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A. D. McIntyre and A. Lielcheriou

Marine Laboratory, Aberdeen.

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Summary

The macrofauna on the beach and in shallow water of a flatfish nursery ground is described. The infauna retained on a $\frac{1}{2}$ mm sieve had a mean density of 755 individuals and biomass of 1.3 g dry wt/m² on the beach, and 3055 individuals and 3.7 g dry weight in the subtidal. The epifauna, dominated by juvenile stages of place and dabs is briefly described. Food chains in the bay are considered. The importance of production in the water column is emphasised, and its possible pathways to the benthos indicated. Predation on the infauna by juvenile flatfish is discussed and it is suggested that since these fish feed to some extent by cropping siphon tips and palps, the productivity of the benthic fauna may be greater than previously suspected.

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Introduction

During 1965 the macrofauna of a sandy bay in a Scottish sea loch was investigated. The work formed part of an extensive study by a larger group, of food chains leading to place, involving sampling of all trophic levels, combined with experimental work.

The area investigated is Firemore, a sandy bay inside Loch Ewe (latitude $57^{\circ}49\frac{1}{2}$ 'N, $5^{\circ}42$ 'W). The bay (Fig. 1) which is about 800 m wide, is enclosed on two sides by rocky headlands and divided into north and south beaches by a central promontory. The substratum changes to shell gravel roughly in line with the headlands, so an isolated pocket of sand from high water mark on the beach to about 8-10 m depth is available for study. Most previous benthos work has been concerned with either the intertidal zone or with the subtidal region deeper than several metres, andlittle is known about the quantitative distribution of the fauna in the area between low water springs and about 5 m depth because of the difficulty of sampling in very shallow water. In the present work it was recognised that the low tide mark does not necessarily separate an assemblage of beach species from a corresponding subtidal assemblage, and the fauna is considered as a whole from the highest point on the beach to the limit of the sand at about 10 m depth.

The bay is sheltered from the prevailing south-west wind, but is exposed to the north. The median diameter of the sand, which is well sorted, ranges from 180 to 260 µ. Profiles constructed at intervals over several years showed that sand movements were considerable on the beach, and were mainly related to alterations of the runnel and ridge system around the mid tide level. A freshwater stream on the scuth beach had a calculated flow of 16 cusec, and while sampling of interstitial water showed it to have a negligible effect in terms of dilution, the very variable course of the stream across the beach produced important scour effects. Annual ranges of temperature and beach salinity are given in Table 1. Salinity of subtidal bottom water varied little throughout the year and averaged 34.00‰.

The Fauna

The fauna was sampled by digging quadrats of $\frac{1}{4}$ or $\frac{1}{16}$ m² mainly on four traverses on the beach and by using a $\frac{1}{10}$ m² Smith-McIntyre grab weighted to 90 kg at various depth zones on subtidal extensions of traverses 1 and 4 out to the limit of the sand (Fig. 1). It was possible to use the grab in a few metres of water close to the beach from an 8 m boat of shallow draft especially rigged to operate heavy gear. The sampling was done in the spring and repeated in the late summer of 1965. All samples were sieved through a $\frac{1}{2}$ mm mesh and dry weights do not include shells of lamellibranchs or echinoderms, or gut contents of Ophelia or Echinocardium.

The fauna is listed in Table 2, and the numbers and weights summarised in Tables 3 and 4. In the intertidal zone numbers of individuals ranged from zero at some of the high water stations to $3856/m^2$ at just below mid-tide level on the south beach. A total of 63 species was found on the beach, but of these only eight were widespread and abundant. Subtidally numbers ranged from $2448/m^2$ in water less than 1 m deep to a maximum of $4045/m^2$ in the 4-6 m depth zone, and altogether 113 species were recorded from the subtidal sand. Most of the individuals were less than 1 g wet weight, and the few heavier animals, such as <u>Echinocardium cordatum</u>, <u>Ammodytes lanceolatus</u>, and some of the thickshelled lamellibranchs, are listed separately in the tables. The overall dry weights on the beach and in the subtidal were 1.27 g and 3.67 g/m²

Some of the main species, such as Nerine cirratulus and Nephtys cirrosa were generally distributed over the sand, but most showed a zonation with distinct peaks. Tellina tenuis occurred mainly from about mid-tide level to a depth of 2 m, where it was replaced by T. fabula, while the other common lamellibranchs such as Dosinia lupinus and Cochlodesma practenue were found deeper than 4 m, and the appearance of Tellina pygmaea and Gari fervensis was associated with the proximity of the shell gravel beyond about 10 m. Of species confined to the intertidal zone, the polychaete Ophelia rathkei, the isopod Eurydice pulchra and the amphipods Bathyporeia pilosa and B. pelagica were the most abundant, while of the related species, B. elegans was mainly, and B. guilliamsoniana entirely confined to the subtidal. In general the number of species increased as the water deepened, the poorest zone being immediately below low water mark. Crustacea (mainly Amphipoda) was the only group which was almost as rich in shallow as in deeper water.

The grab surveys produced information only on the infauna, but sampling with cores gave evidence of a rich interstitial fauna, and hauls with bottom plankton nets, D-nets and dredges indicated populations of small epibenthic organisms, mainly mysids, cumaceans and amphipods. The remaining component of the macrofauna in the bay consists of larger These were sampled with pushnets in shallow invertebrates and fish. water and with beam trawls and a small scale model of a commercial otter trawl in the bay as a whole. The invertebrates included Crangon crangon (L.), Carcinus maenas (L.), Portunus spp., Cancer pagurus (L.), Pagurus bernhardus (L.) and Asterias rubens (L.), while the fish catches were made up regularly of Syngnathus acus (L.), Gobius spp., Trachinus viper Cuvier and Valenciennes, Pholis gunnellus (L.), Trigla sp., Cottus sp., Agonus cataphractus (L.), Spinachia spinachia (L.), Ammodytes lanceolatus Lesauvage and several gadoids. Most of these were not normally abundant, but Ammodytes was occasionally taken in large numbers in the nets and was found buried in the sand during beach sampling, while juvenile gadoids (Gadus morhua L., and Pollachius virens (L.)) migrated into the bay in the summer months. Skate (Raja spp.) and adult plaice (Pleuronectes platessa L.) and dabs (Limanda limanda (L.)) were also present in small numbers but the bay is a flatfish nursery ground, and the bulk of the fish population consisted of the O+ brood of plaice and dabs with juvenile flounders (Platichthys flesus (L.)) locally distributed. Edwards (in preparation) has studied these populations and shown that at the time of maximum density (in June each year) the numbers of juvenile flatfish were less than 2 per m, with a corresponding dry weight of just over 0.02 g.

Discussion

The macrobenthic infauna of the bay consists of animals which feed largely on particulate matter in or on the sand, and which are themselves preyed on chiefly by populations of juvenile flatfish.

Considering first the lower part of this food chain, the average biomass of benthic macrofauna in the bay as a whole is 1.25 g C/m^2 and as this consists mainly of the sort of animals for which Sanders (1956) suggests annual production is about twice standing stock we can estimate the production as about 2.5 g $C/m^2/yr$. The assumption of a 10%2 ecological efficiency suggests an annual requirement of 25 g C/m by this population. An obvious source of food would seem to be the primary production in the substratum but at Firemore, because of the considerable sand movements, this is restricted to attached diatoms for which Steele & Baird (1967) estimated a production of 4-9 g C/m²/yr clearly inadequate for the macrofauna, especially since a rich meiofauna must also be supplied.

A second source of organic matter for the benthos is from the macrophytes which cover the rocks round the bay and in the loch as a whole. Masses of these algae are detached and washed into the bay at certain seasons and finely divided pieces are sometimes seen as a thick suspension in the swash zone. Some of this algal detritus is found in most grab hauls and the quantities retained in a $\frac{1}{2}$ mm sieve averaged almost 8 g dry weight/m. Estimates of the standing stock of macrophytes in the bay are being made, and experiments to determine the rate of breakdown are under way.

A third source of organic matter for the sand fauna is the primary production in the water column. This is estimated at 95 g C/m² annually (Steele & Baird, 1967) and while some of this may be available to the benthos directly it must supply at least one intervening trophic level in the plankton as well as a rich fauna of filter feeders on the rocks. There are several indirect pathways by which this water column production can reach the benthos. The stranding of planktonic copepods on the beach at Firemore in numbers of over 80 individuals per m² has been recorded, and it should be noted that this is a minimum figure since it represents only individuals retained in a $\frac{1}{2}$ mm sieve. The rock fauna also contributes, since in bottom plankton hauls, big numbers of barnacle casts are frequently collected, and grab haul counts at Firemore are sometimes inflated by very numerous barnacle cyprids which appear on the bottom and probably never reach a substratum suitable for settlement.

It would appear then that the water overlying the sand must supply most of the organic matter required by the benthic fauna at Firemore, either by carrying in the breakdown products of seaweeds; or through its own production directly; or indirectly through the plankton or the rock fauna. However, it has been shown (Steele & Baird, 1967) that only 3-5% of the organic matter in the sand is unattached, so that a continuous supply of material and a rapid filtering of water through the sand are essential if the requirements of the benthos are to be met in this way.

Finally, considering the higher levels of the food chain, Edwards (in preparation) has shown that young flatfish populations are the main predators of the benthos at Firemore. There are some interesting aspects of predation by such populations. Young plaice are more or less confined to the sand substratum and are known to migrate into the intertidal zone This migration must affect the patterns of with each rising tide. predation in an area such as Firemore where there is a marked zonation of the benthos. Such species as Magelona, for example, will find predation pressure reduced towards the time of high tide as the fish disperse over a wider area. The quantity of benthic food available to the fish would seem from calculations above to be about 2.5 g C/m /yr. However, Edwards has shown that a large part of the predation consists not of the consumption of whole animals but of the cropping of tips of Tellina siphons and of palps of Polychaeta such as Magelona and various spionids. It may then be that the rate of regeneration of these organs is of as great importance as production of the whole animal, so that a community of apparently low productivity may in fact provide good feeding for juvenile flatfish.

The substrata which make suitable settlement areas for these young flatfish range from quite coarse to comparatively muddy sand. While the

fauna of sand associations is stable, Thorson (1957) indicates that on muddy sand a large number of short-lived species make up the community, and that different species may dominate the fauna in successive years. This supports the observations of Macer (1967) who studied young flatfish on a muddy sand bottom, and reported that different species dominated their stomach contents in 4 successive years. Further work in this field will show how the growth and survival of flatfish are influenced by the benthic community on which they settle.

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	Mean Air temp. in O°C	Mean beach sand temp. in O ^O C	Sea temp. (bottom) in 0°C	Range of beach interstitial salinity in %o
Jan.	4.4	3.2	7•9	15.2-33.5
Feb.	3.2		2	상태, 지하는 것은 감독했다.
Mar.	5.1	7.5	6.4	11.5-34.0
Apr.	8.3		7.3	
May	10.6	11.0	8.3	15.2-34.2
June	12.3	-	8.3	
July	12.4		11.9	이 아이는 것 같아?
Aug.	13.5	13.4	12.0	12.9-34.0
Sept.	11.6		11.6	
Oct.	10.8	11.0	11.7	20.3-33.2
Nov.	4.4		10.7	
Dec.	3.6	1.55	8.5	-

Table 1. Annual range of temperature and salinity.

Table 2.

Chone duneri Malmgren

Fauna of Firemore Bay, showing distribution of species. Numbers 1-4 refer to beach traverses and S to Subtidal records.

POLYCHAETA

CRUSTACEA

T.	UDIOIRDIA			
	Sigalion mathildae		Acidostoma obesum (Bate)	4.
	Audouin and MEdwards	···45	Hippomedon denticulatus (Bate)	S
	Sthenelais limicola (Ehlers)	••••S	Lysianassidae (2 spp.)	S
	Pholoë minuta (Fabricius)	S	Ampelisca brevicornis (A. Costa)	S
	Polynoidae	···45	A. diadema (A. Costa)	····S
	Phyllodoce groenlandica Oersted	···45	A. typica (Bate)	S
	Eulalia sanguinea Oersted	S	Bathyporeia guilliamsoniana (Bate)	.2S
	Eteone longa (Fabricius)	.2S	B. pelagica (Bate)	1234.
		S	B. elegans Watkin	12.45
	E. foliosa Quatrefages	S	B. pilosa Lindström	1234.
	Mystides elongata Southern			•••4•
	Oxydromus propinquus	C	Cressa dubia (Bate)	
	(Marion and Bobretzky)	••••S	Stenothoë marina (Bate)	•••4•
	Hesionidae	••••S	S. monoculoides (Montagu)	•••4•
	Exogone hebes (Webster and Benedict)	••••S	Perioculodes longimanus	n.
	Odontosyllis sp.	••••S	(Bate and Westwood)	····S
	Jolytus sp.	•••4S	Pontocrates arenarius (Bate)	·234S
	Nereidae	•••·S	P. norvegicus Boeck	••••S
	Nephtys hombergii Savigny	•••·S	Atylus swammerdami (MEdwards)	••34S
	N. Longosetosa Oersted	•••4S	A. falcatus (Metzger)	S
	N. cirrosa Ehlers	1234S	Megaluropus agilis Hoek	···45
	N. caeca (Fabricius)	S	Melita obtusata (Montagu)	···45
	Sphaerodorum gracilis (Rathke)	S	Gammarus locusta (L.)	4.
	Glycera rouxii Audouin and MEdwards		Gammaridae juvs.	.2
	Goniada maculata Oersted	••••S	Dexamine spinosa (Montagu)	S
	Glycinde nordmanni (Mamgren)	S	Talitrus saltator (Montagu)	1
	Lumbrineris gracilis (Ehlers)	S	Hyale nilssoni (Rathke)	.2.4.
			Aora sp.	• • • • · · · S
	Orbinia latreillii (Audouin and M	1		
	Edwards)	•••4•	Microprotopus maculatus Norman	••••S
	Scoloplos armiger (O.F. Müller)	••••S	Photidae	••••S
	Scolelepis fuliginosa (Claparède)	12	Amphithoë rubricata (Montagu)	4.
	Nerine bonnieri Mesnil	••••S	Ischyrocerus sp.	4.
	N. cirratulus (delle Chiaje)	1234S	Jassa falcata (Montagu)	••••S
	Aonides oxycephala (Sars)	•••·S	Siphonoecetes dellavallei Stebbing	12345
	Sriophanes bombyx (Claparede)	.2S	Corophium volutator Pallas	S
	Sokroyeri Grube	••••S	Phtisica marina Slabber	S
	Spio filicornis (O.F. Müller)	12.4S	Podalirius typicus (Krøyer)	S
	Pygospio elegans Claparède	.2	Caprellidae	4.
	Polydora sp.	15	Gnathia oxyuraea (Lilljeborg)	S
	Prionospio malmgreni Claparede	S	Cirolana borealis Lilljeborg	S
	P. cirrifera Wirén	····S	Eurydice pulchra Leach	1234.
	Psammodrilus balanoglossoides		Idotea baltica (Pallas)	12.45
	Swedmark	1234.	I. emarginata (Fabricius)	12.45
	Magelona papillicornis O.F. Müller	.2S	Iphinoë trispinosa (Goodsir)	S
	M. filiformis Wilson	S		
	Poscilochaetus serpens Allen	···45	Pseudocuma longicornis (Bate)	••••S
	Paraonis fulgens (Levinsen)	12345	Bodotria scorpioides (Montagu)	••••S
		·2S	Asterope mariae (Baird)	••••S
	Aricidea minuta Southward		Mysidacea	•23•S
	Tharyx sp.	••••S	Copepoda	1234.
	Chaetozone setosa Malmgren	••••S	Hippolyte varians Leach	4.
	Ophelia borealis Quatrefages	••••S	Crangon crangon (L.)	12
	<u>O. rathkei</u> McIntosh	12.4.	Pagurus bernhardus (L.)	••••S
	Travisia forbesii Johnston	••••S	Decapod larvae	•• 34 •
	Notomastus latericeus Sars	•••4S		
	Capitellidae	12.4S		
	Arenicola marina (L.)	.2		
	Owenia fusiformis delle Chiaje	••••S		
	Lagis koreni (Malmgren)	····S	그는 그는 것은 것을 하는 것은 것 같아요. 가슴을 통해 가슴을	
	Lanice conchilega (Pallas)	S		
	Terebellidae	••••S		

....S

(Table 2 continued)

 $\hat{U}_{i}(x_{i}) = u_{i}(x_{i})$

MOL	LUS	CA

Lacuna vincta (Montagu)	1
Littorina littoralis (L.)	4.
Natica alderi Forbes	····S
Philine quadripartita Ascanius	····S
Nucula turgida Leckenby and Marshall	S
Mytilus edulis L.	4.
Montacuta ferruginosa (Montagu)	···45
Mysella bidentata (Montagu)	S
Dosinia lupinus (L.)	S
Venus striatula da Costa	4S
Spisula subtruncata (da Costa)	S
Mactra corallina (L.)	S
Gari fervensis (Gmelin)	S
Abra prismatica (Montagu)	•••·S
Tellina fabula Gmelin	S
T. tenuis da Costa	1234S
T. squalida Montagu	•••·S
T. pygmaea Loven	S
Donax vittatus (da Costa)	S
Cultellus pellucidus (Pennant)	S

MOLLUSCA (Continued)	
Ensis sp.	S
Thracia phaseolina (Lamarck)	S
Cochlodesma praetenue (Montagu)	••••S
ECHINODERMATA	
Asterias rubens L.	••••S
Acrocnida brachiata (Montagu)	S
Ophiura albida Forbes	••••S
Echinocardium cordatum (Pennant)	•••4S
Labidoplax digitata (Montagu)	S
MISCELLANEOUS	
Anthozoa	4S
Nematoda	S
Nemertini	12.45
Oligochaeta	·234S
Sipunculoidea	S
Insect larvae	4.
Chaetognatha	
Phoronis sp.	
Enteropneusta	S
Ammodytes lanceolatus Lesauvage	12.4S
Anguilla anguilla (L.)	S
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	Traverse 1		Traverse 2		Trave	rse 3	Trave	rse 4	Intertidal Mean	
	Dry wt.	Number	Dry wt.	Number	Dry wt.	Number	Dry wt.	Number	Dry wt.	Number
Polychaeta	0.514	414	0.395	889	0.111	52	0.331	111	0.338	366
Crustacea	0.045	157	0.057	302	0.180	325	0.089	320	0.093	285
Tellina tenuis	0.253	35	0.480	55	0.111	14	1.552	147	0.599	63
Others	0.007	12	0.006	24	0.009	82	0.041	42	0 .01 6	40
To	0.819	618	0.938	1270	0.411	473	2.013	620	1.046	754
Large individuals	0.207	1	0.178	1	-	-	0.508	1	0.223	1
Grand total	1.026	619	1.116	1271	0.411	473	2.521	621	1.269	755

Table 3. Firemore, intertidal. March/August, 1965. Mean biomass_per traverse in g/m² dry wt., and numbers of individuals per m².

Firemore, subtidal. April/August, 1965. Mean biomass in g/m^2 dry wt. and numbers of individuals per m² in each depth zone. Table 4.

	< 1 m		1-2 m		2-4 m		4-6 m		6-8 m		8-10 m		Subtidal Mean	
	Dry wt.	No.	Dry wt.	No.	Dry wt.	No.	Dry wt.	No.	Dry wt.	No.	Dry wt.	No.	Dry wt.	No.
Polychaeta	0.575	233	0.798	404	1.116	1123	0.863	1515	0.770	1150	1.082	1130	0.867	926
Crustacea	0.173	1150	0.222	2083	0.191	1467	0.213	2385	0.209	2662	0.248	1790	0.209	1923
Mollusca	0.855	140	1.190	190	0.525	153	0.469	120	0.429	124	0.925	233	0.732	160
Others	0.006	13	0.025	40	0.068	50	0.078	25	0.091	58	0.175	70	0.074	43
Total	1.609	1536	2.235	2717	1.900	2793	1.623	4045	1.499	3994	2•430	3223	1.883	3051
Echinocardium	0.154	< 1	0.070	< 1	3.078	1	1.884	1	0.516	< 1	0.315	< 1	1.003	<1
Other large individuals	0.106	< 1	0.246	3	0.941	6	0.212	1	0.397	2	2.806	9	0.785	4
Grand total	1.869	1536	2.551	2720	5.919	,2800	3.719	4047	2.412	3996	5.551	3232	3.670	3055

