THE AMERICAN WHELK TINGLE, *UROSALPINX CINEREA* (SAY), ON BRITISH OYSTER BEDS

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(Text-figs. 1–10)

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Introduction

Although it is probable that the American slipper limpet (*Crepidula fornicata* L.) was introduced with consignments of American oysters about 70 years ago (see Robson, 1929; McMillan, 1939), it was not until 1928 that it was known that the American oyster pest *Urosalpinx cinerea* (Say) had also become established on British oyster beds. The first record of the occurrence of *Urosalpinx* is that of Orton (1927) who figured American tingles in an article relating to the native rough tingle *Ocenebra erinacea* (L.), the two forms being confused. Later, Orton & Winckworth (1928) corrected this mistake and definitely recorded *Urosalpinx* for the first time. Subsequently, Orton (1930) has recorded the finding of specimens of *Urosalpinx* among material collected in 1920. It is almost certain that this pest had been established in one or two places for several years before it was recognized. The confusion between *Urosalpinx* and *Ocenebra* still persists among many oystermen, who lump them together as tingles, drills, or borers, different terms being employed in different districts.

In 1939 the writer was informed that several tingles had been found a week previously among American oysters received by an east coast oyster merchant. It is not known whether they were alive, but the possibility of fresh introductions will exist as long as American oysters are imported.

In presenting this paper I have to thank Mr R. E. Savage for criticism and advice and Mr H. H. Goodchild for the photograph on p. 483. I am also indebted to a large number of east coast oystermen who have supplied specimens or information, and in particular to Mr F. E. Wombwell and the

foremen and dredgermen of the Tollesbury and Mersea Native Oyster Fishery Company, who assisted me in every way possible.

Distribution

In America *Urosalpinx* occurs from Cape Cod to Florida (Galtsoff, Prytherch & Engle, 1937), while it has also been introduced into San Francisco Bay and to Bermuda.[1] Along the English coast its distribution has not been fully worked out. The two main centres of distribution appear to have been Brightlingsea and West Mersea, Essex (Fig. 1), where for many years American oysters have been laid down. It is very abundant in the River Blackwater and in all the creeks running into the Blackwater to the south of Mersea Island. These creeks are leased to a large number of separate planters, most of whom have at some time or other dealt in American oysters. In Brightlingsea Creeks and in the River Colne *Urosalpinx* is also abundant. Farther south it occurs sparingly in the River Crouch and more abundantly in the River Roach and in the creeks around Paglesham. It seems likely that *Urosalpinx* was recently introduced into the Roach-Crouch river system, probably not long before 1934, for local dredgermen then noted the occurrence of a new type of tingle. These men suggested that they were brought with winkles (*Littorina*) or oysters from West Mersea, the winkles, unobtainable in quantity in the Crouch, being used to keep the oyster pits free of weed. *Urosalpinx* evidently multiplied rapidly, for in one year (1936–7) the company working the grounds in the River Roach paid £9. 5*s*. 0*d*. for tingles collected, at the rate of 1*s*. per 1000, equivalent to approximately 185,000 tingles, many of which, possibly even the majority, would of course be *Ocenebra* and *Nucella*.

On the Kentish coast *Urosalpinx* occurs on the Whitstable beds at the mouth of the River Swale, but it does not thrive on these beds in the same way as in the Essex rivers. The beds at Whitstable are practically in the open sea, and the bottom is hard and quite different from that in the Essex creeks. It clearly does not represent a very favourable habitat for *Urosalpinx*, for it has never become abundant despite the fact that numerous oysters from Essex are laid down annually at Whitstable and small tingles must be carried with them. There is no evidence that *Urosalpinx* occurs in the River Medway, for although I have not dredged there, numerous inquiries among oystermen who work in the Medway, and the showing of specimens, elicited only negative answers, although American oysters have been laid down in the area on several occasions. The beds at Faversham in the River Swale are said to carry no tingles.

Although *Crepidula* now occurs from the Humber to Dorset and the Isle of Wight, and has recently been carried in small numbers to the River Yealm, south Devon, although it may not have established itself there, there are no authenticated records of *Urosalpinx* outside of Essex and Kent. It must be admitted, however, that no intensive search has been conducted in other areas,

[1] Needler has recently recorded (*Bull*. LX, *Fish. Res. Bd. Canada*) the occurrence of *Urosalpinx* in the Northumberland Strait area of the Atlantic coast of Canada.

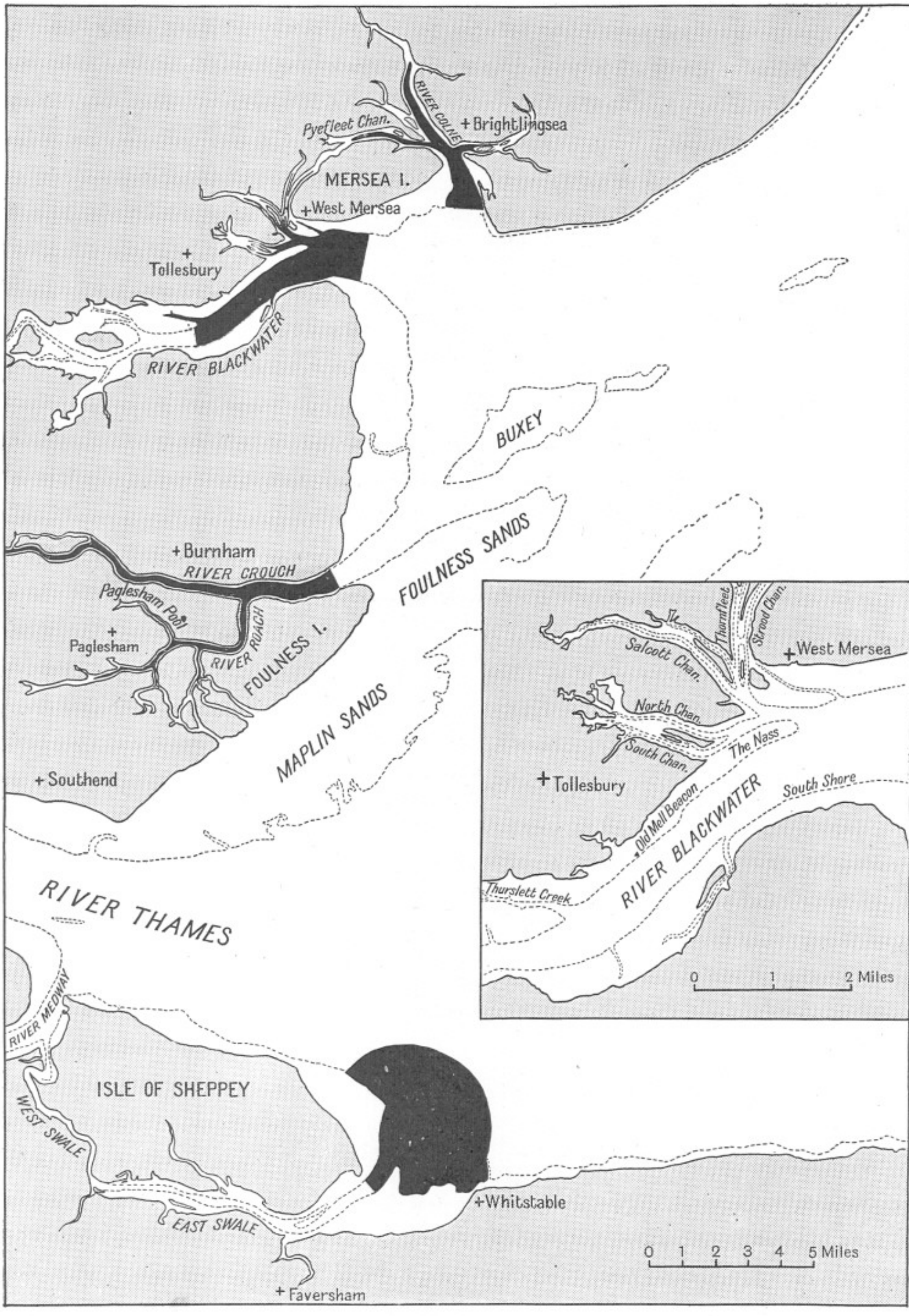

Fig. 1. Chart of the known distribution of *Urosalpinx cinerea* on British oyster beds (from Admiralty Chart). Inset—the Blackwater estuary.

and American oysters have in the past been laid down at several points on the east, south, and north-west coasts, e.g. Cleethorpes and the Orford River on the east, Poole Harbour, Emsworth and Bosham creeks, and the River Yealm on the south, and the Menai Straits in the north-west, while many years ago the beds at Hayling Island were used for wintering oysters from the east coast. If, therefore, as Orton & Winckworth (1928) think, *Urosalpinx* was introduced many years ago with *Crepidula*, an opinion with which the evidence collected by the present writer does not entirely agree, there is a good chance of it occurring wherever American oysters have been laid down. Since *Urosalpinx* lays its eggs in capsules from which the fully formed young tingles emerge, the larval stages being passed in the capsule, it is clear that to infect new localities tingles or their spawn must be carried there along with oysters or cultch.

Until the end of 1939 *Ocenebra erinacea* occurred in fair numbers along with *Urosalpinx* on the east coast oyster beds. Samples of tingles obtained from the River Blackwater in 1938 and 1939 included from 6 to 12 % of *Ocenebra*. Following the extremely cold winter of 1939–40 and the only slightly less cold winter of 1940–1, *Ocenebra* has disappeared from the Blackwater beds; during a fortnight's dredging in May 1941 not a single live specimen was encountered, although empty shells were common. Empty shells of *Urosalpinx* are, on the other hand, only occasionally found, and it seems that the 'great frost' of 1939–40 did not kill off any significant number of *Urosalpinx*; this is hardly surprising, for in its natural home on the Atlantic coast of the U.S.A. it is subjected to much greater extremes of cold and heat than are ever recorded here.

The progressive replacement of *Ocenebra* by *Urosalpinx* in the River Blackwater is well illustrated by some figures given by Orton & Lewis (1931). After the severe winter of 1929 *Ocenebra* was practically wiped out, while *Nucella* was much reduced in numbers—*Urosalpinx*, on the other hand, appeared actually to increase (Table I).

TABLE I. SHOWING THE PERCENTAGE OF *OCENEBRA*, *UROSALPINX* AND *NUCELLA* IN DREDGED CATCHES FROM THE RIVER BLACKWATER (FROM ORTON & LEWIS, 1931)

	Urosalpinx %	*Ocenebra* %	*Nucella* %	Total
1928	7·8	41·2	51	1739
1929	71·2	0·2	28·6	584
1930	77·9	0·11	22	5467

Dredged catches taken in 1941 contained only 1–5 % of *Nucella*, so that this species has also decreased markedly in recent years. During the period 1930–8 *Ocenebra* increased until in 1938 it formed 6–12 % of the catch; it may therefore once again re-establish itself in the Blackwater by migration or transport from outside.

In any river system *Urosalpinx* appears to favour the shallow creeks rather than the main river, and muddy bottoms rather than those of hard gravel or sand. The hard flats off Whitstable seem to be definitely less favourable than, for example, the muddy creeks at West Mersea. Federighi (1931) has shown that the range of salinity tolerated by *Urosalpinx* is much greater than that under which the cultivation of the European native oyster (*Ostrea edulis*) can be carried on.

Migration and movement generally in *Urosalpinx* has been studied in America by Federighi (1931) and Galtsoff *et al.* (1937) with somewhat conflicting results. Federighi, employing tagged drills planted on oyster bottoms at low water, found that even after one month the tagged drills had not moved more than 10–15 ft. from their original situation. It is stated that this was not due to the presence of unlimited food, for drills placed on a hard bottom 20 ft. from an oyster bed did not move towards it. Federighi notes also that contiguous oyster beds in Hampton Roads, Va., which had been left undisturbed for two years, were infested by drills in different quantities; he therefore concluded that significant migration does not take place. Experiments made by Galtsoff *et al.* (1937) did not confirm Federighi's conclusion. Marked drills were released on different types of bottom devoid of oysters and shells, and wire bags, some containing seed oysters and others containing only shells, were planted on the bed at different distances from the drills. In all cases more drills migrated to the bags containing seed oysters than to those containing no live oysters. These experiments were conducted over a period of several months and were thought to show definitely that the migration of drills was influenced by the position of food and that they tend to move towards it at the rate of at least 150 ft. in 48 hr. Galtsoff *et al.* therefore conclude that migration may play an important part in the distribution of drills. It is as well to remember, however, as these authors point out, that under natural conditions the behaviour of *Urosalpinx* is determined by the combined and sometimes antagonistic effects of several factors and cannot be attributed to a single cause.

There is a general belief among Essex oystermen that tingles are able to detect the presence of freshly laid oysters and to move on to them, and several instances were related of tingles which appeared suddenly on oysters laid down at low-water mark on ground previously free of this pest. This move is, however, observed during the breeding season, and it might be argued that the tingles moved on to the oysters from the surrounding clean bottom for the purpose of depositing their spawn. During 1941 a wooden trough 215 cm. long, coated inside with pitch and filled with sea water, was used at Conway to study the movements of marked drills. Food—spat or brood oysters, or barnacled stones—was placed at varying distances from the centre, towards one end of the trough, and the drills lined up at the centre and their movements noted at intervals of 30 min. or more. Ten drills were employed in most experiments and water temperatures were recorded. When the illumination over the whole surface of the trough was the same it was found that the drills moved at random and showed no ability to detect the presence of food or tendency to move towards it. This was true even when the distance between the drills and the food was reduced from the maximum of about 105 cm. to as little as 35 cm. These experiments were repeated a great number of times with identical results. Until steps were taken to even out the intensity of light by appropriate shading, the drills tended to move out of the sun in bright weather and take up a position on the shady side of the trough. Individual drills varied considerably in the degree and rate of their movements, but the maximum rate of creeping for a distance of not less than 90 cm. was 3 cm./min., at a temperature of 14·4° C. This compares favourably with the figure given by Federighi, 2·6–2·8 cm./min. at 26·5° C. This high rate of creeping was only observed once, and in the majority of experiments the most active drill covered the distance of 105 cm. to the end of the trough in 1–1½ hr., a rate of creeping of 1·17–1·75 cm./min. This rate was observed on occasions at all temperatures between 13 and 23° C. At temperatures from 23 to 25° C. only very slight movement occurred, above 25° C. none. Such high temperatures are probably never experienced on British oyster beds, but were frequently exceeded in the laboratory experiments of Federighi without apparently causing any inconvenience to the drills.

Drills moving consistently in one direction at the rate of 1·5 cm./min. would cover a distance of 43·2 m. in 48 hr. The rate of travel observed under natural conditions by Galtsoff *et al.* was 150 ft. (45·72 m.) in 48 hr. This was the minimum rate of travelling for the drills that reached the bags containing seed oysters, and presumed that they travelled in a straight line. It seems certain, therefore, that *Urosalpinx* is capable of moving at this rate; but it has not yet been satisfactorily established that it is able to detect the presence of food and move towards it, and it seems unlikely, from the limited evidence available, that migration is of more than local significance in the distribution of the species.

Growth

The shell dimension most useful in the study of growth rates in gastropods is the height from the tip of the siphonal canal to the top of the spire; this dimension has been employed in this study. In most localities in America the adult *Urosalpinx* is stated (Galtsoff *et al.* 1937) to average slightly over 2·5 cm. in height, but at Seaside, Va., specimens as large as 6 cm. in height are said to be very common. Federighi (1931) found that the largest females from Chesapeake Bay measured 3·3 cm. and the largest males 2·9 cm., but the most usual size was from 2·1 to 2·5 cm. The giants from Seaside, Va., appear to parallel the giant forms of *Nucella lapillus* described by Moore (1936) from the British Museum collection, having been obtained originally from Minehead and Swanage. The present writer has subsequently collected a number of such giants from the River Crouch. The peculiar environmental conditions leading to the production of these giant forms are not known, but in some gastropods parasitism is a factor of importance (Rothschild, 1936).

Urosalpinx on British oyster beds considerably exceeds the size generally reached in America. The largest individuals obtained were 4·3 cm. in height, and the only one sexed of this size was a female. The largest male measured 3·9 cm. Males over 3·5 cm. are always rare, but very large females are not uncommon on grounds which have not been worked intensively. This increase in size of an American form in British waters is also well shown by the slipper limpet, *Crepidula fornicata*.

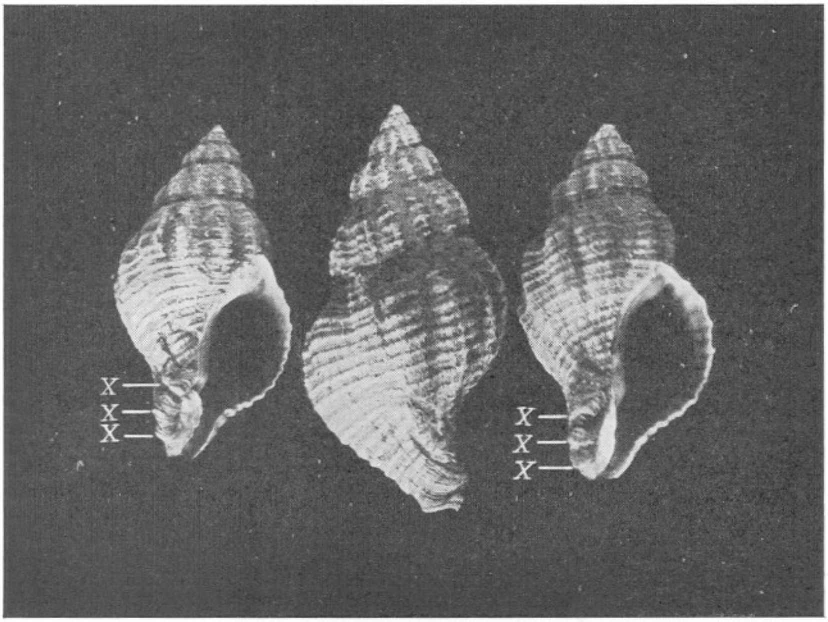

Fig. 2. *Urosalpinx cinerea* Say, showing growth marks (*X*) on the shell bounding the siphonal canal: × 1½.

Apart from the general observation that females grow larger than males the American work contains no information on growth rate or duration of life. This observation is equally true of *Urosalpinx* on British beds, and in the following analysis of growth males and females have been treated separately. Size-distribution curves of catches of females usually show a number of closely approximated peaks, and it appears that the annual increment in height is small after the first few years. This impression is confirmed by a study of the growth marks which may frequently be clearly seen on the tip of the shell bounding the siphonal canal (Fig. 2). Such growth marks in large shells are usually separated from the extreme tip and from each other by 0·1–0·3 cm. Considerable overlapping of successive year groups must therefore occur, and this seriously impedes or prevents altogether the fixing of the position of the peaks in the frequency curves without recourse to further analysis. For this reason wherever possible the analysis of size-distribution curves has been carried out by the freehand drawing method advocated by Buchanan-Wollaston & Hodgson (1929).

TABLE II. SIZE DISTRIBUTION OF *UROSALPINX* SAMPLES COLLECTED FROM THORNFLEET, RIVER BLACKWATER DURING 1941

Shell height	24 May 1941		10 June 1941		8 July 1941		26 August 1941	
cm.	Females	Males	Females	Males	Females	Males	Females	Males
1·6	1	—	1	—	—	—	—	—
1·7	—	—	1	—	—	1	—	—
1·8	1	1	—	—	1	—	—	—
1·9	—	1	—	—	—	1	—	—
2·0	7	1	2	1	3	1	—	—
2·1	—	2	—	2	2	1	—	1
2·2	4	1	1	—	1	2	—	—
2·3	2	—	3	3	5	1	—	—
2·4	1	1	5	2	4	3	2	—
2·5	4	3	15	14	12	5	1	3
2·6	6	9	27	22	19	8	2	2
2·7	12	5	46	27	53	13	3	4
2·8	12	13	55	24	36	23	6	6
2·9	14	9	45	32	46	17	4	4
3·0	6	17	43	24	31	21	3	6
3·1	8	7	34	16	16	9	5	4
3·2	3	3	12	5	7	7	2	3
3·3	5	2	17	4	7	3	—	—
3·4	2	1	4	—	2	3	1	1
3·5	1	—	1	—	—	—	1	—
3·6	3	1	1	—	—	—	—	—
3·7	1	—	3	—	—	—	—	—
3·8	—	—	—	—	—	—	—	—
3·9	1	—	—	—	—	—	—	—

During 1941 a series of four samples of tingles was collected from the beach in Thornfleet (a creek running into the River Blackwater, Essex, near its mouth) at approximately monthly intervals from May to August (Table II). The first lot was collected on 24 May, when tingles were first appearing on the shore at the beginning of the spawning season, and the last on 26 August, when many had already migrated to deeper water. On each occasion all visible tingles were hand collected from stones, old drain pipes, mooring chains, etc., in the region of low-water mark of spring tides. On the same day that the first shore sample was collected a further lot was obtained by dredging in the channel adjacent to the beach. In Fig. 3 the size distribution of the females contained in the four monthly samples from Thornfleet are shown, those of May, June, and July being resolved into their components. The August sample was too small to permit of such treatment, while the May sample contained also those females dredged in Thornfleet on the same day. It will be seen that the modes of successive year groups are separated by an interval of about 0·2 cm., or slightly more in the younger age groups, and rather less in the older ones.

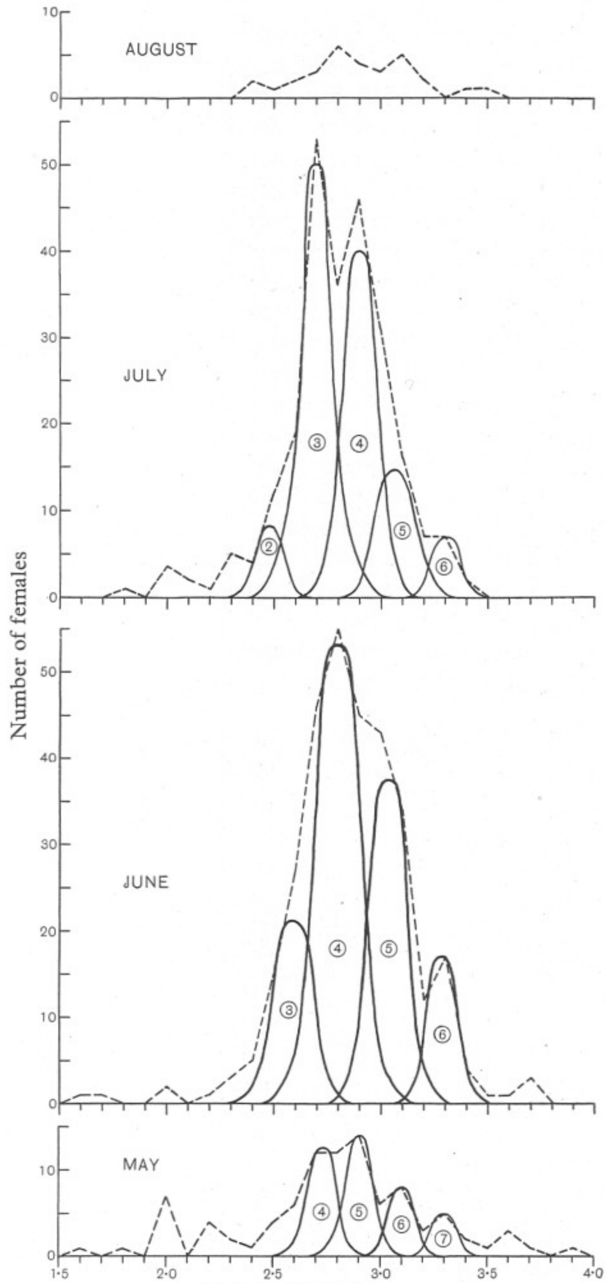

Fig. 3. Size-distribution curves of females from samples of *Urosalpinx* hand collected from the beach of Thornfleet, River Blackwater during 1941. The May sample also includes those dredged in the adjacent channel on the same day. In this and subsequent figures the numbers in the circles represent the probable age of each year group.

The comparison of the May and July groups shows the growth during 1941, up to 8 July, to have been rather less than 0·2 cm., as would be expected.

Comparison of the May and July samples shows the presence in July of two modes on the left-hand side not represented in May. In July these modes lie at 2·47 and 2·7 cm. respectively; but the sample also contains tingles as small as 1·8 cm. which cannot belong to the age group with the mode at 2·47 cm. The latter mode therefore must belong to the 2-year-old group, while the smaller tingles would belong to the 1-year-old class with a mode somewhere in the region of 2·0 cm. This 1-year-old group, which must numerically be the strongest, is very poorly represented on the shore during the summer.

Tingles hatched from egg capsules in July, and reared on small oyster spat in a plunger jar at Conway during 1941, reached a maximum height of 1·2 cm. by the end of the feeding period, the mode of the group being at approximately 1·0 cm. These tingles would start the following season at this size and might be expected to reach about 2·0 cm. by July, i.e. by the end of their first year. Dredged samples of tingles collected during the summer which contain fair numbers of very small tingles usually have a suggestion of a peak around this figure; unfortunately, as yet no method has been devised for collecting adequate samples of these small tingles, the majority of which pass through the rings of an ordinary oyster dredge.

That a growth rate similar to that observed in 1941 prevailed among female tingles in other years is shown by Figs. 4 and 5, which show the results of

TABLE III. SIZE DISTRIBUTION OF *UROSALPINX*

Shell height cm.	River Blackwater 15 July 1939 Females	River Blackwater 15 July 1939 Males	Thurslett Creek R. Blackwater 15 May 1940 Females	River Roach 13 May 1939 Females
1·6	—	—	—	1
1·7	—	—	—	3
1·8	—	—	—	2
1·9	—	—	—	7
2·0	—	—	—	8
2·1	2	2	1	4
2·2	1	2	1	7
2·3	4	6	1	5
2·4	7	4	1	1
2·5	11	7	4	13
2·6	14	7	11	12
2·7	23	14	16	15
2·8	17	9	27	19
2·9	16	9	23	13
3·0	12	5	30	9
3·1	9	2	21	14
3·2	2	1	38	7
3·3	7	—	23	14
3·4	1	—	13	8
3·5	2	—	19	3
3·6	1	—	5	2
3·7	—	—	8	—
3·8	—	—	1	3
3·9	—	—	1	2
4·0	—	—	3	1

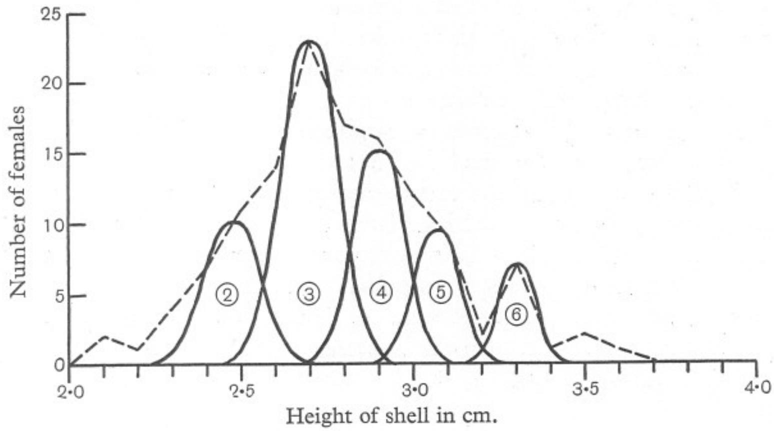

Fig. 4. Size-distribution curves of females from a sample of *Urosalpinx* dredged from the River Blackwater on 15 July 1939.

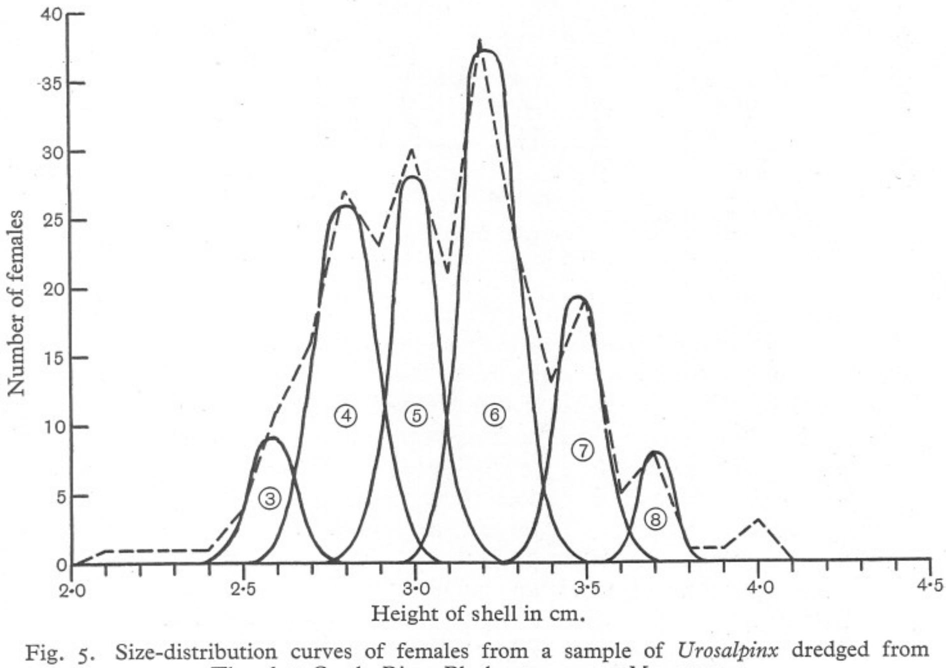

Fig. 5. Size-distribution curves of females from a sample of *Urosalpinx* dredged from Thurslett Creek, River Blackwater, on 15 May 1940.

analysing samples of tingles (Table III) dredged from the River Blackwater in 1939 and 1940. Both samples show a series of successive modes at intervals of about 0·2 cm., the position of the modes agreeing reasonably well with the corresponding sample of the year 1941, when due allowance is made for the lateness of the season in that year.

Although a number of samples of tingles have been collected from other rivers in Essex, only one (included in Table III) contains sufficient females to permit of the resolution of the frequency curve into its components. This sample was obtained in 1939 from the River Roach, a tributary of the Crouch, and is shown in Fig. 6. Successive modes are rather more distant than in the Blackwater collections, being approximately 0·25 cm. apart, indicating a more rapid growth rate in the River Roach. At least seven age groups are represented in this sample, the first mode representing most probably the 3-year-old group (cf. Fig. 2).

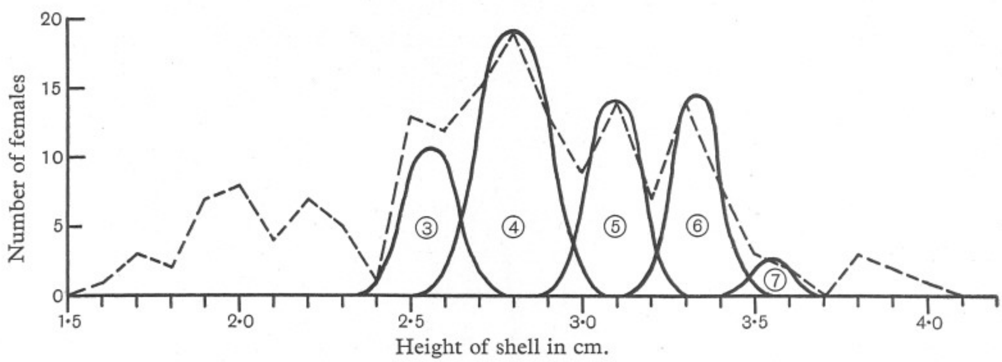

Fig. 6. Size-distribution curves of females from a sample of *Urosalpinx* dredged from the River Roach on 13 May 1939.

Summarizing the information obtained concerning growth rate in female tingles, from both size-frequency curves and the study of growth marks, it seems probable that in July, when a new batch of young emerges from the capsules, the 1-year-old group would average about 2·0 cm. in height, the 2-year-old 2·5 cm., 3-year-old 2·7 cm., 4-year-old 2·9 cm., 5-year-old 3·1 cm., 6-year-old 3·3 cm., 7-year-old 3·5 cm., 8-year-old 3·65 cm., 9-year-old 3·8 cm., 10-year-old 3·9 cm., and thereafter successive age groups would occur at intervals of 0·1 up to 4·3 cm., the largest size recorded. It seems probable that this 4·3 cm. specimen was about 14 years old.

Frequency curves derived from catches of male tingles obtained from Thornfleet in 1941 (see Table II) when analysed show successive modes at intervals of 0·2 cm. or rather less (Fig. 7). The July sample contains representatives of six age groups without taking into account tingles below 2·3 cm. in height. As in the females from these catches, the July sample shows two modes not present in May, so that the first mode in May must comprise indi-

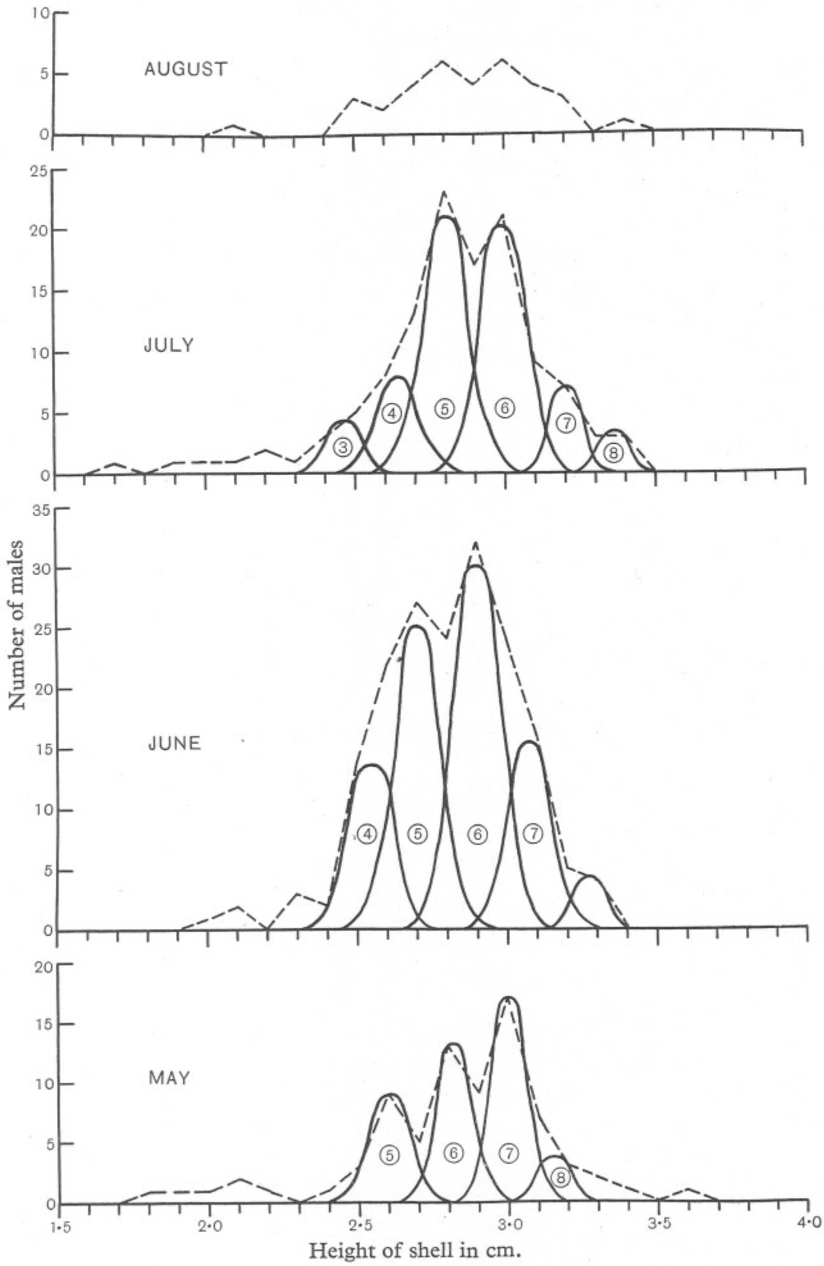

Fig. 7. Size-distribution curves of males from samples of *Urosalpinx* hand collected from the beach of Thornfleet, River Blackwater, during 1941. The May sample also includes those dredged in the adjacent channel on the same day.

viduals at least 3 years old; evidence presented below shows that they are in fact older. The July sample contains tingles down to 1·7 cm. in height which cannot belong to a group with a mode of 2·46 cm., consequently the latter must consist of individuals at least 2 years old. Comparison of Figs. 7 and 8, the latter being the analysis of a sample taken in July 1939 from the River Blackwater (see Table III), reveals an extra mode at 2·3 cm. in the 1939 sample in addition to one at 2·51 cm. corresponding to the first mode (2·46 cm.) in the July 1941 sample. When it is remembered that the 1941 season was very late the slight discrepancy between the position of the modes in the two years is explained. The July 1941 frequency curve (Fig. 7) would therefore, if complete, show a further mode slightly below 2·3 cm., but this age group could not reasonably contain individuals as small as 1·7 cm., the smallest size in-

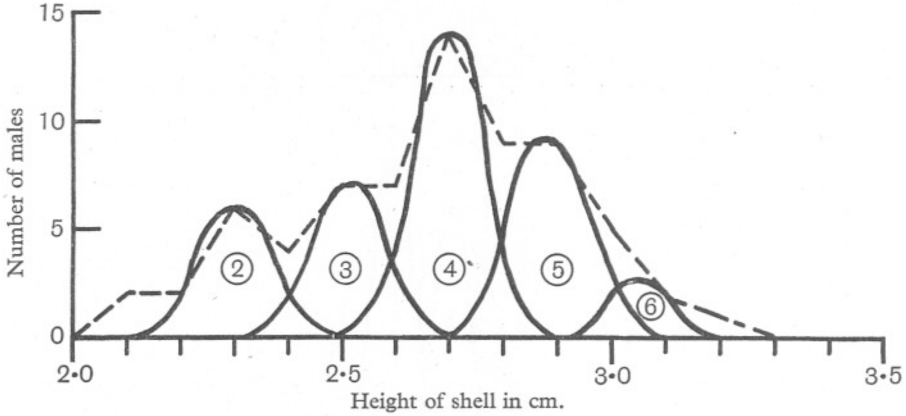

Fig. 8. Size-distribution curves of males from a sample of *Urosalpinx* dredged from the River Blackwater, 15 July 1939.

cluded in the sample, which must belong to a still earlier group. We therefore conclude that the first mode shown by the July 1941 sample (Fig. 7) represents the 3-year-old group and consequently the first mode in May 1941 represents the 5-year-old tingles.

In males growth thus proceeds roughly as follows: 1st summer, 1·0 cm.; 1st year, 1·0–1·8 cm.; 2nd year, 1·8–2·3 cm.; 3rd year, 2·3–2·5 cm.; 4th year, 2·5–2·7 cm.; 5th year, 2·7–2·9 cm.; 6th year, 2·9–3·1 cm.; 7th year, 3·1–3·25 cm.; 8th year, 3·25–3·4 cm.; 9th year, 3·4–3·55 cm.; 10th year, 3·55–3·65 cm.; and thereafter at about 0·1 cm. per annum. The largest male so far collected, viz. 3·9 cm., would therefore be about 13 years old, a similar age to that deduced for the largest female. Although both males and females up to this extreme age may be found on occasion, no substantial number of males over 3·6 cm. or females over 3·9 cm. have been collected, so that the approximate duration of life in *Urosalpinx* is 10 years.

Parasites

During the examination of dredged samples of *Urosalpinx* for sex seven specimens have been found containing what appears to be a very specialized arthropod parasite, probably an isopod, in the liver region. All the tingles so affected came from the oyster beds in the mouth of the River Blackwater. In addition one individual from the same river has been found with the gonad completely riddled with rediae containing cercariae agreeing exactly with *Cercaria sensifera*, which Stunkard & Shaw (1931) have described in *Urosalpinx* from Woods Hole, U.S.A. These authors point out that it is possible that *Cercaria sensifera* is identical with *C. purpurae* (Lebour, 1912), found in *Nucella lapillus* in British waters, although the survival and establishment of an alien trematode is by no means impossible.

Breeding

As in several other carnivorous gastropods the eggs of *Urosalpinx* are deposited in tough horny capsules each of which contains several eggs. The capsules are attached to the substratum in clusters and from them fully formed young tingles emerge. The egg capsules have been described and compared with those of *Nucella* and *Ocenebra* by Orton & Amirthalingam (1929), while the actual method of formation of the egg capsule and the structure of the organs involved has been studied by Fretter (1941) in a variety of British stenoglossan gastropods, including *Ocenebra* and *Nucella*. The deposition of egg capsules usually begins during late April or early May and continues during June and July. Spawning reaches its maximum during June and thereafter declines. During 1940 the first few capsules were found in the River Blackwater in the second week in April, but although the winter had been exceptionally severe the spring was milder than usual. In 1941, when the spring months were exceptionally cold, no spawn was found until the third week of May. During the last fortnight in May, when the water temperature rose steadily from 11·6 to 13·4° C., the number of tingles dredged in the act of spawning and the total amount of spawn caught per day increased steadily. It seems probable therefore that spawning begins each year in British waters when the sea temperature in its seasonal rise reaches 12–13° C. This estimate agrees well with the figure given by Galtsoff *et al.* (1937) for Delaware Bay, U.S.A., where capsule deposition is stated to begin when the water temperature has reached 13·9° C. The bulk of the spawn is deposited during May and June; but small numbers of freshly laid capsules may be found in August, e.g. a sample of spawn collected from the River Blackwater on 27 August 1940 contained about a dozen freshly deposited capsules—a small number contained embryos in early stages of development, but the great majority of the capsules had already hatched or were in process of hatching. The earliest date at which capsules have been seen from which the young tingles had emerged is 2 July (1940); as already mentioned, the first few capsules laid in that year were seen during the second week in April. Several batches of spawn obtained in June 1940 showed no embryos advanced beyond the early shelled stages. In this year, although a few capsules were seen in April no substantial quantity was deposited until May. We may therefore conclude that incubation of capsules under natural conditions occupies about two months.

Further observations made in 1941 confirm the above estimate. Deposition of capsules began in the Blackwater during the third week in May, spawning being in full swing by the first week in June. No hatching had occurred in samples obtained in June, no capsules containing embryonic stages later than morulae; but samples of spawn procured on 23 July showed a large number of capsules with young tingles emerging. The period of incubation was therefore 7–8 weeks.

In the laboratory, incubation of capsules deposited by tingles in experimental tanks at Conway has been carried out in plunger jars, with and without frequent changes of water. The periods of incubation observed were 27–32 days at an average temperature of 22·6° C., and 44–50 days at an average temperature of 18·3° C. According to the records given by Orton & Lewis (1931) of sea temperature in the River Blackwater during the four years 1926–8 and 1930, the mean during the period mid-May to the end of August, when the spawn of *Urosalpinx* is being incubated, varies between 13·5 and 19° C., so that the period of incubation under natural conditions in this river might be expected to exceed slightly the period of 44–50 days recorded above. This expectation accords very well with the period of about two months deduced from observations of the time of commencement of spawning and hatching. In years when the water temperature rises rapidly during spring, spawning may begin in April, but it is not usually general until May or, in late seasons such as 1941, until June. Emergence of young tingles therefore generally occurs about the middle of July.

Federighi (1931) found that the average period of incubation under laboratory conditions of *Urosalpinx* capsules from Hampton Roads, Va., U.S.A., varied between 36 and 44 days with a mean of about 40 days. Water temperature in these experiments varied from 22 to 28° C. Galtsoff *et al.* (1937) give the period of incubation in Delaware Bay as varying from 21 to 53 days. In American waters spawning of *Urosalpinx* apparently occurs throughout the summer and autumn in many localities: e.g. in Delaware Bay it is stated that spawning begins early in April when the water temperature reaches about 14° C. and continues until late November. In Cape Cod waters two separate periods of spawning were observed, the second occurring during the second half of September. There was no evidence until 1941 that a second period of spawning ever occurred in this country, but in that year tingles kept in a tank at Conway spawned intermittently during late August and September, the last capsules being deposited on 30 September. During the latter part of this period water temperature fluctuated between 13 and 17° C. During

September groups of 11, 10, 12 and 14 capsules were laid, all of which, as will be seen later, are less than the usual number deposited in one laying early in the season.

Not a great many opportunities have occurred of noting the number of capsules deposited by a single tingle at one laying, but about a dozen such groups which have been noted during the normal spawning season have ranged from 20 to 35, with an average of 25 per female. This is in fair agreement with the work of Federighi (1931) in America, who found that an average of 28 capsules was deposited by isolated females. Galtsoff *et al.* (1937) state that in Delaware Bay females may deposit as many as 50 capsules, which are grouped in clusters. It is possible therefore that the groups noted above, averaging 25 capsules, may form but a part of the total production of the drills concerned. In practice two or more drills are frequently found spawning together on the same shell, while a large stone or pile of old chain at or about low-water mark may harbour a dozen or more spawning drills. This does not indicate, I think, a social habit among drills but merely the close occupation of the available satisfactory spawning sites. Capsules are deposited at the rate of three or four per day. Orton (1930) states that there is an inshore migration of *Urosalpinx* in spring and early summer, and that the species spawns heavily in shallow water. This is very noticeable in the river Blackwater, but very large numbers spawn also at all depths, and the selection of a spawning site seems to be governed mainly by the presence of abundant 'clocks', stones, or other firm objects, rising well clear of the bottom and offering situations free from silt. *Urosalpinx* kept in a tank at Conway deposited capsules most frequently on the vertical sides of the tank or in situations which were overhung.

On American oyster beds the average number of embryos per capsule is stated to be 9 in Hampton Roads, Va., the numbers varying from 3 to 20, and 8 in Delaware Bay, varying from 0 to 20. On British beds *Urosalpinx* is more prolific, for 1423 capsules from different localities averaged 11·74 embryos per capsule; of this total 823 capsules contained early stages and 600 contained shelled veligers practically ready to hatch. The early stages averaged 12·47 embryos per capsule and the shelled stages 10·74 per capsule. There is therefore a mortality during incubation of 1·73 embryos per capsule, or 13·9%. This figure is much lower than that of Federighi (1931), who found only an average of 5·1 larvae emerging per capsule (the average number of eggs being 8·8)—a loss of 42%. The number of embryos per capsule may vary from 1 to 29 in this country, but in capsules from one parent there is little variation.

If the average number of capsules laid per female in this country is assumed to be 25, from each of which on the average 10·74 drills emerge, then each female drill gives rise to 268·5 young. It is probable that the actual figure is somewhat higher, as Galtsoff *et al.* (1937) have shown that after depositing one group of capsules females may move away and later deposit further batches. It seems likely therefore that from the capsules laid by one female on British beds not less than 300 young drills emerge.

In order to determine at what age and height of shell deposition of egg capsules begins, 21 tingles varying from 1·8 to 2·4 cm. in height were placed in a floating wooden wire-covered cage in one of the tanks at Conway towards the end of June 1941 and a daily examination made for egg capsules. Barnacles were provided as food. Thirteen of the 21 small tingles survived the summer and only three were noted to deposit egg capsules. The largest group of capsules deposited numbered only 13, the others being considerably smaller. Of the 13 tingles remaining at the end of the summer only three were females; these were the largest of the group and were almost certainly 2 years old. The result of this experiment was inconclusive, but suggests that 2-year-old females below 2·5 cm. in height at the beginning of the season deposit a small number of egg capsules. In other lots of tingles two individuals measuring 2·4 cm. and one measuring 2·5 cm. have been noticed in the act of spawning; each of these laid only a small number of capsules in late summer. On the other hand, during May 1941, when breeding was just beginning, it was noticed that the majority of the females 2·2 cm. or less in height had undeveloped gonads and accessory reproductive organs and appeared to be definitely immature. It seems therefore that some of the largest of the tingles below 2·5 cm. in height in July and August, which are probably 2 years old, or possibly unusually small 3-year-olds (see Fig. 2), do spawn to a slight extent, but it is highly probable that the amount of spawn deposited is insignificant in relation to the production of older tingles. The question is of some practical importance, since such small tingles are only retained in very small numbers by the dredge and at present there is no other practicable method of removing them from the beds below low-water mark.

Among the numerous very large females examined only two or three have been found with the gonad in an exhausted condition. None of these was below 4·1 cm. and one was 4·3 cm. in height, the largest size yet recorded; on the other hand, individuals up to 4·1 cm. have been observed in the act of depositing capsules. The latter could not be less than 10–12 years old, so that the reproductive life of each female may extend over 7 years (ignoring the first 2 years when some capsules may be deposited), in each of which she may give rise to 300 young.

It is very noticeable from Fig. 3 how the dominant age group changes during the season among the female tingles collected from the beach in Thornfleet, River Blackwater. In Fig. 9 the composite May sample shown in Fig. 3, which is made up of two separate catches, the one dredged and the other hand collected on the same day, is split up into its components (see Table IV), males and females being graphed separately. The females in the shore sample are seen to belong principally to one year group, which by comparison with Fig. 3 is seen to be the 4-year-old class, with smaller numbers of 3- and 5-year-old tingles. The sample dredged on the same day in the channel adjacent to the beach shows that 5-, 6-, and 7-year-old tingles were also present in numbers in the creek as well as of course large numbers of 1-, 2-, and 3-year-old females which would not be picked up in quantity by the dredge; but the first tingles to come to shore for spawning were mainly 4 years old. The males accompanying these females belong mainly to the 5- and 6-year-old groups (see Fig. 7), with a few younger individuals, but the dredged sample shows that numerous older drills remain in the channel.

In June the 4-year-old females (mode at 2·8 cm.) are dominant on the shore with comparatively small numbers of 3-year-olds and a few smaller tingles, but a month later, in July, the 3-year-olds have enormously increased and form the dominant group, although older tingles are also fully represented, while

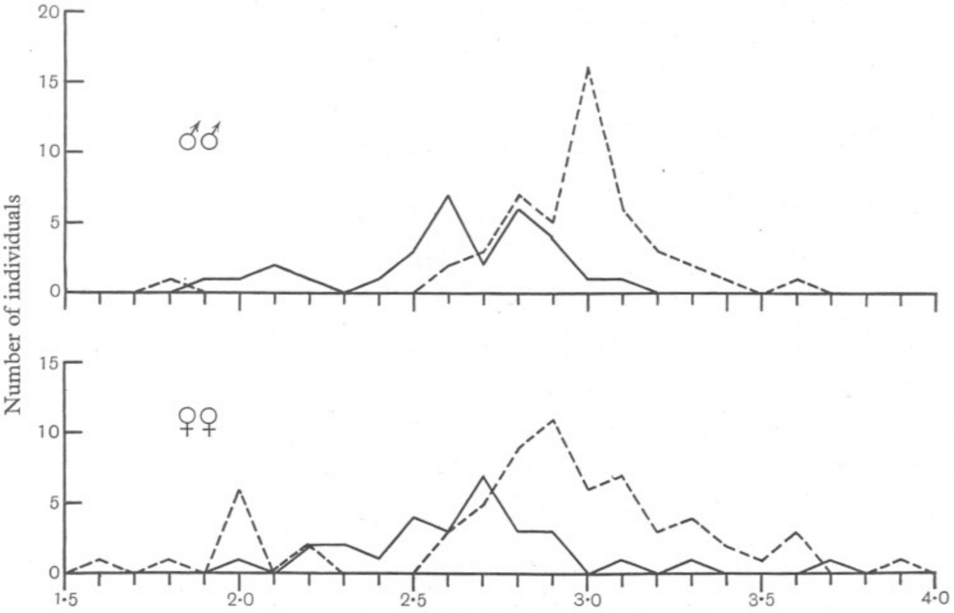

Fig. 9. Comparison of hand-collected (continuous line) and dredged (pecked line) samples of tingles collected on the same day (24 May 1941) from Thornfleet, River Blackwater.

there are a few 2-year-old and even younger tingles. Among males the tendency is similar, for as the season advances the younger age groups appear on the shore in increasing numbers, but the proportion of 1- to 4-year-old males is never commensurate with their numerical strength on the beds.

It should be remembered that these samples from Thornfleet are hand collected and therefore representative of the population on the beach at the time. The females have moved inshore primarily for the purpose of spawning, and it appears therefore that the 3-year-old females spawn about a month after the older groups, while only a few of the 2-year-old and smaller tingles migrate inshore. It has been noted that when such small tingles were isolated some deposited egg capsules, but each drill produced only a fraction of the usual number laid by mature individuals. These facts, taken in conjunction with the absence of significant numbers of 1- and 2-year-old females from the spawning population on the beaches, tend to prove that full spawning does not occur until the tingles are 3 years old.

TABLE IV. SIZE DISTRIBUTION OF DREDGED AND HAND-COLLECTED SAMPLES OF *UROSALPINX* FROM THORNFLEET, 24 MAY 1941

Shell height cm.	Dredged		Hand-collected	
	Females	Males	Females	Males
1·6	1	—	—	—
1·7	—	—	—	—
1·8	1	1	—	—
1·9	—	—	—	1
2·0	6	—	1	1
2·1	—	—	—	2
2·2	2	—	2	1
2·3	—	—	2	—
2·4	—	—	1	1
2·5	—	—	4	3
2·6	3	2	3	7
2·7	5	3	7	2
2·8	9	7	3	6
2·9	11	5	3	4
3·0	6	16	—	1
3·1	7	6	1	1
3·2	3	3	—	—
3·3	4	2	1	—
3·4	2	1	—	—
3·5	1	—	—	—
3·6	3	1	—	—
3·7	—	—	1	—
3·8	—	—	—	—
3·9	1	—	—	—

SEX RATIO

American work gives no indication of any abnormality in the sex ratio of catches of *Urosalpinx*. It has already been recorded, however (Cole, 1941), that the sex ratio in dredged catches from British oyster beds shows some striking peculiarities. Table V gives the proportions of the two sexes in all dredged catches of *Urosalpinx* obtained from the River Blackwater during the years 1938–41. Allowance should be made when studying this table for the fact that the 1941 season was characterized by an abnormally cold spring, the season being reckoned as roughly a month later than usual on the Blackwater. Bearing this in mind it is clear that, generally speaking, males and females are equally abundant in dredged catches of tingles at the outset of the season, but thereafter the proportion of females rapidly increases reaching a peak of over 90% during June and declining again in July and August to approximately 50%. It will be noted also that the seasonal curve of percentage of females follows very closely the intensity of spawning. This suggests that as the females move about and take up their spawning positions they become more

TABLE V. DREDGED CATCHES OF *UROSALPINX* FROM THE RIVER BLACKWATER

Date	Locality	Females	Males	Total	% females
7. iv. 38	R. Blackwater	56	55	111	50·5
10. iv. 40	Thornfleet, R. Blackwater	13	13	26	50·0
2. v. 40	Thornfleet, R. Blackwater	82	58	140	58·1
8. v. 40	Thurslett Creek, R. Blackwater	124	19	143	86·7
15. v. 39	Thurslett Creek, R. Blackwater	55	13	68	80·9
15. v. 40	Thurslett Creek, R. Blackwater	246	33	279	88·2
15. v. 39	South Shore, R. Blackwater	69	28	97	71·1
19. v. 41–27. v. 41	Thurslett—Old Mell Beacon, R. Blackwater	213	75	288	74·0
20. v. 41–29. v. 41	S. Shore, R. Blackwater	58	24	82	70·7
21. v. 41	Nass End, R. Blackwater	65	61	126	51·6
24. v. 41	Thornfleet, R. Blackwater	65	47	112	58·0
10. vi. 41	Thurslett Creek, R. Blackwater	84	13	97	86·6
13. vi. 40	R. Blackwater	57	3	60	95·0
17. vi. 41	Thurslett—Old Mell Beacon, R. Blackwater	112	7	119	93·1
24. vi. 41	Thurslett—Old Mell Beacon, R. Blackwater	149	22	171	87·2
2. vii. 40	R. Blackwater	81	30	111	73·0
15. vii. 39	R. Blackwater	129	68	197	65·5
26. viii. 40	R. Blackwater	92	68	160	57·5

susceptible to capture by an oyster dredge, while the males remain in positions where the dredge rarely captures them. It is known (see Federighi, 1931) that females tend to crawl up on to objects raised off the sea bottom to deposit their spawn, and in these situations they may be particularly liable to capture; but it is highly probable that on most grounds the scraping bar of the dredge digs slightly into the bottom, for the contents of a dredge bag usually includes some mud and a good deal of fine gravel and shell fragments. Nevertheless, female tingles upon objects slightly raised off the bottom may be reasonably considered as particularly liable to be included in a dredge bag; it is therefore likely that the proportion included will increase as the intensity of spawning increases and more females take up spawning positions. It is curious, however, that the males are not with the females or at least crawling among the cultch in search of food. Such evidence as we possess concerning the behaviour of the male tingles does in fact suggest that they are to be found with the spawning females. A sample hand collected on 24 May 1941 from stones, old drain pipes, mooring chains, etc., on the beach at low-water mark in Thornfleet, River Blackwater, includes practically equal numbers of males and females (Table VI), showing that at the beginning of the spawning season males are also on the move and may be found on raised objects alongside the females. The dredged catch from the channel adjacent to the beach, collected on the same day (see Table V) contained only 42% of males. Slightly later in the year at the height of the spawning season similar collections off the same raised objects in Thornfleet gave a preponderance of females (see Table VI), but males were also very numerous, and the percentage of females did not approach the high figures shown by dredged catches at this season. At the end of

TABLE VI. HAND-COLLECTED SAMPLES OF *UROSALPINX* FROM THORNFLEET, RIVER BLACKWATER

Date	Females	Males	Total	% females
24. v. 41	29	30	59	49·2
10. vi. 41	316	176	492	64·2
20. vi. 40	33	23	56	58·9
8. vii. 41	245	119	364	67·3
26. viii. 41	30	34	64	47·0

August another collection from the same raised objects gave approximately equal numbers of males and females. These hand-collected samples show that males are to be found along with spawning females on raised objects throughout the breeding season, at least on inshore grounds; it is all the more remarkable therefore that dredged catches from offshore contain so few males at this season. The difference in size between males and females of the same age will lead to some selection of females by the dredge, for it is clear from the size-distribution curves of dredged catches (e.g. that shown in Fig. 4) that drills below about 2·7 cm. are particularly liable to be lost through the meshes of the dredge bag. Thus the first three year classes of males with modes at *ca.* 1·8, 2·3, and 2·5 cm. at midsummer are likely to be missed, whereas only the first two year classes of females with modes at *ca.* 2·0 and 2·5 cm. are equally liable to pass through the meshes.

The continued collection of large numbers of females and small numbers of males during normal dredging would, in a population with a normal sex ratio, bring about a considerable alteration in the proportion of the two sexes in that population within a few years. For this reason on well-worked grounds such as those in Thurslett Creek, River Blackwater, one might expect to find, at least occasionally, a preponderance of males, yet in the nineteen dredged samples listed in Table V the highest proportion of males is 50%. In a previous note on this question (Cole, 1941) I have mentioned the possibility that sex change in a proportion of the population might be responsible for the observed abnormalities in the sex ratio. There is, however, no evidence whatever to support this hypothesis. During 1941, 20 drills caught in the act of spawning were isolated during the summer and examined in October; 19 were female and one had died. Careful search has been made among thousands of drills for individuals with characters intermediate between those of males and females, but none has been found, yet the sexes are easily recognizable and the penis is quite a large organ, so that if variations occurred in this organ they would be easily detected. The inference to be drawn is that sex change does not occur.

FEEDING

It is extremely difficult to evaluate the destructiveness of tingles, since it is impossible to determine the number of very small oysters killed on the beds. By keeping tingles enclosed with oysters of various sizes some idea of the potential damage may, however, be obtained. This has been done at Conway during the summers of 1940 and 1941. Known numbers of tingles have been enclosed in wooden wire-covered floating cages with ample supplies of either 1- or 2-year-old oysters, and daily counts made of the quantity destroyed. Maximum and minimum water temperatures were also recorded. Drilling may begin as soon as the water temperature exceeds 11–12° C.; this usually occurs during April or early May, but very little feeding occurs at this time as the drills are actively spawning. In June, when the peak of the spawning season has been passed, intensive feeding begins and continues until the water temperature again drops below 11–12° C., usually towards the end of October.

TABLE VII. RATE OF DESTRUCTION OF SPAT AND BROOD OYSTERS BY *UROSALPINX*

Type of oyster	Year	No. of tingles	Oysters destroyed	Period of feeding days	Rate per day per tingle
1-year-old spat	1940	22	701	96	0·332
,, ,,	1940	36	173	10	0·481
,, ,,	1941	39	2168	127	0·438
2-year-old brood	1940	12	45	109	0·034
,, ,,	1941	30	92	98	0·032

In Table VII are given the rates of destruction of 1-year-old spat and 2-year-old brood oysters recorded during 1940 and 1941. For these experiments mixed lots of tingles varying in age from 3 to about 8 years were employed, all collected originally from the River Blackwater. In Fig. 10 the daily rate of destruction of 1-year-old spat in 1941 is correlated with the average daily water temperature. It will be noted from Table VIII that the rate of destruction of spat during July and August is considerably above the final average figure for what was practically the whole feeding period. It is very noticeable how the rate of feeding fell away immediately the water temperature dropped below 14° C. This figure may be regarded as the minimum at which full feeding activity begins. There was no close correlation between water temperature and rate of feeding until mid-July when the breeding season was practically over. During the short period between 22 July and 6 August spat were destroyed at the rate of 0·90 per tingle per day. There is a fairly good general correlation between water temperature and rate of feeding from mid-July onwards, but it is apparent that there is also a seasonal rhythm to some extent overriding the effect of temperature; tingles feed voraciously immediately after the completion of spawning, but thereafter a general decline in the rate of feeding sets in, although it rises and falls also in response to changes in water temperature.

The average duration of the feeding period on the east coast oyster beds may be deduced from records of sea temperature in the River Blackwater covering the five years 1926–30 given by Orton and Lewis (1931). It is apparent that on the average the water temperature exceeds 14° C. about mid-May and again

TABLE VIII. OYSTER SPAT DESTROYED PER DAY DURING 1941 BY 39 *UROSALPINX*, TOGETHER WITH THE MEANS OF THE DAILY READINGS OF MAXIMUM AND MINIMUM WATER TEMPERATURE

Date	Spat destroyed	Average water temperature ° C.	Date	Spat destroyed	Average water temperature ° C.	Date	Spat destroyed	Average water temperature ° C.
June			July			Sept.		
17	1	17	30	36	15·5	10	12	16
18	0	18·5	31	30	15·75	11	26	15·5
19	0	18·5				12	16	14·5
20	0	18·5	August			13	15	14·25
21	0	16	1	36	16·5	14	18	No record
22	0	No record	2	31	18	15	13	14·5
23	2	18	3	40	18	16	11	14
24	4	19	4	31	17·5	17	10	14·5
25	8	19·5	5	48	15·5	18	20	15·25
26	6	19	6	27	13·25	19	8	14·5
27	10	19·25	7	24	13	20	22	14
28	13	18·5	8	16	14	21	8	No record
29	18	No record	9	19	15	22	23	14
30	9	19	10	22	15·75	23	12	14
			11	23	16·5	24	10	14·25
			12	30	16·75	25	10	14·25
July			13	29	15·5	26	13	15·25
1	16	21	14	24	15	27	9	15·5
2	17	21·25	15	26	14·5	28	12	16·25
3	32	22	16	21	13·75	29	9	16
4	27	18·75	17	19	14·5	30	8	15
5	10	19	18	21	15·75			
6	32	19·5	19	24	16·75			
7	15	20	20	22	16·75	Oct.		
8	17	19	21	16	16·25	1	2	13·5
9	27	19	22	11	15·75	2	0	13
10	21	20	23	17	16	3	3	13
11	28	20·5	24	16	15·25	4	3	12·5
12	12	21	25	17	15·25	5	1	No record
13	26	20·5	26	27	16·75	6	1	12·5
14	44	21·5	27	13	16·5	7	4	13·5
15	37	21·25	28	15	15·25	8	1	14
16	19	18·75	29	12	16	9	1	14·75
17	23	16·75	30	11	14·75	10	4	14·75
18	31	17	31	15	15	11	6	14·75
19	23	17				12	3	No record
20	16	No record	Sept.			13	2	13
21	31	16·5	1	28	16	14	2	11·5
22	28	15·75	2	22	16	15	2	11·5
23	29	15·25	3	21	16·25	16	1	10
24	37	17·75	4	24	17	17	1	11
25	45	19·25	5	22	17·25	18	1	10
26	32	18·75	6	31	18	19	2	No record
27	37	No record	7	22	17·5	20	3	11·5
28	43	18·5	8	19	17	21	3	10·75
29	22	18	9	29	17	22	2	10

falls below this level early in October. The duration of the feeding period is therefore approximately 5 months. Assuming an average rate of destruction of 0·385 spat per day, one tingle feeding exclusively on such 1-year-old spat would destroy 59 spat. Valuing these spat at four to the penny, a conservative estimate, the potential saving for each tingle removed is 1*s*. 3*d*. per season.

According to Federighi (1931), *Urosalpinx* from Hampton Roads, Va., U.S.A., begins to feed when the temperature rises above 15° C. and ceases when the temperature falls below 10° C. Similar studies in Delaware Bay (Galtsoff *et al.* 1937) indicate that drilling ceases altogether at 9·5° C. Drilling had not ceased completely at Conway when the water temperature fell below 11° C. (Fig. 10), but activity was practically negligible at temperatures below 13° C. Galtsoff *et al.* (1937) obtained a good correlation between the number of oysters destroyed in baskets let down on to the oyster beds in New Jersey and the prevailing water temperature.

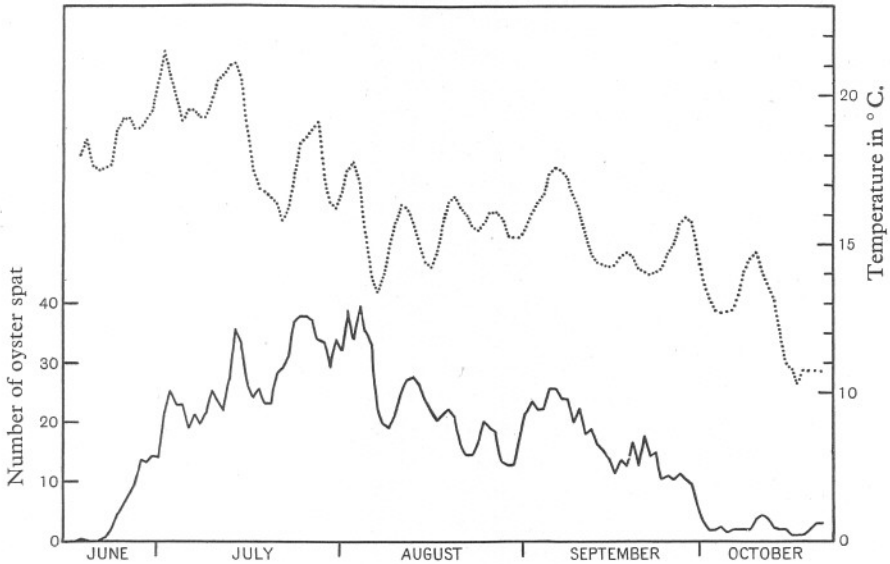

Fig. 10. Daily rate of destruction of oyster spat by 39 *Urosalpinx* during 1941 correlated with water temperature. Figures of both temperature and spat destroyed have been smoothed in threes.

The rate of destruction of spat and larger oysters as determined by American workers is considerably higher than that observed in the experimental cages at Conway. In the U.S.A. the ravages of *Urosalpinx* have been found to vary in different localities. In North Carolina waters a single *Urosalpinx* is stated (Galtsoff *et al.* 1937) to destroy 30–200 oysters in a season, depending on their size; the basis for this statement is not given. Certain other general statements are given, such as that of Nelson (1931), who states that in Delaware Bay *Urosalpinx* kills $1,000,000 worth of oysters annually, and that of Galtsoff *et al.* (1937) who say that there are many localities in Long Island Sound and in Chesapeake Bay where 60–70% of the seed oysters are destroyed annually. These round figures are much on a par with the assertion by Essex cultivators that at least half the spat in the Blackwater is killed annually by tingles, a figure repeated by Orton (1937); there is a great lack of precise information on the subject. The only reasonably precise American determination of the rate of drilling is that of Galtsoff *et al.* (1937), who state that during a 9 weeks season in New Jersey waters each drill destroyed on the average 0·34 adult oysters per week. These workers also state that over 300 spat may be destroyed in a single season by each drill; the basis of this estimate is not given, but one suspects that the rate of destruction of spat has been determined for a short period in midsummer and multiplied by an appropriate factor depending on the relative length of the period of observation and the season of activity. If this is so, the estimate of total damage is clearly much too high, as it has been shown here that the maximum rate of drilling is only maintained for a short period in midsummer after the completion of spawning.

In order to determine the rate of destruction of newly settled spat by young tingles, 20 tingles which had been hatched under laboratory conditions were isolated with a plentiful supply of oyster spat which had settled the same season. The tingles averaged approximately 0·35 cm. in height, while the oyster spat varied in diameter from 3 to 7 mm. The experiment was conducted in a plunger jar with sea water of normal salinity, and the average water temperature during the period of the experiment was 20° C. A total of 162 spat was drilled and destroyed during a period of 140 hr. by the 20 young tingles, giving an average rate of 1·39 spat per day (24 hr.) per tingle. This experiment proves that freshly emerged tingles may cause extensive havoc amongst newly settled spat. At this stage the tingles are for practical purposes immune from capture. Young tingles feeding entirely on such small spat might destroy as many as 100 each during the period July to September inclusive.

Orton (1927), in the course of some preliminary experiments, states that the average time taken for *Urosalpinx* to drill through an oyster was 5·7 days; the size of these oysters is not given, nor the water temperature, but it is implied that the oysters were larger than brood size. It is not suggested, however, that *Urosalpinx* consumed oysters continually at this rate, but that the average rate of drilling in 15 cases was as stated above. His figure for brood oysters 1–2 in. long was 4·1 days (10 oysters), but eight brood oysters nearly bored through had been drilled for an average of 4·5 days before being abandoned. Orton gives a general estimate of the time taken to drill a brood oyster as 5–6 days. This is very different from the average rate of destruction of such oysters as determined at Conway, viz. 33 days; this does not mean that each drill takes 33 days to destroy an oyster, for drills do not continuously attack one oyster after another; considerable periods of inaction occur, so that the rate of drilling, as distinct from the rate of destruction, may be much the same as Orton observed.

The high rate of destruction of adult oysters observed in America (see above) is all the more remarkable when we recall that on the average no less than 33 days was needed to destroy one 2-year-old oyster under experimental conditions at Conway. We are forced to conclude either that *Urosalpinx* has changed its habits under the conditions on British beds or that the shell of *Ostrea edulis* presents a much more effective barrier to *Urosalpinx* than that of *Gryphaea virginica*. In this country the general belief among oystermen is that the American tingle is principally an enemy of the spat and early brood stages and that damage to marketable oysters is negligible. Careful observations on the beds and food-preference experiments at Conway confirm this view.

Food preference has been investigated by enclosing samples of tingles in floating cages with two or more sorts of food and noting daily the number of drills attacking each kind of food. Materials offered as food have been oysters of all ages from early settled spat to 3 years old, mussels, and barnacles. The drills used were obtained from the River Blackwater and were all over 2·5 cm. in height. Certain general conclusions emerge quite clearly from these experiments. Drills offered barnacles or spat oysters (1-year-old) divided their attention about equally between the two kinds of food. Drills offered spat oysters and mussels destroyed practically all the spat before attacking the mussels. When the spat were all finished the mussels were quickly destroyed, drilling occurring chiefly near the thin edge of the shell. Similarly barnacles were more attractive than mussels. Drills offered both spat and brood oysters (2 years old) destroyed practically all the spat before attacking the larger oysters. The latter were then attacked and slowly consumed. It was observed also that tingles showed a distinct preference for spat of thumb-nail size, not attacking very small spat until all the large spat had been destroyed.

We may therefore conclude that oyster spat and barnacles form the principal foods of *Urosalpinx* on the beds in the River Blackwater, but that larger oysters may also be attacked. Similar experiments made in America by Galtsoff *et al.* (1937) placed mussels ahead of seed oysters in the list of foods attractive to drills, barnacles being the most attractive of all. The lack of attractiveness of mussels to drills from the River Blackwater is probably due to the comparative scarcity of mussels in this river system. Orton (1929) has shown that *Ocenebra erinacea*, the British rough tingle, will attack most readily those food species which occur commonly in its normal habitat and that *Ocenebra* from areas where oysters do not occur will not readily attack oysters while other foods are available. It is possible therefore that *Urosalpinx* from, say, Whitstable, where mussels are abundant on certain parts of the ground, would exhibit a strong preference for this food. It is clear that in the River Blackwater *Urosalpinx* is primarily an enemy of the spat stage of the oyster.

Galtsoff *et al.* (1937) conclude from observations of feeding habits that drills are able to detect the presence of food and move towards it. As already noted, careful experiments made at Conway did not confirm this conclusion.

Economic Considerations

Since *Urosalpinx* has no free-swimming stage in its life history, and it is probable that migration is of no more than local significance, it is dependent for distribution upon transportation by human or other agencies to fresh areas.

There is therefore, theoretically, a good chance of localizing this pest and of controlling it in areas where it has already secured a foothold. The latter include, as already noted, the estuaries of the Blackwater, Colne and Crouch and the Kentish Flats off Whitstable. At present two methods of control are practised, in the first place all tingles seen are picked out of dredge hauls and taken ashore and, secondly, all spawn noted is collected and dried. Owing to the general depression in the oyster trade, brought about by the heavy mortality experienced as a result of the severe winters of 1939–40 and 1940–1, the amount of dredging done by the few boats that are now employed is insufficient to keep the pest in check, let alone eradicate it. The present slightly enhanced prices due to the general scarcity of oysters would normally result in rather more intensive working of the grounds; but this is hardly possible now on account of the shortage of suitable men and the operation of certain defence restrictions, e.g. the closing of parts of the oyster beds on the east coast, thus forming reservoirs in which tingles can multiply undisturbed. In normal dredging very few tingles less than three years old are captured, although these are most numerous on the grounds, simply because they are too small to be retained by the dredge bag, the rings of which are an inch across, and further, the close sifting of the dredge contents which is necessary to collect the smallest tingles is not in practice carried out. With the limited amount of labour employed and the scarcity of oysters on the grounds it is necessary to dredge and cull out as expeditiously as possible in order to secure enough oysters to pay for the day's working and consequently thorough sorting of the contents of the dredge bag is hardly possible. Further, many grounds on the east coast, partly as a result of infestation by *Crepidula* and partly as a result of the dying out of the *Zostera* which formerly clothed and consolidated the banks, have in recent years become rather muddy and it is necessary therefore to wash or 'dock' the dredge bag several times, by lifting it almost clear of the water and then dropping it back, in order to wash out mud and facilitate culling of the contents. Trials made by the writer when working on muddy ground at the mouth of the Blackwater showed that washing of the dredge to the extent necessary to free it from mud resulted in the loss of between 75 and 100 % of the tingles. It has been recommended therefore that when dredging to clean fouled ground the usual docking of the dredge before shooting on deck should be omitted and any washing necessary carried out on deck with the aid of buckets. This is a slightly more tedious process but the catch of tingles is likely to be at least trebled.

Since *Urosalpinx* spawn hatches after an incubation period of 6–8 weeks, and the bulk of the spawn is deposited during May and June, hatching of spawn usually begins in early July. Consequently the period from the beginning of spawning, i.e. when the tingles first become active after the winter period of quiescence, until early July is the time during which maximum effort should be made to collect both tingles and spawn. After the beginning of July much of the spawn will have hatched. From other points of view the period from mid-April to early July is a favourable one for working the beds. It serves admirably for the collection and concentration on fresh ground of oysters destined for sale, both when the latter are to be sold as food in the autumn and when they are destined for replanting in other localities. This period is also the most favourable for cultivating the ground, picking out slipper limpets, and working the cultch over so as to render it suitable for picking up a spatfall in the period July to September.

The inefficiency of the dredge in collecting tingles below 3 years old is not so serious a matter as at first appears, for it is probable that the amount of spawn deposited by the small tingles is insignificant in relation to the production of larger tingles. Any reduction in the size of the rings forming the belly of the dredge will inevitably reduce the number of oysters caught per man on grounds carrying a lot of shell, due to the rapid clogging which will occur, and the increased numbers of tingles caught must be balanced against the reduction in the yield per dredge of oysters. It is, however, the practice in the Blackwater to use slightly smaller rings on certain grounds.

Although it is now generally recognized among oystermen on the east coast that tingles are a serious pest, much of the damage done passes unnoticed, for it is only when the clock of a brood or half-ware oyster is found with one of the valves drilled that visible evidence of the damage done is obtained. This will not occur very often, for serious damage to brood and larger oysters only occurs when spat is absent. In this country tingles are mainly an enemy of the spat, but a drilled spat is very rarely seen, for the drilled valve, usually by the nature of the situation of the spat the flat valve, generally becomes detached and broken up almost immediately after the spat gapes. Practically the only evidence of the activity of tingles is therefore the failure of the spatfall to show up the following season. Similarly it is practically impossible to detect the damage done by freshly emerged tingles among the tiny spat of the season; yet it has been shown that these small tingles may destroy these spat at an astonishing rate. Since no method is known or is likely to be devised for trapping these very small tingles the best way of controlling their activities is to prevent them emerging by collecting the spawn before the beginning of July. It will be noted that the time of emergence of tingles coincides with the beginning of the normal spat settlement period.

Until a few years ago a bonus was paid to dredgermen on the basis of the number of tingles and clumps of spawn brought in. This has now been discontinued, partly because of the difficulty of checking the actual numbers and partly because the extra payment for tingles was found to result in what was considered to be undue attention being paid to this aspect of the work on the beds to the detriment of the numbers of oysters taken per man per day. It would probably pay to re-introduce this system where the main task involved is the cleaning and cultivation of ground rather than the collection of oysters. The payment involved was small, e.g. 1*s*. per 1000 on the River Roach. The amount paid out during the year 1936–7 was £9. 5*s*. 0*d*., representing a total of 185,000 tingles and spawn. The main operation on which the company was engaged at the time was the clearing of the ground prior to laying down a large consignment of oysters from Brittany, and the ground was being intensively worked by a large number of boats. The following season payments fell to £3. 11*s*. 6*d*., representing only 71,500 tingles, showing that tingles may be greatly reduced by dredging alone when intensive working of the ground is possible.

As mentioned earlier a conservative estimate of the value of the damage due to a single tingle feeding entirely on oyster spat is 1*s*. 3*d*. per season, while should the tingle prove to be a female and be removed before spawning the potential saving is much greater. It is possible therefore to justify on financial grounds any reasonable sum spent on tingle control, for a man engaged solely upon this work and being paid £3 per week needs to catch only eight per day to pay his way on the basis of the above estimate. When it is realized that on some beaches in the Blackwater river system a man can collect 500 tingles in a few hours from around low-water mark, then there can be no doubt that the detachment of men from normal dredging operations for the work of hand-picking on such beaches is well justified.

In the U.S.A. special tingle traps and dredges have been the subject of large-scale experiment with very encouraging results (see Galtsoff *et al*. 1937). Some of the simpler methods of control advocated in America are already incorporated in normal practice over here. These methods all aim at the removal of drills from oysters after dredging and include screening, forking, hand-picking, etc. This is of course already carried out on British beds; no oysterman in this country knowingly throws a tingle back once it has come on board.

Another method of control strongly advocated by Galtsoff *et al*. (1937) is the use of special dredges fitted with a perforated pan to retain tingles but allow oysters to escape. Although these special dredges have never been tried in England the consensus of opinion is that they would clog up immediately on the clay grounds of the Essex rivers. They might work well on the Kentish Flats, but tingles do not yet present a severe problem there and present methods of control are fairly adequate.

Several different kinds of drill traps have been tried in America, with apparently considerable success. One type of trap takes advantage of the habit of the drills of congregating on objects raised above the bottom for the purpose of depositing egg capsules. Small concrete pillars, wire bags filled with shells, bunches of large shells or tin cans wired together, all are stated to attract spawning drills. They are laid out attached to lines and buoys and fished every few days, being taken up and moved to fresh areas as the catch diminishes. The use of such traps is to be strongly recommended in this country for the habits of the spawning tingles are the same; further, half-sections of large drain-pipes laid down on the beach at low water of spring tides in Thornfleet have attracted large numbers of drills and show that trapping can be carried out with success.

Summary

The American whelk tingle, *Urosalpinx cinerea* (Say), a gastropod enemy of oysters, has been introduced to Britain with American oysters and is now established in the rivers Blackwater, Colne, Crouch and Roach in Essex and on the Kentish Flats off Whitstable. Evidence available concerning the migratory powers of *Urosalpinx* is conflicting, but it is probable that migration is of local significance only in the spread of this pest. To infest new areas tingles or their spawn must be transported by human or other agency, for *Urosalpinx* has no free-swimming larval stage, the eggs being deposited in capsules from which fully formed young tingles emerge.

Females of *Urosalpinx* grow more quickly than males and reach a larger size. In males the annual increase in shell height never exceeds 0·2 cm. after the first 3 years, and is generally rather less. In females an annual increment of 0·2 cm., or slightly more, is general up to the age of about 7 years, after which it gradually falls. Males and females of the same age differ in height by about 0·25 cm. Growth marks are frequently to be seen on the shell and are of value in assessing growth rates. In both sexes a maximum age of 13–14 years may be reached. *Urosalpinx* reaches a much greater average size in Britain than in its natural habitat on the Atlantic coast of the U.S.A.

Females may deposit some spawn during the first 2 years of life, but the amount is insignificant in relation to the production of older tingles. Spawning begins when the water temperature in its seasonal rise reaches 12° C. Adult females may deposit an average of 25 egg capsules at a single laying, but it is possible that further capsules are deposited later in the season. The bulk of the spawn is deposited in May and June on British beds, but a few freshly laid capsules may sometimes be found in August and September. The average period of incubation is about eight weeks. Young tingles usually begin to emerge early in July. The average number of young emerging from each capsule is 11·74. *Urosalpinx* appears to be more prolific on British oyster beds than in America.

Urosalpinx from the River Blackwater exhibits a preference for oyster spat and barnacles over other foods. Oysters larger than spat are not seriously damaged when spat are available. Oyster spat and barnacles are about equally attractive. Tingles confined with oyster spat destroyed them at an average rate of 0·385 per tingle per day over the whole feeding period, but, for a period during July, spat were destroyed at the rate of 0·9 per tingle per day. Two-year-old oysters were destroyed at the rate of 0·033 per tingle per day. The rate of destruction is correlated with water temperature. Drilling may begin when the water temperature exceeds 11–12° C., but little feeding occurs while the tingles are breeding in May and June. Feeding usually ceases early in October and tingles remain quiescent throughout the winter until the water temperature again reaches 12° C., when spawning begins. Freshly emerged

tingles may cause much damage among oyster spat which has recently settled.

Control of this pest is discussed in the light of the information available concerning its biology and distribution.

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