The abundance and morphometric characteristics of the endemic *Pseudodiaptomus brehmi* Kiefer, 1938 (Copepoda: Calanoida: Pseudodiaptomidae) in Lake Taal (Luzon Is., Philippines)

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Pseudodiaptomus brehmi Kiefer 1938 is a very rare freshwater calanoid copepod species, originally known only from the type locality from Lake Naujan, Mindoro Oriental, Mindoro Island, Philippines. Recent studies have documented its presence in Lake Taal, Luzon Island, where it coexists with the invasive freshwater diaptomid *Arctodiaptomus dorsalis* (Marsh 1907). After numerous failed attempts to find *P. brehmi* from the type locality, it has been determined that it has been displaced by *A. dorsalis*, a global invader, making further studies on the Lake Taal population all the more important. This study was undertaken to study the population and morphometric characteristics of the different life stages of *P. brehmi* which were measured for individuals collected in 2009, when very intensive aquaculture occurred in the lake up until 2013, five years after the management and reduction of fish cage culture. This investigation of Lake Taal revealed that some morphometric measurements of *P. brehmi* populations during 2009 and 2013 did not vary in terms of size but population size and reproductive characteristics such as egg diameter and egg sac length varied even though their relative abundance was low compared to that of *A. dorsalis*. All life stages of *P. brehmi* have been noted throughout the year for both 2009 and 2013. Their continued survival in spite of the presence of the invasive diaptomid species may be due to its more demersal habitat, and the fact that Lake Taal is approximately 4 times larger and deeper than Lake Naujan. The results also suggest that its population density has not changed, even though there was a reduction in the intensity of aquaculture practices, nutrient levels and water quality of the lake has not improved. This is the only species of the genus *Pseudodiaptomus* reported from a freshwater lake, other species in the genus have been reported

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from low salinity rivers and estuaries to hypersaline conditions worldwide.

KEYWORDS

Arctodiaptomus dorsalis, Tropical Lakes, Lake Taal, Lake Naujan, Rare, Endemic, Invasive species, Limnology

INTRODUCTION

Lake Taal is a freshwater caldera lake in Luzon Island, Philippines, 13° 59' N 121° 00'E, approximately 25 x18 km in length vs. width, with a surface area of 234 km^2 and a maximum depth of 180 m, that was formed by a series of volcanic eruptions between 500,000 and 100,000 years ago (Ramos 2002). Lake Taal is the Philippines' third largest lake after Laguna de Bay and Lake Lanao (Figure 1). The volcanic lake is still active with the most recent activity occurring from 2010 to 2011 with high rates of CO_2 emissions, seismic activity, increase of 2-3 ºC temperature and pH levels tending more acidic and previous volcanic activity since 1992 was reported by Yamaya et al. (2013). The lake has long drawn the attention of scientists due to its unique geographical location, geological origin and limnological characteristics (Papa and Mamaril Sr. 2011) with zooplankton studies pioneered by the Wallacea Expedition (Woltereck et al. 1941) and recently updated by Papa et al. (2011, 2012b); Papa and Zafaralla (2011) and Papa and Holynska (2013). The lake is connected to the ocean at Balayan Bay through the 8.2 km Pansipit River, with rare saltwater intrusions in the river occurring during strong storms and typhoons, though the intrusion does not reach the lake. The river was navigable using ships until eruptions in the 18^{th} century blocked the connection with volcanic material, which eventually raised the level of the lake (Hargrove 1991). This previous connection to the sea led to several endemic species that evolved and adapted to the desalination of Lake Taal waters, including the rare sea snake, *Hydrophis semperi* Garman 1881, which is one of two "true" sea snake species that are known to live entirely in freshwater, and *Sardinella tawilis* (Herre 1927) a freshwater sardine and main predator of calanoids (Papa et al. 2008). Currently, the zooplankton of Lake Taal is comprised of the two calanoid species *Pseudodiaptomus brehmi* Kiefer 1938 and *Arctodiaptomus dorsalis* (Marsh 1907), one cyclopoid *Thermocyclops crassus* (Fischer 1853), six cladoceran and 15 rotifer species (Papa et al. 2011, 2012b). With the advent of fish cage aquaculture in Lake Taal during the 1970s of the cichlid tilapia (*Oreochromis niloticus* Linnaeus, 1758), whose larvae are zooplanktivores and the milkfish (*Chanos chanos* Forsskål 1775), an herbivore, the lake has suffered from the negative impacts of under-regulated aquaculture practices (Aypa et al. 2008). The number of fish cages reached a high of 12,000 units in 2005 which were concentrated mostly in the north and eastern basins along the shore of the lake. In 2009, the Taal Volcano Protected Landscape Management Plan was implemented to improve the water quality of the lake. This led to the reduction of the number of fish cages to the recommended 8,000 units by 2008 (TVPL-PAMB 2009). However, this regulated management of aquaculture practices within the lake has barely improved the water quality, as intensive feeding and over-stocking of available fish cages still continues to persist in the lake, along with an increase of human habitation around the lake. A recent study has classified the lake as meso-eutrophic, with the zooplankton community found to be characteristic of such elevated nutrient conditions, such as cyclopids and cladocerans with a minority of calanoids (Papa et al. 2011; Perez et al. 2008).

The Wallacea Expedition in 1941 surveyed numerous freshwater lakes in the Philippines (Woltereck et al. 1941) including Lake Taal and Lake Naujan. Lake Naujan on Mindoro Island, at 13°10' N 121°21'E, is approximately 60 km south of Lake Taal, and is about 9 x7 km in length/width, with a surface area of approximately 81 km^2 and a maximum depth of 45 m, and is about one-third the size of Taal. Kiefer (1938) described *P. brehmi* from Lake Naujan and it was later reported by Woltereck et al. (1941). However, there was no report of calanoids in Lake Taal. From 2012 to 2013 numerous attempts by RDS Papa et al. were made to find this species in Lake Naujan without success, though the invasive neotropical calanoid *Arctodiaptomus dorsalis* was always collected. *A. dorsalis* was first recorded in the Philippines in 1991 from Laguna de Bay and must have been present since the mid- or early 1980s (Papa et al., 2012a) and is now found in 19 out of 28 lakes throughout the Philippines (Rizo et al., 2015). It was noted by Reid (2008) that *A. dorsalis* is a very aggressive invasive copepod that rapidly invaded freshwater locations in Central and South America, and she suggested that it may spread outside the New World boundaries. She also reported that males ranged in size from 0.78-1.06 mm and females 0.77-1.13 mm from various worldwide locations compiled from a literature review. *A. dorsalis* from Lake Taal is relatively small in length with the male 0.82 mm and female 0.97mm, and recent studies have discovered *P. brehmi* in Lake Taal along with *A. dorsalis* (Papa and Zafaralla 2011; Papa et al. 2012a; Papa et al. 2012b). As *P. brehmi* is a rare species endemic to Lake Taal, this paper aims to determine the status of the population and determine if the improved aquaculture management practices in the lake have had an effect on the calanoid species pre-2009 population levels.

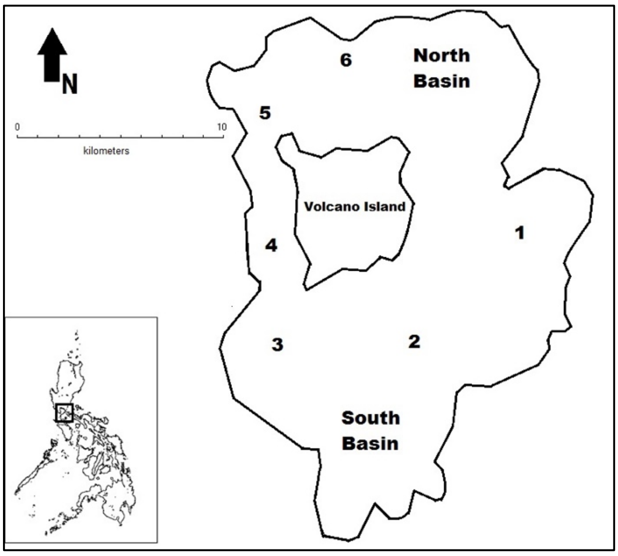

Figure 1. Map showing the six sampling sites in the north and south basins of Lake Taal where *P. brehmi* was collected

MATERIALS AND METHODS

For this study, samples were irregularly collected since 2009 in Lake Taal, and for 2013 from six sites in the mornings between 0430 and 0900 (Figure 1) from June to September 2013 excluding the month of August due to inclement weather. However, due to safety issues, the dawn sampling sites were limited to the south basin (Site 1). Plankton samples were collected by vertical tows from a depth of at least 40m using an 80-μm mesh size conical plankton net (diameter = 30 cm) in areas where average depth is 50m. Each sample was obtained by pooling two replicate hauls, fixed in 70% ethanol, and labeled with locality, time and date of the sampling (Papa et al. 2011). These were stained using Rose Bengal dye ten days after sampling. Additional samples from the University of Santo Tomas – Zooplankton Reference Collection (UST-ZRC) collected from Lake Taal from 2009-2012 and 2014-2016 were also examined. To validate the identity of *Pseudodiaptomus brehmi*, specimens of both sexes were dissected and mounted on slides, for observation, measurement and drawing of morphological features, with the aid of an Olympus CX21 microscope with a drawing tube attachment. All samples were sorted under BestScope and Swift SM90 dissecting microscopes using Stork bill forceps, with adults and copepodids of *P. brehmi* separated from other zooplankton and placed in separate vials. Specimens were photographed individually using an 8-Megapixel Olympus CK2 camera on a phase-contrast microscope. A total of 679 images were processed using ImageJ software version 2.0 for measurements. The length and width of the urosome, prosome and total length were measured in millimeters (mm) for both sexes for adult and copepodid stages (we did not differentiate copepodid stages) (Figure 2). Normality of data distribution was tested using Shapiro-Wilk test. Differences between morphometric measurements of specimens collected from 2009 and 2013 were determined using unpaired Student's t-test and Mann-Whitney U test and illustrated using Box-Whisker plots. Statistical tests were made using PAST v. 1.81 and Microsoft Excel while graphs were generated using SigmaPlot v. 12.0.

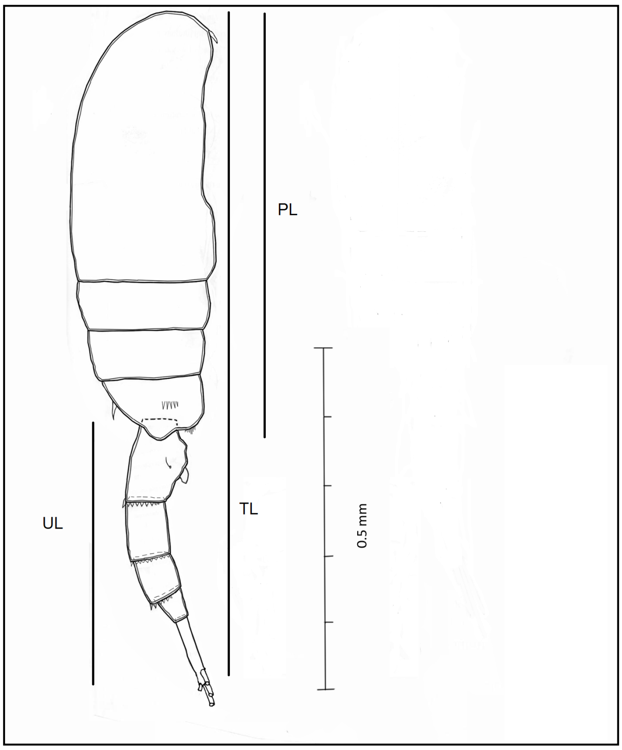

Figure 2. Line drawing of a representative female *Pseudodiaptomus brehmi* specimen (without appendages) with the sites where total length (TL), prosome length (PL) and urosome length (UL) measurements were obtained.

RESULTS AND DISCUSSION

Table 1 presents the relative abundance of adult males and females of *P. brehmi* in Lake Taal for the months of April to October 2013. Total length of adult females (t=1.106, P=0.2695) and copepodids (t=0.85937; P=0.39119), did not vary significantly between 2009 and 2013 while prosome length and urosome length for adult males, females and copepodids and the total length of males showed significant differences (Figure 3 and Table 2). Ovigerous females typically have 4-9 eggs/sac, egg diameter 0.008-0.014 mm and egg sac length 0.022-0.035 mm (Figure 4). In April, females (both adult and juvenile) were dominant compared to adult males, while in May the adults of both sexes were almost equal, providing the maximum number

Table 1. Relative abundance of *Pseudodiaptomus brehmi* collected from Lake Taal during April-October 2013, numbers are a % (percentage) of 100. Juvenile stages not recorded. September and October the percent of ovigerous females was 22 and 14 %, respectively.

Month	April	May	Jun	Jul	Sep	Oct
Male	00	50	22	17	15	07
Female	100	50	78	83	85	93

of males for breeding during June, September and October. Mature ovigerous females were dominant and levels were variable (Table 1). In Thailand, Srinui et al. (2013) reported that ovigerous and spermatophore-bearing females of *P. Siamensis* occurred during June-October. In Lake Taal, there appeared to be a stable population of adult females from April to October, while the population of male copepods gradually decreased, with the monthly ratio of females to males averaging 5:2. The results of this study indicate that *P. brehmi*, though having a thriving population with all life stages observed, is a small component of the copepod assemblage, as few individuals have been recorded throughout the 4-years of observation. The ratio of *P. brehmi* to *A. dorsalis* during the 2013 sampling period was found to be 1:8. The maximum density of *A. dorsalis* was recorded at 20 ind. /liter in January, though the annual mean average was 5-6 ind. /liter (De Leon et al. 2016). We believe that *P. brehmi* has a preferred habitat niche that is deeper than that of the invasive *A. dorsalis* in Lake Taal, which allows it to avoid direct competition for food, space and the advantage ofzpredator avoidance in the surface layers. Even though the population *P. brehmi* in Lake Taal is lower than that of the invasive *A. dorsalis*, it still hasn't been displaced, which is not the case with Lake Naujan, the type locality for *P. brehmi*, where *A. dorsalis* has already been noted to displace *P. brehmi* (Papa et al. 2012a). The relative shallowness of Lake Naujan compared to Lake Taal may have allowed *A. dorsalis* to become a more efficient competitor for food and habitat compared to Lake Taal,

Table 2. Table 2. Summary of Statistical results of *Pseudodiaptomus brehmi* body measurements in all life stages (2009 vs 2013).

	t	P-value
Prosome Length		
Adult Male	-2.4083	0.019062*
Adult Female	5.271	0.00000023749***
Copepodid	4.144	0.00011872***
Urosome Length		
Adult Male	-8.0503	0.000000000036039***
Adult Female	-2.9423	0.003474**
Copepodid	-4.4857	0.000037445***
Total Length		
Adult Male	-4.7509	0.000012723***
Adult Female	1.106	**0.2695**
Copepodid	0.85937	**0.39119**
Egg Diameter	-19.862	2.7701E-23***
Egg Sac Length	20.346	1.0855E-23***

Note: Values in bold face showed no significant difference between 2009 and 2013; (*p<0.05,**p<0.01,***p<0.001)

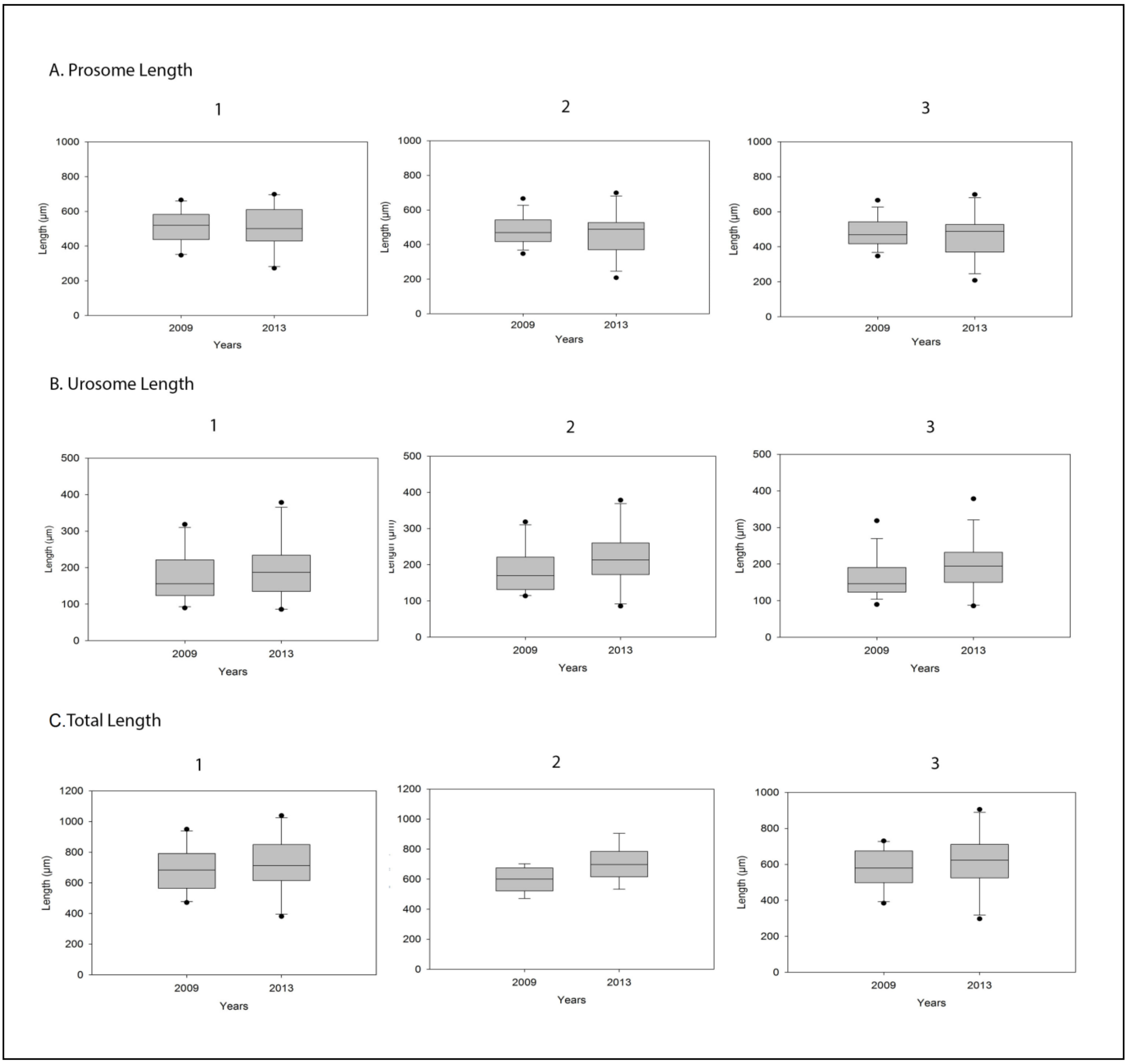

Figure 3. Morphological measurements of *Pseudodiaptomus brehmi*: A. Prosome length (A1: Adult male prosome length; A2: Adult female prosome length; A3: Copepodid prosome length), B. Urosome length (B1: Adult male urosome length; B2: Adult female urosome length; B3: Copepodid urosome length), C. Total length (C1: Total length of adult male; C2: Total length of adult female; C3: Total length of copepodid).

where the depth of the lake may have allowed for *P. brehmi* populations to exist in a separate niche from *A. dorsalis*. Overall, calanoid abundance in Lakes Taal and Naujan (both eutrophic lakes) were much lower compared to the levels of cyclopoids and cladocerans for both lakes (Papa et al. 2012a) and recently (De Leon et al. 2016; Papa, unpublished data; this study). Eutrophic lakes worldwide are typically dominated by cyclopoids and cladocerans rather than calanoids (Dussart and Defaye 2001). For *P. brehmi*, the morphometric measurements of individuals during 2009-2013, show that there is a difference in the body size of different life stages in Lake Taal, specifically for prosome and urosome lengths (for adult males, females and copepodids) but total lengths for adult females and copepodids collected from 2009 and 2013 did not vary significantly. The statistically significant differences in the measurements may have been caused by the unequal sample sizes of specimens collected, as there were fewer specimens collected from 2009 compared to 2013. Furthermore, upon looking at the Box-Whisker plots generated using the data shows that gap between measurements of specimens from 2009 and 2013 are not too large. As such, we cannot attribute the larger size of 2013 samples compared to the 2009 samples as an indication of an improvement in water quality or food availability or even the decrease in predation pressure between these two years, which was the case with *A. dorsalis* (De Leon et al. 2016). Over-all, the results suggest that the shallow nature of Lake Naujan and the depth preferences of the species, may have led to the demise of *P. brehmi* due to the invasion of *A. dorsalis*. It has been noted in previous studies that invasive calanoids such as *Eudiaptomus gracilis* has led to the disappearance of the native *E. padanus* in Lake Candia (Italy) which was attributed to interspecific differences in reproductive rates and juvenile mortality (Riccardi and Giussani, 2007). This is usually the case with calanoid copepods, as there is only usually just one calanoid species found in any given lake, which leads to higher rate of displacement by invasive species.

It appears that further studies into the spatio-temporal variability and feeding habits of *P. brehmi* and *A. dorsalis* populations in Lake Taal may be necessary to see how an invasive species interacts with a native endemic population. If the remaining population of *P. brehmi* from Lake Taal is replaced by *A.*

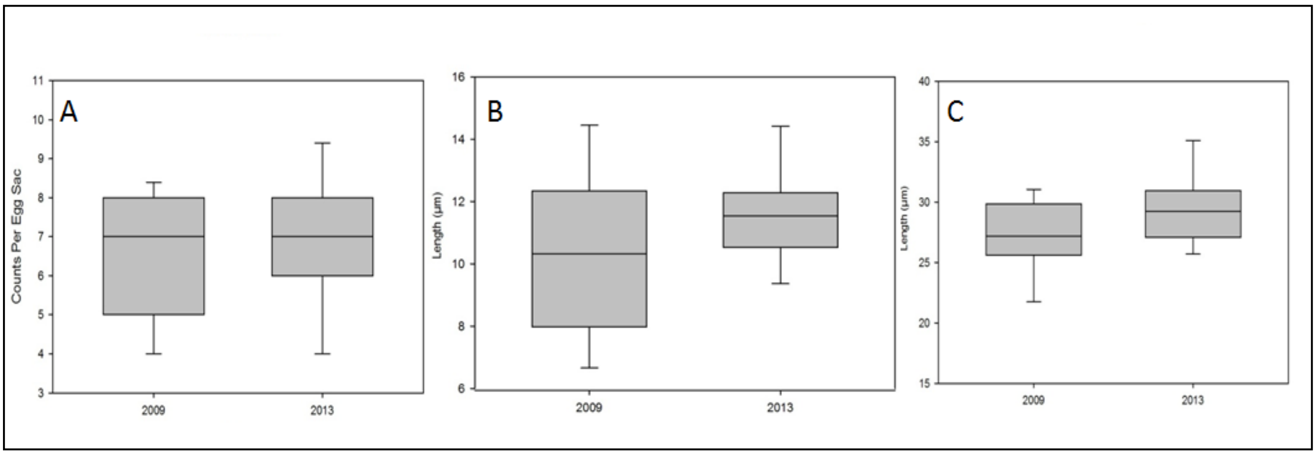

Figure 4. A) Egg counts per sac B) egg diameter and C) egg sac length of *Pseudodiaptomus brehmi.*

dorsalis it may result in the loss of another species from the planet. Members of the Asian Lobus species-group are known to be invasive species as evidenced by the introduction of *P. forbesi* and *P. inopinus* that have developed stable populations along the Pacific coast from Washington to California, USA,
to be invasive spalong the Pacific coast from Washington to California, USA (Orsi and Walter 1991; Cordell and Morrison 1996; Cordell, et al. 2007). Most introductions of invasive species are attributed to the uncontrolled regulations of dumping of international shipping ballast water near shore and/or the importation of animals for aquaculture purposes. Other New World calanoids have been reported in Indo-Pacific waters such as, *Skistodiaptomus palllidus* recently been reported in New Zealand (Duggan et al. 2006, 2014), *P. wrighti* (Johnson 1964) was found in Bangladesh from the freshwater lake Kaptai in 1989 by Hafizuddin and Chowdhury (1996) and *Argyrodiaptomus ferus* from the Pearl River, China by Shen and Tai (1964). Thereby suggesting that other new introductions of non-Asian calanoids may be encountered in future investigations throughout Asia.

As a final note, the primary predator of the zooplankton in Lake Taal is the sardine *Sardinella tawilis*, both juvenile and adults. Adult sardines prefer the larger prey items such as the cyclopoids and calanoids. Year-round food items of the adult sardines were composed of 58% calanoids, 32% cyclopoids and 10% cladocerans and rotifers, while the juvenile fish feed on the copepod larval stages and smaller zooplankton forms. Though calanoid remains found in the gut content analyses done on *S. tawilis* were not identified to genus level, it was observed that the calanoid copepods consumed by *S. tawilis* belonged to Family Diaptomidae which is only represented by *A. dorsalis* in Lake Taal (Papa et al. 2008). Throughout May to June, the adult calanoids were heavily predated by females in preparation for spawning (Joson-Pagulayan 1999). Sardine maximum consumption of calanoid copepods was April-May, which correlated with the lowest density of the copepods. During December-June cyclopoids were the main dietary item, with April-May the highest months of consumption (Papa et al. 2008). The impact of tilapia predation on the zooplankton has so far not been studied in Lake Taal, suggesting that additional studies are needed to shed more light on the interactions between the predator and prey relationships.

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