DEVELOPMENT OF THE POPULATION BIOLOGY OF THE PACIFIC HAKE, *MERLUCCIUS PRODUCTUS*

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ABSTRACT

Pacific hake, *Merluccius productus*, population models have been assembled and manipulated to use in determining research strategies and priorities. Given the present preliminary estimates of life-table parameters, I estimate that the larval mortality rate is 0.135 instantaneous daily mortality, which means that there are an average of 87 survivors for each 100 larvae present the previous day. Ninety-five percent of the spawning takes place between December 19 and March 6 of each year. An equilibrium population requires 3.6 million eggs for each recruit at age 2, and that 217 late larvae become juveniles in mid-June of the same year. Exceptionally high cohorts would have 2173 juveniles, and poor cohorts would have 22 at this period.

The fact that we have not yet observed larger year classes in two adjacent years suggests that a highly successful year class may alter the narrow coastal brood habitat for ensuing cohorts. Mechanisms could include limited food, cannibalism on the new cohort, or population growth of other predators in the brood zone.

INTRODUCTION

The Pacific hake, *Merluccius productus*, in the northeast Pacific Ocean occupies three habitats in its life cycle (figure 1): a 30,000 km^2, narrow feeding habitat populated by adult hake for 6–8 months per year near the continental shelf break of California, Oregon, Washington, and British Columbia (Tillman 1968; Alverson and Larkins 1969; Bailey et al. 1982; Francis 1983; Methot and Dorn 1995); a 300,000 km^2, broad, open-sea area populated by spawning adults in winter, and the resultant embryos and larvae for 4–6 months each year offshore of California and Baja California (Ahlstrom and Counts 1955; Hollowed 1992); and a Baja California and California continental shelf juvenile brood habitat of unknown dimensions (Berry and Perkins 1965; Bailey et al. 1986; Woodbury et al. 1995). The spawning, juvenile nursery, and feeding habitats of the adult appear to be mutually exclusive in both time and space. The hake life cycle may involve a lengthy seasonal migration by the spawning adults (Alverson and Larkins 1969; Alheit and Pitcher 1995).

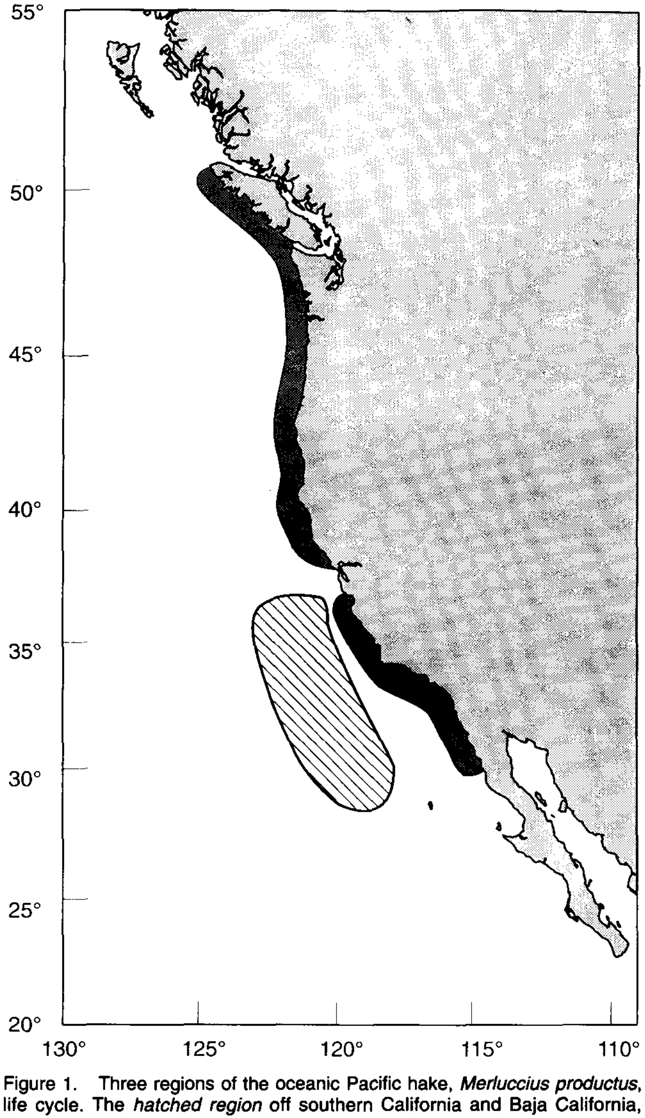

Figure 1. Three regions of the oceanic Pacific hake, *Merluccius productus*, life cycle. The *hatched region* off southern California and Baja California, Mexico, is defined by the 0.275 cm larvae, collected and measured from CalCOFI samples in 1951, and 1963–93. The *narrow strip* covering the upper continental slope, the shelf break, and the continental shelf off British Columbia, Washington, Oregon, and northern California is derived from maps of hake fishing effort (Dorn et al. 1993). The *shaded area* off central and southern California and northern Baja California is postulated to be the distribution of juveniles from the juvenile hake sampled in a general survey (Berry and Perkins 1965), from incidental catch of juvenile hake in anchovy surveys (Bailey et al. 1986), and from incidental catch of juvenile hake in rockfish surveys (Woodbury et al. 1995). The extent of the incidence of O-group hake is not yet defined by these incidental samples.

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Estimated recruitment in Pacific hake varies more than two orders of magnitude (Dorn et al. 1993). The three largest cohorts to recruit came from the spawning years 1980, 1984, and 1977 and accounted for 75 percent (26 billion of the 35 billion recruits at age 2) of the recruitment for the 16-year period 1975–90. The three smallest cohorts to recruit came from the spawning years 1981, 1982, and 1985 and accounted for 0.75 percent of the recruitment for the same 16-year period. The smallest cohorts followed the largest by one or two years.

Most of the hundredfold interannual variability of per capita recruitment rate takes place in the first four months of life in the spawning area or adjacent juvenile nursery areas (Hollowed 1992). The actual mechanisms controlling recruitment are not known. Temperature of the spawning habitat might be directly or indirectly involved, as shown by the fact that five of the largest year classes in the 31 years between 1959 and 1989 (1961, 1970, 1977, 1980, and 1984) have been produced in 20 years classified as warm (>15 degrees off southern California), and no large year classes have resulted from the 11 cold years (Hollowed and Wooster 1992; Methot and Dorn 1995).

Batch fecundity, number of spawnings within season, fertilization rate, and embryonic survival of the Pacific hake are still poorly known. Estimates of standing stock of "advanced oocytes" of the oceanic stock of Pacific hake exist (MacGregor 1966), but the frequency of spawnings per year has not been described for most of the hakes with protracted spawning seasons (Pitcher and Alheit 1995). The possibility of multiple spawnings (Goldberg 1985) and the number of multiple spawnings in Pacific hake is raised by the observations of Alarcón and Arancibia (1993), who have defined the intraseasonal rate of egg batch production in the Chilean hake, *Merluccius gayi*, which is closely related to the Pacific hake (Ho 1989). The embryonic mortality rate (Hollowed 1992) should be reexamined, because it was derived, in part, from the standing stock of "advanced oocytes" of the Puget Sound stock of hake on the assumption of a single spawning (Mason 1986).

The spawning behavior of Pacific hake has not been observed: there are no estimates of the spatial scale of the pattern of spawning adults at the time of spawning. Eggs and larvae are at depths of 40–140 m (Ahlstrom 1959; Smith and Richardson 1977). To some degree, the intensity of aggregation at spawning can be inferred from the statistical distribution of eggs and larvae (Smith and Richardson 1977). Comparable data have been reported for other pelagic spawners such as sardine (Smith 1973), anchovy and jack mackerel (Hewitt 1981), Pacific mackerel and sardinella (Matsuura and Hewitt 1995), and the larvae of the demersal spawning herring (McGurk 1986). The pelagic spawners release eggs in intense patches, presumably to minimize the amount of sperm required for high rates of fertilization (Leong 1989; Mangel and Smith 1990). The importance of the scale and intensity of pattern for estimating abundance is that the sample survey must be adequate to estimate a precise mean. The biological importance of pattern is that the intensity and spatial scale of patchiness may control the rates of predator detection and prey mortality, and the larval pattern controls the feeding rates (McGurk 1986).

Near the time of spawning Pacific hake are distributed offshore of the continental shelf and slope off central and southern California, and northern Baja California, Mexico (figure 1). According to Methot and Dorn (1995), the fishery for adults is conducted far from the spawning area off British Columbia, Washington, Oregon, and northern California, centered on the shelf break. Berry and Perkins (1965), Bailey et al. (1986), and Woodbury et al. (1995) have described the location of juveniles in limited numbers or limited areas from samples in cruises designed for other objectives; the casual synthesis of these samples is represented in figure 1 as a southern image of the adult distribution inshore of the spawning distribution. *Merluccius productus* eggs and larvae are not prominent in the sample summaries of surveys taken off Washington and Oregon (Doyle 1992) and not mentioned in other surveys off the main fishing grounds for Pacific hake (Waldron 1972; Doyle et al. 1993).

Theory and a growing body of empirical studies confirm that population growth, as limited by population density, is focused on a single stage—the "critical stage"—of the life cycle (Charlesworth 1994). For Pacific hake the critical stage does not appear to be in the embryonic or early larval periods. For Pacific hake in an oceanic environment, density-independent controls on population growth rate could happen at every stage in the life cycle. For the purposes of predicting recruitment and projecting responses to environmental regime shifts, it will be necessary to consult more details about the carrying capacity of the habitat by life stage and to examine other environmental features that control survival and somatic growth in the late larval and juvenile stages.

This paper is intended for the use of those wishing to improve our understanding of the population biology of Pacific hake so that useful predictions of recruitment and responses to climate change can be made. This paper includes new and revised information on larval mortality rate and seasonality of spawning. I describe the standard life-table traits of age- and stage-specific rates of mortality and somatic growth, reproduction, and population growth.

METHODS

Several methods have been applied to existing hake data for use in this paper to (1) estimate larval mortality rate adjusted for day:night differences, (2) derive the seasonality of spawning from the incidence and abundance of early larvae, (3) construct a Leslie matrix with which to examine the consequences of multiple spawning behavior, and (4) erect a hypothetical Lefkovitch matrix (Crouse et al. 1987; Caswell 1989) emphasizing the age and size intervals when recruitment rate (critical stage) could be established.

Larval Mortality Rate

The estimates of mortality rate were reconstructed from samples taken from all months. The primary data source for mortality rate is the California Cooperative Oceanic Fisheries Investigations (CalCOFI) database of Pacific hake larvae by length, assembled and maintained by the Coastal Division of NOAA/NMFS Southwest Fisheries Science Center. All hake larvae taken from CalCOFI collections have been counted, but only those taken from 1951 and 1963–94 have been measured. Total data extend from 1951 to 1993. Although the original data are measured to 0.05 cm, I have grouped the sizes into 0.2 cm intervals. The midsize of each interval is 0.275, 0.475, . . . 1.875 cm. All samples were pooled without regard to year, season, or region. I assumed that the general form of the mortality is exponential (constant proportion per unit time), and fitted the equations by the Marquardt method without data transformation:

$$n_t = n_0(e^{-zt})$$

where n_t is the size-specific mean number of hake larvae at estimated age t;

t is the estimated age in days;

n_0 is the estimated number of hake larvae at time 0; and

z is the instantaneous mortality rate.

Ages and growth rates from Hollowed (1992) were used. Day:night differences in catch rate were assembled by a table of hour versus size group. Each hourly catch rate was divided by the mean of the 6 catch rates around midnight (3≤0≥3 hr). Each size was then corrected for day-night bias by dividing the mean abundance by the mean proportion for each hourly sample interval.

Seasonality of Length Groups

Seasonality of each length group was determined by cumulative number by month end starting with October 1. Each empirical cumulative curve was fitted to two models, the logistic and the Weibull. The results of the logistic are not reported here because the maximum time rate of increase is fixed at the midpoint. The Weibull fit can have the maximum rate of increase at any point in the cumulative curve. This is determined iteratively with the other parameters:

$$n_t = K[1 - e^{-\left(\frac{t}{\sigma}\right)^{\tau}}]$$

where n_t is the cumulative number of hake larvae at time t;

t is the number of days after October 1, the nominal start of the spawning season;

K is the upper limit of cumulative number of hake larvae for the season;

σ is the time in days to the middle of the spawning season; and

τ is the shape parameter of the curve.

One estimate of growth rate is available from the comparison of adjacent size classes at the 50 percent point in the season. There are no obvious differences in seasonality among the regions by latitude or distance offshore (Moser et al. 1993). The incidence of hake larvae in the Los Angeles Bight appears to begin to increase before October 1, but this should have little influence on the fit because the major portion of the spawning season is in January–February.

Leslie Matrix Population Model

The Leslie matrix population model requires only information on annual survival and age-specific fecundity. Standing stock of "advanced oocytes" (MacGregor 1971) varies widely in individuals, from 38 to 556 eggs per gram of female. I chose the modal value from 50 females of 200 to avoid conveying a false sense of the precision. New information on number of batches in Chilean hake (Alarcón and Arancibia, 1993) was used in the "strawman" model. I arbitrarily set the number of batches at 10. The annual mortality of adults in the fishery was reported by Hollowed (1992) to be 0.2. Constant annual mortality is but one of three theoretical mortality assumptions. In another assumption—called the Laevastu-Cushing model by Francis (1983)—the mortality rate is a function of population density to a "critical age" (all females mature), and thereafter mortality rate increases with age, presumably due to the "stress" of spawning. A third approach—called the Peterson-Wroblewski mortality model (Peterson and Wroblewski 1984)—assumes that size-specific predation determines mortality rate; in this model the mortality rate of all fish at all stages is inversely proportional to size. In the Hollowed model the mortality stays the same after a brief prerecruit period of changing mortality rate. In the Peterson-Wroblewski model, natural mortality rate is a simple function of size. The Laevastu-Cushing model exhibits a sharply increasing mortality rate with each year of life after maturity.

TABLE 1
Catch Statistics for Oceanic Pacific Hake Larvae

A. Total catch

Length (cm)	Samples #	Average (n/10m^2)	Standard deviation (n/10m^2)	Maximum (n/10m^2)	Day:night bias (p)	Day:night adjusted (n/10m^2)	Fraction positive (p)	Average positive (n/10m^2)
0.275	4188	251.00	2471.00	116292	1.00	251.00	0.68	370.40
0.475	4188	81.70	655.20	22055	0.92	88.80	0.58	152.67
0.675	4188	21.10	244.20	10869	0.87	24.25	0.34	71.93
0.875	4188	6.91	96.20	4196	0.80	8.64	0.19	44.39
1.075	4188	2.27	32.16	1717	0.52	4.37	0.11	41.36
1.275	4188	1.29	18.23	839	0.51	2.53	0.07	36.75
1.475	4188	0.46	4.42	217	0.64	0.72	0.05	15.30
1.675	4188	0.15	1.73	60	0.45	0.33	0.01	28.68
1.875	4188	0.10	1.24	39	0.54	0.18	0.01	20.26
>1.975	4188	0.35	11.95	738	0.36	0.98	0.01	91.30

B. Exponential mortality curve

Age (d)	DN (data)	DN (fitted)	UDN (data)	UDN (fitted)	Positives (data)	Positives (fitted)	Std. dev. (data)	Std. dev. (fitted)
0		1110		1230		1090		11410
11	251.00	252	251.00	251	370.40	366	2471.00	2465
19	88.80	85	81.70	79	152.67	166	655.20	694
27	24.25	29	21.10	25	71.93	75	244.20	195
35	8.64	10	6.91	8	44.39	34	96.20	55
43	4.37	3	2.27	2	41.36	15	32.16	15

C. Parameters

Parameter		SE	CV	r^2	Parameter		SE	CV	r^2
Day:night corrected					Positives				
P_0	1112	58.57	0.05	0.99829	P_0	1085	145.4	0.13	0.97437
imr	−0.135	0.004	0.03		imr	−0.099	0.010	0.10	
Uncorrected for day:night difference					Standard deviation				
P_0	1234	54.87	0.04	0.99899	P_0	14080	1175	0.08	0.99716
imr	−0.145	0.004	0.03		imr	−0.158	0.007	0.04	

imr = instantaneous mortality rate;
P_0 = estimated production at time 0.
Positives—including only those observations with one or more larvae

Lefkovitch Population Model

The Lefkovitch matrix used for this study as a "strawman" model differs from the Leslie matrix in that variable length-stage durations (here in days) are used rather than a fixed interval (for example, 1 year) for a time step. Each stage has three parameters: duration, mortality, and maternity. From these, I calculated (1) the probability of surviving the time step given the daily mortality rate *z*; (2) the joint probability of surviving the time step and proceeding to the next stage given the daily mortality rate *z* and the stage duration *d*; and (3) the daily egg production characteristic of the stage. The values of the daily mortality and stage-duration parameters are the same as in Hollowed (1992) except for the embryonic parameter, which is estimated in this paper, and the tuning parameter (mortality–juvenile II), which is used to balance the matrix for stationarity of population size and constant stage composition. I also explored the consequences of multiple batches of eggs rather than a single spawning.

RESULTS

Larval Mortality Rate

The catch curve from raw data is shown in table 1 with the statistics of number of samples, average number per 10 m^2, standard deviation, and maximum number by .2 cm interval. In addition, table 1 shows values of the day:night bias, the catch curve adjusted for day:night bias, the fraction of samples positive for each size of larvae, and the average number of larvae per positive station.

The time rate of change in numbers assuming an exponential mortality curve is provided for the day:night corrected data, uncorrected data, average per positive station, and standard deviation for each length to 1.075 cm (table 1). For each series, the nonlinear least square fit is also provided.

The statistical table of parameter values, standard error of the values, and coefficients of variation and determination are in table 1. Daily instantaneous mortality rate

TABLE 2
Catch Statistics for Oceanic Pacific Hake Larvae

A. Weibull parameters

Length (mm)	K	Sigma	Tau	Mean	CorCoeff (r^2)
4.75	1.143E+2	1.439E+2	8.299E+0	7.654E+1	0.999

B. Date of birth

	Fraction	Days	Date
Age at 4.75 mm		13	
K*0.025	2.86	92	19–Dec
K*0.5	57.15	138	3–Feb
K*0.975	111.44	168	5–Mar

over all years for early larvae from 0.275 cm to 1.075 cm long is −0.135: in other words, there are, on average, 874 survivors for each 1000 on the previous day (table 1). The assumptions underlying this estimate do not include a value for adult production of spawn, but the intercept of 1112 eggs per 10 square meters is an estimate of egg production, fertilization, and survival to the 0.275 cm stage. This is based on an assumption that survival rate of the embryos, not evaluated here, is the same as for the early larvae. At the end of the early larval period—43 days—the day catch is biased relative to the night catch by a factor of 2 (table 1). The instantaneous rate of decline in sample standard deviation, −0.158, is higher than the rate of decline of the mean per positive station, −0.099. From this difference I concluded that entire patches are disappearing rapidly. The effects of turbulent diffusion and other dispersive mechanisms must be slower.

Seasonality of Length Groups

Approximately 2 percent of the hake spawn is produced before December 19, according to the timing models (table 2; figure 2), and less than 2 percent is produced after March 6. As in the mortality rate tables, these back-calculations assume that fertilization and embryonic survival rates are about the same in all parts of the spawning season. These assumptions will have to be tested.

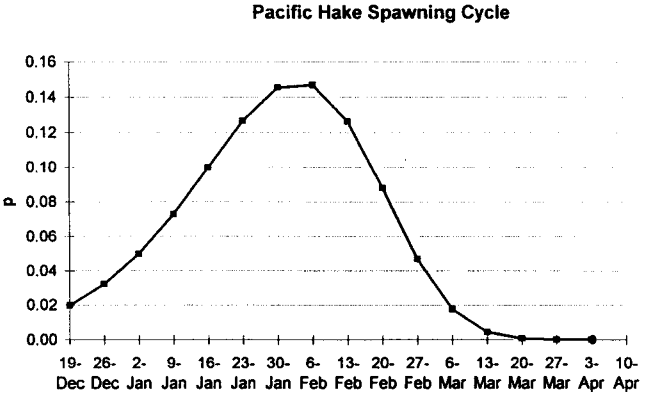

Figure 2. Modeled hake spawning cycle. The Weibull fit allows the shape of the curve to be determined by iteration. It is assumed that eggs are spawned 13 days before the 0.475 cm larvae appear and that the mortality rate from spawning to 0.475 cm larvae is essentially the same at all seasons. Limited hake egg data have been reported by Smith and Richardson (1977).

The importance of multiple batches of eggs depends heavily on the natural and fishing mortality rates as a function of age. When ten batches of eggs allow the life-table model to achieve equilibrium, nine batches—all other things being equal—will cause a Laevastu-Cushing model population to decline to 86.9 percent in 10 years. The Hollowed and Peterson-Wroblewski models decline to 90.9 percent and 90 percent in 10 years. Heavy fishing mortality would cause the population to respond more like the Laevastu-Cushing model. Table 3 presents three differing life-table models for Pacific hake.

For modelling recruitment variability, the Peterson-Wroblewski model maternity schedule is preferred (figure 3). The idea that mortality and trophic efficiency is a function of the actual size is reasonable, and the fecundity curve is very close to the empirically derived constant natural mortality of 0.2 (Hollowed 1992; Dorn 1992; Dorn et al. 1993; see also Francis 1983).

The estimates of mortality for the first two years of life (table 1) represent the stationary solution assuming a fixed population size with the value derived from the Leslie matrix with lambda = 1. Hake O-group mortality (tuned) is highest for the Hollowed model, and lowest for the Laevastu-Cushing model. At equilibrium, to get one recruit at age 2 in the Hollowed model one must start with 5.5 million eggs; the Laevastu-Cushing model requires 2.6 million eggs; and the Peterson-Wroblewski model requires 3.6 million eggs. With the range of recruitment rates of one-hundredfold, we may start with 0.1 the number of eggs in large recruitments and 10 times the number of eggs in poor recruitments.

To further localize the onset of big and poor recruitment, the Lefkovitch model (table 4) may be useful in finding the scope of changes in the first 128 days of life—embryo through late larval stages. With the egg production of the Peterson-Wroblewski model—3.6 million eggs for each recruit at age 2—there would be 217 late larvae moved to the 3.5 cm juvenile I stage in mid-June at equilibrium, 22 in a poor recruitment, and 2173 in a large recruitment.

DISCUSSION

It is important to develop population models of the Pacific hake oceanic population to enable predictions of recruitment and population responses to climatic change. Although the models themselves are probably sufficient as a framework for this round of improvement in our understanding of Pacific hake population dynamics, the parameters available for these models need much improvement. For example, the stock synthesis model

TABLE 3
Leslie Matrix Parameters for Pacific Hake

Age (yr)	Length (cm)	Weight (kg)	Mature (*p*)	Batches (/yr)	e/f/yr #	fe/f/yr #	Hollowed (*m*)	L-C (*m*)	P-W (*m*)
0			0	0	0	0	15.278	14.398	14.568
1	15.73	0.034	0	0	0	0	0.27	0.377	0.53
2	27.53	0.155	0.19	4	2.36E+4	1.18E+4	0.2	0.268	0.36
3	36.26	0.326	0.64	5	2.09E+5	1.04E+5	0.2	0.21	0.30
4	42.73	0.508	0.77	6	4.69E+5	2.35E+5	0.2	0.195	0.27
5	47.53	0.676	0.82	7	7.76E+5	3.88E+5	0.2	0.257	0.25
6	51.08	0.821	0.93	8	1.22E+6	6.11E+5	0.2	0.357	0.24
7	53.71	0.940	0.97	9	1.64E+6	8.21E+5	0.2	0.457	0.23
8	55.66	1.035	1	10	2.07E+6	1.03E+6	0.2	0.557	0.23
9	57.10	1.109	1	10	2.22E+6	1.11E+6	0.2	0.657	0.22
10	58.17	1.166	1	10	2.33E+6	1.17E+6	0.2	0.757	0.22
11	58.96	1.209	1	10	2.42E+6	1.21E+6	0.2	0.857	0.22
12	59.55	1.242	1	10	2.48E+6	1.24E+6	0.2	0.957	0.22
13	59.99	1.266	1	10	2.53E+6	1.27E+6	0.2	1.057	0.22
14	60.31	1.285	1	10	2.57E+6	1.28E+6	0.2	1.157	0.21
15	60.55	1.298	1	10	2.60E+6	1.30E+6	0.2	1.257	0.21
16	60.72	1.309	1	10	2.62E+6	1.31E+6	0.2	1.357	0.21
17	60.86	1.316	1	10	2.63E+6	1.32E+6	0.2	1.457	0.21
18	60.95	1.322	1	10	2.64E+6	1.32E+6	0.2	1.557	0.21
19	61.02	1.326	1	10	2.65E+6	1.33E+6	0.2	1.657	0.21

e/f/yr is eggs per female per year.
fe/f/yr is female eggs per female per year.
L-C is the Laevastu-Cushing life table (Francis 1983).
P-W is the Peterson-Wroblewski life table (Francis 1983).
p is the proportion of females mature (Dorn et al. 1993).
m is the instantaneous natural mortality rate (Hollowed 1992).

TABLE 4
Lefkovitch Estimated and Postulated Matrix Parameters for the Oceanic Stock of Pacific Hake

Stage	Length (cm)	Duration (d)	Mortality (per d)	Maternity (sfe/f/d)
Embryo	egg – 0.4	16	0.135	0
Early larva	0.4 to 1.0	23	0.135	0
Late larva	1.0 to 3.5	89	0.05	0
Juvenile I	3.5 to 6.0	64	0.0200	0
Juvenile II	6.0 to 11.0	128	0.0080	0
Juvenile III	11.0 to 13.5	64	0.0027	0
Juvenile IV	13.5 to 33.3	346	0.000548	0
Pre-recruit	33.3 to 50.0	730	0.000548	10.5
Adult	50.0 to L(inf)	5800	0.000548	199.2

sfe/f/d is surviving female embryos per day.

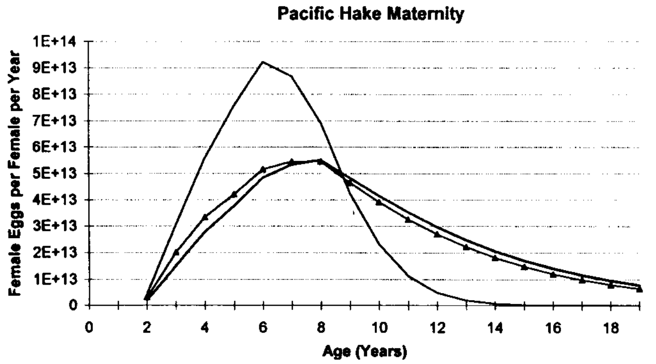

Figure 3. Postulated Pacific hake age-specific maternity function. The *lower solid line* represents the fisheries management life-history model (Hollowed 1992). The *higher solid line* is the Laevastu-Cushing model (Francis 1983) with a density-dependent onset of maturity reaching a maximum at age 6 and with an increase of adult mortality of 0.1 per year. The *line with solid triangles* is the Peterson-Wroblewski curve with the mortality rate a simple function of body length.

(Methot and Dorn 1995) appears to be sufficient for regulating fishing mortality. It is not expected that recruitment will be sensitive to stock size at the levels which have been maintained in the last three decades of fishing; rather, an environment:recruitment model will be necessary for prediction. Given an effective Leslie matrix and a tandem Lefkovitch matrix, one can examine the scope of change that can be detected. From this, the best mix of field studies can be designed to determine the earliest recruitment prediction for each cohort.

The hake life-history strategy differs radically from that of pelagic fishes shallower in the water column. Hake's principal similarity with northern anchovy and sardine life cycles is the intense pattern at time of spawning, which reflects a common need for aggregation before open-sea spawning to conserve sperm in the minutes between release and fertilization of the eggs. Principal differences of the deeper-spawning hake include the rates of mortality, intensity and persistence of patchiness, seasonality of spawning, vertical distribution of spawn, and temperature of the spawning habitat.

Egg and Larval Mortality

It would appear that pooling of all samples has achieved the goal of high precision of the mortality estimate. Of course this stratagem conceals the interannual and interregional differences so critical to understanding variations in mortality rate. It can be seen from the pooled results presented above that precise spatial and temporal egg and larval mortality rates may be attainable only by greatly increasing the sampling effort or by increasing the efficiency of sampling effort through allocation of additional samples in the patchiest areas and times. The uncorrected daily instantaneous rate is 0.145. In terms of the standard error of the fitted data (0.004), the expected ±1.96 S.E. limits of this mortality rate are 0.137 to 0.153, which overlaps broadly with the day:night corrected rate and also with the rate used by Hollowed for the 23-day early larval stage (Hollowed 1992). Since the standard deviation at time of spawning projected for this paper is an order of magnitude higher than the projected mean, it would appear that a few thousand positive samples would be necessary to estimate egg production per unit surface area with useful precision.

Seasonality

Two items of new information are available from the consideration of seasonality: the length of the season tends to support a hypothesis of in-migration, bouts of multiple spawning, and out-migration between October and April; the brevity of the season is an aid to mode-following applications for determining stage duration. If single spawning were the norm, early spawners might leave the feeding grounds late or return to the feeding grounds early; fishing success seems to point to coordinated departures and arrivals on the fishing ground (Dorn 1995). Approximately 35 percent of adults' growth in length is achieved in the spawning portion of the habitat and 65 percent in the feeding portion (Francis 1983). Given the energy expended in migration, aggregation, breeding behavior, investment of eggs with yolk, and formation of multiple batches, it seems likely that important amounts of adult feeding may still occur on the winter breeding grounds. Adult hake and their prey should be directly sampled to verify this.

Vertical Distribution

One of the more important distinctions between hake, which spawn at depth, and anchovy and jack mackerel, which spawn near the surface (Ahlstrom 1959; Moser and Smith 1993), is that the "subeuphotic" spawning habitat may be isolated from Ekman drift, other wind-driven transport, and mixed-layer turbulent diffusion. Similarly, sources of food may be fundamentally different than for the epipelagic larvae (Sumida and Moser 1980, 1984; Ware and McFarlane 1989).

Patchiness and Adequate Sampling

If measures of hake egg production are required, we may use the intercept of the size-specific standard deviation to estimate the number of samples required. For example, the intercept of the original data (table 1) is 1230 eggs per 10 m^2 of sea-surface area, and the intercept of the standard deviation is 14,080. If one required a standard error of 30 percent of the mean (370) by the central-limit theorem and assuming spatial and temporal independence of samples, the number of samples required is 1448; for a standard error of 20 percent of the mean (247) the number of samples required is 3255.

The matrix approach to population models is strategic rather than tactical in that actual projections from the set of parameters presented above (tables 3 and 4) would be valid for the mean population growth rate over many generations. The high variability of recruitment would negate the assumptions of stationarity and constant stage, age, or size distribution required for actually applying these models to practical problems (Bart 1995).

Most work on the early life history of fishes has been conducted on species whose larvae inhabit the upper mixed layer of the ocean. Pacific hake larvae occur somewhat deeper, therefore references to offshore transport of the larvae as described by Power (1986) may not be representative of the direction of transport below the mixed layer. Although much attention has been given to the population dynamics of the subarctic species *Euphausia pacifica* and *Thysonoessa spinifera*, the dominant adult hake food (Mullin and Conversi 1988), the most common euphausiid in the spawning area and depth range of the hake is the temperate species *Nematoscelis difficilis* (Brinton, pers. comm). Although it is clear that Pacific hake recruitment is not controlled by the contemporary changes in spawning biomass, it is not yet known which of the many biological populations and physical events—at many time and space scales—in its spawning and nursery habitats should be explored to understand cause-effect relationships of recruitment rate (Hollowed and Bailey 1989).

Pacific hake recruitment data show that the largest per capita recruitment rates preclude a large recruitment in the subsequent one or two years (Dorn et al. 1993). Is this a general trait in the gadoids? To answer this question, I extracted interannual recruitment standard deviation and lag-1 autocorrelation parameters from a Myers et al. (1990) study of recruitment time series for 50 stocks of North Atlantic gadoids (cod, haddock, pollack, saithe, hake, and the like). For comparison I plotted the same parameters for Pacific hake (Dorn et al. 1993) and Alaskan pollack (Hollowed and Megrey 1989). Figure 4 is a scatterplot of the variance of the natural logs of recruitment versus the autocorrelation (lag 1; ACF1) index. In this plot we find that the Pacific hake is unusual, not for its high variance, but for the combined high variance and negative autocorrelation function. The Alaskan pollack is nominally centered in the same scatterplot. It may be that the distributions from this collection of time series data may be partitioned by the ACF1. Since the environment tends to be autocorrelated, those stocks with ACF1 in the region 0.6–1 may be entrained to envi-

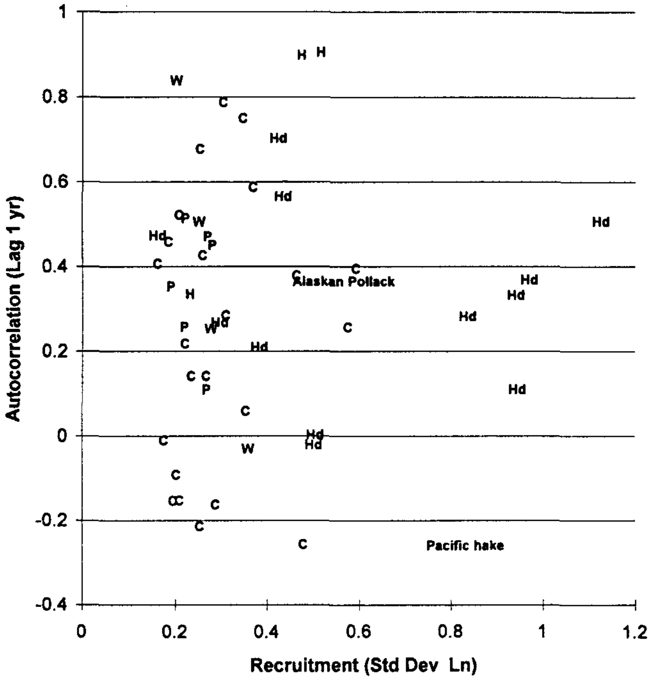

Figure 4. A scatterplot of interannual autocorrelation of the natural log of recruitment and standard deviation of ln recruitment for 49 stocks of gadoids—cod (C), haddock (Hd), pollack (P), hake (H), and whiting (W)) in the North Atlantic (Myers et al. 1990); Pacific hake (Dorn et al. 1993); and Alaskan pollack (Hollowed and Megrey 1989).

ronmentally induced autocorrelation. Those ACF1 in the range of .3–.6 may express only the continuity of large stocks tending to yield large recruitments and small stocks tending to yield small recruitments. The low positive ACF1 0–.3 may be moderate density-dependent lowering of sequential recruitments by way of within-cohort competition for food, slower growth, maturation at smaller sizes, and the like. The negative ACF1 area may be evidence for between-cohort cannibalism or some other more vigorous control on recruitment rate and, ultimately, population size.

What are some density-dependent controls on population growth? One usually refers to competition for food, given limits on production and thus carrying capacity. In addition, we could list aggregation and selectivity of predators, population growth of predators, shortened disease-transmission vectors, and, of course, combinations of these phenomena. Which life stage ("critical stage") would these affect? The compaction of the surviving larvae into the narrow juvenile brood zone is very appealing as a vulnerable stage for density-dependent control. What is the actual mechanism? The fact that we have not yet observed two adjacent larger year classes suggests that a highly successful year class populates a narrow coastal brood zone in sufficient density to influence the survival of the ensuing cohorts by consumption of limited food, by cannibalism on the new cohort, or by stimulating the population growth of the other predators in the brood zone.

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