The growth of herring larvae, *Clupea harengus* L., in the Clyde: an assessment of the suitability of otolith ageing methods

A. J. GEFFEN*

*Scottish Marine Biological Association, Dunstaffnage Marine Research Laboratory,*
*P.O. Box 3, Oban, Argyll PA34 4AD, Scotland*

(Received 10 October 1984, Accepted 29 August 1985)

Wild herring larvae were sampled from the Firth of Clyde, Scotland in 1980 and 1981 to assess the suitability of otolith ageing methods for herring larval studies. The ages and growth rates were estimated directly from otolith ring counts, by comparison of ring counts with the results of validation studies on reared larvae of known age, and by back-calculation. Growth rates based on otolith data were compared with indirect calculations based on length at capture. The assumption of daily ring deposition, even allowing for a period of lag before the initiation of daily ring deposition, led to incorrect predictions for age at yolk-sac absorption, and back-calculations led to overestimated growth rates, indicating that ring deposition does not begin at hatching and that light microscope counts give a rate different from one ring per day in wild herring larvae.

1. INTRODUCTION

Studies of the growth and survival of larvae in the sea are of major importance for the monitoring and management of many commercial fish stocks. The rates of growth and survival are often estimated by temporal changes in the size and abundance of larvae sampled in spawning and nursery areas. Changes in abundance or shifts in length-frequency modes give limited information on larval biology, since they can provide only population estimates and may be biased by sampling. Ageing techniques using otolith ring counts to provide information on individual age, growth rate, and individual history reflecting growth conditions experienced during larval life promise to be valuable tools for larval studies. Based on the assumption that otolith rings are formed on a daily basis, ring counts have been used for growth estimates of northern anchovy (Methot & Kramer, 1979), cod (Gjøsaeter & Tilseth, 1981), Atlantic herring (Lough et al., 1982) as well as other species. Only a few of these studies have included validation of daily ring deposition or compared otolith ageing techniques with traditional methods of estimating larval growth (Townsend & Graham, 1981; Laroche et al., 1982).

The failure and subsequent closure of the Clyde herring fishery in 1980 afforded an opportunity to test several of the ultimate predictions of exploited fish population models. Any changes in the spawning population of Clyde herring that may have been produced by fishing pressure could have had ramifications in the quality and quantity of larvae produced. Larval growth rates may be one indicator of larval quality and are also a necessary input for many mortality models. The growth of spring-spawned herring larvae in the Clyde
was last studied in detail in the 1930s (Marshall et al., 1937, 1939). The present investigation, a limited study of the Firth of Clyde spring-spawned herring larvae, was undertaken to assess the suitability of otolith ageing techniques for growth studies of wild herring larvae and to provide current information on the growth of this population. Larval growth rates were estimated using a simple linear regression model. A linear model was previously chosen as the best fit for Clyde larval herring growth (Marshall et al., 1937). The evaluation of otolith ageing techniques was based on the accuracy in predicting parameters of the linear growth model.

Recent evidence indicates that otolith ring deposition in fish larvae is not a simple process. Species-specific differences have been shown for both the initiation of ring deposition and the rate of ring deposition. Jones (in press) has called for a more rigorous testing of ring deposition models in the laboratory under both optimal and suboptimal growth rates. This study proposes the use of natural otolith marks as an aid to verifying daily ring deposition in field-caught larvae. Distinct, heavy rings on the otoliths are often associated with specific developmental events such as hatching (Marshall & Parker, 1982; Geffen, 1983) or yolk-sac absorption (Geffen, 1982). These developmental events are length-dependent in many species (Doyle, 1975; Methot & Kramer, 1979). It is thus possible to relate specific otolith structures with independently verified larval sizes or developmental stages. For the wild herring larvae sampled in this study, the results of the various ageing methods used were compared and tested by evaluating the accuracy of each in predicting larval age at yolk-sac absorption, an event which coincides with first ring formation in herring larvae (Lough et al., 1982; Geffen, 1982) and whose timing has been verified independently (Blaxter & Hempel, 1966; Ehrlich, 1972).

## II. METHODS

### SAMPLING

The technique of ageing larvae from counts of otolith rings was applied to herring larvae captured in the Firth of Clyde (55°30'N 05°25'W) on 21 May 1980, between 27 April and 1 May 1981, and on 28 May 1981. Larvae were sampled between the Isles of Arran and Bute in 1980 and between the Isles of Sanda (south end of Mull of Kintyre) and Pladda (south end of Arran) in 1981 by oblique haul with a 2-m diameter stramin net (young fish trawl, Southward, 1970). Most of the hauls were taken at night (2200–0500 h). The herring larvae were immediately removed from samples and preserved in 70% alcohol, which was changed after 24 h and replaced with absolute alcohol on return to the laboratory. The standard lengths of alcohol-preserved larvae were converted to fresh standard lengths according to previously determined shrinkage factors (Geffen, 1982).

### OTOLITH PREPARATION

After measuring each larva, it was soaked in water until pliable enough for dissection. The sagittae were removed, mounted on glass slides in immersion oil, and covered with a glass coverslip which was secured in place with fingernail polish. The otoliths were examined at ×500–1000 magnification and the anterio-posterior diameter, the posterior radius, and the posterior radius of the first ring, were measured using an ocular micrometer. The mean number of rings was calculated from three consecutive counts and otoliths giving greater than 5% error in ring counts were discarded from the analysis.

### ESTIMATING THE GROWTH CURVE PARAMETERS

The growth of wild herring larvae was estimated by the linear model:
GROWTH OF HERRING LARVAE

\[ y = mx + b \]

where \( y \) = larval length in mm, \( x \) = age after hatching in days, and \( m \) = larval growth rate.

The methods used to estimate the model parameters for wild herring larvae included traditional length-at-capture techniques as well as an unverified application of back-calculation to primary ring counts. Four methods (known age; daily ring; length-at-capture; back-calculation) were used to estimate \( m \). Each method was incorporated into a growth model and was evaluated by assessing the effect of each \( m \) on the resulting model parameters.

(1) Known-age model

\[ m = \frac{L}{x}, \quad x_{nw} = x_{nl} \]

where \( L \) = larval length in mm, \( x \) = age in days after hatching, \( m \) = growth rate (mm day\(^{-1}\)), \( n \) = otolith ring counts of wild (\( w \)) and reared (\( l \)) larvae. The age of wild larvae was estimated by comparing ring counts of wild otoliths to those of reared larvae of known age. The age of a wild larva with ring count \( (nw) = 19 \), for example, was assumed to equal the age of a laboratory-reared larva with ring count \( (nl) = 19 \). The age of laboratory-reared larvae at any ring number was obtained from herring larvae reared in several laboratory experiments. These larvae were sampled throughout the larval stage (0–110 days after hatching) for validation of daily ring deposition under a variety of growth conditions. These spring-spawned larvae were reared in laboratory tanks (referred to as 120–1 1980, 120–1 1981, and 500–1 1981) and in large outdoor enclosures (referred to as Loch Ewe bags and Norway pond) as described by Geffen (1982). The ring deposition rates measured for each of these laboratory-reared populations were used to predict the ages of individual wild larvae based on the number of rings observed.

(2) Daily ring model

\[ m = \frac{L}{x}, \quad x = n \]

where \( m \), \( L \), and \( x \) are as for known-age model, \( n \) = ring count of individual wild larvae. Here, \( x \) is assumed equal to otolith ring count. Age was estimated using both a direct correspondence between ring number and larval age (Methot & Kramer, 1979; Townsend & Graham, 1981) and a modified model with a lag period representing the time before regular deposition so that \( x = n + 20 \) (Lough et al., 1982).

(3) Length-at-capture model

\[ m = \frac{(L_2 - L_1)}{t} \text{ or } \frac{(L_1 - L_h)}{x} \]

where \( L \) = larval length in mm on consecutive sampling dates (1 and 2), \( t \) = time interval (days) between sampling dates, \( x \) = age estimated from spawning time and water temperature, and \( L_h \) = length at hatching, assumed = 9 mm. As in the two models above, \( m \) = larval growth rate (mm day\(^{-1}\)). The growth of the wild larval populations was estimated indirectly using the lengths of larvae sampled, assuming an average hatching length of 9 mm and calculating the growth during the time estimated to have lapsed since hatching or between sampling trips. Hatching dates were estimated from reports of spawning and spent fish and daily water temperatures.

(4) Back-calculation model:

\[ m = \frac{(L_2 - L_1)}{t}, \quad t = n \]

where \( L \) = larval length (mm) at capture (2) and first ring deposition (1), \( t \) = the interval (days) between these two length measurements, \( n \) = ring count, and \( m \) = larval growth rate (mm day\(^{-1}\)). Assuming daily ring deposition, \( t = n \). Larval length at first ring deposition was obtained using the Fraser-lee modified equation for back-calculation (Bagenal & Tesch, 1968):

\[ r_1(L_1 - c) = r_2(L_2 - c) \]
where \( L = \) larval length (mm), \( r = \) otolith radius (\( \mu \)m), the subscripts 1 and 2 refer to the values at first ring deposition (1) and capture (2), and \( c = \) the constant of the regression of larval length on otolith radius. A close relationship between otolith radius and larval length should be demonstrated before back-calculating growth rates (using a regression analysis for otolith radius and larval length).

These models for growth estimation were tested by predicting the age at yolk-sac absorption (EYS) for individual wild herring larvae, assuming that the first ring coincides with yolk-sac absorption in wild larvae as has been observed in reared larvae (Geffen, 1982). For the wild larvae sampled, the age at yolk-sac absorption was predicted by calculating the time in days required for a larva to grow from hatching length to the length at first ring formation as estimated by each model, based on that estimated growth rate:

\[
x_{\text{EYS}} = \frac{(L_{\text{EYS}} - b)/m}{x_{\text{EYS}} = \text{age at yolk sac absorption as determined by length at first ring formation}}
\]

\( L_{\text{EYS}} \) = length at first ring formation, \( m = \) growth rate, and \( b = \) hatching length (y-intercept), all as estimated by each model.

### III. RESULTS

Herring larvae sampled in the Clyde on 24 May 1980 ranged from 15 to 25 mm in length (fresh length, calculated from alcohol-preserved length and corrected for shrinkage), with a mean length of 16.92 ± 1.16 mm (± 1 s.d., \( n = 85 \)). The larvae captured during the first of the 1981 sampling trips (25 April–1 May) ranged from 13 to 22 mm in length (mean = 19.41 ± 1.60 mm, \( n = 144 \)) and those sampled on 28 May 1981 were 23 to 32 mm in length (mean = 29.44 ± 2.12 mm, \( n = 32 \)).

In general, the otolith rings of wild larvae were distinct and evenly spaced. The number of rings found on the otoliths of larvae collected in May 1980 ranged from five rings in a 19 mm larva to 22 rings in a 24 mm larva (mean = 10.1 ± 3.40). At the end of April 1981 ring numbers in the larvae sampled ranged from 0 in a 15-63 mm larva to 21 rings in a 21.31 mm larva (mean = 10.6 ± 8.52). On the 28th of May 1981 the range was 26 rings in a 26.29 mm larva to 55 rings in a 31.20 mm larva (mean = 39.82 ± 5.51).

There was a strong correlation between larval length (\( y \)) and the number of otolith rings (\( x \)) in 1981 (\( y = 0.32x + 16.27, r = 0.94, t = 36.81; \text{ d.f. 172, } P < 0.0001 \)). The relationship was not so strong in 1980, probably because the range in lengths sampled was much smaller, but the trend was significant (\( y = 0.22x + 16.49, r = 0.5, t = 5.19; \text{ d.f. 82, } P < 0.001 \)). The relationship between larval length and ring number differed significantly between 1980 and 1981 (\( F = 5.12, \text{ d.f. 1,254, } P < 0.05 \)). If ring number was directly related to larval length as in other developmental events, this relationship would be expected to have a similar slope from year to year. The change in slope may indicate that individual variability in some factor such as growth rate itself may have more of an influence than larval length on ring number. Alternatively, if wild herring larvae deposit otolith rings on a daily basis, the differences between 1980 and 1981 indicate that larval growth rate can be extremely variable within the population, as well as between years.

### AGEING AND ESTIMATES OF GROWTH RATE

The various growth rates estimated for the wild larvae sampled in 1980 and 1981 are represented by predictive growth curves in Fig. 1. Depending on which model of estimation was used, a 20 mm larva caught in 1981, for example, could
be from 11 to 38 days old and growing at a rate of 0.11 to 0.61 mm day\(^{-1}\). The estimated growth rates for the wild populations are summarized in Table I. The results of the four methods were compared and evaluated in terms of published values for both reared and wild herring larvae (Table II).

(1) **Known-age model**

The ages of individual wild larvae were calculated from the observed number of otolith rings, based on the ring deposition rates measured in five populations of
### Table I. Growth model \( (y = mx + b) \) parameters estimated by four techniques in two separate years

<table>
<thead>
<tr>
<th>Technique</th>
<th>1980</th>
<th>1981</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>( m ) growth rate (mm day(^{-1} ))</td>
<td>90% C.L. for ( m )</td>
</tr>
<tr>
<td></td>
<td>0.23</td>
<td>--</td>
</tr>
<tr>
<td>Length-at-capture</td>
<td></td>
<td></td>
</tr>
<tr>
<td>120–1 1980</td>
<td>0.07</td>
<td>0.002</td>
</tr>
<tr>
<td>120–1 1981</td>
<td>0.11</td>
<td>0.005</td>
</tr>
<tr>
<td>500–1 1981</td>
<td>0.18</td>
<td>0.009</td>
</tr>
<tr>
<td>Bags</td>
<td>0.16</td>
<td>0.007</td>
</tr>
<tr>
<td>Norway pond</td>
<td>0.20</td>
<td>0.1</td>
</tr>
<tr>
<td>Daily ring</td>
<td>0.22</td>
<td>0.012</td>
</tr>
<tr>
<td>Back-calculation</td>
<td>0.43</td>
<td>( \pm 0.18^\dagger )</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.29</td>
<td>--</td>
</tr>
<tr>
<td>Length-at-capture</td>
<td></td>
<td></td>
</tr>
<tr>
<td>120–1 1980</td>
<td>0.11</td>
<td>0.001</td>
</tr>
<tr>
<td>120–1 1981</td>
<td>0.17</td>
<td>0.001</td>
</tr>
<tr>
<td>500–1 1981</td>
<td>0.27</td>
<td>0.001</td>
</tr>
<tr>
<td>Bags</td>
<td>0.24</td>
<td>0.001</td>
</tr>
<tr>
<td>Norway pond</td>
<td>0.30</td>
<td>0.001</td>
</tr>
<tr>
<td>Daily ring</td>
<td>0.32</td>
<td></td>
</tr>
<tr>
<td>Back-calculation</td>
<td>0.61</td>
<td>( \pm 0.34^\dagger )</td>
</tr>
</tbody>
</table>

*Assumes hatching length of 9 mm (see text for derivation).

†1 S.D. for mean of back-calculated individual growth rates.

### Table II. A comparison of herring larvae growth rates and growth model parameters from various studies

<table>
<thead>
<tr>
<th>Growth conditions</th>
<th>Duration (days)</th>
<th>Temp. (°C)</th>
<th>Growth rate (mm day(^{-1} ))</th>
<th>Age at EYS (days post-hatching)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Laboratory</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>20–1 tank</td>
<td>35</td>
<td>9</td>
<td>0.13</td>
<td>6–10</td>
<td>Werner &amp; Blaxter (1980)</td>
</tr>
<tr>
<td>500–1 tank</td>
<td>95</td>
<td>7–11</td>
<td>0.33</td>
<td>7–10</td>
<td>Geffen (1982)</td>
</tr>
<tr>
<td>310 m(^3) bags</td>
<td>20</td>
<td>--</td>
<td>0.27–0.35</td>
<td>5–10</td>
<td>Gamble *al. (1981)</td>
</tr>
<tr>
<td>4400 m(^3)</td>
<td>27</td>
<td>7–11</td>
<td>0.44</td>
<td>7</td>
<td>Øiestad &amp; Moksness (1981)</td>
</tr>
<tr>
<td>Wild</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Clyde, spring</td>
<td>30</td>
<td>8–10</td>
<td>0.33</td>
<td>--</td>
<td>This study, 1981</td>
</tr>
<tr>
<td>Clyde, spring</td>
<td>70</td>
<td>--</td>
<td>0.45</td>
<td>--</td>
<td>Marshall *al. (1937)</td>
</tr>
<tr>
<td>Clyde, autumn</td>
<td>--</td>
<td>--</td>
<td>0.49</td>
<td>--</td>
<td>Marshall *al. (1937)</td>
</tr>
</tbody>
</table>
reared larvae of known age. Estimated growth curves were constructed using the measured length at the calculated age for each individual. The estimated population growth rates varied, depending on the ring deposition rates measured in each reared population, from 0.07 to 0.20 mm day$^{-1}$ for larvae caught in 1980 and from 0.11 to 0.30 mm day$^{-1}$ for larvae caught in 1981.

(2) Length-at-capture model

Larvae sampled on 21 May 1980 were estimated to be 44–51 days in age at the time sampled, assuming that they hatched during the first week of April. If growth was linear during this time, as indicated for Clyde spring-spawned larvae by Marshall et al. (1937), the growth rate of these larvae (hatching at 9 mm) was 0.23 mm day$^{-1}$. Reports of spent herring indicated that hatching in 1981 occurred between the third week in March and the second week in April (Dempsey & McLaughlin, pers. comm.). Larvae at the end of the first sampling trip, 1 May 1981, were estimated to be from 17 to 42 days old with growth rates of 0.23 to 0.31 mm day$^{-1}$. If the larvae sampled on 28 May 1981 were of the same population, they grew an average of 10 mm in the 30-day interval between samples at 0.33 mm day$^{-1}$. The mean population growth rate estimated for 1981 larvae was 0.29 mm day$^{-1}$. The changeable duration of spawning and variable hatching date make this particular estimation the least precise of the four methods.

(3) Daily ring model

Estimated growth curves were also produced by plotting length of wild larvae against number of rings, assuming that the rate of ring deposition was constant at one ring per day from the time of yolk-sac absorption throughout the larval stage. The population growth rates estimated in this way were 0.22 mm day$^{-1}$ for 1980 larvae, and 0.32 mm day$^{-1}$ for 1981 larvae.

(4) Back-calculation model

Otolith radius in wild larvae was significantly correlated with larval length in 1981 ($r=0.93; t=33.76; df. 172; P<0.001$) and to a lesser extent in 1980 ($r=0.54; t=5.87; df. 82; P<0.001$) when a smaller range of sizes was sampled. Because otolith size increases linearly with larval length, the length of individual larvae at first ring formation and the individual growth rates of larvae could be estimated by back-calculation. The mean lengths at first ring formation and the individual growth rates of larvae could be estimated by back-calculation. The mean lengths at first ring formation estimated in this way were 14.72 mm for 1980 larvae and 13.08 mm for 1981 larvae. The mean estimated individual growth rates were $0.43 \pm 0.18$ mm day$^{-1}$ for 1980 larvae and $0.61 \pm 0.34$ mm day$^{-1}$ for 1981 larvae.

EVALUATION OF OTOLITH RING MODELS

The length-at-capture and daily ring models were closest in estimation of larval growth rate, and showed most similarity to published growth rates (Table II). However, because the estimate of larval growth varied for each model used, further testing was necessary to evaluate the predictive reliability of each model. Earlier studies showed that the first otolith ring in herring larvae is formed at the
time of yolk-sac absorption (EYS) (Lough et al., 1982; Geffen, 1982). The age at EYS has been established in independent rearing studies for spring-spawned Clyde larvae to be 6–10 days (Blaxter & Hempel, 1966; Ehrlich, 1972; Doyle, 1975), depending on egg size and temperature. Because this event could be identified by a distinct otolith structure and the timing of this event had been determined independently, it was chosen as the basis for comparing the predictions of the different ageing methods. Larval length at first ring formation (ring 1) was 16.71 mm in 1980 and 16.59 mm in 1981, using the regression of larval length and ring number. Using these figures and assuming a hatching length of 9 mm, age at EYS was calculated according to the growth rate of each model (Table I). The length-at-capture model predicted age of EYS to be 33 and 26 days, respectively, in 1980 and 1981; the known age model predicted 38–110 and 25–69 days; the daily ring model 35 and 24 days; and the back-calculation model 18 and 12 days.

IV. DISCUSSION

Marshall et al. (1937, 1939) estimated a growth rate of 0.49 mm day\(^{-1}\) in autumn-spawned Clyde larvae and 0.45 mm day\(^{-1}\) in spring-spawned Clyde larvae. Growth rates calculated from the length at date of capture for spring-spawned larvae caught near St. Andrews (east coast of Scotland) by McIntosh & Masterman (1897) were from 0.12 to 0.20 mm day\(^{-1}\). Schnack (1972) reported an average growth rate of 0.35 mm day\(^{-1}\) in spring-spawned North Sea larvae, with a maximum of 0.50 mm day\(^{-1}\). Growth rates measured for autumn-spawned herring larvae in the north-western Atlantic, summarized by Townsend & Graham (1981), range from less than 0.14 to 0.34 mm day\(^{-1}\). Among the estimates summarized, those based on shifts in modal or mean length frequencies ranged from less than 0.14 to 0.28 mm day\(^{-1}\), while growth estimated from otolith rings was 0.34 mm day\(^{-1}\).

With the exception of back-calculations, the growth rates estimated in the present study fit within the range of published growth rates for wild herring larvae. Indirect measurements of growth make many assumptions about hatching times, dispersion, and mixing of age groups, but they seem to be reasonable first estimates of growth, as recorded in the published literature. In contrast, the ageing of these wild larvae using the ring counts of the slowest growing of reared larvae provided the lowest estimate. In most cases this estimate was unreasonably low (0.07–0.15 mm day\(^{-1}\)), indicating that ring counts in rearing experiments can be different from those in the wild, especially in less than optimal rearing conditions. Using the ring counts measured in fast-growing larvae of known age may also lead to incorrect predictions of growth in the wild. If the wild larvae are growing slower than some reared larvae (<0.40 mm day\(^{-1}\)), then it is likely that ring counts in the wild will be lower than one ring per day (Geffen, 1982). Unfortunately, if ring count in herring larvae is dependent on growth rate, wild larvae cannot be aged if the growth rate is unknown.

The increase in mean ring number observed between the first and second sampling trips in 1981 corresponds to the days elapsed between those trips, indicating that ring deposition may have been daily during this time. The growth
rates estimated by the daily ring model agree closely with those of the non-otolith length-at-capture model. This is as expected, since all of the data points used in estimating the slope of the growth curve encompassed a period when ring number increased by an average of one ring per day. The daily ring method was insufficient for predicting events outside this period, however, as demonstrated by unreasonable overestimates of age at first ring formation of yolk-sac absorption. The back-calculation model, on the other hand, overestimated growth in comparison to the length-at-capture model but predicted more closely the age at yolk-sac absorption.

Clearly, in the case of these wild herring larvae, even after first ring formation, ring deposition is not a daily event throughout larval life. Lough et al., (1982) indicated that daily ring deposition in herring larvae begins after the deposition of the third ring, corresponding to 20 days of age. If a lag period is entered into the calculations, to account for the period between hatching and the initiation of daily ring deposition, the resulting growth rates and age at yolk-sac absorption would be 0.41 mm day⁻¹ and 20 days old for both the 1980 and 1981 larvae. The larvae of known age for validation of these studies raised under various growth conditions showed no indication that ring deposition would assume a visible daily pattern at a consistent point in larval life that could be applied to field studies. If ring deposition is not always a linear function of time, it will probably be necessary to determine the inflexion point, i.e., the initiation of daily ring deposition for each spawning group and each year class.

The most significant advantage of using otolith ageing techniques is the ability to produce statistics on individual larvae rather than on populations. Methot (1983) has utilized these methods to group individual anchovy larvae into birth groups on the basis of ring number and compared the mortality of groups spawned at different times of the year. However, there has so far been no attempt to obtain individual growth rates for either wild or reared larvae.

In this study, back-calculation to obtain individual growth rates is used only as a comparative technique. The application of back-calculation to primary increments has not been examined and many of the prerequisite verified procedures have not yet been followed (Beamish & McFarlane, 1983). Although in some cases herring growth rates estimated on the basis of daily ring deposition were similar to measured and published reports of herring growth, experimental data have shown that individual larvae could vary as much as 100% in ring number at the same age (Geffen, 1982). The justification for using methods which can produce acceptable results on the population level, but are incorrect on the individual level, has not yet been addressed.

I wish to thank the director of the Scottish Marine Biological Association for the resources of the Dunstaffnage Marine Research Laboratory, Mr Alex Dunn and the crew of 'R V Calanus' (SMBA), and especially Dr J. H. S. Blaxter for advice and guidance throughout this study. Financial assistance was provided by the Israel Oceanographic and Limnological Research Company Ltd and the Altrusa International Foundation.

References


