Effects of temperature on the development and survival of eggs of four coastal California fishes

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Abstract.—Laboratory experiments were conducted to determine the effects of temperature on egg development and survival of four fish species found off southern California. Our objectives were to further understanding of natural spawning patterns and to aid in identifying and ageing field-collected specimens. An egg-staging procedure was devised and eggs were observed every two hours during development at a range of temperatures (8–28°C). Barred sand bass, *Paralabrax nebulifer*, eggs survived to hatching and produced viable embryos at the highest temperature range (16–28°C), reflecting this species' summer spawning season. Fantail sole, *Xystreurys liolepis*, eggs also hatched at a higher temperature range (16–24°C). This species spawns primarily from summer through fall. Eggs of the two species with winter-spring spawning peaks, white croaker, *Genyonemus lineatus*, and California halibut, *Paralichthys californicus*, had lower temperature-tolerance ranges (12–20°C). Developmental rate at a specific temperature did not significantly differ between species, whereas within tolerance limits, temperature strongly affected rate of development for all species. Time to hatching for all species was inversely related to temperature, and the relationship was approximately exponential. Species-specific differences in egg-stage sequence were observed; embryonic organogenesis in relation to germ-ring migration and blastopore closure was faster for barred sand bass and fantail sole than for white croaker and California halibut.

Manuscript accepted 6 July 1995.
Fishery Bulletin 94:41–48 (1996).

Many studies have examined the influence of temperature on the development and survival of fish during early life history stages (see reviews by Pauly and Pullin, 1988; Pepin, 1991). Since the strength of a year class may be established during early stages (Hjort, 1914; May, 1974), it is important to understand possible causes of mortality during this period. For high egg viability, the timing and location of spawning must coincide with favorable environmental conditions including sea temperature (Alderdice and Forrester, 1968; Riley, 1974; Thompson and Riley, 1981). Additionally, detailed information on the relationship between temperature and the rate of egg development has been used to age field-collected eggs and to backcalculate spawning time (Ferraro, 1980; Thompson and Riley, 1981; Haynes and Ignell, 1983).

We determined the effects of temperature on egg development and survival of four fish species found off southern California: barred sand bass, *Paralabrax nebulifer* (Serranidae); white croaker, *Genyonemus lineatus* (Sciaenidae); California halibut, *Paralichthys californicus* (Paralichthyidae); and fantail sole, *Xystreurys liolepis* (Paralichthyidae). The first three species are important sport and commercial fishes in this area (Lavenberg et al., 1986). The larvae of these species are relatively abundant in the nearshore zone, where white croaker and California halibut spawn most intensely in winter–spring, and barred sand bass in summer (Love et al., 1984; Lavenberg et al., 1986; Walker et al., 1987; Moser and Watson, 1990; McGowen, 1993). Fantail sole larvae are less common off southern California where peaks in abundance occur during late summer and fall (Moser and Watson, 1990). Our primary objective in examining the eggs of these four species was to understand how temperature affects development and survival during the critical early life history period and thus contribute to a better understanding of temporal and spatial spawning patterns in the wild. A secondary objective was to gather information to aid in identifying and ageing field-collected specimens.

Materials and methods

Brood stocks of 5–12 adult fish were held in the laboratory in tanks rang-

ing from 1.8 to 7.6 m diameter and supplied with flow-through coastal seawater at a salinity of 34–35‰. Temperature and photoperiod were maintained at ambient levels simulating natural conditions in nearshore southern California waters (Caddell et al., 1990). Experiments generally began during the spawning season and at a temperature at which spawning would naturally occur for each species (Table 1). The hormones gonadotropin and carp pituitary were used to induce ovarian development of white croaker and fantail sole, respectively, following the methods of Caddell et al. (1990). California halibut brood stock ripened naturally. For each of these three species, eggs were stripped from one female and sperm from 2 or 3 males and these were combined to obtain a single batch of newly fertilized eggs. Barred sand bass spawned naturally in captivity, and newly fertilized eggs floating at the water's surface were collected. The number of individual sand bass participating in a spawning event was unknown. Egg development was initially monitored for each species at five temperatures: 8°, 12°, 16°, 20°, and 24°C. Barred sand bass eggs were also exposed to 28°C water because of their warmer (summer) spawning season. Since fantail sole eggs exhibited high survival at 24°C during the initial experiment, an additional trial was conducted at 28°C in order to establish the upper temperature tolerance limit of sole eggs. This trial was conducted approximately one year later, with incoming water heated to a typical summer–fall temperature (18.5°C) to facilitate gonad maturation.

For each species, an experiment began immediately after egg fertilization. Eggs were stocked in 3-L glass jars at a density of about 100 per liter. The jars contained filtered, UV-light–sterilized seawater at the ambient spawning temperature (Table 1). Jars were placed in temperature-controlled water baths, and jar temperatures were raised or lowered 1°C every 15 minutes until the desired treatment temperatures (see above paragraph) were reached. In order to incubate adequate numbers of eggs, two jars were maintained at each treatment temperature (±0.5°C) for the duration of the experiment. Each jar was mildly aerated to avoid the formation of temperature gradients. Light cycles were maintained at 12L:12D. Every 2 hours until hatching, at least five buoyant eggs per jar were sampled and preserved in 4% formalin. Water in the jars was not exchanged with fresh seawater during the experiments other than as necessary to siphon out dead eggs that accumulated on the bottom.

Eggs were examined with a dissecting microscope to characterize development. We did not illustrate stages of development; eggs of California halibut and fantail sole are illustrated in Oda (1991), and white croaker eggs are illustrated in Watson (1982). We devised a staging classification system based on Ahlstrom (1943) and Walsh et al. (1991) (Table 2). Because the rate of embryonic development in relation to germ-ring migration and blastopore closure varied by species, we could not develop a sequential staging system incorporating all developmental events that could be used for all species. We formulated, therefore, a staging system where some events of embryonic development (stages E, O, and S) were separate from general egg developmental stages I–IX (Table 2).

For each temperature-by-species treatment, a sample size of at least ten eggs per 2-hour time pe-

Table 1

Egg measurements and details of experimental protocol for four southern California fish species spawned in the laboratory. Dates experiments were initiated and water temperatures (T) at which fish were spawned are presented. Thirty laboratory-reared eggs of each species were measured after preservation in 4% formalin for at least one year. Superscripts indicate chorion, yolk, and oil globule mean diameters that differed significantly between species using the Tukey multiple-range test ($P<0.05$).

	Spawning		Egg mean diameter (mm)		
Species	Date	T (°C)	Chorion (SD)	Yolk (SD)	Oil (SD)
Barred sand bass *Paralabrax nebulifer*	17 Aug 1986	18.0	0.85 (0.02)[1]	0.64 (0.03)[1]	0.17 (0.01)[1]
White croaker *Genyonemus lineatus*	19 Apr 1985	15.0	0.81 (0.02)[2]	0.63 (0.02)[1]	0.22 (0.02)[2]
California halibut *Paralichthys californicus*	10 May 1985	16.0	0.75 (0.02)[3]	0.58 (0.02)[2]	0.12 (0.01)[3]
Fantail sole *Xystreurys liolepis*	6 Nov 1985	16.5	0.76 (0.02)[4]	0.61 (0.03)[1]	0.20 (0.01)[4]
2nd trial (28°C)	13 Jan 1987	18.5			

Table 2

Stages of development for laboratory-reared eggs of four California fishes. Each stage begins with the described developmental event. Because the sequence of three embryonic developmental events (stages E, O, and S) differed by species in relation to stages V and VI, they are presented separately.

Stage	Description
I	Cell division; 2–128 celled eggs
II	Multicelled (>128 celled) blastodermal cap evident
III	Segmentation cavity developed
IV	Germ ring formed and embryonic shield visible
V	Germ ring encloses >1/2 of the yolk mass
VI	Blastopore closure
VII	Embryo tail separated from yolk ≤ head length
VIII	Embryo tail separated from yolk > head length
IX	Eggs hatched
Stage	**Description**
E	Thickening of embryonic axis visible
O	Optic vesicles present
S	Somites visible

riod was obtained by combining eggs sampled from the two jars held at each temperature. A sample was determined to be at an egg stage when ≥50% of the eggs in that sample met the stage criteria. Because the duration of each stage differed, we standardized our presentation of egg development in accordance with Ketchen (1956), by spacing egg stages on the vertical axis proportional to the rate of development at a median survival temperature: 20°C for barred sand bass and fantail sole (Figs. 1 and 2), and 16°C for white croaker and California halibut (Figs. 3 and 4).

For each species at each temperature, the rate of egg development was quantified as the slope (β) of age regressed on stage, where age is time (in hours) from fertilization to the nine developmental stages (I–IX). Embryonic developmental stages E, O, and S were not considered in this analysis. Lines were fitted by using least-squares regression forced through the origin. Multiple regression equations were also fitted for each of the four species to estimate age (in hours) of an egg, given developmental temperature and egg stage (I–VIII). Stage IX (hatched) was not included in these predictive equations because this would not be a recognizable stage in field-collected eggs.

Chorion, yolk mass, and oil globule diameters were measured for 30 eggs of each species over a range of developmental stages. To allow for shrinkage, measurements were made after eggs had remained in 4% formalin for at least one year.

Results

Eggs of all four species were buoyant and spherical and had a smooth chorion, unsegmented yolk, and a single oil globule. Mean chorion diameter was significantly different between all species ranging from 0.75 mm (California halibut) to 0.85 mm (barred sand bass) (Table 1; one-way analysis of variance (ANOVA), $F_{3,116}=184.6$; $P<0.001$). Only the mean yolk diameter of California halibut differed significantly from mean yolk diameters of the other species (Table 1; one-way ANOVA, $F_{3,108}=29.3$; $P<0.001$). Mean oil globule diameter varied from 0.12 mm (California halibut) to 0.22 mm (white croaker) and was significantly different between all species (Table 1; one-way ANOVA, $F_{3,108}=320.2$; $P<0.001$).

Embryonic development in relation to germ-ring migration and blastopore closure occurred sooner for

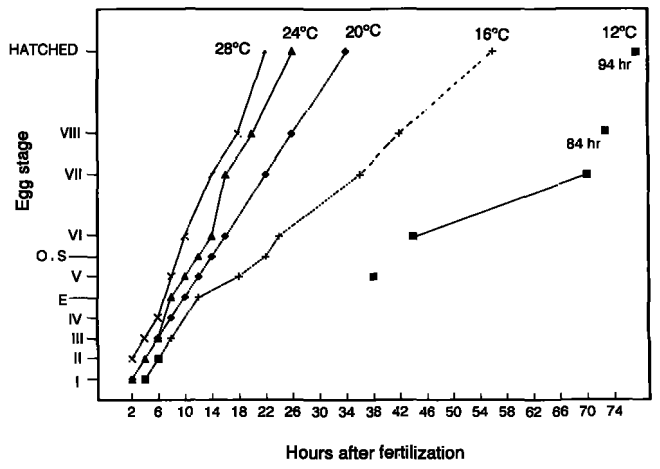

Figure 1

Development of eggs of barred sand bass, *Paralabrax nebulifer*, at five temperatures. Eggs died at 8°C with no cell division evident. At 12°C, many eggs sampled were dead, resulting in a lack of egg-stage observations for some time periods (unconnected points). Hatched larvae from eggs at 12°C were abnormal and soon died. Descriptions of egg stages are presented in Table 2.

barred sand bass and fantail sole eggs than for white croaker and California halibut eggs. For both bass and sole, optic vesicles and somites (stages O and S) were visible in the embryo by the time of blastopore closure, stage VI (Table 2, Figs. 1 and 2). Embryonic development of bass was particularly rapid; the embryonic axis was evident by the time the germ ring enclosed half the yolk mass. In contrast, for both croaker and halibut the embryonic axis was visible just prior to blastopore closure, and optic vesicles and somites appeared after closure (Figs. 3 and 4).

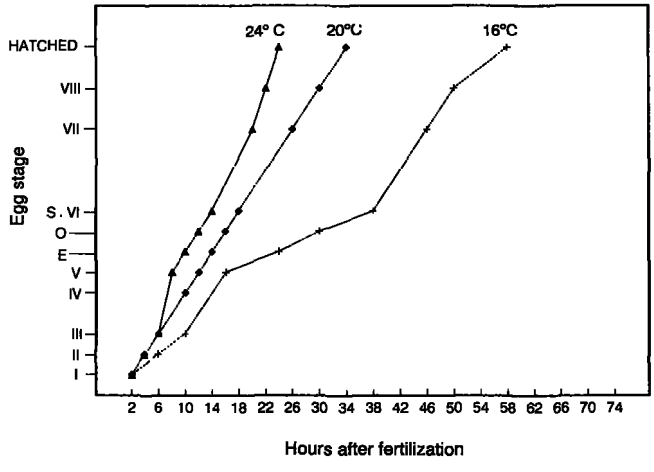

Figure 2

Development of eggs of fantail sole, *Xystreurys liolepis*, at three temperatures. Eggs died at 8°, 12°, and 28°C during stage II. Descriptions of egg stages are presented in Table 2.

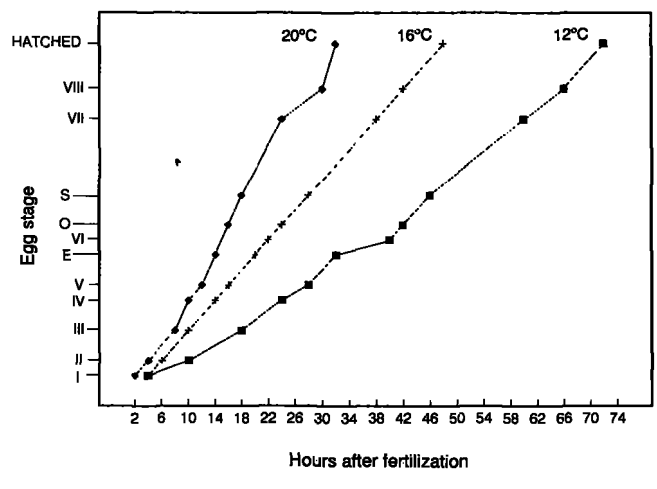

Figure 3

Development of eggs of white croaker, *Genyonemus lineatus*, at three temperatures. Eggs died at 8°C during stage I and at 24°C with no cell division evident. Descriptions of egg stages are presented in Table 2.

Eggs of barred sand bass hatched at a wider range of temperatures, 12–28°C, than did those of the other three species. However, at 12°C bass eggs took much longer to hatch (94 hours) than at higher temperatures, and many sampled eggs were dead (Fig. 1). Bass larvae that hatched at 12°C appeared to be abnormally developed, swam weakly, and soon died. Thus, successful hatching of viable embryos occurred only at 16–28°C for barred sand bass. Fantail sole eggs hatched at 16–24°C (Fig. 2), whereas both white croaker and California halibut eggs hatched at a lower temperature range, 12–20°C (Figs. 3 and 4). Although not quantified, in each treatment most eggs that remained after sampling hatched and all larvae in the samples (except barred sand bass at 12°C) appeared normal and viable. At temperatures where hatching did not occur (8°C for sand bass; 8°, 12° and 28°C for fantail sole; and 8° and 24°C for both white croaker and California halibut), eggs died with little development, reaching at most stage II.

Within survival ranges, eggs of all species developed faster at higher temperatures (Figs. 1–4). The relationship between age and stage was best fitted by a linear function ($Age=\beta stage$; $r^2>0.95$; Table 3). One-way ANOVA was used to test effects of species and temperature on rate of development (β); we could not test interactions between species and temperature with a two-way ANOVA because of missing values due to egg mortalities at temperature extremes. Species had no effect on rate of development (one-way ANOVA, $F_{3,10}=0.20$; $P=0.89$). Pooling across species showed that temperature had a strong effect on rate of development (one-way ANOVA, $F_{4,9}=33.72$; $P<0.001$). A multiple-range analysis (the Tukey test) for the temperature effect showed rates of development at 12°, 16°, and 20°C to be significantly different ($P<0.05$; Table 3).

Because developmental rate at a specific temperature did not significantly differ between species, we examined the general relationship between temperature and age at hatching by pooling data from all species (Fig. 5). This relationship was best fit by an exponential function:

$$\mathrm{Ln}(Age) = 5.395 - 0.090\,(T), \qquad [r^2=0.94, n=14]$$

where *Age* is the time in hours from fertilization to hatching and T is the incubation temperature (°C). Similarly, equations derived for each species to determine egg age at stage and

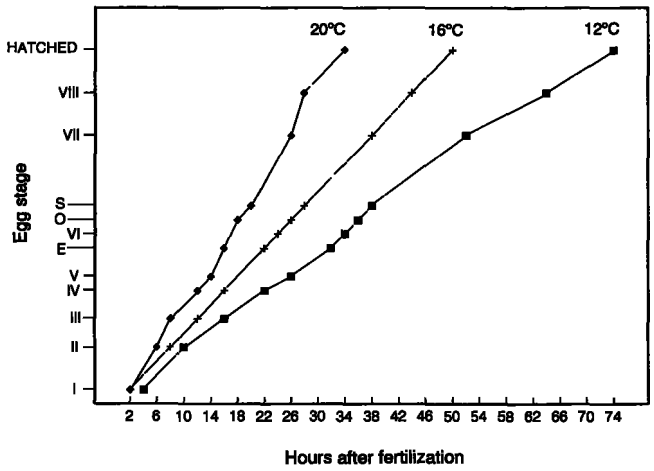

Figure 4

Development of eggs of California halibut, *Paralichthys californicus*, at three temperatures. Eggs died at 8°C during stage I and at 24°C during stage II. Descriptions of egg stages are presented in Table 2.

incubation temperature were best fit by exponential functions (Table 4).

Discussion

Many egg-staging systems have been developed for fishes (Ahlstrom, 1943; Colby and Brooke, 1973; Riley, 1974; Laurence and Rogers, 1976; Ferraro, 1980; Thompson and Riley, 1981; Haynes and Ignell, 1983; Walsh et al., 1991). We found it difficult to devise a system that could be used for all four species because the embryonic development of barred sand bass and fantail sole was faster in relation to germ-ring migration than that of white croaker and California halibut. Species-specific rates of embryonic organogenesis relative to blastopore closure were also noted by Ahlstrom and Moser (1980). Although not commonly considered, these developmental differences could be useful traits in identifying field-collected fish eggs.

Absolute temperature ranges tolerated by eggs of the four species reflect temperatures encountered owing to seasonal spawning patterns off southern California (Love et al., 1984; Lavenberg et al., 1986; Walker et al., 1987; Moser and Watson, 1990; McGowen, 1993). High temperatures successfully tolerated by barred sand bass (16–28°C) and fantail sole (16–24°C) eggs coincide with their summer and late summer–fall spawning seasons. Surface temperatures in the nearshore zone of southern California are generally highest in August, reaching peaks of 20–22°C, and lowest in January or February with temperatures of 13–15°C (Petersen et al., 1986), although unseasonably low temperatures, caused by upwelling, can occur during spring or summer. Both white croaker and California halibut eggs survived only at lower temperatures (12–20°C); peak spawn-

Table 3

Rates of development for eggs of four California fishes reared at five temperatures in the laboratory. Rates are expressed as the slopes (β) of age regressed on stage (Age=β stage). Age is time (hours) from fertilization to the nine egg developmental stages (I–IX); embryonic developmental stages E, O, and S were not considered in this analysis. Dashed lines are temperatures where eggs of that species did not survive. For all regression equations, r^2>0.95. Superscripts indicate means that were significantly different from each other in using the Tukey multiple-range test (P<0.05).

	Temperature (°C)				
Species	12	16	20	24	28
Barred sand bass	9.53	4.95	3.12	2.46	2.04
White croaker	7.54	4.73	3.25	—	
California halibut	7.14	4.98	3.42	—	
Fantail sole	—	5.78	3.38	2.51	—
Mean β	8.07[1]	5.11[2]	3.29[3]	2.49[3]	2.04

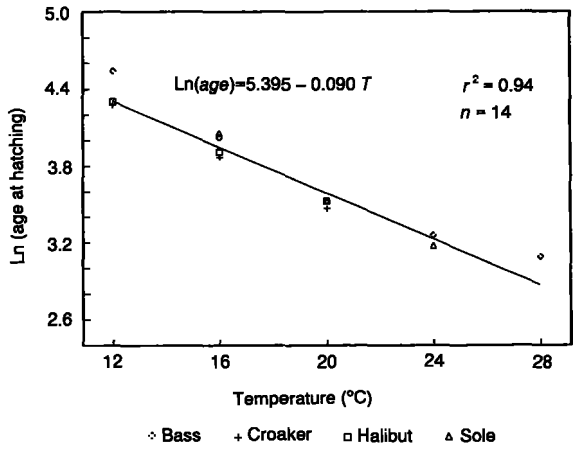

Figure 5

Relationship between egg age at hatching (hours from fertilization to hatching) and temperature (T) for barred sand bass, *Paralabrax nebulifer*, white croaker, *Genyonemus lineatus*, California halibut, *Paralichthys californicus*, and fantail sole, *Xystreurys liolepis*.

Table 4

Regression equations for estimating age (hours) of eggs of four California fishes reared in the laboratory over a range of temperatures. Parameters were calculated for temperatures (T) where eggs survived, producing viable embryos: 16–28°C for sand bass; 12–20°C for croaker and halibut; and 16–24°C for fantail sole. Equations are valid for egg developmental stages (S) I–VIII (1–8 in equations).

Species	Regression equation	R^2
Barred sand bass	Ln (*age*) = 2.039 – 0.062 *T* + 0.328 *S*	0.95
White croaker	Ln (*age*) = 2.876 – 0.105 *T* + 0.327 *S*	0.95
California halibut	Ln (*age*) = 2.542 – 0.084 *T* + 0.330 S	0.91
Fantail sole	Ln (*age*) = 2.363 – 0.080 *T* + 0.348 *S*	0.93

ing of these species occurs in winter–spring when nearshore sea surface temperatures off southern California usually are 13–17°C (Petersen et al., 1986).

Although seasonal spawning peaks of the four species coincide with their temperature tolerance ranges, all species, except sand bass, spawn to some degree thoughout the year. Moser and Watson (1990) examined abundances of California halibut and fantail sole larvae using a 30-year (1951–81) data set with stations from central California to southern Baja California. Densities of sole larvae during the nonpeak winter–spring season were very low; spawning occurred primarily off Baja California where mean sea temperatures were somewhat warmer than off southern California (Moser and Watson, 1990). Halibut displayed a more complex spawning pattern, which varied with location. Halibut were reported to spawn off southern California primarily when water temperatures were lowest (February–March) and to spawn secondarily in July–October (Moser and Watson, 1990). In contrast, off central and southern Baja California, a second spawning stock of California halibut occurred with peak spawning in June–August when temperatures are highest. Since we conducted our experiments with halibut collected off southern California and acclimated to 16°C, it is possible that experiments with eggs from fish collected in other localities or acclimated to other temperatures could result in a different range of survival temperatures.

Like the spawning patterns of California halibut, temporal spawning patterns of white croaker varied with location in a study conducted during 1978–81 by Love et al. (1984). Off southern California, most spawning occurred from November to April, with a peak in February–March; whereas off central California spawning occurred throughout the year, with greatest activity from July through February. Because croaker spawn off southern California during winter when temperatures are lowest, Love et al. (1984) suggested that the colder waters off central California allowed for a longer spawning season. Off Monterey, mean temperatures during June–October (the warmest months) are only 13–14°C; thus, the lower temperature tolerance range observed for croaker eggs probably reflects seasonal spawning conditions in both southern and central California.

Although the absolute temperature ranges that were tolerated differed between species, rates of egg development at a specific temperature did not significantly differ between species (Table 3). However, temperature strongly affected rates of development when data were pooled across species. Hatching times for all four species were inversely proportional to temperature, and the relationship was best fitted by an exponential function. This result is consistent with previous work on eggs of fishes such as Dover sole, *Microstomus pacificus*, cod, *Gadus morhua*, and walleye pollock, *Theragra chalcogramma* (Fonds, 1979; Thompson and Riley, 1981; Haynes and Ignell, 1983). Although these and many studies present results of single species experiments, reviews by Pauly and Pullin (1988) and Pepin (1991) pooled 84 and 124 species, respectively, and they similarly found an exponential relationship between incubation time and temperature. Both reviews also found developmental time to be significantly related to egg diameter. Although in our study mean chorion diameter differed significantly between species, these differences were not great (0.1 mm between the smallest and largest mean chorion diameters; Table 1) and evidently were not large enough to result in significant differences in developmental rate between species. The two reviews had somewhat conflicting conclusions concerning the importance of species-specific differences in developmental rates. Pauly and Pullin (1988) felt that after considering differences in developmental rate due to egg diameter and temperature, taxonomic differences were not important, whereas Pepin (1991) found some evidence for rate differences between groups of similar species.

The temperature range over which eggs hatched was at least eight degrees for fantail sole, white croaker, and California halibut, and possibly more if range endpoints fell outside the extreme temperatures survived. An eight-degree range is typical of other species such as English sole, *Pleuronectes vetulus*, Dover sole, and cod (Alderdice and Forrester, 1968; Irvin, 1974; Fonds, 1979; Thompson and Riley, 1981). Eggs of fantail sole might have tolerated the highest temperature tested (28°C), if we had been able to induce spawning during the more natural summer-fall season instead of winter (Table 1). However, sole brood stock were held at a warmer temperature (18.5°C) typical of their spawning season.

Barred sand bass hatched at a much wider range of temperatures, 12–28°C, although at 12°C embryos were not viable. The adaptive significance of the wider temperature tolerance of barred sand bass is not readily apparent. Field-collected barred sand bass larvae cannot be separated from larvae of two similar sea basses, the kelp bass, *Paralabrax clathratus*, and the spotted sand bass, *P. maculatofasciatus*; thus reports of bass abundance are based on a complex of these three species. Nonetheless, larval abundance of sea basses is the most seasonal of the species we studied, beginning in early summer and peaking in August, and thus bass eggs in the ocean are probably exposed to a narrower range of temperatures (Lavenberg et al., 1986). Perhaps because sea bass have a limited spawning season when waters are warmest, reaching 20–22°C nearshore (Petersen et al., 1986), a broad tolerance to high temperatures results in enhanced bass egg survival. Unseasonally cool temperatures or extended periods of upwelling could result in reduced survival; Lavenberg et al. (1986) reported that fewer sea bass larvae were collected during June and July 1980 when temperatures were anomalously low (Petersen et al., 1986).

Temperature ranges tolerated by fish eggs and larvae are also related to adult geographic distribution. In a study of the nearshore southern California Bight, Walker et al. (1987) found that larvae collected in cooler months were generally of species whose adult northern ranges extend to Canada, whereas larvae abundant during warmer months were species whose ranges extended primarily to Point Conception or northern California. The four species we studied follow this pattern: adults of barred sand bass and fantail sole range to Santa Cruz and Monterey Bay, respectively, whereas white croaker and California halibut both range farther north to British Columbia (Miller and Lea, 1972). All species have been collected as far south as Baja California. Thus, species-specific temperature tolerance ranges for early life history stages of fish may reflect a variety of interrelated factors such as the timing and duration of a species' spawning season, spatial spawning patterns, and adult geographic distributions.

Acknowledgments

Valuable laboratory assistance was provided by L. Abbott, G. Caddell, K. Fujimoto, G. Lattin, R. Lavenberg, G. McGowen, D. Nuygen, J. Petersen, and G. Weins. We thank R. Lavenberg and J. Stephens Jr. for their support and J. Petersen, G. McGowen, J. Rounds, and two anonymous readers for reviewing this manuscript. This study was funded by the California Department of Fish and Game and the Southern California Edison Company.

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