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Research Article

# Revisiting Elton's copepods: lake construction has altered the distribution and composition of calanoid copepods in the British Isles

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## Abstract

It is now widely accepted that the construction of new lakes, ponds and reservoirs facilitates the invasion of non-indigenous aquatic species, due largely to low biotic resistance from native communities. The role played by constructed waters appears to be a particularly frequent feature of zooplankton invasions. Charles Elton, in his classic 1927 book "Animal Ecology", noted that the estuarine calanoid copepod *Eurytemora velox* had invaded constructed inland waters in Britain and highlighted the lack of a key species, *Eudiaptomus gracilis*, in allowing its establishment. At the time, Elton's observations were dismissed and his findings largely consigned to obscurity. Using occurrence records gathered since this time and current knowledge of calanoid copepod ecology and invasion biology, we re-examined the distributions of three species of freshwater calanoid copepods in the British Isles to: 1) determine the legacy of lake and pond construction on their distributions, and 2) reassess the conclusions made by Elton in light of this knowledge. The lack of natural lakes in the south and east of England, and the subsequent widespread development of new lakes and ponds, has altered calanoid copepod distributions. The common *E. gracilis* occurs frequently in the north and west of the British Isles in natural lakes, and is found in the south and east in constructed waters. The estuarine *E. velox* was found only in 3 natural freshwater sites, all in close proximity to the coast, but has been recorded in 23 constructed sites, many of these well inland. Elton noted a general lack of co-existence between *E. velox* and *E. gracilis*, with the relatively slow establishment rates of *E. gracilis* thought key in allowing the estuarine species to invade. However, subsequent collections suggest long-term co-occurrence of these species at some sites. We suggest that *E. velox* has now successfully invaded freshwaters in the British Isles. *Eudiaptomus vulgaris* is not known from natural lakes, but has been recorded in several constructed waters, and appears to have invaded Britain facilitated by lake construction. Current knowledge supports Elton's contention that constructed waters are more readily invaded than natural waters, and that biotic resistance due to the presence of key species is important. While some specific criticisms of Elton's ideas were valid, we argue that Elton's concepts regarding constructed waters and invasions were in many ways correct and prescient of current understanding.

**Key words:** artificial waters, biological invasions, biotic resistance, dams, exotic species, Charles Elton

## Introduction

The construction of lakes, ponds and reservoirs, commonly referred to as "artificial" or "man-made" waters, has increased the number, area and spatial distribution of lakes in many areas globally (e.g., Smith and Lyle 1979; Lowe and Green 1987; Rosenberg et al. 2000). Such waters have been commonly observed to have invasion rates by non-indigenous species greater than those of natural lakes (e.g., Havel et al. 2005; Johnson et al. 2008; Banks and Duggan 2009). Zooplankton provide well recognised examples of this trend. For example, the old world tropical cladoceran *Daphnia lumholtzi* Sars, 1885 invaded a reservoir in Texas, USA, in 1990 and spread to over 125 lakes in North America within a decade of its initial establishment, with reservoirs first to be invaded (Havel et al. 2005). Similarly, the spiny waterflea *Bythotrephes longimanus* (Leydig, 1860), native to Europe and Asia, is known to occur more frequently in constructed than natural lakes in North

America (Johnson et al. 2008). In New Zealand the calanoid copepods *Boeckella minuta* Sars, 1896 and *B. symmetrica* Sars, 1908 from Australia, *Sinodiaptomus valkanovi* Kiefer, 1938 from Japan and *Skistodiaptomus pallidus* (Herrick, 1879) from North America, were (until recently) all only recorded from constructed waters (Duggan et al. 2006; Banks and Duggan 2009; Makino et al. 2010). Parkes and Duggan (2012) found that across New Zealand, zooplankton assemblages differed between natural and constructed waters. Assemblages of natural waters contained planktonic species well adapted to pelagic conditions, with composition governed by trophic state, while in constructed waters assemblages were characterised more by benthic species, with composition associated with opportunity for establishment (e.g., proximity to other lakes). The dominance of poorly adapted species in newly constructed water bodies may reduce the strength of biotic interactions, such as competition or predation, leading to a greater ease of establishment of new arrivals (i.e., reduced biotic resistance). Experimental work suggests that the presence of key native species in natural waters, which may take some time to establish in constructed waters, can provide resistance to invasion by non-native species (Dzialowski 2010; Taylor and Duggan 2012).

In the British Isles, interesting distribution patterns of calanoid copepod species in relation to the construction of new waters were noted in the early 20$^{th}$ century, although these observations were subsequently neglected. In his 1927 book, “Animal Ecology”, the “father of invasion biology” Charles Elton (1927) observed that the estuarine species *Eurytemora velox* (Lilljeborg, 1853) had invaded several constructed inland waters, mostly created less than 20 years prior to observations being made. Lowndes (1929), however, was critical of Elton’s observations, noting that *E. velox* was found in some waters significantly older than suggested by Elton, including one natural lake (Lough Derg, Ireland). Elton (1927, 1929) also noted a general lack of co-existence between the estuarine *E. velox* and the common freshwater species *Eudiaptomus gracilis* (Sars, 1862) in the invaded freshwaters. Elton believed the absence of *E. gracilis* was key in allowing the estuarine *E. velox* to invade. Lowndes (1929), in return, provided a number of examples where these species were known to co-occur. Knowledge of calanoid copepod distributions at this time was in its infancy. With more than 85 years of further observations of calanoid copepods, we re-examine the distributions of calanoid copepods in the British Isles, to reassess the conclusions of Elton (1927, 1929) and Lowndes (1929) in light of current knowledge.

## Methods

The distributions of freshwater calanoid copepod species in the British Isles were examined through literature searches, and the sampling of selected constructed sites in late 2016. Calanoid copepods are better defined morphologically than other zooplankton groups, and generally have distinct geographical native ranges, making them ideal model organisms. Further, other than some alterations to the nomenclature of genera, the taxonomy and species recognised in the British Isles has remained unchanged since the late-1800s (Gurney 1931), providing confidence in the quality of records obtained from literature searches. The distributions of three species were considered; *Eudiaptomus gracilis, E. vulgaris* (Schmeil, 1896) and *Eurytemora velox*. Web of Science, Google Scholar and Google Books were utilised to search for records of copepod occurrences in October 2016, using search terms such as “zooplankton”, “calanoid copepods” and each of the respective species names, combined with geographical specifiers including “British”, “Britain”, “England”, “Scotland” and “Ireland”. Further, publications were examined that had cited Gurney (1931) and Harding and Smith (1960), the primary identification guides for calanoid copepods in the British Isles. Targeted species focused particularly on those that occur in England, as this is where the construction of new waters has been primarily concentrated (Smith and Lyle 1979; Rowan 2010). We did not consider *Mixodiaptomus laciniatus*, *Arctodiaptomus laticeps* and *A. wierzejskii*, as these have distributions restricted primarily to northern, montane and western Irish localities, with sites of occurrence known to be congruent with the history of glacial retreat (Fryer and Joyce 1981). Sites considered were permanent, non-saline, ponds, lakes and reservoirs. Species records were included in the dataset only where the exact location of the waterbody could be ascertained, and where the origin of the waterbody (natural or constructed) could be determined. We accept that not all published records may have been located, particularly in more obscure literature, but believe we have acquired records for the majority of sites examined. As a result, we believe we can be confident in the patterns identified.

To supplement the published data for constructed waters, which are under-represented numerically and spatially in the literature, we conducted new sampling. We sampled 14 ponds from Maidstone, London, Oxford, Cambridge, York, Glasgow and Edinburgh using 70 µm mesh nets, towed multiple times horizontally from the shore. Sites included several constructed waters noted by Elton (1929) to contain the estuarine *Eurytemora velox*, to determine whether populations had persisted:

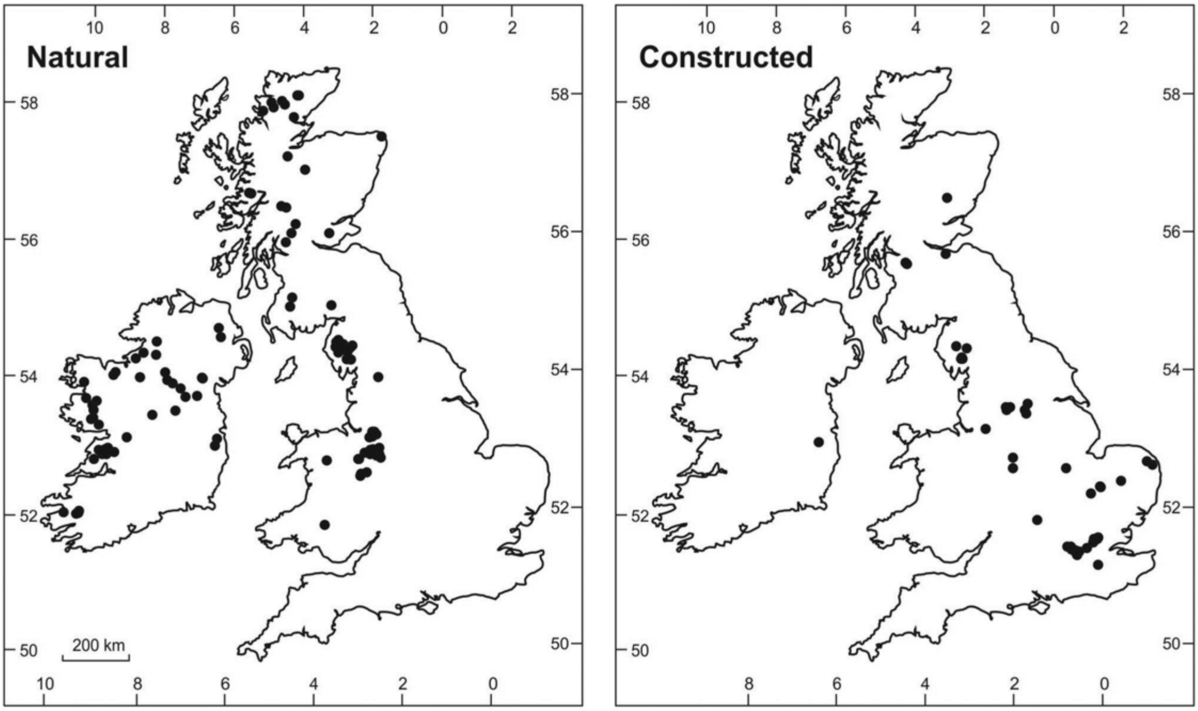


**Figure 1.** Distribution of *Eudiaptomus gracilis* in lakes in the British Isles. Left panel = natural waters; Right panel = constructed waters. For site names, geographical co-ordinates, and publications from which the records are obtained, refer to Supplementary Tables S1 (natural) and S2 (constructed).

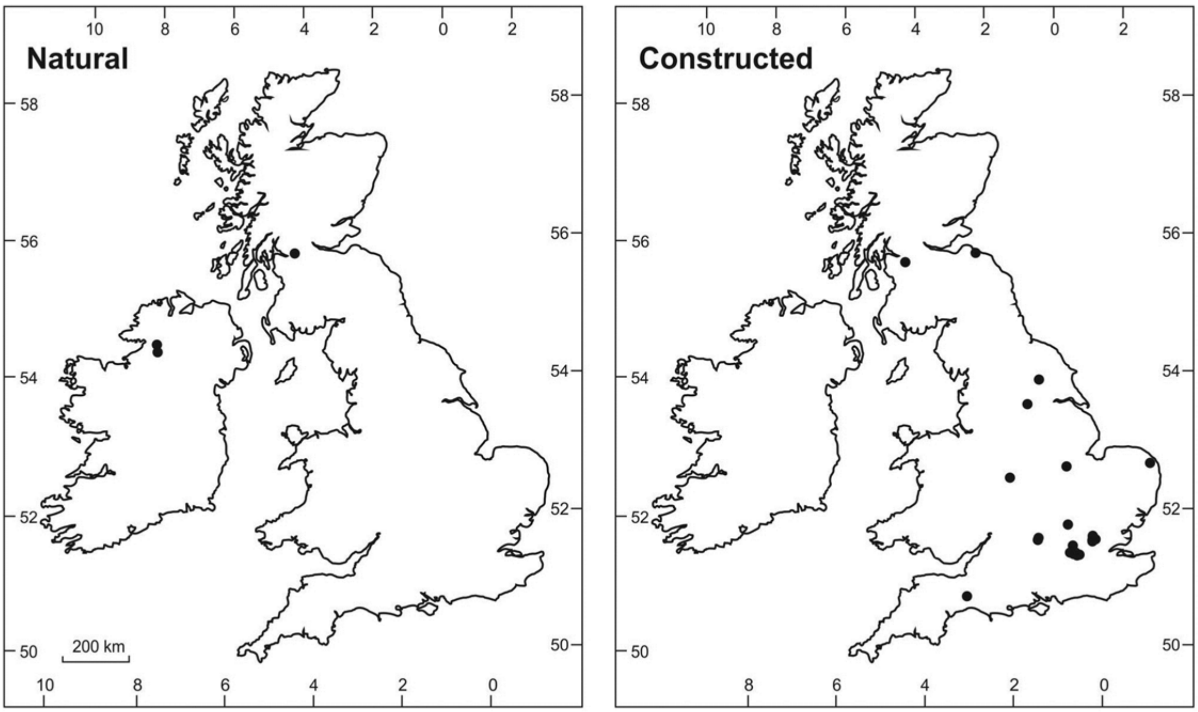


**Figure 2.** Distribution of *Eurytemora velox* in lakes in the British Isles. Left panel = natural waters; Right panel = constructed waters. For site names, geographical co-ordinates, and publications from which the records are obtained, refer to Supplementary Tables S3 (natural) and S4 (constructed).

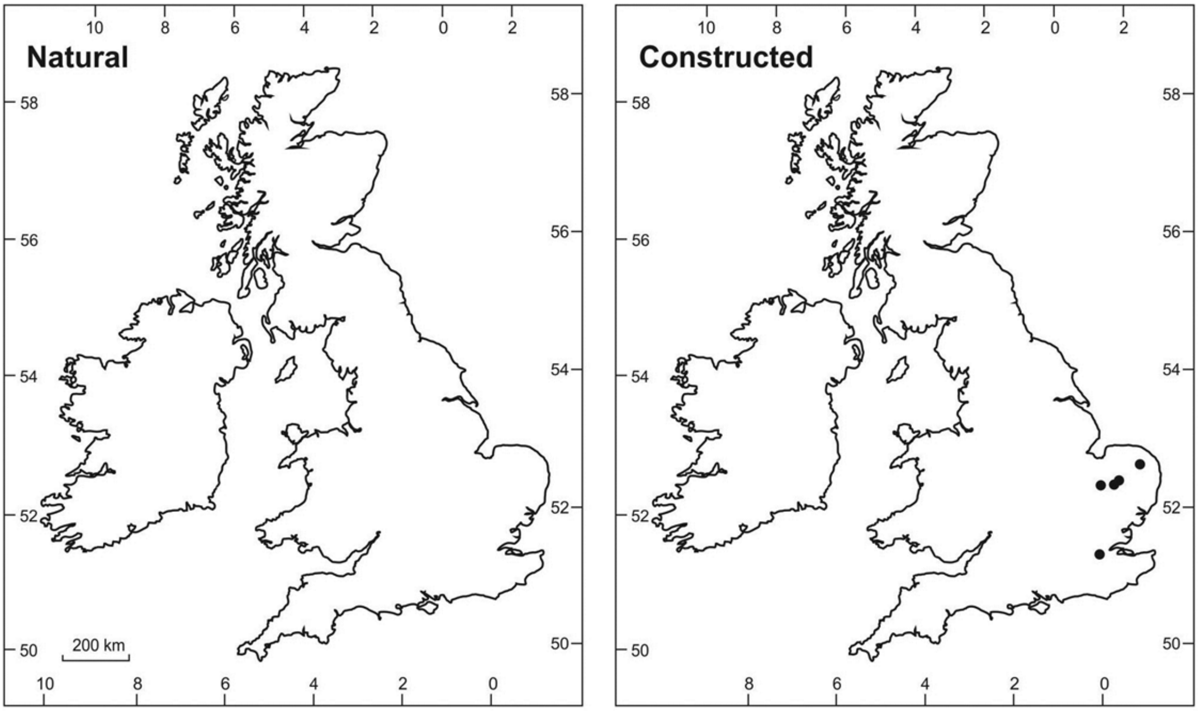


**Figure 3.** Distribution of *Eudiaptomus vulgaris* in lakes in the British Isles. Left panel = natural waters; Right panel = constructed waters. For site names, geographical co-ordinates, and publications from which the records are obtained, refer to Supplementary Table S5 (constructed).

Castlemilk Loch, Glasgow, Scotland (15 October 2016), The Long Water, Hampton Court (23 September 2016), Oxford Botanic Gardens and the Oxford Waterworks Pond (all in England; 29 September 2016). Samples were preserved using isopropyl alcohol for a final concentration of >70%. Entire samples were scanned, and standard taxonomic keys were used to identify the three species (e.g., Harding and Smith 1960). The distributions of freshwater calanoid copepods were plotted according to whether they occurred in natural or constructed water bodies. The differences in frequency of occurrence between water body type was examined using separate Fisher's exact tests for each species.

## Results

The distributions of natural and constructed lakes and ponds identified during our study are congruent with expected distributions, with natural waters primarily in the north and west and constructed waters primarily in the south-east (*sensu* Smith and Lyle 1979; Rowan 2010). *Eudiaptomus gracilis*, a broadly distributed species from Eurasia and Alaska (Reid and Williamson 2010), was recorded in 104 natural water bodies, predominantly in the north and east of the British Isles (Figure 1a; Supplementary Table S1). However, when considering only constructed water bodies, the species has been found in 50 waterbodies and primarily had a south-eastern distribution (Figure 1b; Supplementary Table S2). Considering lakes and ponds with copepod records from this study, this species was far more likely to be recorded in natural than constructed waters (Fisher's Exact Test P value <0.001). The Palearctic estuarine *E. velox* was found in three natural freshwater sites, although these were all close to the coast (<20 km; Figure 2a; Supplementary Table S3). In contrast, *E. velox* was recorded in 23 constructed sites, including a new record from a pond at the University of York, Heslington East campus, filled in August 2010 (Figure 2b; Supplementary Table S4); no other calanoid copepods were recorded at this site. Of the sites we resampled where Elton (1929) noted the presence of *E. velox*, our samples from Castlemilk Loch and the Long Water, Hampton Court contained only *E. gracilis*, the Oxford Waterworks Pond had *E. velox* and *E. gracilis* in roughly equal proportions, while the Oxford Botanic Gardens pond (which held little water) was devoid of either species. Considering lakes and ponds with copepod records from this study, we found *E. velox* in 3 of 106 natural and in 23 of 60 constructed lakes, indicating that this species was far more likely to be found in constructed than natural waters (Fisher's Exact Test P value <0.0001). *Eudiaptomus vulgaris*, an Asiatic and European species (Alfonso and Belmonte 2011), was recorded from no natural lakes, but was found in five constructed waters, primarily in the Norfolk area of south-east England (Figure 3; Supplementary Table S5). A Fisher's Exact Test indicated this species was far more likely to be found in constructed than natural waters (P value <0.01). No new non-indigenous species were recorded during our surveys.

## Discussion

A paucity of natural lakes in the south and east of England, and the subsequent construction of new lakes and ponds by humans, has led to an interesting legacy in the distributions of calanoid copepods in the British Isles. A high proportion of lakes and ponds in the north and west of Britain are natural as a result of the glacial history of these areas. By contrast, the scarcity of such natural waterbodies in southern and eastern England has been offset by a high proportion that have been constructed, mainly to serve as water supply reservoirs (Smith and Lyle 1979; Rowan 2010). The construction of these water bodies has led to opportunities for invasions of species that may not have traditionally occurred in these areas.

The extent of recorded findings of *Eudiaptomus gracilis* throughout the British Isles illustrates the widespread sampling effort for calanoid copepods. Nevertheless, separation of the datasets into natural and constructed sites clearly shows differences between them, with records in natural lakes primarily from the north and west of the British Isles, and in the constructed waters in the south and east. Such a pattern highlights the importance of separating natural and constructed lakes when examining the distributions of freshwater organisms. Waterbodies constructed in the south and east of England have clearly facilitated the occurrence of *E. gracilis* in geographical regions where few natural waters otherwise existed.

*Eurytemora velox* is a common species in weakly brackish areas of estuaries and lagoons around the British Isles, and Europe more broadly (Gurney 1931), but has also invaded a number of freshwaters in England, particularly in the south-east. In natural freshwaters this species has only been recorded from Possil Marsh, Glasgow, and Loughs Derg and Erne, Ireland (Gurney 1931); no new records in natural freshwaters have been made since this time. These three waterbodies, despite being freshwater, are all within 20 km of estuaries, providing a possible local population source. Here we show a widespread presence of this species in constructed waters. Many of the records we identify from constructed waters are far inland (e.g., Oxford City Reservoir, various London Reservoirs, and a University of York pond; Lowndes 1929, Sedal and Duncan 1974; our surveys). While Elton (1929) noted the presence of *E. velox* from only six distinct inland waters, numerous records have been made in constructed waters since this time.

Elton (1927, 1929) noted the presence of *Eurytemora velox* in sites that were all constructed, and that were mostly less than 20 years of age, while the species was absent from older constructed ponds. Soon after, Gurney (1931) similarly noted that *E. velox* had a rather frequent association with constructed waters, even though it was not appreciated at the time that the Norfolk Broads, where this species was known by Gurney to be common, were also constructed (Lambert et al. 1960). Elton (1927) further remarked that where *E. velox* was absent from constructed waters, they all contained *Eudiaptomus gracilis* (i.e., the distributions of these species were mutually exclusive). Based on these observations, Elton argued that *E. gracilis* was slower to disperse, but would eventually displace the less well-adapted *E. velox* in constructed ponds once established, through competition. Such findings support the contention popularised later by Hutchinson (1951), that calanoid copepods of a similar size, or with significant dietary overlap, typically cannot co-exist (see also Chow-Fraser and Maly 1992; Luger et al. 2000). Lowndes (1930) noted the similarity in length of these species, measuring adult *E. velox* at 1.7 mm and *E. gracilis* at 1.5 mm. That *E. gracilis* reduces the probability of establishment of *E. velox* is also in agreement with recent pond-scale experiments, which have shown that the presence of particular key species of zooplankton provide biotic resistance to the establishment of new invaders (Dzialowski 2010; Taylor and Duggan 2012); that is, *E. velox* is unable to invade waters where *E. gracilis* is already present, in accordance with Elton's ideas. Lowndes (1929), however, provided a "Critical Note" in response to Elton's contentions. On the first point, that *E. velox* occurred only in young constructed waters, Lowndes argued that *E. velox* were, in fact, found in some waters significantly older than 20 years, such as the Oxford Waterworks (1853-), and indeed in natural waters such as Lough Derg (Ireland). Our results support Lowndes' contention on this point, that the waters where this species is found are not necessarily young. We re-confirmed presence of the species in the former Oxford Waterworks pond, while Sedal and Duncan (1974) found the species in a number of London reservoirs built as early as 1903. Nevertheless, records of this species are overwhelmingly biased towards constructed waters over natural lakes. Elton's contention of the species being entirely restricted to artificially constructed waters was clearly too "black and white", but he had also identified an interesting trend in invasion biology, not widely appreciated until the beginning of the 21st century.

On Elton's point of the lack of co-existence between *E. velox* and *E. gracilis*, Lowndes provided a number of examples where he believed these species were found to co-occur, including in Lough Derg, Highams Park Lake (London), the Oxford Waterworks, and Oxford Botanic Gardens. In his rebuttal, while Elton could not provide an explanation for the Lough Derg observation, he did note that *E. velox* had apparently died out in Highams Park Lake subsequent to the co-existence observation. For Oxford Botanic Garden, *E. velox* was recorded by Elton himself in 1921 but had been replaced by *E. gracilis* when sampled by Lowndes in 1928 (Elton 1929). Further to this point, Scott (1894) recorded *E. velox* in abundance from Castlemilk Loch, Glasgow, but no diaptomids, whereas our samples from this site, collected in 2016, contained only *E. gracilis*. Similarly, Scourfield (1896) found the Long Water at Hampton Court to contain *E. velox*, whereas our samples also contained *E. gracilis* alone (although it is unclear from Scourfield's paper whether or not *E. gracilis* co-occurred there during his survey). In a good number of cases, therefore, Elton's contention that *E. gracilis* replaces *E. velox* in constructed water bodies has been supported by subsequent research. To date, however, no direct competition experiments have been undertaken between *E. velox* and *E. gracilis*; future studies should be conducted to test the competitive interactions of these species under controlled conditions, to elucidate factors that lead to both coexistence or exclusion.

To further his argument, Elton (1929) presented results of a survey where he showed 87% of natural ponds, versus only 8% of constructed ones, contained *E. gracilis*. His results also indicated that *E. gracilis* occurred in a greater proportion of older constructed ponds than younger, which he used to infer that the process of replacement may take some years. Nevertheless, Elton (1929) argued that the Oxford Waterworks Pond, where co-existence still occurred at that time, was an exception, as it constantly received water from the river by a pipe; he considered the flowing water might allow for co-existence of these species. During our 2016 survey, both species were still found to co-occur at this site (now retired as a reservoir, and known as Hinksey Lake), despite having no obvious flow. A number of further examples of co-existence have been noted, such as among the London water supply reservoirs, where both species are commonplace (Sedal and Duncan 1994). The reasons for such continued co-occurrence requires further investigation. One possibility may be related to the intensity of predation by fish at some sites. For example, Maly and Maly (1997) showed that in the absence of fish predation, species of the calanoid copepod genus *Boeckella* are able to displace species of another genus, *Calamoecia*, through competition for resources. Moderate predation pressure by fish, however, was sufficient to reduce *Boeckella* density and consequently allow co-existence. Nevertheless, it appears that rather than being gradually extirpated, the estuarine *E. velox* has become permanently established due to the construction of new ponds and lakes. As such, lake construction may not only facilitate the invasion of non-indigenous species, but be contributing to a general acceleration of the invasion rate of freshwaters by brackish water species globally (*sensu* Lee and Bell 1999).

Interestingly, Gaviria and Forro (2000) have noted similar trends for the invasion of *E. velox* in mainland Europe, where this species has widened its inland distribution since the early 20th century. Initially found in reservoirs of the Seine, Rhine, Elbe and Volga Rivers, it was recorded from freshwater bodies in Belgium in the 1970s, the Dniepr River in Ukraine, Don River in Russia and the middle Danube River up to Hungary and Slovakia by the 1990s, and Austria by 1994. These authors considered this distribution to be the result either of passive dispersal by bird migration or by inland transport in the ballast water of ships. While the latter is impossible for the inland dispersal in the current British Isles study, the inland movement of an estuarine copepod in association with bird migrations is compelling. For example, large annual migrations of gulls occur within the British Isles between coastal areas and inland waters, with many of the largest inland winter roosts being in reservoirs (Hickling 1954). Interestingly, a related species *Eurytemora affinis*, typical of waters with higher salinities than *E. velox*, has recently been recorded in Cardiff Bay Lake, constructed in 1999 by walling off the sea, but now entirely freshwater (Merrix-Jones et al. 2013).

*Eudiaptomus vulgaris*, which is common in mainland Europe and North Africa (Gurney 1931), appears to be a recent invader in the British Isles. From our dataset, this species has been recorded from no natural ponds and lakes, but from at least five constructed standing waters, particularly around the Norfolk area on the east coast of Britain. Gurney

(1931) also noted its propensity in Norfolk, not only in the Broads district but throughout the county. Although it was not appreciated in Gurney's time that the broads were of human origin, he did suggest that the species was in the process of spreading, and proposed that the species may be a recent immigrant. It is impossible to ascertain, however, whether this species arrived in the British Isles in association with people, or whether the activities of people (in the creation of new habitats) has simply facilitated its establishment. For example, even in the mid-14th century the Norfolk area was one of the most densely populated rural areas of the United Kingdom (Lambert et al. 1960), potentially providing opportunities for introduction via humans with trade. On the other hand, the close proximity of waterbodies in Norfolk to western mainland Europe may also have provided greater opportunities for the latter region to act as a donor region, through transport via wind and rain or by birds (e.g., Proctor 1964; Jenkins and Underwood 1998; Cáceres and Soluk 2002). Outside of our dataset, Gurney (1931) also noted records at Ross in Herefordshire, in the New Forest, and in Richmond and Epping; it was impossible to ascertain from these descriptions whether the records were from natural or constructed waters.

Overall, the construction of new waters in the south and east of Britain has facilitated the establishment of new calanoid copepod species, including the contrasting examples of invasions by a mainland European freshwater species (*E. vulgaris*) and a species common in British estuaries (*E. velox*). Such construction has seemingly provided opportunities for species establishment in the British Isles since mediaeval times. Nevertheless, natural lakes and ponds in the south and east require further investigation, as the distribution of the dominant lake types in various regions of the British Isles may have led to some biases in the sites sampled for zooplankton (i.e., we identified no natural sites which have been examined for zooplankton in the south-east). It is interesting to note that the constructed waters that have been invaded are not only reservoirs, but also other forms of constructed waterbody (e.g., infilled peat diggings, and ornamental ponds). This trend indicates that a lack of biotic resistance is the most compelling factor facilitating invasions at these sites (*sensu* Banks and Duggan 2009; Taylor and Duggan 2016), rather than connectivity and disturbance which may remain important in reservoirs (*sensu* Havel et al. 2005; Johnson et al. 2008). Based on the continued occurrence of *E. velox* at some sites, rather than their extirpation by *E. gracilis* (*sensu* Elton), we suggest that *E. velox* may have successfully invaded freshwaters in the British Isles from brackish environments. Overall, our findings support the contentions of Elton (1927) that constructed waters are more readily invaded than natural waters, and importantly, that reduced biotic resistance—through the lack of a key species—facilitates these invasions. While criticism of Elton's ideas by Lowndes (1929) were valid based on the overtly unequivocal nature of some of his statements, the criticism of Elton's work may have led to a lack of appreciation throughout the 20th century of general trends regarding invasions of constructed waters and their causes, which are now widely accepted by invasion biologists.

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Author contributions: ICD conceived the study, conducted the data collection and wrote the first draft of the paper. RJP facilitated the data collection and contributed to paper writing.

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**Supplementary material**

The following supplementary material is available for this article:

**Table S1**. List of water-bodies where *Eudiaptomus gracilis* have been identified from natural lakes in the British Isles.

**Table S2.** List of water-bodies where *Eudiaptomus gracilis* have been identified from constructed lakes in the British Isles.

**Table S3.** List of water-bodies where *Eurytemora velox* have been identified from natural lakes in the British Isles.

**Table S4.** List of water-bodies where *Eurytemora velox* have been identified from constructed lakes in the British Isles.

**Table S5.** List of water-bodies where *Eudiaptomus vulgaris* have been identified from constructed lakes in the British Isles.

**Appendix 1.** References for supplementary tables.

*This material is available as part of online article from:*
http://www.aquaticinvasions.net/2017/Supplements/AI_2017_Duggan_Payne_Supplement.xls