Measurement of larval striped bass (Morone saxatilis) net avoidance using evasion radius estimation to improve estimates of abundance and mortality

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Abstract. Net avoidance rate increases as a function of larval striped bass size. This causes underestimation of abundance and overestimation of mortality rate. We modeled net avoidance by assuming that fish avoid the net by swimming a radial distance at a right angle to the net axis. This distance, the evasion radius, was estimated by comparing the calculated densities of striped bass larvae from a series of paired tows involving a large and a small net. Iteration and solution models were used to estimate the evasion radius for each millimeter size group of fish in order to estimate the actual density in the environment. Avoidance of the nets increased with fish length. The ratio of actual density in the environment to the measured density in the small net was used to adjust abundances measured in our ichthyoplankton surveys. After adjusting for net avoidance, mortality rates of striped bass larvae from the Sacramento–San Joaquin Estuary were reduced by 10% compared to the unadjusted rates.

Introduction

Quantitative measurements suitable for estimating mortality rates of fish are difficult to make using a single towed net because the probability of capture changes in relation to the selection characteristics of the net for the life stage or size of the target species. Net selectivity is affected by mechanical factors such as mesh size, net dimensions, towing speed, and disturbance ahead of the net caused by the boat or the net, cable and bridles; fish behavior and swimming speed; and environmental conditions such as water clarity (Nielsen, 1983; Nielsen and Johnson, 1983). Net avoidance usually increases with increasing fish size, resulting in underestimation of larger fish abundance and overestimation of mortality rates (Smith and Richardson, 1977). Therefore, correcting for size-dependent selectivity improves the accuracy of abundance and mortality estimates for larval fish.

Fisheries and zooplankton researchers have attempted to estimate the extent of net avoidance. Fleminger and Clutter (1965) conducted a series of tows with different net sizes in an enclosed pool and determined, for several species of zooplankton, an ‘effective radius’ which was directly proportional to the organism’s ability to escape. They also concluded that smaller nets were more easily avoided and the ability to escape varied among species. Barkley (1972) developed a model of avoidance (termed the ‘lethal cone’) which used the net’s speed, the organism’s swimming speed, and position relative to the net to calculate probabilities of capture for different species using field data. His results depended on assumptions about the organism’s speed. Ware and Lambert (1985) used Clutter and Anraku’s (1968) probability of capture as a basis for calculating a probability of capture for Atlantic mackerel (Scomber scombrus). Ware and Lambert (1985)
used this probability of capture to correct the density of juvenile and larval fish
determined from sampling. Their probability of capture model was based on the
burst larval swimming speed of herring larvae and corrected for temperature
effects on swimming speed.

We conducted a study to estimate striped bass (*Morone saxatilis*) larvae avoid-
ance of the net used to survey their concentrations in the Sacramento–San Joaquin
Estuary. Avoidance was determined from a comparison of their concentration in
our standard ichthyoplankton net with their concentration in a large-mouth plank-
ton net with the same mesh. This paper describes the methods used to establish
the relationship of fish size to net avoidance, and compares larva mortality rates
before and after adjusting for net avoidance. Our model’s performance was evalu-
ated by comparing our results to those obtained using the Clutter and Anraku
(1968) model. The ability of striped bass to detect the net and their escape swim-
ming speed necessary to avoid capture were also investigated.

**Method**

Nets were towed repetitively, side by side from different boats on three dates in
May and June 1993 (Table I) in Montezuma Slough, in the Sacramento–San
Joaquin Estuary, California (Figure 1). We sampled this area near the fresh
water–salt water interface because relatively high striped bass densities could be
expected there in years of high river flows. Boat positions were alternated after
each tow to eliminate position effects on catch. The volume of water filtered was
calculated using measurements from a calibrated flowmeter (General Oceanics,
Model 2030) centered in the mouth of each net. Tows were made diagonally from
the bottom to the surface with equal sampling time at each depth. Environmental
data were collected for each tow and consisted of surface water temperature (°C),
water transparency (cm) and surface conductivity (μS) (Table I). Water trans-
parency was measured with a Secchi disk. Conductivity was measured from water
samples taken at the tow site and corrected for temperature. Tows lasted 10 min.

The large (1.50 m²) and small (0.42 m²) mouth nets used (Figure 2) were
designed so that the net efficiencies, the ratios of mouth area to mesh opening
area, were similar. The net efficiency was 5.71 for the large net and 4.71 for the

<table>
<thead>
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<th>Parameter</th>
<th>25 May</th>
<th>2 June</th>
<th>16 June</th>
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<tr>
<td>Paired tows</td>
<td>12</td>
<td>10</td>
<td>10</td>
</tr>
<tr>
<td>Mean Temperature (°C)</td>
<td>19.6</td>
<td>18.5</td>
<td>20.8</td>
</tr>
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<td>Range</td>
<td>19.0–20.0</td>
<td>18.0–19.0</td>
<td>19.4–21.4</td>
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<td>Secchi transparency (cm)</td>
<td>22.4</td>
<td>8.9</td>
<td>23.4</td>
</tr>
<tr>
<td>Mean</td>
<td>18–28</td>
<td>8–11</td>
<td>18–36</td>
</tr>
<tr>
<td>Range</td>
<td>1970</td>
<td>1990</td>
<td>800</td>
</tr>
<tr>
<td>Specific conductance (μS)</td>
<td>1710–2050</td>
<td>1930–2030</td>
<td>580–1080</td>
</tr>
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</table>
small net. The mesh size of both nets was 505 µm. Cod end plastic collecting jars were screened with stainless steel 470-µm-mesh bolting cloth. Earlier trial sampling indicated insignificant day and night differences in catches of larvae, so we sampled only during the day.

Samples were preserved in 5% formalin on the boat and sorted in the laboratory. Striped bass were identified, counted and standard length measured to the nearest millimeter. The mean density, in numbers per 1000 m³, for each millimeter length interval and net size was calculated by dividing the total fish in each length group by the total volume sampled multiplied by 1000. These densities were used to estimate the evasion radius for each length group for each net. Transformation of these data was unnecessary and undesirable because the models for evasion radius require individuals per unit volume (see below).

We modeled net avoidance as an evasion radius that was proportional to standard length. The evasion radius is the linear distance from a point in a plane parallel to the net’s mouth to a point near the net’s perimeter such that a fish can avoid capture by swimming this distance. Modifying the technique of Fleminger and Clutter (1965), we used three mathematical models to estimate the evasion radius and the true density by using the calculated densities from each size net and the net dimensions. The models used the ratio of calculated densities between the small and large nets, and are classified as either a solution or an iteration model.

The following assumptions are used for each model. Variables are defined in Table II.
1. Calculated densities for the large and small nets are less than the actual density, and the calculated density for the large net is greater than the calculated density for the small net \( (ds < dl < da) \). This assumption limited us to the use of 5–29 mm length classes.

Table II. Parameters, symbols and values used in evasion radius and density estimation calculations. Unless a specific value is indicated, the parameter is a variable. The term ‘ind.’ indicates ‘individuals’.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Symbol</th>
<th>Value</th>
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<tbody>
<tr>
<td>Radius, small circular net</td>
<td>Rs</td>
<td>0.366 m</td>
</tr>
<tr>
<td>Radius, large circular net</td>
<td>Rl</td>
<td>0.691 m</td>
</tr>
<tr>
<td>Height, small rectangular net</td>
<td>h</td>
<td>0.57 m</td>
</tr>
<tr>
<td>Width, small rectangular net</td>
<td>w</td>
<td>0.74 m</td>
</tr>
<tr>
<td>Top dimension, large trapezoidal net</td>
<td>a</td>
<td>0.79 m</td>
</tr>
<tr>
<td>Bottom dimension, large trapezoidal net</td>
<td>b</td>
<td>1.52 m</td>
</tr>
<tr>
<td>Height, large trapezoidal net</td>
<td>k</td>
<td>1.3 m</td>
</tr>
<tr>
<td>Area, small circular and rectangular net</td>
<td>As</td>
<td>0.42 m²</td>
</tr>
<tr>
<td>Area, large circular and trapezoidal net</td>
<td>Al</td>
<td>1.50 m²</td>
</tr>
<tr>
<td>Density, small circular or rectangular net</td>
<td>ds</td>
<td>ind. per 10³ m³</td>
</tr>
<tr>
<td>Density, large circular or trapezoidal net</td>
<td>dl</td>
<td>ind. per 10³ m³</td>
</tr>
<tr>
<td>Estimated true density</td>
<td>da</td>
<td>ind. per 10³ m³</td>
</tr>
<tr>
<td>Evasion radius</td>
<td>r</td>
<td>m</td>
</tr>
</tbody>
</table>

Fig. 2. Dimensions and relative sizes of mouth frame openings for the two sampling nets used to evaluate the evasion radius of striped bass larvae.
2. The mouth opening of the net could be approximated by a circle and a rectangle for the small net, and a circle and a trapezoid for the large net. The area used for either shape is the actual area of the net opening.

3. The actual density at the time of sampling is homogeneous in space and time, and is constant for the duration of the tow.

4. Small and large nets were towed for the same length of time, the same speed, the same direction and through the same population.

5. The only cause of difference between the calculated density and the actual density is that fish actively avoid the net.

6. The evasion radius is constant for both nets and is constant at any point along the perimeter of the net.

7. The maximum value of the evasion radius is: \( r < R_s \) for the circular net model and \( r < h/2 \) for the rectangular/trapezoidal net model.

Solution models find an evasion radius value and then use this value to correct the calculated density. We used two types of solution models: analytic and forced. The analytic model solves for the evasion radius and then the calculated densities are corrected to estimate the actual density. Modeling the net openings as circular, we equated the actual density to the calculated density for both large and small nets:

\[
da = ds \times \frac{\pi \times R_s^2}{\pi \times (R_s - r)^2}
\]

\[
da = dl \times \frac{\pi \times R_l^2}{\pi \times (R_l - r)^2}
\]

After setting equations (1) and (2) equal to each other, we solved for the evasion radius \( r \):

\[
r = \frac{(R_l \times R_s \times (1 - (ds/dl)^{0.5}))}{R_l - (ds/dl)^{0.5} \times R_s}
\]

We did not attempt this method for the rectangular and trapezoidal net openings. The equation for the trapezoid becomes a cubic function in \( r \) and its solution is non-trivial. The forced-solution technique does not try to solve for evasion radius, but inputs evasion radii from zero to \( R_s \) (or \( h/2 \) for the rectangular and trapezoidal nets) into equations (1), (2) or equations (3) and (4) (below) for rectangular and trapezoidal nets. As the process continues, the calculated densities converge as the value of the evasion radius approaches its true value (Figure 3). When the calculated densities are equal, the evasion radius is determined. This technique can be used with any net opening shape. We continued to increase \( r \) until the difference between the small and large net corrected densities was <1%.

The iteration model uses an approximation of the actual density to find an approximation of the evasion radius which is used to find a new value of the actual density (Figure 4). This new approximation of the actual density is used to find a
new and more accurate approximation of evasion radius. These iterations were repeated until the difference in successive estimates of the actual density was <1%. The iteration model solves equations (1) and (3) for \( r \), and uses an approximation of the actual density to approximate the evasion radius:

\[
r = R_s \times (1 - (ds/da)^{0.5}) \quad \text{for a circular net opening}
\]

\[
da = ds \times \frac{h \times w}{(h - 2 \times r) \times (w - 2 \times r)} \quad \text{for a rectangular net opening}
\]

Using the quadratic formula, we solved equation (3) for \( r \):

\[
r = \frac{(h + w) - ((h + w)^2 - 4 \times h \times w \times (1 - (ds/da)))^{0.5}}{4}
\]

In both cases, the first estimate of the actual density is the density calculated from the large net. Once an approximation for the evasion radius has been calculated, an approximation for the actual density is determined by correcting the large net density:

\[
da = dl \times \frac{R_l^2}{(R_1 - r)^2} \quad \text{for a circular net opening}
\]

\[
da = dl \times \frac{(a + b) \times k}{((a - 2 \times r) + (b - 2 \times r)) \times (k - 2 \times r)}
\]

\[
\text{for the trapezoidal net opening}
\]

The iteration model asymptotically approaches the actual density and the evasion radius, and cannot overestimate the actual density.
All methods and net geometries result in five models: two for the rectangular/trapezoidal net openings (iteration and forced) and three for the circular net openings (analytic, iteration and forced). We compared the calculated densities and evasion radii of these models to determine whether net mouth geometry had an effect on estimation of density.

We used 6–14 mm abundance indices from the California Department of Fish and Game’s 1991 striped bass Egg and Larva Survey to evaluate the use of the net avoidance correction factors developed in this paper to estimate average mortality more accurately. Methods used for the Egg and Larva Survey are described in Stevens (1977). The abundance index for each millimeter size group is the sum of the products of catch per cubic millimeter and the water volume at each sampling station over all dates and stations sampled, divided by 10 000 for convenience. We regressed the abundance indices, after transformation using natural logarithms, on estimated average age in days for each length group. The slopes of the regressions are estimates of daily mortality. Larval striped bass ages were estimated using a daily increment aging technique on samples of otoliths (California Department of Fish and Game, unpublished data).

We calculated the model’s probability of capture ($PC$) by dividing the small net measured density by the estimated actual density, and compared the results to Clutter and Anraku’s (1968) model. Clutter and Anraku (1968) suggested the following general model [see Ware and Lambert (1985) for an example]:

$$C = 1 - \left(\frac{1}{\pi R^2}\right) \times \left(a \times (R^2 - a^2/4)^{0.5} + 2 \times R^2 \times \sin^{-1}(a/(2 \times R))\right)$$

(5)

where $R$ is the net radius, $C$ is the catch efficiency and ‘$a$’ is the distance, in centimeters, a fish moves between the time of response and the time the net reaches their plane. Setting ‘$a$’ equal to the evasion radius, we calculated Clutter and Anraku (1968) probabilities of capture and then calculated the difference.
between the two probabilities. We did not compare \( PC \) with the Barkley (1972) model because we both define \( PC \) the same way.

Using data in Table I, we used a linear regression model with indicator variables to examine whether striped bass were visually detecting the net. Our working hypothesis is: as water clarity decreases, evasion radius will decrease, \( ds \) and \( dl \) will increase, but the ratio \( ds/dl \) will also increase. Temperature and conductance influence swimming speeds (Webb, 1975) with temperature probably being most important and conductance reducing swimming speed only when at abnormal levels. Temperature was not analyzed as intra- and inter-day variations (Table I) were not significantly different and conductance was in the normal range for striped bass (Table I). We calculated evasion radii for each length for each day of sampling, and coded the data to indicate low- and high-clarity conditions. Coding was done by creating the indicator variable, LCLR, and assigning it the value ‘1’ for 2 June (low water clarity) and ‘0’ for the other dates (high water clarity). Regressing \( r \) on standard length (\( L \)) and LCLR, the regression model to evaluate changes in the intercept is [see Freund and Littell (1991) for a discussion]:

\[
r = B_0 + B_1 \times L + B_2 \times \text{LCLR}
\]

For high-clarity conditions (LCLR = 0), the equation becomes:

\[
r = B_0 + B_1 \times L
\]

and for low-clarity conditions (LCLR = 1) the equation becomes:

\[
r = (B_0 + B_2) + B_1 \times L
\]

If \( B_2 \) is significant, the difference between the two conditions is constant. The regression model to evaluate changes in slope is:

\[
r = B_0 + B_1 \times L + B_2 \times \text{LCLR} + B_3 \times L \times \text{LCLR}
\]

For high-clarity conditions, the equation reduces to equation (6). For low-clarity conditions, the equation becomes:

\[
r = (B_0 + B_2) + (B_1 + B_3) \times L
\]

If \( B_3 \) is significant, the slope is different for the two conditions.

We calculated values of escape speed (\( ES \)) for four detection distances (\( D \)) (250, 500, 1000 and 2000 mm) for 6, 12 and 24 mm striped bass length classes, using our model and that of Barkley (1964). Since Barkley (1964) used a circular net, we used our circular model. Using the geometry in Figure 5 and assuming that a fish will: (i) swim at its maximum escape speed; (ii) swim a course perpendicular to the axis of the net’s path (the shortest path to escape); (iii) detect the oncoming net at a distance \( D \) to have enough time to avoid the net; and (iv) act
independently (i.e. no schooling behavior) (Barkley, 1972); and using a constant net speed \((NS, 850 \text{ mms}^{-1})\) and a constant \(r\) for a given length class, the following relationship for \(ES\) and \(D\) is:

\[
r \times NS = ES \times D \text{ or } ES = (r \times NS)/D
\]

indicating that \(ES\) and \(D\) are inversely related. Barkley’s (1964) model allows a swimming angle \(\theta\) (the angle the fish swim away from the net) based on an axis parallel to the axis of the net and rotated counterclockwise. We calculated \(\theta\) as our model assumes that \(\theta\) is equal to 90°. Using the following formulae [Barkley (1964) with our variable notation], we calculated \(ES\) and \(\theta\):

\[
ES = NS/(1 + D^2/r^2)^{0.5}
\]

and

\[
\theta = \cos^{-1}(1/(1 + D^2/r^2)^{0.5})
\]

**Results**

Estimated actual density was greater than the density calculated from either net (Figure 6). Analysis of the five different models revealed small differences in the estimated true density. Since the largest difference between any two models was <3 individuals per 10^3 m^3, we considered differences between models inconsequential. Although the shape of the net opening appears not to be an important factor in estimating density, we cannot categorically state this because we did not
use nets with circular openings. The forced-solution method sometimes resulted in a negative difference. Since our criterion for stopping the model was ‘less than 1% absolute difference’, the forced-solution model overestimated the actual density in some cases.

There are clear differences in estimates of evasion radius (Figure 7, Table III). Models using a circular shape estimate a larger evasion radius versus a model using a rectangular/trapezoidal shape because for a given ratio of actual to measured densities there is a corresponding ratio in area:

\[
\text{Actual density} = \frac{\text{measured density} \times \text{total area of the net opening}}{\text{(total area of the net opening – area where fish escape)}}
\]

For a given reduction in area, a smaller evasion radius is required for a rectangle than for a circle (Figure 8). Therefore, we used the rectangular/trapezoidal iteration model for density correction as it is closest to the actual shapes of the net openings used and is the most conservative. The circular analytical model will be used for discussion/comparison with other models. As demonstrated above, all models approximate roughly the same actual density.

**Table III.** Standard length (SL), average circular evasion radius (forced, analytic and iteration models AVCRr), average rectangular evasion radius (forced and iteration models AVRTr), small net density (SD) and estimated true density (ED) for the net comparison study in Montezuma Slough, 1993. SL, AVCRr and AVRTr are in millimeters, and SD and ED are in ind. per 10³ m³

<table>
<thead>
<tr>
<th>SL</th>
<th>AVCRr</th>
<th>AVRTr</th>
<th>SD</th>
<th>ED</th>
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<tr>
<td>5</td>
<td>207.80</td>
<td>179.60</td>
<td>1.70</td>
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</tr>
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<td>6</td>
<td>61.40</td>
<td>54.20</td>
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<td>57.08</td>
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<td>7</td>
<td>119.70</td>
<td>104.18</td>
<td>96.55</td>
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</tr>
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<td>8</td>
<td>105.86</td>
<td>93.45</td>
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</tr>
<tr>
<td>9</td>
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<td>182.78</td>
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<tr>
<td>26</td>
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<td>160.60</td>
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<td>224.60</td>
<td>193.13</td>
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The probability of capture (PC) was used to estimate real abundances for evaluating avoidance effects on mortality. The PC is the ratio of measured density in the small net to the estimate of actual density and this relationship for all fish is shown in Figure 9. Because the relationship appeared to be sigmoid, a log-odds or logit transformation was tried to improve the fit of the PC/length relationship.
The difference in $r^2$ between the logit and the non-transformed $PC$ was only 0.0154. The data showed no other strong tendencies and we therefore used a non-transformed $PC$ for calculations. Since we estimate mortality for striped bass in the size range 6–14 mm from our field data, we calculated a $PC$ for this size range by the regression:

$$PC = 0.864 - 0.0394 \times L \quad (r^2 = 0.720, P = 0.0038)$$

Abundance after adjusting the data for net avoidance is compared to the uncorrected abundance (Table IV). The regression for the uncorrected abundance was:

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**Fig. 8.** Comparison of the change in the net mouth area relative to changes in the evasion radius for rectangular and circular net openings.

**Fig. 9.** Linear regression relationship between the probability of capture and striped bass length over the size range 6–29 mm ($r^2 = 0.717, F = 55.89, P < 0.0001$).
\[
\ln(\text{abundance}) = 13.08 - 0.180 \times \text{fish age} \quad (r^2 = 0.996, P = 0.0001)
\]

and the regression for the corrected abundance index was:

\[
\ln(\text{abundance}) = 13.44 - 0.161 \times \text{fish age} \quad (r^2 = 0.994, P = 0.0001)
\]

The daily mortality rate, the slope of the regression, based on avoidance-corrected data was 10.6% lower than the mortality rate based on the uncorrected abundances. Although this difference appears small, it results in a 2-fold difference, 3039 versus 1534, in the numbers of fish surviving from an initial population of one million fish after 36 days.

The Clutter and Anraku (1968) probability of capture was greater than our probability of capture by an average 41.2%. The reasons for this difference are the assumptions concerning the behavior of fish when the net is approaching and escape/extrusion (discussed below). The Clutter and Anraku (1968) model assumes that all organisms will move unidirectionally (left or right) to avoid the net (Ware and Lambert, 1985), while our model assumes that organisms will move radially outward (relative to the axis of the net) to avoid capture (Figure 10), resulting in a larger area where fish can escape and hence a lower probability of capture. We believe that this is the major reason for the observed differences and that the Clutter and Anraku (1968) model overestimates probabilities of capture for striped bass in our study.

The water clarity analysis indicated that as water clarity decreased, the evasion radius increased, contradicting our working hypothesis. Coefficient \(B_2\) was suggestive, but not significant \([-36.82, SE = 22.46, P = 0.1066\) (two-sided), 57 degrees of freedom], only suggesting a constant difference between low- and high-water-clarity sample days. However, coefficient \(B_3\) was significant \([8.99, SE = 3.11, P = 0.0055\) (two-sided), 56 degrees of freedom], indicating a more positive slope (change in evasion radius per unit fork length) for 2 June (LCLR = 1) than either 25 May or 16 June (LCLR = 0).

The differences between our model and Barkley (1964) increase as \(D\) decreases

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**Table IV.** Comparison of abundance and mortality rates for the 1991 striped bass survey data after using the net correction factors to adjust 6–14 mm abundance indices

<table>
<thead>
<tr>
<th>Length group (mm)</th>
<th>Estimated mean age (days)</th>
<th>Abundance index</th>
<th>Probability of capture</th>
<th>Avoidance corrected index</th>
</tr>
</thead>
<tbody>
<tr>
<td>6</td>
<td>4.1</td>
<td>229 208</td>
<td>0.627</td>
<td>365 400</td>
</tr>
<tr>
<td>7</td>
<td>8.8</td>
<td>83 512</td>
<td>0.587</td>
<td>142 201</td>
</tr>
<tr>
<td>8</td>
<td>13.5</td>
<td>53 488</td>
<td>0.548</td>
<td>97 544</td>
</tr>
<tr>
<td>9</td>
<td>18.1</td>
<td>21 232</td>
<td>0.509</td>
<td>42 389</td>
</tr>
<tr>
<td>10</td>
<td>22.8</td>
<td>6408</td>
<td>0.469</td>
<td>13 651</td>
</tr>
<tr>
<td>11</td>
<td>27.5</td>
<td>3104</td>
<td>0.430</td>
<td>7219</td>
</tr>
<tr>
<td>12</td>
<td>32.2</td>
<td>1536</td>
<td>0.390</td>
<td>3934</td>
</tr>
<tr>
<td>13</td>
<td>36.8</td>
<td>576</td>
<td>0.351</td>
<td>1640</td>
</tr>
<tr>
<td>14</td>
<td>41.5</td>
<td>304</td>
<td>0.312</td>
<td>976</td>
</tr>
</tbody>
</table>
and fish size increases (Table V). Also, as $D$ decreases, $\theta$ is farther from $90^\circ$. At $D$ equal to 1000 mm and 2000 mm, the models concur very well with $\theta$ equal to $78^\circ$ or greater (Table V).

Discussion

The main goal of this study was to correct the measured larval striped bass density caught by our egg and larva nets, and make better estimates of larval mortality. In this, we achieved some success. Although high variability in these data allow only a crude correction of larval densities, it is a first step towards an improved estimation of the populations of larval striped bass in this estuary.

Although the evasion radius ($r$) is determined by the ratio of the measured densities from the small and large nets, the densities actually measured may be affected by factors in addition to net avoidance. Our model assumes these other factors to be insignificant, but results indicate otherwise. For example, the calculated evasion radius of 179.6 mm for the 5 mm length class was greater than the 54.2 mm for the 6 mm length class (Table III), indicating that using density ratios as the basis for a correction factor can produce unrealistic results. To examine this further, we will discuss the model’s assumptions.

We assumed that the actual or true density was always larger than the density calculated from either net and that $ds$ was always less than the $dl$. This was a
condition for the model to be able to calculate evasion radii. Since $r$ is in the denominator of the equation for density correction, values of density become asymptotic as $r$ approaches $R_s$ and $R_l$ (Figure 11). Since $R_s$ is less than $R_l$, corrected values of $d_s$ will approach infinity at a faster rate than corrected values of $d_l$. If the $d_s$ is less than $d_l$, the curves of corrected densities will intersect at the evasion radius and at the true density. If $d_s$ is greater than $d_l$, the curves of corrected density will not intersect and the evasion radius cannot be determined.

The actual fish density in the area sampled by both nets was assumed to be homogeneous in space. Alternating boat position and making replicate tows were approaches used to minimize any bias caused by non-random distributions, but this tactic may not have compensated for patchy distributions. If homogeneity was lacking, this would alter the $d_s/d_l$ ratio and either underestimate or overestimate the evasion radius and the estimated true density. To reduce the variability inherent in individual tows, we summed catches for all tows by size and then divided the total catch of each size group by the total water volume sampled. This was justified since the variability of individual paired tows was high, as displayed by a box and whisker plot of the individual ratios of the large net to small net concentrations (Figure 12). The interquartile ranges of the ratios for each length group were above one, except for 5 mm fish, but several length groups exhibited gross outliers.

We also assumed that the distance traveled by the tows was the same for both nets, thus reducing variability. However, if patchiness exists, tows of different lengths would tend to induce more variability into the estimates of density. We observed that the small-net tows covered a greater linear distance than the large-net tows. This was reflected in the differences in flowmeter readings. The mean flowmeter revolutions for the small net tows, 18 052, was significantly greater than

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**Table V.** Escape speed ($ES$) versus detection distance ($D$) and swimming angle ($\theta$) for 6, 12 and 24 mm standard length striped bass larvae from the net comparison study in Montezuma Slough, 1993. ‘G’ indicates results for Gartz et al. (this paper) and ‘B’ indicates results for Barkley (1964). ‘BLS’ stands for ‘body lengths per second’

<table>
<thead>
<tr>
<th>$D$ (mm) and $\theta$ (degrees)</th>
<th>$ES$</th>
<th>$D$ (mm) and $\theta$ (degrees)</th>
<th>$ES$</th>
<th>$D$ (mm) and $\theta$ (degrees)</th>
<th>$ES$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$6$ mm</td>
<td>$12$ mm</td>
<td>$24$ mm</td>
<td>$6$ mm</td>
<td>$12$ mm</td>
</tr>
<tr>
<td>$250$ G</td>
<td>209</td>
<td>34.8</td>
<td>426</td>
<td>35.5</td>
<td>720</td>
</tr>
<tr>
<td>B</td>
<td>203</td>
<td>33.8</td>
<td>381</td>
<td>31.8</td>
<td>549</td>
</tr>
<tr>
<td>$76.2$</td>
<td></td>
<td></td>
<td>63.4</td>
<td></td>
<td>49.7</td>
</tr>
<tr>
<td>$500$ G</td>
<td>104</td>
<td>17.3</td>
<td>213</td>
<td>17.8</td>
<td>360</td>
</tr>
<tr>
<td>B</td>
<td>104</td>
<td>17.3</td>
<td>207</td>
<td>17.3</td>
<td>332</td>
</tr>
<tr>
<td>$83.0$</td>
<td></td>
<td></td>
<td>75.9</td>
<td></td>
<td>67.0</td>
</tr>
<tr>
<td>$1000$ G</td>
<td>52</td>
<td>8.7</td>
<td>107</td>
<td>8.9</td>
<td>180</td>
</tr>
<tr>
<td>B</td>
<td>52</td>
<td>8.7</td>
<td>106</td>
<td>8.8</td>
<td>176</td>
</tr>
<tr>
<td>$86.5$</td>
<td></td>
<td></td>
<td>82.9</td>
<td></td>
<td>78.0</td>
</tr>
<tr>
<td>$2000$ G</td>
<td>26</td>
<td>4.3</td>
<td>53</td>
<td>4.4</td>
<td>90</td>
</tr>
<tr>
<td>B</td>
<td>26</td>
<td>4.3</td>
<td>53</td>
<td>4.4</td>
<td>90</td>
</tr>
<tr>
<td>$88.2$</td>
<td></td>
<td></td>
<td>86.4</td>
<td></td>
<td>84.0</td>
</tr>
</tbody>
</table>
the mean for the large net tows, 15 371 ($t = -4.067$, $P > |T| = 0.0001$). Hence the assumption of equal velocities for the two nets was violated. Apparently, maintaining the large net at the same relative depth (possibly due to higher hydraulic drag) as the small net required the large-net boat to move slower than the small-net boat, resulting in a shorter distance traversed. Because the small net covered more linear distance, the probability of encountering a patch of fish increased, potentially resulting in a larger catch (and potentially a higher $ds$), a higher $ds/dl$ ratio and an underestimation of $r$. However, because the tow distances for both nets were not greatly different, the underestimation of $r$ would not be large, and the error in $r$ is conservative and will not overestimate the actual density, $da$.

Assumptions about the size and shape of the net opening (mouth) need to be considered. Our results indicate that evasion radius is dependent on net opening geometry, but this could be misleading. We used data collected with nets having rectangular/trapezoidal openings and used them in the model with circular openings, yielding the above results. The potential for introduced bias into our results exists. If net avoidance is independent of net opening geometry, different catches and densities would result for nets with the same net opening area, but different geometries. Until the issue of net opening geometry can be resolved, we recommend calculating evasion radii using the actual shape of the net opening. We believe that this will yield usable density correction factors, but evasion radii cannot be compared between other nets and species. Currently, we have no reason to contradict the assumption that the evasion radii are constant for any point along the perimeter of a net. The assumption that evasion radius is constant

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**Fig. 11.** Hypothetical example demonstrating the convergence/lack of convergence depending on whether the density in the small net is larger or smaller than the density in the large net. If the measured density in the small net is greater than that in the large net, no solution is possible.
for any given size net may not be valid, but we believe that net size would have little, if any, significant effect on evasion radius.

Since our evasion radius includes both capture and possible losses through the mesh, i.e. what goes in minus what goes out of the net due to either escapement or extrusion, our probability of capture should be redefined. Tranter (1968) defines the ‘number of plankters in an unbiased sample’ as:

$$y = \frac{x}{(C \times S)}$$

where $C$ is the catch efficiency, $S$ is the mesh selectivity, $x$ is the number of plankters in a sample and $y$ is the corrected number of plankters. If we replace $y$ with $da$ and $x$ with $ds$ or $dl$, we can solve for the quantity $C \times S$, which is equal to our model’s probability of capture. However, our ‘model’s probability of capture’ would be better termed a ‘density correction factor’ because it includes (at least) the probability of capture and the probability of retention. The above illustrates that the evasion radius may not be an escape distance [as with ‘a’ above, see equation (5)], but an index of capture and retention. However, this does not detract from its potential as a method to correct field data and explore some aspects of fish behavior.

Extrusion may be a more likely source of non-retention than escape for very small larvae. Fujimura (1989) demonstrated that retention of 4–8 mm striped bass larvae is nearly equivalent for small nets of 333, 400 and 505 µm meshes, suggesting that extrusion through the 505 µm mesh for the small net is unlikely. However, it is possible that greater hydraulic pressure in the large net might cause extrusion greater than that observed in Fujimura’s comparison using only small nets. In some paired tows, there were larger densities of 5, 6 and 7 mm larvae in the small net relative to the large net, suggesting either extrusion or patchiness. Given the results of this study, we speculate that small larvae were extruded, but we cannot determine to what extent. If the large net is extruding small larvae at a
higher rate than the small net, this would reduce $dl$, possibly resulting in a larger $ds/dl$ ratio, which would result in an underestimation of $r$, and an underestimation of the actual density.

We were unable to measure $ES$, the speed at which larval striped bass avoid the net, but we are able to infer its range. Webb (1975) defined burst speed (high levels of activity for <15 s) as sprints (high steady swimming speeds) and acceleration (high unsteady swimming activity). Some high burst speeds have been reported in the literature. Larval zebra danios [Danio (brachydanio) rerio] have burst speeds of 50–66 body lengths per second (BLS) (Fuiman, 1986) and larval northern anchovy (Engraulis mordax) have maximum burst speeds as high as 28 BLS, but average burst speeds were ~15 BLS (Hunter, 1972). However, these authors reported no ‘burst’ longer than 200 ms. We calculated that a 6 mm larval striped bass would have to swim at 34.8 BLS for roughly 300 ms to avoid the net if it detected it at 250 mm (Table V), an unlikely feat. Meng (1993) reported sustained swimming speeds for 6–9 mm larval striped bass at 3–4 BLS, which would correspond to a detection distance of 2000 mm (Table V). Larval striped bass burst speeds are unknown, but could be faster than their sustained swimming speed. Based on Table V calculations, we infer that $ES$ is <34.8 BLS, but >3.8 BLS. Using Webb (1975), we classify the escape speed as a burst speed, but we cannot infer how much is acceleration and how much is sprint.

As with $ES$, we can infer the range of $D$: the distance at which larval striped bass detect the oncoming net. Secchi transparency did not exceed 250 mm in Montezuma Slough (Table I) and visual cues appear to be unimportant because there was no difference between day and night catches, and the water clarity analysis results were the opposite of what we expected, i.e. higher evasion radii with low visibility conditions. Hence, we infer that detection took place at least 250 mm in front of the net. This is further supported by comparing our model with Barkley (1964) (Table V). At large values of $D$, Barkley’s (1964) swimming angle ($\theta$) approaches 90° to the axis of the net (Table V) for 6 and 12 mm striped bass, which is close to our model’s assumptions concerning larval striped bass behavior. This suggests that $D$ is most likely beyond 250 mm. Since $ES$ at $D = 2000$ mm (see above) was judged too slow, we speculate that $D$ ranges from >250 mm to <2000 mm. There are other cues that could account for this behavior. Clutter and Anraku (1968) reported that acceleration fronts were detected by flowmeters 1500 mm in front of a net rim for a 1-m-diameter net. These fronts could enable fish to detect the oncoming net. Fish could be scattered before the net by boat noise (engines, etc.) or noise/vibration from the tow wire and/or bridle (Clutter and Anraku, 1968); however, these effects would be difficult to determine, without direct observation.

Other factors could be important, but have yet to be evaluated. Functional descriptions of evasion behavior should include the orientation and speed of the evasion maneuver (see laboratory studies of responses to predation; Folkvord and Hunter, 1986). Our model assumes that striped bass swim radially to avoid the net, but without direct observation we cannot confirm this. The schooling behavior of young striped bass is not well known, but Barkley (1972) mentioned that schooling behavior could affect the capturing process when individuals close
to the net ‘warn’ other members of the school farther in front of the net. Given the low water transparency during our study (Table I), schooling behavior seems unlikely, but we cannot discount it. Temperature needs to be evaluated over a broad range and for different sizes of striped bass as temperature directly affects swimming ability. We were unable to evaluate temperature effects due to the small variability in observed temperature.

How well did we measure evasion? The larval striped bass mortality rate was lowered after applying these corrections to 1 year of data, and it empirically appears more realistic, but it may still overestimate true mortality. Further application of these corrections in population models and life tables will help us evaluate the improvement in our abundance estimates. Our experience suggests that net avoidance should be routinely evaluated for any ichthyoplankton survey because the abundance of even small fish may be underestimated by a factor of two. Making better estimates of fish abundance and mortality rates will result in more informed decisions. Our model, though tentative, is an important step in improving striped bass abundance estimates and our understanding of the population in the Sacramento–San Joaquin Estuary.

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