American Fisheries Society Symposium 15:492–498, 1995

Accomplishments and Roadblocks of a Marine Stock Enhancement Program for White Seabass in California

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Abstract.—The Ocean Resources Enhancement and Hatchery Program (OREHP) was established in 1983 to evaluate the feasibility of using cultured fish to enhance depleted populations of white seabass *Atractoscion nobilis* in southern California. This paper describes some of the operational and political aspects associated with developing a marine stock enhancement program. Initial OREHP research was directed toward developing culture protocols, evaluating tagging techniques, identifying population characteristics of wild stocks (including genetics), investigating patterns of postrelease survival, and using computer models to conduct cost-benefit analyses of the stocking program. In 1991 OREHP began an expansion to incorporate a production-scale marine fish hatchery and satellite cage rearing facilities. Operational funds have been secured through extended state legislation and construction funds from a mitigation requirement and private donations. A site for the hatchery has been identified adjacent to a coastal lagoon. All required preconstruction permit applications have been approved. An overlap in the authority of two state agencies with regard to coastal resource issues is being resolved through a memorandum of agreement between these agencies. This agreement stipulates the dedication of money for postrelease and genetic assessments, and the drafting of a written plan describing how fish are to be cultured, distributed, tagged and released.

Based on the experiences of OREHP, we recommend that each species be evaluated individually to determine the efficacy of stocking. The evaluation should consider the biological characteristics and management history of each species. If possible, operational funds should be secured through a dedicated account so the program can be evaluated for several years and so funds cannot be diverted into other unrelated programs. Both scientific and user group advisors should be involved when establishing the goals and oversight responsibilities for the program, and lines of authority for the program should be established early in its development. A high-profile review process should be maintained, and postrelease and genetic assessments should be incorporated into the program as early as possible.

The harvest of many fishery resources at or above maximum sustainable levels worldwide (NMFS 1992) has increased the need for research and development of stock enhancement. The Food and Agriculture Organization of the United Nations (FAO) has reported that approximately 33% of the 200 fisheries it monitors are depleted or overexploited (FAO 1988). The National Marine Fisheries Service (NMFS) has similarly reported that fisheries resources of the United States were fully utilized (26%) or overutilized (28%), and the status of 34% of the stocks is unknown (NMFS 1992). By comparing worldwide population growth with the reported diminishing yields from harvest fisheries, New (1991) concluded that there will be an annual aquaculture production deficit of 50 million tons by the year 2025. Because New (1991) reports current production at around 11 million tons, this more than fourfold expanded production in just over 3 decades will require that the aquaculture industry try to meet this goal through development of three as yet underexploited production methods: (1) the expanded use of inland farms that integrate aquaculture and agriculture, (2) the increased use of off shore sites where the development of protected embayments is not in conflict with aquaculture, and (3) the further development of aquaculture-based fisheries (i.e., stock enhancement) that will augment the natural production capabilities of wild populations. If this expanded food production capability is to be met, it is clear that future fisheries management plans will have to evaluate stock enhancement as a means of helping to maintain or increase food resources and overall resource diversity. This paper describes the case history of a marine stock enhancement program for white seabass *Atractoscion nobilis* in southern California and emphasizes the political and operational aspects of establishing such a program.

Project Background

Marine coastal fisheries provide significant economic value through both commercial and recreational harvests. Venrick (1985) estimated that marine sportfishing contributed more than US$2 billion to the California economy in 1983. Because coastal fisheries represent such a significant resource to California, many sportfishing groups have expressed serious concerns about the declines of key species. In 1982 both an organization of anglers, the National Coalition for Marine Conservation—Pacific Region, and an affiliation of commercial sportfishing vessel owners, the California Sportfishing Association, suggested evaluating the potential for marine fish hatcheries to augment depleted populations of fish in southern California.

In 1983, the California legislature established the Ocean Resources Enhancement and Hatchery Program (OREHP) under the direction of the California Department of Fish and Game (CDF&G) to conduct "basic and applied research on the artificial propagation and distribution of adversely affected marine fish species . . ." (California State Assembly 1983). The legislation established $1 sportfishing and $10 commercial marine fishing stamps to fund this program. It also mandated the formation of an advisory panel to oversee the program with members representing the commercial and sportfishing industries (Sportfishing Association of California and California Gillnetters Association), a conservationist group (National Coalition for Marine Conservation), the aquaculture industry (California Aquaculture Association), the scientific community (University of California and California State University), and CDF&G.

The OREHP advisory panel identified the white seabass as the most appropriate species for use in an experimental stocking program. White seabass is an important sport and commercial species, and catches have declined to low levels. Regulations to manage the white seabass fishery have been in place since 1931 and continue to the present day with some modifications. The regulations include a minimum size limit (711 mm total length [TL]), closed seasons, bag limits, and gear restrictions. Despite the regulations, commercial and recreational fisheries catches have declined (Vojkovich and Reed 1983; Vojkovich, CDF&G, personal communication).

In order to obtain definitive answers regarding the efficacy of stocking marine fish, the advisory panel established specific goals for the program that were used to solicit and evaluate research proposals. These goals were directed toward (1) developing culture techniques, (2) assessing natural population characteristics and postrelease survival, (3) evaluating genetic characteristics of wild and hatchery stocks, and (4) determining the economic feasibility of marine stock enhancement.

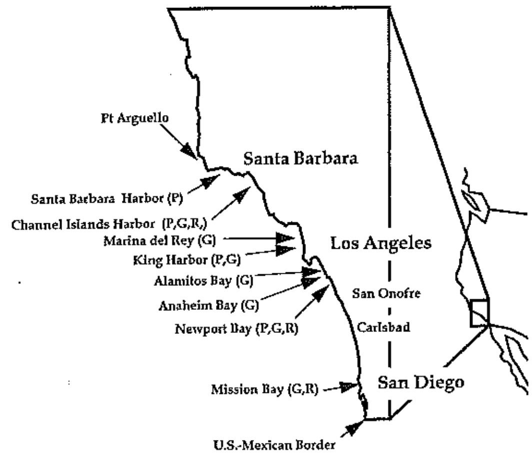

FIGURE 1.—Map of southern California showing culture, release, and assessment areas for white seabass. Key to sites: gill-net sampling (G); cage rearing and release (P); and recapture (R).

Because the funding source for the operation of OREHP is derived from fishers north of the Mexican border and south of Point Arguello, the culture, release, and assessment work has also been confined to this region (Figure 1).

Work Accomplished to Date (1983–1993)

Culture

Culture and stocking research was conducted at the marine laboratory on Mission Bay, California, jointly maintained by Hubbs-Sea World Research Institute and San Diego State University. White seabass broodfish were obtained from several sources, primarily commercial sportfishing vessels. As of this writing the hatchery maintains a breeding population of 33 wild-caught white seabass (18 kg average weight). Effort is being dedicated to increase the total broodfish spawning population to 200 animals—well over the number (i.e., 75) recommended by Bartley and Kent (1990) to ensure the released fish will have minimal genetic effect on the wild population.

Broodfish are divided into separate recirculating-water pools where they are maintained under controlled temperature and photoperiod regimes to induce spawning throughout the year. Eggs are collected and reared through the larval, postlarval, and juvenile stages in culture pools until reaching a size of approximately 65 mm TL (60 days). During this culture sequence, juveniles are weaned from a diet of live and frozen crustacean food to a commercially available pellet. After weaning the juvenile white seabass are transported to cages where they are held for an additional 6–7 months prior to release.

Pre- and Postrelease Assessment

Initial ecological surveys and subsequent attempts to recapture hatchery-reared white seabass used different gear types, including beach seines, beam and otter trawls, experimental gill nets, and hook and line. Experimental gill nets have been the most effective gear because they catch a wide size range of fish (200–850 mm TL), can be used in a diversity of habitats (kelps beds, embayments, and rock reefs) and have relatively high catch rates. Since the gill-net sampling program was initiated in 1988, the majority of effort has been focused within Mission Bay, the primary release site, and along the adjacent open-ocean coast in kelp beds. A hook and line sampling program was initiated in 1992 through the efforts of anglers aboard commercial sportfishing vessels. This program is relatively inexpensive and samples a wide area. Due to the current size limit of 711 mm TL, this method provides data for only larger white seabass.

Prior to release, all hatchery-reared fish are marked for future identification. Oxytetracycline was initially used to mark hatchery-produced fish. This mark was found ineffective for our purposes because it did not last for more than 4 years. Coded wire tags have been used since 1990. This tagging system has enabled identification of the release group to which recaptured fish belong and provided more accurate estimates of growth and patterns of migration.

Genetic Assessment

The genetic diversity of white seabass in southern California has been measured (Bartley and Kent 1990). From genetic analysis of cultured white seabass the program concluded (1) there are no measurable temporal, clinal, or geographic components to the genetic diversity of the white seabass population studied; (2) the genetic diversity of cultured fish from a single spawn is less than that of the wild population; (3) the genetic diversity observed between multiple spawns of cultured broodfish approaches that of the wild population; and (4) a spawning group of at least 75 broodfish is necessary to provide the rarest alleles (approximately 2%) observed in the wild population (Bartley et al. 1995, this volume).

Bioeconomic Assessment

A computer model was developed by L. W. Botsford and R. C. Hobbs (unpublished data) that provides a standard method for evaluating new culture techniques and for estimating the costs to produce fish of different ages prior to release. These culture cost estimates are then used in combination with estimates of postrelease survival to predict the benefits and costs of the program. By use of a calculated, theoretical curve that defines the relationship between the size at release and postrelease survival, the optimal size at release was found to be 210 mm TL when culture costs were considered. This bioeconomic model will be updated as new growth and survival data are gathered.

Planning for Expansion (1991–1994)

Beginning in 1991, OREHP initiated an expansion of the stock enhancement program. A review of the work performed from 1983 to 1991 allowed the advisory panel to recommend to the CDF&G an increase in the size of the experimental rearing and release program. To expand the program in a cost-effective manner, a logistical decision was made to centralize the hatchery operation and to decentralize the grow-out culture by using cage systems operated throughout the southern California range of the experiment. The planning process involved developing funding sources for operational and capital expenses, evaluating cage rearing sites and operators, obtaining prerelease baseline data on the abundance of white seabass, and identifying other potential release areas. A location for a full-scale hatchery was identified and a preliminary design for it developed.

Funding

Operational funds to support the hatchery and assessment work had to be secured to expand OREHP. Support from the local fishing community and legislators resulted in reauthorization of the original legislation and extended the fishing stamp for an additional 10 years to 2003 (California State Assembly 1993).

In the summer of 1991 OREHP representatives approached the California Coastal Commission about including a marine hatchery as part of a mitigation plan for the San Onofre Nuclear Generating Station immediately south of San Clemente, California. Following a 2-year review of the viability of stock enhancement programs by Coastal Commission staff and scientific advisors, the Coastal Commission agreed to release $1.2 million to support the cost of hatchery construction. The cost estimate was based on a preliminary hatchery design, which in turn was based on production capabilities that could be supported by the available operational funds.

Site Selection for Central Hatchery and Cages

During the time funding sources were being sought, potential sites for the main hatchery and cages were being reviewed. It soon became evident that availability of sites within embayments for small-scale cage systems was not as limiting as was the availability of undeveloped land adjacent to a clean seawater supply along the southern California coast for the hatchery.

A suitable site for the hatchery was selected in Carlsbad, California (Figure 1) on property owned by the local utility company, San Diego Gas and Electric Co. (SDG&E), also part owner of the San Onofre Nuclear Generating Station. Through a license agreement with SDG&E, the property was made available virtually free of cost. It is situated adjacent to the outer basin of Agua Hedionda Lagoon, which receives tidal flushing from a coastal inlet, located approximately 300 m away. The site was specifically designated for aquaculture use by a local coastal plan.

Efforts to incorporate cage culture into the overall program for white seabass were initiated in 1991. The cage systems are located in various southern California embayments and are owned and operated by volunteer groups of anglers that have incorporated as nonprofit entities. These systems allow not only an expansion of the culture program by providing more fish of a larger size, but also an expansion of the release program from just San Diego to the entire southern California Bight (Figure 1).

Gill-Net Surveys

In preparation for large-scale releases of white seabass, the gill-net survey was expanded to include embayments where white seabass were cultured in cages, as well as other potential sites in southern California (Figure 1). The primary objective of the expanded gill-net survey is to collect prerelease baseline data on the relative abundances of white seabass and other sympatric fish species in these areas. Areas inhabited by wild white seabass of the same age-class as released fish should represent the most suitable areas for release. This information will also be used to help determine if wild white seabass or other species are being displaced or consumed by stocked fish.

Implementing the Expansion (1993)

Securing Capital Funds

Due to the comprehensive nature of the expanded program, the involvement of coastal resources, and the need to assess the mitigation value of the program for the San Onofre Nuclear Generating Station, several organizational tasks and a series of assurances were required by the Coastal Commission before mitigation moneys could be released.

1. A memorandum of agreement (MOA) must be developed between the two state agencies (CDF&G and California Coastal Commission) that outlines the regulatory authority of the agencies in management of the joint research and mitigation missions of the hatchery program.
2. A panel comprised of representatives from the CDF&G, the California Coastal Commission, the OREHP advisory panel, the Southern California Edison Company, the National Marine Fisheries Service, and the University of California must be formed. The responsibilities of this joint panel are stated in detail in the MOA.
3. A comprehensive hatchery plan must be prepared that details the operational methods by which the goals of the MOA will be accomplished.
4. A coastal development permit must be issued by the California Coastal Commission, permitting the construction of the hatchery facility.

The MOA identified all of the parties involved and the purpose of the agreement. It provided a description of the project and responsibilities for planning and oversight, including the composition of the joint panel. Assurances to be made regarding environmental quality were described as they relate to hatchery and cage system operations. Requirements for a postrelease evaluation program and a genetic quality assurance program were described in detail, including the minimum annual funding requirements to be dedicated to each. Finally, procedures manuals were required for both the hatchery and cage system operations.

TABLE 1.—Permits required for construction of the OREHP hatchery in Carlsbad, California.

Permit	Responsible agency	Time to process	Review and monitoring requirements	Fee
Conditional use	City of Carlsbad Planning Department	8 months	Seventy-three special conditions; annual review of compliance	$3,600
Grading	City of Carlsbad Engineering Department	2 months	Inspection and bonds required by city; approval prior to processing building permit	$6,000
Building[1]	a) City of Carlsbad Building Department b) Carlsbad Unified School District	3 months	City inspection; certificate of occupancy prior to occupying facility	$53,000 $870
Wastewater discharge	Carlsbad Municipal Water District	1 month	Periodic monitoring	$500
Coastal development	California Coastal Commission	10 months	Nineteen special conditions	$4,000
NPDES[2]	Environmental Protection Agency permit issued by California Regional Water Quality Control Board	1.5 years	Waived in lieu of periodic monitoring	$0
404	U.S. Army Corps of Engineers	1.3 years	Three special conditions; postconstruction eelgrass impact report	$500
Total Cost				$68,470

[1]Building permit fee includes $22,000 for sewer and water service; $21,000 for public and community facilities; and $500 for traffic and development impact fees.
[2]National Pollutant Discharge Eliminations System Permit.

The comprehensive hatchery plan addresses the initial objectives for culture, stocking and assessment of white seabass, and included the following:

1. defined enhancement objective or endpoint in units biomass or catch contributed;
2. culture protocols for producing white seabass with a minimum effect on the wild population's genetic variability;
3. methods for tagging fish and managing the resulting database;
4. procedures for juvenile culture and release;
5. methods for transporting the fish from the hatchery to cage systems and from cage systems to release sites;
6. standards for measuring the success of the hatchery;
7. budget and schedule for hatchery construction;
8. procedures manual for cage systems; and
9. provisions for revising the hatchery plan after the first year and biennially thereafter.

The comprehensive hatchery plan is important for several reasons. First, it acknowledges that stock enhancement programs, especially those in their infancy, are part of a dynamic process. Second, it provides a common framework from which to direct research effort. This is especially critical when many organizations and agencies have a vested interest in helping to establish the objectives and assess the results.

Permits and Approvals for Hatchery Construction

The permit requirements for development in California's coastal zone (Table 1) entail a very involved process and often require expert consultation with outside resources. Also, the permit process is site- and project-specific.

On a local level, permits were required that reviewed and approved the use of the site in addition to construction permits (i.e., grading, construction, and tenant improvements). Because the site was previously undeveloped, a Conditional Use Permit was required, which allows the local government to apply special requirements that are tailored to fit the proposed project and thus avoid problems that may be associated with the particular type of use (California Permit Handbook 1992). As part of the Conditional Use Permit, an environmental impact report may be required if a mitigated negative declaration is not found to be sufficient.

At the state level, a Coastal Development Permit was required from the California Coastal Commission. The Coastal Commission retains permit authority over tidelands, submerged lands, and certain lands held in the public trust. Because OREHP is administered by the CDF&G, no formal permit was required by this state agency to culture or release fish.

At the federal level, applications for permits were required by the Regional Water Quality Control

Board and the Army Corps of Engineers. A discharge permit, formally referred to as a National Pollutant Discharge Eliminations System Permit (NPDES), is required by the owner or operator of any facility that discharges waste into any surface waters of the state (California Permit Handbook 1992). Because our anticipated annual production level falls well below the federal requirements (9,090 kg) for a concentrated animal holding facility, we were given a waiver from this permit but were conditioned to conduct periodic monitoring of both hatchery discharge and stormwater runoff. Because the Army Corps of Engineers maintains jurisdiction over all navigable waters, a permit was required to install the seawater intake structure for the hatchery.

Discussion

Because many questions still need to be addressed, the decision to increase the scale of the OREHP experiment has gone through significant critical review. The mission early in the program to address not only the culture problems inherent to enhancement but also the economic and ecological impacts has allowed the program to carefully scale up to its proposed level. However, even with acceptance of the experimental concept and a clear mandate to proceed, OREHP's expansion has been dramatically slowed by the inertia inherent in development projects in the California coastal zone. In fact, the debate over the value of the proposed OREHP hatchery pales in comparison with the effort needed to obtain all of the permits required for construction and operation of the proposed facility.

The procedural hurdles associated with obtaining the necessary permits and approvals to construct and operate the enhancement hatchery are a major deterrent. There are multiple agencies at the federal, state, and local levels with overlapping jurisdictions and different permitting and reporting requirements. Without the help of a professional development consultant, it would be nearly impossible for an organization operated by scientists to identify the numerous agencies from which permits must be obtained The requirements imposed by different agencies on the hatchery project are duplicative and sometimes contradictory. The permitting and reporting requirements of many individual agencies are burdensome and time consuming, and agency staff have little or no apparent incentive to process permit applications on a timely basis.

The experience of OREHP in its effort to develop this relatively modest culture facility has been that even with an overall consensus to construct the hatchery, there exists a bureaucratic logjam. Agency regulations and requirements are designed to allow managed growth, but in their application, they became a discouragement to the execution of the program. The permitting process for the hatchery facility began in July 1991, yet at this writing there are still preconstruction permit applications pending review and approval. The permits acquired thus far have involved two public hearings, an appeal to city council that required an additional public hearing, and a lawsuit that is under review for appeal. In an effort to provide fair public review of development projects, California law has, in effect, allowed single individuals to cause significant expenditures in time and funding to delay and, in some cases by attrition, halt projects that have an overwhelming majority of public support.

In addition to this permitting impasse, pressure continues to be exerted from both sides of the stock enhancement question. Some feel that the maintenance of fishing yields should be accomplished only through the informed management of the existing stock. Many in this group also hold that stock enhancement simply represents a seemingly attractive technical solution to very complicated environmental resource problems, and that its appeal to user groups in the short term cannot really balance the need to correct the underlying causes of the diminished harvest. In addition, because of the significant number of hatcheries built in the Pacific Northwest for salmon *Oncorhynchus* spp. in response to logging and hydroelectric projects, a fear exists that the acceptance of marine stock enhancement as a viable resource management tool might result in its common use for mitigation, allowing further degradation of the coastal environment.

On the other side of the argument, user groups of both recreational and commercial fishers have stated the opinion that the concerns raised by resource managers and the scientific community have little practical merit, and that costs associated with scientific investigations can be eliminated in lieu of supporting increased hatchery production. It can be extremely difficult to convince the lay person that concerns as seemingly esoteric as the genetic variability of the progeny produced in the hatchery may in some way diminish the viability of the wild population.

These on-going arguments often serve only to polarize the debate further on the usefulness of enhancement hatchery programs, ultimately toward limiting the ability to actually test their efficacy. It is incumbent upon the fisheries management community to resist these pressures and apply the best scientific procedures in testing the real potential for fisheries enhancement. If this does not occur, then user groups that control or strongly influence the economic and political resources supporting enhancement programs will cause projects to be performed that lack the scientific structure required to allow adequate assessment of positive or negative impacts.

Based on the experiences of OREHP, we recommend that each species be evaluated individually to determine the efficacy of stocking. The evaluation should consider the biological characteristics and management history of each species. If possible, operational funds should be secured through a dedicated account so the program can be evaluated over several years, or at least until the stocked fish are recruited into the fishery, and so funds cannot be diverted into unrelated programs. Both scientists and user groups should be involved when establishing the goals and oversight responsibilities for the program, and lines of authority for the program should be established early in its development. A high-profile review process should be maintained, and postrelease and genetic assessments should be incorporated into the program as early as possible.

In the case of California's OREHP, we feel that an excellent working relationship has been developed between the scientists conducting the research, the management agencies responsible for the resource, and the user groups providing the funding. With continued scientific review and barring further permitting constraints, the OREHP hopes to further the goal of adequately testing marine fisheries enhancement as a responsible resource management tool.

References

Bartley, D. M., and D. B. Kent. 1990. Genetic structure of white seabass population from the southern California Bight region: applications to hatchery enhancement. California Cooperative Oceanic Fisheries Investigations Report 31:97–105.

Bartley, D. M., D. B. Kent, and M. A. Drawbridge. 1995. Conservation of genetic diversity in a white seabass hatchery enhancement program in southern California. American Fisheries Society Symposium 15:249–258.

California Permit Handbook. 1992. Governor's office of planning and research, office of permit assistance, Sacramento, California.

California State Assembly. 1983. Ocean fishery research. By Larry Stirling. Bill AB 1414, Chapter 982. Sacramento.

California State Assembly. 1993. California ocean resources enhancement and hatchery program. By Dede Alpert. Bill AB 960, Chapter 987. Sacramento.

Food and Agriculture Organization of the United Nations (FAO). 1988. Review of the state of world fishery resources. FAO Fisheries Circular 710, Revision 7.

New, M. B. 1991. Turn of the millennium aquaculture: navigating troubled waters or riding the crest of the wave? World Aquaculture 22(3):28–49.

NMFS (National Marine Fisheries Service). 1992. Our living oceans: report on the status of U.S. living marine resources, 1992. NOAA (National Oceanic and Atmospheric Administration) Technical Memorandum, NMFS F/SPO-2, Silver Spring, Maryland.

Venrick, E. L. 1985. Marine recreational fishing. Pages 38–42 *in* The oceans and the economy of San Diego. University of San Diego, Scripps Institution of Oceanography, San Diego, California.

Vojkovich, M., and R. J. Reed. 1983. White seabass, *Atractoscion nobilis*, in California-Mexico waters: status of the fishery. California Cooperative Oceanic Fisheries Investigations Report XXIV:79–83.

Evolutionary and Conservation Biology of Cichlid Fishes as Revealed by Faunal Remnants in Northern Lake Victoria

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Abstract: *Lake Victoria until recently harbored the world's second richest lacustrine fish assemblage, but it is now experiencing a mass extinction. Here we report on the current status of the endemic cichlid fishes from a preliminary biotic inventory conducted as part of limnological reconnaissance in Kenyan and Ugandan waters during 1989–1992. Sixty-two haplochromine taxa were recovered, half of them new. Some are local endemics, while others are more widely distributed, based on review of earlier collections. Comparison with data from 1982–1984 and 1988 suggests that some shoreline assemblages have been locally stable over the past decade. In addition to littoral rock and vegetation, four kinds of refugia for indigenous fishes are recognized: (1) schools of* Rastrineobola, *(2) benthic microbial mats in deep water, (3) satellite lakes, (4) the oxycline. Reconnaissance by remote operated vehicle (ROV) documented fish kills due to deoxygenation of the water column, indicating the risk of using the oxycline as a refugium. Several species formerly abundant in Lake Victoria were found only in satellite lakes, revealing the importance of these lakes in the conservation of indigenous species. Recent events in Lake Victoria shed light on mechanisms of speciation and mass extinction, insights relevant to conservation planning for the valuable remnants of the lake's indigenous fauna.*

Evolución y conservación biológica de los peces cíclidos de acuerdo a remanentes faunísticos en el lago Victoria

Resumen: *El lago Victoria albergaba, hasta no hace mucho, la segunda fauna lacustre más rica del mundo pero ahora está experimentado una extinción masiva. Nosotros, aqui reportamos el status presente de los peces cíclidos endémicos, de acuerdo a un inventario biótico preliminar realizado como parte de un reconocimiento limnológico en aguas de Kenya y Uganda durante 1989–1992. Fueron recuperadas sesenta y dos taxa de haplochrominas, la mitad de ellas nuevas. Algunas son endémicas locales, mientras que otras están más ampliamente distribuídas, según revisión de colecciones anteriores. Comparaciones con datos de 1982–84 y 1988 sugieren que algunos agrupaminetos costeros han sido estables localmmente en la década pasada. Además de rocas y vegetación litoral, se reconocieron cuatro tipos distintos de refugios para peces: (1) escuelas de* Rastrineobola, *(2) matas microbiales bentónicas en aguas profundas, (3) lagos satélites, (4) la oxiclina. Un reconocimiento con un vehículo operado a control remoto (remote operated vehicle -ROV-) documentó la muerte de peces debido a desoxigenación de la columna de agua, indicando el riesgo de usar la oxiclina como refugio. Numerosas especies anteriormente abundantes en el lago Victoria fueron encontradas en lagos satélites, revelando la importancia de estos lagos en la conservación de especies indígenas. Eventos recientes en el lago Victoria arrojaron luz sobre los mecanismos de especiación y de extinción en masa, este conocimiento es relevante para el planeamiento de la conservación de los valuables remanentes de la fauna indígena del lago.*

Introduction

Until recently, Lake Victoria harbored the world's second richest lacustrine fish assemblage. In 1980, about 90% of the lake's 400+ species and 80% of the fish biomass consisted of haplochromine cichlids. By 1990, they comprised less than 2% of the biomass, and half the endemic species had vanished (Ogutu-Ohwayo 1990; Witte et al. 1992*a*). This mass extinction (see Jablonski 1986) has been attributed to predation by an introduced predatory *Lates,* referred to as Nile perch (*L. niloticus*). First introduced to Lake Victoria in 1954, its numbers exploded in the early 1980s, roughly concordant with the disappearance of the haplochromines (Witte et al. 1992*a*). Although the Nile perch population boom and haplochromine crash correlate in time, it is evident that Nile perch is but one of many causes of the haplochromine decline, most or all anthropogenic (Kaufman 1992). Decimation of the native fishes is coincident with the combined effects of alien introductions, (Ogutu-Ohwayo 1990), eutrophication and hypoxia (Ochumba 1990; Ochumba et al. 1993), overfishing (Cadwalladr 1965), unusually rapid and extreme fluctuations in lake level (Welcomme 1970; Kite 1981), and other profound alterations in the food web and ecosystem dynamics of the lake (Kaufman 1992; Witte et al. 1992*b;* Gophen et al. 1993). The system is still in flux, with water hyacinth, *Eichornia crassipes,* and North American black bass, *Micropterus salmoides,* recently established in the lake basin (Ochumba & Manyala 1992; Twongo 1993).

As a case study for threats facing freshwater biota and resources throughout the world, Lake Victoria provides several extraordinary opportunities (Andrews & Kaufman 1993). Most of the work has been on fish, however; as demonstrated here, these are more poorly known than was previously thought, despite the pioneering efforts of Greenwood (1981) and the Haplochromine Ecology Survey Team, HEST (Witte 1981). In this paper, we contribute to knowledge of the status of Lake Victoria's endemic fishes, as illuminated by preliminary biotic inventory data obtained as part of limnological reconnaissance in Kenya and Uganda (Kaufman 1992; Ochumba et al. 1993; Gophen et al. 1993).

Methods

Data were gathered by members of the Lake Victoria Research Team (LVRT) in Kenya and Uganda during 1989–1992. To assess whether patterns of species survival observed in Mwanza Gulf (Witte et al. 1992*a*) were common to the lake as a whole, fishes were sampled with traps, trawls, trammel nets, and beach seines at established open water and shoreline stations (Gophen et al. 1993). Sampling was also conducted in satellite lakes in the Nabugabo basin of Uganda (Lakes Nabugabo, Manywe, Kayugi, and Kayanja) and the Yala basin of Kenya (Lakes Kanyaboli and Sare). Satellite lakes are small bodies of water isolated from Lake Victoria by papyrus swamps or sand spits (Greenwood 1965*a*). Specimens were fixed in the field in 10% formalin, dehydrated through an ethanol series, and archived in 70% ethanol. Abdomens of large specimens were slit or injected with 10% formalin to preserve stomach contents. Taxonomic nomenclature follows Greenwood (1981) for described taxa. We follow the convention of assigning new taxa to "Haplochromis," followed by a cheironym, which is also placed in quotes (Witte et al. 1992*a*). Live specimens were returned to the laboratory for study of life colors and behavior. When possible, founders were entrusted to the Lake Victoria Fishes Captive Breeding Program as a living archive (Kaufman 1990; Reid 1990; Wilhelm 1993).

Thirty-four exploratory dives (1 m to 47.7 m) were conducted in Kenya by remote operated vehicle (ROV) in December 1987 and December 1990 (Table 1). These covered 16 localities in Kenyan waters, including both Winam Gulf and the open lake. Extensive observations were made at four open-lake LVRT stations and two in Rusinga Channel, Winam Gulf; maps of the study area and station locations can be found in Kaufman (1992) and Gophen et al. (1993).

Results

Sixty-two haplochromine species were recovered in Lake Victoria and the satellite lakes during 1989–1992 (Table 2). All are endemic to the Lake Victoria Basin, with the exception of *Astatotilapia nubila, Astatoreochromis alluaudi,* and *Pseudocrenilabrus* cf. *multicolor.* Half of the recovered species are newly discovered and as yet undescribed (Table 3). Several new species have restricted distributions within Lake Victoria. One species was apparently limited to Mfwangano Island, and a brilliant orange *Neochromis* "kruising" complex was repeatedly observed but not collected on the Bull Islands, off Rusinga Channel. Species seemingly endemic to Rusinga Island were also observed on the recently constructed causeway joining the island to Mbita Point, and on adjacent beaches. Some species were limited to satellite lakes. Four endemic haplochromine species were recovered from the Nabugabo Lakes, Uganda (Greenwood 1965*b;* Ogutu-Ohwayo 1993); *Xystichromis phytophagus* and a large-eyed dwarf ("dwarf bigeye scraper") were limited to Lake Kanyaboli, Kenya. *Oreochromis esculentus* was found in lakes Kanyaboli, Manywe, Kayugi, and Kayanja, but was absent from lakes Victoria and Nabugabo (Ogutu-Ohwayo 1993).

Some species exhibit marked geographical variation

Table 1. Summary of remote operated vehicle dives in 1987 and 1990.

Date	Time	Depth (m)	Location	Duration (mins)
1987 Instrument: Mark V				
12/1/87	10:57	12.3	Rusinga Channel	33
	15:32	28.8	Bridge Island	23
	17:08	21.0	Rusinga Channel	34
12/2/87	9:22	6.0	Mbita Bay	8
	9:40	7.5	Mbita Bay	40
	10:32	13.8	Mbita Bay	16
	14:30	7.2	White Rock Point	24
	15:00	12.3	Gull Shoal Light	57
12/3/87	AM?	4.5	ICIPE Bay	10
	AM?	4.5	ICIPE Bay	10
	AM?	4.5?	ICIPE Bay	30
1990 Instrument: Phantom 300				
12/7/90	11:10	1.5	Kisumu Dock	8
	11:20	1.5	Kisumu Bay	15
12/9/90	9:35	6.0	Ndere Island	40
	13:00	25.5	Gingra Rock	40
	14:40	12.6	Winam Gulf	15
12/10/90	9:00	18.0	Bridge Island	15
	9:15	36.0	Bridge Island	65
	10:21	36.0	Bridge Island	24
	10:50	1.0	Floating Island	5
	11:34	36.0	Bridge Island	74
	14:55	47.7	Rusinga Channel	20
12/11/90	8:30	35.0	Station 33	42
	9:19	1.0	Station 33	3
	10:20	1.0	Bridge Island	25
	12:20	36.0	Kisingere	50
	13:25	26.0	Kisingere	20
	13:59	25.0	Kisingere	23
	14:30	20.0	Kisingere	15
	15:26	30.0	Mfwangano Channel	19
	16:21	19.8	Kisingere	10
12/12/90	10:40	57.0	Siaya	45
	11:50	57.0	Siaya	50
12/13/90	8:00	40.5	Luanda Gembe	45

in coloration. We note that although all "Haplochromis" "rock kribensis" exhibit a characteristic plaid-on-chamois pattern with marked sexual dichromatism, mature males from Uganda are very dark overall, while those from Kenya and Tanzania are much lighter. Tanzanian individuals exhibit a more extensive and brilliant red-orange region on the flank and belly than in either the Kenyan or Ugandan forms. *Neochromis nigricans* populations vary in the extent of red, yellow, black, and iridescent blue in the dorsal fin. "H." "thickskin" varies in the number of vertical bars and in the ratio of orange-red to metallic yellow-green on the dorsum. Other species showed little geographical variation in color or pattern (for example, *Astatotilapia nubila*, "H." "flame-back", *Pseudocrenilabrus* cf. *multicolor*, and *Astatoreochromis alluaudi* from Uganda, Tanzania, and Kenya).

Haplochromine Ecology Survey Team members in Tanzania noted "H." "rock kribensis" to be a scraper-toothed insectivore with a hypotrophic pharyngeal jaw apparatus and fine, pointed, laterally compressed pharyngeal teeth (Witte, personal communication). This morphology was characteristic of Ugandan-derived specimens in the captive breeding program (founders collected by Mr. Bo Selbrink near Entebbe in the late 1970s) and was exhibited by a large, wild male specimen collected in Napoleon Gulf in 1992. However, all specimens captured by us in Kenya since 1989 have hypertrophied pharyngeal jaws, typical of mollusc crushers. The gut contents of the 1989–1992 specimens ($n = 12$) contain insect larvae mixed with bivalve and gastropod shell hash. Three specimens of "rock kribensis" from Kenya in The Natural History Museum, London (lot "Haplochromis nubilus" 1928.1.25.43–47 Pitman), were examined otoscopically; all are near the typical hypotrophic form. Several specimens of this species collected by Robert Dorit in 1983–1984, close to our present collecting locality at Utajo Beach on Rusinga Island, are also hypotrophic. In 1988 the National Museums of Kenya and the British Museum of Natural History led an expedition to Winam Gulf (Harrison et al.

Table 2. Haplochromine taxa recovered from northern Lake Victoria, 1989–1992. Described species are italicized; previously unknown taxa are bolded; species previously known but undescribed are unbolded.

PISCIVORES
Prognathochromis orthostoma
Harpagochromis plagiostoma
Prognathochromis venator (Nabugabo Lakes)
P. serranus
P. "large serranus-like"
Harpagochromis "frogmouth"
H. "grey pygmy"
Prognathochromis "stilleto"
"H." "Omena piscivore"

PAEDOPHAGES
Lipochromis maxillaris

INSECTIVORES
Psammochromis riponianus
Paralabidochromis chilotes
P. chromogynos
P. crassilabris
P. beadlei (Lake Nabugabo only)
Gaurochromis simpsoni (Nabugabo Lakes)
Astatotilapia velifer (Nabugabo Lakes)
A. nubila
"H." "Mbita red anal"
"H." "Mbita goldchest"
"H." "Mbita spot bar"
"H." "Mbita firebelly"
"H." "red littlemouth"
"H." "pink flush"
"H." "Uganda greybar"
"H." "Uganda red flush"
"H." "Hippo Pt. bluebar"
"H." "flameback"
"H." "greenback insectivore"
"H." "deep velvet black"
"H." "aelocephalus-like"
"H." "thickskin"

ORAL SHELLERS
Paralabidochromis plagiodon
Ptyochromis granti
P. xenognathus
P. "xenognathus-like deep"
P. "Hippo Point salmon"
P. "Rusingal oral sheller"
P. "Kisumu oral sheller"
"H." "dwarf oral sheller"
"H." "other oral sheller"

PHARYNGEAL CRUSHERS
Astatoreochromis alluaudi
Labrochromis ptistes
"H." "Kisengare big silver crusher"
"H." "rock kribensis"

EPILITHIC ALGAL GRAZERS
Neochromis nigricans
N. "madonna"
N. "elongatus"
"H." "kruising"
"H." "rockpicker"
"H." "velvetblack"

EPIPHYTIC ALGAL GRAZERS
"H." "dwarf bigeye scraper"
"H." "finebar scraper"
"H." "macula"

PLANT EATERS
Xystichromis phytophagus
Psammochromis acidens

ZOOPLANKTIVORES
"H." nyerei
Yssichromis laparogramma
Y. "Fred Astaire"
Y. "silver bullet"
"H." "golden dart"
"H." "rabbit"

MISSING TROPHIC GROUPS
Phytoplanktivores
Detritivores
Crabeater
Egg stealer
Scale stripper
Cleaners

1989). A specimen of approximately 15 cm standard length that they caught at Rusinga Island is slightly hypertrophic, but less so for its size than specimens from 1989–1992.

Several dozen specimens of the molluscivore *Astatoreochromis alluaudi* were collected during 1989–1992 from Napoleon Gulf, Nabugabo Lakes, and the Mpanga River in Uganda, and from Winam Gulf, Rusinga Island, the Sondu River, and Lake Kanyaboli in Kenya. *A. alluaudi* from Lake Victoria collected between the late 1970s and 1992 were consistently hypertrophic. Size-matched conspecifics from satellite lakes (Nabugabo, Kanyaboli) and rivers were relatively hypotrophic, as described by Greenwood (1965*a*).

Five of our Kenyan stations of 1989–1992 overlap with areas sampled by Dorit in 1982–1984, and by the 1988 Winam Gulf expedition. Comparison of the most abundant and easily diagnosed taxa over time suggests the existence of a characteristic and persistent suite of species at each locality. Examples are listed in Table 4. Many distinctive species previously recorded from our study area were absent, however. Examples are listed in Table 5.

ROV dives on soft bottoms in Winam Gulf (two in Kisumu Harbor and one in the middle of Winam Gulf) revealed loose, rippled sediment and no fish. Dives on hard rock in Winam Gulf and in the open lake revealed live *Caridina nilotica* (the native detritivorous shrimp), scattered live sponges, and the oyster-like mycetopodid bivalve *Etheria elliptica* (Heard & Vail 1976). Dives in Rusinga Channel on what the echosounder indicated would be hard bottom or well-

Table 3. Distribution of Haplochromine species among trophic groups. "Known" = previously known species; "Desc" = previously described species; "Undesc" = previously known but undescribed species; "Found" = species recovered in this study; "New" = previously unknown species discovered in this study; "Total" = total known species.

Trophic Group	*Known*	*Desc*	*Undesc*	*Found*	*New*	*Total*
detritivores/phyt	14	3	11	0	0	14
phytoplanktivores	3	0	3	0	0	3
epilithic grazers	3	1	2	6	2	5
epiphytic grazers	12	5	7	3	2	14
plant eaters	2	2	0	2	0	2
PM crushers	15	8	7	4	1	16
oral shellers	14	8	6	9	6	20
zooplanktivores	21	8	13	6	4	25
insectivores	29	18	11	22	11	41
prawn eaters	13	11	2	0	0	13
crab eater	1	0	1	0	0	1
piscivores	109	42	67	9	5	114
paedophages	24	8	16	1	0	24
scale eater	1	1	0	0	0	1
parasite eaters	2	2	0	0	0	2
other	53	6	47	0	0	54
TOTALS	316	123	193	62	31	349

consolidated sediment (depths 40–50 m) revealed patches about 1–10 m in diameter of sandy sediment with shell hash, windrows of dead snail shells, aggregations of live, crawling snails over sandy sediment, and soft, flocculent mud. In addition, we noted the existence of an unexpected patchy, structured floc on the soft sediment that may represent deep microbial mats. These patches consisted of lacy, filamentous floc layers

Table 4. Haplochromine taxa persistent over time at specific localities.

Site and species		*1982–1984*	*1988*	*1989–1992*
Rusinga Island and Mbita Peninsula				
Astatoreochromis	*alluaudi*			X
Ptyochromis	"Rusinga oral sheller"	X	X	X
	xenognathus	X		X
Paralabidochromis	*chilotes*			X
"Haplochromis"	"rock kribensis"	X	X	X
	"Mbita red anal"			X
	"spot bar"			X
Harpagochromis	"frogmouth"	X	X	X
Rusinga Channel				
Yssichromis	*laparogramma*		X	X
	"Fred Astaire"			X
	"silver bullet"			X
Harpagochromis	"grey pygmy"			X
"Haplochromis"	"dwarf silver crusher"			X
Open Lake, 15–30 m				
Ptyochromis	*xenognathus*			X
Paralabidochromis	*chilotes*			X
"Haplochromis"	"greenback insectivore"			X
Hippo Pt., Kisumu				
"Haplochromis"	"flameback"	X	X	X
Ptyochromis	*granti*	X		X
	"Hippo Pt. salmon"			X
Paralabidochromis	"Hippo Pt. bluebar"	X	X	X
Astatotilapia	*nubila*			X
Lakes Kanyaboli and Sare				
Oreochromis	*esculentus*	X		X
Lipochromis	*maxillaris*	X		X
Xystichromis	*phytophagus*	X	X	X
"Haplochromis"	"dwarf bigeye"			X

Table 5. Distinctive haplochromine species expected but not observed during 1989–1992 sampling in Kenya and Uganda.

Oral Crushers/Shellers
Macropleurodus bicolor
Platytaeniodus degeni
Hoplotilapia retrodens
Ptyochromis sauvagei
Algal Scrapers
Haplochromis obliquidens
Haplochromis lividus
Haplochromis annectidens (Nabugabo)
Xystichromis nuchisquamulatus
Detritivores
Enterochromis spp.
Phytoplanktivores
"H." "regius"
"H." "kribensis"
Paedophages
Lipochromis obesus
Lipochromis parvidens
Pharyngeal Crusher Molluscivores
Labrochromis ishmaeli
Labrochromis pharyngomylus
Egg Stealer
Astatotilapia barbarae
Piscivores
Astatotilapia martini
Prognathochromis dentex group
P. percoides
P. flavipinnis
P. cavifrons
Prawn Eaters
P. tridens group
Psammochromis cryptogramma group

that jiggled but retained their form in the ROV propwash, and they were inhabited by a fauna of small, undescribed haplochromines, including "grey pygmy." Other inhabitants included living *Caridina nilotica* and *Rastrineobola argentea,* with a few dead *Rastrineobola.* Scattered fishes (apparently haplochromines and some that appeared to be juvenile *Lates*) were flushed by the approach of the ROV, but they did not move far ahead and could be observed at close range. The ROV's lights attracted schools of the pelagic cyprinid *R. argentea,* which circled the ROV actively both in the water column and on the bottom.

Conditions in the open lake contrasted with those observed in Rusinga Channel. On a sandy bottom at a depth of 22 m in Kisengere Bay, live *R. argentea* and *C. nilotica* were observed. Lakeward of this in midwater, at 28 m depth over a 40-m bottom, roughly equal proportions of live, dead, and moribund *R. argentea* were seen swirling around the ROV. On the bottom at 40 m depth, no living and 353 dead *R. argentea* were recorded on a 5-minute (0.25 to 0.5 m/sec) ROV flight just above the bottom. Living *C. nilotica* and scattered dead *R. argentea* were seen at four other open lake stations at depths ranging from 30–60 m. Live *R. argentea* were not observed below the oxycline. *C. nilotica* were abundant both at and below the oxycline.

Discussion

The original ecosystem of Lake Victoria is a memory; restoration to prior conditions has been foreclosed by the wholesale loss of indigenous species. These events have, however, opened a unique window on the processes that create, maintain, and destroy biological diversity (Coulter et al. 1986; Goldschmidt & Witte 1992). Research should be accelerated to document the extinction process and ecosystem dynamics. Captive populations of vanishing fishes can briefly extend the time for experimental and genetic study of the fauna (Bruton 1990; Kaufman 1990). Meanwhile, it is essential that interested parties develop a vision and a predictive model for the lake basin's ecological landscape. The objective should be to conserve as much as possible of the indigenous biota while sustaining fisheries and agricultural yields within manageable bounds of uncertainty.

In this regard, we can not overstate the importance of conducting a geographically comprehensive biotic inventory of the lake's flora and fauna, in concert with studies of the lake's physical dynamics. The results reported here, however preliminary, offer guidance for the conservation of indigenous species and ideas about how processes that regulate biological diversity might also be safeguarded. These processes are at the heart of sustainability.

Of primary concern is the incompleteness of our knowledge of the Lake Victoria fauna, as revealed by the fact that half of the 62 haplochromine species recovered in this study were previously unknown (about the same percentage as that encountered by the HEST/TAFIRI team in Mwanza Gulf, Tanzania, ten years earlier; Witte et al. 1981). It is now apparent that Lake Victoria was second only to Lake Malawi in fish species richness. This is not a product of overzealous taxonomists (Hoogerhoud et al. 1983; Hoogerhoud 1984). New ecophenotypes or geographical variants of known species could be mistakenly assigned to new taxa, but haplochromine taxonomists are acutely aware of this issue. They have adopted a highly conservative stance, synonymizing whenever there is doubt (Greenwood 1965*a,* 1980; Hoogerhoud 1984; Witte & Witte-Maas 1987). "H." "rock kribensis" offers a current example. The shift in pharyngeal form during the late 1980s in Kenya and Tanzania, and the differences between Ugandan and other populations, are substantial, yet neither observation can be reflected in their taxonomy until the matter is better resolved. DNA sequence analysis, thus far applied principally to high-level phylogenetic questions

(Meyer et al. 1990) may ultimately inform both the process of differentiation and the nomenclature used to describe it.

Intraspecific variation in form is not always an obstacle; it can provide unique information on environmental change as perceived by the organism (Greenwood 1965*b*; Crowder 1986; Gabriel & Lynch 1992). For trophic relationships in fishes, this approach is superior to stomach content analysis in that morphology reflects an integration of behavior over a period of weeks or months (Hoogerhoud 1986; Kaufman 1990; Witte et al. 1990; Sackley 1992). For example, the shift from insectivory to molluscivory in "rock kribensis" is not unexpected in light of the sharp reduction in standing stocks of most molluscivores and the increased abundance of molluscs (Witte et al. 1992*b*).

The rate of encounter of new taxa has fueled speculation that they might be coming into existence currently (Welcomme, personal communication). This is difficult to test. Except possibly for HEST transects in Mwanza Gulf (Witte 1981), we are unaware of fish sampling efforts in Lake Victoria of sufficient rigor to confirm prior absence of a taxon. The material needed to track the birth of a species is missing. In fact, the volume of Victorian haplochromines in all the world's museums, especially in Africa, is pitiful in view of the perceived importance of this fauna (Greenwood 1984; Barel et al. 1985; Coulter 1986; Miller 1989; Goldschmidt & Witte 1992). It is easy to understand how some species could be missed. For example, "grey pygmy," a diminutive, modestly attired hunter discovered in Rusinga Channel in 1989 and found only in this area, matures at about 5 cm standard length and is the smallest known haplochromine piscivore, based on morphology (Van Oijen, personal communication). *Ptyochromis*, "Rusinga oral sheller," bears superficial resemblance to other *Ptyochromis* species, especially *P. sauvagei*, with which it may have been confused in prior collections.

We were very surprised to have been the first to note certain new taxa that are brightly colored, easily collected, and relatively abundant. Many of the new species exhibit red as a dominant component of male breeding coloration (as discussed in McElroy et al. 1992) and are very conspicuous. For example, three male *Astatotilapia* "flameback" appeared in this study's first sample, a seine haul near downtown Kisumu. The taxon is present in earlier collections, however, as evidenced by voucher photographs almost certainly of this species from Mwanza Gulf, Tanzania (slide #106, 1986, British Museum), and from specimens in the Harvard Museum of Comparative Zoology collected by Robert Dorit from Winam Gulf, Kenya, in 1982–1984. Our first opportunity to observe this species alive came when specimens were exported from Uganda to Laif DeMason, Old World Exotics, Inc., Homestead, Florida, for the aquarium trade. Another distinctive species that paradoxically escaped early notice is "H." "rock kribensis." It was first noted by HEST in Mwanza Gulf, yet we found this species labelled as "*Haplochromis nubilus*" in a 1929 collection deposited at The Natural History Museum, London.

Comparison of trophic representation of the original haplochromines fauna to the 62 taxa that we recovered revealed an apparent deficit in piscivores and surfeit of insectivorous species (Table 3). This is consistent with the results of Witte et al. (1992*b*). Only two piscivores were abundant in our samples: the macrocarnivore *Prognathochromis venator* in the lakes surrounding Lake Nabugabo (Ogutu-Ohwayo 1993) and the paedophage *Lipochromis maxillaris* of Lake Kanyaboli. These occurred in satellite lakes in the absence of *Lates niloticus*. The absence of Nile perch in the satellite lakes is due to there never having been a stocking attempt, and to the presence of papyrus swamps or sand spits preventing Nile perch from entering naturally. Both kinds of barriers have been breached by human enterprise and past changes in lake level, so the continued existence of relict populations of Lake Victoria endemics in satellite lake refugia must be regarded as tenuous. Every effort should be made to secure the integrity of satellite lakes as species refugia. Marginal swamps and rocky reefs are also important refugia for indigenous species in Lake Victoria, as discussed by Witte et al. (1992*b*).

We note four additional refugia: (1) schools of *Rastrineobola argentea*, (2) a structured nephoid resembling benthic microbial mats in deep water, (3) water column and benthos near the oxycline, and (4) satellite lakes. Association of haplochromine zooplanktivores and piscivores with *R. argentea* may help to explain the observation that certain zooplanktivores have been less vulnerable to Nile perch predation than are members of other tropic groups (Witte et al. 1992*a*, 1992*b*). Although *Rastrineobola* is eaten by Nile perch, it is not the preferred prey and does not favor the preferred habitats of Nile perch. The condition factor of perch with *R. argentea* in their stomach is lower than that of specimens recently feeding on *Caridina nilotica* (Asila, personal communication). There has also been a great increase in the abundance of *R. argentea* (Kaufman 1992; Witte et al. 1992*b*). In light of these facts, we postulate that midwater shoals of this pelagic cyprinid are utilized as a shelter by haplochromines of similar shape, color, size, and behavior. The fishery for *Rastrineobola* has recently been expanded, and there are plans to develop a pelagic lift-net fishery for this herring-like species. Such a move could negatively affect the associated haplochromine fauna.

The microbial mat fauna is known only from ROV observations and trawl samples taken in Rusinga Channel, Kenya, at depths of 30–40 m. Unfortunately, samples of the mat itself have not yet been obtained. The region in which it is occurs is unusual in that it is frequently higher in oxygen than equivalent depths in the open lake, from which it is partially cut off by a 20-m rise (Kaufman 1992; Gophen et al. 1993).

Fish (1956), Kolding (1993), and our own observations of recent fish kills in Lake Victoria (Ochumba 1990) indicate that Nile perch are sensitive to low levels of dissolved oxygen, more so than many cichlids. This led Kaufman (1992, for Lake Victoria) and Kolding (1993, for Lake Turkana) to propose that prey species could exploit hypoxic habitats as refugia from Nile perch. A hypoxic refugium near the oxycline in Lake Victoria might even harbor remnant populations of haplochromine species thought extinct, including deepwater insectivores, detritivores, and prawn eaters. Our observations generally support this hypothesis. Since our trawl cable prevented work in depths over 35 m, our sampling of this fauna is limited. Our deepest samples (>30 m), however, contained numerous haplochromines, mostly unidentified insectivores and an oral sheller close to *Ptyochromis xenognathus*. There were, however, few of the detritivorous species that previously dominated the deepwater fauna—a result with potentially severe implications for lake dynamics (Kaufman 1992; Witte et al. 1992*b*). Use of this refugium may impose a high risk (Kolding 1993). If the schools of *R. argentea* that we observed shoaling near the oxycline were trying to exploit the hypoxic refugium, it came at a price, as evidenced by the large numbers that we observed dying and lying dead on the bottom. The physical dynamics of the oxycline are complex (Ochumba et al. 1993). Oxygen levels are spatially and temporally volatile, and local conditions can deteriorate precipitously. The rapid shifts in the oxycline may have caused the mass mortality of *R. argentea*. Although the oxycline may offer ephemeral relief from predation, the consequences of the "hypoxia trap" phenomenon for *R. argentea* could be more significant than the impact of the predator alone.

For *Caridina nilotica* the situation appears to be different. They were most abundant below the oxycline, active and evidently operating as facultative anaerobes. Thus, for *C. nilotica* the hypolimnion may offer escape from what is now its principal predator, the Nile perch (Hughes 1992). Sonar observations coupled to trawling in the open lake confirmed that Nile perch concentrate above the oxycline in dissolved oxygen regimes of more than 3 mg/L. We also noted that fishermen in the open lake moved their gill nets and long lines higher in the water column during periods when we observed shallowing of the oxycline. On several occasions, however, large sonar targets were noted in strata bearing only 1–2 mg/L oxygen. Nile perch trawled under these circumstances had been feeding heavily on *C. nilotica*. Their presence in the trawl does not prove that they were the sonar targets observed, nor that they had foraged at the maximum depth at which the trawl was fished. Nevertheless, we must allow for the possibility that adult Nile perch can dive beneath the oxycline to forage. If commonplace, this behavior bodes ill for the hypoxic haplochromine refugium, and for the stability of the Nile perch population, which would thus be capable of destroying its last reliable food resource.

Our observations at the oxycline suggest that the impact of extinction processes may be determined by the extent to which selective forces interact to eliminate potential refugia. In Lake Victoria, deepwater haplochromines could respond to advancing hypoxia by moving laterally into shallower water, but only at the risk of exposure to Nile perch. Species trying to escape Nile perch by shifting in the opposite direction, toward deeper water, would encounter hypoxia. Selection for mutually exclusive refugia—a "crossed force" hypothesis (Kaufman 1992)—could also help account for the qualitative differences noted between background and mass extinction events (Jablonski 1986).

It is evident from comparison between our samples and earlier collections that populations of certain species have remained intact at specific localities for at least 10 years (Table 4). This lends credence to the notion that intralacustrine fish parks could be a viable conservation mechanism. Satellite lakes, celebrated for their postulated role in speciation (Greenwood 1965*b*), are today functioning as refugia. This is well illustrated by the Nabugabo lakes (Ogutu-Ohwayo 1993) and by Lake Kanyaboli in Kenya. Here *Oreochromis esculentus, Xystichromis phytophagus,* and *Lipochromis maxillaris* were abundant and had been so at least since 1982, when Dorit collected there. All three species were once common in the main lake; *O. esculentus* was the most important food fish in Lake Victoria (Graham 1929), yet today they are rare or extinct in the main lake. The function of satellite lakes as refugia is a welcome observation in terms of conservation and management. Unfortunately, it does somewhat (though not entirely) compromise the popularly accepted view that satellite endemics are examples of speciation by geographic isolation (Greenwood 1965*b*).

The satellite lake refugium is not devoid of threat. Haplochromines throughout the lake basin are in danger of being overfished by their widespread use as long-line bait for Nile perch. Since Nile perch strike only at nonmoving prey, many long liners begin their day by seining for haplochromines or purchasing live haplochromines from others who specialize in this activity. Haplochromines are also still valued as a traditional soup base; this soup is used as a treatment for the symptoms of measles and other diseases. In Lake Nabugabo, we observed fine-mesh gill nets strung two or three deep being used to catch haplochromines and tilapiines in littoral weed beds; these weed beds had been an important refugium for them when predation by fish, rather than man, was the major selective force. Juveniles of the native catfish *Clarias gariepinnis* (*-mossambicus*) are superior to haplochromines as bait because they are more rugged and long-lasting on the hook. *Clarias* aquaculture to supply the bait market should be made a priority; *Clarias* are also desirable food fish in their own right.

It is important to develop conservation strategy in an evolutionary perspective, but doubly so for Victoria, a volatile and dynamic lake basin in a region subject to climate change on a time scale relevant to human enterprise (Kendall 1969). A variety of mechanisms have been proposed to explain the extraordinary species richness of the East African cichlid faunas generally (Greenwood 1965*b*; Kendall 1969; Fryer & Iles 1972; Ribbink et al. 1983; Coulter et al. 1986; Owen et al. 1990; Lowe-McConnell 1993). Lowe-McConnell (1993) and Owen et al. (1990) recognized that speciation pursuant to lake-level fluctuation should be pulsed as alternating cycles of isolation and differentiation, followed by periods of species mixing, attrition, and stasis. Our observations indicate that this expectation is reasonable for the rift lakes, but that speciation dynamics in Lake Victoria are substantially more complex. Understanding this complexity will be important in the development of management strategies that conserve not only extant species, but also the mechanisms necessary to safeguard their integrity over the long term.

With its broad, shallow morphometry, the Lake Victoria Basin allows for speciation in satellite lakes during lake regression (Greenwood 1965*b*) with only a modest change in lake level. In addition, however, the abundance of islands and rocky headlands and pinnacles affords ample opportunity for speciation during island formation through lake transgression (Owen et al. 1990). The isolation and mixing periods for the two mechanisms are out of phase; thus they must operate reciprocally, like a two-cycle pump. Differentiation and mixing would occur at all times, as the relative contribution of each mechanism shifts with any change in lake level, up or down. Thus, speciation dynamics in Lake Victoria should be more rapid, more continuous, and more geographically diffuse than in either Lake Malawi or Lake Tanganyika. This may help explain how the entire haplochromine species flock in Lake Victoria could have arisen in the 12,000 to 14,000 years since the last great desiccation of the lake basin (Kendall 1969; see also McCune et al. 1984; Scholz et al. 1990; Owen et al. 1990).

Human activity brings two new elements to the already very complex picture in Lake Victoria. First, the destruction of papyrus swamps could greatly complicate biogeography and population structure by eliminating barriers to dispersal maintained by chronic hypoxia (Chapman et al. 1993; Ogutu-Ohwayo 1993). Evidence for a recent increase in the lability of the lake level only amplifies this concern (Kite 1981). Second, observations in Lake Victoria (our own samples of Sondu-Miriu and Kusa rivers in Kenya; Basasibwaki, personal communication, for the Nile River) and Lake Nabugabo (Ogutu-Ohwayo, personal communication) suggest that retreat to river mouths is now an important aspect of cichlid population structure. Nile perch may assume the role originally proposed for high salinity as a selective force pushing lacustrine cichlids into isolated river-mouth refugia (Kendall 1969).

It is important for environmental planners to appreciate the volatility of the Lake Victoria fauna and the environment that created it, as well as the vulnerability of the isolating mechanisms that maintain faunal integrity. The morphometry of the Lake Victoria Basin offers a natural, two-fold option for species conservation: the preservation of satellite lakes that retain intact faunas, and the use of those that do not as repositories for indigenous species retrieved from Lake Victoria. After all, satellite lakes were playing a crucial role in biodiversity conservation in Lake Victoria long before humans stumbled upon the idea. In this context, the rescue and captive propagation of Lake Victoria's endangered food fishes and haplochromine species makes real sense (Bruton 1990; Kaufman 1990; Reid 1990; Wilhelm 1993). For maximum benefit, restoration in satellite lakes should be performed in concert with research in evolutionary genetics and experimental limnology. They can be the proving grounds for constructive, large-scale management schemes in the main lake.

We have encountered great skepticism about the notion of ecological restoration of any kind in Lake Victoria, on the grounds that it is unlikely that people could influence so large a system. This is rather ironic. The profound changes recently witnessed in Lake Victoria are clearly attributable to human activities (Kaufman 1992; Witte et al. 1992*b*). There is thus no question that people can rapidly and efficiently alter even a mammoth lake ecosystem. The challenge is to guide such alterations to promote a system that is more sustainable, and therefore more beneficial to both people and wildlife.

Acknowledgments

The authors express their gratitude to colleagues and students on the Lake Victoria Research Team, particularly Richard Ogutu-Ohwayo, Bill Cooper, Moshe Gophen, Bob Hecky, James Maikweki, Paul Sackley, Alistair Economakis, and Simon Agembe, who assisted in every aspect of our studies. The senior author is grateful to Humphrey Greenwood for providing inspiration and encouragement for this work. We thank Frans Witte, Kees Barel, Tijs Goldschmidt, and Martien Van Oijen for their friendly assistance and endless patience in haplochromine taxonomy. Ms. Helga Sprunk expertly piloted a recalcitrant ROV during the December 1990 expedition. Mr. Karsten Hartel and Ms. Jennifer Bush of the Harvard Museum of Comparative Zoology assisted in specimen curation, and Doug Warmoltz of the Columbus Zoo Aquarium assisted in obtaining specimens from the Lake Victoria Fishes Captive Breeding Program. We appreciate the efforts of Marianne Farrington and Lauren and Colin Chapman in reviewing this manuscript. This work was supported by grants from the National Science Foundation (BSER–9016552), the Pew Scholars Program in Conservation and the Environment, the National Oceanic and Atmospheric Administration, the U.S. Agency for International Development, the Institute for Museum Services, and the Conservation, Food and Health Foundation of Boston. Work in Kenya was performed under research permit number OP.13/001/21C 100 to L. S. Kaufman, under the auspices of the Kenya Marine and Fisheries Research Institute, Dr. Ezekiel Okemwa, Director. Work in Uganda was carried out under the auspices of the Ugandan Freshwater Fisheries Research Organization, Dr. Bill Kudhongonia, Director.

Literature Cited

Andrews, C., and L. S. Kaufman. 1993. Captive breeding programs and their role in fish conservation. In Proceedings of the 6th International Congress on Breeding Endangered Species, Jersey Wildlife Preservation Trust, Jersey, England.

Barel, C. D. N., R. Dorit, P. H. Greenwood, G. Fryer, et al. 1985. Destruction of fisheries in Africa's lakes. Nature 315:19–20.

Bruton, M. N. 1990. The conservation of the fishes of Lake Victoria, Africa: An ecological perspective. Environmental Biology of Fishes 27:161–175.

Cadwalladr, D. A. 1965. The decline in *Labeb victorianus* Blgr. (Pisces: *Cyprinidae) fishery of Lake Victoria and associated deterioration in some indigenous fishing methods in the Nzoia River, Kenya. East African Agriculture and Forest Journal 30:249–256.

Chapman, L., C. Chapman, L. Kaufman, and K. Liem. 1993. The role of papyrus swamps as barriers to fish dispersal: A case study and implications for fish diversity in the Lake Victoria Basin. Page 34 in People, fisheries, biodiversity, and the future of Lake Victoria, Report 93–3. New England Aquarium, Boston, Massachusetts.

Coulter, G. W., B. R. Allanson, M. N. Bruton, P. H. Greenwood, R. C. Hart, P. B. N. Jackson, and A. J. Ribbink. 1986. Unique qualities and special problems of the African Great Lakes. Environmental Biology of Fishes 17(3):161–183.

Crapon de Caprona, M. D., and B. Fritzch. 1984. Interspecific fertile hybrids of haplochromine cichlidae (Teleostei) and their possible importance for speciation. Netherlands Journal of Zoology 34(4):503–538.

Crowder, L. 1986. Ecological and morphological shifts in Lake Michigan fishes: Glimpses of the ghost of competition past. Environmental Biology of Fishes 16(1–3):147–157.

Fish, G. R. 1956. Some aspects of the respiration of six species of fish from Uganda. Journal of Experimental Biology 33:186–195.

Fryer, G., and T. D. Iles. 1972. The cichlid fishes of the Great Lakes of Africa. Oliver & Boyd, Edinburgh, Scotland.

Gabriel, W., and M. Lynch. 1992. The selective advantage of reaction norms for environmental tolerance. Journal of Environmental Biology 5:41–59.

Goldschmidt, T., and F. Witte. 1992. Explosive speciation and adaptive radiation of haplochromine cichlids from Lake Victoria: An illustration of the scientific value of a lost species flock. Mitteilyngen Internationale Vereinigung fuer Theoretische und Angewanette Limnologie 23:101–107.

Gophen, M., U. Pollingher, and P. B. O. Ochumba. 1993. Feeding habits of tilapias and the limnology of Lake Victoria. Israel Oceanographic and Limnological Research Report T6/93 Israel Oceanographic & Limnological Research, Kinneret Limnological Laboratory, Tiberias, Israel.

Graham, M. 1929. The Victoria Nyanza and its fisheries. A report on the fishing surveys of Lake Victoria. London Crown Agents for the colonies.

Greenwood, P. H. 1965*a*. Environmental effects on the pharyngeal mill of a cichlid fish, *Astatoreochromis alluaudi* and their taxonomic implications. Proceedings of the Linnoean Society (London) 176:1–10.

Greenwood, P. H. 1965*b*. The cichlid fishes of Lake Nabugabo, Uganda. Bulletin of the British Museum of Natural History (Zoology) 12:315–357.

Greenwood, P. H. 1980. Towards a phyletic classification of the "genus" *Haplochromis* (Pisces, Cichlidae) and related taxa. Part II: The species from Lakes Victoria, Nabugabo, Edward, George, and Kivu. Bulletin of the British Museum of Natural History (Zoology) 39:1–101.

Greenwood, P. H. 1981. The haplochromine fishes of the East African lakes. Kraus Thomson Organization GmbH, Munich, Germany.

Greenwood, P. H. 1984. African cichlids and evolutionary theories. Pages 141–154 in A. A. Echelle and I. Kornfield, editors. Evolution of fish species flocks. University of Maine at Orono Press, Orono, Maine.

Harrison, K., O. Crimmen, R. Travers, J. Maikweki, and D. Mutoro. 1989. Balancing the scales in Lake Victoria. Biologist 36(4):189–191.

Heard, W. H., and V. A. Vail. 1976. Anatomical systematics of *Etheria elliptica* (Pelecypoda:Mycetopodidae). Malacological Review 9:15–24.

Hoogerhoud, R. J. C. 1984. A taxonomic reconsideration of the haplochromine genera *Gaurochromis* Greenwood, 1980 and

Labrochromis Regan, 1920 (Pisces, Cichlidae). Netherlands Journal of Zoology 34:539–565.

Hoogerhoud, R. J. C. 1986. The ecological and taxonomic aspects of morphological plasticity in molluscivorous haplochromines. Annales Musee Royal de L'Afrique Centrale, Zoologie, 251:131–134.

Hoogerhoud, R. J. C., F. Witte, and C. D. N. Barel. 1983. The ecological differentiation of two closely resembling *Haplochromis* species from Lake Victoria (*H. iris* and *H. hiatus*; Pisces, Cichlidae). Netherlands Journal of Zoology 33(3):283–305.

Hughes, N. F. 1992. Nile perch, *Lates niloticus*, predation on the freshwater prawn, *Caridina nilotica*, in the Nyanza Gulf, Lake Victoria, East Africa. Environmental Biology of Fish. 33:307–309.

Jablonski, D. 1986. Mass extinctions: New answers, new questions. Pages 43–61 in L. S. Kaufman and K. G. Mallory, editors. The last extinction. MIT Press, Cambridge, Massachusetts.

Kaufman, L. S. 1988. Challenges to fish faunal conservation programs as illustrated by the captive biology of Lake Victoria cichlids. Pages 105–120 in Proceedings of the 5th International Congress on Breeding Endangered Species, Cincinnati Zoo and Botanical Garden, Cincinnati, Ohio.

Kaufman, L. S. 1992. Catastrophic change in species-rich freshwater ecosystems, the lessons of Lake Victoria. Bioscience 42:846.

Kendall, R. L. 1969. An ecological history of the Lake Victoria basin. Ecological Monographs 39:121–176.

Kite, G. W. 1981. Recent changes in level of Lake Victoria. Hydrological Science Bulletin 26(3):233–243.

Kolding, J. 1993. Population dynamics and life-history styles of Nile tilapia, *Oreochromis niloticus*, in Ferguson's Gulf, Lake Turkana, Kenya. Environmental Biology of Fish. 37:25–46.

Lowe-McConnell, R. 1993. Fish faunas of the African Great Lakes: Origins, diversity and vulnerability. Conservation Biology 7:634–643.

McCune, A. R., K. S. Thomson, and P. E. Olson. 1984. Semionotid fishes from the Mesozoic Great Lakes of North America. Pages 27–44 in A. A. Echelle and I. Kornfield, editors. Evolution of fish species flocks. University of Maine at Orono Press, Orono, Maine.

McElroy, D. M., I. Kornfield, and J. Everett. 1992. Coloration in African cichlids: Diversity and constraints in Lake Malawi endemics. Netherlands Journal of Zoology 41:250–268.

Meyer, A., T. D. Kocher, P. Basasibwaki, and A. C. Wilson. 1990. Monophyletic origin of Lake Victoria cichlid fishes suggested by mitochondrial DNA sequences. Nature (London) 347:550–553.

Miller, D. J. 1989. Introductions and extinction of fish in the African Great Lakes. Trends in Ecology and Evolution 4(2) 56–59.

Ochumba, P. B. O. 1990. Massive fish kills within the Nyanza Gulf of Lake Victoria, Kenya. Hydrobiologia 208:93–99.

Ochumba, P. B. O., and J. O. Manyala. 1992. Distribution of fishes along the Sondu-Miriu River of Lake Victoria, Kenya with special reference to upstream migration, biology and yield. Aquaculture and Fisheries Management 23:701–719.

Ochumba, P. B. O., M. Gophen, and L. S. Kaufman. 1993. Changes in oxygen availability in the Kenyan portion of Lake Victoria: Effects on fisheries and biodiversity. Abstract. Page 33 in People, fisheries, and biodiversity, and the future of Lake Victoria, Report 93–3. New England Aquarium, Boston, Massachusetts.

Ogutu-Ohwayo, R. 1990. The decline of the native fishes of Lakes Victoria and Kyoga (East Africa) and the impact of introduced species, especially the Nile perch, *Lates niloticus*, and the Nile tilapia, *Oreochromis niloticus*. Environmental Biology of Fishes 27:81–96.

Ogutu-Ohwayo, R. 1993. The effects of predation by Nile perch, *Lates niloticus* L. on the fishes of Lake Nabugabo, with suggestions for conservation of endangered endemic cichlids. Conservation Biology 7:701–711.

Owen, R. B., R. Crossley, T. C. Johnson, D. Tweddle, I. Kornfield, S. Davison, D. H. Eccles, and D. E. Engstrom. 1990. Major low levels of Lake Malawi and their implications for speciation rates in cichlid fishes. Proceedings of the Royal Society (London) B240:519–553.

Reid, G. M. 1990. Captive breeding for the conservation of cichlid fishes. Journal of Fish Biology 37(Suppl. A):157–166.

Ribbink, A. J., B. A. Marsh, A. C. Marsh, A. C. Ribbink, and B. J. Sharp. 1983. A preliminary survey of the cichlid fishes of rocky habitats in Lake Malawi. South African Journal of Zoology 18:149–310.

Sackley, P. 1992. Phenotypic plasticity in fishes. M. A. Dissertation. University of Massachusetts at Boston, Boston, Massachusetts.

Scholz, C. A., B. R. Rosendahl, J. W. Versfelt, and N. Rach. 1990. Results of high-resolution echo-sounding of Lake Victoria. Journal of African Earth Sciences 11(1–2):25–32.

Twongo, T. 1993. The spread of water hyacinth on lakes Victoria and Kyoga and some implications for aquatic biodiversity and fisheries. Abstract. Page 42 in People, fisheries, biodiversity, and the future of Lake Victoria, Report 93–3. New England Aquarium, Boston, Massachusetts.

Welcomme, R. L. 1970. Studies on the effect of abnormally high water levels on the ecology of fish in certain shallow regions of Lake Victoria. Journal of Zoology (London) 160:405–436.

Wilhelm, K. 1993. Towards an European species survival plan for the endangered cichlids of Lake Victoria. Pages 33–38 in Meeting of the European Union of Aquarium Curators, Memoires de l'Institut oceanographique Paul Ricard (1992), Marseilles, France.

Witte, F. T. 1981. Initial results of the ecological survey of the haplochromine fishes from the Mwanza Gulf of Lake Victoria, Tanzania: Breeding patterns, trophic and species distribution. Netherlands Journal of Zoology 31:175–202.

Witte, F., C. D. N. Barel, and R. J. C. Hoogerhoud. 1990. Phenotypic plasticity of anatomical structures and its ecomorphological significance. Netherlands Journal of Zoology 40(1–2):278–298.

Witte, F., and E. L. M. Witte-Maas. 1987. Implications for taxonomy and morphology of intra-specific variation in haplochromine cichlids of Lake Victoria. Pages 35–118 in From form to fishery. Ph.D. Dissertation. Rijksuniversiteit Leiden, Leiden, The Netherlands.

Witte, F., T. Goldschmidt, J. Wanink, M. van Oijen, K. Goudswaard, E. Witte-Maas, and N. Bouton. 1992*a*. The destruction of an endemic species flock: Quantitative data on the decline of the haplochromine cichlids of Lake Victoria. Environmental Biology of Fishes 34:1–28.

Witte, F., T. Goldschmidt, P. C. Goudswaard, W. Ligtvoet, M. J. P. Van Oijen, and J. H. Wanink. 1992*b*. Species extinction and concomitant ecological changes in Lake Victoria. Netherlands Journal of Zoology 43(2–3):214–232.

Notes Added in Proof

The epiphytic algal grazer *Haplochromis annectidens* was recovered from Lake Nabugabo during 1993, but is extremely rare. UFFRO was renamed FIRI (Fisheries Research Institute) in 1993.