Ecosystem Alteration by Mosquitofish (Gambusia affinis) Predation

Abstract. *In artificial pools* Gambusia affinis *greatly reduced rotifer, crustacean, and insect populations and thus permitted extraordinary development of phytoplankton populations (2×10^8 cells per milliliter). Other effects included decreased optical transmissivity and increased temperature of the water, decreased amounts of dissolved inorganic phosphorus, and increased amounts of dissolved organic phosphorus, inhibition of* Spirogyra, *and replacement of one annelid,* Chaetogaster, *by another,* Aeolosoma.

The role of fish in determining the nature of aquatic ecosystems has been so underestimated in the past that none of the major monographs on limnology devotes more than a few paragraphs to the subject (*1*). This is understandable since accurate data on fish populations are lacking for most bodies of water and are not easily obtained. Yet in 1935 J. Omer-Cooper observed, in the Libyan Desert, great differences between the biota of springs with and without the African cichlid fish *Tilapia* (*2*). He proposed that "the biological factor is the most important of all the normal ecological factors which affect lakes and ponds . . ." and that "the appearance of a single fresh species in an animal community is more likely to produce a profound effect than any normal chemical or physical change." This and other early observations of the same sort (*3*) passed unheralded, and limnologists have continued to rely principally on physical and chemical factors for explanations of variations in aquatic populations and communities. Only in the last 10 years have the pervasive influences of fish populations become more generally appreciated (*3, 4*).

We have conducted a controlled experiment on the role of the mosquitofish *Gambusia affinis* (Baird and Girard) in artificial aquatic ecosystems. The results show just how extensive the effects of a fish population can be and how fish populations can influence eutrophication. This small, ovoviviparous fish is native to south coastal United States but now has a nearly worldwide distribution, thanks to man's recognition of its appetite for mosquitoes (*5*).

In early October 1970 we placed, in a row, eight plastic pools, 2 m in diameter and 30 cm deep, on the roof of the Life Science Building of San Diego State College. To each was added a 3-cm layer of sand, tap water to a depth of 20 cm, a liter of dry alfalfa pellets as a source of nutrients, and inocula of plankton from a nearby lake and from a laboratory colony of *Daphnia pulex* (*6*). Water levels were maintained by weekly additions. On 23 October, we added 50 *Gambusia*, 3 to 5 cm long, to three of the pools; three pools were kept as controls and the other two pools were left at the ends of the row (*7*). At this time the dominant zooplankton were protozoa and rotifers; insects were represented primarily by mosquitoes and chironomid midges. At intervals thereafter, samples of the phytoplankton (*8*) and zooplankton (*9*) were taken, and insects were collected from the surface (*10*). Phosphorus content was determined (*11*), the benthos was sampled (*12*), the macroscopic algae were harvested (*13*), and water temperature and transparency were measured (*14*) (Table 1).

For most variables there was a large difference between the pools with *Gambusia* and those without. Predation by *Gambusia* on crustacean, insect, and rotifer populations seems sufficient to account for all effects (*15*), although in some instances the causal mechanism remains obscure. On its introduction, *Gambusia* began feeding on *Daphnia* and insects, eventually eliminating them completely. Reduction of *Daphnia* populations permitted temporary increase in the number and variety of planktonic rotifers, which, as a group, do not compete successfully with planktonic cladocerans (*16*); later, for lack of larger prey, *Gambusia* fed on and reduced even the rotifer populations. In control pools, rotifer populations declined as cladoceran populations increased. Copepods, in the form of *Cyclops nauplii*, were found only on the last sampling date.

In pools freed by *Gambusia* of the grazing pressure of zooplankton, a minute blue-green unicell, *Coccochloris peniocystis*, developed into a persistent algal bloom with densities of 200×10^6 cells per milliliter. Correlated effects were very green water, greatly reduced light penetration, and increased afternoon water temperature. This alga was not recorded in control pools (without *Gambusia*), where the water was clear and slightly cooler.

Larger phytoplankters (*17*) showed little response to the presence of fish, an observation not presently understood. In pools with *Gambusia, Haematococcus* occurred both in the plankton and as a bright orange felt on the pool walls. In pools without *Gambusia*, grazing activities of chironomid larvae, mayfly nymphs, and *Daphnia* reduced this felt considerably; nevertheless the alga remained abundant in the plankton.

The cycling of phosphorus, and presumably all other mineral nutrients, was altered by the fish. Particulate phosphorus concentrations probably reflected differences in phytoplankton biomass. The total amount of phosphorus in a dissolved (or colloidal) state was about the same in both sets of pools, but the ratio of the organic to inorganic fraction was quite different in the sets. In part, this difference reflected a shift in the balance between excretion of orthophosphate by insects and zooplankton, and between uptake of orthophosphate and liberation of phosphorus-containing organic compounds by phytoplankton (*18*).

The heavier growth of filamentous algae, almost entirely *Spirogyra*, in pools without *Gambusia* was correlated with greater light penetration, higher concentrations of inorganic dissolved phosphorus, and low phytoplankton populations. For reasons unknown, *Chara* was not affected in the same manner as *Spirogyra*.

In pools without *Gambusia* three families of insects became abundant. Larval chironomids (Diptera) attained exceptional densities in the sediments (*19*), nymphs of the mayfly family Baetidae (Ephemeroptera) numbered in the thousands, and larvae and pupae of the ephydrid genera *Ephydra* and *Brachydeutera* (Diptera) were somewhat less abundant. In pools with *Gambusia* all insects had been eliminated by early December. This is not surprising, but in larger bodies of water *Gambusia*'s predation on benthic organisms would be less intensive. In ponds *Gambusia* has little effect on chironomids (*20*).

The replacement of one species of annelid worm, *Chaetogaster* sp., by a second species, *Aeolosoma* sp., after introduction of *Gambusia* may have the following explanation. *Aeolosoma*, but not *Chaetogaster*, was found in small numbers in zooplankton samples; it possesses numerous, long, hairlike setae which may be useful for clambering about on the surfaces of sediments or in macroscopic vegetation, for example, *Spirogyra* filaments. *Chaetogaster* has a small number of short, stout setae and appears better adapted for existence within sediments (*21*). We can speculate that in pools without *Gambusia*, *Chaetogaster* predominated because only it lived deep enough in the sediments to escape predation or omnivorous browsing by chironomids, mayflies, and other insects. In pools with *Gambusia*, *Chaetogaster* was replaced by *Aeolosoma* because of unfavorable changes in chemical conditions within the sediments or for other reasons.

Our conclusion is that lake and pond ecosystems are strongly influenced by the feeding behavior and population dynamics of animals at the top of the food chain. In other situations where *Gambusia* has been the top predator it has had influences similar to those we found (*22*). Effects of other fish on the zooplankton are well documented, and fish-induced increases in phytoplankton populations have been reported (*3*, *4*). Although some of *Gambusia*'s effects on the benthos were direct, in a deep lake, zooplanktivores dwelling strictly on the surface would influence processes throughout the water column and sediments. For example, if increased zooplanktivory permits an increase in phytoplankton, we should expect correlated changes in the vertical distribution and amounts of photosynthesis, dissolved oxygen, and mineral nutrients;

Table 1. Comparison of the flora and fauna in pools with and without the mosquitofish *Gambusia affinis*. In the column headed *P*, S denotes a statistically significant difference ($P = .10$) between pools with and without *Gambusia*; N indicates nonsignificance (rank sum test).

Organism or condition	Date (1970–1971)	Number of organisms						
		Without *Gambusia*			*P*	With *Gambusia*		
		Pool 1	Pool 3	Pool 5		Pool 2	Pool 4	Pool 6
		Zooplankton (number per 10 liters)						
Daphnia pulex	2 Dec.	42	170	63	S	1	0	0
D. pulex	11 Jan.	346	353	213	S	0	0	0
D. pulex	3 Feb.	2420	610	2480	S	0	0	0
Chydorus sphaericus	2 Dec.	0	0	0	N	0	0	0
C. sphaericus	11 Jan.	1	0	19	N	0	0	0
C. sphaericus	3 Feb.	220	290	620	S	0	0	0
Copepod nauplii	3 Feb.	25	15	5	S	0	0	0
Aeolosoma sp.	11 Jan.	0	0	0	S	31	11	3
Total rotifers	2 Dec.	1646	602	1155	S	3744	5639	8399
Total rotifers	11 Jan.	4	1	6	N	5	2	1
Total rotifers	3 Feb.	55	35	5	N	0	8	5
Monostyla sp.	2 Dec.	65	23	138	S	1777	2906	2673
Lepadella sp.	2 Dec.	0	0	109	S	702	531	3145
Trichocerca sp.	2 Dec.	0	0	0	S	564	570	878
Brachionus quadridentata	2 Dec.	1492	46	908	N	435	1554	460
		Benthic organisms (number per square centimeter of bottom sediments)						
Chironomid midge larvae	7 Feb.	30	23	24	S	0	0	0
Aeolosoma sp.	7 Feb.	0	0	2	N	125	1	49
Chaetogaster sp.	7 Feb.	18	10	14	S	0	1	1
		Insects from water surface collected 15 November to 7 February						
Baetidae, imagoes (dead)		135	18	148	S	0	0	0
Brachydeutera sp., pupae		99	82	61	S	0	0	0
Ephydra sp., pupae*		206	249	453	S	0	0	0
		Phytoplankton (colonies or cells per milliliter)						
Colonial algae†	10 Jan.	13.1	2.2	7.3	N	8.0	38.6	1.5
Colonial algae	2 Feb.	155.9	46.8	34.1	N	74.5	81.4	0.0
Haematococcus lacustris	10 Jan.	17.5	2.9	23.4	S	0.0	2.1	0.7
H. lacustris	2 Feb.	26.3	17.5	41.4	N	86.7	16.1	923.9
Other unicells, > 5 μm‡	10 Jan.	6.5	2.9	27.8	N	6.6	24.6	4.4
Other unicells, > 5 μm	2 Feb.	21.4	24.5	25.4	N	18.0	8.8	44.1
		Phytoplankton (10^5 cells per milliliter)						
Coccochloris peniocystis	10 Jan.	0.0	0.0	0.0	S	111.3	88.1	150.0
C. peniocystis	2 Feb.	0.0	0.0	0.0	S	209.0	222.6	226.5
Other unicells, < 5 μm	10 Jan.	0.0	0.0	0.2	N	0.0	0.0	0.0
Other unicells, < 5 μm	2 Feb.	0.2	0.0	0.0	N	0.0	2.0	2.0
		Macroscopic algae (grams wet weight)						
Spirogyra sp.	6 Feb.	174	273	490	S	32	1	54
Chara sp.	6 Feb.	32	27	14	N	23	27	43
		Phosphorus content of water (micrograms per liter)						
Particulate P	19 Jan.	4.5	19.5	28.5	S	390.0	310.5	398.5
Total dissolved P	19 Jan.	25.5	25.5	27.0	N	15.0	60.0	40.5
Particulate P	3 Feb.	12.4	16.1	8.7	S	235.6	281.5	296.4
Dissolved inorganic P	3 Feb.	13.3	13.2	2.7	S	0.4	0.4	0.19
Dissolved organic P	3 Feb.	21.5	17.8	15.9	S	98.8	30.6	34.7
		Water transmissivity (percentage of light transmitted through 10 cm)						
$\lambda = 4250$ Å (blue-violet)	10 Jan.	57	60	63	S	0.052	0.36	0.11
$\lambda = 6800$ Å (red)	10 Jan.	90	90	96	S	6.4	14	9.5
		Water temperature (degrees Celsius)						
1045 hours P.S.T.	9 Jan.	8.0	7.8	7.7	N	7.9	8.0	7.9
1410 hours P.S.T.	9 Jan.	14.0	14.0	13.6	S	14.9	14.3	14.5

* Includes pupae found attached to *Chara* stems of 7 Feb. † Consisted of *Pandorina morum*, *Pediastrum boryanum*, and *Scenedesmus* spp. None of these, taken separately, showed a significant difference. ‡ Consisted principally of various diatoms, *Trachelomonas* sp., and *Peridinium* sp.

vertical migration of zooplankters; rates of precipitation of organic matter; the chemistry of the sediment-water interface; and the kinds and numbers of benthic organisms.

Species higher in the food chain alter the effectiveness of zooplanktivores. In nature, *Gambusia* and other small fish can rarely effect as extensive changes as we observed in our pools because their populations are limited by piscivores. Probably we could have reversed effects such as the algal bloom by introducing a hungry bass into each pool. A large-scale experiment along these lines is under way in Clear Lake, California, into which *Menidia audens*, a small zooplanktivorous fish, has recently been introduced to feed on planktonic algae and the planktonic larval stages of the gnat *Chaoborus*, both of which tend to be so abundant as to decrease the lake's esthetic value (*23*). *Menidia* has already become abundant there and seems likely to effect at least some reduction in the *Chaoborus* population. However, *Menidia* also feeds heavily on on herbivorous zooplankters (*24*). Hence an unanticipated result may be an increase in phytoplankton populations. The balance that is finally struck will depend greatly on the intensity of predation on *Menidia* by resident piscivores, such as largemouth bass.

These examples suggest that excessive phytoplankton, a principal symptom of eutrophication, may in some cases be more directly a result of man-caused alterations in fish populations than of man-caused increases in nutrient influx (*25*) and that manipulation of fish populations, especially the artificial enhancement of piscivore populations is a potential method for reducing phytoplankton levels. Unfortunately in shallow lakes such "biological control" of phytoplankton might cause increased standing crops of equally undesirable macroscopic vegetation (filamentous algae and higher plants), as evidenced by *Spirogyra*'s growth in our fish-free pools and other observations of the antagonistic relationship between phytoplankton and macroscopic plants (*26*). Whether or not such side effects could be circumvented by the manipulation of other populations or variables is not yet known. But one point is clear: fish deserve a higher place in the conceptual schemes of eutrophication research than they are now accorded.

STUART H. HURLBERT
JOY ZEDLER, DEBORAH FAIRBANKS
Department of Biology, San Diego State College, San Diego, California

References and Notes

1. B. Dussart, *Limnologie—l'Etude des Eaux continentales* (Gauthier-Villars, Paris, 1966); G. E. Hutchinson, *A Treatise on Limnology* (Wiley, New York, 1967), vol. 2; F. Ruttner, *Fundamentals of Limnology*, D. G. Frey and F. E. J. Frey, Transl. (Univ. of Toronto Press, Toronto, ed. 3, 1963); S. A. Sernov, *Allgemeine Hydrobiologie* (VEB Deutsch. Verlag Wiss., Berlin, 1958).
2. J. Omer-Cooper, *Proc. Egypt. Acad. Sci.* **3**, 1 (1948).
3. See review by J. Hrbáček, *Cesk. Akad. Ved. Rada Mat. Prírod.* **72**, 1 (1962).
4. J. L. Brooks, *Syst. Zool.* **17**, 273 (1968); ——— and S. I. Dodson, *Science* **150**, 28 (1965); M. G. Galbraith, *Trans Amer. Fish. Soc.* **96**, 1 (1967); E. Grygierek, *Rocz. Nauk Roln. Ser. B* **81**, 189 (1962); A. Gurzeda, *Ekol. Pol. Ser. B* **6**, 257 (1960); D. W. Hayne and R. C. Ball, *Limnol. Oceanogr.* **1**, 162 (1956); A. Hillbricht-Ilkowska, *Bull. Acad. Pol. Sci.* **2**, 537 (1962); J. Hrbáček, *Verh. Int. Ver. Limnol.* **13**, 394 (1958); ——— and M. Novotna-Dvoráková, *Cesk. Akad. Ved. Rada Mat. Prírod.* **75**, 1 (1965); T. T. Macan, *J. Anim. Ecol.* **34**, 691 (1965); M. Straskraba, *Mitt. Int. Ver. Limnol.* **13**, 106 (1965); L. Wells, *Limnol. Oceanogr.* **15**, 556 (1970).
5. L. T. Dees, *U.S. Bur. Commer. Fish. Fish. Leafl. 25* (1961).
6. This experiment was originally designed as a project for a course in aquatic ecology, and we thank the following students for setting up the pools and for the zooplankton data for 2 Dec.: S. Adair, N. Bailey, J. Blecha, J. Carlberg, S. Lacey, D. Mendola, J. Miller, J. Scholl, and C. Schwalm.
7. Along the row we alternated experimental and control pools. The extra pools at the ends of the row eliminated end effects, such as might be anticipated from aquatic insects flying in from other areas.
8. Water for phytoplankton analysis was collected from a few centimeters below the surface of the pools. Large phytoplankters were concentrated and enumerated on 5.0-μm Millipore filters; small phytoplankters, such as *Coccochloris peniocystis* (2 to 3 μm long), were enumerated in unconcentrated water samples on a hemacytometer. Identification and nomenclature of algae accord with G. W. Prescott ["Algae of the Western Great Lakes area," *Bull. Cranbrook Inst. Sci. No. 30* (Cranbrook, Mich., 1951)] and F. Drouet and W. A. Daily [*Butler Univ. Bot. Stud.* **12**, 1 (1956)].
9. Zooplankton were collected with a rectangular plankton net (mesh aperture ~ 110 μm) the bottom edge of which rode about 3 cm above the sand surface; they were enumerated in a Sedgwick-Rafter counting chamber. Identification of rotifers, annelids, and crustaceans accords with accounts by W. T. Edmondson, C. J. Goodnight, and J. L. Brooks [*Freswater Biology*, W. T. Edmonson, Ed. (Wiley, New York, ed. 2, 1959)].
10. Only ephydrid (*Ephydra, Brachydeutera*) pupae and dead mayfly imagoes were counted and removed. During January and February the surfaces of pools without *Gambusia*, but not those with, were covered with thousands of adult chironomid midges, dead and alive, and their pupal exuviae.
11. Water for phosphorus analysis was collected from mid-depth. Total dissolved phosphorus was determined with water samples filtered through a 0.45-μm Millipore filter, and total phosphorus with samples not so filtered. The perchloric acid–acid molybdate method of J. H. Rigler [*Limnol. Oceanogr.* **9**, 511 (1964)] was used in both cases. Dissolved inorganic phosphorus was determined by the extraction-acid molybdate method of J. Shapiro, W. M. Chamberlain, and J. Barret [*Proc. 4th Int. Conf. Water Pollution Res.*, Prague (1969)] and W. M. Chamberlain and J. Shapiro [*Limnol. Oceanogr.* **14**, 921 (1969)]. Values for particulate phosphorus and dissolved organic phosphorus were obtained by subtraction.
12. Benthic organisms were sampled by taking, from each pool, three cores of sediment, 5 cm in diameter, including 1 to 2 cm of overlying water. The cores were combined, and organisms were concentrated by sieving with a plankton net (mesh 110 μm) and then examined in a Sedgwick-Rafter counting chamber.
13. *Chara* and *Spirogyra* were collected at the end of the experiment and squeezed in a net to remove excess water.
14. Transmissivity determinations were made on unfiltered water with a Bausch and Lomb Spectronic 20 colorimeter using glass tubes having a light path of 1 cm.
15. Turbulence caused by swimming fish and substances excreted by the fish may have had direct effects on the system, but they probably were minor relative to secondary effects arising from reduction of zooplankton populations.
16. Examples of depression of rotifer by cladoceran populations are given by S. H. Hurlbert, M. S. Mulla, H. R. Willson, *Ecol. Monogr.*, in press; G. C. Anderson, G. W. Comita, V. Engstrom-Heg, *Ecology* **36**, 757 (1955); W. Pennington, *J. Ecol.* **5**, 29 (1941).
17. Average linear dimensions (width or length) of *Pandorina, Pediastrum, Scenedesmus*, and *Haematococcus* were 40, 35, 20, and 15 μm, respectively.
18. See E. J. Kuenzler, *J. Phycol.* **6**, 7 (1970), and references therein, for data on liberation of dissolved organic phosphorus by algae.
19. The majority of chironomid larvae were of early instars 0.5 to 3.0 mm long. Identification of later instars by S. Frommer, University of California at Riverside, showed *Tanytarsus* to be the most abundant, with *Tanypus, Cricotopus*, and *Chironomous* also present.
20. E. C. Bay and L. D. Anderson, *J. Econ. Entomol.* **59**, 150 (1966).
21. In their contracted, preserved condition both species were 500 to 800 μm long. *Aeolosoma* was 60 to 70 μm in diameter with setae also 60 to 70 μm long. *Chaetogaster* was 80 to 120 μm in diameter with setae about 25 μm long.
22. In earthen ponds measuring 4 by 6 m, *Gambusia affinis* essentially eliminated crustacean zooplankters, had complex effects on rotifer populations, and caused tenfold increases in phytoplankton populations. The difference in phytoplankton would have been even greater had it not been for the large populations of zooplanktivorous insects (*Notonecta*: Hemiptera that developed in fish-free ponds (S. H. Hulbert, unpublished data). T. Stephanides [*Prakt. Hell. Hydrobiol. Inst.* **9**, 3 (1964)] records the devastation of the invertebrate fauna of a small, otherwise fishless lake on the island of Corfu, Greece, after introduction of *Gambusia*.
23. S. F. Cook and R. L. Moore, *Trans. Amer. Fish. Soc.* **99**, 70 (1970).
24. R. P. Saunders, "A study of the food of the Mississippi silversides, *Menidia andens* Hay, in Lake Texoma," thesis, University of Oklahoma (1959).
25. J. L. Brooks [in *Eutrophication: Causes, Consequences, Correctives* (National Academy of Sciences, Washington, D.C., 1969), p. 236] has suggested that changes in zooplankton populations during accelerated eutrophication in Lake Erie are partly a result of increased numbers of zooplanktivorous fish following decline in numbers of piscivorous fish. Declines in piscivores may be due to their relatively higher oxygen requirements, which more and more often are not met as eutrophication proceeds. Whatever caused the initial decline in a lake's piscivore population, in a marginal situation such a decline could become autocatalytic. Through action and reaction along the food chain, every decrease in the piscivore population would lead to increased phytoplankton populations which, in turn, would render the lake even more unsuitable to piscivores [F. E. Smith, in *ibid.*, p. 631].
26. A. D. Hasler and E. Jones, *Ecology* **30**, 359 (1949); S. Olsen, *Bot. Tidsskr.* **59**, 273 (1964); N. C. Morgan, in *Man-Made Lakes*, R. H. Lowe-McConnell, Ed. (Academic Press, New York, 1966), p. 155.

27. This was supported in part by a grant from San Diego State College Foundation. We thank William E. Hazen and Thomas A. Ebert for reading and commenting on this report.

10 September 1971