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**TEMPORAL AND SPATIAL DISTRIBUTION OF *OSTREA EDULIS* LARVAE
IN KILKIERAN BAY, CO. GALWAY.**

BY

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Temporal and Spatial distribution of *Ostrea edulis* larvae in Kilkieran Bay, Co. Galway, Ireland

by

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ABSTRACT

Concentrations and size distributions of *Ostrea edulis* L larvae were recorded in Kilkieran Bay, Co. Galway, Ireland, during 1984 and 1985. Larvae were most abundant during July and August in both years. Large larvae $\geq 250 \mu\text{m}$ were homogeneously distributed through the vertical water column. Higher percentages of smaller larvae $< 250 \mu\text{m}$ were recorded at stations near the mouth of the bay than at stations on or near the beds. Variations in tidal amplitude and low salinities caused displacement of larvae from the beds. There were no significant losses of larvae from the inner bay.

INTRODUCTION

Oyster stocks in Kilkieran Bay, Co. Galway, have been the subject of several investigations in recent years (Edwards and Wilde, 1959; Barry, 1957, 1976, 1977). These studies have included assessments of concentrations of oyster larvae for prediction of the success of later life stages. Such estimates can be useful if sufficient sampling in time and space allows an accurate description of larval abundance. Location of larval sources and water circulation must be critical factors determining the distribution of larvae accepting the limited vertical mobility of oyster larvae (Korringa, 1951).

Locations of the existing parent stocks which generate larvae are well known (Barry, 1975), but currents and mixing of water masses which ultimately dominate larval movements are not. The volume of water at low water in the inner bay, that is the area contained by a line drawn between Birmore and Dinish Islands (Fig. 1), as calculated by cartographic survey is in the order of $261 \times 10^6 \text{ m}^3$. The tidal prism increases this by about 50% at mean high water. Clearly larvae in this bay are exposed to a highly dynamic system of water circulation.

The objective of the investigation was to record distribution and densities of oyster larvae within the inner bay, and by Eulerian and Lagrangian techniques to decipher some of the small-scale circulation processes which contribute to larval dispersion. These data were then used in the development of models to explain some of the annual variations in recruitment in terms of the losses and gains of larvae to the beds.

MATERIALS AND METHODS

The area sampled

Kilkieran Bay encompasses approximately 5800 ha comprising four major basins; the most northerly Leekin basin, Roskeeda Bay, Camus basin and the southern Kilkieran basin (Fig. 1). The main channel connecting these basins runs along the western side of the bay with a single major outlet between Birmore and Dinish Islands to the south. No major rivers drain into the bay, most of the fresh water input being in the form of run off, normally a relatively minor component of the tidal prism. The bottom is mainly marl with mud predominating in some inlets. The two main oyster beds lie in 1-3 m of water on marl in the Leekin basin (station A) and in Roskeeda Bay (station F).

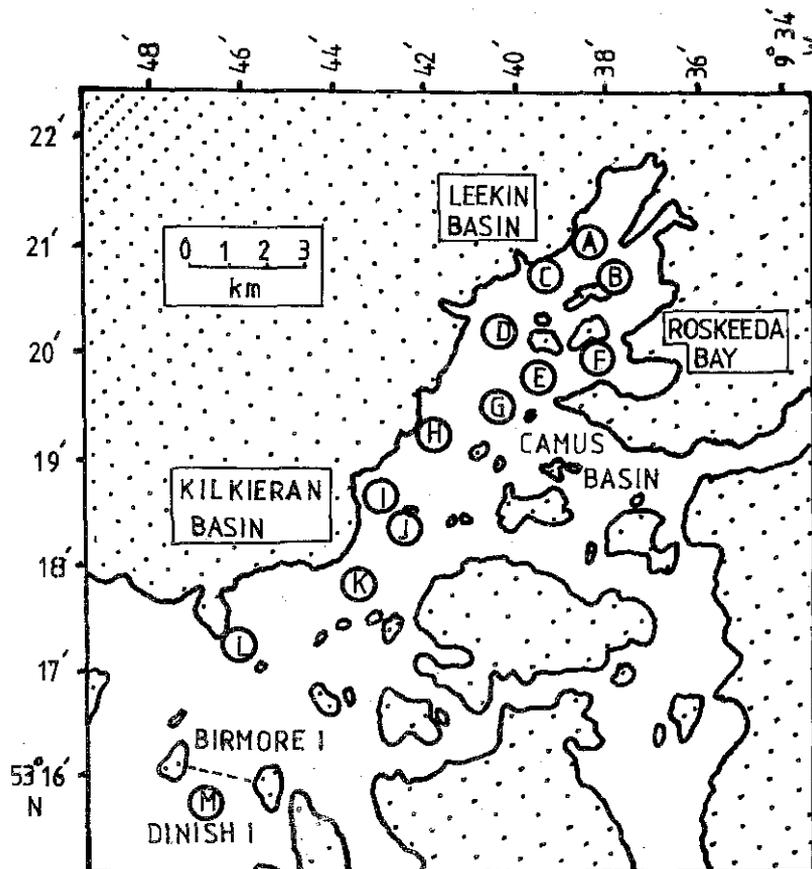


Fig. 1. Map of Kilkieran Bay showing sampling stations.

Larval sampling.

Larval samples were collected in 1984 and 1985 from 30 May to 11 September and 30 May to 2 October respectively to coincide with the breeding season of *Ostrea edulis* in the bay (Wilson and Simons, 1985). During 1984 sampling was carried out at low water ± 1 h at 11 stations (A-K, Fig. 1), while in 1985 samples were taken at high water ± 1 h at 6 stations (E, H, I, K, L and M: Fig. 1).

Samples were collected in 1984 using a hand operated pump calibrated to deliver 100 l water samples, which were taken at 5 m vertical intervals from surface to bottom at each station. Samples were pumped into 90 μ m mesh plankton net squares which were stored with the samples in 1% neutral formalin.

In 1985 larval samples were collected with 90 μ m mesh, 400 mm mouth diameter conical plankton nets. Vertical oblique tows were made from the stationary boat by lowering the weighted net to the bottom and hauling it a measured distance to the surface. The amount of water filtered was quantified with a flowmeter in the net mouth. Between 3.17 and 4.88 m³ were filtered during tows.

Samples were stored in 1% neutral formalin. Larval samples were concentrated in the laboratory by gentle stirring and oyster larvae were counted and individual maximum shell lengths measured on a Sedgewick Rafter cell.

Temperature and salinity readings were made at 5 m vertical intervals from surface to bottom concurrently with sampling at the stations using a temperature/salinity bridge.

Tidal streams.

During 1984 and 1985 the tidal circulation of water bodies in the neighbourhood of oyster beds was followed using drifter buoys. Each drifter consisted of a small surface buoy attached by light rope to a subsurface drogue. The drogue consisted of two 1 m diameter plastic discs set at right angles to bisect each other and weighted to be slightly negatively buoyant. Drogues were positioned at 1, 5 or 10 m below the surface buoy.

Drifters were released over oyster beds at high water neaps or springs and their positions recorded at 30 min intervals during the ebb. The shallowness of the beds necessitated the drogues being set initially at 1m depth, but as the drifters moved into deeper water additional drifters with deeper drogues were launched. Movements from their low water positions during flow tides were recorded in a similar manner on subsequent days. Drifters were used only on calm days to minimise the effect of wind direction on drift.

Temperature and salinity profiles at each location were recorded at 30 min intervals while tracking drifters to monitor mixing in the water body.

Larval fluxes

Export and import of larvae from and to the inner bay were examined in 1985 by measurement of larval fluxes over 12 h tidal cycles at a station situated at the mouth of the bay halfway between Birmore and Dinish Islands. It was impossible logistically to sample synchronously more than one station. The number of stations required to give the best practicable measure of total net flux of larvae through a cross section of the mouth would have been four (Kjerfve, Stevenson, Proehl, Chrzanowski and Kitchens, 1981). However, the use of only one station, while prohibiting an accurate estimate of the total number of larvae being lost or gained in the inner bay, gave a measure of larval numbers moving through the deepest section of the mouth.

Samples were collected and readings made every hour for 12h during both neap and spring tides in June and July. Larvae were collected by vertical/oblique hauls from bottom to surface with a 90 μ m mesh plankton net as described above. Current speed and direction were recorded concurrently with a flowmeter at 5 m depth intervals, as were temperature and salinity.

The instantaneous flux of larvae was calculated as:

$$F_T = V \times W \times D \times C$$

where F_T is the instantaneous flux, V is the depth-averaged instantaneous velocity, W and D are the width and depth of the partial cross-section of the transect respectively and C is the concentration of larvae at the station.

The net flux calculated for each tidal cycle was obtained by expressing instantaneous flux as a function of time (T):

$$F_T = F_N + a \times \sin(2\pi T/12.42)$$

where F_T is the instantaneous flux, F_N is the net flux and a is a coefficient. The tidal period of a complete cycle is assumed to be 12.42 h. This equation fits instantaneous flux as a function of time and is a simplified form of that used by Kjerfve et al. (1981). A sine term is incorporated to explain

variability resulting from tidal oscillations and reduce the standard error of the estimator of F_N . The equation is in the form of a linear model and least squares estimates of F_N and a can be found. Negative fluxes represent imports and positive fluxes exports. A Student's-t test was used to test the null hypothesis $F_N = 0$ ($P < 0.05$) for each tidal cycle.

RESULTS

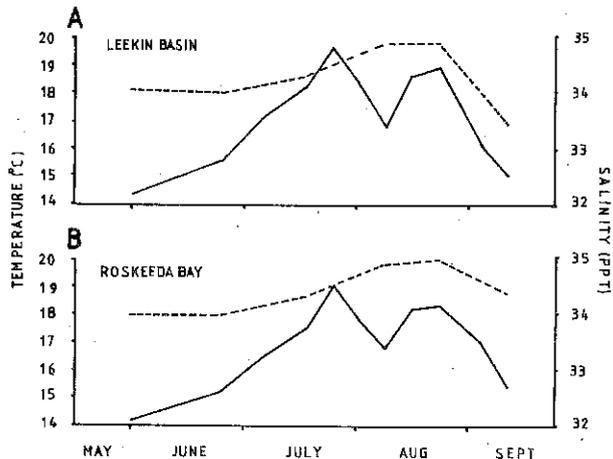


Fig. 2. Average seawater temperatures (°C) and salinities (ppt.) for the Leekin Basin (A) and Roskeeda Bay (B) at low water in 1984. Temperature is plotted as a solid line and salinity as a broken line.

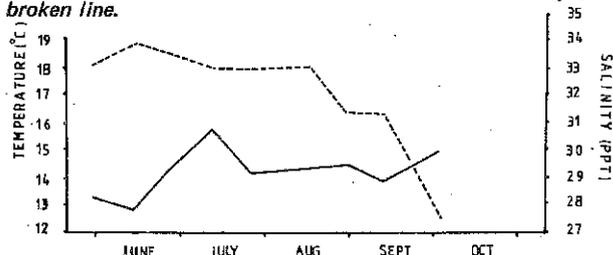


Fig. 3. Average seawater temperatures (°C) and salinities (ppt.) for Roskeeda Bay at high water in 1985. Temperature is plotted as a solid line and salinity as a broken line.

Temperatures and salinities in 1984 and 1985.

Average seawater temperatures and salinities at low water for the Leekin basin (stations A, B and C) and Roskeeda Bay (stations E and F) during 1984 are shown in Fig. 2 A and B respectively. Temperatures were highest in mid-July and mid-August at 19.5°C and 18.9°C in the Leekin Basin and 19.1°C and 18.4°C in Roskeeda Bay respectively. Salinities were relatively high between 34 and 35 ppt. during June to August, but falling in September to a minimum of 33.4 ppt. in the Leekin basin.

Average temperatures and salinities at high water in Roskeeda Bay (station E) for 1985 are given in Fig. 3. Temperature was highest in mid-July at 15.7°C and declined to between 13.9°C and 15.9°C for the remainder of the season. Salinity declined from a maximum of 33.8 ppt. in mid-June to 27.4 ppt. at the beginning of October.

Larval concentrations in 1984 and 1985.

Fig. 4 shows depth-averaged larval concentrations (larvae numbers m^{-3}) for stations A to K over the 1984 sampling period. Oyster larvae were first recorded on 15 June and were present in the plankton throughout July and August, and into the second week in September. The first major peak was recorded at the majority of stations on 12 July being most marked in the Roskeeda Bay stations. A second major peak occurred on 7 August, while concentrations were also relatively high at station C on 24 July. Larval numbers tended to be highest in stations A, B, C, E and F on or close to the oyster stocks. The highest larval count of 840 m^{-3} was recorded at F on 7 August. Concentrations tended to be higher in Roskeeda Bay than in the Leekin basin. The average density of larvae in the Leekin basin (stations A, B and C) was only 63% of that in Roskeeda Bay (stations E and F).

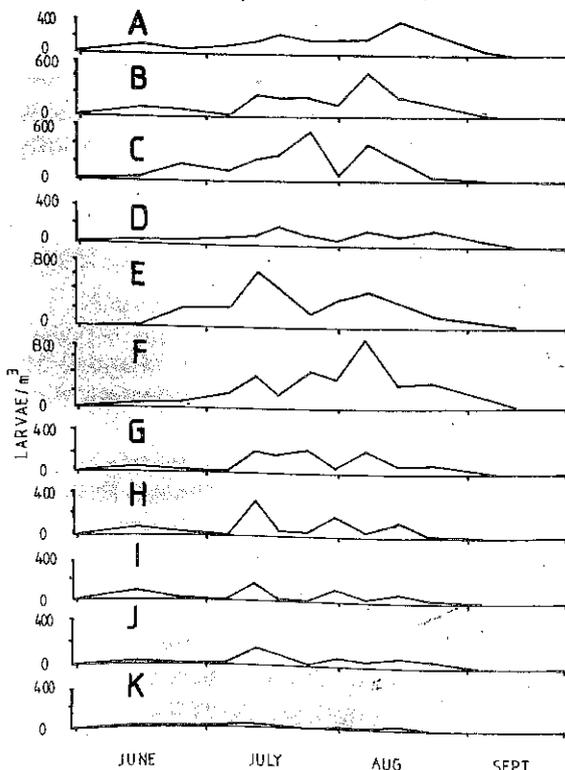


Fig. 4. Average larval concentrations (larvae m^{-3}) at stations A to K during the 1984 season.

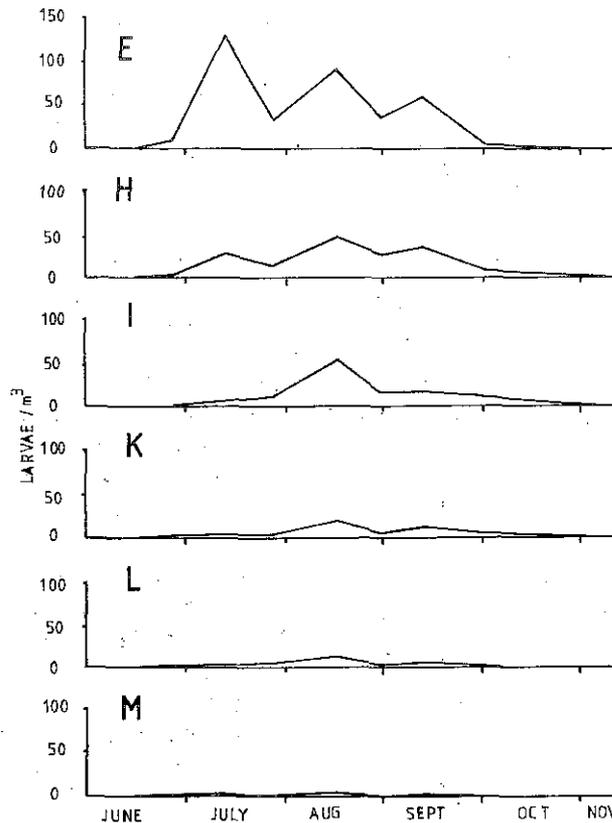


Fig. 5. Average larval concentrations (larvae m⁻³) at stations E, H, I, K, L and M during the 1985 season.

Fig. 5 shows depth-averaged larval concentrations at stations during the 1985 season. Larvae were first recorded on 14 June and were present to 2 October. Peaks were recorded on 12 July, 15 August and 11 September. Larval numbers reached a maximum of 128 m⁻³ at stations E on 12 July (the Leekin basin stations A, B and C were excluded from the 1985 survey). Concentrations were highest on or close to the Roskeeda Bay bed (station E).

Larval distribution with depth.

In 1984 station D was sampled at 1 and 5 m, E, H and I at 1, 5 and 10 m and K at 1, 5, 10 and 15m. Table 1 shows the percentage of larvae recorded at each depth during the season. The number of larvae recorded at each depth at each station on each sampling date have been expressed as a percentage of the total number of larvae in the water column at each station on that date, and a seasonal average with 95% confidence limits for each depth at each station calculated using a standard arosine transformation. There is no evidence of a significant difference ($P < 0.05$) between larval densities at different depths over the season at any of the stations.

Larval size.

The percentage of large larvae at each station with shell lengths $\geq 250 \mu\text{m}$ taken in each sample during the 1984 and 1985 seasons are shown in Tables 2 and 3 respectively. The total percentage of larvae $\geq 250 \mu\text{m}$ shell length taken in each season are also given. In 1984 large larvae were present at one or more stations from 25 June to 7 August. The highest percentage of 16.7% was recorded at station C on 6 July and at B on 1 August. No large larvae were recorded at stations seawards of station G. The percentages for the year varied from 0 to a maximum of 3.03% at station G.

In 1985 larvae $\geq 250 \mu\text{m}$ shell length were first taken in samples on 12 July and were recorded again at some stations on 16 August and 11 September. The highest percentage was 4.59% at E on 12 July. The highest percentage for the season was 3.46% at E. In 1985 some large larvae were taken in the Kilkieran Point basin at K and L although sampling was carried out at high water that year as opposed to low water in 1984.

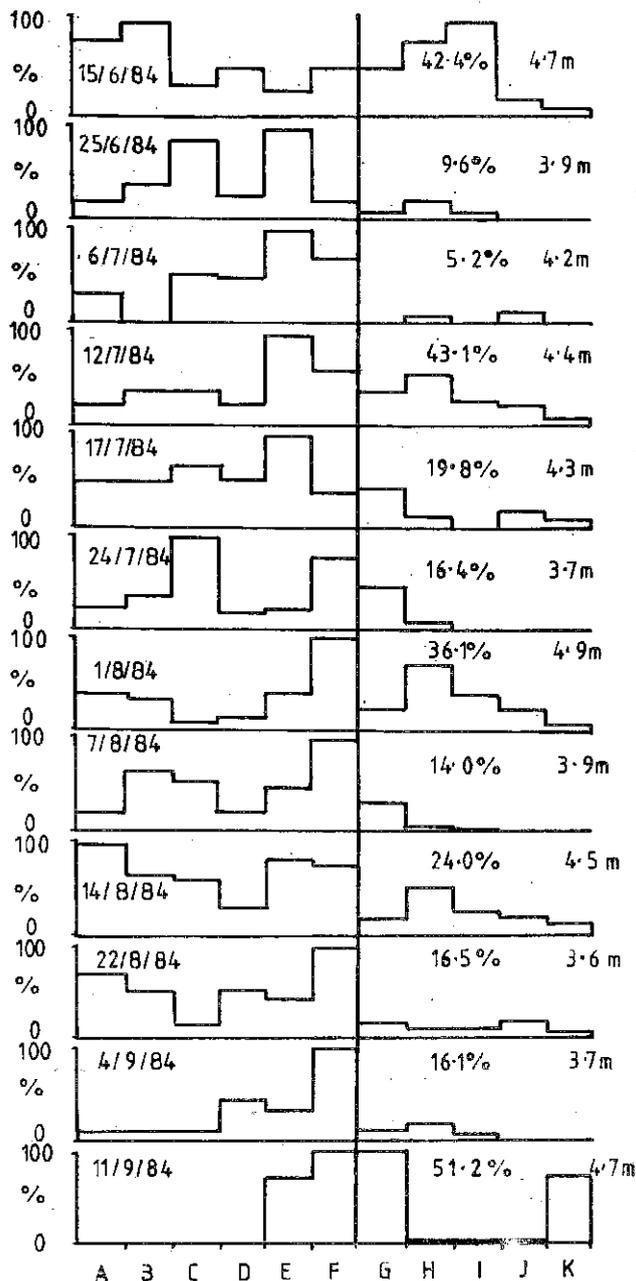


Fig. 6. Larval concentrations at stations expressed as percentages of the maximum concentration in the sample series for each day during the 1984 season. The total percentage of larvae in samples seaward of station F is given with the tidal amplitude (m) above chart datum of the preceding tide.

Larval distributions in relation to tidal cycles and salinity.

The 1984 season was unusually warm with little rainfall. Salinities throughout the bay were high and generally constant. The lowest salinity was 32.7 ppt. at station A on 11 September and the highest was 35.0 ppt. at K on 22 August. There was no evidence of displacement of larvae due to run-off from the land. There were, however, obvious long-term oscillations in the distribution of larvae down the bay (Fig. 4) which were related to variations in tidal amplitude. As the majority of larvae taken in samples averaged 200 μ m shell length it may be assumed that their position down the bay was related to the magnitude of tides in a 2-3 day period preceding sampling. Newly released larvae will be present over the beds initially at stations A-F and thereafter be dispersed by water circulation. In Fig. 6 larval distributions at each station have been plotted for each sampling date. Concentrations have been expressed as a percentage of the maximum concentration recorded on each sampling day. The total percentage of larvae recorded at stations seaward of the beds (G-K) are given in Fig. 6 together with tidal amplitude for the tide one cycle prior to sampling. A relation is apparent between the percentage of larvae at stations G-K and tidal amplitude. A regression of tidal amplitude on total percentage of larvae from G-K gives the linear relation:

$$L = 24.98A - 80.59$$

$$r = 0.745; n = 12$$

where A = tidal amplitude (m), L = the integrated percentage of larvae at stations G-K
r = the correlation coefficient and n = the number of observations.

Hence there is a significant relation ($P < 0.05$) between the distribution of larvae down the bay from the beds and the tidal amplitude. This relation predicts that a higher percentage of larvae pass down the bay at low water springs than at low water neaps when salinity is constant.

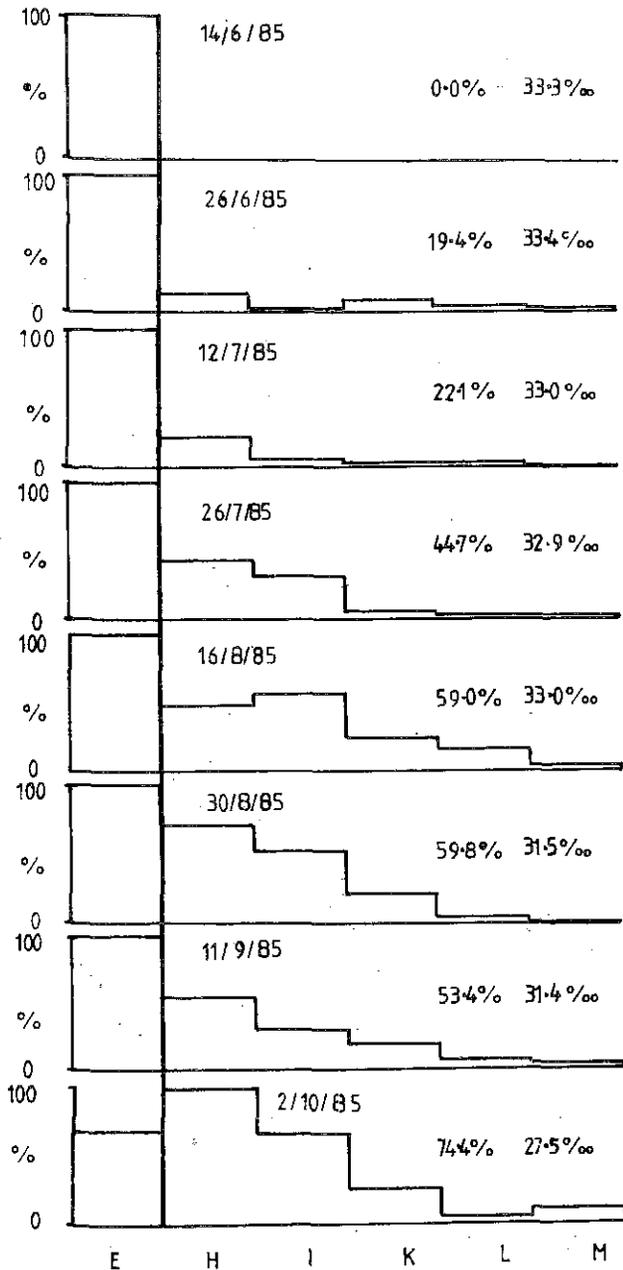


Fig. 7. Larval concentrations at stations expressed as percentages of the maximum concentration in the sample series for each day during the 1985 season. The total percentage of larvae in samples seaward of station E is given with the average salinity (ppt.) at E.

The distribution of larvae at high water in 1985 was quite different. In Fig. 7 larval concentrations expressed as percentages of the maximum concentration recorded on each day are plotted against stations for each sampling date, but unlike 1984 there was no significant relation between tidal amplitude and percentage of larvae at stations seaward of the beds (H, I, K, L and M). Unlike 1984 salinities were depressed due to heavy rainfall. A regression of mean salinity at E on percentage of larvae at stations H-M was significant ($P < 0.05$):

$$L = -9.073 S + 331.924$$

$$r = -0.711; n = 8$$

where L = percentage of larvae at stations H-M, S = the mean salinity at E in ppt., r = the correlation coefficient and n = the number of observations. Hence at high water larvae are displaced seawards by freshwater run-off.

Water movements.

In Fig. 8 paths taken by drifters set at 1 m during ebb and flow from and to the beds are shown. Drifters were tracked during spring and neap tides starting at stations A (Fig. 8 A and B) and F (Fig. 8 C and D) respectively.

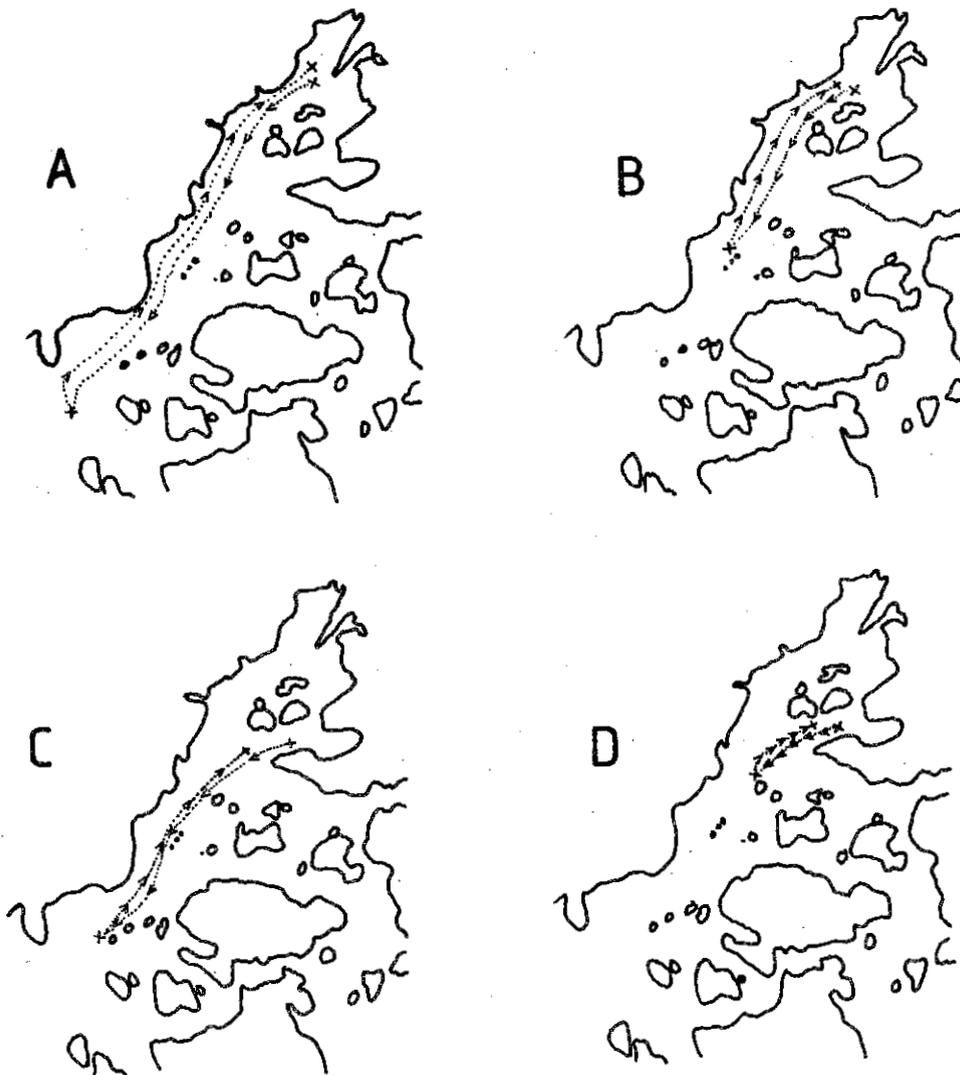


Fig. 8. The paths of drifter buoys set at 1 m during tidal cycles released at high water from stations A (Fig. 8 A and B) and F (Fig. 8 C and D) during springs and neaps respectively.

Ebbing spring tides carry water from the beds down the bay into the Kilkieran basin (Fig. 8 A and C). During tidal flow, however, the Roskeeda water mass takes a more easterly route while Leekin water passes close along the western shore of the bay. This partly segregates the two bodies of water so that they return to their respective basins at high water.

During neap tides Leekin water ebbs down the bay to approximately half way along the path taken at spring tides, and returns to the basin along the western shore (Fig. 8 B). Roskeeda water moves very slowly reaching the western channel at low water and returning with the flow.

There was no evidence of changes in vertical temperature and salinity profiles at the drifter positions during tracking. Drifters set at 5 m and 10 m in deeper water moved approximately half the distance travelled by 1 m drifters.

Larval flux.

Net larval fluxes per unit area and residual currents recorded during a spring and a neap tide at the Birmore-Dinish Island boundary are given in table 4. These results indicate that there were small exports (positive sign) of larvae during both spring and neap tides in July 1985. There were also small residual currents exporting water out of the bay. However, application of the Student's t test showed that neither fluxes nor residual currents were significantly different from zero.

Alternatively losses may be expressed as the proportion of larvae transported during a tidal cycle, which is approximately equal to the net flux expressed as a percentage of the absolute flux, that is the sum of fluxes over a tidal cycle ignoring the sign convention. It was calculated that the percentage of larvae exported during a spring tide was 3.07% of larvae moving across the boundary, while it was 0.5 % during a neap. Once again the results indicate a negligible loss of larvae.

DISCUSSION

Differences between summer water temperatures in Kilkieran Bay in 1984 and 1985 were extreme. This did not effect the timing of the first larval releases, probably due in part to the long-term influence of temperature on gametogenesis in *Ostrea edulis* (Wilson and Simons, 1985). Releases in the study of Barry (1975, 1976, 1977) and in the present study, rose to maxima in early July irrespective of the temperature. Percentages of larvae $> 250 \mu\text{m}$ in Roskeeda Bay were also relatively constant in Barry's records for 1975, 1976 and 1977 and for 1984 and 1985 in the present study at approximately 1 to 4%. The cold summer of 1985 was associated, however, with an extended larval season.

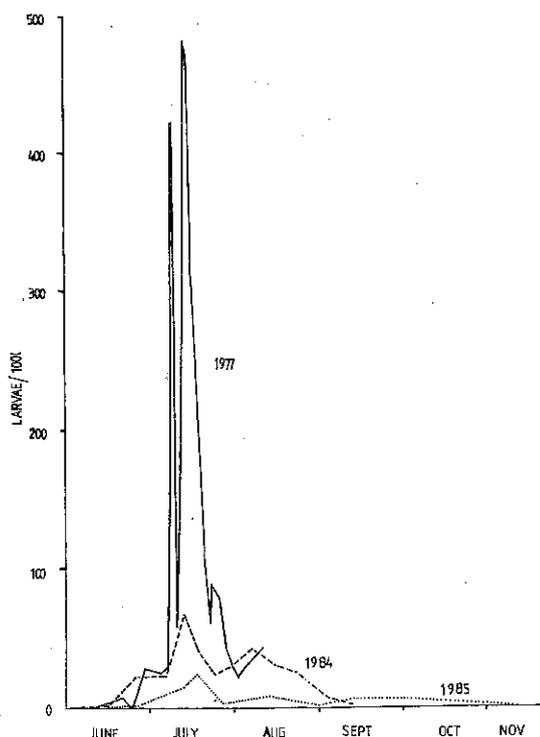


Fig. 9. Larval concentrations in 1977 (state of tide not given) at Outer Roskeeda (Barry, 1977) and concentrations recorded in the present study at E during 1984 (L.W.) and 1985. (H.W.)

Barry (1977) observed that during the three years of his study overall larval concentrations in Kilkieran Bay were low. He suggested that the increase in larval numbers from 1975 to 1977 was in part due to an increase in stock numbers following a cessation of fishing. Korringa (1947) has demonstrated that production of larvae in the Oosterschelde is directly related to the number of broodstock while temperature is of minor importance. This being so, a comparison of Barry's larval counts for Roskeeda Bay with those recorded in 1984 and 1985 must be a cause for considerable concern as to the commercial future of the beds (Fig. 9). There has been a decline in stock numbers between 1977 and 1985 such as to reduce larval numbers approximately twenty-fold. Korringa (1952) has convincingly shown that many European beds disappeared completely where no form of oyster culture was established after wasteful overfishing.

In Kilkieran Bay the majority of oyster larvae originate over shallow beds in the Leekin basin and Roskeeda Bay. The larvae are dispersed vertically through the water column over the beds and in the channels leading seaward. Gravitational flow sweeps larvae off the beds to the western channel where mixing spreads the larvae homogeneously through a water column in excess of 10 m.

The larvae in the channel are carried seaward with the ebb moving as much as 12 km on springs. Although some larvae leave the inner bay they return on the flood. Few larvae are lost from the bay. While larvae from both beds share a common channel to the sea, Roskeeda Bay larvae tend to occupy the easterly side and Leekin larvae the western side of the channel returning to their respective basins at high water.

There was no evidence of a two-layer system in the bay likely to facilitate advection of larvae up the bay (cf. Andrews, 1983; Seliger and Boggs, 1983). When freshwater runoff was significant as in late 1985 it caused displacement of larvae from the Roskeeda bed, so that major concentrations of larvae occurred off the bed at highwater. Many newly released larvae are recycled passing out of the basins, down the channel and back again over several days. Few larvae with shell lengths in excess of 250 μm were recorded in either year of the study. Korringa (1949) suggests that only about 2.5% of larvae reach maturity in the Oosterschelde, Knight-Jones (1952) 1 to 8% and Waugh (1957) 0.4 to 1.5% in the Roach and Crouch rivers. Barry (1977) found the percentage of larvae reaching 250 μm shell length in outer Roskeeda was 3.8% in 1976 and 1.8% in 1977, compared with 2.2% and 3.5% in 1984 and 1985 respectively in the present study. Even allowing for variations in conditions between beds and years the similarity in the proportion of larvae reaching maturity on the different beds is striking. Shell length, however, is not a true indication of the ability of larvae to metamorphose. Larvae depend extensively on lipid reserves accumulated during their pelagic phase and in embryogenesis (Helm, Holland and Stephenson, 1973). Larvae of the same size may have varying levels of lipid depending on their nutritional history. Korringa (1952) states that the number of mature larvae per unit volume of water appears to be a good measure of the intensity of future settlement, and thus can be used with greater accuracy in predicting settling than the so-called "fixation-coefficient" (Lambert, 1946), indicating what percentage of the larvae is mature at a certain moment.

Barry (1976) found as did the present study that the highest percentages of large larvae > 250 μm were on or close to the beds. It is clear that many young larvae are dispersed over considerable distances by tidal circulation, while new broods are repeatedly added to the larval pool. It is possible that the higher percentage of large larvae on the beds is indicative of better growth of the larval fraction resident in these eutrophic areas (Knight-Jones, 1952). Unfortunately measurement of gross primary productivity fails to provide adequate information of the suitability of areas for larval growth (Barry, 1977). It is not the quantity so much as the quality of the phytoplankton which is decisive in larval growth (Korringa, 1952; see also Crisp, Yule and White, 1985).

A second possible explanation for the retention of larger larvae over the beds is that a behavioural mechanism operates such that large larvae sink towards the seabed during ebb only to rise again with the flood. Such a mechanism has been described in *Crassostrea virginica* (Carriker, 1951; Nelson, 1955; Haskin, 1964; Wood and Hargins, 1971). Andrews (1983) has critically reviewed this work and concluded there was little evidence for such a hypothesis (see also Korringa, 1952). Barry (1976) suggests that large larvae concentrate at depth in Inner Roskeeda Bay, but points out that this area experiences peculiar stratification. It is difficult to understand how swimming larvae can maintain positions close to the seabed in turbulent water bodies. Undoubtedly pediveliger larvae close to settlement will tend to congregate on the bottom when swept onto shallow beds (Cranfield, 1973). Pediveligers, however, represented a very small fraction of the sampled larvae.

The most probable explanation for the higher percentages of large larvae over the beds and possibly with depth may lie not in the behaviour of large larvae but rather in the rafting behaviour of newly released larvae which represent the major portion of the larval population. By rising to the surface layers after liberation by the mother young larvae enter a region of the water column which describes the largest excursions from the beds. It is to be expected, therefore, that areas removed some distance from the beds would be dominated by the smaller larvae.

ACKNOWLEDGEMENTS

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Table 1. Total number of larvae recorded at each depth during the 1984 season expressed as an arcsine transformed percentage with 95% confidence limits of the total number taken at all depths at the station.

	D	E	H	I	K
1	46.17 ± 7.25	21.74 ± 6.07	35.89 ± 15.06	21.52 ± 12.42	37.41 ± 17.82
5	43.83 ± 7.25	37.45 ± 10.65	41.12 ± 13.76	47.81 ± 18.16	18.59 ± 11.06
10	—	44.30 ± 11.71	22.72 ± 10.13	28.31 ± 16.64	20.77 ± 12.97
15	—	—	—	—	21.69 ± 11.68

Table 2. Percentage of large larvae at each station with shell lengths ≥ 250 μm taken in each sample during the 1984 season.

Date	Percentage of larvae ≥ 250 μm at each station									
	A	B	C	D	E	F	G	H	I	K
15. 0.84	0	0	0	0	0	0	0	0	0	0
25. 6.84	0	0	0	0	6.06	0	0	0	0	0
6. 7.84	0	0	16.7	0	2.86	0	0	0	0	0
12. 7.84	0	0	0	7.70	4.40	0	0	0	0	0
17. 7.84	0	0	0	8.70	2.90	0	0	0	0	0
24. 7.84	0	9.09	0	0	5.00	0	7.14	0	0	0
1. 8.84	0	15.67	0	0	0	0	0	0	0	0
7. 8.84	0	3.85	0	0	0	4.76	7.69	0	0	0
14. 8.84	0	0	0	0	0	0	0	0	0	0
22. 8.84	0	0	0	0	0	0	0	0	0	0
4. 9.84	0	0	0	0	0	0	0	0	0	0
Totals	0	1.02	1.88	2.14	2.16	1.20	3.03	0	0	0

Table 3. Percentage of large larvae at each station with shell lengths $\geq 250 \mu\text{m}$ taken in each sample during the 1985 season.

Date	Percentage of larvae $\geq 250 \mu\text{m}$ at each station					
	E	H	I	K	L	M
14.						
14. 6.85	0	0	0	0	0	0
26. 6.85	0	0	0	0	0	0
12. 7.85	4.59	2.52	0	0	0	0
26. 7.85	0	0	0	0	0	0
16. 8.85	1.01	0	0	1.11	1.37	0
30. 8.85	0	0	0	0	0	0
11. 9.85	2.17	4.05	0	2.78	0	0
2.10.85	0	0	0	0	0	0
Totals	3.46	1.34	0	1.16	0.85	0

Table 4. Net larval fluxes per unit area (larvae cycle⁻¹ m⁻²) and residual currents (m s⁻¹) recorded during a spring and a neap tide at the Birmore-Dinish Island boundary.

	Spring	Neap
Net larval flux	7138.27 \pm 4356.25	311.64 \pm 53.56
Residual current	0.027 \pm 0.029	0.076 \pm 0.056