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COMPETITION IN THREE CYPRINODONT FISH SPECIES IN THE NETHERLANDS ANTILLES

by

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During a stay in the Netherlands Antilles from 1960 to 1965 the fauna of supersaline waters was studied in relation to the fauna in the sea and in brackish waters. Among the fishes the three most common species in the inland waters are *Cyprinodon dearborni* Meek, *Poecilia* (*Mollienesia*) *sphenops* Valenciennes and *Rivulus marmoratus* Poey, all belonging to the Cyprinodontidae. Although there are small differences in their distribution patterns, the three species may be caught in the same haul of a dipnet. In 48 locations (nrs 1–48 on the maps of Aruba, Curaçao and Bonaire, and in Table 2) one or more waters were investigated. Among these 17 were in open connection with the sea (Table 2).

Various details concerning the localities may be found in WAGENAAR HUMMELINCK's locality descriptions (1933, 1940, 1953).

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In the mangroves and the lagoons open to the sea the three cyprinodont species were often caught together, but in completely landlocked bays, lagoons or ponds as a rule only one of the three species was present. As many as 49 out of 51 landlocked waters held only one species: 23 were inhabited by *Cyprinodon*, 18 by *Poecilia*, and 8 by *Rivulus*. Most striking in this respect were the six very uniform small lagoons of Rif (nr 19), three of which containing *Cyprinodon*, two others *Rivulus* only, and one *Poecilia* only. A similar phenomenon was found in the nine uniform seawater pools (nr. 27) between

TABLE 2

LOCATIONS INVESTIGATED

(* locations *not* in open connection with the sea)

Nr.	iso-lated *	Location	fresh 0–5‰	brack-ish 5–35‰	sea 35–38‰	super-saline 38–70‰	*Cypr.*	*Poec.*	*Riv.*
		ARUBA							
1	*	Tanki Canashitu	+					+	
2	*	Rooi Bringamosa		+				+	
3	*	Rooi San Fuego	+					+	
4		Spaans Lagoen		+	+		+	+	+
5		Rif			+		+	+	
6	*	Fontein	+					+	
7	*	Rooi Prins	+					+	
8	*	Rooi Andicuri	+					+	
		CURAÇAO							
9	*	Dam Noordpunt	+					+	
10	*	Dam Westpunt	+					+	
11		Sta Martabaai		+	+	+	+	+	+
12		Lagoon of San Juan			+		+	+	+
12	*	Saliña of San Juan				+	+		
13	*	San Juanbaai				+	+		
14	*	Cas Abau				+		+	
15	*	Saliña Sint Marie	+	+		+	+		+
16	*	Saliña Sint Michiel		+	+	+		+	
17	*	Slangenbaai			+			+	
18		Piscadera Inner Bay		+	+	+	+	+	+
19		Rifwater		+	+	+	+	+	+
19	*	3 lagoons of Rif			+		+		
19	*	2 lagoons of Rif			+				+
19	*	1 lagoon of Rif			+			+	
20		Waaigat		+	+		+	+	
21	*	Ansingh-plas	+					+	
21		Rooi Asphaltmeer	+				+	+	
22	*	Lagoon Jan Thiel				+	+		
23	*	2 Spaanse Water salt ponds				+	+		
24		Fuikbaai			+		+	+	+
24		Lagoon Fuik			+		+	+	
25	*	Saliña Fuik				+	+		
26	*	Lagun Blancu			+		+		
27	*	4 seawater pools			+		+		
27	*	3 seawater pools			+			+	
27	*	2 seawater pools			+				+

Nr.	iso-lated *	Location	fresh 0–5‰	brack-ish 5–35‰	sea 35–38‰	super-saline 38–70‰	*Cypr.*	*Poec.*	*Riv.*
28		Awa Blancu			+		+	+	
29		Awa di Oostpunt			+		+	+	+
30		St. Jorisbaai			+		+	+	
31	*	Hato	+					+	
32		Plaja Grandi			+		+	+	+
33		Boca Bartol			+		+	+	
		BONAIRE							
34	*	Saliña Bartol			+	+	+		
35	*	Playa Funchi				+	+		
36	*	Slagbaai			+	+	+	+	
37	*	Saliña Tam				+	+		
38	*	Lagun Goto				+	+		
39	*	Saliña Klein Bonaire				+	+		
40	*	Saliña Martinus		+	+	+	+		
41	*	Pos Caraña		+					+
42	*	Pos Jatu largu		+					+
43	*	Pekelmeer				+	+		
44	*	2 Lansbergputten	+						+
45	*	Saliña Plenchi, 2 pools			+	+	+		
46		Lac			+	+	+	+	+
47		Lagun			+	+	+	+	+
48	*	Fontein	+					+	

Lagun Blancu and Awa Blancu: in four of them only *Cyprinodon* was present, in three only *Poecilia*, and in two *Rivulus*.

Exceptionally two cyprinodont species were found together in isolated waters. WAGENAAR HUMMELINCK (1933, p. 321), for instance, mentions the co-occurrence of *Rivulus* and *Cyprinodon* in one of the Lansbergputten (nr 44), although here, in 1963, only *Rivulus* was found by us. In one landlocked bay (Lagun Goto, nr 38) *Cyprinodon* and *Poecilia* were found, and in another (Saliña Sint Marie, nr 15) *Cyprinodon* and *Rivulus*. On the other hand, in 17 bays or lagoons with an open connection with the sea two or all three species were found together (Table 2).

The aim of our investigations was to trace the factors that play a role in the interspecific competition, which apparently is present. To that purpose the biology of the three cyprinodont species was studied, with an emphasis on the ecological relations. The influence of the following factors received special attention: salinity, temperature and desiccation of the environment, and also the aspects concerning propagation, growth (including feeding habits and food competition), and mortality caused by parasitism, by cannibalism and by interspecific predation.

Cyprinodon dearborni Meek

Cyprinodon is often seen in shoals of some dozens or hundreds of specimens in very shallow water, less than 60 cm deep, especially where the bottom is covered by cyanophyceans.

The salinity range of this species is from zero to 130‰; however, the species is not common in water of low salinity. During our investigations it was found in brackish or fresh water only where this water was in contact with water of higher salinity, e.g. in Saliña Sint Marie (nr 15). *Cyprinodon* is most often found in seawater lagoons and in salines with a salinity up to 90‰. They enter occasionally into brines of 130‰ but their stay there seems to be of limited duration. Salinities of over 150‰ seem to be lethal.

In preference tests animals kept in fresh water preferred fresh water, the fishes kept in sea water preferred sea water, and those from supersaline water (70‰ salinity) preferred also their own environment. When transferred to water of different salinity it took at least one day before the new environment was preferred. *Inland* water of any salinity is preferred when tested against pure fresh water or sea water unless the inland water is filtered through activated charcoal. This preference is due to an organic compound present in many types of inland water (KRISTENSEN, in the press).

The temperature range in the Neth. Antilles is so small (26–35°C) that temperature differences are of no importance in respect to the presence of *Cyprinodon*. Now and then salinity *layers* may cause a considerable rise of temperature in the bottom layer (to values of 50–60°C), but in such cases the fish proved to be able to find its way to the cooler layers or to other, unstratified parts of the salines.

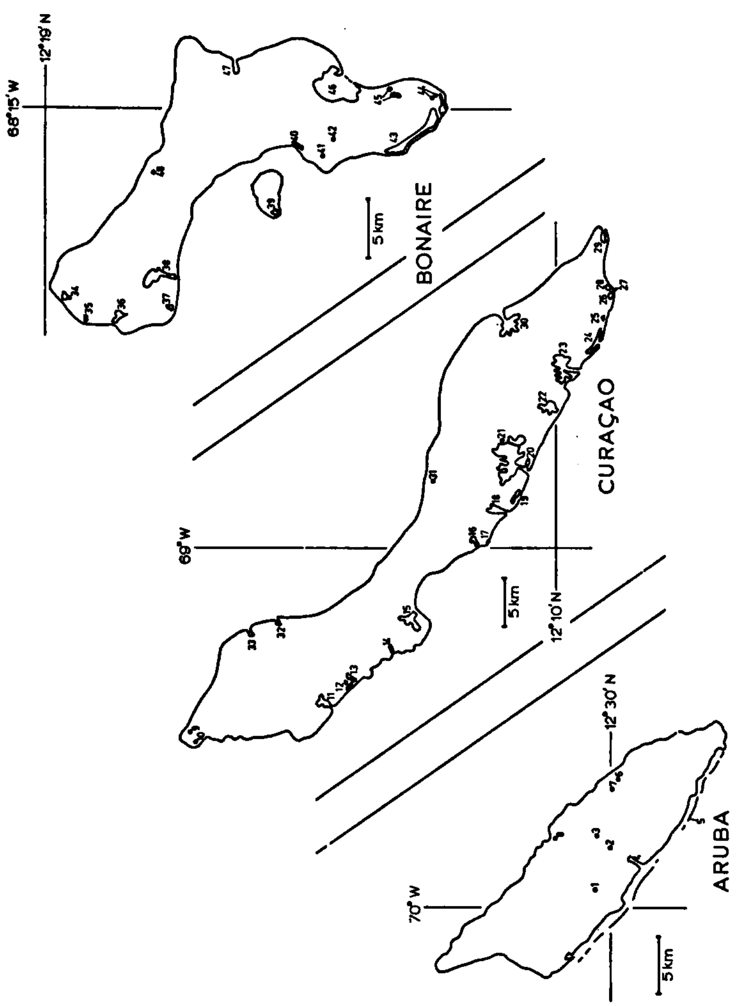

Fig. 160. Sketch map showing the islands of Aruba, Curaçao and Bonaire with collecting locations; see Table 2.

D e s i c c a t i o n of the environment is an important factor, causing mass mortality, especially in shallow salines, either by an increase of salinity to values over 150‰, or simply by complete evaporation of the water. In evaporating pools many species die at a salinity of about 50‰, because of O_2 depletion in the water. *Cyprinodon*, however, is able to avoid suffocation by going to shallow parts of a few cms of depth where the O_2 amount rarely decreases to values of less than approximately 75% saturation. In fact, the lowest value ever measured was in the landlocked San Juanbaai (nr 13) where mass mortality of bivalves and fish occurred, in 1961, as a result of a salinity increase to 52‰. In the bay the oxygen content went down to zero, but along the border, in one cm of water, where *Cyprinodon* was found alive, the oxygen content proved to be 77% (Winkler titration).

Although *Cyprinodon* cannot stand complete evaporation of the water, it will survive for some days hidden under pebbles or between algae if only a film of water is left. The eggs will hatch even after a stay of five days in wet algae or shingle. *Cyprinodon* lacks however, the ability of some other Cyprinodonts to survive a longer period, contrary to e.g. the South American *Cynolebias* species and the African *Notobranchius* species of which the eggs can stand – and even need – a stay of some months out of the water (vide f.i. KOSSWIG, 1963, p. 180).

Propagation. *Cyprinodon* is an oviparous species. Spawning takes place the whole year around. The males, in steel-blue nuptial colours, with orange throat and breast, defend territories of a small size: mostly 50 × 50 cm, but if the population is very dense the areas may be reduced to only 15 × 15 cm. When a mature female enters a territory she is at first attacked by threatening display of the male; but as she does not show any counter-attack and stays in the male's territory, she induces him to quiver on the spot where the clump of some scores of eggs is to be laid. The spawning substratum mostly consists of blue bottom algae or green filamentous algae, but sometimes also pebbles or mud. After spawning the female swims away and the male defends the egg cluster against intruders. More than one cluster, originating from different females, may be found in the same "nest". After hatching the young must find their way without paternal care. The fry keep to the bottom, especially among pebbles and between algae.

Growth. In three months the young have reached maturity at a size of 2.3 cm. From then, the rate of size increase is slower. After half a year they have reached a size of 3 cm. The maximum size is about 4.8 cm. Stomach contents showed that unicellular blue algae form their main diet (see Table 3). In the fresh water of Rooi Asphaltmeer (nr 21) debris of plants and epifauna, and small copepods were also found in their stomachs, and in seawater lagoons also protozoans and copepod nauplii. In supersaline bays *Artemia salina*, especially the nauplii, are often numerous; *Ephydra* larvae were consumed only occasionally here.

Evidence of intraspecific food competition was never observed. Even in extremely dense populations as, for instance, in the locked, shallow inlet to Pekelmeer (nr 43) all individuals had their stomachs filled with unicellular cyanophyceans; the density of nesting males was 45 per sq m, the densest nesting population ever found by us. It was impossible to count the numerous females and immature fish. Nevertheless, growth was not stunted, as maturation took place at the normal length of 2.3 cm. The individual weight in this dense population was also normal: the dry weight of the 34 mm group proved to be 194 mg, a figure that may be found in any *Cyprinodon* population.

Mortality by true cannibalism seems to be nil. Fish fry was never found in the stomachs of *Cyprinodon*. Fish eggs, however, were often present, especially in fish from densely populated landlocked lagoons where *Cyprinodon* was the only fish species present. It is impossible to say whether the population is kept in check by egg predation. Mass attacks by parasites were never observed; only occasionally some nematods, trematods and parasitic copepods were seen, but never in lethal quantities.

Predation, however, seems to be considerable. In the sea, or in bays and lagoons in open connection with the sea, many fish species prey upon adult and juvenile *Cyprinodon*; attacks on adult ones by young barracudas, snappers (Lutianidae), and groupers (Epinephelidae) were observed by us, but there may be quite a lot of other predatory fish species. Juvenile *Cyprinodon* is eaten by even more species, of which *Gobius soporator* and *Poecilia sphenops* were actually observed in the act. In landlocked waters predation by fish will be an exception as *Cyprinodon* is rarely accompanied by other fish species. Here, however, predation by birds is of some importance. Three groups of birds may be mentioned: terns, herons and flamingoes, the last ones however only incidentally (ROOTH, 1965, p. 52). Especially flamingoes of some months old were seen by us hunting *Cyprinodon*, in Pekelmeer (nr 43).

Poecilia sphenops Valenciennes

In the islands Curaçao, Aruba and Bonaire this species is represented by the subspecies *vandepolli* (van Lidth de Jeude). It can be discussed briefly as a special paper has been devoted to this species by FELTKAMP & KRISTENSEN (1969).

Poecilia is often found in water with green filamentous algae, both in very shallow and in deeper water but, in the last case, the fish keeps to the surface where they form shoals of rather small size (some dozens, in most cases). In landlocked small waters the population may be very dense.

The salinity range of *Poecilia* is from zero to 135‰. Its preference for *inland* water, whether fresh or supersaline, is not based on salinity but on an organic compound that is present in many landlocked waters (KRISTENSEN, in the press).

Temperature oscillations do not affect *Poecilia* in its distribution as the temperature range in the Netherlands Antilles is well within the tolerance limits of the species.

Desiccation seems to be an important factor of mass mortality, especially as the species tries to invade pools formed by torrential rains. Afterwards, the pools often become isolated so that the fish population cannot evacuate when the water evaporates.

Poecilia also inhabits supersaline water if there is a salinity range down to 40‰ or less, so that the population can move to parts of lower salinity if necessary. It was only once that mass mortality because of evaporation of supersaline water was observed. That was in 1961 in the saltpans of Cas Abau (nr 14) where a dense population thrived in shallow water with a rather luxurious growth of

Ruppia maritima. As soon as the salinity increased to more than 70‰ *Ruppia* succumbed causing O_2 depletion by decaying. Although the *Poecilia* population crowded near the seepages from the sea the population was almost completely destroyed by suffocation.

Propagation. *Poecilia* is ovoviviparous. The males insert their gonopodium into the genital opening of the females so that the eggs are fertilized in the ovarium cavity. The eggs hatch about 30 days after fertilization. Small females drop litters of only 10, the full-grown ones have between 100 and 200 young per litter. One copulation may result in 8 or even more successive litters because part of the inserted sperm is stored in folds of the ovarium wall, as is the case in all ovoviviparous cyprinodonts. Some, but not all females seem to possess some *testal* tissues too in their ovaria which enable them to produce small litters (of females only) without ever having been in contact with males. This procedure was also observed in other ovoviviparous cyprinodont species (vide, e.g., SPURWAY, 1956, p. 126).

After hatching, the young sink to the bottom and, after a few seconds, they swim to the surface and try to find cover in algae, rootlets etc.

Growth. In contrast to *Cyprinodon*, population differences in growth rate are often found. Sea water seems to favour quick growth, fresh water causes reduced growth. Moreover, crowding also causes stunted growth even if plenty of food is available.

Poecilia is omnivorous (Table 3). Most important quantitatively is the epigrowth on the substratum: the fish are constantly pecking and nibbling, and their stomach contents show a variety of organic debris, small algae, protozoans, fish eggs, *Ephydra* larvae, and other more or less sessile organisms. Besides, they also feed on plankton: copepods, mysids, small fish and – most attractive of all – *Artemia salina*. Insects are only taken occasionally.

Mortality caused by diseases has been observed in brackish and fresh water only. Trematod infections of the *Diplostomum*-type blind the fish and may cause almost complete extermination of an isolated population.

TABLE 3

STOMACH CONTENTS in per cent of presence in *filled* stomachs

(C = *Cyprinodon*, P = *Poecilia*, R = *Rivulus*)

Habitat	Fresh			Brackish			Sea			Supersaline			Brine		
Salinity	0–5‰			5–35‰			35–38‰			38–70‰			70–135‰		
Fish species	C	P	R	C	P	R	C	P	R	C	P	R	C	P	R
Numbers	2	50	4	6	5	0	43	22	26	52	31	2	50	35	0
Cyanophyceae	50	20		50	20		100	18		100	13		88		
Chlorophyceae		24		33	20		9								
Plant debris		100		50	100		26	91		4	32				
Epigrowth		54			80			55			56			9	
Gastropods		22	25				16	50	38						
Artemia										19	32		100	100	
Daphnids		16	25												
Copepods	50	20	50	17	40			32	50		13	50			
Mysids				17	20			27	19						
Ephydra larvae													4	11	
Dipters		14	50		20			18	12		13			6	
Formicids		8	25		20										
Fish eggs							2			12	7		8		
Fish hatchlings		16	25					18	15		7				
Fish juveniles									23			50			

Cannibalism is another important factor controlling population density. Newly born fry are heavily preyed upon by the adults. In locations without filamentous algae or other hiding places near the surface almost no neonati survive the very first day. The young are not safe until they have reached a length of about 13 mm – that is after two weeks.

In the seawater lagoons and in the mangroves *Poecilia* will be preyed upon by the same species as mentioned for *Cyprinodon*, but no pertinent observations were made. However, *Poecilia* is much more alert and is a fast swimmer so they must have better chances of escape than *Cyprinodon*.

Rivulus marmoratus Poey

This species is mostly found in very shallow water. It shows no schooling behaviour but it keeps hidden under pebbles, in and under filamentous algae or in mangrove rootlets.

The *salinity* range of *Rivulus* is from completely fresh water to 70‰. The species is rarely found above 40‰ and is never found in brines of 80‰ like the other two species.

The *temperature* does not play a role in the distribution of the species as it can tolerate a range from 18°C to 36°C.

Desiccation of the habitat will play a less important role than in the other species. *Rivulus* is never seen in briny pools where *Cyprinodon* is exterminated by desiccation almost regularly, and *Rivulus* is never seen in temporary rain pools which *Poecilia* is eager to enter. *Rivulus* was found by us in clusters of algae only wetted by a seepage (in Saliña Sint Marie, nr 15). When their habitat dries up they are able to find their way back to the water by jumping, crawling and wriggling through wet pebbles and mud, covering distances of dozens of metres. The eggs of this species will not lose their viability by a stay of a week or more in wet algae.

Because of their ability to inhabit very shallow water they are never threatened by O_2 depletion as is the case with species inhabiting deeper water.

Propagation. *Rivulus* is an oviparous species. In other *Rivulus* species only the females have a clear ocellus in the caudal peduncle, but in *Rivulus marmoratus* the males may sometimes also have an ocellus. The males show bright orange red flanks, the females are more plainly coloured. The courtship is similar to that in other *Rivulus* species as described, for instance, for *R. urophthalmus* by VAN DEN NIEUWENHUIZEN (1963): male and female swim parallel, at close distance, in the direction of some firm substratum (roots, stones, plants or filamentous algae). Then, the female attaches while quivering a small amount (e.g. 3–8) eggs which are simultaneously fertilized by the male. After a quarter of an hour a second set of eggs are deposited – but the male may very well be some other individual (personal observations). The females are no true females, but are hermaphrodites (HARRINGTON, 1961). If there are no males the ovulated eggs are internally fertilized by the sperm produced by the male part of the ovariotestis of the "females". These eggs are deposited in exactly the same way as when a male is present. The newly spawned eggs show an embryo development in various stages of progress (HARRINGTON, 1963), contrary to the eggs spawned in presence of a male: those eggs do not show any development at the moment of spawning (personal observation).

During the years 1960–1965 that I was able to investigate the *Rivulus* population in the Antilles it was only in 1960 that I found males – very large ones. HARRINGTON (1967) showed that at a temperature of 25°C all young produced are hermaphrodites, but if hatched at lower temperatures (20°C) most of the young (72%) are males. Temperatures in the Neth. Ant. never reach values as low as 20°C, but under experimental conditions I found that the Antillean *Rivulus* hermaphrodites produce males, up to 40%, at temperatures between 20 and 24°C. This temperature range is lower than what is normally found in the Antilles. Only the autumn rains may temporarily lower the water temperature in small pools to 24–25°C. It is not unlikely that the males I found in 1960 were born during autumn rains in 1959 or 1958. The fact that HARRINGTON's *Rivulus* produced males at 20°C, may be due to the fact that HARRINGTON's stock originated from a cooler area, i.e. Florida. Temperature "races" among poikilotherm species are well-known (RUNNSTRÖM, 1928). According to HOEDEMAN (1958, p. 117–120) the Antillean specimens show also *morphological* differences which even induced him to put them into a separate subspecies (*bonairensis*). In *Rivulus* both males and hermaphrodites mature at a size of 35 mm, at the age of three months old. They continue growing for a whole year, reaching a length of 5 cm to 6 cm, the males being one cm greater than the females.

Rivulus is a carnivorous species, taking everything that moves around and is not too big: worms, crustacea, insects, small fish etc. (Table 3). Under experimental conditions it was observed that growth is stunted as soon as no live food is constantly available. Especially in small pools food competition, therefore, may influence the growth rate, but no field observations are available.

Mortality by parasitism was not observed. Cannibalism, however, is a very important factor. At a few weeks old they already start to consume their younger brothers. When they grow older the larger individuals bite off the tail tips of smaller individuals. This aquarium observation is confirmed by the fact that in small pools inhabited by *Rivulus* many specimens show fin damage and other damage, often of a severe nature. They swallow specimens of almost half their size. The adults often devour their own eggs immediately after the spawning act. Of course, many other species will also eat the eggs of *Rivulus*.

Rivulus juveniles and adults will hardly be preyed upon by other fish species as they keep themselves hidden in or near filamentous algae, rootlets, pebbles etc. Only once actual predation was observed; that was in a brackish water pit in Plantation Lima (nr 41), where *Rivulus* was found together with *Eleotris pisonis*. *Eleotris* stomachs proved to contain some young *Rivulus*.

COMPETITION BETWEEN THE THREE SPECIES

The three cyprinodonts seem to inhabit almost the same niche. This explains the fact that, in isolated habitats, as a rule only one of them is present: an example of survival of the fittest in interspecific competition.

Which of the species will survive must depend on small differences in the ecological demands of each species. Some of these differences presented in Table 4 may be summarized here:

If *no shelter* (plants, algae) is present *Cyprinodon* is to be expected.

If the water is *very shallow* (5 cm) *Poecilia* is not to be expected.

In *brackish or fresh water Poecilia* and *Rivulus* are more often found, in *supersaline* and *brine Cyprinodon* is more frequently found.

If periods of *low* O_2 *values* occur *Poecilia* will have a most difficult time.

Temperatures are of no influence at all.

Crowding hardly seems to affect *Cyprinodon*, but it does affect *Poecilia* and *Rivulus*.

Cyprinodon's main source of food (unicellular blue-greens) seems to be almost inexhaustable.

Table 4

Ecological differences between the three cyprinodont species

Ecological Data	*Cyprinodon*	*Poecilia*	*Rivulus*
open water or sheltered	open water	near plants or algae	in or under plants etc.
water depth	3–60 cm	10–200 cm	1–100 cm
preferred zone	near the bottom	near the surface	no preference
extreme salinity range	0–130‰	0–135‰	0–70‰
normal salinity range	36–90‰	0–70‰	0–40‰
temp. tolerance	16–36°C	16–36°C	18–36°C
if water dries up	burried in substratum survival 1 or more days	struggling to death in (wet) substratum	survival in wet algae for 1 or more days
suffocation by O_2 depletion	never observed	only occasionally	never observed
sexes	♂ + ♀	♂ + ♀ (+ ⚥)	(♂ +) ⚥
propagation	oviparous	ovoviviparous	oviparous
food habits	omnivorous	omnivorous	carnivorous
main food	cyanophyceans	plant epigrowth	plankton
cannibalism	only its eggs	hatchlings eaten	small individuals eaten
interspecific predation	none	eats eggs & fry	eats eggs & juveniles
influence lack of food	never observed	stunted growth	starvation observed
mass parasitism	never observed	in fresh water *Diplostomum*	never observed

Poecilia mainly feeds on epigrowth on any substratum, which may become scarce when the fish population grows denser.
Rivulus will starve if no sufficient live food is available.
Cannibalism is hardly of importance in *Cyprinodon*; only the eggs are devoured if the population is very dense. *Poecilia* devoures its neonati almost completely if no shelter is present. *Rivulus* hardly ever eats its own eggs and fry, but as the young grow up they are more often attacked by the adults.
Interspecific predation: *Cyprinodon* does not harm the other two; *Poecilia* takes the eggs and the fry of both the others, and *Rivulus* takes the eggs, the fry and part of the juveniles.
Predation by other fish species or by birds seems to be of little influence.
Parasitism can be of importance with respect to *Poecilia*, but only in exceptional cases.

To check some of these conclusions derived from field observations some simple experiments were carried out.

1) Lack of shelter was tested in an outdoor tank of $3 \times 1 \times 1$ m^3 which was populated by 10 adult *Cyprinodon* (5 males and 5 females), 8 *Poecilia* (3 males and 5 females) and 5 *Rivulus* hermaphrodites. No algae were present. The bottom was covered by coral sand. The fish was fed daily with dogfood (Ken L Ration) and catfood (Kittekat). After two months no offspring of any of the three species was seen although *Cyprinodon* and *Rivulus* were spawning constantly and the *Poecilia* females regularly produced litters. This result may illustrate that, when all three species are confined together in a small area without shelter, no young are to be expected, at least not as long as the adults of all three species are still alive.

In a second experiment green algae (mostly *Enteromorpha* sp.) were introduced into the tank. Two weeks later, already, young *Poecilia* and *Rivulus* were seen moving around in the algae. After two months the tank was emptied. 164 *Poecilia* were found, 88 *Rivulus*, and only 23 *Cyprinodon* youngsters. Apparently, the shelter provided by the algae was more efficient to *Poecilia* and *Rivulus* than to *Cyprinodon*.

2) In order to test the interaction of *Cyprinodon* and *Poecilia* more in detail a set of six aquaria of 24 l was used. Three of the aquaria had no plant growth, the other three had a luxurious algal growth. The bottom was covered by coral lime; 2/3 of the sea water was renewed every week. The fish were fed on dogfood and catfood. The population of both sets, with and without algae was:
tank 1: *Cyprinodon*, 4 males and 4 females
tank 2: *Poecilia*, 2 males and 4 pregnant females
tank 3: *Cyprinodon* (2 couples) and *Poecilia* (2 couples).

After 2½ months both tanks with only *Cyprinodon* had a considerable population increase: in the tank without algae 56, and in the tank with algae 73 youngsters.

In the *Poecilia* tank *without* algae the females together had produced 11 litters, but none of the young had survived, all being consumed by the adults. In the *Poecilia* tank *with* algae 10 litters had been produced, and here 6 juveniles were present – that is a survival of about 1%.

In the tank with mixed population *without* algae *Cyprinodon* had spawned regularly, and *Poecilia* had produced 6 litters, but no young were present. In the tank *with* algae 5 *Poecilia* young had survived, but no *Cyprinodon*.

These few experiments illustrate the picture we got from observation in nature: *Cyprinodon* is able to propagate whether shelter is available or not. *Poecilia* is only able to multiply if shelter is present. If both species are together *Poecilia* will prevent *Cyprinodon* growing up. In nature, only one landlocked location was found where both species lived together; that was Slagbaai (nr 36). Here, however, were two different habitats: a large shallow part with the bottom covered by cyanophyceans, a favoured spot for *Cyprinodon*; the second habitat was a channel, the old inlet of sea water, with a rich growth of filamentous green algae – a typical *Poecilia* habitat. Thus, both species had their own favoured centre, although in most parts of the inhabited area they were found together. Another factor enabling the co-occurrence of both species could be the flow of *Artemia* from the more briny parts to the less saline parts – but this flow was not present every year (HULSCHER-EMEIS & KRISTENSEN, in preparation).

3) The interaction between *Poecilia* and *Rivulus* was studied in aquaria of 10 l, in Holland from 1965 to 1968. Although hundreds of young fish of both species were born, none survived if both species were kept together. In a larger tank, of 150 l, some young of both species survived if plant growth was very dense; survival was much less than 1%.

In the second set of experiments the results were given when *Poecilia* was kept without other species. The results, if *Rivulus* was kept apart, were the following. In an aquarium without plants or algae *Rivulus* young will grow up only if live plankton is continuously available. The adults, however, will start to eat their young as soon as no live food is left. Survival of the young is much higher if plants or algae are present. The denser the plant growth the more young survive.

However, when the youngsters reach a length of 25 mm they become rather aggressive towards each other. Only a few survived if the juvenile population was denser than one per liter of water: mostly only one per 10 liter tank survived. If there was a constant abundance of live plankton some more survived: 3 to 8 per 10 liter aquarium. If the young ones were separated from the beginning mortality was almost nil.

4) Interaction between *Cyprinodon* and *Rivulus* was not studied. In isolated locations they were found together only once, in Saliña Sint Marie (nr 15). There, the population centre of *Rivulus* was a freshwater seepage with green algae, and that of *Cyprinodon* was the shallow supersaline area with cyanophyceans. Although occasionally the fish visited each other's territories, both species kept themselves rather apart.

5) In order to trace the competition between the three species under natural circumstances an experiment was carried out in an old saltpan of about 800 sq m and a depth of 10–30 cm. This abandoned saltpan was situated in the western tip

of Rifwater (nr 19), near the village of Charo. The bottom consisted of black mud and coral limestone pebbles. No plants were present except for some bottom cyanophyceans. During the three months of observation the salinity varied from 51 to 62‰. The saltpan had a small population of *Artemia salina*, and no fish.

Here, 48 adult *Cyprinodon*, 134 adult *Poecilia* and 53 *Rivulus* hermaphrodites were introduced. The *Artemia* was exterminated already within a few days; after four days none could be found. After two months the *Cyprinodon* population looked healthy, but *Poecilia* and *Rivulus* were skinny. Five specimens of each species were caught and were measured and weighed. *Cyprinodon* had a weight of 96% of normal weight, *Poecilia* 80% and *Rivulus* only 72%. No young ones were found. In the course of the third month the number of *Poecilia* and *Rivulus* decreased to less than half the starting number (although no exact countings could be made). In the third month the water quantity decreased because of a general lowering of the waterlevel in the area, and the area covered by water shrank to 40 sq m. At that time all *Rivulus* had disappeared, approximately 30 *Poecilia* were left, and 45 *Cyprinodon* were counted. Part of them could be caught. The fresh weight of 15 *Poecilia* proved to be 69% of the normal weight when length is considered, and 15 *Cyprinodon* had an almost normal weight (96%). No young were seen. At the end of the fourth month only *Cyprinodon* was found, among which some hundreds of juveniles.

This illustrates the view that in shallow lagoons without filamentous algae, *Rivulus* and *Poecilia* will starve by lack of food whilst *Cyprinodon* still thrives. Whether the mortality among *Rivulus* and *Poecilia* was caused by starvation or by other factors, in combination or not, cannot be stated, as direct observations are lacking.

From the experiments and observations mentioned the following picture of the main factors involving competition may be constructed.

Cyprinodon has the advantage of being capable to live solely on unicellular blue-green algae if no other food is present. The species needs no shelter for its fry.

Poecilia has the advantage of being viviparous, producing rather big young, and *Poecilia* is capable of preying upon the eggs and the tiny fry of both other species. Under adverse conditions it consumes its own young so that the population is kept down until conditions have improved. Moreover, it is most strongly attracted by floodings from torrential rains. It struggles against the current and will often manage to reach almost isolated rain pools where the other two cyprinodonts never come (KRISTENSEN, in the press).

The predatory and cannibalistic behaviour of *Rivulus* is still more outspoken than in *Poecilia*. In a very small body of water one hermaphrodite may be present for successive generations as the offspring will only survive when the adult gets senile. Among the offspring only one will survive, as aquarium experiments have shown. Inbreeding may go on for several generations. In aquarium experiments it could be demonstrated that at least five generations of hermaphroditic propagation may occur before normal sexual propagation takes place. When temperatures were exceptionally low, as has been mentioned the hermaphrodites produced two types of young, hermaphrodites and males. These males were *true* males as could be seen from the histological picture of the gonads showing testis tissue only. The "females" caught in Curaçao as well as the ones raised in the laboratory all proved to be hermaphrodites. (Our observations have been mentioned by HARRINGTON, 1968, p. 459). The males proved to be able to fertilize eggs of hermaphrodites of other strains. This, of course, prevents thorough inbreeding of the *Rivulus* populations.

Cyprinodon, Poecilia and *Rivulus* all have their densest populations in inland waters but they have also small but presumably relatively stable populations in the sea or in water that is in open connection with the sea. Only in landlocked waters does competition become so important that as a rule only one of the three species survives.

When comparing the cyprinodont fauna of the Antillean islands with that of the north coast of South America the latter is much richer in species: the mainland has many *Poecilia* species (ROSEN & BAILEY, 1963) and several *Rivulus* species (HOEDEMAN, 1959). As far as is known *Poecilia sphenops* and *Rivulus marmoratus* are the most euryplastic species in their respective genera, as they possess, for instance, an extreme salinity tolerance and an extreme potential in maintaining small populations (even consisting of one individual). Such characteristics make the species well adapted to the environmental conditions that are found in small islands like the Lesser Antilles.

SUMMARY

Cyprinodon dearborni, Poecilia sphenops and *Rivulus marmoratus* seem to fill almost the same niche. In most of the *landlocked* bays, lagoons or pools the three species were not found together. In only two landlocked locations two of the species were found together.

In the locations with an open connection with the sea all three species, or at least two were present.

In landlocked waters interspecific competition seems to play an important role as the niches of the three species overlap to a large extent.

Environmental factors of importance appeared to be:

1) Plant or algal growth is required by *Poecilia* and *Rivulus*.
2) Low salinities seem to be of advantage to *Poecilia* and *Rivulus*, supersaline environments seem to favour *Cyprinodon*.
3) Oxygen depletion may threaten *Poecilia* more than the others.
4) *Cyprinodon* is able to take any food of suitable size but its main food source is formed by unicellular cyanophyceans, a source that is almost inexhaustible. *Poecilia*, although omnivorous, is more particular in its food choice; *Rivulus* is carnivorous and its population depends on the availability of live food.
5) *Cyprinodon* does not prey upon the other two species. *Poecilia* preys upon the eggs and fry of the others, and *Rivulus* also takes juveniles.
6) *Cyprinodon* is hardly ever cannibalistic; it may only consume some of its eggs. Cannibalism in *Poecilia* and *Rivulus* is of great importance. In adverse conditions, it keeps the populations small, which seems to be an advantage in small lagoons or pools.
7) Ovoviviparity and hermaphroditism in *Poecilia* and *Rivulus* may have a special advantage in maintaining very small populations.
8) In isolated waters, predation by other fish species or by birds seem to be of little importance.
9) Mass mortality because of parasitism is an exception.
10) All three species are very able to flee from adverse conditions. If a population is destroyed repopulation will take place from the sea where small, but stable populations are present.
11) Many of the characteristics mentioned are of special advantage in island environments.

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