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The fauna of an inter-tidal mud flat

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Summary—1. An account is given of the fauna of an inter-tidal mud flat (North Bay) in Kyle Scotnish, Loch Sween, Argyllshire.

2. The distribution of the more important species of the fauna over the shore is discussed.

3. Some indications are given of the growth rates of four lamellibranchs, *Macoma, Scrobicularia, Cardium* and *Mytilus.*

4. The changes in the density of the fauna are followed from 1943 to 1946, and the possible beneficial effects of the fertilization of Kyle Scotnish on the bottom fauna of the inter-tidal zone are reviewed.

INTRODUCTION

SOME ACCOUNT has already been given of the bottom fauna of Kyle Scotnish—a northern arm of Loch Sween, Argyllshire (RAYMONT, 1950), but that investigation was confined to the fauna below low water mark. Very little inter-tidal shore exists in Kyle Scotnish, but near the head of the loch there is a fairly extensive mud flat which is designated in the text North Bay (Fig. 1). Although a small stream enters the area, most of the flat is not estuarine. It was thought desirable to investigate the fauna of the mud flat, since most of the work done on muds in Great Britain concerns estuaries (e.g. FRASER, 1932; REES, 1940; BEANLAND, 1940; SPOONER and MOORE, 1940). Since also the main work in Kyle Scotnish has been concerned with the effect on general productivity of the addition of nitrate and phosphate fertilizers, it was decided to attempt to correlate population changes in the mud flat with the effects of fertilization.

The investigation extended over three years commencing in November 1943. Sampling over such a short period cannot give results on which very definite conclusions may be based. Nevertheless, as the work at Loch Sween had to be ended in 1946, the samples have been worked through and some account of the work is presented.

METHODS

Sampling was confined to an autumn (November) and summer (July) period each year. Four transects were planned across North Bay, sited on permanent marks on shore, and three or four stations were selected at approximately equal distances along each of the four lines, beginning near High Water and extending to Low Water (Fig. 1). Altogether fourteen stations were regularly sampled. No exact tidal levels were taken, as the tidal range right at the head of Loch Sween is small, and moreover the tides are irregular, the periods of exposure of the flat being very largely dependent on the prevailing wind.

Various sampling techniques were tried during November 1943 involving the digging of a square (side 0·5 metres) and sieving the material, but such a procedure proved too laborious. In the method finally adopted a quadrat (side 0·5 metres) was dug to a depth of 10–12 cm, the material passed through a coarse (9·5 mm) sieve, and only the larger bivalves exceeding 10 mm length retained in the sieve were counted. At the same station three small " auger " samples were also taken. The auger consisted of a metal cylinder 10 cm diameter, 23 cm height, with a handle at the top. The auger was pushed into the substratum to a depth of 10 cm and then pulled out again with its mud core. Usually the consistency of the mud was such that very little of the core was lost. Each of the auger samples was passed separately through a 1 mm sieve and all the organisms retained were preserved in alcohol and sorted later.

In estimating the total population at any station, the three auger samples were analysed first. Any bivalves exceeding 10 mm length in these samples were discounted, and the numbers of all other organisms then averaged. To this population was added the number of large bivalves *only* (> 10 mm) obtained from the $\frac{1}{4}$m^2 quadrat sample at the same station. The whole population was expressed in numbers per m^2.

The shore of North Bay is covered by a soft mud with a little sand, and with shell and gravel some few inches below the surface. There are a few isolated boulders and some patches of weed (mostly *Fucus vesiculosus*). None of the fourteen sampling stations was sited in weed or near boulders. Even so, the three auger samples at any one station could show considerable differences. Some idea of the great variation which could occur is given for two stations in July 1946, when six auger samples

Table I

Variation in auger samples at two stations: Tr. 4, St. 2 and Tr. 3, St. 4, July 1946. A–F represent actual numbers in 6 samples taken a few feet from each sampling point. The average of 3 samples (A, B and C) has been used for calculating the population per m^2

	Transect 4 Station 2								*Transect 3 Station 4*							
	Samples						*Average A, B, C*	*Average A–F*	*Samples*						*Average A, B, C*	*Average A–F*
	A	*B*	*C*	*D*	*E*	*F*			*A*	*B*	*C*	*D*	*E*	*F*		
Cardium	—	—	2	—	2	—	1	1	5	3	—	—	—	4	3	2
Macoma	—	—	1	—	1	2	+	1	—	2	1	2	—	2	1	1
Hydrobia	35	54	46	26	39	56	45	42	53	20	17	53	17	86	30	41
Littorina	—	—	—	—	1	—	—	+	—	—	—	—	—	—	—	—
Oligochaetes	—	—	—	—	—	—	—	—	—	—	—	4	—	—	—	1
Crustacea	2	1	6	2	1	10	3	4	5	1	—	—	—	—	2	1
Chironomids	—	1	—	—	1	—	+	+	1	—	—	—	—	3	+	1
Nephthys	1	—	—	1	—	2	+	1	1	—	1	1	1	—	1	2
Pygospio	2	5	1	2	1	5	3	3	1	—	—	1	—	—	+	+
Phyllodocids	1	—	—	—	—	—	+	+	—	1	—	—	—	—	+	+
Total	41	61	56	31	46	75	53	52	66	27	19	61	18	95	37	48

(A–F) were taken at a few feet distance radiating from the sampling point, instead of the normal three samples taken close together (Table I). The last columns in Table I, showing the average population based on the usual three augers and also an average based on six samples, indicate that the normal three samples probably give a reasonable picture of the average density of a sampling station. In many of the regular series of samples the agreement between the three auger samples was remarkably good.

The efficiency of the sampling by means of a single $\frac{1}{4}$m^2 quadrat for the larger bivalves was tested by taking two quadrats at each station instead of the usual one. There was normally reasonable agreement between the pairs of samples (Table II). Occasionally there were large discrepancies (e.g. Tr. 1, St. 3 and Tr. 3, St. 3), which appear to have been due mainly to a dense but patchy settlement of *Mytilus*. The bivalve population for July 1946 has been calculated by averaging the two quadrats taken.

The loss during transport of an auger sample has occasionally made it necessary to calculate the average population at a station on the remaining auger samples. On certain occasions also, at the lowest station of a transect, it was necessary to sample the mud fauna with a small grab, as the area remained covered with water for several days owing to the irregular tides. Generally the whole sampling for the fourteen stations took some three to four weeks.

Table II

Variation in quadrat samples. Two $\frac{1}{4}m^2$ *quadrats, A and B, were taken at each sampling station. Numbers indicate the counts of large bivalves* (>10 *mm*) *taken in each* $\frac{1}{4}m^2$ *sample.*

Station	*Macoma*		*Scrobicularia*		*Cardium*		*Mytilus*		*Total*		*Total Average*
	A	*B*	*A*	*B*	*A*	*B*	*A*	*B*	*A*	*B*	
Transect 1:											
1	0	0	36	30	0	0	1	1	37	31	34
2	0	1	3	0	24	3	7	7	34	11	22·5
3	0	0	0	0	10	23	138	56	148	79	113·5
Transect 2:											
1	2	0	4	2	0	0	0	0	6	2	4
2	0	2	35	26	0	0	5	1	40	29	34·5
3	4	0	0	2	0	1	55	55	59	58	58·5
4	0	0	0	0	1	0	3	10	4	10	7
Transect 3:											
1	0	1	5	5	0	1	0	1	5	8	6·5
2	0	0	12	17	1	1	0	0	13	18	15·5
3	0	0	10	11	5	3	16	4	31	18	24·5
4	0	1	1	1	28	12	69	57	98	71	84·5
Transect 4:											
1	0	0	2	12	14	0	0	3*	16	15	15·5
2	0	0	0	0	1	1	0	0	1	1	1
3	0	0	0	0	4	4	0	40	4	44	24

* = 1 Mya *included*

Table III

List of fauna taken in regular samplings in North Bay

Polycladida
Nemertini
Peloscolex benedeni Udekem
Platynereis dumerilii (Audouin & Edwards)
Nereis diversicolor O. F. Müller
Kefersteinia cirrata (Keferstein)
Phyllodoce maculata (L.)
Eteone longa (Fabricius)
Notophyllum sp.
Glycera sp.
Nephthys hombergi Lamarck
Nephthys sp.
Scoloplos armiger (O. F. Müller)
Pygospio elegans Claparède
Pectinaria koreni Malmgren
Arenicola marina L.
Capitella capitata (Fabricius)
Heteromastus filiformis (Claparède)
Fabricia sabella Ehrenberg
Maldanidae
Syllidae
Macoma balthica (L.)
Scrobicularia plana (da Costa)
Cardium edule L.
Mytilus edulis L.
Mya arenaria L.
Modiolus sp.
Kellia suborbicularis (Montagu)
Abra prismatica (Montagu)
Paphia decussata (L.)
Paphia pullastra (Montagu)
Hydrobia ulvae (Pennant)
Littorina littorea (L.)
Littorina littoralis (L.)
Cylichna cylindracea (Pennant)
Philine aperta (L.)
Acera bullata O. F. Müller
Amphipoda
Gammarus sp.
Corophium volutator (Pallas)
Isopoda
Jaera sp.
Idothea granulosa Sars
Sphaeroma rugicauda Leach
Crangon vulgaris L.
Praunus neglecta G. O. Sars
Chironomus salinarius Kieff.
Chironomid larvae
Chironomid pupae
Other larval Diptera
Ophiura texturata Lamarck

In many cases, particularly among soft-bodied animals, the methods of sampling and sieving broke up the material so that identification has not been taken further than the genus. Some animals (chironomid larvae) have not been identified further than family, although the dominant species has been noted. The list of fauna has been constructed mainly from the identification of favourable specimens preserved in good condition.

GENERAL COMPOSITION OF THE FAUNA

Although no account was taken of the small bottom animals (protozoans, nematodes, very small crustaceans, etc.) which were not usually retained by the sieve, more than 40 species were recorded from the area. Of these (Table III) comparatively

Table IV
Average population for whole North Bay area based on 14 *regular stations.*
(*All numbers per* m^2)

	Nov. '43	*July* '44	*Nov.* '44	*July* '45	*Nov.* '45	*July* '46
Bivalves (large)	110	66	44	44	130	125
Bivalves (small)	149	418	233	206	1,064	129
Hydrobia	10,077	7,640	10,143	6,977	13,759	6,961
Chironomids	686	318	454	548	1,526	365
Oligochaetes	2,394	984	948	712	1,288	415
Crustacea	121	29	60	66	56	101
Polychaetes	594	778	936	1,199	470	285
Other organisms	91	91	249	157	415	313
Totals	14,222	10,324	13,067	9,910	18,708	8,694

few appeared to be regular members of the fauna. Four bivalves (*Scrobicularia*, *Macoma*, *Cardium*, *Mytilus*), two gastropods (*Littorina* and *Hydrobia*) and several polychaetes (*Arenicola*, *Nereis*, *Nephthys*, *Heteromastus*, *Pygospio*, *Phyllodoce* and *Eteone*), with two other groups of animals (oligochaetes and chironomid larvae) were the most important numerically. Crustacea were very poorly represented throughout: the average population rarely reached even 1% (Table IV). Echinoderms were practically absent altogether; only an occasional small *Ophiura texturata* was taken.

The gastropod *Hydrobia ulvae* was overwhelmingly dominant in number. The average population calculated for the fourteen stations in North Bay showed that at times *Hydrobia* formed 80% of the total population, and that it never fell below 70% during the whole period of the investigation. *Hydrobia*, with oligochaetes (chiefly *Peloscolex benedeni*), and chironomid larvae (mostly *Chironomus salinarius*)* together dominated the fauna over the whole area, comprising approximately 90% of the whole population (Table V).

There was a slightly lowered percentage for these three organisms in July 1945, which was due to an increase in one species only—*Pygospio*. This polychaete formed 48% of the polychaete population in July 1945 (Fig. 4) and it occurred in 13 of the sampling stations.

In November 1945 young bivalves made an appreciable contribution to the total fauna (Table IV), but only two species were abundant—*Cardium* and to a lesser extent

* I am indebted to Professor A. Thienemann for this identification.

Mytilus. In the summers of 1945 and 1946 young mussels settled in enormous numbers over North Bay, but they usually did not survive for very long probably because of the soft substratum. The ordinary samplings did not reflect the full extent of these temporary settlements, but special collections made in the summer of 1945 after the spatfall in Kyle Scotnish and in two nearby other unfertilized arms of Loch Sween (Linne Mhurich and Sailean More) demonstrated the richness of the settlement in parts of North Bay (Table VI). Larger *Mytilus* were not abundant in North Bay; in fact more were present in Sailean More (Table VI).

Table V

The percentage of Hydrobia, *oligochaetes and chironomid larvae based on the average populations for North Bay*

	Nov. '43	*July '44*	*Nov. '44*	*July '45*	*Nov. '45*	*July '46*
% Hydrobia / Total fauna	71	74	78	70	74	80
% Hydrobia + oligochaetes + chironomids / Total fauna	93	87	88	83	89	89

Table VI

Abundance of large and small mussels in three arms of Loch Sween, Summer, 1945. *Kyle Scotnish is the only fertilized water.* (*All figures are numbers per m*²)

		< 10 *mm*	10–40 *mm*	>40 *mm*
KYLE SCOTNISH—North Bay (Fertilized)	Area 1	9,300	4,300	ca. 10
	Area 2	396,000	556	136
LINNE MHURICH (Unfertilized)	Area 1	0	160	184
	Area 2	32	8	72
SAILEAN MORE (Unfertilized)		9,712	2,088	1,068

Of the " other organisms " in North Bay (Table IV), the commonest were *Littorina littorea* (almost all juvenile), *Cylichna*, nemertines and occasionally *Philine*. The slight rise in " other organisms " late in 1945 and 1946 was accounted for almost entirely by young *Littorina*. *Acera bullata* occurred in fair numbers in the deeper waters of Kyle Scotnish during 1946, and it appeared in the shore samplings during July of that year.

ZONATION

Although the stations were not definitely related to exact tide level, for each transect Station 1 was sited high up on the flat, and the last station (Station 3 or 4) close to low water. Some attempt has therefore been made to relate very broadly the distribution of the more important members of the fauna to level on the shore.

Of the bivalves, *Macoma* was fairly evenly distributed across the shore, while *Scrobicularia* was somewhat more abundant at upper and middle levels (Fig. 2). *Mytilus* was absent near high- and mid-tide levels, and increased towards low water. In Transect 4, however, it was abundant in the middle region as well as towards low water, but still avoided the upper levels (Fig. 2). This difference may possibly be explained by the fact that Transect 4 was taken on a different portion of the shore close to a small permanent stream which ran across the mud (Fig. 1). This difference in distribution was also seen for *Cardium*: while in Transects 1–3 this bivalve was practically absent near high water mark and was common from mid-tide levels and towards low water, in Transect 4 *Cardium* was commonest at the uppermost levels and decreased in abundance down the shore (Fig. 2).

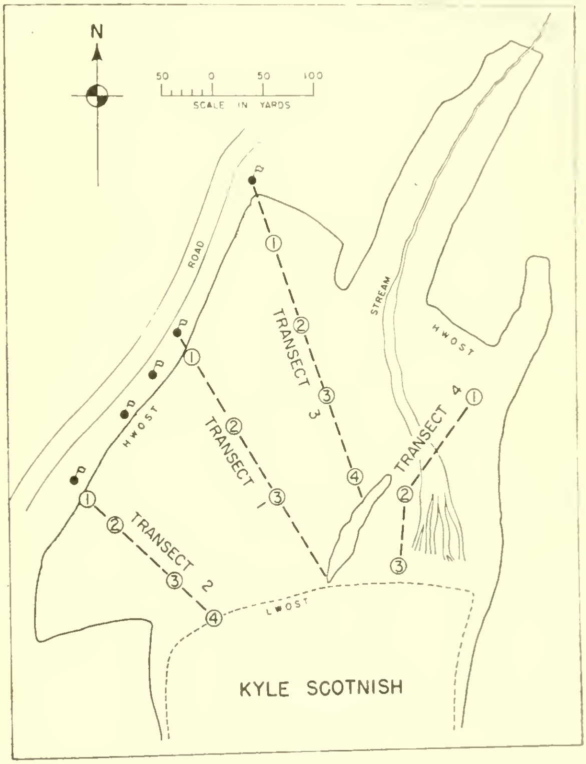

Fig. 1. Sketch map of North Bay mud flat at head of Kyle Scotnish, showing positions of the four Transects. Numbers along Transects indicate Stations. Flagged dots = permanent poles on roadside used for bearings

Some of the polychaetes also showed fairly obvious distributions. *Nereis diversicolor* was hardly represented below mid-levels on the shore and was at its maximum at the uppermost stations (Fig. 2). This distribution applied to Transects 2 and 3; along the other Transects *Nereis* occurred hardly anywhere throughout the sampling period. *Nephthys* contrasted sharply with *Nereis* in that it was practically absent from the upper levels and increased sharply towards low water (Fig. 2). *Nephthys* also occurred quite commonly below low water mark. There is again the suggestion

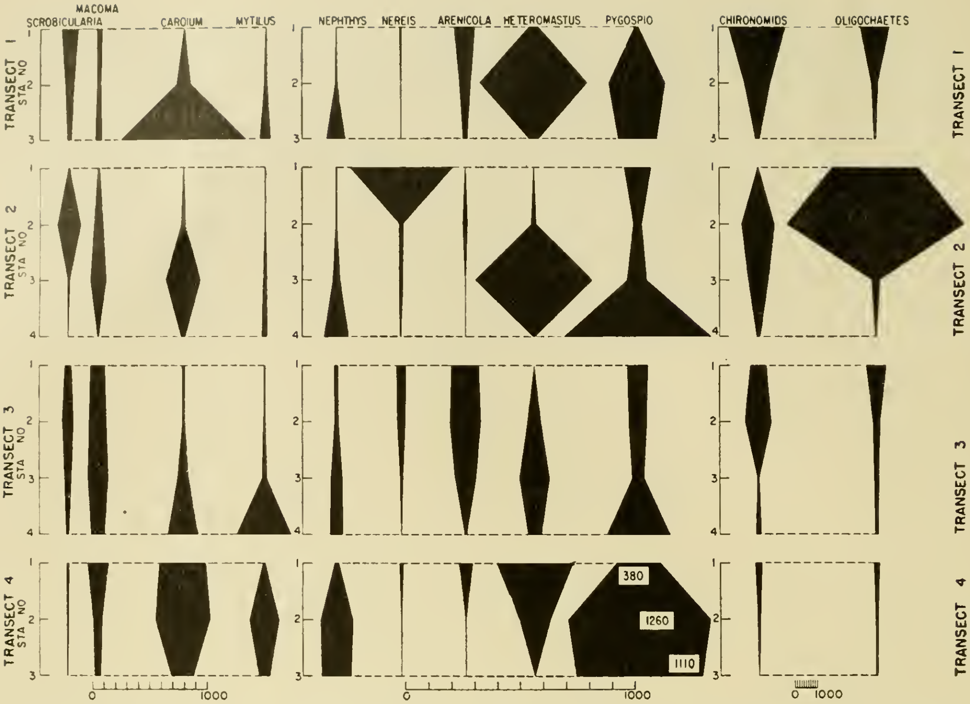

Fig. 2. The distribution of the more important lamellibranchs and polychaetes; also of chironomid larvae and oligochaetes. Along each transect, the stations are taken as equidistant down the shore, St. 1 being near high water mark. The numbers are densities per m² calculated as averages of the populations of 6 sampling dates. Note: A different scale has been used for *Pygospio* in Transect 4

that Transect 4 was generally on a somewhat lower level of the shore. *Nephthys*, for example, was commonest at the mid-station of this Transect instead of at the lower station. *Heteromastus* also appeared to be reaching its maximum density at the high level of the shore in Transect 4, whereas in Transects 1–3 *Heteromastus* was absent

Table VII

The distribution of Hydrobia ulvae *over North Bay. The population of each station is expressed per m² and represents the average of the 6 sampling dates. Numbers in brackets are rounded figures based on averaging 3 July samples*

	Transect 1	*Transect* 2	*Transect* 3	*Transect* 4
Station 1	8,529 (8,300)	6,021 (6,700)	10,593 (9,200)	16,246 (15,300)
Station 2	7,974 (6,700)	9,809 (10,600)	14,366 (10,500)	9,264 (4,600)
Station 3	5,944 (3,100)	9,759 (5,600)	16,149 (12,600)	1,903 (300)
Station 4		283 (300)	12,793 (6,900)	

from the uppermost station, was sparsely distributed towards low tide, and was quite sharply limited to the middle regions of the mud flat (Fig. 2). *Arenicola* appeared to decrease towards low tide levels, especially in Transect 4, while the very abundant *Pygospio*, while occurring across the whole shore, was more abundant at mid- and low-tide levels (Fig. 2).

Both chironomid larvae and oligochaetes (*Peloscolex*) were commonest over the mid- and upper parts of the shore, and decreased sharply towards low-tide mark (Fig. 2). Perhaps they avoided the higher salinities towards low water, although in Loch Craiglin chironomids occurred over the bottom where the salinity was about 30 over most of the year (RAYMONT, 1947). The distribution of juvenile *Littorina* was rather irregular, although on the whole they were less abundant towards low water.

The commonest gastropod (*Hydrobia ulvae*) showed no very clear zonation, being widely distributed with populations of several thousand individuals per square metre over most of the shore (Table VII). It was clear from the analysis of individual samples that *Hydrobia* was extremely patchy, and the averaging of samples probably gave a misleading impression of its real distribution. It seems, however, that *Hydrobia* occurred in only relatively small numbers (below 1,000 per m^2) at the lowest level along Transect 2, and also at the lowest station in Transect 4, where the density did not exceed 450 per m^2 except for one dense patch of some 10,000 individuals recorded in November 1943. Similarly, the lowest level along Transect 1 showed a lower

Table VIII

The changes in total population at the 14 *stations. Two stations* (*Tr.* 2, *St.* 4 *and Tr.* 4, *St.* 3) *were not properly sampled in Nov.* 1945. *The autumn totals show these stations included* (*figures in brackets*), *and also excluded* (*figures unbracketed*). (*Populations to nearest hundred per* m^2)

Station	Autumn Populations			Nov. '43– Nov. '45 % Change	Summer Populations			July '44– July '46 % Change
	Nov. '43	Nov. '44	Nov. '45		July '44	July '45	July '46	
Transect 1:								
1	8,500	8,200	26,400	+211	7,500	15,000	12,800	+71
2	11,800	11,400	13,600	+15	4,200	12,300	12,500	+200
3	3,000	6,000	27,500	+817	5,000	1,900	4,500	−10
Transect 2:								
1	14,700	11,000	10,300	−30	21,900	5,200	7,800	−64
2	21,600	23,300	27,800	+29	15,200	17,900	15,800	+4
3	30,400	9,500	13,400	−56	11,600	7,200	3,800	−67
4	1,700	300	(?)300	−82(?)	1,400	3,100	3,300	+136
Transect 3:								
1	11,100	20,800	13,200	+19	13,700	14,000	5,900	−57
2	14,900	28,000	22,500	+51	13,400	14,600	7,100	47
3	23,000	18,000	22,100	−4	16,800	12,900	11,200	−33
4	13,800	12,400	39,400	+186	12,700	5,700	4,900	−61
Transect 4:								
1	16,700	20,900	21,900	+31	10,100	18,600	23,200	+130
2	17,000	10,600	22,400	+32	7,400	8,200	6,700	−9
3	11,000	2,800	(?)1,100	−90(?)	3,800	2,000	2,200	−42
Total	(199,200) 186,500	(183,200) 180,100	(261,900) 260,500	(+31) +40	144,700	138,600	121,700	−16

Table IX

Changes in density of the main constituents of the fauna at the 14 *regular stations.* (*All numbers per* m^2)

Transect 1 *Station* 1

	Nov. '43	*July* '44	*Nov.* '44	*July* '45	*Nov.* '45	*July* '46
Large Bivalves	80	128	52	72	28	136
Small Bivalves	88	127	127	212	127	84
Hydrobia	6,256	4,961	5,809	9,921	14,289	9,921
Chironomids	788	890	339	1,950	9,286	2,078
Oligochaetes	960	890	1,272	2,502	1,993	382
Crustacea	44	127	—	—	42	85
Polychaetes	212	340	297	42	126	—
Other Organisms	52	—	254	297	509	84
Totals	8,480	7,463	8,150	14,996	26,400	12,770

Transect 1 *Station* 2

	Nov. '43	*July* '44	*Nov.* '44	*July* '45	*Nov.* '45	*July* '46
Large Bivalves	108	48	36	80	152	88
Small Bivalves	24	254	42	84	85	466
Hydrobia	9,472	2,120	7,208	6,233	10,939	11,872
Chironomids	792	—	1,696	3,434	1,060	—
Oligochaetes	220	339	254	636	382	—
Crustacea	20	—	—	—	85	—
Polychaetes	804	1,356	1,865	1,398	467	42
Other Organisms	372	42	296	466	381	—
Totals	11,812	4,159	11,397	12,331	13,551	12,468

Transect 1 *Station* 3

	Nov. '43	*July* '44	*Nov.* '44	*July* '45	*Nov.* '45	*July* '46
Large Bivalves	240	36	28	12	56	454
Small Bivalves	176	255	127	127	6,275	85
Hydrobia	596	4,586	5,427	1,102	20,267	3,689
Chironomids	1,076	—	—	127	42	—
Oligochaetes	492	—	—	—	—	—
Crustacea	48	—	—	42	—	—
Polychaetes	260	128	382	508	679	212
Other Organisms	108	—	4	—	169	42
Totals	2,996	5,005	5,968	1,918	27,488	4,482

Transect 2 *Station* 1

	Nov. '43	*July* '44	*Nov.* '44	*July* '45	*Nov.* '45	*July* '46
Large Bivalves	—	48	—	—	—	16
Small Bivalves	—	42	—	—	42	—
Hydrobia	3,567	10,685	6,190	4,282	6,402	5,003
Chironomids	127	42	—	—	—	—
Oligochaetes	10,192	9,286	3,010	127	42	297
Crustacea	—	—	42	—	—	42
Polychaetes	764	1,102	764	806	509	340
Other Organisms	—	678	1,017	—	3,265	2,247
Totals	14,650	21,883	11,023	5,215	10,260	7,945

Transect 2 *Station* 2

	Nov. '43	*July* '44	*Nov.* '44	*July* '45	*Nov.* '45	*July* '46
Large Bivalves	56	152	140	140	196	138
Small Bivalves	84	339	212	170	212	212
Hydrobia	3,689	11,194	13,653	11,406	9,625	9,286
Chironomids	1,866	1,653	1,145	85	2,968	1,102
Oligochaetes	15,264	1,569	7,378	4,706	13,907	4,155
Crustacea	169	42	84	126	—	127
Polychaetes	466	255	339	1,059	678	84
Other Organisms	—	—	338	254	254	636
Totals	21,594	15,204	23,289	17,946	27,840	15,740

Table IX (cont.)

Transect 2 Station 3

	Nov. '43	*July '44*	*Nov. '44*	*July '45*	*Nov. '45*	*July '46*
Large Bivalves	32	64	16	40	80	210
Small Bivalves	212?	127	296	85	1,865	42
Hydrobia	26,966	10,770	4,918	3,307	9,922	2,671
Chironomids	1,484	85	1,654	1,272	636	339
Oligochaetes	1,145	—	339	297	424	42
Crustacea	—	—	42	42	85	212
Polychaetes	169	423	1,822	1,484	253	169
Other Organisms	423	84	382	721	169	85
Totals	30,431	11,553	9,469	7,248	13,434	3,770

Transect 2 Station 4

Large Bivalves	—	—	4	—	—	28
Small Bivalves	127	84	42	85	16	170
Hydrobia	678	382	85	42	48	466
Chironomids	—	—	—	—	—	1,060
Oligochaetes	—	85	—	—	—	127
Crustacea	42	—	—	170	16	127
Polychaetes	763	805	127	2,801	208	297
Other Organisms	42	—	52	—	—	1,059
Totals	1,652	1,356	310	3,098	288	3,334

Transect 3 Station 1

Large Bivalves	211?	100	164	76	52	26
Small Bivalves	170	127	169	42	127	42
Hydrobia	7,036	11,321	18,276	11,787	10,515	4,622
Chironomids	678	1,103	636	254	1,738	85
Oligochaetes	2,078	806	297	1,230	382	763
Crustacea	297	—	296	42	—	42
Polychaetes	635	253	296	594	296	296
Other Organisms	—	—	636	—	127	—
Totals	11,105	13,710	20,770	14,025	13,237	5,876

Transect 3 Station 2

Large Bivalves	140	136	64	24	84	58
Small Bivalves	42	42	212	211	423	212
Hydrobia	12,126	11,999	26,627	12,762	16,070	6,614
Chironomids	1,357	297	—	170	5,173	—
Oligochaetes	636	339	127	170	678	—
Crustacea	127	84	—	42	—	—
Polychaetes	423	424	933	1,100	—	42
Other Organisms	42	42	—	84	42	169
Totals	14,893	13,363	27,963	14,563	22,470	7,095

Transect 3 Station 3

Large Bivalves	84	80	32	76	132	98
Small Bivalves	64	339	338	296	552	42
Hydrobia	21,212	15,264	17.087	11,575	20,818	10.939
Chironomids	191	—	—	254	—	42
Oligochaetes	701	212	42	—	42	—
Crustacea	—	—	42	85	—	42
Polychaetes	573	762	211	381	212	85
Other Organisms	191	169	212	212	339	—
Totals	23,016	16,826	17,964	12,879	22,095	11,248

Table IX (cont.)

	Nov. '43	July '44	Nov. '44	July '45	Nov. '45	July '46
		Transect 3	*Station* 4			
Large Bivalves	128?	44	56	40	792	338
Small Bivalves	509	128?	255	169	2,586	296
Hydrobia	11,530	12,358	10,049	4,664	34,344	3,816
Chironomids	64	—	890	—	212	42
Oligochaetes	382	—	212	85	127	—
Crustacea	192	64	255	127	381	254
Polychaetes	955	128	551	593	636	169
Other Organisms	—	—	84	42	339	—
Totals	13,760	12,722	12,352	5,720	39,417	4,915
		Transect 4	*Station* 1			
Large Bivalves	127?	48	12	40	108	62
Small Bivalves	84	212	933	1,187	1,018	—
Hydrobia	12,762	7,632	18,656	15,688	20,098	22,642
Chironomids	1,187	382	—	42	—	127
Oligochaetes	933	212	127	127	—	42
Crustacea	678	—	—	42	—	42
Polychaetes	889	1,611	1,145	1,357	424	296
Other Organisms	42	—	42	84	212	—
Totals	16,702	10,097	20,915	18,567	21,860	23,211
		Transect 4	*Station* 2			
Large Bivalves	212?	20	8	12	128	4
Small Bivalves	339	2,459	297	85	1,483	85
Hydrobia	15,137	3,265	7,674	4,664	19,122	5,724
Chironomids	—	—	—	85	254	42
Oligochaetes	297	42	127	42	42	—
Crustacea	42	42	—	212	—	381
Polychaetes	1,018	1,315	2,336	3,053	1,399	423
Other Organisms	—	212	127	42	—	—
Totals	17,045	7,355	10,569	8,195	22,428	6,659
		Transect 4	*Station* 3			
Large Bivalves	126?	16	8	—	16	96
Small Bivalves	170	1,314	212	127	80	64
Hydrobia	10,049	424	339	254	160	191
Chironomids	—	—	—	—	—	191
Oligochaetes	212	—	85	42	16	—
Crustacea	42	42	84	—	176	64
Polychaetes	382	1,994	2,035	1,611	688	1,529
Other Organisms	—	42	42	—	—	64
Totals	10,981	3,832	2,805	2,034	1,136	2,199

population than along the rest of the transect, except for one particularly dense patch of 20,000 individuals per m^2 in November 1945. On the other hand, the lowest station along Transect 3 had a population almost as great as at higher levels, and the population was maintained over the period investigated. There is an indication that Transect 4 exhibited a slightly different distribution from the other transects in that the highest density of *Hydrobia* occurred at the uppermost level, and the population fell off sharply on passing down the shore (Table VII).

CHANGES IN THE POPULATION

The great majority of the stations showed a decline in total population from November 1943 to the following July (Table VIII). This decrease affected most of the members of the fauna (Table IX). The *total* average population in November 1944 was almost identical with that of the previous autumn, but July 1945 showed a decline again.

The counts for November 1943 are not entirely reliable, as the sampling method was still being worked out then. Nevertheless, the order of magnitude of the population is probably correct, and it is important, since that population represents a pre-fertilization autumn density for the North Bay area. Probably the data for July 1944 can also be taken as approximating to a summer *pre-fertilization* density, since, although fertilization began over Kyle Scotnish early in 1944, little effect may be expected for some months (cf. RAYMONT, 1947). In November 1945 the density increased to a relatively high level, but once more declined in the following summer, when there was a particularly marked drop (Tables IV, VIII and IX). In all three years therefore the July population was smaller than in the previous autumn.

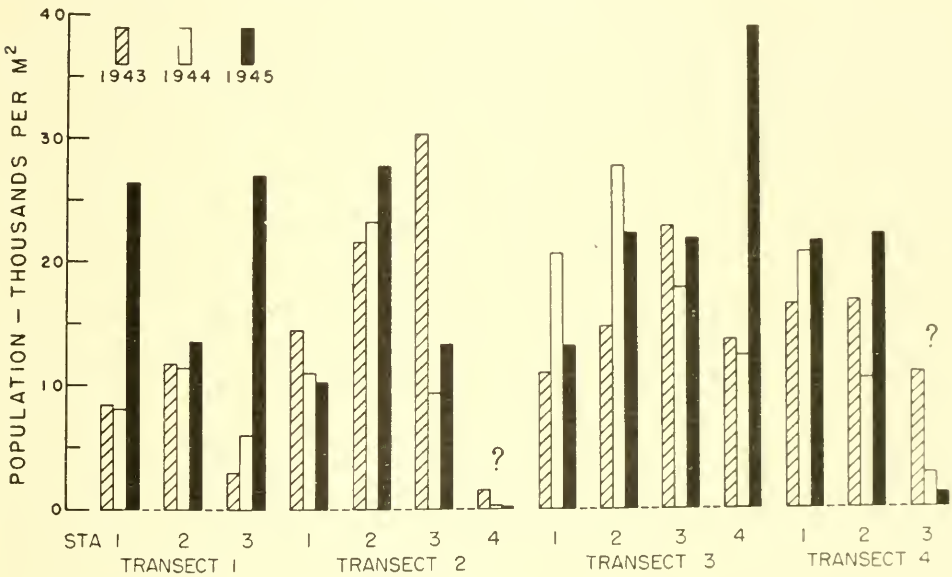

Fig. 3. A comparison of the total populations in November 1943, 1944 and 1945 at each of the 14 regular sampling stations. (Numbers per m².) (The figures at Tr. 2, St. 4 and Tr. 4, St. 3 are doubtful owing to imperfect sampling)

In considering the changes at individual stations it is probably necessary to omit Transect 2, St. 4, and Transect 4, St. 3, since on some occasions the samples could be obtained only by a grab. Of the remaining twelve stations, nine show an increase in population in November 1945 as compared with November 1943 (pre-fertilization), and two stations a decrease (Table VIII; Fig. 3). Owing to the patchiness of the fauna and to sampling errors, small differences (e.g. Transect 1, St. 2; Transect 3, St. 3) should probably be disregarded. If changes exceeding ±30% be regarded as significant, six stations showed a real increase in population—three being really large, while only one station showed a significant decline.

If the July populations are now considered, from Summer 1944 to Summer 1945 there is no obvious change. The total populations when averaged differ by only 4%, and of the individual 14 stations four only show a real increase and five a decrease.

The decline in bottom fauna densities which appeared in every July sampling seems to be more obvious in the summer of 1946. If the population then is compared with that of July 1944, the average population shows a decline, and seven stations show significant decreases as against four showing increases (Tables IV and VIII). Although it is questionable whether a decline of some 16% in the average population from July 1944 to July 1946 is significant, it is at least obvious that the changes in summer population do not parallel those of the autumn.

SIZE DISTRIBUTION OF SOME BIVALVES

An approximate picture of the size distribution of the four common bivalves in North Bay has been obtained. It is likely that, especially where very few small bivalves were taken, the combining of data obtained by the two sampling methods increases

Table X

The size-frequencies of Macoma balthica *in North Bay. The figures are averages per* m^2 *based on* 10 *sampling stations.* (*Tr.* 1, *Sts.* 1, 2 *and* 3; *Tr.* 2, *Sts.* 2 *and* 3; *Tr.* 3, *Sts.* 1, 2 *and* 3; *Tr.* 4, *Sts.* 1 *and* 2)*

Size Groups (mm)	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
July 1944	—	6·5	8	13	4	17	13	19	30	5	5	6	3	2	0·5	0·5
Nov. 1944	4	8·5	8	13	34	13	8	25	30	1	—	3	1	2	0·5	—
July 1945	13	25	13	8	8	0·5	—	13	8	2	2	5	3	2	2	—
Nov. 1945	—	—	8·5	4	8	13	8	8	21	2	5	8	8	3	2	0·5
July 1946	—	—	—	—	—	—	4	4	21	—	—	—	—	—	—	1

Table XI

The size-frequencies of Scrobicularia plana *in North Bay. The figures are averages per* m^2 *based on* 6 *stations.* (*Tr.* 1, *Sts.* 1 *and* 2; *Tr.* 2, *St.* 2; *Tr.* 3, *Sts.* 1, 2 *and* 3). *The columns on the right of the table show the size-frequencies of small* Scrobicularia (<10 *mm*) *

Size Groups (mm)	1–3	4–6	7–9	10–12	13–15	16–18	19–21	22–24	25–27	28–30	31–33	34–36
July '44	28	14	—	1	3	2	1	5	3	14	15	18
Nov. '44	7	28	—	1	1	1	4	5	11	13	15	9
July '45	28	14	49	8	5	6	2	—	7	7	7	7
Nov. '45	—	14	35	1	8	10	6	4	5	9	7	11
July '46	—	—	42	—	4	9	13	10	3	4	5	7

Size Groups (mm)	37–39	40–42	43–45	46–48	49–51	(*mm*) 1	2	3	4	5	6	7	8	9	10
July '44	5	1	—	—	—	—	7	21	7	7	—	—	—	—	—
Nov. '44	1	1	1	1	—	—	—	7	—	14	14	—	—	—	—
July '45	3	1	1	—	—	—	21	7	—	7	7	21	21	7	—
Nov. '45	1	1	5	2	—	—	—	—	—	—	14	21	7	7	—
July '46	7	2	—	—	—	—	—	—	—	—	—	—	14	28	—

* Data for November 1943 omitted as sampling methods then not strictly comparable with later samples.

unduly the proportion of the smaller ones, and thus at 10 mm there may tend to be an artificially sharp break in the distribution pattern. Some confirmation of this, for example, was obtained for the distribution of *Mytilus* in November 1945 (Table XII) when some quadrat counts were also made of small bivalves. Nevertheless a fair indication of the general pattern of the size distribution has been obtained (Tables X, XI, XII, XIII). The growth rates have been based on an examination of modal lengths; the use of growth rings was attempted, but numerous " false rings " interfered with the analysis.

Table XII

The size-frequencies of Mytilus edulis *in North Bay. The figures are averages per* m^2 *based on* 6 *stations.* (*Tr.* 1, *St.* 3; *Tr.* 2, *St.* 3; *Tr.* 3, *Sts.* 3 *and* 4; *Tr.* 4, *Sts.* 2 *and* 3) *

Size Groups (mm)	1–3	4–6	7–9	10–12	13–15	16–18	19–21	22–24	25–27	28–30	31–33	34–36
July '44	75	11	7	—	—	1	0·5	0·5	—	0·5	—	0·5
Nov. '44	—	7	21	—	—	—	—	—	—	—	—	—
July '45	35	21	—	—	—	—	—	—	—	—	—	—
Nov. '45	21	168	294	87	36	13	0·5	—	—	1	1	0·5
July '46	—	7	7	15	14	15	20	20	20	16	15	11

Size Groups (mm)	37–39	40–42	43–45	46–48	49–51	52–54	55–57	58–60	61–63	64–66	67–69
July '44	0·5	0·5	—	—	—	—	1	0·5	—	—	—
Nov. '44	—	—	—	—	—	—	—	—	—	—	—
July '45	—	—	—	—	—	—	—	—	—	—	—
Nov. '45	0·5	—	—	—	—	—	—	—	—	—	—
July '46	4	4	2	1	0·5	0·5	0·5	1	0·5	0·5	0·5

Table XIII

The size-frequencies of Cardium edule *in North Bay. The figures are averages per* m^2 *based on* 6 *stations.* (*Tr.* 1, *St.* 3; *Tr.* 2, *St.* 3; *Tr.* 3, *Sts.* 3 *and* 4; *Tr.* 4, *Sts.* 1 *and* 2). *Note: Up to* 10 *mm length the groups are* 3·5 *mm; thereafter* 4 *mm groupings are used**

Size Groups (mm)	1–3·5	4–6·5	7–9·5	10–13	14–17	18–21	22–25	26–29	30–33	34–37	38–41	42–45	46–49	50–53
July '44	441	42	—	4	1	4	2	2	3	3	3	—	—	3
Nov. '44	98	63	14	1·5	4	2	5·5	2	1·5	2	0·5	0·5	—	—
July '45	52	52	—	1·5	—	1	0·5	0·5	1	1·5	1	—	—	—
Nov. '45	996	396	36	11·5	1	2·5	1·5	5	3·5	2	—	—	—	—
July '46	14	28	35	1	11·5	4·5	7	3	3	1	1	—	0·5	—

* Data for November 1943 omitted as sampling methods then not strictly comparable with later samples.

As regards *Macoma*, almost all individuals were less than 15 mm. The July 1944 and July 1945 collections suggest that young bivalves, less than one year old (O-Group), were about 2–4 mm long (Table X). The November figures indicate a growth to about 5–6 mm, but the distributions for July in each year also suggest another peak at about 8–9 mm. It is suggested therefore that this would represent approximately one year of growth. On this hypothesis there would appear to be little growth from July to the following November, since each autumn has a fairly clear peak at 9 mm. The numbers of *Macoma* larger than 10 mm is very small indeed, but those between 11 and 15 mm may be regarded as in their second year of growth. In summer 1946 there was no successful spatfall. A very few *Macoma* of about 9 mm length (presumably 1 year old) persisted, but all other age groups had disappeared (Table X).

Scrobicularia, though never very numerous, grew to a considerable size in North Bay, a proportion reaching 40 mm (Table XI). In July 1944 and 1945 a new brood of *Scrobicularia* appeared only a few mm long but (as for *Macoma*) no successful spatfall occurred in summer 1946. A difficulty is that in July 1945 the smallest *Scrobicularia* included many of 2–3 mm, but also a large number about 8 mm. When the smallest bivalves (less than 10 mm) are separated into 1 mm groups, it appears that the 2–3 mm individuals were O-Group *Scrobicularia*, and that the 8 mm individuals were probably an older group (Table XI). By November 1944 O-Group *Scrobicularia* reached a length of some 5–7 mm, and the group of 7–9 mm in the following July would presumably be one-year-old bivalves (Table XI). Thus the spat of 1944 reached about 7–9 mm by July 1945, and possibly this was the same year group which attained some 16 mm length by the following November, and about 20 mm by the next July (1946), when they would have been two years old (Table XI). If this is a true interpretation, there was some acceleration in growth rate late in 1945 and during 1946. This could well be a result of fertilization of Kyle Scotnish; the general bottom fauna in the loch did not begin to increase clearly until late 1945 (cf. RAYMONT, 1950).

As regards *Mytilus*, only the lower stations showed an appreciable population and even there mussels, especially large individuals, were extremely sparse until November 1945, when a marked increase appeared. The population then consisted mainly of small individuals, the spat of the previous summer. July 1945 figures, however, showed that very little spat had settled by that time. GAULD (private communication) observed very heavy spatfalls of *Mytilus* over the North Bay area somewhat later in that summer. Some random samplings made in collaboration with Dr. GAULD showed parts of North Bay where tremendously dense patches (even $>$100,000 per m^2) of very small mussels were present. Measurements on some of these collections in August and September showed the great majority of these mussels were below 5 mm—clearly the summer's spat (cf. also Table VI). Although a very large percentage of this spatfall died off very rapidly, by November 1945 a considerable population of young mussels was still present. By the following July the population had declined markedly (Table XII).

Comparison of the three July samplings shows that little spat had settled by that time each summer (Table XII). The somewhat higher figure for July 1944 may indicate a slightly earlier spatfall in that year. The 1944 brood grew to about 8 mm by November, but thereafter they disappeared (Table XII). It is possible that as they grew larger they became smothered in the soft mud substratum. Frost may also have killed them off during the winter.

The abundant 1945 spat which appeared in August and September, mostly $<$5 mm length, attained a length by November 1945 of approximately 9 mm (Table XII). By July 1946, although no new spat had settled, the mussels had definitely established themselves over a considerable part of the shore. Their densities had declined with winter mortality, but there was a fairly rich group ranging from 10 to 35 mm (Table XII). The mode of this group appears to be about 23 mm, and this suggests that the

9 mm peak of November 1945 has now shifted to the 23 mm peak of July 1946. This successful 1945 brood would therefore appear to have grown more than 20 mm in approximately one year. The growth rate is higher than that suggested for *Macoma* and for *Scrobicularia*, but an acceleration was suggested in the growth of *Scrobicularia* over the same period. The success of the 1945 brood of *Mytilus* and the considerable degree of colonization of the North Bay may be due in part to the general rise in productivity with fertilization noted at that time (RAYMONT, 1950).

For *Cardium*, an early spatfall occurred in summer 1944, the majority of cockles in July being about 2 mm. As for *Mytilus*, the population of *Cardium* of more than 10 mm length was generally extremely sparse over North Bay in 1944–45 (Table XIII). It would appear therefore that 1944 was an early spat year but that the brood was unsuccessful.

In 1945, spat was more abundant in the November samples than in July, indicating that the majority of the summer brood had not settled by mid-summer. *Cardium* also followed *Mytilus* in that 1945 appeared to be a much more successful year; over 1,000 small cockles per m^2 had settled by November 1945. All these were less than 10 mm length, and the great majority were in the smallest length class (1–3·5 mm) (Table XIII). A few cockles occurred at this time in the 10–13 mm group, and these may represent a few individuals of the I-Group, i.e. those which had settled in the previous July. By July 1946 a very heavy mortality had occurred, and there was no real spatfall. There was, however, for the first time, some indication of a spread of the somewhat larger cockles (14–25 mm) which probably represented the spat of the previous summer. The numbers, although small, suggest a fairly sharp break in the size distribution between 10 and 13 mm (Table XIII). The numbers of cockles between 10 and 28 mm taken from all six stations added together were:

10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	(Length (mm))
0	0	2	4	20	16	24	8	8	6	8	2	2	8	6	5	2	3	3	(No. per m^2)

This suggests a modal length of about 14–16 mm, indicating a fairly successful brood from the previous summer (1945) which has averaged 15 mm growth in a year. This growth would be an improvement on that for *Macoma* and *Scrobicularia*, but it was not as rapid as that of *Mytilus*.

There is undoubtedly a considerable degree of overlap between this brood and an older age group (20–28 mm). A second peak possibly occurs about 23–24 mm, and this would therefore represent a two year old group of *Cardium*. The very low figures for July 1944 might also indicate one group of cockles varying in size from 18–21 mm (II-Group) and another group of 10–13 mm (I-Group). An enhanced growth rate in 1945 would agree with the results on other lamellibranchs.

It seems clear that 1945 was a fairly successful year for both *Cardium* and *Mytilus*, and that some spread of these bivalves occurred over the North Bay. Although part of the success of the 1945 brood may be correlated with better feeding conditions due to fertilization, the bivalves still experienced the difficulty of establishing themselves for any length of time on a muddy shore, subject to prolonged exposure.

DISCUSSION

The fauna of North Bay is a *Macoma balthica* community, and corresponds well to that studied by SMIDT (1951) in the Danish waddens. The polychaete and lamellibranch species of the infauna are very similar, with *Hydrobia ulvae* as the dominant gastropod. SMIDT quotes *Mytilus edulis* and *Littorina littorea* as the two most important members of the epifauna—a composition that accords well with the North Bay mud flat. One marked difference was the very low numbers of *Corophium* found in North Bay. THAMDRUP (1935), SMIDT (1951), BEANLAND (1940), SPOONER and MOORE (1940) all quote this species as an important member of the *Macoma* community. BEANLAND, and SPOONER and MOORE, suggest that one factor which limits its occurrence is lack of shelter, so that its maximum density is usually near high-water mark. Nevertheless *Corophium* might have been expected to occur abundantly at least at the higher levels of North Bay, which is at the end of a long, sheltered sea-loch. Moreover, *Hydrobia*, which is also said to be sensitive to water movement, was very abundant—in fact dominant numerically—in North Bay. There have been some suggestions that *Corophium* may occur only as a temporary visitor on shore; perhaps sampling only in July and November missed its abundant season. Possibly also *Corophium* competes with other members of the fauna that were plentiful in North Bay (cf. THAMDRUP, 1935).

Another difference between other described *Macoma* communities and North Bay was the importance of chironomid larvae in the latter area. These larvae are not mentioned by THAMDRUP (1935), SMIDT (1951), FRASER (1932), BRADY (1943) or REES (1940). SPOONER and MOORE (1940) do list " dipterous larvae " on a few occasions in their tables, but the numbers are very low, and clearly if there were Chironomidae, they were never of importance. WOHLENBERG (1937) also mentions chironomid larvae in a small area near a fresh water stream, but they did not apparently occur generally over the mud flat. NICOL (1935) found high densities (maximum 39,000 per m^2) in muddy salt pools. Over the North Bay the average population varied between 300 and 1,500 per m^2 from 1943 to 1946, but individual samples gave densities of 2,000–3,000 per m^2 (maximum $>$9,000 per m^2).

Oligochaetes (chiefly *Peloscolex*) were also very abundant in North Bay; the average population for the shore ranged near 1,000 per m^2 for a considerable period, and individual samples amounted sometimes to several thousands (maximum 13,900 per m^2). SMIDT (1951) comments on Oligochaeta (including *Peloscolex benedeni*) as being exceedingly numerous on the higher parts of the waddens, and BRADY (1943) found they occurred in muds off the Northumberland coast, though the densities in North Bay were very much higher. *Peloscolex* was also found by WOHLENBERG (1937).

Most authors state that *Hydrobia* is concentrated in the upper tidal areas (cf. SPOONER and MOORE); in North Bay the lowest stations usually had few. However REES (1940) found it in greater density towards low water, and SMIDT states that the young *Hydrobia* occurred in great numbers in summer and autumn anywhere over the mud flats. This could account for the very dense patches occasionally encountered in North Bay, even at the lowest tidal levels (cf. p. 185). The maximum densities recorded by most workers in Great Britain do not usually exceed 20,000 per m^2 (Table XIV); though NICOL (1935) found up to 32,000 per m^2 at Aberlady, Scotland. The richness of North Bay is therefore apparent. However, the densities there were not as high as those at Skalling (Table XIV). SMIDT (1951) recorded even higher densities for the Danish waddens when O-Group *Hydrobia* were also counted (Maximum 600,000 per m^2).

Of the bivalves typical of the *Macoma* community, *Mya* was taken only rarely in North Bay. *Macoma* seemed able to live over a very broad zone of the shore, though the lowest station of Transects 2 and 4 was quite definitely avoided—*Macoma* occurred only once there during the whole period of sampling. The density of *Macoma*, even in comparatively rich zones, appears rarely to exceed 200–300 per m^2, and North Bay would therefore be quite a dense area. However, THAMDRUP recorded up to 1,000 per m^2 at Skalling, and FRASER far higher densities in the Mersey Estuary (Table XIV).

In general the great majority of individuals in the higher counts in North Bay were young ($<$10 mm); a particularly striking example was the maximum count of 428 per m^2 of which only four exceeded 10 mm. Densities of individuals $>$10 mm rarely rose to 60 per m^2. WOHLENBERG (1937) found $>$6,000 O-Group *Macoma* at Sylt. Similarly the 6,300 individuals per m^2 recorded at Skalling (Table XIV) were all young. SMIDT found even 16,000 O-Group *Macoma* per m^2 in the same area, though he also showed that the stock was reduced to some hundreds per m^2 in a few months.

STEPHEN (1931) believes that *Macoma* breeds about April–May, young individuals appearing by June and reaching a length of some 5 mm by the end of their first autumn. By the end of their second autumn, STEPHEN found an average length of 8–9 mm, and he believes that a heavy mortality occurs after the third summer. The growth rate of *Macoma* in North Bay would seem to parallel closely STEPHEN'S results. Young spat, 2–4 mm, appeared in the July samplings and reached about 5–6 mm by the first autumn (November) and some 9 mm by the following autumn. The conditions for growth in North Bay would appear to be favourable. BRADY (1943), for collections in June, gives an average length of 6 mm for I-Group and 12 mm for II-Group *Macoma*.

THAMDRUP (1935) records *Scrobicularia* at the lower levels at Skalling. SMIDT and WOHLENBERG found it occasionally in soft deposits, and STEPHEN (1930) records it in soft sticky mud in the Firth of Forth. In North Bay this bivalve was widespread in the soft substratum, though it definitely avoided the lowest tidal levels. Thus it was never taken at the lowest station in Transect 2, only once at the lowest station of Transects 1 and 4, and only twice at the lowest station in Transect 3. SPOONER and MOORE (1940) also indicate that *Scrobicularia* is commoner in the upper half of the inter-tidal zone. Except for one extraordinarily dense patch of 1,000 per m^2 recorded by SPOONER and MOORE (1940), the densities of *Scrobicularia* would not appear to exceed 300 per m^2 (Table XIV). SPOONER and MOORE describe the Tamar as a rich *Scrobicularia* area, and they regard this species as generally abundant in sheltered inter-tidal areas in the South of England (cf. also HOLME, 1949). It would appear that North Bay was at least equally rich (Table XIV). The higher densities recorded by SPOONER and MOORE showed a high proportion of young spat. This was also true of the North Bay samples, but counts of 100–150 larger individuals per m^2 were quite common. SPOONER and MOORE do not give details of growth rates, but they remark that specimens $<$12 mm in length include both O-Group and I-Group. This would agree reasonably with the suggestion (p. 192) that in North Bay *Scrobicularia* grew to about 6 mm by the end of their first autumn, to about 8 mm by the following July, and to some 16 mm by the end of the second autumn when some acceleration is postulated.

SPOONER and MOORE have suggested that *Macoma* and *Scrobicularia* may compete, since they seem to have similar feeding habits. The population of *Scrobicularia* in North Bay, while not very large, was about as rich as that of the Tamar Estuary, and possibly therefore *Macoma* was to some extent excluded from North Bay.

Cockles were not very common in North Bay; the density of older individuals never exceeded 80 per m². The much higher figures occasionally recorded showed without exception an overwhelming dominance of young cockles (<10 mm). The densities do not, however, compare unfavourably with those for other areas in Britain, especially as the high populations recorded by STEPHEN and by SPOONER and MOORE were composed mainly of O-Group cockles. By contrast, THAMDRUP found very much higher densities at Skalling (Table XIV); indeed *Cardium* was the most abundant bivalve on the waddens. The maximum quoted even then (4,675) did not take account of O-Group individuals. THAMDRUP showed that several thousand O-Group per m²

Table XIV

Comparison of the densities of some of the members of the fauna in North Bay and in other areas. Numbers are maximal densities per m². Figures in brackets indicate extraordinarily high densities recorded only once

Locality	Tamar	Exe	Bristol Channel	Forth and Clyde	Northumberland	Skalling	Mersey	North Bay
Authority	SPOONER and MOORE (1940)	HOLME (1949)	REES (1940)	STEPHEN (1929, 1930, 1931, 1932)	BRADY (1943)	THAMDRUP (1935)	FRASER (1932)	RAYMONT (this paper)
Hydrobia	10,000–14,000 (28,000)	16,000	18,000	1,400 (3,000)*	—	15,000–46,000 (60,000)	—	10,000–26,000 (34,000)
Macoma	36 (76)	20–30	800	150–200	150–220 (554)	300–1,000 (6,300)	2,000–5,000 (5,900)	250 (428)
Scrobicularia	100–280 (1,000)	230	—	136	—	20–60	—	150–330
Cardium	100–200 (383)	200	—	100–150 (300)	50–160 (192)	2,000–3,000 (4,675)	64	1,000 (6,000)
Pygospio	—	2,540	—	—	—	14,000–20,000	—	2,840
Heteromastus	60–90	—	—	—	—	10–40	—	1,400 (1,740)
Arenicola	3	50–60	—	16 (76)*	40–60	100	—	200–380 (470)
Nereis	1,000 (>3,000)	20 (130)	2,000	110 (396)†	25	100–320	‡	600–700 (890)
Nephthys	100–300 (500)	100	—	36	50–60	90	—	100–210

* = Loch Gilp, Scotland. † = Isle of Barra, Scotland. ‡ = " abundant ", no density quoted.

also occurred, but that the densities declined rapidly during autumn and winter. SMIDT and also WOHLENBERG found even larger settlements of O-Group cockles: SMIDT found 20,000 to 30,000 per m² quite frequently, and WOHLENBERG recorded some 40,000 per m², but he also showed how rapidly those numbers were reduced.

STEPHEN (1931) concluded that *Cardium* bred in summer at Millport, the smallest cockles appearing about August and reaching a length of <6 mm by the end of their first autumn. By the following July these cockles reached 12–13 mm. BRADY (1943) states that in June one-year-old cockles had an average length of 11 mm, and SMIDT (1951) shows in July one-year-old cockles reaching a length of 12 mm, or about 16 mm in a favourable year.

The results of the North Bay collections, and also the results from Loch Craiglin (RAYMONT, 1947) strongly support STEPHEN's view that *Cardium* spawns in summer, but the growth of the cockles up to November in North Bay was somewhat less than STEPHEN found. However, the 1945 spat attained a length of about 15 mm in North

Bay by July 1946, i.e. their growth was of the same order as that given by STEPHEN and BRADY, and (in a favourable year) by SMIDT. This improvement may reflect the better feeding conditions in North Bay in 1945–46.

The density of *Mytilus* was usually very low over the whole of North Bay, the only heavy settlements being at spatfall (August), after which the animals did not come into the regular samplings. CHIPPERFIELD (1953) shows that April–May is the most likely breeding time for *Mytilus* on British coasts; the period of settlement seems to be May to early July. Some authors, however, have recorded settlements in August, and this clearly was the main period for North Bay (p. 192).

Following a heavy spatfall the numbers of *Mytilus* declined very rapidly (cf. other bivalves), so that only once (July 1946) was an appreciable number of the larger mussels found (200–400 per m^2). SMIDT found that the Danish waddens were unsuitable for *Mytilus*; the numbers found were negligible, although on the banks very high densities of mussels occurred. Similarly THAMDRUP recorded densities of 2,000–12,000 mussels per m^2 on the banks, while over the mud flats only an occasional mussel was taken.

The growth rate of young *Mytilus* seems to vary greatly according to conditions (cf. WHITE, 1937; SMIDT, 1951). For example, SMIDT quotes other workers as stating that young spat may grow to 8 mm in less than two months if permanently covered with water, whereas similar spat, left uncovered for a few hours daily, hardly attained 4 mm in three months. WHITE (1937) states that under unfavourable conditions a mussel may add only a few mm in a year, but under good conditions, at St. Andrews, two-year-old mussels ranged from about 30–50 mm. This would indicate a growth at least of some 15–25 mm in a year. The long exposure periods over North Bay would suggest a rather unfavourable environment; nevertheless the 1945 spat grew to 9 mm by November and to about 20 mm in the following July, when these mussels would be one year old. This approximates to the figure mentioned by WHITE, and emphasizes that feeding conditions in 1945/46 over North Bay must have been very good.

Of the polychaetes, *Pygospio* was obviously dominant in North Bay. WOHLENBERG found *Pygospio* at upper tidal levels, though in relatively low densities, but THAMDRUP recorded very high densities, mainly near high water (Table XIV). SMIDT, however, found that very large concentrations of newly settled *Pygospio* ($>$31,000 per m^2) might occur right across the shore. In North Bay *Pygospio* was definitely more abundant at lower tidal levels, but it was so common that there was an average population for the whole mud flat of 160–380 per m^2 (Fig. 4). There are few records of large populations of this polychaete in Britain. However, HOLME (1949) found a density for the Exe Estuary similar to that of North Bay, though the populations are far below those of THAMDRUP for Skalling (Table XIV). BRADY (1943) records up to 600 *Scoloplos* per m^2 and fairly high numbers of *Spio* and *Scolecolepis* in Northumberland muds: perhaps these polychaetes replace *Pygospio*.

Heteromastus filiformis was the next commonest polychaete in North Bay; apart from the sharp decline in July 1946, the average population was 30–290 per m^2 (Fig. 4). *Heteromastus* was quite sharply restricted to mid-tide levels (higher in Transect 4), and the maximal densities were considerably greater than either those recorded by SPOONER and MOORE for the Tamar, or by THAMDRUP for Skalling, Denmark (Table XIV). However, SMIDT (1951) found that in 1947 *Heteromastus* became abundant on the Danish waddens, with some dense patches of mostly young worms exceeding 2,000 per m².

The average population of *Arenicola* over North Bay varied between 30 and 70 per m², apart from the marked decline in July 1946 (Fig. 4). Densities up to 400 per m² occurred over part of the shore (Table XIV). However, *Arenicola* was absent from

Fig. 4. Fluctuations in the density of polychaetes over North Bay. The changes in the total population and in the main species are shown. All numbers represent densities per m² calculated as averages of the populations at 14 sampling stations

a considerable number of stations; possibly it was commoner above mid-tide level, but there was no clear distribution pattern. Many authors have shown that lugworms generally avoid soft substrata and live in essentially sandy bottoms. Thus in Spooner and Moore's work, *Arenicola* hardly ever appeared in the samples. However, in the Exe and off the Northumberland coast small populations of *Arenicola* occurred (Table XIV), and Stephen (1930) found a rich ground in Loch Gilp. Thamdrup found *Arenicola* fairly widely distributed at Skalling, but the densities were <35 per m², except for occasional heavier populations of young worms.

Nereis diversicolor appears to be very restricted in North Bay. Most investigators (STEPHEN, SPOONER and MOORE, BRADY, WOHLENBERG, SMIDT) have found that this species occurs abundantly only at upper tidal levels. This was true also in North Bay, but the only station where the polychaete was really abundant was Transect 2, Station 1, where densities of >800 per m² were recorded (Table XIV). At most stations in North Bay *Nereis* never appeared at any time. HOLME (1949) also found it occurred infrequently in the Exe Estuary, and BRADY's densities for Northumberland are low. STEPHEN recorded fairly small populations for the Forth and Clyde, though he did find a high density on the Isle of Barra (Table XIV). On the other hand, WOHLENBERG (1937) found *Nereis* to be abundant at Sylt, and SPOONER and MOORE (1940) found it was a very common polychaete in the Tamar muds. REES (1940) also recorded high densities for the Bristol Channel (Table XIV). THAMDRUP (1935), in contrast to most workers, did not find *Nereis diversicolor* restricted to the upper tidal zones. His maximal densities were not very large, and varied from year to year (Table XIV). However, SMIDT (1951) has recorded many thousands of young O-Group *Nereis* from the same area, though adults were few. NICOL (1935) also once recorded the extraordinary density of 95,700 *Nereis* per m² (all young) from a salt mud pool at Aberlady.

Nephthys contrasted with *Nereis* over North Bay in being fairly restricted to low tidal levels. There appears to be general agreement that *Nephthys* occurs more frequently towards low tide mark. Although *Nephthys* occurred regularly in North Bay, the numbers were never high (Fig. 4). Indeed, the densities recorded for other areas are mostly rather low. SPOONER and MOORE, however, found somewhat higher populations in the Tamar (Table XIV).

It is clear that, while the fauna of North Bay is rich, comparatively few species reach really high densities (*Hydrobia*, chironomids, *Peloscolex*). These animals, though widespread, appear to be more typical of the upper tidal zones, and were probably favoured by the long and rather irregular periods of exposure over North Bay. The total average fauna varies between 8,700 and 18,700 animals per m² (Table IV), although individual stations showed populations exceeding 25,000 per m² (maximum 39,000). By contrast, BRADY (1943) gives an average density for a Northumberland mud flat of <400 animals per m².

SMIDT (1951) gives figures (Table 21, p. 138 of his paper) for the total numbers of animals per m² for Danish shallow water areas. The extraordinary richness of the Danish waddens (30,000–60,000 per m²) is outstanding, and SMIDT attributes this mainly to the predominance of small species (*Hydrobia*, *Pygospio*, etc.), and to the young of many species. Though the average density in North Bay was not nearly so high, the fauna was rich and, like the waddens, was characterized by the abundance of small animals (*Hydrobia*, *Peloscolex*, chironomids, *Pygospio*), and by young individuals especially of molluscs. The fauna was also similar to that already described by RAYMONT (1947, 1949) for Loch Craiglin, where the total average density rose with fertilization to 16,000 and even 23,000 animals per m², and where the same species (*Hydrobia*, chironomids, young *Cardium*) were dominant.

The results of the population changes over North Bay show a pronounced seasonal fluctuation which is not unexpected in an inter-tidal area. Previous studies in Loch

Sween showed fairly clear seasonal effects, even in the bottom fauna below low-tide mark (RAYMONT, 1947, 1950). But in Loch Craiglin, and in the areas of Kyle Scotnish below low-water mark, the maximum population occurred during the summer, whereas in North Bay the populations in November were consistently larger than in July. In Loch Craiglin, however, the actual months in which the highest densities were experienced were August and September, and a few stations in the loch did show higher densities even in November. In Kyle Scotnish, too, the high " summer " peaks of the bottom fauna represented an average of the three months, July, August and September. It seems clear, as indeed might be expected in a marine area, that the high densities occurred in *late* summer or even afterwards.

It is not surprising that the July samplings should give a lower population than the November samples. Most of the young larvae produced during spring and summer will not have settled and grown to a sufficient size to appear in July samplings. For example, SMIDT (1951) found that the vast majority of *Hydrobia* in June belonged to O-Group, and measured only 0·5 mm. Since they grow only some 2 mm by the winter, it is likely that sampling with a 1 mm sieve in July would miss the majority of the brood. The strong seasonal fluctuation is in fact dominated by *Hydrobia* (Tables IV and V), but the seasonal changes hold also for chironomids, bivalves, oligochaetes and " other organisms ". Chironomids may be expected to oviposit mainly during the summer, and therefore the new larvae will hardly appear in sievings before early autumn. It has also been shown that the main spatfalls of *Cardium* and *Mytilus* occur after July. During the ensuing winter and spring there will be heavy depredations on the bottom fauna, and also the physical conditions (especially frost) over winter will cause the fauna to decline. Little recruitment may be expected before July in the following year.

The results from November 1943 to July 1945 indicated then no real change in the overall population, apart from these seasonal fluctuations. This is borne out by both the average populations (Table IV) and by the results from individual stations (Table VIII, Fig. 3). The rise in November 1945, however, was definite and widespread. The average increase was 40%, and a large number of individual stations showed a rise (Fig. 3, Table VIII).

A rise of only 40% could easily result from a " natural " fluctuation, i.e. it might be attributed to some favourable condition other than increased food supply. Wide variation in the success of year-groups of bottom animals are well known (BOYSEN-JENSEN, 1919; THAMDRUP, 1935; WOHLENBERG, 1937; STEPHEN, 1931, 1932, 1938). Nevertheless it is usual then for some species to show one particular year as a good brood year, while for other species that same year may be very poor (cf. BOYSEN-JENSEN, 1919, for species of bivalves). The fact that so many of the main constituents of the fauna over North Bay showed an increase at the same time (Table IV), lends considerable support to the view that the rise in November 1945 was due to the improved conditions resulting from fertilization. The accelerated growth rate seen in some lamellibranchs (p. 192–193) would also agree with this conclusion.

By July 1946 the average population over the North Bay had declined sharply from the previous high autumn density to reach the lowest value for the period of sampling. This marked fall may be largely explained as a seasonal change as in previous years. It is not easy, however, to account for the especially severe drop in the density of the fauna in 1946. Kyle Scotnish had been stocked with plaice fry in 1945, and a more successful stocking involving ca. 1,500,000 fry was made in the spring of 1946 (GROSS, 1950). To what extent the young flatfish fed over the mud flat at high tide it is impossible to say; nevertheless a considerable increase in the amount of food taken by the fish was inevitable, especially in view of the very high growth rate (cf. GROSS, 1950).

Possibly the drop in the fauna was also partly related to the severe frost in February and March of that year. Thus an extract from the log book states that work was impossible at the head of the loch (i.e. just off North Bay) on 28th February 1946, because of ice. The following day the whole of Kyle Scotnish was covered with ice, and this cleared from the northern parts of the loch only on 5th March. The general bottom fauna of Kyle Scotnish below low-tide mark was not severely checked by these frosts (cf. RAYMONT, 1950) but over an inter-tidal mud flat the bottom animals, except for those burrowing really deeply, would be exposed fully to the severe effects of freezing.

It is significant that almost all the fauna (*Hydrobia*, polychaetes, chironomids, oligochaetes, etc.) showed the great reduction in numbers by July 1946, i.e. it was not an unsuccessful spawning or a poor settlement by merely one important species of the community. On the other hand, the population of large bivalves remained almost stationary from November to July, and indeed the final population (125 large bivalves per m^2) was higher, except for November 1945, than at any other time (Tables IV, XII, XIII). It is these larger bivalves which can burrow away from the surface, some like *Scrobicularia* to a considerable depth, and thus escape, to some degree, adverse conditions. By contrast, the youngest bivalves were decimated over the same period, falling from more than 1,000 to 129 per m^2 (Table IV).

In the earlier years few large bivalves occurred over North Bay (Tables XII and XIII). Probably these molluscs are periodically greatly reduced in numbers by adverse conditions in the area. The lack of the older bivalves is especially true of *Mytilus* which is of course a surface dweller. By contrast, *Scrobicularia*, which burrows deeply, and as older individuals may therefore escape the worst conditions, is not so poorly represented by the older age groups (Table XI).

The only marked exception to the general seasonal fluctuations, and to the large increase in November 1945, was in the polychaete group (Fig. 4). These animals exhibited a fairly steady increase in population from November 1943 onwards, and they reached an average of 1,200 animals per m^2 in the summer of 1945, after which there was a very sharp decline to the summer of 1946 (Table IV). These changes were mainly due to *Pygospio* (Fig. 4). This polychaete was numerically dominant over the whole period November 1943 to July 1946. It also appears to have reproduced in the years 1944 and 1945 sufficiently early for there to be a sharp increase in the polychaete populations in each summer. From November 1943 to July 1944, for example, the population of *Pygospio* more than doubled, and from November 1944 to July 1945 there was an increase of 50%.

Phyllodocidae also contributed to the sharp peak in the summer of 1945 (Fig. 4). The only other polychaete that played a significant part in the overall population changes was *Heteromastus filiformis*—the second most important polychaete. During 1944 there appears to have been a successful brood of *Heteromastus*, so that between July and November of that year the population more than doubled, but the most surprising change was the very sharp decline in *Heteromastus* from July 1945, so that the population was virtually wiped out by the summer of 1946. This was also true of

Nereis diversicolor and *Arenicola marina* (Fig. 4). Not a single *Arenicola* was taken in July 1946, and *Nereis* and *Heteromastus* occurred only in one auger sample (Transect 4, St. 1), at that time. The decline in the polychaete population affected the other species also, though not quite so obviously (Fig. 4); the only exception was *Nephthys*.

The increase in *Heteromastus* and *Pygospio* in 1944, and in *Pygospio* and Phyllodocidae in the following year, may be " natural " fluctuations, though probably the increased food supply in Kyle Scotnish due to fertilization in the early years may have helped in their success. The decline in 1946, in contrast to the rise in the polychaete population below low-water mark, (RAYMONT, 1950) may be attributed to the adverse conditions over the exposed inter-tidal mud flats in the winter. It may not be without significance that *Nephthys* was the only polychaete which did not suffer the decline. This species was sharply limited to the lowest tidal limits on the shore, and it therefore would not be long exposed to freezing. Over the same period *Nephthys* was increasing, together with other polychaetes, in the areas *below* low water in Kyle Scotnish.

It would appear that fertilization, with the resulting increase in food over the North Bay area, had little lasting effect on the density of the bottom fauna. While some increase did occur when other environmental conditions were also favourable, the beneficial effect was more than wiped out by other adverse conditions, and the increase in density was at the most temporary. It is clear, therefore, that increase in food supply alone cannot compensate for other adverse features in the environment. Any attempt at fertilization in inter-tidal areas should therefore be made only in those areas where the species of animals whose increase is desired are either naturally " hardy ", or where the environmental conditions such as temperature, salinity, and so on are constantly favourable.

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