A global review of zooplankton species in freshwater aquaculture ponds: what are the risks for invasion?

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Abstract

Non-native freshwater zooplankton species have been recorded from aquaculture ponds in New Zealand and Italy, while zooplankton invasions elsewhere have implicated the aquaculture industry as the vector for introduction. However, the prevalence of non-native species in international aquaculture facilities is unclear. We undertook a literature review of publications examining zooplankton assemblages in freshwater aquaculture ponds globally to determine; 1) the prevalence of non-native taxa, 2) the quality of the studies undertaken, 3) how well the major freshwater aquaculture nations are represented in studies, and 4) the representation of dominant aquaculture species. Thirty-two suitable publications were found that provided data on zooplankton assemblages from aquaculture facilities. We supplemented this by sampling Huka Prawn Park, Taupō, New Zealand, as knowledge of zooplankton in prawn facilities was scarce. Zooplankton data was obtained for 205 outdoor ponds and experimental tanks, from 39 different aquaculture facilities, across 13 countries. Non-indigenous taxa were recorded from 17.9% of facilities globally. Over half of these publications (53.1%) identified taxa to genus level only, with the remaining 46.9% attempting species level identifications. The high proportion of publications not identifying to species level indicates that non-native species will not be recognised in most studies; 31.8% of facilities were invaded when considering only studies with species level identifications. In total, 234 different taxa were identified (including 184 to species level), with only 4, located in Italy and New Zealand, recognised as non-native; only 3 of these 4 taxa were clearly identified as non-indigenous in their respective publications. Another species has been identified outside of its native range in North American aquaculture facilities, but no co-existing zooplankton species were reported. While aquaculture facilities were found to harbour only a small number of non-indigenous species, our findings indicate that there is a significant lack of taxonomic resolution used in most studies, and a lack of surveys in major aquaculture producing regions and from facilities holding many of the major aquaculture species. Importantly, few zooplankton invaders putatively originating from the aquaculture industry have been found within aquaculture facilities themselves. Overall, it is currently difficult to determine the prevalence of non-indigenous zooplankton species in aquaculture facilities globally, and our results suggest the risk may be far higher than is currently appreciated. As such, we recommend systematic surveys of ponds utilising species level identification from a variety of geographic regions, to better quantify invasion risks by non-native zooplankton taxa from the freshwater aquaculture industry.

Key words: fish farming, non-native, cladoceran, rotifer, copepod, ostracod, earthen ponds

Introduction

Farming of aquatic animals, known as aquaculture, includes the production and keeping of aquatic organisms predominantly for human consumption. Aquatic life is also often produced for non-food purposes, such as for the ornamental trade or to function as biological control agents (Naylor et al. 2001; Bartley 2011). Aquaculture is a growing industry globally. A total of 93.4 million tonnes of produce was taken from aquaculture fisheries in 2014, over 12% of which was from inland ventures. At this time, almost half (44.1%) of the world’s fish production originated from the aquaculture sector rather than from wild fish stocks (Food and Agriculture Organization 2016). With an expanding global
predominantly addressed copepod invasions. For introduction or spread of non-native zooplankton has to date received little attention. Nevertheless, this issuevector responsible for the spread of non-native zooplankton, such as microscopic taxa released in conjunction with cultured stocks, are potentially overlooked (Gollasch 2006; Duggan and Pullan 2017). This bias exemplifies the “smalls rule” in invasion ecology, whereby invasions involving smaller organisms are relatively rarely recognised (Wyatt and Carlton 2002).

Several non-native zooplankton species were recently found during a systematic survey of New Zealand’s freshwater aquaculture facilities. Sampling undertaken at nine aquaculture farms by Duggan and Pullan (2017) resulted in the discovery of three non-native species (Skistodiaptomus pallidus, Daphnia galeata and Nitokra sp.); the first two in outdoor aquaculture ponds, and the latter in an indoor recirculating system. Leading up to this survey, it was suspected that non-native zooplankton taxa were accidentally being translocated from facilities with the release of cultivated grass carp (Ctenopharyngodon idella; Duggan et al. 2014). This was of concern as these fishes were regularly released locally, as they are elsewhere, as a means of controlling invasive macrophytes (Pipalova 2006). Subsequently, Branford and Duggan (2017) sampled 65 New Zealand ponds to determine whether zooplankton transfer with grass carp from aquaculture facilities could be detected. Their study found three non-native zooplankton species (Daphnia pulex, D. galeata and S. pallidus) were more commonly found in ponds stocked with grass carp from aquaculture facilities relative to those that were not. These results suggested that releases from aquaculture facilities represent a key vector responsible for the spread of non-native zooplankton in New Zealand. Nevertheless, this issue has to date received little attention.

The connection between aquaculture and the introduction or spread of non-native zooplankton has predominantly addressed copepod invasions. For example, the non-indigenous calanoid copepod *Arctodiaptomus dorsalis,* native to freshwaters in the southern and central United States, northern South America, the Gulf of Mexico and Caribbean Sea regions, has been found in lakes of the Laguna de Bay in the Philippines; these lakes have also hosted aquaculture facilities for Nile tilapia (*Oreochromis niloticus*) since 1974, which has thus been inferred as the likely invasion vector (Papa et al. 2012). Similarly, the increasing range of *A. dorsalis* into North American waterbodies outside of its native range has also had fish stocking implicated as an invasion vector; *A. dorsalis* has been found in a striped bass (*Morone saxatilis*) farm in Virginia as well as in fish hatcheries in Indiana, Oklahoma and Arkansas, which are all outside of the species’ known native range (Reid 2007). As a final example, the calanoid copepod invader *Boeckella triarticulata* was reported from an aquaculture facility in Italy (Ferrari et al. 1991; Ferrari and Rossetti 2006). Due to the proximity of the fish farm to the Po River, where it was later found to be established, it is likely that *B. triarticulata* escaped from this aquaculture facility into the river. This is problematic as *B. triarticulata* has been documented to have a negative impact on local plankton communities, reducing phytoplankton biomass and outcompeting rotifer species (Ferrari et al. 1991; Ferrari and Rossetti 2006). Nevertheless, few papers have sought to definitively identify the likely vector used by invading zooplankton, by sampling both the non-native species in aquaculture ponds and the precise localities where water or fish have been released from these facilities (e.g., Branford and Duggan 2017; Duggan and Pullan 2017; Ferrari et al. 1991; Ferrari and Rossetti 2006).

Overall, Branford and Duggan (2017) considered the number of invasions recorded by this vector to be underestimated on a global scale based on the number of aquaculture farms that exist worldwide.

The prevalence of non-native zooplankton species in international aquaculture facilities and the risk they present for invasions is unclear. Nonetheless, with farmed fish production set to significantly surpass that of wild fisheries within the next decade (Food and Agriculture Organization 2016; Bostock et al. 2010), the potential risk of aquaculture related escapes is likely to rise. Thus, a clear understanding of the composition of zooplankton assemblages residing within aquaculture ponds is essential for informing management and reducing the prevalence of new invasions worldwide. In response to this issue, this review aims to critically assess studies of zooplankton assemblages reported to inhabit outdoor freshwater aquaculture ponds on a global scale, to determine whether non-native zooplankton species are common, and to determine whether zooplankton species putatively identified as having aquaculture as their vector
for introduction are actually present in aquaculture facilities. Additionally, this work aims to examine whether the quality of these studies is adequate for determining risk and to determine how well the major freshwater aquaculture nations and facilities containing the dominant aquaculture species are represented in zooplankton inhabitant studies.

**Methods**

Web of Science, Scopus, Google Scholar and Google Books were searched for publications addressing zooplankton in outdoor freshwater aquaculture ponds, to compile a species database. To do this, Boolean string searches were completed using a series of keywords and phrases; for example, (aquaculture*) AND (zooplankton OR Cladocera* OR rotifer* OR copepod*). Other keywords utilized in the searches included, but were not limited to: freshwater, ponds, fish farming, aquaculture facility, outdoor pond, earthen pond, fishpond, production pond, community composition, carp, goldfish, catfish, prawn, crustacean and ostracod. Further, we browsed issues of specialist aquaculture journals, such as “Aquaculture”, “Aquaculture International” and “Aquaculture Research”, for further appropriate articles. We accept that our search strategy may not have identified all relevant literature, including potentially some publications whose primary focus was not zooplankton, or those published in more obscure sources. Nevertheless, we believe our resulting dataset includes the majority of appropriate studies, and is robust enough to support our conclusions.

Zooplankton data were gathered from papers that described assemblages living in outdoor freshwater aquaculture ponds, including aquaculture research facilities. Indoor Recirculating Aquaculture Systems were not included as invasion risks for these facilities are considered low relative to pond systems (Duggan and Pullan 2017). We included experimental studies that utilized mesocosms and outdoor tanks that contained water or sediments sourced from aquaculture ponds. Papers were only included in our analysis when we were confident that the ponds were stocked with, or had previously been stocked with, aquaculture species. We excluded papers when the location and number of ponds sampled were not identified, and those containing saltwater zooplankton. Additionally, papers were only included when at least three zooplankton taxa were identified in the publication (i.e., we included only surveys of multiple species), to reduce any bias in the determination of prevalence of species across ponds, facilities and countries.

Species data were compiled into a Microsoft Excel (version 15.33) spreadsheet, with details including the species cultivated, location, and the zooplankton sampling method. As papers utilised different zooplankton sampling methods, such as fish gut contents analysis, or various qualitative or quantitative sampling methods, and as some were one-off snapshots while others were undertaken over longer time periods, we utilized a simple presence/absence analysis in this review. Any obsolete species names were altered to current accepted names, and nauplii and juveniles were designated as “unidentified species” within their taxon group (e.g., cyclopoid nauplii to unknown cyclopoid spp.).

In addition to the literature review, sampling was undertaken at the Huka Prawn Park aquaculture facility in Taupō, New Zealand, due to a paucity of studies identified that examined zooplankton in freshwater prawn farms globally. This aquaculture facility doubles as a popular tourist attraction and is the only producer of the Giant Malaysian River Prawn (Macrobrachium rosenbergii) in New Zealand. Zooplankton were collected from two prawn production ponds, two prawn tourist fishing ponds, a settling pond and the tourist pond stocking brown trout (Salmo trutta) and rainbow trout (Oncorhynchus mykiss) on 6 December 2017, using a horizontal throw net with 40 μm mesh. Samples were preserved using ethanol and returned to the laboratory for identification. Zooplankton were identified using a compound (Olympus BH-2) and/or dissecting microscope (Olympus SZ60) as required, following Shiel (1995) and Chapman et al. (2011), and the species identified were added to the Microsoft Excel spreadsheet database.

In the resulting database, we considered a species to be globally common if it occurred in at least five countries; this represented a value close to half that of all countries identified. Species were ordered into six different taxonomic groups to aid the analysis (cladocerans, rotifers, calanoid copepods, harpacticoid copepods, cyclopoid copepods and ostracods). We then determined the native ranges of the zooplankton species recorded to confirm their status as native or non-native, using guides such as Koste (1978) and Segers (2007), and publications in the “Guides to the Identification of the Microinvertebrates of the Continental Waters of the World” series.

**Results**

Across the 6 ponds sampled at the Huka Prawn Park, a total of 26 taxa were found (Supplementary material Table S1). The Settling Pond had the greatest diversity, with 14 different taxa, while the two fishing ponds and one of the production ponds shared the lowest diversity with 10 taxa each. Overall, the most common
taxa were rotifer species; Brachionus and Keratella species were the most frequently occurring, with B. caliciflorus, B. quadridenatus, K. tecta and K. tropica each found in five of the six ponds sampled. Cladocerans were the second most taxon rich group, with 6 taxa. Chydorus sp. and Daphnia galeata were the most common, each found in five of the six ponds; D. galeata was the only non-native zooplankton species found in the facility. Finally, a single copepod species, the cyclopoid Mesocyclops australiensis, was found in five of the six ponds.

We found 32 publications identifying zooplankton assemblages in freshwater aquaculture ponds (Table 1). Of these, only 14 (46.9%) attempted to describe zooplankton to species level; over half of the papers (53.1%) identified taxa to genus level only. Publications were derived from 13 countries and all major continents, excluding Antarctica. Overall, this review, including our Huka Prawn Park data, produced zooplankton identifications for 234 taxa to genus or species level (i.e., not including 6 taxa identified with lower taxonomic resolution, such as “unidentified cladocerans”), across 39 different facilities and 205 outdoor ponds/experimental tanks. Only 184 were described to species level, with 115 rotifer species making up the majority of these (Table S2, Table S3). This was followed by 41 cladoceran (Table S4), 17 cyclopoid copepod, 6 calanoid copepod (Table S5), 4 ostracod (Table S6), and 1 harpacticoid copepod species (Table S5). This left 50 taxa in the dataset that were described only to genus. Again, rotifers made up the majority of the genus level data with 31 taxa identified, followed by 11 cladoceran and 3 cyclopoid copepod taxa. The remaining taxonomic groups (calanoid copepods, harpacticoid copepods and ostracods) comprised less than three genera each.

Of the 234 taxa identified in this review (Tables S3–S6), 4 were considered non-native species. Two of these taxa were Daphnia species; the North American Daphnia ambigua found in Italy and the Holarctic Daphnia galeata in New Zealand (the latter confirmed using the COI gene; ICD, unpublished data). The remaining two non-indigenous species were calanoid copepods; Skistodiaptomus pallidus, native to North America and found in New Zealand, and Boeckella triarticulata, native to Australia and found in Italy. Only D. ambigua was not clearly identified as non-native in the respective papers, although the authors noted it had been identified in Italy only once previously. In New Zealand, S. pallidus was found in grass carp and goldfish ponds. Daphnia galeata was also found in some of the same facilities, as well as in the Malaysian river prawn and trout ponds at Huka Prawn Park (this study). The two non-native species found in Italy (B. triarticulata and D. ambigua) were both found in channel catfish ponds in the same facility. Arctodiaptomus dorsalis, which has been found in North American aquaculture ponds (Reid 2007), was not included in our list, as other species identified at these facilities were not provided (i.e., data did not meet our criterion of having “assemblages” identified). We have also recently observed North American Daphnia pulex from a New Zealand goldfish farm (unpublished data; Duggan et al. 2012). In total, 17.9% (7) of the 39 aquaculture farms and research facilities (sampled in the literature and this review) contained non-native zooplankton; or 31.8% when considering only the 22 facilities that attempted species level identifications. Furthermore, of the 13 countries sampled in this review, 15.4% (2) housed non-native zooplankton species in their aquaculture ponds. Few zooplankton species were common among aquaculture facilities across the globe (Table S2): eight rotifers identified to species level were found in at least five countries; half of which were Brachionus species. Unidentified copepods were a common occurrence, being reported in seven countries, and Cyclops sp. appeared in five counties. Additionally, four cladoceran taxa were commonly found in at least five countries.

Only 4 of the top 16 inland aquaculture producing countries identified by the Food and Agriculture Organization (2016) had publications suitable for this review (Figure 1). Of the papers found, half were based in Asia (56.3%), while the next largest contributors were North America (15.6%) and Europe (15.6%). The remaining continents were Africa (6.3%), South America (3.1%) and Oceania (3.1%), which each contributed less than 10% of the 32 papers. All studies sampled ponds or tanks at single aquaculture facilities, with the exception of Duggan and Pullan (2017) which surveyed six different facilities in New Zealand, and Körmendi and Hancz (2000) who sampled two facilities in Hungary. The most commonly cultivated taxa across studies were carp species; in particular, grass carp (Ctenopharyngodon idella), silver carp (Hypophthalmichthys molitrix), rohu (Labeo rohita) and common carp (Cyprinus carpio) (Table 1).

Discussion

Are non-indigenous taxa overlooked?

Four non-native species were recognised in our dataset; two were located in New Zealand (Skistodiaptomus pallidus and Daphnia galeata) and two in Italy (Boeckella triarticulata and Daphnia ambigua). Besides D. ambigua, the remaining three species had been identified as non-indigenous in the literature.
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**Table 1.** Information on the facilities, ponds, zooplankton identification and the cultivated species in the 3 publications (and including the Huka Prawn Park data) used in this review. Studies are ordered by country name.

| Reference | Country | Facility/ location | Number of facilities sampled | Number of ponds/tanks sampled | Stocked species | Species level identification attempted |
|-----------|---------|--------------------|------------------------------|-----------------------------|-----------------|--------------------------------------|
| Kalous et al. 2009 | Angola | Integrated fish and duck production system in Bié province | 1 | 2 | Redbreast tilapia (Tilapia rendalli) and ducks | Yes |
| Shil et al. 2013 | Bangladesh | Semi-intensive prawn farm of the Bagerhat district | 1 | 2 | Giant Malaysian river prawn (Macrobrachium rosenbergii) | No |
| Siddique et al. 2010 | Bangladesh | Village Meherchandi of Boalia thana under Rajshahi | 1 | 4 | Giant Malaysian river prawn (Macrobrachium rosenbergii), silver carp (Hypophthalmichthys molitrix) and catla (Catla catla) | No |
| Hossain et al. 2007 | Bangladesh | Rajshahi University Campus | 1 | 1 | “Exotic and indigenous fishes” | No |
| Bhuiyan et al. 2008 | Bangladesh | Taposhie Rabeya Hall, Rajshahi | 1 | 1 | Rohu (Labeo rohita), catla (Catla catla), mrigal (Cirrhinus mrigala), silver carp (Hypophthalmichthys molitrix), mirror carp (Cyprinus carpio), bighead carp (Hypophthalmichthys nobilis) and sarpunti (Puntius gonionotus). | No |
| Rahman et al. 2006 | Bangladesh | Fisheries Faculty Field Laboratory, Bangladesh Agricultural University, Mymensing | 1 | 18 | Rohu (Labeo rohita) and common carp (Cyprinus carpio) | No |
| Rahman and Hussain 2008 | Bangladesh | Rajshahi University campus | 1 | 2 | Rohu (Labeo rohita), catla (Catla catla), mrigal (Cirrhinus mrigala), silver carp (Hypophthalmichthys molitrix), bighead carp (Aristichthys nobilis), grass carp (Ctenopharyngodon idella) and sarpunti (Puntius gonionotus). | No |
| Ibrahim et al. 2008 | Bangladesh | Rajshahi University campus | 1 | 4 | Common carp (Cyprinus carpio), silver carp (Hypophthalmichthys molitrix), rohu (Labeo rohita), catla (Catla catla) and mrigal (Cirrhinus mrigala) | No |
| Chowdhury and Al Mamun 2006 | Bangladesh | Khulna University campus | 1 | 2 | Fish not described | No |
| Ahmed 2004 | Bangladesh | Experimental Pond Facility of the Faculty of Fisheries, BAU, Mymensingh | 1 | 3 | Rohu (Labeo rohita), catla (Catla catla), common carp (Cyprinus carpio), and silver barb (Barbonymus gonionotus) | No |
| Sipaúba-Tavares et al. 2011 | Brazil | The Aquaculture Center at the Universidade Estadual Paulista | 1 | 1 | Pacu (Piaractus mesopotamicus), tambaqui (Colossoma macropomum), pintado (Pseudoplatystoma corruscan) and matrixá (Brycon cephalus) | Yes |
| Adámek et al. 2016 | Czech Republic | Semi-intensive ponds in southern Moravia, Czech Republic | 1 | 2 | Grass carp (Ctenopharyngodon idella), silver carp (Hypophthalmichthys molitrix), bighead carp (Hypophthalmichthys nobilis), pike (Esox lucius), zander (Sizostedion lucioperca), tench (Tinca tinca), European catfish (Silurus glanis), ide (Leuciscus idus) and other fish (e.g. common bream (Abramis brama), white bream (Blicca bjoerkna), roach (Rutilus rutilus), perch (Perca fluviatilis), gibel carp (Carassius gibelio) and ruffe (Gymnocephalus cernua) | No |
| Hlaváč et al. 2016 | Czech Republic | Naděje pond system in the Trbóň region | 1 | 4 | Common carp (Cyprinus carpio) | Yes |
| Körnendi and Hancz 2000 | Hungary | Southern shore of Lake Balaton and catchment area of the Danube | 2 | 6 | Common carp (Cyprinus carpio), silver carp (Hypophthalmichthys molitrix), grass carp (Ctenopharyngodon idella) and bighead carp (Hypophthalmichthys nobilis) | Yes |
## Table 1. (continued)

| Reference          | Country       | Facility/ location                                      | Number of facilities sampled | Number of ponds/tanks sampled | Stocked species                                                                 | Species level identification attempted |
|--------------------|--------------|--------------------------------------------------------|------------------------------|-------------------------------|--------------------------------------------------------------------------------|----------------------------------------|
| Kiran et al. 2007  | India        | Bhadra fish farm, Karnataka                            | 1                            | 1                             | Not described                                                                  | Yes                                    |
| Banerjee et al.    | India        | The research place, Belacab                            | 1                            | 9                             | Indian major carp (*Catla catla*), rohu (*Labeo rohita*), mrigal carp (*Cirrhina mrigala*) and grass carp (*Ctenopharyngodon idella*) | No                                     |
| Jha et al. 2004    | India        | Hatchery Unit of Rainbow Ornaments, Raninagar, Jalpaiguri | 1                            | 21                            | Koi Carp (*Cyprinus carpio* nr. *koi*)                                         | No                                     |
| Milstein and Svirsky 1996 | Israel  | Lohamei HaGetaot farm                                     | 1                            | 18                            | Common carp (*Cyprinus carpio*), tilapia hybrids (*Oreochromis niloticus* × *O. aureus*) and mullet (*Mugil cephalus*) | Yes                                    |
| Milstein et al.    | Israel        | Fish and Aquaculture Research Station, Dor              | 1                            | 10                            | Silver carp (*Hypophthalmichthys molitrix*), Tilapia sp., common carp (*Cyprinus carpio*), grey mullet (*Mugil cephalus*), grass carp (*Ctenopharyngodon idella*) and hybrid bass (*Morone chrysopt × M. saxatilis*) | Yes                                    |
| Milstein et al.    | Israel        | Maagan Michael fish farm                                | 1                            | 12                            | Common carp (*Cyprinus carpio* L.)                                               | Yes                                    |
| Ferrari et al. 1991 | Italy          | Fish farm near Massa Finales, Modena province               | 1                            | 4                             | Channel catfish (*Ictalurus punctatus*)                                          | Yes                                    |
| Duggan and Pallan 2017 | New Zealand | Aquaculture facilities in Northland, Auckland, Waikato, Wellington and Nelson | 6                            | 21                            | Grass carp (*Ctenopharyngodon idella*), ornamental golden tench (*Tinca tinca*), koi carp (*Cyprinus carpio*), giant kokopu (*Galaxias argenteus*), and goldfish (*Carassius auratus*) | Yes                                    |
| This study         | New Zealand   | Huka Prawn Park, Taupō                                 | 1                            | 6                             | Giant Malaysian river prawn (*Macrobrachium rosenbergii*), brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) | Yes                                    |
| Adedeji et al. 2013 | Nigeria  | NIFAGOL Fish farm in Ife North Local Government Area of Osun Stat | 1                            | 6                             | African sharptooth catfish (*Clarias gariepinus*)                               | Yes                                    |
| Goździejewska and Tucholski 2011 | Poland  | Waste-water treatment plant, Olszynnek                  | 1                            | 3                             | Common carp (*Cyprinus carpio*), tench (*Tinca tinca*), European pike-perch (*Sander lucioperca*) and roach (*Rutilus rutilus*) | Yes                                    |
| Kirkagaç 2003      | Turkey        | Fisheries Department of the State Water Works, Keban     | 1                            | 1                             | Grass carp (*Ctenopharyngodon idella*)                                           | No                                     |
| Kirkagaç 2004      | Turkey        | Fisheries Department of the State Water Works, Keban     | 1                            | 1                             | Grass carp (*Ctenopharyngodon idella*)                                           | Yes                                    |
| Kirkagaç and Demir 2004 | Turkey  | Çifteler-Sakaryaşasi Aquaculture and Research Station | 1                            | 4                             | Grass carp (*Ctenopharyngodon idella*)                                           | Yes                                    |
| Fry and Osborne 1980 | United States | University of Central Florida campus                    | 1                            | 3                             | Grass carp (*Ctenopharyngodon idella*)                                           | Yes                                    |
| Geiger et al. 1985 | United States | Marion Fish Hatchery, Marion, Alabama                    | 1                            | 10                            | Striped bass fry                                                                 | No                                     |
| Ludwig et al. 1993 | United States | Fish Farming Experimental Laboratory, Stuttgart, Arkansas | 1                            | 15                            | Reciprocal-cross hybrid striped bass (female white bass (*Morone chrysops*) × male striped bass (*Morone saxatilis*)) | No                                     |
| Mischke et al. 2003 | United States | National Warmwater Aquaculture Center, Stoneville, Mississippi | 1                            | 4                             | Channel catfish (*Ictalurus punctatus*)                                          | No                                     |
| Parmley and Geiger 1985 | United States | Possum Kingdom State Fish Hatchery                     | 1                            | 4                             | No fish stocked during experiment                                                 | No                                     |
Figure 1. World map indicating the top 16 inland aquaculture producing countries in the world highlighted in yellow (China, Myanmar, India, Bangladesh, Cambodia, Uganda, Indonesia, Nigeria, United Republic of Tanzania, Egypt, Brazil, Russian Federation, Democratic Republic of the Congo, Philippines, Thailand and Viet Nam: Food Agriculture Organization 2016). Countries where studies of zooplankton taxa in aquaculture facilities have been published appear in green (Angola, Czech Republic, Hungary, Israel, Italy, New Zealand, Poland, Turkey and United States), unless a country had both publications and was one of the top 16 inland producers, it which case yellow diagonal stripe pattern was added (Bangladesh, Brazil, India and Nigeria).

The New Zealand non-native species were found in grass carp and goldfish ponds, while those in Italy were reported from channel catfish ponds. The distributions of *S. pallidus* and *Daphnia pulex* in New Zealand are associated with grass carp releases from aquaculture facilities (Branford and Duggan 2017). In contrast, *D. galeata* is widely distributed throughout lakes and ponds in New Zealand’s North Island (Chapman et al. 2011), and is likely to have invaded the aquaculture facilities through natural vectors (e.g., waterfowl). The occurrence of *B. triarticulata* in the Italian ponds was this species’ first known record in Europe, while the finding of *D. ambiguа* in the same ponds was only the second record of this species in Italy (Ferrari et al. 1991). Outside of our dataset, *Arctodiaptomus dorsalis* has been identified in aquaculture facilities in Virginia, Indiana, Oklahoma and Arkansas, in the USA (Reid 2007); this species was not included in our dataset for analysis as lists of other species in the ponds were not provided. Further, we have recently identified North American *Daphnia pulex* from a New Zealand goldfish farm (unpublished data; Duggan et al. 2012).

Overall, non-indigenous species were recorded in 17.9% of facilities sampled. Nevertheless, it is probable that many other non-indigenous species exist in aquaculture ponds but are currently undetected. For example, the proportion of facilities with non-indigenous taxa was raised to 31.8% when considering only studies that identified taxa to species level. A lack of taxonomic resolution used in many studies suggests that taxonomic expertise has limited the ability of some authors to identify invaders. Alternatively, zooplankton species are likely to be primarily regarded simply as food items for fish by aquaculture workers, and thus identification to species level may not be a priority. From an invasion perspective, however, it is of concern that many papers in this review identified calanoid copepods with such low taxonomic resolution. For example, “Calanoidа” species were listed as one of the taxa retrieved from the stomachs and ponds of channel catfish fry in the United States (Mischke et al. 2003), on a continent that has been noted as a geographical hotspot for non-native species invasions (e.g., Grigorovich et al. 2003). Overall, out of the eight calanoid copepod taxa identified in this review, only six were identified to species level, which included two non-native taxa (*S. pallidus* and *B. triarticulata*). In some cases, calanoid copepod taxa were only identified to genus level. Of greatest concern, the designation *Diaptomus* sp. was assigned to taxa in eight different papers on two continents (North America and Asia); while still a valid genus for some taxa, this designation was once used for many
species in the family Diaptomidae, but most have since been placed into new genera (e.g., Light 1939). For example, Skistodiaptomus pallidus was described as Diaptomus pallidus. Nevertheless, “Diaptomus” is seemingly still commonly used as a “catch-all” for unidentified diaptomids (the same could be argued for “Cyclops” among the cyclopoid copepods). As calanoid copepods are commonly considered an easy taxon to identify due to their relatively well-defined morphologies, and easily recognised as invaders due to the tendency for individual species to reside in distinct geographical regions, the lack of species identification in these papers raises concerns (Blaxter 1998). It is clear that further work is required to determine whether non-native calanoid copepod species, as well as other poorly identified zooplankton taxa, are a common occurrence in freshwater aquaculture ponds globally.

It is expected that facilities producing fish for release, such as grass carp, will offer the highest invasion risk, as these farms are likely to spread non-native hitchhiking taxa when releasing fish into the wild (see Brandford and Duggan 2017). Nevertheless, it is also probable that aquaculture facilities will pose an invasion risk due to poor management of their outflows, which may directly release taxa into local waterways (Duggan and Pullan 2017). For example, the establishment of the Australian B. triarticulata in Italy was first detected in channel catfish ponds in the north of the country in 1985, and subsequently found in the adjoining River Po (Ferrari et al. 1991). Goldfish farms producing for the aquarium trade may also pose a risk if the hitchhiking species are transported to homes, and then released during aquarium cleaning. Nevertheless, Duggan (2010) found risk species in the aquarium trade to primarily be those that live in benthic habitats, with planktonic taxa unable to survive in home aquaria due to factors such as filtration. Once zooplankton have established in aquaculture facilities, it is also possible that other pathways may aid the spread of non-indigenous taxa, such as accidental transfer by waterfowl visiting aquaculture facilities (Duggan and Pullan 2017). Overall, these issues highlight the need for proper management and identification of protocols to be implemented to reduce invasion risks.

Non-representative sampling geographically and based on common aquaculture species

Out of the 32 publications found suitable for this review, over half (53.1%) described zooplankton taxa only to genus level. Additionally, data were found for only 13 countries, and no more than 7 aquaculture facilities were examined in any individual country. These findings further highlight that there is not only a lack of taxonomic resolution used in the literature, but that there are also biases in the geographic spread of studies. In total, 16 countries are responsible for producing the majority of the globe’s inland aquatic produce (Figure 1); of these, we found studies of zooplankton in aquaculture facilities from only 4 countries. Currently, China is considered the world’s top fish producer for both marine and inland aquaculture, generating over 45 million tonnes of aquatic produce in 2014, which accounted for over 60 percent of the world’s total aquaculture production (Food and Agriculture Organization 2016). Nevertheless, we found no papers describing the zooplankton residing in facilities from this country, demonstrating a significant knowledge gap in zooplankton diversity in aquaculture ponds for the most productive country in the world.

After China, the other top producers of inland aquaculture are Myanmar, India, Bangladesh and Cambodia, respectively (Food and Agriculture Organization 2016). Of these, only India and Bangladesh were found to have produced publications detailing zooplankton species residing in their facilities. Bangladesh contributed the most publications to the review (28.1%), while the larger aquaculture producer, India, offered significantly less (9.4%). Even though Bangladesh offered the most publications overall (9), their studies only examined zooplankton taxa from five different facilities; further, none of these papers described taxa to species level. As Bangladesh alone is estimated to have at least 1.3 million aquaculture ponds (0.15 million hectares; Food and Agriculture Organization 2018a), and our review only found zooplankton information for 37 ponds, this country, along with many of the other major producers, is underrepresented in our dataset. As illustrated in Figure 1, there is a clear mismatch in regions where zooplankton sampling should be a priority and where sampling has been undertaken. Thus, we currently have a poor understanding of zooplankton composition in freshwater aquaculture ponds on a global scale, particularly from countries with the greatest production.

New Zealand is one of the world’s smallest freshwater aquaculture producers, but ponds in seven aquaculture facilities have been examined for zooplankton (including the Huka Prawn facility, surveyed here). This makes New Zealand the most highly studied country in our dataset in terms of the proportion of facilities examined: considering New Zealand has only approximately 30 active freshwater facilities in operation (Daniel Lees, Ministry for Primary Industries, NZ, personal communication, 17 January 2018), sampling of seven represents a large proportion of facilities. As such, zooplankton recorded...
in New Zealand aquaculture facilities to date likely represents a high proportion of the total species that reside in them. Nevertheless, the New Zealand surveys, as with many others, are temporally restricted; we recently recorded *Daphnia pulex* from a goldfish facility in summer, while the sampling of this facility by Duggan (2010) was in winter. In contrast, non-native zooplankton taxa were also found in Italy, but only one aquaculture facility was examined. Italy was estimated to have at least 311 active aquaculture facilities in 2013, and possibly more now (Food and Agriculture Organization 2018b). Comparatively, larger producing countries such as Bangladesh, India and the USA all sampled fewer than seven facilities, representing extremely poor coverage of their many ponds. This may indicate either a lack of research due to this vector being a relatively unappreciated risk, or that funding has not been a priority in this area.

Another factor that illustrates a lack of sampling across all continents is the absence of data from ponds holding some of the most commonly cultivated freshwater aquaculture species. In this review, ponds containing grass carp, silver carp, rohu and common carp were the most frequently surveyed. All of these species are among the most significant freshwater aquaculture species, representing taxa that contributed more than one million tonnes of production in 2008 (Bostock et al. 2010). Other frequently cultured taxa include Nile tilapia, Mozambique tilapia and blue tilapia (Bostock et al. 2010) yet no sampling of ponds of these species could be found in the literature. This illustrates a clear deficit in tilapia pond sampling on a global scale. In addition to the described sampling deficits, other well-known but less frequently cultivated aquaculture taxa were missing from the dataset. For instance, no bivalves were represented; although uncommon in Europe, farming of freshwater bivalves for pearl production is prevalent throughout Asia, with species such as the Asian triangle shell mussel (*Hyriopsis cumingii*), the crown mussel (*Cristaria plicata*) and the swan mussel (*Anodonta* sp.) being cultivated (Sicuro 2015). As well as the top producer, China, this trade is also well established in Bangladesh, where the Indian mussel (*Lamellidens marginalis*) is cultivated for both human consumption and pearl propagation (Sicuro 2015). Similarly, sampling of zooplankton in aquatic crustacean ponds was poor. The giant river prawn (*Macrobrachium rosenbergii*) is one of the top ten most commonly introduced species for aquaculture globally (Bartley 2011), yet only two publications, from Bangladesh, could be found that reported zooplankton species residing in *M. rosenbergii* ponds (Siddique et al. 2010; Shil et al. 2013) and these studies did not attempt species level identifications.

As such, we surveyed the New Zealand Huka Prawn Park facility to supplement our dataset. Further, no freshwater crayfish ponds were represented in our dataset. This is concerning as there are several species of crayfish cultivated for aquaculture worldwide, such as the red claw crayfish (*Cherax quadricarinatus*), native to Australia and Papua New Guinea, which is propagated across several continents (Oceania, North and South America, Europe, Asia: Food and Agriculture Organization 2018c). Another clear sampling deficit identified is the lack of information on zooplankton species residing in facilities producing fish for the warm-water aquarium trade, with no tropical aquarium facilities represented in our dataset.

This is despite knowledge that zooplankton are transported via this trade (Duggan 2010; Duggan et al. 2018). Ornamental crustaceans and aquatic plants for the aquarium trade have been found to harbour zooplankton hitchhikers, indicating such movement is important for the transfer of non-indigenous zooplankton between countries (Patoka et al. 2016a; Patoka et al. 2016b, Duggan et al. 2018). It is particularly alarming that Singapore is not represented in our dataset, considering this country is the greatest producer and exporter of aquarium fish globally (Monticini 2010). From this trade, zooplankton species data could only be found for goldfish farms in New Zealand (for domestic trade only). Surveys are required in this area to eliminate concerns around non-native zooplankton transfer across continents.

Several zooplankton invasions have occurred worldwide that have putatively originated from aquaculture, yet little effort has been made to establish the link between the zooplankton species and the potential donor facilities (e.g., Reid 2007; Papa et al. 2012; Coelho and Henry 2017). For example, the spread of the calanoid copepod *Arctodiaptomus dorsalis* into several waterbodies outside of their native ranges in the United States has been highlighted in the literature. Surveys have found *A. dorsalis* in various fish culture ponds in the United States (Virginia, Indiana, Oklahoma and Arkansas); these records include two findings of *A. dorsalis* in fish hatcheries of Virginia (Vic Thomas Striped Bass Hatchery and Harrison Lake National Fish Hatchery, 2006). In 2005 and 2006, cultured fish stock was supplied from the Harrison Lake facility to the Vic Thomas hatchery, prior to the record of *A. dorsalis* in the latter. This suggests that the Harrison Lake facility was a key site for the spread of *A. dorsalis* to other aquaculture facilities; nevertheless, there appears to be no further research to solidify this link, or of the source of the original introduction to the Harrison Lake facility (Reid 2007). Similarly, in the Philippines, *A. dorsalis* was also found in lakes of Laguna de Bay. Records
suggest that farming of African tilapia may be related to introductions in this region, yet no investigations have seemingly been undertaken to determine if the facilities that supplied the African tilapia also contain *A. dorsalis* (Papa et al. 2012). It is also worth noting that no comprehensive data on zooplankton species residing in aquaculture facilities in the Philippines could be found for this review, further illustrating a lack of records of zooplankton in aquaculture facilities, even in areas where they are most pertinent. Similarly, although *Boeckella triarticulata* is a species commonly found in Australia, we found no publications on zooplankton species in Australian freshwater aquaculture facilities; the lack of such studies in that country inhibits understanding of how *B. triarticulata* was first transported to Italy.

Other non-native zooplankton species that have potentially established due to the aquaculture trade include the cyclopoid copepod *Mesocyclops ogunnum* and the rotifer *Kellicottia bostoniensis*. It is assumed that these species have established in the Middle River Doce, Brazil, in conjunction with exotic fish species likely released by a local fishing club (Peixoto et al. 2010); however, there appears to be no solid evidence to confirm that these species are linked to aquaculture facilities propagating these exotic fishes. The invasion of *Daphnia lumholtzi* in North American reservoirs is also thought to be linked to either the introduction of exotic fishes or the aquarium trade. Again, the evidence does not confirm which invasion vector was responsible for this non-native cladoceran species (Havel and Hebert 1993). Overall, it is clear from the literature that very little effort has been made globally, with the exception of New Zealand, to confirm aquaculture facilities as hotspots for non-native zooplankton. Notably, none of these species have been identified within any aquaculture facility globally (although a *Kellicottia* has been identified to genus).

**Minimal commonalities in zooplankton taxa among countries**

In this review, zooplankton species were only considered globally common when described from a minimum of five countries. As a total of 184 taxa were identified to species level, and only 11 were considered common, this suggests that most regions have their own distinct, primarily locally sourced, assemblages. For example, the calanoid copepod species *Arctodiaptomus floridanus*, first discovered in Florida in 1918, was only identified in central Floridian grass carp ponds in this review (Marsh 1926). In total, eight rotifer species were found to commonly occur in aquaculture facilities across the globe, half of which were *Brachionus* species. It is likely that the distribution of the eight common rotifer species identified in this review was dictated by pond trophic state rather than by widespread movement of zooplankton among facilities globally. For example, three of the most common species identified in this review (*Brachionus calyciflorus*, *Brachionus budapestinensis* and *Filinia longiseta*) are considered to be cosmopolitan species indicative of high trophic state (e.g., Duggan et al. 2001). Nevertheless, this finding is in contrast to the widespread occurrence of *Skistodiaptomus pallidus* among New Zealand aquaculture facilities, but its rarity outside of these ponds suggests movement of species among facilities there is common (Duggan and Pullan 2017).

**Concluding remarks**

Overall, this review has highlighted a serious lack of taxonomic resolution, and coverage of many of the major producing areas geographically, when identifying zooplankton residing in aquaculture facilities. As such, it is currently impossible to conclude whether invasion of non-native species in aquaculture ponds is a global issue. It is clear that much further work is required to gain an adequate understanding of the prevalence of non-native species in aquaculture facilities, and of the connection between zooplankton invaders inferred to be from this industry and their presence in aquaculture facilities. At present, New Zealand is the only country that offers a good representation of the zooplankton assemblages found in their aquaculture facilities. We recommend that aquaculture ponds be systematically surveyed in other countries to determine whether non-indigenous species are as common elsewhere as they are in New Zealand and Italy. Surveys are particularly essential in gaining an understanding of the risk from high producing exporter countries such as China, which are currently data deficient.

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Supplementary material

The following supplementary material is available for this article:

**Table S1.** List of taxa found in six ponds in the Huka Prawn Park aquaculture facility, Taupō.

**Table S2.** The most commonly found zooplankton taxa in our review of aquaculture facilities across the globe.

**Table S3.** Presence of rotifer species found in aquaculture ponds/tanks in various countries and continents across the globe.

**Table S4.** Presence of cladoceran species found in aquaculture ponds/tanks in various countries and continents across the globe.

**Table S5.** Presence of copepod species found in aquaculture ponds/tanks in various countries and continents across the globe.

**Table S6.** Presence of ostracod species found in aquaculture ponds/tanks in various countries and continents across the globe.

This material is available as part of online article from: http://www.aquaticinvasions.net/2018/Supplements/Al_2018_Pearson_Duggan_SupplementaryTables.xlsx