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An Afro-Asian Continental Copepod, *Mesocyclops ogunnus*, found in Brazil; with a new Key to the Species of *Mesocyclops* in South America and a Review of Intercontinental Introductions of Copepods

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With 1 Table and 1 Appendix

Key words: Copepoda, Cyclopoida, *Mesocyclops*, identification key, Brazil, South America, introduced species

Abstract

The Afro-Asian cyclopoid copepod *Mesocyclops ogunnus* ONABAMIRO occurred in samples taken in 1993 in Furnas Reservoir, State of Minas Gerais, Brazil. *Mesocyclops ogunnus* has not been previously collected in South America and is considered to have been recently introduced into Brazil.

The African species *Mesocyclops kieferi* VAN DE VELDE was recently reported for the first time from South America, from reservoirs in the State of São Paulo, Brazil, in the same watershed as Furnas. *Mesocyclops kieferi* was probably also introduced into South America.

We provide an upated key to identification of the 15 species and subspecies of *Mesocyclops* that are now known from South America.

There are presently 21 known or supposed instances of intercontinental introductions of freshwater and coastal brackish-water Copepoda, involving 18 species. Most introductions into coastal waters involve calanoids; in inland waters, records of exotic cyclopoids, including three species of *Mesocyclops*, predominate. Exotic copepods have in some cases replaced indigenous species, but there is as yet little evidence of other ecological effects of introductions of these crustaceans.

Introduction

The study of species introductions in ecosystems has gained importance recently. Three elements have contributed to this trend. First, the number of planned and accidental introductions has increased. Second, the level of concern about the nature and magnitude of undesirable effects of such introductions has been rising. Third, accumulation of general knowledge of world faunas has facilitated recognition of exotic species.

Ecology can be defined as the study of abundance and distribution of organisms in nature (ANDREWARTHA & BIRCH 1974). It is well known that community structure becomes modified with time and that the array of species is continuously undergoing losses and additions. Ecologists are interested in questions such as why organisms appear in or disappear from systems, or, in another, perhaps more interesting approach, why some exotic organisms are able to colonize a new environment successfully and others are not.

The potential impact that a newcomer will have on the community structure depends on factors besides its ecological competence. Ecosystems are capable of counteracting or "buffering" external influences to some extent. They are, however, open systems, with energy, nutrients, and organisms constantly entering and leaving. An ecosystem's structure at a given time can be seen as the result of the interactions between all these factors and the system's buffering potential. This internal homeostatic capability can be measured as resilience, resistance, and stability (PIMM 1984). Therefore, changes in nutrient levels or introduction of a single species in a given ecosystem can modify its structure, if the modification transcends the system's homeostatic potential. Attention to the effects of exotic species on an ecosystem can provide clues to its basic mechanisms.

Copepods and other aquatic animals and plants are easily transported, either as active individuals or as resistant stages (e.g. REID & REED 1994; SARS 1901; SAUNDERS 1993; SAUNDERS et al. 1993). Human-mediated movement seems to have been going on for a long time and by various vectors such as ship ballast (solid and water), with fish and shellfish transported for aquaculture, and with aquatic and terrestrial plants (CARLTON & GELLER 1993; LEPPÄKOSKI 1984; LOCKE et al. 1991; MILLS et al. 1993).

We report the finding of an Afro-Asian cyclopoid copepod, *Mesocyclops ogunnus*, in a reservoir in Brazil. There is some evidence that *M. ogunnus* has been recently introduced into the reservoir. Because several other congeners have been added to the list for South America in recent years, we also provide an updated identification key to the genus *Mesocyclops*. In addition we list other known or supposed instances of transcontinental introductions of freshwater and estuarine copepods, and review the little accumulated information on effects of these introductions on indigenous copepod species and aquatic fauna in general.

Material and Methods

Species of Copepoda were determined in non-quantitative plankton samples taken bimonthly from February–August 1993 at six stations in Furnas Reservoir. Furnas is a large reservoir on the Rios Grande and Sapucaí in the south of the State of Minas Gerais (MG), partly bordering the State of São Paulo, at 20°40′S 46°19′W. The reservoir was closed in 1962; the present flooded area is 1459 km^2 and the volume is 22,950,000 m^3; the maximum depth (at the dam) is 90 m and the mean depth is 13 m (FURNAS/ELETROBRAS 1992). The stations were located over most of the length and both major branches of the reservoir, and were described in more detail by REID & PINTO-COELHO (1994). The stations included: "Dam", just upstream from the dam at Alpinópolis; "Rio Turvo Bridge", equidistant between the dam and the confluence of the Rios Grande and Sapucaí; "Fazenda Shangrilá" at the confluence of the Rios Grande and Sapucaí near the ferry crossing to the town of Guapé, about 20 km from the dam; "Porto Fernandes", about midway along the Rio Grande arm of the reservoir near the old Guapé-Cristais ferry crossing; "Itaci", at the town of Carmo do Rio Claro, near the ferry crossing to Itaci, on the arm of the reservoir formed by the Rio Sapucaí; and "Fama", near the village of Fama at nearly the upstream end of the reservoir on the Rio Sapucaí arm.

Voucher specimens of all species of copepods found were deposited in the collections of the National Museum of Natural History, Smithsonian Institution (USNM).

Results

Six species of Copepoda occurred in the samples (REID & PINTO-COELHO 1994). *Argyrodiaptomus furcatus* (SARS) f. *exilis* DUSSART, *Notodiaptomus iheringi* (WRIGHT), and *Thermocyclops minutus* (LOWNDES) were taken at every locality, although not in every sample. *Scolodiaptomus corderoi* (WRIGHT) occurred at Rio Turvo Bridge in February and at Porto Fernandes in April, June and August. *Thermocyclops decipiens* (KIEFER) was taken in most samples, except Porto Fernandes in June and August.

Mesocyclops ogunnus ONABAMIRO was present at the dam and Rio Turvo Bridge (in February–March), Fama (March, April, June), Itaci (March, June), and Porto Fernandes (April). The species was also present in one of two tanks sampled at the Furnas Hydrobiological and Fish Hatchery Station in December 1993.

Discussion

A. *Mesocyclops ogunnus* ONABAMIRO 1957

Synonymy:

Mesocyclops ogunnus ONABAMIRO 1957: 125, Figs. 7–12. – KIEFER 1981: 155, 181, Fig. 15. – DUMONT & VERHEYE 1984: 320. – VAN DE VELDE 1984: 3, 4, 6–11, 13, 31–36, Figs. 19–22, Table 1. – DUSSART & FERNANDO 1986: 291. – GOPHEN 1986: 294–297, Tables 1, 2. – DUSSART 1987: 154. – DUSSART & SARNITA 1987: 2731. – DUMONT & MAAS 1988: 4, 6, Table 1. – DUSSART & FERNANDO 1988: 241, 250–251, Figs, 28–30. – GOPHEN 1988: 375–378, Table 2. – JEJE 1988: 171, 173, 174, 176, 177, 183, Figs, 21–26, Table 1. – BONOU et al. 1991: 287–303. – BOXSHALL & BRAIDE 1991: 208, 209, 212, Figs. 64, 66. – FRANKE 1991: 61–62, 265, 266, 272, 430. – JEJE & FERNANDO 1992: 247, 241. – REID & KAY 1992: 331, 336–339, Fig. 3d–f.

Mesocyclops leuckarti (CLAUS). – LINDBERG 1957: 134, 135. – RAHM 1964: 19, 26, 32, 36, 40. – DUSSART & GRAS 1966: 78, 81, 84 [partim]. – GOPHEN 1976: 271–277, Tables 1–4. – GOPHEN 1977: 513–517, Tables 1–5. – GOPHEN & LANDAU 1977: 167, Tables, 3, 4, 6. – GOPHEN 1978: 17–22, Figs. 1, 2, Tables 1–4. – VAN DE VELDE 1978: [partim]. – GOPHEN 1979a: 199–207, Table 4. – GOPHEN 1979b: 41–42, Fig. I. – GOPHEN 1980a: 48, 49, Table 1. – GOPHEN 1980b: 67–75. – GOPHEN 1981a: 15. – GOPHEN 1981b: 416. – GOPHEN & SCHARF 1981: 4.

Mesocyclops thermocyclopoides HARADA. – KIEFER 1981: 163 [partim].

Mesocyclops sp. 1 DUMONT et al. 1981: 615.

Mesocyclops. – GOPHEN et al. 1990: 455. – AZOULAY & GOPHEN 1992: 243–249.

Material examined: Dam and Rio Turvo Bridge (combined sample), 26 Feb 1993, 1 ♀ dissected on slide and 1 ♀, preserved in 70% ethanol, USNM 259644. Itaci and

Fama (combined sample), 3–4 Mar 1993, 10 ♀♀ ethanol-preserved, USNM 259643. Additional specimens in collection of R. M. PINTO-COELHO, Departamento de Biologia Geral, UFMG.

Mesocyclops ogunnus was redescribed by VAN DE VELDE (1984); additional morphological details were provided by BOXSHALL & BRAIDE (1991), DUSSART & FERNANDO (1988), JEJE (1988), and REID & KAY (1992). *Mesocyclops ogunnus* is easily distinguished from most congeners by the presence of a row of spines on the maxillular palp, a character shared only with the African *Mesocyclops salinus* SARS. Additional principal diagnostic characters of *M. ogunnus* include the pediger 5 with several lateral and a few dorsal spines, the seminal receptacle with broad horizontal lateral arms and long curved pore-canal, the caudal ramus with naked medial surface and with spines at the bases of the lateral and lateralmost terminal caudal setae, the antenna basipodite with a row of spines on the distal part of its caudal surface, the leg 1 basipodite lacking a medial spine, the leg 4 coupler with 2 small blunt marginal prominences, the leg 4 basipodite with 2 groups of long slender spines on its posteromedial surface, and the leg 4 endopodite article 3 terminal spines subequal in length and spinulate along most of their margins. The specimens from Furnas Reservoir agree with this diagnosis and with other published morphological details.

Mesocyclops ogunnus was originally described from stagnant pools near the River Ogun, Nigeria, and occurs over most of Subsaharan Africa, the Near East, and South and Southeast Asia. It is one of the most eurytopic species of the genus, common and often abundant in all types of epigean freshwater habitats, including organically polluted ponds (JEJE 1988; JEJE & FERNANDO 1992; REID & KAY 1992; VAN DE VELDE 1984), saline ponds (VAN DE VELDE 1984), and brackish coastal lagoons (BONOU et al. 1991; DUMONT & MAAS 1988; LINDBERG 1957; RAHM 1964). Extensive information on physiology, development, sex ratios, trophic relationships, culture, short- and long-term population numbers, biomass and seasonal changes, spatial distribution and migratory behaviour of this species in Lake Kinneret, Israel was reported (under the name *Mesocyclops leuckarti* in earlier articles) by AZOULAY & GOPHEN (1992); GOPHEN (1976, 1977, 1978, 1979a, 1979b, 1980a, 1980b, 1981a, 1981b, 1986, 1988); GOPHEN & LANDAU (1977); GOPHEN & SCHARF (1981); GOPHEN & THRELKELD (1989); and GOPHEN et al. (1990). BONOU et al. (1991) studied the development and growth rates of *M. ogunnus* in aquaculture ponds at Layo, Ivory Coast.

This is the first report of *Mesocyclops ogunnus* in the Americas. The record satisfies several of the criteria of CHAPMAN & CARLTON (1991) for distinguishing introduced species: it has not been found previously on the continent, particularly in relatively well-collected southeastern Brazil including Minas Gerais (REID et al. 1988); it occurs in an artificial habitat (a reservoir); it appears to have a restricted distribution in Brazil; the population in Brazil is disjunct from the species' known distribution in Africa and Asia; and it is unlikely to have been passively dispersed naturally from the Old World. Although there are no earlier zooplankton samples available from Furnas Reservoir, we presume that the population in Furnas has appeared recently. This presumption is supported by the fact that ROLLA et al. (1990) reported the native congeners *Mesocyclops longisetus* and *Mesocyclops meridianus*, but did not find *M. ogunnus* in Volta Grande Reservoir, on the Rio Grande downstream from Furnas. (The copepod species reported by ROLLA et al. (1990) were determined by J. W. REID.)

The route of entry of *M. ogunnus* into Furnas is unknown. Although introduction along with exotic fish might seem possible, there is no evidence to suggest that this is the case. No African species of fish is known to exist in the reservoir. Tilapias have been introduced into some reservoirs in southern Brazil, but government fish hatcheries in São Paulo and Minas Gerais obtained their stocks from populations reared in northeastern Brazil (D. M. RIBEIRO & W. P. DE SÁ JUNIOR, personal communications). Although *M. ogunnus* was found in samples taken in December 1993 from a tank at the Furnas Hydrobiological and Fish Hatchery Station, this population could have been brought in with water from the reservoir itself. Plankton in the tilapia hatcheries in northeastern Brazil has not yet been investigated; in any event it seems unlikely that copepods could have survived a double transplant sequence.

MATSUMURA-TUNDISI et al. (1990) and TUNDISI et al. (1991) reported another African species, *Mesocyclops kieferi* VAN DE VELDE, in reservoirs along the Tietê River, State of São Paulo. *Mesocyclops kieferi* is broadly distributed across West Africa, the Rift Valley, and the Arabian Peninsula (VAN DE VELDE 1984). MATSUMURA-TUNDISI et al. (1990) noted that collections in Barra Bonita Reservoir in 1985–1986 did not contain *M. kieferi*, but that the species was present "in great abundance" in November 1988. This time sequence and the fact that *M. kieferi* has been reported from no other location in South America suggests that *M. kieferi*, like *M. ogunnus*, is a recent introduction. Both the Tietê and the Rio Grande are major tributaries of the Rio Paraná, and it seems likely that these cyclopoids will rapidly enter other waters of this immense system.

Appendix 1 presents an updated key to the species of *Mesocyclops* known until now from South America. Species from the Antilles and Central America are not included, because the taxonomic status of several remains to be clarified, and some species have been collected but not yet described (J. W. REID, unpublished data).

B. Intercontinental Introductions of Copepods

In Table 1 we list a number of known or supposed intercontinental introductions of free-living continental and estuarine copepods. It is usually difficult to evaluate records of copepods found far from their "normal" range, for reasons discussed by CHAPMAN & CARLTON (1991). Natural passive dispersal of copepods as well as other small aquatic animals with resistant life stages is undoubtedly constantly occurring, and the temporary establishment of isolated populations may be more frequent than is presently supposed (REID & REED 1994; SAUNDERS et al. 1993). Widely distributed soil-dwelling copepods such as *Phyllognathopus viguieri* (MAUPAS) are often common in greenhouse soils and in recesses of tropical plants (BORUTSKII 1952; LANG 1948; LEHMAN & REID 1993) and are probably frequently transported by the ornamental plant trade, so that it may be difficult or impossible to

Table 1. Known and presumed intercontinental introductions of continental and estuarine freeliving Copepoda, and possible vectors.

Species	Introduction	Native Range	Possible vector
Calanoida			
Acartia tonsa Dana[a]	Europe	Indo-Pacific, Americas?	Ballast water (LEPPÄKOSKI 1984; REMY 1927)
Boeckella triarticulata (THOMSON)	Italy	Australasia	With Chinese carp (I. FERRARI et al. 1991; STELLA 1989 [1991])
Eurytemora affinis (POPPE)[a]	Laurentian Great Lakes	European, North American coasts	Ballast water (FABER & JERMOLAJEV 1966; MILLS et al. 1993; SAUNDERS 1993)
Pseudodiaptomus forbesi (POPPE & RICHARD)[a]	USA west coast	East Asia	Ballast water (CARLTON 1985; CORDELL et al. 1992; ORSI & WALTER 1991)
Pseudodiaptomus inopinus BURCKHARDT[a]	USA west coast	Indo-Pacific	Ballast water (CORDELL et al. 1992)
Pseudodiaptomus marinus SATO[a]	USA west coast	East Asia	With shellfish and/or ballast water (CARLTON & GELLER 1993; CORDELL et al. 1992; FLEMINGER & KRAMER 1988; ORSI & WALTER 1991)
Pseudodiaptomus marinus	Hawaii	East Asia	Ballast water (JONES 1966)
Pseudodiaptomus trihamatus WRIGHT[a]	Brazil	Indo-Pacific	With prawns (*Penaeus monodon* FABRICIUS) (MEDEIROS et al. 1991)
Sinocalanus doerri (BREHM)[a]	USA west coast	Asia	Ballast water (CORDELL et al. 1992)
Sinodiaptomus sarsi (RYLOV)	Western USA[b]	China	Tropical aquatic plants (LIGHT 1939; WILSON 1959)
Cyclopoida			
Apocyclops panamensis (MARSH)	Ivory Coast	Western Atlantic coasts	Unknown (DUMONT & MAAS 1988)
Limnoithona sinensis (BURCKHARDT)[a]	USA west coast	China	Ballast water (F. FERRARI & ORSI 1984)
Mesocyclops kieferi VAN DE VELDE	Brazil	Africa	Unknown (MATSUMURA-TUNDISI et al. 1990; TUNDISI et al. 1991)
Mesocyclops ogunnus ONABAMIRO	Brazil	Africa, Asia	Unknown (Present report)
Mesocyclops ruttneri KIEFER	Austria[c]	East Asia	Tropical plants (KIEFER 1981)
Mesocyclops ruttneri	Southern USA	East Asia	Rice culture (REID 1993; REID & MARTEN 1994)
Oithona davisae FERRARI & ORSI[a]	California	Asia	Ballast water (F. FERRARI & ORSI 1984)
Thermocyclops crassus (FISCHER)	Costa Rica	Old World	Unknown (COLLADO et al. 1984; REID 1989)
Thermocyclops crassus	Northeast USA (Lake Champlain)	Old World	Ballast water (DUCHOVNAY et al. 1992
Harpacticoida			
Attheyella aliena NOODT	Germany[c]	Unknown	Tropical plants (NOODT 1956)
Nitokra hibernica (BRADY)	Laurentian Great Lakes	Europe	Ballast water (CZAIKA 1978)

a Estuarine species, some of which may inhabit continental fresh waters.
b Introduced population did not persist.
c Discovered in greenhouse; wild populations not established.

infer where a particular population may have originated. We undoubtedly know far less than we ought to about the processes and possibilities for introducing exotic aquatic invertebrates.

Table 1 indicates a preponderance of intercontinental introductions of calanoid copepods over cyclopoid and harpacticoid species. However, considering freshwater species only, there are more records of cyclopoids, most of these comparatively recent. Cyclopoids in general are particularly resistant to difficult environmental conditions. Many are facultative omnivores and can survive long periods with almost no food, cannibalizing their young in extreme situations. We suggest that because most monitoring programs emphasize plankton, the predominantly planktonic calanoids are most likely to be noticed. Increased efforts toward monitoring benthic copepods and studies including all taxa present are likely to result in more discoveries of exotic cyclopoids and harpacticoids.

Introductions of copepods appear to have been effected through a variety of transport modes (Table 1), although in most cases the vector can only be guessed. Ship ballast water is commonly implicated in intercontinental transport of coastal marine and estuarine species (CARLTON 1985; CARLTON & GELLER 1993; FLEMINGER & KRAMER 1988; LOCKE et al. 1991; and other references in Table 1). For instance, the Chilean coast has been colonized by several exotic marine species, apparently by this means (reviewed by CARLTON & GELLER 1993). Freshwater species may also be transported in ballast water, which is the most likely vector of the exotic copepods *Eurytemora affinis*, *Thermocyclops crassus* and *Nitokra hibernica* into the Laurentian Great Lakes system. [The European *N. hibernica* was first identified from Lake Ontario by CZAIKA (1978) and has been recently found in several localities in the Great Lakes. This case will be treated in more detail elsewhere (P. HUDSON & J. W. REID in prep.)]. LOCKE et al. (1991) found more than 28 copepod species, including 12 freshwater species, in ballast water of ships entering the Great Lakes.

Several authors have speculated about the possibility of transport of free-living copepods through aquaculture. The first South American report of an introduced brackish-water coastal species was provided by MEDEIROS et al. (1991), who found *Pseudodiaptomus trihamatus* in prawn culture ponds in Natal, northeastern Brazil. Similarly, FLEMINGER & KRAMER (1988) favored a route via culture of shellfish from Japan rather than via ballast water to account for the appearance of the East Asian neritic marine-estuarine *Pseudodiaptomus marinus* in Southern California embayments. Two freshwater copepods may have travelled with exotic fish. *Boeckella triarticulata* may have arrived in nothern Italy along with Chinese carp (I. FERRARI et al. 1991; STELLA 1989 [1991]). Although the most likely route of *Eurytemora affinis* into the Laurentian Great Lakes is presumed to have been via ballast water (MILLIS et al. 1993), SAUNDERS (1993) suggested that this calanoid may also have "hitchhiked" with fish. SAUNDERS (1993) also traced the recent appearance of *E. affinis* in widespread, isolated locations in the south central conterminous United States and suggested that it may have travelled with introduced striped bass, *Morone saxatilis* (WALBAUM). Of course, ectoparasitic copepods easily move with their fish or shellfish hosts (e.g. FRYER 1968; OGUTU-OHWAYO 1992; STOCK 1993; TAYLOR et al. 1984).

Some introductions have been associated with transport of tropical plants, or with rice culture. Imported tropical plants have long been fruitful collecting sites for copepods and other small aquatic animals. *Sinodiaptomus sarsi* may have arrived in California with ornamental plants from Asia (LIGHT 1939). *Mesocyclops ruttneri* and *Attheyella aliena* were discovered in greenhouses, but did not establish wild populations (KIEFER 1981; NOODT 1956 respectively). Recently, *M. ruttneri*, apparently an Asian species, was found in ricefields in the south central United States (REID 1993; REID & MARTEN 1994).

The means of introduction of some copepod species, as in the cases of *M. ogunnus* and *M. kieferi*, remain even more a matter for speculation. The only verified New World records of the Old World cyclopoid *Thermocyclops crassus* are from a few artificial and natural ponds in Costa Rica (COLLADO et al. 1984; New World records reviewed by REID 1989), and from Lake Champlain in the Laurentian Great Lakes system (DUCHOVNAY et al. 1992). How *T. crassus* came to Costa Rica and to Lake Champlain is a mystery. DUMONT & MAAS (1988) suggested that *Apocyclops panamensis*, which is widespread and often extremely numerous in western Atlantic brackish coastal waters from the eastern United States to Brazil, might be a recent arrival in the Ebrié Lagoon, Ivory Coast. Brackish-water ponds have been constructed for aquaculture in the area (BONOU et al. 1991; DUMONT & MAAS 1988), but there is no information on possible means of transport.

In most cases, no effects of exotic species on indigenous copepod populations have been established, and most observations are preliminary and anecdotal. CORDELL et al. (1992) observed that the introduced *Pseudodiaptomus inopinus* is apparently coexisting with the formerly co-dominant natives *Eurytemora affinis* and *Scottolana* (= *Coullana*) *canadensis* (WILLEY) in the Columbia River on the west coast of the United States.

Sinocalanus doerri and *Pseudodiaptomus forbesi*, which recently arrived in the Sacramento-San Joaquin Estuary in California, may be indirectly affecting local populations of *E. affinis* (ORSI et al. 1983). On the other hand, AMBLER et al. (1985) suggested that *S. doerri* may be exploiting a vacant niche in the riverine boundary (oligohaline section) of this estuary, and found no observable changes in the native diaptomid and cyclopid populations, which usually had been low in that section. FLEMINGER & KRAMER (1988) noted that the indigenous *Pseudodiaptomus euryhalinus* was absent from Southern California embayments invaded by *Pseudodiaptomus marinus*. However, these authors and CORDELL et al. (1992) cautioned that no data exist to support the attribution of this change to exclusion or displacement by *P. marinus*. The Afro-European calanoid *Calanipeda aquae-dulcis* KRITSCHAGIN, which entered the Aral Sea between 1965 and 1970, has replaced the previously dominant calanoid *Arctodiaptomus salinus (*DADAY) (ALADIN & WILLIAMS 1993). REID & MARTEN (1994) noted that *Mesocyclops ruttneri* is distributed allopatrically with the native *Acanthocyclops vernalis (*FISCHER) in some ricefields in the south central United States, suggesting possible competitive exclusion. In Barra Bonita Reservoir, São Paulo, MATSUMURA-TUNDISI et al. (1990) collected the two native species *Mesocyclops longisetus* and *Mesocyclops brasilianus* in 1985–1986, but only *M. longisetus* and *M. kieferi* in November 1988. This sequence seems to indicate that *M. kieferi* may be supplanting *M. brasilianus* in Barra Bonita.

The general effects of entrance of exotic copepods into aquatic ecosystems are so far hardly studied. In the Sacramento-San Joaquin Estuary, the striped bass preferred two indigenous copepods, *Cyclops* sp. and *E. affinis*, over *S. doerri* and *P. forbesi* in feeding trials. Factors of prey behavior, habitat preference and reproductive cycles apparently reduce the availability of the introduced species to young bass (MENG & ORSI 1991).

Introductions of aquatic organisms are increasing worldwide at a rapid rate (CARLTON & GELLER 1993). Invasions of the Laurentian Great Lakes are well documented; two species of free-living copepods [*Eurytemora affinis*, Table 1; and *Skistodiaptomus pallidus* (HERRICK) from the central United States], two cladocerans *[Bythotrephes cederstroemi* SCHOEDLER and *Eobosmina coregoni* (BAIRD)], a parasitic branchiuran (*Argulus japonicus* THIELE), and the especially economically damaging zebra mussel [*Dreissena polymorpha* (PALLAS)] are among the species with planktonic life stages that have appeared in the lakes in this century (GARTON et al. 1993; MILLS et al. 1993). Introductions of fish and planktonic and benthic crustaceans, together with increasing salinization and reduced nutrient input, have greatly altered the biota of the Aral Sea (reviewed by ALADIN & WILLIAMS 1993). The cladoceran *Bythotrephes longimanus* LEYDIG, recently established in several reservoirs in the Netherlands, has greatly increased the predation pressure on native daphnids (KETELAARS & VAN BREEMEN 1993). Although no such spectacular effects are known to have resulted from introductions of copepods alone, faunistic changes, albeit subtle in some cases, must inevitably result. In most cases, discoveries of introduced copepods are quite recent and the reasons for any observed faunistic changes are difficult to determine because of normal short-term environmental and community fluctuations (AMBLER et al. 1985; CORDELL et al. 1992; ORSI & WALTER 1991). Long-term monitoring and attention to population dynamics of the total plankton and fish communities in localities where exotic species have becom established will doubtless document more cases of pro found changes in community equilibria.

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Appendix 1.

Key to females of species of *Mesocyclops* occurring in South America. Morphological features employed were defined and/or illustrated by BOXSHALL & BRAIDE (1991), DUSSART (1987), JEJE (1988), PETKOVSKI 81986), REID (1985), and VAN DE VELDE (1984). Principal taxonomic references were DEFAYE & DUSSART (1988 [1989]), DUSSART (1987), DUSSART & FRUTOS (1985 [1986]), KIEFER (1981), PETKOVSKI (1986), REID (1985), REID & REED (1994), and VAN DE VELDE (1984).

1. Leg 1 basipodite medial expansion lacking spine . . . 2
– Leg 1 basipodite medial expansion with spine 4
2. Pediger 5 with hairlike spinules on each side 3
– Pediger 5 naked laterally . . . . . *kieferi* VAN DE VELDE [Brazil (introduced); Africa, Yemen]
3. Caudal ramus with hairlike spinules on medial surface; maxillular palp lacking spines on surface . . . . *aspericornis* (DADAY) (Argentina, Brazil, Colombia, Venezuela, Antilles; pantropical)
– Caudal ramus lacking hairs on medial surface; maxillular palp with row of spines on surface . . . *ogunnus* ONABAMIRO [Brazil (introduced); Africa, Near East, South and South-east Asia]
4. Coupler (intercoxal plate) between 4th swimming legs with 2 large dentiform prominences on distal margin 5
– Coupler of 4th legs with 2 small rounded prominences, or none 11
5. Seminal receptacle with broad, somewhat recurved lateral arms 6
– Seminal receptacle with narrow lateral arms, recurved or not 8
6. Seminal receptacle with lateral arms strongly recurved 7
– Seminal receptacle with lateral arms nearly perpendicular to long axis of body; caudal ramus short (about 2.5 times longer than broad), leg 4 endopodite article 3 about 2.5 times than broad . . . . *longisetus* (THIÉBAUD) sensu stricto (South and Central America, Mexico)
7. Caudal ramus 3.6–4.4 times longer than broad, leg 4 endopodite article 3 about 4 times longer than broad . . . . *longisetus* var. *araucanus* LÖFFLER (Chile, Tierra del Fuego)
– Caudal ramus about 3.2 times longer than broad, leg 4 endopodite article 3 about 3.1 times longer than broad . . . . *longisetus* var. *curvatus* DUSSART (Brazil; probably elsewhere in South America; Guadeloupe, Honduras, southern United States, Canada)
8. Caudal ramus at least 4.5 times longer than broad . . 9
– Caudal ramus much shorter 10
9. Leg 4 endopodite article 3 at least 2.5 times longer than broad, medial terminal spine of this article shorter than lateral terminal spine . . . . *annulatus* (WIERZEJSKI, sensu stricto (Argentina, Bolivia, Chile, Paraguay, Peru, Uruguay)
– Leg 4 endopodite article 3 about 2.1 times longer than broad, medial terminal spine at least 1.25 times longer than lateral terminal spine . . . *annulatus diversus* HERBST (Brazil)
10. Seminal receptacle, anterior part much expanded, semicircular; lateral arms narrow, not tapering; leg 4 coupler, 2 acute prominences triangular, stout . . . . *ellipticus* (KIEFER) (Brazil, Venezuela, Haiti)
– Seminal receptacle, anterior part slightly expanded; lateral arms tapering laterally; leg 4 coupler, 2 acute prominences long, incurved . . . . *paranaensis* DUSSART & FRUTOS (Argentina, Brazil, Paraguay)
11. Seminal receptacle, lateral arms narrow, not tapering . 12
– Seminal receptacle, lateral arms broad or narrow, tapering laterally 13
12. Seminal receptacle, anterior margin straight or convex, posterior expansion narrowing posteriorly; leg 5 article 2, medial spine armed with 2 rows each of about 9 small spinules . . . . *meridianus* (KIEFER) (Argentina, Bolivia, Brazil, French Guiana, Paraguay)
– Seminal receptacle, middle of anterior margin concave, posterior expansion widening posteriorly; leg 5 article 2, medial spine with few (about 5–6) large spinules . . . . *pseudomeridianus* DEFAYE & DUSSART (French Guiana)

13. Leg 4 endopodite article 3, medial terminal spine longer than lateral terminal spine 14
– Leg 4 endopodite article 3, medial terminal spine shorter than lateral terminal spine . *meridionalis* DUSSART & FRUTOS (Argentina, Brazil)
14. Leg 4 endopodite article 3, setae on medial margin reaching at least end of medial terminal spine; leg 1, spine on basipodite short, strong, regularly barbed . . . . *brasilianus* (KIEFER) (Brazil, Colombia, Venezuela; possibly Peru and Nicaragua)
– Leg 4 endopodite article 3, setae on medial margin reaching about 1/2 length of medial terminal spine; leg 1, spine on basipodite long, slender, bearing long hairlike spinules proximally, tiny spinules distally . . . . *venezolanus* DUSSART (Venezuela, Honduras, Canada)