Long-lived Reef Fishes:

The Grouper-Snapper Complex

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POLICY

The American Fisheries Society (AFS) recognizes that reef fishes must be conservatively managed to avoid rapid overfishing and stock collapse because reef fish communities comprise slow-growing, late maturing fishes such as groupers and snappers. Therefore, the Society recommends that for such species, fishing mortality should be maintained at or near natural mortality. In addition, AFS cautions that an imbalance in the normal sex ratio may occur rapidly during harvesting of many reef fishes, thus leading to stock collapse because many reef fish species mature first as female but then become male later in life; most of the older, larger individuals in the population are male. Thus, conventional management modeling tools such as Spawner Biomass Per Recruit may lead to overly optimistic conclusions and should be used with caution. Many reef fish species form predictable, localized, seasonal spawning aggregations that are very vulnerable to overharvesting. Such aggregations should be protected.

The AFS supports the establishment of networks of large Marine Protected Areas and the development of individual transferable quotas, along with more conventional management measures to help maintain and restore reef fish populations and their habitats. The AFS encourages its members to become involved by providing technical information needed for protection of long-lived reef fishes to international, federal, state, and provincial policy makers so decisions are made on a scientific, rather than emotional or political, basis.

A. Issue definition

The status of most reef fish stocks is unknown in the southeastern United States and Mexico (Atlantic, Gulf of Mexico and Gulf of California). Stock information is available for only 22 out of 73 reef fish species off the U.S. in the Atlantic and 5 out of 55 species in the Gulf of Mexico (NMFS 1997; SAFMC 1999). Virtually nothing is known about the status of reef fish stocks in the Gulf of California, except that at least four species of grouper have been recognized to be threatened (Huntsman 1994; Hudson and Mace 1996). Unfortunately, this lack of information is often interpreted as absence of a problem. Only five of those species for which the status is known are considered healthy stocks. Some of the larger, long-lived species have been widely extirpated by overfishing and considered to be at risk of extinction (Musick 1998; Huntsman et al. 1999). Clearly, changes in fisheries management are needed that invoke a new ethic in fishing practices and incorporate effective conservation while maintaining the health and viability of marine ecosystems.

B. Background

The worldwide demand for fishes has increased dramatically in the last several decades, primarily because of human overpopulation (Brown et al. 1995), but also because of per-capita increases in consumption (Hardin 1968; Holdren and Ehrlich 1974; Ehrlich 1994) and an increased ability to locate and capture fish through advances in fishing technology (Dayton et al. 1995). Members of the reef fish complex of warm-temperate and tropical regions appear to be particularly at risk. In the southeastern United States alone, for example, species currently either overfished or in danger of being so include red porgy (*Pagrus pagrus*) (Harris and McGovern 1997), black sea bass (*Centropristis striata*) (Vaughan et al. 1995), gag (*Mycteroperca microlepis*) (McGovern et al. 1998b), scamp (*M. phenax*), snowy grouper (*Epinephelus niveatus*) (Wyanski et al. 2000), red grouper (*E. morio*) (Schirripa et al. 1999), warsaw grouper (*E. nigritus*), Nassau grouper (*E. striatus*) (Carter et al. 1994), speckled hind (*E. drummondhayi*), jewfish (*E. itajara*) (Sadovy and Eklund 1999), red snapper (*Lutjanus campechanus*), vermilion snapper (*Rhomboplites aurorubens*) (Zhao and McGovern 1997; Zhao et al. 1997), white grunt (*Haemulon plumieri*), and tilefish (*Lopholatilus chamaeleonticeps*) (SAMFC 1993). Jewfish and Nassau grouper have been so heavily overfished that they are protected and are candidates for the Endangered Species List (Sadovy and Eklund 1999). Warsaw grouper and speckled hind may soon follow. The fishery for red porgy in the U.S. Atlantic was closed in 1999 because of extremely low spawning potential. The economic value of this species complex makes protecting the sustainability of the fishery a critical consideration for this region (1996 landings in the Gulf of Mexico of roughly 16 million pounds, an ex-vessel value near US$36 million, Waters 1997).

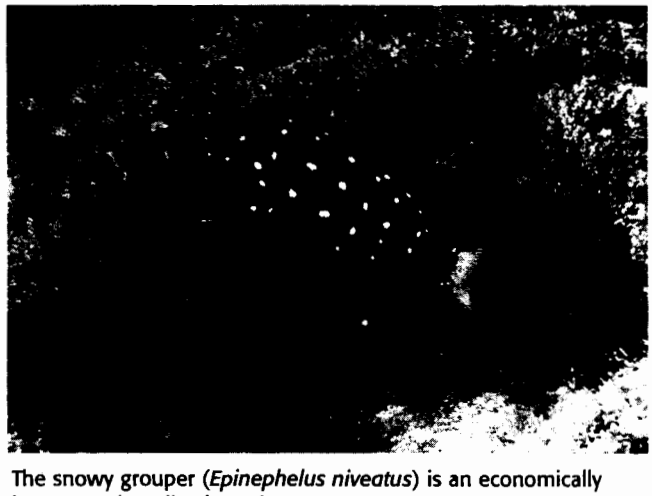
Life history. Many economically important reef fish species share a suite of life history characteristics that make them particularly susceptible to overexploitation. In addition, their behavioral characteristics exacerbate the problem. These species exhibit slow growth and late maturity (Musick 1999); high site fidelity; ontogenetic (development from embryo to post-embryo stages), seasonal and spawning migrations; complex social structure; and sex reversal (Coleman et al. 1999). At least eight (about 73%) of the most overfished species are protogynous hermaphrodites—they switch from female to male later in life. This complex life history and behavior explains why conventional management measures have entirely failed to stem the effects of commercial and recreational fishing pressure on this important group (Coleman et al. 1999).

Large, economically important reef fishes tend to be long-lived. Life spans range from about 25 to 40 years in warsaw grouper, jewfish, wreckfish (*Polyprion americanus*) (Manooch and Mason 1987; Bullock et al. 1992; Sedberry et al. 1999a), gag (Harris and Collins 2000), snowy grouper (Wyanski et al. 2000), blackbelly rosefish (*Helicolenus dactylopterus*) (White et al. 1998) and a number of snapper species (Zhao et al. 1997; Manooch and Potts 1997; A. Johnson, National Marine Fisheries Service [NMFS] Panama City Laboratory, pers. comm.), to as high as 53 years in red snapper (Goodyear 1995). Even small reef species like damselfish can live more than 15 years (Kohda 1996). Some of these maximum ages are likely to be underestimates because they were estimated from over-exploited populations. Ages at maturity range from 3 to 5 years in gag (Collins et al. 1987; Harris and Collins 2000; A. Johnson, NMFS Panama City Laboratory, pers. comm.) to 5–7 years in jewfish (Bullock et al. 1992) and red snapper (Goodyear 1995). The very low natural mortality rates in these large reef species (from 0.1 to 0.2 per year; Pauly 1980, 1997) imply that to sustain the species, only a small portion of the biomass (perhaps as low as 10%, Walters and Pearse 1996) can be harvested each year.

Fishing mortality. Fishing mortality rates are closer to 0.35–0.92 (30–60% annually), and fishing effort typically concentrates on the largest, oldest individuals, which supply the bulk of the reproductive output in any stock. The repeated result is a significant truncation in both the age and size structures of the population (Cuellar et al. 1996; Harris and McGovern 1997; Zhao et al. 1997; McGovern et al. 1998b). In red snapper, for example, virtually the entire catch is of relatively small (35–45 cm), young (3–5 year old) individuals, many of which are just reaching sexual maturity (Goodyear 1995) in a species that can live up to 53 years and reach sizes of 90 cm. The negative effect of the loss of large females on the reproductive potential of the population is obvious; one red snapper at 61 cm produces as many eggs as 212 red snapper at 42 cm (PDT 1990). Similarly, one gag at age 8 produces as many eggs as 48 gag at age 3 (Collins et al. 1998).

The largest, oldest individuals of some species are selectively removed from fished stocks both because they are the target of more intense fishing and because they frequent (at least seasonally) habitat that fishers can locate with relative ease, such as high-relief reefs and shelf-edge outcrops (Man et al. 1995; Koenig et al., in press). Gilmore and Jones (1992) have reported that larger gag and scamp may be more available to fishing gear because they outcompete smaller fish for bait. Many species like Nassau grouper, gag, scamp, tiger grouper (*M. tigris*), red hind (*E. guttatus*), and jewfish form consistent aggregations (always containing the largest, oldest individuals in the population) only during the spawning season (Domeier and Colin 1997). Migration of some species that aggregate may further increase susceptibility to fishing gear. For example, unpublished Marine Resources Monitoring Assessment and Prediction (MARMAP) program tagging data indicate that gag migrate long distances from North and South Carolina to south Florida where they are more accessible to fishing pressure due to the narrowing of the continental shelf off Florida (McGovern, pers. observ.). Other species, such as the deepwater wreckfish, yellowedge grouper (*E. flavolimbatus*), snowy grouper, and warsaw grouper may also form aggregations, but few data are available. This strong site fidelity, both to nonspawning habitat and to spawning sites to which they migrate annually, makes them vulnerable to fishers equipped with readily available electronic navigational and echo sounder equipment, with potentially devastating consequences.

Species with short spawning seasons that form a few large aggregations are more susceptible to severe overexploitation than are those with longer windows of opportunity for spawning in numerous smaller aggregations (Coleman et al. 1999). Nassau grouper, for example, form large aggregations of up to 10,000 individuals (Smith 1972) in a few specific locations around the full moons of December and January (Colin 1992)—a total spawning window of roughly 10 days. Of the nearly 50 Caribbean aggregations known for Nassau grouper, at least 10 have been annihilated by fishing (Sadovy and Eklund 1999). Gag and scamp, by comparison, form smaller aggregations (<100 individuals; Gilmore and Jones 1992; Koenig, pers. observ.) distributed widely along the outer continental shelf (50–100 m depth) from the eastern Gulf of Mexico to North Carolina (Coleman et al. 1996; McGovern et al.



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The snowy grouper (*Epinephelus niveatus*) is an economically important, long-lived species.

1998b; Y. Sadovy, Department of Ecology and Biodiversity, University of Hong Kong, pers. comm.). Gag spawning aggregations observed in the Atlantic off Florida in 1980 by Gilmore and Jones (1992) no longer exist at those sites, as a result of intense fishing pressure (Koenig et al., in press). Jewfish spawning aggregations, concentrated at depths ranging from 30 to 50 m along the southeast and southwest coasts of Florida, were heavily exploited from the 1960s through the 1980s by divers using powerhead-tipped spears and by both commercial and recreational fishers. The population suffered such a dramatic decline that the fishery was closed in 1990 (Sadovy and Eklund 1999).

Studies on spawning-site fidelity in bluehead wrasse (*Thalassoma bifasciatum*) demonstrate that subsequent generations of fish must learn the locations of specific spawning sites (Warner 1990). More recently, Luckhurst (1998) has provided evidence that spawning site fidelity in red hind is an acquired trait. In addition, the loss of spawning aggregations in several grouper species due to overfishing, despite their proximity to more healthy spawning stocks (Stevenson et al. 1998), would strongly suggest that spawning fidelity is a learned behavior in many reef fish species. When heavy fishing on aggregations removes the experienced fish, new recruits cannot find the aggregations, which can then collapse as functional spawning units. This appears to be what happened in orange roughy (*Hoplostethus atlanticus*) and Nassau grouper; aggregations were fished out and have not returned (Clark and Tracey 1993; Sadovy and Eklund 1999). Aggregation fishing has also been implicated in the declining male:female sex ratios of gag and scamp in both the Atlantic and the Gulf of Mexico (Coleman et al. 1996; Koenig et al. 1996; McGovern et al. 1998b; Harris and Collins 2000). In the Gulf of Mexico, the percentage of male gag in the catch has fallen from about 17% in the late 1970s (Collins et al. 1987; Hood and Schlieder 1992) to 2–4% in the early 1990s; that of scamp from about 36% to 18% (Coleman et al. 1996). In the Atlantic, the percentage of male gag has fallen from 19% during 1978–1982 to 6% in 1995; and the percentage of male scamp has dropped from 36% during 1979–1981 to 22% during 1996.

Although the significance of male loss is poorly understood, it is highly probable that such losses negatively affect reproductive success at the population level (Chapman et al. 1999). For the U.S. Atlantic population of red porgy (another protogynous reef fish), reproduction remained adequate to sustain a stable population until 1982. The population and reproduction collapsed due to severe overfishing (Huntsman et al. 1995). Harris and McGovern (1997) reported that red porgy in the U.S. Atlantic had a smaller size at age, smaller size at maturity (females) and underwent transition from females to males at smaller sizes during 1991–1994 than during 1979-1981. The root cause of fishing-induced changes in sex ratio may be a disruption of the social structure of aggregations (Shapiro 1987), which alters the reproductive output of the spawning group if sex change is socially mediated. If sex change is size- or age-related, then fishing in this manner could be selecting against recovery by removing the age or size classes in which sex change occurs. In either case, no management plans currently in effect are designed to preserve the size, age, social structure, or the natural sex ratios of reef fish stocks.

C. *Management*

Recruitment. The late planktonic stages of 40 of 73 species in the South Atlantic Fishery Management Council (SAFMC) Snapper/Grouper management unit cannot be identified to species, and this has limited the analysis of recruitment of planktonic stages to benthic (bottom) habitats (Lindeman et al., in press). However, early life history patterns and recruitment have been described for several important species. Often, each stage in the life history of a reef fish is associated with a different habitat and has very different recruitment dynamics (Gulland 1982; Frank and Leggett 1994; McGovern, pers. observ.). For example, all species of grouper and snapper spawn on offshore reefs, produce larvae in the open ocean that may disperse over hundreds of kilometers in the course of 20–50 days and experience high density-independent mortality (Brothers et al. 1983; Keener et al. 1988; Jones 1991; Coleman et al. 1996; Lindeman et al., in press). Larvae transported to nearshore nursery habitats settle as juveniles in seagrass beds, mangroves, oyster reefs, and marshes. Such species include gag, black grouper (*M. bonaci*), Nassau grouper, jewfish, black sea bass, gray snapper (*L. griseus*), lane snapper (*L. synagris*), hogfish (*Lachnolaimus maximus*), white grunt, and to some extent red grouper. Recruitment of larvae to post-settlement habitats in groupers that spawn in aggregations often occurs in pulses, following a planktonic period of about 40 days) (Keener et al. 1988; Shenker et al. 1993). Because spawning and recruitment in aggregating spawners are episodic events, they are subject to the vagaries of environmental conditions, and unfavorable conditions such as low water temperature during planktonic stages can drastically reduce year-class strength (McGovern and Olney 1998). Juveniles move offshore after a nursery grow-out period and eventually recruit into adult populations. Although these characteristics make reef fishes particularly tractable for description of recruitment processes, the same characteristics may make them largely unsuitable for management by conventional methods.

Reef fish stock assessments. Management methods for reef fishes in the southeastern United States are based on catch-at-age data. The data are used in virtual population analysis (VPA) to reconstruct cohort-specific stock abundances and fishing mortality rates on the basis of past catches. The outcome of the VPA is then used to make annual recommendations for the total allowable catch (TAC). The greatest problem of VPA is that it provides only hindsight information on a particular year class that has already passed through the fishery, but no information on the year classes that need managing. Estimates of current year class size based on historical trends impose a risk of underestimated fishing mortality, overestimated stock biomass, and misplaced optimism about the stock's condition (Walters and Hilborn 1992; Walters and Maguire 1996; Myers et al. 1997).

The predictive capability of recruitment forecasting allows management to anticipate problems and make preemptive adjustments to fishing pressure (de Lafontaine et al. 1992). Fishery-independent surveys of juvenile abundance have important implications for improving traditional assess-

ments that are based on fishery-dependent catch-at-age data. Fishery-independent surveys of estuarine juvenile gag (McGovern, unpublished data) and offshore life history stages of several species (Vaughan et al. 1995; Cueller et al. 1996; Harris and McGovern 1997; Sedberry et al. 1998; Zhao and McGovern 1997; McGovern et al. 1998b) conducted by the MARMAP program have been used to explain year-class strength and tune VPA analyses. In addition, MARMAP surveys provide real-time abundance estimates for many species (red porgy, black sea bass, vermilion snapper, etc.) on an annual basis (McGovern et al. 1998a).

Spawning potential ratio (SPR), as it is traditionally determined, has also proved less effective for protogynous reef fishes than for the cold-temperate fishes for which it was originally intended (e.g., Gabriel et al. 1989; Shelton and Morgan 1994). The emphasis in determining SPR has been and continues to be on the female's reproductive contribution, that is, egg production and the assumption that it is a valid measure of stock reproductive capacity. We know little about how declining numbers of male groupers affect reproductive output, but such declines almost certainly do. The fallacy is in the assumption that egg production is equivalent to zygote production (Levitan and Petersen 1995), since there may not be sufficient males to fertilize the available females.

Coleman et al. (1999) suggest that the reproductive capacity of a protogynous species could be severely compromised at harvest levels far below those that might affect recruitment in gonochoristic species. Current SPR methods measure the decline in reproductive potential only as the numbers (= biomass) lost, and the largest fish (all male) are usually the first to be removed by a fishery. Thus, a large percentage of the population (mostly female) survives and SPR wrongly predicts a relatively small change in reproductive output. In reality, a 90% decline in males, which made up a relatively small percentage of the original population could be equivalent to a 90% loss of reproductive potential. The SPR as typically determined for protogynous fish is very unlikely to be a valid measure of the stock's reproductive capacity.

Conventional management. Conventional management is based on management of individual species. However, reef species are part of a complex. Restrictions that are placed on individual species are ineffective because these "protected" species continue to be caught and suffer mortality when fishers target co-existing species that are not restricted.

Size limits and prohibited species. Size limits are intended to exclude from the fishery immature fish (lower size limit), the fish that have greatest reproductive potential (upper size limit), or both (slot limit). Lower size limits supposedly ensure against growth overfishing because they are generally set at sizes that allow most individuals at least one opportunity to reproduce. However, as depth of capture increases, so does release mortality of fish of all sizes (Rogers et al. 1986; Collins 1999; Parker 1999; Wilson and Burns 1996; Dixon and Huntsman, NMFS, Beaufort, North Carolina, unpublished data). In addition, because of the diversity of the reef fish community, nontargeted species will continue to be caught, even after quotas and bag limits are filled. Presumably anglers and commercial fishers will release fish caught in excess of the limits, but these fish are subject to the release mortality suffered by undersized fish. Because the vast majority of economically important reef species occur in a wide range of depths and stock declines cause fisheries to contract to areas of highest abundance, which are typically at greater depths, size limits and species prohibition become ineffective. Not only are the immature and first-year spawners unprotected, but the positive effects of a fortuitously large recruitment year can be significantly depressed by the high release mortality associated with a size limit. Such unreported discards were one of three dominant factors leading to the collapse of the Canadian cod fishery (Myers et al. 1997). The mortality of discarded fish not included in the catch-at-age data are unavailable to VPA. With regard to species prohibition, such regulations do nothing to protect deeper water species such as snappers and groupers, which are either already dead or moribund when captured. Size limits and species prohibition are therefore most effective when restricted to hardy species that carry out their life cycles in relatively shallow water.

Effort limitations. Effort limitations, such as bag limits for recreational fishing and trip limits and individual transferable quotas (ITQs) for commercial fishing, effectively protect both juvenile and adult stocks. A bag limit makes the fishery more inefficient but may do little to reduce fishing mortality if either the number of trips or the number of individuals fishing increases, or if release mortality occurs in bycatch of prohibited species (Coleman et al. 1999). Trip limits similarly restrict the allowable catch size per trip, but they are easily circumvented, and their potential benefits offset, by increases in days fished or trips taken (Huntsman and Vaughan, NMFS, Beaufort, North Carolina, unpublished data).

Time and space closures. Temporal and spatial-temporal restrictions typically imposed on a single-species basis prohibit fishing either during a particular time or for a short time over a particular area. However, this method is often ineffective because fishers will shift effort to times outside the closed period (Coleman et al. 1999). In addition, the species will still be taken and mortality will occur as fishers target other species.

D. Conclusion

Because of the ecological and behavioral characteristics of reef fish, none of the management tools cited above has been effective for their management. Rather, the management strategy with the greatest promise is the use of marine reserves or Marine Protected Areas (MPAs) spatially restricted absolute no-take zones, particularly when accompanied by reduced TAC to preclude effort shifts. However, this is the least-often employed management tool in the United States. The only examples of marine reserves in the southeastern United States are the Experimental *Oculina* Research Reserve (EORR) off the Atlantic coast of Florida and the newly designated no-take zones of the Florida Keys National Marine Sanctuary. Even the EORR is not a true no-take reserve because it allows trolling for coastal pelagics, and its closure is for only a prescribed period of 10 years. Furthermore, since the very slow growing deep-water coral, *Oculina varicosa*, has been destroyed and grouper spawning aggregations depleted, there is little hope that the EORR will be able to function as a true reserve for many years.

MPAs have worked in other areas of the world. For example, Sedberry et al. (1999b) found that MPAs in Belize, Central

America, had a higher diversity of fishes than in areas that were not protected. Various grouper and snappers were larger and more abundant in reserves. Populations of herbivorous forage species were reduced to what were probably natural levels in the presence of protected predators.

Besides protecting stocks, permanent spatial closures also protect physical habitat, age structure, perhaps genetic diversity of the stock, and community structure within the ecosystem (PDT 1990; Murray et al. 1999). Agardy (1997) reviewed these aspects of marine fishery reserves extensively, so we address in detail only the issue of protecting essential fish habitat. This aspect of reserve use is important because even greatly reduced fishing mortalities cannot compensate for habitat degradation caused by harmful nonfishing and fishing practices (Pauly 1997). For many reef fish species, essential habitats include estuarine nursery grounds, mid-shelf reefs, and outer-shelf reefs.

Reef fish in nearshore habitats have suffered most from human activities that lead to point and nonpoint sources of pollution and to structural alterations such as canalizations and water-diversion projects, which diminish or eliminate juvenile habitat. Seagrass beds in Tampa Bay, Florida, for example, have declined by about 80% since the 1960s; beds in Florida Bay have been so badly degraded that they may no longer be useful as nursery habitat (Butler et al. 1995). Coastal mangrove habitats have also undergone considerable loss to coastal development. Mangroves are important habitat for juvenile reef fishes in tropical areas. In the temperate coastal waters of the South Atlantic states, oyster reef habitat is important for gag, grey snapper, sheepshead (*Archosargus probatocephalus*), Atlantic spadefish (*Chaetodipterus faber*), and perhaps others. Oyster reef is being destroyed by harvesting and siltation caused by coastal development, further reducing nursery habitats. Although no estimates are available of the economic losses to fishery production associated with seagrass losses, quantitative estimates of potential fishery production clearly support adoption of protective measures.

Offshore reef habitats, particularly those important to bottom-dwelling fishes, are susceptible to destruction by mobile trawl and dredge gear (Dayton et al. 1995; Pauly 1997). Thus, in addition to the direct loss of fish populations, habitat and community structure are lost through the use of inappropriate gear (Koenig et al., in press).

It is important to restore and protect fish habitat integrity by establishing networks of MPAs. Reserves provide an insurance policy for management (Murray et al. 1999). Fisheries managers continue to put their trust in the single basket of stock assessment, ignoring high variability in recruitment, environmental factors, and the influence these factors have on predictions of stock health. These assessments as a consequence are usually overly optimistic. MPAs provide significant insurance against recruitment variability, habitat destruction, uncertainties in stock assessment, and most importantly, against our vast ignorance of ecosystem function.

Recommendations

A. Reef fishes must be very conservatively managed to avoid rapid overfishing and stock collapse.

1. Reef fish communities comprise slow-growing, late-maturing fishes such as groupers and snappers that have very low rebound potentials. In such species, fishing mortality (F) should be maintained at or near natural mortality (M).
2. Many reef fish species are protogynous hermaphrodites which means that most of the larger, older individuals are males. Thus, managers should keep in mind that when such species are harvested an imbalance in the normal sex ratio may occur rapidly thus leading to stock collapse.
3. Many reef fish species form predictable, localized, seasonal spawning aggregations that are very vulnerable to overharvesting. Such aggregations should be protected.

B. Conventional management modeling tools such as VPA and SPR may lead to overly optimistic conclusions when assessing reef fishes and should be used with caution.

C. Networks of large Marine Protected Areas (MPAs) should be established along with more conventional management procedures to help restore and maintain reef fish populations and habitats.

D. Individual transferable quotas (ITQs) should be considered in reef fish management plans to limit fishing effort.

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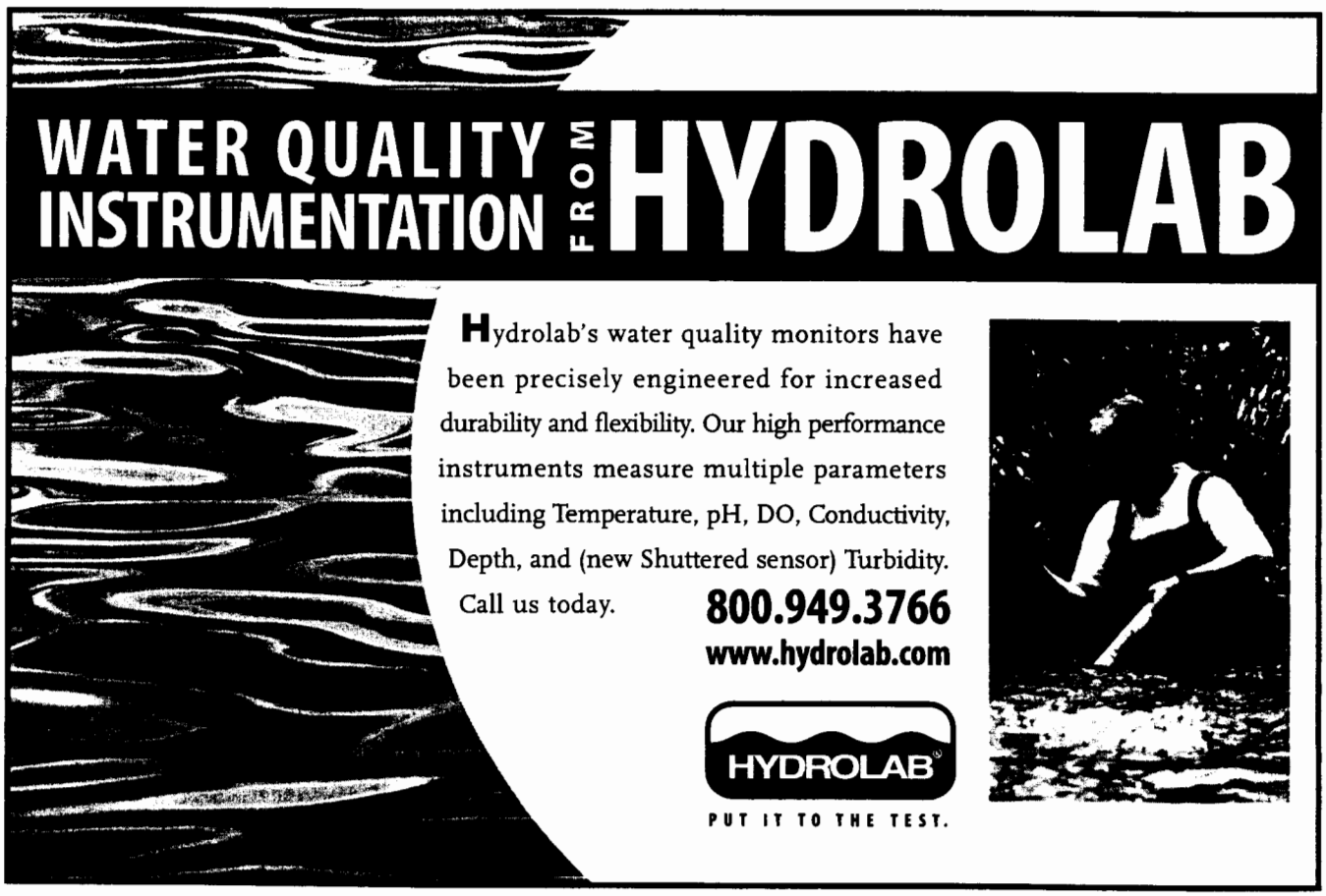
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