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Arctodiaptomus dorsalis (Marsh): A Case History of Copepod Dispersal

Janet W. Reid

Research Associate
Virginia Museum of Natural History
Martinsville, Virginia 24112

ABSTRACT

The planktonic copepod crustacean *Arctodiaptomus dorsalis* (Marsh) was found in ponds at two warmwater-fish hatcheries in Virginia in the summer of 2006. Because no permanent population is known to exist north of Florida in the eastern United States, the Virginia populations are considered to be introduced. These discoveries provided the impetus for a review of the distribution of this species, based on previously published records, as well as unpublished records derived from museum collections and inquiries of colleagues. This review provided new evidence that the core range of *A. dorsalis* lies in tropical and subtropical lowlands bordering the Gulf of Mexico and Caribbean Sea, from the southern United States through Central America and northern South America, plus the Greater Antilles. There are outlying, published records from Arizona, California, Missouri, Oklahoma, South Carolina, Texas, and Virginia in the United States; the Central Highlands of Mexico; and the Colombian Highlands. Previously unpublished records from Arkansas, Florida, Indiana, Maryland, Michigan, Oklahoma, Texas, Puerto Rico, and Colombia are given herein. Several of the outlying populations were likely established through human agency, via transport of fish or aquatic plants; at least one population, in South Carolina, did not persist. The species has become established in the south-central Mississippi River basin, from Texas as far north as Missouri, and possibly also in Indiana and southern Michigan, primarily in eutrophic impoundments and fish hatcheries although it is not known whether all of the populations previously reported in the region have survived. The population in Indiana has apparently persisted since at least 1980. These observations suggest that *Arctodiaptomus dorsalis* has the potential to extend its range farther north and south, into suitable, eutrophic waterbodies, aided by inadvertent local introductions. Cases of intercontinental introductions of copepods are briefly reviewed.

Key words: Colombia, Copepoda, Crustacea, exotic species. fish hatchery, new records, Puerto Rico, United States.

INTRODUCTION

Questions regarding the geographical distributions, ecological requirements, colonizing capabilities, and dispersal mechanisms of freshwater zooplankton species have engaged limnologists since the early stages of the discipline of freshwater biology. Recently, artificial introductions of freshwater organisms have received much attention, particularly where they affect indigenous aquatic communities, or have the potential to do so. Herein, I briefly review instances of transcontinental introductions of copepod crustaceans. I also provide new information on the distribution of the Neotropical calanoid *Arctodiaptomus dorsalis* (Marsh, 1907), and discuss the possibility that this species is extending its range northward in North America and southward in Colombia, perhaps facilitated by human activities.

Cases of transcontinental introductions of planktonic crustaceans into North American waters include the Afro-Asian-Australian cladoceran *Daphnia lumholtzi* G. O. Sars, 1885 (Havel & Shurin, 2004; Benson et al., 2006); the northern-European cladoceran, the spiny water flea *Bythotrephes longimanus* Leydig, 1860 (first identified as *B. cederstroemii* Schödler, 1877) (Liebig & Benson, 2006); and several copepods, especially in the Laurentian Great Lakes (Hudson & Lesko, 2003).

Reid & Pinto-Coelho (1994) reviewed the 21 cases of intercontinental introductions of freshwater and estuarine copepods known to that date. Since then, several more cases have been documented, or suggested. Species of Cyclopoida predominate: the Afro-Asian cyclopoid *Mesocyclops ogunnus* Onabamiro, 1957, besides becoming established in reservoirs in central Brazil (Reid & Pinto-Coelho, 1994; Matsumura-Tundisi & Silva, 2002), has appeared in ponds in the Cayman Islands (Suárez-Morales et al., 1999), and recently in a plant tray and a pond in the Florida Keys (Hribar & Reid, 2008). The supposedly Asian *Bryocyclops muscicola* (Menzel, 1926) appeared in several locations in Florida (Reid, 1999; Bruno et al., 2005; Reid & Hribar, 2006; Hribar & Reid, 2008); the Asian *Apocyclops dengizicus* (Lepeshkin, 1900) in Virginia and Maryland (Reid et al., 2002); the European *Megacyclops viridis* (Jurine, 1820), in Lake Superior (Hudson & Lesko, 2003); the Asian *Mesocyclops pehpeiensis* Hu, 1943, in southeast Mexico (Suárez-Morales et al., 2005); and the South American *Paracyclops bromeliacola* Karaytug & Boxshall, 1998, in Florida (Reid & Hribar, 2006).

Species of Calanoida include the North American *Skistodiaptomus pallidus* (Herrick, 1879) and the Asian *Sinodiaptomus valkanovi* Kiefer, 1938, in New Zealand (Duggan et al., 2006). The Australasian calanoid *Boeckella triarticulata* (Thomson, 1883), first found in northern Italy in the 1980s, has recently reappeared there (Ferrari & Rossetti, 2006).

There are relatively few records of harpacticoids. The Ponto-Caspian *Nitokra incerta* (Richard, 1893) has been found near the mouth of the Detroit River in Michigan (Grigorovich et al., 2001). The European *Nitokra hibernica* (Brady, 1880), which was first reported from Lake Ontario in 1978, is now common in all of the Great Lakes except Lake Superior (Hudson & Lesko, 2003). The euryhaline, European *Schizopera borutzkyi* Monchenko, 1967 was first reported from Lake Michigan by Horvath et al. (2001), and has since spread into Lake Erie (Hudson & Lesko, 2003).

Known instances of range expansions of planktonic copepods within the same continent are much fewer. *Skistodiaptomus pallidus*, which was first found in the north-central and plains states (Wilson & Yeatman, 1959), seems to have colonized the eastern states beginning with North Carolina and Virginia sometime after 1940 (Saunders, 1975); its presence west of the Rocky Mountains was first noted in 1970 (Byron & Saunders, 1981). *Eudiaptomus gracilis* (G. O. Sars, 1862), which is common throughout most of Europe, began to appear in lakes in northern Italy in the late 1980s, where it is now displacing the native *Eudiaptomus padanus* (Burckhardt, 1900) (Riccardi & Giussani, 2007). The best-studied case is that of the circumboreal temorid calanoid copepod *Eurytemora affinis* (Poppe, 1880), which formerly occurred only in brackish coastal waters, and has in the past 70 years invaded many inland, fresh waterbodies in North America, Europe, and Asia (Lee, 1999; Benson, 2006). Its Palaearctic congener *E. velox* (Lilljeborg, 1853) has similarly moved from coastal into inland waters in Europe during the past century (Gavíria & Forró, 2000). The estuarine harpacticoid *Heteropsyllus nunni* Coull, 1975, known originally from the coast of South Carolina, has appeared in the Great Lakes (Horvath et al., 2001; Hudson & Lesko, 2003).

The large diaptomid calanoid copepod genus *Arctodiaptomus* is primarily Palaearctic; 6 of its 37 species are known to occur in the Americas. Of these, *Arctodiaptomus dorsalis* (Marsh, 1907) has extended the farthest south, through Central America to northern South America, and is considered to be essentially Neotropical (Suárez-Morales & Reid, 2003; Suárez-Morales et al., 2005). It was originally described by Marsh (1907, as *Diaptomus dorsalis*) from Guzman and Milneburg, two now-extinct towns formerly located near New Orleans, Louisiana. The species was subsequently reported from elsewhere in the southern and southwestern United States; Mexico; several countries in Central America; the Bahamas, Cuba, and Haiti in the Antilles; and northern Colombia and Venezuela in South America. Although *A. dorsalis* is most common in lowlands bordering the Gulf of Mexico and Caribbean Sea, there are many reports of populations outside that region: in the central Mexican and Colombian highlands, and in Arizona, central California, Oklahoma, northern Texas, Maryland, Missouri, and South Carolina in the United States. *Arctodiaptomus dorsalis* has highly distinctive morphological characters, including, in most populations, dorsal projections on the posterior thorax of adult females, from which it derives its name. Its biology has been well studied, particularly in Florida, where it is often dominant in the plankton of eutrophic ponds and lakes across the central and northwestern parts of that state (Bruno et al., 2005, and references therein).

Arctodiaptomus dorsalis usually occurs in perennial ponds, lakes, and impoundments. It can survive in subterranean waters: in addition to many cenotes (sinkhole lakes) in the Yucatan Peninsula (e.g., Suárez-Morales et al., 1996; Suárez-Morales & Reid, 2003), it was found in phreatic groundwater in a cave in Cuba (Bowman, 1979), and in the Split Sink cave system, Florida (Bruno et al., 2005). The only record from a natural, temporary waterbody is from a seasonal floodplain pond in Missouri (Havel et al., 2000). *Arctodiaptomus dorsalis* may be able to overwinter by means of resting eggs. Although I have been unable to locate a report of resting eggs of this species, its presence in a temporary waterbody suggests that it does have this capability, as do many species of diaptomids, including several congeners (Williams-Howze, 1997). Like most diaptomids, it is a selective phytoplankton grazer; it prefers diatoms but will also ingest cyanobacteria (blue-green algae) and chlorophytes (Cisneros et al., 1991; Ahlgren et al., 2000). It is often dominant in eutrophic waterbodies, such as throughout central Florida. Elmore (1983) suggested that *A. dorsalis* cannot survive under conditions of low food concentrations. This species also dominates the crustacean zooplankton in moderately productive Guatemalan lakes (Deevey et al., 1980). It occurs in waters of a rather wide range of chemistry: Cole (1961, 1966) reported that in one of the Arizona ponds where *A. dorsalis* was found, the chloride content was 950 mg/L, and the standard conductivity was 1,900 µmhos ($1.9\ S{\cdot}m^{-1}$), i.e., in the oligohaline range. The Keystone Reservoir in Oklahoma, which drains semi-arid salt plains, is also rather saline, with measured conductivities of 1,114 to 4,672 µmhos when *A. dorsalis* was collected there in 1967-1968 (Kochsiek et al., 1971). Its rather small size (0.77-1.13 mm for females, 0.78-1.06 mm for males) may allow it to maintain substantial populations under heavy predation pressure from planktivorous fish (Deevey et al., 1980). Like many diaptomids that are planktonic in permanent waterbodies, its body is transparent, another anti-predator adaptation. A more important factor may be that, when food is not limiting, it can produce a large number of small, fast-developing eggs, and its nauplii and copepodids develop quickly compared to other diaptomids, i.e., it is an *r*-strategist (Elmore, 1983).

In waterbodies at higher latitudes and altitudes, *A. dorsalis* may appear mainly in the warmer seasons. In the Atchafalaya River basin floodplain complex, Davidson et al. (1998) found that it was a minor component of the crustacean plankton, and increased in abundance only in late summer. Davidson et al. (1998) further reported that this increase was correlated with higher dissolved oxygen concentrations, maintained by high algal populations, in summer.

Although morphologically distinct, *A. dorsalis* was described by four workers under different names: *Diaptomus dorsalis* (Marsh, 1907), *Diaptomus dampfi* (Brehm, 1932 and 1939; from Lake Petén, Guatemala); *Diaptomus proximus* (Kiefer, 1936; from Haiti); and *Diaptomus alter* (Herbst, 1960; from Lake Managua, Nicaragua). The shared identity of the first three taxa was noted by Wilson & Yeatman (1959) and Cole (1976), and was discussed in detail by Collado et al. (1984) and Dussart & Fernando (1985). Suárez-Morales & Elías-Gutiérrez (2001) were able to obtain specimens from Lake Petén, and confirmed their suspicion that the species there is indeed *A. dorsalis* (as earlier reported by Deevey et al., 1980). As Collado et al. (1984) remarked, the reasons for this confusion include the inevitable differences among specialists in preparation, perception, observation, and illustration of complex structures, and the limited material available to some authors. The reluctance of taxonomists to assign newly discovered, unfamiliar material to a known taxon, slight differences from published descriptions, and occurrences far from the type locality probably also played a part in the proliferation of names.

During a "BioBlitz" 24-hour biological survey held in June 1996 in the Kenilworth Park and Aquatic Gardens in Washington, D.C., I collected a single male of *A. dorsalis* in an outdoor artificial pond. This record was reported in an unreviewed, online checklist of the copepod crustaceans of the District of Columbia (Reid, 1996), but has not been published elsewhere. This species may have been brought in by human agency, possibly along with ornamental water plants. The Asian cyclopoid *Mesocyclops pehpeiensis* Hu, 1943 (reported as *M. ruttneri* Kiefer, 1981, which has since been synonymized with *M. pehpeiensis*), was also present in Kenilworth ponds and greenhouse tanks. Neither species has been found in any other waterbody in the District of Columbia (Reid, 1996; Reid, unpublished data).

Arctodiaptomus dorsalis occurred in plankton samples taken in July 2006 from two fish ponds at the Vic Thomas Striped Bass Hatchery in Brookneal, Campbell County, Virginia. A collection in August 2006 from ponds at the Harrison Lake National Fish Hatchery in Charles City County, Virginia, which supplied fish to the Brookneal facility in 2005 and 2006, also yielded *A. dorsalis* in large numbers. This species was not present in plankton samples from two other warmwater-fish hatcheries in Virginia, the King and Queen Fish Cultural Station at Stevensville in King and Queen County, and the Buller Fish Cultural Station in Smyth County, also in August 2006.

Existing summaries of the distribution of *A. dorsalis* are regional in focus (e.g., Bowman, 1986; Reid, 1990; Suárez-Morales, 1991; Bruno et al., 2005; Suárez-Morales et al., 2005). Therefore, I review published records, add several, previously unpublished records derived from museum holdings, personal collections, and records communicated by colleagues, and provide a detailed map of the resulting known distribution of *A. dorsalis*.

METHODS

Copepods were collected with a small plankton net, transported in plastic bags in an insulated container on ice to the laboratory, sorted, and fixed and preserved in 70% ethanol or isopropanol. The species contained in the samples were identified primarily through the keys by Reed (1994) and Wilson & Yeatman (1959), with recourse to more recent literature when necessary. The specimens from D.C. are deposited in the collection of the Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution (USNM). The specimens from Arkansas, Indiana, and Virginia are deposited in the collection of the Department of Recent Invertebrates, Virginia Museum of Natural History (VMNH), and the Crustacea Catalogue Database numbers are provided.

Material examined:

Arkansas: 10 females and 10 males, fish culture ponds at the University of Arkansas Pine Bluff Aquaculture/ Fisheries Center, Lonoke, Lonoke County (Site 15 in Fig. 1, Site 18 in Fig. 2), June 13, 2007, leg. S. Kumaran, det. J. W. Reid (VMNH 1478).

District of Columbia: 1 male, Kenilworth Park and Aquatic Gardens (Site 1 in Fig. 1, Site 13 in Fig. 2), lily display pond, 4 October 1996, leg. S. W. Syphax and J. W. Reid, det. J. W. Reid (USNM 278173).

Indiana: 20 females, 20 males, and 20 copepodids, Cikana State Fish Hatchery (Site 12 in Fig. 1, Site 10 in Fig. 2), Martinsville, Morgan County, sample combined from several ponds, 5 September 2006, leg. D. Jessup, det. J. W. Reid (VMNH 1316).

Virginia: 2 females and 2 copepodids, Pond 1, Vic Thomas Striped Bass Hatchery (Site 2 in Fig. 1, Site 16 in Fig. 2), Brookneal, Campbell County, 24 July 2006, leg. det. J. W. Reid (VMNH 1263). 10 females, 10 males, and 100 copepodids, Pond 4, Vic Thomas Striped Bass Hatchery, Brookneal, Campbell County, 24 July 2006, leg. det. J. W. Reid (VMNH 1264). 20 females and 20 males, combined from Ponds B1, B2, C1, E1, E2, E3, E4, E5, F1, F2, C2, and C3, all fresh water, Harrison Lake National Fish Hatchery (Site 3 in Fig. 1, Site 15 in Fig. 2), Charles City County, 3 August 2006, leg. det. J. W. Reid (VMNH 1276). 20 females and 20 males, Pond F5, salinity 1.5 ‰, temperature 35 °C, Harrison Lake National Fish Hatchery, Charles City County, 3 August 2006, leg. det. J. W. Reid (VMNH 1277).

Colombia: 5 males, 55-gallon drums, Hacienda Fircal, Vereda La Esperanza, Mesa de los Santos, Municipio Puedecuesta, Santander, leg. M. F. Suárez and O. Vargas, det. J. W. Reid (specimens temporarily at USNM; to be transferred to VMNH; Site 8 in Fig. 1). This record was briefly noted as "Colombia" by Reed (1994).

Puerto Rico: 2 females and 1 copepodid, Canal de Sague, Langostiños del Caribe, Sabana Grande (Site 7 in Fig. 1), 14 June 1990, leg. C. Aranda and M. Rivera, det. J. W. Reid (USNM 284703). 13 females and 10 males, Ponds 164, 166, and 173, Langostiños del Caribe, Sabana Grande, 16 August 1990, leg. M. F. Suárez and C. Aranda, det. J. W. Reid (USNM 284704). These records were briefly noted as "Puerto Rico" by Reid (1990).

The published reports used to compile the distribution map in Figure 1, listed by country and department, province, or state, are as follows:

United States: California (Suárez-Morales & Elías-Gutiérrez, 2001), Florida (Marsh, 1929; Suárez-Morales & Elías-Gutiérrez, 2001; Bruno et al., 2005, and references therein; Reid & Hribar, 2006), Louisiana (Marsh, 1907, 1929; Davidson, 1996; Davidson et al., 1998, 2000; Suárez-Morales & Elías-Gutiérrez, 2001), Mississippi (Harris, 1978), Missouri (Havel et al., 2000), Oklahoma (Robertson, 1970, 1972; Kochsiek et al., 1971), South Carolina (Taylor et al., 1993), Texas (Smith et al., 1978, 1979).

Mexico: Aguascalientes (Dodson & Silva-Briano, 1996; Silva-Briano & Suárez-Morales, 1998), Campeche (Suárez-Morales, 2003), Morelos (Álvarez-Silva & Gómez-Aguirre, 2000b; Álvarez-Silva & Campos-Verduzco, 2001; Suárez-Morales & Elías-Gutiérrez, 2001; Gómez-Marquez et al., 2003), Quintana Roo (Suárez-Morales & Rivera-Arriaga, 2000; Suárez-Morales & Elías-Gutiérrez, 2001; Suárez-Morales, 2003), Tabasco (Álvarez-Silva & Gómez-Aguirre, 2000b; Álvarez-Silva & Campos-Verduzco, 2001; Gutiérrez-Aguirre & Suárez-Morales, 2001; Suárez-Morales & Elías-Gutiérrez, 2001; Álvarez-Silva et al., 2002), Veracruz (Torres-Orozco & Zanatta, 1998; Álvarez-Silva, 1999; Álvarez-Silva & Gómez-Aguirre, 2000a), Yucatán (Suárez-Morales et al., 1996; Suárez-Morales, 2003).

Guatemala: Petén (Brehm, 1932, 1939; Deevey et al., 1980; Suárez-Morales & Elías-Gutiérrez, 2001), Izabal (Brinson & Nordlie, 1975).

Nicaragua: Lake Nicaragua (Cole, 1976; = Lake Cocibolca, Ahlgren et al., 2000), Lake Xolotlán (= Lake Managua, Herbst, 1960; Cisneros & Mangas, 1991; Cisneros et al., 1991).

Costa Rica: San José (Collado et al., 1984; Dussart & Fernando, 1985; Schaper, 1999); Alajuela, Cartago, and Guanacaste (Collado et al., 1984; Dussart & Fernando, 1985).

Colombia: Antioquia (Ramírez & Díaz, 1997; Buitrago, 1998; Estrada-Posada, 1999, 2006; Jaramillo & Gavíria, 2003; Gallo-Sánchez et al., 2004).

Venezuela: Aragua (González, 1968).

Bahamas: New Providence (Segers et al., 1995).

Cuba: All provinces (Smith & Fernando, 1978); Sancti Spíritus Province (Bowman, 1979, as Las Villas Province; Suárez-Morales & Elías-Gutiérrez, 2001).

Haiti: Laguna Rincón (Kiefer, 1936).

In their review of freshwater copepods from northwestern North America, Chengalath & Shih (1994) listed *A. dorsalis* from Alaska and British Columbia, without further details. Neither A. Robertson (in litt., 2006) nor I have been able to trace the source of these listings, and they appear doubtful, given the confirmed range of the species. Therefore, they are not included in Fig. 1.

Unpublished records of *A. dorsalis* from collections in the Virginia Museum of Natural History and the National Museum of Natural History, personal, unpublished determinations, and unpublished records provided by G. Carter, S. Dodson, S. Gavíria-Melo, P. L. Hudson, A. Robertson, and B. Torke are presented in Figs. 1 and 2. These records are as follows:

United States: Oklahoma: Cleveland County, unnamed, 0.1 acre (0.04 ha) pond, collected in June 1975 by J. P. Magovern, and identified by the late T. E. Bowman (USNM 190874; Site 4 in Figs. 1 and 2).

Communicated by A. Robertson (personal collection): Texas: Steedman Marsh in Hagerman National Wildlife Refuge, Grayson County, 28 August 1970 (Site 6 in Figs. 1 and 2). Arkansas: Old River Lake in Pulaski County, collected on August 22, 1971 (Site 5 in Fig. 1, Site 7 in Fig. 2). Florida: (1) drainage canal along US 27 on the Dade/Broward County line, 16 August 1965; (2) along US 27 in Broward County, 16 August 1965; (3) north of Lake Ida, Delray Beach, Palm Beach County, 17 August 1965; (4) pond in Sarasota, Sarasota County, 31 July 1967; (5) pond along Route 4 near Venice, Sarasota County, 31 July 1967; (6) pond on Longboat Key, Sarasota County, 31 July 1967; (7) flooded area about 3 miles (4.8 km) south of Tarpon Spring, Pinellas County, 20 March 1970; and (8) small lake near Dunedin, Pinellas County, 30 October 1976. (The Florida records are indicated individually by triangles in Fig. 2, but are not numbered.)

Communicated by S. I. Dodson (personal collection): Indiana: Cikana State Fish Hatchery, Martinsville, Morgan County, 39.4449 N, 86.3810 W, 2 June 2005, leg. B. Torke (Site 12 in Fig. 1, Site 10 in Fig. 2). Oklahoma: Fort Gibson Reservoir, Cherokee County, 35.94 N, 95.22 W, 15 July 1995, leg. J. Havel (Site 13 in Fig. 1, Site 12 in Fig. 2).

Communicated by P. L. Hudson and G. Carter (personal observations): Michigan: Edwin S. George Reserve, Livingston County, experimental tanks containing fish and zooplankton, 2006 (Site 14 in Fig. 1, Site 17 in Fig. 2).

Colombia: From S. Gavíria-Melo (personal observations): Antioquia: La Fé Reservoir, Medellín, 1999, 2001; Lago Botanical Garden in Medellín and Porce II Reservoir, 2001 (Site 9 in Fig. 1); Chocó, Ciénaga de Bojayá, lower Atrato River, 6° 32' N, 76° 56' W, 1992 (Site 10 in Fig. 1); Cauca: Salvajina Reservoir, 2° 45' N, 76° 50' W, 1991 (Site 11 in Fig. 1).

RESULTS

All but one of the ponds examined at the Harrison Lake National Fish Hatchery in August 2006 contained populations of adults and juveniles of *A. dorsalis*. Many of the adult females were carrying egg sacs. Another species of diaptomid, *Skistodiaptomus pallidus* (Herrick, 1879), was also present, in smaller numbers, in several of the ponds. *Skistodiaptomus pallidus*, but not *A. dorsalis*, occurred in Harrison Lake itself, which supplies water to the hatchery ponds. Both of the ponds examined at the Vic Thomas Striped Bass Hatchery contained *A. dorsalis*, but no other calanoid species. No individuals of *A. dorsalis* appeared in collections made at the King and Queen or Buller facilities, or in nearby impoundments surveyed in August 2006.

The records of *A. dorsalis* indicate a somewhat disjunct distribution (Fig. 1). Most records are from lowland areas in a region extending from the southern United States around the Gulf of Mexico and the Caribbean to northern South America, plus the Greater Antilles. Other concentrations of records appear at higher latitudes in Texas, Oklahoma, Arkansas, and Missouri. *Arctodiaptomus dorsalis* has been recorded

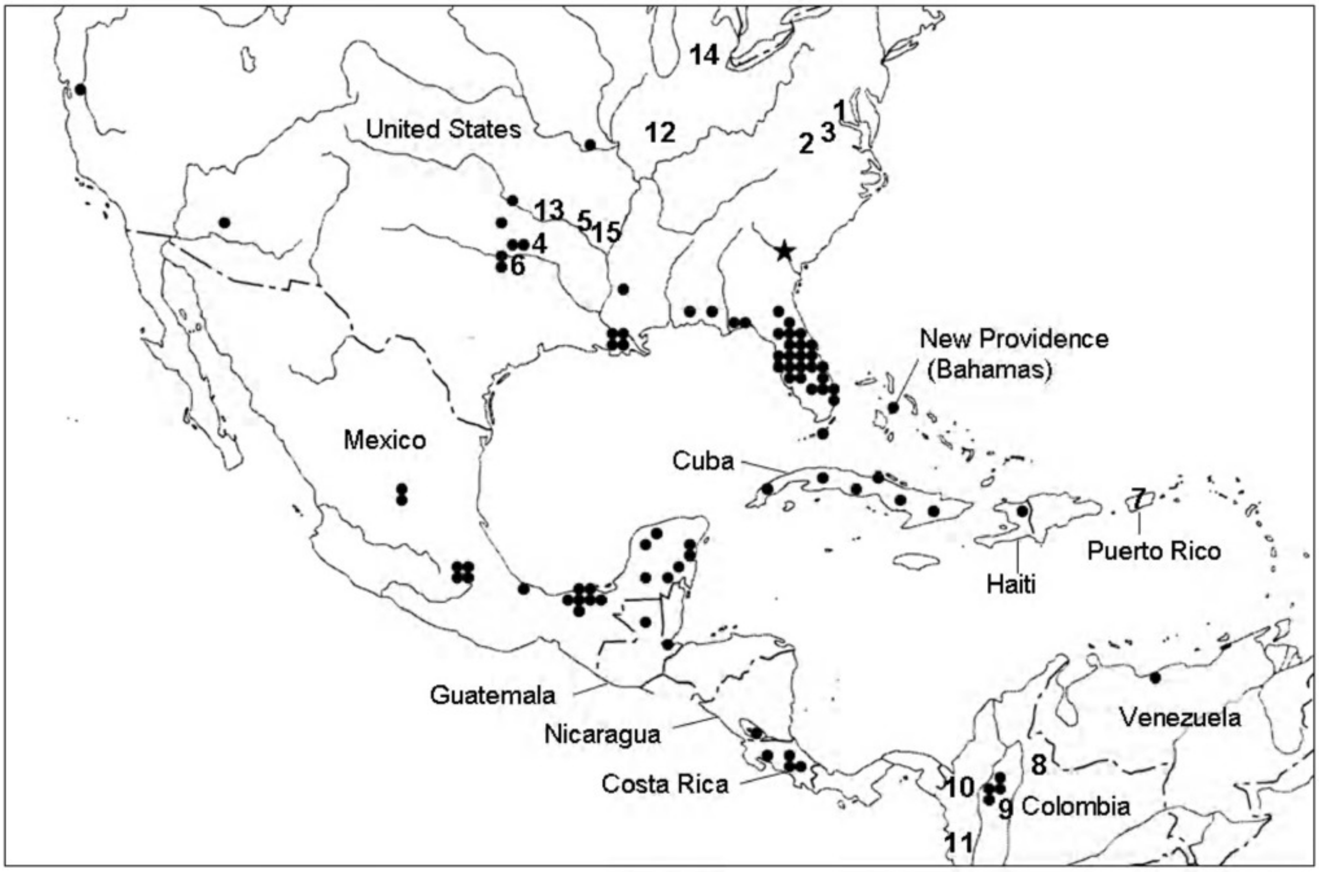

Fig. 1. The known distribution of *Arctodiaptomus dorsalis*. Circles represent published records; most indicate individual records, although where several local waterbodies were investigated, a single circle represents this group. The star indicates an apparently introduced population (in South Carolina) that did not persist. Numbers represent previously unpublished records (see text for locations).

from higher elevations in the states of Aguascalientes and Morelos, Mexico; and the province of Antioquia in Colombia. The population studied by Jaramillo-L. & Gavíria (2003) in Lago Santander, Rionegro, at an elevation of 2100 m in Antioquia, is the highest on record. There are disjunct records from Arizona, California, Indiana, Maryland, Michigan, South Carolina, and Virginia in the United States; and from Cauca Province in Colombia.

DISCUSSION

In certain lowland areas around the Caribbean Sea and Gulf of Mexico, *Arctodiaptomus dorsalis* is extremely common (Fig. 1). In their review of records of copepods in Florida, Bruno et al. (2005) listed this species from 37 named lakes and ponds, as well as several other waterbodies in 23 counties; Reid & Hribar (2006) and Hribar & Reid (2008) reported records from the Florida Keys; and the new records by Robertson given herein add nine additional localities. In Louisiana, Davidson (1996) and Davidson et al. (1998, 2000) found the species in 11 of 30 sites prospected in the lower Atchafalaya River basin. *Arctodiaptomus dorsalis* is also common in the cenotes (subterranean sinkhole lakes) of the Yucatán Peninsula, where it can be very abundant (Suárez-Morales et al., 1996; Suárez-Morales & Rivera-Arriaga, 2000). Deevey et al. (1980) reported it as dominant in the plankton of all ten lakes that they surveyed in the Petén lake district of Guatemala.

Outside this lowland region, reports of *A. dorsalis* are sparser and more widely separated. For instance, in more than 250 samples of calanoids in the mountainous state of Aguascalientes, Mexico, collected over a period of several years, Silva-Briano & Suárez-Morales (1998) reported this species from only two localities. In a general survey covering the drainage basins of six tributaries of the Mississippi River in northern Mississippi, Harris (1978) found *A. dorsalis* only in "a large creek with little or no current" in the Yazoo River drainage, where it was abundant in late summer. In a recent study of floodplain waterbodies along the Little Tallahatchie River in the same general area, Frisch et al. (2005) did not record this species. Havel et al. (2000) reported *A. dorsalis* from a temporary pond, one of 30 sites that they examined in the floodplain of the Missouri River in Missouri. None of the few other regional surveys of planktonic copepods carried out in recent decades in the central and southeastern United States has reported *A. dorsalis*: North Carolina (Clamp et al., 1999), Wisconsin (Torke, 2001), the Great Lakes region (Hudson & Lesko, 2003). Samples of plankton taken in 38 large and small lakes, ponds, and reservoirs in 24 counties in Virginia from 2002 through 2006 have not contained this species (J. W. Reid, unpubl. data).

Most of the records of *A. dorsalis* in South America are from impoundments and are quite recent, particularly in Colombia. Gavíria (1989, 1994) included no records of *A. dorsalis* in his checklists of copepods from Colombia. Since 1994, *A. dorsalis* has been found in several reservoirs and lakes around Medellín in Antioquia Province (Ramírez & Díaz, 1997; Buitrago, 1998; Estrada-Posada, 1999, 2006; Jaramillo & Gavíria, 2003; Gallo-Sánchez et al., 2004). S. Gavíria-Melo (in litt., August 2006) has collected this species in the Salvajina Reservoir in Cauca Province, at 2° 45' N, the southernmost record in South America. The known distribution in Colombia now includes Antioquia, Cauca, and Chocó provinces (locality data herein; Gavíria & Aranguren, 2007). S. Gavíria-Melo (in litt., August 2006) is of the opinion that *A. dorsalis* is presently expanding southward in Colombia.

The single record from Venezuela (González, 1958) is from an artificial lake in the botanical garden of the Universidad Central in Caracas. Dussart (1984) failed to find this species in collections in northern Venezuela made at 38 localities and in habitats ranging from major lakes and reservoirs to rivers, swamps, bogs, etc.

The record provided by Gavíria-Melo from the Ciénaga de Bojayá in Cauca Province, northern Colombia, fits the pattern of circum-Caribbean, natural, lowland waterbodies that seems to represent the core range of *A. dorsalis*. This may, therefore, represent a natural population.

The sequence and pattern of collections in the central and eastern United States (Fig. 2) suggest that *A. dorsalis* has extended its range into this region in recent decades, and also that this expansion was aided, at least partly, by inadvertent transport along with fish. In the first general survey of diaptomid copepods in Oklahoma, Kingsbury (1966) did not report this species from any of the 92 lakes and ponds examined. In his subsequent, extensive survey and comprehensive listing of diaptomids in Oklahoma, Robertson (1970) recorded *A. dorsalis* from only two localities: a pond at the Durant Fish Hatchery in Bryan County, collected in May 1967; and the Fisheries Research Lab at Noble in Cleveland County, collected in May 1969. Nearly all of the subsequent records from this region are from artificial ponds and reservoirs, many of which are likely to have been stocked with fish; or from fish-culture ponds, i.e., most recently at the University of Arkansas Pine Bluff Aquaculture/Fisheries Center in Lonoke. There is no information as to whether the small pond in Cleveland County, Oklahoma, was natural or artificial (new record herein). The recent record by Havel et al. (2000) from a natural floodplain pond may indicate that *A. dorsalis* can establish populations in relatively unimpacted waterbodies.

The population of *A. dorsalis* in L Lake, a nuclear-reactor cooling reservoir constructed in 1984-1985 on the United States Department of Energy Savannah River Site in South Carolina, may have been introduced along with fish, and eventually disappeared (Taylor et al., 1993). L Lake was stocked with bluegill, *Lepomis macrochirus* Rafinesque, 1819, and largemouth bass, *Micropterus salmoides* Lacépède, 1802, in 1986-1987. Both *Skistodiaptomus pallidus* (Herrick, 1879) and *A. dorsalis* were abundant during the warm months of 1986 and 1987, at the cooler end of the reservoir (water temperature 24-32 °C). An accidental introduction in 1987 and consequent population explosion of threadfin shad, *Dorosoma petenense* (Günther, 1867), was followed by an abrupt decline in all crustacean zooplankton by the next summer. The reactor ceased operation at the end of 1988. Thereafter, *Eurytemora affinis* replaced the diaptomids. Taylor et al. (1993) attributed this shift to predation pressure from threadfin shad, rather than to alterations in the reservoir's temperature regime, because the reactor continued to warm the water periodically during 1988. *Arctodiaptomus dorsalis* has not been seen in L Lake or any other waterbody on the Savannah River Site since 1989 (A. DeBiase, in litt., August 2006), and was not included in a recent checklist (DeBiase & Taylor, 2005).

The pattern and nature of the habitats of other disjunct records are also suggestive of introductions. In his survey of the diaptomids of Arizona, Cole (1961) recorded *A. dorsalis* only from four small, permanent ponds (Papago Ponds) in the Tempe-Scottsdale-Phoenix region. Both Cole (1961, 1966) and Robertson (1972) assumed that these were naturally occurring populations. However, because these waterbodies were artificial and had been used as experimental ponds for rearing fish (Cole, 1966), and, furthermore, because *A. dorsalis* has not been reported again from Arizona, this occurrence may well have been an introduction.

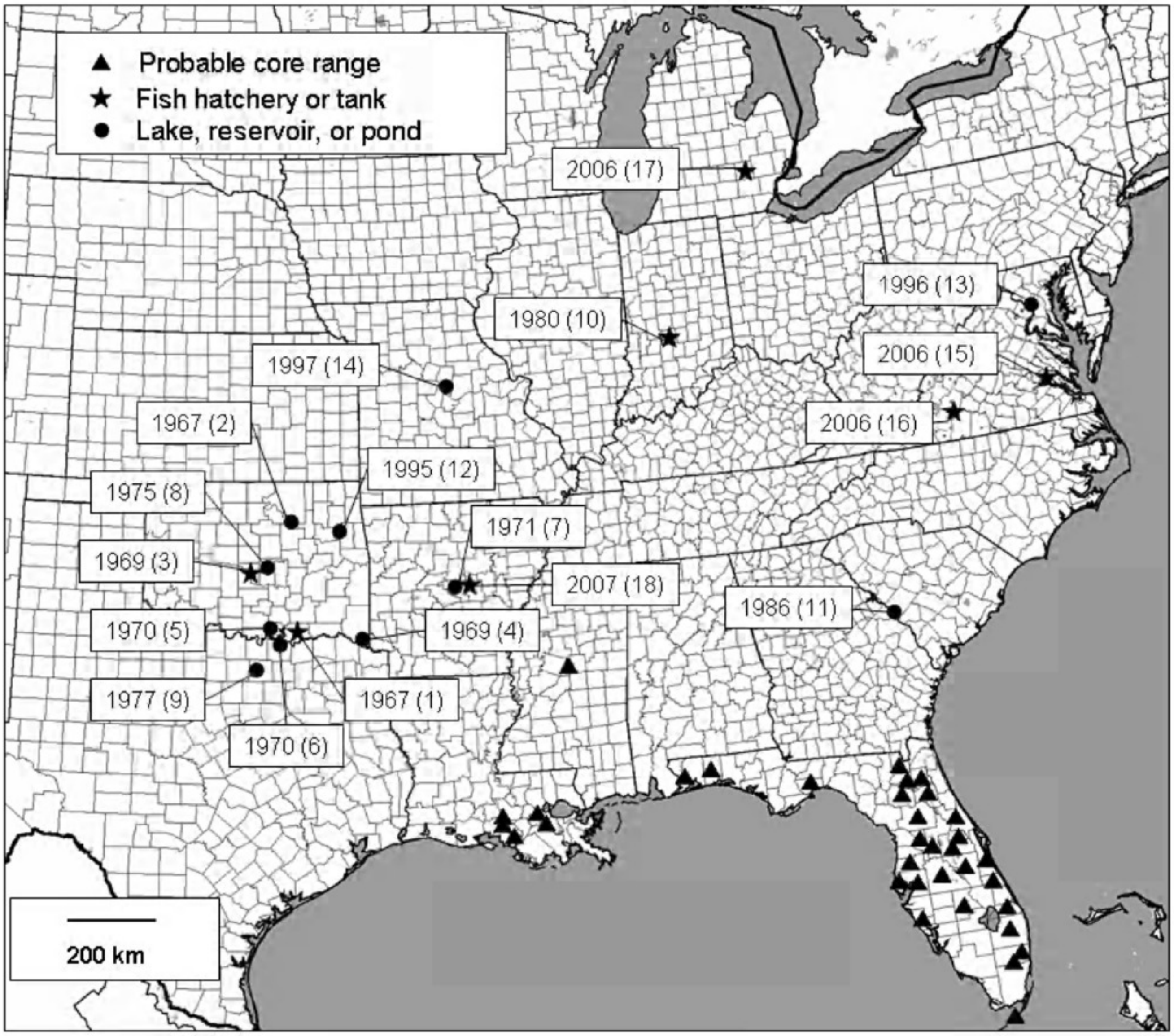

Fig. 2. Localities in the central and eastern United States where *Arctodiaptomus dorsalis* has been recorded. For localities outside its supposed core range, the year when *A. dorsalis* was first recorded is given, followed by the number of the locality in parentheses. 1 – Pond at Durant Fish Hatchery, Bryan County, Oklahoma (Robertson, 1970); 2 – Keystone Reservoir, Pawnee County, Oklahoma (Kochsiek et al., 1971); 3 – Fisheries Research Lab, Noble, Cleveland County, Oklahoma (Robertson, 1970); 4 – Unnamed pond, Cleveland County, Oklahoma (record given herein); 5 – Lake Texoma and pond on largest of group of islands in Lake Texoma, Marshall County, Oklahoma (Robertson, 1972); 6 – Steedman Marsh, Hagerman National Wildlife Refuge, Grayson County, Texas (record given herein); 7 – Old River Lake, Pulaski County, Arkansas (record given herein); 8 – Breedlove Lake, McCurtain County, Oklahoma (Robertson, 1972); 9 – Golf course pond, North Texas State University, Denton, Texas (Smith, 1977; Smith et al., 1978, 1979); 10 – Cikana State Fish Hatchery, Martinsville, Morgan County, Indiana (records given herein); 11 – L Lake, United States Department of Energy Savannah River Site, South Carolina (Taylor et al., 1993); 12 – Fort Gibson Reservoir, Cherokee County, Oklahoma (record given herein); 13 – Artificial pond, Kenilworth Aquatic Gardens, Washington, D.C. (Reid, 1996); 14 – Temporary floodplain pond near the Missouri River in Missouri (Havel et al., 2000); 15 – Ponds, Harrison Lake National Fish Hatchery, Charles City County, Virginia (record given herein); 16 – Ponds, Vic Thomas Striped Bass Hatchery, Brookneal, Campbell County, Virginia (record given herein); 17 – Experimental tanks, Edwin S. George Reserve, Livingston County, Michigan (record given herein); 18 – Fish culture ponds, University of Arkansas Pine Bluff Aquaculture/Fisheries Center, Lonoke, Lonoke County, Arkansas. Localities presumed to be part of the core range of *A. dorsalis* (indicated by solid triangles) are those given by Marsh (1907, 1929), Harris (1978), Davidson (1996), Davidson et al. (1998, 2000), Bruno et al. (2005), Reid & Hribar (2006), and Hribar & Reid (2008).

The occurrence at the Kenilworth Aquatic Gardens in the District of Columbia is also probably an introduction. The diaptomids may have traveled along with ornamental aquatic plants.

The occurrences in Virginia also seem to be introductions. The Harrison Lake facility supplied fish to the Vic Thomas Striped Bass Hatchery and to the King and Queen Fish Cultural Station in 2005 and 2006, but to no other hatcheries (M. Odom, in litt., August 2006). The source of the population at the Vic Thomas facility was most likely the Harrison Lake hatchery. *Arctodiaptomus dorsalis* has not appeared in collections from 38 other lakes and ponds in the Virginia mountains, Piedmont, and Coastal Plain made from 2001 through 2006 (Reid, unpublished data).

The population at the Cikana State Fish Hatchery in Indiana may have been introduced prior to 1980, when a study by T. Schwartz (unpublished Indiana Department of Natural Resources Technical Paper, communicated by D. Jessup) reported it as a major dietary component of larval walleye, *Sander vitreus* (Mitchill, 1818). B. Torke collected *A. dorsalis* at the hatchery in 2005, and it was still present in September 2006. The Cikana hatchery is a warmwater-coolwater facility producing walleye, sauger, channel catfish, fathead minnows, and smallmouth bass. The ponds are earthen and filled by deep wells on the property. The only sources of fish for this hatchery outside Indiana are the Jake Wolf Memorial Fish Hatchery in Illinois, and hatcheries in Illinois and Ohio (D. Jessup, in litt., August 2006). Therefore, there is no direct link to Florida or any other obvious source of this population; one can speculate that it was seeded along with fish.

The record from tanks at the Edwin S. George Reserve in southern Michigan is now the northernmost in the central United States. In 2006, these tanks were stocked with zooplankton, bluegill, and *Chaoborus* sp. from nearby lakes. In the 1980s, redear sunfish *Lepomis microlophus* (Günther, 1859) were stocked in another local lake; the source of the sunfish was likely one or more hatcheries in Indiana or Michigan (G. Carter, in litt., January 2007). Redear sunfish have been widely stocked in southern Michigan since the 1950s, and have established reproducing populations in many waterbodies (Towns, 2003). It is therefore conceivable that populations of *A. dorsalis* may have been seeded along with the fish. Intensive surveys in ponds and lakes in the Great Lakes region (Hudson & Lesko, 2003) and in Wisconsin (Torke, 2001) have not recorded *A. dorsalis*.

The case of the Sacramento River in California is even less clear. According to J. Orsi (in litt., August 2006), over the course of the long-term plankton-sampling program in the Sacramento-San Joaquin Delta conducted by the California Department of Fish and Game, diaptomid copepods were only identified to species level in 1972-75 and again in 1984, at which time voucher specimens were deposited in the NMNH. *Arctodiaptomus dorsalis* was at most a very minor component of the crustacean zooplankton, because it was not among the four diaptomid species listed by Orsi & Mecum (1986). In the 1980s, the diaptomid populations declined sharply, possibly because of competition from introduced Asian calanoids *Sinocalanus doerrii* (Brehm, 1909) and *Pseudodiaptomus forbesi* (Poppe & Richard, 1890). In the late 19th Century, railroad tank cars were filled with water and striped bass *Morone saxatilis* (Walbaum, 1792) from a New Jersey river and shipped to California; this may have been the route of introduction of *Eurytemora affinis* to the Delta (Orsi, 2000, and in litt., August 2006). The eastern species *Skistodiaptomus pallidus* was also found in the Sacramento-San Joaquin estuary in 1973 (Byron & Saunders, 1981).

It has been widely assumed that human-induced alterations of the landscape have created opportunities for many species to expand their ranges. Saunders (1975) noted the large number of eutrophic impoundments in Virginia, which were apparently easily colonized by *S. pallidus*. Byron & Saunders (1981) noted that eutrophication of a marina embayment in Lake Tahoe may have allowed *S. pallidus* to survive in that small part of the lake. Lee & Bell (1999) suggested that the proximate causes of the continental invasions by *Eurytemora affinis* and *E. velox* were the impoundment of brackish waters, turning them fresh; the construction of reservoirs, multiplying the number of lentic habitats; and human-mediated dispersal through shipping traffic (ballast), fish transport, or intentional introduction.

Transport along with stocked fish has been implicated in several cases of introduced copepod populations. One such possible case was reported by Ishida & Ohtaka (2006), who found *E. affinis* in the Tsugaru-Juniko lake complex in Japan, where it was not recorded prior to the 1950s; *E. affinis* is now widespread in the larger lakes containing fish. Similarly, the Australasian-South American *Boeckella triarticulata* was first recorded in Italy in fish ponds in the 1980s, and subsequently disappeared. It was recently reported in the Po River by Ferrari & Rossetti (2006), who proposed the stocking of allochthonous fishes or importation with crop seeds as the most likely vectors.

Arctodiaptomus dorsalis is a native American freshwater species. It has not previously been considered as invasive, and relatively few records have previously been considered to represent introductions. However, in spite of the obvious gaps in time and space, and the inability to document the exact routes and sources of its movements, the data presented here indicate that *A. dorsalis* is expanding its range. Chapman & Carlton (1991) proposed six criteria to aid in assessing whether a species is introduced on the "provincial scale," i.e., within the same biogeographic realm. The geographical and habitat distribution of *A. dorsalis* in the areas where it may be introduced satisfy most of these criteria, as follows:

Criterion 1: Appearance in local regions where not found previously. As discussed above, *A. dorsalis* has been collected in several regions that were relatively well sampled prior to its appearance, in particular California, Oklahoma, the upper Midwestern states, South Carolina (Savanna River site), Virginia, and central Colombia.

Criterion 2: Initial expansion of local range subsequent to introduction. Unfortunately, there are insufficient regional surveys to document in detail the appearance or disappearance of this species. However, the geographical and temporal pattern of the records of *A. dorsalis* in reservoirs in Oklahoma, Texas, and Arkansas hints that this species may have been able to expand its range in that region, and possibly northwards from there. The pattern in central Colombian reservoirs is similar.

Criteria 3 and 4: Association with human mechanism(s) of dispersal; and association with or dependency on other introduced species. As discussed above, *A. dorsalis* is closely associated with cultured and stocked fish, and also possibly with transport of ornamental aquatic plants.

Criterion 5: Prevalence or restriction to new or artificial environment(s). Outside its supposed core range, *A. dorsalis* is almost exclusively found in fish-culture ponds and other constructed waterbodies including large reservoirs.

Criterion 6: Relatively restricted distribution on a continent compared to distributions of native species. Even in Oklahoma, northern Texas, and central Arkansas, the records of *A. dorsalis* are rather discontinuous, and it has not been reported from many apparently suitable habitats (such as by Robertson, 1970, 1972). Outside this region, the records are geographically distant from each other.

I speculate that the original range of *A. dorsalis* included mainly ponds and lakes in the warm lowlands around the Gulf of Mexico and the Caribbean, from the southern United States possibly to northwestern Colombia, and including Cuba and Dominica. Occasionally, populations may have been able to establish slightly farther north, as for instance in central Mississippi. From there, it was passively transported and succeeded in establishing itself in the Mexican and Colombian highlands, one location in Venezuela, and several locations in the United States, most successfully in the lower Mississippi basin (Texas, Oklahoma, Arkansas), and then as far north as Missouri, Indiana, and Michigan. There it could be classified as a stage IVb invader (localized but dominant) sensu Colautti & MacIsaac (2004).

The movements of *A. dorsalis* and the other calanoids that are expanding their ranges may be promoted by some of the same factors. Passive transport, especially via the operations of warmwater-fish hatcheries, seems to have played the primary role. Another factor may be the proliferation of impoundments, many of them eutrophic, and the eutrophication of many natural waterbodies.

Particular biological traits of *A. dorsalis* that could have facilitated these movements include its propensity for eutrophic conditions, wide range of food items, and resistance to fish predation. Genetic selection may have also played a part, as in the case of *E. affinis* (Lee, 1999; Lee & Bell, 1999).

The rapid changes in aquatic habitats – their creation, eutrophication, and introduction of exotic fauna and flora – caused by humans over the past century have facilitated the entry and establishment of many species into regions and habitats where they were not formerly present. These changes may be allowing *A. dorsalis* to expand its range.

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