



Behaviour and habitat of *Neohela monstrosa* (Boeck, 1861) (Amphipoda: Corophiida) in Norwegian Sea deep water

Lene Buhl-Mortensen^a, Anne Helene S. Tandberg^a, Pål Buhl-Mortensen^a
and Andrew R. Gates^b

^aBenthic Communities and Coastal Interactions, Institute of Marine Research, Bergen, Norway; ^bNational Oceanography Centre, University of Southampton, Waterfront Campus, Southampton, UK

ABSTRACT

There are few in situ observations of deep-sea macrofauna, due to the remoteness of this ecosystem. Visual surveys conducted for marine management by MAREANO, (marine area database for Norwegian waters) and the petroleum industry (by SERPENTS, scientific and environmental remotely operated vehicle partnership using existing industrial technology) have provided unique material of visual information from large areas in the Norwegian Sea. The distribution, density and behaviour of the deep-sea amphipod *Neohela monstrosa* (Boeck, 1861) is described based on videos and samples from the Norwegian Sea. This amphipod is common on mud bottoms at 200–2181 m depth in the area. Dense communities were found in stands of the arctic sea pen *Umbellula encrinus* at more than 1000 m depth where temperatures were below 0° C. The mean density of *N. monstrosa* observed for larger areas was 4/100 m² but densities of 15–36 individuals per m² were found in local patches. It is domicolous which is characteristic of the superfamily Corophiida and digs burrows in soft muddy bottoms primarily by using large shovel-like gnathopods to scoop the sediment out. The amphipod was observed pushing and rolling sediment balls out of its burrow, which were probably held together with amphipod silk. It digs out an upper 3 to 4 cm wide burrow with a horizontal side burrow a couple of centimetres down. *Neohela monstrosa* appears to feed on newly settled detritus that it collects from the surface sediment through the use of its long antennae while the burrow is mainly used for protection against predators such as demersal fish. Newly released juveniles are probably kept in the burrow for protection. Based on the local high density of *N. monstrosa* together with its habit of making long burrows, we suggest that there is significant bioturbation associated with the presence of *N. monstrosa* in deep sedimentary habitats of the Norwegian Sea, which likely provides an important ecosystem function.

ARTICLE HISTORY

Received 28 November 2014
Accepted 5 June 2015
Online 14 August 2015

KEYWORDS

Neohela; behaviour; density; bioturbation

Introduction

The amphipod *Neohela monstrosa* (Boeck, 1861) belongs to the family Unciolidae within the infraorder Corophiida (suborder Senticaudata). This species has an arctic–boreal

distribution and has been documented from arctic and subarctic parts of the Northwest Atlantic, southwards to the Gulf of St. Lawrence to the south of New England; Greenland; and the Northeast Atlantic from Svalbard to the Kattegat (Stephensen 1933; Enequist 1949; Udekem d'Acoz 2007). In the Fram Strait it has been registered from 2470 m (Bergmann et al. 2011), and Sars (1895) reports it from 300–600 m depth off western and northern Norway where it occurs both in fjords and on the shelf and slope (Buhl-Jensen 1986; Enequist 1949; Buhl-Mortensen 1996). It is also frequent in Skagerrak and in Swedish fjords (Enequist 1949; Miskov-Nodland et al. 1999).

Neohela monstrosa is a large amphipod; the adult female is typically 25 mm and the male 28 mm (Sars 1895). It has a very distinct morphology, and Sars (1895) notes that this peculiar-looking species cannot be confused with other amphipods due to the long and slender body, and extremely elongated antennae and legs (Figure 1). Enequist (1949) suggests that its long antennae and legs are an adaption to the loose sediments of its habitat, with the long legs keeping it on top of a watery sediment and the antennae adapted to collect fine particles.

It is a poor swimmer that lives mainly endobenthically, belonging to what Sainte-Marie and Brunel (1985) define as the 'lowermost supra benthos', defined by the swimming activity of amphipods swimming away from the bottom. It is presumed to feed mainly on detritus. When dividing Skagerrak amphipods into "food-ecological" groups, Enequist (1949, p. 429) positioned *N. monstrosa* in group IV, A, 2 which is 'Burrowing forms exclusively utilizing the detritus occurring in the bottom material underneath the surface' (group IV), 'Forms ingesting the detritus uniformly distributed in the bottom substrate' (A) and 'Forms digging hollows, burrows or tunnels in the material' (2).

In general, detailed information on habitat, density of occurrence and behaviour is lacking for most deep-sea organisms. Soft-bottom amphipods mostly feed on detritus and live more or less buried in the sediment (Lincoln 1979). Due to their small size and remote habitat, there are few *in situ* studies of deep-sea amphipods. However, Enequist (1949) provides detailed observations from aquarium studies for several amphipod species including *N. monstrosa* (Figure 2). For most of these species, studies on behaviour have not been pursued, and field studies on habitat, population density and behaviour are lacking. Recent technological development has strongly improved the ability for visual inspection of deep-sea habitats, and *in situ* observations of their inhabitants are rapidly accumulating (e.g. Mortensen et al. 2008; Buhl-Mortensen et al. 2010; Purser et al. 2013). In this paper we use video records, supplemented by grab, trawl and sled samples, to describe the habitat, density and behaviour of *N. monstrosa* in the Norwegian Sea (221–2167 m depth).

Materials and method

The material for this study was collected as part of the Norwegian national mapping programme MAREANO (marine area database for Norwegian waters; www.mareano.no), supplemented by remotely operated vehicle (ROV) observations at Norwegian hydrocarbon exploration wells made available through the SERPENT Project (scientific and environmental ROV partnership using existing industrial technology; www.serpentproject.com).

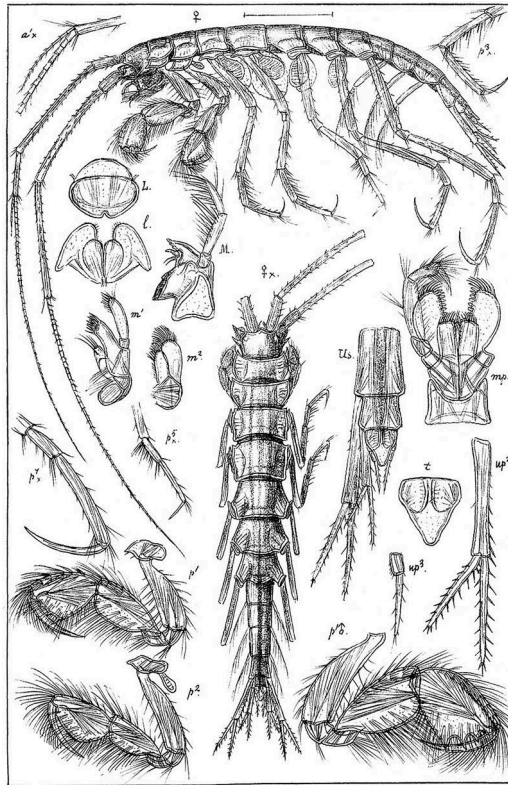


Figure 1. Morphological description of *Neohela monstrosa* (from Sars 1895).

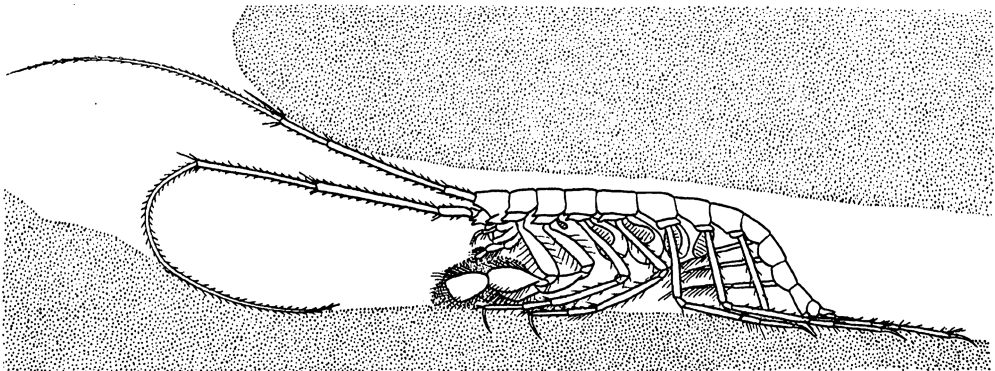


Figure 2. Enequist kept *Neohela monstrosa* in aquarium and published this drawing with the following text: '*Neohela monstrosa* shovelling mud out of its burrows' (copied from Enequist 1949).

Samples and observations from the MAREANO mapping programme

Neohela monstrosa was recorded from 22 stations in the area mapped by MAREANO in the period 2006–2009 (Figure 3; Table 1) as part of wider surveys of the deep-sea habitats and benthic fauna. It was recorded on video at 13 stations, in beam trawls at five stations, by

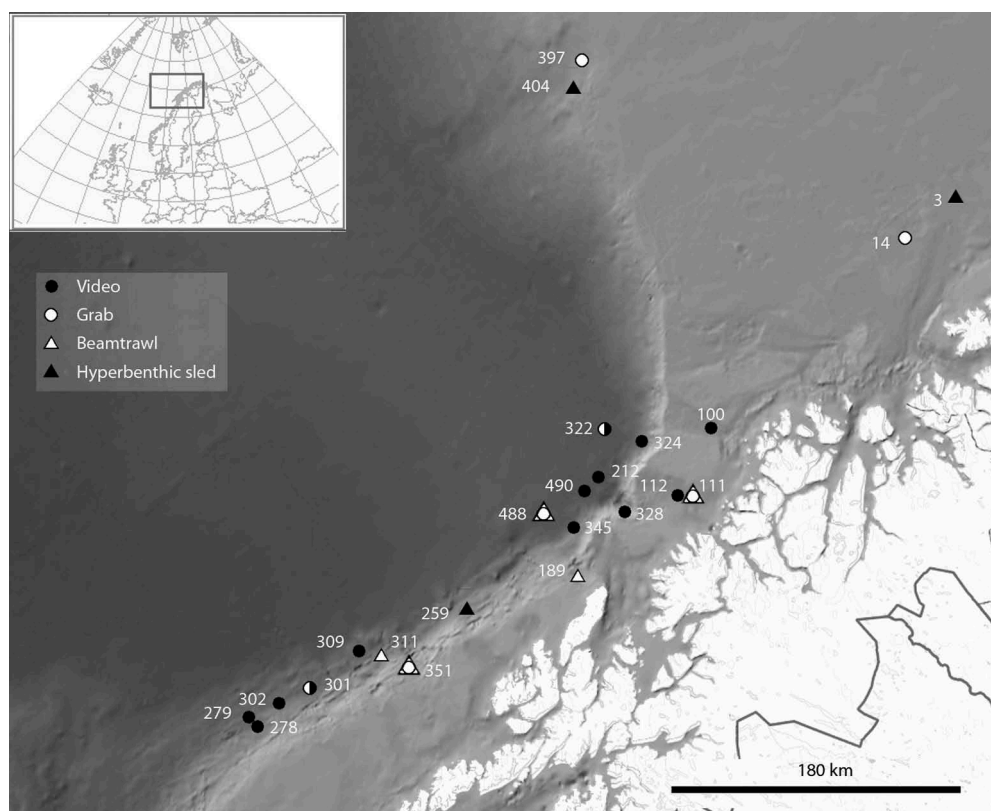


Figure 3. Position of localities where *Neohela monstrosa* was sampled or observed in the material from MAREANO (marine area database for Norwegian waters), period 2006–2009 (for detailed information see [Table 1](#)).

epibenthic sled at three stations and in seven grab samples. This material was used to estimate the density of *N. monstrosa* both in larger areas and in densely populated smaller patches. Observations of behaviour were from close-up video records.

At each site, seabed video was recorded with a high-definition video camera along 700-m-long transects using the towed video platform 'CAMPOD'. It was towed behind the survey vessel at a speed of 0.7 knots with a near-constant altitude of 1.5 m above the seabed, controlled by a winch operator. Geopositioning for the video data was provided by a hydroacoustic positioning system (Simrad HIPAP and Eiva Navipac software) with a transponder mounted on CAMPOD, giving a position accurate to 2% of water depth. All organisms were identified to the lowest possible taxon and counted, or quantified as % seabed coverage following the method described by Mortensen and Buhl-Mortensen (2005). Abundance data (the number of organisms counted divided by the area observed) were standardised as the number of individuals per 100 m² (Mortensen et al. 2009; Dolan et al. 2009).

Neohela monstrosa specimens were collected as part of samples for documentation of the infauna using a large Van Veen grab (0.2 or 0.25 m²). Samples were gently washed over a 1-mm sieve. Epifauna was sampled by beam trawl (mesh size 2 mm, 2 m opening width, 5 min hauls; see Bergman et al. 2009 for gear description) and

Table 1. Information on video from MAREANO and SERPENT, and samples from MAREANO including station number or name, position, depth and bottom temperature.

Station	Equipment	Longitude	Latitude	Depth (m)	Temp (°C)
MAREANO					
189	BT	15.7340	69.3834	891	
311	BT	12.6728	68.9004	1316	−0.8
14	Grab	21.7435	71.1135	186	5.7
397	Grab	15.9409	72.2476	637	4.5
111	Grab, BT	17.6254	69.7966	367	6.5
351	Grab, BT	13.0950	68.8436	805	
488	Grab, BT	15.1901	69.7131	2192	−0.9
3	Sled	22.4142	71.3312	421	5.0
259	Sled	13.9750	69.1841	1912	
404	Sled	15.7689	71.9213	624	4.8
100	Video	18.0215	70.1548	317	7.0
112	Video	17.4278	69.8177	409	
212	Video	16.1393	69.9174	1817	
278	Video	10.8435	68.5245	1587	
279	Video	10.6814	68.5494	2044	
302	Video	11.1126	68.6330	1903	
309	Video	12.3040	68.9213	1950	
324	Video	17.0874	70.1421	583	
328	Video	16.4802	69.7389	872	
345	Video	15.5777	69.5622	1850	
490	Video	15.8957	69.8457	2181	
301	Video, grab	11.6165	68.7126	1919	
322	Video, grab	16.1762	70.2048	2008	
SERPENT					
Asterix	Video	5.29	67.02	1340	−0.84
Gro	Video	3.94	66.15	1380	−0.95
Dalsnuten	Video	3.54	66.57	1452	−0.83
Edvarda	Video	4	64.2	1730	~−0.5
Haklang	Video	7.059	67.047	1250	−0.94

Note: BT, beam trawl; MAREANO, marine area database for Norwegian waters; SERPENT, scientific and environmental ROV partnership using existing industrial technology.

hyperfauna was sampled with an Rothlisberg and Percy-sled (mesh size 0.5 mm, 1 m opening width, 10 min hauls; see Rothlisberg and Percy 1977 and Buhl-Jensen 1986 for a description). Sampled fauna was fixed in 5% buffered formalin until sorting and identification in the laboratory.

Observations from the SERPENT project

Additional video data were available south of the MAREANO survey area through the SERPENT Project. Video transect surveys were carried out using ROVs (Oceaneering Magnum) launched from drilling rigs at five hydrocarbon exploration locations in the Norwegian Sea between 1250 and 1730 m depth (Table 1). Video-transect surveys comprised eight transects of 100–200 m in length radiating from the well centre and recorded in standard definition. The locations of these surveys were disturbed by drill cuttings (Gates and Jones 2012). The standard-definition video data were of insufficient quality to confidently calculate the density of *N. monstrosa* from the SERPENT ROV video transects, but estimates of abundance of burrows were determined. At each location, high-resolution digital stills photography (Kongsberg OE14–208) was used to document benthic megafauna (Jones and Gates 2010). These images were collected opportunistically during ROV operations.

The movements of the antennae of *N. monstrosa* were observed on 5 minutes long standard definition video clip recorded at 1340 m depth at the Asterix exploration drilling site in the Norwegian Sea in an area disturbed by drill cuttings.

Results

The *Neohela* species group is under taxonomic revision and a new species has recently been described Udekem d’Acoz (2007). Udekem d’Acoz (2007, p. 33) states that ‘In literature, *N. monstrosa* has been recorded down to 2222 m (Sars 1895) but all records below 700 m should be considered as very suspect and could refer to *N. lamia* sp. nov. or even additional new species’.

Habitat

Within the study area, *N. monstrosa* has a depth range from 22 to 2167 m in arctic–boreal waters (bottom temperatures varying between –0.94 and +6.95°C), and the substratum is dominated by mud or sandy mud (Tables 2 and 3). On the slope at 700–1000 m depth it co-occurs with the sea pen *Umbellulla encrinus* Linnaeus, 1758 (Cnidaria: Pennatulacea), forming a sea pen and burrowing fauna habitat resembling the shallower *Funiculina* Lamarck, 1816 – *Nephrops* Leach, 1814 habitat, a common variety of the habitat ‘seapen and burrowing megafauna communities’ listed as one of the threatened and/or declining habitats by Oslo-Paris (OSPAR) convention (OSPAR Commission 2008).

Table 2. Densities of *Neohela monstrosa* per 100 m² from video observations, together with depth and sediment quality. Percentage of surface cover is estimated from video.

Video Transect station	Neohela ind/100 m ²	Depth (m)	Surface sediment composition (%)					
			Mud and sandy mud	Sand	Pebble	Cobble	Boulder	Bedrock
MAREANO								
100	0.2	317	15.0	85.0				
112	0.5	409	60.0	40.0				
324	0.2	583	11.6	74.1			13.8	0.4
328	0.2	872	85.3			0.3	0.6	13.8
278	0.1	1587	73.0	22.3		4.1	0.5	
212	0.1–0.3	1817	98.0			2.0		
345	0.2	1850	100.0					
302	0.2–0.5	1903	92.0	8.0				
301	0.3–4.0	1918	100.0				0.1	
309	0.3–0.5	1950	81.6		12.0	4.0	2.4	
322	1.4–2.9	2010	91.3	8.1	0.4	0.1		
279	0.1	2044	99.3			0.8		
490	1.7	2181	95.9		0.4	2.3	1.4	
SERPENT								
Asterix	2.2	1340	100					
Gro	0.11	1380	100					
Dalsnuten	0.5	1452	100					
Edvarda	5.11	1730	95				5	

Note: MAREANO, marine area database for Norwegian waters; SERPENT, scientific and environmental ROV partnership using existing industrial technology.

Table 3. Density of *Neohela monstrosa* on sampling stations per 100 m² from epibenthic sled and beam trawl and per m² from grab samples, together with information on depth and temperature.

Station no.	Neohela	Depth	Temp.
Epibenthic sled	(ind/100 m ²)	(m)	(°C)
3	0.47	432	5.0
404	0.98	623	4.8
259	0.12	1899	
Beam trawl	(ind/100 m ²)	(m)	(°C)
111	0.22	367	6.5
189	1.22	881	
311	12.31	1330	−0.8
351	0.53	730	
488	0.29	2241	−0.9
Van Veen grab	(ind/m ²)	(m)	(°C)
14	16	221	5.7
100	8	323	7.0
100	8	323	7.0
111	4	366	6.5
111	4	365	6.5
301	5	1935	
301	10	1937	
322	5	1999	
351	35	765	
351	15	765	
351	5	765	
397	4	636	4.5
488	4	2167	−0.9

Abundance

Based on counting of observed amphipods within 200-m-long video transect sequences, the density varies between < 1 and up to 4 per 100 m² (Table 2). Results from beam trawl and epibenthic sled samples provide slightly higher density ‘estimates’ up to 12 individuals per 100 m² for larger areas (Tables 2 and 3). Local-scale observations from video and grab samples, however, showed that *N. monstrosa* often forms densely populated patches or colonies of 10–35 individuals/m². Clearly, density estimates based on long video sequences or hauls with beam trawl or epibenthic sled represent minimum estimates while video close-ups and grab samples from patches reveal local densities that are up to 10 times higher.

Video results from frame grabs showed that *N. monstrosa* is patchily distributed. Counting the burrows within areas where *N. monstrosa* has been observed revealed that the normal patch size varies in spatial extent between 10 and 30 m (Figure 4). Typically, a densely populated area consisted of a mixture of small and large burrows, presumably belonging to individuals of different sizes (Figure 5).

The density of *N. monstrosa* burrows at the five SERPENT sites is shown in Table 2. Inspection of burrows with close-up video footage and still photography showed *N. monstrosa* were present in the burrows at four of the five locations. At Asterix, the closest *N. monstrosa* burrow was 94 m from the well, compared to cerianthids which were found less than 40 m away. Other epibenthic megafauna common at the sites where *N. monstrosa* were present include cerianthids and the asteroid *Pontaster tenuispinus* (von Düben & Koren, 1846) (at all five sites), large numbers of ophiuroids at Asterix

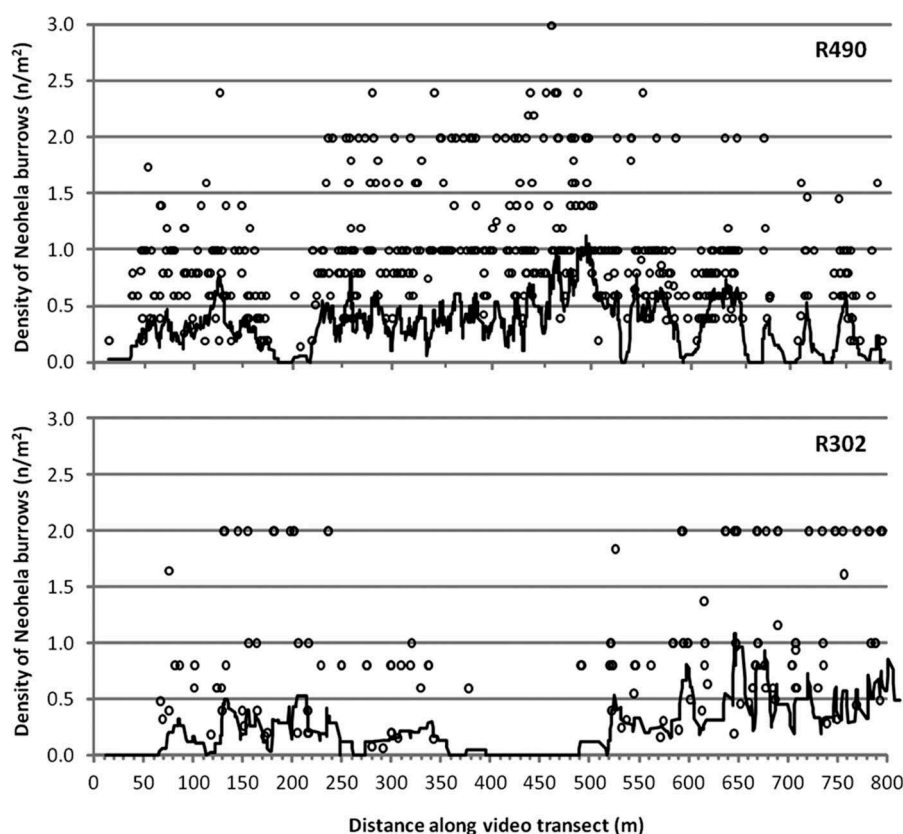


Figure 4. Density of small burrows most likely representing *Neohela monstrosa* along the video lines from stations 490 and 302. Patches are indicated by separate peaks in abundance. The solid lines in the plots of two selected stations represent a moving average. These two stations did not have the highest density of amphipod observations, but numerous small burrows useful for estimating patch sizes.

and Gro [collected specimens were identified as *Ophiocten gracilis* (G.O. Sars, 1871)] and the glacial eelpout (*Lycodes frigidus* Collett, 1879).

Tunnel description and behavioural observations

The burrows often have a funnel-shaped upper part, 3–10 cm wide, with a horizontal side burrow occurring a couple of centimetres below the surrounding seabed surface (Figures 6a–c). We observed *Neohela* pushing and rolling sediment balls, which seem to be kept together by amphipod ‘silk’, out of its burrow (Figures 7a–c). This was done primarily using the large shovel-like gnathopods. From the video observations, it is clear that the normal position for *Neohela* is in the opening of its burrow. The video observations at Asterix of a specimen in this position showed a constant waving and sweeping motion of the second antennae, sometimes alternating the left and right sides, other times simultaneously (Figure 8a and b), while the first antennae remain in

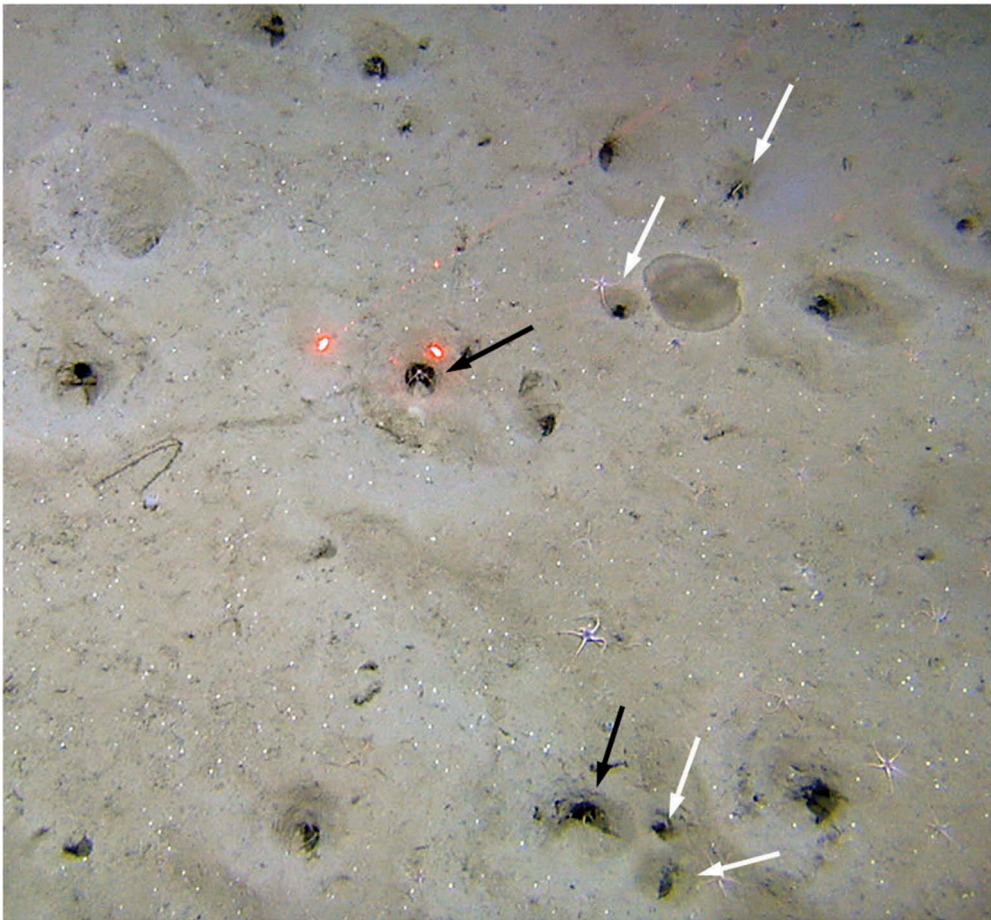


Figure 5. Typical distribution of *Neohela monstrosa* burrows in a densely populated area. The photo from a video transect at station 301 at 1935 m depth shows ~15 burrows made by small (white arrows) and large (black arrows) individuals. Scale is indicated by two laser spots that are 10 cm apart.

a more upright position, and it often sweeps the antennae along the sediment surface, which may draw collected particles towards the mouth.

When disturbed by the presence of an ophiuroid arm, the specimen retreated rapidly a short distance inside the burrow. In a period of approximately 2 minutes 40 seconds, the specimen completed seven sweep motions with the second antennae (counted on the animal's right side) between two disturbances (ophiuroid arm and sediment tumbling into burrow).

Discussion

Distribution and abundance

Identification of *Neohela* specimens to the species level from from *in situ* video records is challenging because of the small morphological details necessary for identification. However, close-up footage of the organisms suggested the genus *Neohela*, and the



Figure 6. A common position for *Neohela monstrosa* is in the opening of the burrow; (a, b) show the amphipod holding a ball of mud between the gnathopods. c. A burrow with antennae extending from a side tunnel.



Figure 7. A *Neohela monstrosa* digging out sandy mud from its burrow. In sequence, the photos show movement of a sediment ball from the bottom of the burrow (a) to the edge (c). Photos are taken from a MAREANO video record (see Supplemental material).

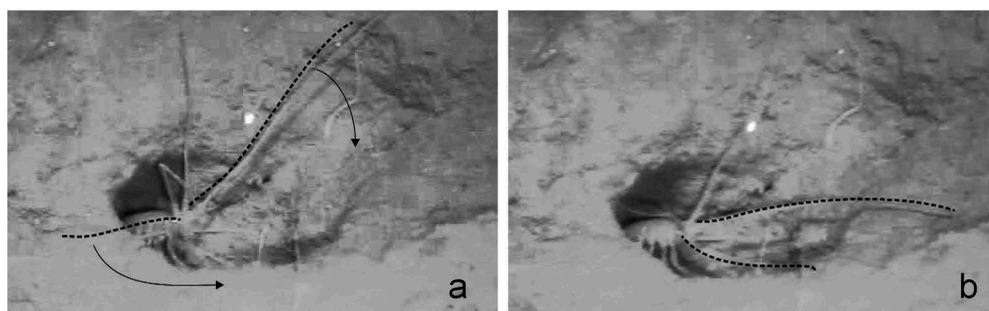


Figure 8. *Neohela monstrosa* waving the second antennae in a sweeping motion while the first antennae remain in a more upright position. Movement is indicated with arrows, and the position of the second antennae is indicated with a dotted line (from video observations at Asterix; see Supplemental material).

sizes of the burrows and specimens observed are too large to represent *N. lamia* (Udekem d'Acoz pers. comm.). Furthermore, the sampled specimens were all identified as *N. monstrosa* in all cases. Thus, we are convinced that the specimens observed on video are *N. monstrosa*. An additional area of uncertainty is whether or not all the small burrows in an area are made by this amphipod, or whether they are still inhabited, which cannot be determined without sampling.

Table 4. Density estimates for *Neohela monstrosa* based on different sampling gears from the same MAREANO (marine area database for Norwegian waters) station.

Stations	Grab (ind/m ²)	Beam trawl (ind/100 m ²)	Video (ind/100 m ²)
301	5–10		0.31–4.03
322	5		1.35–2.89
351	5–35	0.53	
488		0.29	4

Our data highlight the importance of multiple approaches to sampling the deep sea. Epibenthic sleds and beam trawls alongside photographic and video methods are important to describe the benthic megafaunal invertebrate assemblage (Table 4). *N. monstrosa* digs deep burrows, and density estimates based on sled and beam trawl samples that accumulate organisms mainly from the sediment surface from long tows (400 m) will represent minimum values that underestimate densities. In contrast, at some locations the large numbers of *N. monstrosa* that were sampled by Van Veen grab (covering 0.2–0.25 m²) suggest densely populated small patches; thus, information from video analysis that allows for patch identification and calculation of burrows proved the most reliable estimate of density.

In the densest patches, *Neohela* was present with 15–36 individuals per 100 m², and the sizes of burrows indicated inhabitants of varying size. The upper part of the burrows reaches several centimetres into the sediment and often has a side burrow (Figure 6c). According to Enequist (1949), the side burrow can easily be 10 cm or more in length; thus, when occurring in dense populations, as observed in the Norwegian Sea, *N. monstrosa* must be an important bioturbator that could increase surface layer, irrigation and oxygenation at depth.

Behavioural observations

Video documentation is an effective method to collect *in situ* behavioural information that is an important supplement to the thorough aquarium observations made by Enequist (1949). The digging behaviour of *N. monstrosa* was earlier observed in aquaria by Enequist (1949), who noted that it was simultaneously reworking the sediments with its mouthparts when pushing out sediment. He also noted that *N. monstrosa* could dig a ~2-cm-deep hole quickly, from which a horizontal burrow was built. One day's digging activity resulted in a 10-cm-long burrow that often had two openings. However, our observations could not support the existence of the two openings to the burrow as observed by Enequist, which we believe may be an artefact from keeping this deep-sea species in an aquarium for observations.

The burrow-digging primarily using the large shovel-like gnathopods confirms the aquarium observations made by Enequist (1949). In addition, our observations show that the sediment is pushed out as mud balls that seem to be kept together by amphipod 'silk'. Glands for production of amphipod 'silk' for the purposes of nest-building are common among species in the superfamily Corophioidea (Kronenberg et al. 2012) to which Unciolidae belongs. These glands that are positioned in the bases of pereopods

3–4 and open through pores at the tips of the dactyls are considered to be a major evolutionary innovation of corophiideans (Myers and Lowry 2003).

Neohela monstrosa is typically seen with the head in the opening of the burrow and antennae widely spread. Enequist also noted this position at the burrow entrance and reported that the pleiopods are not used to ventilate the burrow. Our observations showed *N. monstrosa* often sweeps the antennae along the sediment surrounding its burrow, probably drawing collected particles towards its mouth, indicating that the amphipod feeds by collecting newly settled organic-rich particles from the sediment surface. This is in line with a suggestion by Enequist (1949) who believed that the digging of a burrow was not part of a feeding process, and noted that the pleiopods are not used to ventilate the burrow and that the amphipod is mainly positioned in the entrance.

The burrow appears to be important for protection for this large amphipod species, similar to what has been suggested for the burrowing decapod *Nephrops norvegicus* (Rice and Chapman 1971) that easily could fall prey to demersal fish species like the Glacial eelpout (*Lycodes frigidus*; Figure 9). *Neohela monstrosa* has been found in stomachs of Longfin hake (*Phycis chesteri*) off Atlantic USA (Sedberry and Musick 1978) and in Cod (*Gadus morhua*) stomachs from the Gulf of Saint Lawrence (Sainte-Marie and Brunel 1985). The burrow might also provide important protection for newly released juveniles. Amphipods are brooders and release the juveniles from a brood chamber looking like miniature adults. Many amphipods protect their offspring, either in their burrows or on their antennae. The newly released juveniles are very vulnerable and maternal care seems to be essential (Thiel 1998). The video records show that the burrows occur in different sizes that correspond to the size of the inhabitant (see Figure 7); presumably it is a demanding task to build and sustain a burrow, and newly released juveniles probably stay in the mother's burrow, as has been observed for other domicolous amphipod species (Thiel 1998).

Anthropogenic disturbance

Neohela monstrosa is present in habitats subject to anthropogenic disturbance from oil and gas exploration. At drilling locations, our observations showed reduced abundance close to the well, in line with previous studies of benthic megafauna from the deep

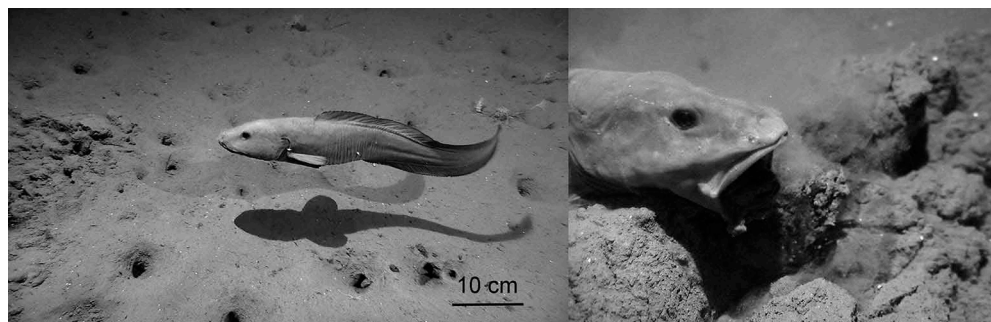


Figure 9. Glacial eelpout (*Lycodes frigidus*) is often observed in the same habitat as dense populations of *Neohela monstrosa* and may represent an important predator from which the latter has to hide in its burrow.

Norwegian Sea (Gates and Jones 2012). It is important that the efforts are made to improve the understanding of the behaviour and local-scale variability of deep-sea species in areas undergoing anthropogenic impacts, especially as industries move into deeper and less explored areas. The abundance of burrows encountered at these sites was undoubtedly reduced by drill cuttings. At Asterix, the closest *N. monstrosa* burrow was 94 m from the well, compared to cerianthids which were found less than 40 m away. Background studies would show greater abundance because cuttings deposition significantly reduces megafaunal abundance (Gates and Jones 2012).

In conclusion

- *Neohela monstrosa* occur in patches with a density that can reach 15–36 individuals per m² on mud or sandy mud bottoms at 200–2181 m depth off Northern Norway.
- The locally high density of *N. monstrosa* together with its habit of making deep and long burrows indicates that it is a major bioturbator.
- *Neohela monstrosa* normally is positioned in the opening of its burrow, which is used for protection against predators, where it feeds on newly settled detritus that it collects from the surface sediment through the use of its long antennae.

Acknowledgements

The MAREANO programme (www.mareano.no) which is supported by the Norwegian Ministry for the Environment and the Ministry of Trade, Industry and Fisheries provided unpublished data from samples and videos. SERPENT, which is supported by hydrocarbon exploration companies detailed at www.serpentproject.com/part.php, provided ROV observations. SERPENT thanks Kerstin Kröger for assistance with survey work at sea.

Disclosure statement

No potential conflict of interest was reported by the authors.

Supplemental material

Supplemental material for this article can be accessed here: <http://dx.doi.org/10.1080/00222933.2015.1062152>

References

- Bergmann M, Soltwedel T, Klages M. 2011. The interannual variability of megafaunal assemblages in the Arctic deep sea: preliminary results from the HAUSGARTEN observatory (79°N). *Deep-Sea Res I*. 58:711–723.
- Bergmann MJN, Birchenough SNR, Borja Á, Boyd SE, Brown CJ, Buhl-Mortensen L, Callaway R, Connor DW, Cooper KM, Davieas J, et al. 2009. Guidelines for the study of the epibenthos of subtidal environments. Copenhagen: International Council for the Exploration of the Sea. (ICES Techniques in Marine Environmental Sciences No. 42.) 88 pp.
- Buhl-Jensen L. 1986. The benthic amphipod fauna of the west-Norwegian continental shelf compared with the fauna of five adjacent fjords. *Sarsia*. 71:193–208.
- Buhl-Mortensen L. 1996. Amphipod fauna along an offshore-fjord gradient. *J Nat Hist*. 30:23–49.

- Buhl-Mortensen L, Vanreusel A, Gooday AJ, Levin LA, Priede IG, Buhl-Mortensen P, Gheerardyn H, King NJ, Raes M. 2010. Biological structures as a source of habitat heterogeneity and biodiversity on the deep ocean margins. *Mar Ecol.* 31:21–50.
- Collett R. 1879. On a new Fish of the Genus *Lycodes* from the Pacific. *Proc Zool Soc London* 47:381–382.
- Dolan MFJ, Buhl-Mortensen P, Thorsnes T, Buhl-Mortensen L, Bellec VK, Bøe R. 2009. Developing seabed nature-type maps offshore Norway: initial results from the MAREANO programme. *Norw J Geol.* 89:17–28.
- Enequist P. 1949. Studies on the soft-bottom amphipods of the Skagerak. *Zoologiska Bidrag Från Uppsala.* 28:295–492.
- Gates AR, Jones DOB. 2012. Recovery of Benthic Megafauna from Anthropogenic Disturbance at a Hydrocarbon Drilling Well (380 m Depth in the Norwegian Sea). *PLoS One.* 7:e44114.
- Jones DOB, Gates AR. 2010. Deep-sea life of Scotland and Norway. Southampton (UK): Ophiura press; p. 80 pp.
- Kronenberg K, Moore PG, Halcrow K, Vollrath F. 2012. Spinning a marine silk for the purpose of tube-building. *J Crustacean Biol.* 32:191–201.
- Lincoln RJ. 1979. British marine Amphipoda: Gammaridea. London: British Museum (Natural History); 657 p.
- Miskov-Nodland K, Buhl-Mortensen L, Høisæter T. 1999. Has there been a fauna change in the Skagerrak?: a comparison of the present amphipod fauna with observations from 1933/37. *Sarsia.* 84:137–155.
- Mortensen PB, Buhl-Mortensen L. 2005. Coral habitats in The Gully, a submarine canyon off Atlantic Canada. In: Freiwald A, Roberts JM, editors. Cold-water corals and ecosystems. Berlin: Springer-Verlag; p. 247–277.
- Mortensen PB, Buhl-Mortensen L, Gebruk AV, Krylova EM. 2008. Occurrence of deep-water corals on the Mid-Atlantic Ridge based on MAR-ECO data. *Deep-Sea Res II.* 55:142–152.
- Mortensen PB, Dolan MFJ, Buhl-Mortensen L. 2009. Prediction of benthic biotopes on a Norwegian offshore bank using a combination of multivariate analysis and GIS classification. *ICES J Mar Sci.* 66:2026–2032.
- Myers A, Lowry J. 2003. A Phylogeny and a New Classification of the Corophiidea Leach, 1814 (Amphipoda). *J Crustacean Biol.* 23:443–485.
- OSPAR Commission. 2008. OSPAR list of threatened and/or declining species and habitats. Reference number 2008–6.
- Purser A, Thomsen L, Barnes C, Best M, Chapman R, Hofbauer M, Menzela M, Wagner H. 2013. Temporal and spatial benthic data collection via an internet operated Deep Sea Crawler. *Methods Oceanogr.* 5:1–18.
- Rice AL, Chapman CJ. 1971. Observations on the burrows and burrowing behaviour of two mud-dwelling decapod crustaceans, *Nephrops norvegicus* and *Goneplax rhomboides*. *Mar Biol.* 10:330–342.
- Rothlisberg PC, Percy WG. 1977. An epibenthic sampler used to study the ontogeny of vertical migration of *Pandalus jordani* (Decapoda, Caridea). *Fishery Bull Natl Oceanic Atmos Adm US.* 74:994–997.
- Sainte-Marie B, Brunel P. 1985. Suprabenthic gradients of swimming activity by cold-water gammaridean amphipod Crustacea over a muddy shelf in the Gulf of Saint Lawrence. *Mar Ecol Prog Ser.* 23:57–69.
- Sars GO. 1871. Nye Echinodermer fra den norske Kyst. *Vidensk. Selsk. Forhandl. Christiania.*
- Sars GO. 1895. An account of the Crustacea of Norway. Volume 1. Amphipoda. Parts 1 and 2, 248 pls. Christiania, Bergen: Cammermeyer; 730 pp.
- Sedberry GR, Musick JA. 1978. Feeding strategies of some demersal fishes of the continental slope and rise off the Mid-Atlantic Coast of the USA. *Mar Biol.* 44:357–375.
- Stephensen K. 1933. The Godthaab expedition 1928. Amphipoda. *Meddelelser om Grønland.* 79:1–88.
- Thiel M. 1998. Extended parental care in marine amphipods. I. Juvenile survival without parents. *J Exp Mar Biol Ecol.* 227:187–201.

- Udekem d'Acoz CD. 2007. The genera *Haliragoides* and *Neohela* in the North Atlantic, with the description of two new deepwater species from Norway and Svalbard (Crustacea: Amphipoda). *Cahiers de Biologie Marine*. 48:17–35.
- von Düben MW, Koren J. 1846. Öfversigt af Skandiniaviens Echinodermer [Overview of Scandinavian Echinodermata]. *Kungl Svenska Vetenskapsakademiens Handlingar* 1844. 229–328, plates VI–XI.