THE VALUE OF PATTERN IN THE DISTRIBUTION OF YOUNG FISH

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A hypothesis is proposed that the "patchy" character of pelagic larval fish distributions is adaptive and may be considered a life history trait co-evolved with a suite of other behavioral traits and physiological characteristics which together assure optimum larval survival. Specific differences in larval "patchiness" are implied and these differences may be explained in biological terms. A method is described which uses the counts of sized larvae from plankton samples to describe the development of pattern with larval age. "Patchiness" at age curves are presented for the northern anchovy (*Engraulis mordax*) and the jack mackerel (*Trachurus symmetricus*). An attempt is made to explain the dissimilarities between the curves in terms of specific differences in feeding behavior, sibling cannibalism and the development of social behavior.

INTRODUCTION

A universal charactersitic of both plant and animal populations is the 'non-random nature of their distributions. When mapping a population, it is often found that the spacing between organisms is more regular than that which would be due to chance alone; on the other extreme, relatively dense concentrations of organisms may be found to be surrounded by areas of relatively low densities (i.e., aggregated pattern or patchiness). Classic explanations for these observations are resource monopolization and/or territoriality in the case of uniform distributions, and environmental heterogeneity in the case of patchiness (Pielou, 1974). Social behavior may also explain patchiness in the population distribution of certain mammalian, avian, insect and fish taxa (Wilson, 1975, and numerous references cited within).

In the pelagic marine habitat, phytoplankton patchiness is probably caused by environmental discontinuities in nutrient supply, sunlight and grazing pressure. Patchiness among invertebrate and vertebrate groups is often attributed to social behavior; advantages include reduction of predation,

enhancement of reproductive activities, increased efficiency of movement and population regulation (e.g., Clutter, 1969; Brock and Riffenburgh, 1960). However, there are occasions where patchiness is not so readily explained; specifically the aggregated pattern encountered when sampling fish eggs and larvae at a stage prior to the onset of social behavior. The observed patchiness of ichthyoplankton may be explained as the result of parental behavior to achieve efficient fertilization; if this were the only reason natural selection would favor those characteristics which inhibit egg dispersion and thus maximize zygote formation. One would expect convergence in egg geometry, batch size, and general spawning behavior.

Convergence is not observed: some species lay ovoid eggs while others lay spheroid eggs; some eggs have embossed patterns of ridges on their surface while others are smooth; some fish are batch spawners while others are serial spawners; some release large numbers of small yolked eggs while others release fewer but larger yolked eggs. All of these features have an effect on the dispersion of eggs and it may be that fertilization and the subsequent dispersal pattern of the young are both being optimized. I am proposing

that larval patchiness does indeed contribute to survival specifically by facilitating visual contacts between larval which appear to be essential to the ontogeny of schooling behavior (Shaw, 1970; Williams and Shaw, 1971). From this viewpoint, pattern is considered one of a suite of co-evolved characters which together describe the life history of the larval phase. The patchiness of planktonic eggs and larvae is initially determined by parental spawning behavior (Smith, 1973) and the physical forces which drive oceanic diffusion. If increased social contacts between larvae contribute to their survival then spawning behavior is subject to selection, particularly with respect to the initial scale and intensity of egg patches. It follows that the intensity of egg patchiness may have evolved to complement the average diffusion conditions in the sea and that anomolous environments may inhibit or enhance the development of schooling behavior.

The positive aspects of larval patchiness are reduced by the detrimental effects of increased competition for food and, in some species, sibling cannibalism (Mayo, 1973). The pelagic larvae of various fish species, or at least groups of species, differ widely in morphology, growth rate, visual acuity, swimming ability, prey selectivity, and tendency to cannibalism. If we acknowledge the existence of density-dependent events in the larval and early juvenile stages (e.g., feeding, ontogeny of schooling, settling success for demersal fishes) then pattern must be included in the above list.

This paper presents the initial investigation of the hypothesis that patchiness is an important characteristic of larval existence. It is limited to the question: do differences exist between two species in their larval dispersion patterns and can these differences be explained by differences in other characteristics of their life history? The index used to quantify patchiness is briefly reviewed and pattern is traced, as a function of larval age, for a carangid (*Trachurus symmetricus*) and an engraulid species (*Engraulis mordax*).

QUANTIFYING PATTERN

Two classes of methods are used to reconstruct population pattern from sampling information: those that employ distance as a continuous variate and those that use numbers-per-quadrat as a discrete variate (Pielou, 1977). The first methodology relies on distance sampling to measure the spatial distribution of individuals (e.g., the distance to the nearest neighbor from randomly chosen individuals is used as a variate). The second methodology uses as a variate the number of individuals counted in a randomly chosen quadrat encompassing some finite space. When the population does not distribute itself into natural quadrats (such as in the organs of parasite hosts), distance sampling is preferred because the delimitation of artificial quadrats imposes a scale on the pattern detectable. However, distance sampling is possible only for sessile animals and plants or when a synoptic picture of the distribution of motile animals is possible. Planktonic populations are most directly sampled using quadrats where the quadrat size is defined as the volume of water captured in a bottle or filtered by a net.

The results of a survey may be presented as a histogram of numbers-per-quadrat which, in the case of an aggregated population, is skewed with a disproportionately large proportion of the organisms retained in a small number of samples. The histogram may be summarized by an estimate of the population mean and variance. Several indexes, sensitive to pattern intensity, have been derived as a function of the mean and variance. Some are affected by population density such as the variance/mean ratio, "index of clumping" (David and Moore, 1954) and "mean crowding" (Lloyd, 1967). Others are unaffected by density, such as Morista's (1959) "index of dispersion" and Lloyd's (1967) "patchiness". Density independence is an attractive feature because it allows the use of these measures to compare the pattern of populations irrespective of their abundance levels.

These indices measure the intensity of pattern but not the scale (or grain) of pattern. Intensity is defined as the extent to which local density varies from place to place and scale is the relative spatial extent over which the whole range of densities is found. The resolution of these indices (i.e., the minimum scale at which pattern intensity may be detected) is the distance traversed with an oblique plankton tow.

The index used here is Lloyd's (1967) "patchiness" which is a function of "mean crowding." Lloyd has defined mean crowding ($\overset{*}{m}$) as "the mean number per individual of other individuals in the same quadrat." Thus:

$$\overset{*}{m} = \frac{\displaystyle\sum_{i=1}^{Q} x_i(x_i - 1)}{\displaystyle\sum_{i=1}^{Q} x_i} = m + \left(\frac{\sigma^2}{m} - 1\right)$$

where the population is distributed into Q quadrats x_i is the count of organisms in the ith quadrat, σ^2 is the population variance, and m is the population mean. Thus, mean crowding ($\overset{*}{m}$) is the mean density improved by the amount that the variance to mean

ratio exceeds unity. In a randomly dispersed population the variance equals the mean, and $\overset{*}{m}$ and m are also the same.

Patchiness is mean crowding standardized by the mean density:

$$\frac{\overset{*}{m}}{m} = 1 + \frac{\sigma^2 - m}{m^2}$$

and may be considered to measure how many times more crowded an average individual is relative to an individual in a population with the same mean density but randomly dispersed.

It can be shown (Hewitt, unpubl. MS) that a random removal of a fraction of the population (density independent mortality) reduces mean crowding proportionately but patchiness remains unchanged. Thus, mean crowding is something that is experienced by the individual and depends on the absolute abundance. Patchiness is a property of pattern and is independent of population density; two populations can exhibit the same degree of patchiness even though their densities differ (Pielou, 1977).

In order to arrive at a standard error for the sample estimate of population patchiness, I have assumed the underlying distribution to be negative binomial (Lloyd, 1967, Zweifel and Smith, this volume). The negative binomial distribution is specified by two parameters: the mean (m) and k (the reciprocal of k has been used as an index of patchiness, e.g. Waters, 1959, Cassie, 1962). The population variance is related to m and k:

$$\sigma^2 = m + \frac{m^2}{k}$$

Thus:

$$\frac{\overset{*}{m}}{m} = 1 + \frac{1}{k}$$

The sample estimate of patchiness is by analogy:

$$\frac{\overset{*}{x}}{x} = 1 + \frac{1}{\hat{k}}$$

Where $\hat{k}$ is the maximum likelihood estimate of k (Bliss and Fisher, 1953). This method is particularly attractive in the case of highly contagious populations because it makes use of the entire sample distribution rather than its summary form: the mean and variance. The expression for the standard error of the sample estimate of patchiness was given by Lloyd as:

$$S.E.\left[\frac{\overset{*}{x}}{x}\right] \cong \frac{1}{\hat{k}^2}\left[\widehat{var(k)}\right]^{.5}$$

where var (k) is the sampling variance for k.

THE FISH

The gross morphology of the northern anchovy larva (*Engraulis mordax*) is characteristic of clupeoid fish larvae: elongate body, small fins, and a small terminal mouth (Fig. 1a). Except for the yolk-sac stage and a short period after yolk-sac absorption, growth in length is approximately linear with age over the time that the larvae are susceptible to capture (Zweifel and Lasker, 1976, Fig. 2), although Hunter (1976) has described growth over the entire larval period as curvilinear.

Northern anchovy are initially euryphagous but soon adjust their diet to the eggs. nauplii, and copepodid stages of small copepods; the size of prey eaten increases with age (Arthur, 1976). Anchovy are able to persist for up to 20 days on a euryphagous diet (Lasker et al., 1970) but growth is depressed.

In the process of feeding, a northern anchovy larva assumes a sinusoidal posture and sculls toward the prey; at a short distance the larva straightens its body, drives forward and captures the prey. If a strike is unsuccessful, repeated efforts are seldom made toward the same prey (Hunter, 1972).

Northern anchovy larvae are capable of short (0.1–0.2 sec) swimming bursts with an average speed of 15 body lengths per second but this mode of swimming behavior is increasingly rare with age. The dominant form of larval swimming, used for prey search. is a beat and glide mode similar to that of the adults (Hunter, 1972). While this behavior results in a slow speed of advance, Vlymen (1974) has calculated that it has relatively high metabolic efficiency.

The larva of the jack mackerel (*Trachurus symmetricus*) rapidly changes from an elongate shape to a deep bodied form with a large jaw structure and eyes (Fig. 1b). No clear cut distinction exists between larvae and juveniles; the larval period is considered to end at the completion of fin formation (Ahlstrom and Ball, 1954). Initial growth is slow (Theilacker, 1978) but must accelerate at a later age to a value greater than that for the anchovy because 1 year old jack mackerel are larger than 1 year old anchovy despite the fact that the jack mackerel were spawned later in the year (Wine and Knaggs, 1975; Spratt, 1975; Kramer and Smith, 1970, 1971).

The larval growth curve for jack mackerel (Fig. 2) was approximated to fit the growth of laboratory reared larvae (Theilacker, 1978; and pers. comm.) and field caught larvae aged by R. Methot using daily otolith increments. Reduction in growth rate was not observed at the end of the larval phase (Theilacker, pers. comm.) as it was for the anchovy.

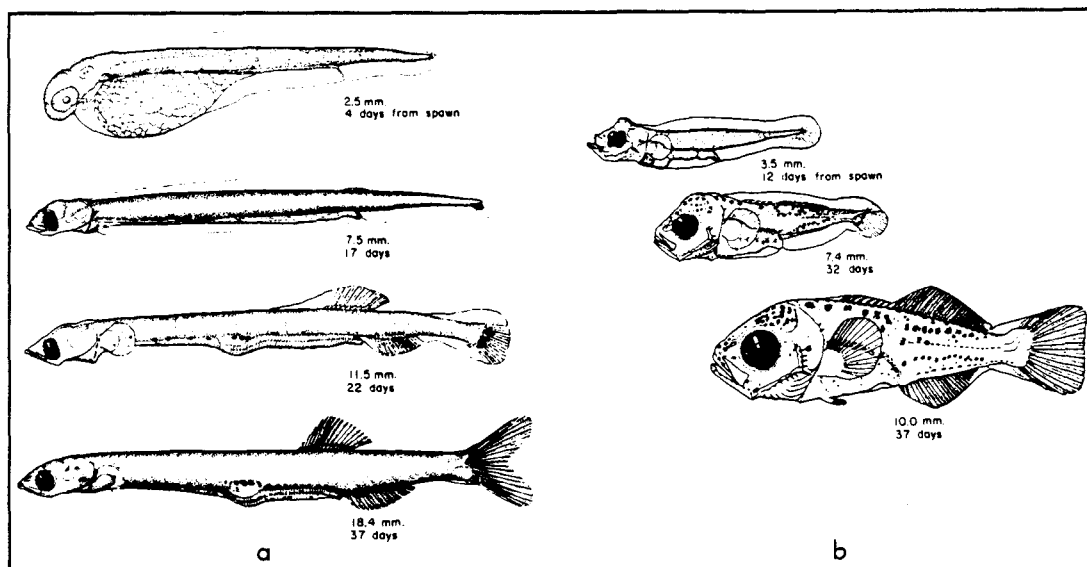Jack mackerel larvae consume larger prey as they grow and rapidly shift from naupliar to copepodid

Figure 1. (a) Four developmental stages of the larva of the northern anchovy, *Engraulis mordax*. From Kramer and Ahlstrom 1968. (b) Three developmental stages of the larva of the jack mackerel, *Trachurus symmetricus*. From Ahlstrom 1969.

stages as preferred food items (Arthur, 1976). A shift to larger prey implies a shift to more rare prey because the density of food particles in the sea decreases exponentially with particle size (Sheldon and Parsons, 1967; Sheldon et al., 1972). Vlymen (1977) and Arthur (1977) described similar distributions in the coastal waters off California; a jack mackerel larva eating copepodites would find its prey 1–2 orders of magnitude less abundant than the naupliar stages eaten by anchovy larvae. Arthur (1977) also finds the different naupliar stages to have a similar type of contagious distribution whereas copepodid stages are more uniformly distributed. Jack mackerel larvae feed with a simple biting lunge and do not employ the more time consuming coil, advance, and strike mode of the anchovy.

The swimming of jack mackerel larvae has not been described although Hunter and Kimbrell (1980) has observed that a morphologically similar larva (deep, robust body) of the Pacific mackerel (*Scomber japonicus*) increases its cruising speed from 2 to 3 body lengths over the larval period. Theilacker (pers. comm.) states that jack mackerel larvae swim at a steady moderate speed and do not engage in high speed bursts as the Pacific mackerel do. On the basis of the contrast between beat and glide swimming and continuous tail beat swimming, one may expect differences to exist between the anchovy and jack

mackerel in their searching ability and metabolic requirements, with the jack mackerel expending more energy to search a larger volume of water.

In contrast, the clupeoid larva swims at a slower rate, expending less energy and searches a smaller volume of water; its preferred food is smaller and therefore more common. The carangid larva eats rarer prey and must search further for it; its higher locomotor ability aids in the search for food and maintains the frequency of contacts between dispersed individuals. High larval densities may be less detrimental to the feeding success of anchovy than jack mackerel; whereas low larval densities may be less detrimental to successful school formation among jack mackerel than anchovy. Thus, it seems reasonable that the formation of dense patches of eggs and slow dispersion rates favor clupeoid larvae, while low egg densities would be more favorable to the more active larvae. Table 1 summarizes larval characteristics of the northern anchovy and the jack mackerel relevant to distribution pattern.

THE DATA

Counts of anchovy and jack mackerel larvae from the California Cooperative Oceanic Fisheries Investigations (CalCOFI) ichthyoplankton collections were examined and enumerated by size
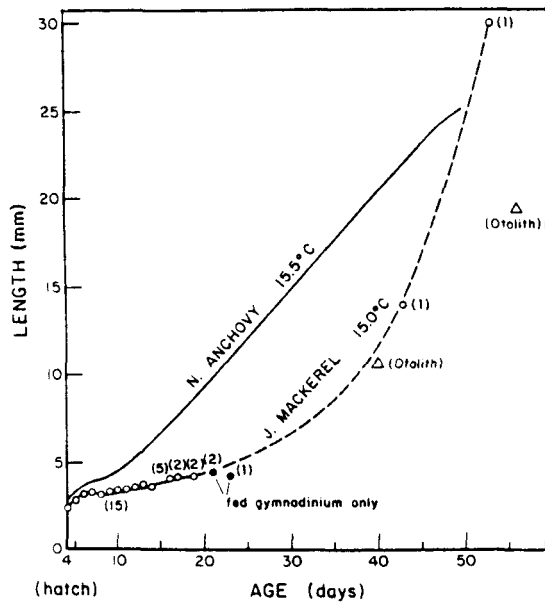
Figure 2. Larval growth curves (length at age) for the northern anchovy and the jack mackerel. Northern anchovy growth is based on the Laird-Gompertz model fit by Zweifel and Lasker (1976) and further elaborated by Zweifel and Smith ms. The growth curve for jack mackerel was fitted by eye to data on laboratory reared fish and two field caught fish; the numbers in parentheses indicate the number of fish at a given age whose length was measured; each of the first 11 points (up to 10 days age) are the average of 15 fish (Theilacker, 1978).

classes. Data was available for the anchovy for stations occupied between 1951 and 1969 and for the jack mackerel between 1961 and 1969. Because the interpretation of zero counts is ambiguous (they either represent samples drawn from outside the animal's habitat or they are true zeros resulting from the patchy character of egg and larvae distributions), only those samples which captured a larva of any size were selected. This analysis pooled sized larvae counts from 11 650 samples (out of 25 360) which were positive for any size anchovy larvae and from 1 879 samples (out of 9 459) which were positive for any size jack mackerel larvae. The two sets of samples were assumed to be representative of each species habitat and the dispersion of larvae among these samples was examined.

The decrease in mean number of larvae per sample with time (size was translated to age using the growth curves) is interpreted as the result of mortality. A crude mortality estimate, based on a linear transformation of the exponential curve, obtained an instantaneous mortality of 0.16 for the anchovy and 0.18 for the jack mackerel.

Dispersion was evident from the initial increase in positive samples even though the abundance of larvae was decreasing at a substantial rate (Fig. 3b). The proportion of positive samples for anchovy larvae increased and reached a maximum after 18 days; during this same time the cohort suffered an order of magnitude decrease in numbers. The jack mackerel achieved maximum dispersion after about 10 days and rapidly disappeared from a large portion of the samples.

Evidence for an increase in patchiness is described in Figure 3c where mean larval abundance is plotted against age. The closed squares are the mean number of larvae per sample throughout the habitat and their decline with age is the result of mortality. The open squares are the mean number of larvae per sample positive for that age larvae and are a measure of local abundance in that portion of the habitat where they are found. The mean per positive sample will decrease in response to mortality and may decrease or increase in response to dispersion or aggregation. For the anchovy the open and closed squares diverged at 18 days suggesting that the effect of mortality on local density is somewhat offset by increasing patchiness; a similar increase in patchiness is observed for the jack mackerel beginning at an earlier age.

The anchovy exhibited an initially high degree of patchiness, achieved a maximum dispersion at about 18 days and showed a rapid increase in patchiness thereafter (Fig. 4). The jack mackerel started out less patchy and achieved maximum dispersion at an earlier age.

Table 1. Summary of larval characteristics relevant to distribution pattern.

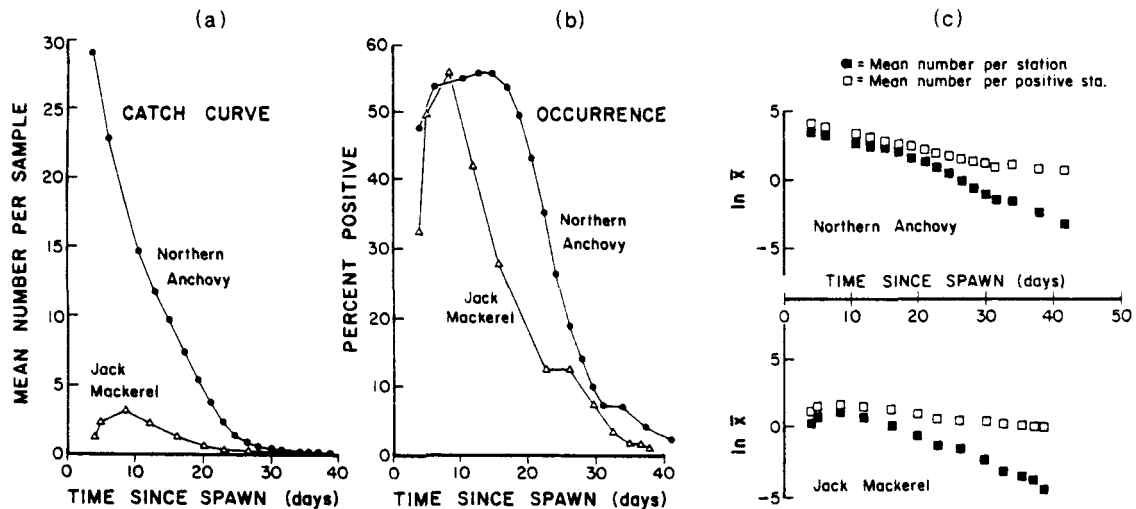| Characteristic	Northern anchovy	Jack mackerel
Swimming ability	Poorly developed	Well developed
Prey	Small size, abundant and patchy	Large size, uniformly rare
Volume of water capable of searching	Small	Large
Dispersion	Low	High
Expected contact between larvae necessary for development of schooling behavior	High	High

Figure 3. (a) Catch curve of larvae expressed as mean number of larvae per sample by age categories. The first two jack mackerel groups are undersampled relative to the other classes as a result of rapid growth in the yolk-sac stage and extrusion of small larvae throughout the meshes of the net. (b) The proportion of samples positive for larvae of a particular age. (c) The natural logarithms of the mean number of larvae per sample and the mean number of larvae per sample positive for larvae of a particular age. Change in the mean number per sample indexes mortality; change in the mean number per positive sample indexes patch density and is sensitive to mortality and dispersion. A divergence of the means is interpreted as evidence of increasing patchiness.

DISCUSSION

The curves described by Figure 4 were obtained from pooling data over large temporal and spatial regimes and as such represent average conditions for the period considered. Patchiness is a non-dimensional quantity best used to describe the character of pattern as a population trait rather than as perceived by the individual. The index used here is defined as a measurement of how many more times an individual is crowded relative to an individual in a randomly dispersed population of the same size. Jack mackerel larvae are never more than 1 / 10 as abundant as equal-aged anchovy larvae yet the development of their pattern shows a similarity to that of the anchovy. Both fish are initially patchy, disperse, and then become patchy again. The increase in patchiness may be due to a response to food gradients (Hunter and Thomas, 1974), or to uneven predator pressure, or hydrographic features, or movements observed early in the development of social behavior (Shaw, 1960, 1961; Jorne-Safriel and Shaw, 1966). Whatever the cause, patchiness maintains continued contact between larvae necessary to the integration of approach/withdraw and approach/orient behaviors. The merging of such opposing reactions has been shown to be essential to the development of schooling behavior (Williams and Shaw, 1971).

The jack mackerel was not only less abundant but less patchy than the anchovy in the early larval phase. Presumably this pattern is an evolutionary response to the relative scarcity of jack mackerel larval food. Apparently the initial intensity of patchiness was high enough to insure that the larvae were never completely dispersed to a random pattern. If complete dispersal had occurred, the larvae would have had little or no contact between them and subsequent schooling behavior would have been adversely modified (Williams and Shaw, 1971) or non-existent. Jack mackerel larvae were never significantly more patchy than anchovy larvae even though they were much less abundant. Presumably the more active larvae are capable of maintaining contact between more widely separated individuals.

The curves in Figure 4 describe the evolution of pattern for two very different larvae. They lend credence to the idea that pattern is species specific or at least specific to larval types and that pattern is important to larval events. The next phase in this work will be to determine a similar curve for a pelagic larva that does not eventually school. Patchiness will also be examined in particular years, seasons, and subportions of the habitat and then compared with the long term mean. Particular attention will be directed toward correlations with seasonal variation in
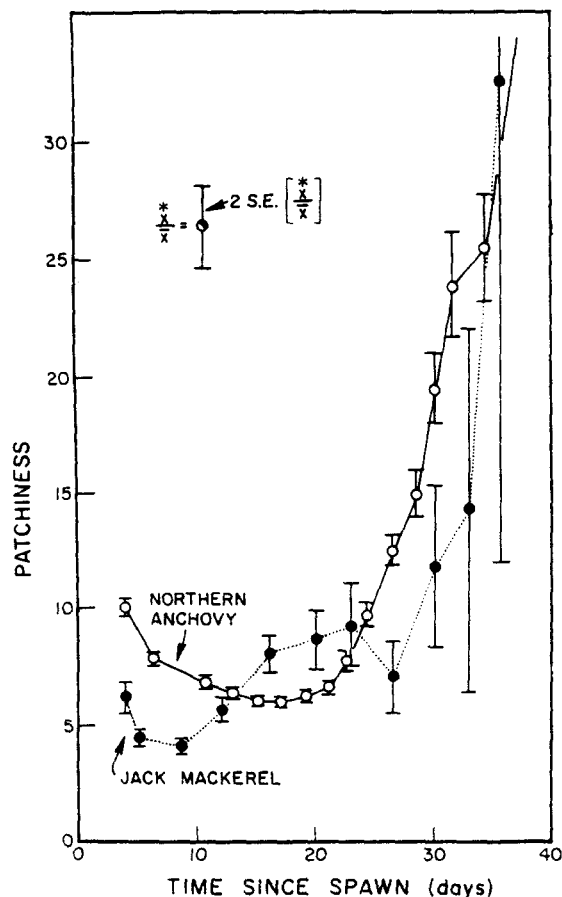
Figure 4. Lloyd's (1967) index of patchiness as a function of larval age, where patchiness measures the degree of departure from a random dispersion pattern.

spawning biology, geographic expansion (or contraction) of the spawning area, anomalies in horizontal mixing, and, finally, survival variation in the late larval, early juvenile phase.

Smith and Lasker (1978) have noted that while the anchovy population has increased approximately by an order of magnitude between 1951 and 1969, the number of large larvae has remained relatively constant. It is apparent that there must have been large variations in survival through the late larval phase to account for the increase in anchovy numbers. Abundance of older larvae yields little information as to the future success of recruitment and it may be that the important predictive factor is not how many larvae have survived but rather their dispersion pattern.

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