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Rapid Communication

New kid on the block: first record of juvenile American lobster, *Homarus americanus* H. Milne Edwards, 1837, in European waters

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Abstract

A juvenile American lobster, *Homarus americanus,* H. Milne Edwards, 1837, was recorded for the first time in European waters in August 2019, with the capture of a single early benthic phase specimen during surveys along the North East England coast. Identification was determined by a combination of morphological and molecular approaches. The record raises serious questions of whether the species is now breeding in the region, with associated implications for its invasiveness. The mechanisms of introduction, invasion status, risks to native shellfisheries, and directions of future study are discussed.

Key words: invasive species, United Kingdom, reproducing, breeding, North Sea, benthic

Introduction

Native to the northwest Atlantic coast, the American lobster, *Homarus americanus*, H. Milne Edwards 1837, is an introduced species in Europe (CABI 2019). The main vector of introduction is the importation of live lobster for consumption – over 13 metric tons was imported into Europe from America and Canada in 2019. This inevitably leads to illegal or accidental releases and escapes from holding facilities (SwAM 2016).

To date, adult *H. americanus* have been found in the wild in many European countries, such as Norway, Sweden, Ireland, England, Croatia, Iceland, and France (Stebbing et al. 2012a; van der Meeren et al. 2010; Pavičić et al. 2020). In the UK, American lobster was first recorded in 1988, with 26 reports up to 2011, and a further 162 to 2018 (136 of which were recovered from a mass release of 361 individuals off Brighton as part of a religious ceremony in 2015) (Stebbing et al. 2012a; Barrett et al. 2020).

Evidence of *H. americanus* becoming established and breeding in European waters is less clear, and primarily consists of hybrid offspring reported in

Sweden and England, where larvae from berried *H. americanus* females were identified genetically (Øresland et al. 2017; Barrett et al. 2020; Ellis et al. 2020). Berried *H. americanus* females carrying unhybridized eggs have also been reported in England, but it is unclear whether breeding had occurred locally, or before or during transport or holding (Jørstad et al. 2011; Stebbing et al. 2012a; Barrett et al. 2020). There is currently no evidence of larval or juvenile *H. americanus* occurring or surviving in the wild in the UK.

Concern over the possible establishment of *H. americanus* in European waters stems from the clear threat to the native European lobster, *Homarus gammarus* (Linnaeus, 1758), and the fisheries it supports. Landings of *H. gammarus* by UK vessels exceeded 3,400 tons in 2019, worth over £46 million. These two lobster species occupy similar niches, sharing habitat preferences and diets (SwAM 2016). *Homarus americanus* has a competitive advantage, due to its larger size, greater aggression, and higher fecundity (van der Meeren et al. 2010). They have been observed to prey upon *H. gammarus* in the wild (Øresland et al. 2017). There are additional threats of contagious diseases such as Gaffkaemia and Epizootic Shell Disease, which *H. americanus* can carry and spread to *H. gammarus* (Stebbing et al. 2012b; Davies and Wootton 2018).

Actions to reduce the threat to *H. gammarus* to date include a ban on live American lobster imports into Norway, and a call by the Swedish Government for the European Commission to ban live imports more widely. In the UK, the threat is acknowledged by the classification of "priority species" by the GB Non-Native Species Secretariat, and the launch of a recent campaign by CEFAS to encourage fishermen and the public to report sightings, with the aim of increasing knowledge on the status (CEFAS 2020).

This paper presents the first record of a wild-caught juvenile *H. americanus* in UK waters, which raises serious questions of whether the species is now breeding in the region, with associated implications for its invasiveness.

Materials and methods

A juvenile American lobster was collected off the coast of Sunderland, North East England (54°56.536N; 001°16.599W) in August 2019 (Figure 1). The specimen was collected during benthic monitoring surveys by Van Veen grab (0.01m^2), at a depth of 38.4 m, in medium silt. The sample was sieved on-board with a 0.5 mm mesh sieve, and residual sediment containing macrofauna was immediately fixed in 10% phosphate buffered formalin. The macrofauna samples were transported to the Benthic Solutions Ltd taxonomy laboratory for analysis where they were transferred to 70% industrial methylated spirit during laboratory processing and species identification. Morphological features used to taxonomically identify

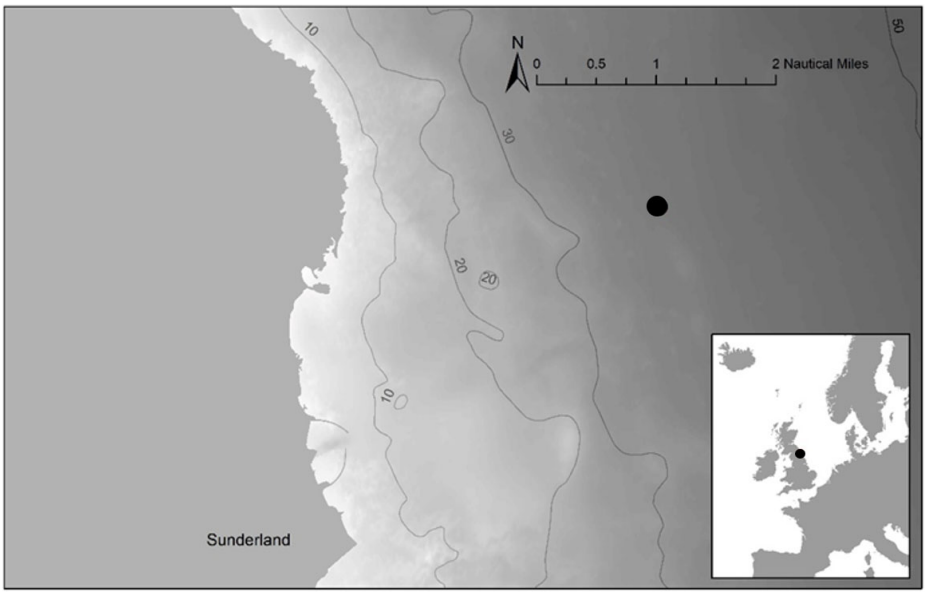

Figure 1. Capture location of *Homarus americanus* juvenile specimen from muddy sediment off the coast of Sunderland (indicated by filled dot). Coordinates: 54°56.53800N; 001°16.59900W.

H. americanus and distinguish the American lobster from the congeneric European lobster *H. gammarus* are normally based on colour patterns in adult individuals and the presence of one or more spines on the ventral surface of the rostrum (Holthuis 1991; Factor 1995). Despite considerable information available on the morphology of young *Homarus* lobsters (Charmantier et al. 1991), it remains difficult to make a positive identification of juvenile specimens of *H. americanus* solely based on taxonomic features. Indeed, larval and young lobsters undergo morphological developmental stages before they reach maturity and display the distinguishing characters typical of mature specimens (Factor 1995). Even on adult individuals, the reliability of taxonomic methods to correctly identify *H. americanus* is considered debatable (Stebbing et al. 2012a). Therefore, upon primary visual identification, the juvenile American lobster specimen was retained, measured, and photographed, before being digested for molecular species identification.

The whole lobster sample was initially homogenised in sufficient G2 lysis buffer (Qiagen) and Proteinase K to provide a 10% w/v homogenate, and was digested for 3 hours at 56 °C. A further lysis step was later undertaken using 350 µl Qiagen ATL buffer, 42 µl 0.5 M EDTA and 20 µl Proteinase K, incubated overnight at 65 °C, with the resultant homogenate treated with 6µl RNase A for 30 minutes at 37 °C. To maximize the prospects of obtaining DNA compatible for downstream analysis, genomic DNA was then isolated from this digest via two methods; a salting-out (SO) protocol (Jenkins et al. 2018) and a phenol chloroform isoamyl alcohol (PCI) protocol (Sanbrook et al. 1989). These methods yielded 1.87 µg and 1.92 µg of DNA, respectively, each eluted to a 25 µl solution.

Genomic DNA was genotyped at 26 single nucleotide polymorphism (SNP) loci (Jenkins et al. 2018), which provide powerful species assignment

Figure 2. Juvenile specimen of American lobster (*Homarus americanus*) collected off the coast of North East England. Poor condition of specimen due to sample undergoing sieving and preservation in Formalin prior to specimen discovery. Photo by A. Lodola.

in *Homarus* and *Nephrops* (Ellis et al. 2020). Genotyping and scoring of SNPs was carried out on a Fluidigm EP1 platform following the protocol of Jenkins et al. (2019), except that the genotyping array chip used was a Fluidigm Flex Six IFC. Three units of the Fluidigm Flex Six IFC were used, each of which screens 12 individuals across 12 SNP assays. In each unit, DNA from both extraction methods of the target specimen were run, alongside species controls of 2x *H. gammarus*, 2x *H. americanus* and a *H. americanus x gammarus* hybrid, all of which had known genotypes (Ellis et al. 2020), and 4x *Nephrops norvegicus*, whose genotypes were unknown, as well as a negative control. The multilocus genotypes of these test samples were supplemented by data from 147 other individuals from these four clawed lobster taxonomic groups (Ellis et al. 2020; Jenkins et al. 2019), and the software Snapclust (Beugin et al. 2018) was used to calculate maximum-likelihood estimations of their membership probabilities under expectations of four genetic clusters (k = 4), as executed in the adegenet v2.1.3 package (Jombart and Ahmed 2011) in R (R Core Team 2020).

Results

The juvenile lobster measured 12 mm in total length with 4.5 mm carapace length, likely making this a recently settled post-larva of one of the first benthic lifestages (i.e. instar IV–VI). The specimen did not display any colour pattern due to preservation in formaldehyde and was missing most of its appendages, including all pereopods, whereas it retained most pleopods, all uropods and telson (Figure 2). The main morphological trait which allowed visual recognition of the specimen as *H. americanus* was the presence of one ventral spine on the rostrum (Figure 3). Moreover, this young specimen showed the following distinguishing features of *Homarus* species (Factor 1995) which allowed differentiation from the other Nephropid lobster, *Nephrops norvegicus*, found in UK waters: carapace with distinct median dorsal groove extending from rostrum to posterior margin and without observable sub-dorsal carina, telson slightly narrow distally with posterior

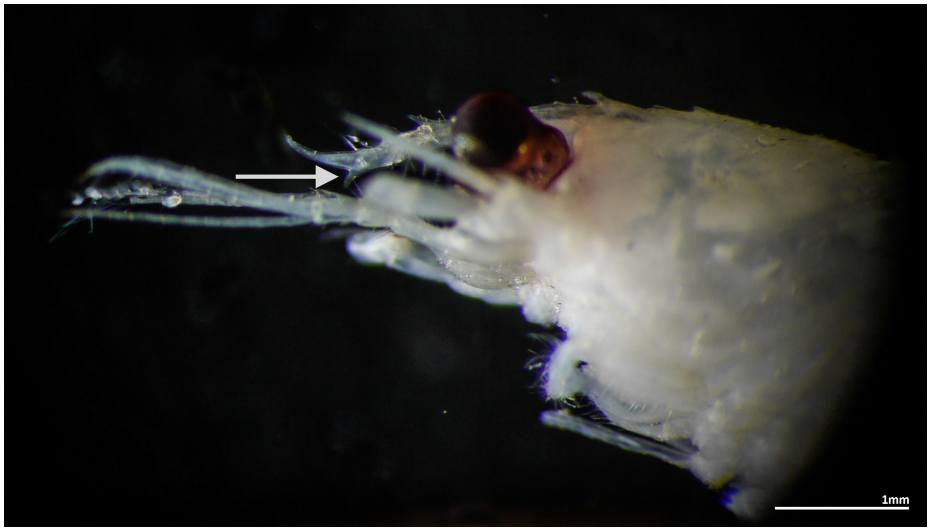

Figure 3. Detail of the ventral spine on the rostrum (indicated by arrow) of the juvenile specimen of *Homarus americanus*. Photo by A. Lodola.

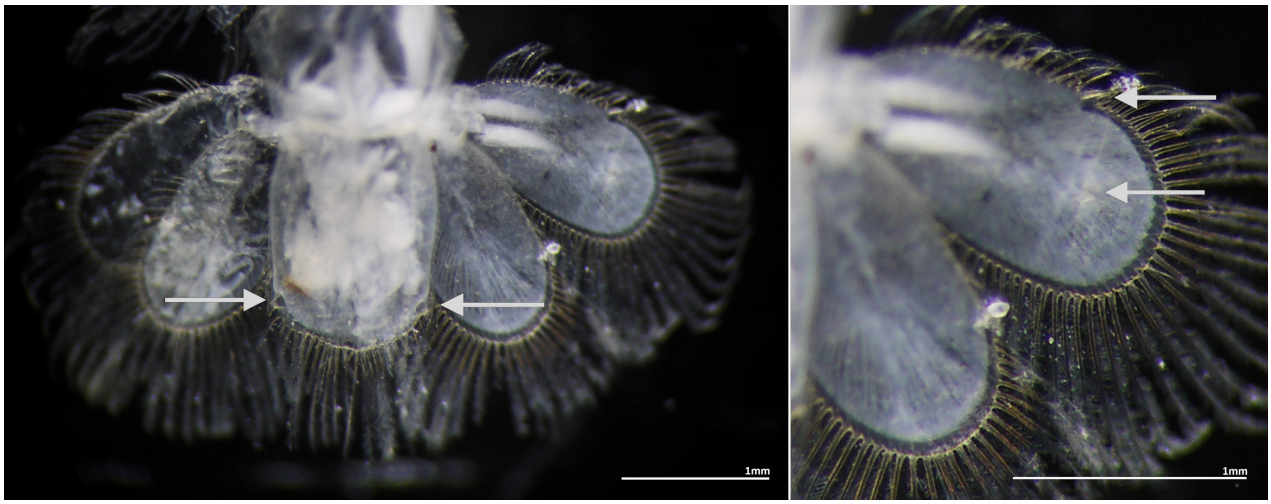

Figure 4. Telson and uropods of the juvenile specimen of *Homarus americanus*. Left, detail of small postero-lateral spines on the telson (indicated by arrows). Right, exopod lateral spine and transverse carina (indicated by arrows). Photo by A. Lodola.

margin convex and with a pair of small postero-lateral spines (Figure 4), uropods oval in shape, bearing a very small distal spine on the outer margin, exopods with a faint transverse carina showing early signs of denticulation (Figure 4).

Despite the propensity for formalin preservation to degrade DNA and inhibit molecular amplification techniques (Koshiba et al. 1993; Do and Dobrovic 2015), the target specimen was successfully genotyped at 23 of the 26 SNP loci, including all 12 of those providing the greatest assignment power to distinguish between the two *Homarus* species (Ellis et al. 2020). Assignment analysis using Snapclust confirmed the specimen as *H. americanus* and was unequivocal in classifying the specimen as belonging to the same cluster as 38 known *H. americanus* individuals included in the analysis, with a membership probability of > 0.99999 to this species group.

Discussion

The specimen described in this study is, to the best of our knowledge, the first early benthic phase *H. americanus* recorded in Europe. Although berried females have been recorded several times in the UK (Barrett et al. 2020), until now there was no evidence of successful transition from eggs to benthic phase. This raises questions about the route of entry for this juvenile, increasing concerns over breeding occurring in UK waters, and possible establishment.

Many previous records of *H. americanus* in the UK have been acknowledged as recent releases due to the presence of banded claws, lack of biofouling, and small geographic spread near to known release sites (Stebbing et al. 2012a). For this juvenile specimen, release at this life stage is implausible. Landing of berried female *H. americanus* is illegal throughout their native range (Jury et al. 2019), and were a landed female to extrude and fertilise eggs at some point during holding, the efficiency of the seafood supply chain seriously limits any prospect of a ~ 9-month developmental period enabling hatching in captivity. Additionally, water treatment requirements from UK holding facilities housing American lobster (Beard and McGregor 2004) should ensure no live larvae reach the sea. Therefore, extrusion and hatching in the wild by a mature *H. americanus* is assumed as the origin of this juvenile. There are two scenarios by which a conspecific spermatophore could have been obtained to enable fertilisation; mating either with a native male prior to capture, or with a fellow introduced male following release in the UK.

Introduced female American lobsters have mated interspecifically in the wild with *H. gammarus* males, creating hybrid clutches (Øresland et al. 2017; Ellis et al. 2020), yet female *Homarus* tend to favour conspecific males regardless of their size and dominance status (van der Meeren et al. 2008). It is possible that two or more adults are present and bred locally, especially since the specimen was found near Sunderland, where an adult was reported in 2017 (Barrett et al. 2020). Alternatively, conspecific mating between our specimen's parents may simply have occurred prior to capture in the USA or Canada; most lobsters typically extrude and fertilise eggs a full year after actually receiving a spermatophore during copulation, and larger lobsters are capable of storing enough sperm from a single mating to fertilise clutches in two successive years (Waddy and Aiken 1990). As such, it is arguably most likely that our *H. americanus* specimen derives from a female who mated in its native range, was legitimately landed while egg development remained internal, and who only extruded and fertilised these eggs following import to the UK, either before or after its release into UK waters.

The discovery of this specimen provides strong evidence that all life stages of *H. americanus* are capable of surviving and settling in local conditions in North East England coastal waters. Evidence of successful larval development

raises concerns over whether introduced *H. americanus* have progressed towards the next phase of invasion, establishment, where the introduced species becomes capable of maintaining a viable and self-sustaining population (Sakai et al. 2001). Many invasive species remain in a lag phase after becoming established and before expansion and spreading (Kowarik 1995). It is possible that this is the case with American lobsters in Europe, with increasing evidence suggesting possible establishment, but remaining at low levels. If *H. americanus* is established, it is thought they would be impossible to eradicate (SwAM 2016). Establishment and expansion of *H. americanus* in the UK has the potential to significantly impact local European lobster fisheries, with major ecological and economic implications if native populations declined. There is also risk to other resident commercial crustacean taxa, such as the edible crab (*Cancer pagurus*) and Norway lobster (*Nephrops norvegicus*), as well as squat lobsters in deeper water (SwAM 2016).

It is likely that there are many more American lobsters present in the UK than are reported, and the true scale of their establishment is unknown. Despite reporting mechanisms in place, and recent education campaigns (CEFAS 2020), it is possible that some fishermen do not report catches of American lobster, either due to the administrative burden or fear of the introduction of additional regulatory restrictions, or a loss of income from having to submit the lobster to the authorities.

The discovery of a single juvenile *H. americanus* is likely to underestimate their actual abundance by an even greater extent, given that early benthic phase lobsters are extremely difficult to locate and study in European waters (Linnane et al. 2001), and are rarely found in grab samples. Most taxonomic surveys of pelagic or benthic environments tend to lack the resolution to identify immature decapods even to genus level, so it is possible that more larvae or juveniles have remained undetected in recent years. Given that this sample was opportunistically collected during a broad benthic grab survey, it seems highly unlikely that there are not more juvenile *H. americanus* in UK waters. It is also noteworthy that this specimen was retrieved from a silt seabed; although native juvenile American lobsters are most abundant in shelter-providing cobble ground (Wahle and Steneck 1991), there is evidence that mud can serve as a recruitment habitat for early benthic phases (Dinning and Rochette 2019), and cohesive fine sediments enabling stable burrow excavation have been previously proposed as a potentially important habitat for settling European lobsters, via mesocosm studies (Howard and Bennett 1979). This ecotype should be further surveyed in the hope of yielding more juvenile *Homarus* sp. in Europe. Emerging environmental DNA survey techniques for inshore waters (e.g., Mynott 2020) offers promise for less invasive and wider monitoring of invasive and native marine species.

Combining morphological features with molecular testing has long been recognized as the best approach for distinguishing American and European

lobsters, and our taxonomic characterisation is both robust and convincing, given that both techniques independently identified this juvenile as *H. americanus*. Although colour patterns can offer a good indication, colour variation and intermediate patterns are known to occur in both species (Jørstad et al. 2007). The key feature often used, the presence of a ventral spine on the rostrum of *H. americanus* (Holthuis 1991), is also not completely diagnostic due to the occasional occurrence of this feature in European and hybrid lobsters (Devescovi and Lucu, 2000; Jørstad et al. 2007), or its absence in American lobsters (Ellis et al. 2020). Molecular testing is therefore pivotal in achieving positive and confident identification of *H. americanus*, particularly in juveniles, where morphological features are often lacking or underdeveloped. However, it is important to remain vigilant when working with juvenile Nephropid lobsters, as early recognition of something unusual is key to allow for further testing as performed in this study.

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Authors' contribution

A.T-M – sampling design, data collection, interpretation, funding provision, writing (original draft); C.D.E – methodology, data collection, interpretation, writing (original draft); A.L – methodology, data collection, writing (original draft); C.M-R – methodology, data collection; J.R.S – interpretation, writing (review and editing); C.F – interpretation, funding provision, writing (review and editing).

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