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A REVIEW OF THE DISTRIBUTION OF MARINE TALITRIDAE (AMPHIPODA) IN IRELAND, INCLUDING THE RESULTS OF A NEW SURVEY OF SANDY BEACHES

BY

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ABSTRACT

Talitrid amphipod crustaceans were recorded at about 240 sites around Ireland using both published records and recent seashore surveys. Five species were present, the beachfleas *Orchestia gammarellus* and *O. mediterranea*, and sandhoppers *Talitrus saltator*, *Talorchestia deshayesii*, and *Talorchestia brito*. This is the first record of the last-mentioned species in Ireland and it was present at only two sites. In general, species occurred on all coasts indicating that local rather than regional factors influenced their occurrence. Analysis of the co-occurrence of species, field observations on microhabitats, and contrasting occurrence of species in sandy beach and wider sampling surveys, indicated that *T. saltator* and *T. deshayesii* prefer coarser and finer sand, respectively, whereas *O. gammarellus* prefers gravel and stony substrata. The absence of *O. mediterranea* from 89 beaches surveyed indicates it is not found on sandy beaches. The two sites with *T. brito* had a large median sand grain size supporting observations elsewhere in Europe that the species inhabits more wave exposed sandy beaches. The findings show the species have similar habitats in Ireland as elsewhere in Europe. Talitrids can be used to define two distinct biotopes, supralittoral sand with burrowing *Talorchestia* and *Talitrus* species, and supralittoral gravel with *O. gammarellus*. Further field studies may demonstrate a mid to upper shore sand biotope characterized by *T. brito*, and a supralittoral drift weed on rock or salt-marsh biotope characterized by *O. mediterranea*. The microhabitats of the species are further defined based on the results of this study and a review of the literature. A working model of the spatial distribution of the species in relation to sea level and substrata is proposed.

INTRODUCTION

Amphipod crustaceans of the family Talitridae occur worldwide in the 'strandline', which marks the boundary between the marine and terrestrial environments (Wildish, 1988). Some species are fully terrestrial but are not considered in this

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paper as only one such species, an introduction, occurs in Ireland (Costello, 1993). Seashore talitrids are convenient species to survey because (a) their habitat is narrowly defined around the upper limit of the tide, (b) their habitat is more accessible and safer to work in than deeper littoral and sublittoral habitats, and (c) qualitative sampling requires no special equipment. Although their abundance varies seasonally, they can be sampled in their habitat throughout the year (Lagardère, 1966). Because of this ease of sampling, it is reasonable to expect that the absence of a species from a sample is real and not due to sampling error. They thus have considerable potential as suitable species for environmental impact and monitoring studies. Amphipods have been found to be useful bioindicators due to their widespread distribution, abundance, and sensitivity to pollutants (Reish, 1993; Thomas, 1993). For the above reasons, and the findings that for a given species their body metal concentrations are correlated with metal bioavailability in the environment, talitrid amphipods have been shown to be suitable biomonitors for metals (Rainbow et al., 1989, 1993, 1998; Moore et al., 1991; Weeks & Moore, 1991; Weeks & Rainbow, 1991; Rainbow & Phillips, 1993; Rainbow, 1992, 1995).

The classification of littoral marine biotopes in Britain and Ireland defined only one talitrid strandline biotope, but Connor et al. (1997) felt further studies were required to identify others. Hudson & Reynolds (1985) reviewed the distribution of Talitridae in Ireland and recorded four species, the beachfleas *Orchestia gammarellus* (Pallas, 1766) and *O. mediterranea* A. Costa, 1853, and sandhoppers *Talitrus saltator* (Montagu, 1808) and *Talorchestia deshayesii* (Audouin, 1826). They found "little overlap" in species distributions and each species was recorded on muddy, sand, and gravel substrata. This contrasts with studies on Sherkin Island in south-west Ireland (Rees, 1980) and in other countries which found *Talitrus* and *Talorchestia* species on sand, *Orchestia* species on wrack (decaying fucoid seaweed stranded at the high tide mark), shingle and in salt marshes, and species of all genera to sometimes occur together (Dahl, 1946; Reid, 1947; Jones, 1948; Williamson, 1948; Den Hartog, 1963; Lagardère, 1966; Vader, 1968, 1970; Karlbrink, 1969; Ingólfsson, 1977; Williams, 1978; Lincoln, 1979; Moore, 1984; Bellan-Santini et al., 1984; Bellan-Santini, 1993). Since Hudson & Reynolds' (1985) study, we have sampled 89 new localities and found literature records for 14 additional localities, so there are now records of talitrids from 238 seashores. This larger database permitted a re-evaluation of whether talitrids in Ireland differed in their habitats from other countries, and whether more than one talitrid biotope can be defined.

METHODS

The present study sampled the strandline habitat for talitrids during a wider survey of marine biotopes in Ireland as part of the BioMar-LIFE project (Costello, 1995). About 130 seashores were surveyed in Ireland from 1993 to 1996 (Picton & Costello, in press), of which 89 were sediment shores, and from 68 of which talitrids were identified (fig. 1). Further records of species occurrence have been found in the literature (fig. 1). Together, this provides the most comprehensive distribution data for any marine family in Ireland.

Talitrids were found by disturbing drift weed, cobbles and gravel, and digging in the sand. In addition, core samples of sediment were taken at 66 sites, but these would have excluded coarse gravel and driftweed material from which

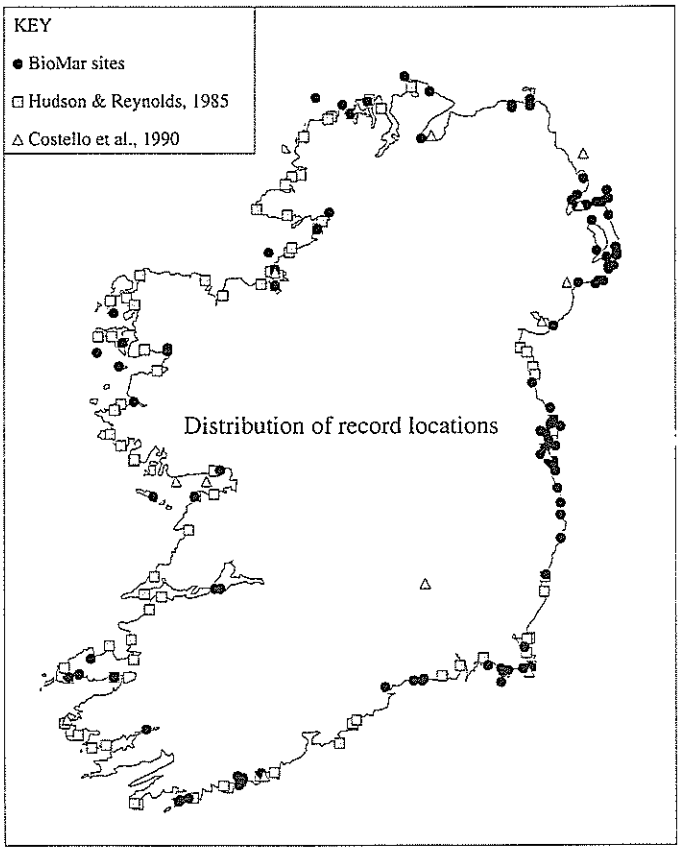

Fig. 1. Map of sampling locations in Ireland by this study (solid dots), Hudson & Reynolds (1985) (stippled squares), and other publications cited by Costello et al. (1990) (triangles). The position of sites from the latter two sources is indicative and readers should refer to these publications for more exact details of their sampling sites.

specimens were also collected. It was often not possible to collect cores because of the presence of stones in the sand. In the granulometric analysis a 5 g to 10 g sub-sample was agitated in water and particle size distribution determined by laser analysis (using a Malvern MasterSizer X SB.OD system). This analysis excluded material coarser than 2 mm diameter, and where such material (gravel, cobbles or maerl) typically occurred, it was noted in the biotope description. Specimens were collected by hand and preserved in alcohol for identification in the laboratory. Voucher specimens were lodged in the National Museum of Ireland (collection number NMI.31.1993).

RESULTS

Five species were recorded in the present survey of beaches, namely *Orchestia gammarellus* (14 sites), *Talitrus saltator* (59 sites), *Talorchestia deshayesii* (62 sites), and *Talorchestia brito* (Stebbing, 1891) (2 sites). In addition, *O. mediterranea* is recorded in the literature (Costello et al., 1990). Combining the new data with published records, it is clear that the first four species occurred on all coasts (figs. 2, 3). The most widespread species, *O. gammarellus*, occurred inland at the uppermost reaches of some estuaries (fig. 2a), an area rarely sampled during the reported studies. Although occurring on all coasts of Ireland, *O. mediterranea* was not common (fig. 3b) and was not sampled in the present survey of beaches. This study provides the first record of *T. brito* in Ireland, but only at single sites in the north-west and south-east of the country (fig. 3b).

The presence of species in our beach survey contrasts with their known distribution in Ireland, namely that *O. mediterranea* was absent, and *T. saltator* and *T. deshayesii* more widespread than *O. gammarellus*. Over the 68 sites surveyed, 71% (48) had both *T. saltator* and *T. deshayesii*, 9% (6) had these two species with *O. gammarellus*, 8% (5) *T. deshayesii* and *O. gammarellus*, and 4% (3) had *T. saltator* or *T. deshayesii* alone. There were single sites with combinations of *T. saltator* with *O. gammarellus*, *T. saltator* with *T. brito*, and *T. saltator* and *T. deshayesii* with *T. brito*.

Descriptions of sites from visual observations indicated that sites with only *T. saltator* and *T. deshayesii* consisted of fine to medium sand, while sites with *O. gammarellus* also had varying amounts of shells, stones, and cobbles present. Sites with mixtures of species had a mixture of these substrata present. Granulometric analyses of sediment core samples from 39 sites was biased towards sites with both *T. saltator* and *T. deshayesii*.

Of the 8 sites where talitrids were not found, 3 consisted of cobbles and boulders where collecting can be difficult, and 3 were very muddy. In the latter

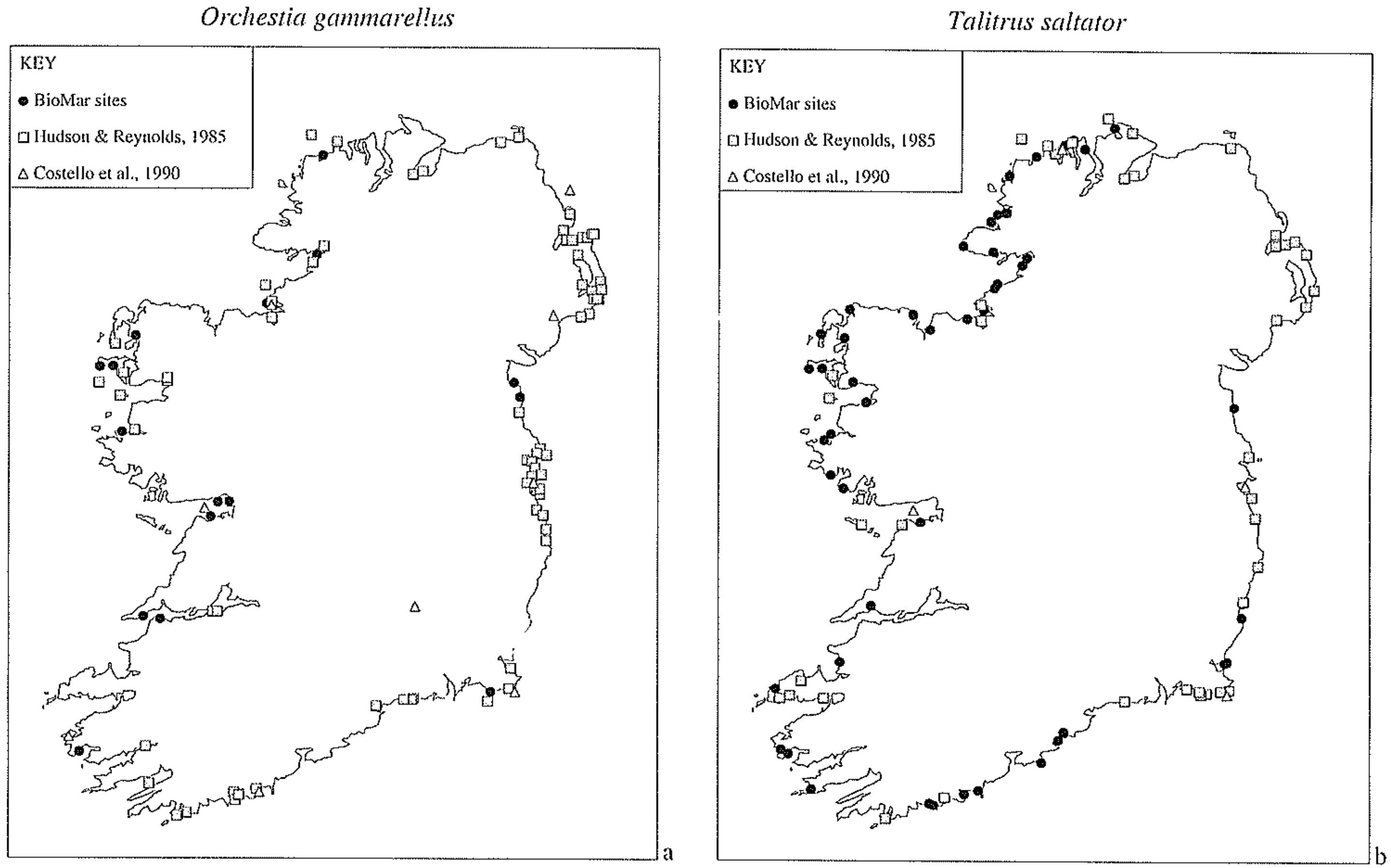

Fig. 2. Distribution of a, *Orchestia gammarellus* (Pallas, 1766); b, *Talitrus saltator* (Montagu, 1808); as found in this (solid dots) and previous (squares and triangles) studies in Ireland. The apparently inland location of *O. gammarellus* is at the head of an estuary.

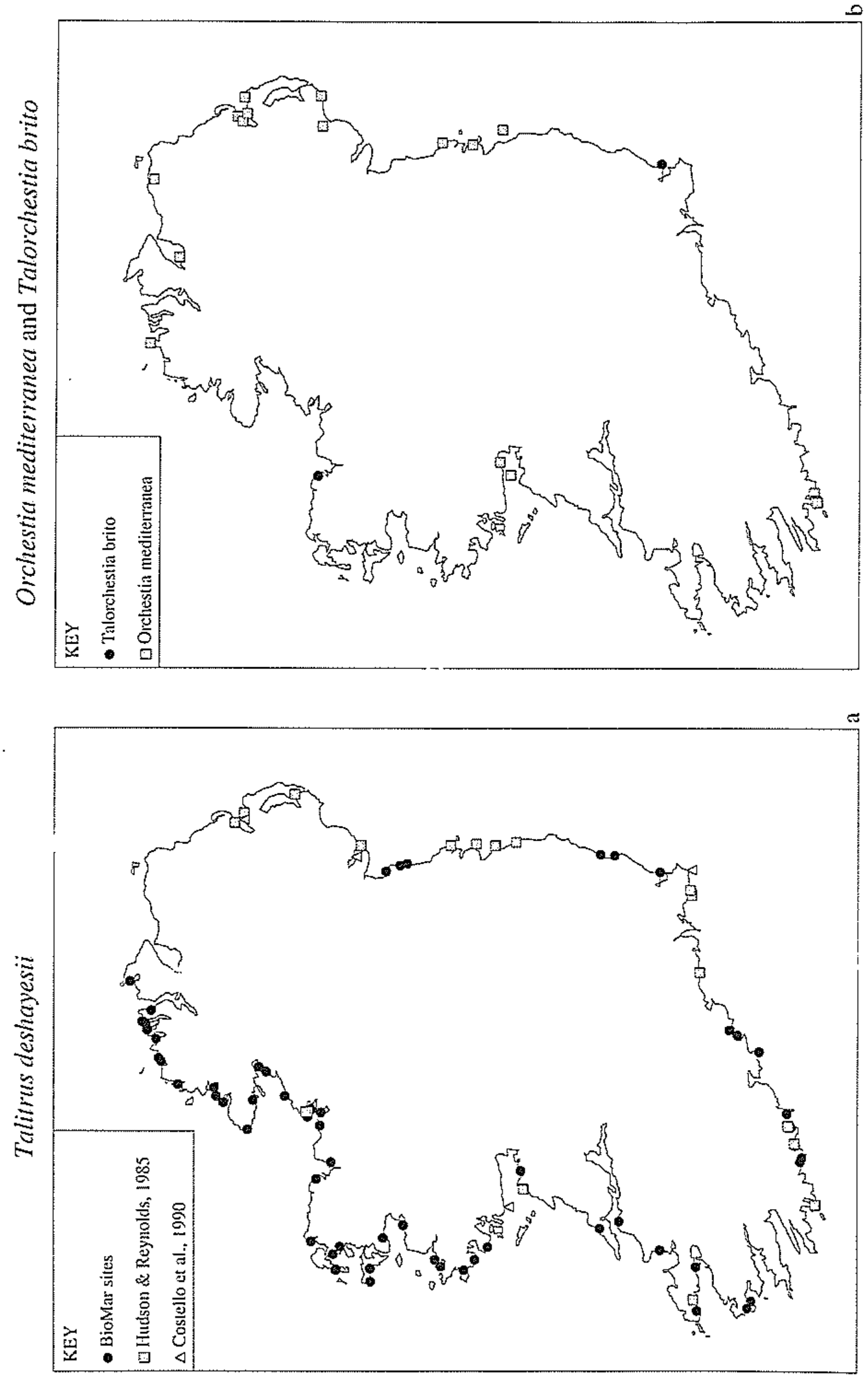

Fig. 3. Distribution of a, *Talitrus deshayesii* (Audouin, 1826); as found in this (solid dots) and previous (squares and triangles) studies in Ireland; and of b, *Orchestia mediterranea* A. Costa, 1853 (squares) and *Talorchestia brito* (Stebbing, 1891) (solid dots).

TABLE I

The lowest (min.) and highest (max.) values for the median and mean grain size, sorting coefficient, and percent mud content for the sediment sites where each species occurred. Results are expressed in Φ units ($-\log_2$ mm)

Species	No.	Median Φ		Mean Φ		Sorting Φ		% Mud content	
		min.	max.	min.	max.	min.	max.	min.	max.
Talitrus saltator (Montagu, 1808)	59	0.191	0.917	0.12	2.39	0.29	1.13	0.0	3.0
Talorchestia deshayesii (Audouin, 1826)	52	0.192	0.917	0.12	2.38	0.29	1.13	0.0	3.7
Orchestia gammarellus (Pallas, 1766)	13	0.191	0.333	1.59	2.39	0.37	0.99	0.1	3.7
Talorchestia brito (Stebbing, 1891)	2	0.266	0.502	1.00	1.89	0.34	0.65	0.0	0.1

three (a) the median grain size was < 0.14 phi whereas the other 5 sites were > 1.91 phi, and (b) the mud content was 2.3%, 35.5%, and 52.1%, but < 3.7% for other sites. The commonest species, *T. saltator* and *T. deshayesii*, occurred in a wide spectrum of sand types (table I). However, *O. gammarellus* was limited to sites with a median grain size of < 0.3 phi, and mean of > 1.5 phi. The two sites with *T. brito* had minimal mud content and their lowest median grain size was greater than that for the other talitrid species (table I).

There was further sampling at stations on the middle and lower shore of each beach (i.e., two stations per site) to identify biotopes that may be associated with a type of 'talitrid beach'. The biotopes occurring below the talitrid zone were (1) gravel and sand characterized by the polychaete *Scolelepis foliosa* (Audouin & Milne-Edwards, 1833) (at 12 stations), (2) gravel and sand characterized by the isopod *Eurydice pulchra* (Leach, 1815) and non-talitrid burrowing amphipods (*Haustorius*, *Bathyporeia*, *Pontocrates*) (35 stations), (3) gravel and sand characterized by the bivalve *Angulus tenuis* (Da Costa, 1778) with polychaetes (45 stations), and (4) muddy sand characterized by the polychaete *Arenicola marina* (Linnaeus, 1758) and bivalve species (14 stations). Often two different biotopes occurred below the talitrid zone. The biotopes were associated with *T. saltator* and *T. deshayesii* in 71-94% of instances (table II). These species were more often (89 and 94%) associated with the *Eurydice pulchra* than the *Arenicola* biotope. *Orchestia gammarellus* was associated with the *Arenicola* (36%) and *Angulus* (24%) biotopes more often than with the *Scolelepis* and *Eurydice* biotopes (9% each). The only other biotope at the two beaches with *Talorchestia brito* was the *Eurydice* biotope.

TABLE II

The number of times a species of talitrid occurred in association with biotopes recorded below the strandline zone at the beaches surveyed in this study. The percentage of examples of that biotope associated with a talitrid species is also given

Species	No.	*Scolelepis*	%	*Eurydice*	%	*Angulus*	%	*Arenicola*	%
Talitrus saltator (Montagu, 1808)	59	0	3	3	4	2	1	0	1
Talorchestia deshayesii (Audouin, 1826)	62	9	5	1	9	7	2	0	1
Orchestia gammarellus (Pallas, 1766)	14	1	9	3	9	1	4	5	6
Talorchestia brito (Stebbing, 1891)	2	0	0	2	6	0	0	0	0
Talitrids absent	8	1	9	2	6	5	1	3	1
Number of stations biotope present		12	100	35	100	45	100	14	100

DISCUSSION

Species occurrence in Ireland

The results of this study indicate that all five species have had adequate dispersal abilities to find suitable habitats around Ireland. It is thus the local environmental conditions, probably on a scale of centimetres to metres, that determine their distribution. Our observations confirm that all species prefer moist dark conditions, and have behaviours that allow them to avoid desiccation by burrowing in sand or hiding under cobbles and driftweed (Morritt, 1998). Although the biology of the most widespread species in Ireland, *O. gammarellus*, has been studied (e.g., Moore & Francis, 1985a, b, 1986a, b; Morritt, 1987, 1989; Morritt & Spicer, 1996a, b), there is little comparative information for the other species on which to determine their environmental limitations. The widespread distribution of *O. gammarellus* may reflect the fact that it can tolerate temperatures from 0 to 30°C, salinities from 1 to 60 psu, and anoxia for 5 h at 10°C (Moore & Francis, 1986a).

The lack of records of five other talitrids present in Europe may reflect a lack of sampling rather than absence from Ireland. *Platorchestia platensis* (Krøyer, 1845), a so-called 'cosmopolitan' supralittoral species, appears to live in the same habitat as *O. gammarellus* (cf. Karlbrink, 1969; Bellan-Santini, 1993; Rainbow & Phillips, 1993). *Orchestia aestuarensis* Wildish, 1987 has recently been described from Britain, and appears to inhabit brackish eulittoral parts of estuaries (Wildish, 1970b, 1988). *Orchestia cavimana* Heller, 1865, is widespread in Europe on land near brackish and fresh waters (Den Hartog, 1963; Wildish, 1970b). *Orchestia* *roffensis* Wildish, 1969, is known only from driftwood in the supralittoral of salt marshes in Britain (Wildish, 1987). *Orchestia microphthalma* Amanieu & Salvat, 1963, is associated with driftwood in the supralittoral in the west of France (Lagardère, 1966). Karlbrink (1969) suggested *P. platensis* was expanding its distribution in Sweden, so it may not have colonized Ireland. However, Karlbrink (1969) also found *P. platensis* harder to catch than *O. gammarellus*, which increases the chances of it being overlooked. The species *O. cavimana*, *O. aestuarensis*, and *O. mediterranea* are morphologically similar but inhabit fresh, brackish, and marine waters, respectively (Wildish, 1987). Ireland has considerably fewer freshwater species of any taxa than Britain (McCarthy, 1986), and the latter than continental Europe, reflecting the marine barriers to dispersal. Thus *O. cavimana* may not yet have colonized Ireland.

Summary of species habitat preferences

Our field observations in Ireland, and observations elsewhere in Ireland (Rees, 1980) and Europe (Dahl, 1946; Reid, 1947; Jones, 1948; Karlbrink, 1969; Vader, 1970; Moore, 1984; Bellan-Santini, 1993), find that the sand-hoppers *Talitrus saltator* and *Talorchestia deshayesii* live in sand whereas the beach-flea *Orchestia gammarellus* inhabits gravel and cobbles with decaying seaweed. These lifestyles have been termed substratum 'modifying' and 'non-modifying' (McIntyre, 1963) and 'burrowers' and 'nestlers' (Griffiths, 1976), respectively. The former two species typically occurred together in the present study, in the Netherlands (Den Hartog, 1963), and in southern Sweden (Karlbrink, 1969). However, our field observations, but not granulometric analysis, suggested that *T. deshayesii* prefers finer sand than *T. saltator*, such as occurs on seashores more sheltered from wave exposure. Karlbrink (1969) found *T. deshayesii* to occur lower in the supralittoral than *T. saltator*, and Williamson (1951a) found the latter more tolerant of lower humidity. These data indicate that *T. deshayesii* prefers finer and wetter sand, as occurs in the lower supralittoral on less wave exposed beaches, than *T. saltator*. Wim Vader (pers. comm.) has found that juveniles of both species occur lower on the beach than adults. Neither *T. saltator* (cf. Williams, 1978) nor *O. gammarellus* (cf. Wildish, 1970a) appear to have a tidal rhythm of activity, suggesting their behaviour is independent of the tide because they live above the high tide mark.

Sampling of sediment cores is biased towards sand dwelling species, whereas hand collecting in all available habitats can record all species. *Orchestia gammarellus* can occur many metres inland from the strandline, including amongst sand dunes during stormy weather (Healy & McGrath, 1998), and does not require a sand habitat (Reid, 1947; Jones, 1948; Den Hartog, 1963; Ingólfsson, 1977; Costello et al., 1990; Morritt, 1998). Although it extends further into the terrestrial environment than *T. saltator*, it is more sensitive to desiccation and must thus inhabit more humid microhabitats (Morritt, 1987, 1998). *O. gammarellus* typically crawls into crevices under stones, vegetation in salt-marshes, and amongst seaweed debris. It is strongly thigmotactic in contrast to the sand burrowing species (Williamson, 1951a; Morritt, 1998). It is possible that *O. gammarellus* is often overlooked where it hides deep in shingle and cobbles, or occurs above the strandline amongst terrestrial vegetation and material.

The absence of *Orchestia mediterranea* in our recent survey of beaches suggests its habitat was not sampled. Previously, we have found it on rocky shores in Lough Hyne, south-west Ireland (MJC), in light traps (designed to capture insects) beside a salt-marsh (Costello et al., 1990), and on salt-marshes in muddy bays near Carna west of Ireland (DMcG). In all these cases the sites were very sheltered from wave action. Hamond (1967) and Moore (1984) found *O. mediterranea* amongst the upper shore brown alga *Pelvetia* in a saltmarsh, and "below the *Pelvetia* zone", respectively. Similarly, Den Hartog (1963) found *O. mediterranea* amongst *Pelvetia*, *Fucus spiralis*, and in salt-marshes in the Netherlands. *Orchestia mediterranea* is rarely recorded above the high water mark (i.e., strandline) in Britain (Reid, 1947; Jones, 1948; Moore, 1984), Den Hartog (1963) found it lower on the shore than *O. gammarellus* in the Netherlands, and Wildish (1988) considered it eulittoral. It would also appear more aquatic than *Talitrus saltator*. *Orchestia mediterranea* (i) has been recorded in plankton (Hamond, 1967), and (ii) was associated with driftweed in the neuston of Galway Bay (Tully & O'Céidigh, 1987), whereas the apparently commoner *O. gammarellus*, was not. In addition, in *O. mediterranea* (iii) the position of males carrying females prior to copulation is more adapted to an 'amphibious' condition whereas *T. saltator* adopts a position more suited to a terrestrial lifestyle (Williamson, 1951b), (iv) its activity has a tidal rhythm whereas in *O. gammarellus* it does not (Wildish, 1970a), (v) is a better swimmer, with more suitably adapted swimming legs (pleopod rami), than *O. gammarellus* (cf. Williamson, 1951c), and (vi) tends to move on its side in an aquatic gammarid manner in contrast to *O. gammarellus* (cf. Morritt, pers. comm.) which walks vertically. Futhermore, (vii) the uptake of copper is mainly from the water in *O. mediterranea* but from the diet in *O. gammarellus* (cf. Weeks & Rainbow, 1993). It thus seems that *O. mediterranea* is more aquatic and eulittoral than supralittoral. It may also be more closely associated with seaweed drift than the other talitrid species in Ireland, uses this to disperse, and may occur on driftweed wherever it settles in the eulittoral. Its rarity in the present survey of beaches reflects the limited sampling of the eulittoral in comparison to the supralittoral.

The apparent rarity of *Talorchestia brito* may reflect limited sampling of its preferred habitat, and Costello et al. (1990) predicted it would occur in Ireland. The species is widespread in Europe (although maybe not in Britain) and is found below the supralittoral and lower on the shore than *T. saltator* and *T. deshayesii* (cf. Reid, 1947; Williamson, 1948; Den Hartog, 1963; Lagardère, 1966; Vader, 1968, 1970; Lincoln, 1979). In the Netherlands (Den Hartog, 1963) and Mediterranean (Bellan-Santini, 1993) it inhabits wave exposed beaches, which is supported by the observations in the present study. It occurs on coarse sand (Williamson, 1948; this study), and Lagardère (1966) never found it in estuarine conditions. The preference for being below the strandline, on coarse sand, and on more wave exposed coasts may reflect a lower tolerance to desiccation, and/or intolerance to silt. Lagardère (1966) found *T. brito* to eat filamentous green algae and diatoms, whereas *T. saltator* fed on seagrass (*Zostera*) and seaweed debris. However, these diets may not reflect preferences but rather the food available to the species, as found for *O. gammarellus* by Moore & Francis (1985a).

Associated biotopes

The sand living *Talitrus* and *Talorchestia* species were more often associated with the coarse sand *Eurydice* and *Scolelepis* biotopes below the strandline. In contrast, *O. gammarellus* was more often associated with the finer and muddier sand *Arenicola* and *Angulus* biotopes where talitrids were less frequently found (table II). Finer sediments retain more water and are more likely to be anoxic within centimetres of the surface. It is likely that *Talitrus* and *Talorchestia* species will not burrow in finer muddy sands, whereas *O. gammarellus*, not burrowing in the sand, may prefer a sediment with a wetter surface. All these talitrids require a high humidity to survive (Williamson, 1951a; Karlbrink, 1969).

Spatial distribution model

From the now available information and literature it is possible to outline the spatial distribution of the species known to occur in Ireland in relation to zonation (height above sea level) and substratum (fig. 4). This model indicates that the talitrid biotope may be subdivided into a sandy beach strandline biotope characterized by *T. saltator* and *T. deshayesii*, and a mixed gravel strandline biotope with *O. gammarellus*. Below this zone, wave exposed sandy beaches may have a *T. brito* dominated biotope. However, because of the mobility of the strandline habitat due to the effects of tide and wind, it may be difficult to distinguish between above and below supralittoral talitrid biotopes in the field. It should also be noted that these are mobile species. They can migrate up

Zone		SUBSTRATUM				
		Soil, Leaf litter Saltmarsh,	Shingle, Gravel	Decaying and drift seaweed	Coarse sand	Fine sand
Land		Og	Og	Og		
Spray		Og	Og	Og Ts Td	Ts Td	Td
Strandline		Og	Og	Og Ts Td Om Tb	Ts Td Tb	Td
Eulittoral	upper	Om	Om	Om Tb	Tb	
	lower					
Sublittoral						

Fig. 4. A diagrammatic representation of the hypothesized spatial distribution of the Talitridae in relation to vertical zonation and substratum based on both this study and the literature. Og = *Orchestia gammarellus* (Pallas, 1766), Om = *Orchestia mediterranea* A. Costa, 1853, Ts = *Talitrus saltator* (Montagu, 1808), Td = *Talorchestia deshayesii* (Audouin, 1826), Tb = *Talorchestia brito* (Stebbing, 1891).

and down the shore with the tide, time of day and night, and depending on seasonal weather conditions (Lagardère, 1966; Karlbrink, 1969; Wildish, 1988). The diagram also illustrates that it is to be expected that the species distributions will overlap in many localities, and that there are habitats where only one species may occur. Further field studies in Ireland may add a driftwood habitat and associated talitrids, such as *O. microphthalma* and *O. roffensis*, to this diagram.

Further information on the physiological requirements of the species, especially *O. mediterranea*, *T. brito*, *T. saltator* and *T. deshayesii*, would enable the prediction of local site suitability for the species, and their consequent use as indicators of coastal habitat quality. Littoral amphipods are the most sensitive species on beaches to oil pollution (Weslawski et al., 1997) so the absence of species from the habitats they should occur in may be a useful indicator of pollution. Furthermore, analysis of the talitrid species *Orchestia gammarellus* (cf. Rainbow et al., 1989; Moore et al., 1991), *Talitrus saltator* (cf. Rainbow et al., 1998), and *O. mediterranea* and *Talorchestia deshayesii* (cf. Weeks & Moore, 1991; Weeks & Rainbow, 1991), can provide baseline levels of metal bioavailability in coastal waters. Such baseline information on metal levels, and predictive knowledge of where talitrids should occur, would be particularly useful where pre-impact information on species distribution is not available, as is often the case in marine pollution incidents.

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