FIELD METHODS FOR THE BEHAVIORAL STUDY OF FORAGING ECOLOGY AND LIFE HISTORY OF HERBIVOROUS CORAL-REEF FISHES

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Behavioral studies of coral-reef fishes have provided many insights into the ecological and evolutionary processes occurring in the marine environment. Work with herbivorous species has proven especially fruitful in this regard, both because their algal food resources can be quantified within the context of specific environmental or demographic conditions, and because these variables can often be manipulated within controlled field experiments. My studies of coral-reef fishes exploit this unique research opportunity by integrating a suite of methods that, together, identify how specific ecological factors affect fish behavior and life history. In this paper, I outline this integrative approach with a discussion of basic techniques including: methods for the capture and marking of fishes; protocols for assessing the life history characteristics of growth, reproduction, and mortality; and, procedures for monitoring fish behavior and resource availability under a variety of natural and experimental conditions.

INTRODUCTION

Adult coral-reef fishes are extremely well suited for the study of ecological and evolutionary processes. This utility stems, to a large extent, from a dispersive juvenile phase that can expose adults to a wide variety of physical and demographic environments. In response, adult reef fish typically express a suite of labile, adaptive responses to specific environmental conditions, producing concordantly complex and variable patterns of social organization and behavior in different locations. These behaviors are easily quantified in the field and, thus, well suited for comparative and experimental studies. The relative ease with which individuals or entire populations can be manipulated offers further opportunities to examine how aspects of individual fitness such as growth, reproduction, and mortality shift as the result of experimentally induced changes in behavior. This basic approach has repeatedly provided important insights and answers to ecological and evolutionary questions during the last twenty years (Sale, 1991).

While the advent of SCUBA remains the most significant technological advance for the underwater study of coral-reef fishes, many other useful technologies have emerged during the last twenty years to facilitate the capture, marking, and monitoring of these animals and their resources. Indeed, researchers now face a potentially confusing array of possible field methodologies for the study of coral-reef fishes. During my studies of herbivorous reef fishes over the last fifteen years, I have tried, embraced, refined, or discarded a variety of techniques, and this paper provides a general overview of these, and related methods. This account is by no means a comprehensive review of current techniques, and interested readers should also peruse recent texts on reef fish ecology and behavior (*e.g.*, Pitcher, 1986; Sale, 1991; and references therein). While many of the methods described here have been specifically applied during studies of herbivorous reef fishes, a majority should also prove applicable to other species or aspects of underwater research.

METHODS

CAPTURING FISH

The capture of fish remains a crucial (and often rate-limiting) step towards a study's successful completion. Information on identity, sex, condition, fecundity, size, age, and growth typically require having a fish in hand at least once. Although pursuit and capture can traumatize fish (a state that behavioral scientists wish to avoid), such negative aspects are minimized with practice and patience. This is important to remember, especially when a particular method proves initially unfruitful or counter-productive. Although somewhat dated, Randall's (1963) review of methods for the capture of reef fishes remains an excellent reference on this topic. Note, however, that some popular devices for fish capture (*e.g.*, anesthetics and spears; Baldwin *et al.*, this volume) may prove unsuitable during behavioral studies of herbivorous fishes because of the fish's sensitivity to chemicals or its small size.

Nets: Numerous netting techniques work well for capturing reef fishes. Many smaller species and juveniles (up to ~ 50 mm) may be captured simply with a hand net of appropriate mesh size. I generally custom-build my hand nets onto frames of stainless steel rod, but simple aquarium nets, though rather flimsy, also work well for slower or very small species. It is often more effective to drive the fish with one hand towards a stationary net held in the other hand, rather than chasing the fish with the net itself. Alcohol from a squirt bottle is an effective irritant to fishes and can be sparingly used to drive them from holes and crevices (this can also be mixed with an anesthetic; see Gibson, 1967; Baldwin *et al.*, this volume).

Smaller non-herbivorous species attracted to baits (*e.g.*, wrasses) can often be caught in hoop or lift nets (fig. 1A). Broken urchins, crabs, or other local invertebrates work well for species that feed on plankton or glean along the benthos. Larger baits, that diffuse slowly (*e.g.*, tethered pieces of cooked or raw fish, squid, etc.), can also be effective, particularly in surgy conditions. A "model" bottle (*sensu* Myrberg and Thresher, 1974) containing a conspecific can also be used as "bait" to attract or distract strongly territorial species such as damselfishes. Lift netting is best done in pairs, with one individual holding the raised net while the other removes fish.

Small (1 - 2 m in height) "wall" nets, deployed in a rough "V" shape, are extremely effective for capturing vagile, medium-sized (50 - 250 mm), resident fishes on coral reefs (*e.g.*, parrotfishes, surgeonfishes, butterflyfishes, grunts, etc.). I typically use a net with a three sided, floored, central section and five to ten meter arms lined along the bottom with weights or leadline (fig. 1B; also see Baelde, 1990 for larger design). For wary fish, I use transparent monofilament netting for all but the distal arms. Taking a few minutes to ensure that all holes and gaps are closed along the base of the entire net is time well spent. Fish driven slowly towards the net mouth should be spooked into the end section just as they recognize the cul-de-sac for what it is. Once the fish enter the floored section, the net arms can be quickly closed over the entrance, effectively making an open-topped box from which the fish can be removed using a hand net. Smaller fish (< 35 mm) can be caught in this manner using fine meshed netting, however these nets are often easily damaged by larger fish or through snagging on corals. Smaller species are also more prone to predation while in the net. Choose mesh size carefully, since a seine for one sized fish becomes a lethal gill net for smaller individuals. Deployed nets should never be left unattended on reefs.

Small trawls, though generally not recommended for work on or near coral reefs (they can easily damage large sections of live coral), can be quite effective for non-selective collecting in grassbed and sand-halo areas adjacent to reefs. In Caribbean grassbeds, various parrotfish (*e.g.*, *Sparisoma radians*, *S. rubripinne*, *S. chrysopterum*, *S. automarum*, *Cryptotomus roseus*), wrasses (*e.g.*, *Halichoeres poeyi*, *Doratonotus megalepis, Xyricthys splendens*), and many other species (*e.g., Monacanthus ciliatus, Alphestes afder, Haemulon* spp.) may be captured in abundance using this method. Rays, scorpionfish, urchins, and other potentially injurious species can be hidden within a bolus of grass in the codend, so caution is needed when emptying the net. Fish traps, another relatively non-selective collecting method, will also capture fish in these areas. Smaller fish often get eaten by larger individuals in traps, so mesh size and compartmentalization within the trap are important considerations (*e.g.*, Newman and Williams, 1995). Fish flesh or invertebrates (crab, clams, urchins) are often used as bait, although many herbivorous fishes are attracted to white objects such as ceramics or coconut meat. In some areas, local fishermen may exploit your efforts by emptying traps in your absence and, like nets, fish traps should be checked regularly. Researchers have also captured fish using barbless fishing hooks (*e.g.*, Burke and Winn, 1995), but this method is extremely unselective.

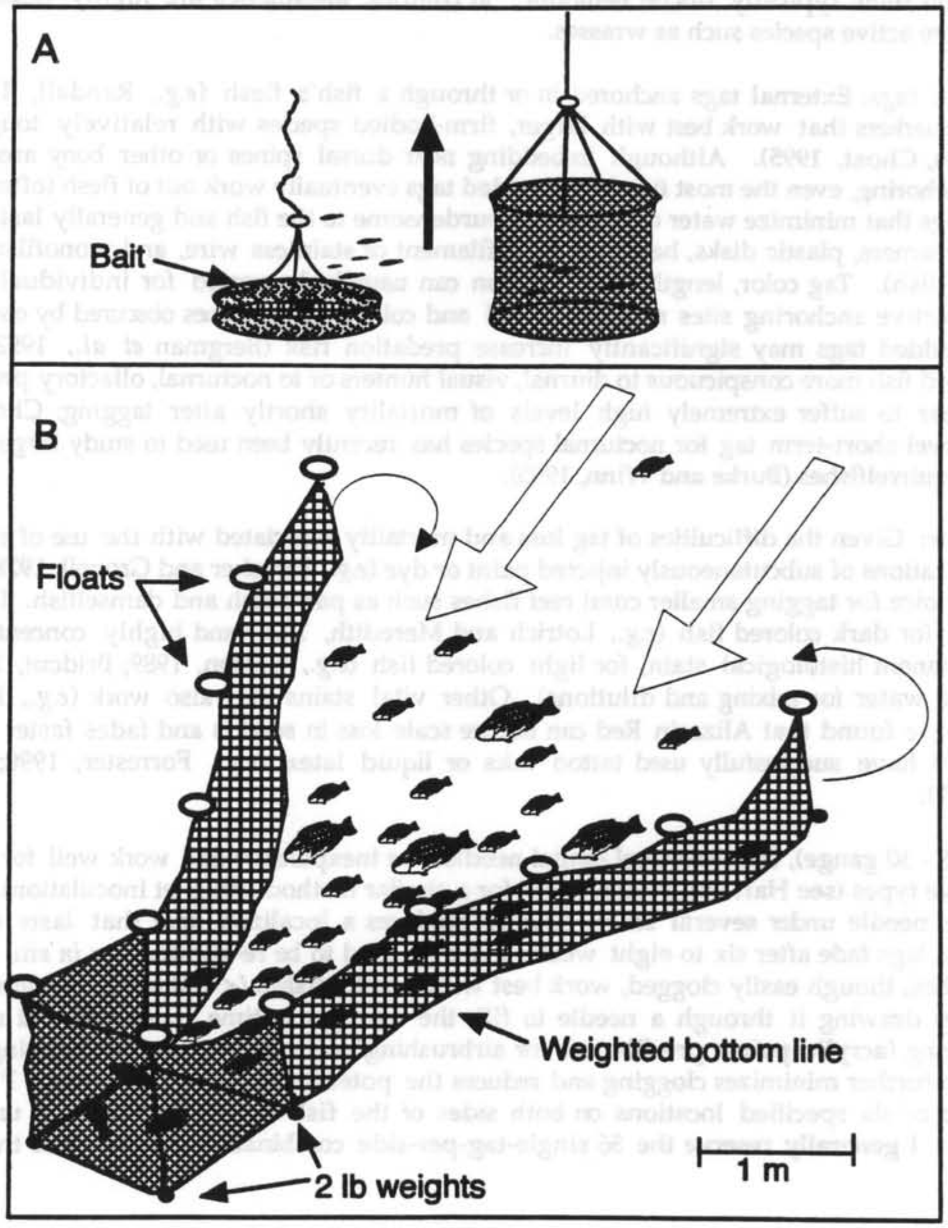

Figure 1. Net arrangements for capturing coral-reef fishes. A) Baited hoop or lift net; B) Wall net with floored central section.

FISH TAGGING

A variety of individual and cohort tagging methods have been developed for studies of reef fishes (*e.g.*, Parker, 1990; Bergman *et al.*, 1992). Choice of tagging method depends upon a number of factors including: fish size, color, scale type, skin and flesh characteristics, habits and habitat, whether the tag must be recognizable in the field (vs. in the hand), and sensitivity to handling. Some fish (*e.g.*, nocturnal species such as pempherids) are easily stressed by handling and exposure to sunlight or desiccation. Under these circumstances, it may be best to hold the fish in a net bag and apply the tag underwater. Highly diluted anesthetics such as Quinaldine and MS-222 or Metomidate (1- (1 phenylethyl) - 1H imidazone 5 carbolxylic acid methyl ester), a true hypnotic that significantly minimizes handling stress (Mattson and Riple, 1989) may ease handling and further reduce stress. I avoid anesthetics when working with parrotfishes and damselfishes because of their sensitivity to the chemicals and their typically docile behavior. In contrast, anesthetics are highly recommended for handling more active species such as wrasses.

Imbedded tags: External tags anchored in or through a fish's flesh (*e.g.*, Randall, 1961) provide conspicuous markers that work best with larger, firm-bodied species with relatively tough skin (*e.g.*, surgeonfishes, Choat, 1995). Although imbedding near dorsal spines or other bony areas generally improves anchoring, even the most firmly embedded tags eventually work out of flesh (often in weeks to months). Tags that minimize water drag are less burdensome to the fish and generally last longer (*e.g.*, floy tags, streamers, plastic disks, beads on monofilament or stainless wire, and monofilament marked with nail polish). Tag color, length, and position can usually be varied for individual recognition, although effective anchoring sites may be limited and color often becomes obscured by overgrowths of algae. Imbedded tags may significantly increase predation risk (Bergman *et al.*, 1992), either by making tagged fish more conspicuous to diurnal, visual hunters or to nocturnal, olfactory predators (*e.g.*, scarids appear to suffer extremely high levels of mortality shortly after tagging; Choat *et al.*, in press). A novel short-term tag for nocturnal species has recently been used to study larger (>150 mm) grunts and squirrelfishes (Burke and Winn, 1995).

Injections: Given the difficulties of tag loss and mortality associated with the use of external tags, unique applications of subcutaneously injected paint or dye (*e.g.*, Thresher and Gronell, 1978) remain my method of choice for tagging smaller coral reef fishes such as parrotfish and damselfish. I prefer white acrylic paint for dark colored fish (*e.g.*, Lotrich and Meredith, 1974) and highly concentrated Alcian Blue, a permanent histological stain, for light colored fish (*e.g.*, Clifton, 1989; Bridcut, 1993; always use deionized water for mixing and dilutions). Other vital stains may also work (*e.g.*, Kelly, 1967), although I have found that Alizarin Red can induce scale loss in scarids and fades faster than Alcian Blue. Others have successfully used tattoo inks or liquid latex (*e.g.*, Forrester, 1990; Knapp and Warner, 1991).

Small (26 - 30 gauge), stainless-steel dental needles are inexpensive and work well for a variety of fishes and dye types (see Hart and Pitcher, 1969 for a similar method using jet inoculation). Shallowly inserting the needle under several scales usually produces a localized spot that lasts for weeks to months (most tags fade after six to eight weeks and may need to be re-applied for *in situ* recognition). Smaller needles, though easily clogged, work best with smaller fishes (< 100 mm). Straining the dye or paint first by drawing it through a needle to fill the syringes is time consuming, but substantially reduces clogging (acrylic paints pre-filtered for airbrushing are recommended). Changing the needle every 2-4 fish further minimizes clogging and reduces the potential for skin infections. Placing marks at one or two of six specified locations on both sides of the fish allows hundreds of unique tagging combinations. I generally reserve the 36 single-tag-per-side combinations for fish less than 50 mm in length.

Methods such as freeze-branding (*e.g.*, Berge 1990; Lajeone and Bergerhouse, 1991), heat branding (*e.g.*, Jones, 1987; Hargreaves, 1992) and subdermal insertions of film (*e.g.*, Huegel *et al.*, 1977), coded wire (*e.g.*, Brodziak *et al.*, 1992), or fluorescent filaments (*e.g.*, Beukers *et al.*, 1995; Crook and White, 1995) should also work with an impressive variety of adult and juvenile coral reef fishes. Some of these techniques do not allow individual recognition, however, and may require having the fish in hand for tag recognition. Other cohort tagging methods such as fin clipping (*e.g.*, Sale, 1971) and immersion (to band otoliths) in tetracycline (Schmitt, 1984), alizarin red (Beckman and Schulz, 1996), or fluorochrome (Lang and Buxton, 1993) will also work with reef fishes.

MONITORING FISH

Ecological studies of fish generally examine life-history variables (*i.e.*, growth, reproduction, survivorship, or their proxies) relative to specific aspects of a fish's behavior or environment. Collecting this information typically requires an assortment of methodologies that not only directly measure life-history variables, but also monitor environmental conditions relative to where and how specific individuals behave. These include techniques for mapping and measuring aspects of the reefal environment (*e.g.*, rugosity, demography, food availability, water quality, etc.) as well as methods for monitoring a fish's behavior (*e.g.*, feeding and swimming rates, territorial defense, social interactions, etc.).

Growth: Measures of growth require the recapture of a previously measured fish. Researchers often simply monitor changes in fish length (generally using standard length, the distance from snout to caudal peduncle, to obviate inaccuracies caused by changes in fin length unrelated to growth). Some fish, particularly older ones, change length slowly and require long time spans before recapture. Although length and weight are strongly related, under most conditions fish weight will provide a more accurate measure of somatic growth (although gut and gonad condition can affect weight and introduce unwanted variance). For reef fish, I use a portable digital balance accurate to 0.01 grams, housed in a Plexiglas box with hinged lid. This sits atop a tripod or permanent post erected in shallow water near the reef. Because fish grow indeterminately, it may be necessary to repeatedly measure growth through time to develop an accurate profile of growth patterns. Few data of this nature are available, although recent work (Robertson and Clifton, unpub. data) reveals that individuals can show consistent patterns of growth and/or shrinkage on a variety of temporal scales.

Reproduction: Rates of reproduction can be estimated in a variety of direct and indirect ways. For demersal spawners, egg output can be directly assessed simply by counting eggs. This is often facilitated by providing an artificial substrate for females to lay on (*e.g.*, Robertson *et al.*, 1990). Many workers line nests with thin mylar sheets that can be removed, measured, and replaced with a minimum of disturbance. Areal measures of egg mass often provide good estimates of total egg number, although this relationship must be established for the range of egg densities encountered. During a recent study of damselfish reproductive activity in which egg density was quite variable, I photographed egg masses daily to record patterns of egg acquisition and loss. If egg density is constant, simply measuring the dimensions of the egg mass (*e.g.*, Petersen and Hess, 1991) or tracing its outline for later digitizing can provide accurate estimates of egg numbers (*e.g.*, Knapp and Warner, 1991). Output from broadcast spawners can also be estimated directly by immediately collecting eggs from the water column with a fine mesh (brine-shrimp) net swept back a forth at the point of egg release (*e.g.*, Petersen *et al.*, 1992).

Alternative methods can provide good indirect measures of reproductive output. Stripping of eggs or sperm can be done with many fish by capturing them just before the spawning period. Relationships between egg output and gonad size allow fecundity to be estimated (albeit, destructively) from gonad weights (Clifton, 1995). In terms of reproductive investments, time spent in reproductive activities (*e.g.*, courtship, territory defense, egg guarding) may also provide important estimates of reproductive investment.

Survivorship: Accurately estimating natural rates of fish mortality remains one of the more problematic aspects of studying the ecology of coral-reef fish. Mortality studies typically demand large sample sizes of individually recognizable fish, and long-lived species require monitoring over large time-spans. Emigration from the study area must simultaneously be monitored. Although fish tagging is often necessary for these studies, tagging itself may influence mortality and must also be controlled for.

Though time and labor intensive, the best data on mortality come from repeated censuses of known (usually tagged) individuals. This approach obviously works best for site-based (territorial or limited homerange), short-lived species that can be checked daily or weekly for presence or absence (*e.g.*, Caribbean damselfishes, wrasses, and smaller parrotfishes). I control for tag affects by concurrently censusing a (usually smaller) cohort of untagged, individually recognizable fish (*e.g.*, using scars, size, color patterns, etc.) in the same area. Relative mortality rates can sometimes be estimated from the stomach contents of predators (*e.g.*, Clifton and Robertson, 1993).

Mapping: Many adult reef fish are relatively sedentary, and thus easily mapped. To do so, however, often first requires a map of the reef itself. Simple maps are often sufficient and are easily made by two divers using compass and large measuring tape to mark the reef at regular north-south and east-west intervals. Careful orientation along both axes is initially critical to ensure accuracy, however line-of-sight orienting works well after that. Choice of grid size depends on the density and homerange of the study organism as well as water clarity and the detail needed (*e.g.*, sample size, whether location of behaviors and identity of individuals will be recorded, etc.). Many researchers prefer working on patch reefs, where the adult population is discrete, and problems of adult movements are minimized.

Behavior: Fish behaviors often reveal the mechanisms by which aspects of the physical or demographic environment influence a individual's life history. Information on feeding patterns, swimming rates, predator avoidance, spawning activity, and social interactions may all provide important clues. The simplest way to monitor and quantify many behaviors is to simply record their occurrence on an underwater slate. Time budgets can be easily estimated by using an underwater timer (*e.g.*, Casio watch) and observing focal animals for set periods of time (*e.g.*, Clifton, 1990). Data on more complicated behaviors can be facilitated with a variety of tools including hand counters (useful for monitoring short-term, discrete behaviors such as bites), underwater tape recorders, or underwater event recorders. A small, programmable computer, housed within a water-tight PVC bag, allows virtually unlimited data collection possibilities (*e.g.*, Clifton, 1995).

Food: The best estimates of the quality and quantity of food available to fishes on coral reefs come from studies of herbivorous fishes. Scrapings of algal cover from natural substrate or from ceramic tiles work well for grazing species such as parrotfish (*e.g.*, Clifton, 1991) or surgeonfish but may not be appropriate for selectively browsing species (*e.g.*, damselfishes). The quality of algae as food can be estimated in terms of percent organic matter as well as nutritive content (*e.g.*, nitrogen, carbohydrates, lipids, short-chain fatty acids). Algal quantity can be estimated from the amount of algae present within a known area, usually measured as dry weight, or better, ash-free dry weight (*e.g.*, Clifton, 1989). For ephemeral food sources such as benthic diatoms and epiphytic algae that accumulate quickly, renewal rates can be estimated from areas protected from grazing (*e.g.*, using hardware cloth over a set of tiles; Clifton, 1995).

Food availability for non-herbivorous fishes can also be quantified by a variety of methods (*e.g.*, plankton nets for planktivores, sand, rubble, or turf collections for detritivores and benthic gleaners, visual censuses of prey for piscivores); however, the spatial and temporal variance associated with the availability of non-algal foods generally demands extremely intensive sampling regimes.

CONCLUSION

Methods papers quickly age as technological advances and innovations redefine the bounds of our research. This paper is no exception, and the techniques championed here should be judged accordingly. Underwater research and related methodologies reflect an ever-evolving challenge to do things quickly, cheaply and well, and even the most basic, time-tested techniques will no doubt undergo fine-tuning during subsequent applications. More important than any method is the reason for its development: the need to collect data as inobtrusively and as accurately as possible. This goal should remain our focus as technological advances in areas such as computerization and remote sensing promise to further broaden the limits of underwater study.

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