Contribution of Early Life Stages to Interannual Variability in Recruitment of Northern Anchovy (*Engraulis mordax*)

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We tested Hjort's and Lasker's hypotheses that the abundance of recruits in fishes is determined at an early life stage. Using 13 yr of data on components of population dynamics of the well-studied northern anchovy (*Engraulis mordax*), we reconstructed the abundance of anchovy in each year at three stages: eggs, 4.5-d-old yolk-sac larvae, and 19-d-old larvae. No abundance measure was significantly correlated with age 1 recruits, resulting in rejection of Hjort's and Lasker's hypotheses. We give reasons why the low correlations are not an artifact of estimation error. The lack of correlation exists because of the large variability (CV = 171%) in survival rate between age 19 d and age 1 yr. Therefore, attempts to understand interannual variability in recruitment in this, and perhaps other, marine fish species may have to rely not only on data on eggs and larvae, but especially on data on abundances estimated after 20 d, closer to the age at recruitment.

Les hypothèses de Hjort et de Lasker, selon lesquelles le nombre de recrues chez les poissons est déterminé au cours des premiers stades de vie, ont été testées. À partir des données couvrant une période de 13 ans provenant des études sur la dynamique des populations de l'anchois du Pacifique (*Engraulis mordax*), on a retracé l'abondance annuelle des anchois à trois stades différents, soit les stades oeuf, alevin vésiculé de 4,5, et alevin de 19. On n'a observé aucune corrélation significative entre les différentes mesures d'abondance et le nombre de recrues d'âge 1, et les hypothèses de Hjort et de Lasker ont donc été rejetées. On explique pourquoi ces faibles corrélations ne résultent pas d'un artefact dû à l'erreur d'estimation. L'absence de corrélation s'explique par la grande variabilité (CV = 171 %) du taux de survie entre les âges 19 j et 1 a. Pour comprendre la variabilité interannuelle du recrutement chez l'anchois, et peut-être chez d'autres espèces de poissons marins, les données concernant les oeufs et les alevins peuvent être insuffisantes; peut-être serait-il préférable de se fier surtout aux données sur l'abondance après l'âge de 20 j, c'est-à-dire à un âge plus rapproché du moment du recrutement.

One of the best examples of a paradigm in fish population biology is Hjort's (1913, 1926) hypothesis that the annual abundance of recruits (year-class strength) is established at an early life stage, soon after larvae absorb their yolk sac. This hypothesis was based on the observed high mortality rates of these young fish, and on their planktonic nature, which potentially makes them extremely vulnerable to starvation, predation, and transport by movement of water away from habitats favorable to subsequent growth and survival. This "critical period" hypothesis has stimulated considerable research and has formed the foundation of many attempts to explain interannual variability in recruitment (e.g. Bannister et al. 1974; Cushing 1975; Sinclair et al. 1985). May (1974) and W. C. Leggett (pers. comm.) reviewed the literature and showed that there is not strong support for Hjort's hypothesis, yet it still

is the basis of considerable research (e.g. Walsh et al. 1981; Wroblewski 1984; and others).

Lasker's (1975, 1981) stable ocean hypothesis is a special case of Hjort's paradigm. Lasker proposed that wind-driven turbulent mixing of the upper ocean could cause high mortality of first-feeding fish larvae through dissipation and dilution of patches of larval food. Consistent with this is the observation that starvation is the major source of mortality for first-feeding larvae (Theilacker 1986), although this does not appear to be a direct cause of death for older larvae (O'Connell 1980). The second part of Lasker's hypothesis was that these turbulent mixing conditions would lead to a poor year-class.

Recently, Peterman and Bradford (1987) tested the turbulent mixing mechanism of Lasker's stable ocean hypothesis and found that, indeed, high mortality rates of young northern anchovy (*Engraulis mordax*) larvae (up to age 19 d) occurred in years when spawning seasons had many periods of high-speed winds. Years with few periods of high winds were asso-

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ciated with low larval mortality rates. If Hjort and Lasker are correct in hypothesizing that mortality at this early stage has a strong influence on subsequent recruitment, then we should expect a positive correlation between the number of larvae surviving through this early larval period and subsequent recruitment. We arbitrarily defined recruitment as the abundance of fish of age 1 yr.

For the northern anchovy, previous analyses (Ahlstrom 1965; Methot 1983; Smith 1981) suggest that the number of surviving larvae is *not* related to recruitment. However, no correlation statistic was calculated in these cases either because of too few years of data (Methot 1983) or because only qualitative indices of recruitment were available. Both limitations have been rectified; estimates of age 1 recruitment since 1965 are now available from stochastic virtual population analysis (VPA) (Methot 1986, 1988).

In this paper, we reconstruct the annual abundance of northern anchovy at each of several early life stages, using in most cases annual observations on components of egg production and on mortality rates of eggs and larvae. We then estimate the extent to which interannual variation in abundance at each of these early life stages contributed to interannual variation in abundance of age 1 recruits of northern anchovy from 1965 to 1985. Thus, we test Hjort's and Lasker's hyotheses for this northern anchovy population.

Methods

We used data on the central population of northern anchovy, which spawns primarily during January–April in waters off the coast of southern California. This species is one of the dominant fish in the California Current, with a mean spawning biomass of 500 × 10³ metric tonnes (t) from 1965 to 1985 (Methot 1986), and it has been intensively studied since the 1950's by the California Cooperative Oceanic Fisheries Investigations (CalCOFI) (see annual volumes of CalCOFI Reports and Smith 1985).

To initiate the reconstruction of abundances of early life stages (eggs, yolk-sac larvae, and 19-d-old larvae or prerecruits), we used numbers of fish at each age from 1 to 5+ yr estimated for 1965–85 by Methot's (1986) VPA (Table 1).

Egg Production, *E*

Total egg production by the anchovy population in a given year, E_j, was estimated by

$$(1) \quad E_j = \sum_{i=1}^{5} 0.5 N_{ij} \, p_{ij} \, F_{ij} \, S_{ij} \, ,$$

where i = age-class, j = year, 0.5 = fraction of females (Bindman 1986), N_{ij} = number of adults by age and year, from Table 1, p_{ij} = proportion of fish mature in each age by year, F_{ij} = batch fecundity (eggs per female per spawning), and S_{ij} = spawning frequency, or number of spawnings per year per female of age *i*.

A constant sex ratio was used because annual estimates are unreliable due to small samples and a tendency for segregation between sexes in survey catches (Klingbeil 1978).

The proportion of females of a given age which was mature was set = 1.0 for ages ≥2 based on Parrish et al. (1986) and, for age 1 fish only, was made an increasing function of the mean January–February water temperature as measured at Scripps pier

TABLE 1. Millions of fish at time of spawning in each age group of the central population of northern anchovy. Data from Methot's (1986) virtual population analysis. This table only shows data for those years that were relevant to the analysis (other years had no data on early life stages).

Year	Age 1	Age 2	Age 3	Age 4	Age 5+
1965	10 794	5 744	1 965	1339	635
1966	5 494	5 695	2 917	959	924
1969	14 241	7 779	1 707	473	528
1972	56 233	26 496	5 151	1013	375
1975	17 806	21 822	17 177	6118	2547
1978	9 390	13 462	1 211	754	1099
1979	76 561	3 457	4 276	355	500
1980	58 144	24 737	885	966	170
1981	45 273	18 913	6 634	208	233
1982	15 537	11 063	3 319	908	47
1983	51 305	3 667	1 728	392	84
1984	24 174	17 641	1 046	438	107
1985	54 693	8 980	5 718	313	150

(Methot 1986). For years when the fraction of mature age 1 fish was estimated from field samples (Methot 1986), we used the mean of this estimate and the one predicted for that year from the water temperature by Methot's (1986) temperature-dependent function (Table 2). This approach reflects the imprecision of the field samples. In years without field samples, we used Methot's function and the observed temperature to estimate age 1 maturity.

Because northern anchovy are multiple spawners with an indeterminate annual fecundity (Hunter and Macewicz 1980), we estimated the number of eggs produced per mature female per year from two components: eggs per female per spawning (batch fecundity) and number of spawnings per year per female (spawning frequency).

Batch fecundity, F

Eggs per female per spawning (*F*) was calculated from the batch fecundity relations reported by Hunter et al. (1985), which are linear functions of female weight:

$$(2) \quad F_{ij} = a + b(0.95 W_{ij}).$$

The weight of each female of age *i* in year *j* was multiplied by 0.95 because Hunter et al.'s (1985) batch fecundity relations used gonad-free weight which is 95% of total weight (Hunter and Macewicz 1980). Table 2 gives the annual values for the *a* and *b* parameters in equation (2); long-term mean parameter values (Hunter et al. 1985) were used in years when field estimates of batch fecundity relations were not available. Annual weights of female spawners at each age (Table 3) were obtained from California Department of Fish and Game surveys (Methot 1986). Again, long-term means were used for years when it was not possible to estimate weights from field samples.

Spawning frequency, S

Parrish et al. (1986) showed that older females produce more egg batches per year than small females. We therefore used the following relation between number of egg batches per female per year (spawning frequency, *S*) and weight:

$$(3) \quad S_{ij} = c + d W_{ij},$$

where $c = -6.136$, $d = 1.2878$, and W_{ij} = weight (grams). Paramaters *c* and *d* were estimated by linear regression of our "adjusted" version of Parrish et al.'s (1986) data for number

TABLE 2. Annual parameter estimates for components of egg production and mortality of eggs and larvae by the year in which spawning occurred. Maturity, p_1, is the fraction of age 1 females which were mature in year j. Fecundity parameters a and b refer to equation (2); missing parameter estimates were filled in with long-term means, denoted by an asterisk. Embryo mortality parameters α and t refer to equation (4) and larval mortality parameters β and u to equation (5). Age 1 recruits are those resulting from spawning in the year given in column 1. Data sources are given in the text.

Year (j)	Maturity (p₁)	Fecundity		Embryo mortality		Larval mortality		Age 1 recruits (10⁶)
		a	b	α	t	β	u	
1965	0.28	−1104*	583*	0.19	4.91	2.42	18.27	5 494
1966	0.57	−1104*	583*	0.42	4.91	1.84	20.35	7 911
1969	0.82	−1104*	583*	0.19	4.79	2.15	18.33	23 675
1972	0.10	−1104*	583*	0.25	4.54	1.73	18.35	68 509
1975	0.23	−1104*	583*	0.44	4.89	1.88	18.95	10 617
1978	0.99	−1104*	583*	0.59	4.24	1.66	19.47	76 561
1979	0.55	−4410	658	0.48	4.91	2.22	18.62	58 144
1980	0.98	−1891	535	0.36	3.05	1.22	18.63	45 273
1981	0.92	−1979	714	0.38	3.10	1.53	18.56	15 537
1982	0.75	−180	586	0.36	4.42	1.81	18.13	51 305
1983	0.96	−1002	559	0.46	3.82	2.05	18.88	24 174
1984	0.94	−554	505	0.36	4.26	1.47	19.74	54 693
1985	0.63	−2040	648	0.28	4.93	2.13	20.96	47 011

TABLE 3. Total weight (g) per spawning fish. Data from Methot (1986), derived from California Department of Fish and Game winter surveys. Years with missing data (denoted by an asterisk) were filled in with the long-term mean for that age.

Year	Age				
	1	2	3	4	5+
1965*	8.7	14.6	18.3	21.2	24.3
1966*	8.7	14.6	18.3	21.2	24.3
1969*	8.7	14.6	18.3	21.2	24.3
1972*	8.7	14.6	18.3	21.2	24.3
1975*	8.7	14.6	18.3	21.2	24.3
1978	10.4	15.4	19.7	22.2	22.2
1979	9.2	18.3	21.7	24.8	24.3
1980	7.1	15.0	17.9	24.8	29.5
1981	9.8	13.4	18.3	20.2	27.7
1982	9.5	16.6	18.8	21.2	22.2
1983	8.9	11.0	17.5	19.7	24.3
1984	4.8	12.4	13.8	18.8	22.2
1985	10.6	15.4	18.4	21.2	24.3

of egg batches for fish aged 1, 2, and 3 yr on our mean spawning weight at those ages ($r = 0.996$).

We "adjusted" Parrish et al.'s (1986) data as follows. These authors provided age-specific monthly spawning frequencies (number of egg batches per female per year) for each age 1–3 and age 4+ fish, averaged over many years. However, for age 1 fish, the spawning frequencies in Parrish et al. (1986) were calculated from samples which included immature fish. To obtain an estimate of spawning frequency of mature age 1 fish only, we divided Parrish et al.'s (1986) spawning frequency for all age 1 fish by the average fraction of age 1 fish that matured during those years. This fraction was 0.905, as estimated by the fraction of age 1 fish mature during March, the month with the highest mean proportion of spawning age 1 fish (Parrish et al. 1986). This method assumed that the fish that were immature in that month would not spawn at all that year. In addition, the monthly spawning frequencies for all ages were divided by 0.95, a correction for sampling bias noted by Parrish et al. (1986). The resulting "adjusted" estimates of spawning fre-

quency were used to estimate the parameters of equation (3) by regression.

The number of spawnings each year for mature age 1–3 fish was the sum of the monthly spawning frequencies for each age over the 12-mo interval, December–November. November was the month with least spawning and formed a natural break in the annual spawning cycle.

We then estimated the spawning frequencies for each age in each year from equation (3), using weights of spawning females of each age in that year. The product of the components shown in equation (1) thus gave an estimate of the total number of eggs produced each year by the central population of northern anchovy.

Early Larvae, L

Lo (1985) calculated the mean instantaneous daily mortality rate of each annual cohort of eggs between time of spawning and mean age of yolk-sac larvae. We used her "Series 2" estimates of this rate, α (see Table 2). Lo also estimated the time between these two stages, t, for each year (Table 2) because it was affected by water temperature (Lo 1983). The mean age of yolk-sac larvae from data in Table 2 averaged 4.4 d from time of spawning; such larvae were 3–4 mm in length (Lo 1983). Standard CalCOFI sampling cruises for eggs and larvae were made only every third year between 1966 and 1978; thus, our analysis here is limited to the 13 yrs sampled by CalCOFI between 1965 and 1985, when both age 1 recruitment data and egg mortality data were available (see section on Recruits below). We used Lo's (1985) equation to calculate the number of eggs surviving to mean age of yolk-sac larvae (L_j):

(4) $L_j = E_j e^{-\alpha_j t_j}$

where α_j = instantaneous daily mortality rate in year j and t_j = temperature-dependent mean age of yolk-sac larvae in year j, in days since fertilization. Annual values for the α_j and t_j parameters are given in Table 2. In this species, first feeding of larvae is initiated only after the yolk is absorbed (Theilacker and Dorsey 1980). Thus, abundance of the yolk-sac larvae, L_j from equation (4), is estimated just prior to onset of first feeding.

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Prerecruit Larvae, PR

Lo (1985) also estimated for each year the mortality coefficient of larvae from the mean age of yolk-sac larvae (just before the start of first feeding) to an average of 19 d after spawning (~10 mm length). Larvae larger than this were not included in the analysis because of their increased ability to avoid standard bongo nets (Smith 1981; Hewitt and Methot 1982: Folkvord and Hunter 1986; Lo 1986). This early larval period spans yolk-sac absorption, initiation of first feeding, and the early larval stage up to 19 d of age. To simplify terminology, we refer to the latter, 19-d-old larvae as prerecruits. Lo (1985) assumed that mortality rate varied with larval age, and she estimated the duration of this period for each year. Table 2 gives her annual estimates of the β mortality coefficient and times at the beginning and ending of this period, t and u, respectively. We then calculated for each year the survival of yolk-sac larvae, L_j, to prerecruits, PR_j, with Lo's (1985) equation:

$$(5) \quad PR_j = L_j (u_j/t_j)^{-\beta_j}$$

where t_j = same as in equation (4) and u_j = mean age of larvae at end of the sampled period in year j, in days since fertilization.

Recruits, R

Because no field estimates exist for annual mortality rates between prerecruits (19-d-old larvae) and age 1, we obtained annual estimates of abundance of age 1 recruits, R_j, from Methot's (1986) virtual population analysis. These recruits (Table 2) represent abundance as of 15 February each year. Thus, the 1966 estimate of 5494 × 10⁶ age 1 fish is the recruitment at age 1 resulting from spawning in early 1965. Because no reliable adult age structure data were available before 1965, our data set for age 1 recruits was restricted to 1965 and later. This excluded the pre-1965 data on earlier life stages from our analysis of the effect of these early stages on subsequent recruitment.

Life Table

To compare the extent of mortality suffered by a cohort during each life stage up to recruitment, we calculated standard survival rates (s, not to be confused with S, which is spawning frequency as defined above) and instantaneous mortality rates for each year:

$$(6) \quad \begin{aligned} s_{j1} &= L_j/E_j, \\ s_{j2} &= PR_j/L_j \\ s_{j3} &= R_j/PR_j \end{aligned}$$

where the second subscript, $k = 1, 2,$ or 3, on s indicates the life phase. These fractions surviving were also converted to total instantaneous mortality rates for the respective periods:

$$(7) \quad M_{jk} = -\log_e (s_{jk}).$$

We used statistics on these 13 yearly M_{jk} to construct a life table for the central population of northern anchovy.

Analysis

We took natural logarithms of abundances at all stages to calculate correlations because recruitment of marine fishes is frequently lognormally distributed (Hennemuth et al. 1980) and because logarithms of our abundances did not deviate substantially from a normal distribution (although there were too few data points to test this formally).
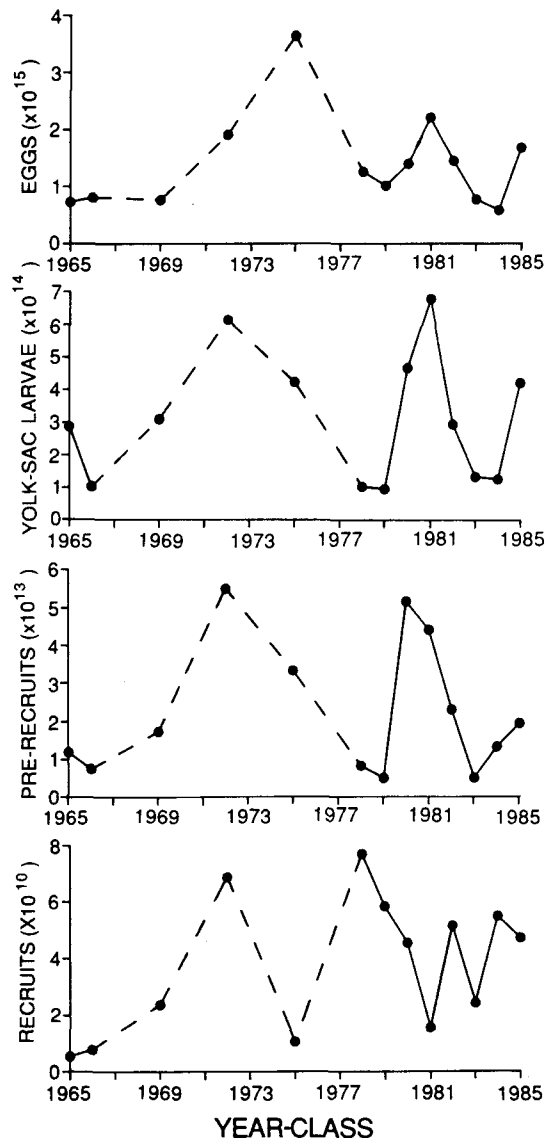
Fig. 1. Estimated abundances of early life stages for the central population of northern anchovy by year-class. Abundances of the first three stages are from this paper, and age 1 abundances are from Methot's (1986) VPA. Broken lines connect CalCOFI survey years before 1978, in which early life history variables were estimated only every third year from 1966 to 1978. Actual abundances in non-CalCOFI years could have been much higher or lower than the locations of the broken lines; dashes are provided only to aid comparison of observed points.

Results and Discussion

Recruitment Variability

Figure 1 shows estimated annual abundances of each life stage for the northern anchovy and Table 4 gives summary
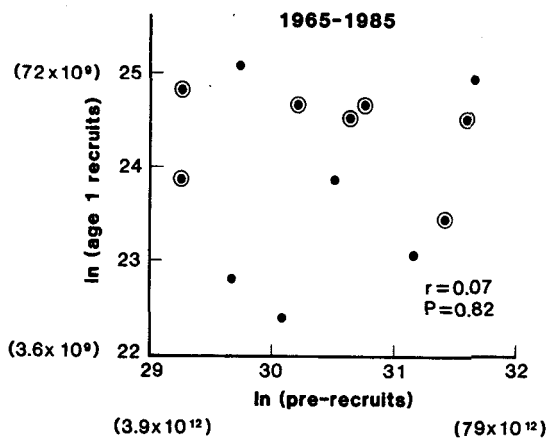
1965–1985

Fig. 2. Relationship between log,(prerecruit abundance, ~age 19 d) and resulting abundance of log,(age 1 recruits) for 1965–85 year-classes. Circled data points are from those years in which all components in the reconstruction of prerecruits were observed (see General Discussion section).

TABLE 4. Summary statistics of the 13 yr of abundances of northern anchovy, in numbers at each stage. Geometric mean column is the mean of the natural logs of abundances.

Stage	Arithmetic mean	Standard deviation	CV	Geometric mean
Eggs	1.40×10^{15}	8.39×10^{14}	0.599	34.74
Larvae (4.5 d)	3.12×10^{14}	1.99×10^{14}	0.638	33.16
Prerecruits (19 d)	2.26×10^{13}	1.76×10^{13}	0.780	30.44
Recruits (1 yr)	3.76×10^{10}	2.42×10^{10}	0.643	24.07

statistics.

Analysis of our 13 yearly abundances of early life stages and age 1 recruitment does not support Hjort's or Lasker's hypothesis that recruitment is established at an early stage in northern anchovy. No correlation between abundance at early life stages and recruitment was significant, including the one between age 1 recruits and prerecruits (those larvae which survived through 19 d) (Fig. 2; Table 5). Thus, even though the wind speed index of turbulent mixing explained 65% of the interannual variation in larval mortality during the "critical" first-feeding phase (Peterman and Bradford 1987), the numbers of larvae surviving through this period were not correlated with subsequent recruitment (r was only 0.07). Hjort's and Lasker's hypotheses thus are not applicable to our 13 yr of data.

Mortality between the larval stage at 19 d old and age 1 is sufficiently variable among years to destroy the correlations between abundance at all early life stages and recruitment. However, variable mortality *prior to* 19 d is not the cause of these low correlations. Lo's (1985) estimates of mortality rates and time at stage varied among years but still led to significant correlations between egg abundance and resulting yolk-sac larvae and between these larvae and subsequent prerecruits (Table 6). Yet neither the correlation between eggs and age 1 recruits nor the correlation between yolk-sac larvae and age 1 was significant (Table 5). Based on instantaneous mortality rates (Table 7), mean survival through the stage from prerecruits to age 1 was lowest of the three stages (Table 8); only 0.34%

TABLE 5. Correlations, r, between reconstructed abundances at early life stages and subsequent age 1 recruitment from that same cohort for the central population of northern anchovy. In each correlation, the log, was taken of both abundance variables. P is the probability for the null hypothesis H_0: $r = 0$, and sample size = 13 yr in all cases. Average age since spawning is given in parentheses.

Beginning stage	Ending stage	r	P
Eggs	Age 1	0.04	0.89
Yolk-sac larvae (4.5 d old)	Age 1	−0.09	0.76
Prerecruits (19-d-old larvae)	Age 1	0.07	0.82

TABLE 6. Correlations, r, between reconstructed abundances at life stages prior to recruitment for the central population of northern anchovy. Log, of both abundances were used in each correlation, and sample size = 13 yr in all cases.

Beginning stage	Ending stage	r	P
Across one stage			
Eggs	Yolk-sac larvae (4.5 d old)	0.66	<0.015
Yolk-sac larvae (4.5 d old)	Prerecruits (19-d-old larvae)	0.91	<0.001
Across more than one stage			
Eggs	Prerecruits (19-d-old larvae)	0.67	<0.014

TABLE 7. Statistics on instantaneous mortality rates (M) of northern anchovy, calculated from 13 yr of reconstructed abundances at successive life stages. SD_M is the standard deviation of M. The mean daily M was calculated as the mean total M from the beginning to the end of the period, divided by the duration of the period (in days).

Beginning of period	End of period	Mean duration of period (d)	Mean total M over period	SD_M	Mean daily M
Eggs	Yolk-sac larvae	4.4	1.584	0.544	0.360
Yolk-sac larvae	Prerecruits	14.6	2.711	0.343	0.186
Prerecruits	Age 1 recruits	346	6.378	1.170	0.018

of the 19-d-old larvae survived to age 1 recruits, on average. Most important, however, this stage was the most variable, having a coefficient of variation (CV) in survival rate of 1.71, almost three times that of the egg-to-larval stage (Table 8). Thus, the interannual variability in mortality between successive early life stages (egg-to-larvae, larvae-to-prerecruits) was not sufficient to destroy a significant correlation between abundances at those stages, but the large variability in the fraction of fish surviving from prerecruits to recruits did destroy any correlation between abundance at earlier life stages and age 1 recruitment. Therefore, recruitment strength is not determined at the early life stages.

As originally stated, Hjort's and Lasker's hypotheses about sources of interannual variation in recruitment referred

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specifically to the importance of the early larval stage, within a few days of yolk-sac absorption. However, for the anchovy population analyzed here, the early larval stage averages only 14.5 d in duration, which is only a small portion of the total duration as larvae (about 20%; Hunter and Coyne 1982) and a smaller portion of the egg-to-recruitment period. Based on the highly variable mortality after age 19 d reported here, it appears that the "critical period" (if one exists) is more likely to occur at a later stage than the early one discussed by Hjort and Lasker.

Our low correlation between 19-d-old larvae and age 1 abundance does not imply that the lack of correlation will also hold when abundance of prerecruits gets very low and outside the range of our data. Extremely low abundance of prerecruits could lead to significantly decreased recruitment, but our data do not permit a test of this hypothesis.

Regardless of the reason for lack of correlation between abundances of prerecruits and recruits, current data clearly show that it is not possible to forecast age 1 abundance from larval abundance at 19 d or before. If forecasts are needed, they will have to be made from population measures taken at an age between 19 and 365 d. Indeed, Methot (1986) showed that a reasonable index of age 1 recruits is the proportion of age 0 (not yet 1 yr old) fish caught by the Mexican commercial fishery during their 9th through 12th mo of life, just prior to becoming age 1 fish. The proportion of these age 0 fish reflects the size of the incoming year-class: the arcsine or angular transform (Sokal and Rohlf 1969, p. 386) of the proportion of these age 0 fish is significantly correlated with the $\log_e$ of age 1 fish ($r = 0.75$, $r^2 = 0.57$, $P < 0.01$). An identical analysis of the proportion of age 0 fish in their *third* quarter of life (6–9 mo old) shows much lower correlation with age 1 fish ($r = 0.33$, $r^2 = 0.11$, $P > 0.4$), as does the relation between this third quarter index and our $\log_e$(prerecruit abundance) ($r = -0.07$). The fourth quarter correlations particularly confirm that better forecasts of recruitment will arise from samples at ages closer to age 1 than the early larval stage.

Life Table

Mean instantaneous *daily* mortality rates for the three periods described here decrease with increasing age and size of northern anchovy up to age 1 (last column of Table 7), as has been found for numerous other species (e.g. Cushing 1974; Dahlberg 1979; Peterson and Wroblewski 1984). The means of the reconstructed abundances on which the M values in Table 7 are based appear reasonable because the mean instantaneous mortality rate for each period (plus symbol in Fig. 3) agrees well with theoretical expectations and with rates observed for other fishes at a similar size (Fig. 3). Note that the mean instantaneous daily mortality rate of 0.018 for the period between prerecruits and age 1 applies over a longer time (averaging 346 d) than the larger daily mortality rates at previous stages. The net result is a large mean total instantaneous mortality over the period from prerecruits to recruits (~6.4, Table 7).

The mean daily instantaneous mortality rates for the first two periods in Table 7 are slightly different from those in Smith's (1985) summary life table: 0.25 and 0.16 instead of the 0.36 and 0.186 estimated here. This is partly because Smith's estimates were from a subset of the 13 yr used here. Our value of 0.018 for the daily mortality rate from prerecruits to age 1 recruits falls within Smith's range for that period (0.01–0.05).

General Discussion

Estimation Error

Some readers may believe that the low correlation between abundances of prerecruits and recruits (Fig. 2) is due to errors in estimation of the components of the reconstruction process, rather than due to biological reality. There are a number of lines of evidence which suggest that estimation errors are *not* the explanation for this low of correlation.

First, the correlation was still low ($r = -0.21$, $P = 0.64$) when we only included data from those years in which all components were observed, rather than estimated by filling in the long-term mean. The points included (circled dots in Fig. 2) thus had less error embedded in them than the points in the original analysis. Note that these seven relatively error-free points covered the same range in abundance of prerecruits as the original 13 (Fig. 2), yet no significant correlation emerged.

Second, imprecision in the mortality estimates prior to 19 d was probably not the cause of the low correlation between our reconstructed abundance at that age and age 1 recruits. Lo's (1985) annual mortality coefficients for the periods between eggs and 19-d-old larvae were based on a large number of ichthyoplankton tows (~1000) (Lo 1986). Also, the high correlations in Table 6 among eggs, yolk-sac larvae, and prerecruits were all statistically significant and show that variation in mortality rates due to natural and sampling variability at those early stages contributes little to the low correlations between those early stages and recruitment (all of the latter r values were near zero, Table 5).

In addition, one must assume an unreasonably large amount of estimation error in the abundance of prerecruits to show that the correlation of 0.07 found here between prerecruits and recruits was derived from a stronger true underlying correlation. Under the assumption that the $\log_e$(prerecruits) are normally distributed, we used methods described by Snedecor and Cochran (1967, p. 165) to reestimate the correlation coefficient with estimation error removed from the prerecruit abundance. With parameters estimated from the correlation of $\log_e$(recruits) on $\log_e$(prerecruits), extremely large estimation errors are required to strengthen the correlation. For example, if estimation error accounts for 50% of the total variation in $\log_e$(prerecruits), the correlation coefficient only increases from 0.07 to 0.10; if it accounts for 80% of the variance in X, r is only increased to 0.16. Therefore, we conclude that estimation error alone is not sufficient to give rise to the low correlation that we observed.

Finally, the estimates of age 1 abundance appear precise. The time series of abundance of recruits which was used here was from one VPA based on one set of assumptions used by Methot (1986). However, two other time series of recruits were derived using other assumptions, and all three are significantly correlated (all $r > 0.83$, Methot 1986). In part, this consistency among the different time series of recruits arose because Methot (1986) used in his VPA four independent data sets on age compositions, which were in turn highly correlated (r values ranged from 0.61 to 0.99). Thus, it is unlikely that imprecise estimates of age 1 abundance are the cause of the lack of correlation between prerecruits and age 1 recruits.

Given these reasons, estimation error does not appear to be an important factor in our results. The lack of correlation between prerecruits and age 1 recruits in northern anchovy appears real and it is caused by the highly variable survival rate during that lengthy period.

TABLE 8. Statistics on proportion of northern anchovy cohorts surviving. Following standard formulae for lognormal distributions (Aitchison and Brown 1966), we calculated these statistics for survival rates (proportions) from the mean, μ, and variance, σ^2, of the corresponding instantaneous mortality rate (M) data shown in Table 7. Median of the 13 yr of survival rates was $e^{-\mu}$, their mean was $e^{(-\mu+(\sigma^2/2))}$, and their coefficient of variation (CV) was $(e^{\sigma^2}-1)^{0.5}$. Last column shows mean fraction of initial eggs which survived through to the end of the period indicated.

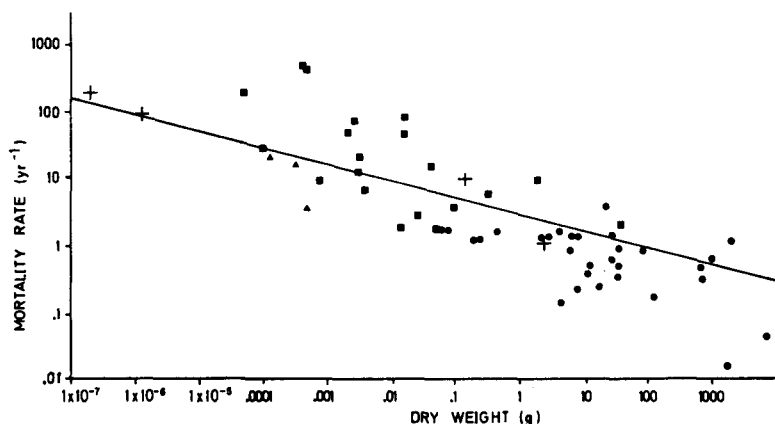| Beginning of period	End of period	Mean duration of period (d)	Median survival rate over period	Mean survival rate over period	CV	Mean daily survival rate	Mean fraction of eggs
Eggs	Yolk-sac larvae	4.4	0.205	0.238	0.587	0.722	0.238
Yolk-sac larvae	Prerecruits	14.6	0.066	0.070	0.353	0.833	1.67×10^{-2}
Prerecruits	Age 1 recruits	346	1.7×10^{-3}	3.4×10^{-3}	1.712	0.984	5.66×10^{-5}

FIG. 3. Instantaneous mortality rates of different species of fish and chaetognaths in relation to body weight. Plus symbols are for the three early life stages of northern anchovy discussed here, plus anchovy adults. All data except northern anchovy are from Peterson and Wroblewski (1984). Mean body weight of northern anchovy during each of the three early life history periods in the life table was the weighted average (weighted by abundance) calculated from a survivorship curve derived from our estimated instantaneous daily mortality rate for that period (shown in Table 7) and a growth curve. We used Hunter's (1976) growth curve of dry weight vs. age for eggs to 19-d-old larvae, and from then until age 1, we used Methot's (1981) observed lengths at age converted to dry weight by his length–weight relationship.

We concur with May (1974) and W. C. Leggett (pers. comm.) that there is evidence to doubt the generality of Hjort's hypothesis that mortality of first-feeding larvae is a strong determinant of year-class strength. If we are to improve our understanding of causes of variability in recruitment of northern anchovy, research must be done on all life stages, especially those closer to age 1. Methot's (1986) correlations between recruits and proportion of age 0 fish in the Mexican catch underscore the importance of understanding the sources of variability in mortality even during the last 3 mo prior to recruitment as age 1 fish. Although the majority (57%) of interannual variability in age 1 abundance is accounted for by that fourth quarter index, there still is a large amount (43%) of unexplained variability in that period.

Other Species

Much of the research on the early life history of northern anchovy has been directed toward back-estimation of spawning biomass (Lasker 1985). But in addition, the CalCOFI program

has been useful from the viewpoint of providing data to rigorously test hypotheses about sources of variability in recruitment of northern anchovy. However, it is not possible to extend our conclusions to other marine fish species with pelagic larvae because they differ from northern anchovy in the physical habitat and the species complexes of predators, competitors, and food organisms. Such differences could lead to differences in the mechanisms that cause variability in recruitment. However, to the extent that fish larvae of similar size face similar problems everywhere, our results suggest that early larval sampling programs alone will provide only a partial understanding of sources of variation in recruitment.

The question concerning the general appropriateness of data on early larval abundances alone can be answered partly by examining the literature that reports analyses of correlations between abundance of recruits and abundance at some earlier life stage. Such correlations are normally used to forecast recruitment for management purposes. Therefore, the summary

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TABLE 9. Summary of reported correlations between abundances at early and later life stages. Sizes of fish, when reported, are given in parentheses below the age. References: A, Cushing (1974); B, Bannister (1978); C, Rauck and Zijlstra (1978); D, Tormosova (1980); E, Postuma and Zijlstra (1974); F, Burd (1985).

Species	Beginning stage	Ending stage	N (yr)	Correlation	P	Reference
Baltic cod	30-d-old larvae	Age 1 group	6	0.81	0.05	A
	Age 0 group	Age 1 group	6	0.90	0.015	A
North Sea plaice	Eggs	Age 2	10	0.25	0.49	B
	Age 0 group	Age 2	14	0.71	0.005	C
North Sea sole	Age 0 group	Age 2		Low		C
	Age 1 group	Age 2	12	0.68	0.13	C
North Sea haddock	First-feeding larvae (≥6 mm)	Age 2	7	0.60	0.15	D
North Sea herring						
Downs stock	30-d-old larvae	Age 3	15	0.34	0.22	E
	30-d-old larvae	Age 0	13	0.76	<0.01	F
Doggerbank stock	Small larvae (<11 mm)	Age 3	9	0.58	0.10	E
	Large larvae (≥11 mm)	Age 3	9	0.71	0.025	E
Bank stock	20-d larvae	Age 0	11	0.66	0.027	F

of published correlations in Table 9 may be biased towards significant cases because nonsignificant results would be less likely to be reported in the literature. Even so, results in Table 9 are diverse; some stocks show significant correlations and others do not. This diversity of results emphasizes the varied effect of different physical and biological processes on the relative variability in mortality at early and late life stages. Future investigations could fruitfully use a comparative approach (Bakun 1986) to determine which habitat factors are more variable for species such as northern anchovy, which show a low correlation between early larval abundance and recruitment, than for species showing a high correlation.

Table 9 also supports the intuitive reasoning that the closer that abundance samples are taken in time, the more likely a significant correlation is to exist between those abundances. This is demonstrated by Baltic cod (*Gadus morhua*), North Sea plaice (*Pleuronectes platessa*), North Sea haddock, (*Gadus aeglefinus*), North Sea sole (*Solea solea*), Downs herring (*Clupea harengus*), and Doggerbank herring (Table 9). For example, the Downs herring stock in the North Sea showed a lower correlation between abundance of 1-mo-old larvae and an index of recruitment at age 3 (Postuma and Zijlstra 1974) than was observed between those larvae and an index of age 0 fish. Such evidence supports our finding that in the northern anchovy, abundance of age 1 recruits may be better correlated with abundance at some stage closer to age 1 than the currently sampled 19-d-old larvae.

Acknowledgments

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