Stock structure of gray triggerfish, *Balistes capriscus*, on multiple spatial scales in the Gulf of Mexico

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SEDAR41-RD45

6 August 2014

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ABSTRACT

Ingram, G. Walter, Jr., Ph.D., University of South Alabama, May 2001. Stock structure of gray triggerfish, *Balistes capriscus*, on multiple spatial scales in the Gulf of Mexico. Co-Chairs of Committee: Robert L. Shipp and James H. Cowan, Jr.

In recent years a demand has been created for gray triggerfish (GTF) due to an increase in regulations on other reef species and the increased awareness of its excellent flesh. The objectives of this dissertation are to provide insights into stock structure on large and small-scales, and to provide population parameters necessary for future management. I used descriptions of larval distribution, values of selected population parameters, and mark-recapture to evaluate the degree of stock homogeneity of GTF.

Movement patterns of GTF were described by employing a mark-recapture study. Of the 1235 GTF tagged off the Alabama coast from March 22, 1995 through October 20, 2000, encounter histories for 270 individuals were obtained. GTF exhibited high annual site fidelity (0.63-0.87 per year) with small pulses of movement during tropical cyclones on the scale of a few kilometers. Management of GTF may be facilitated by the implementation of no-take marine reserves.

Age, growth, mortality and reproductive data were collected on 1,849 GTF from July 19, 1996 to October 20, 2000. GTF were found to live to 9 years of age, reach a theoretical maximum fork length of 583 mm, and spawn from May to August. Population parameters of GTF appeared heterogeneous on multiple spatial scales. At the local scale, GTF appeared to have differences in growth and mortality parameters, which may have been attributable to differential fishing pressure between reef areas off Alabama. On a Gulf-wide scale, temporal differences in growth and mortality parameters may have resulted from differential exploitation, and precluded meaningful comparisons of parameters.

The distribution of larval/juvenile GTF in the Gulf was analyzed using data collected during surveys of the Southeast Area Monitoring and Assessment Program from 1990-1993. This indicated that larval/juvenile distribution is affected by hydrography and distribution of spawning grounds. GTF may have a prolonged pelagic phase and exhibit homogeneous stock structure in relation to genetic variability. However, if young GTF are entrained within currents that retain them in the same area from which they were spawned, the result would be a mostly self-recruiting population or sub-population.

CHAPTER 1: GENERAL INTRODUCTION

1.1 Introduction

Reef fishes represent important commercial and recreational resources in the Gulf of Mexico (Gulf). Within the past decade and a half, many concerns have arisen over the future of some reef fish stocks. Many economically and ecologically important species in the snapper/grouper complex currently are estimated to be overfished, with declining recreational and commercial landings of many species (GMFMC, 1989). The Reef Fish Fishery Management Plan was implemented in November 1985 by the Gulf of Mexico Fishery Management Council (GMFMC) to rebuild declining reef fish stocks. There are numerous species managed under this plan, including the gray triggerfish (GTF), the subject of this dissertation.

The gray triggerfish, *Balistes capriscus*, ranges in the western Atlantic Ocean from Nova Scotia to Argentina, including the Gulf of Mexico. In the Gulf, the GTF is a reef fish inhabiting both natural and artificial reefs in waters from 10 m (Smith, 1976; Johnson and Saloman, 1984) to 106 m (Kevin Rademacher, pers. comm.[1]) in depth as adults. Fishery independent data provided by National Marine Fisheries Service (NMFS) in the form of videos taken of reefs in the Gulf indicate that GTF are distributed from

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[1] National Marine Fisheries Service, Pascagoula, Mississippi

south Texas around the northern Gulf to just north of the Florida Keys with increased concentration of adults associated with the numerous artificial reef permit areas (Kevin Rademacher, per. comm.). Early life stages include demersal eggs and pelagic larvae (Richards and Lindeman, 1987), and for extended periods of time, the GTF is planktonic and associated with seaweed and flotsom (mostly *Sargassum* spp., Dooley, 1972).

Until recently GTF were not prized by recreational and commercial fishermen. Hence, the GTF did not support an economically important directed fishery in the Gulf. However, an increase in regulations on other reef species and the increased awareness of the excellent flesh of GTF have created a demand for this previously underutilized fishery resource. This increase in demand can be seen in both commercial and recreational landings of GTF the in Gulf (Figure 1.1; Harper and McClellan, 1997) from 1986-1996. After 1990 a sharp decline in landings occurred.

The goal of this dissertation is focused on two main objectives: to provide insights about stock structure on large and small-scales, and to provide population parameters that are necessary for future management. In this dissertation, the term 'stock' refers to the population of GTF in the Gulf, and is synonymous with the term 'population.' These results are a needed addition to the currently depauperate information on the population ecology and population dynamics of GTF in the Gulf. If the current trend of increasing popularity of GTF continues, a stock assessment of GTF in the Gulf will be necessary in the near future. The results of this project also provide important information that will assist in the development of a fishery management plan for this species.

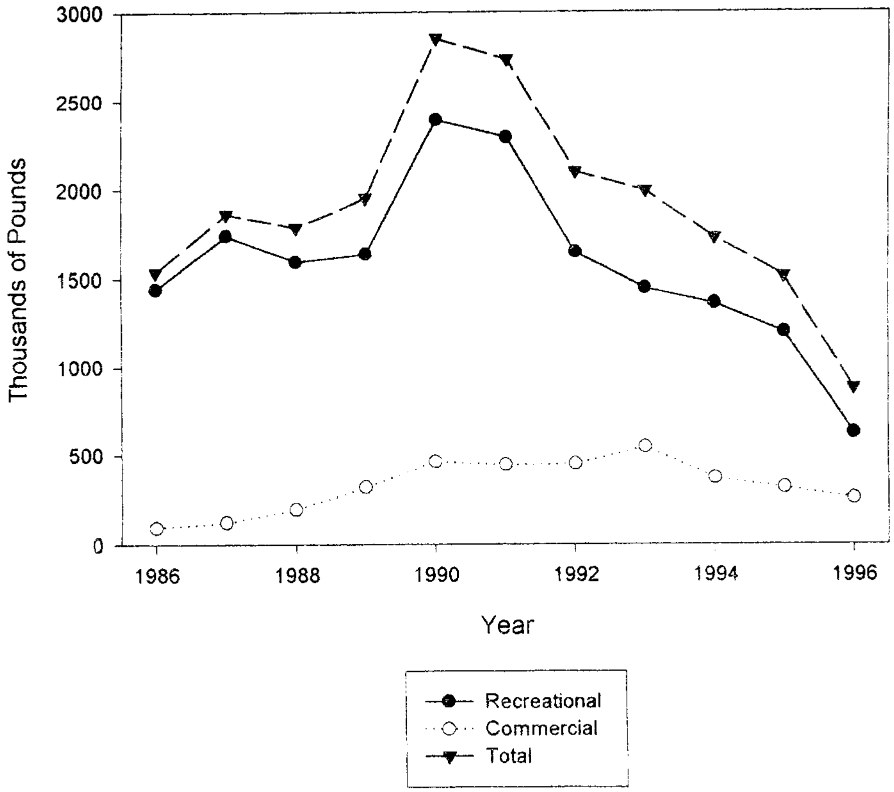

Figure 1.1. Recreational and commercial landings of gray triggerfish in the Gulf of Mexico.

1.2 Generalized Linear Models

In fisheries biology, and the field of biology in general, there are many discrete response variables, which have event counts (i.e. count data) as possible outcomes. Throughout this dissertation, count data are described with many different types of generalized linear models, which include logistic regression models, Poisson regression models and negative binomial regression models.

Logistic regression is used to model binary response variables, for which the response measurement for each sample is a "success" or "failure." For a binary response Y and a quantitative explanatory variable X, let $\pi(x)$ denote the probability of "success" when X takes the value x. This probability is the parameter for the binomial distribution, in which the mean and variance of a binomial distribution with N trials are $E(Y) = N\pi$ and $\mathrm{Var}(Y) = N\pi(1 - \pi)$, respectively. The logistic regression model has the linear form for the logit of this probability,

$$\operatorname{logit}[\pi(x)] = \log\left(\frac{\pi(x)}{1-\pi(x)}\right) = \alpha + \beta x .$$

The equation indicates that $\pi(x)$ increases or decreases as an S-shaped function of x. An alternate equation uses the exponential function e^x, in the form:

$$\pi(x) = \frac{e^{(\alpha+\beta x)}}{1+e^{(\alpha+\beta x)}} ,$$

where the parameter β determines the rate of increase or decrease of the S-shaped curve. However, parameter interpretation while in this equation form is convoluted and unintuitive (McCullagh and Nelder, 1989; Agresti, 1996; Mark Carpenter, per. comm.[2]).

Perhaps the simplest way to interpret the parameters is by taking the inverse natural log of both sides of the original linear equation. Therefore, the odds of "success" are:

$$\frac{\pi(x)}{1-\pi(x)} = e^{(\alpha+\beta x)} = e^{\alpha}\left(e^{\beta}\right)^{x}.$$

This exponential relationship provides an interpretation of β: the odds increase multiplicatively by e^{β} for every one-unit increase in x (McCullagh and Nelder, 1989; Agresti, 1996; Mark Carpenter, per. comm.).

Next, the Poisson distribution is a potential probability model for many types of count data. It is indexed by a parameter μ, its mean. Let y denote a possible outcome for the Poisson variate. The formula for Poisson probabilities is:

$$P(y) = \frac{e^{-\mu}\mu^{y}}{y!} \qquad y = 0, 1, 2, \ldots$$

The possible outcomes for y are nonnegative integers. Also, let $E(Y)$ denote the expected value of variable Y, which is the mean of its probability distribution. Let Var(Y) = $\sigma^2(Y)$

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[2] Department of Mathematics and Statistics, University of South Alabama, Mobile, Alabama

denote its variance, $\sigma(Y)$ its standard deviation. Therefore, the Poisson mean parameter is also the variance of the distribution. That is:

$$E(Y) = \mathrm{Var}(Y) = \mu, \qquad \sigma(Y) = \sqrt{\mu}$$

(McCullagh and Nelder, 1989; Agresti, 1996; Mark Carpenter, per. comm.).

A Poisson loglinear model is a generalized linear model that assumes a Poisson distribution for Y. If μ denotes the expected value of for a Poisson variate y, and X denotes an explanatory variable, then the Poisson loglinear model, which is employed to perform Poisson regressions, has the form:

$$\log \mu = \alpha + \beta x .$$

For this model, the mean satisfies the exponential relationship:

$$\mu = e^{(\alpha + \beta x)} = e^{\alpha}\left(e^{\beta}\right)^{x} .$$

A one-unit increase in X has a multiplicative impact of e^{β} on μ (McCullagh and Nelder, 1989; Agresti, 1996; Mark Carpenter, per. comm.).

Count data often show greater variability in the response counts than one would expect if the response distribution truly were Poisson. If this is the case, the response variances will be much larger than response means, whereas Poisson distributions have identical means and variances. This phenomenon is known as overdispersion. A common cause of overdispersion is heterogeneity among subjects. If the resulting Poisson regression model has significant lack-of-fit due to overdispersion of data, the negative binomial regression may be a better model to use, which would adjust model variances without significantly changing the parameter values (McCullagh and Nelder, 1989; Agresti, 1996; Mark Carpenter, per. comm.).

The negative binomial distribution is described by two parameters: the mean (m) and a dispersion parameter (k) such that the probability of observing a specific value x is:

$$\Pr(X = x) = \binom{k+x-1}{k-1}\left(\frac{m}{k}\right)^{x}\left(1+\frac{m}{k}\right)^{-(k+x)}$$
$$m, k > 0, x = 0,1,2,\ldots$$

The arithmetic mean (m) measures location, and k measures the dispersion of the negative binomial distribution. As $k \to \infty$, this distribution approaches a Poisson distribution. However, as $k \to 0$ (i.e., the population becomes more clumped), the distribution approaches a logarithmic series. Therefore, at a given scale, k can be interpreted as the degree of clumping in the population. The Poisson assumption of spatial independence is relaxed with the negative binomial distribution (McCullagh and Nelder, 1989; Agresti, 1996; Mark Carpenter, per. comm.).

The loglinear negative binomial regression model closely resembles that of the Poisson regression model save for the aforementioned dispersion parameter located in the systematic component of the model. The parameters of the log negative binomial are interpreted exactly like those of the Poisson model (i.e. by taking the inverse natural log of both sides of the regression model and describing the multiplicative effect of each parameter on μ) (McCullagh and Nelder, 1989; Agresti, 1996; Mark Carpenter, per. comm.).

There are two primary statistics used in evaluating parameter significance, lack-of-fit, and the significance of each step in the model building process of the aforementioned models: the deviance (likelihood-ratio statistic) and Pearson's chi-square statistics. Pearson's chi-square statistic is defined as:

$$X^2 = \Sigma \frac{(y_i - \mu_i)^2}{\mu_i}$$

(McCullagh and Nelder, 1989; Agresti, 1996; Mark Carpenter, per. comm.).

The deviance statistic is asymptotically a chi-square random variable with the degrees of freedom equal to the number of observations minus the number of parameters in the model (i.e., df = n-p-1) and is defined as:

$$\text{Deviance} = 2\Sigma y_i \log\left(\frac{y_i}{\hat{\mu}_i}\right).$$

For most models, lack-of-fit and parameter significance can be evaluated by using both the Pearson's chi-square and deviance statistics. If a model has insignificant lack-of-fit, then the corresponding p-value of each statistic should be large. Conversely, if a model has significant lack-of-fit, then the corresponding p-value of each statistic should be small. When testing the significance of individual parameters, a low p-value indicates a parameter is significant (McCullagh and Nelder, 1989; Agresti, 1996; Mark Carpenter, per. comm.).

However, for models of rare events data both statistics may not be appropriate to evaluate lack-of-fit, and may be at completely opposing ends of the significance spectrum. In other words, for rare events data, Pearson's chi-square may indicate insignificant lack-of-fit (i.e. have a high p-value) while the deviance statistic may indicate significant lack-of-fit (i.e. low p-value)(Mark Carpenter, per. comm.).

Even though deviance may not be an appropriate statistic with which to evaluate lack-of-fit, McCullagh and Nelder (1989) indicated that using the significance of a reduction in deviance to evaluate the addition of more parameters to a model is appropriate because deviance partitions associated with model parameters are additive where Pearson's chi-square is not.

1.3 Approach and Rationale

Under the most widely accepted management paradigm, species like GTF that have pelagic larval and juvenile life history stages are assumed to belong to a genetically homogenous or unit stock (Ricker, 1975; Gulland, 1983; Richards and Lindeman, 1987). While this may be true, previous studies (Beaumariage, 1964; Johnson and Saloman, 1984) suggest that adult GTF exhibit high site fidelity and thus may be prone to localized differences in population demographics (Gulland, 1983); fishes that exhibit high site fidelity may also be highly susceptible to localized overexploitation as fishing pressure increases (Bohnsack, 1989). Although not directly calling into question the unit stock hypothesis for GTF, this does suggest that adult GTF may better be managed with respect to local demographics (i.e. with respect to management units within a unit stock).

Gulland (1983) suggested that data derived from several sources could be used to provide information on stock separation: distribution of fishing, spawning areas and larval/juvenile distribution, values of population parameters, morphological or physiological characteristics, and tagging. Of these, I used descriptions of larval distribution, values of selected population parameters, and mark-recapture to evaluate the degree of stock homogeneity of GTF.

I used mark-recapture (i.e. tag-recapture) to describe movement patterns and site fidelity of GTF. I reasoned that if fish tagged off the Alabama coast in one area are frequently recaptured in other areas, then the same stock likely occurs throughout the waters off Alabama. If not, then the stock may be separable into management units (MU's). If different MU's are present, I hypothesized that there may be differences between population parameters (here growth, reproductive and mortality parameters) of GTF in different reef areas off Alabama.

I compared values of selected population parameters on multiple scales to gain insight on GTF stock structure. On a relatively local scale, I reasoned that if there are little differences in growth and/or mortality of GTF between individual reefs and/or between clusters of reefs within the same area, then local separation of GTF into smaller MU's may not be warranted. On a slightly larger scale, I reasoned that if there are little differences in growth, mortality and/or reproductive parameters of GTF between artificial-reef permit areas off Alabama then local separation of GTF into smaller MU's may not be warranted at the permit-area scale. On a relatively larger scale, I reasoned that if there are significant differences between the population parameters for GTF in the north-central Gulf compared to other areas of the Gulf, then there might be separable MU's within the unit stock.

Finally, on an even larger scale, I reasoned that a description of larval distribution of GTF would provide insight into the stock dynamics of this species. If there is a clear separation of adult and larval distributions, then recruitment to reefs may not be derived from local sources.

CHAPTER 2: MOVEMENT AND SITE FIDELITY OF GRAY TRIGGERFISH

2.1 Introduction

Until recently, the focus of adult reef fish studies has been primarily on relatively sedentary taxa (e.g., Pomacentridae, Labridae; Jones, 1991; but see Ingram and Patterson, In press). This has somewhat diverted attention from the issue of fish movement and its effect on spatial and temporal patterns in population size and structure. However, even in species exhibiting high site fidelity, estimates of population parameters have a hidden element associated with the balance of immigration and emigration. Of more mobile species, it is expected that patterns of distribution across reef systems on large spatial scales will be determined by movement and habitat selection following recruitment to adult reef habitat (for review, Jones, 1991).

Difficulties in quantifying movement make this one of the most challenging demographic parameters to estimate. It can only be measured directly by observing individually recognized or tagged fish shifting from one place to another, and then estimating the net effects on other population parameters. Because movement may be unpredictable and instantaneous, it may be difficult to detect without continuous observation (Jones, 1991). Given these inherent difficulties, it is not surprising that many

1.1), which peaked in the early 1990s after the close of the red snapper fishery. Marine reserves may provide an effective management tool to overcome the weaknesses of current management practices, especially with regard to ecological complexity and the effects of shifts in fishing effort between species due to imposition of regulations (Bohnsack, 1993; Lauck et al., 1998).

The utility of a marine reserve depends on the life histories and behavior of the species under management. I reason that reef species exhibiting high site and/or area fidelity may profit from the shelter of a no-take marine reserve. Also, I reason that tropical cyclones may facilitate the export of adult biomass from no-take marine reserves in the northern Gulf (Ingram and Patterson, In press; Patterson, 1999; Watterson, 1998; Watterson et al., 1998) by causing an increase in movement, thereby restocking surrounding areas.

One of the most important uses of a marine reserve may be to serve as a refuge from fishing pressure for some or all of the species in the area. By releasing such fishing pressure, a population may then become structured by natural mortality instead of fishing mortality (Bohnsack, 1992). Thus, reserves may increase the density, average size, and spawning stock biomass (SSB) of species in the reserve, even large predatory species like carangids and lutjanids (e.g., Plan Development Team, 1990; Polunin and Roberts, 1993; Roberts, 1995; Russ and Alcala, 1996). Because larger individuals tend to have higher reproductive output, a population now structured by natural mortality with a greater abundance of larger and older individuals in a marine reserve may have a much higher reproductive output (Bohnsack, 1992). Hence, marine reserves could possibly enhance fisheries by acting as centers of dispersal of propagules and adults into the areas surrounding the reserve.

To date, there have been few studies concerning movement of adult gray triggerfish. Ofori-Danson (1990) reported that gray triggerfish off the west African coast in the eastern Atlantic Ocean move from cold coastal waters as a result of seasonal upwelling (during the third quarter of the year) to join an offshore stock, which is present throughout the year. In contrast, Beaumariage (1964) and Johnson and Saloman (1984) reported that Gulf of Mexico fish may be less migratory. For example, Beaumariage (1964) found that 38 of 103 gray triggerfish that were tagged and released in the northeastern Gulf were recaptured by investigators (36.9% recovery rate) in the approximate area of initial capture and release.

Thus, the purpose of this chapter is to describe the movement patterns of gray triggerfish off the Alabama coast and to accomplish two goals. The first objective of this chapter is to provide insight into the stock structure of GTF off the Alabama coast by describing the propensity for, direction and velocity of movement, and site fidelity of GTF inhabiting natural or artificial reefs. A finding of a high likelihood or velocity of movement would support the unit stock hypothesis (Gulland, 1983). However, a finding of high site fidelity and little or no movement could be evidence that fish in different areas constitute different MU's within the unit stock, especially if localized differences in growth, reproductive and survival parameters can be demonstrated (Gulland, 1983). The second objective of this chapter is to provide insight on the utility of marine reserves as a management tool for GTF stocks in the northern Gulf.

For mark-recapture studies, both Cormack-Jolly-Seber (CJS) model theory and corresponding ring recovery model theory (Brownie et al., 1985) for time-specific effects is well developed and established. Many mark-recapture studies on fish can generate both live recaptures and dead recoveries from fish that are harvested or found dead throughout the year. Burnham (1993) provides a basic generalization of the CJS and ring recovery model for the simultaneous analysis of live recapture and dead recovery data. The basic model (Burnham, 1993) gives an estimate of the following parameter set: S for survival, r for the probability of recovery of an individual that is dead, p for the recapture probability of an individual that is alive, and F for the probability that an individual remains on the study area (fidelity) and hence is available for recapture. Thus, the joint recovery and recapture model provides unbiased estimates of S assuming that r is constant regardless of where the animal dies. If r varies geographically (i.e. if r declines as animals emigrate from the study area), then the estimates of S will still be biased.

Before I can make strong inferences about the unmarked (untagged) population, there are several assumptions about the tagged population that must be met. These assumptions include: 1) tagging does not affect the mortality of the tagged GTF; 2) all GTF have the same probability of being captured whether they were tagged or not; 3) tagging does not affect the growth of tagged GTF; 4) tagging does not effect the behavior of tagged GTF; 5) tagged GTF were recognized as such; and, 6) tags recovered by fishers were all reported (Seber, 1982; Krebs, 1989; Nielsen, 1992; Patterson, 1999). In this chapter, I first present the methods used during the tagging studies, as well as the methods by which the aforementioned assumptions were tested. I then present the

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2.2 Materials and Methods

2.2.1 Study Area

GTF were tagged during two studies off the Alabama coast. The first study took place from March 22, 1995 through July 20, 1998. During this study, GTF were opportunistically tagged from June 20, 1995 through February 25, 1998 as part of a red snapper (*Lutjanus campechanus*) tagging study (MarFIN Grant number NA57FF0054, Robert L. Shipp, principle investigator) over nine artificial reef sites. These reefs were located between 20 and 32 km south-southeast of Dauphin Island, Alabama, in the Hugh Swingle General Permit Area for artificial reef deployment (Figure 2.1). The artificial reefs were constructed eighteen months prior to the start of the tagging study to allow sufficient time for fouling of the reef material and attraction of fish. The artificial reefs were constructed from a variety of materials. These included newspaper bins, shopping carts, 55-gallon plastic drums, and a tractor-trailer truck bed. The reefs were deployed in a 3 × 3 grid and were between 4 and 16 km apart. Each reef site was given a directional

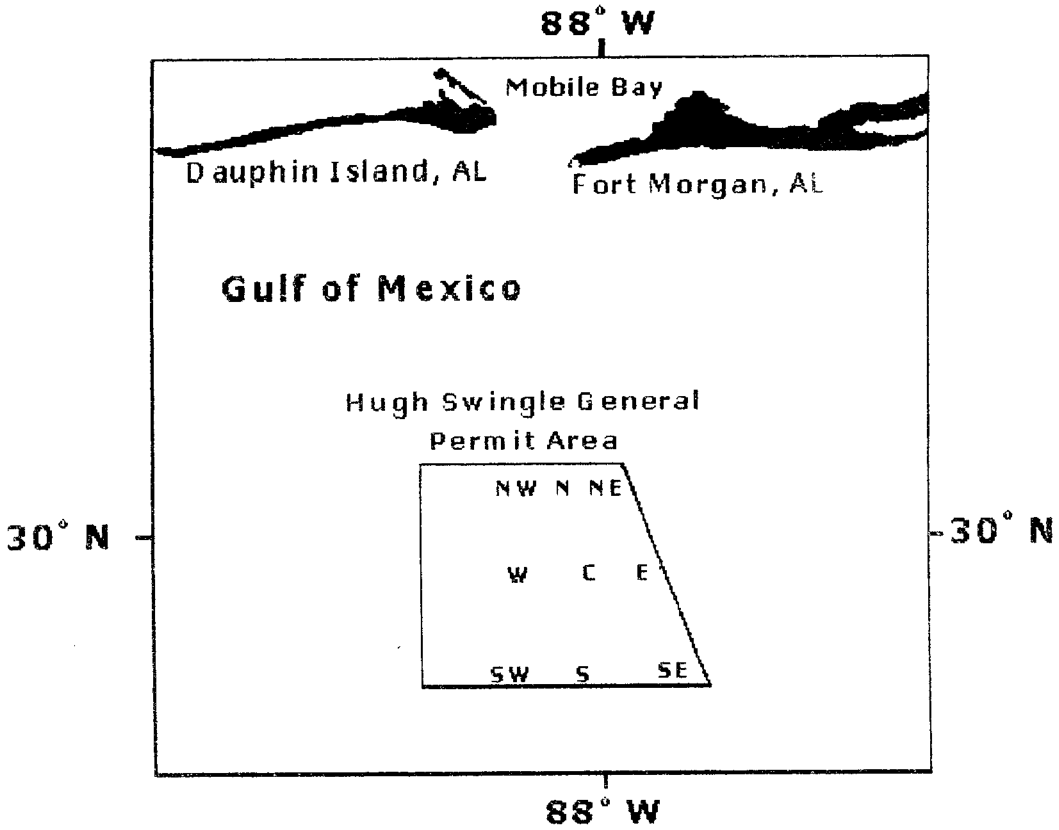

Figure 2.1. Artificial reef tagging stations in the Hugh Swingle General Permit Area.

name according to its location in the grid. Reefs in each row occupied a similar depth. The northern, central and southern reefs were at depths of approximately 21, 27 and 32 m, respectively. During this study, 22 tagging trips were made to capture and tag GTF. During each tag and recapture operation (each cruise), at least 3 stations were sampled. Because GTF were exclusively tagged over artificial reefs during this project, this project will henceforth be known as that artificial reef study (ARS).

The second tagging study took place between October 1, 1997 and October 20, 2000. Gray triggerfish were captured in two natural reef areas in the north-central Gulf off Dauphin Island, Alabama (Figure 2.2). These areas were chosen due to high historical catch of GTF on these sites by recreational anglers. Each of the two areas was arranged into a cluster of tagging stations. The first area was a cluster of six tagging stations located in the northeast corner of the Hugh-Swingle General Reef Permit Area in approximately 20 m of water, proximal to the Southeast Banks. The stations, denoted as the Inshore Site, consist of natural hard-bottom, and are approximately 0.1-1.5 km apart within the Southeast Banks site. The other area was a cluster of four tagging stations located south of the Hugh-Swingle General Reef Permit Area in approximately 32 m of water, and denoted as Offshore Site (Figure 2.2). The stations at the Offshore Site also consist of natural hard-bottom, but are more dispersed than the stations in the Inshore Site (i.e. approximately 2.9-5 km apart). Tagging stations within each area were named first according to the area (i.e. Inshore, I or Offshore, O), and then to the order in which each was initially sampled (i.e. A, B, C, D or E), or replaced if the original stations were "lost" to tropical cyclones during the study (i.e. R). During this study, 34 tagging trips

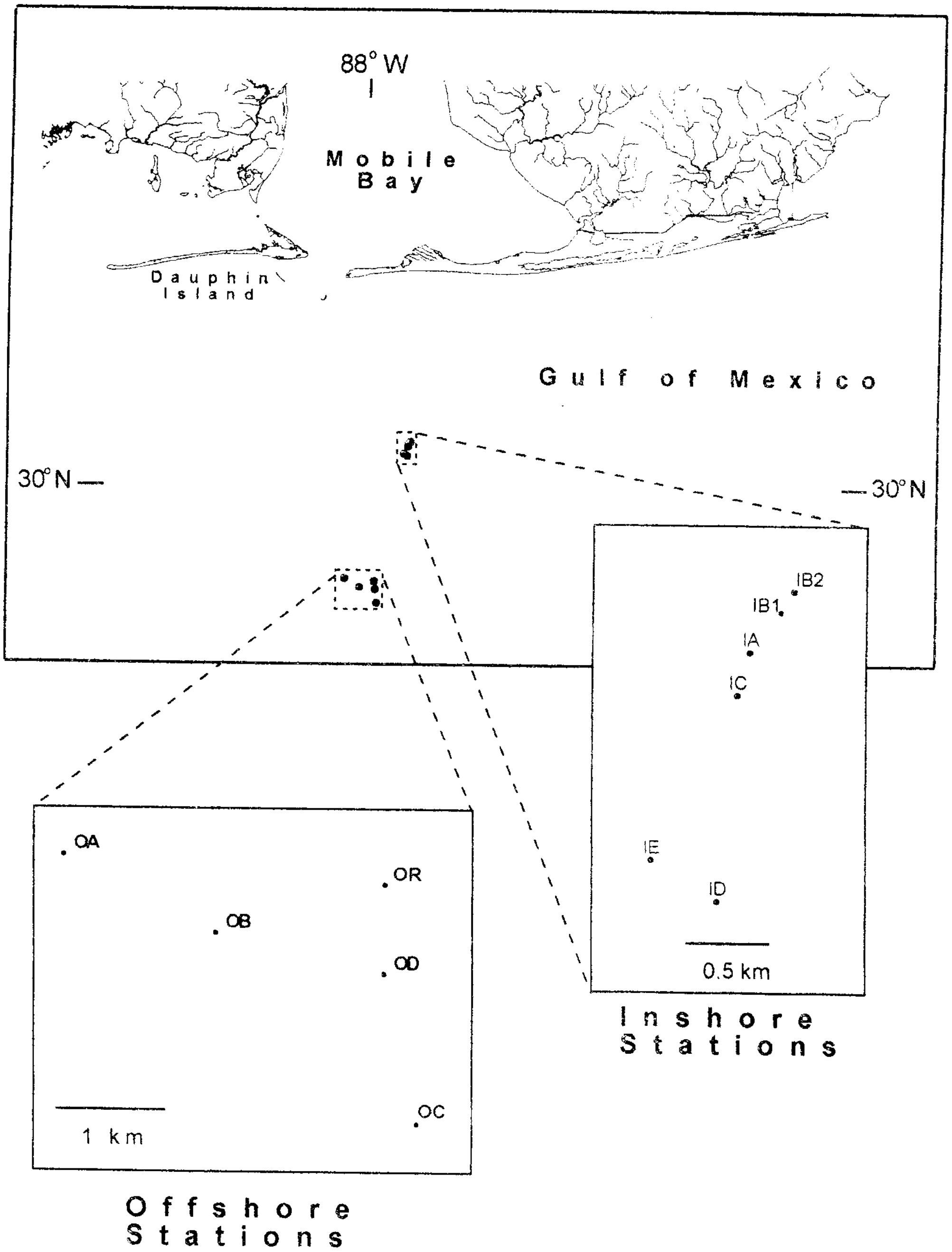

Figure 2.2. Natural reef tagging stations in the north-central Gulf of Mexico

were made to capture and tag GTF. Either the Offshore Site or the Inshore Site was sampled per cruise, not both. When the Offshore Site was visited, 3 to 5 stations were usually sampled. When the Inshore Site was visited, 6 tagging stations usually were sampled.

Due to passage of a tropical cyclone, stations OB and OD were "lost," probably due to the deposition of sand over these hard-bottom outcroppings. These stations were repeatedly checked to determine if they would uncover with time, but on July 21, 1999, I added station OR (Offshore Replacement) to help compensate for the loss of stations. Because GTF were exclusively tagged over natural reefs during this study, it will henceforth be referred to as the natural reef study (NRS).

2.2.2 Tagging Protocols

The basic protocol for tagging was similar for both studies and consisted of one to two GTF tag and recapture cruises each month, depending on weather conditions. Tag and recapture cruises were made aboard the chartered fishing boat *Lady Ann* out of Dauphin Island, Alabama.

Upon arrival at each site, a Model 25, Sea Bird Electronics, Inc., conductivity, temperature, and depth data logger (CTD) was used to record a water column profile of temperature, salinity, and dissolved oxygen concentration to determine if movement of GTF was dependent upon these environmental parameters. GTF were captured over reef sites with rod and reel fished with straight-shank, barbed hooks. During the ARS, the target of the study was red snapper; therefore, 3/0 size hooks were used. However, in order to better target GTF, I used 1/0 size hooks during the NRS. Once hooked, GTF were retrieved slowly from the bottom (approximate retrieval rate < 0.5 m/s) and placed into an aerated holding tank with running seawater. Fish captured at each station were measured for total length (TL) and fork length (FL). Elongated fin rays at the top and bottom lobes of the caudal fin can cause high variability in measurements of total length (Johnson and Saloman, 1984; Menezes, 1985; Manooch and Drennon, 1987; Ofori-Danson, 1989). Therefore, FL was used in all statistical analyses concerning length-dependent data.

Each triggerfish then was tagged with an individualized Floy® FM-89 internal anchor tag. Tags were inserted into a small incision made in the abdominal cavity, a method proven to be effective in the ARS. When released, the condition of the triggerfish were visually assessed based upon the following scale (Patterson, 1999; Ingram and Patterson, In press; Patterson and Ingram, In press): (1) GTF immediately oriented itself toward the bottom and swam down vigorously; (2) GTF appeared disoriented upon entering the water, oriented toward the bottom but swam erratically; (3) GTF appeared very disoriented upon entering the water and remained at the surface; and (4) GTF was either dead or unresponsive upon entering the water.

Tags in the ARS were yellow, Floy® internal-anchor, monofilament-core tags. Initially, tags in the NRS were yellow, Floy® internal-anchor, monofilament-core tags and were used to tag GTF from October 1, 1997 through November 18, 1998. However, due to tag loss, presumably by removal by other fish during the ARS and the first part of the NRS, tag type was switched after 18 November for the remainder of the study to orange, Floy® internal-anchor, stainless-steel-core tags to reduce tag loss. Both types of tags had similar dimensions in anchor size, length and diameter of tubing. Regardless of tag type, each was marked with a tag number, the word "reward," and a phone number for fishers to report tag recoveries. Recaptures by other fishers within and outside of the tagging areas were an important source of data, especially if GTF moved from the tagging stations. Therefore, a $5 reward was offered per tag as incentive to fishers to report tag returns, with a chance to win $500 in a drawing of tag returners at the end of the study.

The occurrence of tropical cyclones during each study provided a unique natural experiment to investigate the effects of tropical cyclones on movement of GTF. During the ARS, Hurricane Opal passed within 40 km of the artificial reef tagging stations on October 4, 1995 with maximum sustained winds of 200 km hr^{-1}. During the NRS, Hurricane Georges passed within 50 km of the natural reef tagging stations on September 28, 1998 with maximum sustained winds of 150 km hr^{-1}. During both the ARS and the NRS, movement was compared between fish that were at large during a tropical cyclone (i.e. GTF that were tagged before the occurrence of the tropical cyclone and recaptured after the occurrence of the tropical cyclone) and fish that were not at large during a tropical cyclone (i.e. GTF that were tagged before and recaptured before, or GTF that tagged after and recaptured after the occurrence of a tropical cyclone).

2.2.3 Statistical Treatment of Data

Several two-group comparisons were made while analyzing size data of recaptured GTF. These included comparisons between the FL of fish captured and tagged during the ARS versus those during the NRS, and the FL of fish recaptured on my tagging cruises versus those recaptured by recreational fishers during both the ARS and the NRS. For each comparison, if both data sets passed the Kolmogorov-Smirnov test for normality ($\alpha = 0.05$) then they were compared using a t-test ($\alpha = 0.05$). If one or both of the data sets failed the Kolmogorov-Smirnov test, they were compared using a Mann-Whitney rank sum test ($\alpha = 0.05$).

Statistical analyses were performed to test the aforementioned assumptions, and were based on those of Patterson (1999). Assumptions were tested on data from the NRS, because the data with which to test the aforementioned assumptions was explicitly collected during this study. Assumptions that were not tested included the assumption that all GTF caught by fishers were reported, and that tagging did not alter the behavior of GTF. The statistical methodology by which I tested the remaining assumptions is presented below. Regardless of whether the assumptions were statistically tested or not, all assumptions, and the consequences of not meeting them in these tagging studies are discussed.

A large sample Z-test for proportions ($\alpha = 0.05$) was used to test the assumption that tagging had no effect on mortality of tagged GTF. I assumed that fish released in any condition but condition one, according to the previously mentioned release condition scale, did not survive to be recaptured. Therefore, it is was taken that the proportion of

GTF released in conditions two to four was the acute mortality rate due to tagging. I then statistically determined if acute mortality rate was significantly greater than 0. If so, I used logistic regression to model acute mortality rate as a function of depth from which the GTF was captured, and fish size (mm FL). The dependent variable for this model, condition, was assumed to be binomially distributed as a condition-1 or not. The variable depth was based on average depth of inshore tagging stations (24 m) versus offshore tagging stations (33 m), and was assigned as shallow versus deep, respectively.

The assumption that all tagged fish were recognized as such could not be directly tested. However, I again used a logistic regression to model the rate of external tag loss of tagged GTF. This provided a means by which to correct for tag loss in future analyses. To accomplish this, I modeled the binomial variable of tag retention against time at large for each fish, and tag type following the methods of Patterson (1999). To ascertain whether a tag was lost or not, I used only GTF recaptured over my tagging stations. If most of the external part of the tag was missing, usually there was a small part of the tag core remaining on the outside of the GTF or a tagging scar. In either case, tag condition was assigned as lost. I assumed that I recognized all tagged fish, whether or not the external part of the tag was missing.

The last assumption to be tested was the assumption that tagged and untagged GTF have an equal probability of being captured (POC) (Patterson, 1999). Here, I assumed that this assumption was met (Patterson, 1999), even though direct comparisons of the POC of tagged and untagged members of the population were not made. However, the recovery rate and the numbers of multiple recaptures of individual fish provide insight into the POC of tagged individuals. Recovery rate was reported as percentage of tagged fish that were recaptured.

Catch per unit effort (CPUE) was calculated for each tagging trip by counting the number of fishers actively fishing for GTF on each tagging cruise, assessing the length of time that these fishers sampled GTF for tagging, and counting the number of GTF captured. A multiple regression was used to determine if there was a significant effect of season, depth and/or hydrographic parameters (i.e. dissolved oxygen, temperature and salinity) on CPUE. A Fisher's least-significant-difference test ($\alpha = 0.05$) was used to describe any differences found in class variables. Seasons in this chapter, and in Chapter 3 correspond to quarters of a year (i.e. January – March = Winter; April – June = Spring; July – September = Summer; and October – December = Fall).

2.2.4 Description of Site Fidelity and Movement

Analysis of survival and site fidelity using the Burnham model (1993) was accomplished by using the computer program MARK, which takes into account information generated by both live recaptures and dead recoveries. Data were formatted as individual capture histories (i.e. a list of zero's and one's, which indicated live recapture(s) and dead recovery of each individual GTF during the study) with the corresponding individual covariates (i.e. size of fish, season, distance of tagging area from shore, temperature, salinity, and/or dissolved oxygen concentration). Because of the encounter histories coding used in MARK, I was unable to combine data from the ARS and NRS for development of a model, which simultaneously compares both studies.

With MARK, the maximum likelihood estimates of survival, site fidelity, recapture rate, and recovery rate of GTF were determined by analyzing many different models based on different combinations of covariates. The model which best describes survival and fidelity was chosen based upon a combination of Akaike's information criterion (AIC) and the number of parameters in the model. The simplest model (i.e. the model which estimates the fewest parameters) with the highest AIC is considered to be the most parsimonious model. In addition, MARK places a 95% confidence interval around each parameter estimate, making parameter comparisons possible.

Site fidelity also was estimated for GTF using a method described by Patterson (1999). Initially, the decay of recaptures over time at large of GTF was estimated by using the model:

$$\mathrm{N}_t = \mathrm{N}_0 e^{-Dt},$$

where N_t was the number of recaptures after a time at large (t), N_0 was the initial number of recaptures, and D was a decay constant within which was confounded tag loss (D_{tagloss}), emigration from tagging sites (IE), and total mortality (Z), which represents the combination of fishing mortality (F) and natural mortality (M) (i.e. $D = D_{\mathrm{tagloss}} + Z + IE$). Next, by adjusting D for tag loss, and subtracting decay due to total mortality estimated from catch curve analysis of the GTF collected for age estimation (see Chapter 3), I estimated emigration (IE) assuming both natural and fishing mortality (i.e. total mortality Z) was occurring. Next, the decay constant was also adjusted assuming there was only natural mortality (*M*) occurring. The instantaneous natural mortality rate of GTF was estimated using Hoenig's method (1983). Annual site fidelity (Ψ) was then estimated using the model:

$$\Psi = e^{-IE}.$$

Finally, site fidelity was also analyzed for GTF tagged during both the ARS and the NRS by plotting the cumulative frequency of recaptures of GTF versus distance from the point of tagging and release to the point of recapture.

To describe the movement patterns of GTF, I estimated the distance traveled from the tagging stations, the number of days at large, and the direction of movement, if any, of all recaptured fish. Velocity of a recaptured fish was estimated by dividing the distance moved by the time the fish was at large. Two-way comparisons were used to determine if there was a significant study effect (i.e. ARS and NRS) and/or a significant effect of hurricane status on both the distance moved and velocity of fish. At-large hurricane status was assigned to fish in the following manner. Fish at large during tropical cyclones were those fish tagged before and recaptured after the occurrence of a tropical cyclone, and fish not at large during tropical cyclones were those fish tagged and recaptured before the occurrence of a tropical cyclone or tagged and recaptured after the cyclone. For each comparison, if both data sets passed the Kolmogorov-Smirnov test for normality ($\alpha = 0.05$) then they were compared using a two-way ANOVA ($\alpha = 0.05$). If one or both of the data sets failed the Kolmogorov-Smirnov test then they were compared using a Friedman's two-way nonparametric ANOVA ($\alpha = 0.05$). To test if direction of movement, if any, was random, the Rayleigh test for randomness ($\alpha = 0.05$; Batschelet, 1981) was employed. Generalized linear models were employed (SAS for Windows, v.8) to partition the variance in both the distance moved and velocity data to determine if these parameters varied as were a function of study, year, season, GTF size at recapture, hydrographic data at the time of tagging (i.e. salinities, temperatures, and dissolved oxygen levels), and/or the presence of tropical cyclones.

2.3 Results

2.3.1 Overall Study Results

During the ARS, 201 GTF were tagged (Table 2.1). Of these, encounter histories for 44 individuals were obtained. Four individuals were recaptured more than once (i.e. two individuals were recaptured twice and two individuals were recaptured three times). This resulted in 50 total recaptures, 19 (38 %) of which were made and reported by recreational fishermen. The mean time at large for GTF in this study was 190 days. The longest time at large for a fish in the ARS was 949 days, for an individual that moved 4.1 km. The greatest distance moved by a GTF in this study was 8.6 km for a fish that was at large for 54 days, during which time Hurricane Opal passed nearby the tagging stations.

During the NRS, 1,034 GTF were tagged (Table 2.2). Of these, encounter histories for 226 individuals were obtained. Forty-seven individuals were recaptured more than once (i.e. 35 individuals were recaptured twice, 8 individuals were recaptured

Table 2.1. Dates of tagging cruises, stations sampled and numbers of gray triggerfish tagged and recaptured during the artificial reef study.

DATE	STATIONS SAMPLED	NUMBER OF FISH TAGGED	NUMBER OF FISH RECAPTURED
6-20-95	W, S, SW	13	-
6-21-95	E, SE, C	14	-
8-29-95	SE, E, NE	0	2
9-13-95	NW, W, SW	29	4
9-14-95	N, C, S	0	0
11-30-95	S, SE, NW, C	1	0
12-12-95	N, SW	1	0
2-27-96	SW, W, NW	2	0
3-22-96	N, C, S	8	0
3-29-96	NE, SE, E	9	0
5-1-96	S, SE, C	5	0
6-12-96	SW, S, W, N, C	19	2
8-7-96	SE, NE, N	11	2
10-31-96	C, W, NW, SW	12	2
11-1-96	NE, E, SE	10	0
12-2-96	N, C, S	5	3
12-9-96	NE, E, SE	15	3
3-26-97	NW, N, NE	9	1
3-27-97	SW, S, C	7	3
4-29-97	NW, N, NE	3	2
9-18-97	NW, N, NE, E	11	1
9-23-97	C, SE, S	0	1
11-3-97	NW, N, NE	4	3
11-5-97	W, SW, S, C	8	2
2-25-98	NW, N, NE	5	0

Table 2.2. Dates of tagging cruises, stations sampled and numbers of gray triggerfish tagged and recaptured during the natural reef study.

DATE	STATIONS SAMPLED	NUMBER OF FISH TAGGED	NUMBER OF FISH RECAPTURED
11-19-97	Inshore	47	-
11-25-97	Inshore	32	2
3-6-98	Offshore	9	-
3-26-98	Inshore	22	8
5-20-98	Offshore	28	0
6-11-98	Inshore	22	8
8-4-98	Inshore	14	3
10-14-98	Offshore	52	0
10-19-98	Inshore	51	6
11-18-98	Offshore	62	8
11-25-98	Inshore	109	7
12-1-98	Offshore	28	4
1-27-99	Inshore	25	3
3-22-99	Offshore	8	7
4-28-99	Inshore	111	14
7-21-99	Offshore	17	5
8-4-99	Inshore	47	14
10-22-99	Inshore	33	17
11-23-99	Offshore	28	15
12-16-99	Inshore	20	7
2-2-00	Offshore	12	11
2-25-00	Inshore	26	9
3-28-00	Offshore	10	15
5-23-00	Inshore	30	7
5-30-00	Offshore	6	4
5-31-00	Inshore	16	15
6-20-00	Inshore	13	9
6-21-00	Offshore	2	1
7-5-00	Inshore	17	5
7-27-00	Offshore	2	1
8-3-00	Inshore	1	1
8-8-00	Offshore	6	5
9-5-00	Inshore	111	20
10-2-00	Offshore	17	6

three times, 3 individuals were recaptured four times and 1 individual was recaptured five times). This resulted in 290 total recaptures, 49 (16.9 %) of which were made and reported by recreational fishermen. The mean time-at-large for GTF in this study was 194 days. The longest time-at-large for a GTF in the NRS was 1,006 days, for a fish that was recaptured five times at the point of tagging. The greatest distance moved by a GTF in this study was 22.5 km for a fish that was at large for 166 days, during which time Hurricane Georges passed nearby the tagging stations.

The median FL of GTF tagged during the ARS was significantly greater than those tagged during the NRS (Mann-Whitney rank sum test, T = 158987.500, $p < 0.001$). The mean FL (± standard error) of GTF (n=201) that were tagged during the ARS was estimated to be 326 (± 1.8) mm, while the mean FL (± standard error) of GTF (n = 1,034) that were tagged during the NRS was estimated to be 297 (± 1.2) mm (Figure 2.3).

The mean FL of GTF recaptured on my tagging cruises was not significantly different than that of GTF recaptured by recreational fishers (t-test, $t_{d.f.=35} = 1.619$, $p = 0.114$). During the ARS, the mean FL (± standard error) of tagged GTF that were recaptured on my tagging trips was 352 (± 10) mm, while the mean FL (± standard error) of tagged GTF that were recaptured by recreational fishers was 389 (± 68) mm.

Similarly, the median FL of GTF recaptured on my tagging cruises was not significantly different from those recaptured by recreational fishers during the NRS (Mann-Whitney rank sum test, T = 3652.500, $p = 0.276$). During the NRS, the mean FL (± standard error) of tagged GTF that were recaptured on tagging trips was 319 (± 2.0) mm, while the mean FL (± standard error) of tagged GTF that were recaptured by

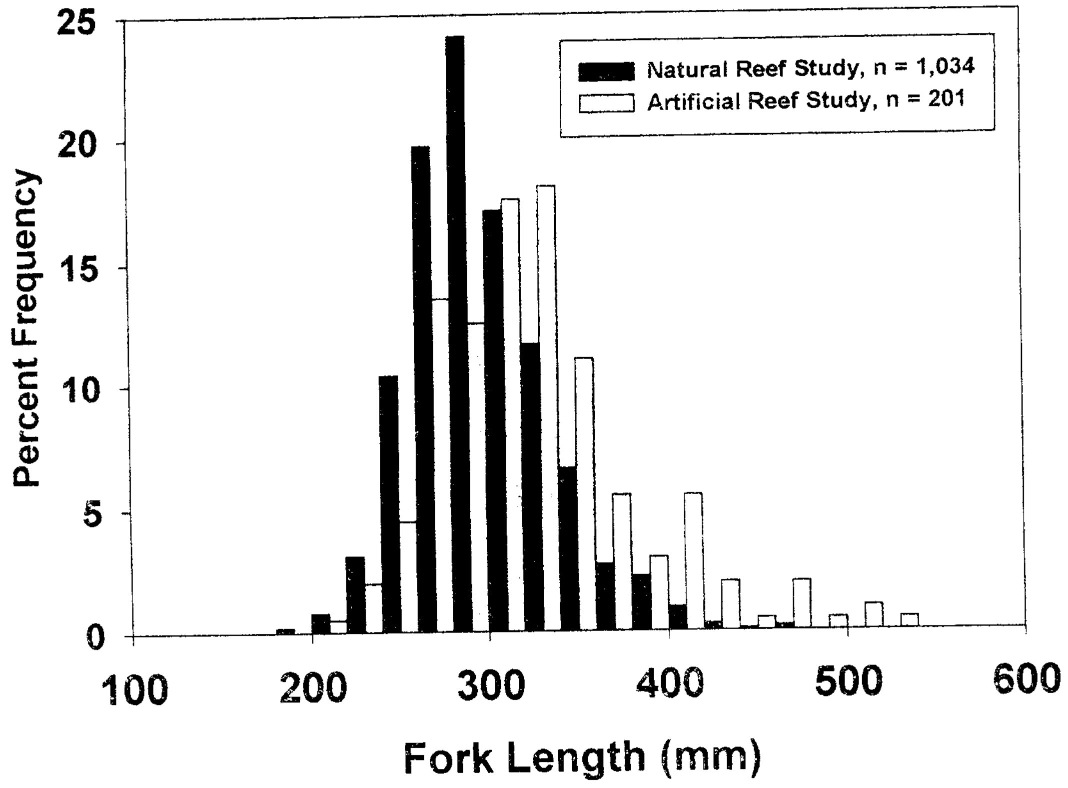

Figure 2.3. Length-frequency distributions of gray triggerfish tagged during the artificial and natural reef studies.

recreational fishers was 333 (± 8.7) mm. It is interesting to note however, that in both studies, the mean size of fish recaptured by recreational fishers was larger than the mean size of fish recaptured at my tagging stations, even though differences were not statistically significant.

2.3.2 Tagging Mortality

Generally, GTF were very hardy and resilient tagging subjects. Acute mortality of GTF due to tagging was estimated to be 1.5 %, but this percentage was statistically significant from zero (Z-test, $p < 0.05$). Out of 1,271 releases (i.e. this included all releases during the NRS – initial releases and subsequent releases after recaptures), four GTF were released in condition-2, 14 were released in condition-3 and one was released in condition-4.

The logistic regression model of GTF condition versus depth of tagging station had insignificant lack-of-fit ($\chi^2_{\text{d.f.} = 1269} = 1271.0$; $p = 0.4789$), but the addition of the depth variable did not significantly reduce the deviance of the model from that of the intercept alone ($p = 0.0807$). In contrast, the logistic regression model of GTF condition for all releases, regardless of when it was captured and released, versus FL at tagging and/or release had insignificant lack-of-fit ($\chi^2_{\text{d.f.} = 1267} = 1202.9$; $p = 0.9000$), and the addition of the FL variable significantly reduced the deviance of the of the model from that of the intercept alone ($p = 0.0031$). This model was represented by the following equation:

$$\hat{p}(m) = \frac{e^{-8.9151+0.0151(\mathrm{FL})}}{1+e^{-8.9151+0.0151(\mathrm{FL})}},$$

where $\hat{p}(m)$ is the probability of a GTF being released in a condition other than condition one, which may be an indication of acute mortality due to tagging and/or handling, and FL is fork length. This model is illustrated in Figure 2.4, and is transformed and its effects interpreted as multiplicative changes in the odds of a GTF being released in a condition other than condition-1 (see Chapter 1). These model results indicate that station depth had little effect on acute tagging mortality, and that for every millimeter increase in FL of GTF, there is a 1.5 % (95 % confidence interval: 0.5, 2.5 %) increase in the odds of a GTF being released in a condition other than condition-1, suggesting that small fish handle the stress of tagging better than larger fish.

2.3.3 Tag Loss

Of the 50 GTF that were tagged with monofilament-core tags and recaptured, 42 (84 %) retained the external portion of their tags. By comparison, of the 127 GTF that were tagged with steel-core tags and recaptured, 125 (98.4 %) retained the external portion of their tags. Combined results indicate that steel-core tags were retained better than monofilament-core tags, and that tag retention decreased with time for both tag types. Model results are detailed below.

Of the single-variable logistic models, the model for tag retention with tag type initially had the lowest deviance (deviance = 64.5395), compared to the model with time

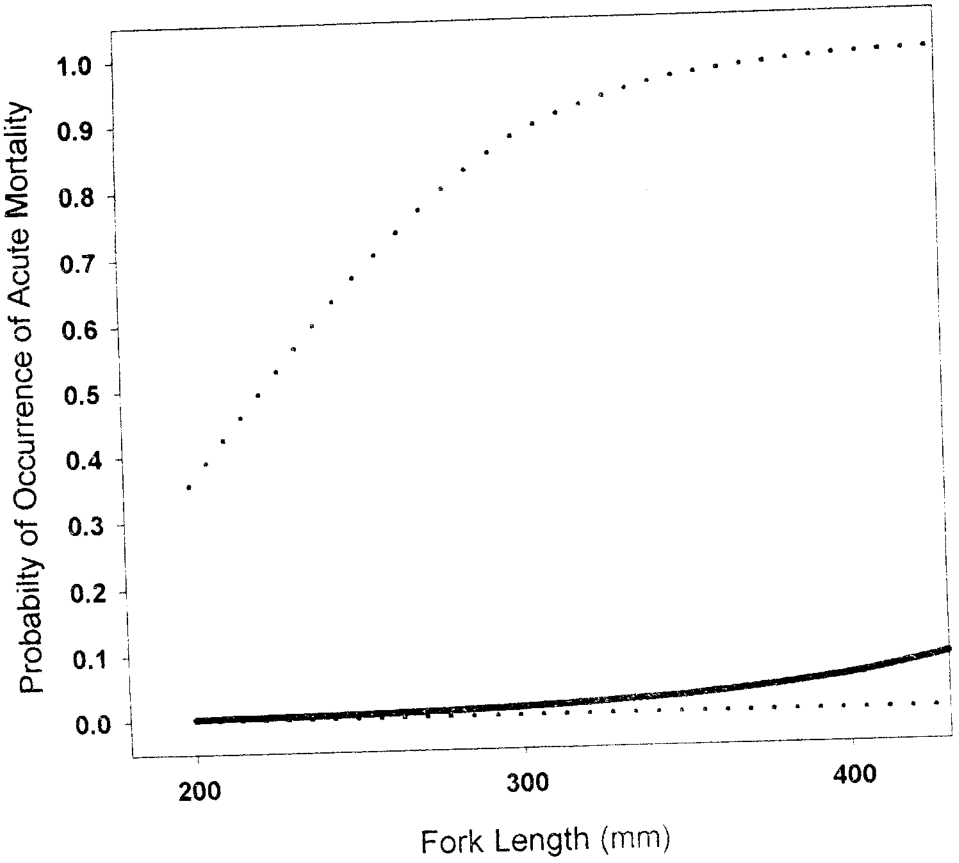

Figure 2.4. Logistic regression of the probability of releasing gray triggerfish in a release condition other than condition-1 (with 95% confidence intervals).

at large (deviance = 72.7236). The logistic model with tag type, which was essentially a contingency table analysis, had insignificant lack-of-fit ($\chi^2_{\text{d.f.} = 175} = 177.00$; $p = 0.4435$). Also, tag type had a significant effect on tag retention ($p = 0.0022$). Next, the time at large variable was entered into the model. The addition of time at large into the model significantly reduced the model deviance ($\text{deviance}_{\text{1st model}} - \text{deviance}_{\text{2nd model}} = 64.5395 - 59.5277 = 5.0118$; $\text{d.f.}_{\text{1st model}} - \text{d.f.}_{\text{2nd model}} = 175 - 174 = 1$; $p = 0.0252$), and the new two-variable model also had insignificant lack-of-fit ($\chi^2_{\text{d.f.} = 174} = 119.1427$; $p = 0.9995$). Thus, I concluded that the two-variable model best described tag retention in GTF. Because tag type was bivariate, the relationship between tag retention and time at large could be separated into two logistic models – one for monofilament tag retention over time, and one for steel tag retention over time. These models are represented by the following equations:

$$\hat{p}_{\text{mono tag retention}} = \frac{e^{2.6036 - 0.0038(\text{time})}}{1 + e^{2.6036 - 0.0038(\text{time})}}$$

and

$$\hat{p}_{\text{steel tag retention}} = \frac{e^{5.2318 - 0.0038(\text{time})}}{1 + e^{5.2318 - 0.0038(\text{time})}},$$

where $\hat{p}$ is the estimated probability of tag retention. For every one-day increase in time at large, there is a 0.38 % (95 % confidence interval: 0.03, 0.72%) decrease in the odds of retaining the external portion of a tag, regardless of tag type. The models differed only in their intercepts, and this implies that monofilament-core tags are retained less over time than are the steel-core tags (Figure 2.5).

2.3.4 Probablity of Capture

The last assumption to be tested was the assumption that all GTF have an equal probability of being captured. Recovery rate was estimated to be 21.9%, and rate of multiple recaptures (i.e. the percentage of fish that were recaptured more than once) was 20.7%. The insight into probability of capture provided by these rates is discussed below.

2.3.5 CPUE

CPUE (fish angler-hour^{-1}) varied among tagging trips (Figure 2.6). The multiple regression procedure indicated that CPUE was not significantly related to local environmental conditions (i.e. temperature, salinity and dissolved oxygen, as independent variables were insignificant ($p = 0.8123$, $p = 0.1982$, $p = 0.0734$, respectively, and all two-way interaction terms were insignificant, $p > 0.10$). Hydrographic data, collected via CTD on a number of tagging cruises during the NRS are illustrated in Appendix 1. The multiple regression procedure indicated that depth of tagging stations had no significant affect on CPUE ($p = 0.6101$). Finally, the multiple regression procedure indicated that season of tagging trip significantly affected CPUE ($p = 0.0477$). Mean CPUE was higher in fall (mean CPUE ± standard error = 3.16 ± 0.401) than in other seasons (mean CPUE

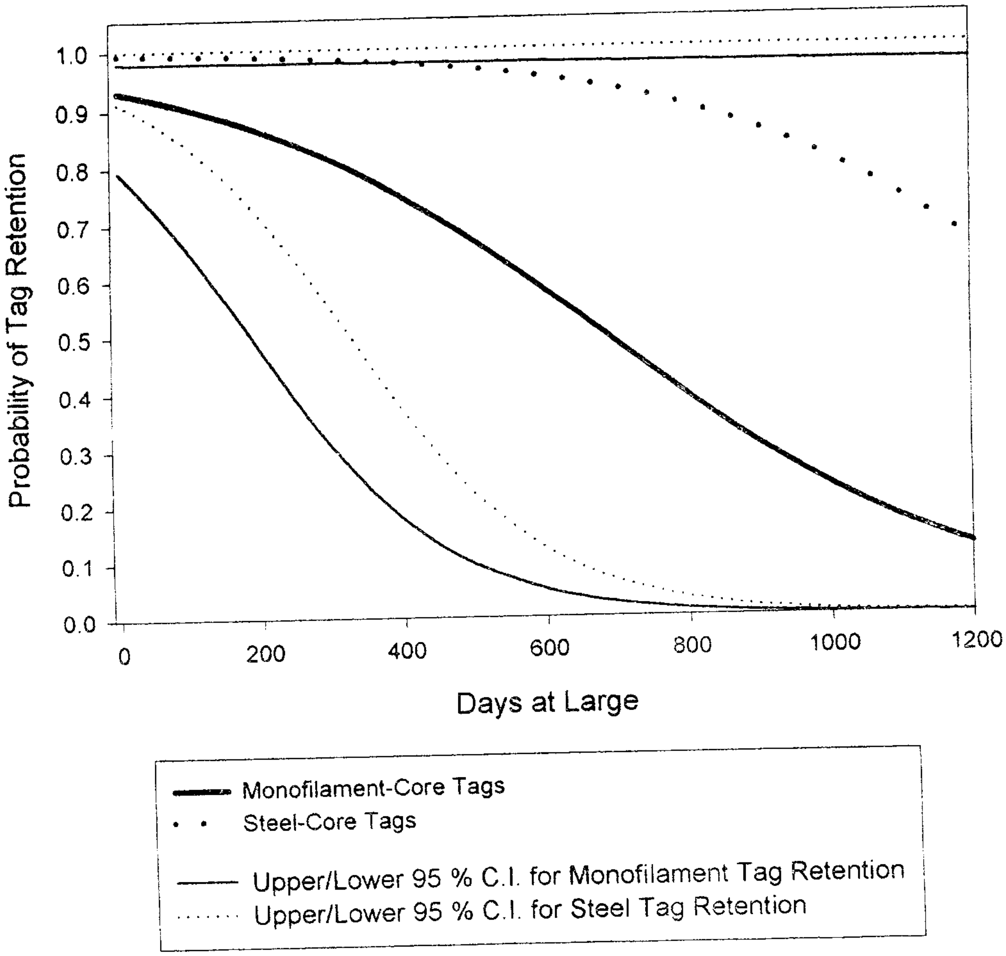

Figure 2.5. Logistic regression of monofilament- and steel-core tag retention over time (with 95 % confidence intervals).

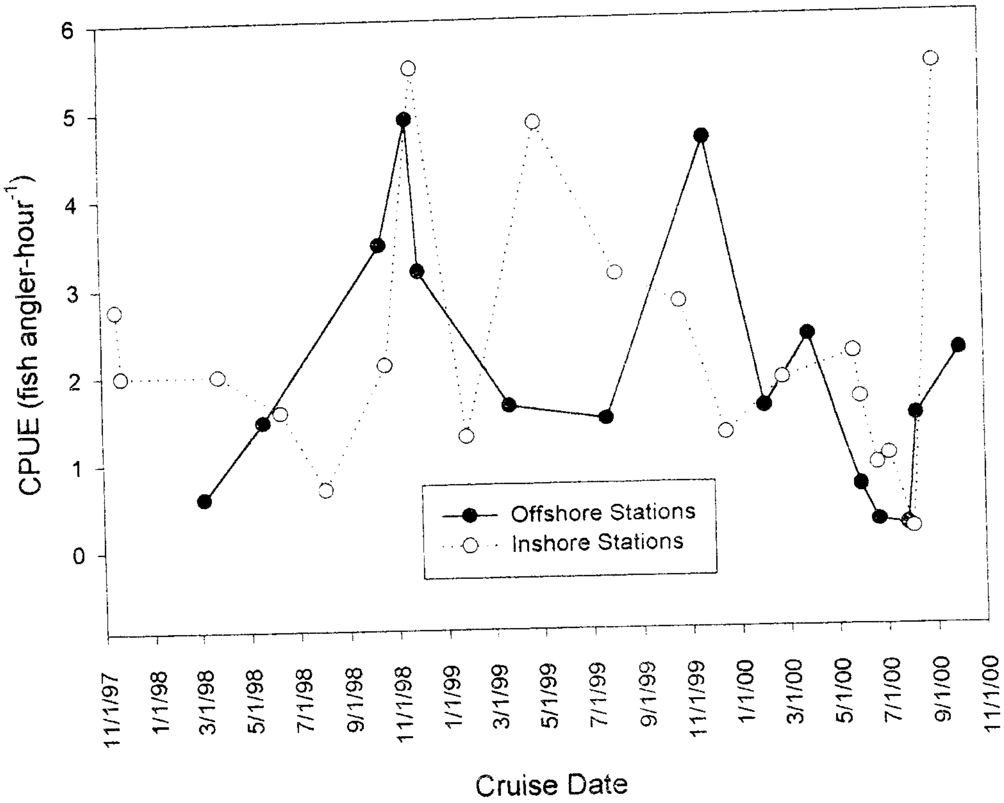

Figure 2.6. Catch-per-unit-effort of gray triggerfish for each cruise during the natural reef study.

± standard error = 1.69 ± 0.496, 1.69 ± 0.625 and 1.62 ± 0.216 for winter, summer and spring respectively) (Fisher's least-significant-difference test, $\alpha = 0.05$)(Figure 2.7).

2.3.6 Site Fidelity and Movement

With the computer program MARK, the maximum likelihood estimates of survival, fidelity, recapture rate, and recovery rate of GTF were determined by analyzing many different models. For the ARS, the model which best described the data was the fully reduced model and included only single estimates of each parameter (i.e., *S*, *p*, *r* and *F*). This model was the most parsimonious with the lowest AIC value of 467.89 and gave estimates (± standard error) of *S*, *p*, *r* and *F* of 0.485 year^{-1} (± 0.159), 0.108 year^{-1} (± 0.027), 0.124 year^{-1} (± 0.035) and 0.226 year^{-1} (± 0.121), respectively. However, even with the data adjusted for overdispersion, with a dispersion parameter estimated to be 2.382, there was still significant lack-of-fit in the model ($\chi^2_{\text{d.f.} = 193} = 459.71496$; $p < 0.0001$).

For the NRS, the parameters of *S*, *p*, *r* and *F* were estimated for both the Inshore Site and the Offshore Site, separately, due to aforementioned sampling protocol, which treated each tagging site separately. For both tagging sites, the model which best described the data was the model that had single estimates of *S* and *F*, but had multiple estimates of both *p* and *r* that related to the live recaptured rate for each cruise and dead recovery rate during the time period between each tagging cruise (i.e., time-related effects). For the Inshore Site, *S* and *F* (± standard error) were estimated as 0.811 year^{-1} (± 0.053) and 0.318 year^{-1} (± 0.052), respectively. This model was the most

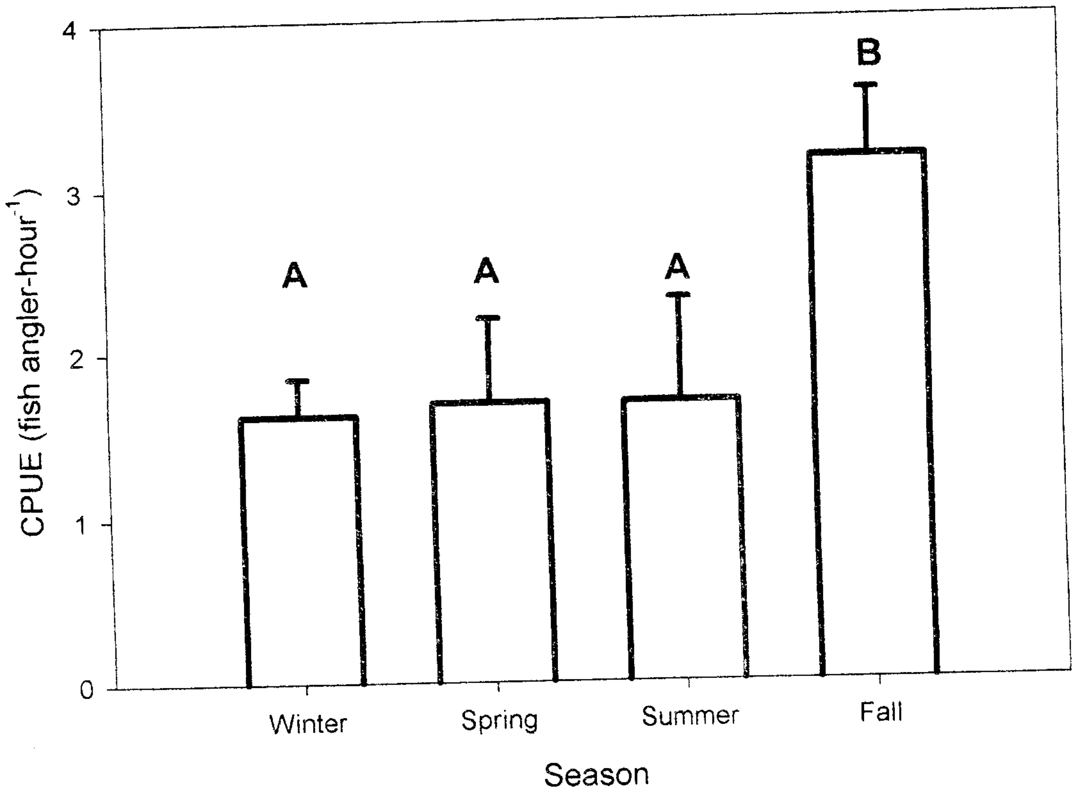

Figure 2.7. Seasonal catch-per-unit-effort of gray triggerfish. Difference in letters represents a significant difference in means among seasons ($\alpha = 0.05$). Error bars represent one standard error.

parsimonious with the lowest AIC value of 1830.33. However, even with the data adjusted for overdispersion, with a dispersion parameter estimated to be 2.468, there was still significant lack-of-fit in the model ($\chi^2_{\text{d.f.} = 719} = 1774.6020; p < 0.0001$). For the Offshore Site, S and F (± standard error) were estimated to be 0.670 year^{-1} (± 0.096) and 0.346 year^{-1} (± 0.081), respectively. This model was the most parsimonious with the lowest AIC value of 697.49. However, even with the data adjusted for overdispersion with a dispersion parameter estimated to be 2.514, there was still significant lack-of-fit in the model ($\chi^2_{\text{d.f.} = 265} = 666.10602; p < 0.0001$). Therefore, in all the above cases, results from models ran with MARK were uninterpretable due to significant lack-of-fit.

Site fidelity for GTF was also estimated using the methods of Patterson (1999) by first estimating the instantaneous rate of decay in recaptures over time (D ± standard error = 1.0010 year^{-1} ± 0.1342). The data with which this model was developed was initially corrected for the number of tagged GTF that were at large, due to the increase in the number of tagged GTF at large over time. Also, the average length of time between tagging trips was 31.3 days. Therefore, the time intervals for model development were set at 30 days for simplicity. Next, the instantaneous rate of decay in recaptures over time was adjusted for tag loss according to the aforementioned logistic regression representing external tag retention over time (D_{adj} ± standard error = 0.9562 year^{-1} ± 0.1335). This difference in the rate of instantaneous decay in recaptures over time due to the instantaneous rate of tag loss (L = 0.0448 year^{-1}) was transformed to give an annual estimate of tag loss (4.38% year^{-1}).

The instantaneous rate of emigration (IE) was then estimated two ways. First, IE was estimated by assuming fishing and natural mortality were equal to the total mortality of GTF off the Alabama coast ($F + M = Z$), which was estimated through catch curve analysis. The instantaneous total mortality rate, as estimated from catch curve analysis of recreationally caught GTF for which age was estimated analyzing annuli in the first dorsal spine (see Chapter 3)($Z \pm$ standard error = 0.8169 year^{-1} ± 0.0751), was subtracted from D_{adj} to provide an estimate of the instantaneous rate of emigration assuming both F and M (i.e., Z) were present ($IE_Z = 0.1393$ year^{-1}). Annual site fidelity assuming both F and M (i.e., Z) were present (Ψ_Z) of GTF was estimated to be 87% year^{-1} (Figure 2.8).

Next, the instantaneous rate of emigration was estimated by assuming only natural mortality (M) was present. Natural mortality was estimated to be 0.4988 year^{-1} using Hoenig's method (1983), where $\ln(M) = 1.44 - 0.982(\ln(\text{maximum age}))$, which in the case of GTF was 8.8 years (see Chapter 3). The natural mortality rate was subtracted from D_{adj} to provide an estimate of the instantaneous rate of emigration assuming only M was present ($IE_M = 0.4574$ year^{-1}). Annual site fidelity (Ψ_M) of GTF was estimated to be 63 % year^{-1} when only M was present.

Finally, site fidelity was also analyzed for GTF tagged during both the ARS and the NRS by plotting the cumulative frequency of recaptures of GTF versus distance from the point of tagging and release to the point of recapture (Figure 2.9). This analysis indicated, regardless of at-large hurricane status, that 66.7 %, 76.2 % and 100 % of recaptured GTF were recaptured at the point of release, within 2 km and within 9 km of the point of release, respectively, during the ARS. Similarly, 73.4 %, 92.3 % and 100 %

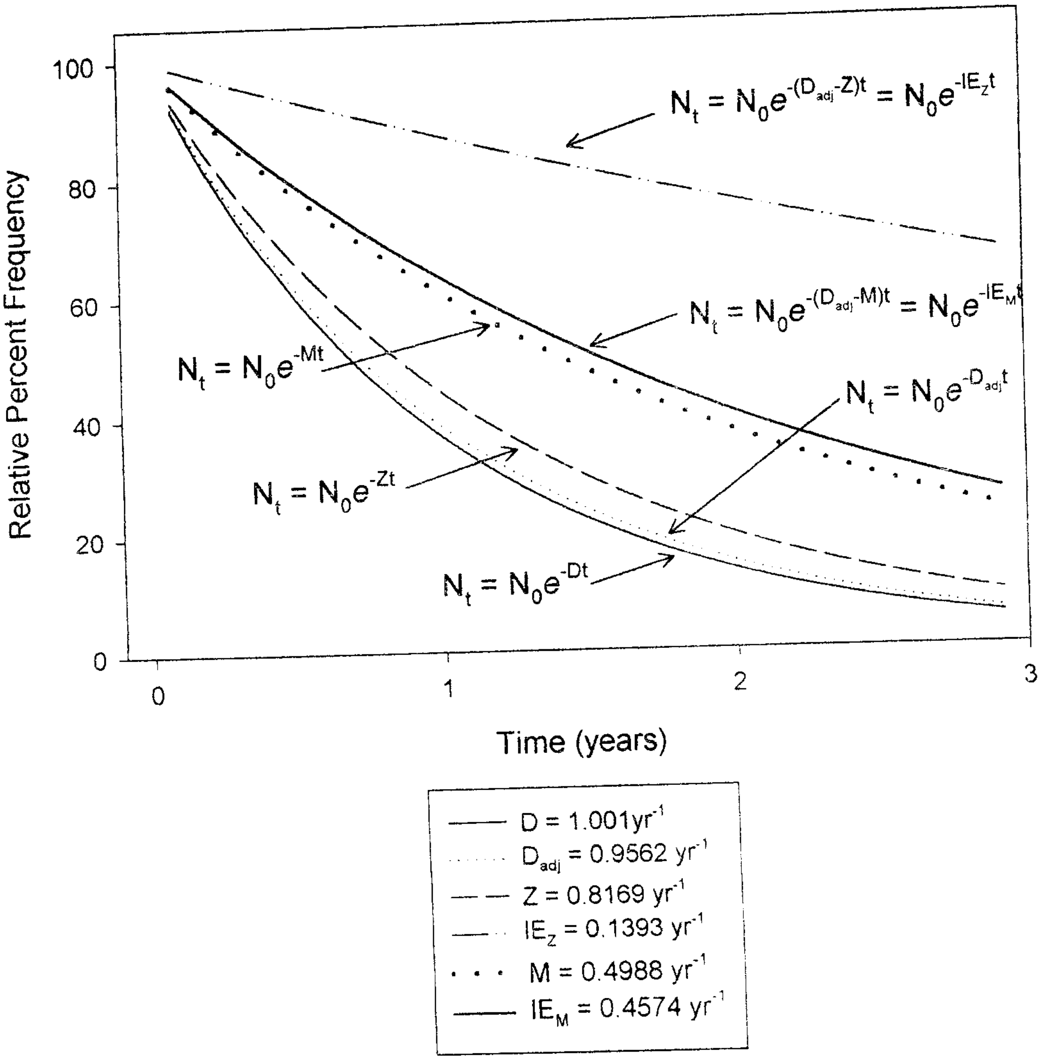

Figure 2.8. Decay curves used in calculating instantaneous emigration rate and, utimately, annual site fidelity.

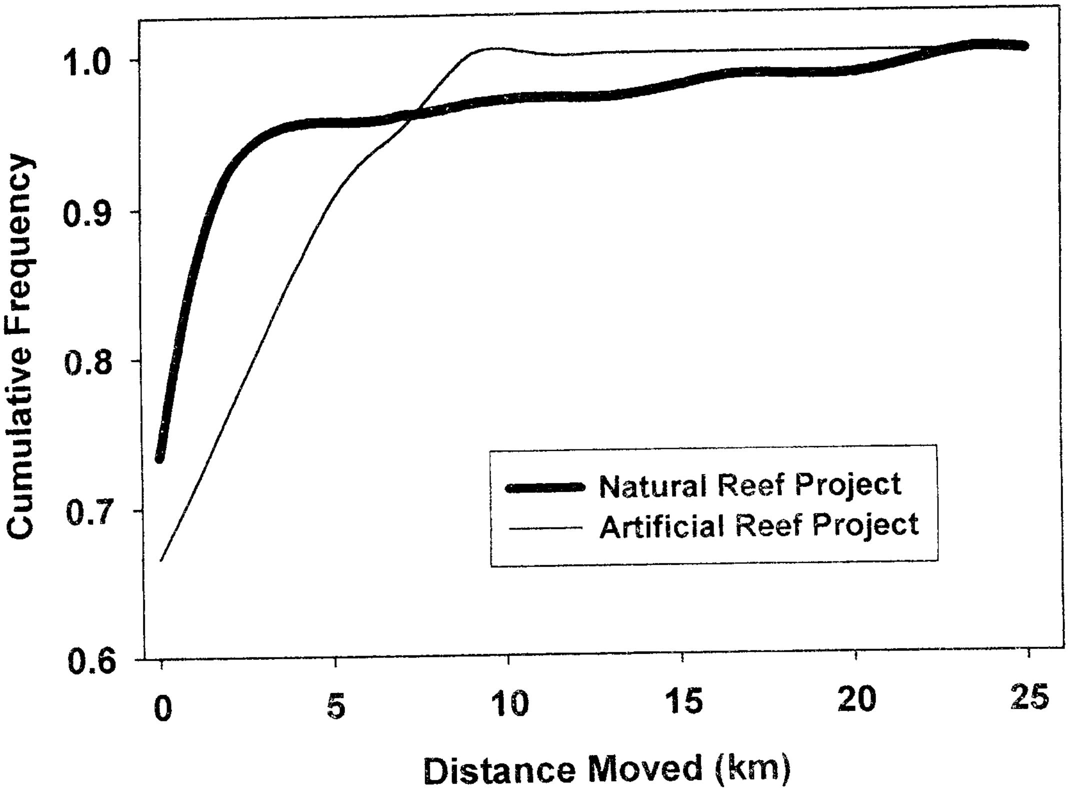

Figure 2.9. Cumulative frequency of gray triggerfish recaptured within a given distance from the point of tagging.

of recaptured GTF were recaptured at the point of release, within 2 km and within 25 km of the point of release, respectively, during the NRS.

The greatest effect on magnitude of movement of GTF was that of tropical cyclones. Friedman's two-way nonparametric ANOVA indicated that the greatest effect on distance moved of GTF was that of tropical cyclones ($p < 0.0001$). It also indicated there was not a significant study effect ($p = 0.3889$). The estimated median distance moved of GTF not at large during tropical cyclones (0 km) was significantly less than for fish at large during tropical cyclones (3.75 km). Likewise, Friedman's two-way nonparametric ANOVA indicated that the greatest effect on velocity of GTF was that of tropical cyclones ($p < 0.0001$). It also indicated there was not a significant study effect ($p = 0.4900$) on velocity. The estimated median velocity of GTF not at large during tropical cyclones (0 m day^{-1}) was significantly less than velocity of GTF at large during tropical cyclones (25 m day^{-1}). In addition, movement of GTF at large during tropical cyclones was generally to the northwest (5.11 km at 133°), and was significantly different from random (Rayleigh Test, $p < 0.05$) (Figure 2.10). Movement of GTF not at large during tropical cyclones was not significantly different from random ($p > 0.10$).

Because of the zero-inflated and overdispersed nature of both the distance moved and velocity data, I used a negative-binomial-type regression approach to model movement of GTF. Also, because there were numerous multiple-recaptures in the data, the regression was run with each individual tagged GTF as a repeated measure. The repeated-measures, negative binomial regression run on data from ARS and NRS combined supported the finding that distance moved by GTF was most affected by

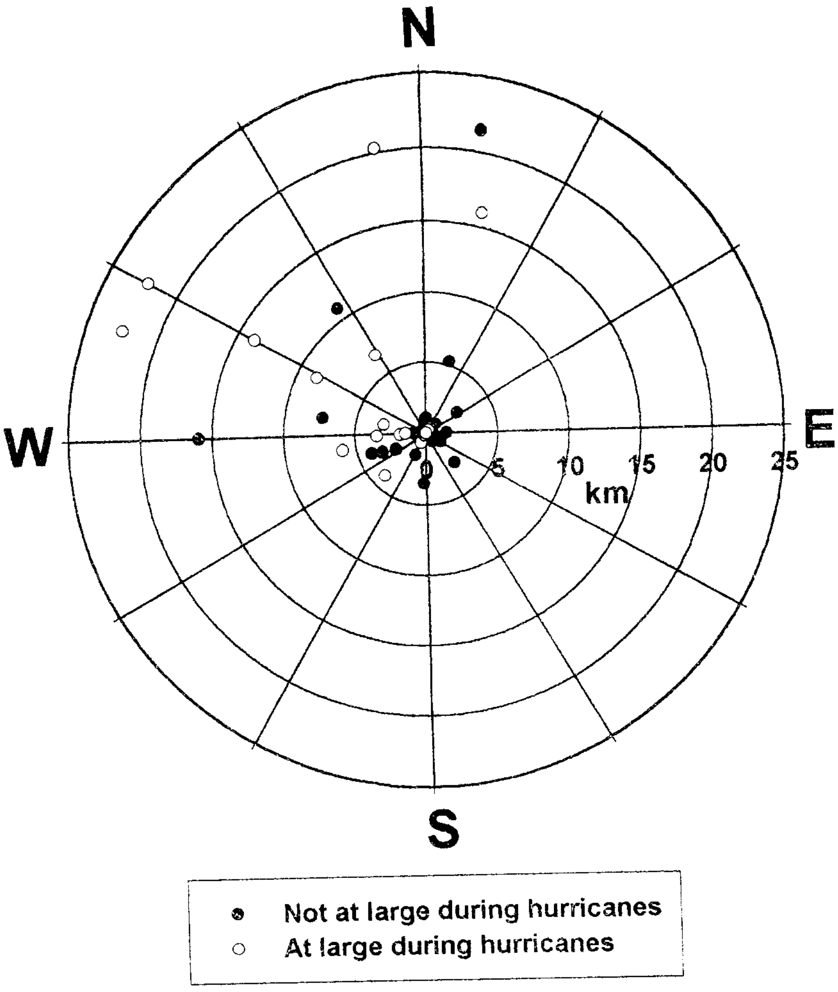

Figure 2.10. Polar graph of gray triggerfish movement during and not during tropical cyclones. Twenty-two fish at large during storms were recaptured at the point of release. One hundred and thirteen fish not at large during storms were recaptured at the point of release.

tropical cyclones ($\chi^2_{\text{d.f.} = 1} = 10.71$; $p = 0.0011$), and had insignificant lack-of-fit ($\chi^2_{\text{d.f.} = 322} = 181.8364$; $p = 1$). The model in which distance moved (m) was the dependent variable and the at-large hurricane status (i.e., GTF at large during tropical cyclones versus GTF not at large during tropical cyclones) was the bivariate independent variable is represented by the following equation:

$$\ln \hat{\mu}_d = e^{8.8769} e^{-2.7413(\text{if no hurricane})} e^{0(\text{if hurricane})},$$

where $\hat{\mu}_d$ is the mean distance moved (m), and the dispersion parameter was estimated to be 27.4899 (95 % confidence interval: 21.9999, 34.3500). This equation can be divided into the following pair of equations, each describing a different at-large hurricane status:

$$\ln \hat{u}_{\text{no hur}} = e^{8.8769} e^{-2.7413}$$

and

$$\ln \hat{\mu}_{\text{hur}} = e^{8.8769},$$

where $\hat{\mu}_{\text{no hur}}$ is the estimated mean distance moved (m) of GTF not at large during hurricanes and $\hat{\mu}_{\text{hur}}$ is the estimated mean distance moved (m) of GTF at large during hurricanes. By solving these equations, overall mean distance (± standard error) moved by GTF at large and not at large during hurricanes was computed to be 7164 m (±323) and 462 m (±34), respectively.

The repeated-measures, negative binomial regression indicated that the effect of at-large hurricane status on velocity of GTF also was significant ($\chi^2_{\text{d.f.} = 1} = 7.15$; $p = 0.0075$), but the model had significant lack-of-fit ($\chi^2_{\text{d.f.} = 319} = 837.9013$; $p < 0.0001$). However, the model, in which velocity (m day^{-1}) was the dependent variable and the year of recapture was the independent variable also was significant ($\chi^2_{\text{d.f.} = 5} = 36.08$; $p < 0.0001$). The model had insignificant lack-of-fit ($\chi^2_{\text{d.f.} = 317} = 313.3014$; $p = 0.5481$) and was represented by the following equation:

$$\ln \hat{\mu}_v = e^{1.2685} e^{2.7675(\text{if } 1995)} e^{0.4132(\text{if } 1996)} e^{-0.8230(\text{if } 1997)} e^{2.2502(\text{if } 1998)} e^{-0.9294(\text{if } 1999)} e^{0(\text{if } 2000)},$$

where $\hat{\mu}_v$ is the estimated mean velocity (m day^{-1}), and the dispersion parameter was estimated to be 12.6685 (95 % confidence interval: 9.9089, 16.1967) and mean velocity of GTF recaptured during the year 2000 was used as a reference. Individual year parameters for recapture years 1995 and 1998 were the only significant recapture year parameters ($\chi^2_{\text{d.f.} = 1} = 5.62$; $p = 0.0178$ and $\chi^2_{\text{d.f.} = 1} = 16.54$; $p < 0.0001$, respectively). All other year parameters were not significantly different from the reference year 2000. Therefore, the above regression model can be divided into three individual models describing velocity of GTF recaptured in 1995, 1998, which were years in which major hurricanes passed over the tagging stations or all other years in the study in which there were no hurricane effects:

$$\ln \hat{\mu}_{v1995} = e^{1.2685} e^{2.7675},$$

$$\ln \hat{\mu}_{v1998} = e^{1.2685} e^{2.2502}$$

and

$$\ln \hat{\mu}_{v1996,1997,1999,2000} = e^{1.2685} e^{0},$$

where $\hat{\mu}_{v\ 1995}$ is the estimated mean velocity of GTF recaptured in 1995, $\hat{\mu}_{v\ 1998}$ is the estimated mean velocity of GTF recaptured in 1998 and $\hat{\mu}_{v\ 1996,1997,1999,2000}$ is the estimated mean velocity of GTF recaptured in all other years of study. By solving these equations, estimated mean velocity (± standard error) of GTF recaptured during 1995, 1998, and all other years of study was computed to be 57 m day^{-1} (± 4.37), 34 m day^{-1} (± 2.36) and 4 m day^{-1} (± 1.35), respectively.

2.4 Discussion

2.4.1 The Present Study

To my knowledge these studies (i.e. ARS and NRS) are the most comprehensive studies ever conducted concerning movement patterns and site fidelity of GTF. These tagging studies were sufficient in scope, and had a large enough number of tags recaptured, especially the NRS, with which to accomplish the goals previously outlined.

2.4.2 Tagging Mortality

Tagging had little apparent effect on acute mortality of GTF. Acute mortality rates in this study were low compared to other species. For example, Patterson (1999) indicated that acute mortality rate of red snapper (*Lutjanus campechanus*), which inhabits similar habitats as adult GTF, when tagged with similar internal anchor tags was 15 %. Also, Wallin et al. (1997) indicated that the mortality rate of common snook (*Centropomus undecimalis*) tagged with internal anchor tags was 8.1 % after 30 days of observation; nearly all fish had inflammation or a proliferation of epithelial cells at the tag insertion site, and a few individuals had anchors inserted through the peritoneum and into the swim bladder. Moreover, reported tagging mortality rates of striped bass (*Morone saxatilis*) have ranged from 3 to 67 % after tagging and release, due to the type of anchor tag, the handling of the fish while tagging and the amount of internal injury caused by tagging (Bettoli and Osborne, 1998; Henderson-Arzapalo et al., 1999).

Out of the 19 GTF released in a condition other than condition-1, two (11 %) were recaptured and released again in condition-1, indicating that some proportion of the GTF that were assumed to have died as a result of the tagging process actually survived. Also, a GTF tagged on November 19, 1997 was recaptured on a tagging cruise six days later, and the incision wound around the shaft of the tag was completely healed. However, the logistic regression, which modeled the probability of occurrence of acute mortality, indicated that acute mortality due to tagging increased slightly with GTF size. Overall, my findings suggest that acute tagging mortality was low, although I was unable to observe GTF after the moment of release and was thus unable to estimate longer-term mortality rate.

2.4.3 Tag Retention

Tag retention for GTF decreased both as a function of tag type and time-at-large. Toward this end, it was apparent that the tags became fouled with time. Fouling of the external portion of the tag by barnacles, bryozoans and algae may increase both drag and tag loss, make the tag more visible to other fish that might attempt to consume the tag, make the GTF more vulnerable to predation, or make the tag unrecognizable as such (Dunning et al., 1987; Scott et al., 1990; Nielsen, 1992; Wallin et al., 1997; Bettoli and Osborne, 1998; Buzby and Deegan, 1999; Henderson-Arzapalo et al., 1999; Patterson, 1999). Ventral placement of tags may have also made the tags less visible to fishers (Nielsen, 1992; Patterson, 1999).

Monofilament-core tags exhibited higher loss rates than did steel-core tags, presumably due to increased durability of steel-core tags. Henderson-Arzapalo et al. (1999) recommended that while monofilament-core tags offer increased flexibility and reduction in drag, they should only be used in short-term studies due to increased loss relative to other tag types.

The consequences of tag loss may be important to my results, especially during the early parts of this study when monofilament tags were used. If tagged GTF were not recognized as such, under reporting by fishers could have negatively biased estimates of likelihood and magnitude of movement (Nielsen, 1992; Henderson-Arzapalo et al., 1999; Patterson, 1999).

2.4.4 Probability of Capture

I assumed that tagged and untagged fish have the same probability of being captured by hook and line, and that tagging did not affect the behavior of tagged GTF. Although no data are available to permit a statistical test of this assumption, 21.9% of GTF tagged and released were recaptured at least once. This recovery rate is much higher than those reported for other species. For example, Patterson (1999) reported a recovery rate of 14.6% for red snapper tagged off Alabama. In addition, Stevens and Sulak (In review) reported recovery rates of tagged red drum (*Sciaenops ocellatus*), spotted seatrout (*Cynoscion nebulosus*), black drum (*Pogonias cromis*), and common snook (*Centropomis undecimalis*) to be 3.1, 0.7, 2.6, and 16.4%, respectively. Moreover, Fowler and Stobo (1999) reported recapture rates for groundfish of 20.7 (cod, *Gadus* *morhua*), 3.5 (haddock, *Melanogrammus aegelfinus*), 6.4 (pollock, *Pollachius* spp.), and 9.5% (plaice, *Pleuronectes platessa*). However, Beaumariage (1964) found that 36.9% of GTF that were tagged and released in the northeastern Gulf were recaptured, which may indicate a negative effect of tagging on POC. In addition to a high recovery rate, 20.7% of all GTF recaptured during the NRS were recaptured multiple times, including one individual that was recaptured five times. Therefore, I concluded that tagging did not decrease the probability of capture.

2.4.5 Tagging Effects on Growth

The assumption of that tagging had no effect on growth was not met. The tagging process negatively affected growth of GTF. The growth rate of tagged fish was significantly less than that of fish aged through analysis of the first dorsal spine, and this issue is discussed in more detail in Chapter 3.

Differences in growth due to tagging could bias estimates of movement. If distance moved and/or velocity is a function of size, then estimates of movement of for tagged GTF would differ from the untagged population. However, because no significant relationship was found between movement and size, I reason that estimates of movement through tagged fish may represent movement in the untagged portion of the population off the Alabama coast.

GTF tagged during the ARS were found to be significantly larger in FL than in the NRS. This result may be attributable to differences in hook sizes between the ARS and the NRS. After interviewing a number of local, reputable fishers, it was suggested that the larger hook size (3/0) and the resulting larger bait placed on that hook during the ARS may have biased the size of GTF at capture toward larger GTF. However, it was also suggested that the smaller hooks (size 1/0) and smaller bait used during the NRS probably did not reduce the catch of larger GTF. Therefore, the difference in size of GTF tagged above artificial versus natural reefs may be biologically significant, and resulted from the availability of larger GTF inhabiting artificial reefs. In addition, mortality may have been higher on fish sampled during the NRS due to public knowledge of Southeast Banks in which is located the Inshore Tagging Site (see Chapter 3). This may have led to the reduction in larger fish on tagging sites of the NRS.

2.4.6 Reporting of Recaptures by Fishers

The assumption that all recaptured GTF were reported was not statistically tested. However, this may be the most important assumption concerning bias in estimates of distance moved, velocity and site fidelity. All recaptures made on tagging cruises were assumed to be recognized and recorded, but reporting rate of fishers was not estimated for this study. An underreporting of recaptures by fishers results in an under estimation of distance moved and velocity, and an over estimation of site fidelity of GTF. Results from other studies suggest this problem is real. The reporting rate of spotted seatrout tagged in Alabama waters was estimated to be around 50 % (James J. Duffy, per. comm.[1]). Similarly, the reporting rate of sciaenids off Texas was estimated to be 29 %, with low reporting rate attributable to lack of recognition of tagged fish (Matlock et al.,

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[1] Alabama Department of Conservation/Marine Resources Division, Dauphin Island, Alabama

1981; Green et al., 1990). Therefore, tag loss of GTF may have likewise contributed to underreporting of recaptures.

Patterson (1999) speculated that reporting rates of red snapper were probably low due to resentment by fishers of increases in red snapper regulations. Recent management actions aimed at GTF may have contributed to underreporting in a similar way. For example, the Gulf of Mexico Fishery Management Council recently imposed a 12-inch total length minimum size limit for GTF and GTF are part of the aggregate reef fish bag limit in Gulf waters. Thus, fishers may fear that information provided by tags may lead to a subsequent increase in regulations for GTF and, therefore, hesitate to report them.

2.4.7 CPUE

Higher estimates of CPUE of GTF observed in the fall were initially believed to result from seasonal stratification of the water column above tagging stations, as was the case with red snapper catch-per-tagging-site (CPTS) in the same area by Patterson (1999), who reported a positive relationship between dissolved oxygen concentration and CPTS. Due to seasonal heating and subsequent stratification of the water column in the northern Gulf, oxygen concentrations may become depleted from lack of water column turnover during summer months (Patterson, 1999). Dissolved oxygen levels increase during the fall as the water column overturns due to storms (Patterson, 1999).

I speculate that the increase in CPUE of GTF in the fall is associated with the spawning cycle of GTF. Spawning of GTF off Alabama peaks in June and July and then decreases in August, which then is followed by an increase in CPUE (see Chapter 3).

The increase in CPUE may result from relaxation of territoriality of GTF following spawning (see Chapter 3). However, if the fall-increase in CPUE is strictly related to the spawning cycle, CPUE should only be low during summer months. Therefore, increased CPUE during the fall also may result, in part, from an increase in aggression of GTF due to a decrease in prey abundance, following the drop in temperature during fall mixing of the water column, as suggested for red snapper by Patterson (1999).

2.4.8 Site Fidelity and Movement

Estimates of site fidelity of GTF for both the ARS and the NRS obtained using the software package MARK were found to be uninterpretable due to lack-of-fit. The joint encounters model (Burnham, 1993) depends on data from both my recaptures over tagging sites and recaptures made by fishers, and lack-of-fit may have been caused by a number of violations of assumptions of this model. First, it is assumed that fishing pressure is the same on both the tagging stations and other areas around the tagging stations. Because I attempted to tag GTF through the year, regardless of season, there may have been differences in fishing pressure between tagging stations and the surrounding area, with fewer recreational fishers participating in the fishery during winter months. Also, if fishing pressure was the same, but recreational fishers did not report tags, recovery rate, *r*, would be biased low. Moreover, with a low number of tag recoveries, maximum likelihood estimates of recovery rate would tend toward 0 or 1, increasing model lack-of-fit due to the small sample size of recoveries.

Another assumption of the joint encounter model, which is essential in estimating site fidelity, is the assumption that all recoveries made by fishers were made at sites other than the tagging stations. Several fishers indicated that they made recaptures of GTF in close proximity to tagging stations. This could have affected estimation of site fidelity by biasing it low, and/or increased model lack-of-fit. Finally, tag loss may have biased estimates of survival high, which would in turn bias estimates of site fidelity low.

When decline in the number of recaptures over time was modeled for GTF during the NRS, assuming either no fishing mortality of GTF tagged over tagging stations or that fishing mortality occurred, resulting estimates of site fidelity were relatively high. The estimate of Ψ_M (no fishing) was a little more than half that of the estimate of Ψ_Z (with fishing). If F occurred, or if M was higher than estimated by using Hoenig's method, then the estimate of Ψ_M would be higher. Because some fishers indicated capturing GTF in close proximity of tagging stations, the actual value of annual site fidelity probably lies somewhere between Ψ_M and Ψ_Z (i.e. between 63 % and 87 %, respectively). Finally, because of the large number of recaptures during the NRS, I reasoned that this data would be sufficient to provide reliable estimates of annual site fidelity without the possible increase in variation in the decay models resulting from the addition of ARS data.

Finally, site fidelity of GTF was addressed by analyzing the cumulative frequency distribution of GTF recaptured within a given distance from the initial point of tagging and release, during both the ARS and the NRS. Regardless of study or at-large hurricane status, GTF exhibited high site fidelity with the majority of fish being recaptured within only a few kilometers of the site of tagging.

Territorialism is reported as being predominant among balistids, and there have been many studies on balistid social systems. Territoriality in triggerfishes has been described by Fricke (1980; *Odonus niger* and *Pseudobalites fuscus*), Nellis (1980; *Canthidermis sufflamen*), Thresher (1984; *Sufflamen verres*), Gladstone (1994; *Pseudobalites flavimarginatus*), Ishihara and Kuwamura (1996; *Sufflamen chrysopterus*), and Kuwamura (1997; *Rhinecanthus aculeatus*). In all cases both male and female triggerfishes are territorial, especially during their corresponding spawning seasons.

Although no formal study exists of GTF territoriality, they anecdotally have been reported as such by many scuba divers and spear fishers, who reported being "attacked" as they entered the "territory" of a GTF. Also, GTF have been observed on video as being territorial in nature, defending an area (male GTF) or defending a nest (female GTF) with a haremic-type social structure (Andrew Strelcheck, per. comm.[2]; Kevin Rademacher, per. comm.[3]). The possible territorial nature of GTF may contribute to high apparent site fidelity.

The most significant effect on both distance moved and velocity of GTF in both the ARS and the NRS was that of tropical cyclones. Both the nonparametric tests and the negative binomial regressions developed for combined ARS and NRS data agree in the effects of hurricanes on distance moved and velocity. Namely, GTF exhibit an increase in movement during tropical cyclones, with tendencies toward vectored movement

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[2] University of South Alabama. Department of Marine Sciences, Mobile, Alabama

during tropical storms to the west-northwest. For fish not at large during hurricanes, movement was random in nature. The Hugh Swingle General Reef Permit Area is located to the west and north of the tagging stations occupied during the NRS, and during the ARS the stations were actually located within the Hugh Swingle General Reef Permit Area. GTF may have moved toward this area if the low relief natural reefs they occupied were altered or covered by sediment during tropical cyclones. However, of the few GTF tagged above the two stations within the offshore site "lost" during Hurricane Georges, none were subsequently recaptured. Estimates also indicated that GTF moved little when not affected by tropical cyclones, reflecting, perhaps, only small-scale movement between other reefs nearby the tagging stations.

2.4.9 Utility of Marine Reserves

High site fidelity is paramount for management of GTF stock(s) in the Gulf, because adults may be prone to localized differences in population demographics (Gulland 1983; Jones, 1991, for review). Also, fishes that exhibit high site fidelity also may be highly susceptible to localized overexploitation as fishing pressure increases (Bohnsack, 1989). Yet, despite high site fidelity as adults, GTF mature at an early age, and have larvae and juvenile life history stages that are pelagic through the first year of life, permitting dispersal of propagules out of the no-take areas (Harper and McClellan, 1997)(see Chapters 3 and 4). Thus, I reason that management of species with similar

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[3] National Marine Fisheries Service, Pascagoula, Mississippi

movement patterns and life history characteristics as GTF may be facilitated by the implementation of no-take marine reserves.

CHAPTER 3: AGE, GROWTH, REPRODUCTION AND MORTALITY OF GRAY TRIGGERFISH

3.1 Introduction

3.1.1 Age and Growth

There have been relatively few age and growth studies of gray triggerfish and results from these studies have differed. GTF growth rate based upon annuli of the first dorsal spine was estimated by Ofori-Danson (1989) off the coast of Ghana in western Africa following a tremendous increase in standing stock biomass there (from ~ 10 kg ha^{-1} in 1968 to ~ 3000 kg ha^{-1} in 1977; Pease, 1984). Ofori-Danson's estimates of the von Bertalanffy parameters were $L_\infty = 408$ mm and $K = 0.43$ $year^{-1}$. Johnson and Saloman (1984) conducted a study by sampling the hook and line fishery for GTF off the coast of Panama City, Florida. They used methods similar to those reported by Ofori-Danson to estimate size-at-age in the northeastern Gulf, and reported that fish reached a larger maximum length ($L_\infty = 466.0$ mm) but grew more slowly ($K = 0.382$ $year^{-1}$) than GTF off the West African coast. Wilson et al. (1995) and Hood and Johnson (1997) also studied GTF growth in the northern and eastern Gulf, respectively. Wilson et al. (1995) found that estimated ages of GTF landed by the commercial fishery in Louisiana ranged from 1 to 11 years, with the majority of the fish sampled being two to six years old. The mean age of females (3.9 years) was slightly, but not significantly, higher than that of males (3.3 years). Also, based on length-frequency data, GTF were reported to recruit to the commercial fishery at age 2, with a decline in age-class strength after age 3. Hood and Johnson (1997) studied the age and growth of GTF from the eastern Gulf and found that von Bertalanffy growth model (parameters: females, $L_{\infty} = 421$ mm, K = 0.329 year^{-1}; males, $L_{\infty} = 664$ mm, K = 0.156 year^{-1}; combined sexes, $L_{\infty} = 645$ mm, K = 0.152 year^{-1}) tended to underestimate growth when compared to empirical estimates of sizes-at-age. Also, they reported rapid growth in young GTF with an average length of 276 mm FL for one-year-old specimens. In addition, Escorriola (1991) sampled both the recreational and the commercial fisheries off the Carolinas on the U.S. east coast and found estimates of growth parameters that differed from those both of Johnson and Saloman (1984) and Hood and Johnson (1997). Escorriola (1991) also used methods similar to Ofori-Danson, and further suggested that GTF have a larger maximum length ($L_{\infty} = 571.0$ mm) and a slower approach to that maximum length (K = 0.199 year^{-1}) than fish off the coast of northwest Florida in the Gulf studied by Johnson and Saloman (1984). All of these differences could be due to environmental effects on growth rate, or the fish could be members of different stocks.

3.1.2 Reproduction

A study of the reproductive ecology of GTF was performed on specimens from Ghana in West Africa (Ofori-Danson, 1990). Ofori-Danson defined the breeding season as October to December by assigning each gonad collected to a specific maturity level based upon five gonad maturity categories. Peak spawning occurred in the warmer months, which in Ghana are November and December. First time spawners were 133 - 157 mm in FL, 50.0 - 70.5 g, and one year old. Fecundity (F) was correlated with fork length (FL) and was described by the linear regression log F = 1.176 + 1.642 log FL.

In the Gulf of Mexico, there have been a number of studies concerning the reproductive biology of GTF. Dooley (1972) estimated the spawning season to be from July to October in the Gulf based upon the presence of small, recently spawned GTF in samples. Wilson et al. (1995) reported that ovarian histology indicated that GTF captured off Louisiana are iteroparous and spawn during late spring and summer (April through August), with a peak in the gonosomatic index (GSI) in June for both male and female fish.

Hood and Johnson (1997) similarly reported iteroparity in GTF and suggested that ovarian histology indicated that fish captured off west Florida spawn during summer and early fall (June through September) with a peak in the GSI in August for female fish, and in September for male fish. Mature females with ovaries containing vitellogenic oocytes were first observed in June, and were present through September. Spent females were observed from September through October. From October to March most fish had developing gonads that contained primary growth oocytes and some atretic bodies. Finally, maturing gonads first appeared in April and were present through August in fish from the eastern Gulf (Hood and Johnson, 1997).

Hood and Johnson (1997) also report that 87.5% of the female fish were sexually mature by age 1, and no immature males were observed. The smallest mature male observed was 110 mm FL (age 0). Batch fecundities in fish from the eastern Gulf ranged from 213,912 to 1,172,854 oocytes from fish ranging from 267 to 388 mm FL, and relative batch fecundity had a mean of 13,809 oocytes per gram ovary and ranged from 6,318 to 24,188 oocytes per gram (Hood and Johnson, 1997).

3.1.3 Mortality

Jones (1991) reviewed patterns of mortality in reef fishes and reported that data on mortality are difficult to obtain, and may differ widely among locations. Jones (1986) provided estimates of mortality for juvenile damselfishes *Pomacentrus wardi* and *P. amboinensis*, and mortality rates were greater on shallow reefs than deeper reefs in the same reef area. On a larger scale, mortality rates of red snapper, *Lutjanus campechanus*, tagged above the same nine artificial reefs as used in the ARS (see Chapter 2) differed greatly (i.e. instantaneous fishing mortality ranged from 0.047 to 0.620 year^{-1}) (Watterson, 1998). Watterson (1998) also estimated instantaneous fishing mortality of red snapper inhabiting publicly known reefs off the coast of Alabama and Florida to be much higher (i.e. 1.12 year^{-1}) than the more private artificial reefs off the Alabama coast during the ARS.

Hood and Johnson (1997) estimated instantaneous total mortality of recreationally and commercially caught GTF off the west Florida coast to be 0.836 and 0.825 year^{-1}, respectively. Instantaneous total mortality for GTF off the coast of Panama City Beach, Florida was estimated to be 0.67 year^{-1} (Johnson and Saloman, 1984).

3.1.4 Fin Rays and Spines

In fisheries, age and growth information provides a means by which to assess the environmental and endogenous conditions affecting the well-being of a fish (DeVries and

Frie, 1996). Estimates of age and growthrate are useful in evaluating prey availability, habitat suitability, or the affect of specific management actions on target species. Although age and growth are related and typically used in conjunction in fisheries science, they describe two different aspects of fish biology. Growth can be defined as the change in body size (length, weight, etc.) between specific points in time. Age is a cumulative, quantitative description of how long a fish has lived (DeVries and Frie, 1996).

There are many ways to determine the age of a fish. First, age can be determined by direct observation. This is the most accurate way of age determination, but it can be very costly and labor-intensive. For these reasons, it is usually only used in fisheries as a validation tool, and generally in an aquaculture setting (DeVries and Frie, 1996). Second, length-frequency analysis can be used to estimate the age of fish. This procedure of plotting the frequency of individuals as a function of length may appear simple. However, the variation of the length of individuals within each age class as fish grow older generally increases relative to differences between age groups, blurring differences in lengths among ages. This is just one of many reasons that makes this technique more difficult than it initially appears (DeVries and Frie, 1996).

Finally, the analysis of hard parts in fish can be used to estimate age. In recent years, this technique is the most frequently used method for aging fish. Hard parts that have been used in estimating fish age are scales, otoliths, fin spines and rays, cleithra, vertebrae, opercal bones, and dentary bones. The use of hard parts to estimate age is based on the presence of countable, annual "marks" or "rings" radiating from the center of the hard part. The formation of these rings is related to times of slow and fast growth, usually fall-winter and spring-summer, respectively (Casselman, 1983; DeVries and Frie, 1996).

The methods of using fin rays and spines are very similar, and offer several advantages over otoliths and other bony structures such as scales. Fin rays and spines can be removed and processed more easily than some scales and most otoliths (Casselman, 1983). When using rays or spines, it is not always necessary to kill the fish or significantly mutilate the carcass when sampling, which may reduce the market value of a commercially harvested species (Casselman, 1983). The method of using soft rays is especially useful because, like scales, rays can be removed from many species of fish at the time of capture and compared with the corresponding structure at the time of recapture (Casselman, 1983). Also, because annuli on scales result from a different process than those on bones, there is no reason to assume that annuli on both structures will be equally prominent throughout the life of the fish. Annuli in fin rays and spines can remain prominent in older fish when scale annuli are not identifiable (Beamish, 1981). Finally, fin rays can be used to assess the credibility of ages assigned by other methods (Beamish, 1981).

Determining age from fin spines and rays requires that they be sectioned near the base in an exact transverse plane to assure that all annuli present are exposed. The exact location of the section depends on the species. A dremmel saw, fine jeweler's saw, or some other thin-sectioning device can be used to section spines and rays (DeVries and Frie, 1996). The thickness of the section must be adjusted to assure that it is thin enough for annuli to be visible. Sections may require soaking in solutions containing acetic acid or bleach to remove unwanted tissue from the spine or ray surface to make observation and quantification easier (DeVries and Frie, 1996). Sections are best viewed under a microscope, although they can be projected with a microfiche projector (similar to scales, DeVries and Frie, 1996), or viewed using video imaging systems inclusive of microscopes.

Although fin spines and rays are useful in the estimation of age and growth in fish, there are disadvantages. In older fish the core can undergo resorption and become more vascularized, obscuring and even eliminating the first few annuli (Casselman, 1983). This can result in underestimation of age, as has been reported for several oceanic pelagic fishes: bluefin tuna, *Thunnus thynnus* (Compeán-Jimenez and Bard, 1983); albacore, *T. alalunga* (González-Garcés and Fariña-Perez, 1983); Atlantic skipjack tuna, *Euthynnus pelamis* (Antoine et al., 1983); little tunny, *E. alletteratus* (Cayre and Diouf, 1983; Johnson, 1983); sailfish, *Istiophorus platypterus* (Hedgepeth and Jolly, 1983; Prince et al., 1986); blue marlin, *Makaira nigricans* (Hill et al., 1989); and swordfish, *Xiphias gladius* (Berkeley and Houde, 1983; Ehrhardt, 1992; Tserpes and Tsimenides, 1995). In addition, fin spines and rays in older fish are similar to scales because, like growth bands on the edge of scales, the distal annuli may be so close together that they appear to coalesce, making optical resolution and correct age assessment difficult or even impossible (Casselman, 1983). Finally, fin rays and spines can possess pseudoannuli that are similar to annuli, but which are associated with checks and zones that are somewhat incomplete and irregular, and are usually found only in one part of the structure, and often not in all structures. Although they are sometimes prominent, they are not associated with the growth zone that forms during the principal annual cessation or reduction in growth rate that produces the annulus (Casselman, 1983). This problem can be correctly addressed with the validation of the hard part.

Whenever age and growth parameters are estimated from hard parts, it is necessary to both verify and validate the use of that hard part. Verification can be accomplished when annuli are counted by more than one scientist, or when the same scientist counts annuli in each hard part more than once. This can provide some measurement of the precision of age estimation when using hard parts (Casselman, 1983; DeVries and Frie, 1996). Validation refers to the accuracy of age estimation when using hard parts. Usually some type of marginal increment analysis (MIA) and/or comparison between length- and age-frequencies is used to validate the use of a specific hard part by confirming that the rings are in fact produced annually (Wilson et al., 1983).

Fin spines and rays have been used in many studies to estimate age and growth of fish. Table 3.1 lists the species for which age estimation was performed using fin spines or rays. This table includes how this method of age estimation has been applied, and whether the estimates were verified or validated.

While otoliths are still the method of choice in aging fish (DeVries and Frie, 1996), some species have small, hard to read otoliths that inhibit age estimation. This is true for GTF, whose otoliths are small and fragile. During preliminary examination of hard parts of GTF, they were found not to contain annual rings, or rings of any type with which to estimate age. Therefore, for this study I follow the methods of Johnson and Saloman (1984), Ofori-Danson (1989), Wilson et al. (1995) and Hood and Johnson (1997), and use the first dorsal spine of GTF in age estimation.

Table 3.1. Review table on the use of fin rays and spines as age estimators. Some species, which were not included in Table 1, primarily utilized fin rays as aging structures, include Pacific salmon, *Oncorhynchus* spp. (Bilton and Jenkinson 1969); white sucker, *Catostomus commersoni* (Beamish and Harvey 1969); lingcod, *Ophiodon elongatus* (Beamish and Chilton 1977); walleye pollock, *Theragra chalcogramma* (Beamish 1981); and Pacific cod, *Gadus macrocephalus* (Beamish 1981).

Species	Application	Verification / Validation	Comments	Literature Cited
dogfish shark, *Squalus acathias*	Age estimation in *S. acathias* is made possible by a semi-regular series of dark bands of pigment associated with ridges in the spine enamel of the second dorsal spine, which may be indicative of annual changes in growth.	In the study preformed by Ketchen (1975) of 410 readable spines, there was complete agreement in the reading of only 22%. No firm criteria was established for recognition and rejection of false checks or acceptance of those thought to be genuinely annual, due to the lack of some type of validation, such as MIA.	The fact that many spines showed irregular spacing between supposed winter checks (annuli) was ignored, and it was assumed that all complete bands were annuli. The enamel on some of the larger dogfish were severely worn and annuli destroyed, which could have led to an underestimation of age.	Ketchen 1975
lake sturgeon, *Acipenser fulvescens* white sturgeon, *A. trans-montanus*	In each study, age and growth information was estimated from microscopically examined annuli exposed on transverse sections of first pectoral fin rays.	Neither study discussed precision of age estimates, but validity was discussed in Probst and Cooper (1954) and assumed in Semakula and Larkin (1968).	Probst and Cooper (1954) compared length- and age-frequencies distributions of sturgeon caught in several Wisconsin lakes and found a strong correlation, which indicates that the age estimates in this study are accurate.	Probst and Cooper 1954 Semakula and Larkin 1968
marine catfish, *Arius heudeloti, A. parkii, A. latis-cutatus*	Age and growth information was estimated for each species by microscopically examining annuli exposed on transverse sections of the first dorsal spines.	For verification counts of annuli were made by two investigators. The marginal increment ratio of individual fish was plotted on a monthly basis and indicated that on annulus was formed per year for fish under 5-6 years of age.	Preliminary observations of pectoral and dorsal spines indicated that the best readings were obtained from dorsal spines. In this study, there was a high percentage of illegible spines in older fish.	Conand et al. 1995

Table 3.1, cont.

bluefin tuna, *Thunnus thynnus*	The first dorsal spine was taken to estimate age and growth and to determine if a relationship exists between the growth increments exposed on spine sections and fish migration patterns.	Verification method not mentioned. Back-calculation of fork lengths indicated that growth bands are formed twice a year and the growth curve calculated for bluefin tuna closely approximated previous estimates derived from other aging methods.	The formation of growth bands in the dorsal spines of the tuna appeared to be related to their spring and fall migration patterns. Growth bands were progressively obscured by the increase in size of the vascularized core increased as the size of the fish increased.	Compeán-Jimenez and Bard 1983
Atlantic skipjack tuna, *Euthynnus pelamis*	The first dorsal spine was used to estimate age and growth.	The precision of counts between eight different readers was assessed. Only one specimen produced total agreement. The assumption of two growth bands per year was not validated.	Growth bands were also obscured by the increase in size of the vascularized core.	Antoine et al 1983
little tunny, *E. alletteratus*	The first dorsal spine was used to estimate age and growth.	Two readers (Cayre and Diouf 1983) had good precision in estimating age with an index of average percent error of 10.5%. The assumption of one doublet or one growth band per year was not validated in either study.	Growth bands were also obscured by the increase in size of the vascularized core. Johnson (1983) found 96% of the growth bands in the first dorsal spine agreed with the number of ridge groups found on the 33rd caudal vertbra from the same fish.	Cayre and Diouf 1983; Johnson 1983
albacore, *Thunnus alalunga*	The first two dorsal spines were used to estimate age and growth.	There was 85% agreement between the two readers. The assumption of two growth bands per year was not validated.	Growth bands were also obscured by the increase in size of the vascularized core.	González-Garcés and Fariña-Perez 1983

Table 3.1, cont.

sailfish, *Istiophorus platypterus*	The forth dorsal spine was used to estimate age and growth (Hedgepeth and Jolly 1983). Comparisons were made between dorsal spines and otoliths as age estimators (Prince etal. 1986).	Three readings of each spine by two readers were made independently (Hedgepeth and Jolly 1983). The assumption of one growth band per year was not validated (Hedgepeth and Jolly 1983).	Prince etal. (1986) found that the build up of oil in the dorsal spines caused resorption of centermost growth bands and an underestimation of age in older fish. Therefore, otoliths would probably be a better source of age and growth information.	Hedgepeth and Jolly 1983; Prince etal. 1986
blue marlin, *Makaira nigricans*	Otoliths, vertebrae, and anal and dorsal fin spines were evaluated for legibility and interpretability of growth patterns, ease of collection and processing, and the precision of the resultant annulus counts for use in estimating age.	Dorsal and anal fin spine counts had the best agreement. The growth zones were assumed to be annual and were not validated.	The fin spines were more practical in terms of ease of collection, processing, legibility, and interpretation. However, in larger fish the inner growth zones were resorbed and had to be replaced statistically.	Hill et al. 1989
swordfish, *Xiphias gladius*	The second anal fin spine was used to estimate age and growth in all studies.	Sections were read twice by a single reader (Berkeley and Houde 1983). The data collected by Berkeley and Houde (1983) were validated to be annual by Ehrhardt (1992) by studying the seasonal growth of relative marginal increments. Tserpes and Tsimenides (1995) each read all spines and used marginal increment ratio to validate that the growth bands were annuli.	The core of these spines often contains globules of oil that may obscure the focus and the first few growth bands, causing an underestimation of age.	Berkeley and Houde 1983; Ehrhardt 1992; Tserpes and Tsimenides 1995
queen triggerfish, *Balistes vetula*	The first dorsal spine was used to estimate age and growth.	Verification was not addressed in this study. Validation of annuli was accomplished using MIA and focus to ring measurements.	Spines were easily sampled and easily processed.	Manooch and Drennon 1987
gray triggerfish, *B. capriscus*	The first dorsal spine was used to estimate age and growth in each study.	Johnson and Saloman (1984) and Ofori-Danson (1989) did not address precision and did not validate growth bands as annuli. Escorriola (1991) used two people to read growth bands and had good precision. He also used MIA to validate growth bands as annuli.	Spines were easily sampled and easily processed.	Johnson and Saloman 1984; Ofori-Danson 1989; Escorriola 1991

3.1.5 Mathematical Representations of Growth

There are many mathematical functions that have been used to describe growth in fish. Common to these functions is a dependency on parameters that can be easily determined and then compared between stocks. Since the application of the von Bertalanffy growth function by Beverton and Holt (1957) to the yield-per-recruit problem, this function has been used widely in fisheries biology to describe and estimate growth in fishes. There are two different methods of determining the parameters of the von Bertalanffy growth function. The first method uses weight- and length-at-age data to estimate the growth parameters L_∞ (theoretical maximum length), W_∞ (theoretical maximum weight), K (Brody growth coefficient) and t_0 (theoretical age when length or weight is zero) for both length and weight, using the following equations:

$$L_t = L_\infty\left(1 - e^{-K(t-t_0)}\right) \text{ and/or } W_t = W_\infty\left(1 - e^{-K(t-t_0)}\right)^3 ,$$

where L_t is the length at time t and W_t is the weight at time t. This method of using age estimates from spines or otoliths, and length and weight measures is well described by Ricker (1975) and has been used by fisheries scientists to estimate and describe growth in many fish including those of the genus *Balistes* (Johnson and Saloman, 1984; Menezes, 1985; Manooch and Drennon, 1987; Ofori-Danson, 1989; Escorriola, 1991; Wilson et al., 1995; Hood and Johnson, 1997).

Secondly, data obtained from capture-recapture studies has also been used to estimate growth in fish (e.g. Sutter et al., 1991). Fabens (1965) described a method which uses capture-recapture data to estimate the parameters of the von Bertalanffy growth function. This method uses initial length (y_i) and the increment of growth (d_i) over time at large (recapture interval = Δ_i) to estimate the growth parameters of L_∞ and K:

$$d_i = (L_\infty - y_i)\left[1 - e^{(-K(\Delta_i))}\right].$$

In addition, Kirkwood (1983) combined both age-length and length-increment data to estimate von Bertalanffy growth curve parameters, and presented statistical measurements to test the adequacy of the curve's fit to both types of data sets.

3.1.6 Goals and Objectives

Age and Growth. The goal of this chapter is to provide insight into stock structure of GTF by comparing local-scale and large-scale age and growth parameters. Comparisons of estimates growth rate derived for fish inhabiting individual reefs are made to provide insight into small-scale stock structure in relation to growth parameters. Likewise, estimates of the von Bertalanffy growth parameters for GTF from two different artificial reef permit areas in the north-central Gulf off the coast of Alabama (i.e., the Hugh Swingle General Reef Permit Area and the Don Kelly North General Reef Permit Area) are compared (Figure 3.1). Differences in growth parameters fish from these two areas could be an indication of stock separation (Gulland, 1983) on a relatively local scale. Also, the results of this study are compared with those of studies from other areas of the Gulf. As seen in Chapter 2, GTF exhibit high site fidelity. If growth parameters off Alabama differ from those from than other regions of the Gulf, this may indicate that

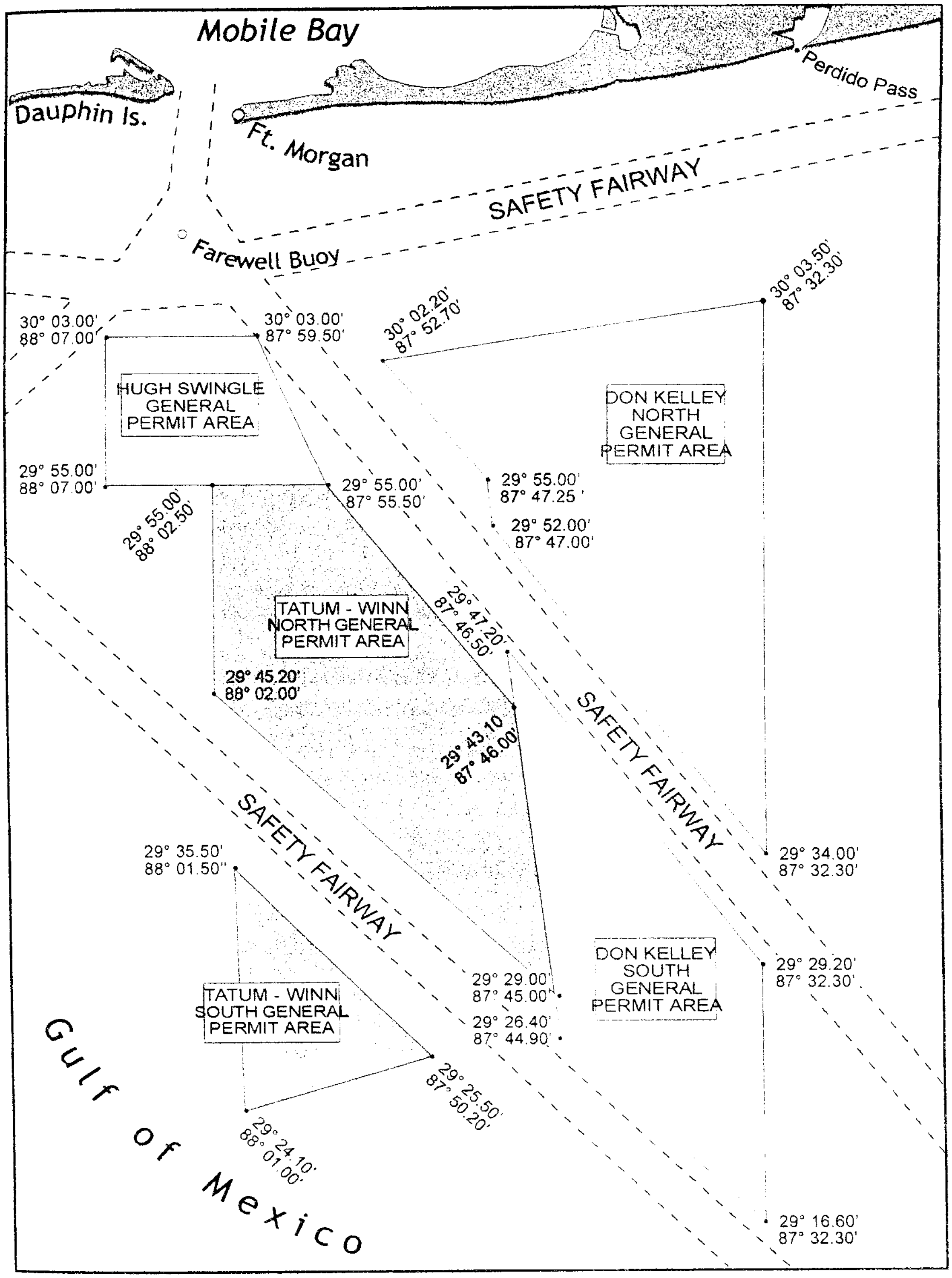

Figure 3.1. General permit areas off the Alabama coast for artificial reef construction.

GTF should be managed with respect to differences in discrete management units (MU's) within the large or Gulf-wide scale.

Reproduction. Another goal of this chapter is to accurately describe the reproductive biology of GTF off the Alabama coast (i.e., provide data on size-fecundity relationships, reproductive seasonality, sex ratios at age, and maturation schedules) and to compare the reproductive parameters of fish captured in the Hugh Swingle General Reef Permit Area to those of fish from the Don Kelly General Reef Permit Area. I reason that if there are significant differences between the reproductive parameters obtained from fish in one reef permit area when compared to the other (i.e. localization of reproductive parameters), then, like differences in growth rates, the need for MU's within the unit stock may be indicated. Also, the results of this study are compared with those found in studies from other areas of the Gulf.

Mortality. The final goal of this chapter was to describe mortality of GTF off the Alabama coast on multiple scales. Mortality rates were compared between GTF captured in Don Kelly North and Hugh Swingle General Permit Areas and between tagging sites of the NRS (see Chapter 2). I reason that differences in mortality rates may indicate differences in fishing pressure between areas. Due to high site fidelity (see Chapter 2), I reason that differences in fishing pressure and resulting mortality rates between areas may lead to differences in age structure between areas, and subsequent localization in growth and reproductive parameters.

3.2 Materials and Methods

3.2.1 Age and Growth

GTF captured by charter boats off Dauphin Island and Orange Beach, Alabama were sampled to collect the data with which to estimate growth. In addition, I sampled fish landed at various local fishing tournaments, and captured in bottom trawls off the coast of Louisiana during the 1998 Summer Groundfish Survey conducted as part of the South East Area Monitoring and Assessment Program (SEAMAP) by the National Marine Fisheries Service. Specimens (n = 1,849) inclusive of all samplings for this project were collected from July 19, 1996 to October 20, 2000.

Of the 1,849 GTF sampled for hard parts for age and growth analysis, 650 were harvested from the Hugh Swingle General Permit Area; 909 were harvested from the Don Kelly North General Permit Area; 80 were collected during SEAMAP trawling cruises; and 210 were sampled at various local, hook-and-line and spear-fishing tournaments.

Nine-hundred-and-twelve female, 892 male and 45 GTF of undetermined sex were collected. When sampled, each specimen was measured for fork length (mm), total length (mm), and total weight (to the nearest 0.01 kg). The gonad from each specimen was taken to determine the sex of the fish, and the first dorsal spine of each fish was collected. Finally, if a charter boat landed the fish, the charter boat captains were interviewed to determine the permit area in which each fish was captured.

The first dorsal spine was removed by cutting the membrane between the first and second dorsal spine toward the joint where the condyle articulates with the first basal pterygiophore using a heavy sharp knife (line A, Figure 3.2). After the membrane was

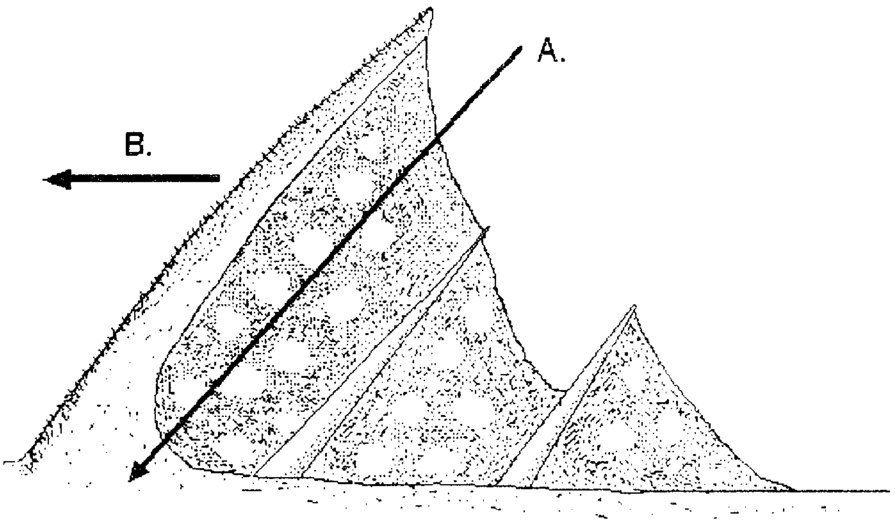

Figure 3.2. Illustration of removal of the first dorsal spine of gray triggerfish.

cut, the knife was inserted anteroventrally into the condyle socket at the posteroventral base of the first dorsal spine, and any connective tissue holding the spine in place was removed. Next, the spine was removed from the socket by distally applying pressure to the posterior surface of the spine, moving it anteriorly until the condyle 'popped' out of the socket (line B, Figure 3.2). Finally, any remaining tissue still attached to the spine was cut, separating the spine from the fish.

A modified combination of the methods of Johnson and Saloman (1984), Manooch and Drennon (1987), and Hood and Johnson (1997) was used to estimate the age of GTF using the first dorsal spine. The shaft of each dorsal spine was cut about 5-10 mm above the condyle. Figure 3.3 shows the best place to make the transverse section in the extracted spine. The sectioning plane, illustrated by line B in Figure 3.3, was the best position to section the spine. The section at line A resulted in more closely spaced annuli, and a section made at line C would result in annuli which may be obscured by the convolutions in the condyle of the spine. Therefore, the section made at line B provided the most widely spaced annuli with the best resolution.

A Hilquist model 800, water-cooled thin sectioning machine with a diamond blade (Cowan et al., 1995) was used to section GTF spines. This saw allows accurate cuts at high speed. To make a transverse section, the spine was held horizontally, perpendicular to the saw blade. Then, while holding the spine as steady as possible, the first cut was made as illustrated on line B in Figure 3.3. This resulted in two portions of the spine – the distal portion and the proximal portion containing the condyle. After this cut was made, the cut surface of the distal portion was polished using the polishing lap of the Hilquist saw. After the cut surface was ground, the distal portion of the spine was

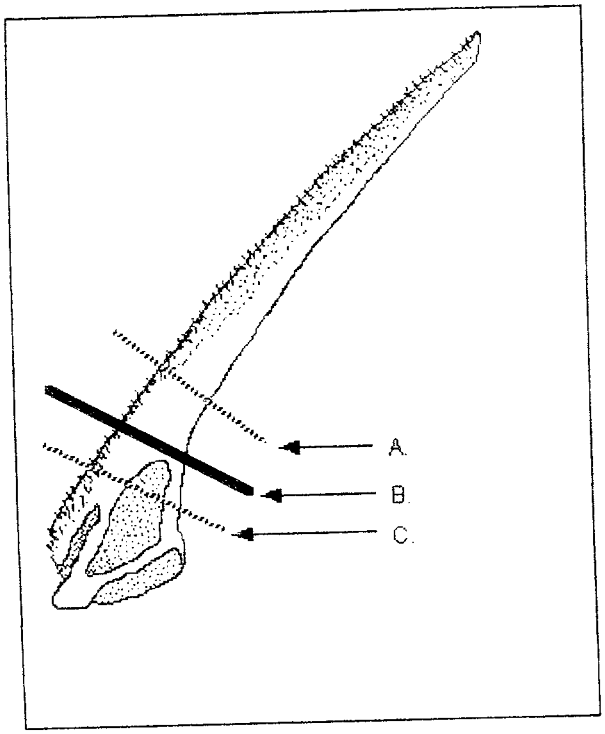

Figure 3.3. Positioning of a correct transverse section in the first dorsal spine of gray triggerfish.

cemented to the petrographic slide with the plane of the cut parallel to the plane of the slide. The spine was cemented to the slide with ultra-violet epoxy (Loctite #349) and allowed to cure for two to three minutes. After curing, the slide with the mounted distal portion of the spine was placed into the slide-holding lever-arm associated with the Hilquist's cutting blade. The second transverse cut was made using this lever-arm to guide the spine across the blade. The result was a spine section with an initial thickness of approximately 0.5 to 1 mm. The final thickness of the section was adjusted using a dial caliper on the grinding lap, which indicates the distance of the spine section and lever arm from the grinding lap in units of micrometers (i.e. the thickness of the thin-section). A microscope set at 40x magnification was used to monitor the clarity of the section, as the thickness of the section was adjusted by grinding. The thickness of the thin-section was adjusted to around 400 μm to achieve sufficient resolution when examining the spines at a magnification of 40x.

A generalized spine section was illustrated in Figure 3.4. The areas of summer and winter growth in a gray triggerfish spine section were translucent and opaque, respectively, opposite the pattern generally found in otoliths. These annuli radiated outward from the focus. The focus in a spine section was the main channel of vascularization for the spine. The spine radius was measured as the distance from the focus to the margin of one of the posterior lobes, as seen in Figure 3.4.

A section was best viewed with either a compound or dissecting light microscope set at a magnification of 40x. Illuminated from below, the translucent rings in the section were relatively clear and well defined. The rings were counted from the focus to the margin of one of the posterior lobes along the radius (Figure 3.4). In order to insure a

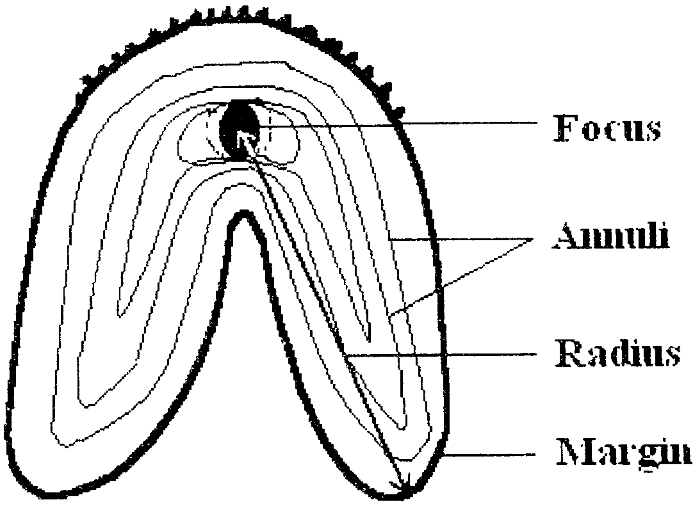

Figure 3.4. Generalized section of the first dorsal spine of gray triggerfish.

definitive margin on the posterior lobes, I removed the skin from between the lobes and covering the lobes. This enabled the production of a section with a smooth, readable, and measurable margin.

Two readers independently enumerated annuli in the first dorsal spines. If the spines were deemed either unreadable, or if the readers disagreed in annulus counts, then those sections were not used for age estimation or included in any further analysis. After enumeration of the annuli, the biological age of the gray triggerfish was estimated by adjusting for a June-July spawning date (i.e. July 1 spawning date) in the northern Gulf of Mexico (Wilson et al., 1995 and see Chapter 4); adjusting for an annulus formation date between December and February (i.e. January 1 formation date (Wilson et al., 1995 and see below); and adjusting for the date of capture.

To validate these translucent rings as annuli, I conducted a relative marginal increment analysis on the spines using a modified combination of methods used by Manooch and Drennon (1987) and Ehrhardt (1992). Various measurements (spine radius, distance of the last annulus to the margin) were obtained for a sub sample of 280 specimens (15 %). I plotted the monthly average relative marginal increment. The relative marginal increment was the distance from the distal edge of the last translucent band to the edge of the spine (marginal increment) divided by the radius of the spine. The mean monthly relative marginal increment was calculated and plotted over the course of a year. Also, I plotted the monthly percent-frequency of the presence of a translucent margin in GTF spines. If valid, the annuli would indicate the age of each fish, and with both age and length/weight data, the von Bertalanffy growth parameters could be derived using a nonlinear regression procedure (SAS for Windows, v.8).

Sex-specific and overall age-length keys were developed for all GTF collected for hard-part analysis, and excluding those specimens collected at tournaments and during SEAMAP cruises. Sex-specific nonlinear length-weight relationships were developed using the following model:

$$\mathrm{W} = a\mathrm{FL}^{b},$$

where W is the weight (kg) at fork length (FL) in mm, a is a constant and b is the exponent of the power function (Ricker, 1975). Finally, a linear regression of fork length on total length (TL, mm) was developed using length data both from the mark-recapture study from Chapter 2, and from length data collected during this study.

Von Bertalanffy parameters were estimated for male GTF, female GTF and for combined sexes, and compared with parameters from other age and growth studies (e.g. Johnson and Saloman, 1984; Wilson et al., 1995; Hood and Johnson, 1997). Von Bertalanffy parameters also were estimated for GTF captured within the Hugh Swingle General Reef Permit Area and were compared (see below) to those estimated for GTF in the Don Kelly North General Reef Permit Area. In addition, the von Bertalanffy growth parameters were determined using a nonlinear solution of Faben's method (1965), which used mark-recapture data to calculate growth parameters. These data, consisting of change in length and corresponding time at large, were obtained during the tagging study described in Chapter 2. The parameters obtained from Faben's method were compared to those obtained using age-length data based on analysis of the first dorsal spine to determine if each method provides a similar biological interpretation. In addition, von

Bertalanffy parameters estimated for different sexes and for GTF inhabiting different permit areas were compared.

Von Bertalanffy growth models were compared statistically using the methods of Bernard (1981). This method employs a Hotelling's T^2 statistic ($\alpha = 0.05$), which can simultaneously compare parameters from multi-parameter models, in which all parameters are highly correlated. In this case, the statistic is employed to determine a difference between von Berttalanffy growth models by simultaneously comparing all model parameters. For Hotelling's T^2, both sets of parameter estimates (i.e., L_∞, K and t_0) are assumed to be drawn from two, trivariate normal, joint probability distributions with a common variance structure. Asssuming a common variance-covariance matrix allows for the pooling of variance estimates when the actual variance structure is unknown. If this assumption is violated and the variance-covariance matrices are different, then the probability of a Type I error (α), and correspondingly the power of the T^2 test, may deviate from tabulated values with similar degrees of freedom. However, when sample sizes are similar, the effects of different variances are trivial. Also, the assumption of a normal, joint, probability distribution is important to the test. Large sample sizes increase the robustness of the T^2 statistic to non-normally distributed data; parameters are means in a trivariate, normal distribution and like all means become normally distributed at large sample sizes.

Negative binomial regression also was employed to elucidate differences between growth of female and male GTF, and for differences in growth of GTF harvested from the Hugh Swingle General Permit Area versus those harvested from the Don Kelly North General Permit Area. This was accomplished in each scenario by describing the deviance in the dependent variable fork length of GTF with the independent variable of age of each GTF. Then to test differences in growth between sexes, or between fish harvested from different permit areas, I included either a bivariate sex variable (i.e. male versus female) or a bivariate area variable (i.e. Hugh Swingle versus Don Kelly), respectively, in each model.

To elucidate differences in growth on a small scale, I compared differences in change in fork length over time at large of GTF tagged over each tagging station during the NRS (see Chapter 2). I developed a negative binomial regression with growth rate (i.e. change in fork length/time at large) as the dependent variable and tagging stations (i.e. IA, IB1, IB2, IC, ID, IE, OA and OC) as independent class variables. Because all of the inshore tagging stations were in similar water depths (20 m), and the offshore tagging stations were in similar water depths (32 m), depth-specific growth rate was also evaluated using negative binomial regression (SAS v.8).

3.2.2 Reproduction

Gonosomatic Indices (GSI). Gonads were removed from 454 male and 613 female GTF, and were immediately placed in 4 % formaldehyde solution for at least two weeks for preservation. Before placement in formaldehyde solution, the gonads were weighed (to the nearest 0.1 g).

A GSI was calculated for each fish. GSI for female GTF was calculated using the following equation:

$$GSI_F = 100\ \%\ [\text{gonad weight(kg)}/\ \text{total body weight(kg)}],$$

GSI for males was calculated using the following equation:

$$GSI_M=100\{100\ \%\ [\text{gonad weight(kg)/total body weight(kg)}]\}.$$

Due to the small size of the male gonad, the initial male GSI, which represented the percent of total body weight that was gonad material, was multiplied by 100 to allow a more straightforward comparison between spawning periodicity of male and female GTF. Sex-specific, monthly means of GSI of males and females were examined for changes in relative gonad size.

Maturation Schedules. Gonad tissue samples were sampled and histologically analyzed to describe the maturation schedule of male and female GTF. A section of gonad tissue was taken from a randomly selected area of each ovary and testis. Histological preparations were made and mounted by the Histology/Pathology Department at the Louisiana State University, School of Veterinary Medicine using standard techniques (Hinton, 1990, for review).

Histological sections of gonads were examined microscopically and assigned to maturation categories described by Hood and Johnson (1997), who used modified classification schemes developed from West (1990) and Wallace and Selman (1981) for females, and Hyder (1969) for males. The following developmental stages were used in describing ovarian development of in GTF:

Immature: Only primary growth oocytes are present in this stage, which is characterized by little cytoplasm with a centrally located nucleus. The nucleus contain either one large basophilic nucleous (a chromatin nucleolar oocyte) or several small nucleoli usually found at the nuclear periphery (a perinucleolar oocyte).

Resting: This stage is similar to immature ovaries except that atretic bodies, which are indication of past spawning, and an increased number of folds in the ovigerous lamellae are present.

Maturing: This stage is characterized by the presence of cortical alveoli (yolk vesicle) oocytes, which are recognizable by the appearance of the chorion and yolk vesicles in the cytoplasm that give rise to the cortical alveoli.

Mature: This stage is characterized by vitellogenic oocytes as the most advanced oocyte present in the ovary. Vitellogenic oocytes have yolk granules, which are initially small, but as the oocyte develops, fuse and eventually form a continuous mass of yolk fluid.

Hydrated: This stage is characterized by the presence of late-stage vitellogenic oocytes and hydrated oocytes. Hood and Johnson (1997) reported that hydrated oocytes have an amoeboid shape that results from dehydration of the histological imbedding process.

Atresia: this stage is characterized by massive atresia of all remaining vitellogenic oocytes.

The following developmental stages were used in describing testicular development of GTF:

Immature: This stage is characterized by the presence of spermatogonia and spermatocytes in the central lobules, but no tailed sperm are observed in the lumen of the lobule.

Developing: Testes in this stage are similar to the immature stage; however, developing testes can have tailed sperm in the lumen of the lobule.

Mature: This stage is characterized by the testis having primarily spermatocytes, spermatids and free spermatozoa in the lumen of the lobule.

Ripe: Testes in this stage is characterized as having only free spermatozoa in the lumen of the lobule.

Spent: This stage is characterized by the testis having few free spermatozoa in the lumen of the lobule and early stages of spermatogenesis occurring in the peripheral lobules.

Percent frequency of GTF in each stage of gonad development per month was plotted for each sex.

<u>Batch Fecundity, Spawning Frequency and Total Annual Fecundity</u>. Modified histological techniques of Brown-Peterson et al. (2000) were employed to estimate batch fecundity. All oocytes undergoing final oocyte maturation (FOM), which precedes hydration, were enumerated using a light microscope at 100X magnification. Mid- to late-stage vitellogenic oocytes that were greater than 400 μm in diameter were considered to be undergoing FOM. Six fields of view per slide (i.e. per fish) were inspected, and only the oocytes undergoing FOM were counted. Each field of view had an area of 2.44 mm^2, and this area was multiplied by the average diameter of oocytes counted in that field to give the number of oocytes undergoing FOM per volume. The total number of oocytes per volume of histological section inspected was then multiplied by the volumetric displacement of the ovary. Of the 44 females classified as mature with oocytes undergoing FOM, 39 were used to estimate batch fecundity.

Statistical relationships between batch fecundity and age (years), FL (mm) and weight (kg) were developed. The relationship between batch fecundity and age was modeled using the following equation:

$$f = ae^{b(\mathrm{age})},$$

where a and b are model constants and f is batch fecundity (number of eggs per batch). The relationship between batch fecundity and fork length was modeled using the following equation:

$$f = ae^{b(\mathrm{FL})},$$

where a and b are model constants, f is batch fecundity. The relationship between batch fecundity and weight was modeled using the following equation:

$$f = a + b(\mathrm{W}),$$

where a and b are model constants, f is batch fecundity and W is weight (kg).

The incidence of females with oocytes undergoing FOM provided an estimate of spawning frequency during the spawning season (Hunter and Macewicz, 1985). The mean percent-frequency of females with ovaries containing oocytes undergoing FOM per day was estimated. One hundred percent divided by this rate indicated the mean interval between spawnings (days)(i.e. spawning frequency). The mean number of spawnings per spawning season was estimated by dividing the length of the spawning season by the spawning frequency. Mean total annual fecundity was estimated by multiplying the mean number of spawnings by mean batch fecundity.

The reproductive parameters of fish captured in the Hugh Swingle General Reef Permit Area and of those from the Don Kelly North General Reef Permit Area were compared using ANOVA with month, area and a multiplicative interaction term. In addition, the reproductive parameters estimated in this study were compared to those from other studies around the Gulf (i.e., Louisiana, Wilson et al., 1995; West Florida, Hood and Johnson, 1997).

3.2.3 Mortality

I used catch curve analysis (Ricker, 1975) of age-frequency distributions to estimate survival rate of GTF. I modeled the exponential decay in numbers with age (years) with the following model:

$$\mathrm{N}_t = \mathrm{N}_0 e^{-Zt},$$

where N_0 is the number of fish at age zero, N_t is the number of fish at age t (years) and Z is the instantaneous total mortality rate. Z was estimated by modeling the decay of number with age, starting with age three. The decay model was started with this bin since it was the peak in the age-frequency histogram and assumed to be the age at which all GTF are fully recruited to the recreational fishery off Alabama. Other scientists (i.e. Johnson and Saloman, 1984; Wilson et al., 1995) also report that GTF are fully recruited to the hook and line fishery by age 3 years. Once Z was estimated, I estimated annual survival (S) using the following equation:

$$S = e^{-Z}$$

Also, to estimate natural mortality, I used Hoenig's method (1983), where instantaneous natural mortality rate was estimated using the following equation:

$$\ln(M) = 1.44 - 0.982(t_{\max}),$$

where M is the instantaneous natural mortality rate and $t_{\max}$ was the maximum age of GTF in the sample. With both estimates of Z and M, I then estimated the instantaneous fishing mortality rate (F) off the Alabama coast by assuming the following relationship:

$$Z - M = F.$$

I used the above methods to estimate *Z*, *M* and *F* based upon age-frequency data derived from age estimates from first dorsal spines, excluding all tournament fish and all fish collected by SEAMAP. In addition, I estimated *Z*, *M* and *F* for fish harvested by recreational fishermen from the Hugh Swingle General Permit Area versus those harvested from the Don Kelly North General Permit Area. Finally, I estimated *Z*, *M* and *F* of GTF tagged over inshore versus offshore tagging sites. This was accomplished by transforming the estimated fork-length-at-tagging to age-at-tagging data using the von Bertalanffy growth function for combined sexes.

3.3 Results

3.3.1 Age and Growth

Marginal Increment Analysis. Of the 1,849 first dorsal spines collected and analyzed for age estimation, 4.16 % were deemed unreadable, and readers disagreed on annulus counts on 4.49 % of the spines. Therefore, 1,690 (91.35 %) spines were used in GTF age estimation.

The marginal increment analysis indicated that a translucent annual mark forms in the spine from December to early February, and a secondary mark forms in July (Figure 3.5). The frequency of translucent margin of the first dorsal spine indicated that 100 % of GTF have a translucent margin in the month of January (Figure 3.6). The frequency of fish having a translucent margin decreased through April and was minimal in May and June. There was a secondary peak in August, followed by a subsequent decrease in the

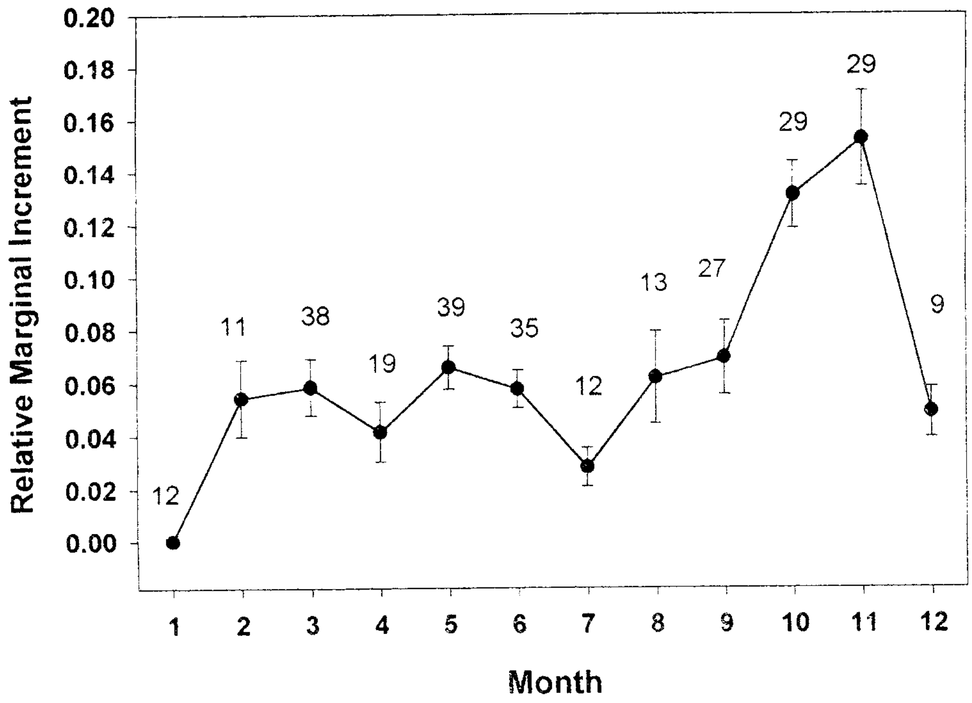

Figure 3.5. Average relative marginal increment of the first dorsal spine of gray triggerfish. Error bars represent standard error, and numbers above symbols represent sample size.

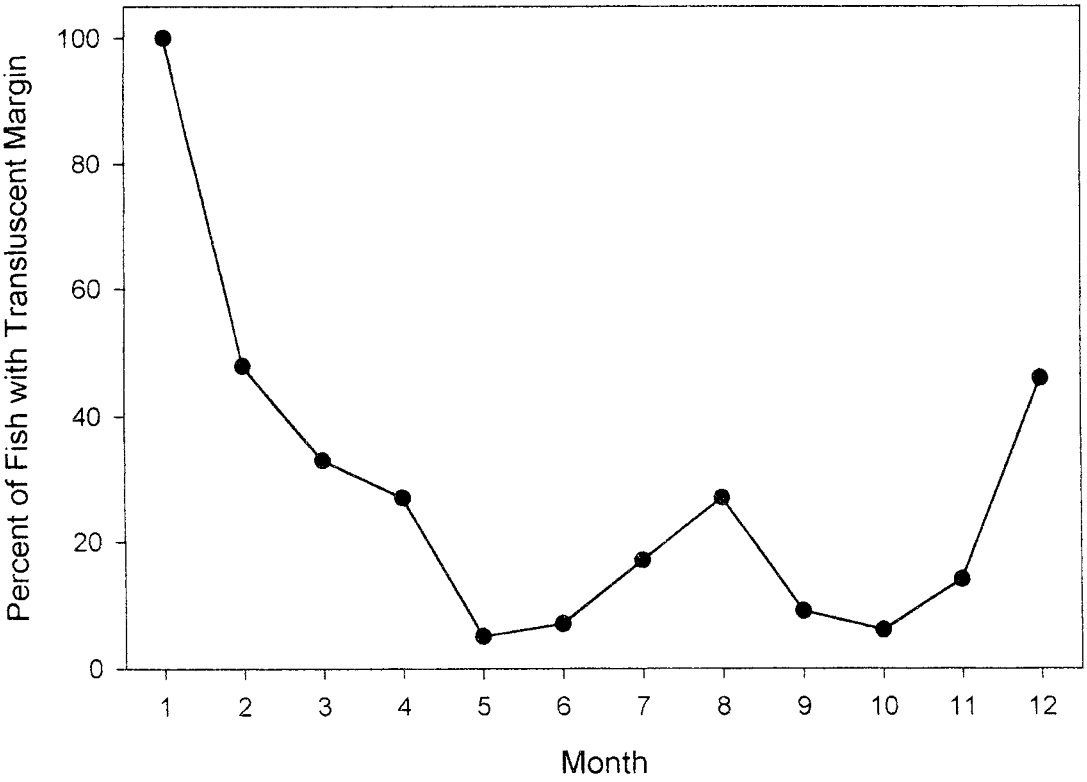

Figure 3.6. Monthly percent frequency of a translucent margin in the first dorsal spine of gray triggerfish.

fall. This pattern suggested that an annulus formed from December through February, and a spawning check or false annulus formed in August.

There were several occurrences of false annuli in GTF spines. Such false annuli are shown in the image of a spine section of a seven-year-old female gray triggerfish in Figure 3.7. In Figure 3.7, each annulus is marked with a black dash, and the false annuli are those marks falling between annuli. These marks were easy to discern in early annuli because of their high relative width, as as shown for the annuli 3 and 4 in Figure 3.7, compared to later annuli. Finally, there appeared to be formation of a settlement mark around the focus in many specimens, which is discussed in Chapter 4.

Sex-Specific Growth. Sex-specific and overall age-length keys and tables of mean fork length at age were developed for all GTF collected for hard-part analysis (Tables 3.2 – 3.4 and 3.8), and excluding those specimens collected at tournaments and during SEAMAP cruises (Tables 3.5 – 3.7 and 3.9). The mean age (±standard error) of males and females collected during this study was estimated to be 3.50 years (± 0.054) and 3.40 years (± 0.048), respectively, including all fish in the sample and 3.44 years (± 0.047) and 3.44 years (± 0.039), respectively, excluding all tournament and SEAMAP collected fish. Differences in mean ages between male and female GTF were not significantly different (ANOVA; $\alpha = 0.05$) in both of the above cases. The oldest GTF in the sample was a female that was estimated to be 8.8 years of age. The oldest male was estimated to be 8.1 years of age.

The mean fork lengths (±standard error) of males and females collected during this study were estimated to be 363 mm (± 2.68) and 326 mm (± 2.15), respectively,

Figure 3.7. Spine section of a seven-year-old, female gray triggerfish.

Table 3.2. Percent length composition of female gray triggerfish collected for age and growth analysis, including all tournament fish, and all fish collected during SEAMAP cruises. Percentages shown are row percentages.

	Age in Years									
FORK LENGTH (MM)	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**TOTAL NUMBER OF FISH**
50-99	100.00									3
100-149	100.00									23
150-199	72.73	18.18	9.09							11
200-249	12.50	75.00	12.50							8
250-299	1.06	25.93	39.15	29.63	3.70	0.53				189
300-349	0.59	8.85	38.05	35.40	13.57	3.24	0.29			339
350-399		2.60	12.99	42.86	31.17	9.74		0.65		154
400-449			1.85	14.18	35.19	24.07	22.22	1.85		54
450-499				3.57	17.86	35.71	17.86	10.71	14.29	28
500-549						75.00	25.00			4
550-599									100.00	1
TOTAL NUMBER OF FISH	39	91	226	251	125	53	19	5	5	814

Table 3.3. Percent length composition of all male gray triggerfish collected for age and growth analysis, including all tournament fish, and all fish collected during SEAMAP cruises. Percentages shown are row percentages.

	Age in Years									
FORK LENGTH (MM)	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**TOTAL NUMBER OF FISH**
50-99	100.00									2
100-149	100.00									23
150-199	68.75	31.25								16
200-249	14.29	57.14	28.57							7
250-299	7.69	41.67	43.96	6.59						91
300-349	1.02	14.80	47.45	29.08	7.65					196
350-399		5.21	24.48	37.50	27.08	5.21	0.52			192
400-449			7.09	33.33	41.13	16.31	1.42	0.71		141
450-499			1.05	12.63	20.00	41.05	17.89	7.37		95
500-549				6.25	18.75	25.00	18.75	25.00	6.25	16
550-599						50.00	50.00			2
TOTAL NUMBER OF FISH	46	86	193	195	147	77	24	12	1	781

Table 3.4. Percent length composition of all gray triggerfish (combined sexes) collected for age and growth analysis, including all tournament fish, and all fish collected during SEAMAP cruises. Percentages shown are row percentages.

	Age in Years									
FORK LENGTH (MM)	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**TOTAL NUMBER OF FISH**
50-99	100.00									5
100-149	100.00									46
150-199	70.37	25.93	3.70							27
200-249	11.76	64.71	23.53							17
250-299	3.14	30.66	41.11	21.95	2.79	0.35				287
300-349	0.73	10.99	41.76	33.15	11.17	2.01	0.18			546
350-399		4.24	19.21	40.11	28.81	7.06	0.28	0.28		354
400-449			5.61	28.06	39.80	18.37	7.14	1.02		196
450-499			0.81	10.48	20.16	39.52	17.74	8.06	3.23	124
500-549				5.00	15.00	35.00	20.00	20.00	5.00	20
550-599						33.33	33.33		33.33	3
Total number of fish	85	181	431	455	277	130	43	17	6	1625

Table 3.5. Percent length composition of all female gray triggerfish collected for age and growth analysis, excluding all tournament fish, and all fish collected during SEAMAP cruises.

	Age in Years									
FORK LENGTH (MM)	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**TOTAL NUMBER OF FISH**
200-249	14.29	71.43	14.29							7
250-299	0.55	24.31	40.33	30.39	3.87	0.55				181
300-349	0.60	9.06	38.97	35.05	12.99	3.02	0.30			331
350-399		2.74	13.01	44.52	30.14	9.59				146
400-449			2.63	21.05	39.47	26.32	10.53			38
450-499					44.44	33.33	22.22			9
500-549						50.00	50.00			2
550-599									100.00	1
Total number of fish	4	83	223	244	113	39	8		1	715

Table 3.6. Percent length composition of all male gray triggerfish collected for age and growth analysis, excluding all tournament fish, and all fish collected during SEAMAP cruises.

	Age in Years								
FORK LENGTH (MM)	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**TOTAL NUMBER OF FISH**
200-249	20.00	60.00	20.00						5
250-299	6.74	42.70	43.82	6.74					89
300-349	1.06	15.43	46.81	29.79	6.91				188
350-399		5.75	26.44	41.38	22.99	3.45			174
400-449			8.18	39.09	39.09	12.73	0.91		110
450-499			2.13	19.15	23.40	38.30	10.64	6.38	47
500-549					25.00	25.00	25.00	25.00	4
Total number of fish	9	80	184	186	108	39	7	4	617

Table 3.7. Percent length composition of all gray triggerfish (combined sexes) collected for age and growth analysis, including all tournament fish, and all fish collected during SEAMAP cruises.

	Age in Years									
FORK LENGTH (MM)	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**TOTAL NUMBER OF FISH**
200-249	14.29	64.29	21.43							14
250-299	2.53	29.96	41.88	22.38	2.89	0.36				277
300-349	0.75	11.32	42.08	33.21	10.57	1.89	0.19			530
350-399		4.59	20.18	42.81	26.30	6.12				327
400-449			6.76	34.46	39.19	16.22	3.38			148
450-499			1.79	16.07	26.79	37.50	12.50	5.36		56
500-549					16.67	33.33	33.33	16.67		6
550-599									100.00	1
Total number of fish	13	167	419	438	224	78	15	4	1	1359

Table 3.8. Mean fork length of female, male and all (combined sexes) gray triggerfish collected for age and growth analysis, including all tournament fish, and all fish collected during SEAMAP cruises.

	Age in Years								
MEAN FORK LENGTH (MM) STANDARD ERROR N	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
Male	168	296	330	375	407	449	475	485	521
	9.6	5.0	2.9	3.3	3.7	4.6	7.9	7.2	
	46	86	193	195	148	77	24	12	1
Female	146	291	310	330	362	403	438	437	490
	9.3	3.9	2.0	2.4	3.9	8.2	8.5	23.5	20.1
	39	91	226	251	125	53	19	5	5
Combined Sexes	158	293	319	349	386	430	458	471	495
	6.8	3.1	1.8	2.2	3.0	4.7	6.4	9.8	17.2
	85	182	431	456	278	130	43	17	6

Table 3.9. Mean fork length of female, male and all (combined sexes) gray triggerfish collected for age and growth analysis, excluding all tournament fish, and all fish collected during SEAMAP cruises.

	Age in Years								
MEAN FORK LENGTH (MM) STANDARD ERROR N	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
Male	283 7.0 9	304 3.9 80	330 2.9 184	372 3.1 186	402 4.2 109	443 6.4 39	471 12.8 7	482 9.5 4	0
Female	289 15.2 4	295 3.7 83	311 2.0 223	329 2.4 244	359 4.1 113	384 8.1 39	432 19.1 8	0	567 1
Combined Sexes	285 6.4 13	299 2.7 168	319 1.7 419	347 2.1 439	380 3.2 225	413 6.1 78	450 12.5 15	482 9.5 4	567 1

including all fish in the sample and 361 mm (± 2.17) and 328 mm (± 1.59), respectively, excluding all tournament and SEAMAP collected fish. Differences in mean fork length between males and females were significantly different (ANOVA, $\alpha = 0.05$) in both of the above cases.

The linear regression between TL (mm) and FL (mm) of GTF is illustrated in Figure 3.8 (Table 3.10, for model equation). In addition, the nonlinear length-weight (mm-kg) relationships for both male and female GTF are illustrated in Figure 3.9 (Table 3.10, for model equations).

The von Bertalanffy growth functions for males, females and combined sexes, including all fish sampled during tournaments and all fish sampled by trawl during SEAMAP cruises are illustrated in Figure 3.10 (Table 3.10, for model equations). These indicate that males attain a larger size than females. Hotelling's T^2 statistic indicates a highly significant difference in von Bertalanffy growth functions between males and females ($T^2 = 141681.8, p << 0.001$). Male GTF attain a larger asymptotic maximum length. The difference (with 95 % confidence intervals) in L_∞ parameters between male and female growth functions is 83.6 mm (80.7 to 86.6 mm). Males approach that length at a slower rate of growth. The difference (with 95 % confidence intervals) in Brody growth coefficients, K, between male and female growth functions is -0.0078 year^{-1} (-0.0104 to -0.0052 year^{-1}). In addition, males had a higher theoretical age at 0 mm fork length. The difference (with 95 % confidence intervals) in t_0 parameters between male and female growth functions is 0.2334 year (0.2142 to 0.2527 year).

The negative binomial regression run with FL (mm) as the dependent variable and age (years) and sex as the independent variables indicated that males attain a larger size

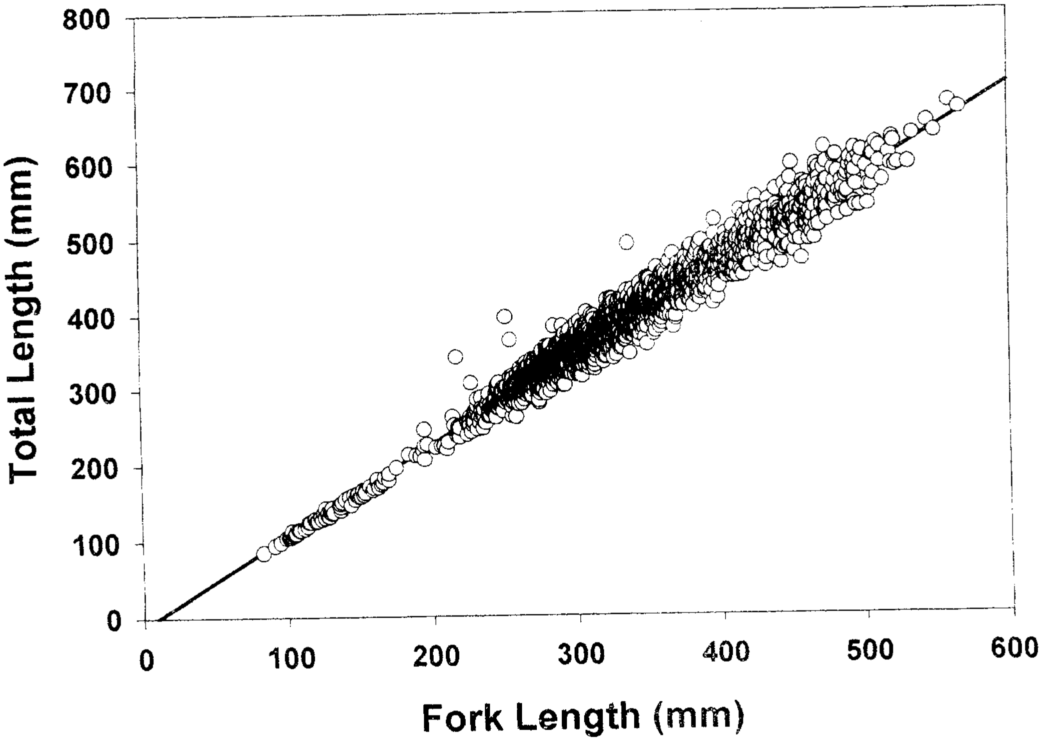

Figure 3.8. Linear regression of total length versus fork length of gray triggerfish.

Table 3.10. Morphometric, and 2-, and 3-parameter von Bertalanffy (2- and 3-VB) growth equations for gray triggerfish.

Equation-Type	**Equation**	**Intra-model Parameter Correlations**	**R^2**
TL vs. FL	$TL = -10.5017 + 1.1889(FL)$	--	0.96
Male length-weight	$W_m = 0.0698FL^{1.0075}$	--	0.97
Female length-weight	$W_f = 0.0627FL^{1.0079}$	--	0.96
Combined Sexes (3-VB)	$L_t = 583\left(1 - e^{(-0.1830(t+1.5786))}\right)$	$R_{L_\infty,t_0} = -0.78$ $R_{L_\infty,K} = -0.98$ $R_{K,t_0} = 0.89$	0.99
Male (3-VB)	$L_t = 598\left(1 - e^{(-0.1997(t+1.3731))}\right)$	$R_{L_\infty,t_0} = -0.77$ $R_{L_\infty,K} = -0.98$ $R_{K,t_0} = 0.88$	0.99
Female (3-VB)	$L_t = 514\left(1 - e^{(-0.2075(t+1.6065))}\right)$	$R_{L_\infty,t_0} = -0.76$ $R_{L_\infty,K} = -0.97$ $R_{K,t_0} = 0.88$	0.99
Hugh Swingle (3-VB)	$L_t = 574\left(1 - e^{(-0.2040(t+1.3448))}\right)$	$R_{L_\infty,t_0} = -0.73$ $R_{L_\infty,K} = -0.98$ $R_{K,t_0} = 0.84$	0.99
Don Kelly North (3-VB)	$L_t = 579\left(1 - e^{(-0.1853(t+1.4848))}\right)$	$R_{L_\infty,t_0} = -0.76$ $R_{L_\infty,K} = -0.98$ $R_{K,t_0} = 0.86$	0.99
Hard Parts (2-VB)	$L_t = 450\left(1 - e^{(-0.4630(t))}\right)$	$R_{L_\infty,K} = -0.95$	0.98
Tagged Fish (2-VB Faben's Method)	$d_i = (403 - y_i)\left(1 - e^{(-0.3675(\Delta_i))}\right)$	$R_{L_\infty,K} = -0.96$	0.65

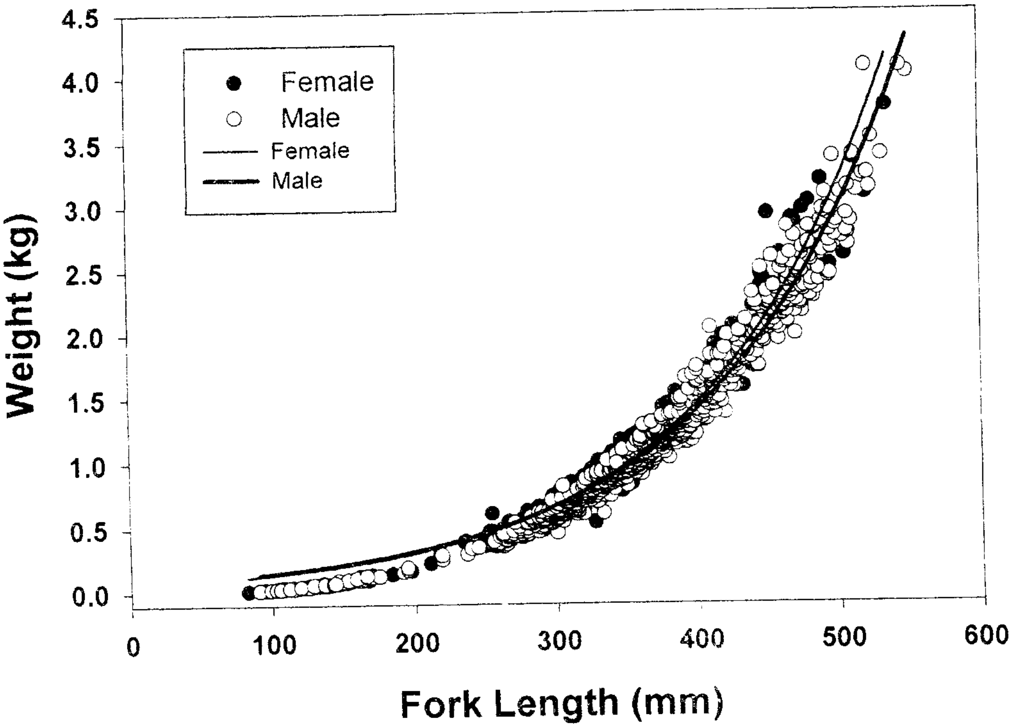

Figure 3.9. Length-weight relationship of male and female gray triggerfish.

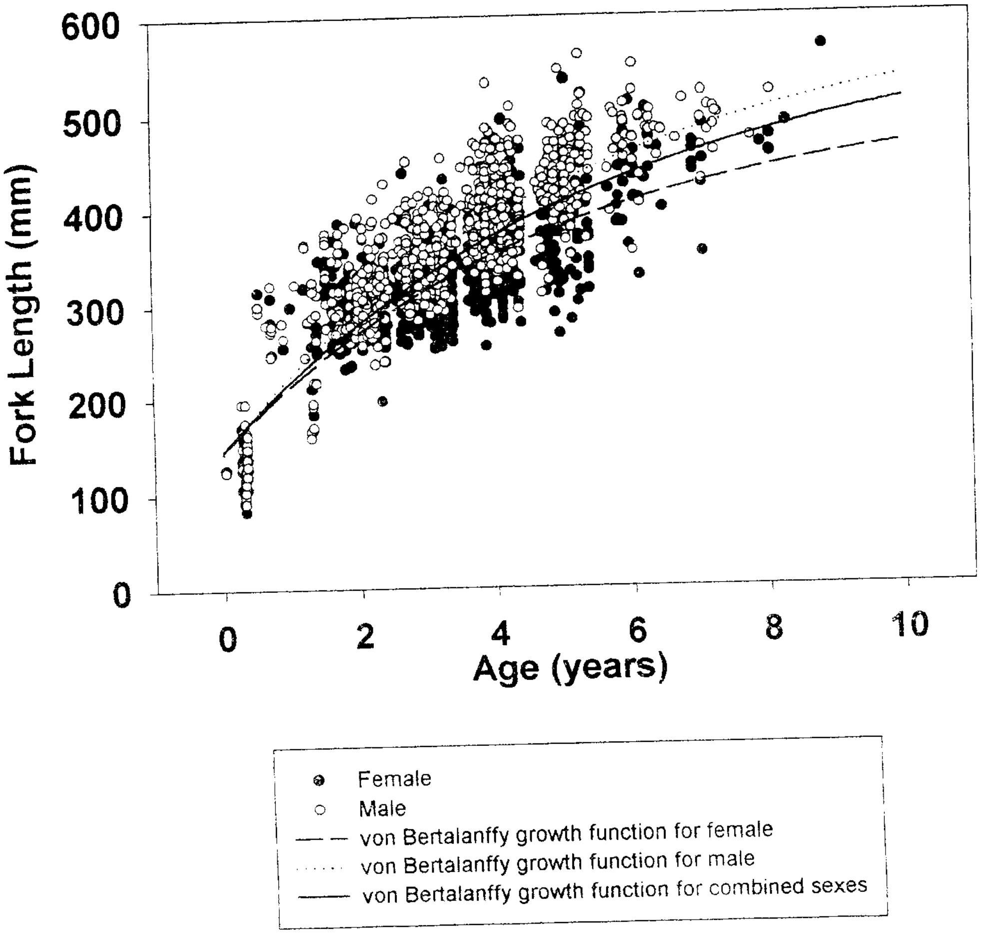

Figure 3.10. Von Bertalanffy growth functions for gray triggerfish.

than females (Table 3.11, for model equations). Due to the categorical nature of the sex variable (i.e. M and F), this equation could be broken down into two equations – one for each sex (Table 3.11). Size at age increased 13.97 % per year of age for both male and female GTF. However, the equation for females shows a smaller intercept (209 mm) than for the equation for males (228 mm). Therefore, growth rates may have been the same for both sexes, but females were consistently smaller in fork length than males.

Area-Specific Growth. Area-specific von Bertalanffy growth functions could not be estimated without the inclusion of data for larger GTF sampled at tournaments, and those smaller fish collected during SEAMAP cruises. Otherwise, the area-specific models did not converge (SAS v.8).

The von Bertalanffy growth functions for GTF harvested by recreational fishers in the Don Kelly North General Permit Area, and in the Hugh Swingle General Permit Area differed slightly (Figure 3.11; Table 3.10, for equation). Hotelling's T^2 statistic indicated a significant difference in von Bertalanffy growth functions between GTF captured in different permit areas ($T^2 = 13381.05422, p << 0.0001$). Hugh-Swingle harvested fish attain a smaller asymptotic maximum length. The difference (with 95 % confidence intervals) in L_∞ parameters between growth functions is –5.4 mm (-8.5 to –2.3 mm). Hugh-Swingle harvested fish approach that length at a higher rate of growth. The difference (with 95 % confidence intervals) in Brody growth coefficients, K, between growth functions is 0.0187 year^{-1} (0.0164 to 0.0210 year^{-1}). Hugh-Swingle harvested fish have a higher theoretical age at 0 mm fork length. The difference (with 95 %

Table 3.11. Negative binomial growth equations for gray triggerfish.

Equation-Type	Equation	Dispersion Parameter	*p*-value for Lack-of-Fit Test
Male vs. Female Growth	$\ln FL = e^{5.4299} e^{-0.0882(\text{if female})} e^{0(\text{if male})} e^{0.1308(\text{age})}$ $\ln FL_{\text{female}} = e^{5.3417} e^{0.1308(\text{age})}$ and $\ln FL_{\text{male}} = e^{5.4299} e^{0.1308(\text{age})}$	0.0218	0.9887
Don Kelly North vs. Hugh Swingle Growth	$\ln FL = e^{5.5539} e^{-0.0251(\text{if Don Kelly})} e^{0(\text{if Hugh Swingle})} e^{0.0900(\text{age})}$ $\ln FL_{\text{Don Kelly}} = e^{5.5288} e^{0.0900(\text{age})}$ and $\ln FL_{\text{Hugh Swingle}} = e^{5.5539} e^{0.0900(\text{age})}$	0.0103	0.3989
Tagging Station-Specific Growth Rate	$\ln G = e^{-1.6256} e^{-0.7951(\text{if IA})} e^{-0.7712(\text{if IB1})} e^{-0.5784(\text{if IB2})} e^{-0.6566(\text{if IC})} e^{-0.5440(\text{if ID})} e^{-0.5373(\text{if IE})} e^{0.0427(\text{if OA})} e^{0(\text{if OC})}$	0.0000	1
Inshore vs. Offshore Growth Rate	$\ln G = e^{-2.3083} e^{0.7028(\text{if offshore})} e^{0(\text{if inshore})}$	0.0000	1

Figure 3.11. Von Bertalanffy growth functions for gray triggerfish harvested from the Hugh Swingle and Don Kelly North General Permit Areas.

confidence intervals) in t_0 parameters between growth functions is 0.1400 year (0.1248 to 0.1552 year).

The negative binomial regression run with FL as the dependent variable and age and permit area of harvest (i.e. Hugh Swingle or Don Kelly North General Reef Permit Areas) as the independent variables indicated that fish harvested in the Hugh Swingle General Reef Permit Area (Table 3.11, for equation) indicates a slightly larger size-at-age for Hugh-Swingle harvested fish. Because the area variable was categorical, this equation could be broken down into two equations – one for each area (Table 3.11, for equation). Size at age increased 9.42 % per year of age for fish harvested in both areas. However, the equation for Hugh Swingle harvested fish showed a larger intercept (258 mm) than for the equation for Don Kelly harvested fish (252 mm).

Growth of Tagged and Untagged Fish. A von Bertalanffy growth function was estimated from analysis of annuli in the first dorsal spines of all GTF collected for hard parts analysis and compared to the von Bertalanffy growth function estimated using Faben's method for those tagged during the study described in Chapter 2 (Figure 3.12). To directly compare growth functions between methods, a two-parameter von Bertalanffy growth function was computed for all fish based on hard parts analysis (Table 3.10, for equations). Hotelling's T^2 statistic indicated a highly significant difference in von Bertalanffy growth functions between the two, aforementioned methods (T^2 = 105168.2122, $p << 0.001$), with tagged GTF attaining a smaller asymptotic maximum length; the difference in L_∞ parameters between growth functions (with 95 % confidence intervals) is -47.45 mm (-49.20 to -45.71 mm). The tagged fish also approached L_∞ at a

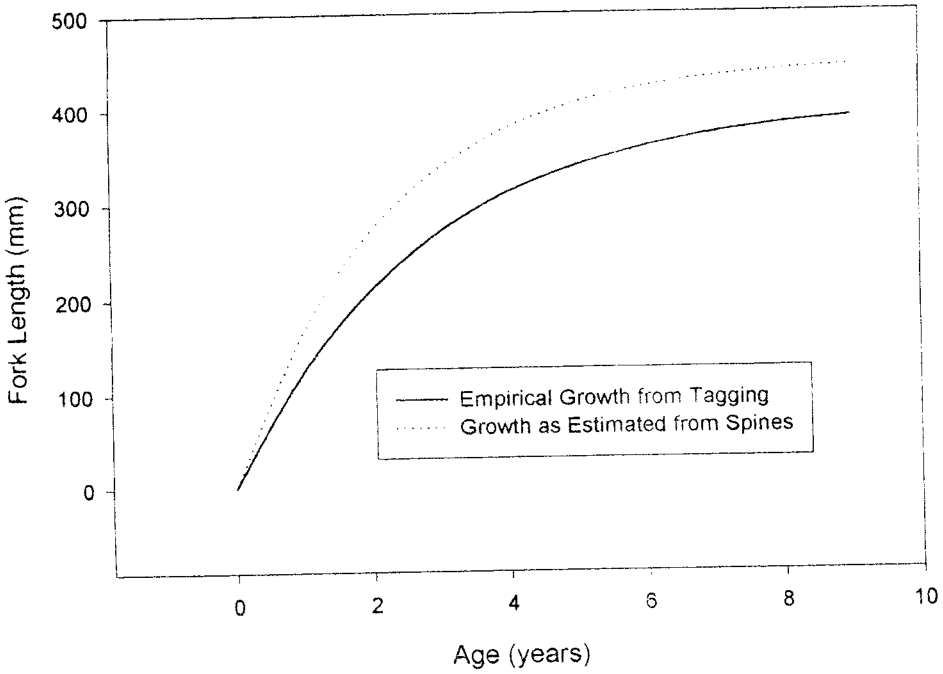

Figure 3.12. Von Bertalanffy growth functions based on empirical measurements from tagging and on age estimates from the first dorsal spines of gray triggerfish.

lower rate of growth; the difference in Brody growth coefficients, K, between growth functions (with 95 % confidence interval) is -0.0955 year^{-1} (-0.1018 to -0.0893 year^{-1}).

Growth of Fish Over Small Spatial Scales. The negative binomial regression employed to elucidate differences in growth on a small scale showed there were significant differences in growth rate of GTF tagged above different tagging stations (Table 3.11, for equation).

Due to trends of lower growth in fish tagged over the inshore stations, the data were grouped into depth strata (i.e. offshore stations and inshore stations) and growth rate was estimated as a function of station status (Table 3.11, for equation). Therefore, the mean growth rate (with a 95 % confidence interval) on the offshore tagging stations was estimated to be 0.20 mm day^{-1} (0.12 to 0.33 mm day^{-1}), and the mean growth rate (with a 95 % confidence interval) on the inshore tagging stations was estimated to be 0.10 mm day^{-1} (0.08 to 0.12 mm day^{-1}). The growth rate of GTF tagged over offshore stations was significantly greater than that of GTF tagged above inshore stations (negative binomial regression, $p < 0.0001$).

3.3.2 Reproduction

Both histological condition of maturity, and GSI indicate that spawning activity for both male and female GTF increases in May, peaks during June and July, and then decreases during August (Figures 3.13 - 3.15). Sex-specific plots of GSI versus age and fork length provide insight into size and age at maturity for GTF (Figures 3.16 – 3.19).

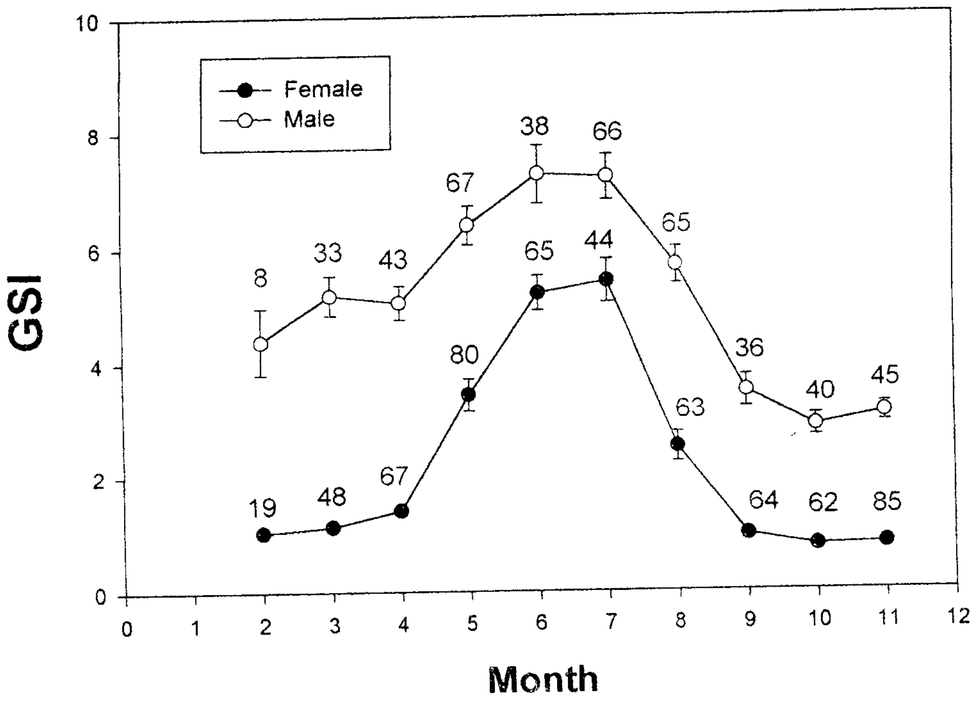

Figure 3.13. Mean monthly gonosomatic indices for male [100*(gonad weight as % body weight)] and female (gonad weight as % body weight) gray triggerfish. Error bars represent standard error and numbers represent monthly sample sizes.

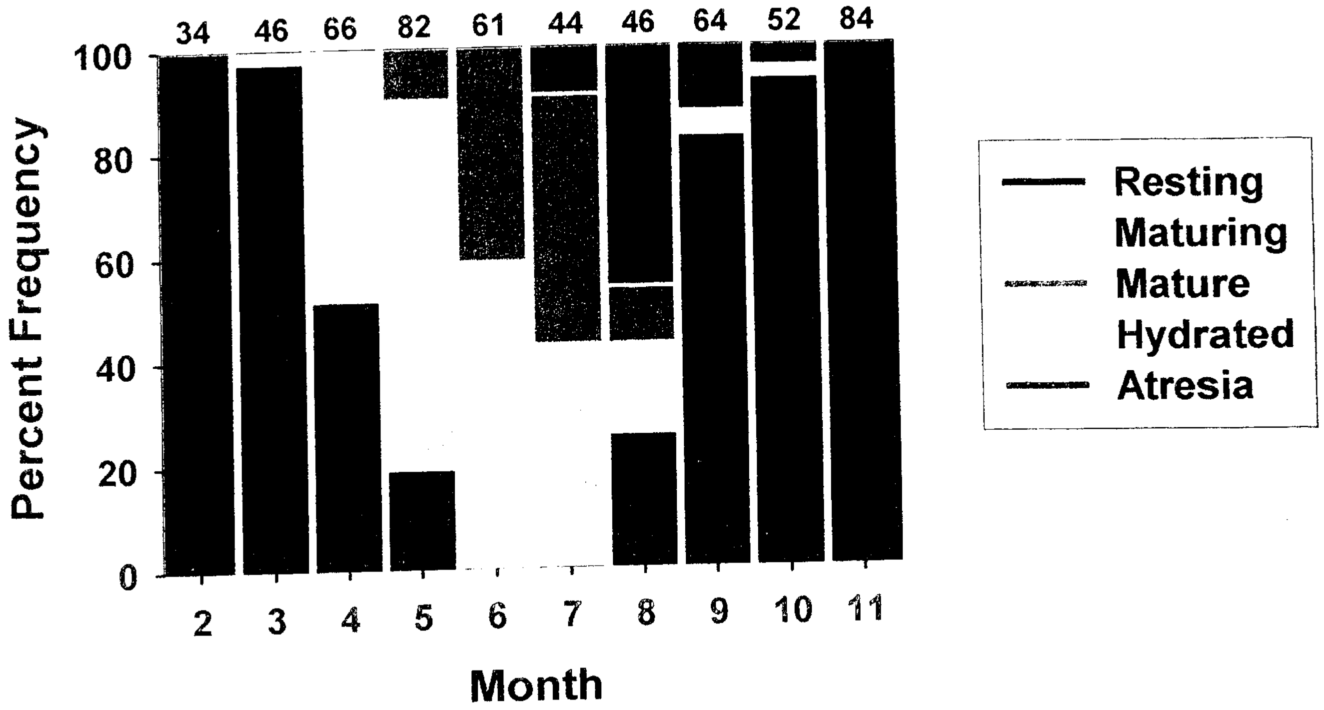

Figure 3.14. Monthly histological condition of female gray triggerfish gonads. Numbers on the upper axis represent monthly sample sizes.

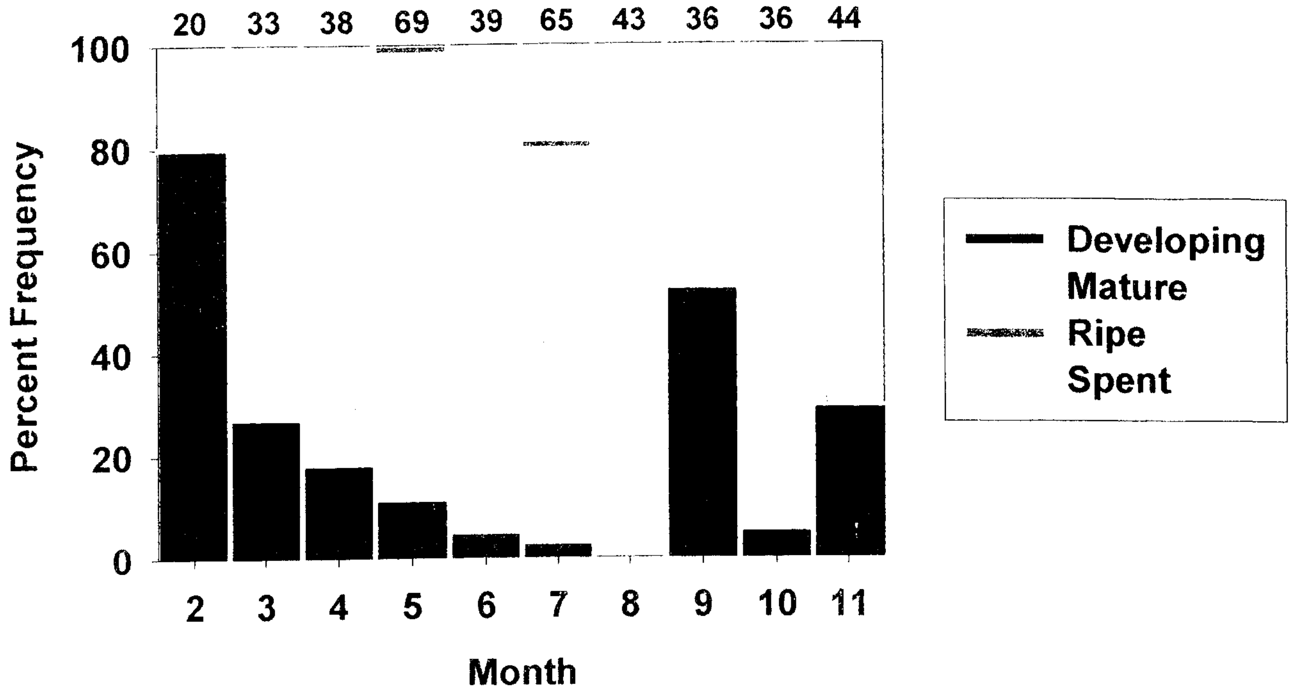

Figure 3.15. Monthly histological condition of male gray triggerfish gonads. Numbers on upper axis represent monthly sample sizes.

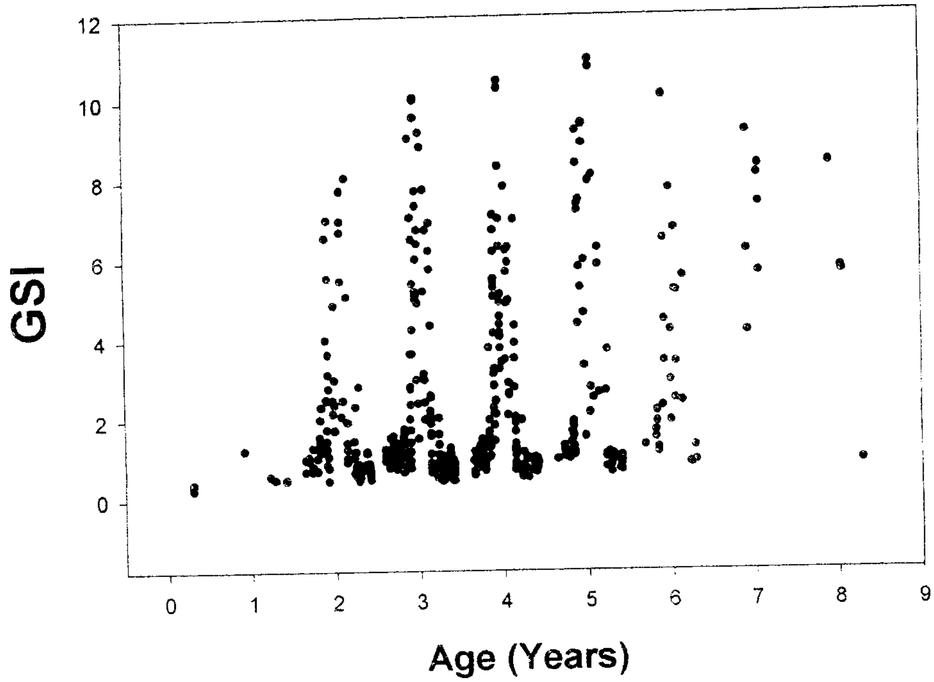

Figure 3.16. Gonosomatic index (gonad weight as % body weight) versus age of female gray triggerfish.

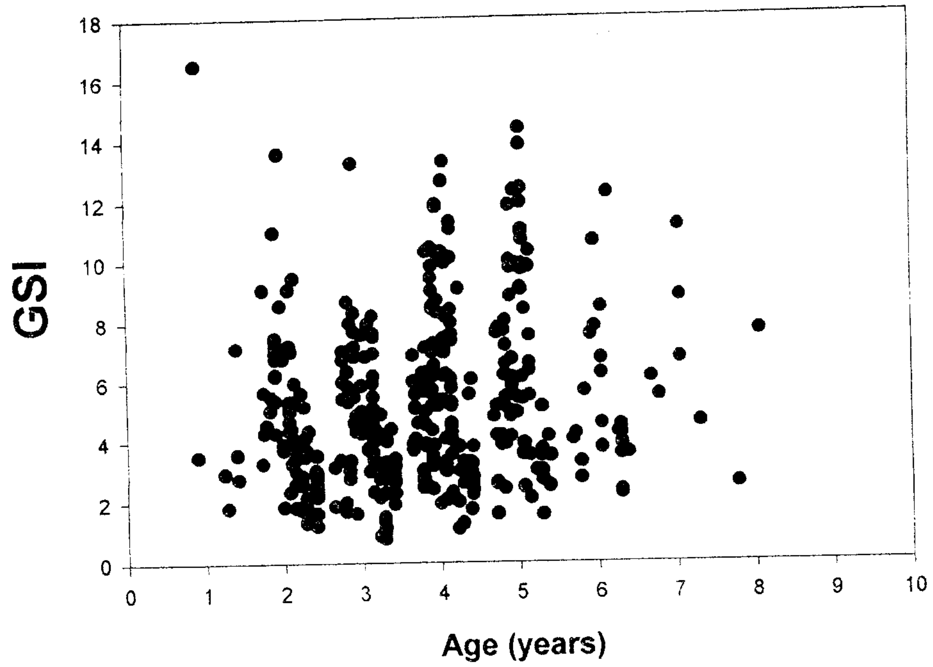

Figure 3.17. Gonosomatic index [100*(gonad weight as % body weight)] versus age of male gray triggerifsh.

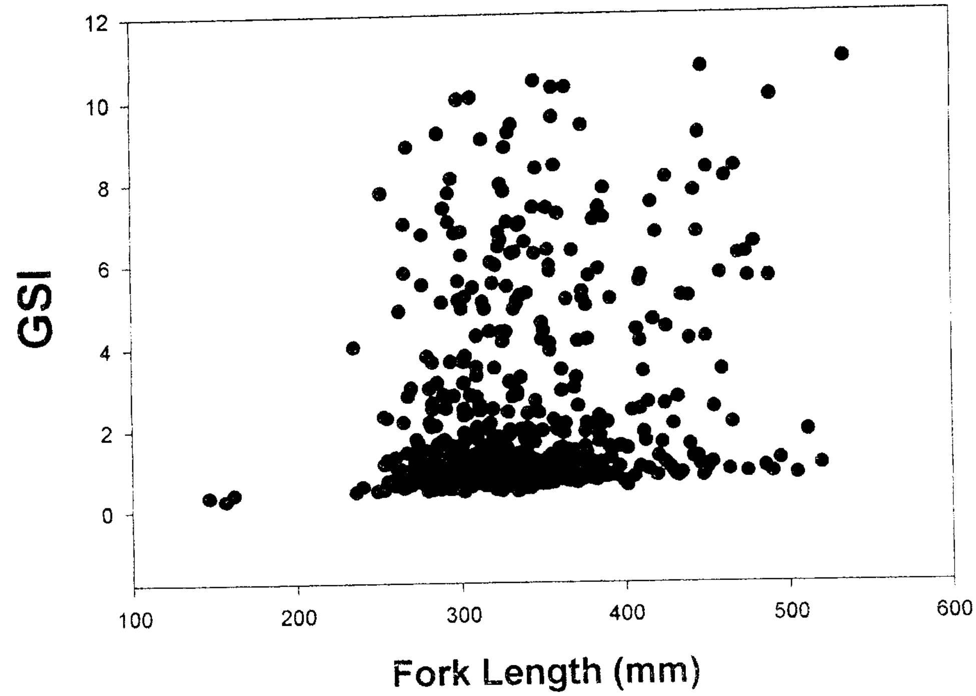

Figure 3.18. Gonosomatic index (gonad weight as % body weight) versus fork length of female gray triggerfish.

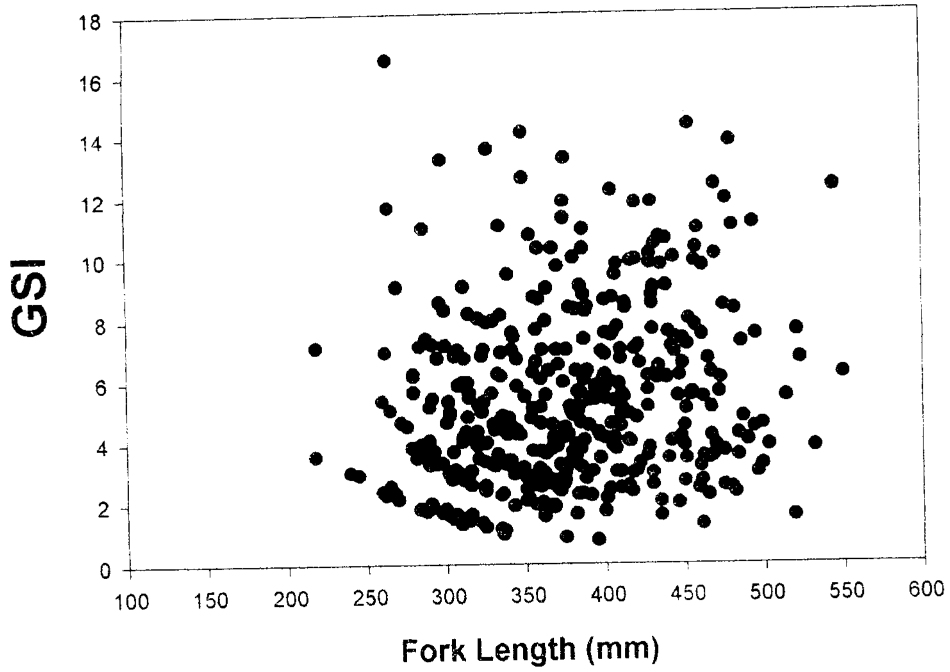

Figure 3.19. Gonosomatic index [100*(gonad weight as percent body weight)] versus fork length of male gray triggerfish.

These plots indicate that 1-year-old males (>250 mm fork length) and 2-year-old females (>250 mm fork length) exhibit seasonal maturation cycles associated with spawning.

No hydrated oocytes were found in histological sections of females. Therefore, I enumerated oocytes undergoing FOM to estimate batch fecundity. Mean diameter (± standard error) of oocytes undergoing FOM was estimated to be 418 µm (± 1). Of the 613 females from which gonads were taken, 59 were observed to be at FOM stage. Of these, 34 were used to estimate batch fecundity. Batch fecundity estimates ranged from 96,379 to 2,649,027 oocytes undergoing FOM per ovary. The mean (± standard error) number of oocytes undergoing FOM per gram was estimated to be 8,015 (± 247). The batch fecundity-fork length relationship (Figure 3.20), batch fecundity-age relationship (Figure 3.21), and batch fecundity-weight relationship (Figure 3.22) all indicated an increase in fecundity with size and age.

The mean percent (± standard error) of females spawning per day during the spawning season was 27.3 % (± 4.6). The mean interval between (± standard error) spawnings was estimated to be 3.7 days (± 0.6). Females with ovaries containing oocytes undergoing FOM were observed from late May to late August (~ 90 days). Therefore, the mean number of spawnings (± standard error) per spawning season was estimated to be 24.3 (± 4.1). Mean total annual fecundity (± standard error) was estimated to be 17,071,634 eggs year^{-1} (± 2,010,787).

The area-specific GSI for females per month indicated a month lag in the onset of ovary development for fish captured in the Hugh Swingle General Reef Permit Area when compared to those captured in the Don Kelly North General Reef Permit Area (Figure 3.23). The ANOVA procedure performed for females indicated that permit area

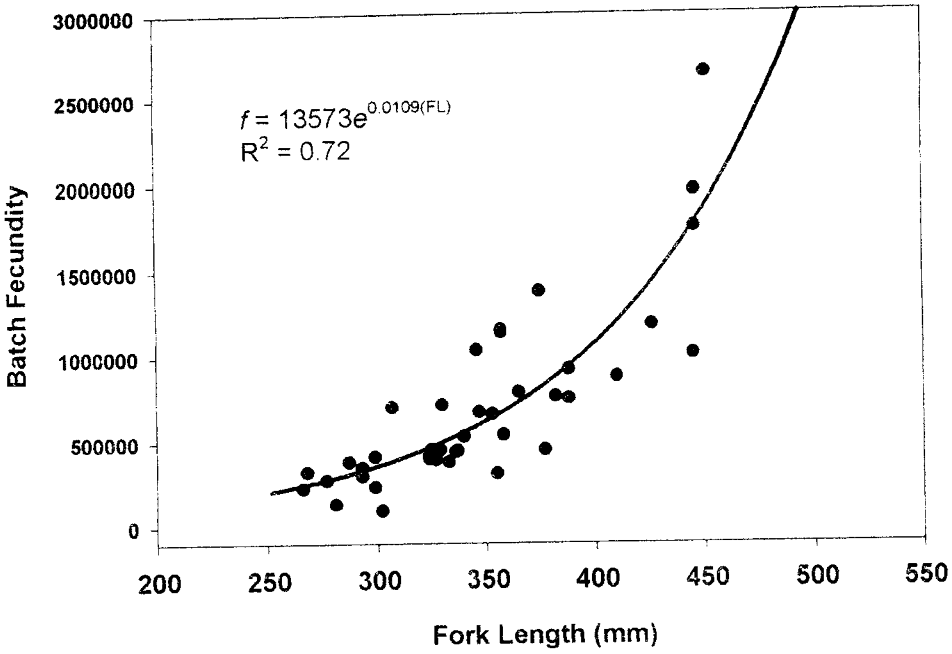

Figure 3.20. Batch fecundity versus fork length of gray triggerfish.

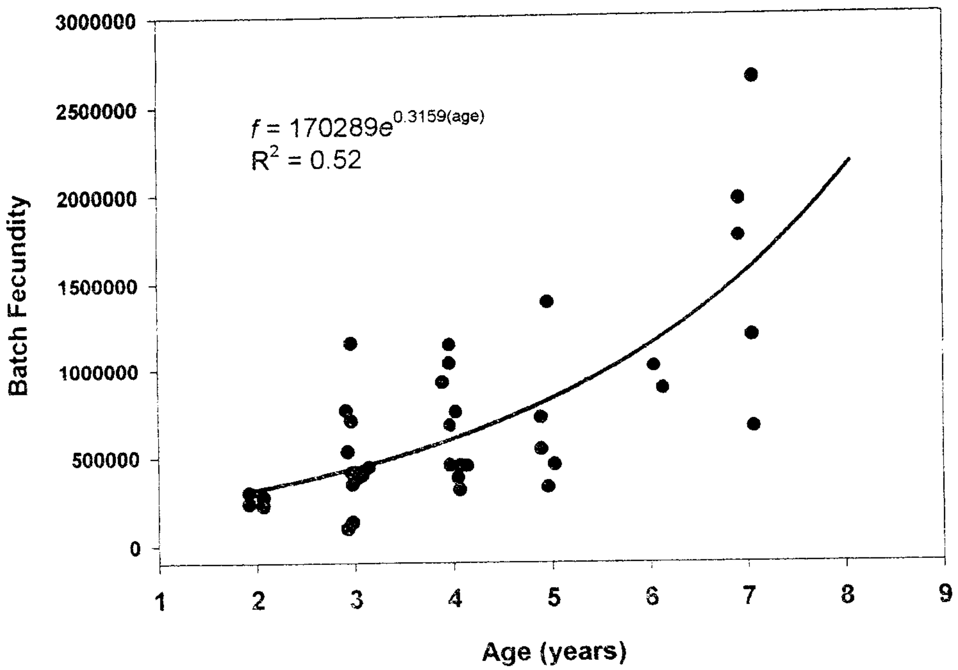

Figure 3.21. Batch fecundity versus age of gray triggerfish.

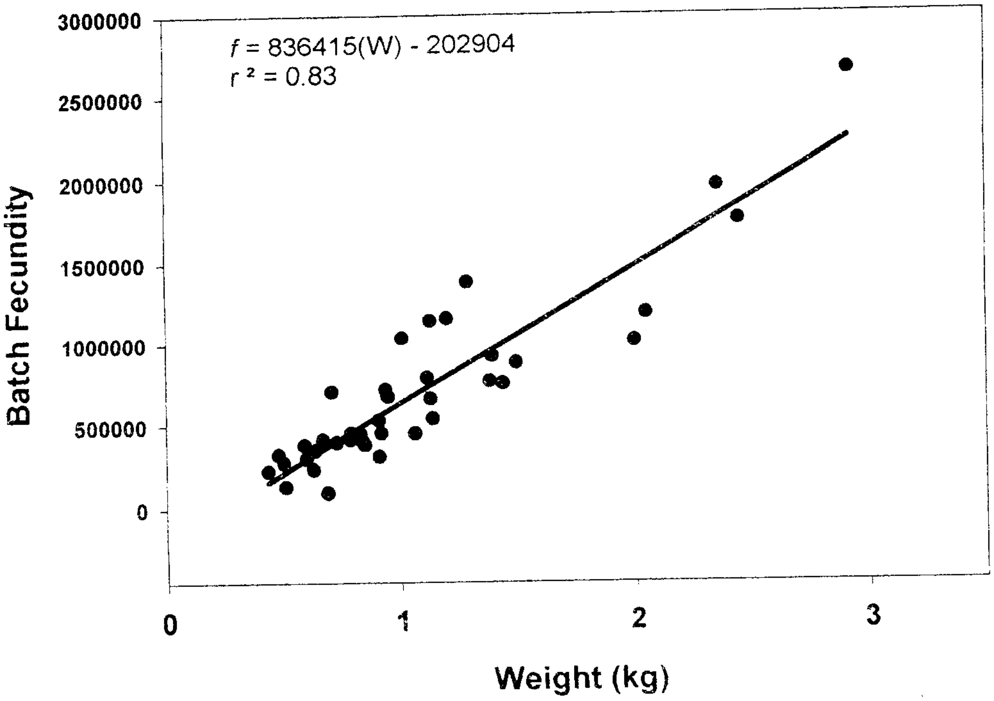

Figure 3.22. Batch fecundity versus weight of gray triggerfish.

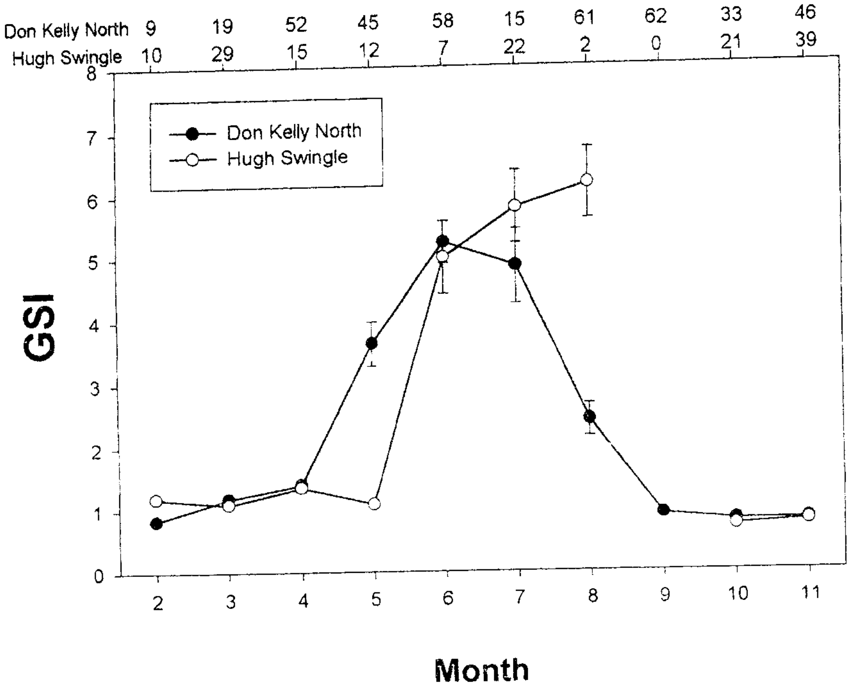

Figure 3.23. Mean monthly gonosomatic indices (gonad weight as % body weight) for female gray triggerfish captured in the Don Kelly North and Hugh Swingle General Permit Areas. Error bars represent standard errors, and the numbers on the upper axis represent monthly sample sizes.

of captured, month and their interaction were all significant effects on GSI (i.e., p = 0.0063, $p < 0.0001$ and $p < 0.0001$, respectively) and the resulting model had a coefficient of determination of 58.4 %.

The area-specific GSI for males per month indicated a decrease in GSI of fish captured in the Hugh Swingle General Reef Permit Area during the month of May and a steep decrease in the GSI in August, when compared to those captured in the Don Kelly North General Reef Permit Area (Figure 3.24). The ANOVA procedure performed for males indicated that permit area of capture, month and their interaction were all significant effects on GSI (i.e. $p = 0.0273$, $p < 0.0001$ and $p = 0.0021$, respectively) and the resulting model had a coefficient of determination of 38.3 %.

3.3.3 Mortality

Instantaneous total annual mortality rate (Z ± standard error) and subsequently annual survival (S ± standard error) for all fish sampled for hard parts was estimated to be 0.82 year^{-1} (± 0.08) and 0.44 year^{-1} (± 0.04), respectively (Figure 3.25). One and two-year-old GTF were found to be 7.3 % and 41.4 % recruited, respectively, to the recreational fishery after back calculation. M was estimated to be 0.50 using Hoenig's method (1983), and F was estimated to be 0.32.

Instantaneous total annual mortality rate (± standard error) of fish harvested from Don Kelly North General Permit Area (Z_{DK}) versus those harvested from the Hugh Swingle General Permit Area (Z_{HS}) was estimated to be 0.75 year^{-1} (±0.12) and 0.97 year^{-1} (±0.04), respectively (Figure 3.26). After subtracting M as estimated earlier by Hoenig's method, and assuming the remaining mortality component of Z could be

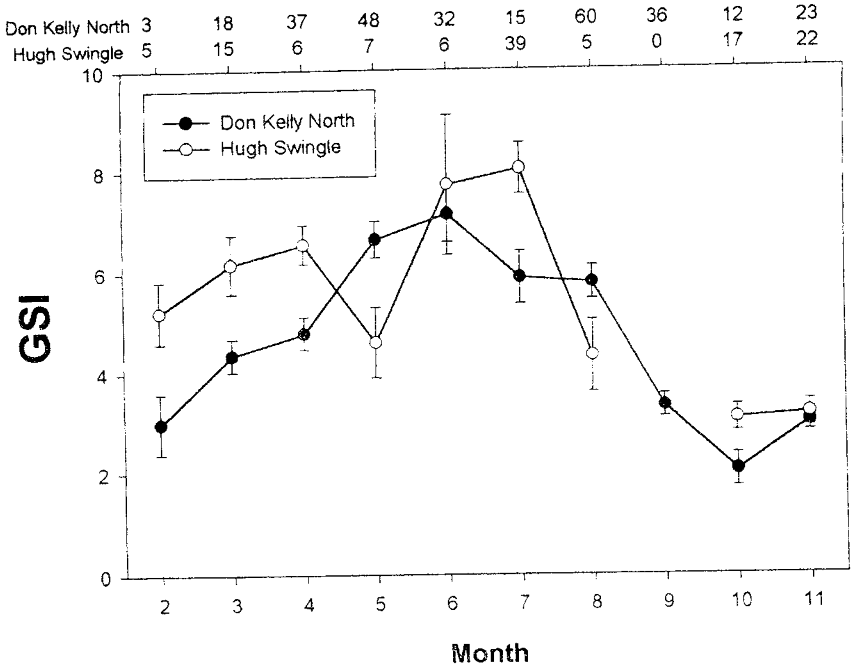

Figure 3.24. Mean monthly gonosomatic indices [100*(gonad weight as % body weight)] for male gray triggerfish captured in the Don Kelly North and Hugh Swingle General Permit Areas. Error bars represent standard errors, and the numbers on the upper axis represent monthly sample sizes.

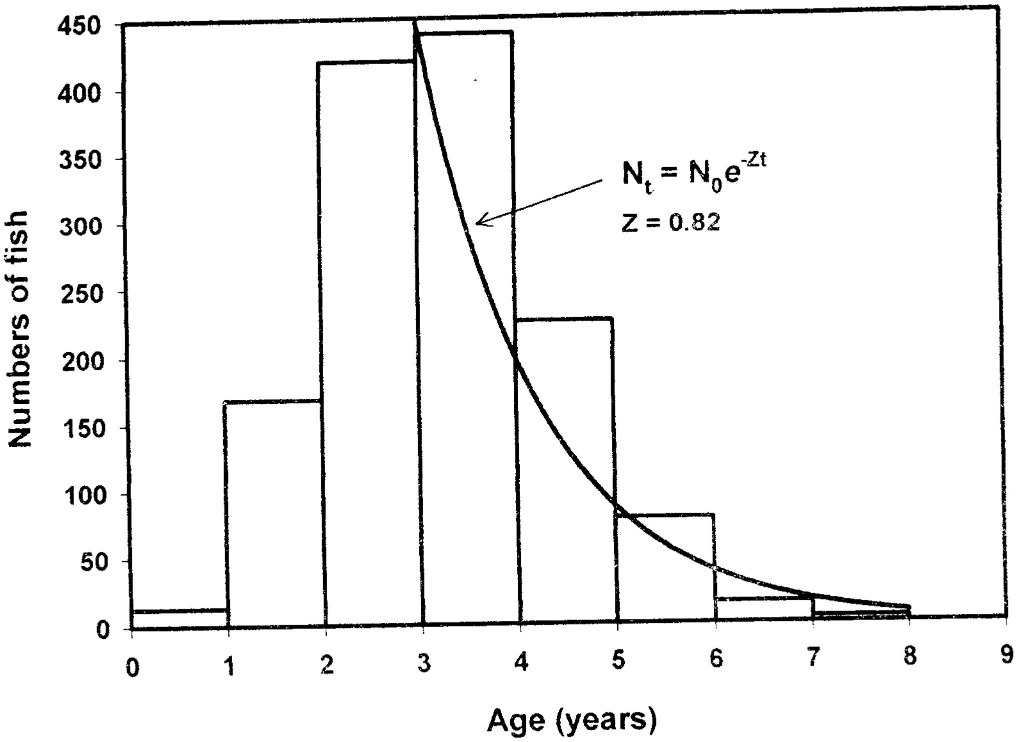

Figure 3.25. Age-frequency distribution of gray triggerfish captured by recreational fishers off the Alabama coast, excluding tournament fish and fish collected by SEAMAP, and a plot of the decay in number of fish over time used to estimate total mortality (Z).

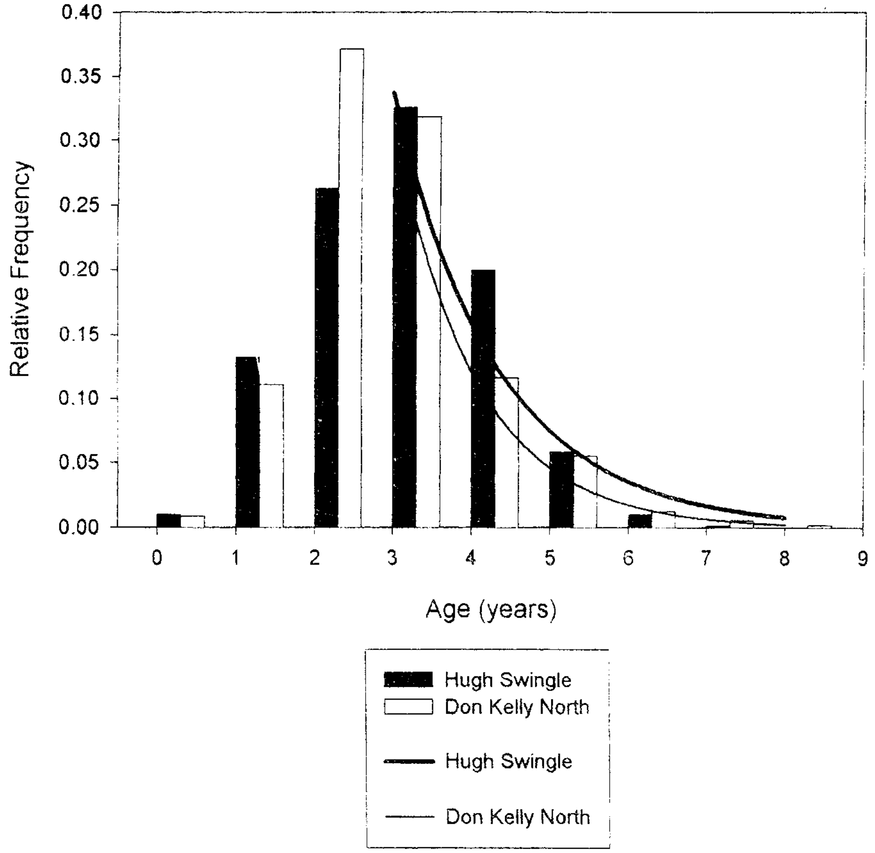

Figure 3.26. Age-frequency and decay of frequency of gray triggerfish over time for fish captured in the Hugh Swingle and Don Kelly North General Permit Areas.

attributed solely to fishing, estimates of F were estimated to be 0.25 year^{-1} and 0.47 year^{-1}, for Hugh Swingle harvested fish (F_{HS}) and Don Kelly harvested fish (F_{DK}), respectively.

Instantaneous total annual mortality rate (± standard error) of GTF tagged above inshore stations (Z_{I}) versus those tagged above offshore stations (Z_{O}) was estimated to be 1.59 year^{-1} (±0.02) and 0.86 year^{-1} (± 0.03), respectively (Figure 3.27). After subtracting M and assuming the remaining mortality component of Z could be attributed solely to fishing, F estimates were estimated to be 1.09 year^{-1} and 0.37 year^{-1}, for inshore (F_{I}) and offshore (F_{O}) stations, respectively.

3.4 Discussion

3.4.1 Annulus Formation

My interpretation of patterns in GTF growth, catch-per-unit-effort (CPUE), reproduction, and increment formation in spines, as well as the relatedness of these patterns, is summarized in Figure 3.28. Both the relative marginal increment analysis, and the monthly condition of the margin of the first dorsal spines indicate that a translucent annual mark forms in December-February, and that a spawning check forms in some fish during July-August. Both of these time periods represent periods of slow somatic growth and low CPUE. The spring increase in CPUE corresponds with spring growth as indicated in the first dorsal spine by the formation an opaque band.

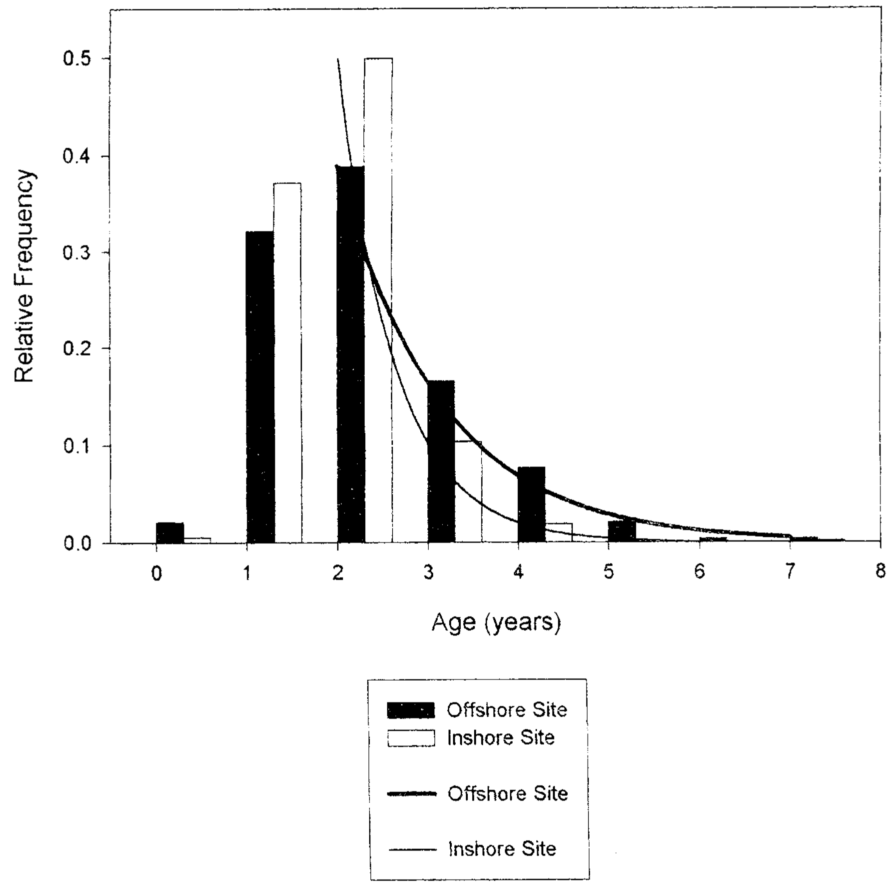

Figure 3.27. Age-frequency and decay in frequency of gray triggerfish with age for fish tagged at Inshore and Offshore Tagging Sites.

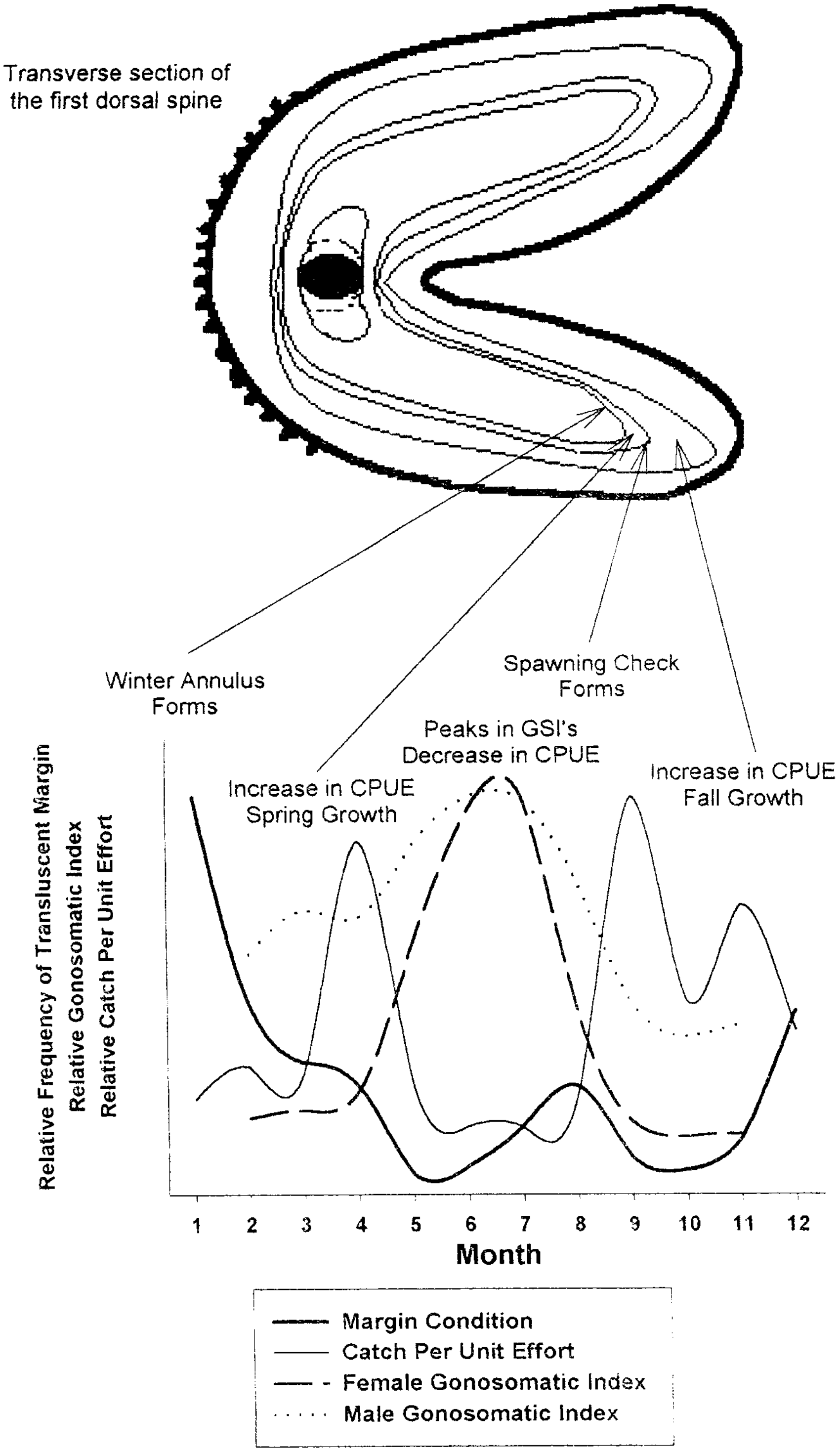

Figure 3.28. Annulus formation in the first dorsal spine of gray triggerfish.

I reason that changes in CPUE directly correspond to changes in feeding activity and not to changes in abundance, and provide a rough index of feeding activity. In Chapter 2, GTF were reported to have high site fidelity. Therefore, seasonal changes in abundance due to emigration/immigration should not be the cause of changes in CPUE.

During the summer months, as both male and female gonosomatic indices (GSI's) of spawning activity peaked, CPUE dropped to its lowest point during the year. After the peak in spawning activity and the observed CPUE minimum, CPUE began to increase, and a spawning check forms as indicated as another translucent band in some spines. The formation of these spawning checks probably is attributable to reproductive behavior. During the spawning season, the territorial male GTF prepare a number of nests (see Chapter 2). Males then coax females to the nests, not allowing them to leave. I suggest that this haremic spawning behavior, which has been described for many other species of triggerfishes (e.g., Fricke, 1980; Nellis, 1980; Thresher, 1984; Gladstone, 1994; Ishihara and Kuwamura, 1996; and Kuwamura, 1997), may affect growth of both males and females, possibly leading to the formation of false annuli in the spine.

Finally, the annulus is completed when the wide opaque band indicative of fall growth forms in the spine, which is correlated with sustained high levels of CPUE. The formation of the next winter annual mark corresponds with the decrease in CPUE during the winter. With the pattern of annulus formation established, enumeration of annuli and age estimation was straightforward.

There also appears to be a settlement mark that forms near the focus in the first dorsal spine of most GTF sampled (~ 89 %). The settlement mark is a translucent ring encircling the focus. Due to the mark's close proximity to the focus, even in small fish

(80 – 100 mm fork length) less than 1 year old, it is assumed to be associated with the period of transition between pelagic and demersal habitats. The settlement mark was the only mark in the first dorsal spine resorbed by increased vacularization in larger and older fish, and thus did not affect estimates of age.

3.4.2 Data Sets

Initially, it might have been confusing to the reader that I included statistics describing both the entire sample of GTF, and the sample excluding tournament and SEAMAP collected fish. Statistics concerning the entire sample were aimed at characterizing all fish available for analysis, thus representing the largest ranges of size and age. The statistics concerning only those captured in the Hugh Swingle General and the Don Kelly North Permit Areas were aimed at characterizing the recreational fishery off the Alabama coast. SEAMAP captured fish were the smallest and youngest in the overall sample. Those sampled at tournaments were the largest and oldest fish that I encountered. For all mortality estimates, and for estimates of growth derived from negative binomial regression, no tournament or SEAMAP-captured fish were used. Only in derivation of estimates of von Bertalanffy growth parameters did I use data from both tournament and SEAMAP-captured GTF, because the algorithm used by SAS V.8 did not converge without the data on large and small GTF. Lack of convergence was probably due to the sensitivity of the von Bertalanffy growth function to data from large and small fish. Without these fish in the data set the model was essentially linear. Therefore, some of the growth functions may have been biased by non-random or selective sampling, such as bias introduced when sampling tournament fish (Goodyear, 1995). However, sampling large fish at tournaments, and small fish from SEAMAP trawls was deemed useful because GTF of these sizes and ages were rarely landed otherwise.

3.4.3 Gulf-Wide Growth and Mortality Statistics

The average age of male and female GTF captured off the Alabama coast was nearly identical, based on data excluding tournament and SEAMAP-captured fish. However, both von Bertalanffy and negative binomial growth parameters indicated that males attain a larger size than females. These sex-specific parameters, and the von Bertalanffy parameters for combined sexes of Alabama GTF, are different from similar estimates from other regions of the Gulf. For example, Alabama fish apparently attain a larger asymptotic length, but approach that theoretical maximum length more slowly than estimated for fish sampled from the hook and line fishery off Panama City Beach, Florida during the late 1970's and the early 1980's (Johnson and Saloman, 1984). Johnson and Saloman also reported that fish off northwest Florida obtain a higher maximum age (i.e. male = 13 years; female = 12 years) than Alabama GTF. Likewise were the findings of Wilson et al. (1995), who sampled commercially caught GTF off Louisiana (i.e. maximum age = 11 years). For fish caught off the west coast of Florida, Hood and Johnson (1997) reported that females had a smaller asymptotic length than males, and males approach that asymptote at half the rate of females. When compared to Alabama GTF, females from west Florida had a smaller asymptotic length but approach that asymptote faster; males have a larger asymptotic length and approach it slower; and, for combined sexes, GTF have a larger asymptotic length and approach it slower.

Differences in estimates of mortality rates of GTF in this study, versus those from other regions of the Gulf may, in part, explain differences in von Bertalanffy growth parameters between those regions, given that the size-age structure of the stock (or MU within the stock) affects the estimated values of said parameters. Hood and Johnson (1997) estimated instantaneous total mortality of recreationally and commercially caught GTF off the west Florida coast to be 0.83 $year^{-1}$ and 0.82 $year^{-1}$, respectively, which was very similar but slightly higher than the above reported instantaneous total mortality rate estimated for Alabama GTF (i.e., 0.82 $year^{-1}$). Instantaneous total mortality estimated for GTF off the coast of Panama City Beach, Florida was estimated to be 0.67 $year^{-1}$ by Johnson and Saloman (1984), which is lower than that estimated in this study or by Hood and Johnson (1997).

On the Gulf-wide scale growth and mortality parameters cannot be directly compared because differences may be attributable to changes in fishing pressure over time. Landings (Figure 1.1) and mortality estimates of GTF collected in the late 1970's and early 1980's indicate little exploitation (i.e. probably a lack of targeting of GTF by fishers during this time)(Johnson and Saloman, 1984). With later studies (i.e. Wilson et al., 1995 and Hood and Johnson, 1997; Harper and McClellan, 1997, for review), data were collected after landings had peaked and were on the decline (Figure 1.1). Due to increases in regulations on other reef fishes and the increased desire of GTF as table fare, I reason that GTF were exploited more during the earlier to mid 1990's than during the 1970's and 1980's. This may explain the larger estimates of mortality between studies. For the current study, data were collected during the late 1990's and the year 2000. Currently, GTF may be fully exploited, especially in view of the fact that during the past

4 years the red snapper fishery has closed in the late summer to early fall, and has reopened in the spring. Fishers target GTF during this time to supplement their catch (per. obs.), and during the fall CPUE of GTF is higher than in other seasons (see Chapter 2). Moreover, as indicated earlier GTF off Alabama have a higher estimate of fishing mortality than in previous studies, which may be indicative of increases in fishing pressure. Therefore, temporal differences in growth and mortality parameters resulting from different levels of exploitation may preclude any meaningful comparisons of growth and mortality to gain insight into stock structure at this scale.

3.4.4 Local Growth and Mortality Statistics

Growth of tagged GTF (see Chapter 2) apparently was affected by the tagging process. The growth rate of tagged fish was significantly less than those aged through analysis of the first dorsal spine. There are many ways that the tagging process may have reduced the growth rate. First, the incision, tag insertion and subsequent healing process associated directly with tagging could have reduced growth rate (Henderson-Arzapalo et al., 1999). Moreover, if the tag wound became infected during the healing process, growth rate may have been further reduced (Henderson-Arzapalo et al., 1999). Also, growth rate may have been affected by the energetic consequences of the increase in drag caused by the tag, especially if the external portion of the tag became fouled (Henderson-Arzapalo et al., 1999). In contrast, Patterson (1999) reported no reduction in growth rate of abdominally tagged red snapper off the Alabama coast.

It is also possible that observed differences in mortality of GTF are attributable to differences in growth rates, and subsequently the size-age structure of fish sampled in each case. Total mortality was estimated to be relatively high for GTF sampled during the tagging study, versus those sampled for age estimation. Because growth and mortality have been shown to be negatively correlated (Houde, 1987), slow growth in tagged GTF may have directly affected other vital rates. Finally, differences in growth rate may be due to a difference in fishing mortality between the areas in which GTF were tagged, and the areas from which fish were collected for hard-part analysis. If fishing mortality is higher in areas where tagging occurred, then faster growing individuals which recruit to the fishery first may have been removed more quickly from that area, leaving slower growing individuals behind, thus lowering the apparent growth rate of GTF in tagging areas (Ricker, 1975; see below).

Intuitively, one would expect higher fishing pressure closer to shore. The Southeast Banks Area off the Alabama coast, in which is located the Inshore Site, is publicly known as an excellent place to capture GTF. Both anecdotal evidence, as indicated by charter boat captains from Dauphin Island, Alabama, and many publications of the Alabama Department of Conservation and Natural Resources, Marine Resources Division, make this case.

Observed differences in growth rate between fish tagged above Inshore and Offshore Sites could have resulted from the effects of tagging on smaller fish at stations within the Inshore Site, versus the effects of tagging on larger fish at stations within the Offshore Site. Small GTF may have suffered greater long-term tagging effects than larger GTF. Long-term effects of tagging on individual GTF, however, were not the topic of this research. However, as suggested earlier, tagging did significantly affect growth rate. Szedlmayer and Shipp (1994) reported that laboratory held red snapper, which were tagged with internal anchor tags, showed no signs of infection or stress and did not experience significant tagging mortality. GTF are laterally flattened when compared to red snapper, and Neilsen (1992) suggested that internal anchor tags are appropriate for more robust species. Insertion of the internal anchor tag may penetrate farther into the viscera in species like GTF, and thus cause decreases in growth due to stress of tagging (Henderson-Arzapalo et al. 1999).

The differences in growth rates between Inshore and Offshore Sites may be due to a combination of individual growth heterogeneity, and size-selective mortality. The more aggressive and/or faster growing individuals may have been removed more quickly in areas of higher fishing mortality because they recruit to the fishery earlier than do slower growing individuals. The selective removal of faster growing individuals may explain the slower growth rates of GTF in areas of higher fishing mortality (Ricker, 1975), and has been seen in a number of other species. Reductions in growth of the temperate reef fishes red porgy (*Pagrus pagrus*; Harris and McGovern, 1997) and vermilion snapper (*Rhomboplites aurorubens*; Zhao et al., 1997) resulted from sustained overexploitation that has selectively removed individuals predisposed towards rapid growth and larger size. Moreover, Kristiansen and Svåsand (1998) used a combination of mark-recapture data and an individual-based growth and mortality model to describe selective removal of faster-growing coastal cod (*Gadus morhua*) and subsequent depression in mean growth rates over time.

This decrease in growth rate coupled with an increase in mortality rate seems counterintuitive to the idea of density-dependent growth (Beverton and Holt, 1957). The notion that growth rate is correlated to population size (i.e. as mortality increases and population size decreases, more resources are available for those remaining, allowing for an increase in growth) has been described for many fresh water species (e.g., Donald and Anderson, 1982; Fox and Flowers, 1990; and Le Cren, 1965; Walters and Post, 1993, for review). However, in the marine environment, examples of density-dependent growth in adult fish are few, except for reef fishes. Negative density-dependent effects (i.e. reduced growth rate and increased mortality) have been evaluated for many species of reef fishes (e.g. Doherty, 1982, 1983; Thresher, 1983; Jones, 1987). Such density-dependent effects indicate that competition is occurring probably because of limitation of resources or behavioral interactions (Jones, 1991, for review). Moreover, Bannister (1977) summarized density-dependent growth in North Sea plaice (*Pleuronectes platessa*), a demersal flatfish and non-reef species, which increased in mean length at age, due to increases in fishing mortality and subsequent decreases in population size. In the case of the present study, I reason that differences in growth rates of GTF between Inshore and Offshore Sites are due to increased size-selective mortality on fish associated with the Inshore Site, and any density-dependent affects may be eclipsed by increased size-selective mortality.

GTF mortality off the Alabama coast appears to follow north to south, and east to west gradients (Figure 3.29) decreasing with distance from shore, and from east to west. Intuitively, one can understand the decrease in fishing mortality with the increase in distance from shore, because recreational fishing effort in small boats probably decreases in the offshore direction. The east-west decrease in fishing mortality also may be attributable to a decrease in fishing pressure, as the largest charter boat fleet in Alabama is based in Orange Beach, a town on the Alabama-Florida border. There are

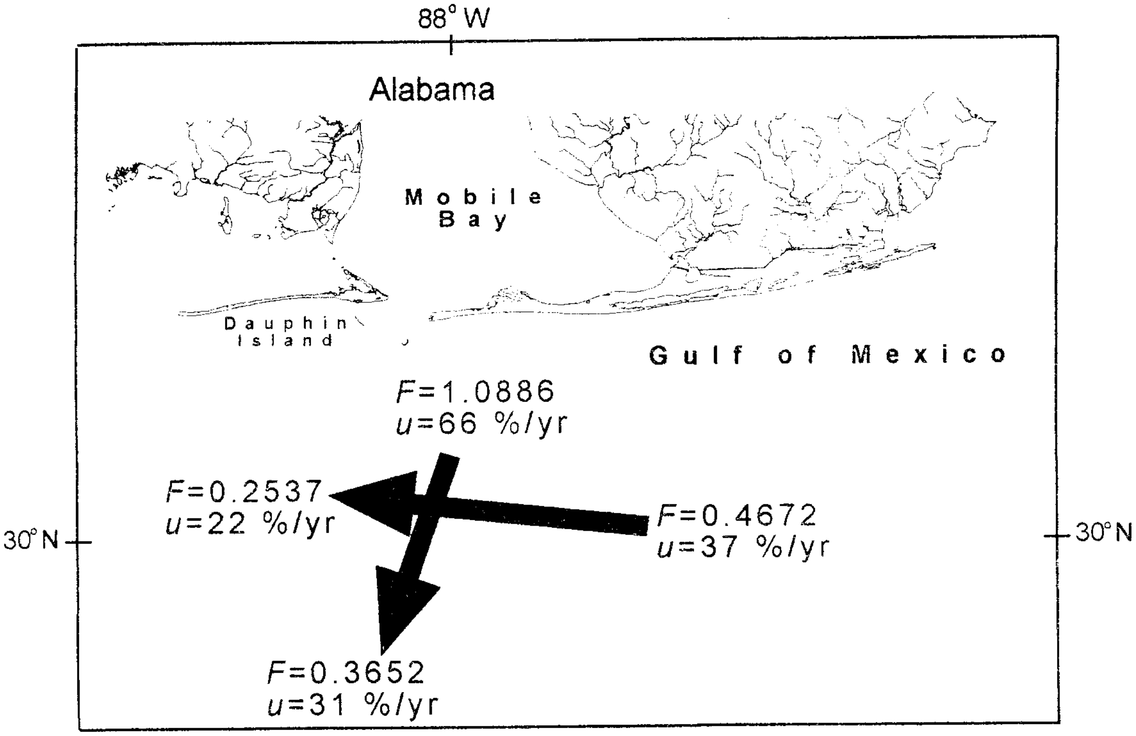

Figure 3.29. Spatial trends in mortality of gray triggerfish off the Alabama coast. Estimates of instantaneous fishing mortality (*F*) and annual rate of exploitation due to fishing (*u*) as transformed by Ricker (1975) are provided.

approximately 200 vessels in the charter boat fleet in Orange Beach, comparerd to 10 vessels in the charter boat fleet on Dauphin Island (James Duffy, per. comm.[1]). Orange Beach is located almost due north of the Don Kelly North General Permit Area, and Dauphin Island is located due north of the Hugh Swingle General Permit Area. I have no direct measurements of fishing effort by these two fleets. However, as most charter boat captains minimize the distance traveled to minimize fuel costs and maximize profit of each fishing trip, there is probably more fishing pressure in the Don Kelly Area.

3.4.5 Reproductive Dynamics and Statistics

Both histological condition of maturity and GSI indicated that GTF spawn from May through August. These results are similar to those of Wilson et al. (1995) who reported that ovarian histology and GSI indicated that gray triggerfish captured off Louisiana spawn during late spring and summer. In contrast, my samples indicate that GTF off Alabama begin and cease to spawn earlier in the year than those studied by Dooley (1972), who estimated the spawning season to be from July to October in the northern Gulf. Hood and Johnson (1997) reported that ovarian histology indicated that gray triggerfish captured off west Florida spawn during summer and early fall (June through September) with a peak in the GSI in August for female fish and in September for male fish. For Alabama, mature females with ovaries containing vitellogenic oocytes were first observed in May, and were present through August. Whereas, for west Florida GTF, mature females with ovaries containing vitellogenic oocytes were first observed in June and were present through September. Atretic females were observed from

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[1] Alabama Department of Conservation, Marine Resources Division, Dauphin Island, Alabama

September through October for west Florida GTF and from July through October for Alabama GTF. From October to April most Alabama GTF had developing gonads that contained primary growth oocytes and some atretic bodies.

GTF off Alabama appear to begin to spawn and cease to spawn one month earlier than do fish off west Florida. This difference in the temporal position of spawning season is counterintuitive to that seen in other fishes. For example, gag grouper (*Mycteroperca microlepis*) spawn earlier in south Florida than those in north Florida (Andrew Strelcheck, per. comm.[2]). Likewise, other serranids (i.e., *Epinephelus striatus*, *E. guttatus* and *Cephalopholis fulva*) show a pattern of winter spawning at low latitude and spring-summer spawning at high latitudes (Robertson, 1991). I have no conclusive explanation for this pattern of earlier spawning in Alabama fish. However, it may have resulted from the presence of mild winters in the 1998 and 1999 study years (CWRC, 1998, 1999, 2000), especially if warm temperatures are a cue for the initiation of spawning activity.

Relatively, few studies have been conducted on the duration of balistid spawning seasons, but results are consist with my and previous studies of GTF. *Monacanthus hispidus* spawns off South Carolina from May to November, with a peak in activity during July (Hildebrand and Cable, 1930). *Odonus niger* and *Pseudobalistes fuscus* from the Red Sea, and *Sufflamen verres* from the Gulf of California similarly spawn only during the warmer parts of the year (Fricke, 1980; Thresher, 1984). Data for six species in as many genera in the western Atlantic all suggest long spawning seasons, with peaks of activity in the spring, the fall or both (Randall, 1964; Munro et al., 1973; Aiken, 1975).

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[2] University of South Alabama. Department of Marine Sciences, Mobile, Alabama

Overall, estimates of batch fecundity and size-fecundity relationships were similar between Alabama and west Florida GTF, but estimates of GTF mean egg diameter (418 µm) were slightly smaller with those of other balistids. Triggerfish eggs have been described for species in five genera, *Balistes*, *Odonus*, *Pseudobalistes*, *Balistapus*, and *Sufflamen* (Garnaud, 1960; Fricke, 1980; Lobel and Johannes, 1980; Thresher, 1984), and all are spherical, slightly over 500 µm in diameter, and translucent. The number of oocytes undergoing FOM per gram was lower for Alabama fish, which could have resulted from the differences between methods of oocyte enumeration used in this study, versus those of Hood and Johnson (1997).

Spawning frequency of GTF appears similar to that of red snapper (approximately every 3.5 days, Melissa Woods, per. comm.[3]) inhabiting similar areas. In addition, this estimate seems reasonable when compared to incubation times of demersally deposited eggs of triggerfishes (12 to 58 hours) as reported by Thresher (1984). I reason that if the estimated time between spawnings is less than incubation time, then spawning frequency results are counterintuitive.

The estimates of reproductive seasonality between permit areas were found to be significantly different. However, the validity of this difference between GSI's in the Hugh Swingle and the Don Kelly North General Permit Areas were questionable, due to the small, monthly sample sizes of gonads from fish from the Hugh Swingle General Permit Area. If the relatively small samples were not truly representative of GTF in that permit areas than statistical differences may have been invalid.

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[3] University of South Alabama, Department of Marine Sciences, Mobile, Alabama

3.4.6 Stock Structure

In this chapter, growth, mortality, and reproductive parameters in combination with information on site fidelity presented in Chapter 2 are used to gain insight into stock structure. On the Gulf-wide scale, insight into stock structure cannot be gained, due to temporal differences in fishing pressure. In order to compare growth and mortality estimates from areas throughout the Gulf a comprehensive, Gulf-wide study would need to be conducted. During the current study, while fishing pressure may have differed in specific areas off the Alabama coast, it was assumed that temporal changes in fishing pressure did not occur. Therefore, heterogeneity in stock structure on this local level may be associated with the combination of distribution of fishing pressure and high site fidelity, and subsequent localization of growth rates. In addition, if localization of growth and mortality is actually occurring, then throughout the Gulf sampling may need to be conducted on local-scales to elucidate stock structure on the Gulf-wide scale. Thus, determination of Gulf-wide stock structure of GTF may be an arduous task.

CHAPTER 4: MODELING THE OCCURRENCE AND ABUNDANCE OF GRAY TRIGGERFISH LARVAE USING GENERALIZED LINEAR MODELS.

4.1 Introduction

Most reef fishes have a pelagic larval stage but are benthic as adults, resulting in a life history with two distinct and very different phases. Ninety-six percent of reef fish families have pelagic early life histories (Leis, 1991). Because many adult reef fish are relatively sedentary (Sale, 1980) and the pelagic stage may disperse at scales from meters to thousands of kilometers, the pelagic stage is more likely to determine the geographical range of population units than the adult stage. Such is the case for GTF. In Chapter 2, I concluded that GTF exhibit high site fidelity as adults, but the balistids as a family are reported to have demersal eggs and pelagic larvae (Leis, 1991).

The early life history of gray triggerfish has been reviewed from Senegal (Caveriviere et al., 1981; Caveriviere, 1989), and off Brazil (Matsuura and Katsuragawa 1981). Larval developement from Brazil was reviewed by Matsuura and Katsuragawa (1981). Longley and Hilderbrand (1942) and later Dooley (1972) described fish up to 100 mm to commonly occur in *Sargassum spp.* and about bits of flotsam. Aiken's (1983) study in Jamaica found juveniles among mangroves and in sargassum, and suggested larvae are transported by oceanic currents. In addition, the length of GTF pelagic phase during early life has been described as prolonged and indeterminate (Richards and Lindeman, 1987). GTF begin colonizing hard bottom habitat at approximately 160-170 mm SL (Vose and Nelson, 1994). Therefore, oceanic circulation, and the associated hydrography of the circulating water masses, may play a large role with respect to the distribution of larvae and juveniles, concentrating larvae into "clumps" associated with specific water masses.

In the U.S. Gulf of Mexico (Gulf), the dominant circulation feature is the Loop Current, which enters from the Caribbean through the Yucatan Channel and then exits through the Florida Straights. However, the Loop Current is not the major feature driving circulation over the continental shelves in the Gulf. The periodic shedding of eddies, both cyclonic and anti-cyclonic, from the Loop Current can modify circulation patterns on the west Florida shelf, Mississippi-Alabama shelf and Texas-Louisiana shelf. On the inner west Florida shelf, the circulation consists of longshore currents caused from wind stress (Mitchum and Sturges, 1982; Marmorino, 1983), and the mid- to outer-shelf is dominated by geostrophic flow. This leads to a mean southerly flow to the south in summer (Mitchum and Sturges, 1982). The circulation on the Mississippi-Alabama inner shelf is dominated by geostrophic flow or circulation due to wind stress. Both cases result in a mean westward flow (Chew et al., 1962; Schroeder et al., 1987). On the Texas-Louisiana shelf, the circulation is dominated by a large cyclonic gyre. Throughout most of the year the gyre is driven nearshore by wind stress, and near the shelf break an eastern flow is present throughout most of the year. During late summer (July-August) changes in wind direction cause reversals in the nearshore flow and the gyre system subsequently breaks down (Cochrane and Kelly, 1986).

Gray triggerfish are reported to spawn in the Gulf from late spring through early fall (Hood and Johnson, 1997; Wilson et al., 1995; and see Chapter 3). Therefore, I reason that there should have been an increase in larval and juvenile occurrence and abundance during and after this spawning period in areas corresponding to high concentrations of adults. If the spatial distribution of larvae and juveniles matches the distribution of adult fish, the extent of the spawning area for this species in the U.S. Gulf can be described. If the larval/juvenile distributions do not match the distribution of adult fish, a distant source of larvae may be indicated. Also, if the pelagic phase during the early life of GTF is in fact prolonged and indeterminate (Richards and Lindeman, 1987) and larvae/juveniles associate with flotsam, suggesting they could be transported long distances by oceanic currents (Aiken, 1983), the distribution and occurrence may be a function of hydrographic parameters associated with specific water masses (i.e. temperature, salinity and chlorophyll-*a* concentrations).

This chapter covers three aspects of the early life history of GTF. First, I describe the temporal and spatial distribution of larval and juvenile GTF in the U.S. Gulf using data collected during resource surveys of the Southeast Area Monitoring and Assessment Program (SEAMAP), and compare the distribution of early life history stages with that of adult GTF. Next, I describe the degree of association between GTF larval/juvenile occurrence and abundance and environmental parameters. Finally, I provide size ranges of specimens captured in neuston tows, bongo tows and bottom trawls to estimate the size distributions of larvae and juveniles in both pelagic and demersal environments to provide insight into the length of the pelagic phase during the early life history of this species.

This chapter aims to describe the occurrence (presence/absence) and the abundance (number of specimens captured per 10 minute neuston tow) of GTF larvae/juveniles in the northern Gulf using three types of generalized linear models: logistic, Poisson and negative binomial regressions (see Chapter 1). I describe the distribution of larvae and juveniles in the U.S. Gulf using data collected during numerous surveys of the Southeast Area Monitoring and Assessment Program (SEAMAP).

4.2 Materials and Methods

Larval/juvenile GTF collected in bongo and neuston tows during seasonal SEAMAP resource surveys from 1990 – 1993 were examined to describe their temporal and spatial distribution in the U.S. Gulf. Collections were taken using standardized procedures (Richards et al., 1993) during four time periods: Spring, April – May; Summer 1, June – July; Summer 2, August – early October; and Fall, late October - November (Table 4.1). During each of these time periods multiple cruises occurred, and these cruises were combined within each time period to provide temporal categories in the sampling regime for analysis purposes. During the Spring cruises the majority of the sampling was conducted off the shelf (> 200 meters water depth). During the Summer 1, Summer 2 and Fall cruises each year the majority of the sampling was conducted on-

Table 4.1. Yearly sampling time periods of gray triggerfish larvae and juveniles.

Sample Time Period

Sample Years	Spring	Summer 1	Summer 2	Fall
1990	4/20 - 6/30	6/9 - 7/28	9/2 - 10/18	10/16 - 11/17
1991	4/17 - 5/22	6/15 - 7/13	8/21 - 10/4	10/14 - 11/18
1992	4/22 - 5/23	6/12 - 7/13	8/30 - 10/19	10/18 - 11/10
1993	4/26 - 6/15	6/12 - 7/21	8/31 - 10/18	10/15 - 11/14

shelf (< 200 meters water depth). Collection stations were approximately 30 nautical miles (~ 56 km) apart, and samples were taken at all times of the day or night. Measurements of temperature, salinity, and chlorophyll-*a* concentration were taken approximately one meter below the surface at collection stations (Donaldson et al., 1993, 1994 and 1996; Sanders et al., 1992).

Larval GTF (< 10 mm) were identified using the larval description of Matsuura and Katsuragawa (1981). Juvenile GTF between 10 and 25 mm in body length were identified based on anal and dorsal fin element counts, and larger juvenile specimens (> 25 mm) were identified using pigmentation patterns.

Body length in larvae prior to notochord tip flexion was measured from tip of the snout to the tip of the notochord. After notochord flexion body length was measured from the tip of the snout to a vertical line through the posterior edge of the hypural plate.

Body lengths of neuston-collected GTF were statistically compared with those of bongo-collected individuals. Statistical comparisons were made between gear-types and between sampling time periods within each gear-type. The comparison of body length between gear-type was performed using a t-test ($\alpha = 0.05$) or a nonparametric equivalent (Mann-Whitney Rank Sum Test, $\alpha = 0.05$) if the data was non-normally distributed. Likewise, tests between time periods within each gear type were performed using a one-way ANOVA ($\alpha = 0.05$) or the nonparametric equivalent (Kruskall-Wallis One Way Analysis of Variance on Ranks, $\alpha = 0.05$) if the data was non-normally distributed.

Logistic regression was used to predict the presence/absence of larvae/juveniles in neuston tows. The method was deemed most appropriate because of numerous zeros in the occurrence data for larval/juvenile GTF. First, occurrence was modeled against the following variables: surface temperature, surface salinity, surface chlorophyll-*a* concentration, depth, time period and year. Next, Poisson and negative binomial regression-type models were employed to determine which of the aforementioned variables best describe larval/juvenile abundance in neuston tows.

The reduction in deviance method (McCullagh and Nelder, 1989; see Chapter 1) was used to build the most parsimonious models. I began the reduction in deviance method by starting with the one-variable model with the most insignificant lack-of-fit. I then compared the deviance of the two-variable model with the most insignificant lack-of-fit and determined if the reduction of model deviance was significant. This process continued with the addition of new variables until there was no further significant reduction in deviance. The new models, which had the most insignificant lack-of-fit, contained all variables that were previously included in the best fitting models of lower variable count. This method was used to build both the logistic model describing larval/juvenile occurrence and the Poisson model describing their abundance.

I described spatial distributions of larvae collected during the Summer 2 time frame to elucidate any patterns of local or upstream larval sources. Position and larval/juvenile abundance were plotted during the Summer 2 time frame for each sample year. Distributions of larvae/juveniles were compared among years.

To gain insight into the size distributions of GTF in the pelagic and demersal stages of their early life, I compared size distributions based upon standard lengths of specimens collected in both neuston and bongo tows during the SEAMAP surveys to the size distribution based on fork lengths of specimens collected from October 28 through November 11, 1998 during the Fall Groundfish Survey (Figure 4.1). GTF were collected using a trawl in the northern Gulf during this survey, which is conducted annually by the National Marine Fisheries Service.

I used data presented in Chapter 3 to estimate size-at-settlement from a pelagic to a demersal habitat. The sub-sample of 280 specimens used in Chapter 3 to conduct a marginal increment analysis was used to determine if a relationship existed between fork length and the corresponding spine radius, and a linear regression was developed. I estimated fork-length-at-settlement using this linear relationship. The length from the spine focus to the settlement mark along the spine radius (see Chapter 3) was entered as the radius to estimate the corresponding fork length of the specimen at settlement. The settlement mark in the first dorsal spine was a translucent ring encircling the focus of the spine. Due to this mark's close proximity to the focus, even in small fish (80 – 100 mm fork length), the mark was assumed to be associated with the period of ontogenetic transition between pelagic and demersal habitats. This process was completed for 235 of the 280 specimens used in Chapter 3, whose first dorsal spines contained a settlement mark.

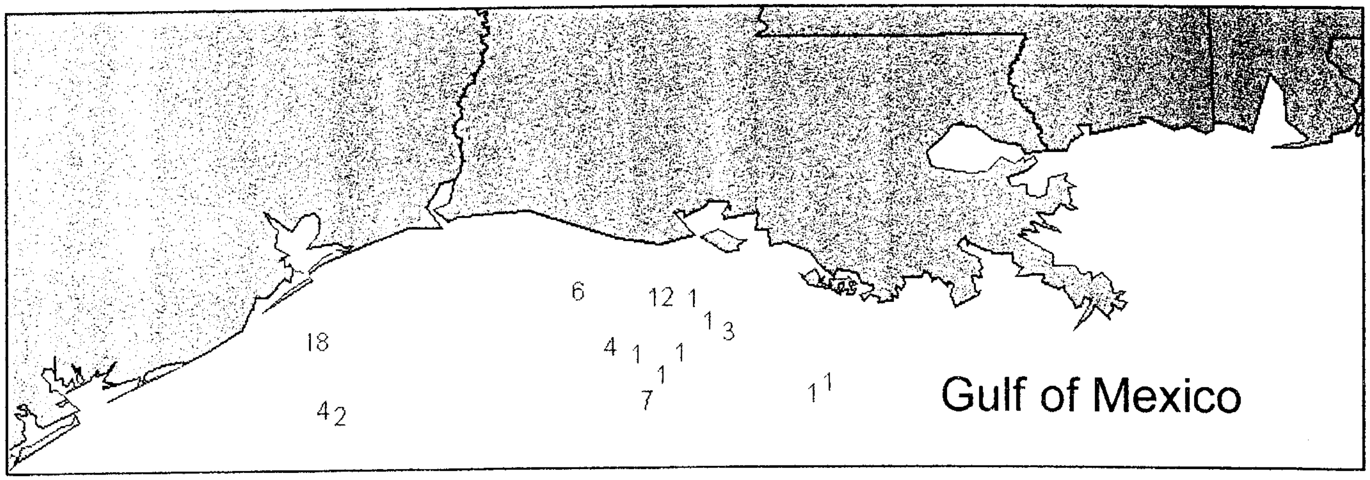

Figure 4.1. Position and abundance of gray triggerfish collected in trawls during the Fall Groundfish Survey of 1998.

4.3 Results

4.3.1 Empirical Results

There were 1,940 neuston samples taken during the four years of SEAMAP surveys included in these analyses (Table 4.2). The highest number of samples was taken in 1990 and the lowest in 1992. Of the four sampling time periods, the highest number of samples was taken during Spring and Summer 2 and the lowest during Summer 1 and Fall. Overall, the total number of stations where GTF were collected was 121, yielding a percent occurrence (i.e. occurrence/number of neuston samples) of 6.2 %. GTF occurred in 9.8 % and 4.6 % of neuston tows during the 1991 and 1993 sampling years, respectively, representing the highest and lowest rates of occurrence in any sampling year. GTF occurred in 12.0 % and 2.1 % of neuston tows during the Summer 2 and Spring sampling time periods, respectively, representing the highest and lowest percent occurrence over the time series. Fifty-seven larvae (< 10 mm) and 218 juvenile GTF were collected during this time series in bongos and neuston tows. Of the 275 specimens collected, 232 (84.1%) were collected during the Summer 2 sampling period.

GTF occurred predominantly on the continental shelf off the Louisiana-Texas coast with few occurrences on the west Florida Shelf during the Summer 2 time frame of each sampling year (Figure 4.2). Occurrence of GTF off Louisiana-Texas was consistent throughout the time series during this time period. Occurrence on the west Florida Shelf, and off Mississippi-Alabama was sporadic in nature, with relatively few occurrences in these areas.

Table 4.2. Sample size, occurrence and abundance of gray triggerfish larvae and juveniles collected in neuston tows.

	n	Occurrence	Percent Occurrence 100% (Occurrence/n)	Total Abundance
Overall	1940	121	6.2	276
Year				
1990	612	33	5.4	55
1991	439	43	9.8	62
1992	361	21	5.8	120
1993	527	24	4.6	39
Time Period				
Spring	868	18	2.1	29
Summer 1	175	12	6.9	14
Summer 2	748	90	12.0	232
Fall	149	1	0.7	1

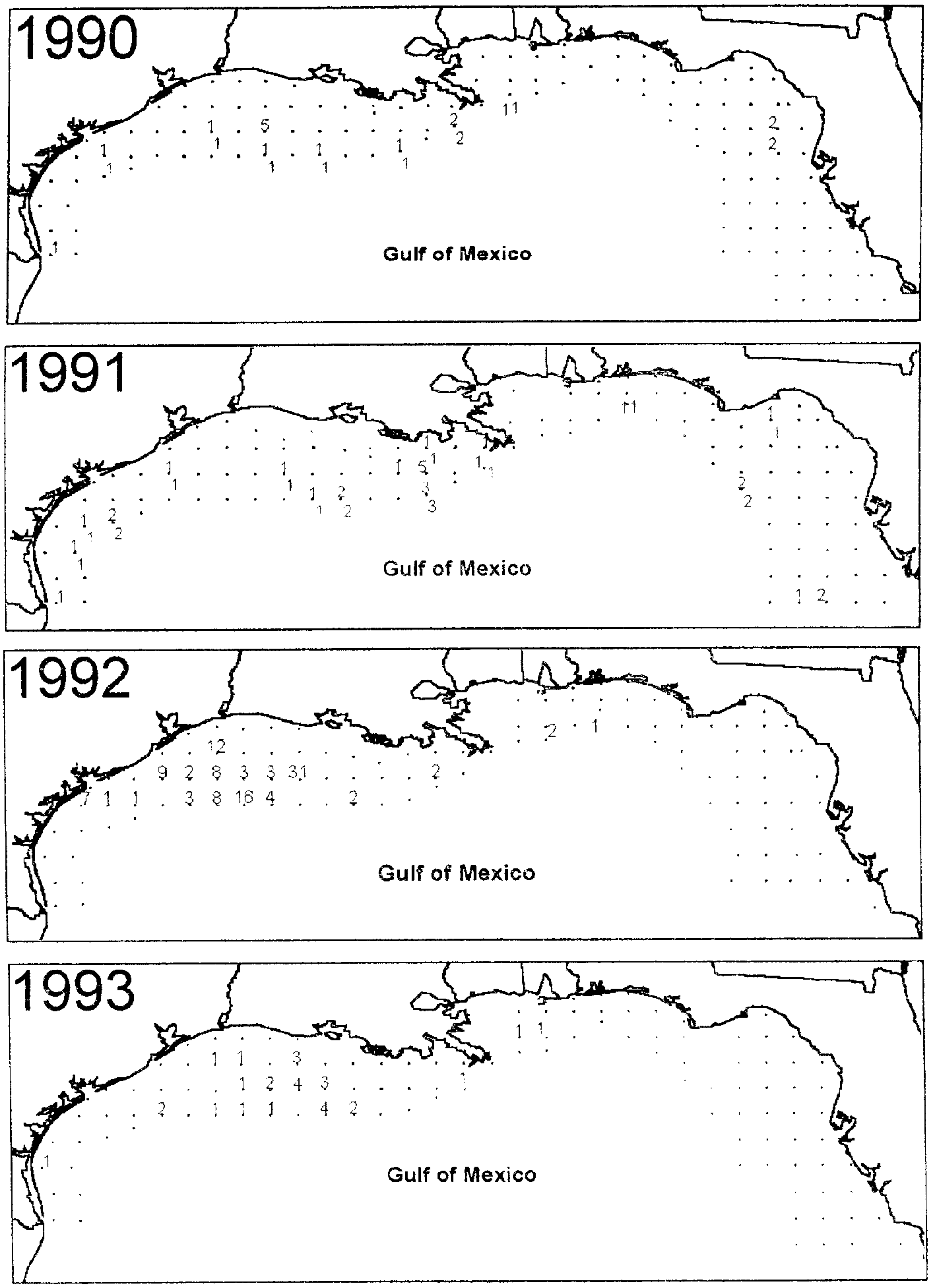

Figure 4.2. Distribution of gray triggerfish larvae and juveniles collected in neuston tows during Summer 2 of 1990 through 1993.

Body length measurements were obtained for 250 and 25 larvae/juveniles in neuston and bongo tows, respectively. The mean (± standard error) and median of body length (mm) of fish collected in neuston tows was 16.9 mm (± 0.71) and 13.6 mm, and by bongo tows was 14.8 mm (± 2.68) and 10.2 mm, respectively. The difference in the median values between bongo and neuston-collected GTF is greater than would be expected by chance (Mann-Whitney Rank Sum Test: $p = 0.038$).

There were seasonal differences in size of GTF taken in bongo, but not in neuston tows. Fish collected in Spring bongo collections were significantly larger than those taken in Summer 1 collections (One Way ANOVA, $p = 0.038$) (Figure 4.3). There was no significant difference between median standard lengths of GTF collected by neuston during the four time frames each year (Figure 4.4) (Kruskall-Wallis One Way Analysis of Variance on Ranks, $p = 0.446$).

There were 71 GTF collected by trawl during the 1998 Fall Groundfish Survey, having a mean fork length (± standard error) of 138 (± 4.0) mm (Figure 4.5). A significant linear relationship existed between fork length and the corresponding spine radius (Figure 4.6), and proportional back calculation based on this relationship provided a mean estimate of fork length (± standard error) at settlement to demersal habitats of 81.2 (± 1.32) mm (Figure 4.7).

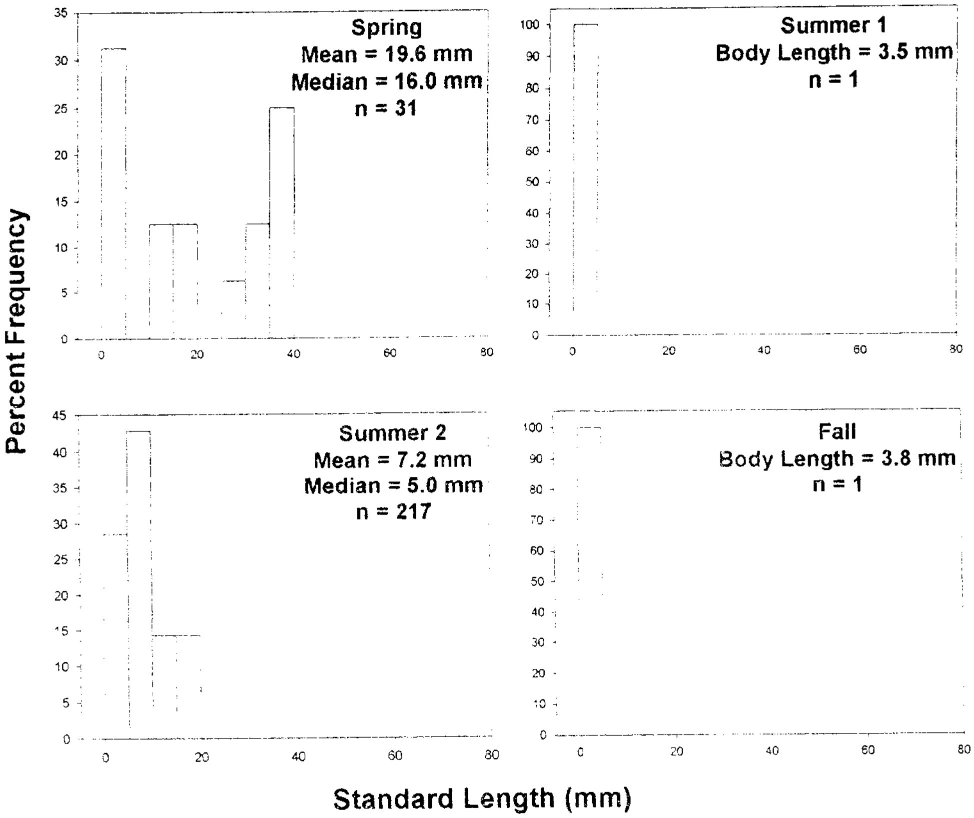

Figure 4.3. Seasonal length-frequency of larval/juvenile gray triggerfish collected in bongo tows.

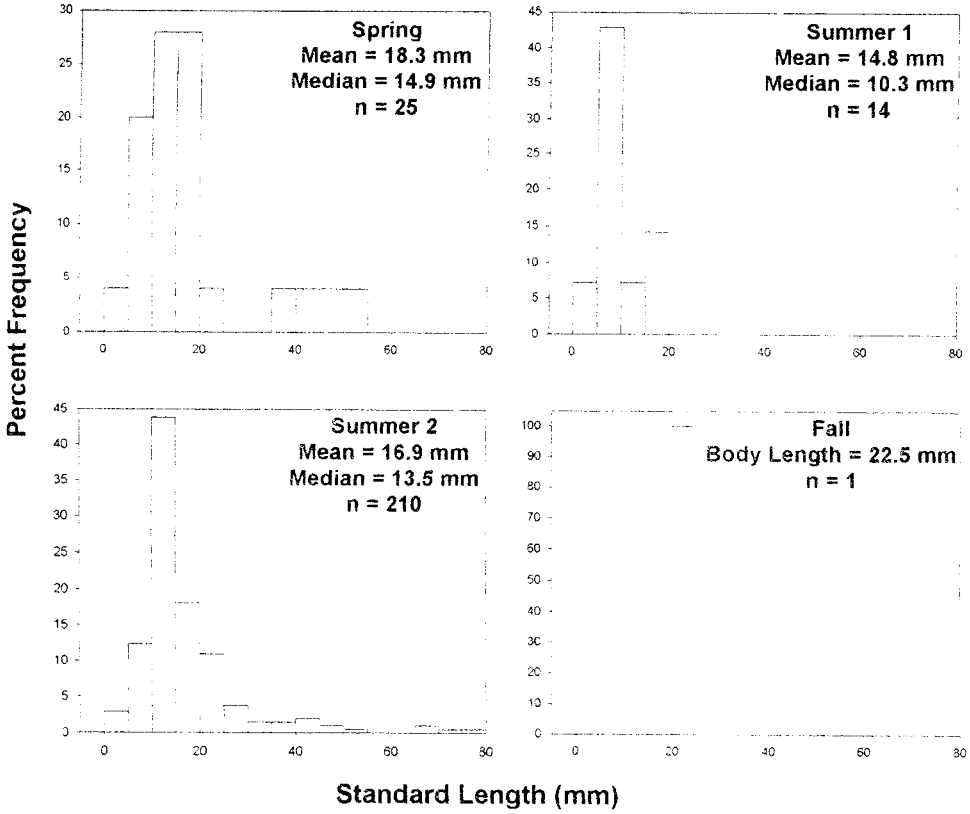

Figure 4.4. Seasonal length-frequency of larval/juvenile gray triggerfish collected in neuston tows.

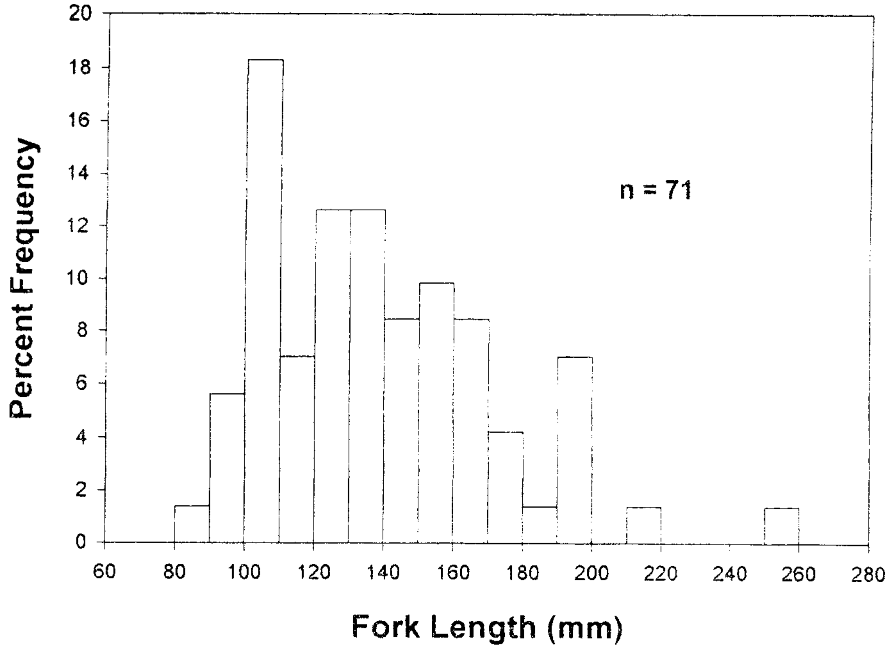

Figure 4.5. Length-frequency of gray triggerfish collected by trawl during the Fall Groundfish Survey.

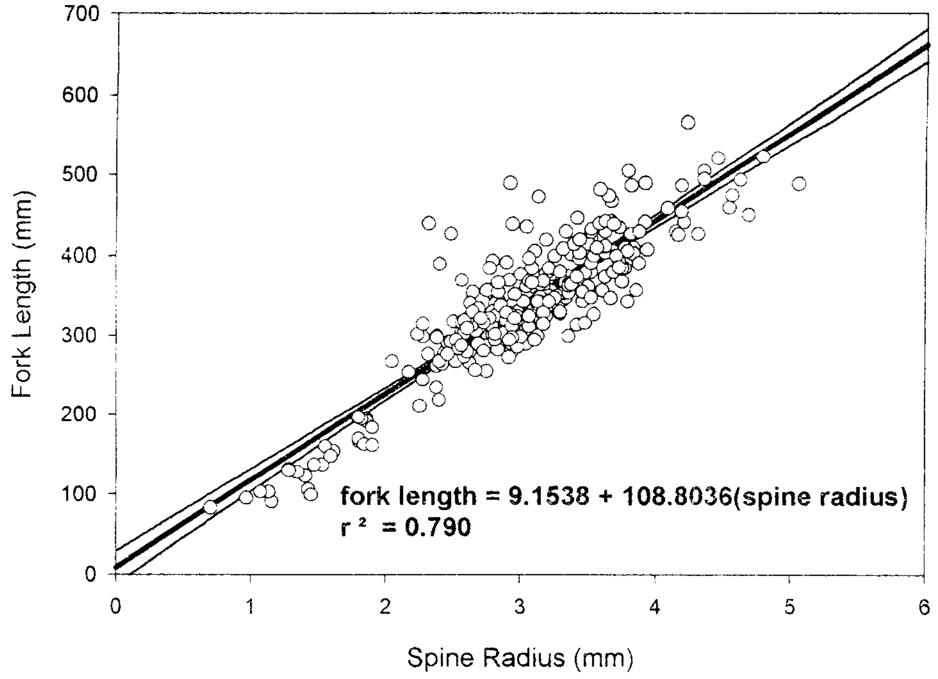

Figure 4.6. Linear regression between fork length and the radius of the first dorsal spine of gray triggerfish, with 95 % confidence intervals.

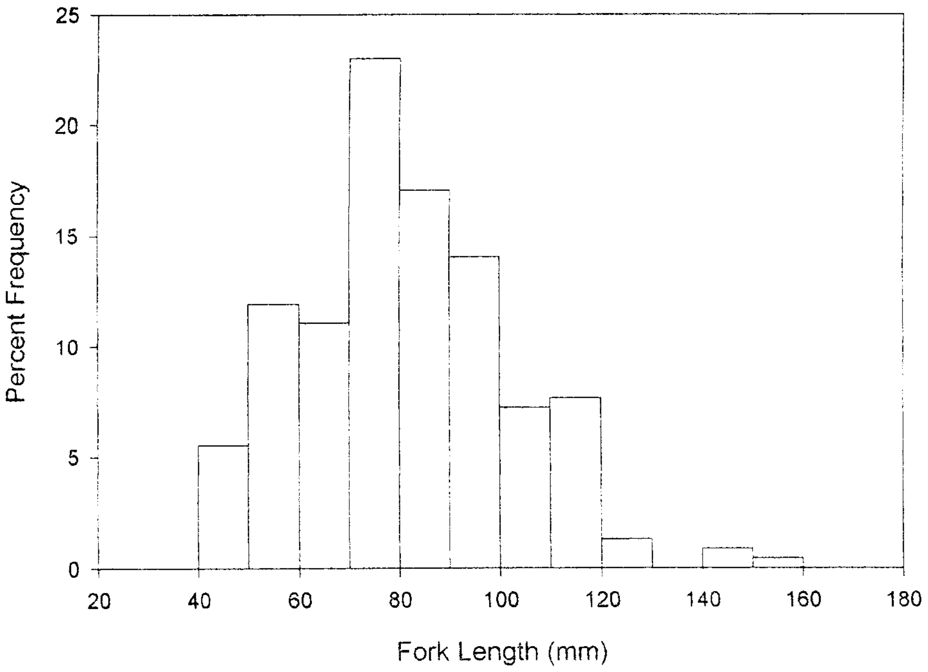

Figure 4.7. Length-frequency of gray triggerfish at settlement to demersal habitats.

4.3.2 Modeling Results

Both occurrence and abundance of larvae and juveniles were positively related to temperature and salinity, and negatively related to chlorophyll-*a* concentration, suggesting that GTF larvae associate with warm, high-salinity water containing low concentrations of phytoplankton. Also, occurrence and abundance both were significantly lower during 1990, and abundance was significantly higher during 1992, than in other sampling years. Finally, both occurrence and abundance were significantly lower in the Spring than in other sampling seasons.

The results of all possible logistic regressions of GTF occurrence and environmental parameters, and the resulting model-building pathway based on deviance reduction are summarized in Table 4.3. There was significant (i.e. α=0.05) reduction in deviance with all parameters except station depth. Therefore, I did not include station depth in the final five-variable logistic regression model. Also, all logistic models used in the model building procedure had insignificant lack-of-fit with respect to both Pearson's chi-square and deviance lack-of-fit statistics.

The interpretation of the logistic model parameters is best described using the exponential relationship between the mean and the independent variables, thereby interpreting the parameters as multiplicative changes in the odds of occurrence (see Chapter 1). Interpretation of the parameters in the resulting logistic model is straightforward (Table 4.4).

Among years, 1990 is the only significant parameter ($\alpha = 0.05$) with a 52 % reduction in the odds of GTF occurring in a neuston tow in the study area. Among the

Table 4.3. Logistic model building pathway and lack-of-fit statistics. Note: All stepwise reductions in deviance significant at $\alpha=0.05$.

Model Variables	DF	Deviance	Pearson'sChi-Square
One variable model temperature	1940	830.4343 (p=1.00000)	1538.1677 (p=1.00000)
Two variable model temperature, chlorophyll	1755	758.1377 (p=1.00000)	1534.1493 (p=0.99995)
Three variable model temperature, chlorophyll, salinity	1732	739.7313 (p=1.00000)	1680.4120 (p=0.80895)
Four variable model Temperature, chlorophyll, salinity, year	1729	724.6647 (p=1.00000)	1772.4627 (p=0.22834)
Five variable model temperature, chlorophyll, salinity, year, time period	1726	716.8528 (p=1.00000)	1600.1566 (p=0.98555)

Table 4.4. Logistic model parameters.

Parameter	Multiplicative change in odds	95% Confidence Interval	*p*-value
Intercept	1.96×10^{-10}	7.27×10^{-14}, 5.27×10^{-7}	< 0.0001
Year			
1990	0.4814	0.2554, 0.9076	0.0238
1991	0.8778	0.4928, 1.5638	0.6585
1992	1.0010	0.5168, 1.9389	0.9977
1993	0.0000		
Time Period			
Fall	0.3033	0.0377, 2.4416	0.2622
Spring	0.4031	0.1923, 0.8450	0.0161
Summer I	0.7342	0.3426, 1.5731	0.4268
Summer II	0.0000		
Environmental Parameters			
Temperature	1.8239	1.4408, 2.3089	< 0.0001
Salinity	1.1078	1.0111, 1.2138	0.0279
Chlorophyll	0.6537	0.4561, 0.9368	0.0206

four time periods, Spring is the only significant parameter ($\alpha = 0.05$) with a 60 % decrease in the occurrence of GTF during this time period. Among environmental parameters, there is an 82 % increase, an 11 % increase, and a 35 % decrease in the odds of occurrence for every unit increase of temperature, salinity and chlorophyll, respectively.

The results of all possible Poisson regressions of GTF abundance and environmental parameters, and the resulting model-building pathway are summarized in Table 4.5. There was significant (i.e., $\alpha = 0.05$) reduction in deviance as each parameter was added, starting with time period and ending with surface salinity. However, there was no significant reduction in deviance with the addition of station depth to the model. Therefore, station depth was not included in the final, five-variable Poisson regression model.

All Poisson models used in the model building procedure had significant lack-of-fit with respect to Pearson's chi-square (Table 4.5), including the final five-variable model. Therefore, the five-variable model was built as a Poisson regression model, but was reevaluated as a negative binomial regression model in order to compensate for overdispersion in the data and reduce the model's lack-of-fit. This resultant model had 1726 degrees of freedom and a Pearson's chi-square statistic equal to 1728.3242 ($p = 0.47971$).

The interpretation of the negative binomial model parameters is best described using the exponential relationship between the mean and the independent variables, thereby interpreting the parameters as multiplicative changes in the mean abundance

Table 4.5. Poisson model building pathway and lack-of-fit statistics. Note: All stepwise reductions in deviance significant at $\alpha=0.001$.

Model Variables	DF	Deviance	Pearson's Chi-Square
One variable model time period	1940	1599.1951 (p=1.00000)	9147.6936 (p<0.00001)
Two variable model time period, chlorophyll	1773	1410.8175 (p=1.00000)	6627.3446 (p<0.00001)
Three variable model time period, chlorophyll, year	1770	1294.7012 (p=1.00000)	4966.4243 (p<0.00001)
Four variable model time period, chlorophyll, year, temperature	1749	1203.7940 (p=1.00000)	3811.8173 (p<0.00001)
Five variable model time period, chlorophyll, year, temperature, salinity	1726	1160.3224 (p=1.00000)	4265.6654 (p<0.00001)

(Table 4.6). Among the year parameters, 1990 and 1992 are both significant parameters ($\alpha = 0.05$) with a 56 % decrease and a 179% increase in the abundance of GTF larvae in the study area in 1990 and 1992, respectively. Of the time period parameters, Spring is the only significant parameter ($\alpha = 0.05$) with a 55 % decrease in GTF larval abundance. Next, there is a 120 % increase, a 12 % increase, and a 51 % decrease in the abundance of GTF for every unit increase of temperature, salinity and chlorophyll, respectively.

4.4 Discussion

This two-step modeling approach used to describe both abundance and occurrence of GTF larvae and juveniles is similar to the approach performed by Stefánsson (1996) and Lyczkowski-Shultz and Link (In review). However, instead of using a linear regression to describe abundance using only the non-zero responses, I employed the Poisson and negative binomial regressions to describe abundance and included all data, thus avoiding the loss of valuable biological and statistical information contained within the zero data (McCullagh and Nelder, 1989; Agresti, 1996; Mark Carpenter, per. comm.[1]). Also, the probability distributions associated with these models allowed for modeling of dependant variables with both categorical and continuous dependent variables, whereas point estimates derived from the delta-distribution, which is also an appropriate probability distribution for modeling zero-inflated data (Aitchison, 1955; Pennington, 1983), would have been insufficient.

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[1] University of South Alabama, Department of Mathematics and Statistics, Mobile, Alabama

Table 4.6. Negative binomial regression model parameters.

Parameter	Multiplicative change in odds	95% Confidence Interval	*p*-value
Intercept	$1.38x10^{-10}$	$1.30x10^{-14}$, $1.50x10^{-7}$	< 0.0001
Year			
1990	0.4401	0.2145, 0.9029	0.0252
1991	0.8598	0.4387, 1.6868	0.6605
1992	2.7930	1.3944, 5.5942	0.0038
1993	0.0000		
Time Period			
Fall	0.2192	0.0243, 1.9759	0.1761
Spring	0.4545	0.2107, 0.9806	0.0444
Summer I	0.3419	0.1437, 0.8134	0.8134
Summer II	0.0000		
Environmental Parameters			
Temperature	2.2098	1.6769, 2.9121	< 0.0001
Salinity	1.1208	1.0205, 1.2308	0.0171
Chlorophyll	0.4905	0.2276, 1.0571	0.0690

The occurrence of GTF in the Gulf was best modeled as a rare event; however, evaluation of lack-of-fit Poisson-type models may be problematic for this type of data (Figure 4.8, Table 4.2). Therefore, deviance was used only to evaluate significance of variable addition to the model, and Pearson's chi-square was used to evaluate lack-of-fit of the models (McCullagh and Nelder, 1989; Agresti, 1996; Mark Carpenter, per. comm.).

Although not formally correlated during this study, many scientists (Dooley, 1972; Longley and Hilderbrand, 1942; Aiken, 1983; James Franks and Eric Hoffmayer[2], per. comm.) have reported an association of young GTF with *Sargassum* spp. In addition, many similar species (i.e. balistids and monocanthids, Camin, 1997; Kimura et al., 1998) and many species of reef fishes (i.e. pomacentrids, Low et al., 1997; haemulids, acanthurids, and sparids, Ornellas and Coutinho, 1998; Leis, 1991, for review) have been reported to associate with *Sargassum* spp. As *Sargassum* spp. is commonly associated with oceanic waters with high salinity and temperature, the distribution of such floating habitats may in turn control the distribution of reef fish species that associate with floating habitat during the pelagic phase (Low et al., 1997; Kimura et al., 1998; Ornellas and Coutinho, 1998). Therefore, I reason that the patchy nature of floating habitats may contribute to the overdispersed nature of young GTF abundance data.

Increased abundance and occurrence of young GTF in neuston tows during the Summer 2 time frame mirrored the observed spawning season. In the Gulf, GTF spawn from late spring through early fall (Hood and Johnson, 1997; Wilson et al., 1995; and see

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[2] Gulf Coast Research Laboratory, Ocean Springs, Mississippi

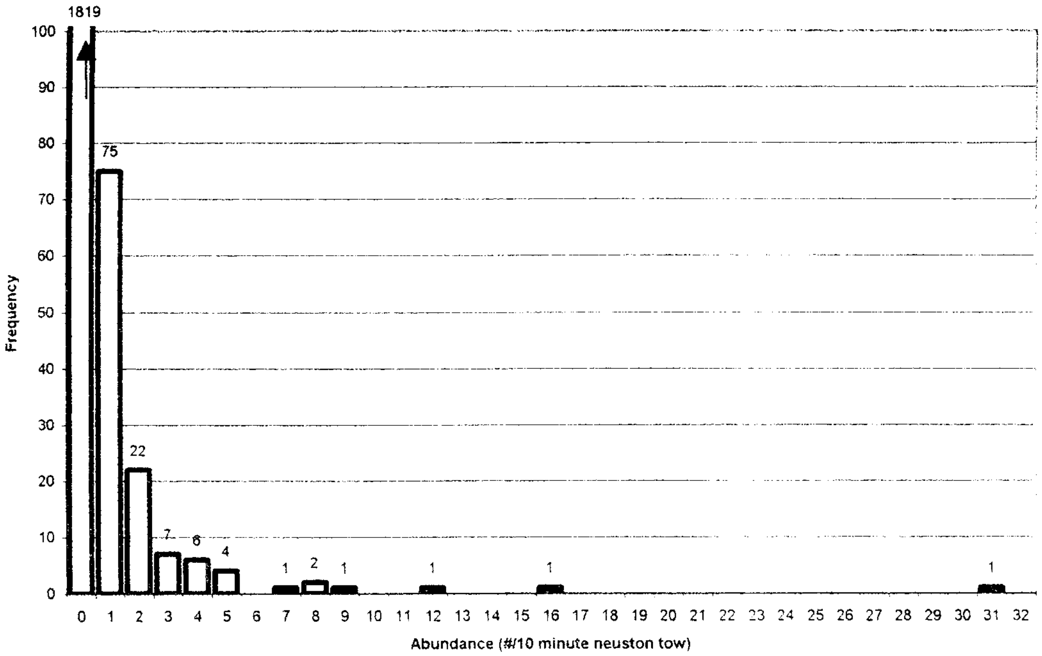

Figure 4.8. Distribution of gray triggerfish abundance collected in neuston tows.

Chapter 3). When the demersal eggs of a species like GTF hatch, it is inferred that the young fish seek the refuge of floating habitats (Leis, 1991).

Reasons for yearly differences in occurrence and abundance were not as easily discerned. Higher occurrences or higher abundances between sampling years may be due to increased reproductive success leading to more larvae, or there may have been more *Sargassum* spp. or other floating habitat with which larvae and juveniles could associate. Larvae and juveniles occurred in more neuston tows during the 1991 sampling year. However, there was a greater abundance of larvae and juveniles during the 1992 sampling year. This indicated that patchiness of larvae and juveniles varies in both space and time.

The pattern in seasonal distribution and abundance of larvae and juveniles may reflect the distribution of spawning grounds. Higher occurrences and abundances of larvae and juveniles during the Summer 2 time period off the Louisiana-Texas coast was probably due to proximity to the Flower Garden Banks, an extensive natural reef area in the northern Gulf. GTF have been observed inhabiting this reef area (Kevin Rademacher, per. comm.[3]). As mentioned earlier, GTF inhabiting these reefs probably spawned during the 2-3 months prior to the Summer 2 time period each sampling year. Other areas of GTF larval concentrations may indicate proximity to other important spawning grounds.

GTF collected in bongo tows were smaller than those collected in neuston tows, which may indicate that bongo-collected fish were still in the water column and had not yet associated with floating structure on the surface. Comparison of the size distribution

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[3] National Marine Fisheries Service, Pascagoula, Mississippi

n bongo and neuston collections suggest that they begin to associate with ɔbjects at about 15mm. Bongo tows sampled the water column from the surface ottom or 200 m, while neuston tows only sampled surface waters.

1aximum size of GTF collected during this time series was 73 mm, whereas to 100 mm have been reported to be common in *Sargassum spp.* (Longley and ınd, 1942; Dooley, 1972; Aiken, 1983). Vose and Nelson (1994) reported that the Atlantic coast of Florida began colonizing hard bottom habitat at ıately 160-170 mm standard length. While the length-frequency distribution of ? trawl-collected GTF in the Gulf certainly contained fish of the settlement size by Vose and Nelson, the mean size of GTF in the SEAMAP collection indicated settlement size. The mean back-calculated size at settlement based on ıt marks in the first dorsal spine, indicated a size at settlement less than half that by Vose and Nelson (1994). The length-frequency distribution of back d size of GTF at settlement to demersal habitat was similar to the size at ıt of queen triggerfish (*Balistes vetula*) in the Caribbean Sea (i.e., 49 – 70 mm ›bertson, 1988).

ettlement marks in otoliths of reef fishes are common and have been validated in ıes for back-calculation and estimation of settlement date and duration of the ic larvae/juvenile stages (Wilson and McCormick, 1997, 1999, for review). This ms when the growth rates of reef fishes are lowered due to the transition from ic to the benthic environment. Likewise, environmental transitions can cause ıarks in fin spines (see Chapter 3). Therefore, due to this mark's close proximity to the focus, even in small fish (80 – 100 mm fork length), I reason that it is a settlement mark representing the relatively slower growth during the ontogenetic transition between pelagic and demersal habitats.

The length of the pelagic phase was characterized for GTF as being prolonged and indeterminate by Richards and Lindeman (1987). GTF may choose to inhabit structure in surface waters until suitable demersal habitat is found. GTF may be pelagic from a few weeks to several months, perhaps up to a year (Dooley, 1972). This may place GTF larvae/juveniles at the mercy of not only oceanic currents, but also the abundance of surface habitat within those currents and the availability of suitable demersal habitat below those currents.

If GTF larvae become entrained within cyclonic or anti-cyclonic currents that retain the larvae in the same area from which they were spawned, the result would be a mostly self-recruiting population or sub-population. Many scientists have described larval retention of reef fishes by local oceanographic processes. Limouzy-Paris et al. (1997) described how meanders and spin off eddies of the Florida Current may act to retain larval reef fishes in coastal areas of the Florida Keys. Likewise, Porch (1998) simulated settling rates and retention of larvae of southeast Florida fishes. Settling rates were greatly affected by hydrodynamics. Eddies and gyres associated with the Florida current front can retain between 0.07 and 41% of the larvae with planktonic life spans on the order of 1 month, which implies that southeast Florida reef fish populations should be able to replenish themselves without relying on upstream sources of recruitment. Moreover, reef fish populations associated with isolated oceanic islands, like Bermuda, are primarily replenished by larvae that are spawned locally and retained in the vicinity of the island due to local oceanographic processes (Schultz and Cowen, 1994). In the northern Gulf, the circular currents on the shelf on either side of the Mississippi River Delta may act to retain GTF larvae in each area. Cross-shelf mixing of larvae, or the introduction of larvae from the Caribbean Sea may occur with the periodic shedding of Loop Current eddies.

CHAPTER 5: CONCLUSIONS AND RECOMMENDATIONS FOR FUTURE MANAGEMENT

5.1 Dissertation Goals Revisited

The goals of this dissertation, as outlined in Chapter 1, were met. Almost 1,900 GTF were sampled for analysis of age, growth and reproduction, and over 1,200 individuals were tagged to study movement patterns. In addition, four years of SEAMAP survey data were used to study the distribution of larval and juvenile GTF during the pelagic phase of their early life. This was the most in-depth study concerning population dynamics and stock structure of GTF on multiple spatial scales ever conducted.

5.2 Stock Structure

Adult GTF off Alabama exhibit high site fidelity. High site fidelity may result from the territorial nature of adult fish (see Chapter 2). Bohnsack (1989) infers that fishes exhibiting high site fidelity may be more easily overexploited. In the case of GTF in this study, loss of older age classes resulting from increases in fishing pressure in publicly known fishing grounds is apparent. In the long term, selective removal of large, fast-growing members of the population may be resulting in decreased growth rates of survivors (see Chapter 3).

Population parameters of adult GTF are heterogeneous on multiple spatial scales. Estimates of growth rates on the scale of individual reefs (tagging stations) indicate high variability, which precludes a finding of stock heterogeneity on this small scale. However, at a slightly larger scale (i.e. at the reef-complex or reef-permit-area scale), adult GTF appear to have differences in specific population parameters; differences may be attributable to differential fishing pressure between reef areas. On a Gulf-wide scale, temporal differences in growth and mortality parameters may result from different levels of exploitation, and may preclude any meaningful comparisons of growth and mortality to gain insight into stock structure (see Chapter 3).

The length of the pelagic phase of young GTF is characterized as being prolonged and indeterminate by Richards and Lindeman (1987). GTF may choose to inhabit structure in surface waters until suitable demersal habitat is found, and may be pelagic from a few weeks to several months. Although not addressed in this study, triggerfishes associate with *Sargassum* spp. patches and other flotsom during their pelgic phase (see Chapter 4). GTF may exhibit homogeneous stock structure in relation to genetic variability, due to a prolonged pelagic phase and the potential of wide dispersal (Richards and Lindeman, 1987). However, if young GTF are entrained within cyclonic or anti-cyclonic currents that retain them in the same area from which they were spawned, the result would be a mostly self-recruiting population or sub-population (see Chapter 4).

5.3 Management Recommendations

With increasing regulations on other reef fishes, and the increased awareness of the excellent flesh of GTF, a harvest quota will probably need to be set for this species. This can be accomplished by seasonal closures, size limits and/or bag limits. However, due to high site fidelity of GTF, this species would probably benefit, and best be managed by the implementation of no-take marine reserves. GTF may be territorial (see Chapter 2), have an early age at maturity (see Chapter 3), and have an early life history stage that may be pelagic through the first year of life (see Chapter 4). By releasing fishing pressure, a population of GTF may then become structured by natural mortality instead of fishing mortality (Bohnsack, 1992). Thus, reserves may increase the density, average size, and spawning stock biomass of species in the reserve (e.g. Plan Development Team, 1990; Polunin and Roberts, 1993; Roberts, 1995; Russ and Alcala, 1996). Because larger GTF have higher reproductive output, a population now structured by natural mortality with a greater abundance of larger and older individuals in a marine reserve will have a much higher reproductive output (Bohnsack, 1992). Due to the prolonged nature of the pelagic phase in early life, young GTF can be exported from marine reserves while associating with *Sargassum* spp. and bits of flotsam on ocean currents, and serve to restock adjacent and possibly distant reef areas with recruits. In addition, due to an increase in movement in the presence of tropical cyclones, adult GTF may emigrate from marine reserves to surrounding areas. Hence, marine reserves may enhance the GTF fishery by acting as centers of dispersal of young and adults into areas surrounding the reserves (Plan Development Team, 1990; Bohnsack, 1992; Polunin and Roberts, 1993; Roberts, 1995; Russ and Alcala, 1996).

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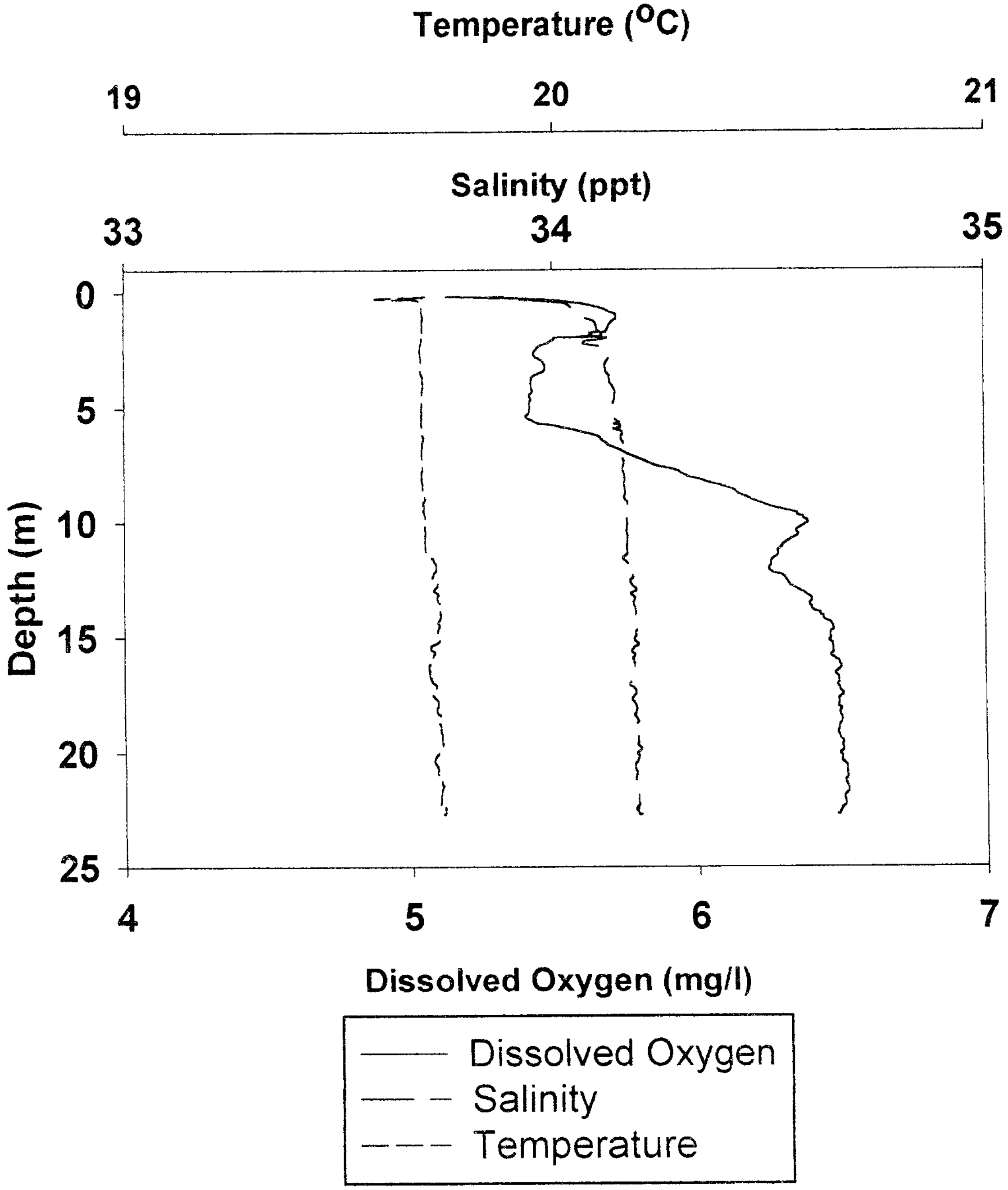
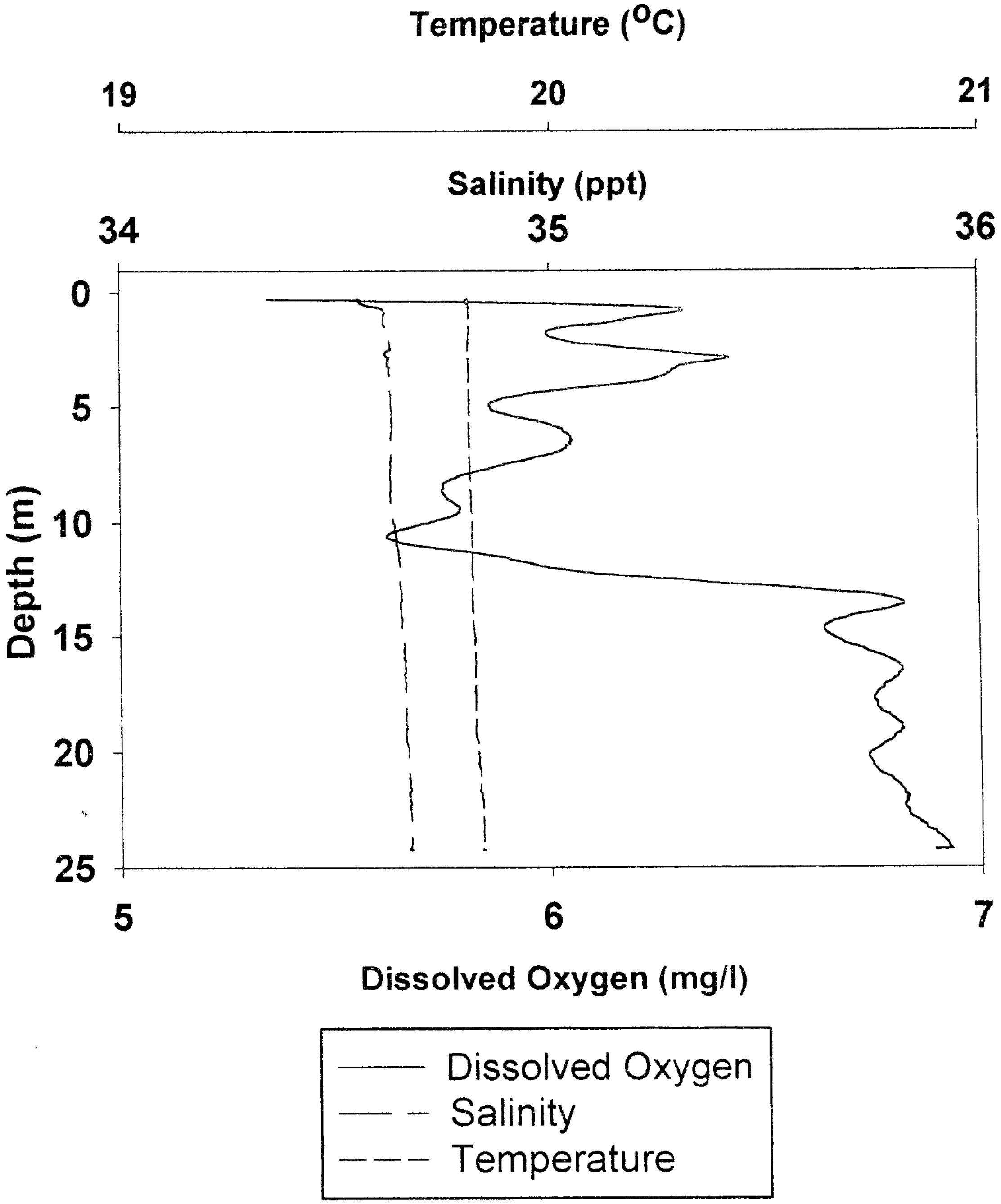
APPENDIX

Appendix. Water column profiles of temperature, salinity and dissolved oxygen taken at tagging sites. Profiles are in chronological order, and labeled with date of data collection.

11-19-1997

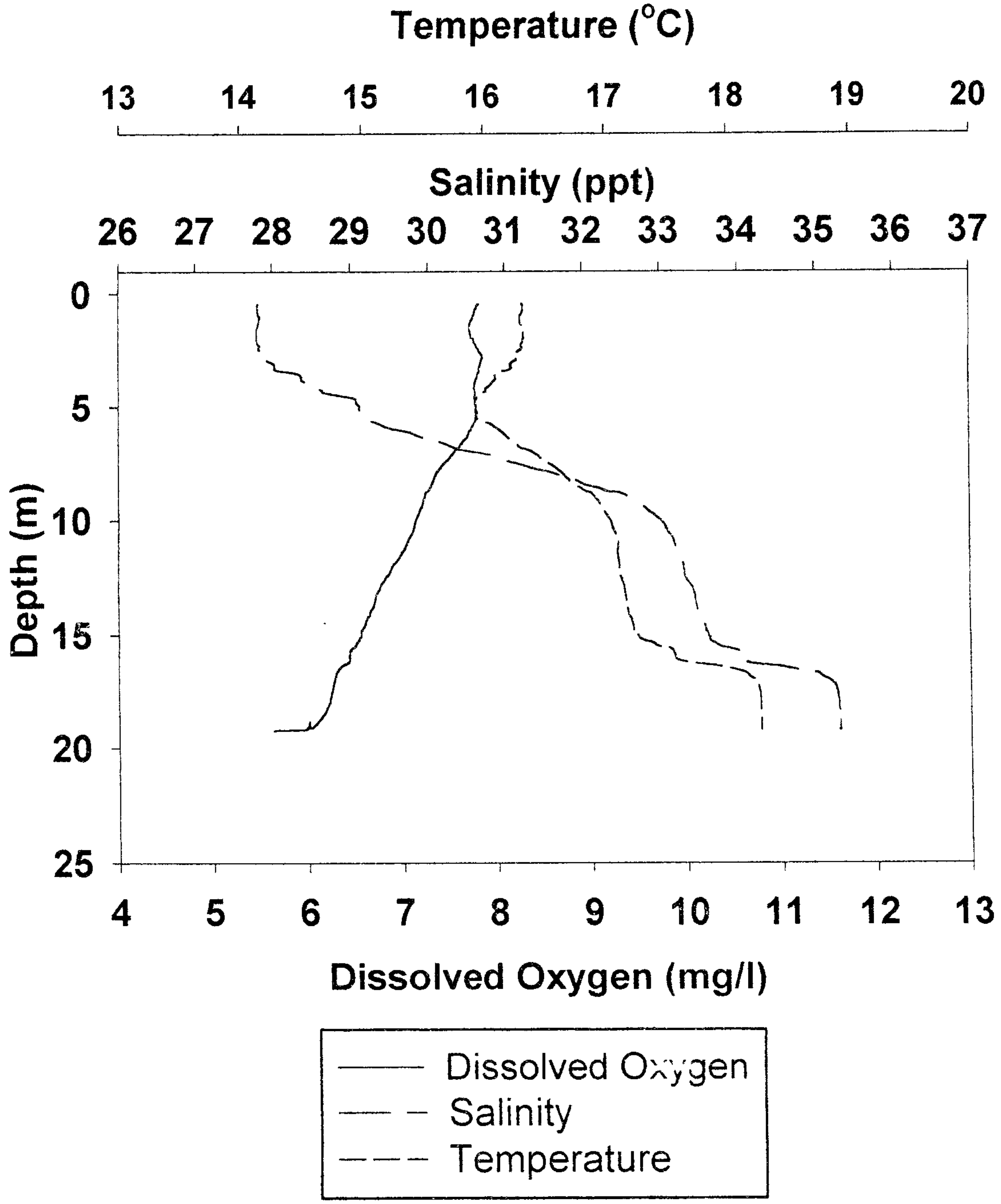

Temperature (^oC)
19
20
21
Salinity (ppt)
33
34
35
Depth (m)
0
5
10
15
20
25
4
5
6
7
Dissolved Oxygen (mg/l)
Dissolved Oxygen
Salinity
Temperature

11-25-1997

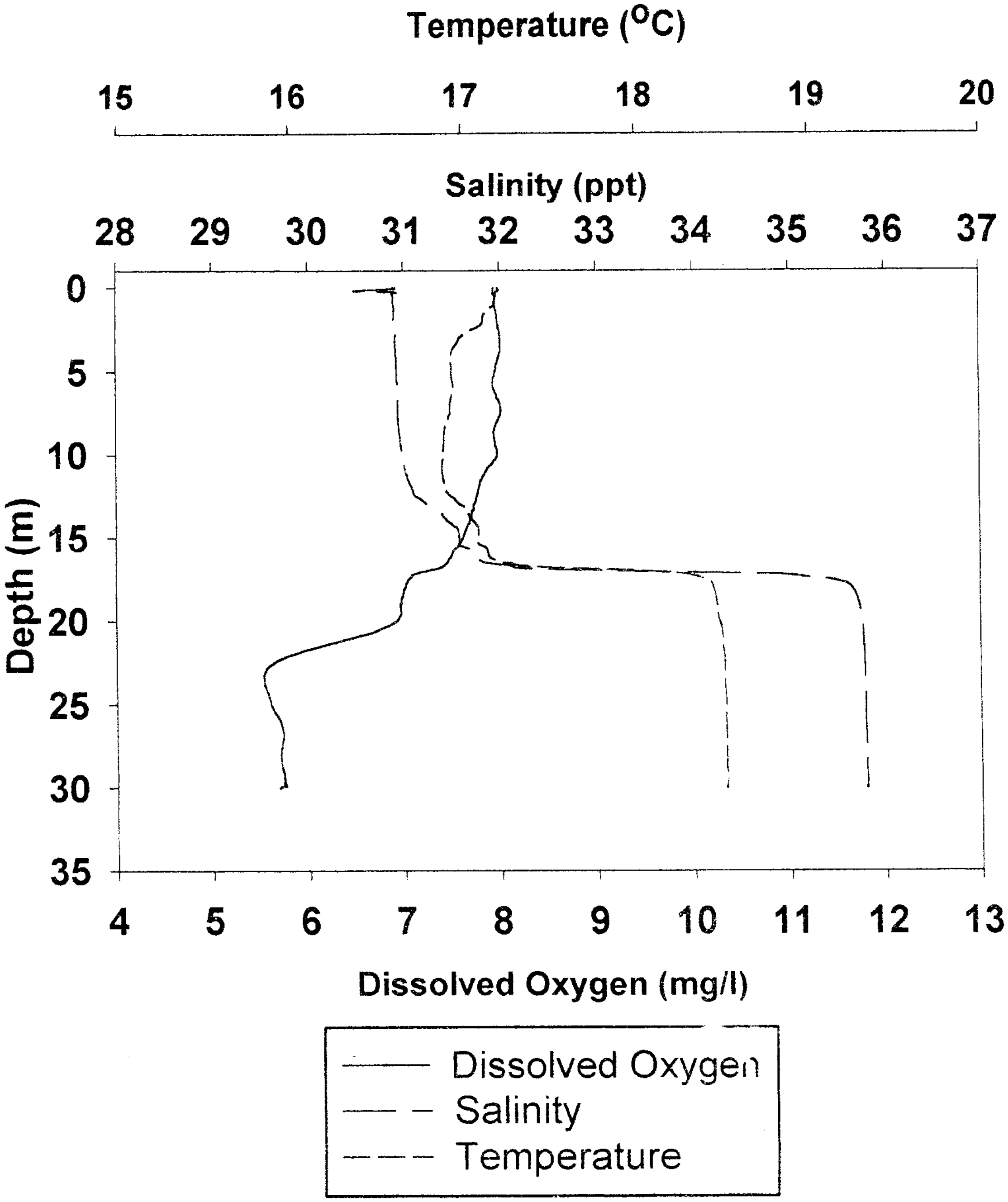


Temperature (°C)
19
20
21
Salinity (ppt)
34
35
36
Depth (m)
0
5
10
15
20
25
5
6
7
Dissolved Oxygen (mg/l)
Dissolved Oxygen
Salinity
Temperature

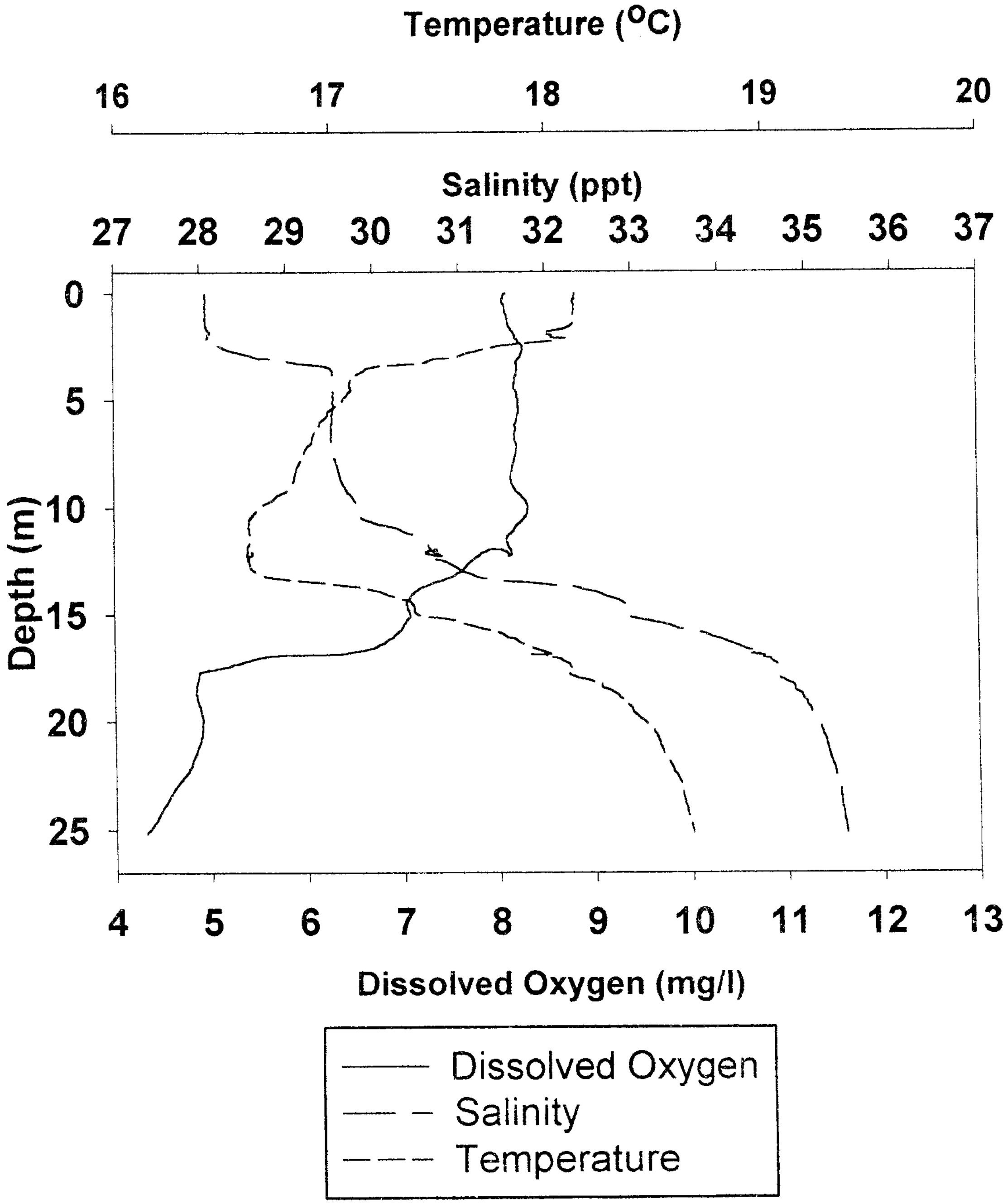
2-25-1998


Temperature (°C)
13
14
15
16
17
18
19
20
Salinity (ppt)
26
27
28
29
30
31
32
33
34
35
36
37
Depth (m)
0
5
10
15
20
25
4
5
6
7
8
9
10
11
12
13
Dissolved Oxygen (mg/l)
Dissolved Oxygen
Salinity
Temperature

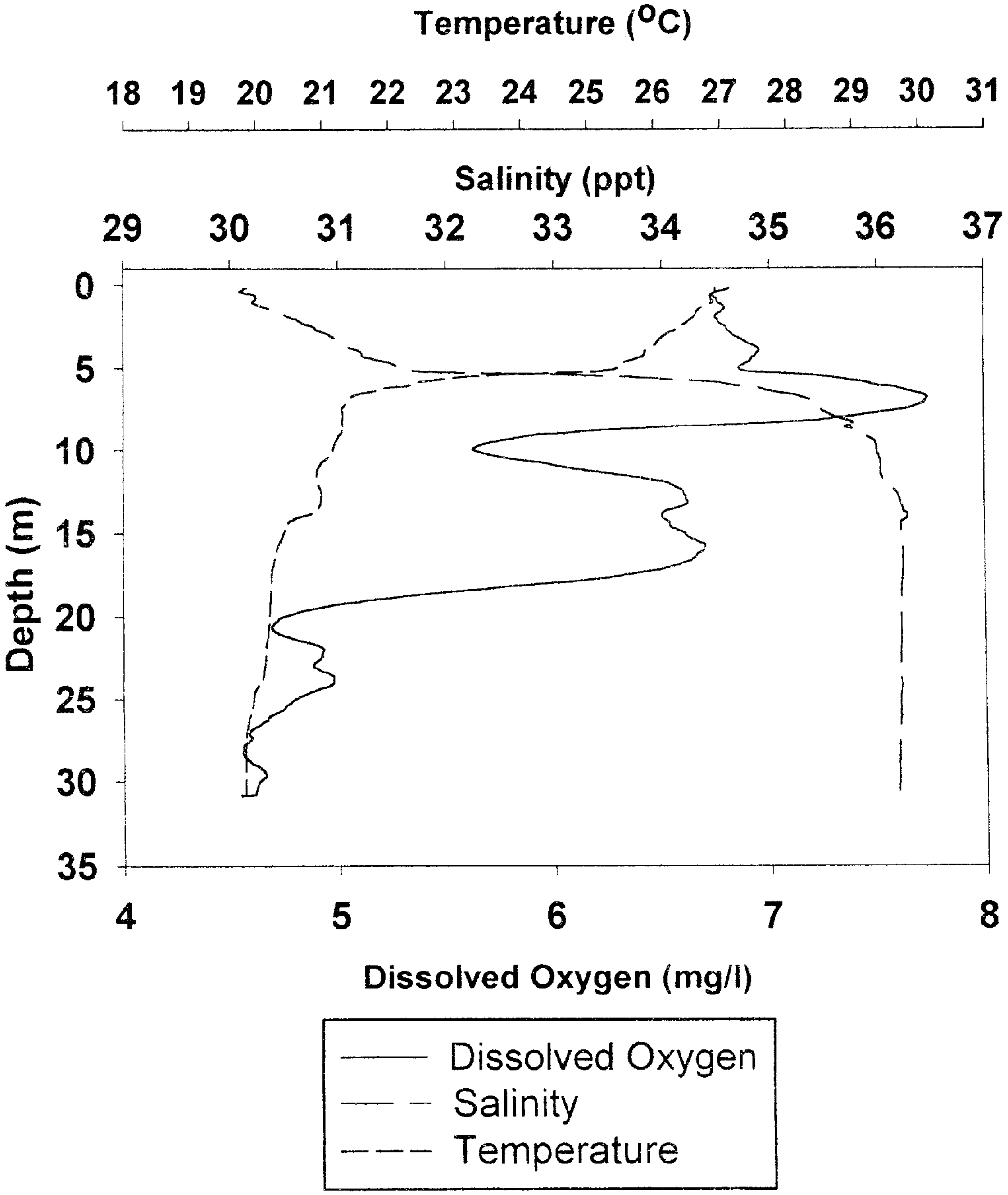
3-5-1998


Temperature (°C)
15
16
17
18
19
20
Salinity (ppt)
28
29
30
31
32
33
34
35
36
37
Depth (m)
0
5
10
15
20
25
30
35
4
5
6
7
8
9
10
11
12
13
Dissolved Oxygen (mg/l)
Dissolved Oxygen
Salinity
Temperature

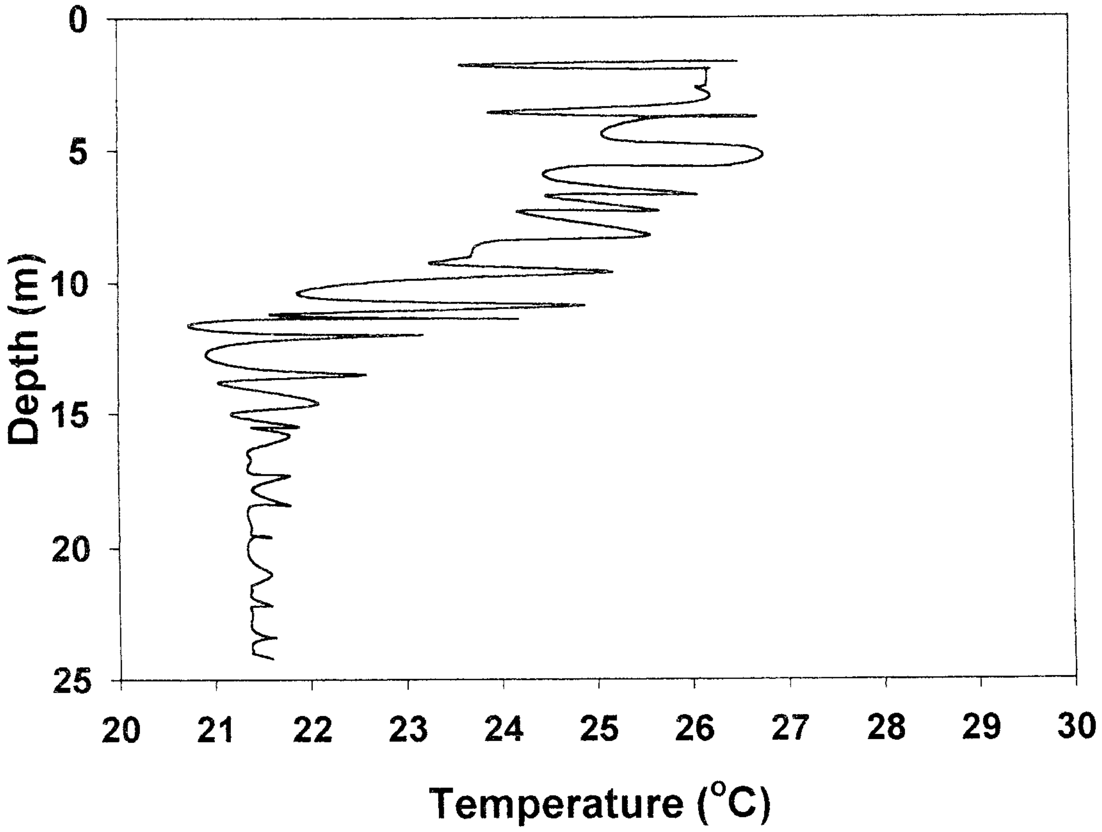
3-26-1998


Temperature (°C)
16
17
18
19
20
Salinity (ppt)
27
28
29
30
31
32
33
34
35
36
37
0
5
10
15
20
25
Depth (m)
4
5
6
7
8
9
10
11
12
13
Dissolved Oxygen (mg/l)
Dissolved Oxygen
Salinity
Temperature

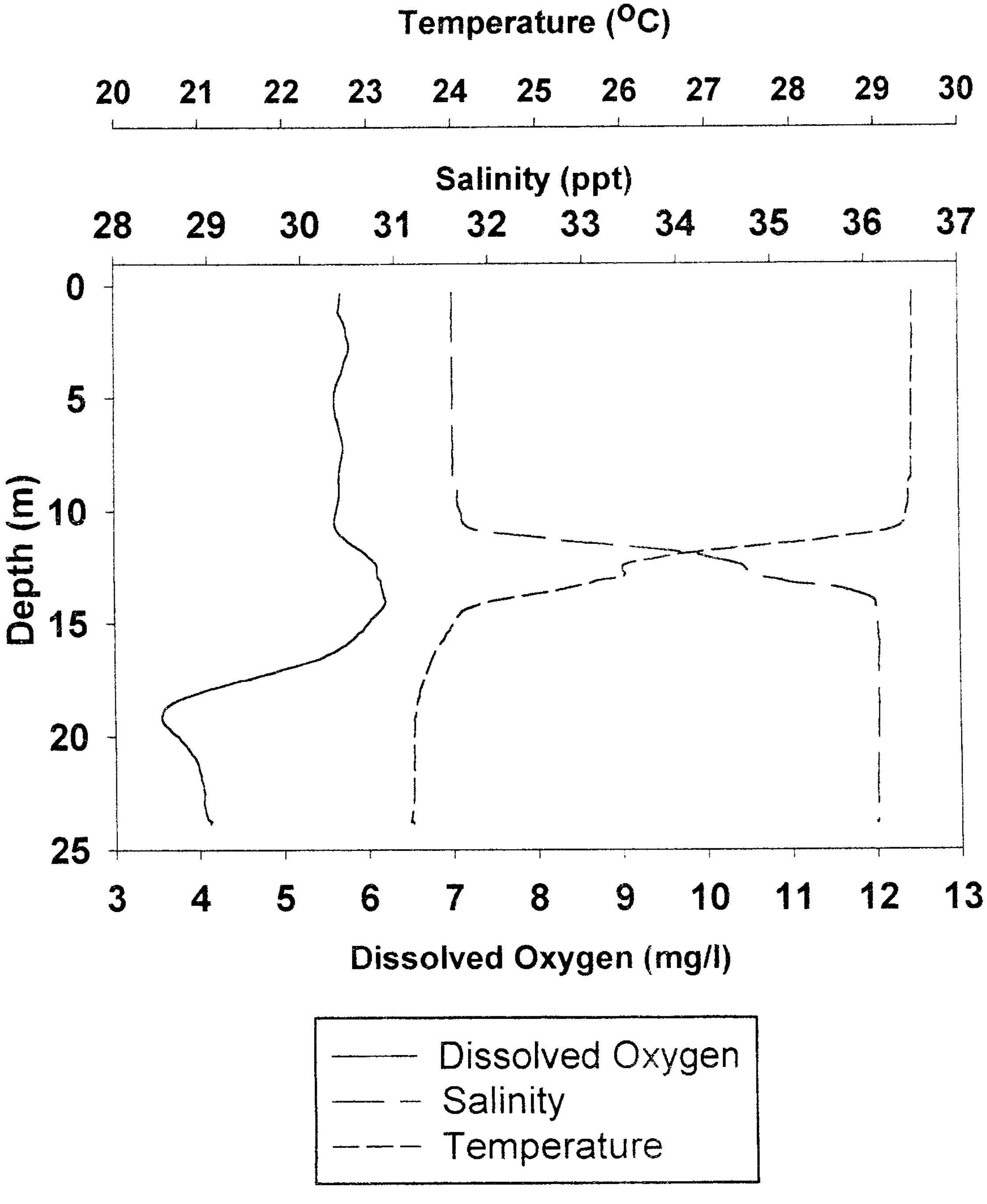
5-20-1998


Temperature (^oC)
18 19 20 21 22 23 24 25 26 27 28 29 30 31
Salinity (ppt)
29 30 31 32 33 34 35 36 37
Depth (m)
0 5 10 15 20 25 30 35
4 5 6 7 8
Dissolved Oxygen (mg/l)
Dissolved Oxygen
Salinity
Temperature

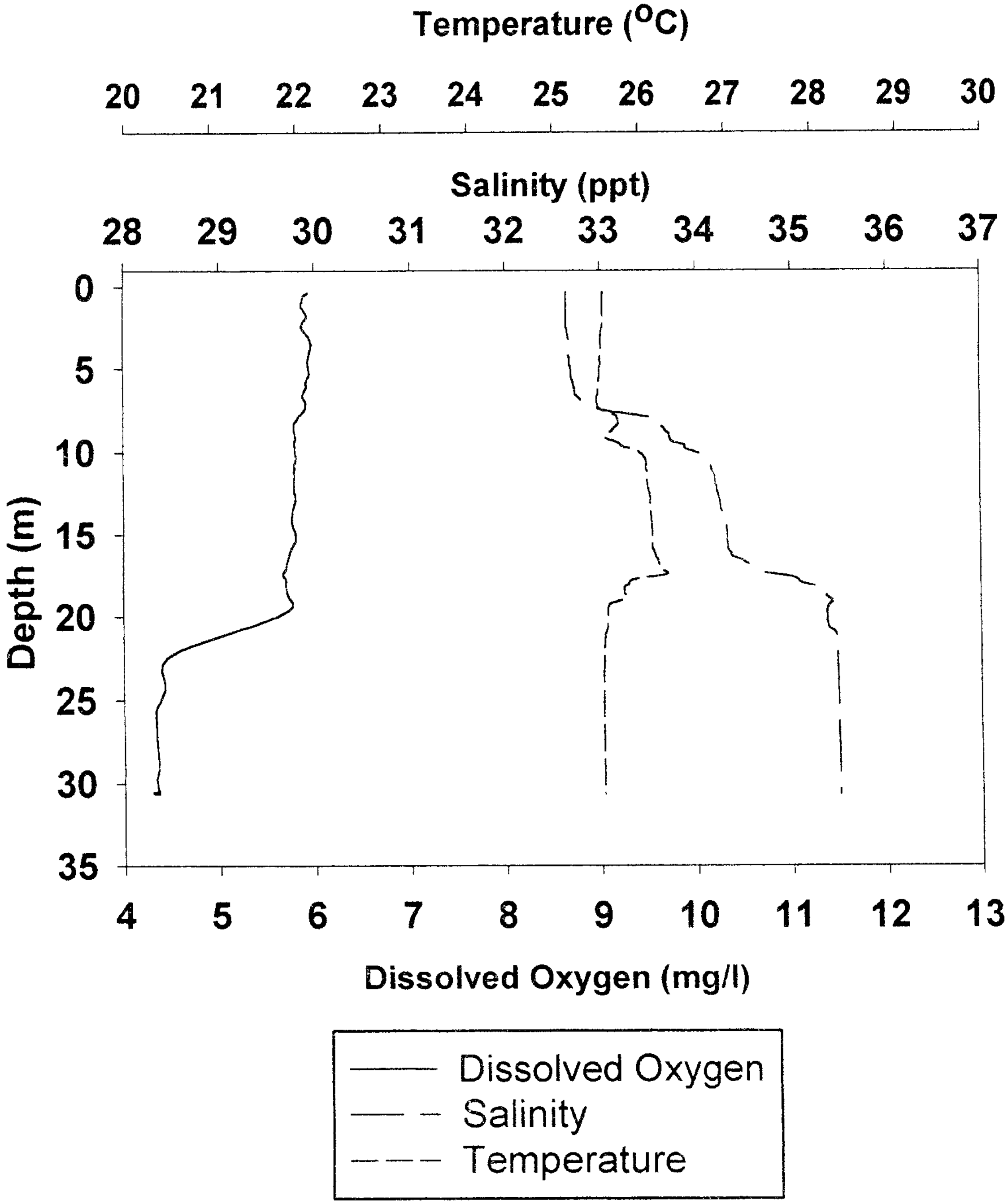
6-11-1998


0
5
10
15
20
25
Depth (m)
20
21
22
23
24
25
26
27
28
29
30
Temperature (°C)

8-4-1998


Temperature (°C)
20
21
22
23
24
25
26
27
28
29
30
Salinity (ppt)
28
29
30
31
32
33
34
35
36
37
Depth (m)
0
5
10
15
20
25
3
4
5
6
7
8
9
10
11
12
13
Dissolved Oxygen (mg/l)
Dissolved Oxygen
Salinity
Temperature

10-14-1998


Temperature (°C)
20
21
22
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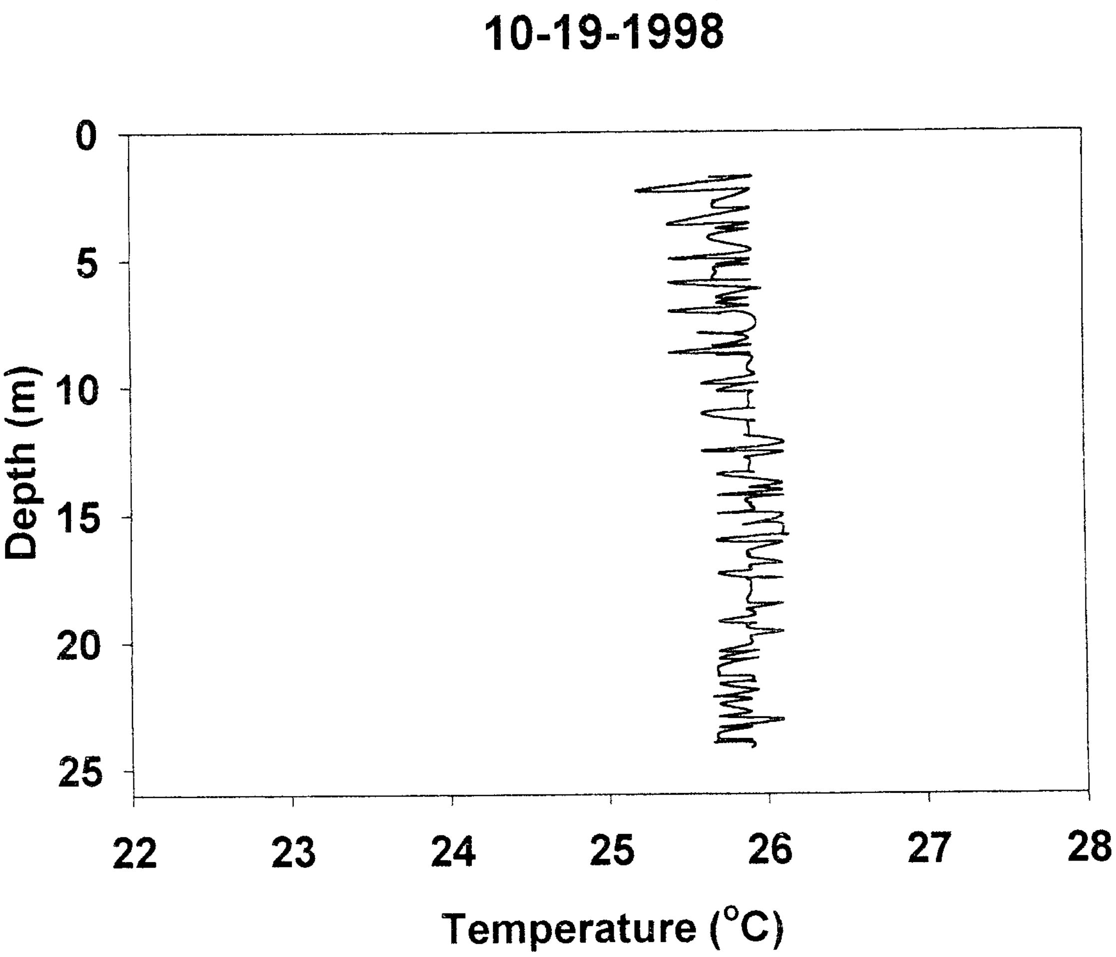
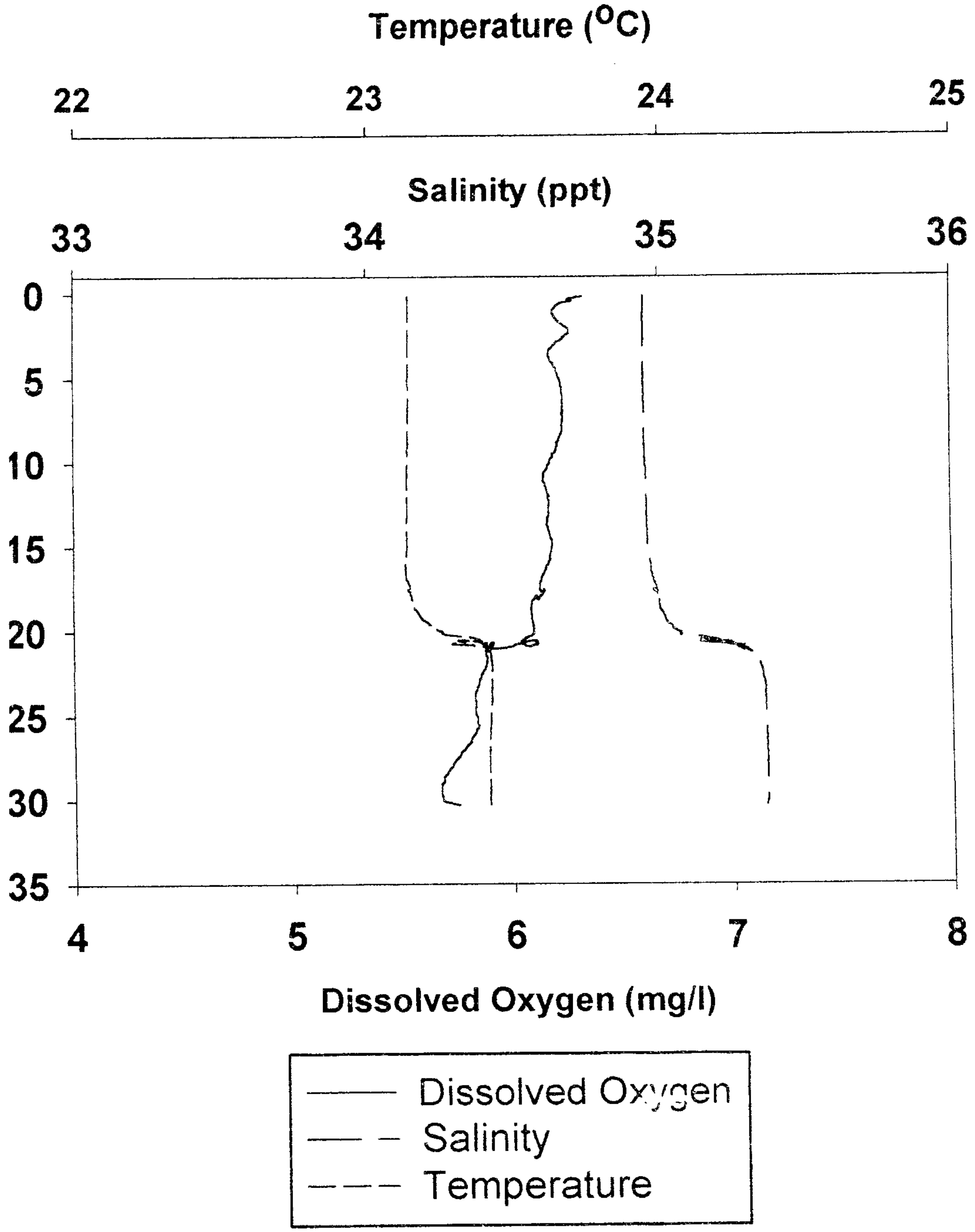
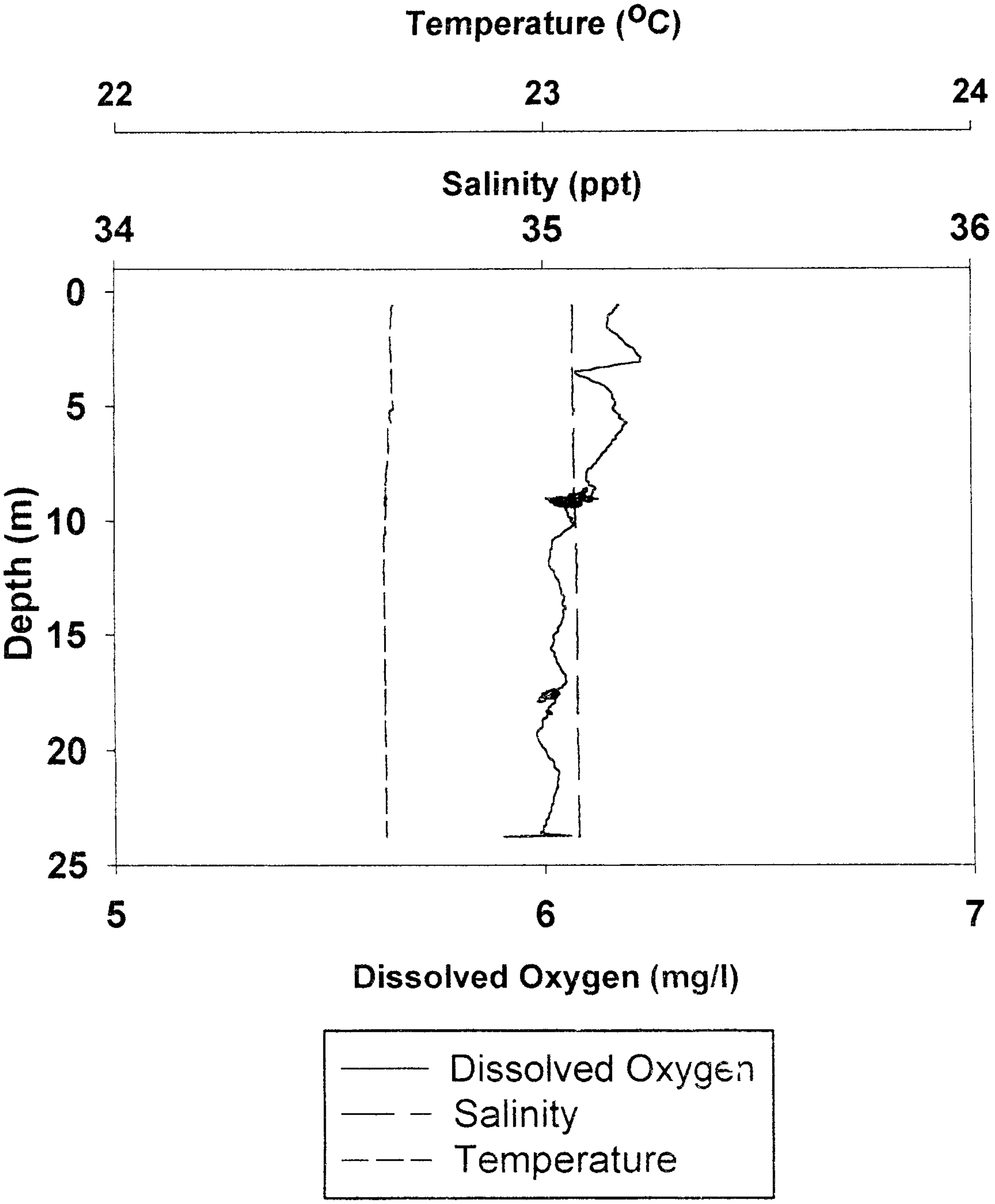
24
25
26
27
28
29
30
Salinity (ppt)
28
29
30
31
32
33
34
35
36
37
Depth (m)
0
5
10
15
20
25
30
35
4
5
6
7
8
9
10
11
12
13
Dissolved Oxygen (mg/l)
Dissolved Oxygen
Salinity
Temperature


10-19-1998
0
5
10
15
20
25
Depth (m)
22
23
24
25
26
27
28
Temperature (°C)

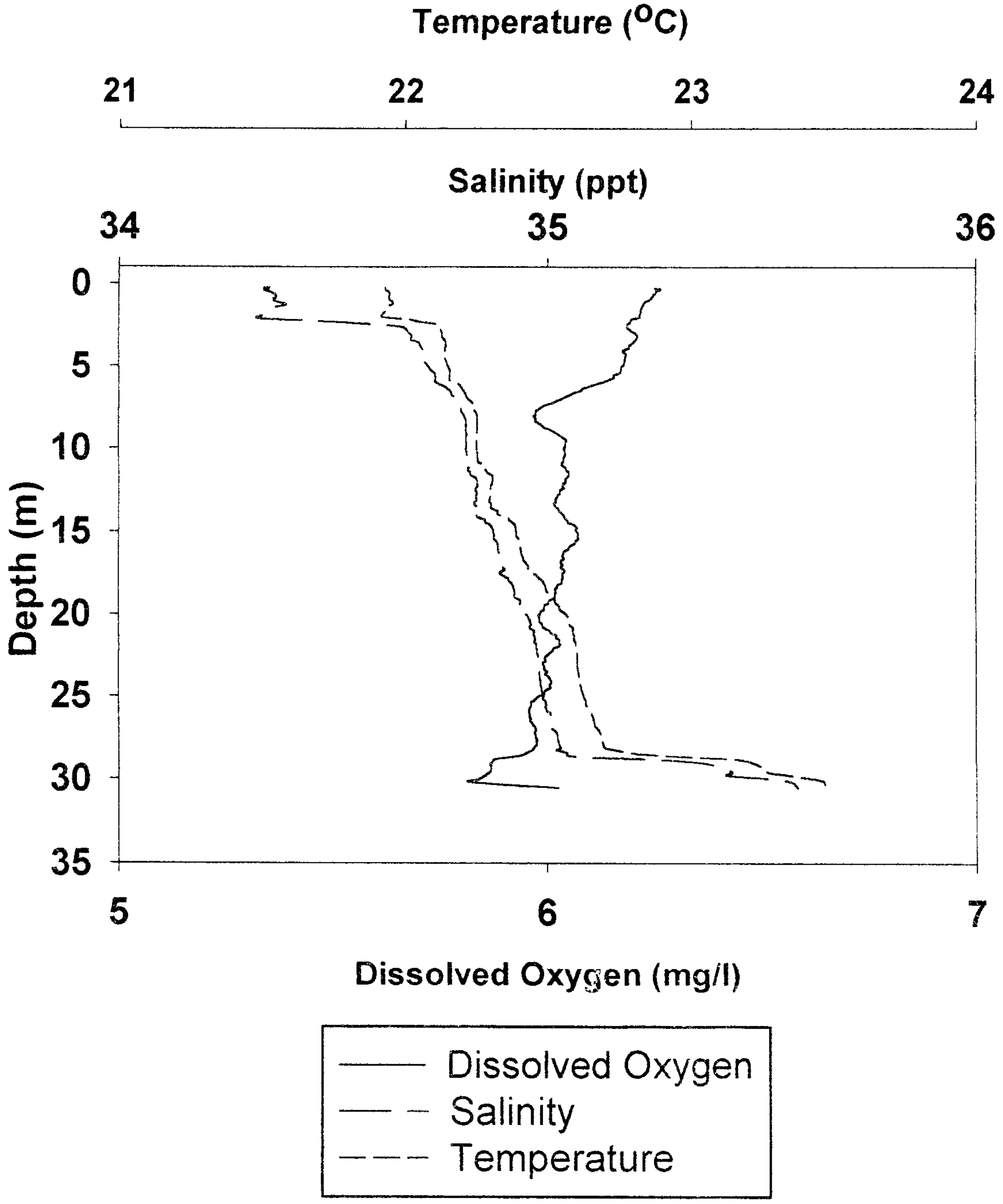
11-18-1998


Temperature (^{O}C)
22
23
24
25
Salinity (ppt)
33
34
35
36
0
5
10
15
20
25
30
35
4
5
6
7
8
Dissolved Oxygen (mg/l)
Dissolved Oxygen
Salinity
Temperature

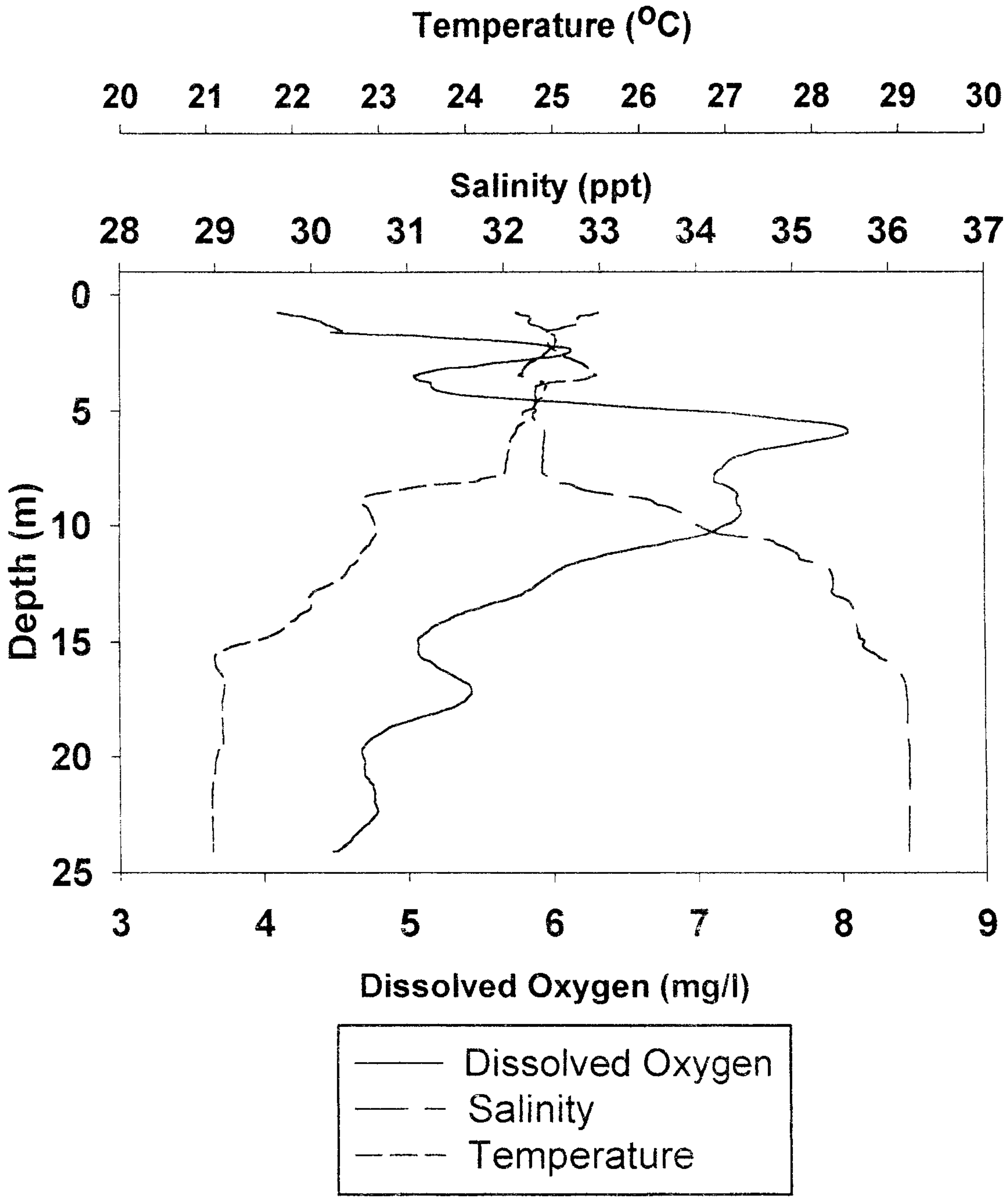
11-25-1998


Temperature (°C)
22
23
24
Salinity (ppt)
34
35
36
Depth (m)
0
5
10
15
20
25
5
6
7
Dissolved Oxygen (mg/l)
Dissolved Oxygen
Salinity
Temperature

12-1-1998



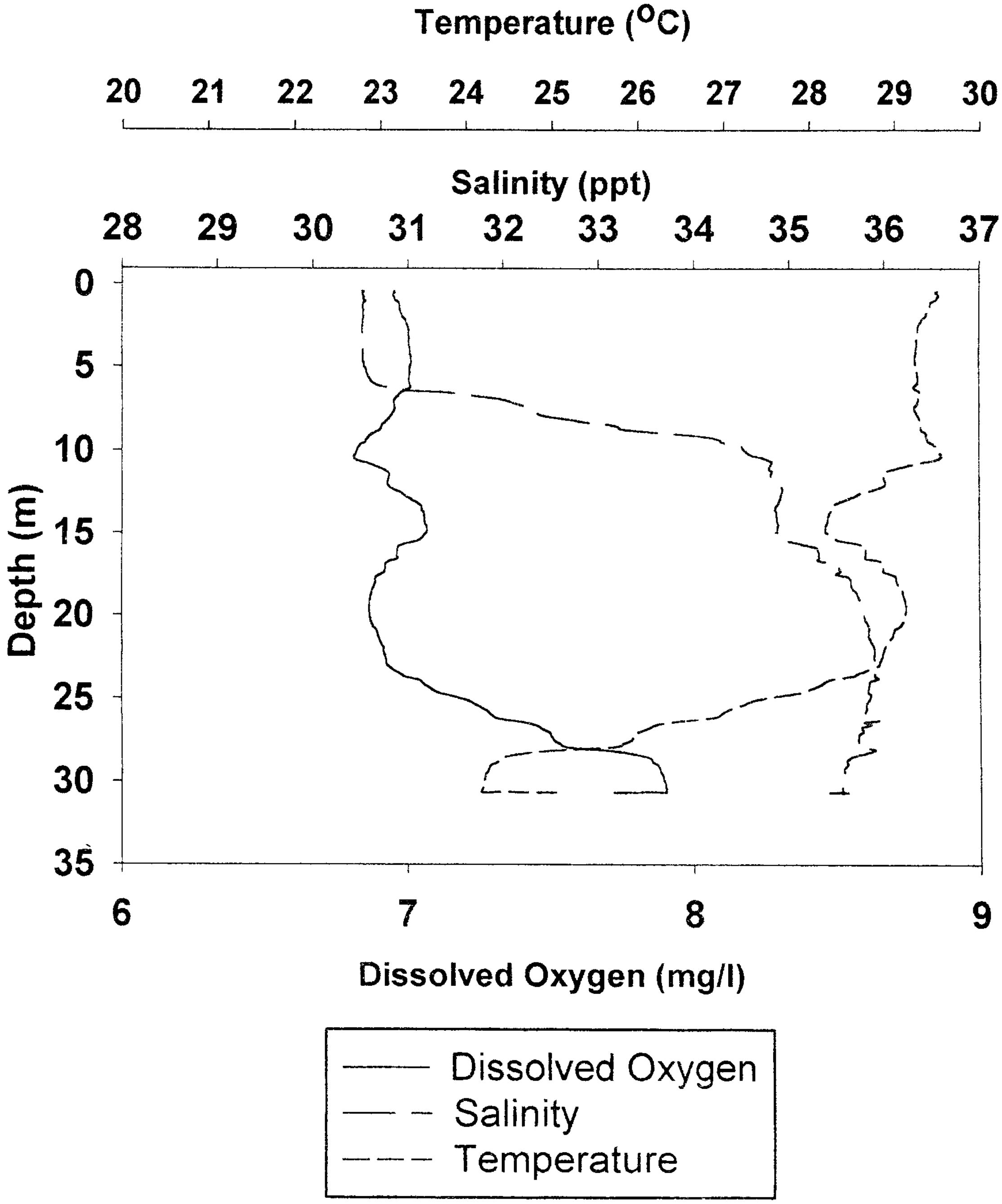
Temperature (°C)
21
22
23
24
Salinity (ppt)
34
35
36
0
5
10
15
20
25
30
35
Depth (m)
5
6
7
Dissolved Oxygen (mg/l)
Dissolved Oxygen
Salinity
Temperature

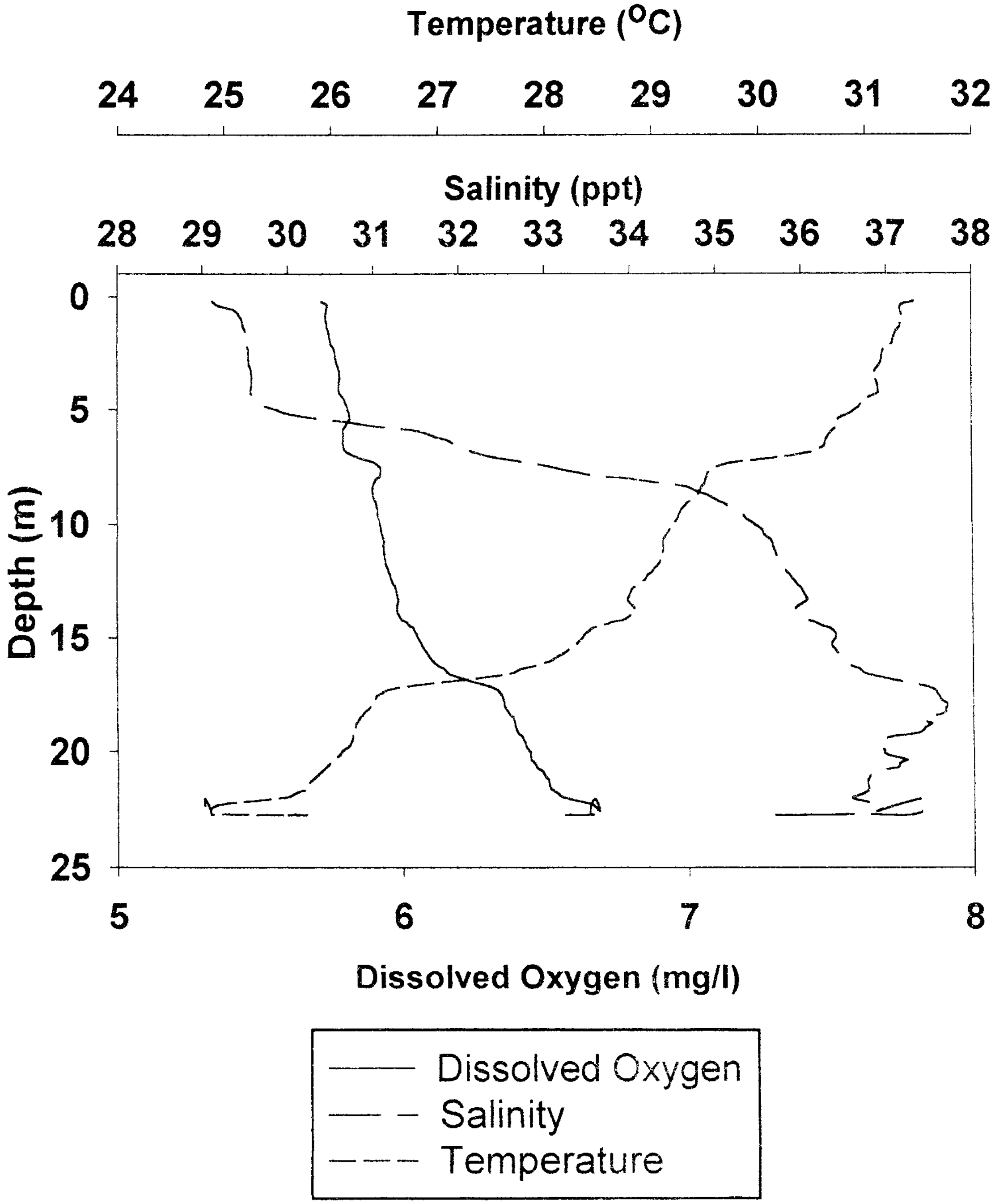


4-28-1999

Temperature (^{O}C)
20 21 22 23 24 25 26 27 28 29 30
Salinity (ppt)
28 29 30 31 32 33 34 35 36 37
Depth (m)
0 5 10 15 20 25
3 4 5 6 7 8 9
Dissolved Oxygen (mg/l)
Dissolved Oxygen
Salinity
Temperature

7-21-1999

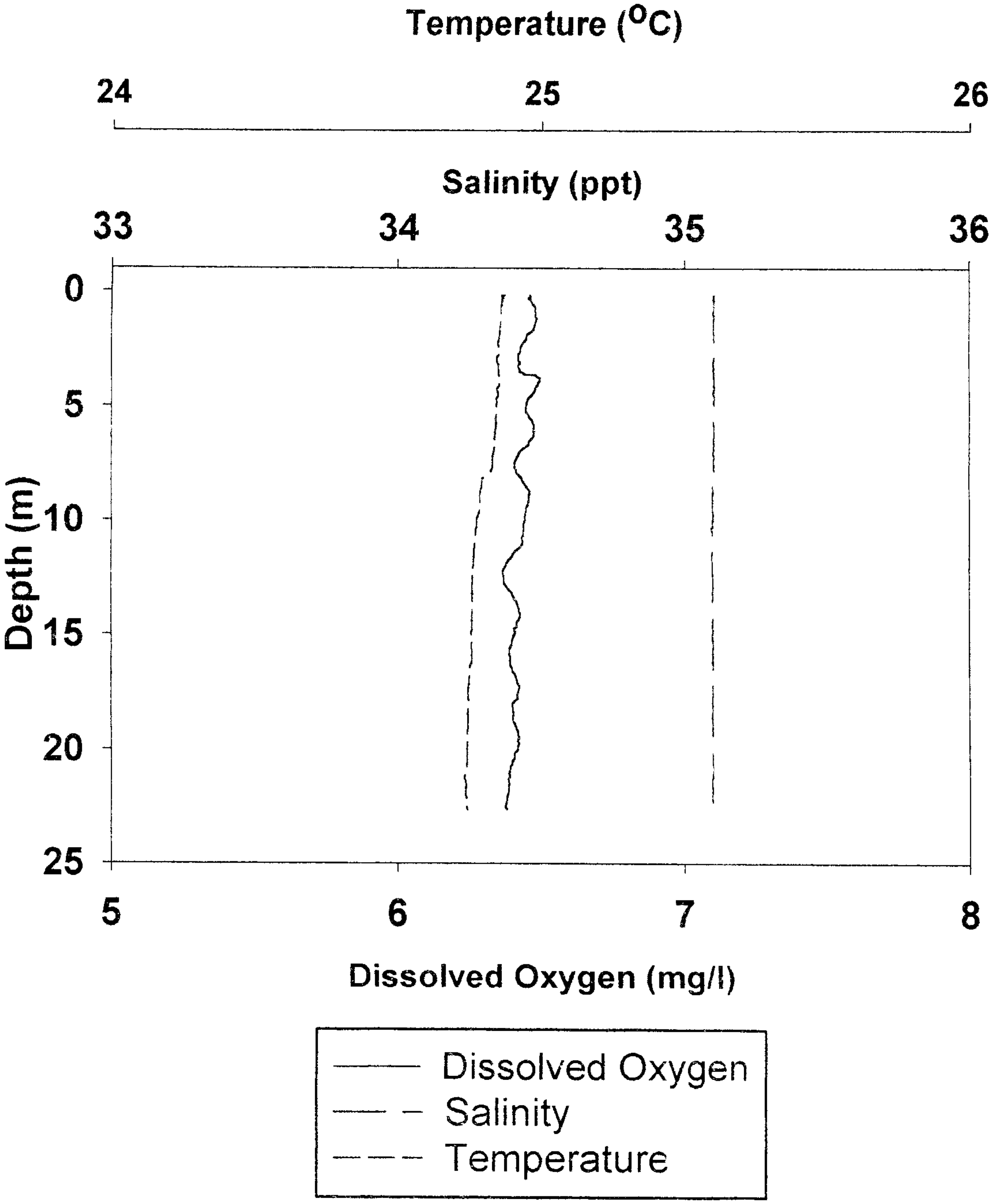

Temperature (°C)
20
21
22
23
24
25
26
27
28
29
30
Salinity (ppt)
28
29
30
31
32
33
34
35
36
37
Depth (m)
0
5
10
15
20
25
30
35
6
7
8
9
Dissolved Oxygen (mg/l)
Dissolved Oxygen
Salinity
Temperature



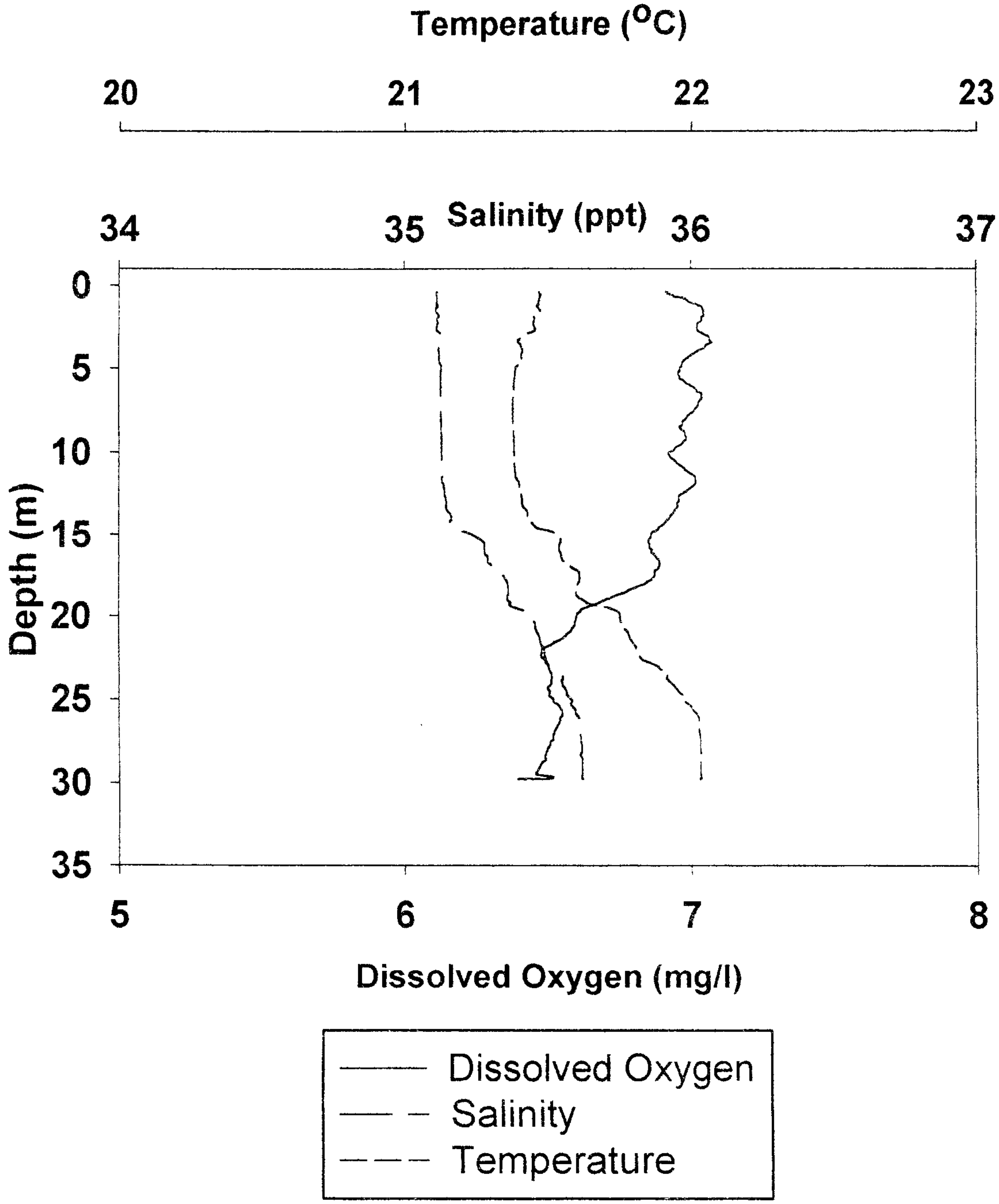
8-4-1999

Temperature (°C)
24
25
26
27
28
29
30
31
32
Salinity (ppt)
28
29
30
31
32
33
34
35
36
37
38
Depth (m)
0
5
10
15
20
25
5
6
7
8
Dissolved Oxygen (mg/l)
Dissolved Oxygen
Salinity
Temperature

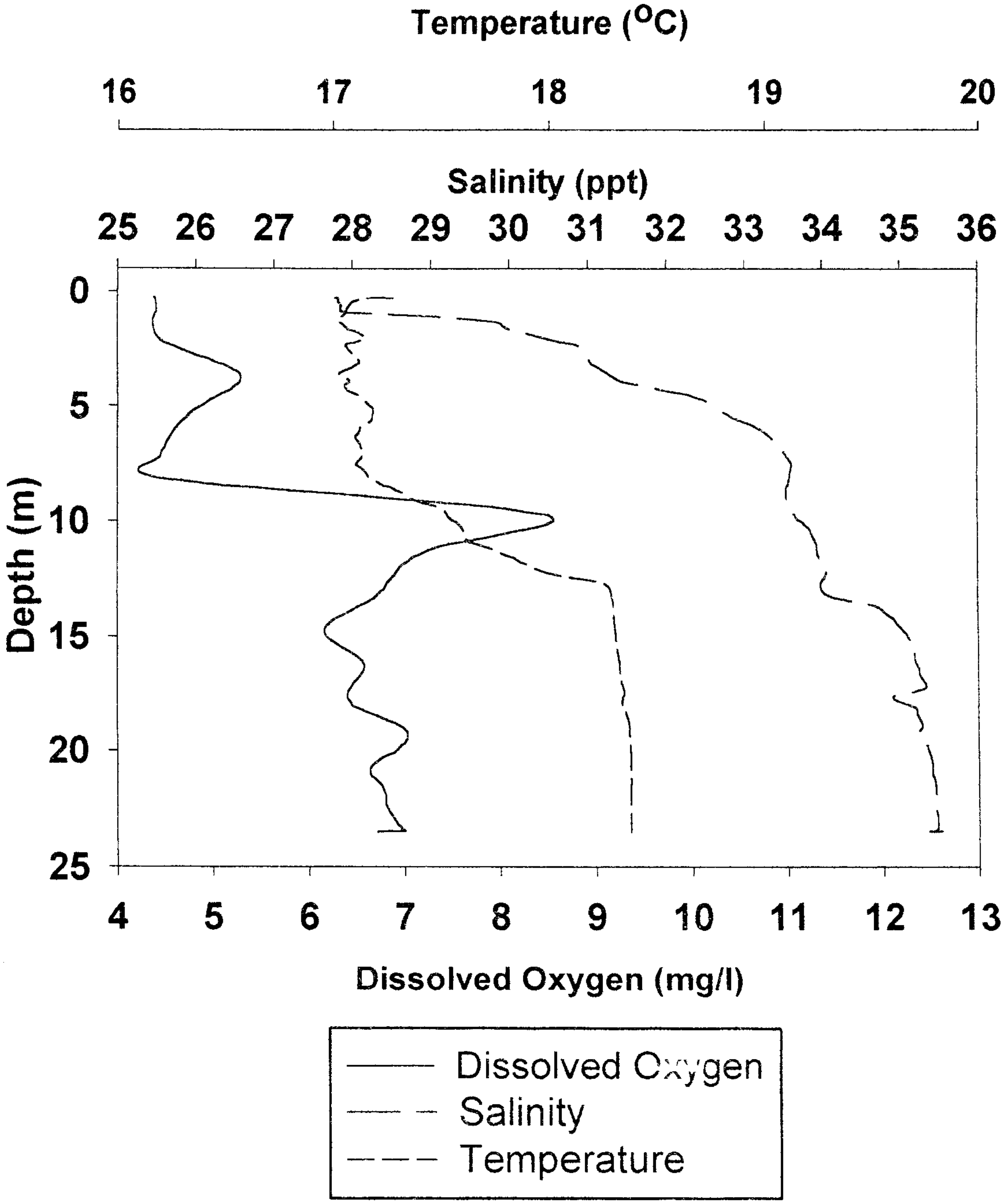
10-22-1999


Temperature (°C)
24
25
26
Salinity (ppt)
33
34
35
36
0
5
10
15
20
25
Depth (m)
5
6
7
8
Dissolved Oxygen (mg/l)
Dissolved Oxygen
Salinity
Temperature

11-23-1999


Temperature (°C)
20
21
22
23
Salinity (ppt)
34
35
36
37
Depth (m)
0
5
10
15
20
25
30
35
5
6
7
8
Dissolved Oxygen (mg/l)
Dissolved Oxygen
Salinity
Temperature

12-7-1999


Temperature (^{O}C)
16
17
18
19
20
Salinity (ppt)
25
26
27
28
29
30
31
32
33
34
35
36
Depth (m)
0
5
10
15
20
25
4
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9
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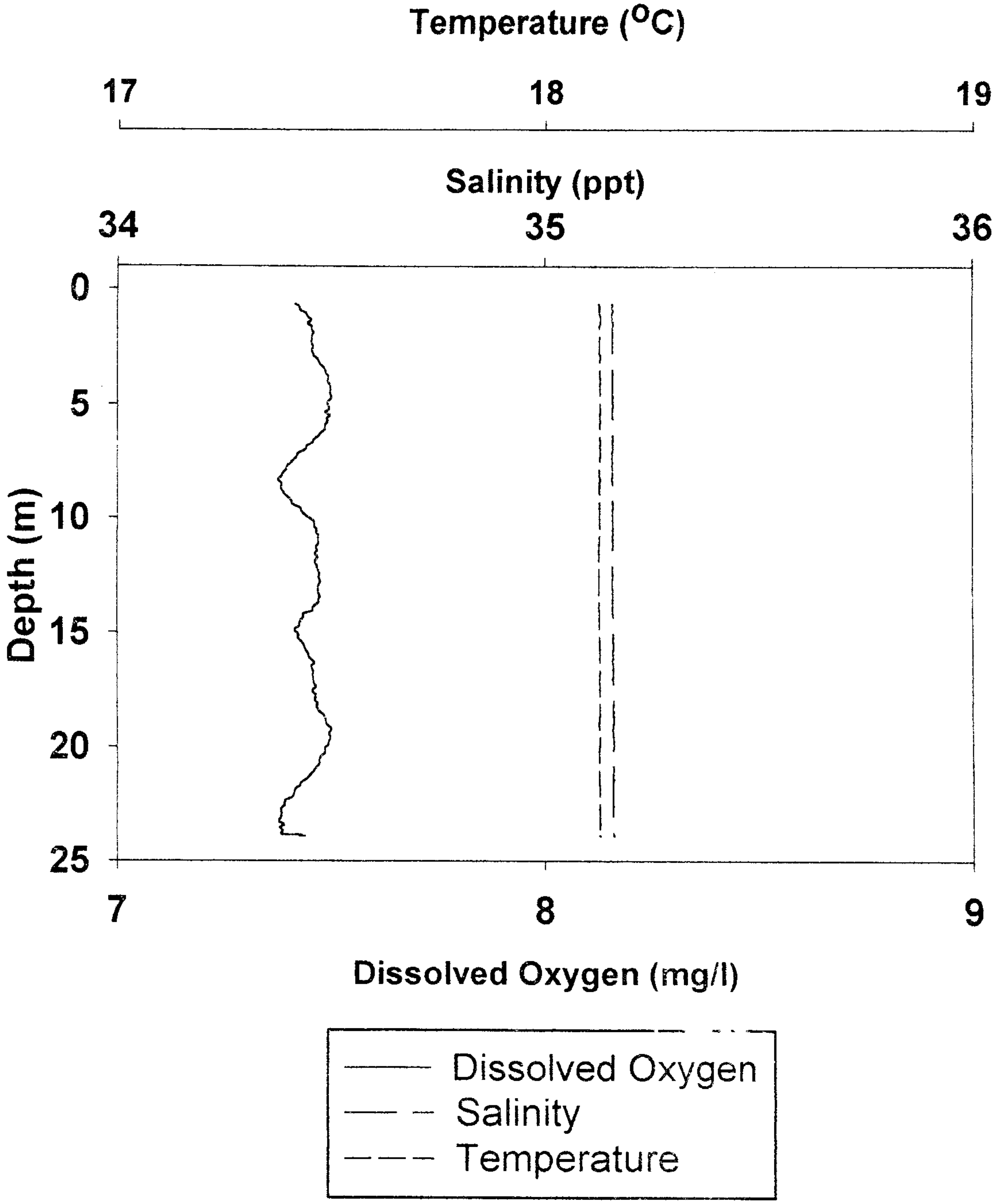
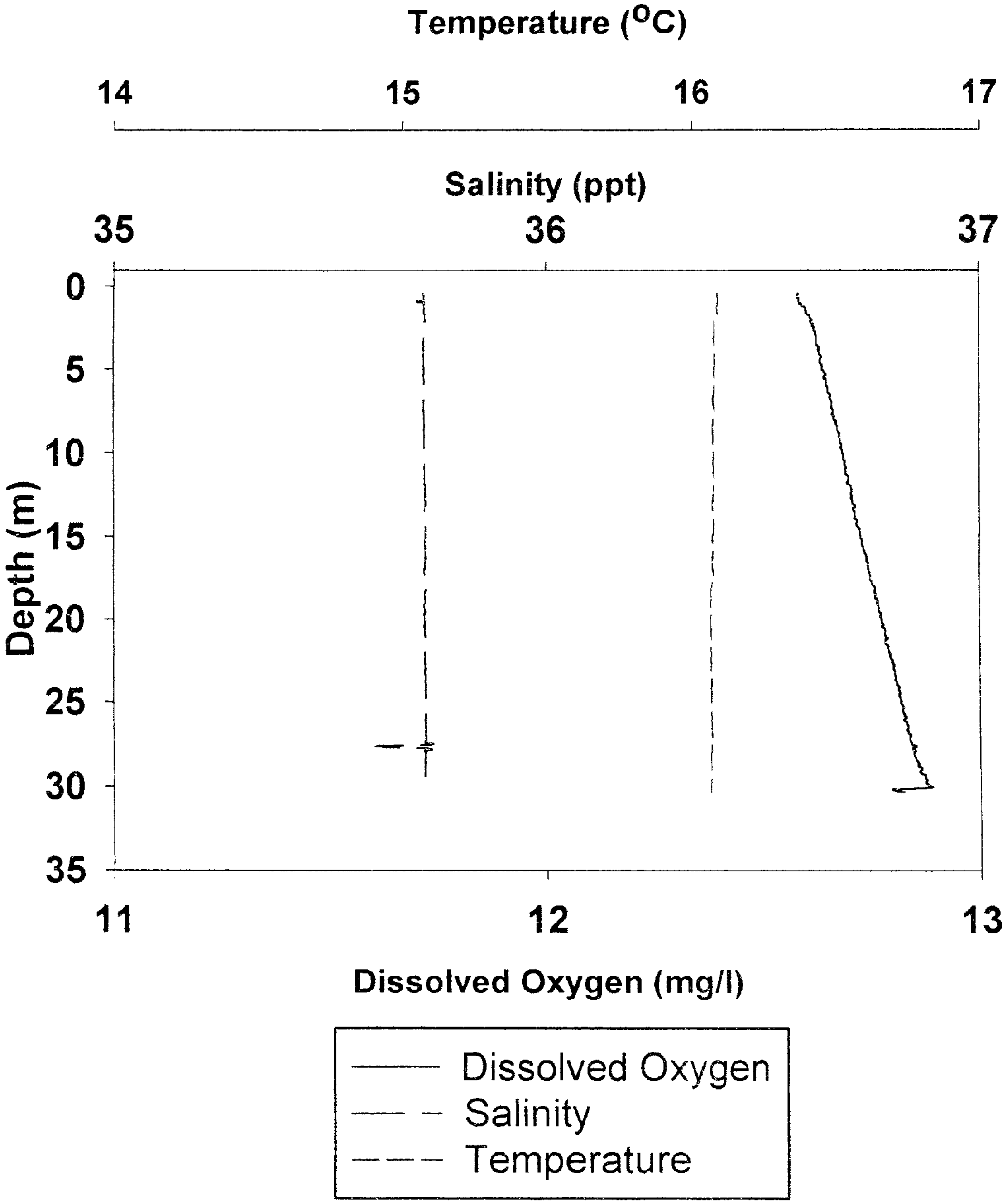
11
12
13
Dissolved Oxygen (mg/l)
Dissolved Oxygen
Salinity
Temperature

12-16-1999



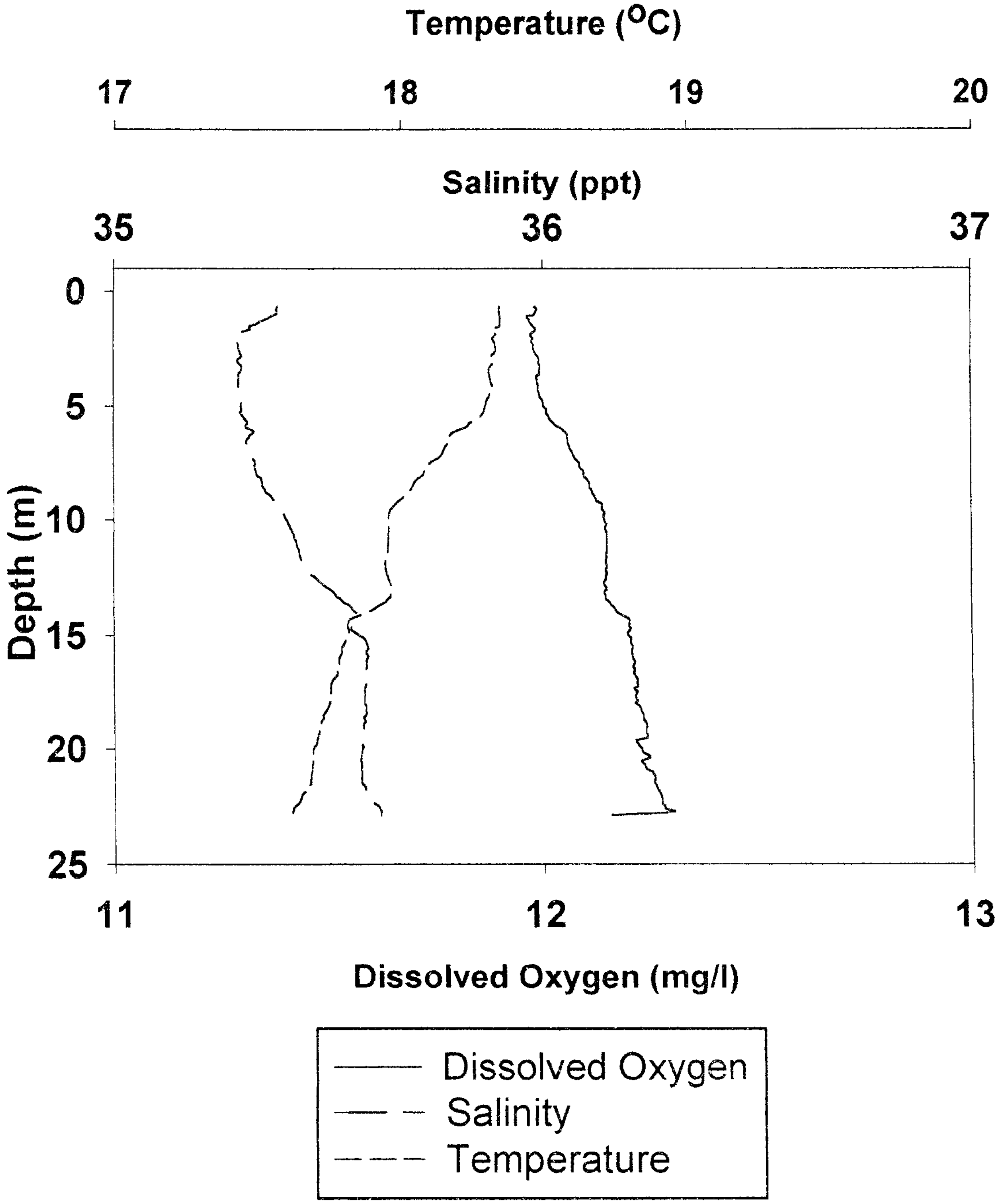
Temperature (^{o}C)
17
18
19
Salinity (ppt)
34
35
36
Depth (m)
0
5
10
15
20
25
7
8
9
Dissolved Oxygen (mg/l)
Dissolved Oxygen
Salinity
Temperature

2-3-2000



Temperature (^{o}C)
14
15
16
17
Salinity (ppt)
35
36
37
Depth (m)
0
5
10
15
20
25
30
35
11
12
13
Dissolved Oxygen (mg/l)
Dissolved Oxygen
Salinity
Temperature

2-25-2000



Temperature (^{O}C)
17
18
19
20
Salinity (ppt)
35
36
37
Depth (m)
0
5
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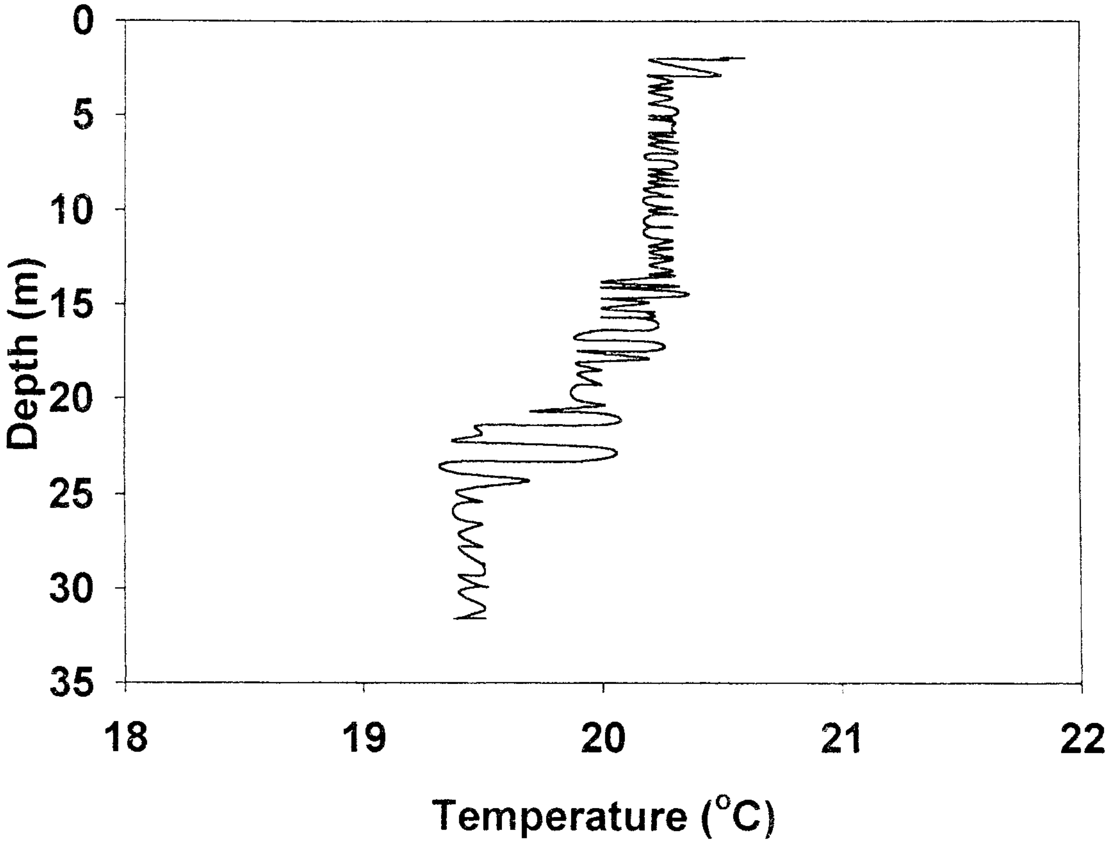
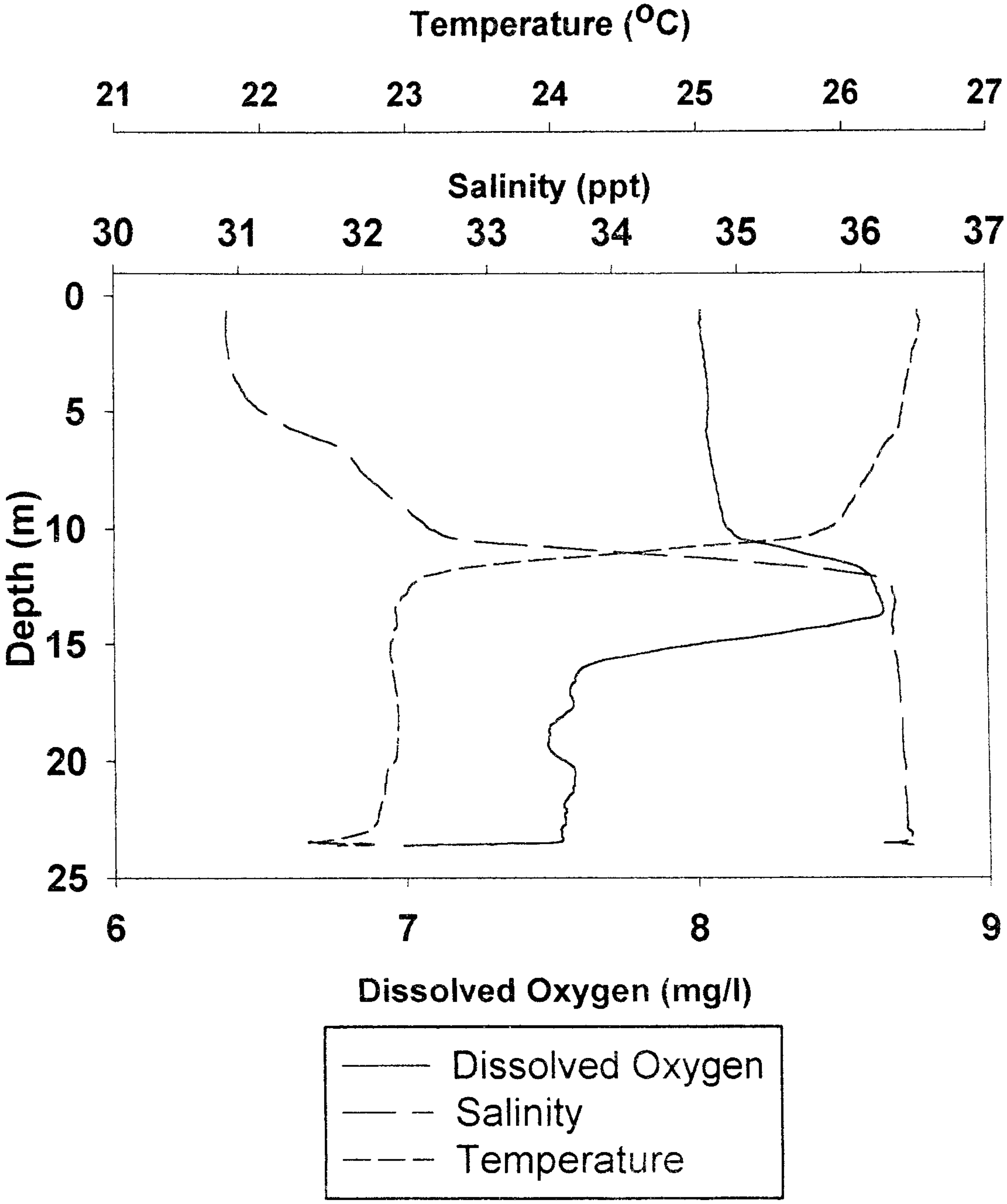
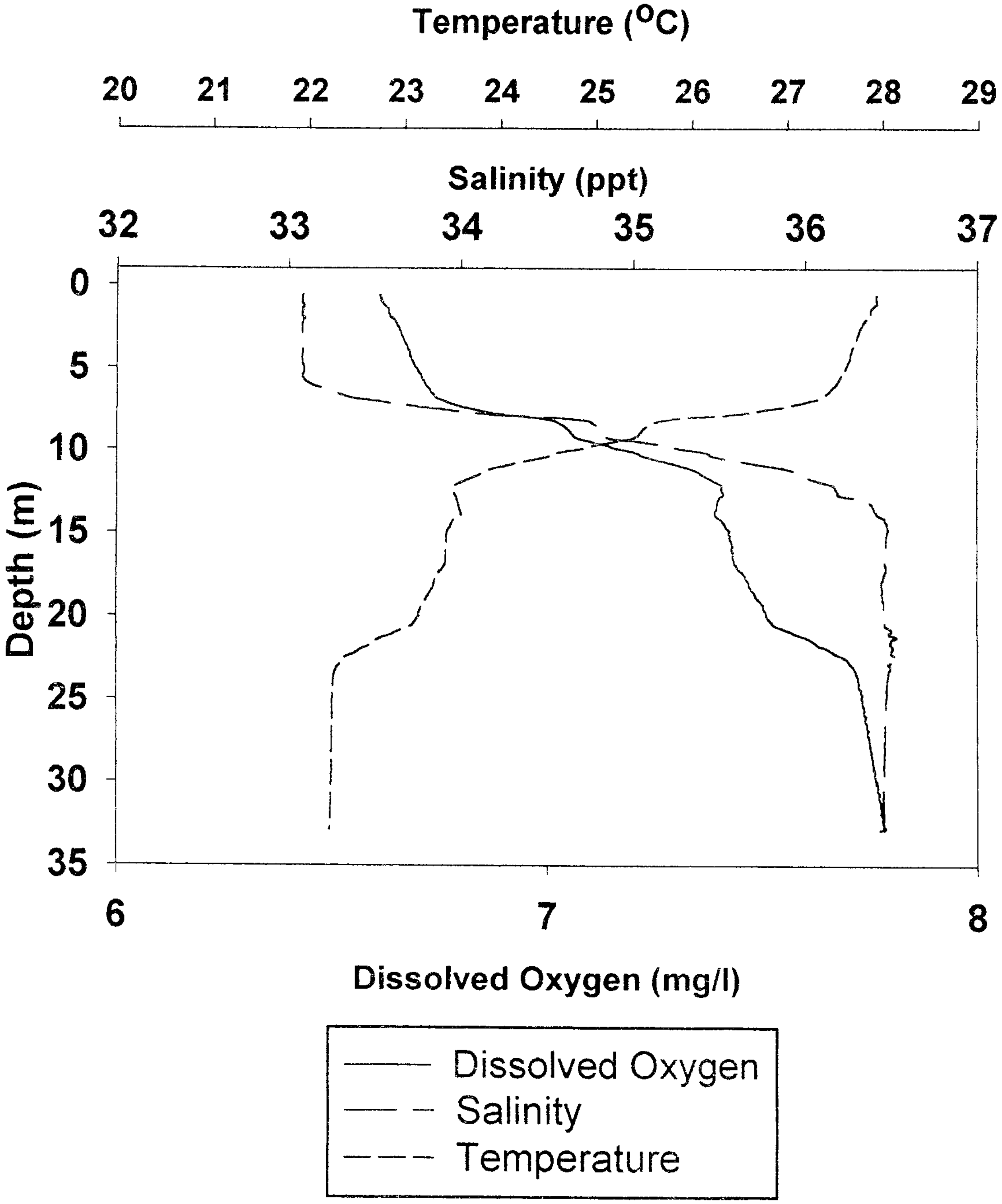
20
25
11
12
13
Dissolved Oxygen (mg/l)
Dissolved Oxygen
Salinity
Temperature


3-28-2000

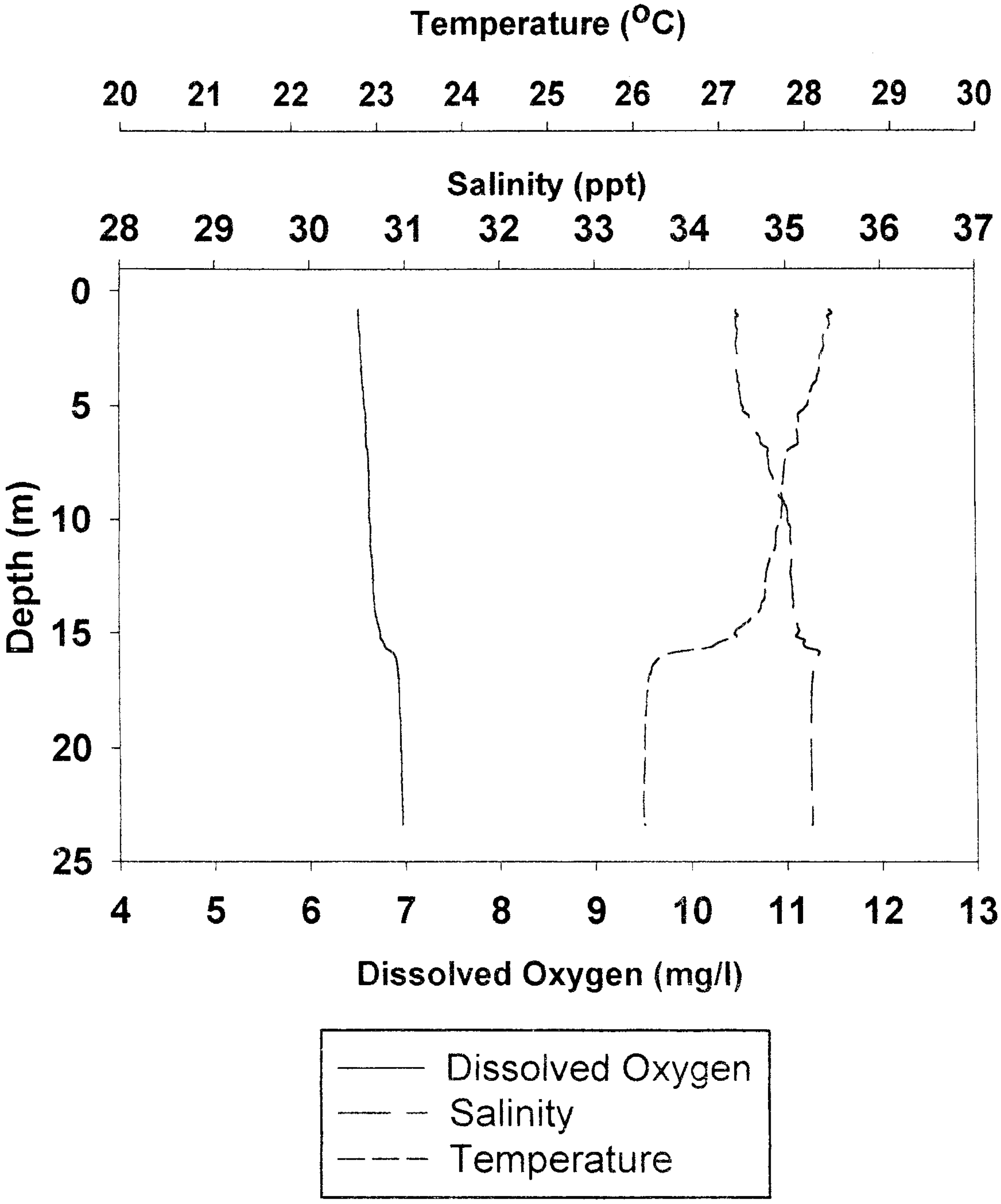
5-23-2000


Temperature (^{o}C)
21
22
23
24
25
26
27
Salinity (ppt)
30
31
32
33
34
35
36
37
Depth (m)
0
5
10
15
20
25
6
7
8
9
Dissolved Oxygen (mg/l)
Dissolved Oxygen
Salinity
Temperature

5-31-2000

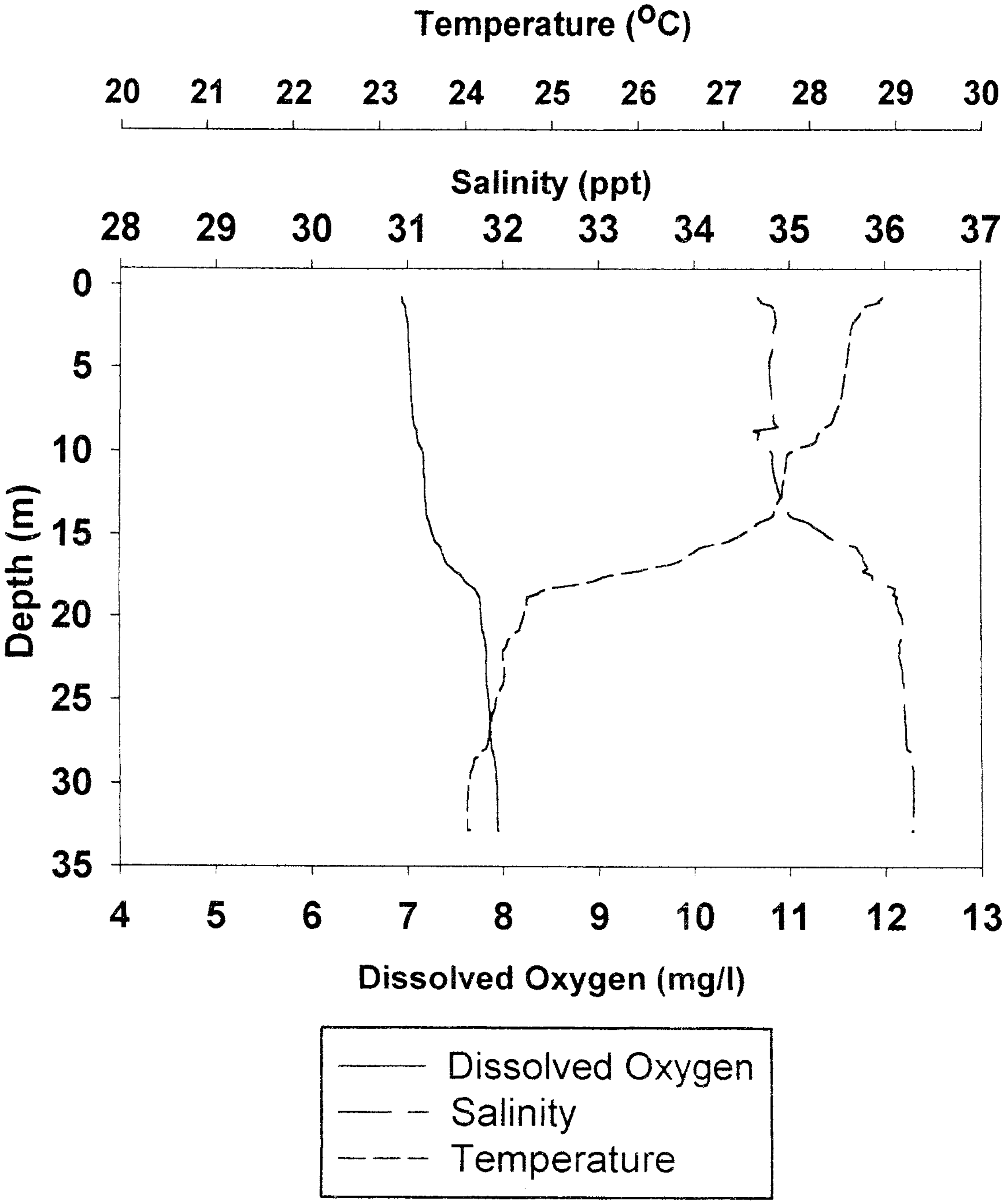

Temperature (°C)
20
21
22
23
24
25
26
27
28
29
Salinity (ppt)
32
33
34
35
36
37
0
5
10
15
20
25
30
35
Depth (m)
6
7
8
Dissolved Oxygen (mg/l)
Dissolved Oxygen
Salinity
Temperature

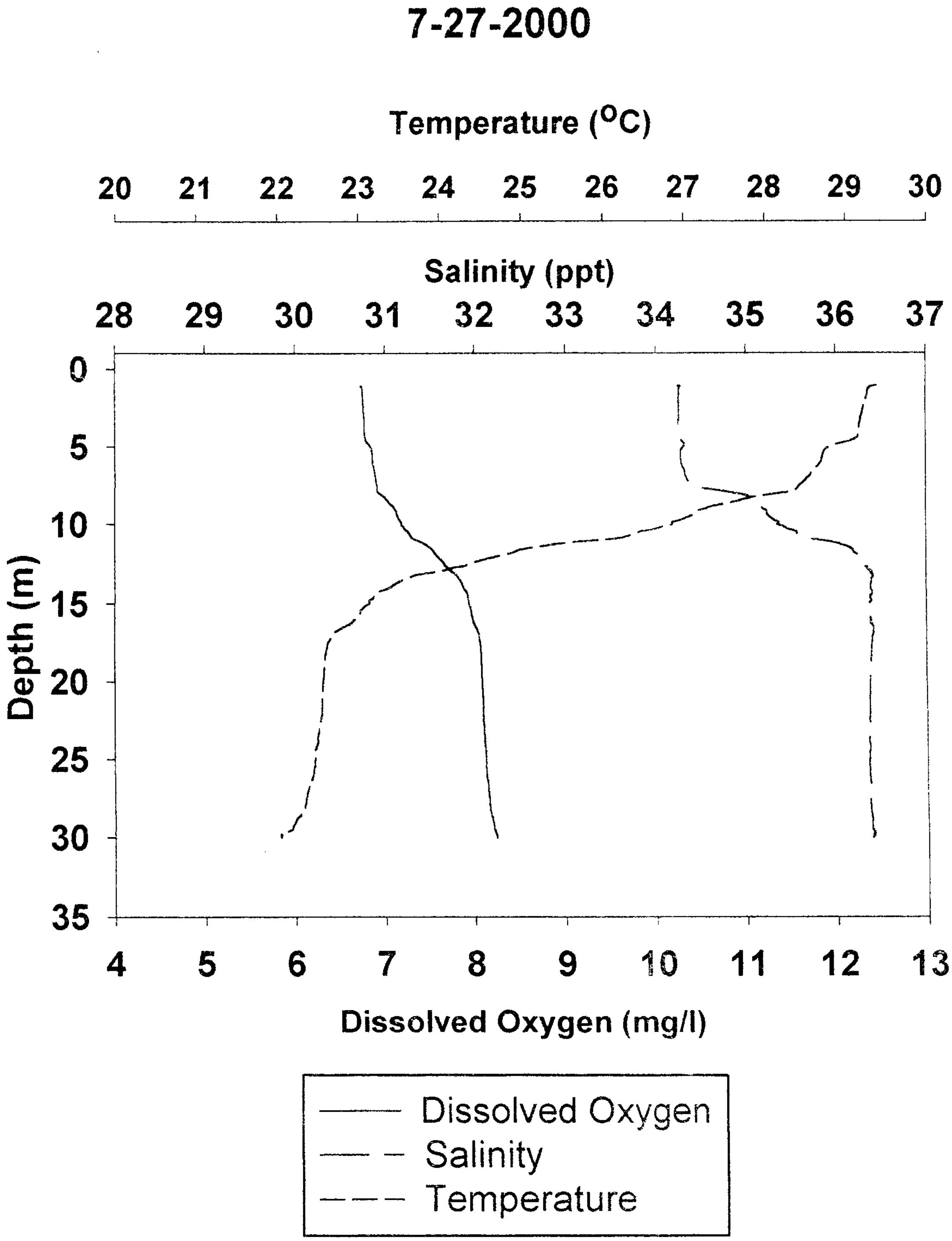
6-20-2000



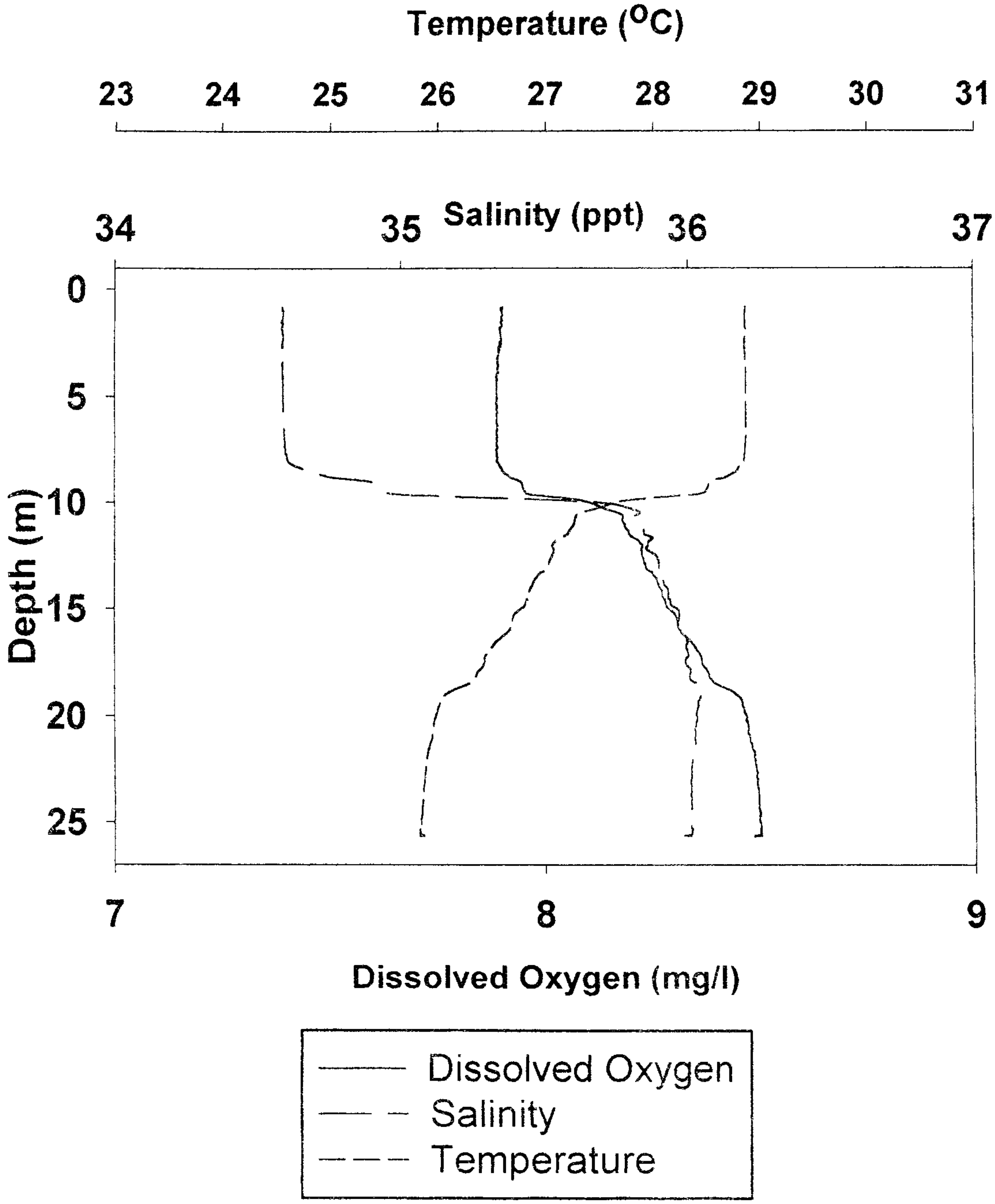
Temperature (^{O}C)
20 21 22 23 24 25 26 27 28 29 30
Salinity (ppt)
28 29 30 31 32 33 34 35 36 37
Depth (m)
0 5 10 15 20 25
4 5 6 7 8 9 10 11 12 13
Dissolved Oxygen (mg/l)
Dissolved Oxygen
Salinity
Temperature

6-21-2000

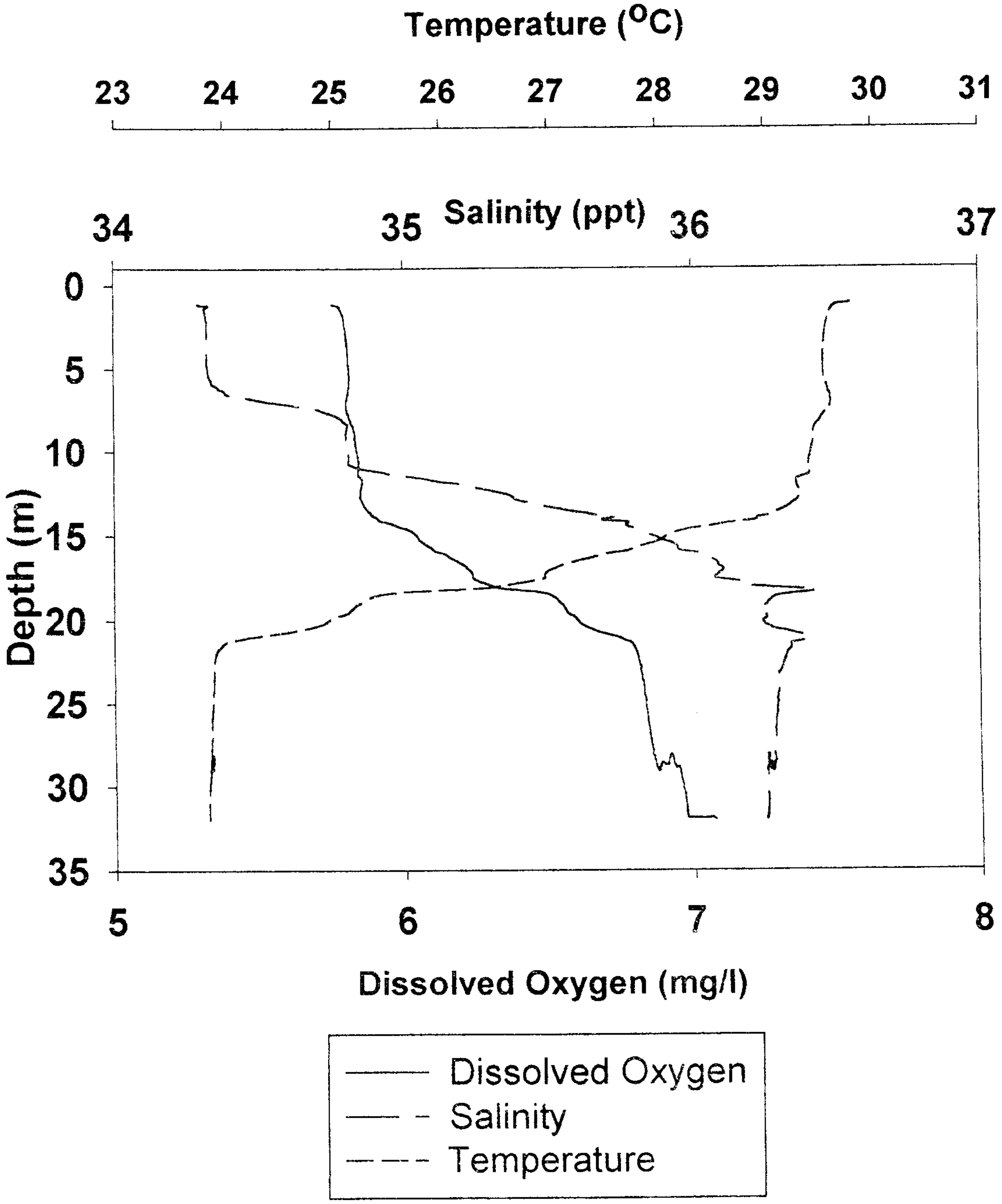

Temperature (°C)
20 21 22 23 24 25 26 27 28 29 30
Salinity (ppt)
28 29 30 31 32 33 34 35 36 37
Depth (m)
0 5 10 15 20 25 30 35
4 5 6 7 8 9 10 11 12 13
Dissolved Oxygen (mg/l)
Dissolved Oxygen
Salinity
Temperature


7-27-2000
Temperature (°C)
20
21
22
23
24
25
26
27
28
29
30
Salinity (ppt)
28
29
30
31
32
33
34
35
36
37
Depth (m)
0
5
10
15
20
25
30
35
4
5
6
7
8
9
10
11
12
13
Dissolved Oxygen (mg/l)
Dissolved Oxygen
Salinity
Temperature

8-3-2000


Temperature (°C)
23
24
25
26
27
28
29
30
31
Salinity (ppt)
34
35
36
37
Depth (m)
0
5
10
15
20
25
7
8
9
Dissolved Oxygen (mg/l)
Dissolved Oxygen
Salinity
Temperature

8-8-2000


Temperature (°C)
23
24
25
26
27
28
29
30
31
Salinity (ppt)
34
35
36
37
Depth (m)
0
5
10
15
20
25
30
35
5
6
7
8
Dissolved Oxygen (mg/l)
Dissolved Oxygen
Salinity
Temperature