

## Research Article

## Diel and seasonal variations in the population dynamics of *Hemimysis anomala*, a non-indigenous mysid: implications for surveillance and management

Andrew D. Nunn\* and Ian G. Cowx

Hull International Fisheries Institute, Department of Biological Sciences, University of Hull, Hull, HU6 7RX, UK

E-mail: [a.d.nunn@hull.ac.uk](mailto:a.d.nunn@hull.ac.uk) (ADN), [i.g.cowx@hull.ac.uk](mailto:i.g.cowx@hull.ac.uk) (IGC)

\*Corresponding author

Received: 25 March 2012 / Accepted: 9 May 2012 / Published online: 21 May 2012

### Abstract

This study investigated diel and seasonal variations in the population dynamics of *Hemimysis anomala*, a non-indigenous mysid originating from the Ponto-Caspian region. There were strong diel variations in the abundance (catch-per-unit-effort; CPUE) of *H. anomala*, with CPUE being low during the day but increasing by up to an order of magnitude at night. Abundance also varied seasonally, with CPUE increasing from mid-May to a peak in late June/early July, followed by a crash in mid-July. However, the seasonal variations in abundance were apparent only in nocturnal surveys, with CPUE during the day being low throughout the study. There were also seasonal variations in population structure (life stages, length distributions, sex ratios, reproductive state, fecundity). The nocturnal behaviour of *H. anomala* renders it difficult to assess its geographical distribution or population dynamics using only diurnal surveys or inappropriate sampling methods, which could underestimate the size, structure, reproductive potential and sustainability of non-indigenous populations of this invasive species. Surveillance programmes for *H. anomala* should therefore be conducted at night, at intervals throughout the year and targeting likely habitats using site-specific methods of proven effectiveness.

**Key words:** diel variation, *Hemimysis*, invasive, population dynamics, seasonal abundance

### Introduction

Biological invasions have increasingly become a global concern during the past two decades, both in terrestrial and aquatic ecosystems (Lodge 1993; Moyle and Light 1996; Mack et al. 2000; Manchester and Bullock 2000; Gherardi 2007). The potential impacts of non-indigenous species are numerous, and include loss of indigenous species, shifts in ecosystem functioning and socio-economic issues. Until 2004, only two species of mysid [*Mysis relicta* Lovén, 1862 and *Neomysis integer* (Leach, 1814)] had been recorded from UK fresh waters. *Hemimysis anomala* G. O. Sars, 1907, a species indigenous to the Ponto-Caspian region, was first recorded in the UK in 2004, in the catchment of the River Trent, central England, with subsequent investigations revealing that it was present in a number of canals, floodplain waterbodies and the main stem of the river (Holdich et al. 2006; Stubbington et al. 2008). Non-indigenous populations of the species have also been reported from Ireland, mainland Western Europe

and North America (Salemaa and Hietalahti 1993; Ketelaars et al. 1999; Borcharding et al. 2006; Pothoven et al. 2007; Wittmann 2007; Minchin and Holmes 2008; Wittmann and Ariani 2009; Marty et al. 2010); a detailed history of the invasion of Europe and North America by *H. anomala* is provided by Audzijonyte et al. (2008). One of the most frequently cited impacts following invasion by *H. anomala* has been predation (Ketelaars et al. 1999; Borcharding et al. 2006). *Hemimysis anomala* is largely zooplanktivorous, and could potentially cause changes in ecosystem functioning by increasing the predation pressure on particular components of the zooplankton, possibly leading to a reduction in grazing pressure on phytoplankton and in water clarity. There is also concern that *H. anomala* may compete with indigenous species for resources (Dumont and Muller 2010). This may be of particular importance to larval and juvenile fishes, the majority of which are zooplanktivorous and vulnerable to competition (Nunn et al. 2012). As there may be a causal link between the survival of fish larvae and

zooplankton dynamics (see Nunn et al. 2012), competition with *H. anomala* could have negative implications for fish recruitment success.

A number of studies have reported diel variations in the abundance of *H. anomala*, usually related to migrations from daytime refuges to open water at night (Salemaa and Hietalahti 1993; Ketelaars et al. 1999; Borchering et al. 2006; Pothoven et al. 2007; Walsh et al. 2010). Furthermore, Boscarino et al. (2012) and Brown et al. (2012) observed ontogenetic shifts in the diel behaviour of *H. anomala*, with juveniles migrating earlier in the evening and remaining higher in the water column at dawn than the more photophobic adults. Seasonal variations in population demographics (life stages, length distributions, sex ratios, reproductive state, fecundity) have also been described, both from the species' indigenous and introduced ranges (Salemaa and Hietalahti 1993; Ketelaars et al. 1999; Borchering et al. 2006; Stubbington et al. 2008; Dumont and Muller 2010; Brown et al. 2012). Notwithstanding, knowledge of the diel and seasonal aspects of *H. anomala* ecology is limited and requires further research (Lantry et al. 2010; Walsh et al. 2010). Furthermore, the implications of diel and seasonal variations in population dynamics for the surveillance and management of non-indigenous populations of *H. anomala* remain largely unexplored.

A prerequisite for successful management strategies is an effective surveillance programme, which should minimise the likelihood of invasions by detecting non-indigenous species before they establish self-sustaining populations (Britton et al. 2011). Surveillance programmes must also be able to detect changes in temporal and spatial structure relating to species distributions and abundances if management is to be effective (Cowx et al. 2009). However, surveillance programmes will only be effective if the chosen sampling strategies and methods are able to detect non-indigenous species at low levels of abundance, to avoid false-negative results through imperfect detection (Britton et al. 2011). The aim of this study was to investigate diel and seasonal variations in the population dynamics of *H. anomala*. The specific objectives were to: (1) compare the abundance of *H. anomala* between day and night ( $H_1$ : diurnal surveys underestimate abundance); (2) compare the seasonal variations in the abundance of *H. anomala* in diurnal and nocturnal surveys ( $H_1$ :

diurnal surveys underestimate seasonal variations in abundance); and (3) examine seasonal variations in the population structure (life stages, length distributions, sex ratios, reproductive state, fecundity) of *H. anomala* ( $H_1$ : diurnal surveys underestimate seasonal variations in population structure). The rationale was that diel and seasonal variations in the population dynamics of *H. anomala* could lead to underestimates of the size, structure, reproductive potential and sustainability of non-indigenous populations and, consequently, to invasions if only diurnal surveys are conducted. The implications of diel and seasonal variations in population dynamics for the surveillance and management of *H. anomala* are discussed, and recommendations for surveillance strategies for non-indigenous populations are provided.

## Methods

The study area was a boating marina (52.9476 °N, 1.09361 °W, surface area ~1 ha, max. water depth ~2 m) that is connected to the River Trent by a 30-m long × 20-m wide channel. The site, which is close to where *H. anomala* was first observed in 2004, was chosen after five individuals were captured there by the first author in November 2006 and subsequently in June, July, August and October 2009. The substratum consisted largely of gravel and silt, and vegetation (mainly *Acorus calamus* L., *Glyceria maxima* (Hartm.) and *Sparganium erectum* L.) was present in the shallow water along the shoreline. Moorings for boats consisted of floating pontoons. Traps were set in seven replicate locations along the shoreline (<1.5-m deep) of the marina at fortnightly intervals between May and July 2010. Qualitative samples of *H. anomala* (if present) were also collected fortnightly between May and July and monthly between August and October with a single sweep of a 240-µm-mesh dip net under a floating pontoon. Each trap was constructed using two transparent 2-L bottles, one without a top and the other without a bottom, with the latter inserted into the former and the join sealed with adhesive tape (Odenwald et al. 2005; Wittmann 2007, personal communication). Previous studies have demonstrated that *H. anomala* is more efficiently captured with traps than with hand-nets (Odenwald et al. 2005; Wittmann 2007). The traps were baited with *Spirulina* flake fish food, laid horizontally on the substratum, and emptied

every 3 h during five 24-h periods (total no. samples = 245 [seven trapping locations  $\times$  seven samples trap<sup>-1</sup> survey<sup>-1</sup>  $\times$  five 24-h surveys]). All *H. anomala* were preserved in 4% formalin solution prior to examination at the laboratory.

At the laboratory, all *H. anomala* were counted and measured (total length,  $L_T$ ; nearest 0.1 mm).  $L_T$  was measured from the tip of the rostrum to the distal end of the telson. Individuals were classified as either adult males, adult females or juveniles, with females further classified as either "virgin", "breeding" or "depleted". Males were identified by the presence of an elongated exopod on pleopod IV and females by the presence of a marsupium; breeding females were characterised by the presence of ova or embryos in the marsupium, while virgin and depleted females, respectively, were characterised by their small or empty marsupium (Ketelaars et al. 1999; Borcharding et al. 2006). Juveniles were identified by their lack of either elongated pleopods or a marsupium, and were generally <5.6 mm  $L_T$  (Borcharding et al. 2006; Holdich et al. 2006). For breeding females, fecundity was calculated as the number of ova or embryos in the marsupium.

All data were tested for normality and homogeneity of variances using one-sample Kolmogorov-Smirnov and Levene tests, respectively. The abundance of *H. anomala* in the traps was expressed as no. h<sup>-1</sup> (i.e. catch-per-unit-effort; CPUE), and diel variations in abundance (objective 1) were investigated by plotting CPUE over time for each 24-h survey. The maximum and mean ( $\pm$  S.D.) CPUE were calculated for diurnal (08:00, 11:00, 14:00, 17:00, 20:00) and nocturnal (23:00, 02:00, 05:00) samples (all surveys combined), and median CPUE was then compared between day and night using a Mann-Whitney *U*-test. In addition, the relative frequency of occurrence (%*O*) and relative abundance (%*A*) of *H. anomala* was calculated: %*O* = ( $O_d O_n^{-1}$ )  $\times$  100 and %*A* = ( $A_d A_n^{-1}$ )  $\times$  100, where  $O_d$  was the number of diurnal samples (all surveys combined) that contained *H. anomala*,  $O_n$  was the number of nocturnal samples (all surveys combined) that contained *H. anomala*,  $A_d$  was the mean CPUE of *H. anomala* in diurnal samples (all surveys combined), and  $A_n$  was the mean CPUE of *H. anomala* in nocturnal samples (all surveys combined). Seasonal variations in the abundance of *H. anomala* (objective 2) were assessed by plotting mean CPUE ( $\pm$  S.D.) in diurnal and nocturnal samples during each survey over time, and mean CPUE was then

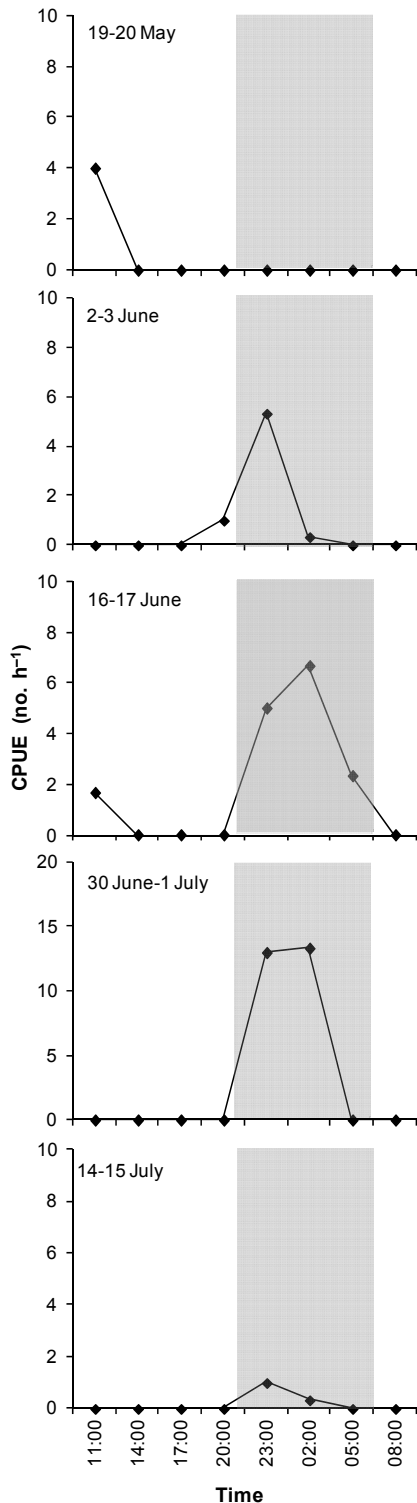
compared between day and night for each survey using an independent-samples *t*-test. Seasonal variations in population structure (objective 3) were investigated by plotting length-frequency histograms (0.2 mm length classes) for adult male, adult female and juvenile *H. anomala* for each survey. Mean  $L_T$  and length distributions were then compared between males and females using independent-samples *t*-tests and two-sample Kolmogorov-Smirnov tests, respectively. In addition, seasonal variations in the reproductive state of female *H. anomala* were investigated by calculating the relative (%) abundance of breeding, depleted and virgin individuals for each survey, as well as the mean ( $\pm$  S.D.) fecundity of breeding females.

## Results

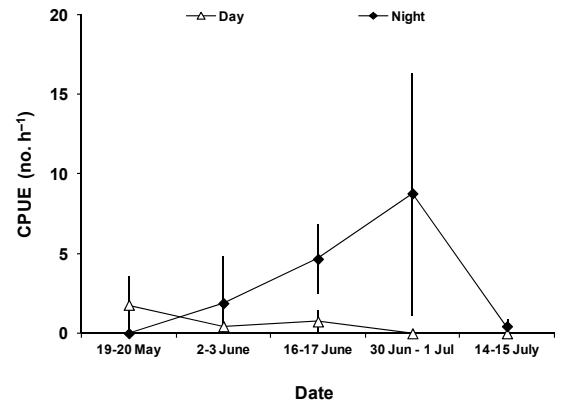
There were strong diel variations in the abundance of *H. anomala*, with CPUE generally being low during the day and peaking at night (Figure 1). Indeed, CPUE was invariably zero during the day (88% of daytime samples; max. = 4.00 h<sup>-1</sup>, mean  $\pm$  S.D. from all surveys combined = 0.27  $\pm$  0.87 h<sup>-1</sup>) but increased dramatically at night (max. = 13.33 h<sup>-1</sup>, mean  $\pm$  S.D. from all surveys combined = 3.16  $\pm$  4.64 h<sup>-1</sup>), when CPUE was up to an order of magnitude higher than during the day (Mann-Whitney *U*-test,  $P$  = 0.001). The relative frequency of occurrence and relative abundance of *H. anomala* in diurnal samples was 30% and 9% of nocturnal samples, respectively.

There were also seasonal variations in the abundance of *H. anomala*, with CPUE increasing from mid-May to a peak in late June/early July, followed by a crash in mid-July (after which trapping ceased, but qualitative sampling continued) (Figure 2). However, the seasonal variations were apparent only in nocturnal surveys, with CPUE during the day being low throughout the study (Figure 2). Differences between day and night were statistically significant in the mid- and late June surveys only (independent-samples *t*-tests,  $P$  = 0.005 and  $P$  = 0.034). No *H. anomala* were captured after mid-July (i.e. in August and September) until October (when some were captured using a dip net from under a floating pontoon).

There were seasonal variations in the population structure of *H. anomala*. In mid-May, the population was dominated by juveniles (modal  $L_T$  = 5.0 mm), with adults being less



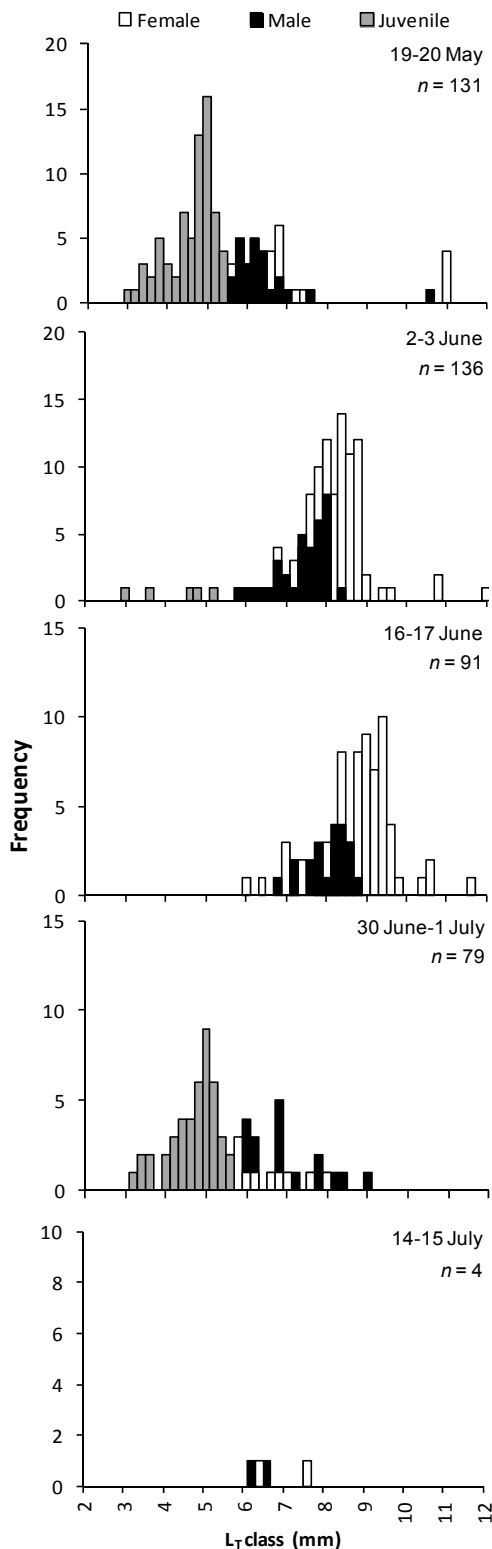
**Figure 1.** Diel variations in the catch-per-unit-effort (CPUE) of *Hemimysis anomala* in a boating marina on the River Trent, England. Nocturnal samples are indicated by the shaded area.



**Figure 2.** Seasonal variations in the mean ( $\pm$  S.D.) catch-per-unit-effort (CPUE) of *Hemimysis anomala* in a boating marina on the River Trent, England, in diurnal (five samples per survey) and nocturnal (three samples per survey) samples.

abundant (Figure 3). By contrast, in early and mid-June the population was dominated by adults, and juveniles were scarce (Figure 3). There were significant differences in the mean  $L_T$  (independent-samples  $t$ -tests,  $P < 0.001$  and  $P = 0.002$ ) and length distributions (two-sample Kolmogorov-Smirnov tests, both  $P < 0.001$ ) of males and females in early and mid-June (Table 1, Figure 3). By late June/early July, the population was dominated by a new cohort of juveniles (modal  $L_T = 5.0$  mm), whereas only adult *H. anomala* were captured in mid-July (Figure 3). Females were more abundant than males from mid-May to mid-June, whereas males were more abundant than females in late June/early July (Table 1).

There were seasonal variations in the reproductive state of female *H. anomala*. No breeding females were observed in mid-May, but relative abundance increased to  $\sim 75\%$  in early and mid-June before declining to  $< 20\%$  by late June/early July; there was then a second peak in mid-July when 100% of females were breeding (Table 1). The relative abundance of depleted females was low throughout the study period (Table 1). As anticipated, virgin females followed the opposite pattern to breeding females, with peaks in relative abundance occurring in mid-May and late June/early July (Table 1). There were seasonal variations in the fecundity of adult female *H. anomala*. No gravid females were observed in mid-May, but the peak in fecundity occurred only a fortnight later



**Figure 3.** Seasonal variations in the total length ( $L_T$ ) distributions (0.2 mm classes) of adult male, adult female and juvenile *Hemimysis anomala* in a boating marina on the River Trent, England.

(Table 1). Fecundity then steadily declined through June and July (Table 1). Maximum fecundity of *H. anomala* was 54 ova/embryos (Table 1).

### Discussion

*Hemimysis anomala* exhibited strong diel variations in abundance, with CPUE generally being low during the day and peaking at night. This can probably be explained largely by the nocturnal behaviour (rather than an absence) of *H. anomala*. Ketelaars et al. (1999) and Borcharding et al. (2006) observed that *H. anomala* undertook diel vertical migrations in deep (>20 m) waterbodies, being pelagic at night and demersal during the day, and identified light intensity as the proximate factor controlling the behaviour. A number of other studies have related diel variations in abundance to changes in various aspects of the light regime (Lindström 2000; Pothoven et al. 2007; Walsh et al. 2010; Boscarino et al. 2012; Brown et al. 2012). In shallow waterbodies, diel vertical migrations may be replaced by horizontal migrations between refuges in the littoral zone during the day and open water at night, as has been observed for some zooplankton species and *N. integer* (Debus et al. 1992; Lauridsen et al. 1996). Indeed, during the present study, a large swarm of *H. anomala* formed under a floating pontoon during the day and then dispersed into open water at night (AD Nunn, personal observation). A similar phenomenon was observed by Borcharding et al. (2006), Dumont (2006) and Pothoven et al. (2007), with Stubbington et al. (2008) detecting a positive association between the amount of cover provided by anthropogenic structures and the occurrence of *H. anomala* in the littoral zone.

There were also seasonal variations in the abundance of *H. anomala*, with CPUE increasing from mid-May to a peak in late June/early July, followed by a crash in mid-July; none were captured thereafter until October. By contrast, Stubbington et al. (2008) observed that densities peaked in September and then gradually declined until January, with no *H. anomala* observed during February or March. However, juveniles then appeared in April and abundance increased until July before, similar to this study, declining in August. Borcharding et al. (2006), whose study was conducted over the winter, found that the abundance of *H. anomala* increased from

**Table 1.** Seasonal variations in the population dynamics of *Hemimysis anomala* in a boating marina on the River Trent, England.

Date	mean $L_T$ (mm) $\pm$ S.D.			$L_T$ range (mm)			Ratio $\text{♂}:\text{♀}$	$B$	$D$	$V$	$F_{mn}$	$F_{mx}$
	♂	♀	J	♂	♀	J						
19-20 May	6.4 $\pm$ 1.0	6.8 $\pm$ 1.5	4.6 $\pm$ 0.6	5.5-10.5	5.6-11.0	3.0-5.4	0.68	0%	11%	89%	–	–
2-3 June	7.4 $\pm$ 0.6	8.1 $\pm$ 0.8	4.2 $\pm$ 0.9	5.8-8.3	5.9-11.9	2.9-5.2	0.36	75%	11%	14%	27 $\pm$ 6	46
16-17 June	8.0 $\pm$ 0.5	8.7 $\pm$ 1.0	–	6.8-8.8	6.0-11.6	–	0.30	73%	26%	1%	25 $\pm$ 9	54
30 June-1 July	6.9 $\pm$ 0.9	6.4 $\pm$ 0.8	4.6 $\pm$ 0.6	5.6-8.9	5.6-8.0	3.2-5.5	1.90	17%	0%	83%	–	19
14-15 July	–	–	–	6.2-6.6	6.4-7.5	–	–	100%	0%	0%	–	17

$L_T$  total length, ♂ male, ♀ female, J juvenile,  $B$  breeding,  $D$  depleted,  $V$  virgin,  $F_{mn}$  mean fecundity,  $F_{mx}$  max. fecundity, – insufficient data

September to a peak in December, before declining to a minimum in April. In this study, the pattern of seasonal variations in abundance was apparent only in nocturnal surveys, because CPUE during the day was low throughout the period. Indeed, CPUE was invariably zero during the day but increased dramatically at night, when abundance was up to an order of magnitude higher than during the day. This has important implications for the assessment and management of non-indigenous *H. anomala* populations, as surveillance programmes conducted only during the day are unlikely to be effective at detecting this nocturnal species (and may produce false-negative results) and will, therefore, underestimate population abundance and distribution.

It is possible that the population crash observed in the current study was a natural seasonal cycle linked to changes in water temperature or food availability, as has been documented in other aquatic invertebrate species (Sommer et al. 1986; Panov and McQueen 1998). Predation by fishes may also have been a factor, as has been observed for zooplankton communities (Hrbáček et al. 1961; Brooks and Dodson 1965; Lazzaro 1987), with larval and juvenile fishes in particular having the potential to suppress populations of large zooplankton species (Mehner and Thiel 1999; Nunn et al. 2012). However, no *H. anomala* were observed in the diets of 0+ perch *Perca fluviatilis* L. or roach *Rutilus rutilus* (L.) in the study area in 2009 or 2010 (LH Tewson, personal communication), despite being present and occasionally abundant. Conversely, the population crash may have been part of a ‘boom-and-bust’ cycle related to the invasion process (Williamson and Fitter 1996; Simberloff and Gibbons 2004), as has been observed in other species, as there appear to be few, if any, published examples of *H. anomala* sustaining massive populations over

more than a few years. Continued monitoring of this and other non-indigenous populations may corroborate or refute this theory.

In mid-May, the population of *H. anomala* was dominated by juveniles, whereas adults were dominant in early and mid-June. By late June/early July, the population was dominated by a new cohort of juveniles, whereas only adult *H. anomala* were captured in mid-July. This has ramifications for the assessment and management of non-indigenous *H. anomala* populations, as juveniles are smaller than adults and so are more likely than adults to avoid detection during routine sampling programmes, which could delay the implementation of management strategies at certain times of the year. There were significant differences in the mean  $L_T$  and length distributions of male and female *H. anomala*, mainly because of the presence of large females; this corroborates studies by Salemaa and Hietalahti (1993) and Ketelaars et al. (1999). There were also seasonal variations in sex ratio, with females more abundant than males from mid-May to mid-June, and males more abundant than females in late June/early July, which could possibly be related to differential mortality between males and females (Ketelaars et al. 1999).

No breeding females were observed in mid-May, but relative abundance increased to ~75% in early and mid-June before declining to <20% by late June/early July; there was then a second peak in mid-July when 100% of females were breeding. This, together with the occurrence of two cohorts of juveniles, suggests that *H. anomala* bred at least twice between May and July, and possibly also in April (as juveniles were present in May). Similarly, Borchherding et al. (2006) observed two cohorts per year, one in April/May and one in September/October, but suspected that there could be a third. Indeed,

Dumont and Muller (2010) observed that *H. anomala* reproduced three times a year, in March/April, June/July and September/October. No gravid females were observed in mid-May, but the peak in fecundity occurred only a fortnight later; fecundity then steadily declined through June and July. These results corroborate those reported in the literature (Salemaa and Hietalahti 1993; Ketelaars et al. 1999; Borcharding et al. 2006). The seasonal variations in reproductive state and fecundity are important, as they could lead to underestimates of the reproductive potential or sustainability of non-indigenous *H. anomala* populations if surveys are conducted at inappropriate times of the year (e.g. when breeding activity or fecundity are low).

*Hemimysis anomala* is one of the most invasive aquatic species in Europe and North America (Wittmann 2007; Audzijonyte et al. 2008), with the potential to disperse through canal networks and colonise the lower reaches and estuaries of major rivers (Stubbington et al. 2008; Brown et al. 2012). In addition, the rehabilitation of floodplain ecosystems by connecting man-made waterbodies to rivers (Nunn et al. 2007a) may facilitate consolidation and expansion of its populations, as well as those of other non-indigenous species already present or introduced in the future (Nunn et al. 2007b). It is therefore essential to establish effective surveillance and management strategies to help control the species' dispersal and impacts. Resource use may be substantially greater over the diel cycle than during daylight or darkness alone, suggesting that estimates of niche breadth based solely upon diurnal (or nocturnal) studies are potentially inaccurate (Copp 2008). Similarly, the nocturnal behaviour of *H. anomala* (and other species) renders it difficult to assess its geographical distribution or population dynamics using only diurnal surveys or inappropriate sampling methods, which could underestimate the size, structure, reproductive potential and sustainability of non-indigenous populations of this invasive species. In this study, few *H. anomala* were captured during the day, despite being present in large numbers at night. Indeed, the relative frequency of occurrence ('detection efficiency') of *H. anomala* in diurnal samples was only 30% of nocturnal samples. Furthermore, the relative abundance of *H. anomala* in diurnal samples was only 9% of nocturnal samples, and fecundity could not be accurately determined from diurnal surveys as

only two gravid females were captured during the day.

It should be borne in mind that the semi-quantitative (i.e. CPUE) data in this study were obtained using traps, and that it is possible that other (passive or active) methods may have produced different results and, therefore, conclusions. Other methods that have been used to study *H. anomala* include various nets, dive surveys and lights, but all have biases or limitations related to their efficacy in particular habitats or waterbodies (Salemaa and Hietalahti 1993; Ketelaars et al. 1999; Borcharding et al. 2006; Pothoven et al. 2007; Stubbington et al. 2008; Walsh et al. 2010). For example, Brooking et al. (2010) stated that, despite intensive monitoring, *H. anomala* was detected only in nocturnal zooplankton tows and fish diets, indicating that it may go undetected in traditional surveys. Similarly, Stubbington et al. (2008) considered that the occupation of anthropogenic structures by *H. anomala* during the day renders net-based surveys ineffective in shallow waterbodies. It is thus essential that surveillance programmes are designed using methods of known efficacy to optimise management outcomes (Britton et al. 2011). Surveillance programmes for *H. anomala* should therefore be conducted at night, at intervals throughout the year and targeting likely habitats using site-specific methods of proven effectiveness.

## Acknowledgements

The authors would like to thank Colwick Park for access to the marina and Colwick Boat Club for the use of their facilities during the 24-h surveys. No funding was received to conduct the surveys reported in this paper. The paper benefited greatly from the constructive criticism of two anonymous referees.

## References

- Audzijonyte A, Wittmann KJ, Vaeniola R (2008) Tracing recent invasions of the Ponto-Caspian mysid shrimp *Hemimysis anomala* across Europe and to North America with mitochondrial DNA. *Diversity and Distributions* 14: 179-186, <http://dx.doi.org/10.1111/j.1472-4642.2007.00434.x>
- Borcharding J, Murawski S, Arndt H (2006) Population ecology, vertical migration and feeding of the Ponto-Caspian invader *Hemimysis anomala* in a gravel-pit lake connected to the River Rhine. *Freshwater Biology* 51: 2376-2387, <http://dx.doi.org/10.1111/j.1365-2427.2006.01666.x>
- Boscarino BT, Halpin KE, Rudstam LG, Walsh MG, Lantry BF (2012) Age-specific light preferences and vertical migration patterns of a Great Lakes invasive invertebrate, *Hemimysis anomala*. *Journal of Great Lakes Research* (in press), <http://dx.doi.org/10.1016/j.jglr.2011.06.001>

- Britton JR, Pegg J, Gozlan RE (2011) Quantifying imperfect detection in an invasive pest fish and the implications for conservation management. *Biological Conservation* 144: 2177-2181, <http://dx.doi.org/10.1016/j.biocon.2011.05.008>
- Brooking TE, Rudstam LG, Krueger SD, Jackson JR, Welsh AB, Fetzer WW (2010) First occurrence of the mysid *Hemimysis anomala* in an inland lake in North America, Oneida Lake, NY. *Journal of Great Lakes Research* 36: 577-581, <http://dx.doi.org/10.1016/j.jglr.2010.04.004>
- Brooks JL, Dodson SI (1965) Predation, body size, and composition of plankton. *Science* 150: 28-37, <http://dx.doi.org/10.1126/science.150.3692.28>
- Brown ME, Morse R, O'Neill K (2012) Spatial, seasonal, and diel distribution patterns of *Hemimysis anomala* in New York State's Finger Lakes. *Journal of Great Lakes Research* (in press), <http://dx.doi.org/10.1016/j.jglr.2011.04.011>
- Copp GH (2008) Putting multi-dimensionality back into niche: diel vs. day-only niche breadth separation in stream fishes. *Fundamental and Applied Limnology* 170: 273-280, <http://dx.doi.org/10.1127/1863-9135/2008/0170-0273>
- Cowx IG, Harvey JP, Noble RA, Nunn AD (2009) Establishing survey and monitoring protocols for the assessment of conservation status of fish populations in river Special Areas of Conservation in the UK. *Aquatic Conservation: Marine and Freshwater Ecosystems* 19: 96-103, <http://dx.doi.org/10.1002/aqc.968>
- Debus L, Mehner T, Thiel R (1992) Spatial and diel patterns of migration for *Neomysis integer*. In: Köhn J, Jones MB, Moffat A (eds), *Taxonomy, Biology and Ecology of (Baltic) Mysids (Mysidacea: Crustacea)*. Rostock University, Rostock, pp 79-82
- Dumont S (2006) A new invasive species in the north-east of France, *Hemimysis anomala* G. O. Sars 1907. *Crustaceana* 79:1269-1274, <http://dx.doi.org/10.1163/156854006778859560>
- Dumont S, Muller CD (2010) Distribution, ecology and impact of a small invasive shellfish, *Hemimysis anomala* in Alsatian water. *Biological Invasions* 12: 495-500, <http://dx.doi.org/10.1007/s10530-009-9453-0>
- Gherardi F (ed) (2007) *Biological Invaders in Inland Waters: Profiles, Distribution and Threats. Invading Nature – Springer Series in Invasion Ecology, Volume 2*. Springer, Dordrecht, The Netherlands, 733 pp
- Holdich D, Gallagher S, Rippon L, Harding P, Stubbington R (2006) The invasive Ponto-Caspian mysid, *Hemimysis anomala*, reaches the UK. *Aquatic Invasions* 1: 4-6, <http://dx.doi.org/10.3391/ai.2006.1.1.2>
- Hrbáček J, Dvorakova M, Korinek V, Procházková L (1961) Demonstration of the effect of fish stock on the species composition of zooplankton and the intensity of metabolism of the whole plankton association. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* 14: 192-195
- Ketelaars HAM, Lambregts-van de Clundert FE, Carpentier CJ, Wagenvoort AJ, Hoogenboezem W (1999) Ecological effects of the mass occurrence of the Ponto-Caspian invader, *Hemimysis anomala* G.O. Sars, 1907 (Crustacea: Mysidacea), in a freshwater storage reservoir in the Netherlands, with notes on its autecology and new records. *Hydrobiologia* 394: 233-248, <http://dx.doi.org/10.1023/A:1003619631920>
- Lantry BF, Walsh MG, Johnson JH, McKenna JE Jr (2010) Occurrence of the Great Lake's most recent invader, *Hemimysis anomala*, in the diet of fishes in southeastern Lake Ontario. *Journal of Great Lakes Research* 36: 179-183, <http://dx.doi.org/10.1016/j.jglr.2009.12.002>
- Lauridsen TL, Pedersen LJ, Jeppesen E, Sondergaard M (1996) The importance of macrophyte bed size for cladoceran composition and horizontal migration in a shallow lake. *Journal of Plankton Research* 18: 2283-2294, <http://dx.doi.org/10.1093/plankt/18.12.2283>
- Lazzaro X (1987) A review of planktivorous fishes: their evolution, feeding behaviours, selectivities, and impacts. *Hydrobiologia* 146: 97-167, <http://dx.doi.org/10.1007/BF00008764>
- Lindström M (2000) Eye function of Mysidacea (Crustacea) in the northern Baltic Sea. *Journal of Experimental Marine Biology and Ecology* 246: 85-101, [http://dx.doi.org/10.1016/S0022-0981\(99\)00178-1](http://dx.doi.org/10.1016/S0022-0981(99)00178-1)
- Lodge DM (1993) Biological invasions: lessons for ecology. *Trends in Ecology and Evolution* 8: 133-137, [http://dx.doi.org/10.1016/0169-5347\(93\)90025-K](http://dx.doi.org/10.1016/0169-5347(93)90025-K)
- Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* 10: 689-710, [http://dx.doi.org/10.1890/1051-0761\(2000\)010\[0689:BICEGJ\]2.0.CO;2](http://dx.doi.org/10.1890/1051-0761(2000)010[0689:BICEGJ]2.0.CO;2)
- Manchester SJ, Bullock JM (2000) The impacts of non-native species on UK biodiversity and the effectiveness of control. *Journal of Applied Ecology* 37: 845-864, <http://dx.doi.org/10.1046/j.1365-2664.2000.00538.x>
- Marty J, Bowen K, Koops MA, Power M (2010) Distribution and ecology of *Hemimysis anomala*, the latest invader of the Great Lakes basin. *Hydrobiologia* 647: 71-80, <http://dx.doi.org/10.1007/s10750-009-9990-7>
- Mehner T, Thiel R (1999) A review of predation impact by 0+ fish on zooplankton in fresh and brackish waters of the temperate northern hemisphere. *Environmental Biology of Fishes* 56: 169-181, <http://dx.doi.org/10.1023/A:1007532720226>
- Minchin D, Holmes JMC (2008) The Ponto-Caspian mysid, *Hemimysis anomala* G.O. Sars 1907 (Crustacea), arrives in Ireland. *Aquatic Invasions* 3: 247-249, <http://dx.doi.org/10.3391/ai.2008.3.2.19>
- Moyle PB, Light T (1996) Biological invasions of fresh water: empirical rules and assembly theory. *Biological Conservation* 78: 149-161, [http://dx.doi.org/10.1016/0006-3207\(96\)00024-9](http://dx.doi.org/10.1016/0006-3207(96)00024-9)
- Nunn AD, Harvey JP, Cowx IG (2007a) Benefits to 0+ fishes of connecting man-made waterbodies to the lower River Trent, England. *River Research and Applications* 23: 361-376, <http://dx.doi.org/10.1002/rra.993>
- Nunn AD, Bolland JD, Harvey JP, Cowx IG (2007b) Establishment of self-sustaining populations of non-native fish species in the River Trent and Warwickshire Avon, UK, indicated by the presence of 0+ fish. *Aquatic Invasions* 2: 190-196, <http://dx.doi.org/10.3391/ai.2007.2.3.6>
- Nunn AD, Tewson LH, Cowx IG (2012) The foraging ecology of larval and juvenile fishes. *Reviews in Fish Biology and Fisheries* 22: 377-408, <http://dx.doi.org/10.1007/s11160-011-9240-8>
- Odenwald C, Krug K, Grabow K, Martens A (2005) Eine Reusenfalle zum Nachweis von *Hemimysis anomala* (Crustacea: Mysidacea). *Lauterbornia* 55: 97-105
- Panov VE, McQueen DJ (1998) Effects of temperature on individual growth rate and body size of a freshwater amphipod. *Canadian Journal of Zoology* 76: 1107-1116, <http://dx.doi.org/10.1139/z98-025>
- Pothoven SA, Grigorovich IA, Fahnenstiel GL, Balcer MD (2007) Introduction of the Ponto-Caspian bloody-red mysid *Hemimysis anomala* into the Lake Michigan basin. *Journal of Great Lakes Research* 33: 285-292, [http://dx.doi.org/10.3394/0380-1330\(2007\)33\[285:IOTPB\]2.0.CO;2](http://dx.doi.org/10.3394/0380-1330(2007)33[285:IOTPB]2.0.CO;2)
- Salemaa H, Hietalahti V (1993) *Hemimysis anomala* G. O. Sars (Crustacea: Mysidacea) – immigration of a Pontocaspian mysid into the Baltic Sea. *Annales Zoologici Fennici* 30: 271-276
- Simberloff D, Gibbons L (2004) Now you see them, now you don't: population crashes of established introduced species. *Biological Invasions* 6: 161-172, <http://dx.doi.org/10.1023/B:BINV.0000022133.49752.46>



- Sommer U, Gliwicz ZM, Lampert W, Duncan A (1986) The plankton ecology group model of seasonal succession of planktonic events in fresh waters. *Archiv für Hydrobiologie* 106: 433-472
- Stubbington R, Terrell-Nield C, Harding P (2008) The first occurrence of the Ponto-Caspian invader, *Hemimysis anomala* G. O. Sars, 1907 (Mysidacea) in the U.K. *Crustaceana* 81: 43-55, <http://dx.doi.org/10.1163/156854008783244816>
- Walsh MG, Lantry BF, Boscarino B, Bowen K, Gerlofsma J, Schaner T, Back R, Questel J, Smythe AG, Cap R, Goehle M, Young B, Chalupnicki M, McKenna JE (2010) Early observations on an emerging Great Lakes invader *Hemimysis anomala* in Lake Ontario. *Journal of Great Lakes Research* 36: 499-504, <http://dx.doi.org/10.1016/j.jglr.2010.04.012>
- Williamson MH, Fitter A (1996) The characters of successful invaders. *Biological Conservation* 78: 163-170, [http://dx.doi.org/10.1016/0006-3207\(96\)00025-0](http://dx.doi.org/10.1016/0006-3207(96)00025-0)
- Wittmann KJ (2007) Continued massive invasion of Mysidae in the Rhine and Danube river systems, with first records of the order Mysidacea (Crustacea: Malacostraca: Peracarida) for Switzerland. *Revue Suisse de Zoologie* 114: 65-86, <http://dx.doi.org/10.1007/s10530-008-9257-7>
- Wittmann KJ, Ariani AP (2009) Reappraisal and range extension of non-indigenous Mysidae (Crustacea, Mysida) in continental and coastal waters of eastern France. *Biological Invasions* 11: 401-407, <http://dx.doi.org/10.1007/s10530-008-9257-7>