Abstract.– Laboratory experiments were conducted to determine how growth and survival of early-life-history stages of California halibut *Paralichthys californicus* are influenced by temperature, and how optimal temperature ranges may change with ontogeny. As halibut developed from eggs to juveniles, highest survival occurred at increasingly higher temperature ranges. Within tolerance limits, growth and development rates of all early-life-history stages were directly proportional to temperature. Eggs hatched successfully at 12, 16, and 20°C; at 8 and 24°C they died prior to embryo formation. Larval survival 17 days after hatching was 23–46% at 16, 20, and 24°C, but almost all larvae died at 12°C after an initial period of high survival. At 8°C, larval development ceased at the early yolksac stage. Survival of 3-month-old juvenile halibut was significantly greater at 20, 24, and 28°C (57–76%) than at 16°C (31%). Temperature also affected settlement rate; when the temperature of 1-month-old larvae was raised from 16°C to 20°C, settlement occurred about a week sooner than settlement of larvae remaining at 16°C. Tolerance ranges of halibut early-life-history stages determined in the laboratory approximate temperatures encountered by halibut in the field; high densities of newly-settled halibut larvae and juveniles have been collected in shallow areas of bays where temperatures are often higher than the open ocean inhabited by young larvae. These warmer inshore nursery grounds could enhance growth and survival of halibut juveniles.

Effects of Temperature on Early-life-history Stages of California Halibut Paralichthys californicus

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The California halibut *Paralichthys californicus* (family: Paralichthyidae) is important to commercial and recreational fishermen in central and southern California. Adult halibut spawn in nearshore waters (Frey 1971, Lavenberg et al. 1986) and eggs hatch in about 2 days at 16°C (Gadomski et al. 1990). Lavenberg et al. (1986) collected halibut larvae year-round within the 75m contour of the Southern California Bight, with greatest abundance during winter and spring. When larvae are about 1-month-old and 8mm standard length, they metamorphose and settle to the bottom (Allen 1988, Gadomski et al. 1990). Although spawning has not been observed in bays and estuaries, high densities of newly-settled halibut larvae and juveniles have been collected in these areas, often in waters as shallow as one meter (Allen 1988, Kramer 1990). It is not known at what stage of development inshore movement occurs, and whether the mechanism of transport is passive or active. The advantages of estuarine nursery areas for juvenile fishes have been often cited (McHugh 1967, Pearcy and Myers 1974, Boehlert and Mundy 1988). Estuaries commonly have greater food availability and protection from predation and adverse weather conditions.

As early development progresses, halibut may experience an increasingly higher range of temperatures due both to the distribution changes described above and to seasonal temperature differences. When eggs and young larvae are in nearshore waters of southern California during winter and spring, typical surface temperatures are about 13–17°C (Petersen et al. 1986). Juveniles in inshore waters during summer months commonly experience temperatures above 20°C, and shallow areas may be as warm as 24°C (Kramer 1990). Thus, one advantage of inshore migration might be higher temperatures, which could result in enhanced juvenile growth.

Fishes generally have temperature ranges at which growth and survival are optimum. These may differ with age; young of some species prefer warmer temperatures than adults (Norris 1963, McCauley and Huggins 1979). Early-life-history stages may also have different optimal temperatures, which may reflect field temporal and spatial distributions. For example, sole *Solea solea* larvae from North Sea coastal regions require

higher temperatures for successful development than sole eggs, probably because sole's spring spawning cycle results in larval abundances later in the season when sea temperatures are warmer (Irvin 1974, Fonds 1979).

Our purpose was to determine how growth and survival of California halibut may be influenced by temperature during development from egg to 3-month-old juvenile, and how optimal temperature ranges may change with ontogeny. Additionally, we were interested in how temperature may influence the timing of an important stage of flatfish development—settlement. We examined the possibility that month-old pelagic larvae passively transported to warmer inshore waters would settle significantly sooner due to a faster development rate than those remaining in colder offshore areas, resulting in selective settlement of shallow coastal nursery grounds. Larvae remaining pelagic due to colder waters would have a continued chance of transport inshore. The results of this study will aid in better understanding how oceanographic conditions may influence the survival of halibut early-life-history stages in the field.

Methods

Egg development

Eggs and sperm were stripped from ripe field-collected California halibut and combined in petri dishes. Approximately 300 fertilized eggs were placed in each of ten 3 L glass jars containing filtered, ultraviolet-light sterilized seawater (35%) at an ambient temperature of 16°C. To establish and maintain desired temperatures, jars were placed in temperature-controlled water baths. A low level of aeration was provided in each jar to avoid the formation of temperature gradients. Soon after fertilization, temperatures in eight jars were raised or lowered 1°C/15 minutes from 16°C to 8, 12, 20, and 24°C, resulting in two replicates of each temperature treatment. Light cycles simulated natural conditions (12L:12D). Every 2 hours until hatching, temperatures were recorded and at least five live eggs were sampled from each jar and preserved in 4% formalin. Because of the short experimental duration, water in the jars was not exchanged with fresh seawater during the experiment; when eggs in all jars had hatched or died, the experiment was terminated. To monitor development, egg series were examined using a dissecting microscope.

Larval growth and survival

An experiment was initially conducted to determine the influence of temperature on starvation rate of newly-hatched halibut larvae. Fertilized eggs were obtained from natural spawns from brood stock held in an outdoor 5 m diameter tank with a flow-through seawater system (for a further description of brood stocks, see Caddell et al. 1990). Seventy-five late-stage eggs (with developed embryos) were placed in each of ten 3 L glass jars of sterilized seawater at an ambient temperature of 16°C. Jars were in temperature controlled water baths and light aeration was provided. Temperatures in eight jars were raised or lowered 1°C/15 minutes from 16°C to 8, 12, 20, and 24°C; each temperature treatment was replicated. Light cycles simulated natural conditions (12L:12D). Twenty percent of the water volume was replaced with fresh seawater twice weekly; at this time, ammonia and salinity levels were monitored. Dead halibut larvae were removed and counted daily until total starvation had occurred.

To determine how growth and survival of halibut larvae are temperature-dependent, the above experiment was repeated except food was added. Gadomski and Petersen (1988) found that for greatest survival, first-feeding halibut required food by the day of total yolk absorption. Full yolk depletion occurs 6 days after hatching at 16°C, but yolk absorption time varies with temperature (Gadomski et al. 1990). In the current study, we fed rotifers *Brachionus plicatilis* to halibut larvae after eye pigmentation and mouth development, but before total yolk absorption. Rotifers were stocked at 15/mL, following the methods of Gadomski et al. (1990), and supplemented thereafter as needed to maintain this density. Dead halibut larvae were removed and counted daily. Seventeen days after hatching, notochord lengths of surviving larvae were measured.

Because final survival was the same (zero) for all starvation trials, we compared survival curves of starved and fed larvae using the Mantel-Haenszel test (Matthews and Farewell 1985, Gadomski and Petersen 1988). This method tests the null hypothesis that incremental survival rates, computed between successive sampling times, are similar throughout the observation period. Rapid decomposition of deceased larvae resulted in accumulative totals of survivors and mortalities in some trials at the end of the experiment to be less than the original stocking density of 75. The Mantel-Haenszel test compensated for this by adding the "lost" mortalities to each experimental day proportionate to the known number that had died that day. First we tested if replicates could be combined; then we tested for a significant difference between survival curves of each experiment (starved and fed): 12°C vs. 16°C, 16°C vs. 20°C, and 20°C vs. 24°C. Because of

their similarity, survival curves of 12°C starved and 12°C fed trials were additionally compared.

For the fed trials, analysis of variance (ANOVA) was used to test for significant differences in final survival [ln(number alive + 1)] and also differences in mean larval length between temperatures; if significant differences were found, Duncan's multiple range test was applied.

Juvenile growth and survival

Twenty-five 30-day-old pelagic larvae, which had been held at a mean ambient temperature of 16.7°C (SE 0.1), were stocked in each of twelve indoor 15 L black fiber-glass tanks (40 cm diam., 12 cm depth) at 16°C. Water quality was maintained using a slow-drip flow-through system and tank aeration; ammonia and salinity levels were monitored weekly. A natural cycle of light and dark (12L:12D) was provided. Temperatures were raised using aquarium heaters in nine tanks 0.5°C per day from 16°C to 20, 24, and 28°C, resulting in three replicates per temperature. Fish were fed rotifers and newly-hatched brine shrimp nauplii (*Artemia* sp.) to excess. Dead fish were removed and counted daily and, in the last 15 days of the experiment, measured if not badly decomposed. The experiment was terminated when fish were 97 days old; survivors were counted and standard lengths determined. ANOVA and Duncan's multiple range test were utilized to test for significant differences in final survival and size between temperatures. Student's t-test was used to test for significant differences in mean standard lengths between 16°C and 20°C mortality and survivor groups.

Larval settlement

The settlement rate of a group of larvae held constantly at 16°C was compared with that of a group of larvae from the same cohort exposed to 20°C when a month old. These two temperature regimes were designed to simulate temperatures halibut larvae would encounter in the field if they (1) remained in colder offshore waters, or (2) were transported to warmer inshore areas when a month old.

Fifteen 30-day-old pelagic larvae that had been held at a mean temperature of 15.9°C (SE 0.1) were transferred to each of six indoor 15 L black fiberglass tanks at 16°C. Temperatures were raised 2°C a day to 20°C in three of the tanks while keeping

three tanks at 16°C. Light cycles simulated natural conditions (12L:12D). Tanks were aerated to maintain water quality and avoid the formation of temperature gradients. Three times a week, 20% of the volume of water in each tank was replaced with fresh seawater; at this time, salinity and ammonia levels were monitored. Larvae were fed rotifers and newly-hatched brine shrimp to excess. Dead larvae were removed and counted daily. Each tank was observed for 10 minutes twice daily (morning and afternoon) and the numbers of settled and pelagic larvae counted; the mean values of these two daily observations were used to calculate percent settled larvae per tank per day. We defined "settled" larvae to be individuals that remained on the tank bottom (on their side) for at least 5 seconds during an observation period. This behavior occurs before metamorphosis is complete (Gadomski et al. 1990). When 100% settlement was observed in all tanks, fish were removed and standard lengths determined. Student's t-test was utilized to test for a significant difference in mean fish lengths between temperature treatments.
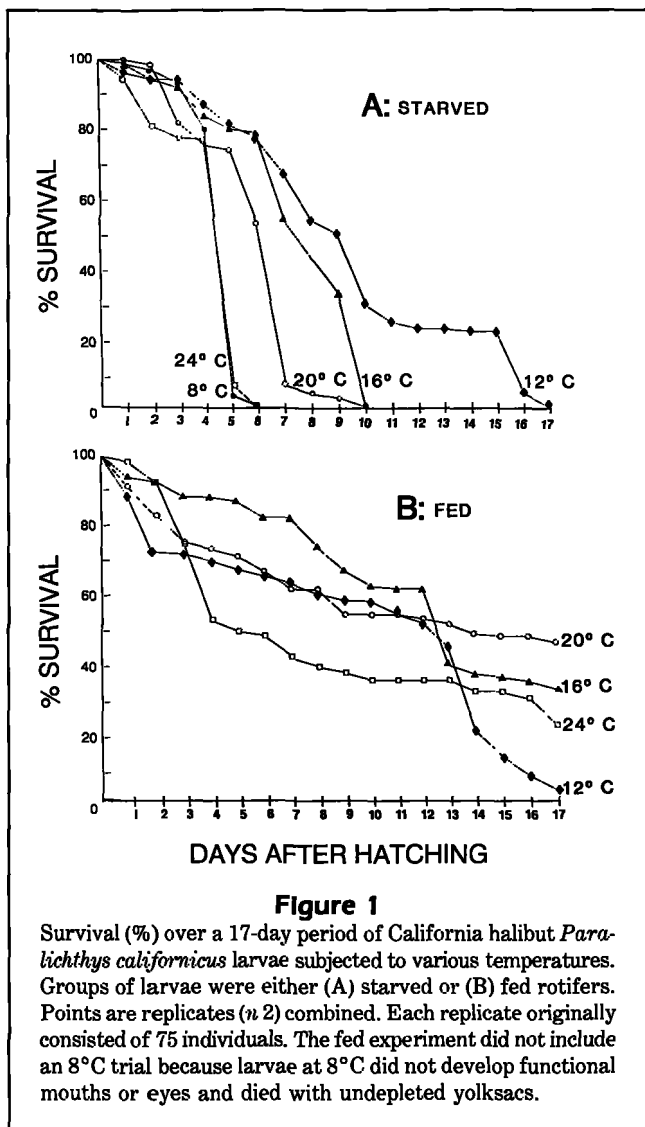
Results

Egg development

Halibut eggs are buoyant and about 0.8 mm in diameter with a single 0.14 mm oil globule. Eggs developed to hatching at 12, 16, and 20°C (Table 1). At 8°C, eggs did not develop beyond the 32-cell stage, and at 24°C cell divisions were abnormal and ceased during early development. Time to hatching was inversely propor-

Table 1

Egg development rates of California halibut *Paralichthys californicus* at five temperatures. Times (hours) after fertilization at which developmental events (I–VII) were first observed are presented. Two replicate jars were maintained at each temperature, with initially 300 recently-fertilized eggs per replicate; every 2 hours until hatching, at least five live eggs were sampled from each jar and egg development noted.

		Hours post-fertilization				
	Mean temp. (°C): SE (°C):	8.4 (0.2)	12.4 (0.1)	16.0 (0.1)	20.8 (0.1)	23.9 (0.6)
I	2–128 cells	4	4	2	2	2
II	Multicelled blastodermal cap	Dead	10	8	6	6
III	Germ ring >1/2 down yolk mass		26	18	14	Dead
IV	Embryo visible		32	22	16	
V	Blastopore closed		34	24	18	
VI	Tail separated from yolk mass		52	38	26	
VII	Eggs hatched		74	50	34	

Figure 1

Survival (%) over a 17-day period of California halibut *Para-lichthys californicus* larvae subjected to various temperatures. Groups of larvae were either (A) starved or (B) fed rotifers. Points are replicates (*n* 2) combined. Each replicate originally consisted of 75 individuals. The fed experiment did not include an 8°C trial because larvae at 8°C did not develop functional mouths or eyes and died with undepleted yolksacs.

Table 2

Mean notochord lengths of larval California halibut *Paralich-thys californicus* 17 days after hatching at four temperature treatments. Two replicates were maintained at each tempera-ture, with initially 75 late-stage eggs per replicate. *N* = com-bined number of surviving larvae in the two replicates.

Temperature (°C)			Notochord length (mm)	
Mean	SE	*N*	Mean	SE
12.3	(0.2)	4	3.92	(0.09)
16.2	(0.1)	45	4.80	(0.07)
20.0	(0.1)	69	5.31	(0.07)
24.1	(0.1)	34	5.94	(0.03)

beyond the yolksac stage with unpigmented eyes and nonfunctional mouths (thus the fed experiment did not include an 8°C trial). At 24°C, however, dead larvae had pigmented eyes, functional mouths, and completely depleted yolks.

Survival curves of 20 and 24°C fed larvae were statistically similar, while the 12 and 16°C fed trials differed ($P<0.05$). At 24°C, mortality initially was high, perhaps due to temperature acclimation prob-lems, but then mortality was gradual, paralleling the 20°C curve. At 16°C, survival initially was highest, but dropped after 12 days. Survival was high for fed larvae at 12°C until the end of the second week when the mor-tality rate increased, resulting in almost total mortal-ity by day 17 (Fig. 1B). Although this survival pattern approximates the starved 12°C counterpart, the two curves are significantly different ($P<0.01$; more larvae in the fed trial survived longer). Fed larvae at 12°C initiated feeding (since food was observed in their guts) but survival enhancement was only short-term.

Final survival of fed larvae at 16°C was intermediate to final survival values at 20°C and 24°C; final survival was highest at 20°C and nearly zero at 12°C (Fig. 1B). Final survival did not significantly differ between tem-perature treatments (P 0.14), however. At experimen-tal end, mean notochord lengths of surviving fed larvae were directly proportional to temperature (Table 2) and significantly different between all temperatures ($P<0.05$).

Juvenile growth and survival

Replicates (*n* 3) did not differ and were combined for analysis. Survival of 97-day-old fish at 16°C was sig-nificantly ($P<0.05$) lower than survival at 20, 24, or 28°C (Fig. 2); there were no significant survival dif-ferences between the three higher temperatures. Final mean standard length at 16°C did not differ signif-

tional to temperature: 74, 50, and 34 hours at 12, 16, and 20°C, respectively. Although not quantified, most eggs remaining (the initial number was reduced by sampling) at each temperature hatched. No abnormal yolksac larvae were observed.

Larval growth and survival

Replicates (*n* 2) of survival curves at each temperature for starved and fed larvae were combined for analysis since they were not significantly different ($P<0.05$). Survival curves of 12, 16, 20, and 24°C starved trials were significantly different ($P<0.01$), with starvation time (6-17 days) inversely proportional to temperature (Fig. 1A). Total mortality occurred first at temperature extremes, 8 and 24°C, which had similar mortality curves. Larval development at 8°C never progressed

Table 3

Mean standard lengths of 97-day-old juvenile California halibut *Paralichthys californicus* at four temperature treatments (acclimated when 1 month old from 16.7°C). Three replicates were maintained at each temperature, with initially 25 larvae per replicate. *N* = combined number of surviving juveniles in the three replicates.
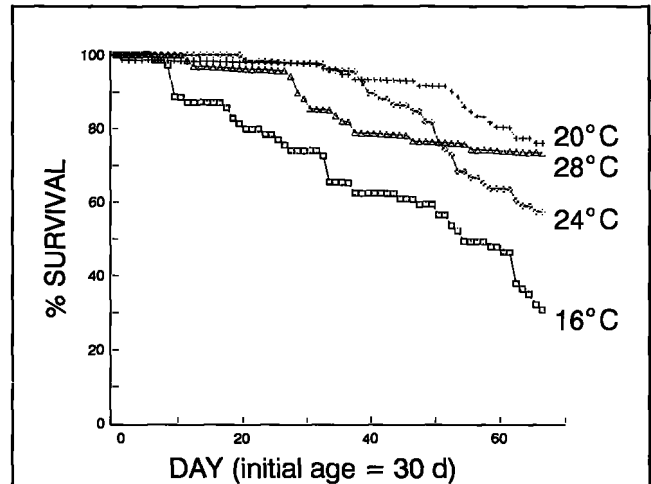
Temperature (°C)			Standard length (mm)	
Mean	SE	*N*	Mean	SE
16.1	(0.1)	23	18.48	(0.93)
19.7	(0.0)	57	18.10	(0.39)
23.7	(0.1)	43	24.24	(0.57)
27.5	(0.0)	55	26.92	(0.71)

Figure 2

Survival (%) over a 67-day period of California halibut *Paralichthys californicus* larvae and juveniles at four temperatures. Larvae held at 16.7°C were transferred into experimental containers when 30 days old. Points are replicates (*n* 3) combined. Each replicate initially consisted of 25 larvae.

icantly from 20°C ($P < 0.05$), but final mean length was significantly larger at 24°C, and larger at 28°C than 24°C (Table 3). These results were unexpected, since all previous experiments have demonstrated greater growth at 20°C than 16°C (Gadomski et al. 1990). Measurements of dead fish removed during the last 15 days of the experiment, however, indicated that smaller individuals were dying at 16°C than at 20°C, which biased the final growth data. Mean standard lengths at 16°C of fish that died during two time periods—the five (days 63–67) and fifteen (days 53–67) day intervals before the end of the experiment—were similar, 12.68 mm (SE 0.77, *n* 8) and 12.57 mm (SE 0.49, *n* 14), respectively, and were significantly smaller ($P < 0.01$) than mean mortality lengths at 20°C for these same two time periods, 17.46 mm (SE 2.02, *n* 3) and 16.21 mm (SE 1.12, *n* 8). The mean standard length (12.68 mm, SE 0.77, *n* 8) of fish that died near the end of the experiment (days 63–67) at 16°C was also significantly smaller ($P < 0.05$) than the final mean standard length of surviving individuals at 16°C, 18.48 mm (SE 0.93, *n* 23), indicating that size-selective mortality had occurred.

Larval settlement

There were no significant differences in survival between temperatures ($P < 0.01$), with individual tank survival ranging from 80% to 93%. Larvae settled sooner at 20°C (actual mean temperature 20.0°C, SE 0.0) than 16°C (15.8°C, SE 0.1) (Fig. 3). At 20°C, 50% had settled by 6–8 days after transfer from 16°C, and all were settled by 10 days after transfer (when 40 days old). In contrast, at 16°C, 50% settlement did not occur until 12–15 days after transfer, and the last few larvae did not settle until 21–22 days (when 51–52 days old).

At the end of the experiment, larvae held at 20°C were significantly larger ($P < 0.01$) than those at 16°C.
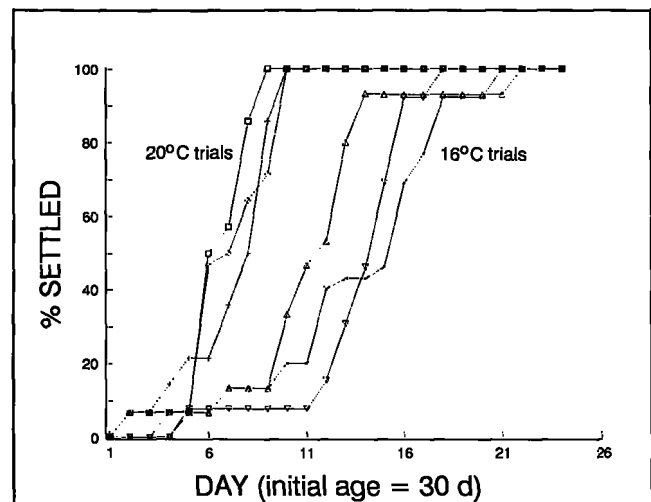
Figure 3

Percent of California halibut *Paralichthys californicus* settled per day at 16°C and 20°C. Larvae held at 16°C were transferred into experimental containers when 30 days old. Three replicate trials were conducted at each temperature. Each replicate initially consisted of 15 larvae.

At the beginning of the experiment (when transferred from 16°C), 30-day-old larvae had a mean length of 6.74 mm (SE 0.10, *n* 15) with 80% still exhibiting incomplete notochord flexion [the remaining 20% had achieved full flexion (standard length)]. All exhibited full elongation of the second to sixth dorsal rays

[dorsal ray elongation is characteristic of larvae of many pleuronectiform fishes; rays regress during metamorphosis (Ahlstrom et al. 1984, Gadomski et al. 1990)], and no eye migration was evident. At experimental end, 53-day-old larvae at 16°C had a mean length of 8.75 mm (SE 0.16, n 38), while at 20°C, mean larval length was 12.88 mm (SE 0.23, n 40). All fish at both temperatures had achieved standard length and had fully migrated eyes. Those at 16°C were somewhat less developed, however, since 8% still had slightly elongated dorsal rays. The remainder at 16°C and all fish at 20°C exhibited normal length dorsal rays characteristic of juveniles.

Discussion

Temperature tolerance experiments have been conducted on eggs and larvae of many fish species (Houde 1974, Laurence and Rogers 1976, Laurence 1978, Ferraro 1980, Bolla and Holmefjord 1988). The temperature tolerance range of California halibut eggs in the current study was at least 8 degrees (12-20°C), and probably more if the range endpoints fell between 8-12°C and 20-24°C. This 8-degree range is typical of other flatfish species such as English sole *Parophrys vetulus*, sole *Solea solea*, and winter flounder *Pseudopleuronectes americanus* (Alderdice and Forrester 1968, Irvin 1974, Fonds 1979, Buckley 1982). Absolute temperatures tolerated varied among species, however, and were reflective of field habitat temperatures; sole *S. solea* eggs survived slightly lower temperature exposures than halibut (8-16°C), whereas English sole and winter flounder eggs (found in colder waters) tolerated much lower temperatures, 4-12°C and 2-10°C, respectively.

Temperature tolerance ranges may change with ontogeny. Halibut larvae exhibited a higher temperature tolerance range (16-24°C) than halibut eggs, a pattern which has also been demonstrated for sole *S. solea* (Irvin 1974, Fonds 1979) and yellow perch *Perca flavescens* (Hokanson and Kleiner 1974). Additionally, sole (Devauchelle et al. 1987) and yellow perch (Hokanson and Kleiner 1974) temperature tolerances were higher for late-stage eggs than for eggs at early developmental stages. Similarly in our study, larval halibut experiments initiated with late-stage eggs resulted in a higher range of temperature tolerance than experiments initiated with recently fertilized eggs. As larval halibut development progressed, temperature tolerance ranges also increased; soon after hatching, the highest mortality rate occurred at 24°C, whereas mortality of older larvae was greater at 12°C and 16°C (Fig. 1B).

At low temperatures, biochemical reactions, and thus metabolic rates and growth, of poikilotherms are reduced (Laurence 1975). For all halibut early-life-history stages, the lowest tested temperatures adversely affected growth and survival. Larval halibut may have a minimum necessary growth rate for survival, as suggested by Gadomski and Petersen (1988), and reported for larvae of other fish species (Jones 1973, Beyer and Laurence 1980, Govoni et al. 1986). At 8°C, development of halibut larvae halted soon after hatching when larvae still had significant amounts of yolk, unpigmented eyes, and nonfunctional mouths. Ehrlich and Muszynski (1982) found that at low temperatures, yolk-sac California grunion *Leuresthes tenuis* encountered problems with fat metabolism. At 12°C, survival of fed halibut larvae initially was high and ingestion was observed, but by 17 days after hatching almost all larvae were dead. This type of survival pattern was also reported by Laurence (1975) for winter flounder *Pseudopleuronectes americanus*, which survived in the laboratory at 2°C for 5 weeks with a very slow development rate, and then died before metamorphosis; larvae at higher temperatures of 5 and 8°C developed normally. Similarly, Laurence (1978) found that larval cod *Gadus morhua* and haddock *Melanogrammus aeglefinus* could only survive for limited periods after hatching at lower tested temperatures, with variable and elevated oxygen consumptions indicating physiological stress.

The temperature tolerance ranges of halibut eggs and larvae in the laboratory approximate temperatures these stages usually encounter in the field; deviations from normal sea temperatures could affect survival. During winter and spring, nearshore (1-20 km from shore) sea surface temperatures off southern California usually range between 13 and 17°C (Petersen et al. 1986). Vertical mixing during the winter season generally produces uniform temperatures throughout the water column. In late-spring and summer, surface waters warm as high as 20-22°C, and a thermocline develops (Petersen et al. 1986). Late-spring and summer upwelling events may disrupt this temperature stratification, however, transporting deep colder waters to the surface (Dorman and Palmer 1981). Our study has shown that halibut larvae can endure 12°C for a short period during the first 3 weeks after hatching, but years with prolonged periods of this temperature might result in high larval mortality. Since 1920, there have been only three instances when surface temperatures at the Scripps Pier off San Diego remained below 12.5°C for as long as 2 weeks, and these were all in the time period of December–February (E. Stewart, Scripps Inst. Oceanogr., La Jolla, CA). Temperatures considered lethal for halibut eggs and larvae ($\leq 8°C$) were never recorded at this site. In

contrast, areas north of Point Conception, California commonly have extended periods of temperatures below 12°C (SIO 1955–85, Parrish et al. 1981). Low northern California ocean temperatures may possibly limit the geographic range of larval halibut abundance, although areas off northern California are also characterized by strong offshore surface transport (due to upwelling), which in itself limits survival of pelagic fish eggs and larvae (Parrish et al. 1981).

Growth and development rates of halibut eggs and larvae in the laboratory increased with temperature increase. We did not determine the upper temperature tolerance limit of halibut larvae, but the highest temperature tested, 24°C, exceeds normal southern California ocean temperatures. Swift development of pelagic eggs and larvae in the field may be advantageous, since these stages are particularly vulnerable to predation (Bailey 1981). Conversely, faster development requires that more food be available, or starvation may quickly occur; we found that newly-hatched halibut larvae died sooner from starvation at higher temperatures (Fig. 1A), since yolk absorption was faster. Thus, warm ocean temperatures would increase starvation-related mortality of larval halibut in the field during periods with inadequate available food, while cold temperatures might decrease mortality.

Juvenile halibut had a higher temperature tolerance range than halibut eggs and larvae; survival of 3-month-old halibut was significantly lower at 16°C than at 20–28°C. Juvenile growth rates at 20, 24, and 28°C were directly proportional to temperature. Surviving juveniles were similarly sized at 16°C and 20°C (Table 3), but this final size data are biased because fish that died at 16°C were significantly smaller than those that died at 20°C. The less robust, slower-growing fish at 16°C died, perhaps indicating that young juveniles, like larvae (Laurence 1977, Houde and Schekter 1980), require a minimum growth rate for survival that was unattainable for some individuals at 16°C.

The higher temperature range required for best survival of juvenile halibut reflects observed spatial and temporal distribution patterns. High densities of newly-settled larval and juvenile halibut have been collected during spring and summer in southern California bays where waters may be as warm as 24°C (Allen 1988, Kramer 1990); solar heating of very shallow waters could result in even higher temperatures. Juveniles in shallow areas of bays and estuaries may thus have the advantage of enhanced growth and survival due to warmer waters, in addition to other advantages, such as increased food availability and protection. Larval cohorts that settle and remain in open-coast areas do not have these advantages, and could experience low survival. As an example of this, in 1988 Kramer (1990, 1991) collected most newly-settled halibut juveniles in

open-coast areas, whereas bays contained larger sized juveniles; Kramer suggested that individuals that settled on the open coast eventually moved into bays or died. However, Kramer (1991) did not find a significant difference in growth rates of smaller juveniles (≤40 mm standard length) from bay versus coastal locations.

The El Niño years of 1982 and 1983 may be an example of warm ocean temperatures enhancing juvenile halibut survival, both in open-coast areas and during normally colder seasons. Higher densities of juvenile halibut were collected in bays in 1983 (Allen 1988). Additionally, strong fishery catches of halibut 1982 and 1983 year-classes have been reported (Miller 1990, Pattison and McAllister 1990).

The mechanism of larval or juvenile halibut entry into bays, and the stage at which entry occurs, are unknown. Kramer (1990) found newly-settled halibut almost exclusively in southern California bays in 1987, whereas in 1988 most settled in shallow open coast areas and then possibly moved into bays. English sole *Parophrys vetulus* have been reported to enter bays both during and after metamorphosis (Misitano 1976, Boehlert and Mundy 1987, Rogers et al. 1988). Plaice *Pleuronectes platessa* settle in deeper waters and move into shallow areas after metamorphosis (Lockwood 1974). For both English sole and plaice, tidal stream transport is an important migration mechanism (van der Veer and Bergman 1986, Boehlert and Mundy 1987). Other physical factors that have been suggested to mediate shoreward migration of larval and juvenile fishes are often associated with river discharge (salinity; olfactory cues) (Creutzberg 1961, Boehlert and Mundy 1987), and are thus not as applicable in drier southern California, where rainfall is only 25–40 cm/year (Petersen et al. 1986). Temperature differences between near and offshore areas might be an important cue (Boehlert and Mundy 1988, Miller 1988), although the ability of halibut larvae and young juveniles to seek preferred temperatures has not been demonstrated.

High inshore densities of juvenile halibut are likely a combination of passive larval transport to coastal areas, followed by active inshore movement of larvae or juveniles mediated by environmental stimuli. Shoreward transport of pelagic fish eggs and larvae to coastal nursery grounds has been demonstrated to enhance cohort survival (Nelson et al. 1976, Parrish et al. 1981). Onshore and offshore surface water transport in nearshore southern California areas is sporadic and associated with late-spring and summer downwelling and upwelling events (Winant 1980, Dorman and Palmer 1981). Another possible mechanism of onshore transport is surface slicks generated by tidally forced internal waves (Kingsford and Choat 1986, Shanks

1988). Additionally, halibut eggs and larvae may be transported parallel to the shore, since a narrow near-shore current with a generally southward surface flow often occurs within 10–20km of the coast (Tsuchiya 1980, Winant and Bratkovich 1981).

The passive transport of pelagic halibut larvae off southern California is thus influenced by a variety of currents and oceanographic conditions. Our results indicate that halibut larvae that encounter warmer waters during transport may settle much sooner than those remaining in colder waters (Fig. 3). Therefore, larvae carried by alongshore currents might eventually settle near the entrances of bays or estuaries due to warmer waters in these areas. Larvae transported offshore during upwelling events would experience lower temperatures (Dorman and Palmer 1981), resulting in delayed settlement and the possibility of eventual shoreward transport into shallow coastal or inshore nursery areas where warm temperatures could stimulate settlement.

The ability of pelagic larvae of many marine invertebrates to delay settlement until an appropriate habitat is available has been well documented (Scheltema 1974, Doyle 1975). Fish larvae have not commonly been demonstrated to have this ability, although Victor (1986) reported that bluehead wrasse *Thalassoma bifasciatum* can extend the duration of the planktonic larval period after attaining settlement size by reducing growth rate. We found that halibut larvae at 16°C took about a week longer to 50% settlement than larvae reared initially at 16°C and then exposed to 20°C when 1 month old; one individual at 16°C was pelagic 12 days after all larvae had settled at 20°C (Fig. 3). Although the observed longer period to settlement at 16°C vs. 20°C was to some degree a direct growth response to temperature, halibut larvae in colder waters may additionally be capable of delaying settlement for a limited period until encountering the appropriate cue, higher temperatures. This trait would enhance larval halibut survival by increasing the likelihood of settlement in warmer inshore areas.

Acknowledgments

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