Surbrook, C. C. Sheppard, J. S. Boyd, H. C. Zindel, C. J. Flegal, *Proc. Int. Symp. Livestock Wastes* (American Society of Agricultural Engineers, St. Joseph, Mo., 1971), p. 193.
35. N. B. Andrews, *The Response of Crops and Soils to Fertilizers and Manures* (Mississippi State University, State College, ed. 2, 1954); R. I. Cook, *Soil Management for Conservation and Production* (Wiley, New York, 1962), pp. 46–61; S. L. Tisdale and W. L. Nelson, *Soil Fertility and Fertilizers* (Macmillan, New York, 1966).
36. R. E. Linton, *Cornell Ext. Bull.* No. 1195 (1968).
37. J. R. Miner, *Iowa Agr. Exp. Sta. Spec. Rep.* No. 67 (1971).
38. U.S. Department of Agriculture, *Crop Production* (Crop Report Board, Washington, D.C., 1970).
39. President's Science Advisory Committee, *Report of the Environmental Pollution Panel* (White House, Washington, D.C., 1965), p. 172.
40. C. J. Willard *Ohio Agr. Exp. Sta. Bull.* No. 405 (1927).
41. H. D. Tate and O. S. Bare, *Nebr. Agr. Exp. Sta. Bull.* No. 381 (1946); pp. 1–12; R. E. Hill, E. Hixon, M. H. Muma, *J. Econ. Entomol.* **41**, 392 (1948); C. L. Metcalf, W. P. Flint, R. L. Metcalf, *Destructive and Useful Insects* (McGraw-Hill, New York, 1962), p. 510; E. E. Ortman and P. J. Fitzgerald, *Proc. Ann. Hybrid Corn Ind. Res. Conf.* **19**, 38 (1964); R. E. Robinson, *Agron. J.* **58**, 475 (1966).
42. L. C. Pearson, *Principles of Agronomy* (Reinhold, New York, 1967), pp. 73–84.
43. National Academy of Sciences, *Principles of Plant and Animal Pest Control* II, Publication 1597 (National Academy of Sciences, Washington, D.C., 1968), pp. 256–257.
44. H. B. Sprague, *N.J. Agr. Exp. Sta. Bull.* **609**, 1 (1936).
45. R. D. Munson and J. P. Doll, *Advan. Agr.* **11**, 133 (1959).
46. J. S. Drew and R. N. Van Arsdall, *Ill. Agr. Econ.* **6**, 25 (1966); D. L. Armstrong, J. K. Leasure, M. R. Corbin, *Weed Sci.* **16**, 369 (1968); F. W. Slife, personal communication.
47. R. J. Delroit and H. L. Ahlgren, *Crop Production* (Prentice-Hall, Englewood Cliffs, N.J., 1953), pp. 572–573); P. W. Michael, *Herbage Abst.* **39**, 59 (1969).
48. G. F. Sprague, *Corn and Corn Improvement* (Academic Press, New York, 1955), pp. 643 and 663.
49. National Academy of Sciences, *National Research Council Publication* No. 1232 (National Academy of Sciences, Washington, D.C., 1964), pp. 77–89; *ibid.*, No. 1684 (1969), pp. 38–45.
50. D. D. Harpstead, *Sci. Amer.* **225**, 34 (1971).
51. U.S. Department of Agriculture, *Agr. Econ. Rep.* No. 147 (1968).
52. H. Jiler, *Commodity Yearbook* (Commodity Research Bureau, Inc., New York, 1972), pp. 252–253.
53. National Academy of Sciences, *Resources and Man* (Freeman, San Francisco, 1969), p. 143.
54. G. Borgström, *Principles of Food Science* (Macmillan, New York, 1968), vol. 2, p. 376.
55. U.S. Department of Agriculture, *Agricultural Statistics 1970* (Government Printing Office, Washington, D.C., 1970), pp. 28 and 430.
56. ———, *Fats and Oils Situation* (Economics Research Service, FOS-257, Washington, D.C., 1971).
57. G. R. Conway, *Environment, Resources, Pollution, and Society* (Sineurer Associates, Inc., Stamford, 1971), pp. 302–325; S. Pradhan, *World Sci. News* **8**, 41 (1971).
58. J. N. Black, *Ann. Appl. Biol.* **67**, 272 (1971).
59. U.S. Department of Agriculture, *Agricultural Statistics 1967* (Government Printing Office, Washington, D.C., 1967), pp. 34–35.
60. ———, *Crop Production, 1971 Annual Summary* (State Report Service, 1972).
61. ———, *Agr. Res. Ser. Stat. Bull.* No. 216 (1957).
62. ———, *Stat. Rep. Serv. Bull.* No. 408 (1967).
63. R. S. Berry and M. F. Fels, *The Production and Consumption of Automobiles. An Energy Analysis of the Manufacture, Discard, and Reuse of the Automobile and its Component Materials* (Univ. of Chicago, Chicago, 1973).
64. U.S. Department of Agriculture, *Bur. Agron. Econ. Bull.* No. FM 101 (1953).
65. U.S. Bureau of the Census, *Statistical Abstract of the U.S., 93rd Edition*, (Government Printing Office, Washington, D.C., 1972), pp. 600–601.
66. H. F. DeGraff and W. E. Washbon, *Agr. Econ.* No. 449 (1943).
67. U.S. Bureau of the Census, *Census of Agriculture* 1964 II (1968), pp. 909-955.
68. E. O. Heady, H. C. Madsen, K. J. Nicol, S. H. Hargrove, *Report of the Center for Agriculture and Rural Development*, prepared at Iowa State University, for the National Water Commission (NTIS, Springfield, Va., 1972).
69. A. W. Epp, *Nebr. Exp. Sta. Bull.* No. 426 (1954).
70. T. S. Thorfinnson, M. Hunt, A. W. Epp, *Nebr. Exp. Sta. Bull.* No. 432 (1955).
71. *Corn Grower's Guide* (W. R. Grace and Co., Aurora, Ill., 1968), p. 113.
72. U.S. Bureau of the Census, *Statistical Abstract for the United States, 92nd Edition* (Government Printing Office, Washington, D.C., 1971), p. 496.
73. ———, *Statistical Abstract of the United States, 86th Edition* (Government Printing Office, Washington, D.C., 1965), p. 538.
74. U.S. Department of Commerce, *Census of Transportation*, III (3), (Government Printing Office, Washington, D.C., 1967), pp. 102–105.
75. Interstate Commerce Commission, *Freight Commodity Statistics, Class I Motor Carriers of Property in Intercity* (Government Printing Office, Washington, D.C., 1968), p. 97; ———, *Freight and Commodity Statistics Class I Railroads* (Government Printing Office, Washington, D.C., 1968); ———, *Transportation Statistics* I, V, VII (Government Printing Office, Washington, D.C., 1968).
76. U.S. Department of Transportation, *Highway Statistics* (Government Printing Office, Washington, D.C., 1970), p. 5.
77. *Handbook of Chemistry and Physics* (Chemical Rubber Company, Cleveland, 1972), Table D-230.
78. A. J. Payne and J. A. Canner, *Chem. Process Eng.* **50**, 81 (1969).
79. G. Leach and M. Slesser, *Energy Equivalents of Network Inputs to Food Producing Processes* (Univ. of Strathclyde, Glasgow, 1973).
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Species Introduction in a Tropical Lake

A newly introduced piscivore can produce population changes in a wide range of trophic levels.

Thomas M. Zaret and R. T. Paine

By chance or by intention, man has often introduced new species to an ecosystem. The results have ranged from little or no effect to large-scale changes, often accompanied by catastrophic consequences (*1*). Although there have been many such species introductions over the past century, there is little documentation of community effects other than some general information about vertebrate introductions (*2*) and some experimental studies concerning the effects of herbivores on vegetation (*3*). Noticeably absent is the situation in which there has been sufficient qualitative or quantitative information concerning the preceding conditions of the ecosystem to permit a quantitative statement about changes resulting from the species introduction. Even in the field of biological control, where serious studies of this nature have been continuing for more than seven decades, accurate predictions of the effects of a new species on a given ecosystem are, even at the most basic level, not yet possible (*4*).

Historically, fish introduction (or culture) has provided a rich source of protein in many tropical areas. Introductions, however, are not without a

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potential ecological cost. As many governments in the tropics turn increasingly to freshwater fish as a source of animal protein, it seems important to be able to predict the long-term consequences of altering natural freshwater ecosystems. Further, if data on introductions of fish to tropical lakes were available, they would be valuable to the development of a general theory of freshwater community structure and organization.

For at least three centuries before 1958, Lake Atitlán, a large, tropical, and surely one of the world's most beautiful lakes, had sustained fisheries for small native fishes, probably *Poecilia sphenops* and *Cichlasoma nigrofasciatum*, as well as a substantial crab-catching operation (*5*). The fish, which were smoke-cured, consumed, and, if there were any excess, sold in the market, and crabs (*Potamocarcinus guatemalensis*) provided the native Guatemalan Indian population with an important source of protein as well as a small extra cash income. In 1958, through the efforts of a well-meaning fish biologist, the game fish *Micropterus salmoides*, the largemouth bass, was introduced, along with *Pomoxis nigromaculatus*, the black crappie. *Micropterus* fed voraciously on the small native fishes, and the result, a totally unexpected one, is that now, some 15 years after the introduction, the local fish populations, along with the crabs, are gone, both decimated by *Micropterus*. The few large *Micropterus* in the lake are taken only by those individuals fortunate enough to own skin-diving equipment (and they do not include the local Indians). Gone is an accessible and, in this region of the world, critical source of protein, as well as the extra income once generated by the local fish populations. Clearly the ecological cost of this species introduction was great and the benefit slight.

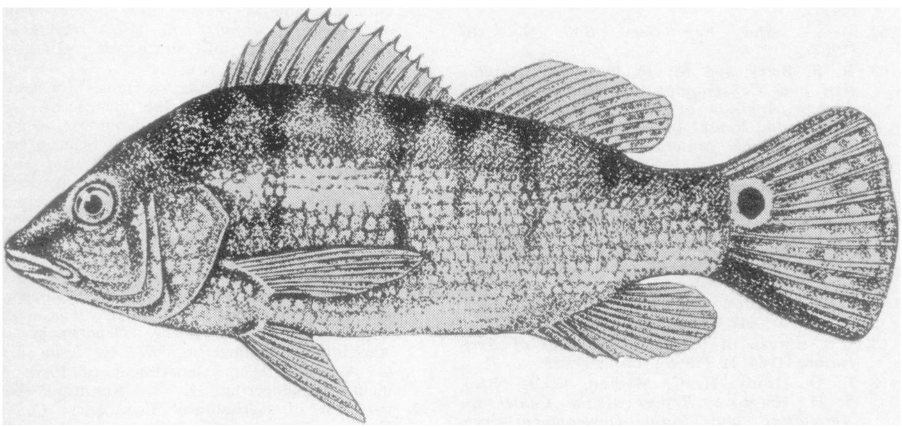

Fig. 1. *Cichla ocellaris* (Bloch and Schneider), showing ocellus (eyespot) at base of caudal peduncle [from Sterba (*11*), probably 1 year old, 24 to 32 cm TL].

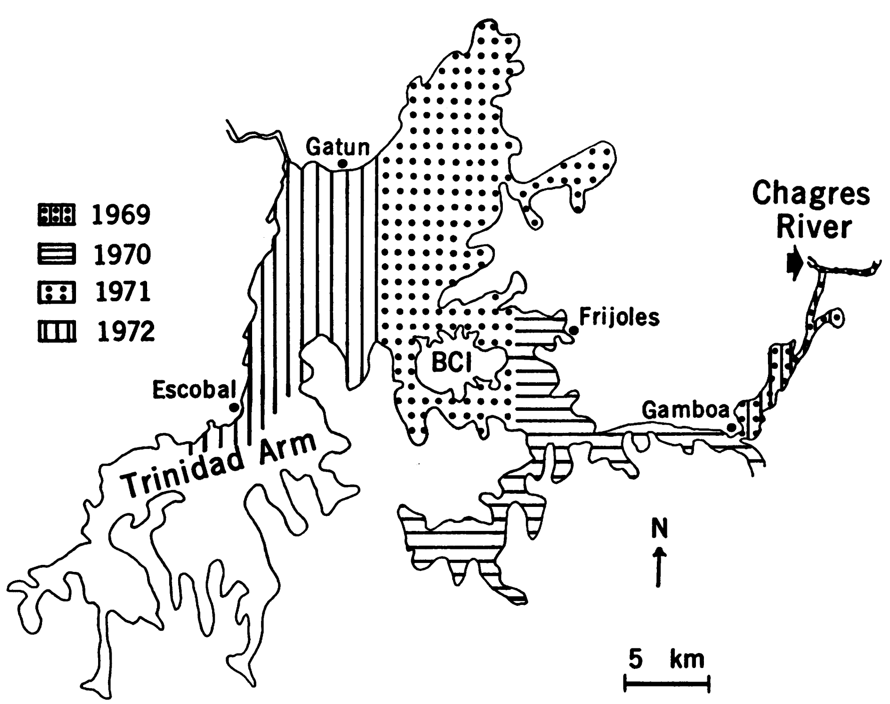

Fig. 2. Map of Chagres River and Gatun Lake, showing estimated extent of *Cichla* population by August of each year, 1969 through 1972. The extensive shoreline development is omitted from map outline. *Cichla* was first introduced in the upper Chagres (arrow), spread toward Barro Colorado Island (*BCI*), and, as of 1972, has not yet spread throughout the Trinidad Arm.

History of Cichla

In 1967, *Cichla ocellaris* (Bloch and Schneider) (*6*), a cichlid fish native to the Amazon River and its tributaries in northern South America, was introduced to Gatun Lake, a large (surface area of 42,315 hectares) body of fresh water in the Panama Canal Zone (*7*). This piscivore, bright yellow with black vertical bars, derives its pseudonym of "Peacock Bass" from its bass-like shape and, specifically, from the conspicuous ocellus (eyespot), black encircled by a gold ring, located at the base of the caudal peduncle (Fig. 1). *Cichla*, which commonly reaches 2 kilograms in weight and 50 centimeters TL (total length, from tip of snout to end of caudal fin) was thought to have been introduced as a boon to sportsmen because it has a reputation as a fine fighter, as well as being delicious (*8*). Owing to the success and popularity of this fish, a number of local residents have each taken credit for the "first introduction" of *Cichla*. In fact, in 1965, a local businessman, with the cooperation of the Panamanian government, arranged the transfer of approximately 100 fingerlings from rearing tanks in Buga, Colombia, to Panama. These fingerlings were put into a small impoundment with the hope of their eventually providing fish and fishing for the employees of his company and the residents of the neighboring community as well. During the rainy season, the waters of this impoundment, formed by damming the Quebrada Ancha creek, overflow and eventually reach the Rio Gatuncillo, a small tributary at the northern end of the Chagres River (Fig. 2). It is probable that by late 1966, during the rainy season, some of these fish entered this small tributary and spawned and that by 1967 *Cichla* had traveled the approximately 8 kilometers to the Chagres River itself. Since its initial introduction, *Cichla* has been casually introduced, often successfully, in rivers and ponds all over the isthmus, there being no apparent or effective controls or regulations in Panama and the U.S. Canal Zone regarding introductions of new species.

So far, *Cichla* has completely lived up to all expectations; its capture has provided entertainment for fishermen, and its taste has pleased many palates. Further, it is the only freshwater fish sold for consumption in this area. However, in a situation reminiscent of that in Lake Atitlán, one unforeseen effect of this introduction has been dramatic changes in the biotic community of Gatun Lake, with repercussions that have affected the entire lake ecosystem. We had been conducting investigations of this ecosystem for several years before the advent of *Cichla*, and this article documents qualitative and quantitative changes caused by the introduction of this single, piscine predator, whose actions have affected populations from the tertiary consumers down to the primary consumers and, in all probability, the primary producers as well (*9*).

Spread of Cichla

Cichla is a strictly piscivorous predator inhabiting the Amazon River system (*10, 11*). Since its natural habitat is a river, the initial introduction in Panama to the Chagres River was fortuitous. In this habitat, the *Cichla* population, feeding voraciously on the abundant, smaller native fishes along the river banks, increased rapidly in numbers. By early 1970, probably 2 years after the initial introduction, *Cichla* had traveled down the Chagres River, and catches were reported in the area near Gamboa (Fig. 2), where the river enters Gatun Lake's eastern boundary. The *Cichla* population, apparently ineffectively opposed by any natural competitors or predators, had increased to the point where it was not uncommon to find sportsmen on any given weekend who had caught 30 or more *Cichla*, with an average SL (standard length, from tip of snout to end of vertebral column) of 30 cm. By June 1970, *Cichla* were sighted near the small village of Frijoles, apparently having traveled along the eastern side of the lake. No significant progress of the population was noted for the following 7 months, but in the spring of 1971, *Cichla* appeared in our sampling areas around Barro Colorado Island (*BCI* in Fig. 2), and spread toward Gatun, at the northernmost end of the lake (*12*). At the present time, the fish population is spreading to the last remaining unexploited area of the lake, the Trinidad, or Southwest, Arm.

The fish have not diffused haphazardly throughout the lake, but have moved as a wave, with a leading edge composed of subadults, in such a way that the dynamics of the *Cichla* populations at the edge are significantly different from those in the rear. The total fish community is still a long way from equilibrium.

There are only two main processes slowing the spread of *Cichla* throughout Gatun Lake. First, although there do not seem to be any natural predators making a significant dent in the population, man's fishing is very intensive and, especially in recent years, has certainly contributed toward reducing the rate at which *Cichla* spread through the lake. Second, the species itself is very territorial during the breeding season, both parents remaining with the schools of fry for probably 60 days or more, and each *Cichla* pair probably breeds for a considerable portion of each year and probably remains in the same vicinity during breeding activities. Thus immigrants to previously unexploited habitats will probably be immature, thereby introducing a reproductive lag into the rate of population expansion.

Effect on Native Fishes

As *Cichla* has spread through the lake, its voracious predatory habits have had a devastating effect on the native fish populations. One can see the results by comparing fish census data taken before the introduction of *Cichla* with those taken after the population had moved through an area. In our sampling areas, located around Barro Colorado Island, the more common diurnal fishes found abundantly in previous years included the species listed in Table 1. The values in Table 1, obtained from field observations over the past 6 years, illustrate how *Cichla* has effectively eliminated six of the eight previously common fish species and drastically reduced a seventh.

During the summer of 1972, we attempted to substantiate further the differences in the structures of the fish communities. We made two complete

Table 1. Diurnal Barro Colorado Island fish species with percentage change following *Cichla* appearance.

Family	Species	Change: Increase (%)	Change: Decrease (%)
Atherinidae	*Melaniris chagresi*		50
Characinidae	*Astyanax ruberrimus*		100
	Roeboides guatemalensis		90
Cichlidae	*Aequidens coeruleopunctatus*		100
	Cichla ocellaris	100	
	Cichlasoma maculicauda	50	
Eleotridae	*Gobiomorus dormitor*		90
Poeciliidae	*Gambusia nicaraguagensis*		100
	Poecilia mexicana		100

Table 2. 1972 fish collections contrasting a non-*Cichla* site in the Trinidad Arm region with a *Cichla* site near the shores of Barro Colorado Island.

Family	Species	Non-*Cichla* No.	*Cichla* No.
Atherinidae	*Melaniris chagresi* (*23*)	200	0
Characinidae	*Astyanax ruberrimus*	160	0
	Compsura gorgonae	120	0
	Hoplias microlepis (*24*)	0	1
	Hyphessobrycon panamensis	2	0
	Pseudocheirodon affinis	7	0
	Roeboides guatemalensis	195	21
Cichlidae	*Aequidens coeruleopunctatus*	10	0
	Cichla ocellaris	0	14
	Cichlasoma maculicauda	7	36
	Neetroplus panamensis	4	0
Eleotridae	*Eleotris pisonis*	4	99
	Gobiomorus dormitor	42	10
Poeciliidae	*Gambusia nicaraguagensis*	22	0
	Poecilia mexicana	17	2
Other (*25*)		0	1

fish collections comparing the Trinidad Arm, where *Cichla* has not yet invaded, and where the fish community represents the pre-*Cichla* conditions, with Barro Colorado Island, where the *Cichla* population has recently peaked (Table 2). In the Trinidad Arm region, the site we chose was relatively shallow ($\leq$ 5 meters), with dense vegetation, mainly *Hydrilla* sp., lining the shore. At this site, we made a large semicircle (30 m by 5 m) with a 1.27-cm mesh nylon net. The net was attached to the shore, with the ends 10 m apart, to form the letter "D." The second site, along the shores of Barro Colorado Island, was a comparable cove, depth $\leq$ 5 m, with the same species of dense vegetation lining the banks and choking much of the waters. A 30 m by 5 m nylon net closed off the mouth of the cove, leaving an area approximately 30 m by 25 m. The results are presented in Table 2. The Barro Colorado Island site had a total surface area, volume, and shoreline several times that of the Trinidad Arm site. A census of the fishes at each site had been taken previously by direct observation.

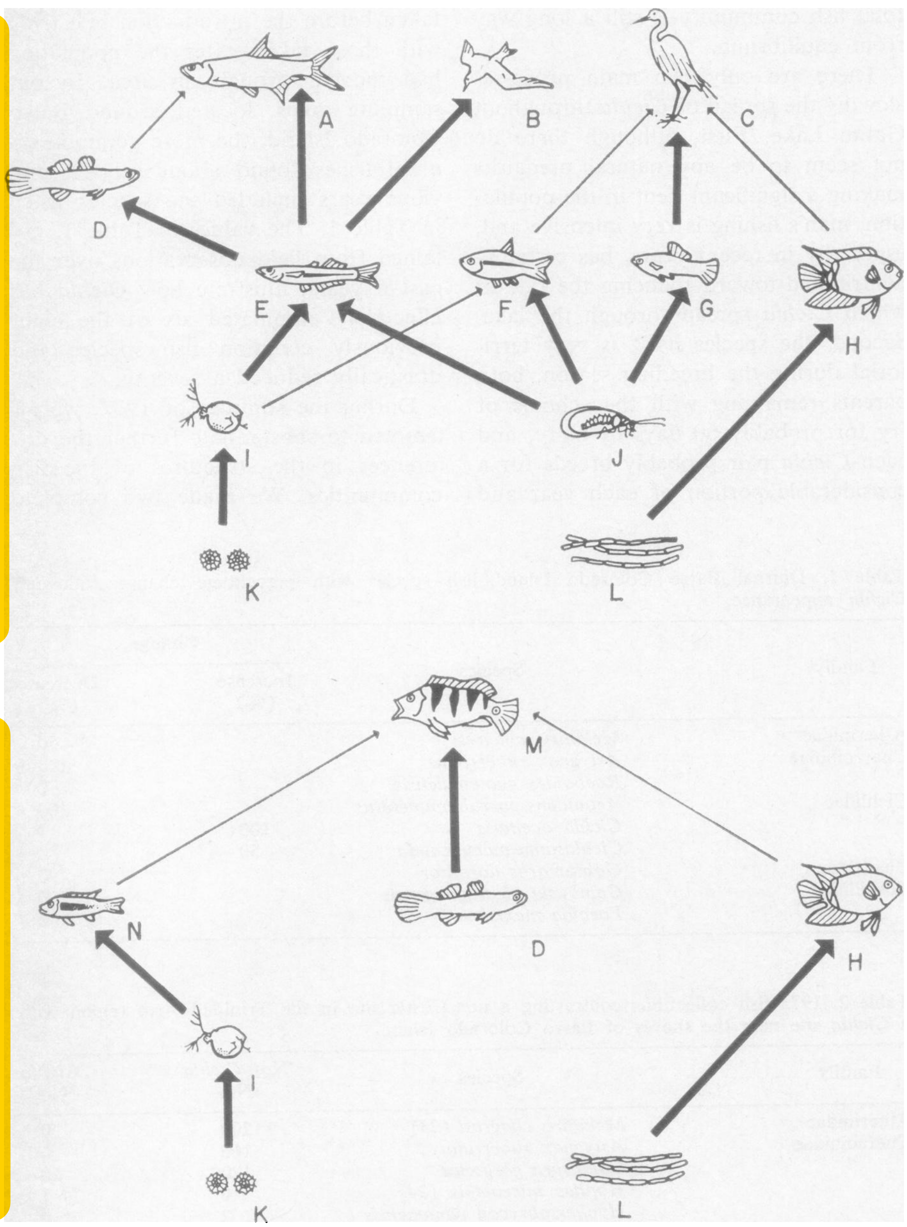

Fig. 3. Generalized food webs of common Gatun Lake populations, contrasting pre-*Cichla* (or present non-*Cichla*) regions (top) with *Cichla* regions (bottom). Thick arrows indicate that food item is of major importance to predator or herbivore, thin arrows indicate minor importance. Key to species: (A) *Tarpon atlanticus*; (B) *Chlidonias niger*; (C) several species of herons and kingfishers; (D) *Gobiomorus dormitor*, (E) *Melaniris chagresi*; (F) characinidae, including four common species; (G) poeciliidae, including two common species—one exclusively herbivorous, *Poecilia mexicana*, and one exclusively insectivorous, *Gambusia nicaraguagensis*; (H) *Cichlasoma maculicauda*; (I) zooplankton; (J) terrestrial insects; (K) nannophytoplankton; (L) filamentous green algae; (M) adult *Cichla ocellaris*; (N) young *Cichla*.

The Trinidad Arm community is composed of 14 fish species, 11 of which, in terms of their percentage of the biomass, contribute significantly. These are the genera *Melaniris, Astyanax, Compsura, Pseudocheirodon, Roeboides, Aequidens, Cichlasoma, Neetroplus, Gobiomorus, Gambusia,* and *Poecilia*. In contrast, the Barro Colorado Island site shows seven fish species present, but dominated heavily, in terms of percentage of biomass, by *Cichla* and *Cichlasoma*. This comparison indicates (excluding *Hoplias*) that, of the 11 previously important species, *Cichla* has completely eliminated seven and has reduced three others. One, *Cichlasoma*, has apparently increased. [The increase in *Cichlasoma* is probably due to the elimination by *Cichla* of species that formerly fed on the *Cichlasoma* fry, thereby seriously limiting the population. *Eleotris*, although abundant numerically, is a very small species, most of those we found being $\leq$ 2 cm SL. The role of this fish in the lake is not understood and is omitted from further discussion, although it seems that *Cichla*'s presence is resulting in an increase of this smaller species. The presence of a substantial number of *Roeboides* came as a surprise because this species was never seen during our numerous diving activities. *Roeboides* primarily feeds by ingesting scales of other fishes (*13*) and apparently has survived *Cichla* by remaining in the midst of the dense aquatic foilage where it must await other fishes darting in for cover.] The results from these fish collections basically support the generalizations we made after several years of observing the associations of *Cichla* with the native fish communities.

Cichla's Effect on the Food Web

Cichla predation affects most directly the secondary consumers, and these changes are most easily observed. However, these secondary consumers are related to and dependent upon other lake populations, and thus any change in the population of prey fishes must result in second- and third-order effects throughout other trophic levels. Figure 3 presents a generalized view of the trophic structure of Gatun Lake, based on information from stomach analyses and direct observations.

The top of Fig. 3 represents the pre-*Cichla*, or non-*Cichla*, community, and the bottom, the community when the *Cichla* population is at its numerical maximum. The arrows indicate whether a food species makes up a major (thick arrow) or minor (thin arrow) proportion of its consumer's diet.

Melaniris chagresi is a key species in the lake food web (*14*), with three higher-level species feeding heavily on it. Schools of young *Melaniris* are commonly found up to 100 m from shore and so are at least partially protected from *Cichla* predation, which is confined to the shore regions. However, schools of older *Melaniris* concentrate along the shore while feeding and breeding, and thus predation falls most heavily on these larger, more mature individuals. Adult *Melaniris* are commonly recovered from *Cichla* stomachs. Figure 4 depicts the changes in the *Melaniris* population, derived by comparing the period before *Cichla* were present with the period afterward. The pre-*Cichla* data were collected during a 14-month, consecutive period (January 1969 to February 1970), and the *Cichla* data were collected from July to August 1971 and from June to September 1972. Figure 4A presents the numbers of *Melaniris* adults that passed the Dock Sampling Station (off Barro Colorado Island) in the daytime. The numbers were obtained by direct observation, which is easily done with these fish because they swim as a school near the surface of the water and can be counted easily. Figure 4A shows a greater than 90 percent reduction in *Melaniris* adults in 1971 and 1972; Fig. 4B gives pre-*Cichla* and *Cichla* data with regard to the total number of young *Melaniris*. Each data point represents the mean number of *Melaniris* from nighttime net tows taken over a 100-m towing tract at the Buoy Sampling Station (off Barro Colorado Island); there were between one and six tows per sample date. These samples give an accurate population estimate of young *Melaniris*. Both A and B of Fig. 4 indicate the marked decrease in the *Melaniris* population after the appearance of *Cichla*. The reduction of young is caused by the reduction in adults, rather than by direct predation by *Cichla*. If we had long-term quantitative data for other fish species, we would expect to see a similar decrease in population.

Second-Order Effects—Zooplankton

Young *Melaniris* feed almost exclusively on zooplankton throughout the year. The predation pressures that these fish exert determine the composition and distribution of the zooplankton species, as has been demonstrated for *Ceriodaphnia cornuta* (Sars) (*15*). This species consists of two morphologically distinct forms: one possesses "horns," pointed extensions of the exoskeleton on the head, fornix, and tail region; the other does not have these specialized structures. Unhorned *Ceriodaphnia* possess a reproductive advantage over their horned relatives and predominate in all lake areas where the two *Ceriodaphnia* forms coexist in the absence of predation. However, *Melaniris* shows a greater electivity for the unhorned forms, and in those regions of Gatun Lake where this planktivore occurs, differential predation results in both *Ceriodaphnia* forms occurring in more equal numbers. We predicted, therefore, that, if the *Melaniris* population decreased, the percentage of horned *Ceriodaphnia* would also.

Figure 4C presents seasonal data on the percentage of horned *Ceriodaphnia* at the Buoy Sampling Station, where the numbers of young *Melaniris* are known (Fig. 4B). The values for 1971 and 1972 include the lowest ever recorded from this station, indicating an almost complete absence of *Melaniris* predation.

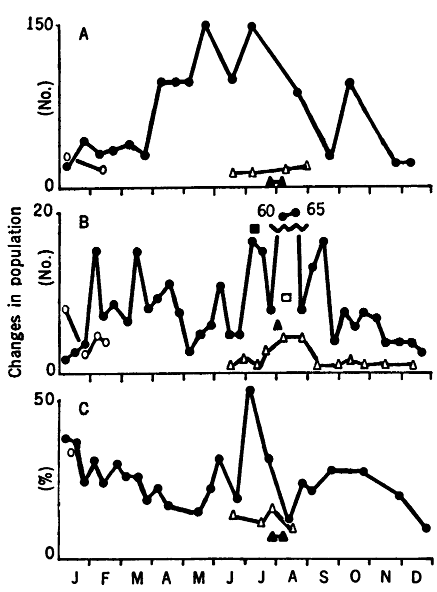

Fig. 4. Population changes in (A) adult *Melaniris chagresi* from Dock Sampling Station; (B) young *Melaniris chagresi* from Buoy Sampling Station; and (C) horned morphs of *Ceriodaphnia cornuta* from Buoy Sampling Station, contrasting pre-*Cichla* years with *Cichla* years in the Barro Colorado Island region. Pre-*Cichla* years: 1967 (■); 1968 (□); 1969 (●); 1970 (○); *Cichla* years: 1971 (▲); 1972 (△).

Second-Order Effects—Vertebrates

In Gatun Lake there are several populations of tertiary consumers that are primarily dependent on *Melaniris* as their food source. Atlantic tarpon, *Tarpon atlanticus*, are present in the Panama region from late spring until early fall; in fact, some of the world tarpon catch records come from this area. Some tarpon regularly enter Gatun Lake by way of the Panama Canal locks, and, once within the lake, they pursue and feed on the numerous schools of *Melaniris*. Immature *Chlidonias niger*, the common black tern, that remain near Gatun Lake during the winter perch on the tree stumps and channel markers of the lake in flocks often numbering over 150. These terns follow the tarpon chasing the *Melaniris* schools. Those *Melaniris* which leap from the water in a final attempt to escape the tarpon are seized and eaten by the hovering terns, while many others are taken from below by the tarpon. It is rather difficult to monitor the seasonal populations of these two tertiary-consumer populations because of their mobility, and our data come from direct observations. Tarpon and terns are normally seen around the waters of Barro Colorado Island almost every day during the months of May through October. However, during the summer months of 1971 and early summer 1972, these two populations were not seen in the region. During this same period of absence from the Barro Colorado Island region, the tarpon and terns were commonly seen in the non-*Cichla* areas of the lake. This same trend appears to be true for such fishing birds as kingfishers and herons, which feed on small fishes (*16*) and which have become much less common in the *Cichla* regions of Gatun Lake.

Second-Order Effects—Insects

Many of the prey fishes fed primarily on insects, including the most common fishes, such as the characins *Astyanax* and *Roeboides* (*17*), adult

Melaniris (*14*), and *Gambusia* (*18*). With the absence of these species, one would expect some change in the local insect populations. However, measuring changes in insect populations for the Gatun Lake area would be, at best, a very tenuous prospect, even if there were good records, which there are not. The only data that were collected consistently and that date from the period before the introduction of *Cichla* concern mosquitoes. Mosquito abundance is a matter of concern because malaria was once a serious problem in the Panama region.

At the present time, the Division of Sanitation of the Panama Canal Company keeps a constant vigil in the form of a weekly "mosquito index," which consists primarily of the genera *Anopheles, Culex*, and *Mansonia*. Since the two areas of mosquito light traps used to obtain the mosquito index are located in the two major Canal Zone cities, Balboa and Cristobal (at opposite ends of the canal), and since the organophosphate Baytex is used regularly there to control the mosquito populations, data from these areas are of little value for our study. However, there are some records from Gamboa, a small town on the Chagres River close to the area where the river enters Gatun Lake and near the region where *Cichla* was flourishing by 1969. Mosquito control in Gamboa is only partial, primarily local applications of 5 percent DDT in kerosene. The average mosquito take in the light traps reaches more than three orders of magnitude greater than that of Balboa and Cristobal. The mosquito data at the Gamboa station were first collected in 1968 (pre-*Cichla*) and have been continued since that time. The monthly averages for 1968 to 1971 are plotted in Fig. 5. They show that the total mosquito populations were at their lowest in 1968 and that there was a dramatic increase in 1969, coinciding with the period when the *Cichla* population was, in all probability, peaking in the region. This is followed by years of somewhat lower abundance, although still appreciably higher than the low of 1968. Each monthly average in 1968, with one exception, is the lowest value for that respective month in the 4 years during which data were collected.

There has also been an interesting change in the type of malaria occurring in the Canal Zone. Until 1969, more than 95 percent of malaria victims carried *Plasmodium vivax* as the disease agent, while less than 5 percent carried *P. falciparum*. Starting in 1969, however, there was an abrupt change. Since then, 60 percent or more of the malaria victims have carried the *P. falciparum* agent, and the most serious outbreaks (in 1971 at Las Cumbres, an artificial lake, and in 1972 at Escobál, located just at the narrow section before the Trinidad Arm) have consisted primarily of *P. falciparum* cases. Both of these outbreaks, involving several hundred people, have occurred in areas near waters containing *Cichla* (*19*).

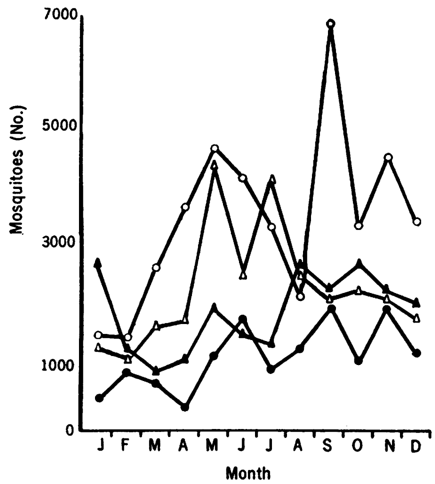

Fig. 5. Monthly averages of total number of mosquitoes of the genera *Anopheles, Culex*, and *Mansonia*, from Gamboa Chagres River Jungle Edge Station, one light trap per night, four nights per week, contrasting pre-*Cichla* year with *Cichla* years. Pre-*Cichla* year: 1968 (●). *Cichla* years: 1969 (○); 1970 (▲); 1971 (△).

We wish to reiterate that the preceding information must be taken very cautiously. There are other possible explanations for the apparent changes in mosquito abundance, the most likely being changes in aquatic vegetation or precipitation, the latter often a correlate of mosquito abundance. However, whereas the mosquito population increased most sharply, and to its highest levels, in 1969, the rainfall data taken from Barro Colorado Island showed little annual change, going from 2238 millimeters in 1968 to 2194 mm in 1969. In 1970, when the rainfall increased approximately 1.5 times, to 3226 mm, the total mosquito levels dropped. The rainfall for 1971 was 2162 mm. These data suggest strongly that some factor other than rainfall was important in determining the mosquito population levels.

Some Predictions

Our present efforts are concerned with monitoring changes in the Gatun Lake populations, including such aspects as the predator and its population structure, the rate of movement of the predator population through the lake, alterations in the prey communities as the predator spreads its influence, and the subsequent second- and third-order changes in the higher and lower trophic levels. Coupled with this long-term data-gathering are a series of field and laboratory experiments designed to elucidate such interactions among populations as predator food preferences, prey removal rates, and the effects of prey escape on the rate of predator spread throughout the system. We are developing a heuristic model to describe the effects on a freshwater ecosystem of a newly introduced, top-level predator.

There are also several areas concerning the basic ecological theory of freshwater systems that we hope to examine over the next few years. We present, therefore, several predictions that we will be directly testing in Gatun Lake. We base these predictions on the assumption of no further fish introductions.

1) The predatory nature of *Cichla* is having dramatic effects on the native populations of fish species. We predict that we will be able to determine, for any given locale in Gatun Lake, a coefficient of predation pressure (namely, the magnitude and time element of the predation force) by simply examining the spectrum of the secondary-consumer populations and their relative numbers in that location.

2) The habits of the chief planktivorous fish in Gatun Lake, *Melaniris chagresi*, confine its influence solely to those areas of the lake within 100 m of the shore. We predict that, as *Cichla* removes *Melaniris* from these shore-associated regions of the lake, there will be an increase in the total zooplankton density and also in the average body size of the largest species (*22*). Under these conditions, very small zooplankton species, including rotifers, would be expected to diminish in numbers as well.

3) It has been suggested that, when planktivorous fish effect changes in the composition of the zooplankton community, there are corresponding changes at the level of the primary producer as well and that this may be a primary

control of algae abundance (20). This result has taken place in small-scale laboratory experiments and also in experiments in large artificial ponds (21). Although there appear to be no gross chemical differences in the water of different areas of Gatun Lake (22), there does apear to be a lower phytoplankton standing crop in those areas characterized by *Cichla* predation. We predict that we will find a continuance of this pattern—namely, that the species composition and abundance of phytoplankton will be related directly to the coefficient of predation pressure.

It appears that it is the magnitude and direction of predation, and predation alone, which is now the overriding factor in determining the structure of populations in the Gatun Lake ecosystem, from the tertiary consumers down to the primary producers, as long as the lake retains its nonequilibrium status. We expect that this influence will subside as the lake ecosystem returns to, or at least approaches, some form of equilibrium.

Summary

Probably in early 1967, a piscivore from South America, *Cichla ocellaris*, was introduced to Gatun Lake in the Panama Canal Zone. As this predator population spread through the lake, the initial effect was dramatic reductions in almost all secondary consumers. These species reductions produced, in turn, second- and third-order changes at other trophic levels of the ecosystem. The resulting changes in the lake community can be seen best by examining the general Gatun Lake food web. The decrease in numbers of the important planktivore *Melaniris* has resulted in changes within the zooplankton community, as illustrated by the cladoceran *Ceriodaphnia*. The tertiary-consumer populations, such as tarpon, black terns, kingfishers, and herons, formerly dependent on small fishes for food, appear less frequently in the *Cichla* areas of the lake. There has also been, possibly, a resurgence of the local mosquito populations (which are malaria vectors), caused by the reduction in the populations of insect-eating fishes. Even the primary producers may be affected by this introduction. Although at present the Gatun Lake ecosystem is undergoing rapid changes, we anticipate an eventual return to some form of equilibrium. However, it will be some time before we can evaluate the permanence or transience of the many changes produced in the trophic levels by the introduction of a single, top-level predator to this lake system.

References and Notes

1. C. S. Elton [*The Ecology of Invasions by Animals and Plants* (Wiley, New York, 1958)] presents a wealth of historical information concerning the effects of species introductions.
2. W. I. Aron and S. H. Smith, *Science* **174**, 13 (1971).
3. J. L. Harper, *J. Ecol.* **55**, 247 (1967).
4. P. DeBach, *Biological Control of Insect Pests and Weeds* (Reinhold, New York, 1964).
5. F. W. McBryde, *Cultural and Historical Geography of Southeast Guatemala* (Smithsonian Institution, Washington, D.C., 1947), p. 124.
6. There has been some taxonomic confusion concerning the species of the genus *Cichla*. Only two species are recognized by C. H. Eigenmann and W. R. Allen [*Fishes of Western South America* (Univ. of Kentucky, Lexington, 1942), pp. 401–403]. A. Machado-Allison [*Acta Biol. Venez.* **7**, 459 (1971)] has described a third species, *C. intermedia*, and from his work we have reconfirmed the identity of the Gatun Lake species as *C. ocellaris*, not the naturally co-occurring *C. temensis* (Eigenmann and Allen).
7. Gatun Lake was formed in the early 1900's by the damming of the Chagres River near the present-day site of Gatun. The river basin, which was subsequently inundated, had been extant for at least 11,300 continuous years, judging from bottom sediment cores analyzed by A. S. Bartlett, E. S. Barghoorn, R. Berger, *Science* **165**, 389 (1969).
8. *Panama Canal Rev.* (February 1971), p. 11.
9. The plant and animal components of a community may be arranged according to their method of obtaining nutrition by placing them in "trophic levels" (from the Greek *trophe*, nutrition). All organisms obtaining their food in the same number of energy steps are classed in the same trophic level. Thus green plants, which obtain nutrition in a single energy step, are in the first trophic level and are known as primary producers, whereas herbivores are in the second trophic level and are called primary consumers. Herbivore-eating carnivores are secondary consumers, carnivore-eating carnivores are tertiary consumers, and so on. Those individuals belonging to the highest trophic level are top-level carnivores, and they may sometimes occupy up to a fifth trophic level, as *Cichla* does in Gatun Lake.
10. R. H. Lowe-McConnell, *J. Linn. Soc. London Zool.* **45**, 103 (1964); H. A. Knöppel, *Amazonia* **2**, 257 (1970); R. H. Lowe-McConnell, *J. Linn. Soc. London Zool.* **48**, 255 (1969) gives some additional information, including breeding behavior of *Cichla*.
11. G. Sterba, *Freshwater Fishes of the World* (Vista, London, 1962), p. 690.
12. The presence of *Cichla* at the northern end of the lake may have been aided by local anglers, since at least one has reported to us that he transplanted up to 60 fish sometime in 1970.
13. C. M. Breder, *Bull. Amer. Mus. Nat. Hist.* **57**, 127 (1927); J. Géry, *Vie Milieu* (Suppl. 17) (1964), pp. 459–460; T. R. Roberts, *Proc. Calif. Acad. Sci.* **38**, 383 (1970).
14. Most of the following information on the ecology of *Melaniris* comes from T. M. Zaret, *Copeia* **1971**, 341 (1971).
15. T. M. Zaret, *Ecology* **53**, 248 (1972); *Limnol. Oceanogr.* **17**, 171 (1972).
16. F. Haverschmidt [*Birds of Surinam* (Oliver and Boyd, London, 1968)] describes the feeding habits of birds whose range includes the Panama region.
17. G. S. Myers, *Stanford Ichthyol. Bull.* **7**, 206 (1960); T. M. Zaret and A. S. Rand, *Ecology* **52**, 336 (1971).
18. Members of this genus are commonly called "mosquito fish" because they eat mosquitoes. They were, therefore, frequently used in biological control.
19. Las Cumbres is a small, man-made lake in a private residential area; it possibly held *Cichla* as early as 1967. The 1972 outbreak of malaria at Escobál involved 330 cases, caused by *Plasmodium falciparum* exclusively. It is possible that, since *P. falciparum* has been present in the area for many years, a new vector may be involved. Such was the case in Brazil in the late 1930's, when the introduction of a new vector, *Anopheles gambiae*, produced a malaria epidemic reportedly responsible for the deaths of 20,000 people (*1*, pp. 19–20). Although the recent development of the *Cichla* population has coincided remarkably with the increase in the incidence of falciparum malaria, only the mosquito data hint at any possible causal relationship.
20. This result can be expected, given the results of the effects of planktivores on the zooplankton community [J. L. Brooks, *Syst. Zool.* **17**, 272 (1968); ——— and S. I. Dodson, *Science* **150**, 28 (1965)].
21. J. Hrbáček, M. Dvorakova, V. Korínek, *Verh. Int. Verein. Theor. Angew. Limnol.* **14**, 192 (1961); D. J. Hall, W. E. Cooper, E. E. Werner, *Limnol. Oceanogr.* **15**, 839 (1970); S. H. Hurlbert, J. Zedler, D. Fairbanks, *Science* **175**, 639 (1972).
22. An extensive chemical analysis of Gatun Lake is being conducted by the Panama Canal Company Miraflores Water Laboratory.
23. *Melaniris* was not captured in our fish collection because these relatively fast-moving and highly mobile schools can avoid the net before it is in position, whereas other species swim directly into the weeds for protection and are later captured. However, a school of 200 *Melaniris* was in the area and was counted at the time of our collection. Since most of the *Gambusia* and *Poecilia* living on the periphery of the sites were also able to escape, the numbers in Table 2 come from the preceding observational count.
24. *Hoplias* is a relatively large piscivore that hunts primarily at night or dawn. It is observed rarely, but we have seen it in both *Cichla* and non-*Cichla* regions of the lake.
25. Includes one small pipefish, *Oostethus lineatus*.
26. We thank the Smithsonian Tropical Research Institute for its cooperation and financial assistance and the staff for their critical and stimulating discussion, especially A. S. Rand and I. Rubinoff, who provided data and advice. We also thank J. P. McLaren and the Division of Sanitation, Panama Canal Company, for kindly providing us with mosquito data and other unpublished data; C. Leck for his data concerning tern population distribution around Barro Colorado Island in 1968 and 1969; and J. Johnson and A. Johnson for their hospitality and information at Lake Atitlán. M. Perrone, S. Schroder, and K. Weers provided assistance in the field work during the summer of 1972, as did A. Rodoniche and N. Smythe. We thank A. Spight for the food web illustrations and S. Shimada for manuscript typing. Finally, thanks to our curious and friendly guide José, who seemed always to be there when we needed him in our Central American fieldwork. Support during 1971 by Organization for Tropical Studies Pilot Proposal N70-22 to T.Z. and in 1972 by a National Science Foundation grant GB-33396 to R.T.P. and T.Z.

Species Introduction in a Tropical Lake: A newly introduced piscivore can produce population changes in a wide range of trophic levels

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