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An analysis of publications on *Daphnia lumholtzi* in freshwater ecosystems

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ABSTRACT

An analysis of publications on *Daphnia lumholtzi* in freshwater ecosystems

Biological invasions can threaten biodiversity worldwide through the loss of native species. *Daphnia lumholtzi*, Sars, 1885 is a native cladoceran from Australia, southwest Asia, and North Africa, and was recently recorded in the Neotropical region. We performed a scientometric analysis of scientific papers published between 1976 and 2016 to evaluate the studies that documented the occurrence of *D. lumholtzi* and assess the influence of local (temperature) and spatial factors (geographic distance) on the species distribution. Research articles were collected by the Thomson Reuters database (www.isiwebofknowledge.com) in December 2016. We observed that the number of articles increased over the years and that the species occurred in a great variety of environments, predominantly in reservoirs. Studies were performed using different approaches, most of them using descriptive and predictive designs. Furthermore, we observed that there was no significant relationship between *D. lumholtzi* abundance and both local (temperature) and spatial (geographic distance) factors. However, when we analyzed the occurrence of the species with temperature, we found that the species frequently occurred between 21 ºC and 27 ºC, and the greatest number of studies reported *D. lumholtzi* at 24 ºC. We observed a tendency for *D. lumholtzi* to occur in aquatic environments with higher temperatures. Therefore, we suggest experimental studies that evaluate the effect of temperature changes on the survival of this species, which could be impacted by climate change.

Key words: biological invasion, Cladocera, invasive species, zooplankton

RESUMO

Análise de publicações de* Daphnia lumholtzi *em ecossistemas aquáticos

As invasões biológicas são processos importantes no cenário global, uma vez que constituem umas das principais ameaças não só para a biodiversidade, através da perda de espécies nativas, mas também para o desenvolvimento econômico. Daphnia lumholtzi *Sars, 1885 é um cladócero nativo da Austrália, sudoeste da Ásia e Norte da África, e foi recentemente registrado na região Neotropical (Brasil e Argentina). Foi realizada uma análise cientométrica de trabalhos científicos publicados entre 1976 e 2016 para avaliar os estudos que registraram a ocorrência de* D. lumholtzi *e verificar a influência de fatores locais (temperatura) e espaciais (distância geográfica) na distribuição da espécie. Os artigos resultantes da pesquisa foram coletados pela base de dados Thomson Reuters (www.isiwebofknowledge.com) em dezembro de 2016. Foi possível observar que o número de artigos aumentou ao longo dos anos e que a espécie esteve presente em uma grande variedade de ambientes, predominantemente em reservatórios. Além disso, não foi encontrada uma relação significativa entre a abundância de* D. lumholtzi *e os fatores locais (temperatura) e espaciais (distância geográfica). No entanto, quando analisamos o gráfico de ocorrência das espécies com temperatura, observamos que a mesma foi encontrada frequentemente na faixa de temperatura correspon-*

dente entre 21 ºC e 27 ºC, e o maior número de estudos foi registrado em 24 ºC. Foi observado uma tendência de ocorrência de D. lumholtzi *em ambientes aquáticos com temperaturas mais elevadas. Portanto, faz-se necessário estudos experimentais que avaliem o efeito da temperatura sobre a ocorrência desta espécie, visto que pode ser de suma importância em caso de mudanças de temperatura devido às mudanças climáticas.*

Palavras chave: *biologia das invasões, Cladocera, invasão de espécies, zooplâncton*

INTRODUCTION

Biological invasions (i.e., the successful establishment and spread of species outside their native range) constitute serious threats to the integrity of natural aquatic ecosystems (Simberloff *et al.*, 2013). Invasions may cause the loss of biological diversity through extinctions of native species, besides causing alterations in habitats and in the transfer of matter and energy in these environments (Stewart & Sprules, 2011). Aiming to solve this global problem, the interest in invasive species has substantially grown in recent decades (Strayer, 2010), particularly in freshwater ecosystems (Lowry *et al.*, 2013).

Although many years of investigation provided greater knowledge on the propagation and potential impacts of certain invasive species, the effects of biological invasion are poorly studied (Havel *et al.*, 2015). Moreover, the prediction on the geographic extension and invasive success of non-native species are still difficult to measure (Moyle & Marchett, 2006; Hayes & Barry, 2008).

Understanding patterns related to the rates of establishment and dissemination of non-native species is crucial to the management of biological invasions (Parkes & Duggan, 2012). In general, the process of biological invasion is composed of several stages, such as geographic isolation, which acts as the first filter for the dispersal of non-native species (Havel *et al.*, 2015). Local environmental filters (biotic and abiotic) can partially determine the success or failure of these species (Mcgill *et al.*, 2006; Zhang & Liu, 2011). Although the synergism of these factors is important in the invasion process, it is known that anthropogenic impacts facilitate the overcoming of natural barriers (Espínola & Julio-Júnior, 2007; Havel *et al.*, 2015; Bomfim *et al.*, 2016), accelerating the colonization process of a new environment by a non-native species.

Recent studies of freshwater zooplankton have revealed a variety of successful invaders in different environments, countries, and continents (José de Paggi, 2002, Serafim-Júnior *et al.*, 2003; Simões *et al.*, 2009; Bomfim *et al.*, 2016). These planktonic organisms have resting stages, asexual reproduction, rapid population growth, and phenotypic plasticity, assuring strong invading potential (Dodson & Frey, 2001).

Daphnia lumholtzi (Crustacea: Branchiopoda) is a planktonic species native to the subtropical regions of Africa, Asia, and Australia (Benzie, 1988). Since its invasion in the southern United States in 1990, *D. lumholtzi* has rapidly invaded a wide variety of habitats, including reservoirs, flood-plain lakes, and large rivers (Frisch *et al.*, 2013). This species shows morphological characteristics that may facilitate its dispersal and reduce its vulnerability to predation by small planktivorous fish, due to the presence of spines in the lateral parts of the helmet, anterior region of the head and posterior region of the carapace, which are larger than those observed in other *Daphnia* species (Lienesch & Gophen, 2001; Effert & Pederson, 2006). Moreover, their ability to produce resting eggs increases their survival rates and facilitates dispersal over long distances, increasing the probability of reaching new habitats (Riccardi *et al.*, 2004; Panov *et al.*, 2007).

The successful invasion of *D. lumholtzi* may also be credited to their ability to access different environments and tolerate the environmental conditions of the new habitat (Swaffer & O'brien, 1996). Recent studies showed that *D. lumholtzi* is usually not abundant at the same time of year as other cladoceran species and therefore, direct competition between groups is unlikely (Work & Gophen, 1999; Havel & Graham, 2006), leading to the conclusion that this alien species fills a 'vacant niche' (Work & Gophen, 1999).

Studies reported that temperature is also a

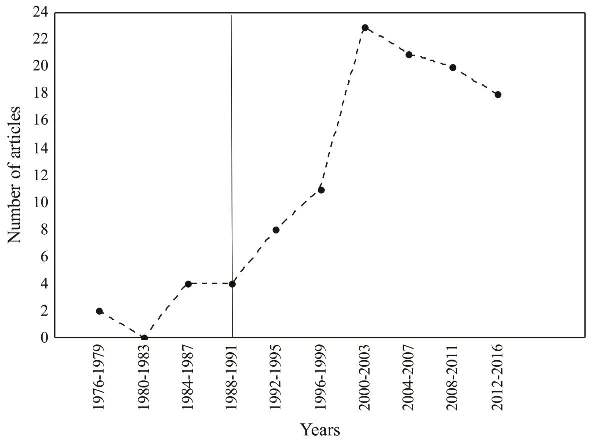

Figure 1. Temporal trend of the number of papers indexed in Thomson Reuters databases, addressing studies on *D. lumholtzi* during the scientometric survey. *Tendência temporal do número de artigos indexados nas bases de dados da Thomson Reuters, abordando estudos sobre* D. lumholtzi *durante a pesquisa cientifica.*

relevant factor for the invasive success of *D. lumholtzi* (Work & Gophen, 1999; Havel & Graham, 2006). It is known that temperature may have an important effect on the distribution and abundance of these organisms, defining tolerance limits (Wetzel, 2001). Within these intervals, temperature directly regulates the survival, reproduction, growth rate and distribution of these organisms (Brazner *et al.*, 2005; Heino *et al.*, 2009). Therefore, this environmental variable may act as a facilitating or inhibiting mechanism for the establishment of the species in a certain aquatic environments (Lennon *et al.*, 2001). Therefore, we aimed to evaluate the studies that registered occurrence of *D. lumholtzi* through scientometric analysis, and assess the influence of local (temperature) and spatial factors (geographic distance) on the species distribution.

MATERIAL AND METHODS

We performed a scientometric analysis based on research articles indexed in the Thomson Reuters database (www.isiwebofknowledge.com) citing "*Dapnhia lumholtz*" or "*D. lumholtzi*" published prior to December 31, 2016. For this, we used the scientific production catalogued as an indicator of results.

We categorized articles according to (1) the temporal tendency of publication; (2) climatic zone (temperate, tropical, and polar); (3) type of environment (lake, river, and reservoir); (4) location by continent (Europe, North America, Central America, South America, Asia, Africa, and Oceania); (5) study focus (ecological: related to the occurrence and distribution of the species and their respective environmental function; or zoological: including taxonomic, biological, and molecular studies that indicate the genetic origins of populations of *D. lumholtzi*); and (6) study design (descriptive -comparative studies, predictive-studies based on predictive models with or without ecological theory, experimental- studies performed in the laboratory under controlled environmental conditions, and review- literature review). We also gathered and standardized data on the average abundances of *D. lumholtzi* (individuals/m3) through the information extracted from text and figures, the range of temperature in which the species was registered, and the geographic coordinates in articles that provided this information.

The years of publication were grouped into intervals of six years between 1976 and 2016. Therefore, the articles were grouped into 10 time intervals: 1976–1979, 1980–1983, 1984–1987, 1988–1991, 1992–1995, 1996–1999, 2000–2003, 2004–2007, 2008–2011, 2012–2016. We

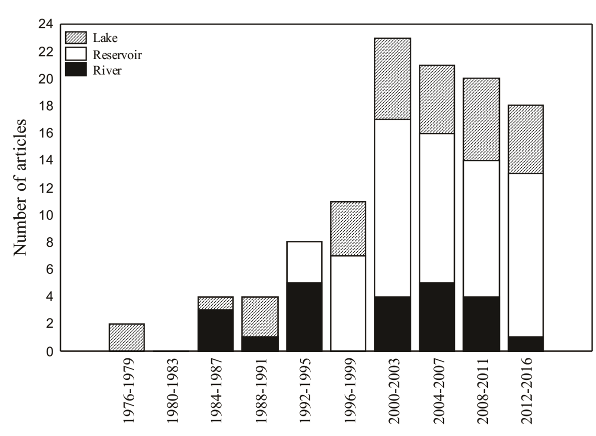

Figure 2. Number of articles citing *D. lumholtzi* in each type of aquatic environment in the scientometric survey. *Número de artigos que citam* D. lumholtzi *em cada tipo de ambiente aquático na pesquisa cientifica.*

produced a distribution graph to visualize optimum temperature and temperature range that the species occurred. Finally, we used regression tree (MRT) analysis (De'ath and Fabriciu, 2002) to verify which time interval was relevant to mark an effective change in the *D. lumholtzi* publications scenario and a Mantel test (Legendre and Legendre, 1998) to investigate the influence of temperature (local factor) and geographic distance (spatial factor) on *D. lumholtzi* abundance. For this, three matrices were calculated: *D. lumholtzi* abundance (Bray-Curtis dissimilarity matrix with species abundance), temperature (Euclidean distance matrix), and geographical distance matrix (Euclidean distance matrix). The significance of the results ($p<0.05$) was determined using 999 permutations.

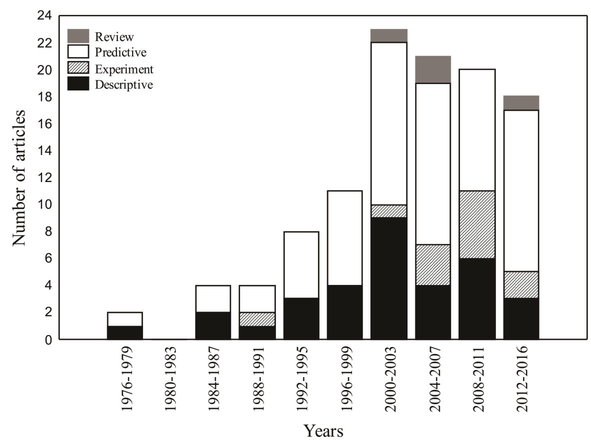

Figure 4. Number of articles classified according to the design employed in studies conducted in the period of the scientometric survey. *Número de artigos classificados de acordo com o delineamento empregado em estudos realizados no período da pesquisa cientifica.*

RESULTS

We collected 109 research articles regarding *D. lumholtzi* in the Thomson Reuters database, published between 1976 and 2016 (see references list used in supplementary information, available at http://www.limnetica.net/en/limnetica). The increase in scientific production was observed in 1992, as suggested by MRT. The threshold year was 1991, and from that year on, there was an increasing number of publications over time, with a peak in the interval 2000–2003 (n = 23) and similar values in the next periods (Fig. 1).

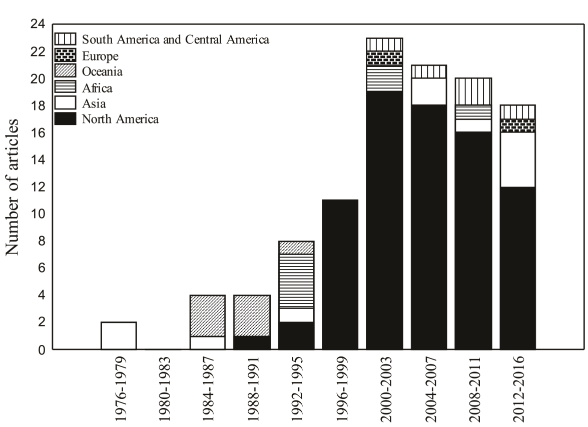

Figure 3. Number of publications recorded for each continent during the period considered in the scientometric survey. *Número de publicações registradas para cada continente durante o período considerado na pesquisa cientifica.*

Regarding the distribution of species in the different climatic zones, most studies were performed in the subtropical climate (n = 66), followed by tropical climate (n = 25). When considering the types of environments, most studies were performed in reservoirs (n = 55), followed by lakes (n = 31), and rivers (n = 23) (Fig. 2).

Considering geographic location, North America showed the highest number of scientific publications (n = 77), followed by Asia (n = 11), Africa (n = 7), and Oceania (n = 7). The lowest number of publications was found in South America and Central America (n = 5), followed by Europa (n = 2), and there were no studies conducted in Central America. We also observed that Asia and Africa pioneered studies on *D. lumholtzi*. Moreover, we observed that North America was the dominant continent in our research from 1992 (Fig. 3).

Most studies were descriptive (n = 32) or predictive (n = 61). Articles with predictive design were registered during most time intervals, with a greater number of studies at the beginning of the 1990s, when the number of published articles also increased. Experimental studies were published beginning in 1984 (n=12), and similar to review articles, showed a lower number of

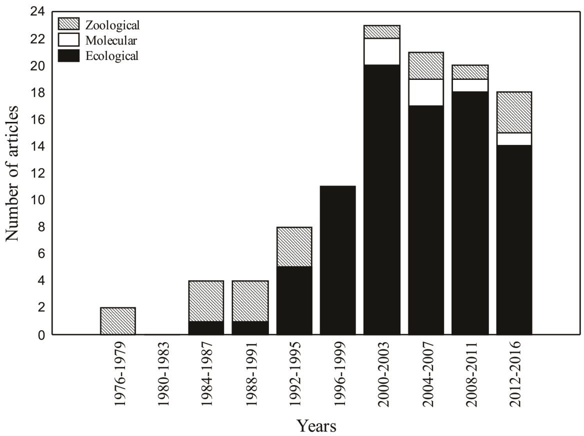

Figure 5. Number of publications classified according to the central focus of the article during the period of the scientometric survey. *Número de publicações classificadas de acordo com o enfoque central do artigo durante o período da pesquisa cientifica.*

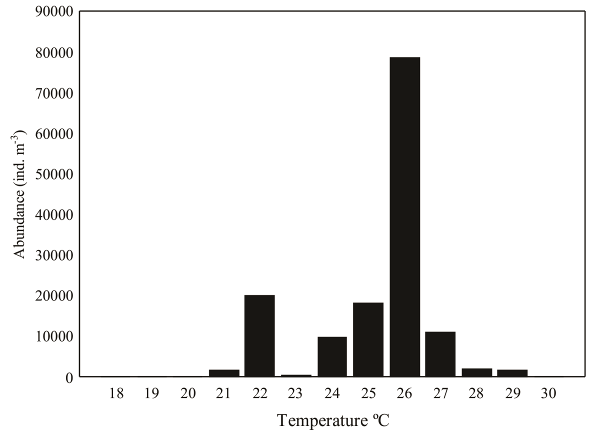

Figure 6. Number of publications classified according to the relation between abundance and temperature variation. *Número de publicações classificadas de acordo com a relação entre abundância e variação de temperatura.*

publications than the other designs employed during the analyzed period (n = 4) (Fig. 4).

Most articles focused on ecology (n = 85), which were followed by zoological (n = 18) and molecular studies (n = 6). Ecology studies were published during the most intervals and were the only study focus from 1996-1999. Zoological studies were published from 1976–1979, 1984-1991, 2000-2003, 2004-2007, 2008-2011 e 2012-2016, whereas molecular studies were published only after the year 2000 (Fig. 5).

There was no relationship between *D. lumholtzi* abundance and local (temperature) or spatial (geographic distance) factors (Mantel test, p>0.05). However, when we analyzed the graph of occurrence of the species and temperature, we found that *D. lumholtzi* was frequently occurring at temperatures between 21 ºC and 27 ºC, and the greatest number of studies reported *D. lumholtzi* at 24 ºC (Fig. 6).

Although many articles did not report both abundance and temperature, it was possible to observe that the highest mean abundance of the species (78.533 individuals/m^{-3}) was registered at 26 ºC (Fig. 7).

DISCUSSION

The increase in the number of publications on *D. lumholtzi* over time can be indicative of the growing recent interest in the distribution and ecology of invasive and the possible impacts that they may have in aquatic ecosystems (Lowry *et al.*, 2013; Sousa *et al.*, 2017). The low number of articles found before the 1990s possibly reflects the scarcity of knowledge within the scientific community of biological invasions, since it only became widely recognized after the publication of Charles Sutherland Elton's book "*Ecology of invasions by animals and plants*" in 1958 (Ricciardi & Macisaac, 2008). Furthermore, the first record of this *D. lumholtzi* outside of its native area was published only in mid-1993 (Havel & Hebert, 1993).

The prevalence of ecology-focused studies may be explained by the fact that zooplankton species constitute great models testing ecological theories. These organisms link producers and higher trophic levelsand have small body size and high abundance (Sommer, 1996); these characteristics facilitate sampling, allowing robust statistical analyses and consequently, portray a more realistic picture of the environment (Bohonak & Jenkins, 2003). Regarding anthropogenic impacts, which have drastically altered conditions of water bodies (Jeppesen *et al.*, 2015), different incentives to drive ecological research have emerged. Concomitant with the need to understand ecological relationships between species, which are determinant for their survival in the environment, those modifications anthropic also allow the identifica-

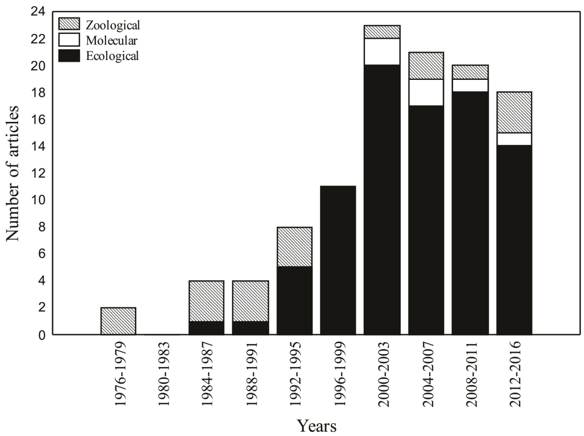

Figure 7. Number of publications classified according to the registered temperature during the period of the scientometric survey. *Número de publicações classificadas de acordo com a temperatura registrada durante o período da pesquisa cienciométrica.*

tion of ecological events not previously directly observed (Bohonak & Jenkins, 2003).

The publication of research articles on *D. lumholtzi* with molecular emphasis began only in the year 2000. This area of knowledge is still considered recent, since the discovery of DNA structure occurred in 1953 (Watson & Crick, 1953). From that study, new possibilities of molecular research emerged, which were further applied in studies of organisms (Schwind *et al.*, 2013). In addition, currently molecular identification methods are being used more frequently performed to indicate the origin of *D. lumholtzi* populations and to recreate invasion routes of non-native individuals (Havel *et al.*, 2000).

Daphnia lumholtzi is native to tropical and subtropical regions, such as the South Asia and North Africa, which explains why studies originated on these continents (Benzie, 1988). Most publications in the analyzed period were concentrated in the south-central region of North America. Since its first recorded occurrence in North America in the mid-1990s (Fey & Cottingham, 2011), *D. lumholtzi* showed a rapid dispersal among aquatic environments in the United States and is currently widely distributed throughout the North America (Havel & Medley, 2006). Since it is considered an invasive species in the tropics, it is likely that its physiology allows adaptation to warm summer conditions in the United States, leading to higher abundances (Havel *et al.*, 1995). The likely explanation for the dispersal vector of *D. lumholtzi* between continents is related to the introduction of resting eggs, concomitant to the introduction of exotic fish of great commercial interest, such as tilapia (*Tilapia mossambica*) and Nile perch (*Lates niloticus*) (Sorensen and Sterner, 1992; Havel & Hebert, 1993). Fluvial connections among reservoirs also aid dispersal rates (Magnuson *et al.*, 1990; Amoros & Bornette, 2002).

The higher incidence of *D. lumholtzi* populations in reservoirs indicated that these environments have an important role in invasion, since they serve as stepping-stones for further invasions. River damming for reservoir construction alters the morphology of the system, abiotic characteristics, and functioning dynamics, affecting aquatic communities and favoring the processes of introduction and establishment of non-native species (Parkes & Duggan, 2012). Specifically, reservoirs provide new habitats for passively dispersing numerous zooplankton species that cannot persist in strong unidirectional flow, making ideal habitats for the maintenance of populations of planktonic invasive species like *D. lumholtzi* (Havel & Shurin, 2004; Havel *et al.*, 2005; Johnson *et al.*, 2005; Sousa *et al.*, 2017). This is a worrying scenario, since future projections point to a significant expansion of these systems along rivers (Ferreira *et al.*, 2014), which would increase populations of cladoceran *D. lumholtzi* that could provide inocula to natural lakes (Havel *et al.*, 2005).

Although the influence of temperature on the abundance of *D. lumholtzi* was not observed, this species showed a higher frequency of occurrence at higher temperatures and with a higher abundance found during summer than in winter, when they were less abundant or absent (Havel and Graham, 2006). The lack of articles comparing the occurrence of this species during winter and summer, as well as their occurrence at extreme temperatures (temperatures below 16 ºC and above 30 ºC) may have contributed to the non-significant correlation between temperature and abundance. Geographic isolation is an important barrier in the process of species invasion (Simberloff, 2009; Parkes & Duggan, 2012). However, in our study, geographic distance did not significantly influence the abundance of *D. lumholtzi*. This may be related to the fact that zooplankton species produce resting stages that can be transported by migratory birds (Figueirola *et al.*, 2003), wind, or rain (Jenkins & Underwood, 1998) and hatch under favorable environmental conditions (Hairston, 1996; Bomfim *et al.*, 2016).

CONCLUSIONS

Results showed that the increase in the number of publications on distribution, abundance, and ecological aspects of *D. lumholtzi* evidenced the concern of researchers on its invasive potential and the need to identify possible effects of the presence of this species in local communities. We also observed, although not evaluated by ourselves, a tendency of occurrence of *D. lumholtzi* in aquatic environments with higher temperatures. Unfortunately, there is a lack of studies with this bias, so we suggest studies that evaluate the effect of temperature on the occurrence of this species, because it may be significantly impacted by climate change.

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