1 October 1971, Volume 174, Number 4004 SCIENCE

Ship Canals and Aquatic Ecosystems

Equilibrium has not been achieved since the Erie, Welland, and Suez canals were built.

William I. Aron and Stanford H. Smith

Through a combination of ecosystem homeostasis and the perversity of man and nature, oftentimes the significant biological changes effected by environmental modifications are not detected until long after the initial change has taken place. The immediate impact, which may range from the spectacular to the undetectable, is a deceptive measure of the long-term and often more important changes in the ecosystem. Two major engineering achievements illustrate this premise: (i) construction of the Erie Canal, which provided access from the Atlantic Ocean to the Great Lakes, and the Welland Canal, which bypassed the block between Lakes Ontario and Erie created by Niagara Falls (Fig. 1), and (ii) construction of the Suez Canal between the Red Sea and the Mediterranean Sea. The Erie Canal was opened to Lake Ontario in 1819 and to Lake Erie in 1825, and the Welland Canal was opened in 1829 (*1*). The Suez Canal was opened in 1869. In both areas there was a long lag between the physical connection and the appearance of major biological changes. In the Great Lakes the changes, when they finally occurred, were explosive and resulted in major shifts in the abundance, composition, distribution, and growth of the fish fauna throughout the lakes. Changes that followed the opening of the Suez, although more gradual, were also dramatic. These examples serve as a backdrop to speculations about the biological implications of the proposed sea-level canal in Central America.

Dr. Aron is director of the office of ecology and environmental conservation, National Oceanic and Atmospheric Administration, Washington, D.C. 20230. Dr. Smith is senior investigator at the Great Lakes fishery laboratory of the U.S. Fish and Wildlife Service, Ann Arbor, Michigan 49107. This paper is dedicated to the memory of Heinz Steinitz, whose scholarship and persistent enthusiasm opened many new pathways to our knowledge of the Suez Canal region.

Canals and the Great Lakes

The catch data from the Great Lakes fisheries over the past 100 years reveal continual changes in species abundance. Less than a dozen species have been major contributors (over 1 million pounds per year) to the catch (*2*) and, despite an intensive, selective fishery, major and permanent changes in these species were sporadic and usually local until the influence of marine invaders was manifested. This influence became apparent in the late 1800's in Lake Ontario (*3*) and has become apparent during the last three decades in the other deep Great Lakes (Superior, Michigan, and Huron). The changes reflect the complex interactions resulting from exploitation and from the impact of exotic species which entered the lakes through canals. The changes which have occurred in Lake Erie (the shallowest of the Great Lakes) and which have accelerated in recent years (*4*) are not included in this discussion because we lack data about the additional interactions resulting from pollution (*5*).

Evidence anticipating the events which were to occur throughout the four deep Great Lakes was first noted in Lake Ontario, the lowermost of the lakes and the first to be reached by a canal system. The alewife (*Alosa pseudoharengus*) was first recognized in Lake Ontario in the spring of 1873, when at least three observers reported it was present in abundance. The best evidence suggests that it entered the lake through the Erie Canal (*3*). The first section of the canal, which allowed barges to move between New York City and Lake Ontario, opened in 1819, 54 years before the first recorded observation of the alewife in the lake. Earlier entrance of the alewife through the St. Lawrence River appears to have been prevented by the abundance of large piscivores, particularly the Atlantic salmon (*Salmo salar*) and the lake trout (*Salvelinus namaycush*). The Atlantic salmon, the most abundant, declined sharply during the 1860's, and the lake trout underwent a decline that apparently started in the late 1860's. Timing of these declines was coincident with the establishment of alewives in Cayuga and Seneca lakes in New York, within the Lake Ontario drainage, via the Erie Canal (*3*).

The initial reaction of many fishery observers to the sharp increase of alewives in Lake Ontario was positive because they expected this prolific and abundant species to provide forage for the more valuable predators. The concurrent decline in the 1870's of the once very abundant lake herring (*Leucichthys artedi*) alarmed some people, but others believed that the alewife would be a more valuable and productive fish. Optimism was short-lived; by the 1890's the abundance of all major game and commercial species of the lake had declined (Fig. 2). Although the Atlantic salmon and lake trout declined during periods of inten-

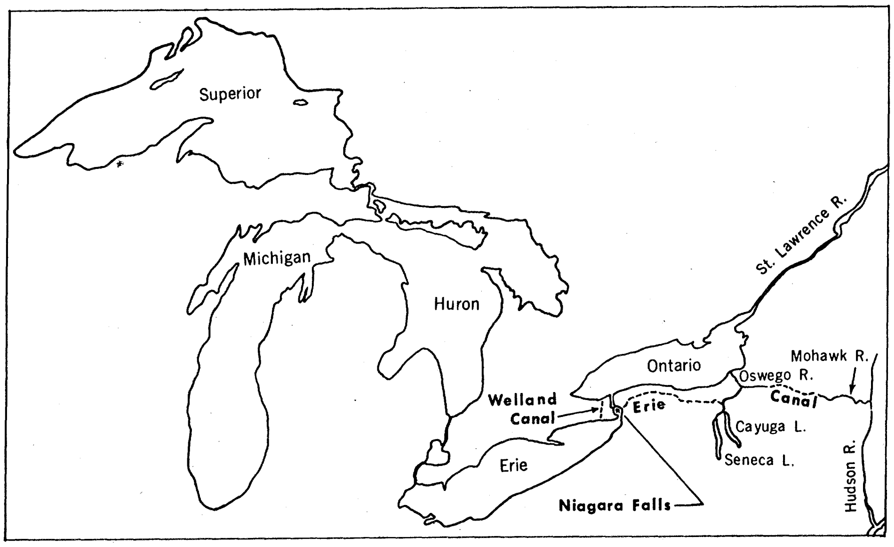

Fig. 1. The Great Lakes and the location of the Erie and Welland canals. The maximum and mean depths (in feet) of each lake are, respectively: Superior, 1333 and 487; Michigan, 923 and 276; Huron, 750 and 195; Erie, 210 and 58; Ontario, 802 and 283.

sive fishing, a reduction in fishing effort after the early 1870's preceded the declines of other species. This timing tends to reduce the likelihood that fishing was the dominant factor in the general collapse of the fish stocks.

These changes in the fishery and the fish stocks of Lake Ontario were amply documented in successive reports of the U.S. Fish Commissioner. The report for 1872–73 on the first survey of the Great Lakes by the commission observed: "From the information received from Lake Ontario it is evident that the fisheries are more reduced than in either of the other lakes" (*6*). In the report for 1887 Smith and Snell noted: "fishing as a means of livelihood along the shores of the great lake (Ontario) and the St. Lawrence River, especially in American waters, is rapidly decaying . . ." (*7*). Commenting on conditions in 1893, the 1895 report (*8*) noted that the collapse of the Lake Ontario fishery was more pronounced than in any body of water in the United States. The 1897 report of the Commissioner of Fisheries, Game and Forests of New York stated: "Part of the decrease in the fisheries can be explained by the stringent laws governing the commercial fishermen, but the main cause is the scarcity of fish" (*9*).

Although the alewife remained the prime suspect contributing to the decline of the fish stocks in the 1890's (*10*), the sea lamprey (*Petromyzon marinus*) probably was a contributing factor as early as the 1880's. The sea lamprey was not mentioned in discussions of fish stocks in Lake Ontario during 1860–80, although it was well known in nearby Cayuga Lake in the 1870's (*11*). There were reports, however, of sea lampreys in Lake Ontario in the 1880's, and it caused serious problems in the 1890's (*12*). Although evaluation is not complete, available evidence gives strong support to the possibility that the sea lamprey entered the Lake Ontario drainage via the Erie Canal. It probably became established first in Cayuga and Seneca lakes during the mid-1800's and then moved down into Lake Ontario as the alewife did. The establishment of the sea lamprey in Lake Ontario later than the alewife could be attributed to the lamprey's longer life cycle. The sea lamprey aroused much less attention in Lake Ontario than it did later in the other Great Lakes, probably because the fishery and fish stocks had already collapsed before it became abundant.

If it had not been for the Welland Canal (Fig. 1) these marine invaders and the havoc they caused might have been contained in Lake Ontario. The white perch (*Morone americana*) is believed to be the only species that reached Lake Erie via the western extremity of the Erie Canal (*13*). The sea lamprey was the first marine invader to pass through the Welland Canal. Its possible impact on the upper Great Lakes was first noted by Hubbs and Brown in 1929 (*14*):

> The occurrence of the sea lamprey in Lake Erie is a recent discovery. The specimens collected at Merlin, November 8, 1921, were the first for the lake to be scientifically reported. Dr. John Van Oosten in the fall of 1927 saw one which had been caught near Sandusky and W. M. Tidd collected one there in the spring of 1928. At the same place Professor E. L. Moseley saw another about two weeks before Mr. W. D. Bates sent us the specimen from near Rondeau. Mr. Bates told Dr. Van Oosten that he occasionally takes the large lamprey in his nets.
>
> There can be little question as to the recentness of the establishment of the species in Lake Erie. That it immigrated into Lake Erie from Lake Ontario through Welland Canal is extremely probable. Since the species is much larger than the native lamprey of Lake Erie, *Ichthyomyzon concolor*, and is known to be very destructive to food fishes in Cayuga Lake, New York, and elsewhere, its establishment in Lake Erie adds another potential factor to those responsible for the depletion of the great fisheries of this important lake.

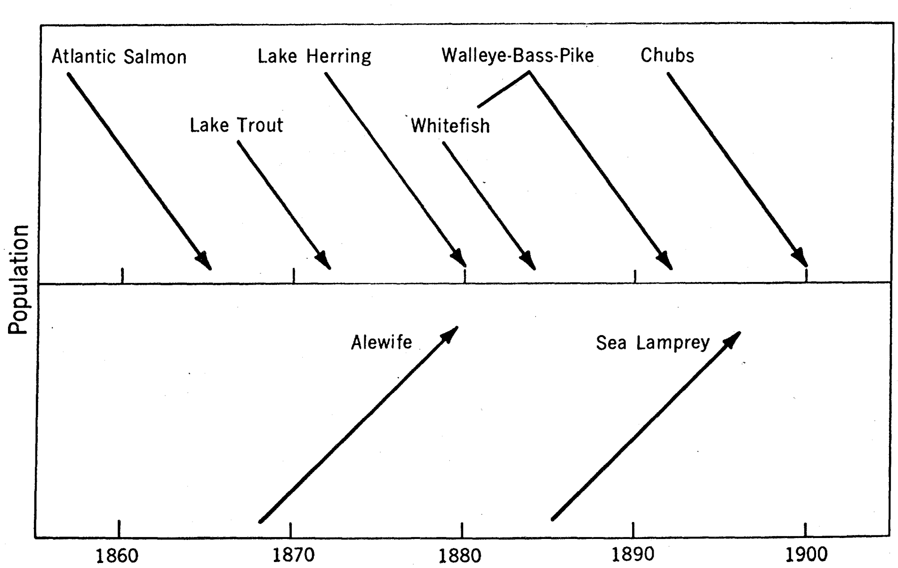

Fig. 2. Trends in fish stocks described for Lake Ontario for the period preceding and following the establishment and increase of the alewife and sea lamprey.

In the later article, Hubbs and Pope (*15*) made an even more prophetic comment confirming the occurrence of the sea lamprey in Lake Michigan:

> The sea lamprey is no doubt not only spreading but also increasing in numbers in the Great Lakes. There is good reason to expect that it will follow the history of the smelt, eventually reaching to the limits of the Great Lakes and greatly increasing in numbers. [The smelt (*Osmerus mordax*) was an intentionally introduced exotic species that has spread throughout the Great Lakes (*16*), and has been suspected of causing substantial ecological disruption in recent years (*17*).] The multiplication of the lamprey has been at a slower rate than that of the smelt, and will continue so, because the life cycle is much longer: Gage . . . estimates the larval life of *Petromyzon* as four or five years, and the immature period of adult life as one and one-third to three and one-third years. In time, however, the sea lamprey may well attain an abundance equal to or greater than that maintained in Lake Ontario and in Cayuga Lake. If that not improbable end be reached, this large and destructive bloodsucking parasite will add one more very serious factor to those already depleting the supply of lake trout, whitefish, suckers, catfish and other commercial fishes in the Great Lakes.

The problems anticipated by Hubbs and others in the upper Great Lakes were well under way by the 1940's. The sea lamprey became established in Lake Huron in 1932 (*18*), and lake trout had started declining sharply by 1940 (*19*). Sea lampreys were first recorded in Lake Michigan in 1936 and in Lake Superior in 1946; within two decades after these first records lake trout were declining rapidly in each lake.

Before the establishment of the sea lamprey, lake trout production was unusually stable in all three upper lakes and was highest in Lake Michigan (Table 1). The history of the catch was similar in the three lakes although timing differed somewhat. Catches in Lake Michigan, for example, increased in 1879 during the development of the fishery. Production was highest during 1890–1911 and was characterized by periods of relative stability at slightly lower levels in 1912–26 and 1927–39 (*20*). The catch increased briefly in 1940–44, after which it underwent the collapse attributed to sea lamprey predation. Lake trout neared extinction by the mid-1950's due to a complete failure of natural reproduction after 1948 (*21*). The lake trout was probably most heavily exploited in Lake Michigan; this factor may have contributed to variations in the catch before the population collapsed. The production and stocks were even more stable in Lakes Huron and Superior before the establishment of the sea lamprey.

The abundance of sea lampreys was relatively low in each of the three upper Great Lakes at the time when lake trout stocks started to decline (*20*). The lake trout was unquestionably the prime target of the sea lamprey as it was the only abundant species of large fish that inhabited the colder (subthermocline) regions of the lakes preferred by the sea lamprey. That the decline of lake trout in Lake Michigan was particularly abrupt is possibly due to the interaction of increasing predation by the lampreys and greater exploitation by the commercial fishery (*20*). The burbot (*Lota lota*) was also a large deepwater predator in the three upper lakes. Fishing records did not provide a measure of abundance for this species because there was little market for it; however, its decreasing appearance in experimental and commercial nets indicates that it declined simultaneously with the lake trout as lamprey predation increased.

A second important deepwater fishery in Lake Michigan was based upon the chubs (*Leucichthys* spp.) which are smaller than the lake trout and burbot, less valuable to the fishery, and less desirable prey for large lampreys. As the lake trout declined both the fishermen and the sea lamprey altered their targets for predation (*22*). The change in the fishery was reflected by a catch of chubs in 1949 of 7 million pounds; the catch then increased to an annual rate above 10 million pounds during 1951–57. Earlier catches had been as low as 2 million pounds.

The consequence of this extreme pressure of high commercial production and sea lamprey predation on the

Table 1. Lake trout production (thousands of pounds) and sea lamprey abundance [expressed as a percentage of the mean counts of spawning runs; Smith (*20*)] in Lakes Huron, Michigan, and Superior from 1930 to 1966.

Year	Huron*		Michigan		Superior	
	Lake trout	Sea lamprey	Lake trout	Sea lamprey	Lake trout	Sea lamprey
1930	2993		5441		4019	
1	3263		5632		4321	
2	3457	(E)†	5470		4191	
3	3313	—	5212		3461	
4	3138	—	4957		4634	
1935	3812	—	4873		4994	
6	3538	—	4763	(E)†	4829	
7	3094	—	4988	—	4784	
8	3017	—	4906	—	4835	
9	2622	—	5660	—	4052	
1940	1979	—	6266	—	3938	
1	2002	—	6787	—	4153	
2	1528	—	6484	—	4320	
3	976	—	6860	—	4376	
4	676	50‡	6498	—	5292	
1945	290	68	5437	—	4848	
6	68	90	3974	3‡	4975	(E)†
7	19	111	2425	16	4250	—
8	14	145	1197	27	4401	—
9	4	275	343	43	4322	—
1950	<1	210	54	148	4699	—
1	<1	216	11	345	4184	—
2	<1	105	4	90	4227	—
3	<1	130	<1	252	3785	24‡
4	<1	113	<1	199	3522	45
1955	<1	153	<1	164	3104	53
6	<1	122	0	155	2340	138
7	0	91	0	165	1515	223
8	<1	61	0	80	1426	114
9	<1	31	<1	68	1106	141
1960	<1	84	<1	52	503	221
1	<1	53	<1	101	371	228‖
2	0	58	<1	63	327	47
3	1	52	26	59	213§	66
4	1	30	<1	36	208	39
1965	1	15	<1	26	226	38
6	<1	36	<1	9‖	228	23

* Excluding Georgian Bay and North Channel. † Indicates year of first evidence of establishment of sea lamprey (*18*). ‡ First year for which sea lamprey counts are available. ‖ Year in which the first round of chemical treatment of lamprey spawning streams was completed. § The lake trout fishery was closed in mid-1962, and subsequent production was limited to the number required for biological assessment; production hence does not reflect abundance (*28*).

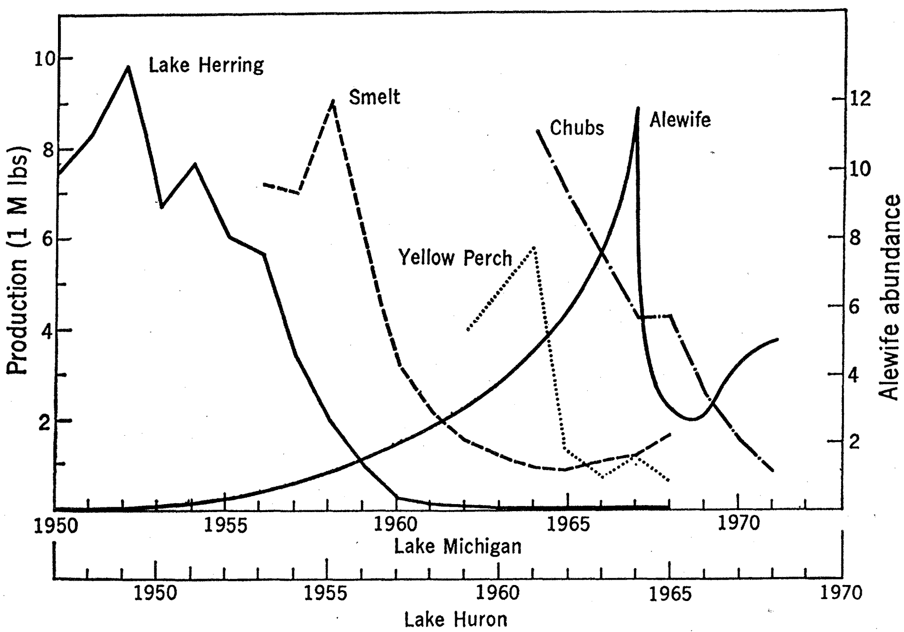

Fig. 3. Generalized population trend of the alewife, based on available abundance data from Lakes Michigan and Huron, superimposed to match the year of peak abundance for the lakes and showing the successive declines in the production of lake herring, smelt, and yellow perch for Lake Michigan, and chubs for Lake Huron.

chub population was severe. A fishery survey of Lake Michigan in 1960–61 showed major changes in the species composition and abundance of chubs. Of the seven species of chubs that inhabited Lake Michigan the two largest (*Leucichthys johannae* and *L. nigripinnis*) had apparently become extinct, and the four species of intermediate size (*L. alpenae, L. kiyi, L. reighardi,* and *L. zenithicus*) had been seriously depleted (*22*). The smallest and slowest growing chub, the bloater (*L. hoyi*), was favored during this period and became very abundant. It had been a primary food of the lake trout (*23*), and most were too small to be taken profitably in commercial gill nets or to serve as prey for the sea lamprey. As the supply of larger chubs declined during the late 1950's, the commercial gill net catch declined and the abundance of sea lampreys decreased.

When the sea lamprey reached maximum abundance in Lake Michigan during the mid-1950's, it was observed more frequently in shallower areas of the lake where it preyed heavily on whitefish (*Coregonus clupeaformis*), suckers (*Catostomus* spp. and *Moxostoma* spp.), and walleyes (*Stizostedion vitreum vitreum*), all of which suffered sharp reduction in stocks. The deepwater fishery, supported only by chubs, increased to a new high of 12.7 million pounds in 1960, much of which consisted of small bloaters which were taken in trawls and sold as animal food.

An almost unnoticed but significant event that led to even more extreme disruption in Lake Michigan was the establishment of the alewife, which was first reported in 1949. Alewives were uncommon in the early 1950's but started an explosive increase in the late 1950's that culminated in a peak during the winter of 1966–67 (*3*).

The first records of alewives above Niagara Falls are from Lake Erie in 1931, 58 years after the first official record in Lake Ontario (*3*). The species has never become abundant in Lake Erie, possibly because of the continued high abundance of predators and also because of the lack of deep water where alewives concentrate in winter months to avoid extremely cold water. Alewives were first captured in Lake Huron in 1933, in Lake Michigan in 1949, and in Lake Superior in 1954 (*24*).

Lakes Huron and Michigan also provided examples of the decline of predators as a condition for alewife establishment. Following the first record in Lake Huron (*25*), observations of alewives were sparse until the early 1950's when a population increase was evident in South Bay (*26*); in 1956 they were taken in large numbers in Saginaw Bay (*24*). Thus alewives did not thrive in Lake Huron until after the extreme reduction of the lake trout during the mid-1940's by sea lamprey predation. In fact, alewives failed to appear in Lake Michigan until 1949, after the lake trout population there had collapsed and when lake trout stocks in Lake Huron had been reduced to a remnant. It appears that the lake trout —and perhaps other large predators such as burbot and walleye, which declined as the lake trout declined—not only delayed the increase of alewives in Lake Huron but also prevented their penetration into Lake Michigan.

Scattered measures of alewife abundance in Lake Superior indicate that alewives also multiplied there after the lake trout population was reduced by the sea lamprey (*3*). Lake trout abundance reached a low about 1960–62, and the reduction was greatest in eastern Lake Superior, where alewives were common in 1963. After chemical control reduced the sea lamprey population in 1962 (*27*), the abundance of lake trout started to increase (*28*); coincidentally, alewives appeared to be reduced after 1963. Lake trout abundance more than doubled during 1962–68 (*29*). In 1968 reports of alewives in Lake Superior were rare, and most of the individuals seen were taken from lake trout stomachs (*3*).

The changes in fish stocks that accompanied and followed the population increase and dominance of the alewife in Lake Ontario occurred in a sequence and at time intervals that were to be repeated as the alewife became abundant in Lakes Huron and Michigan. In general, the sequence has been a decline of the abundant shallow-water planktivores accompanied by a short-term increase of minor piscivores in the first decade after alewife establishment, a decline of minor piscivores in the second decade, and a decline of deepwater planktivores during the third decade as alewives became extremely abundant. The increase in alewives was followed by a severe decline of the two most abundant shallow-water planktivores, the lake herring (Fig. 3) and the emerald shiner (*Notropis atherinoides*). The yellow perch (*Perca flavescens*) and smelt are minor inshore piscivores that increased during the rise in abundance of alewives, but then declined sharply as alewives became extremely abundant. The stocks of chubs, which are deepwater planktivores, collapsed after the period of extreme alewife abundance.

The most spectacular consequences of the alewife population explosion are probably the massive spring die-offs which litter the beaches with dead fish in late spring and early summer. These die-offs were common in Lake Ontario in the late 1870's and in Lake Michigan during the 1960's. Lake Michigan had an extremely heavy die-off in 1967, the year of peak alewife abundance (*30*). Spring die-offs are characteristic of alewives whenever they are abundant in large freshwater lakes. The causes of die-offs are complex and incompletely explained. The conspicuous die-offs, however, are most common during spring and summer when spawning alewives are concentrated near shore, where they are subjected to sharp changes in water temperature. When alewives move to shallow water to spawn they cause another costly problem, less conspicuous to the public, by clogging municipal and industrial water intakes.

The only major benefit of the alewives in the Great Lakes has been associated with the introduction of Pacific salmon. Chinook salmon (*Oncorhynchus tshawytscha*) introductions into Lake Ontario were started in the 1870's in an attempt to replace the Atlantic salmon. Alewives were abundant at that time, and the chinook grew well. Common reports of capture in the lake and of spawning runs indicated good survival, considering the relatively small numbers planted (and perhaps the early state of development of hatching, rearing, and planting techniques). After similar plants in Lake Michigan during the 1870's, when no alewives were present, the very few fish that were recovered showed only modest growth, and the lack of reports of spawning runs indicated poor survival.

In contrast to the early salmon introductions in Lake Michigan, a recent plant of 659,000 coho salmon (*Oncorhynchus kisutch*) smolts in 1966, in the absence of competition by other large predators and in the presence of a superabundance of alewives, showed fast growth similar to that of coho salmon in the marine environment. Survival was excellent. More than 30 percent of the fish planted were recovered by fishermen or accounted for in spawning runs. Mature fish averaged about 10 pounds in the fall of 1967 (*31*). Chinook salmon planting, which was started in 1967, is also resulting in good growth and survival.

Planting of coho salmon in Lake Superior since 1966, when alewives were very sparse, have resulted in only fair growth and survival.

No major attempt was made to counter the problems caused by the alewife and sea lamprey until recent years, after the fish stocks and the fisheries of the upper Great Lakes had become severely disrupted and there were no other lakes to which fishermen could move, as they did when fish populations collapsed in Lake Ontario in the late 1800's. A major attempt is being made to control the sea lamprey in the upper lakes by applying a selective chemical to kill sea lamprey larvae in spawning streams (*27*). As lamprey control measures are being applied, introduction of approximately 10 million trout and salmon (mostly lake trout and Pacific salmon) are being made each year to establish stocks of large predators. The large predators may, in turn, reduce alewife abundance.

It is premature to predict the outcome of the Great Lakes story. The chain of events precipitated by canal construction and amplified by other man-induced effects is incomplete. It is still uncertain whether present lamprey control methods will be sufficient to reduce predation below the level of substantial damage to large piscivores. After 9 years of reduced sea lamprey populations and 11 years of intensive stocking of lake trout in Lake Superior there is still no evidence of widespread or significant recovery of lake trout spawning stocks or natural reproduction. The degree of reduction of alewives in Lake Michigan, where the heaviest predator introductions are being made, is still not clear, and there is no basis for anticipating the degree of recovery of the various species that declined as alewives became abundant. Restoration of favorable and productive fish stocks in the Great Lakes may be difficult, however; for both the alewife and the sea lamprey, even when they were at low abundance during their establishment, caused severe reductions of previously very abundant and valuable species.

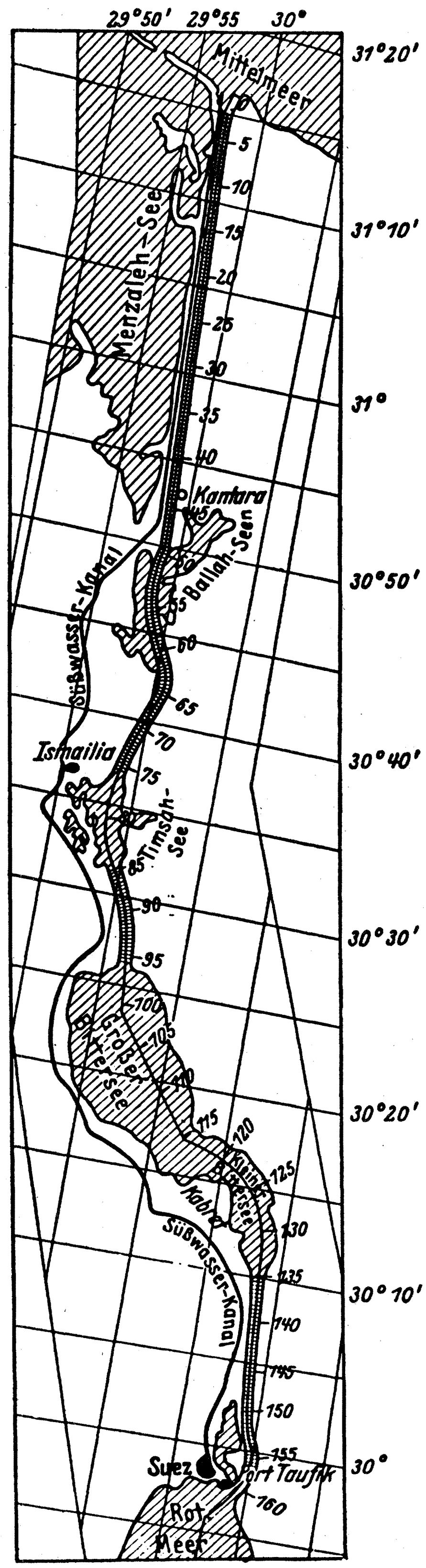

Fig. 4. Suez Canal.

Effects of the Suez Canal

The ecological history of the Suez Canal may be best characterized as inadequate. Although many biological problems of the dispersal of biota via the Suez Canal were recognized early [in 1865, 4 years before the opening of the canal, Vaillant (cited by Keller, *32*) expressed his conviction that the new channel "will doubtlessly bring about an interchange of the species"], little was done to promote their study. The early works of de Lesseps (*33*), Fuchs (*34*), Keller (*32*), Tillier (*35*), and, in particular, Fox (*36*), leader of the 1924 Cambridge University Expedition, seemed to have closed the door to all but occasional visits by isolated biologists to the canal area. The urgent plea in 1919 by W. Steinitz (*37*) went unheard. He wrote, "The Suez Canal is, apart from the recently completed Panama Canal, the only place on earth where two totally separated faunal provinces can freely interchange. . . ."

The Suez Canal is about 160 kilometers long and about 50 to 100 meters wide (Fig. 4). It was originally dredged to a depth of nearly 8 meters; it has no locks. It is not, however, without significant barriers, which prevent the simple exchange of biota between the two seas. The prime barriers are the Bitter Lakes, which at the time the canal was first opened had salinities up to 68 per mille (*38*) and as a consequence were an important obstacle to the movement of plants and animals. Second, and probably no less important, the basic edaphic conditions of the canal are not conducive to dispersal. The canal lacks a hard bottom and through most of its history its waters were highly turbid due to the constant movement of ships and the frequent dredging operations that were required for maintenance. The canal was also polluted slightly by the merchant ships. Finally, the "brackish barrier" (*39*) resulting from the flow of the Nile River probably has had some effect on movements, although its importance is somewhat controversial.

Possibilities of biotic exchange existed between the Red Sea and Mediterranean before the opening of the Suez Canal. Since eustatic changes of the sea level occurred during the Pleistocene and during interglacial periods, the sea probably covered the present-day isthmus. In later times, from the 13th century B.C. until late in the 8th century A.D., channels and natural waterways maintained a connection between the two seas. [This pre-Suez history was reviewed by Por (*40*), who suggested that only a few species exist in the Mediterranean that might be suspected of originating from the Red Sea before the 1869 opening of the canal or which may be considered as tropical relics.] This judgment is a posteriori and, according to Por, therefore open to criticism, particularly in view of the fact that our knowledge of the Mediterranean biota is still incomplete.

The first information on the migration of the Red Sea and Mediterranean faunas into the Suez Canal was recorded in 1882 by Keller (*32*). W. Steinitz in 1929 (*41*) recognized Indo-Pacific elements off the Israeli Coast. By 1970 his son, H. Steinitz, was able to compile a list of 140 marine animals that had moved from the Red Sea into the Mediterranean and 42 in the opposite direction (*42*).

The successful migrants, according to Por (*40*) fall into two ecological groups: (i) the strong swimming littoral fishes, peneid shrimp, and portunid crabs; and (ii) the biota of the littoral level bottoms, with a severe restriction on those that have pelagic larvae. These groups result from the highly stratified salinity structure of the Bitter Lakes and the probability that the lakes are not crossed by any through-going current. With the exception of a few good swimmers, Por contends that every prospective migrant has to stop and settle for at least one generation in the Bitter Lakes. Por likewise discounts the importance of the role of passive transport (attachment to ship hulls or redistribution through ballast waters).

The one-sided nature of the exchange between the two seas is obscured by a simple listing of successful migrants because none of the Mediterranean migrants into the Red Sea are commonplace; most records are based upon one or a few specimens. On the other hand, many of the Red Sea species that entered the Mediterranean are now found commonly in the latter sea. Among the fishes, for example, 30 Red Sea species may be found in the Mediterranean, of which 16 have been reported since 1953 (*43*). Only three or four of these species may be regarded as rare; the remaining ones either constitute an important part of the commercial fishery or serve as food for commercially important species. For example, the goat fish, *Upeneus moluccensis*, a Red Sea species, is now commercially important in the fisheries of Turkey and Greece, and the lizard fish, *Saurida undosoquamis*, another migrant, forms the main catch of trawlers off Mersin, Turkey (*44*).

The essentially unidirectional nature of dispersal is, possibly, best explained by combining the views of Por and Ben-Tuvia. Por dismissed the suggestion by most previous workers that a northward current in the canal could account for the pattern which has become evident. He described the eastern Mediterranean as a zoogeographical "cul-de-sac," a tropical sea, undersaturated with Atlantic-temperate fauna. The high-salinity, warm, nutrient-impoverished waters of the eastern Mediterranean are not conducive to the success of species adapted to more temperate seas. Ben-Tuvia, in considering the ichthyofauna, points out the higher number of species contained in the Red Sea, as compared to the eastern Mediterranean. He says. "The high number of species in this region is an expression of a diversified adaptation to the various ecological biotopes of tropical and subtropical waters. Thus it can be expected that the more vigorous Indo-Pacific species are able to compete with the indigenous species of the eastern Mediterranean, while the less numerous east Atlanto-Mediterranean species are less likely to be adapted to the Red Sea conditions."

In large part this explanation of the success of Red Sea species in the Mediterranean accounts for the failure of the reverse dispersal. Not only are the Atlantic-temperate forms poorly adapted to succeed in the Red Sea, but the Red Sea itself is a typical tropical sea with a population at equilibrium with its environment.

The basic inadequacy of the data makes it impossible to recount the changes brought about by the Suez Canal in detail comparable to that used in describing the changes caused by canals in the Great Lakes. It is important to note, however, that a lag did ensue between the opening of the canal and the resultant biological consequences. That this lag is real and cannot be blamed on the neglect of observing scientists is borne out largely by the changes in the commercial fisheries.

Of particular interest for this discussion is the probability that several environmental changes will largely serve to accelerate the dispersal. When Egypt started operating the canal in the middle 1950's, she undertook a major program for deepening the passage from 8 to 11 meters. This deepening undoubtedly improved circulation through the canal. The salinity of the Bitter Lakes, 68 per mille in 1869, had decreased to 52 per mille by 1924 and is now about 41 per mille (*38*), or about the same as the salinity at either entrance to the canal.

The closure of the Suez Canal to shipping has almost certainly been a boon to the biota. The waters of the canal, now undisturbed by either ships or dredging, have never before been as clear or as quiet. Piers and port installations have not been maintained, and algae and sessile fauna have been left to thrive.

Finally, the impoundment of the Nile in 1964 by the Aswan Dam basically eliminated the "brackish barrier." This most recent engineering accomplishment, however, has its negative side effects for the marine biota; it deprives the nutrient-deficient Levant basin of its prime nutrient source. The long-term consequences of this change are most uncertain; however, a significant decline in the local sardine fishery has already been noted (*45*).

It should be fairly clear that the eastern Mediterranean is still in a condition of disequilibrium. Competitive pressures between the Atlantic and Red Sea species will probably increase because of both the declining nutrient supply and the improved opportunities for dispersal. In terms of effective utilization of incoming energy through all trophic levels, it is almost a truism to suggest that when equilibrium is finally attained, the ecosystem will be more efficient than in the past. This improved efficiency, however, in no way suggests that the ultimate composition of the biota of the eastern Mediterranean will be more valuable to man. It is also reasonable to suspect that, with the exception of a few more or less cosmopolitan species, the prime impact of the Red Sea biotic intrusion will be limited to the eastern Mediterranean.

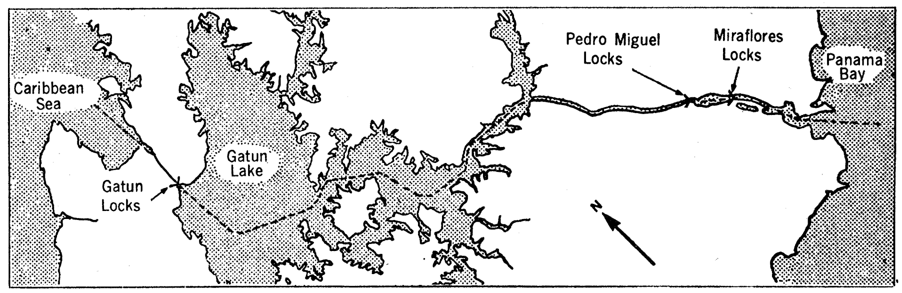

Fig. 5. Panama Canal.

Proposed Central American Canal

The release of the Atlantic-Pacific Interoceanic Canal Study Commission report, "Interoceanic Canal Studies, 1970," which recommended the construction of a new sea-level canal not far from the existing Panama Canal, marked another step in the continuing controversy regarding the possible ecological impact of such a canal. Boffey (*46*) reported the concern of Ernst Mayr, chairman of a National Academy of Sciences Committee on Ecological Research for the Interoceanic Canal over the minimization of the potential dangers of canal construction in the commission's report.

As might be expected, particularly during this period of "environmental concern," the plans for a new sea-level canal have drawn a great deal of attention and controversy. At one extreme, Lamont Cole, when discussing the possibility of canal construction through the use of atomic energy said, "I think this is the most irresponsible suggestion that I can remember since Admiral Byrd's senile proposal to blow ice caps off Antarctica" (*47*). Likewise, just the title of John C. Briggs's paper (*48*) on the subject, "The sea level canal: potential biological catastrophe," reflects something of the controversy created by the issue. At the other side, however, John Sheffey, executive director of the Canal Commission, has said that the environmental consequences of canal construction will not be particularly significant. He has been quoted as saying, "The possibilities of any serious disruption to nature are very remote," and, "the potential threat to biota is so insignificant that it doesn't merit spending a lot of money on it" (*47*).

If we are to believe the lessons provided by the Great Lakes and the Suez Canal, we must anticipate that a sea-level canal will cause changes in the Atlantic and Pacific ecosystems, and that these changes might be modest, if noticeable, in the next half-century, but might ultimately be great. The available information, however, does not permit a value judgment as to whether these changes will be positive, negative, or neutral in their impact on man.

The studies conducted to date in the Panama Canal region are too limited to provide either predictive capability or even the minimum ecological insight that would be needed to delineate potential problem areas. The existing Panama Canal joins the Atlantic and Pacific oceans at a point where the Central American Isthmus is about 80 kilometers wide (Fig. 5). More than half the length of the canal is occupied by Gatun Lake, a major freshwater barrier to the dispersal of biota between the two oceans. Menzies (*49*) successfully towed specimens wrapped in cheesecloth through the canal at a speed of 10 knots, and Chesher (*50*) examined the possibility of biotic transfer through ballast water of ships. In both studies one could conclude, as Chesher did [although Rubinoff (*51*) discounts Chesher's arguments and points out several errors in his paper] that biota could transit the existing canal and that the failure of colonization so far demonstrates that a sea-level canal would create little or no threat to the marine biota. Likewise, although a number of marine species such as the tarpon and snook are known to have invaded the fresh waters of Gatun Lake and presumably occasionally pass through the locks in both directions (*51*), only one species of fish—a small goby (*Gobiosoma nudum*)—has actually been found to have traversed the canal from the Pacific to the Atlantic (*52*). This lack of major transfer could also be used to support a prediction that the consequences of the opening of a sea-level canal would be trivial.

We must remember, however, that the existing Panama Canal was first opened in 1914 and that the freshwater block imposed by Gatun Lake presents a very significant obstacle to dispersal. We must also remember that 58 years passed between detection of abundant populations of alewives in Lake Ontario and their first occurrence in Lake Erie, and that some 40 years passed between the time the sea lamprey was known to be established in Lake Ontario and the time it was first found in the Upper Great Lakes. For both the alewife and sea lamprey the first major biological impact occurred more than 50 years after the environmental modification in Lake Ontario, and another 50 years passed before the disruption started what is just now reaching a state of extreme instability in the upper lakes. The situation in the Suez is much the same, although more poorly documented and still in a state of flux. In the case of the Suez Canal, we would further contend that the real impact of the environmental alteration was somewhat masked by the basic sterility of the environment. Had major fisheries existed in the eastern Mediterranean, as they did in the Great Lakes, the changes would have been more noticeable.

Appropriate studies in advance of canal construction should be undertaken, if for no other than practical reasons. Although we cannot share John Briggs's (*48*) extremely pessimistic outlook in terms of species extinction (he predicted the loss of anything from 1000 to more than 5000 species), we nevertheless take little comfort in the view that sea-level canal construction will result in adjustment, not tragedies. These adjustments may be viewed in a positive light—the occupancy of a vacant niche or the displacement of a congeneric or confamiliar species from a niche by the new arrival which may be better adapted. These changes could be viewed as leading to a better use of the food chain and potentially improved yields of commercially valuable fish, as appeared to be the case when the alewife first appeared in abundance in Lake Ontario. Ultimately, however, it became clear that the alewife used only a fraction of the niches occupied by species that it displaced, thus reducing total fish productivity (*3*).

Aside from the losses to commercial fishermen, the monies spent on cleaning up the results of massive die-offs of alewives, and the losses to the recreational and tourist industries, Canada and the United States have already spent nearly $20 million to control the sea lamprey. Now that a basic technique of control has been worked out, the annual cost of the lamprey abatement program in Lake Superior is approximately $500,000. Assuming substantial success, the projected annual net benefit of this program to just the lake trout fishery is $2.1 million. This projection is based on a lake trout catch of 4 million pounds. Lamprey control throughout the Great Lakes may cost $2.6 million annually, but the benefits will be greater if problems of the alewife can be reduced, and, in doing so, alewives can be eaten by salmonids.

For comparison, the fisheries of the Panama Bight alone annually produce about 66 million pounds of food fish and 149 million pounds of fish used for fish meal. Included with the food fish are roughly 28.6 million pounds of shrimp.

The predictions of scientists in the 1930's concerning the sea lamprey are a tribute to their insight, based upon knowledge of the Great Lakes ecosystem, where detailed observations and data have accumulated for more than a century. For the waters off Central America, however, the benchmark data necessary for predictive capability are generally lacking, except perhaps in the case of several important commercial fisheries. The marine fauna and flora of Central America are poorly known, not only in terms of their ecological interactions, but also, perhaps more disturbingly, even in terms of their kinds and distributions. A basic survey of the area remains to be undertaken which should include the total tropical biota from either side of the isthmus. Laboratory work and behavioral studies must be accomplished to evaluate the potential of interbreeding, the possible introduction of diseases and possible interactions of commercially valuable species. The raw data to permit the development of predictive models must be obtained if we are to diagnose the problems posed by a sea-level canal in advance of construction. Likewise, we must have these data to permit a thorough evaluation of the changes after such a canal is opened to take advantage of, as Carl Hubbs (*53*) points out, "an opportunity of the ages to carry on research on species and faunas that are almost certain to be intermixed, particularly from the Pacific into the Atlantic."

References and Notes

1. H. Hatcher, *Lake Erie* (Bobbs-Merrill, New York, 1945).
2. H. J. Buettner, *U.S. Bur. Commer. Fish. C.F.S. 4825* (1968), p. 22.
3. S. H. Smith, *Trans. Am. Fish. Soc.* **99**, 754 (1970).
4. V. C. Applegate and H. D. Van Meter, *U.S. Fish Wildl. Serv. Fish. Leafl. 630* (1970).
5. A. M. Beeton, *Trans. Am. Fish. Soc.* **90**, 153 (1961).
6. J. W. Milner, "Report on the fisheries of the Great Lakes; the result of inquiries prosecuted in 1871 and 1872," *Rep. U.S. Commer. Fish. 1872–1873* (1874).
7. H. M. Smith and M. Snell, "Review of the fisheries of the Great Lakes in 1885," *Rep. U.S. Commer. Fish. 1887* (1891).
8. H. M. Smith, "Report of the division of statistics and methods of the fisheries," *Rep. U.S. Commer. Fish. 1895* (1896), p. 93.
9. J. N. Cobb, *N.Y. Comm. Fish Game For. Annu. Rep. 1897* (1898), p. 205.
10. H. M. Smith, "Fisheries of the Great Lakes," *Rep. U.S. Commer. Fish. 1892* (1894), p. 361.
11. R. L. Wigley, *U.S. Fish Wildl. Serv. Fish. Bull. 154* (1959), p. 561.
12. J. R. Dymond, J. L. Hart, A. L. Pritchard, "The fishes of the Canadian waters of Lake Ontario," *Univ. Toronto Stud., Publ. Ont. Fish. Res. Lab. 37* (1929).
13. W. B. Scott and W. J. Christie, *J. Fish. Res. Board Can.* **20**, 1189 (1963).
14. C. L. Hubbs and D. E. S. Brown, *Trans. R. Can. Inst.* **17**, 1 (1929).
15. C. L. Hubbs and T. Pope, *Trans. Am. Fish. Soc.* **66**, 172 (1937).
16. J. Van Oosten, *ibid.*, p. 160.
17. E. Anderson, thesis, University of Minnesota (1969); *Diss. Abstr.* **31**, 1383B (1970).
18. V. C. Applegate, *U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 55* (1950).
19. R. Hile, *Trans. Am. Fish. Soc.* **76**, 121 (1949).
20. S. H. Smith, *J. Fish. Res. Board Can.* **25**, 667 (1968).
21. P. H. Eschmeyer, *Trans. Am. Fish. Soc.* **85**, 102 (1957).
22. S. H. Smith, *ibid.* **93**, 155 (1964).
23. J. Van Oosten and H. J. Deason, *ibid.* **67**, 155 (1938).
24. R. R. Miller, *ibid.* **86**, 97 (1957).
25. H. H. MacKay, *Copeia* **2**, 97 (1934).
26. W. B. Scott, *Trans. R. Can. Inst.* **34**, pt. 2. 111 (1963).
27. N. S. Baldwin, *Limnos* **1**, 20 (1968).
28. W. Dryer and G. R. King, *J. Fish. Res. Board Can.* **25**, 1377 (1968).
29. *Great Lakes Fish. Comm. Annu. Rep. 1968* (1969), p. 71.
30. E. H. Brown, Jr., *Great Lakes Fish. Comm. Tech. Rep. 13* (1968), p. 20.
31. D. P. Borqueson, *Fish. Div. Mich. Dep. Nat. Resour. Fish. Manage. Rep. 3* (1970), p. 3.
32. C. Keller, *Neue Denkschr. Schweiz. Naturforsch. Ges. 28* (1882).
33. F. de Lesseps, *C. R. Acad. Sci.* **78** (1867); **82** (1868).
34. T. Fuchs, *Denkschr. Kais. Acad. Wiss. Wein Math.-Naturwiss. Kl.* **38**, 25 (1878).
35. J. D. Tillier, *Mem. Soc. Zool. France* **15** (1902).
36. H. M. Fox, *Trans. Zool. Soc. London* **2**, 1 (1926); *ibid.* **2**, 842, 863 (1929).
37. W. Steinetz, "Denkschrift zur Begrundung einer zoologischen Meeresstation an der Kuste Palastinas" (Private publ., Breslau, 1919).
38. O. H. Oren, *Prog. Oceanogr.* **5** (1969).
39. G. Thorson, "Animal migration through the Suez Canal in the past, recent years and future," 3rd Symp. Eur. Biol. Mar., Arcachon (1968), p. 1 (mimeographed).
40. F. D. Por, "One hundred years of Suez Canal —a century of lessepsian migration," *Syst. Zool.* **20**, 138 (1971).
41. W. Steinitz, *Int. Rev. Hydrobiol.* **22**, 1 (1929).
42. H. Steinitz, "A critical list of immigrants via the Suez Canal," manuscript.
43. A. Ben-Tuvia, "Revised list of the Mediterranean fishes of Israel," *Israel J. Zool.* **20** (1), 1 (1971).
44. ———, *Copeia* **2**, 255 (1966).
45. A. A. Aleem, *Sci. Rev. Gen. Fish Comm. Mediterr. 43* (1969).
46. P. M. Boffey, *Science* **171**, 355 (1971).
47. M. Mueller, *ibid.* **163**, 165 (1969).
48. J. C. Briggs, *BioScience* **10**, 44 (1969).
49. R. J. Menzies, *Nature* **220**, 802 (1968).
50. R. H. Chesher, *Limnol. Oceanogr.* **13**, 387 (1968).
51. I. Rubinoff, *Biol. Conserv.* **3**, 33 (1970).
52. R. W. Rubinoff and I. Rubinoff, *Nature* **217**, 476 (1968).
53. C. Hubbs, personal communication, 1971.

54. Supported in part by the Smithsonian Foreign Currency Program. We thank P. Eschmeyer, H. Steinitz, D. Por, I. Rubinoff, V. Springer, C. Hubbs, D. Cohen, and D. Brown for their help.