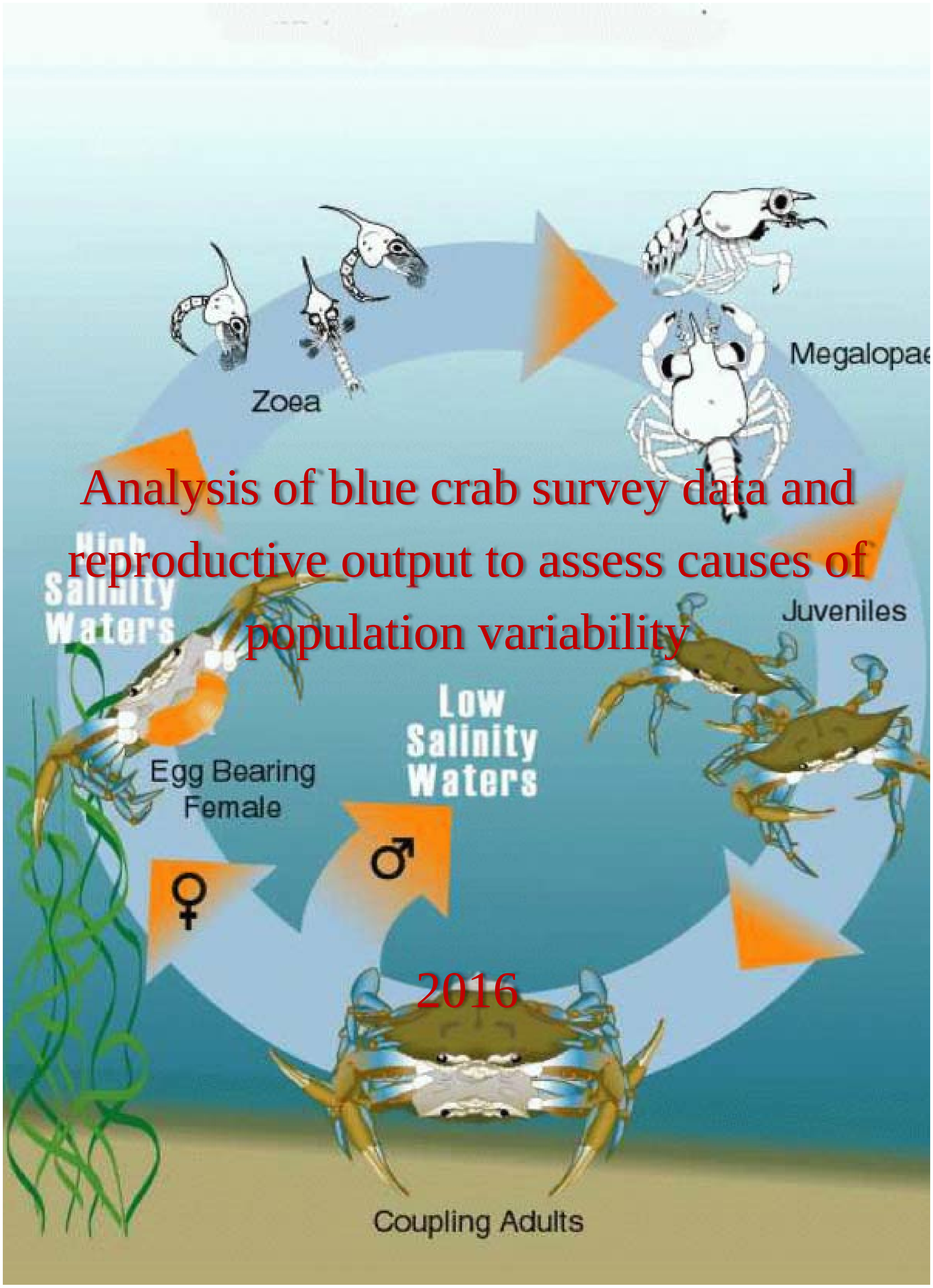
Analysis of blue crab survey data and reproductive output to assess causes of population variability



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Scope #4: CBSAC Research Needs – Analysis of blue crab survey data and reproductive output to assess causes of population variability

Final Report

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Executive Summary

We evaluated a series of hypotheses to explain the relatively low survival of the 2011 year class evident in the winter dredge survey as age-0 crabs in 2012 and as age-1+ crabs in 2013. We assembled a data base of six fishery independent surveys that employed different gears and had different spatial and temporal coverages.

We conducted extensive quality assurance / quality checks of the fishery-independent data. This involved ensuring that each time series used consistent date, location and structural formats for observations. We also evaluated whether the spatial locations reported in the surveys were congruent with a map of the shoreline of the Chesapeake Bay and the presumed statistical strata used in design-based estimates. These efforts resulted in the production of a single, unified database of fishery—independent surveys that will be of high utility for future analyses and stock assessments. **We strongly recommend that this database is maintained and extended in future years.**

We evaluated hypotheses related to the reliability of estimates of the 2011 year class as age-0 crabs in 2012 and as age-1 crabs in the 2013 in the winter dredge survey. One suite of hypotheses explored potential biases in the estimation of the 2011 year class as age-0 crabs in 2012. Specifically, we assess whether the WDS estimate of age-0 abundance in 2012 was an over-estimate of the true abundance of the 2011 year class. We found no evidence that the size distribution of age-0 crabs in 2012 was any different to the size distributions in other survey years. Similarly, we found no evidence that the spatial distribution of age-0 crabs in 2012 was any different to the spatial distribution of age-0 crabs in other years in the survey. **We conclude that the 2011 year class of blue crab likely was very strong, and its abundance was reasonably well estimated by the winter dredge survey in 2012.**

We also evaluated hypotheses related to the survival of the 2011 year class between when it was age-0 in 2012 and age-1+ in 2013. We found compelling evidence of a declining trend in relative survival baywide from 1990-2014. When evaluated at a finer spatial resolution, evidence indicates that the relative survival of juvenile crabs in northern regions shows a strong declining trend, whereas relative survival of juvenile crabs in southern regions shows a positive, increasing trend. **We conclude that any mortality source that is hypothesized to account for this trend must be stronger in the northern regions than in the southern regions.**

Analysis of environmental parameters, routinely collected during the winter dredge survey, were not related to, and could not explain the low relative survival of the 2011 blue crab year class. **Additional analysis of environmental data is required to fully evaluate the potential impacts of environmental factors.**

Analysis of red drum removals in the recreational fishery suggest that the abundance of red drum may have been 10 fold higher than average. Blue crab relative survival was lowest in a year when red drum recreational catches were their highest. However recreational catch of red drum was not higher in areas of particularly low relative survival of blue crab (Maryland waters) and vice versa. Also, the data are highly clumped, such that the 2012 observation is highly influential in any statistical analysis. Additional analysis with fishery-independent data is required for a full evaluation of the role of red drum in the decline of the 2011 blue crab year class.

We evaluated the expected lifetime brood production of female blue crab in the Chesapeake Bay using a monthly life table. We reviewed all available empirical data to estimate an expected frequency of brood production. These data suggest that crabs have the potential of producing broods approximately monthly during the spawning season. We also estimated the survivorship schedule of blue crab based upon the best available scientific information from the most recent stock assessment. **When combined in a life table, these data indicated that the expected lifetime number of broods for a female blue crab in Chesapeake Bay is 1.4 – 2.3 broods per female.** This estimate is relatively insensitive the changes in the fishing mortality rate, but is sensitive to changes in the background natural mortality rate.

Statement of Problem

The blue crab (*Callinectes sapidus*) supports the most valuable commercial fishery in the Chesapeake Bay. In 2008 management measures were implemented that sought to conserve the number of mature, egg bearing females that survived to reproduce. This approach combines biological reference points derived from the most recent stock assessment (Miller et al. 2011) with an evaluation of current stock status derived from the baywide winter dredge survey (Chesapeake Bay Stock Assessment Committee 2014). These management measures achieved considerable success when first implemented (Fig. 1), but several recent years of poor fishery performance has raised questions about their efficacy. In particular, the 2011 year class of blue crab appeared to be a time series maximum when surveyed as age-0 crabs in the 2012 winter dredge survey. However, this year class failed to recruit to the fishery, and as age-1+ crabs in the 2014 winter dredge survey was a near record low. This unexpected performance of winter dredge survey has highlighted the need to re-evaluate the information content of all fishery-independent surveys and particularly the utility of fishery-independent surveys that are not currently used in the assessment (e.g., summer, fall and winter data from the VIMS trawl survey and the Chesapeake Bay Multispecies Monitoring and Assessment Program, ChesMMAP). These additional data may provide information on the patterns of distribution, growth and mortality during the course of the fishing year.

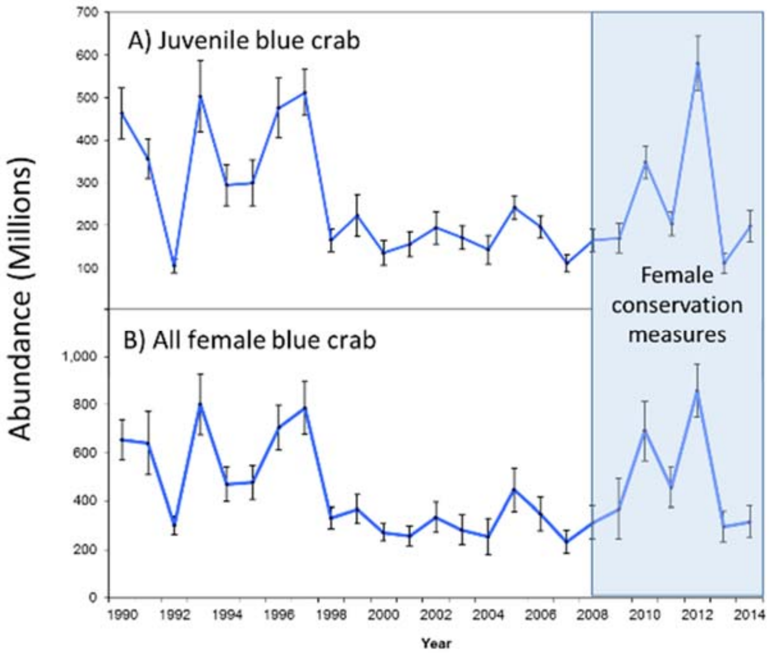


Figure 1. Time series of blue crab abundance estimated from the winter dredge survey for A) juveniles and B) all female crabs

Scope of Work

We conducted analyses that focused on two aspects of Scope #4: CBSAC Research Needs. Specifically, we addressed **TASK A**) **Analysis of the summer survey data from the VIMS trawl survey** by analyzing fishery-independent data from the VIMS trawl survey, the Chesapeake Bay Multispecies Monitoring and Assessment Program (ChesMMAP), the Maryland trawl survey, and the winter dredge survey to determine their potential for improving our understanding of the abundance and population dynamics of blue crab, particularly the dynamics since 2012. Additionally we addressed **TASK C) Assess how many broods each adult**

female can produce over a lifetime by undertaking a synthesis of existing data and new modeling work.

Task A: Analysis of Survey Data

Integration of available data

Our first action to address this task was to obtain and evaluate the available fishery-independent survey data for blue crab. Requests were sent to data holders for six fishery-independent surveys (Table 1). These surveys include surveys that have been previously used in blue crab assessment activities (e.g., the winter dredge survey, the VIMS trawl survey and the MD trawl survey), but also included surveys that have not previously been explored. We requested metadata that would allow us to understand the survey design employed, any changes in survey design during the survey, the gear used and any information on gear efficiencies that were available from each data holder.

All data were imported into an Access database for quality assurance / quality control check to remove errors from the data and to improve the efficiency and effectiveness of subsequent statistical analyses. We used the ChesMMAP data management procedure as a standard to which all other data sets were made to conform. All dates were converted to the same format, both within and between surveys. Latitude and longitude values were converted to decimal degree values, and a consistent standard of longitude used (i.e., 68° 30′ W was represented as -68.5 Longitude). A consistent value was substituted for any missing values.

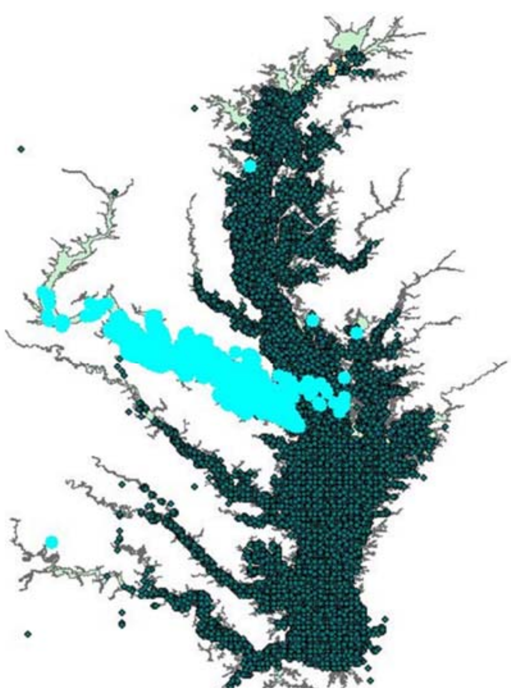


Figure 2. Examples of incorrect allocation of stations to strata from the winter dredge survey. Stations shown in light blue were defined as Potomac River strata locations within the original winter dredge survey dataset.

All station locations were verified in a GIS system to ensure that they were within the Bay and within the specified strata. Numerous stations in most surveys were shown to be outside of the Bay or not within the strata that was indicated by the sampling program (Fig. 2). Where possible, we examined each individual station that was outside its designated area to see if simple transcription errors could have resulted in the misspecification of the station. When possible, station locations were revised. Finally, information from each survey was then separated into tables that provide station/tow characteristics and tables that provided biological data for each haul.

Table 1. Summary of fishery-independent surveys available for analysis

Survey	Duration	Spatial coverage	Temporal coverage	Design	Gear	Total number of stations available
MD seine survey	1998-2014	Shoreline stations in upper bay, Choptank, Nanticoke, Patuxent and Potomac Rivers	July, Aug., Sept.	Fixed sites	30.5 x 1.2 m bagless beach seine (6.4 mm mesh)	
MD blue crab summer trawl survey	1990-2014	Chester, Choptank and Patuxent Rivers, Tangier, and Pocomoke Sounds	Monthly (May – October)	Stratified fixed	16’ semi-balloon otter trawl	5,507
VIMS blue crab and juvenile trawl survey	1955-2014	VA waters of CB[1]	Monthly	Stratified random	30’ semi-balloon otter trawl (1.5” mesh)	41,096
Winter dredge survey (WDS)	1990-2014	Bay wide	Winter synoptic	Stratified random	8' Virginia commercial dredge	41,531
Chesapeake Fishery Independent Survey (CHESFIMS/TIES)	1995-2006	Bay wide	Spring, summer, autumn	Stratified random	18 m^2 midwater trawl (6-mm mesh)	3,309
Chesapeake Multispecies Monitoring and Assessment Program (ChesMMAP)	2002-2014	Bay wide	Bimonthly	Stratified random	45’, 4-seam otter trawl (3” mesh)	4,752

[1] The sampling gear and design of the VIMS blue crab and juvenile trawl survey has changed substantially over time

The different surveys employed different strata designations, and so it was necessary to provide a new consistent strata definition for all surveys. We developed four new regional descriptor variables for each survey. New_Reg1 was a latitudinal variable based on the strata designation from the ChesMMAP program (Fig. 3A). New_Reg2 was a variable that separated stations located in the main stem of the Bay from stations located in tributaries (Fig. 3B). New_Reg3 was a variable that combined New_Reg1 and New_Reg2. Finally New_Reg4 was a variable that provided more specific station location such that specific regions (e.g., Potomac River) could be identified. This approach required us to make informed decisions about allocation of stations to particular values of New_Reg4. For example, we had to clearly define geographic limits to Pocomoke Sound and the James River.

Considerable effort has been invested in developing, revising and unifying the available survey data. We recommend management agencies maintain and update the database on an ongoing basis to provide a consistent and accurate resource that can be used for future analyses and assessment activities.

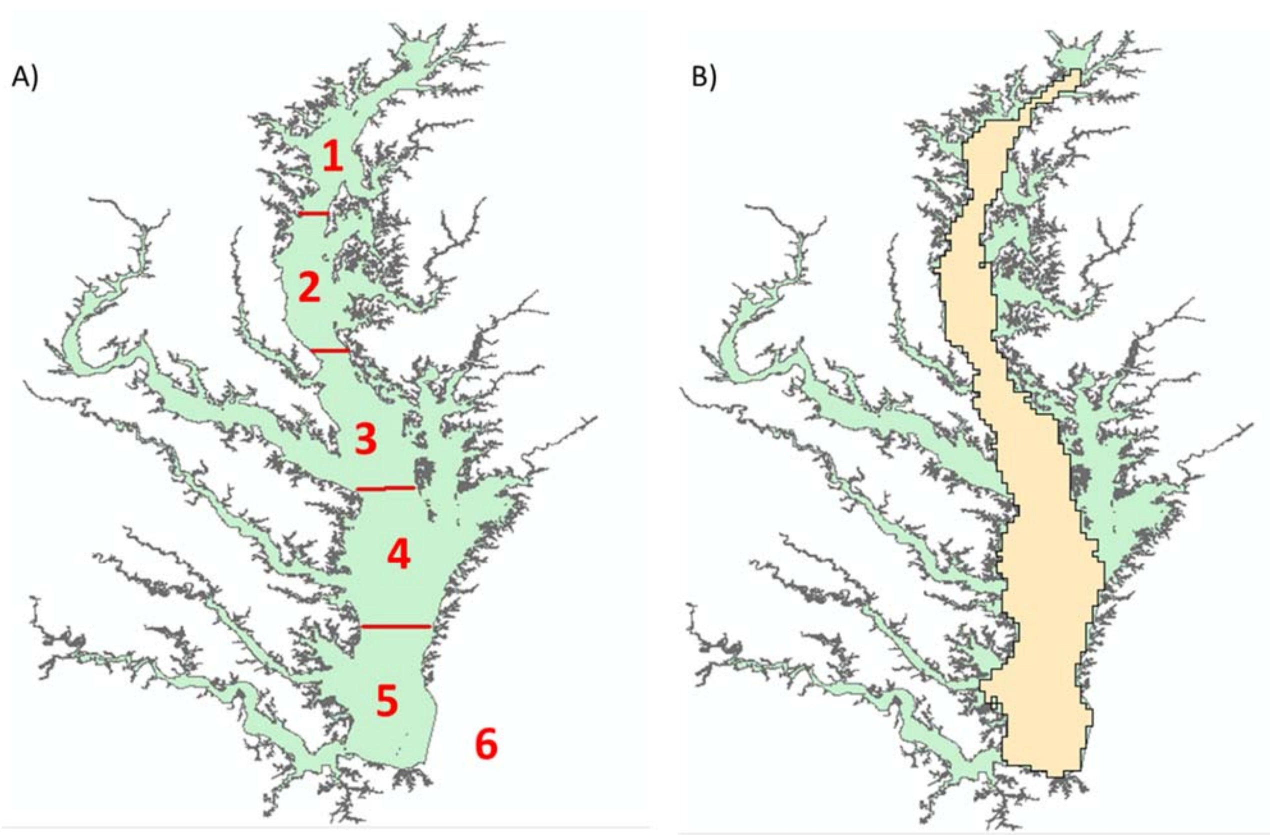


Figure 3. New regional definitions used in analysis. A) Location of New_Reg1 latitudinal strata, and B) mainstem (yellow) versus tributary (Green) locations

Evaluation of Hypotheses

The principal objective of this project was to evaluate potential explanations as to why the strong 2011 year class of blue crab, which produced one of the highest recorded age-0 abundances in the 2012 winter dredge survey failed to lead to equally strong age-1+ abundance in the winter dredge survey in 2013. We developed two hypotheses to explain the failure of the 2011 year class to produce a strong age-1+ abundance in the 2013 winter dredge survey.

H1: The WDS estimate of age-0 abundance in 2012 was an over-estimate of the true abundance of the 2011 year class.

- H1A: The availability of age-0 crabs to the WDS in 2012 was higher than in previous years, such that the survey abundance was artificially inflated.
- H1B: The spatial distribution of age-0 crabs in the 2012 winter dredge survey was unusual such that it biased the statistical weighting assumed in the survey design.

H2: The 2011 year class was very abundant and was correctly indexed as age-0s in the 2012 winter dredge survey, but experienced unusual levels of mortality so that the abundance of the 2011 year class as age-1+ in the 2013 winter dredge survey was low. The high levels of mortality was a result of:

- H2A: Colder than average temperatures in 2012 led to slow growth and high rates of mortality of the 2011 year class prior to being indexed as age-1+ crabs in the 2013 winter dredge survey.
- H2B: The 2011 year class experienced high mortality as age 1+ crabs during 2012 as a result of predation, possibly by red drum or striped bass.

Size distributions of crabs in 2012 winter dredge survey

Hypothesis H1A suggests variation in the availability of age-0 blue crab to the survey. Ralph and Lipcius (2014) have shown that a substantial fraction of the age-0 crabs are not fully vulnerable to the winter dredge survey because they are either too small or in water shallower than can be sampled by the winter dredge survey. One explanation of the high abundance of age-0 crabs in 2012 could be that age-0 blue crab were more available to the survey, for some reason, than in other years. If this hypothesis is correct, we expect to see differences in the size distribution of crabs in 2012 compared to other years.

We applied an iterative expectation-maximization algorithm in the statistical package mclust (Fraley and Raftery 2006) in the R statistical language to estimate the mixture of normal distributions that best described the abundance and size distribution of blue crab in each of the surveys. This algorithm estimates the parameters for a given number normal distributions (mean, variance and proportion of observations) that best fit the observed size frequency. We fit two normal distributions to the size frequency data for each year, representing age-0 and age-1+ cohorts.

We estimated the parameters for the optimal mix of normal distributions for each year of the winter dredge survey from 1990-2014. Figure 4 shows the strong agreement between the observed modal structure in the size frequency data (open bars) and the normal distributions (red solid lines) fit to these data for 1990. Fits were similarly strong for other years (Appendix A). Inspection of the fits to each year of the winter dredge survey indicate that the proportion of age-0 crabs in the 2012 survey was high (0.73), but not unusually so (Table 1). The average proportion of age-0 crabs in the survey is 0.54. Similarly high proportions of age-0 crabs were also observed in 1997, 1999 and 2005. The mean of the smaller mode in the size distribution in 2012 (21.14 mm carapace width, cw) was the second smallest observed in the time series and below the average (25.72 mm cw). Taken all together, these data indicate that the age-0 distribution in the 2012 winter dredge survey was not substantially different than other age-0 age classes observed in the time series. Indeed the high proportion of small crabs observed in 1997, 1999 and 2005 provide a specific opportunity to test if these age-0 age classes also experienced a high level of mortality as age-1 crabs in the following year in subsequent analyses.

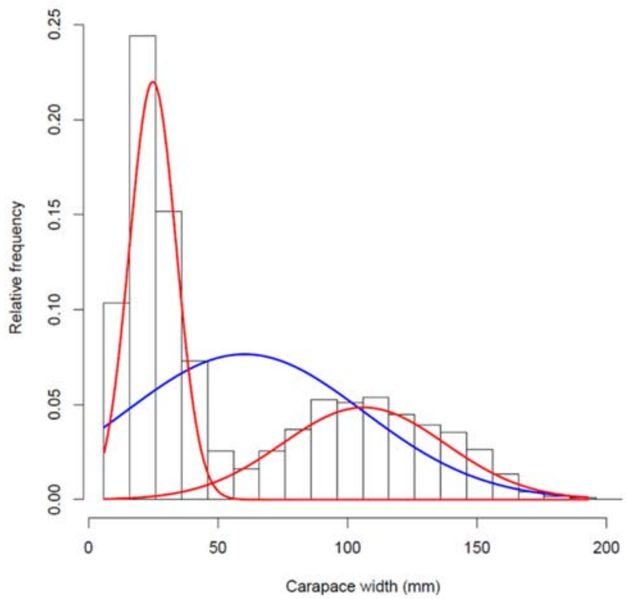


Figure 4. The optimal mixture of normal distributions for one (blue) or two (red) normal distributions fit to the 1990 winter dredge survey

Table 2. Parameter estimates of two normal distributions fitted to the winter dredge survey 1990-2014

Year	Observations	Smaller mode			Larger mode		
		Mean	SD	Proportion	Mean	SD	Proportion
1990	6,412	24.91	81.38	0.56	106.32	991.74	0.44
1991	8,295	27.49	62.76	0.45	119.49	857.28	0.55
1992	3,844	31.23	184.76	0.31	133.35	595.61	0.69
1993	3,886	26.37	67.35	0.51	118.60	873.07	0.49
1994	3,741	27.89	103.71	0.50	120.80	829.20	0.50
1995	2,687	26.00	80.27	0.54	112.26	893.94	0.46
1996	6,694	29.49	124.31	0.65	123.08	788.26	0.35
1997	5,958	21.49	43.84	0.71	119.18	1035.64	0.29
1998	3,304	28.57	137.28	0.41	125.33	679.65	0.59
1999	2,162	31.13	230.53	0.71	128.80	644.26	0.29
2000	1,995	26.44	149.12	0.44	131.74	487.24	0.56
2001	1,509	25.48	90.59	0.51	121.57	793.46	0.49
2002	1,884	23.26	125.48	0.53	126.28	916.08	0.47

2003	2,656	23.91	77.13	0.37	115.57	870.36	0.63
2004	2,672	24.72	146.48	0.50	122.83	765.45	0.50
2005	4,472	31.70	169.48	0.73	128.73	745.74	0.27
2006	4,090	23.26	59.83	0.65	123.33	1237.13	0.35
2007	2,102	24.17	77.16	0.43	120.40	944.34	0.57
2008	2,199	26.34	98.75	0.62	125.11	1010.33	0.38
2009	3,271	24.14	84.28	0.49	132.07	622.43	0.51
2010	5,985	20.09	65.80	0.57	126.74	754.74	0.43
2011	4,497	25.31	102.54	0.48	130.19	608.54	0.52
2012	7,804	21.14	43.74	0.73	96.59	1931.31	0.27
2013	2,581	21.39	70.72	0.46	129.73	545.34	0.54
2014	2,439	27.14	115.30	0.65	129.67	592.43	0.35

Spatial distribution of crabs in 2012

The winter dredge survey was designed as a stratified random survey (Table 1 - Sharov et al. 2003; Volstad et al. 2000). A range of stratifications have been explored over the course of the survey, particularly in the early years. In initial surveys strata were based on latitudinal and substrate types. However, simulation results indicated that the stratification could be simplified to three strata without loss of efficiency. Stratification has been consistent since 1993. The application of the stratified random design assumes the area-based weighting of the strata is appropriate. Specifically, it assumes that densities of crabs (number of crabs per unit area) are more similar within strata than they are between strata. If this is not the case, the efficiency of stratification is reduced. If the spatial distribution of age-0 crabs in 2012 was atypical, then the estimate of age-0 abundance may be biased or imprecisely estimated.

To test this hypothesis, we compared results from two different approaches to estimating bay wide abundance. Jensen and Miller (2005) developed and applied a geostatistical model to estimate abundance of crabs in the winter dredge survey. This approach is free of the assumptions inherent in the stratified random design that underlies the winter dredge survey. However, using data from the winter dredge survey up to 2002, Jensen and Miller reported that the geostatistical (model-based) and the stratified random (design-based) approaches produced similar estimates of abundance.

To assess whether changes in the spatial distribution of crabs in 2012 affected the estimate derived from the winter dredge survey, we developed a Bayesian geostatistical model to estimate abundance in the winter dredge survey. Details of the approach are forthcoming in a manuscript in preparation for submission to a peer-reviewed journal (Liang et al. in prep). Preliminary results indicate, as found by Jensen and Miller, a strong concordance between design-based estimates derived from the winter dredge survey and model-based estimates derived from the geostatistical analysis. For example, when estimated total crab abundance,

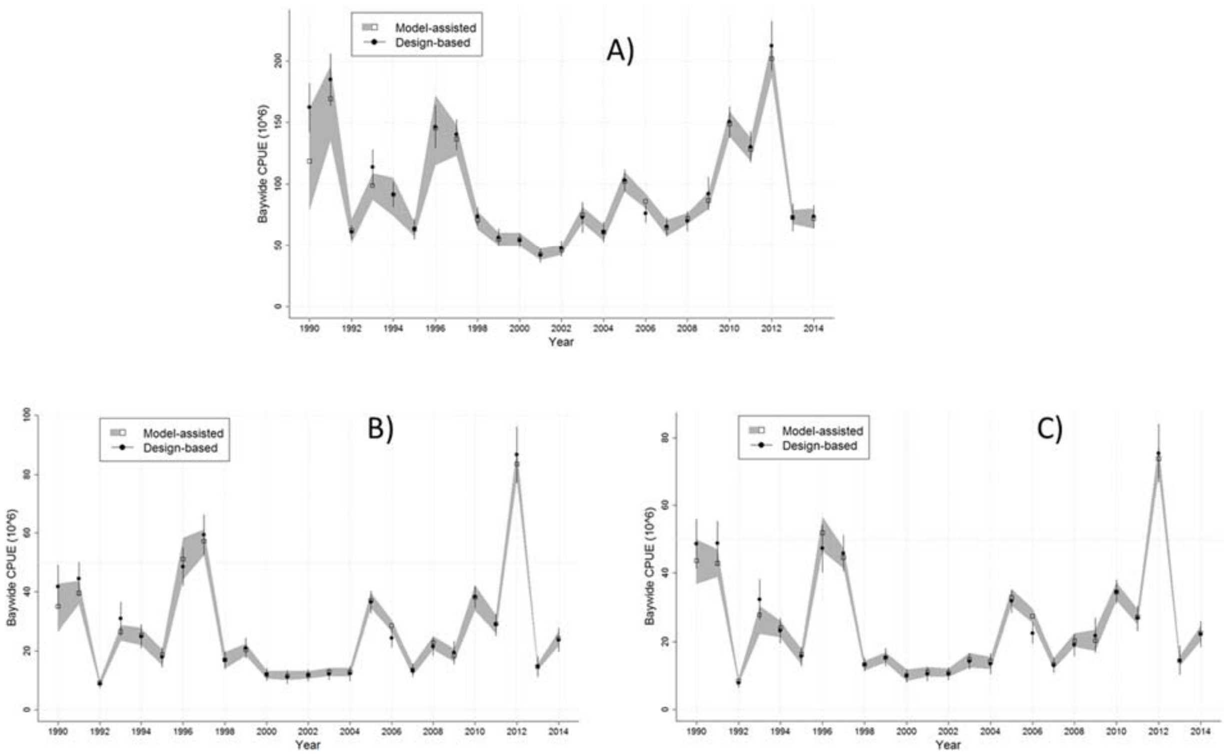


Figure 5. Comparison of design-based (solid) and model-based (open symbols) estimates of abundance of a) all crabs, b) age-0 female crabs and c) age-0 male crabs

design-based estimates were always within the confidence bands of the model-based estimates (Fig. 5A).

A similar conclusion holds for age-0 female crabs (Fig. 5B), and age-0 male crabs (Fig. 5C) as well. These findings suggest that there is no reason to believe that the distribution of age-0 crabs in 2012 produced biases in the statistical weightings of the different strata in the winter dredge survey. Further, in simulation studies which examined the efficiency of model-based, model-assisted and design-based approaches we found that, because of the large sample size of the winter dredge survey, design-based estimates were less biased than either model-based or model-assisted methods (Fig. 6).

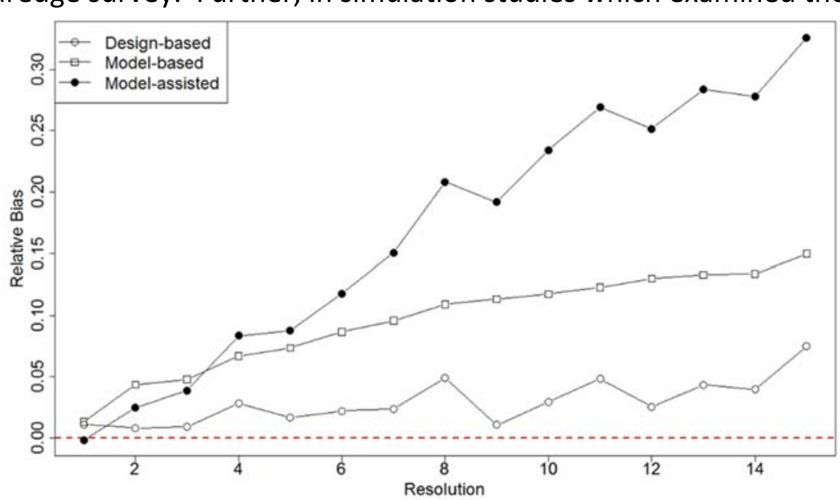


Figure 6. Relative bias of design-based, model-based and model-assisted approaches to estimate abundance of blue crab in Chesapeake Bay based on simulation studies.

Our analyses found no evidence of a substantial change in the size distribution or spatial distribution of age-0 blue crab in the winter dredge survey in 2012. Our analyses cannot be definitive because we do not know the true abundance or distribution of age-0 blue crab, because large areas of shallow water are not sampled by the winter dredge survey. However, our geostatistical analyses provide no evidence of a shift in the spatial distribution of age-0 blue crab in 2012.

We conclude from these analyses that the 2011 year class of blue crab, as indexed by the age-0 abundance in the 2012 winter dredge survey was likely extremely strong.

<u>Relative mortality rates of blue crab cohorts</u>

To assess patterns of mortality, we generated indices of relative mortality calculated as

$$RelSurv_{2012} = \frac{Age - 1 + \ CPUE_{2013}}{Age - 0 \ CPUE_{2012}}$$

If the numerator and denominator of this index are accurate estimates of abundance, the $RelSurv_i$ index must be equal to or less than one. However, we note that because age structure in the age-1+ cohort cannot be refined, it is possible that the value of the index for an individual year could exceed one. Additionally, age-0 blue crab are not fully vulnerable to the survey gear (Ralph and Lipcius 2014). For example, the abundance of age-0 crabs in the winter dredge survey in 1990 was 46.46 million crabs, whereas the abundance of age-1+ crabs in the winter dredge survey in 1991 was 48.19 million crabs, yielding a relative survival of crabs > 1 for 1990 in the winter dredge survey.

We estimated RelSurv values by year and region for all surveys, paying particular attention to the pattern of survival of the 2011 cohort. Considering the winter dredge survey, we found evidence of a gradual decline in relative survival between 1990-2014 (Fig. 7). Moreover, the relative survival of the 2011 cohort as reflected in abundances of age-1+ in 2013 and age-0 crabs in 2012 is the lowest in the time series.

If we assume that the adults are randomly distributed among regions in the winter dredge survey, it is possible to examine $RelSurv_i$ for different regions in the winter dredge survey. We calculated $RelSurv_i$ values for the latitudinal strata in the main stem of the Bay (Fig. 3). These estimates indicated a latitudinal trend in relative survival (Fig. 8). A complete suite of plots is provided in Appendix B.

Figure 8 indicates a strong negative trend in relative survival in the most northern region (Region 1), whereas in contrast there is a positive trend in relative survival in the most southern region (Region 5). Inspection of patterns in tributaries and main stem regions within the northern half of the Bay indicate that the negative trend in relative survival is a consistent

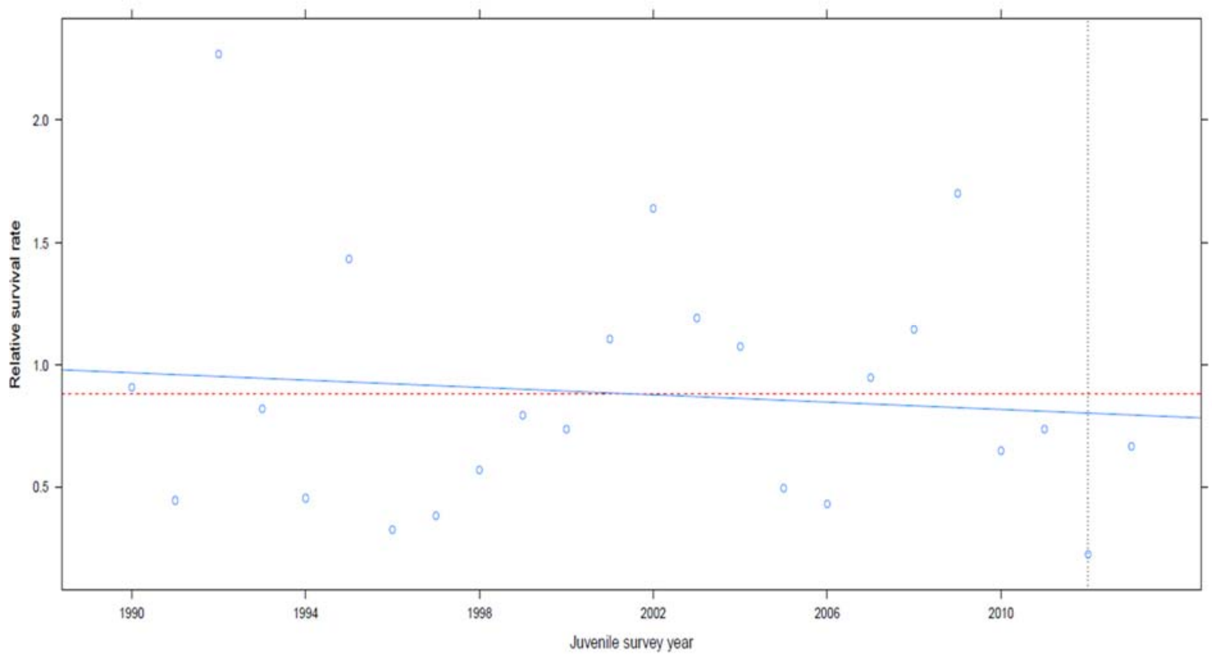
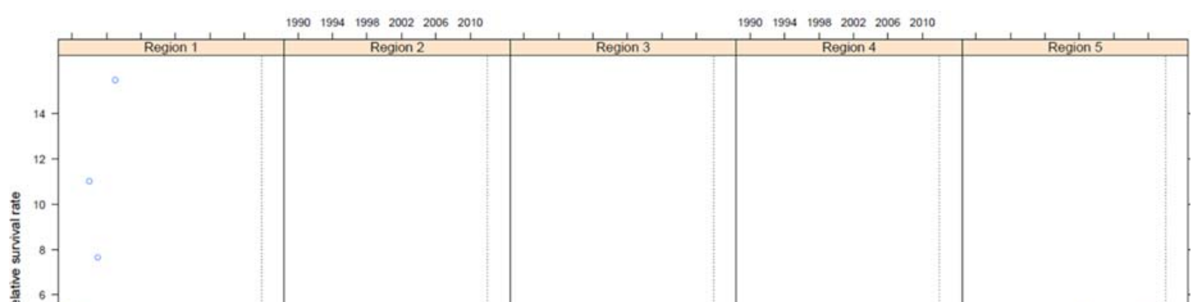


Figure 7. Estimates of relative survival from the winter dredge survey from 1990-2014. Shown are relative survival values for individual years (open symbols), the average for the time series (red dashed line), and lines the least squares regression of the individual relative survival estimates to survey year (solid blue line).

Figure 8. Estimates of relative survival from the winter dredge survey from 1990-2014 by latitudinal region from north (Region 1) to south (Region 5). Shown are relative survival values for individual years (open symbols), the time series average (red line), and a least squares fit of the data to survey year (blue line).



pattern. Similarly, inspection of patterns in tributaries and the main stem regions within the southern half of the Bay support a uniform conclusion of positive trend in relative survival. Indeed, this pattern is most obvious when the principal tributaries are considered (Fig. 9). Moreover, closer inspection of the individual data points in this figure suggest that the relative survival for 2012 is close to the time series low only for the more northern regions. For example, the relative survival in 2012 is or is close to the time series low in the three most northerly strata (Regions 1-3, Fig. 8), whereas the relative survival for 2012 is closer to the time

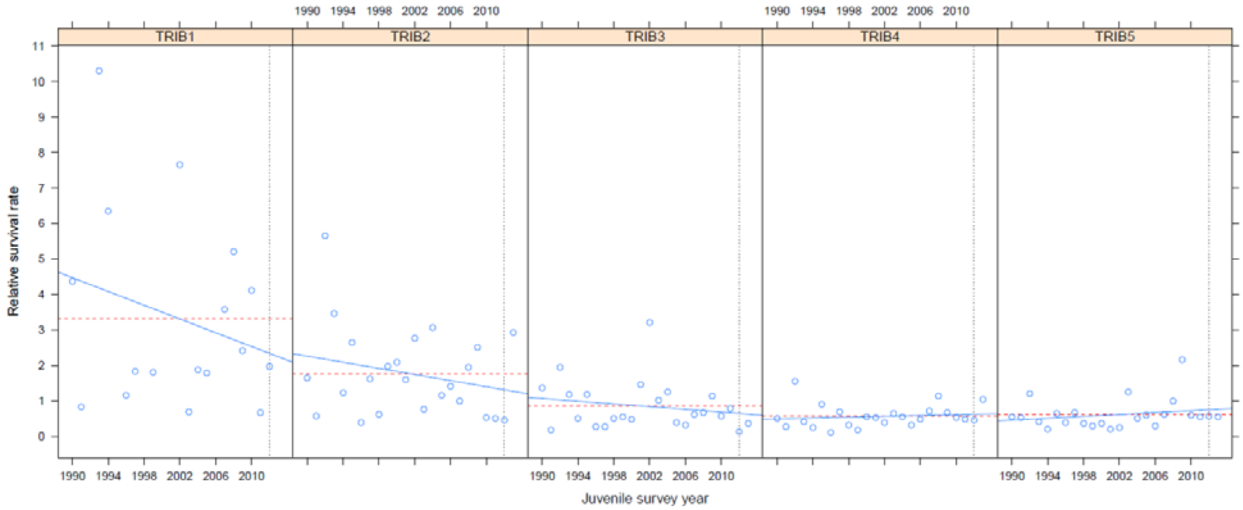


Figure 9. Estimates of relative survival from the winter dredge survey from 1990-2014 for the principal tributaries from north (Region 1) to south (Region 5). Shown are relative survival values for individual years (open symbols), the time series average (red line), and a least squares fit of the data to survey year (blue line).

series average for the southerly strata (Regions 4-5, Fig. 8). This leads to the inference, that whatever factors were responsible for the low relative survival in 2012 were expressed more clearly in the more northerly regions than in the more southerly regions.

<u>Environmental conditions</u>

There is clear evidence from estimates of overwinter mortality that cold temperatures can induce high levels of mortality (Sharov et al. 2003). We explored the effects of salinity and temperature, the two commonly measured environmental variables, on estimates of relative survival. We focus here on temperature, but results for salinity are similar. We calculated the average relative survival and water temperature for each latitudinal region of the winter dredge survey for each year (Fig. 10). There was no significant relationship between the regional average water temperature and average relative survival. The five values for 2012 (solid symbols in Fig. 10) do not appear anomalous, but rather fit the pattern established in other years.

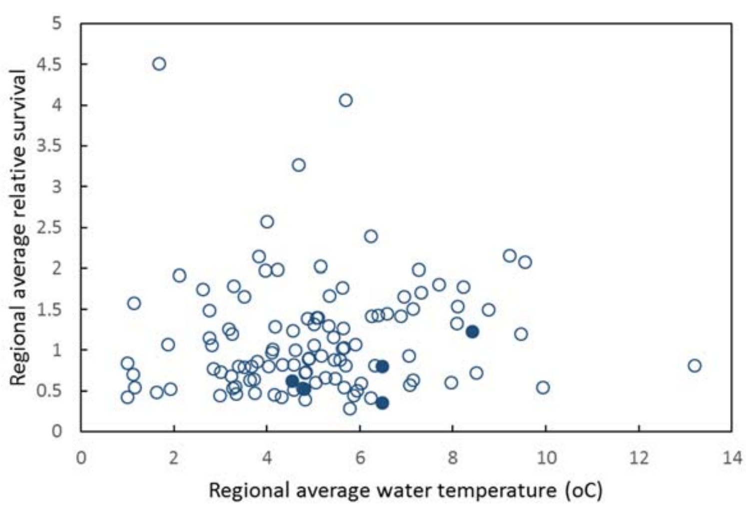


Figure 10. Relationship between regional average water temperature and relative survival for 1990-2011 and 2013 (open symbols) and 2012 (closed symbols) for each latitudinal region in the main stem of the bay.

Finer evaluation of temperature patterns do reveal that March 2013 temperatures in Maryland were the warmest on record. Whether these warm temperatures caused crabs to break diapause early is unknown, but if crabs did break diapause they could have been more vulnerable to predation. In summary no environmental variable, routinely measured in the winter dredge survey, appears to predict the low relative survival observed in 2012.

Red Drum Predation as an explanation of low survival

Many stakeholders have suggested that an unusual abundance of red drum in the Chesapeake Bay during 2012 was responsible for the low RelSurv of the 2011 year class after they were surveyed as age-0 crabs in the 2012 winter dredge survey. No reliable, fishery-independent surveys of red drum were available for the relevant time period. Accordingly, we used estimates of the total recreational removals for red drum in inland water (NOAA designation of non-oceanic) of Maryland and Virginia estimated by the Marine Recreational Program (MRIP). We obtained estimates of the (A +B1+ B2) removals from regional agencies. We regressed the three estimates of relative survival of the 2011 year class (RelSurv = T1+/T0; RelSurvFem = (Fem1+-Fem2)/Fem0; RelSurvMale=(Male1+-Male2)/Male0). The two sex specific estimates were developed because it was possible to estimate age-1 abundance as the difference between age-1+ and age-2.

Inspection of these data support the notion that red drum abundance in the Chesapeake Bay was particularly high. Indeed, the 2012 recreational removals were more than 10 times the time series average recreational removals of red drum in Chesapeake Bay. Plots of RelSurv against recreational removals all indicate that the 2012 point is different to rest of the time series (Fig 9). It is tempting to infer the presence of a negative relationship between relative survival of blue crab cohorts and abundance (as measured by recreational removals) of striped bass from these plots. However, we caution that the 2012 red drum data point is an extreme outlier and therefore any resulting regression relationship is strongly influenced by the single observation in 2012 of red drum abundance that was 10 fold higher than average.

In our evaluation of the spatial distribution of relative survival patterns (Figs. 8 and 9), we suggested that any mechanism hypothesized to explain the low relative survival of the 2011 year class had to be such that it produced lower relative survival in the more northerly regions, and average survival in more southerly regions. To examine whether the distribution of red drum, as reflected in the distribution of recreational harvests of red drum, exhibits this characteristic, we regressed z-transformed estimates of red drum recreational removals for Maryland with estimates of relative survival for blue crab in Maryland waters, and z-transformed estimates of red drum recreational removals in Virginia with estimates of relative survival of blue crab in Virginia waters (Fig. 12). We found no compelling evidence of a difference in the relationship between relative survival and red drum removals in the two states.

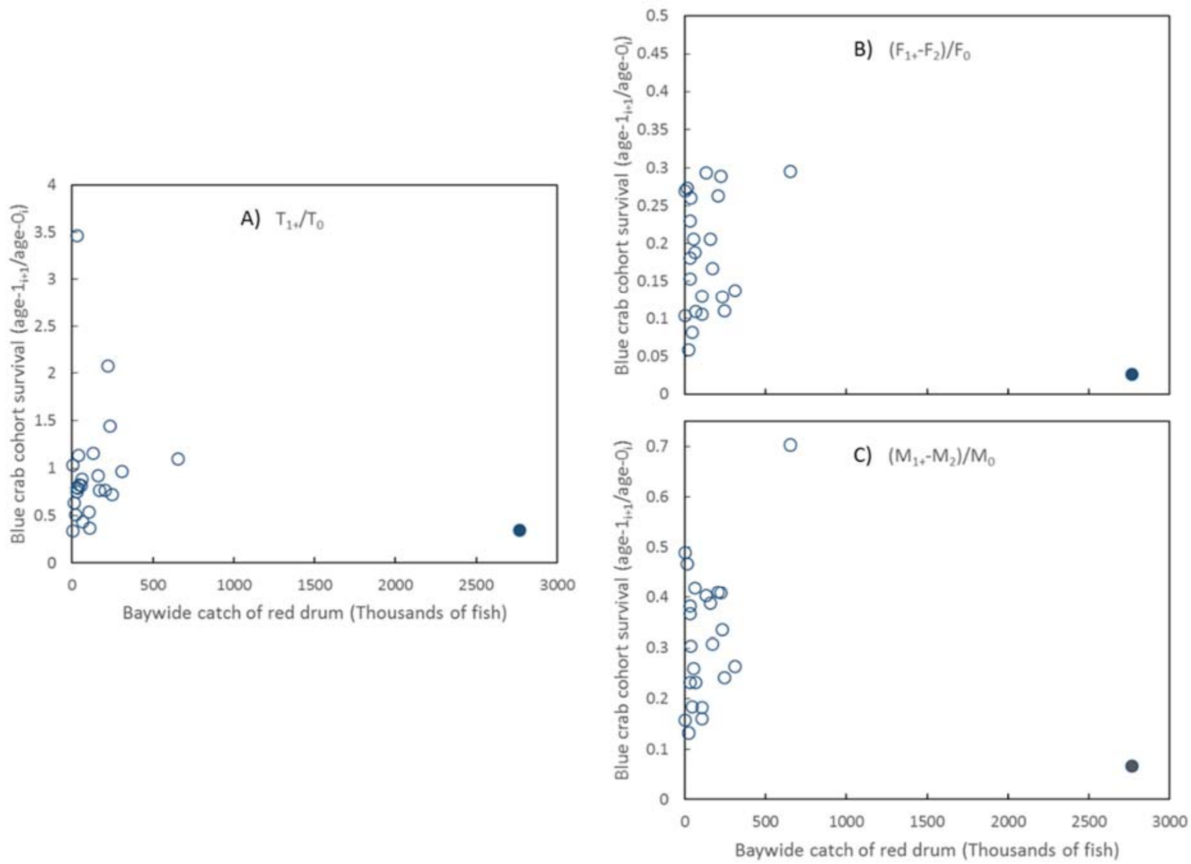


Figure 11. Relationship between recreational removals of red drum and indices of relative survival of blue crab. The datum for 2012 is shown as a solid symbol. Indices are shown for A) Relative survival of all juveniles, B) Modified relative survival of juvenile females and C) Modified relative survival of juvenile males. The extent of the y-axis for the female and male plots have been clipped to remove one high relative survival value for each series.

In summary, our analyses of relative survival in the winter dredge survey indicate that the relative survival of the 2011 year class between 2012 and 2013 was the lowest on record over the 24 years of the survey. Further, the low survival was evident in northern regions, more so than in southern regions. Specifically, the relative survival of the 2011 year class in the winter dredge survey in the northern region was the lowest on record. In contrast, although the relative survival of the 2011 year class in the southern region was one of the lowest five values in the time series, it was not the lowest. Thus, we conclude that any mortality source that is responsible for this pattern must be more intense in northern regions than in southern regions. Red drum, as indexed by their recreational removals, were 10 fold higher in the Chesapeake Bay in 2012 than on average. The high abundance of red drum coincides with a record low relative survival of blue crab. Although consumption of blue crab by red drum as an explanation of the low relative survival of blue crab is consistent with the temporal pattern of relative survival, it does not match the spatial pattern. Additionally, we note that our index of red drum abundance is crude, and its values are unevenly distributed, such that the extremely high recreational harvest in 2012 is an outlier, thereby making interpretation of any mechanism

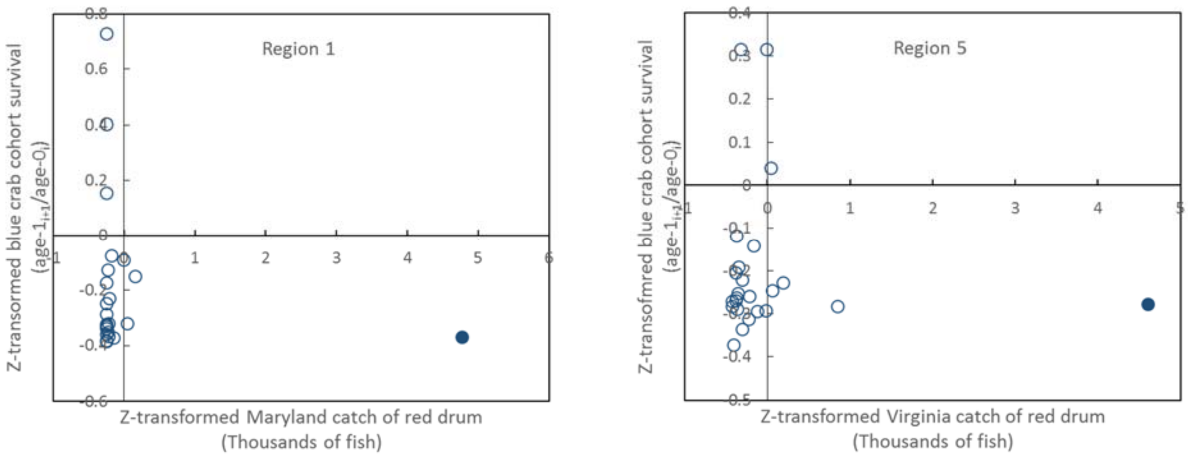


Figure 12. Plots of z-transformed relative survival and z-transformed recreational red drum removals for A) Maryland and B) Virginia. The data for the 2011 year class are shown in solid symbols

difficult. Moreover, the distribution of recreational catches of red drum do not match the spatial pattern in relative survival – in that relative survival was lower in more northerly waters, but recreational harvest seem as extreme in both regions (Z- transformed catches are between 4-5 in both regions).

Task C: Expected lifetime brood production

Over the last decade or so there has been considerable interest in the reproductive biology of blue crab, both as it relates to the estimation of key parameters for population models (Miller 2001; Miller 2003; Miller et al. 2011), and because of concerns over changes in the sex ratio in the blue crab population in the Chesapeake Bay (Ogburn et al. 2014; Wells 2009). The classical understanding of the reproductive biology of blue crab was reviewed by Jivoff et al. (2007), and is only summarized here. Briefly, pre-pubertal females undergo a functional terminal molt. It is known that mature females can molt again in the field, but it is an uncommon event. Mating in blue crab is a complex behavioral and hormonal cascade that involves males searching for, identifying and defending pre-pubertal females. When a female is receptive, the male uses his chelae to position the female so that mating can occur. Mating occurs immediately after the female has completed the molt, but before the new carapace hardens (Van Engel 1958). During the mating, the male inserts his primary pleopod into the external opening of the female reproductive tract. The male transfers both seminal fluid and spermatophores to the female (Jivoff et al. 2007). These male reproductive products are stored in spermathecae in the female. The male then guards the recently inseminated female to prevent other males mating with the female, although there is some evidence of multiple paternity in the field (Jivoff 1997). Subsequently, the female uses these stored male reproductive products to produce multiple broods of offspring.

There are three central questions in understanding the reproductive biology of blue crab from the viewpoint of the species' population dynamics. What is the expected number of broods for a female crab? What is the batch (per brood) fecundity? What is the role of the sex ratio during reproduction (termed the operational sex ratio) on reproductive output? We address each question in turn.

Expected lifetime number of broods

It is known that females in the Chesapeake Bay are capable of producing multiple broods because of reports of collections of females with egg scars on their abdomens. Because of the occurrence of the functional terminal molt in females, females mate only once in their lifetime, and thus the sperm transferred to the female on this single mating is responsible for the females total lifetime reproductive output.

Estimating the expected lifetime number of broods requires knowledge of the frequency of brood production, and the mortality schedule of mature females. Van Engel (1958) reported that in the Chesapeake Bay female crabs produce 1-3 broods a year. These values were inferred from patterns of release of offspring rather than from direct observation. Several studies have measured the frequency of brood production in blue crab. Hines et al. (2003) reported on the results of experiments conducted at Indian River Lagoon, FL that followed brood production by three cohorts of crabs. Mated, female crabs were held in 1 x 2 x 1m tanks and monitored for eight months. Hines et al (2003) report that females in this sub-tropical environment can produce up to 7 broods from a single mating (Fig. 13). Broods were produced approximately monthly in most crabs, although some crabs could produce two broods within some months (Fig. 13). Combining these data and Van Engels' original estimate of three broods per season for Chesapeake Bay crabs with expected levels of mortality, Hines et al. (2003) concluded that expected maximum lifetime number of broods per female was 7 in the Chesapeake Bay and 17 for crabs in Florida. The next substantive observations of brood production in blue crab were completed by Dickinson

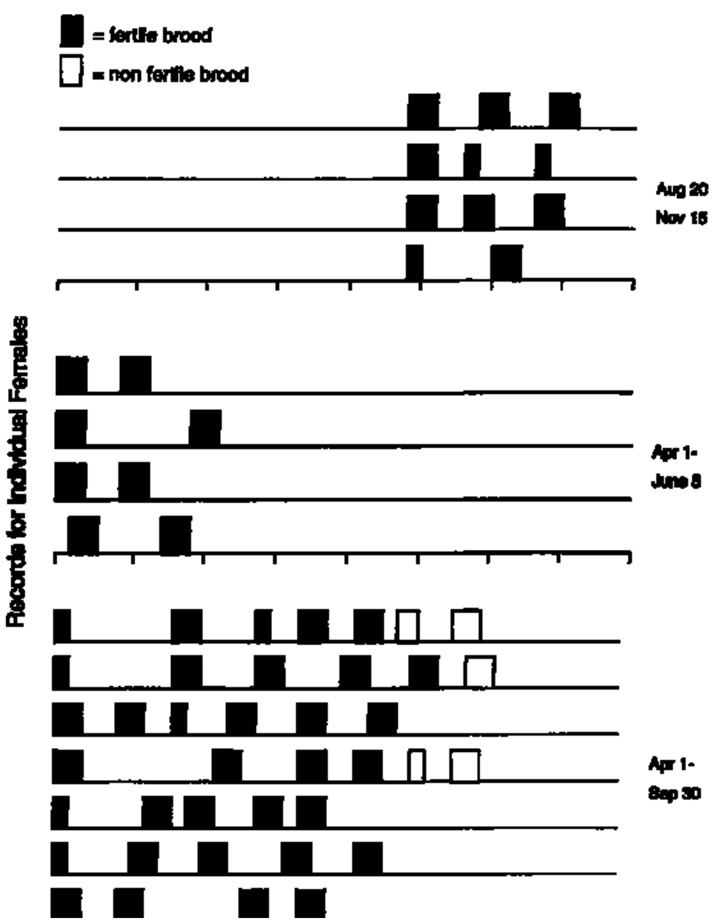


Figure 13. Brood production by individual female blue crab in experimental studies conducted in Florida (see Hines et al. 2003 for details)

et al. (2006), who quantified brood production by females caged in the field in North Carolina over 18 weeks. These authors conclude that females could produce 8 broods per 25 week spawning season, giving a brood production frequency of a brood every 22 days. Darnell et al (2009) refined the Dickinson et al. study. These authors report female blue crab in North Carolina could produce up to seven broods in their lifetime (2 seasons), with the frequency of production being temperature-dependent.

We developed at life table approach to estimate the expected lifetime number of broods for blue crab. The life table used a monthly resolution. The life table assumed a cohort of crabs began life as new juvenile crabs settling in the Chesapeake Bay in September (Table 3).

These crabs produced their first brood in June of the following year Based on existing literature (Hines et al. 2003, Dickenson et al. 2006, Darnell et al. 2009), broods were produced approximately monthly thereafter until November. Brood production this late is unlikely, but the assumption means that the overall estimate of the expected lifetime number of broods is conservative. Females that survived would start producing egg broods in June of the following year, continuing to the November. This pattern would repeat in model year 3 if females survived. This translates to a maximum lifetime number of broods of 18. These calculations allow definition of the maternity schedule (m_x curve), which defines the timing and level of reproductive output.

Table 3. . Monthly life table for blue crab in Chesapeake Bay

year	Month	x	N_x	ℓ_x	m_x(broods)	$\ell_x m_x$(broods)	ℓ_x modified	$\ell_x m_x$ modified	m_x(eggs)	$\ell_x m_x$(eggs)	$\ell_x m_x$(eggs) x
1	9	0	1	1	0	0			0	0	0
1	10	1	0.927743	0.927743	0	0			0	0	0
1	11	2	0.860708	0.860708	0	0			0	0	0
1	12	3	0.798516	0.798516	0	0			0	0	0
1	1	4	0.740818	0.740818	0	0			0	0	0
1	2	5	0.687289	0.687289	0	0			0	0	0
1	3	6	0.637628	0.637628	0	0			0	0	0
1	4	7	0.591555	0.591555	0	0			0	0	0
1	5	8	0.526414	0.526414	0	0			0	0	0
1	6	9	0.468447	0.468447	1	0.468446521	1	1	1.904	0.891922176	15.28397841
1	7	10	0.416862	0.416862	1	0.41686202	0.889881771	0.889881771	1.904	0.793705285	15.11214864
1	8	11	0.370958	0.370958	1	0.370957912	0.791889566	0.791889566	1.904	0.706303865	14.79282815
2	9	12	0.330109	0.330109	1	0.330108684	0.70468809	0.70468809	1.904	0.628526934	14.3605834
2	10	13	0.293758	0.293758	1	0.2937577	0.627089085	0.627089085	1.904	0.559314661	13.8441565
2	11	14	0.26141	0.26141	1	0.261409623	0.558035146	0.558035146	1.904	0.497723921	13.26732885
2	12	15	0.242521	0.242521	0	0	0.517713472	0	0	0	0
2	1	16	0.224997	0.224997	0	0	0.480305301	0	0	0	0
2	2	17	0.20874	0.20874	0	0	0.445600115	0	0	0	0
2	3	18	0.193657	0.193657	0	0	0.413402604	0	0	0	0
2	4	19	0.179664	0.179664	0	0	0.383531573	0	0	0	0
2	5	20	0.15988	0.15988	0	0	0.341297755	0	0	0	0
2	6	21	0.142274	0.142274	1	0.142274072	0.303714651	0.303714651	1.904	0.270889832	10.83125905
2	7	22	0.126607	0.126607	1	0.126607103	0.270270131	0.270270131	1.904	0.241059924	10.09751808
2	8	23	0.112665	0.112665	1	0.112665353	0.240508463	0.240508463	1.904	0.214514832	9.394033515
3	9	24	0.100259	0.100259	1	0.100258844	0.214024097	0.214024097	1.904	0.190892838	8.723039146
3	10	25	0.089219	0.089219	1	0.089218517	0.190456143	0.190456143	1.904	0.169872057	8.08590992
3	11	26	0.079394	0.079394	1	0.079393932	0.169483449	0.169483449	1.904	0.151166047	7.483323993
3	12	27	0.073657	0.073657	0	0	0.157237166	0	0	0	0
3	1	28	0.068335	0.068335	0	0	0.145875757	0	0	0	0
3	2	29	0.063397	0.063397	0	0	0.135335283	0	0	0	0
3	3	30	0.058816	0.058816	0	0	0.125556427	0	0	0	0
3	4	31	0.054567	0.054567	0	0	0.116484158	0	0	0	0
3	5	32	0.048558	0.048558	0	0	0.103657129	0	0	0	0
3	6	33	0.043211	0.043211	1	0.04321072	0.092242589	0.092242589	1.904	0.082273211	5.169390384
3	7	34	0.038452	0.038452	1	0.038452432	0.082084999	0.082084999	1.904	0.073213431	4.739544642
3	8	35	0.034218	0.034218	1	0.034218118	0.073045944	0.073045944	1.904	0.065151297	4.34168245
4	9	36	0.03045	0.03045	1	0.03045008	0.065002254	0.065002254	1.904	0.057976952	3.973972184
4	10	37	0.027097	0.027097	1	0.027096971	0.057844321	0.057844321	1.904	0.051592633	3.634597777
4	11	38	0.024113	0.024113	1	0.0241131	0.051474607	0.051474607	1.904	0.045911343	3.321777504
4	12	39	0.021458	0.021458	0	0	0.045806314	0	0	0	0

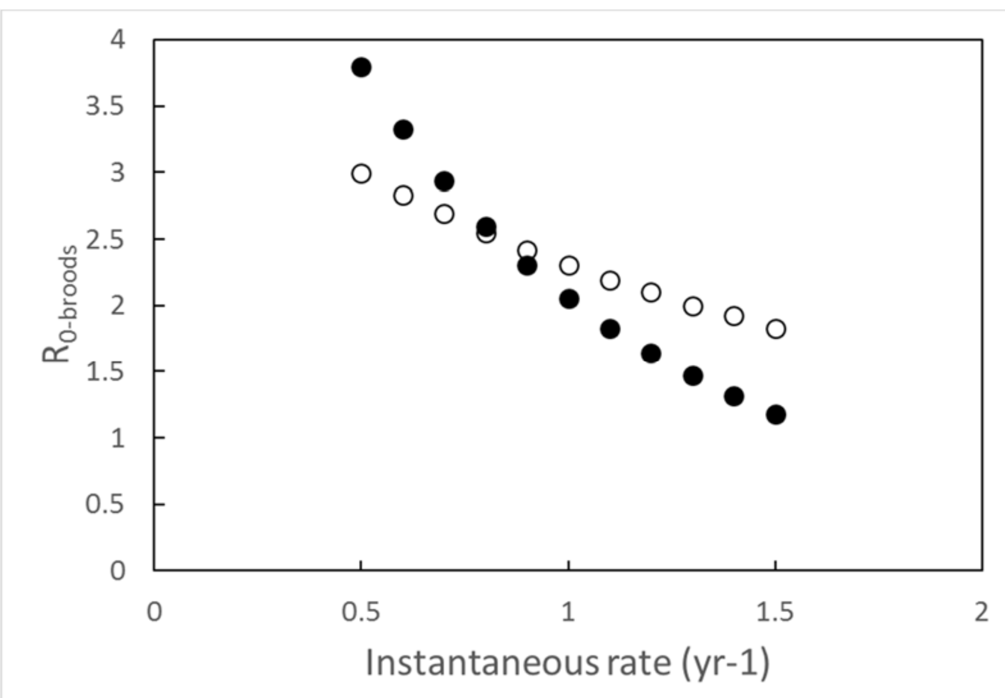
However, this maximum lifetime number of broods has to be weighted by the probability that a female survives. We used an estimate of the instantaneous mortality rate, M=0.9 yr^{-1} = 0.075 $month^{-1}$, to estimate survival (Miller et al. 2011). This mortality rate was applied to months when female crabs were too small to have recruited to the fishery, or for months when the fishery was not in operation (December – May). In months when females had grown sufficiently large to recruit to the fishery, and when the fishery was in operation (June – November), an instantaneous fishing mortality rate, F=1 yr^{-1} = 0.0833 $month^{-1}$, was added to the natural mortality rate. Together these assumptions allow estimation of the survivorship (ℓ_x) curve.

Following life table methods, the expected monthly reproductive output can be defined as $\ell_x \cdot m_x$ and the expected lifetime reproductive output as

$$R_{0-broods} = \sum_{x=1}^{n} l_x \cdot m_x$$

Given these base assumptions, the expected lifetime number of broods produced by a female blue crab is $R_{0\text{-broods}}$=2.307 broods. This estimate is sensitive to assumptions regarding M and F. As both M and F increase the estimate of $R_{0\text{-broods}}$ declines (Fig. 14). The response of R0-broods is more sensitive to changes in M, which operates during all months than it is to changes in F, which only operates from June – November on mature females. The overall conclusion from this analysis is that for reasonable values of M and F, the expected lifetime number of broods produced per female is between 2- 3. We note that if the original value of broods

Figure 14. . Response of expected lifetime brood production to changes in instantaneous mortality rates. Data shown are for changes in natural mortality rate, M (solid symbols) and changes in the fishing mortality rate (open symbols).



per season given by Van Engel (1958) and reported by Hines et al. (2003) of three broods per season is correct, then the average lifetime number of broods per female is reduced to 1.42 broods.

Expected lifetime number of offspring

It is trivial to extend this analysis to estimate the expected lifetime egg production using estimates of fecundity per brood. Prager et al. (1990) conducted an extensive study of fecundity patterns in Chesapeake Bay blue crab and concluded that number of zoea produced was an increasing linear function of female carapace width. This translates to an average fecundity per brood of 3.2 million eggs. Because life tables are female specific, we need to divide this number by the sex ratio, to yield an average number of female offspring per brood of 1.6 million. Thus, the expected life time reproductive output of female blue crab in the Chesapeake Bay is 3.2 – 4.8 million female offspring.

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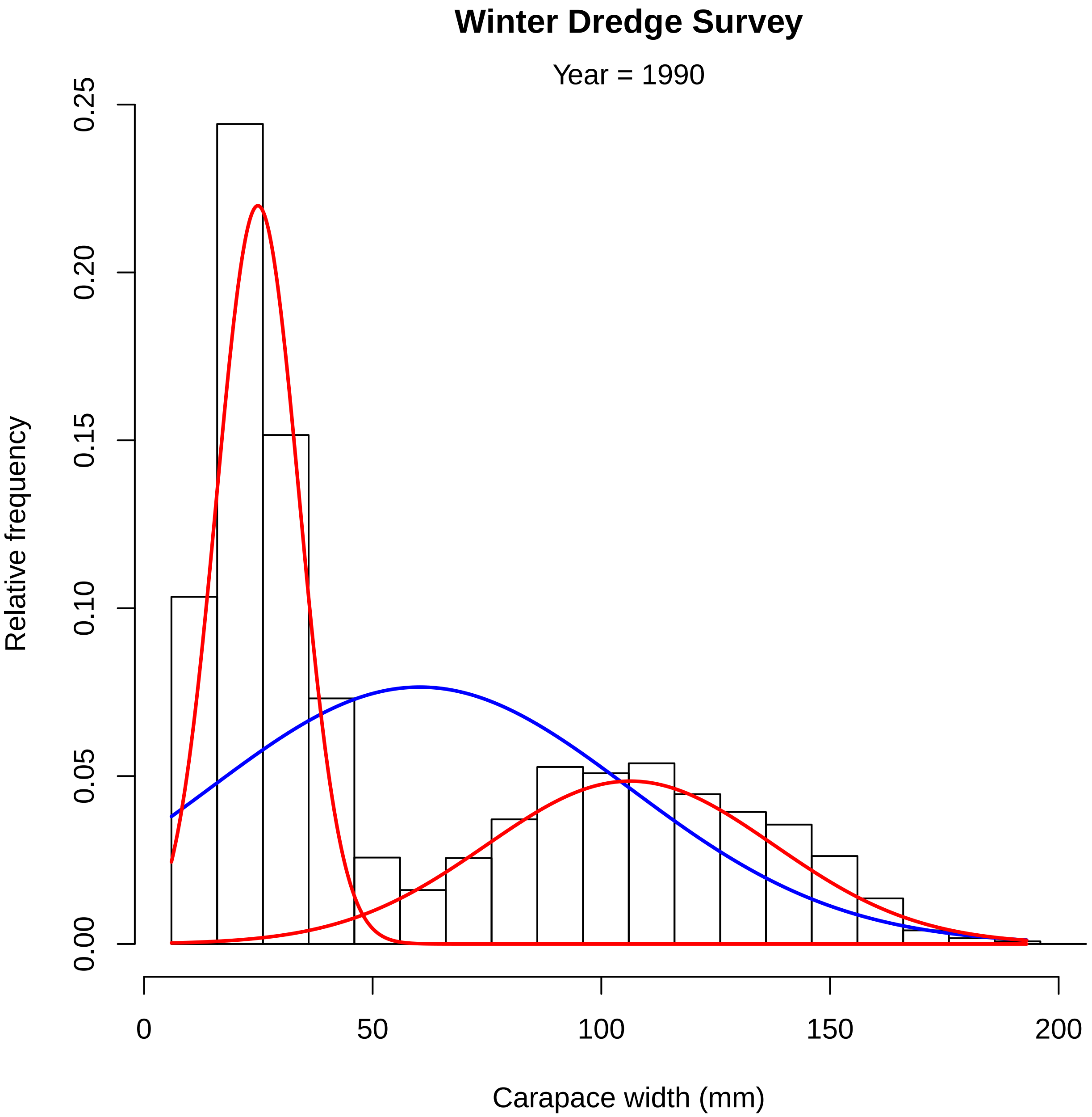
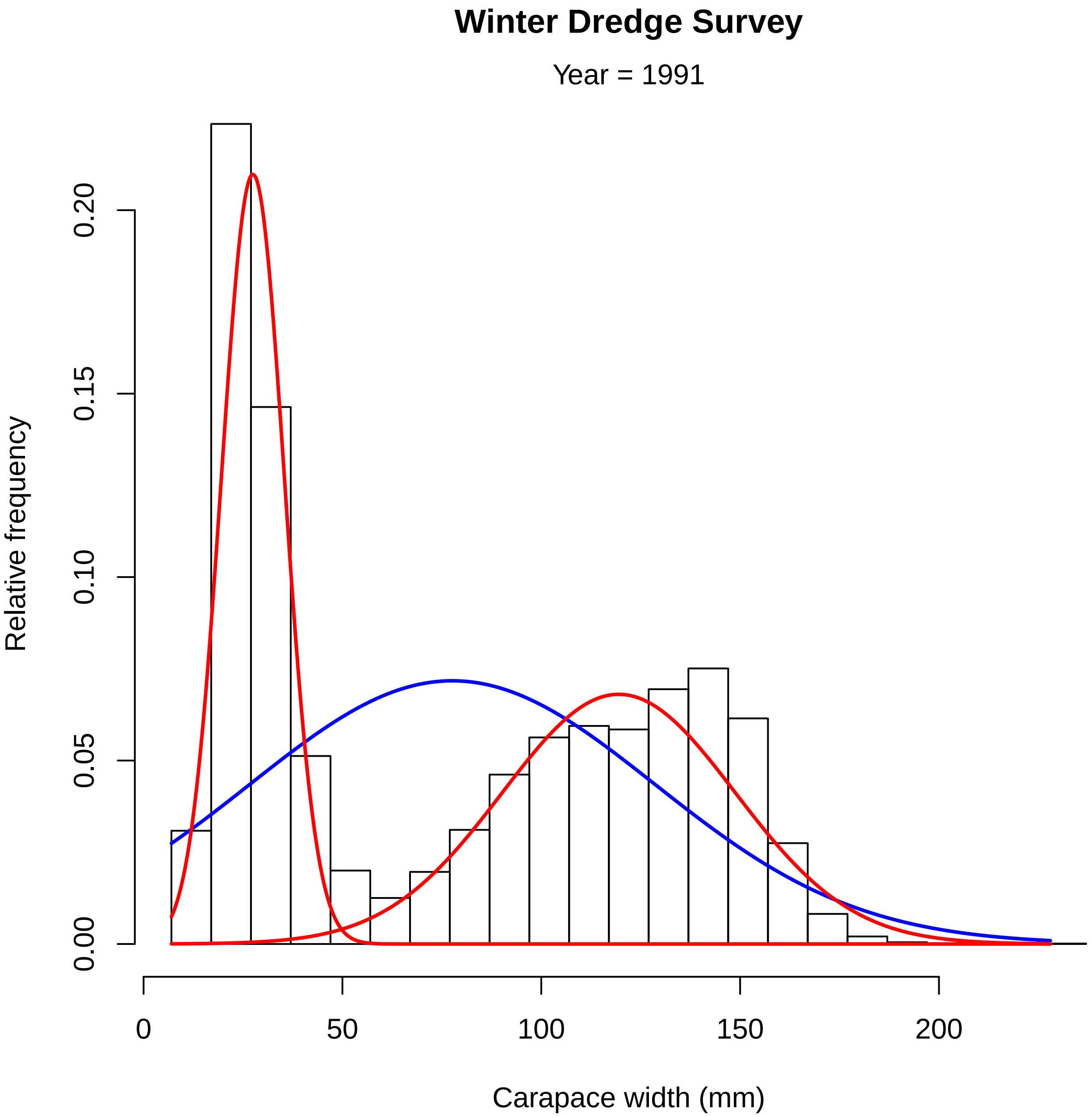
Appendix A

Mixture model fits to the size distribution of the winter dredge survey


Winter Dredge Survey
Year = 1990
Relative frequency
0.00
0.05
0.10
0.15
0.20
0.25
0
50
100
150
200
Carapace width (mm)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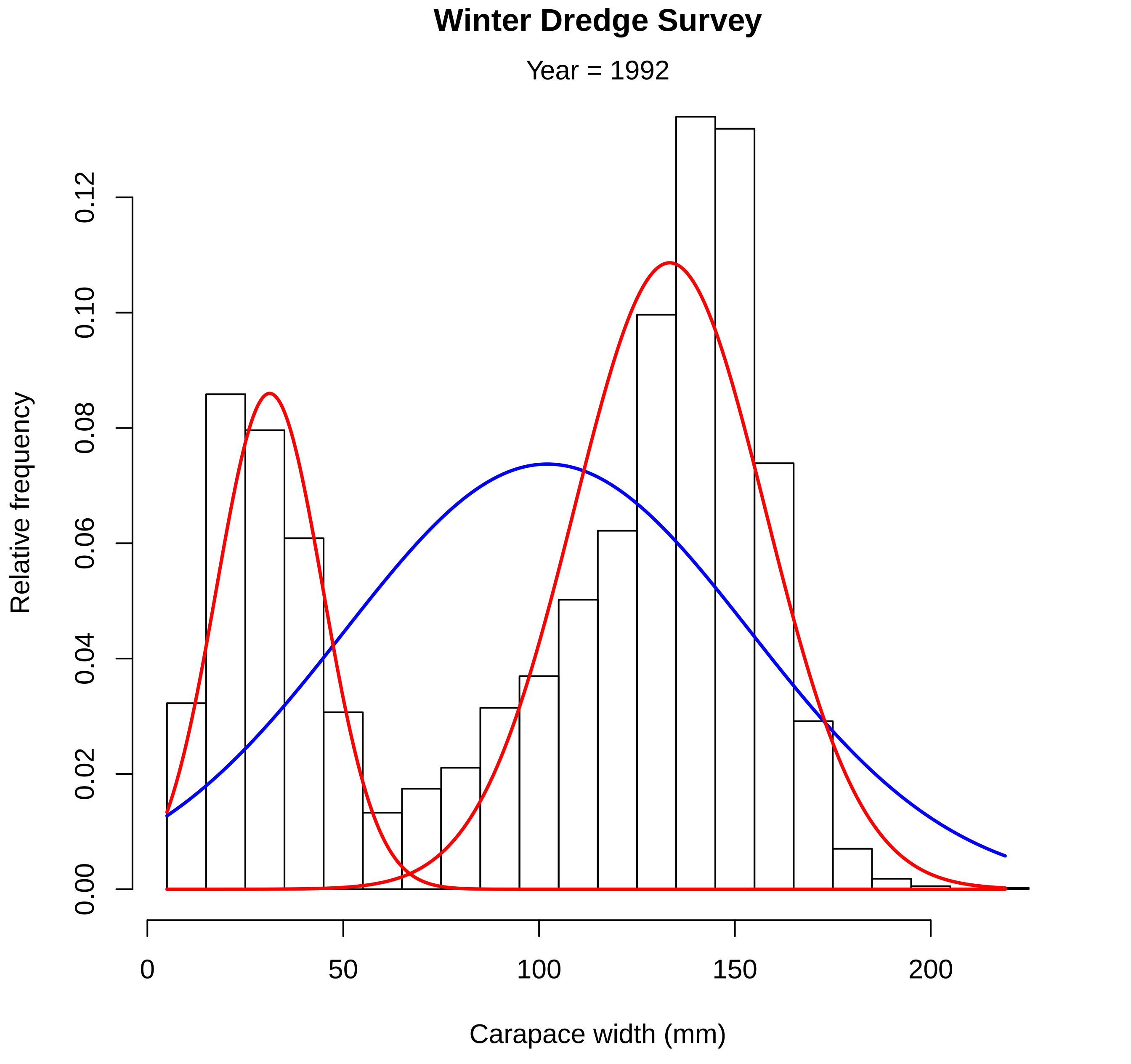
0.15
0.20
0
50
100
150
200
Carapace width (mm)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0.08
0.10
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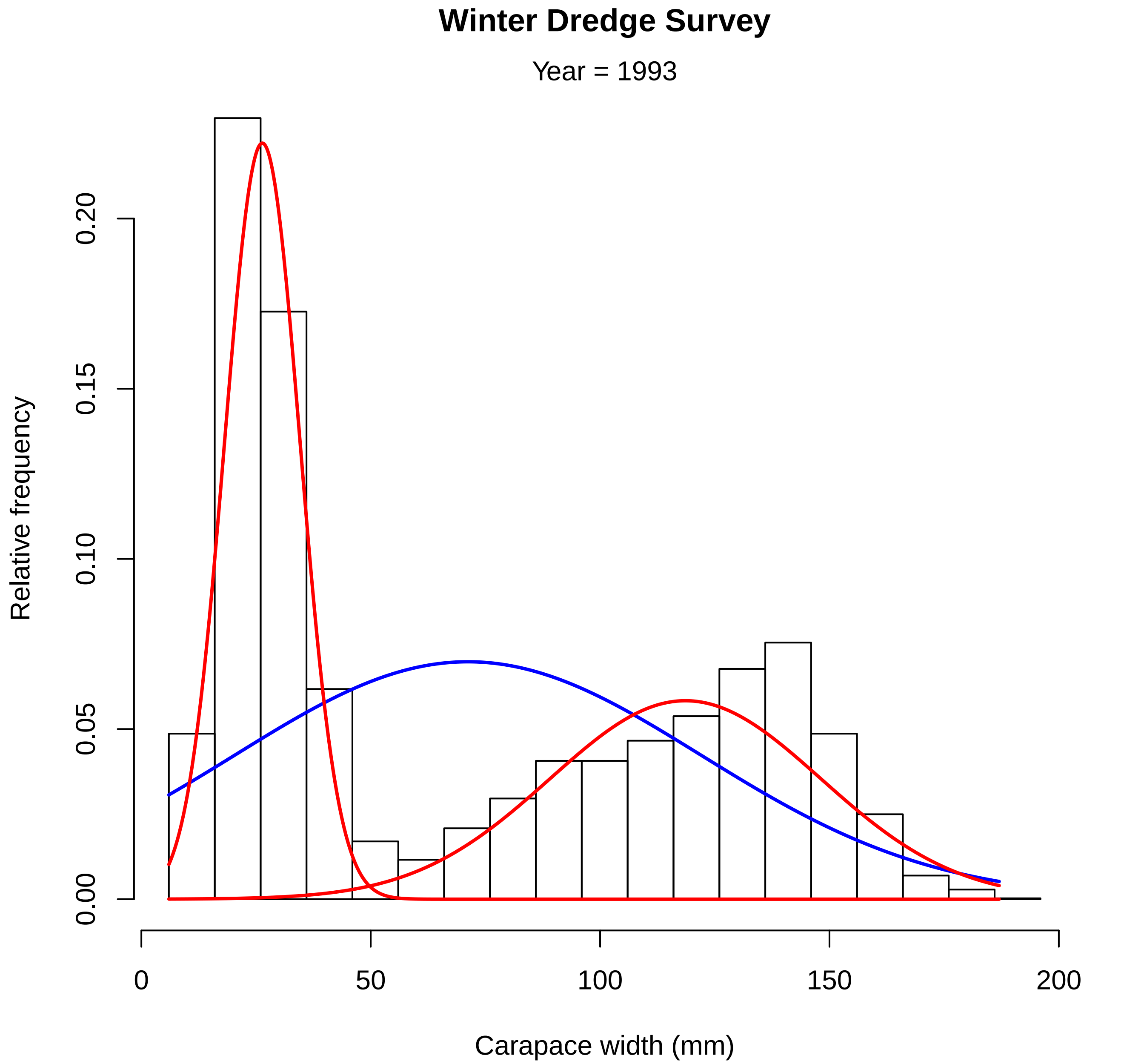
0
50
100
150
200
Carapace width (mm)



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0.20
0
50
100
150
200
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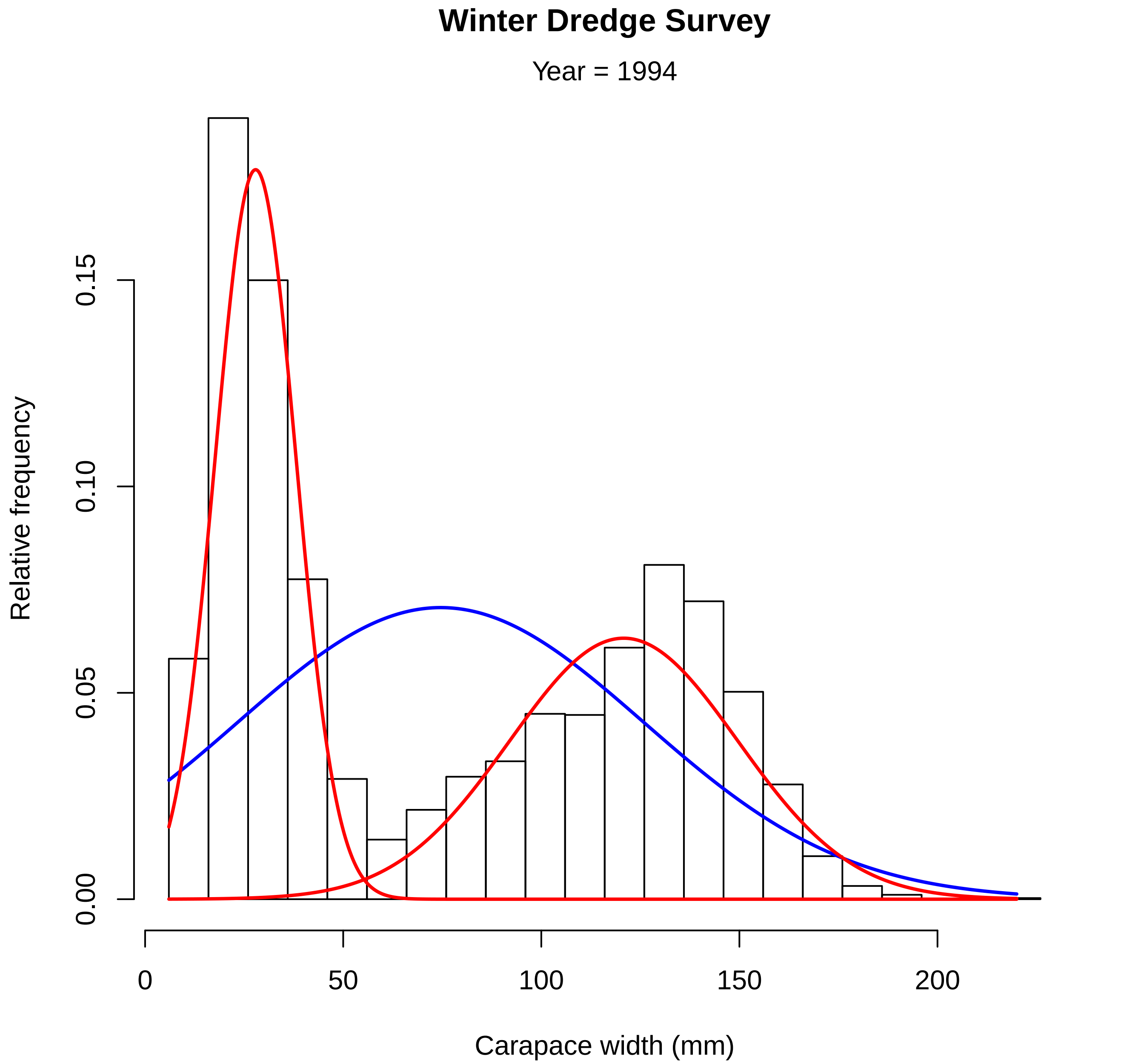

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150
200
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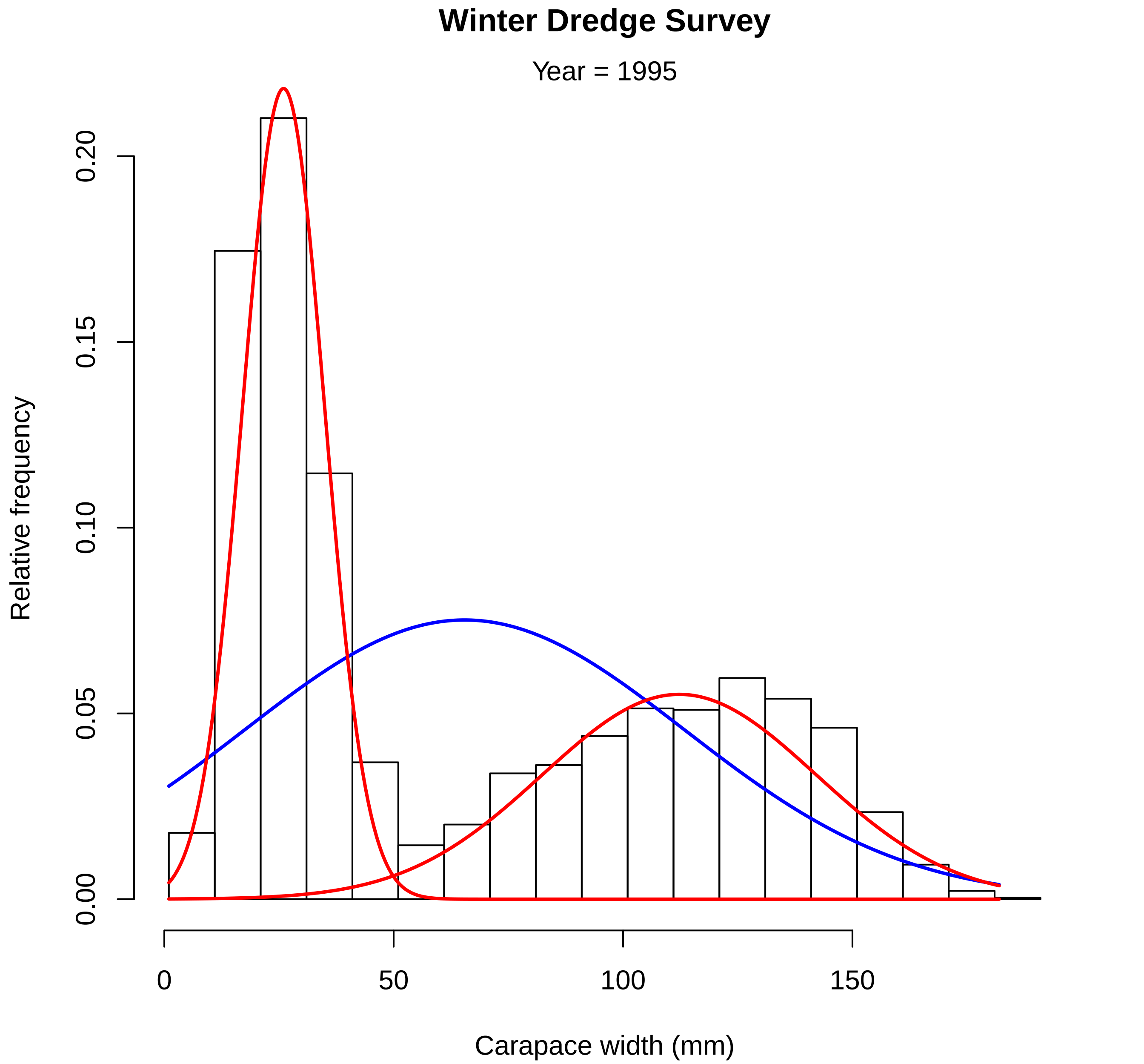

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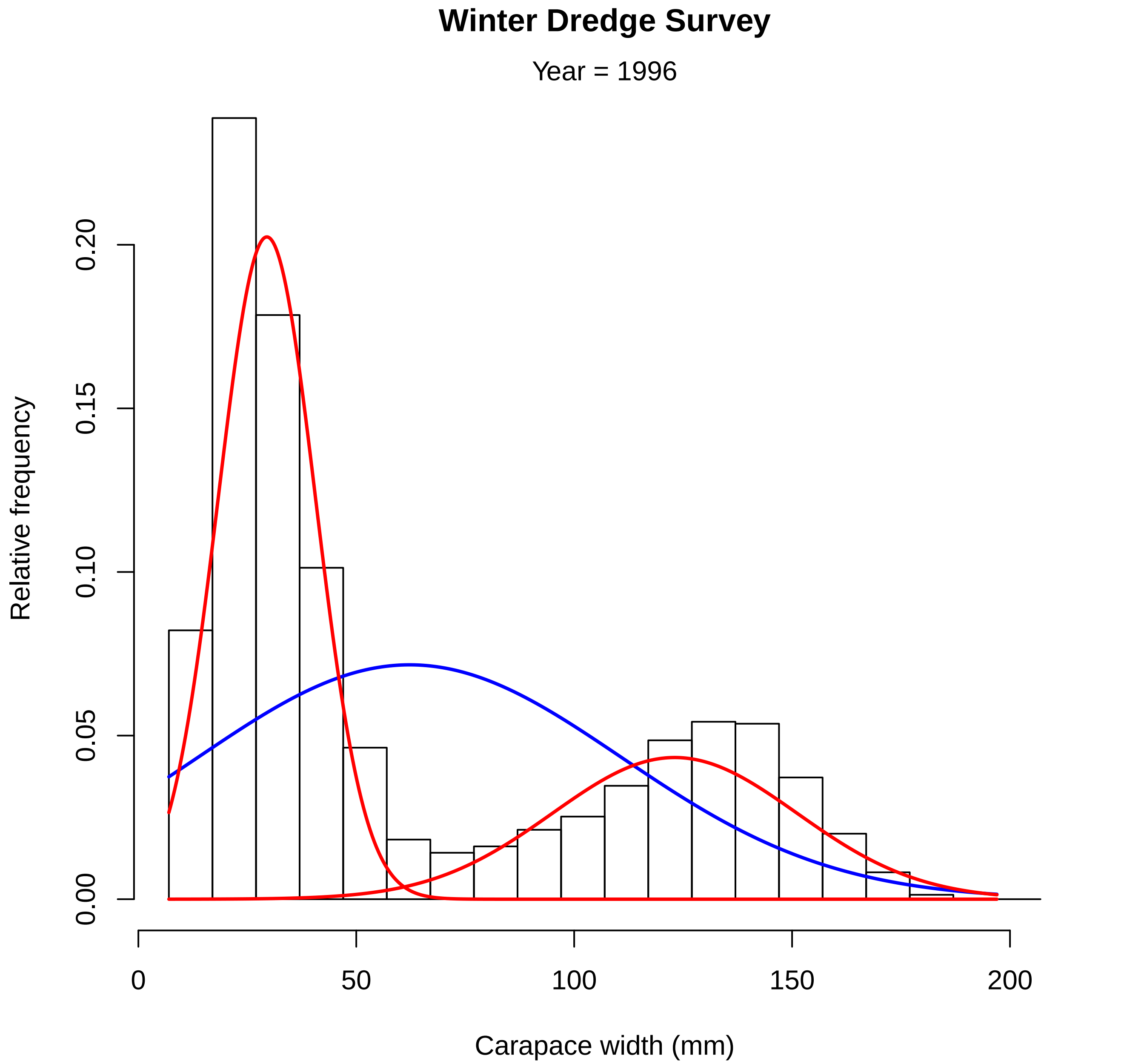
50
100
150
Carapace width (mm)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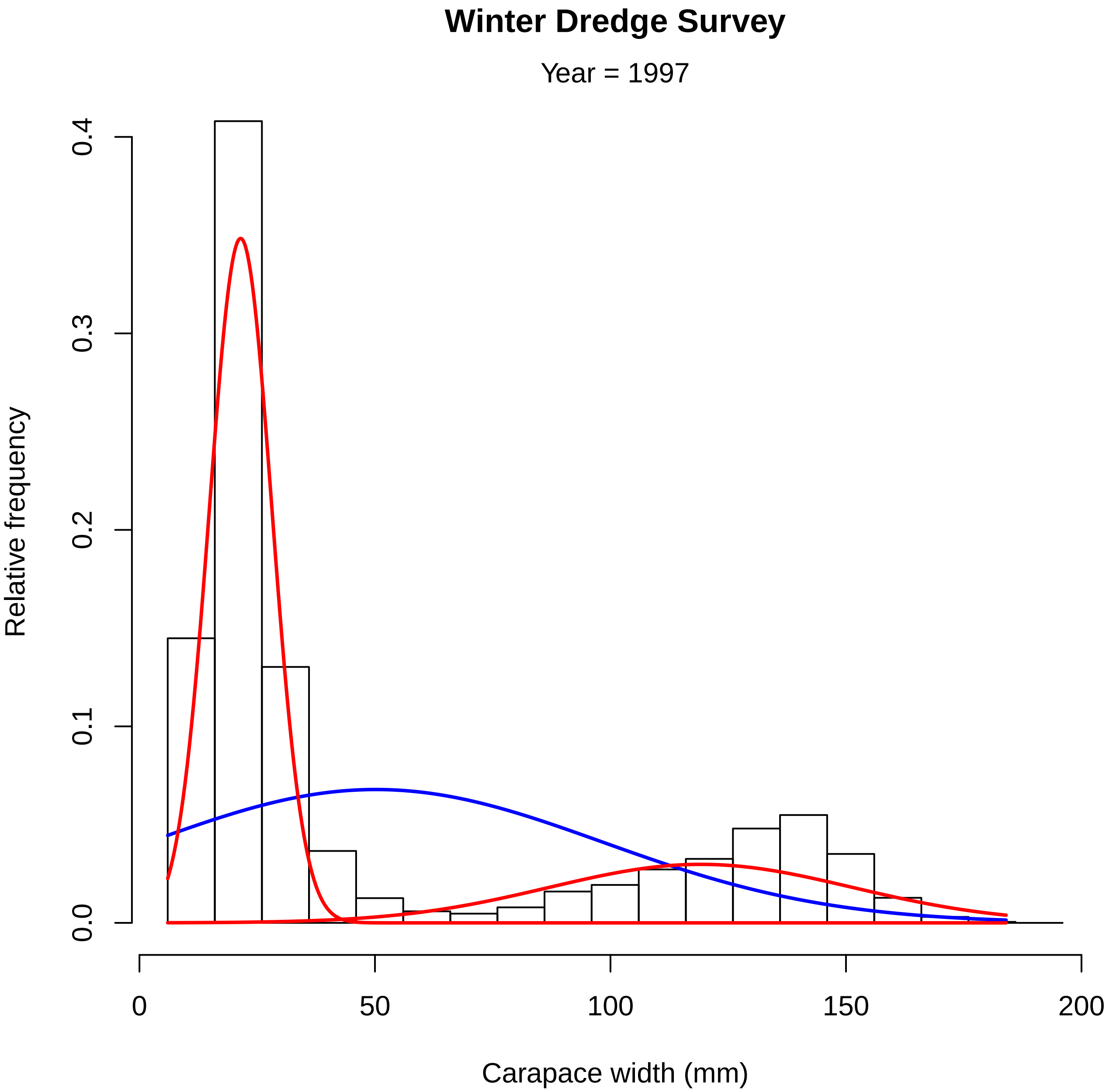
Carapace width (mm)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50
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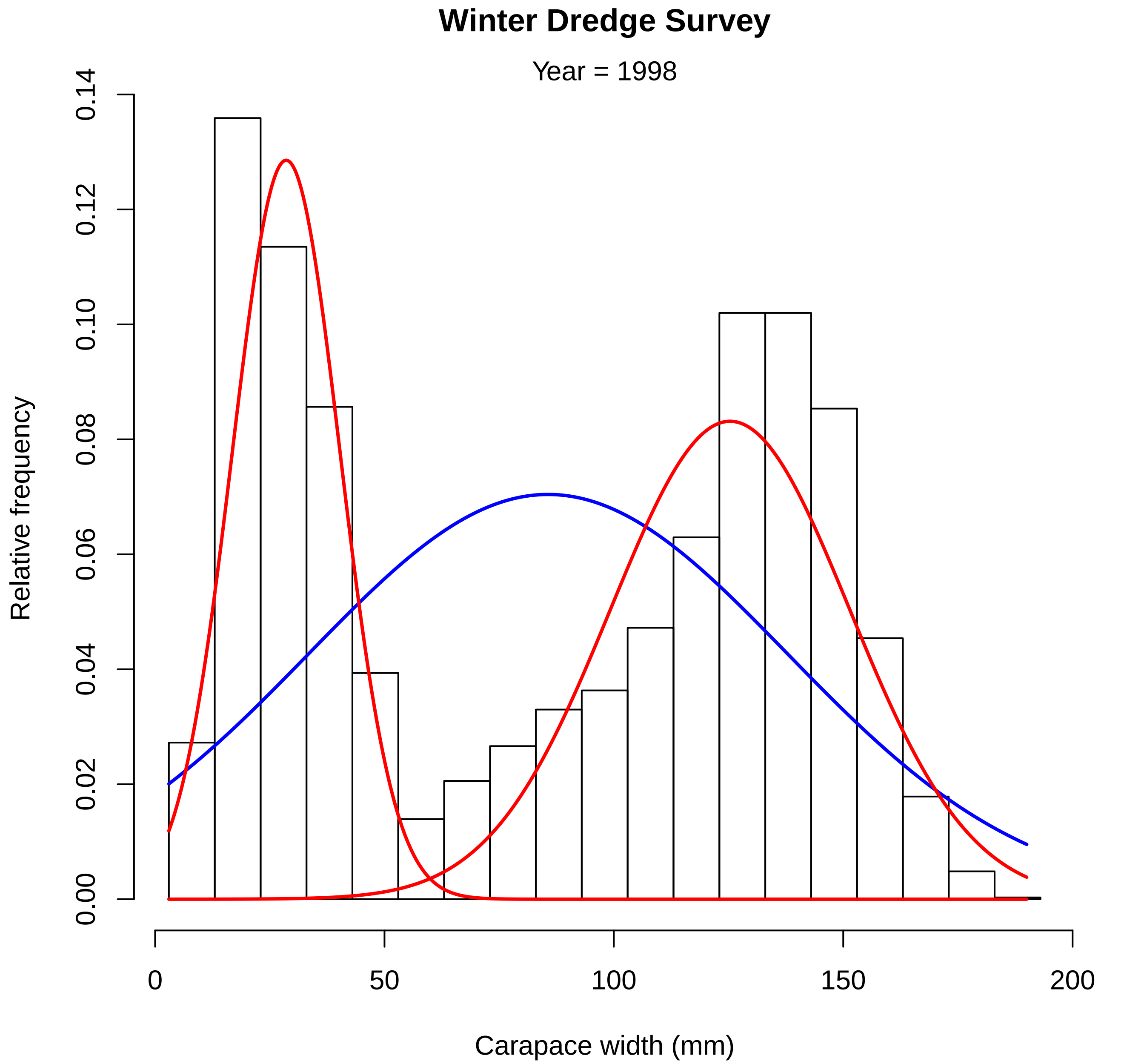
150
200
Carapace width (mm)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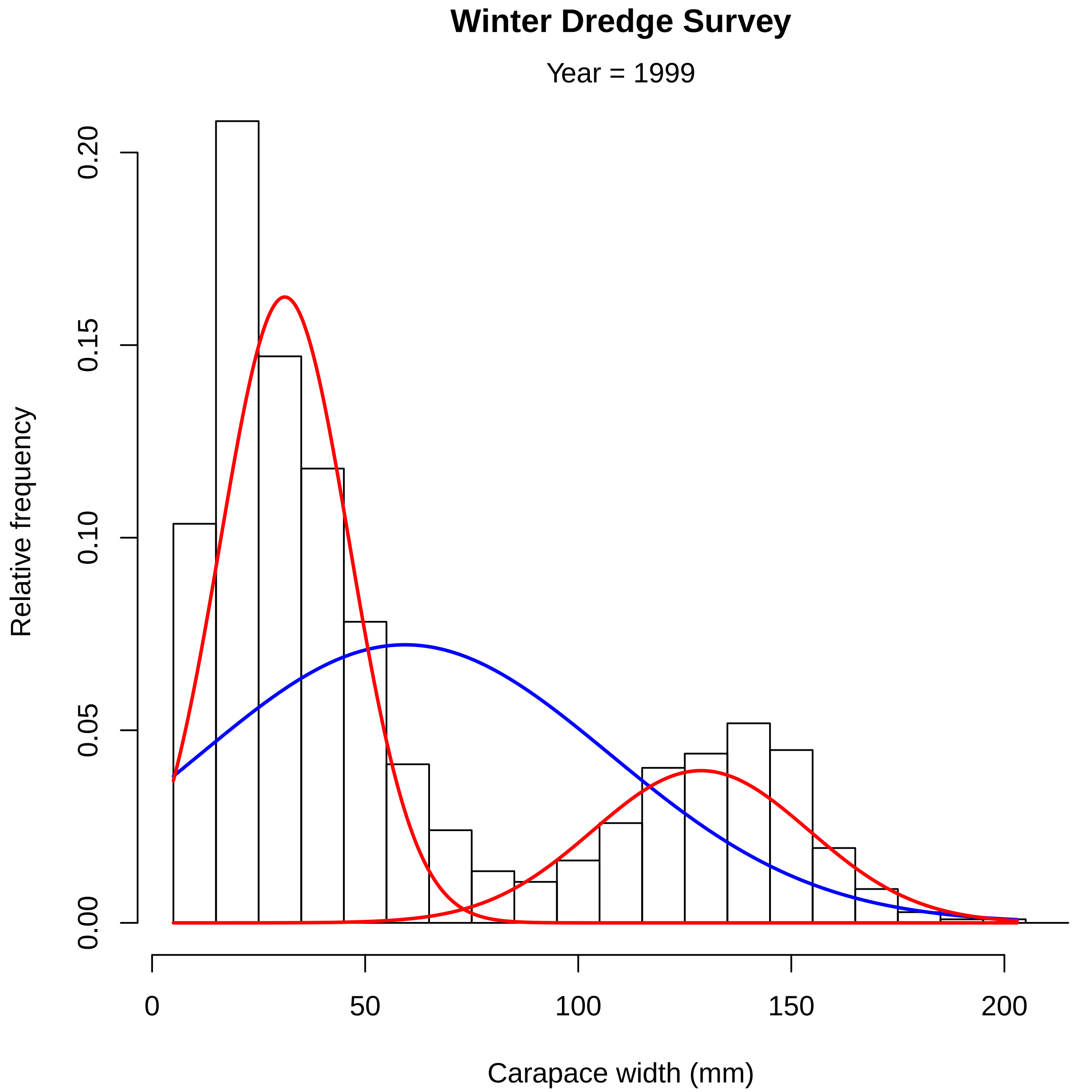
150
200
Carapace width (mm)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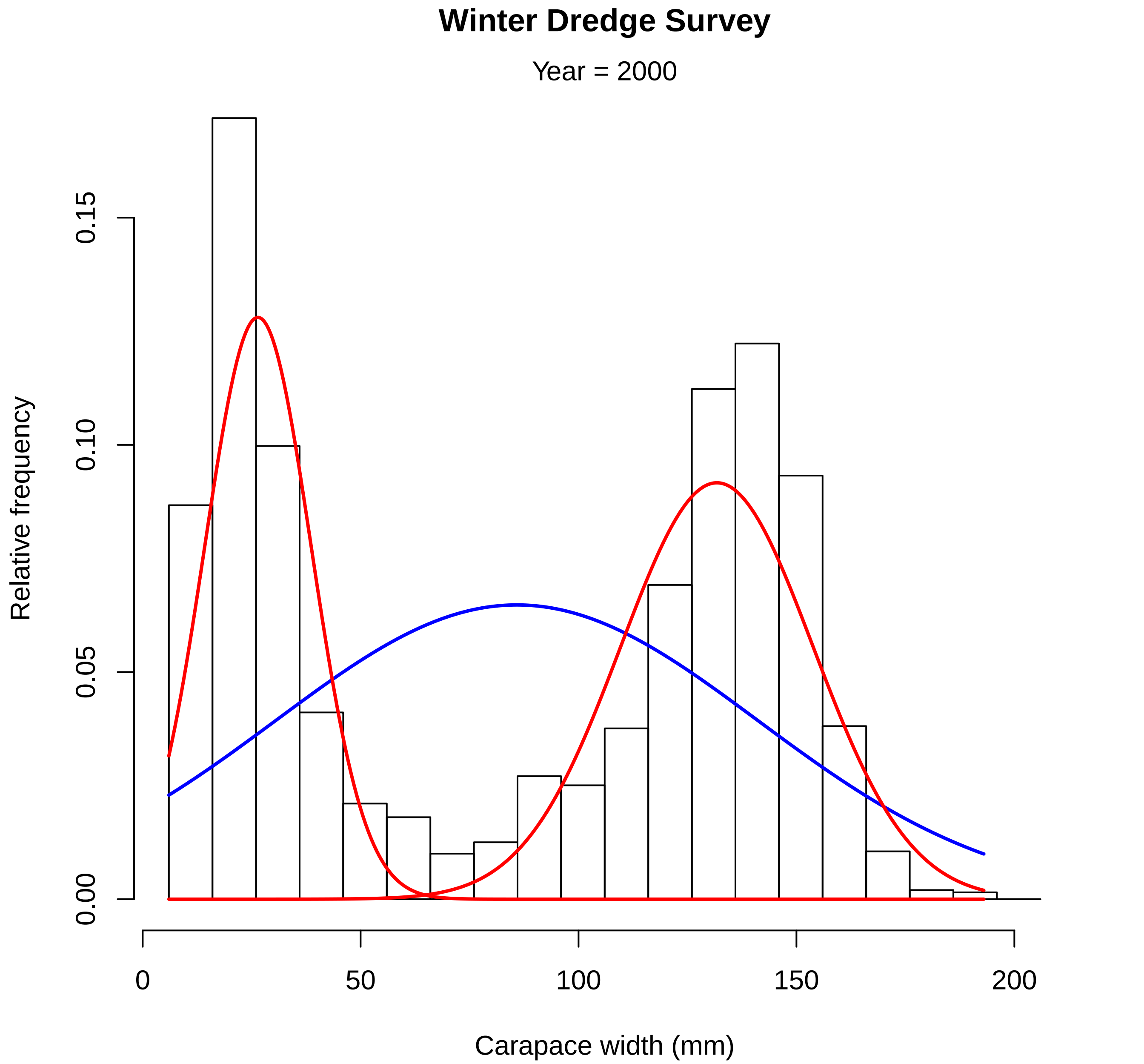
100
150
200
Carapace width (mm)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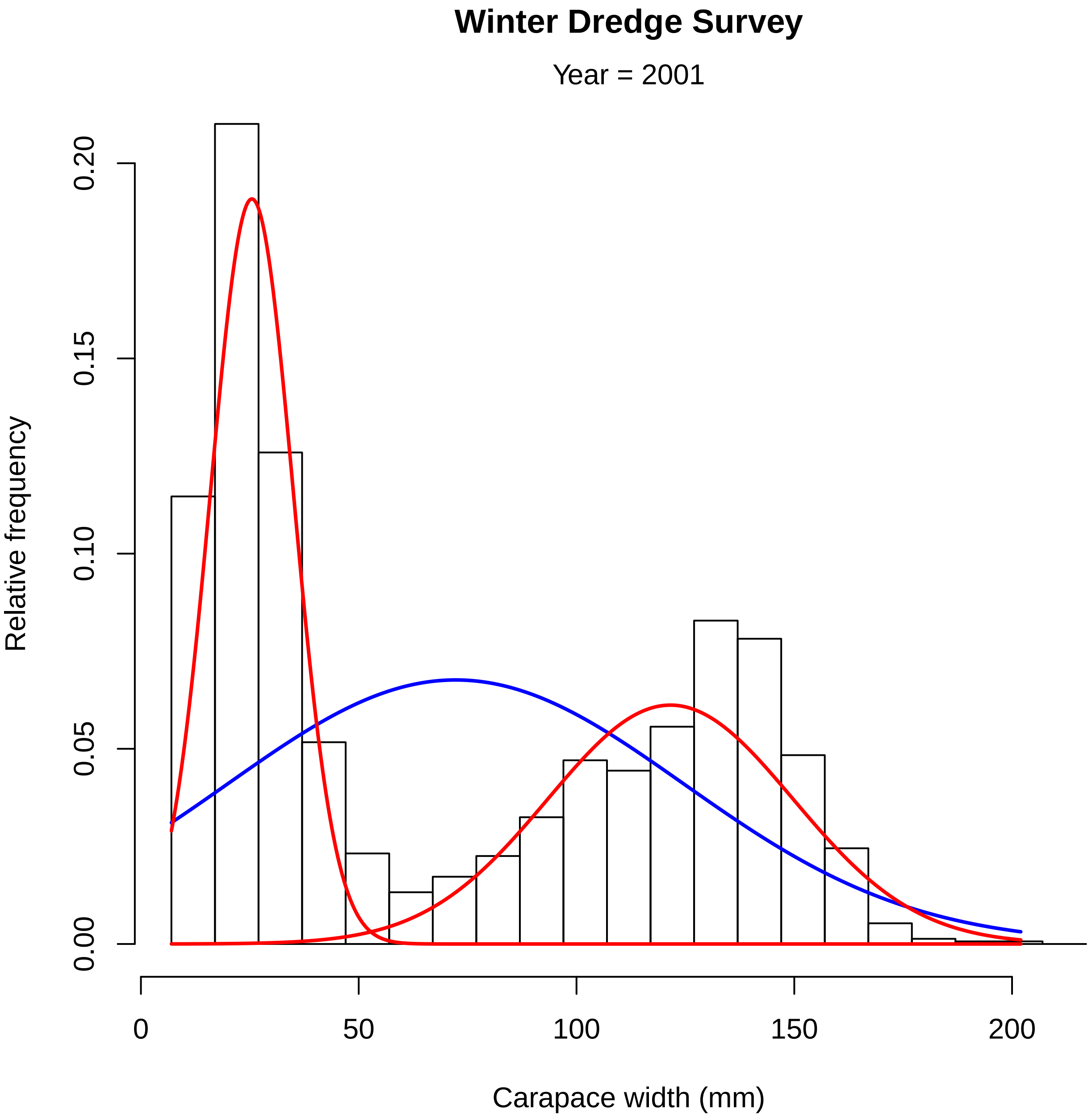
0.15
0
50
100
150
200
Carapace width (mm)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0.15
0.20
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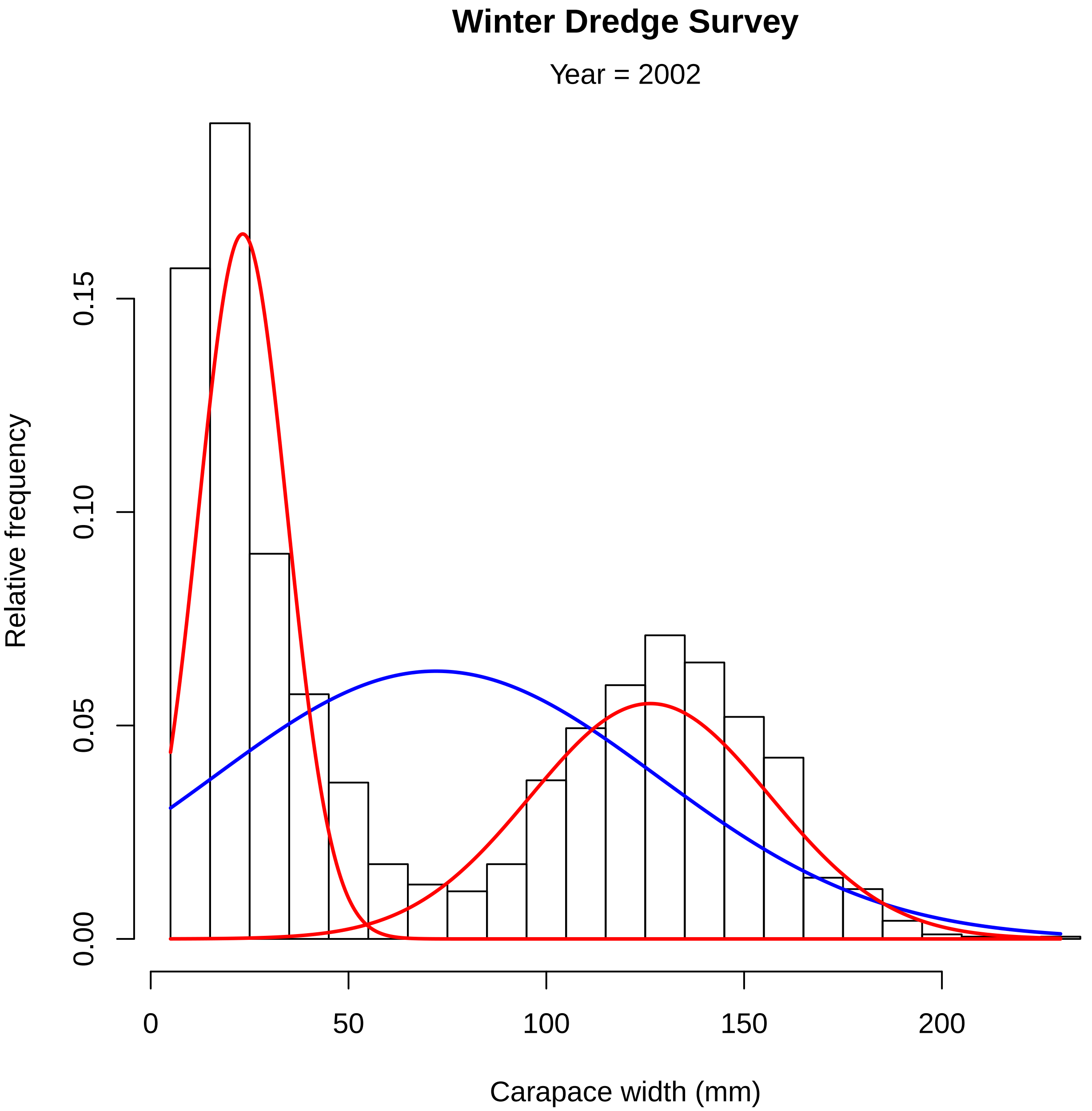
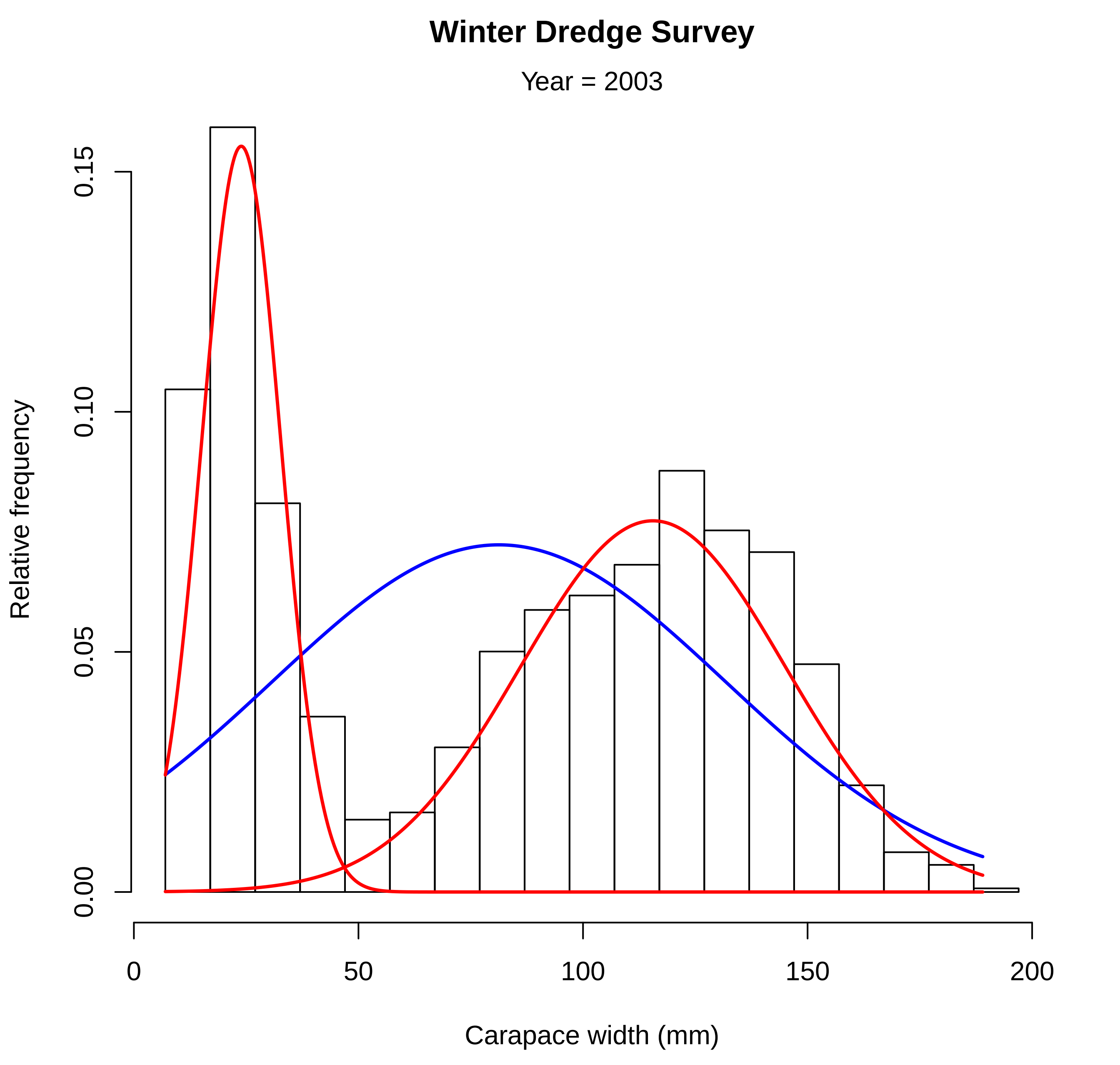
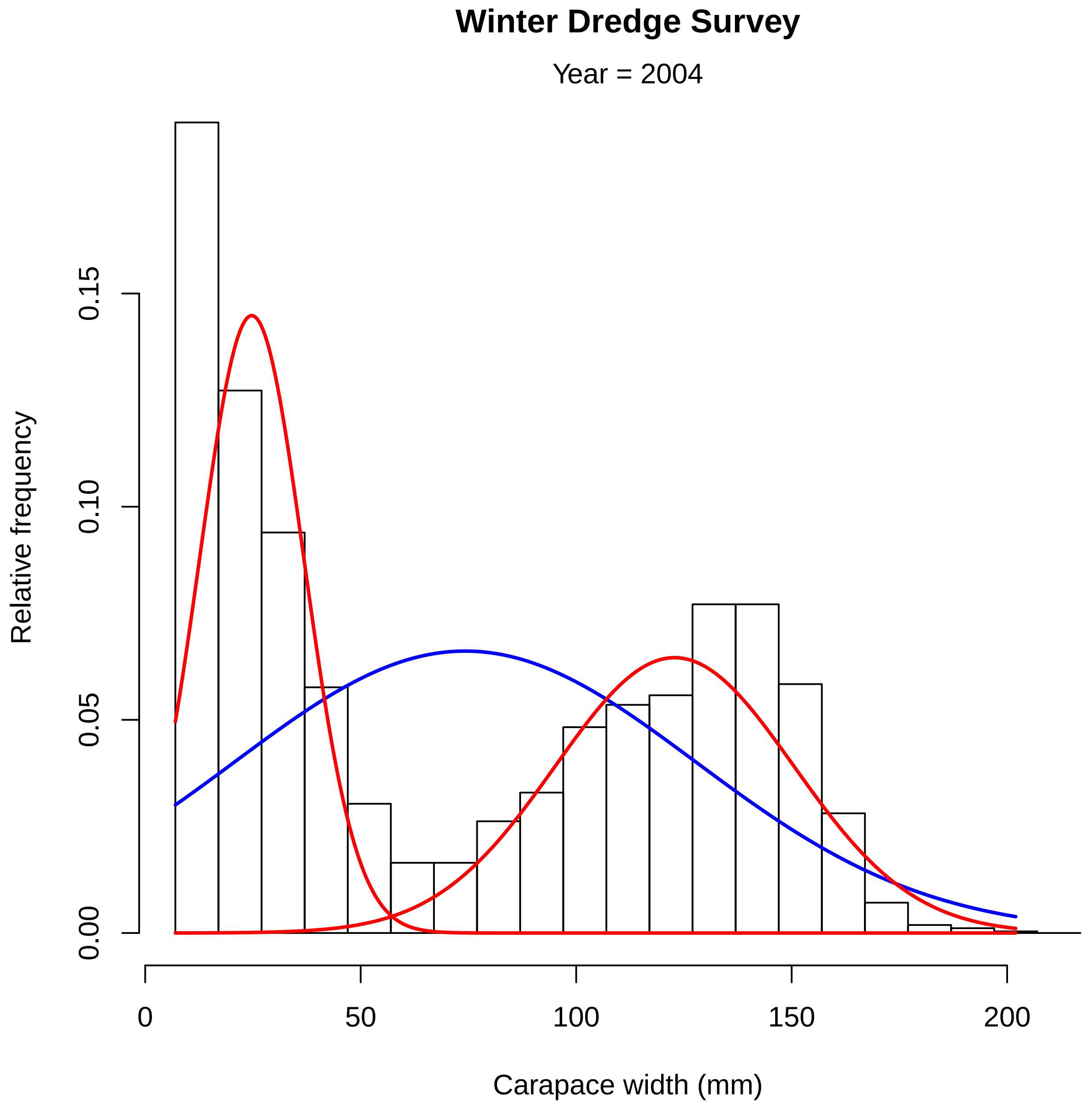
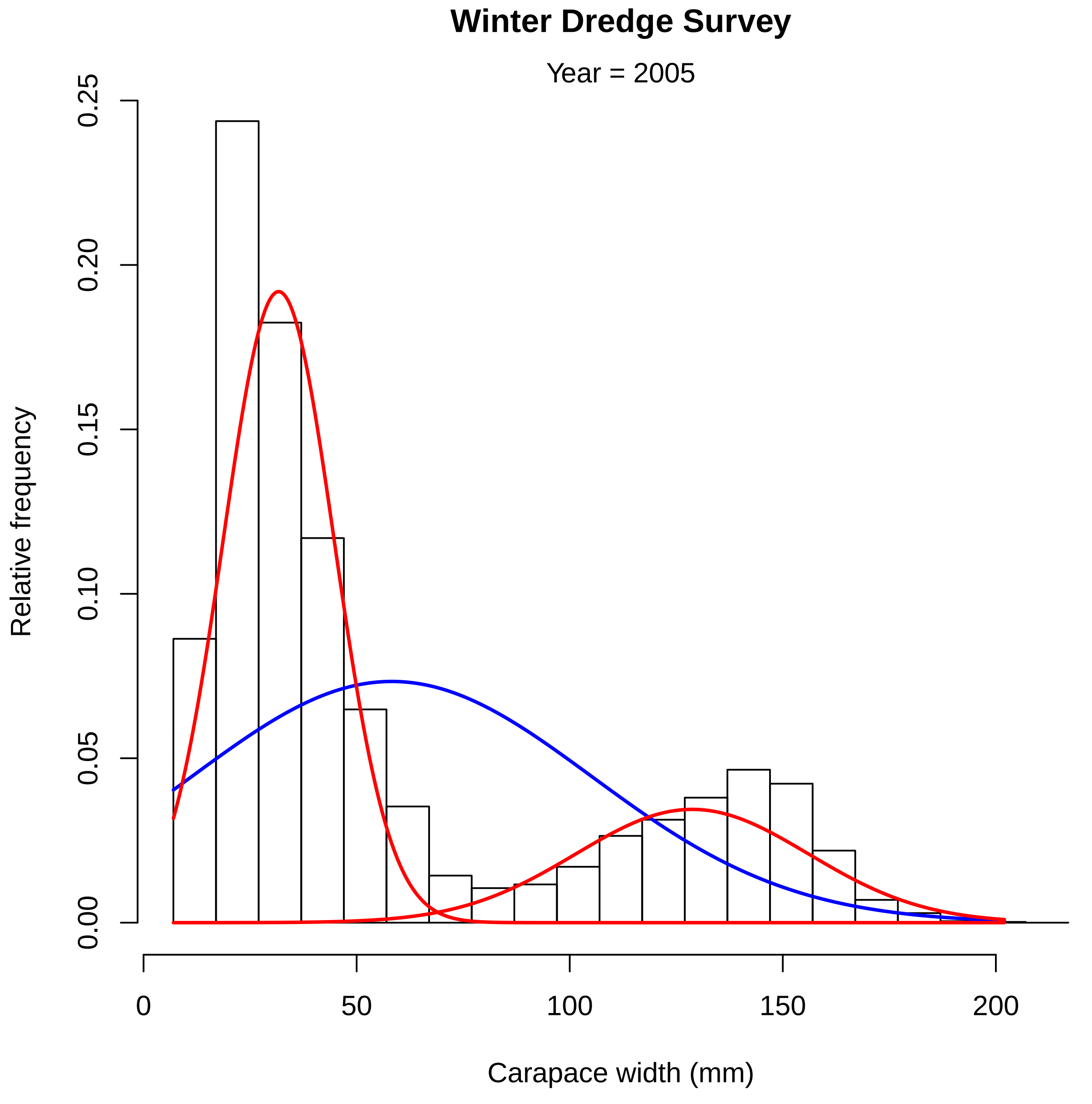
50
100
150
200
Carapace width (mm)

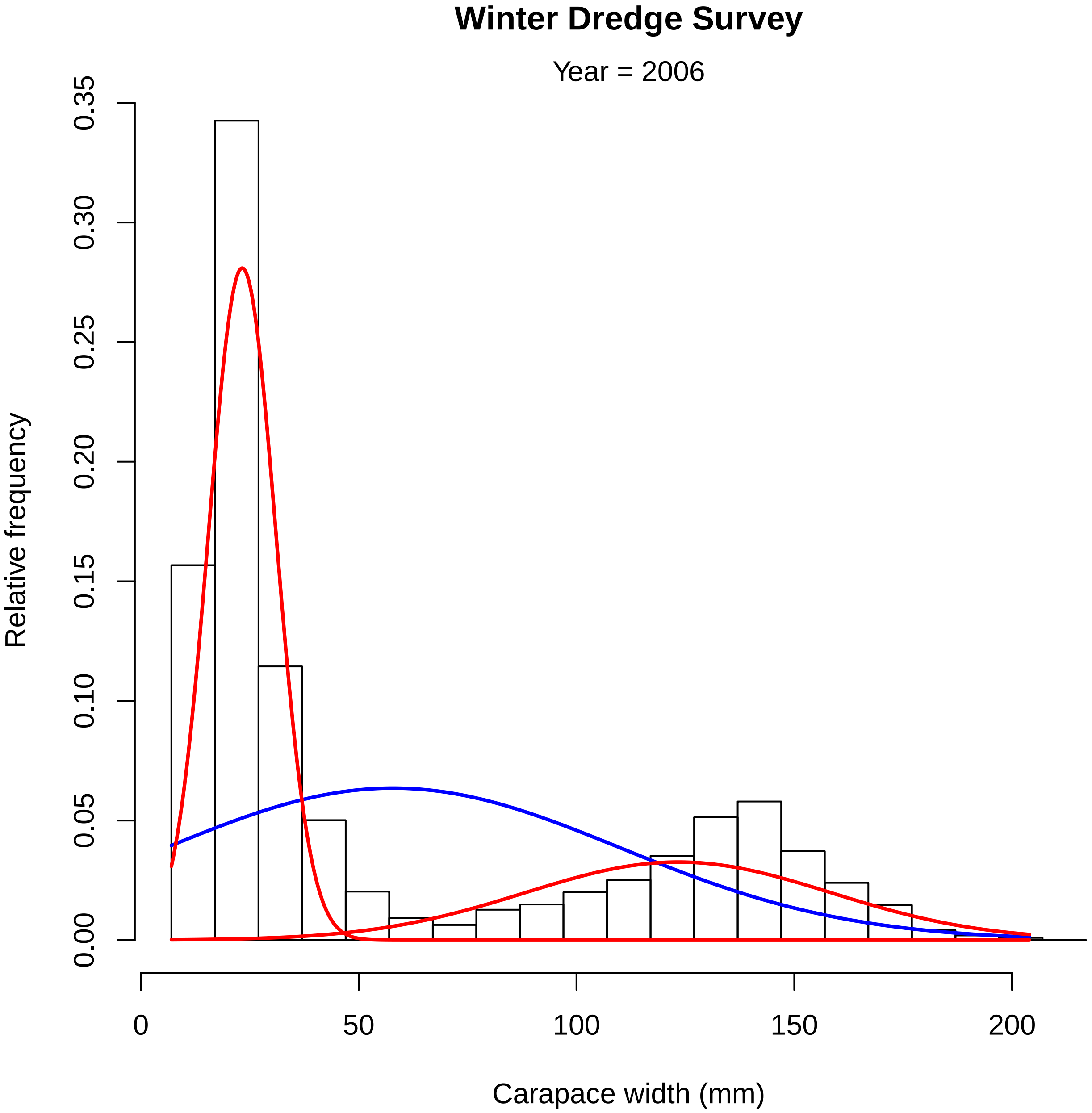

Winter Dredge Survey
Year = 2002
Relative frequency
0.00
0.05
0.10
0.15
0
50
100
150
200
Carapace width (mm)

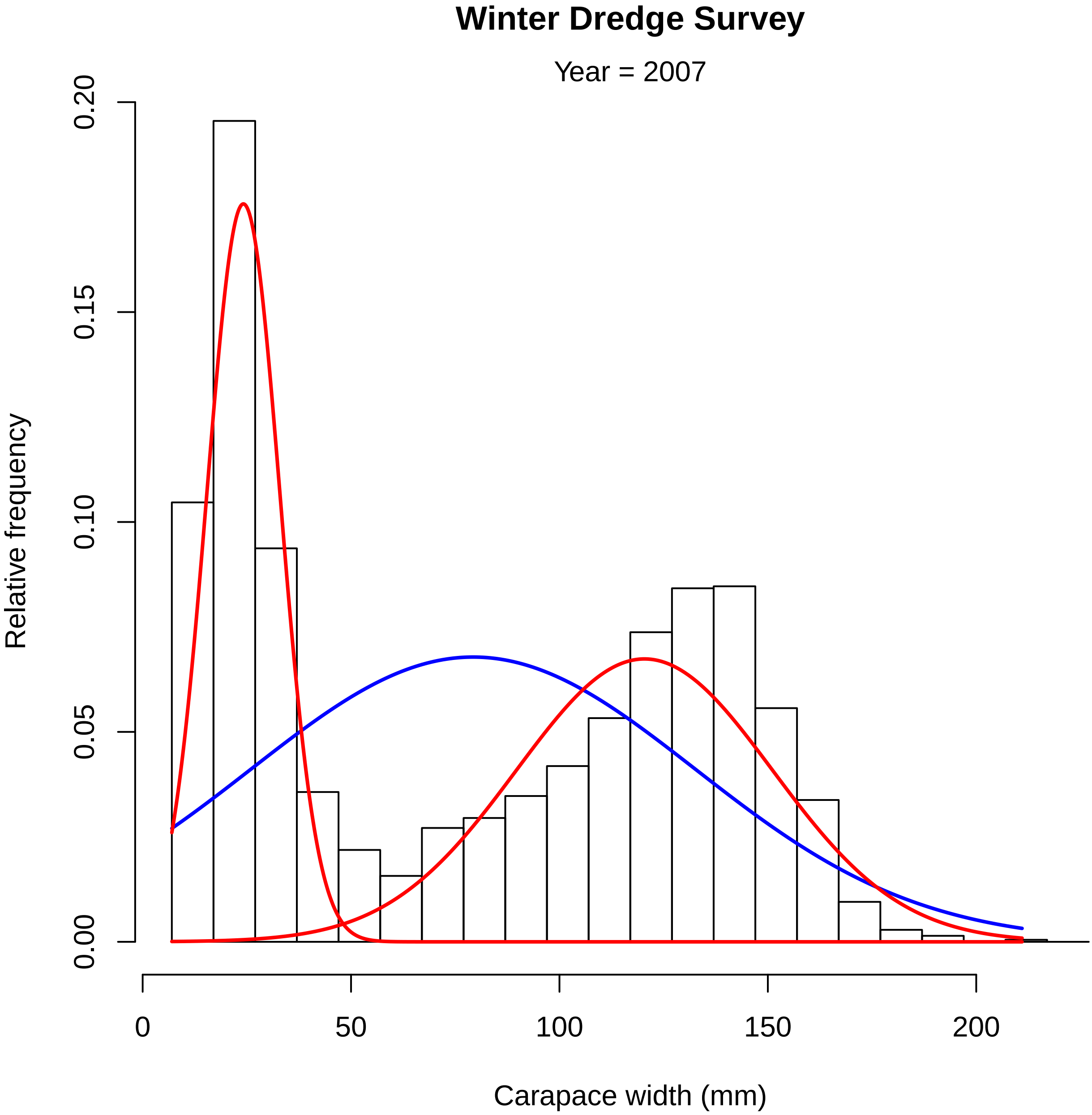

Winter Dredge Survey
Year = 2003
Relative frequency
0.00
0.05
0.10
0.15
0
50
100
150
200
Carapace width (mm)



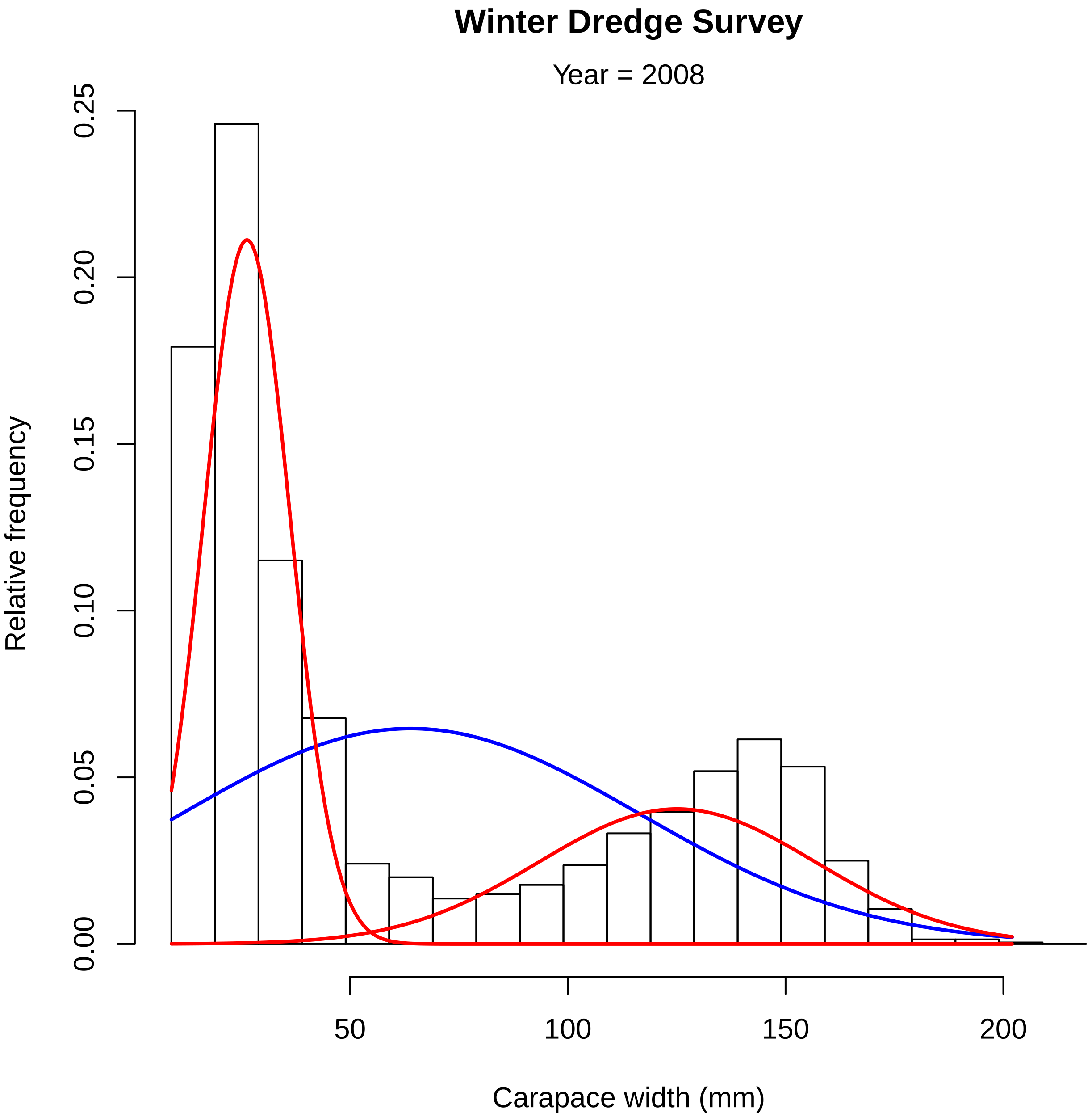
Winter Dredge Survey
Year = 2004
Relative frequency
0.00
0.05
0.10
0.15
0
50
100
150
200
Carapace width (mm)

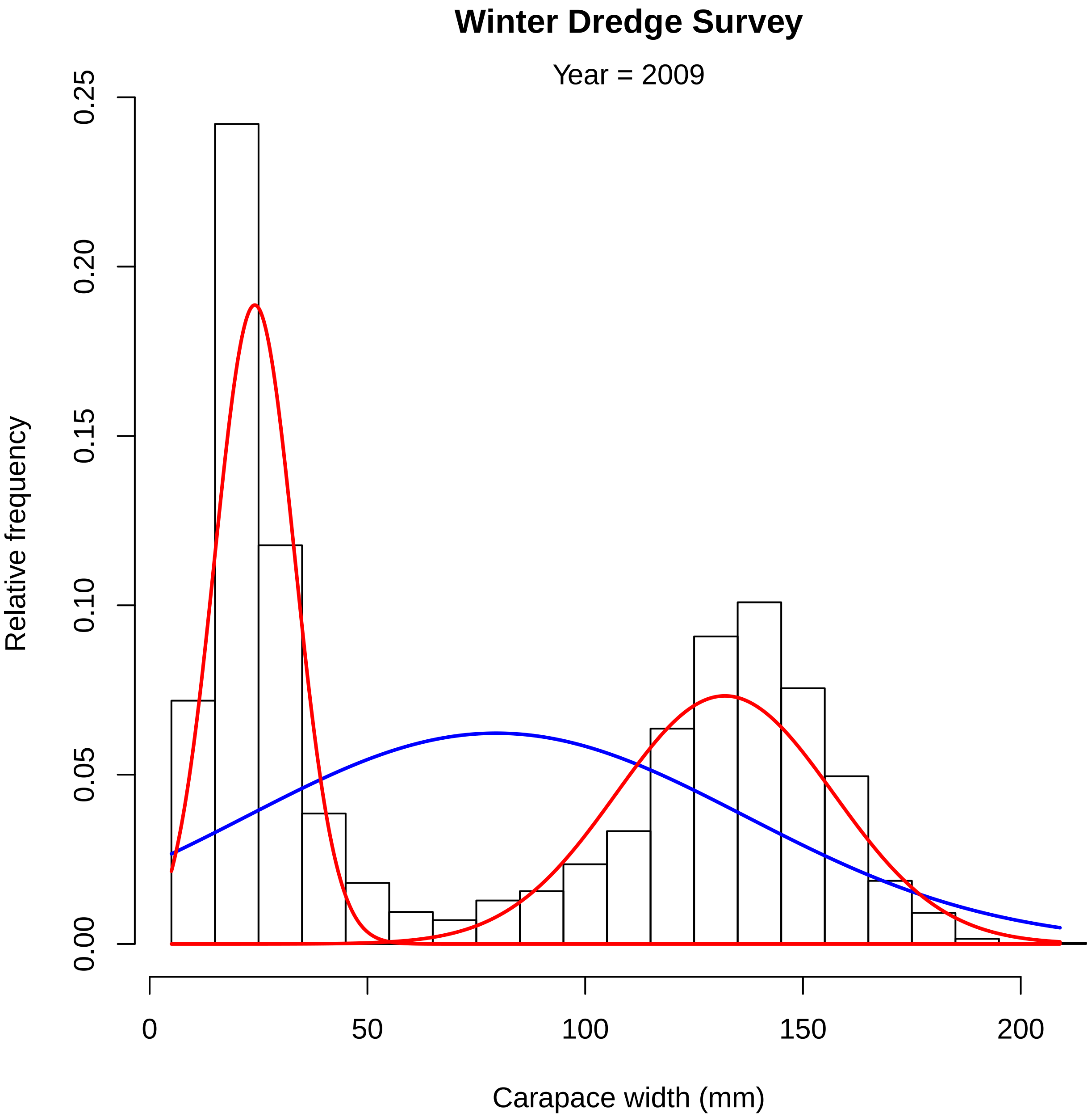

Winter Dredge Survey
Year = 2005
Relative frequency
0.00
0.05
0.10
0.15
0.20
0.25
0
50
100
150
200
Carapace width (mm)


Winter Dredge Survey
Year = 2006
Relative frequency
0.00
0.05
0.10
0.15
0.20
0.25
0.30
0.35
0
50
100
150
200
Carapace width (mm)

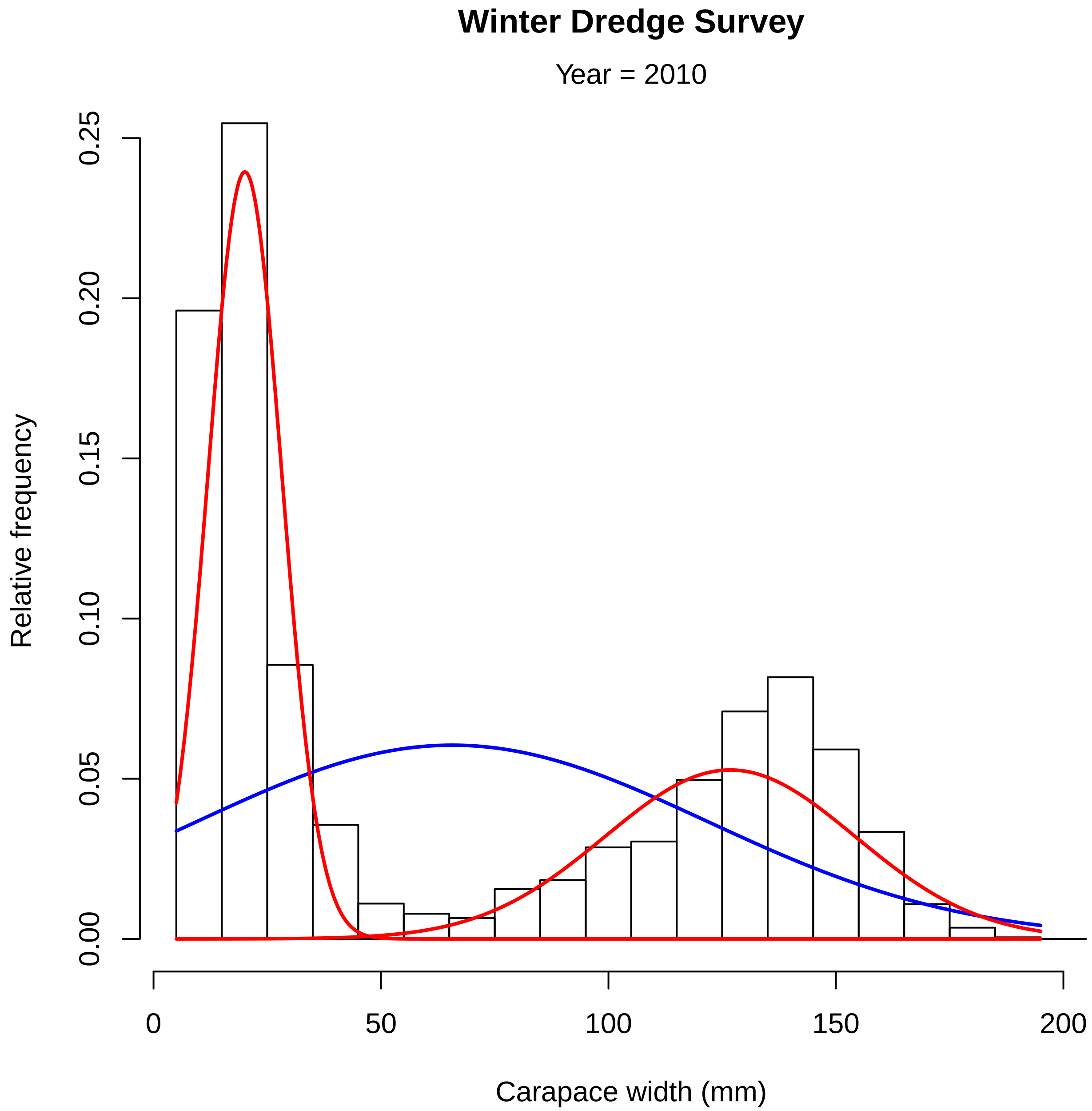


Winter Dredge Survey
Year = 2007
Relative frequency
0.00
0.05
0.10
0.15
0.20
0
50
100
150
200
Carapace width (mm)

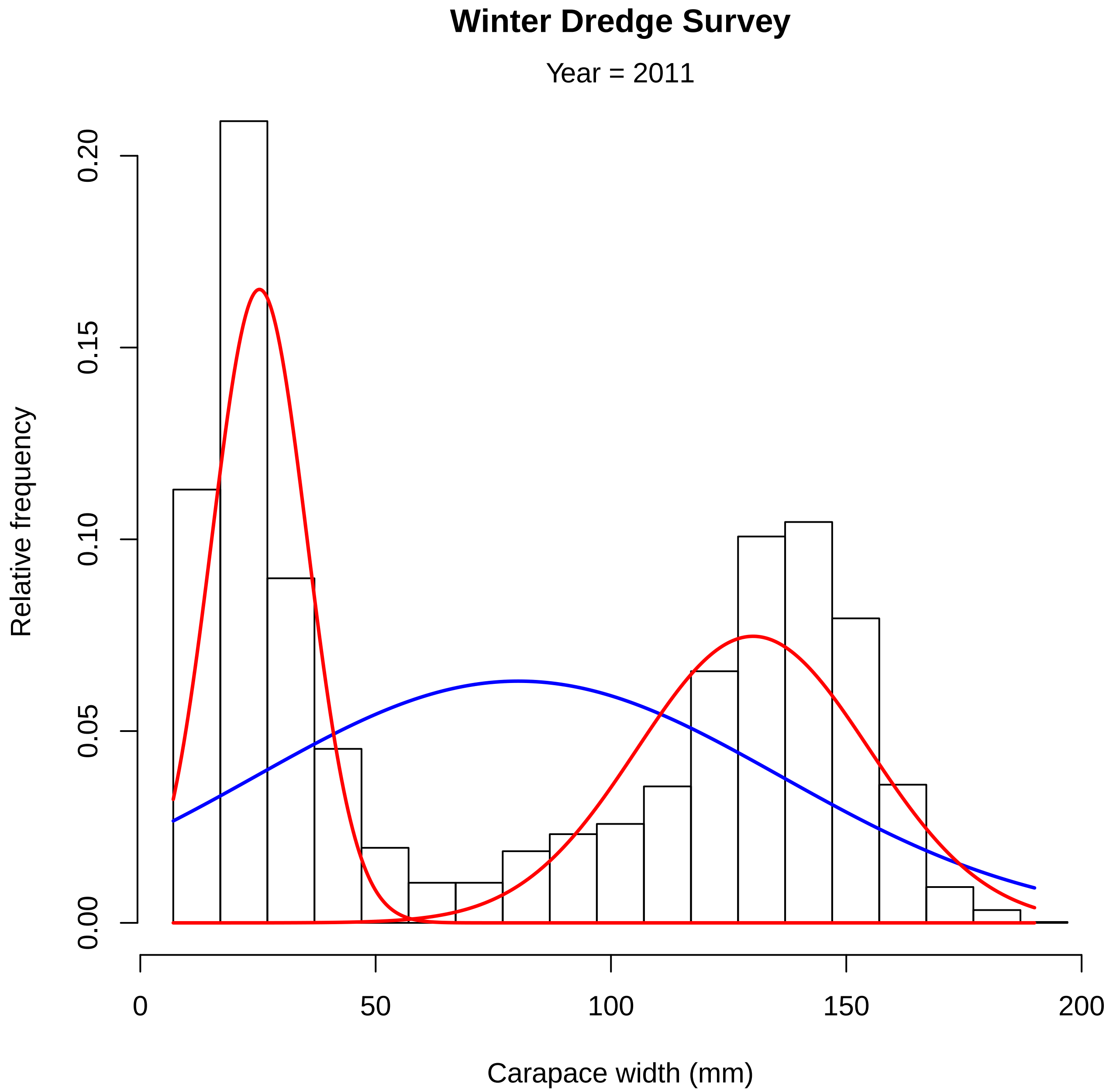

Winter Dredge Survey
Year = 2008
Relative frequency
0.00
0.05
0.10
0.15
0.20
0.25
50
100
150
200
Carapace width (mm)

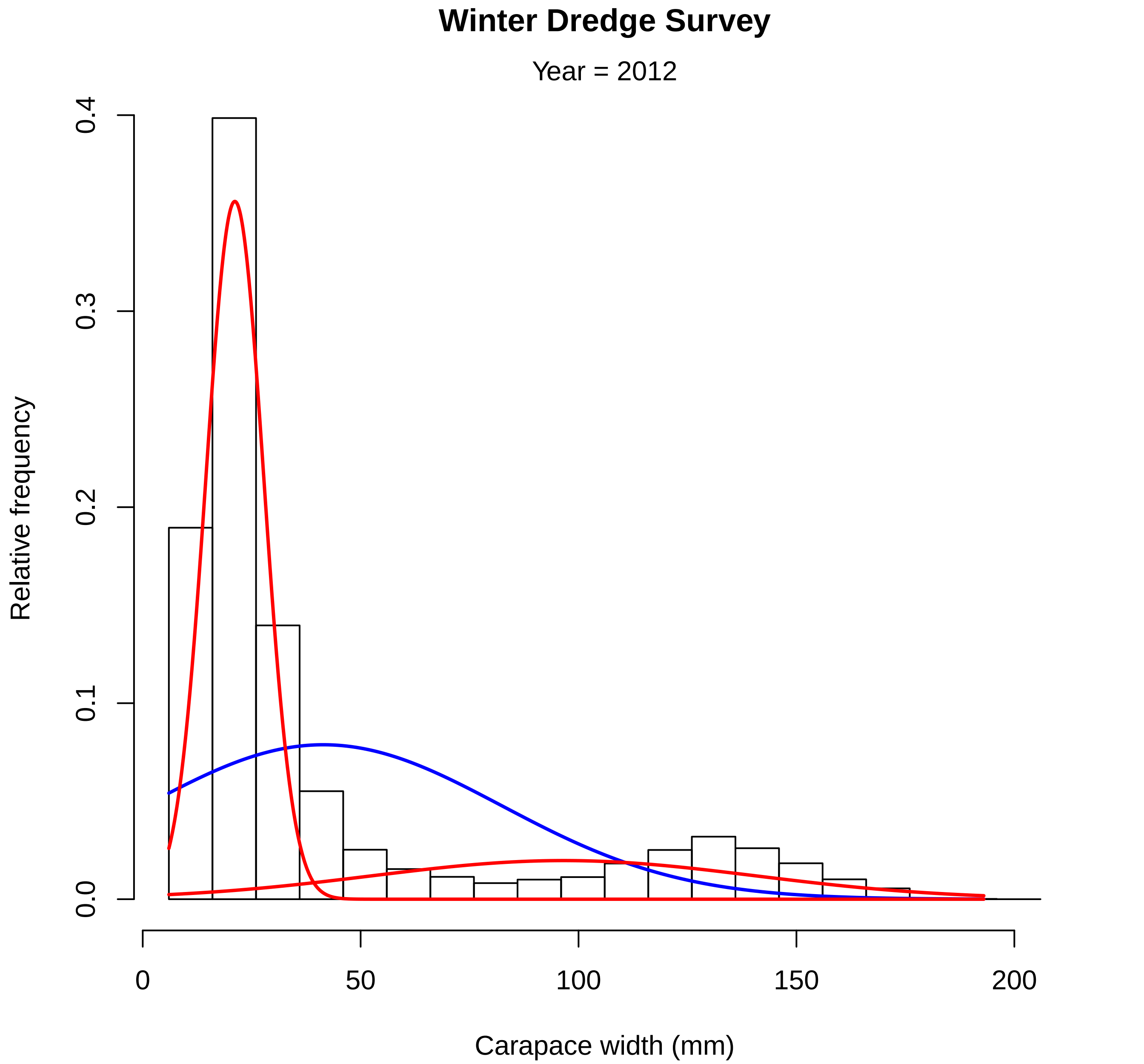


Winter Dredge Survey
Year = 2009
Relative frequency
0.00
0.05
0.10
0.15
0.20
0.25
0
50
100
150
200
Carapace width (mm)

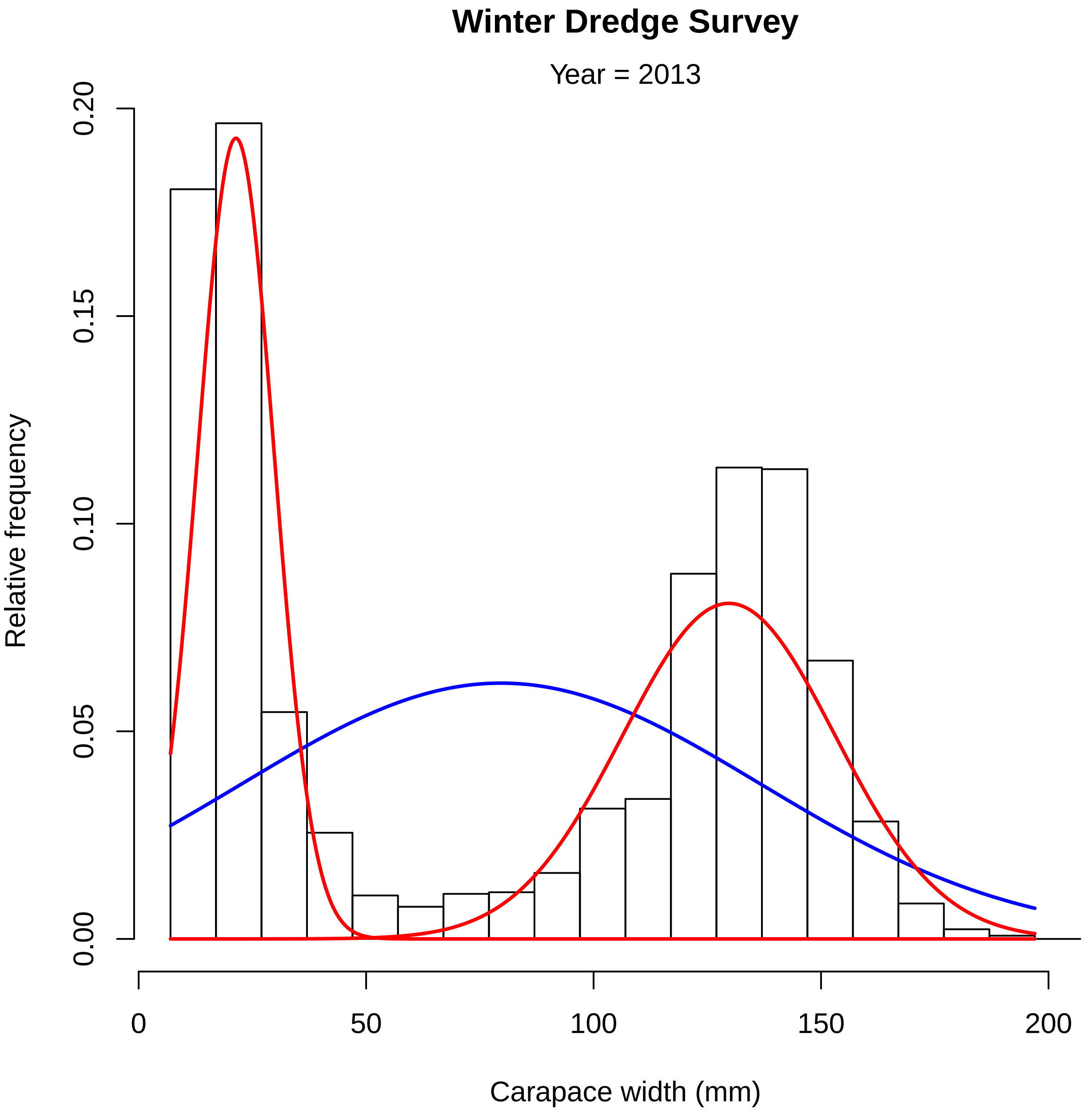


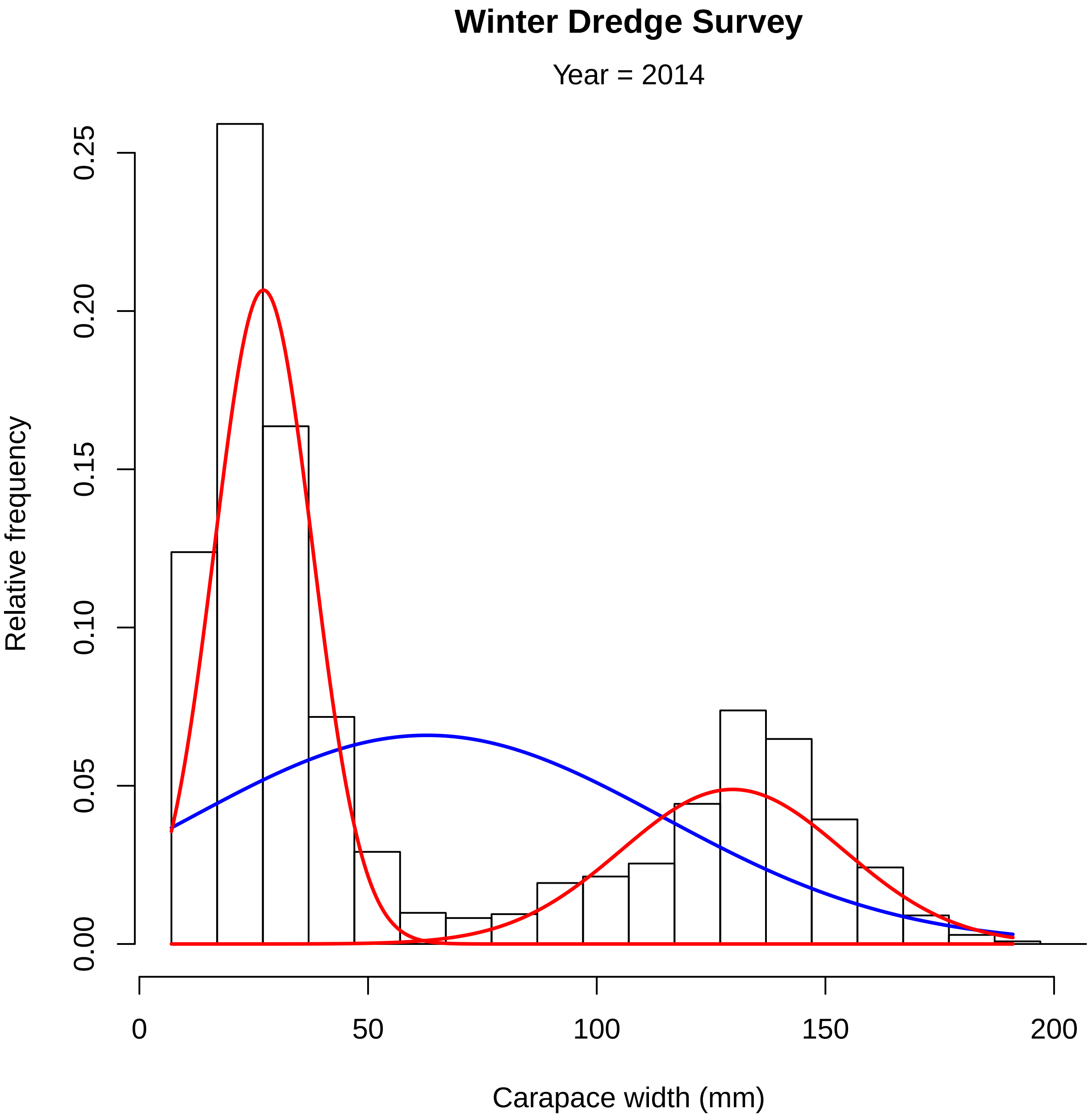
Winter Dredge Survey
Year = 2010
Relative frequency
0.00
0.05
0.10
0.15
0.20
0.25
0
50
100
150
200
Carapace width (mm)


Winter Dredge Survey
Year = 2011
Relative frequency
0.00
0.05
0.10
0.15
0.20
0
50
100
150
200
Carapace width (mm)



Winter Dredge Survey
Year = 2012
Relative frequency
0.0
0.1
0.2
0.3
0.4
0
50
100
150
200
Carapace width (mm)


Winter Dredge Survey
Year = 2013
Relative frequency
0.00
0.05
0.10
0.15
0.20
0
50
100
150
200
Carapace width (mm)



Winter Dredge Survey
Year = 2014
Relative frequency
0.00
0.05
0.10
0.15
0.20
0.25
0
50
100
150
200
Carapace width (mm)

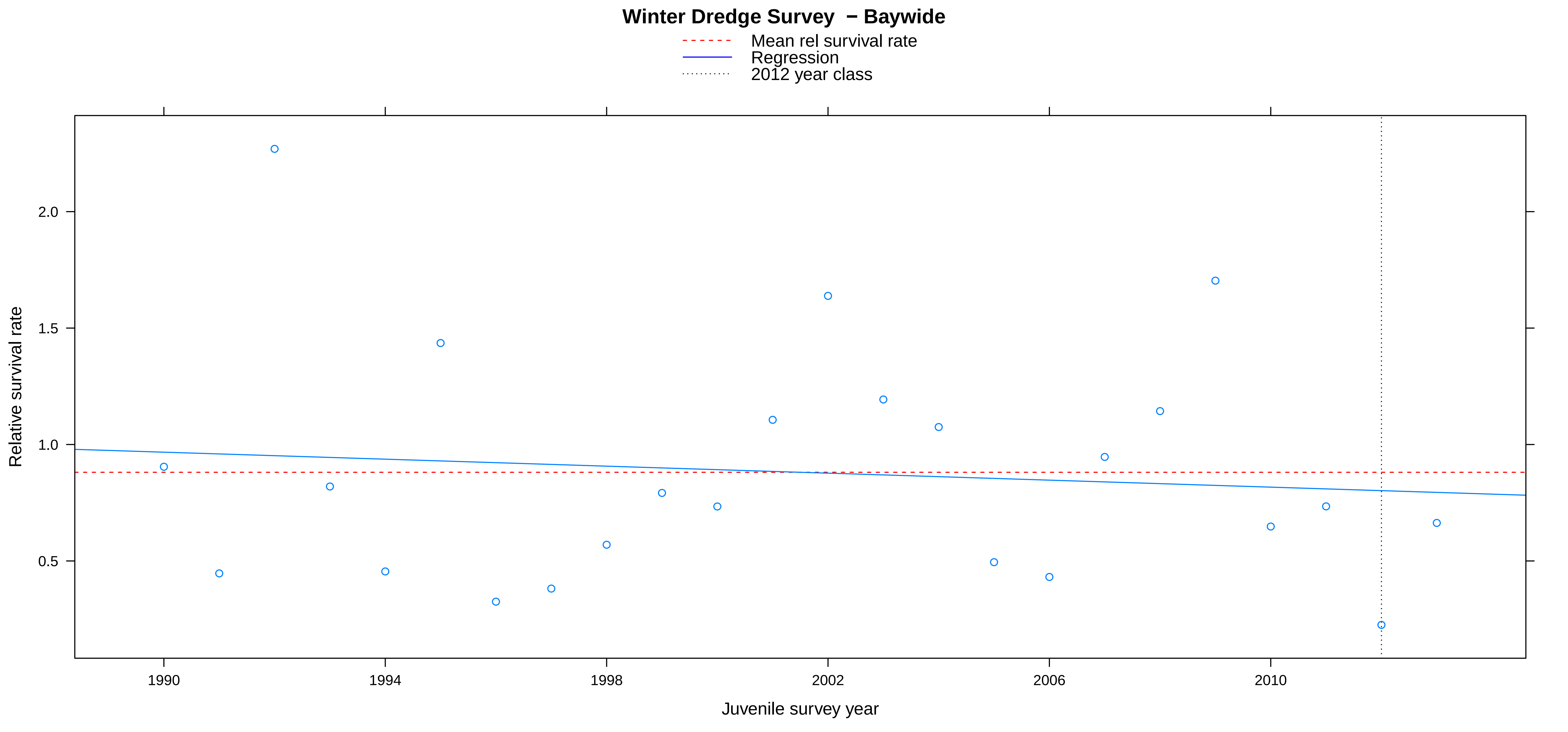
	Year	Nobs	1 sample proportion	Smaller mode proportion	Larger mode proportion
1	1990	6412	1	0.564979645	0.435020355
2	1991	8295	1	0.454755918	0.545244082
3	1992	3844	1	0.30596202	0.69403798
4	1993	3886	1	0.514111713	0.485888287
5	1994	3741	1	0.497115383	0.502884617
6	1995	2687	1	0.542539806	0.457460194
7	1996	6694	1	0.649913003	0.350086997
8	1997	5958	1	0.706505411	0.293494589
9	1998	3304	1	0.409972	0.590028
10	1999	2162	1	0.710956128	0.289043872
11	2000	1995	1	0.435952763	0.564047237
12	2001	1509	1	0.513109644	0.486890356
13	2002	1884	1	0.525747246	0.474252754
14	2003	2656	1	0.374258674	0.625741326
15	2004	2672	1	0.495183673	0.504816327
16	2005	4472	1	0.726444516	0.273555484
17	2006	4090	1	0.654412962	0.345587038
18	2007	2102	1	0.427142729	0.572857271
19	2008	2199	1	0.619843566	0.380156434
20	2009	3271	1	0.486573197	0.513426803
21	2010	5985	1	0.57270119	0.42729881
22	2011	4497	1	0.475715993	0.524284007
23	2012	7804	1	0.731123897	0.268876103
24	2013	2581	1	0.462144778	0.537855222
25	2014	2439	1	0.65111677	0.34888323

	year	Nobs	1 dist Mean	Smaller mode n	Larger Mode Mean
1	1990	6412	60.32439177	24.91205423	106.3159175
2	1991	8295	77.64918626	27.48752959	119.4860644
3	1992	3844	102.1032778	31.22584504	133.3491219
4	1993	3886	71.18399382	26.36958539	118.601503
5	1994	3741	74.61748196	27.89478504	120.804163
6	1995	2687	65.46036472	26.00361722	112.2553787
7	1996	6694	62.25276367	29.48580393	123.0824242
8	1997	5958	50.15978516	21.48766045	119.1798352
9	1998	3304	85.66101695	28.56907955	125.3304831
10	1999	2162	59.36447734	31.13480745	128.8004999
11	2000	1995	85.83659148	26.44116541	131.7433852
12	2001	1509	72.26441352	25.47917377	121.5690617
13	2002	1884	72.11836518	23.2633613	126.2780585
14	2003	2656	81.26430723	23.90548399	115.5708748
15	2004	2672	74.25	24.72444325	122.8305348
16	2005	4472	58.24798748	31.70493796	128.7347952
17	2006	4090	57.8405868	23.25631142	123.330306
18	2007	2102	79.29400571	24.16937595	120.3968876
19	2008	2199	63.88994998	26.34039832	125.1143457
20	2009	3271	79.55212473	24.13632002	132.0695335
21	2010	5985	65.65981621	20.08816779	126.7387068
22	2011	4497	80.3004225	25.31190129	130.1949809
23	2012	7804	41.42696053	21.13942596	96.59252258
24	2013	2581	79.66137156	21.38542405	129.7341863
25	2014	2439	62.91143911	27.13864552	129.6737933

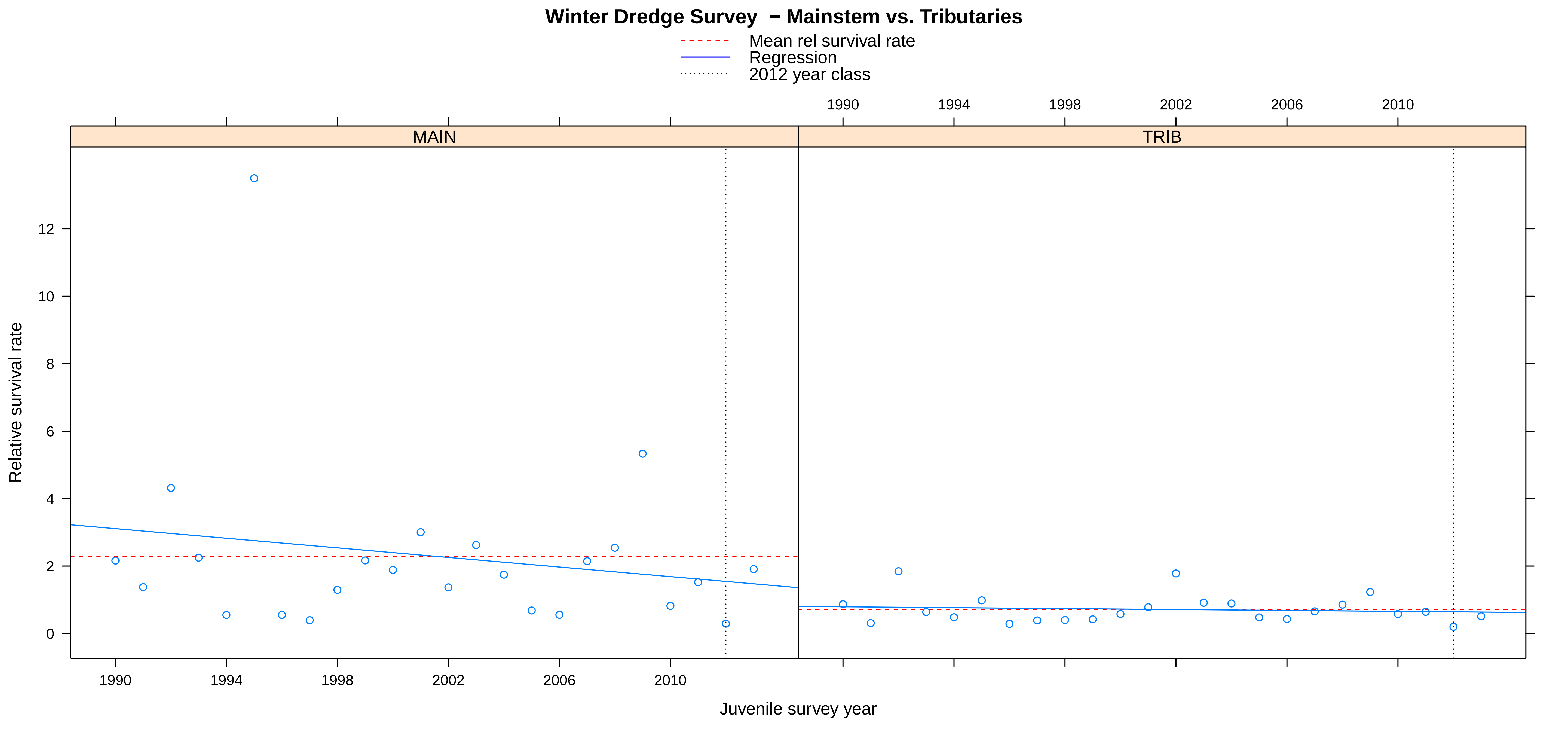
	Year	Nobs	1 sample variance	Smaller mode variance	Larger mode variance
1	1990	6412	2106.072562	81.38375628	991.7351125
2	1991	8295	2594.572771	62.76112921	857.2759884
3	1992	3844	2684.530697	184.7555608	595.6119284
4	1993	3886	2583.829502	67.35244676	873.0714629
5	1994	3741	2626.512595	103.7114076	829.1956923
6	1995	2687	2298.867707	80.26785278	893.9360356
7	1996	6694	2349.955232	124.312848	788.2602371
8	1997	5958	2313.880813	43.84077961	1035.642883
9	1998	3304	2722.099376	137.2754963	679.651797
10	1999	2162	2310.270487	230.5282925	644.2585628
11	2000	1995	3066.484576	149.1157716	487.2350311
12	2001	1509	2739.541086	90.58915416	793.4622802
13	2002	1884	3146.395225	125.4807408	916.0770044
14	2003	2656	2541.26975	77.13431946	870.3551972
15	2004	2672	2864.923278	146.4757405	765.4523673
16	2005	4472	2198.051427	169.4756961	745.7423481
17	2006	4090	2731.604416	59.83240652	1237.126346
18	2007	2102	2839.708994	77.15981141	944.3357394
19	2008	2199	2744.24255	98.75110578	1010.33066
20	2009	3271	3270.873391	84.27772371	622.4288279
21	2010	5985	3143.646013	65.7978105	754.7360092
22	2011	4497	3111.454999	102.5358235	608.5424713
23	2012	7804	1670.439693	43.7439255	1931.31413
24	2013	2581	3244.037985	70.71718143	545.3431989
25	2014	2439	2670.037257	115.3001104	592.426021

Appendix B

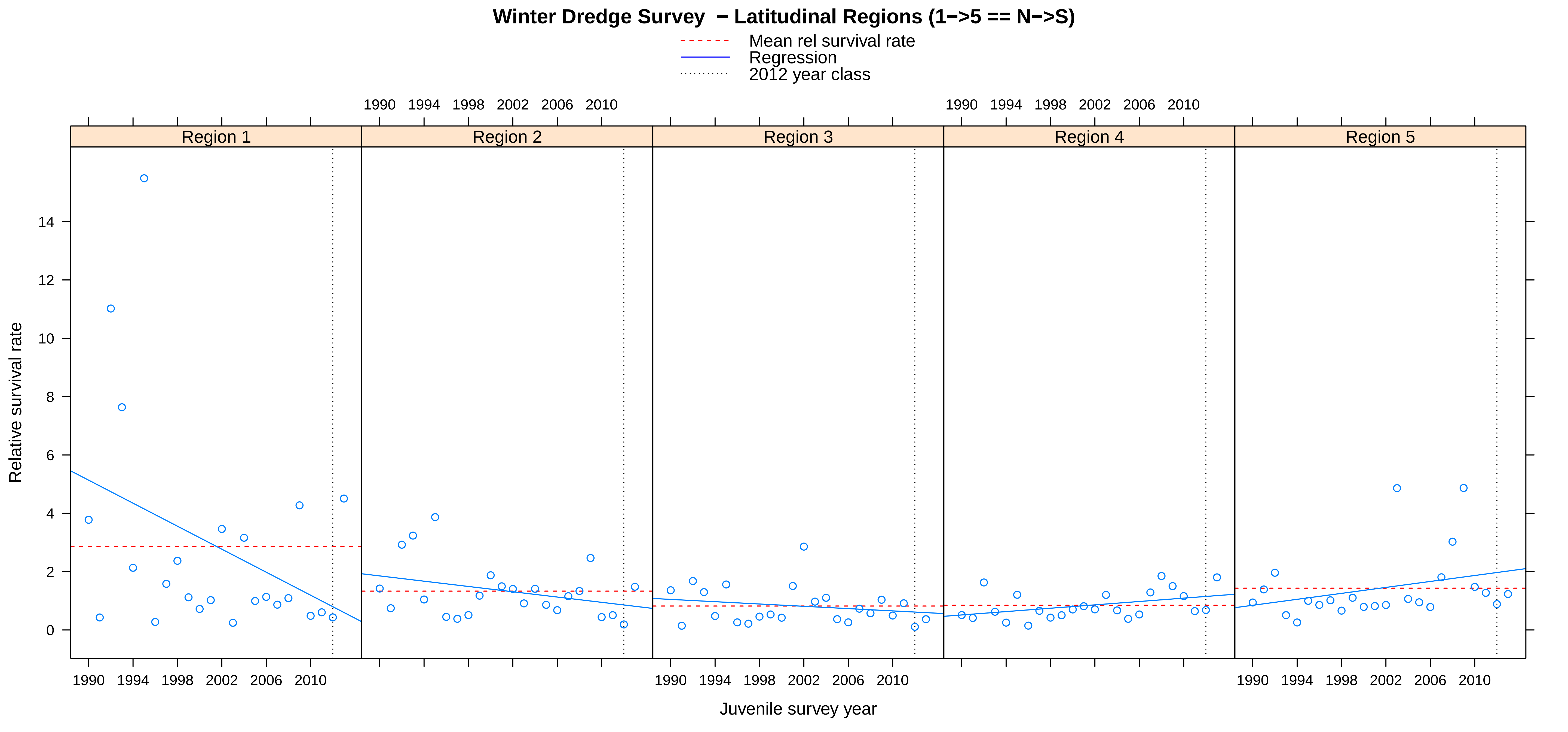
Spatial patterns in relative survival



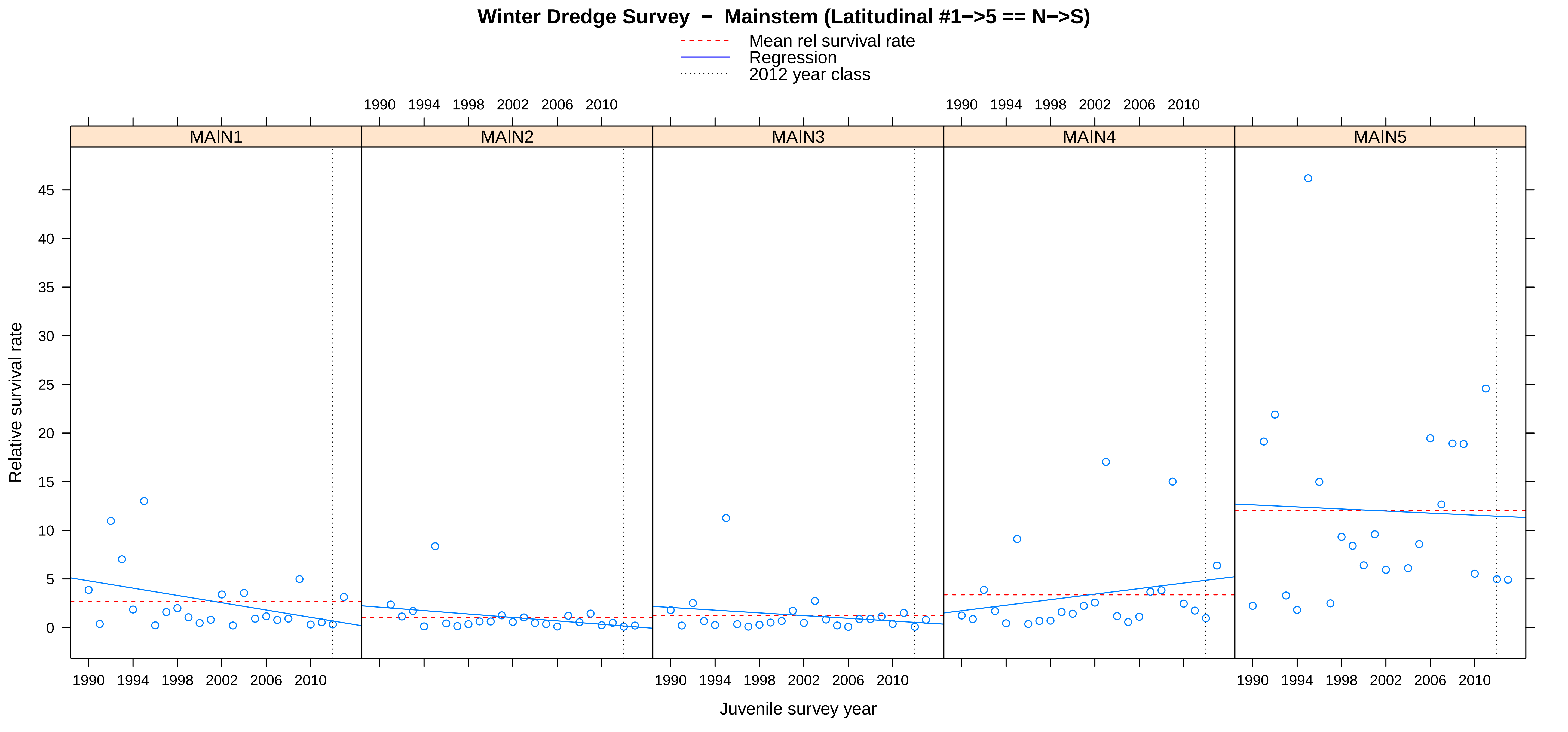
Winter Dredge Survey − Baywide
Mean rel survival rate
Regression
2012 year class
Relative survival rate
2.0
1.5
1.0
0.5
1990
1994
1998
2002
2006
2010
Juvenile survey year



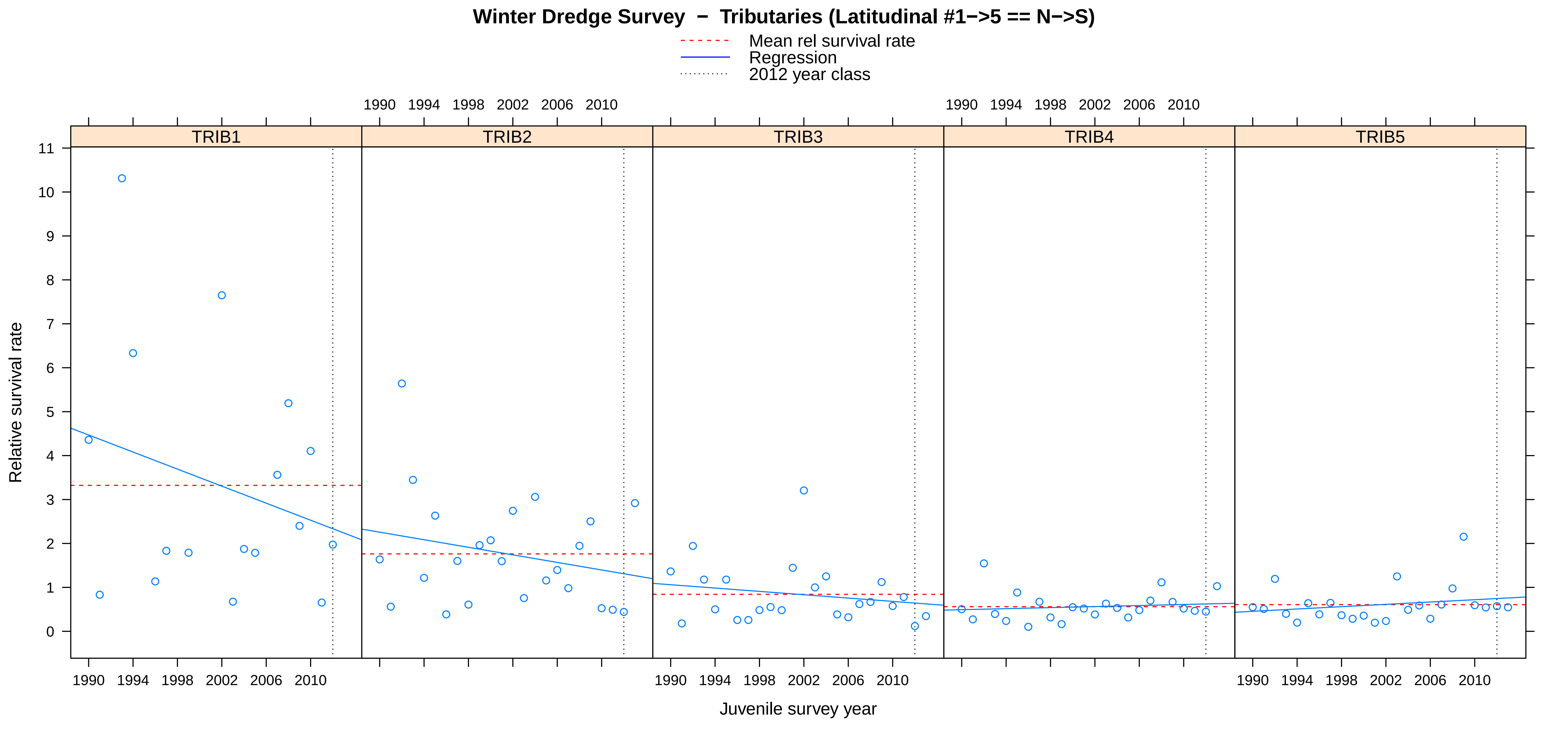
Winter Dredge Survey − Mainstem vs. Tributaries
Mean rel survival rate
Regression
2012 year class
MAIN
TRIB
Relative survival rate
0
2
4
6
8
10
12
1990
1994
1998
2002
2006
2010
Juvenile survey year

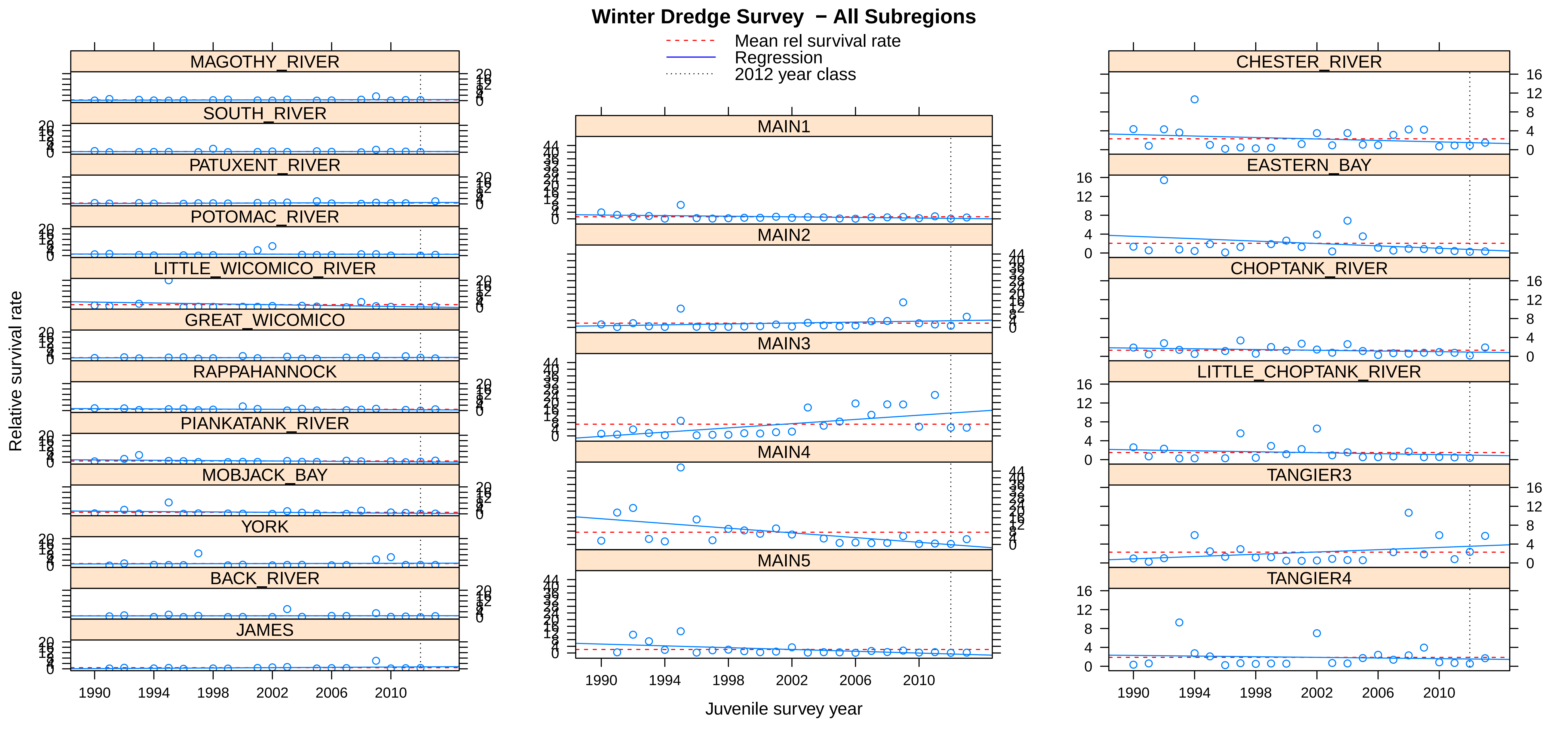


Winter Dredge Survey − Latitudinal Regions (1−>5 == N−>S)
Mean rel survival rate
Regression
2012 year class
Region 1
Region 2
Region 3
Region 4
Region 5
Relative survival rate
0
2
4
6
8
10
12
14
1990
1994
1998
2002
2006
2010
Juvenile survey year

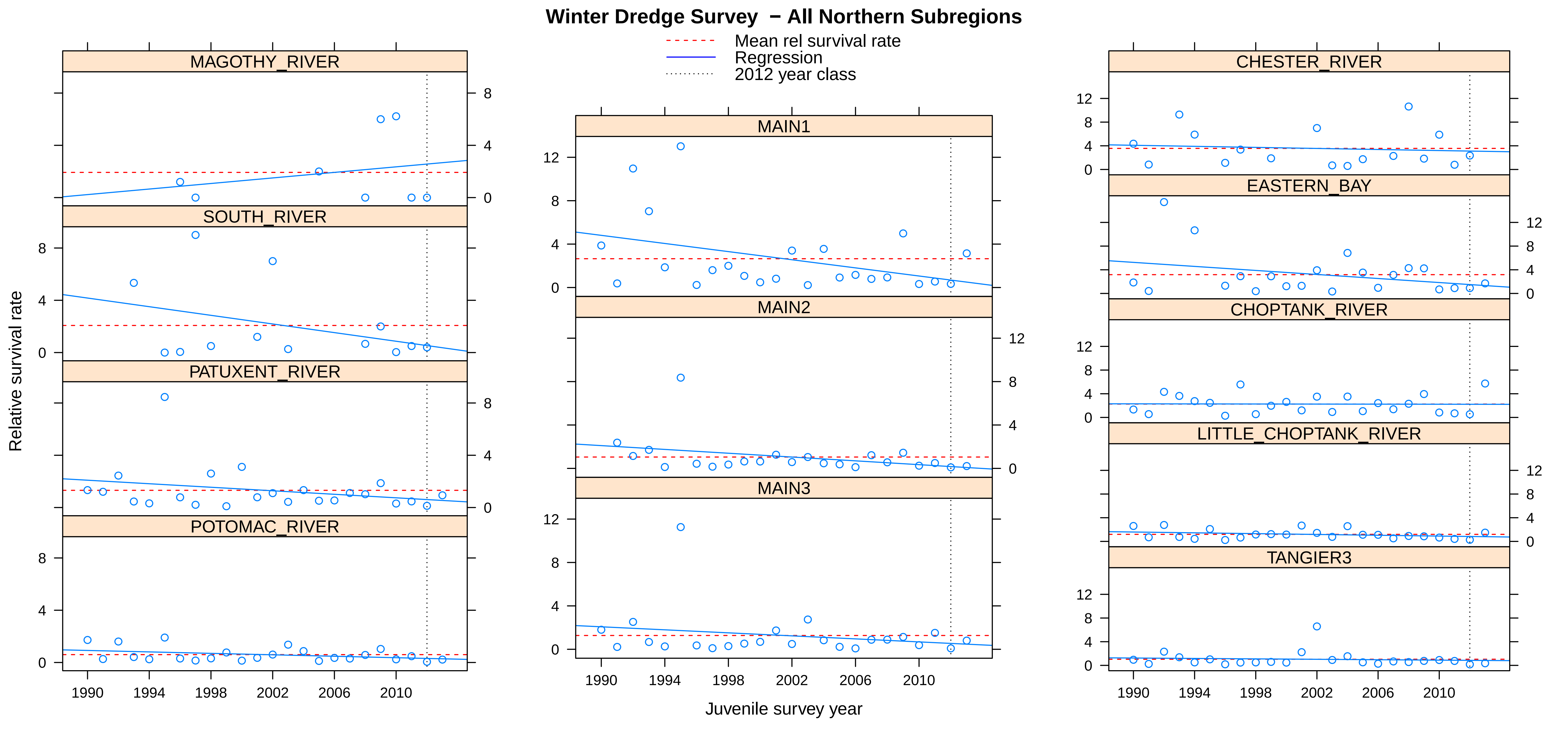


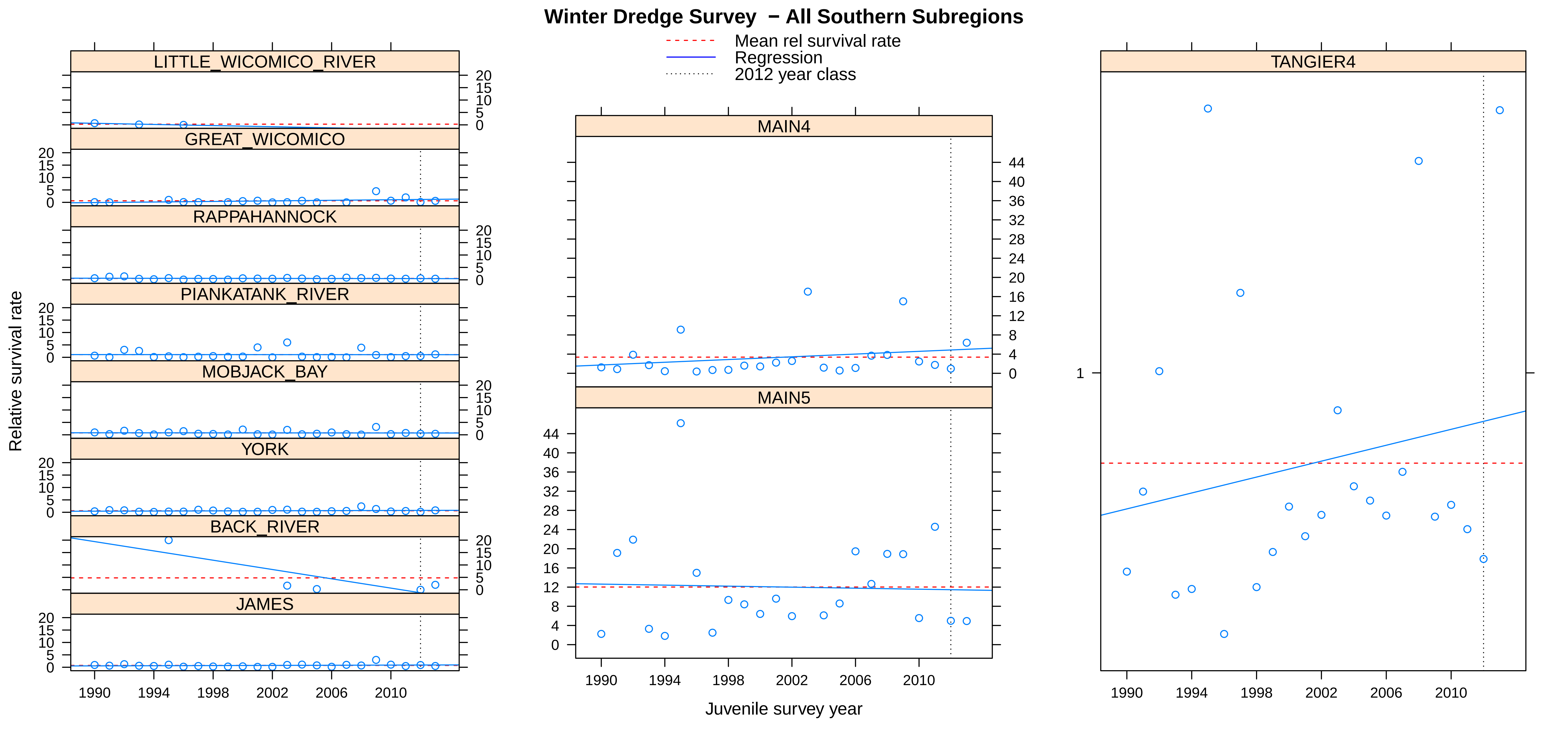
Winter Dredge Survey − Mainstem (Latitudinal #1−>5 == N−>S)
Mean rel survival rate
Regression
2012 year class
MAIN1
MAIN2
MAIN3
MAIN4
MAIN5
Relative survival rate
Juvenile survey year
0
5
10
15
20
25
30
35
40
45
1990
1994
1998
2002
2006
2010

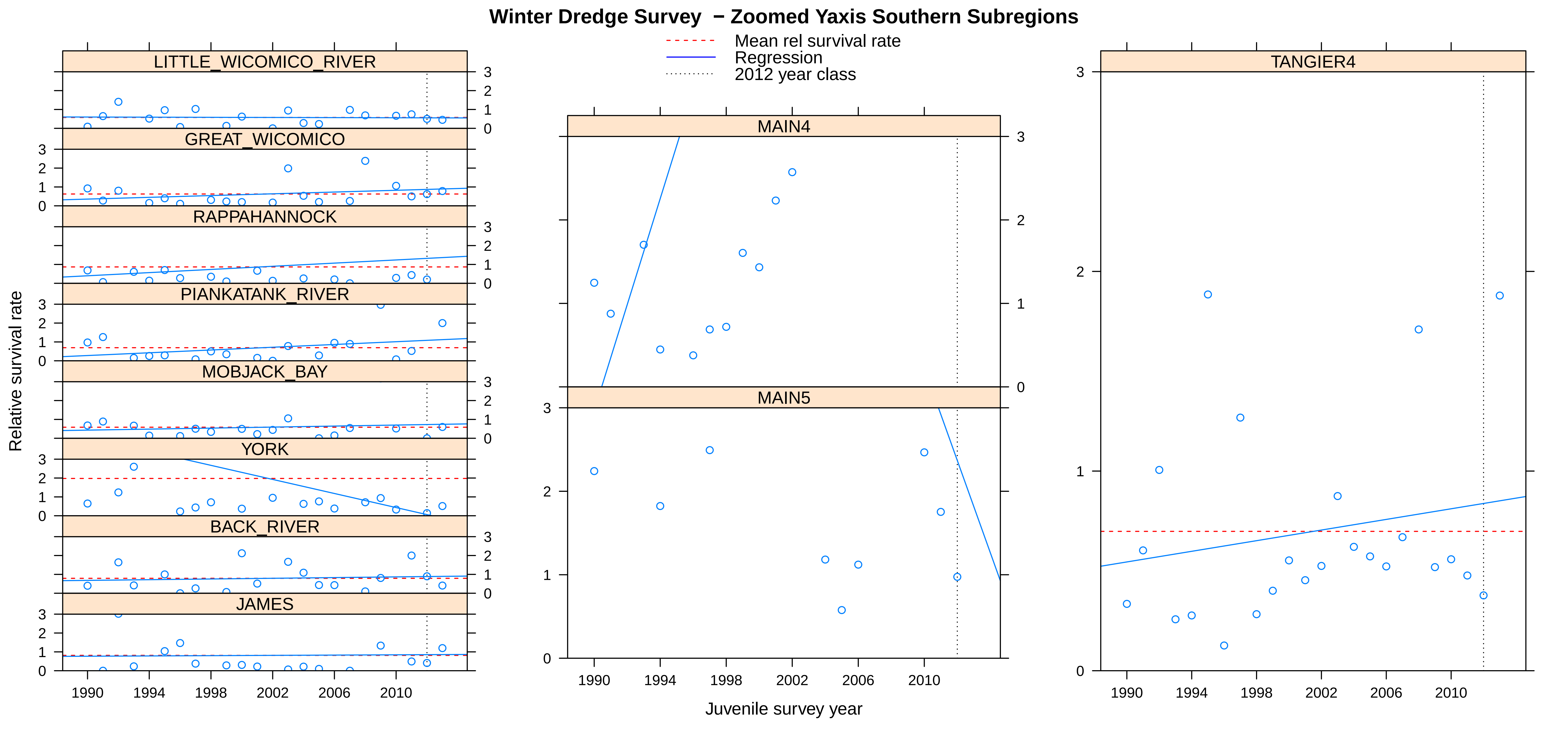

Winter Dredge Survey – Tributaries (Latitudinal #1−>5 == N−>S)
Mean rel survival rate
Regression
2012 year class
TRIB1
TRIB2
TRIB3
TRIB4
TRIB5
Relative survival rate
Juvenile survey year
1990
1994
1998
2002
2006
2010
0
1
2
3
4
5
6
7
8
9
10
11



Winter Dredge Survey − All Subregions
Mean rel survival rate
Regression
2012 year class
MAGOTHY_RIVER
SOUTH_RIVER
PATUXENT_RIVER
POTOMAC_RIVER
LITTLE_WICOMICO_RIVER
GREAT_WICOMICO
RAPPAHANNOCK
PIANKATANK_RIVER
MOBJACK_BAY
YORK
BACK_RIVER
JAMES
MAIN1
MAIN2
MAIN3
MAIN4
MAIN5
CHESTER_RIVER
EASTERN_BAY
CHOPTANK_RIVER
LITTLE_CHOPTANK_RIVER
TANGIER3
TANGIER4
Relative survival rate
Juvenile survey year
1990
1994
1998
2002
2006
2010


Winter Dredge Survey − All Northern Subregions
Mean rel survival rate
Regression
2012 year class
MAGOTHY_RIVER
SOUTH_RIVER
PATUXENT_RIVER
POTOMAC_RIVER
MAIN1
MAIN2
MAIN3
CHESTER_RIVER
EASTERN_BAY
CHOPTANK_RIVER
LITTLE_CHOPTANK_RIVER
TANGIER3
Relative survival rate
Juvenile survey year
0
4
8
12
1990
1994
1998
2002
2006
2010


Winter Dredge Survey − All Southern Subregions
Mean rel survival rate
Regression
2012 year class
LITTLE_WICOMICO_RIVER
GREAT_WICOMICO
RAPPAHANNOCK
PIANKATANK_RIVER
MOBJACK_BAY
YORK
BACK_RIVER
JAMES
MAIN4
MAIN5
TANGIER4
Relative survival rate
Juvenile survey year
1990
1994
1998
2002
2006
2010



Winter Dredge Survey − Zoomed Yaxis Southern Subregions
Mean rel survival rate
Regression
2012 year class
LITTLE_WICOMICO_RIVER
GREAT_WICOMICO
RAPPAHANNOCK
PIANKATANK_RIVER
MOBJACK_BAY
YORK
BACK_RIVER
JAMES
MAIN4
MAIN5
TANGIER4
Relative survival rate
Juvenile survey year
0
1
2
3
1990
1994
1998
2002
2006
2010