A Method for Correcting Catches of Fish Larvae For the Size Selection of Plankton Nets

David A. Somerton and Donald R. Kobayashi

ABSTRACT: Length distributions of fish larvae obtained with plankton nets are usually biased because large larvae avoid the net and small larvae are extruded through the meshes. Sueh bias is often corrected by determining the ratio between a standard net and a test net with either zero extrusion or zero avoidance. However, when avoidance of the test net with zero extrusion or when extrusion through test net with zero avoidance differs from the standard net, then the usual method of correcting for size selection results in biased estimates. For such situations, we propose a method that explicitly considers both differential extrusion and differential avoidance and that provides estimates of variance for the corrected length-frequency distributions. The method was applied to length-frequency data for the Hawaiian anchovy or nehu, *Encrasicholina purpurea*. It was shown that a 1 m plankton net with 0.335 mm mesh dropped vertically through the water column during the day effectively samples nehu larvae only between 2.25 and 6.75 mm, roughly one-third of the total length range.

For many aspects of larval fish ecology, accurate estimates of length distribution are imperative, yet the length distribution of larvae obtained with a plankton net is nearly always biased because large larvae avoid the net and small larvae are extruded through the meshes. Previous research on methods to correct larval catches for such size selection has focused on either extrusion (Lenarz 1972) or avoidance (Barkley 1972; Murphy and Clutter 1972), implicitly assuming that the two aspects of size selection are independent. Although this assumption seems reasonable, situations arise in which the problems of estimating extrusion and avoidance are unavoidably linked.

Nearly all empirical or analytical studies of avoidance and extrusion are based on the premise that the number of larvae captured by a plankton net (N_o) is proportional to the number

David A. Somerton and Donald R. Kobayashi: Southwest Fisheries Center Honolulu Laboratory, National Marine Fishery Service, NOAA, Honolulu, HI 96822-2396.

originally in the path of the net (N):

$$N_o = P_c\, N, \qquad (1)$$

where the proportionality constant (P_c) varies with larval length. P_c can be considered as the probability of capturing a larva, and this, in turn, can be considered as a product of an entry probability (P_e) and a retention probability (P_r):

$$P_c = P_e P_r; \qquad (2)$$

where P_e is equal to 1 minus the probability of a larva avoiding the net and P_r is equal to 1 minus the probability of a larva being extruded through the meshes, given that it has entered the net.

Since an estimator for N can be obtained by combining and rearranging the above equations,

$$N = \frac{N_o}{P_e P_r}, \qquad (3)$$

the problem of correcting for size selectivity is one of estimating P_e and P_r for each length interval.

To estimate P_e or P_r, catches of a standard net are usually compared with those obtained by some test net used to sample the same population of larvae. In this paper, we will refer to these comparisons as either entry or retention experiments. Assuming catches are standardized to reflect equal filtration volumes, the general form of a net comparison is

$$\frac{N_{os}}{P_{es} P_{rs}} = \frac{N_{oi}}{P_{ei} P_{ri}} = N, \qquad (4)$$

where the second subscript refers to the standard net (s) and to the test net used in either an entry experiment ($i = e$) or a retention experiment ($i = r$). Expressed in words, Equation (4) states that the corrected catches from the standard and test nets are both unbiased estimates of the true abundance of larvae and are therefore equal.

For an entry experiment, an appropriate test net is one that has no larval avoidance (i.e., $P_{ee} = 1.0$) over the size range of interest. After substituting this value for the entry probability and rearranging terms, Equation (4) can be expressed as

$$\frac{N_{os}}{N_{oe}} = \frac{P_{rs}}{P_{re}} P_{es} . \qquad (5)$$

Likewise, for a retention experiment, an appropriate test net is one that has no larval extrusion (i.e., $P_{rr} = 1.0$). After substituting this value for the retention probability and rearranging terms, Equation (4) can be expressed as

$$\frac{N_{os}}{N_{or}} = \frac{P_{es}}{P_{er}} P_{rs} . \qquad (6)$$

To simplify Equations (5) and (6) further, previous studies have assumed that either the larval retention of the test net used in an entry experiment was identical to that of the standard net (i.e., $P_{rs} = P_{re}$; Barkley 1972; Murphy and Clutter 1972) or that the larval entry into the test net used in a retention experiment was identical to that of the standard net (i.e., $P_{es} = P_{er}$; Lenarz 1972; Colton et al. 1980; Leak and Houde 1987). With these assumptions, Equations (5) and (6) become

$$\frac{N_{os}}{N_{oe}} = P_{es} , \qquad (7)$$

and

$$\frac{N_{os}}{N_{or}} = P_{rs} . \qquad (8)$$

In other words, entry and retention probabilities of the standard net were estimated as the ratio of the catches of the standard and test nets within each length interval.

When neither assumption can be made, the estimation procedure is complicated in two ways: First, P_{es} and P_{rs} cannot be estimated as simple ratios of the catches of the standard and test nets because they additionally depend on other unknown entry and retention probabilities. This means that P_{es} and P_{rs} cannot be estimated independently for each length interval and must instead be expressed as functional relationships of

larval length and estimated simultaneously for all size intervals. Second, the equations for the entry experiment, Equation (5), and the retention experiment, Equation (6), contain both P_{es} and P_{rs}; therefore, the two probabilities are confounded and must be estimated jointly.

In this paper, a method is described for estimating the entry and retention probabilities for this more difficult situation, and this method is then applied to correct the length-frequency distribution of larval Hawaiian anchovy or nehu, *Encrasicholina purpurea*, obtained with plankton nets.

MATERIALS AND METHODS

The standard plankton net that we used to sample eggs and larvae of nehu was constructed of 0.335 mm Nitex[1] and measured 1 m in diameter and 5 m long. The net was not towed but deployed instead by our allowing it to drop vertically through the water column until it hit the bottom, then retrieved with a line attached to a choke collar surrounding the mesh approximately 15 cm from the mouth of the net.

Retention and entry experiments were conducted on 28 March 1988 within Pearl Harbor, HI. The retention experiment consisted of 10 paired net drops, in which the standard net and a test net were deployed simultaneously at one location during daylight hours when the standard net was normally used. The test net was identical to the standard net in all dimensions, but it had a smaller mesh size (0.183 mm). The entry experiment was conducted at each of three nearby (<0.5 km distance) locations and consisted of five deployments of the standard net during the day and five deployments of the same net the following night at each location. Since sampling could not be paired in this experiment, we were concerned that patchiness and horizontal movement of fish by tidal currents might alter the length distribution between day and night sampling. To reduce this, the sampling locations chosen had weak tidal currents, and in addition, sampling was partitioned between three locations rather than concentrated at one. Water depth at all sampling locations was approximately 12 m. The sample obtained from each deployment of each net was stored separately in 10% buffered formalin.

During the retention experiment, the test net

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[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

appeared to become clogged with algae despite efforts to clean it between deployments. To determine whether the test net was indeed clogged and filtered less water than the standard net, we assumed filtration volume was proportional to the catch of nehu eggs and used a paired t-test to compare egg catches between nets. The test net caught significantly fewer eggs ($P < 0.05$); therefore, the test net was assumed to have filtered less water. To correct for the difference in filtration volume, larval catches in the test net were multiplied by the ratio of the egg catch of the standard net to that of the test net in each pair of deployments.

Nehu larvae were subsequently measured to the nearest 0.1 mm by using a video digitizing system (Optical Pattern Recognition System produced by Biosonics, Inc., Seattle, WA). For preflexion and early flexion larvae, length was measured from the snout to the end of the notochord. For larvae with fully formed tails, length was measured from the snout to the base of the caudal fin rays. The length distributions were not corrected for shrinkage due to preservation, but since all samples were maintained in preservative for about the same length of time, it is unlikely that shrinkage varied among samples.

The entry and retention probabilities were estimated by simultaneously fitting Equations (5) and (6) to the length-frequency data by using nonlinear regression, but before this could be done, three problems had to be solved. First, the entry and retention probabilities could not be estimated independently for each length interval; therefore, Equations (5) and (6) had to be modified so that the probabilities were expressed as functions of larval length. Retention probabilities were chosen to vary with length as logistic functions and thus have the form $P = 1/(1 + ae^{-bl})$, where a and b are parameters to be estimated and l is larval length (Ricker 1975). Entry probabilities, because they are decreasing functions of length, were chosen to have the form $P = 1 - (1/(1 + a\ e^{-bl}))$. After the logistic functions were substituted for the two entry probabilities (P_{es} and P_{er}) and two retention probabilities (P_{rs} and P_{re}) in Equations (5) and (6), the resulting statistical model had eight parameters.

Second, variability in the catch ratio changed with larval length, owing to the change in sample size, and necessitated the use of weighting factors in the regressions (Draper and Smith 1981). The weighting factors used were equal to

$1/var(N_{os}/N_{oi})$, where var is the variance and N_{oi} can be either N_{or} or N_{oe}. Variance of the catch ratio was approximated by using the delta method (Seber 1973):

$$var(N_{os}/N_{oi}) = (1/N_{oi})^2\ var(N_{os})$$

$$+\ (N_{os}/N_{oi}^2)^2\ var(N_{oi})$$

$$-\ 2\ (N_{os}/N_{oi}^3)\ cov(N_{os},N_{oi})\ ,\quad (9)$$

where cov indicates covariance. The number of larvae captured in each length class (N_o) was assumed to vary as a multinomial random variable. The variance of N_o was therefore expressed as $N_*P(1 - P)$; where N_o is either N_{os}, N_{or} or N_{oe}; N_* is the sum of N_o over all length intervals; and $P = N_o/N_*$. Although the covariance between the catches of the standard and test nets could be estimated for the retention experiment, it could not be estimated for the entry experiment because sampling was not conducted pairwise. However, the covariance term for the retention experiment was, for all size intervals, approximately 100 times less than the sum of the two variance terms (Equation (9)). On this basis, we assumed that the covariance term was generally small and could be ignored in both the entry and retention experiments.

Third, since the catch ratios fluctuated widely and often became infinite in the larger length intervals where sample sizes were small, the length distributions were truncated prior to fitting the equations. For the entry experiment, truncation occurred at the smallest length interval with zero catch by the test net. For the retention experiment, however, this rule resulted in an extremely narrow length range because the catches obtained with the test net were zero at relatively small lengths. To circumvent this problem, the inverse of Equation (5) was fit to the data, and truncation occurred at the smallest interval with zero catch by the standard net. Weights were calculated by using Equation (9) after substituting N_{os} for N_{oi} and vice versa.

Once Equations (5) and (6) had been fit to the data, the values P_{rs}, P_{re}, P_{es}, and P_{er} were estimated by evaluating the logistic functions at each 0.5 mm length interval using the parameter estimates. P_c for the standard net was calculated for each length interval as the product of the estimates of P_{es} and P_{rs}. Length-frequency data from nehu larvae were then corrected for extru-

sion and avoidance by dividing each N_o by the
estimated value of P_c for the appropriate length
interval. To better visualize the effect of this
correction, we chose N_o from a data set that was
considerably larger ($N = 4,178$) than those used
in the net comparisons because histograms of
this larger data set were smoother in appear-
ance. This larger data set comprises all larvae
that we have measured to date (including those
obtained in the net comparisons) and that were
collected during the day by the standard net.

The variance of the estimated value of N was
approximated by using bootstrapping (Efron and
Gong 1983): 1) each of the four experimental
length-frequency data sets was randomly sub-
sampled with replacement to produce four new
samples with the same sample sizes as the orig-
inals; 2) Equations (5) and (6) were fit to the four
synthetic samples by the methods described
above; 3) P_{es}, P_{er}, P_{rs}, P_{re}, and P_c were esti-
mated for each length interval; and 4) N for each
length interval was estimated by dividing the N_o
from the large sample of nehu length-frequency
data by the estimated value of P_c. This pro-
cedure was repeated 500 times, generating 500
independent estimates of P_c for each length. To
reduce variance owing to rare but extremely

large estimates of N produced when P_c was near
0, the data were trimmed by eliminating the 25
largest estimates within each length interval (5%
of the sample). After data trimming, the vari-
ance was calculated among the remaining 475
independent estimates.

The variances of P_{es}, P_{er}, P_{rs}, and P_{re} were
also calculated from the same 500 independent
estimates (no data trimming was required). A
two-sample t-test incorporating these variances
was then used to test for significant differences
between P_{es} and P_{er} and between P_{rs} and P_{re}
within each length interval.

RESULTS AND DISCUSSION

The estimated entry probabilities for the stan-
dard net (P_{es}) decreased from 1.00 for 3 mm
larvae to near 0.00 for 10 mm larvae, whereas
the entry probabilities for the small mesh net
(P_{er}) decreased from 0.95 for 3 mm larvae to near
0.00 for 8 mm larvae (Fig. 1). When the apparent
difference in entry probabilities between the two
nets was examined statistically for each 0.5 mm
length interval between 2.5 and 10.75 mm, P_{er}
was found to be significantly less than P_{es} (two-
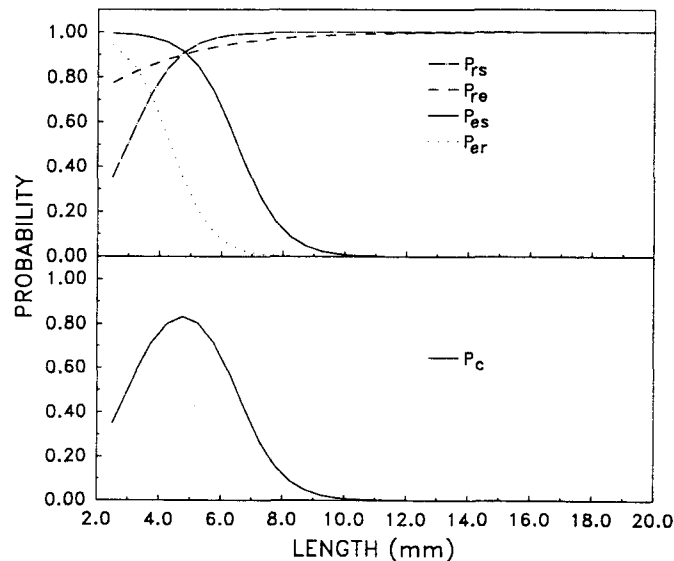sample, one-tailed t-test; $P < 0.05$) for all length

FIGURE 1.—Entry probabilities for the standard (P_{es}) and test nets (P_{er}) and reten-
tion probabilities for the standard (P_{rs}) and test nets (P_{re}) are shown by 0.5 mm
length intervals (upper panel). Capture probability (P_c) for the standard net is
shown by 0.5 mm length interval (lower panel).

intervals ≥4.25 and ≤6.75 mm. This result is surprising because the two nets were identical except for mesh size which, by itself, is unlikely to influence avoidance. However, the catch of nehu eggs in the test net was significantly less than in the standard net (paired t-test, $P <$ 0.05), indicating, to the extent egg catches can be used as a measure of filtration volume, that the test net was likely clogged by abundant filamentous algae in Pearl Harbor during sampling. Such clogging not only decreased the apparent amount of water entering the test net but also may have slowed the sinking rate, allowing larvae to avoid the net more easily.

The estimated retention probabilities for the standard net (P_{rs}) during the day increased from about 0.35 for 2.5 mm larvae to nearly 1.00 for 6.0 mm larvae (Fig. 1). At night, however, the standard net appeared to have higher retention probabilities in the smallest length intervals (P_{re}; Fig. 1). When this difference was examined statistically (two-sample t-test), P_{re} and P_{rs} were not significantly different at $P \leq 0.05$ in any length interval, but they were significantly different at $P \leq 0.15$ within the two smallest length intervals. Although the differences between P_{re} and P_{rs} are relatively small, considering the same net and method of deployment were used during both day and night sampling, it is surprising that any differences were detected. One possible explanation is that the density of small larvae, rather than the retention probability, was higher at night. This could have occurred either because, by chance alone, the density of small larvae was higher in the patches sampled at night or because the mean density was higher as a result of eggs hatching between the day and night sampling. However, the addition of new larvae is unlikely because, at the time of year when our sampling occurred (March), nehu eggs hatch during the morning and new larvae would therefore have been equally available to both our day and night sampling (Clarke 1989). A second explanation is that the greater retention of small larvae at night is real and at least partially due to morphological changes increasing the catchability of larvae between the day and night sampling periods. Evidence for this is weak; however, Clarke (1989) reported that during March nehu larvae display considerable development of their eyes, mouth, and pectoral fins between midday and early evening of their third day of life. Development of such features might increase catchability relative to equal-sized, but undeveloped, larvae.

Regardless of the reasons, over some length ranges, $P_{rs} \neq P_{re}$ in the entry experiment and $P_{es} \neq P_{er}$ in the retention experiment; both cases are violations of the assumptions implicitly made when entry and retention probabilities are estimated as simple catch ratios (i.e., catch of standard net/catch of test net). The effect of ignoring this can be judged from plots of entry and retention probabilities estimated from simple catch ratios and estimates of P_{es} and P_{rs} using our method (Fig. 2). Entry probabilities estimated from simple catch ratios are similar to P_{es} for larvae ≥4.0 mm but are increasingly less than P_{es} at smaller lengths. This region of underestimation corresponds approximately to the length interval in which the retention of larvae differed between day and night (Fig. 1). Retention probabilities estimated from simple catch ratios are similar to P_{rs} at larval lengths <4 and >8 mm, but are considerably larger than P_{rs} at intermediate lengths. Again, this region of overestimation corresponds approximately to the length region in which avoidance differed between the standard and test nets (Fig. 1). Violation of the assumptions therefore leads to bias in estimates of entry and retention probabilities based on simple catch ratios.

The success of a net comparison, however, also depends upon the validity of several other assumptions. Foremost are the assumptions that no avoidance of the test net occurred in the entry experiment ($P_{ee} = 1.0$) and no extrusion through the test net occurred in the retention experiment ($P_{rr} = 1.0$). Violations of these assumptions lead to positive bias in the estimates of P_{es} and P_{rs}. For the entry experiment, P_{ee} was definitely higher than P_{es} over a broad range of sizes because more larvae were caught at night and a sizable fraction of the catch was larger than the largest larva caught during the day (Fig. 3). But no evidence indicates P_{ee} remained equal to 1.0 for size intervals ≤14.0 mm (the size of the largest larvae caught during the day), as is required to obtain unbiased estimates. For the retention experiment, P_{rr} was definitely higher than P_{rs} because more small larvae were captured with the test net (Fig. 3). But, again, no evidence indicates P_{rr} remained equal to 1.0 for size intervals ≥2.00 mm, the smallest size category.

Still another assumption is that, in each of the two experiments, the standard and test nets both sampled the same population of larvae. For the retention experiment, the assumption is certainly valid because the two nets were deployed
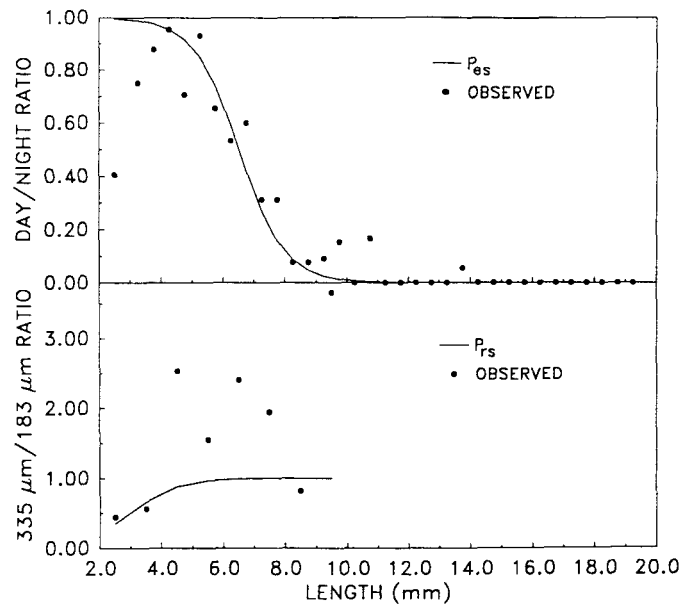
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FIGURE 2.—Estimated values of P_{es} and the day to night catch ratio by 0.5 mm length intervals obtained in the avoidance experiment (upper panel). Estimates of P_{rs} and the 0.335 mm standard net to the 0.183 mm test net catch ratio by 1.0 mm length intervals obtained in the extrusion experiment (lower panel).

simultaneously from a small boat. For the entry experiment, however, deployment of one of the nets occurred approximately 10 hours after the other, and any patchiness in the larval distribution coupled with advective movement could have substantially altered the characteristics of the population sampled. We attempted to minimize this problem by increasing the sample size, relative to the retention experiment, and by partitioning the sampling among three locations rather than by concentrating it at one. Sampling variability, however, may still have been responsible for some of the differences between the day and night size distributions. This problem has been encountered in other studies using day and night comparisons to estimate entry probabilities (Murphy and Clutter 1972), and the only effective solution is increased sample sizes.

Since the method of estimating entry and retention probabilities proposed here requires more effort than that using simple catch ratios, it is important to determine at the outset whether the assumptions that $P_{rs} = P_{re}$ and $P_{es} = P_{er}$ have been violated so that the appropriate method of analysis can be chosen. Some indica-

tion of the validity of these assumptions can be obtained by examining plots of catch ratios as a function of larval length (Fig. 2). Two cases are evident in our data. First, if the assumptions are met, catch ratio should be a monotonically increasing or decreasing function of larval length because extrusion and avoidance are monotonic functions of larval length. This is not true in the avoidance experiment where the catch ratios increased for lengths ≤4 mm and decreased thereafter. Second, if the assumptions are met, catch ratios cannot be >1.0, because, except by chance alone, catch in the standard net is less than the catch in the test net. This is not true for the extrusion experiment where the catch ratios in some length intervals are >2.0. If either of these conditions are evident in plots of catch ratios, the method of estimating entry and retention probabilities proposed here is preferable to simple catch ratios.

Although we considered the problem in which both $P_{rs} \neq P_{re}$ and $P_{es} \neq P_{er}$, this is the most general of several related problems that could be approached with slight variations in our methodology. One example occurs when either $P_{rs} \neq P_{re}$ or $P_{es} \neq P_{er}$ but not both. In this case, either
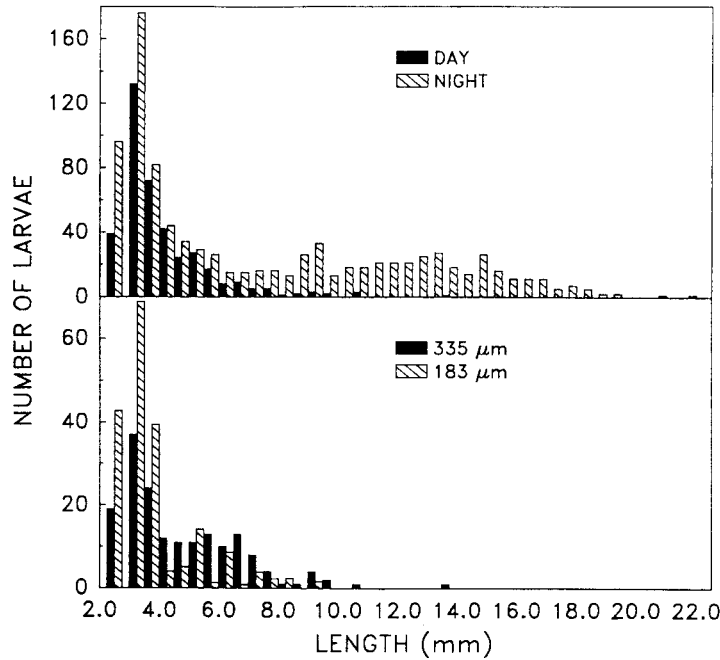
FIGURE 3.—The number of larvae by 0.5 mm length intervals captured in Pearl Harbor, HI, in March 1988. The entry experiment (upper panel) used a 0.335 mm standard mesh net during the day and night. The retention experiment (lower panel) used both a 0.183 mm mesh test net and a 0.335 mm standard mesh net during the day.

Equation (5) or (6) could be simplified by deleting either P_{rs}/P_{re} or P_{es}/P_{er}, but parameter estimation would still require a simultaneous fit of the two equations to the catch ratios. A second example occurs when only an entry experiment or retention experiment is conducted and the appropriate assumption is violated. In this case, the entry and retention probabilities still must be expressed as functions of larval length, thus requiring that nonlinear regression be used to fit either Equation (5) or (6) to the catch ratios.

The efficacy of the standard net at sampling nehu larvae can be judged in two ways. First, it can be judged by the length range sampled with a P_c = 1.0; that is, the range that requires no correction for extrusion and avoidance. For the standard net, P_c reaches a maximum of 0.86 at 4.25 mm and remains above 0.75 only over the interval 3.75–5.50 mm (Fig. 1). In other words, no interval within the larval length range of nehu (2.5–25.0 mm) is sampled completely with the standard net.

A second way of judging the efficacy of the standard net is by the length range than can be corrected, with sufficient precision, for extrusion and avoidance. The effect of correcting a large sample of nehu length frequencies for extrusion and avoidance can be seen in the frequency distributions before and after N_0 was divided by the estimated value of P_c (Fig. 4). The precision of this correction can be gauged from the estimates of the variance of N (Fig. 5). Note that variance increases gradually with length until 6.75 mm and, thereafter, increases at a greatly accelerated rate. If 6.75 mm is chosen as the upper bound on the length interval within which the estimated numbers are considered sufficiently precise, then only one-third of the larval length range could be corrected to reflect the true length distribution. Thus, judging from either perspective, the standard net is a relatively ineffective tool for sampling nehu larvae.

Variance of the corrected length-frequency distribution was used above to define some length range that can be corrected for extrusion and avoidance with sufficient precision, but estimates of variance have other important uses,
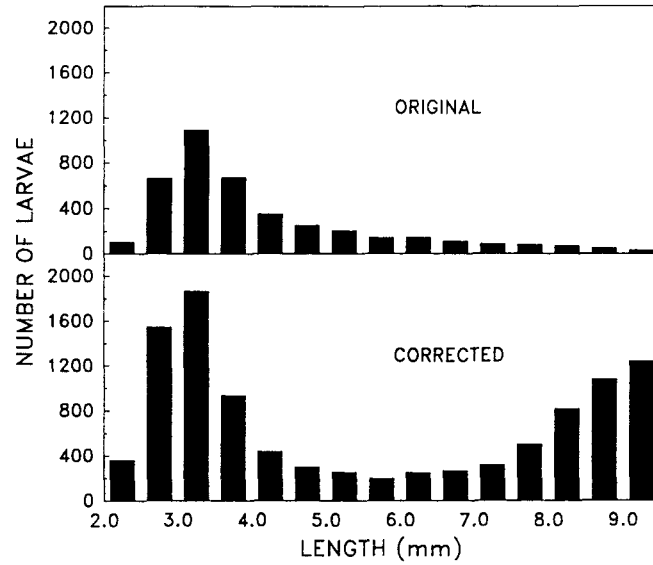
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FIGURE 4.—Length distribution of nehu larvae by 0.5 mm intervals before correction for extrusion and avoidance (upper panel) and after correction (lower panel).
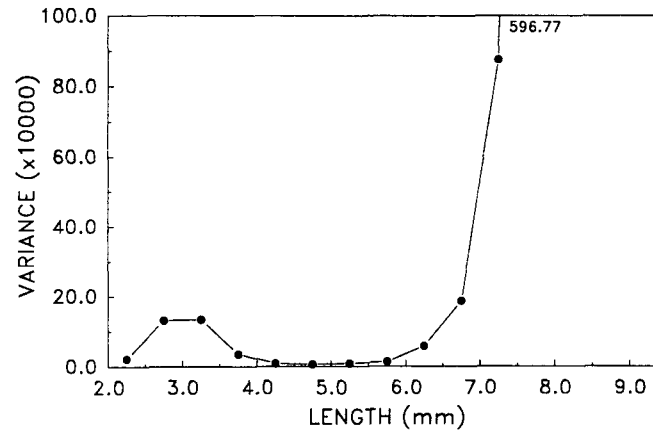

FIGURE 5.—Bootstrap estimate of variance of the corrected number of larvae by 0.5 mm length intervals.

especially when the corrected length-frequency distributions will be subsequently used to estimate mortality rates. Whether mortality is estimated by using methods that require converting length-frequency distributions to age-frequency distributions (Leak and Houde 1987) or by using some form of length-based method (Wetherall et al. 1987), precision of the mortality estimates will depend on the precision of corrected length-

frequency distributions. Thus, procedures used to estimate mortality from larval length-frequency distributions should include weighting factors that incorporate the size-specific variances of the corrected length-frequency distributions.

Most of the problems associated with violations in the assumptions $P_{rs} = P_{re}$ and $P_{es} = P_{er}$ could be eliminated with proper attention to the

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design of the entry and retention experiments. When these assumptions are violated, unbiased estimates of entry and retention probabilities can sometimes be obtained by restricting the analysis to either large or small larvae to ensure that avoidance and extrusion do not simultaneously influence the size distribution. If the size range of interest must be as broad as possible, however, then the methods described in this paper can be used to correct for differential extrusion and avoidance and unbiased length-frequency distributions can thereby be obtained.

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