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IRISH INTERTIDAL MEIOFAUNA: A MODICUM OF PROGRESS

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ABSTRACT

Sporadic records of meiofauna on Irish shores appear from the 1860s onwards. These and more recent records of metazoan meiofaunal taxa are reviewed. Meiofaunal abundance and diversity are related to the habitats' structural complexity.

Overall abundances of up to two hundred individuals below each square centimetre of sand beach surface and of one thousand per gram wet weight of plant have been recorded on Co. Down beaches. Distributions and abundances of meiofauna vary with sub-habitats as for example shown by work on Oligochaeta and Acari. An example of sub-habitat differences in abundance is given for flatworms in a sand beach with *Arenicola* burrows. Biomass data is absent from the literature but data for one Co. Down beach is presented.

In spite of the paucity of information on our beach meiofauna, Irish work led to the first published EM pictures illustrating meiofaunal adaptation at the ultrastructural level and to the elaboration of the concept of the thiobios.

A small amount of work has been conducted on behaviour and physiology of meiofauna from Irish beaches but very little is known of their energetics. Some work on meiofaunal respiration has illustrated the foolhardiness of applying laboratory algorithms to field populations unless population density and adaptation to environmental temperatures are considered. Although meiofauna may provide a very good means of monitoring pollution, to date there appear to be only five Irish studies considering possible anthropogenic affects; these relate to oil spill detergent, Pb, sewage discharge, the presence of intertidal oyster trestles and seaweed harvesting respectively.

In conclusion some progress has been made but it is clear that a great deal of work on faunistics, population ecology, species interaction and energetics remains to be done before the role of meiofauna in Irish beaches can be properly assessed.

INTRODUCTION

The history of meiobenthic research extends forward from mid-nineteenth and early twentieth century taxonomic descriptions, for example of Kinorhyncha (Dujardin 1851) and acochlid opisthobranch Gastropoda (Kovalevsky 1901), to present-day studies which range from ultrastructure to community energetics. The paper on the distribution and organisation of the 'microfauna' of the Bay of Kiel by Remane (1933) can be taken as the foundation stone of present studies. This paper compared the distribution, abundance, morphology and feeding of major taxa in three main biotopes – namely phytal, sand and mud. Remane's (*l. c.*) descriptions included a number of biocoenoses (i.e. characteristic habitats and their fauna) which could be found intertidally; these included sand with the gastrotrich *Turbanella hyalina* Schultze, *Arenicola marina* (L.) detritus-rich sand, the seaweed *Fucus vesiculosus* L. and *Zostera marina* L. plants. After Remane's seminal paper, work continued mainly in Europe, on a taxonomic and morphological basis until the 1960s (see Swedmark 1964) when further ecological (reviewed by McIntyre 1969) and experimental studies (Boaden 1962) began. By this time the term 'meiofauna', apparently first used by Mare (1942), had come into general use to describe the fauna which generally passed through the 1 or 2 mm mesh used in sorting the macrofauna from benthic samples.

In Ireland as elsewhere the earliest studies composed of or incorporating meiofaunal records were on a taxonomic and/or faunistic basis such as Brady and Robertson (1869), Halbert (1920) on Acarina and Southern (1910, 1912) on Annelida and Turbellaria respectively. The latter paper resulted from part of the Royal Irish Academy's Clare Island Survey, as did several other papers cited in the references (those from Volume 31 of the Proceedings). In the 1960s meiofaunal studies began to include behavioural and experimental work (e.g. Boaden 1968). The volume edited by Higgins and Thiel (1988) remains a good manual for sampling, preservation and other techniques. Giere (1993) provides an excellent introductory text to the history and status of meiobenthic biology at the end of the twentieth century; this book cites about nine hundred and forty references of which nine are mainly based on work from Ireland. It may be said that our knowledge of Irish meiofauna remains sparse. It is the purpose of the present paper to summarise what is known about the island's intertidal meiofauna to date and to help stimulate work which may help fill the considerable gaps in our knowledge.

THE MEIOFAUNA

The following list must not be taken as exhaustive since it does not, for instance, include various meiofaunal records mentioned incidentally among more general faunal lists – an example could be the polychaete *Dinophilus taeniatus* Harmer often found in rock-pools and recorded in Williams (1954).

Protista

The Protista in general and the Ciliata in particular provide an extremely important component of meiofaunal biotopes. Mulisch *et al.* (1986) list six species of folliculinid (Ciliata Heterotrichida) found intertidally on spirorbid polychaete shells from Strangford

Lough, Co. Down, but there appears to be no other work on the Irish coastline citing free-living ciliate species. Giere (1993) and Patterson *et al.* (1988) should be consulted for further information about the role of Protista in the meiofaunal community.

Foraminiferans have been neglected in many meiofaunal studies but are important in some habitats such as intertidal mud (Ellison 1984). The great Irish naturalist Joseph Wright published many papers on foraminiferans including littoral and deep water species from about 1870 to the early 1900s. The reader is referred to the list in Heron-Allen and Earland (1913) who list many species occurring in shore sand and from shallow-water dredgings in the Clare Island area. The occurrence of some Foraminifera in Bull Island (Dublin) sediment is cited by Healy (1975).

Cnidaria

There are relatively few meiofaunal cnidarians. *Protohydra leukarti* Greef is common in high-shore muddy sands in Strangford Lough and, being of world-wide distribution, is presumably common in similar and brackish-water sediments elsewhere in Ireland. *Halammohydra schulzei* Remane has been found intertidally at Black Island in the Strangford Lough Narrows (Boaden 1966). A curious medusoid form, probably a species of *Eleutheria,* was found to be common on low-shore red algae in the Lough Narrows in September 2000; it 'walked' on the weed thalli using the ventral branches of its capitate tentacles (pers. obs.). A few more meiofaunal cnidarian species probably remain to be found on our beaches.

Gnathostomulida

Sterrer (1971) described the 'new' gnathostomulid *Austrognatharia boadeni* from detritus-rich shell gravel at Green Island in the Strangford Lough Narrows and Sterrer (1969) listed six species of the genus *Pterognathia* from various localities near Portaferry, Co. Down. *Gnathostomula paradoxa* Ax is common in intertidal fine sand in Strangford Lough (pers. obs.). Further investigations of detritus-rich sands could easily double the number of species known from Irish shores.

Platyhelminthes

The marine turbellarians are common in littoral sediments and in low-shore phytal habitats where they are often the third or fourth most common metazoans. Knowledge of their ecology was summarised by Boaden (1995). Acoel species sometimes have population blooms particularly in mud and muddy sands and in phytal habitats. Rhabdocoels especially the Kalyptorhynchia are particularly common in tidal flats and Seriata, especially the Otoplanidae, may dominate in coarse wave-swept sediments. Southern (1912) listed eleven turbellarian species of meiofaunal size occurring intertidally at Clare Island and twenty nine at Blacksod Bay – with seven species in common. His posthumous paper on Turbellaria of Ireland (Southern 1936), which gives thirteen earlier references to Irish Turbellaria, includes records for fifty eight species which had been found intertidally. Boaden (1966) lists fifty turbellarian species from Strangford beach sediments. There are further Co. Down records of some of these and seven other identified species in Maguire (1977). The 'red acoel' in the latter paper has subsequently been identified as *Paratomella* *rubra* Dörjes. The type locality for the retronectid *Retronectes terpsichore* Sterrer and Rieger (1974) is at Green Island, Strangford Lough. An estimation is made that the known number of species on Irish beaches is less than a fifth of those actually occurring.

Gastrotricha

There appear to be no records of marine Gastrotricha in Ireland prior to 1966 when Boaden listed twenty-eight species from Strangford Lough. All but one of these (*Tetranchryoderma coeliopodium* Boaden) have been found intertidally in the area, albeit some at ELWS. Maguire (1977) described three new species from intertidal sand from the Strangford area. The world database for marine gastrotrichs prepared by Hummon (details from hummon@ohio.edu) gives various Irish west coast localities where the gastrotrich fauna has been sampled but does not give further details yet other than the number of species (e.g. at Castlegregory six chaetonotoids and six macrodasyoids). Marine gastrotrichs are more or less limited to marine sands and gravels and are often the third to fourth most abundant metazoans in sand beaches. A general account of the biology of gastrotrichs is presented by Boaden (1985). The number of currently known species on Irish beaches probably represents less than a third of those occurring.

Nematoda

Nematoda are often the most abundant metazoans in the benthos; Platt and Warwick (1980) stressed their significance in the littoral ecosystem. Little is known of their distribution in Ireland in spite of excellent early work by Southern (1914b) who, commenting on his extensive records from the Clare Island Survey, stated that species found on weed or under stones on the shore usually belonged to well-known species but those in sand and mud 'were usually either new or very rare'. Platt (1973) described nine new species from the northern fine-sand flat of Strangford Lough from where he also reported on the ecology of these and a further seventy-five species (Platt 1977). He also described two new species from South Bay on the Outer Ards Peninsula coast (Platt 1983). Our current knowledge probably represents less than a tenth of species occurring on Irish shores.

Annelida

Meiofaunal polychaetes are common in intertidal sediments and on rocky shores but are not commonly recorded in the literature. Southern (1910, 1914a) lists polychaetes from the Dublin bay area (with shore records mostly from Sandymount and Howth) and from the Clare Island area. Littoral meiofaunal species included the so-called 'archiannelids' *Nerilla antennata* Schmidt and *Protodriloides flavocapitatus* (Uljanin) and *Fabricia sabella* Ehrenberg. Boaden (1966) listed eight species from shell gravel and five (those not given a specific location) from fine intertidal sand in Strangford Lough. Healy (1975) listed various annelids, some of meiofaunal size, from North Bull Island. She also studied the intertidal distribution of Oligochaeta in Co. Wexford (1979, 1996a) stating that both meiofaunal and macrofaunal oligochaetes are dominant between HWN and HWS in all but one of the sand beaches studied; three main habitat types for exposed rocky shore oligochaetes, namely rock crevices and cracks, algal and animal 'mats' and pools were described at Carnsore Point where 12 species were found. Two of the new species encountered were described later (Healy 1996b). Healy and Bolger (1984) included references to species occurring in salt marshes. Present knowledge probably represents less than a quarter of our meiofaunal annelid species.

Crustacea

Meiofaunal crustaceans, particularly copepods and ostracods, are often the second or third most abundant metazoans in shore sediments and among seaweed. However, as is the case with other taxa, relatively little is known of their occurrence on Irish shores. Farran (1912) working on Clare Island survey material, listed some ostracods (mainly from earlier records by Norman 1905) and a hundred and twenty species of copepods, many from intertidal habitats. A paper by Roe (1958) listed one hundred and six species of harpacticoid copepods including 6 new species and two she had previously described (Roe 1955) from a variety of habitats on the shore at Dalkey, Co. Dublin. Roe (1960) also listed copepods from Lough Ine from where she described two further species. Holmes (1980, 1981, 1984, 1987) has extended the list of crustaceans from the Lough with records which include many copepods from a wide variety of intertidal habitats including weed and gravel. O'Riordan (1971) studied harpacticoids on the Irish east coast at twelve littoral stations in Counties Louth and Dublin; fifty-three of the sixty species found were meiobenthic. There is little recent information about the west coast although Bodin and Jackson (1987) described a new harpacticoid from intertidal sand at Mweenish Island, Galway. Wells (1963) gave a number of intertidal records of meiobenthic copepods plus the interstitial isopod *Microcharon harrisi* Spooner from low-water shell gravel in Strangford Lough.

The biology of meiobenthic harpacticoids was excellently reviewed by Hicks and Coull (1983). Since this review and that on algal meiofauna by Hicks (1985), Jarvis and Seed (1996) have published data from North Wales on the abundance and diversity of meiofauna, particularly harpacticoids, in the algae *Pilayella* and *Polysiphonia* growing on *Ascophyllum*. Holmes and O'Connor (1990) have published a checklist of harpacticoids currently known from Ireland and Holmes and Gotto (2000) one of the cyclopoids; the former group is particularly common in sand and the latter in phytal and muddy habitats.

It has not been usual to consider commensal forms as part of the benthic meiofauna, however the reader is referred to the numerous papers by Gotto and various co-workers for some account of commensal copepods (see Gotto 1993) including many occurrences in Ireland.

Various Irish records of Ostracoda are included in the classic work by Brady and Norman (1889). Many species occur in littoral mud and the group is abundant in phytal habitats. Athersuch *et al.* (1990) is excellent for identification and general distribution records although there is little specific reference to Ireland rather than the British Isles because of the widespread distribution of many species. Our current knowledge in Ireland may represent less than a sixth of the occurring intertidal meiofaunal crustacean species.

Acari

Early reviews of marine mites including records of species in Ireland are given by Brady (1875) who recorded one littoral species and Halbert (1915, 1920), the latter papers recording twenty species. Bartsch (1985) incorporated these species and twenty-one others from the Strangford Lough Narrows and adjacent Irish Sea in her list of Halacaridae recorded from Ireland. Somerfield and Jeal (1995) compared the distribution of mites on exposed and sheltered Irish shores and found that the range of species were essentially similar on the two shore types. The same authors (1996) investigated the distribution of halacarids among macroalgae in Mulroy Bay and the Strangford Narrows and found different genera were characteristic of the upper and lower shores. Somerfield (1991) gives further distributional data. This is probably the best-studied major taxon of Irish intertidal meiofauna, so only a few species may remain to be found.

Mollusca

The young of many gastropod species may be found among algae in the low intertidal zone but a number of species, for example *Skeneopsis planorbis* (Fabricius) and many members of the Rissoidae and Rissoellidae remain of meiofaunal size throughout their life. Southgate (1982) studied a population of *Rissoa parva* (da Costa) in red algal turf in Bantry Bay; most specimens were less than 3 mm in height and they occurred in 'a rich and varied cryptofauna'. Colgan (1930) recorded various small prosobranchs from the shore of Co. Dublin. Three interstitial opistobranch species including abundant *Hedylopsis brambelli* Swedmark and the prosobranch *Caecum glabrum* (Montagu) were recorded from low-water coarse shell sand in the Strangford Narrows by Poizat (1979). Boaden (1966) also recorded three aplacophorans including two unidentified species from Narrows shell gravel. *H. brambelli* is abundant in many small patches of shell sand with pebbles between *Laminaria* zone boulders in the Narrows and emerges to feed on hydroids on the pebble surfaces when samples of the biotope are placed in aquaria (pers. obs.). Nunn has produced checklists of the molluscan fauna of localities including Strangford Lough (1994) and Clare Island (2002) which include data for meiofaunal sized species. The majority of Irish intertidal meiofaunal molluscans are probably known except for a few low shore interstitial forms such as species of *Pseudovermis,* acochlidiaceans and aplacophorans. A checklist of all the currently known Irish marine molluscs is to be published as a CD ROM (Nunn *et al.* in prep.).

Others

Meiofaunal representatives of some other taxa, fairly well known elsewhere, have single or occasional littoral records from Ireland. Murray (1911) recorded the marine tardigrade *Echiniscoides sigismundi* (Schultze) among sediment washed from algae under Achill Bridge, Co. Mayo and Boaden (1966) records *Batillipes mirus* (Richter) from intertidal fine sand: thus, at least for marine forms, Murray's comment 'Irish water-bears appear to have no history' remains apt. The sipunculoid *Golfingia minuta* (Keferstein) has been recorded by Southern (1910) from Sandymount, Howth and by Boaden (*l.c.*) in Strangford Lough where it is common in detritus rich shell gravel. Kinorhynchs are fairly common in intertidal muds and muddy sand but the only Irish littoral records known to the author are by Southern (1914b) for *Echinoderes dujardinii* Claparède in intertidal algae from Blacksod Bay and Boaden (1966) for *Echinoderes* sp. in Strangford Lough fine sand.

The latter paper also records the meiofaunal holothurian *Leptosynapta minuta* (Becher) from Strangford Narrows shell gravel. One would expect some twenty or more meiofaunal species from these major taxa to be found on Irish beaches, particularly if more muddy habitats are investigated.

Habitats and meiofaunal abundance

Meiofaunal abundance and diversity are broadly related to the structural complexity of the habitat. This is well established for algal habitats (Myers and Southgate 1980; Gibbons 1991) and is also the case for the small animals living in mussel clumps (Tsuchiya and Retière 1992). This is discussed by Hicks (1985) and by Healy (1996a) who also demonstrated that increased cryptofauna diversity resulted from increased structural complexity of barnacle populations at Carnsore Point, Co. Wexford. It is also true on the County Down coast that medium to coarse shell gravels (providing that they do not dry out) provide a greater size range of interstices than finer sediments and have a correspondingly species-rich, but not necessarily more abundant, meiofauna than finer sediments (pers. obs.). Eleftheriou and Nicholson (1975) demonstrated increased meiofaunal densities with decreased wave exposure in some Scottish beaches. It has also been shown, for example by Reise (1981) that biogenic structures in sediment increase faunal diversity and abundance. The general rule that meiofaunal species diversity increases with habitat complexity is therefore hypothesised.

Values for meiofaunal abundance in the literature are sometimes difficult to compare because of the different and sometimes ambiguous units used, for example ind. 10 cm^2 has been used both for the number of individuals from sand beneath a surface area measuring 10×10 cm (*i.e.* 100 cm^{-2}) and for the number from a core of 3.57 cm diameter *i.e.* from beneath a 10 cm^{-2} area of sediment surface. It is far better to express densities as per 1 m^2 or 1 cm^2 to avoid such ambiguity.

Table 1 reports densities of meiofauna from some Irish beach sediments and Table 2 from some algae. Data on abundance of nematode species from Strangford Lough (Platt 1977) was later re-used by Lambshead *et al.* (1983) in the verification of cumulative percentage species abundance versus species rank graphs (that is *k*-dominance curves) as the most appropriate way to assess species diversity.

Within habitat distribution

Habitats such as intertidal seaweeds and sand flats provide a number of sub- or micro-habitats. It is clear, for example, that zonation of meiofauna may occur according to height on the shore in relation to tidal parameters (e.g. Giere and Pfannkuche 1982), however even at one tidal height there will be horizontal and vertical patterns of distribution. Thus Boaden and Platt (1971) working at South Bay, Co. Down, showed that dominant species of nematodes had population centres at different depths within the sand column. This has also been shown for turbellarians and gastrotrichs in the beach at Ballymaconnel, Co. Down by Boaden (1977). Such patterns of vertical distribution have often been linked to sediment oxygenation as measured by redox potential. Examples are the important work by Fenchel (1969) on ciliates and Boaden's (1981) discussion concerning the within-sediment

Table 1. Meiofaunal density in some Co. Down sand beaches. Densities have been recalculated from original data and expressed as number of individuals below 1cm^{-2} of the sediment surface. Poizat's samples were to 5cm depth and ice extracted. All others were $MgCl_2$ or Ludox extracted and of sufficient depth to include the surface, RPD and upper black sand layers. Abbreviations such as HWN½MTL mean half way between the indicated tidal levels. M_d is median grain size in microns

Locality	Tidal level	M_d µm	Ind.cm^{-2}	Source
Strangford and Adjacent Area				
Narrows	LWN	687	1.1	Poizat 1979
Narrows	LWN	1160	6.2	Poizat 1979
Doctor's Bay	MTL½LWN	140	148.5	Maguire 1977
Hanna's Mill	MTL½LWN	122	128.5	Maguire 1977
South Bay	MTL½LWN	150	73.1	Maguire 1977
South Bay	HWN½MTL	220	74.0	Boaden and Platt 1971
Greyabbey	HWN½MTL	150	29.5	Boaden and El-Hag 1984
Ballymaconnel	MTL½LWN	165	134.5	Maguire 1977

depth distribution of turbellarian taxa on various Co. Down beaches. The situation is made more complex by tidal and seasonal vertical migrations which for example have been linked to conditions of oxygenation (Fenchel and Riedl 1970) or depth of the RPD layer (Platt 1977 – working on the north Strangford tidal flat) and to disturbance by waves (Boaden 1968, Rieger and Ott 1970).

Work by Johnston (1981) at Doctor's Bay Kircubbin, Co. Down showed that different sand flat subhabitats such as *Arenicola* burrow head shafts or undisturbed sediment from surface pools had different population densities of the various taxa – see Table 3. This can easily lead to errors in determining overall abundance unless the sampling regime ensures that the subhabitats are represented by their correct proportion. For example calculation of the overall mean density of Copepoda from the measured percentage occurrence of each subhabitat gives a mean of 6.1 individuals per 1 cm^{-2} but random sampling (48 cores in the area) gave a mean of 11.2. In addition to the different abundances in sediment subhabitats it is characteristic for sediment meiofauna to occur in small patches (Heip 1975). This has been reported for two gastrotrich and one turbellarian species in Northern Ireland beaches by Boaden (1985, 1995 respectively).

Meiofauna in phytal habitats also can display different subhabitat distribution, for example Hicks (1985) gave a) within holdfasts, b) the base of fronds in association with sediment and c) the frond surface as the main areas of meiofaunal occurrence on intertidal algae. On the other hand Somerfield and Jeal (1996) working on marine mites from Ireland cited four main types of occurrence on emersed plants namely a) on the dry surface layer of fronds, b) on damp fronds, c) on the lower stipe and among the holdfasts and d) on the surface substratum between holdfasts.

Boaden *et al.* (1995) and Boaden (1996) working on *Fucus serratus* L. meiofauna from

Table 2. Abundance and density of meiofauna on intertidal algae from Strangford Lough. *Fucus serratus* data (except weight) from Boaden (1995). Other data from author's records. *Polysiphonia* samples consisted of individual tufts scraped from *Ascophyllum*.

Locality	Algal Species	Total in sample	Plant area (m^{-2})	Plant dry wt (g)	Plant wet wt (g)	Density (individuals per unit)
Narrows LWN						
'Site 9A'	*Fucus serratus* L.	900323	4.01	7571	–	2.25 ind.cm^{-2} frond
						12.1 ind.g^{-1} dry wt.
Opposite Walter Rock	*Scytosiphon lomentaria*	95	–	0.48	0.03	Mean of the samples
	(Lyngybe)	63	–	0.65	0.06	121.7 ind.g^{-1} wet wt.
		73	–	1.04	0.09	2997.6 ind.g^{-1} dry wt.
..	*Cladophora sp.*	14800	–	15.25	3.17	970.5 ind.g^{-1} wet wt.
						4668.8 ind.g^{-1} dry wt.
Kircubbin MTL	*Polysiphonia lanosa (L.)*	722–866			0.045–0.031	Mean of the 5 tufts
	5 tufts					761,0 ind.g^{-1} wet wt.

the Strangford Lough Narrows showed that the presence of epifauna greatly enhanced the meiofaunal abundance and that, at some sites, this was related positively to the amount of silt retention due to the surface configuration (spinosity) of the epifaunal colonies. These papers also showed that the density of meiofauna (per cm of the epifaunal surface) increased from the basal through mid to distal portion of the *Fucus* plants but, since there was much more epifauna in the central parts of the plant, meiofaunal density per unit thallus area was highest in the mid-region (Boaden 1996).

The Thiobios

Fenchel and Riedl (1970), mainly using distributional data from the east coast of the United States, drew attention to the occurrence of metazoan meiofauna in the sulphide-rich layers of sandy marine sediments. Boaden and Platt (1971) reporting on temporal changes in vertical distribution of meiofauna at South Bay, Co. Down, coined the term 'thiobios' for the redox potential discontinuity (RPD) and black (anaerobic) sand layers and their inhabitants as a convenient expression for these layers and 'the living system of the sulfide biome' as they had been called by Fenchel and Riedl (*l.c.*). Four groups of

Table 3. Comparison of mean densities (shown on diagonals as individuals.cm^{-2}) of major taxa between four subhabitats on a fine sand beach inhabited by *Arenicola marina*. The% occurrence of each habitat was measured by mapping twelve 25 × 25 cm quadrats. ME emersed sediment (plain or rippled surface) 52%, MP sediment from surface pools samples 40%, MH sediment from head-shafts 2.5% and MT sediment from tail mounds 5.5%. Results are from thirty-nine to forty-nine 2 cm depth 2.9 cm diameter core samples for each subhabitat. Significant differences are shown as p< 0.05*, p<0.01 and p< 0.001*** according to the Mann-Whitney U-test, ns is non-significance. (Data from Johnston 1981).**

Nematoda

	ME	MP	MH	MT
ME	48.3			
MP	ns	59.3		
MH	***	***	30.9	
MT	***	***	ns.	28.6

Copepoda

	ME	MP	MH	MT
ME	3.3			
MP	***	9.9		
MH	***	*	161	
MT	***	***	***	9

Ostracoda

	ME	MP	MH	MT
ME	1.0			
MP	ns	1.2		
MH	**	***	0.4	
MT	*	***	ns	0.5

Gnathostomulida

	ME	MP	MH	MT
ME	1.3			
MP	ns	2.2		
MH	ns.	ns.	3.4	
MT	**	***	***	0.3

Turbellaria

	ME	MP	MH	MT
ME	0.8			
MP	***	3.4		
MH	***	***	8.3	
MT	***	ns	***	3.2

Annelida

	ME	MP	MH	MT
ME	2.6			
MP	*	4.5		
MH	ns	ns	4.8	
MT	***	***	***	0.5

species were defined according to their vertical distribution within sand on Co. Down beaches by Maguire (1977); two of these groups citing particular gastrotrich and flatworm species were characteristic of the thiobios. Maguire and Boaden (1975) used one of these species, the gastrotrich *Megadasys* (*Thiodasys*) *sterreri* (Boaden), to explore features of thiobiotic biology and demonstrated this species' ability to exist anaerobically for a period of at least four months and to respire anaerobically using carbon dioxide in a reversed Krebs cycle sequence. Boaden (1980) found thiobiotic population density equivalent to 78.8 individuals below 1 cm^{-2} of surface sand at Millin Bay, Co. Down – this has led the author to suspect that the thiobiotic component has often been under-represented in samples taken elsewhere. Information on the ecology and adaptations of thiobiotic meiobenthos has been summarised by Giere (1992, 1993).

Behaviour and tolerances

Remane (1933) gave some limited information on the salinity tolerances of meiofauna but little further information emerged until the 1960s when a number of authors began to relate behaviour and tolerances of species to their intertidal distribution (e.g. Boaden 1963; Gray 1966; Jansson 1966). Factors investigated included bacteriology, granulometry, light, temperature and water flow. The initial papers of this type concerning Irish beaches were those by Boaden (1968) and Boaden and Erwin (1971) which described responses of meiofauna at South Bay, Co. Down to various factors. The first of these papers was particularly concerned with responses to tidal movement mediated *via* currents and vibration; it also contained the first published pictures of meiofaunal ultrastructural adaptation. The second paper was principally concerned with the gastrotrich *Turbanella hyalina* Schultze and its avoidance of sand inhabited by the polychaete *Protodriloides symbioticus* (Giard) – a response to a heat-labile substance produced by the latter species; it also summarised responses of the *T. hyalina* to current, temperature, oxygenation, contact, light, vibration, pressure fluctuation and granulometry as well as a gregarious response and attraction to sand mediated *via* bacteria. Johnston (1981, also see Boaden 1995) working with material from Doctor's Bay, Strangford Lough, showed that the flatworm *Monocelopsis otoplanoides* Ax was attracted to *Arenicola marina* (L.) head shaft sand by a heat-labile substance emanating from *Arenicola*.

The responses of the seriate flatworm *Monocelis lineata* (Müller) occurring in the meiofauna on *Fucus serratus* plants from the Strangford Lough were studied by Boaden (1996) who showed that it would select damaged in preference to undamaged *Flustrellidra hispida* (Fabricius) colonies and the latter in preference to *F. serratus* thallus without such epifauna; *M. lineata* also showed negative phototaxis, positive rheotaxis and movement to areas of 17–18°C within a temperature gradient.

Respiration and energetics

In order to assess the overall importance of meiofauna within the littoral ecosystem it is necessary to investigate factors such as food preferences, energy assimilation and population turnover. Unfortunately, relatively little is known about some of these and several of the assumptions made in the literature may be unwarranted (Coull and Bell 1979). It is generally understood that meiofauna can contribute 30–50% of sediment biomass but only about 10% in the phytal. The first biomass data including both macrofauna and meiofauna for an Irish beach is presented in Table 4. McLachlan and co-workers have made extensive studies of sand surf-dominated beaches in South Africa (see McLachlan and Romer 1990) and in Europe work has been carried out on sand- and mud-flats (e.g. Kuipers *et al.* 1981, Warwick and Price 1979). These papers give a production-to-biomass ratios for meiofauna plus microfauna as 65:1 and for meiofauna alone as 8.4:1 respectively.

The general proportion for the meiobenthic contribution to the total energetic budget of an average benthic biotope is estimated as about one quarter (Giere 1993). The only paper that begins to address the energetics of meiofauna in Irish beaches is by Boaden and El-Hag (1984) who produced a partial oxygen budget for a fine sand beach at Greyabbey, Co. Down, which calculated meiofaunal respiration at 40ml.h^{-1} m^{-2} of beach. This was

Table 4. Calculated biomass for major meiofaunal groups and macrofauna in the medium sand beach at Rossglass, Co. Down, March 1985. Five replicate meiofaunal core samples of 3.2 cm diameter were taken to a depth of 10 cm at five approximately equally vertically spaced stations. Macrofauna was from 1 mm sieving of two 50 × 50 cm, 50 cm deep, quadrats at each beach level. The sampled area between mid- and low-tide was affected by a small beach stream. Biomass was calculated from average length and breadth dimensions of specimens in each major taxon assuming animals to be cylindrical and having a specific gravity of 1.33 (Wieser and Kanwisher 1961). From original data.

	Estimated biomass wet weight $g.m^{-2}$					
	HWN	**HWN½MTL**	**MTL**	**MTL½LWN**	**LWN**	**Mean**
Nematoda	0.56	0.84	0.31	0.24	1.56	0.702
Polychaeta	0.00	0.06	0.45	0.22	0. .22	0.190
Turbellaria	0.00	0.18	0.32	0.03	0.08	0.122
Copepoda	0.01	0.05	0.06	0.01	0.46	0.118
Insecta	0.45	0.00	0.00	0.00	0.00	0.090
Nemertea	0.00	0.22	0.00	0.00	0.11	0.066
Ostracoda	0.00	0.00	0.00	0.00	0.07	0.014
Gastrotricha	0.01	0.01	0.01	0.01	0.01	0.010
Acarina	0.00	0.00	0.01	0.00	0.00	0.002
All meiofauna	**1.03**	**1.36**	**1.35**	**0.51**	**2.51**	**1.352**
Macrofauna	**2.12**	**5.14**	**6.36**	**2.10**	**11.66**	**5.476**

only about 15% of the macrofaunal value. This paper illustrated that the meiofaunal taxa considered all had a minimum respiration rate at between 12–14°C which corresponded to the annual average ambient sand temperature, and furthermore that the respiration rate per animal decreased with the number of individuals being used for each oxygen uptake determination. Further details of this are given by Boaden (1985, 1989, 1995). The work implies that it is unwise to extrapolate laboratory data showing Q_{10} type responses of respiration with temperature change to field conditions where the fauna has been 'conditioned' by the ambient temperature; furthermore the density of the species and any gregarious response affecting activity must be considered.

ANTHROPOGENIC EFFECTS

Pollution

Coull and Chandler (1992) have reviewed laboratory and field studies concerning pollution effects on meiofauna. There are two fully published Irish studies. Boaden and Bleakley (1974) conducted laboratory experiments on harpacticoid copepods and the polychaete *Protodriloides symbioticus* from Ballymaconnel, Co. Down and treated part of this beach with an oil spill remover; concentrations in excess of 100ppm were found to give persistent toxic effects. Roberts and Maguire (1976) using material from Co. Down found limited interaction of lead with intertidal sediment and its meiofauna, probably because of absorption onto particle surfaces. Some unpublished work by Johnston (1981) partly reported by Boaden (1978, 1995) indicated decline in meiofaunal abundance and diversity caused by a sewage-polluted beach stream at Doctor's Bay, Strangford Lough.

Other causes

Unpublished work by Skjaeggestad (1997 and Skjaeggestad and Boaden (2005)) has shown that oyster culture on intertidal trestles affected the abundance of meiofauna in the underlying sediment and in sediment between the trestle rows when compared with the adjacent control site. All the major taxa studied other than the Turbellaria had significantly lower densities under the trestles (Table 5).

The relationship between sediment parameters and the variations in abundance at and between the sites in the course of a year were analysed by multiple linear regression using stepwise variable selection. The most important factors were found to be Chl*a* content for nematodes, temperature and Eh for copepods, temperature for turbellarians, sediment mean grain size and Eh for kinorhynchs and organic carbon content for tardigrades.

Boaden and Dring (1980) in studying the effects of harvesting *Ascophyllum* demonstrated a subsequent coarsening of shore sediment which led to an apparent doubling of meiofauna to about 70 ind.cm^{-2} with a significant increase of crustaceans (mainly copepods) from about 2 to 8 ind.cm^{-2}.

CONCLUSIONS

Our knowledge of the meiofauna of Ireland is rather limited. Although there were some early faunistic studies which included meiofaunal organisms, most of our current knowledge of the distribution of metazoan meiofauna around Ireland is limited to Strangford Lough and the adjacent Co. Down coastline, Dublin Bay and Co. Wexford, although somewhat more is known about the distribution of phytal mites. There is thus a need for more meiofaunal survey work, particularly on the Atlantic coastline. Studies

Table 5. Mean sediment meiofaunal abundance (ind.cm^{-2}) over one year at Paddy's Point, Strangford Lough in low water control (C), between oyster trestle (B) and under oyster trestle sites (T). Cores were of 1 cm^{-2} surface area taken to 5cm depth. $F_{2,40}$ values and probabilities are from three way repeated anovas. Differences between sites are indicated as for example T<B, T<C meaning trestle sites had lower abundance than both between-trestle and control sites. (Data from Skjaeggestad 1997)

	Control C	Between B	Trestles T	F value	p <	Differences
Nematoda	390	300	160	143	0.001	T<B T<C
Copepoda	13.0	13.5	2.0	58	0.001	T<B T<C
Turbellaria	4.7	4.7	4.8	2	0.14	ns
Kinorhyncha	4.1	2.2	0.9	38	0.001	T<C B<C
Tardigrada	2.1	3.0	1.5	23	0.001	T<B

of muddy habitats are also required. Some information is available about the general abundance of the meiofauna (and in particular gastrotrichs and turbellarians) in Co. Down beaches and about Oligochaeta and Acari elsewhere. There is also some information about habitats and sub-habitats on rocky shores, in seaweeds and in sand. Work on vertical distribution of sediment meiofauna on Co. Down beaches has led to the concept of the thiobios and to a little consideration of the biochemistry and ultrastucture of meiofaunal species. There is extremely little information relating to meiofaunal energetics and the role of meiofauna within the intertidal ecosystem of Irish shores. It is clear from work elsewhere that meiofaunal organisms, although of little size, are a major component of the littoral ecosystem. Without their consideration we cannot be really pleased with the state of our knowledge of Irish shores.

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