscripts are not presented here, but the information was useful in providing depth and balance to the ideas and data we do present. In this regard, we are particularly grateful for the shared opinions and findings of Drs. K. M. Bailey and A. W. Kendall, Jr. We also thank S.J. Westrheim for several helpful comments on this manuscript.

1.2 Unit Stocks and Their Relationships

Electrophoretic analyses have not identified significant regional genetic differences between pollock in various areas of the eastern Bering Sea (Grant and Utter 1980), and currently the fishery is managed as a single stock. However, regional morphometric differences occur between populations located north vs. south of the Pribilof Islands (Serobaba 1977). Regional differences in adult growth (Lynde 1984) and recruitment patterns (Francis and Bailey 1983) also have been observed. These differences suggest that more than one "production unit" may exist within the eastern Bering Sea. However, a problem exists in identifying the recruitment origin of fish over the Aleutian Basin, since virtually no fish younger than four years old have been found there (Okada and Yamaguchi 1985; Traynor and Nelson 1985, see also 1.8).

1.3 The Fishery

1.3.1 Relative Size and Importance. The pollock fishery currently ranks as the most productive single-species fishery in the world (Food and Agriculture Organization 1977, 1978, 1979, 1980; Bakkala and Wespestad 1983). Since 1971, total annual harvests from the North Pacific, the Sea of Japan, the Sea of Okhotsk and the Bering Sea average about 5.1 million mt. The commercial catch from the eastern Bering Sea and Aleutian Basin area, where the largest concentration of pollock is found, averaged nearly 1.3 million mt from 1970 until recently when harvests have been reduced, partly by catch restrictions, to just under 1 million mt (Bakkala et al. 1981, 1987; Bakkala and Wespestad 1983). During 1981, pollock comprised 68% of the total reported commercial harvest (live weight) from the eastern Bering Sea shelf (Incze and Schumacher 1986). The harvest from the eastern Bering Sea during 1982 accounted for 40% of the entire U.S. commercial harvest within the 200-mile Fisheries Conservation Zone (FCZ) (Wespestad and Terry 1984).

1.3.2 Age at Recruitment. Pollock begin to recruit to the fishery at age 1, but this age comprises a minor component of the harvest (Bakkala and Traynor 1984). The fishery consists primarily of age 2 and older animals.

1.3.3 Characteristics of Harvested Fish. Ages 2 through 5 years account for the bulk of the total catch (Bakkala and Traynor 1984). Size distribution depends on relative year-class abundance (Bakkala and Traynor 1984) and on the gear type used. Using parameters for the von Bertalanffy growth equation and the length: weight relationship given by Smith (1981), most of the harvested fish (ages 2-5) can be characterized as ranging from ca. 24-42 cm fork-length and 96-496 g wet weight.

1.3.4 Types and Selectivity of Gear. Three main products result from the pollock fishery: surimi (made from minced flesh), frozen, both blocks and fillets and roe. Surimi fisheries take pollock of all sizes, whereas the others target on the larger adults. The surimi fishery consists of large factory trawlers with bottom and midwater trawls or (presently) foreign mothership fleets composed of large floating factory ships and small catcher vessels using pair trawl, Danish seine and stern trawl gear. The freezer fishery consists of large factory trawlers and smaller independent stern trawlers using bottom gear. These vessels target on turbot (*Atherestes stomias*) and Pacific cod (*Gadus macrocephalus*), as well as pollock. The roe fishery employs midwater trawls and targets on aggregations of spawning adults (see 1.3.5). Recently, joint venture arrangements have evolved whereby U.S. fishing vessels (primarily crabber-trawlers) transfer their catch at sea to foreign floating processors (Lynde 1981).

1.3.5 Distribution of Fishing Effort. The surimi factory trawlers fish year-round on the slope and outer shelf but remain primarily north of the Pribilof Islands during winter. The mothership fleet fishes primarily over the slope and outer shelf during summer and fall. The freezer trawlers fish year-round on the shelf and slope. The roe fishery is directed at spawning aggregations near Unimak Pass and in the Aleutian Basin from January to April. In 1984, for the first time, the Aleutian Basin area accounted for the majority of the foreign fishing effort. Much of the effort occurred east of the U.S.-U.S.S.R. convention line but outside the 200 mile FCZ.

1.4 Distribution and Abundance of the Population

Adult pollock appear to avoid cold water of the middle shelf region during winter, thereby becoming more concentrated over the outer shelf and slope. The comparatively concentrated distribution probably continues until springtime spawning, when the fish migrate further onto the shelf, then gradually disperse. Catch per unit effort (CPUE), therefore, should be greater during winter and early spring. Interannual variability of bottom water temperature over the middle shelf during summer and fall may affect the degree of dispersal (Lynde 1984). Spatial patterns of abundance also may be affected by patterns of recruitment. During early to mid-1970s, greater than average CPUE and greater fishing effort were concentrated north of the Pribilof Islands, while the reverse was true during the late seventies. Francis and Bailey (1983) speculate that this was due to regional differences in recruitment and that fish from each region may effectively constitute different "production units."

1.5 Current Status of Stocks and of Management Measures

The abundance of pollock has been estimated by trawl surveys (Wakabayashi et al. 1985) and by various CPUE analyses. Trawl samples, however, may not produce a reliable index of abundance because a substantial portion of the stock remains above the depth sampled and the proportion of stock missed by trawls is not necessarily constant. CPUE analyses by Low and Ikeda (1980), which are consistent with trends shown by other methods of analysis, indicate a gradual decrease in commercially harvestable stocks from 1968 to 1972, followed by a substantial decrease of approximately 48% from 1972 to 1977. From 1977-1981, stocks remained approximately at the 1977 level, with the lowest level estimated for 1980 (Low and Ikeda 1980). Trawl estimates, available for only a few of the aforementioned years, also indicate a severe decrease in stocks in 1980. Although supporting the finding of reduced populations in 1980, trawl estimates cannot be used quantitatively for the reasons stated above. Cohort analyses of data from commercially harvested fish indicate the same trend in stock abundance as CPUE analyses (Bakkala and Wespestad 1983).

The fishery for pollock currently is managed as part of the multispecies fishery of the eastern Bering Sea. Allowable harvest of pollock is adjusted upward or downward according to the results of stock assessments (trawl surveys and CPUE data) relative to previous years. Adjustments are made within the context of trying to maintain a relatively constant total harvest of finfish from the eastern Bering Sea, so decisions are somewhat influenced by the status of other fish stocks in the region.

1.6 Recruitment Variability

Cohort analyses of the pollock catch between 1974 and 1980 indicate that recruitment at age 1 varied between 5 and 35 billion fish, with a coefficient of variation (CV) of 44% (Francis and Bailey 1983). When fish caught to the southeast and northwest of the Pribilof Islands were analyzed separately, the CV for the southeastern Bering Sea increased an estimated 3 to 6 times, indicating, according to Francis and Bailey (1983), that variability in recruitment was much greater there (see 6.0 for possible reasons). Year classes for 1972 and 1973 and the 1978 year class were strong to the northwest and to the southeast of the Pribilofs, respectively. Analyses of the 1973 to 1981 shelf and slope populations by Wespestad and Terry (1984) and Lynde (1984) agree with these findings. Length-frequency data for pollock sampled by midwater trawls in the southeastern Bering Sea during 1979 and 1980 suggest a strong 1978 year class relative to those for 1979 and 1980 (Bakkala and Traynor 1984). These observations indicate significant latitudinal, as well as interannual, variations in recruitment. Notwithstanding the general concept of the eastern Bering Sea as a single ecosystem, such spatial variations are not inconsistent with the vast size of the shelf.

1.7 Age Determination and Validation

The current method of age "determination" (actually, estimation) of adult fish is counting rings (interpreted as annular features) on saggital otoliths—work conducted by the National Marine Fisheries Service, Seattle. Precision (repeatability) of ring counts has been well-quantified, but the relationship between ring counts and age (i.e., accuracy in the assignment of age) has not been validated independently. There is considerable variability between ring counts and length of individual fish, indicating that some error in the estimation of age is likely.

1.8 Age Composition of the Population

Although pollock live to be as old as 15 years, ages 1-7 account for 80% of the total population over the shelf and slope areas. The dominance of individual year classes was estimated by Bakkala et al. (1985) from survey and fisheries data. For example, the 1978 year class was numerically prominent in the fishery from 1980 through 1983 and accounted for much of the harvested biomass of this species from 1981 through 1983 . Earlier fisheries data are discussed by Francis and Bailey (1983, also see 1.6). In the Aleutian Basin, there are virtually no juvenile nor adult pollock under age 4 (Traynor and Nelson 1985), suggesting that adults recruit to the Basin primarily from other areas. This presents a dilemma, since spent fish (Okada and Yamaguchi 1985) and larvae (Waldron 1981) have been found over the basin.

2 SPAWNING ADULTS

2.1 General Description

2.1.1 Size and Age Ranges. Both male and female pollock begin to attain sexual maturity at about 25 cm body length (age 2-3); 50% are mature by 31-34 cm (age 3-4) and 90% by 40-45 cm (age 5-6) (Bakkala and Smith 1978).

2.1.2 Type of Spawning Behavior. Ova from pollock apparently develop in batches (Zver'kova 1977; Sakurai 1982). Gorbunova (1954) and Serobaba (1971) identified three year classes of developing oocytes, two of which were said to be released each year. Shew (1978) differentiated two size classes (≤ 59 mm and ≥ 59 mm diameter). Sakurai (1982) raised pollock in captivity and observed individuals spawning 2-5 times over a period of 18 days. He estimated that animals in the field may spawn 10 or more times per year. Hinckley (1986) characterized the development of oocytes as partially synchronous, that is asynchronous up to completion of yolk development and synchronous thereafter. She described two groups of oocytes which can be distinguished after yolk development is completed by the maturing group, the only group that will spawn in a single year. The number of synchronized (batch) spawnings still is unknown.

2.1.3 Fecundity. Considerable uncertainty exists in estimates of average fecundity/size relationships. According to Lynde (1984), the estimated fecundity for a female of 50 cm fork length ranges from 222,400 to 487,900 eggs. However, these estimates include oocytes that would not be spawned in the same year (Hinckley, pers. comm.). Hinckley (1986) gives estimates of 207,781 and 228,745 eggs for a female of 50 cm fork length from the Aleutian Basin and the shelf/slope environments, respectively. Hinckley's work also provides 95% confidence intervals for the estimates.

2.2 Distribution and Abundance

2.2.1 Duration of Spawning. Peak spawning occurs in February and March in the Aleutian Basin, March and April along the slope and outer shelf and April and May over the middle shelf (see Francis and Bailey 1983). Spawning over the middle shelf apparently is influenced by bottom water temperature, which can change dramatically between years (Incze and Schumacher 1986).

2.2.2 Large-scale Patterns. After (or perhaps during) spawning, there is a general dispersal of adults from the slope and outer shelf to the middle, and, in some years, also to the inner shelf domain for feeding. The extent of this migration appears to be modified by the presence or absence of a cold (sometimes as low as -1.5°C) middle-shelf bottom water mass. Concentrations of pollock were located primarily in outer shelf waters in 1975 and 1976, when bottom water was cold over the middle shelf, but extended onto the middle shelf in warm years (Bakkala and Alton 1983; also see catches and bottom water temperature in Francis and Bailey 1983: 54). With the onset of the winter season, adults retreat from the cold (-1.5 to 0.0°C) bottom water of the inner and middle shelf regimes and aggregate on the outer slope where the water is warmer (ca. 3°C) due to the intrusion of oceanic water from the Aleutian Basin (Serobaba 1968; Shimada et al. 1983).

2.2.3 Small-scale Patterns. In places where bottom depth exceeds 100 m, active spawners have been observed in midwater shoals and inactive spawners at lower depths (Serobaba 1974; Sakurai 1982).

2.2.4 Maximum and Mean Abundances. The average density of adult pollock for the entire shelf and slope ranged between 32.2 and 133.0 kg/ha during 1975 to 1983, based on demersal survey data (Bakkala and Traynor 1984), but the density may exceed 300 kg/ha in some areas. However, these surveys underestimate pollock biomass because a substantial portion of the stock remains in water above the near-bottom depths sampled by bottom trawls.

2.2.5 Vertical Distribution. Adult pollock adopt a semidemersal (bathypelagic) distribution, occurring primarily within 50 m of the bottom. Adults older than age 3 rarely are found in the upper water column.

2.3 Feeding

2.3.1 Habitat. Adults feed primarily in the mid-to-low water column. Few, if any, strictly benthic organisms are taken as prey.

2.3.2 Prey Species. As pollock grow, there is an increasing preference for larger food items. Therefore, the relative dietary importance of copepods decreases while that of fish increases. Fish prey species include myctophids, herring, gadoids, cottids, hexagrammids and zoarcids (Bailey and Dunn 1979; Wespestad 1979; Dwyer et al. 1986), but the largest percentage of fish (often more than 75% by weight) eaten by adult pollock over the eastern Bering Sea shelf and slope are juvenile pollock (Takahashi and Yamaguchi 1972; Francis and Bailey 1983). Lynde (1984), based on preliminary results of an analysis of the diet of adult pollock (Dwyer et al. 1986), found that the important prey species for various size categories during different seasons were (1) copepods for small adults (<35 cm) during summer, (2) euphausiids for all adult-size categories during spring and summer, (3) young-of-the-year pollock for all sizes during autumn and (4) juvenile pollock for larger adults (>35 cm) during winter.

2.3.3 Prey Density Requirements. Not applicable.

2.3.4 Factors Affecting Availability of Prey. The degree of cannibalism may vary interannually, depending on climatological conditions (see 5.5.2). Little is known about factors affecting the abundance and availability of other prey organisms.

2.3.5 Temporal Patterns of Energy Storage. Seasonal cycles of energy storage related to reproductive effort were addressed in general ways (gonadosomatic and hepatosomatic indices) by Serobaba (1971) and Sakurai (1977, 1982).

2.3.6 Evidence of Food Limitation. Based on 1981-1983 data, the percentage of empty stomachs was highest during winter (about 35%) and lowest during spring and summer (about 8%) (Dwyer et al. 1986). Estimated daily ration was highest in summer (43% and 64% of body weight for pollock <40 cm and >40 cm, respectively) and declined during winter to 6% and 36% for the two size categories, respectively. Therefore, if food limitation is a factor for adults, and this is debatable, it probably occurs during winter. During this period, juvenile pollock exceed the size range utilizable by small adult predators but are still vulnerable to larger adults.

2.4 Predation

2.4.1 Predator Species. Predators of adult pollock include marine mammals, especially the northern fur seal, *Callorhinus ursinus* (Kajimura and Fowler 1984), and large piscivorous fish. Fishes with the greatest probable impact (in approximately decreasing order) are Pacific cod (*Gadus macrocephalus*), Greenland turbot (*Rheinhardtius hippoglossoides*), large-mouthed flounders (*Atherestes stomias* and *A. evermanni*) and sculpins (*Myoxocephalus polyacanthocephalus*, *M. groenlandicus* and *Hemitripterus bolini*) (J. Allen, Nat. Mar. Fish. Serv., Seattle, pers. comm.).

2.4.2 Effect on Spawning Adults. Data are not sufficient to estimate the degree of predation on spawning adults.

2.5 Other Factors Affecting Adults

2.5.1 Biotic. Parasitism at times may be substantial (Mamaev et al. 1965), but the effect of parasitism on survival and spawning success of adults is unknown.

2.5.2 Abiotic. No abiotic factors other than temperature are presently known to affect spawning (see 2.2.2).

2.5.3 Total Mortality. Estimates of average natural mortality vary from 0.3, based on Pauly's (1979) method (R. Francis, Fish. Res. Inst., Univ. Washington, pers. comm.) to 0.65, a value derived by Chang (1974), using an age:length key. Recently, Bakkala and Wespestad (1983) and Lynde (1984 and unpubl. data) used variations of cohort analysis to estimate the overall natural mortality as 0.4 and 0.5, respectively. Average instantaneous fishing mortality estimates ranged from 0.107 in 1978 to 0.259 in 1983, with a coefficient of variation of 34% during the period 1978 to 1980 (Bakkala and Wespestad 1983). As ages 1 and 2 are not fully recruited, they experience less than the estimated average fishing mortality.

2.6 Laboratory Holding and Rearing

J. Hendee (Inst. Mar. Sci., Univ. Alaska, Seward, pers. comm.)was able to maintain juvenile pollock in large circular tanks (approx. 2,700 l) until they matured and spawned (1.5 to 2 y). No injected hormones were required to induce spawning, and fish survived spawning, apparently in good health. Fish were fed as much herring and other foods as they would consume, dissolved oxygen was maintained below saturation and temperature was kept below 7°C. Adult fish, caught by hand-line, have been maintained for 2 to 3 months until they were ready to spawn (K. Bailey, Nat. Mar. Fish. Serv., Seattle, pers. comm.).

3 EGGS

3.1 General Description

Eggs are round with a smooth chorion and have a homogeneous yolk (clear and unsegmented) without an oil globule (Gorbunova 1954; Dunn and Matarese 1985). Average diameter is approximately 1.5 mm and observed range 1.3 to 1.9 mm (Nishama and Haryu 1981; Dunn and Matarese 1985). For eggs in net samples, the average size varies geographically and temporally but apparently not as a function of developmental stage (Nishiyama and Haryu 1981; see Lynde 1984 and Incze et al. 1984 for discussion of possible causes and consequences).

3.2 Distribution and Abundance

3.2.1 Duration of Egg Stage. Development time of pollock eggs ranges from about 14 days at 5°C to about 25 days at 2°C (Hamai et al. 1971). Daily development of eggs at 5°C has been examined, and it is possible to estimate the age, in days, of eggs collected from the plankton if this temperature prevailed throughout development (A.E. Matarese et al., unpubl. data).

3.2.2 Large-Scale Patterns. Pollock eggs have been found from February to July but are most abundant mid-March to mid-May (Serobaba 1968; Waldron 1981), when they may dominate the planktonic fish egg assemblages of the eastern Bering Sea, e.g., in April 1978 constituting 97% of planktonic fish eggs sampled (Waldron and Vinter 1978). Eggs occur first in March in oceanic waters over the Aleutian Basin and continental slope and later (April, May) over the shelf (Nishama and Haryu 1981; Francis and Bailey 1983). Spawning fish may not enter the middle shelf in significant numbers following cold winters (see 2.2.2), a source of interannual variability in distribution of eggs (see 6). Peak abundance of eggs was of similar magnitude in most surveys conducted from 1959 to 1982, but comparatively low abundances were observed in 1977 and 1980, and there was considerable interannual variability in the areal extent and the geographical locations of the high abundance regions (see Fig. 1 in Incze et al. 1984). Kim and Kendall (1983) divided the eastern Bering Sea into 37 subareas and recorded the number of eggs and larvae sampled during each research cruise from 1977 to 1979. Estimated abundance of pollock eggs was compared with estimated reproductive potential of the adult population.

3.2.3 Small-scale Patterns. No data are available for examination of abundance variations of eggs for length scales of less than 10 km. Data for 10-km intervals are available from a 1981 survey conducted by Kendall et al. (Nat. Mar. Fish. Serv., Seattle, unpubl. data).

3.2.4 Maximum and Mean Abundances. Maximum abundance of eggs estimated from single oblique plankton tows can exceed 1000 m^{-2} or 14 m^{-3} (Waldron and Vinter 1978). The latter value most probably is an underestimate of actual density because the depth of tow exceeded the depth where most eggs are found (station 25-1 of Waldron and Vinter's (1978) study), and because small-scale patchiness is overlooked by the sampling method. Mean abundance over significant areas can exceed 100 m^{-2} (see Kim and Kendall 1983, Incze et al. 1984).

3.2.5 Vertical Distribution. Eggs are found mainly in the upper 20 m in the eastern Bering Sea (Serobaba 1974; T. Nishiyama et al., unpubl. data). The neuston layer is not enriched in eggs, although they are frequently found there (Waldron and Vinter 1978; Nishiyama and Haryu 1981).

3.3 Feeding

Not applicable.

3.4 Predation

3.4.1 Predator Species. Bailey and Stehr (1986) found greatest predation on eggs by planktonic amphipods (*Parathemisto* sp.); other invertebrates examined included euphausiids, medusae and ctenophores. Planktivorous fish probably consume some eggs when "filter-feeding" (as compared to directed predation), but the importance of this loss cannot be evaluated without additional information on the feeding behavior of the abundant nektonic planktivores.

3.4.2 Effect of Predation. The impact of predation on egg survival cannot be evaluated at this time.

3.5 Other Factors Affecting Eggs

3.5.1 Biotic. Substantial mortality at hatching has been observed in the laboratory but has not been quantified or verified for samples collected at sea (A. J. Paul and M. E. Clarke, pers. comm.). Other biotic factors with significant impact have not been identified.

3.5.2 Abiotic. Temperature is of potential significance for survival of eggs because in cold waters development time is slowed. However, the sources of mortality that might interact with prolonged egg development, such as predation, are not well known and, in turn, might also be affected by cold temperatures.

3.5.3 Total Mortality. No published calculations on egg mortality rates exist.

3.6 Laboratory Holding and Rearing

For laboratory studies of eggs and later stages, reproductive products from mature pollock can be stripped or expressed into a beaker or other vessel. After fertilization, eggs are transferred to an aquarium where temperature can be adjusted to control hatching times.

4 LARVAE

4.1 General Description

Pollock larvae are tadpole shaped, with characteristic pigment patterns permitting easy separation from most Bering Sea gadoids (Matarese et al. 1981; Dunn and Vinter 1984). Length is approximately 4 mm at hatching (Walline 1983) and increases to approximately 22 mm when the full complement of adult fin rays develop; they then are considered juveniles (Haryu 1980). The average estimated dry-weight growth during larval development is from 0.07 to 15.8 mg. Walline (1983) estimated the linear growth rate of ethanol-preserved larvae from samples collected in the Bering Sea during June and July 1979. His estimates for growth rates, based on age determined from otolith structures, were 0.2 and 0.35 mm body length d^{-1} for yolk-sac and post-yolk larvae, respectively. Incze et al. (1984) used these data to estimate carbon growth as 7.5% of body carbon d^{-1} for post-yolk larvae. Clarke (1984) observed much lower growth rates (on the order of 0.17 to 0.23 mm d^{-1}) for larvae sampled during April and May 1980 and 1981. Regional differences in estimated growth rate were identified more frequently than interannual differences between these two years. Both Walline (1983, 1985) and Clarke (1984) applied a linear regression to their data. Nishimura and Yamada (1984), using larvae collected off Japan, and Bailey and Stehr (1986), using laboratory-reared larvae, showed nonlinear growth rates that were considerably lower than Walline's or Clarke's, particularly before age 35 days. Bailey and Stehr (1986) used a Gompertz growth equation to describe increase in weight as a function of age. Nishiyama (1981) and Bailey and Stehr (1986) gave formulae for length to weight conversions of field-caught and laboratory-reared larvae, respectively. The lower estimates of linear growth given by the latter authors yield substantially lower weight-specific or carbon-specific growth rates than noted above (Incze et al. 1984). It is not known how much environmental vs. technical variations in preparation and reading of the otoliths were responsible for the differences in reported growth rates, particularly between those of Walline (1983, 1985) and Clarke (1984), who studied pollock from the same region.

4.2 Distribution and Abundance

4.2.1 Duration of Larval Stages. Yolk-sac and post-yolk stages of larval development in the southeastern Bering Sea last approximately 15 and 36 days, respectively (Incze et al. 1984). Yolk-sac absorption is complete at approximately 7-mm body length.

4.2.2 Large-scale Patterns. Knowledge of large-scale distribution patterns of larvae is limited by the small number of surveys. However, considerable interannual differences in peak abundance and the extent of the area over which larvae are abundant have been recorded (Incze et al. 1984).

4.2.3 Small-scale Patterns. Data on small-scale distribution of larvae for length scales of less than 10 km are not available. Data on variability in abundance at 10-km intervals are available from the 1981 survey of Kendall et al. (Nat. Mar. Fish. Serv., Seattle, unpubl. data).

4.2.4 Maximum and Mean Abundances. Maximum abundance of larvae from single oblique plankton tows can exceed 570 m^{-2} or 2 m^{-3} (Waldron and Vinter 1978). The latter estimate of abundance, like that for eggs (see 3.2.4), probably is low. Mean abundances in some years can exceed 30 m^{-2} over large areas (Incze et al. 1984).

4.2.5 Vertical Distribution. Most larvae (all sizes) occur in depths of 10-30 m (Walline 1983; Dagg et al., 1984). No pronounced diel vertical migrations have been observed, although a slightly deeper and more dispersed distribution sometimes has been seen at night compared to daylight hours (Walline 1983).

4.3 Feeding

4.3.1 Habitat. Feeding presumably occurs in depth of 10-30 m. As larvae are visual predators, they are influenced by factors affecting light intensity in the visible spectrum. The action spectrum has not been defined for larval pollock, but the light intensity threshold for feeding of 5-mm larvae is approximately 0.2 to 0.4 lux using standard indoor lighting (Paul 1983). A convenient comparison of light intensities is shown in Figs. 2-30 of Blaxter (1970). It has been estimated that at the time of first feeding adequate light is available for 10-12 d^{-1} within the depth range occupied by most pollock larvae in the southeastern Bering Sea (Paul 1983).

4.3.2 Prey Species. Feeding begins about 5 and 9 days after hatching at 3 and 5°C, respectively (Paul 1983); this is before yolk sac absorption is complete. Pollock larvae primarily feed on copepod nauplii and eggs at first-feeding and continue to do so until yolk is absorbed (Clarke 1978). Small copepods of the genus *Oithona* sometimes also are abundant in larval stomachs (Clarke 1978). In post-yolk larvae, copepod nauplii and small *Oithona* spp. remain numerically abundant in the diet, but copepodid stages of *Pseudocalanus* and *Acartia* spp. and of juvenile euphausiids become more important in terms of their contribution to ingested ration (Incze et al. 1984). A preliminary carbon budget and an analysis of prey contribution to total carbon needs of larval pollock were presented by Incze et al. (1984). They estimated that daily ingestion must be approximately 16-17% of body weight to support estimated rates of *in situ* growth and metabolism of post-yolk larvae. These calculations were based on the highest published linear growth rates (see also 4.1). Stomach content data of Clarke (1978) showed a gradual, rather than sudden, increase in mean number of copepod prey consumed per larva as larval length increases. This is consistent with the absence of marked morphological changes during larval development. A comparatively sudden increase in mean number of calyptopes (juvenile euphausiids) was found in larvae longer than approximately 14 mm in Clarke's study, but it is not known whether this increase was due to chance availability of prey or to increased predatory capability of the larvae. Features of developing larval pollock that are probably relevant to predation on large organisms are the development of maxillary teeth at 11-12 mm larval length and the ossification of the vertebral column and caudal fin rays at 11 to 16 mm larval length (J. Dunn, Nat. Mar. Fish .Serv., Seattle, unpubl. data).

4.3.3 Prey Density Requirements. In laboratory studies, first-feeding larvae consumed from one to four copepod naupli^{-1} in a 12-h light (3 lux) period at 5.5°C at initial prey concentrations ranging from 8 to 50 l^{-1} (averaged for all larvae in each experimental container; Paul 1983). Because the experimental vessels used were small, prey were sometimes potentially limiting at lower initial densities, for instance, when eight larvae were added to containers with eight prey. Nonetheless, the mean percentage of larvae actually feeding (10-14%) and the number of prey consumed per feeding larvae (1-4 prey) were essentially the same over the range 8-50 prey l^{-1} (see Table 2 of Paul 1983 for details). However, the mean percentage of larvae feeding does not necessarily reflect what can be expected at sea. Paul (1983) purposely used very young larvae to ensure that his experiments pertained to the first-feeding condition; thus, some larvae probably weren't ready to feed. In feeding experiments, Clarke (1984) used larger containers and also larvae that had been maintained in vessels with prey organisms prior to their use in his experiments. The possible effects of container size on larval behavior, however, were not evaluated by either Paul (1983) or Clarke (1984). Although Clarke's results are not strictly comparable with those of Paul (1983), she observed an average of 15% feeding at 10 nauplii l^{-1}. A much higher proportion, up to an average of 56.8%, fed at 20-24 nauplii l^{-1}. On average, it appears that naupliar densities of approximately 10 l^{-1} are sufficient to ensure feeding of active yolk-sac pollock larvae. These densities are commonly encountered in the Bering Sea when first-feeding larvae are present (Paul 1983; Clarke 1984). The prey density requirements for successful feeding of older larvae are unknown. The prey requirements (required ingested ration) have been estimated by Incze et al. (1984) for various species of prey and evaluated with respect to stomach content data published by Clarke (1978). The absolute values (number of prey required) need to be adjusted for various estimates of growth rate (see discussion in 4.3.2), but the relative contribution of each prey type would not be affected.

4.3.4 Factors Affecting Availability of Prey. The abundance and availability of food organisms for larval pollock in the eastern Bering Sea (shelf and slope environments) appear to be determined primarily by factors affecting rates of reproduction and growth of the numerically abundant, small copepods of the genus *Pseudocalanus* and perhaps also reproduction of euphausiids and growth of the juvenile stages. Over the basin, other species of copepod may become important as prey (see discussions of zooplankton communities by Motoda and Minoda 1974; Cooney and Coyle 1982; Smith and Vidal 1984, 1985). There is some indication that naupliar prey commonly are not limiting to first-feeding larvae (see 4.3.3); however, there is evidence that standing stocks of *Pseudocalanus* spp. during April and May can vary by nearly an order of magnitude from year to year (Walsh 1983; Incze et al. 1984). One major factor affecting abundance of small copepods early in spring appears to be temperature (Walsh 1983; see also Vidal 1980), but other factors, such as overwintering stocks, also may be important. There is currently no knowledge of how variation in abundance of copepods affects the feeding success of larger pollock larvae.

4.3.5 Temporal Patterns of Energy Storage. Not applicable.

4.3.6 Evidence of Food Limitation. These is no evidence of food limitation at the present time.

4.4 Predation

4.4.1 Predator Species. Numerous species of seabirds are known to consume larval pollock (Smith 1981; Kajimura and Fowler 1984), but the incidence of catch and the total impact relative to other sources of mortality probably are low (D. Schneider, Univ. California, Irvine, from data of G. Hunt, D. Schneider and others, pers. comm.). Potentially significant predators include planktivorous fish, scyphozoan and hydrozoan medusae and euphausiids.

4.4.2 Effect on Larvae. No estimates of the importance of predation on larval pollock are available.

4.5 Other Factors Affecting Larvae

4.5.1 Biotic. Potentially significant biotic impacts on survival have not been identified.

4.5.2 Abiotic. If cold temperatures slow larval growth, which seems probable, the length of time during which larvae could be exposed to predators would be increased. However, more must be known about predators of larval pollock, as well as the response of the predators to cold temperatures, before such a mechanism could be implicated as an important cause of interannual variations in year-class survival. Other abiotic influences on the survival of pollock larvae in the southeastern Bering Sea have not been identified.

4.5.3 Total Mortality. Estimates of total larval mortality for the eastern Bering Sea are not available.

4.6 Laboratory Holding and Rearing

First-feeding larvae produced in the laboratory or on board ship from eggs (see 2.8) can be held for 2 to 3 weeks by maintaining appropriate temperatures (see 3.2.1). Bailey and Stehr (1986) have raised larvae to the juvenile stage in the laboratory, but there may be difficulty rearing larvae at sea due to stress imposed by motion (Clarke 1984).

5 JUVENILES

5.1 General Description

Pollock enter the juvenile phase upon completion of fin-ray development at about 22 mm standard length, approximately 50 days after hatching. Metamorphosis is gradual with only slight morphological changes between the larval and juvenile phases. Pollock remain in the juvenile phase until about 25 cm (age 2-3, see 2.1.1).

5.2 Distribution and Abundance

5.2.1 Duration of Juvenile Stage. Pollock usually enter the juvenile phase in late June or early July and grow to about 100 mm by December and to 200 mm by the end of the following year.

5.2.2 Large-scale Patterns. Juvenile pollock are widespread throughout the eastern Bering Sea, although they apparently are rare in the Aleutian Basin (see 1.2). Unlike adults, juveniles do not avoid, or at least they occur in, water as low as 0°C. Data concerning interannual variability are limited, since juveniles do not occur with regularity in demersal trawl surveys or the commercial catch. However, they were sampled effectively by hydroacoustic-midwater trawl surveys conducted in the eastern Bering Sea during 1979 and 1982. The estimated abundance of juveniles differed greatly between these two years, reflecting differences between the large 1978 year class (76.9 billion age-1 fish estimated in 1979) and the poor 1981 year class (1.0 billion age-1 fish estimated in 1982) (Traynor 1983).

5.2.3 Small-scale Patterns. Schooling behavior and other aspects of patchy distribution of juveniles have not been documented.

5.2.4 Maximum and Mean Abundances. Traynor (1983) estimated the average density of 0-age pollock in a middle shelf area during 1982 to be 6.65 million fish/km^2, which he considered a conservative estimate. No such estimates exist for previous years.

5.2.5 Vertical Distribution. Juvenile pollock are pelagic. The presence or absence of a strong thermocline appears to influence the vertical distribution of 0-age juveniles. Juveniles have been found above a strong thermocline but mixed throughout most of an isopycnal water column (Francis and Bailey 1983).

5.3 Feeding

5.3.1 Habitat. Feeding occurs primarily within the upper mixed layer (Walline 1983).

5.3.2 Prey Species. Copepods and euphausiids are the primary prey of juvenile pollock (Takahashi and Yamaguchi 1972; Walline 1983), and amphipods occasionally are important (Bailey and Dunn 1979). Cooney et al. (1980) found a distinct difference in the diet of early 0-age (20-60 mm), late 0-age (60-100 mm) and age-1 (100-200 mm) juveniles sampled over the southeastern shelf. Early 0-age juveniles fed almost exclusively on copepods of the genus *Pseudocalanus*. Larger 0-age juveniles supplemented this diet with larger copepods, such as *Metridia* sp. and *Eucalanus* sp., as well as barnacle nauplii, pteropods, appendicularians and fish (unclassified); age-1 juveniles fed primarily on large copepods and euphausiids. However, these generalizations may be influenced by the areal distribution of samples.

5.3.3 Prey Density Requirements. No data available.

5.3.4 Factors Affecting Availability of Prey. Periods of extended thermal stratification may help concentrate both 0-age pollock and their prey. Sambrotto and Goering (1983) associated interannual variability in zooplankton and phytoplankton production on the shelf with variability of wind stress. They suggest that a balance of vertical mixing necessary for infusion of nutrients and stability necessary for proper light conditions is required for maximum biological production in the upper mixed layer. For the production of zooplankton, variations in total annual primary production probably are not important over the middle shelf, where the grazing community does not appear to be food limited (Dagg et al. 1982).

5.3.5 Temporal Patterns of Energy Storage. No data available.

5.3.6 Evidence of Food Limitation. Evidence of food limitation for juveniles is generally lacking. Walline (1983) examined the growth of individuals by counting increments, presumed to be daily growth rings, on otoliths. A total of 30 juveniles, collected during 1978, 1979 and 1981, were examined. Although juvenile growth rates differed between sampling stations, the variability was not as high as one might expect. Juveniles seemed to be growing at a roughly constant rate, 0.55 mm body length d^{-1}. This may be an indication that food limitation was not critical during these years. However, the limited sample-size and the uncertainty associated with estimating ages from otoliths prevent any strong conclusions.

5.4 Predation

5.4.1 Predator Species. A wide variety of predators, ranging from marine mammals and marine birds (Kajimura and Fowler 1984) to fish (including adult pollock) and invertebrates (Smith et al. 1984), prey on juvenile pollock. The most important predators are adult pollock.

5.4.2 Effect on Juveniles. A rough estimate of annual pollock consumption by marine mammals, using data from McAllister (1981), is about 500,000 mt (Kajimura and Fowler 1984, Table 10). Based on the length frequencies of pollock in stomach samples of marine mammals (Kajimura and Fowler 1984), it is not unreasonable to assume that juvenile fish contribute 1/3 to 1/2 of the above amount. Hunt et al. (1981) estimated that consumption of juvenile pollock by marine birds in the eastern Bering Sea averaged between 150,000 and 300,000 mt per year. Predation by fish species has not been quantified, although cannibalism probably accounts for mortality at least similar to that due to mammals or birds. Taking the lower bounds of these estimates and conservatively assuming an average weight of 60 g (average wet weight for age-1 juveniles) results in an estimated mortality of about 10 billion 0-age and age-1 individuals per year due to predation. These very tentative numbers at least suggest that predation may be an important factor in determining year-class strength since population estimates of age-1 juveniles range from 6.5 to 76.9 billion (Lynde 1984).

5.5 Other Factors Affecting Juveniles

5.5.1 Biotic. No data available.

5.5.2 Abiotic. Periods of extended thermal stratification may isolate 0-age juveniles from adults (see 2.2.5 and 5.2.5), therefore, cannibalism may be reduced, but predation by marine mammals and birds may increase. During years in which the cold bottom water mass persists over the middle shelf, adults may be partially excluded and the middle shelf area may then serve as a refuge from cannibalism.

5.5.3 Total Mortality. No accurate estimates of juvenile mortality exist.

5.6 Laboratory Holding and Rearing

See 2.6.

6 CURRENT HYPOTHESES ON FACTORS AFFECTING YEAR-CLASS ABUNDANCE

The following is not an exhaustive account of research possibilities but a brief summary of themes presently receiving the most attention. Experiments with first-feeding pollock larvae in the laboratory (Paul 1983) and at sea (Dagg et al. 1984; Clarke 1984) and estimators of naupliar prey abundance (Cooney et al. 1978; Cooney 1979; Clarke 1984) indicate that first-feeding pollock larvae usually should encounter sufficient food densities in their depth habitat in the southeastern Bering Sea. It is possible that later larvae may encounter low abundance of their principal prey as estimates have been shown to vary by as much as an order of magnitude in some years (Incze et al., 1984) and the growth rate may be affected. Reduced growth rate increases exposure (time) to potential predators and thus may indirectly affect survival. Mortality experienced during hatching of eggs, while it may be significant, should be relatively constant and, therefore, would not appear to be an important source of interannual variability in year-class abundance. Predation on eggs and larvae, however, might not only be significant but also show large interannual variations due to variation in abundance of predators. Variations in the abundance and activity of predators and the duration of egg and larval stages may interact to significantly affect the extent of predatory losses.

Predation on juvenile pollock, particularly 0-age fish, appears to be extensive; a major source of predatory losses is cannibalism by older pollock (Bailey and Dunn 1979; Dwyer et al., 1986). Francis and Bailey (1983) postulate that early autumn breakdown of stratification may significantly increase cannibalism by vertically overlapping the depth ranges of 0-age and older fish. The hypothesis is attractive because of the possibilities for interannual variation. Early autumnal mixing has the impact of exposing smaller fish than normal to adult pollock predators and increases the total amount of exposure time. Changes in the vertical distribution of 0-age fish in response to vertical mixing were shown by Traynor (1986). However, comparatively colder bottom water may resist vertical mixing in late summer and fall because greater turbulent energy is required to mix across a steeper thermal gradient. Thus, variations in bottom water temperature, in conjunction with wind energy, may influence the timing of fall breakdown of the thermocline and subsequent cannibalism on 0-age pollock.

The spatial distribution of abundant year-classes may be affected by the abiotic environment. Eggs spawned over the outer shelf of the southeastern Bering Sea are transported northwestward and may ultimately contribute to a "production unit" of fish primarily associated with that region. Differences in transport may be substantial for some years. In contrast, heavy spawning over the middle southeastern shelf presumably leads to recruitment of juveniles in the southeast since advection out of this region appears to be negligible (Kinder and Schumacher 1981; Francis and Bailey 1983). Bottom water temperature of the middle shelf influences the migration of spawning fish (see 2.2.2) and so may be a major influence on the spatial pattern of recruitment. This hypothesis addresses only spatial distribution of recruitment during the juvenile phase; year-class strength presumably will be influenced by other factors.

The relationship of spawning over the Aleutian Basin to recruitment on the shelf needs to be investigated. Likewise, the source of recruits to the Basin must be investigated. Recruitment (at different stages in the life history) between these two broad areas may be interrelated by planktonic transport to the shelf and juvenile or adult migrations to the Basin.

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WALLEYE POLLOCK, *Theragra chalcogramma*, IN THE GULF OF ALASKA

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1 BACKGROUND

1.1 Literature Search

All pertinent papers in scientific journals through 1986 and various reports, such as Northwest and Alaska Fisheries Center (NWAFC) technical memoranda and processed reports and Outer Continental Shelf Environmental Assessment Program (OCSEAP) annual and final reports, were used in the literature search. Because of the scarcity of published papers, we are very grateful for the many items of interest obtained from talks with various NWAFC and University of Washington scientists.

1.2 Unit Stocks and Their Relationships

Two hypotheses have been proposed:

Two-stock hypothesis—An east-west separation of stocks exists in the vicinity of Kodiak Island. This hypothesis is based on observed east-west differences in the relative abundance of two prominent year-classes. Size and age of adult pollock consistently increased from the southwestern Kodiak and Shelikof Strait region westward through the Chirikof region and into the Sanak-Unalaska region (Hughes and Hirschhorn 1979). A closer association of western pollock with Bering Sea pollock than with pollock from the area south of Kodiak or in the eastern Gulf of Alaska was found through a biochemical genetic study (Grant and Utter 1980).

One-stock hypothesis—Biomass within a single spawning area (Shelikof Strait) during the spawning season was estimated at 2-4 million mt, comparable to the total known adult standing stock from Kodiak to the Shumagin area, and maximum summer catches were taken to the west of Shelikof Strait (Strickland and Sibley 1985).

1.3 The Fishery

1.3.1 Relative Size and Importance. About 66% of the total Gulf of Alaska groundfish catch by foreign trawl fisheries during 1977-1981 was pollock (annual mean, 170,000 mt) (Alton and Deriso, 1983b). Hydroacoustic surveys of spawning pollock in Shelikof Strait showed pollock biomass of 3.8, 2.4, 1.8 and 0.7 million mt during peak spawning (March) of 1981, 1983, 1984 and 1985, respectively (Nelson and Nunnallee 1985).

1.3.2 Age at Recruitment. Reports of age at recruitment to the fishery vary. Generally, catches of pollock less than age-2 are negligible. Age-2 pollock occurred in the catch during 1978 and 1980, while they were scarce during 1979 and 1981 (Alton and Deriso 1983b).

1.3.3 Characteristics of Harvested Fish. Female pollock are larger and heavier than males, and both show seasonal variability. Based on measurements of pollock caught in the Gulf of Alaska by all nations during 1976-1982 (Alton and Kim, unpubl. data), during the main spawning season (Apr.-June) mean lengths are 39.04 cm and 41.42 cm and mean weights are 488.6 g and 587.2 g for males and females, respectively. They become progressively longer and heavier until the next spawning season, reaching a maximum mean length of 42.75 cm and 45.20 cm and mean weight of 657.3 g and 785.6 g for males and females, respectively. Pollock in Shelikof Strait midwater trawl samples showed an annual increase in length over a four-year period (1981-1984); mean lengths (sexes combined) were 32.2, 34.0, 39.1 and 43.6 cm, respectively (Nelson and Nunnallee 1984).

1.3.4 Types and Selectivity of Gear. Two types of vessel, large factory trawlers and small or large freezer trawlers, were used in the Japanese fishery . The factory trawler, the largest Japanese fishery, produces minced fish (surimi) and frozen fish. The catch by small freezer trawler increased substantially in 1981 and exceeded that of larger vessels. Detailed information on foreign fisheries in the Gulf of Alaska is given by Wall et al. (1981). The U.S. catcher vessels in joint-venture fisheries are small stern trawlers, ranging between 25 and 50 m in length (Alton and Deriso 1983b).

1.3.5 Distribution of Fishing Effort. The Catch per Unit Effort (CPUE) of pollock in the Japanese fishery in the Gulf of Alaska increased from 0.211 in 1973 to 9.153 ton per hour in 1982 (Yamaguchi and Okada 1983). These values were standardized for frozen-fish factory trawlers of 2,505-3,504 GRT.

Pollock fisheries were concentrated in the Shumagin-Chirikof-Kodiak area during the third and fourth quarters of the year until 1981. After the discovery of the Shelikof Strait spawning ground, however, the major pollock catch has occurred in the Chirikof area during the first quarter of the year (Table 1).

1.4 Distribution and Abundance of the Population

Greatest abundance of pollock is on the continental shelf between 100 and 300 m; however, they may occur on or near the bottom, as well as at mid- and near-surface depths. Beyond the shelf, adult pollock have been found in the upper water layers (Alton and Deriso 1983b).

About 91% of the pollock biomass lies west of 148°W longitude. General summer onshore and winter offshore migrations of bottom fish correspond to the general pattern of bottom currents on the shelf (Alton 1981). However, pollock gather in Shelikof Strait before spring spawning time. Subsequently, post-spawners migrate very rapidly outside the Strait; for example, the mean biomass in 1983 was reduced from 2.5 million mt in March to 0.8 million mt during April (Nelson and Nunnallee 1984).

In addition to seasonal on- and offshore migration, pollock shift their location in the water column as the season changes. Fishing records indicate that pollock are mainly at 100-200 m depth during winter and at 50-150 m depth during summer (Niggol 1982).

There has been a dramatic increase in the size of the Gulf of Alaska pollock stock since the early 1960s. Based on survey catch data, changes in stock density increased sharply from 20 kg/h in 1961 to 621 kg/h in 1975 (Alton and Deriso 1983b). Commercial CPUE data showed a 43-fold increase between 1973 and 1982 (Yamaguchi and Okada 1983).

1.5 Current Status of Stocks and of Management Measures

Estimates of exploitable biomass and exploitable annual surplus production (ASP) have increased continuously. Biomass and ASP, respectively, were 719,000 mt and 120,000 mt in 1976 and 2,176,000 mt and 524,000 mt in 1981.

1.6 Recruitment Variability

Estimates of year-class strength at age 3 by Alton and Deriso (1983b) were 0.5, 0.4, 1.74, 2.57, 2.32 and 2.16 billion fish from the 1973 to 1978 year classes, respectively. The average was 2.2 billion fish per year during 1975-1978, while the 1973 and 1974 year-classes were relatively unimportant in the fisheries.

1.7 Age Determination and Validation

Age determination of pollock can be made from examination of otoliths, scales, dorsal fin rays and pectoral fin rays. Otolith break-burn and surface reading methods are used by American scientists (e.g., NWAFC) for eastern Bering Sea and Gulf of Alaska pollock, and the dorsal fin ray is used by Canadian scientists (e.g, PRS) for pollock off British Columbia. Both are good

Table 1. Temporal and spatial distribution of foreign and joint venture walleye pollock catch in the Gulf of Alaska during 1977-1985 (Berger, NWAFC, pers. comm.).

		Areas					
Year	Quarter	Shumagin	Chirikof	Kodiak	Yakutat	SE*	Total
	1	2388.00	690.50	1820.00	497.30	131.70	5528.20
1977	2	471.20	532.80	2479.60	935.80	45.80	4465.20
	3	20052.10	1597.30	7107.20	1524.40	527.50	30308.50
	4	38583.70	19755.20	16609.80	1510.30	572.40	77031.40
	Total	61495.70	22575.80	28016.60	4467.80	1277.40	117833.30
	1	1238.78	10730.42	2297.69	208.19	61.30	14536.38
1978	2	3681.10	29237.15	2813.72	837.33	210.64	36779.94
	3	9435.52	882.85	6896.06	1039.42	587.90	18841.75
	4	16945.21	2166.13	4463.94	453.17	130.50	24158.95
	Total	31300.61	43016.55	16471.41	2538.11	990.34	94317.02
	1	16.18	632.30		48.02		696.70
1979	2	938.51	5619.79	6153.23	104.09	51.92	12867.54
	3	18093.68	3963.36	17830.25	2999.42	377.38	43264.09
	4	11169.01	18968.72	15064.62	1676.39	126.15	47004.89
	Total	30217.58	29184.17	39048.10	4827.92	555.45	103833.22
	1	7628.40	4644.00	42.83	0.00		12315.23
1980	2	8215.39	18124.61	5919.45	480.20	39.08	32778.73
	3	18641.77	3505.47	12164.98	3088.72	318.35	37719.29
	4	12274.04	9323.07	9015.82	629.29	76.07	31318.29
	Total	46759.60	35597.15	27143.08	4198.21	433.50	114131.54
	1	8260.74	19400.28	128.00	21.20		27810.22
1981	2	2831.84	8365.82	2450.70	309.80	79.13	14037.29
	3	18651.74	22637.73	4769.47	3943.92	510.50	50513.36
	4	17836.10	31525.85	1746.95	3298.76	411.20	54818.86
	Total	47580.42	81929.68	9095.12	7573.68	1000.83	147179.73

Table 1. Temporal and spatial distribution of foreign and joint venture walleye pollock catch in the Gulf of Alaska during 1977-1985 (Berger, NWAFC, pers. comm.) - cont'd.

		Areas					
Year	Quarter	Shumagin	Chirikof	Kodiak	Yakutat	SE*	Total
	1	299.09	63586.62	1769.10	0.40		65655.21
1982	2	14721.52	9631.15	3029.97	1.90		27384.54
	3	17219.44	17973.32	2132.60	8.47		37333.83
	4	8133.83	23727.06	4280.39	15.00		36156.28
	Total	40373.88	114918.15	11212.06	25.77		166529.86
	1	128.30	122199.74	6898.90	1.60		129228.54
1983	2	3667.32	2675.92	1550.03	0.70		7893.97
	3	21718.38	1858.01	3723.44	19.40		27319.23
	4	14302.41	33177.82	3547.33	19.50		51047.06
	Total	39816.41	159911.49	15719.70	41.20		215488.80
	1	349.54	173958.72	3060.56			177368.82
1984	2	681.53	4200.97	1338.41			6220.91
	3	25010.78	15293.83	17021.62			573236.23
	4	24447.68	20861.68	20138.16			65447.52
	Total	50489.53	214315.20	41558.75			306363.48
	1	8.36	196642.55	10115.20			206766.11
1985	2	1014.61	12906.01	204.67			14125.29
	3	1025.87	14.35	5637.79			6678.01
	4	34018.07	1818.70	6040.84			41877.61
	Total	36066.91	211381.61	21998.50			269447.02
Mean		42677.85	101425.54	23362.59	3381.81	851.58	170569.33

*SE: Southeastern Gulf of Alaska.

indicators of the age of pollock, while scale readings may underage them (Lai 1985).

1.8 Age Composition of the Population

Age frequency distributions based on catch data generally indicate that recruitment and highest catch occurred at age 2 and age 4, respectively. Because the 1978 year class was very strong, both the numbers recruited at age 2 and the catch in subsequent years were noteworthy.

2 SPAWNING ADULTS

2.1 General Description

2.1.1 Size and Age Ranges. On the basis of 1973-1975 spring surveys, sexual maturity was reached at age 3, and mean length at first maturity was 29 to 32 cm for males and 30 to 35 cm for females. Sexual composition fluctuated around 50% at 20 to 45 cm fork length, but females became dominant at fork lengths greater than 45 cm (Hughes and Hirschhorn 1979).

2.1.2 Type of Spawning Behavior. Pollock are iteroparous and spawn only once a year (Miller et al. 1986). Spawning in Shelikof Strait typically occurs within a 10- to 20-day period (E. Nunnallee, NWAFC, pers. comm.).

2.1.3 Fecundity. For Shelikof Strait pollock, fecundity estimates range from about 95,000 to 1,000,000 for those ranging from 30 to 69 cm in length and 225 to 2000 g in weight (Miller et al. 1986). The estimates were determined as follows: Fecundity/length and fecundity/weight relationships were described by $F = 1.2604 * L ** 3.2169$ and $F = 387.4551 * W ** 1.0160$ for pollock 35 to 65 cm in length, where F = number of eggs, L = fork length in cm and W = gutted weight in grams.

2.2 Distribution and Abundance

2.2.1 Duration of Spawning. Peak spawning in Shelikof Strait occurs from the end of March to early April, after which intense spawning activity declined rapidly but incidental spawning persisted into late May. Spawning time varied little from year to year (A. Kendall, NWAFC, pers. comm.). During research cruises, spawning pollock have been observed at 127 locations between 142°-157°W longitude; 82% occurred within the 150-300 m depth interval. The seasonal distributions of spawning activity were 11%, 30%, 37%, 18% and 4% in February, March, April, May, and June-August, respectively (Hirschberger and Smith 1983).

2.2.2 Large-scale Patterns. Neither the spatial nor temporal distribution and abundance of pollock in the Gulf of Alaska are well understood. In general, it is assumed that most of the resource lies in the central-western regulatory areas, i.e., westward from the vicinity of Prince William Sound to Unimak Pass, an onshore spawning migration occurs during early winter and, after spawning, pollock outmigrate, then disperse to the whole Gulf area. The overall pattern of pollock distribution shows the highest abundance in regions where the continental shelf is indented, providing sheltered areas, such as the Kodiak shelf, and the lowest abundance in exposed areas such as the Yakutat shelf (Strickland and Sibley 1985).

2.2.3 Small-scale Patterns. Spawning aggregations in Shelikof Strait follow the narrow contours of the bottom trough (below 200 m depth) between Puale Bay and Cape Atushagvic (A. Kendall, NWAFC, pers. comm.). There is some indication that segregation by age occurs, and no conspicuous diel migration of spawners was found in Shelikof Strait (E. Nunnallee, NWAFC, pers. comm.).

2.2.4 Maximum and Mean Abundances. Mean density on the Shelikof Strait spawning ground was 0.638 kg/m^2 during March, 1981, but it sharply decreased to 0.251 kg/m^2 during April (Nelson and Nunnallee 1984).

2.2.5 Vertical Distribution. As noted in section 1.4, pollock are located near bottom during spawning. Toward the end of the spawning period (May), they change their location in the water column; echograms taken during May cruises (1981 and 1985) showed that most walleye pollock schools were located at the midwater level.

2.3 Feeding

2.3.1 Habitat. Pollock are classified as facultative planktivores; their feeding realm is epibenthic and benthic (Simenstad 1979).

2.3.2 Prey Species. Stomach contents of adult pollock from several bays and shelf areas near Kodiak were examined, and the average number and weight of prey items per stomach determined (Rogers et al. 1979a, b; Jewett and Powell 1979). There is a seasonal variability in prey items. Members of the Pandalidae comprised over 80% by weight of stomach contents during summer (July and August), while during winter

(November) and spring (May) the main food items were Gadidae (65%) and Pandalidae (26%). The percentage of euphausiids in stomachs increased from 3.1% in May to 10.9% in July, but their importance as food became negligible after August. While shrimp and fishes were important prey of pollock around Kodiak Island, the most important prey in Lower Cook Inlet were mysids, which comprised 91% of the Index of Relative Importance (IRI) during fall (Simenstad 1979).

2.3.3 Prey Density Requirements. No data available.

2.3.4 Factors Affecting Availability of Prey. The abundance of the main food items, zooplankton and nekton, is strongly affected by the amount of phytoplankton and variations in abiotic phenomena, such as temperature, current, wind force and direction, nutrients, upwelling and downwelling. However, because of the complexity of the ecosystem and the scarcity of data, these relationships are poorly understood for the Gulf of Alaska.

Facultative planktivorous fish competing with pollock for food in the Gulf of Alaska include: Pacific Ocean perch (*Sebastes alutus*), Pacific cod (*Gadus macrocephalus*), yellow Irish lord (*Hemilepidotus jordani*), arrowtooth flounder (*Atheresthes stomias*), flathead sole (*Hippoglossoides elassodon*), butter sole (*Isopsetta isolepis*) and Dover sole (*Microstomus pacificus*) (Simenstad 1979). Alton (1981) associated the recent increase in size of pollock stock to overfishing of Pacific ocean perch, which has a depth distribution that overlaps that of pollock and a similar prey spectrum and therefore may be a competitor, a predator or both.

2.3.5 Temporal Patterns of Energy Storage. No data available.

2.3.6 Evidence of Food Limitation. Strickland and Sibley (1984) suggested that food supplies for pollock may be limited in the Gulf of Alaska, based on smaller individual sizes and lower growth rate in strong year-classes.

2.4 Predation

2.4.1 Predator Species. According to Frost and Lowry (1981), the major pollock predators in the north Pacific are marine mammals, birds and fishes. Several mammal predators may affect pollock populations. Pollock were a major item in stomachs of harbor seals (*Phoca vitulina richardsii*), with 25% and 35% occurrence in 1980 and 1981 surveys, respectively, and northern fur seal also may feed on pollock (Pitcher 1980, 1981). In the northern Gulf, the Steller sea lion (*Eumetopias jubatus*) population, ranging from 95,000-135,000 in number, is a major predator (Longhlin and DeLong 1983); Pitcher (1981) found pollock in 67% of the stomachs examined and they comprised 58% of the total volume, while Calkins and Pitcher (1982) reported only 39% occurrence but the same total volume. Predation pressure on pollock by various whales and porpoises has not been determined as little is known of their diets or population sizes (A. Erickson, Univ. Washington, pers. comm.). Known fish predators are Pacific cod and arrowtooth flounder (Feder 1979).

2.4.2 Effect on Spawning Adults. According to Livingston (1977), total pollock consumption by marine mammals in the Gulf of Alaska was estimated at 338,000 mt per year.

2.5 Other Factors Affecting Adults

2.5.1 Biotic. The parasites of pollock include nematodes, cestodes and microsporidians. Arthur et al. (1982) reported the following parasites in British Columbia pollock: *Pleistophora* sp., *Pseudophyllidean plerocercoids* and *Phocanema decipiens* in musculature; Contracaecum-type larvae and *Hysterothylacium aduncum* larvae in the body cavity; *Anisakis simplex* larvae and *Nybelinia surmenicola* in both sites.

2.5.2 Abiotic. Sea water properties probably affect pollock behavior and distribution patterns. During the 1981 spawning season in Shelikof Strait, over 80% of the spawners were in 5.0-5.5°C seawater (S. Kim, unpubl. data).

2.5.3 Total Mortality. Full recruitment fishing mortality rates at age 3 obtained from catch-age analyses were 0.16, 0.16, 0.15, 0.11, 0.10 and 0.07 from 1976 to 1981, respectively; 1973-1978 year classes averaged 0.13 per year (Alton and Deriso 1983b). An estimate of natural mortality for adult pollock, derived by Megrey (1985), is 0.35 for ages 6-10, based on Japanese catch-at-age/effort data collected during 1976-1981.

2.6 Laboratory Holding and Rearing

No data available.

3 EGGS

3.1 General Description

Pollock eggs are transparent, round, planktonic and pelagic. The size range is 1.20-1.85 mm (Matarese et al. in press).

3.2 Distribution and Abundance

3.2.1 Duration of Egg Stage. The NWAFC ichthyoplankton team recognizes 21 stages in the development of pollock eggs. Duration of each stage depends on sea water temperature (cumulated hours for development) = EXP (A + B * Temperature), where A and B are constants for each cell stage (R. Bates, NWAFC, pers. comm.).

3.2.2 Large-scale Patterns. In the western Gulf of Alaska, pollock eggs were found mainly during February through June but also in small numbers from September to November (Dunn et al. 1984). Peak spawning occurs in early April in Shelikof Strait, with maximum abundance of eggs in the area between Cape Kekurnoi and Cape Atushagvik. Low abundance of eggs occurred nearshore and toward the margins of the spawning aggregation in Shelikof Strait (Bates and Clark 1983).

3.2.3 Small-scale Patterns. Pollock eggs apparently are spawned at depth, then move upward in the water column until their specific gravities balance that of the surrounding water. They stay at this depth until increased weight causes them to sink toward the bottom (S. Kim, unpubl. data).

3.2.4 Maximum and Mean Abundances. Egg abundance varies from year to year; it may be biased by sampling procedure and gear deployed. During the 1981 survey, maximum egg density was around 60,000 eggs/m^2 in Shelikof Strait (R. Bates, NWAFC, pers. comm.). On the Kodiak shelf during April-May in 1972, the maximum was 10,465 eggs/m^2 and the mean was 179 eggs/m^2 (Dunn and Nauplin 1974). Mean catch in several bays near Kodiak ranged from 0 to 0.089 eggs/m^3 between March and August and in November 1978 and in March 1979 (Rogers et al. 1979a).

3.2.5 Vertical Distribution. Based on a 1978 Kodiak survey, pollock eggs were distributed throughout the water column between 0-121 m (Kendall et al. 1980). However, results from vertical sampling in 1985 and 1986 showed that over 90% of the eggs occurred below 150 m. Eggs were severely clumped and formed strong patches in the bottom layer (S. Kim, unpubl. data).

3.3 Feeding

Not applicable.

3.4 Predation

3.4.1 Predator Species. It is believed that pollock, larvae of other fishes, amphipods and euphausiids consume pollock eggs. During the 1985 ichthyoplankton surveys conducted by NWAFC, the depth of maximum concentration of eggs was coincident with that of chaetognaths, and a few to 200 eggs were found in stomachs of adult pollock (A. Matarese, NWAFC, pers. comm.).

3.4.2 Effect of Predation. No data available.

3.5 Other Factors Affecting Eggs

3.5.1 Biotic. No data available.

3.5.2 Abiotic. Low temperatures probably prolong developmental stages of eggs and therefore would result in increased predation rates. Strickland and Sibley (1984) have explored the ability of larval and juvenile pollock to remain near their spawning grounds by examining the fine structure of currents in the vicinity of Kodiak Island and Shelikof Strait. Troughs provide increased shelf break length and have current patterns that tend to reduce advective removal and include intrusions of slope water that remain at 3-5°C all year. Therefore, the velocity of the Alaskan Stream is greatly reduced here, and at least one persistent countercurrent has been identified shoreward of the shelf break. Several intermittent and persistent eddies, produced in part by irregularities in coastline and bathymetry, have been observed, and subsurface cyclonic flow has been documented within troughs. Tidal currents also are greatly reduced northwest and southeast of Kodiak Island. Furthermore, the seasonal onset of the mean southwesterly wind pattern and coastal upwelling in the Shelikof region, coincident with the spring minimum in the Kenai Current, would tend to retard advective losses at that time, especially near the surface. These observations suggest that reductions in the strength of the Kenai Current and the strong upwelling conditions are favorable for survival of pollock eggs and larvae. Strickland and Sibley (1984) note the similarity between longitudinal distributions of pollock and coastal upwelling in the Gulf. Upwelling could have a negative effect by transporting eggs offshore, but this effect could be offset by a simultaneous reduction in southwestward transport of surface water.

3.5.3 Total Mortality. No data available.

3.6 Laboratory Holding and Rearing

In laboratory studies, Puget Sound pollock eggs required 9 and 18 days for hatching at 8°C and 5°C, respectively (Bailey and Stehr 1986).

4 LARVAE

4.1 General Description

Newly hatched pollock larvae of the Kodiak shelf showed no variation in mean length at various depths. Mean length was 4.1 mm for larvae taken between 0-66 m and 4.2 mm for those between 66-121 m (Kendall et al. 1980). They estimated larval lengths to be 2-8 mm (mean 4.3 mm) in spring and 5-37 mm (mean 19.1 mm) in summer. For larvae of the Kodiak nearshore area, Rogers et al. (1980b) reported mean sizes of 3.5 mm at hatching, 13 mm during April and May, 16-38 mm during summer, and over 38 mm during October. In contrast, survey results, based on a 1981 cruise in Shelikof Strait, showed that mean length of larvae was about 3 mm at hatching and 4 mm and 8 mm, respectively, during April and May (Dunn et al. 1984); maximum lengths were 4 mm during March 5 to 18, 5 mm during March 13 to April 8, 10 mm during April 16 to May 2 and 15 mm during May 20 to 28 (Bates and Clark 1983). Walline (1983) determined that the estimated hatching dates of pollock larvae south of the Alaska Peninsula in 1980 were later toward the west, varying from March 25 in the vicinity of Trinity Island to May 2 near Unimak Island.

4.2 Distribution and Abundance

4.2.1 Duration of Larval Stages. Larval growth was estimated from daily otolith measurements (A. Kendall, pers. comm.). During the 1983 spring season, mean growth rate was 0.21 mm per day. Transformation to juveniles probably occurs during mid-summer, because 0-age juveniles are found in August surveys.

4.2.2 Large-scale Patterns. In general, larvae were found from March to June throughout the western Gulf of Alaska (Dunn et al. 1984). Abundance was high in Shelikof Strait but low to the east of Kodiak Island and west of about 158°W. Abundance increased from March to April, peaked in April and declined thereafter. South of Kodiak Island, peak larval abundance occurred during late April and early May (Rogers et al. 1979a, b).

4.2.3 Small-scale Patterns. No data available.

4.2.4 Maximum and Mean Abundances. High abundance at Shelikof Strait ranged from 10,000 to 100,000 larvae/10 m^2 (Dunn et al. 1984). Over the Kodiak shelf during the spring of 1972, maximum densities were 12,118 larvae/10 m^2, with a mean abundance of 192 larvae/10 m^2 (Dunn and Nauplin 1974).

4.2.5 Vertical Distribution. Pollock larvae, like the eggs, are positively buoyant (S. Kim, unpubl. data). Highest numbers of larvae were found in the upper layers (0-66 m) off Kodiak Island (Kendall et al. 1980) and in Shelikof Strait (20-50 m) (A. Kendall et al., unpubl. data).

4.3 Feeding

4.3.1 Habitat. (See 4.2.5.)

4.3.2 Prey Species. No data available for the Gulf of Alaska. However, Georgia Strait pollock larvae (4-22 mm) eat copepods and their eggs (Barraclough 1967).

4.3.3 Prey Density Requirements. No data available.

4.3.4 Factors Affecting Availability of Prey. No data available. But it is believed that copepod nauplii represent the major food of pollock larvae.

4.3.5 Temporal Patterns of Energy Storage. No data available.

4.3.6 Evidence of Food Limitation. No data available.

4.4 Predation

4.4.1 Predator Species. Dolly Varden are documented predators (Blackburn et al. (1980), but most fishes, including pollock, may consume pollock larvae.

4.4.2 Effect on Larvae. No data available.

4.5 Other Factors Affecting Larvae

4.5.1 Biotic. No data available.

4.5.2 Abiotic. (See 3.5.2.)

4.5.3 Total Mortality. No data available.

4.6 Laboratory Holding and Rearing

Experiments on first feeding larvae were carried out by Paul (1983). He found a mean digestion rate of 5 h and a light threshold of 0.2-0.4 lux for capturing prey (copepod nauplii). Larvae reared and fed at 5.5°C were more successful at capturing prey than cohorts reared and fed at 3°C. The relationship between temperature and nauplii concentration during larval feeding is (arcsine % of larval feeding : P) = 0.48 + (4.38 * T) + (0.04 * NC), where T is temperature and NC is nauplii concentration. In laboratory studies, the yolk-sac period of pollock larvae lasted 5 days at 8-9°C, and after 5 weeks of feeding, larvae reached about 25 mm (Bailey and Stehr 1985).

5 JUVENILES

5.1 General Description

Juvenile pollock may occur in bays during October when the length is over 3.8 cm (Rogers et al. 1980a). Blackburn et al. (1980), however, found 4-cm pollock in July 1978 in Kachemak and Kamishak bays. Their data on length frequency by time of capture showed continuous growth: 0-age pollock increased from 4 cm in July to 12 cm in October and age-1 pollock from 12 cm in early June to 19 cm by late August.

The length distribution of juvenile pollock, based on 1980-82 data, showed two distinct modes, 0-age and age-1. Mean lengths in 1980, 1981 and 1982, respectively, were 9.2 cm, 9.9 cm and 8.5 cm for 0-age (about 6 months) and 19.2 cm, 23.9 cm and 20.0 cm for age-1 pollock (Smith et al. 1984). In general, Gulf of Alaska pollock juveniles were smallest in the southwest and length increased toward the northeast along the Alaska Peninsula (Walters et al. 1985).

5.2 Distribution and Abundance

5.2.1 Duration of Juvenile Stage. Smith et al. (1984) recognized three groups of juveniles: 0-group (5-15 cm), 1-year-olds (16-23 cm) and 2-year-olds (24-31 cm) in 1980 and 1982 survey data.

5.2.2 Large-scale Patterns. Recruitment of some age-1 juveniles to the fisheries occurred in the Chirikof region at the mouth of Shelikof Strait but not farther west in the Shumagin region (Janusz 1983). Several incidental catches were reported from Kodiak banks, inside waters of southeastern Alaska, Prince William Sound and Cook Inlet. Densities of 0-age pollock were highest southwest of the main spawning area (e.g., Wide Bay, Shelikof Strait), then declined in the bays to the southwest along the Alaska Peninsula, while the density of age-1 pollock declined from south to north. Especially high densities of 0-age and age-1 pollock were found at the southwestern tip of Kodiak Island, Alitak region (Smith et al. 1984). The 0-group showed less continuous spatial distribution, while the age-1 group showed relatively continuous distribution along the Alaska Peninsula (Walters et al. 1985).

There are large variations in distribution and abundance from year to year, e.g., estimates of 0-group pollock were 42.4 million, 256.6 million, and 30.7 million fish for the 1980, 1981 and 1982 year-classes, respectively (Smith et al. 1984).

5.2.3 Small-scale Patterns. No data available.

5.2.4 Maximum and Mean Abundances. On the basis of 1980-1982 surveys, highest overall densities of 0-age, age-1 and age-2 pollock were 0.1642 individuals/m^2 in 1980, 0.0492 individuals/m^2 in 1981 and 0.0055 individuals/m^2 in 1982, respectively (Smith et al. 1984).

5.2.5 Vertical Distribution. During the 1985 spawning season in Shelikof Strait, age-1 juvenile pollock separated from the main spawning group in midwater, usually in a single layer; in some places, three layers were noted (E. Nunnallee, NWAFC, pers. comm.). Juveniles apparently perform vertical diel migrations, while spawners do not. Smith et al. (1984) and Walters et al. (1985) showed that the highest densities were at depths of 20-140 m. Age-1 juveniles were found at greater depths than 0-group pollock during 1980 to 1981, but there was no difference in their vertical distribution in 1982.

5.3 Feeding

5.3.1 Habitat. No data available.

5.3.2 Prey Species. Composition of prey species is highly variable with season and size of pollock. In spring at Cook Inlet, the main food was Tanner crab megalops (66%) and gammarid amphipods (13%) (Blackburn et al. 1980). During May in Kodiak bays, juvenile pollock (about 15 cm long) fed most heavily on chaetognaths (69% in weight) and calanoid copepods (21%). By August, mysids (73%) and euphausiids (26%) had become the major food items. Pandalid shrimp, fishes, euphausiids, mysids and calanoid copepods predominated in the diet of 15-30 cm juveniles (Rogers et al. 1979b). In the northwestern Gulf of Alaska in fall 1980, the main food (by dry weight) of age-1 pollock from bays and nearshore waters was euphausiids (46.6%) and epibenthic animals, caridean shrimp (17.8%), fishes (14.8%) and mysids (12.8%) (Walters et al. 1985). The food items (by volume) of juvenile pollock (<25 cm) in southeastern Alaska embayments were determined by Clausen (1983); euphausiids were the dominant food in winter and spring (34% and 78%), mysids were dominant in summer and fall (36% and 22%), shrimp and fishes were important during fall and winter and copepods were important in summer (11%). For large juveniles and adults (25-35 cm), the feeding pattern was similar; shrimp became the dominant food item in summer and fall (19% and 21%), more polychaetes were included and copepods were excluded as food items. (See also 2.3.2.)

5.3.3 Prey Density Requirements. No data available.

5.3.4 Factors Affecting Availability of Prey. No data available.

5.3.5 Temporal Patterns of Energy Storage. No data available.

5.3.6 Evidence of Food Limitation. No data available.

5.4 Predation

5.4.1 Predator Species. Pacific cod are known to eat juvenile pollock 10-31 cm in length (Clausen 1980). Other predators are probably the same as those of adult pollock (see 2.4.1.).

5.4.2 Effect on Juveniles. No data available.

5.5 Other Factors Affecting Juveniles

5.5.1 Biotic. Some age-2 juveniles (0.7%) have pseudobranchial tumors (McCain et al. 1980). The growth rate of pollock with tumors was apparently depressed in that they were 15% shorter than normal (McCain et al. 1979).

5.5.2 Abiotic. No data available.

5.5.3 Total Mortality. No data available.

5.6 Laboratory Holding and Rearing.

No data available.

6 CURRENT HYPOTHESES ON FACTORS AFFECTING YEAR-CLASS ABUNDANCE

Year-class strength and annual recruitment variability probably cannot be explained by a single cause and effect relation. Biological factors such as prey-predator relationships and growth and mortality rates are closely related to abiotic factors. The pollock spawning period is nearly fixed every year, while peak phytoplankton production and, in turn, zooplankton production (the major food item for pollock larvae) vary from year to year depending on sea surface temperature and water column stability. Therefore, if the time of egg hatching and peak copepod nauplii production were not matched, pollock larvae might grow slowly and undergo more serious predation by larger zooplankton. This so-called match-mismatch hypothesis (Cushing 1975) might be applied to explain interannual variation of pollock recruitment. On the other hand, if the water temperature is very cold, eggs and larvae need a longer time to develop and are vulnerable to predation for a longer period. Low temperatures during spawning would be detrimental to forming a successful year class. Aside from these two problems, density independent factors such as transport from the spawning area are also important. From an ecological point of view, the spawning location is well adapted to average oceanic transport processes. Early stages should drift to nursery areas or should be restrained near the spawning area if spawning occurred at a good nursery site. It is evident that eggs and larvae advected offshore have low survival rates. Sometimes this can be avoided by vertical positioning of larvae in the water column whether it is active vertical migration or passive movement through adjustment of specific gravity, since Shelikof Strait shows typical estuarine characteristics in flow pattern. Strickland and Sibley (1984) hypothesized that pollock year-class success depends on the combination of several climatic stimuli such as seawater temperature, water stability, precipitation and wind, as well as biological responses to them.

A holistic ecosystem simulation approach was introduced by Laevastu and Larkins (1981). This large-scale simulation is based not only on ecosystem simulation but also on a variety of larger scale meteorological and oceanographic models.

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MARKET SQUID, *Loligo opalescens*, IN THE NORTHEASTERN PACIFIC

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1 BACKGROUND

1.1 Literature Search

This report is based on journal or symposium papers on the market squid, *Loligo opalescens*, from the northeastern Pacific. Particularly helpful were California Fish and Game bulletins, such as Fields' (1965) account of all that was known of the biology of *L. opalescens* at the time and Bulletin 169 (1978), containing papers on oceanographic and acoustic, as well as biological aspects of the market squid.

1.2 Unit Stocks and Their Relationships

Loligo opalescens occurs along the west coast of North America from central Baja California to southeastern Alaska (Street 1982; Jefferts 1983). At the present time, it is not known whether these stocks are related or discrete. However, morphometric, electrophoretic and genetic research, e.g., Ally and Keck (1978), is being conducted in the hopes of identifying the unit stocks and their relationship to one another.

1.3 The Fishery

1.3.1 Relative Size and Importance. Commercial landings have been reported only in California. Between 1970 and 1980 the annual commercial catch of *L. opalescens* averaged 9.072 mt from Monterey Bay and southern California, the main fishing grounds. The squid fishery, which serves the local fresh and bait markets, traditionally was ethnic. Recently, small experimental fisheries have sprung up along the Oregon coast, in Puget Sound, and along the southeastern Alaska coast (R. Starr, pers. comm.). However, it is hypothesized that the Pacific Northwest resource, especially in Puget Sound and off the Washington coast, may be larger than such ventures have indicated (R. Mercer, pers. comm.).

1.3.2 Age at Recruitment. For the most part, *L. opalescens* recruit to the fishery when they are sexually mature and ready to spawn, which occurs between ages 1 and 2. Animals from winter spawning reproduce in the second summer, while those from summer spawning reproduce in the second winter and are larger than winter spawners (Jefferts 1983).

1.3.3 Characteristics of Harvested Fish. *L. opalescens* is a relatively small squid; adult spawning individuals range from about 100 to 200 mm dorsal mantle length (DML). Mature males are somewhat longer (110 to 190 mm) than mature females (100 to 180 mm) and their weight exceeds that of a female of the same length.

1.3.4 Types and Selectivity of Gear. Depending on location, tradition, law and desired condition of the squid, several types of gear are used to harvest *L. opalescens*. The gear includes gill and lampara nets and brails; purse and beach seines, midwater and shrimp trawls and jigs (Kato and Hardwick 1975). Except on the traditional fishing grounds in Monterey Bay, lights are used with several gear types to draw the squid to the surface. Jigging and brailing provide a superior product; they also are most selective, yielding a greatly reduced incidental catch. Seining and lampara net catches can have their by-catch reduced by brailing out incidental species before the catch is brought on deck. Trawling is basically nonselective (Kato and Hardwick 1975; Dewees and Price 1982).

1.3.5 Distribution of Fishing Effort. Traditionally, commercial fishing effort for *L. opalescens* has been centered around Monterey Bay and in southern California around the Channel Islands. Subsequently, other fishing sites, e.g., around Catalina Island, in southern California, have been productive. Monterey squid catches tend to reflect abundance, while southern California catches are more indicative of market price and cannery interest than availability (R. Spratt, pers. comm.)

Total squid landings from Monterey and southern California reported by the California Department of Fish and Game for 1945-1980 ranged from about 1,000 to 20,000 mt. Landings for 1981-1984 were 23,326, 16,281, 1,358 and 195 mt, respectively. In Oregon and Puget Sound, *L. opalescens* landings of 136.4 mt and 39.5 mt, respectively, were reported in 1983. Due to the experimental nature of the Oregon and Washington fisheries, these data do not necessarily reflect the abundance of squid.

1.4 Distribution and Abundance of the Population

From acoustic and video surveys of a surface area of 298 km^2 near Catalina Island, the total number of squid was estimated to be 122,907,865, weighing approximately 3,033 mt (Cailliet and Vaughn 1983). *L. opalescens* is known to migrate inshore to spawn but little is known about the geographic or depth distribution during nonreproductive seasons. Juveniles and immature squid are collected at times in otter and midwater trawls, purse seines and in the stomachs of predatory nekton (Fields 1965; Cailliet et al. 1979).

1.5 Current Status of Stocks and of Management Measures

Loligo opalescens is generally thought to be an underutilized resource along the extent of its range. However, in concentrated fishing areas, such as Monterey Bay, both the abundance and size of the squid have been decreasing. It is not known whether these significantly reduced catches are due to overfishing or to natural changes in abundance. In the mid 1900s, Monterey fishermen succeeded in banning the use of lights on the traditional fishing grounds in an attempt to discourage land-based processors from attracting the squid to the docks (R. Spratt, pers. comm.). In 1984, the Oregon Department of Fish and Wildlife established a 9 mt per boat, per day, trip limit for *L. opalescens.* This action was largely in response to the local processors' concern over their ability to handle unpredictable fluctuations in squid landings and still produce a top quality product (R. Starr, pers. comm.).

1.6 Recruitment Variability

Stock-recruitment relationships and recruitment variability are not known.

1.7 Age Determination and Validation

Based on statolith readings, adult *L. opalescens* vary between 9 months and 2 years (Spratt 1978). Laboratory studies demonstrated that this species could spawn successfully between 8 and 9 months after hatching (Yang 1981).

1.8 Age Composition of the Population

No data are available.

2 SPAWNING ADULTS

2.1 General Description

2.1.1 Size and Age Ranges. Females are considered to be sexually mature when eggs are present in the oviduct and males are mature when spermatophores are present in the spermatophoric sac. The size at maturity is variable for both sexes. The smallest mature male and female *L. opalescens* reported by Fields (1965) had a dorsal mantle length (DML) of 72 mm and 81 mm, respectively. Generally, DML of mature males ranges from 110 mm to 190 mm and of females from 100 mm to 180 mm (Fields 1965). Weight of *L. opalescens* under 120 mm is about the same for both sexes, whereas weight of larger males exceeds that of females of the same length. In the commercial catch, average weights for males and females of average DML of 150 mm and 140 mm were 70 g and 50 g, respectively (Fields 1965).

Fields (1965) used population data that indicated both sexes reached a mean DML of 65 mm at 12 months and 120 mm at 24 months. At 36 months, males measured 165 mm and females 150 mm. Spratt (1978) combined age (statolith ring counts) with DML data to calculate the mean, range and standard deviation value for 3-month intervals throughout the life cycle. The average mean for each 3-month interval from 3 to 21 months was approximately 25, 60, 70, 88, 120, 138 and 137 mm.

2.1.2 Type of Spawning Behavior. After a single annual spawning event, both male and female *L. opalescens* die. There are two peak spawning seasons (see 2.2.1), although eggs have been observed year-round (Fields 1965; Recksieck and Frey 1978; Jefferts 1983). *L. opalescens* is a demersal spawner. The females anchor egg capsules, by means of a thin stalk, to previously laid egg capsules or to the substrate. The preferred substrate is generally mud, sand or gravel. Large clusters of egg capsules may be formed; some are up to 12 m in diameter and 1.3 m in height (McGowan 1954; Field 1965).

2.1.3 Fecundity. An egg capsule may contain up to 300 eggs and a female may extrude up to 20-30 capsules during a spawning event (Fields 1965; Hurley 1977; Jefferts 1983).

2.2 Distribution and Abundance

2.2.1 Duration of Spawning. *L. opalescens* spawn throughout the year, but the population exhibits biannual spawning peaks. Such events generally are progressive and occur early in the year in the southernmost parts of the range (Bernard 1980). In southern California, the main spawning peak occurs from December through February and in Monterey Bay from February through April. Peak spawning in Oregon is in spring and early summer and in the Straits of Juan de Fuca in mid- to late summer. Spawning activity peaks in Puget Sound from December through February and in southeastern Alaska from March through May (Bernard 1980; Street 1982; Jefferts 1983). As the spawning schedule is variable, peak activity may occur earlier or later than indicated.

Successful rearing experiments have made it possible to supplement information gained from field data. Yang et al. (1980, 1983a) reared *L. opalescens* to the subadult. Subsequently, Yang et al. (1983b, 1986) twice reared them to viable second generations in closed seawater systems. In both experiments, growth was fast initially, increased exponentially in the first 2 months, then slowed to a logarithmic rate (8.35% and 5.6-1.6%, respectively). Growth rings on statoliths corresponded to one per day for the first 65 days. In the two experiments, maximum size was 116 mm DML and weight 63 g and life span was 248 days; maturation occurred at about the same time for both sexes (day 92 and day 100) and spawning occurred between day 175 and day 222 and day 196 and day 239, respectively.

2.2.2 Large-scale Patterns. Spawning aggregations of *L. opalescens* occur throughout its range. Sexually mature *L. opalescens* migrate seasonally to shallow inshore spawning grounds to mate and lay their eggs (McGowan 1954; Fields 1965; Kato and Hardwick 1975). Spawning grounds are located in sheltered bays or coves, often near submarine canyons. Egg capsules have been observed in depths ranging from 3 to 180 m (McGowan 1954; Fields 1965). Major spawning grounds are Monterey Bay, waters around Santa Rosa, Santa Cruz and Santa Catalina islands and several coastal localities in southern California (Recksieck and Frey 1978).

2.2.3 Small-scale Patterns. *L. opalescens* forms dense schools nearshore to mate and to spawn.

2.2.4 Maximum and Mean Abundances. Using underwater video equipment with and without night lights, Vaughn and Recksieck (1978) estimated a school to be 99.6 squid/m^3 and 7.3 squid/m^3, respectively. Population abundances are unknown.

2.2.5 Vertical Distribution. Spawning *L. opalescens* adults are found in depths of 5 to 40 m, as demonstrated by the presence of eggs (Bernard 1980). Occasionally eggs are found in depths up to 200 m (Spratt, pers. comm.).

2.3 Feeding

2.3.1 Habitat. *L. opalescens* tend to feed primarily in the water column but benthic organisms, particularly on the spawning grounds, also play a part in their diet (Kaspor and Cailliet 1978).

2.3.2 Prey Species. *L. opalescens* feeds mainly on crustaceans, the most important being euphausiids, mysids and megalops larvae (Fields 1965). Juvenile gastropods, nereid polychaetes, fish and dead or dying squid play a lesser role. Egg-like spheres and sand particles also have been found in stomach contents of *L. opalescens*. In a field study, stomach content analysis revealed that males tended to ingest cephalopod parts more frequently and to eat more megalops per meal than did females (Karpov and Cailliet 1978).

2.3.3 Prey Density Requirements. Not applicable.

2.3.4 Factors Affecting Availability of Prey. Factors affecting the abundance and availability of food organisms are largely water quality related. Since *L. opalescens* spawn mostly in sheltered bays, local industrial discharges could alter the local community structures. Other factors include competition with crustacea-eating fishes, productivity, temperature and circulation of the water body.

2.3.5 Temporal Patterns of Energy Storage. *L. opalescens* is a voracious predator until the time of spawning, when both sexes, especially the female, tend to eat less (Karpov and Cailliet 1978).

2.3.6 Evidence of Food Limitation. No available data.

2.4 Predation

2.4.1 Predator Species. A study was carried out in Monterey Bay by Morejohn et al. (1978) to determine the extent of predation by marine fishes, seabirds and marine mammals on *L. opalescens*. The stomach contents of most fish and of some of the seabirds and mammals were evaluated by an index of relative importance (IRI) developed by Pinkas et al. (1977). The IRI was calculated by summing the numerical and volumetric percentages of prey and multiplying by the frequency of occurrence expressed as a percentage.

Of the nearly 2,000 marine fish examined, 19 species had consumed *L. opalescens*, and it ranked first (IRI = 3,745) in the diet of the curlfin turbot, *Pleuronichthys decurrens*. *L. opalescens* had a DML of mainly 2 or 3 mm; less than 5% were between 100 mm and 110 mm. *L. opalescens* ranked second in the diet of four marine fish: lingcod, *Ophiodon elongatus* (IRI = 3,188); speckled sanddab, *Citharichthys stigmaeus* (IRI = 2,000); Pacific sanddab, *C. sordidus* (IRI = 866); silver salmon, *Oncorhynchus kisutch* (IRI = 581). DML range of *L. opalescens* in silver salmon was between 30 and 130 mm but was not determined for the other three fishes.

The thirteen species of birds examined all consumed *L. opalescens*, and it ranked first in the diet of four birds: the rhinoceros auklet, *Cerorhinca monocerata* (IRI = 12,810); black-legged kittiwake, *Rissa tridactyla* (IRI = 6,149); California gull, *Larus californicus* (IRI = 2,192); sooty shearwater, *Puffinus griseus* (IRI = 1,480); short-tailed shearwater, *P. tenuirostris* (IRI = 1,360). DML range of *L. opalescens* in the first two and last two seabirds was 10-110 mm, 50-120 mm, 30-180 mm and 40-150 mm, respectively.

Of the marine mammals in Monterey Bay, Morejohn et al. (1978) were able to collect samples from only nine species. *L. opalescens* was first in the diet of the Alaskan fur seal, *Callorhinus ursinus* (IRI = 11,400). The marine mammals with the highest biomass that feed heavily on this squid are the California sea lion, *Zalophus californicus*; the harbor porpoise, *Phocoena phocoena*; and Dall's porpoise, *P. dalli*. DML range of *L. opalescens* from the sea lion and the two porpoises was 95-175 mm, 56-135 mm and 47-174 mm, respectively. Morejohn et al. (1978) point out that the market squid, anchovy and rockfish are the important prey items for most marine mammals and that the dependence of marine fish, seabirds and marine mammals on market squid, anchovy, rockfish and euphausiids cannot be overemphasized.

2.4.2 Effect on Spawning Adults. If *L. opalescens* is preyed upon after it has mated and spawned, predation is of no consequence to year-class recruitment. However, if predation is heavy prior to such activities, the effect could be severe. Because so little is known about the relationship of stocks to one another, the magnitude of the effects of predation and fishing are unknown.

2.5 Other Factors Affecting Adults

2.5.1 Biotic. Two types of parasites have been reported to infest *L. opalescens*. They were found in the eye, stomach, digestive caeca, mantle cavity and the mesenteries. An infection rate of 77% was found in one study, but no mention was made of the effect or impact (Jefferts 1983). Fields (1965) noted that occasionally pleurocercoid larvae of tetraphyllidean cestodes are found in the caecum or elsewhere.

2.5.2 Abiotic. The temperature of the water appears to have a significant effect on the timing and duration of spawning. The presence of squid in high concentrations on the spawning grounds seems to be tied to the warming of the water that follows by several months the cessation of upwelling. It is thought that a warming trend may trigger spawning by stimulating the optic gland that regulates the maturation of male squid gonads and sperm production. The optic gland also may be affected by day length (McInnis and Broenkow 1978; Hardwick and Spratt 1979).

2.5.3 Total Mortality. There are no data on adult mortality prior to spawning. Once on the spawning ground the squid are preyed upon by birds, fish, marine mammals and man. Squid mortality is 100% after spawning (Fields 1965; Recksieck and Frey 1978; Jefferts 1983).

2.6 Laboratory Holding and Rearing

In two laboratory studies, sexually mature *L. opalescens* that were raised from the egg were successfully mated and subsequently laid viable eggs; the maximum life span was 248 days and they reached a DML of 115 mm. Mortality was caused by fin or skin damage and by spawning activities (Yang et al. 1983b, 1986).

3 EGGS

3.1 General Description

Eggs of *L. opalescens* are in capsules and range from 2 to 2.5 mm in length and from 1.3 to 1.6 mm in width (Fields 1965; Jefferts 1983). The egg capsules contain from 180 to 300 eggs and are approximately 1.2 cm in diameter, ranging in length from 5 to 20 cm (Fields 1965). They are attached by filaments to the substrate or to egg capsules previously attached to the bottom (Bernard 1980).

3.2 Distribution and Abundance

3.2.1 Duration of Egg Stage. The rate of embryonic development is dependent on water temperature. The approximate number of days for eggs to hatch at various temperatures was 90 at 8°C, 60 at 10°C, 30 at 13.6°C and 15-23 days at 16°C (McGowan 1954; Fields 1965; Bernard 1980; Jefferts 1983). In laboratory experiments, eggs developed in 30 days at 15°C (Yange et al. 1983b).

3.2.2 Large-Scale Patterns. Spawning occurs in sheltered bays and inlets. Egg capsules, arranged on the bottom in dense clumps or thin layers, are generally found in depths ranging from 15 to 40 m but have been collected in depths of 200 m (McGowan 1954; Spratt, pers. comm.). Egg capsules are present throughout the year; however, peak abundances follow peak spawning times.

3.2.3 Small-scale Patterns. The distribution of eggs is dependent upon suitable conditions for spawning and for the incubation of eggs. The body of water needs to be somewhat protected and well oxygenated, with a sand or mud substrate (Fields 1965).

3.2.4 Maximum and Mean Abundances. Diver surveys conducted off La Jolla, California, in 1954 found that, of the 1,600 km^2 surveyed, 50% of the bottom was covered by *L. opalescens* egg cases. Three sampling quadrants of 100 m^2 each were selected to determine the number of eggs spawned in this area. Each quadrant contained about 10,400 egg cases per m^2 and the total number of eggs thought to be present was 8.32×10^9. Later surveys, considering a mean number of 212 eggs per case, suggest that 1.7×10^{12} eggs were spawned at La Jolla in 1954 (Okutani and McGowan 1969).

3.2.5 Vertical Distribution. Under normal conditions, egg capsules remain attached to the bottom or to each other throughout incubation. However, if an egg capsule breaks loose and is still intact, it is possible that the eggs will hatch (Jefferts 1983).

3.3 Feeding

Not applicable.

3.4 Predation

3.4.1 Predator Species. Predation apparently is infrequent while eggs are in the egg capsules (McGowan 1954; Fields 1965). Predators include various species of starfish, a *Lytechinus* urchin and possibly a worm, *Capitella ovincola*, which is found in the egg capsules. According to Fields (1965), *Capitella ovincola* appears to inhabit the intermediate jelly coating without interfering with successful development and hatching.

3.4.2 Effect on Eggs. As the abundance, selectivity or rates of predation are unknown, the effect of predation on the survival of eggs has not been determined.

3.5 Other Factors Affecting Eggs

3.5.1 Biotic. No data available.

3.5.2 Abiotic. No data available.

3.5.3 Total Mortality. Field and laboratory studies indicate that egg mortality during any stage is very low (McGowan 1954; Yang et al. 1980). Egg cases in the middle of dense clusters may get too little oxygen, resulting in the death of some of the eggs (Yang, pers. comm.).

3.6 Laboratory Holding and Rearing

Eggs are easily maintained in a laboratory if well oxygenated, temperature-controlled seawater is available. For a detailed discussion on technique see Hurley (1976), Hanlon et al. (1979) and Yang et al. (1980, 1983a, b, 1986).

4 LARVAE

4.1 General Description

L. opalescens does not have a true larval stage; eggs hatch as miniature adults with disproportionate small fins, which are called hatchlings (Fields 1965; Yang et al. 1983a). The mean hatching size is 2.7 mm mantle length (Hurley 1976; Yang et al. 1983b, 1986). Shortly after hatching, the mantle is firm, cylindrical and 1.5 to 2 times as long as wide (Okutani and McGowan 1969). Hatchlings can live up to several days on the yolk sac. In two laboratory experiments, after the yolk sac was absorbed, instantaneous growth rates averaged 1.69% per day (Yang et al. 1983a) or 1.75% per day (Yang et al. 1983b), and there was a wide disparity in length among squids of the same age. No weight measurements are available.

4.2 Distribution and Abundance

4.2.1 Duration of Larval Stages. As squids do not go through metamorphic changes as do other mollusks, stages from hatchlings to juveniles are not delineated. However, there do seem to be subtle physiological and behavioral changes at about 15 mm DML, or at approximately 50 days of age. Squid less than 15 mm DML are not able to maintain a stationary position against a current and generally do not school (Yang et al. 1980). A change in swimming posture during the positioning phase of attack also occurs with squid larger than 15 mm DML (Yang et al. 1983a, b).

4.2.2 Large-scale Patterns. Large-scale patterns for *L. opalescens* are poorly understood. Fields (1965) theorized that young squid, upon hatching, swim toward light, thus reaching the surface where they become dispersed by currents. Few hatchlings have been found in surface, mid- or bottom water near the spawning grounds (McGowan 1954; Okutani and McGowan 1969) . However, more recent work has shown that the largest number of hatchlings were collected by towing a small plankton net, mounted on a sled, over the bottom near a major spawning ground. This finding has led researchers to suggest that *L. opalescens* hatchlings may be quickly dispersed to deeper water offshore by bottom currents (Recksieck and Kashiwada 1979). *L. opalescens* hatchlings are present year-round but their peak abundances follow peak spawning events by several weeks. The exact timing is dependent on the temperature of the water.

4.2.3 Small-scale Patterns. No data available.

4.2.4 Maximum and Mean Abundances. A study, conducted by the CALCOFI program off La Jolla, California, in January 1955, found abundance of *L. opalescens* hatchlings to be approximately 4 to 6 per km^3. It was estimated that these squid were not more than a month old (Okutani and McGowan 1969).

4.2.5 Vertical Distribution. (See 4.2.1.)

4.3 Feeding

4.3.1 Habitat. Being weak swimmers, hatchlings feed on organisms that drift by them on the surface or mid-level in the water column (Yang et al. 1983a, b).

4.3.2 Prey Species. Squid hatchlings feed on small planktonic crustaceans: crab larvae, copepods (*Acartia tonsa* and *Labidocera* sp.), penaeid shrimp myses, post larvae (*Penaeus duorarum*) and, in the laboratory, brine shrimp (*Artemia* sp.). Also in the laboratory, the surface living copepods, *Anomalocera ornata*, the bottom living mysids, *Mysidopsis almyna*, and fishes were consumed when they swam into the immediate vicinity of the hatchlings (Yang et al. 1983a, b).

4.3.3 Prey Density Requirements. No data for prey density requirements for hatchlings in the wild are available. For rearing in the laboratory, Hurley (1976) calculated that a 1-day-old hatchling would require 23 *Artemia* sp. nauplii or two anchovy (*Engraulis mordax*) larvae per day to meet normal metabolic needs. A 7-10 mm, approximately 2-month-old, hatchling would require 225 nauplii or 20 anchovy larvae per day. Actual food consumption observed in the laboratory for a day-old hatchling was 150 nauplii or 14 anchovy larvae and, for a 60-day-old hatchling, 1500 nauplii or 135 anchovy larvae (Hurley 1976).

4.3.4 Factors Affecting Availability of Prey. All significant biotic and abiotic changes in the water body concerned could have an effect on the abundance and availability of prey species.

4.3.5 Temporal Patterns of Energy Storage. Not applicable.

4.3.6 Evidence of Food Limitation. No data available.

4.4 Predation

4.4.1 Predator Species. According to Fields (1965), principal predators of *L. opalescens* hatchlings are ctenophores, arrow worms and siphonophores. Hatchlings also probably are heavily preyed upon by fishes, birds and marine mammals (see 2.4.1). Morejohn et al. (1978) found that the curlfin turbot, *Pleuronichthys decurrens*, fed extensively on post-hatch *L. opalescens* (2-3 mm DML) on the spawning grounds. Some had consumed in excess of 600 post-hatch squid.

4.4.2 Effect on Larvae. No data available.

4.5 Other Factors Affecting Larvae

4.5.1 Biotic. No data available.

4.5.2 Abiotic. No data available.

4.5.3 Total Mortality. Laboratory studies have suggested that mortality may be high after the yolk has been exhausted and the young squid must forage. This transitional stage led to approximately 85% mortality in the first 30 days post hatching in one study (Hurley 1976) but only 42% mortality over the first 20 days in other laboratory studies (Yang et al. 1980).

4.6 Laboratory Holding and Rearing

In Hurley's (1976) experiments, *L. opalescens* attained 13 mm DML and Hanlon et al. (1979) were able to keep hatchlings alive until they reached 17 mm DML (approximately 80 days old), but Yang et al. (1980, 1983a) reared them to subadults and Yang et al. (1983b, 1986) from the egg to the second generation. All of these researchers agree that starvation, resulting from an inability to supply the right type or amount of food, was the primary cause of death in the hatchling stage. Fields (1965), however, found that death in the first 10 days after hatching was due mainly to fungal infections, resulting from injuries caused by the hatchling hitting the side of the aquarium.

5 JUVENILES

5.1 General Description

Laboratory studies have shown that at 15 mm DML *L. opalescens* become more powerful and maneuverable swimmers, begin to school, accept different types of prey and are found deeper in the water column than smaller squid. At this stage they are approximately 7-80 days old (Yang et al. 1983a, b, 1986).

5.2 Distribution and Abundance

5.2.1 Duration of Juveinle Stage. As previously stated, the "juvenile stage" begins at around 15mm DML or 70-80 days of age and continues until sexual maturity. Size at sexual maturity averages about 100mm DML at an age of approximately 1 year (Fields 1965; Spratt 1978). In laboratory experiments (Yang et al. 1983b, 1986) maturation occurred slightly earlier in the third experiment (Yang et al. 1986): males on day 93 at 29 mm ML and 1.15 g wet weight and females on day 92 at 33 mm ML and 1.71 g wet weight.

5.2.2 Large-scale Patterns. Juvenile *L. opalescens* are believed to generally occur in the pelagic environment offshore. However, trawl samples have indicated that some young squid (<40 mm) remain in or return to sheltered bays near the spawning grounds (Fields 1965). According to Bernard (1980), spawning schools may include a high proportion of immature individuals. However, juvenile *L. opalescens* only occasionally are collected in bottom and mid-water trawls, and their occurrences are so few and sporadic that their distributional patterns, migrations or interannual variability cannot be assessed (see 1.4.).

5.2.3 Small-scale Patterns. Laboratory studies of captured squid indicate that juvenile *L. opalescens* (1) are obligate schoolers, (2) exhibit parallel orientation of individuals and strong cohesiveness and (3) maintain school structure primarily by visual cues (Hurley 1978). Field observations show that juveniles are usually found in schools made up of animals of about the same size (Fields 1965; Hurley 1978). On average, the maximum difference in size of individuals within a school was about 25 mm DML (Hurley 1978). She also suggested that the main function of schooling behavior may be defense against predation. When feeding undisturbed in the laboratory, no obvious schooling behavior existed, but when the plexiglass aquaria were tapped the squid immediately grouped together (Hurley 1978). There are no data regarding patchiness during this stage.

5.2.4 Maximum and Mean Abundances. No data available.

5.2.5 Vertical Distribution. Juvenile squid are visual predators and usually are in the water column during daylight hours (Karpov and Cailliet 1978). At dusk, squid migrate upwards, probably following the surface migration of plankton (Bernard 1980).

5.3 Feeding

5.3.1 Habitat. Juvenile *L. opalescens* are both demersal and pelagic feeders (Fields 1965; Loukashkin 1977; Karpov and Cailliet 1978). Feeding occurs mostly during daylight hours in 20-50 m of water (Bernard 1980).

5.3.2 Prey Species. *L. opalescens* is a carnivore that feeds heavily on crustaceans, fish, polychaetes and cephalopods, including *L. opalescens* (Fields 1965; Loukashkin 1977). According to Karpov and Cailliet (1979), juvenile *L. opalescens* primarily consume euphausiids, *Euphausia pacifica* and *Thyanoessa spinifera*. Noncrustaceans also play a small role in their diet. Whole cephalopods were identified as *Gonatus* sp. and *L. opalescens*. Gastropods, cumaceans, megalops larvae, the anchovy, *Engraulis mordax*, and bottom debris were also ingested (Karpov and Cailliet 1979). In the laboratory, juveniles were fed on benthic palaemonid shrimps, mysids and killifishes, *Fundulus similis*. They were especially attracted to silversides, *Menidia beryllina*, probably because they swam in the middle of the water column. When feeding on fishes or shrimps, the squids ate only the flesh, discarded the fish heads and bones or, in the case of crustaceans, the entire exoskeleton. In the laboratory environment, competition, intraspecific aggressiveness and cannibalism were rarely observed (Yang et al. 1983a, b).

Yang et al. (1983a, b) found that in aquaria young squid can prey upon organisms ranging from 300 µm to 3 times their mantle length. This is accomplished by grasping the prey with their arms and tentacles, then using their beak, located in the buccal mass, to tear off small chunks of flesh. Large juvenile and adult squid consume an average of 14.4% dry body weight per day and digest prey at a rate of 0.29% of squids dry body weight per hour (Karpov and Cailliet 1978).

5.3.3 Prey Density Requirements. No data available.

5.3.4 Factors Affecting Availability of Prey. A study conducted on pelagic assemblages in Monterey Bay showed that *L. opalescens* and the Pacific hake, *M. productus*, were associated in both shallow and deep mid-water trawls during the summer. Both species feed primarily on the vertically migrating euphausiids, *T. spinifera* and *P. pacifica* (Morejohn et al. 1978; Cailliet and Karpov 1979). Although *L. opalescens* are day feeders and *M. productus* night feeders, they do utilize the same resource. Less frequent euphausiid predators, occurring with *L. opalescens* either seasonally or at varying depths in the water column, are: *Porichthys notatus*, *Clupea harengus pallasi*, juvenile rockfish (*Sebastes* spp.), *Perilus simillimus*, *Citharichthys stigmaeus* and *C. dordidus*. The significance of these species as competitors to *L. opalescens* is not known (Morejohn et al. 1978).

5.3.5 Temporal Patterns of Energy Storage. No data available.

5.3.6 Evidence of Food Limitation. No data available.

5.4 Predation

5.4.1 Predator Species. A wide variety of marine mammals, fish and sea birds feed on juvenile *L. opalescens* of all sizes (see 2.4.1).

5.4.2 Effect on Juveniles. No data available.

5.5 Other Factors Affecting Juveniles

5.5.1 Biotic. No data available.

5.5.2 Abiotic. Timing and intensity of upwelling and current regimes may have a significant impact on the abundances and availability of prey for *L. opalescens* juveniles. These factors also may be important in determining the squids' exposure to predators and their ability to be transported to more favorable environments.

5.5.3 Total Mortality. No data available.

5.6 Laboratory Holding and Rearing

Yang et al. (1983b, 1986) have successfully raised *L. opalescens* through the juvenile stage to sexual maturity and viable second generation progeny (see 2.6).

6 CURRENT HYPOTHESES ON FACTORS AFFECTING YEAR-CLASS ABUNDANCE

California market squid landings have fluctuated widely over the past 64 years, ranging from 195 to 23,326 mt; 1983 and 1984 (El Niño years) yielded unusually low squid catches in the Monterey Bay and southern California fisheries according to California Department of Fish and Game data. Catches have been high in Oregon and Washington in the past few years (see 1.3.1), but historical statistics of incidental squid catches suggest fluctuating abundances (T. Bettinger, pers. comm.). In attempting to explain fluctuations in abundance in California, McInnis and Broenkow (1978) looked at year-to-year variations in water temperature in Monterey Bay. They found that good squid catches tended to follow warm temperature anomalies by 18 months, while poor landings followed periods of anomalously low temperatures. This led them to suggest that temperature may affect the survival and growth of juvenile *L. opalescens* by influencing food availability. The warming trend associated with El Niño was followed by greatly reduced abundances, possibly due to delay in upwelling resulting in food for *L. opalescens* hatchlings being unavailable. It also has been suggested that low abundances resulted from the squid migrating north to more favorable water conditions. However, this theory seems unlikely because the squids' jet-propelled swimming has a low metabolic efficiency. Using a tunnel respirometer, O'Dor (1982) discovered that large scale migrations by *L. opalescens* would impose high metabolic costs (around 12.5 j/kg/m). He estimated this amount to be nearly five times that of a salmon of a similar size. *L. opalescens* has a sustainable speed (0.36 m/s) that is only about half that of a salmon (O'Dor 1982).

Another major source of speculation regarding population dynamics is whether this species is represented by one or more stocks. On the basis of the occurrence of two distinct spawning seasons throughout its range, Fields (1965) postulated that there might be two distinct populations. In further attempts to distinguish stocks, Kashiwada et al. (1979) did extensive beak measurements, Ally and Keck (1978) and Christofferson et al. (1978) ran various biochemical and electrophoretic tests and Evans (1976) and Kashiwada and Recksieck (1978) developed morphological indices. Bernard (1980) postulated that size differences within spawning schools appear to be a function of age in a genetically homogeneous population rather than a result of two distinct populations. Basically, all the researchers concluded that more work needed to be done. At present, both the Washington Department of Fish and Game and the Oregon Department of Fish and Wildlife are undertaking similar studies. Along with fluctuations in abundances, there also appear to be fluctuations in the size of squid landed over time. Fields (1965) noted that the mean mantle length of spring and summer males decreased from 160 mm ML in 1948 to 130 mm ML in 1952. In the same period, females deceased from 152 mm ML to 140 mm ML. They remained at the reduced size until 1962, then increased to the 1948 size. He concluded that predator-prey relationships might have been responsible rather than overfishing. The reduction in squid size coincided with the near disappearance of the California sardine. This might imply that either there was a reduction in a food resource common to both the squid and sardine or that the sardine may have been a major prey item. Recent catches of squid in California, Oregon and Washington have all yielded "smaller than normal" animals, but no explanation is immediately obvious.

Many questions remain regarding this species' life cycle, seasonal distributions, life span, abundances, migrations and stock structure. We know, however, that *L. opalescens* does play a major role in the flow of energy and recycling of nutrients in the pelagic nearshore environment and is a major intermediate link in the food web of the California Current ecosystem.

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PACIFIC HALIBUT, *Hippoglossus stenolepis*, IN THE GULF OF ALASKA

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1 BACKGROUND

1.1 Literature Search

This report is based mainly on scientific and technical reports (and references therein) of the International Pacific Halibut Commission (IPHC). The IPHC, originally the International Fisheries Commission, was established between Canada and the United States in 1923 as the first international convention for the joint management of a marine fishery, the Pacific halibut (*Hippoglossus stenolepis*). The data base is the most extensive of any North American fishery. A large amount of "grey literature" on the biological and oceanographic environment of the Gulf of Alaska, including NOAA's Outer Continental Shelf Environmental Assessment Program (OCSEAP) reports, NOAA's National Marine Fisheries Service (NMFS) "processed reports" and Pacific Marine Environmental Laboratory (PMEL) "technical memoranda," is included as information not otherwise available. I am indebted to many staff members at IPHC for having shared their opinions and recent progress with me.

1.2 Unit Stocks and Their Relationships

Pacific halibut in the Gulf of Alaska undergo extensive migrations in an easterly and southerly direction. Egg and larval drift, compensatory contranatant juvenile emigration and adult movements were considered by Skud (1977). Stocks in the two major regulatory areas (see 1.3.5) were found to intermingle extensively at all life history stages. There is an indication of a high degree of interrelationship, e.g., strong tagging evidence for stock intermingling between the Bering Sea and the Gulf of Alaska (Best 1968, 1970; Skud 1977; Figs. 119-120 in Bell 1981).

Biochemical racial studies, based on samples from British Columbia to the Bering Sea, indicated overall genetic uniformity among all stocks, except in a single heterogeneous area in southeastern Alaska (Tsuyuki et al. 1969; Utter, cited in Skud 1977). In contrast, mercury content studies revealed significant differences between adjacent regions (Hall et al. 1976). Stock heterogeneity can be a possible interpretation of this difference. Regional morphometric differences clustering on either side of Cape Spencer, such as head-length values and meristic characters (e.g., vertebral and median fin ray counts), have been reported (Bell 1981).

1.3 The Fishery

1.3.1 Relative Size and Importance. The Pacific halibut fishery is one of the most valuable luxury food fisheries in North America and usually has a landed value among the top five species. Total annual harvests in the Gulf of Alaska of the world's largest flatfish averaged 50.4 million lb from 1929-1985, with a peak yield of 74.9 million lb in 1962 (IPHC 1984). Since 1981, catches have been increasing steadily; a 1985 harvest of 55.1 million lb, worth about $50 million, was predicted. The 1986 catch limit has been raised to 66.4 million lb, with an expected value of $100 million for the fishermen and more than twice that for the processing industry (D. McCaughran, IPHC, pers. comm.). Bering Sea landings accounted for only 3% of the total: After a severe depletion during the 1960s attributable to trawling fleets, strict catch restrictions were levied and the fishery is slowly recovering (Hoag 1976, Hoag and French 1976).

1.3.2 Age at Recruitment. Halibut presently recruit to the fishery at age 7-8, depending upon prevailing growth rates and stock conditions. Most halibut in the North American setline catches range from ages 8-15 (IPHC 1978). Due to their higher growth rates, females recruit earlier than males, generally by 2-3 years (see 2.1.1).

1.3.3 Characteristics of Harvested Fish. Females grow faster and live longer than males, and both have shown increasing growth rates since the 1920s, presumably due to changes in population density and/or environmental conditions. The fishery is limited by an 81 cm length minimum, with a common range of 100-150 cm and an average length of 120 cm. Weight distribution in the commercial catch ranges from 10-300 lb, with a 25-30 lb average.

1.3.4 Types and Selectivity of Gear. Halibut are marketed as fresh and frozen steaks, fillets or roasts, and there is no modern processing for roe or meal by-products. The technique employed commercially includes fixed-hook setlines or longlines, and snap-on gear widely introduced in the 1970s. The gear unit of standard effort is a "skate," with 100 short baited-hook lines (gangions) attached to a groundline at 18-ft intervals. The versatile snap method incorporates easily removable gangions attached with metal clips to the groundline, and therefore can vary hook spacing with encountered halibut concentrations. This method is advantageous for smaller boats that alternate between fisheries in-season. Traditional setline craft include the characteristic halibut schooners, while other ships such as seiners and trollers are also used.

1.3.5 Distribution of Fishing Effort. For the most part, the commercial fleet operates from Oregon to the Bering Sea in specific areas or grounds where halibut tend to concentrate during spring and summer. Catches take place along shelf bottom areas wholly within the 200-mile Fisheries Conservation Zones of the U.S. and Canada. Most fishing is conducted between 30 and 250m, with "soak" times from 4-48 hours (12 average). The season currently is divided into a series of short (2- to 12-day) openings staggered among the three major IPHC regulatory areas, which have their respective catch limits strictly set each year. The 1985 regulatory areas for the Gulf of Alaska include three subareas: 2C, all waters off the coast of Alaska south and east of Cape Spencer; 3A, all waters between Cape Spencer and Cape Trinity, Kodiak Island; 3B, all waters between Cape Trinity and a line extending southeast from Unimak Island. Subareas 2A and 2B are U.S. and B.C. waters, respectively, and the Bering Sea (Area 4) has four subareas. Fishing effort in the Gulf of Alaska is concentrated near Kodiak Island where population abundance is usually highest.

1.4 Distribution and Abundance of the Population

Halibut are demersal, living on or near bottom in 3-8°C water. Most are caught in summer in depths of 30-300m as they move from deep slope areas to shallower banks and coastal waters (IPHC 1978). A seasonal movement related to spawning involves their return to the shelf edge in winter, as documented by tagging records.

Migrations often are extensive along the coast; however, distance and direction differ substantially between seasons, years and fish size or age. The longest record is 2500 miles (Aleutians to Oregon). Emigration from most regions has been observed, but no adults released in the Gulf have been recovered in the Bering Sea. The easterly and southerly migrations in the Gulf occur predominantly at the juvenile stage, counterbalancing the northwestward egg and larval drift (Skud 1977). New methodology for estimating migration rates within and between areas has been developed at IPHC and is being incorporated into management stock estimation procedures (Quinn et al. 1985).

Catch per unit effort (CPUE) is greatest where adults concentrate over the summer feeding grounds; values are particularly high on banks along the wide continental shelf of the western Gulf of Alaska. During the late 1970s and early 1980s, CPUE increased sharply off Alaska, while remaining stable at a low level off British Colombia. Differences in setline catchability (effectiveness) between areas were considered a likely cause (Hoag et al. 1984), and environmental factors affecting regional differences in recruitment have been investigated (Parker 1988; Parker, in press). Migration variability is also an important dynamic impacting abundance and distribution patterns from year to year. A new method, migratory cohort analysis, is currently being employed to incorporate migration rates between areas (Deriso and Quinn 1983; Quinn et al. 1985).

1.5 Current Status of Stocks and of Management Measures

Halibut stocks are approaching historical highs above maximum sustainable yield (MSY) in the northeastern, central and western Gulf of Alaska. MSY, however, is below average off British Columbia and in the Bering Sea, but improving. Stocks currently are managed by IPHC as a single species fishery in the Gulf of Alaska and Bering Sea. Productivity is measured at IPHC as annual surplus production (ASP) and constant exploitable yield (CEY) and can be relatively indexed by a comparison of the more stable (and currently favored) CEY management goal with the traditional long-term goal of MSY (Quinn et al. 1985). Current IPHC population assessment methods include estimation by CPUE data from the commercial fishery and regional catchability differences (Quinn et al. 1985). Original cohort analysis was completed by Hoag and McNaughton (1978). Catch-age data are considered adequately precise and accurate to estimate exploitable biomass by geographic assessment areas. Two methods, catch-age analysis with CPUE partitioning and migratory catch-age analysis, are used. The latter may lessen the sensitivity of estimates to CPUE data and catchability changes if applied to the migratory cohort analysis technique (see 1.3). Short-term assessment of estimating ASP involves two methods, blind-response and biomass-partitioning, whereas long-term assessment involves CEY and MSY, the results of which determine current catch limits.

Several methods of determining long-term stock abundance trends are presented by Quinn et al. (1984). Throughout the history of the managed fishery (1929-present), surplus production was greater than the catch until 1950, equalled it until 1960, was smaller until 1973 and subsequently again exceeded the catch. Large ASP changes from catch-effort analysis are due to unprecedented CPUE changes. There is considerable evidence supporting a density-dependent production trend (Deriso 1985). Under prevailing environmental conditions, the population appeared to have reached MSY levels by the late 1950s, following sustained improvements under IPHC controls. Since 1975, the commercial catch has been held at the lowest level in its history and is below ASP (Quinn et al. 1984). This action, together with reduction of incidental catch mortality that has long been a serious problem, is the strategy of IPHC to rebuild the stock so that population biomass and fishery yield will be increased.

1.6 Recruitment Variability

Relative year-class strength has been estimated recently by (1) cohort analysis, using catch-age data and assumed values for natural and fishing mortality, and (2) CPUE indices weighted by habitat size in each region, adjusted by gear selectivity values for each age class and partitioned by relative regional densities (Quinn et al. 1982; Parker 1988; Parker, in press).

Various historical methods of recruitment estimation for halibut, e.g., Fukuda (1962), Southward (1968), Cushing (1971), Hoag and McNaughton (1978) and Schmitt and Skud (1978), also have been proposed. Cushing (1971) suggested the relatively less variable historical catches in halibut and other flatfishes have been due to the stabilizing tendency of recruitment with respect to the parent stock, i.e., the greater the density dependence the greater the stability. Deriso (1985) presented spawner-recruit analysis according to a Ricker-type relation and argued that density-dependent mechanisms appear to have driven recruitment variability. Higher levels of recruitment and/or growth rates seem to result from low mature stock sizes, as indicated by both the age-structured and CPUE methods. If so, management goals to maximize yields would require stock size to be limited. Aside from the few particularly large recruitment year classes (1951, 1955, 1961, 1970, 1972, 1973 and 1975), the recently rebuilt stock increase tends to accompany a mildly decreasing recruitment trend (see Fig. 4, Deriso 1985).

Age 8, when halibut begin to enter the commercial fishery, is probably the youngest age class for which reasonable estimates of abundance can be made. Deriso (1985) presented biomass estimates for 8-year-olds vs. mature adults. A moving average has been used with Deriso's estimates for ages 8-10 to smooth variable sampling success by the fishery during this early recruitment period (Parker 1988; Parker, in press).

1.7 Age Determination and Validation

Saggitae otoliths (surface-read summer-winter paired rings called annuli) have been used since 1933 at IPHC for ageing. Precision or repeatability of ring counts has been well established, while only recently has work been underway to independently validate accuracy in ring counts and actual age. A comparison of the otolith readings with growth and length-at-liberty of tagged fish revealed good agreement. Considerable variability occurs between ring counts and fish length due to known differential growth rates by sex. Since 1982, some tagged halibut have been injected with oxytetracyclene, producing a check mark in the otolith that fluoresces with UV light exposure. Age readings can be corroborated upon recapture according to the number of annuli. By 1987, total recoveries are expected to provide sufficient data for proper evaluation of the technique's reliability in validating age estimates (C. Blood, IPHC, pers. comm.). Digital image analysis of otoliths is currently being developed at IPHC to facilitate an automated procedure for ageing, and preliminary results show good agreement with direct reading (P. Neal, IPHC, pers. comm.).

1.8 Age Composition of the Population

Commercial landings (about 40,000 fish per year), supplemented by research cruises, have been sampled by IPHC for age and size composition since 1933. However, these data may not be representative of the population as factors such as size or sex segregation between fishing grounds and gear selectivity with respect to fish size, together with size limits, port sampling problems and varying price structures, all contribute to sampling bias (Quinn et al. 1983). Nevertheless, information on age composition is essential for estimating abundance, age structure, recruitment, growth and mortality.

Various methods and sampling designs utilized since the 1960s, including recent models developed at IPHC to convert age composition from landings to that of the actual population (which differ significantly from each other), were presented and discussed by Quinn et al. (1983). The entire halibut fishery spanning the coast from California to Alaska and the Bering Sea has been divided into 60-mile-wide statistical areas for analytical purposes with landings assigned by time intervals. The catch from these areas can be combined as needed into regions and subareas (see Fig. 1, Quinn et al. 1983). The percent of each age in the annual commercial catch is reported each year as catch, CPUE and average weight by regulatory areas (IPHC Annual Report series). Although Pacific halibut may live for over 40 years, ages 10-17 account for about 80% of the population biomass, and most of the commercial catch is comprised of ages 10-15.

2 SPAWNING ADULTS

2.1 General Description

2.1.1 Size and Age Ranges. Size and maturity of Pacific halibut varies with regions in the Gulf of Alaska and has changed over time. Males usually attain sexual maturity by about 70 cm body length. Maturity occurs much earlier in males than in females and is more difficult to discern; 50% are mature by age 8 (60-80 cm). On average, 50% of females are mature by 115-125 cm (ages 11-12) and 90% by 150 cm (age 15); age of females at maturity ranges from 8-16 years (Schmitt and Skud 1978, St-Pierre 1984).

2.1.2 Type of Spawning Behavior. Ovarian examinations have revealed that only small numbers of ova to be released during spawning periods are ripe at any one time; thus batch spawning is likely, as it is impossible for an ovary to hold at one time all the ripe ova it will shed in a season (Thompson 1914, Kolloen 1934, Novikov 1964, St-Pierre 1984). There is disagreement on whether mature halibut spawn annually (IPHC 1978, Vernidub 1936, Novikov 1964, Bell 1981); it is believed by some that maturation may be prolonged so that females spawn only every two or more years. However, St-Pierre (1984) concluded from analyses of winter research data that spawning must occur annually.

2.1.3 Fecundity. Schmitt and Skud (1978) noted that fecundity-at-age has more than doubled since the 1920s, while fecundity-at-length and at-weight have changed only slightly. For example, an average age-12 female produced 330,000 eggs in 1927, but 740,000 in 1973, a 124% increase. This is related to a long-term population decline since the 1940s and a coincident compensatory increase in growth rates. Recruitment was found to be inversely related to fecundity before 1955 but has paralleled it since, indicating a density-dependent relationship. Halibut fecundity is best estimated by size (Kolloen 1934) and is high, as are losses due to prolonged egg and larval drift and the lack of parental care. A 120 cm female produced 646,000 eggs in 1927 as compared to 573,000 in 1973, and a 40 kg female produced an estimated 1,575,000 in 1927 but 1,227,000 in 1973 (Schmitt and Skud 1978).

2.2 Distribution and Abundance

2.2.1 Duration of Spawning. Peak spawning occurs from the last week of December to the third week of January; movements to and from the spawning grounds are predominantly in November, February and March (St-Pierre 1984). Batch spawning (see 2.1.2) extends this stage through a gradual shedding of ripe ova over an unknown number of weeks. Seasonal maturation of sex products appears to vary among individuals of both sexes. For example, some females may have completed spawning before others begin at the same location; males always release milt before the earliest and after the latest spawning females. This pattern occurs coastwide, probably ensuring maximal fertilization of the most egg releases (St-Pierre 1984).

2.2.2 Large-scale Patterns. Gulf of Alaska research data from 1924 show active adult migrations between winter spawning grounds along the continental slope and summer feeding grounds on the shelf (St-Pierre 1984). Tagging records document the dispersal of the spawning population, e.g., adults tagged in the Gulf have not been recovered in the Bering Sea; however, a few juvenile Pacific halibut do occur there (Best 1977). A major spawning activity from Dixon Entrance to Kodiak Island is suggested by the number of mature females reported. Prevailing migratory movements of adults indicate a net influx of migrants into the central region from these outlying areas, thereby tending to reduce the age at 50% maturity in the central section (Schmitt and Skud 1978). This pattern is also reflected by the distribution in mean age of females along the coast. Their eastward and northward movements appear to be confirmed by the counter movements observed in summer recoveries of winter-tagged fish. The speed of these seasonal movements is difficult to ascertain with data from a summer fishery, but incidental recoveries in other fisheries indicate the potential for long migrations (over 100 miles) soon after spawning.

2.2.3 Small-scale Patterns. Although spawning is widespread in the Gulf of Alaska, spawning concentrations are intensified with interannual consistency at several known locations, such as: Cape St. James and Langara and Frederick islands in British Columbia waters; Yakutat, Cape Suckling-Yakataga, Portlock Bank and Chirikof Island in the Gulf of Alaska; and probably in a few areas along the Aleutian Islands, as indicated by 60 years of commercial and research catches of mature halibut during winter months. Some degree of aggregating behavior has been noted among spawning females and males (often separately), at least just prior to releasing eggs and milt, particularly on the banks adjacent to active spawning grounds (St-Pierre, IPHC, pers. comm.).

2.2.4 Maximum and Mean Abundances. Density estimates have been derived by apportioning estimates of exploitable biomass by subarea (from cohort analysis with CPUE-partitioning, see 1.4) according to measures of bottom area (cf. Table 1, Appendix Table. 7, Quinn et al. 1985). In 1984, these values ranged from 0.248 kg/ha in subarea 2A to 5.2 kg/ha in subarea 2C, with an average density of 3.01 kg/ha of adult halibut for the entire Gulf of Alaska shelf and slope areas.

2.2.5 Vertical Distribution. Known spawning grounds in the Gulf are in deep waters (200-500 m) just beyond the continental shelf break. According to Thompson and Van Cleve (1936) and Van Cleve and Seymour (1953), eggs are released primarily at bottom depths of 270-405 m and 75-400 m in the Gulf of Alaska and British Columbia waters, respectively.

2.3 Feeding

2.3.1 Habitat. Adult halibut are primarily benthic apex predators of widely varied epibenthic prey types but often leave bottom to feed on bathypelagic or even pelagic fishes, such as herring.

2.3.2 Prey Species. Adult halibut are strong swimmers and vigorous carnivores. They are opportunistic feeders and, as they grow beyond 80 cm, their preferences shift from small to larger crustaceans and especially to fish and octopus (Thompson 1916). Recent examination of the stomach contents of over 300 halibut indicated that the principal prey are Pacific sand lance (*Ammodytes hexapterus*), walleye pollock (*Theragra chalcogramma*), octopus (*Octopus* spp.) and Tanner crab (*Chionoecetes bairdi*) (Best and St-Pierre 1986). Pacific cod (*Gadus macrocephalus*) was the third most important fish prey species); other prey were sable fish (*Anoplopoma fimbria*), rockfish (*Sebastes* spp.), sculpins (*Cottidae*), arrowtooth flounder (*Atheresthes stomias*) and other flatfish, Pacific herring (*Clupea harengus pallasi*) and various clams and shrimp (IPHC 1978, St-Pierre and Best 1986). Crabs with carapace widths over 7 in have been found in halibut stomachs.

There is evidence of occasional cannibalism on juveniles by adults. In a study on the possibly adverse effect of cannibalism on stock recruitment by adults encroaching onto nursery areas, about 7% of examined stomachs contained juvenile halibut (Best and St-Pierre 1986). Cannibalism was not noted in recent studies in areas west of Kodiak occupied by large numbers of juveniles, but no estimates of their availability at the time of fishing exist. The influence of cannibalism on recruitment remains unknown but is likely to be insignificant.

2.3.3 Prey Density Requirements. Not applicable.

2.3.4 Factors Affecting Availability of Prey. Little is known of factors affecting abundance or availability of the halibut prey base. However, there is some evidence of selectivity in halibut feeding habits (McIntyre 1953, Simenstad et al. 1977). Large adults feed voraciously and may temporarily deplete local prey species of choice.

2.3.5 Temporal Patterns of Energy Storage. There is no information on energy storage related to reproduction, beyond the generalization that more active summer feeding is likely to be an important precursor for winter spawning activity in the less productive deep waters.

2.3.6 Evidence of Food Limitation. Seasonal differences in stomach contents of adult halibut have not been documented. In the IPHC 1978 study (see 2.3.2), 16% of stomachs from 82-144 cm fish in Hecate Strait and 20% of 82-153 cm fish in the Gulf of Alaska were empty. Existing data from stomach contents account for a wide range of body weight but are insufficient to suggest possible daily ration percentages for halibut of any age. In general, prey scarcity appears to be an unlikely problem for adult halibut, except perhaps in winter before spawning.

2.4 Predation

2.4.1 Predator Species. Adult halibut have few predators capable of overtaking them, particularly in bottom environments. Studies based on the examination of stomach contents of thousands of fishes were reviewed by Best and St-Pierre (1986), and only a few predators of halibut had been reported (Simenstad 1977, Jewett 1978, Jewett and Powell 1979, Hunter 1979). Predation on hooked halibut is a consistent problem with setline gear, e.g., by Pacific sleeper sharks (*Somniousus pacificus*) (Thompson 1915, Gotshall and Jow 1965) and particularly by marine mammals, such as Steller sea lions (*Eumetopias jubata*) who mutilate so much of the local catch that fishermen often have to change grounds (Thompson 1915, Imler and Sarber 1947, Wilke and Kenyon 1952, Kenyon and Schaffer 1955, Thorsteinsen and Tensink 1962, Spalding 1964). Actual predation of free halibut by marine mammals appears exceedingly rare, as analyses of sea lion, harbor seal (*Phoca vitulina*) and fur seal (*Callorhinus ursinus*) stomachs from the Gulf of Alaska and Bering Sea attest (Imler and Sarber 1947, Pitcher and Calkins 1977, Perez and Bigg 1980, Lowry et al. 1982). Killer whales (*Orcinus orca*) may be more effective, but their stomach contents rarely have been analyzed (Pike and MacAskie 1965, Rice 1968). Cannibalism appears limited to juveniles.

2.4.2 Effect on Spawning Adults. Data are insufficient to estimate the importance of predation on spawning adults.

2.5 Other Factors Affecting Adults

2.5.1 Biotic. Halibut appear to have fewer parasites than most marine fish; therefore, parasitism is unlikely to be a significant problem for survival or spawning success (Bell 1981).

2.5.2 Abiotic. No abiotic factors other than temperature are presently known to affect spawning.

2.5.3 Total Mortality. Estimates of natural mortality have been derived from catch curve analysis of catch-age composition with assumptions for an unexploited stock (IPHC 1960) and from tagging records (Myhre 1967). The latter method produces higher rates but suffers from several biasing problems. From corroborating work completed subsequently, the rate used at IPHC remains at 0.2 (R. Deriso, IPHC, unpubl. data).

Setline fishing mortality is based on catch-age and cohort analyses, with age classes apportioned by gear selectivity curves (Deriso et al. 1985). Estimates ranged from 0.031 for age 8 to 0.191 for ages 15-20 in 1984, with interannual variability ranging from 0.018 (age 8) to 0.427 (age 17) since 1955. Ages 8-9 are not fully recruited and generally experience less than the estimated average setline fishing mortality. Incidental fishing mortality was near 33% per cohort during the 1960s and has been reduced by at least half since then (Deriso, IPHC, pers. comm.). Estimated exploitable biomass is currently adjusted by a 28% exploitation rate to provide the CEY scientific recommendations for annual catch limits (see 1.5, Quinn et al. 1985).

2.6 Laboratory Holding and Rearing

Adult halibut have been held in various types of marine aquaria (see also 3.6). Tomlinson and Baker (1973) reported that 5 female and 3 male halibut were maintained in an aquarium until sexually ripe (21 months), the first such development in captivity.

3 EGGS

3.1 General Description

The bathypelagic halibut eggs are round; the clear glassy outer surface is punctured by numerous minute holes, giving a honeycombed appearance. The comparatively large yolk is colorless and without oil globules; the perivitelline space is very small and there are no markings around the micropyle (Thompson 1915). Ova size varies geographically and interannually, but the relationship of egg size to fish size or age is unknown.

Variation in egg size is also a function of preservation method and time prior to measurement. Eggs taken in net hauls range from 2.9-3.8 mm in diameter and average 3.3 mm (see Table 10, Thompson and Van Cleve 1936).

3.2 Distribution and Abundance

3.2.1 Duration of Egg Stage. Time of hatching varies with the temperature of the water. Thompson and Van Cleve (1936) assumed slow development (approximately 15 days) at the cold depths (3.5-6.5°C), whereas Van Cleve and Seymour (1953) estimated 23 days at 4.7°C and 11 days at 9.7°C. In the laboratory, eggs hatched after 20 days at 5°C and 12.5 days at 8°C (Forrester and Alderdice 1973). The effect on daily egg development of variable temperatures encountered in deep layers in the Gulf of Alaska is as yet uninvestigated.

3.2.2 Large-Scale Patterns. According to Thompson and Van Cleve (1936), very few eggs have been found from December to March along the Gulf of Alaska coast. They occurred mainly in the deep water (100-200 m) along the shelf break (over 425 m), but also at intermediate depths over the slope. Eggs are distributed throughout the region between Yakutat and Cape Chiniak (except in southeast Alaska north of Dixon Entrance), as well as off the Queen Charlotte Islands and Cape St. James, where distribution was consistent from year to year. Central Gulf occurrences were concentrated along the slope edge within 40 miles of the 1800m contour and not more than 15 miles inside the 180m contour. Egg scarcity noted by Thompson and Van Cleve (1936) was thought to indicate a lack of spawning west of Cape Chiniak and over banks south of Cape St. James. Van Cleve and Seymour (1953), however, found that many eggs released off Cape St. James drifted into deeper water as they were carried north along the west coasts of the Queen Charlotte Islands. Horizontal distribution appears to be limited more by the presence of denser intermediate water layers than by actual depth range as the eggs drift (mostly alongshore) with prevailing deep circulation.

3.2.3 Small-scale Patterns. No data are available on abundance variations within the scale of patchiness over space and time.

3.2.4 Maximum and Mean Abundances. It is difficult to discern a range of abundance density for halibut eggs in the field, because of their rarity in the plankton, as well as the scarcity of sampling attempts. From early surveys (with single oblique tows), a crude estimate of 0.001 m^{-3} to 0.01 m^{-3} (January maximum) may be calculated (see Fig. 55 and Table 15, Thompson and Van Cleve 1936). This is likely to be an underestimate due to much of the towing being outside the depth of high ova density, and to small-scale patchiness. Density was about 10 times greater on western than on southern spawning grounds. "Density contour" maps of egg distributions around Cape St. James during January of each year (1935-1946) provide a general indication of abundance (see Figs. 6-16, Thompson and Van Cleve 1936). However, problems with representative samples and other sampling design inadequacies were partially responsible for a failure to obtain statistically significant relations between egg production and spawning biomass or recruitment in the region.

Subsequently, Schmitt and Skud (1978) estimated annual potential egg production from the fecundity-weight relationship and spawning stock biomass, from cohort analysis numbers-at-large (see Hoag and McNaughton 1978) and mean weight-at-age from unpublished commercial fishery sampling data.

3.2.5 Vertical Distribution. Based on 1928-1934 Gulf of Alaska data, Thompson and Van Cleve (1936) described and depicted (Fig. 59) the vertical distribution of halibut ova according to depth of haul and position over the continental slope. Ova were found along the outer shelf and the deep waters outside at temperatures of 3.5-6.5°C; 98% of the stations were at depths over 275 m and 67% over 400 m; 88% of the ova were at depths between 85 and 425 m, 68% between 85 and 212m and the remainder down to 680 m. No eggs were found in surface layers. Off British Columbia, Van Cleve and Seymour (1953) found eggs at depths of 75-400 m in 4.7-9.7°C waters with specific gravity ranging from 1.0254 to 1.0266. Eggs appeared to lie within or below the intermediate layer of strong density gradients, depending on their density as they developed.

3.3 Feeding

Not applicable.

3.4 Predation

3.4.1 Predator Species. No data are available.

3.4.2 Effect of Predation. No data are available.

3.5 Other Factors Affecting Eggs

3.5.1 Biotic. No data are available.

3.5.2 Abiotic. Temperature is an important factor in successful egg development, as shown by the early surveys of egg distributions and projected hatching times. In laboratory experiments, slowed and aborted development occurred with decreasing temperatures and considerable mortality at higher temperatures; 7°C was optimal for hatching, and hatching efficiency and time to hatching varied with temperature (Forrester and Alderdice 1973). Slowed development may decrease survival by delaying normal density changes and the resultant rise in the water column for favorable transport in surface layers.

3.5.3 Total Mortality. Although no data are available to calculate total egg mortality, an assumption of 1-3% survival may be considered reasonable (St-Pierre, IPHC, pers. comm.). Van Cleve and Seymour (1953) calculated that 10% of eggs might survive to hatching at 6.38°C, the average temperature at which eggs have been caught over the years, and they assumed much higher mortalities at higher or lower temperatures. Quinn's (1981) model demonstrated an early decline in population abundance was due partially to a sharp decrease in egg survival in the 1940s, implying a change in the biological recruitment mode.

3.6 Laboratory Holding and Rearing

Forrester and Alderdice (1973) incubated Pacific halibut eggs at various temperature regimes from 2-12°C. Hatching occurred at temperatures of 5 to 8°C, and time to 50% hatching at 8°C and 5°C was 12.5 and 20 days, respectively. Incubation of eggs at 6°C produced the largest larvae. No attempt was made to feed the larvae and yolk sac absorption was carefully monitored. Larvae have not been reared beyond stage 2; however, a cooperative study between IPHC and the U.S. Fish and Wildlife Service to rear larvae is now underway (S. Kaimmer, IPHC, pers. comm.).

4 LARVAE

4.1 General Description

Pacific halibut larvae undergo remarkable metamorphic transitions as they develop through a variable and protracted 5-7 month pelagic phase. Thompson and Van Cleve (1936) presented a detailed description of twelve continuous stages, including detailed drawings and photographs of each stage. A brief synopsis follows: The newly hatched Stage 1 larva emerges in a highly elongated symmetrical tadpole shape, 7.8 to 15 mm in length. It is nearly circular in cross section and gradually tapers to the posterior notochordal tip. The head is bent vertically around the large yolk (3 mm long), with a characteristically undeveloped short snout and an eye on each side. Pigment is entirely lacking except in the retina of the eye. The larva remains in an upright position and continues feeding off the yolk until Stage 3 (11.2-18.5 mm) initiates postlarval development. Primitive pigmentation (scattered chromatophores) and comparatively great length distinguish halibut larvae from those of other species at a similar stage. Myotome counts can also be used for distinguishing them. By Stage 4 (13.6-17.8 mm) the larva is dependent on captured food and the body shape begins to flatten. By Stage 7 (14.7-19.9 mm), the length-depth ratio has increased substantially and asymmetry is more apparent. Migration of the left eye, begun in Stages 5-6, continues toward the right until Stage 7, and the first signs of postlarval pigment and the grouping of chromatophores appears in Stage 8. The characteristic halibut pattern is established by Stage 9 (18.4-23.7 mm); the body is flattened and pigmentation on the left side is beginning to fade. By Stage 11 (18.7-24.6 mm), the left eye has passed over the dorsal head margin and the pectoral fin begins to take adult form. Adult coloration, as well as form, are recognizable by Stage 12 (22.3-28.8 mm, average 26.0 mm); the eyes are very large, postlarval pigmentation is nearly lost in the general deepening of color and the left side is white and blind.

4.2 Distribution and Abundance

4.2.1 Duration of Larval Stages. The yolk-sac stages last approximately 2 to 3 months (through Stage 2, 13.4 mm body length). Development through the remaining larval stages (3 to 12) takes an additional 3 to 4 months, then the adult form is attained and the pelagic phase ends. All 3- to 4-month-old larvae captured were in the upper 100 m.

4.2.2 Large-scale Patterns. In the Gulf of Alaska, larval horizontal and monthly distribution patterns differ markedly according to stage (see Figs. 65-70, Thompson and Van Cleve 1936). Data for some stages, however, are limited. Newly hatched larvae were found beyond the shelf break over bottom depths exceeding 400 m (Thompson and Van Cleve 1936). Stage 2 larvae (2-3 months old) were scattered over the entire Gulf north of 56°N and Stages 3-4, having begun an inshore movement as they entered the surface layers, were found in increasing numbers in shallower shelf regions. Few larvae older than Stage 5 were found outside the shelf break; from Stage 10 they occurred only in shallow inshore areas, even intertidally along the Kodiak Island south coast (Thompson and Van Cleve 1936).

Once larvae are in the surface layers inshore, cyclonic coastal circulation transports them alongshore and cross-shelf in the typical convergent downwelling pattern. This involves the Alaska Coastal Current system, which is broad on the east side but, on the west, is a narrow "Kenai Current" component that is tightly constrained against the Kenai Peninsula and continues through Shelikof Strait and beyond Kodiak Island along the Alaska Peninsula (Royer et al. 1979; Royer 1979, 1981b, 1983; Schumacher and Reed 1980, 1986; Reed 1981). This inner shelf coastal flow is regarded as distinct from the oceanic forcing of the shelf-break flow which is associated with the Alaska Current and Alaskan Stream (Hayes and Schumacher 1976, Schumacher et al. 1978, 1979). It is possible that some larvae are lost from onshelf transport by veering out of the southwestward flowing Alaskan Stream (offshelf) and moving east and northeast around the Gulf of Alaska gyre in the recirculation that has been observed south of Kodiak Island (Reed 1980a).

The circulation pattern for larvae beyond the shelf break presumably is as follows. Newly hatched larvae in deep water would be carried westward, drifting with the cyclonic oceanic flow (Alaska Current in the east, narrowing into the swifter Alaskan Stream to the west (Reed et al. 1980, Royer 1981, Reed 1984)). The recently described "Haida Current" off northwestern British Columbia and southeastern Alaska flows as a narrow jet over the continental slope predominantly from November through February (with a peak in January) and may provide an important transport mechanism for offshore larvae down to 500m (Thomson and Emery 1986).

In the central part of the Gulf of Alaska (139-147°W, north of 55°N), larval distribution followed a circular pattern (Figs. 66-68, Thompson and Van Cleve 1936), suggesting some transport from the northern Gulf to the south, and then east toward southeastern Alaska. This "eddy" feature (perhaps similar to the one described by Reed 1980a) might carry larvae to the coastal shallow areas in time for a May or June completion of metamorphosis. The high abundance of juveniles in Shelikof Bay, as well as a high tag recovery rate in British Columbia of releases there, supports this eventuality, though further study is needed (Skud 1977). The outer edge of an anticyclonic eddy that recurs periodically during the spring off Sitka, Alaska (likely topographically steered, see Swaters and Mysak 1984) may affect the lateral distribution of halibut larvae along the continental slope (Tabata 1982), with possible interactions with the Haida Current.

The possibility of larval transport from the Gulf of Alaska into the Bering Sea was suggested by Thompson and Van Cleve (1936) and Vernidub (1936). Such circulation has been documented by subsequent studies (e.g., Uda 1963, Dodimead et al. 1963, Favorite and Fisk 1971, Schumacher et al. 1982).

4.2.3 Small-scale Patterns. No data are available.

4.2.4 Maximum and Mean Abundances. Pacific halibut larvae are exceedingly rare in the plankton even at times of peak abundance, and crude estimates are likely to be conservative. To obtain abundance data, extremely high rates of filtration were used (Thompson and Van Cleve 1936, Table 15) and there was considerable variation in stage and month. Larvae were most abundant in March (averaged over the years), with 2.3 larvae per 60-min haul, or nearly $0.001 m^{-3}$. A gradual scattering and decrease in postlarval density is evident in the western regions from March to June. In

June 1985, successful tows by IPHC with a 3m Tucker trawl system compared double-oblique haul sampling of surface-bottom-surface with that of the upper layer only (50m), where late-stage larvae would be expected to accumulate (Parker 1988). Densities of 0.002m^{-3} and 0.003m^{-3} were estimated at a shallow (100m bottom) station south of Kodiak Island and a shallower station (50m) in Unimak Pass, respectively. At the latter station, there were many young (5-9) stages (see Hagen 1986).

4.2.5 Vertical Distribution. Vertical distribution at each larval stage was described by Thompson and Van Cleve (1936, see Figs. 60-64). The youngest larvae were taken mainly between 400 and 700m in waters of uniform density (high) and temperature. By Stage 3, they began their upward movement to an intermediate depth (170-935m) and Stages 5-9 were found mainly about 85mm nearer inshore. Finally, Stages 10-12 completed the onshore drift and settled near bottom in shallow bays, where most were taken in bottom trawl hauls averaging 12m depth.

No evidence of diel vertical migration exists, nor do any differences by month or region. One study, suggesting diel migrations in late May 1983, west of Shelikof Strait, involved only 10 larvae collected in neuston tows (upper 15 cm) at night, and no larvae were collected in day tows (A. Kendall, Natl. Mar. Fish. Serv., Seattle, pers. comm.).

4.3 Feeding

4.3.1 Habitat. Larval feeding should follow depth locations discussed in 4.2.5. Light intensity undoubtedly would affect visual targeting but minimum levels, relevant bandwidths and the consequent daily feeding periods are unstudied. First feeding may be a critical factor in survival, considering the apparent depth of Stage 3 and given the essential but narrow time/light window.

4.3.2 Prey Species. Feeding begins as yolk-sac absorption nears completion (late Stage 2). No quantitative stomach analyses have been carried out, but qualitative examinations and generalized relative proportions by depth and location were made on the May 1985 larval recoveries (Parker 1988). A high proportion of euphausiids (mostly *Thysanoessa longipes* and *T. spinifera* and *Euphausia pacifica*) were identified in the hauls containing halibut larvae, followed by, in decreasing order: copepods, mainly *Neocalanus cristalus*, *Calanus pacificus* and *Eucalanus bunjii;* decapod larvae, mainly megalops; crab zoeae and megalops; a carnivorous copepod, *Euchaeta elongata*; and amphipods. A few of these cohabitants were found in the stomachs of halibut larvae; one contained six megalops and a C-3 copepod, another contained euphausiids, unidentified zoea and megalops, and juvenile amphipod remnants. Others had pieces of euphausiid and megalops, but few could be identified to species.

4.3.3 Prey Density Requirements. No data are available.

4.3.4 Factors Affecting Availability of Prey. No data are available.

4.3.5 Temporal Patterns of Energy Storage. Not applicable.

4.3.6 Evidence of Food Limitation. No data are available.

4.4 Predation

4.4.1 Predator Species. No data are available.

4.4.2 Effect on Larvae. No data are available.

4.5 Other Factors Affecting Larvae

4.5.1 Biotic. No data are available.

4.5.2 Abiotic. Temperatures of 3.5°-4.5°C increase development times. Unusually cold conditions, particularly if extended in time, would thus increase the vulnerable period for predation. Salinity variations also may affect such vulnerability. For example, if an unusual depression of isohalines persisted (excessively high freshwater runoff with a lowered pycnocline), larvae would remain deeper longer even as their specific gravity decreases, thus restricting a timely rise to upper layers for feeding and subsequent development.

4.5.3 Total Mortality. No estimates are available.

4.6 Laboratory Holding and Rearing

Laboratory rearing of yolk-sac larvae was carried out by Forrester and Alderdice (1973) with no attempts to feed them. Antero-posterior yolk-sac length was over 50% of the total preserved length of 5.3-7.8 mm for the first hatched larvae. The ratio decreased in larvae hatching later. Pigmentation appeared 2 to 4 days after hatching. Larvae survived to a maximum of 10 days after hatching, increasing in length for the first 3-4 days, then regressing in size with yolk-sac absorption.

5 JUVENILES

5.1 General Description

After the 6-7 month pelagic larval phase, the young halibut (about 25 mm length) settle to the bottom in shallow inshore nursery areas. They have the adult form with fully developed fin rays and differentiated sides, one colorless and blind and the other with developing adult pigmentation (initially spotted), and two very large eyes.

Extensive IPHC surveys of nursery areas began in 1955 in British Columbia (Hardman and Southward 1957) and were subsequently extended to the north and west and further offshore into southeast Alaska and eventually across the Gulf to Unimak Island. Tagging was done in conjunction with the trawl surveys to estimate the importance of different nursery areas on recruitment to the fishery. Results of the 1967 through 1980 surveys have been reported by Best (1969a, 1969b, 1974) and Hardman (1982); they include length and age composition for all halibut under 65 cm long (see 5.2.2). Ages were determined from otoliths by subsampling, and an age-length key was constructed annually (Hardman and Southward 1965).

5.2 Distribution and Abundance

5.2.1 Duration of Juvenile Stage. The juvenile phase is considered by management to span from metamorphosis until the time of entering the commercial fishery. They are historically defined as halibut below a total length of 65 cm and less than 6 years of age (IPHC 1978), although technically the juvenile phase ends when sexual maturity is attained (see 2.1). Juveniles usually recruit to the fishery by age 7, yet have entered as early as age 4, depending upon the prevailing growth rate and the condition of the stocks (Bell 1981). Growth rate was high in the 1970s with low stock abundance, and recruitment was at an earlier age. A minimum commercial size limit was imposed at 66 cm until 1973 when it was extended to 81 cm.

5.2.2 Large-scale Patterns. Juveniles are widely dispersed throughout Gulf of Alaska shelf regions, as shown by IPHC surveys. They remain inshore for 1 to 3 years, and therefore are usually unavailable to the commercial fishery. As they become older, they move offshore to depths of 100 m and beyond (IPHC 1964) and migrate eastward and southward, in contrast to the passive drift of eggs and larvae (Skud 1977, see 1.4).

In general, juveniles tend to remain closer inshore than adults. Recoveries of tagged juveniles indicated that some from the Bering Sea and western Gulf of Alaska migrated as far south as British Columbia and others moved into the Bering Sea from the western Gulf, and vice versa. Many juveniles are taken incidentally in trawls for other groundfish, constituting a serious problem for management, e.g., a sharp decline of the larger juveniles resulted from the Japanese sablefish setline fishery (Bell 1981). Surface and bottom temperatures were taken daily in Gulf of Alaska surveys, and the latter values showed subtle differences that usually fell within the tolerance range. Thus temporal and spatial changes in juvenile distribution are difficult to discern, as compared to those in the Bering Sea, which are more distinctly related to the variable presence of different water masses (Best 1974 and Hardman 1982). Seasonal warming tends to increase the dispersal of juveniles over the shallower shelf areas for summer feeding. Large juveniles move the greatest distances and utilize a wider range (particularly as compared to the denser congregations on feeding grounds in the Bering Sea). Though the pattern is not as distinct as in the Bering Sea or as extensive as that of adults, juveniles return to deeper offshore areas into the winter period. Colder waters may limit their migration and distribution. Relatively low summer temperatures tend to restrict migration because normal feeding grounds within the range of preferred temperature are reduced in size and at a level which is not maintained as long.

An analysis of the IPHC surveys for interannual variations in abundance and distribution by age revealed some problems. The abundance indices were unreliable and of poor predictive value due to changes in juvenile availability and/or sampling error. They did not agree with other measures of year-class abundance at either the egg or adult stages, and mortality estimates in between stages could not explain the differences. Large changes in distribution seemed evident among survey regions. Eastern Gulf of Alaska surveys tended to assess older juveniles than those in the west (and Bering Sea), due to distributional differences and/or sampling bias (Schmitt, IPHC, pers. comm.). Absolute abundances were found to be highest, in descending order, in the Chirikof, Chiniak, Unimak and Cape St. Elias regions (Schmitt 1985).

5.2.3 Small-scale Patterns. Data from IPHC surveys suggest that juveniles school by size (Best 1977). Distinct patchiness in catch variability of younger juveniles appeared to occur more often at shallow inshore stations.

5.2.4 Maximum and Mean Abundances. Juveniles are least abundant in the northeastern Gulf of Alaska (Icy Bay to Cape Spencer) and more abundant in the southwestern part (Kodiak Island to Unimak Pass) than to the east of Kodiak. Great density differences between the juvenile survey regions were nearly identical to those in absolute abundances among most regions, because bottom areas for each index region in the Gulf of Alaska were nearly equal. Estimates of mean historical abundance per area are currently being derived at IPHC (St-Pierre, in prep.).

5.2.5 Vertical Distribution. Juveniles are limited to their benthic habitat during the temperature-related seasonal interchange between summer feeding and dispersal over shallower flats to deeper offshore areas in winter. The surveys indicate a tendency for the greatest abundance to be at depths less than 110m. Larger juveniles tend to dominate catches in deeper water.

5.3 Feeding

5.3.1 Habitat. Feeding is primarily within the benthic realm, but bathypelagic prey species and even some pelagic fishes such as herring and salmon have been identified (Best and Hardman 1982).

5.3.2 Prey Species. Qualitative studies of stomach contents of 2,709 juveniles from 1976-1981 IPHC surveys were reported by Best and Hardman (1982) and Best and St-Pierre (1986). Previously, similar studies had been reported for 0- and 1-year-olds from northern British Columbia and southeast Alaska (Hardman and Southward 1957, IPHC 1960). Eighty-nine percent contained food, and prey were reported in order of frequency of occurrence, grouped by 10 cm halibut length increments. The smallest juveniles ate small crustaceans (mainly shrimp and crabs). Prey in the stomach contents of larger juveniles in decreasing order of occurrence were Tanner crab (*Chionoecetes bairdi*), hermit crab (*Paguiridae* spp.), Pacific sand lance (*Ammodytes hexapterus*), sand fish (*Trichodon trichodon*) and walleye pollock (*Theragra chalcogramma*). Diet for juveniles of similar size varied considerably, indicating their highly opportunistic feeding behavior. In some areas, a large number of 0-age rock sole (*Lepidopsetta bilineata*) were consumed by juveniles in 1977, while very few were observed in 1976. Rock sole were also an important prey species for juveniles in the Kodiak Island area in some years (IPHC 1978, Hunter 1979). Hunter (1979) also reported that halibut under 30 cm feed mainly on shrimp (*Crangon* spp.), those between 30 and 60 cm depended less on crustaceans and more on pollock and sand lance and, for those over 60 cm, pollock and Tanner crab were the most utilized food. Rogers et al. (1980) reported clams, shrimps, hermit crabs and Tanner crabs in stomach contents of young halibut from otter trawls in summer off Kodiak Island. Tanner crabs were the primary component of stomach contents of juveniles from Cook Inlet (Feder 1977). The stomach contents of 10 0-age juveniles captured at less than 15m depths at 5 sites near Juneau, Alaska in 1985 contained 28% harpacticoid copepods, 26% amphipods and 24% shrimp (Sturdevant and Shirley, pers. comm.).

5.3.3 Prey Density Requirements. No data are available.

5.3.4 Factors Affecting Availability of Prey. No data are available.

5.3.5 Temporal Patterns of Energy Storage. No data are available.

5.3.6 Evidence of Food Limitation. No data are available.

5.4 Predation

5.4.1 Predator Species. A wide variety of fish and invertebrate predators consume juvenile halibut (Best and St-Pierre 1986). Species composition of catches in the IPHC juvenile surveys was variable in number and species at various locations around the Gulf of Alaska (see Best and Hardman 1982).

5.4.2 Effect on Juveniles. Apparently cannibalism by adult halibut is limited, as observed in several nursery area studies (see 2.3.2). No data are available on other aspects of predation.

5.5 Other Factors Affecting Juveniles

5.5.1 Biotic. No biotic impacts on juvenile survival have been identified.

5.5.2 Abiotic. Other than temperature, abiotic impacts on juvenile survival have not been identified (see 5.2.1)

5.5.3 Total Mortality. Juvenile mortality due to incidental catches in other fisheries was estimated by year class (1857-1978) (Fig. 13, Table A.21, Schmitt 1985). Quinn (1981) estimated a relative age-structured mortality rate schedule for juvenile progeny expected from estimated egg production of the spawning stock.

There are problems with estimation of interannual mortality variations (see 5.2.1).

5.6 Laboratory Holding and Rearing.

No laboratory work has been carried out with juvenile halibut.

6 CURRENT HYPOTHESES ON FACTORS AFFECTING YEAR-CLASS ABUNDANCE

Efforts are continuing at IPHC to capture larvae in selected areas around coastal Gulf of Alaska (Parker, St-Pierre, Trumbull, see 4.2.4). Many long-term time series of oceanographic and meteorological data were developed for various analyses aimed at discerning relationships between the physical environment and recruitment; the findings are reviewed in detail elsewhere (Parker and Schumacher 1984; Parker 1988; Parker, in press). The potential influence of wind-forcing and associated coastal transport processes during the winter season upon larval drift and eventual year-class strength was the primary focus.

Little is known of seasonal ambient levels of secondary production in the Gulf of Alaska, let alone the required prey densities for halibut larvae at various stages in their protracted pelagic phase. The sampling carried out since 1985 by the NOAA Fishery Oceanography Experiment (FOX), together with stomach analyses of captured larvae, should provide needed information. There is likely to be substantial interannual variability in localized production cycles and resultant predator abundance, in light of considerations on the mixed layer dynamics and turbulent wind-mixing discussed in sections 4.3.4. Reduced survival and/or growth rates would result in poorer years, increasing exposure to predation. Such losses would vary with predation conditions and with the duration of egg and larval stages that may be significantly influenced by unusual environmental fluctuations. Nutrient availability (e.g., from central Gulf upwelling with Ekman pumping and coastal Ekman convergence according to the temporal gradient in wind stress curl over the Gulf), timing/duration and intensity of spring production, subsurface chlorophyll maximum layers (vertical stability and shear layers), and variations in the coastal and oceanic circulation (wind- and/or freshwater-driven, by season) represent important factors that may interact to affect early life history success and recruitment.

Transport of eggs and larvae may present substantial differences from year to year, with discernable spatial patterns of variation in abundance and ultimately recruitment. Interannual variations in the Alaska Coastal Current system, particularly vigorous in the western Gulf, greatly affects the alongshore and cross-shelf drift of larvae as they rise into surface layers from deeper waters. Recent data may make it possible to project likely spawning sites. Such trajectories are poorly understood, and research into the actual rates of buoyancy increase with development would be instructive. Mechanisms that control the onshelf flux and entrainment of slope water are thus important, including bathymetric steering via deep trough features cut into the shelf, the Haida Current and related flows, eddies such as the "Sitka Eddy" (Tabata 1982), shelf-break upwelling and simple wind-driven Ekman onshore flow.

The latter process, together with the winter maximum in the coastal circulation cycle, is chiefly the result of seasonal and event-scale winds that appear to conform to interannual variations in the intensity and position of the Aleutian Low atmospheric pressure system. Emery and Hamilton (1985) (see also Hamilton and Emery 1985) found intensified Aleutian lows to be associated with warm coastal waters and high coastal sea levels, and attempted to relate Northeast Pacific oceanic conditions with ENSO (El Niño/ Southern Oscillation) episodes. Their winter mean-pressure index, like that of the North Pacific Oscillation (NPO) of Rogers (1981), correlates well and indicates that the winter season (critical for larval transport) produces the largest interannual atmospheric variability over the Gulf of Alaska. The incidence and duration of blocking-high pressure ridge phenomena in winter and early spring also may affect coastal circulation patterns and, in turn, the biological environment, through reduced or delayed regional atmospheric forcing patterns (White and Clark 1975). A shift in the position of major storm tracks may be instrumental here, in some years generating conditions of transport and/or turbulence that may lead to enhanced recruitment.

The extent to which recruitment variability not explained by the effects of spawning biomass (density-dependence) may have been driven by ocean variability was investigated (Parker 1988; Parker, in press). Significant relationships were found between these variants, within the four subareal management regions encompassing the entire Gulf of Alaska shelf.

Substantial interannual variations were found to exist in the regional environmental series, and alongshore wind energy alone accounted for nearly one quarter of the recruitment variations in the energetic northwest Gulf. Multiple regression models, which included derived geostrophic winds, adjusted sea level, surface atmosphere pressure and freshwater discharge, explained up to 65% of the residual variance in year-class abundance. The latter estimates were based on CPUE, cohort and catch-age analyses of the commercial fishery data, adjusted for migration rates, habitat area, age-specific gear selectivity and incidental catch mortality. The results clearly suggest that interannual fluctuations in the intensity and consistency of critical alongshore and cross-shelf transport processes, including shelf-slope exchange mechanisms, are related to Pacific halibut recruitment success, and further research is encouraged.

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