

Upogebia deltaura (Crustacea: Thalassinidea) in Clyde Sea maerl beds, Scotland

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Burrows inhabited by *Upogebia deltaura* (Crustacea: Thalassinidea) were studied over a two-year period on two maerl beds at 10 m below Chart Datum (CD) in the Clyde Sea area, Scotland. Labelled burrows proved to be stable features on each ground, with animals able to withstand the impacts of scallop dredging and storm disturbance by re-building the damaged upper sections of their burrows. Resin casts excavated using an air-lift showed that these burrows were inhabited by single individuals. Burrows were deeper, larger and more complicated than was previously thought typical for *U. deltaura* and other members of the genus. Mapping of burrow systems revealed average densities of 2.9 ind m⁻² with up to ten openings m⁻². These elusive animals were the deepest burrowing megafauna (to 68 cm) and the most abundant large crustaceans within the maerl bed habitat.

INTRODUCTION

Maerl beds are calcareous gravels built up over 100s–1000s of years by the accumulation of unattached nongeniculate Corallinaceae (Rhodophyta). They occur worldwide (Bosence, 1983; Foster et al., 1997) forming near-shore habitats that typically exhibit high benthic biodiversity and biomass (Cabioc, 1968; Keegan, 1974; Bosence, 1979; Mora Bermúdez, 1980). European maerl beds are of conservation importance (Council Directive 92/43/EEC, 1992) although numerous activities currently threaten these habitats, notably direct exploitation (Cabioc et al., 1997), eutrophication (Grall & Glémarec, 1997a,b) and towed demersal fishing gear (Hall-Spencer, 1995, 1998). The present study was carried out as part of a wider investigation into the impacts of scallop dredging on the ecology of maerl habitats (BIOMAERL, 1998).

Preliminary *in situ* observations on maerl grounds at several sites in Scotland revealed that large burrows of similar external appearance were common and important features of the habitat. Use of a range of remote sampling gear on maerl beds in the Clyde Sea area failed to capture the organisms responsible but subsequent use of a diver-operated air-lift, following methods developed on Irish maerl grounds (Keegan & Könnecker, 1973), revealed that these burrows were occupied by the thalassinidean shrimp *Upogebia deltaura* (Leach).

Thalassinideans are commonly known as mud-shrimps since most species, including *Upogebia* spp., are found in muddy sediments. *Upogebia deltaura*, however, has been recorded in association with coarser sediments (gravels and shell-sands) for example in Norway (Samuelsen, 1974), Sweden (Gustafson, 1934; Tinberg, 1986), Scotland (Astall et al., 1997) and the Irish Sea (Swift, 1993; Hughes & Atkinson, 1997). A search of records show that maerl beds may be an important habitat for *U. deltaura*, since these shrimps have been located amongst maerl throughout the north-east Atlantic with records from

Kilkerrin Bay, Ireland (Keegan, 1974), the Fal Estuary, England (Hardiman et al., 1976), the Bay of Brest, France (J. Grall, personal communication) and the Ria de Arosa, Spain (A. Sánchez-Mata, personal communication). The southern extent of *U. deltaura* is not known due to sparse records and taxonomic confusion. Dworschak (1983) described three burrows attributed to *U. deltaura* from the Adriatic Sea, but indicated, based on unpublished information, that they could have been those of *U. mediterranea* which was subsequently confirmed (P.C. Dworschak, personal communication). The situation is now further complicated by the possibility that *U. mediterranea* Noel (Noel, 1992) may be a subspecies of *U. nitida* (A. Milne Edwards) (d'Udekem d'Akoz, 1995).

There have been few published studies on the biology of *U. deltaura* in contrast with those carried out on other upogebiids (Ott et al., 1976; Dworschak, 1983, 1987a,b, 1988, 1992; Mukai & Koike, 1984; Posey et al., 1991; Nickell & Atkinson, 1995). Recent work on the behaviour and physiology of *U. deltaura* (Astall et al., 1997) emphasized difficulties experienced with investigating their burrows *in situ*. Attempts to cast burrows in the field using polyester resin were only partially successful due to difficulties in extracting casts from the coarse substratum. The present contribution describes a successful adaptation of the methods used by Astall et al. (1997) to obtain burrow casts of these elusive animals. The prevalence and dynamics of these burrow systems were investigated on Clyde maerl grounds and monitored to determine the effects of natural (storms) and human (scallop dredge) disturbances.

MATERIALS AND METHODS

Sampling sites

This study was carried out on two maerl beds in the Clyde Sea area, Scotland (Figure 1) where tides are semidiurnal with a mean range of 3.1 m on springs and

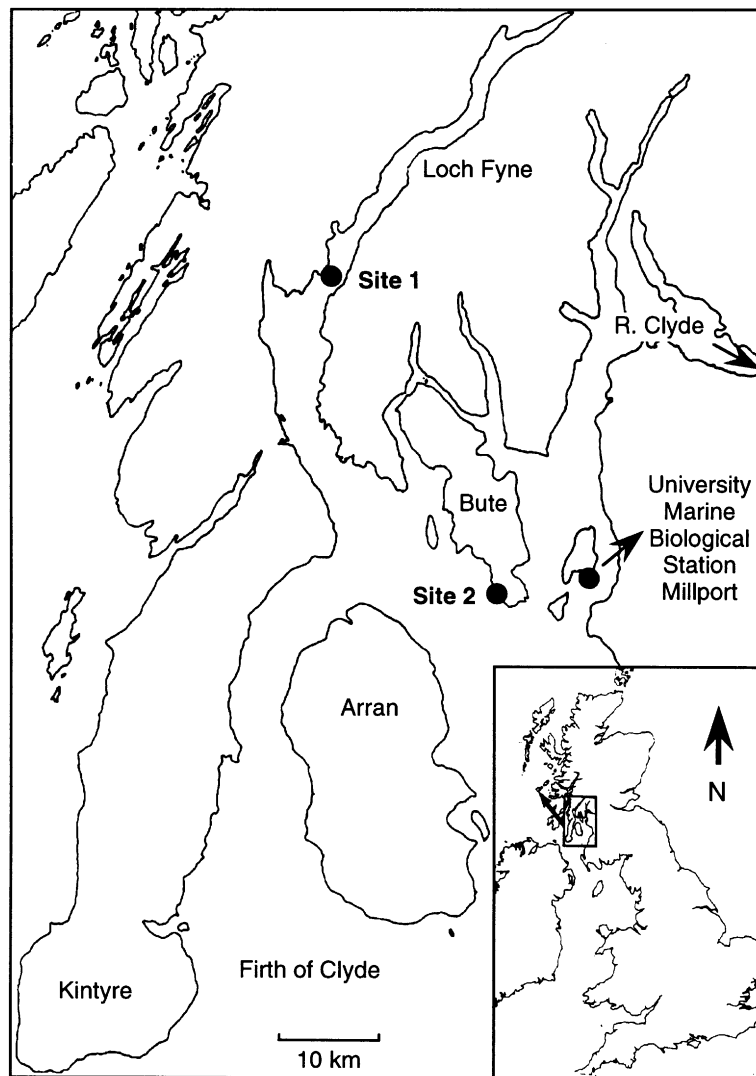


Figure 1. Map showing location of field study areas and the Marine Station in the Clyde Sea area, south-west Scotland.

1.8 m on neaps. The sites were Creag Gobhainn (Site 1) in Loch Fyne ($56^{\circ}00.601'N$ $005^{\circ}22.148'W$, position determined by Trimble Differential Global Positioning System) and Stravanan Bay (Site 2) ($55^{\circ}45.323'N$ $005^{\circ}04.265'W$) off the Isle of Bute. Site 2 had been heavily impacted by scallop dredging in recent years whereas Site 1 was unimpacted due to the prohibitive presence of a seabed telecommunications cable lain in 1968. Visual inspections of the distribution of *Upogebia deltaura* burrows were carried out during ~ 70 SCUBA dives in these areas during 1996–98. Each bed was marked with a permanent buoy at -10 m CD as a datum for diving operations and the sites were investigated at approximately two monthly intervals from May 1996–June 1998.

On each sampling occasion, salinity and temperature were measured 10 cm above the bottom and a current meter (Model 308, Valeport Ltd, Devon, UK) was deployed on spring, neap and mid-tides for periods of 5–36 hours, 1 m above the bottom.

Granulometry

Sediment samples were taken at -10 m CD on both sites using 10 cm diameter, 25 cm long hand-held cores.

Three replicate cores were taken at Site 1 which was level and relatively homogeneous, Site 2 was megarippled (see below); three replicate cores were taken on peaks of the megaripples and three on the troughs to quantify differences in their granulometry. Cores were horizontally sectioned at 4 cm intervals and subjected to granulometric analysis following Folk (1974).

Remote sampling

The two maerl deposits were sampled bimonthly during 1996–98 using replicate 0.1 m^2 van Veen grabs (totals of 85 taken at Site 1 and 105 at Site 2) and a 75 cm-wide ring-dredge (totals of 12 taken at Site 1 and 14 at Site 2). On one occasion divers took measurements of the pits excavated by these sampling devices at Site 2.

Appearance of burrow openings

Throughout, the external appearance of burrows were photographed using a Nikonos V camera, 35 mm lens, 64 ASA Kodachrome film, YS-60 Sea & Sea strobe and standard close-up attachments. At Site 2, three hand-held stainless steel Senckenberg box cores (8×15 cm area,

20 cm long; Bouma, 1969) were used to retrieve the top sections of *U. deltaura* burrows in September 1996. On return to the laboratory, these box cores were sectioned vertically to reveal burrow lumens and organisms embedded in the burrow lining.

Air-lifting

Methods for the use of an air-lift on maerl sediments followed those of Keegan & Könniker (1973). At each site, six 1 m² quadrats were excavated at 4 cm intervals to give depth-stratified samples to 72 cm below the surface of the deposit in June–July 1996. The density and orientation of *U. deltaura* burrows were recorded together with the burrowing depth of other species of megafauna.

Burrow casts

Burrow casts were made at both sites using techniques adapted from those described by Atkinson & Chapman (1984). Polyester resin (manufactured by Scott Bader, marketed as SP701PA by Trylon Ltd, Wollaston, UK) was thinned using 10% by volume of styrene monomer and mixed with peroxide catalyst (2% by volume) in a 7 l plastic watering can. In initial casting exercises (September/October 1996) divers slowly poured the resin directly into the narrow burrow openings, a process that took up to an hour per burrow. Subsequently (November/December 1996) the top 4 cm of maerl was scraped aside to remove the narrow openings and reveal the wider lumen of the descending shaft. Ten centimetre diameter plastic collars were then placed around selected burrow openings to minimize spillage of resin. Burrow openings were identified by pushing numbered flags (constructed from PVC tape attached to lengths of aluminium welding rod) into the sediment beside burrow openings, within each collar. Casts were recovered the day after the resin was poured, with divers using an air-lift to excavate the casts and a Nikonos V camera (see above) to photograph burrow orientation *in situ*. In the laboratory, casts were photographed, measured and weighed. Burrow volume was computed from cast weight and resin density (1.2). Burrow terminology follows that of Nickell & Atkinson (1995), based on that of Frey (1973). Thus, 'opening' describes an aperture at the sediment surface, 'shaft' describes a vertical or dominantly vertical structure, 'tunnel' describes a structure with an oblique to horizontal orientation, 'sump' describes a downwardly directed blind-ending shaft and 'burrow system' refers to a relatively complex individual burrow.

On retrieval, some casts contained embedded *U. deltaura*—these specimens were injected with 4% formalin and their size was determined from X-ray photography of the cast. Measurements of carapace length were taken from the tip of the rostrum to the posterior edge of the carapace, following the methods of Tunberg (1986).

Burrow mapping

A 2×5 m area of seabed was marked out using pegs to give a grid of ten 1 m² quadrats at each site. The densities of burrows and burrow openings were surveyed in November/December 1996. Each quadrat was investigated for visible openings. When one was located it was

irrigated using a hand-operated pump (Alvey Reels, Australia) fitted with a nozzle of 1 cm internal diameter. Connected openings were indicated by a plume of fine sediment which was forcibly ejected from the lumen of the burrow system. These openings were mapped on a writing 'slate' and the distances between openings were measured. This process continued over several dives until all of the burrows within the 10 m² area had been mapped. Where burrows connected to openings outside a quadrat, the proportion of the burrow within the area was estimated. For example, where burrows had two openings within a quadrat and one outside, this was counted as 0.67 of a burrow within that quadrat.

Effects of wave disturbance

At each site, a gauge (Figure 2) designed to measure changes in sediment macro-topography due to wave action (see Napier, 1993), was used approximately bimonthly between May 1996 and June 1998. The 2.4 m long gauge was photographed 15 times along a 32 m transect running south-west starting from a permanent site marker on each maerl bed. Resulting photographs were used to record changes in seabed topography along the two transects. Divers recorded the effects of wave-induced sediment transport on the appearance and spatial arrangement of *U. deltaura* burrow openings. Ten of the burrows mapped within each 2×5 m area (above) were selected haphazardly and marked with pre-labelled aluminium rods in November/December 1996. These marked burrows were re-examined bimonthly up to June 1997 to monitor changes in burrow density and position.

Effects of scallop dredging

In May 1996 a gang of three standard Newhaven scallop dredges (each 75 cm wide) were towed between marker buoys laid out at -10 m CD at each site, following methods given by Hall-Spencer (1995). They were towed at the usual commercial speed of 3.5 km h⁻¹ over approximately 100 m which left dredged areas of ~250 m². Immediately after dredging, divers equipped writing slates counted *U. deltaura* burrow openings in 40 1 m² quadrats on dredge tracks and 40 1 m² quadrats on the adjacent maerl. Quadrat placement was haphazard. Notes were also made on damage to visible fauna and changes in seabed topography. These surveys of dredge tracks and adjacent seabed were repeated approximately bimonthly at each site over a subsequent period of 12 months.

RESULTS

Sampling sites

At both sites, *in situ* visual inspections of the distribution of *Upogebia deltaura* burrows in the period 1996–98 revealed that they were strongly associated with the maerl substratum. At Site 1 the *U. deltaura* burrows occurred within maerl that formed a bank running parallel to the shore along a gently sloping strip covering an area of 17.5 ha between -6 m and -14 m CD. At Site 2 the *U. deltaura* burrows occurred within maerl over an area of 6.75 ha from -6 m to -14.7 m CD on a shoal



Figure 2. Sediment profile gauge in use at Stravanan Bay (Site 2) one week after storms in February 1997. The coarse surface layer of maerl gravel is thrown into megaripples 11 cm high ($\lambda=1.2$ m) overlying a relatively stable layer of sediment with a higher proportion of sand and fines.

situated ~ 500 m off the coast of the Isle of Bute. The depth distribution of *U. deltaura* was similar at both sites. Maerl graded into sandy and rocky areas shallower than -6 m CD where there were no burrowing thalassinideans present. Below -15 m CD, the maerl at both sites became more muddy and air-lifting in the area showed that *U. deltaura* was replaced by *Upogebia stellata* (Montagu). The only thalassinideans present in the permanently marked areas at -10 m CD were *U. deltaura*.

Salinity and temperature were very similar at the two sites, variations in bottom water salinity were slight (31–33 psu) and temperature readings ranged from 6.0°C (February 1997) to 14.1°C (September 1997). Bottom currents at Site 1 were generally faster (up to 54 cm s^{-1}) than at Site 2 (up to 11 cm s^{-1}).

Granulometry

The top 4 cm of sediment collected in cores at both sites was very coarse (40–70% gravel) with the proportion of sand and mud increasing with depth into the cores. The megarippled topography of the maerl at Site 2 (see

Figure 2) exhibited pronounced differences in granulometry with clean gravel ($<4\%$ fine sand and mud) on the ripple peaks compared with more mixed sediment ($\sim 15\%$ fine sand and mud) in the ripple troughs. The subsurface sediment at Site 2 was coarse with 50% gravel, 31% coarse sand, 14% fine sand and 4% mud at 20–24 cm below the surface of the deposit. At Site 1, the sediment surface was level, overlying predominantly coarse sand with 12% gravel, 49% coarse sand, 24% fine sand and 14% mud at 20–24 cm below the sediment surface.

Remote sampling

Dives made immediately after van Veen grab and ring-dredge sampling revealed that the grabs penetrated <15 cm into the sediment and the ring-dredge <23 cm. Both types of gear often exposed the distinctive lumens of *U. deltaura* burrows (see below) but none of the 190 0.1 m^2 grab samples or the 26 qualitative ring-dredge samples caught *U. deltaura*.

Appearance of openings

At both sites, burrow openings were flush with the sediment surface (cf. the mounds or funnel openings found in some thalassinidean species—see Nickell & Atkinson, 1995) and were markedly constricted to diameters <7 mm. Many burrow openings were not visible to divers since they were occluded by the open lattice arrangement of the surface layer of maerl gravel. The most obvious burrow openings were surrounded by circular patches (to 12 cm in diameter) of fine grey sediment that had been ejected from the burrow (Figure 3A). This ejected sediment contrasted with the pink live maerl and the brown to black maerl gravel that lay dead on the surface. No obvious seasonal differences in external burrow morphology were discerned. When probed, coarse shell and maerl fragments collapsed into the wider, underlying burrow shaft revealing distinctive smooth walls and a circular transverse section (Figure 3B). When these damaged openings were revisited some minutes later, *U. deltaura* were sometimes seen repairing the walls of the openings from within the burrow. Throughout this study (115 h of *in situ* observations) no mud-shrimps were seen on the sediment surface.

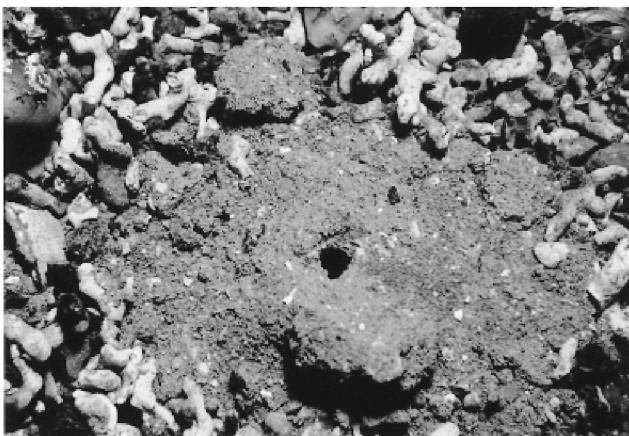


Figure 3. Surface view of a *Upogebia deltaura* burrow. (A) Showing constricted aperture (6 mm diameter) flush with the maerl bed surface and surrounded by fine sediment ejected from the burrow below. (B) Surface constriction removed by hand to show circular lumen of burrow shaft descending into the gravel below, lined with a smooth layer of mud.

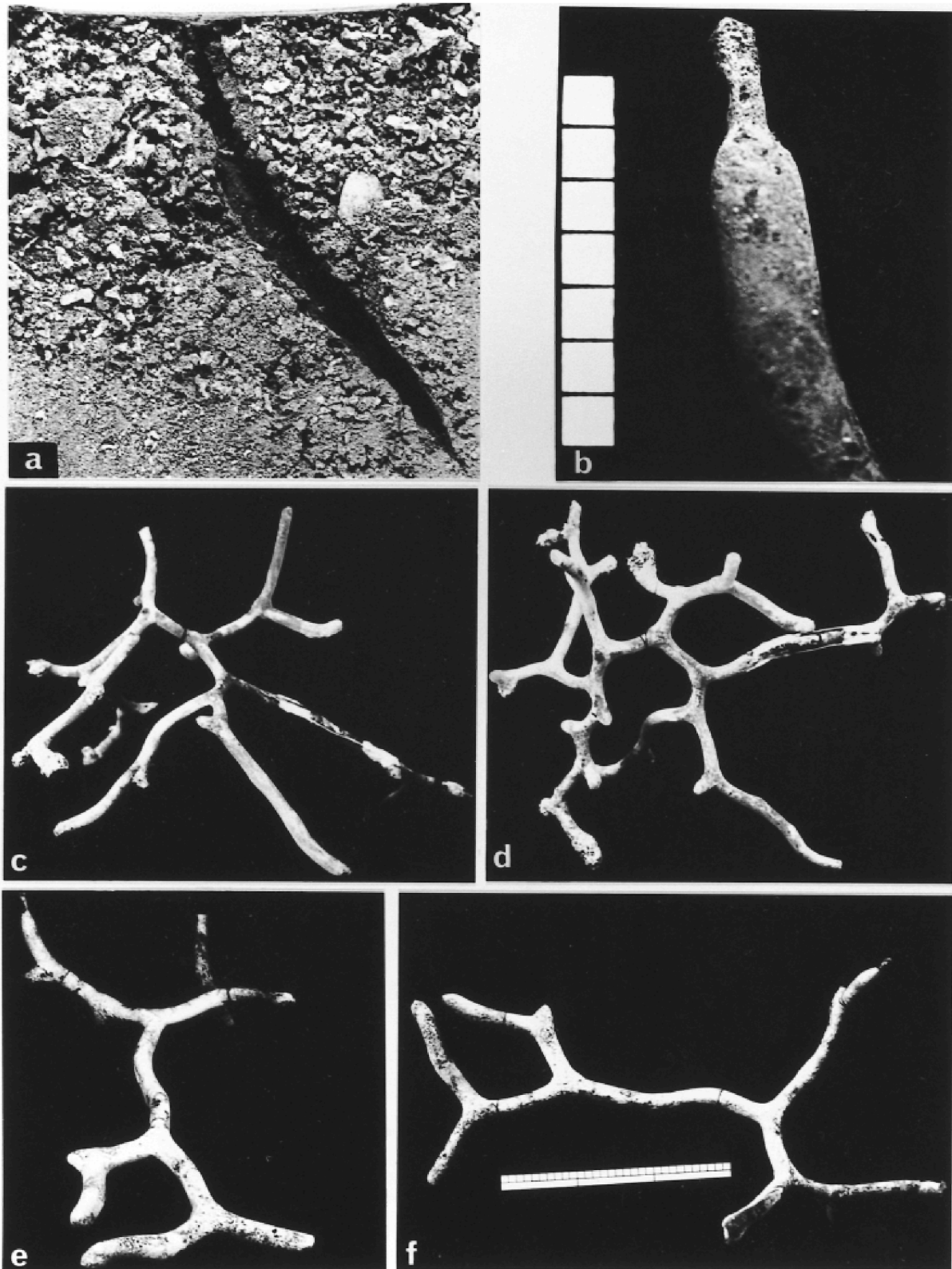


Figure 4. *Upogebia deltaura* burrow construction. (A) Vertically sectioned box core, note the coarse granulometry of the maerl gravel and the mud-lined burrow lumen (arrow), core width: 15 cm. (B) Resin cast of burrow opening showing surface constriction and descending shaft. (C) Cast 1 side view. (D) Cast 1 surface view with position of trapped *U. deltaura* indicated (arrow). (E) Cast 4 side view with two openings uppermost. (F) Cast 4 surface view. Scale bars: B, 7 cm; C–F, 30 cm.

Subsurface burrow morphology and associated fauna

Each of the vertically sectioned Senckenberg cores showed that burrows were lined with a distinct layer of mud 4–8 mm thick that the inhabitants had pushed into

the interstices of the surrounding gravel to form a very smooth tube of circular transverse section. The light brown colour of the burrow wall sediment indicated that it was well oxygenated. This colour contrasted with the darker, reduced sediment in deeper parts of the sediment

Table 1. *Burrowing megafauna co-occurring with Upogebia deltaura on maerl beds at Site 1 (Creag Gobhainn, Loch Fyne) and Site 2 (Stravanan Bay, Bute), showing the maximum distances at which these animals were found below the sediment surface. Six 1 m² quadrats were excavated at each site during June–July 1996 using an air-lift at –10 m CD. Nomenclature follows that of Picton & Howson (1997).*

Species	Maximum depth below maerl surface (cm)	
	Site 1	Site 2
<i>Cerianthus lloydii</i> Gosse	40	44
<i>Golfingia elongata</i> (Keferstein)	40	—
<i>Golfingia vulgaris vulgaris</i> (de Blainville)	36	—
<i>Glycera rouxi</i> Audouin & Milne-Edwards	44	36
<i>Nereis longissima</i> Johnston	32	16
<i>Nephtys hombergi</i> Savigny	16	28
<i>Chaetopterus variopedatus</i> (Renier)	28	28
<i>Terebellides stroemi</i> M. Sars	24	—
<i>Pista cristata</i> (O.F. Müller)	24	—
<i>Eupolymnia nebulosa</i> (Montagu)	20	24
<i>Upogebia deltaura</i> (Leach)	68	68
<i>Lutraria angustior</i> Philippi	40	—
<i>Ensis arcuatus</i> (Jeffreys)	—	32
<i>Moerella donacina</i> (Linnaeus)	28	—
<i>Clausinella fasciata</i> (da Costa)	20	28
<i>Tapes rhomboides</i> (Pennant)	40	—
<i>Dosinia exoleta</i> (Linnaeus)	28	28
<i>Mya truncata</i> Linnaeus	52	52
<i>Echinocardium pennatifidum</i> Norman	28	28
<i>Neopentadactyla mixta</i> (Ostergren)	—	48
<i>Thyone fusus</i> (O.F. Müller)	40	—
<i>Thyonidium drummondii</i> (Thompson)	40	—

column. The surface shafts averaged 19 mm in diameter and narrowed down to ~7 mm within 2–6 cm of the seabed surface (Figure 4A,B). The narrow conduits to the overlying water column were not mud-lined. Each core contained individuals of the bivalve *Mysella bidentata* (Montagu) (to 3 mm in length) embedded on the innermost surface of the burrow linings.

Table 2. *Morphometric data for eight >50% complete casts of Upogebia deltaura burrows taken at –10 m CD on maerl at Site 2 (Stravanan Bay, Isle of Bute) in November–December 1996. Apart from number of burrow openings, total burrow depth and % cast completion (based on in situ measurements) data refer to measurements taken on cast portions of the burrows.*

Cast	No. of openings	Burrow depth (cm)	% cast complete	Cast volume (cm ³)	Cast opening diameter (mm)	Mean cast diameter	Cast length (cm)	No. of cast junctions	No. of cast sumps	Animal present in cast	Carapace length (mm)
						(mm ±SD) (N=10)					
1	3	55	80	1428	—	18.0 ±0.8	321	19	4	+	18.5
2	3	45	90	1176	6.0–6.2	24.7 ±1.2	165	8	3	+	22.0
3	2	44	80	1194	—	22.7 ±2.2	230	11	2	—	—
4	2	40	70	516	6.0–6.4	20.0 ±0.9	112	6	2	—	—
5	2	37	80	282	4.2–6.3	16.2 ±0.7	101	8	3	+	17.4
6	2	31	55	612	3.6–5.0	19.7 ±0.9	123	7	3	—	—
7	2	23	80	552	—	19.3 ±1.2	97	5	1	—	—
8	2	23	55	408	—	23.3 ±2.4	70	2	0	+	17.1

Air-lifts

At both sites, once the top 4 cm layer of maerl had been removed it was possible to clearly see the mud-lined shafts of *U. deltaura* burrows descending into the sediment below. The six 1 m² quadrats at Site 1 contained 2–7 descending shafts in the upper layer, those at Site 2 had 3–10 descending shafts. The burrow walls were firm and could be traced into the sediment using the air-lift. Each burrow had one occupant and separate burrow systems came to within a few centimetres of each other within the three-dimensional lattice of the sediment below, but on no occasion were they observed to join. At both sites, most tunnels were in the 20–32 cm depth range and the deepest sump portions of the burrow systems were up to 68 cm below the sediment surface. Other species of burrowing megafauna (e.g. the holothurian *Neopentadactyla mixta* (Ostergren)) were abundant on both maerl beds and were found at considerable depths within the sediment (Table 1). *Upogebia deltaura* was consistently the deepest-burrowing organism present, followed by mature individuals of *Mya truncata* L. The largest *U. deltaura* collected was an ovigerous female (total length 62 mm).

Burrow casts

The technique initially used, whereby resin was poured directly into the narrow burrow openings, provided casts showing distinctive near-surface constrictions (Figure 4B). However, this method was time-consuming and the openings often became blocked so that only small portions of the burrow were cast. Removal of the top section of burrows allowed resin to be poured more quickly and gave eight casts that were >50% complete. Complete resin casts were not obtained due to blockages created either by the body of the inhabitant, by back filling of the burrow by the animal or due to seawater trapped within the burrow lumen. Typical casts (1 & 4 in Table 2) are shown in Figure 4C–F showing the depth and complicated nature of these structures. Characteristics of the eight >50% complete casts are provided in Table 2. Use of an air-lift enabled the casts to be recovered without breakage. An added advantage was that the tunnels and

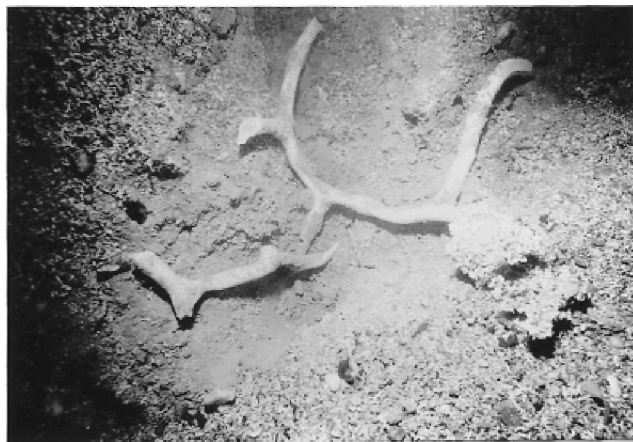


Figure 5. Resin-cast *Upogebia deltaura* burrow photographed *in situ* after excavation using an air-lift to enable accurate reconstruction of its orientation.

shafts of the portions of the burrow that had not been cast could be traced through the maerl gravel due to their firm mud-lined walls. Photographs taken with the casts *in situ* (Figure 5) allowed accurate orientation of the casts. Consistent features of the casts were their circular transverse section and regular diameter along shafts and tunnels which constricted at openings to the surface and widened at blind endings. All junctions were bifurcate. Casts of the tunnels and shafts were very smooth, usually with *Mysella bidentata* attached. Sumps, in contrast, were rough with pieces of maerl gravel attached indicating that they were not lined with mud to the same degree.

A combination of resin casting and use of an air-lift showed that each burrow was inhabited by a single individual and did not link up with other burrow systems. Four of the eight >50% complete resin casts had a *U. deltaura* embedded within the resin, the lengths of which are given in Table 2.

Burrow mapping

Table 3 shows the numbers of burrow systems encountered in 2×5 m areas marked out on each site. Use of a pump revealed the position of openings that were occluded by surface maerl when a plume of fine sediment was ejected from the burrow system. At both sites, the majority of burrows had two openings (68%) and the remainder had three. Two-holed burrows covered a smaller area, on average, with openings as little as 11 cm apart, whereas some of the structures with three openings

were very extensive with openings up to 145 cm apart. Site 2 had the highest density of *U. deltaura* with a mean of 2.9 burrows m⁻² and 3–10 openings m⁻². Site 1 had a mean of 1.9 burrows m⁻² and 2–7 openings m⁻².

Effects of wave disturbance

At both study sites, burrow densities remained remarkably stable over the 1996–1998 period. At Site 1, ten marked burrow openings remained in the same configuration throughout a seven-month monitoring period. This site was relatively sheltered and remained undisturbed by wave action throughout the survey; no changes were recorded in the gross topography of the ground from 1996–1998 with dead *Aequipecten opercularis* (L.) shells seen lying in the same position on the sediment surface throughout. By contrast, Site 2 was more exposed to prevailing south-westerly winds. For most of the period the sediment remained stable but large-scale shifts in the coarse upper layer of maerl occurred during two storms in the winter of 1996/1997 and one in January 1998 leading to a rearrangement of the gravel megaripples (Figure 2). Observations in the weeks after these storms showed that the mixed sediments of the subsurface (>12 cm) layer of maerl had been unaffected allowing *U. deltaura* to remain in place. Seven burrow markers were relocated after the storms of 1996/1997, the adjacent *U. deltaura* had rebuilt the surface portions of their burrows to conform to the shifted maerl topography.

Effects of scallop dredging

At both sites, dives undertaken immediately after fishing revealed distinctive 2.5 m wide tracks where teeth on the three dredges had raked through the top 10 cm of sediment, bringing fine sediments to the surface and leaving a trail of smashed sessile megafauna such as the bivalve *Ensis arcuatus* (Jeffreys) and the heart-urchin *Spatangus purpureus* O.F. Müller. Bodies of *U. deltaura* were not amongst the carrion visible on the sediment but nearly all burrow openings had been erased. The shrimps rebuilt the upper sections of their burrows within a week. After one month there were no significant differences in the densities of burrow openings on impacted and unimpacted areas of the maerl beds (ANOVA, $P > 0.05$). At Site 1, a mean density of 4.52 m⁻² openings (SE=1.3, N=40) were recorded on the dredge track compared with 4.02 m⁻² (SE=0.9, N=40) on the adjacent control area. At Site 2, a mean of 7.70 m⁻² openings (SE=2.5, N=40) were

Table 3. Distribution and abundance of *Upogebia deltaura* burrows recorded in 2×5 m² plots on maerl at -10 m CD at Site 1 (Creag Gobhainn, Loch Fyne) and Site 2 (Stravanan Bay, Bute) in November–December 1996.

Site	No. of burrows examined	No. with 2 openings	No. with 3 openings	Distance between openings on burrows with 2 openings (cm)			Distance between openings on burrows with 3 openings (cm)			No. of openings m ⁻² (N=10)			No. of burrows m ⁻² (N=10)		
				Min	Mean ±SD	Max	Min	Mean ±SD	Max	Min	Mean ±SD	Max	Min	Mean ±SD	Max
1	24	16	8	14	35.1 ±25.0	84	14	34.8 ±28.4	111	2	4.5 ±1.4	7	0.6	1.9 ±0.7	3.3
2	38	26	12	11	38.7 ±21.2	94	12	32.6 ±23.5	145	3	7.0 ±2.2	10	1.3	2.9 ±0.9	4.3

recorded on the dredge track compared with 6.64 m^{-2} (SE=2.1, N=40) on the adjacent control area.

The dredge tracks were easily visible to divers for 12 months after the initial disturbance at Site 1 whereas they were erased by shifting sediment during winter storms in 1996/1997 at Site 2. Thus at both sites, while many large, sessile organisms on or near the sediment surface were killed by the scallop dredges, the density of newly constructed burrow openings showed that survival rates of *U. deltaura* were high.

DISCUSSION

This study showed that *Upogebia deltaura* was abundant in maerl beds of the Clyde Sea area with complex and extensive burrows that affected the structure of these habitats. Although *U. deltaura* are relatively large animals (up to 62 mm total length in this study) and can be abundant in near-shore sediments [e.g. Tunberg (1986) found mean densities of 5.0 ind 0.1 m^{-2}], even basic aspects of their biology such as growth rates, longevity and reproductive habits are poorly known because the animals are so difficult to collect. The importance of deep-burrowing megafauna can often be overlooked since most sampling methods (e.g. grab sampling, coring, Naturalist's dredge, surveys with cameras/divers) rarely reveal their presence, leading to underestimates of their distribution and abundance. Even heavy equipment such as $20\times 28\text{ cm}$ by 45 cm deep Reineck box corers cannot be relied upon to capture *U. deltaura* quantitatively (Swift, 1993). Thus records are sparse, but coarse near-shore sediments appear to be the preferred substrata of *U. deltaura* (see introduction and below). Many of the records for *U. deltaura* come from maerl beds occurring from Scotland to Spain (Hardiman et al., 1976; Keegan, 1974; J. Grall & A. Sánchez-Mata, personal communication). The main maerl-forming species in this region of the north-east Atlantic are *Phymatolithon calcareum* (Pallas) Adey & McKibbin, *Lithothamnion glaciale* Kjellman and *L. corallioides* (P. & H. Crouan) P. & H. Crouan which colonize sedimentary substrata and build calcareous gravel banks through fragmentation and growth (BIOMAERL, 1998; Hall-Spencer, 1998). Thus these maerl-forming species may be an important source of habitat for *U. deltaura*.

The two species of *Upogebia* known to occur in Scotland overlap in their sediment preferences, with *U. stellata* obtained from fine muds (Nickell & Atkinson, 1995) to muddy gravels (present study) and *U. deltaura* found in fine muds (personal observation) to coarse gravels (present study). These two species are reported to occur together at Salcombe, southern England (de Morgan, 1910) and in shallow Norwegian waters (Samuelsen, 1974). However, Gustavson (1934) noted that they occurred at different depths in Gullmarfjord, Sweden. He recorded a distinct *U. deltaura* zone at 10–14 m depth in 'clay-mixed sand, often mixed with coarse gravel' with a *U. stellata* zone at depths below 25 m in 'clay-mixed sand'. It is clear from Poulsen (1941), however, that *U. deltaura* also occurs at depth (50 m) in Swedish waters. Detailed observations at sites in the Clyde Sea area indicate that where these species occur in the same general area, *U. stellata* is commoner in finer grade muddy sands and

U. deltaura is commoner in coarser grade muddy gravels which usually results in *U. deltaura* occurring in shallower water than *U. stellata*. The sediment preferences of the juveniles and adults of these species would merit further experimental investigation. Being a large, robust species (de Morgan, 1910) *U. deltaura* may be able to exploit coarse substrata that are difficult to access by smaller species such as *U. stellata*.

Upogebia deltaura is principally a suspension feeder (Pinn et al., 1998) and lines its burrow with mud to allow a laminar flow of water as it irrigates the burrow to feed. The method by which *U. deltaura* consolidates the burrow wall has not been investigated but may involve the application of secretions from glands in the hind-gut, as shown for *Upogebia pugettensis* (Dana) by Thompson (1972), and/or by plastering the mud lining with secretions from glands on the appendages used to manipulate burrow walls, as shown in two species of the closely related thalassinidean genus *Callianassa* (Dworschak, 1998).

It is clear from our diving observations and from the literature (Dworschak, 1983; Tunberg, 1986) that upogebiids can be very common and, due to their size, they are likely to be significant contributors to total biomass. Upogebiids have been shown to pass large volumes of water through their burrows during feeding and irrigation activities (Dworschak, 1981). For *U. deltaura*, through burrow flow rates of $4.2\text{--}34.1\text{ ml min}^{-1}$ have been reported (Astal et al., 1997). As shown by other workers (Ott et al., 1976; Astal et al., 1997), such extensive, deep burrows increase the area of the water/sediment interface and introduce oxygenated conditions at depth in the sediment column as evidenced by an oxic zone surrounding the burrow wall. A large variety of fauna is associated with *Upogebia* burrows, where they are able to penetrate deeper into the sediment than in the absence of these shrimps (Dworschak, 1983). The burrows also increase the structural complexity of the habitat; within gravelly sediments their mud-lined burrows provide loci for organisms such as *Mysella bidentata* which is known to associate with the burrows of other species (Ockelmann & Muus, 1978; Nickell et al., 1995).

The cryptic, narrow burrow openings of upogebiids result in them being overlooked or underestimated in abundance, especially in coarse sediments like maerl where their burrow openings are often occluded. The present study has shown that the burrows of *U. deltaura* can be far more complicated and extensive than the relatively simple structures described for this species from laboratory observations (Astal et al., 1997), though burrow casts taken in the field by these authors suggested greater complexity. Upogebioid burrows described in the literature (Dworschak, 1983; Nickel & Atkinson, 1995) are less complex than those described here for *U. deltaura*, but all share common features. These include U- or W-shaped upper sections, bifurcate branches and blind-ended descending sumps. The complexity of *U. deltaura* burrows lies in their large size and the amount of branching. In this study, *U. deltaura* were found to live singly in their burrows, a trait that appears to be typical of upogebiids as a group (Dworschak, 1983). In common with most thalassinideans, they probably leave their burrows only rarely. They are predated upon by demersal fish, having been found in the stomachs of rays (*Raja*

clavata L.), haddock (*Melanogrammus aeglefinus* (L.)) and cod (*Gadus morhua* L.) (Selbie, 1914; Poulsen, 1941; Tunberg, 1986). Suctorial feeding (Osse & Muller, 1982) may account for this, perhaps when the upogebiid signals its presence when tending a burrow opening.

The depth of these burrows coupled with the ability of the occupants to withstand hypoxia (Astall et al., 1997) makes them resilient to natural perturbances such as large sediment shifts during storms, as observed in this study, or severe cold (0.8°C; Tunberg 1986). While commercial scallop dredges have a high impact on sessile organisms on or near the sediment surface (Thrush et al., 1995; Curry & Parry, 1996; Hall-Spencer et al., 1999) our observations have shown that the deep-burrowing habit of upogebiids confers resistance to disruption by towed demersal fishing gear since they are able to repair the upper sections of their burrows and survive at high densities, even on grounds that are dredged extensively for scallops.

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