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Research Article

An intra-continental invasion of the temperate freshwater copepod *Skistodiaptomus pallidus* (Herrick, 1879) (Calanoida, Diaptomidae) in tropical Mexico

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Abstract

The freshwater planktonic calanoid copepod *Skistodiaptomus pallidus* (Herrick, 1879), native to cold and temperate latitudes in the United States, has recently been identified as having non-indigenous populations in Western Europe and New Zealand. A further non-indigenous population of this species is recorded here from a large inland reservoir in the State of Sinaloa, northwestern Mexico. This copepod species can be distinguished from its congeners mainly by its pincer-like distal process of the second exopodal segment of the right fifth leg of the male. This is the first record of *S. pallidus* in tropical latitudes and its presence in Mexico is far outside of its known intra-continental range. This introduction is attributed to human agency and deemed as a recent arrival. The local fisheries and aquaculture activities in the surveyed reservoir are the most probable vectors of this introduction but avian transportation by migrating pelicans is also possible. Because of the competitive abilities of this species and the connectivity of this reservoir, it is expected that *S. pallidus* will spread to other man-made locations in Mexico.

Key words: freshwater zooplankton; Neotropical freshwater fauna; crustacean introductions; copepod species introduction

Introduction

The freshwater copepod genus *Skistodiaptomus* Light, 1939 comprises small or medium-sized diaptomids. The generic diagnostic characters include the presence of a single seta on antennular segment 11 in the female, a much reduced female fifth leg terminal exopodite, and a right male antennule with strong spines on segments 10, 11 and 13 (Dussart and Defaye 2002). Currently, the genus is known to contain eight species: *S. bogalusensis* (Wilson and Moore, 1953), *S. carolinensis* Yeatman, 1986, *S. mississippiensis* (Marsh, 1894), *S. oregonensis* (Lilljeborg, 1889), *S. pallidus* (Herrick, 1879), *S. pygmaeus* (Pearse, 1906), *S. reighardi* (Marsh, 1895), and *S. sinuatus* (Kincaid, 1953) (Boxshall and Halsey 2004; Reid and Williamson 2010). All the known species of *Skistodiaptomus* are native to North America, with the genus absent from South and Central America; most species have restricted distributions (Suárez-Morales et al. 2005, Dussart and Defaye 2002). *Skistodiaptomus pallidus* is relatively widely distributed, having spread across the cold-temperate areas of the United States (Byron and Saunders 1981), but it is largely restricted to latitudes north of the 30°N. This species has been regarded as native to the north-central plain states of the United States, northeast to New York and in states in the Mississippi River basin, Montana, Wisconsin, Michigan, Georgia, Texas, and west to Colorado (Pennak 1989; Torke 2001; Thum and Stemberger 2006). This calanoid copepod has been recognized as a non-indigenous species outside of the United States, with recent records in New Zealand and Germany (Duggan et al. 2006; Brandorff 2011).

The freshwater copepod fauna of Mexico has been investigated in different regions (Suárez-Morales and Reid 1998; Elías-Gutiérrez et al. 1999; Suárez-Morales et al. 2010) and several non-native species of cyclopoids have been recorded from this country (Suárez-Morales et al. 2011); however, no non-indigenous diaptomid calanoids have been hitherto reported.

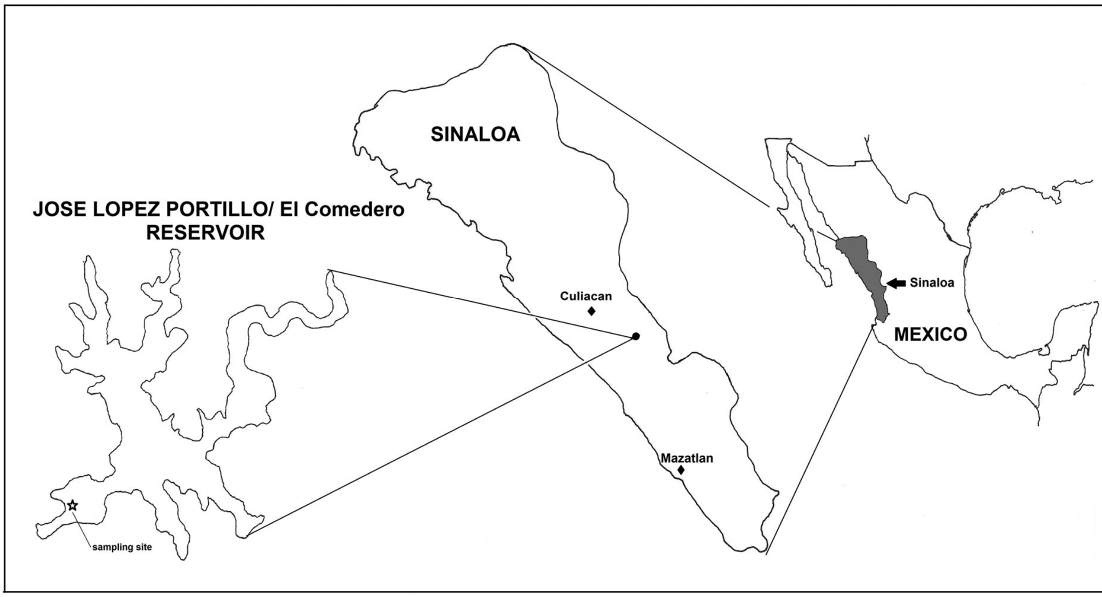

Figure 1. Geographic location of the El Comedero reservoir in Sinaloa, Mexico, the site where *Skistodiaptomus pallidus* was recorded.

A biological survey was carried out in the large reservoir José Lopez Portillo, also named "El Comedero", in the Mexican State of Sinaloa, northwestern Mexico. Zooplankton samples were obtained during 2004, 2005 and 2010 to determine the composition and abundance of planktonic crustaceans. In samples from March 2010 we detected several adult male and female diaptomid copepods. The taxonomical examination of this material resulted in the identification of *S. pallidus*. Because there are few taxonomical illustrations of this species, we present complementary morphological data about this copepod, particularly in reference to the male fifth leg. The record of this species is presented herein as an accidental introduction to this system in an area well outside the known distribution of the species. We discuss the probable route of introduction to the surveyed area.

Material and methods

Adult males and females of *Skistodiaptomus pallidus* were collected during a biological survey of the El Comedero reservoir. The study aimed to determine the composition, diversity, and distribution of the freshwater zooplankton of this large reservoir that is used for fishing and aquaculture (Beltrán 2003). Zooplankton was collected bi-monthly throughout 2010 using a Wisconsin-type plankton net with a mesh size of 90 µm. Samples were fixed and preserved with 4% formalin solution. Copepods were sorted and transferred to 70% ethanol for preservation and storage. The taxonomic analysis of the copepods involved dissection of appendages, preparation of microscope slides using glycerol as a mounting medium, and illustrations prepared with the aid of a camera lucida.

The José López Portillo reservoir, also known as El Comedero, is located in the municipality of Cosala in the state of Sinaloa, northwestern Mexico (Figure 1). The area is crossed by two important rivers: the San Lorenzo and the Elota. The former river flows through the county of Cosala, enters the municipality of Culiacan, and flows into the Pacific Ocean. The reservoir has a catchment area of 8 919 km^2 and has an average annual runoff of 1 572 million m^3. To take advantage of this important hydrologic basin the El Comedero reservoir has a total capacity of 3 399 million m^3, being the fourth largest in the state. Conductivity of El Comedero reservoir water ranges from 142 to 203 µS cm^{-1}, temperature between 21.9 (January) and 31.2°C (July), and dissolved oxygen between 5.5 (January) and 8.7 mg/l (September).

Results

Family Diaptomidae Baird, 1850
Subfamily Diaptominae Kiefer, 1932
Skistodiaptomus pallidus (Herrick, 1879)
(Figures 2-3)

Material examined. One adult ♂, collected March 4, 2004 from El Comedero reservoir, in the Mexican State of Sinaloa, northwestern Mexico (24°34'14.40"N; 106°48'30.13"W), plankton sample, collector G. Arroyo, one specimen dissected on two slides, mounted in glycerol and sealed with Entellan ®, deposited in collection of Zooplankton of El Colegio de la Frontera Sur (ECOSUR), Chetumal, Mexico (ECO-CHZ-08583). One adult ♂, undissected, same site, date, and collector, ethanol-preserved, vial (ECO-CHZ-08584). Four adult ♀♀, collected March 2010 from same locality, date and collector, plankton sample, specimens un-dissected, ethanol-preserved (ECO-CHZ-08581). One adult ♀, specimen dissected on two slides, mounted in glycerol and sealed with Entellan ®, same locality and collector (ECO-CHZ-08582).

Morphology

Female. Body length excluding caudal setae (1.17-1.28 mm, average 1.23 mm, n=10) and proportions as in Pennak (1989) and Brandorff (2011), including a long cephalothorax and a one-segmented urosome (Figure 2A), metasomal wings weak and symmetrical, not expanded laterally, armed distally with spine-like sensilla and hair-setae (Figure 2D). Genital double somite with weak rounded expansion on anterior half, right margin with patch of minute spinules (Figure 2A,D), genital field ventrally protuberant (Figure2C). Antennules 25-segmented, relatively long, reaching beyond caudal setae (in Figure 2A the antennule is not stretched backwards and in Figure 2B it is cut short for illustration purposes). Fifth legs symmetrical (Figure 2E) as in Pennak (1989), Reid and Williamson (2010), and Brandorff (2011).

Male. Body length (1.05-1.20 mm, n=4) and proportions as in other descriptions, including slender cephalothorax (Figure 3A), symmetrical fifth pedigerous somite with posterior spiniform sensillae and numerous short hair-like setae (Figure 3A). Right geniculate antennule with 22 segments, geniculation between segments 18 and 19 (Figure 3B), segments 10 and 11 with spiniform process, segment 13 with a relatively long spine, longer than that on segment 11 (Figure 3C). Segments 14-16 lack spiniform processes (Figure 3B). Antepenultimate segment lacking process on distal inner margin; segment 22 with short distal spiniform process (Figure 3D). Fifth leg (Figure 3E) as in Pennak (1989), Reid and Williamson (2010), and Brandorff (2011), but with basipod of left leg with patch of spinules on middle and distal inner surfaces and first exopod with row of hair-like seta on inner margin (Figure 3G). Also, endopod of left leg with patch of spinules along inner margin (Figure 3F).

Physical and chemical conditions

During sampling of zooplankton in March 2010 the water temperature was 23.5°C, conductivity 142 µS cm^{-1}, oxygen 7.6 mg/l, and pH was 8.1. Chlorophyll a concentration in this month was the lowest of the year at 0.33 µg l^{-1}.

Discussion

Only one other species of the genus *Skistodiaptomus* has been recorded from the Neotropical region, *S. oregonensis* (Suárez-Morales and Reid 1998; Dussart and Defaye 2002). *Skistodiaptomus oregonensis* cannot be confused with *S. pallidus* because of the peculiar pincer-like structure of the distal exopodal segment of the right male fifth leg (Figure 3G), among other characters. Hence, it is confirmed here that the non-indigenous diaptomid copepod *S. pallidus* is present in northwestern Mexico. The body size of both females and males is as reported by Brandorff (2011). Based on genetic and molecular studies, Thum and Derry (2008) stated that there are at least four different lineages currently contained in the nominal species *S. pallidus*. However, the reproductive isolation among populations has not been tested and there are no morphological characters known to reflect these lineages; in any case, the presence of any one of these presumed lineages in Mexico is unexpected.

The biogeography of *S. pallidus* in North America was described by Byron and Saunders (1981) as historically occurring primarily in the central sector of the United States and the Mississippi Valley states with a recent expansion into the northeastern United States resulting from the construction of numerous artificial aquatic systems. A different pattern was

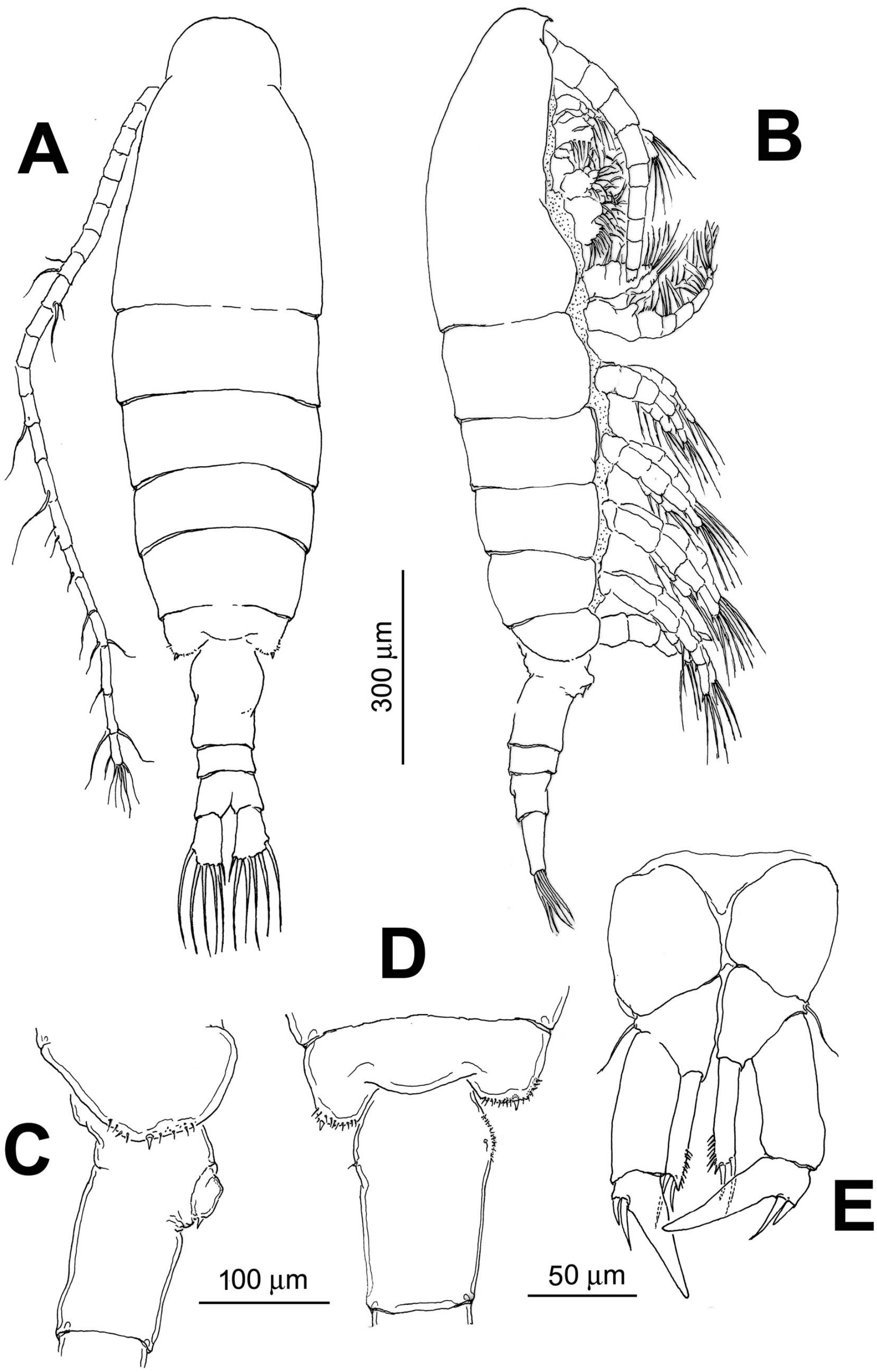

Figure 2. *Skistodiaptomus pallidus*. Adult female from Sinaloa, Mexico. **A**. habitus, dorsal view; **B**. same, lateral view; **C**. fifth pedigerous somite and genital somite, lateral view; **D**. same, ventral view; **E**. fifth leg.

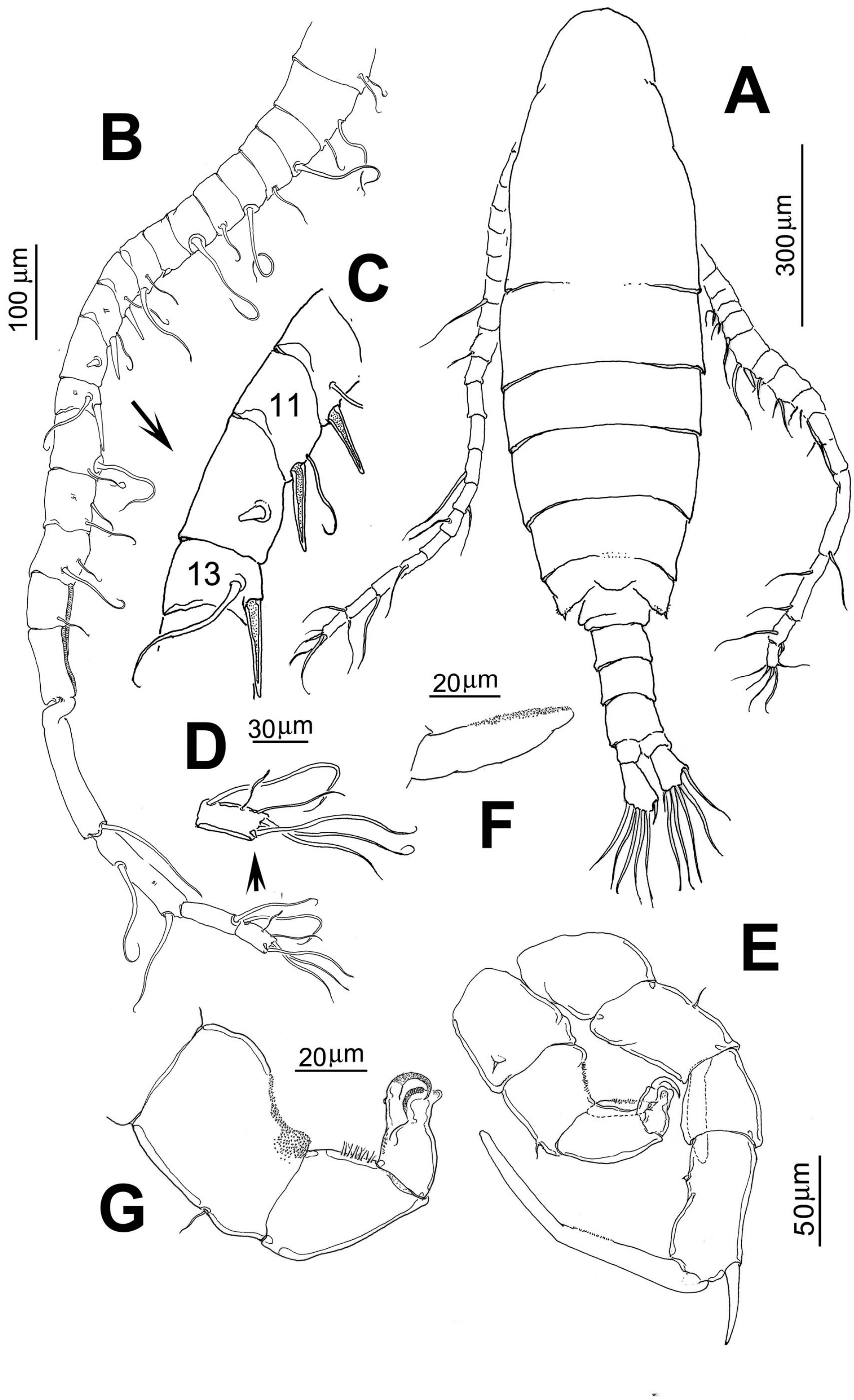

Figure 3. *Skistodiaptomus pallidus*. Adult male from Sinaloa, Mexico. **A**. habitus, dorsal view; **B**. right geniculate antennule; **C**. detail of antennular segments 10-13; **D**. detail of last antennular segment; **E**. fifth legs; **F**. detail of endopod of left fifth leg; **G**. detail of left fifth leg showing ornamentation of segments.

proposed by Stemberger (1995) and supported by the results by Thum and Derry (2008), explaining the current distributional patterns by colonization processes of different areas from glacial refugia. The occurrence of this species in Mexico cannot be explained by these patterns. Recent records of *S. pallidus* outside North America suggest that it is rapidly establishing populations in different geographic areas, including Europe and New Zealand, particularly in man-made aquatic habitats (Duggan et al. 2006; Brandorff 2011). It was found in constructed ponds and also among live fish food sold in an aquarium store in Auckland, New Zealand. According to Duggan et al. (2006), New Zealand populations of *S. pallidus* are still restricted in distribution and, despite the well-known abilities of this copepod to spread and colonize new areas (Byron and Saunders 1981; Krieger and Klarer 1991), eradication was considered possible at that time. Later on, Banks and Duggan (2009) reported two further populations in New Zealand, including one far outside of Auckland, suggesting that the spread of this species is an irreversible process. In Germany it was found also in man-made aquatic systems (Brandorff 2011), thus agreeing with recent surveys in New Zealand (Banks and Duggan 2009; Taylor and Duggan 2012, Parkes and Duggan in press) and our findings of this species, being apparently restricted to this large reservoir of Sinaloa, Mexico. This is a morphologically distinct species that might have been easily distinguished from other copepod surveys carried out in central and northern Mexico (Suárez-Morales and Reid 1998; Suárez-Morales et al. 2010) and it was not observed in previous local samplings carried out in 2004 and 2005. Therefore, based on this information, and pending the results of samplings in natural and man-made systems of adjacent areas, it is speculated that the population of *S. pallidus* found in the surveyed area invaded this man-made system recently.

The physical and chemical conditions at El Comedero differ from the usual range reported for *S. pallidus*; this species usually inhabits beta-mesotrophic (with intermediate productivity levels) to eutrophic habitats but the surveyed area is a highly oxygenated oligotrophic system, with relatively low values of phosphorus PO_4 (0.02–0.20 mg l^{-1}), nitrogen (NO_2: 0.001–0.023 mg l^{-1}, NO_3: 0.132–0.176 mg l^{-1}), and chlorophyll *a* (0.33–1.72 µg l^{-1}). In addition, *S. pallidus* is known to prefer cool waters <12°C. However, the temperature was 24° when this species was collected in El Comedero. The pH and conductivity ranges recorded at El Comedero are both within the range of this copepod (7.5–8.6 and 77–660 µS cm^{-1}, respectively) (Kipp and Benson 2010).

This species has been hitherto recorded mainly from high, cold-temperate latitudes in North America (e.g. Montana 46°N, Ontario 43°, Lake Tahoe 39°), and as an introduced species in Germany (53°N) and New Zealand (37°S). The southernmost records in North America are from Mississippi, Texas, and Georgia (30-32°N) (Duggan et al. 2006; Thum and Derry 2008; Brandorff 2011). This is the first record of *S. pallidus* from tropical areas, at latitudes below 30°N; it is recorded herein at 24°N in north-western Mexico. This is also the first diaptomid copepod known as an invader in Mexico; several Nearctic species of diaptomids are known to be distributed in Mexico as a result of natural dispersal and processes of radiation including post-glacial stranding (Granados-Ramírez and Suárez-Morales 2003; Suárez-Morales et al. 2005) but the disjunct distribution of *S. pallidus* (the nearest record along the Pacific coast is Lake Tahoe), and the fact that the species is well outside of its known climate regime and latitudinal range, suggest that it represents an intra-continental introduction of a Nearctic diaptomid species into a fully tropical zone. The tropical diaptomid *Arctodiaptomus dorsalis* (Marsh) shows the opposite pattern of introduction; it had not been previously recorded north of Florida in North America until Reid (2007) reported it from temperate latitudes in the United States. It is also expected that *S. pallidus* will spread to other areas of northern and central Mexico because of its ability to spread using human mediated transport vectors and its highly competitive features. *Skistodiaptomus pallidus* is an efficient predator, consumes algae, and can become cannibalistic when resource availability is low (Williamson and Vanderploeg 1988). This latter point may be important in the oligotrophic conditions of El Comedero. Overall, *S. pallidus* commonly becomes dominant in invaded systems over local species (Byron and Saunders 1981), but this is known only for non-tropical latitudes. Hence, the potential impact of this highly competitive temperate copepod is unpredictable when it is introduced to tropical communities.

One possible vector for introduction of copepods to new areas includes dispersal via migrating birds (Reid and Reed 1994; Green and Figuerola 2005). There are reports of passive dispersal of copepods by avian transport in North America generally involving the southward migration of northern species (Saunders et al. 1993). Diapausing eggs have been reported for *S. pallidus* (Dowell 1997), and this diaptomid is potentially able to survive transportation in this manner. The American white pelican *Pelecanus erythrorhynchos* Gmelin, 1789 breeds in areas of north-central and western United States. It spends the late fall and winter in different regions of Mexico (Mendoza-Salgado et al. 2011) and may be a suitable vector for diapausing eggs of *S. pallidus*. Populations of this pelican are known to dwell at El Comedero during fall and winter.

It is well known that human activities related to aquaculture and shipping are major vectors for the dispersal of aquatic organisms (Holeck et al. 2004; Wonham et al. 2005). The only case in which the vector of this invasive diaptomid has been identified is in New Zealand, where *S. pallidus* was introduced via dumping of aquarium contents wherein present as live food (Duggan et al. 2006). Ballast water is yet another possibility of introduction, but because of the distance between the coastline and the El Comedero reservoir (80 km), it is unlikely that *S. pallidus* was introduced this way, as reported by Brandorff (2011) on the German coast. In different geographic areas of North America, the introduction of *S. pallidus* has been attributed to handling of bait buckets, fishing equipment, by recreational boaters, with hatchery stock, or through natural dispersal (Mills et al. 1993; Reid and Hudson 2008). In Sinaloa, Mexico the activities related to fishery and hatchery stocks probably represent sources of introduction although aquarium live food cannot be discarded as a vector. The reservoir is intensively used for fish culturing, including the tilapia *Oreochromis aureus* (Steindachner, 1864), the channel catfish *Ictalurus punctatus* (Rafinesque, 1818), and the largemouth black bass *Micropterus salmoides* (Lacépede, 1804). The local activities linked to aquaculture and fisheries, including live food, hatchery stock incorporation, and aquarium products are thus proposed as the probable vector of this introduction.

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