Indices of larval king mackerel (*Scomberomorus cavalla*) abundance in the Gulf of Mexico for use in population assessments

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Abstract—The stock status of the Gulf of Mexico migratory group of king mackerel *(Scomberomorus cavalla)* is currently evaluated by using age-based sequential virtual population analysis (VPA). We examined king mackerel larval occurrence and abundance indices from annual ichthyoplankton surveys, developed an age-adjusted abundance index, and questioned whether larval indices of abundance are useful for calibrating the king mackerel VPA. Gulf of Mexico king mackerel larval occurrence and abundance increased over a fourteen-year time series from 1982 to 1995 and were highly correlated with spawning stock size. Correlations between stock size and larval occurrence, and between stock size and larval abundance, were 0.82 and 0.84, respectively. The correlation between larval occurrence and stock size for the years 1986–95 increased to 0.91, owing to the addition in 1986 of a fall survey with added coverage during peak spawning. Daily instantaneous mortality rate (Z) was estimated by regression of larval catch curves. Although a large amount of interannual variability in mortality rates was noted, no statistical differences were detected among years. The instantaneous daily mortality rate estimated by pooling all years, $Z = 0.53$, was used to develop an age-adjusted index for king mackerel in order to eliminate the influence of variable larval age composition among years. This adjusted index did not improve correlations between stock size and larval abundance (r=0.78). For now, indices of larval occurrence and unadjusted larval abundance from ichthyoplankton collections reflect trends in spawning stock size and provide useful variables for calibrating the king mackerel VPA.

Manuscript accepted 4 April 2000.
Fish. Bull. 98:684–691 (2000).

The king mackerel *(Scomberomorus cavalla)*, a western Atlantic member of the family Scombridae, ranges from Massachusetts to Brazil (Shipp, 1986). This highly migratory, coastal pelagic species can attain a maximum size of 1.7 m and 45 kg (Robins and Ray, 1986) and ages of more than 20 years (DeVries and Grimes, 1997). King mackerel support valuable commercial and recreational fisheries that are regulated in the southeastern coastal states and Gulf of Mexico under the Coastal Migratory Pelagic Resources Fishery Management Plan. These fisheries were largely unregulated in the late 1970s and early 1980s when fishing mortality was high, and thus stock size was reduced. As a result, management by quota was implemented in the 1985–86 fishing year. The current management regime for king mackerel fisheries recognizes only two stocks off the U.S. southeast coast: an Atlantic migratory group and a Gulf of Mexico migratory group. There is, however, some disagreement as to whether there are one or two distinct stocks in the Gulf of Mexico (Johnson et al., 1994; DeVries and Grimes, 1997; Gold et al., 1997; Roelke and Cifuentes, 1997).

Reproduction in this highly fecund, serial spawning species occurs from May through early October and peaks in September along both the U.S. Gulf of Mexico and southeast Atlantic coasts (McEachran et al., 1980; Finucane et al., 1986; Grimes et al., 1990). Data on the abundance and distribution of king mackerel larvae indicate that spawning occurs chiefly over the mid to outer continental shelf of the northern Gulf of Mexico (McEachran et al., 1980; Grimes et al., 1990). Grimes et al. (1990) suggested that spawning occurs over shallower depths in the region from west Louisiana to northwest Florida and may be associated with oceanographic features, especially the discharge plume of the Mississippi River. Absolute growth rates of king mackerel larvae were observed to range from 0.54 to 1.33 mm per day and were slightly higher for larvae from the Mississippi River plume when compared to other locations in the Gulf and southeast Atlantic coast (DeVries et al., 1990).

Population size of Gulf-group king mackerel is estimated biennially by scientists of the Mackerel Stock Assessment Panel (Gulf of Mexico and South Atlantic Fishery Management Councils) using an age-based sequential virtual population analysis (VPA). This VPA is implemented by using ADAPT (Conser and Powers, 1990; Powers and Restrepo, 1993). The king mackerel VPA is calibrated or tuned by using various indices of abundance based on fisheries dependent catch-per-unit-of-effort and fisheries independent resource survey data. Survey estimates of annual abundance and frequency of occurrence of king mackerel larvae were first considered as tuning variables for the king mackerel VPA by the 1996 Mackerel Stock Assessment Panel.[1] Although fre-

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[1] Mackerel Stock Assessment Panel. 1996. 1996 Report of the Mackerel Stock Assessment Panel. Gulf of Mexico Fishery Management Council, Lincoln Center, Suite 331, 5401 West Kennedy Blvd, Tampa, FL 33609 and South Atlantic Fishery Management Council, Southpark Bldg., Suite 306, 1 Southpark Circle, Charleston, SC 29407.

quency of occurrence was ultimately accepted as a tuning variable, abundance was not because larval catches had not been adjusted for age. Interannual differences in age composition of sampled larvae could contribute a large amount of variation in estimates of mean annual abundance because of the exponential decline in numbers of larvae with age. Furthermore, it was thought that survey estimates of larval abundance would be too variable to be of value as an index of stock size owing to the highly variable nature of larval mortality rates.[2] In our study, we developed an age-adjusted larval index for king mackerel and evaluated the appropriateness of using larval indices in calibrating the king mackerel VPA.

Materials and methods

King mackerel larvae in the Gulf of Mexico have been collected annually since 1982 during Southeast Area Monitoring and Assessment Program (SEAMAP) ichthyoplankton surveys conducted by the states of Florida, Alabama, Mississippi, Louisiana, and by the National Marine Fisheries Service. Larvae were captured in oblique tows from near bottom to the surface with a 61-cm, 0.333-mm-mesh bongo net by following standardized SEAMAP collection procedures (Richards et al., 1993). Survey stations were typically located 55.56 km apart in a fixed grid, and sampled at all times of day or night. Collections were taken west of 88°W longitude in June and July from 1982 to 1985. Starting in 1986, gulf-wide samples were also collected in late August, September, and early October. Catches of king mackerel larvae were standardized to account for sampling effort and expressed as number of larvae under 10 m^2 of sea surface (no./10 m^2). Annual mean abundances, i.e. the indices not adjusted for age composition of larval catches, were based on arithmetic means. Use of the delta-distribution (Pennington, 1983) did not lower estimates of standard error.

The age composition of king mackerel larvae captured at each station was estimated by converting lengths to ages with a least squares regression model based on the length and age of larvae (n=47) collected in September 1986 from the Gulf of Mexico and Atlantic Ocean and aged by counting otolith growth increments[3] (DeVries et al., 1990). Two additional techniques for assigning larval ages from lengths were considered, namely a probability age-classification matrix (Scott, et al., 1993) and discriminant analysis, but these were found to be ineffective owing to the small number of aged larvae. Once ages were assigned, individual catch curves for each year of the time series from 1982 to 1995 were constructed from the descending arm of $\log_e$-transformed catch-at-age data (Ricker, 1975) by using the regression procedure of SAS (SAS Institute Inc., 1990). A dummy-variable model was used in the regression procedure to fit a single model for all years with test statements that tested for homogeneity of intercepts and of slopes. Instantaneous daily mortality rates and an age-adjusted index of abundance were then calculated.

The age-adjusted index for king mackerel was based on the abundance of a single age class to eliminate the influence of variable larval age composition among years. We arbitrarily chose one-day-old larvae as the standard age class on which to base the age-adjusted index. We estimated the density of one-day-old larvae at each station by back-calculating and summing their numbers from older age classes using an estimate of daily instantaneous mortality rate. The density of one-day-old king mackerel larvae at each station was estimated as

$$I_{y,s} = \sum_{i=1}^{k} N_{y,s,i} e^{Z(i-1)},$$

where $I_{y,s}$ = the number of one-day-old larvae under 10 m^2 of sea surface (y=year; s=station); and
$N_{y,s,i}$ = the number of larvae under 10 m^2 of sea surface of each age class represented in the sample (i=age class).

Annual mean age-adjusted index of larval abundance was estimated as the average of station values.

Annual estimates of spawning stock size (ages 1 through 11+ years) were obtained from a VPA of king mackerel.[4] No king mackerel larval occurrence data from SEAMAP were used to tune this VPA. However, the VPA used for the most recent stock assessment was calibrated with larval occurrence data. Residual plots from regressions between the VPA estimate of stock size indices of larval abundance exhibited no particular pattern; therefore data were not transformed for correlation analyses. Correlation between the VPA estimate of spawning stock size and three SEAMAP larval indices were then estimated by using the correlation procedure of SAS (SAS Institute Inc., 1990). Larval indices used were 1) frequency of occurrence; 2) mean abundance of all larvae captured unadjusted for age; and 3) mean abundance of age one-day larvae.

Results

The SEAMAP survey king mackerel larval frequency of occurrence index ranged from 0.02 (SE=0.017, CV=100%) in 1983 to 0.32 (SE=0.038, CV=12%) in 1995 (Table 1). The survey larval abundance index (no./10 m^2) ranged from 0.23 (SE=0.228, CV=100%) in 1983 to 5.15 (SE=0.924; CV=18%) in 1995 (Table 1). Mean frequency of occurrence and abundance of king mackerel larvae varied more during the first four years of the time series when observations were available from only the early part of the spawning season, i.e. summer months. However, both frequency of occurrence and abundance have increased over

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[2] Powers, J. E. 1996. Personal commun. Southeast Fisheries Science Center, Miami Laboratory, Miami, FL 33149.

[3] DeVries, D. 1996. Personal commun. Southeast Fisheries Science Center, Panama City Laboratory, Panama City, FL 32407.

[4] Legault, C. 1998. Personal commun. Southeast Fisheries Science Center, Miami Laboratory, Miami, FL 33149.

the fourteen-year time series (Fig. 1A, Table 1). Variability decreased after 1986, when the fall SEAMAP ichthyoplankton survey was added which both extended coverage into the time period of peak king mackerel spawning and increased the number of samples. Coefficients of variation (100 × SE/mean) have been less than 20% for both frequency of larval occurrence (1989–95) and larval abundance (1992–95) for the most recent years of the time series (Table 1). Also an expansion in the areal distribution of king mackerel larvae has been apparent since 1986 (Fig. 2).

A total of 798 king mackerel larvae ranging in length from 1.6 to 10.1 mm were collected from 1982 to 1995 (Table 2). A quadratic equation best described the relationship between larval king mackerel age and length data (Fig. 3). Catch-at-age was calculated from the estimates of larval density and age frequencies and then used to construct annual catch-at-age curves for survey-captured king mackerel larvae. Over the time series, larvae ranged in age from 2 to 11 days, and estimates of instantaneous daily mortality rates for individual years ranged from 0.35 in 1985 to 0.70 in 1992 (Table 3). A single catch-at-age regression for all years combined indicated no significant difference among slopes (i.e. instantaneous mortality rates) or among intercepts. Therefore, a pooled regression model was fitted. The slope of the pooled regression gave an estimate of instantaneous daily mortality rate (Z) of 0.53 (Table 3) and was subsequently used to backcalculate the abundance of one-day-old larvae and generate the age-adjusted index of king mackerel larval abundance.

VPA estimates of king mackerel spawning stock size ranged from 46.03×10^5 individuals in 1985 to 101.93×10^5 individuals in 1995 (Fig. 1A). Survey larval frequency of occurrence and estimates of stock size corresponded with a correlation of 0.82 over the entire time series, 1982–95, and 0.92 for the period 1986–95 (Fig. 1A). The king mackerel survey index of larval abundance (unadjusted for age) was also highly correlated with spawning stock size (Fig. 1A). The correlation, 0.84, was the same for both periods of comparison, all survey years, and years since 1986. Our attempt to adjust larval abundance for age did not improve the correlation between the abundance index and spawning stock size. The correlation with spawning stock size was, however, higher after fall surveys began, 0.78 versus 0.65, but these values were both lower than those for the “uncorrected” abundance index and the index based on frequency of occurrence (Fig. 1B).

Discussion

Hunter and Lo (1993) asserted that fish eggs and larvae can be used not only to estimate the biomass of a fish stock but also to monitor trends in relative stock abundance. Indices of relative abundance are less costly to produce than biomass estimates from ichthyoplankton data, but they are also less precise. The CVs of the most precise biomass estimates based on ichthyoplankton data range between 20% and 30%. Whether adjusted for growth and mortality of larvae or not, ichthyoplankton indices are “surprisingly sensitive to major changes in stock abundance” (Hunter and Lo, 1993). It should be of no surprise that our indices based on abundance and frequency of occurrence of king mackerel larvae from SEAMAP collections in the Gulf of Mexico closely tracked trends in adult abundance over the time

Table 1

SEAMAP annual estimates of king mackerel larval mean abundance and frequency of occurrence (n=number of stations, CV=100×SE/mean).

		Number/10 m^2			Frequency of occurrence		
Year	n	Mean	SE	CV (%)	Mean	SE	CV (%)
1982	77	0.83	0.464	56	0.09	0.033	36
1983	59	0.23	0.228	100	0.02	0.017	100
1984	74	1.19	0.413	35	0.18	0.045	25
1985	94	0.36	0.178	49	0.06	0.025	40
1986	225	1.10	0.286	26	0.10	0.020	20
1987	216	0.69	0.161	23	0.12	0.022	19
1988	125	0.97	0.319	33	0.11	0.028	25
1989	129	2.08	0.714	34	0.19	0.034	18
1990	129	1.67	0.357	21	0.21	0.036	17
1991	129	1.33	0.368	28	0.18	0.034	19
1992	167	2.00	0.338	17	0.28	0.035	12
1993	175	3.22	0.546	17	0.30	0.035	12
1994	176	2.82	0.503	18	0.26	0.033	13
1995	155	5.15	0.924	18	0.32	0.038	12

series. Annual estimates of mean king mackerel occurrence were more precise than the estimates of larval abundance, and CV's for both king mackerel indices were comparable to CVs of ichthyoplankton-based estimates for other species (Hunter and Lo, 1993). Larval abundance of Atlantic bluefin tuna, a species that poses a more intractable sampling problem than does king mackerel, namely an immense spawning area (the open Gulf) and lower overall abundance, has been used as a tuning variable in population assessments by VPA (Scott et al., 1993).

The use of a simple larval index for monitoring stock size is not unprecedented. Data from larval surveys of Atlantic herring (*Clupea harengus harengus*) in the North Sea have been used since 1967 as the sole source of information on stock size or in combination with catch statistics or acoustic surveys, or both (Heath, 1993). One of the two larval indices for North Sea herring, the larval abundance index, employs only larvae less than 10 mm in length (up to 15 days old). The correlation between this larval index and stock size became weaker with increasing age of larvae owing, it was surmised, to interannual variation in mortality and dispersal. The potential influence of varying mortality rates and dispersal were likewise minimized in our study because most king mackerel larvae collected during the SEAMAP surveys were less than 5 mm and no more than ten days old. The other larval herring abundance index for the North Sea, the larval production estimate, utilizes all size and age groups to estimate the abundance at hatching and requires estimates of growth and mortality rates. Both herring indices are calculated annually; however, the actual use of each in VPA assessment is dependent on survey coverage in time and space in relation to spawning events for that year.

Our attempt to account for differences in larval age composition among years by adjusting the index for mortality of larvae did not improve the correlation with stock size. There are a number of reasons for this outcome. It is very likely that the limited age-at-length data available for conversion of king mackerel lengths to age probably resulted in imprecise assignment of ages. Overestimation of age by a single day would result in a 70% error in the backcalculated abundance of age one-day fish, and a 41% error if underestimated. Hauser and Sissenwine (1991) noted that estimates of larval production using "back-calculation techniques," as we did to estimate the abundance of one-day-old king mackerel larvae, will be biased if the growth rate used is incorrect or if mortality is size dependent, or both conditions transpire. It is also likely that the assumption of constant mortality rate, an integral part of catch curve analysis, did not hold for king mackerel larvae. Bailey et al. (1996a; 1996b) found that early mortality rates of walleye pollack larvae were not only highly variable among years but declined as larvae became older. Furthermore, the observation that instantaneous mortality rates of king mackerel larvae among years were not significantly different may be caused by the low number of larvae caught and the small number of age classes represented in collections (Comyns, 1997). However, an age-adjusted index calculated with annual estimates of mortality rate had a much poorer correlation with stock size; therefore we did not report these data. Our estimate of mortality (Z=0.53) may be biased high owing to net selectivity, i.e. avoidance of the net by larger larvae. To correct this bias, we truncated the upper 20% of the size distribution and recalculated mortality rates and an age-adjusted index. Although the mortality estimate was lower (Z=0.43), the correlation between stock size and the age-adjusted index based on this mortality rate did not differ from the correlations based on nontruncated distributions.

Another measure of king mackerel stock size was considered, namely the VPA-generated estimate of egg pro-

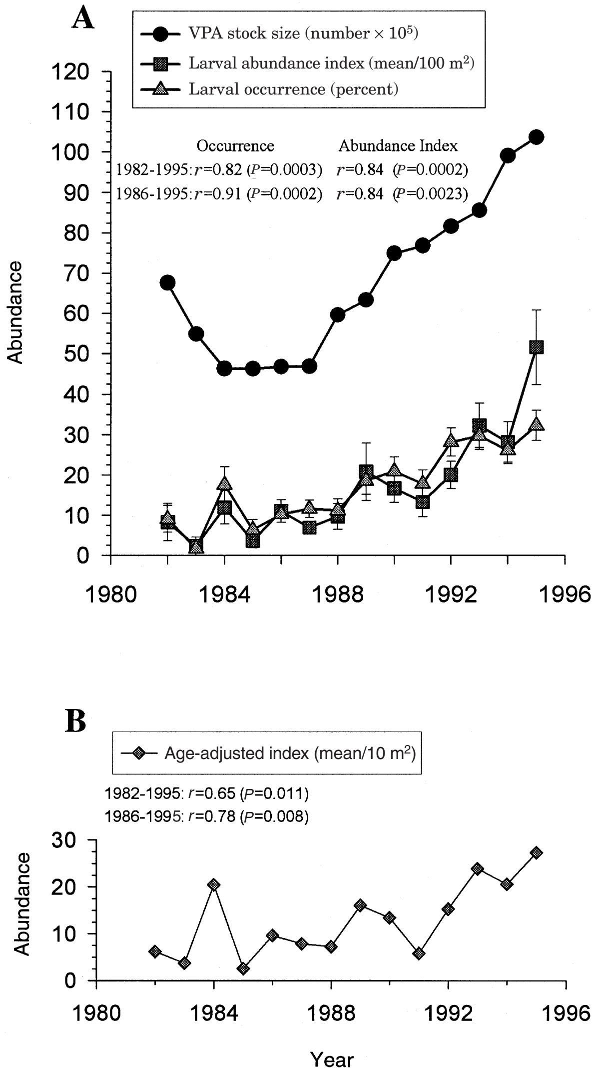

Figure 1

(**A**) King mackerel adult spawning stock size (number × 10^5 of fish in the 1 through 11+ age groups) estimated by VPA, survey larval index of abundance (mean number under 100 m^2 of sea surface ±SE), and survey larval frequency of occurrence (percent of stations where larvae were captured ±SE). (**B**) Annual age-adjusted larval index of abundance (mean number under 10 m^2 of sea surface).

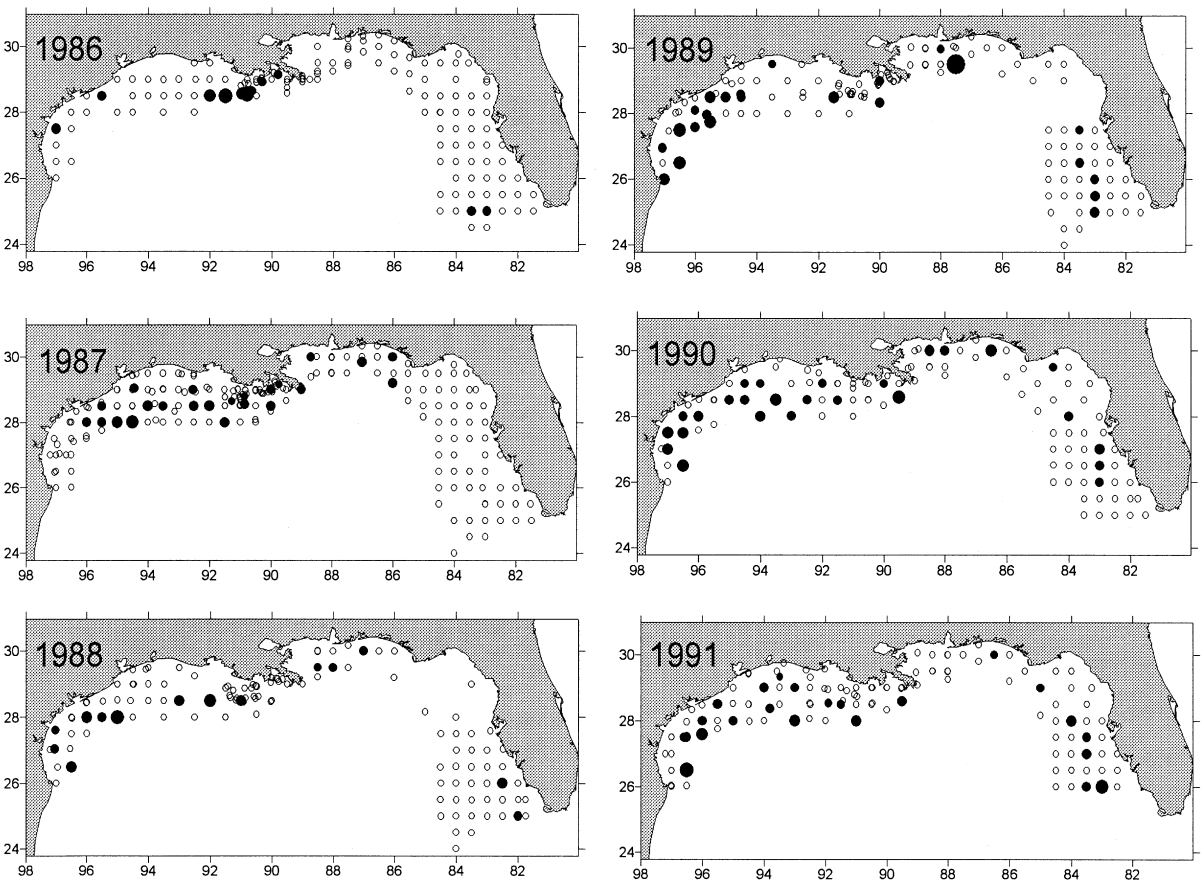

Figure 2

King mackerel larval density at each station sampled during SEAMAP surveys from 1986 to 1995 (○=zero catch; ●= from 1 to 82 larvae/10 m^2 [symbol size scaled accordingly]).

duction (number-at-age × relative fecundity-at-age). This measure accounts for the presumably greater contribution of older and larger fish to overall reproductive output; therefore it would seem a better correlate of larval occurrence and abundance than numbers of fish. However, we found egg production to be somewhat less correlated with larval indices than were numbers of fish, perhaps owing to the use of a constant fecundity-at-age distribution to estimate king mackerel egg production. Significant interannual differences in relative fecundity have been demonstrated for a wide variety of fishes (Bagenal, 1966; 1967; Bagenal and Braum, 1971; Hunter et al., 1985; Rijnsdorp, 1991; Koslow et al., 1995). But there is insufficient data on fecundity of king mackerel over the time series to ascertain the influence of interannual variability on this parameter, and in turn, on larval production.

Application of growth and mortality rates to refine or adjust larval indices of relative abundance may be moot because determinants of larval survival, i.e. predation or starvation rates, or both, appear to be unrelated to spawning stock abundance (Hunter and Lo, 1993). It has been argued that larval occurrence provides a more useful index of stock size because stock size and the geographic area occupied by eggs and larvae may be correlated, as is the case for Pacific sardines (*Sardinops sagax*) and northern anchovy (*Engraulis mordax*), especially at low population levels. (Mangel and Smith, 1990; Smith, 1993; Hunter and Lo, 1993; MacCall, 1988). However, Mangel and Smith (1990) suggest that a switch from presence and absence data to actual counts would be necessary when the spawning biomass increases to a level where “virtually all stations have eggs.”

King mackerel in the Gulf of Mexico are rebounding from the low levels of the late 1970s and early 1980s (Powers and Restrepo, 1993), and the increases are reflected in larval occurrence and abundance. A switch to a larval abundance index may be required to follow trends in stock size as larval abundance rises if the uncorrected abundance index at some future time no longer corresponds to stock size. Adjustment of the king mackerel larval abundance index would require annual estimates of mortality and growth rates by direct aging of survey-caught larvae. For now, both the index of larval occurrence and the unadjusted index of abundance from SEAMAP collec-

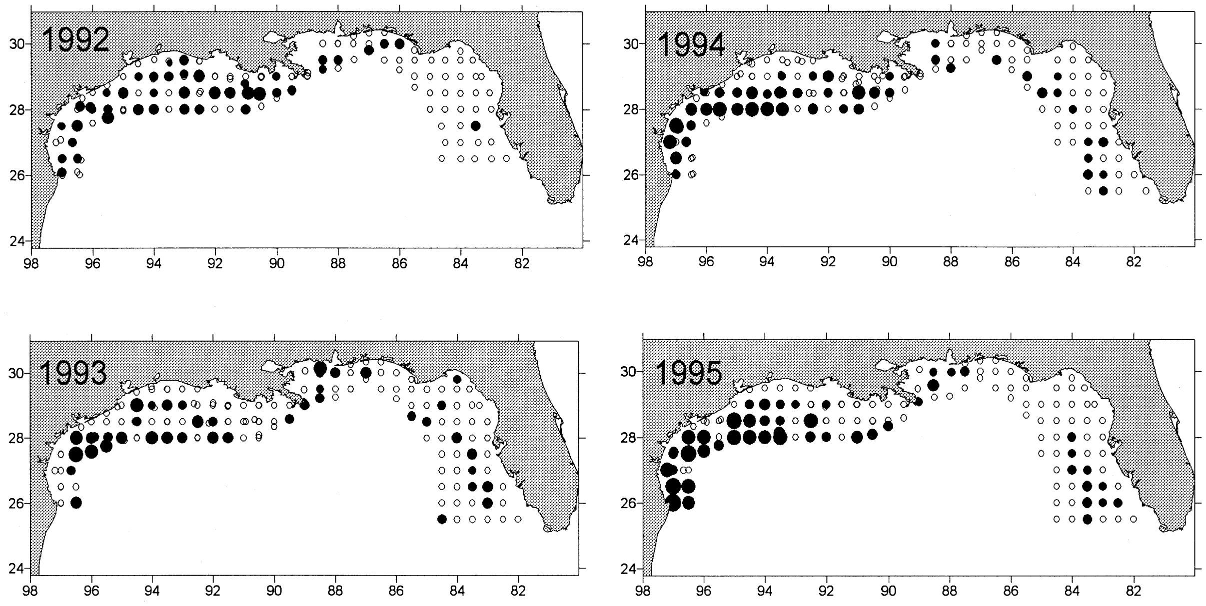

Figure 2 (continued)

Table 2

Average length (mm) and age (days) of king mackerel larvae collected during annual surveys (*n*=number of larvae measured).

		Length				Age			
Year	*n*	Mean	SE	Min	Max	Mean	SE	Min	Max
1982	29	3.4	0.231	2.0	6.0	4.47	0.257	2.81	7.25
1983	4	4.9	0.860	4.0	7.5	6.08	0.880	5.13	8.71
1984	20	4.7	0.467	2.2	8.7	5.84	0.494	3.05	9.81
1985	12	3.8	0.330	1.9	5.5	4.89	0.369	2.69	6.74
1986	63	3.9	0.170	1.8	8.0	4.94	0.183	2.57	9.18
1987	35	4.3	0.267	1.9	7.5	5.39	0.297	2.69	8.71
1988	28	3.6	0.245	2.0	6.8	4.62	0.270	2.81	8.04
1989	58	3.5	0.171	2.0	10.0	4.53	0.182	2.81	10.91
1990	49	3.6	0.232	1.6	9.8	4.64	0.249	2.32	10.74
1991	33	3.1	0.209	1.8	6.0	4.06	0.236	2.57	7.24
1992	86	3.3	0.157	1.7	8.5	4.28	0.171	2.45	9.63
1993	137	3.3	0.133	1.7	10.1	4.27	0.142	2.45	10.99
1994	105	3.4	0.164	1.8	9.6	4.35	0.177	2.57	10.58
1995	139	3.2	0.100	1.8	8.1	4.18	0.111	2.57	9.27

tions reflect trends in spawning stock size and provide useful variables for calibrating the king mackerel VPA.

Acknowledgments

The authors wish to thank Doug DeVries at the NMFS Panama City Laboratory for giving us his larval king mackerel age and length data. Joe Powers and Chris Legault of the NMFS Miami Laboratory supplied king mackerel VPAs for the various iterations of this manuscript. Rosanne Brasher supplied indispensable assistance with the SEAMAP database. Scientists at the Polish Sorting and Identification Center in Szczecin, Poland, sorted and identified larvae from collections. Kim Williams, Collections Manager of the SEAMAP Archiving

Center in St. Petersburg, Florida, facilitated our work by furnishing king mackerel specimens and data. This time series would not have been possible without the labor of the crews of the NOAA ships *Chapman* and *Oregon II,* and field biologists of the NMFS laboratories and state agencies participating in SEAMAP cruises. Scott Nichols, Director of the NMFS Mississippi Laboratories, gave us encouragement, incentive and comments on an early draft of the manuscript. We greatly appreciate the comments and suggestions of Chris Legault, James H. Cowan, Bruce Comyns, and one anonymous reviewer who improved the manuscript.

Table 3

Individual annual and pooled catch curve parameters. ($\log_e$(number) = $\beta_0 + \beta_1$ *Age*; n=number of age groups.)

Year	n	β_0	β_1	r^2
1982	4	0.323	–0.444	0.86
1983	2	0.063	–0.366	1.00
1984	4	1.657	–0.505	0.51
1985	3	–0.824	–0.345	0.09
1986	7	1.343	–0.638	0.83
1987	5	–0.032	–0.431	0.41
1988	6	–0.631	–0.557	0.82
1989	5	1.638	–0.629	0.67
1990	7	1.642	–0.654	0.88
1991	6	0.643	–0.573	0.63
1992	7	1.757	–0.700	0.71
1993	8	1.485	–0.509	0.94
1994	8	1.332	–0.574	0.91
1995	7	2.187	–0.636	0.84
Pooled (1982–1995)	78	0.940	–0.529	0.65

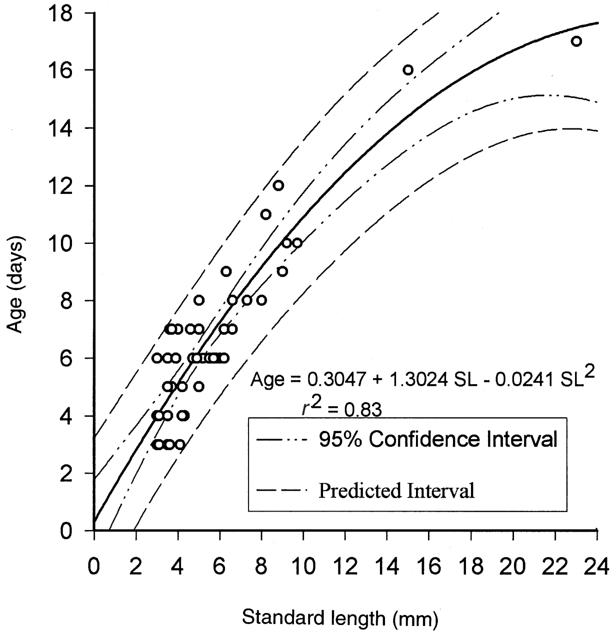

Figure 3

Relation between age and standard length (SL) with 95% confidence limits for king mackerel. Data from DeVries et al. (1990).

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