Estimates of Age, Growth, and Settlement from Otoliths of Young-of-the-Year Kelp Bass (Paralabrax clathratus)

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Abstract.—Settled young-of-the-year (YOY) and older juvenile kelp bass (Paralabrax clathratus) were collected off the coast of southern California during the summers of 1989 and 1990. Daily rings on the sagittae of settled YOY kelp bass were used to determine age, estimate growth, and construct ring width profiles for each fish. Laboratory-reared larvae revealed that ring deposition began on the third day after hatching, and confirmed the daily periodicity of ring deposition. The combined 1989–90 growth curve could be described as a linear regression with the equation (length (mm)) = 14.67 + 1.69(age(days)) (r = .96), resulting in an average daily growth of 0.59 mm/day for the first 90 days of life. Back-calculated spawn dates suggested a possible lunar periodicity around the full moon. Settlement checks and otolith ring widths were used to determine the time of settlement and explore the possibility of delayed settlement in this species. The average age-at-settlement was calculated to be 30 days, with a range of 25–36 days. Only a single case of delayed settlement was evident from the increment-width profiles of 22 fish.

The kelp bass Paralabrax clathratus is one of three congeneric species in the family Serranidae found off the coast of southern California. Traditionally a popular sport fish, local southern Californian P. clathratus populations fell off dramatically after heavy post-WWII fishing (Young 1963), but ranked second in the Commercial Passenger Fishing Vessels (CPFV) catch of 1992 (Oliphant 1993). The kelp bass is generally believed to be a long-lived, slow-growing species, and may reach an age of over thirty years and sizes up to 680 mm (Young 1963).

Kelp bass are broadcast spawners with widely dispersed larvae (Beckwitt 1983; Waples and Rosenblatt 1987; Walker et al. 1987). However, with the exception of differentiation based on mitochondrial DNA (Graves et al. 1990), the eggs and early larvae of the three local species of Paralabrax are largely indistinguishable (Butler et al. 1982), and have traditionally been treated as a single entity in distributional studies (Walker et al. 1987). This has resulted in an unclear picture of the actual abundances and distributions of P. clathratus during its planktonic phase. This ambiguity typifies current understanding of kelp bass early life history. Butler et al. (1982) described the developmental stages of the kelp bass from egg to juvenile using specimens reared in the lab and caught in the field, while Carr (1989, 1994) studied the effect of macroalgal assemblages on the recruitment of post-larval kelp bass to the nearshore benthic habitat. Despite these studies,

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however, wide gaps still remain in our knowledge of the period between hatching and settlement, knowledge which is important to the intelligent management of the kelp bass fishery.

Otoliths provide a record of the early life history of individual fish from which information not only on age, but also on temporal distribution of spawning (Mid- daugh 1981), growth (Geffen 1982; Volk et al. 1984), larval duration and the timing of settlement (Victor 1982; McFarland et al. 1985) can be obtained. Because a number of studies have reported instances of non-daily growth ring deposition (Taubert and Coble 1977; Neilson and Geen 1985; Bailey and Stehr 1988), it is imperative to validate the daily deposition of growth rings for each species studied, and to standardize the treatment of confounding factors such as sub-daily rings (Fowler 1989). The purpose of this study was to use information derived from otoliths to characterize the early life history of the kelp bass. More specifically, the objectives of this project were to: 1) determine the onset of otolith ring deposition and validate its daily periodicity in kelp bass larvae, 2) estimate average daily growth for settled young-of-the-year (YOY) fish caught in the field, 3) back-calculate birth dates and determine temporal spawning patterns with relation to seasonal and lunar periodicity, 4) estimate average age- and length-at-settlement for larvae, and 5) look for any sign of slowed growth (as evidenced by a change in daily ring width) due to delayed settlement.

Methods

Validation of Daily Ring Deposition

In the summer of 1991, a laboratory experiment was conducted to determine the onset and daily periodicity of sagittal ring deposition in kelp bass larvae. Fertilized eggs of known spawn date (from adults spawned in the lab) were hatched and the larvae reared in 70 L seawater tanks under shaded natural lighting and a mean temperature of 19.6°C (range 19.0°C–20.5°C).

Larvae were reared on a diet of rotifers, which were maintained at a mean concentration of 2000–3000 rotifers/L of seawater in the 70 L tanks for the duration of the experiment. A daily sample of ten larvae from a 28 July spawn were collected on days 1, 2, 3, 4, 5, and 9 after hatching and preserved in 70% alcohol. Larvae from an August 8th spawn were kept under identical conditions but left to grow out until after metamorphosis. Because of a mass mortality in the second week, the only sample obtained from this spawn consisted of three fish collected 18 days after hatching. Sagittae from each lab reared larva were extracted and mounted on slides as described under Otolith Extraction and Preparation. No further preparation was needed, and the sagittae were viewed under oil immersion at 1000X. Their growth increments were counted and a regression line constructed to test whether there was a significant deviation from the expected age/ring ratio of 1:1.

For the purposes of this study, a daily growth ring (or increment) was defined as one hyaline and one opaque band, and increment widths were measured from the inner edge of one opaque band to the inner edge of the next (Geffen 1982). Daily and subdaily increments were differentiated using the criteria established by Campana (1984).
Field Collection

Post-settlement kelp bass were collected from drift algae on soft bottom habitats at 19 different stations in the southern California Bight during the summers of 1989–1990 (Fig. 1). At each station, four 5 min benthic tows were taken at 5 m and 10 m depths using beam trawls deployed from two 5.2 m Boston Whalers. The beam trawls had a horizontal opening of 1.6 m and a vertical opening of 0.34 m. The netting of the trawl consisted of 3 mm mesh in the wings and 2 mm knotless mesh in the codends.

In 1989, four mainland and eight island stations were sampled once a month from May through August (Fig. 1). Sampling involved 96 tows per month (except in May, when only 80 tows were made; weather conditions prevented sampling at the Santa Rosa stations), for a total of 386 tows.

In 1990, eleven mainland stations were targeted from July through September (Fig. 1). Of these eleven, nine were sampled at 5 m and 10 m depths, while the shallow embayment stations of Mugu Lagoon and Alamitos Bay were sampled only at the 5 m depth. Due to the silt bottom at these last two stations, it was necessary to sample with a 2 m otter trawl, rather than the beam trawl used for the rest of the study. The same otter trawl was used to sample Marina Del Rey. Sampling in 1990 involved 80 tows per month (except in August, when only 72 tows were conducted because the Marina Del Rey station was omitted), for a total of 232 tows.

Specimens of kelp bass from individual trawl catches were sorted, identified, and frozen on dry ice for transport to the laboratory.
Otolith Extraction and Preparation

In the laboratory, frozen kelp bass were thawed, remeasured to the nearest 0.01 mmSL using digital calipers, and weighed to the nearest 0.1 g wet weight on a Mettler PE3000 precision scale. Using a Wild dissecting microscope with polarizing filters, the three sets of otoliths (sagittae, lapilli, and asterisci) from settled fish were extracted and mounted medial side down on standard microscope slides using a cyanoacrylate (Superb) medium. Preliminary grinding tests proved the sagitta to be the best otolith for ring visibility, and only these otoliths were used for the remainder of the study. Once mounted, the sagittae were ground and polished on a sagittal plane using 40, 15, 12, 3, and 1 micron 3M lapping films and a special grinding platform devised by Jensen (1990). Each grade of lapping film was used successively in descending numerical order until increment rings could be clearly seen from the focus to the outer edge of the otolith using a light microscope.

Otolith Counts and Increment-Width Measurements

After grinding, all sagittae were viewed under oil at 400X on an Olympus BH2 microscope fitted with an Olympus BH-DA Camera Lucida drawing attachment. This superimposed the image of the otolith over a Jandel 2210 Digitizing Board interfaced with a personal computer. Used in conjunction with the Sigmascan software from Jandel, this system made it possible to simultaneously count the number of rings on each sagitta and determine their widths to the nearest 1 micron. Increment counts and widths were recorded for each sagitta using the digitizing board and a moveable puck by following an eyepiece crosshair superimposed on the otolith's image. Otoliths were not viewed at a higher magnification so that the entire length of the otolith could be surveyed without having to move the microscope stage, which would have interrupted the counts and may have introduced greater errors in accuracy and/or precision. To reduce bias, sagittae were assigned numbers and then counted at random, without knowledge of prior counts. Each sagitta was counted and measured on three separate occasions, and the resulting means were used to back-calculate birth dates, construct growth curves, and compile increment-width profiles for each fish. All sagittae were counted along the best visible axis. The posterior long axis was the most commonly counted axis, since it consistently displayed the clearest growth rings. For standardization, only the otoliths measured along this axis were used to construct increment-width profiles.

A two stage approach was used to determine age-at-settlement for those fish whose otoliths provided increment-width data. First, settlement checks and secondary primordia were visually identified on individual sagittae using the definitions in Victor (1982). Second, increment widths were plotted as a function of age for each individual otolith. Marks were then placed on the resulting increment graphs to indicate the age at which the settlement check occurred for each fish; visible settlement checks could thereby be used to identify any change in increment widths that might be associated with settlement. The resulting graphs were then used to determine the age-at-settlement for each fish.

In the few cases where secondary primordia were found, their day of appearance was noted, since they have been associated with the onset of metamorphosis.
and settlement in some flatfish (Koutsikopoulos et al. 1989; Sogard 1991; Toole et al. 1993).

The increment-width graphs were also used to investigate the possibility of delayed settlement. Following Cowen (1991), the graph of each individual fish was scrutinized for any sudden changes in increment widths that would allow the profile to be subdivided into pre-competent, post-competent, and post-settlement stages. Linear regressions were then fitted to the pre- and post-competent stages and their slopes compared by one-way analysis of covariance (ANCOVA) to confirm any significant drop in increment width (and presumably fish growth) that would be indicative of a delayed settlement phase.

An estimate of the length of post-larval fish at settlement was made by averaging the length of those YOY kelp bass determined to have settled just prior to capture.

Statistical Analyses

All descriptive statistics and linear regressions were generated using the Axum software (Trimetrix Inc., Seattle, Washington) package for personal computers. Analyses of variance (ANOVAS) and one-way analyses of covariance (ANCOVAS) were generated using the Complete Statistical System (Statsoft Inc., Tulsa Oklahoma).

Results

Laboratory Validation

Hatchery-reared larvae emerged approximately 36 hours after fertilization, and yolk sac absorption was complete by the third day after hatching. Sagittal ring counts from the 24 collected larvae were plotted against the age (days post-hatching) of the fish, resulting in the linear regression \( \text{Age (days)} = 1.82 + 0.97 \text{ (ring count)} \) \( r = 0.99, P < 0.01 \) (Fig. 2). Ring deposition began on the third day after hatching and corresponded with yolk sac absorption. Two days were therefore added to all subsequent ring counts used for aging in this study. A one-way analysis of covariance (ANCOVA) indicated no significant difference \( P > 0.05 \) between the slope of the regression line (Fig. 2) and the expected slope of 1/1 (one ring per day), thereby validating the daily periodicity of ring deposition in kelp bass larvae. However, because none of the larvae survived to the settlement stage, the continued daily deposition of increment rings after metamorphosis and settlement must be assumed.

Length-Frequency Distributions of Kelp Bass Catches

A total of 111 settled young-of-the-year (YOY) and older juvenile kelp bass were taken during the years 1989–1990. Length-frequency distributions for the two sampling years were highly skewed to the left (Fig. 3). Back-calculated spawn dates suggest that spawning does not begin until May of each year (see results below). Assuming a May first start to the spawning season, and an average daily growth rate of 0.6 mm/day (see results below), one can conservatively assume kelp bass smaller than 25 mmSL in June, 50 mmSL in July, 75 mmSL in August, etc., to be YOY spawned that season. Using these estimates, YOY kelp bass made up 56% \( (N = 63) \) of the combined 1989–1990 kelp bass catch, with 27% of these
1991 Lab Validation
Regression of Ring Counts and Known Ages

\[ (\text{Age}) = 1.82 + 0.97(\text{Ring Count}) \]

N=24

- expected regression
- experimental regression

No. of Increments

Fig. 2. Results of the 1991 laboratory validation experiment comparing the experimental regression of age based on otolith ring counts (solid line, \( r = .99 \)) to the expected regression (dashed line). Analysis of covariance (ANCOVA) showed no significant differences between the lines. Values next to data points indicate the number of otoliths which yielded that result.

being newly settled fish \( \leq 10 \text{ mmSL} \) which had probably settled less than a week prior to capture. This bias towards smaller fish is probably a result of the sampling gear, which may have been slow enough for larger juvenile and adult fish to avoid. However, the presence of older juvenile fish up to 200 mmSL in the 1989

1989-90 *Paralabrax clathratus*
Length Frequency Distribution

Fig. 3. Length frequencies (grouped in 5 mmSL increments) for all kelp bass sampled in 1989–1990.
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sample (Fig. 2) also raises the possibilities that fish settling at many of our stations did not survive to grow larger, or migrated out of these soft bottom areas to more preferred habitats soon after settlement. Comparison of captured fish length-frequency distributions between the two types of nets (otter and beam trawls) used in 1989 showed no differences between the two gear types (two sample t test, $P > 0.2$). In 1989, 83 settled YOY and older juvenile kelp bass were captured ranging in size from 8.5 mm to 200 mmSL (mean = 64.5 ± 52.41 mm SD). Settled YOY fish ($\leq 10$ mmSL) made up 41% of the catch, while smaller percentages of one and two-year-old juveniles were clustered around 90 mm and 180 mmSL, respectively (Fig. 3). Newly settled fish made up 38% of the YOY catch.

In 1990, 28 settled YOY kelp bass were captured ranging in size from 9.3 mm to 16.4 mmSL (mean = 11.38 ± 1.8 mm SD). Newly settled fish made up 29% of the total catch, and no older juveniles were captured (Fig. 3).

Age and Growth

Otolith counts taken from settled YOY kelp bass sampled in 1989–1990 were used to determine age-length relationships and estimate growth rates for fish caught in the field. A linear regression of growth was used for samples of both years.

Of the 34 settled YOY kelp bass caught in 1989, 16 had otoliths suitable for counting after preparation. These fish ranged in size from 8.6 mm to 39.5 mmSL, and their length-age relationship was represented by the linear regression (length (mm SL)) = 14.49 + 1.69(age (days)) ($r = .96, P < 0.01$). The average daily growth predicted by the model for fish in this size range was 0.59 mm/day.

Of the 28 settled YOY kelp bass caught in 1990, ranging in size from 9.3 mm to 16.4 mmSL, 20 had otoliths suitable for counting after preparation. Their length-age relationship was described by the linear regression (length) = 10.90 + 2.04(age) ($r = .92, P < 0.01$), and the average daily growth predicted was 0.49 mm/day.

Results of a one-way ANCOVA indicated no significant difference between the two regressions ($P > 0.05$), allowing the two sample years to be combined. This resulted in the linear length-age regression (length) = 14.67 + 1.69(age) ($r = .96, P < 0.01$) and an average daily growth of 0.59 mm/day (Fig. 4).

Back-Calculation of Birth Dates

Using the combined age-length regression from above, the ages of all 62 settled YOY kelp bass sampled in 1989–1990 were estimated and used to back-calculate their birth dates. Graphed by month, the results indicated a pattern typical of a summer spawner (Fig. 5), although apparent spawning peaks should be viewed with caution considering the limited number of specimens. Spawning in 1989 was low in May, increased sharply in June, and then decreased somewhat in July. Because no sampling was done in September of 1989, August spawning could not be characterized. Back-calculated birth dates in 1990 produced a pattern similar to 1989, with spawning beginning in June and rising steadily through July and August.

Back-calculated birth dates were also used to investigate any evidence of a lunar influence on spawning periodicity. Only those fish with otolith counts were used for this analysis ($N = 36$). A frequency distribution was constructed by
grouping birth dates in 7-day intervals centered on the four phases of the moon. In 1989 peaks occurred around the full and first quarter moons (Fig. 6A), while peaks in 1990 centered around the full and third quarter moons (Fig. 6B). The greatest number of individuals were spawned in the seven days around the full moon in both 1989 and 1990, with lesser numbers around the first quarter in 1989, and the third quarter in 1990 (Fig. 7). Although these results suggest a

![Graph of 1989-90 Paralabrax clathratus Combined Length/Age Regression](image)

Fig. 4. Combined age-length regression for YOY kelp bass collected during the summers of 1989 and 1990 ($r = .92$). Dotted lines represent 95% confidence limits.

![Graph of 1989-90 Paralabrax clathratus Back-Calculated Spawn Dates](image)

Fig. 5. Back-calculated birth dates by month for YOY kelp bass collected from 1989–1990. Ages were calculated from the combined 1989–1990 age-length regression (Figure 4).
relationship between kelp bass spawning and the lunar cycle, a larger sample size and a time series analysis are needed to bring this relationship into sharper focus.

**Timing of Settlement**

Graphs of mean daily increment width were constructed for 22 otoliths. Of the 22 otoliths profiled, 12 exhibited settlement checks or secondary primordia which were visible under light microscopy (Fig. 7). The mean age of settlement for these 12 individuals was estimated at 30 days (±2.6 days SD), with a range of 27–36 days. In the ring-width profiles for these 12 fish (see Fig. 8 for examples), the age at which these checks occurred corresponded closely with a peak in increment width the day before settlement, a phenomenon previously linked with the time of settlement in a number of fish species (Victor 1986; Cowen 1991). Using this information, the time of settlement for eight of the remaining ten increment profiles was estimated by determining the day on which this increment width peak occurred. From these data the average age at settlement for 20 of the 22 fish profiled was estimated to be 30 days (±2.7 days SD), with a range of 25–36 days which was virtually identical to the previous estimate for the 12 fish. The two remaining profiles exhibited no distinct increment width jumps, and were omitted from the analysis.

Averaging the mean daily increment widths for all 22 fish indicates that incre-
ment width increases steadily from approximately 3 microns during the first few days of larval life to 8 microns just prior to an age when settlement occurs (Fig. 9). This suggests that growth rates were accelerating up to the point when larvae became competent to settle. Settlement checks in individual fish were generally evident after increment widths greater than approximately 10 microns were reached. Post-settlement widths leveled off at about 15 microns and remained relatively constant throughout the remaining days of the oldest fish (age = 47 days), suggesting that growth rates were also constant and no longer accelerating as they were in the larval phase.

Qualitative examination of the increment width profiles revealed four fish exhibiting patterns characteristic of delayed settlement (Fig. 10). The boundary between the pre- and post-competent stages was identified as a peak and subsequent decrease in increment width occurring some time before settlement (Cowen 1991). These competency peaks for the four fish suspected of delayed settlement corresponded with the earliest ages-at-settlement reported above, while the actual settlement age for these same fish fell, predictably, as the high end of the range.

Comparison of the pre- and post-competent regressions for each profile by one-way ANCOVA revealed significant differences ($P < 0.05$) between the slopes in only one of the four fish tested (Fig. 10D). These results suggest that these four
Fig. 8. Representative graphs showing the correspondence of settlement checks (closed triangles) and secondary primordia (open triangles) with an increase in daily increment width. (A) 1989 43rs = right sagitta from the forty-third YOY kelp bass collected in 1989, (B) left sagitta from the sixty-fourth YOY kelp bass from 1989, (C) left sagitta from the twenty-third YOY kelp bass collected in 1990, (D) right sagitta from the twenty-seventh YOY kelp bass collected in 1990. Bars represent ± one standard error (SD) around the mean.

Fig. 9. Mean daily increment widths for 1989–1990 YOY kelp bass over the first 48 days of life. Three readings were averaged for each of 22 fish for a total N = 66. Numbers above and below line indicate decreasing sample sizes as younger fish dropped out of the calculations. Bars represent ± one standard error around the mean.
Possible Examples of Delayed Settlement

Fig. 10. Examples of increment width profiles from four YOY kelp bass which may have undergone delayed settlement. (A) 1989 50RS = right sagitta from the fiftieth YOY kelp bass collected in 1989, (B) left sagitta from the forty-second YOY kelp bass collected in 1989, (C) left sagitta from the twenty-ninth YOY kelp bass collected in 1990, (D) right sagitta from the seventeenth fish collected in 1990. Settlement check = closed triangles. Bars represent ± one standard error around the mean.

fish may have undergone a slow-growth phase which delayed their time of settlement, although quantitative confirmation was difficult to obtain.

The smallest settled YOY kelp bass captured was 8.59 mmSL and determined to be 31 days old from otolith counts. To determine the average size at settlement, fish between the ages of 25–36 days (the range of settlement ages determined earlier) were presumed to have been captured immediately after settlement. These fish ranged in size from 8.59–12.71 mmSL and averaged 10.3 mmSL.

Discussion

Reproduction and Spawning

Data from back-calculated spawn dates (Fig. 5) show the pattern of a summer spawner, although the time of peak spawning activity could not be determined due to logistical limits on the duration of sampling each summer. Studies characterizing the spawning season of kelp bass on the basis of seasonal gonad maturation (Smith and Young 1966) and the presence of larvae from the three species of Paralabrax in the ichthyoplankton from the southern Californian Bight (Walker et al. 1987), indicate that spawning activity begins in May, peaks in August or September, and ceases by October. Recent work by Oda et al. (1993) suggests
that kelp bass are late afternoon spawners, and may be capable of daily spawning during their reproductive season.

Although the reproductive behavior of kelp bass has not been thoroughly studied, adults of the species are known to form offshore spawning aggregations (Feder et al. 1974). Johannes (1978) proposed that similar strategies in tropical fishes may serve the dual purpose of enhancing larval dispersion while avoiding nearshore benthic reef predators which might feed on eggs and small larvae. One danger incurred by offshore spawning is the possibility of larvae being swept out to sea and lost. Parrish et al. (1981) investigated the effects of the California Current and upwelling events in central California on the distribution patterns of marine fishes. They found that spawning activities in a large number of species coincided with the net onshore flow characteristic of central California waters in the late winter and early spring. These onshore currents would tend to transport the eggs and larvae of pelagic spawners back toward shallower waters. Internal waves may play a similar role in the onshore transport of fish larvae in the neuston (Shanks 1988). Transforming larvae of California halibut, Paralichthys californicus, have been shown to migrate from bottom to surface waters at night (Kramer 1990), and may be utilizing internal waves to reach nearshore nursery grounds (Moser and Watson 1990). Recovery of drift bottles released less than twenty miles offshore in the southern California Bight is greatest from March through October (Schwartzlose 1963), indicating that onshore flow is high during the summer months when kelp bass spawning occurs.

Back-calculated spawn dates also suggested a relationship between spawning activity in kelp bass and the lunar cycle (Figs. 6–7). Data from both years showed that spawning peaks coincided with the full moon. Spawning around the full moon has been widely documented for many tropical fish families, including two species of epinepheline serranids (Johannes 1978). Less is known regarding temperate serranids, but at least one species of sea bass from the mid-Atlantic Bight, the gag (Mycteroperca microlepis), has been shown to spawn around the full and new moons (Keener et al. 1988). More important than the lunar cycle itself, however, may be its relationship to the tidal flux. Middaugh (1981) found that the Atlantic silverside, Menidia menidia, spawned during daytime flood tides on the full and new moons. The author suggested that spawning during incoming high tides may increase fertilization success. Conversely, some tropical species spawn in conjunction with out-going spring (new and full moon) tides to facilitate offshore transport and distribution of pelagic eggs (Johannes 1978). It is not known whether kelp bass spawning is correlated with spring or ebb tides, but the association between spawning and the full moon, in conjunction with the one month larval period, suggest that lunar and/or tidal cycles may play an important role in both the time of spawning and settlement in this species.

Validation of Increment Initiation and Daily Periodicity

The chronological sequence from fertilization to yolk sac absorption reported in the hatchery validation experiment are consistent with that found by Butler et al. (1982) for laboratory-reared kelp bass larvae. In addition, results from the validation study determined that initial sagittal ring deposition occurred on the third day after hatching, and corresponded with yolk sac absorption. This correspondence is common in marine fishes (Brothers et al. 1976; Victor 1982; Geffen
1982; Tzeng and Yu 1988), although onset of ring deposition has also been shown to begin prior to hatching (Radkte and Dean 1982) and at hatching (Brothers et al. 1976; Bolz and Lough 1988). Although ring deposition was found to be daily during the larval period, the failure to raise kelp bass past the settlement stage left open the question of continued daily deposition in juveniles. There is, however, little reason to believe that daily deposition would not continue past the larval stage.

**Daily Growth Estimates**

The use of otolith increments in the construction of growth curves assumes that daily deposition of rings is not interrupted by environmental or physiological factors. Some studies have shown non-daily ring formation under conditions of starvation (Bailey and Stehr 1988), elevated feeding (Neilson and Geen 1985), and abnormal photoperiod (Taubert and Coble 1977) and temperature regimes (Neilson and Geen 1985). Other studies on a variety of species, however, have shown no disruption of daily periodicity under varying conditions of these same factors (Maillet and Checkley 1990; Campana and Neilson 1982, 1985), although increment quality and width were often affected. The most serious challenge to the concept that daily growth rings are an accurate index of age comes from a study on larval herring, *Clupea harengus*, which found increment deposition to be less than daily in larvae exhibiting suboptimal growth rates (Geffen 1982). Despite these very real concerns, however, there is little reason to doubt the daily formation of increments in fish exhibiting adequate growth rates (see Campana and Neilson 1985 for review).

The estimated average daily growth rate from the combined 1989–1990 data presented here was 0.56 mm/day for fish less than 90 days old. Daily growth rates reported for other temperate eastern Pacific fishes range from 0.20–0.23 mm/day for settled YOY white seabass, *Atractoscion nobilis* (Franklin 1991), to 0.76–1.11 mm/day for settled YOY California halibut, *Paralichthys californicus* (Jensen 1990). Due to the limited age range of YOY kelp bass used to construct the growth curves in the present study, a linear regression was deemed adequate to describe the relationship between growth and age. It is assumed that this line would begin to flatten out as growth approached an asymptote during the late juvenile/adult stage, thus more closely resembling the von Bertalanffy growth model more commonly employed in growth studies. Increment analysis showed that ring width increased steadily until the time of settlement, after which point rings became more irregular and no longer exhibit a net increase in width (Fig. 10). Assuming a constant positive correlation with fish growth, this would result in an age-length regression that would appear exponential during the larval phase, linear for the early juvenile stage, and then begin to flatten out as the older fish grew more slowly.

**Age at Settlement**

Settlement checks are a common means used to determine the duration of the planktonic phase of fish species with pelagic larvae (Campana and Neilson 1985; Victor 1986, 1991; Wellington and Victor 1989). Such checks are presumed to be a result of stress associated with a transition from a pelagic to a demersal habitat, although direct evidence of this is scarce (Campana and Neilson 1985).
Formation of a settlement check has been validated, however, for at least one family of fishes, the labrids (Victor 1982; Cowen 1991). As mentioned before, changes in physiological and environmental conditions which may occur at metamorphosis and settlement have been associated with a change in otolith increment width. Settlement checks have also been shown to be associated with such changes in increment width (Fowler 1989, Cowen 1991), allowing for a way to double check the validity of visually identified settlement marks.

The average age-at-settlement reported in this study is comparable with the average settlement age of 35 days for white seabass, *Atractoscion nobilis* (Franklin 1991), and 28 days for California halibut, *Paralichthys californicus* (Jensen 1990). There is often, however, a large range of variation among species, even within families. Victor (1986), for example, reported a range of mean ages from 15 to 121 days among one hundred species of labrids, while Brothers et al. (1983) found a range of means between 19 and 74 days among twelve families of fishes from the Great Barrier Reef.

The average length at settlement of kelp bass of 10.3 mmSL reported here is somewhat overestimated, because the fish used in the calculations were assumed to have settled just prior to capture. The two events may actually have been separated by several days, thus adding any fish growth during these intervening days to the estimate. The actual average may be closer to 9 mmSL, a value somewhat smaller than that of 11 mmSL found by Butler et al. (1982) for metamorphosing laboratory-reared kelp bass larvae.

Whether the larvae of fishes are capable of playing an active role in determining where and when they settle out of the water column has received much attention in recent years. Boehlert and Mundy (1988) list studies on a variety of fish taxa which show that the immigration of larvae into estuarine nursery grounds involves an active behavioral process. Carr (1994), however, showed that the correlation between settlement of kelp bass larvae and the presence of algae was probably passive in nature. Regardless, the ability to delay settlement until a suitable habitat is reached, either by active or passive means, could prove valuable in areas where such habitat is scarce or patchy in distribution. The ability of larvae to delay metamorphosis and settlement, especially in the absence of suitable settlement cues, has been documented for a variety of invertebrate taxa (see Jackson and Strathmann 1981 for review). This delay is often correlated with a marked decrease in growth, presumably due to the reduced survival of larger larvae in the plankton (Scheltema 1971). Precompetency is the term used to describe the period of development up to the point when the larvae is physiologically able to settle, while postcompetency describes the period of reduced growth between competency and settlement (Jackson and Strathmann 1981). Evidence for similar mechanisms in teleosts have been reported in at least two cases (Victor 1986; Cowen 1991). Through field collections and subsequent otolith analysis, Victor (1986) showed that some post-larval bluehead wrasse, *Thalassoma bifasciatum*, went through a slow growth phase and concomitant decrease in increment width prior to settlement. His results indicated that fish exhibiting a longer larval stage grew more slowly just prior to settlement. Cowen (1991) reported similar results for the California sheephead, *Semicossyphus pulcher*, in which time of settlement was more closely correlated to fish length than age. Species in both studies exhibited a wide range of settlement ages (38–78 days and 37–78 days, respectively) com-
pared to that reported here for YOY kelp bass (25–36 days). In view of this small range of values, it is not surprising that relatively few cases of delayed settlement were identified. Only four possible examples were found in the increment-width profiles of 22 fish, as opposed to 10 out of 11 cases found by Cowen (1991). This suggests that there may be some physiological inflexibility in the duration of the larval phase in kelp bass, although these results must be viewed with caution due to the small sample size.

The results of this study help to characterize the early life history of the kelp bass and the environmental factors that may play a role in determining the abundance and distribution of YOY that will eventually find their way into adult stock populations. The effects of lunar phase and tide on spawning and settlement, the limiting effect of larval availability, and the importance of various environmental cues in the settlement of recruiting larvae, are all areas ripe for future research. Such research is crucial if the recreational fishery for this popular sport fish is to be properly managed.

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