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Effects of Life History and Physical Variables on Winter Distribution of Blue Crabs in Chesapeake Bay

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Effects of Life History and Physical Variables on Winter Distribution of Blue Crabs in Chesapeake Bay

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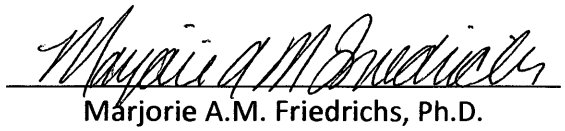

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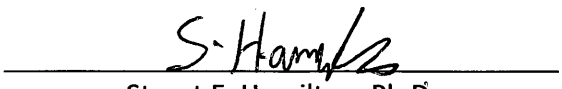

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ABSTRACT

The blue crab (*Callinectes sapidus*) is one of the most valuable fisheries in the Chesapeake Bay. Due to fishing pressure and environmental conditions over the past two decades, the population has experienced severe fluctuations in estimated abundance, ranging from 249-828 million crabs. I hypothesized that variability in spatial distribution over these years would correlate with these fluctuations in abundance and with various physical and biotic variables. To examine these hypotheses, I analyzed long-term data from the bay-wide blue crab winter dredge survey (WDS), which samples population abundance when water temperature falls below 10°C, usually from late November to mid-March. At this time blue crabs cease activity and enter a torpid state, enabling effective sampling of the bay-wide population in the absence of migration.

The analyses involved two-stage, Generalized Additive Models (GAMs) to assess the roles of temperature, salinity, depth and seagrass in predicting blue crab overwintering distribution from 1991 to 2004 for each age and gender class. The first stage corresponds to presence data while the second relates density data. Inputs included data from a combination of the WDS, geostatistical methods, the VIMS aerial submerged aquatic vegetation (SAV) survey, and hydrodynamic model output of the Chesapeake Bay Regional Ocean Modeling System (ChesROMS).

Physical variables were often significant when modeling blue crab distribution. Temperature and salinity were significant in most models for all crab classes, while depth was significant in more female models than male models. The effect of seagrass was generally not significant, but this may be due to selective sampling of large juveniles. Generally, smoothed functions were in agreement with previous literature.

Female presence had a positive relationship with depth at depths less than 18 m, at which point juvenile female presence decreased for depths greater than 18 m as they tend to stay in the shallow tributaries. Adult female presence continued to increase with depth until 24 m, at which point the smoothing functions deviated in shape. For males, depth was only significant in half of the years, with no noticeable trend in the smoothing functions.

Salinity was a significant predictor variable for juveniles, with curves exhibiting a shallow rise with salinity until 15-20 then a sharp decline, as juveniles remain in the shallower tributaries, coves and lagoons. Adult males followed a similar pattern, except that there were fewer males present in low salinities possibly due to the behavior of males whereby they remain close to the mouths of tributaries to intercept prepubescent females. Adult female presence had a positive relationship with salinity, as expected from their migration to the mouth of the bay prior to spawning. In some years females exhibited a bimodal relationship, possibly reflecting a sudden chilling of bottom water when migration of upper and lower bay females was halted.

Temperature was significant in almost every stage one model; however, the smoothing functions showed little generality. In addition, temperature was the hardest variable to

interpret due to the way that the temperature effect was handled. The temperature taken at the time a sample was taken by the WDS was not necessarily an indication of the environmental conditions at the time a crab buried in the bottom to overwinter. Instead, the day the bottom water became 10^{o}C at the sample point was used. This metric is useful in relation to the other points of that year, with earlier days indicating upper bay and tributary points and later days indicating lower bay sites. Maps made the relationships clearer, but this study highlighted the importance of the temperature variable as well as the need to refine the way temperature is studied in terms of interpretability, and the onset and duration of winter.

An effect due to seagrass, which is often cited as important nursery habitat for juveniles, was not significant in almost all models. This may have been due to the fact that the WDS was not designed to survey the young-juvenile segment of the population and tends to catch only the larger juveniles. The WDS effectively samples juveniles larger than 20-30 mm carapace width; these juveniles leave seagrass beds for non-structured habitat, which could explain the lack of a relationship with seagrass.

The study highlights interesting gaps of knowledge in blue crab ecology, particularly the importance and difficulty in measuring the effect of temperature in overwintering behavior, the need for a juvenile winter survey, and gives evidence to the difference in behavior of male and female juveniles.

Effects of Life History and Physical Variables on Winter Distribution of Blue Crabs in Chesapeake Bay

INTRODUCTION

The blue crab *(Callinectes sapidus),* a dominant species in Chesapeake Bay, is a principal component of the food web and also supports one of the Bay's most valuable fisheries (Fogarty & Lipcius 2007; Hines 2007; Lipcius et al. 2007). The blue crab is an integral part of the food web as a benthic predator, as well as an important prey item for pelagic fish species (Figure 1). In its range, over 101 species prey on blue crabs, including fishes, reptiles, birds, mammals and invertebrates (Guillory & Elliot 2001). The blue crab diet is diverse, consisting of benthic and epifaunal invertebrates, including bivalves, crustaceans, and polychaetes, fishes, and detrital matter (Tagatz 1968; Laughlin 1982; Hines et al. 1990; Mansour 1992). As such, they provide an important connection between the benthos and the water column (Baird & Ulanowicz 1989).

In addition to being a key part of the food web in Chesapeake Bay, watermen depend on the Bay's resources, including the blue crab harvest, to support their families and communities (Paolisso 2002). There are over 5,000 licensed commercial watermen (3,676 in Maryland (MDNR) and 1,649 in Virginia (VMRC)) that rely on the blue crab harvest. Since the mid-1990s, dockside value of the bay catch exceeded $40 million annually (National Marine Fisheries Service 2012). In addition to commercial value, recreational fishers also enjoy the summer tradition of harvesting and eating this iconic species.

However, overfishing (Miller et al. 2011), habitat degradation (Johnson et al. 2010), disease (Johnson et al. 2010) and global climate change (Hines et al. 2010) threaten the population and the fishery. The Chesapeake Bay blue crab population has declined for much of the late 1990s and 2000s (Figure 2). From 1992 to 2000, spawning stock abundance and biomass dropped 81% and 84%, respectively (Lipcius & Stockhausen 2002). There were also drops in larval abundance and recruitment (Lipcius & Stockhausen 2002), which remained at low

levels until 2008 (Miller et al. 2011). Recruitment overfishing, when high fishing pressure prevents the stock from replacing itself, and habitat degradation are cited as the leading causes of this decline (Lipcius & Stockhausen 2002). However, disease and global climate change could also be factors in the decline (Hines et al. 2010; Johnson et al. 2010).

From 1998 to 2002, around 60% of the blue crab stock was harvested each year (Miller et al. 2005). While overfishing may or may not be the primary cause of the blue crab decline, it is the easiest factor to mitigate. Managers and stock assessment committees have used a number of fishery-independent surveys, such as the VIMS and Maryland trawl surveys, Calvert Cliffs pot survey, and the winter dredge survey, to inform management. These surveys show that the lowest level of recorded blue crab density occurred in 2008 with an average of 26.6 crabs 1000 m^{-2}. Previously, the lowest documented abundance occurred in 1968. Whether or not the stock was overfished was determined by the threshold exploitation rate that maintained 10% of the spawning potential and the target as 20% of the spawning potential (Miller et al. 2011). Various regulations have been implemented to limit the blue crab harvest including mandatory days off, limiting time on the water to 8 hours daily, increasing the minimum size limit, and restrictions on where and when to fish (State of Maryland 2001, 2002). For example, in Virginia, a 1,700 km^2 spawning stock sanctuary was implemented in June 2000 that covers the migration corridor and spawning grounds used by females reaching the lower bay. In 2002, Virginia expanded the sanctuary to 2,400 km^2. In addition, waters deeper than 10.7 m are off limits from June 1st to September 15th. This corridor is effective and thought to protect as many as 70% of spawning stock females (Seitz et al. 2001a, b; Lipcius et al. 2003). Tagging studies found mature females in the sanctuary were 3 to 6 times less likely to get caught than females outside of the sanctuary (Lambert et al. 2006). While the corridor protects some gravid females,

known as sponge crabs, they may still be caught on the way to deep water or in the deep channel waters of Maryland (Aguilar et al. 2008). Most fisheries have temporal or spatial closures, but only a few will employ the most extreme form of regulation - complete closure of a fishery. In 2008, with historically low abundances of blue crabs the Winter Dredge Fishery, the only Chesapeake Bay blue crab fishery active in winter, was closed and as of yet has not been reopened. Following the closing, abundance estimates have increased with the most gain in mature female abundance (Miller et al. 2011).

In addition, habitat degradation, loss, and fragmentation, most notably due to the reduction of submerged aquatic vegetation (SAV) from poor water quality and weather events, have been suggested to have negatively affected the small juveniles that use the beds as a predator refuge (Hovel & Lipcius 2001; Sharov et al. 2003; Fogarty & Lipcius 2007). Large scale declines of seagrass occurred in the late 1960s and early 1970s (Orth & Moore 1983). From 1993 to 2006, SAV coverage in the lower bay continued on a downward trend from around 10,000 ha to 5,000 ha. After 2006, there was a shift back up to 9,000 ha in 2010 (Orth et al. 2010). This latter positive trend may loosely correlate with the recent rise in blue crab abundance. However, these recent years are still only 15% to 30% of the Bay's historical, pre-1970s, SAV distribution (Moore et al. 2004).

Furthermore, given the right conditions, several blue crab pathogens and parasites (*Vibrio* spp., *Hematodinium perezi, Paramoeba perniciosa* and *Loxothylacus texanus*) could deplete the stock. Shields and Overstreet (2007) offer an extensive review of blue crab diseases. However, there is little data on how parasitism or pathology affects the blue crab, or on a broader scale, how diseases may change the number of crabs in the bay. Even less is known about diseases and parasites of blue crab prey and predators. For example, reductions in

major prey items like oyster and clams due to disease could also lead to major shifts in blue crab diet (Johnson et al. 2010).

Finally, global climate change could affect blue crab by altering physical variables. Water temperature, which affects all vital processes such as growth, feeding, reproduction, and ontogenetic habitat shifts (Kennedy 1990; Edwards & Richardson 2004), is expected to increase. As sea level rises, spatial and temporal variability in salinity is predicted to increase in the Chesapeake Bay (Najjar et al. 2010). These changes in salinity may affect the cue for migration. Moreover, the extent of areas experiencing low dissolved oxygen (DO) and the duration of low DO events are expected to increase and may reduce foraging efficiency (Aumann et al. 2006) and alter migration routes of mature females down the estuary (Aguilar et al. 2005). Direct effects of changes in physical variables are the focus of most climate change scenarios, but the indirect effects may be more important (Harley et al. 2006). To the blue crab population, the biggest threat associated with climate change may be changes in wind and water circulation. The currents carry larvae onto coastal shelf waters to develop and then back into the Bay a few months later. A change in circulation patterns could carry those offspring far from the Bay to inhospitable waters and cripple blue crab recruitment. Other indirect effects may also prove important. For example, as sea level rises, marine waters will intrude into the estuary and may enhance disease invasions into the bay (Kennedy 1990). Behavioral changes such as adults moving to fresher waters to escape disease, may mitigate some of these effects (Berteaux et al. 2004). Additionally, a pervasive low DO regime may affect the distribution of benthic habitat on which small recruits rely (Diaz & Rosenberg 2008). While blue crabs have a wide set of tolerances, their ability to adapt will rely on the magnitude, duration and onset of these climate affects.

Traditional stock assessment methods have not been very effective in managing most fisheries. Of the 441 stocks of species groups for which FAO has compiled assessments, 52% are fully exploited, 17% are over-exploited, and 7% are depleted (FAO 2005). Hence, around ¾ of stocks must be continuously monitored and the regulations adjusted. In the past, ecological management was infeasible as marine systems were harder to sample mostly due to the level of available technology. However, ecosystem based fisheries management, a more holistic approach which integrates life history, environmental effects and interspecific interactions, is currently possible and could reduce uncertainty in predicting population dynamics (Botsford et al. 1997; Pitcher et al. 2009). However, ecosystem dynamics are controlled in part by hydrodynamic and atmospheric processes that regulate temperature and salinity. These processes influence productivity (Richardson et al. 1998), zooplankton community dynamics (Krause & Trahms 1983) and by extension, fish community dynamics. Management should incorporate these factors, especially in light of increasing variability due to global climate change (Frid et al. 2006). Life history and environmental factors have not been considered in most models of blue crab populations and should be included in light of the extensive evidence from field and laboratory experiments.

Blue Crab Life History

The blue crab spans the shallow coastal waters of Nova Scotia, Canada, to Pampas, Argentina (Williams 1974, 1984). Evidence suggests the genus evolved in the coastal ocean of the American tropics (Norse 1977). Adults mate and spawn in warm waters but can tolerate a wide range of temperature and salinity regimes. Conversely, larvae must develop in high

salinities and warm temperatures (Costlow & Bookhout 1965), deviations from which result in a lower hatch rate and fitness (Sandoz & Rogers 1944). These temperature and salinity developmental constraints lead to a complex life history strategy that varies with latitude (Smith 1997). In lower latitudes, due to the prevailing warmer waters, crabs can reach maturity in a year; however, in the colder higher latitudes, maturity occurs in the second season after development (Ju et al. 2003). These latitudinal differences and their effects on crab behavior can be seen on a scale as small as the lower and upper Chesapeake Bay. For example, crabs cannot molt below 10°C (Brylawski & Miller 2003). The warmer waters of the lower Bay allow a proportion of the fast growing female crabs to molt to maturity in the fall, while the rest overwinter and molt to maturity the following spring. In the colder, upper Bay, females require the full two years to reach maturity. This leads to two periods of mating in the lower Bay versus a single peak in the upper Bay (Hines et al. 1987; Gibbs 1996). To comprehend the spatial distribution of blue crabs, these latitudinal differences and blue crab life history must be integrated into investigations.

In the Chesapeake Bay, blue crab larvae are released near the entrance of the bay in the late spring or summer where they are transported in the offshore waters over the continental shelf (McConaugha et al. 1983). They develop in the coastal ocean for 1-2 months and go through seven or eight zoeal stages (Costlow et al. 1959). By late summer and fall, they metamorphose into the megalopal stage and are transported back to the mouth of the estuary where they use selective tidal stream transport to move into the tributaries (Forward et al. 2003; Figure 3)

The time of settlement and the habitats selected in the recruiting stage are primary factors in juvenile blue crab distribution (Forward 1989; Forward et al. 1996, 2003). Megalopal

settlement is correlated to moon phases, with higher settlement at the new and full moons than during waning and waxing moons (van Montfrans et al. 1990, 1995; Metcalf et al. 1995; Olmi 1995). Large scale disturbances, such as hypoxia, can alter distribution patterns of adult blue crabs, and thus increase cannibalism on juveniles (Eggleston et al. 2005). The current paradigm is that blue crabs preferentially settle in structured habitats like submerged aquatic vegetation (Heck & Thoman 1984; Orth & van Montfrans 1987) and after reaching approximately 20 mm carapace width (CW- the distance between lateral spines) they move to unstructured habitats (Hines et al. 1987; Orth & van Montfrans 1987; Pile et al. 1996).

Several lines of evidence support this model. First, chemicals released from seagrass, macroalgae and humic acid induce metamorphosis in megalopae (Forward et al. 1994, 1996, 1997). In addition, shallow structured habitats like seagrass and marsh can act as valuable nurseries for species with complex life cycles by enhancing survival, movement and growth rates relative to nearby unstructured areas (Heck & Thoman 1984; Beck et al. 2001; Heck et al. 2003; Minello et al. 2003). Small juvenile crab densities are highest in association with structured habitat, particularly seagrass, and lower on non-structured soft bottoms, though density is also affected by salinity, temperature and DO (Heck & Orth 1980; Everett & Ruiz 1993; Perkins-Visser et al. 1996; Pile et al. 1996; Moksnes et al. 1997; Ryer et al. 1997; Etherington & Eggleston 2000; Heck & Spritzer 2001; Hovel & Lipcius 2001, 2002; Rakocinski et al. 2003). This may be due to reduced predation by visual predators (Heck & Thoman 1984; Orth & van Montfrans 2002). Conversely, for older juveniles, multiple studies suggest unvegetated habitat is important due to high prey densities in sand and mud (Mense & Wenner 1989; Rakocinski et al. 2003; Lipcius et al. 2005; Seitz et al. 2005). Finally, tethering experiments in the York River suggest that juveniles

between 25 and 55 mm CW survive longer in upriver sand and mud than in seagrass and the lower river (Lipcius et al. 2005)

However, movement after reaching 20 mm CW may not be the only case of juvenile migration. Small juveniles can undergo secondary dispersal due to environmental or biological conditions (Etherington & Eggleston 2000; Reyns & Eggleston 2004; Forward 2005). In their first year, Chesapeake Bay juveniles can grow up to or greater than 100 mm CW. Some females may grow fast enough to copulate and spawn by the end of their first summer, but the vast majority will copulate, gather reserves, and overwinter, waiting until the following season to spawn (Van Engel 1958; Ju et al. 2003). By their second summer crabs are in the age 1+ class and females molt to maturity (Hines 2007). Since crabs have no hard structures that are retained through ecdysis, age structure is based on size. Winter dredge survey size frequency distributions exhibit a bimodal distribution with a split at 60 mm CW (Figure 4), corresponding to the boundary between the age-0 and age 1+ classes. After a female receives a sperm packet she will cease molting and migrate to the lower bay to produce broods and incubate the eggs until larvae are released at the mouth of the bay (Van Engel 1958; Millikin & Williams 1984). In contrast, males remain in the tributaries and upper estuary and continue to grow and molt. In the Chesapeake, mature males range in size from 87-227 mm CW (Millikin & Williams 1980; Williams 1984).

In the winter, males and juveniles generally stay in the tributaries but migrate towards deeper water to bury (Hines et al. 1987; Sharov et al. 2003; Aguilar et al. 2005). Females have a much longer two-phase migration after mating. The first phase occurs in fall after insemination when females follow a temperature or photoperiod cue to move to the lower estuary to produce and incubate their broods (Turner et al. 2003; Aguilar et al. 2005). The more saline waters (> 20) encourage egg development and hatching (Davis 1965). In the Chesapeake, when

the temperature drops below 10°C the females bury in the sediment for the winter (Aguilar et al. 2005). They emerge in the spring and may move as much as 200 km along the deep channels of the mainstream rather than shallow nearshore routes to complete phase one (Tankersley et al. 1998). The second phase occurs when ovigerous females migrate from the lower estuary to the mouth to hatch their eggs and release the larvae into the water column (Tankersley et al. 1998). Females prefer a mix of sand and silt during spawning (Schaffner & Diaz 1988) as this promotes the formation of egg membranes and attachment strands (Kuris 1991). The spawning season in the Chesapeake lasts up to five months and could allow multiple broods per female (Dickson et al. 2006). Female blue crabs can have as many as 6 million eggs in the first brood; however, later broods are smaller and the number of embryos that develop declines by up to 40% from the 1st to 4th brood (Hines et al. 2003; Darnell et al. 2009).

Adult Overwintering Blue Crab Distribution

Schaffner and Diaz (1988) assessed winter distribution patterns of adult blue crabs in the Chesapeake Bay. Blue crabs showed a preference for sediments containing 41 – 60% sand. They were more often found in basins rather than shoals and spit areas, and at depths greater than 9 m (Schaffner & Diaz 1988).

When the WDS was initiated, the main purpose was to provide fishery managers with a monitoring tool for the Chesapeake Bay blue crab population. In addition to the population and mortality estimates the survey has provided since the 1990s, the survey has also informed studies of distribution and abundance. Jensen et al. (2005, 2006) used geostatistics to explore distribution, while spatial variability in winter mortality was assessed by Bauer and Miller (2010).

Jensen et al. (2005) analyzed 13 years of WDS data (1990-2003) to examine distribution and abundance of mature female crabs using a two-stage generalized additive model with depth, salinity, temperature, distance from the mouth of the Bay, distance from SAV and bottom slope. They found depth and distance from the mouth of the bay were dominant variables for predicting female abundance, followed by temperature and salinity. Depth and distance from the mouth of the bay are static variables and are inadequate for determining inter-annual variability. The authors stated that other factors not included in their models must be playing a role; these may include the onset of cold winter, density-dependent habitat selection, and to a lesser extent, hypoxia and sediment type. This study expands on the work of Jensen et al. (2005) by examining these processes in WDS data for males, females and juveniles separately, rather than just the mature females as examined by Jensen et al. (2005). Accurate estimates of temperature and salinity were garnered from the ChesROMS hydrodynamic model, depth from WDS, and a new seagrass effect variable utilizing both distance and area of closest seagrass was added.

Factors and Predictor Variables

Temperature and salinity affect the temporal and spatial distribution of crabs (Hines et al. 1987; Steele & Bert 1994). In blue crabs, 10˚C is the lowest temperature required for activity (Brylawski & Miller 2006; Smith & Chang 2007) and in the Chesapeake Bay, it is the temperature at which crabs bury. Temperature had two functions in this study. All WDS tows taken above 10˚C were eliminated from the analysis. Also, the time a crab has to migrate to the mouth varies by year because of temperature. If the onset of winter is early, crabs will bury sooner and

may or may not be in prime overwintering habitat. If winter comes slowly, crabs will have a longer time to migrate and the data may show a higher concentration of females towards the mouth of the bay. Thus, temperature is a key factor in determining overwintering spatial distribution. However, the temperature taken at each tow is not a reliable indication of when the crabs buried. A more appropriate metric for the temperature effect is the day in winter when bottom water temperature reached 10˚C for every given sample point in the bay. There are no daily records of bottom temperature for every part of the bay for the last 20 years, but there are models for bottom water temperature until 2005, such as the ChesROMS model. These models perform well when compared to station data and were used to approximate the day at which bottom temperature at any given point reaches and stays at 10˚C for 24 hours after November 1st.

Salinity affects blue crab behavior depending on age and sex. In general, the highest densities of crabs occur in mesohaline and polyhaline (18-30) zones (Orth & van Montfrans 1987; King et al. 2005; Lipcius et al. 2005). In some systems, juvenile abundance is highest in low salinities (Lipcius et al. 2005; Posey et al. 2005), due either to reduced abundance of predators or to greater availability of benthic prey such as the Baltic clam (Seitz et al. 2005). In contrast, mature females concentrate in deeper saline waters of the lower bay where they overwinter prior to spawning the following spring and summer (Van Engel 1958; Schaffner & Diaz 1988; Lipcius et al. 2001, 2003; Seitz et al. 2001b, 2003; Aguilar et al. 2005) . This study used the bottom water salinity value of every station when the temperature reached and stayed at 10˚C for 24 hours after November 1st. This was to ensure that the bottom water salinity had maintained winter stability. Observations of the bottom salinity data show relatively constant values after bottom water has reached 10˚C and support that there is little covariation between

temperature and salinity estimates. Distance to the mouth of the bay was an important predictor variable in Jensen et al. (2005). However, for this study it was highly correlated to the salinity variable. Given the choice between distance to the mouth or salinity, salinity was included because distance to the mouth is static and will not vary by year.

Depth and sediment type also determine locations where crabs bury during winter (Schaffner & Diaz, 1988); highest abundances of mature blue crabs occurred at depths greater than 9 m and in areas between 41% and 60% sand. The interplay between depth and optimal sediment type likely affects insulation, whereby deeper waters have more constant temperatures whereas shallow waters have higher variance and accompanying physiological stress. Sediment maps did not exist for the Chesapeake Bay and hence were not included, but depth was taken from the WDS.

Seagrass effect, a combination of the area of closest seagrass and distance to the closest seagrass, is the only biological variable included in these analyses and may be important for determining juvenile overwintering density. Once inside the bay, megalopae settle in seagrass or other structured habitats where they metamorphose into the first benthic instars (Heck & Thoman 1984; Orth & van Montfrans 1987; Etherington & Eggleston 2000). Juveniles either remain in this habitat until they are 20 to 30 mm carapace width at which point they migrate to unvegetated habitat, or they exhibit secondary dispersal cued by environmental or biological conditions (Etherington & Eggleston 2000; Reyns & Eggleston 2004; Forward 2005). While the dredge survey is limited to sampling habitats deeper than 2 m, useful trends from the limited data may inform future research surveys.

Overall objective

The overall goal of this thesis was to use and modify existing methods to develop a better understanding of the possible mechanisms driving overwintering distribution of blue crabs. Specifically I used a two-stage Generalized Additive Model (GAM) to analyze the blue crab distribution data from the winter dredge survey in regards to temperature, salinity, depth and a combined effect of distance and area of seagrass. By assessing and understanding overwintering distribution in light of the previous literature, we can expand the tools of management and highlight gaps in blue crab knowledge.

METHODS

Winter Dredge Survey

The winter dredge survey (WDS), a stratified random survey, was originally developed to evaluate the bay-wide blue crab stock annually by assessing the size, sex, abundance and mortality of the population above 15 mm carapace width (CW) each year. Every November through March since 1989, 877 to 1500 random stations deeper than 1.5 m have been sampled bay-wide. The data collected include crab sex, crab size, depth and location of the beginning and end of each tow. For some locations and years, temperature, dissolved oxygen, salinity, sediment type, bottom type and bycatch were also recorded (Figure 5).

The original design, based on a pilot survey in 1989 (Rothschild et al. 1992), underwent varying stratification and sub-stratification, sample allocations, area towed, and replicate tows per site. Although Schaffner and Diaz (1988) found sediment type to be important for burying behavior, sediment type as a stratum was removed from the survey in 1992 due to the lack of

an accurate bay-wide sediment map which could lead to bias from inaccurate substratum weights, tow length sampling more than one sediment type, inconsistent sediment distribution over time from currents and tidal effects, and cost. Paired tows were removed due to correlation (r^2~0.5-0.7) between the tows. Sharov et al. (2003) found that stratification by river and major parts of the bay, with sub-stratification by sediment type and paired tows exhibited only marginal improvement to the models and were discarded. In 1994, the design reached consistency with three strata (Upper Bay and Rivers, Intermediate Bay, and Lower Bay), established total area sampled (9,812 km^2), a greater number of stations sampled (1,287-1,500) and single tows. Each tow covers about 100 m, lasts one minute at 3 knots, and is done with a 1.83-m-wide commercial crab dredge with a 1.3-cm-wide mesh liner. The survey is conducted by two vessels- a dead-rise in Maryland and a modified passenger transport boat in Virginia. Catchability differences between the two vessels were taken into account by including a vessel variable in the model. More details about the design can be found in Vølstad et al. (2000) and Sharov et al. (2003).

One limitation is that the survey does not representatively sample juveniles since the boats can only tow in depths greater than 1.5 m and the dredge mesh only consistently retains crabs above 15 mm CW. Other constraints include inconsistent sampling on different substrates, sampling after the crabs have finished overwintering, and exclusion of deeper sites close to shore due to boat access.

For this study, crab sex and size were used to differentiate the crab classes for the models with crabs < 60 mm CW considered juveniles (Age 0+) and crabs > 60 mm CW as adults (Age 1+). Tow area was used to standardize crab abundance. Station location was used in calculating physical variable estimates from the ChesROMS model and in the GIS calculations of

distances and areas. Sample day was used in conjunction with the ChesROMS model to omit samples taken when temperature was above 10^{o}C. Average depth of the tow was added as a predictor variable in the GAM model.

Aerial Seagrass Survey

Annual bay-wide seagrass area and distributions were derived from the VIMS Submerged Aquatic Vegetation Program's annual aerial survey (Orth et al. 2010). The survey produces annual aerial photographs taken at an altitude of approximately 4,000 m, yielding a scale of 1:24,000 (1 map cm: 24,000 real world cm). This translates to a scale of 7.5 minute quadrangles, or a box with an area of 7.5 minutes of longitude by 7.5 minutes latitude. National Mapping Accuracy Standards for 1:24,000-scale mapping mandate that 90% of the features in the spatial coverage be within 14 m of their exact location on the face of the Earth. At 1:24,000 scales, a 0.5 mm line covers 12.5 m on the ground. Therefore, the smallest resolvable object on a 1:24,000 scale map must be 14 m in size. The survey is taken during the peak growing season of seagrass, and covers over 4,000 km of flight line. The photographs are georectified and orthographically corrected to produce photomosaics. Each seagrass bed is outlined and the density of seagrass within each bed or subsection within the bed is estimated and classified into one of four groups: 1, very sparse (< 10%); 2, sparse (10-40%); 3, moderate (40-70%); and 4, dense (70-100%). The data are ground-truthed opportunistically in collaboration with other parties and have confirmed the location of some beds as well as found beds too small to be detected in the aerial photographs.

The seagrass distributions are constrained in that the flights generally occur from May to July and may not represent the seagrass available when crabs begin to overwinter. The survey also misses seagrass beds smaller than 14 m^2. However, there are no other data of this sort at a sufficiently high resolution or spatial coverage.

This study used the annual seagrass photomosaics in conjunction with GIS to measure the distance of each sampling point to the closest seagrass bed and its area. Both the distance and area estimates were used to create the seagrass effect variable which was weighted by the bed's distance from seagrass. The following function was used to determine the weight:

$$weight = 1 - \left[\frac{1}{1 + \exp -(distance\ to\ seagrass\ (km) - 5)}\right]$$

The function maximizes the effect of seagrass for a few kilometers until a threshold at 5 km, then drops to nearly zero by 10 km (Figure 6). The equation is an approximation and derived from the distances of seagrass beds in the tributaries to habitats utilized by older juveniles and adults. Seagrass effect was calculated by multiplying the area of seagrass closest to a point by this weight.

ChesROMS

Chesapeake Bay Regional Ocean Modeling System (ChesROMS) is a primitive equation model that constitutes the hydrodynamic component of the Chesapeake Bay Prediction System. ChesROMS is based on the Regional Ocean Modeling System (ROMS) and configured with physical and biogeochemical processes important for shallow estuaries. Primitive equations are

the standard set of nonlinear differential equations used in atmospheric models and consist of equations describing continuity, thermal energy and the conservation of momentum.

Bathymetry was extracted from the high resolution coastal relief model data from NOAA's National Geophysical Data Center. An orthogonal curvilinear grid (100x x 150y x 20z) was chosen to follow the deep channel and complex coastlines. This version of the ChesROMS model (Scully 2010) provided temperature and salinity estimates, which have been validated with historical data from the Chesapeake Bay Program, real time measurements, and satellite remote sensing. While the model estimates temperature well, the model underestimates salinity variability. See http://www.myroms.org/Papers/roms.pdf for details of the ROMS model and http://ches.communitymodeling.org/models/ChesROMS/index.php for ChesROMS.

The ChesROMS model constrained the analysis in a number of ways. First, the simulation used in this analysis extended from 1991 to 2005. In addition, around 100 sampling points each year were removed because they were shallow sites out of the model domain. Finally, the model grid cells have the lowest resolution of any data used. For example, the largest cell is about 1 km x 3 km in the xy plane. Hence all sample points taken in that cell will have the same value.

The model was used to calculate (1) on what day after November 1st a station point reached < 10°C for two consecutive days, (2) the day after February 1st that it took a station point to reach above 10°C for two consecutive days, and (3) bottom salinity from the day it reached below 10°C when the water column would have presumably stabilized for winter. The first two measurements were used to exclude samples taken when the bottom water temperature was above 10°C. The day the temperature turned 10°C and salinity were also included in the GAM models.

GIS

Considerable progress has been made in all areas relating to blue crab dynamics. In the past, however, survey data had proved cumbersome to analyze spatially. Geographic Information Systems (GIS) tools allow easy conversion of spatial data into information about a given area of the earth. However, scale should be considered *a priori*. For example, had the dredge survey, seagrass survey, and ChesROMS model been specifically structured for this project, the data would have been taken at the appropriate scale to match the scale of the ecological phenomenon (overwintering crab distribution). However, this is not the case. To reconcile the differing scales of the data the worst or largest scale data should be used. In this study that is the ChesROMS data with an average horizontal cell size in the bay of 1.5 km x 0.5 km.

Measuring tools of GIS provide robust analyses, ranging from simple area calculations to complex connectivity analyses. These tools were used to calculate the total area of each contiguous SAV bed (including *Zostera marina, Ruppia maritima*, and macroalgae) from 1990 through 2004. Euclidean, or straight line distances, as well as modified straight line distances to account for obstacles were also used. To prevent distances or paths from crossing land, a cost raster was created that assigned a high cost to traveling on all "land" cells. These distance tools were used to calculate the distance to the mouth of the Bay and distance to the nearest SAV bed, and then linked with the contiguous SAV bed map to find the area of closest SAV.

These tools rely on the use of raster data, rather than vector data, to store spatial information. Raster data are easy to store digitally and manipulate mathematically, but only

one attribute can be displayed at a time. Once the raster data were complete, the vector data from each dredge year were overlaid on the raster for each attribute, and the value of the raster cell extracted for each station.

GAM

From the dredge survey, the abundance of each crab class was acquired and served as the dependent variable in the analysis. The independent or predictor variables came from various sources. The dredge survey provided depth, the seagrass survey provided the distance to seagrass and area of seagrass, which were used to calculate seagrass effect, and ChesROMS provided the temperature proxy and salinity estimate.

Regression analyses focus on the relationship between dependent and independent variables. The goal of this research was to relate number of crabs to various predictor variables; however, a multiple regression framework is inappropriate due to the assumption that the response variable follows a normal distribution. Count data, like the number of crabs caught, especially in a case where many observations are zeros, are better approximated using a Poisson, gamma or negative binomial distribution (Gardner et al. 1995). Generalized linear models can accommodate any distribution in the exponential family due to its link function ($g_i(y)$) replacing y. However, given the number and nature of the variables being explored, the assumption of linearity is inappropriate. Linearity was evaluated through the smoothing functions and estimated degrees of freedom.

A Generalized Additive Model (GAM), first proposed by Hastie and Tibshirani (1986), does not assume linearity and instead uses the data to build functions that relate each predictor

variable to the response. The simple regression coefficients ($B_0 \ldots B_n$) in linear models are replaced with a non-parametric smoothing function of the predictor variable ($f_0 \ldots f_n$).

Multiple Regression

$$Y = B_o + B_1(X_1) + B_2(X_2) + B_3(X_3) + B_4(X_4) + \ldots B_pX_p$$

Generalized Linear Model

$$g_i(Y) = B_o + B_1(X_1) + B_2(X_2) + B_3(X_3) + B_4(X_4) + \ldots B_pX_p$$

Generalized Additive Model

$$g_i(Y) = f_o + f_1(X_1) + f_2(X_2) + f_3(X_3) + f_4(X_4) + \ldots f_pX_p$$

The smoothing function may be based on cubic spline smoothing or locally weighed scatterplot smoothing (LOESS). In the cubic spline case, each predictor variable is graphed with the response variable then modeled using third order cubic functions pieced together. In LOESS, polynomial functions of any order are fit to localized areas called neighborhoods. The degree of smoothing relies on the size of the neighborhood in which a single point is estimated. If neighborhoods are too small then the function will be choppy, noisy and overfit. This could lead to models that include noise and can only fit that particular data set. If neighborhoods are too large the functions may be underfit and lose trends. In this case, models may be too general and not show important predictor variable effects on the response variable. The strength of a GAM analysis lies in the flexibility of the predictor variables; however, GAMs are prone to being overfit and harder to interpret than their linear counterparts.

Generalized Additive Models were used to describe the relationship between each crab class and the above predictor variables. One large GAM, including year as a variable was run but more than half of the years appeared significant in the model. Hence each year was run individually. The data were graphed and appeared zero-inflated, meaning there were higher proportions of zeroes in the data than that of the corresponding candidate model families. The distribution of the count data also indicated possible Poisson overdispersion, where variance is larger than the mean. A correlation matrix indicated that some variables may be collinear with each other. These issues were addressed in the analysis. To address the high proportion of zeroes in the data, a two-stage GAM was used. The first-stage GAM analyzed the presence and absence of crabs, while the second stage GAM analyzed the density of crabs when present.

In the first stage, a GAM where the response variable follows a binomial distribution with a complementary log-log link (cloglog) was used to analyze presence-absence. Usually logit links are used with the binomial distribution; however, our data have a disproportionate amount of zeros and do not fit the assumption that 0s and 1s are approximately equal. A cloglog link, like the standard logit, is also a sigmoid function but as probability increases the transformation approaches infinity slower than either the logit or probit links. Unlike the logit and probit, cloglog is asymmetric, which makes it suitable for data with an extreme value distribution. The following is the cumulative distribution function for cloglog where X is the independent variable, Y is the dependent variable and B is the regression coefficient:

$$ln\{-ln[1 - Pr(Y_i = 1)]\} = X_iB$$

In the second stage, only the samples with presence were analyzed. AIC was used to determine that the density data fit a negative binomial distribution better than a Poisson or a Poisson corrected for overdispersion.

While different distributions and links were used for each stage, the rest of the methods remain constant for both stages. The full model is given by

$$Y = \text{factor}(V) + s(D) + s(Temp) + s(Sal) + s(SGE)$$

Where V = vessel, D = depth, Temp = Julian day that bottom temperature turned $10^{o}C$, Sal = bottom salinity on the Julian day that bottom temperature turned $10^{o}C$, and SGE = a weighted effect of seagrass with distance and area of seagrass as inputs. Although not indicated in the equation, a master model containing year as a factor was run. However, there were significant differences between years and hence, each model was run for every year. The vessel term, which accounts for the different boats used in the survey, remained unsmoothed while the main effects were smoothed with individual 5-knot, penalized regression splines. [Knots are the join points in smoothing functions.] Keele (2008) gives a general rule to use 3 knots if there are less than 40 observations and 5 knots if there are more than 100. The penalized regression spline is the default smoothing function in R's mgcv package and differs from a piecewise 3^{rd} order polynomial spline only in where the knots are placed and how model complexity is controlled through penalized likelihood maximization where a penalty is added for each smoothing function.

Assumptions were validated through graphical diagnostics. Histogram and QQ plots assessed normality, residual versus linear predictor plots assessed homogeneity of variance,

effective degrees of freedom evaluated nonlinearity, and mapping the residuals in space assessed autocorrelation.

To summarize the important predictor variables for crab presence/absence and crab density the significant terms were tallied through the years for each crab class. The significant smoothed functions were also evaluated.

RESULTS

Collinearity was evaluated through scatterplots of each combination of predictor variables and Kendall's tau (τ), a rank correlation coefficient used when the distribution of the parameters is non-normal. Both showed a strong positive correlation (τ = 0.57-0.68) between salinity and distance to mouth of the bay for all 14 years of the study (Appendix A). Due to this relationship, distance to the mouth of the bay was dropped from the models as salinity is more likely to have a causal effect on crab distribution.

Temperature and salinity exhibited strong correlation for five years ($\tau \geq 0.5$) but the collinearity between these was deemed insufficient to eliminate one of the variables. Instead the model results will be interpreted in light of this possible relationship. Evaluation of the scatterplots revealed linear patterns, probably due to the large scale of the ChesROMS data where multiple tows conducted near each other will have the same temperature and salinity estimate due to the tows being in the same ChesROMS cell. The full model was run for every year and crab class with significance at the alpha ≤ 0.05 level (Appendix B).

For the stage one GAM (presence/absence), temperature day was important for every class, appearing in 65 out of 70 models. Salinity and depth appeared significant 62 and 49 times

respectively, while seagrass effect was only significant in 10 models (Appendix C). For the stage two GAM (density), temperature day was important for every class, appearing in 47 out of 70 models. Salinity and depth were significant 40 and 33 times, whereas the seagrass effect was only significant in 11 models (Appendix D). In general, first stage GAMs had more significant variables than second stage GAMs, probably due to the number of observations for each stage. For stage one, N ranged from 1122 to 2521, and for stage two N ranged from 106 to 1152. The penalized regression spline fits of each predictor variable on either crab presence (stage one) or crab density (stage two) for each year and class (Figure 7) showed a variety of shapes. If the p-value was > 0.05, the fit was not significant and the p-value was provided instead of the fit. Note that for the GAM script in R's mgcv package, alpha at 0.05 is not strict due to uncertainty in lambda when calculating the effective degrees of freedom using cross validation. If the degrees of freedom were known, there would be less uncertainty around alpha. Simulation from Wood (2006) found that p-values close to 0.05 can be half their correct values when the null hypothesis is true. Hence smoothing functions with p-values less than 0.001 and greater than 0.2 can be readily trusted while anything in between should be taken with caution. Better estimates could be obtained through bootstrapping, had computational power and time not been an issue. If the focus had been on prediction rather than exploration and mechanisms, bootstrapping would have been the method of choice.

In most models for juvenile females, presence increased with depth until peaking at 12-24 m, after which the relationship became less stable. Density decreased with depth in four out of the five significant smoothing functions. Salinity was significant for crab presence every year and the smoothed models follow the same pattern. In general, salinity had a positive effect on crab presence until about 6 m where there was a steep decline. The predictor functions for

density were more heterogeneous, but most curves show a humped relationship with highest density at 3 and 6 m. Temperature and presence show a general decline except for 1992, 2002 and 2003, which had ambiguous curvilinear relationships. For density, four of the six significant relationships had a linear decline. Seagrass effect was only significant in two of the 14 years for both the presence and density GAMs.

Mature female presence increased with depth until leveling at 24 m, after which the relationship was less certain. Density also increased with depth until 18 m except in 1992, 1998 and 2004. There was an increase in crab presence and density with salinity for most years; some years had a bimodal relationship. There was a general decline in presence until temperature day 345 at which point the relationship was less certain. For density, the peak was between days 345 and 350. Some years also had a peak at the earliest temperature day; however there were few data points close to the lowest temperature days. Seagrass effect was only significant in four of the presence GAMs and three of the density GAMs, but showed a negative relationship in all but one smooth.

For all years but 2003, juvenile male presence increased with depth until 12-15 m, at which point presence decreased. Presence and salinity followed the same general pattern as the one described for juvenile females; however, the relationship between density and salinity curves was not consistent. In general there were lower densities at the lowest and highest salinities, except for 1995, 2002 and 2003. Presence and temperature had a negative relationship except for 1992, 1994 and 2001. Density and temperature also had a negative relationship except for 1992 and 1993. Seagrass effect was not significant in the presence models and only significant in one density model.

Adult male presence with depth was significant for eight years. Except for 2003 and 2004, depth and presence shared a positive relationship until 24 m at which point the pattern was inconsistent. Density was significant in five years with three showing a negative relationship with depth. Highest presence was between 10 and 20 every year, with most years at 15. Salinity and density were only significant for three years but had a negative relationship in two years. Temperature and presence had a negative relationship except in 2001 and 2003. The smoothing functions for density and temperature were driven by clustering around temperature days. Years with even spread along temperature days had a negative relationship with density.

The output included two measures of goodness of fit (Appendix B): the adjusted r-squared is an estimate of the proportion of variance explained and the deviance explained. Deviance explained uses null deviance, which is the deviance for a model with just a constant

$$Deviance\ Explained = \frac{Null\ Deviance - Residual\ Deviance}{Null\ Deviance}$$

term, and residual deviance, which is the deviance of the fitted model. The latter is a generalization of r^2, best suited for data with non-normal errors (Wood 2006) and will be the goodness of fit measure analyzed in this study. Adult females had the least average deviance explained for stage one at 9.7%, followed by adult males (13.6%), juvenile females (15.2%) and juvenile males (16.1%). Stage two also has adult females having the least deviance explained (18.1%) followed by juvenile females (20.2%), juvenile males (21.1%) and adult males (24.1%).

Cross validation, a technique to assess how accurately a model can predict in practice, was not used with these data. The purpose of this study was exploratory. Thus, the data were

used to construct models rather than validate models for prediction. Cross validated models of the adult female crabs can be found in Jensen et al. (2005)

Assumptions

Graphical diagnoses validated model assumptions. Histograms and QQ plots evaluated normality, residual versus fitted value assessed homogeneity of variance, and response versus fitted values assessed model fit. Non-linearity was assessed through the smoothing functions (Figure 7) and the estimated degrees of freedom (edf, APPENDIX B). Higher edf indicates higher non-linearity in the smoothing spline. Temporal autocorrelation did not need to be addressed since each year was evaluated individually. Spatial autocorrelation was minimal at the broad scale of this study and was evaluated by mapping the residuals of all 140 models (APPENDIX D). No one class or area had predominantly skewed negative or positive residuals, though some areas may have had more extreme positive and negative residuals than other areas. Sample points were randomly chosen and had approximately even spread through the years, though in some years there were gaps in sampling (APPENDIX D).

DISCUSSION

Blue crab spatial distribution was predominantly a function of physical variables, with substantial variation by age class and gender. Temperature and salinity were significant in almost every stage one model regardless of crab class. Depth was more important in predicting

female presence than male presence, while seagrass effect had little power in predicting either presence or density.

Depth

Female smoothing functions for presence had a general increase with depth until 18 m, at which point juvenile female presence decreased with depth because they remained in the tributary shallows. Adult female presence continued to increase with depth until 24 m at which point the smoothing functions deviated in shape. The deeper depth coincides with the migration destination of adult females to the mouth of the bay. While depth appeared important in most female models, depth was only significant for half of the male models. Interestingly, juvenile and adult male smoothing functions, while not the same shape, were also important for most of the same years. Juvenile male curves, when significant, were similar to the juvenile female curves, which peaked in presence at 18 m. These data demonstrate that juvenile male depth distribution was similar to that of males in terms of significance of depth as a predictor variable and to that of juvenile females in terms of the smoothing function shape. This may indicate that juvenile males and females should be treated separately and suggests investigating the size at which juvenile males and females begin to exhibit different patterns in depth distribution.

Salinity

Salinity was a significant predictor variable for juveniles in all years except 2004. The curves exhibited a shallow rise with increasing salinity until a peak around 15-20, then a sharp decline afterwards. This was expected as juveniles remain in the rivers. Adult males followed a similar pattern with the exception that the smoothing function was humped with fewer males in low salinities. This supports the assumption that males tend to stay in the middle and downriver parts of the bay to mate with pre-pubescent females traveling from upriver lower salinity waters. Adult female presence followed an interesting progression pattern. As expected, there was an increase in presence with higher salinity since females migrate towards the mouth of the bay. However, some years showed a distinct two humped smooth, possibly reflecting the migration of upper and lower bay females that had to overwinter before heading to the mouth. Some years had a linear smooth, indicating that both of these groups arrived at the mouth of the bay before overwintering. Variation between these two shapes was also apparent (Figure 8). Again, the density GAMs could not be generalized well due to inconsistent shapes. However, it appears that juveniles shared the same curves in a given year and that females had higher densities between 25 and 30.

Temperature

Temperature was the predictor variable that was significant in every stage one model save five. However, it is also the hardest variable to interpret due to both the low resolution of the ChesROMS model as well as the way that the temperature effect was handled. The scale bar for temperature day changed each winter, reflecting both the onset and duration until all bottom water reached 10^{o}C. For example, compare the smoothing functions for adult females in

1996 and 2003 (Figure 9). Given the range of temperature days, 1996 was a year with an earlier onset of cold but gradual cooling, whereas 2003 was a year when the onset of cold was a week later but the entire Chesapeake chilled two times faster. Air temperature data from four weather stations near Virginia Beach close to the southern limit of the Chesapeake, (US1VAVBC004, US1VAVBC0013, US1VAVBC015, USC00440385) (NCDC 2012), although limited in that they only provide monthly averages, supported the trend. The mean monthly temperature in November 1996 (16.1^{o}C) was the lowest November temperature, whereas 2003 (22.4^{o}C) had the highest average November temperature for 1991-2004. Hence the onset of cold temperatures on land also appeared to be earlier in 1996 than 2003. In 1996, December temperatures dropped by 5% from November, compared to a 40% drop in 2003 to 13.3^{o}C. This corresponds to the quick chill in 2003.

The 1996 stage one smoothing function indicates high presence of females at the earliest temperature day, 310, and a lesser presence around day 350. In 2003 there was one hump, with presence greatest on day 327. Given the slow chilling of 1996, one might expect all female crabs to have arrived at the mouth of the bay. However, there was a large proportion of presence data close to the days that chilled quickly. The trends are clearer when mapped spatially. The spatial distribution shows that in 1996 the eastern shore of Maryland and the tributaries chilled around the same time (Figure 10). In contrast, the mainstem had a more gradual cooling with more crabs at the mouth. Hence, the hump towards the beginning of the smoothed function was for those crabs caught in Maryland during the tributary cold snap, while the other hump was for those crabs that made it to the mouth of the bay.

For density, most positive densities were near day 350 which corresponded to temperature days close to the mouth. The density trend was best seen for densities greater

than 5 crabs (Figure 11). For 2003, given the quick chill, the crabs may not have started to migrate. However, comparing the 1996 and 2003 maps, crabs were caught lower in the tributaries in 1996 (Figure 10 and Figure 11). This indicates that the female crabs from the tributaries and Maryland had already started their migration when the sudden chill caused them to overwinter. In the smoothing function density was homogenous until day 338 when the smooth dipped towards the negative, indicating that there was no clumping in the lower bay. This is also better shown in the map (Figure 11). There were certainly more crabs in the lower bay than the upper bay. However, given the quick chill, many upper bay points had approximately the same temperature day value as the lower bay points.

The temperature smoothing functions were hard to interpret. Hence, smoothing functions were compared not by the specific shape but by the repetition of particular shapes across classes. In general, juvenile males and adult males had the same general smooth shapes for 10 years, whereas juvenile females only had similar smoothing functions as juvenile males for 5 years. This again provides evidence for the difference in behavior of juvenile males and females. Temperature was only significant in half of the stage two GAMs, though when significant the trend was generally the same as its stage one counterpart (Figure 12). Patterns in female presence with temperature showed an inverse relationship with that of females and salinity. When salinity had a "w"-shaped curve, the temperature curve had an "m" shape. When salinity was positively shaped, temperature was negatively shaped. This collinearity between temperature and salinity was only detectable with mature females, probably due to the wider temperature and salinity ranges experienced by mature females as compared to the other crab classes. The inverse shape was unexpected, given that the hypothesis was that temperature would follow the same pattern as salinity in predicting female crab presence, though this may

have been due to the difficulty in interpreting temperature. While temperature day showed the onset and general chilling rate, other factors such as the temperature at which female crabs are cued to migrate could improve the parameter.

Importance of the findings

The only study of a blue crab population at this broad scale was by Jensen et al. (2005), who used two stage GAMs to evaluate and predict adult female distribution. While crab and depth data were taken from the same source, salinity, temperature and seagrass effect were handled differently and resulted in different curves. Jensen et al. (2005) interpolated the December bottom temperatures and salinities from the Chesapeake Bay Water Quality Monitoring Program and used the resulting maps to assign values to each point every year. The greatest similarity was that seagrass effect did not appear significant in many models for either study. Depth had the same smoothing function shapes for stage one but different shapes for stage two (Figure 13). This difference could be attributed to the sample sizes and the difference in omission of points. For stage one, sample size (1122-2521) was sufficiently large to produce the same curves for both studies even though Jensen et al. (2005) reserved a fourth of the data for cross validation and this study omitted all points taken above 10^{o}C. The sample sizes for stage two were far lower (131-568), which could account for the difference in smoothing function shapes. For salinity, only two smoothing functions could be compared between the studies and those did not have similar smoothing function shapes (Figure 14). Temperature curves were incomparable due to the way temperature was handled.

This was the first study examining the spatial distribution of males and juveniles of different age classes at the population scale, and should aid in resolving problems associated with management actions. For example, recent increases in adult females coupled with a commercial fishery that targets large males may cause a ratio discrepancy (Gascoigne et al. 2009; Carver 2005). This could lead to an Allee effect, defined as the positive correlation between population density and individual fitness. For blue crabs, this manifests as sperm limitation (Hines et al. 2003) from a scarcity of large males reducing female reproductive success. A refined spatial model using the data from this study could identify potential sanctuaries for large males during the crab-potting season.

Seagrass is often cited as an important nursery habitat for juvenile blue crab (Heck & Toman 1981; Ruiz et al. 1993; Moksnes et al. 1997; Ryer et al. 1997; Orth & van Montfrans 2002). However, like Jensen et al. (2005), this study did not find seagrass to be an important predictor variable for any crab class, even juveniles. There are many potential explanations for this seeming lack of importance of seagrass. First, seagrass may not be important in winter. Second, there may be an issue with scale. The previous studies found significant effects of various attributes of seagrass on juvenile blue crabs at small spatial scales (Perkins-Visser et al. 1996; Pile et al. 1996; Shulman 1996; Heck & Spitzer 2001; Hovel & Lipcius 2001, 2002), but this may not translate to significant effects at the population level. Third, there could be a problem with the way in which the seagrass variable was formulated. There is a temporal discrepancy between the surveys; the SAV aerial survey occurs during the summer while seagrass densities are at their highest (Orth et al. 2011), whereas the WDS occurs in the winter, after an annual defoliation. Finally, the dredge survey was not designed to survey juveniles and is estimated to only sample 20% of the juvenile population (Ralph & Lipcius, *unpublished data*). Churchill (1919)

observed a negative relationship between crab size and distance to shore, with the smallest crabs found at depths of only several cm. Winter suctions support the relation (Orth & van Montfrans 1987). Since the boats used in the WDS cannot dredge in less than 1.5 m of water, the WDS tends to only sample larger juveniles (> 30 mm CW). Previous studies suggested that seagrass is a nursery habitat for juveniles only until they reach 20-30 mm CW, at which point they move towards lower salinity waters and unvegetated habitats (Minello et al. 2003; Seitz et al. 2003, 2005; Lipcius et al. 2005, 2007). While seagrass was not found to be an important predictor variable, this study does not provide evidence against seagrass as a nursery habitat.

Management is moving toward a more holistic approach, namely ecosystem based fisheries management, with the goal to manage fisheries in context of the environment. This means management must take into consideration how species react to climate change, physical and biological interactions, and the potential adaptation of a species in range or life history (Field & Francis 2005). The goal of this incorporation is to optimize the resilience of both the species and ecosystem. Resilience is the extent to which a population or ecosystem can absorb persistent natural or anthropogenic agitation and recover without degradation or flipping into alternative states (Hughes et al. 2005). This study demonstrated the importance of physical variables in predicting blue crab abundance at the population scale, while refined models may be useful in designating essential fish habitat and provide a tool to explore possible ramifications on overwintering abundance from changing temperatures and salinities due to global climate change.

Limitations and suggestions for future research

Deviance explained, a goodness of fit value, only explained 4-40% of the data. This could be due to a number of reasons. First, the severe overdispersion of the data may not have been controlled sufficiently by using the complementary log-log link function for stage one models and negative binomial distribution for stage two models. Additionally, points taken at sites after the site had been fished would result in lower survey catches and these data would hide trends. However, this would only affect the lower-bay mainstem sites where dredging was allowed. Further, data for some potentially important predictor variables were unavailable. Sediment type, which Shaffner and Diaz (1988) found important in female crab distribution, could not be added to this model as reliable sediment maps do not exist for the whole bay. Dissolved oxygen may be important, as crabs tend to avoid hypoxic areas. While hypoxia is prevalent in summer, the occurrence of hypoxia may change the type of bottom encountered in the winter. Given more time, hypoxia estimates could be estimated from the ChesROMS model. Density dependence could also obfuscate trends. The ideal free distribution theory (Fretwell & Lucas 1970) states that animals will distribute proportionally to resources available. Hence, years with low numbers of crabs may have most crabs in the highest quality habitat, whereas years with high abundance may have crabs dispersed in lesser quality areas. Finally, there may be significant interaction effects between depth, salinity and temperature, but exploring those interactions requires more complex analyses.

An interesting future study could redesign part of the winter dredge survey to take samples in high-density areas. This could further define the stage two trends. Additionally, some female salinity curves seemed to continue in a positive linear fashion past 25, begging the question of whether adult female crabs have migrated outside the bay. If so, there would be a segment of the population unsampled by the dredge survey. In 2003, between January and

March, dredge samples were taken outside of the bay and found very few blue crabs (Lipcius et al. 2003). The winter of 2002-2003 had both an early onset and quick chilling; the first site to reach 10°C was on day 307 (November 3) and the last site day 343 (December 8). Given the unusually warm weather during the winter of 2012 and the possibly warming waters due to global climate change, the issue may need to be re-addressed.

The estimates of temperature and salinity from the ChesROMS model appeared significant in most GAMs. However, there were drawbacks given the large cell size of the model and the limitation to only generate estimates between 1991 and 2005. Higher-resolution models of the physical parameters in the Chesapeake Bay for the years after 2005 should become more easily accessible. If so, future GAMs could begin to model years when the commercial dredge fishery was closed and provide a more in-depth assessment of how that management action affected the population. Furthermore, the models may provide maps of potential no-take areas useful for management if the winter dredge fishery were to re-open. Thus, this investigation can serve as the foundation for several new lines of investigation and their management applications.

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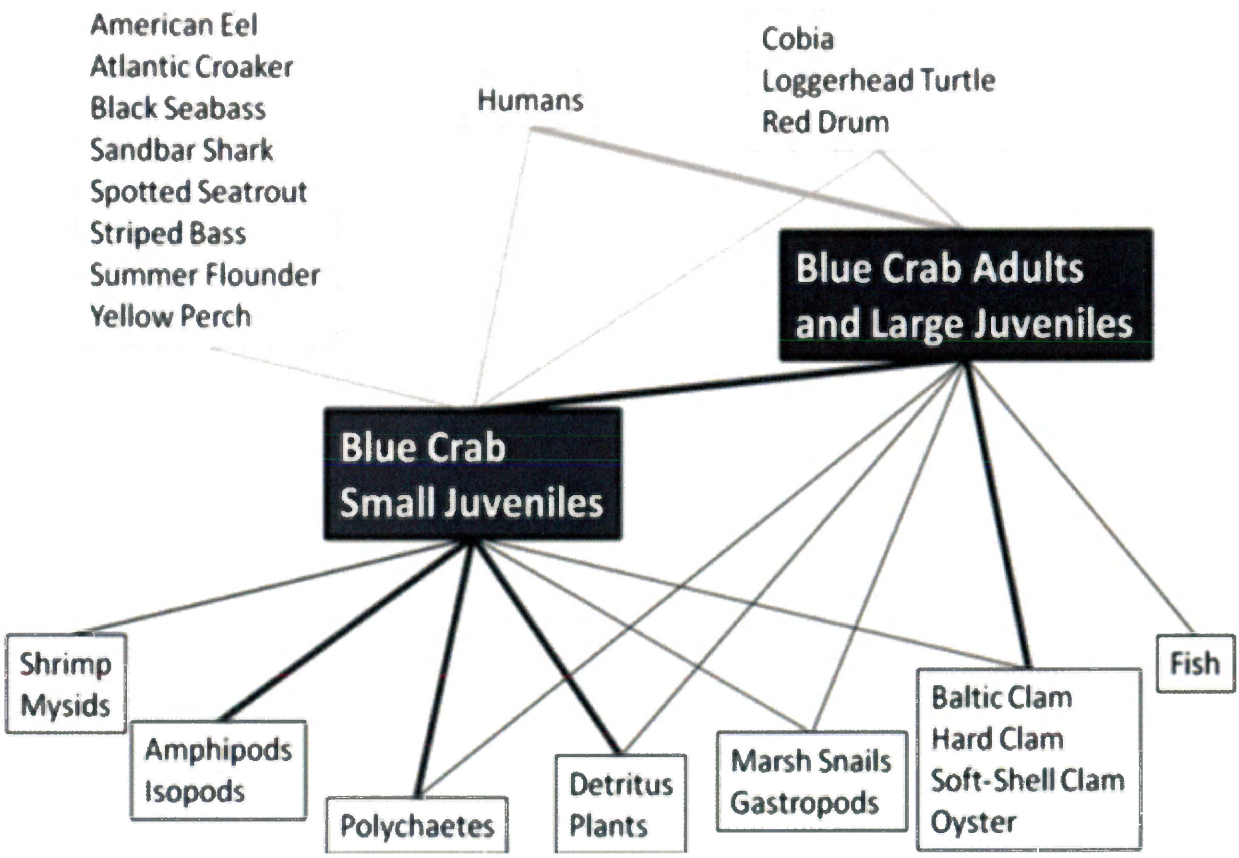


Figure 1. The blue crab's role in the Chesapeake Bay food web. Darker and thicker lines correspond to stronger connections as determined from stomach content studies. Taken from Lipcius et al. (2007).

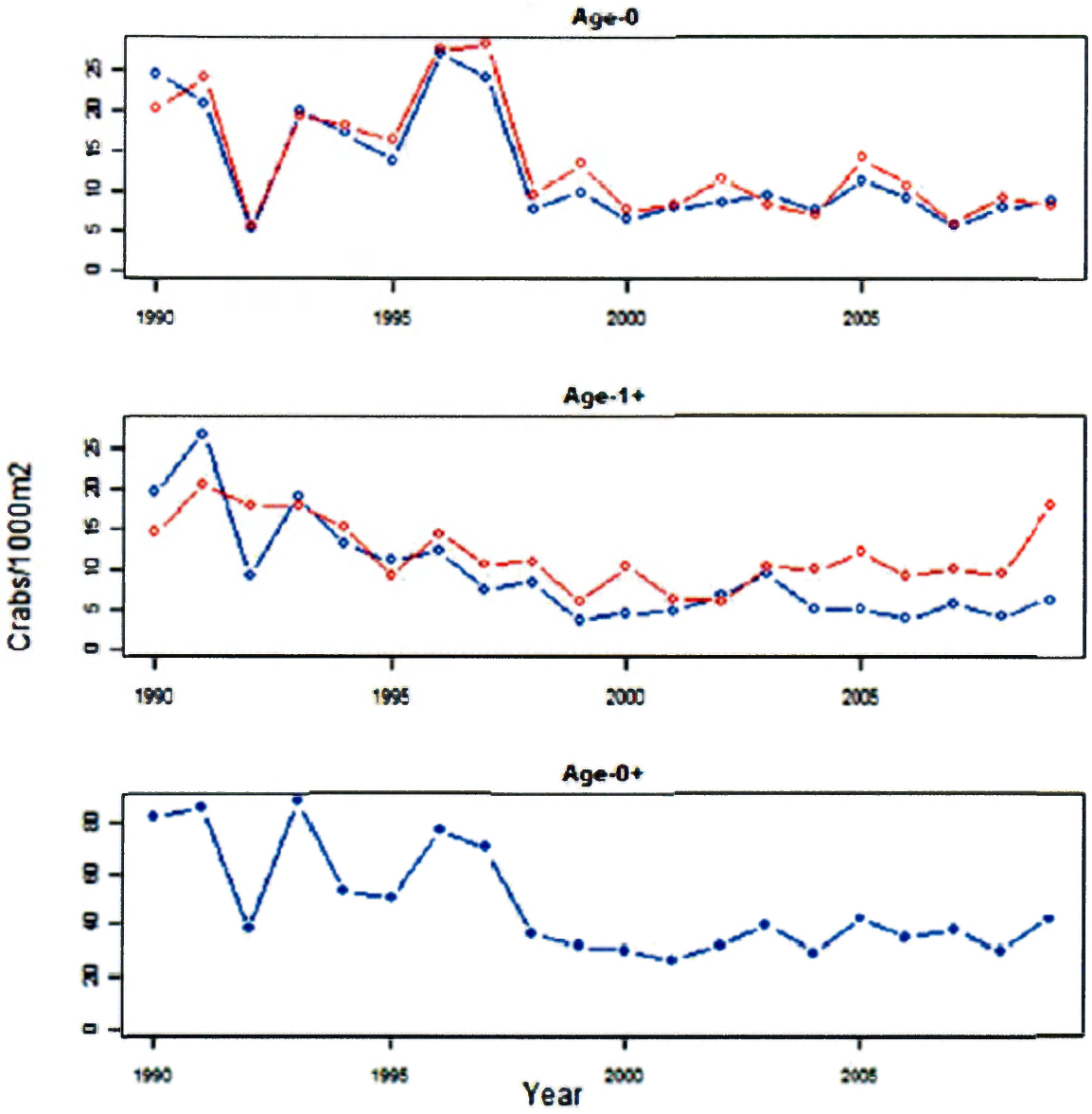


Figure 2. Time series of average baywide crab densities from the winter dredge survey. Trends are for age-0, age1+ and all crabs combined for both males (blue) and females (red). Taken from Miller et al. 2011.

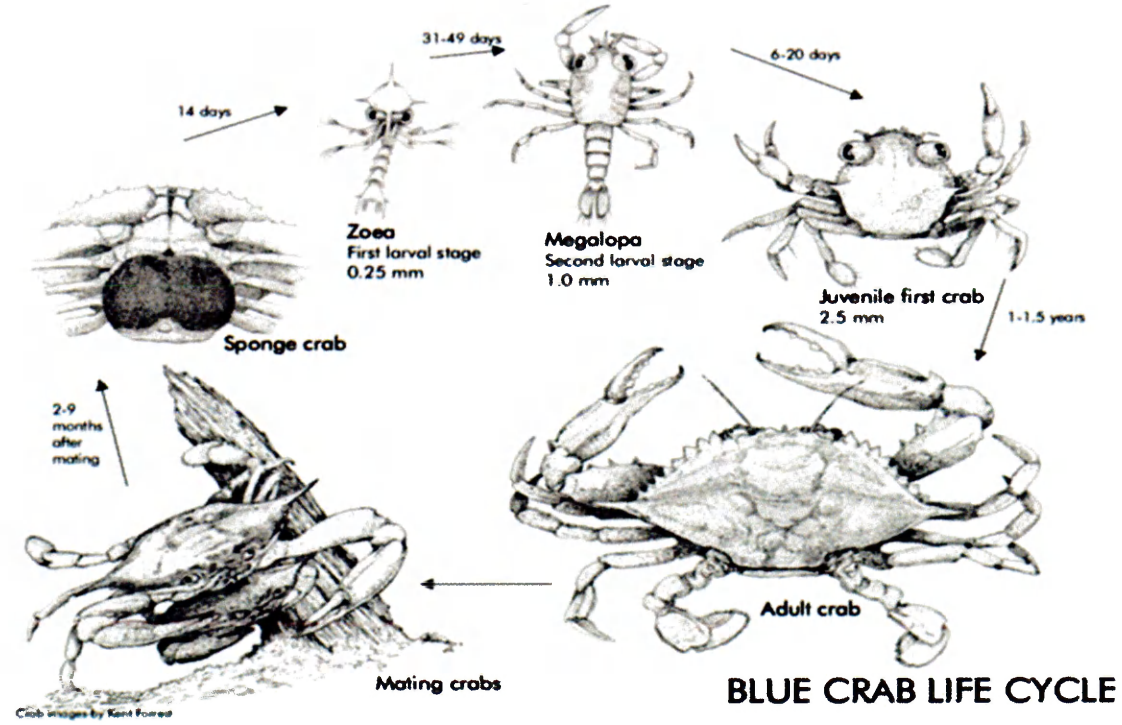


Figure 3. Life history of the blue crab. Drawing by Kent Forest.

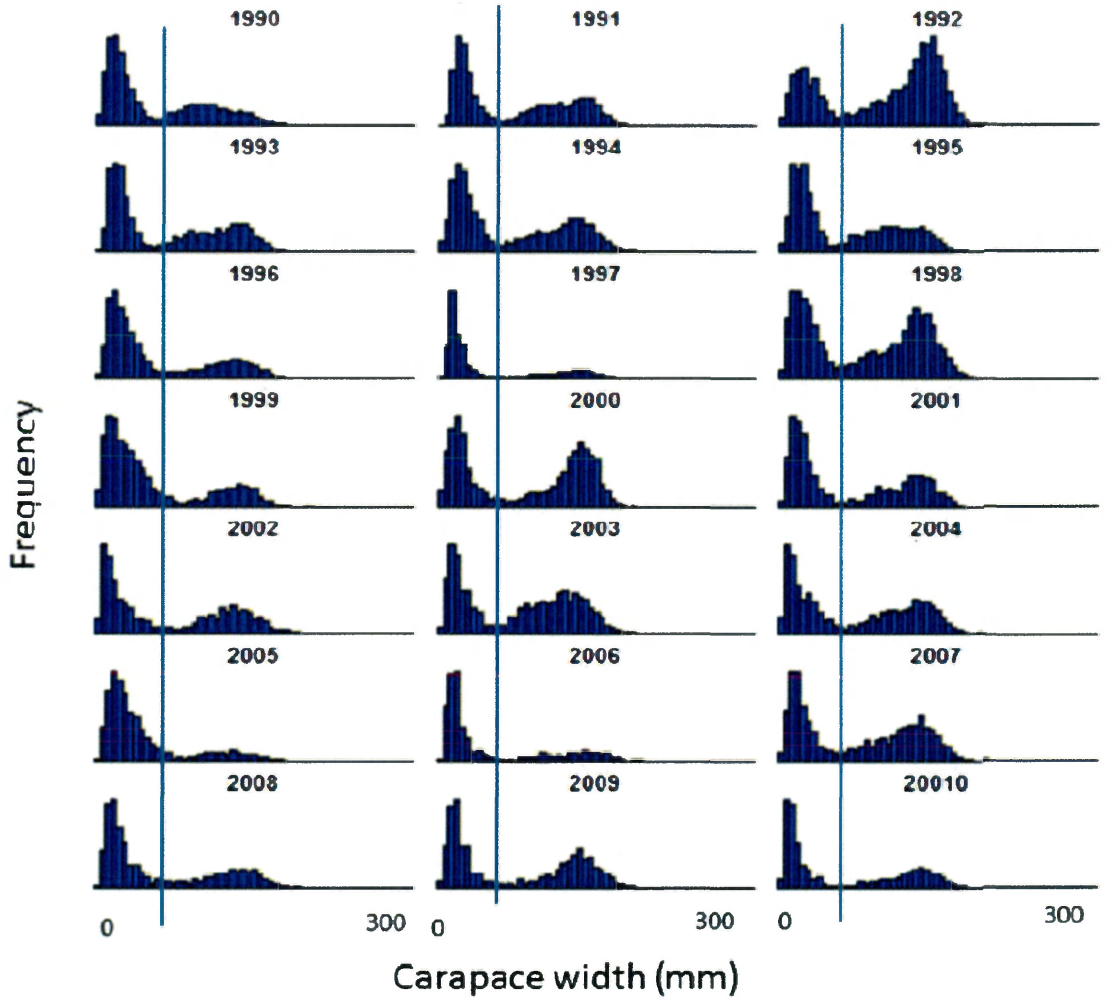


Figure 4. Size frequency histograms from the blue crab winter dredge survey from 1990 to 2010. The blue line corresponds to the 60 mm CW line. Taken from Miller (2011).

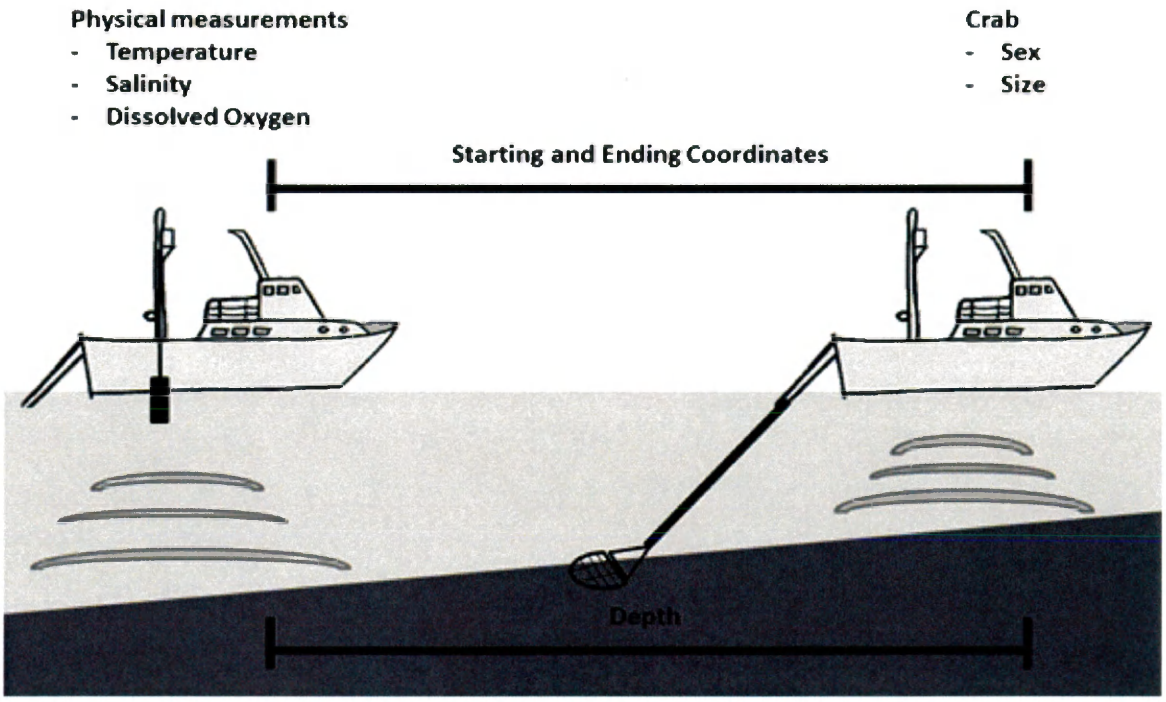


Figure 5. Schematic of data taken in one dredge tow.

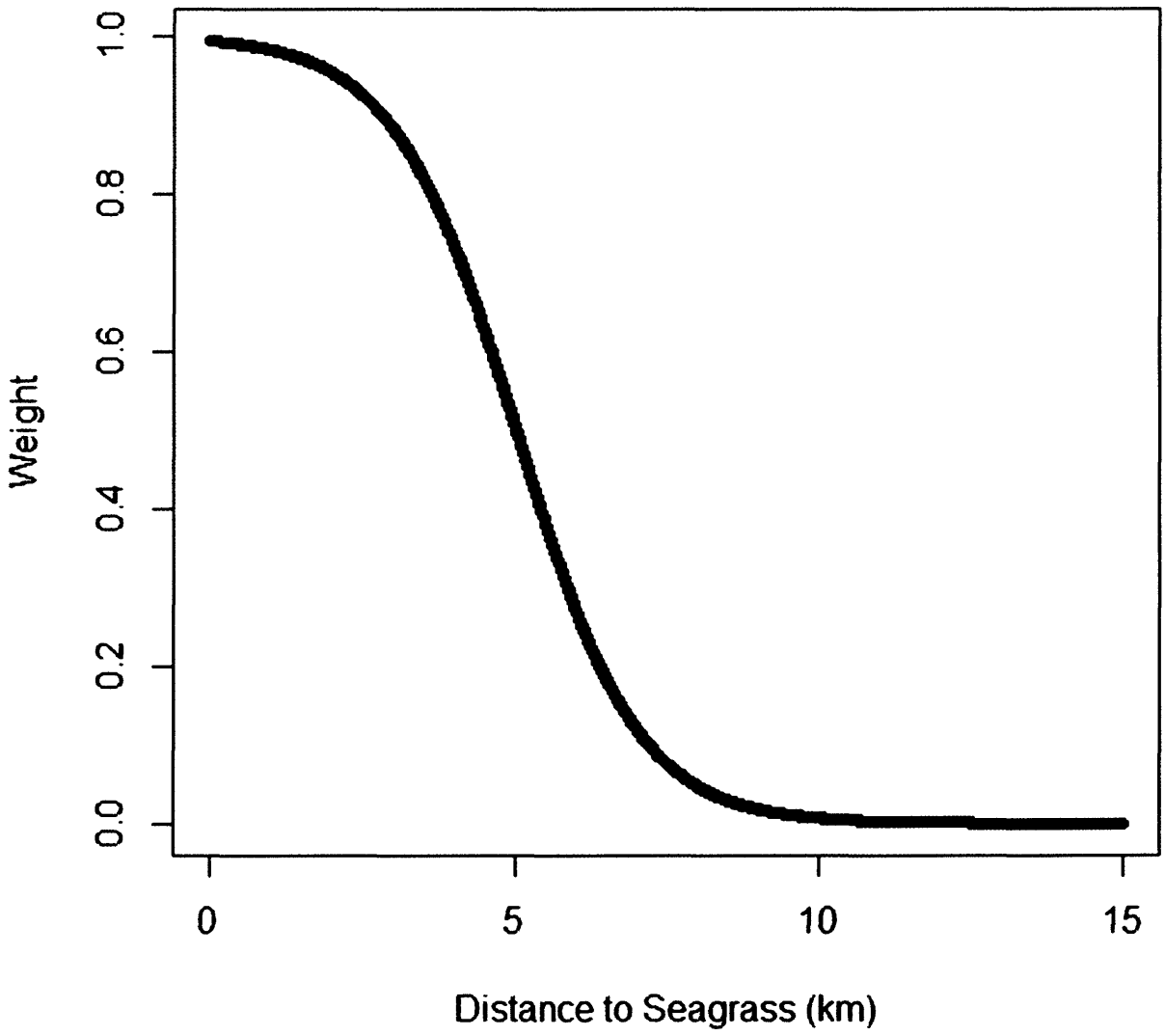


Figure 6. Weighing function for the seagrass effect variable.

Figure 7. Smoothing functions for both stages of the GAMs for each year (1991 - 2004), displayed for each age/sex class separately. D = depth, Temp = day the bottom water temperature reached 10^{o}C and remained below 10^{o}C for 2 consecutive days from the ChesROMS model, Sal = bottom salinity on the day the bottom water temperature reached 10^{o}C, SGE = combined effect of area of the nearest seagrass bed and distance to that bed. Stage 1 is the presence/absence GAM; given presence, Stage 2 is the density GAM. F0 includes female crabs < 60 mm CW, F1+ includes females > 60 mm CW, M0 includes males < 60 mm CW, and M1+ includes males > 60 mm CW. In cases where the p-value of the smoothed term was > 0.05, the smoothing function was replaced by the p-value. The shading indicates the confidence band, which takes into account uncertainty in the smoothing function and the mean.

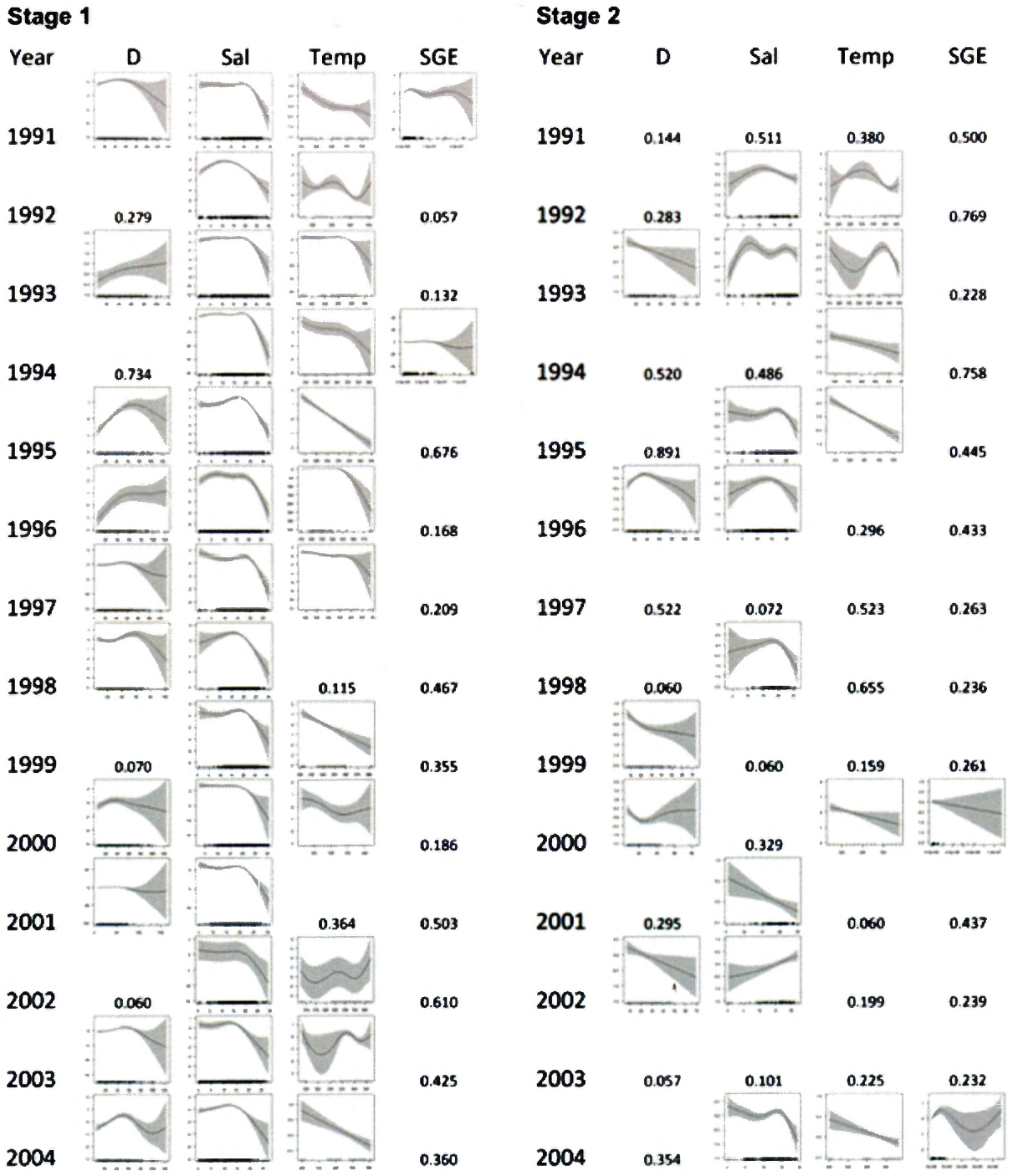

Stage 1
Year
D
Sal
Temp
SGE
1991
1992
0.279
0.057
1993
0.132
1994
0.734
1995
0.676
1996
0.168
1997
0.209
1998
0.115
0.467
1999
0.070
0.355
2000
0.186
2001
0.364
0.503
2002
0.060
0.610
2003
0.425
2004
0.360
Stage 2
Year
D
Sal
Temp
SGE
1991
0.144
0.511
0.380
0.500
1992
0.283
0.769
1993
0.228
1994
0.520
0.486
0.758
1995
0.891
0.445
1996
0.296
0.433
1997
0.522
0.072
0.523
0.263
1998
0.060
0.655
0.236
1999
0.060
0.159
0.261
2000
0.329
2001
0.295
0.060
0.437
2002
0.199
0.239
2003
0.057
0.101
0.225
0.232
2004
0.354

Figure 7.1. F0

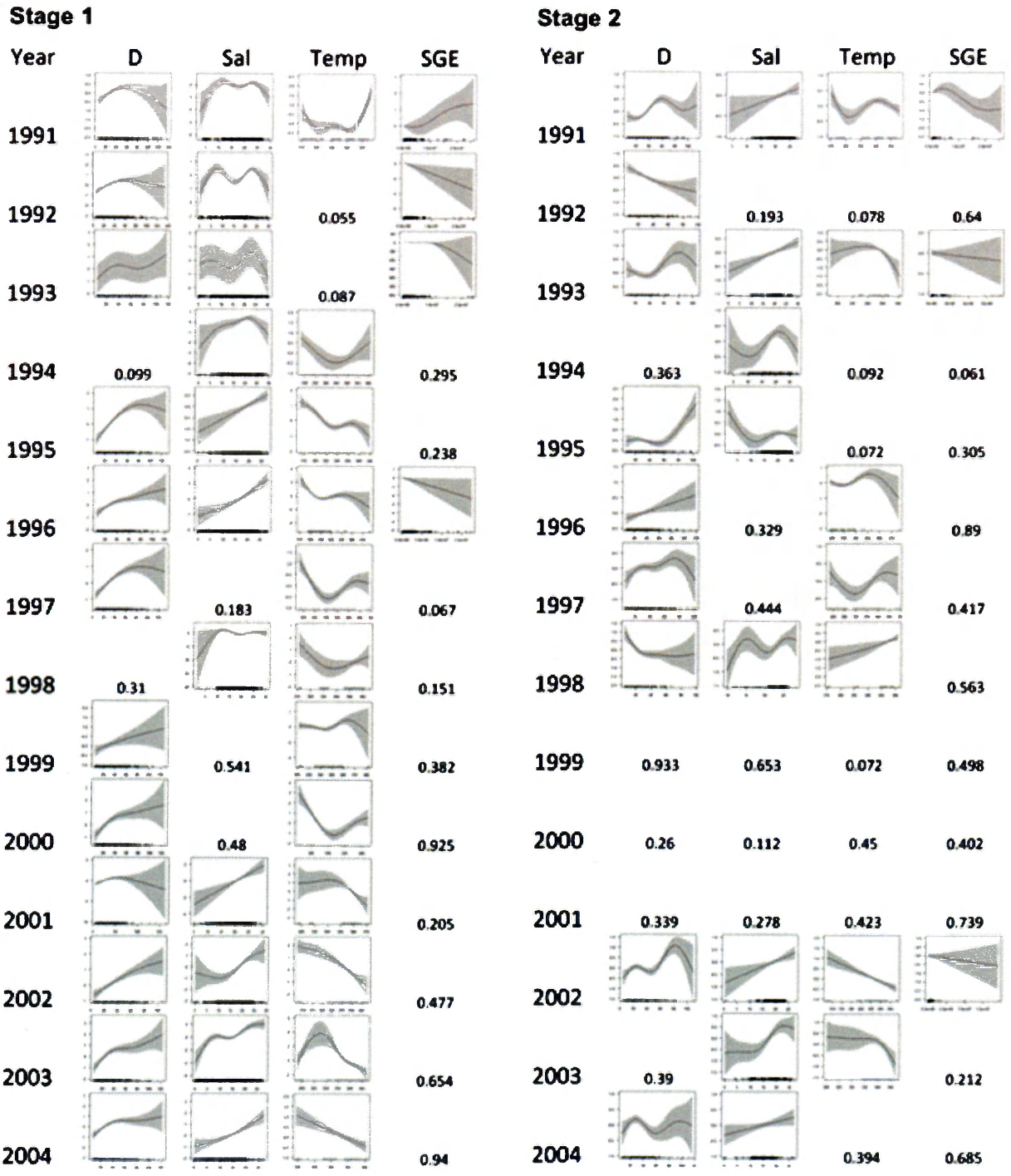

Stage 1
Year
D
Sal
Temp
SGE
1991
1992
1993
1994
1995
1996
1997
1998
1999
2000
2001
2002
2003
2004
0.055
0.087
0.099
0.295
0.238
0.183
0.067
0.31
0.151
0.541
0.382
0.48
0.925
0.205
0.477
0.654
0.94
Stage 2
Year
D
Sal
Temp
SGE
1991
1992
1993
1994
1995
1996
1997
1998
1999
2000
2001
2002
2003
2004
0.193
0.078
0.64
0.363
0.092
0.061
0.072
0.305
0.329
0.89
0.444
0.417
0.563
0.933
0.653
0.072
0.498
0.26
0.112
0.45
0.402
0.339
0.278
0.423
0.739
0.39
0.212
0.394
0.685

Figure 7.2. F1+

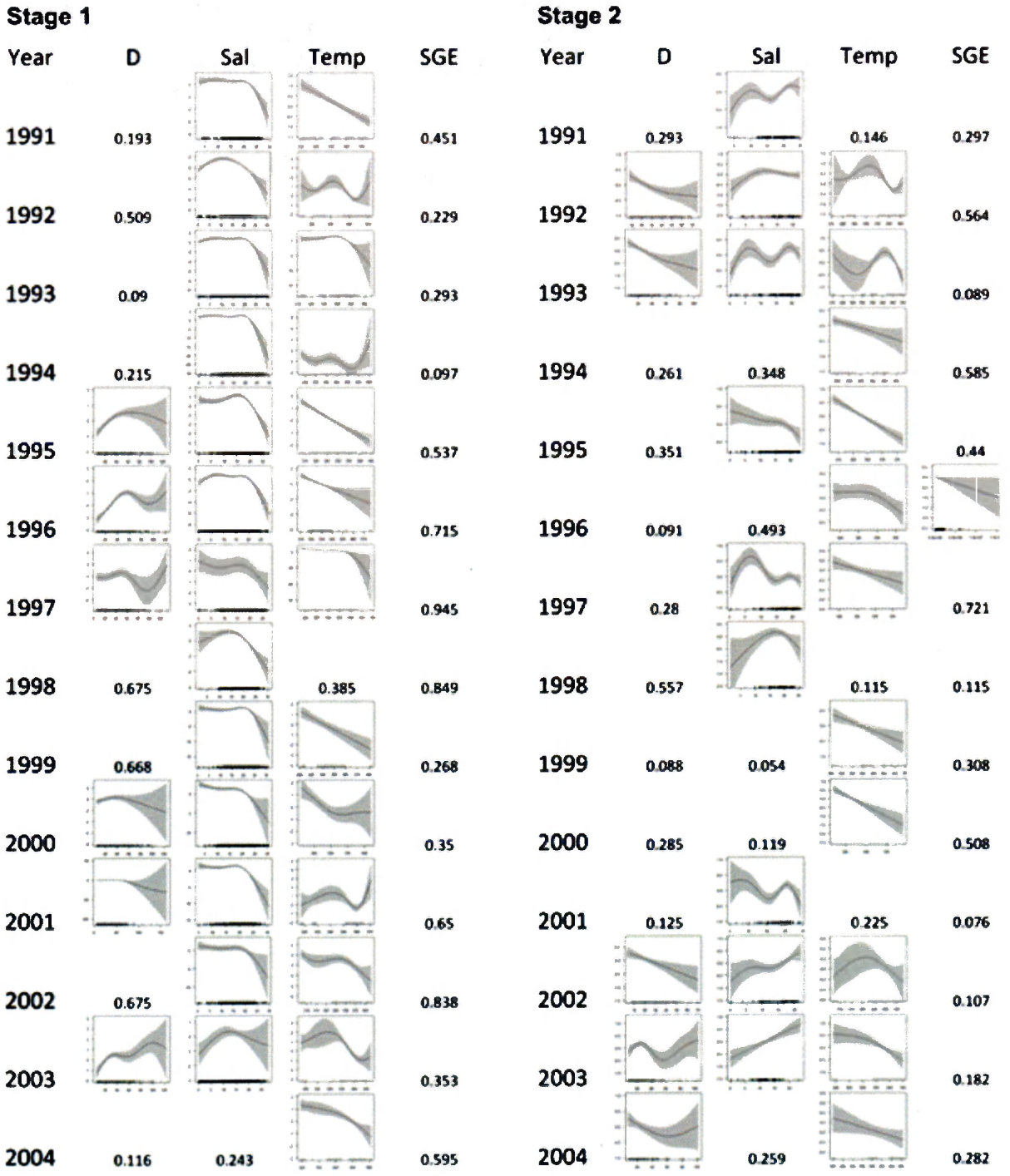

Stage 1
Year
D
Sal
Temp
SGE
1991
0.193
0.451
1992
0.509
0.229
1993
0.09
0.293
1994
0.215
0.097
1995
0.537
1996
0.715
1997
0.945
1998
0.675
0.385
0.849
1999
0.668
0.268
2000
0.35
2001
0.65
2002
0.675
0.838
2003
0.353
2004
0.116
0.243
0.595
Stage 2
Year
D
Sal
Temp
SGE
1991
0.293
0.146
0.297
1992
0.564
1993
0.089
1994
0.261
0.348
0.585
1995
0.351
0.44
1996
0.091
0.493
1997
0.28
0.721
1998
0.557
0.115
0.115
1999
0.088
0.054
0.308
2000
0.285
0.119
0.508
2001
0.125
0.225
0.076
2002
0.107
2003
0.182
2004
0.259
0.282

Figure 7.3. M0

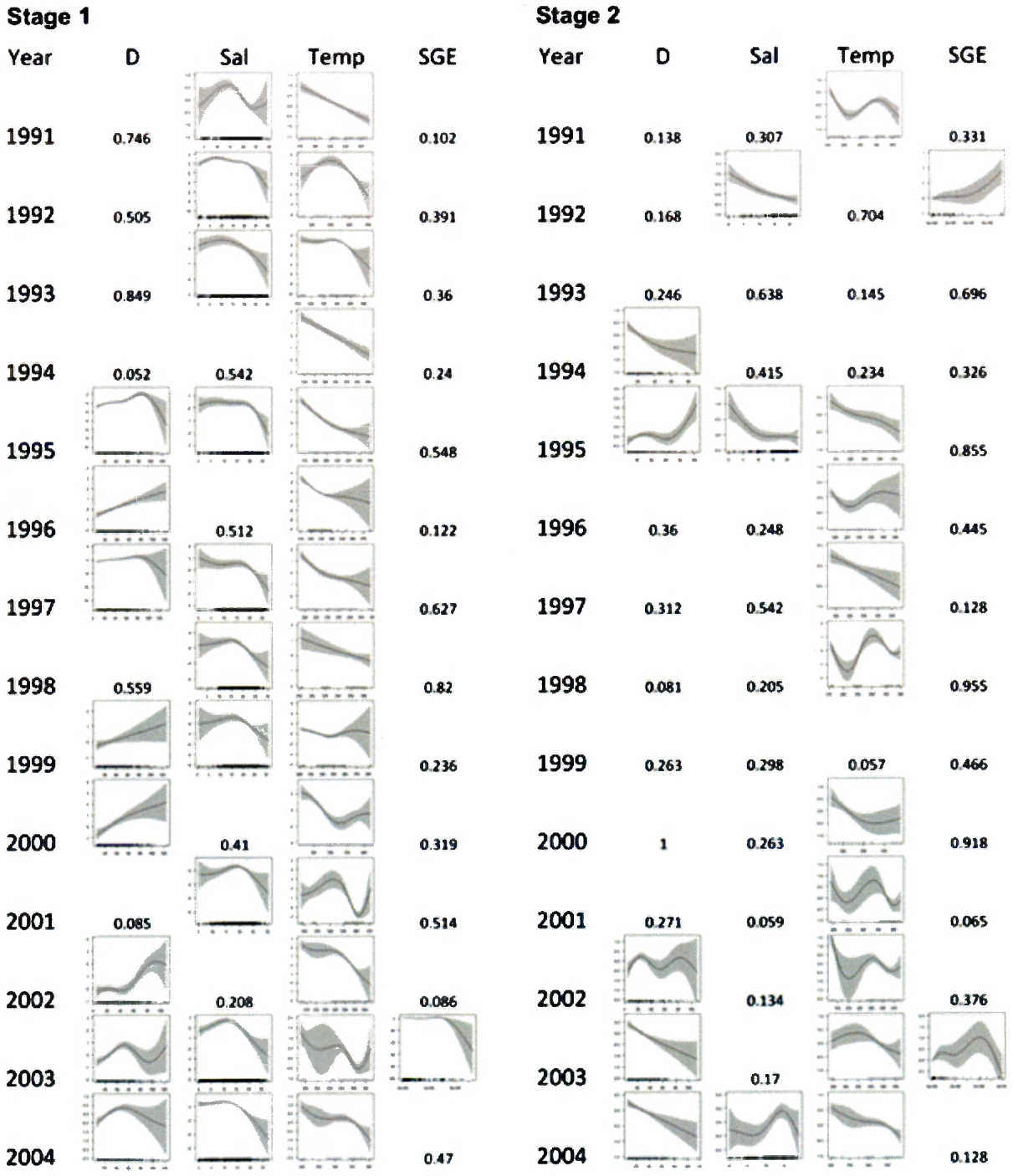

Stage 1
Year
D
Sal
Temp
SGE
1991
0.746
0.102
1992
0.505
0.391
1993
0.849
0.36
1994
0.052
0.542
0.24
1995
0.548
1996
0.512
0.122
1997
0.627
1998
0.559
0.82
1999
0.236
2000
0.41
0.319
2001
0.085
0.514
2002
0.208
0.086
2003
2004
0.47
Stage 2
Year
D
Sal
Temp
SGE
1991
0.138
0.307
0.331
1992
0.168
0.704
1993
0.246
0.638
0.145
0.696
1994
0.415
0.234
0.326
1995
0.855
1996
0.36
0.248
0.445
1997
0.312
0.542
0.128
1998
0.081
0.205
0.955
1999
0.263
0.298
0.057
0.466
2000
1
0.263
0.918
2001
0.271
0.059
0.065
2002
0.134
0.376
2003
0.17
2004
0.128

Figure 7.4. M1+

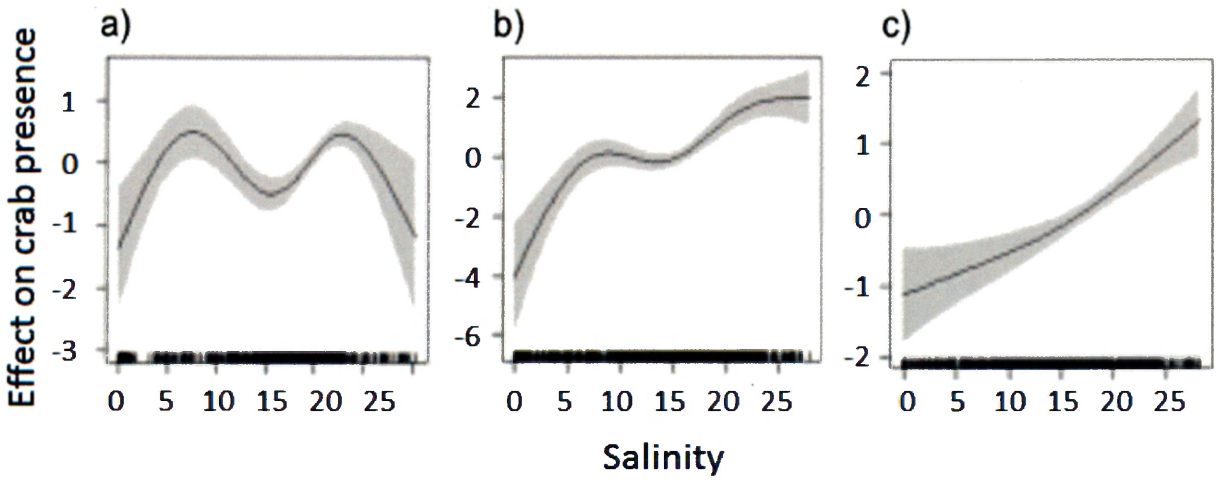


Figure 8. Smoothing functions of the GAM relating salinity to the presence/absence of female crabs > 60 mm CW for a) 1991, b) 2003, and c) 2004. Sal = bottom water salinity on the day the bottom water temperature reached 10°C. The shading indicates the confidence band which takes into account uncertainty in the smoothing function and the mean.

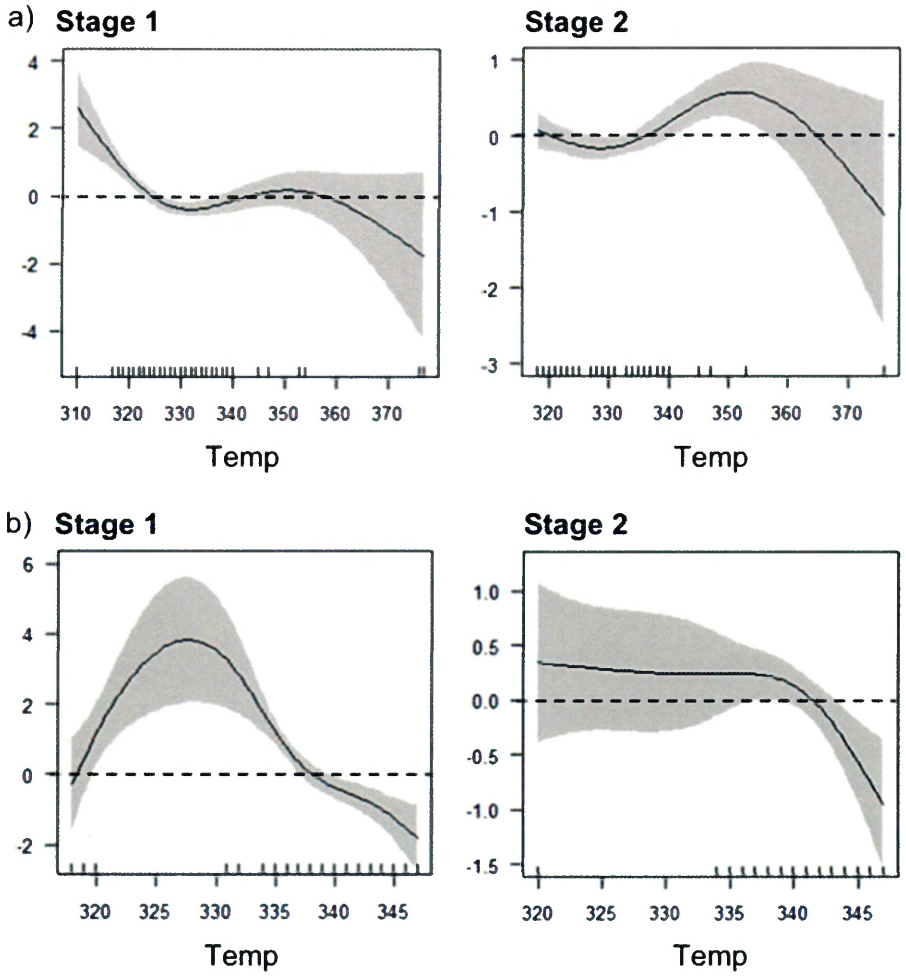


Figure 9. Smoothing functions of both stages of the GAM relating temperature to female crabs > 60 mm CW for a) 1996 and b) 2003. Temp = day the bottom water temperature reached 10°C and remained below 10°C for 2 consecutive days from the ChesROMS model. Stage 1 is the presence/absence GAM; given presence, Stage 2 is the density GAM. The shading indicates the confidence band which takes into account uncertainty in the smoothing function and the mean. The ticks above on the x-axis indicate sampling points.

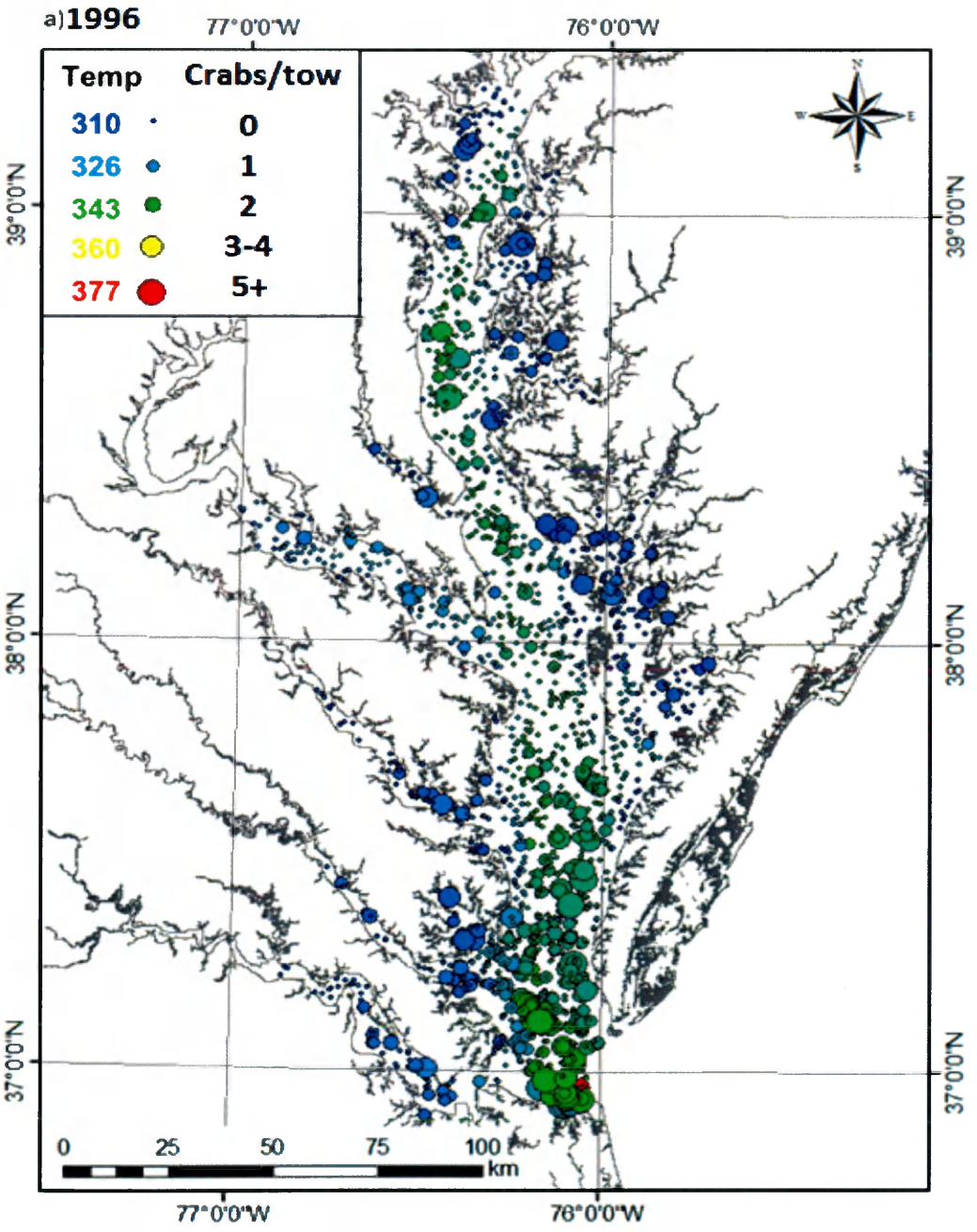
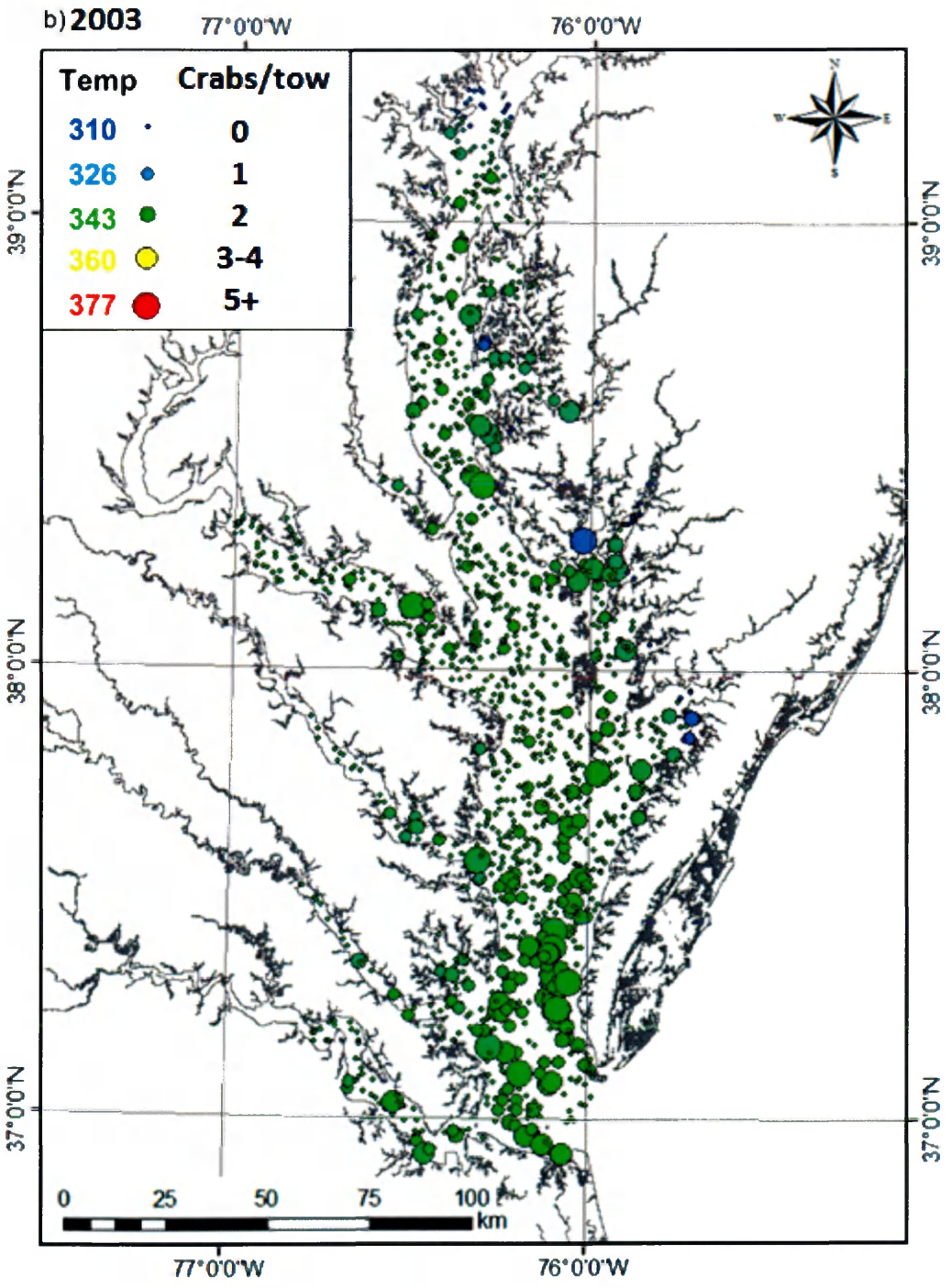


Figure 10: Spatial distribution of female blue crabs > 60 mm CW in relation to the day the bottom water temperature reached 10^{o}C based on the Winter Dredge Survey in a) 1996 and b) 2003.


b) 2003
77°0'0"W
76°0'0"W
Temp
Crabs/tow
310
0
326
1
343
2
360
3-4
377
5+
39°0'0"N
38°0'0"N
37°0'0"N
0
25
50
75
100
km

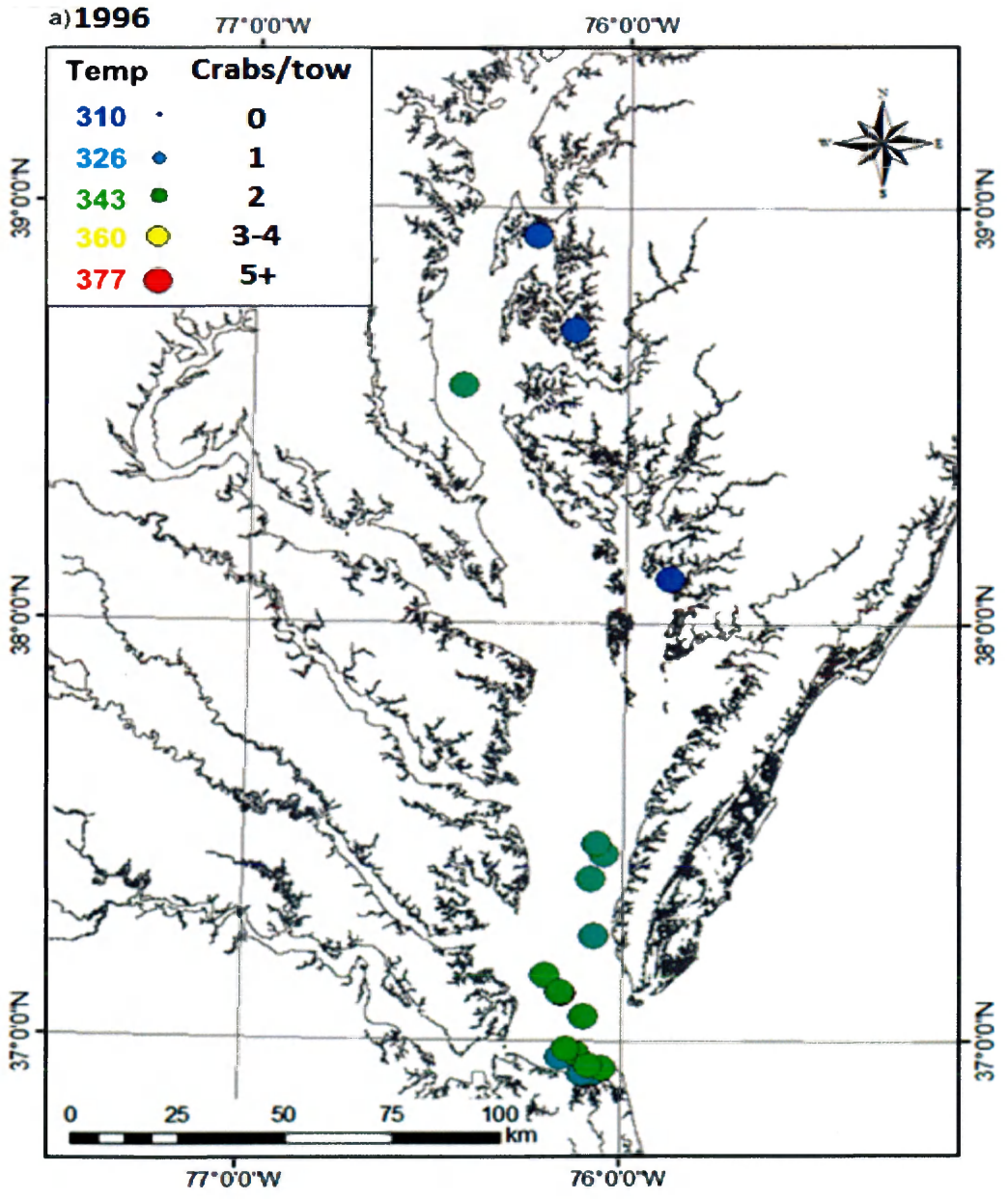
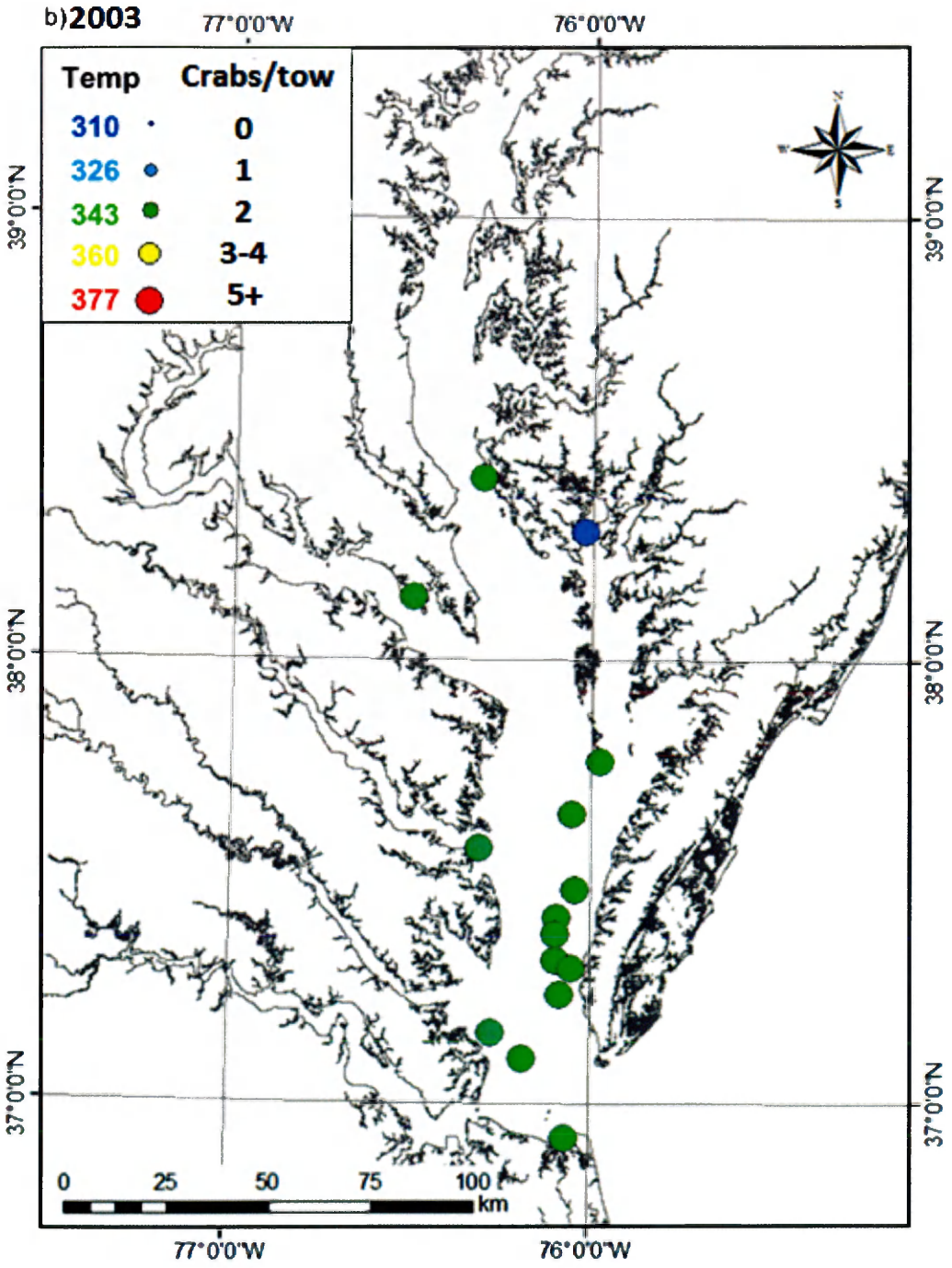


Figure 11: Spatial distribution of female blue crabs > 60 mm CW, where each site had > 5 crabs, in relation to the day the bottom water temperature reached 10^{0}C based on the Winter Dredge Survey in a) 1996 and b) 2003.


b)2003
77°0'0"W
76°0'0"W
Temp
Crabs/tow
310
0
326
1
343
2
360
3-4
377
5+
39°0'0"N
38°0'0"N
37°0'0"N
0
25
50
75
100
km

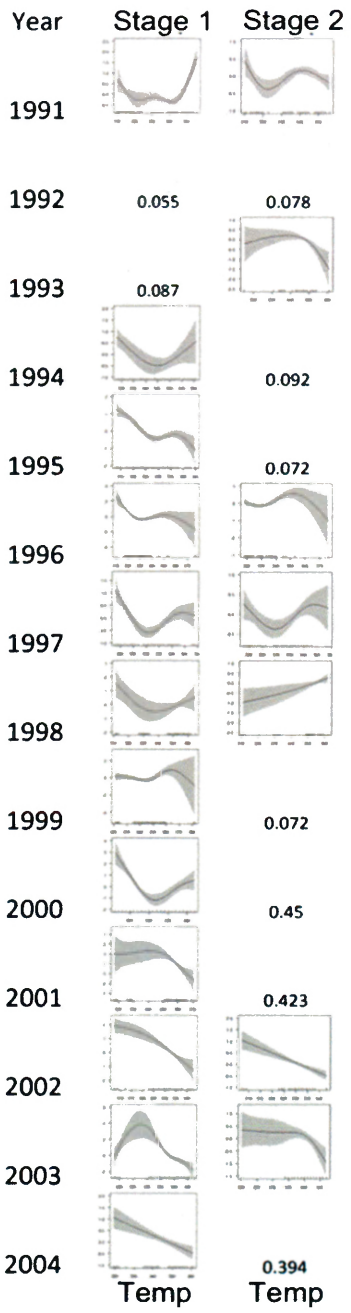


Figure 12: Smoothing functions of both stages of the GAM relating temperature to female crabs > 60 mm CW for each year (1991 – 2004). Temp = day the bottom water temperature reached 10°C and remained below 10C for 2 consecutive days from the ChesROMS model. Stage 1 is the presence/absence GAM; given presence, Stage 2 is the density GAM. In cases where the p-value of the smoothed term was > 0.05, the smoothing function was replaced by the p-value.

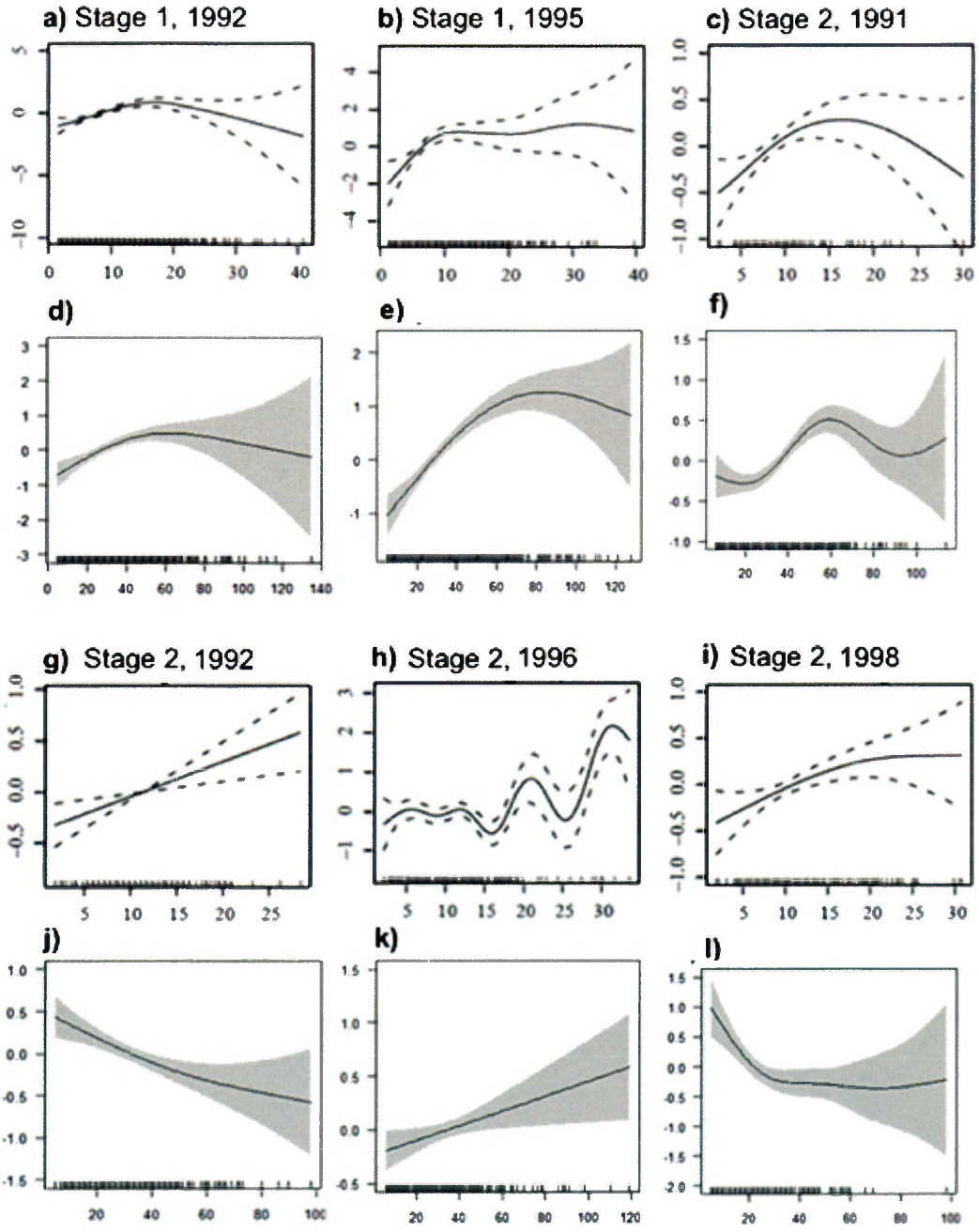


Figure 13: Comparison of the smoothing functions of the GAMs relating depth to female blue crabs > 60 mm CW from Jensen et al. (2005 - a – c and g - i) and this study (d – f and j - l). For both studies, depth measurements were from the WDS sample sites, but note that Jensen used meters as the depth unit while this study used feet.

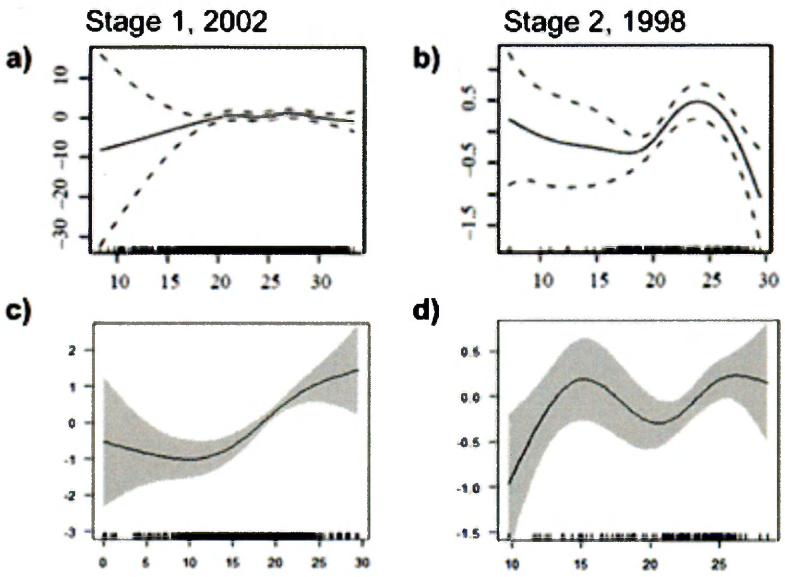


Figure 14: Comparison of the smoothing functions of the GAMs relating salinity to female blue crabs > 60 mm CW from Jensen et al. (2005 - a and b) and this study (c and d). Salinity was measured differently in Jensen et al. (2005) as compared to this study (see text for details).

Appendix A

Figure A: Correlation matrices for the independent variables used in the GAMs for each year (1991– 2004). D = depth, DM = distance to the mouth of the Chesapeake Bay, Temp = day the bottom water temperature reached 10^{o}C and remained below 10^{o}C for 2 consecutive days from the ChesROMS model, Sal = bottom water salinity on the day the bottom water temperature reached 10^{o}C, SGE = combined effect of area of the nearest seagrass bed and distance to that bed. Upper panels have the Kendall tau, a non-parametric rank-correlation coefficient. Diagonal panels are the histograms for each variable. Lower panels are scatterplots of each pair of variables.

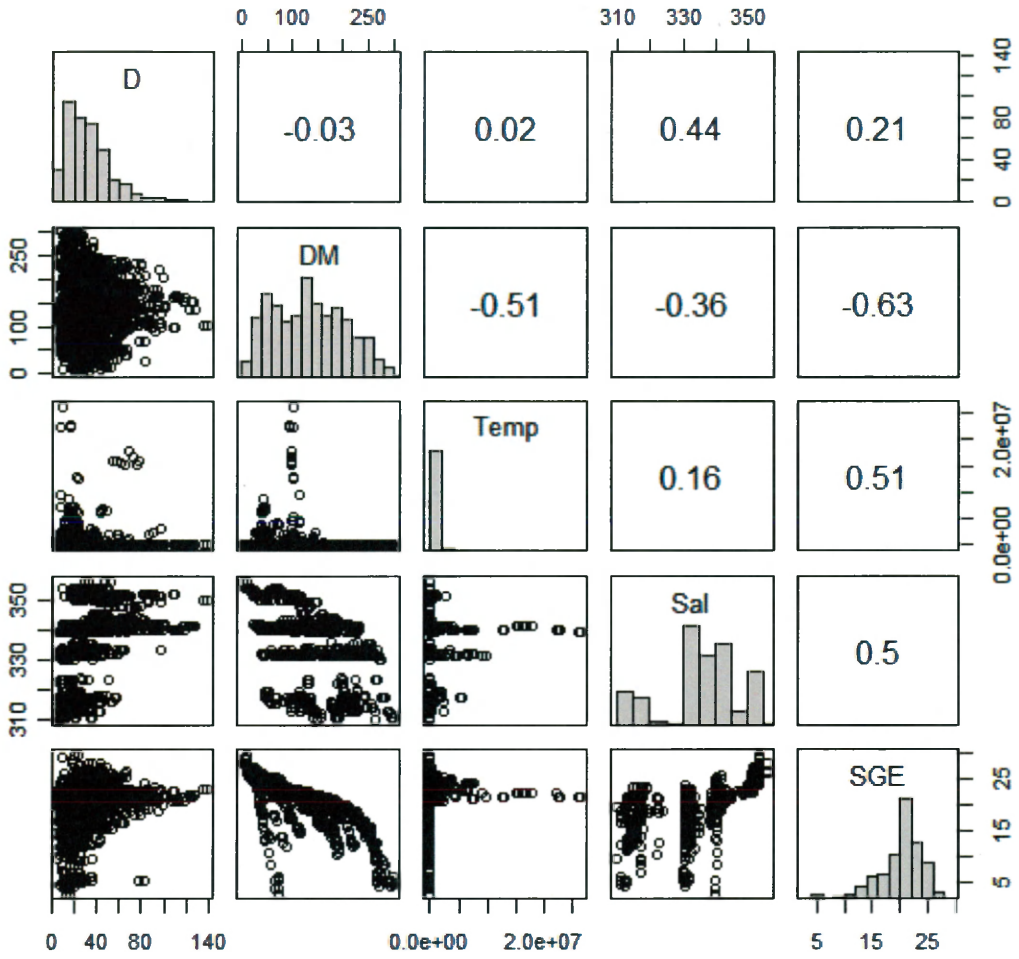


Figure A.1: 1991

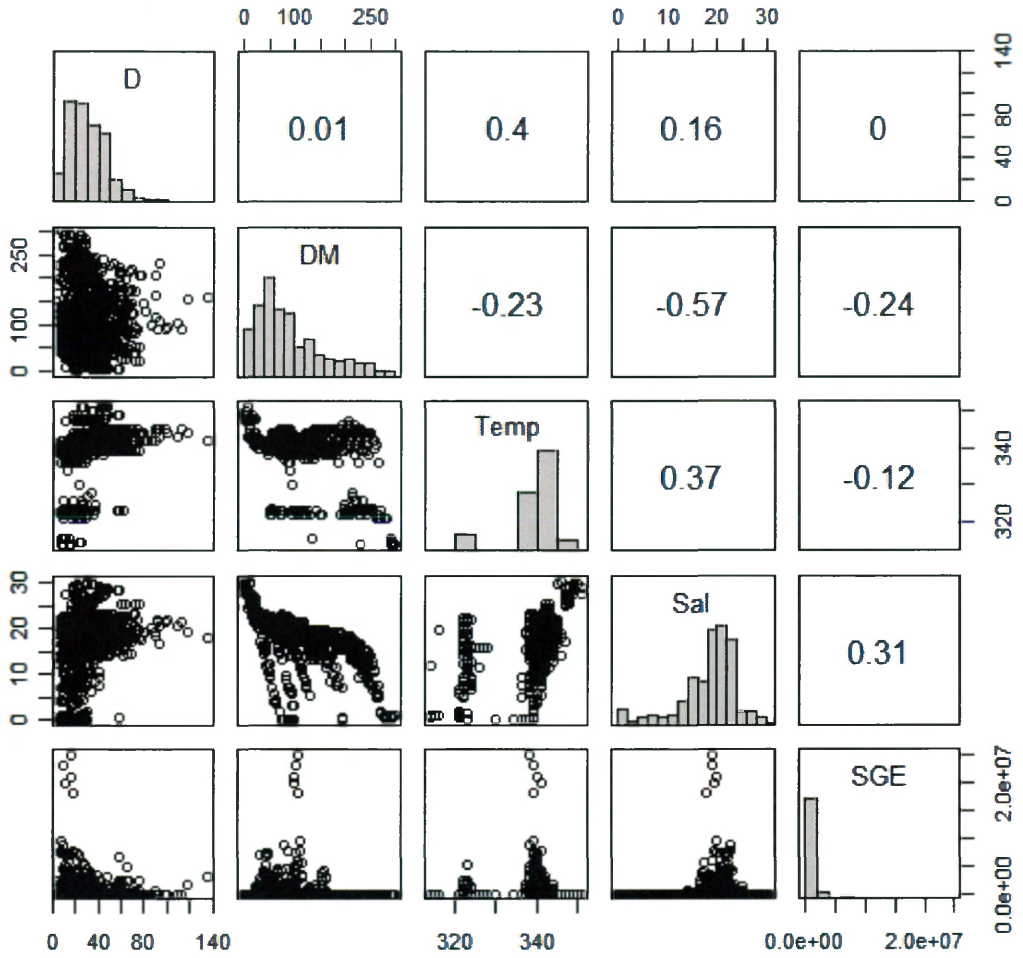


Figure A.2: 1992

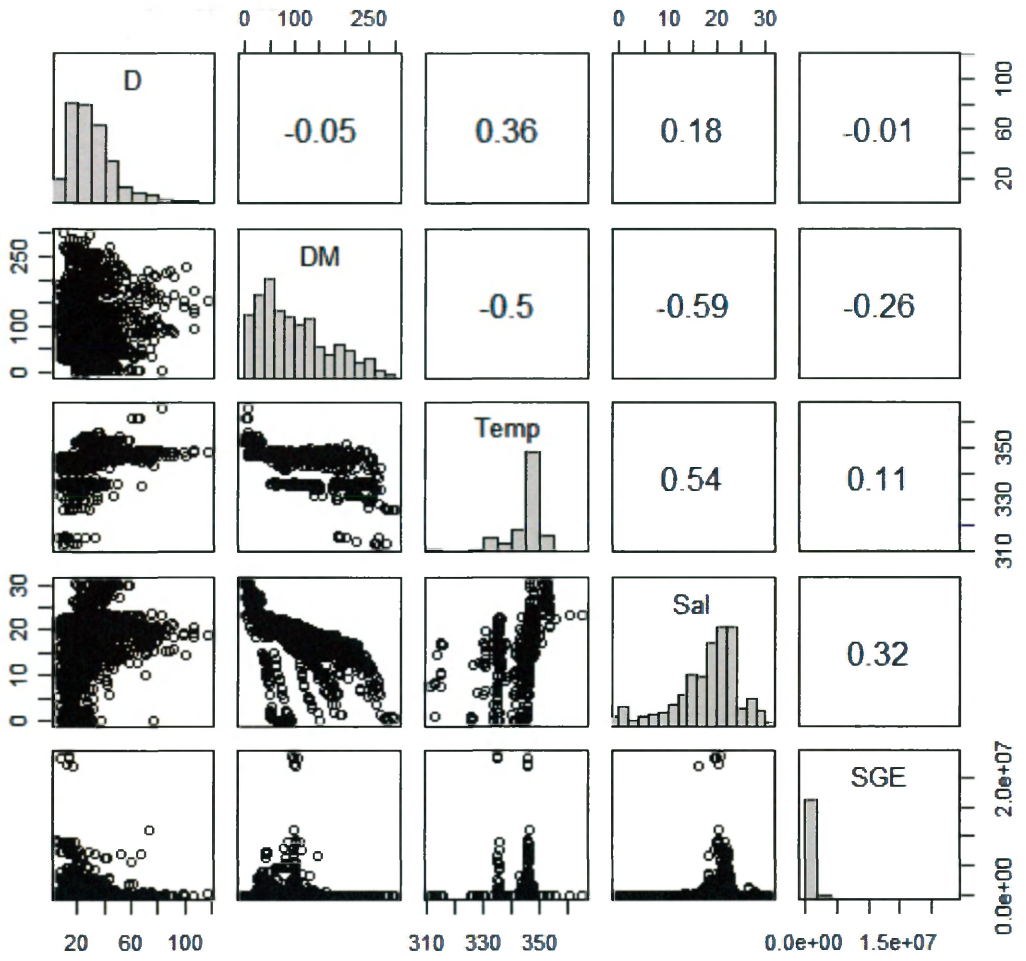


Figure A.3: 1993

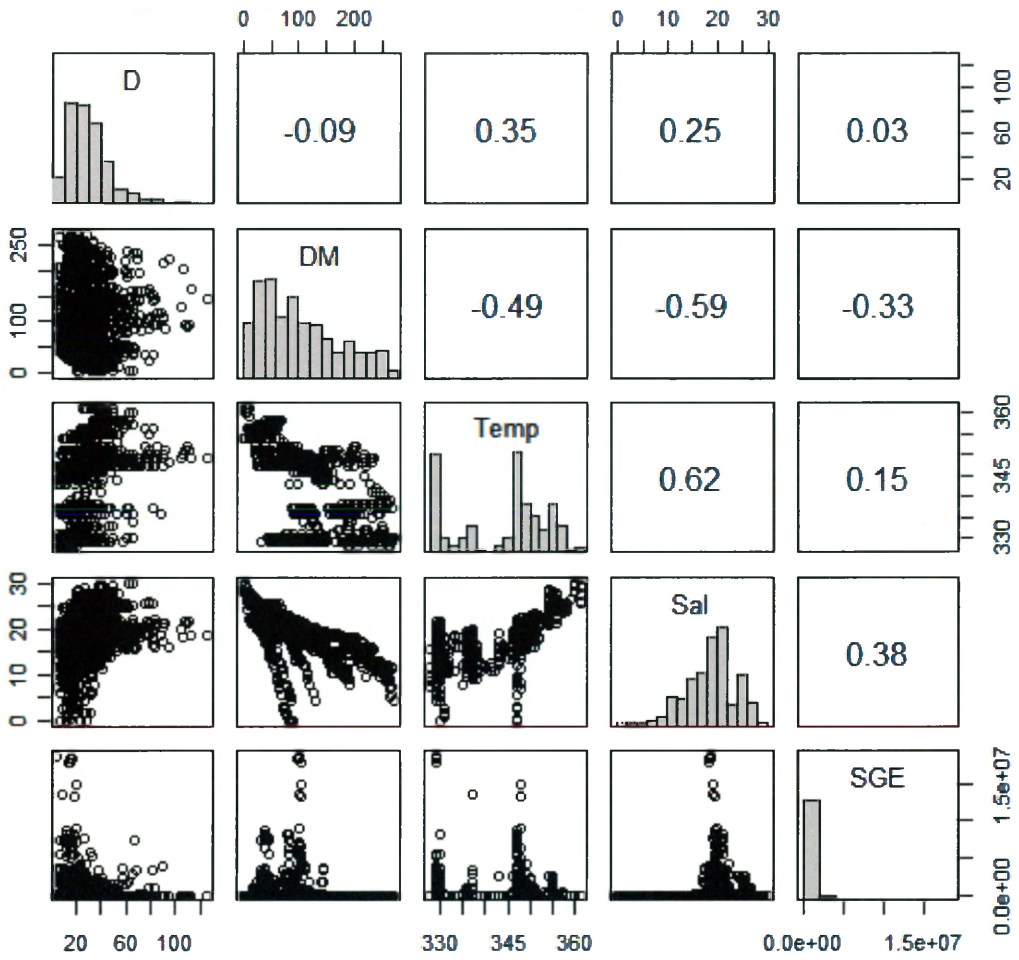


Figure A.4: 1994

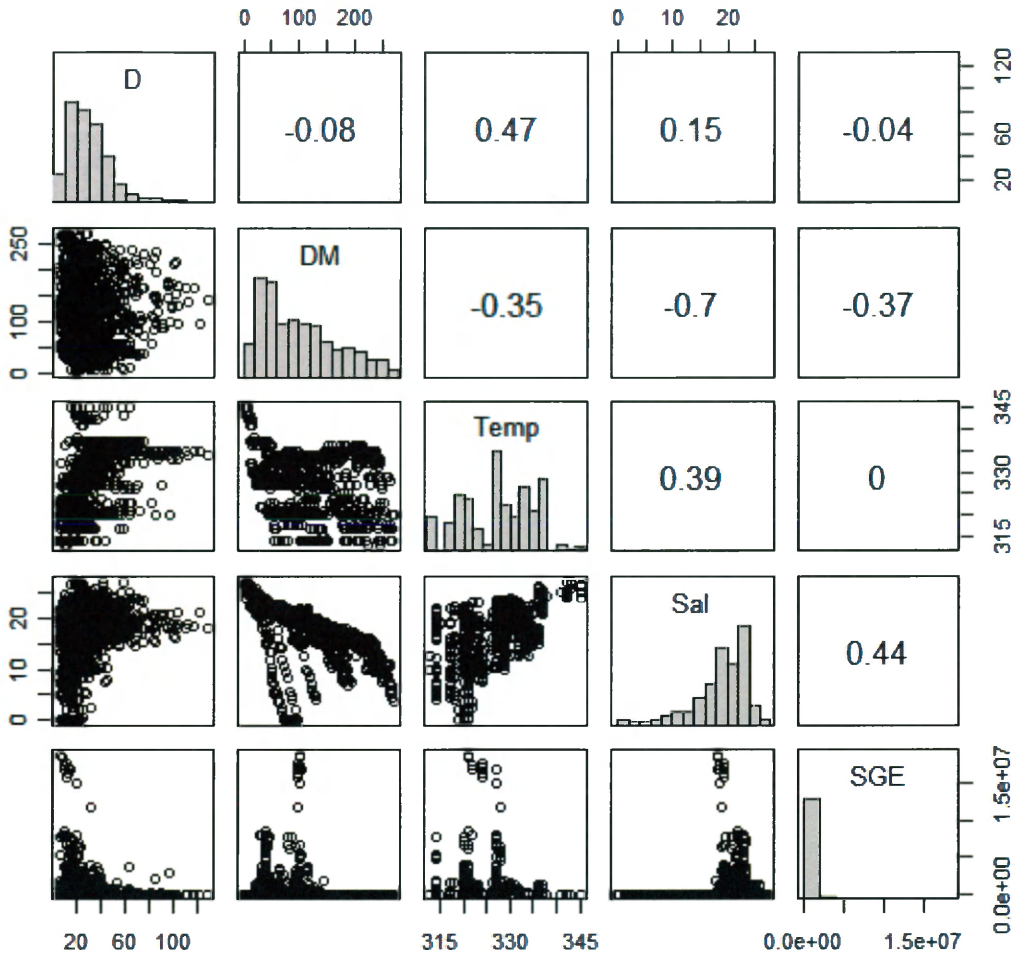


Figure A.5: 1995

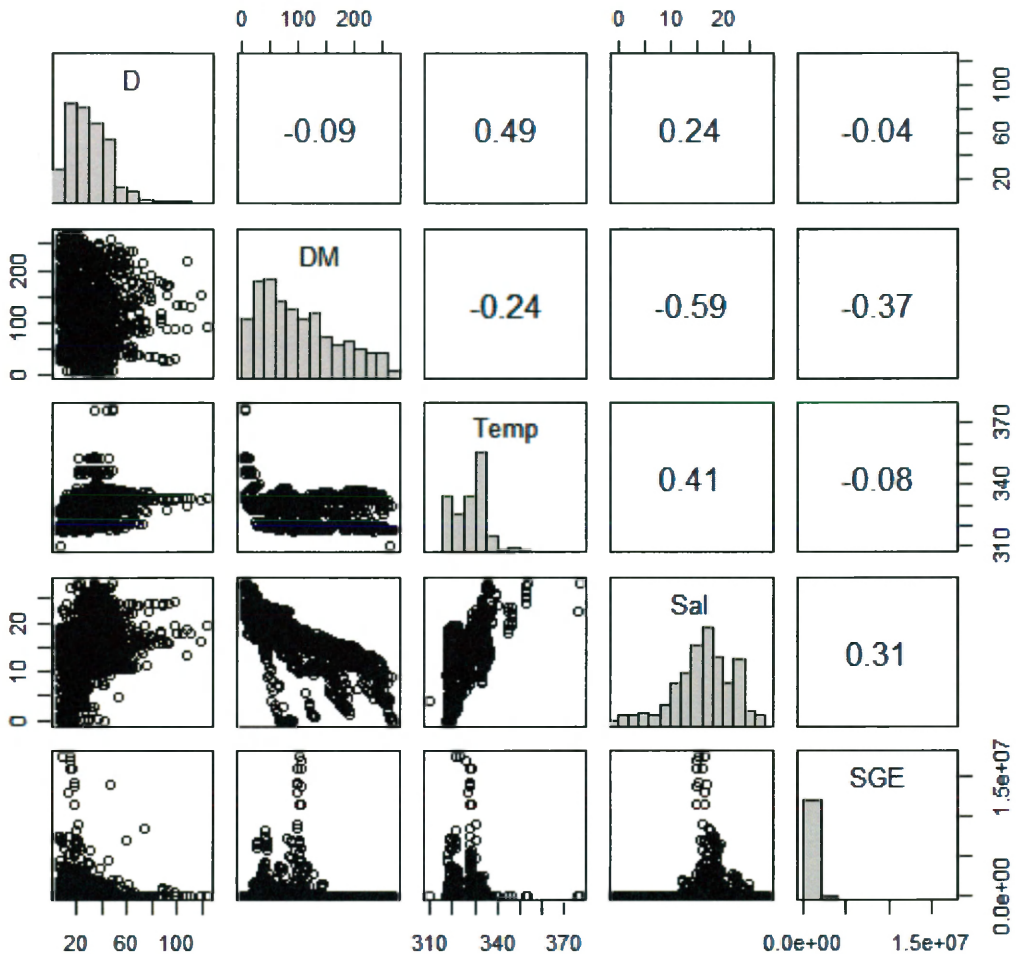


Figure A.6: 1996

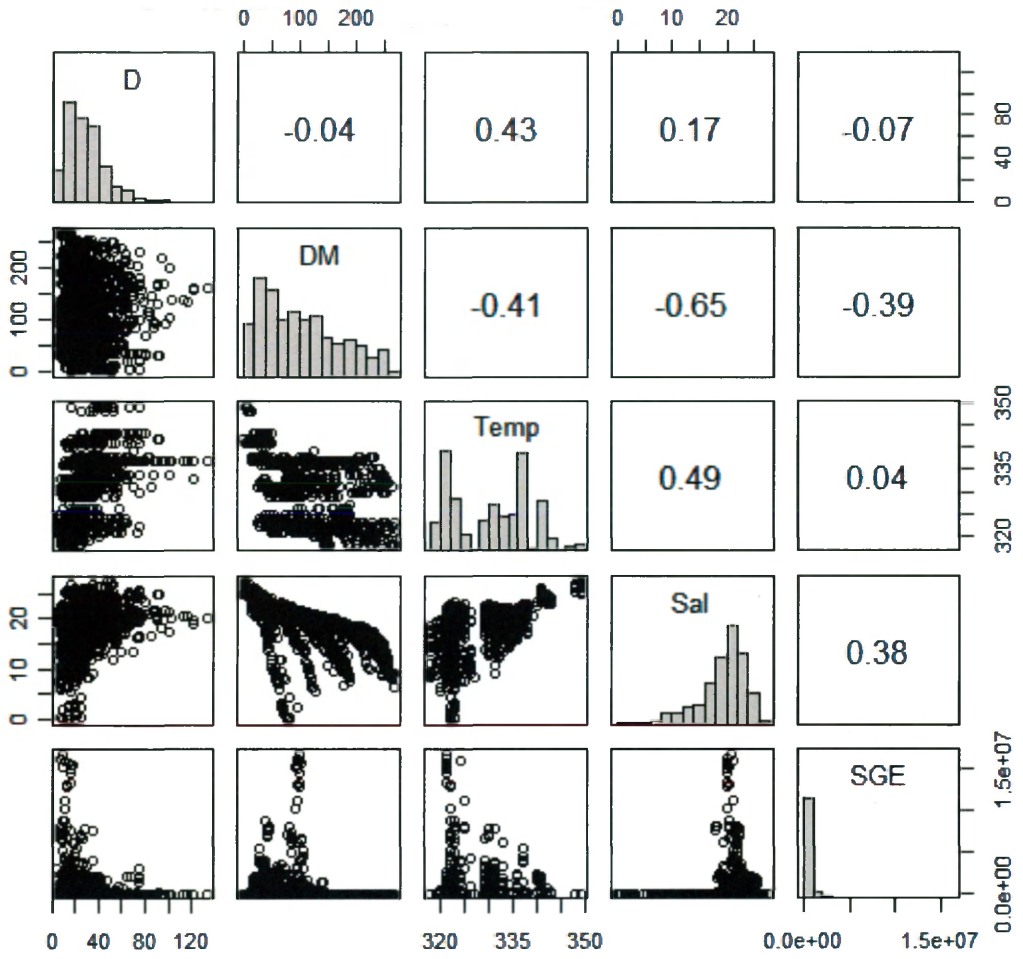


Figure A.7: 1997

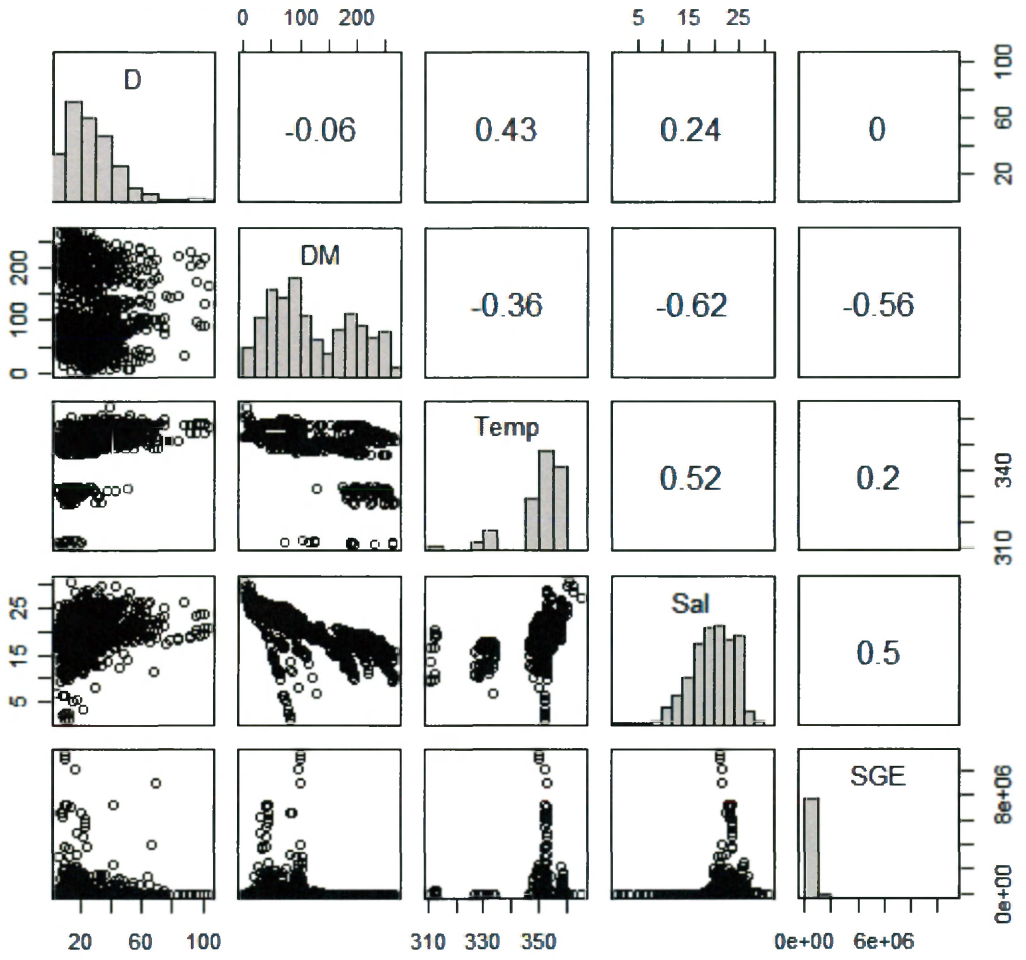


Figure A.8: 1998

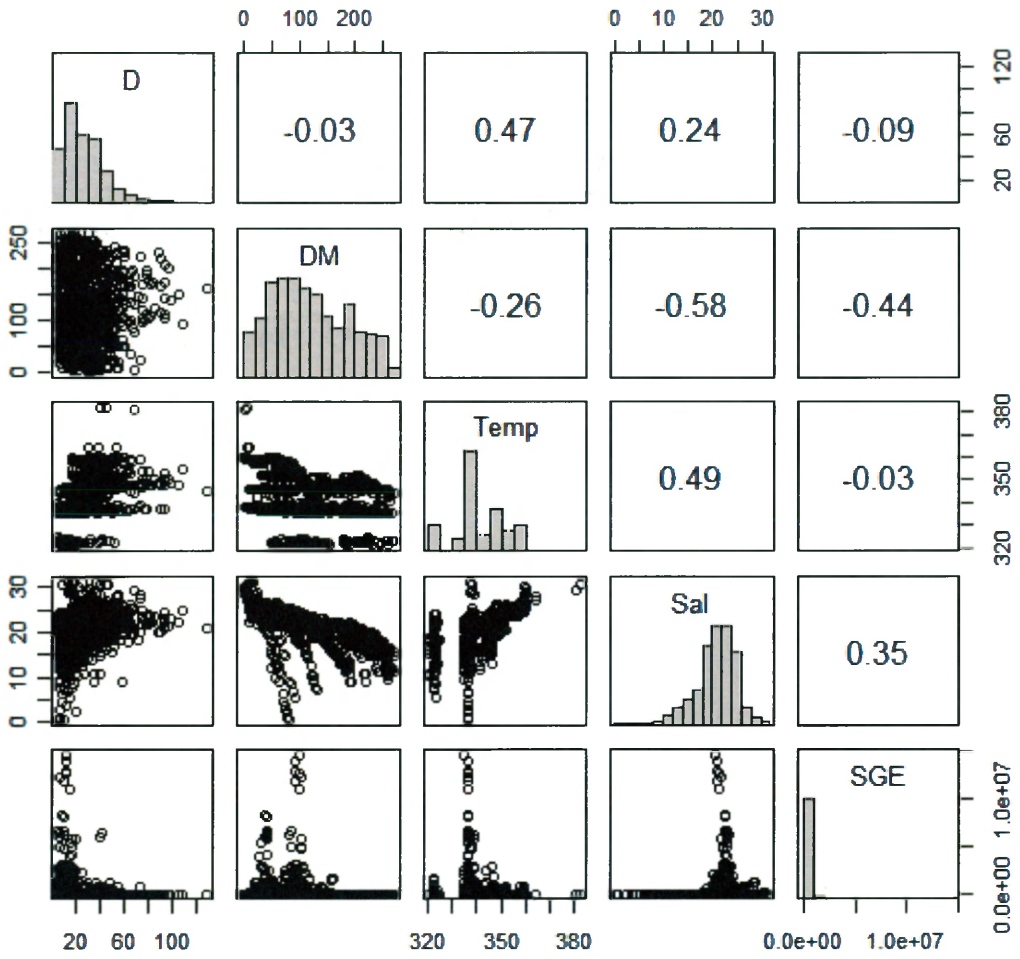


Figure A.9: 1999

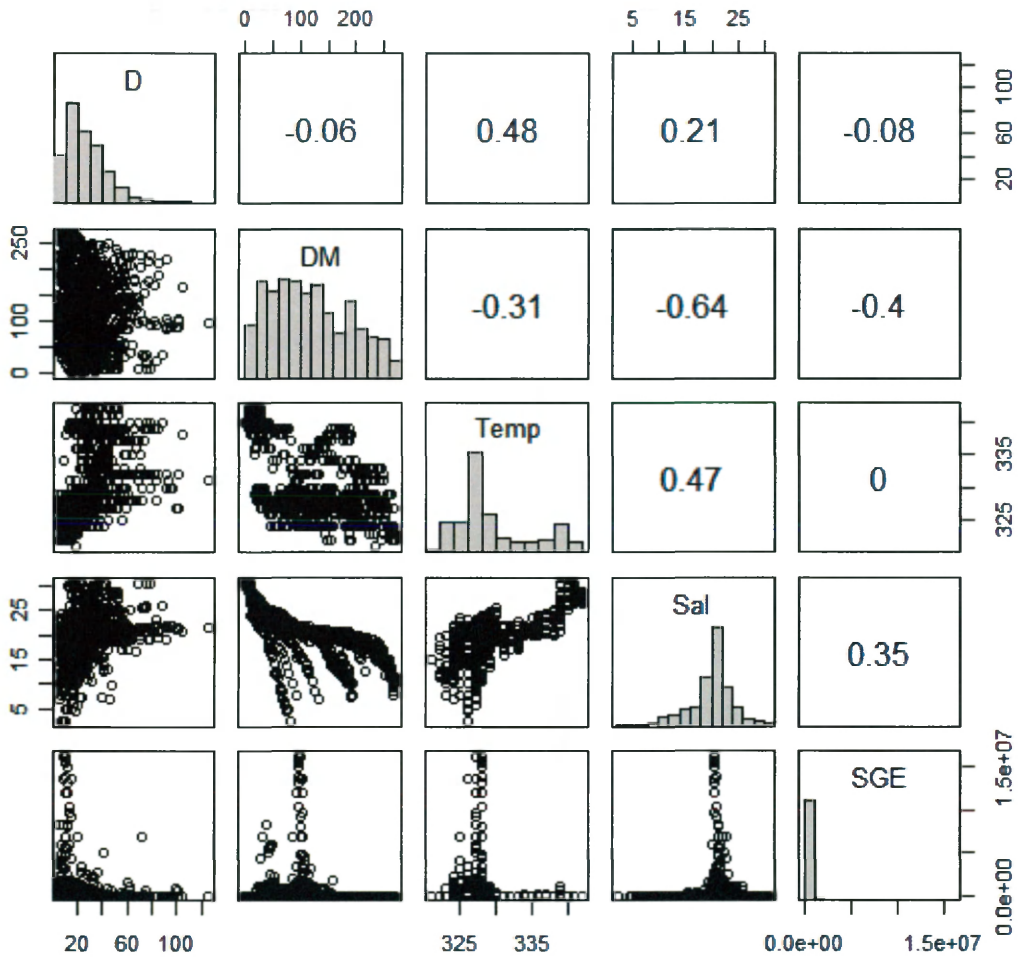


Figure A.10: 2000

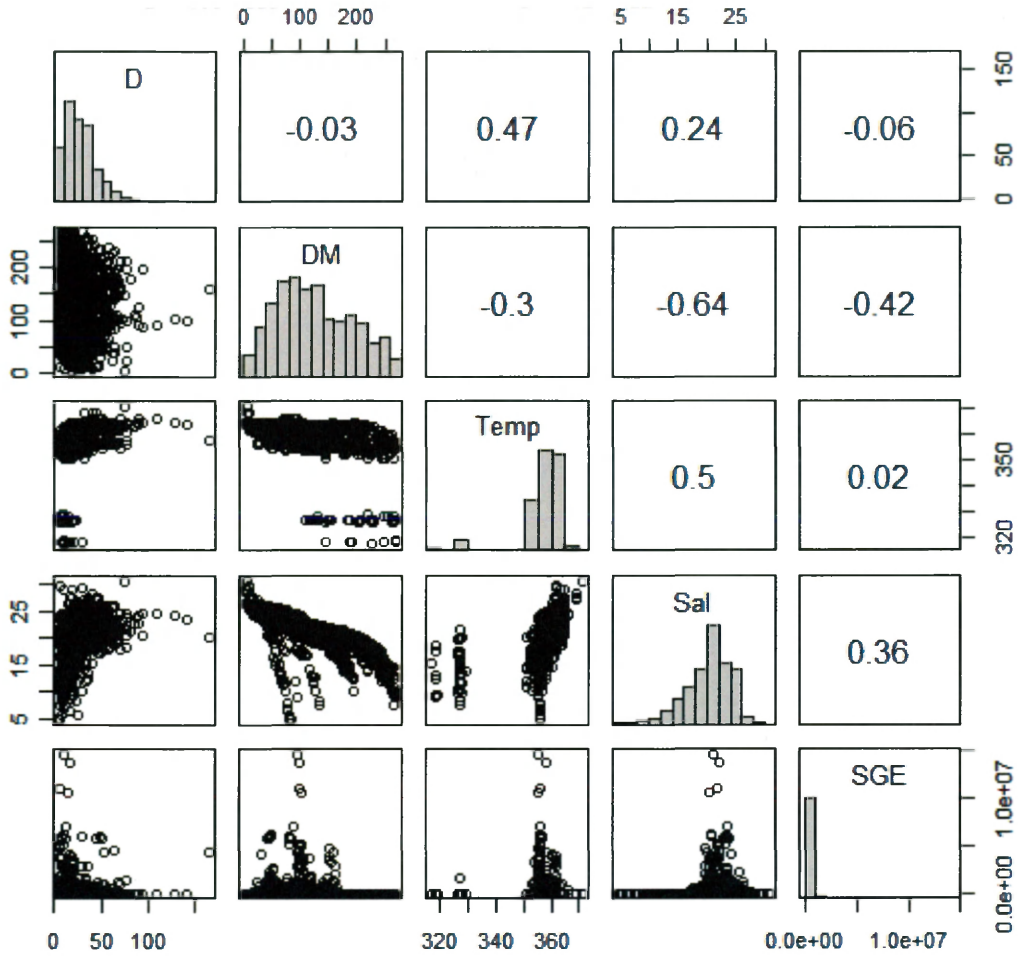


Figure A. 11: 2001

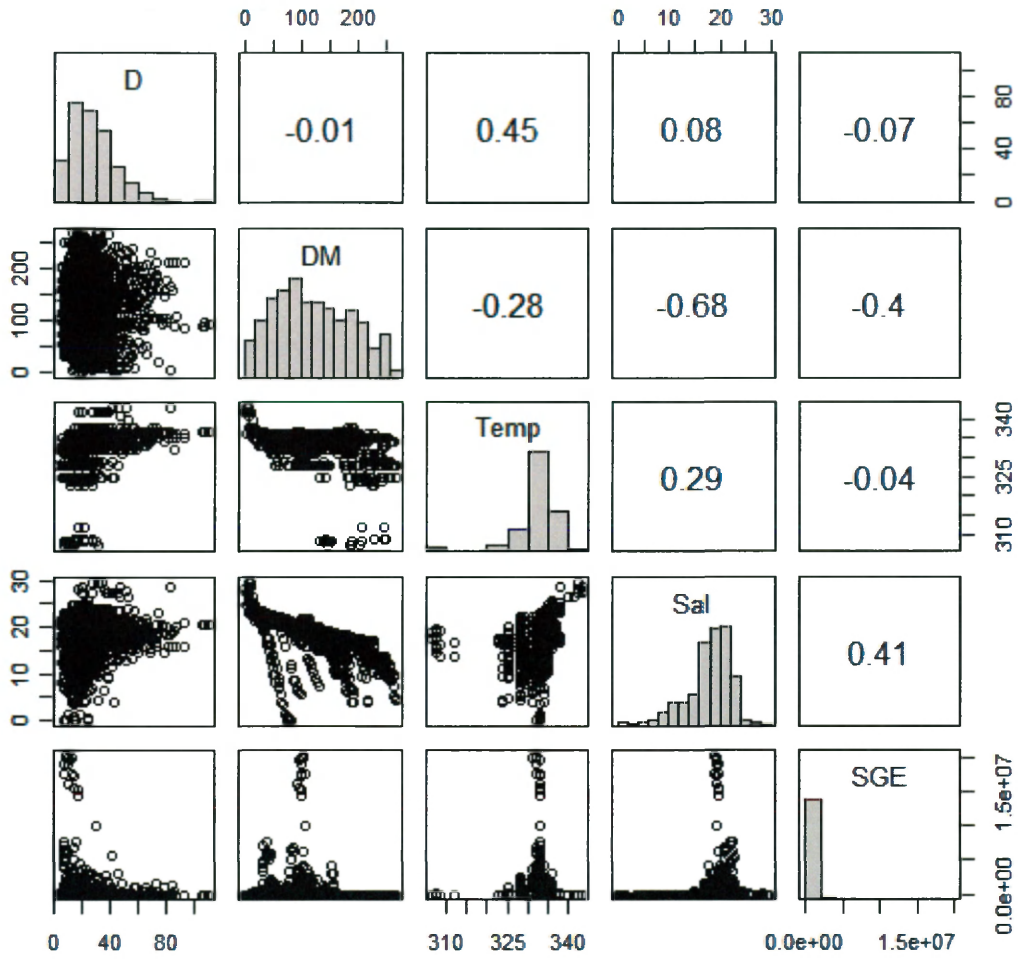


Figure A.12: 2002

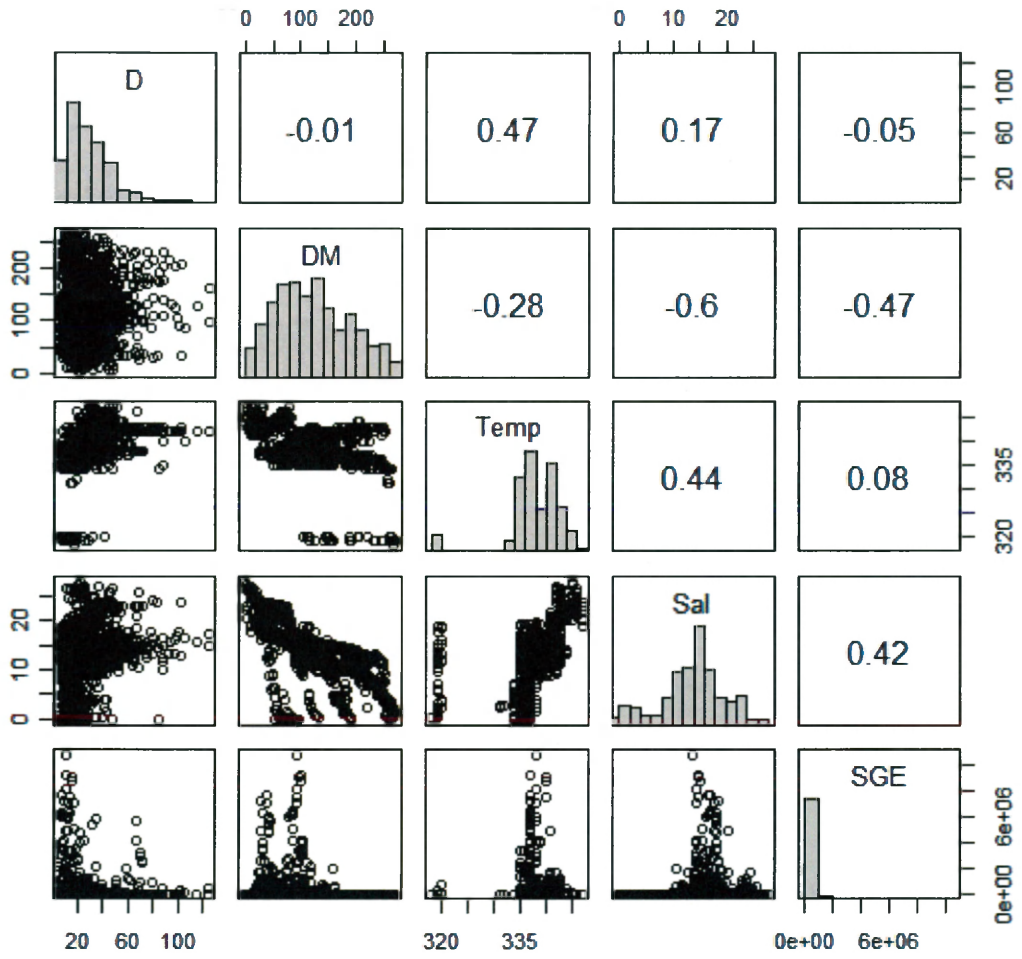


Figure A.13: 2003

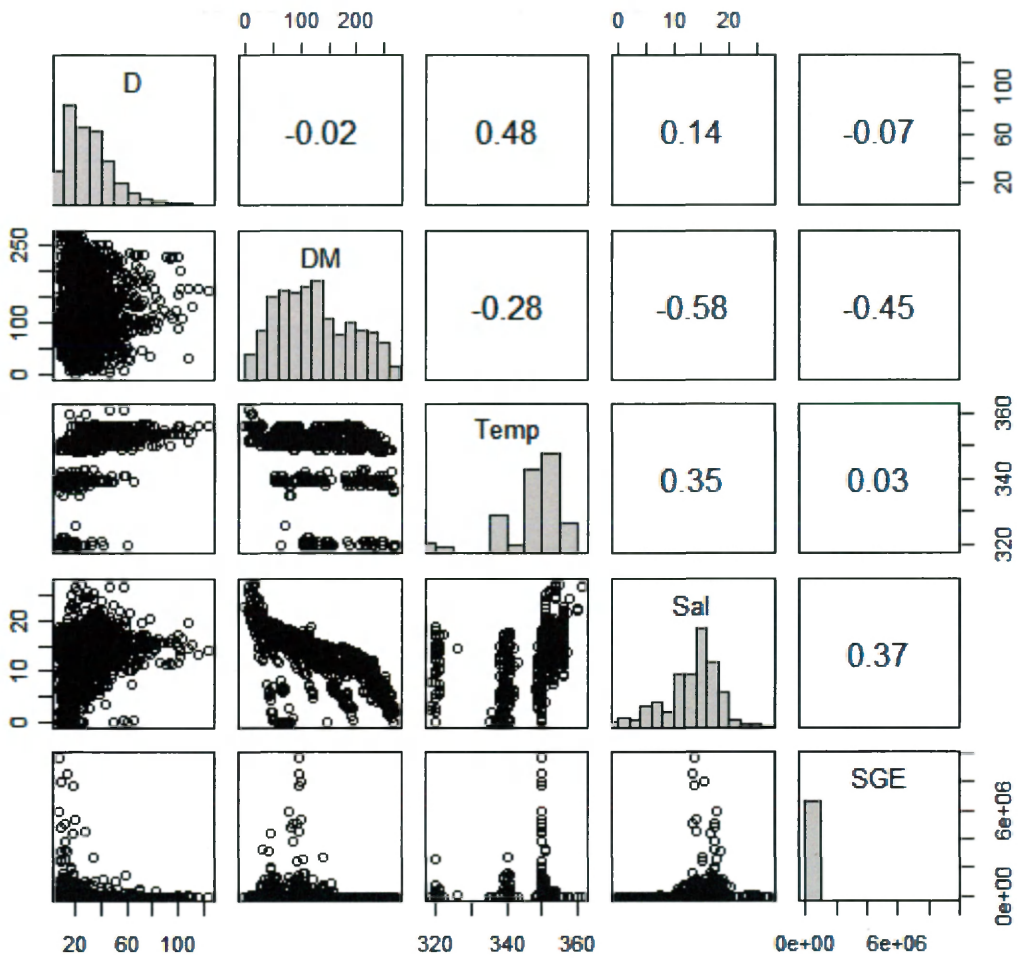


Figure A.14: 2004

Appendix B

Table B: Model output from GAMs by year (1991 – 2004). D = depth, Temp = day the bottom water temperature reached 10^{o}C and remained below 10^{o}C for 2 consecutive days from the ChesROMS model, Sal = bottom water salinity on the day the bottom water temperature reached 10^{o}C, SGE = combined effect of area of the nearest seagrass bed and distance to that bed. Stage 1 is the presence/absence GAM; given presence, Stage 2 is the density GAM. F0 includes female crabs < 60 mm CW, F1+ includes females > 60 mm CW, M0 includes males < 60 mm CW, and M1+ includes males > 60 mm CW.

Table B.1: 1991

Sex/Age Class	GAM	n	*edf*				*p-value*					r^2	% dev
			D	Sal	Temp	SGE	V	D	Sal	Temp	SGE		
Total	1	2521	2.895	2.864	3.88	1.001	0	0	0	0	0.209	0.077	0.061
Total	2	1132	2.995	1	3.858	2.685	0.005	0.113	0.002	0	0.454	0.025	0.07
F0	1	2521	2.637	3.81	2.29	3.749	0	0.003	0	0	0.002	0.053	0.083
F0	2	339	1.078	1	1	1	0.875	0.144	0.511	0.38	0.5	0.024	0.059
F1	1	2521	2.462	3.925	3.833	2.318	0	0	0.002	0	0.033	0.141	0.118
F1	2	568	3.727	1	3.63	2.795	0.053	0	0.039	0.004	0.018	0.08	0.226
M0	1	2521	2.197	3.888	1.001	1.694	0	0.193	0	0	0.451	0.078	0.103
M0	2	325	2.85	3.784	1	1	0.004	0.293	0.001	0.146	0.297	0.053	0.146
M1	1	2521	1	3.46	1	1	0.01	0.746	0	0	0.102	0.077	0.078
M1	2	443	3.275	2.998	3.685	1	0.01	0.138	0.307	0	0.331	0.06	0.202

Table B.2: 1992

Sex/Age Class	GAM	n	edf				p-value					r^2	% dev
			D	Sal	Temp	SGE	V	D	Sal	Temp	SGE		
Total	1	1418	2.525	3.937	3.598	1.001	0	0	0	0	0.012	0.139	0.115
Total	2	668	1.587	2.673	3.489	2.631	0	0	0	0	0.058	0.165	0.309
F0	1	1418	2.964	3.427	3.823	2.393	0	0.279	0	0	0.057	0.22	0.22
F0	2	280	1	2.631	3.536	1.308	0.001	0.283	0.008	0	0.769	0.127	0.264
F1	1	1418	2.231	3.984	2.949	1.001	0.002	0	0	0.055	0.015	0.067	0.068
F1	2	356	1.595	3.294	1	1.531	0.069	0	0.193	0.078	0.64	0.029	0.104
M0	1	1418	1	3.553	3.895	2.178	0	0.509	0	0	0.229	0.231	0.226
M0	2	274	1.735	2.743	3.77	1	0	0.002	0.013	0	0.564	0.149	0.294
M1	1	1418	1.001	3.818	2.571	1	0.102	0.505	0	0	0.391	0.133	0.152
M1	2	226	1.739	1.849	1	2.456	0.001	0.168	0	0.704	0.001	0.075	0.241

Table B.3: 1993

Sex/Age Class	GAM	n	*edf*				*p-value*						
			D	Sal	Temp	SGE	V	D	Sal	Temp	SGE	r^2	% dev
Total	1	1494	3.706	3.843	3.03	1.001	0	0	0	0	0.026	0.09	0.076
Total	2	682	2.902	1	3.886	1.826	0	0.004	0.002	0	0.039	0.085	0.186
F0	1	1494	1.679	3.907	3.572	1	0.004	0.025	0	0	0.132	0.084	0.113
F0	2	309	1	3.847	3.425	1	0.002	0.032	0	0.001	0.228	0.123	0.223
F1	1	1494	3.146	3.912	1	3.763	0	0.002	0	0.087	0	0.102	0.103
F1	2	304	3.527	1	3.151	1	0	0.001	0	0.009	0.516	0.119	0.195
M0	1	1494	1.572	3.915	3.318	1.001	0	0.09	0	0	0.293	0.118	0.139
M0	2	302	1.579	3.856	3.44	1.449	0.036	0.002	0.001	0.001	0.089	0.099	0.224
M1	1	1494	1	2.572	3.002	1	0.005	0.849	0.005	0	0.36	0.105	0.13
M1	2	239	1	1	3.012	1.539	0	0.246	0.638	0.145	0.696	0.045	0.191

Table B.4: 1994

Sex/Age Class	GAM	n	edf				p-value					r^2	% dev
			D	Sal	Temp	SGE	V	D	Sal	Temp	SGE		
Total	1	1627	1	3.801	3.59	1.001	0	0.001	0.001	0	0.116	0.175	0.146
Total	2	526	2.379	3.101	3.469	3.721	0	0.124	0.001	0	0.006	0.098	0.25
F0	1	1627	1.409	3.951	2.947	2.931	0	0.734	0	0	0.042	0.259	0.278
F0	2	230	1	1	1.104	1	0.318	0.52	0.486	0.007	0.758	0.008	0.088
F1	1	1627	1	3.551	2.43	2.912	0	0.099	0.001	0	0.295	0.059	0.076
F1	2	227	1	3.373	1	2.39	0.035	0.363	0	0.092	0.061	0.012	0.123
M0	1	1627	1	3.969	3.873	1	0	0.215	0	0	0.097	0.232	0.263
M0	2	208	1.542	1.828	1.103	1	0.01	0.261	0.348	0.007	0.585	0.042	0.155
M1	1	1627	3.657	2.776	1	1.491	0	0.052	0.542	0	0.24	0.206	0.247
M1	2	186	1.859	1.994	1	2.585	0	0.001	0.415	0.234	0.326	0.125	0.242

Table B.5: 1995

Sex/Age Class	GAM	n	*edf*				*p-value*					r^2	% dev
			D	Sal	Temp	SGE	V	D	Sal	Temp	SGE		
Total	1	1737	3.254	3.16	3.4	1	0	0	0	0	0.304	0.191	0.147
Total	2	898	3.344	3.475	3.901	3.103	0.025	0	0.002	0	0.005	0.097	0.259
F0	1	1737	2.648	3.567	1.001	1.3	0.065	0	0	0	0.676	0.234	0.227
F0	2	480	1.001	3.429	1.001	3.34	0.009	0.891	0.022	0	0.445	0.087	0.242
F1	1	1737	2.571	1.003	3.802	2.874	0	0	0	0	0.238	0.126	0.118
F1	2	447	3.206	3.271	1.001	3.583	0.073	0	0.028	0.072	0.305	0.115	0.222
M0	1	1737	2.496	3.678	1.336	1.668	0	0	0	0	0.537	0.248	0.243
M0	2	438	3.437	2.783	1	1	0.307	0.351	0.011	0	0.44	0.058	0.201
M1	1	1737	3.906	3.707	2.281	1.001	0.021	0	0.002	0	0.548	0.183	0.189
M1	2	308	3.411	2.543	2.373	1	0.018	0	0	0.002	0.855	0.032	0.222

Table B.6: 1996

Sex/Age Class	GAM	n	edf				p-value					r^2	% dev
			D	Sal	Temp	SGE	V	D	Sal	Temp	SGE		
Total	1	1798	3.091	3.367	3.487	1	0	0	0.012	0	0.029	0.187	0.148
Total	2	888	1.639	3.568	3.514	3.38	0	0.243	0.002	0.018	0.026	0.06	0.133
F0	1	1798	2.932	3.948	3.945	1.558	0.002	0	0	0	0.168	0.23	0.214
F0	2	511	3.125	2.661	1.001	3.631	0	0	0.013	0.296	0.433	0.114	0.187
F1	1	1798	2.541	1.837	3.515	1.001	0.64	0	0	0	0.038	0.063	0.072
F1	2	332	1	2.081	3.359	1.249	0.299	0.018	0.329	0.001	0.89	0.079	0.158
M0	1	1798	3.785	3.95	1.227	1.028	0	0	0	0	0.715	0.216	0.197
M0	2	490	1.86	1.762	2.003	1	0	0.091	0.493	0.022	0.044	0.056	0.097
M1	1	1798	1.318	2.272	2.567	1	0.011	0	0.512	0	0.122	0.098	0.121
M1	2	244	1.714	1	2.96	1	0.028	0.36	0.248	0.012	0.445	0.066	0.154

Table B.7: 1997

Sex/Age Class	GAM	n	*edf*				*p-value*						
			D	Sal	Temp	SGE	V	D	Sal	Temp	SGE	r^2	% dev
Total	1	1716	2.604	3.299	3.377	1	0	0	0	0	0.076	0.1	0.079
Total	2	751	2.678	3.442	2.752	1	0.004	0.141	0.099	0	0.329	0.046	0.109
F0	1	1716	3.079	3.784	3.598	1.001	0	0	0	0	0.209	0.107	0.139
F0	2	294	1	2.976	2.848	1.785	0.029	0.522	0.072	0.523	0.263	0.077	0.201
F1	1	1716	2.417	1	3.489	1	0	0	0.183	0	0.067	0.083	0.079
F1	2	389	3.674	3.363	3.22	2.169	0	0.031	0.444	0.005	0.417	0.068	0.173
M0	1	1716	3.859	3.08	3.79	1	0.001	0.005	0.002	0	0.945	0.108	0.15
M0	2	264	1	3.839	1	1	0.073	0.28	0	0.016	0.721	0.108	0.221
M1	1	1716	3.722	3.24	2.43	1.206	0.856	0	0.004	0	0.627	0.108	0.141
M1	2	256	1	3.095	1	2.241	0.264	0.312	0.542	0.002	0.128	0.014	0.093

Table B.8: 1998

Sex/Age Class	GAM	n	*edf*				*p-value*					r^2	% dev
			D	Sal	Temp	SGE	V	D	Sal	Temp	SGE		
Total	1	1122	2.734	2.589	1.965	1	0	0	0	0.048	0.658	0.044	0.041
Total	2	436	2.911	3.709	3.553	1	0	0.003	0	0.005	0.888	0.097	0.322
F0	1	1122	3.262	3.077	2.244	1.786	0	0.012	0	0.115	0.467	0.083	0.09
F0	2	248	1	3.038	1	1.404	0	0.06	0.005	0.655	0.236	0.079	0.326
F1	1	1122	1.723	3.886	2.372	1	0	0.31	0.001	0.025	0.151	0.089	0.123
F1	2	135	3.151	3.709	1.274	1	0.787	0.001	0.022	0.016	0.563	0.15	0.275
M0	1	1122	1	2.914	1.441	1	0	0.675	0	0.385	0.849	0.091	0.095
M0	2	184	2.849	2.476	3.513	3.448	0	0.557	0.022	0.115	0.115	0.026	0.3
M1	1	1122	1	3.055	1.135	1	0	0.559	0	0.028	0.82	0.062	0.089
M1	2	106	1.889	3.485	3.904	1	0.077	0.081	0.205	0	0.955	0.176	0.406

Table B.9: 1999

Sex/Age Class	GAM	n	*edf*				*p-value*					r^2	% dev
			D	Sal	Temp	SGE	V	D	Sal	Temp	SGE		
Total	1	1347	3.698	2.384	3.852	1.357	0	0	0.004	0	0.811	0.059	0.053
Total	2	475	3.24	3.798	1.593	2.126	0.013	0	0.001	0.01	0.004	0.077	0.182
F0	1	1347	2.11	3.464	1	1.74	0	0.07	0	0	0.355	0.098	0.123
F0	2	176	2.181	2.888	1.887	1.383	0.003	0.005	0.06	0.159	0.261	0.197	0.311
F1	1	1347	1.287	3.464	3.769	1.889	0	0.033	0.541	0.003	0.382	0.09	0.097
F1	2	226	1.08	1.255	3.713	1	0.032	0.933	0.653	0.072	0.498	0.056	0.157
M0	1	1347	1	3.834	1	1.798	0.006	0.668	0	0	0.268	0.098	0.141
M0	2	142	1.71	3.487	1	1	0.085	0.088	0.054	0.002	0.308	0.059	0.272
M1	1	1347	1.079	2.549	3.484	1.873	0.237	0.05	0.037	0.001	0.236	0.061	0.092
M1	2	163	3.466	1	1	1	0.001	0.263	0.298	0.057	0.466	0.117	0.219

Table B.10: 2000

Sex/Age Class	GAM	n	edf				p-value					r^2	% dev
			D	Sal	Temp	SGE	V	D	Sal	Temp	SGE		
Total	1	1440	2.897	1.017	3.739	1	0	0	0	0	0.937	0.081	0.076
Total	2	424	3.075	1	3.265	1.453	0	0.088	0.397	0	0.25	0.138	0.286
F0	1	1440	2.477	3.71	2.629	1.89	0	0.021	0	0.016	0.186	0.102	0.148
F0	2	181	2.913	1	1	1	0.014	0.009	0.329	0.036	0.334	0.167	0.296
F1	1	1440	2.569	2.926	3.39	1	0	0	0.48	0	0.925	0.111	0.146
F1	2	180	2.675	1	1	1	0.046	0.26	0.112	0.45	0.402	0.052	0.133
M0	1	1440	2.172	3.498	2.433	2.675	0	0.182	0	0	0.35	0.12	0.167
M0	2	167	1.946	1	1	1	0	0.285	0.119	0	0.508	0.123	0.271
M1	1	1440	1.584	2.824	3.384	1	0.82	0	0.41	0	0.319	0.059	0.112
M1	2	113	1	1	2.113	1	0.909	1	0.263	0.007	0.918	0.004	0.163

Table B.11: 2001

Sex/Age Class	GAM	n	edf				p-value					r^2	% dev
			D	Sal	Temp	SGE	V	D	Sal	Temp	SGE		
Total	1	1350	2.87	3.737	3.662	1.754	0	0	0	0	0.212	0.077	0.068
Total	2	459	1	3.207	3.6	3.147	0.039	0	0.016	0.068	0.127	0.027	0.154
F0	1	1350	2.946	3.763	1	1.644	0	0.003	0	0.364	0.503	0.075	0.099
F0	2	235	1.003	1	1	1.698	0.06	0.295	0.008	0.06	0.437	0.045	0.109
F1	1	1350	2.338	1.001	2.312	1	0.03	0.001	0	0.001	0.205	0.047	0.076
F1	2	131	1.905	1.668	1.966	1.487	0.256	0.339	0.278	0.423	0.739	-0.005	0.096
M0	1	1350	2.844	3.803	3.869	1	0	0.044	0	0.005	0.65	0.102	0.138
M0	2	213	1.955	3.864	1	3.792	0.34	0.125	0.002	0.225	0.076	0.039	0.14
M1	1	1350	1.987	3.042	3.983	1	0.025	0.085	0.003	0	0.514	0.065	0.103
M1	2	135	1	2.344	3.846	1.954	0.005	0.271	0.059	0.015	0.065	0.138	0.315

Table B.12: 2002

Sex/Age Class	GAM	n	edf				p-value					r^2	% dev
			D	Sal	Temp	SGE	V	D	Sal	Temp	SGE		
Total	1	1386	3.489	1	3.829	1	0.662	0	0.002	0	0.089	0.131	0.108
Total	2	520	3.869	1	2.124	1.05	0.147	0	0	0	0.016	0.114	0.314
F0	1	1386	2.101	3.758	3.919	1.859	0.743	0.06	0	0	0.61	0.137	0.19
F0	2	204	1	1.452	2.1	1	0.673	0.022	0.001	0.199	0.239	0.107	0.173
F1	1	1386	1.786	3.009	1.982	1.541	0.552	0	0	0	0.477	0.066	0.074
F1	2	245	3.902	1	1	1	0.513	0	0.005	0	0.359	0.117	0.238
M0	1	1386	1.49	3.625	3.295	1.833	0.283	0.675	0	0	0.838	0.186	0.224
M0	2	212	1	3.019	2.001	1	0.688	0.003	0.004	0.044	0.107	0.087	0.185
M1	1	1386	3.694	2.905	3.149	1	0.206	0	0.208	0	0.086	0.191	0.205
M1	2	212	3.758	1.001	3.868	1.423	0.106	0.05	0.134	0	0.376	0.04	0.374

Table B.13: 2003

Sex/Age Class	GAM	n	edf				p-value					r^2	% dev
			D	Sal	Temp	SGE	V	D	Sal	Temp	SGE		
Total	1	1385	3.67	3.327	2.559	1.002	0.032	0	0.001	0	0.337	0.074	0.061
Total	2	589	1.671	1	2.288	1.76	0.022	0.013	0	0	0.31	0.053	0.167
F0	1	1385	3.1	3.207	3.808	1.677	0.068	0	0	0.016	0.425	0.069	0.09
F0	2	266	2.95	2.352	1.836	1	0.046	0.057	0.101	0.225	0.232	0.047	0.18
F1	1	1385	2.977	3.893	3.859	1	0.119	0	0	0	0.654	0.132	0.137
F1	2	215	1	3.427	2.791	1	0.895	0.39	0.004	0.025	0.212	0.001	0.181
M0	1	1385	3.641	2.487	3.347	1	0.208	0	0.001	0	0.353	0.078	0.11
M0	2	140	3.573	1	1.792	1	0.099	0.007	0	0.002	0.182	0.161	0.28
M1	1	1385	3.764	3.205	3.721	3.866	0.361	0	0	0	0.03	0.104	0.113
M1	2	335	1.455	2.892	2.419	3.661	0.515	0	0.17	0.044	0.026	0.139	0.299

Table B.14: 2004

Sex/Age Class	GAM	n	edf				p-value					r^2	% dev
			D	Sal	Temp	SGE	V	D	Sal	Temp	SGE		
Total	1	1369	3.89	3.834	1.001	1.622	0.873	0	0	0	0.391	0.124	0.096
Total	2	742	1	3.605	2.862	3.634	0.002	0.003	0.003	0	0.103	0.145	0.185
F0	1	1369	3.671	3.492	1	1	0.327	0	0	0	0.36	0.136	0.119
F0	2	492	1.903	3.769	1	3.328	0.003	0.354	0.002	0	0.001	0.102	0.176
F1	1	1369	2.736	1.855	1	1	0.637	0	0	0	0.94	0.06	0.065
F1	2	235	3.62	1	1	1.485	0	0.01	0.049	0.394	0.685	0.059	0.255
M0	1	1369	1	1.13	2.137	1	0.005	0.116	0.243	0	0.595	0.051	0.061
M0	2	141	2.074	1.283	1	1.71	0.648	0.045	0.259	0.042	0.282	0.047	0.172
M1	1	1369	2.517	3.265	2.922	1.534	0.3	0	0	0	0.47	0.15	0.135
M1	2	496	1	3.54	2.761	2.831	0.001	0	0.014	0	0.128	0.189	0.259

Appendix C

Table C.1: Parameter significance in GAM models by year (1990 – 2004). D = depth, Temp = day the bottom water temperature reached 10°C and remained below 10°C for 2 consecutive days from the ChesROMS model, Sal = bottom water salinity on the day the bottom water temperature reached 10°C, SGE = combined effect of area of the nearest seagrass bed and distance to that bed. Stage 1 is the presence/absence GAM; given presence, Stage 2 is the density GAM.

	GAM	V	D	Sal	Temp	SGE
1990	1	1.00	0.50	1.00	1.00	0.50
	2	0.50	0.25	0.50	0.50	0.25
1991	1	0.75	0.25	1.00	0.75	0.25
	2	0.75	0.50	0.75	0.50	0.25
1992	1	1.00	0.50	1.00	0.75	0.25
	2	1.00	0.75	0.75	0.75	0.00
1993	1	1.00	0.00	0.75	1.00	0.25
	2	0.75	0.25	0.25	0.50	0.00
1994	1	0.75	1.00	1.00	1.00	0.00
	2	0.50	0.50	1.00	0.75	0.00
1995	1	0.75	1.00	0.75	1.00	0.25
	2	0.75	0.50	0.25	0.75	0.25
1996	1	0.75	1.00	0.75	1.00	0.00
	2	0.50	0.25	0.25	0.75	0.00
1997	1	1.00	0.25	1.00	0.50	0.00
	2	0.50	0.25	0.75	0.50	0.00
1998	1	0.75	0.50	0.75	1.00	0.00
	2	0.75	0.25	0.00	0.25	0.00
1999	1	0.75	0.75	0.50	1.00	0.00
	2	0.75	0.25	0.00	0.75	0.00
2000	1	1.00	0.75	1.00	0.75	0.00
	2	0.25	0.00	0.50	0.25	0.00
2001	1	0.00	0.50	0.75	1.00	0.00
	2	0.00	1.00	0.75	0.75	0.00
2002	1	0.00	1.00	1.00	1.00	0.25
	2	0.25	0.50	0.50	0.75	0.25
2003	1	0.25	0.75	0.75	1.00	0.00
	2	0.75	0.75	0.75	0.75	0.25
2004	1	1.00	0.50	1.00	1.00	0.50
	2	0.50	0.25	0.50	0.50	0.25

Table C.2: Parameter significance in GAM models over all years (1990 – 2004). D = depth, Temp = day the bottom water temperature reached 10°C and remained below 10°C for 2 consecutive days from the ChesROMS model, Sal = bottom water salinity on the day the bottom water temperature reached 10°C, SGE = combined effect of area of the nearest seagrass bed and distance to that bed. Stage 1 is the presence/absence GAM; given presence, Stage 2 is the density GAM. F0 includes female crabs < 60 mm CW, F1+ includes females > 60 mm CW, M0 includes males < 60 mm CW, and M1+ includes males > 60 mm CW.

	GAM	V	D	Sal	Temp	SGE
F0	1	**0.71**	0.36	**0.57**	0.43	0.07
	2	**0.71**	**0.71**	**1.00**	**0.86**	0.14
F1	1	0.43	**0.64**	**0.57**	**0.50**	0.07
	2	**0.71**	**0.86**	**0.78**	**0.86**	0.28
M0	1	**0.50**	0.36	**0.64**	**0.78**	0.07
	2	**0.86**	0.36	**0.93**	**0.86**	0.00
M1	1	**0.64**	0.36	0.21	**0.71**	0.14
	2	**0.50**	**0.57**	**0.71**	**1.00**	0.07

Appendix D

Figure D: Spatial distribution of the residuals from both stages of the GAM models for all years (1990 – 2004) by sex/age category. Stage 1 is the presence/absence GAM; given presence, Stage 2 is the density GAM. F0 includes female crabs < 60 mm CW, F1+ includes females > 60 mm CW, M0 includes males < 60 mm CW, and M1+ includes males > 60 mm CW. Stage 1: a) F0, b) F1, c) M0, d) M1; Stage 2: e) F0, f) F1, g) M0, h) M1.

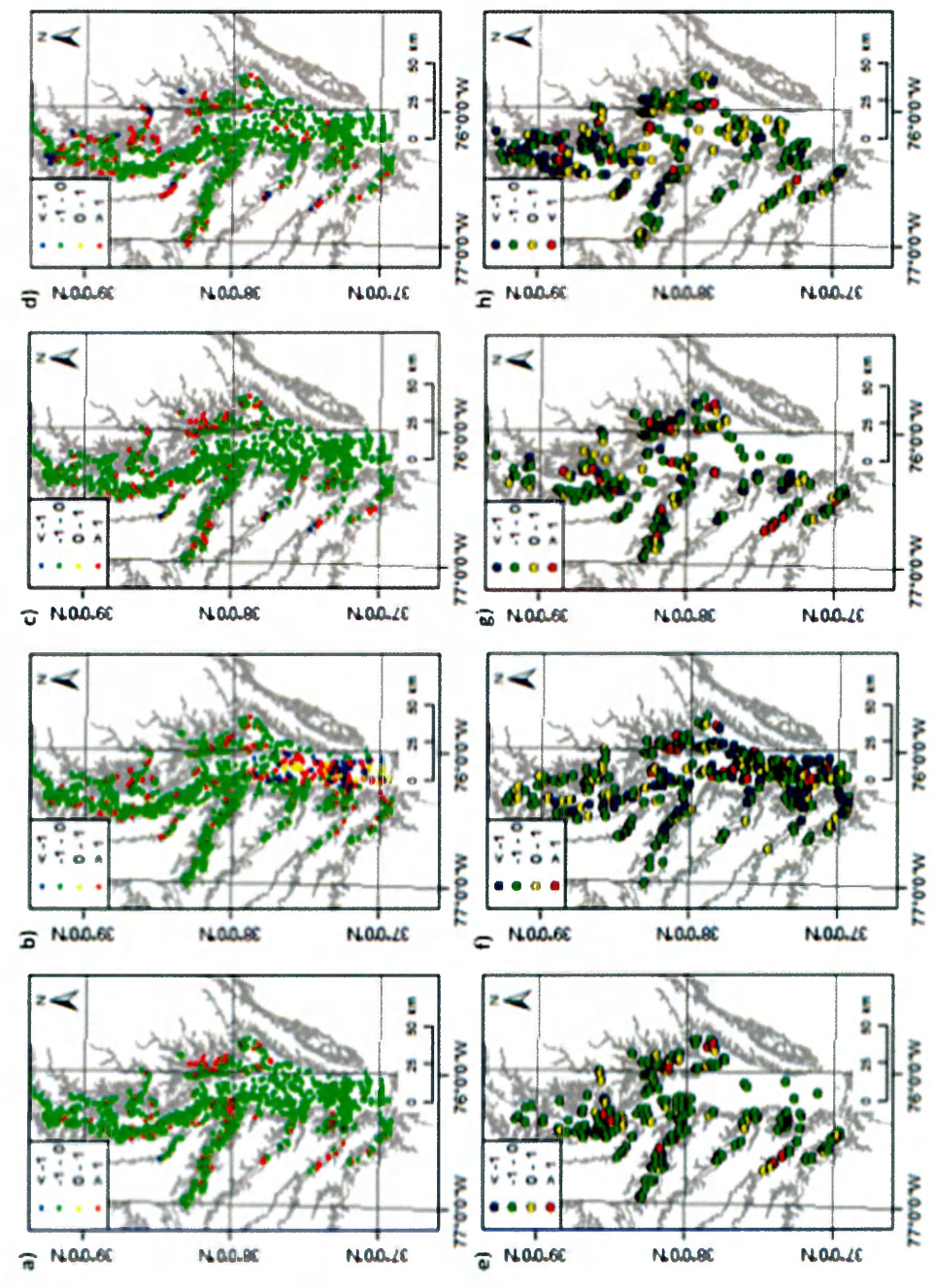


Figure D.1: 1991

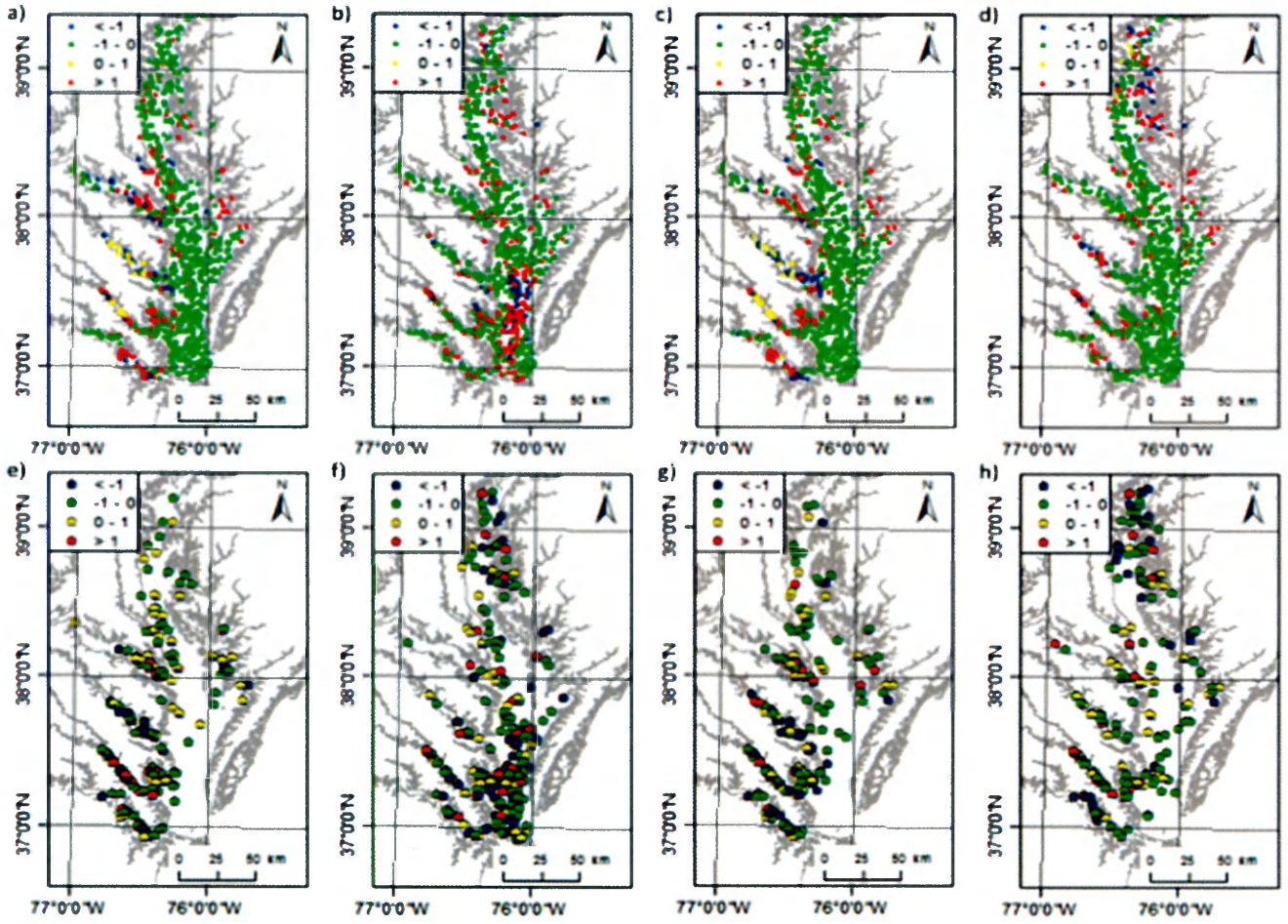


Figure D.2: 1992

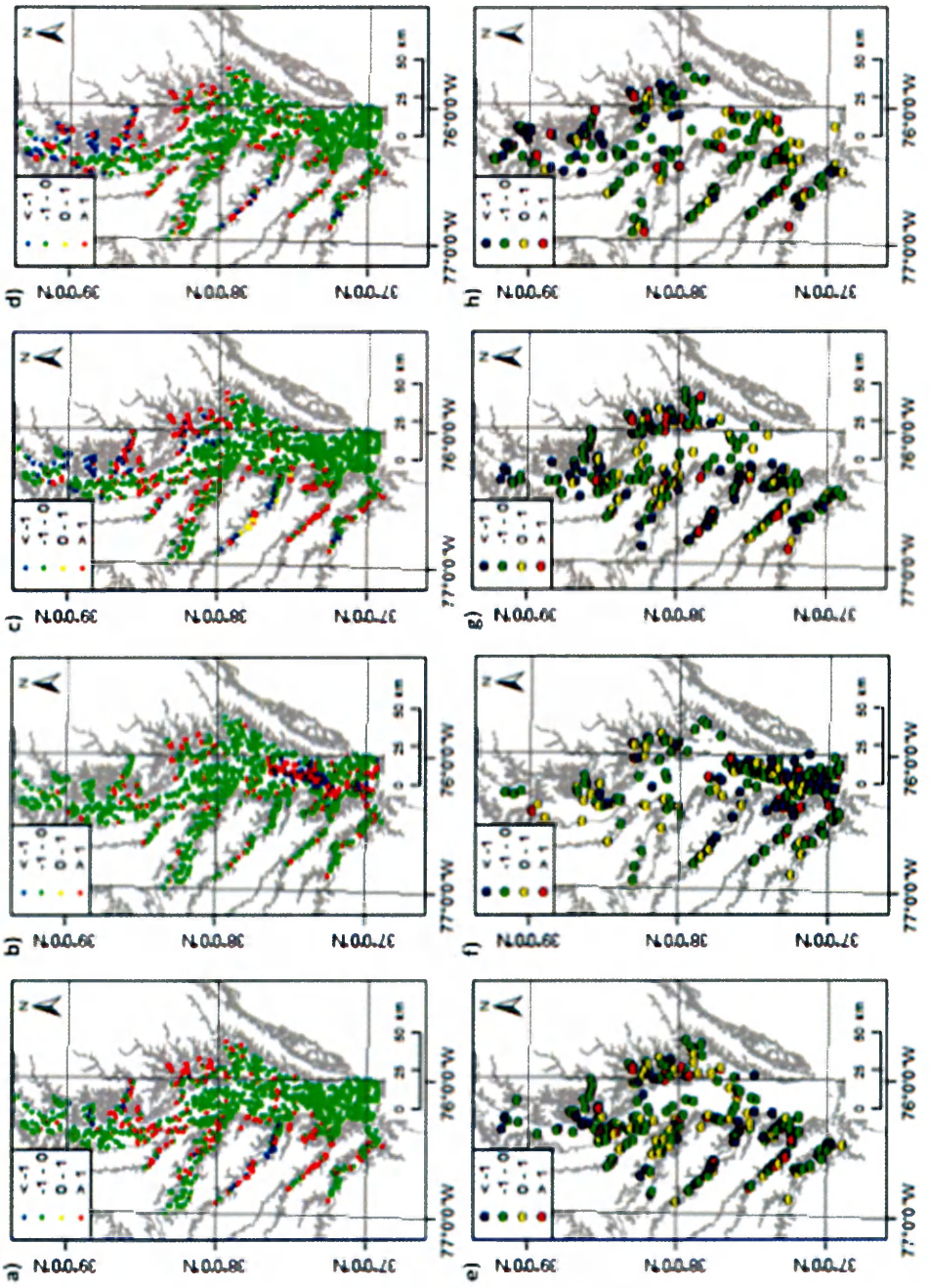


Figure D.3: 1993

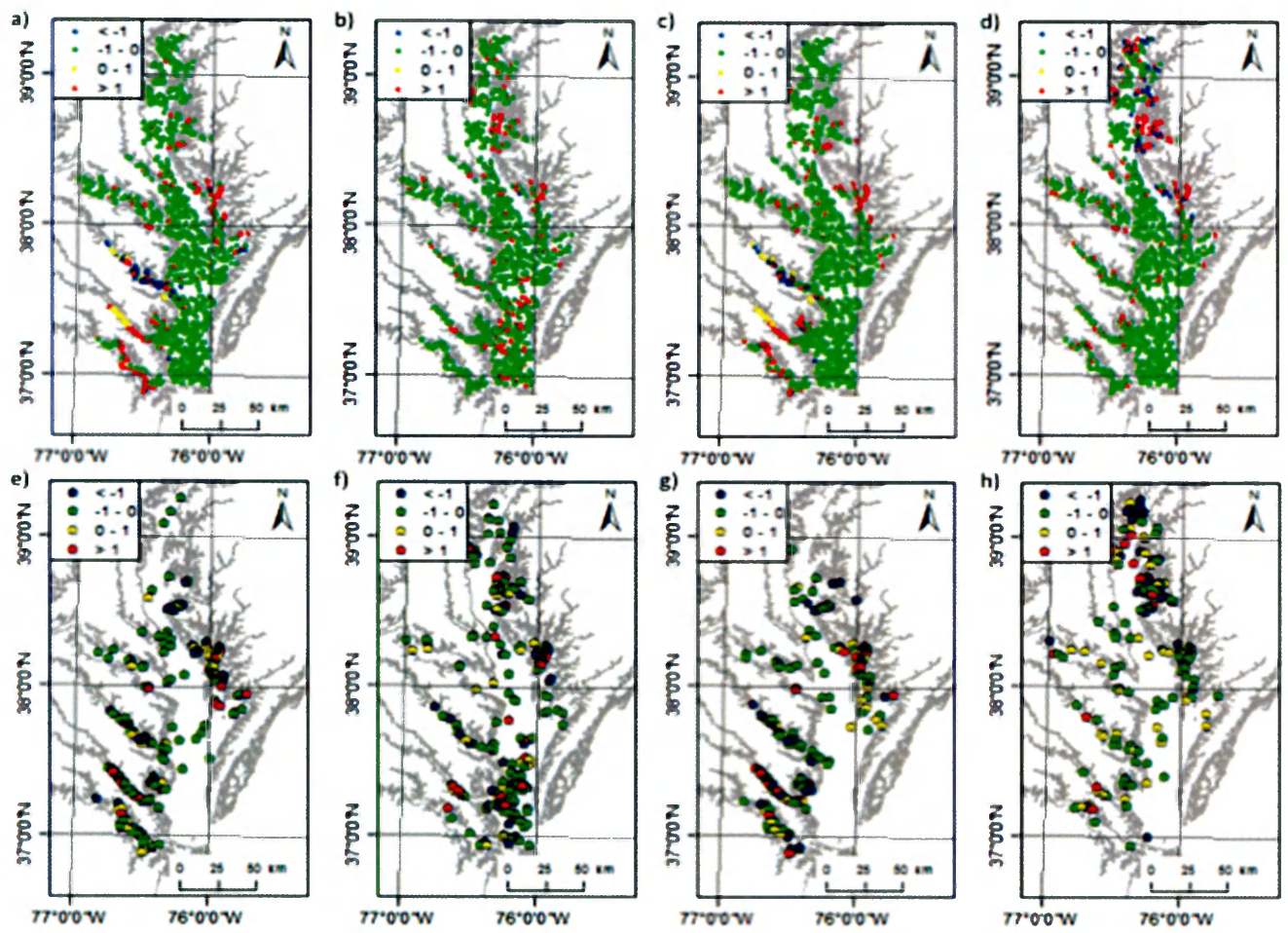


Figure D.4: 1994

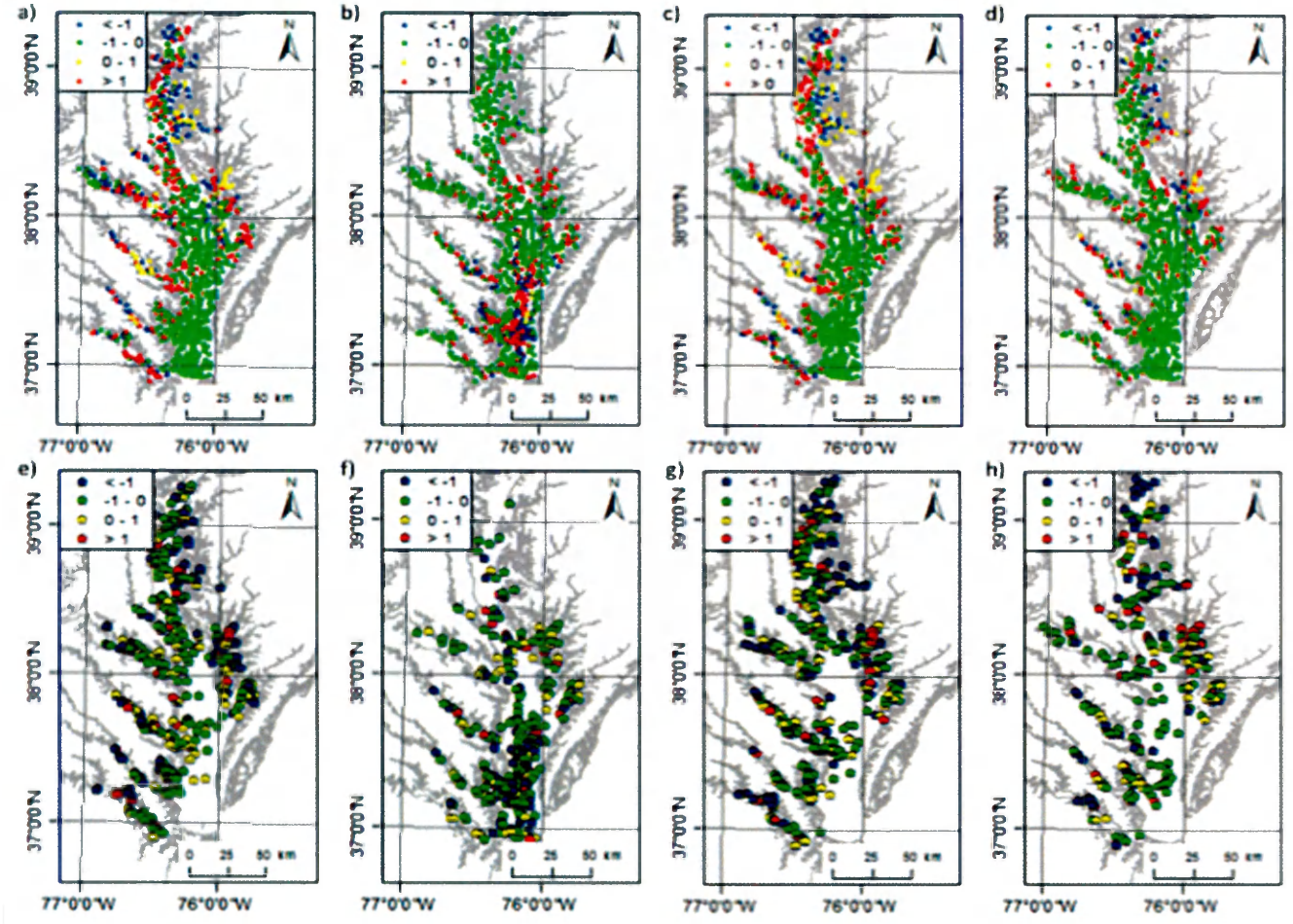


Figure D.5: 1995

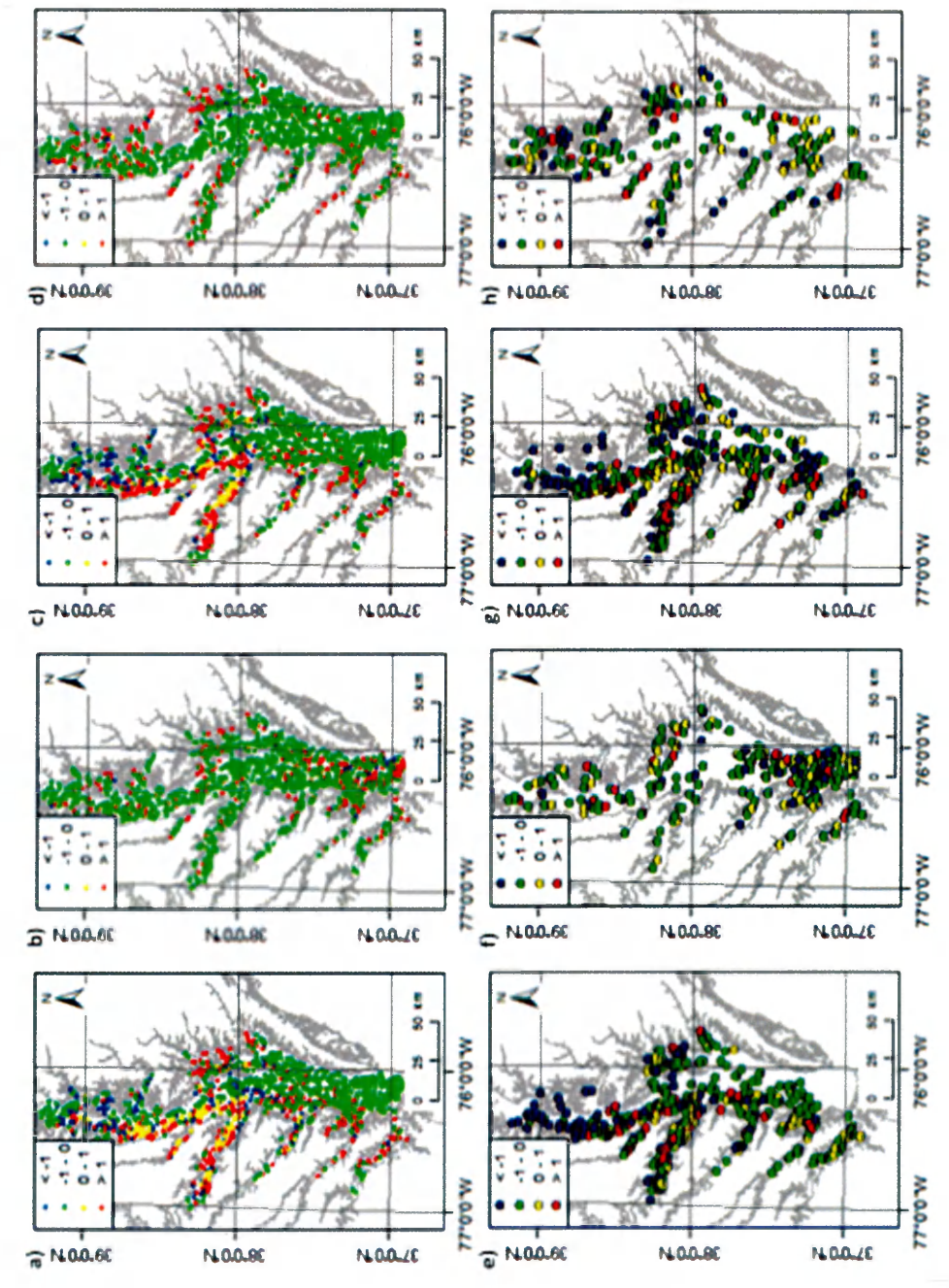


Figure D.6: 1996

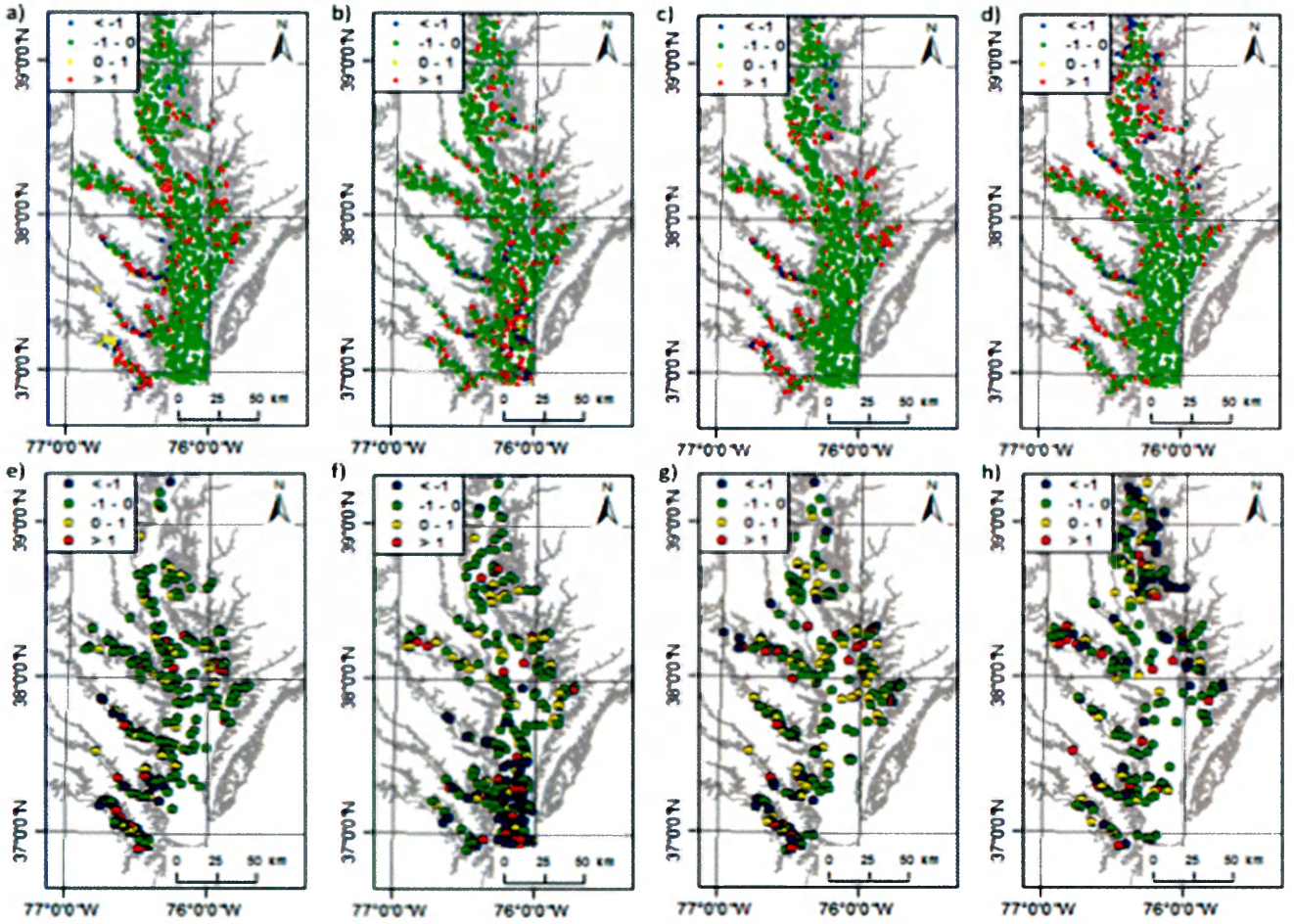


Figure D.7: 1997

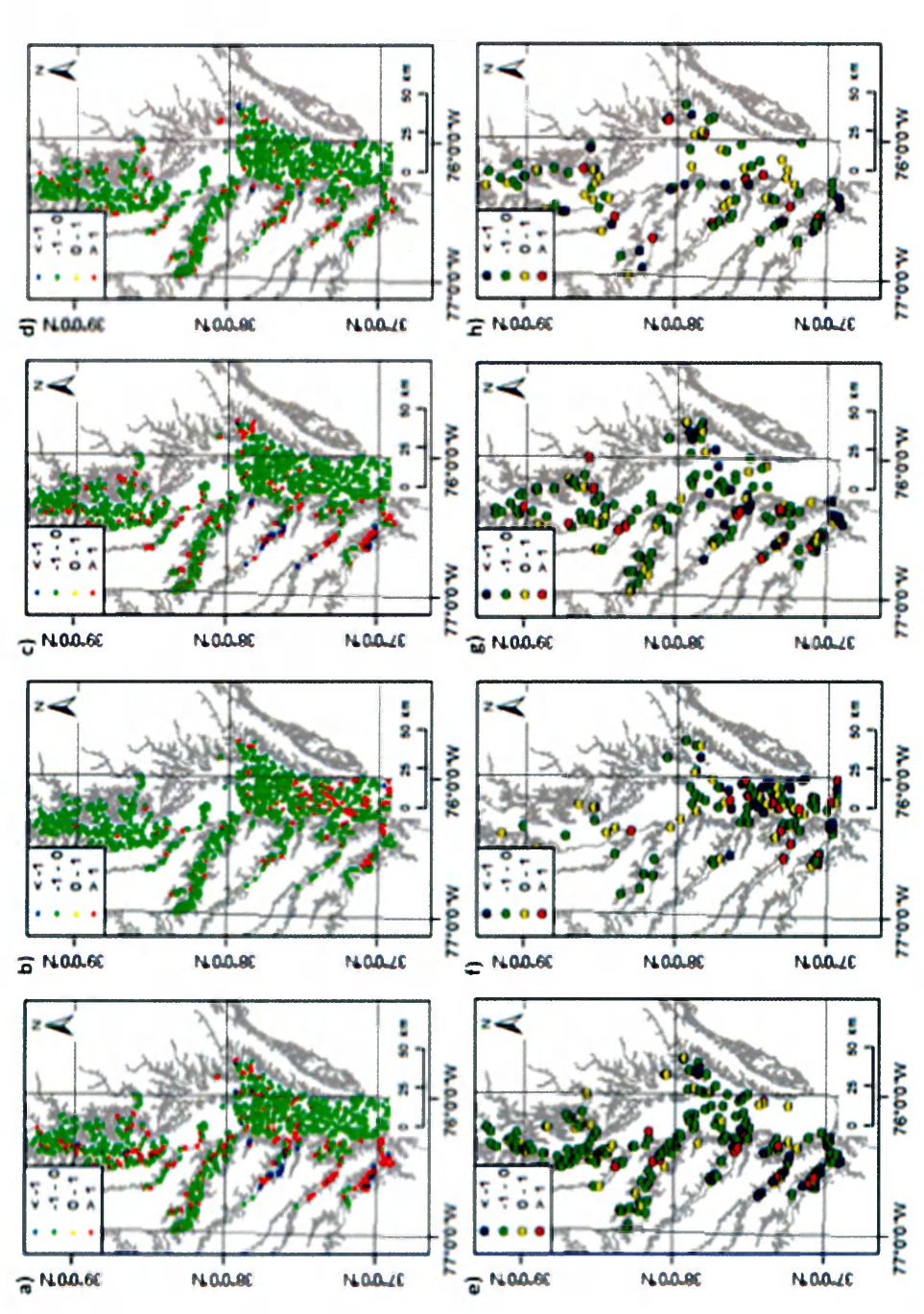


Figure D.8: 1998

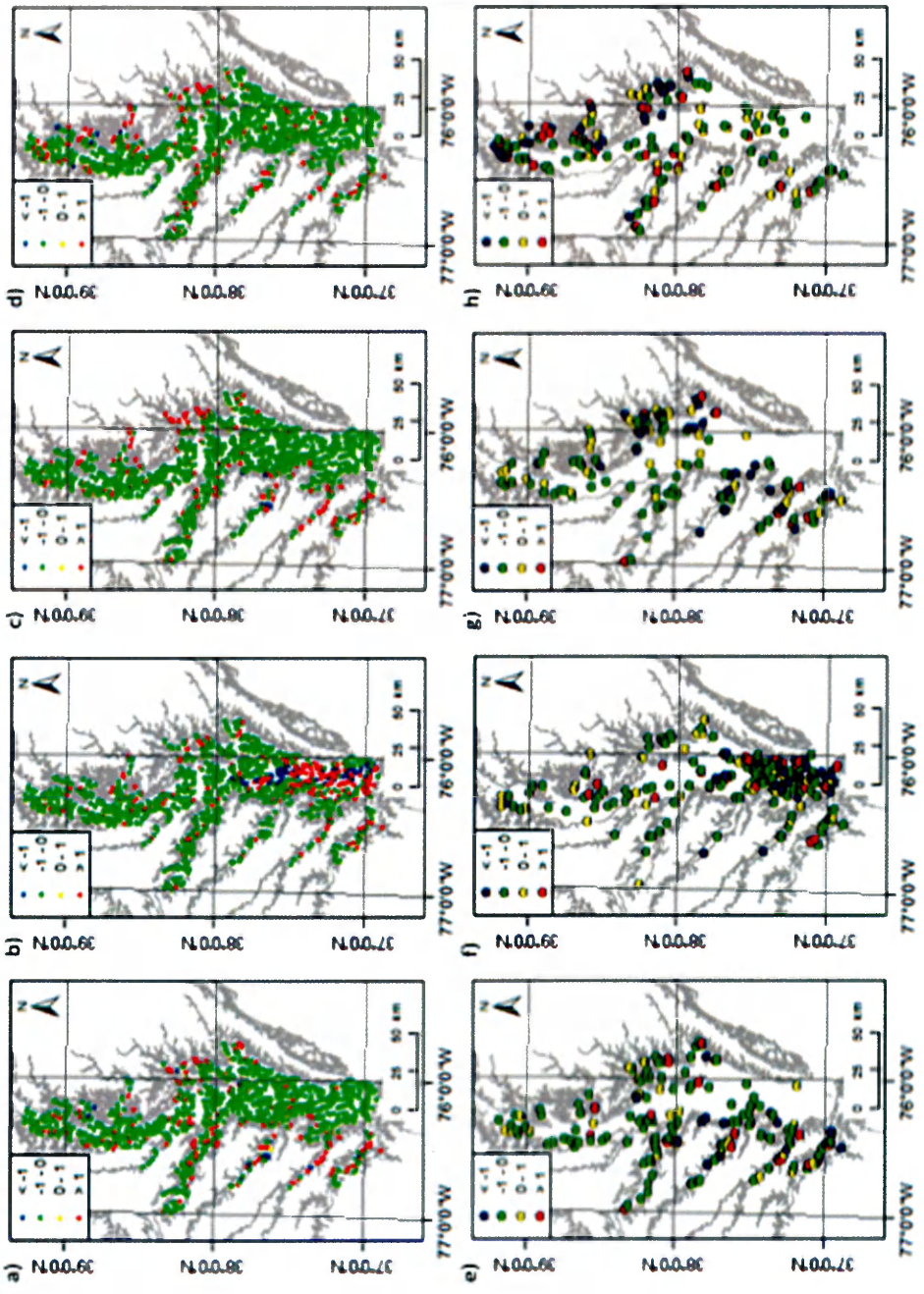


Figure D.9: 1999

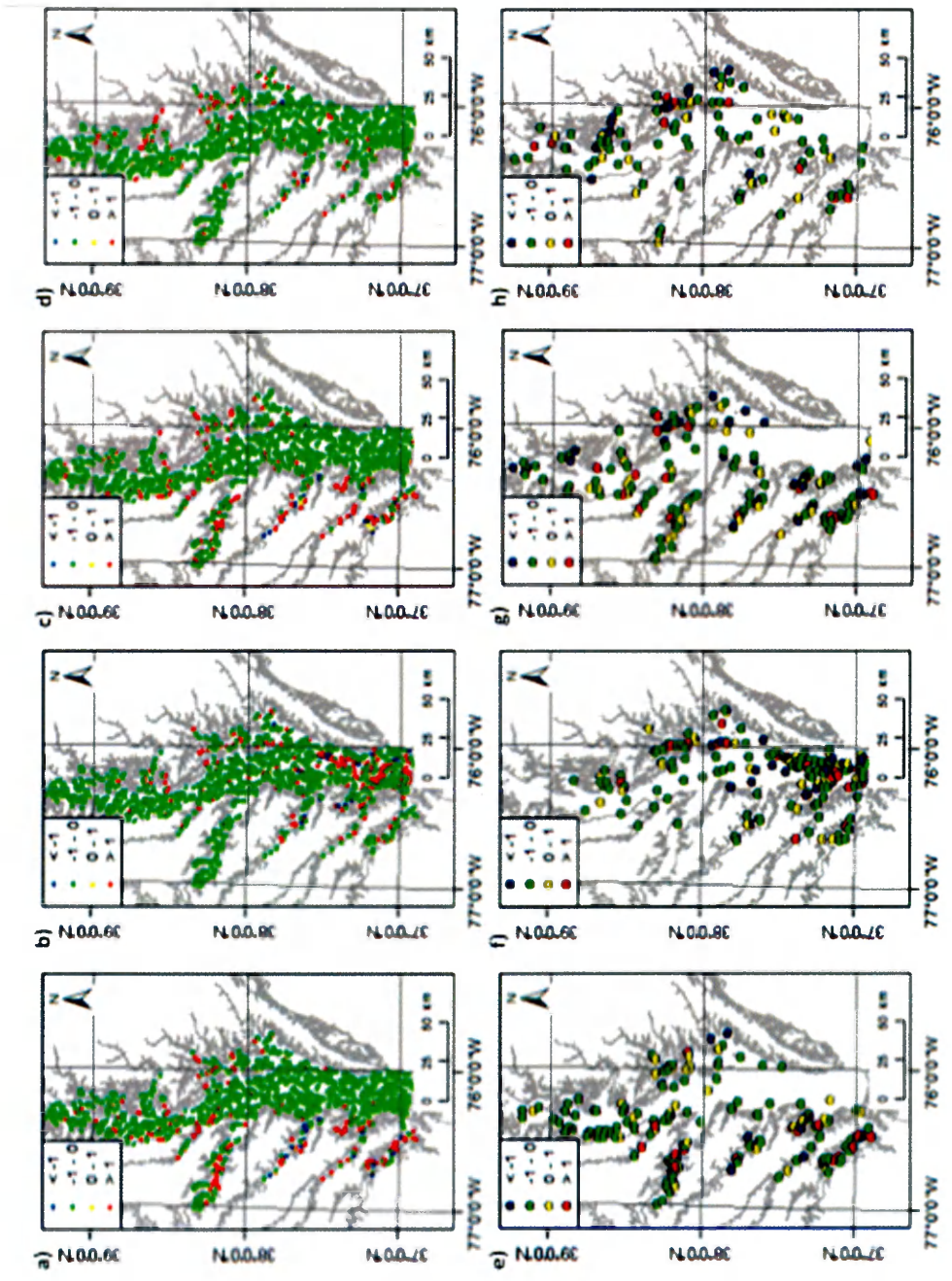


Figure D.10: 2000

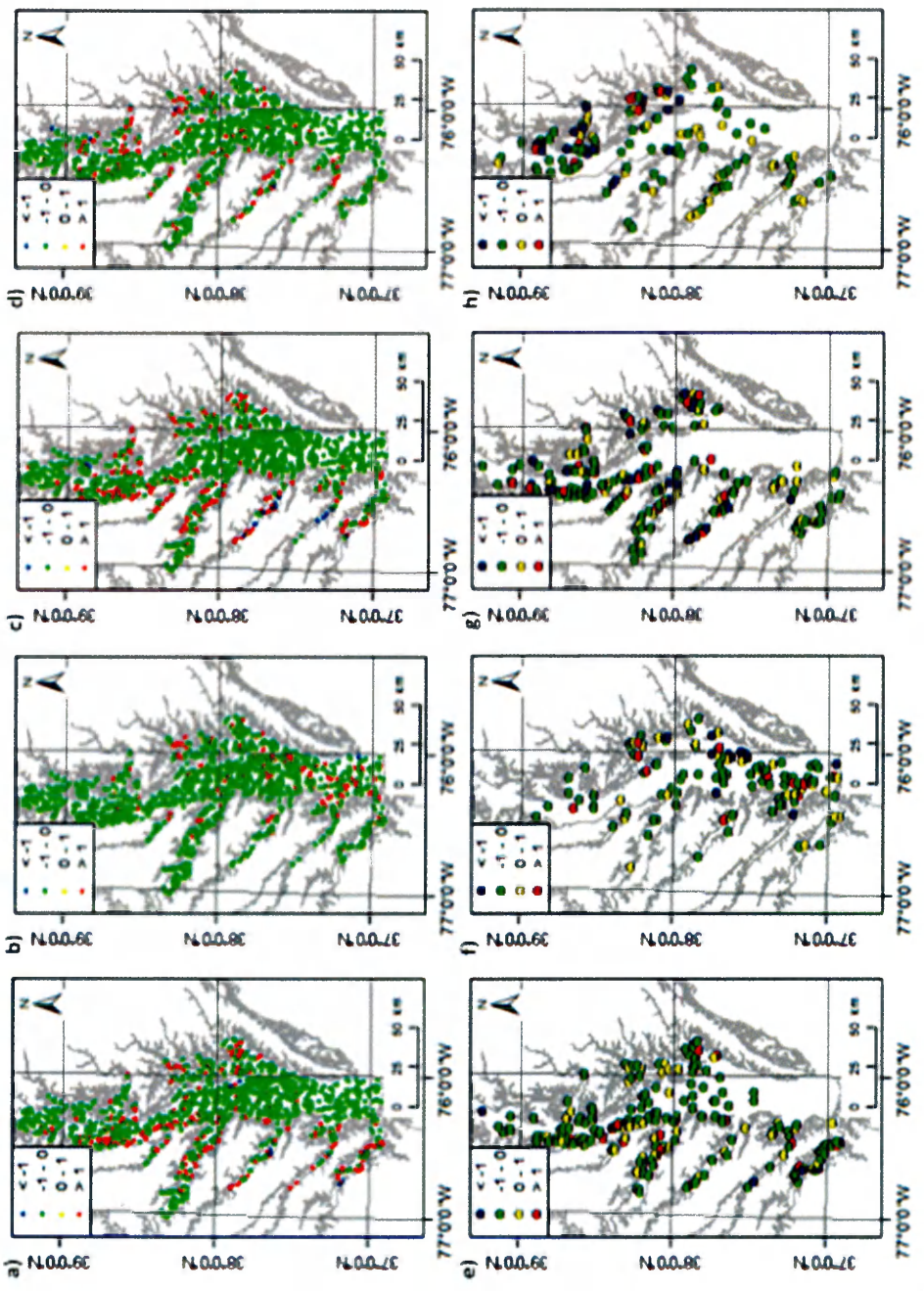


Figure D.11: 2001

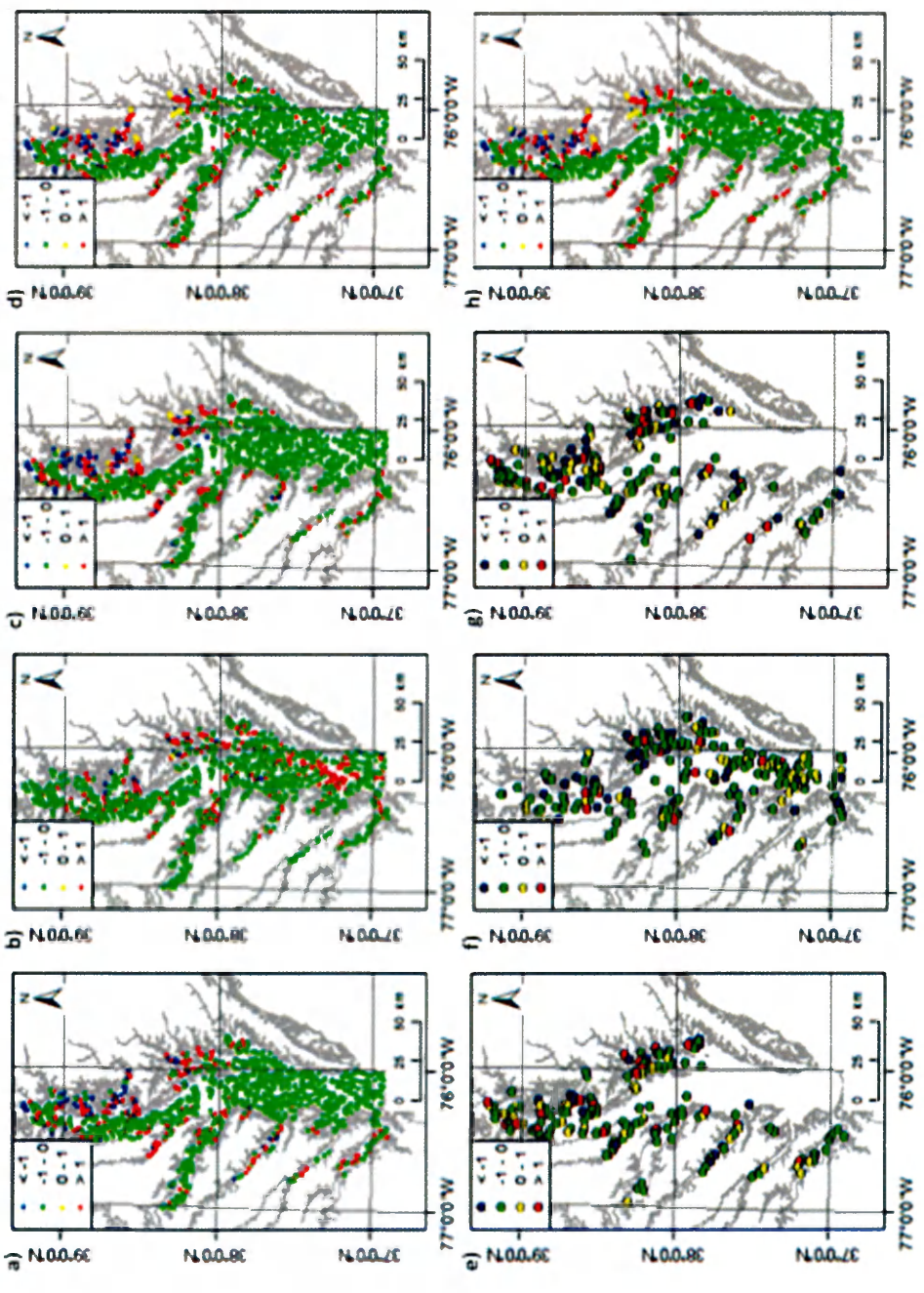


Figure D.12: 2002

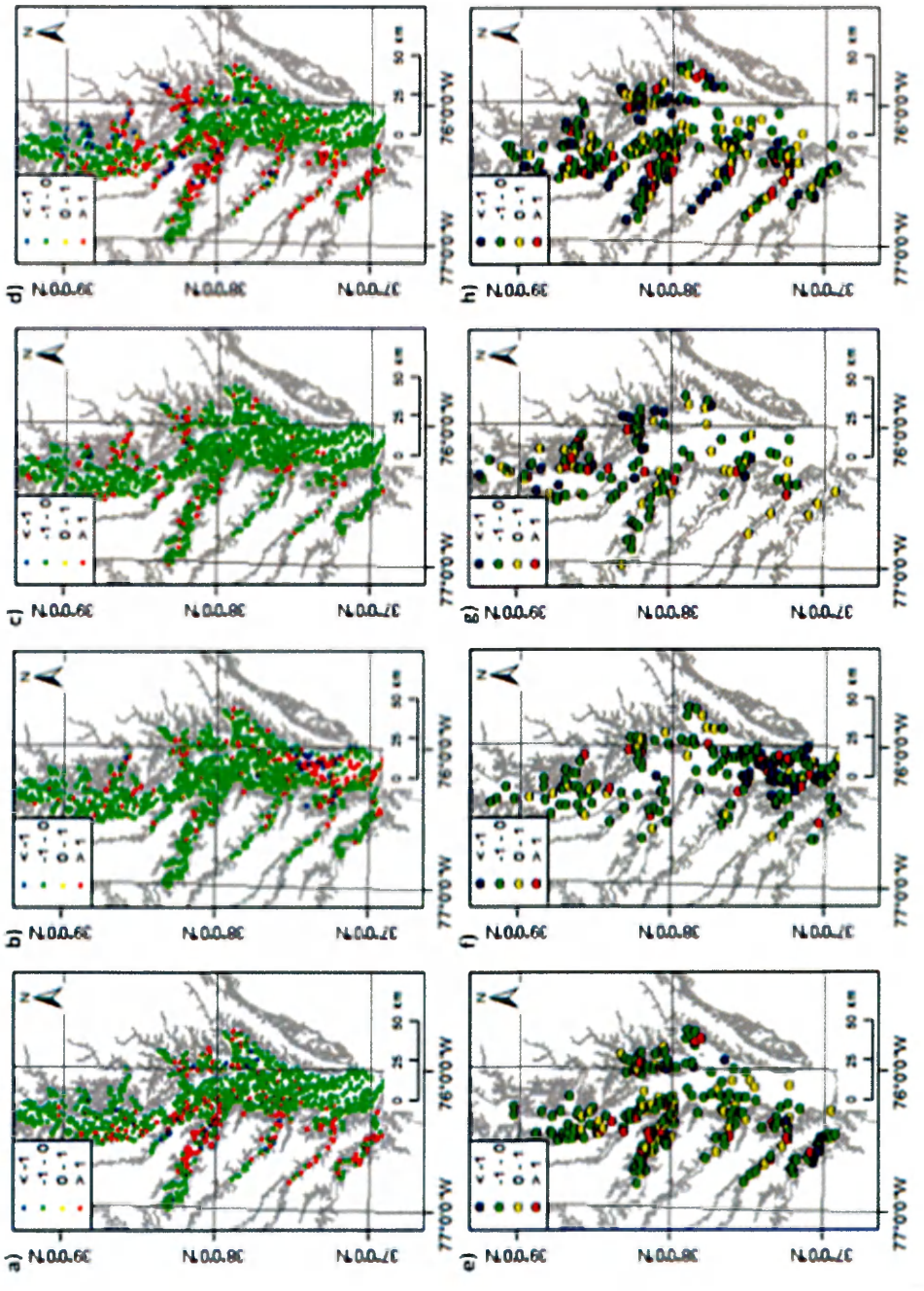


Figure D.13: 2003

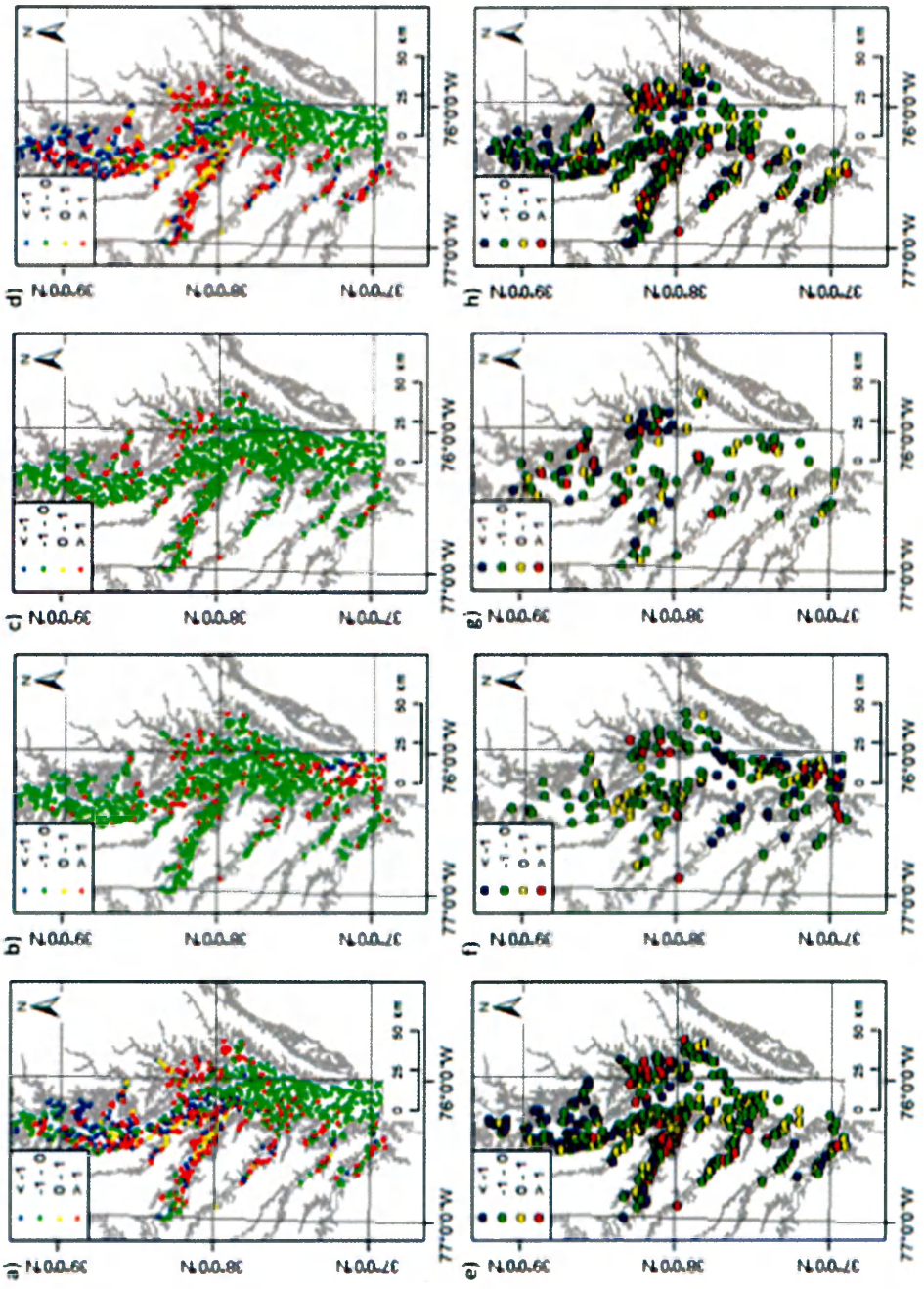


Figure D.14: 2004

VITA

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Born in Winston-Salem, North Carolina, January 31, 1984. Graduated from R.J. Reynolds High School in 2002. Completed the Multicultural Initiative in Marine Science Undergraduate Program (MIMSUP) six month intensive marine science program in Anacortes, Washington, in 2005. Graduated from the University of North Carolina at Chapel Hill, in 2006 with a B.S. in Biology. Completed the Multicultural Students at Sea Together (MAST) program in the Chesapeake Bay during summer 2006. Interned for the U.S. Fish and Wildlife Service working with Gulf Sturgeon in2006. Taught outdoor education seasonally in the San Bernardino Mountains, California, 2007 and 2008. Volunteered for the World Wide Organization for Organic Farming in Chasignelles, France, Summer 2008. Entered the masters program in the School of Marine Science, The College of William & Mary in August 2008 as a Hall-Bonner Fellow.