Factors Influencing Year-Class Strength and Growth of Young-of-the-Year
Summer Flounder (Paralichthyidae: *Paralichthys dentatus)*

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APPROVAL SHEET

This thesis is submitted in partial fulfillment of

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DEDICATION

This thesis is dedicated to my parents, Mary and Paul, for their endless love, encouragement, and support.

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FACTORS INFLUENCING YEAR-CLASS STRENGTH AND GROWTH OF

YOUNG-OF-THE-YEAR SUMMER FLOUNDER

INTRODUCTION

Summer Flounder, *Paralichthys dentatus,* management is guided by a coast-wide

stock assessment to ensure sustainable commercial and recreational fisheries along the

US Atlantic coast (Terceiro 2012). The stock assessment uses catch data from these

fisheries, as well as data from fishery-independent surveys, to estimate abundance of

the stock. During the past quarter-century, Summer Flounder spawning stock biomass

has increased, but recruitment has remained highly variable (Terceiro 2011), and the

relationship between spawning stock biomass and recruitment is unclear.

Understanding Summer Flounder recruitment dynamics, including effects of biotic and

abiotic factors on year-class strength, is necessary to better inform stock assessment

models.

A broad range of physical and environmental factors may influence growth,

survival, and recruitment of young-of-the-year (YOY) Summer Flounder, from the pelagic

egg and larval stage to the demersal juvenile stage. Summer Flounder are distributed

from Nova Scotia to Florida (Gutherz 1967; Grimes et al. 1989) and are most abundant

in the mid-Atlantic region (Wilk et al. 1980). Adult Summer Flounder migrate from

estuarine and coastal areas to the continental shelf to spawn from September to

February; peak spawning occurs off the Virginia coast during November (Smith 1973;

Morse 1981). Pelagic Summer Flounder larvae rely primarily on selective tidal stream

transport for delivery into coastal bays and estuaries such as Chesapeake Bay (Hare et

al. 2005). Summer Flounder larvae are negatively buoyant, and their position in the water column depends on tidal phase: larvae are found near the bottom during ebb and slack tides and in the water column during flood tides (Hare et al. 2006). After competing metamorphosis, Summer Flounder settle on the bottom in nursery habitats and exhibit relatively fast growth during their first year of life (Szedlmayer et al. 1992; Tuckey and Fabrizio 2013).

Many hypotheses have been advanced to account for observed annual fluctuations in abundance of fishes, and most invoke a coupling between environmental and biological processes (Houde 2008). Climate variability, which influences temperature and salinity regimes (Gibson and Najjar 2000; Najjar et al. 2010; Xu et al. 2012) and circulation (Scully 2010) in Chesapeake Bay, may drive recruitment patterns of shelf-spawning species such as Summer Flounder (Wood and Austin 2009). Variations in nursery habitat characteristics, such as food availability, predation, temperature and salinity (Gibson 1994) may differentially influence growth and survival of juvenile fishes in these areas (Fitzhugh et al. 1996; Phelan et al. 2000; Sogard et al. 2001). Temperature strongly influences feeding rates and growth (Brett 1979; Gibson 1994), which is variable within a year-class and also among nursery habitats (Chambers et al. 1988; Sogard and Able 1992; Ciotti et al. 2010). Fast growth during the first year of life is critical for survival (e.g., Campana et al. 1989; Tupper and Boutilier 1995; Campana 1996), and may be influenced by the density of conspecifics (e.g., Craig et al. 2007; Tuckey 2009; Martino and Houde 2012).

My research objectives were to understand factors influencing year-class strength (Chapter 1) and growth (Chapter 2) of young-of-the-year Summer Flounder in Chesapeake Bay from 1988 to 2012. In Chapter 1, I examined effects in winter (December-April) of wind, freshwater discharge, temperature and salinity on observed year-class strength (measured as abundance of YOY Summer Flounder in August, September, and October). I also investigated the method used to estimate YOY Summer Flounder year-class strength in Chesapeake Bay from fisheries-independent survey catches, considering the time period and location of catches used for these calculations, as well as distributional assumptions of catches. In Chapter 2, I examined biotic and abiotic factors that contribute to variation in growth of Summer Flounder after they have settled on the bottom in nursery habitats (June to November). Factors examined included region, density of conspecifics, temperature, salinity, depth, dissolved oxygen, and prey abundance. Results from this research provide insight on the factors contributing to recruitment variability and growth of YOY Summer Flounder in Chesapeake Bay.

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CHAPTER 1: FACTORS INFLUENCING YEAR-CLASS STRENGTH OF YOUNG-OF-THE-YEAR SUMMER FLOUNDER IN CHESAPEAKE BAY

ABSTRACT

Species that spawn along the coast (such as Summer Flounder *Paralichthys dentatus*) rely on the connectivity between spawning grounds and estuarine nursery habitats. Environmental conditions within nursery areas may affect the growth and survival of young-of-the-year (YOY) fishes, thereby influencing year-class strength. In this study, I examined effects of environmental conditions during the larval stage of Summer Flounder on the observed abundance of YOY Summer Flounder in nursery areas in Chesapeake Bay. Furthermore, the method of calculating YOY Summer Flounder recruitment in Chesapeake Bay from fisheries-independent survey data, and the time period and locations of catches used for these calculations, was assessed to obtain measures of recruitment that best reflected abundance of YOY Summer Flounder in Virginia estuarine waters. I used a delta-lognormal model to estimate annual, stratified mean abundance for Summer Flounder based on catches from Chesapeake Bay and the James, York, and Rappahannock rivers. About 75% of the variation in annual abundance of Summer Flounder from 1988 to 2012 was explained by a multiple linear regression model of year-class strength as a function of wind, freshwater discharge, temperature, salinity, and a categorical factor accounting for time. Average surface water temperature in Chesapeake Bay from January-April had a significant positive effect on Summer Flounder abundance. The effect of average east wind speed in December on Summer Flounder abundance was dependent on time period such that higher wind speed resulted in greater abundance during the early portion of the time series, but abundance remained relatively constant with increasing wind during the later portion of the time series. Based on the influence of physical and environmental factors on Summer Flounder abundance in Virginia estuaries, I suggest the use of a coupled physical-biological model to predict Summer Flounder year-class strength and larval delivery from continental shelf spawning grounds to inshore nursery areas.

INTRODUCTION

Many species that spawn along the Atlantic coast, including Summer Flounder

Paralichthys dentatus, Atlantic Croaker *Micropogonias undulatus*, and Bluefish

Pomatomus saltatrix, rely on the connection between the ocean and estuarine habitats

to successfully complete their life cycles (Able 2005; Able and Fahay 2010). Because eggs

and larvae occur in continental shelf waters, these life stages often depend on wind and

currents for transport to inshore nursery areas (Norcross and Austin 1988; Valle-

Levinson 2001; Hare et al. 2005). Environmental conditions within nursery areas may

affect the growth and survival of young-of-the-year (YOY) fishes, thereby influencing

their abundance (Houde 1989a). For most fishes, abundance of the YOY stage serves as

a measure of year-class strength, or recruitment success, which is highly variable from

year to year. Pronounced environmental variation in temperate estuaries likely

contributes to recruitment variability in species that use nursery areas in these systems.

Chesapeake Bay serves as an important nursery area in the mid-Atlantic region and is

used by a number of commercially and recreationally valuable species (Kemp et al.

2005; Murdy and Musick 2013), including Summer Flounder, the species of interest for

this study.

In addition to the effect of spawning stock biomass on recruitment, the

relationship between abundance of recruits in nursery habitats and stock abundance

(most commonly measured as spawning stock biomass) may also be influenced by

variations in environmental factors and habitat characteristics (Rice et al. 2005). Fishes

exhibit a variety of species-specific or population-specific stock-recruitment

relationships that relate stock abundance to abundance of recruits (Ricker 1954;

Beverton and Holt 1957; Jennings et al. 2001). Some examples of stock-recruitment

relationships for flatfish stocks in marine waters of the United States and Canada

include strong positive correlations between spawning stock biomass and recruitment

(such that recruitment increases as spawning stock biomass increases), weak

relationships between spawning stock biomass and recruitment (such that recruitment

at low levels of spawning stock biomass is similar to recruitment levels at high levels of

spawning stock biomass), or no discernible relationship at all (Rice et al. 2005).

Additionally, variable patterns in stock-recruit relationships have been observed for the

same flatfish species in different geographic regions (e.g., Common Sole from the

western and eastern English Channel; Rice et al. 2005). Furthermore, measurement

error of spawner abundance, recruit abundance, or both, can make underlying stock-

recruit relationships difficult to discern (Walters and Ludwig 1981). Environmental

conditions may be important drivers of YOY Summer Flounder recruitment because of

the influence of these factors on Summer Flounder throughout their first year of life,

from the pelagic egg and larval stage in shelf waters to the demersal juvenile stage in

inshore nursery areas.

Summer Flounder spawning stock biomass has increased during the last quarter-

century, but recruitment has remained highly variable (Terceiro 2011), so much so that

the relationship between spawning stock biomass and recruitment for Summer

Flounder is unclear. Based on previous evidence relating environmental effects and recruitment in fishes (e.g., Myers 1998; Martinho et al. 2009; Nyitrai et al. 2013), I hypothesize that recruitment variability in Summer Flounder may be associated with physical and environmental factors in addition to spawning stock biomass. As noted, the large variations in recruitment and spawning stock biomass through time, and the potential for biased measurement of spawner and recruit abundance, may obscure the relationship between spawning stock biomass and recruitment and establishes the need for further studies of physical and environmental drivers of recruitment.

The method of calculating an index of Summer Flounder recruitment for Chesapeake Bay from fisheries-independent survey catches may affect the ability to discern the stock-recruitment relationship. I therefore examined Summer Flounder catches from a bottom trawl survey (the Virginia Institute of Marine Science (VIMS) Juvenile Fish Trawl Survey) across multiple spatio-temporal domains to estimate annual recruitment indices for Chesapeake Bay Summer Flounder. I explored estimation of an index of abundance for YOY Summer Flounder using a design-based estimator because the VIMS trawl survey uses a stratified random design (Cochran 1977). Stratum means were estimated in 2 ways: using a geometric mean (Cochran 1977; Chittenden 1991) or using a delta-based estimate that allowed explicit modeling of zero catches (Lo et al. 1992; Maunder and Punt 2004). Catches of zero Summer Flounder are common, especially in years of low abundance, and therefore the delta-based estimate may be preferred. Because the Summer Flounder catch data examined in this study are the only fishery-independent survey data used in the current stock assessment to gauge

abundance of YOY Summer Flounder from Virginia waters (Terceiro 2012; Tuckey and Fabrizio 2013), appropriate abundance calculations are important for developing management plans for this species.

Summer Flounder occur from Nova Scotia to Florida (Gutherz 1967), but this species is most abundant in the mid-Atlantic region where they are managed as a single stock (Wilk et al. 1980; Terceiro 2012). Adult Summer Flounder migrate from estuaries to the continental shelf to spawn from September to February; peak spawning occurs off the Virginia coast during November (Smith 1973; Morse 1981). The extended spawning period of adult fish produces cohorts of eggs and larvae that are differentially vulnerable to physical processes which, in turn, affect the timing of larval delivery to estuaries (Hare et al. 2005). Summer Flounder pelagic larvae occur in shelf waters, and settle on the bottom in nursery areas after completing metamorphosis (Keefe and Able 1993). In Chesapeake Bay, larval stages of Summer Flounder are typically encountered as ichthyoplankton from December to April, with peak ingress at the York River occurring in January and February (Ribeiro et al., *in review*).

In this study, I used a linear model to explore the effects of environmental factors on YOY Summer Flounder abundance in Chesapeake Bay for the period 1988 to 2012. Because the relationship between Summer Flounder spawning stock biomass and recruitment is unclear, considerations of other factors influencing recruitment, such as physical and environmental characteristics, may lead to better understanding of year-class strength variations in Summer Flounder. Successful transport of larvae from shelf

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habitats into mid-Atlantic estuarine nurseries may be mediated by wind speed and direction, with favorable conditions leading to a greater number of larvae advected into nursery areas (Epifanio and Garvine 2001; Hare et al. 2005). Because freshwater discharge alters estuarine circulation in Chesapeake Bay (Pritchard 1952), freshwater flow may affect the number of larvae that enter and are retained in nursery areas. As larvae are transported from shelf waters into estuarine nursery areas, they typically must transition from relatively high ocean salinity to lower estuarine salinity; therefore, salinity may be an important consideration in the model. Summer Flounder larval development, metamorphosis, and behavior are influenced by temperature, such that cooler temperatures lead to slower larval development (Keefe and Able 1993; Keefe and Able 1994) and presumably, higher natural mortality rates (Houde 1989b). The environmental factors reasoned to be influential on YOY Summer Flounder abundance included wind, freshwater discharge, temperature and salinity; these conditions were considered during the time that Summer Flounder larvae are pelagic and cohorts begin entering Virginia estuaries (December-April; Ribeiro et al., *in review*).

METHODS

Index of Abundance Calculation

Monthly catch data of Summer Flounder from the VIMS bottom trawl survey

(Tuckey and Fabrizio 2013) were used to estimate annual abundance of young-of-the-

year fish from 1988 to 2012 in Chesapeake Bay. Young-of-the-year Summer Flounder

are identified using monthly length thresholds estimated from historical length-

frequency histograms (Tuckey and Fabrizio 2013; also see Chapter 2, Table 3). The

survey staff deploy a 9.14-m semi-balloon otter trawl with 38.1-mm stretched mesh and

6.35-mm cod-end liner to sample fishes and invertebrates throughout the Virginia

portion of Chesapeake Bay and in the James, York and Rappahannock rivers (Figure 1).

Samples are collected monthly from a random stratified sampling design with depth and

region defining the strata (Fabrizio and Tuckey 2009): three regions in Chesapeake Bay

(bottom, lower and upper bay) are partitioned into six strata (western and eastern shore

(1.2-3.7 m), western and eastern shoal (3.7-9.1 m), central plain (9.1-12.8 m) and deep

channel (≥12.8 m)); the James, York and Rappahannock rivers comprised four regions

(bottom, lower, upper and top) with four depth strata in each region (1.2-3.7 m, 3.7-9.1

m, 9.1-12.8 m and ≥12.8 m). Each month, 111 stations are sampled (22 stations in each

river and 45 stations in the bay). Additional information about the survey and sampling

protocol is found in Tuckey and Fabrizio (2013).

Catches of YOY Summer Flounder in September, October and November in the

Chesapeake Bay and the lower rivers were used to calculate an index of abundance for

the species; this period was chosen because Summer Flounder are most abundant

during this time and are highly vulnerable to the gear (Tuckey and Fabrizio 2013). The

index of abundance (and hence, the recruitment index) for Summer Flounder is

calculated using a geometric mean catch weighted by stratum size (Tuckey and Fabrizio

2013). The weighted geometric mean is obtained by transforming the catch (in

numbers) using the natural log (ln(n+1), n=number of individuals, 1 is added to account

for 0 catches because ln(0) is undefined), calculating the mean catch per tow of the log-

transformed data in each stratum, weighting those means by stratum area and

estimating the stratified mean for the sampling domain according to the following

calculation (Cochran 1977):

$$\bar{y} = \sum_{i=1}^{L} W_i \ \bar{y}_i \tag{1}$$

where $\bar{y}$ is the stratified mean, W_i is the weight of stratum i determined using the

stratum area, $\bar{y}_i$ is the mean catch in stratum i, and L is the total number of strata (n=53

strata). The estimated mean ($\bar{y}$) is back-transformed to yield a geometric mean (GM)

catch per tow for each year according to the following conversion (Chittenden 1991;

Tuckey and Fabrizio 2013):

$$GM = e^{\bar{y}} \tag{2}$$

Fisheries catches, such as those from research surveys, are typically distributed

as a lognormal distribution and may be characterized by a high proportion of zero

catches (Pennington 1983; Pennington 1996; Maunder and Punt 2004). Because tows

with zero catches are encountered, and the logarithm of zero is undefined, a small

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positive constant (most commonly 1) may be added to each observation to enable log transformation (McArdle et al. 1990; Maunder and Punt 2004). However, this method of accounting for zero catches is biased, and may lead to underestimates of the population variance (McArdle et al. 1990). The bias increases with the number of zero catches (McArdle et al. 1990). Furthermore, the selection of the positive constant (most typically, 1) is arbitrary because addition of other small constants (e.g., 0.1) leads to widely varying stratified means (Maunder and Punt 2004). Because of these and other concerns, the weighted geometric mean should be considered as a measure of relative abundance that is interpretable only for the series of observations from a given survey.

An alternative to using the geometric mean to estimate mean abundance for each stratum is to use the delta approach (Maunder and Punt 2004). Typically, the delta-lognormal model has been used when the distribution of non-zero catches is lognormal. With this approach, zero catches and non-zero catches are modeled separately, and a binomial model is used to describe the occurrence of zero catches. Abundance estimates are then calculated using the log-transformed product of the mean and the proportion of non-zero catches (Aitchison 1955; Lo et al. 1992):

$$\bar{y}_{\Delta i} = P_i * e^{\left(\mu + \frac{\sigma_\mu^2}{2}\right)} \tag{3}$$

where $\bar{y}_{\Delta i}$ is the delta lognormal mean in stratum i, P_i is the proportion of positive tows in stratum i (calculated by dividing the number of positive tows [tows with one or more Summer Flounder] by the total number of tows in the stratum), μ is the mean of the log transformed positive catches in stratum i, and σ_μ is the standard deviation of the log-

transformed catches in stratum i. Note that the delta-lognormal mean is adjusted by $\frac{\sigma_\mu^2}{2}$ to account for bias imparted on estimates of the mean due to the skewed nature of the lognormal distribution (Sprugel 1983). I calculated an index of abundance for Summer Flounder using the delta model in each stratum, and weighting the delta-based means by stratum size following methods in Fabrizio et al. (*in prep*).

Prior to implementation of the delta approach, it was necessary to properly describe the distribution of the non-zero catches in each stratum. I used the 'Fitdistr' function in R to examine the fit of the normal, gamma, and lognormal distribution to the stratum-specific catch data. Because catches may exhibit different distributions due to characteristics such as depth and region which varied by stratum, I examined the catch data for each stratum separately. Furthermore, I combined stratum-specific catches across years (1988 to 2012) which allowed for appropriate sample size for identification of the underlying distribution of the catch. The best description of the stratum-specific distribution of the catch data was identified by comparing Akaike's information criterion (AIC) for each distribution fit; smaller AIC values indicated better fit to the data (Anderson 2008). Delta (Δ) AIC values were calculated for each stratum, and represent the difference in the AIC values among the best fitting model (ΔAIC=0) and alternative models (ΔAIC>0; Anderson 2008).

In addition to investigating an alternative method for calculation of the Summer Flounder index of abundance, I also examined the effect of using catch data from alternative spatial and temporal domains of the random stratified survey. The spatial

and temporal domains used to calculate the Summer Flounder index of abundance have

been used for at least two decades without evaluation. I examined the selection of

these domains because YOY Summer Flounder abundance in Chesapeake Bay has varied

widely in the last 25 years (Tuckey and Fabrizio 2013), and because environmental

conditions in the bay and rivers likely have changed during that time period. For

example, we know that water temperatures in the mid-Atlantic region have increased in

the last two decades (Najjar et al. 2000; Hayhoe et al. 2007), and this may have affected

distributions and abundances of fishes in this region. Currently, the Summer Flounder

index of abundance is calculated using catch data from the Bay and the lower James,

York and Rappahannock rivers (Figure 1). In addition to being captured in these regions,

Summer Flounder are routinely captured in the upper rivers, but those regions have not

been considered in abundance calculations because abundance of Summer Flounder in

the upper rivers is generally low. Because Summer Flounder abundance is typically

highest in the Bay and in the lower James River, I also investigated the utility of these

areas. Thus, I calculated the index of abundance for Summer Flounder based on catch

data from the following spatial domains: (1) the currently used domain (bay and lower

rivers); (2) the entire sampling domain (i.e., the bay, and lower and upper rivers); (3) the

bay; (4) the bay and lower James River; and (5) the lower bay and lower James River.

Alternative 2 allows for assessment of the effect of including catches in the upper rivers

on Summer Flounder abundance calculations. Alternatives 3, 4, and 5 reduce the need

to process samples from larger spatial domains, and thus may be more efficient if such

indices were found to be reasonable representations of annual abundance of YOY

Summer Flounder.

Similarly, I examined catch data from multiple temporal domains. YOY Summer

Flounder are frequently encountered by the trawl survey beginning in early summer

(June). Summer Flounder begin to leave Virginia estuaries in late fall, typically in October

and November (Wilk et al. 1980; Capossela et al. 2013; Henderson et al. 2014). Due to

this seasonal movement, a significant portion of the population may not be available to

the trawl in November, and indeed, few fish are routinely captured December. To

ensure sufficient sample size at the stratum level, I considered catches from a minimum

of three-months. In this manner, a minimum of three samples occurred in a given

stratum for a given three-month period: two to four stations are selected each month in

each stratum in the Bay, and one to two stations are selected each month in each

stratum in the rivers (Fabrizio and Tuckey 2009). The temporal domains I examined

included: (1) September-November, which is the period currently used to calculate the

index of abundance, (2) August-November, or the current time period plus an

additional summer month, (3) July-November, or the current time period plus two

additional summer months, (4) June-November the current time period plus three

additional summer months, and several three-month periods earlier than that currently

used: (5) June-August, (6) July-September, and (7) August-October.

Spatial and temporal variations in the index of abundance were examined in

SAS ® (SAS Institute, Cary, NC) using a two-step process for abundance estimation:

calculation of a mean for each stratum, followed by calculation of a stratified mean

weighted by stratum area (equation 1). Spatial variations were examined first: I

calculated a yearly index of abundance for each alternative spatial domain, and used a

simple graphical comparison of the resulting indices to evaluate the effect of selecting a

different spatial domain. I identified the spatial domain of interest by using the current

spatial domain as a benchmark against which alternatives were evaluated; unless

evidence supported alteration of the spatial domain, the current spatial domain was

retained. Using the selected spatial index, I examined alternative temporal domains and

again used graphical comparisons to evaluate the effect of variations in temporal

domain. No statistical test was used to select the 'best' spatial or temporal domains for

sampling because the various indices were not independent, thus violating a

fundamental statistical assumption (Quinn and Keough 2002).

Environmental Factors

Environmental factors included in the model were chosen based on biological reasoning,

and were believed to be those that exert influence on Summer Flounder larvae. I chose

to examine wind, freshwater discharge, temperature and salinity during winter when

Summer Flounder larvae are pelagic and begin entering Virginia estuaries (Ribeiro et al.,

in review).

<u>Wind Speed and Direction in Winter</u>

Because peak Summer Flounder spawning occurs in continental shelf waters

during winter (Morse 1981), I examined wind speed and direction during December,

January, and February when the greatest number of larvae would likely be influenced by wind-driven transport into Chesapeake Bay. Monthly average wind speed and direction records for these months, from 1 Dec 1987 to 29 Feb 2012, were obtained from the National Centers for Environmental Prediction and National Center for Atmospheric Research (http://www.esrl.noaa.gov/psd/data/gridded/data.ncep. reanalysis.html). Note that December wind speed and direction from the prior year were considered together with January and February wind data for the year of interest (e.g., December 1987 data were considered to influence the 1988 year class).

Monthly average wind speed measurements were calculated for 8 sectors based on wind direction: north, northeast, east, southeast, south, southwest, west, and northwest (J. Shen, unpublished). Monthly average wind speed and direction were represented by U and V components, where the U component represents east-west wind and the V component represents north-south wind. I calculated average wind speed (magnitude) for each month by combining wind vectors in the U and V direction using the following standard equation (Serway and Faughn 2003):

$$\text{Total Wind Speed} = \sqrt{U^2 + V^2} \tag{4}$$

To identify the wind direction that was most influential on YOY Summer Flounder abundance, total wind speed and direction (for all 8 directions) during December, January and February for 1987 to 2012 were correlated with mean Summer Flounder abundance from 1988 to 2012. I used the correlation (CORR) procedure in SAS with an *a priori* alpha level of 0.05 to determine the strength of the linear relationship

(Quinn and Keough 2002) between wind and Summer Flounder abundance. Because average east wind in December was the only wind factor significantly correlated with Summer Flounder abundance (Table 2: r=0.43, P=0.03, see Results below), only this factor was included in the model.

<u>Annual Freshwater Discharge in Winter</u>

To calculate annual freshwater discharge (reported as ft^3/sec) during winter into Chesapeake Bay, I used daily freshwater discharge records from the United States Geological Survey (USGS; http://waterdata.usgs.gov/nwis) for eight tributaries of Chesapeake Bay (Figure 2). These eight tributaries account for more than 80% of the total freshwater flow into Chesapeake Bay, with the Susquehanna (51.3%), Potomac (15.9%) and James (8.9%) rivers contributing the greatest percentage of freshwater (Table 1, M. Brush unpublished data; Schubel and Pritchard 1986). I used daily freshwater discharge from 1 Dec 1987 to 29 Feb 2012 with the exception of data for the Mattaponi River which were not available prior to 1 Dec 1989. Because the Mattaponi River accounts for less than 1.3% of freshwater flow into Chesapeake Bay (Table 1), discharge data from this river were omitted from calculations of annual discharge in 1988, when flow observations were not available. I calculated total daily freshwater discharge into Chesapeake Bay by summing the daily discharge rates for the 8 rivers. Total cumulative freshwater discharge from December-February was calculated for each year (1988 to 2012) and used as a factor in the linear model. Note that December flow rates from the year prior were used in discharge calculations for the year of interest

(e.g., daily discharge observations for December 1987 were used for the 1988

cumulative discharge calculation).

Winter Temperature and Salinity in the Bay

Surface temperature and salinity values were obtained from the Chesapeake Bay

Program's approximately monthly monitoring of environmental conditions (Water

Quality Monitoring Database available at www.chesapeakebay.net/data); these monthly

data were temporally interpolated (M. Brush, unpublished data) to provide daily surface

temperatures and salinities for the Chesapeake Bay (Figure 3). I used these daily

interpolated observations to calculate mean surface water temperature and salinity in

Chesapeake Bay over a four-month period (from January-April) for each year (1988 to

2012). I used temperature and salinity observations from only Chesapeake Bay because

all Summer Flounder must encounter these Bay conditions prior to settling either in the

Bay or in its tributaries.

Environmental Effects on YOY Summer Flounder Abundance

Environmental factors (wind speed and direction in winter, freshwater discharge

in winter, and temperature and salinity in winter) considered in the linear model of YOY

Summer Flounder abundance were standardized (mean=0, standard deviation=1) prior

to analysis to equalize the scale of measurement and to allow direct comparison of

effect size (Quinn and Keough 2002). Model diagnostics included examination of

tolerance (to check for multicollinearity among explanatory factors) and patterns in the

residuals (to ensure variance homogeneity and lack of structural issues; Quinn and

Keough 2002). The initial statistical model fitted to the data using the MIXED procedure

in SAS was:

$$Y_i = \beta_0 + \beta_1(WIND)_i + \beta_2(DIS)_i + \beta_3(TEMP)_i + \beta_4(SAL)_i + \varepsilon_i,$$

where Y_i =   YOY Summer Flounder index of abundance in the ith year (i=1988 to 2012), assumed to be normally distributed;

β_0 =   overall mean index of abundance for the population during 1988 to 2012;

β_{1-4} =   partial regression coefficients accounting for the effect of each factor (WIND, DIS, TEMP, and SAL) on Y_i holding all other factors constant;

$WIND_i$ =   mean east wind speed in December in year i;

DIS_i =   total freshwater discharge from December-February in year i;

$TEMP_i$ =   mean surface water temperature in lower Chesapeake Bay from January-April in year i;

SAL_i =   mean surface salinity in lower Chesapeake Bay from January-April in year i; and

ε_i =   random unexplained error, assumed to be normally distributed with mean of 0 and standard deviation of σ_ε^2.

All factors in the model were considered fixed effects. Although this model

accounted for approximately 14% of the total variation in YOY abundance, model

residuals revealed a pattern indicating poor model fit: residuals were positive in the

early years, but negative in the later years, indicating a systematic (but abrupt) change

in the effect of wind, freshwater discharge, temperature, or salinity on YOY abundance

and suggesting an incorrect model structure (Figure 4). To address the structural

deficiency of the model, I constructed a categorical variable, 'period.' The 'early' period

consisted of the years with mostly positive residuals (1988 to 1999), and the 'late'

period consisted of the years with mostly negative residuals (2000 to 2012).

Additionally, I used interaction plots to discern the presence of potential interactions

between period ('early', 'late') and the environmental variables (wind, freshwater

discharge, temperature and salinity; Figure 5). The interaction between mean wind

speed and period was included in the final model because the effect of wind speed on

YOY abundance differed during the early period compared with the late period

(different slopes of the best fit lines to the 'early' and 'late' period wind-speed data).

The final statistical model fitted to the data using the MIXED procedure in SAS was:

$Y_i = \beta_0 + \beta_1(WIND)_i + \beta_2(DIS)_i + \beta_3(TEMP)_i + \beta_4(SAL)_i + \beta_5(PER)_i + \beta_6(WIND_i * PER_i) + \varepsilon_i,$

where Y_i, β_0, $WIND_i$, DIS_i, $TEMP_i$, SAL_i and ε_i are defined previously and

$PER_i =$ period variable, 'early' (1988 to 1999) or 'late' (2000 to 2012), for year i;

$WIND_i * PER_i =$ interaction between mean east wind speed in December and period in year i; and

$\beta_{5-6} =$ partial regression coefficients accounting for the effect period (PER) and the interaction between wind speed and period (WIND*PER) on Y_i holding all other factors constant;

As before, all factors in the model were considered fixed effects. I examined

residuals from this model to assess model fit and the assumption of homogeneity of

variance; I also examined tolerance to assess collinearity of factors (Quinn and Keough

2002). Index values predicted by the model were compared with observed index values

graphically.

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RESULTS

Index of Abundance Calculation

The index of abundance that I selected to represent young-of-the-year

abundance employed the delta-lognormal calculation method and included Summer

Flounder catches from the Chesapeake Bay and the lower James, York, and

Rappahannock rivers during August, September and October. The weighted geometric

mean catch per tow and the delta-lognormal catch per tow for YOY Summer Flounder

exhibited strikingly similar patterns through time (Figure 6). However, I selected the

delta-lognormal calculation because the delta calculation better accounts for zero

catches (it does not require the addition of an arbitrary constant to zero catches as does

the geometric mean calculation). Furthermore, the non-zero catches in each of the 53

strata exhibited a lognormal distribution (Table 3). In a single stratum, the gamma

distribution gave a reasonable description of the non-zero catches (ΔAIC < 2, Upper

James River, 3.7-9.1m depth); because the gamma or lognormal distribution could be

used in this specific case, I chose the lognormal distribution because that distribution

best described the non-zero catches in the majority (98%) of strata. Most (79%) of the

Delta AIC values for the normal and gamma distributions were greater than nine,

indicating little support for the distributional fit (Anderson 2008). Therefore, neither the

normal nor the gamma distribution could be used to adequately model catches at the

stratum level.

Regardless of the spatial domain considered, the index of abundance exhibited similar patterns through time (Figure 7). As long as the Chesapeake Bay was included in the index, the deviation in the YOY abundance value was minimal, suggesting that catches in the bay drive the YOY abundance index. When abundance is calculated from catches in the Chesapeake Bay and upper and lower rivers, the calculated index is lower than that estimated from other spatial domains. This results because Summer Flounder abundance is lower in the upper portions of the rivers, yielding lower calculated abundance values. Conversely, if Summer Flounder catches from the lower Chesapeake Bay and lower James River are the only catches considered in the calculation of the index of abundance, the result is a higher index value because Summer Flounder are most abundant in these areas. I conclude that the current spatial scale used to calculate abundance for Summer Flounder (Chesapeake Bay and lower rivers) is reasonable, and therefore did not alter the spatial domain of the index.

Although the index calculated for multiple temporal domains exhibited similar patterns from 1988 to 2012, catches during August, September, and October are likely to best represent abundance of YOY fish in the Chesapeake Bay region (Figure 8). In general, abundance is lowest when calculated from catches in June-August and July-September. Indices calculated during this time period are lower because Summer Flounder may not have fully recruited to the gear in June and July, or because they are unavailable to the gear due to their occurrence in shallow nursery habitats (habitats shallower than 1.2 m are not sampled by the trawl survey). Indices of abundance calculated from Summer Flounder catches in September-November and August-

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November are generally higher compared with indices calculated from other time periods; these indices may be inflated by higher catch rates of Summer Flounder in November. In November, Summer Flounder concentrate in the lower James River and the lower Chesapeake Bay before leaving the bay (pers. obs.).

Environmental Effects on YOY Summer Flounder Abundance

The final model contained the following factors: average east wind speed in December, freshwater discharge from December to February, mean surface water temperature and salinity in lower Chesapeake Bay from January to April, and a categorical factor accounting for time. This model accounted for 75% of the variation in Summer Flounder abundance for the period 1988 to 2012 (R^2=0.75). The R^2 value was calculated by using model residuals from the full model and residuals from the null model ((null model residual – full model residual)/null model residual; Singer 1998). I examined model assumptions and determined that none of the factors exhibited collinearity (all tolerance values were greater than 0.1, Table 4), and no pattern was present in the residuals to indicate heterogeneity of variance (Figure 9). Observed and predicted abundance values showed similar patterns through time (Figure 10).

The early period (1988 to 1999) was characterized by higher Summer Flounder abundance compared with the later period (2000 to 2012): during the early period the mean index was 3.34 fish per tow (95% CI: 2.03-4.65), and during the later period the mean index was 1.25 fish per tow (95% CI: 0.73-1.77). The overall mean index value predicted for the time series (intercept) was 1.14 fish per tow (95% CI: 0.87-1.41).

Average wind speed in December differentially influenced Summer Flounder abundance

during the early period compared with the later period: a significant interaction was

present between time period (early, late) and east wind speed in winter (F=14.49,

P<0.01). During the early period, stronger average east wind speeds in winter

corresponded to higher abundance values, whereas in the later period, abundance was

similar regardless of wind speed (Figure 5). Mean winter temperature in the surface

waters of Chesapeake Bay was a significant factor in the model (F=7.43, P=0.01),

suggesting that as water temperature in the Bay increased, YOY Summer Flounder

abundance also increased (model estimate = 0.56, 95% CI: 0.35-0.77). Neither mean

salinity (F=0.24, P=0.63) nor total freshwater input (F=0.29, P=0.60) were significant

factors in the model.

DISCUSSION

Surface water temperature during winter in Chesapeake Bay significantly influenced Summer Flounder year-class strength from 1988 to 2012 in Chesapeake Bay and its tributaries. The significant positive effect of temperature on abundance was expected, as higher temperatures within the range observed over this time period typically lead to greater survival and higher growth rates of larval and juvenile Summer Flounder (Szedlmayer et al. 1992; Keefe and Able 1993; Bengtson 1999). Increased surface temperatures can lead to increased phytoplankton primary production (Harding et al. 2002), providing greater food resources for Summer Flounder growth in the estuary (Malloy and Targett 1994).

I did not detect an influence of salinity or freshwater discharge on year-class strength. This may be because the average salinity during winter from 1988 to 2012 ranged from 15.4 to 24.7 psu, which may not influence larval Summer Flounder abundance and subsequent year-class strength because larval survival is not noticeably affected by salinities within this range (Specker et al. 1999). Freshwater discharge in Chesapeake Bay during winter may not alter estuarine conditions significantly enough to affect the number of Summer Flounder larvae that enter and are retained in Chesapeake Bay.

Higher observed abundances of YOY Summer Flounder in the early period may be due to variations in spawning stock biomass (SSB), changes in age composition of

spawners, or regional variability in environmental conditions that promote greater survival of YOY in their nursery habitats. I explore the likelihood of each of these possible explanatory mechanisms below.

Summer Flounder SSB has increased more than eight-fold during the last quarter century, from 7,040 million metric tons in 1989 to 57,020 million metric tons in 2011 (Terceiro 2012). Moreover, this increase has been somewhat linear. Throughout the time period of increasing SSB, recruitment of Summer Flounder has been highly variable, suggesting that SSB and recruitment are not strongly related (Figure 11; Terceiro 2012; Tuckey and Fabrizio 2013). The highest recruitment of Summer Flounder to Chesapeake Bay occurred during years of low SSB (e.g., 1990, 1991, 1994). Later in the time series, when SSB was high, recruitment was generally relatively low. However, both relatively low (e.g., 2011) and high (e.g., 2008) recruitment were observed in recent years when SSB was high.

The age composition of spawning fish has changed as the Summer Flounder stock was rebuilt (Terceiro 2012), and because older individuals may contribute disproportionally more recruits to the population compared with younger individuals, changes in the age composition of spawners may have influenced recruitment of Summer Flounder (Hilborn and Walters 1992; Quinn and Deriso 1999).The percentage of age-3 and older Summer Flounder in the commercial and recreational fisheries catch (in numbers) has increased from only 4% in 1993 (when age-0 and age-1 fish predominated the catches), to 80% in 2011 (Terceiro 2012). In addition, in marine fishes

reproductive output typically increases with body size (Jennings et al. 2001), and older, larger fish may produce a greater number of eggs, with higher survival rates, compared with that produced by younger fish (Birkeland and Dayton 2005). For Summer Flounder, fecundity increases with increases in length and weight (Morse 1981), but no studies have been published on variations in egg viability with age of female spawners. A population with a greater number of experienced spawners (fish that have spawned in previous years) and an expanded age structure is more likely to produce a large year class (Buckley et al. 1991; Murawski et al. 2001). Because fishing typically removes the older, larger individuals from a population (Berkeley et al. 2004; Beamish et al. 2006; Hsieh et al. 2010), and because Summer Flounder were historically overfished (Terceiro 2011; Terceiro 2012), the older, larger individuals were likely less abundant in the early period (1988 to 1999). Contrary to what would be expected, high recruitment was observed during this early period when smaller, younger fish were dominant among spawning fish. In recent years, Summer Flounder spawning stock biomass and the age structure of spawners have both increased, suggesting abundance of recruits should have been higher in recent years, but this was generally not observed. These findings support the hypothesis that environmental effects may be driving recruitment variations in Summer Flounder, at least for the annual population sizes of YOY fish observed over the last 25 years in Chesapeake Bay and the lower tributaries.

Finally, Summer Flounder abundance may also be influenced by long-term, regional-scale environmental variability that was not accounted for in the model I used to describe variation in year-class strength for this species. Wood and Austin (2009)

described a significant regime shift in recruitment patterns of multiple species of fishes

within Chesapeake Bay such that anadromous fish recruitment began to be favored over

shelf-spawning fish recruitment in 1992; they examined annual recruitments for the

period 1968 to 2004. Recruitment of Summer Flounder (a shelf-spawning species) in

Chesapeake Bay was highest in 1991, and in recent years has remained relatively low

compared with that of earlier years; the observed changes in Summer Flounder

recruitment patterns may be related to the regime shift postulated by Wood and Austin

(2009).

Relationships between environmental factors and recruitment have been

examined in numerous studies, but are rarely used to predict recruitment in practice

(Myers 1998). Myers (1998) examined nearly 50 cases where published environment-

recruitment correlations were re-examined with new data. In many cases, the observed

environment-recruitment correlations were no longer valid when re-tested with new

data. The few correlations that were confirmed when re-examined were associated with

populations near the northern or southern limits of a species' range; these correlations

frequently involved the relationship between temperature and recruitment. Near the

center of a species' range, environment-recruitment relationships typically fail.

Because Chesapeake Bay is near the southern limit of estuarine nursery areas for

Summer Flounder, changes in environmental effects may be more discernible here.

Aside from the examination of influential physical and environmental factors on

Summer Flounder year-class strength, results from this study show that the random

stratified sampling design of the trawl survey appears to provide sufficient samples with

which to gauge patterns in abundance through time. Patterns in abundance can be detected regardless of the calculation method used (geometric mean or delta lognormal mean) or time period and spatial domain of catches considered. The delta-lognormal method is a reasonable approach to calculate Summer Flounder abundance and does not require the use of an arbitrary constant. Thus, the modified index of abundance calculation method will be suggested for incorporation into subsequent Summer Flounder stock assessments. Summer Flounder catches from August to October from the Chesapeake Bay and lower James, York and Rappahannock rivers likely captured the population of Summer Flounder in Chesapeake Bay during a time period when the population size of Summer Flounder is relatively constant, and fish are large enough to be consistently available and vulnerable to the trawl. Although the yearly delta-lognormal index of abundance values were similar for all spatial scales considered, I included catches from multiple rivers in the index of abundance estimate (versus using the Bay and lower James River only) because each region may be characterized by different habitats, environmental conditions, and predator-prey communities that result in variations in growth and, presumably, survival of YOY Summer Flounder. YOY Summer Flounder in the rivers are typically smaller than conspecifics found in the bay; furthermore, growth is dependent on density of conspecifics (Chapter 2). To obtain a reasonably accurate representation of the Summer Flounder population in Chesapeake Bay, I suggest including catches from multiple rivers so that region-specific variations are reflected in the estimate of abundance.

To further investigate the interplay of physical and environmental factors on

Summer Flounder recruitment, a coupled physical-biological model could be applied; these models have become increasingly common to understand fish recruitment (Miller 2007). For example, a coupled individual-based hydrodynamic model has been used to study larval transport of the Common Sole *Solea solea* from spawning areas to nursery grounds in the English Channel (Rochette et al. 2012), and a particle-tracking hydrodynamic model has been used to assess the influence of behavior on larval oyster dispersal in Chesapeake Bay (North et al. 2008). Important considerations prior to the application of this type of model to Summer Flounder include the incorporation of larval characteristics (such as behavior, mortality, and growth) and variations in the location of Summer Flounder spawning areas. Initial exploratory model runs using a three-dimensional hydrodynamic model (Hong and Shen 2012) to investigate Summer Flounder larval transport indicated the importance of fish behavior in predicting larval transport into Chesapeake Bay (J. Shen, pers. comm.). Although the precise spawning location(s) of Summer Flounder are unknown, and are likely variable from year to year, centers of abundance of adult Summer Flounder from offshore trawl survey data can be used to estimate spawning location.

Results from this study exemplify the importance of external factors on Summer Flounder year-class strength. As climate warms, environmental factors examined in this study are expected to change in ways that will likely influence fish recruitment patterns. Climate change is hypothesized to alter conditions in Chesapeake Bay by: increasing water temperature, decreasing dissolved oxygen levels, increasing streamflow, and increased regional precipitation (Najjar et al. 2010). Climate change is also expected to

lead to alterations in wind patterns including increased intensity of storm events such as tropical cyclones (Knutson et al. 2012). Alterations in wind patterns could affect transport of Summer Flounder larvae and other shelf-spawning species. In addition, acidification of the oceans associated with increased atmospheric CO_2 levels (Doney et al. 2009) may have a deleterious effect on Summer Flounder. For example, laboratory studies of Summer Flounder subjected to elevated CO_2 levels (such as those associated with ocean acidification) suggest that reductions in survival, tissue damage and alterations in skeletal elements can be expected during larval stages (Chambers et al. 2013). Increased variations in environmental conditions associated with climate change are of importance for the assessment of Summer Flounder recruitment because these variations may influence year-class strength and subsequent production of the stock.

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TABLES

Table 1. Long-term (1988 to 2012) percentage of mean daily freshwater flow calculated using records from USGS gauging stations at the 8 major tributaries of Chesapeake Bay (M. Brush, unpublished). Respective land areas of each watershed are also listed, courtesy of http://chesapeake.usgs.gov/featuremeasuringnutrient-sedimentloads.html.

River	Percentage of Flow	Land Area (km^2)
Susquehanna	51.3	70,189
Potomac	15.9	30,043
James	8.9	16,192
Rappahannock	2.1	4,134
Appomattox	2.8	3,476
Pamunkey	2.3	2,792
Mattaponi	1.3	1,562
Patuxent	1.0	995

Table 2. Average wind direction for selected months and correlation coefficients for the relationship between wind direction and the delta lognormal index of abundance for young-of-the-year Summer Flounder from 1998 to 2012. Wind direction data are from the National Centers for Environmental Prediction and National Center for Atmospheric Research. N is the number of years considered for analysis; N values less than 25 occur because wind direction data were missing. Pearson's correlation coefficient and associated P-values are given, and significant correlations (P<0.05) are indicated in bold.

Wind Direction	Month	N	Correlation	P
North	December	25	0.003	0.99
North	January	25	0.110	0.63
North	February	25	0.021	0.92
Northeast	December	25	-0.086	0.68
Northeast	January	25	0.071	0.74
Northeast	February	25	-0.034	0.87
East	**December**	**25**	**0.430**	**0.03**
East	January	25	0.115	0.59
East	February	25	-0.069	0.74
Southeast	December	23	-0.103	0.64
Southeast	January	25	0.175	0.40
Southeast	February	24	-0.319	0.13
South	December	25	-0.191	0.36
South	January	24	0.227	0.29
South	February	25	-0.037	0.86
Southwest	December	25	0.207	0.32
Southwest	January	25	0.083	0.69
Southwest	February	25	-0.235	0.26
West	December	25	0.142	0.50
West	January	25	-0.376	0.06
West	February	25	0.097	0.65
Northwest	December	25	-0.036	0.87
Northwest	January	25	-0.033	0.88
Northwest	February	25	-0.114	0.59

Table 3. Akaike's information criterion (AIC) for fit of the normal, gamma or lognormal distribution to non-zero Summer Flounder catches from 1988 to 2012 in Virginia estuaries. Catch distributions were examined by stratum (Figure 1), and catch data were combined across years for analysis. Delta (Δ) AIC values indicated the difference in AIC of the model and the AIC of the model with the lowest AIC value among the models considered. The description column provides details of the location examined, including the depth range of the stratum (m). Together, the location and description uniquely define each stratum.

| | | | ΔAIC | |
Location	Description	Normal	Gamma	Lognormal
Bottom Bay	West 1.2-3.7m	59.80	11.15	0
Bottom Bay	East 1.2-3.7m	28.95	7.70	0
Bottom Bay	West 3.7-9.1m	278.28	55.64	0
Bottom Bay	East 3.7-9.1m	213.89	41.61	0
Bottom Bay	Central 9.1-12.8m	404.24	68.90	0
Bottom Bay	≥ 12.8m	229.37	31.33	0
Lower Bay	West 1.2-3.7m	69.10	12.26	0
Lower Bay	East 1.2-3.7m	23.13	5.76	0
Lower Bay	West 3.7-9.1m	277.41	53.27	0
Lower Bay	East 3.7-9.1m	234.70	40.71	0
Lower Bay	Central 9.1-12.8m	291.08	49.54	0
Lower Bay	≥ 12.8m	521.37	96.52	0
Upper Bay	West 1.2-3.7m	65.54	12.23	0
Upper Bay	East 1.2-3.7m	31.58	7.55	0
Upper Bay	West 3.7-9.1m	194.48	40.70	0
Upper Bay	East 3.7-9.1m	233.16	41.35	0
Upper Bay	Central 9.1-12.8m	376.85	42.49	0
Upper Bay	≥ 12.8m	309.85	58.27	0
Bottom York	1.2-3.7m	90.63	10.48	0
Bottom York	3.7-9.1m	101.86	20.95	0
Bottom York	9.1-12.8m	271.37	48.33	0
Bottom York	≥ 12.8m	162.72	39.06	0
Lower York	1.2-3.7m	123.05	24.48	0
Lower York	3.7-9.1m	235.95	51.71	0
Lower York	9.1-12.8m	54.70	12.77	0
Upper York	1.2-3.7m	290.06	59.56	0
Upper York	3.7-9.1m	213.89	45.94	0
Upper York	≥ 9.1m	36.72	9.40	0
Bottom Rappahannock	1.2-3.7m	59.74	8.70	0
Bottom Rappahannock	3.7-9.1m	71.86	14.45	0
Bottom Rappahannock	9.1-12.8m	54.62	12.12	0

Table 3. Continued

| | | | ΔAIC | |
Location	Description	Normal	Gamma	Lognormal
Bottom Rappahannock	≥ 12.8m	314.37	67.19	0
Lower Rappahannock	1.2-3.7m	82.12	17.28	0
Lower Rappahannock	3.7-9.1m	24.48	5.10	0
Lower Rappahannock	9.1-12.8m	50.53	11.07	0
Lower Rappahannock	≥ 12.8m	235.53	55.43	0
Upper Rappahannock	1.2-3.7m	54.58	13.69	0
Upper Rappahannock	3.7-9.1m	82.56	21.49	0
Upper Rappahannock	≥ 9.1m	29.74	7.85	0
Top Rappahannock	1.2-3.7m	10.52	3.19	0
Top Rappahannock	3.7-9.1m	28.65	6.91	0
Bottom James	1.2-3.7m	38.66	7.38	0
Bottom James	3.7-9.1m	331.60	65.71	0
Bottom James	9.1-12.8m	77.86	16.87	0
Bottom James	≥ 12.8m	458.93	96.14	0
Lower James	1.2-3.7m	40.33	9.72	0
Lower James	3.7-9.1m	138.78	29.72	0
Lower James	9.1-12.8m	195.48	40.27	0
Upper James	1.2-3.7m	61.13	14.75	0
Upper James	3.7-9.1m	67.34	18.23	0
Upper James	≥ 9.1m	41.10	11.35	0
Top James	1.2-3.7m	6.68	2.17	0
Top James	3.7-9.1m	3.79	1.14	0

Table 4. Tolerance values for factors used in the multiple linear regression to describe changes in Summer Flounder abundance from 1988 to 2012 in the Chesapeake Bay region. Tolerance values less than 0.1 indicate collinearity among predictor values (Quinn and Keough 2002).

Factor	Tolerance
Temperature	0.92
Salinity	0.25
Average east wind in December	0.87
Total Freshwater Discharge	0.25

FIGURES
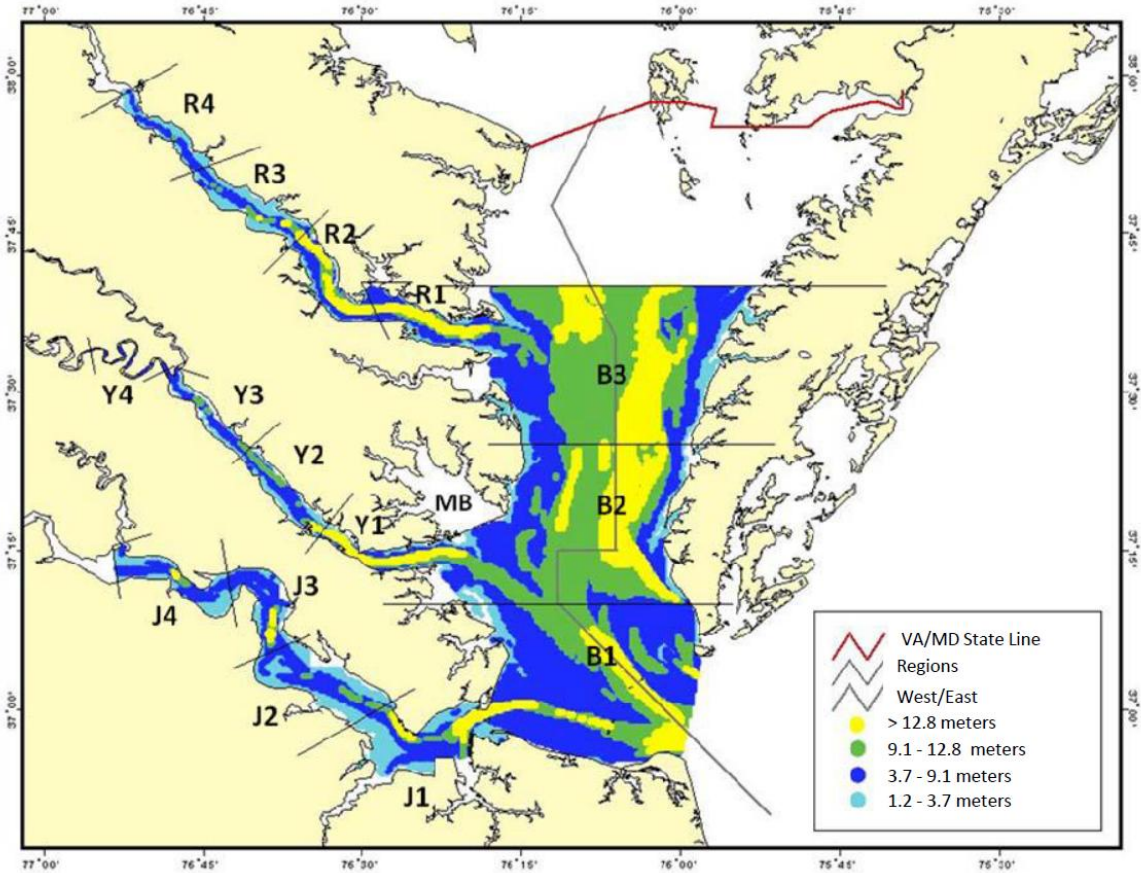
Figure 1. Random stratified sampling design used to sample young-of-the-year Summer Flounder in Chesapeake Bay and the James, York, and Rappahannock rivers (from Tuckey and Fabrizio 2013). Colored areas indicate the 4 depth strata sampled (1.2-3.7 m, 3.7-9.1 m, 3.7-9.1 m and >12.8 m). The black lines demarcate the followng geographic strata:

Chesapeake Bay Mainstem	B1	Bottom Bay
	B2	Lower Bay
	B3	Upper Bay
James River	J1	Bottom James
	J2	Lower James
	J3	Upper James
	J4	Top James
York River	Y1	Bottom York
	Y2	Lower York
	Y3	Upper York
	Y4	Top York
Rappahannock River	R1	Bottom Rappahannock
	R2	Lower Rappahannock
	R3	Upper Rappahannock
	R4	Top Rappahannock
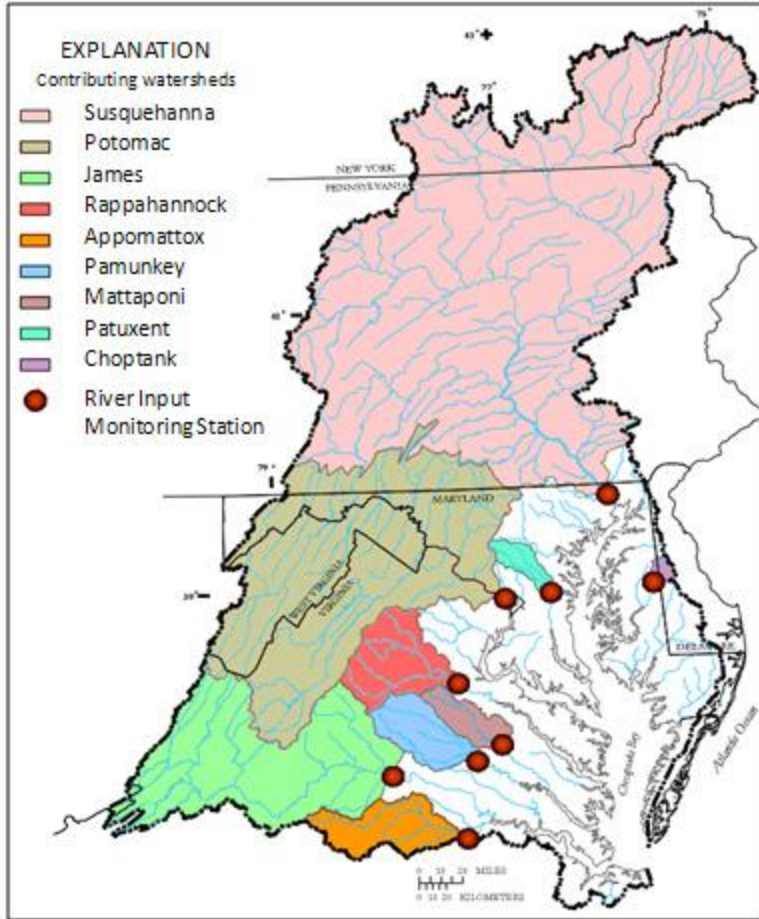
Figure 2. Streamflow gauge sites (red dots) in the Chesapeake Bay watershed where daily discharge rates (reported as ft^3/sec) were measured. Eight major tributaries of Chesapeake Bay (Susquehanna, Potomac, James, Rappahannock, Appomattox, Pamunky, Mattaponi, and Patuxent rivers) were considered in the calculation of total freshwater discharge into Chesapeake Bay. The Choptank River was excluded due to its minimal discharge rate. Figure courtesy of http://chesapeake.usgs.gov/featuremeasuringnutrient-sedimentloads.html.
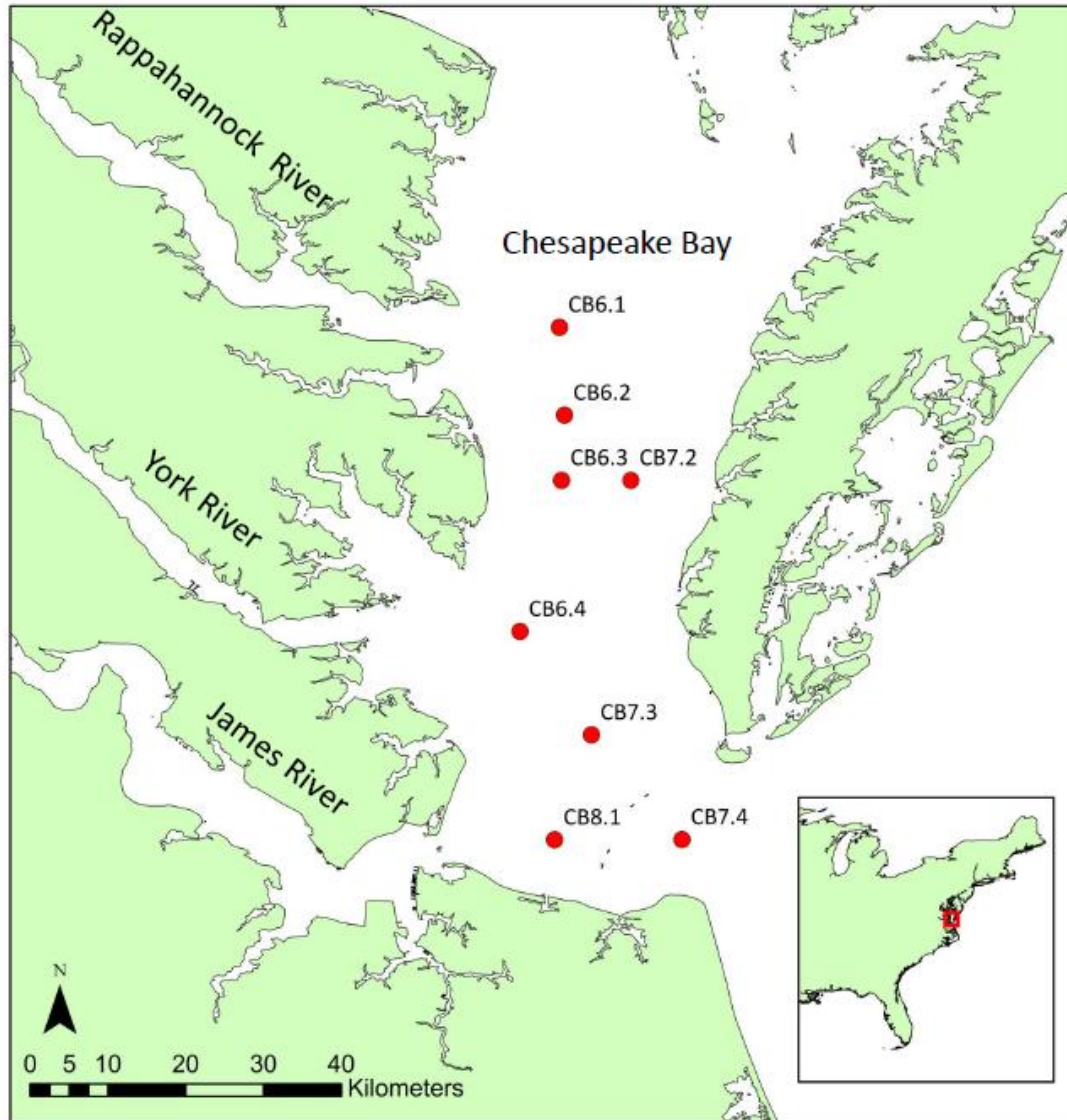
Figure 3. Location of temperature and salinity stations monitored by the Chesapeake Bay Program (red dots) and considered for input in the model of environmental conditions and year-class strength of Summer Flounder in the Chesapeake Bay region. Daily surface temperature and salinity values were interpolated from approximately monthly monitoring data collected at each site (M. Brush, unpublished).
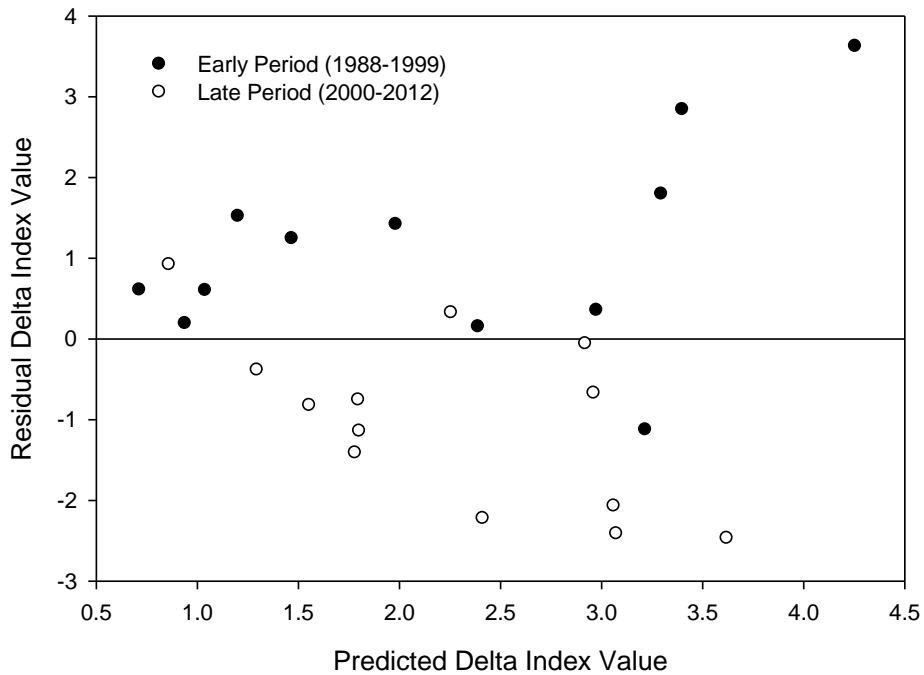
Figure 4. Residuals from the initial model describing changes in the Summer Flounder index of abundance in Chesapeake Bay from 1988 to 2012 using average east wind in December, total freshwater discharge from December-February, and average surface water temperature and salinity from January-April. Model residuals during the early (filled circles) and late periods (open circles) are indicated; note that the majority of residuals from the early period are positive, and the majority of residuals from the late period are negative.
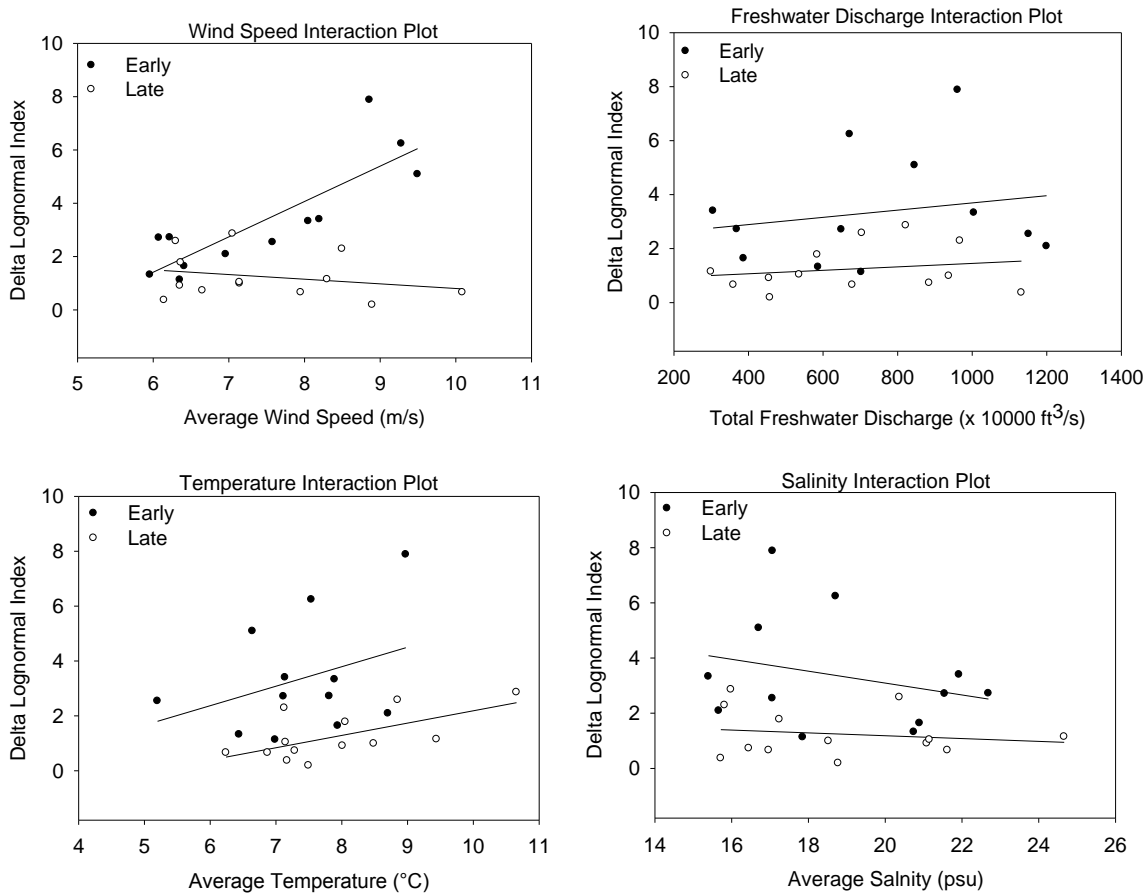
Figure 5. Interaction plots for period and environmental variables examined in the model of young-of-the-year Summer Flounder abundance, 1988 to 2012. Wind speed is the average east wind in December; freshwater is the total freshwater discharge from December-February; temperature is the average surface water temperature in the Bay from January-April; and salinity is the average surface water salinity in the Bay from January-April. Period is a categorical factor to designate early (1988 to 1999; filled circles) or late (2000 to 2012; open circles) years. Lines on the graphs are the best fit linear relationship to the data points for each period and are shown for ease of interpretation only. Parallel lines indicate no interaction between the factor of interest and period.
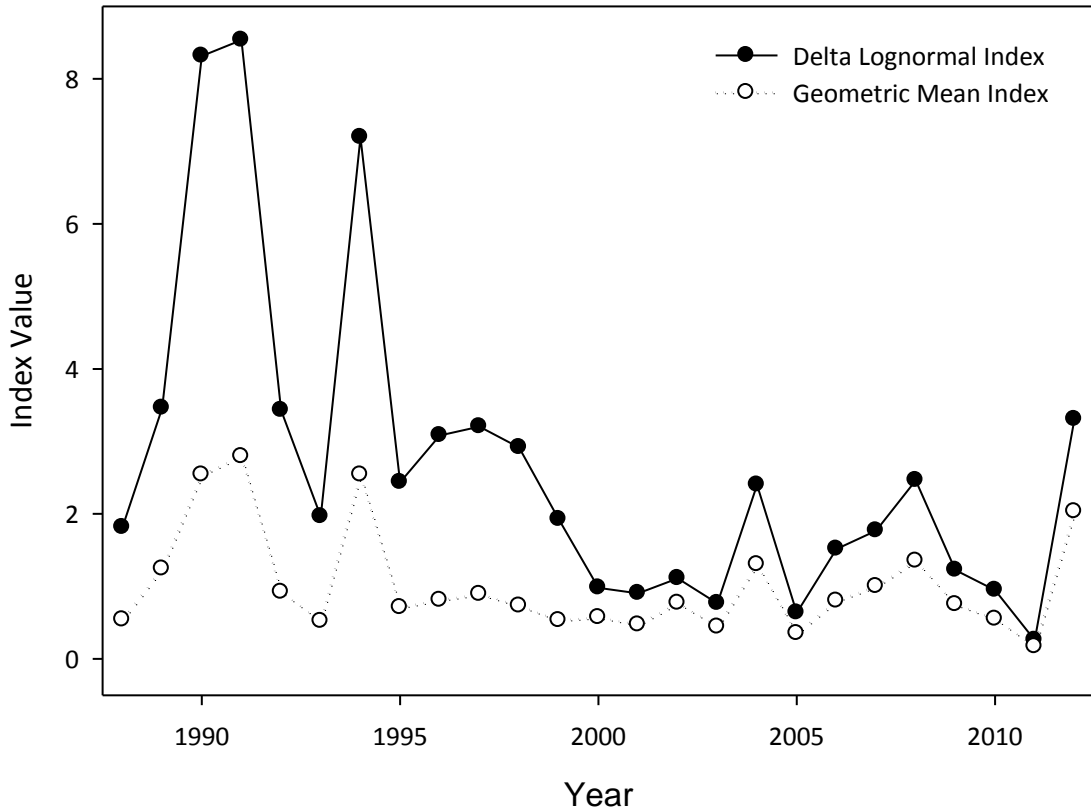
Figure 6. Relative abundance of Summer Flounder in the Chesapeake Bay and the bottom and lower James, York and Rappahannock rivers during September, October, and November from 1988 to 2012. Two indices of relative abundance are depicted here, both of which represent a stratified mean: one is calculated from the delta lognormal stratum means and the other, from the geometric stratum means.
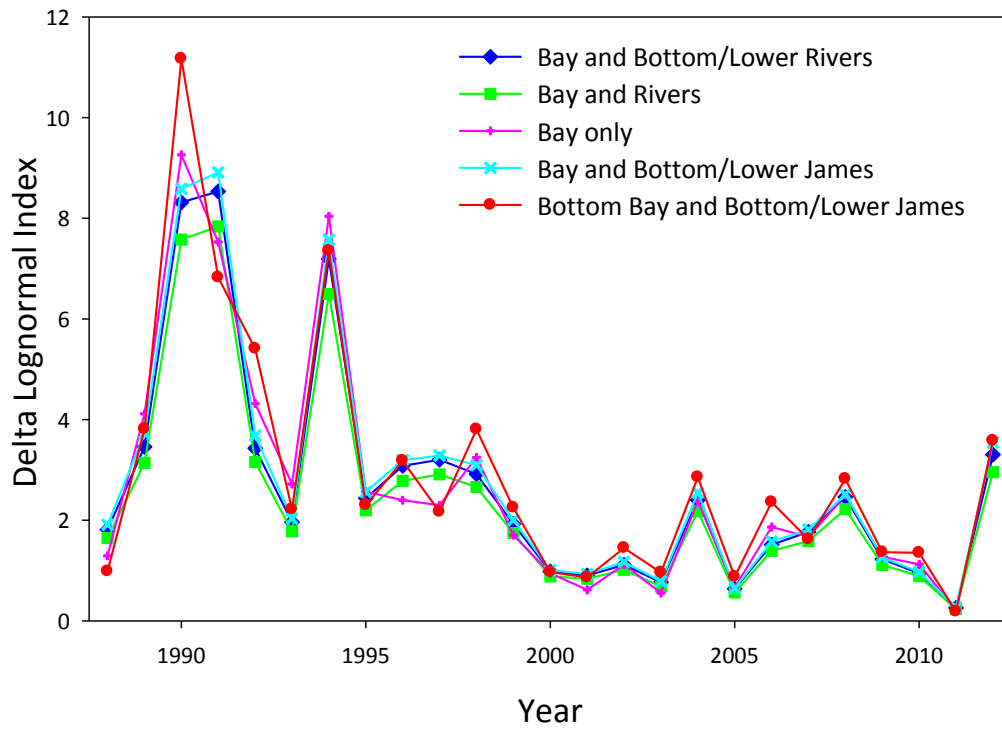
Figure 7. Delta lognormal indices of abundance for young-of-the-year Summer Flounder calculated from catches in September, October and November from 1988 to 2012. The five indices were developed from 5 spatial domains of sampling as indicated in the legend and depicted in Figure 1.
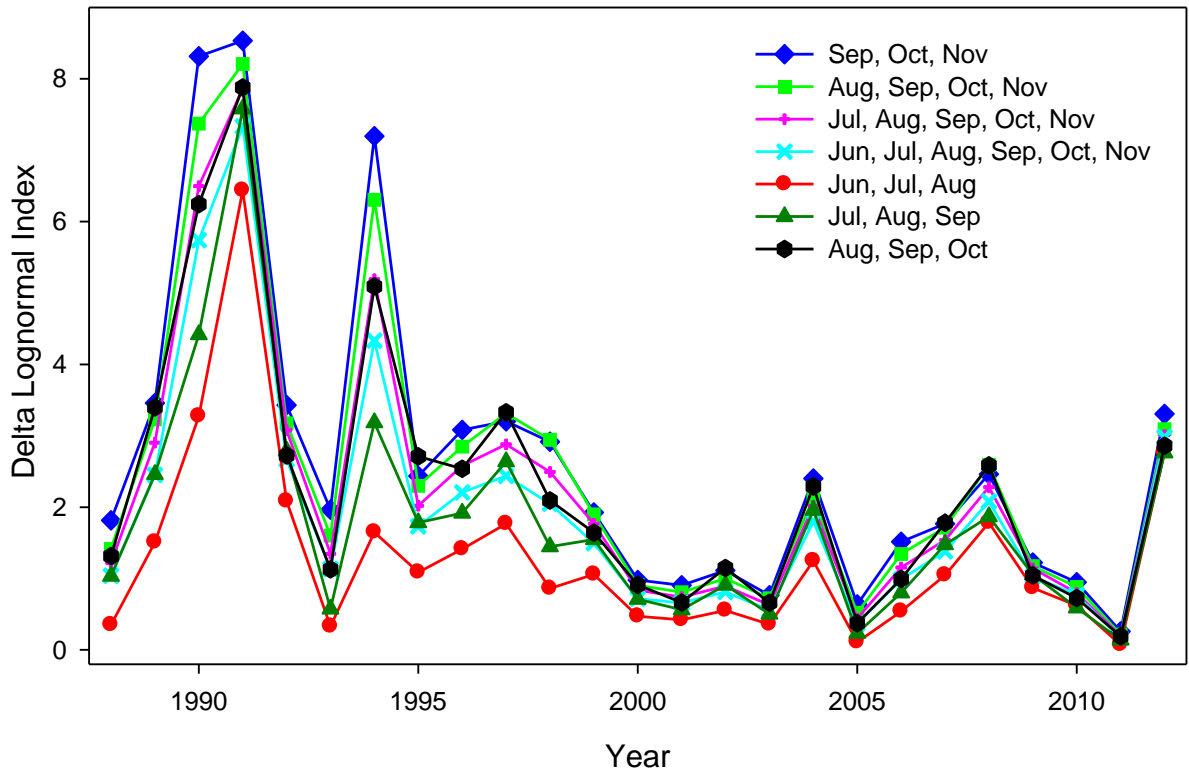
Figure 8. Delta lognormal indices of abundance for Summer Flounder calculated from catches in the Chesapeake Bay and the lower James, York and Rappahannock rivers from 1988 to 2012. The 7 indices were developed for 7 temporal domains of sampling, as indicated in the legend.
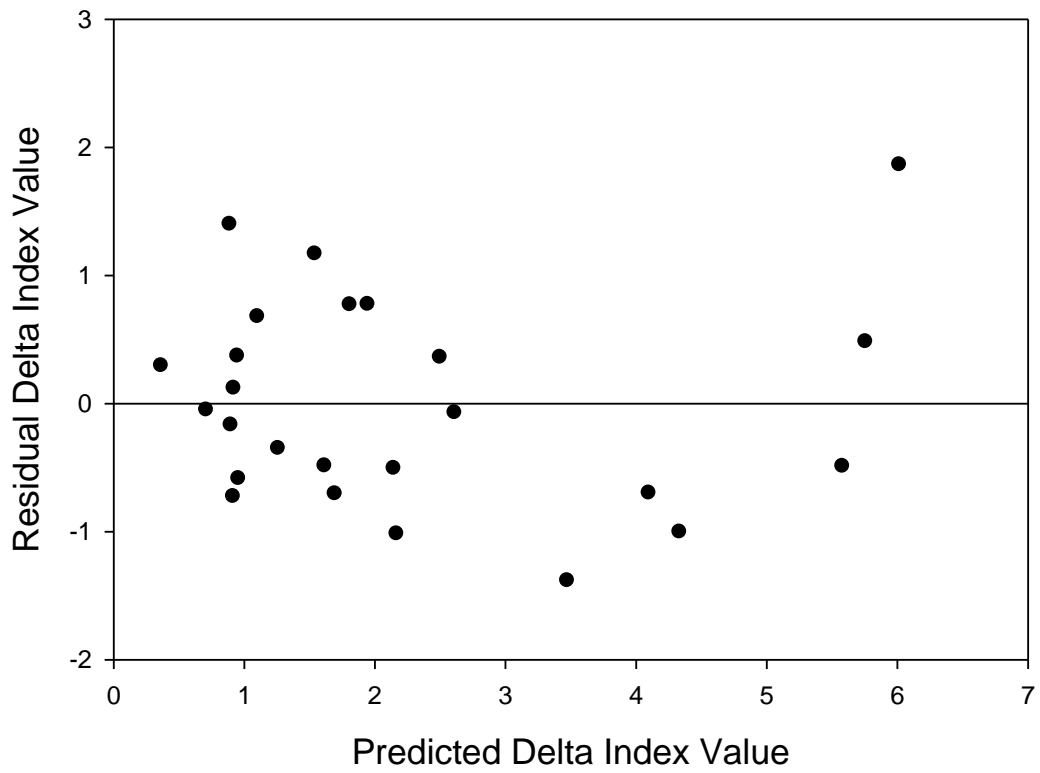
Figure 9. Residuals from the model describing changes in the Summer Flounder index of abundance in Chesapeake Bay from 1988 to 2012 using average east wind in December, total freshwater discharge from December-February, average surface water temperature and salinity from January-April, and a categorical factor accounting for time.
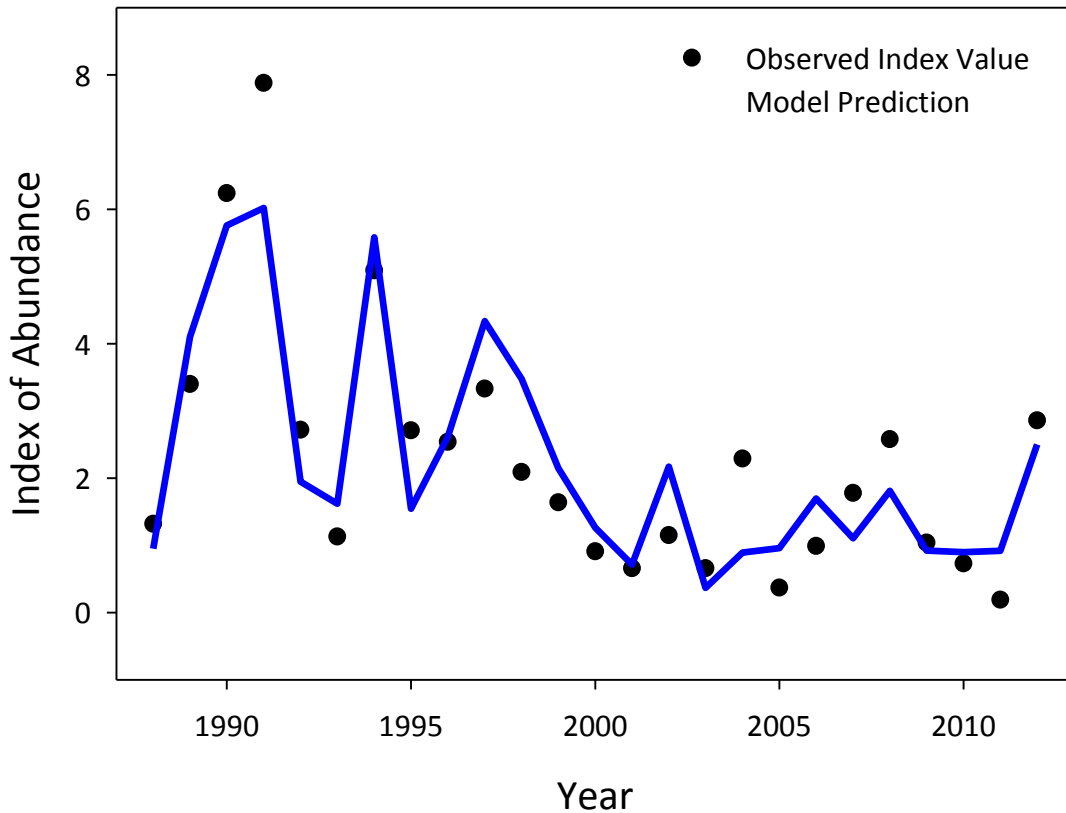
Figure 10. Observed (filled square) and model-based (line) estimates of the delta-lognormal of abundance for young-of-the-year Summer Flounder in the Chesapeake Bay region from 1988 to 2012. Observed values are calculated using a delta-lognormal approach from catches of Summer Flounder in Chesapeake Bay and the lower James, York and Rappahannock rivers during August, September, and October. A general linear model of Summer Flounder abundance was used to obtain the model based predictions; factors in the model include average east wind in December, total freshwater discharge from December-February, average surface water temperature and salinity from January-April, and a categorical factor accounting for time. Approximately 75% of the variation in the index of abundance is explained by the model.
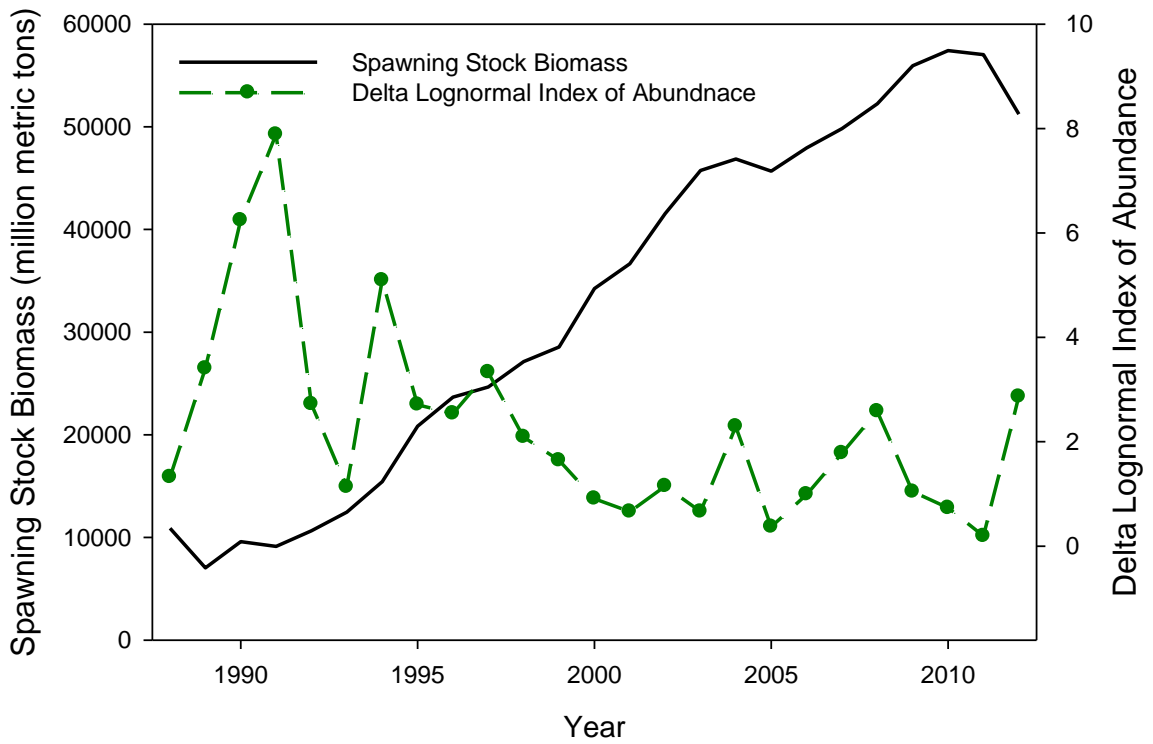
Figure 11. Summer Flounder spawning stock biomass for the mid-Atlantic stock (line; Terceiro 2012) and the index of abundance of young-of-the-year Summer flounder (dash line and filled circles) calculated using a delta-lognormal approach and using catches of Summer Flounder in the mainstem of Chesapeake Bay and the lower James, York and Rappahannock rivers during August, September, and October from 1988 to 2012.

CHAPTER 2: FACTORS INFLUENCING GROWTH OF YOUNG-OF-THE-YEAR SUMMER FLOUNDER IN CHESAPEAKE BAY

ABSTRACT

During the last quarter-century, management of Summer Flounder along the Atlantic coast resulted in significant increases in abundance such that rebuilding targets were recently achieved. Although spawning stock biomass is high, recruitment of young-of-the-year (YOY) Summer Flounder remains variable. Chesapeake Bay is one of the principal nursery areas for this species, but processes such as growth and survival that affect production of YOY Summer Flounder in this estuary have not been explored. Here, I investigated the relationship between fish size and abundance of recruits from the 1988 to 2012 year classes of Summer Flounder from Chesapeake Bay. I also considered the effects of environmental factors on growth because conditions in the bay vary spatially and during the time that fish are in the nursery area; these environmental variations may therefore contribute to variable growth within a year class. To describe growth, I used monthly length observations from YOY fish captured by bottom trawl from the lower Chesapeake Bay and the mouths of the three major Virginia tributaries (James, York, and Rappahannock rivers) where Summer Flounder are commonly observed. I applied a generalized additive model to describe spatial, temporal, and environmental effects on observed sizes; I also considered the density of Summer Flounder and an index of prey abundance as factors in the model. Summer Flounder in Chesapeake Bay exhibited density-dependent growth and spatially related differences in length (larger fish in the Bay and smaller fish in the rivers). Additionally, low (<13°C) and high (>26°C) temperatures and low salinities (<10 psu) had a negative effect on length, indicating that fish found in these environments were typically smaller than conspecifics inhabiting areas of moderate temperatures and higher salinities. Variable nursery habitat conditions in temperate estuaries can influence the growth and production of Summer Flounder year classes. As water temperatures in Chesapeake Bay continue to increase as a result of changing climate, YOY Summer Flounder growth may be negatively affected.

INTRODUCTION

Juvenile fishes inhabiting temperate estuaries are subjected to large fluctuations in temperature, salinity, and dissolved oxygen on daily and seasonal scales (Able and Fahay 2010); these fluctuating conditions may lead to variability in growth and subsequent survival (Gibson 1994; Houde 2008). Growth rates of fishes are typically fastest during their first year of life, when fast growth is critical for survival (e.g., Campana et al. 1989; Tupper and Boutilier 1995; Campana 1996). Fish growth may also be influenced by abundance, which can affect the size structure of the cohort such that smaller fish sizes are observed when density of conspecifics is high. Indeed, density-dependent growth has been documented for juvenile estuarine fishes including American Shad *Alosa sapidissima* (Tuckey 2009), Striped Bass *Morone saxatilis* (Martino and Houde 2012), and Spot *Leiostomus xanthurus* (Craig et al. 2007). In habitats where size-selective predation is an important component of juvenile mortality, larger individuals are more likely to survive than smaller ones (Miller et al. 1988; Witting and Able 1993; Sogard 1997) and may therefore make a greater contribution to year-class strength (Houde 2008). Fishes that use shallow temperate estuaries during their first year of life, such as Summer Flounder *Paralichthys dentatus,* are subject to variations that occur naturally in these systems as well as human-induced alterations to these habitats.

Growth rates of young-of-the-year flatfish are variable within a year-class and among nursery habitats (Fitzhugh et al. 1996; Phelan et al. 2000; Pihl et al. 2000; Sogard et al. 2001), reflecting the plasticity of growth in these fishes. Juvenile Winter Flounder *Pseudopleuronectes americanu*s and Southern Flounder *Paralichthys lethostigma* both exhibit variable growth rates. Variable growth rates of YOY Winter Flounder in Atlantic estuaries have been attributed to variations in temperature and dissolved oxygen concentration (Phelan et al. 2000; Sogard et al. 2001). Similarly, variable growth rates in YOY Southern Flounder in a mid-Atlantic estuary were attributed to a combination of factors including temperature, dissolved oxygen levels, the onset of piscivory, and prey availability (Fitzhugh et al. 1996). I expect that Summer Flounder may exhibit similar variations in growth because the distribution of this species overlaps that of Southern Flounder, which range from Chesapeake Bay to Texas (Murdy and Musick 2013), and Winter Flounder, which are most abundant between the Gulf of Saint Lawrence and Chesapeake Bay (Able and Fahay 2010). Furthermore, Summer Flounder and Southern Flounder are congeners. In the North Atlantic, growth rates of another Pleuronectid, the European Plaice (*Pleuronectes platessa*), were affected by the density of juveniles in the nursery (Pihl et al. 2000; Geffen et al. 2011; Ciotti et al. 2014). In this study, I investigated factors that contribute to variation in growth of YOY Summer Flounder in Chesapeake Bay, Virginia, including environmental conditions and abundance of conspecifics.

Estuaries along the mid-Atlantic coast from Massachusetts to North Carolina serve as nursery habitat for YOY Summer Flounder (Able and Fahay 2010); however, few

YOY Summer Flounder occur in estuaries north of Delaware Bay. Chesapeake Bay is a

principal nursery area for this species (Norcross and Wyanski 1994). During the last

quarter-century, management of Summer Flounder along the Atlantic coast resulted in

significant increases in abundance such that rebuilding targets were recently achieved.

Recruitment of YOY Summer Flounder in Chesapeake Bay is variable among years

(Tuckey and Fabrizio 2013), and shows little relationship to adult spawning stock

biomass (Terceiro 2011). Within a year class, individual YOY Summer Flounder may

exhibit large variations in length (pers. obs.), which may reflect that a year class

comprises multiple cohorts. These cohorts arise because adult Summer Flounder spawn

in continental shelf waters during an extended period of time, typically from September

to February in the mid-Atlantic Bight (Smith 1973; Morse 1981). This protracted

spawning results in multiple cohorts of eggs and larvae entering Chesapeake Bay from

December to April (Ribeiro et al., *in review*). Compared with other estuarine fishes,

Summer Flounder exhibit relatively fast growth and individuals may exceed 290 mm

total length (TL) by the end of their first year of life (Szedlmayer et al. 1992; Tuckey and

Fabrizio 2013); length at maturity ranges from 240 to 270 mm TL for males and from

300 to 330 mm TL for females (Morse 1981). As a result of the fast growth of age-0 fish,

a portion of the population may reach maturity by the end of their first year of life; a

recent stock assessment estimated that 38% of age-0 Summer Flounder were mature

(Terceiro 2006), but this proportion is likely to vary annually based on variations in

growth.

Based on what has been reported for other flatfishes, I postulated that YOY Summer Flounder growth is variable within a year class, and that this variation is related to physical and environmental conditions, prey availability, and density of conspecifics. In particular, I expected temperature (Malloy and Targett 1994), dissolved oxygen concentration (Stierhoff et al. 2006; Stierhoff et al. 2009), and prey abundance (Malloy and Targett 1994) to affect Summer Flounder growth. In laboratory experiments, juvenile Summer Flounder grew faster at 14-18°C than did conspecifics exposed to colder temperatures (2-10°C); however, salinities between 10-30 psu had no effect on growth of juveniles (Malloy and Targett 1991). A reduction in the growth rate of juvenile Summer Flounder was observed when fish were exposed to dissolved oxygen levels between 3.5 and 5 mg/l, with further reductions in growth in hypoxic (<2.0 mg/l) conditions (Stierhoff et al. 2006). Negative effects of low oxygen conditions on juvenile Summer Flounder growth have also been observed in the wild (Stierhoff et al. 2009). Finally, growth rate is highly dependent on the feeding rate of juvenile Summer Flounder (Malloy and Targett 1994), therefore, prey abundance is likely an important determinant of growth. Although laboratory experiments can be useful to elucidate factors affecting growth, field studies are needed to provide a more realistic assessment of growth under a wide variety of conditions experienced by wild fish. Observations of the size of wild fish from temporally intense samples can yield insights on the relationship between fish size and the environmental conditions from which such samples were collected.

To assess growth of YOY Summer Flounder, several approaches have been considered including direct measurements of growth, use of length-frequency analysis, use of back-calculated length from individual fish, and the traditional length-at-age modeling approaches. Direct measurements of individual growth include the use of RNA:DNA ratios (e.g., Rooker and Holt 1996; Buckley et al. 1999; Ciotti et al. 2010), field caging experiments (e.g., Sogard 1992; Dahlgren and Eggleston 2000; Phelan et al. 2000), and tagging studies (e.g., Fabrizio et al. 2001; Henderson and Fabrizio 2013). Methods to directly measure growth were not used for this study because of the inability to examine growth for more than a few year classes of fish, and the large sample sizes that would have been required to assess growth under a wide variety of environmental conditions. Examination of empirical length frequencies through time can be used to measure growth by modeling changes in the mean and variance of daily length frequencies (e.g., Baba et al. 2004). This type of modeling approach is data-intensive, and is best applied to daily length measurements from the same group of individuals. These daily length measurements are more feasible for sessile organisms (e.g., freshwater clam *Corbicula japonica*) compared with mobile organisms such as fish. Individual growth can also be described using back-calculated length-at-age (Francis 1990). Fish length at a prior date is estimated by back-calculating length from fish hard parts (most commonly, the fish otolith); growth estimates are derived from comparisons of measured length at the time of capture to the back-calculated length at an earlier date assuming annual or daily increment formation (Francis 1990). For some flatfish, growth increments are formed on the otolith with constant frequency, allowing for the

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back-calculation of length-at-age (Nash and Geffen 2005). However, this approach is not

viable for YOY Summer Flounder because otolith increment formation is not daily during

the pelagic larval stage (Szedlmayer and Able 1992). Furthermore, otoliths of YOY

Summer Flounder do not exhibit a settlement check to permit determination of the

settlement date (pers. obs.; Szedlmayer, pers. comm.). Although increments are clearly

visible on the otoliths of YOY Summer Flounder, the periodicity of formation is unknown

and thus daily age cannot be determined. Growth can also be described using length-at-

age models, such as the von Bertalanffy growth model (Beverton and Holt 1957) or

variants thereof (Porch et al. 2002; Kimura 2008). However, length-at-age models

require data on the age of fish. For fishes whose age cannot be estimated or is

unknown, a common practice in fisheries is to assign fish ages by assuming a common

hatch date for the year class (e.g., Bishop et al. 2006). Due to the protracted spawning

period of Summer Flounder (Morse 1981), and the extended period of larval entry into

Chesapeake Bay (December-April; Ribeiro et al., *in review*), it is not reasonable to assign

a common hatch date to an entire year class of YOY Summer Flounder. Because Summer

Flounder age cannot be determined, I identified an alternate approach to describe

changes in Summer Flounder length during their time in nursery areas within

Chesapeake Bay and the lower James, York, and Rappahannock rivers.

I used length observations of young-of-the-year Summer Flounder from a

temporally intensive trawl survey in Chesapeake Bay and modeled length with a

generalized additive model (GAM). A GAM is a non-parametric version of a generalized

linear model that allows for non-linear relationships between the response (length) and

the explanatory factors (e.g., environmental conditions). The non-linear components in the model follow smoothing functions that are determined from the data, rather than *a priori* by assuming a parametric relationship (Wood 2006; Zuur et al. 2009). Because they are highly flexible, GAMs have been widely applied in fisheries (Cheng and Gallinat 2004; Maunder and Punt 2004; Venables and Dichmont 2004). For example, the spatial distribution of mature female blue crabs *Callinectes sapidus* in Chesapeake Bay (Jensen et al. 2005) was modeled with a GAM, and GAMs were used to relate biotic and abiotic factors to the distribution of fish in Pamlico Sound (Bacheler et al. 2009) and Chesapeake Bay (Buchheister et al. 2013). GAMs were also used to examine the effect of water temperature, food abundance, and salinity on growth rates of juvenile Winter Flounder (Meise et al. 2003).

The objective of my study was to determine the effects of conspecific density, prey abundance, region, time, temperature, salinity, depth, and dissolved oxygen concentration on observed lengths of YOY Summer Flounder from multiple year classes that recruited to estuarine waters of Virginia between 1988 and 2012. Due to differences in the quality of estuarine nursery areas, some habitats within Chesapeake Bay may differentially influence growth and survival (Beck et al. 2001). For example, competition, prey availability, and environmental factors may vary spatially throughout the occupied nursery area. For Summer Flounder, both biotic and abotic factors may influence observed sizes of fish. I hypothesized that Summer Flounder length depends on fish density: smaller individuals should be observed during years of high density. Additionally, based on previous laboratory and field studies of flatfish growth, I

hypothesized low temperature, low salinity, and low dissolved oxygen levels would

result in smaller mean length observations.

METHODS

Fish Sampling

Summer flounder lengths from the 1988 to 2012 year classes were obtained from samples collected by the Virginia Institute of Marine Science (VIMS) Juvenile Fish Trawl Survey (hereafter, 'trawl survey'). The trawl survey operates year-round in Virginia's estuarine waters, and uses a 9.14-m semi-balloon otter trawl with 38.1-mm stretched mesh and 6.35-mm cod-end liner towed for 5 minutes along the bottom (Tuckey and Fabrizio 2013). The survey employs a random stratified sampling design with depth and region used to define strata in the Virginia portion of Chesapeake Bay and in the major tidal tributaries. For this study, I used samples from the Chesapeake Bay and from the lower James, York and Rappahannock rivers. Seventy-eight stations were sampled monthly (11 stations in the lower portion of each river and 45 stations in the bay; Figure 1). I considered Summer Flounder captured between June and November of each year. Before June, Summer Flounder are not frequently encountered in bottom trawl catches, possibly due to their small size or occurrence in shallow areas (<1.2 m) that are not sampled by the survey. Summer Flounder begin to leave Virginia estuaries in late fall (Capossela et al. 2013; Henderson et al. 2014), such that by late November, most fish have typically moved out of Chesapeake Bay. Therefore, encounter rates decline markedly in December because many fish are not available to the trawl. Furthermore, and perhaps more importantly, initiation of fall migration may be size

dependent (Capossela et al. 2013); such differential behaviors may affect estimates of mean size from trawl samples collected in December.

To express abundance of each year class, I estimated Summer Flounder mean catch in each stratum using a delta-lognormal model (Chapter 1). Because catches from research surveys typically follow a lognormal distribution and have a high proportion of zeros, the delta-lognormal model is often used (Pennington 1983; Pennington 1996; Maunder and Punt 2004). With this approach, zero catches and non-zero catches are modeled separately, and abundance estimates are then calculated using the log-transformed product of the mean and the proportion of non-zero catches (Aitchison 1955; Lo et al. 1992):

$$\bar{y}_{\Delta i} = P_i * e^{\left(\mu + \frac{\sigma_\mu^2}{2}\right)} \tag{1}$$

where $\bar{y}_{\Delta i}$ is the delta lognormal mean in stratum i, P_i is the proportion of positive tows in stratum i (calculated by dividing the number of positive tows (tows with one or more Summer Flounder) by the total number of tows in the stratum), μ is the mean of the log transformed catches in stratum i, and σ_μ is the standard deviation of the log transformed catches in stratum i. Next, I used a design-based estimator (Cochran 1977) to calculate the stratified mean, which was used as the index of abundance for the year class:

$$\bar{y} = \sum_{i=1}^{L} W_i \ \bar{y}_{\Delta i} \tag{2}$$

where $\bar{y}$ is the stratified mean, W_i is the weight of stratum i determined using the

stratum area, $\bar{y}_{\Delta i}$ is the delta-lognormal mean catch in stratum i, and L is the total

number of strata (n=53 strata). Abundance calculations were implemented in SAS ®

(SAS Institute, Cary, NC) using code specifically designed for analysis of trawl survey

data. The index of abundance serves as a measure of Summer Flounder density under

the assumption that the area swept by the trawl is constant; this is a reasonable

assumption because tow duration and vessel speed are held relatively constant during

the survey and the same protocols are implemented each year. Catches of YOY Summer

Flounder from August, September, and October were included in the estimate of density

because fish captured during this time period are likely to best represent abundance of

YOY fish (Chapter 1).

Environmental Conditions and Prey Abundance

       The environmental conditions considered in the model of Summer Flounder

length were collected by trawl survey personnel; chlorophyll-*a* measurements were

taken from the Chesapeake Bay Program were used as a proxy for prey abundance.

Temperature (°C), salinity (psu), and dissolved oxygen (mg/l) measurements reflect the

conditions of bottom water, and are collected at the completion of each tow; depth (m)

is recorded during the tow. These environmental conditions are associated with each

fish length. To investigate the effect of prey on Summer Flounder growth, chlorophyll-*a*

concentrations were used as a proxy for prey abundance. Although YOY Summer

Flounder include a variety of invertebrates in their diet, during their first year of life,

diets consist primarily of mysid shrimp (*Neomysis* spp.; Latour et al. 2008).

Unfortunately, information about mysid shrimp abundance in Chesapeake Bay is lacking. Chlorophyll *a* reflects primary production, and is believed have a positive relationship with secondary production and fish yield (Nixon 1982; Ware and Thomson 2005). Chlorophyll-*a* (mg/m^3) measurements were obtained from the Chesapeake Bay Program Water Quality Monitoring Database (www.chesapeakebay.net/data). The approximately monthly data were temporally interpolated (M. Brush, unpublished data) to provide daily chlorophyll-*a* estimates for surface waters throughout the Virginia portion of Chesapeake Bay and the lower James, York, and Rappahannock rivers (Figure 2); these daily chlorophyll-*a* estimates were used to calculate monthly average chlorophyll-*a* estimates for the model. Because the Chesapeake Bay program sampling is not uniformly distributed through time (there are variations in the numbers of days between sampling), calculating the mean of interpolated daily chlorophyll-*a* estimated ensures that the values are uniformly weighted through time (M. Brush, pers. comm.).

Statistical Analysis

A GAM was used to describe spatial, temporal, and environmental effects on length of Summer Flounder collected between July and November (1988 to 2012). Factors in the model included region, Summer Flounder density, time (capture date), temperature, salinity, dissolved oxygen, depth, and prey abundance. Region (REG) and density (DENS) were considered categorical factors in the model; the results are presented in terms of the levels of those factors. Four regions were defined to account for spatial variation in conditions or resources throughout the study area: (1) Chesapeake Bay; (2) lower Rappahannock River; (3) lower York River; and (4) lower

James River (Figure 3). Because of the relatively short time series (n=25 years), and due to the possible non-linear effect of fish density on observed fish sizes, I modeled the effects of fish density as a categorical factor. The delta-lognormal stratified index of abundance, considered a measure of Summer Flounder density, was partitioned into four density categories of approximately equal number of observations: 0-1, 1-2, 2-3, or greater than 3 fish per tow (Figure 4).

The continuous factors, capture date (DATE, ordinal date), temperature (T, °C), salinity (S, psu), dissolved oxygen (DO, mg/l), depth (DEPTH, m), and prey abundance (PREY, chlorophyll-*a*, mg/m^3) were modeled with non-parametric smoothing functions. Capture date was included in the model to account for increases in length with time and seasonal effects associated with Summer Flounder movement out of the bay in the fall. To account for a potential lag between chlorophyll-*a* and benthic production (Hagy et al. 2005; Nixon et al. 2009), I included chlorophyll-*a* measurements lagged by 0 to 5 months. A lagged chlorophyll-*a* value indicates that chlorophyll-*a* measurements in a previous month were used as a proxy for prey abundance in the month of interest (e.g., a one-month lag considers chlorophyll-*a* measured in May, and Summer Flounder lengths measured in June). The full GAM was:

$$Y_i = a + \alpha_1*(REG) + \alpha_2*(DENS) + g_1(DATE) + g_2(T) + g_3(S) + g_4(DEPTH) + g_5(DO) + g_6(PREY) + e_i$$

where Y_i = Summer Flounder length (mm);
a = intercept, overall mean Summer Flounder length;
α_1 = estimated mean effect of region (REG) on Summer Flounder length;
α_2 = estimated mean effect of density (DENS) on Summer Flounder length;
g_{1-6} = nonparametric smoothing functions for capture date (DATE), temperature (T), salinity (S), depth (DEPTH), dissolved oxygen (DO)

and prey (PREY);

e_i = random unexplained error, assumed to be independent and normally distributed.

Each GAM was fitted in R using the 'mgcv' package (version 3.0.3; R Development Core Team 2014). Because I fit several models to the data (the full model and reduced models), I used Akaike's information criterion (AIC) to select the best model from among those considered (Zuur et al. 2009); smaller AIC values indicate better model fit (Anderson 2008). Delta (Δ) AIC values were calculated for each model, and represent the change in the AIC value from the best fitting model (ΔAIC=0 for the best fitting model, ΔAIC>0 for other models; Anderson 2008). To examine collinearity among the factors considered, I calculated Pearson correlation coefficients (Zuur et al. 2009) and tolerance statistics (Quinn and Keough 2002). Model diagnostics were examined using the 'gam.check' command in R ('mgcv' package) and included an evaluation of the normality assumption (Quantile Quantile (Q-Q) plot and histogram), the homogeneity of variance assumption (residual pattern), and model fit (examination of fitted values and observed values; Zuur et al. 2009).

RESULTS

Young-of the-year Summer Flounder captured in Virginia estuarine waters from

June to November during 1988 to 2012 (n=13,047 fish) exhibited large variations in

length for any given month, and as expected, increasing mean length through time

(Figure 5). The full model which included region, density, capture date, temperature,

salinity, depth, dissolved oxygen, and prey, provided the best fit to the data (lowest AIC

value, Table 1). The percent deviance changed little among the reduced models and the

full models indicating that all models were capable of describing the majority of the

variation in fish length (68.2-69.5%). However, large changes in AIC values occurred for

some of the reduced models (394.7-2547.4 units; Table 1). Models with delta AIC values

greater than about 9-14 units are generally considered to have relatively little support

(Anderson 2008). Thus, the full model was required to adequately describe changes in

length of YOY Summer Flounder.

Model assumptions were reasonably met and collinearity was absent among the

independent factors (all tolerance values were greater than 0.1; tolerance values less

than 0.1 suggest collinearity among variables; Quinn and Keough 2002). The Q-Q plot

(Figure 6) and the histogram of residuals (Figure 6) indicated that the normality of errors

was a reasonable assumption of the selected model (Wood 2006; Zuur et al. 2009).

Ideally, the points on the Q-Q plot would form a straight line; I observed some deviation

from that pattern at the lower end of the plot (large negative residuals) and attributed

large residuals to the few small fish observed during any given month. For example, in

August most YOY Summer Flounder are between 100 and 225 mm, although a few fish between 50 and 100 mm were observed in some years (Figure 5). Predicted lengths for fish smaller than 100 mm may be less similar to the observed mean length, and therefore these observations would be associated with larger residuals. The histogram indicates a relatively normal, bell-shaped distribution of residuals, further supporting the use of the GAM for these data. The residual vs. linear predictor plot (Figure 6) showed slightly increasing variation with increasing values of the linear predictor, suggesting larger residuals among larger fish. The response vs. fitted values plot (Figure 6) showed a positive linear relationship, indicating that the assumption of homogeneity of variance was reasonable for these data. In both the residual vs. linear predictor plot and the response vs. fitted value plot, some observations are clearly below the large scatter of observations (i.e., some predicted values have large negative residuals); these observations are also depicted on the left side of the the Q-Q plot. The large negative residuals in these diagnostic plots comprised approximately 2% of all observations, and therefore were not of concern.

All factors in the GAM (region, density, capture date, temperature, salinity, depth, dissolved oxygen, and prey) were significant (Table 2): about 69.3% of the variation in Summer Flounder length observations were explained by this model (deviance explained = 69.3%, Table 1). The inclusion of capture date in the model allowed for adjustment of the predictions for expected intra-annual increases in fish length through time and for seasonal migration effects. Because this GAM is an additive model, the effects of fish density, region, water temperature, salinity, depth, dissolved

oxygen, and chlorophyll *a* represent effects that are adjusted for capture date, thereby allowing for the interpretation of the effects of environmental and population conditions independently of collection date. That is, the effect of temperature on fish length is the effect in addition to the effect of capture date and other factors in the model.

Fish density had a significant effect on the observed mean fish length (Table 2A; Figure 7). Relative to the highest density category (3+ fish per tow), fish in the lower density categories (0-1, 1-2, and 2-3 fish per tow) were significantly larger (P<0.001). The largest fish, on average, occurred in years of lowest densities (0-1 fish per tow), and mean lengths decreased with increasing density. Based on model estimates of mean length (Table 2A) and compared with Summer Flounder mean lengths during years of high density (3+ fish per tow), Summer flounder were 28.0 (0.8) mm larger when density was 0-1 fish per tow, 24.2 (0.8) mm larger when density was 1-2 fish per tow, and 12.6 (0.7) mm larger when density was 2-3 fish per tow (mean with standard error in parentheses).

Fish size varied significantly by region (Table 2A; Figure 8). Relative to the mean size of Summer Flounder in the Chesapeake Bay, fish in the James, Rappahannock, and York rivers were significantly smaller (P<0.001). Additionally, mean fish length in the James, Rappahannock, and York rivers were different from each other. Based on model estimates of mean length (Table 2A) Summer Flounder in the James, Rappahannock, and York rivers were 6.1 (0.8) mm, 9.9 (1.0) mm, and 14.6 (0.8) mm smaller,

respectively, (mean with standard error in parentheses) than Summer Flounder in Chesapeake Bay.

Mean fish length was also significantly affected by capture date, water temperature, salinity, depth, dissolved oxygen, and chlorophyll-*a* concentrations (Table 2B). These factors have an estimated degree of freedom (edf) value greater than 1 (Table 2B), indicating that non-linear smoothing functions (and not linear models) were appropriate for describing the effect of these continuous factors. Capture date effects on mean length reflected the expected pattern of increasing fish length through time (Figure 9A). From June to September (day 150 to day 250), capture date had a negative effect on length: Summer Flounder are typically smaller, on average, during this time period. From September to November (day 250 to day 330), capture date had a positive effect on mean length: Summer Flounder are typically larger, on average, during this time period. This is not a particularly informative result, but confirmed that the model reflected the increasing size of fish during their time in nursery areas. Water temperatures less than 13°C or greater than 26°C had a negative effect on mean length such that fish encountered at these temperatures were typically smaller than those sampled between 13 and 26°C (Figure 9B). Water temperatures between 13 and 23°C have a positive effect on mean fish length and may represent optimal temperatures for YOY Summer Flounder in the Chesapeake Bay region. Salinities less than 10 psu had a negative effect on observed mean fish length, but salinities greater than 10 psu had no appreciable effect on length (Figure 9C). Depths from 1.2 to 20 m had little to no effect on observed mean length; depths greater than 20 m had a positive effect on length

suggesting that larger fish are typically found in deeper waters (Figure 9D). Mean fish

size was invariant to dissolved oxygen concentrations between 0.13 and 15.65 mg/l

(Figure 9E). The effect of chlorophyll-*a* concentrations on mean fish length was variable

when chlorophyll-*a* ranged between 3.2 and 7 mg/m^3; however, chlorophyll-*a*

concentrations greater than 7 mg/m^3 had a positive effect on mean length (Figure 9F).

DISCUSSION

Using monthly length data representing 25 year classes, I found evidence of spatially related differences in mean length and density-dependent growth in young-of-the-year Summer Flounder. Possible explanations for spatial variation in length may be related to annual differences in Summer Flounder settlement patterns, or to within-year variation in resources, predation pressure, or environmental conditions. More specifically, Summer Flounder larvae may settle in the Bay earlier in the year compared with settlement in other habitats, therefore, on any given date, fish in the Bay may be older and larger compared with fish elsewhere. Additionally, resources (such as prey) and abundance of predators may vary by region and may influence growth and density of Summer Flounder. Summer Flounder mean length differences by region do not seem to follow a latitudinal cline: mean fish sizes in the York River were most dissimilar to fish sizes in the Bay. Although I was unable to examine the effect of predator abundance, chlorophyll a appeared to provide a suitable proxy for prey abundance and suggested that larger mean sizes of Summer Flounder were observed when chlorophyll-a concentrations were high (>7 mg/m^3). Although I did not include Summer Flounder from the upper portions of the rivers in this analysis (they are captured less frequently in these locations), Summer Flounder have been observed to use these habitats, which appear to be sub-optimal for growth given the lower salinities in these locations.

Although not previously reported, density-dependent growth of Summer Flounder may have implications for both spawning stock biomass (SSB) and the use of length thresholds to delineate YOY fish (Table 3). The onset of maturation in Summer Flounder is size dependent (Terceiro 2006); therefore, Summer Flounder that grow fastest and are largest after their first year of life are more likely to be mature and contribute to the production of the stock. Furthermore, in years of low density, fish may attain larger sizes after their first year of life due to density-dependent growth, and a higher proportion of fish may be mature by age-0 compared with years of high density.

Young-of-the-year Summer Flounder are identified using monthly length thresholds estimated from consideration of historical length-frequency histograms (Tuckey and Fabrizio 2013); based on the GAM results, these length thresholds may be too conservative in some years, especially in years of low density when fish growth is higher. I examined the length-frequency distributions of all Summer Flounder captured monthly by the trawl survey from 1988 to 2012 (Appendix A), and noted the occurrence of Summer Flounder whose lengths were greater than the month-specific length threshold. Ideally, the age of the fish (0 or 1 year) would be determined to assess the validity of the age-class designation, but fish ages are not available for this time series of data. My investigation specifically focused on size of Summer Flounder observed in August, September, and October because these are the months from which catch data are used to calculate the YOY Summer Flounder index of abundance. In some years, YOY fish may exceed the length-threshold value for any given month, and this is most likely to occur when YOY density is low. For example, in 2003 (a year of relatively low

density), fish larger than the length threshold may actually be age-0 fish (Figure 10).

Results for August 2003 suggest at least two groups of Summer Flounder were present: two distinct distributions from about 150 to 240 mm and another from 275 to 400 mm. Some fish in the first group include fish that exceed the length threshold for age-0 fish and would thus not be included in the count of age-0 fish. However, in September and October, the distinction between groups is not as clear; this could be a result of the rapid growth of age-0 fish or inadequate sampling in August. Fish exceeding the length threshold in any given month are excluded from calculations of abundance, which may lead to under-estimation of YOY Summer Flounder abundance if these individuals are indeed fast-growing age-0 fish.

Optimal and sub-optimal conditions for growth of YOY Summer Flounder in Chesapeake Bay can be defined by water quality conditions and depth. Because temperature is a dominant factor controlling feeding and growth in fishes (Brett 1979; Gibson 1994), excessively low or high temperatures may result in growth limitation (Weatherley et al. 1986); this is consistent with what I observed among Summer Flounder in Chesapeake Bay. Summer Flounder use Chesapeake Bay as a nursery area throughout the summer months, but high water temperatures (>26°C) during this time may lead to sub-optimal growth. Optimal growing salinity for Summer Flounder has been described as 10 to 30 psu (Malloy and Targett 1991), and my modeling results supported this laboratory finding. Low salinities (<10 psu) had a negative effect on growth; this effect may be related to physiological processes because individuals from these habitats are presumed to use more energy to osmoregulate, and therefore

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relatively less energy can be used for growth (Boeuf and Payan 2001). The positive

effect of depths of 20 to 30 m on mean length likely reflects ontogenetic behavioral

changes among Summer Flounder: as fish grow they move out of shallow habitats into

deeper water. Smaller fish may inhabit shallow water because the risk of predation is

thought to be lower in these habitats (Gibson et al. 2002; Manderson et al. 2004; Ryer

et al. 2010).

Although dissolved oxygen was a significant factor accounting for variations in

fish length, Summer Flounder mean length responded minimally to changes in dissolved

oxygen. Based on previously reported results (Stierhoff et al. 2006), I expected to

observe a negative effect of low oxygen levels (<5 mg/l) on fish size. Two reasons are

proposed – one physiological, the other behavioral – to explain why I may not have

observed an effect of dissolved oxygen concentration on length. Adult Summer Flounder

exhibit a high tolerance to low oxygen conditions, and can tolerate low dissolved oxygen

to about 2.3 mg/l (Capossela et al. 2012): if larger juveniles exhibit a similar tolerance to

these conditions, then the distribution of juvenile Summer Flounder may be invariant to

dissolved oxygen greater than 2.3 mg/l. Additionally, Summer Flounder may exhibit a

behavioral response and escape habitats characterized by low oxygen conditions (Brady

and Targett 2010): if YOY Summer Flounder escape low dissolved oxygen habitats, then

they would be unavailable to the trawl. Summer Flounder captured in low oxygen areas

(<5 mg/l) may have been actively escaping those conditions or may not have been

inhabiting these poorly oxygenated waters for extended periods of time.

I expected that low chlorophyll-*a* levels would have a negative effect on length, and higher chlorophyll-*a* levels would have a positive effect on length. This pattern was generally observed, but in future studies a clearer relationship between prey abundance and mean fish length may be detected by using mysid shrimp abundance as an indicator of prey abundance. Although information on mysid shrimp abundance in Chesapeake Bay is currently unavailable, a random stratified sampling regime to assess abundance of this species in Chesapeake Bay is under development (C. Sweetman, VIMS dissertation research).

The GAM applied to 25 years of Summer Flounder length data described the majority of variation in length through time using 7 independent factors (69.3% deviance). Multiple factors may contribute to the 30% deviance that cannot be explained by the model including 1) genetic differences among YOY fish within a year class; 2) characteristics of the spawning fish; 3) the incidence of parasitic infections in YOY Summer Flounder; and 4) measurement error and random unexplained variation. Although Summer Founder are currently managed as a single stock along the Atlantic coast of the United States, studies suggest the existence of one to three Summer Flounder stocks in this region (based on meristics and morphometrics, mark-recapture studies, cell constituents, and genetic diversity summarized in Terceiro 2011). Multiple stocks could result in increased genetic variability among Summer Flounder if mixing of progeny from the multiple stocks occurs in the bay. Such mixing of recruits from different genetic stocks may potentially lead to variable growth rates (Burke et al. 2000) as was observed in Summer Flounder in Chesapeake Bay. In marine fish, older, more

experienced spawners (fish that spawned in previous years) are more likely to produce

viable eggs and larvae compared with younger individuals (Buckley et al. 1991;

Murawski et al. 2001). Also, growth variation may result from parasitic infections among

a subgroup of fish. In Chesapeake Bay, Jansen and Burreson (1990) documented the

occurrence of 38 species of parasites in Summer Flounder, some of which are lethal

(Burreson 1984) or elicit an inflammatory response (Jansen and Burreson 1990) that

may reduce growth; parasitism of Summer Flounder in Chesapeake Bay is currently not

monitored. Finally, measurement error (either of fish length or other factors considered

in the model) and random, unexplained variation may also contribute to the 30%

deviance that cannot be explained by the model.

This study is the first to apply generalized additive models to examine changes in

length of wild captured fish. As such, this approach may serve as a useful tool to assess

the effect of different biotic and abiotic factors on mean fish length. The results from

this study potentially identified optimal growth conditions for Summer Flounder, which

could be used to denote critical nursery areas for this species in Chesapeake Bay.

Although most results were consistent with those in the literature on Summer Flounder,

I found that temperatures >26°C adversely affected Summer Flounder length. As water

temperatures continue to warm in Chesapeake Bay as a result of changes in climate

(Hayhoe et al. 2007; Najjar et al. 2010), YOY Summer Flounder growth and production

may be negatively affected.

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TABLES

Table 1. Generalized additive models considered in the analysis of biotic and abiotic factors on young-of-the-year Summer Flounder size (Y_i) from the 1988 to 2012 year classes collected in Virginia estuarine waters. Percent deviance explained, AIC, and delta-AIC (ΔAIC) are presented for the full model (listed first) and alternate reduced models. Symbols in the models are: the model intercept (a), estimated mean effects (α_1, α_2) for each level of region (REG) and density (DENS), nonparametric smoothing functions(g_{1-6}) for capture date (DATE), water temperature (T), salinity (S), depth (DEPTH), dissolved oxygen (DO), prey (PREY), and random unexplained error (e_i). Prey effects were lagged from 0 to 5 months. The k value is a smoothing parameter in the model, and when a k value is given this indicates manipulation from the default setting. The k value influences the number of knots (similar to inflection points) within a smoothing function; k values were altered due to observed overfitting of the spline function to the data (Ciannelli and Chan). The best model (lowest AIC value) is in bold.

Model	% Deviance Explained	AIC	ΔAIC
$Y_i=a + \alpha_1*(REG) + \alpha_2*(DENS) + g_1(DATE) + g_2(T) + g_3(S) + g_4(DEPTH) + g_5(DO) + g_6(PREY, no lag, k=7) + e_i$	**69.3**	**117672.6**	**0**
$Y_i=a + \alpha_1*(REG) + \alpha_2*(DENS) + g_1(DATE) + g_2(T) + g_3(S) + g_4(DEPTH) + g_6(PREY, no lag, k=7) + e_i$	69.5	119734.2	2061.6
$Y_i=a + \alpha_1*(REG) + \alpha_2*(DENS) + g_1(DATE) + g_2(T) + g_3(S) + g_6(PREY, no lag, k=7) + e_i$	69.4	119776.4	2103.8
$Y_i=a + \alpha_1*(REG) + \alpha_2*(DENS) + g_1(DATE) + g_2(T) + g_3(S) + g_6(PREY, 1 month lag, k=7) + e_i$	69.3	119823.9	2151.3
$Y_i=a + \alpha_1*(REG) + \alpha_2*(DENS) + g_1(DATE) + g_2(T) + g_3(S) + g_6(PREY, 2 month lag, k=5) + e_i$	69.0	119936.7	2264.1
$Y_i=a + \alpha_1*(REG) + \alpha_2*(DENS) + g_1(DATE) + g_2(T) + g_3(S) + g_6(PREY, 3 month lag, k=6) + e_i$	68.8	120036.3	2363.7
$Y_i=a + \alpha_1*(REG) + \alpha_2*(DENS) + g_1(DATE) + g_2(T) + g_3(S) + g_6(PREY, 4 month lag, k=7) + e_i$	69.3	119837.2	2164.6
$Y_i=a + \alpha_1*(REG) + \alpha_2*(DENS) + g_1(DATE) + g_2(T) + g_3(S) + g_6(PREY, 5 month lag, k=5) + e_i$	68.4	120100.5	2427.9
$Y_i=a + \alpha_1*(REG) + \alpha_2*(DENS) + g_1(DATE) + g_2(T) + g_3(S) + g_4(DEPTH) + g_5(DO) + e_i$	68.3	118067.3	394.7
$Y_i=a + \alpha_1*(REG) + \alpha_2*(DENS) + g_1(DATE) + g_2(T) + g_3(S) + g_5(DO) + e_i$	68.2	118108.7	436.1
$Y_i=a + \alpha_1*(REG) + \alpha_2*(DENS) + g_1(DATE) + g_2(T) + g_3(S) + g_4(DEPTH) + e_i$	68.4	120181.2	2508.6
$Y_i=a + \alpha_1*(REG) + \alpha_2*(DENS) + g_1(DATE) + g_2(T) + g_3(S) + e_i$	68.3	120220.0	2547.4

Table 2. Effect of region, density, capture date, temperature, salinity, depth, DO, and prey on young-of-the-year Summer Flounder mean length from the best fit generalized additive model (Table 1). Summer Flounder lengths from the 1988 to 2012 year classes collected from Virginia estuarine waters were used for this analysis. The model intercept (indicating mean Summer Flounder length) and estimated mean effects for the categorical factors in the model are provided in section A, with associated standard errors, *t*-values, and approximate significance (*P* values). Region estimates for the James, Rappahannock, and York rivers represent expected changes in fish size relative to sizes observed in Chesapeake Bay. Density estimates are relative to the category that includes year classes of the highest density (3+; see Figure 5). The continuous, smoothed terms in the model are listed in section B, with associated estimated degrees of freedom (edf), *F* values, and approximate significance *(P* values). Edf values >1 denote nonlinear smoothers.

A

Parameter	Estimate	Standard Error	*t*-value	*P*
Intercept	181.7995	0.5266	345.212	<0.001
Region: James	-6.0843	0.8039	-7.569	<0.001
Region: Rappahannock	-9.9299	1.0866	-9.138	<0.001
Region: York	-14.5590	0.8362	-17.410	<0.001
Density 0-1	28.0432	0.8035	34.899	<0.001
Density 1-2	24.1550	0.7903	30.565	<0.001
Density 2-3	12.5820	0.6487	19.397	<0.001

B

Smooth terms	edf	*F*	*P*
s(Ordinal Date)	8.225	1182.728	<0.001
s(Temperature)	8.945	81.508	<0.001
s(Salinity)	7.933	6.802	<0.001
s(Depth)	7.399	5.225	<0.001
s(DO)	7.983	10.049	<0.001
s(Prey, no lag)	5.759	67.490	<0.001

Table 3. Length thresholds for YOY Summer Flounder, by month, based on length-frequency analysis (Tuckey and Fabrizio 2013). Catches from months indicated in bold are used to estimate an index of abundance for Summer Flounder.

Month	Length (mm)
January	290
February	290
March	60
April	100
May	140
June	170
July	200
August	**225**
September	**250**
October	**275**
November	290
December	290

FIGURES
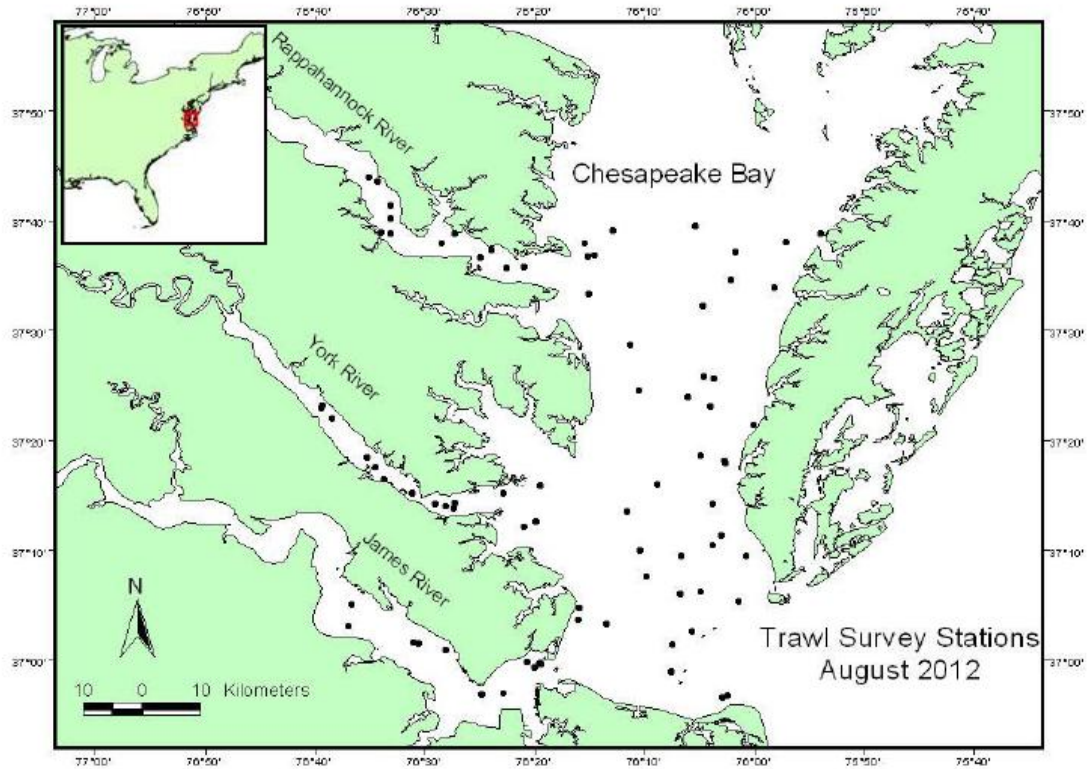
Figure 1. Sampling locations (filled circles) in August 2012 in Chesapeake Bay and lower James, York and Rappahannock rivers. Sample sites for each month and year were selected randomly from a stratified sampling design. Figure courtesy of W. Lowery.
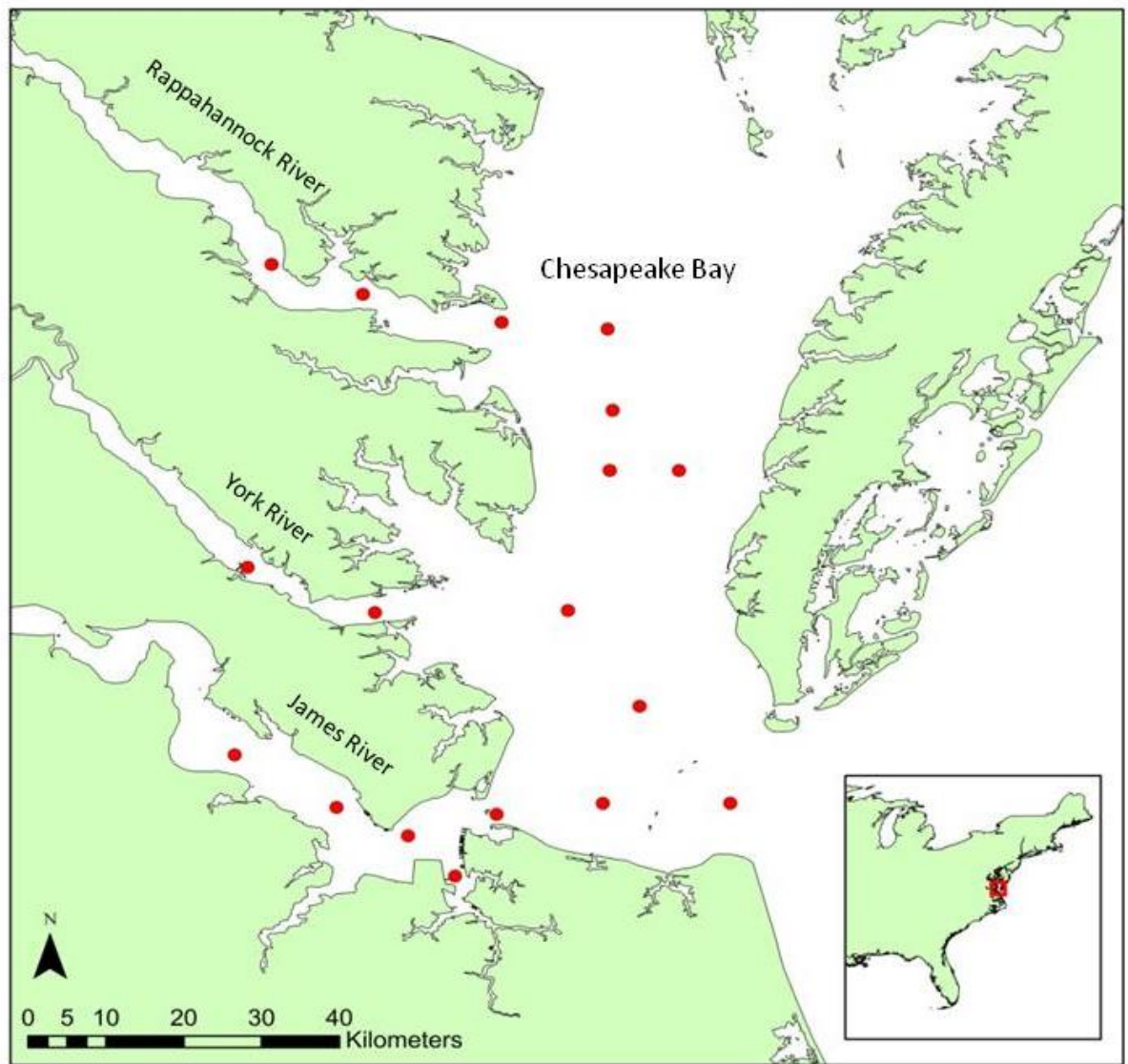
Figure 2. Stations monitored by the Chesapeake Bay Program in the Virginia portion of Chesapeake Bay and the lower James, York and Rappahannock rivers (filled circles). Daily surface chlorophyll-*a* values from these stations were interpolated from monthly monitoring data for June to November, 1988 to 2012 (M.Brush, unpublished).
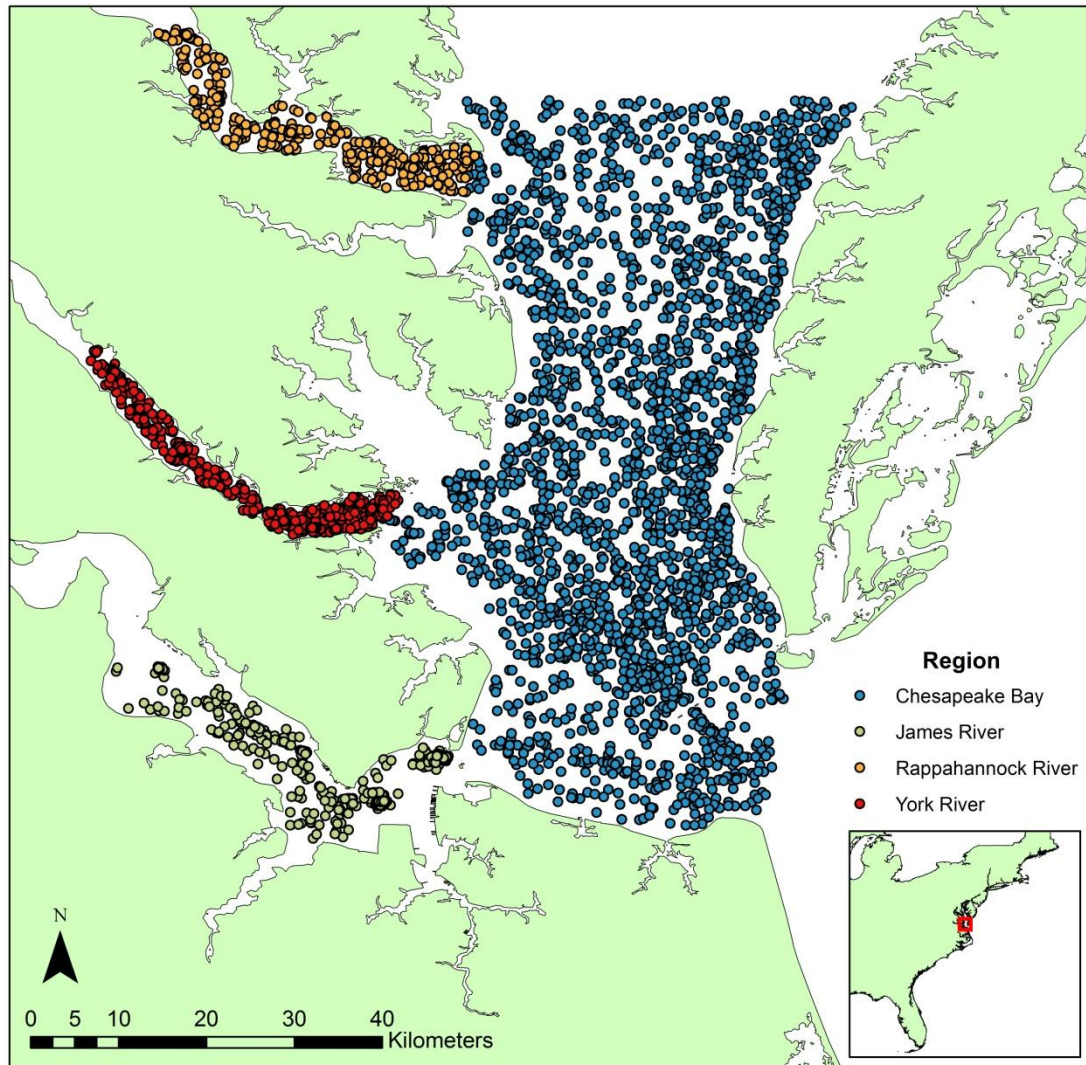
Figure 3. Sampling locations (filled circles) where Summer Flounder were captured in each region from 1988 to 2012: Chesapeake Bay (blue), lower Rappahannock River (orange), lower James River (green), and lower York River (red).
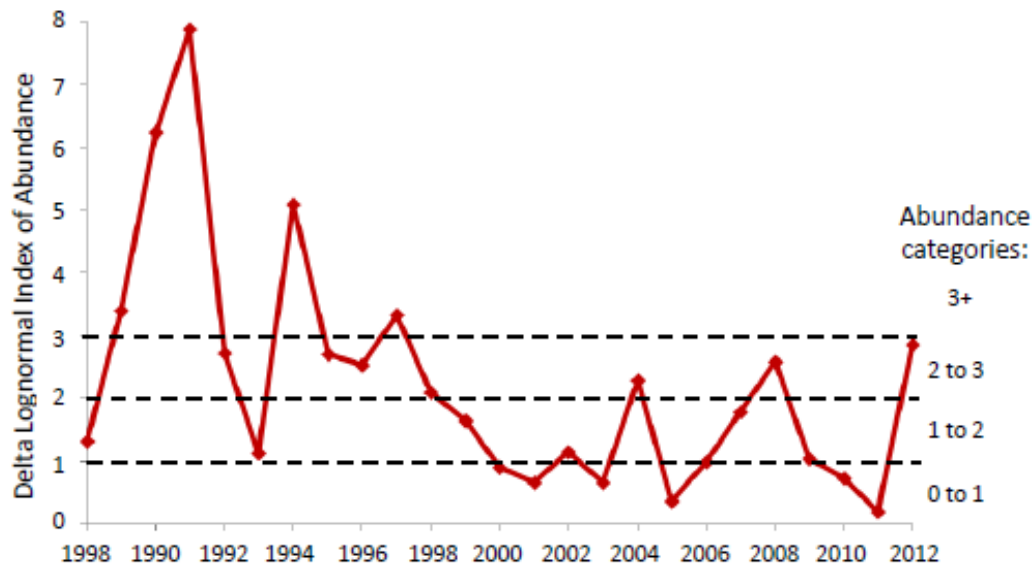
Figure 4. Temporal variation in the index of abundance for Summer Flounder from the 1988 to 2012 year classes collected in the Chesapeake Bay and lower James, York and Rappahannock rivers. The index was calculated using a stratified mean based on the delta-lognormal estimate of mean abundance in each stratum; catches from August, September, and October were included in this calculation. Four categories of approximately equal numbers of observations were used to discretize abundance data for further analysis; the discrete abundance categories are indicated on the right axis.
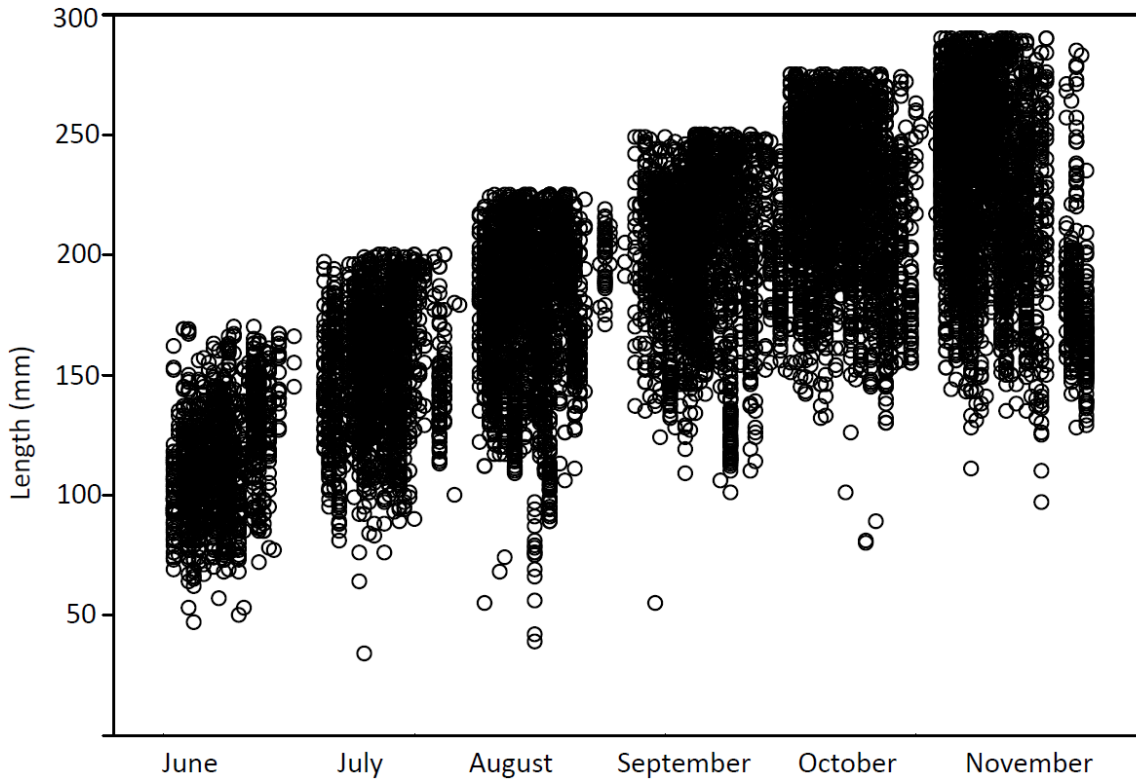
Figure 5. Total length of young-of-the-year Summer Flounder from the 1988 to 2012 year classes collected in Virginia estuarine waters (n=13,047). The truncation indicates the length threshold used to designate young-of-the-year fish (see Table 3). Note the variation and range in length for any given month.
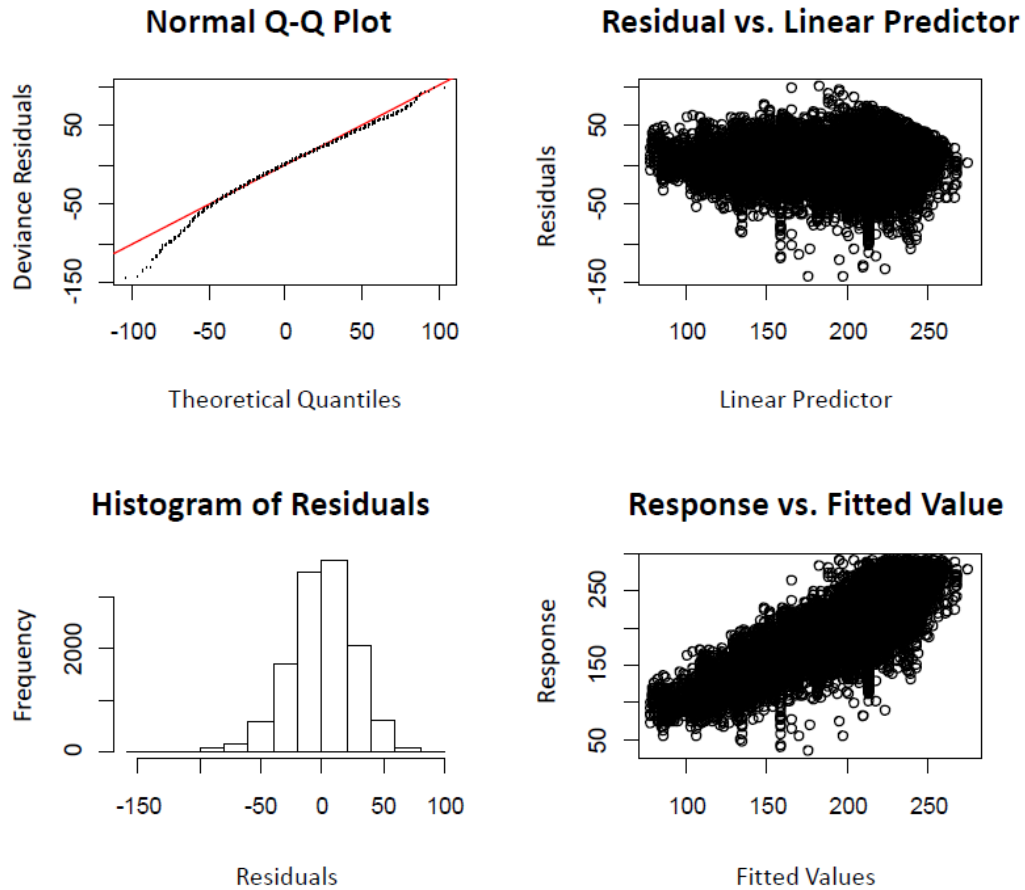
Figure 6. Diagnostic plots for the generalized additive model of the effects of conspecific density, prey abundance, region, capture date, temperature, salinity, depth, and dissolved oxygen concentration on observed lengths of YOY Summer Flounder from multiple year classes that recruited to estuarine waters of Virginia between 1988 and 2012. Plots were created using the 'gam.check' function in R. The Q-Q plot presents the quantiles of the observed length distribution with those of the normal distribution (theoretical quantiles).
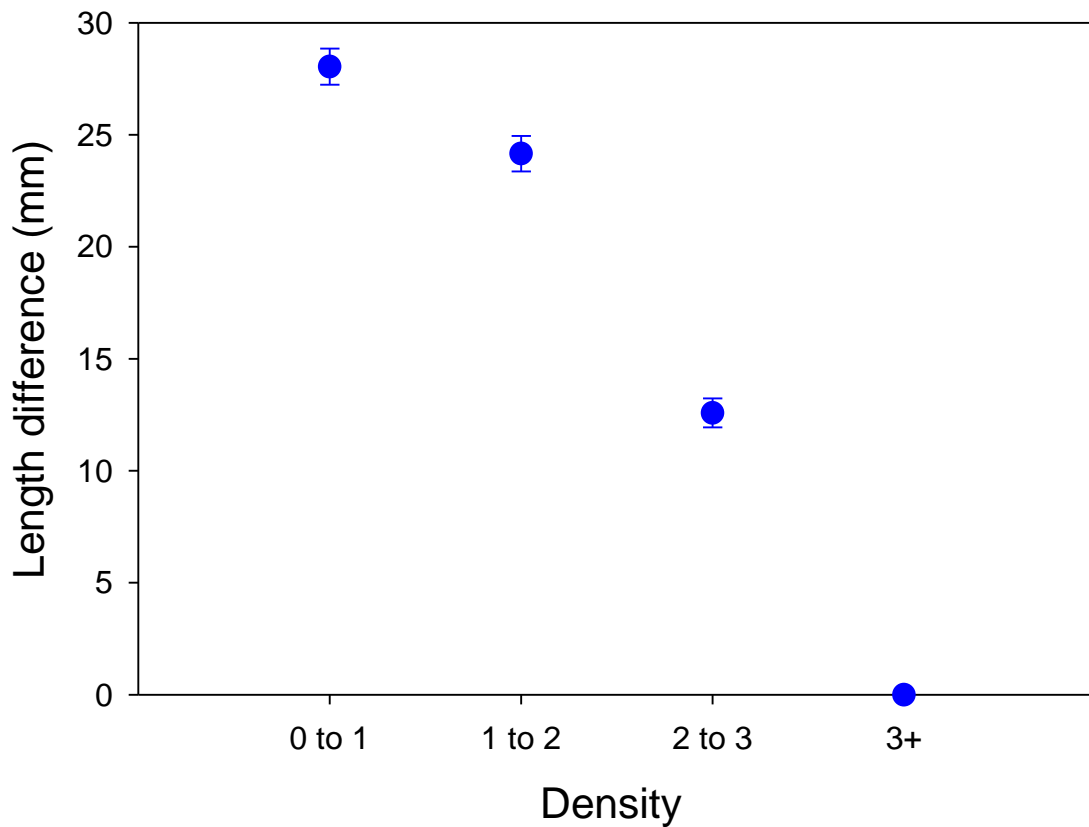
Figure 7. Effect of density on young-of-the-year Summer Flounder mean length from the 1988 to 2012 year classes in estuarine waters of Virginia relative to size of Summer Flounder in the 3+ density category. The length differences presented are the mean effect of each density category on Summer Flounder length estimated by the generalized additive model (Table 2). Fish in the lower density categories were significantly larger than fish in the highest density category (3+ fish per tow). The largest fish occurred at the lowest abundance (0-1 fish per tow), followed by significantly smaller fish lengths as abundance increased. Error bars represent model-based standard errors.
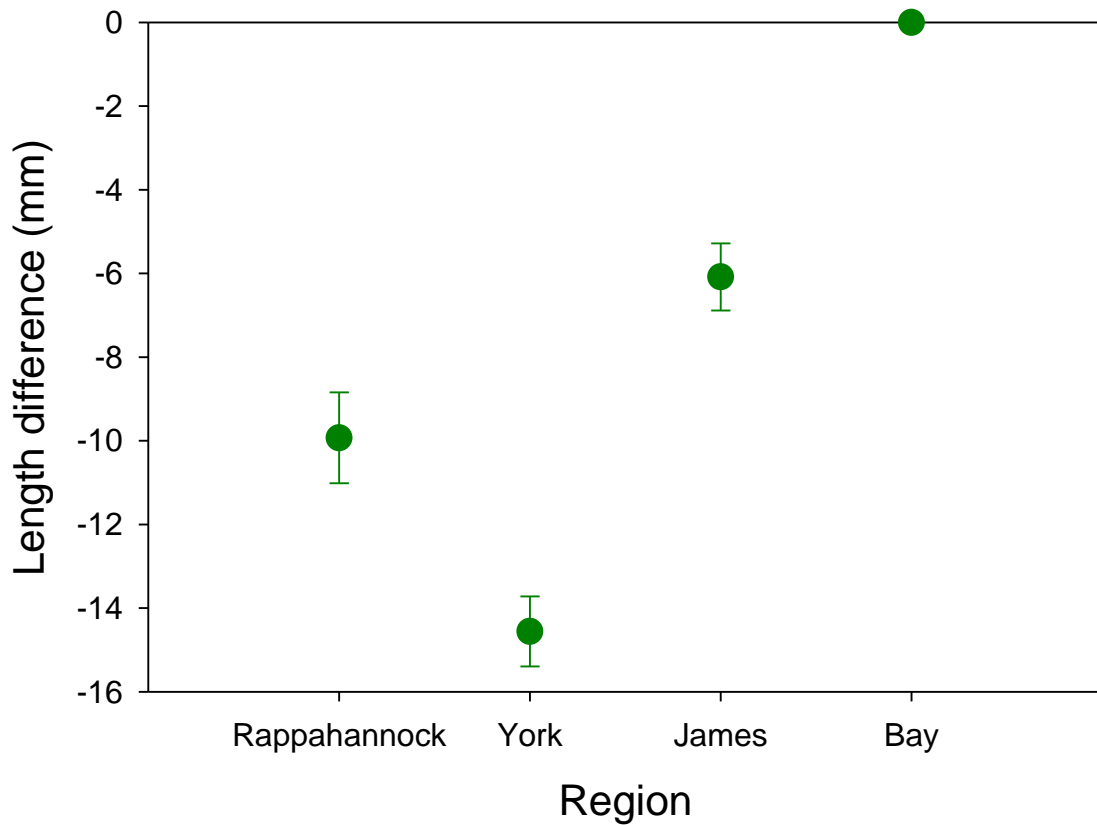
Figure 8. Spatial effect of region on young-of-the-year Summer Flounder mean length in the Rappahannock, York and James rivers relative to the Chesapeake Bay for the 1988 to 2012 year classes. The length differences presented are the effect of each region on Summer Flounder mean length estimated by the generalized additive model (Table 2). Fish in the Rappahannock, York, and James rivers were significantly smaller than fish observed in the Bay. Additionally, fish lengths in the Rappahannock, York, and James rivers were significantly different from each other. Error bars represent model-based standard errors.
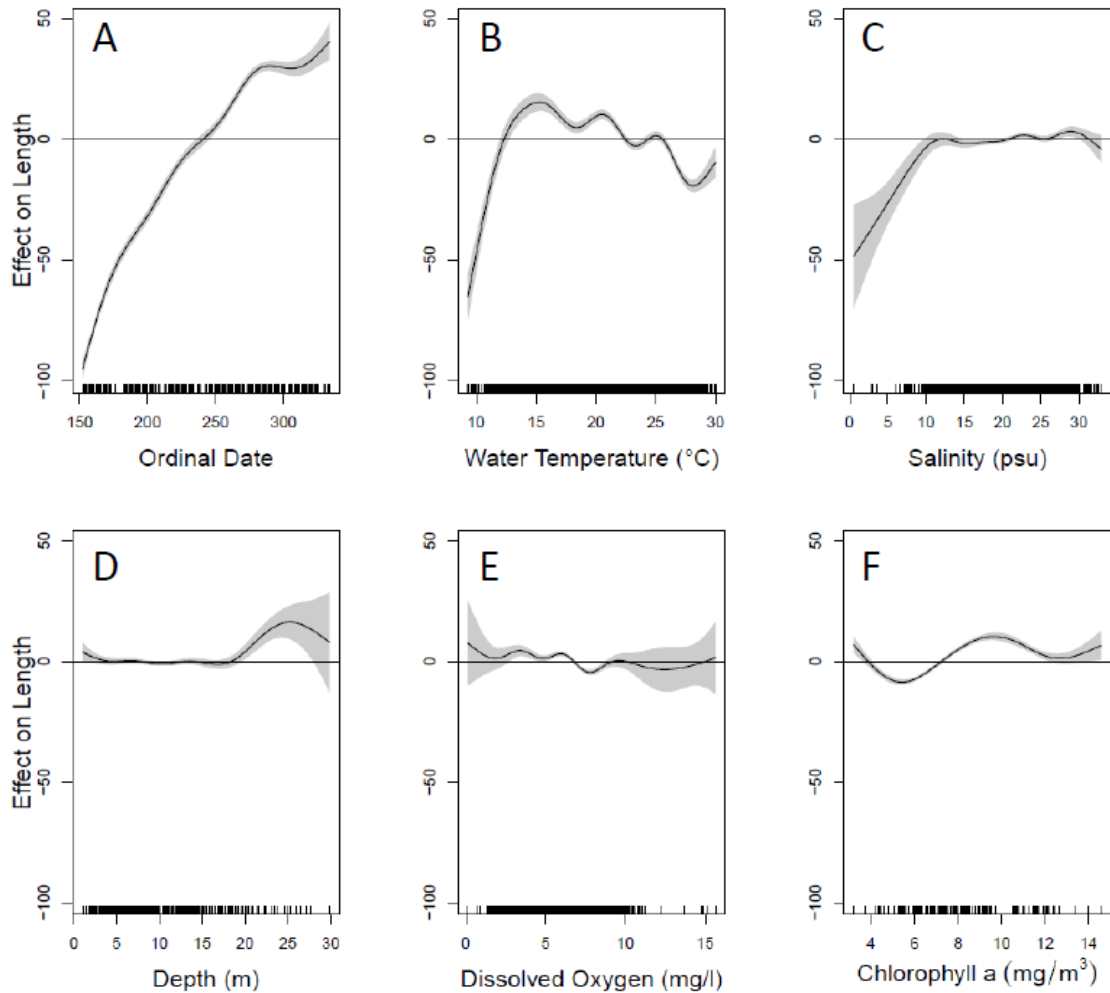
Figure 9. Effect of capture date (A), water temperature (B), salinity (C), depth (D), dissolved oxygen (E), and chlorophyll-*a* concentration (F) on young-of-the-year Summer Flounder mean length from the 1988 to 2012 year classes collected in Virginia estuarine waters. The black hash marks on the x-axis indicate observed values, the black line represents the smoothing function (gray shading indicates ±2 standard errors). The horizontal line at 0 indicates no effect on length, negative values indicate a negative effect on length and positive values indicate a positive effect on length. Capture date was included in the model to adjust other model effects for increases in fish length through time.
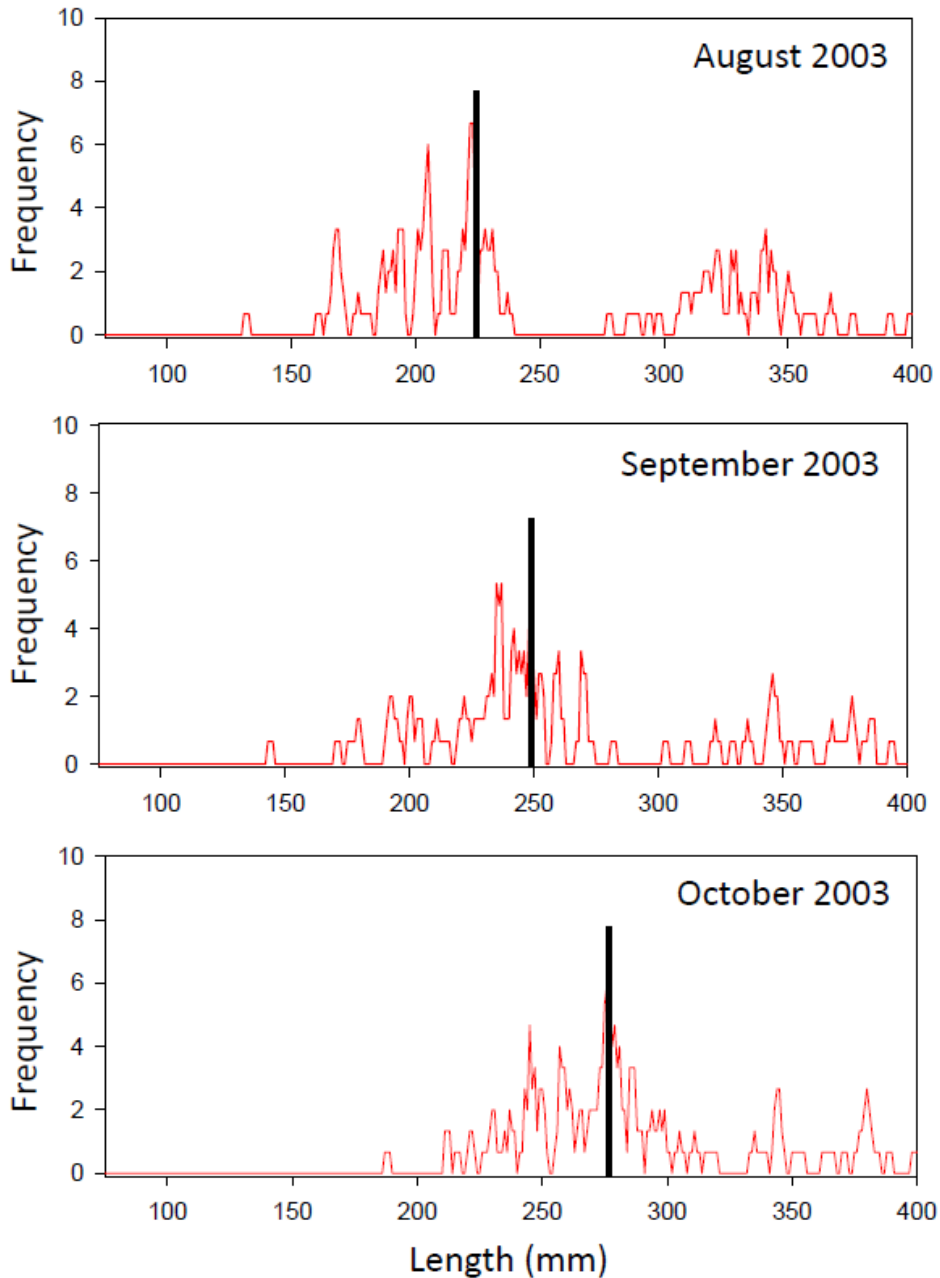
Figure 10. Monthly length-frequency distributions of Summer Flounder collected in Virginia estuarine waters for the 2003 year class in August, September, and October. Length-frequency thresholds used to designate young-of-the-year fish are indicated with a solid black line. It is possible that some fish that are larger than the threshold may actually be age-0 fish, but ages are not available for these samples.

APPENDIX

Appendix A. Length-frequency histograms of Summer Flounder from Virginia estuarine waters; fish were captured by the VIMS juvenile fish trawl survey in January to December for 1988 to 2012. Histograms for the months used to calculate the index of abundance for young-of-the-year Summer Flounder (August, September, and October) are in red.

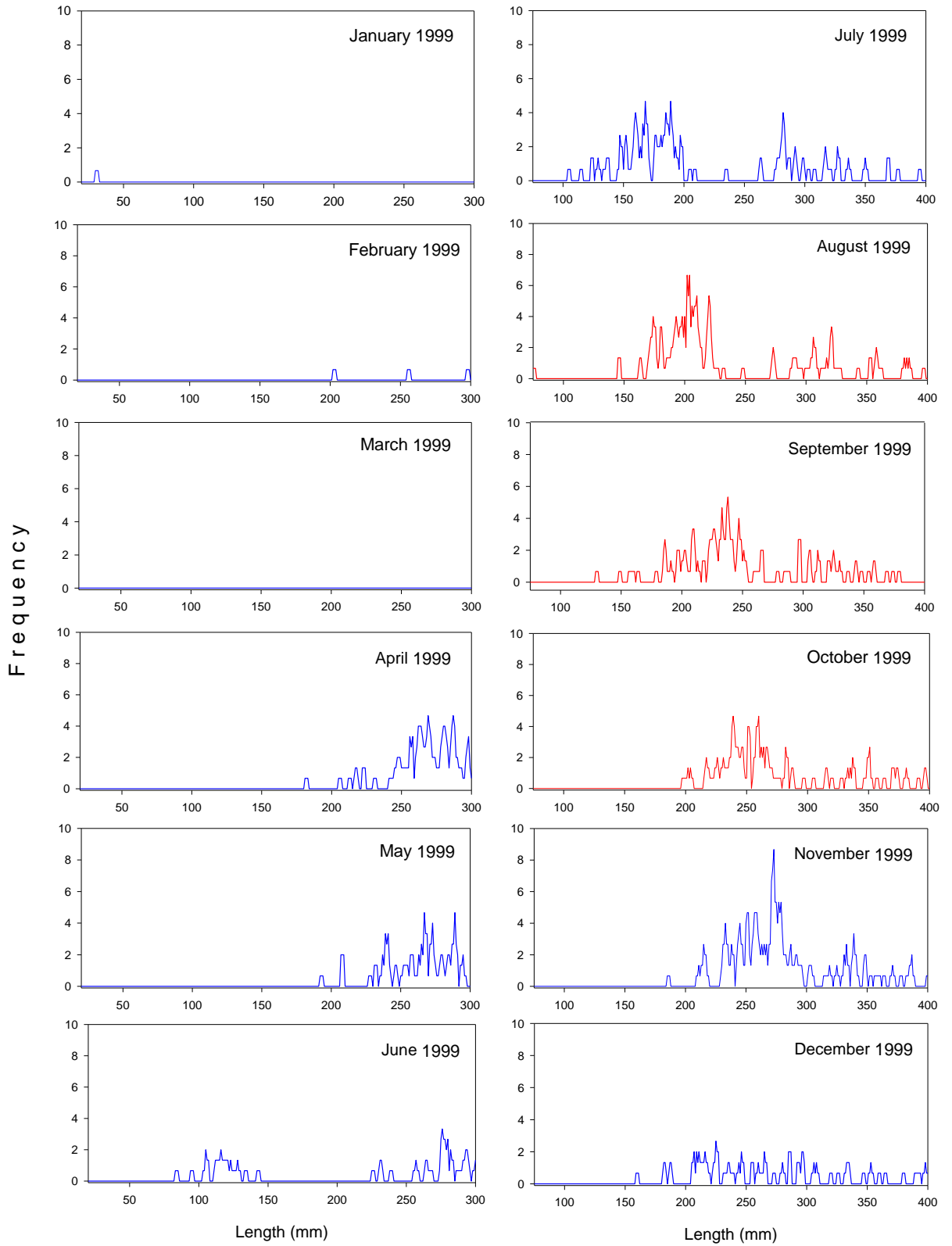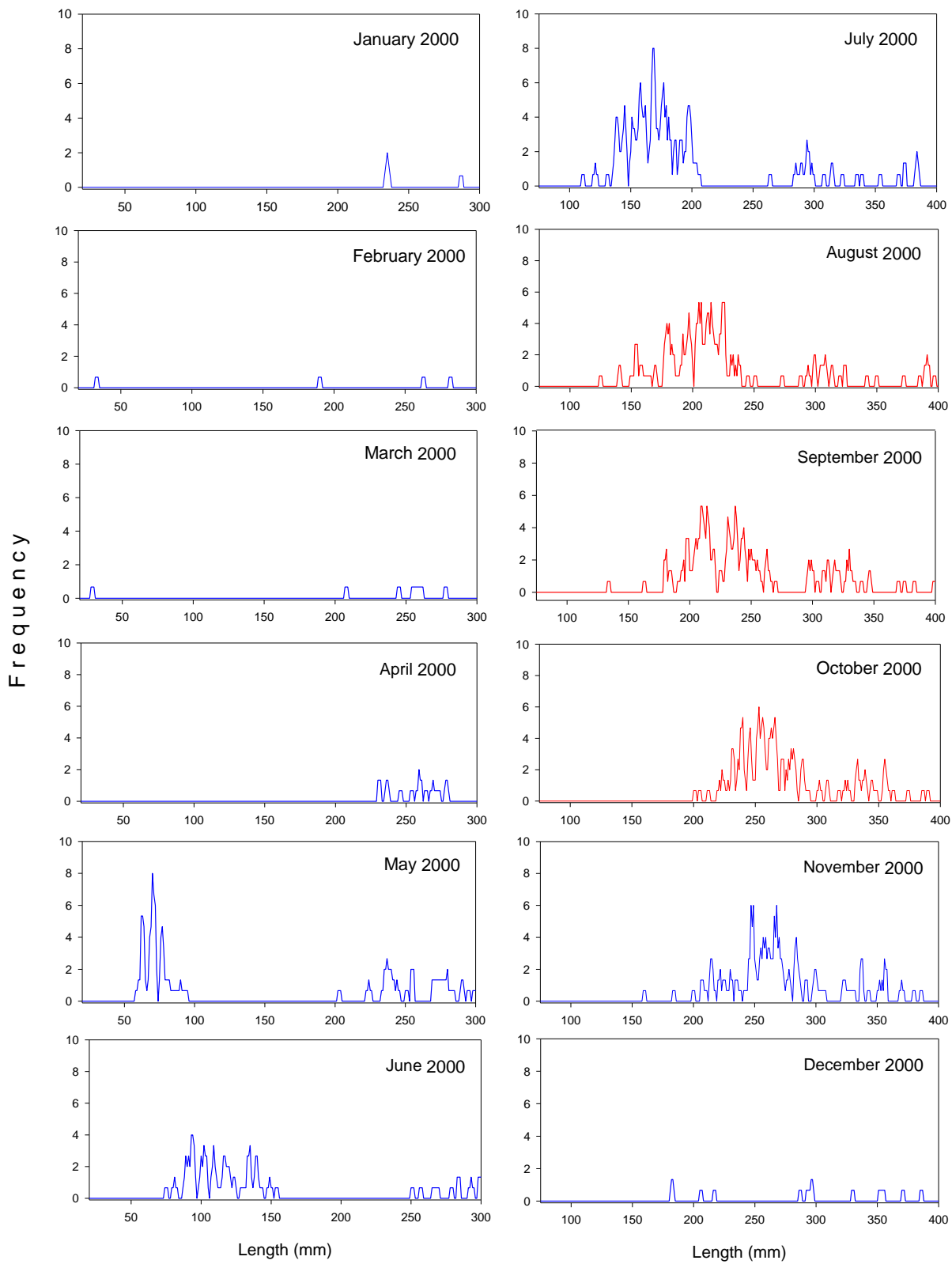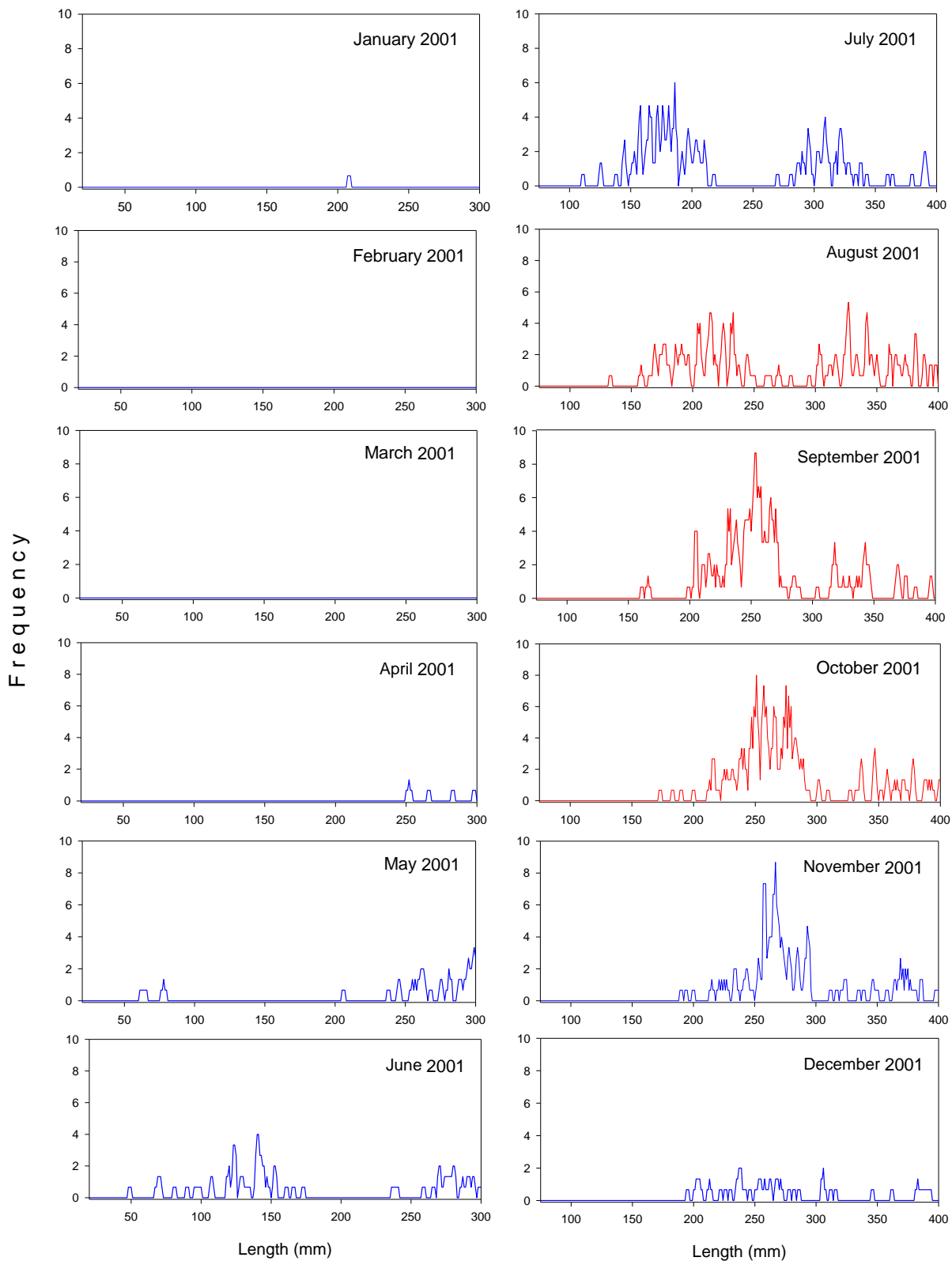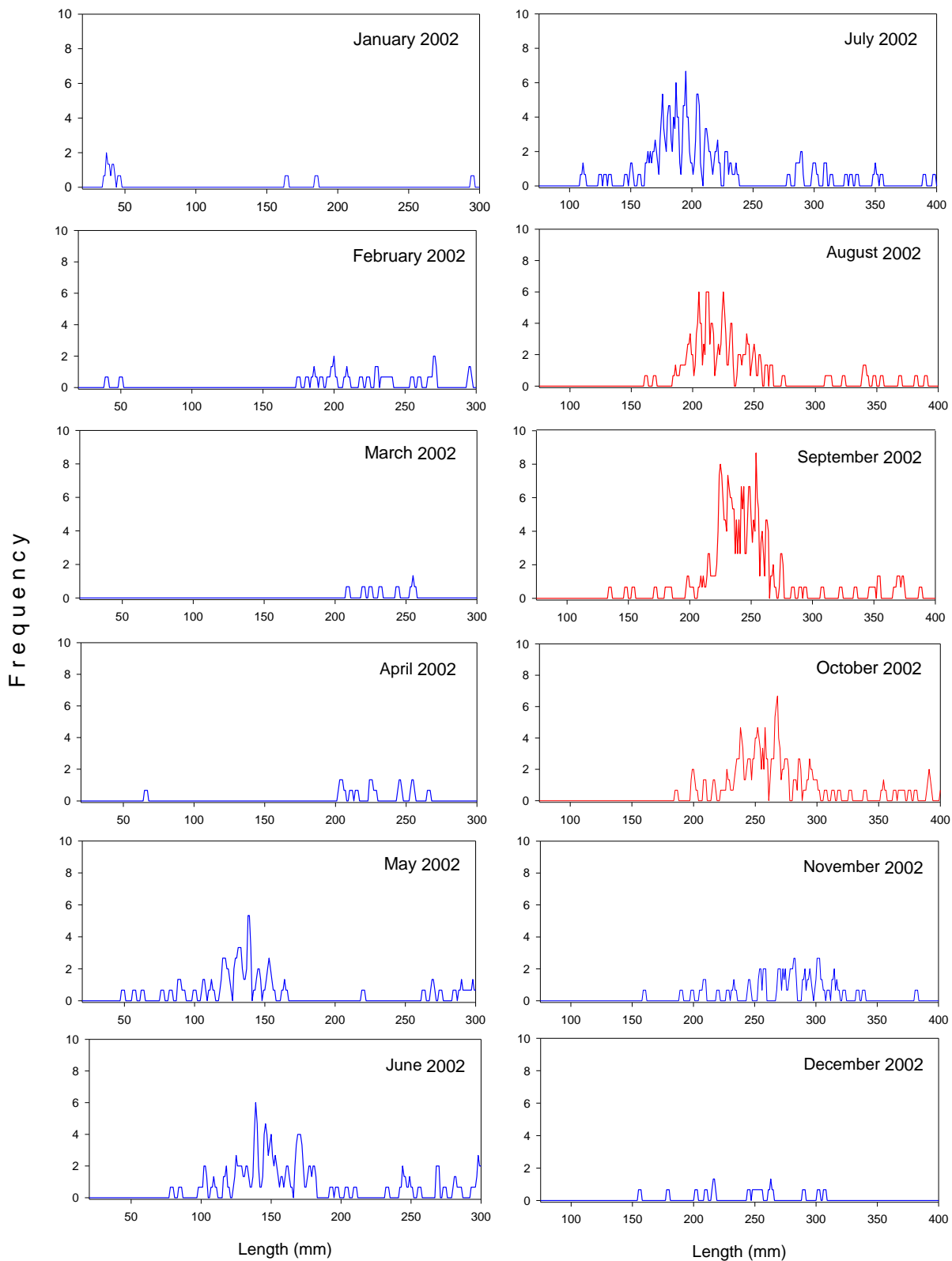# 1988 Length Frequency
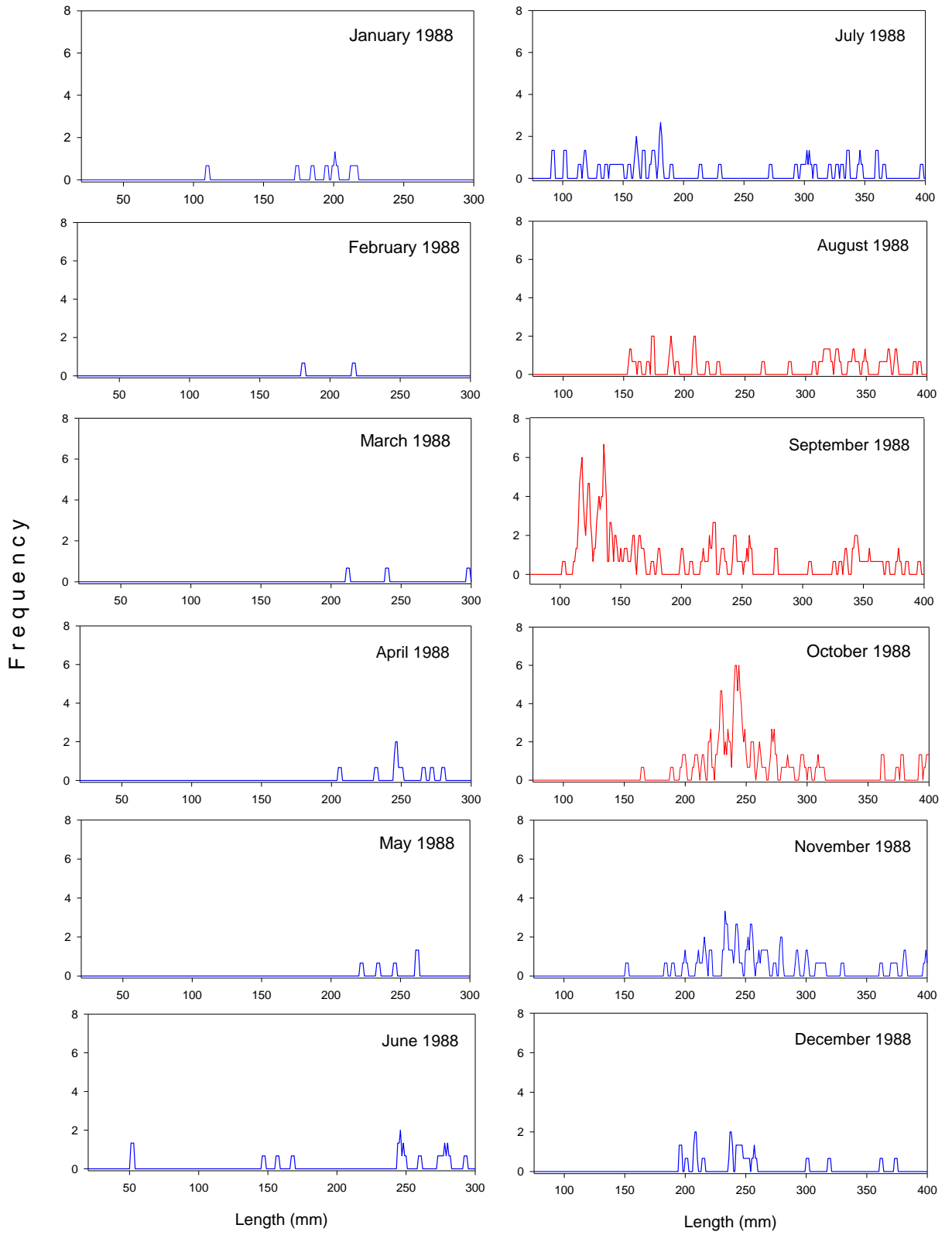
1989 Length Frequency

1990 Length Frequency

January 1990

February 1990

March 1990

April 1990

May 1990

June 1990

July 1990

August 1990

September 1990

October 1990

November 1990

December 1990
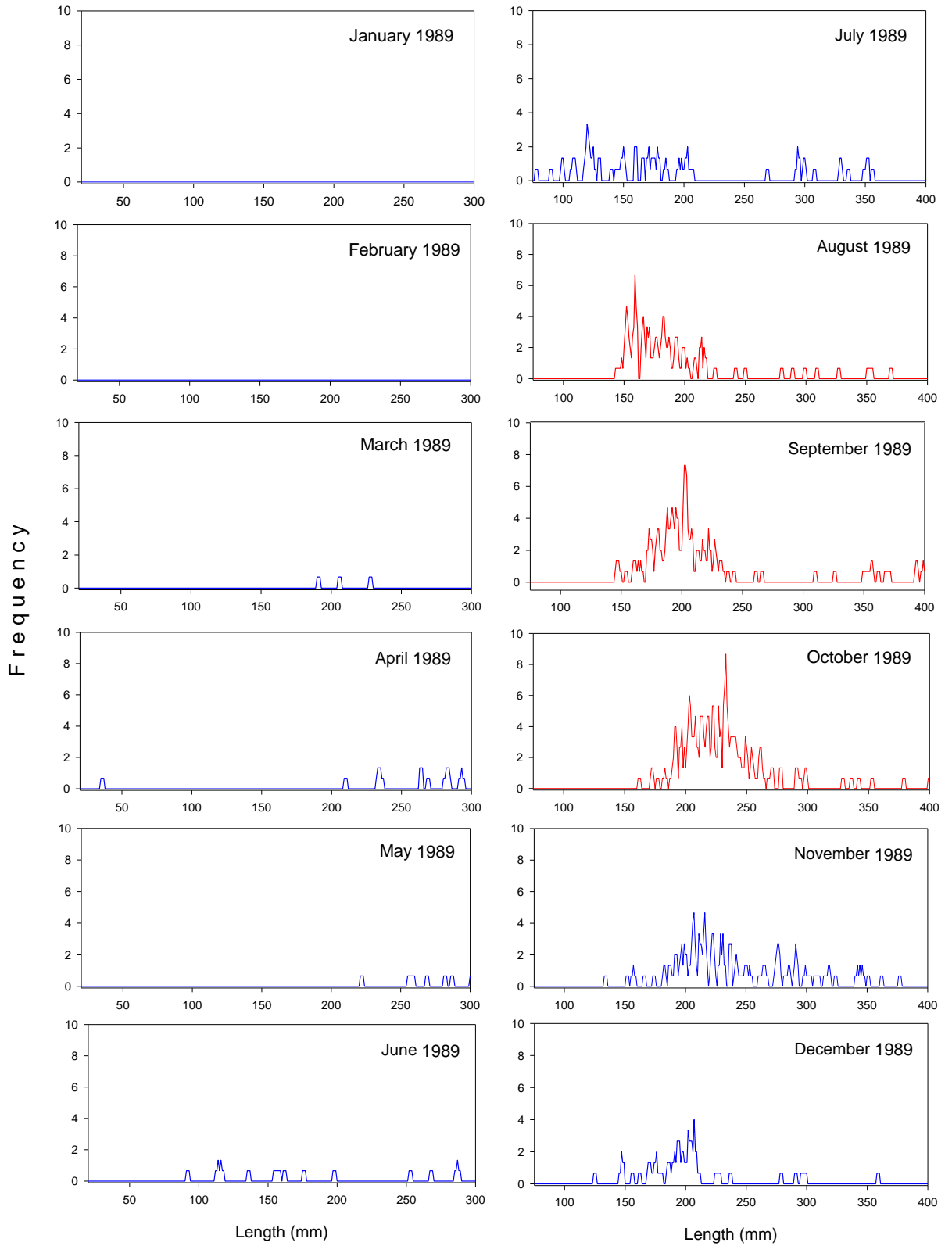
Length (mm)

Length (mm)
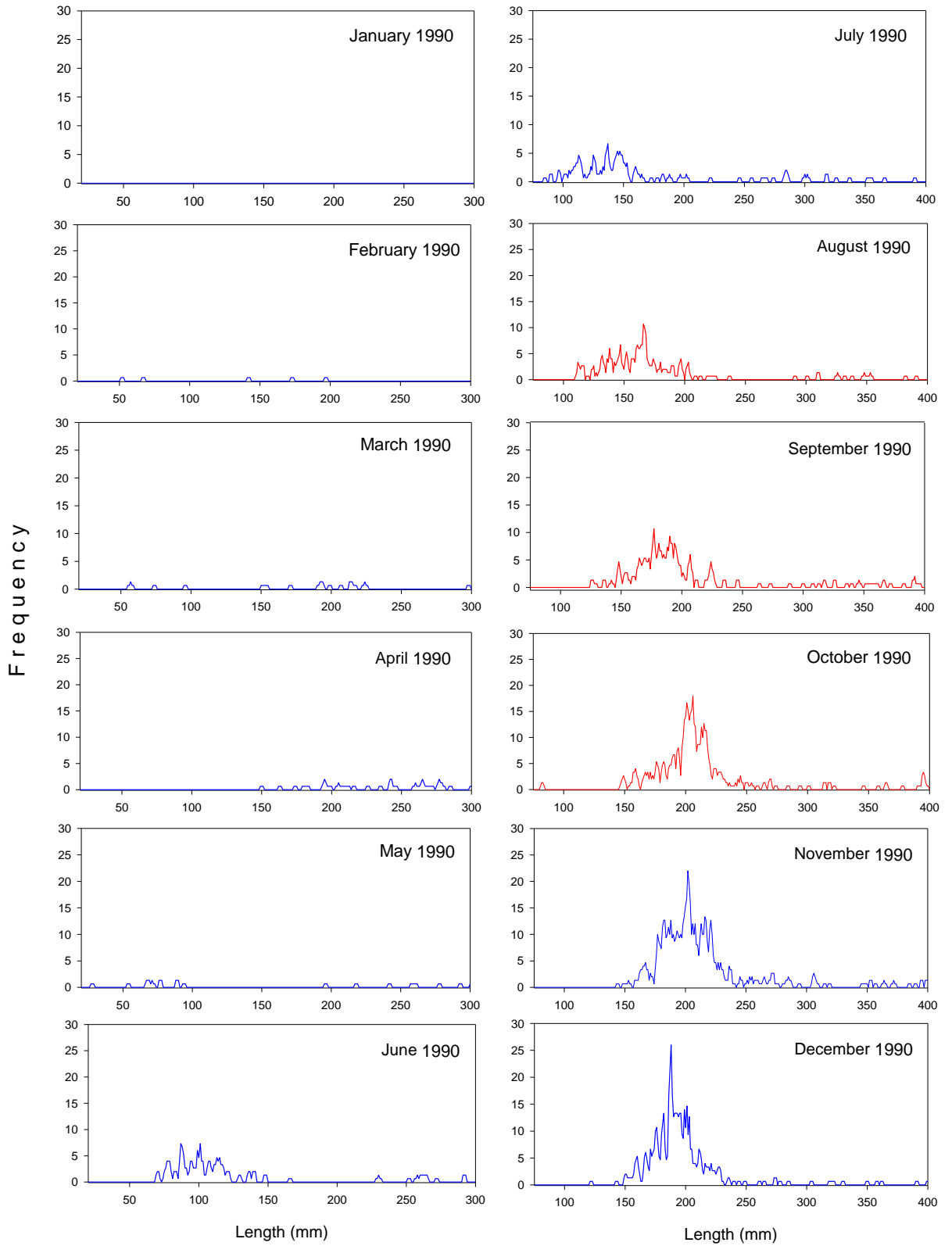
Frequency

1991 Length Frequency
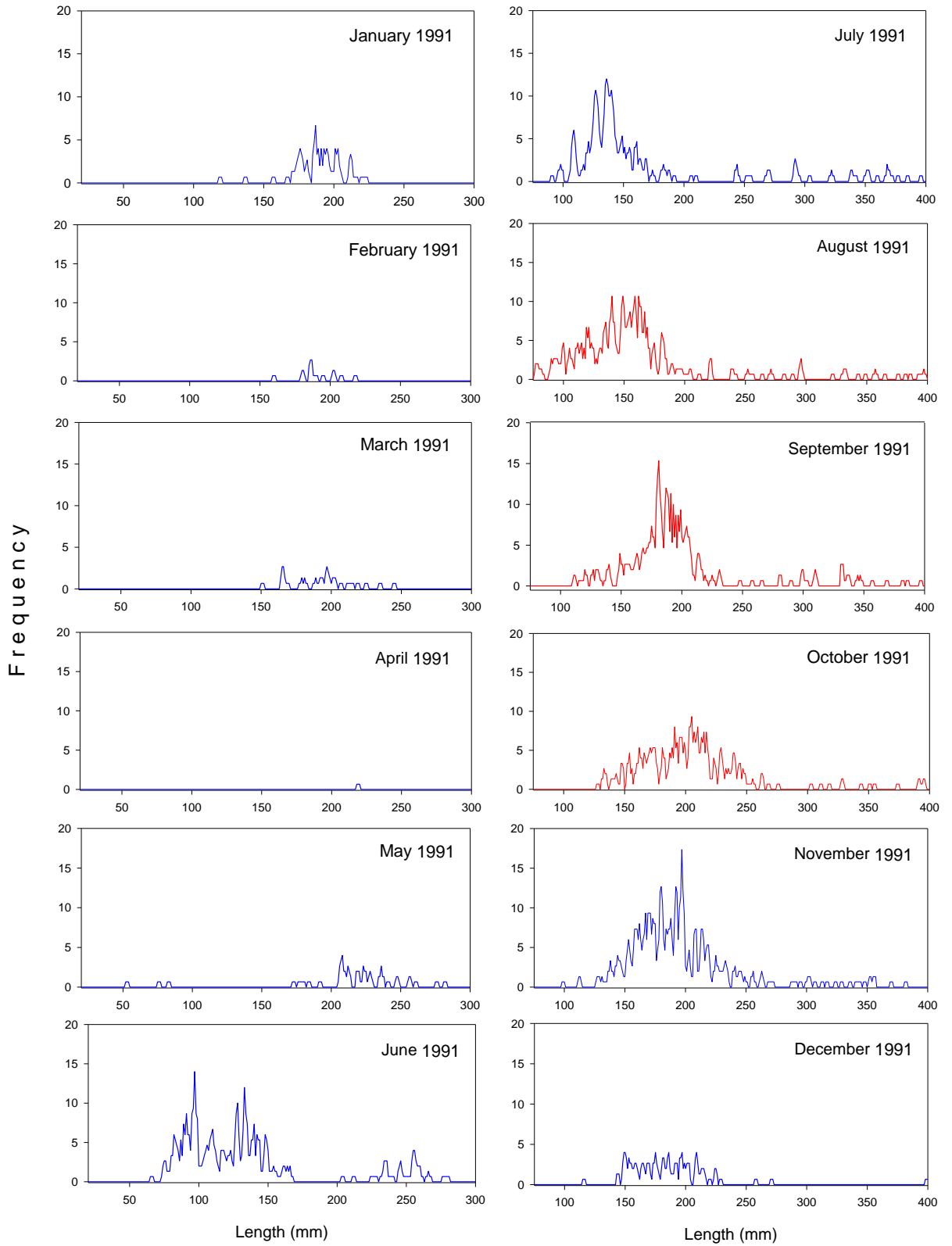
1992 Length Frequency
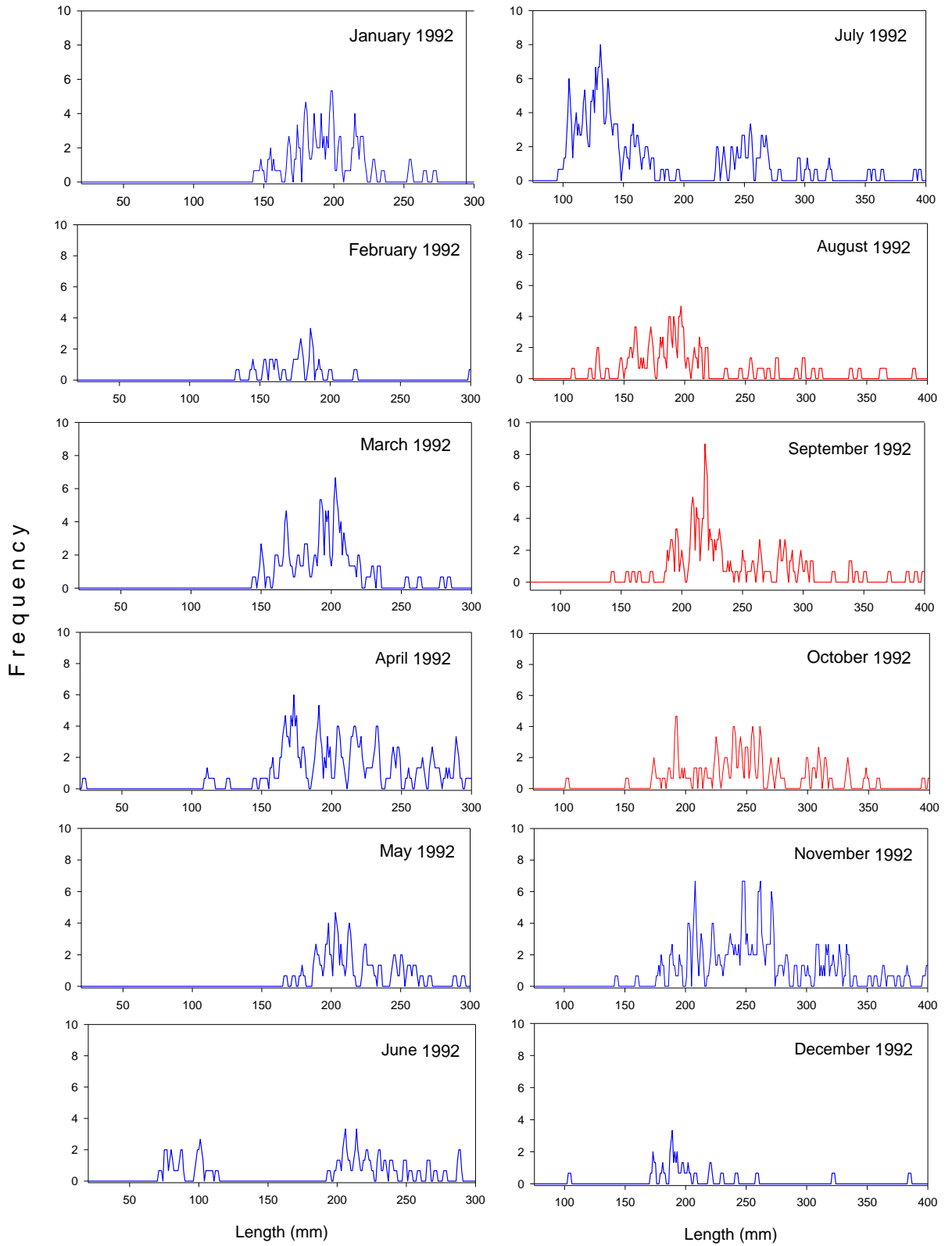
1993 Length Frequency
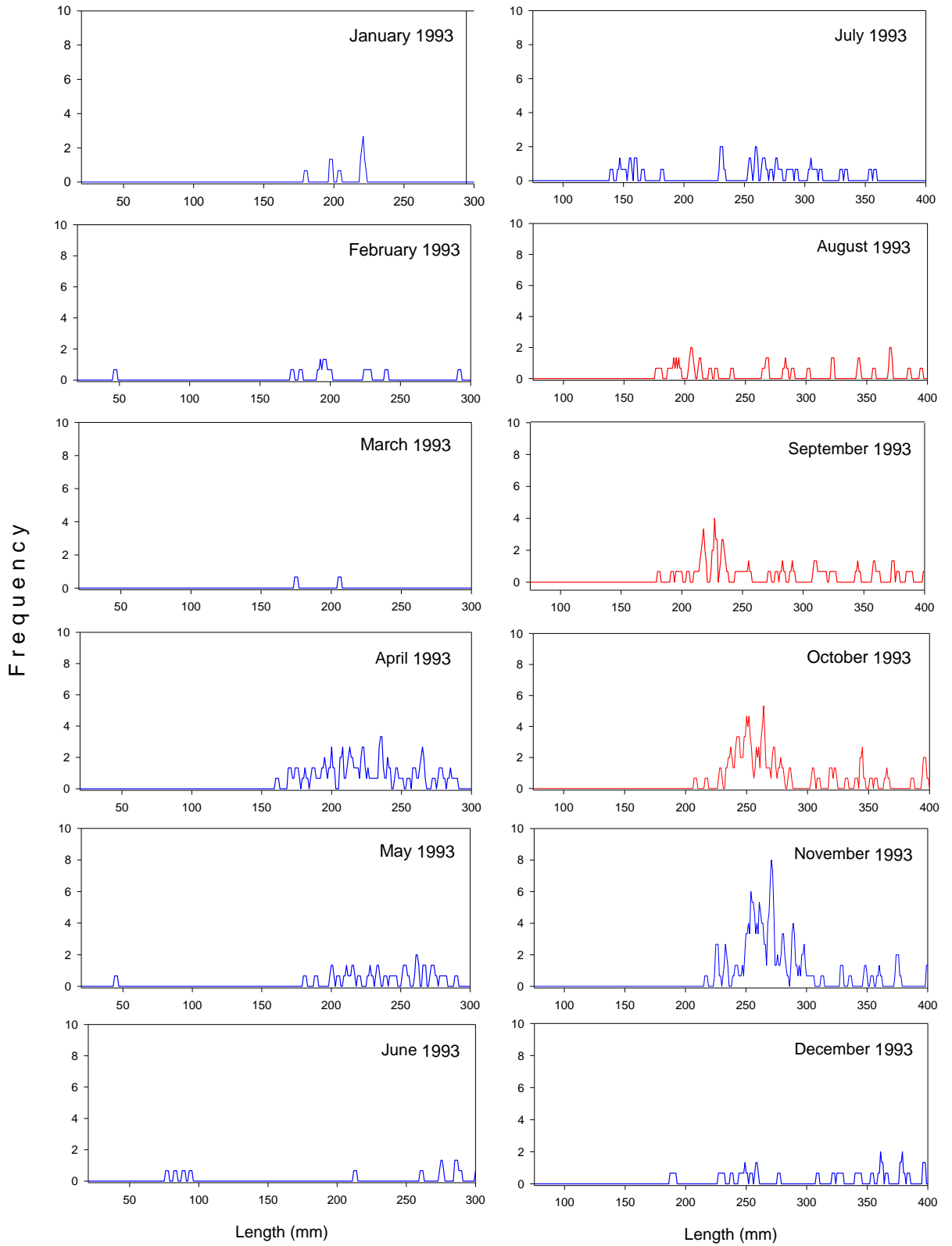
1994 Length Frequency
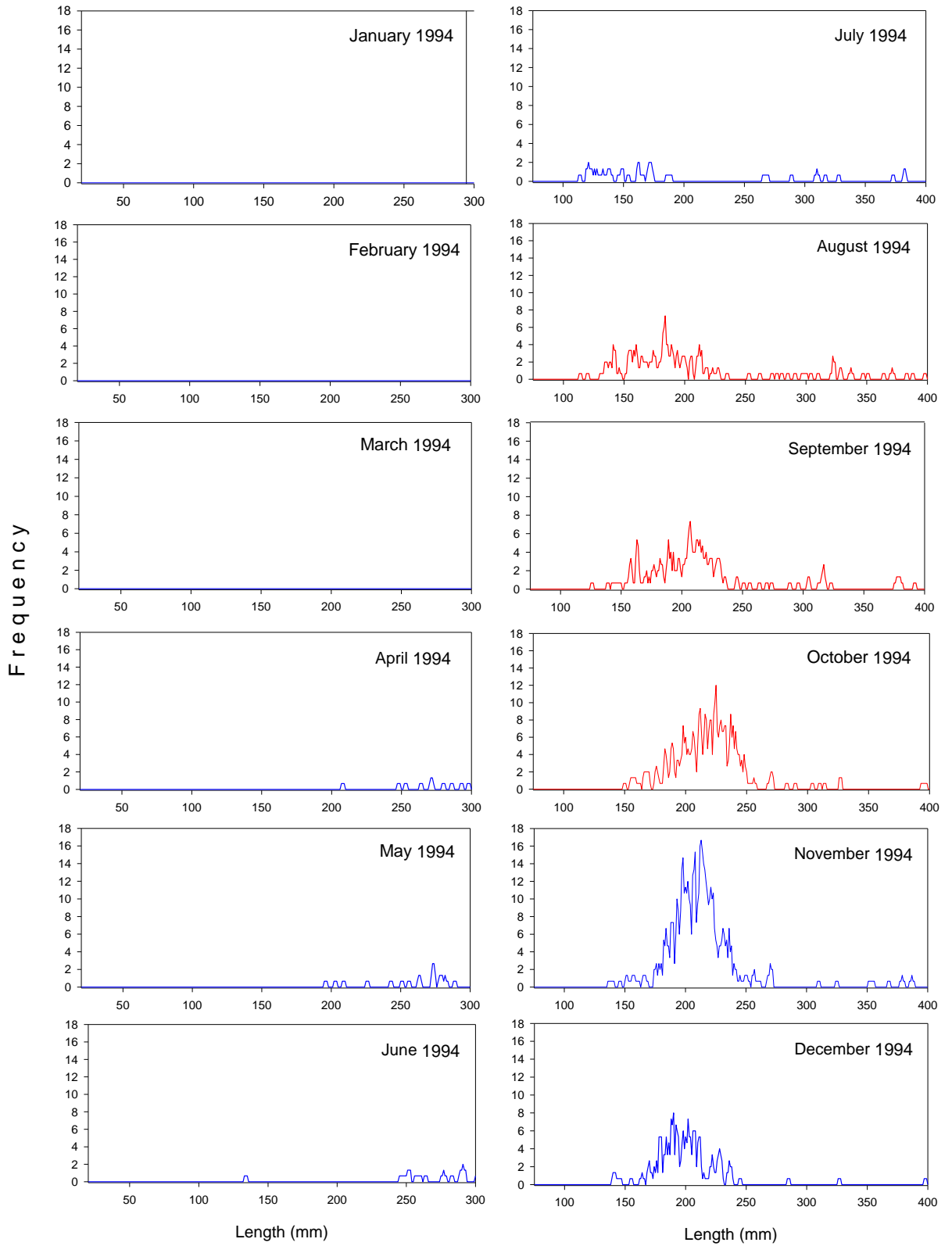
1995 Length Frequency
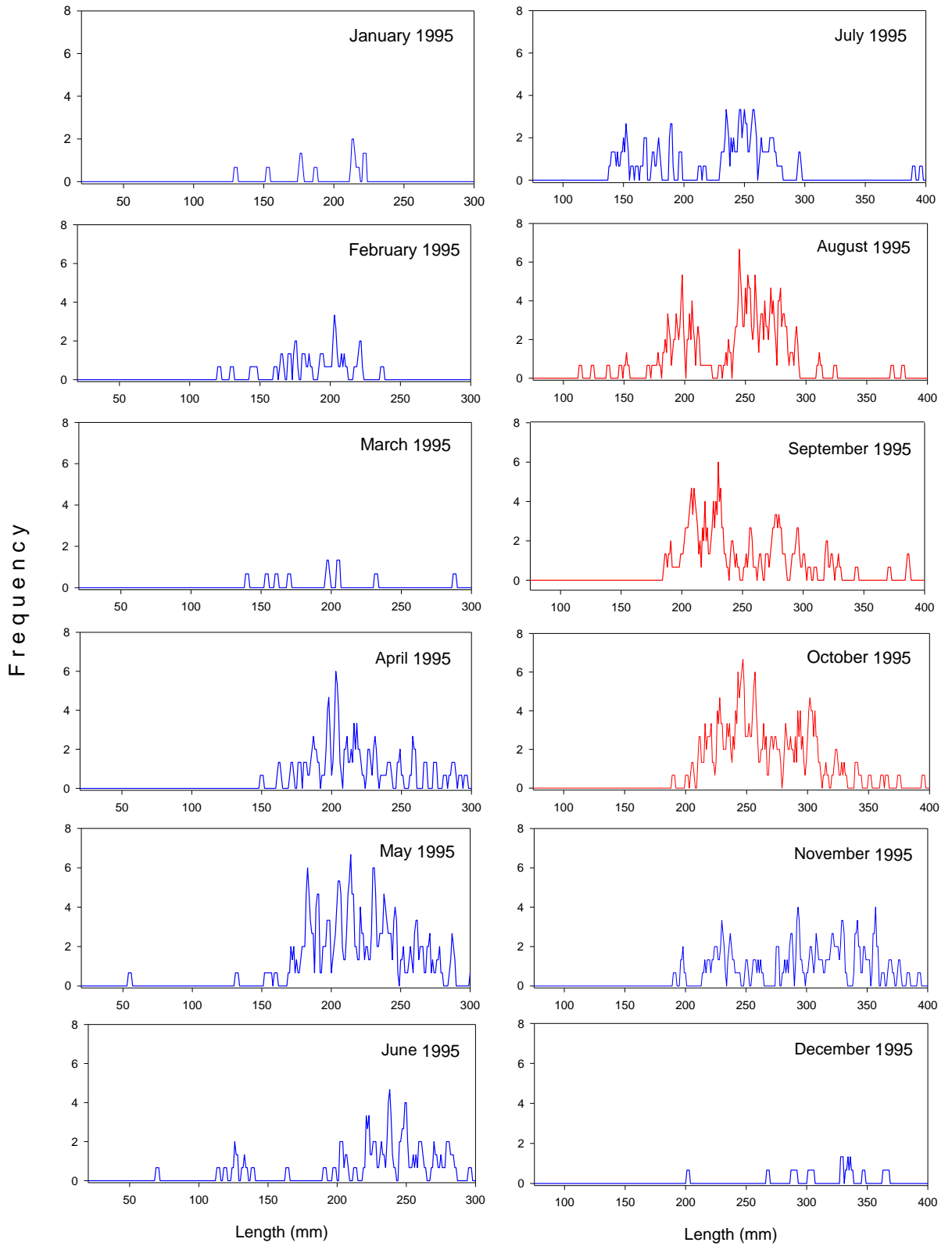
1996 Length Frequency

1997 Length Frequency

January 1997

February 1997

March 1997

April 1997

May 1997

June 1997

July 1997

August 1997

September 1997

October 1997

November 1997

December 1997
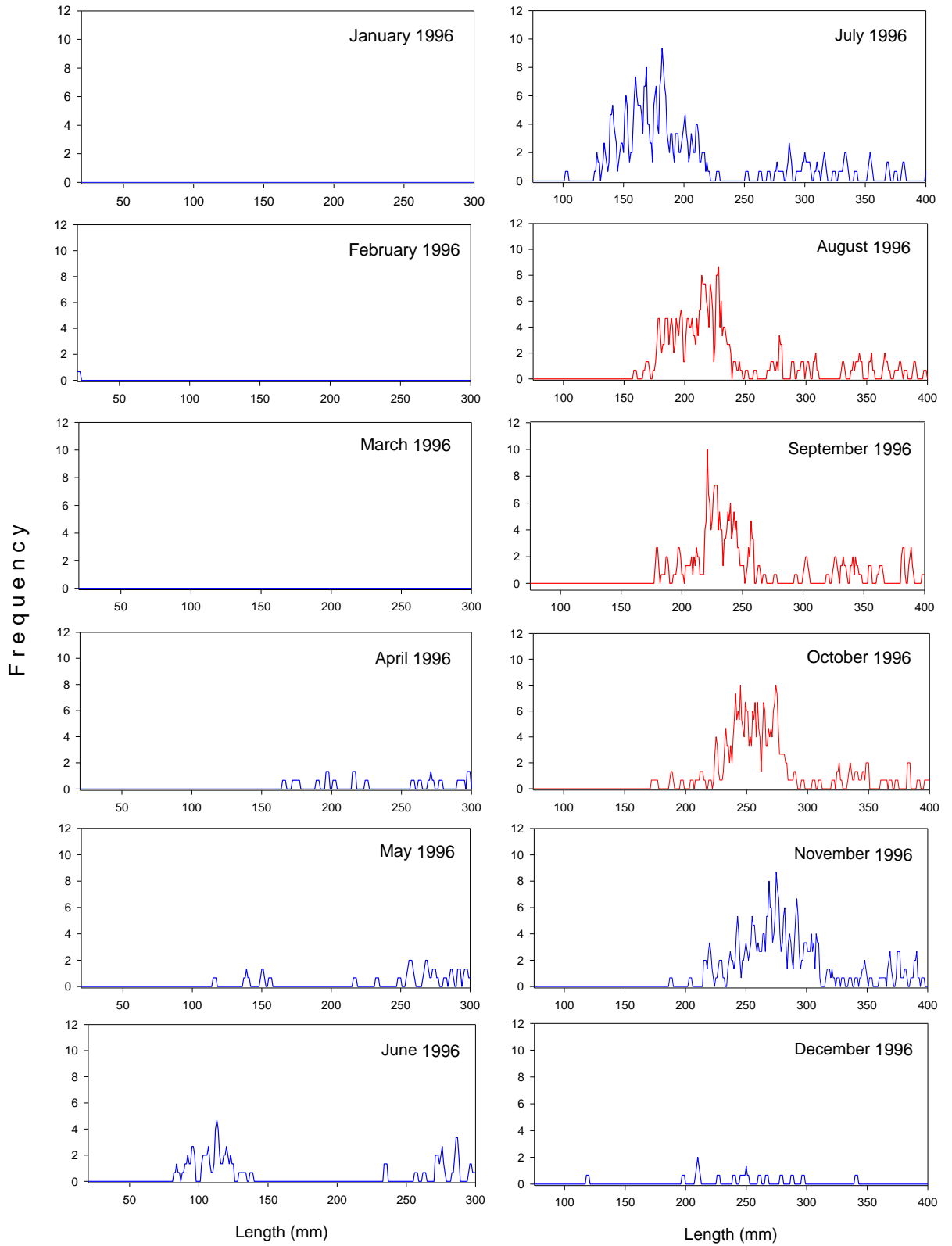
Frequency
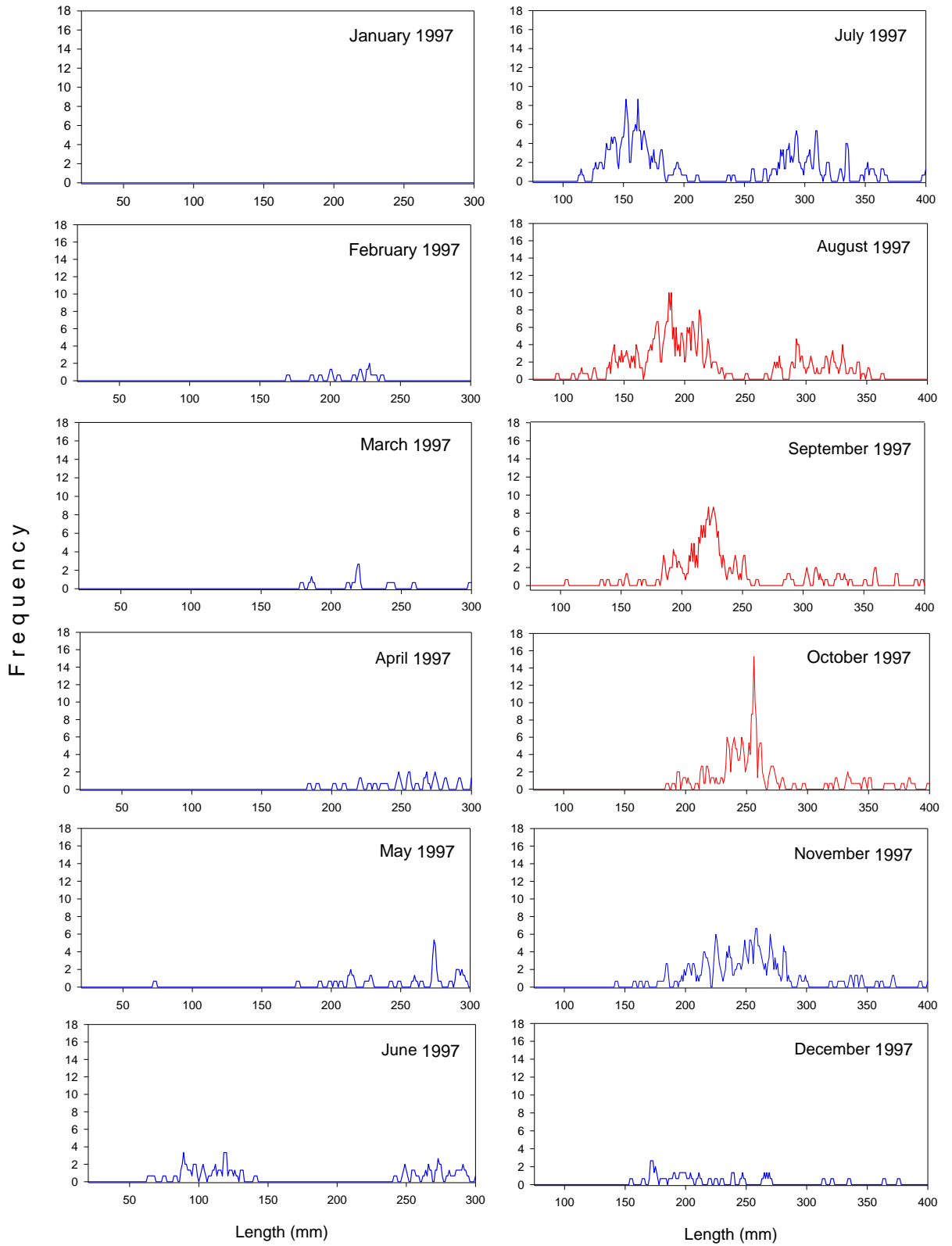
Length (mm)

Length (mm)

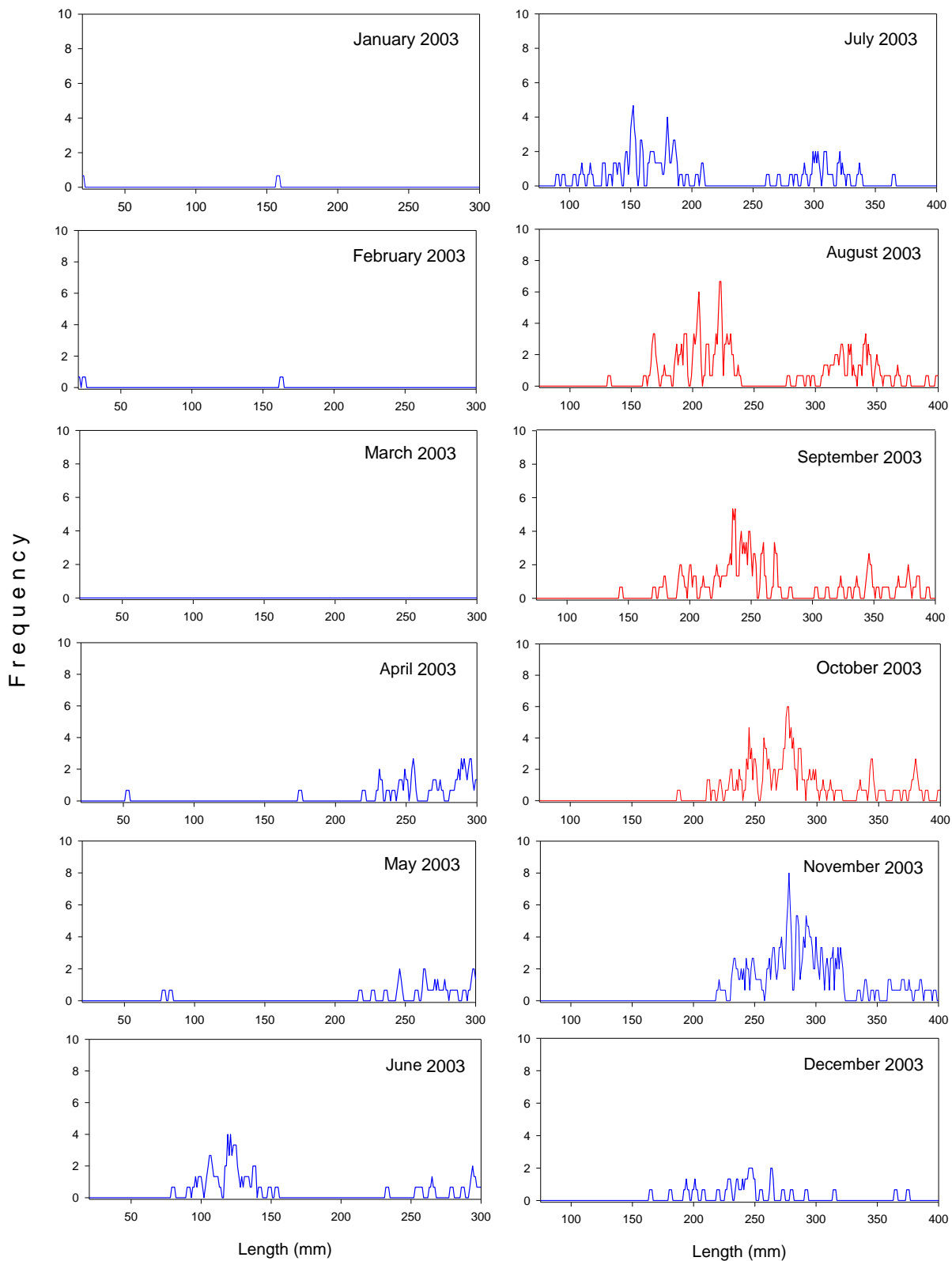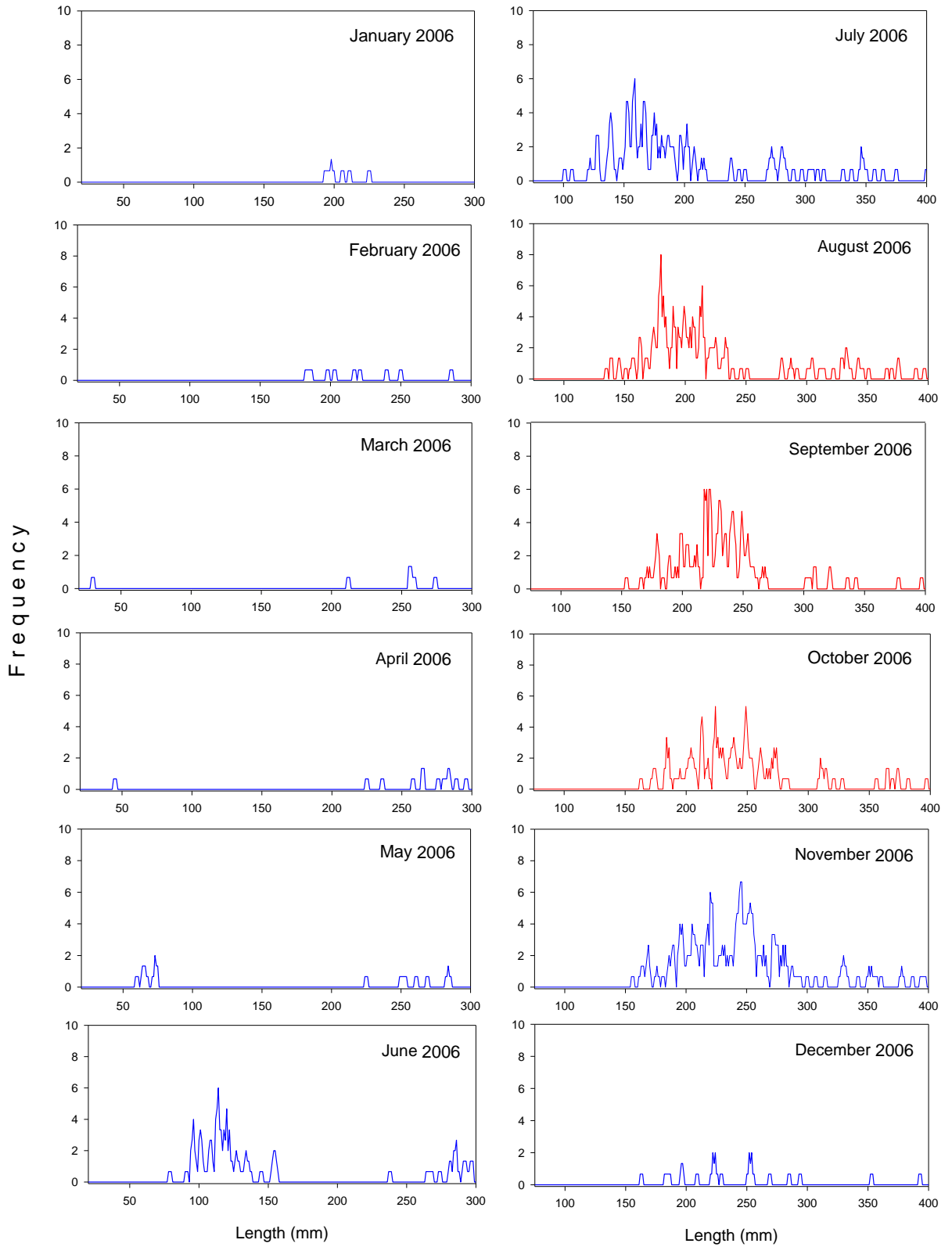# 1998 Length Frequency
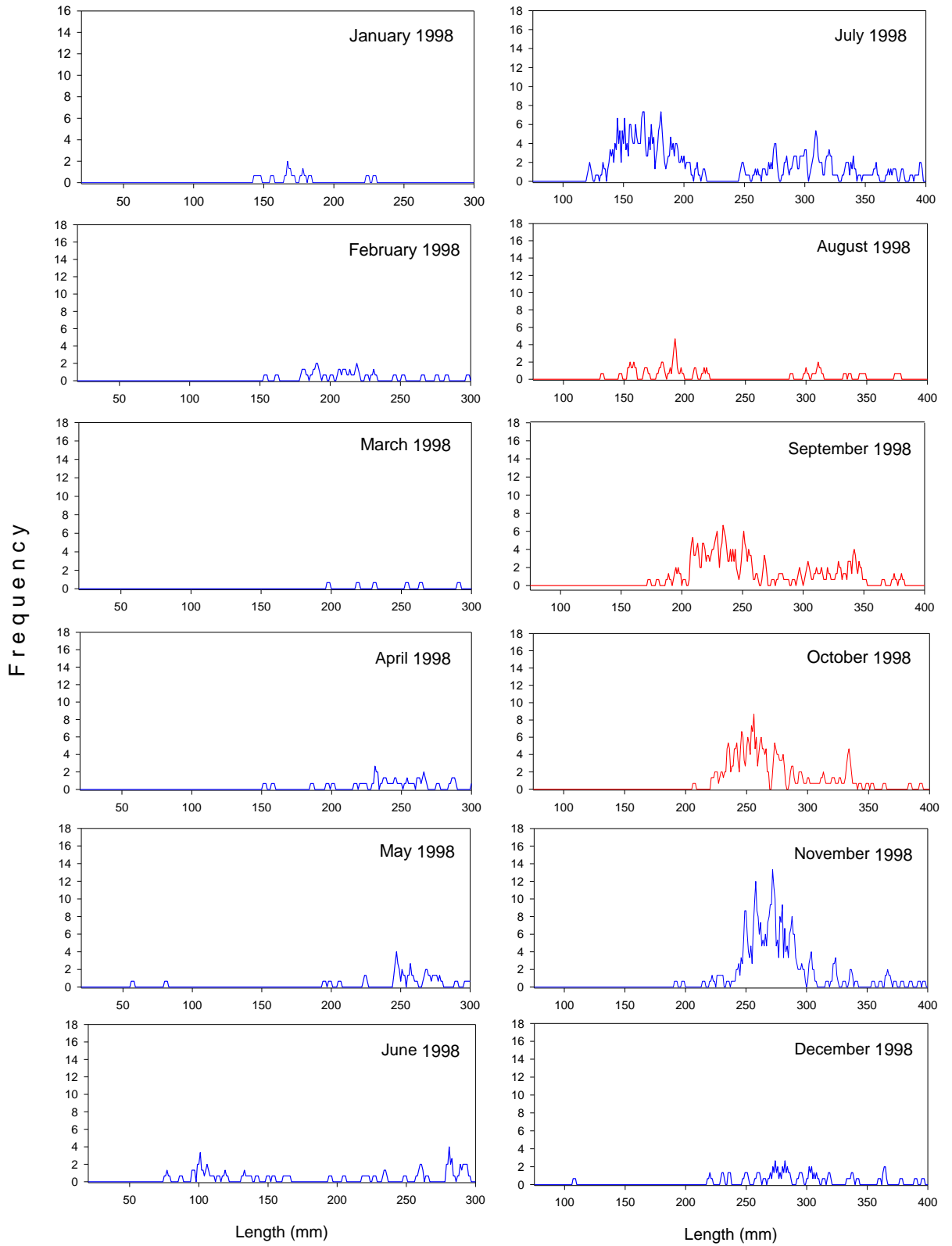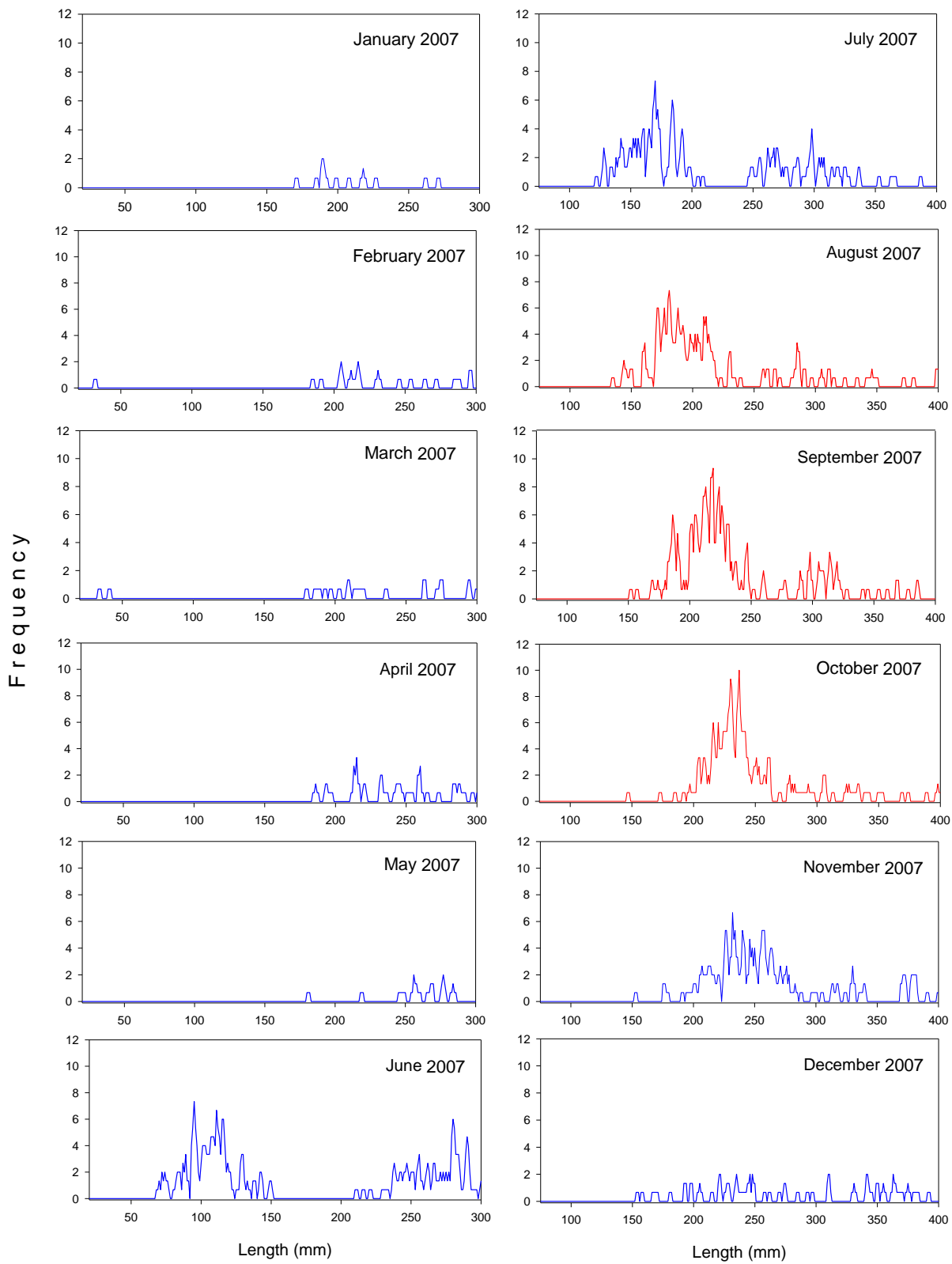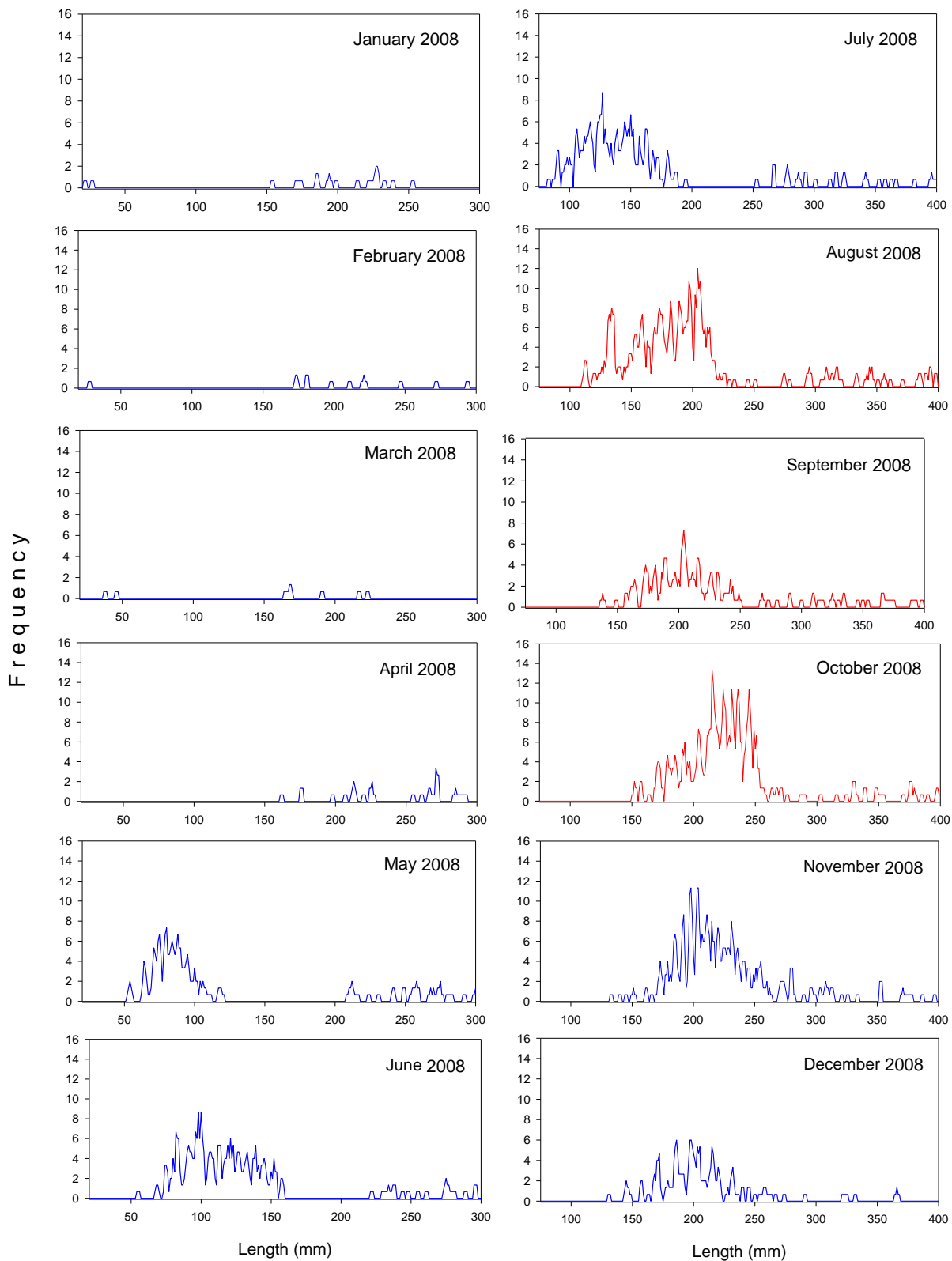
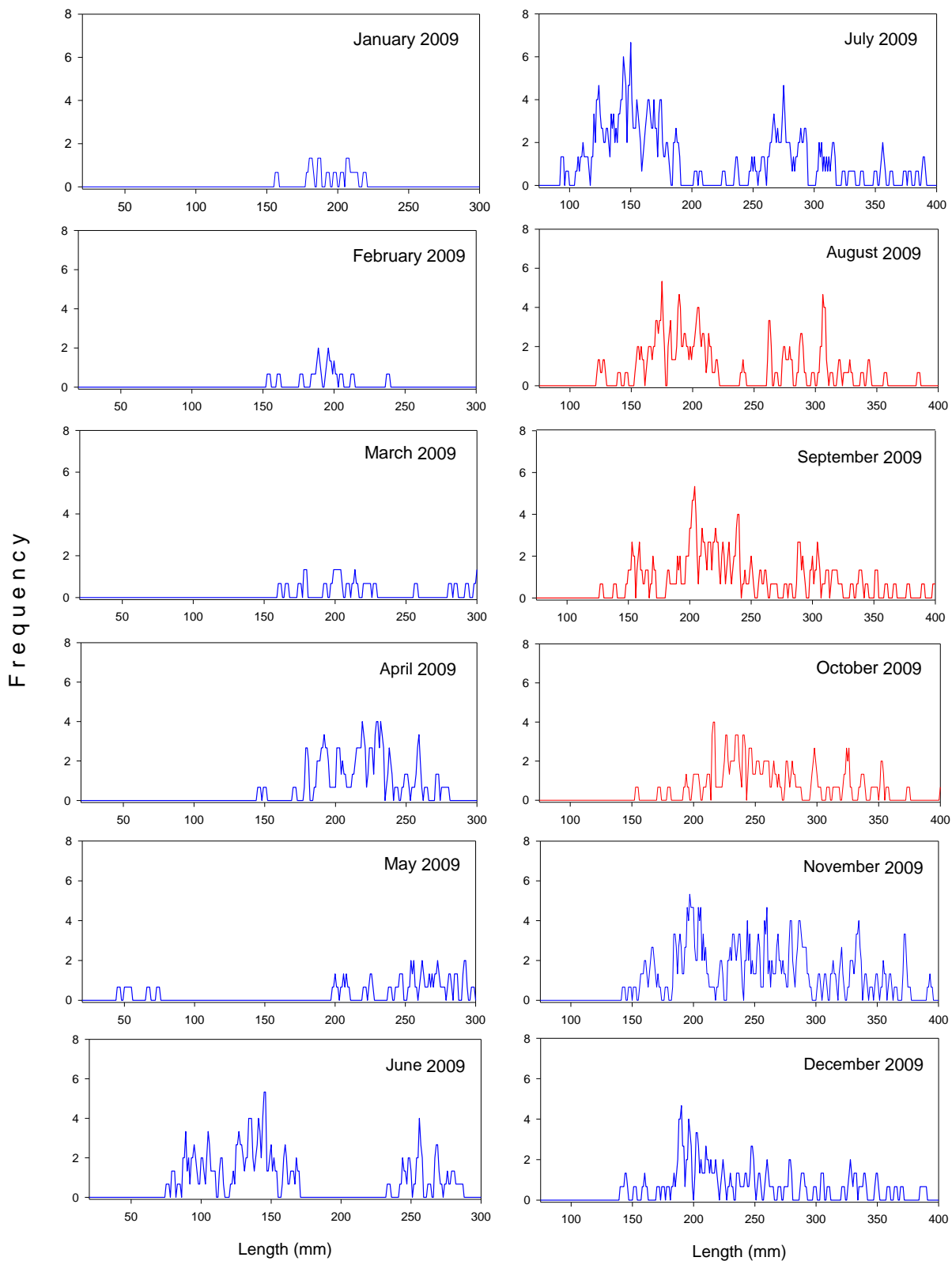# 1999 Length Frequency

2000 Length Frequency

2001 Length Frequency

January 2001

February 2001

March 2001

April 2001

May 2001

June 2001

July 2001

August 2001

September 2001

October 2001

November 2001

December 2001

Frequency

Length (mm)

Length (mm)

2002 Length Frequency

January 2002

February 2002

March 2002

April 2002

May 2002

June 2002

July 2002

August 2002

September 2002

October 2002

November 2002

December 2002

Length (mm)

Length (mm)

Frequency

2003 Length Frequency

January 2003

February 2003

March 2003

April 2003

May 2003

June 2003

July 2003

August 2003

September 2003

October 2003

November 2003

December 2003

Frequency

Length (mm)

Length (mm)

2004 Length Frequency

Frequency
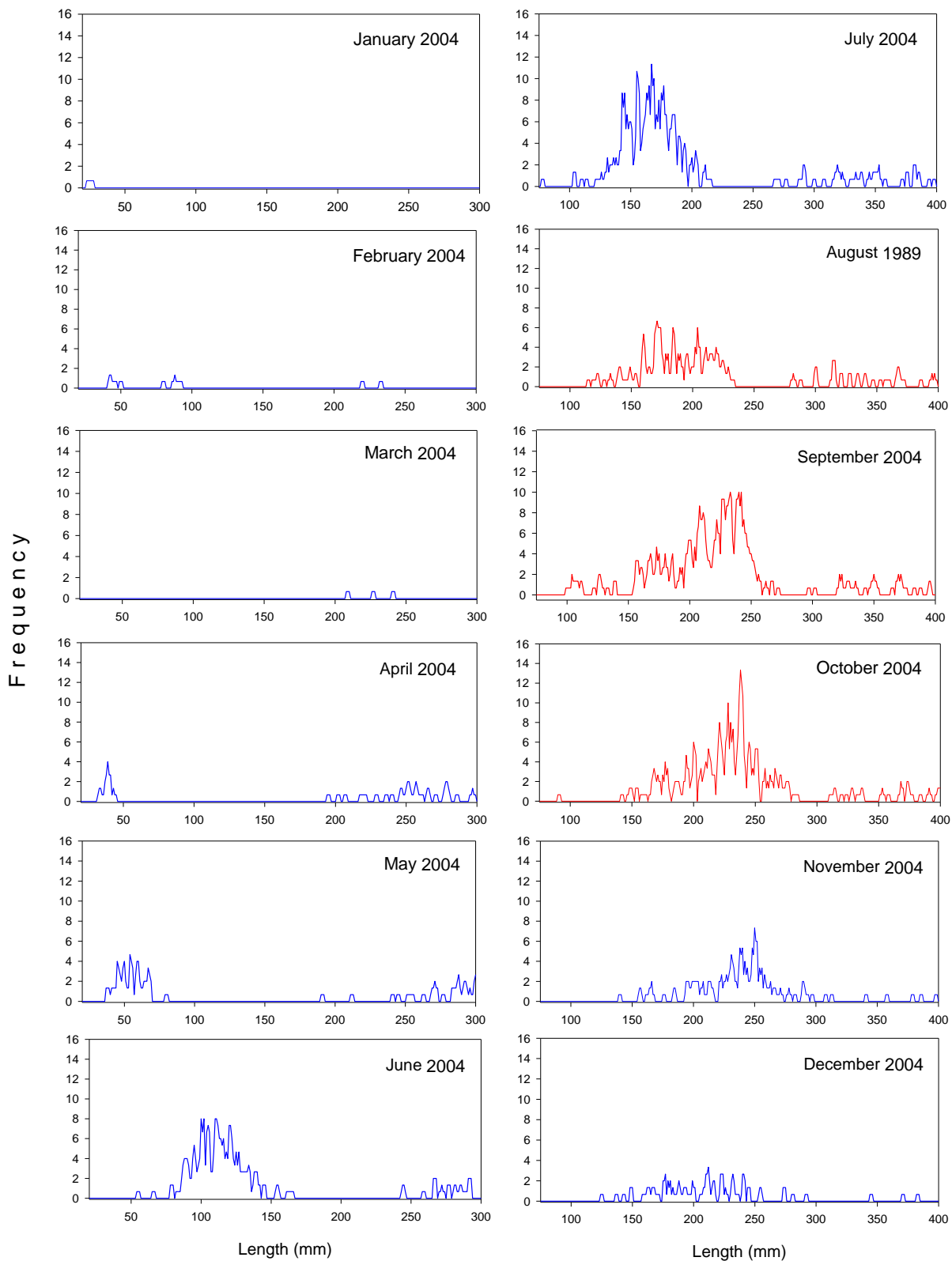
Length (mm)

2005 Length Frequency

Length (mm)
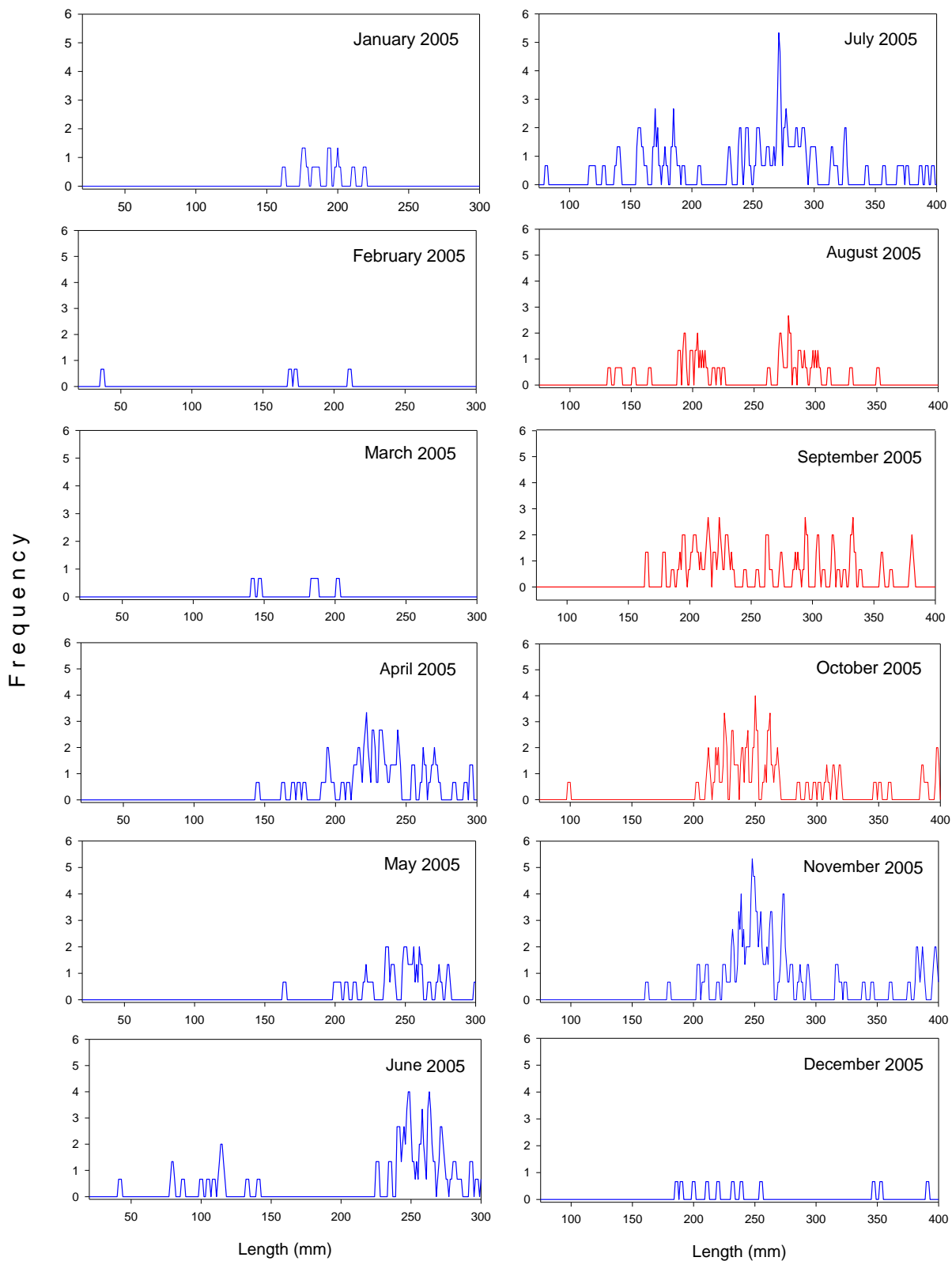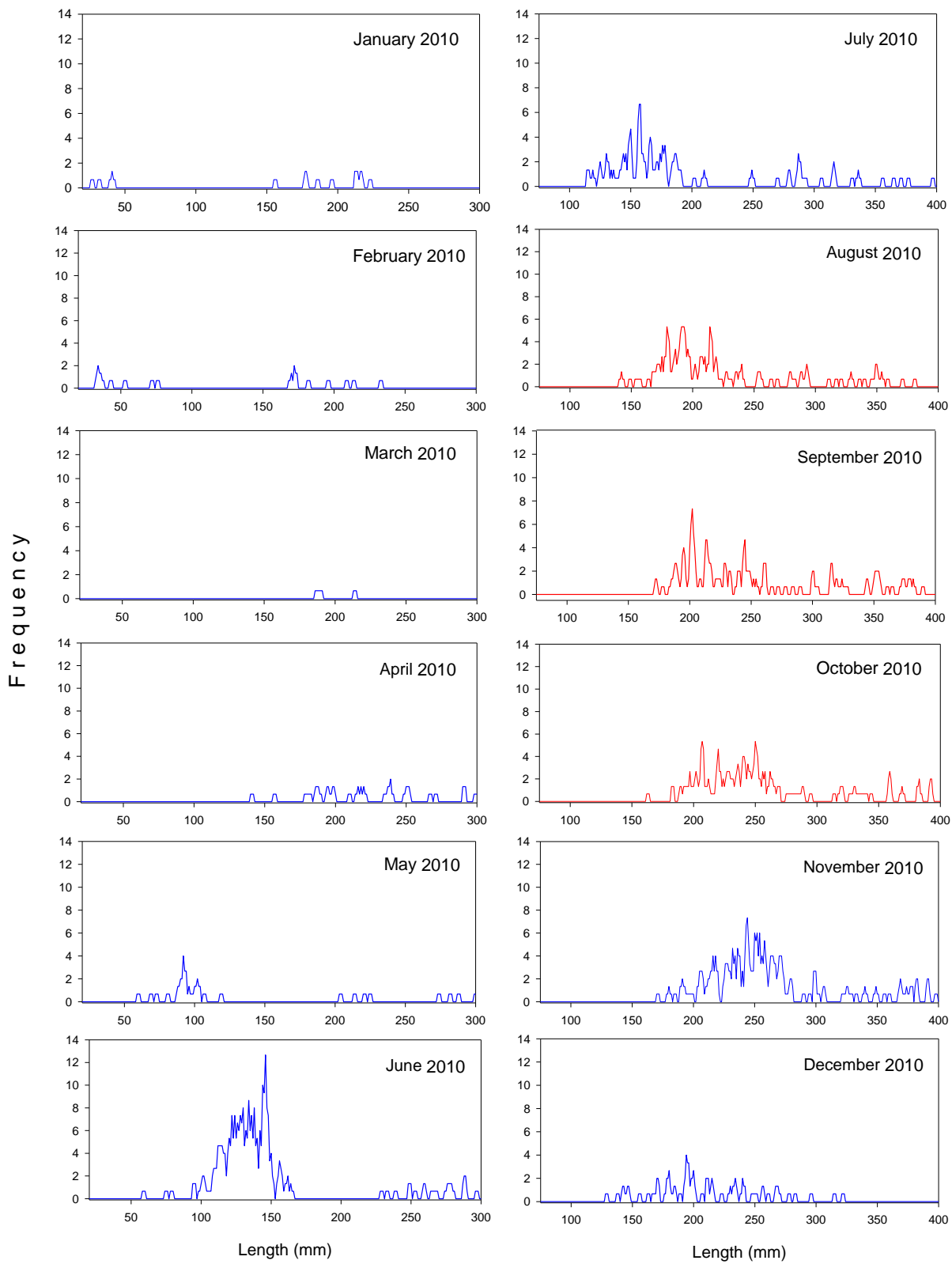
Frequency
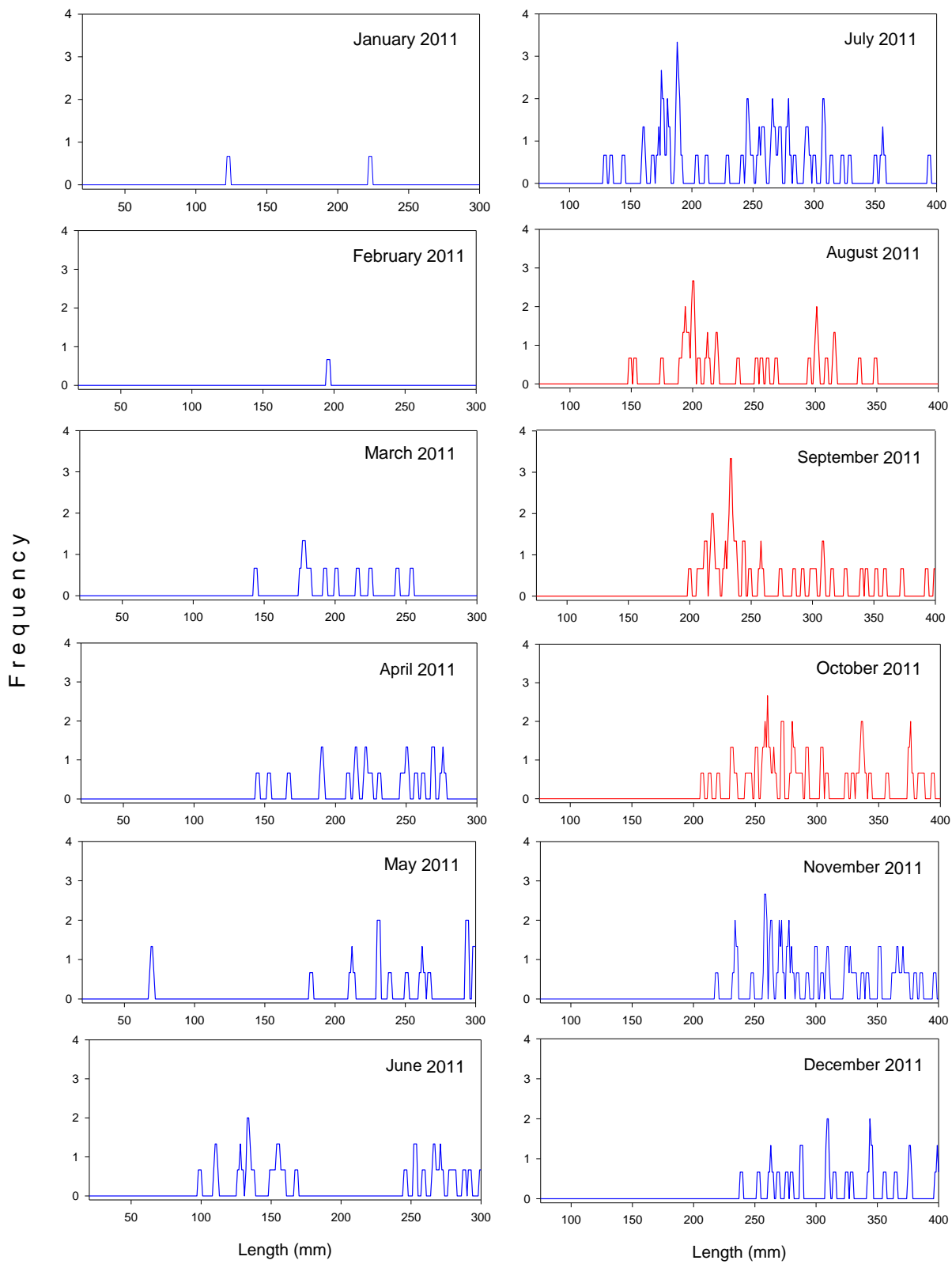
2006 Length Frequency

2007 Length Frequency

Frequency

Length (mm)

2008 Length Frequency

Frequency

Length (mm)

Length (mm)

2009 Length Frequency

Length (mm)

Length (mm)

Frequency

2010 Length Frequency
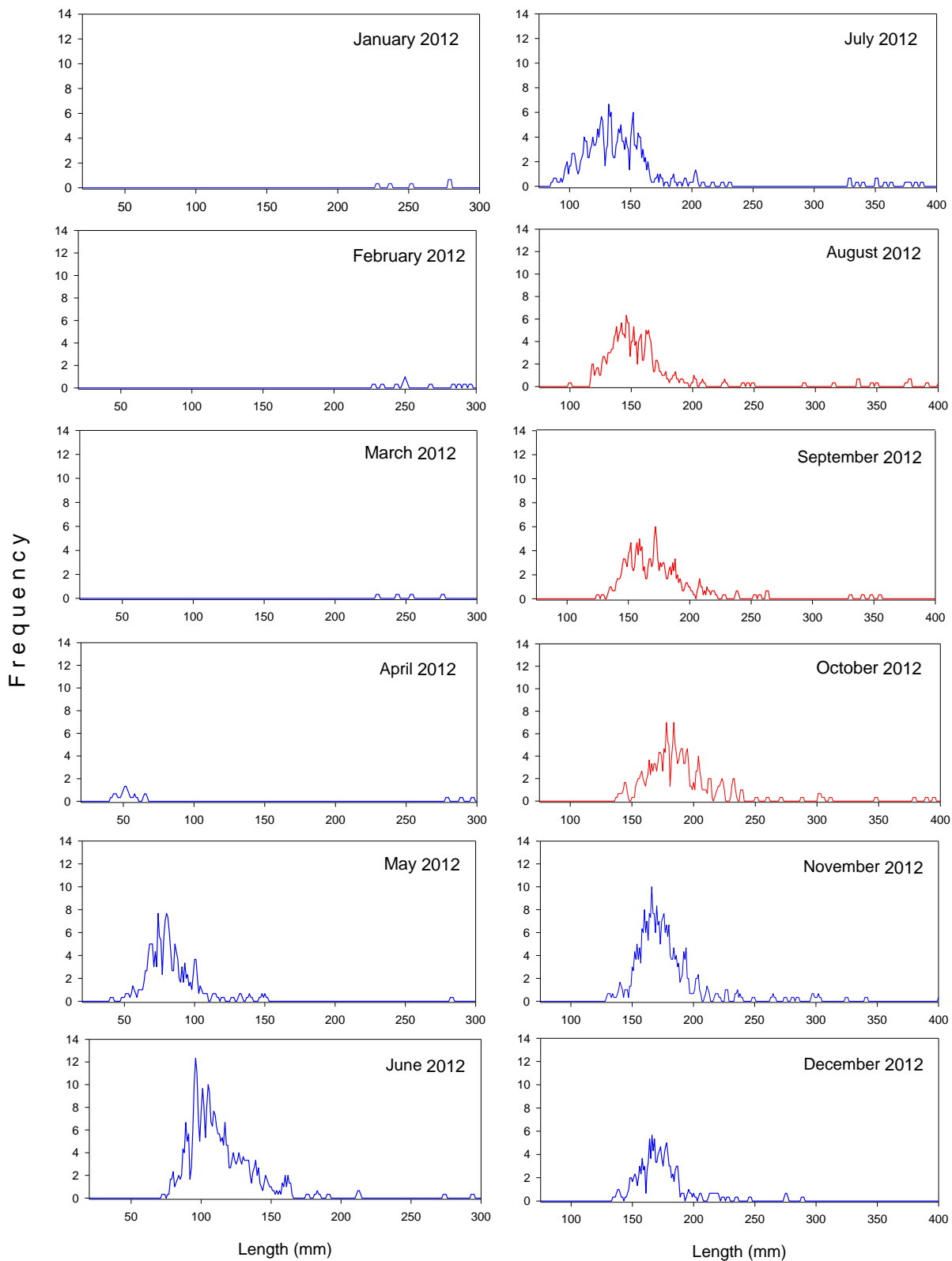
2011 Length Frequency

2012 Length Frequency

Frequency

Length (mm)

Length (mm)

VITA

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