Age-related protandry in the scallop *Chlamys varia* (L.) on the west coast of Ireland

Gavin M. Burnell

*Chlamys varia* is a successive protandric hermaphrodite. It is thus usual to find an imbalance of the sex ratio, with males predominating among small scallops and females among the larger animals. In an attempt to clarify the relationship between age, height, and sex change in *C. varia*, the proportion of males was examined in two populations (Lough Hyne, Co. Cork, and Inner Roskeeda, Co. Galway, Ireland) which had large differences in growth rate. Although individual scallops could not be aged, the construction of von Bertalanffy growth curves using Manzer–Taylor plots gave an accurate estimate of height–age relationships. Because the growth rates were so different between the sites there was no overlap of height/age data. Despite the difference in growth rate, the percentage frequency of males at comparable ages was the same, suggesting that the timing of the sex change was similar and not affected by the environment or the growth rate. If age rather than size is the important sex-determining factor, then it could be acting through the number of sexual resting periods experienced by each individual. By having sex change linked to age rather than size, an individual scallop minimizes the risk of being in a population with an imbalanced sex ratio and thus maximizes its chance of contributing to the gene pool.

**Introduction**

*Chlamys varia* (L.) is a lamellibranch mollusc of the family Pectinidae. It is a small scallop which rarely exceeds 60 mm in height. It is normally attached to the substrate by a byssus extended from just above the anterior projection of the hinge (ear). It is reported from Denmark to the Iberian Peninsula, in the Mediterranean, off the coast of West Africa to Senegal, and is common on the west coast of the British Isles (Tebble, 1976; Earl and Erwin, 1978).

The Irish population is widely distributed along the west coast from Co. Cork to Co. Donegal, but is only abundant within sheltered bays from the sublittoral to 10 m depth (Rodhouse and Burnell, 1979). A commercial dredge fishery exists for *C. varia* on the Atlantic coast of France, but in Ireland there is no organized harvesting. However, a few are taken for local consumption either by hand-picking at low water spring tides or as a by-catch of the oyster (*Ostrea edulis* L.) fishery. Most biological studies on *C. varia* have been carried out on French populations. In particular, its sexuality and reproductive cycle were studied by Lubet (1959), Reddiath (1962), and Lucas (1965) and an ecophysiological study was carried out by Shafee (1980) on a *C. varia* population in the Rade de Brest.

*C. varia* is a successive protandric hermaphrodite (Lubet, 1959; Lucas, 1965). It is thus usual to find an imbalance of the sex ratio, with males predominating among small scallops and females among the larger animals. A similar reproductive mode has been reported for *C. distorta* (da Costa) and *Glycymeris glycymeris* (L.) (Lucas, 1965). Lubet (1959) felt that sex change in *C. varia* was related to age. But because of the wide range of heights observed in each age class, Lucas (1965) reviewed Lubet's data and concluded that it was not possible to satisfactorily deduce the age from shell height. Lucas (1965) studied sex change in relation to height and showed that the mean height of males was significantly (p < 0.01) smaller than that of females, but that the decline in the proportion of males with increasing height was in irregular oscillating steps. He concluded that the timing of sex change from male to female was not constant.

Rodhouse and Burnell (1979) had shown that Lough Hyne *C. varia* achieved a significantly larger shell size.
(L_{max} = 77.0 \text{ mm}) than those in Inner Roskeeda Bay (L_{max} = 50.0 \text{ mm}). Given the difference in growth rates between the sites it should therefore be possible to test Lubet's hypothesis that sex change in *C. varia* is related to age rather than size.

**Materials and methods**

Inner Roskeeda Bay, Co. Galway, is a semi-enclosed inlet of approximately 1 km² on the west coast of Ireland with a full tidal range of 3.7–5.0 m. Lough Hyne (L. Hyne), Co. Cork is a marine lake, 0.8 km², on the south coast of Ireland connected to the sea by a narrow channel. The topography of the lake results in a much reduced tidal exchange (1–2 m) compared with that on the open coast.

One hundred *C. varia* from Inner Roskeeda and 100 from the north shore of L. Hyne were gathered by scuba diving and individually marked using numbered plastic labels attached with epoxy resin. At each site the scallops were held in a 12 mm mesh, seven-compartment Japanese lantern net approximately 2 m off the seabed in 5 m (mean low water) of water. Indigenous and transferred animals were held in alternate compartments at 50 per compartment. The experiment was run from 12 December 1979 to 30 November 1980 in L. Hyne and from 16 January to 5 December 1980 in Inner Roskeeda. The L. Hyne lantern net was changed to reduce fouling on 2 May 1980 and the Inner Roskeeda net was changed on 15 May 1980.

The indigenous scallops used to determine growth rate at each site also served as controls for a reciprocal transfer experiment between the two sites. This showed that the observed differences in growth rate were environmental rather than genetic, since transferred animals assumed the growth rates of the indigenous population (Gosling and Burnell, 1988).

For determination of sex, *C. varia* were collected in July 1980 by scuba diving at both sites. At this time, gonads were ripe and sex was easily determined. Whenever possible, approximately 50 animals were collected from each 10 mm size class (20–29 mm, 30–39 mm height, etc.). Sections of gonad were stained with Ehrlich's haematoxylin and counterstained with eosin. Sex was determined by microscopic examination and the percentage of males calculated for each size class.

**Results**

Growth over one year was determined by measuring the shell height increment for individually labelled scallops. The data for scallops grown at each site were plotted by the method of Manzer and Taylor (1947) and the values of $L_{\infty}$ and $K$ in the von Bertalanffy growth equation were calculated. Assuming that length at zero time ($t_0$) was 0, the growth curve for seven years was calculated for each site. These are shown in Figure 1. This gave estimated height–age data for scallops at both sites. L. Hyne scallops grew fastest, achieving 35 mm (minimum French market size) after one year, which was 9 months faster than those ongrown in Inner Roskeeda. In order to determine the significance of the observed difference in growth rates the instantaneous growth rate (G) based upon height was calculated using the equation:

$$G = \frac{\log_{e} h_{t} + 1 - \log_{e} h_{t+1}}{1 \text{ (year)}}$$

where $h_{t}$ and $h_{t+1}$ are height of the scallop at the beginning and end of the year respectively. The mean instantaneous growth rates ($G$) and standard deviations are given in Table 1 for each size class at both sites. The $G$ values for each size class at each site were tested for significance using Student's *t*-test. The results are included in Table 1.

The smallest scallops (10–19 mm) showed no significant difference in growth rate between sites. All other size classes for which comparative data were available showed significant ($p < 0.05$) differences in G with L. Hyne scallops growing faster than those from Roskeeda. The percentage frequency of male *C. varia* occurring in each size class (height) at both sites is shown in Figure 2. *C. varia* > 60 mm height were rarely found at Inner
Table 1. Levels of significant difference (t-test) between mean instantaneous growth rate \(G\) for *C. varia* ongrow in Lough Ine and Inner Roskeeda. * = \(p < 0.05\), n.s. = not significant, s.d. = standard deviation, \(n\) = sample number.

<table>
<thead>
<tr>
<th>Height (mm)</th>
<th>I. Roskeeda (G \pm \text{s.d.} (n))</th>
<th>L. Ine (G \pm \text{s.d.} (n))</th>
<th>Level of significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>10–19</td>
<td>0.90 0.15 (13)</td>
<td>1.14 0.05 (2)</td>
<td>n.s.</td>
</tr>
<tr>
<td>20–29</td>
<td>No data</td>
<td>0.67 0.10 (4)</td>
<td></td>
</tr>
<tr>
<td>30–39</td>
<td>0.24 0.06 (5)</td>
<td>0.51 0.09 (7)</td>
<td>*</td>
</tr>
<tr>
<td>40–49</td>
<td>0.12 0.06 (22)</td>
<td>0.29 0.06 (17)</td>
<td>*</td>
</tr>
<tr>
<td>50–59</td>
<td>0.07 0.04 (26)</td>
<td>0.14 0.05 (17)</td>
<td>*</td>
</tr>
<tr>
<td>60–69</td>
<td>No data</td>
<td>0.07 0.05 (19)</td>
<td></td>
</tr>
<tr>
<td>70–79</td>
<td>No data</td>
<td>0.05 0.03 (7)</td>
<td></td>
</tr>
</tbody>
</table>

Roskeeda and so a comparison with the larger L. Hyne animals was not possible. Animals at both sites showed a decrease in the frequency of males as height increased, which concurs with the previous research of Lubet (1959) and Lucas (1965) that this species is a successive protandric hermaphrodite. Only one hermaphrodite gonad was found among the 956 gonads examined histologically during this study and the reciprocal transfer experiment (Burnell, 1983). This specimen was not a true hermaphrodite, with a morphologically distinct male and female part, but consisted of mixed male and female follicles as described by Reddiath (1962) for hermaproditic *C. varia*.

Height–age data were obtained from Figure 1 and combined with sex–height data (Fig. 2) to give Table 2. From Figure 2 it can be seen that the rate of decrease in the percentage frequency of males is approximately linear in Inner Roskeeda. In L. Hyne the decrease is also linear and at the same rate once scallops are greater than 59 mm (i.e., > 2 years old, Table 2). Figure 2 also shows that the size class at which 60% of scallops are males is 30–39 mm in Inner Roskeeda and 60–69 mm in L. Hyne.
Acknowledgements

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References


Table 2. The percentage frequency occurrence (%) of male C. varia at Inner Roskeeda and Loch Ine in each 10-mm size class and the corresponding age in years estimated from Figure 1.

<table>
<thead>
<tr>
<th>Height (mm)</th>
<th>I. Roskeeda Male %</th>
<th>n</th>
<th>Age (yr)</th>
<th>L. Hyne Male %</th>
<th>n</th>
<th>Age (yr)</th>
</tr>
</thead>
<tbody>
<tr>
<td>20–29</td>
<td>100.0</td>
<td>19</td>
<td>1.4–2.3</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>30–39</td>
<td>57.4</td>
<td>47</td>
<td>2.4–4.0</td>
<td>76.5</td>
<td>34</td>
<td>0.8–1.0</td>
</tr>
<tr>
<td>40–49</td>
<td>44.9</td>
<td>49</td>
<td>4.1–8.0</td>
<td>85.1</td>
<td>47</td>
<td>1.1–1.6</td>
</tr>
<tr>
<td>50–59</td>
<td>24.5</td>
<td>49</td>
<td>8.1</td>
<td>78.1</td>
<td>32</td>
<td>1.7–2.5</td>
</tr>
<tr>
<td>60–69</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>62.7</td>
<td>59</td>
<td>2.6–4.6</td>
</tr>
<tr>
<td>70–79</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>39.7</td>
<td>53</td>
<td>4.7</td>
</tr>
<tr>
<td>80–89</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>18.2</td>
<td>53</td>
<td>–</td>
</tr>
</tbody>
</table>

age relationships for the two populations. Despite these differences the percentage frequency of males at comparable ages is very similar, suggesting that the timing of the sex change is constant and not affected by the environment either directly or indirectly. If age rather than size is the important determining factor then it could be acting through the number of sexual resting periods experienced by each individual. The small number of hermaphrodites observed in this and other studies (Lubet, 1959; Reddiath, 1962; Lucas, 1965) and the fact that the proportion of hermaphrodites in a population was not directly related to the rate of sex change (Lucas, 1965) point to sex changes taking place while the gonad is in the resting stage. This could mean that hermaphrodites are unusual intermediates resulting from an incomplete sex change.

When age-specific sex ratios are investigated in protandrous hermaphrodites, there is often a fairly sharp change in the sex ratio at a particular age (Warner, 1975). However, the change is not sharp in species where environmental and/or social influences are evident (Buroker, 1983). Environment would not appear to be an important factor in the Irish populations, but as changes can occur occasionally from female to male (Lucas, 1965) there may be social interactions of the type described for Crassostrea gigas (Buroker, 1983) where sex determination is influenced (via chemical secretions?) to some extent by a relationship between contiguous individuals. The trigger for changing sex is not known, but could be related to the amount of winter storage products.

By having sex change linked to age rather than size an individual scallop minimizes the risk of being in a population with an imbalanced sex ratio and thus maximizes its chance of contributing to the gene pool. For example, if sex change were related to size, then in a fast growing environment like L. Hyne, two or three seasons of poor recruitment might result in a dearth of males.

Age-related protandry in the scallop

Table 2. The percentage frequency occurrence (%) of male C. varia at Inner Roskeeda and Loch Ine in each 10-mm size class and the corresponding age in years estimated from Figure 1.

