GROWTH AND COHORT DYNAMICS OF LARVAL PACIFIC HAKE (*MERLUCCIUS PRODUCTUS*)

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ABSTRACT

Size-specific mortality rates and stage-based models predict that fast-growing fish larvae experience lower mortality than slow-growing larvae. We provide empirical evidence that supports this hypothesis, by comparing otolith size-at-age of young larval Pacific hake (*Merluccius productus*) with back-calculated otolith size-at-age from older larvae collected about 45 days later. The mean back-calculated size-at-age of the larvae surviving beyond 45 days was greater than the average population growth rate of younger larvae sampled earlier. Thus hake larvae with slow growth rates appear to have suffered higher mortality than larvae with faster growth rates.

INTRODUCTION

Size-selective mortality is a common topic in fishery biology, but most investigations focus on the effects of fishing (Parma and Deriso 1990; Rijnsdorp and Jaworski 1990; Buijse and Houthuijzen 1992; Hanson and Chouinard 1992). Correlations of body size and mortality indicate that larger organisms have lower mortality rates (Peterson and Wroblewski 1984). Individual-based models (Lomnicki 1978; DeAngelis et al. 1993; Cowan et al. 1996) and stochastic stage-based models (Lo et al. 1995) also predict that faster-growing individuals have higher survival rates.

Although size-selective mortality is believed to be a major factor in larval fishes (McGurk 1986; Houde 1987; Anderson 1988; Miller et al. 1988; Pepin 1988, 1989, 1991; Bailey and Houde 1989; Beyer 1989; Cowan et al. 1996), few field data exist to support this hypothesis. Both starvation and predation are size dependent (Rosenburg and Haugen 1982; Margulies 1993). Smaller larvae are more vulnerable to starvation because they have smaller energy reserves to withstand food deprivation (Beyer and Laurence 1980; Rosenburg and Haugen 1982; Margulies 1993). Smaller larvae are more vulnerable to predation (Shepard and Cushing 1980; Bailey and Batty 1983; Bailey 1984; Purcell 1986). Size-selective vulnerability to predation in hake larvae has been demonstrated in the laboratory (Bailey 1984). However, Brown and Bailey (1992) were unable to demonstrate size-selective mortality in walleye pollack larvae in the field.

Some evidence for size-selective mortality has been reported for juvenile fishes. Post and Prankevicius (1987) found evidence for size-selective mortality in one of two

populations of yellow perch (*Perca flavescens*) on the basis of otolith growth history. West and Larkin (1987) reported evidence for size-selective mortality in juvenile sockeye salmon (*Oncorhynchus nerka*) in Babine Lake, British Columbia. Their results were criticized by Mosegaard (1990) because the correlation between fish length and otolith length was too low for indirect selection on fish length to shift otolith sizes as much as was observed. Between-drainage differences in otolith size–fish size may explain West and Larkin's result (Mosegaard 1990). Fitzhugh and Rice (1995) could not reject the null hypothesis of no size-selective mortality when back-calculation variability was incorporated into simulations of juvenile southern flounder (*Paralichthys lethostigma*) growth. Size-selective mortality has been demonstrated for gulf menhaden (*Brevoortia patronus*) and king mackerel (*Scomberomorus cavalla*; Grimes and Isely 1996). Meekan and Fortier (1996) found selection for fast growth in larval Atlantic cod (*Gadus morhua*), and Campana (1996) found that year-class strength was correlated with faster growth of larval and juvenile Atlantic cod. Thus, although size-selective mortality is often incorporated in models, empirical evidence for this phenomenon in larval fish has only recently been reported.

Population dynamics of Pacific hake are characterized by large year classes separated by two to three years of poor recruitment (Dorn 1995). While the exact cause of this variability is unknown, the strength of an incoming year class is detectable in the first 1–3 months after spawning (Hollowed and Bailey 1989). Thus, growth rates may be critical to larval survival as well as in the dynamics of recruitment in the coastal stock of Pacific hake (Woodbury et al. 1995).

As part of an investigation on the recruitment of Pacific hake, we studied the growth of larvae during a 4-month period. To investigate whether hake larvae experience size-selective mortality, we compared the otolith size-at-age of young larval hake with repeated measures of otolith size-at-age of older larvae with the same back-calculated hatch dates collected in the same area approximately 45 days later.

METHODS

Larval hake were sampled on three cruises. During January 4–23, 1995, larvae were captured with a standard CalCOFI 1-m bongo net hauled obliquely between
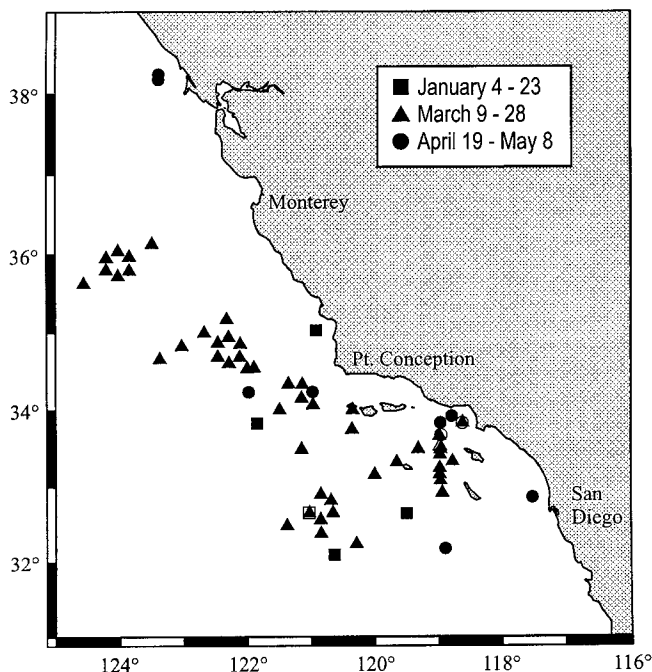
Figure 1. Locations of positive samples for Pacific hake (*Merluccius productus*) larvae during 1995 cruises: January (*squares*); March (*triangles*); and April–May (*circles*).

210 m and the surface. During March 9–28, 1995, larvae were collected with a standard CalCOFI 1-m bongo net and with a 1-m² multiple opening/closing net and environmental sensing system (MOCNESS) hauled obliquely between 300 m and the surface. During April 19–May 8, 1995, larger larvae were collected with a 10-m² MOCNESS hauled obliquely between 300 m and the surface. Samples were collected in the California Current between 32°5.1'N and 38°13.5'N and between 117°31.8'W and 124°33.1'W (figure 1).

Plankton samples from the bongo nets in January and March were preserved in 80% ethanol buffered with 20 millimolar tris(hydroxymethyl)aminoethane. Hake larvae were removed from the plankton at the shore laboratory and stored in 70% ethanol. Larvae collected with the 10-m² MOCNESS and bongo net in April–May were sorted at sea and preserved in buffered 80% ethanol.

To compare catch rates of hake larvae in the 505-micron-mesh, 70-cm bongo net and catch rates in the 3-mm-mesh, 10-m² MOCNESS, we compared the log of percent frequency of all hake larvae (N = 124,064) caught in the bongo during March and April from 1978 to 1986 to the log of percent frequency of hake larvae (N = 1,435) caught in March 1992 with the 10-m² MOCNESS. Catch rates were compared on the log scale to highlight any differences in the larger sizes.

Before removing the otoliths, we measured the standard length or length to the tip of the notochord of each larva to the nearest 0.1 mm with an ocular micrometer.

Otoliths were extracted with microprobes while the larva lay on a glass slide. After drying, the otoliths were fixed to the slide with the histological compound EUKITT.

Otolith increments were counted and measured with the technique of Methot and Kramer (1979). A high-resolution television camera mounted on a compound microscope projected the image of the otolith onto a monitor of a closed-circuit television system. Distance along a standardized path and the number of increments observed were recorded on a microcomputer interfaced to a video coordinate digitizer and television system. Data on average increment width were recorded and analyzed with a program that "counts" increments by evaluating the distance along the radius from the center to the outer edge of the otolith divided by average width at each radius (Methot 1981).

We counted increments on both sagittae whenever possible by placing nondrying immersion oil on the histological compound and using oil-immersion lenses of 40× and 63×. The sagittae had been mounted or remounted distal side up, and the increments were counted in a straight path from the focus to the tip of the rostrum on otoliths where the rostrum and postrostrum could be differentiated. For small larvae, where two of the three pairs of otoliths are nearly equal in size, and round, we selected two otoliths with the most visible increments, and counted in a straight line from focus to the edge of the otolith. When increments were difficult to see, we polished the otoliths with either 12- or 30-micron imperial lapping paper until the increments became visible. Widths were measured for two increments at a time along two transects for each otolith. One transect began at the focus and proceeded toward the outer edge, the other began at the margin and overlapped the first transect.

Since both otoliths may not have been recovered from each larva, results from left and right sagitta were tested to determine any bias. The percent agreement within ±1 day was 78.9, and the agreement within ±2 days was 93.8. Since the index of precision (Chang 1982) was 0.0142, results were average from both otoliths. If both otoliths were not recovered, we used the count for the single otolith.

The daily formation of otolith microincrements was validated by Bailey (1982). Hake larvae form the first increment 2–3 days after hatching (Bailey 1982). For the age in days, we used two more than the number of increments.

A Gompertz growth equation (Zweifel and Lasker 1976) was fitted to size-at-age data from the March and April–May cruises by means of nonlinear regression (figure 2). Because the variance was heteroscedastic, we used the reciprocal of the variance for each 10-increment segment to weight the regression.
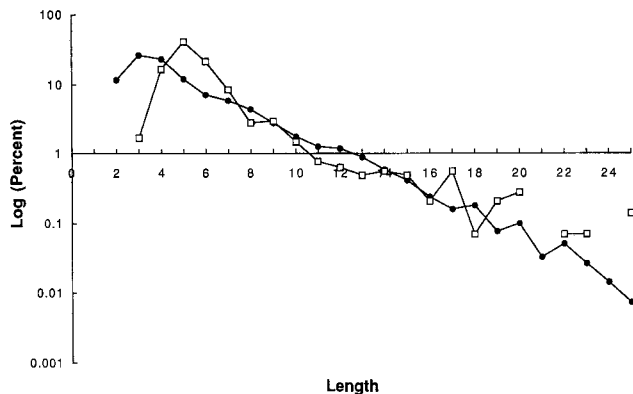
Figure 2. Percentage of Pacific hake (*Merluccius productus*) larvae in 1-mm size categories collected by 70-cm bongo nets (*filled circles*; N = 124,064) and 10-m² MOCNESS (*open squares*; N = 1,435).

Hatch dates were back-calculated from the age and the date of capture. We compared the hatch date distributions from the March and April–May cruises to confirm that back-calculated growth rates were compared to size-at-age of larvae hatched during the same part of the spawning season (within-season cohort).

Otolith size was measured from the focus to the maximum radius of the otolith (rostrum). An allometric relation was fitted with geometric regression (Ricker 1973).

To test whether surviving larvae were larger at size than the population, we compared otolith size-at-age from larvae collected during the March cruise to otolith size-at-age from the April–May cruise by using repeated measure analysis of covariance (Chambers and Miller 1995). Body-length-at-age trajectories of surviving larvae were back-calculated from size at hatching to size at capture and plotted with size-at-age from the March larvae for illustrative purposes. Since few late larvae were collected north of Point Conception during the April–May cruise (figure 1), only larvae collected south of Point Conception from both the March and April–May cruises were included in the comparison. Large larvae, whose otoliths had begun to form secondary primordium, were also excluded.

RESULTS

The catch rates of the 70-cm bongo net and 10-m² MOCNESS differ greatly for the smallest larvae (figure 2). The bongo net catches many more 2- and 3-mm larvae than the MOCNESS because the smaller larvae are extruded through the 3-mm mesh of the MOCNESS. Larvae of 8 to 16 mm are represented equally in the catch of the two nets. In the size classes larger than 16 mm, the numbers of larvae are few, and the differences may represent sampling error.

The size-at-age of early larvae (≤20 d) is not significantly different for the January and March cruises
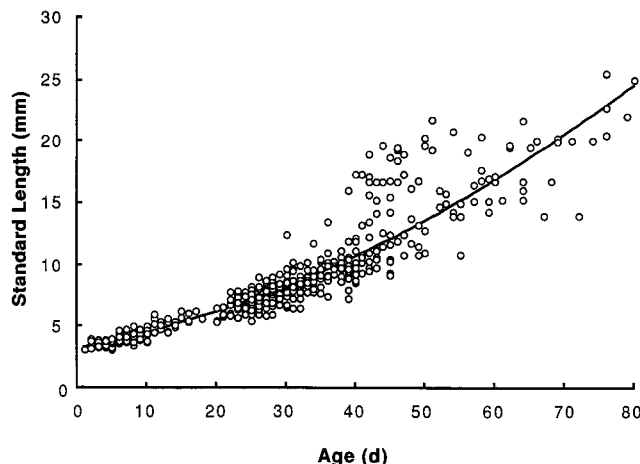

Figure 3. Size-at-age of Pacific hake (*Merluccius productus*) larvae. The Gompertz growth curve was fitted to all data. See text for details of fitted line.
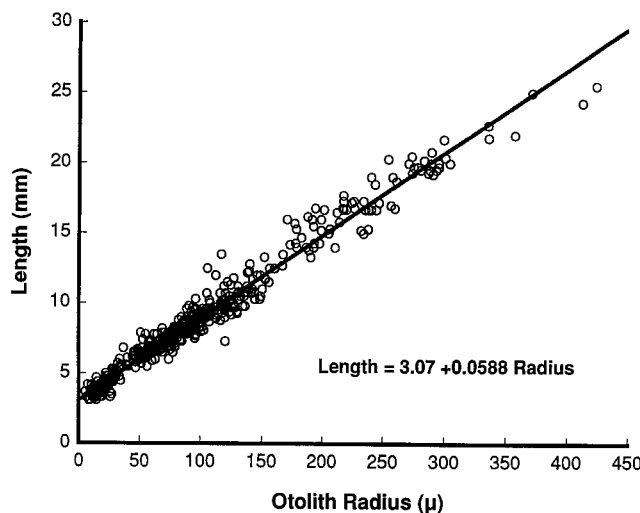

Length = 3.07 +0.0588 Radius

Figure 4. Allometric relation of body length and otolith radius of Pacific hake (*Merluccius productus*) larvae. Fitted line is geometric regression.

(ANCOVA, $P > .05$). Therefore, we pooled all specimens from both cruises. The growth rate is described by the linear equation

$$L = 3.02 + 0.156 \star t$$

where L is body length in mm and t is time in days ($N = 187$, $R^2 = .74$, $p = .001$).

The growth rate of hake larvae up to 89 days is best described by the Gompertz equation:

$$L = L_0 e^{(a(1-e^{(-gt)}))}$$

where L is standard length, t is age in days, and L_0 is length at hatching (figure 3). For hake larvae from March and April–May 1995, $L_0 = 3.16$, $a = 3.64$, $g = 0.0101$. The residual mean square of this regression is 1.00 ($r^2 \cong 0.76$).

Fish size is linearly related to maximum otolith radius (figure 4). Residuals from this regression show no trend
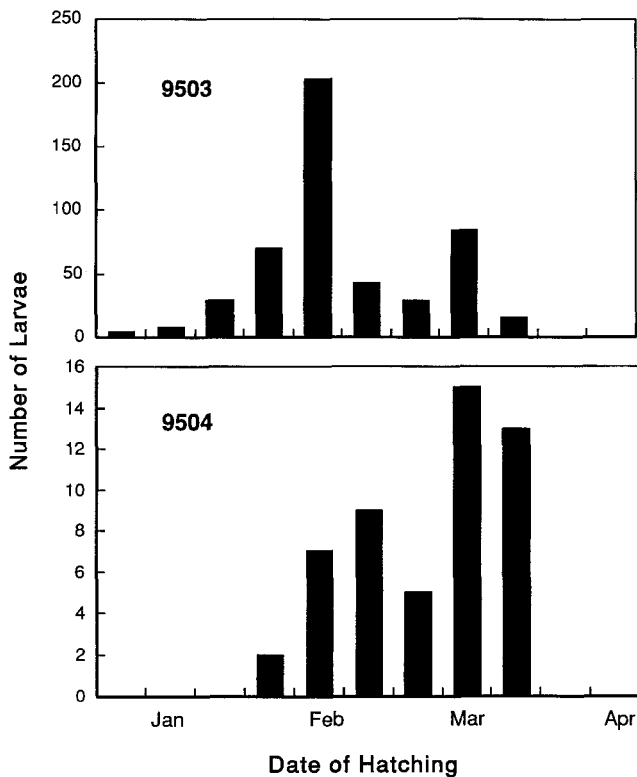
Figure 5. Hatch date distributions of Pacific hake (*Merluccius productus*) larvae for cruises 9503 and 9504. Histogram is based on ten-day intervals beginning January 1, 1995.

with otolith size (figure 5). A step-wise linear regression indicates that otolith size explained 96% of the variance of fish size (table 1). Variance in age accounts for only 3% of the variance in fish size (table 1). The geometric mean regression of length (*L*) on otolith radius (*R*) is:

$$L = 3.07 + 0.0588 \star R$$

The distributions of hatch dates are similar for the March and April cruises (figure 6). Both distributions are bimodal, with a peak in mid-February and a second peak in mid-March. The relative decrease in the first peak from the first cruise to the second cruise may be due to the greater total mortality of these older larvae. An alternative interpretation would be that the age of the older larvae has been underestimated. This would both shift the hatch date peak and overestimate the growth

TABLE 1
Step-Wise Linear Regression of Fish Length
on Otolith Radius and Age

Variable	Coefficient	Standard error	Standard coefficient	P(2-tail)
Constant	3.007	0.058	0.000	0.000
Radius	0.057	0.001	0.956	0.000
Age	0.009	0.004	0.034	0.047

rates of the survivors. The clarity of daily increments in larval hake otoliths makes that interpretation unlikely.

Mean otolith size-at-age from larvae caught in April–May is significantly different from otolith size-at-age from larvae collected in March (RM-ANCOVA $P < 0.000$). Back-calculated size-at-age trajectories of the April–May surviving larvae are plotted with size-at-age of March larvae in figure 6 to illustrate the difference. These differences in size-at-age indicate that slow-growing larvae survive less well than fast-growing larvae.

DISCUSSION

In order to demonstrate that survivors have higher growth rates than larvae sampled earlier, it is necessary to show that neither net selected for faster- or slower-growing larvae. The greatest difference in the catch curves of hake larvae in the two nets is in the smallest larvae (figure 2). Although there is significant extrusion of 3- and 4-mm hake larvae in the 10-m² MOCNESS, from 5 to 16 mm the catch rates of the two nets are virtually the same. Comparing the catch rate of larvae larger than 16 mm is difficult because of the few larvae represented in the 10-m² MOCNESS samples. To date, only 1,435 hake larvae have been collected with the MOCNESS; thus one larvae represents .07 percent. Because 124,064 larvae have been collected in the bongo net during the months of March and April since 1978, the bongo catch curve is accurate for larvae up to 25 mm. Since the 10-m² MOCNESS adequately samples larvae as small as 5 mm (figure 2), it is unlikely that the MOCNESS undersampled slower-growing individuals.

Size-at-age and growth rates of young hake larvae (≤20 d) did not differ in January and March and were almost identical to those reported by Bailey (1982). Thus the early growth of hake larvae may vary little from season to season. Size-at-age of field-collected larvae up to 80 days are also similar to those reported by Bailey (1982). However, Woodbury et al. (1995) have found significant interannual variation in growth rates of larvae older than about 80 days.

Size-selective mortality in larval fish has been an accepted fact since Houde (1987) speculated on its role in recruitment variability. Many models have incorporated size-selective mortality (Lo et al. 1995; Cowan et al. 1996), but direct empirical evidence for this phenomenon remains elusive. Many investigators have been unable to detect this phenomenon in the field, perhaps because of problems with back-calculation (Brown and Bailey 1992; Fitzhugh and Rice 1995). In this study, however, we used otolith size-at-age rather than back-calculated growth to detect size selection.

Back-calculated growth rates from larvae that have survived for at least a month are, however, significantly faster than those of the cohort. This is strong evidence
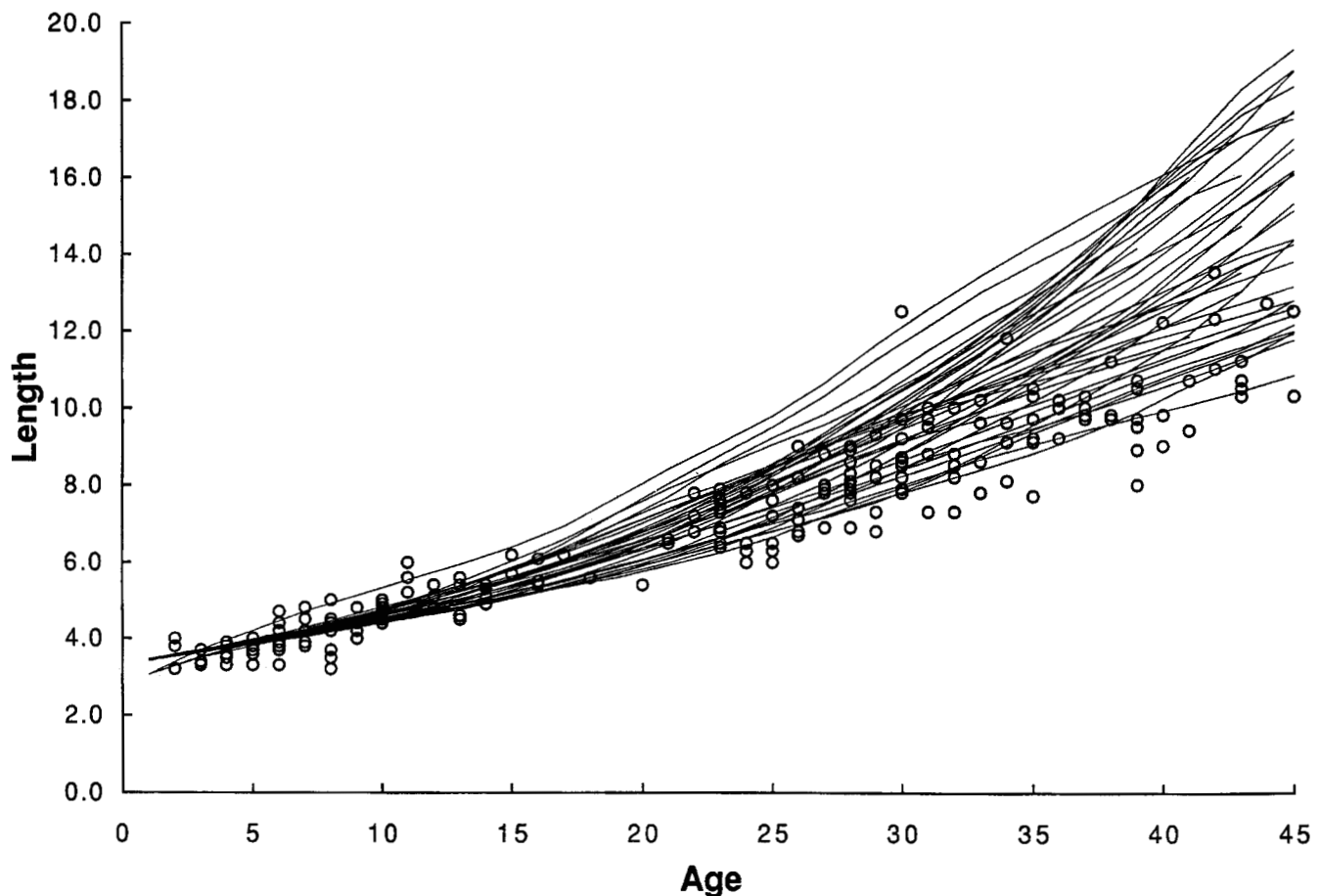
Figure 6. Size-at-age (*circles*) of 207 Pacific hake larvae collected south of Point Conception, and growth trajectories (*lines*) of larvae collected about 45 days later in the same area.

for size-selective mortality. The larvae with the fastest growth rates are the ones that survive. These data support conclusions of stochastic stage-based models (Lo et al. 1995) and individual-based models (Cowan et al. 1996).

Size-selective mortality in the early life history of fishes has also been demonstrated for fish eggs (Rijnsdorp and Jaworski 1990). In the case of fish eggs, mortality (predation) can be either neutral or positive for smaller eggs. In the case of fish larvae, mortality (predation and starvation) can be positive for smaller, slower-growing individuals. It is also conceivable that predation can be positive for larger, faster-growing, and more active individuals. This is certainly true for juveniles entering a fishery (Parma and Deriso 1990; Rijnsdorp and Jaworski 1990; Buijse and Houthuijzen 1992; Hanson and Chouinard 1992). Faster-growing, more active larvae may also be vulnerable to higher predation, if predators detect prey by their movements. In the case of Pacific hake larvae, the evidence from otolith size-at-age indicates that slower-growing larvae suffer higher mortality.

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