Overwinter Survivorship and Relative Mortality of Young-of-the-Year Black Sea Bass (*Centropristis striata*) on the Northeast United States Continental Shelf Between 1967-2007

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Abstract of the Thesis

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As global ocean temperatures continue to increase, marine fauna are redistributing themselves to remain in preferred water temperatures. The Northwest Atlantic has experienced a number of species distribution shifts over the last few decades and black sea bass (*Centropristis striata*) is one of these species. Black sea bass are extending the northern extent of their range to include the southern Gulf of Maine where historically they have existed in very low abundance. The ability of black sea bass to expand their distribution is partially dependent upon the ability of the northern stock to survive winter. Specifically, the ability of young of the year (YOY) to survive their first winter is important to the success or failure of continued ranged expansion. In order to test the ability of YOY to survive winter a series of experiments were conducted to examine growth at low temperatures, lower thermal tolerance and overwintering ability. Results indicated that YOY black sea bass stopped growing at 6°C and weight loss began below 6°C at a range of salinities. In the acute thermal tolerance experiment exposure to temperatures below 5°C for nine days resulted in 11.5% mortality. Interestingly, mortality continued to occur even after the temperature increased slowly to 10°C. Continued mortality at temperatures above 5°C indicates that irreparable damage was likely endured by the fish at temperatures below 5°C. The overwintering experiment indicated that all fish will die when exposed to temperatures of 5°C and 3°C within 32 days. Fish held at 5°C, however, lived significantly longer than fish at 3°C. In addition, fish in 15 psu lived significantly longer than fish at 35 psu at both temperatures. Using survival analysis an accelerated failure time model was created to quantify the rate of mortality during the overwintering experiment. Within the model, temperature, salinity and their interaction were significant variables, but mass was not. Using the accelerated failure time model to estimate survivorship on the NE US continental shelf during winter, daily winter bottom temperature and bottom salinity hindcasts from the Regional Ocean Modelling System (ROMS) between 1967-2007 were used to force the survivorship model. Relative estimated survivorship on the shelf was compared to the relative abundance of YOY caught in the NMFS spring trawl surveys during the same period by visual inspection of maps and by correlation analysis. Although there were many years where the amount of suitable overwintering habitat and YOY abundance were high (and vice versa), there was no statistically significant correlation between suitable habitat and YOY abundance following spring. It is likely that other factors in addition to temperature and salinity during winter are affecting the relative abundance of YOY black sea bass in the spring trawl survey.

Dedication Page

I would like to dedicate this thesis to my wife, Charlotte, who has given me her unwavering support as I went back to school and throughout the entire process of conducting my experiments. She consistently encouraged me to keep working hard when courses were tough and was always willing to lend a hand in the lab on the weekends. I could not have done it without her support or help and I am forever grateful.

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Chapter 1: Overwinter mortality and growth rate of young-of-the-year black sea bass in relation to temperature, salinity and size

Introduction

Black sea bass, *Centropristis striata,* supports recreational and commercial fisheries throughout its range (Musick and Mercer 1977). They range from the Florida peninsula to Massachusetts with two stocks divided at Cape Hatteras (Musick and Mercer 1977, Bowen and Avise 1990). The northern and southern stock are genetically distinct (McCartney and Burton 2011, McCartney et al. 2013) and are assessed and managed separately. In the northern stock, seasonal temperature variability elicits a seasonal offshore and southward migration that is not observed in the southern stock (Able et al. 1996, Moser and Shepherd 2009). In the summer, both mature and immature adults are associated with structure in coastal waters of the Northeast US. The offshore migration begins in response to temperature and photoperiod and has been shown to occur when bottom temperatures are typically the warmest on the shelf (Fabrizio et al. 2013).

Young of the year (YOY) black sea bass can be found in bays and estuaries in the late summer to early fall. YOY black sea bass move out of estuaries in the fall and it is thought that they also move offshore like the adults. However, little is known about their distribution once they leave estuaries. They may be able to build energy reserves in coastal marine habitats while bottom temperature is still warm, but it is unknown where the majority of YOY black sea bass in the northern part of their range overwinter. The ability of YOY black sea bass at the northern extent of their range to survive winter depends on the timing and extent of their seasonal migration offshore to escape colder nearshore waters and their ability to survive cold water temperatures (Able et al. 1996).

Overwintering is an important source of mortality for many temperate marine fishes. For example, Hurst and Conover (2002), found that at low temperatures YOY striped bass (*Morone saxatilis*) have higher survivorship (87%-100%) at an intermediate salinity of 15 psu than at a salinity of 30 psu (0% - 65%). They also observed that the majority of mortality (61%) occurred when temperatures fell to 2°C and that mortality was unrelated to length or feeding. In an earlier study, Hurst and Conover (1998) found that recruitment of age-0 YOY striped bass to age-1 was significantly correlated to size, but the extent of overwintering mortality varied depending on the duration and severity of the winter. Furthermore, in a study of YOY Atlantic croaker (*Micropogonias undulatus*), overwinter survivorship was partially a function of size with smaller individuals living longer than larger individuals (Lankford Jr and Targett 2001). In the same study, survival was significantly higher at 7ºC (99% survival) than at 1ºC (0% survival) and at higher salinities. The authors concluded that winter severity plays an important role in overwinter survivorship and recruitment.

In a fresh water species, white crappy, winter severity, not size or feeding regiment, negatively correlated with overwinter survival (McCollum et al. 2003). Slightly less than half of the fish survived during severe winters compared to 97% during mild winters. During severe winters energy density was similar among live and dead fish leading the authors to conclude that osmoregulation dysfunction caused mortality at temperatures lower than 4°C rather than starvation. Similarly, white perch, *Morone americana*, was found to have osmoregulation difficulties at 2.5°C, but at 4°C starvation was considered the primary driver of mortality (Johnson and Evans 1996).

The relationship between winter mortality, size, temperature and salinity is not confined to fish. Bauer and Miller (2010) found in laboratory experiments that juvenile blue crabs (*Callinectes sapidus*) survived significantly longer at higher treatment temperatures (5°C) and that relatively larger crabs survived longer than smaller ones. Male and female crabs had similar survivorship at the low temperature (3°C) and 10 psu treatments. A study of the surf clam population on the NE US continental shelf found a decline in the population associated with episodic warming of bottom water rather than gradual warming (Narváez et al. 2015).

For ectotherms, the thermal tolerance range dictates growth by limiting the temperature range that efficient respiration can take place. Assimilated energy not devoted to respiration is portioned to growth, excrement and nitrogenous waste. Aerobic scope is fundamentally dictated by external water temperature, considered by Fry (1971) to be a “controlling” factor. A controlling factor can be considered a stimulus that affects the rate or pace of metabolism. Pörtner and Knust (2007) have labelled the link between thermal tolerance and aerobic scope as the oxygen and capacity-limited thermal tolerance. At extreme temperatures oxygen supply is unable to meet demand because the circulatory and ventilation systems are not physiologically capable. When this occurs the animal will attempt to compensate with anaerobic metabolism or other mechanisms to protect against cellular degradation (Pörtner and Knust 2007). Some temperate species have the ability to expand their thermal tolerance windows through acclimation thereby increasing aerobic scope (Pörtner and Knust 2007).

A species’ specific thermal range varies with the life history. In early life stages, thermal windows are narrow, but in general they widen in the juvenile/early adult stage and become narrow again in the adult stages (Portner and Peck 2010). This indicates that the range of temperatures that fish allocate energy towards growth varies throughout life with the largest thermal window for growth typically in the juvenile stages. However, the extent that a specific species is able to grow depends on the duration that it is exposed to its thermal window. Species located in temperate regions, such as the Northeast US, experience a wide range of temperatures between summer and winter, and therefore, varying amounts of time in the thermal window that promotes growth. For many species in this region, winter months are associated with little or no growth, weight loss and size-selective mortality (Post and Evans 1989, Sogard 1997). In a study of YOY cunner, tautog, black sea bass and smallmouth flounder winter temperatures were found to slow growth to the extent that any growth that was measured was near measurement error (Hales and Able 2001). Weight loss due to the use of lipid reserves was found in YOY striped bass during laboratory overwintering experiments, but the authors concluded that weight loss and subsequent starvation did not account for the size-dependent mortality observed because live specimens collected from the wild actually had lower energy levels than the replicates that died during the experiment (Hurst et al. 2000). The authors suggest that there are possible confounding stressors such as osmoregulation failure.

Fish are rarely in water that is isosmotic with their bodies and marine fish must constantly drink water and excrete salts in order to maintain homeostasis. The ability of fishes to maintain homeostasis is reliant upon active ion pumping, a temperature dependent process, and passive ion diffusion, a temperature independent process (Hochachka 1988). When temperatures approach a fishes' lower thermal tolerance, usually near 0°C in temperate species, active ion pumping is hindered and homeostasis cannot be maintained resulting in ion concentrations in the blood plasma similar to the surrounding water that eventually causes death (Belkovskiy et al. 1991, Hurst 2007). Reduced activity of Na$_+$ K$^-$ATPase at low temperatures also affects the central nervous system by reducing synapse transmissions and effectively impeding nerve communication to carry out essential bodily functions (Cossins and Bowler 1987).

The NW Atlantic is one of the fastest warming regions on earth (Friedland and Hare 2007, Lozier et al. 2008), and black sea bass has seemingly responded by expanding their geographic range to the extent that they are now commonly found in the southern Gulf of Maine during spring and summer where they had only been found occasionally in the past (Bigelow and Schroeder 1953). One potential mechanism for this range expansion is that overwintering mortality is reduced as temperatures on the Northeast shelf have increased especially over the last decade. Black sea bass, the northernmost grouper (Family Serranidae) species on the east coast of the United States, is considered a warm water species in the Northeast US. They emigrate to warmer waters at the northern extent of their range during winter to stay within their preferred thermal range (Steimle 1999). The extent to which they need to migrate to escape their lower thermal tolerance will decrease as water temperatures in the region increase. As a result, with climatic warming black sea bass will be able to establish their center of biomass further and further north as water temperatures increases which will require novel management practices that can adapt to this change in the population distribution. As one of the most vulnerable periods in their life history, the ability to survive their first winter will likely be critical to recruitment dynamics and the distribution of the population.

In this study, I quantified growth rates at low temperatures and then conducted an acute exposure experiment to identify the lower thermal tolerance to be examined in overwintering experiments. An overwintering experiment was then performed to create an accelerated failure time model that was used to estimate relative mortality on the NE US continental shelf. Specifically, my hypotheses for these three sets of experiments were:

Growth Experiment:

- Higher temperatures and intermediate salinities will provide the fastest growth rates.

Acute Exposure Experiment:

- Mortality will increase once temperatures decline below 4°C, but once temperature increases again, mortality will cease.

Overwintering Survivorship and Growth Experiment:

- Mortality will be higher at colder temperatures and lower salinity treatments
- Survival will be size dependent with larger individuals surviving for longer periods of time than smaller individuals

Materials & Methods

Growth Experiments

YOY black sea bass were collected from Oak Beach and the Peconic Bays in Long Island New York between August and October 2013. Fish from Peconic Bays were captured during the NY DEC trawl survey. Fish were transferred to Flax Pond Laboratory in East Setauket, NY where they were held at ~20°C and a salinity of 29 in four 1,100-L recirculating tanks prior to the start of the experiment. Once all the fish were collected salinity was increased by ~1 psu day^{-1} to 34 psu in two of the tanks while the other two tanks remained at 29. The salinities were held at these values while the temperatures in each tank were reduced by ~1°C day^{-1} until the first experimental temperature (12°C) was reached. When the desired temperature was achieved, the fish were randomly selected from the holding tanks, weighed, measured (TL) and placed into an individual container (~4L). The individual containers were placed in sea tables (~650L/table) (Figure 1) acting as a water bath with the corresponding temperature and salinity treatment. Each container had a continuous flow (~1L min^{-1}) of water provided by a spigot located directly above the bucket. The fish were allowed to acclimate for one week prior to the start of the next phase of the experiment. In the next phase, the temperature was decreased again by ~1°C day^{-1}

while maintaining the same salinities. Until the next desired temperature (8°C) was achieved. For the 6°C treatments, the same procedures and experimental design was used except that the fish were held in a temperature controlled-temperature room. The fish were held at the experimental temperatures for 90 days in each treatment.

Photoperiod was adjusted to reflect winter light levels (~9 h light/15 h dark). Fish were fed finfish starter pellets ad libitum every day throughout the course of the experiment. Any leftover food and feces were siphoned from the individual containers once daily. Ammonium, nitrite and nitrate levels were monitored daily and water changes were done once per week. Each fish was provided shelter in the form of a 3.5” x 1.5” (length x diameter) PVC pipe. At the end of experiment each fish was measured (TL) and weighed.

To determine the growth rates of the fish in each treatment specific growth rate (SGR) was calculated. SGR (% mass day^{-1}) was used to estimate the mean percent mass gained or lost in each treatment. SGR was calculated from the instantaneous growth rate (G) as: SGR = (e^G - 1) x 100, where G = (ln final mass – ln initial mass) x day^{-1}. Differences in SGR were analyzed using a two-way Analysis of Variance (ANOVA). Significant differences among temperature and salinity treatments and their interaction were determined using Tukey’s multiple comparison test (α=0.05).

Acute Exposure Experiment

To test the lower thermal tolerance of YOY black sea bass, twenty-six fish acclimated to 10°C and a salinity of 29 psu had temperature reduced by ~1° day^{-1} until 3°C – 4°C was reached. The fish were held at this temperature range for 9 days. The temperature was then increased by approximately 1°C day^{-1} to 10°C. Photoperiod was (~9 h light/15 h dark). Mortality was checked once daily. Dead fish were measured and weighed and the date of mortality recorded. The experiment was conducted for 33 days. Fish were fed ad libitum once daily and any uneaten food and feces were siphoned once daily. Ammonium, nitrite and nitrate levels were monitored daily and water changes were done once per week. Identical to the growth experiment, each fish was held in an individual container with a spigot providing flow (~1L min^{-1}) to each container. Cumulative mortality was calculated as a percentage before the one week exposure period, during the nine day exposure period and after the exposure period.

Overwintering survivorship and growth

Similar to the growth and acute mortality experiments, fish were collected from Oak Beach in Great South Bay and Peconic Bays between September and November 2014 and then transported and held in holding tanks at Flax Pond Laboratory in East Setauket, NY. The holding system consisted of four 1,100 L tanks divided into two recirculating systems with in-line chillers. While in the holding tanks all fish were held at the same temperature (~20°C) and a salinity of 29 psu. Salinity was adjusted to experimental treatment values 35 psu and 15 psu by ~1 day^{-1} after enough replicates were collected (n = 144). To achieve experimental temperatures (3°C and 5°C), water was decreased by ~1°C day^{-1}. Once the desired temperature was reached, fish (n=36) were randomly selected and transferred to an individual container (~3L) within a water bath (650L sea table) after being measured (TL) and weighed. Each replicate received continuous flow (~0.5L/min) into the container via a spigot located directly above the container. Each container was checked once daily for mortality. Dead fish were measured and weighed. Fish were fed fin-fish starter pellets ad libitum once daily. Uneaten food and feces were removed once daily. Photoperiod was adjusted to reflect winter hours (~9 h light/15 h dark).

Survival analysis was conducted to quantify mortality in each treatment using the *survival* package in RStudio version 0.99.335 (Terry Therneau 2015). Survival analysis requires time until event and status for each replicate. In this experiment, time until event was the time until death measured in days from the first day a fish was placed in a container and status was a binary variable indicating whether the mortality event occurred or was censored. If a replicate does not die or the time of a mortality event is unknown it is considered censored. In R, this is referred to as the survival object (Crawley 2012). An important attribute of survival analysis is that it allows the user to pick distributions which do not have constant variance or normal errors since time until death usually changes the longer the subject is exposed to the treatment (Crawley 2012). Survival analysis uses the time until death to estimate a survival function S(t) and a hazard function h(t). The survival function describes probability of survival while the hazard function estimates the instantaneous risk of mortality (Crawley 2012). The graphical output of a survival analysis comes in the form of a Kaplan-Meier curve which consists of two pieces of information: the number of deaths and the number of survivors at each point and is called with the survfit function in R (Crawley 2012).

To determine if survival among the treatments was the same a log-ranked test (Harrington and Fleming 1982) using the R function survdiff was used ($\alpha=0.05$). In the survdiff function the argument rho can either be 0 or 1. A value of $\rho = 0$ returns the Mantel-Haenszel test which accounts for large amounts of censoring and gives equal weight to an event regardless of when it occurs. A value of rho = 1 returns the Wilcoxon test which gives more weight to early events and when little censoring is observed. Censoring is when the exact date of event is unknown or when the subject survives to the end of the experiment without the event occurring.

To test whether initial mass, salinity and/or temperature had a significant effect on overwintering survival an accelerated failure time model was fit to the data. An accelerated failure time model was chosen over a proportional hazard model because the accelerated failure time model allows estimates to be made past the last observation (Crawley 2012). In the model, the predictor variables (mass, salinity and temperature) were treated as continuous variables (Hosmer and Lemeshow 1999). To determine the most parsimonious model, backward elimination was used starting with all effects and interactions. The model was concurrently fit with all available distributions (Weibull, logistic, log-logistic, extreme, exponential and Rayleigh) to determine the shape of the mortality curves. The best model was chosen by using the Akaike's information criterion (AIC) statistic. The best performing model was verified by graphing observed versus predicted mortality to visualize how well the model fit to observed data.

In addition to quantifying mortality during the overwintering experiment, specific growth rates were also estimated for each fish using the same methods as the growth experiment. Differences in SGR were analyzed using a two-way Analysis of Variance (ANOVA). Significant differences among temperature and salinity treatments and their interaction were determined using Tukey's multiple comparison test (α=0.05).

Results

Growth Experiments

Growth experiments were conducted at 6°, 8° and 12°C and subsequent growth during the overwintering experiments at temperatures of 3°C and 5°C. Experiments were conducted at different times and at different salinities. As a result, the two groups of treatments were analyzed separately.

In the growth experiment, temperature, salinity and their interaction significantly affected growth. (Table 1, Figure 2). Growth of YOY black sea bass was significantly higher for both the 12°C treatments compared to 8°C and 6°C treatments ($p < 0.0001$). Growth at 12°C was significantly lower at 29 psu compared to 34 psu ($p < 0.001$). This pattern of growth was not observed in the 8°C and 6°C treatments where there was no difference in growth across salinity treatments ($p = 0.5$ and $p = 0.6$, respectively). Weight loss (SGR = -0.042 ± 0.056, mean ± SD) was observed for the 6°C and 34 psu treatment but not observed at higher temperatures.

In the overwintering experiment, temperature, salinity and their interaction were again significant. Growth at 5°C was significantly different between salinity treatments with -0.212 ± 0.075 and -0.880 ± 0.149 for the low and high salinity treatments, respectively ($p < 0.0005$). No significant difference in growth was observed in the 3°C treatments (-1.736 ± 0.241 and -1.138 ± 0.183) ($p < 0.48$). Fish at the 12°, 8° and 6°C were observed consistently feeding during the course of the experiment, but replicates in the 5°C and 3°C were never observed feeding.

Acute Exposure Experiment

During the course of the experiment (33 days) 13 of the 26 fish died which accounted for 50% mortality (Figure 3). Fish experienced 100% survival while the temperature was decreased from 10°C to 3–4°C during an 11 day period. Three fish (11.5%) suffered mortality after 9 days at the acute temperature range. However, mortality of an additional ten fish (38.5%) continued even as the temperature increased gradually to 10°C.

Overwintering Experiment

Higher survivorship was observed in both the low salinity treatments compared to the high salinity treatments. Maximum survival (32 days) was observed at the 5°C and 15 psu. Survival at 5°C and 15 psu was 100% for seven days and decreased steadily for the remainder of the experiment. Mortality in the 5°C and 35 psu treatment was more abrupt compared to the lower salinity treatment. Median survivorship was observed at day 19 and 13 for the 5°C, low and high salinity treatments, respectively. Replicates in the low temperature (3°C) and 15 psu treatment had maximum survivorship of 7 days and an average of 4.5 days. Fish exposed to 3°C and 35 psu suffered acute mortality, surviving a maximum of 3 days and an average of 1.36 days. No censoring was observed in any of the treatments over the course of the experiment. The accelerated failure model indicated that temperature, salinity and their interaction significantly affected the mortality rate of YOY black sea bass (Table 4). Initial mass was not statistically significant in any of the model iterations, so it was removed from the final model. The survdiff function indicated that survivorship among each treatment was significantly different ($p < 0.0001$). The Weibull distribution that included temperature, salinity and their interaction had the lowest AIC value so it was selected as the best model (Table 5). The probability of survivorship [S(t)] at time *t* was:

$$\mathrm{S}(t, \mathrm{x}, \beta, \lambda) = \exp\{-\mathrm{t}^{\lambda} * \exp[(-\lambda)(1.078 + 0.448(temperature) - 0.112\,(salinity) + 0.018\,(temperature * salinity))]\}$$

where t is number of days less than 6°C and λ is the shape parameter. Predicted values using the Weibull model visually fit well to the observed data (Figure 5). Predicted survival was highest in the 5°C and 15 psu treatment followed by the 5°C and 35 psu (Figure 5). Predicted survivorship was higher between day 1 and day 2 at 3°C and 15 psu.

Temperature and salinity were relatively constant throughout the experiment (Table 3). However, a cold room malfunction in the 3°C and 35 psu treatment caused the temperature to spike between days two and three. Since 85% (n = 30) of the fish died by day three the remaining fish (n=6) were not included in the survival analysis. All 6 fish eventually died within 13 days even though the temperature increased slightly and then decreased again. The removal of these replicates did change which distribution was chosen, but not the variables (salinity, temperature and their interaction) that were included in the final model. Prior to death, fish were observed lying down on their lateral side or swimming erratically.

Discussion

Results from the three experiments indicate that YOY black sea bass stop growing at 6°C, begin losing weight below 6°C and that the lower lethal thermal tolerance is near 3-4°C. Fish exposed to 5°C will survive a maximum of 32 days at 15 psu and a minimum but even less (~20 days) at 35 psu. At 3°C YOY black sea bass suffered 100% mortality within 7 days. At low temperatures it was the combined effects of temperature and salinity that affected the rate of mortality. It is important to point out that fish at 3°C and to a lesser extent 5°C showed symptoms of reduced nervous system functionality indicating damage to the nervous system and likely other tissues.

Size was not a statistically significant factor in determining the rate of survival. These findings are supported by Hales and Able (2001) who also observed that size was not significant to determining survivorship in overwintering YOY black sea bass. In one overwintering experiment and three subsequent experiments testing the effects of temperature-rate reduction and salinity on survivorship, Hurst and Conover (2002) also found that size (length) and the rate of temperature decline were not significant in determining survivorship of YOY striped bass. The most significant factor determining survivorship was salinity leading the authors to conclude that suitable overwintering habitat in the Hudson River estuary is dictated more by salinity than temperature.

Size-dependent mortality is not always an insignificant factor determining mortality rates. Other studies have shown size to be an important predictor of winter survival. Lankford and Targett (2001) observed that overwintering YOY Atlantic croaker exhibit size-dependent mortality resulting in smaller fish living significantly longer than larger fish. The disparity of survivorship between sizes was attributed to exposure to acute temperatures (1°C, 3°C and 5°C) and low salinity values between 2 psu and 10 psu. The croaker suffered significantly less mortality at 7°C and 26 psu suggesting that winter severity and salinity distributions within overwintering estuaries are critical to YOY Atlantic croaker. Size dependent mortality often results in smaller fish dying before larger fish because energy reserves of smaller fish are depleted more quickly (Sogard 1997).

(Post and Evans 1989) observed weight loss between the fed and unfed YOY yellow perch, a fresh water species, but only the unfed treatments suffered mortality with smaller individuals dying before larger ones. This suggests starvation and not exposure to acute lower thermal tolerance as the cause of death. Overwintering blue crabs have also been observed to exhibit size-selective mortality. In a laboratory experiment conducted by Bauer and Miller (2010), carapace length along with temperature and salinity positively correlated with survivorship. At the temperatures (3°C and 5°C) and salinities (15 and 30 psu) tested, smaller crabs died significantly faster than larger crabs but this pattern was more pronounced at 3°C and 15 psu.

Results from this growth experiment on black sea bass suggest that 6°C is the temperature where growth ceases and weight loss begins. SGR at 6°C in the low salinity treatment was slightly above zero (0.018), and SGR in the high salinity treatment was slightly negative. The weight loss trend continued at temperatures below 6°C regardless of salinity (Figure 2). Hales and Able (2001) observed that YOY black sea bass growth was extremely slow, 0.017mm/day for 69 days, when the average temperature was 5°C. Furthermore, in a tag and recapture experiment, Able and Hales (1997) found that YOY black sea bass had reduced growth rates in late fall (mid-November – December) compared to summer or spring. The seasonal variability of growth is a response to temperature variability experienced in the estuaries with warmer water causing higher growth in black sea bass, but prey availability may also affect growth rates in the field.

The general trend of a thermal threshold below which growth is reduced occurs consistently in other fish species that are exposed to seasonal temperature variability. Malloy and Targett (1991) found that mean growth efficiency of juvenile summer flounder (*Paralichthys dentatus*) was significantly lower at 6°C than at 14°C or 18°C, and slow growth rates and mortality occurred at temperatures below 6°C. Similarly, YOY striped bass require at least 10°C for positive growth (Hurst and Conover 1998). Sogard and Able (1992) found latitudinal variations in growth rates of YOY winter flounder (*Pseudopleuronectes americanus*) via otolith microstructure. Growth of the winter founder was positive near 6°C. The latitudinal variations in size were attributed to the local estuary water temperature in which they settled and the timing of settlement. At the southern extent of their range along the New Jersey coast, YOY winter flounder benefitted from the co-occurrence of settling earlier and doing so in a year with relatively warmer winters allowing them to jump start growth before the water increased to suboptimal temperatures. The authors attributed variation in growth rates to warmer water temperatures, potentially, but acknowledge that they were not sure of the mechanism behind the variation. Overwintering experiments of YOY tautog (*Tautoga onitis*), YOY cunner (*Tautogolabrus adspersus*), YOY smallmouth flounder (*Etropus microstomus*) and YOY black sea bass did not produce measureable length increases except in YOY black sea bass which was extremely slow (~1mm over 69 days) (Hales and Able 2001). Black sea bass suffered 100% mortality during the experiments likely due to being exposed to their lower thermal tolerance leading the authors to confirm YOY black sea bass undergo obligatory migrations during winter in the NE US. Smallmouth flounder experienced 33% mortality while mortality of tautog and cunner was the lowest with 14% and 3%, respectively (Hales and Able 2001). The stark difference between mortality but not growth of these species during overwintering experiments indicates that the lower thermal tolerances among these species is very different even though they have overlapping distributions and utilize the same nursery habitat prior to their first winter. Because growth was almost undetectable during the overwintering experiments yet length differences were observed with wild-caught fish between fall and spring, this led the authors to conclude that size selective mortality as a function of winter duration and severity was likely the driving mechanism for length differences in wild populations. Furthermore, the differences between mortality allude to their different overwintering strategies where black sea bass and smallmouth flounder emigrate out of estuaries and onto the continental shelf yet tautog and cunner are able to remain in the estuaries. The results from these studies highlight the need to understand the physiological contraints and life history characteristics of each species when considering the effects of climate on population-level processes.

In addition to weight loss observed at temperatures below 6°C, the interaction between temperature and salinity at 5°C seemed to exacerbate weight loss. At 5°C, the higher salinity treatment caused significantly more weight loss than the low salinity treatment. However, in the 3°C treatments there was no significant difference in weight loss between salinities. This indicates that temperature and not salinity likely plays a more significant role in weight loss as the temperature approaches the fishes' lower lethal limit and supports Fry's paradigm that temperature is a controlling factor in fishes. The low temperature low salinity treatment 3°C and 15 psu did suffer more weight loss than the 5°C and 15 treatment further indicating that temperature more than salinity drives growth.

YOY black sea bass demonstrated positive growth above 6°C. YOY black sea bass grew significantly more quickly at 12°C than 8°C regardless of salinity value. Even though there was only a 5 psu salinity difference between the salinity treatments, fish at 12°C experienced significantly more rapid growth at 34 psu than 29 psu. In warmer experimental conditions, temperature and salinity were both found to be significant for juvenile weak fish (*Cynoscion regalis*), and this species was also found to have optimal growth at higher salinities (Lankford Jr and Targett 1994). Juvenile flathead grey mullet (*Mugil cephalus*) had significantly less growth at salinities near 35 psu compared to fresh water while adults demonstrated the opposite preference for salinity (Cardona 2000). The variation in growth based on salinity is likely evidence of specific habitat utilization at different ages.

Results from the acute exposure experiment suggests that temperatures below 5°C cause irreparable damage to black sea bass that lead to high mortality even when temperatures increase above 5°C . Although mortality was observed in only half of the fish, the majority of this mortality (77%) occurred after the temperature was increased. This suggests that even though brief periods of exposure to cold temperatures may not have immediate repercussions, irreversible damage to the fish may eventually lead to death even when the water has increased to a more suitable temperature. These results are supported by experiments conducted by Hales and Able (2001) which found that mortality of YOY black sea bass increases sharply around 2-3°C, and that the individuals who were able to survive this environment eventually died as the temperature began to increase to 7-8°C. Our results are further supported by Sullivan and Tomasso (2010), who demonstrated that the lower mean lethal thermal limits for juvenile black sea bass was 2.7°C. Atwood et al. (2001) observed the lower limit to be one degree higher (3.7°C). These results are in accordance with the prevailing physiological understanding that the lower lethal limit for most temperate fishes is near the freezing point of blood plasma (0°C) (Hurst 2007). Since black sea bass are known to make an offshore and southern seasonal migration during winter in the northern extent of their range it makes sense that their lower lethal limits would be higher than YOY tautog and cunner that are able to spend winter in near shore estuaries without emigrating (Hales and Able 2001).

Temperature, salinity and their interaction were significant in determining the time until death of YOY black sea bass. Mortality at 3°C was faster than at 5°C due to the fact that 3°C is approaching their lower thermal tolerance (Atwood et al. 2001, Hales Jr and Able 2001, Sullivan and Tomasso 2010). In previous experiments, the lower lethal tolerance was found to be near 2°C for slightly older fish (Schwartz 1964). YOY black sea bass in our experiments exhibited the highest rate of survival at 15 psu. Other laboratory experiments have demonstrated that some fish survive longer when exposed to intermediate salinities. Hurst and Conover (2002) found that YOY striped bass survived significantly longer at 15 psu compared to 30 psu or 35 psu. Juvenile weak fish were found to survive longer at salinity 5 if they when previously acclimated to intermediate salinities of 12 psu and 19 psu (Lankford Jr and Targett 1994). Furthermore, Berlinsky and Watson (2000) found that juvenile black sea bass at 23°C had significantly more growth at 20 psu than 30 psu. This is likely due to less energy being allocated to osmoregulation that can be used for respiration or growth.

Current stock assessments and fish population models of many valuable species do not explicitly account for overwintering mortality (Hurst 2007). However, overwintering mortality is particularly important in the NW Atlantic where sea surface temperature can fluctuate on the order of at least 20°C between summer and winter (Schroeder 1966). Therefore, estimates of overwintering mortality are increasingly more important for building more informative models and better management plans that are able to meet fisheries management goals. Using the accelerated failure model produced in this study, future studies should examine the relative survivorship of YOY black sea bass by using winter historic bottom water temperatures and salinities on the NE US continental shelf, which may provide insight to recruitment dynamics associated with the severity and duration of winter. Estimated survivorship and eventual recruitment of overwintering fish during their first year of life will become increasingly important as the NE US continental shelf warms potentially providing suitable overwintering habitat further north.

Table 1 F statistics, residuals, degrees of freedom (df) and p-values of temperature, salinity and their interaction for the growth experiments at 6°, 8° and 12°C and salinities of 29 and 34 psu.

	F-value	Residual/df	df	p-value
Temperature	152.01	144	2	< 0.0001
Salinity	7.28	144	1	0.007
Interaction	9.73	144	2	0.0001

Table 2 F statistics, residuals, degrees of freedom (df) and p-values for temperature, salinity and their interaction of growth during the overwintering experiments at 3° and 5° C and 15 psu and 35 psu.

	F-value	Residual/df	df	p-value
Temperature	15.1	73	1	0.0002
Salinity	11.65	73	1	0.001
Interaction	7.95	73	1	0.006

Table 3 Mean and standard deviation values of temperature, salinity and fish biomass during the overwintering experiment.

Treatment	Temperature (Mean±SD)	Salinity (Mean±SD)	Mass (g) (Mean±SD)
3°, 15	3.90° ± 1.20°C*	14.98 ± 0.11	3.39 1.016
3°, 35	3.20° ± 0.42°C	34.99 ± 0.29	4.02 1.50
5°, 15	5.19° ± 0.47°C	14.79 ± 0.29	4.23 2.11
5°, 35	4.74° ± 0.26°C	34.66 ± 0.24	4.18 2.08

*These values represent the mean±SD with two days of high temperature removed. The mean±SD with these two outliers is 5.04° ± 3.44 °C.

Table 4 Test statistics of temperature, salinity and their interaction using a Weibull distribution for YOY black sea bass exposed to two temperatures (3°C and 5°C) and two salinities (15 psu and 35 psu).

Parameter	df	Estimate	SE	Lower 95% CL	Upper 95% CL	Wald chi-quare	Pr>chi-square
Intercept	1	1.078	0.302	0.485	1.67	3.57	0.0003
Temperature	1	0.448	0.073	0.305	0.591	6.14	< 0.0001
Salinity	1	-0.112	0.011	-0.135	-0.089	-9.75	< 0.0001
Temperature: Salinity	2	0.018	0.002	0.013	0.024	6.82	< 0.0001
Scale	1	0.323	0.067	-1.261	-0.998	-16.81	< 0.0001

Table 5 Number of parameters, log-likelihood and AIC values for possible accelerated failure models.

Exponential	**# Parameters**	**Log-likelihood**	**AIC**
mass*temperature*salinity	8	-400.30	816.60
mass+temperature*salinity	5	-400.50	811.06
mass*temperature+salinity	5	-402.60	815.28
mass*temperature	4	-411.20	830.36
mass*salinity	4	-450.50	909.00
mass+temperature+salinity	4	-403.10	814.14
mass+temperature	3	-412.30	830.57
mass+salinity	3	-450.80	907.64
temperature*salinity	4	-400.60	809.11
temperature+salinity	3	-403.20	812.37
mass	2	-454.10	912.15
temperature	2	-412.70	829.30
salinity	2	-451.40	906.71
Extreme			
mass*temperature*salinity	9	-384.00	785.95
mass+temperature*salinity	6	-386.20	784.48
mass*temperature+salinity	6	-392.50	796.98
mass*temperature	5	-419.90	849.81
mass*salinity	5	-493.80	997.61
mass+temperature+salinity	5	-393.10	796.23
mass+temperature	4	-421.80	851.63
mass+salinity	4	-494.00	996.01

temperature*salinity	5	-387.20	784.30
temperature+salinity	4	-394.70	797.37
mass	3	-503.10	1012.11
temperature	3	-421.90	849.88
salinity	3	-494.00	994.04
Gaussian			
mass*temperature*salinity	9	-386.20	790.34
mass+temperature*salinity	6	-386.70	785.47
mass*temperature+salinity	6	-389.50	791.00
mass*temperature	5	-409.90	829.71
mass*salinity	5	-478.30	966.57
mass+temperature+salinity	5	-389.60	789.20
mass+temperature	4	-410.60	829.12
mass+salinity	4	-478.60	965.13
temperature*salinity	5	-386.70	783.47
temperature+salinity	4	-389.60	787.25
mass	5	-478.30	966.57
temperature	3	-410.60	827.24
salinity	3	-479.40	964.71
Log Logistic			
mass*temperature*salinity	9	-324.20	666.34
mass+temperature*salinity	6	-326.10	664.25
mass*temperature+salinity	6	-344.70	701.47
mass*temperature	5	-381.50	772.95
mass*salinity	5	-454.60	919.23
mass+temperature+salinity	5	346.60	703.21
mass+temperature	4	-385.60	779.20
mass+salinity	4	-456.00	919.96
temperature*salinity	5	-326.20	662.33
temperature+salinity	4	-347.10	702.24
mass	3	-462.70	931.40
temperature	3	-386.40	778.73
salinity	3	-458.70	923.43
Logistic			
mass*temperature*salinity	9	-376.50	770.95
mass+temperature*salinity	6	-377.30	766.56
mass*temperature+salinity	6	-379.50	771.04
mass*temperature	5	-400.70	811.47
mass*salinity	5	-483.60	977.16
mass+temperature+salinity	5	-379.90	769.74
mass+temperature	4	-402.30	812.66

mass+salinity	4	-483.80	975.67
temperature*salinity	5	-377.30	764.57
temperature+salinity	4	-379.90	767.78
mass	3	-487.00	980.03
temperature	3	-402.40	810.76
salinity	3	-485.40	976.76
Log normal			
mass*temperature*salinity	9	-345.20	708.45
mass+temperature*salinity	6	-346.60	705.13
mass*temperature+salinity	6	-353.20	718.31
mass*temperature	5	-386.30	782.67
mass*salinity	5	-448.10	906.28
mass+temperature+salinity	5	-354.00	717.91
mass+temperature	4	-388.30	784.55
mass+salinity	4	-449.00	906.06
temperature*salinity	5	-347.20	704.50
temperature+salinity	4	-355.00	717.91
mass	3	-457.20	920.36
temperature	3	-389.90	785.70
salinity	3	-451.30	908.51
Rayleigh			
mass*temperature*salinity	8	-331.70	679.48
mass+temperature*salinity	5	-332.80	675.52
mass*temperature+salinity	5	-340.50	690.96
mass*temperature	4	-367.60	743.19
mass*salinity	4	-486.80	981.53
mass+temperature+salinity	4	-342.70	693.43
mass+temperature	3	-371.60	749.20
mass+salinity	3	-487.00	980.09
temperature*salinity	4	-332.80	673.61
temperature+salinity	3	-343.00	692.09
mass	2	-495.30	994.53
temperature	2	-372.60	749.16
salinity	2	-487.30	978.55
Weibull			
mass*temperature*salinity	9	-312.50	643.00
mass+temperature*salinity	6	-315.60	643.18
mass*temperature+salinity	6	-329.80	671.52
mass*temperature	5	-367.00	744.00
mass*salinity	5	-448.40	906.77
mass+temperature+salinity	5	-334.40	678.84

mass+temperature	4	-371.40	750.85
mass+salinity	4	-448.70	905.45
temperature*salinity	5	-315.70	641.42
temperature+salinity	4	-335.00	677.95
mass	3	-452.60	911.10
temperature	3	-372.50	750.91
salinity	3	-449.30	904.50


Figure 1 Experimental design used for all experiments referenced in this study

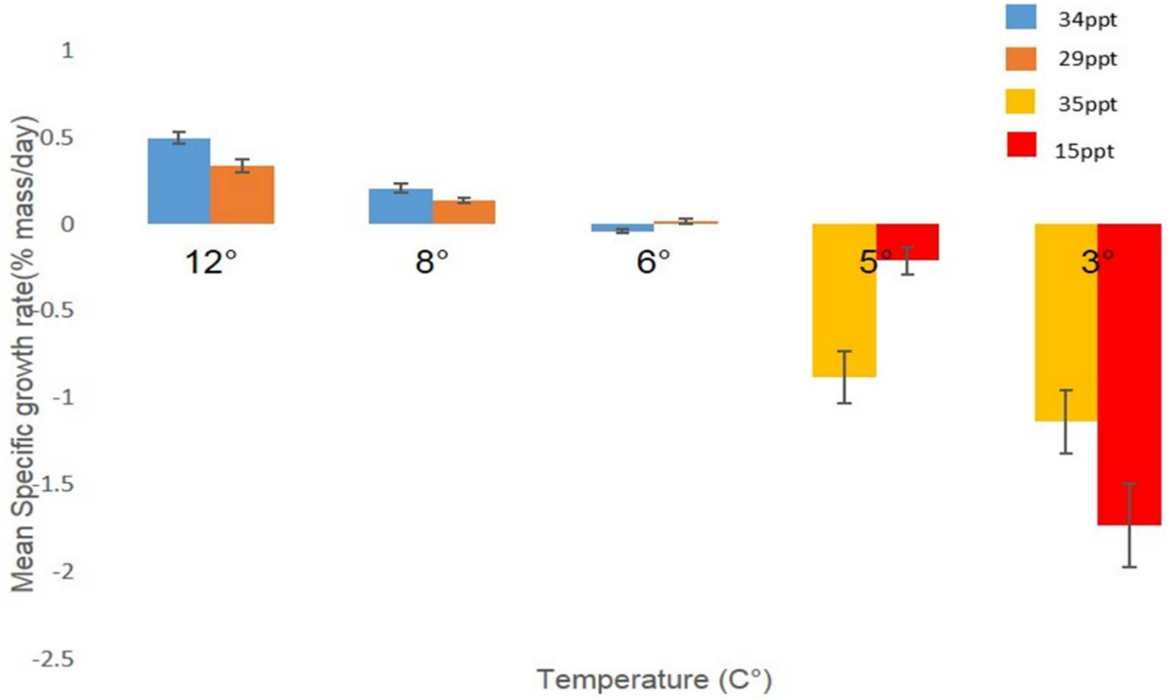

Figure 2 Specific growth rates (%mass/day) at five temperatures and four salinity treatments. The 12°, 8° and 6° treatments were conducted solely as a growth experiment while the 3°C and 5°C treatments were the subsequent growth results of the overwintering experiment.

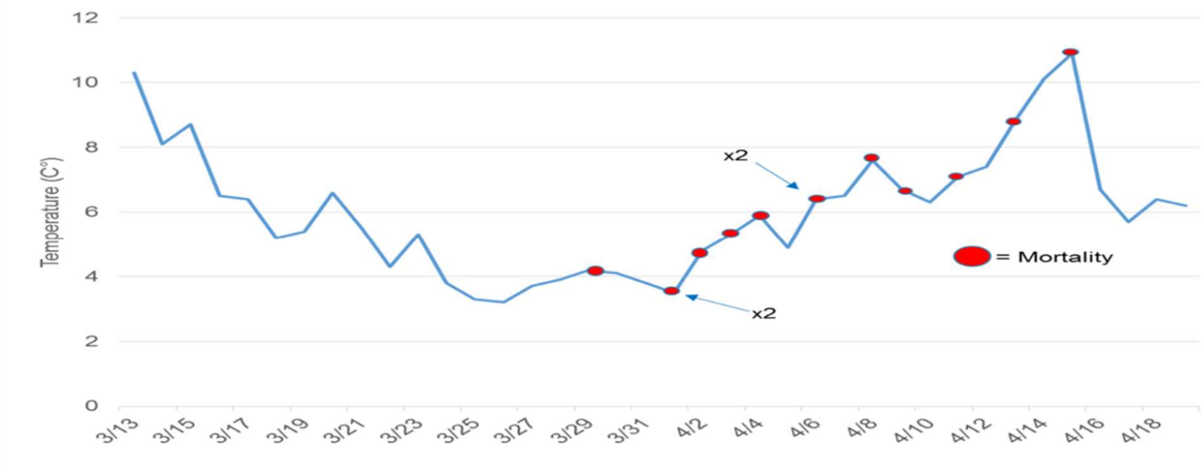

Figure 3 Temperature (blue line) and days with mortality (red circles) during the acute exposure experiment.

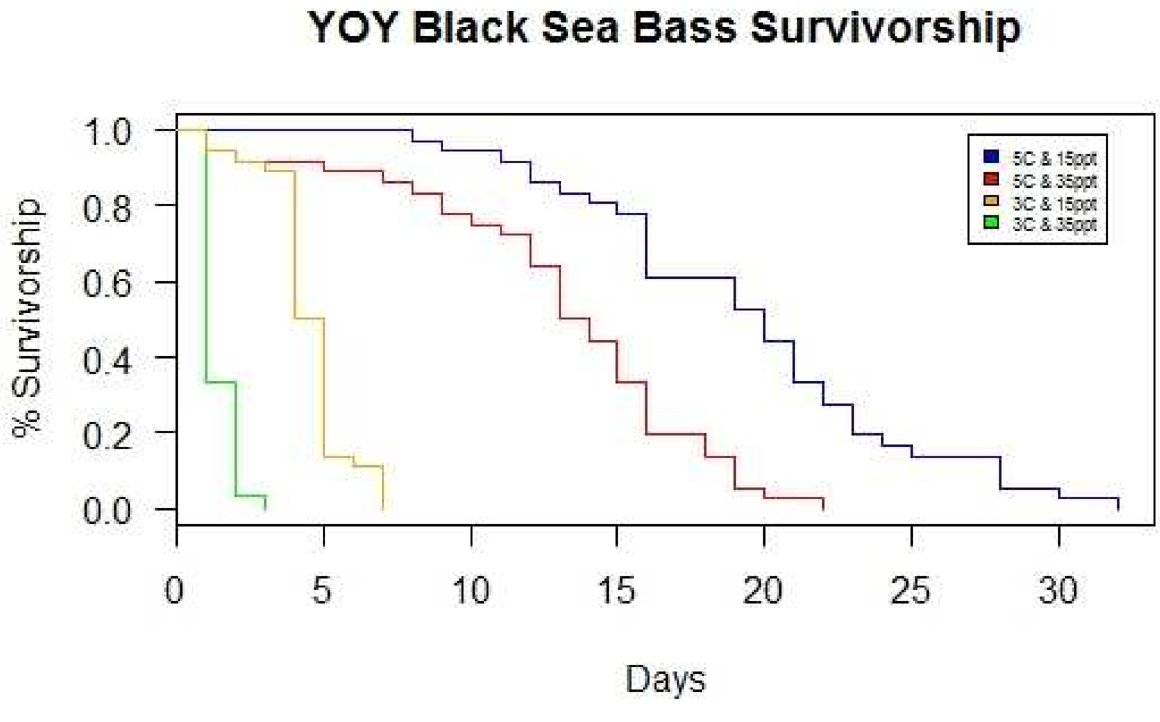

Figure 4 Kaplan-Meier curves depicting percent survivorship in each treatment over the duration of the experiment.

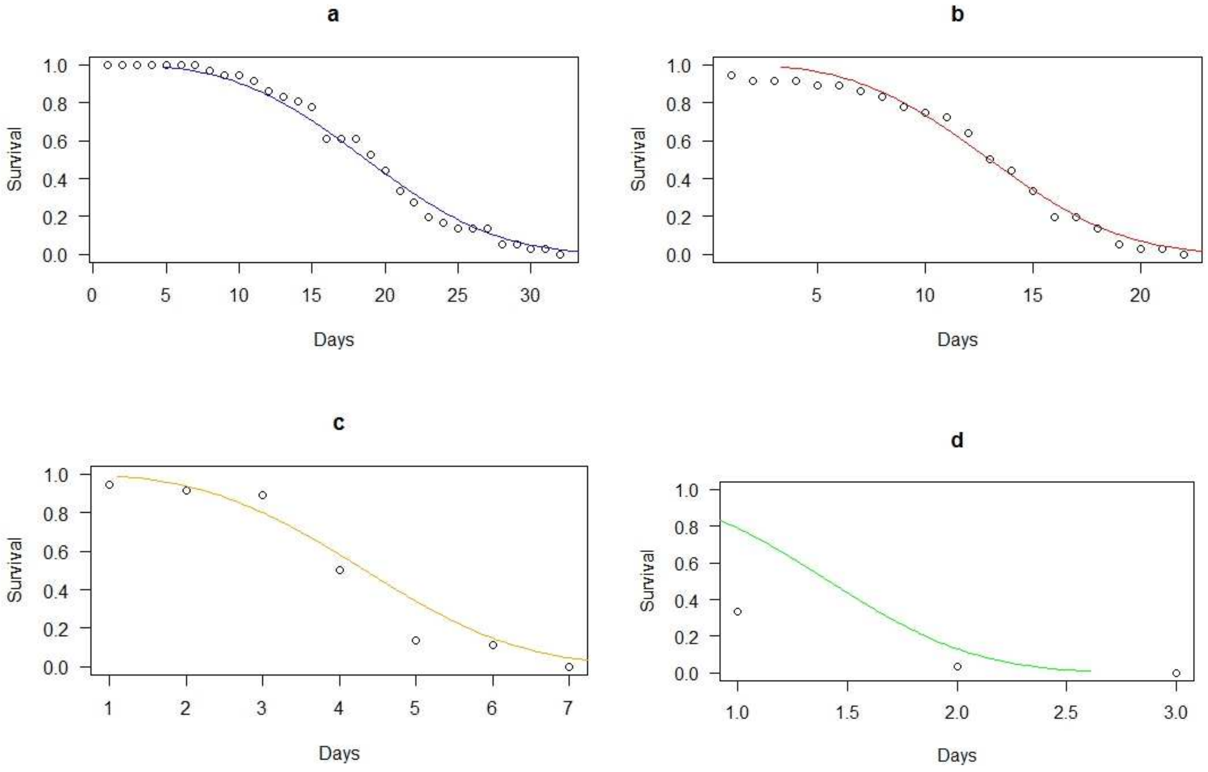

Figure 5 Predicted survival functions formed from the accelerated failure model with a Weibull distribution (lines) versus observed survivorship (circles). Graph a refers to the 5°C and salinity 15 treatment, b =5°C and salinity 35, c = 3°C and salinity 15 and d = 3°C and salinity 35.

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Chapter 2: Relative Survivorship of young-of-the-year black sea bass on the NE US continental shelf

As one of the fastest warming regions in the world (Friedland and Hare 2007, Belkin 2009), many fish species have shifted to higher latitudes in the Northwest Atlantic (Weinberg 2005, Nye et al. 2009, Overholtz et al. 2011, Pinsky and Fogarty 2012, Pinsky et al. 2013). The effects of increasing water temperature on marine fauna extends from the ecosystem level, by dictating which species' habitats overlap, all the way down to the cellular and molecular level where temperature affects vital bodily functions, especially at physiological thermal extremes (Parmesan and Yohe 2003, Lester et al. 2007, Portner and Peck 2010, Poloczanska et al. 2013). The over-arching influence of temperature acts as a dictating force that influences large scale processes like species abundance and distribution (Perry et al. 2005). Shifts in the distribution and abundance of fish as a result of temperature increases is well documented (Frank et al. 1990, Shuter and Post 1990, Nye et al. 2009, Pinsky et al. 2013), and the common theme among these studies is that fish are moving to remain in preferred water temperatures. The general trend is towards higher latitudes by either shrinking or expanding their range, shifting their center of biomass or moving to greater depths (Frank et al. 1990, Shuter and Post 1990, Nye et al. 2009, Pinsky and Fogarty 2012).

The physiological link between distribution shifts and temperatures changes in the environment is the species' ability to supply oxygen to its tissues (Pörtner and Peck 2010). Conceptually, within a species' thermal range, respiration occurs more efficiently at certain temperatures than others, and therefore species will tend to seek out favorable temperatures as one way of promoting fitness. This results in species shifting to remain in temperatures that support efficient respiration. Since species with similar preferred temperatures overlap geographically it is possible to observe whole assemblages shifting over time. Along the NE US continental shelf Lucey and Nye (2010) found species assemblages in Mid-Atlantic Bight (MAB), Southern New England (SNE), and the Gulf of Maine resemble former assemblages of the adjacent region to its south. These shifts in abundance and distribution are more pronounced at northern and southern range limits (Shuter and Post 1990) because the extreme ends of a species' geographical range also tend to be at the species physiological thermal limits where oxygen demands are not as easily met (Deutsch et al. 2015). In the Northwest Atlantic, black sea bass are at the northern extent of their range and since the 1970's their center of biomass has been shifting polewards (Henderson personal communication). They were extremely rare in the Gulf of Maine from 1973-1982, but are now frequently caught there (Figure 1).

As the oceans continue to warm (Solomon 2007, Stocker 2013) black sea bass will likely continue shifting their distribution to remain in preferred water conditions. The mechanism that allows a northward range expansion of the black sea bass population lies partially in the ability of young-of-the-year (YOY) black sea bass to survive winter. Their survival depends on not only the timing and duration of water temperatures below their thermal tolerance, but also the extent of their seasonal migration offshore to escape cooler nearshore waters and their ability to survive cool water temperatures (Able et al. 1996). If YOY black sea bass increase their relative survivorship during their first winter, they will be much more likely to reach maturity, spawn and contribute to future cohort classes. If this occurs in many locations throughout the northern population, the population will grow and create a unique challenge to fisheries managers to manage new or growing fisheries that did not previously exist. In fact, the NOAA NEFSC fall survey data shows that YOY black sea bass have distributed themselves further north over the last five decades (Figure 1). If warm winters ensue it is possible that the fish will recruit to age-1 thereby establishing local self-sustaining populations of black sea bass.

From a physiological perspective there are two mechanisms that are considered primary drivers of overwintering mortality: starvation and osmoregulatory failure (Hurst 2007). As ectotherms, water temperature dictates the metabolic rates of fish. In general, warm water temperatures cause basal (resting) metabolic rate in fish to increase, which in turn increases oxygen consumption (aerobic scope), and results in the fish using more energy while at rest (Fry 1971). This means that fish will have to use more energy simply to remain at rest. During cooler temperatures, metabolic rate and aerobic scope decrease resulting in less energy being used due to reduced metabolic demand. However, when temperatures drop below a physiological threshold the fish will cease eating and will rely on energy stores usually in the form of lipids to maintain minimal metabolic demands (Griffiths and Kirkwood 1995, Hurst 2007). The amount of energy stores available and how quickly they are used largely depend on body size, and the rate at which they are depleted depends on temperature. Larger fish generally have more energy stores, and use them more slowly than smaller fish because weight-specific basal metabolism decreases as size increases (Hurst 2007). This means that a smaller fish of any particular species will use proportionally more energy than their larger conspecifics only to remain at rest. This puts juveniles at higher risk of mortality during winter conditions particularly in temperate climates where water temperatures can range 20°C between winter and summer (Schroeder 1966). In addition to the effects of low temperature and size on metabolic rates and energy use, low temperatures also affect osmoregulation.

For any animal to maintain appropriate ion concentrations within their cells, active ion pumping through transmembrane channels must be balanced with passive diffusion of ions through the cell membrane. At cold temperatures this balance breaks down and fish are not able to effectively maintain favorable ion concentrations (Hochachka 1988). According to Cossins and Bowler (1987), the inability to maintain homeostasis results in the malfunction of the central nervous system by preventing synapse transmission. If synapse transmission deteriorates, then communication between the brain and body breaks down leading to the subsequent failure of essential bodily functions. Size and temperature dependence of metabolic rates and stored energy reserves as well as the ability to maintain osmoregulation at low temperatures varies across fish species so specific experiments must be conducted to define the limits for individual species of interest.

There is growing body of literature that examines overwintering survival in marine and freshwater fauna. Studies have generally focused on temperate regions where aquatic taxa are subject to seasonal changes in temperature and food availability and, therefore, growth restraints, but the literature covers overwintering mortality from Florida to the North Sea (Storey and Gudger 1936, Simpson 1953). In multiple species the ability to survive overwintering is highly correlated to size, temperature and salinity (Griffiths and Kirkwood 1995, Johnson and Evans 1996, Hurst and Conover 1998, Bauer and Miller 2010).

A study of roach (*Rutilus rutilus*) and perch (*Perca fluviatilis*) in Northern Ireland found both species to be affected by a short growing season due to cooler summer temperatures caused by interannual temperature variability (Griffiths and Kirkwood 1995). Size-selective mortality was found in both species. The authors attributed weight loss and overwintering mortality to energy allocation trade-offs between fat and protein. For white perch, an estuarine fish found in temperate regions of North America, starvation and osmoregulatory failure were found to dictate mortality at 4°C and 2.5°C (Johnson and Evans 1996). Hurst and Conover (1998) observed evidence of size-selective mortality of YOY striped bass during winter in the Hudson River correlating with more severe winter conditions. The authors observed that recruitment of age-1 fish was not correlated to YOY abundance suggesting overwintering mortality plays a part in how many fish survive their first winter. Furthermore, optimal overwintering habitat was correlated to regions of intermediate salinity, 15 psu (Hurst and Conover 1998). Salinity and temperature was also important to blue crab, a commercially and recreationally valuable species along the US East Coast. Laboratory experiments of blue crabs established that survivorship was significantly size-dependent and that the crabs were more susceptible to mortality at 3°C than 5°C and at lower salinities (Bauer and Miller 2010). The authors hypothesized that the physiological mechanisms behind the mortality could be linked to oxygen and capacity-limited thermal tolerance and osmoregulatory dysfunction. Bauer and Miller (2009) used the results from their laboratory experiments to estimate winter mortality of blue crabs in Chesapeake Bay, and found that spatial and interannual variability of winter duration and winter severity was highly correlated to mortality. Furthermore, in a study of the surf clam population along the NE US Narvaez et al. (2015) found warmer bottom temperatures have an adverse affect on growth that results in starvation and an overall population decline.

Hare and Able (2007) observed that the abundance of juvenile Atlantic croaker in North Carolina and New Jersey positively correlated to an increase in overwintering habitat due to above average bottom water temperatures forced by a positive NAO. The authors also found a positive correlation between adult catch and a positive NAO. This allowed the authors to build a conceptual model of the Atlantic croaker’s east coast population based on the NAO as the forcing mechanism of temperature in the ecosystem (Hare and Able 2007). In contrast to Atlantic croaker, a study of yellowtail flounder at the southern extent of its range, found that recruitment was negatively correlated to the NAO (Sullivan et al. 2005). When the NAO index was negative, spring water temperatures were cooler and specifically, the extent of the Mid-Atlantic cold pool, in which juvenile yellowtail flounder are found to occupy, is larger.

To determine if winter temperatures have warmed on the shelf to promote black sea bass population expansion at the northern edge of its range, I used the model of survivorship developed in Chapter 1 in combination with estimates of winter temperature to quantify the amount of habitat that would allow enhanced survivorship. I hypothesized that:

1) Relative survivorship will have latitudinal pattern on the shelf with higher survivorship predicted at southern latitudes.
2) Relative abundance will increase with increasing area of the shelf estimated to be in suitable habitat.
   Relative abundance will decrease with increasing area of the shelf estimated to be in unsuitable habitat.

Materials & Methods

To obtain a clearer understanding of YOY black sea bass overwintering survivorship, results from a previous overwintering experiment were used to construct an accelerated failure time model. During the laboratory experiments YOY black sea bass were exposed to 3°C and 5°C and salinity of 15 psu and 35 psu. Results suggest that YOY black sea bass are not able to survive winters that have a significant number of days <6°C. In my experiments, fish survived at 5°C and 15 psu for a maximum of 32 days, and 21 days at 35 psu. In the 3°C treatments, mortality was acute with fish surviving for a maximum of 7 days at the intermediate salinity and only 3 days at 35 psu. In all treatments, the amount of days survived was much shorter than the average winter duration in the NE US.

An accelerated failure time model was created using the survival package in the R statistical language. The best model of survivorship included temperature, salinity and their interaction as the significant variables. Initial mass was not significant to quantifying the rate of mortality in the experiment. The Weibull distribution provided the best fit for the observed data. Using the coefficients for temperature, salinity and their interaction a survivorship and hazard function were developed to describe the pattern of mortality during the experiment.

To estimate relative survivorship along the NE US coast the Regional Ocean Modelling System (ROMS) was used to hindcast daily bottom water temperature and daily bottom salinity between 1959 and 2007. ROMS is a ‘free surface, terrain following primitive equations ocean model” (http://www.myroms.org/index.php). It has a wide range of applications from tracking sea ice movements in the Barents Sea to tracking eddy formations in the Gulf Stream (Budgell 2005, Kang and Curchitser 2013), respectively. It has also previously been used to force a model of surfclam population dynamics with estimates of bottom water temperatures along the NE US coast (Narváez et al. 2015). ROMS was chosen for three main reasons: accuracy of winter bottom water temperatures, high resolution of relevant spatial coverage and an extensive time series of 50 years. ROMS has a resolution of 7 km x 7 km and is able to estimate bottom water temperature at depths within 1m from the seafloor. A full evaluation of the accuracy with which ROMS predicts bottom temperatures was beyond the scope of this work, but observed bottom water temperatures from February to October 2003-2006 were not significantly different from those in the model based on a nonparametric Wilcoxon Signed Ranks test on 2395 CTD casts that matched spatially and temporally with ROMS grid points (personal communication, Ryan Rykaczewski). The ROMs model was slightly warmer (0.06ºC) than observed bottom temperatures, but typically less than the average daily standard deviation in most regions. We deemed this a reasonable approximation and therefore, in the absence of observed winter temperature and salinity that extended further back in time, used temperature and salinity from the ROMS model to force the survivorship and hazard functions described above. Maps of percent survivorship on the NE US continental shelf between the Gulf of Maine and Cape Hatteras were created for each year between 1959 and 2007. Percent survivorship across the shelf in each year was divided into bins of 10%. The number of pixels (7 km x 7km boxes) in each 10% bin was summed and multiplied by $49km^2$ to obtain the area on the shelf estimated to be at that survivorship. Because there may be some biases in the ROMS model we considered a wide threshold to quantify habitat of good survival (70-100%).

Using daily bottom temperature and bottom salinity output from the ROMS hindcasts to force the survivorship model we estimated relative percent survival for each day in each grid cell. Winter duration was calculated as the number of days below 6°C which was the minimum temperature growth was observed in our experiments, and it was also the minimum temperature black sea bass were caught in a survey of the MAB likely indicating avoidance of temperatures below 6°C (Musick and Mercer 1977).

To determine if the survivorship model combined with ROMS output was able to estimate relative survivorship in the field, the NOAA NEFSC spring and fall bottom trawl survey data were used. Since 1963 in the fall and 1968 in the spring, approximately 300-400 stations have been sampled from Cape Hatteras, NC to the Gulf of Maine and Scotian Shelf in a stratified random survey design. Consistent with the 2004 black sea bass stock assessment, the offshore strata were used to estimate the relative abundance of black sea bass in the spring because the fish are located on the shelf at the end of their overwintering period (NEFSC 2004). Fish less than 14cm were considered YOY black sea bass based on length frequency distribution from the spring time series between 1968 and 2007 (Figure 2), and the mean stratified abundance per tow was calculated to estimate the relative abundance of YOY in each year. Individuals less than 14cm is also deemed to be the relevant cutoff by the stock assessment to reflect juvenile fish (NEFSC 2004, 2011). The fall survey encompasses both inshore and offshore strata starting in 1973. Fish between 14 – 20cm were pulled from the survey data to represent age-1 fish (Figure 3).

Results

The ROMS model indicated that typically at least 40% of the Northeast US continental shelf was unsuitable for black sea bass survival in winter in most years (Figure 4). In general, survivorship did follow a latitudinal pattern with higher survivorship in southern latitudes near the Chesapeake Bay. In cooler winters unsuitable habitat stretched from the Chesapeake Bay region to the Gulf of Maine west of the 200m isobaths. The extent of this area is reduced in warmer years when higher survivorship regions occur near the Chesapeake Bay and southern New Jersey. There was no linear trend in suitable or unsuitable habitat over time, but rather there was considerable interannual variation in habitat predicted to support high black sea bass survival over the 49-year time period, and thus high variation in winter temperature and duration. The predictions of habitat in which there is over 90% survivorship reflect the steep survivorship curves in the accelerated failure model where juveniles die rapidly once the temperature drops below 6^{o}C even for a short amount of time. Most of the variation in winter survivorship is captured by the amount of habitat in the 1-30% and 70-100% categories and thus, we focused on these winter habitats for our analysis. The upper three (70-80, 80-90, 90-100%) and lower (1-10,10-20 and 20-30%) three percentile bins exhibited relatively high correlations among each other so they were grouped together to represent unsuitable (1-30%) and suitable habitat (70-

100%) respectively (Table 1). However, the area corresponding to 1-30% survival (unsuitable winter habitat) was not correlated with the area corresponding to 70-100% survival (suitable winter habitat, Table 1). Hereafter we refer to these two classifications as unsuitable and suitable habitat.

While there does not appear to be any trend in total area of low survivorship during the time series, the 1960s had generally low survivorship (Figure 5). The average CPUE between 1967-2007 was 0.54. Estimated areas of suitable habitat were among the largest in 1974, 1986, 1995 and 2002 and were associated with above average CPUE (1.16, 0.91, 0.66, 0.82), respectively (Figure 6). This trend is represented in the figures by an increase of estimated suitable habitat along the shelf break and Chesapeake Bay region. Conversely, 1968, 1982, 1993 and 2004 unsuitable habitat was large and was followed by springs with lower than average CPUE of YOY black sea bass (0.46, 0.12, 0.33, 0.45), respectively (Figure 6). ROMS also predicted extremely cold winters with relatively large areas of low survivorship in the early-mid 1980s, late 1990s, 2001, 2003, 2006 and 2007, however these years were not necessarily associated with the lowest recruitment. For example, unsuitable habitat in 1984 and 2001 was expansive yet the following spring experienced above average CPUE (0.92 and 1.29), respectively (Figure 7). In contrast, the winters of 1991 and 2006 had an expansive amount of suitable habitat yet the following spring CPUE was below average (0.20 and 0.28) respectively (Figure 7).

Although, there does seem to be a relationship between good recruitment years and bad recruitment years and the maps of estimated survivorship, the estimated amount of area at any particular range of survivorship did not demonstrate a strong correlation with the observed abundance of YOY black sea bass on the NE US continental shelf based on the spring. The correlations between unsuitable and suitable habitat and the abundance of YOY in the spring trawl survey was $\rho = 0.010$ and 0.20 ($p = 0.96$ and 0.17), respectively (Figures 8, 9).

Discussion

Although maps of relative YOY survivorship picked up the peaks of black sea bass abundance, the correlations between overwintering survival and relative survivorship of YOY black sea bass were low and not statistically significant indicating that other factors must be considered to understand overwintering survivorship and the population dynamics of black sea bass. Habitat quantity and quality defined by temperature, salinity and duration of winter are only a piece of what may account for overwintering mortality. Other possible explanations for low correlations may be that our estimate of juvenile survival is poor, winter temperature are not well estimated by ROMS, some behavior such as burrowing are not compensated for in our survivorship model or some other aspect of the seasonal cycle like the delayed onset of fall may explain recruitment patterns.

Our estimates of recruitment may not accurately reflect the true recruitment or overwintering survival of the population since we based our estimates solely on the relative abundance of juveniles from fishery independent survey data without correcting for adult population size. It is well established that the spawning stock biomass (SSB) plays a significant role in recruitment in addition to environmental factors (Ricker 1954, Beverton and Holt 1957, Cushing et al. 1996). Generally, the higher the SSB the more potential for recruitment because more mature adults will likely spawn more eggs and increase the chance of offspring to recruit into the population up to a point where at very high levels of SSB density dependence reduces recruitment. This relationship has enabled fishery scientists to make estimates of recruitment based on estimates of the spawning stock biomass as well as set biological reference points for fished stocks. In this study we were unable to account for the effect of SSB so our index of juvenile survivorship is not corrected for the size of the adult population contributing offspring. In the latest stock assessment for black sea bass, the estimates of SSB were not accepted and as such it would be inappropriate to attempt to use these estimates of SSB with such high uncertainty to create a reliable index of recruitment that accounts for SSB (NEFSC 2011). However, the general trend in SSB follows the trend in YOY abundance with high numbers early in the time series, low from 1980-1998, and then an increase since 2000 suggesting our index of juvenile abundance is a reasonable estimate of juvenile survival and recruitment. Our inability to come up with a strong metric of recruitment and juvenile survival highlights the need to gather more information on this data-poor stock in order to better assess and manage the resource.

To estimate winter bottom temperatures we used the data predictions of a ROMS model for the east coast of the United States (Kang and Curchitser 2012). Evaluating the accuracy of the bottom temperatures was beyond the scope of this project, but could be completed using CTD data that extends back to the late 1970s. However, the ROMS model reasonably estimates bottom temperatures when evaluated from 2003-2006 in a previous study (personal communication, Ryan Rykaczewski).

There may be behavioral factors that influence winter survival that we did not account for in our survivorship model. Burrowing has been observed in previous overwintering experiments of tautog, smallmouth flounder and black sea bass (Hales and Able 2001). According to Hales and Able (2001), black sea bass burrowed in sand as a response to sudden reduction in temperature below 6°C, and the authors bring up the fact that if fish in the wild exhibit this behavior while overwintering and then die detection of this moratlity event would be difficult.

Burrowing is a behavior exhibited by many marine species. Tilefish in the Hudson submarine canyon were discovered in vertical structures they constructed to presumably seek refuge from predators because their means of egress from the burrow was tail first indicating a structure to hide in and not to ambush prey (Able et al. 1982). Many species of groupers, a relative of black sea bass, exhibit burrowing behavior (Jones et al. 1989, Coleman et al. 2010). Burrowing by blue crabs while overwintering has been observed in the field and in overwintering survivorship experiments. Although it was not a significant factor determining survival, reduced mortality was observed in crabs with substrate (Bauer and Miller 2010). Brown and white shrimp also display a burial behavior response to cooler temperatures in the northern Gulf of Mexico (Aldrich et al. 1968). Burrowing in soft substrate may provide a slight advantage to survival of YOY black sea bass if the substrate is even slightly warmer than the overlying water and/or if the substrate itself insulates the fish from cold temperatures. Future studies should incorporate substrate in addition to controlled temperature and salinity to quantify the relationship, if any, between survivorship and burrowing.

In addition to uncertainty in our estimate of recruitment, another climate-related factor affecting survivorship may be summer duration rather than winter duration. Recent analysis of satellite SST at 10 locations on the NW Atlantic shelf from the northern Scotian Shelf to Virginia indicates that summers are getting longer in 9 of the 10 sites (Andrew Thomas, personal communication). While spring temperatures generally have not occurred progressively earlier over the last 30 years, the onset of cooling in the fall has occurred progressively later. Increased summer duration and late cooling of SST in the fall has the potential to benefit YOY black sea bass preparing to overwinter. A longer summer means a longer growing season that provides the opportunity to accumulate more energy reserves that can be used to prevent starvation at cold temperatures. In addition to obtaining more body mass, longer summers may allow the fish extra time to move to preferred overwintering habitats before temperatures drop to undesirable temperatures.

To test the feasibility of this hypothesis, we calculated how long it might take a juvenile black sea bass to reach favorable habitat using literature values for swimming speed in a similar species. In the European sea bass *Dicentrarchus labrax*, the laboratory-derived optimal swimming speed at $7^{o}C$ is $0.32\ m\ s^{-1}$ (Claireaux et al. 2006). This is the speed that minimizes energy expenditure per unit of travel distance and in general this speed is faster when temperatures are higher. Based on an approximate swimming rate of 0.3 m/s for European sea bass and a distance of 170 km from Democratic Point Long Island to the 200m isobaths estimated using Google Earth, black sea bass could reach the shelf break in about a week and could reach as far south as the Chesapeake Bay in approximately 19 days. Although these are only approximations, even an additional few days of favorable temperatures may allow an emigrating fish to reach substantially better overwintering grounds further south. The possibility of later fall cooling should be investigated in future studies.

Table 1 Correlation values between estimates of survivorship area.

	0 -1%	*1 - 10%*	*10 - 20%*	*20 - 30%*	*30 - 40%*	*40 - 50%*	*50 - 60%*	*60 -70%*	*70 - 80%*	*80 -90%*	*90 - 100%*	*1-30%*	*70 - 100%*	*log Spring YOY*
0 -1%	1													
1 - 10%	0.420178	1												
10 - 20%	0.16724	0.676699	1											
20 - 30%	0.23829	0.609835	0.793586	1										
30 - 40%	0.154299	0.600893	0.624884	0.823591	1									
40 - 50%	0.145488	0.463187	0.543052	0.666201	0.71909	1								
50 - 60%	0.122933	0.310491	0.25519	0.384513	0.571973	0.801667	1							
60 -70%	0.094979	0.235054	0.234779	0.375085	0.502749	0.736171	0.746899	1						
70 - 80%	0.183439	0.202352	0.044747	0.259501	0.402076	0.648545	0.680434	0.795967	1					
80 -90%	0.216651	0.118447	-0.02291	0.230123	0.398807	0.573893	0.55403	0.602171	0.836687	1				
90 - 100%	0.481935	0.064659	-0.18477	0.099748	0.206513	0.216202	0.23563	0.177422	0.409407	0.635453	1			
1-30%	0.35862	0.939951	0.86853	0.814385	0.723995	0.581854	0.346476	0.291956	0.194037	0.11686	0.010468	1		
70 - 100%	0.465257	0.085723	-0.16302	0.133842	0.258268	0.305049	0.322306	0.284747	0.532167	0.739235	0.988899	0.03693	1	
log Spring YOY	0.396003	0.139464	-0.18091	-0.11885	-0.13629	-0.17023	-0.01138	-0.06634	-0.05639	-0.05679	0.246986	0.010775	0.208110798	1

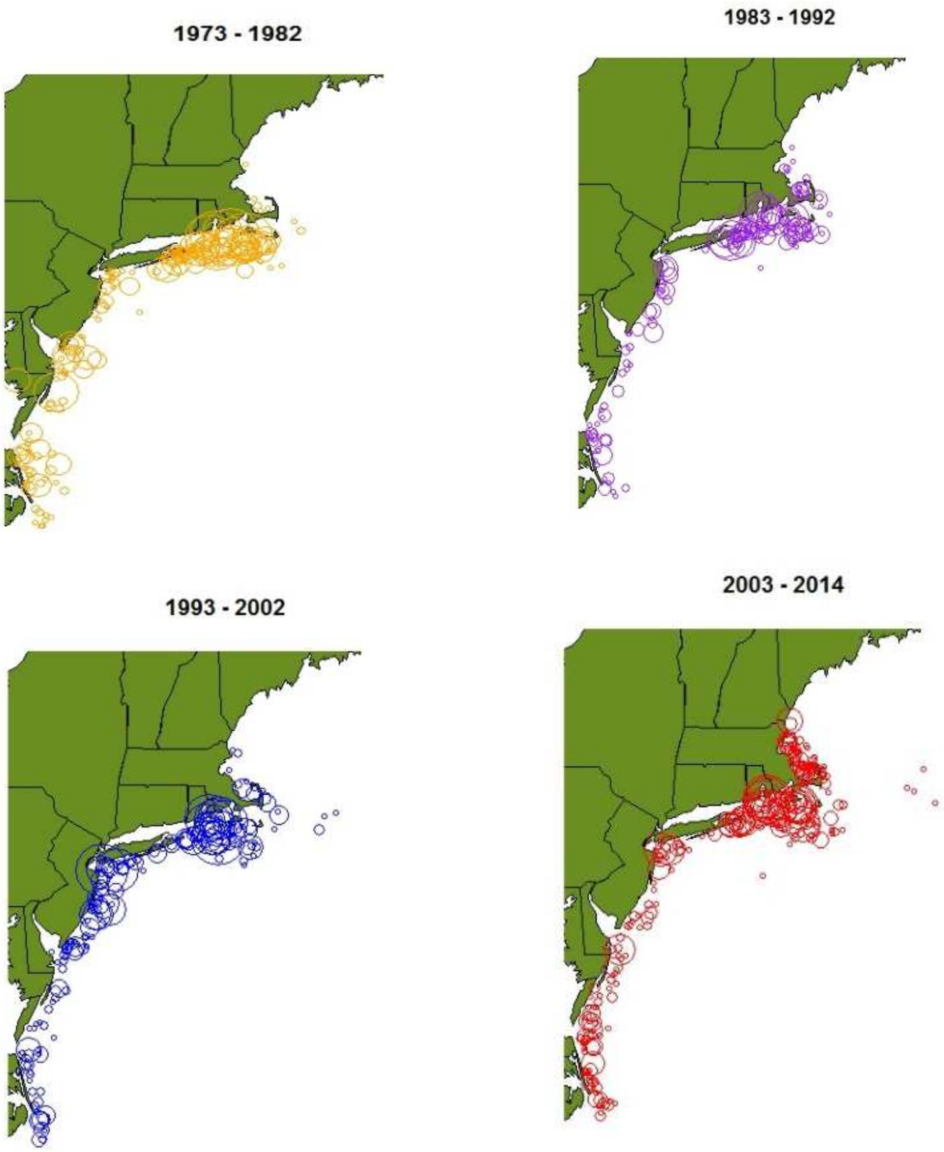


Figure 1 Fall abundance of YOY black sea bass in the NEFSC bottom trawl survey by decade. Larger circles indicate more individuals caught at that site.

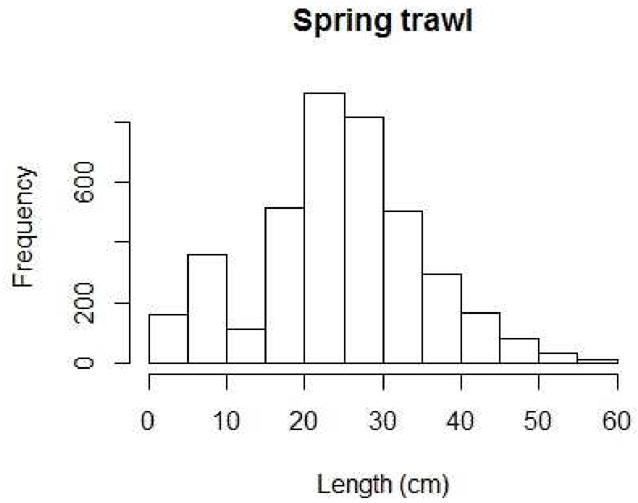


Figure 2 Length frequency of black sea bass caught by the NMFSC spring trawl survey from 1968-2007.

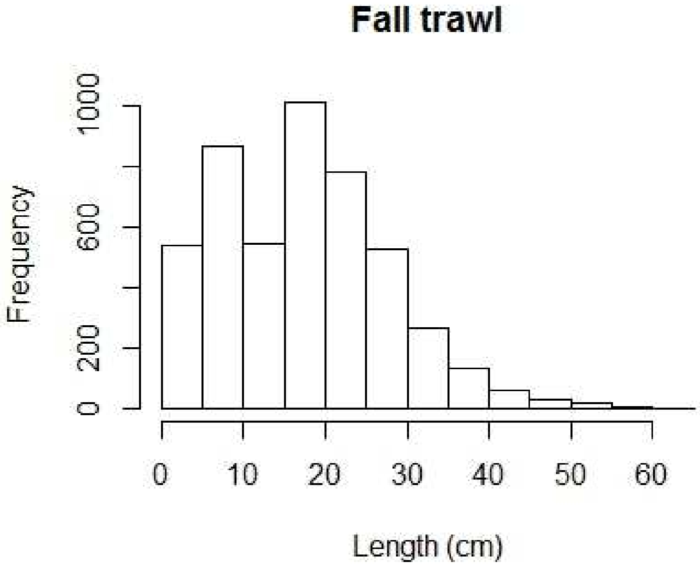


Figure 3 Length frequency of black sea bass caught by the NMFSC fall trawl survey from 1973-2007.

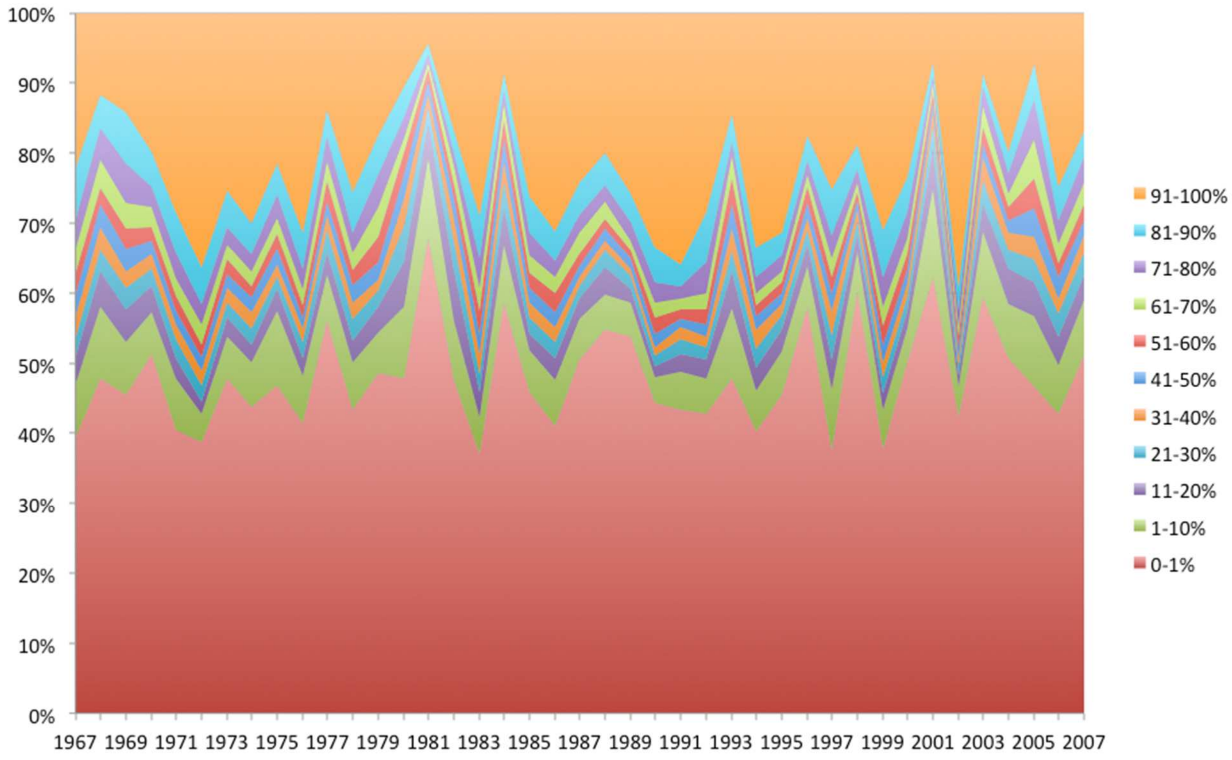
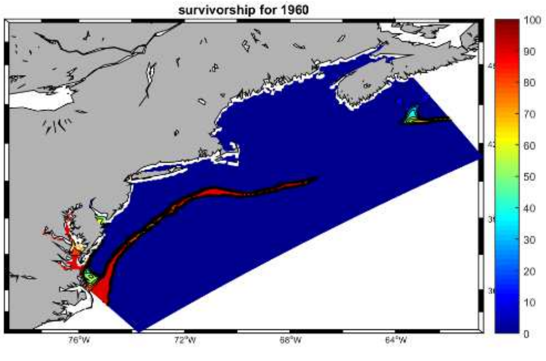
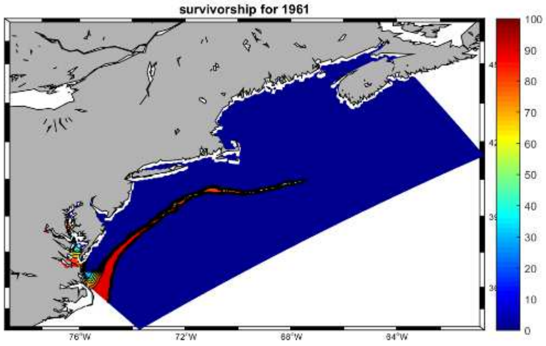


Figure 4 Proportion of the Northeast US shelf in each 10% survivorship bin of YOY survivorship.

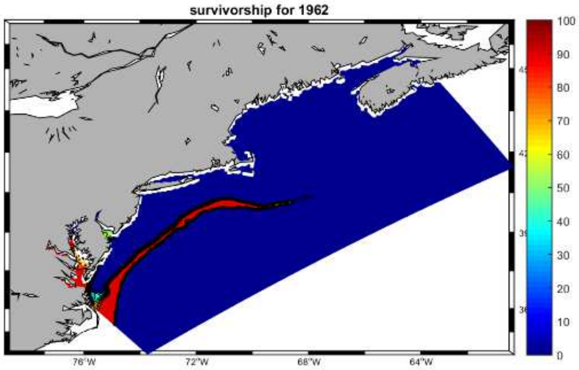
survivorship for 1960



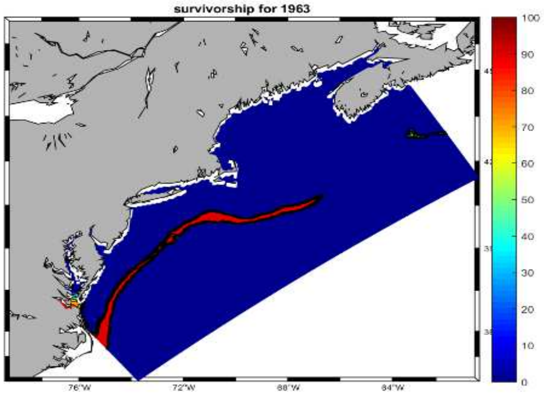
survivorship for 1961



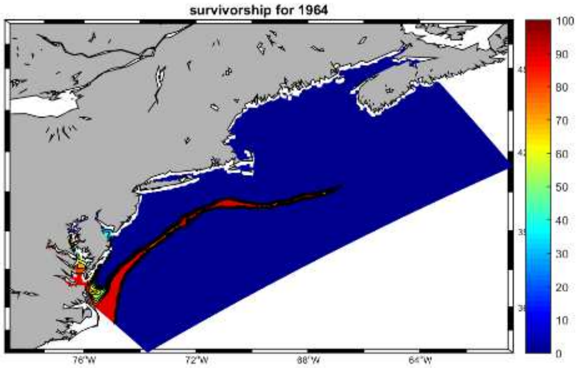
survivorship for 1962



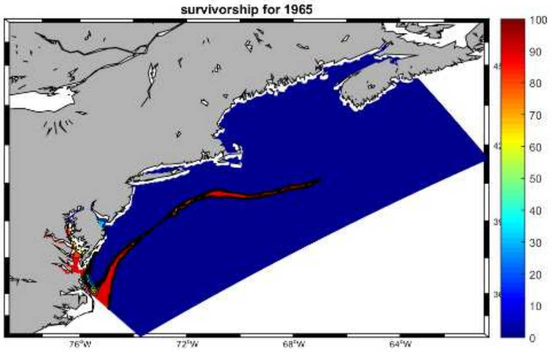
survivorship for 1963



survivorship for 1964



survivorship for 1965



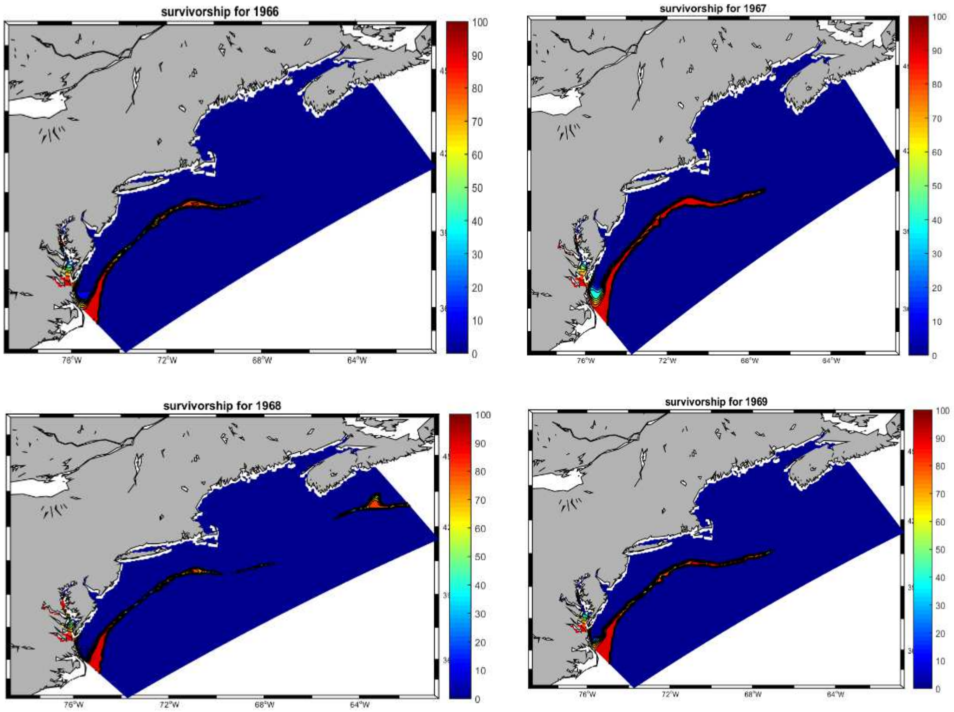


Figure 5 ROMS estimated survivorship during the 1960’s.

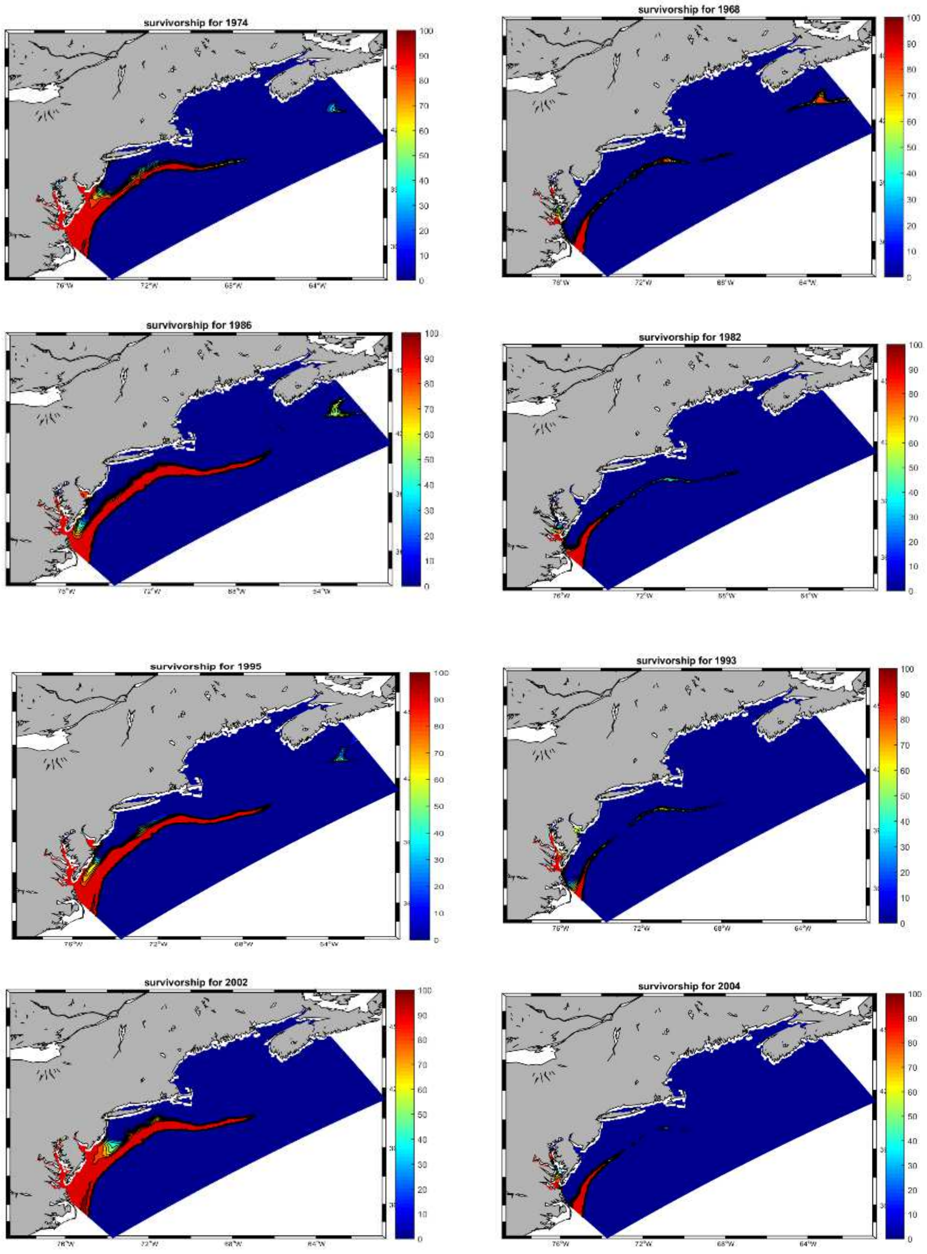


Figure 6 Estimated survivorship of YOY black sea bass during winter on the NE US continental shelf. The four figures on the left represents years with large amounts of suitable habitat and above average CPUE. The four figures in the right column illustrate years with low estimated survivorship and low CPUE.

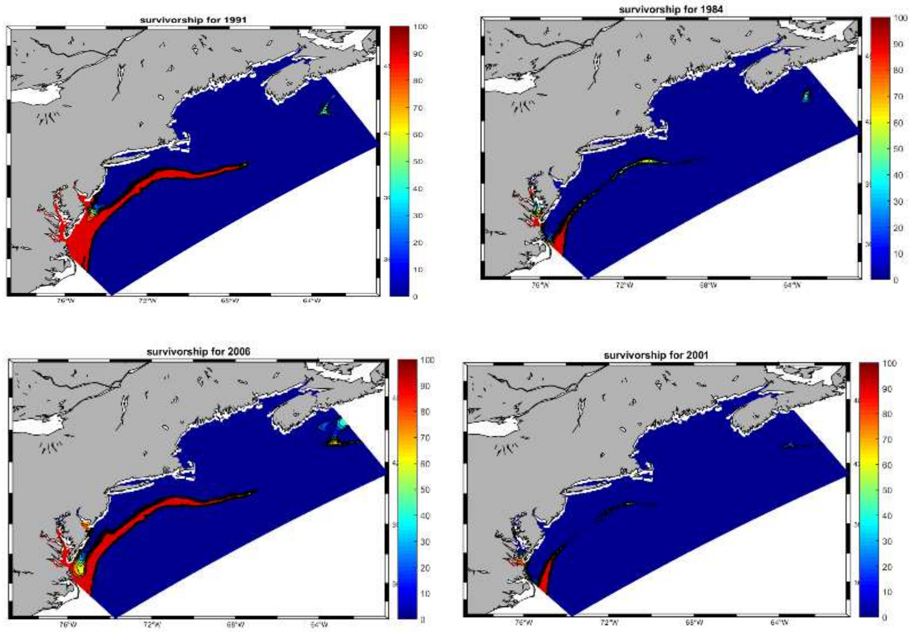


Figure 7 Estimated survivorship of YOY black sea bass during winter on the NE US continental shelf. Figures in the left column represent years with high estimated winter survivorship but below average CPUE in the NMFS spring trawl survey. The right column illustrates years with low estimated winter survivorship but above average CPUE in the spring trawl survey.

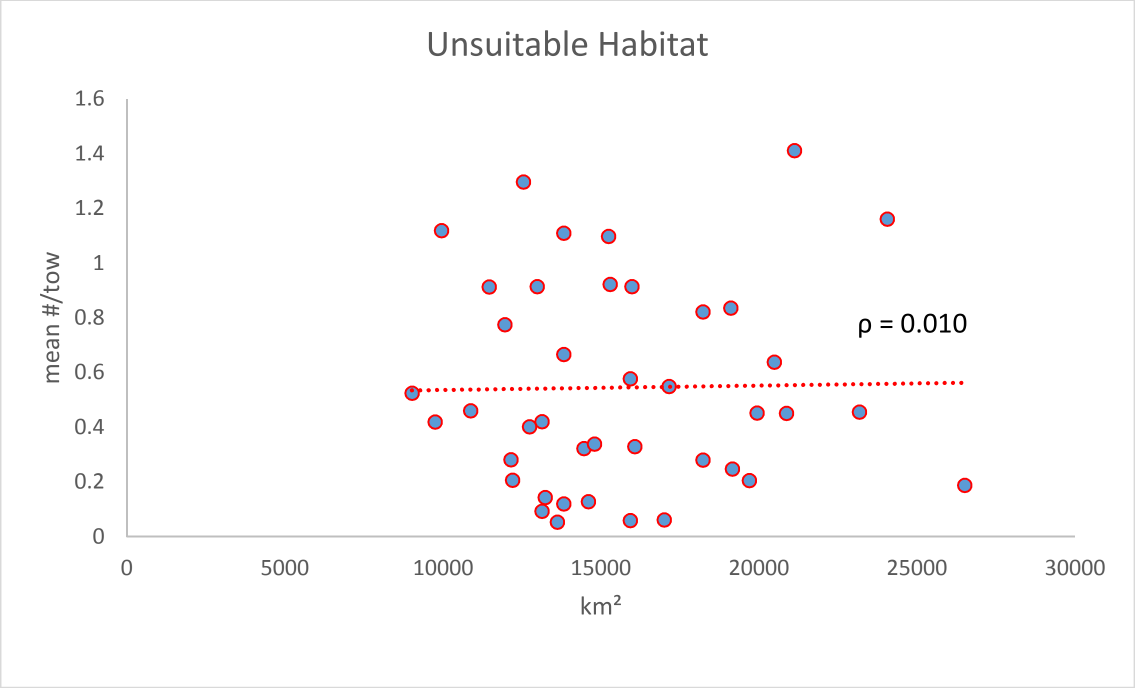


Figure 8 Correlation between unsuitable habitat in winter and CPUE in spring.

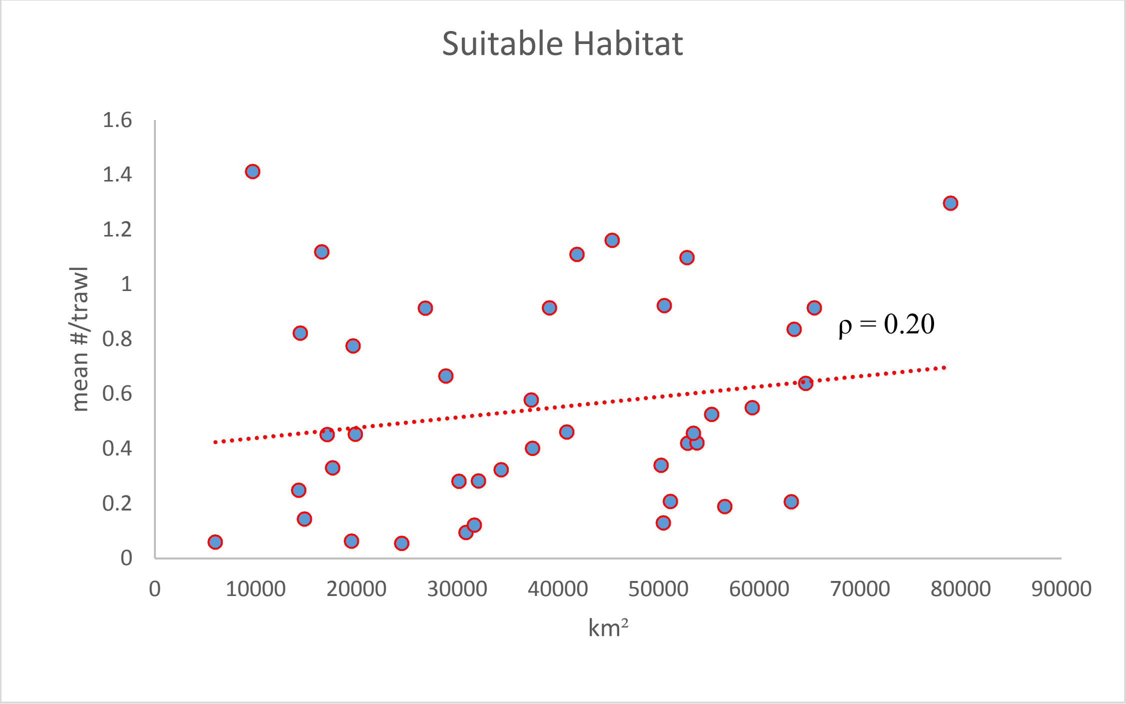


Figure 9 Correlation between suitable habitat in winter and CPUE in spring.

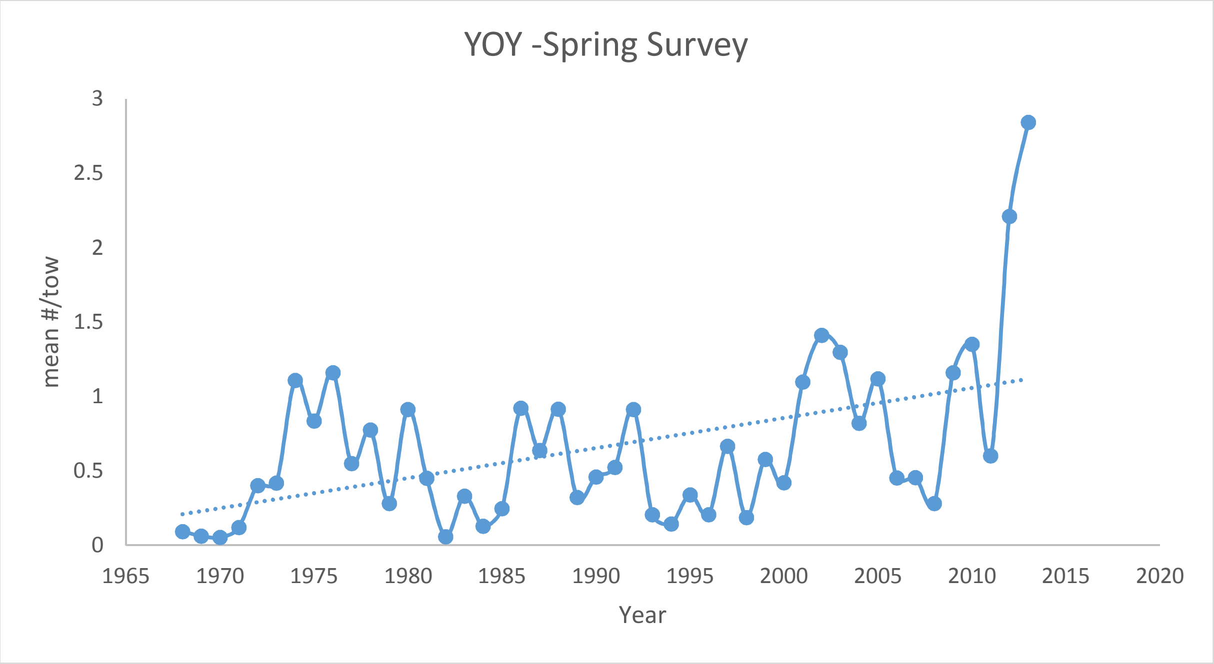


Figure 10 Mean number per tow of YOY black sea bass from the NMFS spring trawl survey from 1968 – 2013.

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