

Research article

The spiny-cheek crayfish, *Orconectes limosus* (Rafinesque, 1817) [Crustacea: Decapoda: Cambaridae], digs into the UK

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Abstract

The invasive, plague-carrying, North American spiny-cheek crayfish, Orconectes limosus, has apparently only recently reached the UK despite being first introduced into continental Europe in 1890. A number of populations have now developed over a wide geographic area in England. It is thought that these have arisen from deliberate introductions by anglers or from aquarium pets being released by the general public. O. limosus probably poses as great a threat to the indigenous white-clawed crayfish, Austropotamobius pallipes, in the UK as does the North American signal crayfish, Pacifastacus leniusculus. Like the signal crayfish, O. limosus burrows extensively. A developing lake population of O. *limosus* has been studied by trapping and direct observation for the first time in the UK to see whether it could be controlled before it spreads to adjacent lakes and a river. Although large numbers appear to be present they are not easily caught in traps and the CPUE over the year of trapping was low (1.28). although in certain months, i.e. September and October, it was relatively high (2.0). Trap catches were dominated by adult males. Mating and egg-laying took place in the spring. A berried female of 62 mm CL and a male of 65 mm CL were found, which were probably at least four years old. A review of the life-history of O. limosus is also undertaken as there appears to be some variation within Europe, with two periods of mating being reported for some populations. The only way to control the population would appear to be by chemical or physical (dewatering) means.

Key words: crayfish, Orconectes limosus, burrowing, life-history, Austropotamobius pallipes, threat, UK

Introduction

The spiny-cheek crayfish, Orconectes limosus (Rafinesque 1817), was the first non-indigenous crayfish to be intentionally introduced into Europe from the USA (Hamr 2002, Holdich 2002). After its introduction into Germany in 1890, secondary introductions were made into other parts of Germany and into Poland and France, in an attempt to make up for losses of the economically important noble crayfish, Astacus astacus (L.), through crayfish plague (Machino

and Holdich 2006, Holdich et al. 2006a). Ironically, *O. limosus* acts as a vector of crayfish plague (Vey et al. 1983), like other North American crayfish studied, so its introduction was a further 'nail in the coffin' for indigenous crayfish. Due to the fact that it does not live for long, i.e. usually less than four years, has small chelipeds with little meat, and rarely reaches the preferred size for commercial use, i.e. 10 cm total length, it never fulfilled its role as a replacement for *A. astacus* from the gastronomic point of view in Europe, as other species are much preferred. O. limosus has also spread naturally through rivers and canals as well as being accidentally transferred by man, e.g. when caught up in fishing nets (Holdich et al. 2006a) and via the crayfish trade (Troschel and Dehus 1993). It is thought to have entered western rivers in Germany via the Elbe-Oder-Rhine Canal from the River Oder system near its original point of introduction (Troschel and Dehus 1993). It is commonly used as fish bait and as fish food, and this has led to its introduction into new sites and countries. It is one of the commonest crayfish in now continental Europe, occupying at least 20 countries, although it has yet to reach the Iberian Peninsula or Scandinavia (Holdich et al. 2006a). In Germany, it has colonised most of the major river systems thus making any attempts to reestablish A. astacus impossible (Dehus et al. 1999). It has invaded Belarus from Poland within the last 10 years and is now common in some rivers, including the River Neman that drains into the Baltic Sea (Alekhnovich et al. 1999). Investigations from 1991-1996 in Belgium showed that O. limosus occurred in 103 out of 388 ponds and 30 out of 120 streams investigated (Arrignon et al. 1999). In Poland, populations of O. limosus increased from 57 in 1959 to at least 1383 by 2004 (Holdich et al. 2006a), and out of 300 lakes recently examined in NE Germany, 214 were found to have O. limosus (Schulz and Smietana 2001). It was first recorded in Italy in 1991, probably having being introduced with fish stocks, and is now common in northern parts (Gherardi et al. 1999). O. limosus is gradually spreading eastwards in Europe and is now widespread in western parts of the Czech Republic (Petrusek et al. 2006). In Hungary, its colonisation speed has been calculated to be more than 13 km yr⁻¹ in the River Danube (Puky and Schád 2006) and, whilst the main catch in Hungary was A. astacus in the 1990s, it is now dominated by O. limosus (Holdich et al. 2006a). Recently it has been found in Croatia (Maguire and Gottstein-Matočec 2004) and Serbia (Karaman and Machino 2004). It will probably spread into Bulgaria, Romania and the Ukraine via the River Danube before long (Machino and Holdich 2006).

All these observations show that *O. limosus* is a fast-spreading, invasive species, which poses a serious threat to indigenous crayfish species, so its apparent recent introduction into the UK (see below) is a worrying development.

Distribution in the UK

Despite its introduction into continental Europe in 1890 and, as indicated above, its subsequent spread, O. limosus was not recorded in the UK until 1995, when a male specimen was purchased from an aquarist centre in southern England (Foster 1995). The first occurrence in the wild (2000) was from the lawn of a garden in East Sussex (National Grid Reference: TO 395 370) (www.searchnbn.net). Subsequently, a number of populations have been reported and the main source seems to be from anglers introducing them into fish ponds to improve production, or members of the public releasing aquarium pets into natural waters. It is also possible that they could be transferred in consignments of fish from commercial fish farmers or as a result of them being used as bait.

The first actual population of *O. limosus* was reported from a catfish pond in Warwickshire, West Midlands (SP 079 592) in 2001 (see Annex for geographic coordinates). Although its origins are unknown it seems likely they were introduced to supplement the food of the fish. In 2002 it was reported that the crayfish had been found approximately 5 km downstream of the pond in the River Arrow (PJ Sibley, pers. com. 2002).

A number of populations have developed in north London associated with the River Lee catchment: 1. pond in Enfield (TQ 369 986); 2. Small River Lee (TQ 370 988); 3. Lee Navigation - various sites from TQ 364 955 to TQ 351 904; 4. Walthamstow Reservoir (Warwick Reservoir East) (TQ 348 888) (see Annex for geographic coordinates). The source of the Enfield population may have been a local person who kept exotic pets, who got rid of his crayfish when he relocated (J England, pers. com. 2004), and they have spread from there into the R. Lee catchment in a relatively short space of time (D Ahern, pers. com. 2006). The first three sites, which are known from the year 2004, are subject to regular monitoring by the Environment Agency, whilst the fourth is from 2003 (J England, pers. com. 2004; D Ahern, pers. com. 2006). In addition to O. limosus, three other non-indigenous species occur in the catchment, i.e. the narrow-clawed crayfish, Astacus leptodactylus Eschscholtz, Pacifastacus leniusculus (Dana), and the red swamp crayfish, Procambarus clarkii (Girard) (D Ahern, pers. com. 2006).

Although a number of sightings of *O. limosus* have been reported from Essex (2005, Abberton Reservoir, TL 977 182) and Suffolk (2005, R. Waveny, Beccles boatyard, TM 421 913) in the east of England, none have yet to be confirmed as that species, and those examined have turned out to be *A. leptodactylus* (R Brown, pers. com. 2006), which also has relatively spiny sides to the carapace, and can also have a sharp spine on the carpus of the cheliped as in cambarid crayfish (Holdich et al. 2006a, Pöckl et al. 2006).

A population of non-indigenous crayfish was reported from a water-filled gravel pit known as Clifton Pond (actually it is more like a large lake) near Nottingham (SK 523 335) in 2002, and these were originally identified from photographs as the North American signal crayfish, P. leniusculus, as they appeared to have red undersides to the claws and were burrowing extensively into the margins of the pond (Figure 1). Coots had been seen eating the crayfish (Figure 2). However, when live specimens were examined in 2005 they were found to be O. limosus. It was subsequently divulged by an angler that they had been introduced (possibly in 2000) by a carp angler. As the carp angler died soon after it has not been possible to determine the origin of the crayfish or how many were introduced. This population is the focus of the current paper.

The most recent finding (2006) concerns a population near Ancaster (Lincolnshire) in Eastern England at a caravan/camping site that has several lakes. The crayfish have been there at least 5 years and possibly much longer. The initial records came from Roach Pool and were reported by an angler (PJ Sibley, pers. com. 2006), and a subsequent visit by the Environment Agency also found them in Carp Pool (SK 974 436) a short distance away (R Page, pers. com. 2006).

Materials and Methods

Site description

A system of water-filled gravel pits, some dating back to the 1920s, and covering an area of 222 ha, exists to the west of the city of Nottingham in the East Midlands region of England. Much of the area was designated as a Site of Special Scientific Interest in 1964, on the basis of the importance of resident breeding and overwintering bird populations. Most of the pits are connected to allow passage of barges that



Figure 1. Crayfish burrows exposed after a drop in water level behind the reed beds in Clifton Pond (2005). (Photo: DM Holdich).



Figure 2. A coot attacking a crayfish on the banks of Clifton Pond (2002). Although this crayfish (inset) looks like the signal crayfish, *P. leniusculus*, none were found in subsequent studies, so it is presumed to be a spiny-cheek crayfish, *O. limosus* (see inset). (Photo: J. Black).

transport gravel from western pits to a processing plant in the east. The River Erewash, which drains an area of extensive industry, including coal mining, and is relatively polluted, enters the pits at Coneries Lagoon and this water mixes with that in the connected pits.

The exception is Clifton Pond, which is isolated, although water from it can enter the adjacent River Trent that is separated from it by only a few metres in places via a one-way outflow flap valve when water levels exceed the height of the drop-board sluice on the nature reserve side of the outflow. Water levels in Clifton Pond are maintained from ground and rain water but in dry months the level can drop by as much as 1.5 m leaving areas of deep muddy substrate exposed. Clifton Pond (Figure 3) is 16 ha in surface area and 4 m deep in places. From the air a significant area appears quite shallow. It has steep banks, which makes launching a boat difficult. It tends to shelve off quickly from the banks into deeper water making manual searching hazardous, although in places there is a narrow shelf. An extensive area of *Phragmites* reeds has been planted in front of the left (north-western) bank in order to provide habitat for birds (Figure 4).



Figure 3. View across Clifton Pond from in front of the transect line (arrow), which carries on near to the reed bed on the left. (Photo: DM Holdich).



Figure 4. Shallow muddy area close to reed bed where observations of mating and burrowing were made in April 2006. (Photo: DM Holdich).

In summer months the pond becomes hypertrophic and there is extensive growth of algae and macrophytes (mainly Canadian pond weed, *Elodea canadensis*), which makes it difficult to make direct observations and to ensure that traps reach the bed of the pond. Extensive blooms of blue-green algae are also present in summer months.

Trapping and manual searching

At the beginning of August 2005, 23 traps, based on the Swedish 'Trappy' design, were laid overnight along a transect from the reed bed on the left shore across Clifton Pond to the right shore (Figure 3), which was lined mainly by willows. Each trap was attached to a wooden float by means of a rope and was lowered until it reached the pond floor, or was caught on vegetation. The depth of water was 1.5-2 m at all points along the transect. Six crayfish (three male and three female were caught) and it was at this time that it was discovered that the crayfish were *O. limosus* (Figure 5) and not *P. leniusculus* as previously thought. The traps



Figure 5. An adult male *O. limosus* with its characteristic spiny cheeks (arrow and lower inset), orange tipped legs (upper inset), and abdominal stripes. (Photos: DM Holdich).

were reset and left over three nights. Eight crayfish were caught (six males and two females). A week later, ten traps were placed behind the reed beds for three nights and 14 males and five female crayfish were caught. Although the numbers caught were low the position of the transect was deemed suitable for a longer term study rather than the reed bed area, which was subject to fluctuations in water level. Trapping was carried out under an appropriate licence from the Environment Agency with each trap carrying a numbered, dated tag (Figure 6).

Subsequently, each month from September 2005 to October 2006, except for November

2005, 20 crayfish traps were baited with kipper and placed via a motorboat along the transect across the pond (Figure 3). The traps were weighted with a metal bar attached to the underside, but because of the extensive growth of weed in the summer months (starting in May) they may not have always settled on the pond bed. They were left overnight and then raised the following morning between 0815 and 0915. All individuals caught were sexed and the carapace length measured in mm (see below). Manual searching using a pond net was carried out for at 20 minutes amongst the marginal least vegetation and rubble between the shore and the transect line. When the water was clear burrows were searched for.



Figure 6. An Environment Agency tag that has to be placed in all traps by law. (Photo: J Black).

As *O. limosus* is a non-indigenous species it is not permitted by law to put live individuals back into the environment once caught (Holdich et al. 2004), therefore all individuals caught were subsequently frozen and then disposed of.

Carapace length

Carapace lengths (from the tip of the rostrum to the junction of the carapace and abdomen) categories are given in 5 mm intervals (1: 4.0-8.9, 2: 9.0-13.9, 3: 14.0-18.9, 4: 19.0-23.9, 5: 24.0-28.9, 6: 29.0-33.9, 7: 34.0-38.9. 8: 39.0-43.9, 9: 44.0-48.9, 10: 49.0-53.9, 11: 54.0-58.9, 12: 59-63.9, 13: 64-68.9) as used by Holdich et al. (2006b). A linear correlation between carapace length and total length in *O. limosus* has been shown by Brink et al. (1988) in Dutch populations, and this has recently been confirmed for both sexes in a French population (D Baldry, pers. com. 2006).

Temperature

The temperature of the marginal water at 10 cm depth was taken each month at approximately 0800 using a mercury thermometer. In addition, temperatures from further out in the pond near to the centre of the transect line and at a variety of depths were obtained using a digital thermometer by staff in the Geography Department at the University of Nottingham, who were involved in a study of the gravel pits.

Results and Observations

Trapping

The longer term study started in October 2005. In total, 307 crayfish were caught during 12 trapping exercises, only 20 of which were females (including three berried females).

The majority of crayfish trapped were in the larger CL categories, i.e. 8 - 35, 9 - 64, 10 - 68 and 11 - 26 (Figure 7). Three individuals in CL category 12 (60, 60 and 62 mm) were also trapped. Some smaller individuals were occasionally found in the traps, i.e. CL categories 3 - 2, 4 - 9 and 5 - 5 from August to October.

Overall, the CPUE averaged 1.28 over the 12 months. Catches varied considerably with the highest number being in September and October 2006 when 40 were caught on each occasion (CPUE 2.0) (Figure 8). The lowest catch was in July 2006 when only two individuals were trapped (CPUE 0.1).

Manual searching

In early August 2005 whilst searching for crayfish burrows, 14 crayfish in the CL categories 2 (6) and 3 (8) were caught amongst Canadian pond weed in the shallows behind the reed beds (Figure 4). In subsequent months individuals were usually caught in the margins along the shore in front of the transect line (Figure 3) except during periods of low temperature (1.0-3.0°C) and when the plant growth was at a minimal level in December-March inclusive. In December 2005 the margins were frozen over on occasions.

In late April 2006 some very large individuals were found patrolling on the mud flat by the

reeds, including mating pairs, a male of 65 mm CL (category 13) and a berried female of 63 mm CL (category 12) (see below).

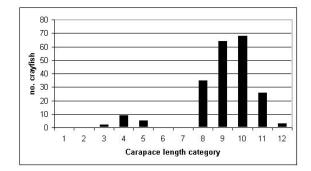


Figure 7. Numbers of crayfish caught by trap per carapace length category

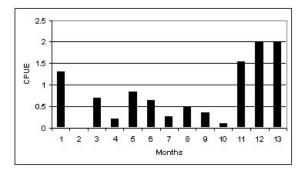


Figure 8. Catch per unit effort with traps shown on a monthly basis starting October 2005 (1) and ending October 2006 (13). No samples were taken in November 2005 (2)

Despite only catching two individuals in the traps (Figure 7) in late July 2006, many juvenile crayfish were found in the pond margins in front of the transect line in CL category 1 (14), 2 (14) and 3 (11). In August individuals in CL categories 3 (2) and 4 (2) were caught in the margins. (Individuals in these categories were also caught in the traps in August). Berried females were present in April, so these juveniles represented at least three different growth stages derived from eggs produced at that time. The 5 mm CL categories are only arbitrary and more than three stages may be represented.

Mating and berried females

In late April 2006, before the macrophytes had started to grow extensively, many adults including mating pairs (Figure 9) - the males with well-developed copulatory stylets (Figure 10), and berried females (Figure 11) were found in very shallow (2-5 cm) water on the surface of



Figure 9. A mating pair found in shallow water on the mud surface in April 2006 (see Fig. 4). (Photo: J Black).



Figure 10. Ventral view of male showing the copulatory stylets and the ischial hook on the second walking leg (arrow) characteristic of F1 males. (Photo: DM Holdich).

the mud near the reed bed (Figure 4). Some individuals were found mating out in the open and berried females were seen moving around.

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Figure 11. A berried female found in shallow water on the mud surface in April 2006. Note that some of the eggs are dead having been attacked by fungi. The position of the seminal receptacle is shown by the arrow. (Photo: DM Holdich).

Berried females were only found in the traps in the month of May, when three were trapped in the CL categories 8 and 9.

Burrows

In late April 2006 the water in Clifton Pond was very clear. It was very shallow by the reed beds, and there was very little weed growth. After the traps had been lifted the opportunity was taken to examine the pond margins near the reed bed (Figure 4) for any signs of burrows. Many adults were seen in burrows (Figures 12, 13). The burrows were often circular in outline when on the mud surface (Fig. 12), but at the edge of the mud shelf they took on a more characteristic Dshape (Figures 12, 13). No occupied burrows were seen in other months, even when the weed had died back in October 2006 and the same area once again had shallow water.

Colour and moulting

Very few adult crayfish were found in the traps or by manual means that were as clean as that shown in Fig. 5 from June 2006. Usually, they



Figure 12. An *O. limosus* on the pond floor close to a number of burrows. Note that algae are starting to grow and by the following month (May) were, along with macrophytes, very extensive. (Photo: J Black).



Figure 13. A crayfish about to emerge from its burrow. Note that it is covered in silt. (Photo: J Black).

were almost black as shown in Figure 11. This is presumably a consequence of living amongst sediment, the true colour only being revealed after moulting. The black coloration could be removed by hard scrubbing. Recently moulted individuals were mostly found in the traps and by manual search in June-July 2006.

Predation

Clifton Pond contains a wide variety of fish, including large carp that were seen foraging amongst the marginal vegetation and could presumably eat the crayfish. A large number of birds are associated with the pond, including herons, cormorants and wildfowl, although only coots have been seen attacking the crayfish out of water (Figure 2). In some months when the water was shallow crayfish carcasses could be seen in the shallows and mud flats, which had been attacked and eaten (rather than being moult casts).

Behaviour

When the traps were lifted, crayfish were often found clinging to a trap or just about to enter via the tapered funnel, indicating that they were active in daylight hours. This activity is backed up by observations of adults moving about in the shallows during daytime. It is not known if they were active at night although it is presumed so, as other populations have been found to be.

When handled, individuals often took up a curled posture with claws crossed and clamped together, rather than exhibiting the aggressive 'claws raised' posture that most crayfish species display when disturbed. This probably makes it difficult for all but the largest fish to swallow them.

Temperature

At approximately 0800 the temperature of the marginal water was found to be similar to that recorded further out on the pond – see below, except that from December to March it ranged from $1-3^{\circ}$ C.

In addition, temperatures from further out in the pond near to the centre of the transect line and at a variety of depths were obtained by staff in the Geography Department at the University of Nottingham, who were involved in a study of the gravel pits. Interestingly, temperatures did not vary much with depth. When the trapping started in October 2005 the temperature was 13.91°C at the surface and 13.76°C at 1.5 m. Temperatures were similar in early November, but then in late November they dropped significantly to 4.84°C at the surface and 4.95°C at 2.0 m. Low temperatures were maintained throughout the water column until mid-March, but by 20 April 2006 they had risen to 11.51°C at the surface and 11.18°C at 2.0 m. There was a 5.0°C rise by 18 May and a further 4.0°C rise by 15 June. By mid-July the surface temperature had reached 23.36°C and that at 1.8 m was 19.83°C. Temperatures throughout the water column then started to decline, and by the month of the last trapping session (October 2006) had reached 14.46°C at the surface and 14.52°C at 1.5 m, being slightly higher than that recorded in October 2005.

Discussion

Origins

According to the literature there has only been one successful introduction of O. limosus into Europe from the USA, i.e. in 1890 when 100 individuals were put in a 0.1 ha fish farm pond near Berneuchen in Germany (now Barnówek, Poland) close to the River Mietzel, east of Berlin (now R. Myśla, Poland) (Ďuriš 1999). It is possible, therefore, that this population has been the source of all the O. limosus now in Europe (Schulz and Smietana 2001). However, the actual origin of the O. limosus stock is not so clear. They were sent to Europe by the US Fish Commission and the source is usually quoted as the Delaware River area - the type locality of O. limosus is in fact the Delaware River near Philadelphia, Pennsylvania (Hobbs 1989), but the documentation does not actually mention where the introduced crayfish came from (Holdich et al. 2006a, Y Machino, pers. com. 2006). An additional source of O. limosus in Europe has come via the aquarium trade, but usually it is not known where the crayfish originally come from. The populations in north London waters are thought to be the result of aquarium stock being deposited in a nearby pond (see above).

Habitat

Hamr (2002) states that in North America, *O. limosus* inhabits soft-bottomed, silty, turbid waters such as found in large rivers, wide streams and lakes with abundant vegetation, although in Canada it has been found occupying stony streams with a moderate current. In Europe it is known from a wider range of habitats including cool, fast waters, but preferring calm, deep waters such as found in ponds and lakes, which may be organically rich and polluted (Holdich et al. 2006a). Although usually found in lowland waters, in Morocco (North Africa), introduced populations have become established at altitudes between 1400 and 2078 m a.s.l (Holdich et al. 2006a).

Tolerance

Orconectes limosus is very tolerant of environmental conditions and can be found living in a wide range of water types and quality (Holdich et al. 2006a). The water quality at the Nottingham site is high if based on the diversity of macroinvertebrate life that lives there, i.e. 28 families and 38 species in 1999 (DM Holdich and H Johnson, pers. obs). However, it does become highly eutrophic in the summer months. One of the reasons O. limosus has not proved popular as a food item is because the public perceive it as living in eutrophic or polluted waters (Gherardi et al. 1999). Indeed, Pöckl (1999) mentions that in Austria O. limosus has reached a high density in a waterbody that is oily and muddy, with other aquatic fauna indicating low water quality. It appears able to tolerate drying conditions for many weeks (Laurent 1988), and is capable of moving across land, even in winter (D Baldry, pers. com. 2006). It would seem that low temperature is not an obstacle to activity or to mating (see below) in O. limosus.

Colonisation

The O. limosus introduced into the Nottingham site appear to have spread through the lake very quickly, even though they have only been in there four or five years. Although studies were restricted to the western end of the lake, individuals have been found at the far eastern end, where a route to the adjacent R. Trent might be possible in times of high water. The speed with which O. limosus can colonise a lake is well shown for Lake Geneva (Dubois et al. 1999). Although this crayfish was known to be present in the lake in 1976, the real invasion did not start until 1986 when a fishmonger released an unknown quantity of crayfish into the lake in the south-east corner at the harbour of Meillerie (France). They subsequently spread eastwards and westwards aided by strong currents. Internal deep currents carried them to the deepest parts of the lake (306 m) and they are now encountered everywhere in the lake. Large quantities are caught by fishermen in their nets and traps, but the yield is unprofitable because people do not want to buy them (Dubois et al. 1999). Also, removing them from nets can be very tedious.

Burrowing

The fact that *O. limosus* has been seen burrowing at the Nottingham site is interesting as there have been few other observations of this species burrowing, although Hamr (P Hamr, pers. com. 2005) thinks that the burrows created by the Nottingham population (Figures 12, 13) look similar to those of other Orconectes species in North America, and suspects that O. limosus, like them, is a burrower. Hasiotis (1993) has compared the types of burrows made by O. immunis (Hagen), O. nais (Faxon) and O. virilis (Hagen) in artificial conditions and found that they burrowed into banks as well as directly into the substratum. If water levels fell then they continued to dig down as far as they could, remaining dormant once the lowest water level was reached. Often a chimney (pile of spoil) was created at the entrance to the burrow. Some of those created by the Nottingham population may well have had two entrances as there was often a circular opening in the horizontal substrate near to a D-shaped entrance on an underwater bank edge (Figure 12). This type of burrow would be unusual for a crayfish that spends most of its time in open water, i.e. a tertiary burrower in the North American classification of burrowing crayfish devised by Hobbs (1981). It is possible that the period of burrowing and their occupation is connected to the breeding season as occupied burrows were only observed in the spring in the Nottingham population.

For European populations, Kozák (P Kozák, pers. com. 2006) has not seen O. limosus creating proper burrows in the Czech Republic, although this may be due to the nature of the habitats he studied. However, Ďuriš (Z Ďuriš, pers. com. 2006), also from the Czech Republic, has observed that O. limosus may dig itself into soft substrata, and on one occasion a gallery of burrows on 2-3 levels was seen. Laurent (PJ Laurent, pers. com. 2006) has not observed the species burrowing in Lake Geneva or rivers and ponds in Morvan, France, despite having examined many populations. Neveu (2006) states that O. limosus is not normally a burrower, although he has observed them in short burrows between the roots of macrophytes in a lake (A Neveu, pers. com. 2006). Baldry (D Baldry, pers. com. 2006), who has been studying the invertebrates in Cessy Lake in central eastern France for the last 11 years, has never seen burrows made by O. limosus.

Life history

Before commenting on the life history of *O. limosus* in the Nottingham population, a review of what is known for other populations in provided below so that a comparison can be made.

According to Momot (1988), the maximum size reached by O. limosus in North America is 50-54 mm CL, with female maturity occurring at 20-25 mm CL. The length reached in year 0 is 25, year 1 - 35, year 2 - 45 and year 3 - 55 mm Cl. He stated that the typical orconectid life cycle was about 3-4 years, with females producing only one brood a year. Depending on their size females usually laid their eggs in April or May. The eggs remained attached to the female for 1-3 weeks depending on temperature, hatching in May or June, after which the juveniles moved into the littoral zones of lakes. Growth varied considerably, but those released in May reached 30 mm total length by July in lower latitudes, but not until September at higher levels. Maturity was not usually reached until the end of the second growing season when five to ten moults had taken place, after which males usually moulted twice a year and females once. This resulted in males usually being larger than females. Mating usually took place in early spring or late summer with the male transferring the sperm to the female's seminal receptacle (Figure 11) using copulatory stylets (Figure 10). As with other cambarid crayfish the shape of these stylets varied (as do the chelipeds) depending on whether the male was in the sexually active Form I or sexually inactive Form II.

However, none of the studies made in Europe have mentioned the phenomenon of cyclic dimorphism, unique to cambarid crayfish (Payne 1997). The traditional view is that the final moult of the juvenile male produces a breeding form known as FI, which is distinguished by a number of morphological features including modified copulatory stylets, shape of chelae, and hooks developing on certain walking legs. At the end of the breeding season the FI stage moults back to a quasi-juvenile form known as FII. At the next breeding season the FII stage moults back to the FI stage, but as Payne (1997) points out there are exceptions to the rule, and in at least one species the FII stage is the last juvenile stage, the next being an FI stage which remains until death.

According to Hamr (2002), mating in both American and European populations of O. *limosus* takes place in spring and eggs are carried from March to May. Crayfish hatch and become free-living in May-June and measure 18-30 mm CL the following January. Maturity occurs in the second summer at 25-35 mm CL (1+) and the average life span is 2 years, although a maximum life span of 4 years and 61 mm CL has been reported. However, Hamr (2002) noted that in some Canadian (Québec) populations mating took place in September-October and again in March-April with eggs being deposited at the end of May and hatching taking place in late June. Maturity occurred at 15-16 months (45 mm CL) with most females becoming berried in their second year; a small number producing another brood in their third year. A heavy winter mortality of up to 88% was also noted. Hamr (pers. com. 2006) stated that he knew of no evidence that showed that female orconectids mated in the autumn produced eggs before the following spring.

Momot (1988) only referred to the Polish study of Orzechowski (1973) for European populations of O. limosus. This was carried out in a 1600 ha reservoir with a maximum depth of 20 m. Crayfish reached a maximum of 50 mm CL and had a maximum life span of 48 months. Maximum egg number was recorded as 228. Piesik (1974) stated that an O. limosus population in Poland mated in the autumn but that females did not lay their eggs until spring. S'mietana (P S'mietana, pers. com. 2006) has recorded O. limosus mating in late August, but mostly in October in Poland, but females did not deposit their eggs until the end of April and beginning of May. Egg incubation took 4-5 weeks depending on temperature. However, one study in Poland has shown a second mating in the spring. S'mietana kept crayfish in captivity at similar temperatures to outside and they mated during the whole of the autumn, winter and spring, only ceasing when temperatures declined below 8.0-9.0°C.

Egg carrying in the Czech Republic is usually in May, seldom in June (Z Ďuriš, pers. com. 2006). Kozák is currently studying the reproductive process in O. limosus (P Kozák, pers. com. 2006). He has found that O. limosus mates at least twice (autumn and spring), and in one case another worker found that they mated throughout the winter in a flooded gravel pit. The spring mating has been found to occur in March-April with females carrying eggs from the end of April to the beginning of June (approx. 6 weeks), but none have been recorded as carrying eggs in the winter months. Petrusek (A Petrusek, pers. com. 2006) has also observed O. limosus in the Czech Republic mating both in autumn (mid-October) and in early spring (start of April in 2006, even when the locality was still covered in ice). Out of 200 females examined none were found to carry eggs in the winter.

Stuki (1999) compared the life history and behaviour of seven crayfish species in Switzerland, including a lake and a river population of O. limosus. He found O. limosus mating from the end of August until the beginning of April the next year, but females with eggs were not found until mid-April. Hatching took place at the end of May and in June, as with indigenous crayfish species in Europe, and also the introduced P. leniusculus, but the egg incubation time was much shorter being 49 days for the lake population and 55 days for the river population. He noted that O. limosus was active both during the night and day. In spring and summer crayfish were mainly found in refuges during diurnal hours, becoming active at night. From autumn until the spawning of eggs in mid-April, crayfish were active during diurnal and nocturnal hours. In the river population many crayfish were observed wandering round the river bed from November to January, peaking in the river population between December and March when the water temperature was 6-7°C, and between September and December in the lake population when the water temperature was 7-16°C. At the onset of sexual maturity at 1+ the average female size was 22.0 mm CL, although no sizes were given for males. The average pleopodal fecundity in the lake population was 138 eggs (range 31-372) and the average number of juveniles was 64 (range 30-100). Average egg diameter was 1.79 mm, the smallest of all the crayfish studied, e.g. those of A. pallipes, were 2.87 mm. Juveniles were found to grow fastest in the lake population and by the end of the first growing season (November, December) were of 18 mm CL, which is smaller than the figure given by Momot (1988) (see above).

Brink et al. (1988) studied populations of *O. limosus* in the Rhine River and Meuse River in the Netherlands. They were able to sample the crayfish caught on the cooling-water intakes of a mining company and a power station. Highest numbers of crayfish were collected in April to September. From October to March more males than females were found, but in April the situation became reversed. This suggests that males were more active in the winter months. The number of crayfish caught generally increased with increasing temperature. They found berried females occurring from the middle of March until June, with highest numbers in April. Brink et al. (1988) stated that this was the same for a population in the Rhine-Marne Canal in France, but that studies in Poland, the former East Germany, and North America recorded the first berried females in May, even though water temperatures were similar. Larger females were found to carry their eggs earlier in the season than smaller ones. Females with attached developing juveniles were found in May, suggesting that embryonal development took about one month in the Netherlands. Juveniles appeared in June in the 0-10 mm carapace range, by August they showed a mean carapace length of 18 mm, reaching 30 mm CL by the end of the year. This was similar to the situation found by other workers in East Germany (Pieplow 1938) and Poland (Orzechowski 1984). Moulting individuals were recorded from June to September. The maximum length of individuals recorded in the Dutch populations was 55 mm CL, which was similar to those found in East European countries, but larger than in North America, where crayfish with a carapace length greater than 40 mm were rarely found (Smith 1981). Brink et al. (1988) suggested that this size difference may be due to differences in climate or food conditions.

Neveu (2006) compared the characteristics of six species of crayfish in France. He found that the age of first maturity of a pond population of O. limosus was 1 year. The period of egg incubation was 3 months. The potential fecundity ranged from 320-340 eggs, whilst the actual fecundity varied between 60-200 eggs. Length at the first maturity was 48 mm TL and in the second summer 90 mm TL. Longevity was given as 3 years. Neveu (A Neveu, pers. com. 2006) found that in outdoor tanks in Rennes (NW France) O. limosus regularly mated at 15-16°C, but also at 3-5°C in 1990-91. Eggs were deposited in late March and juveniles became independent at the end of May; the same was found in a study by Krach (thesis 1978) near Nancy (eastern France). Neveu also provided data from a study by Jestin (thesis 1979) in Créteil Lake near Paris, who found O. limosus mating from September-November and again intensively) during March-April. (more However, pairs were also found during the whole of the winter by electric trawling, and also in July.

Baldry (D Baldry, pers. com. 2006), who is currently studying *O. limosus* from Cessy Lake in eastern France, has never caught any with eggs, despite many females being trapped. Mating has been observed in early April and again in October and November. Using traps, relatively large numbers of crayfish have been caught compared to the Nottingham study. Interestingly, whilst the catch was 100% male in May 2006 it was 78% female in June. Baldry found that *O. limosus* were most active during the night, although significant numbers were also active at day.

At first glance the life history of the Nottingham population of O. limosus would appear to involve a single period of reproduction with mating in the spring followed by egg carrying and release of juveniles in the summer (July). However, the fact that mating individuals and berried females were found together in April complicates the issue. It is possible, as so few females were trapped and none were found by manual searching in October of 2005 or 2006, plus the fact that no November sampling took place, that an autumn period of mating was missed. Those females found with eggs in April may have been stimulated to lay eggs and fertilize them with stored sperm by the rise in water temperature between March and April 2006. Females mated in April may have been those not mated in the previous autumn, and presumably laid their eggs some time later. Certainly in July and August juveniles in the carapace categories 1-4, which cover the size range 4.0-23.9, were found in the lake margins, possibly indicating that they had become independent over a period of time. Alternatively, there may only be one period of mating in April and those berried females found had been mated in the weeks prior to the sampling that month and had laid their eggs soon after. It seems likely that CL categories 1-5 are formed in year one, although category 5 may also occur in year 2. All the berried females bar one were in CL categories 8 or 9, which would seem to suggest that they were in at least their third year, the exception being in category 12, which along with a large male of 65 mm CL (CL category 13) may have been even older. In the current study no differences were noted between males caught at any time of the year and they all appeared to be at the FI stage with a distinct grasping hook on the ischium of the second pair of walking legs (Figure 10). The low CPUE using traps for O. limosus has also been found by other workers, e.g. Brink et al. (1988), although others have had much more success (D Baldry, pers. com. 2006). In many other studies where CPUE values have been given they vary considerably with species, season and location. Why so few females were caught in traps during the present study is unknown, although in many studies of various species it has been mentioned that females are trap shy compared to males. Again, however, this is not born out by Baldry's study (see above).

Impact on other biota

In Europe, O. limosus has been implicated in the demise of many indigenous crayfish populations through competition and crayfish plague (Laurent 1988, Holdich 1999, Souty-Grosset et al. 2006). In North America it appears to have displaced O. virilis in the lower St Lawrence River (Hamr 2002). However, both Bohl (1999) and Pöckl (1999) state that for Germany and Austria respectively, O. limosus tends to inhabit large rivers and the lower reaches of their tributaries. It tends not to penetrate small tributaries and thus does not pose a threat to indigenous crayfish populations living there.

Its large numbers are likely to have a marked impact on the fresh water environment, although this has yet to be quantified. It is not known if the crayfish in Clifton Pond are having any negative impact at the present time. Another cambarid crayfish, *P. clarkii*, has been shown to completely alter the trophic dynamics of lakes and wetlands in Spain (Rodriguez et al. 2005).

Spread and control in UK

Although there are relatively few populations of O. limosus in the UK at present those that have been discovered have all been reported since 1999. None are currently a threat to the indigenous cravfish, A. pallipes. However, as an invasive species the potential for spread is real and, with its ability to act as a vector of crayfish plague, it presents an additional threat to the already endangered A. pallipes (Holdich et al. 2004). If O. limosus is able to produce two bursts of recruitement, i.e. juveniles in early and late summer, then its ability to quickly colonise new localities will be considerably enhanced and may explain how it has become established so quickly in Clifton Pond. Man would seem the most likely culprit to spread it, but it is equally possible that predators, particularly birds, could aid the process. As a burrower it also poses an additional threat to the freshwater environment.

As has been shown, legislation is a relatively unsuccessful tool for trying to control nonindigenous invertebrates such as cravfish (Holdich and Pöckl 2005). However, it is better to have it than not, and the UK probably has the most stringent cravfish legislation in Europe (Sibley 2003, Holdich et al. 2004). With two exceptions it is prohibited to keep any species of non-indigenous crayfish anywhere in the UK without a licence (Holdich et al. 2004). The exceptions are P. leniusculus in the south of England where they are numerous populations in the wild, and the tropical redclaw crayfish, Cherax quadricarinatus (von Martens), which can be kept in heated, covered aquaria. Because of the threat they pose to the indigenous crayfish, A. pallipes, three out of the five nonindigenous crayfish present in the wild in the UK, i.e. A. astacus, A. leptodactylus and P. leniusculus, were placed on Schedule 9 of the Wildlife & Countryside Act in 1992, effectively classifying them as pests. However, P. clarkii and O. limosus have yet to be treated similarly and this needs to be addressed by the relevant authorities, especially for O. limosus, which is geographically widespread, and could become a real threat to the future survival of A. pallipes (see above). The use of crayfish for bait purposes is now banned in the UK under a bylaw issued by the Environment Agency in 2003 (Holdich and Pöckl 2005), as the practice may have contributed to the spread of non-indigenous crayfish and crayfish plague in the past.

It is not known how large the population of *O. limosus* in Clifton Pond is as CPUE results cannot be used to calculate this. However, the CPUEs in August-October 2006 were higher that in autumn 2005, possibly indicating that the population is increasing, despite all captured crayfish being removed during the year. Markrecapture methods were not attempted to estimate numbers as in the authors' experience they involve a lot of time and effort for very little reward in relatively large water bodies.

As the Nottingham population is very close to a major river as well as an extensive series of interconnected lakes it would seem advisable to consider ways of eradicating it. It is unlikely that trapping would be effective in this respect due to the low CPUE recorded in most months, and also because of the very low number of females caught. Holdich et al. (1999), in their review of possible methods for controlling nuisance populations of crayfish, came to the conclusion that the only sure method was to use biocides. However, there are objections to using synthetic biocides in aquatic ecosystems in the UK, and natural substances would have to be used, and then only in closed systems. Peav et al. (2006) have developed a system that is currently being trialled on some Scottish populations of P. leniusculus - a pest species in the UK (Holdich et al. 2004). This involves the use of natural pyrethrum and results obtained so far look promising. The exercise, however, involves a lot of time and effort, not to mention considerable cost. An alternative solution might be to drain down Clifton Pond after removing the fish. However, it would be very difficult to ensure that no juveniles escaped in the water being removed and, due to the fact that adults burrow, even drying out for a considerable time might not result in their complete demise. Once water levels were restored the survivors would emerge to breed once more, as has happened when this method has been used to try and eradicate P. leniusculus. Meanwhile, the introduced crayfish are serving their original purpose, i.e. they are providing food for the carp, as well as other fish and numerous birds.

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Annex

Records of established populations of Orconectes limosus in England 2001-2006*

Location	Record coordinates			
	Latitude, °N	Longitude, °W	First record date	Collector
Catfish pond, Warwickshire	52° 13.83'	1° 53.03'	2001	Environment Agency, UK
River Lee, Enfield, London	51° 40.14'	0° 01.07'	2004	Environment Agency, UK
Small R. Lee, London	51° 40.26'	0° 01.12'	2004	Environment Agency, UK
Lee Navigation, London	51° 38.49'	0° 01.65'	2004	Environment Agency, UK
Lee Navigation, London	51° 35.79'	0° 02.93'	2004	Environment Agency, UK
Walthamstow Reservoir, London	51° 34.93'	0° 03.22'	2003	Environment Agency, UK
Clifton Pond, Nottingham	52° 53.77'	1° 13.36'	2005	D. Holdich and J. Black
Carp Pool, Ancaster, Lincs	52° 58.87'	0° 32.90'	2006	Environment Agency, UK

*Full reference to the data: Holdich D and Black J (2007) The spiny-cheek crayfish, Orconectes limosus (Rafinesque, 1817) [Crustacea: Decapoda: Cambaridae], digs into the UK. Aquatic Invasions 2 (1): 1-16