

# The impact of invasive fish on an endemic *Cyprinodon* species flock (Teleostei) from Laguna Chichancanab, Yucatan, Mexico

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## U. Strecker

Zoological Museum, University of Hamburg,  
Hamburg, Germany

**Abstract** – Species that invade a new environment often may lead to population declines of endemic species. Here I document the invasions of an African cichlid (genus *Oreochromis*) in 1988 and the Mexican *Astyanax fasciatus* (Characidae) in 1996 into Laguna Chichancanab (Yucatan, Mexico), and the impact on an endemic *Cyprinodon* species flock and the poeciliid *Gambusia sexradiata*. After the invasion of *Astyanax fasciatus*, their relative abundances decreased enormously, most likely caused by predation on the fry. One species, *Cyprinodon simus*, might have even gone extinct or just occurs in extremely reduced numbers. Furthermore, it was observed that the percentage abundance of the detritivorous *Cyprinodon beltrani* increased significantly, in contrast to all other *Cyprinodon* species. This study also revealed that infestation by metacercaria (black spots) of an ectoparasitic trematode and of an endoparasitic nematode increased in the *Cyprinodon* spp. following the introduction of *Oreochromis*. Whereas the infestation by trematodes decreased after a period of 6 years, the prevalence and intensity of infestation by nematodes stayed at a high level. In contrast, in *G. sexradiata* the parasite load remained always very low.

**Key words:** exotic fish; *Oreochromis*; *Astyanax*; parasite load; sympatric speciation; pupfish

U. Strecker, Zoological Museum, University of Hamburg, Martin-Luther-King Pl. 3, 20146 Hamburg, Germany;  
e-mail: strecker@uni-hamburg.de

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## Introduction

In several lakes, the introduction of new species into delicate aquatic ecosystems has caused a decline or even extinction of endemic species for various reasons, including predation, food competition and disturbance of mate recognition (Kornfield & Carpenter 1984; Goldschmidt et al. 1993; Lowe-McConnell 1993; Villwock 1993; Seehausen et al. 1997). Generally, the causes of population declines were not assessed until long after an invasion. In contrast, I monitored the influence of introduced fish species on the fish fauna in Laguna Chichancanab (Yucatan, Mexico) starting immediately after the appearance of one exotic species and including the period of invasion of a second one.

The native fish fauna of Laguna Chichancanab is composed of the livebearing tooth carp *Gambusia sexradiata* Hubbs (Poeciliidae) and an endemic *Cyprinodon* species flock (Cyprinodontidae). The flock consists of seven species (*Cyprinodon beltrani* Alvarez, *Cyprinodon esconditus* Strecker, *Cyprinodon labiosus* Humphries & Miller, *Cyprinodon maya* Humphries & Miller, *Cyprinodon simus* Humphries & Miller, *Cyprinodon verecundus* Humphries, *Cyprinodon suavium* Strecker (Humphries & Miller 1981; Humphries 1984; Strecker 2002, 2005) and a number of specimens which cannot be allocated to any of the described species and were initially considered as hybrids by Humphries & Miller (1981). However, it is unclear whether the latter individuals include representatives of morphological plasticity within species

and/or hybrids (Strecker et al. 1996) or more yet unidentified species, like *C. verecundus*, *C. esconditus* and *C. suavius* which were recognised and described later. Laboratory experiments indicate that reproductive isolation is not complete in all species (Strecker 1996, in press; Strecker & Kodric-Brown 1999, 2000; Kodric-Brown & Strecker 2001). Studies of the gut contents have shown that all species feed on bottom sediments. However, while one species, *C. beltrani*, exclusively relies on these sediments, the other species and the unidentifiable specimens have additionally become carnivorous, developing a preference for species-specific prey items and displaying incipient trophic niche partitioning (Horstkotte & Strecker 2005).

In 1988, African cichlids (aquacultural stocks of *Oreochromis*) invaded the lake following damage to aquaculture facilities caused by hurricane Gilbert (Stevenson 1992; Strecker 1993; Schmitter-Soto & Caro 1997). Eight years later in 1996 the native neotropical characid *Astyanax fasciatus* (Cuvier) was discovered in the lake (Strecker 2002) following hurricane Roxana (1995) which caused vast inundations in that area. Both aliens are now highly abundant (U. Strecker, personal observations).

Compared with other lakes in which sympatric speciation has occurred, the ecological system of Laguna Chichancanab is much less complex due to its small size, depauperate fauna and the nearly constant tropical conditions. This simplicity facilitates a study of the ecological consequences of invasive species. In this paper, I describe the habitat of Laguna Chichancanab and analyse the effects of the above-mentioned invasions on the endemic species flock and *G. sexradiata*. In particular, I studied changes in the relative and percentage abundance of the *Cyprinodon* species to assess the impact of the detritivorous/planktivorous cichlids and that of the carnivorous *A. fasciatus*. Furthermore, I analysed the indirect consequences of these invasions on the infestation load in fishes of the parasites *Contracaecum* sp. (Anisakidae, Nematoda) and *Crassiphiala* cf. *bulboglossa* Haitsma (Diplostomatida, Trematoda) passed on by fish-eating birds.

## Materials and methods

### Sampling

The sampling sites (A–H) are shown in Fig. 1. The locations A, B, C, E and G correspond to 1, 2, 3, 6 and 5, respectively, of Humphries & Miller (1981) and Humphries (1984). Sampling times were in December 1990, July 1991, December 1992, 1993 and January 1996, April 1997, March 1998, 1999 and November 2000. Not all sampling sites were accessible in every study year. Sampling of fish was done with a net

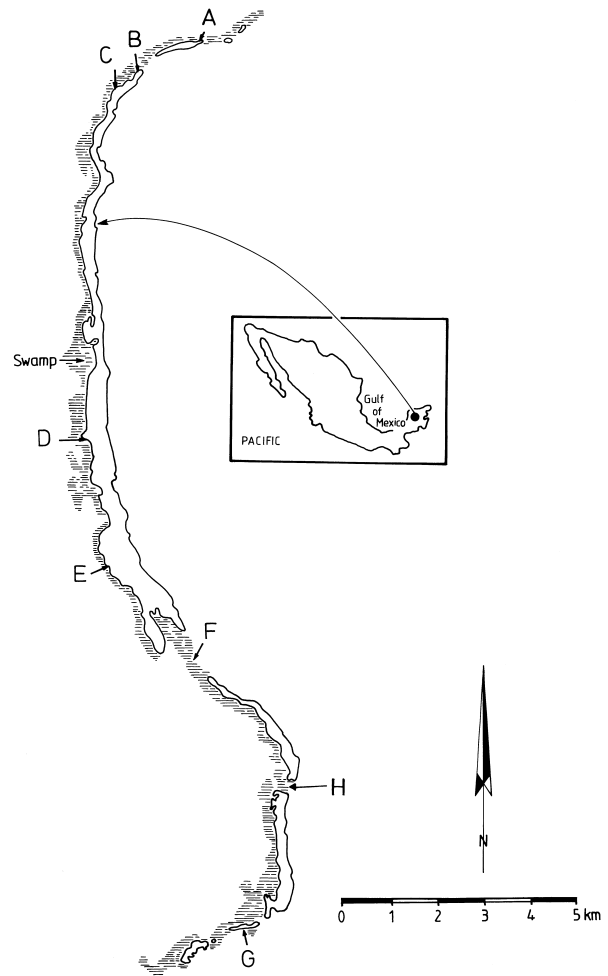


Fig. 1. Map of Laguna Chichancanab showing sampling sites.

(mesh width 0.5×0.5 cm) about 5 m long pulled by two persons from about 5 m offshore to the shore. Maximum sampling depth was 1.20 m. Occurrences of fishes offshore and in the littoral zone were studied by snorkelling. Plankton sampling was by a plankton net (55  $\mu$ m). Samples of water from the surface were collected for chemical analysis.

### Parasites

Trematode infestation was diagnosed by the presence of externally visible black spots. Specimens having at least one black spot were classified as infested. In total 3350 *C. beltrani*, 84 *C. esconditus*, 475 *C. labiosus*, 281 *C. maya*, 103 *C. simus*, 434 *C. verecundus* and 1362 unidentifiable specimens were analysed including museum material from the University of Michigan Museum of Zoology (UMMZ) collected in 1974 before the cichlid invasion in 1988. Additionally, 336 *G. sexradiata*, 214 cichlids and 61 *A. fasciatus* from Laguna Chichancanab were included. For comparison 180 specimens of the sister species of the flock

*Cyprinodon artifrons* Hubbs were studied from coastal marine lagoons near Chuburna Puerto (Yucatan).

Infestation by nematodes was determined after opening the body cavity. The number of nematodes per specimen, as well as the number of specimens infested, was counted. In total 109 *C. beltrani*, 52 *C. esconditus*, 106 *C. labiosus*, 63 *C. maya*, 65 *C. simus*, 99 *C. verecundus* and 103 unidentifiable specimens were analysed. Also 80 *G. sexradiata* from Laguna Chichancanab and 60 *C. artifrons* from coastal lagoons near Chuburna Puerto (Yucatan) were studied.

Statistical methods

For statistical tests only sampling sites with comparable data sets were chosen. The percentage abundance of the different *Cyprinodon* species was assessed in 1992, 1993, 1997, 1998, 1999 and 2000 at sampling sites A, B, C and E. In 1998 and 1999 sampling sites E and A, respectively, were not accessible. For comparison of mean percentage abundance before (1992 and 1993) and after the invasion of *A. fasciatus* (1997–2000) a *t*-test for percentages was performed (Knußmann 1992).

The relative abundances of *Cyprinodon* spp. and *G. sexradiata* were calculated from the number of fish collected in the first catch: 1992 (sampling sites A, B, C and E; for *G. sexradiata* only in A and C), 1997 (A, B, C, F, G and H), 1998 (A) and 2000 (A, B, C and G).

Infestation by parasites was statistically analysed using a two-tailed chi-square test. Where appropriate, the significance of *P*-values were adjusted following Bonferroni sequential corrections for multiple simultaneous tests (Rice 1989), with an initial alpha value of 0.05/*k*, *k* being the number of tests.

Results

The habitat

The lake comprises several basins that are continuously filled with water and connected by narrow

passages (Fig. 1). Together they are about 20 km long. The largest width of the lake is about 300 m. In most parts the depth is less than 3 m, although depths of 12.5 m have been measured (Covich & Stuiver 1974). The eastern shore is bordered by a steeply ascending landscape whereas the opposite shore is bordered by a vast plain. Seasonal rainfalls (May to September) periodically inundate the flat plain. After hurricanes Gilbert in 1988, Roxana in 1995 and Isidor in 2002, the water level rose more than 1 m causing extensive flooding of the adjoining plain. In each instance high water levels persisted for at least 1 year.

At sampling site F, alongside the bridge near San Diego, water from the southern basin may develop a strong flow at times of higher water levels, flowing northwards through a narrow pipe situated under the bridge, suggesting that intralacustrine springs in the southern basin have higher flows than those in the north. The substrata range from solid rock to areas of crystalline gravel and, in deeper parts, muddy sediments or fluffy colloidal humin precipitates.

Salinity measured at the water surface ranges from 3.5 to 5.6 ppt in the northern basin and from 1.2 to 2.9 ppt in the southern basin. Freshwater influx from the groundwater apparently causes the reduced salinity here. Ionic concentrations are lower after heavy rainfalls as shown for data collected in 1996 and 1997, following hurricane Roxana (Table 1). Water clarity varied from clear to turbid. At about 200 m from the lake at the northern margin of the floodplains groundwater is accessible in a hole that is about 1 m<sup>2</sup> in diameter and located above the normal inundation level of the lake. Such habitat types are called ‘Ojo de Aqua’ by the local people. In contrast to Laguna Chichancanab the water here is suitable for drinking because the amount of magnesium is lower and considerably different from that of the lake except for localities F and H (Table 1).

Submerged macroscopic vegetation consists of at least three species of *Chara* (*Chara zeylanica* Klein ex Wild, *Chara cienegaensis* Tindall, *Chara*

Table 1. Water chemistry of Laguna Chichancanab and the adjacent Ojo de Agua.

Year	1950†	1967‡	1991	1993		1996		1997		
Sampling site	D	D	A	A	Ojo	D	F	B	F	H
Na <sup>+</sup>	105	340–400	190	320	119	216	134	203	132	117
K <sup>+</sup>	3	20–24	16	19.8	6.4	16	9.3	14.5	9.2	7.4
Mg <sup>2+</sup>	253	360–425	380	349	98	227	151	217	147	130
Ca <sup>2+</sup>	813	600–700	c. 800	749	559	631	552	561	444	423
Cl <sup>-</sup>	138		276	423	546	257	146	246.2	152.2	131.3
SO <sub>4</sub> <sup>2-</sup>	2959	2750–2950	2476	3700	1311	2247	1661	2225.9	1584.4	428.7
HCO <sub>3</sub> <sup>-</sup>	71			32	3.6	136	242	81.7	110.1	94.0
‰	4.3	4.3	4.2	5.6	2.96	3.73	2.9	3.5	2.5	1.2

†Illescas-Pasquel (1950).

‡Covich & Stuiver (1974).

*hornemanni* Wallmann) that densely cover the lake bottom in shallow areas. The eulitoral and the above-mentioned inundation plain support extensive growths of salt-tolerant sedges (cf. *Cladium jamaicense* Crantz) and isolated specimens of mangrove (*Conocarpus erecta* Linnaeus). During dry seasons the local people burn large portions of these areas. At elevations above the inundation level, the common Yucatan forest plant communities are found.

Besides the fish and fish preying birds [e.g., *Phalacrocorax olivaceus* (Humboldt), *Casmerodius albus* (Linnaeus)], aquatic vertebrates include two reptiles, *Crocodylus moreletii* Dumeril & Bibron and *Chrysemys ornata* Grey and *Bufo valliceps* Wiegmann (Amphibia) tadpoles. The invertebrate fauna is depauperate and characterised by benthic marine and freshwater species. Ostracod species (*Cytheridella alosa* Tressler, *Darwinula furcibdominis* Keyser, *Darwinula stevensoni* Brady and Norman, *Physocypria pseudocrenulata* Furtos, *Cypridopsis* sp., *Heterocypris* sp., *Eucypris* cf. *serrato-marginata* Furtos), the amphipod *Hyaella azteca* Saussure and the bivalve *Lucina* sp. are abundant. The snail *Pyrgophorus coronatus* (Pfeiffer) is very common. The only decapod crustacean is *Procambarus llamasii* Villalobos.

The plankton is also depauperate, with high abundances of only a few phytoplanktonic species (Volvocales; Diatomea: *Campylodiscus*, *Navicula*, *Cymbella*; Dinoflagellata: *Peridinium*). Among the zooplankton, the rotifer *Keratella cochlearis* (Gosse) and rare specimens of an undetermined harpacticid copepod were found in moderate numbers. In shallow zones, a large proportion (c. 90%) of the plankton consists of small oval bodies about 200 µm long. These appear to be faecal pellets of the bivalve *Lucina* sp.

The fauna of the Ojo de Agua consists of three blind troglobitic crustacean species widely spread in the Yucatan groundwater system, *Mayaweckelia cenoticola* Holsinger, *Antromysis cenotensis* Creaser, *Typhlatya pearsei* Creaser (Wilkens 1982; Iliffe 1993). Particularly remarkable is the occurrence of a thermosbaenacean, *Tulumella unidens* Bowman &

Iliffe, which is only recorded from underground waters close to the Caribbean coast of Yucatan (Iliffe 1993). The primary freshwater fish *Rhamdia guatemalensis* Guenther (Pimelodidae) is also present. Another, much larger, groundwater access (Actun Há) is near the village of Kantemo, about 3 km from Laguna Chichancanab, where the Yucatan cave fish *Ogilbia pearsei* (Hubbs) and *Ophisternon infernale* (Hubbs) and several blind crustaceans [*Creaseriella anops* (Creaser), *Creaseria morleyi* (Creaser)] have been found. This indicates that the whole ensemble of Yucatan troglobites exists in close contact to the lake and might occasionally get introduced into it by underwater freshwater springs.

Invasion of *A. fasciatus* (Characidae) into Laguna Chichancanab

*Astyanax fasciatus* was first observed in the Laguna Chichancanab system at the northernmost end of Laguna Esmeralda (San Diego bridge, collection site F; Fig. 1) in January 1996. At that time it occurred in low abundance and had not yet spread north of the sampling site at Balneario Dziuché. However, by April 1997 it occurred throughout the lake system. After this, *A. fasciatus* became highly abundant. For example, in 2000 at sampling site G, 513 specimens were caught with one seine haul.

Percentage and relative abundances of the *Cyprinodon* species flock and *G. sexradiata*

*Cyprinodon beltrani* was the most abundant member of the species flock and showed an increase of the percentage abundance after the invasion by *A. fasciatus* ( $P < 0.05$ , after Bonferroni correction, Table 2). Contrary to this, all other *Cyprinodon* spp. show a decrease of the percentage abundance after the invasion, which is not significant for *C. esconditus* and *C. simus*. The unidentifiable specimens were the second-most abundant group with 29.4% (before the invasion) and 19.8% (after the invasion). The corresponding values for the other species of *Cyprinodon* were as follows: *C. labiosus* (9.5% and 6.5%), *C. verecundus* (9.3% and 4.5%), *C. maya* (3.6% and

Table 2. Mean percentage abundances of *Cyprinodon* spp. for the time periods before (1992 and 1993) and after (1997–2000) *Astyanax fasciatus* had spread in Laguna Chichancanab to sampling sites A, B, C and E.

	<i>C. beltrani</i>	<i>C. esconditus</i>	<i>C. labiosus</i>	<i>C. maya</i>	<i>C. simus</i>	<i>C. verecundus</i>	Unidentifiable specimens
Before <i>A. fasciatus</i>	46.0 (35.5–56.8)	2.0 (0–6.9)	9.5 (0.6–25.5)	3.6 (0–14.6)	0.3 (0–1.0)	9.3 (0–36.8)	29.4 (8.0–43.1)
After <i>A. fasciatus</i>	66.8 (45.6–80.4)	1.3 (0–5.1)	6.5 (0–19.2)	1.2 (0–3.6)	0.1 (0–1.9)	4.5 (0–13.1)	19.8 (2.0–51.0)
t-test value	14.3	0.6	6.0	3.6	2.3	5.1	8.2
Significant after Bonferroni correction	sign.	n.s.	sign.	sign.	n.s.	sign.	sign.

In 1998 and 1999 sampling sites E and A, respectively, are missing (for details see Materials and methods). Ranges in brackets.

1.2%), *C. esconditus* (2.0% and 1.3%) and *C. simus* (0.3% and 0.1%).

*Cyprinodon esconditus* was absent in several catches (53.1%) and was never found at sampling site F. *Cyprinodon simus* was even rarer (absent in 68.8% of all catches) and was absent at sampling sites D and E. This is the only species of the flock that has gradually become rare during the study period. The last records of *C. simus* are from sampling sites C and F in 1998 (Table 3). During the study period large schools, previously observed by Humphries & Miller (1981), were never detected by snorkelling.

After the appearance of the cichlids, no *C. maya* specimens were observed with a standard length (SL) surpassing 5 cm. In contrast, Humphries & Miller (1981) and Wilkens (observation in 1971) report larger individuals up to 8.5 cm SL.

The relative abundance of *Cyprinodon* spp. and of *G. sexradiata* decreased drastically from 1992 to 1997 (Fig. 2). The number of smaller *Cyprinodon* specimens ( $\leq 2.0$  cm SL) and of *G. sexradiata* remained at a very low level in 1998 and 2000. In contrast, the number of larger *Cyprinodon* specimens had increased in 2000, but reached only half the amount found in 1992.

#### Parasite loads

During the study period all members of the *Cyprinodon* flock were subjected to increasing infestation by two helminths, *C. cf. bulboglossa* Haitsma (Diplostomatida, Trematoda) and *Contracaecum* sp. (Anisakidae, Nematoda). Significant differences between the infection rates among *Cyprinodon* spp. were observed for both parasites (chi-square test,  $P = 0.001$  for *Crassiphiala* cf. *bulboglossa* and  $P < 0.0001$  for *Contracaecum* sp.). Infestation by *C. cf. bulboglossa* is by intermediate metacercaria stages causing black spots on the fish epidermis (Scholz et al. 1995). The prevalence of *C. cf. bulboglossa* in the *Cyprinodon* flock, in general, can be classified into three sequential phases: (i) increasing prevalence during 1974–1991 and 1991–1992; (ii) stable high levels of prevalence from 1992 to 1997/1998; and (iii) a reduced prevalence after 1997/1998 (Fig. 3). As an exception, *C. verecundus* showed a significant increase in parasites between 1991 and 1992 only ( $P = 0.0001$ ). In *C. maya*, a high infestation level was already reached by 1991 (77.8%) which remained more or less stable until 1999 and decreased significantly in 2000 ( $P = 0.033$ ). In the unidentifiable specimens the increase in parasite infestation was prolonged until 1996 (Fig. 3). In *C. esconditus* and *C. simus* the number of data is low or missing in some years. However, when looking at data with sample sizes

$N > 10$ , in principle the development of the infestation rate is comparable to the other species. In *C. simus* it was low in 1974 reaching a high level in 1996. Also for *C. esconditus* high prevalence was found in 1993 and 1999 with a significant reduction in 2000 (Fig. 3).

For *G. sexradiata*, the prevalence of black spots was very low [1990 1.4% ( $N = 146$ ); 1991 0.0% ( $N = 54$ ); 1992 2.1% ( $N = 95$ ); 1998 0.0% ( $N = 41$ )]. The sister species of the *Cyprinodon* species flock, *C. artifrons* from coastal lagoons, was not infested in 1992, 1998 and 1999 ( $N = 60$  per year). In cichlids, the frequency of infestation with black spots was between 1.4% ( $N = 214$ ; 1992) and 9.5% ( $N = 97$ ; 1997). In *A. fasciatus* no trematode metacercaria were found ( $N = 61$ ; 1997).

The second parasite is the third stage larva of *Contracaecum* sp. Type 2 (Moravec et al. 1993). Strong infestation of *Cyprinodon* species can be recognised from outside by the protruding anterior belly region of the fish. This condition was not present in any specimens of museum material collected in 1974 ( $N = 700$ ). Generally, increased infestation by *Contracaecum* during the study period was observed in the species of the flock in terms of percentage of parasitised specimens and number of nematodes per individual which show a comparable pattern (Table 4). When comparing the number of infested specimens in the beginning of the 1990s with the last year of the study (1999) in most species a significant increase can be observed: *C. beltrani* (1991/1999;  $P = 0.0001$ ), *C. labiosus* (1991/1999;  $P = 0.0001$ ), unidentifiable specimens (1991/1999;  $P = 0.0001$ ), *C. verecundus* (1992/1999;  $P = 0.0001$ ). Contrary to this, in *C. maya* no significant increase was observed (1992/1999;  $P = 0.303$ ) because the infestation level was already high in 1992. For *C. simus* and for *C. esconditus* not enough data are available.

No *Contracaecum* nematodes were detected in *C. artifrons*, the sister species of the Laguna Chichancanab flock (1992, 1998, 1999;  $N = 20$  per year). Also, no nematodes were detected in *G. sexradiata* (1990, 1991, 1992, 1998;  $N = 20$  per year).

#### Discussion

Derivation and development of the Laguna Chichancanab ichthyofauna

The surface freshwater ichthyological community of the northern Yucatan peninsula is composed of *Cichlasoma urophthalmus* Guenther (Cichlidae), *G. sexradiata* and *Gambusia yucatanana* Regan (Poeciliidae) and the primary freshwater fish *R. guatemalensis* (Pimelodidae) as well as the characid *A. fasciatus*, which is restricted to cenotes and lagoons

Table 3. Percentage abundance of *Cyprinodon* spp. between 1990 and 2000 at the different sampling sites (A–G, see Fig. 1).

Year	Sampling site	1990							1991							1992							1993							1996							1997							1998							1999							2000						
		G	C	D	G	A	B	C	G	C	E	A	B	C	E	A	B	C	G	A	B	C	E	C	F	A	B	C	E	A	B	C	G	A	B	C	E	F	G	A	B	C	E	F	G	A	B	C	G	B	C	E	A	B	C	E	A	B	C	E	G			
N		156	1304	103	239	155	150	611	133	304	496	93	232	299	133	21	359	151	122	232	52	149	166	417	122	169	159	305	271	349	226	362	38																															
<i>C. beltrani</i>		37.2	81.0	76.7	87.0	56.8	54.7	41.4	36.0	52.9	52.0	35.5	38.4	35.1	20.0	76.2	82.2	89.4	72.9	92.4	98.1	45.6	67.5	68.6	87.5	63.9	62.3	54.4	66.5	61.3	48.2	75.5	100																															
Unidentifiable specimens		50.0	10.5	6.8	13.0	36.1	8.0	19.8	14.3	43.1	34.9	37.7	40.9	45.2	10.0	23.8	9.8	2.0	10.7	0	1.9	51.0	16.9	21.8	0	20.1	25.8	26.6	25.3	17.1	18.4	7.2	0																															
<i>C. esconditus</i>		2.6	0.4	0	0	1.3	0.7	1.5	5.3	0	0	0	6.9	1.3	0	0	0.3	0	2.5	0	0	0.7	1.2	0.7	0	0	0	0	0	0	0	0	0																															
<i>C. verucundus</i>		0.6	3.1	10.7	0	2.0	10.0	11.0	36.8	0	0.2	3.2	11.2	2.7	0.8	0	1.9	5.3	12.3	1.5	0	0	3.6	3.1	0	3.6	3.8	13.1	0	3.2	9.1	4.1	0																															
<i>C. simus</i>		5.1	0.2	0	0	0.6	0.7	0	0	1.0	0	0.4	1.3	58.5	0	0	0	0	6.1	0	0	0	0	1	12.5	0	0	0	0	0	0	0	0																															
<i>C. maya</i>		4.5	1.2	3.9	0	2.6	14.6	0.8	3.8	2.0	1.8	3.2	0	3.7	10.7	0	2.2	2.6	0.8	0	0	0.7	2.4	0.2	0	2.4	0.6	0	3.6	1.2	0	0	0																															
<i>C. labrosus</i>		0	3.6	1.9	0	0.6	11.3	25.5	3.8	2.0	10.1	20.4	2.2	10.7	0	0	3.6	0.7	0.8	0	0	2.0	8.4	4.6	0	10.0	7.5	5.9	4.6	13.0	19.2	10.2	0																															

N, number of specimens.

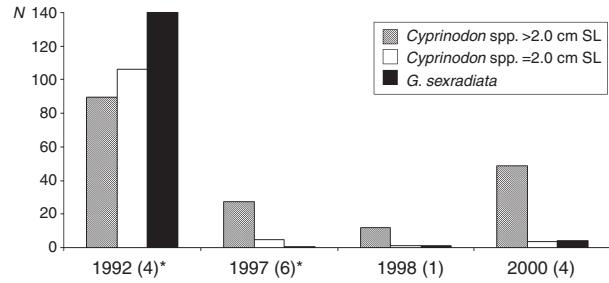


Fig. 2. Relative abundance of *Cyprinodon* spp. and *Gambusia sexradiata*. Number of catches per year are in parentheses; asterisk indicates two catches for *G. sexradiata*. SL, standard length.

close to the coast (Wilkins 1982). The sister species of the *Cyprinodon* species flock, *C. artifrons* (Lacépède), is not a native component of this assemblage. It is a species adapted to marine and extremely hypersaline salinities and is distributed in habitats along the Yucatan coast.

The ichthyofauna of Laguna Chichancanab originally contained only one derivative of the described freshwater species spectrum, *G. sexradiata* (Humphries & Miller 1981; Wilkins 1982). The lake is superficially isolated from surface freshwaters as well as from the coast. However, it has been shown above that the characteristic Yucatan cave fauna, including fish like *R. guatemalensis*, occur nearby and may have access to the lake by submerged springs or by underground pathways. Therefore, it might be concluded that the superficial geographical isolation only plays a minor role with respect to the colonisation of the lake. I assume that the salinity, which lies at the level of the ‘species minimum’ in the salinity gradient scale (Remane 1958), is much more important in explaining the depauperate character of the floristic and faunal community and the low number of fish species compared to other lakes. The observation that *A. fasciatus*, in contrast to *R. guatemalensis*, is able to live and reproduce in the lake since it was introduced may be caused by the greater salinity tolerance of its fry (max. 7 ppt, Wilkins 1982; H. Wilkins, personal communication). However, this finding does not explain why *A. fasciatus* has not colonised the lake at earlier times. A possible explanation could be that the salinity of the lake was once or periodically subjected to drastic increases in years with lower precipitation (Table 1). The long-term salinity depends on the lake water level, which is correlated with the freshwater influx. The more water the lake contains, the lower the salinity is, which is intensified by the stratification of water layers of different salinities, which is typical of saline lakes. After a large freshwater influx the overlying water lens will develop lower salinity and simultaneously expand.

Covich & Stuiver (1974) assumed that the salinity was higher before the refilling of the lake which

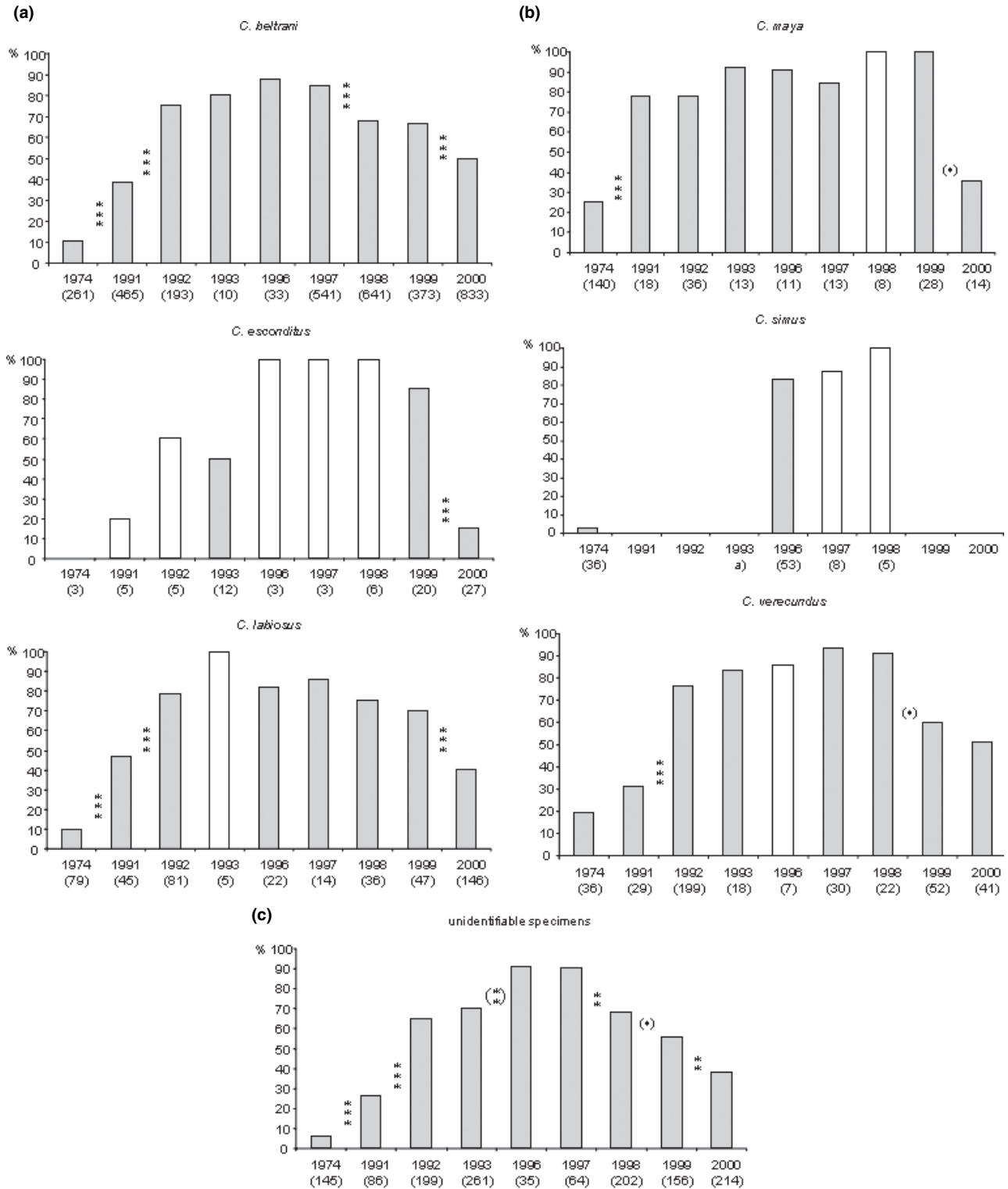


Fig. 3. Percentage of *Cyprinodon* spp. infested by *Crassiphiala* cf. *bulboglossa* between 1974 and 2000. The number of specimens studied is in brackets. White bars indicate sample size  $N < 10$ . (a) Only one *Cyprinodon simus* was caught in this year and this was infected. Asterisks indicate significance level (\* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.0001$ ), asterisks in parenthesis are not significant after Bonferroni correction.

occurred from 7750 to 7260 years BP. Aside from this and subsequent fluctuations, the lake salinity between 1300 and 1100 years BP (AD 800–1000) was the highest of the past 8000 years (Hodell et al. 1995). It

was furthermore shown that bicentennial oscillations in precipitation influenced drought frequency in the Yucatan during the past 2500 years (Hodell et al. 2001). During drier climates the lake volume was

Table 4. Percentage of *Cyprinodon* spp. infested by *Contracaecum* sp. (upper lines) and mean number of nematodes per specimen (middle lines) and sample sizes (lower lines) in the different years of the study period 1991–1999.

	1991	1992	1993	1994	1995	1996	1997	1998	1999
<i>C. beltrani</i>	9.1	23.7	20.0			71.4			77.8
	0.1	0.4	0.2			2.2			2.1
	22	38	10			21			18
<i>C. esconditus</i>		0	58.3			100	100	100	80.0
		0	0.8			3.0	5.7	2.8	2.2
		5	12			3	3	4	25
<i>C. labiosus</i>	10.0	51.7	80.0					89.7	81.8
	0.1	1.0	80.0					3.5	3.4
	10	29	5					29	33
<i>C. maya</i>		90.0	100			100	100		100
		4.1	4.2			6.4	7.4		7.4
		10	13			9	8		23
<i>C. simus</i>						39.6	100	75.0	
						0.7	5.1	2.8	
						53	8	4	
<i>C. verecundus</i>	28.6	28.6	92.3				85.7		83.9
	0.3	0.7	6.2				3.6		3.5
	7	35	12				14		31
Unidentifiable specimens	18.8	55.6	68.8			83.3		90.9	89.5
	0.2	1.3	1.3			2.4		3.7	2.6
	16	18	16			12		22	19

reduced and gypsum saturation was exceeded. Under such dry conditions, gypsum precipitates not only in shallow water near the lakeshore, as today but also throughout the entire lake (Hodell et al. 2001). Thus invasion and extinction of native Yucatan freshwater fish species, like *A. fasciatus*, in Laguna Chichancanab may have repeatedly occurred during the evolution of the flock of *Cyprinodon* species.

#### Infestation by parasites

The two parasites analysed in this study are dispersed widely in fishes of the Yucatan freshwater cenotes (Moravec et al. 1995a,b; Scholz et al. 1995). Their final hosts are fish-eating birds (e.g., kingfisher, cormorant, heron, fish eagle). I observed an increase of parasite loads in the *Cyprinodon* flock after the introduction of the cichlids (Fig. 3, Table 4). It is likely that the Laguna Chichancanab became more attractive for fish-preying birds (and humans) due to the cichlids having a greater size (max. 25 cm SL) than the *Cyprinodon* species, occurring in large numbers (own observations), and being more accessible as a nectonic species for diving birds. Consequently, a greater amount of infectious stages (eggs and enclosed larvae) may have dropped into the lake with bird faeces, as is also described for other lakes (Wisniewski 1957; Chubb 1970; Esch 1971; Zander 1998).

The first intermediate host of *C. cf. bulboglossa*, is probably the snail *P. coronatus* which is found in the cenotes of the Yucatan (Ditrich et al. 1997), and is also

most abundant in the shallow littoral of the Laguna Chichancanab, in which *Pyrgophorus* shells have been found to occur since about 8000 years ago (Covich & Stuiver 1974). Thus, cercaria, being released from the snail, would be spread throughout the habitat. The different *Cyprinodon* species show a comparable prevalence starting with a low level in 1974 to a high one, indicating a similar infestation risk for all species (Fig. 3). Only in *C. maya* was a high infestation level found as early as 1991. As one of the major food items of *C. maya* is the snail *P. coronatus* (Horstkotte & Strecker 2005) it is likely that this high prevalence might be due to its stronger exposure to the intermediate host.

The degree of infestation by the nematode *Contracaecum* sp. also shows a divergent pattern of increase in *C. maya* compared to the other species of the flock. *Cyprinodon maya* shows the highest and most rapid infection rate (Table 4). It is possible that this also can be attributed to differences in food preferences. According to Moravec et al. (1995a,b, personal communication) small crustaceans like ostracods are the intermediate hosts for this parasite. Dietary studies have shown that *C. maya* is reliant on ostracods as a major prey item besides the snail *P. coronatus* whereas the other carnivorous species feed on ostracods to a much lesser amount (Horstkotte & Strecker 2005). Therefore, this food preference may cause a higher exposure of *C. maya* to the parasite compared to the other species, leading to the high prevalence that was found.

The high infestation of the flock with parasites could be caused by its derivation from a coastal marine ancestor, which like *C. artifrons* was originally living in habitats in which these parasites do not occur (Olsen 1974). This might be supported by *G. sexradiata*, which shows only low or missing infestation in Laguna Chichancanab. It originates from Yucatan freshwater habitats and was therefore probably adapted to these parasites.

For *C. cf. bulboglossa* a decrease of infestation was observed during the study period in all members of the flock (Fig. 3). This could be explained by immunoreaction having developed after the exposure to this parasite. It was shown for *Fundulus heteroclitus* (Linnaeus) (Cyprinodontidae) that rapid changes in an MHC class II locus at the inferred antigen-binding region can be achieved within a few generations (Cohen 2002). Therefore, the decrease could reflect the development of defence mechanisms against the parasite like immunoresponses.

#### Influence of the cichlids

The only data on percentage abundance of the *Cyprinodon* species prior to the introduction of the cichlids



were published by Humphries & Miller (1981). Their data differ from those observed in this study in the period before the *Astyanax* invasion took place for *C. beltrani* (68–85% vs. 35.5–56.8%), for *C. labiosus* (2–13% vs. 0.6–25.5%) and for *C. maya* (6.5–18% vs. 0–14.6%). These differences may be explained by the fact that Humphries & Miller (1981) only included these three species, but did not consider the unidentifiable specimens called ‘hybrids’ by them, representing the second-most abundant group in this study, *C. simus*, and the three species described in later years, *C. verecundus* (Humphries 1984), *C. esconditus* (Strecker 2002) and *C. suavium* (Strecker 2005). Also the study performed by Fuselier (2001) is not comparable because only four species were analysed. However, this study shows that despite the introduction of the cichlids, the higher percentage abundance of *C. beltrani* compared to that of carnivorous forms has been maintained. As shown by Horstkotte & Strecker (2005), the cichlids and members of the species flock differ in the composition of bottom sediments that they ingest. The cichlids are able to access deeper layers of bottom sediments with their much larger and stronger mouths and also utilise other deeper areas of the lake for feeding than the members of the species flock (own observations). Therefore, food competition for bottom sediments might be reduced.

Prior to the invasion of the cichlids, *C. simus* occurred in large schools consisting of 50–1000 individuals (Humphries & Miller 1981). During the entire study period no such schools have been observed and only a few solitary specimens have been caught, with the exception of sampling site F in 1996 (Table 3). Humphries & Miller (1981) observed *C. simus* feeding on zooplankters, whereas I found a nearly complete absence of them in surveys throughout the study period. I suggest that the decrease of *C. simus* might be due to food competition with juvenile cichlids which rely on such prey according to Trewavas (1983). Sampling site F is the only place where *C. simus* was always found in comparatively high numbers until 1998 (Table 3). As shown above, this sampling site differs from all other locations because of the temporary development of a strong current during higher water levels. Based on these data it cannot be decided whether this species today is extinct or just occurs in extremely reduced numbers.

The large body sizes of *C. maya* documented prior to the cichlid invasion (Humphries & Miller 1981, H. Wilkens, personal observations in 1971) have not been detected in all the collections made subsequently. This finding might be associated with the high level of parasitism and/or the negative influence of the cichlids on the development of *Chara* vegetation due to bioturbation (feeding, bower building) and deposition of large amounts of faeces causing the death of *Chara* vegetation within large areas. As the ostracods are

living in the thalli of these plants (Horstkotte & Strecker 2005), this might have diminished one of the major food source of this species. Such decline of ostracods resulting from environmental changes was also shown for Lake Tanganyika (Cohen et al. 1993).

#### Influence of *A. fasciatus*

After *A. fasciatus* invaded the whole lake system the relative frequency of all carnivorous members of the flock decreased, whereas that of *C. beltrani* increased (Table 2). This is probably not due to food competition, because there is only minor overlap in the use of food items between *A. fasciatus* and the members of the species flock (Horstkotte & Strecker 2005). Furthermore, the number of *Cyprinodon* spp. and *G. sexradiata* per first catch was drastically lower since 1997 indicating a reduction of absolute numbers of specimens in Laguna Chichancanab (Fig. 2). The number of smaller *Cyprinodon* spp. showed an even stronger decrease. This strong decrease of specimens is probably due to the fact that *A. fasciatus* is preying on fish fry and juveniles, previously documented in *A. fasciatus* by Schmitter-Soto (1998). In contrast to *Cyprinodon* spp., *G. sexradiata* and *A. fasciatus* use similar food resources (Horstkotte & Strecker 2005) and, therefore, the pronounced decrease in *G. sexradiata* might be caused by both food competition and predation on fry.

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