Year-Class Strength and Survival of O-Group Clupeoids[1]

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Global marine fish catch has been stable over the past decade but the clupeoid contribution has declined from one-half to one-third of the marine fish catch. This decline appears to be caused by changes in recruitment success during heavy fishing pressure. Theoretical population approaches and correlative environmental indices are not yet sufficient for setting catch limits. For some time the direct measurement of current biomass appears to be necessary for setting clupeoid quotas. Precision and cost studies on the estimation of biomass with current methods indicate that a standard error of estimate less than 25% cannot be justified based on the increased long-term yield of the stock. Assembly of a prospective life-table for the central subpopulation of the northern anchovy (Engraulis mordax) allows the discussion of intra-population and environmental controls on growth of the population. Using reasonable values for survival and growth in the embryonic, larval, and juvenile stages in the context of a life-table allows one to evaluate the stages where recruitment is controlled. From this manipulation it appears that significant decreases in recruitment could originate at any stage but marked increases in recruitment are only likely to arise from lower mortality rates in the embryonic and larval stages. The late larval stage of the anchovy could exhibit remarkable control on the level of recruitment through plasticity of the inter-action between growth rate and survival. Maximum cohort biomass of the anchovy occurs late in the first year of life but current measures of juvenile survival and biological production are inadequate to explore density-dependent survival and growth rates.

La prise globale de poissons marins a été stable au cours de la dernière décennie mais le pourcentage de clupéidés est passé de la moitié au tiers de ce total. Ce déclin semble être causé par des variations du succès du recrutement quand la pression par pêche est élevée. Les modèles théoriques de population et les indices environnementaux corrélatifs ne permettent pas encore de fixer les limites des prises. Pour quelque temps, la quantification directe de la biomasse actuelle semble nécessaire pour l'établissement des contingents de clupéidés. Des études sur la précision et les coûts des estimations de la biomasse, à l'aide des méthodes actuelles, indiquent qu'on ne peut justifier un écart-type de l'estimation inférieur à 25% en fonction du rendement accru du stock à long terme. L'ébauche d'une table de survie éventuelle pour la sous-population d'anchois du Pacifique (Engraulis mordax) permet une discussion des contrôles environnementaux et intra-population sur la croissance de la population. En utilisant des valeurs raison-nables concernant la survie et la croissance chez les stades embryonnaires, larvaires et juvéniles, dans le contexte d'une table de survie, on peut évaluer les stades où le recrutement est contrôlé. D'après cette manipulation, il semble que les baisses importantes du recrutement peuvent se produire à n'importe quel stade, mais que les accroissements marqués du recrutement ne proviendront probablement que de faibles taux de mortalité aux stades embryonnaires et larvaires. À cause de la plasticité de l'interaction entre le taux de croissance et la survie, le stade larvaire avancé de l'anchois pourrait exercer un contrôle frappant sur le niveau de recrutement. La biomasse maximale de la cohorte chez l'anchois a lieu vers la fin de la première année de vie. Toutefois, les quantifications actuelles de la survie des juvéniles et de la produc-tion biologique ne permettent pas d'étudier la survie reliée à la densité ni les taux de croissance.

Marine fish catch has been stable over the past decade at 45 million tons per annum but the clupeoid contri-bution has declined from one-half to one-third the marine fish catch (Anonymous 1981a). This has occurred through a chronic decline of herring catch and a drastic decline of the anchovy catches partly moderated by a recovery of sardine fisheries (Anonymous 1981a). In 1980, clupeoids

represented 80% of the meal and oil fishery products, about 15% of the canned and cured fish, and 7% of the fresh or frozen fish (Anonymous 1981b). The major genera in the commercial fishery are the pilchard or sardine (Sardinops spp. and Sardina pilchardus, 7 million metric tons (t)), the anchovy (Engraulis spp., 3 million t), the oil sardine (Sardinella spp., 2 million t), and the herring, menhaden, sprats, and thread herring (Clupea spp., Brevoortia spp., Sprattus spp., Opisthonema spp., at 1 million t per genus per year). Fisheries are conducted on all ages and sizes of the clupeoids, and variations in recruitment have immediate effects on the fishery. In the past 30 yr the anchovy catch has ranged between one half and 15 million

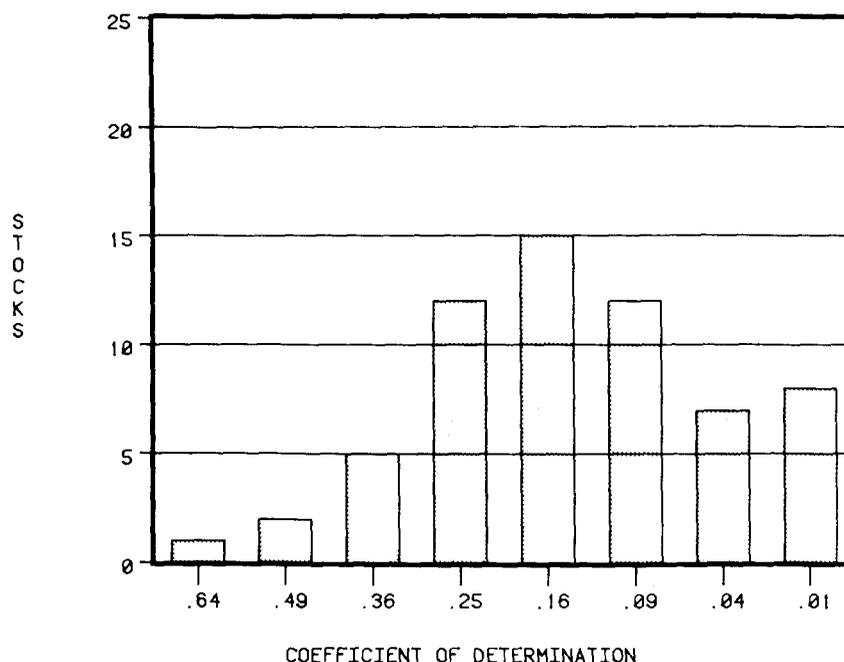Can. J. Fish. Aquat. Sci., Vol. 42, 1985

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FIG. 1. Frequency distribution of indices of density dependence based on Tanner (1966). The coefficient of determination is the square of the correlation coefficient of the population growth rate versus the population size. All 62 values differ significantly from unity.

$t \cdot yr^{-1}$, sardine has varied between 1 and 7 million $t \cdot yr^{-1}$, and herring from 1 to 5 million $t \cdot yr^{-1}$. Most of this variation has been caused by changes in recruitment success during heavy fishing pressure.

Ten years have passed since Parrish (1973) stated at the Aarhus Symposium on Fish Stocks and Recruitment "... in most species for which detailed information is available, these (population regulation) factors operate mainly during the early stages of development (i.e. between the egg and the end of the first year of life) so that year-class strength is determined and population control mechanisms for most fish stocks operate before the individuals enter the exploited phase."

Improvement of the long-term management of clupeoids stocks will include (1) specialized studies on population size and environmental controls of reproductive success and (2) implementation of measurement and prediction procedures for controlling the impact of fishing pressure on clupeoid stocks.

The theory and application of population modeling does not appear to have much immediate promise for management of clupeoid stocks. A good example of the inadequacy of "density-dependent" controls on population growth is reported by Tanner (1966). Figure 1 is a summary of 111 time series of the relative amount of population change controlled by population size. In the 62 population time series where density and population growth were significantly negatively correlated, the degree of control was very low. Essentially, only 16% of the population growth was controlled by population size. More recently, MacCall (1980a) deduced that as little as 10% of the variation in mortality rate in the northern anchovy (*Engraulis mordax*) could be attributed to density-dependent causes.

Garrod and Colebrook (1978) have presented a large correlation matrix for 22 yr (1950–71) of recruitment of 18 North Atlantic stocks. If large-scale environmental features were a dominant influence on recruitment, independent of stock size and density, one would expect three modes: a positive mode would arise from stock pairs whose recruitment is favored by the same environmental features (i.e. positively correlated recruitment), a negative mode would arise from pairs of stocks in which an environmental change would simultaneously increase the recruitment of one stock and decrease recruitment of the other, and a central mode would arise from indifference of stock pairs' recruitment to general environment.

Figure 2 is a frequency diagram of the 153 stock pairs coefficients of determination (r^2). Coefficients of determination arising from negative correlations are separated from those arising from positive correlations. If one assumes no serial coherence with this length of time series, $P =$ values of r^2 in excess of 0.25 ($0.05 < t < 0.01$) is strong evidence of association in the statistical sense that such a value would not likely arise by chance; however, a coefficient of determination as low as 0.25 on the interannual scale would have very little use in fisheries management or biological oceanography. More than two thirds of the pairs were positively correlated. This implies that certain general features of the environment such as lethal temperatures, turbulent mixing, and productivity have a weak large-scale, long-term control on population success, irrespective of population reproductive size.

General population theory and wide-scale environmental measurements may never provide adequate (Fig. 1 and 2) information for generating periodic decisions necessary to restore
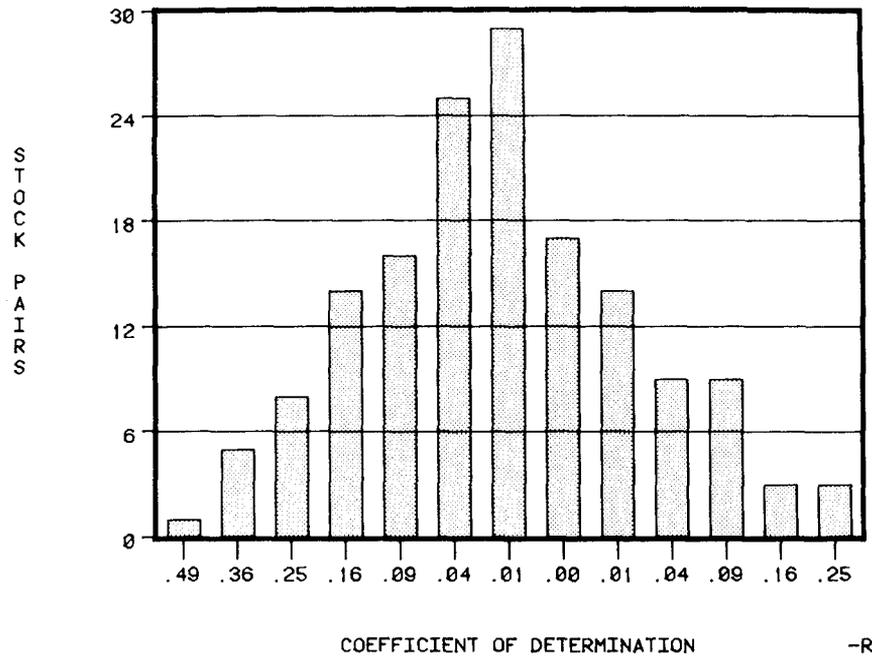
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FIG. 2.   An index of environmental dependence based on Garrod and Colebrook (1978). The coefficient
of determination is the square of the correlation coefficient of all pairs of 18 North Atlantic stocks.

and sustain clupeoid fisheries. Until predictions of recruitment success are effective, management of clupeoids will depend on assessments of stock size and direct measures of recruitment. Gulland (1982) stated that "... the point in their lifespan (fishes) in which increased understanding would seem to be most rewarding is in the early life stages before recruitment ... The practical value of such an improvement in our scientific knowledge in terms of better management of the world's fish resources is considerable." It is the purpose of this paper to explore characteristics of the early life stages of the northern anchovy and the practical value of new procedures for restoration and management of clupeoid fish stocks.

Mechanisms of Population Control

The habitats of clupeoids are not known in sufficient detail to decide for any species what mechanisms other than fishing control reproductive success, population size, and potential fishery yield. The sheer logistics of mounting population/ habitat studies with sufficient geographic scale, spatial intensity, and temporal continuity and competent samplers have so far prevented adequate explanations of annual fluctuations of clupeoid reproductive success. For convenience, most work on the stock-recruitment problem has had to accompany stock assessment activities. Similarly, most analytical work has been concentrated on the commercial sizes and planktonic stages. The result is that time series data are too simple and the occasional experimental approaches are too short-term to provide adequate information on the basis of recruitment overfishing in clupeoids.

I shall defer to the second section how early and how precise a

recruitment prediction must be to be worth the cost of producing the estimate. For the purpose of this section I will assume that timely knowledge of recruitment success will be valuable for effective tactical management of clupeoids and some knowledge of recruitment variability will encourage strategic approaches to the limitation of overall fishing effort and associated capital facilities.

This section contains a prospective life-table of the northern anchovy central subpopulation. This is intended to focus the discussion in the subsequent elements of this section on where the life-cycle and in what manner the density-dependent and environmental mechanisms serve to control population size in *E. mordax*. The second element is a description of some density-dependent mechanisms. Lastly, environmental mechanisms are discussed.

General Features of an Anchovy Population

Vulnerability to predation and starvation changes so radically during the life cycle of a clupeoid that it is useful to erect a life-table as a guide to stages in which population size control by intrapopulation or environmental means may be effected. It is the purpose of this section on the population characteristics of the central subpopulation of the northern anchovy to describe the entire life cycle. While we have detailed knowledge of only the adult and planktonic stages (Smith and Lasker 1978), we can deduce the intermediate parameters for a first approximation. This is accomplished by the artifice of a stationary population model. New estimates of fecundity and growth (Hunter and Leong 1981; Mallicoate and Parrish 1981) for this subpopulation can be used with estimates of embryonic mortality (Picquelle and Hewitt 1983) and larval growth (Methot and

TABLE 1. Estimated and postulated life history characteristics for the central subpopulation of the northern anchovy (sources in parentheses).[a]

Category	Length (mm)	Mortality rate (daily)	Growth rate (mm·d⁻¹)	Age (d)	Initial dry wt (g)	Initial number	Principal food	Principal predators
Embryo	Egg–4	0.25 (1)	—	0–7	3×10^{-5} (6)	3.50×10^{15}	Yolk	Filtering, biting (9, 10, 11, 12)
Early larva	4–10	0.16 (3)	0.5 (4)	8–19	2×10^{-5} (7)	4.74×10^{14}	Dinoflagellates, nauplii (8)	Biting
Late larva	10–35	0.05	0.325 (4)	20–96	5×10^{-4} (6)	6.94×10^{13}	Microcrustacea (6)	Fish, birds
Early juvenile	35–60	0.02	0.5 (4)	97–146	5×10^{-2} (6)	1.48×10^{12}	Microcrustacea, diatoms (4)	Fish, birds, marine mammals
Late juvenile	60–85	0.01	0.35	147–217	3×10^{-1}	5.44×10^{11}	Copepods, diatoms (4)	Fish, birds, marine mammals
Prerecruit	85–110	0.01	0.087	218–504	9×10^{-1} (7)	2.67×10^{11}	Copepods, diatoms (4)	Fish, birds, marine mammals
Early adult	110–135	0.0027 (2)	0.025 (5)	505–1504	2×10^{0} (7)	1.52×10^{10}	Copepods, euphausiids, diatoms	Fish, birds, marine mammals
Late adult	135–160	0.0027 (2)	0.02 (5)	1505–2754	4×10^{0} (7)	1.02×10^{9}	Copepods, euphausiids, diatoms	Fish, birds, marine mammals

[a]Sources: (1) Picquelle and Hewitt 1983, (2) Hanan 1980, (3) Hewitt 1982, (4) Methot 1981, (5) Mallicoate and Parrish 1981, (6) Hunter 1976, (7) Hunter and Leong 1981, (8) Lasker 1975, (9) Hunter and Kimbrell 1980, (10) Lillelund and Lasker 1971, (11) MacCall 1980b, (12) Theilacker and Lasker 1974.

Kramer 1979; Methot 1981) to postulate a total life cycle stationary model.

In Table 1 I have listed the assumed characteristics of the anchovy population. Citations for the properties for which we have any data are listed. These parameters or their range are known only for time periods we have been fortunate enough to observe. The primary utility of listing the known and assumed values is to direct the discussion below to a small number of specific characteristics of the population, and to speculate how these might be influenced by the population size and the environment within the first year.

For all but two of the stages, the population is divided into 25-mm length groups. The first two stages, the embryonic and early larval, are divided from each other on the basis of the onset of feeding: the transition to late larva is arbitrarily set at a length of 10 mm.

The fecundity schedule from which the initial number in Table 1 is derived is found in Table 2. In this instance the fecundity rate is controlled only by the number of batches of eggs per year and the number of eggs per batch at a fixed rate per adult gonad-free weight. I have assumed no weight- or age-specific change in the eggs produced per gram of female. We have no estimate of the variability of the number of batches per year but the batch fecundity appears to vary on the order of 20% on an interannual basis (Hewitt 1982). I also do not know whether the season of slower spawning is based on many females spawning at a slow rate or a few females spawning at the normal rate.

A schematic drawing of a cohort of northern anchovy is illustrated in Fig. 3. The mortality and biomass curves are distorted by the log–log plot of numbers and biomass on age in order to emphasize the role of the early stages. The biomass of the cohort undergoes four transitions, which may be instructional for the study of recruitment. Three of the changes occur in

the larval stage and one in the juvenile stage. For the purpose of this discussion, I will first point out some functional anatomical features for each stage and follow with a simple model of their mortality and growth.

Embryo

The embryonic stage is characterized by rapid loss in weight per individual and rapid decline in numbers. As a relatively large member of the zooplankton, the egg is subject to passive filtration. It is also probably vulnerable to biting as the visual distortion of the clear egg, the increasing visual contrast, and later motions of the developing embryo heighten the detectability by mechanoreceptors and vision. The vulnerability may also be heightened at hatching as the protective integument of the egg is lost: clues for chemoreception by predators may also increase. Lillelund and Lasker (1971) described the mortality associated with chance contact of yolk-sac larvae with copepods even when no feeding by the copepods occurs. Theilacker and Lasker (1974) evaluated the predation by euphausiids on yolk-sac larvae. Also, there appear to be many malformed embryos in nature (E. Sandnop, Southwest Fisheries Center, pers. comm.; H. Santander, Instituto del Mar del Peru, Collao, Peru, pers. comm.; E. Stevens, Southwest Fisheries Center, pers. comm.) at all stages; some may live through the yolk-sac period but are too distorted for successful first feeding. The anchovy requires high food density at first feeding; layers (Lasker 1975) and horizontal patches of food (Vlymen 1977) are a condition for successful first feeding. The embryos are never very far from low lethal temperatures (Brewer 1976) in the water column (12°C at 50 m depth; Eber 1977). The adults appear to skirt lethally cold patches of newly upwelled water (Lasker et al. 1981), and embryonic mortality could be caused by lateral advection into those areas. Lastly, chronic and widespread colder-than-average water temperatures would retard develop-

TABLE 2. Life and fecundity table for the females of the central subpopulation of the northern anchovy.

Age (yr)	Number	Weight $(g)^a$	Fecundity[b]				
			b	f	n	N	Cumulative
0	1.74×10^{15}	—	—	—	—	—	—
1	2.11×10^{10}	12.8	532	7	24 000	5.00×10^{14}	5.00×10^{14}
2	7.88×10^{9}	16.5	532	20	77 000	6.92×10^{14}	1.38×10^{15}
3	2.90×10^{9}	20.7	532	20	110 000	3.19×10^{14}	9.58×10^{14}
4	1.07×10^{9}	24.4	532	20	130 000	1.39×10^{14}	5.56×10^{14}
5	3.92×10^{8}	27.8	532	20	148 000	5.80×10^{13}	2.90×10^{14}
6	1.44×10^{8}	31.5	532	20	168 000	2.41×10^{13}	1.45×10^{14}
7	8.24×10^{7}	35.5	532	20	189 000	1.56×10^{13}	1.09×10^{14}
Sum						1.75×10^{15}	3.94×10^{15}
Mean generation time (yr)							2.25

^{a}Grams wet weight for a representative female.

$^b b$ = batch fecundity in eggs per gram of female; f = frequency of batches per year; n = number of fertilized female eggs per female adult per year assuming 50:50 sex ratio; N = total number of fertilized female eggs spawned by all females of that age in a year; — = immature.
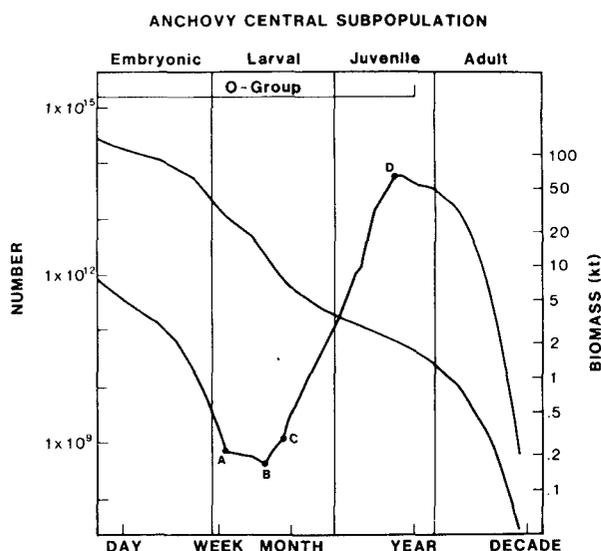
ANCHOVY CENTRAL SUBPOPULATION

Fig. 3. Cohort estimates of number and biomass of northern anchovy central subpopulation. Values are based on a series of exponential mortality equations for each stage of the life cycle in approximate stationarity.

ment and prolong the highest mortality rate phase of the life cycle.

Larval period

In the larval period, the cohort biomass rate of decline is arrested at point A (Fig. 3) but the growth in weight of the individual larva is insufficient to balance weight loss of the cohort through mortality. At point B the cohort begins its net growth and this growth advances to a sustained high rate at point C. The break at point A may represent a radical change in vulnerability to filtration predation. At this length (5 mm) we see the first demonstrable change in day and night sampling with a 1-m net. Day–night differences in evasion are about 3:1 at this length (Smith 1981). O'Connell (1981) and Hunter and Coyne (1982) have described the onset of schooling and associated

anatomical, sensory, and behavioral characteristics. By point B the larva has eye retractor muscles, red muscle and red blood corpuscles, and night vision. Plankton net capture of this stage (15 mm) is a rarity. Point C may represent the faster weight gain and lower mortality aided by the onset of metamorphosis into the adult form (Methot 1981; Hunter and Coyne 1982). The lateral line is formed, respiration is through gills rather than cutaneous, red muscles are in layers, the stomach is formed, and the degree of tolerance to starvation is greatly increased. Sustained high growth rate probably still requires the detection of highly aggregated food supplies (Lasker and Zweifel 1978; Vlymen 1977; Owen 1981).

Juvenile

The maximum biomass of the cohort is achieved at point D in Fig. 3. Methot (1981) pointed out that the elaboration of gill rakers in the juvenile may coincide with the maximum rate of coastal upwelling and diatom abundance (Tont 1981). Methot (1981) also briefly described the concentration of juveniles in the continental borderland. Since the juvenile stage is at a maximum point of biomass and appears to be concentrated in a small fraction of the adult habitat, this would appear to be an extremely vulnerable point for the recruitment to the population by either density or environmentally mediated controls on population growth.

In this simple model, the life cycle is controlled by three factors in each stage. The first factor is the initial number that originates from the previous stage. The second factor is duration or the reciprocal of daily growth rate. The third factor is instantaneous mortality. In Fig. 4, these three factors are illustrated. The contrast of the mortality rate and duration of the early stages may be emphasized by comparison with the nearly horizontal curve of adult mortality. Since these curves are based on stationarity, any combination of increased stage-specific mortality that intersects the adult line will lead to a recruitment below the replacement value. To evaluate the importance of these parameters, it will be convenient to perturb each parameter for each stage.

Mortality

In Table 3, the parameters controlling the hypothetical O-group of the northern anchovy have each been perturbed

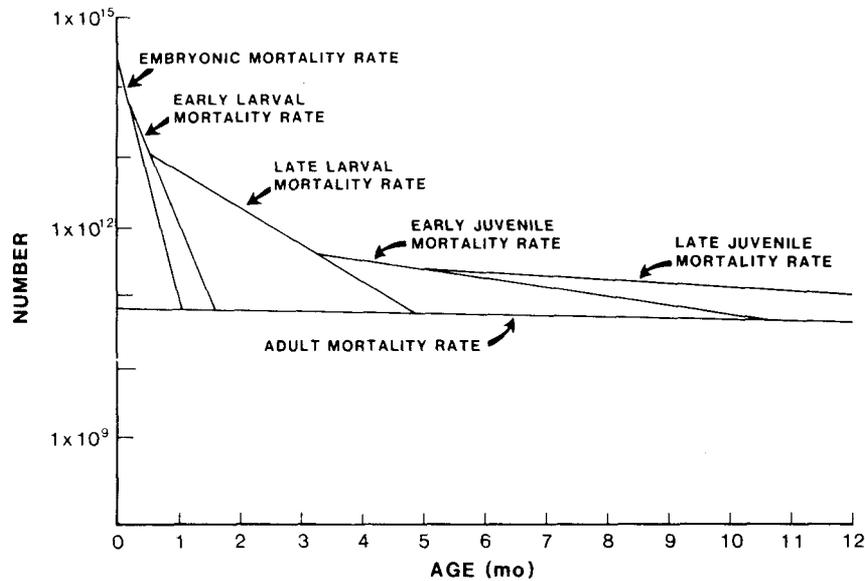*Can. J. Fish. Aquat. Sci.*, Vol. 42, 1985

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FIG. 4. A diagram of the O-group mortality curves to compare the joint effects of stage duration and stage mortality rate on the resulting adult population of northern anchovy central subpopulation.

sufficiently to effect a fivefold decrease or increase in the level of recruitment. It should be remembered at this point that we do not know if the values we have estimated for parameters so far are central in an interannual sense. The early larval mortality parameter is probably the best known on an interannual scale. The value 0.16 is the mean of 21 annual values in the period between 1951 and 1979. The range is 0.03 and 0.24, and Hewitt (1982) found that the higher values of mortality are associated with higher rates of larval production and wider distribution of the spawn. Interannual variability in embryonic mortality for the brief period between 1979 and 1983 has also been large, with estimated rates ranging from 0.00 and 0.41 in five estimates.

It is interesting to note that no manipulation of the juvenile mortality rates over a period encompassing 4 mo and 50 mm growth in length will result in a fivefold increase in the number of recruits. All the other values for mortality appear reasonable.

Duration

When one deals with duration of the stage or growth rate, it is also seen that a fivefold increase in recruitment cannot solely originate in modification of the juvenile periods' values. At the embryonic stage, the duration is controlled by temperature alone and the parameter requiring that this stage be completed in 1.6 d is not reasonable; thus, a fivefold increase in recruitment does not appear to be a reasonable outcome in this stage alone. The temperature required to lengthen this stage to 14.5 d is nearly lethal as well (Zweifel and Lasker 1976). The observed variations in growth rate in recent years would not support the idea of plasticity to the necessary extent to change the recruitment fivefold (Methot 1981), and field-measured durations of this stage are not distinguishable from the same value measured in laboratory conditions. The late larvae parameter values are as reasonable at both extremes of duration as they are in mortality.

The juvenile and prerecruit duration parameters still retain sufficient plasticity to permit fivefold decreases in recruitment but the only source of a fivefold increase would be the sustained

growth at $0.2 \, mm \cdot d^{-1}$ for more than 4 mo. The observations necessary to evaluate this are not yet documented.

Adult

We see in Table 2 that the mean generation time is over 2 yr; thus, a fully functional model of this population would require that adjacent years of recruitment be assembled into the resultant adult portion of the population with its own growth, mortality, and fecundity rates. This is beyond the scope of this paper, but it is worthwhile to note that adult mortality rates of the small clupeoid species may well vary significantly. R. D. Methot (pers. comm.) has observed this phenomenon in the northern anchovy. The number of eggs per batch per gram of female appears to vary on the order of a few tens of percent (Hunter and Leong 1981) rather than the fivefold discussed for the other population-controlling parameters. The number of batches per year could well be quite changeable. From the seasonality of the larval production over the past 30 yr (Hewitt 1982), the northern anchovy would not likely vary more than two- or three-fold in the annual rate of fecundity. More directed study on seasonality of adult reproductive behavior is required.

Some Density-Dependent Mechanisms

Some unusual circumstances of density dependence in the northern anchovy are caused by the fact that all but 30 d of a 5-yr life cycle is spent in schools (Hewitt 1981; Hunter and Coyne 1982) and the schools are often found aggregated into school groups (Fiedler 1977). This means that the more obvious forms of competition for food and space appear to be compromised by aggregation behavior. The following section contains comments on competition, cannibalism, and the stimulation of aggregation and growth of predator populations.

Competition

The dimensions of anchovy schools are of the order of tens to hundreds of metres, with most schools in the lower range, and possibly half of the fish are in the few schools more than 90 m in

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TABLE 3. Parameter[a] changes leading to a fivefold decrease or increase in recruitment for the central subpopulation of the northern anchovy. Experimental values underlined (see Table 1 for references).

Stage	Instantaneous mortality (daily)	Stage duration (d)	Growth rate (mm·d⁻¹)
Embryo			
Stationary	0.250	8	—
1/5	0.454	14.5	—
5×	0.048	1.6[b]	—
Early larva			
Stationary	0.160	12	0.500
1/5	0.297	22.2	0.270
5×	0.026	1.9[b]	3.158[b]
Late larva			
Stationary	0.050	77	0.325
1/5	0.072	110	0.227
5×	0.029	44.5	0.559
Early juvenile			
Stationary	0.020	50	0.500
1/5	0.053	131	0.190
5×	Inf.[b]	Inf.[b]	Inf.[b]
Late juvenile			
Stationary	0.010	71	0.350
1/5	0.033	232	0.108
5×	Inf.[b]	Inf.[b]	Inf.[b]
Prerecruit			
Stationary	0.010	287	0.087
1/5	0.016	449	0.056
5×	0.0044	126	0.200

[a]Parameters in the equation $NT(I - 1) \exp [-Z(I)T(I)]$ where $NT(I - 1)$ is the number at the beginning of interval I, Z is the instantaneous rate of mortality, T is the time in days, and $NT(0)$ is the annual fecundity (both sexes).

[b]Unreasonable values or Inf. (infinity).

diameter. The maximum observed size of a school is about 400 m (Mais 1974). A common density within a school is 15 kg·m⁻² (Hewitt et al. 1976). When one considers a single school (Smith 1978) the food available in the water column would be the accumulated excess of production over consumption for the interval since the last school occupied that area. Anchovy schools at any instant occupy less than 1% of their habitat (Smith 1981) but the chances of reencountering an area or encountering an area already fed upon by another school is relatively high for time periods of weeks. All these events together might cause the schools or school groups to move apart where production of food was inadequate, whereas schools might congregate in areas where food production exceeds consumption. At some population size for anchovy, or at some joint biomass of all the plankton-feeding members of a coastal pelagic guild, competition could occur between schools or among school groups.

Competition could occur between adults and juveniles if the adults deploy over a wide area for feeding when productivity is high and reassemble on the brood habitat with the juveniles at the approach of spawning time. By that time, the juveniles are nearly a year old and their food requirements are the same as the adults. The juveniles will have invested most of their energy intake into growth in length and will have relatively less fat than

the adults. The outcome, limiting to the population growth rate, might be to delay the onset of spawning by the O-group and lessen the number or repetitive batches spawned by adults.

There is evidence that all or most juveniles go through a coastal phase (Methot 1981) in water less than 90 m (50 fathoms) deep. In the major brood area for the northern anchovy the mainland coast contains 17% and the coastal islands contain 7% of the 25 000 km² brood area. Based on capture rate the shallow waters contained at least 70% of the juveniles. Thus, while a habitat calculation based on Fig. 3 might show food to be sufficient, intraspecific food-limited growth could be a factor for juveniles at large population sizes.

Competition is not likely to be a factor in the early larvae of northern anchovy. Growth rates in the sea are similar to those in the laboratory under rich feeding conditions (Methot 1981).

In summary, competition for food is not likely to be a consideration for early larvae. Competition for food should be considered for late larvae (Cushing 1983).

Competition, if any, for juveniles in a cohort may be exaggerated if most of the juveniles must pass through a small, shallow coastal segment of their habitat. Competition between the adult and juvenile segments of the population could be intense at the winter zooplankton and phytoplankton minimum when the adults assemble on the brood grounds at spawning time. Lastly, competition among adults is likely to be between schools that occupy their local habitat intensely and may reoccupy it frequently.

Cannibalism

Cannibalism is a potential density-dependent, population-limiting mechanism for the northern anchovy. Depending on the population size, cannibalism could be important as incidental to filter feeding, it could be accentuated by directed filtering on high egg concentrations, or by switching from biting to filtering behavior.

If schools must perpetually move to support their high food requirement, the population cannibalism would merely entail a school encountering the patch of eggs deposited by it or another school. From the distribution of fish schools I would expect the reencounter of a patch of eggs by the school that spawned it to be a constant probability at all population sizes or a decreasing probability with increased population size. The encounter and incidental filtration of embryos by a different school (than that which spawned it) would be an increasing function of population size.

Eggs of anchovy disperse after being spawned. Hunter and Dorr (1982) found that filtering anchovy would filter selectively in anchovy egg concentrations of 1·L⁻¹ or more. This raises the possibility that rather than incidental cannibalism, at certain population levels directed filtration could represent an important shift in the impact of egg cannibalism on the population growth rate.

A third density-dependent mechanism would be switching from biting to filtering at high population sizes. If the preferred food at low anchovy population sizes were herbivorous crustaceans obtained by biting, the probability of egg cannibalism would be low. If the population size actually decreased the population sizes of herbivores, the additional phytoplankton production and the shortage of crustaceans could increase the incidence of filtering to the extent that population growth rate would be controlled.

Brief observations of cannibalism in the northern and Peruvian anchovy (Hunter and Kimbrell 1980; MacCall 1980b;

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Santander et al. 1983) indicate that under current population sizes (very low for both stocks), cannibalism is responsible for a relatively small fraction of the mortality of the spawn. If cannibalism becomes an important regulator of the population growth rate it could occur by (1) directed filtering on dense aggregations of eggs, (2) encounter of other schools' patches of eggs, and (3) the anchovy population switching from biting to filtering feeding behavior.

Aggregation and growth of predator populations

The rapid development, mortality, and dispersal of embryos and larvae of the anchovy would make less likely the aggregation and growth of populations that prey on these stages. There is evidence for reproductive success of coastal birds changing in response to juvenile anchovies. It seems likely that populations of marine mammals and fishes could respond to adult anchovies as well. Anderson et al. (1982) described the improved rates of survival of young of the endangered brown pelican population. Should that success continue, the pelican could in turn begin to exercise control of the juvenile survival rate, particularly if most juveniles must pass through the nearshore region, as postulated by Methot (1981).

Scale deposition rates (Soutar and Isaacs 1974) of the major temperate fish stocks were collectively 3 to 5 times greater at the turn of the century (Smith 1978). This coincides with a population minimum of the northern fur seal harvest in 1911, which has been accompanied by a resurgence of the fur seal population and a concomitant decrease in the scale deposition rate (Anonymous 1977, p. 242). The current fur seal population consumes about 1 million t of pelagic fish per year in the Northeast Pacific (Lander and Kajimura 1982). If the high populations of the early part of this century stimulated the growth of the predatory populations this could be an important form of density-dependent control of the anchovy population.

Some recent years of poor recruitment per spawner in the northern anchovy have also been years of unusual Pacific mackerel (*Scomber japonicus*) abundance on the brood grounds (R. D. Methot, pers. comm.). To the degree that the mackerel aggregates on the schooled anchovy juveniles, this could be considered an important density-dependent factor in the regulation of the anchovy population. A second phase of this interaction would be if the mackerel population increases in later years as a result of the abundance of anchovy.

Thus we see that marine birds, mammals, and fishes could establish and control growth rates for a clupeoid fish population such as the anchovy. Only in the case of the guanay off Peru (Tovar 1983) and pelican feeding on anchovy juveniles (Anderson et al. 1982) have sufficient data been collected to establish a convincing link to anchovy population control by the mechanism of aggregating or stimulating the population growth of a predator population.

Environmental Mechanisms

The high-seas support no clupeoid stocks in the temperate zone. Usually in the study of the environment of clupeoid stocks we are examining the interaction of the open-sea environment in juxtaposition with the coastal and neritic ones which comprise the clupeoid habitat. The definition and interpretation of these zones must be done with care as exemplified by the writings of Bakun and Parrish (1982), Bernal and McGowan (1981), Chelton (1982), Chelton et al. (1982), Colebrook (1977), Hewitt and Method (1982), Lasker et al. (1981), Owen (1980), Parrish and MacCall (1978), and Smith and Eppley (1982). The

mechanism invoked must match the spatial, temporal, and other biological characteristics of the species for which population control is implied. For example, the California Current exhibits laminae of epipelagic fishes in which the clupeoid pair, sardine and anchovy, occupy intermediate areas; onshore are the speciose rockfishes and abundant flatfishes aligned to the bathymetric features of the coast and their interaction with the passing currents. Offshore of the clupeoid pair are the oceanic species of pelagic schooling fish, the jack mackerel (*Trachurus symmetricus*) and the saury (*Cololabis saira*) (Loeb et al. 1983). These are widespread over the transition zone of the Northeast Pacific.

The mechanisms to be discussed below are (1) lethal conditions, (2) biological production, (3) changes in the biological community, and (4) physical and chemical changes in the habitat. Many of the mechanisms to be discussed differ from density-dependent mechanisms only in that the decrease in population growth rate is incidental to the environmental change rather than being a direct result of the interaction of population density and the carrying capacity of the environment.

Lethal temperature, oxygen, etc.

A relatively large fraction of the sardine eggs spawned were placed in sites where the temperature at 10 m of depth (13°C) is known to be lethal to embryonic stages before first-feeding can occur. In 1953, lethal (Ahlstrom 1965) temperatures swept the major spawning grounds of the northern subpopulation of the Pacific sardine (*Sardinops sagax*) and no spawning was detected there. After the warming trend in 1958, virtually all sardine spawning was located in the southern California bight where spawning had previously been excluded. It may be seen that density-independent controls of stock size may be more restrictive to the spawning grounds than the feeding grounds; thus, studies of these features will have to be carefully placed in time and space and be adaptively conducted to estimate the population effect.

Biological production

Based on the early work of Murphy (1966) and Ryther et al. (1971) and later writings by Walsh (1981) and Smith and Eppley (1982), it seems plausible that stocks of clupeoids could achieve sufficient biomass to approach the limits of productivity. Neither the current measures of fish biomass, fish food requirements, nor biological production are adequate to test this hypothesis because the interaction of the disappearance of food and the increased energy of searching for the remainder cannot be studied until a clupeoid population is found whose density is near the carrying capacity. Since the clupeoid populations constitute a significant nitrogen source, the primary limitation on production would be the time between the renitrification of the environment and the elaboration of plankton edible by the clupeoid stock involved. The poleward and offshore migrations of the temperate clupeoids might reflect a behavior brought about by limitations of biological production and the relative standing stocks of food (Lasker 1970) in the two environments. Excellent measures of recruitment would be necessary for detecting subtle effects of limits of biological production; given the mobility of the juveniles at maximum cohort biomass, recruitment failure studies would require intensive regional measures of feeding and food availability.

Biological production is not yet measured routinely over oceanic areas of significant size relative to the distribution of clupeoids. For the most part, secondary production is unmeasureable by present techniques, and the elaborate methods

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necessary to estimate primary production in a broad geographic area have defeated attempts to obtain a seasonally and geographically satisfying estimate of primary production in any upwelling coastal area. Eppley et al. (1979) reported the primary production in a small area of the Southern California Bight and Smith and Eppley (1982) compared the time series with that of the northern anchovy biomass in that small area. The main barriers to temporally and spatially coherent measures of primary production are that the primary production will likely be very patchy in space and episodic in time (Tont 1976).

There are some data with which to form plans for studies of primary and secondary production off California. Colebrook (1977) analyzed the CalCOFI biomass data and found a clear pattern for the major elements of the biota. He found that there were two clear planes of variability: one was associated primarily with the California Current and the other was cross-shore near the coast. The organisms associated with the subarctic flow from the transition zone were in the "functional groups" Thaliacea, Siphonophora, and Medusae. Organisms whose orientation was primarily cross-shore were in the functional groups Copepoda, Euphausiacea, and Chaetognatha. Another description of the same data may be found in Fleminger et al. (1974); they described the coastal upwelling as extending the habitats of the temperate ocean toward the tropics adjacent to the coast in a narrow band.

Similarly, in a phytoplankton community study, Malone (1971) described a geographic division oriented to the coast. In the vast majority of the oceanic area and most of the time that the nannoplankton did not dominate was during episodes of coastal upwelling; at that time the production was primarily by large diatoms. Malone found that the geography of the bloom could be described by the presence of chlorophyll a greater than 0.5 mg$\cdot$m^{-3} at the surface. Long time-series of episodic diatom blooms were described by Tont (1981), and the nature of the episodes was described by Tont (1976). Tont found that most of the diatom biomass was detected in three blooms per year and the duration of the upwelling effect was slightly more than 1 mo.

Given these diagnostic features of primary production, the spatial and temporal description of interannual change should be approximated usefully by ships under cloud cover and by satellites when conditions are favorable. Smith and Eppley (1982) found that statistical relationships among the levels of production were exponential. That is, the relationship among primary production, zooplankton volume, and anchovy larval abundance was highly nonlinear. Larval growth and survival and recruitment should be compared with simple indices of the area influenced by upwelling. Alvariño (1980) has already begun the characterization of the spawning habitat in terms of the invertebrate communities there and in nonspawning areas.

Walsh (1981) illustrated the problem with biological productivity measurements by reporting a "time-series" of primary production with a range of 1966 to 1978 off the coast of Peru. He stated that the 1966 values are high because they were taken in a high chlorophyll area at the shelf break and that the 1976–77 data are low because repeated time-series stations were taken within a low chlorophyll area near the coast. This means that 101 of 185 stations are not representative. He failed to mention in the text, but listed in tables, the fact that 149 of the 185 samples reported were taken at 15° south in an area where Santander (1981) showed that there are usually few anchovies. Also, 159 of the 185 samples reported were from February through May and only 4 samples were during the austral winter in August and September. Walsh also chose to calculate an overall average from cruises or citations that varied in number of samples from 4 to 43. Thus, we see that someone constructing a model that includes primary production off Peru is forced to use an invalid set of samples. The average rate of carbon fixation was 3.98 g C$\cdot$m$^{-2}\cdot$d^{-1}. The situation is little better off California where there are many measurements within 30 km of the coast, and 1 yr of primary productivity reported (Owen 1974) with 38 stations spread over 12 mo and 250000 square nautical miles (M^2). Of these, only three were in the habitat of the central subpopulation of the northern anchovy in February–March of 1969, one station in May–June, two stations in August–September, and two stations in November–December.

It would appear from this that it may be some time before a primary production time-series of sufficient extent, coherence, and duration is availalable with which to consider a fundamental property of eastern boundary currents, the habitat of massive clupeoid populations.

Changes in the biological community

Loeb et al. (1983) described the large-scale spatial relationships of the organisms constituting the community that normally contains the schooling pelagic clupeoids, anchovy and sardine, delineating also the offshore, inshore, subarctic, and subtropical boundaries of this community. One may see from the time-series work of Bernal and McGowan (1981) that the relative size of these zones and the clupeoid habitat off California may be quite changeable. Colebrook (1977) estimated that the subarctic boundary and strength of the California Current parallel to the coast was the most important influence on biota and that a second significant plane of variability existed onshore and offshore.

There is frequently little distinction between those changes in the biological community that are brought about by the population in question and those that are merely incidental to other environment changes. For example, if the anchovy stimulated the aggregation and growth of predatory populations in its habitat and these populations grew to control the anchovy, the incidental effect on the cohabitant sardine might well be determined to be density independent. Thus, it is the origin of the change rather than the effect of the change that distinguishes between these phenomena and those described above.

Physical and chemical changes in the habitat

Advection — Chelton et al. (1982) concluded that large-scale variations in the flow of the California Current play the dominant role in controlling zooplankton biomass by advection of nutrients. Their argument is strongly supported by the coherent response of the zooplankton volume over a very large oceanic area (240 × 1000 M) to changes in flow between 1955 and 1959, and supported by the rest of the time-series between 1951 and 1979. Murphy (1966) in his study of the sardine population noted that the annual rate of flow into the habitat was 47×10^{12} m$^3\cdot$yr^{-1} and that the zooplankton transported in was 0.6 g$\cdot$m^{-3} and that transported out of the California Current region was 0.05 g$\cdot$m^{-3}. He estimated that the imported zooplankton was equal to one standing crop but acknowledged that the species composition was different. Transport over most of the area is simple but a narrow band near the coast is complex (Hickey 1979), and one would need to know the orientation of various phytoplankton, zooplankton, and fish species to these general areas to interpret these results more fully. Haury and Shulenberger (1982) were unable to confirm the nutrient transport hypothesis of Chelton et al. (1982).

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Wind-stress curl — Chelton (1982) used the wind-stress curl data assembled and reported by Nelson (1977) to describe a mechanism for the addition of nutrients to the euphotic zone by upwelling in a zone about 60 M offshore. This effect would extend between San Francisco and northern Baja California. No time-series or source water analyses are yet available to evaluate the range of this phenomenon or its effect on zooplankton and pelagic schooling fishes.

Isopycnal shoaling — Isopycnal shoaling is a large-scale effect caused by geostrophic tilting of isopycnals (uplift of entire density structure at coastal margin of gyres). As these isopycnals are inserted into the euphotic zone, productivity is enhanced. When the long-term, large-scale time-series of salinity (Chelton et al. 1982) is compared with advection, it appears that neither horizontal nor vertical advection is dominant for nutrient addition to the California Current. They emphasized that the vertical motion is not due to classical wind-induced coastal upwelling but is associated with geostrophic tilting of isopycnals from large-scale, low-frequency changes in the transport; thus, both horizontal and some vertical advection are caused by the flow of the California Current.

Wind-driven coastal upwelling — Barber and Smith (1980) characterized coastal upwelling ecosystems by several quantifiable features: (1) midwater oxygen minimum layers, (2) highly organic sediments, (3) anoxia, (4) denitrification and hydrogen sulfide events in subsurface waters, (5) large bird populations, and (6) guano deposits.

Source water — The physical introduction of deeper water into the euphotic zone, whether by isopycnal shoaling, coastal wind-driven upwelling, or wind-stress curl, generally has the effect of cooling and adding nutrients. The exceptions are, of course, when the source water is itself warm or nutrient free. Barber and Chavez (1983) emphasized the relationship of the qualities of the source water for upwelling to the response of the euphotic zone.

Since the California upwelling zone is not well defined or as extreme as the criteria established by Barber and Smith (1980), it will be useful to organize some measures that can be estimated from a variety of platforms in addition to the standard surveys. Surface chorophyll *a* in the range $0.5–10 \, mg \cdot m^{-3}$ should be a useful boundary feature. Copepod biomass above $10 \, g \cdot 1000 \, m^{-3}$ in the upper 140 m and euphausiid biomass over $2 \cdot 1000 \, m^{-3}$ in the upper 140 m should also serve as ready guides to the outer limit of the upwelling impact zone. Since these macroplankton have taken several weeks (copepods) or months (euphusiids) to respond to the upwelling enrichment, one should not expect these values at the site of upwelling.

Why is the recruitment to the central subpopulation of the northern anchovy so variable? To echo Gulland's (1982) theoretical paper, "Why is the recruitment to the central subpopulation of the northern anchovy not so variable?" At the beginning of the Mechanisms of Population Control section, we posed an extremely simple model of eight arbitrary stages in the anchovy life cycle. Following the lead of Shepard and Cushing (1980), the controlling parameters of each stage were the mortality and growth rates (Murphy 1961) of a stage of fixed length interval. The obvious reason why recruitment can vary is that relatively minor changes in these exponents can singly change the outcome severalfold. If these parameters are correlated with each other in a cohort, their joint effects would be devastating. If the later fate of the cohort is ultimately controlled by the carrying capacity of the environment, some of the early life stage losses or gains could be nullified. If the growth rate and the mortality rate were each adjusted independently and stochastically on a weekly basis, there would be a strong temporal averaging process. Similarly, if weekly cohorts encountered radically different conditions, there would be a second temporal averaging process. Thirdly, if the environment with respect to growth and mortality rate were structured as a mosaic, each sector of which had different rates, there would be yet another averaging process. Thus, we see that the answer to the question of why recruitment is constant is that temporal averaging within each cohort, temporal averaging among cohorts, and spatial averaging all taken together would likely enforce a certain level of stability on the eventual population size. Given the expense of confirming theory, development of predictions, and establishing monitoring systems with which to implement management recommendations (for stocks distributed over thousands of square kilometres of coastal ocean) the practical questions of costs must be raised. This is the subject of the next section.

Evaluations and Predictions

Thirty years ago, the chief problem in clupeoid fisheries was to define the stocks that had not yet been fished. Most of the catch of clupeoids in the past three decades was from stocks that had not yet been evaluated at the beginning of that period. While there are still isolated stocks of clupeoids that have not been fished, their potential yield appears small relative to those stocks that have been fished. Thus, with regard to the biological and economic yield from this taxonomic group, the largest remaining unexploited resource is effective stock management.

The physical yield from the clupeoid stocks may be expected to follow rather simple (Blaxter and Hunter 1982) (even if elaborate in total) biological rules for reproduction and harvest in a varying environment. The economic yield will probably be dominated for some years by increasing values caused by the increase of the human population and the conversion of the catch from relatively low value products of fish meal and oil to higher valued canned and cured products. Restoration of the stocks under the condition of higher demands and higher values is a first management priority. Higher stocks may be expected to yield more for less fishing effort, recover from natural variations faster, and provide other values as forage for coastal birds and migratory predators such as marine mammals and larger fishes.

Clupeoid O-Group Biological and Economic Models

Lenarz (1971) explored some economic consequences of management of the recovery of the Pacific sardine stock and the subsequent long-term yield as a function of the precision of management advice. Characteristics of sardine recruitment elucidated by Murphy (1966) were incorporated into the model. These were the reproductive capacity, recruitment variability, and the tendency for annual recruitment success to be linked with the previous years' recruitments, namely that recruitment failures tended to occur in runs, as did successes. He explored the management tools, quota, and fishery closure. Above a fixed biomass level fishing mortality was controlled and below that level the fishery was closed.

The simulation by Lenarz (1971) did not consider the economic effects of the yield but explored long-term average yield and yield per unit-of-effort as a function of management

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policy and the precision of estimates on which the policy was based. The policy of total closure at a fixed biomass increased the long-term yield about 1% but increased the yield per unit of fishing mortality by 0.4. Allowing the upper limit of fishing mortality to rise to 1.05 resulted in small long-term *gains* in average yield but significant *losses* in yield per unit of fishing effort. Precision management to maximize biological yield and yield per unit of fishing effort resulted in a closure of the fishery in 25% of the years for periods up to 4 yr. The quality of the biomass estimates had a moderate effect on yield and yield-per-effort when crude estimates were used, but 10% increases in yield and yield-per-effort resulted from improving the multiplicative error factor from 4 to 1.5.

Huppert et al (1980b) combined a biological model, a biomass-dependent yield-per-effort fishing model, and an economic yield model to explore the benefits of different management policies for the reduction segment of the northern anchovy fishery. They also included stochastic variability in actual recruitment and in the estimation of stock biomass. Their management policy included (among other things) a maximum on total catch and a closure of the fishery when the biomass was below set limits. Their management policy was based on a biomass estimate and they allowed the standard error of estimate to improve from 0.4 to 0.05 (about 2.5 to 1.05 on the Lenarz scale). The cost of the survey was scaled to the sampling effort and cost of a survey using 500 samples (1978 dollars). They assumed that survey costs were proportional to the number of samples and that the standard error of estimate decreased as the square root of the number of samples.

Huppert (1981, p. 73) concluded that the diminishing returns of value from the catch per unit of survey cost became negative between proportional assessment standard errors of 0.30 and 0.25. Further work of a similar nature was used to demonstrate the added value of allocating a portion of the catch based on the spawning biomass estimate and another portion at midyear based on a hypothetical recruitment estimate (Huppert et al. 1980a). They found that a very accurate and precise estimate of recruitment (0.1 standard error as a fraction of the mean) (Anonymous 1983) could augment the spawning biomass estimate usefully only if the annual cost of the recruitment survey was materially less than $250\,000 \cdot yr^{-1}$. They did not explore the value of a recruitment survey without a spawning biomass survey.

The scale of the fishery in the work of Huppert et al. (1980a, 1980b) and Huppert (1981) is probably too small to apply directly to the fishery commodities of a global clupeoid fishery, but some dimensions would be interesting to expand to that scale. If we incorporate the data for the Lenarz (1971) model of the value of a sardine recovery and the data from Huppert et al. (1980a, 1980b) and Huppert (1981) for improving the precision of management, we should be able to project the management research and management tactical costs for restoring and sustaining global clupeoid yields.

The expected monetary value for an annual 400 000 t catch of northern anchovy (fished for reduction to meal and oil) is $4 million, or about $10 annually per metric ton of yield. Herring have yielded 3 million t for a long period, rose to nearly 5 million t for a brief period, and then fell to 1 million t currently. Anchovies have yielded 15 million t briefly and now yield 2.5 million t. Assuming that the combined restored catch could be approximately 10 million t, the restored values would be $75 million above the harvesting and processing costs for anchovy and $20 million for herring.

The additional value of precision management could exceed the costs of the northern anchovy fishery by $40\,000 \cdot yr^{-1}$ or $0.10 \cdot t^{-1}$ (this assumes an optimum fleet size and processing facilities, and annually adjusted quotas). If all clupeoids were managed this way, and the marginal biological yields were used for meal and oil, the restored 25 million t clupeoid yield would support $2.5 million from precision management. Thus, the long-term clupeoid yield would have a perpetual expected monetary value of the order of $250 million annually at 1978 costs and values. Development and implementation of precision management techniques would yield an additional $2.5 million annually with existing methods.

Bell et al. (1975) project a fivefold increase in price for fishmeal by the year 2000 (approximately 15 yr), and this they projected would accompany a decline in supply from a maximum of 30 million to 15 million t (Anonymous 1982). They also projected a conversion of products from the clupeoid stocks to maintain a level price-function for sardines while doubling the tonnage used to 2.5 million t. Even with the improvement in human fertility trends (Coale 1983), the human population will triple by the year 2100. Thus, we find that the expected monetary values of Huppert (1981) could be a moderate underestimate.

In summary, there has been a transition in research objectives for clupeoid fisheries in the past 30 yr from exploratory fishing to define new stocks to management research to restore depleted stocks and maintain the production of existing stocks. Increasingly realistic biological models of population growth combined with economic models of fishing efficiency and monetary value can assist us in establishing perspective on the perpetual values of existing uses of clupeoid stocks. The most expensive segments for management advice can probably be coupled for several species in the temperate and tropical areas to increase efficiency. The restored biological yield of clupeoids would approach 25 million t, and rise in prices for fish meal and the conversion of end products from clupeoid stocks from meal and oil to canned and cured products will tend to increase the expected monetary values. The projected yield of $2.5 million from precision management of the restored clupeoid stocks represents the costs and precision of methods as they existed in 1978. It would seem that reduction of costs of management advice is more urgent than increases in precision for sustained management of naturally variable clupeoid stocks.

Recruitment Prediction

Huppert et al. (1980a) evaluated recruitment assessment but did not involve prediction; thus, the economic value of recruitment prediction as a function of lead time and precision has not yet been explored. The values would appear to arise from planning alternate uses for fleet and processing plants during the inevitable closures. Other values might arise from early increases in quotas after the recovery of the stock and earlier closures following the projection of poor recruitment. The research objectives under this topic should involve cost and precision studies of new methods and the merger of recruitment prediction technology and tactics for several stocks in a region, and for the global adaptation of fundamental progress in recruitment studies.

Predictions of stock size in the clupeoids will have three characteristic elements: (1) the size of the spawning stock, (2) the locations, growth, and survival of the juveniles, and (3) the survival rate (R. D. Methot, pers. comm.) and the fecundity of adults. For the purposes of this paper, the sections to follow will

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emphasize direct measures of the O-group and environmental influences. The emphasis will be on the development and implementation of low-cost indices of recruitment in clupeoids.

Direct O-Group Studies

Current methods of study of the O-group clupeoid seem confined to labor and ship-time intensive direct sampling; the quality of the samples, in terms of representivity, precision, and accuracy, is in question. The strategy of conversion to lower cost methods rests heavily on the question of when the size of the incoming year-class is determined. It is also possible that the time of recruitment determination changes among years.

A new method for determining the location of juvenile anchovies and directing samples to determine growth and survival has been developed and tested (Hewitt et al. 1976; Holliday 1980). The method consists of three steps: (1) mapping schooled fish targets with conventional sonar, (2) estimating fish size with gas-bladder resonant return of broad-band sound, and (3) trawling to determine species composition. Discrimination of bladder-bearing fish from squid and pelagic crab aggregations is possible, and the length and age of anchovies can be evaluated to a 25-mm length category or 60-d age group for larval and juvenile anchovies between 10 and 110 mm in length. Adult anchovies can be discriminated from the juveniles and larvae, and these latter could be separated into late larvae (10–35 mm), early juveniles (35–60 mm), and late juveniles and prerecruits (60–85 and 85–110 mm, respectively). The precision of the measurements should be within the useful range because continuous line-transect surveys can be partitioned into independent estimates and weighted for representativeness. This method would probably detect recruitment failure and distinguish between moderate and exceptionally large year-classes. Such a method might also replace direct spawning biomass estimates in some years and furnish the continuity needed for management purposes in years when the biomass is too low or so high as not to require direct measures for setting quotas or closures.

Until one knows the success and dependability of the environmental indicators and predictors of recruitment discussed below, it will not be possible to define the direct O-group measurements necessary for perpetual management of clupeoids. It is likely, though, that the current status of O-group direct evaluation techniques will have to be improved to test and evaluate the environmental indices for long-term operational annual recruitment predictions. Thus, the development of direct measures of recruitment will accelerate the postulation (Bakun and Parrish 1982), evaluation (Parrish and MacCall 1978), and implementation of efficient environmental prediction of clupeoid recruitment.

Environmental Prediction of Recruitment

The eventual efficient predictors of recruitment will likely entail inexpensive observations taken at high frequency over vast areas for a multitude of purposes. For the purpose of predicting recruitment the generalized measurement will be evaluated for its effect on growth and survival mechanisms of several categories in the life cycle of clupeoids. Examples of key life cycle events are the successful transition from embryonic to first-feeding larvae (Lasker 1975), maintenance of the feeding larvae in food conditions leading to fast growth and proximity to the juvenile brood grounds (Hewitt and Methot

1982), conversion from carnivory to omnivory at 60 mm for northern anchovy (Methot 1981), and the achievement of maximum cohort biomass (point D in Fig. 3) all in the first year of life.

Clupeoid populations appear to occupy the habitat rather intensely (Ryther et al 1971; Murphy 1966; Lasker 1970; Hunter and Leong 1981; Smith and Eppley 1982; Cushing 1982); thus, measures of primary and secondary productivity could serve to evaluate the timing and intensity of spawning and subsequent survival of growth of the cohort. This approach could be extremely useful where several schooling coastal pelagic species occupy overlapping planktivorous niches. Virtually all the techniques discussed up to now were directed at fishery population management. New economies could be realized by merging measurements for the regulation of multispecies fisheries such as are commonly pursued for clupeoids, scombrids, carangids, and gadoids in the upwelling areas and continental boundary currents.

Environmental measurements may be obtained from standard survey cruises, platform-of-opportunity data, and coastal measures of temperature, salinity, chlorophyll, and sea level. Estimates of temperature and chlorophyll can now be made by satellite or airplane (Lasker et al. 1981; Pelaez and Guan 1982). Large area averages of turbulence, transport, and upwelling can now be obtained from meteorological data fields (Bakun and Parrish 1982). Coastal birds may be monitored for chick production, survival, and growth (Anderson et al, 1982; Tovar 1983) and marine mammals are often monitored (Anonymous 1977). The primary inhibition in the use of the above indicators is that they are more in the realm of individual, intensive, short-term research and they have not yet been forged into the system necessary for effectiveness as a perpetual management tool.

For schooling coastal, pelagic fishes, including the clupeoids, it can be foreseen that the estimation of small-scale spatial intensity of their food will be more important than measurements integrated through depth and space. Holliday (1980) described systems for evaluating forage using multifrequency ultrasound (megahertz), and mergers with pumps and nets are natural applications of this acoustic tool. As in the case of direct measurements of the O-group clupeoids, these techniques will be useful for defining the indicative or predictive indirect measures we need to evaluate plankton composition, spatial pattern and productivity as controls on clupeoid juvenile growth rate and survival and adult fecundity.

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