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An investigation of timed-tethering: A method for study of coral reef piscivory.

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An Investigation of Timed-Tethering: A Method for Study of Coral Reef Piscivory

by
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Abstract

In this work, I compared several existing methods of studying piscivory (predation on fish) with a new method. While testing methods was the primary goal of my work, I was also able to test some hypotheses. This study focused on methods because, in coral reef ecosystems, work on predation has been hampered by a lack of methods suitable for its study. In coral reef fishes, studies have found correlations to support the hypothesis that predation has a major impact on the structure of assemblages (Hixon 1991).

The new method, timed-tethering, allows one to measure how long a tethered fish survives before being eaten, as opposed to the previous non-timed tethering technique, which measured presence/ absence of tethered prey after an interval as an index of predation risk (Minello 1991).

I used these new timed-tethers to study survival of juvenile french grunts, *Haemulon flavolineatum.* This work was done in Tague Bay, St. Croix, U.S.V.I. Several tethering studies were done, one study in conjunction with censuses to determine what patterns existed in piscivore and prey numbers.

Results of the censuses showed significantly more juvenile grunts on the back reef, and more piscivores on the fore reef. Results of a survival analysis of the timed-tether data revealed that piscivory was more intense on the fore reef than the back reef. These results suggest that higher densities of piscivores may result in higher predation pressure. The other tethering studies I ran showed no evidence of a pattern in predation

with respect to distance from the reef. One did find a significant difference in predation with time of day (more predation during the nocturnal period than during the diurnal, the reverse of previously held ideas about the effect of time of day).

In conclusion, I found the timed tethers to be a useful additional method for study of patterns in the intensity of piscivory. I conclude that they can give different information than the non-timed tethers, and therefore can address different hypotheses. Such timed-tethers are a valuable new method to study piscivory, especially since so few methods already exist.

DEDICATION

I would like to dedicate this to my nephews, Christopher (age 4),

Zachary (3), and Andrew (2) Ha, and my young friends,

Steven (7), Jennifer (4), and Christopher (3) Frick.

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Chapter One: Introduction, Objectives, and General Methods

Introduction

This thesis investigates the effect of piscivory on prey populations. The main purpose of this study is to compare and contrast methods of comparing spatio-temporal patterns in piscivory on coral reefs. The methods I intend to compare are non-timed tethering (presence/absence), timed tethering (survival duration), and piscivore censusing (number of piscivores). While investigating these methods, I also investigate several hypotheses. My general question is, "To what extent does piscivory structure coral reef fish populations?"

Before beginning a review of the literature on studies of predation in coral reef ecosystems, I would like to define some terms. First, community or assemblage is used to refer to the whole group of organisms of all species living in the specified area. Community or assemblage structure refers to the composition of that group of species. In general, a piscivore is anything that captures and eats live fish, including other fish, gastropods, people, whales, squid, porpoises, etc. In this study, the definition of piscivore is narrowed down to those fish that prey on other fish (fish that are piscivorous). The reason for this is because the devices mentioned earlier are designed to measure only piscivory by fish. This is quite a reasonable restriction, since few of the other kinds of piscivores mentioned previously are likely to prey on the type of fish (juvenile) used in this study. For a caveat, however, see Chapter 2, section III, and Chapter 3.

All the work described in this thesis was done in Tague Bay, St. Croix, United States Virgin Islands. For a detailed description of this site, see the study site section under General Methods. Briefly, this site consists of an off-shore bank-barrier reef, the seaward side of which is called the fore reef, and the landward side of which is called the back reef.

Reasons to study predation.

Methods for comparing patterns in piscivory are needed because predation is acknowledged as potentially a very important factor in evolution and ecology. Darwin (1859) mentioned predation as one method through which natural selection could occur. In fish, predation can affect prey fish community (or assemblage) structure in several ways. It can influence guild structure (Zaret 1980), the distribution of fish in space and time (Werner et al. 1983), and the age structure of fish populations (Wright et al. 1993). The importance of predation on fish (piscivory) is such that one model of the structure of coral reef fish communities proposes piscivory as key. This is the predation disturbance model, as originated by Talbot et al. (1978). In this model, predators remove enough prey fish to keep the prey from ever competing for resources.

Hixon (1991) reviewed the evidence to support this model, and put the support he found into three classes, circumstantial, correlational, and experimental.

Circumstantial Evidence

The first class consists of circumstantial evidence and includes arguments such as the ubiquity of piscivores, and the presence of chemical, morphological, and behavioural defenses in prey organisms. The ubiquity of piscivores suggests that, since piscivores occur in every system so far studied, they must be having some sort of impact. Defenses known include chemical (including poisons in the mucus, skin, or flesh, or venom), morphological (such as spines, bony armor, and modified scales), and behavioural mechanisms (such as activity patterns, spatial patterns, and schooling), all serving to protect individuals from predators. Thompson (1978) summarizes the ways prey fish can avoid predation. He includes defenses, and some others such as life history traits, mutualistic relationships, and mimicry.

Correlational Evidence

The second class of evidence is correlational evidence; that is, existence in nature of correlations expected if predation were having an impact on prey populations. Correlations between shelter availability and prey numbers, and between piscivore abundance and prey abundance are among those Hixon reviews. Hixon also includes survivorship patterns in this group, though they are not correlations. Since his review summarizes the evidence so well, I will describe below only particularly relevant cases, or ones he did not mention.

Hixon and Beets (1989, 1993) examined the effects of refuge structure on the composition of prey fish assemblages on artificial coral reefs. They found that the type

and availability of refuge strongly affected the composition of prey fish communities. Shulman (1984) found that, for all the species she studied, recruitment and early survivorship were strongly limited by refuge availability. This sort of relationship between survival and shelter availability is not found only in coral reef systems. Fraser and Cerri (1982) found that freshwater stream fishes are more likely to go into areas that contain piscivores if those areas includes shelter sites.

Shulman et al. (1983) found a negative correlation between predator abundance and prey abundance. They found that french grunts recruited in lower numbers to reefs that were home to snappers, a family of piscivorous fishes. Hixon and Beets (1993) also found a negative correlation between recruitment and piscivore density. They found that as the number of piscivores increased, the maximum number of prey decreased. From this, they concluded that piscivores set an upper limit on the number of prey fish that can occupy a reef. In this study, they did not find a negative relationship among reefs between the average abundances of predator and prey, as would be the case if predators acted chronically (consistently over time). They did, however, find a negative relationship between abundance of predators and maximum number of co-occurring prey. In other words, piscivores were observed to set a maximum on prey numbers, but did not affect prey populations that were below this maximum. Only when the prey population goes above this maximum do piscivores reduce prey numbers. From these results, they concluded that piscivory acted sporadically (occasionally, when prey populations go over the maximum) rather than chronically (at all times, as would be the case if they had found a correlation between abundances of predators and prey) on prey

fish abundances.

Survivorship patterns suggesting high rates of mortality via predation were found by Shulman & Ogden (1987), working on grunt recruitment on St. Croix. They found that 99.9% of grunts died in the first year of life, and suspected that piscivory was the cause of most of this mortality. The Type III survivorship curve they found is the one expected from the predation disturbance model. Sale and Ferrell (1988) also looked at survivorship, but in a larger number of species. They found 20 to 80 percent mortality in the first six weeks of a fish's post-settlement life. Aldenhoven (1986) studied a reef fish (*Centropyge bicolor*) on the Great Barrier Reef, and measured mortality rates for various ages of fish. This study found up to 30 percent mortality of juvenile fish in 2.2 months. These studies provide much indirect evidence to support the idea that piscivores influence prey community structure.

Experimental Evidence

Hixon's third class of evidence consisted of manipulative studies, of which he could find only four; Bohnsack (1982), Stimson et al. (1982), Thresher (1983), and Doherty and Sale (1986). Bohnsack's study (1982) was a "natural experiment" rather than a manipulative experiment. He quantified fish abundances on fished and unfished reefs. He thought that piscivores would suffer a greater reduction in numbers, than would other species, as a result of fishing, since many piscivores are sought after by humans. Some prey fish he studied showed patterns one would expect if piscivory were important,

i.e. larger populations of prey fish occurred on reefs that had fewer piscivores. However, he concluded that the evidence presented was insufficient to support the predation disturbance model, since the abundances of some prey species showed no pattern, or patterns opposite of that expected.

Stimson et al. (1982) attempted to remove piscivorous muraenid eels (chiefly *Lycodontis undulatus*) from selected reefs in Hawaii. However, they were unable to show a reduction in the numbers of piscivores. They speculated that their method of trapping and releasing piscivores allowed the piscivores to home in on and return to the reef from the distant release point.

Thresher (1983) cleared some reefs of all fish other than the study species (*Acanthochromis polyacanthus*), cleared some of just planktivores, and left others as controls. The patterns of prey fish survivorship he observed suggested the possibility of a piscivore effect, since the fish on reefs from which piscivores were removed showed higher survivorship than on the same reefs a year earlier. However, since his sample sizes were too small for statistical analysis, some doubt remains.

Doherty and Sale (1986), caged some areas of reef to exclude piscivores, but still permit settlement of juvenile prey fishes. They monitored post-settlement juvenile fish populations, to uncaged, caged and half-caged areas. They used the differences between the rates at which juveniles accumulated in the habitats as their measure of differences in predation. Especially in one class of fish (site-attached ones), they found that prey-fish survivorship was higher in the cages than in either the uncaged or partially caged areas. This suggests that piscivory reduced the numbers of fish present below their maximum,

thus supporting the predation disturbance model. Although these studies supported the model, none were definitive.

Two other manipulative studies that support the predation disturbance model exist that were not discussed by Hixon. Belk (1993) studied sunfish (*Lepomis spp.*) in a large pond in Georgia. In this study, both conspecific density and predation risk were manipulated. Belk showed that competition was not very important in this system, since conspecific density had little effect on growth rates or lipid content. However, significant effects were found in predation risk experiments. Growth rates were higher in vegetated areas (low risk), as opposed to open areas (high risk). Mortality, in a tethering study (in which sunfish were attached to monofilament line and left out for a time to be eaten), was shown to be higher in the open areas. These results suggest a pattern very much like that predicted by the predation disturbance model, if one considers the vegetated areas as analogous to the reef in the model. The vegetated areas were shown in this study to be able to support more fish than unvegetated areas, with no significant decrease in growth rates from the unvegetated areas. This means that fish present in the vegetated areas were not competing for resources. Since Belk considered the experimental pond to be a heavy predation environment, this would lead one to the conclusion that the number of prey fish was limited by piscivores to a level below that which allows competition to take place.

Caley (1993) removed piscivores from reefs with the anesthetic quinaldine. He showed that most species of recruit and resident fishes were more abundant on reefs from which predators had been removed. This is the strongest support so far, in a manipulative experiment, for the predation disturbance model.

When taken in total, all of the evidence, from all three classes, presents a consistent argument that piscivory is an important factor in coral reef fish ecology. Note, however, that the predation disturbance model is an ecosystem model, while the methods I intend to compare are for determining patterns in piscivory. As such, these methods study more the behavioural interactions between piscivore and prey, although there are implications for the ecology of both predator and prey. For this reason, this work is not intended to prove or disprove the predation disturbance model. I include this model here only to show how important piscivory may be to the ecology of coral reefs, and hence why any methods at all are needed to study it.

Difficulties in Studying Piscivory

Hixon's (1991) review indicated how little attention had been directed to the role of piscivory. He also pointed out that few methods exist for doing manipulative field experiments on the role of piscivory.

Several reasons exist for the paucity of work (especially manipulative field experiments) on piscivory in coral reef systems. The first reason is the relative infrequency of observable predation events (Zaret 1979). Helfman (1989) observed Atlantic trumpetfish, Aulostomus maculatus (a diurnally active piscivore), for nineteen hours, and observed eight successful predation events. This comes out to about one every two hours, which is quite infrequent, especially given the difficulty of using SCUBA (see below). Sweatman (1984) observed that lizardfish, Synodus englemani (another diurnally

active piscivore), ate a mean of 1.8 prey per day (13 hours). This means that feeding events are rare for this species of piscivore, as well. Collections of piscivores such as those made by Randall (1967) yield many empty stomachs, as a result.

A second difficulty is that piscivores often have activity periods unsuited to direct daytime observation. Most piscivores are crepuscular (Hobson 1979), making direct (visual) and indirect (photographic) means of observation difficult and costly. Direct observational studies are therefore difficult, especially when this difficulty is combined with the first.

Third, most piscivores have large home ranges, roaming over large areas, making them difficult to follow, especially in low light. This also means that studying these fishes on a scale appropriate to their home range size is difficult. Often, their home range size is so large that it makes manipulation of piscivore densities on any reasonable scale (such as a patch reef) very difficult. Piscivores such as billfish, tuna and sharks range over especially large areas. Clemens and Flittner (1969) found that tuna can roam across the entire north Pacific Ocean. Other piscivores seem to have smaller home ranges, but little work has been done on home range size of reef-associated piscivores. Casual observations support the idea that reef-associated piscivores roam over larger areas than their prey.

Finally, many other methods used to study predator-prey interactions on land are either not applicable underwater or are vastly more difficult and costly to apply there. For example, using electronic devices such as transmitters and recorders is difficult in saltwater. In addition, the experimenter's time is limited to the length of time one can

safely SCUBA dive. As described subsequently, other methods have been tried and found lacking.

As discussed earlier, Hixon (1991) found only four manipulative studies have been done on piscivory. He found flaws in each. Bohnsack (1982) studied piscivores removed by spear fishing; Stimson et al. (1982) attempted removal of piscivores by trapping; Thresher (1983) removed piscivores with poison. Doherty and Sale (1985) excluded piscivores with cages. They concluded, among other things, that this method was not very suitable to study of piscivory. To quote: "His experience [referring to Lassig, 1982], however, showed that caging is inappropriate as a technique for studying the long-term effects of removing predators. Our experiences with the logistics and artifacts of caging suggest that it is a frustrating approach even for short-term studies. Recent studies of temperate reef fish populations have suggested that there may be better approaches (Choat 1982)."

Tethering and Timed-Tethering

One method that has appeared promising is tethering. This method involves attaching a prey organism via a suture or fishhook to a piece of light monofilament. The

other end of the monofilament is attached to the substrate. Many such tethered prey are put out, and they are checked by the experimenter after an interval of time. The number of prey missing (and presumed eaten) and the number remaining are then recorded. These data provide a relative assessment of the intensity of predation at different times or places. I would like briefly to review the previous work using tethering.

Tethering studies give only a relative measure of predation pressure (Wilson et al. 1990). They are incapable of providing an absolute measure, as a tethered organism is unable to avoid predators as it would normally. Escape, concealment, and schooling are some of the most obvious anti-predator behaviours impossible to mimic while using tethering. Thus, tethered prey are more vulnerable to predation than natural prey, and one cannot use tether data to estimate absolute predation pressure on a normal (non-tethered) individual. However, their use as a relative measure is possible, since all the tethered organisms are equally vulnerable (save for the factor(s) being investigated).

Many studies have used tethering to examine marine predation. Most of these studies have examined the effects of the type of habitat on predation intensity. Studies have been done using crabs as the prey (Heck and Thoman 1981, Heck and Wilson 1987, and Wilson et. al. 1987, 1990). These studies all looked at how submerged vegetation acts as a predation refuge, and all found that such vegetation did act to reduce predation significantly.

Herrnkind and Butler (1986) used tethering to study predation on the juvenile spiny lobster (*Panulirus argus*). They examined the effect of substrate as refuge, and looked for differences between times of day. In this study, more complex substrata

(vegetated) were found to significantly lower predation. However, time of day did not have a significant effect.

Three studies have used fish of the genus *Fundulus* as the prey species in a tethering experiment. These studies looked at the effects of various aspects of habitat on predation intensity. McIvor and Odum (1988) examined the effect of the type of channel bank (erosional vs. depositional) on predation in intertidal creeks; Rozas and Odum (1988) studied the effects of vegetation as refuge from predation; Rozas (1992) looked at the effects of the origin of channels (natural vs. human origin) on predation intensity. McIvor and Odum (1988) found significantly higher predation on erosional banks. Rozas and Odum (1988) found significantly lower predation in vegetated habitats. The last study (Rozas 1992) failed to show a significant effect. These three studies used two additional statistical tests to those mentioned above (paired t-tests, and the replicated goodness-of-fit test).

Only one tethering study to date has examined predation on a coral reef fish species. Shulman (1985) examined predation on juvenile french grunts (*Haemulon flavolineatum*) (which will be referred to from now on as 'grunts'). She used tethering to look for differences in predation intensity with distance from the reef (sometimes called the halo effect). She checked the tethered grunts after several intervals of time, rather than one interval, as the previous experiments did. To analyze her results, she used the Wilcoxon rank order test, and she found that predation intensity was significantly higher nearer to the reef.

A recent improvement on tethering involves the use of a timer attached to the

tether to measure how long each fish survived before being eaten. Somerton et al. (1988) first published an account of such a device, and Boggs (1992) used a similar device. These two studies used dead bait on the tethers, unlike the above papers that used live prey organisms. Somerton et al. (1988) compared corrosion timers and digital timers. Corrosion timers involved the exposure of metal to saltwater corrosion upon taking of the bait, while the digital timers used reed switches and magnets to start a stopwatch upon the taking of the bait. Digital timers were found to work better because they were reusable, required less time to use, and were more precise than the corrosion timers. Boggs (1992) used the digital timers of Somerton et al. (1988) to measure when the tethered bait was taken, as an indirect way of measuring how deep in the pelagic zone a long line bait was when it was taken.

Minello (1993) also devised a timer for tethered animals, of a design unlike those used by Somerton et al. (1988) and Boggs (1992). His used a digital watch that, once the connection to the battery was broken and reconnected, would not begin counting until another switch was closed. This button was rewired so that the predation event closed the switch. He found that significantly more shrimp were eaten, and were eaten more quickly, when tethered in sandy (non-vegetated) habitats than when tethered in vegetated habitats.

In this research, I use a device similar in many ways to those just described. This device is based on a design by N. Collins of the University of Toronto (Collins, personal communication). It is in essence the same type as that of Somerton et al (1988) and Boggs (1992), but different in construction and use. Unlike both of these researchers, I

used live prey, as Minello (1993) did. I call the device I used the timed-tether, or, for short, the "timer."

I adapted these timers to marine use, and tested their utility for studying predation intensity on coral reef fish. I also investigated whether they were a significant improvement over the existing method of tethering, without timers. Although the primary goal of this thesis was to test the method, I also simultaneously tested some hypotheses about piscivory.

Hypotheses

Many existing hypotheses about piscivory's effects on prey fish ecology either have not been tested, or have not been thoroughly examined. For this reason, I chose to investigate three of hypotheses. The first of these hypotheses is that piscivory on coral reefs varies with time of day. That piscivory is higher at certain times of day is a well-established idea. Hobson (1979) argued that during the day, prey fish and predators are both able to see well, and thus prey defenses are at their peak during the day. The only predators able to feed successfully at this time are those that avoid these defenses, by remaining immobile until a fish strays too close, or by stalking prey. One fish that uses this strategy is the lizardfish (Sweatman 1984). At night, however, too little light exists for most predators to feed. During the crepuscular period, piscivores are most active, especially those that chase down prey. These piscivores can catch prey fish unable to cope with the rapidly changing light conditions that occur at this time. Other studies

(Hobson 1972, Ogden and Ehrlich 1977, McFarland et al. 1979) also argued similarly. The pattern that these studies suggest is that piscivory is highest during the crepuscular period (dawn and dusk), intermediate during the diurnal (day), and lowest during the nocturnal (night).

The second hypothesis is that piscivory is more intense on the fore reef than the back reef. Wright et al. (1993) manipulated piscivore density in a temperate marine system, and found that predation was higher when more piscivores were present. This, with anecdotal accounts, and later experimental evidence (see chapter 3), that piscivores are more dense on the Tague Bay fore reef, leads one to the expectation that piscivory will be higher on the fore reef. One could consider the sides of the reef to be merely different habitats, but the sides of the reef also vary in other factors, such as depth, and current patterns.

The final hypothesis is that piscivory is more intense closer to the reef. Shulman (1985) did two kinds of experiments that both found this sort of effect. In one (also described, in part, earlier), she manipulated habitat and distance of these habitats from the reef. She found that recruitment was lower nearer to the reef, suggesting predation on newly settled fish is higher. In her second experiment, she tethered prey fish (juvenile grunts) at different distances from the reef. From this, she found that mortality was highest near the reef.

Use of Juvenile Fish as Prey

The effects of piscivory are commonly thought to be most severe on juvenile fish. Werner et al. (1983), working in freshwater, found a significant effect of piscivores only on the smallest size class of their study species. Wright et al. (1993), found that the two types of prey they used showed different responses to predation due to their different size-frequency distributions, with the smaller fish species showing the most pronounced effects. Piscivory, therefore, seems size-dependent, with smaller fish being more vulnerable. For this reason, I investigated piscivory with juvenile (=small) fish. The survivorship studies mentioned earlier also support use of juveniles as prey. Aldenhoven (1986) found higher mortality rates on juvenile fish than on any other age group. Shulman and Ogden (1987) found high mortality rates in juvenile grunts (99.9 %). Sale and Ferrell (1988) found high mortality rates on some species of juvenile reef fishes, as well.

General Objectives

The specific hypotheses used in this thesis were described and explained above, however, I would like to briefly summarize them here.

My hypotheses are as follows:

H_1: Intensity of piscivory varies with time of day, highest during the crepuscular period and lowest at night.

H_0: No pattern in intensity of piscivory exists with respect to times of day.

H_1: Intensity of piscivory varies with sides of the reef, highest on the fore reef.

H_0: No pattern in intensity of piscivory exists with respect to side of the reef.

H_1: Intensity of piscivory varies with distance from the reef, highest near the reef.

H_0: No pattern in intensity of piscivory exists with respect to distance from the reef.

General Methods

Study Species

The juvenile french grunt (*Haemulon flavolineatum*) was used in all but one of the experiments as the prey species. The other prey species used was the Beaugregory damselfish (*Pomacentrus leucostictus*).

The juvenile french grunt (hereafter 'grunts') is common on the reefs of Tague Bay, especially on the back reef. It has been studied before, most notably by Shulman (1984, and by McFarland et al. (1979). The family of which they are a member consists of a large (making up a large part of the community structure in most systems) group of nocturnally active carnivores. These fish congregate over relief during the day, and move out over seagrass beds at night to feed. The grunt is always present on the reefs of Tague Bay (and elsewhere). The grunts used were approximately 3-5 cm in total length (tip of snout to end of tail), and were caught on the back reef, since they are easier to collect there, and more common there as well. Grunts of this species can reach up to one foot (

0.33 m) in total length (Böhlke and Chaplin 1968). Grunts of the size used in this study are less than a year old, although no actual age determination of the fish was done. Mortality due to handling was virtually non-existent.

Beaugregories are diurnally-active herbivores, and are highly site-attached and territorial. They occur on both sides of the reef in Tague Bay, but seem more common on the back reef, where all the ones used for tethering were caught. The ones used for tethering were 3-5 cm in total length, and were less than a year old. Mortality due to handling was variable (for a discussion of handling mortality, see the discussion in Part III of Chapter 2).

Study Site

All the work described in this paper was done in Tague Bay, St. Croix, U.S.V.I. Earlier authors, such as Ogden and Ehrlich (1977), McFarland et al. (1979), and Shulman (1984, 1985) describe this site in more detail.

Timed-Tethers

In this Master's thesis, I used the timed tethers to look for hypothesized differences in predation risk. All the experiments performed in this thesis with the timed-tethers were very similar to each other. What follows is a description of the timers as

used in the final study, when their use had been perfected as much as possible. The sections (in Chapter 2) describing early work with the timers (before they were perfected) detail some minor differences in techniques

The timers were made from an inexpensive digital watch movement (the working parts of a watch, i.e., everything but case and strap), set to the stopwatch mode. The movement was wired to an AA battery, and simple switching circuitry, and embedded in clear marine epoxy (Figures 1, 2). The movement was attached to two reed switches, which open and close by magnetic fields. The first switch controlled the starting/stopping of the stopwatch. The second switch controlled the resetting of the stopwatch. The first switch was embedded close to a magnet such that an external steel plate placed over the magnet opened the switch (nullified the magnetic field's effect on the switch), and when removed, closed the switch. A second magnet was also used to provide more holding force on the plate (more resistance to being pulled off). This second magnet did not affect either switch. The plate was separately attached by 40 lb. test monofilament fishing line to the timer, and to an angler's swivel-snap clasp. This swivel-snap was attached to the tether. The second switch (used to reset the stopwatch) was activated by a small magnet carried by the experimenter. A detailed protocol for construction of timed-tethers can be found in Appendix A.

Grunts for tethering were caught with hand nets, barrier nets and quinaldine at various locations on the back reef. Fish were held less than 48 hours before being used, and in most cases, less than 1 hour. They were held in seawater, refreshed (new seawater

Figure 1: The timed-tether device as used in this study. For scale, the movement is 3 cm in diameter. A- Watch movement B- AA battery. C- Magnet that provides the holding force on the plate. D- Smaller magnet (Allied Electronics stock # 808-0026) that provides the magnetic field to close the start/stop reed switch when the plate is not on the timer. E- Reed switch (SPST, Allied Electronics stock # 808-0004) that starts and stops the stopwatch. F- Reed switch (same as above) that controls the resetting (to zero) of the stopwatch. G - Epoxy embedding material (Gugeon West System brand resin # 105, hardener #206). H- Steel plate. I- Swivel-snap.

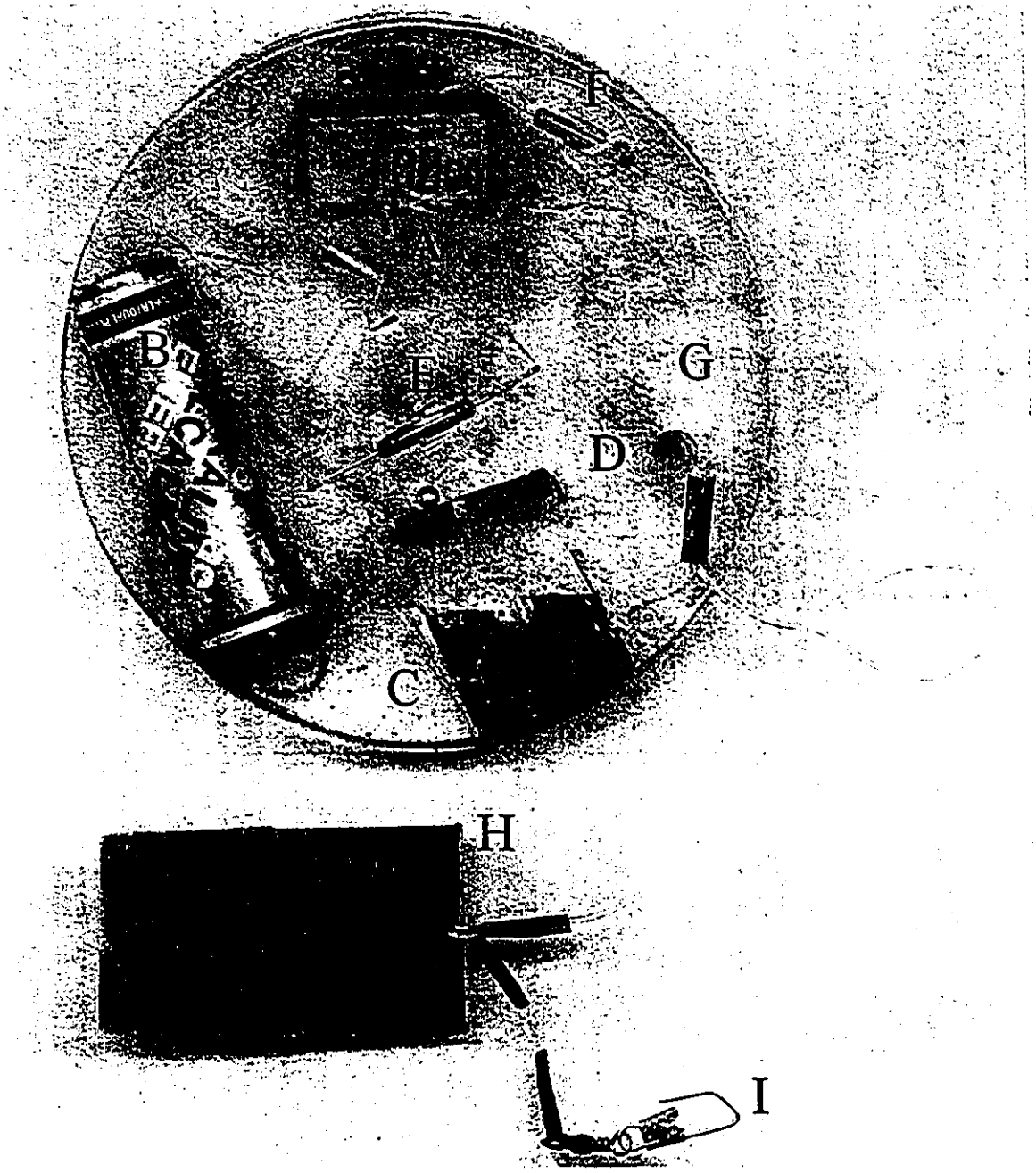
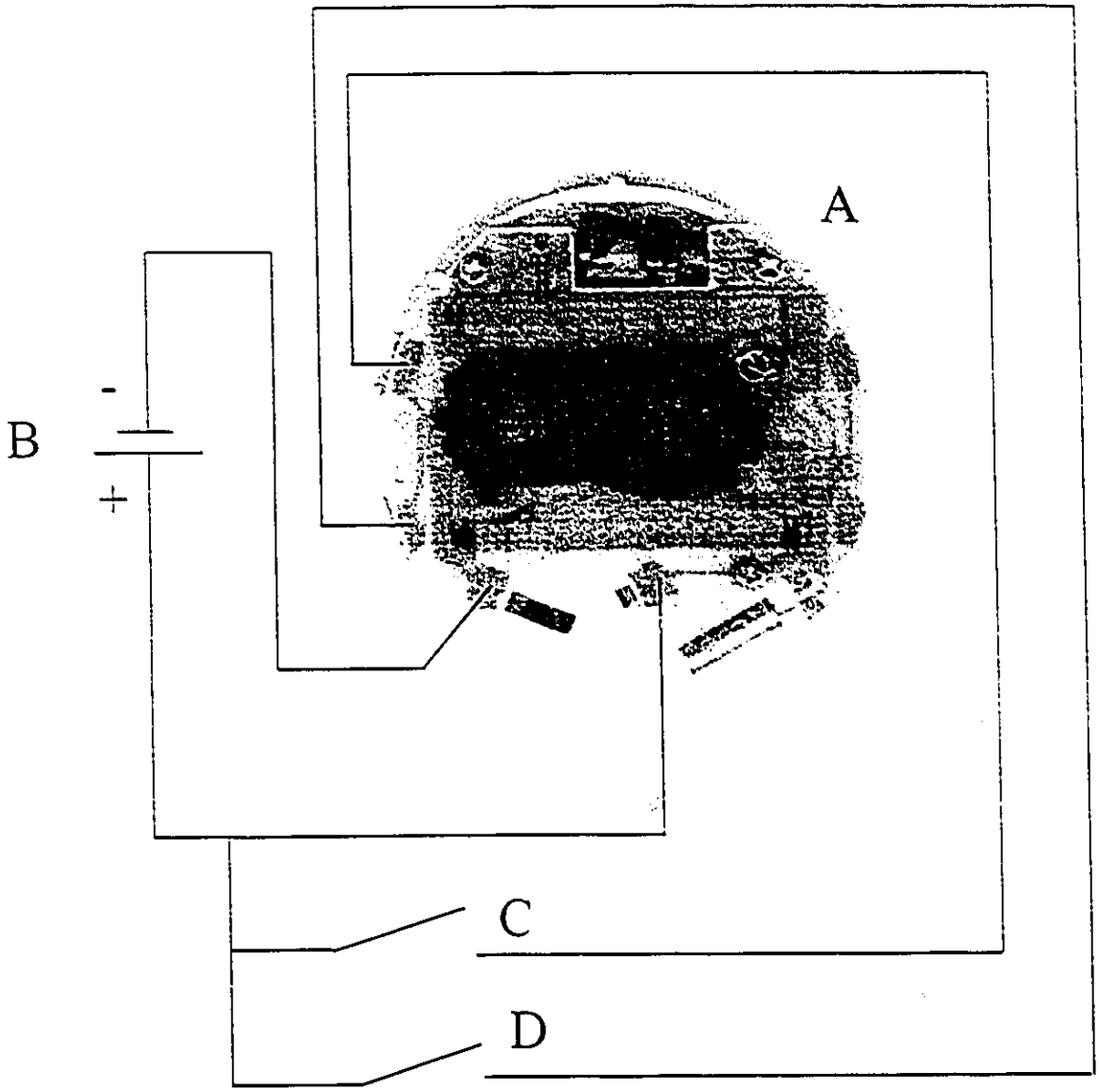

F
B
E
G
D
C
H
I

Figure 2: Circuit Diagram of the tether-timer. Watch (A), face down. The positive and negative contacts of the battery (B) are shown as the + and - signs. The positive pole (+) is connected to the two reed switches and the positive pole of the watch. The one wire from the negative pole (-) connects the battery to the negative pole of the watch. Switch C controls the starting/ stopping of the timer. As described above, one lead is connected to the positive pole of the battery, and the other is wired to the correct contact on the circuit board of the watch (the top right one, on this watch). Switch D controls resetting the timer. Again, one end is connected to the positive pole of the battery, and the other connected to the correct contact (the bottom right one, in this case).


A
B
-
+
C
D

added) once every 12 hours, and aerated with an air pump and air stones. Mortality due to holding was small, less than 5% (estimated). The fish were attached to 15 cm monofilament tethers (4 lb. test), with a loop at the other end. Under anesthetic, fish were sutured through the dorsal musculature, above the anus, and tied to the tether. Each fish was then separately bagged for transport, to simplify handling. Timers were placed out on the reef, fastened down with a 30 cm roofing nail, and the clock reset with a small magnet. Each timer was spaced at least 4 m away from its neighbors. The fish was removed from its bag, and the loop attached to the swivel snap-clasp on the timer. The stopwatch was started by removing the plate from the reed switch, and replacing it. The experimenter then left. When the predation event occurred, the grunt was eaten by the piscivore, snapping the light monofilament of the tether. The pull of the strike removed the plate from its position over the magnet, thus stopping the clock. On my return, I recorded times, and how many timers had fish remaining.

Data Analysis

Two kinds of data were obtained from these timed tethers. The first kind was collected when the fish was eaten during the experiment, three hours in this case. For these, there were a definite number of minutes, the length of time the fish survived before being eaten. The second kind occurred when the fish survived the entire time (three

hours). Survival analysis (Cox 1972, Cox and Oakes 1984, Singer and Willett 1993) is designed to incorporate both kinds of data into its significance tests.

Survival analysis gives as part of its output a survivorship graph. This graph is strictly speaking a step function. However, it likely provides a more realistic estimate of such values to assume a straight line relationship between points on this curve (J. C. Ha, personal communication). This is what I have done in the following analyses. Figures show the straight-line relationship (rather than the step), and estimates of medians are taken from these. In all cases, the results of comparisons involving the medians are all qualitatively the same using such values as they would be using the step-function values.

All survival analyses were performed using the Systat survival module. Figures included in this thesis are output of the Kaplan-Meier estimation function in Systat's survival module, after suitable stratification. Significance tests are the Cox test function in the same module. Both Kaplan-Meier estimation and Cox tests are described by Cox (1972).

Chapter Two: Tethering Studies.

Part I: Beaugregory tethering experiment of Summer 1994

Materials and methods

In this study the methods described above were used with a few modifications. First, the timers were not moved every day, so only one location was tested. Second, fewer timers (six to eight) were used each day than described above. Third, the timers were held down with two-pound dive weights rather than steel nails. Fourth, timers were checked and results analyzed after twenty-four hours. Finally, the prey species used were juvenile beaugregory damselfish, Pomacentrus leucostictus.

I designed this study to determine, "Does distance from the reef affect predation pressure on the juvenile beaugregory damselfish?" As detailed in the introduction, my hypothesis was that predation pressure would be higher nearer to the reef (i.e. farther from the shore), and lower, farther away (a 'halo' effect). My null hypothesis was that no pattern exists. The distances used were five meters and twenty meters from the edge of the back reef. In the tract of reef used, the edge of the reef was clearly visible as the line where the coral rock substrate of the reef ended, and the sandy subsrate of the lagoon

Day	Time put out	5 m	20 m
1	3:30 pm	4	3
2	12:45 pm	4	3
3	11:45 pm	4	4
4	2:00 pm	4	3
5	12:45 pm	3	4
6	12:30 pm	3	4
7	12:20 pm	3	4

Table One: Number of timers used out by day and distance from the reef, and the approximate time of day when they were placed out. From the experiment described in Part I of Chapter 2. See text for details.

started. Since timers were put out over the course of several days, days were used as blocks in the analysis. Forty-seven timers in total were put out over the course of seven days. It was originally intended that each block (day) consists of eight timers, four at each distance, but vagaries of field work prevented this. Consequently, between five and eight timers were used each day, with at least two at each distance (Table 1).

Results

Forty-two of these forty-seven timers were triggered. The data were analyzed with survival analysis, and neither blocks (days), nor the main effect (distance) were significant according to Cox tests.

Discussion

These results support the null hypothesis that no pattern exists with respect to distance from the reef. However, these results are insufficient to determine whether there is a "halo" effect in this situation. They suggest that if an effect exists, these two distances are not far enough from one another to show such an effect significantly. Previous work on this type of effect (Shulman 1985), although conducted with a different prey species, used distances of twenty-five and zero meters from the reef. She found a

significant effect. Future work should include a wider range of distances, such as zero, twenty-five and one hundred meters from the reef, to be able to claim conclusive results.

Part II: Grunt tethering experiment done in the Summer of 1994

Materials and methods

The modifications to the general methods are as the above experiment, except that juvenile french grunts were used in this experiment. In addition, the timers were moved to another site 50 m along the reef after four days testing, in order to test for differences between locations.

The question this study was designed to investigate is the same as the above, with the sole change being the different prey species used. Thus the question was "Does distance from the reef affect predation pressure on the juvenile french grunt?" The same two distances were used in this experiment, 5 m and 20 m from the edge of the back reef, and days were used as blocks in this experiment (Table 2).

Day	Time Put Out	5 m	20 m
1	1:45 pm	3	4
2	12:05 pm	4	4
3	11:50 am	4	4
4	10:50 pm	4	3
5	11:50 am	6	4
6	12:30 pm	0	2
7	11:40 am	3	4
8	11:50 am	3	4

Table 2: Number of timers used out by day and distance from the reef, and the approximate time of day when they were placed out. From the experiment described in Part II of Chapter 2. See text for details.

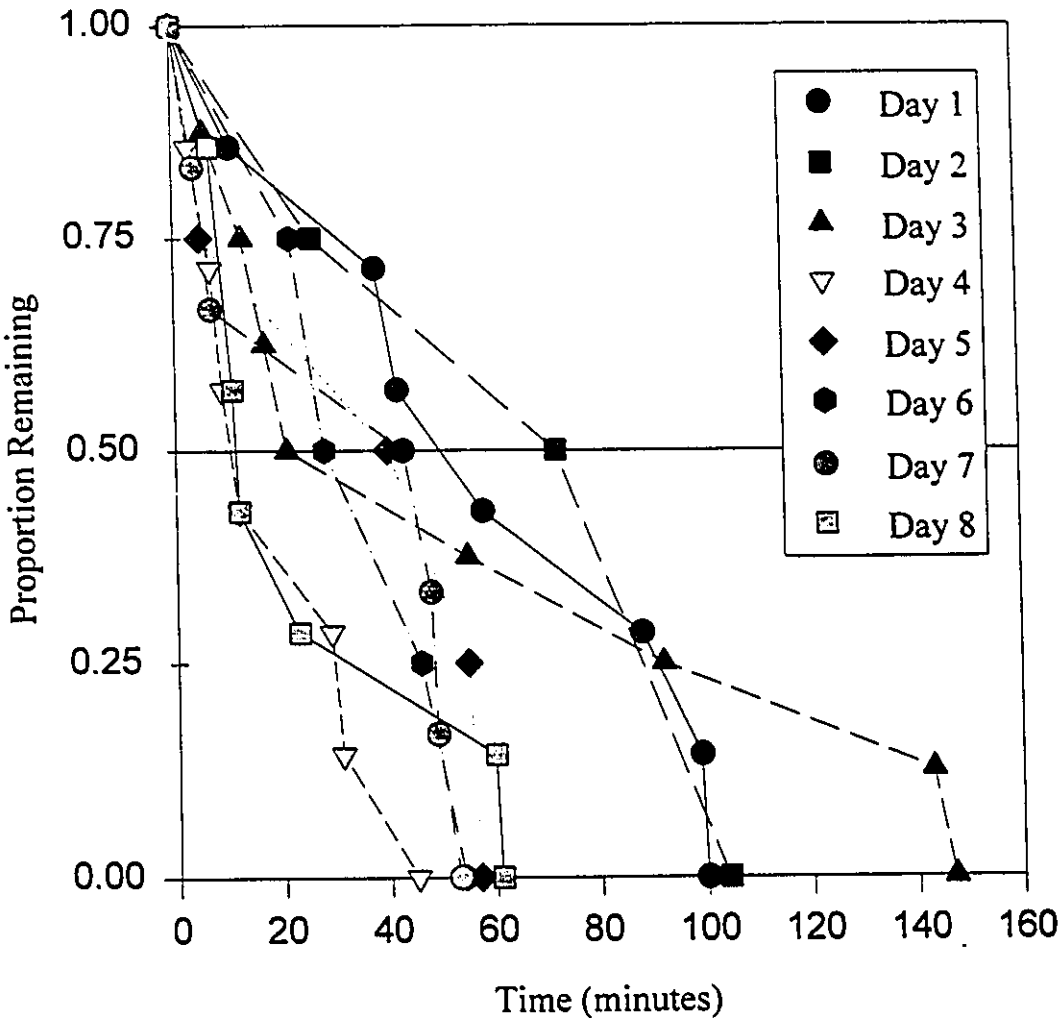


Figure 3: Survivorship of tethered juvenile french grunts in summer 1994, compared only among days (all other factors pooled). The rate at which fish are taken by predators differs among days. This factor is significant (Cox test p=0.011, df=1).

Day	Median (minutes)
1	50
2	72
3	21
4	11
--Change of location--	
5	40
6	28
7	43
8	11

Table 3: Median values for curves from Figure 3. The location switch is the change in the placement of the timers, moving them 50 m down the reef in order to test the effect of spatial location on predation rates.

Results

In this experiment, fifty-six timers were put out over the course of eight days. The same timer problems plagued this experiment as well, so that blocks of eight were not always possible. Again, between five and eight timers were used each day, roughly half at one distance, and half at the other (Table 2). Forty-seven of these were triggered upon return twenty-four hours later (Figure 3, Table 3). Survival analysis of these data showed that the only significant effect was the blocking factor (days, $p=0.011$ $df=1$). The most parsimonious Cox log-linear model included only day.

Discussion

These results suggest three things. First, they suggest that distance from the reef is not a strong factor influencing predation pressure on juvenile french grunts, contrary to the results of Shulman (1985). However, the same caveat as that made above should be made here, that these results may instead mean that the distances were not extreme enough, or that the test lacked power. Further studies into this factor should note this (see next section).

The second implication of these results concerns the effect of blocking. The clear message of the significant effect of blocks is that predation varied over the course of days,

implying that predation is quite patchy over time. I have found no evidence from the literature about this sort of patchiness. One factor possibly inducing patchiness is the large territory/home range size of the piscivore. Patrolling of the home range may take piscivores away from specific parts (i.e., the area where the timers are) of its home range for varying lengths of time. Future studies should investigate further this apparent patchiness in piscivore feeding, and attempt to find the cause(s).

The third possibility (seen best in Table 3) is that piscivores are learning the location of the tethered prey. The apparent increase in predation pressure (shown as the reduced median survival time in Table 3) over time implies that piscivores are consuming the prey more quickly, presumably by knowing where to look. This is confirmed by the way that predation pressure jumps up after the location of the timers was changed. Although the median from day five of the experiment (the first day at the new site) does not rise to the level of the median from the first day (at the original site), it is still higher than the median on day four (the last day at the original site). This implies that piscivores learned the location of the timers. Future work should move timers further apart, and move them every day, to avoid this effect as much as possible.

Part III: Tethering experiment conducted in January 1995

Materials and Methods

The method used in this study was the same as that described in the general methods, with a few exceptions. Timers were spaced two m apart, and linked via a thin nylon cord to be more readily found at night. Timers were picked up and moved about 100 m along the reef every day, to minimize the chance of piscivores learning where to find tethered prey. Timers were checked and data recorded three hours after being put out.

This study was designed to examine three questions. First, like the previous experiments, I wanted to investigate whether distance from the reef affects predation intensity. My hypothesis is that predation is higher nearer to the reef. For this, I studied two distances, one and 25 m from the edge of the reef, more extreme than in the last study. Second, I wished to look for effects of the side of the reef on predation intensity. My hypothesis was that predation would be more intense on the fore reef. The third question addressed by this study is whether time of day influences predation intensity. My hypothesis was that predation would be more intense during the diurnal

		1 m	1 m	25 m	25 m
Day	Side	Day	Night	Day	Night
1	Back	10	10	10	10
2	Fore	11	10	11	10
3	Back	10	10	10	10
4	Back	10	10	10	9
5	Fore	10	10	10	8

Table Four: Number of timers used out by day, side of reef, time of day, and distance from the reef. From the experiment described in Part III of Chapter 2. See text for details.

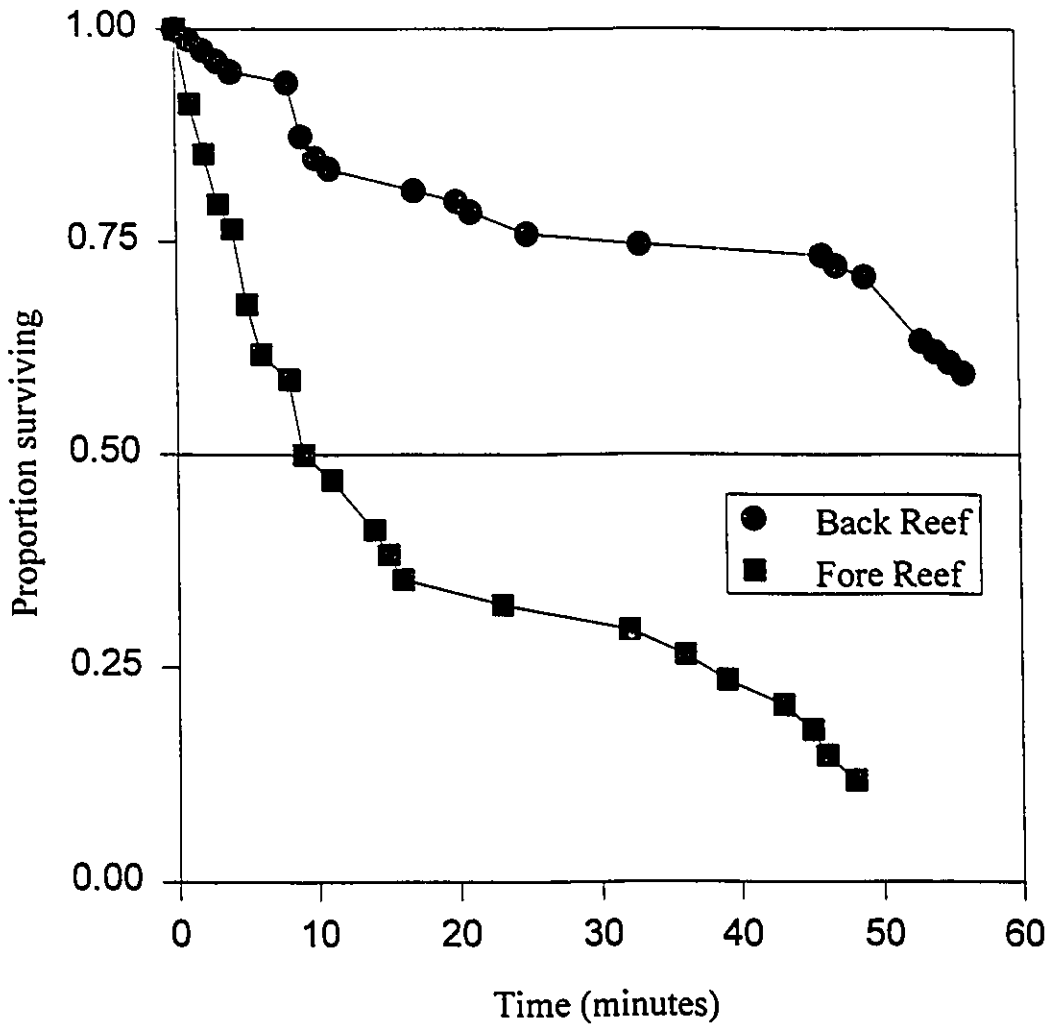


Figure 4: Survivorship of tethered juvenile french grunts in January 1995, compared between sides of reef only, all other factors being pooled. The rate of mortality differs between fore and back reef. The median survival time on the fore reef is 9 minutes. The median survival time on the back reef is not determinable. These two curves differ significantly (Cox log-linear test,$p<0.001$ df=1).

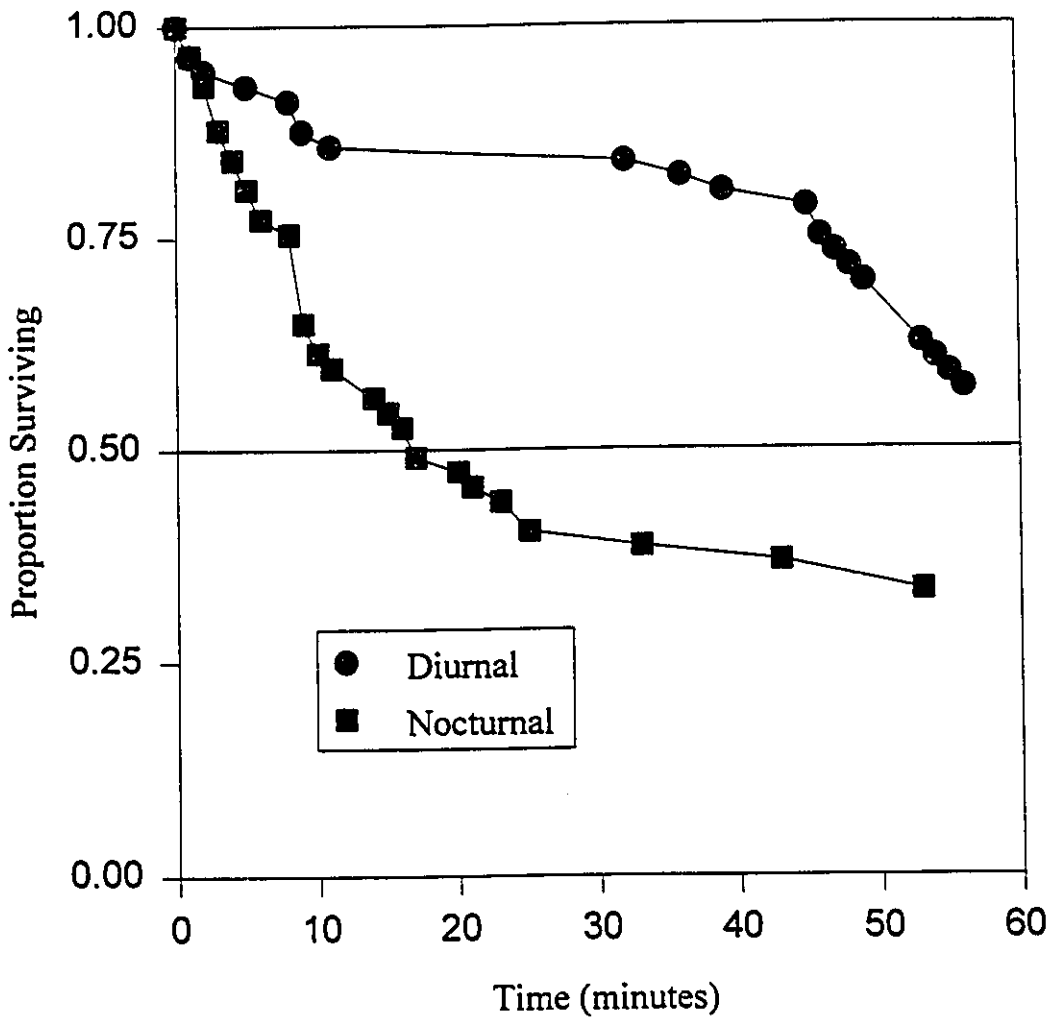


Figure 5: Survivorship of tethered fish in January 1995, compared between times of day only, all other factors being pooled. Rate of mortality differs between the diurnal period and the nocturnal period. As in Figure 4, the median for the back reef is not determinable (the curve never reaches the 0.5 level). The median survival time during the nocturnal period is 17 minutes. These two curves differ significantly (Cox log-linear test, p=0.001 df=1).

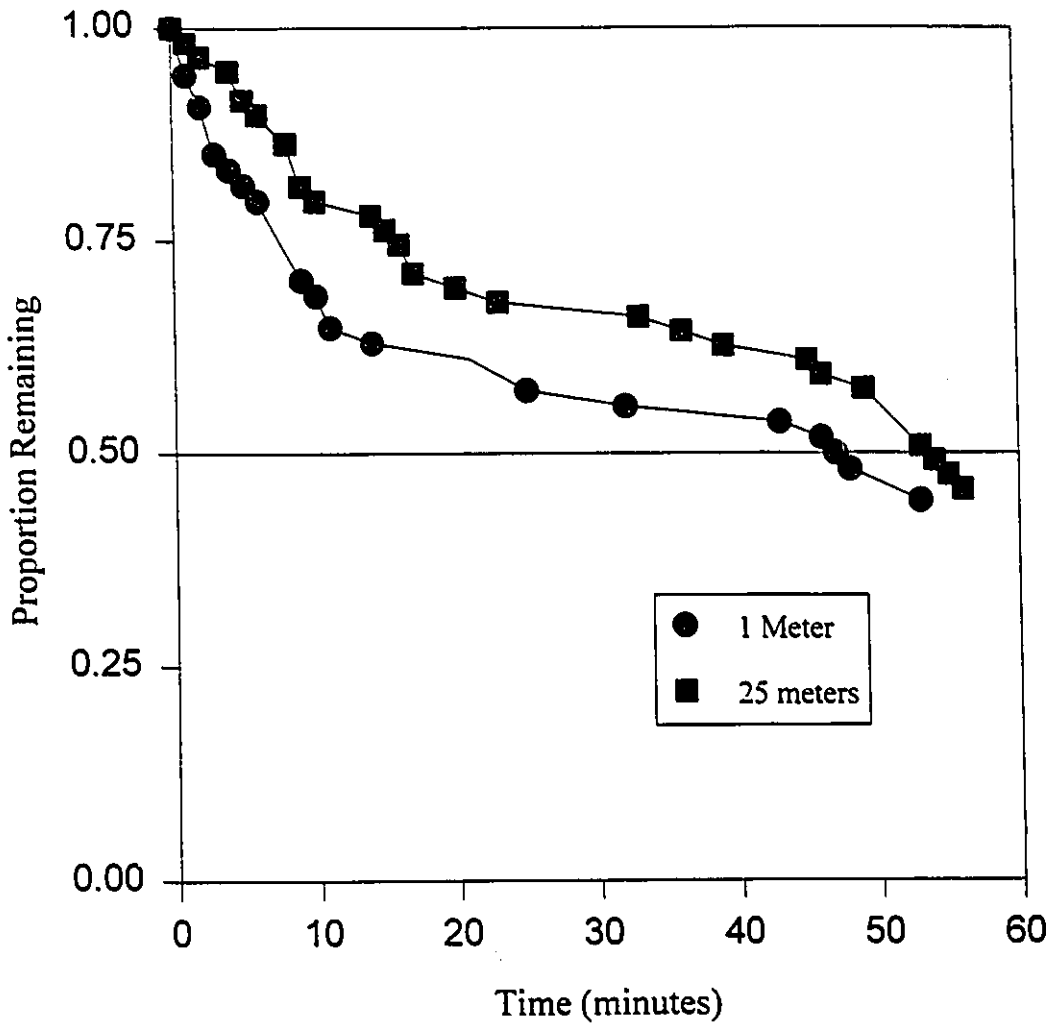


Figure 6: Survivorship of tethered fish in January 1995, comparing distance from the reef, all other factors being pooled. The median survival time at one meter from the reef is 47 minutes. The median survival time at twenty-five meters from the reef is 50 minutes. These two curves show a trend in the expected direction, but the effect is not significant (Cox log-linear test, p=0.907, df=1).

period than during the nocturnal. For this factor, I used two levels, nocturnal and diurnal (the crepuscular period was not studied because field logistics prevented its inclusion).

One hundred ninety-four timers were put out over the course of five days (Table 4). Originally, it was intended that ten timers per side per time of day per distance (or 80 timers per full day of the experiment) be used. However, doing both sides of the reef each day was logistically impractical, so different sides of the reef were done on separate days (or 40 timers per full day). This was done for five days (three on the back reef, and two on the fore reef). The discrepancy remaining (200-194=6 timers) is the result of timer failures of the kind that occurred in earlier experiments. Sixty-two of the 194 timers were triggered, and fifty-one had live fish remaining on them after three hours. This totals 113 timers. Of the remaining 81 timers placed out, tethered fish of 39 were being consumed by gastropods when checked three hours later. The other 42 suffered from various forms of timer failure while underwater (mainly wiring shorts). These 81 data points were omitted from the analysis.

Results

Survival analysis of the data revealed that the best model was the model including side of reef and time of day, which were each significant according to the Cox test (side of reef $p<0.001$ df=1, time of day $p=0.001$ df=1). Distance from the reef and blocks (days) were not significant and did not contribute significantly to the best model. Figures 4 and 5 show the resulting survival curves for analysis by side of reef and time of day,

respectively. The median survival time on the fore reef was 9 min. The median survival time on the back reef was not determinable, as the curve never reached that low (see Figure 4). For figure 5, the median survival time during the diurnal period was again not determinable (see Figure 5). During the nocturnal period, the median time was 17 min. Figure 6 shows the non-significant resulting survival curve from the analysis of distance from the reef, for comparison. The median at the one meter distance was 47 min. The median at twenty-five meters distance 50 min.

Discussion

These results support two of my expectations, showing that predation is higher on the fore reef than the back, and that predation is more intense at night than during the day. No support was found for the hypothesis about the effects of distance from the reef, however. The pattern of predation with respect to side of reef supports anecdotal accounts of greater abundances of piscivores on the fore reef. However, an effort to quantify these differences in piscivore abundances was not successful. A further effort should be made to quantify these differences (see below).

The pattern of predation with respect to time of day does not support the previously unsubstantiated observation that piscivory should be higher in the diurnal period because there are more diurnally-active piscivores (Hobson 1979). Unfortunately, logistic constraints prevented the inclusion of the crepuscular period in this experiment.

Further research into this factor should attempt to include the crepuscular period, as it is generally held to be the most vulnerable time for prey fish on the reef (Hobson 1979)

The lack of evidence of a pattern in distance from the reef sheds further doubt on the importance of this factor in affecting predation on these prey fish. Shulman (1985) found a significant effect of distance on predation on juvenile french grunts. She used a Wilcoxon rank order test on non-independent data, which violates one of its assumptions. However, this non-parametric test is fairly robust in the face of this violation, but it does lose power (J. C. Ha, personal communication). Her relatively large sample size (n=64), and her low p value (p=0.004) suggest that there is still a significant effect. A more important difficulty with her conclusions is with her design. She tested only two distances from the reef, and, more importantly, she used zero and twenty meters as her distances. Zero meters implies on the edge of the reef, and hence it seems she may have confounded her results. In effect, she was testing two different habitats, rather than two distances. For this reason, I didn't use zero meters as a distance in any of my studies, the major difference between my work and hers. So, to conclude that there is no effect of distance, a final study designed to answer this question is needed. This experiment should include zero, one, 25 and around 80 m as the distances from the edge of the reef at which the timers are placed. Two of these distances are those used by Shulman (1985), and so a direct comparison in order to check her results is possible. One meter is included for comparison with my work, and eighty meters as an extreme distance. These distances also avoid the problem of confounding effects mentioned above. More distances could be used, but these, at a minimum, should be included in any experiment

of this sort.

One problem arose during this experiment. As noted above, at the end of three hours, 39 of the tethered fish (out of 194) were being consumed by snails. No actual predation events (capture of a live fish) were observed, so as to be able to determine whether this was piscivory or simple scavenging, but at least one of the gastropod species (*Oliva reticularis*) can capture live fish (a piscivore). I cannot conclusively determine from this study whether the fish being consumed were captured alive or dead. However, I believe that the snails were preying mostly upon dead or moribund prey and were not truly piscivorous. (Unfortunately, the general state of the fish when being put out was not noted during this experiment.) I came to this conclusion because of work done the following summer. In setting out to start the timer experiment laid out in Chapter 3, I caught 20 fish (using the method outlined in the general methods) of the same size (3 to 4.5 cm TL) as those used in the present experiment. These fish I then tethered, and placed out on the reef. Upon checking them, I found that few (3) of the timers had been triggered, but the grunts were gone from all of them. The three fish on the triggered timers had been preyed upon, but the others had died before being eaten, and then fed upon by scavengers. I had noted upon putting them out, however, that most of these were moribund. The next day, I caught larger grunts (4.5 to 6.5 cm TL), and reduced the handling time to a minimum. Fewer fish were moribund, and all but six of the timers, upon checking, had been triggered, and the prey fish gone. Therefore, I believe that many of the fish used in the current experiment were either quite moribund or dead, and therefore easy prey for any scavenger, like these snails.

Part IV: Conclusions

I found little evidence from three experiments and two species of prey fish to support the idea that a 'halo' effect exists around the back reef. No effect of distance from the reef was observed, but one final experiment is necessary before putting this hypothesis to rest entirely. I did find that blocking by days is important, since piscivory seems patchy with respect to time, at least.

Both time of day and side of reef were significant factors affecting the intensity of predation on juvenile grunts. However, my results failed to support the traditional hypothesis regarding time of day, by finding higher predation at night. As for side of reef, I found higher predation on the fore reef, supporting a yet unquantified observation that more piscivores are found on the Tague Bay fore reef.

These studies demonstrated the effectiveness of timers for measuring relative differences in the intensity of predation on fish. This has important consequences, not only for scientific methodology, but potentially for fisheries and other applied work, as well. This new method is one of the few that works well for scientific studies on predation, adding another tool to the toolkit. It also could be used by fisheries workers to find out where piscivorous fishes are most abundant. This is important because such fishes are often the most sought-after for human consumption. Groupers (Serranidae) and snappers (Lutjanidae), to name two, are among the best tasting fish available from coral

reef fisheries (personal observation). For these reasons, this work has potentially broad effects on both pure science and applied science.

Chapter 3: Comparison of Methods.

Introduction and Objectives

As described in the introduction, there are reasons to expect that piscivory may be more frequent on the fore reef than on the protected back reef. In this section of my thesis, I report the results of several experiments examining this hypothesis.

To answer the question, "Do sides of the reef differ in intensity of piscivory?," or, in other words, "Is piscivory a possible explanation for the pattern seen in juvenile french grunt distribution?," I did three things. First, I quantified the qualitative observations I had made earlier (see Chapter 2), that piscivores seemed to be more abundant on the fore reef. Second, I used the timed-tethers to see if a pattern in intensity of piscivory could be seen that paralleled the patterns in french grunt and piscivore distributions. Third, I tested the new technique to see whether snail predation was significantly altering timed-tether results.

Materials and Methods

Part I- Quadrat Censuses

In this study, I wanted to determine if a pattern in piscivore and prey densities could be found between sides of the reef. To do this, I set up five semi-permanent 500 m^2

quadrats, marked with standard flagging tape, on each side of the reef. Each quadrat was censused three times, and each time all ten quadrats were censused in haphazard order over two days or less. Censuses of a quadrat were separated by at least four days. The first censuses were done on June 15-16, the second June 27-28, and the third July 2. Each census was conducted during the daytime hours, in order to count piscivores active during the same time of day as the tethered fish were present (see Part II, below).

The quadrats were 50 X 10m (500 m^2), with the long axes parallel to the reef crest. To count fishes in them, I swam along one long side, looking into the quadrat, and noting on a slate all large, mobile piscivores. The other side of the quadrat was marked clearly enough to be easily seen, thus only piscivores within the confines of the quadrat were counted. When I reached the end of the long axis, I swam up the short axis and counted small and/or cryptic fish. I then swam about two m up the long axis, and then back down through the quadrat to the opposite long axis continuing to count small and/or cryptic species. This was repeated in a back and forth pattern until I reached the other short axis. During these quadrat censuses, to save time, I counted only piscivores and juvenile grunts.

Number of piscivores and number of species of piscivores on each side of the reef were contrasted with repeated-measures ANOVAs. Number of juvenile grunts was analyzed with a chi-squared contingency table analysis.

Part II- Timed-tether experiment

The general methods described earlier were used in this experiment, exactly as described.

Part III- Verification of validity of timer data.

In this experiment, I wanted to verify that snails did not significantly prey on tethered grunts, and that a tethered fish could not trigger a timer by itself. To do this, I put cages over timers, and screen bottoms under timers. Cages were used to exclude fish piscivores, while the screen bottoms were used to exclude snail piscivores *(Oliva reticularis)*. Bottoms could effectively exclude snail piscivores because the snails in question were of the type that shelter in the sandy substrata, and attack fish from underneath. Screen bottoms would therefore prevent snails from using the sandy substrata as concealment from which to attack the prey fish. Exclusion of each piscivore type was a factor in a factorial experiment. The four treatments in this experiment were cage only, bottom only, neither, and both. Cages were made of half-inch (12.5 mm) mesh hardware cloth, and were 1 m x 1m x 0.33 m high. Bottoms were made of 2 mm mesh window screening, and were 1 m x 1 m in area. Treatments including both a bottom and a cage were simply the above cages with window screening sewn onto the bottom edges with sailmakers' thread. Cages and the combination treatments were fastened down with rebar stakes and cable ties. The bottom only treatments were fastened down with large

roofing nails, and weighted at two ends with lengths of rebar to keep them spread out.

Five replicates were done each day, over two days. Each day, the spatial arrangement of treatments was randomized. Treatments were laid out along a line in the sand, about four meters from and parallel to the back reef. I slightly modified the procedure for using timers compared with that described above. The treatment was set out before the timer was put down, and the treatment (cage or screen, or both) was fastened down as much as possible before putting in the timer and tethered fish. The fish were caught, tethered, and put out on timers. I then finished fastening down the treatments, where needed, and left. I returned twenty-four hours later to check the timers, and record data. The data were analyzed with a chi-squared contingency table analysis.

Results

Part I- Quadrat Censuses

A broad definition of piscivore was used during the censuses, excluding only members of families I knew did not include piscivores. Families included in the piscivore counts were Lutjanidae, Serranidae, Holocentridae, Carangidae, Sphyraenidae, Muraenidae, Synodontidae, Aulostomidae, Priacanthidae, Scombridae, Bothidae, and Scorpaenidae (Table 5). The data were later categorized into piscivores and non-piscivores according to Randall (1967).

Scientific Name	Common Name
Gymnothorax moringa	Spotted Moray
Synodus intermedius	Sand Diver
Tylosaurus crocodilus	Houndfish
Aulostomus maculatus	Trumpetfish
Epinephelus cruentatus	Graysby
E. fulva	Coney
E. guttatus	Red Hind
Caranx ruber	Bar Jack
Ocyurus chrysurus	Yellowtail Snapper
Lujanus analis	Mutton Snapper
L. apodus	Schoolmaster
L. gruseus	Gray Snapper
L. mahoghani	Mahoghany Snapper
Sphyraena barracuda	Great Barracuda
Scomberomorus regalis	Cero

Table 5: Species of censused fish classified as piscivorous by Randall (1967). These species were counted in quadrats.

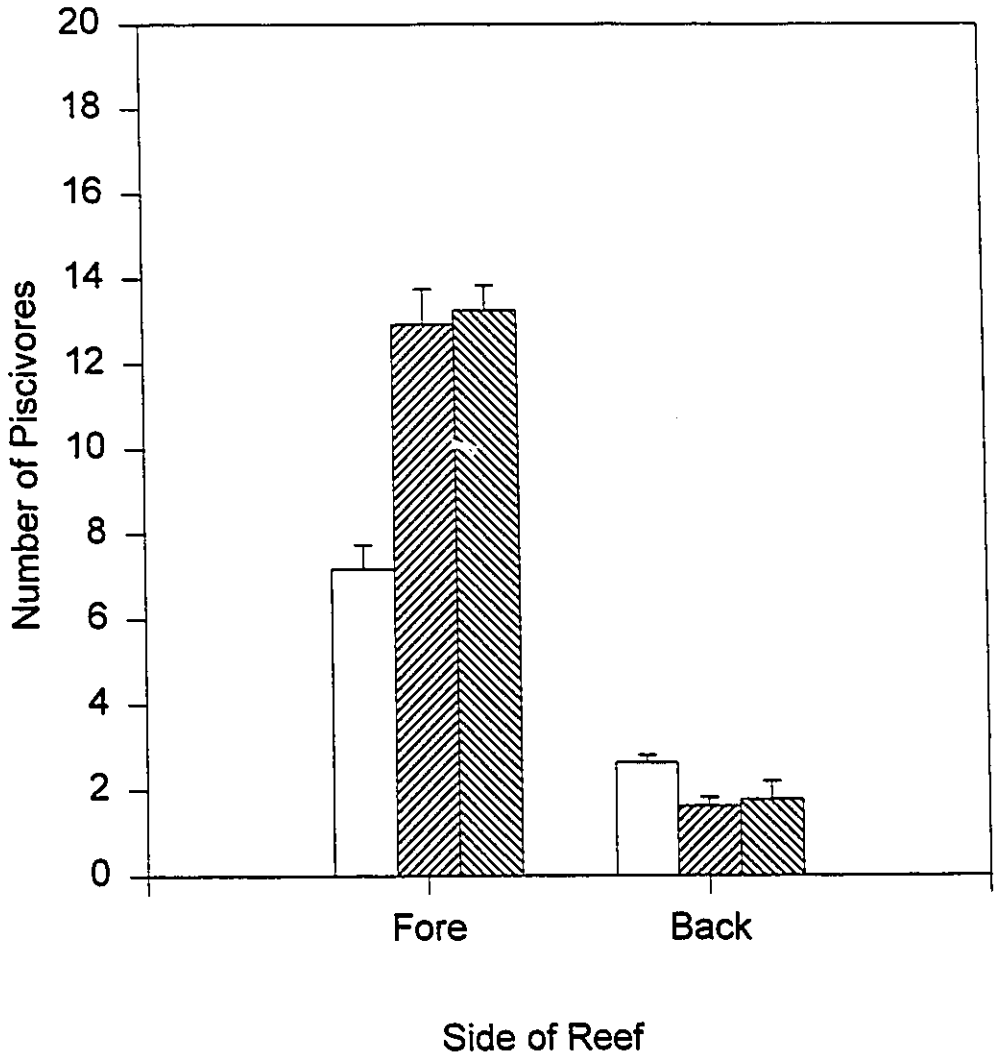


Figure 7: Mean number of piscivores recorded in 50 m X 10 m quadrats. Each bar represents the back-transformed mean of the five quadrats censused on that side of the reef on that date. Error bars are one standard error, also back-transformed. All ten (five per side) quadrats were sampled on three successive dates at least four days apart (June 15-16, June 27-28, July 2). Significantly more piscivores were present on the fore reef (repeated-measures ANOVA, F=12.687, df=1, p=0.007).

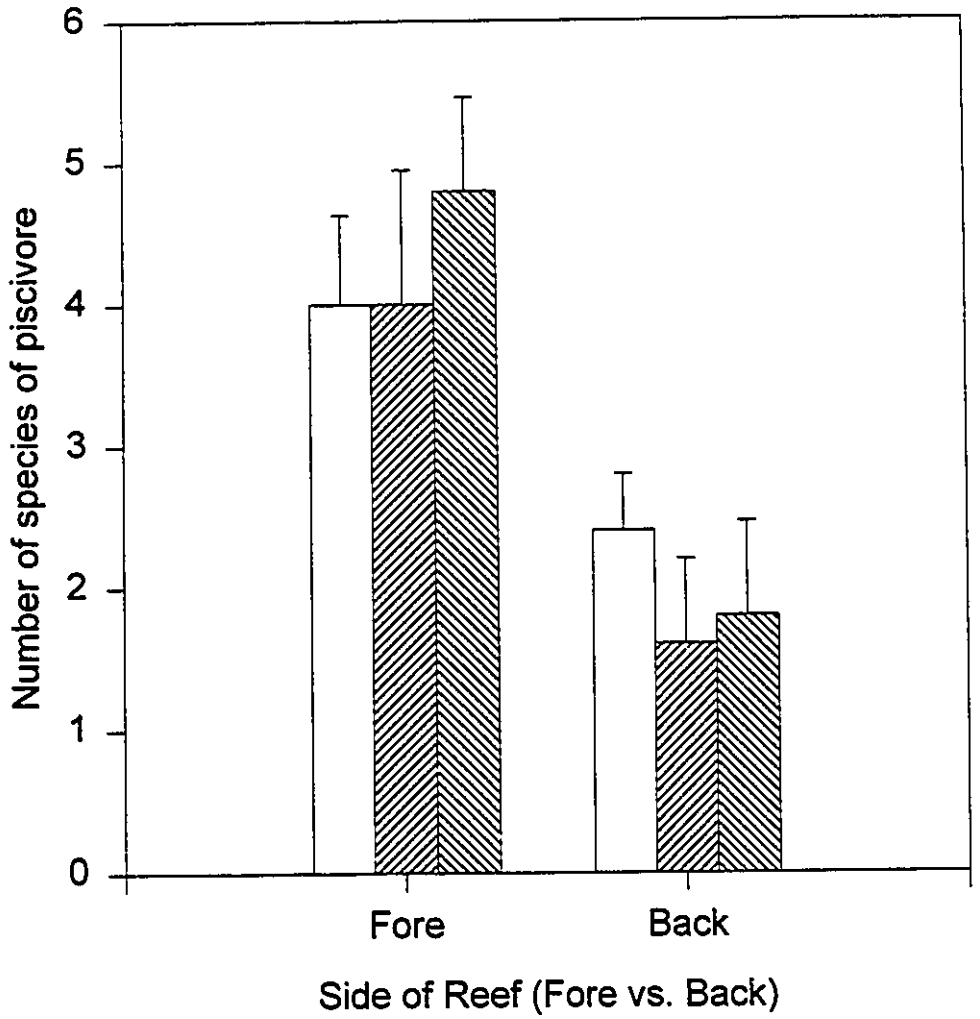


Figure 8: Mean number of species of piscivore counted in 50 m X 10 m quadrats. Each bar represents the mean of the five quadrats censused on that side of the reef on that date. Error bars are one standard error. All ten (five per side) quadrats were sampled on three successive dates at least four days apart (June 15-16, June 27-28, July 2). Significantly more species of piscivores were present on the fore reef (repeated-measure ANOVA, F=9.280, df=1, p=0.016).

Since the variances of counts of juvenile grunts could not be homogenized, I analyzed them by breaking the data down into categories (present/absent), and using a chi-square contingency table test. Grunts were found eight times in fifteen site*days (three census dates times five sites) on the back reef, and were never observed in fifteen site*days on the fore reef. Grunts occurred significantly more often on the back reef than on the fore reef (Pearson χ^2= 10.909, df= 1, p=0.001).

The data on piscivore numbers were transformed using a log (Y+1) transformation, to normalize the variances. The repeated measures ANOVA using the transformed data demonstrated a significant difference (Repeated measures ANOVA, F= 12.687, df=1, p= 0.007) between sides of the reef. The fore reef averaged 21 piscivores per census, while the mean of the back reef quadrats was 2.4 piscivores per census.

The repeated measures ANOVA demonstrated that the two sides of the reef differed significantly in piscivore species numbers (Repeated measures ANOVA, F= 9.280, df= 1, p= 0.016). The forereef averaged 4.3 piscivore species per census, while the backreef averaged 1.9 piscivore species per census.

Part II- Timed-tether experiment

Table six shows the numbers of timers used for each treatment. The results of the this experiment show that rate of loss of tethered fish is more gradual on the back reef than on the fore reef (Figure 9). The intensity of piscivory was lower on the back reef.

Day	Fore	Back
1	10	10
2	10	10
3	12	10
4	12	10
5	12	9
6	11	10
7	11	10
8	11	10

Table Six: Number of timers used by day and distance from the reef. From the experiment described in Part II of Chapter 3. See text for details.

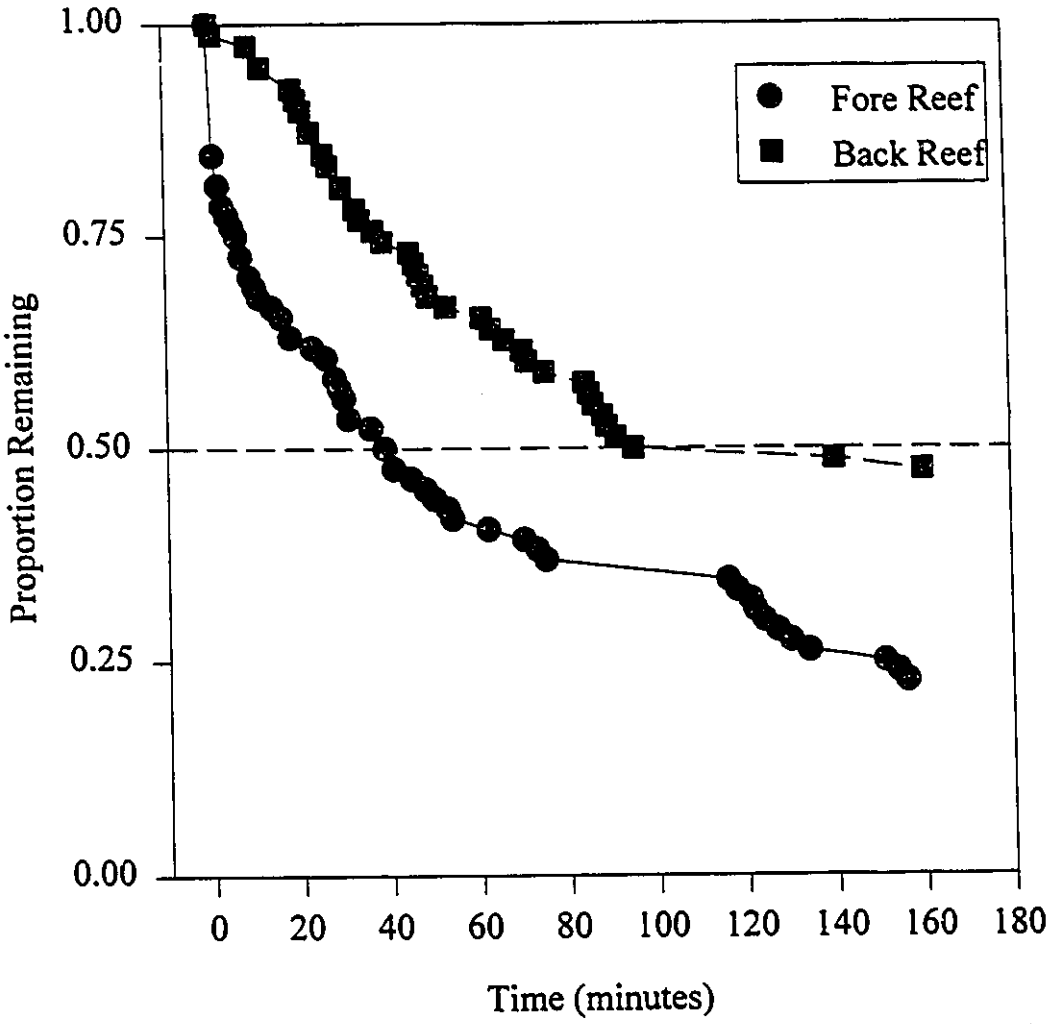


Figure 9: Result of survival analysis for juvenile grunts tethered in Summer 1995. 168 fish were tethered, 89 on the fore reef, and 79 on the back reef. Of the fore reef fish, 19 survived three hours, and 65 had been eaten after three hours. Of the back reef fish, 37 survived, while 41 were eaten. The dashed line on the figure shows Y equal to 0.5, or the median. This intersects the back reef curve (the circles) at 39 minutes, and the fore reef curve (squares) at 95 minutes. Piscivory was significantly more intense on the fore reef (Cox test, $p<0.001$, df=1).

	Bottom present	Bottom absent
Cage present	10	10
Cage absent	3	5

Table 7: Results of the experiment to test operation of the timers. Orthogonal treatments are presence or absence of a cage preventing access to the prey by piscivorous fish, and the presence or absence of a floor preventing access by a gastropod predator. Numbers are numbers of timers (out of 10) untriggered after 24 hours under each treatment.

These two curves are significantly different (Cox test $p<0.001$ df=1), and the median survival time, the place where the curves intercept the line at the 0.5 level, was 95 minutes on the back reef, and 39 minutes on the fore reef.

Part III: Verification of validity of timer data.

Significantly fewer (χ^2 contingency table, Mantel-Haenszel χ^2= 16.482 df=1 $p<0.001$) timers were triggered under a cage (none, in fact; Table 7). No significant difference existed between bottom and no bottom (χ^2 contingency table, Mantel-Haenszel χ^2= 0.792 df=1 p=0.374). Also, no interaction existed (χ^2 contingency table, Mantel-Haenszel χ^2= 0.346 df=1 p=0.556) .

Discussion

The results of the first study show the pattern expected, in that there were more piscivores and fewer juvenile grunts observed on the fore reef. In fact, small fish of many species seemed less common there. This suggests that piscivory may be more intense on the fore reef. The results of the second experiment supported this conclusion, since they show more intense piscivory on the forereef. These results lead one to conclude that piscivory is one possible reason to explain the pattern in juvenile grunt abundance. However, since this study did not examine other possible causes, such as water movement patterns, food availability, or competition, I cannot say that piscivory is the only or even the most important of these causes. Even if one assumes piscivory to be an

important factor, no evidence exists from this study about whether grunts settle on both sides equally and are consumed more on the fore reef, or whether grunts have evolved to settle preferentially on the back reef to avoid predators.

The important result of this study is the evidence of the usefulness of timed-tethering. The results above show that enough data for analysis can be gathered with reasonable amounts of work and money. Further, they show that this method can provide different data (such as patterns in predation over the course of the experiment) than earlier methods of tethering (without timers).

The results of the third experiment also support use of this method. Exclusion of fish piscivores with a cage eliminated triggering of timers over a 24 hour period. This leads one to conclude that the prey fish cannot trigger timers alone. The lack of a significant effect of exclusion of snail piscivores shows that snail predation did not significantly affect the results. These results show that neither of the anticipated difficulties with the timer method were operating in the system studied. However, future work done with timers will likely require that this sort of experiment be done to show that other systems do not fall prey to such difficulties.

One further improvement to this method, and any tethering method, is possible. Use of some sort of recording device, such as a camera or video camera to allow one to know the species of predators eating the tethered organism would provide useful information. This sort of recording, using still cameras triggered by the predation event, has been done in studies of nest predation (Picman 1987, Major 1991, Ouchley et al 1994). Of course, the use of a video camera would preclude the need for timers, since

video cameras can record time on the tape. These tether-timers cannot record what ate the tethered grunt, only when it was eaten. Unfortunately, due to time and cost constraints, I was unable to do such recording in this study. Therefore, for my quadrat censuses, I had to assume that the group of fish preying on tethered grunts was those classified as piscivores according to Randall (1967, see Table 5). Without such recordings, I am unable to verify that this assumption is true. The only evidence from this study identifying species of piscivores responsible for predation is the observations by the divers of fish seen eating a tethered grunt or in highly suspicious proximity to a recently-eaten grunt. Piscivores observed in such conditions include red hinds (*Epinephelus guttatus*), lizardfish (*Synodus intermedius*), graysby (*Epinephelus cruentatus*), Mutton snapper (*Lutjanus analis*), coney (*Epinephelus fulvus*), yellowhead wrasse (*Halichoeres garnoti*), and sand tilefish (*Malacanthus plumieri*). All but the last two are piscivores according to the definition used in the quadrat censuses (anything classed as piscivorous according to Randall 1967). The last two are generalist carnivores (not limited to fish), and the sand tilefish was found by Randall (1967) to eat fish. However, neither is classed as a piscivore according to the above definition. I believe these two observations to be abnormal, in that these two species ate fish less than half a minute after the fish was attached to its timer and released from the bag it had been transported in. Often, tethered grunts are moribund immediately after having been released. This is possibly due to low oxygen levels in the bag in which they are transported. The fish soon become much more active. Usually, other fish are not in the vicinity during the period of moribundity. In this case only, however, the yellowhead

wrasse and the sand tilefish were attracted to the diver (unlike most fish), and attacked the fish while still moribund. Neither of these two fish was observed to eat more than one tethered grunt. Since both species are carnivores, and likely scavenge food when available, the moribund fish was likely seen by both as dead or dying food available to be eaten. In future work, to avoid this, a better way of holding fish before being put on the timers should be devised. In this study, such cases in no way compromise the timer's usefulness as a relative measure of piscivory. However, it does highlight the practicality of identifying the species of piscivore responsible for each predation event.

This leads into the difficulty in defining a piscivore. Randall 's (1967) gut content analyses are subject to interpretation. Is any species found with fish in its gut a piscivore? Besides the obvious problem of whether the prey fish was alive (making that fish species a piscivore) when eaten or not alive (making that fish species a scavenger), there is the problem of how many guts of that species must contain fish to make the entire population a piscivore. Perusal of gut content studies like Randall (1967) reveals that many species of fish can be found to have eaten fish as some small proportion of their diet. Ontogenetic diet shifts could potentially further cloud this issue.

The best way to define a species of fish as piscivorous would be to follow many individuals of that species around the reef and count how often they capture and eat a live fish. Besides the difficulty of the diver's presence influencing the study fish's behavior, there are the difficulties outlined in the introduction in observational studies on piscivores. The question then becomes, "What is the next best way?" One other way is through gut content analysis, like that of Randall (1967). Another way is by videotaping

tethered fish, as discussed earlier. The problems with gut analysis, described above, include whether a prey fish was alive when eaten, and how much fish a carnivore species must eat to be a piscivore. The problem with videotaping is the possibility of scavengers eating moribund tethered prey and the high cost/time investment necessary.

Conclusions

In this study I have shown that a prey species, the juvenile french grunt was significantly more common on the back reef in Tague Bay, U.S.V.I., while piscivores were more common on the fore reef. Using a new tethering technique, I demonstrated more intense piscivory (higher predation pressure) on the fore reef. In addition, I conclude that the new technique is a useful addition to earlier methods of tethering, since it provides different information. Finally I found no evidence of design flaws in a factorial piscivore exclusion experiment. Timed tethering is recommended as a good way of studying predation underwater, although subject to some restrictions.

Chapter 4: General Discussion and Conclusions.

Using a new tethering technique, I showed more intense piscivory (higher predation pressure) on the fore reef in two separate experiments. In addition, I have shown that grunts were significantly more common on the back reef in Tague Bay, while piscivores were more common on the fore reef. These two experiments together show that patterns in piscivore distribution inferred from patterns in relative predation pressure on prey fish can actually be seen in the distribution of naturally-occurring piscivores.

I found time of day was a significant factor affecting the intensity of predation on juvenile grunts. However, my results failed to support the traditional hypothesis regarding time of day, by finding higher predation at night. This suggests that a reexamination of the traditional beliefs about the effects of time of day is in order. More experiments should be done to examine this hypothesis. Piscivore censuses should be attempted at night, if possible, and additional tethering experiments should be done. Future tethering experiments designed to investigate this hypothesis should investigate the crepuscular period, as well.

I found little evidence from three experiments and two species of prey fish to support the idea that a 'halo' effect exists around the back reef. No effect of distance from the reef was observed. Some doubt exists about the validity of Shulman's findings, so there still is uncertainty about how important this factor is.

I found that blocking by days is important, since piscivory seems patchy with respect to time, at least. In addition, I found no evidence of design flaws (i.e. prey

triggering timers by themselves or gastropods preying on tethered fish) in a factorial piscivore exclusion experiment.

In terms of the most important aim of this thesis, the development of the new method, several points can be made. First, this work has shown effectively that timed-tethers are a scientifically useful method, meaning it is both scientifically valid, and feasible logistically.

However, a comparison must also be drawn with earlier methods. Is this new method in any way an improvement? Examining the results in this light, an important point must be made. This technique is different, but not necessarily better than untimed tethering, which yields only binary data. The two techniques give different information, and therefore can be used to answer different questions. Timed tethers give ordinal data from which one can calculate means, medians, and graphs such as Figure 3. This gives the experimenter more insight into what the patterns are in predation over the course of the experiment. However, the timed-tethers cannot be recommended over the non-timed tethers in every case. The more costly, nature (both in time and money) of the timed-tethers prevents this. If the cost of the two methods were equivalent, then it would behoove one to always use the timed-tethers, since more information can be gained, and insights not necessarily planned for may be gained. However, with limited resources on the part of the researcher, the question is what kind of information one needs to address the hypothesis (es). If a simple contrast between relative levels of predation between two levels of a factors (two sites, times of day, etc.) is needed, then non-timed tethers are the most cost-efficient method to use. For example, the experiment using timers described in

Chapter 3 is one such experiment. In that, a contrast between two sides of the reef was the sole purpose of the experiment. No comparisons of the patterns in predation over time were needed, so a non-timed tethering experiment would have worked as well.

Only in cases where the patterns in predation over time are needed would the timed-tethers be the best method. One example of this is the second experiment described in Chapter 2 (shown in Figure 3). In this, I compared the slopes of the curves for different days and locations, and was able to come to some conclusions about predator learning.

This work is intended to find a good method of determining spatio-temporal patterns of piscivory in coral reef fish ecosystems. In the past, many of the methods used in coral reef predation studies were originally adapted from terrestrial methods. Manipulations of predator density, either by removing or excluding predators, is a common method in terrestrial and marine temperate predation studies (Taylor 1984). Studies using these two approaches are common, while another, less common approach is manipulating prey density (Taylor 1984). Studies of the interactions of predator and prey, such as determining predation rates is often done via observational methods, either watching predator capture prey, or by coming across prey carcasses. As discussed in the introduction, such methods are largely unworkable in coral reef fish systems. No equivalent to tethering, either untimed or timed, has been found in the terrestrial predation literature.

Much evidence exists to support the contention that piscivory plays an important role in coral reef fish ecology. Most experimental studies done on piscivory have had

little to conclude, unfortunately. Piscivory may be important, but has not been well studied.

Use of this method will provide much-needed insight into at least the patterns of piscivory on coral reefs, if not the effects of piscivory on coral-reef fish community structure. First, it will shed light on a previously shadowy area, giving some experimental evidence to support or reject long-held ideas about spatio-temporal patterns of piscivory. These ideas have remained untested due to a lack of methods to investigate piscivory experimentally. The new method described in this study will help remedy this lack.

The second reason is the economic value of this method. My study species, the french grunt, is commercially caught and eaten by local fisheries, not only in St. Croix, but also in most other parts of the Caribbean. More importantly, timers have the potential to give information about where piscivores can be found, in space and time. Many piscivores are highly valued by people as good to eat (Bohnsack 1982). Grouper and snapper are two benthic coral-reef fish families considered the best eating by many (personal observation). Both families include many piscivores. Information gained on intensity of piscivory through timers could be a way for fisheries managers to assess stocks of such commercially valuable species.

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Appendix A: How to make a tether-timer.

Part one: Finding the right materials. Refer to Figures one and two. For one timer, you will need (all measurements are rough estimates, actual amounts may vary):

-One watch movement, part A (see below)

-One AA battery, part B (see below)

-two reed switches, parts E & F (Allied Electronics stock #808-0004)

-one small magnet, part D (A.E. Stock #808-0026)

-one large magnet, part C (see below)

-30 cm wire (Radio Shack wrapping wire)

-solder (any kind)

-150 mL (combined) epoxy (Gugeon West system resin # 105, hardener # 206)

-2 cm x 3.5 cm steel plate (must be steel to work w/ magnet)

- 15 cm monofilament fishing line (40 lb test)

-four crimp-on connectors (size #4, with 40 lb test line)

-one swivel snap-clasp (size 12)

-clear packing (or box-sealing) tape

-pure silicone spray lubricant

-one standard size petri dish (4 cm inner diameter)

Finding the right watch movement can be difficult. First of all, it must have a

stopwatch feature. Second, and most difficult, is finding one that has contacts for the switches and at least one battery pole on the back, not on the inside. Do not buy watches without contacts exposed on the back. The large magnet is just a radio shack magnet split in half by brute force (and vise grips).

Now I'll describe the procedure I found best to make one timer (multiply for more):

1) Take the AA battery and solder four wires to the positive pole. Soldering to batteries can be hard (Rayovac's seem to work better). You must get the metal of the battery contact quite hot before the solder will stick to it. Because of this, I use the soldering stand to hold the battery and the wires, since they get so hot.

2) Solder a wire to the negative pole.

3) Now the watch needs to be soldered to wires that can be later connected to components. (See figure 2 from my thesis). On the watches I used most commonly, the negative contact was on the front side of the circuit board, and all the other contacts were on the back side. This necessitates taking the circuit board off of the watch. To do this, remove the four screws holding the circuit board to the plastic case. Gently remove the circuit board, sliding it sideways. Be very careful with the board and the LCD glass. Set the plastic case and the LCD aside. Using the soldering stand to hold the circuit board, solder a wire to the negative contact.

4) Flip the board over, and solder a wire to the positive contact, and one each to the (from the back) top left button contact, the bottom left contact, and the bottom right contact.

5) Let the solder cool, and then carefully screw the circuit board back onto the plastic case

holding the LCD.

6) Set the modified watch movement aside. Solder wires roughly 4 cm long to each wire coming out of each of the two reed switches.

7) Now take the standard petri dish, and place the battery into it, in the position shown in Figure 1, making sure that all wires are pointing up and away from the center of the dish (to avoid getting epoxy on them).

8) Next, the magnets and reed switches must be placed correctly. To do this, first place the larger magnet (the Radio Shack magnet split in half) into the petri dish in the position shown in Figure 1. Once this is in position, tape it down with a small piece (roughly 1 cm x 3 cm) of the clear packing tape.

9) Place the second magnet used to activate the switch in the position shown in Figure 1. This need not be exact. Tape this magnet down with clear packing tape. I found it best to use a long thin strip running the length of the magnet (roughly 3 mm x 5 cm).

10) Place one of the reed switches running parallel to the activating magnet so that the wire leading from the glass is exactly 11 mm from the nearer long edge of the activating magnet. Tape this switch down using a piece of tape roughly 1 cm x 2.5 cm, running perpendicular to the glass.

11) Tape down the other reed switch in approximately the position shown in Figure 1. The exact position is not critical, it only need be as far away from the magnet as possible.

12) The next step is to test the first reed switch using a multimeter, to ensure that the switch is at the correct distance from the magnet. Connect the leads of this switch to a digital multimeter, set to test continuity or resistance. Without any steel plate over the

magnet, the switch should be closed. Place a steel plate over the magnets and switch (on the underside of the petri dish). With this plate in place, the switch should be open. If the switch is not closed and the plate is not in place, then move the activating magnet closer to the reed switch. If the switch is closed, and the plate is in place, then move the magnet further away from the reed switch. If movements are necessary, do them, and re-test, repeating this as often as needed.

13) Pull all the lead wires up out of the way of the epoxy that will be poured. Spray some of the silicone lubricant into a container and, using a small paintbrush, brush silicone lubricant over all exposed areas of the dish, including underneath the battery, but not under the magnets or switches. The silicone allows the epoxy to be removed easily from the petri once it has set. However, tape does not stick to silicone, so it must be applied after the components have been taped down. In addition, the components must not be coated in epoxy, so that they become embedded correctly in the epoxy. Hence, the need for the paintbrush.

14) Next, mix the epoxy according to the instructions, and pour 3 mm of epoxy into the dish containing the two magnets, two switches, and battery. This layer should just cover the tops of the switches and magnets, but not the wires or the top of the battery. Allow sufficient time for curing (24 hours)

15) Now the watch movement can be wired into the other components. Solder wires together as shown in Figure 2., being sure that the watch is face-down. Note that the wire leading to the bottom right contact, and one of the wires leading to the positive pole do not get connected to anything.

16) The timer should now be working as it should, that is, the timer starts or stops when the plate is placed on the magnets and removed. If the watch is in the wrong mode, the stopwatch mode can be entered by touching together the two unconnected wires (mentioned above).

17) After all the wires are connected, press all the movement and the wires, except the two just mentioned, down into the petri dish, so that they are below the level of the rim (to ensure that they become embedded). The other two wires must be standing straight up, above the rim of the dish. Tape may be used to hold down the wires and/or movement.

18) Mix epoxy, and fill the petri dish until the watch movement is covered. Allow epoxy to cure.

19) Check timer for correct operation. The heat generated by the curing of the epoxy around the watch movement may have caused the watch to re-enter standard time mode. If this has happened, put the watch back into stopwatch mode using the above-mentioned wires.

20) Once normal operation has been achieved, press all wires (including the two free ones) below the level of the rim of the petri dish, and fill the petri dish to the rim with epoxy. Allow the epoxy to cure.

21) Remove the timer from the petri dish. Check for normal operation. Usually 20% of timers do not work correctly at this stage. Depending on the needs of the researcher (and builder), in some cases steps can be taken to repair timers that do not function. Some simple problems that I have repaired include the watch not being set to stopwatch mode.

This repair can be done by scraping away epoxy to reveal the wires used to change the watch's mode (mentioned earlier), and using them to change the mode. Another defect is the wrong distance between the start/stop reed switch and the activating magnet. The magnet can be removed (with a drill and coping saw), and a hollow in the epoxy made for it nearer to or farther from the switch, as needed, and then re-coated in epoxy. It is not recommended to try moving the switc, as it is glass-enciosed, and therfore delicate. One last defect is a broken connection between wires, or between wire and component. These occur because the wire is quite thin, and will break if flexed too much. This can be repaired oftentimes by drilling or scraping to expose the wire(s), and re-soldering, and coating the repair in epoxy. Some defective timers, however, must be discarded.

22) Examine completed timer carefully for any air bubbles or other areas where the surface of the epoxy may be open. Such areas can allow water in, so if any such areas are found, coat them with some additional epoxy.

23) Cut a plate of steel, roughly 2 cm x 3.5 cm. Bend roughly 5 mm of the longer dimension up to a 90 degree angle. Drill a 2 mm diameter hole in the center of the perpendicular piece using an electric drill and appropriate drill bit.

24) Drill a 5 mm hole in the body of the timer, being careful not to drill through any essential components. Loop a 10 cm length of 40 lb test fishing line through this hole, and secure with a crimp-on connector. Loop the other end through the hole in the plate, and secure with another connector.

25) Using a 5 cm length of the same fishing line, loop one end through the hole in the plate and secure as above. Connect the other end to the swivel-snap clasp.

A tether timer cost roughly $15 in consumables to build, the largest portion of this cost being the watch. This cost estimate include a watch costing US$ 6, however, bulk watches can be had for less. As yet, none of my timers has stopped functioning as a result of the battery dying, so the useful life of a tether-timer is unknown. However, it is certainly more than 2 years, and likely more, since the battery being used is much larger than the battery it is designed for. About batteries, I've used only AA batteries before, but I planned to try AAA batteries in my next models.