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December 1989

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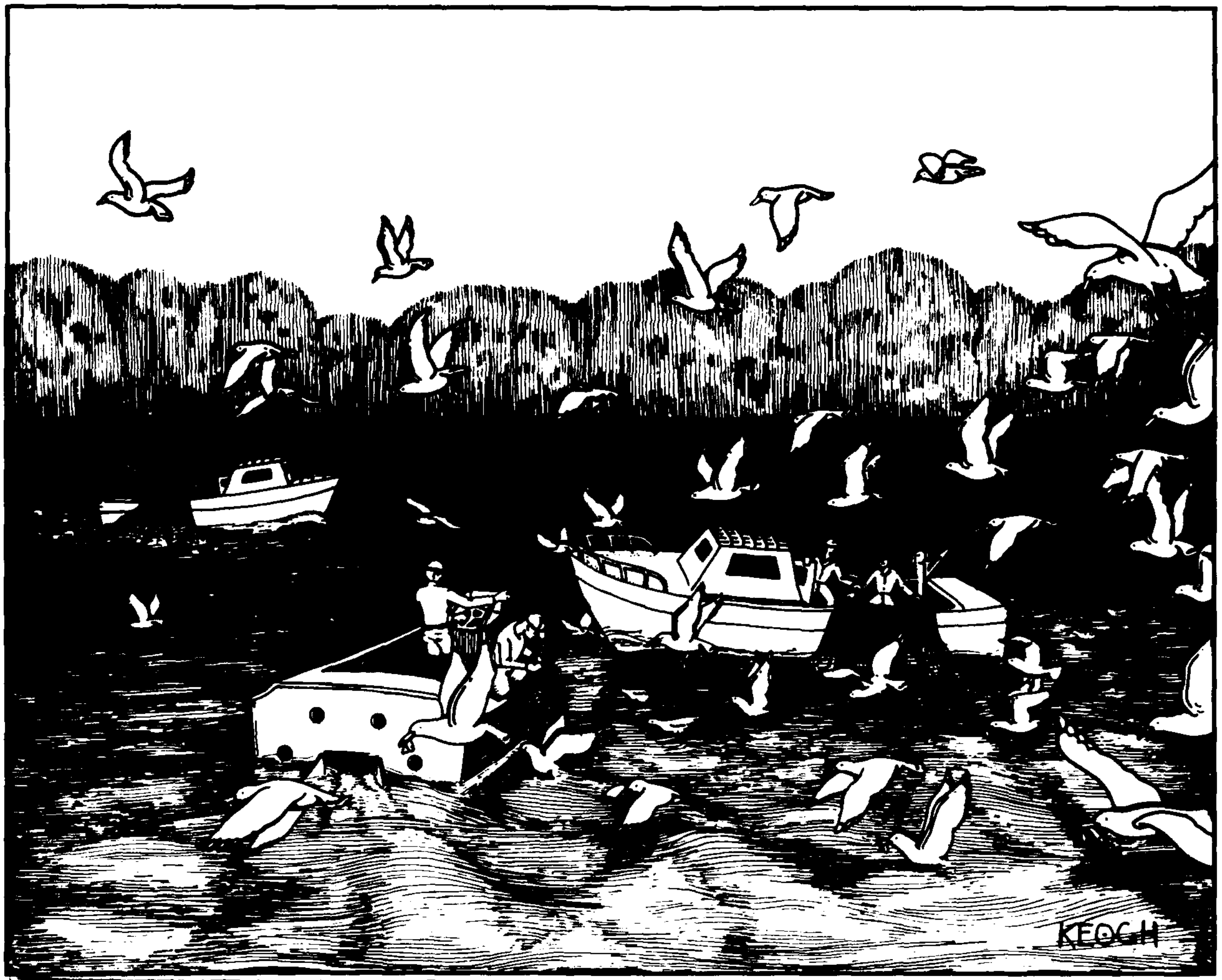
Species Profiles: Life Histories and Environmental Requirements of Coastal Fishes and Invertebrates (Pacific Northwest)

PACIFIC HERRING



Fish and Wildlife Service
U.S. Department of the Interior

Coastal Ecology Group
Waterways Experiment Station
U.S. Army Corps of Engineers

Biological Report 82(11.126)
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Species Profiles: Life Histories and Environmental Requirements of Coastal Fishes and Invertebrates (Pacific Northwest)

PACIFIC HERRING

by

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PREFACE

This species profile is one of a series on coastal aquatic organisms, principally fish, of sport, commercial, or ecological importance. The profiles are designed to provide coastal managers, engineers, and biologists with a brief comprehensive sketch of the biological characteristics and environmental requirements of the species and to describe how populations of the species may be expected to react to environmental changes caused by coastal development. Each profile has sections on taxonomy, life history, ecological role, environmental requirements, and economic importance, if applicable. A three-ring binder is used for this series so that new profiles can be added as they are prepared. This project is jointly planned and financed by the U.S. Army Corps of Engineers and the U.S. Fish and Wildlife Service.

Suggestions or questions regarding this report should be directed to one of the following addresses.

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Vicksburg, MS 39180

CONVERSION TABLE

Metric to U.S. Customary

Multiply	*By*	*To Obtain*
millimeters (mm)	0.03937	inches
centimeters (cm)	0.3937	inches
meters (m)	3.281	feet
meters	0.5468	fathoms
kilometers (km)	0.6214	statute miles
kilometers	0.5396	nautical miles
square meters (m^2)	10.76	square feet
square kilometers (km^2)	0.3861	square miles
hectares (ha)	2.471	acres
liters (l)	0.2642	gallons
cubic meters (m^3)	35.31	cubic feet
cubic meters	0.0008110	acre-feet
milligrams (mg)	0.00003527	ounces
grams (g)	0.03527	ounces
kilograms (kg)	2.205	pounds
metric tons (t)	2205.0	pounds
metric tons	1.102	short tons
kilocalories (kcal)	3.968	British thermal units
Celsius degrees (° C)	1.8 (° C) + 32	Fahrenheit degrees

U.S. Customary to Metric

inches	25.40	millimeters
inches	2.54	centimeters
feet (ft)	0.3048	meters
fathoms	1.829	meters
statute miles (mi)	1.609	kilometers
nautical miles (nmi)	1.852	kilometers
square feet (ft^2)	0.0929	square meters
square miles (mi^2)	2.590	square kilometers
acres	0.4047	hectares
gallons (gal)	3.785	liters
cubic feet (ft^3)	0.02831	cubic meters
acre-feet	1233.0	cubic meters
ounces (oz)	28350.0	milligrams
ounces	28.35	grams
pounds (lb)	0.4536	kilograms
pounds	0.00045	metric tons
short tons (ton)	0.9072	metric tons
British thermal units (Btu)	0.2520	kilocalories
Fahrenheit degrees (° F)	0.5556 (° F - 32)	Celsius degrees

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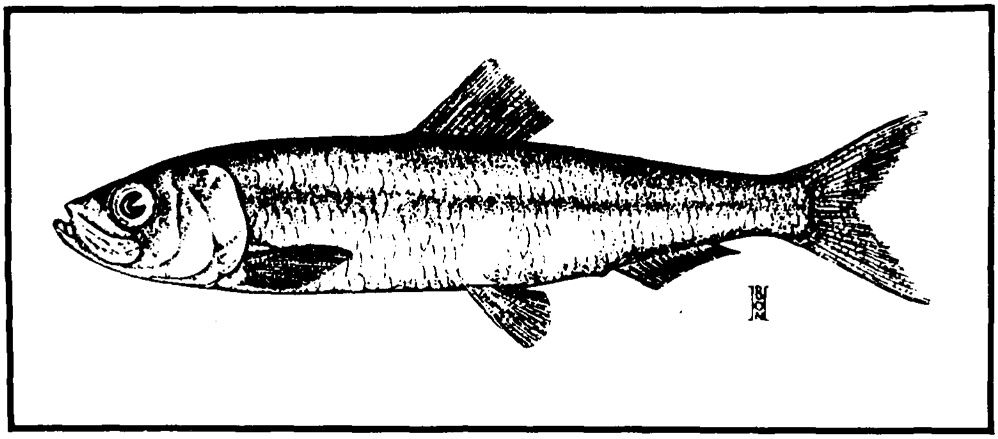

Figure 1. Pacific herring (from Hart 1973).

PACIFIC HERRING

NOMENCLATURE/TAXONOMY/RANGE

Scientific name	*Clupea harengus pallasi* (Valenciennes 1847)
Common name	Pacific herring
Class	Osteichthyes
Order	Clupeiformes
Family	Clupeidae

Geographic range: Geographic distribution of this subspecies extends from northern Baja California well into arctic Alaska and the U.S.S.R., Japan, and the Yellow Sea. It is commercially caught throughout most of its subarctic range.

MORPHOLOGY/IDENTIFICATION AIDS

Body elongate, depth about 4-4.5 in standard length (SL), considerably compressed but variable. Head compressed; mouth terminal, moderate in size, directed moderately upward, lower jaw extending to point below eye; teeth lacking on jaws, ovate patch of fine teeth on vomer. Operculum without striae. Fins: dorsal (1), 15-21; anal, 13-21; pectorals, about 17; pelvics, about 9, abdominal, each with fleshy appendage at base; caudal forked. Lateral line absent. Scales large, cycloid, 38 to 54 along midside, modified along midventral line with keels moderately developed anterior to pelvic fins and strongly developed between pelvic fins and anus. Vertebrae, 46 to 55. Gill rakers, 20 + 45. Color bluish green to olive on dorsal surface, shading to silvery on ventral surface, dusky on peritoneum. Length to 18 inches.

Recognition: Silvery, lacking black spots on sides of body. Also without spines or adipose fin, no scales or striae on head or gill cover, no modified scales on side of tail fin, no teeth on jaws, keels along midventral line only moderately developed (see Figure 1).

The above description is based entirely on the taxonomic accounts of the Pacific herring presented by Clemens and Wilby (1961); Miller and Lea (1972); and Hart (1973).

The elongate form of the larva is easily confused with other species. The posterior position of the anus and the absence of an adipose fin separate clupeid larva from others including sand lance, stichaeid, and osmerid larvae.

REASON FOR INCLUSION IN SERIES

The Pacific herring has a long history of exploitation for human consumption and reduction fisheries for animal feeds and as an item of trade. It also provides food for a wide variety of pelagic, intertidal, and avian predators. The Pacific herring is particularly susceptible to the influences of shoreline development because its spawning grounds are limited to rather specific intertidal and shallow subtidal locations. This and other life history characteristics also make it susceptible to overfishing. The larval stage is sometimes abundantly found in shallow, nearshore waters that are susceptible to shore-based environmental impacts.

LIFE HISTORY

Spawning

Pacific herring, *Clupea harengus pallasi*, spawn primarily on vegetation and substrates in intertidal or shallow subtidal waters (Hay 1985). Substrate spawning within the genus *Clupea* is unique to *C. harengus* and occurs in both the Pacific and Atlantic subspecies (Whitehead 1985). Spawning grounds of Pacific herring are typically in sheltered inlets, sounds, bays, and estuaries rather than along open coastlines (Haegele and Schweigert 1985a). Hay and Outram (1981) noted that the locations of spawning grounds were consistent from year to year. The general distribution and major spawning sites of Pacific herring in the Pacific Northwest are shown in Figure 2. Koons and Cardwell (1981) provided a detailed map of spawning sites in Puget Sound.

Within the range of the species, there is a latitudinal cline in spawn timing. Spawning may begin as early as October in California (J. Spratt, California Department of Fish and Game, Monterrey; pers. comm.) and continue as late as July in northern Alaska (Haegele and Schweigert 1985b). Spawning peaks in February and March in the Pacific Northwest. Regardless of the calendar month, spawning is apparently timed to coincide with "local spring" conditions (Ware 1985), a period of increasing plankton productivity.

Within a season, spawning occurs in "waves" of several days each separated by a little over 1 to several weeks. Larger fish within a stock tend to spawn first and smaller fish later (Hay 1986). In the actual spawning event, a rapid response in females is triggered by the presence of milt in the water column (Stacey and Hourston 1982). Thereafter, the behavior of males and females within the spawning school is simultaneous and nearly identical. Spawning waves are usually completed within 1 or 3 days and may occur either during the day or at night (Hay 1986). Stacey and Hourston (1982) provided an excellent detailed description and illustration of the spawning sequence.

Eggs and Larvae

The eggs of Pacific herring adhere to vegetation and other solid substrates and may vary in density "from a few thinly scattered eggs to more than 20 layers" (Haegele and Schweigert 1985b). Densities are highest in the lower intertidal and upper subtidal zones. The fertilized eggs average 1.2-1.5 mm in diameter (Hart 1973); incubation time is about 2-3 weeks (Hay and Fulton 1983).

At hatching, Pacific herring larvae "depend on endowed yolk to survive" (Lasker 1985). Yolk-sac larvae move actively in the wild (Westerhagen and Rosenthal 1979). Acuity of the larval eye is low (the minimum separable angle is about 3 to 4 degrees in larvae <12 mm long) but is sufficient in larvae 10-12 mm long to detect prey at short distances (Blaxter and Jones 1967). The yolk-sac stage is generally completed within a week; after that, condition factor (weight/volume) begins to increase, coinciding with the onset of feeding (Westerhagen and Rosenthal 1979).

Larval distribution depends on local current patterns (Eldridge 1977) but may be modified

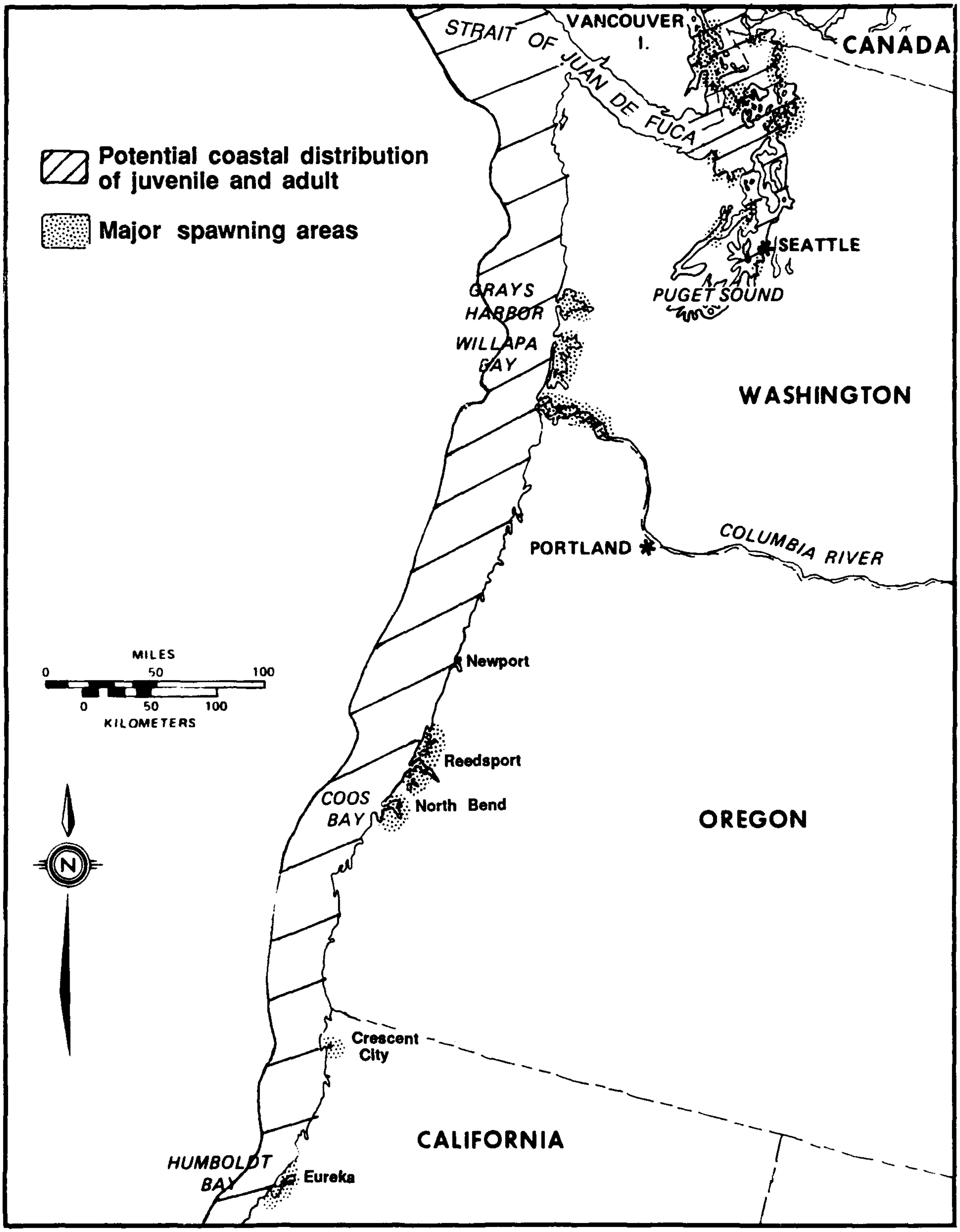

Figure 2. Distribution of the Pacific herring in the Pacific Northwest Region. Shaded areas show known spawning grounds.

by daily vertical migrations--down by day, up by night (Hourston and Haegele 1980). Survival in these early stages therefore depends on stable current patterns that promote larval retention in areas favorable to feeding and growth (Stevenson 1962).

Juveniles and Adults

Larval Pacific herring metamorphose 2 to 3 months after hatching (Hourston and Haegele 1980; Hay 1985) and begin to school when they reach lengths of 25-40 mm (Hart 1973). During the first summer after having been spawned, juveniles gather in large schools and remain primarily in inshore waters (Hay 1985; Stocker et al. 1985). Juveniles may gather after their first summer and move offshore until maturation (Stocker et al. 1985) or they may remain inshore until their first spawning (Hay 1985). First-year juveniles that move offshore live mainly in waters with depths of 150-200 m. Schools of immature fish (second and third year) are found in areas with depths of 100-150 m (Hourston and Haegele 1980). These offshore "juvenile schools" appear to remain separated from offshore schools of adults (Haist and Stocker 1985). Age at first maturity is generally 2-5 years but increases with increasing latitude (Hay 1985) and decreases with increasing exploitation (Ware 1985).

Not all stocks of Pacific herring make this extensive offshore migration. Many small resident populations remain in coastal inlets and bays (Stevenson 1955). Some stocks migrate offshore in the spring after spawning and return from their offshore feeding grounds to inshore waters during the late fall and early winter of each year. The large schools of adults may arrive inshore weeks or even months before the spawning season (Hourston 1980). The move from inshore "holding" areas to spawning sites may simply be from deep water to the adjacent shallows (Hardwick 1973) or may cover long distances in a short time. On the west coast of Vancouver Island, BC, a tagged herring moved 150 km in 6 days (Haegele and Schweigert 1985b). Migratory and non-migratory stocks may mix while both are inshore but apparently separate before spawning (Hay 1985).

GSI and Fecundity

The gonadosomatic index (GSI) is an expression of gonadal weight as a percentage of total body weight. It has been found to provide "a sensitive and quantifiable estimate of maturity" for Pacific herring (Hay and Outram 1981). Since much of the fishery for Pacific herring is for their eggs, or roe, such an index can be extremely useful in correctly timing the fishery to maximize egg yield. The seasonal pattern of gonadal development for male and female Pacific herring from the lower eastern coast of Vancouver Island, BC (adjacent to Puget Sound, WA) is shown in Figure 3. GSI is lowest in the months after spawning and then begins to increase sharply in the fall. Large herring attain a higher maximum GSI than do the smaller adults (Hay 1985). The GSI of female Pacific herring during the spawning season was estimated at 29% (Gunderson and Dygert 1988).

Males begin gonadal development earlier, develop faster, and reach a lower maximum GSI than females (Hay and Outram 1981). Hay (1986) wrote that the "energy investment of

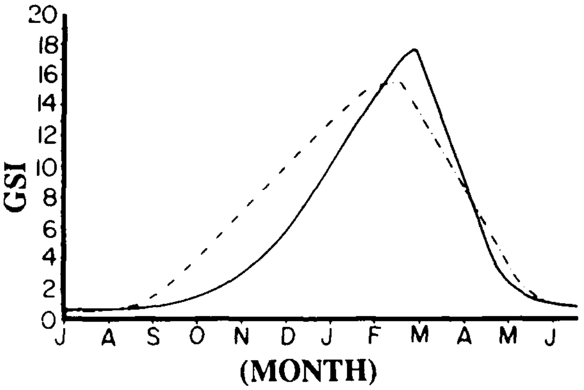

Figure 3. Seasonal pattern of gonadosomatic index (GSI = gonad weight + whole body weight X 100%) in a resident stock of Pacific herring (adapted from Hay and Outram 1981). Solid line is females; dashed line is males. The pattern shown here may not be the same for migratory stocks. Most populations have a maximum GSI above 25%.

Pacific herring in gonadal development is substantial--ovaries usually exceed 25% of the total body weight." Peak GSI in females may be as high as 30%-32% (Hay and Outram 1981; Hay 1986). Reduction of the number of mature oocytes by atresia prior to spawning was found in experimental impoundments and may occur naturally (Hay and Brett 1988).

The estimation of fecundity in Pacific herring has been related by various researchers to length, weight, or age (see Table 1). A pattern of decreasing length-specific fecundity with increasing latitude is widely reported (Katz 1948; Paulson and Smith 1977; Hay 1985). However, exceptions within more restricted geographic areas (specifically coastal British Columbia) have also been noted (Nagasaki 1958). Hay (1985) discounted the roles of GSI and egg size in explaining the widespread latitudinal differences. He suggested instead that the more southern stocks "have a steeper length-weight relationship." A similar explanation was given by Paulson and Smith (1977).

Although herring from northern stocks are characterized by decreased size-specific fecundity, they are also characterized by greatly increased maximum size (Katz 1948; Paulson and Smith 1977). Their average and maximum

Table 1. Equations for the estimation of fecundity in Pacific herring.

Equation[a]	Source	Location
$F=7.98\ (\times 10^{-4})\ L^{3.171}$	Quisheng (1980)	Yellow Sea
$F=4.2\ (\times 10^{-4})\ SL^{3.316}$	Paulson and Smith (1977)	Prince William Sound, AK
$\log F=3.25 \log SL + 0.08 \log A - 3.17$	Nagasaki (1958)[b]	Northern British Columbia
$F=2.33\ (\times 10^{-3})\ L^{3.028}$	Hay (1985)[c]	Northern British Columbia
$F=555\ W^{0.782}$	Ware (1985)	Straits of Georgia, 1974
$F=111\ W^{1.120}$	Ware (1985)	Straits of Georgia, 1980
$\log F=2.16 \log SL + 0.32 \log A - 0.90$	Nagasaki (1958)[b]	Southern British Columbia
$F=4.19\ (\times 10^{-4})\ L^{3.372}$	Hay (1985)	Southern British Columbia
$F= -63920.9 + 496.6\ SL$	Rabin and Barnhart (1977)	Humboldt Bay, CA
$F= -56788.4 + 443.4\ SL$	Hardwick (1973)[d]	Tomales Bay, CA

[a] Abbreviations: F = fecundity (number of eggs), L = length (mm), SL = standard length (mm), A = age (yrs), and W = whole wet weight (g).

[b] Nagasaki (1958) did not actually measure standard length but approximated it by measuring from "tip of snout to end of silvery area on the peduncle."

[c] Hay (1985) did not specify whether female "length" was measured as standard, fork, total, or some other measure of fish length.

[d] Based on data presented by Hardwick (1973, Table 1).

fecundities, therefore, are actually higher. Female Pacific herring from Siberian stocks, in fact, are reported to reach 370 mm SL and have an estimated fecundity in excess of 134,000 eggs (Katz 1948). The fish may be larger because they are older. Older fish may be more ubiquitous in northern waters because of sporadic recruitment and the absence of substantial fisheries.

GROWTH

The average length of Pacific herring at the time of hatching is 7.5 mm (Hart 1973). Alderdice and Hourston (1985) estimated a growth rate of 0.48-0.52 mm/day during the first 15 days after hatching. Estimations were based on field samples from Nanoose Bay, Vancouver Island, BC, at ambient temperatures of 8.8-9.1 °C. This rate is two to three times the growth rate observed by Boehlert and Yoklavich (1984) for larvae of similar age raised in the laboratory at a temperature of 10 °C and salinity of 15 ppt. Larvae metamorphose into juveniles at a length of 25-40 mm about 10 weeks after hatching (Hart 1973; Hourston and Haegele 1980). Scales begin to appear at this time and the juveniles develop the general appearance of adults.

Haist and Stocker (1985) concluded that the growth rate of juvenile Pacific herring was equally moderated by temperature conditions and density-dependent factors. They suggested, however, that density-dependent effects on adult growth rate would be evident only in severely reduced stocks. Spratt (1981) found no significant difference in the growth rates of males and females. Size-at-age data are summarized in Table 2. Trumble and Humphreys (1985) calculated von Bertalanffy growth equations for stocks from San Francisco Bay and the eastern Bering Sea. Growth rate was higher in San Francisco Bay ($K = 0.59$ vs. $K = 0.18\text{-}0.35$), but maximum size was greater in the eastern Bering Sea ($L_{\infty} = 299\text{-}314$ mm vs. $L_{\infty} = 208$ mm). This same inverse relation between K and L_{∞} along a latitudinal gradient was noted for stocks in the vicinity of Puget Sound (Gonyea and Trumble 1983). Growth was slowest and maximum size greatest in the Strait of Georgia ($K = 0.36$, $L_{\infty} = 263$ mm). Growth rate was near its highest ($K = 0.59$) and maximum size at its lowest ($L_{\infty} = 197$ mm) in Case Inlet. The differences, however, may result because the Strait of Georgia stocks are migratory while the Case Inlet stocks are resident. Less than 2 degrees of latitude separate the two areas.

Pacific herring may attain a total length of 18 inches (Miller and Lea 1972) and weight of 550 g (Ware 1985). Longevity may exceed 15 years, but few live longer than 9 years (Ware 1985). A review by Gunderson and Dygert (1988) listed longevity at 10 years. They presented the size and age of a female at 50% maturity as 209 mm and 3 years.

THE FISHERY

History and Products

Native Americans have for many centuries used nets, traps, and mazes to capture Pacific herring for use as a fresh or salted food source, for trade, and for bait (Hourston and Haegele 1980; Trumble and Humphreys 1985). In the early 1900's, dry salted herring and canned herring were important products for human consumption. Large quantities were also reduced to fish meal and oil. Market demand or processing capacity usually limited catches (Hourston 1980). From about a decade after World War II until the early 1970's, demand for herring and for human consumption declined and Pacific herring supported only a relatively minor fishery in California (Spratt 1981). To the north, at the center of the Pacific herring's abundance, British Columbia reduction fisheries prospered until the mid-1960's, when a major decline occurred. The decline was apparently precipitated by continued heavy fishing through a period of several years of poor recruitment (Hourston 1980; Ware 1985).

The removal of Japanese import quotas in the early 1970's opened a new market to U.S. and Canadian herring fishermen. The product of this fishery was the eggs (roe) of mature females for use as kazunoko (i.e., caviar), a far more valuable product than other uses of Pacific herring. Consequently, roe fisheries had

Table 2. Size of Pacific herring at different ages.

	Age (years)									Source and location
	1	2	3	4	5	6	7	8	9	
W[a]		56.5	90.0	112.5	136.0	155.5	-	-	-	Haist & Stocker (1985), Strait of Georgia
W[b]	22.1	66.0	86.7	106.3	130.6	147.9	164.6	180.1	201.4	Spratt (1981), Tomales Bay
W[b]	18.5	57.9	75.9	95.6	116.8	130.5	149.8	156.6	-	Spratt (1981), San Francisco Bay
BL[c]	113.0	164.0	180.0	193.0	207.0	216.0	224.0	231.0	240.0	Spratt (1981), Tomales Bay
BL[c]	113.0	161.0	175.0	188.0	200.0	200.0	216.0	219.0	-	Spratt (1981), San Francisco Bay
L[d]	90.3	153.6	197.9	232.0	255.4	278.4	291.9	-	-	Naumenko (1979), eastern Bering Sea

[a]W = mean whole wet weight (g) for males and females combined from Haist and Stocker (1985, Table 1).

[b]W = expected whole wet weight (g); calculated from observed mean body length (this table) and length/weight relationships provided by Spratt (1981):

Tomales Bay $W = 0.2125(x10^{-4})\ BL^{2.9316}$

San Francisco Bay $W = 0.4278(x10^{-5})\ BL^{3.2317}$.

[b]BL = mean body length; Spratt (1981) measured "body length" from "the tip of the snout to the end of the silvery part of the body."

[d]L= mean length; Naumenko (1979) did not mention whether "length" was measured as standard, fork, total, or some other measure of fish length.

been initiated coastwide by 1973 (Hardwick 1973; Trumble and Humphreys 1985), and have now become the predominant fishery for Pacific herring. Landings in California, Oregon, and Washington since 1979 are shown in Table 3.

The possibility of stable, substantial markets and high prices for a quality product in roe fisheries led to the development of fleets that by the 1980's had many times the needed catching capacity, especially since effort shifted to concentrate on the dense aggregations which typify this species' prespawning behavior. To prevent overharvest and to avoid exceeding processing capacity, most State or Provincial governments now manage these nearshore stocks by using limited entry permit systems for very brief openings--sometimes as short as 15 minutes (Hourston 1980; Trumble and Humphreys 1985). The season for a large general area may be longer (sometimes 3 months). The culturing of prespawning fish in impoundments is probably not a viable alternative at this time because the current fishery is doing well. Should impoundment be recommended in the future, experiments on impounded fish showed that mortality was low. Age-, length-, and weight-specific fecundity were in the range of fish in the wild. Density and cover had no detectable influence on mortality (Hay and Brett 1988; Hay et al. 1988).

Herring for human consumption, other than as sac-roe, still command a market share;

Table 3. Pacific herring landings in short tons (2,000 lb) in California, Oregon, and Washington, 1977-86. Data provided by State management agencies.

	Landings (short tons)							
State	1979	1980	1981	1982	1983	1984	1985	1986
California	4,623	7,103	6,313	11,331	10,515	2,989	8,305	8,620
Oregon	88	70	74	72	73	89	82	[a]
Washington[b]	4,263	3,273	966	1,202	666	425	464	493

[a] Data not available.

[b] The sac-roe fishery in Washington has been closed since 1981 except for a brief opening in 1982. Data for 1983-86 are for the bait fishery only.

however, this and other fisheries for Pacific herring are much smaller than the roe fishery. Pacific herring is widely used for bait by recreational and commercial salmon trollers, halibut longliners, and crabbers. Small fisheries also remain that harvest fish for reduction to fish meal and for animal food in zoos and aquaria (Trumble and Humphreys 1985).

Another product of herring fisheries, and more recently of developing aquacultural interest, is spawn-on-kelp. As the name suggests, both the eggs and the algal substrate on which they have been laid are harvested. The alga is often a kelp species but may be any of a number of other algae as well--e.g., *Gracilaria* (Hardwick 1973). The harvest of algae blanketed with naturally spawned eggs had been practiced in California since 1965 (Hardwick 1973). Again, this caviar-like product is exported almost entirely to Japan. However, the expansion of Japanese import markets in the early 1970's encouraged the development, led by British Columbia fishermen, of a more reliably available product through aquacultural practices. In the closed pond method, schools of nearly ripe adults are encircled by nets and held until they have spawned on the fronds of kelp that have been placed in the enclosure. In 1985, the spawn-on-kelp fishery in northern California began to use an open-pond method in which fronds of *Macrocystis pyrifera* brought in from southern California are attached to rafts in the vicinity of known spawning grounds (J. Spratt, pers. comm.). The egg-laden fronds provide a useful technique to provide spawning substrate at particular times and thereby control the timing of egg release. Possible conflicts with the roe fishery, however, have caused a hesitancy to develop spawn-on-kelp fisheries in both Puget Sound and California. An experimental spawn-on-kelp operation run by Native Americans may be developed in Port Gamble Bay, Washington (Dwane Day, Washington Department of Fisheries, Olympia; pers. comm.). Interest has also been expressed in developing a spawn-on-kelp fishery in Coos Bay, Oregon (Jerry Butler, Oregon Department of Fish and Wildlife, Newport; pers. comm.).

Stocks

Haegele and Schweigert (1985) indicated that the variety of spawning sites and times made it difficult to identify genetically distinct stocks of Pacific herring. They remained convinced, however, that efforts should be made to maintain stock diversity because if the time of spawning is genetically influenced, then the reestablishment of lost stocks may be impossible. The identification of separate Pacific herring stocks has been attempted by a number of methods, including patterns of fecundity (Katz 1948), parasitism (Arthur and Arai 1980), and growth (Gonyea and Trumble 1983). A complicating factor in the maintenance of stock diversity is the mixing, particularly in stocks exploited by offshore food or reduction fisheries, that may occur before stocks separate for spawning (Buchanan 1983; Fried and Wespestad 1985).

Of the "12 known spawn areas" in California (Trumble and Humphreys 1985), only San Francisco and Tomales Bays support major herring stocks. Based on information presented by Spratt (1981, Table 3) for 1973-80, only about 1% of the total California catch is taken in the Pacific Northwest region (Humboldt Bay and Crescent City). Pacific herring stocks in Oregon are relatively small but stable (Trumble and Humphreys 1985). Yaquina Bay is the only Oregon bay that supports a commercial roe fishery, but Coos, Umpqua, and Tillamook Bays support smaller bait and recreational fisheries (Jerry Butler, pers. comm.). Most of the Pacific herring fisheries in Washington are in Puget Sound rather than along the open coastline. Gonyea and Trumble (1983) suggested the existence of at least three separate stocks (Strait of Georgia, Northern Hood Canal, and Case Inlet) in the vicinity of Puget Sound.

Population Dynamics and Management

Hourston and Haegele (1980) estimated that of all stages in the life history of the Pacific herring, larvae experienced the greatest mortality (>99%). They further estimated an average mortality of 20% at the egg stage and a total annual mortality (A) of 50% for adults (= an instantaneous total mortality, Z, of 0.69). Egg mortality may sometimes be much higher. Hardwick (1973) estimated a loss to predation alone of 56%-99% and suggested that two-thirds of this mortality occurred within the first 3 days of spawning. By assuming some degree of compensatory decrease in predation, however, he suggested that a harvest by spawn-on-kelp fishermen of "10% of the eggs spawned would not significantly reduce the number of eggs that hatch." High egg loss may only occur south of British Columbia on the U.S. coast, where total egg production in an area is typically small and there may be no swamping of predators with many more eggs than they can consume. In British Columbia, where up to 30,000 t may be spawned over several days in one area, egg loss rates are much smaller. Hourston and Haegele (1980) cited a correlation between juvenile abundance and abundance at recruitment as evidence that year-class strength is determined by the time Pacific herring have reached the juvenile stage.

In a review of Pacific herring management, Trumble and Humphreys (1985) wrote that "most estimates of instantaneous natural mortality (M) [for adults] fall very consistently in the range of 0.4-0.5." Similar but slightly lower estimates were given by Fried and Wespestad (1985, M = 0.39) and by Schweigert and Hourston (1980, M = 0.36). Stocker et al. (1985) reported that the instantaneous natural mortalities in the Strait of Georgia ranged from 0.31 to 0.71. A review by Gunderson and Dygert (1988) lists M at 0.56, as estimated from the gonadosomatic index (GSI). They found a positive correlation for 20 different species of fish, between M and GSI, indicating that the GSI of those species can predict the natural mortality rates for fishery management models. Schweigert and Hourston (1980) reported a mean instantaneous fishing mortality (F) for 1972-79 of 0.59 for a heavily exploited Canadian stocks.

By combining the instantaneous rates of natural and fishing mortality from Schweigert and Hourston's study (1980), a total instantaneous mortality rate ($M + F = Z$) of 0.95 can be calculated. This translates to an annual mortality rate ($A = 1 - e^{-Z}$) of 61%. Trumble and Humphreys (1985) reported Z values of 0.50 (A = 39%) for a relatively unexploited stock and 0.62 (A = 46%) for an exploited stock in Puget Sound. Hourston (1980) reported that "apparent annual mortality rates, from 75% to over 90%, did not depress the abundance of the stocks" in the 1950's. Annual mortality rates of 75% and 90% translate to Z values of 1.39 and 2.30, respectively.

Another common expression of the influence of fishing pressure on stocks is the exploitation rate (E) which expresses instantaneous fishing mortality as a percentage of instantaneous total mortality (i.e., $E = F/Z$). Judging from the

Pacific herring's ability to compensate for exploitation through increased growth and decreased age at maturity, Ware (1985) estimated that E should not exceed 0.2-0.3 to avoid adversely affecting stock resilience. Similarly, Fried and Wespestad (1985) considered the balance between yield and maintenance of the spawning stock to produce a suggested exploitation rate of 0.2. Also rather conservative in his estimate, Spratt (1981) suggested a quota of not more than 20% of the previous year's spawning biomass for California roe fisheries.

Smith (1985) concluded that "theoretical population approaches and correlative environmental indices are not yet sufficient for setting catch limits . . . direct measurement of current biomass appears to be necessary for setting clupeoid quotas." On the basis of direct estimation techniques such as hydroacoustics and spawning ground surveys, U.S. management agencies generally set quotas as a percentage (usually <20%) of the standing stock.

ECOLOGICAL ROLE

Feeding Habits

If other environmental conditions are sufficient for successful hatching, it is likely that larval survival is dependent on timing in relation to predation and food supply (Blaxter and Hunter 1982; Alderdice and Hourston 1985). Larval Pacific herring begin feeding during or immediately after the yolk-sac stage, at a length of 9.5-11.0 mm (Westernhagen and Rosenthal 1981; Lasker 1985). Earliest food consists mainly of copepods, invertebrate eggs, and diatoms (Hart 1973). As larvae, clupeoids "are characterized by straight, relatively undifferentiated guts" (Boehlert and Yoklavich 1984).

In laboratory aquaria, Boehlert and Yoklavich (1984) fed ^{14}C-labeled rotifers to a group of small larvae (mean notochord length, NL, = 10.3 mm). Assimilation efficiency ranged from 44% to 59%. In another group of larger larvae (mean NL = 13.8 mm), which were fed brine shrimp nauplii, assimilation efficiency ranged from 38% to 68%. In both groups, assimilation efficiency was inversely related to ingestion rate. Even with the decrease in assimilation efficiency, however, overall energy uptake was greater at high food density. This pattern of maximizing energy by maximizing the number of prey taken may enable larval herring to better exploit patchy food sources (Boehlert and Yoklavich 1984).

If larvae are unable to feed soon after hatching, they may "give up" (Lasker 1985) and die of starvation. McGurk (1984) noted a decrease in growth and an increase in mortality with increasing age of first feeding and increasing temperature. The time from exhaustion of the yolk-sac to the age of irreversible starvation decreased from 8.5 d at 6 °C to 6 d to 10 °C. McGurk further suggested that catastrophic mortality due to starvation may occur in 18%-36% of natural populations of first-feeding Pacific herring larvae. Westernhagen and Rosenthal (1981) attributed the occurrence of emaciated larvae in 1976 in the Strait of Georgia to poor food supply during the critical period (sensu Hjort 1914). Contrary to theory, however, they noted that this same 1976 year-class yielded an extremely good recruitment. This finding seems to cast doubt on starvation as a singular cause of year-class failures and supports the conclusion of Cushing (1985) that we should perhaps "consider predation and starvation as equivalent factors, not exclusive ones."

By the time of metamorphosis, barnacle and mollusk larvae, bryozoans, rotifers, and larval fish are included in the diet, but copepods still predominate (Hart 1973). Levings (1983) noted that the diet of juveniles 45-55 mm long depended on invertebrates that live in eelgrass beds, such as decapod larvae, harpacticoid and calanoid copepods, gammarid amphipods, and barnacle larvae. During summer, while the fish attain lengths of 70-100 mm, copepods remain an important diet item (Hart 1973). As the herring mature, copepods may be superseded by euphausids. However, since they then move into deeper offshore waters where sampling is difficult, little is known about their feeding until they return as adults for spawning.

Pacific herring undertake daily vertical migrations. At dusk, they move up in the water column and begin to disperse and feed. Ingestion may either be by visually mediated particle feeding or, when particle size is less than 300-400 μm, by filter-feeding (Blaxter 1985). The herring may gather near the bottom during the day, but are frequently observed in midwater schools at that time.

During their spawning migration and the inshore "holding" period, Pacific herring may reduce their intake or stop feeding altogether (Ware 1985). Stacey and Hourston (1982) examined feeding response in laboratory-held Pacific herring during various seasons. Feeding response was reduced during October and November (the usual period of spawning migration) and was at its lowest during February and March (the period immediately before spawning). Herring resume feeding heavily after spawning and continue to feed through the summer as they move offshore (Stacey and Hourston 1982). Over summer and early fall, herring increase in oil content and condition factor (Ware 1985). These stored lipids apparently support the energy requirements of the herring as they again move inshore and undergo the gonadal development that precedes spawning.

This pattern of feeding offshore and spawning inshore represents a movement of considerable energy from offshore to inshore waters. Hay and Fulton (1983) estimated that "about 22% of the total herring spawning stock biomass is released as milt and eggs." They noted that this is a small portion of the carbon budget over an annual cycle, but may be "substantially higher than maximum estimates of primary productivity" over the period from spawning until larval emergence. Hay and Fulton (1983) suggested that the heavy organic input of eggs and milt may promote a burst of secondary production, especially in the form of increased microzooplankton that feed on the organic matter. They additionally suggested that the emergence of larvae from the same spawn may coincide with this increased zooplankton availability. In other words, the larval herring may thus be the beneficiary of this burst in local productivity.

Sources of Mortality

The earliest source of mortality is the failure of eggs to hatch because of unsuitable environmental conditions, such as salinity and temperature (Alderdice and Hourston 1985). Other identified sources of mortality at the egg (or zygote) stage include physical destruction by wave action during storms (Hay and Miller 1982), intertidal exposure and desiccation (Haegele and Schweigert 1985b), suffocation due to high egg densities or silting (Haegele and Schweigert 1985b), and most especially, predation. The list of known egg predators is long, but birds are most consistently cited as the major predator (Hardwick 1973; Hourston and Haegele 1980; Alderdice and Hourston 1985). Birds that feed on eggs in California include the California gull (*Larus californicus*), mew gull (*L. canus*), glaucous-winged gull (*L. glaucescens*), western gull (*L. occidentalis*), coot (*Fulica americana*), and surf scoter (*Melanitta perspicillata*) (Hardwick 1973). Gulls feed directly on the eggs. Diving ducks may cause mortality either by direct consumption or by dislodging the egg-laden algae and setting them adrift to wash ashore.

Predation on larval herring may be extremely high (Hourston and Haegele 1980). Medusae and other pelagic invertebrates may be the major predators. Arai and Hay (1982) demonstrated in laboratory aquaria that several species of medusae common to coastal waters were capable of feeding on Pacific herring larvae. Field surveys led them to believe that "the hydromedusae *Sarsia tubulosa* and *Aequorea victoria* may be the most abundant during the time of peak herring larval abundance." Both species were collected with herring larvae in their stomachs. Ctenophores and chaetognaths may also be important predators of larvae (Stevenson 1962). Juveniles of a common pelagic hyperiid amphipod, *Hyperoche medusarum*, may occur in high numbers along with abundant Pacific herring larvae and may prey on the larvae (Westerhagen and Rosenthal 1976). Hourston and Haegele (1980) suggested that juvenile salmonids on their seaward migration would feed on larval herring. Other fishes and invertebrates that have been observed to prey on herring eggs include sturgeon (*Acipenser* sp.), smelt (family Atherinidae), surfperches (family Embiotocidae), and crabs (probably *Cancer* sp.) (Hardwick 1973). Hourston and Haegele (1980) also noted that even juvenile and adult Pacific herring, when in the vicinity of the spawning grounds, may feed "voraciously" on the eggs and newly hatched larvae of their own species.

Again, little is known of predation on juvenile herring. Adults are susceptible to predation while holding inshore before and during the spawning season. Among the predators that feed on herring at these times are salmon, seals, sea lions, killer whales, dogfish, and birds (Hourston and Haegele 1980). Pacific herring were the most important prey of the northern fur seal, *Callorhinus ursinus*, in the inshore waters of the northern coast of Washington (Perez and Bigg 1986). Pacific herring, containing 2.17 kcal/g, were among the prey with the highest energy content. When herring are feeding offshore, important predators include hake, sablefish, dogfish, Pacific cod, and salmon.

ENVIRONMENTAL REQUIREMENTS

Salinity

Salinities at which apparently viable Pacific herring eggs have been found range from 3 to 35 ppt (Alderdice and Velsen 1971; Alderdice and Hourston 1985; Haegele and Schweigert 1985b). Reported optima fall in a somewhat narrower range of 12-26 ppt (Alderdice and Velsen 1971). In their own study, Alderdice and Velsen observed maximum egg and larval survival in the range of 13-19 ppt, around an optimum of 17 ppt. Galkina (1957), cited by Haegele and Schweigert (1985b), noted a sharp decrease in the successful fertilization of eggs at salinities below 5 ppt. Alderdice and Hourston (1985) determined an "incipient lethal limit" (3-day LC_{10} with 3-day-old larvae) in the range of 27.5-31.7 ppt. The lower 72-hour median tolerance limit, or the limit at which 50% mortality occurred at 72 hours of exposure, was 2.8-5.2 ppt for larvae 0-9 days old (Alderdice et al. 1979). The upper limit was 33.0-35.8 ppt, but substantial mortality is expected above 20 ppt.

Temperature

The range of temperatures at which naturally spawned eggs have been observed is fairly broad, ranging from below 0 to 14 °C (Alderdice and Velsen 1971; Haegele and Schweigert 1985b). However, most natural spawnings occur between 3 and 9 °C (Alderdice and Velsen 1971). Again, in their own studies, Alderdice and Velsen determined that optimum egg development occurred in the range of 5.5 to 8.7 °C and that survival of eggs and larvae was highest at about 8.7 °C. They also noted that abnormalities developed in the lower jaws of larvae from eggs incubated at 4.0 to 4.7 °C. Alderdice and Velsen (1971) suggested that 10 °C represented an approximate upper limit to natural spawning in the Pacific Northwest. However, water temperatures of 10 to 12 °C are about average for natural spawning grounds in California (J. Spratt, pers. comm.).

Optimal temperatures for juvenile and adult Pacific herring seem to be a few degrees higher than those for eggs or larvae. Of the environmental factors analyzed by Haist and Stocker (1985), sea surface temperature best fits their model for juvenile growth. The suggested optimum temperature was 12.2 °C. In their adult surplus energy model (energy for somatic and gonadal growth), an optimum temperature of 11.4 °C was estimated.

Temperature and Salinity Interaction

Alderdice and Velsen (1971) provided an extensive review of the literature that dealt with the effects of temperature and salinity on Pacific herring. Most studies dealt with only the egg and larval stages. Alderdice and Velsen (1971) concluded that "Pacific herring eggs are considered euryhaline and stenothermal." More specifically, their review led them to conclude that "Pacific herring populations on the North American coast are confined to regions providing protected spawning waters of reduced salinity (8-28 ppt S) at temperatures between about 5.0-5.5 °C and 8.8 or 9 °C," and that the size of these populations is related to the physical extent of the regions that provide these spawning requirements. Alderdice and Hourston (1985) narrowed these ranges when they concluded that the Pacific herring "appears to have an optimum salinity-temperature maximum for physiological performance during its early life history in the region of 12-17 ppt at temperatures near 6.5-8.3 °C." They also determined that reproductive success occurs over a wide range of temperature and salinity and that salinity plays a major role below 7 °C but not above that temperature.

Substrate

Since the Pacific herring is a pelagic rather than demersal species throughout most of its life history, information on substrate use is entirely related to spawning and egg deposition. References to the specificity of spawning substrate selection vary considerably. Hardwick (1973) stated that once the herring have moved into shallow waters, "they spawn on whatever substrate is available." Haegele and Schweigert (1985b), on the other hand, observed that "eggs are laid almost exclusively on marine vegetation, algae and sea grasses, although quite frequently eggs adhere to the rocky substrate to which the algae are attached." Within the vegetation as a substrate category, however, they found that herring "do not appear to favor one type . . . over another." Some of the plants commonly used as egg deposition sites include the seagrass *Zostera* and several brown or red algae of the genera *Macrocystis, Fucus*, and *Gracilaria*. Statements of preference or of selectivity in on-site substrate use that are based on nonmanipulative field studies must be tempered by the understanding that what is "available" may have been strongly biased by rather specific site selection.

During laboratory observations of Pacific herring spawning behavior, Stacey and Hourston (1982) noted that "rigidity and texture appear to be important components of suitable substrates." In general, a suitable substrate was judged to be one that was "rigid, smooth, and free of sediment." Haegele and Schweigert (1985b) similarly noted that spawn was deposited on substrates "free from silting." Apparently, the presence of sediment on a substrate is sufficient to inhibit certain behavioral transitions in the normal spawning sequence (Stacey and Hourston 1982).

The use of vegetation as a spawning substrate raises a very practical consideration for fishery management. Two resources, the herring and the algae upon which they spawn, must be managed. As Hardwick (1973) pointed out in the case of Tomales Bay, "a continued supply of *Gracilaria* is essential to a viable herring egg-on-seaweed fishery." Unfortunately, this fishery ended in 1977 because of silt contamination of the product (J. Spratt, pers. comm.).

Oxygen

I found no reference to the oxygen requirements of any Pacific herring life history stage other than the eggs. Alderdice and Hourston (1985) suggested a minimum ambient oxygen concentration of 2.5 mg/ml at the egg's surface. In other words, to achieve this ambient oxygen concentration for deeper layers within an egg mass, water column oxygen concentration must be much higher. The amount higher depends, of course, on the water's ability to penetrate the egg mass and, therefore, upon water movement. Haegele and Schweigert (1985) suggested that eggs elevated from the bottom on vegetation could avoid siltation and receive better circulation for waste removal and oxygenation.

Contaminants

Of the life stages of the Pacific herring, the larvae is most sensitive to the water-soluble fraction (WSF) of crude oil. The LC_{50} (concentration at which median or 50% mortality occurred was 0.37 ppm WSF and the LC_{50} for indirect exposure (exposure of prey later consumed) was 6 ppm WSF (Carls 1987). Larval growth was correlated with larval feeding, and both were reduced after WSF exposure. Exposure may affect growth by causing biochemical changes or by reducing feeding rate. In clean water, larvae rapidly depurated hydrocarbons from tissues, and survivors resumed growth and feeding (Carls 1987).

CONCERNS

Various authors whose papers I reviewed expressed concerns regarding informational needs or management. Some of these are discussed below.

One rather surprising generalization made by Cushing (1985) was that "management of herring stocks based on a great expenditure of research has not been very successful." In view of such management difficulties, the very basic concerns of others take on a special importance--especially with respect to coastal development policy. I refer to the statement by Trumble (1983) that "there is no clear instance of a stock successfully moving its spawning area as a result of destruction or major alteration of their original spawning area." A study of the transplantation of eggs concluded that though eggs hatched, a new spawning population did not become established (Hay and Marliave 1988). Clearly, the maintenance of relatively undisturbed, quiescent areas of vegetation is a valid concern.

Also pertinent to the maintenance of functional spawning grounds is the avoidance of activities (e.g., dredging) which would cause silting immediately before, during, and two to three months following the spawning season. The inhibition of spawning behavior, suffocation of eggs, and destruction of product quality were mentioned earlier. It also seems likely to me that a heavy loading of suspended sediment would be ingested or feeding inhibited during a period critical to the nutrition of both adult and newly hatched larvae. Boehlert and Morgan (1985) noted that sediment at "low suspension levels" roughly equivalent to natural conditions actually enhanced larval feeding abilities. Higher loads, as might be expected in catastrophic events, inhibited feeding.

Other specific concerns relate to the biology of the species and the efficiency of fishery management. Alderdice and Velsen (1971) believed that there was a need for the systematic collection of temperature and salinity measurements at the spawning site and for the examination of temperature and salinity tolerances of eggs and larvae from "representative stocks over the range of the species." Such data could be used to build a data base for correlating recruitment with environmental factors. Hay (1985) noted that the time and place at which recruits join the spawning population, the patterns of larval dispersal and mortality, and the distribution and ecology of 0-group juveniles were all areas that are poorly understood. Haegele and Schweigert (1985b) were concerned with the maintenance of genetic diversity in order to assure no further reduction in the production capacity of herring stocks. Trumble and Humphreys (1985) thought that there was a need to better separate the effects of natural mortality and fishing in explaining stock declines. These same authors, as well as Wilimovsky (1985), expressed concern with the availability and precision of pre-season quota estimates to better prepare the herring roe industry. Wilimovsky additionally asked fishery managers to more formally consider the risks of management decisions and the value of the information on which those decisions are based.

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16. Abstract (Limit: 200 words)

Species profiles are literature summaries of the taxonomy, morphology, distribution, life history, ecological role, and environmental requirements of coastal aquatic species. They are prepared to assist coastal managers, engineers, and biologists in the gathering of information pertinent to coastal development activities. The Pacific herring has a long history of exploitation for human consumption, animal feed, and trade. It also provides food for a wide variety of pelagic, intertidal, and avian predators. The herring roe fishery has dominated catches since Japan opened its market to imports in the early 1970's. Pacific herring spawn in quiescent, nearshore areas, primarily on marine vegetation. Spawning peaks in the Pacific Northwest region during February and March. Larvae remain inshore, transform into juveniles after 2-3 months, then move offshore in the fall. Adults move inshore on their spawning migration in late fall and early winter. Optimum physiological performance during the early life history is achieved at about 12-17 ppt salinity at temperatures near 6.5-8.3°C. It is important to avoid siltation at or near the spawning grounds in order to prevent disruption of spawning behavior or smothering of eggs.

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