Changes in the spatial patchiness of Pacific mackerel, *Scomber japonicus*, larvae with increasing age and size

Yasunobu Matsuura

Instituto Oceanográfico da Universidade de Saõ Paulo
Cidade Universitária, Butantan, Saõ Paulo 05508, Brasil

Roger Hewitt

Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
P.O. Box 271, La Jolla, California 92038

Several investigators have suggested that the spatial patchiness of fish eggs and larvae may be an important factor in the recruitment process (Smith, 1973; Lasker, 1978; Hewitt, 1981; Houde and Lovdal, 1985; McGurk, 1986). Patchiness has been linked to success in foraging (Hewitt, 1981), ontogeny of schooling behavior (Hewitt, 1981), and predation mortality (McGurk, 1986, 1987). Contagion in the dispersion of ichthyoplankton has been described for Pacific sardine, *Sardinops sagax*, eggs (Smith, 1973); northern anchovy, *Engraulis mordax*, and jack mackerel, *Trachurus symmetricus*, larvae (Hewitt, 1981); haddock, *Melanogrammus aeglefinus*, eggs (Koslow et al., 1985); several taxa found in Biscayne Bay including bay anchovy, *Anchoa mitchilli*, eggs and larvae (Houde and Lovdal, 1985); Atlantic herring, *Clupea harengus harengus*, larvae (Henri et al., 1985); Pacific herring, *Clupea harengus pallasi*, larvae (McGurk, 1987); bluefin tuna, *Thunnus maccoyii*, larvae (Davis et al., 1990); Brazilian sardine, *Sardinella brasiliensis*, larvae; and scaled sardine, *Harengula jaguana*, larvae (Spach, 1990).

The patchy distribution of fish eggs and larvae is initially introduced by the spawning behavior of adult fish. In order to guarantee successful fertilization in a pelagic environment, eggs must be laid when the adults are highly aggregated, and spawning and fertilization must occur almost simultaneously (Hewitt, 1981). Alternately, demersal spawners may deposit their eggs in batches that incubate on a substrate before releasing a cohort of larvae into the pelagic environment (McGurk, 1987). Thereafter, eggs or hatching larvae, or both, disperse, principally in horizontal directions; distribution patterns during this period are primarily influenced by dispersal, diffusion, and transport (Smith, 1973). After a few days or weeks, larvae begin to reaggregate, an activity that becomes more evident in the juvenile stages of most schooling pelagic fishes.

Patchiness-at-age curves for several species of pelagic schooling fishes have been shown to exhibit a characteristic "U" shape: high initial patchiness, followed by a rapid decline as the eggs or newly hatched embryos, or both, passively disperse, followed by an increase in patchiness as the developing fish begin to aggregate in schools (Hewitt, 1981; McGurk, 1987; Spach, 1990). Patchiness-at-age curves for fish eggs and larvae have been in-

terpreted in terms of species-specific differences in life history traits such as adult reproductive behavior and larval feeding ecology, size, growth, and mortality (Smith,1973; Hewitt, 1981; Koslow et al., 1985; McGurk, 1987). Insight into the function of patchiness may be improved by comparing how patchiness changes with age and size for species with different life histories.

In this note, we present patchiness-at-age and patchiness-at-size curves for Pacific mackerel, *Scomber japonicus*, larvae and compare them with similar curves for other pelagic fish larvae.

Material and methods

Data base

The data used in this work came from the California Cooperative Oceanic Fisheries Investigations (CalCOFI) ichthyoplankton data base. These data are available from the CalCOFI on-line data system (Anon., 1988). Details of station and ichthyoplankton data were published in a series of CalCOFI ichthyoplankton data reports (NOAA Tech. Memo., NMFS, SWFSC, numbers 70–88, 92–100, and 102–105). Size-specific catches of Pacific mackerel larvae, collected from 1953 through 1981, were extracted and summarized for the analyses reported here.

Pacific mackerel larvae were collected with 1-m ring nets from 1953 through 1975 and with bongo nets thereafter. Sampling methods and laboratory procedures were described by Kramer et al. (1972). Out of 23,963 CalCOFI stations sampled from 1953 to 1981, plankton samples from 1,011 stations contained at least one Pacific mackerel larva. The 1,011 stations where larva were collected were assumed to define the Pacific mackerel's

habitat, and these stations comprised the data set used in the analyses.

Size-frequency analysis

Frequency distributions of larval catches by size were assembled and a negative binomial model was fit to each distribution. The negative binomial has been used to describe aggregated distributions of ichthyoplankton (Hewitt, 1981; Zweifel and Smith, 1981; Smith and Hewitt, 1985). The model is specified by the mean (m) and the index of dispersion (k); the variance (σ^2) is related to m and k as

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

Lloyd's (1967) index of patchiness (P) was used to describe the intensity of the distribution pattern at various larval sizes where

$$P = 1 + \frac{\sigma^2 - m}{m^2}.$$

The index has been used by several investigators to describe ichthyoplankton patchiness (Smith, 1973; Hewitt, 1981; Houde and Lovdal, 1985; McGurk, 1987) and may be considered as a measure of how many times more crowded an average individual is relative to an individual in a population with the same mean density, but one which is randomly dispersed. The index is independent of density and the scale of sampling (Pielou, 1977; Hewitt, 1982) which allows comparisons of patchiness between relatively abundant yolk-sac larvae and less abundant older larvae. By substituting the expression for the variance of the negative binomial,

$$P = 1 + \frac{1}{k},$$

where k was estimated by using a maximum likelihood estimate expression (Bliss and Fisher, 1953; Smith and Hewitt, 1985). The standard error of the sample estimate of patchiness was estimated by following Lloyd (1967):

$$se(P) \cong \frac{1}{k^2}\sqrt{\widehat{\text{var}(k)}},$$

where $\widehat{\text{var}(k)}$ is the sampling variance of k.

Adjusting for shrinkage and converting to age

Initial size measurements were obtained from larvae preserved in 5% buffered formalin. Preserved size was converted to live size by using the shrinkage rate obtained for jack mackerel larvae from Theilacker (1980). To convert from larval size to larval age, we used the growth curve obtained from laboratory reared larvae with water temperature ranging from 16.8 to 19.2°C (Hunter and Kimbrell, 1980):

$$t = \frac{\ln(SL/3.4432)}{0.05968},$$

where t = age in days since hatching (= 0 age), and SL = standard length in live size (mm). The incubation period (from spawn to hatch) was assumed to be 2.3 days.

Results and discussion

Frequency distributions of larval catches by size are presented in Table 1. The corresponding live sizes, ages, mean abundances per tow, and patchiness parameters are also presented in Table 1. Larvae less than 3.5 mm in length appear to be undersampled in comparison to larger sizes. Pacific mackerel larvae grow rapidly through the first two size classes and therefore are vulnerable to capture for a relatively short period of time; small larvae are also more likely to be extruded through the meshes of the sampling net (Smith and Richardson, 1977).

The change in patchiness with age suggests that recently hatched Pacific mackerel larvae were highly aggregated and dispersed rapidly until approximately five days after spawning (Fig. 1). Patchiness gradually increased with age until 9.2 days, then decreased slightly and continued to increase with age thereafter.
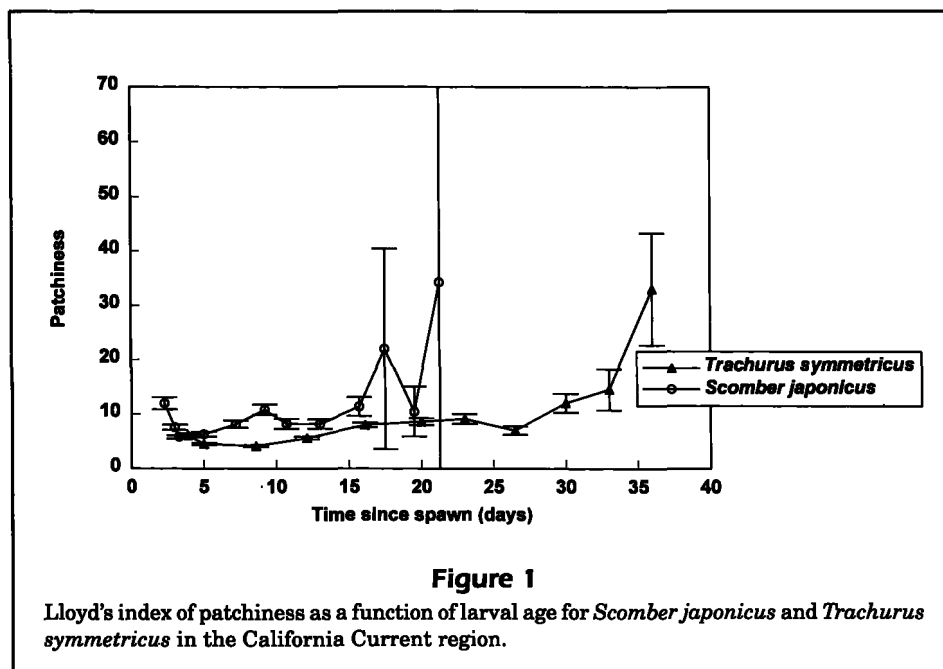
Morphological and behavioral changes of developing Pacific mackerel larvae are summarized in Table 2 and illustrated in Figure 2. A functional visual sensory organ is formed in Pacific mackerel larvae at 6.0–6.5 mm and completed at approximately 8 mm.[1] Although caudal and pectoral fins begin development at 3.5 mm, swimming speed increases rapidly with size only after the pelvic, anal, and dorsal fins are formed at approximately 9.6 mm (Watanabe, 1970; Hunter and Kimbrell, 1980). Hunter and Kimbrell (1980) reported that schooling behavior did not begin until 14 mm, although an increase in patchiness at 4.6 mm is apparent from the plankton catches. It may be that the ontogeny of schooling behavior in Pacific mackerel involves a prolonged period of contact between larvae that is necessary for the successful integration of approach-withdraw and approach-orient behaviors (Shaw, 1960, 1970; Williams and Shaw, 1971). This phenomenon may be statistically recognizable as an increase in patchiness but not visually recognizable as coordinated social behavior.
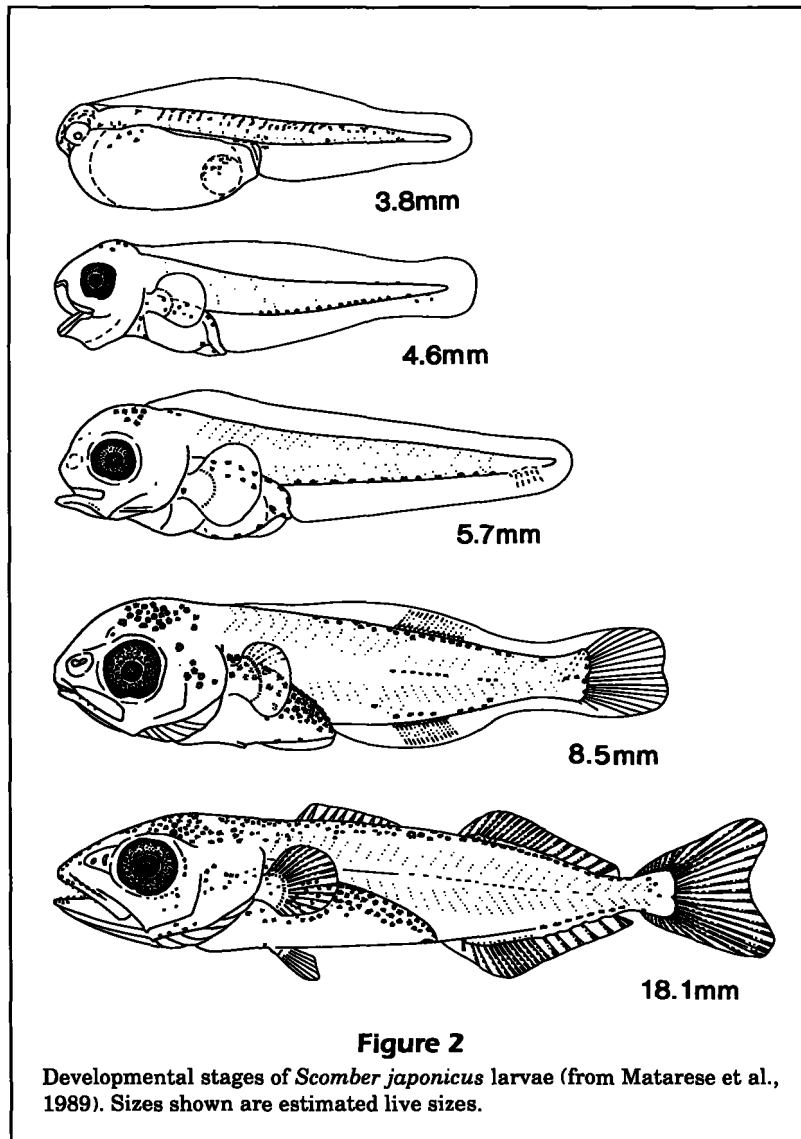
[1] O'Connell, C. Southwest Fisheries Science Center, Nat. Mar. Fish. Serv., NOAA, P.O. Box 271, La Jolla, California.

Table 1

Size-specific catch statistics for *Scomber japonicus* larvae collected during CalCOFI surveys from 1953 through 1981. A total of 8,396 larvae were caught at 1,011 stations out of a total of 23,963 CalCOFI stations.

Catch	Preserved size (mm) Live size (mm) Age since spawn (days)											
	2.00 3.10 2.3	2.50 3.30 3.0	3.00 3.50 3.3	3.50 4.00 5.0	4.00 4.60 7.2	4.50 5.20 9.2	5.00 5.70 10.7	5.75 6.50 13.0	6.75 7.70 15.7	7.75 8.50 17.5	8.75 9.60 19.5	9.75 10.70 21.3
Number of larvae/sample												
0	825	671	571	698	774	806	849	836	908	970	980	995
1	93	149	195	143	112	113	90	99	80	26	28	13
2	34	66	81	63	56	35	34	39	9	10	2	2
3–4	28	42	70	52	36	29	23	17	5	3	1	1
5–8	18	31	42	29	18	16	11	15	6	2	0	0
9–16	5	30	27	15	11	8	3	4	2	0	0	0
17–32	4	15	14	10	2	2	1	1	1	0	0	0
33–64	3	4	5	1	1	2	0	0	0	0	0	0
65–128	1	2	4	0	1	0	0	0	0	0	0	0
129–256	0	1	2	0	0	0	0	0	0	0	0	0
Total larvae	709	1,823	2,334	1,088	762	762	350	400	193	67	36	21
Number of samples	1,011	1,011	1,011	1,011	1,011	1,011	1,011	1,011	1,011	1,011	1,011	1,011
Mean per sample	0.701	1.803	2.309	1.076	0.754	0.754	0.346	0.396	0.191	0.066	0.036	0.021
Variance	13.101	67.540	97.629	10.823	13.885	7.421	1.415	1.936	0.933	0.155	0.050	0.036
k	0.092	0.152	0.209	0.189	0.140	0.102	0.139	0.139	0.097	0.048	0.106	0.030
Patchiness	11.91	7.57	5.79	6.30	8.15	10.76	8.21	8.19	11.33	21.98	10.42	34.28
SE (patchiness)	1.09	0.48	0.32	0.44	0.67	0.94	0.91	0.86	1.71	18.42	4.54	39.78

Figure 1

Lloyd's index of patchiness as a function of larval age for *Scomber japonicus* and *Trachurus symmetricus* in the California Current region.

Figure 2
Developmental stages of *Scomber japonicus* larvae (from Matarese et al., 1989). Sizes shown are estimated live sizes.

Table 2

Behavioral and morphological changes in developing *Scomber japonicus* larvae.

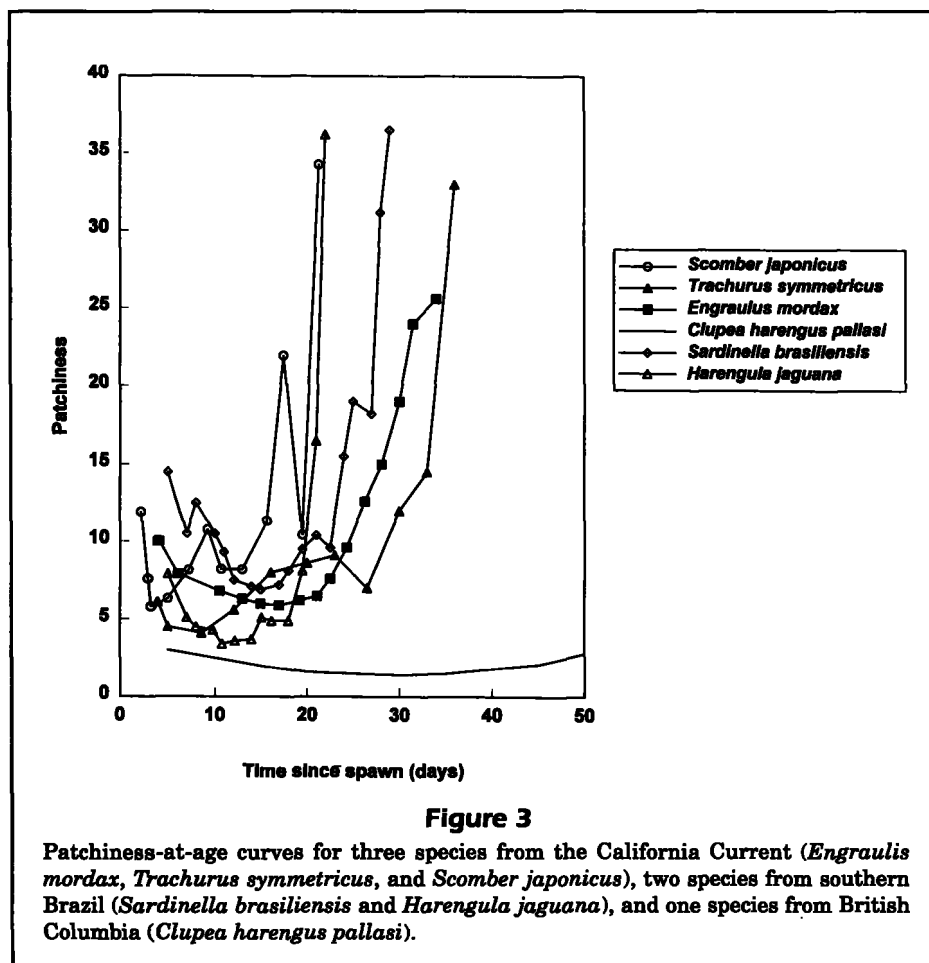|	Measurements																	
Live size	3.1	3.3	3.5	4.0	4.6	5.2	5.7	6.5	7.7	8.5	9.6	10.7	11.8	12.9	14.0	15.1	16.2	17.3
Swimming speed (cm/sec)[1]		0.4	0.6	0.7	0.9	1.0	1.3	1.8	2.1	2.6	3.1	3.7	4.4	5.0	5.7	6.5	7.3	
Cannibalism[1]								sibling cannibalism between 8 and 15 mm										
Schooling[1]														oriented swimming				
Patchiness		11.9	7.6	5.8	6.3	8.2	10.8	8.2	8.2	11.3	22.0	10.4	34.3					
Feeding ability[2]			Mouth opening and yolk absorption at 4 mm															
Fin formation[2]		CF, PF at 3.5 mm						PvF, AF, DF at 9.6 mm										
Visual sensory organ[3]				developed between 6.5 and 7.7 mm														

[1] Hunter and Kimbrell (1980).
[2] Watanabe (1970); CF = caudal fin, PF = pectoral fin, PvF = pelvic fin, AF = anal fin, DF = dorsal fin.
[3] O'Connell (unpub. data).

Patchiness-at-age curves for six species (*Engraulis mordax* and *Trachurus symmetricus*, Hewitt, 1981; *Clupea harengus pallasi*, McGurk, 1987; *Sardinella brasiliensis* and *Harengula jaguana*, Spach, 1990; and *Scomber japonicus*, reported here) describe a similar sequence: a high index is observed at the youngest larval ages, a low index is observed at one or two weeks after spawn, and thereafter the index increases suggesting the onset of schooling behavior (Fig. 3). The highest index of patchiness at early larval age was observed for *S. brasiliensis* (*P*=14.5). This can be attributed to intensive spawning behavior of adult sardine, short incubation time (Matsuura, 1983), and fast larval growth (Yoneda, 1987) relative to the other species. The lowest index of patchiness was observed for *C. harengus pallasi* (*P*=3.5) collected in a small inlet on the west coast of Vancouver Island, British Columbia; McGurk (1987) noted that this may be a reflection-dispersed prey. Houde and Lovdal (1985) reported that fish larvae in Biscayne Bay, Florida, were only slightly more patchy (*P*=1.3) than their prey, which was abundant and not aggregated (*P*=1.06). Henri et al. (1985) also

reported low patchiness values (*P*=1.63–3.52) for *Clupea harengus harengus* larvae collected in the St. Lawrence estuary, Quebec. Hewitt (1981) discussed differences in patchiness-at-age curves for *E. mordax* and *T. symmetricus* in terms of their prey availability and foraging strategies. In contrast to *T. symmetricus*, *E. mordax* exhibited an initial high degree of patchiness and slowly dispersed before showing a rapid increase in patchiness at about 18 days of age. *Trachurus symmetricus* larvae were approximately 1/10 as abundant, exhibited lower initial patchiness, and achieved maximum dispersion at an earlier age. *E. mordax* depend on small, but abundant, prey; they have poorly developed swimming capabilities and can effectively forage only through a small volume of water. In contrast, *T. symmetricus* depend on large, but rare, prey items; they have well-developed swimming capabilities and are able to search through relatively large volumes of water.
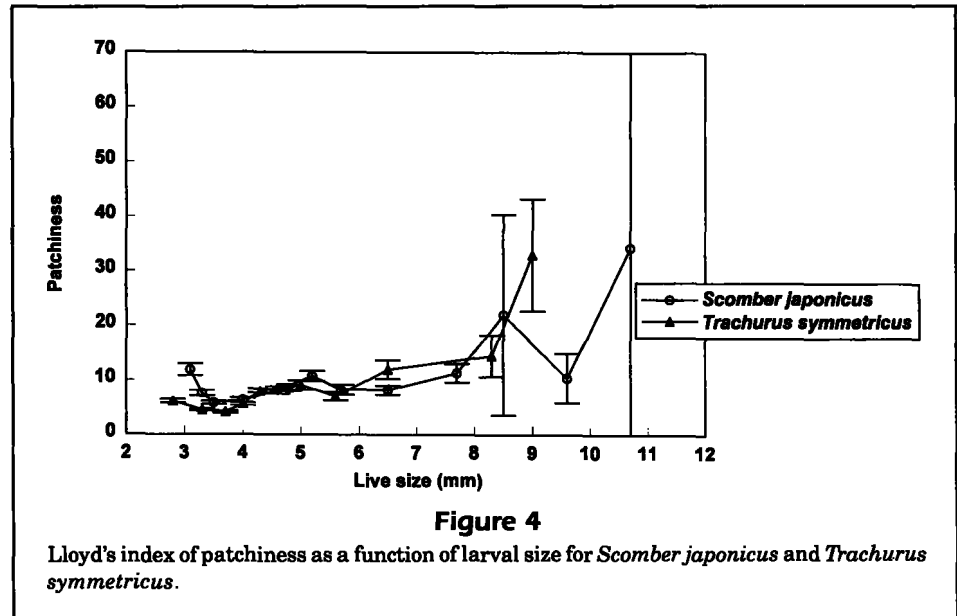
In comparison to the four clupeoid species, the increase in patchiness was observed to occur at an early age for both *S. japonicus* and *T. symmetricus*. *Scomber japonicus* and *T. symmetricus* larvae share similar morphologies and life history traits. Hunter and Kimbrell (1980) noted that Pacific mackerel larvae may be characterized as having fast growth, rapid swimming abilities, high metabolism, a dependence on increasingly larger prey, and a tendency for cannibalism. Sibling cannibalism may be an important survival strategy for mackerel larvae, where larger individuals prey on smaller ones. Grave (1981) reported that by the time Atlantic mackerel, *Scomber scombrus*, larvae were 12 mm long, 83% of the food items in their diet were other mackerel larvae. High initial dispersal, followed by aggregation of similar-sized larvae may be mechanisms for reducing sibling cannibalism. Although the patchiness-at-age curves for *S. japonicus* and *T. symmetricus* are distinct (Fig. 1), the patchiness-at-size curves are almost coincident (Fig. 4), suggesting that change in patchiness

Figure 3

Patchiness-at-age curves for three species from the California Current (*Engraulis mordax*, *Trachurus symmetricus*, and *Scomber japonicus*), two species from southern Brazil (*Sardinella brasiliensis* and *Harengula jaguana*), and one species from British Columbia (*Clupea harengus pallasi*).

may be a size-dependent phenomenom.

Acknowledgments

Figure 4

Lloyd's index of patchiness as a function of larval size for *Scomber japonicus* and *Trachurus symmetricus*.

Literature cited

Anon.
1988. CalCOFI on-line data system, user's manual. NOAA, SWFSC, La Jolla, p.1–9.
Bliss, C. I., and R. A. Fisher.
1953. Fitting the negative binomial to biological data and a note on the efficient fitting of the negative binomial. Biometrics 9:176–200.
Davis, T. L. O., G. P. Jenkins, and J. W. Young.
1990. Patterns of horizontal distribution of the larvae of southern bluefin (*Thunnus maccoyii*) and other tuna in the Indian Ocean. J. Plankton Res. 12(6):1295–1314.
Grave, H.
1981. Food and feeding of mackerel larvae and early juveniles in the North Sea. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 178:454–459.
Henri, M., J. J. Dodson, and H. Powles.
1985. Spatial configurations of young herring (*Clupea harengus harengus*) larvae in the St. Lawrence estuary: importance of biological and physical factors. Can. J. Fish. Aquat. Sci. 42 (Suppl. 1):91–104.
Hewitt, R. P.
1981. The value of pattern in the distribution of young fish. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 178:229–236.
1982. Spatial pattern and survival of anchovy larvae: implications of adult reproductive strategy. Ph.D. diss., Scripps Institution of Oceanography, Univ. Calif., San Diego.
Houde, E. D., and J. D. A. Lovdal.
1985. Patterns of variability in ichthyoplankton occurrence and abundance in Biscayne Bay, Florida. Estuarine Coastal Shelf Sci. 20:79–103.
Hunter, J. R., and C. A. Kimbrell.
1980. Early life history of Pacific mackerel, *Scomber japonicus*. Fish. Bull. 78:89–101.
Koslow, J. A., S. Brault, J. Dugas, and F. Page.
1985. Anatomy of an apparent year class failure: the early life history of the Browns Bank haddock *Melanogrammus aeglefinus*. Trans. Am. Fish. Soc. 114:478–489.

Kramer, D., M. Kalin, E. Stevens, J. Thrailkill, and J. Zweifel.
1972. Collecting and processing data on fish eggs and larvae in the California Current region. U.S. Dep. Commer., NOAA Tech. Rep. NMFS Circ. 370:1–38.
Lasker, R.
1978. The relation between oceanographic conditions and larval anchovy food in the California current: identification of factors contributing to recruitment failure. Rapp. P.-V Reun. Cons. Int. Explor. Mer 173:212–230.
Lloyd, M.
1967. Mean crowding. J. Anim.Ecol. 36:1–30.
Matarese, A. C., A. W. Kendall Jr., D. M. Blood, and B. M. Vinter.
1989. Laboratory guide to early life history stages of northeast Pacific fishes. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 80, 652 p.
Matsuura, Y.
1983. Estudo comparativo das fases iniciais do ciclo de vida da sardinha-verdadeira, *Sardinella brasiliensis*, e da sardinha-cascuda, *Harengula jaguana*, (Pisces: Clupeidae) e nota sobre a dinâmica da populaçaõ da sardinha-verdadeira na região sudeste do Brasil. Assoc. Professorship thesis, Univ. São Paulo.
McGurk, M. D.
1986. Natural mortality of marine pelagic fish eggs and larvae: role of spatial patchiness. Mar. Ecol. Prog. Ser. 34: 227–242.
1987. The spatial patchiness of Pacific herring larvae. Environ. Biol. Fish. 20(2):81–89.
Pielou, E. C.
1977. Mathematical ecology. J. Wiley and Sons, New York, 385 p.
Shaw, E.
1960. The development of schooling behavior in fishes. Physiol. Zoo. 33(2):79–86.
1970. Schooling in fishes: critique and review. *In* L. R. Aronson et al. (ed.), Development and evolution of behavior: essays in memory of T. C. Schneirla, p. 452–480. Freeman, San Francisco.

Smith, P. E.
1973. The mortality and dispersal of sardine eggs and larvae. Rapp. P.-V. Reun. Cons. Int. Perm. Explor. Mer 164: 282–292.

Smith, P. E., and S. L. Richardson.
1977. Standard techniques for pelagic fish egg and larva surveys. FAO Fish. Tech. Pap. 175, 100 p.

Smith, P. E., and R. P. Hewitt.
1985. Anchovy egg dispersal and mortality as inferred from close-internal observations. CalCOFI Rep. 26:97–110.

Spach, H. L.
1990. Estudo comparativo da distribuição espaço-temporal e de padrões de agregação de ovos e larvas de *Harengula jaguana*, *Sardinella brasiliensis* (Clupeidae: Osteichthyes) e *Engraulis anchoita* (Engraulidae: Osteithyes) na costa sudeste do Brasil. Ph. D. diss., Univ. São Paulo.

Theilacker, G. H.
1980. Changes in body measurements of larval northern anchovy, *Engraulis mordax*, and other fishes due to handling and preservation. Fish. Bull. 78:685–692.

Watanabe, T.
1970. Morphology and ecology of early stages of lfe in Japanese common mackerel, *Scomber japonicus* Houttuyn, with special reference to fluctuation of population. Bull. Tokai Reg. Fish. Res. Lab. 62:1–283.

Williams, M. M., and E. Shaw.
1971. Modifiability of schooling behavior of fishes: the role of early experience. Am. Mus. Novit. 2448:1–18.

Yoneda, N. T.
1987. Criação em laboratório de larvas da sardinha-verdadeira, *Sardinella brasiliensis* e estudo dos incrementos diários nos otólitos. M.S. thesis, Univ. São Paulo.

Zweifel, J. R., and P. E. Smith.
1981. Estimates of abundance and mortality of larval anchovies (1951–75): application of a new method. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 178:248–259.